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Modeling Gag (*Mycteroperca Microlepis*) Population Dynamics to Predict Optimal Reserve Strategy

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THE FLORIDA STATE UNIVERSITY
COLLEGE OF ARTS AND SCIENCES

“MODELING GAG (*Mycteroperca microlepis*) POPULATION DYNAMICS TO
PREDICT OPTIMAL RESERVE STRATEGY”

By
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I dedicate this to my family who has been behind me every step of the way.

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ABSTRACT

Marine reserves are proposed not only as a management strategy but also as a proxy for un-fished conditions. As fishing pressures have risen over time, scientists have had no way to control for fishing in populations being studied. With the help of models, we can begin to understand the effects of heavy fishing on populations by comparing them with “un-fished reserves” that are simulated by the model. I have done this using the species *Mycteroperca microlepis* (commonly known as gag) to build an explicit, individual-based model that looks at the effects of fishing on population dynamics. In order to better understand how to manage this species, I have created a model that has incorporated factors that have, up to now, been largely ignored: (1) explicit dispersal and connectivity between spawning grounds and seagrass nursery habitat, (2) pre- and post-dispersal density dependence, (3) stage-structured population, (4) spatially explicit and stage-specific movement, (5) stochastic population dynamics, and (6) the exploration of percent, placement, and size of marine reserves both by themselves and coupled with other management techniques. A sensitivity analysis on all parameters was performed using Latin Hypercube Sampling to determine which parameters had the greatest effect as well as which output variables were affected most. I found that (1) fishing exaggerated the skewed population demography of this protogynous hermaphrodite, (2) the effects of fishing had a much greater significant effect on effective population size than total population size, (3) sex ratio in the form of the fertility function did not have a significant effect on population demography, total, or effective population size, (4) spatial distribution has a significant effect, usually as an interaction, on effective population size therefore increasing its susceptibility to fishing pressure, (5) output variables were sensitive to life history aspects including natural mortality, sex change, fecundity, and recruitment, which were all highly correlated with multiple output variables, (6) effective population size was the most sensitive to change as compared to other output variables, and (7) size limit (where age limit was used as a proxy), reserves, and spatial variation in fishing were found to be effective management strategies when used both alone and in suites. This model can be used as a basis to be modified for other species in the Gulf of Mexico by changing life history methods. Overall, this model will be beneficial in better understanding the effect of fishing on the population structure and genetic viability of the population, and for predicting proper management strategies in a manner that is both habitat and species specific.

CHAPTER 1

INTRODUCTION

Many studies model population growth with the primary goal of understanding how the life history of a species interacts with environmental factors to determine its growth (Beverton and Holt 1959, Hutchings 1993, Klemetsen et al 2003). In fish populations, much work has been done to show the effects of fishing on population growth in an effort to both increase catch and conserve species (Beverton and Holt 1957, Fogarty and Murawski 1998). As valuable economic and agricultural resources, fisheries will continue to be harvested but the way in which harvesting occurs must undergo significant changes as stocks continue to be depleted. Frequently, species are fished to the verge of economic extinction, forcing fisheries to move on to the next species and leaving species as well as entire ecosystems greatly damaged. This “roving bandits” mentality (Steneck and Wilson 2010, Berkes 2010) must be done away with if fisheries are to become sustainable, renewable resources.

While artisanal uses of marine protected areas have been in practice for millennia (Johannes 1984), it is only recently that new methods of fisheries conservation and management have begun to be explored in the form of the actual establishment of marine reserves. Though work has been done on terrestrial reserve systems for quite some time, there are additional factors that must be taken into account for marine reserves that make them more complicated. While some of the foci of marine and terrestrial reserves are shared, such as environmental and population stochasticity and maintenance of genetic variation, they differ in others like spatial variation and modes of dispersal. Where terrestrial reserves focus on the effect of fragmentation, e.g. the island biogeography theory, the most important concept in marine reserves is connectivity between reserve areas and surrounding unprotected zones (Gerber et al, 2003). The importance of connectivity in marine reserves is generally based on two key factors: the common dispersive larval stage of marine life cycles and the currents that carry them (Gaines, et al 2003). A reserve that ignores these factors of connectivity can prove to be ineffective at managing a species with mobile juvenile stages. The movement of adults between habitats can also prove to be an important factor in many species.

1.1 Past Theoretical Studies of Fisheries Reserves

Some of the earliest theory on marine reserves comes from Beverton and Holt's (1957) study of the effects of spatial variation in fishing mortality on the population dynamics of plaice in the North Sea. Interestingly, their original "protected areas" were zones that were naturally unacceptable for trawling, too distant to reach, and even included minefields left over from World War II. In this seminal work, they also discussed the then-novel concept of creating "no-take" areas as a possible management tool. Beverton and Holt concluded that protected areas were the most effective when the fishery was already facing severe overfishing, but otherwise yield per recruit did not increase within the reserve (Figure 1.1). While encouraging, the Beverton and Holt model made a number of unrealistic assumptions, such as random, uniform diffusion out of reserves, and even the authors felt that a much more detailed knowledge of fish movements would be required.

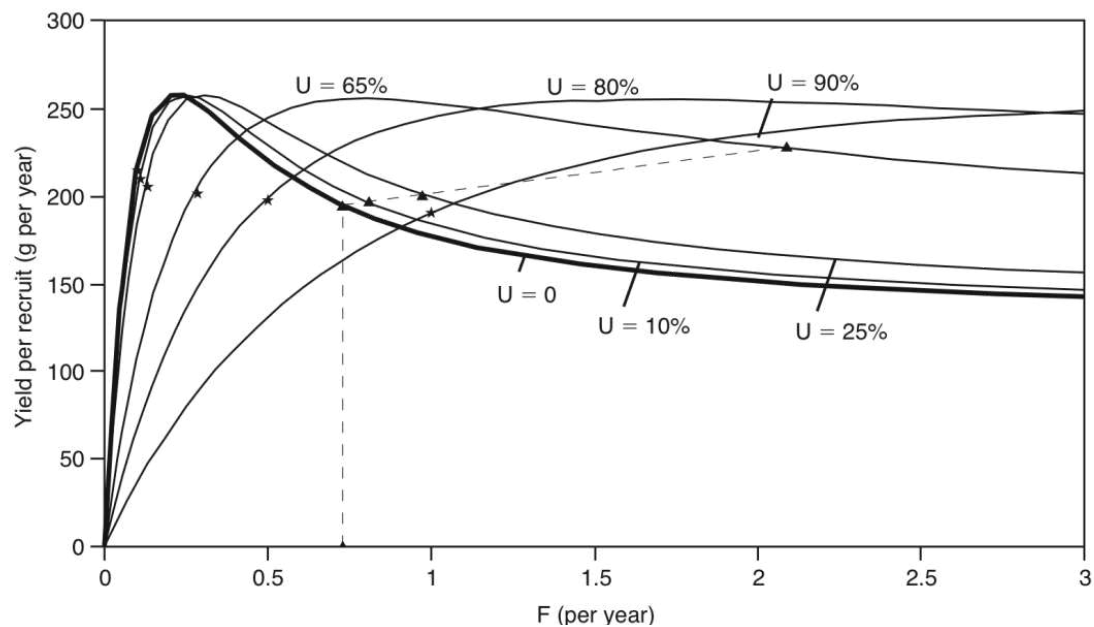


Figure 1.1 Beverton and Holt's (1957) original figure showing yield per recruit for different size of unfishable areas (U), where F is fishing mortality on the harvested areas per year

Relatively little seems to have been done with marine reserves models (or marine protected areas – MPAs) for the next 30 years, although New Zealand enacted the Marine Reserves Act in 1971 and the first reserve, Cape Rodney-Okakari Point Marine Reserve, was formed there in 1977 (Sobel and Dahlgren, 2004). At the time, more traditional methods of fisheries management were implemented, such as fleet and gear control. However, increasing numbers of fisheries collapses seems to have stimulated further models on marine protected areas in the 1990's (see reviews in Guenette et al. 1998 and Gerber et al. 2003). These models were for a wide variety of marine species including cod, shrimp, reef fish, and sea urchins. Most of these models confirm Beverton and Holt's main conclusion that marine reserves may not be effective management tools in general and when they are effective, it may only be when there is very high fishing effort. Guenette et al. (1998) suggest that one of the conclusions to be drawn from these models is that reserves should provide resistance to stock collapse, even if they don't effectively increase fisheries take. The popularity of marine reserves has been growing exponentially over recent years, with the number of studies dealing with reserves rising from close to zero in 1990 up to approximately 160 per year in 2005 (Halpern, Encyclopedia of Earth). It is understandable that we want to learn more about how these reserve systems work, optimum situations for reserves, and the benefits and costs associated with forming reserves. Ideally, we would also keep some areas unfished so that we will have a "control" environment in nature for future empirical work.

In order to study the performance and applications of reserves, I have built a model to test reserve theory as it applies to a specific species, *Mycteroperca microlepis*, commonly known as "gag". The species as well as the model itself will be described in detail shortly, but knowledge of the model is necessary in order to compare the present model to prior models and their assumptions. My model is individual based so that each individual of the population can be tracked in order to make statements about the population in its entirety, in addition to allowing stochasticity to function along every step of the model. The methods of the model act on these individuals to allow them to function as a distinct unit in the population that is able to interact with other individuals. In addition to interactions, individuals can also be acted upon by the environment as it is defined in the model. Basic life history aspects including sexual maturity, fecundities, sex change, and recruitment are all included in the model. Space has also been included to determine the spatially specific application of marine reserves as a management tool.

Incorporating space into the model also allows for the inclusion of behaviors such as small and large-scale migrations. All of these factors are critical to creating the most accurate model possible for the species and will be discussed in more detail when the model and methods are outlined.

Assumptions of Past Models

The two major reviews of fisheries models (Guenette et al. 1998, Gerber et al. 2003) both conclude that the existing models are oversimplified and are based on highly unrealistic assumptions. Predicting the effectiveness of marine reserves for fisheries will require that attributes of the species, their environment, the fisherman themselves, and all resulting interactions thereof be incorporated into the models. Here, I will address some of these areas.

Equally Distributing Larvae

Gerber (2003) points out that the majority of models assume equally distributing larval-pool dispersal. However, this is obviously not the case, except for some self-recruiting species (Botsford et al. 2001, Hastings and Botsford 2006, Kaplan et al. 2009). As pointed out by Gaines (2003), currents can also play a major role in the uneven dispersal of larvae, suggesting that the inclusion of a hydrodynamic component in the model is important. Some models approach this problem by coupling a hydrodynamic model with the species model (Hinckley et al. 1996), or by creating sub-models for each stage of the life cycle to model specific movement patterns, i.e. current- and turbulence-dependent larval distribution (Stockhausen et al. 2000).

Resident Adults

Though some species are sedentary (e.g. goliath grouper, *Epinephelus striatus*), others move extensively as adults (e.g., bluefin tuna, *Thunnus thynnus*). Completely ignoring adult movement disregards the defining aspect of connectivity in marine ecosystems. Although field studies examining spillover effects from MPAs concentrate heavily on adult movement, models have yet to take this important factor into account. As the empirical work of Halpern, et al. (2010) shows, adult movement is extremely important for the success of reserves and the sustainability of fisheries outside reserve areas. Models seeking to determine effectiveness of reserves must account for mobility of the adults that are to be protected by the reserve. Failing to

account for adult movement will not only give false results as to the protective effect of the reserve for that species, but will also fail to predict the economic sustainability of the fishery and the presence and degree of a spillover effect (Smith et al. 2008).

Post-Dispersal Density Dependence

While we know that the population size of adults for any given species has an effect on the number of larvae produced, I expect that most models (e.g. Quinn et al. 1993) assumed that the population needing protection were so far under the carrying capacity that density effects would not apply to such populations. But once a marine reserve is formed with the goal of increasing density, it is necessary to make sure that density effects both before and after dispersal are taken into account. Empirical studies have shown that density inside marine protected areas increases since fish have a higher survival rate provided there is suitable habitat (Harmelin-Viven et al. 2008). Also, density still affects other stages, even if adults are far from any carrying capacity.

Deterministic Population Dynamics

We know that there can be significant demographic and environmental stochasticity in natural populations (Lee et al. 2011, McMahon et al. 2009, Mullan et al. 2009): we see a great deal of variance in marine populations, for example, years of both high and low recruitment are common (Murphy et al. 1990, Coleman, personal communication). Assuming recruitment levels to be the same each year in the model could end up masking problems that could occur if recruitment was very low in certain years. Thus, including appropriate stochasticity in events such as yearly recruitment is vital to making sure our management strategies hold even in the face of random stochastic events, such as hurricanes, red tides, or similar events that result in years with very few recruits. Environmental stochasticity can be an important factor in predicting the effects of marine reserves (Langlois and Ballantine 2005). Using data collected from 20 no-take zones in New Zealand, Langlois and Ballantine (2005) demonstrated that any model of marine reserves must be specific to the location, habitat, and species to accurately predict the outcome of establishing the reserve. They also show that currents as well as both small-scale and large-scale migrational movement as complicating factors.

Species Specific Life History

Gerber, et al (2005) showed the importance of species life history on the effectiveness of reserves. Their model shows that while population growth rates increase across all species when a reserve is added, the degree to which the reserve is effective depends strongly on the dispersal of the species. They suggest the synthesis of known life history data for species with marine reserve theory to build models that can more accurately predict the efficacy of marine reserves. Though much theoretical work on marine reserves has concluded that marine reserves may only be beneficial under very high fishing pressure (Beverton and Holt 1959), Gaylord et al. (2005) pose that when species-specific details are taken into account, marine reserves can actually have a significant positive effect in many cases which may translate into higher fisheries yields outside the reserve. In addition to maintaining high connectivity between reserves, they propose that adult and larval spatial patterns, the structure of the population, and life history and behavioral aspects such as longevity, age-dependent fecundity, and rate of movement are critical to determining how effective the reserve will be for a species.

Spatial Management Techniques

Few models have explored rotating reserves, addressing the possibility of rotating the placement of reserves in the same way we rotate crops or hunting areas on land. We have already discovered in terrestrial systems that letting one area “rest” while focusing our efforts on other areas allows the stock to build up in the resting area. This option could also satisfy the fishermen who are opposed to the idea of closing an area permanently. Closely related to this is the “spillover effect”, which is the theory that a protected area will have higher densities on the outskirts of the reserve. Sanchirico and Wilen (1999) showed that fishermen will move to areas of higher rent (where rents are defined as the value of area if it was to be sold or traded). These areas could be a newly opened reserve (on the rotating reserve system) or the edges of the reserve. This is important to consider because when fishing becomes highly concentrated in these areas, it is likely that the population could be fished out quickly. This implies that additional management strategies may be needed in addition to reserves to keep this from occurring. Rotating reserves may be a problem of relative rates, where the period of rotation must match not only the doubling time of the target species but also the time it takes for a newly opened reserve

to be reduced. While this may be difficult in practice, the theory could and should be explored through sophisticated modeling.

Territorial use rights in fisheries (TURFs) and zoning are other spatially explicit management techniques that allocate certain areas to specific fishermen. This causes fishermen to take a long-term management approach in fishing since they no longer must compete with other fishermen for their catch and are instead interested in maintaining the health and numbers of fish at their specific sites. This essentially causes fishermen to self-manage the species within their turf or zone. Incorporating a model with spatial distribution of fishermen as well as fish would also require sophisticated modeling and extensive human behavior data, but would provide very useful insight into these types of alternative management approaches.

Reserves are yet another spatially explicit management technique that places additional protections in certain areas, up to and including enforcement of “no-take” zones. Though reserves constitute a relatively new field that has much left for us to learn, we must be careful not to ignore other systems of management that may work just as well or better based on environment or species.

Non-Spatial Management Strategies

It is important to remember that establishing marine reserves is not the only management strategy: size limits, and daily and annual catch limits including both traditional catch limits as well as individual transferrable quotas (ITQs), also known as catch shares, or individual, non-transferrable quotas (INTQs) are all methods for conservation and management of fisheries (Branch, 2009, Castilla, 2000). It is also important to remember that multiple management techniques may be used together and may be more effective in suites. Thus, while I am interested in the dynamics of marine reserves especially as they apply to grouper in the Gulf of Mexico, my model is focused on comparing multiple different management options to determine the best fit for gag.

1.2 The Species

Gag (*Mycteroperca microlepis*, Family Serranidae, Subfamily Epinephelinae) is a shallow-water reef fish that is found along the southeastern U.S. coast of the Atlantic and throughout the Gulf of Mexico, specifically along the West Florida Shelf and also along the Yucatan Peninsula (Briggs 1958, McGovern 2005). Adult gag weigh on average between 5 and 10 kg and reaches a mean length of 550mm at sexual maturity between the ages of 3 and 6 years (Collins, et al 1998). Adult gag are benthic-feeding piscivores that spawn on deep (90-120 m) offshore reefs while juveniles inhabit seagrass nursery and shallow reef habitats (Fitzhugh, et al 2005, Koenig and Coleman 1998).

Gag are sequential, protogynous hermaphrodites: each fish matures as a female, and females must then transition to become males (Shapiro 1987). It is often the largest and most aggressive females in a school that will change sex, which is thought to be triggered by absence or scarcity of males (Coleman, et al 1996) and the frequency of younger or smaller females (Alonzo and Mangel, 2003). There is also a relationship between age and probability of transition, where 50% age at transition is 10.7 years (Fitzhugh, et al 2006). This life cycle is shown in detail in Figure 1.2. Coloration can, in general, be used to differentiate males from females. Some adults are heavily pigmented on their ventral side, and studies have shown that 91.7% of the time these heavily pigmented individuals are males. Only 5% were females and the remaining 3.3% were transitionals (Collins, et al 1997), suggesting that pigmentation is a trait most closely associated with males. The locations of these critical habitats can be seen in Figure 1.3.

Female gag form pre-spawning aggregations that move from offshore reefs to nearshore reefs a month or so before the spawning season, presumably to take advantage of the higher productivity inshore. They then join males on aggregation sites. After the spawning season, females return to deep-water reefs. Males tend to stay at spawning sites year round. Some females are known to migrate from the coast of South Carolina to the northeastern Gulf of Mexico prior to the spawning season (Coleman et al. 1996, McGovern et al. 2005, Chris Koenig, personal communication). Thus, the population is divided between the more mobile female (although females are quite sedentary on sites outside of seasonal migrations) and the sedentary male. Peak spawning occurs in February and March (Fitzhugh, et al 2005) and larval

movement into seagrass beds takes approximately 40-50 days. Juveniles continue to grow in the nutrient-rich nursery habitat of the seagrass beds over the next five to six months until they move to nearshore reefs in autumn, where they stay until they mature (Koenig and Coleman, 1998). Juveniles in the seagrass beds experience extremely low mortality, with 95-100% survival (Koenig and Coleman, 1998) until they reach the nearshore reefs where they experience approximately the same natural mortality as adults (Chris Koenig, personal communication).

Gag has been listed as vulnerable since 1996 by the International Union for the Conservation of Nature, but it is currently marked as “Least Concern” and decreasing (www.iucnredlist.org, April 5, 2011), and the most recent stock assessment found that gag are “overfished and undergoing overfishing” (SEDAR Update Assessment, 2009). Gag supports a highly valuable fishery in the southeastern United States both for commercial hook and line fisheries and recreational fisheries. The sustainable catch was estimated in 2002 to be 5 million pounds, but this level has been exceeded by an average of 50% each year from 2002 to 2007 (Ocean Conservancy 2007). The recreational bycatch may be the most devastating, however, with 2.7 million fish (about 6.5 million pounds) being discarded because they are below size limits (see Figure 1.4). In fact, recreational fishing far exceeds that of commercial fishing pressure applied to gag, where total recreational removal from the population totaled approximately 14 million pounds in 2003 while commercial removals totaled only 3 million pounds in the same year (Figure 1.4). Though these fish have 86% and higher chance of surviving if caught in water shallower than 44m, they have less than a 33% chance of surviving if caught any deeper (Wilson and Burns 1996). Gag, as a reef fish, are also susceptible to popular recreational fishing activities such as spear fishing, where size limits may not be followed due to the inability to measure before capture, resulting in dead discards due to small size (Florida Fish and Wildlife Conservation Commission, personal communication). This, of course, is also true of hook and line fishing, however there is a greater chance of survival in this case depending on the depth at which fish are caught (citation). As an overfished species, special attention needs to be paid to gag and maintaining sustainable harvest levels both in the best interest of the species and the fishery itself.

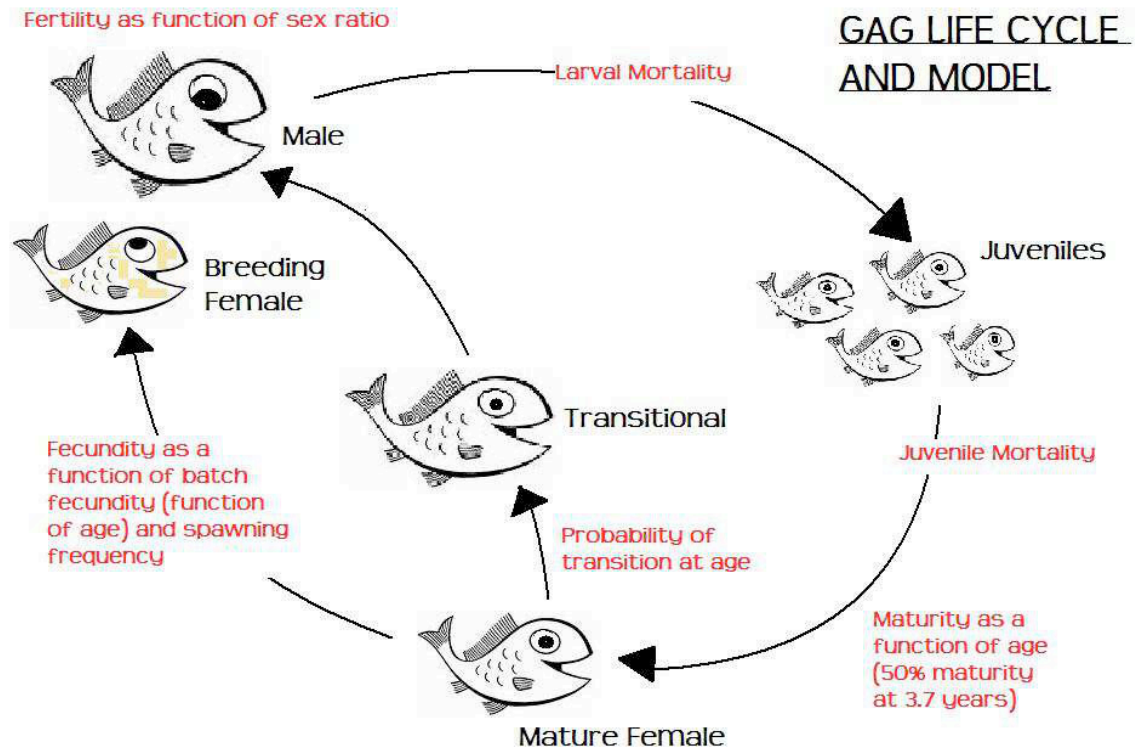


Figure 1.2 The life cycle of gag, including important transitions used in the current model

As a protogynous hermaphrodite, gag are all born female and may go through transition in order to become a male.



Figure 1.3 Habitats of gag including seagrass beds, nearshore reefs, offshore reefs, and shelf edge reefs

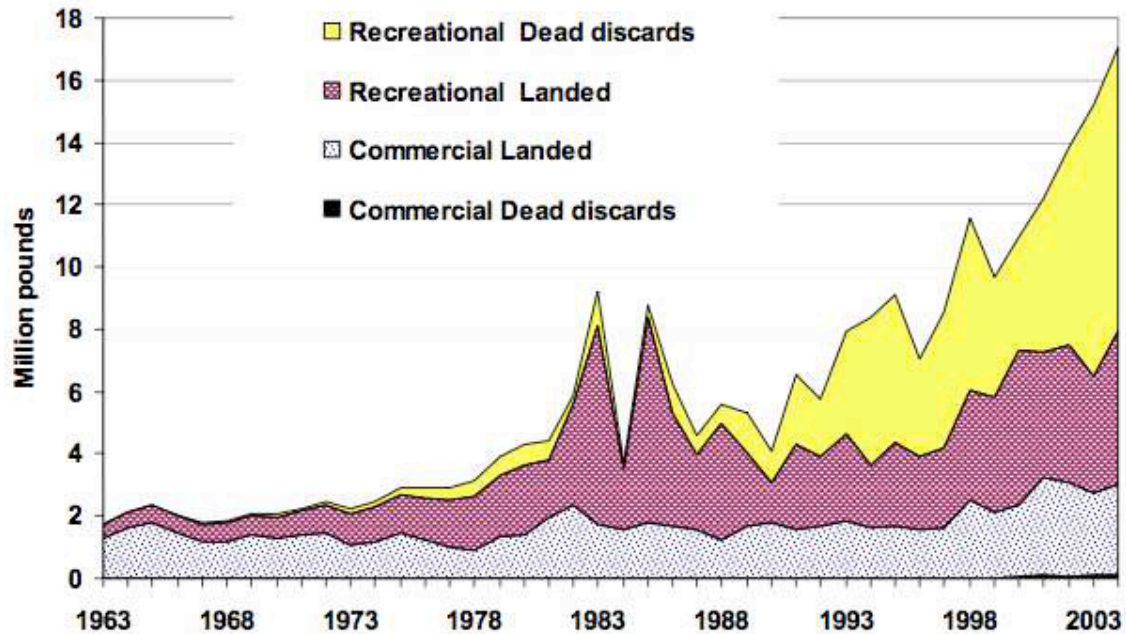


Figure 1.4 Gag landings and discards from 1963 to 2003 in the Gulf of Mexico (SEDAR Stock Assessment, 2006)

1.3 The Vulnerable Life History

Gag are susceptible to fishing pressure because of specific aspects of their life history. These include (1) aggregating in specific locations to spawn, (2) relatively sedentary males that stay at the spawning aggregation sites year round, (3) protogyny: females change sex to become males, and (4) behavioral differences between females, transitionals, and males. The individual-based model presented in this thesis includes these factors in predicting patterns in population abundance and growth.

As is typical of most protogynous fish, gag have a skewed sex ratio, with a higher abundance of females as compared to males. When this characteristic is coupled with the formation of spawning aggregations, fishing pressures for larger individuals become selective on males, (and perhaps transitionals and large females) and the ratio becomes skewed even further. It is important to note that it is commercial fishermen that most commonly target these aggregations, since recreational fishermen often stay in much closer proximity to the coast. Coleman et al (1996) showed that over the previous 20 years, the percent of male gag declined in

the population from 17% to 1%. In contrast, there was little to no change in the sex ratio of red grouper (*Epinephelus morio*), which are protogynous but do not aggregate to spawn (Coleman et al. 1996). Because it is a common practice for fisherman to deplete the fish population on a given site, entire spawning populations can be wiped out, including all of the males. Harvesting of both sexes is detrimental to the population but it is the removal of males that has the largest effect on population growth because of the naturally skewed sex ratio. It seems logical that a protogynous fish should be able to compensate for a skewed sex ratio by developing a higher rate of transition from female to male. However, if sex change is also disrupted by fishing or takes a sufficiently long time, then the natural sex ratio cannot naturally re-establish.

The final characteristic of gag that I evaluate in my model is their behavior. Females are less aggressive and less likely to be taken by both commercial and recreational fishers (Heppell 2005). Males are also usually higher in the water column, making them easier to access, and are also much more aggressive in taking baited hooks (Gilmore and Jones, 1992). When females in other protogynous species begin the transitional phase, they also adopt this aggressive behavior (Gilmore and Jones, 1992, Shapiro, 1987), making transitional females just as likely as males to be caught by hook and line methods (Coleman, et al. 1996, Heppell 2007). Transitional gag also stay at the spawning aggregation with males while they go through the transition period, making them more susceptible to capture. Thus, the transitional phase in this species may also be disrupted by fishing.

In order to put the effects of fishing into perspective, it is important to contrast natural and fishing mortalities. Mortality due to fishing of breeding-age individuals (approximately 4-12 years) is catch-curve estimated at 0.52 annually, while mortality from natural causes, such as aging or predation, is only about 0.15 annually (McGovern, et al. 2005). Stable fishing has been estimated to be 0.30 annually (SEDAR Data 10, 2006). In addition to these effects on population numbers, removing large numbers of males and breeding-age females will also affect genetic variation and effective population size of the population considerably.

Reproductive capacity of the population will be considerably diminished as a result of the previously mentioned skewed sex ratio. As shown by Alonzo and Mangel (2005), fertilization rates will be high when both the sperm and egg production are high. However, if sperm production falls relative to egg production (which may be occurring in gag), then the rate of fertilization will decrease. This is supported by evidence of unspawned eggs in females and

formation of atretic bodies. Coleman et al (1996) suggested this atresia may be a result of reduced numbers of males at spawning sites, to which females respond through resorption of yolked eggs.

All of the previously mentioned factors contribute to the shrinking of the effective population size of gag. Whenever there are fewer of either sex, the effective population size will be reduced. Specifically, when there are fewer males than females, “minimal inbreeding” can be induced in the population (Caballero, 1994). Inbreeding depression mimics the effects of genetic drift by reducing the amount of genetic variation in the population and increases the chance of alleles being identical by descent. Decreasing the effective population size can increase the strength of drift by reducing the size of the population that is able to pass on its genes to the next generation. Thus the probability of a gene being fixed will be much greater, reducing the genetic variation in the population.

As a major fishery in the Gulf of Mexico (as well as along the southeastern coastline of the Atlantic), gag is very important to consumers as a key food source and to fisheries from an economical perspective (FWRI, 2008, SEDAR Update Assessment, 2009). Current fishing practices will prevent this key fishery from being sustainable over any long period of time. As the total population size decreases, so does the effective population size. In the case of gag, this problem is exacerbated by the ever-decreasing numbers of males as a result of a naturally skewed sex ratio coupled with a fishery that increasing male susceptibility to capture. As proposed by Coleman et al (1996), an Allee effect (reduced population growth at low population size) could cause spawning failures across the population. This is based on the findings of large numbers of females that were mature but reproductively inactive as a result of limited numbers of males on spawning sites. This issue highlights the need to better understand the effects of fishing practices both on population growth itself and on population genetics.

1.4 Current Protections

Currently, federal and state regulations for both commercial and recreational fisheries intended to protect gag from overfishing include quotas, bag limits, size limits, seasonal closures, International Fishing Quotas (IFQ’s), and even some marine protected areas (see Table 1.1 for

more details and comparison). Commercial fisheries are regulated by size limits as well as total catch quotas that are established based on assessments of the species. Commercial fishermen must also respect fishing restrictions within marine reserves. Since many species are controlled by regulations at both the state and federal levels (which can differ), fishermen must abide by the more strict regulation. For example, in Florida, the gag seasonal closure is usually from February 1-March 31, however, a temporary federal rule has closed the gag fishery from January 1-May 31 of 2011. A recreational fisherman, therefore, must abide by the federal regulation in the case where state and federal regulations do not coordinate. There is also a variation from state to state as to where state waters end and federal waters begin; most states have a three-mile limit though Florida and Texas have different limits. Federal waters in Florida and Texas begin nine nautical miles from the coastline and extend to the 200-mile limit of the Exclusive Economic Zone (EEZ), whereas federal waters in Alabama, Louisiana, and Mississippi begin 3 nautical miles from the coastline and extend to the limit of the EEZ. The federal authority in charge of setting management standards for the Gulf of Mexico is the Gulf of Mexico Fishery Management Council (GMFMC), which operates under the National Oceanic and Atmospheric Administration (NOAA). Both state and federal law agencies have their own law enforcement to ensure that these rules are followed, and some state law enforcement officers are federally deputized in order to be able to enforce federal violations (Florida Fish and Wildlife Conservation Commission, personal communication). Management of fisheries can only ever be as good as the effort that is available to enforce such regulations, and many management activities have failed due to lack of enforcement (Smith et al. 2007, Smith et al. 2008, Chris Koenig, personal communication). Theoretical models generally show a “perfect world” scenario of how species and fisheries should respond to management activities. However, they can also be used to explore some of the more complex scenarios that occur in the real world.

Table 1.1 Comparing federal and state regulations on commercial and recreational fishing of gag grouper in the Gulf of Mexico

Recreational Fishing Limits				
State	Bag Limit	Size Limit (min)	Seasonal Closure	Reserves
Alabama	n/a	n/a	February 1 – March 31	n/a
Florida (Monroe & Atlantic Counties)	2	22"	February 1 – March 31	n/a
	1	24"	January 1 – April 30	n/a
Louisiana	5	22"	February 15 – March 15 ⁴	n/a
Mississippi	5	22"	n/a	n/a
Texas	2	22"	n/a	n/a
Federal	Bag Limit	Size Limit	Seasonal Closure	Reserves
NOAA/GMFMC	2	22"	February 1 – March 31 ¹	8 ^{2,3}
Commercial Fishing Limits				
NOAA/GMFMC	IFQ: 7.5 MP ⁵	24"	Only 100,000 lbs released to date	8 ^{2,3}

1- A temporary federal rule is currently in effect that closes the gag fishery from January 1, 2011 through May 31, 2011.

2- Some reserves are part of the same sanctuary, but have different coordinates (i.e. East and West Flower Garden Bank, and North and South Tortugas Ecological Reserve).

3- Some reserves are closed to all fishing whereas others are closed only during certain time periods that are specific to the reserve.

4- Louisiana Wildlife and Fisheries Commission has closed state waters to harvest of gag effective January 6, 2011.

5- Gutted weight; subject to IFQ allocations and protocols

1.5 Questions

The purpose of my model is to answer questions concerning the effects of fishing, marine reserves, and other management pertaining to gag, while attempting to overcome the limiting assumptions of prior models. I will explore the sensitivity of gag to natural stresses in the form of natural mortality as well as human-induced stresses in the form of fishing pressure. The specific questions I will be asking are (1) What are the population dynamics in the absence of fishing? (2) How does fishing affect the gag demographics? (3) How does fishing affect the effective population size vs. the total population size? (4) How does sex ratio affect the gag demographics and effective population size (in the form of enforcement of fertility constraints)? (5) Does the spatial distribution of the species increase its susceptibility to increased fishing pressure? (6) Which model parameters have the most significant effect on the output variables of the model? (7) Which output variables are most sensitive to changes in model parameters? and (8) What modeled management strategy or suites of modeled management strategies have the greatest effect on this species in terms of their effect on effective population size? Finally, I would like to briefly explore and discuss realistic management strategies for this species and potential marine policy implications on state and federal levels.

1.6 Hypotheses

While I expect population dynamics without fishing to still exhibit a skewed population sex ratio, I predict that fishing will further skew population demographics even more than what is seen naturally. I propose that fishing will exacerbate the problems associated with the life history of gag even further. The practices of both commercial and recreational fishermen are likely to affect the two most sensitive life stages of gag: males and juveniles (in the form of bycatch). Males are easily found and caught since they stay year-round on shelf edge aggregations. There is also a high abundance of juvenile gag in seagrass bed habitat, which is most accessible to recreational fishing practices.

I expect that fishing will have a much more significant effect on the effective population size than on the total population itself. A common mistake in management is the misperception that a

species is unaffected by fishing by looking only at the total population size. In species such as grouper, where life history pre-disposes it to overfishing, total population size is likely to be misleading in terms of the overall health of the population. Looking at other statistics such as effective population size may reveal the real status of the population.

Sex ratio obviously has a direct effect on population demography, but more importantly is its role in determining the fertility of the population. Even though older female gag are highly fecund, their fecundity is moderated by an extremely low male:female sex ratio (Coleman et al. 1996). Over years and generations, a small skew can diverge sharply due to this negative feedback loop. Therefore, I hypothesize that there will be a negative, non-linear relationship between the sex ratio and fertility as well as sex ratio and effective population size.

Spatial distributions should be integral in determining a management plan for any species. Since gag have both sedentary and highly mobile stages, incorporation of this movement into the model should more accurately predict how the species would respond to management. I expect that varying fishing pressure by location will have a significant effect on the effective population size. Incorporating spatial distributions is also important for determining the effectiveness of marine reserves, as well as other management techniques. I expect that varying size and placement of reserves will have a significant effect on the both total and effective population sizes.

I expect that certain life stages and transitions will be most sensitive to changes. I also expect effective population size to be more sensitive to varying the parameters of the model, since total population size is likely to mask the real state of the populations. The sensitivity analysis will (1) allow managers to see which stages and habitats should garner the most attention, (2) allow scientists to see which variables of population dynamics need further study and testing in order to have the most accurate data possible for future models and management decisions, and (3) to help both scientists and managers know which output variables they should be testing. This analysis and subsequent work will allow policy makers and managing agencies to best direct their efforts and raise public awareness in the proper areas.

Finally, I expect that protecting males will be the most important factor in management of the species, and that strategically placed marine reserves will be the most effective tool with which to do this. I also expect that suites of management tools will be even more effective than any one management strategy alone.

CHAPTER 2

METHODS

2.1 The Individual Based Model

I created a model to incorporate life history aspects including protogyny, fecundities, maturity rates, and basic reproduction to study the population dynamics of gag. It was built with a Java platform, using object oriented programming to create an age-based, Individual Based Model (IBM). The defining feature of an IBM is that it creates and tracks individuals in a population as well as the population as a whole. Other factors that have been included are variation in reproductive behaviors, stage-dependent migration that occurs in time steps of one month, methods to test effects of fisherman behavior, marine reserve placement and size, minimum age limits to fishing (a proxy for minimum “size” limits), stochasticity in yearly recruitment, and variable fishing mortality. A flowchart of the model can be seen in Figure 2.1 and describes the steps that an individual “fish” would experience. Each fish is assigned an age, position, school for females (the school determines which aggregation a group of females will return to), fecundity, and determined to be reproductively mature or immature (individual methods are shown in light gray). The model loops over all individuals (in light gray) while applying population level methods. Movement occurs monthly (as indicated by everything shown in dark gray), while other methods are only applied during the month that corresponds to the actual gag life cycle. For instance, the spawning method only occurs during month 3, or March, which is the middle of gag spawning season (though gag spawning runs from January through April, for the purposes of the model it only occurs during one month). Methods shown in black are run each year, including changing sex, calculating mortalities and fecundities, subsampling of the population, and aging. This current model simulates the life cycle of many individual fish, based on data from stock assessments and values obtained by cited authors, while also keeping track of a sufficiently large number of individuals that population-level dynamics can be analyzed and predictions can be made based on the parameters given in the model.

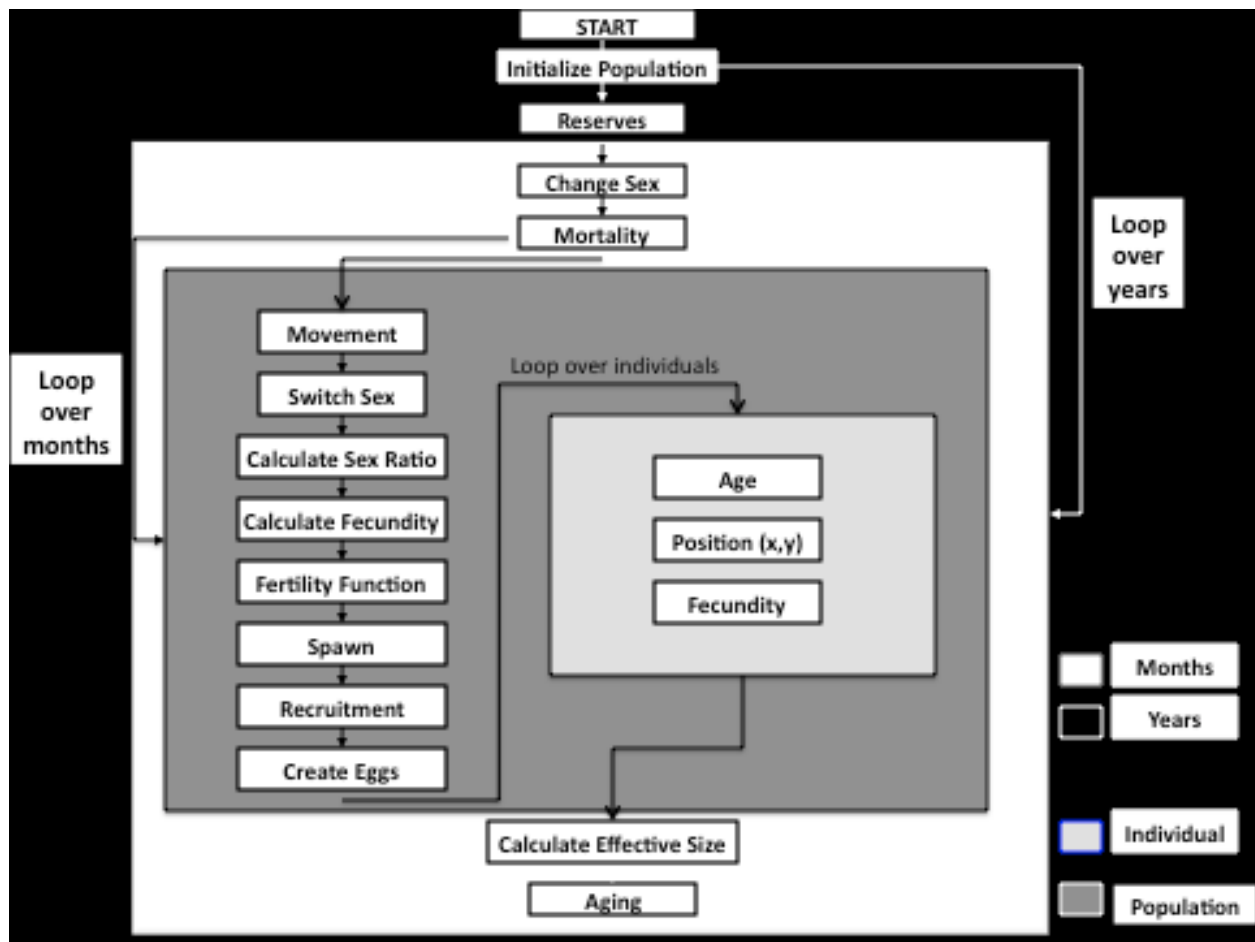


Figure 2.1 Flowchart for IBM for gag
(1) Adjusting for sex ratio occurs within the fertility function (explained below).

2.2 Model Parameters and Methods

A number of different life-history methods and parameters were required in order to run the model (a table of parameters can be seen in Table 2.1) and were estimated from available data. While most parameters are a function of age, they can also be calculated as a function of length. To make a more simplified model, I have chosen to use age-based functions of life history methods throughout the model (movement is stage-based), due to the strong correlation between age and increased length (Figure 2.2), the higher frequency of age-based functions in

the literature, and the need for a uniform metric in the model. While age, length, and weight functions are all available for certain parameters, age-based functions are most commonly found. Each of the parameters used in the model is discussed in further detail below.

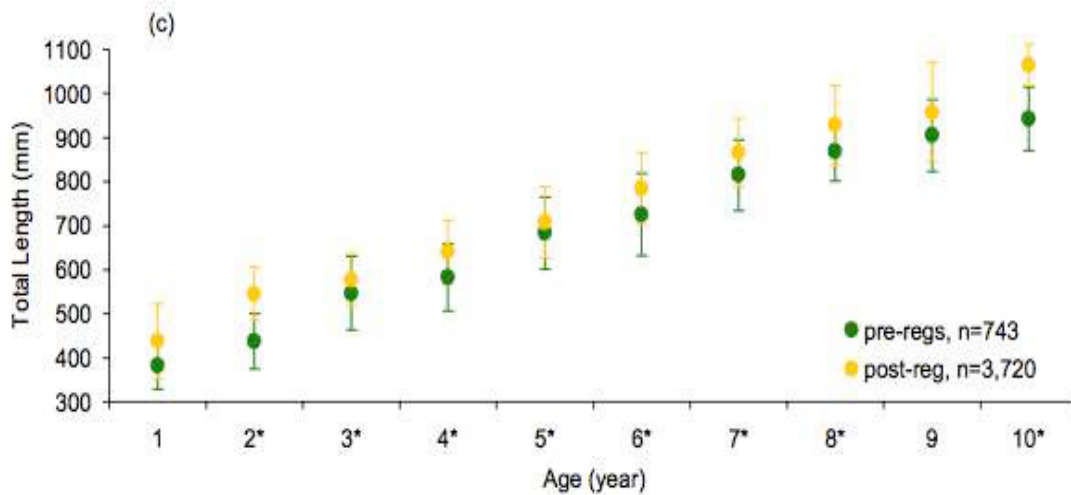


Figure 2.2 Pre-regulatory data (1979-1989) compared to post-regulatory data (1999-2005) for size at age
Asterisk indicates significant statistical differences between groups determined by a Welch two sample t-test (Lombardi-Carlson, et al 2006).

Initialization of the Population

The population is initialized at a population size of 50,000, where 60% of the population are juveniles, 30% are females, and 10% are males. This was the largest population size that the model could run without using all the memory. The model was run for 100 years before results were outputted, and results were taken for 30 years after that, totaling 130 years. Initial individuals were assigned a random age, aggregation or school, and position all of which are dependent on whether the individual's sex.

Maturity

Maturity is calculated as a function of age, with 50% of the population reaching maturity at the age of 3.7 years (Fitzhugh, et al 2006). The regression function for the proportion of the population that is mature based on age is:

$$M = e^{-e^{-(6.42 + 1.81 \times AGE)}}$$

This equation, illustrated by the graph in Figure 2.3, was used to calculate the probability that any individual was mature. Stochasticity was included in this process by assigning each individual a random probability and determining whether that value was greater or less than the probability of maturity as determined by this equation. Once an individual is determined to be mature, they can then be assigned a fecundity and they are available for spawning. As long as an individual is immature, it is included in the “Juveniles” subgroup and behaves accordingly. Once an individual matures, it is removed from “Juveniles” and added into the “Female” subgroup of the model. It is important to remember that while an immature individual is in the “Juveniles” subgroup, it’s sex is still female, however the “Females” subgroup is reserved for mature females only. This allows distinctions to be made in habitat and movement patterns between immature females (juveniles) and mature females in order for stage-specific behaviors to be assigned.

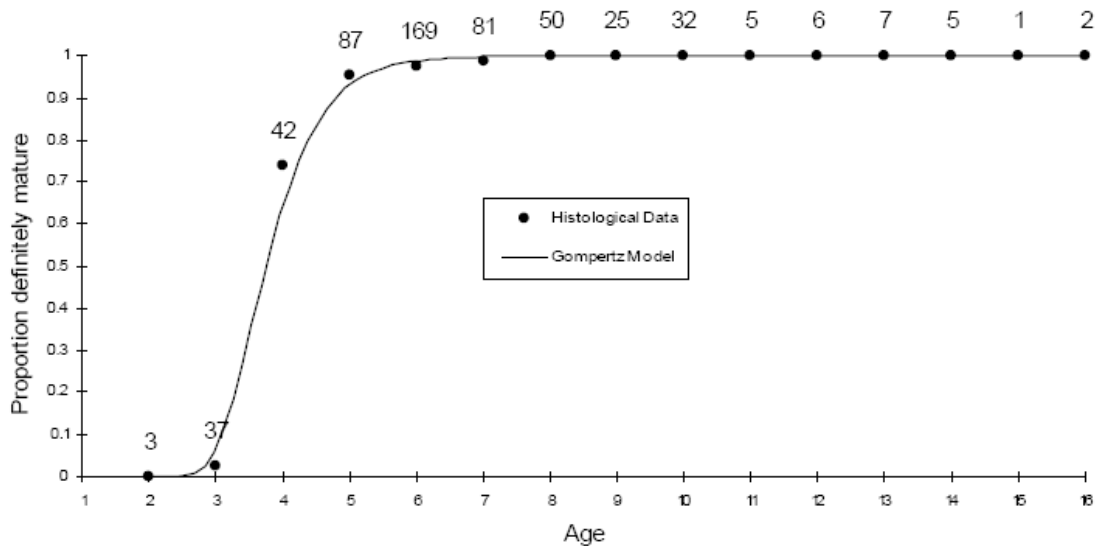


Figure 2.3 Maturity as a function of age
Proportion definitely mature as a function of age with 50% age at maturity = 3.7 years, with $r^2 = 0.6$, $n = 552$ (Fitzhugh, et al 2006)

Fecundity

Fecundity is estimated as a function of spawning frequencies and batch fecundity, where batch fecundity itself is a function of age. Batch fecundity, in thousands, is estimated by the regression equation:

$$F_{batch} = (80.997 \times AGE) - 151.2$$

This equation, illustrated by the graph in Figure 2.4, calculates the fecundity of a female each time she spawns. Annual spawning frequency is estimated at 25 spawns per female per year, age-averaged. So annual fecundity at age, defined as the amount of contribution of a female of a certain age to the next generation measured by the number of eggs produced, is equal to the number of spawns per female per year, or annual spawning frequency, multiplied by the batch fecundity at age:

$$F_{total} = 25 \times [(80.997 \times AGE) - 151.2]$$

This equation is used since fecundity is calculated for females only once per year, provided the female is mature. The total number of offspring for the population per year is calculated by summing the fecundities of all females. This number is the total possible recruitment, however, other factors such as larval mortality, stochasticity, and a carrying capacity for seagrass beds must be applied, and is discussed in the Carrying Capacity method.

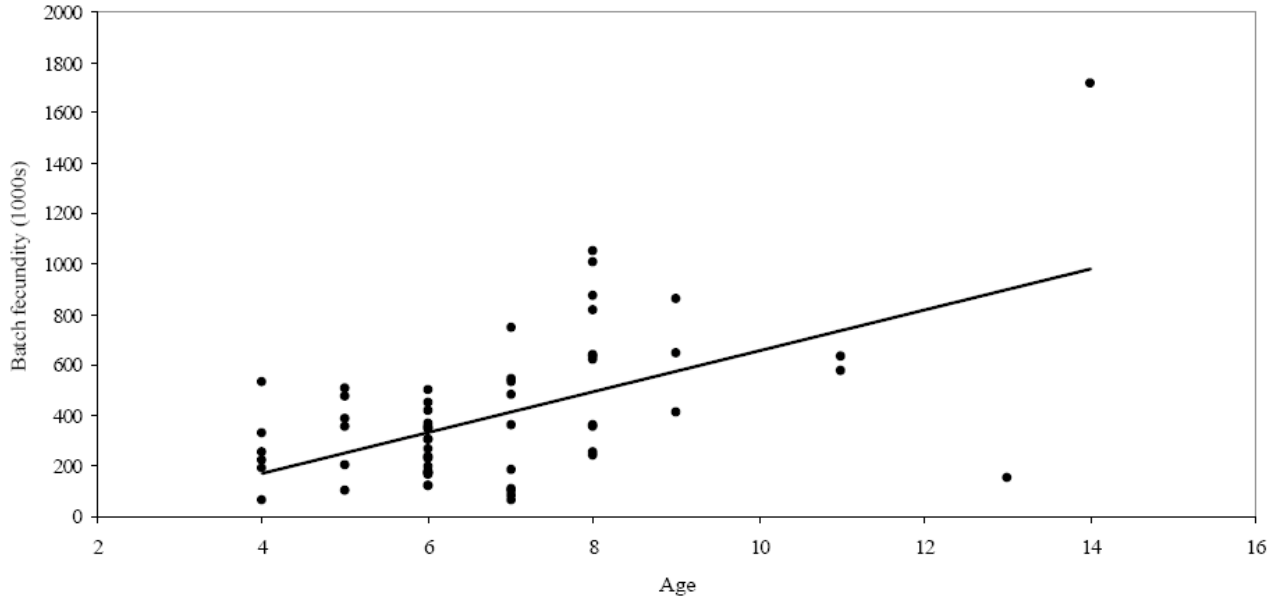


Figure 2.4 Batch fecundities as a function of age
 Linear regression of fecundity as a function of age where $r^2 = 0.30$ and $n=61$ (Fitzhugh, et al 2006)

Fertility

Since the sex ratio is believed to have an effect on the population and population genetic variation, a method was included to adjust fecundities based on the sex ratio. This equation is not always used in the model, but instead can be included or not in order to test the effect of recruitment that is variable depending specifically on the proportion of males in the population. The fecundity equation I used in the model is taken from Heppel, et al. (2006):

$$\psi = f_{max} \times (1 - e^{(-\theta \times p_{male})})$$

where Ψ represents the proportion of eggs that are actually fertilized (as apposed to how many are produced, which is calculated in the Fecundity method), f_{max} is the maximum fertilization rate which was set to 0.8 (the value used for high fishing scenarios, Heppel, et al 2006), θ is the parameter representing fertilization ability, and is set to a “high fertility” value of 80, and p_{male} is the proportion of males in the population calculated at each yearly time step directly before

reproduction occurs. If there are no males in the population at the time of reproduction, then spawning does not occur and the model ends the run.

Recruitment

A carrying capacity was enforced in the recruitment stage of the population in order to simulate the density dependence that is enforced on any population. In this case, the carrying capacity is found in the limited habitat of the seagrass beds for juvenile fish. In order to introduce this limiting factor, I used a step-wise function (Heppel, et al. 2006), where if the possible number of recruits is less than the carrying capacity, then the following equation calculates the number of total recruits for the year:

$$Recruitment = Fecundity \times Survival_{larval} \times \gamma$$

But if the possible number of recruits is greater than the carrying capacity, then the number of total recruits for the year is calculated by the equation:

$$Recruitment = K \times Survival_{larval} \times \gamma$$

where K is the carrying capacity of the seagrass beds and γ is a random number drawn from a gamma distribution (with $\theta = 1$ and $k = 5$). The shape of the gamma distribution most resembles the distribution of recruitment rates from 1988 to present (SEDAR, 2006). I determined that the random numbers should come from a gamma distribution by running simulations with random numbers taken from both Poisson and gamma distributions to determine which was representative of the population in nature. The distribution of recruitment rates for gag showed a pattern very similar to a gamma distribution using the parameters mentioned above, but very dissimilar from a Poisson distribution, as compared to the recruitment rates from 1988 to present from the stock assessment.

Female-to-Male Transition

This transition is the probability that an adult female will switch to become a male. This probability is a function of age, with 50% of the females transitioning by 10.7 years of age

(Fitzhugh, et al 2006). The proportion of individuals that are female in a population was calculated by age by Fitzhugh (2006), where sex was determined by pigmentation with males being pigmented where females are not. Fish that have only some pigmentation but are not fully pigmented were counted as male because they are assumed to have completed transition by the next spawning season. The equation fit to this proportion and used in my model is:

$$pr(trans) = \frac{1}{1 + e^{-(6.89 - 0.637 \times AGE)}}$$

I used this equation to calculate the proportion of females who change sex each year based on age alone (see Figure 2.5). When this equation is used, the number of females that enter the “transition” stage will be removed from the female population immediately, and then added to the male population the following year. This equation is applied to female fish only after they reach maturity.

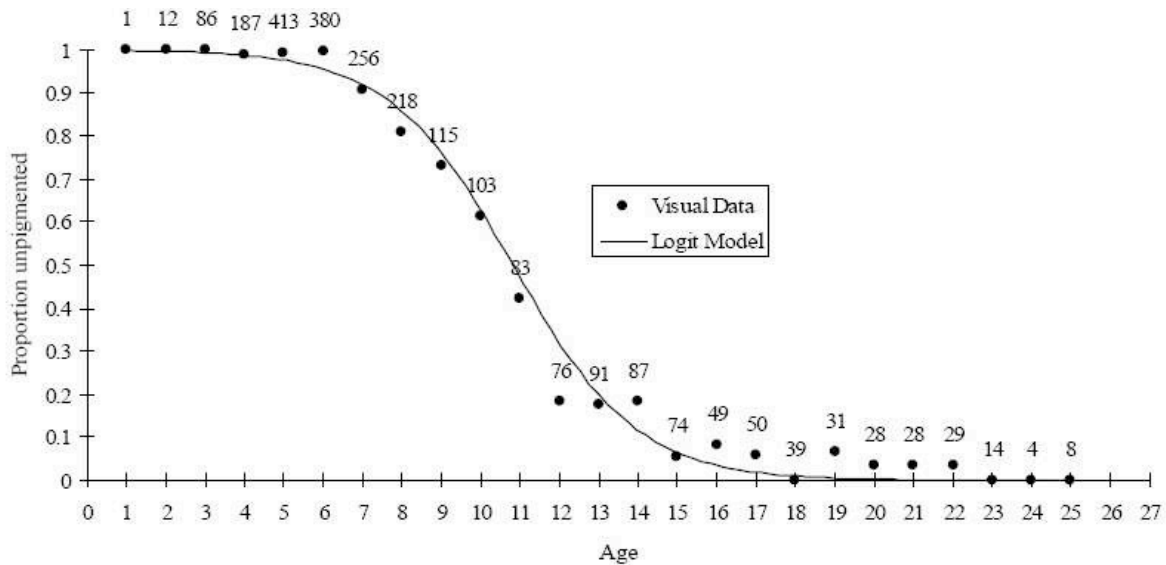


Figure 2.5 Proportion of fish remaining female as a function of age
Proportion of fish remaining females as determined by pigmentation, where $r^2 = 0.57$ and $n=2462$ (Fitzhugh, et al 2006)

It is also thought that female-to-male transition may be dependent on the frequency of younger (or smaller) females relative to the female whose probability of transition is in question. For example, if a school of females arrives at an aggregation and finds that there are no males or depleted males, then the oldest, or largest, female may be more likely to undergo transition. This probability is described by the equation:

$$p_c(age) = \frac{1}{1 + e^{-\rho(F_i - F_c)}}$$

Where $p_c(age)$ is the probability of switching as a function of age, ρ is the slope of the probability function retrofitted to stock assessment data (SEDAR, 2010), F_c is the frequency at which 50% of individuals are expected to switch sex, and F_i represents the frequency of mature females that are younger than the selected female for whom the probability is being determined. F_i is calculated in the model in the following way:

$$F_i = \frac{N_{younger}}{N_{total}}$$

This relationship between transition, age, and frequency of younger females was described for protogynous hermaphrodites by Alonzo and Mangel (2003) and was applied to gag by modifying the slope of the function to fit the data for this species (see Figure 2.6). The above function takes into account both age of the potentially switching female as well as the frequency of younger females. The model was run with this scenario to determine the effect of the hypothesized case that females change sex based on social factors and not purely by age alone.

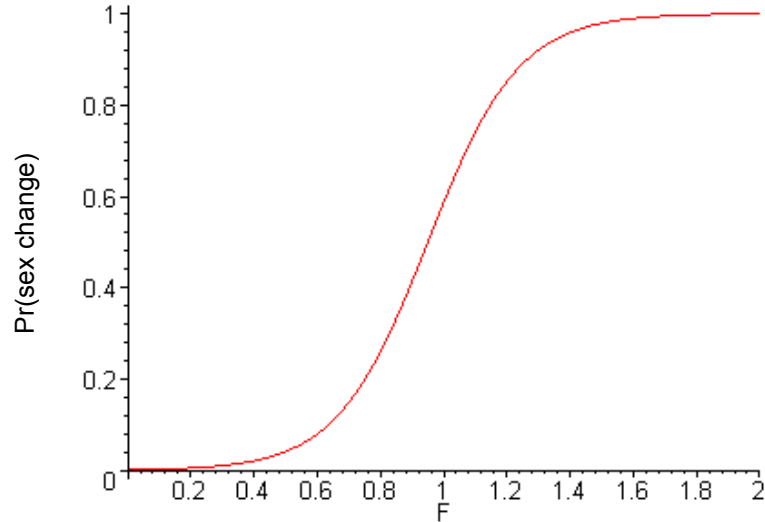


Figure. 2.6 Probability of sex change as a function of age and frequency of younger females

Population Growth

Population growth will occur as propagated by the fecundities, mortalities, and reproductive events that occur in the population and will not be fit to any other equation. The population was started with an initial size of 50,000 and allowed to grow. Growth will only be regulated by a carrying capacity in the seagrass beds, as supported by stock assessment data (2010), which enforces density dependence on the juvenile stage of the population as they enter the seagrass bed habitat.

Aging

Aging simply adds a year to the fish's age at every time step. It also removes fish that are older than 30, which is the maximum known age for gag (Lombardi-Carlson, et al. 2006). It is important to note, however, that individuals greater than 13 years of age are rare, thus a natural mortality equation was needed to remove most individuals after this age and before that of 31.

Mortality

Larval mortality values were determined by running a simulation of the population with different larval mortality values and also with different values for parameters such as fishing and

fertility in order to determine what value yields a stable population across all cases. The mortality values were determined for six cases: (1) fishing at 0.5 with fertility function (2) no fishing with fertility function (3) fishing at 0.25 with fertility function (4) no fishing with no fertility function (5) fishing at 0.5 with no fertility function (6) fishing at 0.25 with no fertility function. Each run went for 30 years, after an initial 10 year burn-in period. The initial population size was set at 10,000 individuals and the carrying capacity was set at 15,000. Larval mortality was most stable at 99% mortality so this value was used in the model.

I considered fish of age 1 as juveniles in the seagrass beds to have virtually no mortality once they successfully enter the seagrass bed habitat (note that density dependent mortality acts on juveniles as they enter the seagrass bed habitat and must compete for space). After about 6 months in the seagrass, juveniles move off to the nearshore reefs in the fall where they assume the same level of age-dependent natural mortality as well as the same probability of fishing mortality as adults. In the model, mortalities were only calculated once per year, therefore juvenile gag are exempt from mortality from natural causes until age 2. Since juveniles are given an age of 1 once they get to the seagrass beds, there is only a 3 month period where juveniles are exempt from natural mortality which is inconsistent with the reality that juveniles assume approximately adult-level of natural mortality once they move to nearshore reefs in the fall. Once the juveniles reach age 2, individuals were assumed to have relatively constant mortality over time. Therefore, probability of natural mortality is calculated for each individual in the model using the following equation:

$$Mortality_{nat} = 0.4298 \times AGE^{-0.488}$$

Where natural mortality is a function of age as seen in Figure 2.7.

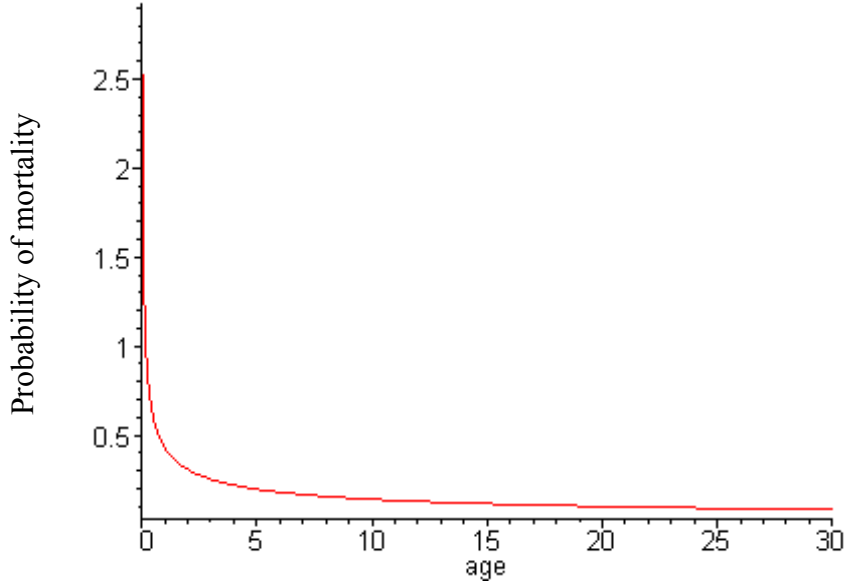


Figure 2.7 Probability of mortality from natural causes as a function of age

A different method is used to describe mortality caused by fishing. The proportion of the population surviving to time t is represented by:

$$\frac{N_t}{N_0} = e^{-Z \times t}$$

where Z is the constant instantaneous rate of mortality. Since our time steps are in years, this was equal to the annual rate of mortality. Since mortality can come from both natural causes and from fishing, two values will be described by McGovern, et al. (2005): $Z_{\text{NAT}} = 0.15$ and Z_{FISH} . However, in the model I decided to use the equation for natural mortality that was based on age instead. This Z value was used to calculate probability of mortality from fishing as an annual rate. Fishing mortality (Z_{fish}) was varied to examine the difference in effects of no fishing as well as fishing at both low and high levels of fishing, where sustainable fishing mortality was set to $Z_{\text{fish}} = 0.25$ and high fishing mortality was set to $Z_{\text{fish}} = 0.5$. In the model, natural mortality was applied to the population first and was followed by fishing mortality depending on the specified fishing pressure. Fishing pressure applied was also generally assumed to be the same for both males and females in the model. While this is likely not the case, no relationship

between sex and fishing pressure has yet been concluded. In the model, this was taken into account in spatially variable fishing where aggregations that are usually dominated year round by males were either assigned a higher fishing pressure or were “protected” by being assigned a lower fishing pressure. This was the only method by which sex-dependent fishing was imposed.

Fishing mortality can be made spatially variable in order to exercise differential fishing pressures that may be experienced by aggregations (which is likely a result of only commercial fishing, as recreational fishermen rarely make trips to deep water aggregations): higher to reflect likely current conditions where fisherman can target aggregations or lower to test the management technique of protecting all aggregations. The age at which fish are eligible to be caught can be changed to reflect the common management strategy of imposing size limits on fish that can be kept, or in this case “age limits”.

Movement

Space was incorporated into the model in two dimensions, with x and y both being set to 120 units. Individual fish move throughout this space with movement dependent on both life stage and time. The model used a monthly time step as well as a yearly time step, so that some methods were imposed only yearly while others, such as movement, were imposed monthly. The variation in movement by stages can be seen in Figure 2.8.

Eggs are assigned an initial position with x set to 0 and y set to a random number between 0 and 120. These coordinates are used because they describe the strip of model space where the aggregations are found, which is where reproduction occurs and eggs are produced. Once eggs are fertilized during spawning, they are turned into pelagic larvae.

Pelagic larvae move randomly for the first month after they are produced, with random movement occurring based on a “current speed”, equal to 120 units per time step, that carries them positively, negatively, or with no movement in the y direction, and only positively in the x direction. By the second month, their position is set to the sea grass beds where they transition to become benthic juveniles.

Benthic juveniles are initially assigned a random position in the seagrass beds by giving them an x value of 120 and a random y value between 0 and 120. Benthic juveniles can then move within the defined “seagrass space” at a defined rate of swimming of 2 units per time step. They are only allowed to move a certain distance before their movement will be “weighted” to

move back towards the seagrass. They stay in the seagrass until the fall (month nine), when they move off to nearshore reefs. They are allowed to move randomly (at the same swim rate) around the nearshore reef model space where they remain until they mature and are entrained into the female population.

In the model, mature females spend the majority of the year near offshore reefs, where they are able to move randomly at a swim rate of 16 units per time step. They form pre-spawning aggregations and move into the nearshore reef model space during months 9, 10, and 11, where they move randomly at the 16 units per time step swim rate. During month 12, they move back to the deeper offshore reefs, where they stay during month 1 as well, moving randomly at the same swim rate. Females are assigned schools that they travel with to the shelf edge aggregations during month two to spawn (in month three). Based on female behavior, females will either travel to the closest aggregation to spawn from their location on the offshore reef, or they will return to the same aggregation with their school each year. After spawning during month three, females randomly move about the model space at the same swim rate until month nine when they return to the nearshore reefs.

Males, on the other hand, experience very little movement (Coleman et al., in press). They are assigned to an aggregation, where they stay year-round within a distance of 5 units. When they reach the bounds of their aggregation space, their movement is weighted back towards their assigned space at a swim rate of one unit per time step.

Movement is thus based not only on the stage of the individual, but also on the time of the year in order to simulate realistic movement patterns.

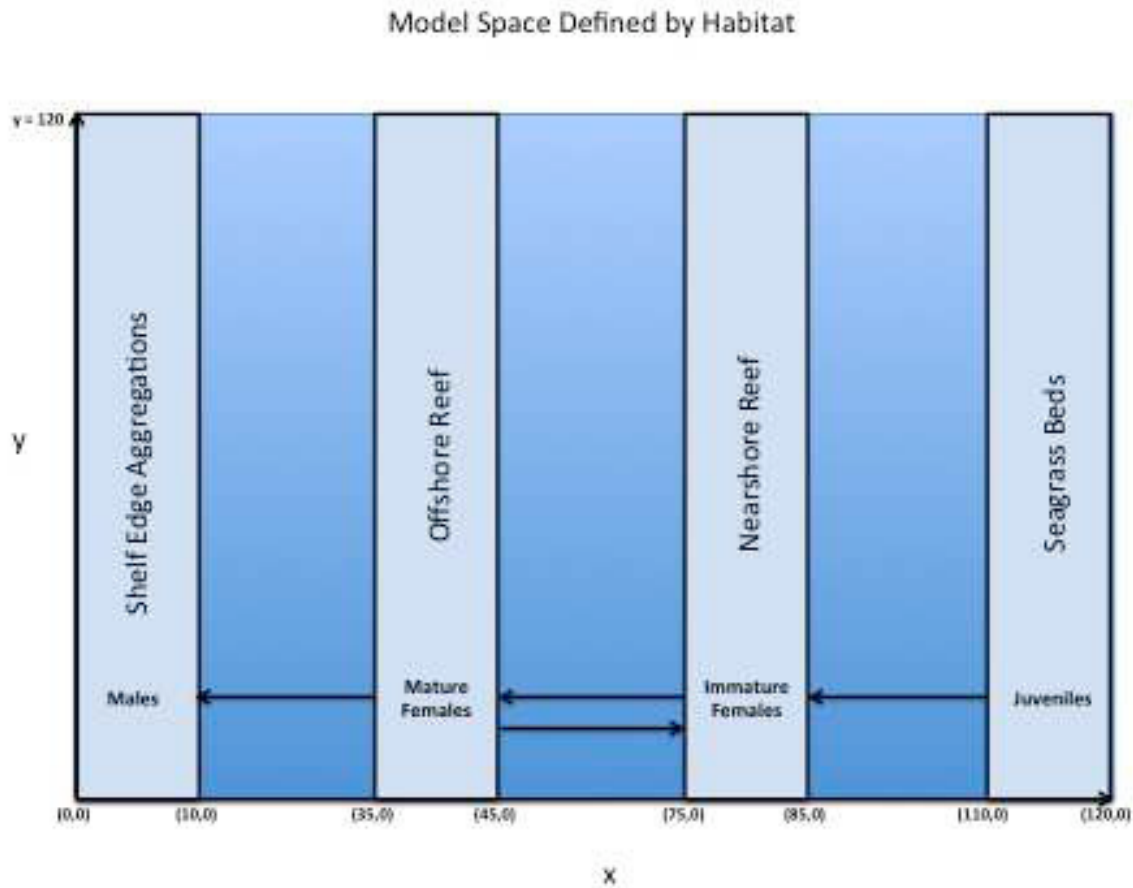


Figure 2.8 Diagram of model space and stage-dependent movement patterns

Spawning

Spawning in the model occurs at aggregations where males are located only when the sex ratio is positive, meaning males are present in the population. Females move to the shelf edge aggregations during month two and spawning occurs during month three. First, each aggregation is evaluated to determine whether or not males are present. If males are present, then spawning proceeds. If not, any females that arrive at that aggregation will not spawn and therefore will not contribute to the recruitment that year. Total possible recruitment, or the number of total eggs produced, is calculated by summing over the fecundities of all mature females that arrive at an aggregation where males are present. If females exercise the behavior of returning to the same aggregation each year, then they will move with their school to the “matching” aggregation. However, if females do not exercise this behavior, they will move to the closest aggregation.

Then, each female whose position matches the aggregation position will be allowed to spawn at that location that year. While the male behavior of remaining at aggregations is important, it is not tested in this model because the sedentary behavior of males is well-known and established (Coleman citation). Therefore, male behavior was set to be sedentary so that they remain at the aggregations year round.

Marine Reserves

Marine reserves are handled in the model by creating a reserve matrix that represents the model space with dimensions of 120x120 units and is initially filled with the value, “1”. Percent of area protected is varied from 0% to 100% in increments of 10%. Based on the percent protected, a certain percent of the model space is then “reserved” and changed to the value, “0”. To create reserves based on the amount of protected area desired, fishing mortality rate for each fish is multiplied by the value of the number in the reserve matrix that corresponds to that individual’s current position. Thus, if a fish is in a position that corresponds to the value of “0” in the reserve matrix, the fishing pressure applied to that individual is now zero and it is subjected only to mortality from natural causes. The percent of the model space that is protected is varied by habitat, creating 5 different protection scenarios (see Figure 2.9). The first scenario applies the percent protected to the entire model space, applying protection across habitats. The second scenario applied percent protected to the shelf edge aggregation habitat only, which has dimensions of 10 units in the x direction by 120 units in the y direction. The third scenario applies protection to offshore reef habitat only, the fourth to nearshore reef habitat only, and the fifth to seagrass bed habitat only. This allows both percent and location of marine reserves to be tested for gag.

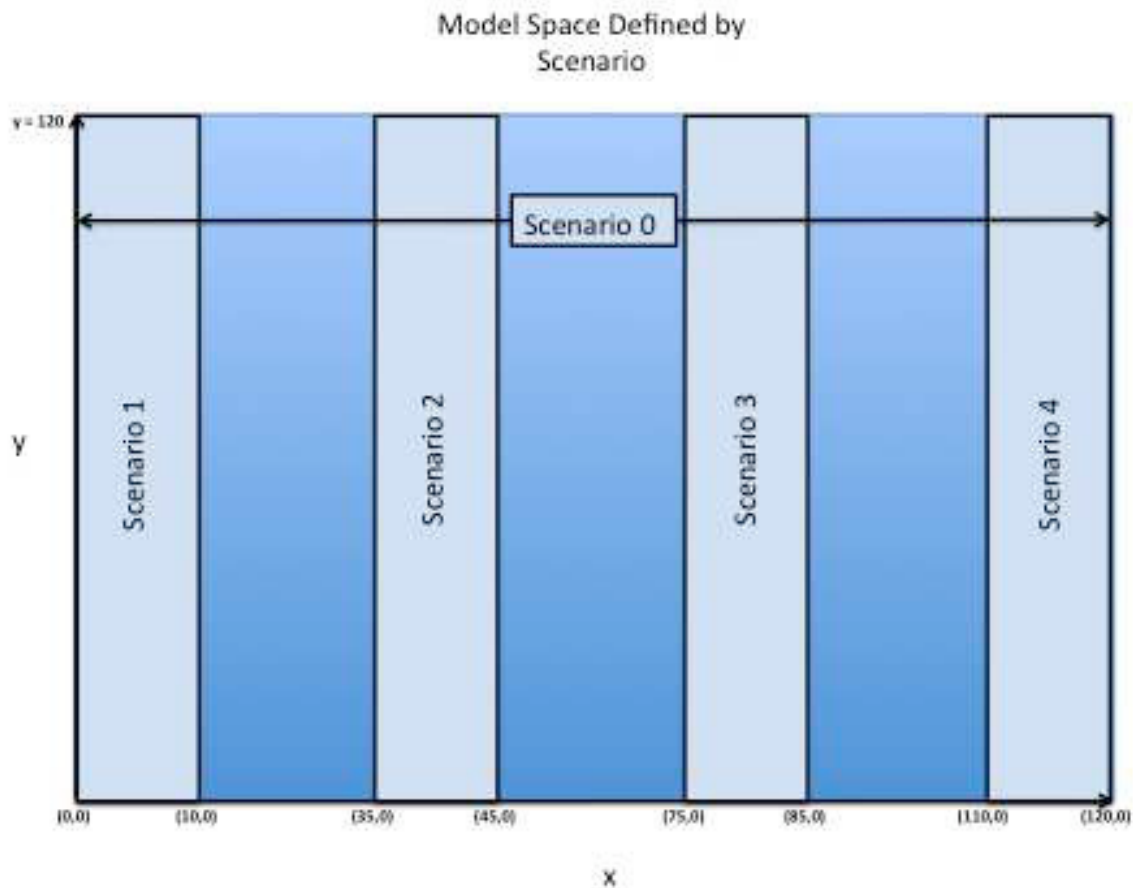


Figure 2.9 Diagram of model space designated by habitat with defined protection scenarios

Other Management Strategies

Marine reserves are not the only management strategy to be tested in the model. More traditional management strategies such as size limits (or in this case where age is used as a proxy for size, “age limits”), catch limits, and variable catch limits. Age limits are varied so that fish can be taken as early as age 1 and as late as age 30. Fishing mortality is thus enforced only after the fish reaches the specified age. Total catch limits are enforced by varying the fishing pressure using a no fishing scenario, a sustainable fishing pressure scenario ($Z_{\text{fish}} = 0.25$), and a high fishing pressure scenario ($Z_{\text{fish}} = 0.5$). Variable catch limits operate spatially to simulate 2 scenarios: one where fishing pressure is higher in aggregations which is thought to be the case since aggregations contain sedentary males that are more susceptible to capture (as are the

breeding age females found at aggregation sites during spawning season), and one where aggregations have lower fishing pressure to simulate a management technique that restricts fishing to lower levels in designated areas without making it into a no-take protected area.

Effective Population Size

Effective population size is calculated for the population to represent the portion of the population that is genetically viable. I used the inbreeding effective population size to measure the population since the skewed sex ratio likely contributes to a limited breeding population size. The following equation was used to calculate inbreeding effective population size, which is most commonly used for conservation purposes:

$$N_e = \frac{4(N_m \times N_f)}{N_m + N_f}$$

Since stochasticity operates heavily within this model, I took the harmonic mean of the values of effective population size each year for the last 30 years of each model run. I determined that the 100-year burn in period was adequate to minimize any effects of initial equilibration by running tests to assure that there were no trends still occurring after 100 years. It was shown that the population essentially reached an equilibrium around 50 years (see Figure 2.10). The following equation was used to calculate the harmonic mean:

$$Mean_{harmonic} = \frac{n}{\sum_{0}^n \frac{1}{N_{en}}}$$

Where n is equal to 30, which is the output period, and N_e refers to the value obtained from the previous equation for effective population size. This allows a mean to be taken over 30 years to minimize any random effects that may impact effective population size in any given year to allow more accurate comparison of this output variable between different scenarios. The generation time was determined by averaging the spawning females over the last 30 years of a

130-year period and was found to be 5.8 years. Therefore, calculating the harmonic mean over the last 30 years averages over approximately 5 generations.

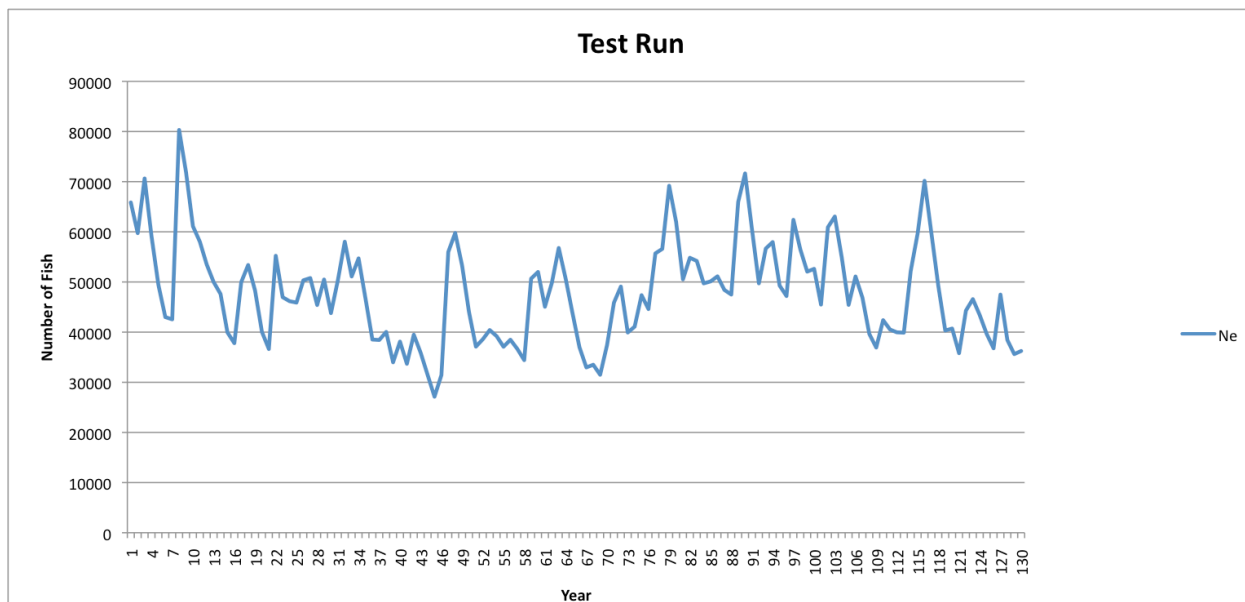


Figure 2.10 Single run test of equilibrium of the population over a span of 130 years

Statistical Analysis

I performed a sensitivity analysis to determine which parameters in the model have the greatest effect on the output variables: total population size, effective population size, and sex ratio. Though sensitivity analyses of individual based models are often performed by increasing or decreasing parameter values one at a time, I performed Latin Hypercube sampling instead (McKay et al. 2000, Megrey and Hinckley, 2001). Rather than testing parameters one at a time, LHS varies parameters simultaneously, which is advantageous because it avoids redundancy in testing every single parameter and combination of parameters. Latin Hypercube Sampling works by sampling from the probability distributions of each parameter used in the model. To do this, LHS divides the probability distribution for each parameter into “n” number of sections and samples each without replacement. This results in stratified sampling from each parameter distribution. The resulting data set can then be used in place of the model parameters to obtain output variables. A correlation test using Spearman’s Rank Correlation was then used to determine which parameters have the highest correlation, or effect, on each of the output

variables. Sensitivity was measured not only by the significance of the correlation but also whether the correlation was negative or positive. This can also be performed in reverse to test which output variables are most sensitive to changes in parameters. I tested 17 parameters in my model (which can be seen in Table 2.1 and are described in Table 2.2) and 3 output variables: total population size, sex ratio, and effective population size. Each run of the model used different values for the 17 parameters and output results. This was done 50 times to obtain 50 values for each output variable. These were then tested for correlations using Spearman's rho with a p-value confidence level of 5%.

Table 2.1 Table of parameters including ranges used in sensitivity analysis

Variable	Parameter	Value	Range (min)	Range (max)	Description
Input Parameters					
Natural Mortality	$p_1 * \text{age}^{(-p_2)}$	$p_1 = 0.4298$	0	1	Mortality rate from natural causes applied to all individuals over age 1
		$p_2 = 0.488$	0	1	
Fishing Mortality	Z_{fish}	Low = 0.25	0	1	Mortality rate from fishing applied to all individuals over age limit
		High = 0.5			
Transition (age)	$(1 + e^{-(p_1 - p_2 * \text{age})})^{-1}$	$p_1 = 6.89$	-	-	Probability of transition as a function of age only
		$p_2 = 0.637$	-	-	
Transition (frequency)	$(1 + e^{-p_1 * (F_i - F_c)})^{-1}$	$p_1 = 7$	1	30	Probability of transition as a function of both age and frequency of younger females
Maturity	$e^{(-e^{-(p_1 + p_2 * \text{age})})}$	$p_1 = 6.42$	0.1	20	Probability that an individual is mature as a function of age
		$p_2 = 1.81$	1	5	
Fecundity	$p_1 * [(p_2 * \text{age}) - p_3]$	$p_1 = 25$	1	100	Fecundity of individuals as a function of age, where p_1 represents the number of times a female spawns per year
		$p_2 = 80.997$	20	100	
		$p_3 = 151.2$	1	500	
Fertilization Rate	$F * p_1 * (1 - e^{(-p_2 * \text{SR})})$	$p_1 = 0.8$	0.01	1	Maximum fertilization rate, where fecundity (F) is adjusted for each individual by accounting for sex ratio (SR)
		$p_2 = 80$	1	100	
Aggregations	n_{agg}	10	1	100	Number of spawning aggregations
Schools	n_{school}	10	1	100	Number of female schools
K (larval)	$\text{juv}_{\text{avg}} * \gamma$	$\gamma = \text{random gamma}$	-	-	The carrying capacity is set to the average juvenile population size and adds stochasticity
Age Limit	L_{age}	1	1	30	Minimum age that fish can be kept if caught

Table 2.1 - continued

Variable	Parameter	Value	Range (min)	Range (max)	Description
Input Parameters					
Variable Fishing Mortality	Z_{var}	0	0	1	Probability of fishing that can be varied spatially
Recruitment	$\Sigma[F]*(1-p_1)*\gamma$	$p_1 = 0.99$	0	1	Recruitment adjusts the sum of fecundities (F) by larval survival ($1 - p_1$), and stochasticity (γ)
		$\gamma = \text{random gamma}$	0	1	
Female Swimrate	S_{female}	16	1	-	Units per time step that females can travel
Juvenile Swimrate	$S_{juvenile}$	2	1	-	Units per time step that juveniles can travel
Current	S_{larval}	60	1	-	Current speed that determines how many units per time step larvae travel
MPA	$p_{protected}$	varies	0	1	Percent of model space or percent of habitat type that is protected
Initial Males	p_{male}	0.1	-	-	Percent of initial population that are males
Initial Females	p_{female}	0.3	-	-	Percent of initial population that are females
Initial Juveniles	$p_{juvenile}$	0.6	-	-	Percent of initial population that are juveniles
Output Variables					
Total Population Size	$N_m + N_f + N_j$	-	-	-	Sum of all individuals in the population
Sex Ratio	N_m/N_f	-	-	-	Ratio of males to females
Effective Population Size	$4(N_m*N_f)/(N_m+N_f)$	-	-	-	Inbreeding effective population size which adjusts population size for variance in reproductive success

*If a parameter is used in the model but not varied in the sensitivity analysis, ranges are not shown.

Table 2.2 Table of input parameters and descriptions used in sensitivity analysis

Parameter	Description
Natural Mortality 1	Controls slope of the natural mortality function
Natural Mortality 2	Controls age specific mortality rates
Fishing Mortality	Probability of an individual being removed from the population
Probability of Sex Change	Slope of the function that determines probability of sex change
Maturity 1	Absolute maturity at age
Maturity 2	Slope of maturity function
Fecundity 1	Spawning frequency per year
Fecundity 2	Rate at which fecundity increases with age
Fecundity 3	Absolute fecundity at age
Fertility 1	Rate of fertilization
Fertility 2	Fertilization coefficient
Number of Aggregations, Schools	Number of aggregations and associated schools
Age Limit	Age limit at which individuals can be removed from the population (proxy for size limit management technique)
Aggregation Fishing	Probability of an individual being removed the population only from aggregation locations
Recruitment 1	Larval mortality
Recruitment 2	Stochasticity of yearly recruitment
Percent Protected	Percent of specified habitat protected

CHAPTER 3

RESULTS

The model was run to produce results for four different scenarios, each related to specific questions about gag population dynamics and management: (1) no reserves, (2) reserves, (3) variable fishing on aggregations, and (4) a sensitivity analysis. Each scenario was run 5 times to get an average value for all output variables shown. Exceptions did occur for scenarios that, due to variability and low populations sizes, ran less than 5 times and these exceptions are noted where they occur. It is also important to note that in all figures, the total population size shown does not include the larvae produced each year but does include the number of juveniles in the population.

3.1 No Reserves

The model was first run without reserves, but varying other parameters in order to answer the following questions: (1) How does fishing affect the effective population size vs. the total population size? (2) How does sex ratio affect the population demography and effective population size (in the form of enforcement of fertility constraints)? (3) Does the spatial distribution of the species increase its susceptibility to increased fishing pressure? and (4) How does fishing affect the population demography?

Life History and Behavior

Life history and behavior were both varied to understand the interactions between these aspects and fishing pressure. Data were collected from a factorial design including aggregations, fishing, age limit, fertility, and behavior and analyzed with an ANOVA. I varied spatial distributions by changing the number of aggregations (10, 50, or 100), which varies the distribution of sedentary males as well as distributing females among different numbers of aggregation during spawning months. Fishing was imposed at three levels: none ($F=0$), low ($F=0.25$), and high ($F=0.5$). One management technique was tested by changing the age limits at

which fish can be caught and kept (removed from the population) in scenarios where fishing was implemented. When the fertility function was implemented, female fecundity was adjusted based on the sex ratio; otherwise, the fertility was assumed to be constant. Female behavior refers to females returning to the same aggregation each year when behavior = true, and females migrating to the closest aggregation each year when behavior = false. Each of these parameters were explored with different spatial distributions in effect. The base scenarios, where no fishing occurs, are shown for 10, 50, and 100 aggregations in Figure 3.1, 3.2, and 3.3, respectively. These graphs are included here in order to give perspective as well as create a baseline for variation. Similar figures for all scenarios can be found in the Appendix.

Certain scenarios resulted in a population crash: when 100 aggregations were put in place, age limit was set to 1 year old, and fishing was high ($F=0.5$). The resulting populations of size 0 sometimes create distribution problems with the data, violating the heterogeneity assumptions of an ANOVA. So, the ANOVA results should be interpreted cautiously, but I feel the results are clear and informative nevertheless.

Three main effects were shown to significantly affect effective population size: aggregations, fishing, and age limit (Table 3.1, Figure 3.4). Though all were highly statistically significant, fishing had the greatest effect by far, so that increasing fishing from $F=0$ to $F=0.5$ resulted in a 40% decrease in the log of the effective population size. Increasing age limit from 1 year to 4 years old resulted in a 7% increase in the log of the effective population size and aggregations do not have an effect on the means of the effective size but are significant because increasing the number of aggregations in conjunction with increased fishing and low age limit causes population crashes. The other two main effects, female aggregation behavior and use of a fertility function, had no significant effects on effective population size (Table 3.1); all interaction terms including these variables were also not significant.

All three two-way interactions among these significant main effects were also highly significant, with the interaction between fishing and age limit being the strongest (Table 3.1, Figure 3.5). Increasing fishing from $F=0$ to $F=0.5$ when age limit was set to 1 year old resulted in a 60% decrease in the log of the effective population size, whereas increasing fishing while setting the age limit to 4 years old resulted in a 40% decrease in the log of the effective population size. The effect of fishing depended on age limit in part because the populations often crashed at the highest rate of fishing and an age limit of 1 (Figure 3.5). The number of

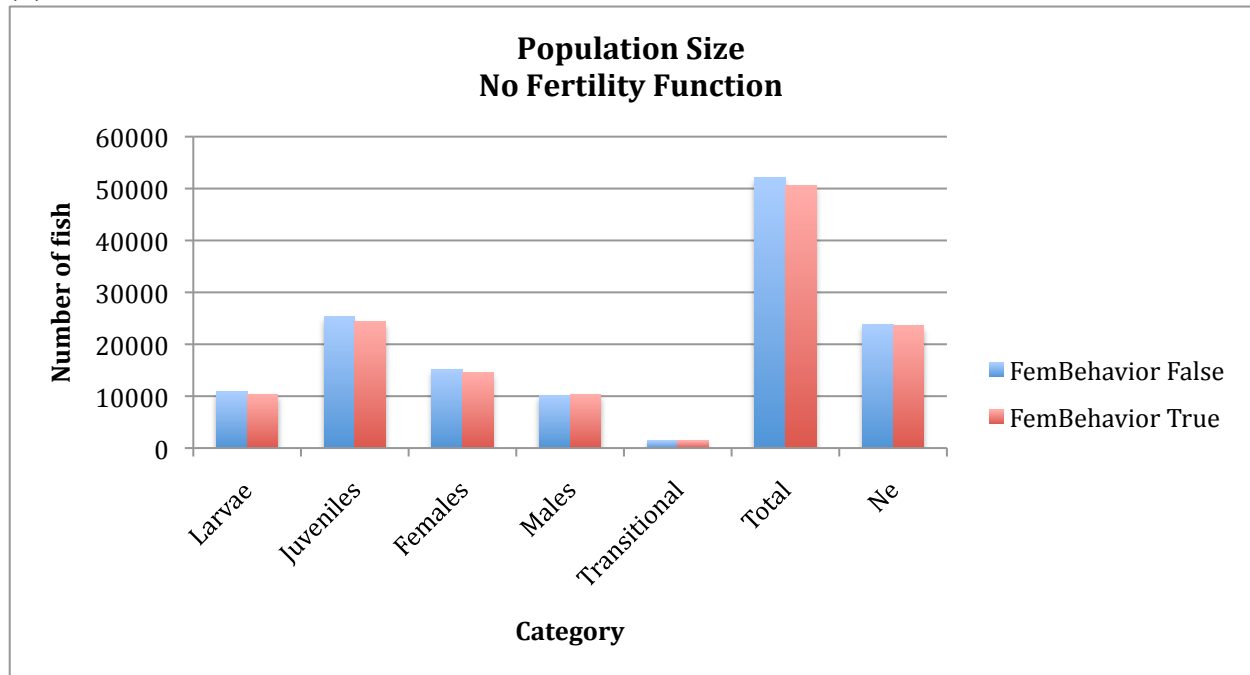
aggregations also interacted with the age limit and fishing because these population crashes tended to occur at larger aggregation sizes; increasing fishing from $F=0$ to $F=0.5$ at 10 aggregations caused a 35% decrease in the log of the effective population size while increasing fishing at 50 and 100 aggregations caused a 45% decrease in the log of the effective size. Aggregation and age limit interacted so that increasing the age limit from 1 year to 4 years at 10 aggregations only caused a 7% decrease in the log of the effective size, which did not seem to differ much when aggregation number was increased and is likely only a significant interaction because of the population crashes. The three-way interaction between these variables was also highly significant, apparently because population crashes were more likely when the age limit was low (1 year), fishing was high ($F=0.5$), and fish were distributed between 100 aggregations.

The same test was done for these variables in relation to the total population size and showed similar results (Table 3.2, Figure 3.6). One difference was that the effect on total population size was much less than the effects of each variable on effective population size. When fishing is increased, the log of the effective population size (adding 100) declines around 40%, whereas the log of the total size declines only 10%. The three significant variables were again number of aggregations, fishing level, and age limit. The same two- and three-way interactions were significant, while fertility and female behavior again had no effect. The two way interaction between fishing and age limit shows that increasing fishing while lowering age limit negatively effects the total population size; increasing fishing from $F=0$ to $F=0.5$ when age limit is set to 1 year old results in a 47% decrease in the log of the effective population size while setting the age limit to 4 years old results only results in a 6% decrease in the log of the effective size (Figure 3.7, Graph A). A similar effect is seen for the interaction between aggregation number and fishing: increasing both fishing and number of aggregations have strong, negative effects on total population size (Figure 3.7, Graph B). The interaction between number of aggregations and age limit also shows that increasing the number of aggregations while reducing the age limit has a significant negative effect on total population size (Figure 3.7, Graph C). Each significant main effect can be seen in Table 3.2, and the effect each treatment variable had on total population size is shown in Figure 3.6. Two-way interactions are shown in Figure 3.7.

To summarize these results, fishing had the strongest effect on both the effective population size and total population size when no refuges are used in the model. Aggregation number and the age limit also had significant effects on both effective and total population sizes.

Variables affecting effective population size showed a stronger effect than when these same variables affected total population size. Sex ratio, in the form of the fertility function, was not found to affect either the total or effective population sizes. While the spatial distribution in the form of the number of aggregations had a significant effect on both total and effective sizes, female behavior in relation to this spatial distribution did not. The interaction between the number of aggregations and level of fishing was highly significant, suggesting that spatial distribution does indeed increase the susceptibility of the species to increased fishing pressure.

(a)



(b)

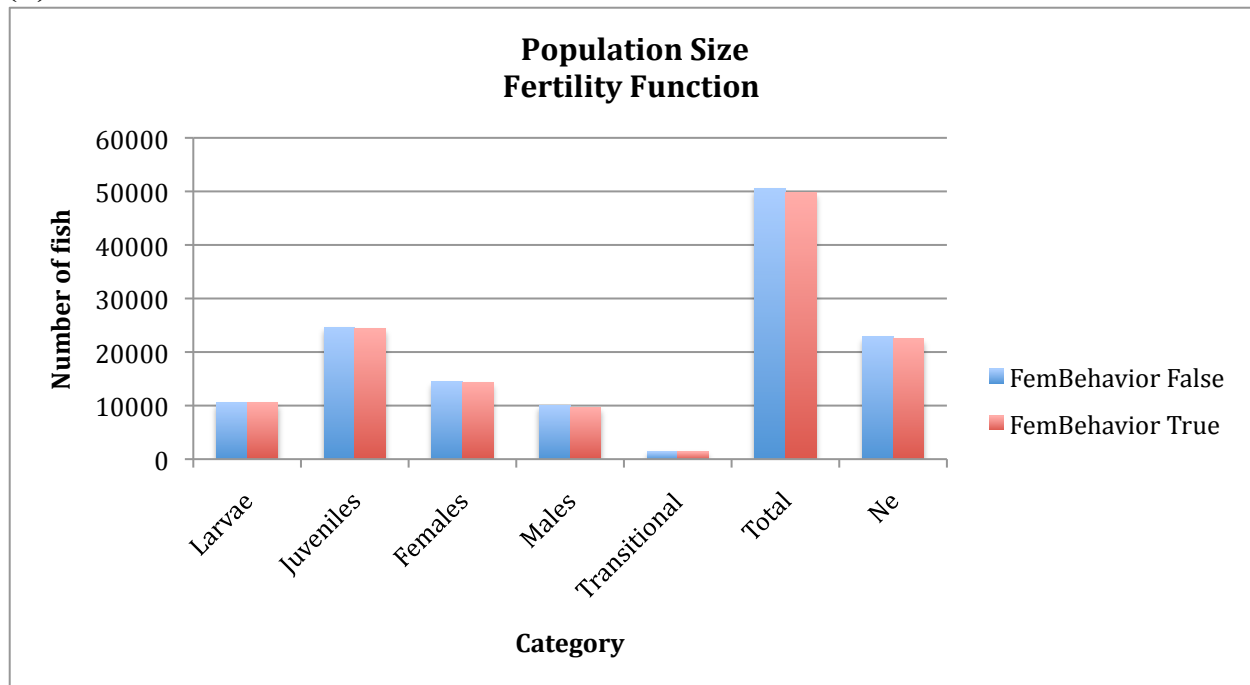
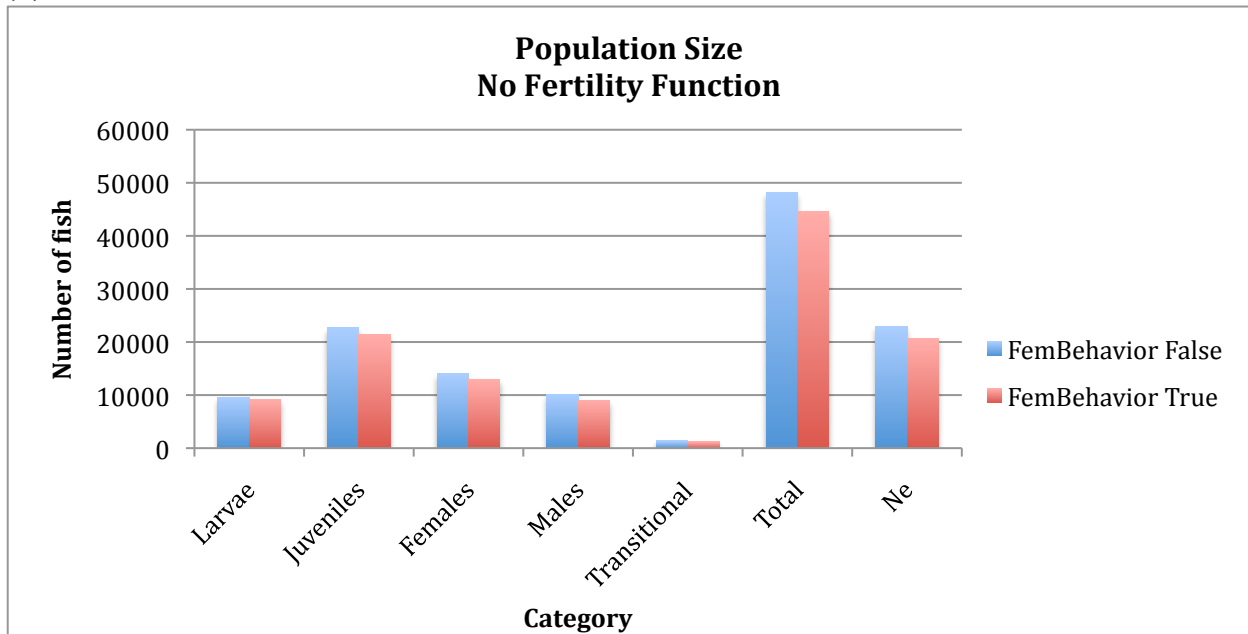


Figure 3.1 Population size with no fishing ($F=0$) and 10 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included

(a)



(b)

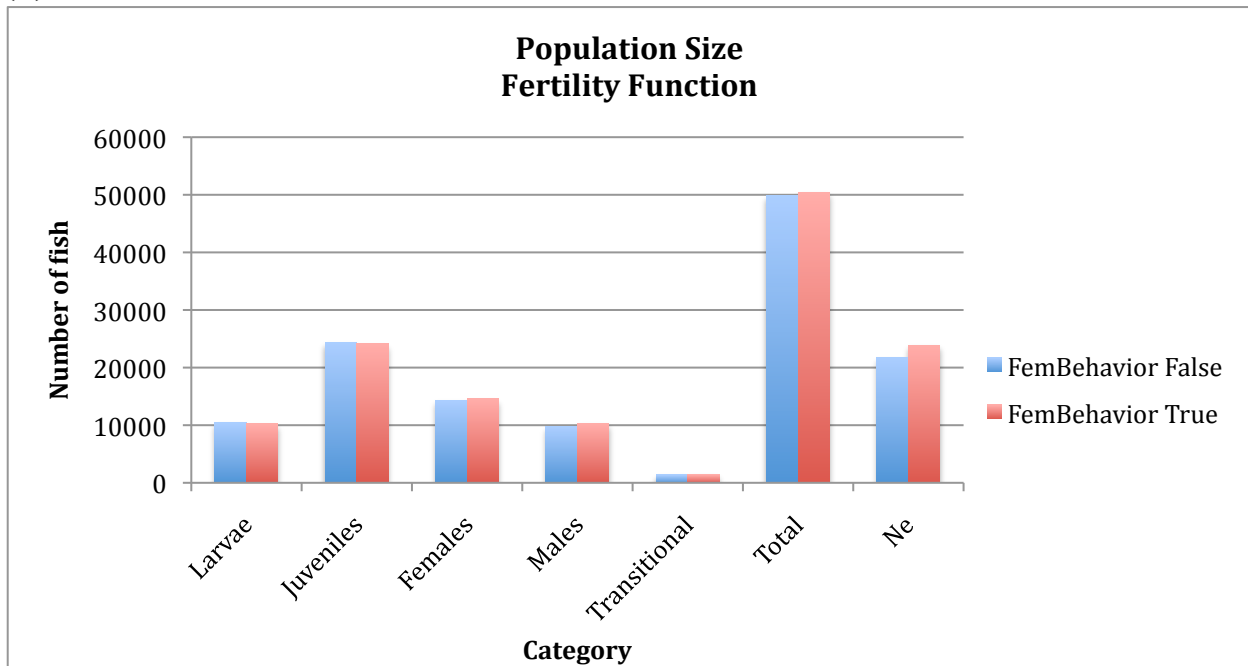
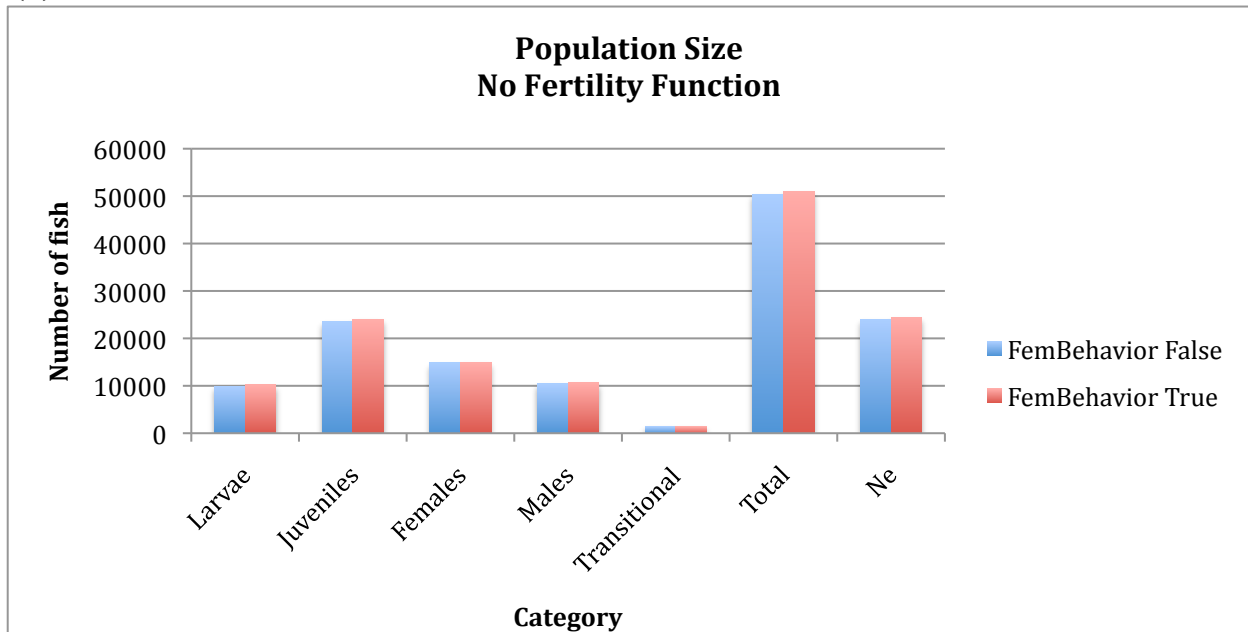


Figure 3.2 Population size with no fishing ($F=0$) and 50 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

(a)



(b)

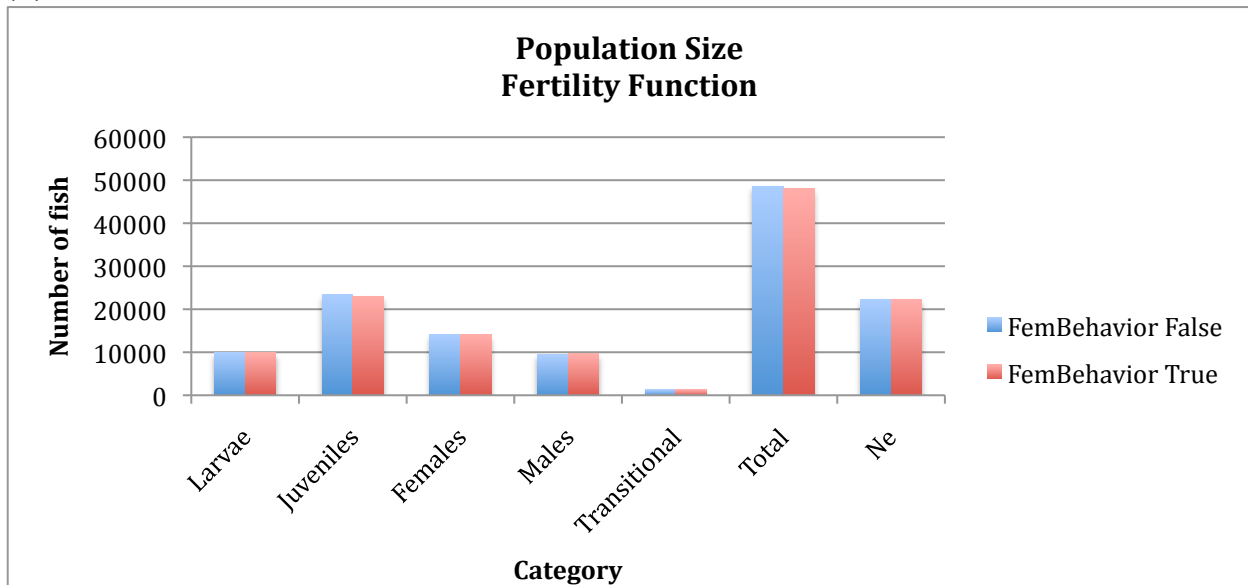


Figure 3.3 Population size with no fishing ($F=0$) and 100 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

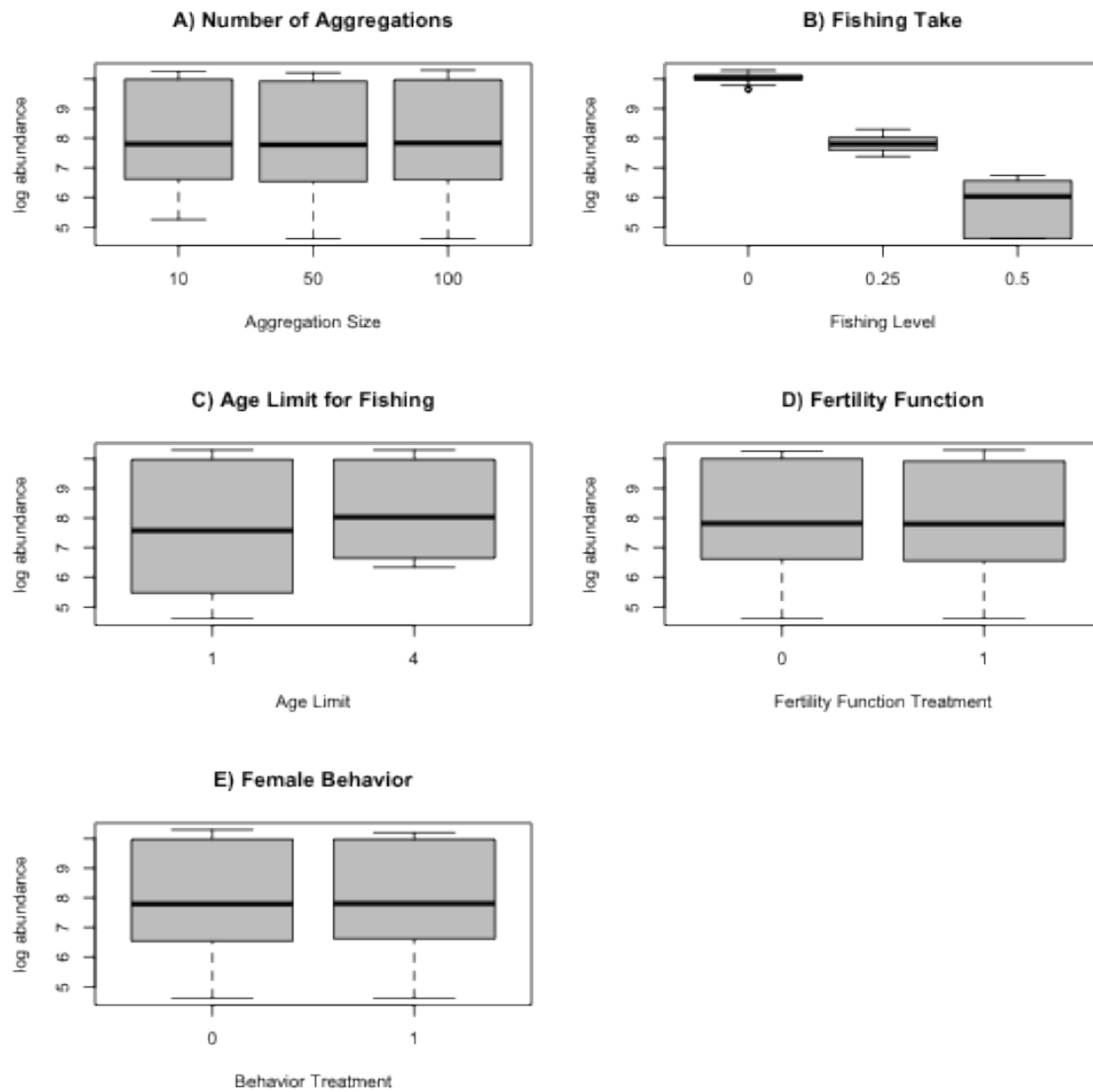


Figure 3.4 Main effects of aggregation, fishing, age limit, fertility function, and female behavior on effective population size
 *The y-axis is log abundance with 100 uniformly added to account for zeroes in the data.

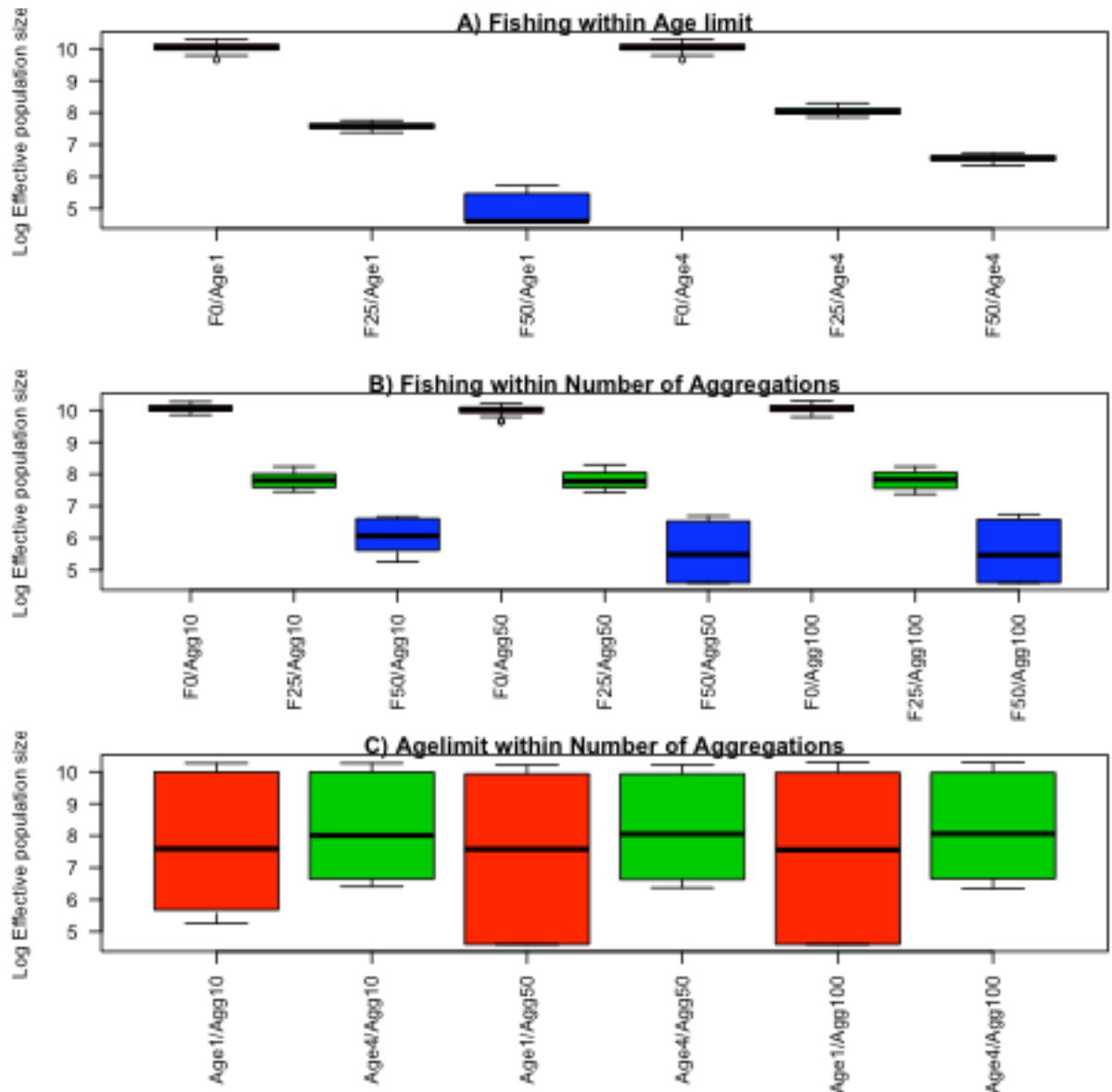


Figure 3.5 Interaction effects of aggregation, fishing, and age limit on effective population size

*The y-axis is log abundance with 100 uniformly added to account for zeroes in the data.

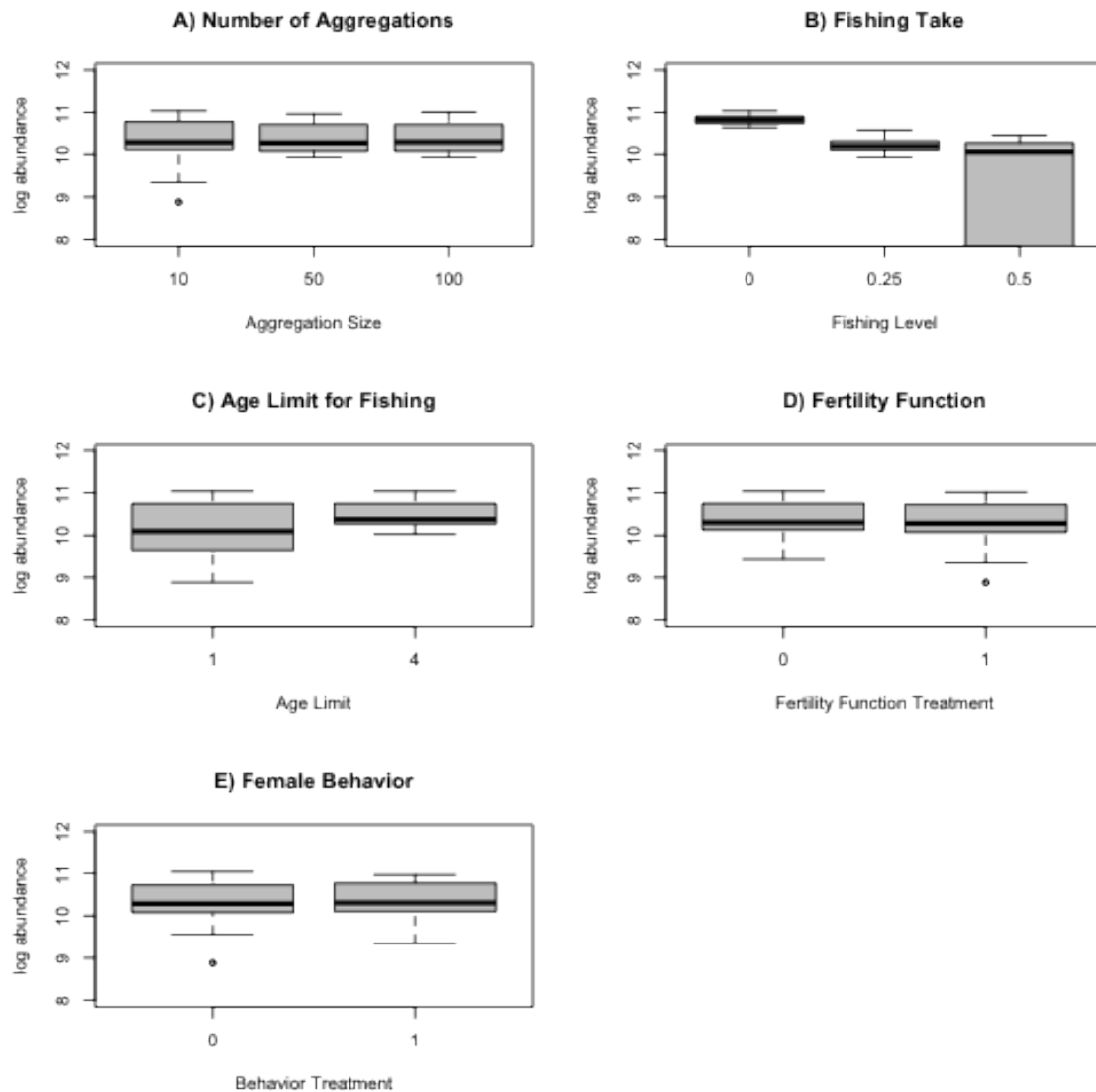


Figure 3.6 Main effects of aggregation, fishing, age limit, fertility function, and female behavior on total population size

*The y-axis is log abundance with 100 uniformly added to account for zeroes in the data. The range of the y-axis was also restricted in order to better show the effects of each treatment. It is important to note that there are some outliers that have been deleted only for ease of interpretation of these graphs, but not from the ANOVA results.

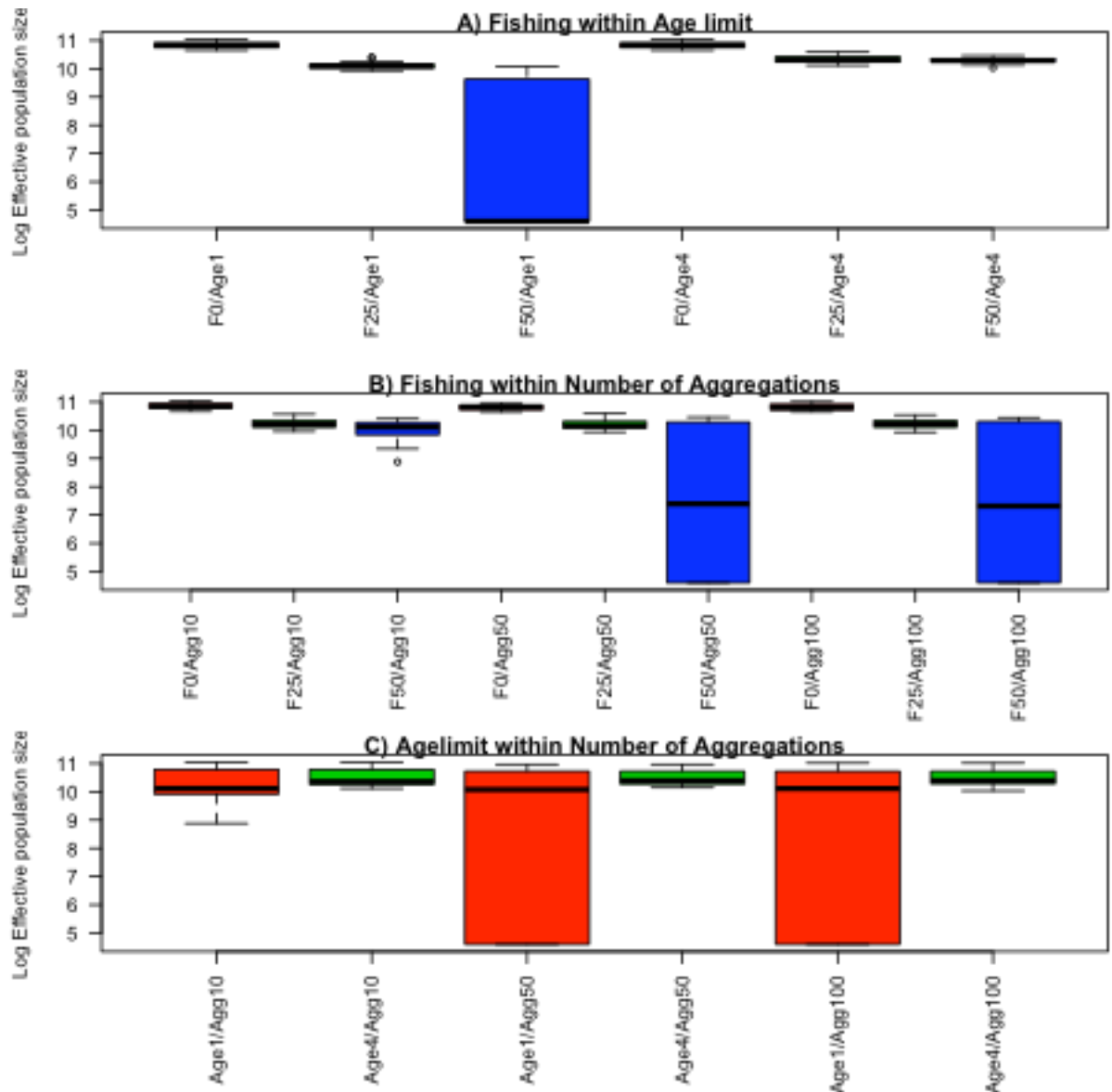


Figure 3.7 Interaction effects of aggregation, fishing, and age limit on total population size

*The y-axis is log abundance with 100 uniformly added to account for zeroes in the data. The range of the y-axis was also restricted in order to better show the effects of each treatment. It is important to note that there are some outliers that have been deleted only for ease of interpretation of these graphs, but not from the ANOVA results.

Table 3.1 Significant effects on effective population size when no reserves are present
All non-significant effects have been deleted from the ANOVA results and only significant effects are shown. All parameters in the table have one degree of freedom.

Significance legend: <0.001 '***' 0.001 '**' 0.01 '*'

<u>Effect</u>	<u>F value</u>	<u>Pr(>F)</u>
aggregation	46.99	3.20e-11 ***
fishing	32830.54	< 2.2e-16 ***
agelimit	1339.57	< 2.2e-16 ***
aggregation:fishing	61.09	6.37e-14 ***
aggregation:agelimit	47.24	2.85e-11 ***
fishing:agelimit	1205.58	< 2.2e-16 ***
aggregation:fishing:agelimit	62.69	3.19e-14 ***

Table 3.2 Significant effects on total population size when no reserves are present
All non-significant effects have been deleted from the ANOVA results and only significant effects are shown. All parameters in the table have one degree of freedom.

Significance legend: <0.001 '***' 0.001 '**' 0.01 '*'

<u>Effect</u>	<u>F value</u>	<u>Pr(>F)</u>
aggregation	58.92	1.63e-13 ***
fishing	539.18	< 2.2e-16 ***
agelimit	250.82	< 2.2e-16 ***
aggregation:fishing	83.33	< 2.2e-16 ***
aggregation:agelimit	58.37	2.07e-13 ***
fishing:agelimit	335.44	< 2.2e-16 ***
aggregation:fishing:agelimit	86.86	< 2.2e-16 ***

Population Demography

Shifts in the gag demographics can help to explain how the spatial distribution of the species affects its susceptibility to increased fishing pressure. To compare the differences in population structure that result from varying the number of aggregations, the percentages of each stage were determined at each level of fishing. The main differences can be seen when comparing each fishing level and age limit. The biggest effect of aggregation number can be seen when there are 100 aggregations and a fishing age limit of 1. With this combination, the population crashes and no data can be obtained. To simplify presentation, only the results from runs with 10 aggregations are shown below. The results at all other aggregation levels show some very similar patterns across treatments, so only a subset of the results are shown here to illustrate important conclusions. These graphs use the scenario where neither the fertility function or female behavior is implemented, as neither of these factors affect the effective or total population size. Age limit was also varied, though some scenarios would not run at certain age limits and fishing levels, which is noted where applicable.

When there is no fishing (Figure 3.8), there are only very slight differences in population demography. While the abundances of larvae, juveniles, females, and transitionals stay relatively constant, there is slightly more variability in males.

With low fishing and an age limit of 1 year (Figure 3.19), all groups stay constant for each aggregation scenario. With low fishing and an age limit of 4 years, there is slight variability in males and juveniles by only 1% (Figure 3.10). Otherwise, all other stages stay constant.

In Figure 3.11, high fishing is implemented and an age limit of 1 is enforced. This graph looks much different than others, as females, males, and transitionals close to 0% of the population, which is taken over mainly by juveniles. In this case, the run with 10 aggregations was the only run able to be completed. All other aggregation scenarios collapsed.

Figure 3.12 shows the scenario where high fishing is implemented but a higher age limit of 4 years is imposed. One difference from the other fishing levels is that transitionals show a higher percentage than males at 10 and 50 aggregations. Otherwise, the population remains relatively constant.

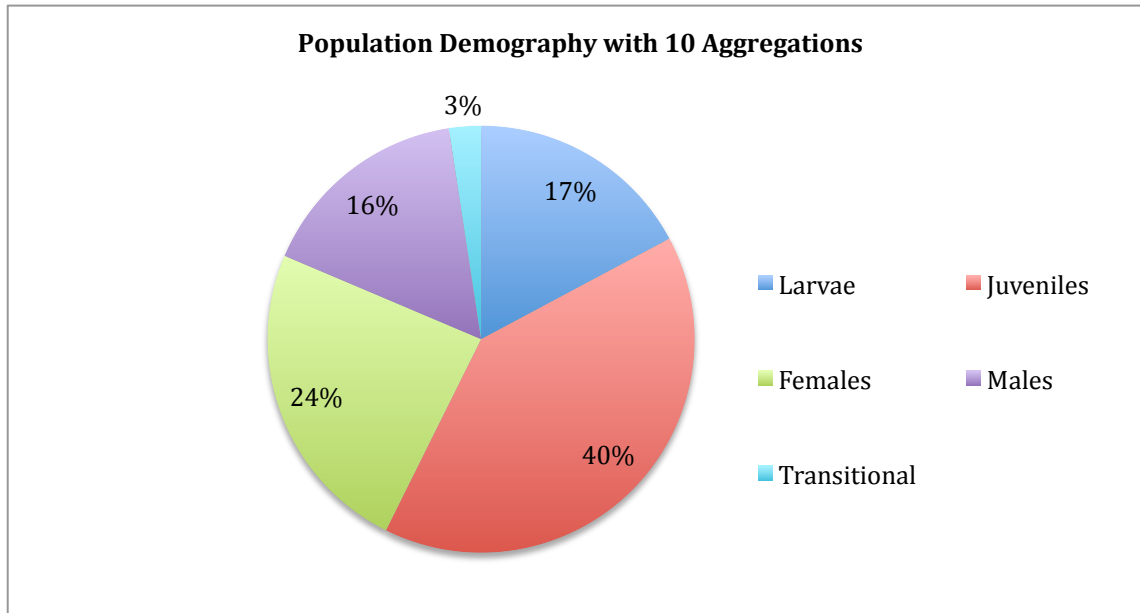


Figure 3.8 Population demography with varying aggregations and no fishing ($F=0$)

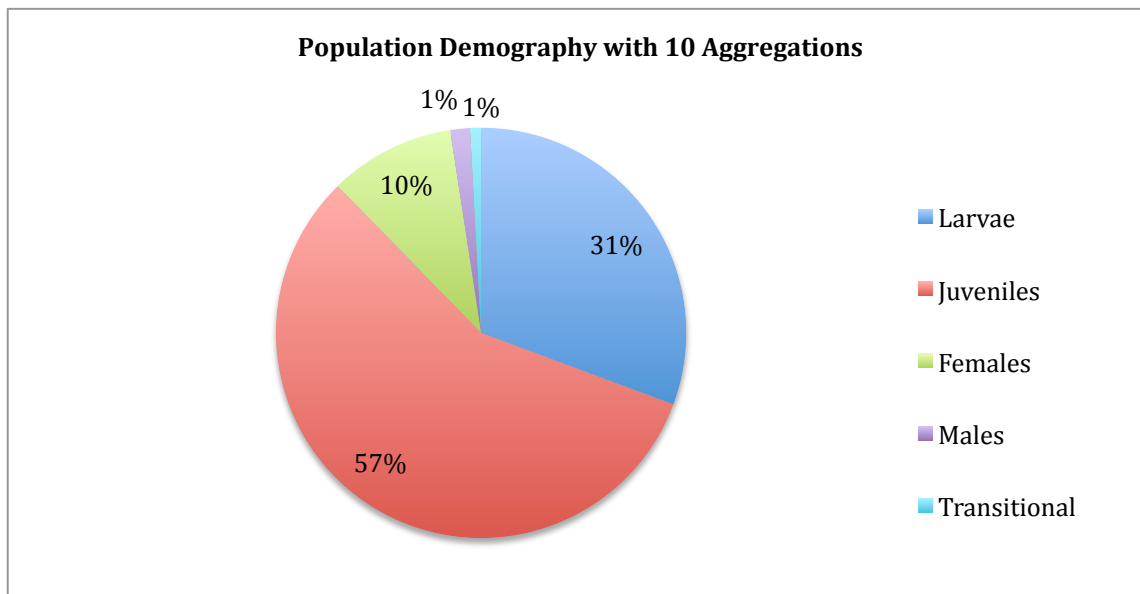


Figure 3.9 Population demography with varying aggregations and low fishing ($F=0.25$) and age limit of 1 year

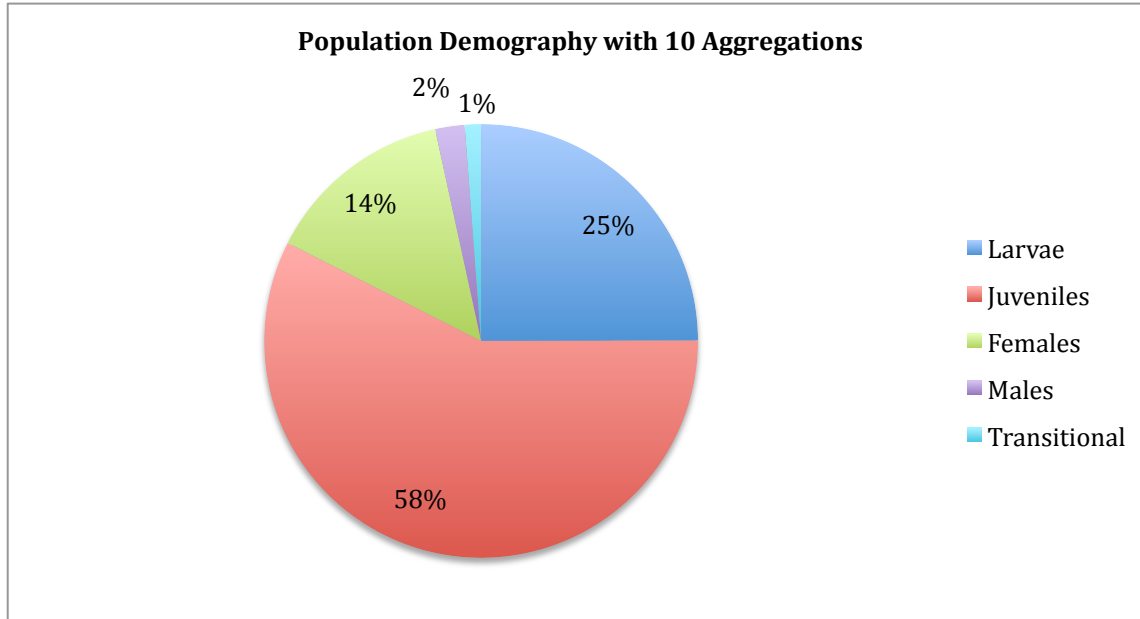


Figure 3.10 Population demography with varying aggregations and low fishing ($F=0.25$) and age limit of 4 years

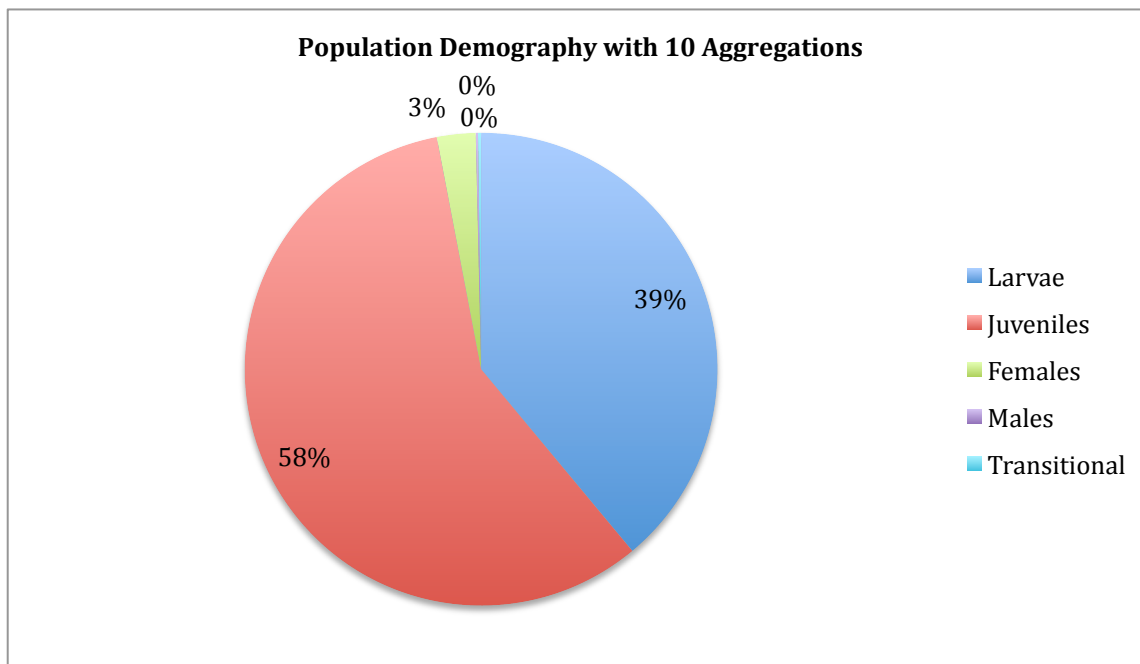


Figure 3.11 Population demography with varying aggregations and high fishing ($F=0.5$) and age limit of 1 year

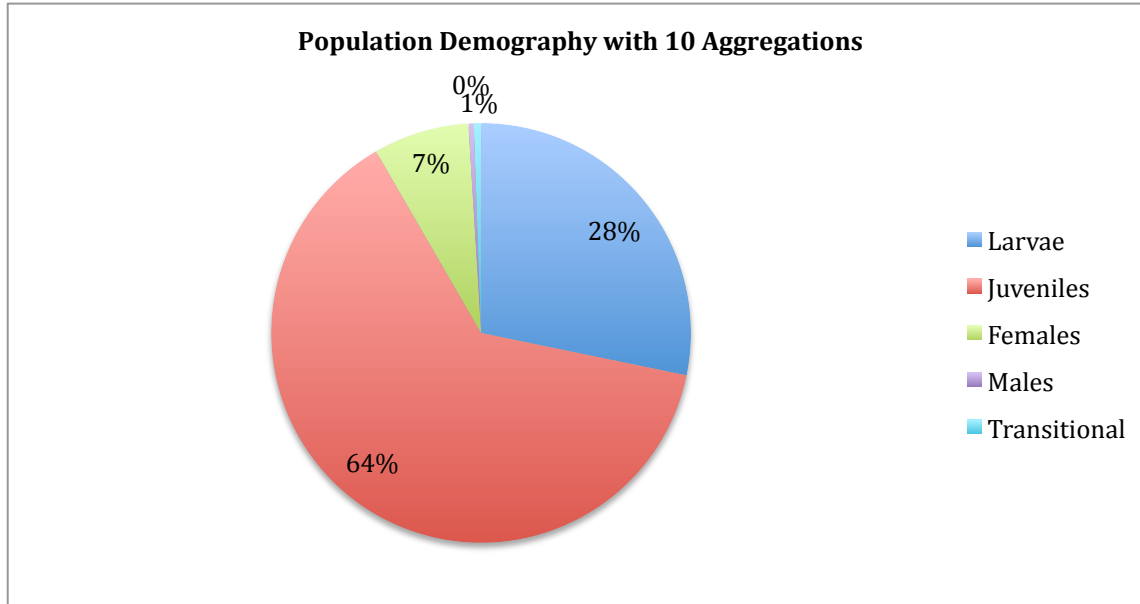


Figure 3.12 Population demography with varying aggregations and high fishing ($F=0.5$) and age limit of 4 years

3.2 Reserves

Reserves were imposed in order to answer the following question: What management strategy or suite of management strategies would be optimal for this species in terms of their effect on effective population size? Varying both the size and placement of reserves over certain habitats tested optimal reserve strategy. Reserves were run varying number of aggregations, age limit for fishing, fishing pressure, percent of reserve that is protected, and habitat protected (refuge "scenario". The number of aggregations was once again varied between 10, 50, and 100; age limit was set to either 1 or 4; fishing pressure was set at either low ($F = 0.25$) or high ($F = 0.5$) levels; percent protected was varied in increments of 10% between 10%-90%; and the habitat protected is varied from reserve scenario 0-4 (where each scenario is described in Chapter 2). These parameters were analyzed with an ANOVA to determine their effect on effective population size, using percent protected as a covariate. Once again, there were runs that produced a zero value for effective population size, which violates the assumption of heterogeneity for ANOVA analyses. However, I believe the results from the analysis are still informative although they should be interpreted cautiously.

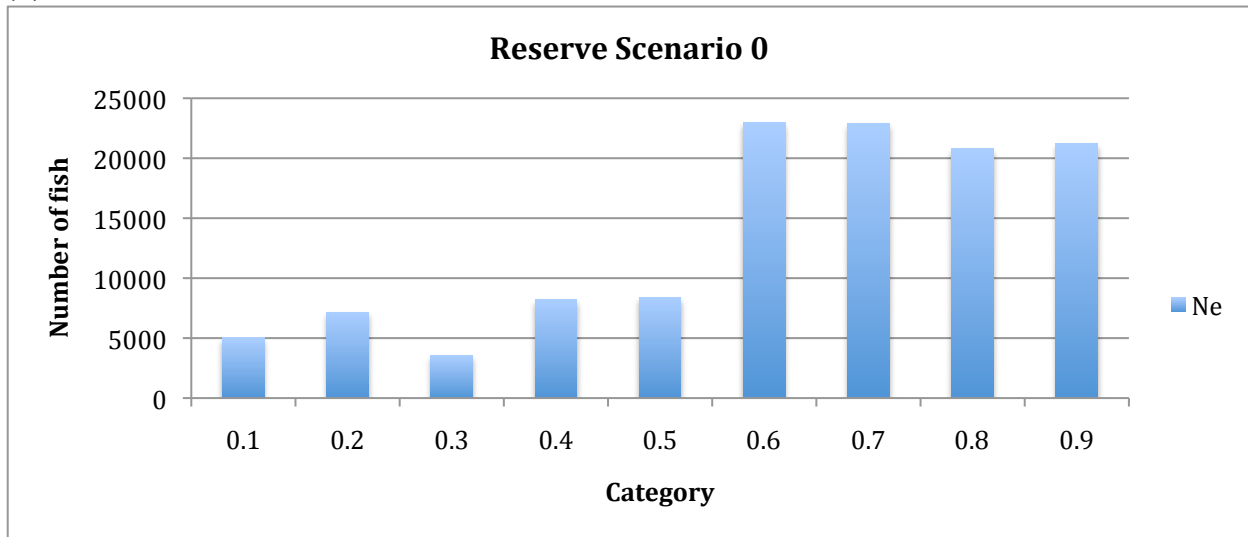
Many parameters were shown to have a significant effect on the effective population size in the reserve scenarios, with the largest effects due to fishing and the reserve scenario (Table 3.3). Increased fishing from 0.25 to 0.5 decreases average effective size by more than an order of magnitude (Fig. 3.2b), as was also seen in No Reserves results, above.

In general, the most distinctive result occurs using Scenario 0, which varies the percent protected over the entire model space, or “Gulf of Mexico” (Figure 3.13, Graph A). A very noticeable threshold for protection appears at approximately 60% of the model space protected, so that increasing the percent protected over 60% dramatically increases the log of the effective size of the population. Other scenarios (such as Scenario 1 shown in Figure 2.19b which varies the percent protected over the aggregation habitat), do not show clear trends as the percent protected is varied. However, both Scenario 1 and especially Scenario 0 do have increased the population numbers compared to Scenarios 2, 3, and 4, which protect offshore reefs, nearshore reefs, and seagrass beds, respectively.

Aggregation was shown to have an effect because of its interaction with fishing and age limit, which caused the population to crash under certain conditions (Figure 3.14). These conditions were usually at high fishing levels and low age for the fishing limit, as was as low percent protection with Reserve Scenarios 2, 3, and 4. This explains the higher order terms that were found to be significant (Table 3.3, Figure 3.15). Table 3.3 shows all significant main effects and interactions with confidence levels greater than 5%; due to the many parameters and interactions, the rest were deleted from the table.

In summary, Reserve Scenarios 0 and 1 were shown to have the greatest effect on effective population size. A threshold of 60% of habitat protection was also observed to increase the effective size when it was reached. The suite of management strategies here included the establishment of reserves, age limit, and fishing level. All three of these main effects were significant as were their interactions. A high age limit combined with low fishing ($F=0.25$) and reserves had a significant positive effect on effective population size. There were not any treatments that did not have a significant effect, suggesting that all management strategies tested do in fact affect the effective size of the population though there are certain combinations of strategies that may be more beneficial for this species that will be discussed in the next chapter.

(a)



(b)

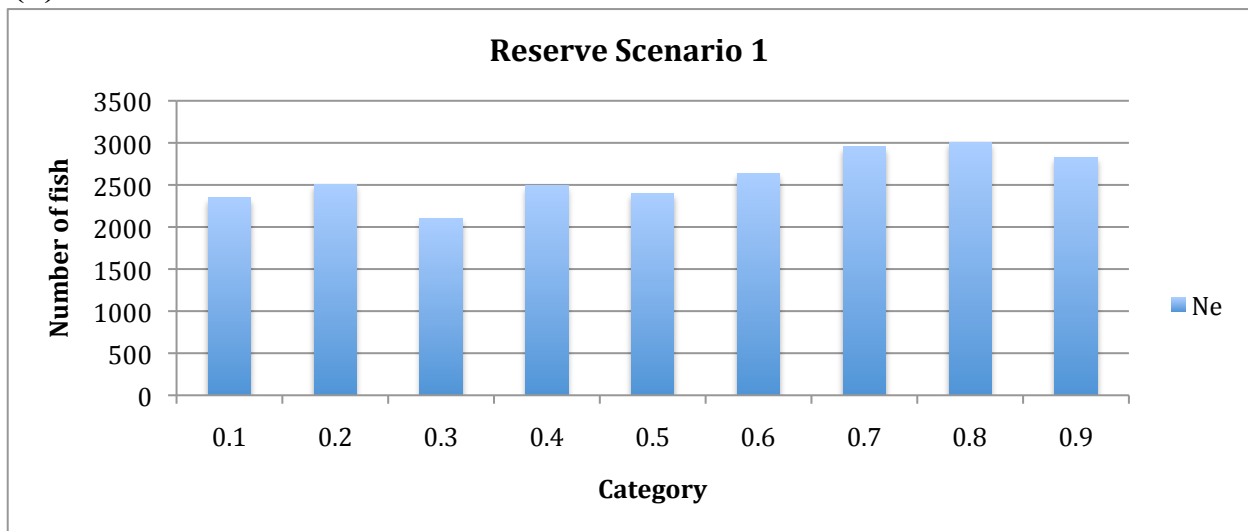


Figure 3.13 Population size with reserves and low fishing ($F=0.25$), and age limit of 1 year at 10 aggregations

Only two scenarios are shown here: (a) Reserve Scenario 0, or protection of the entire model space, and (b) Reserve scenario 1 where only the aggregation habitat was protected.

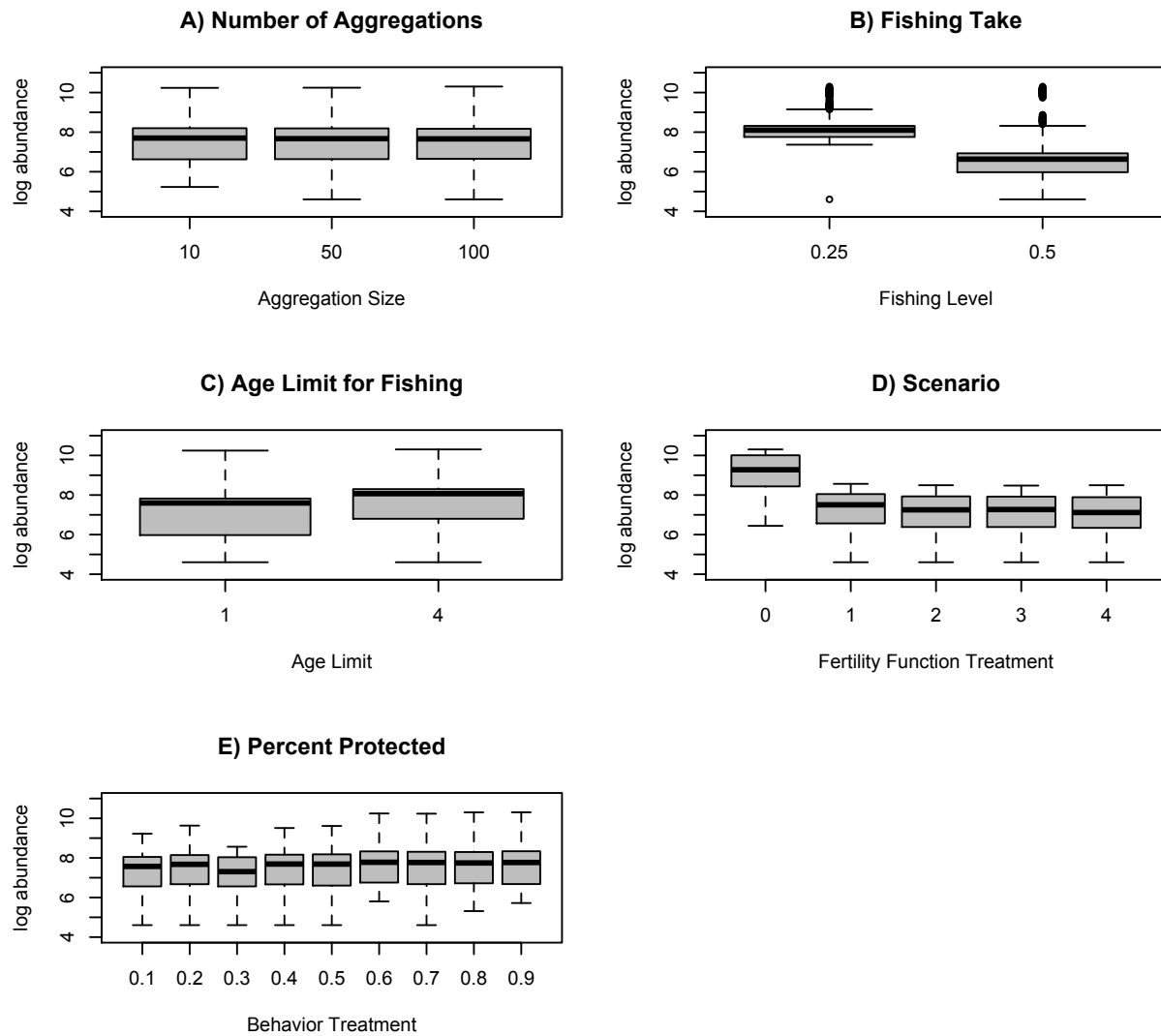
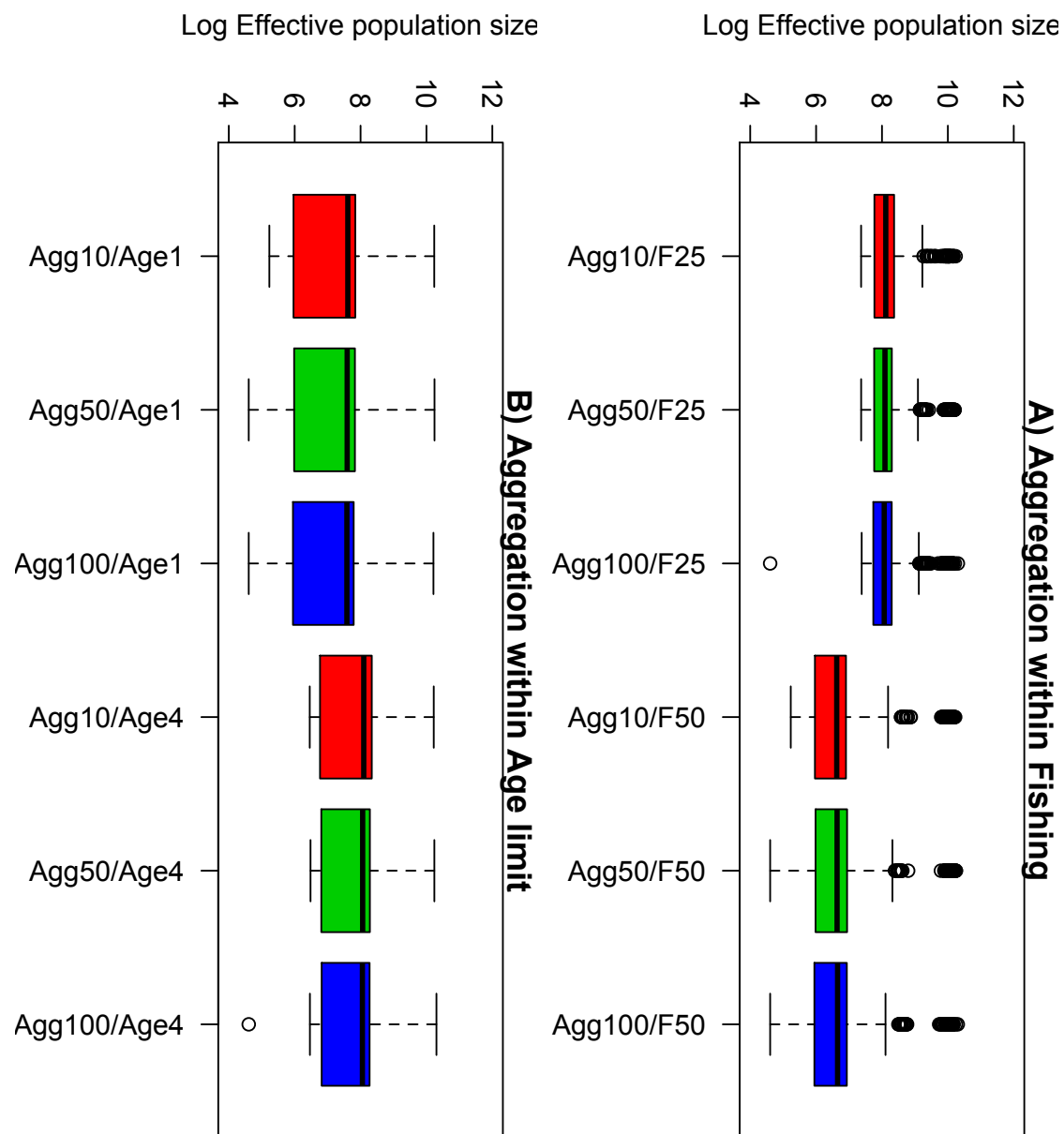
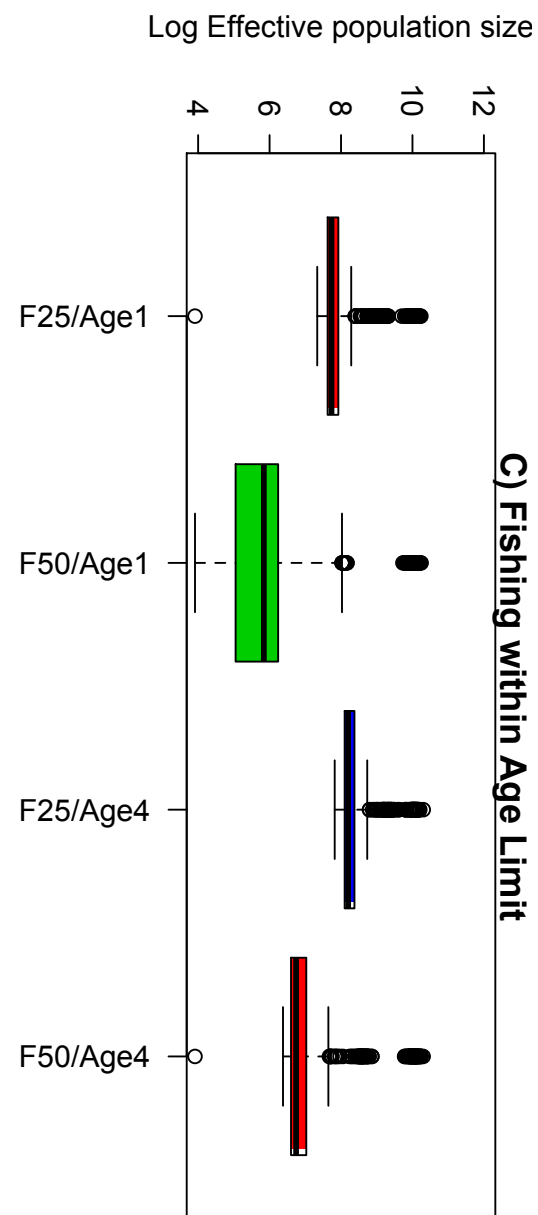
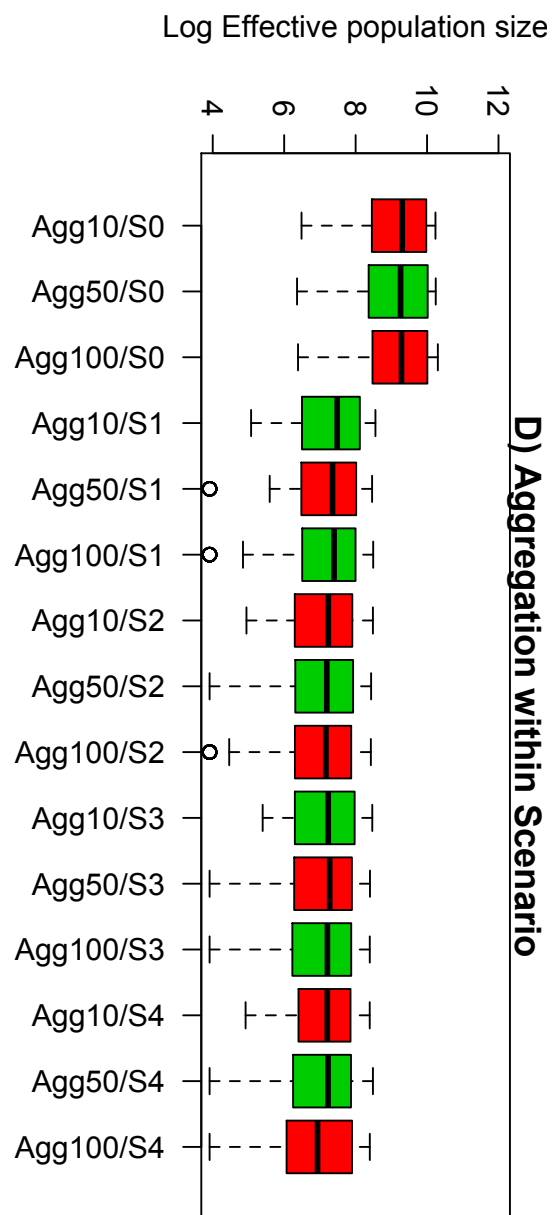
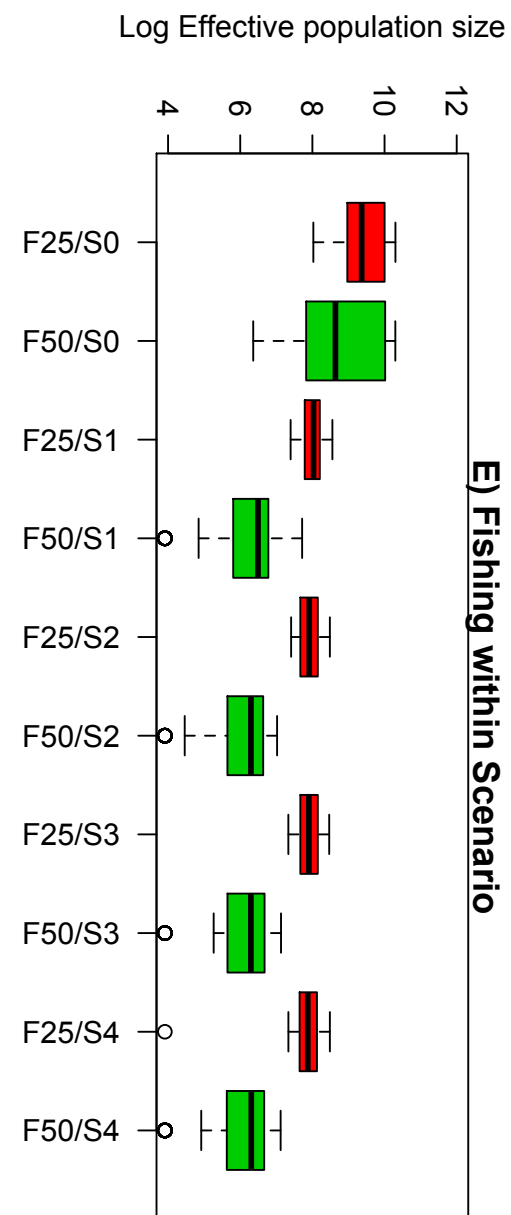
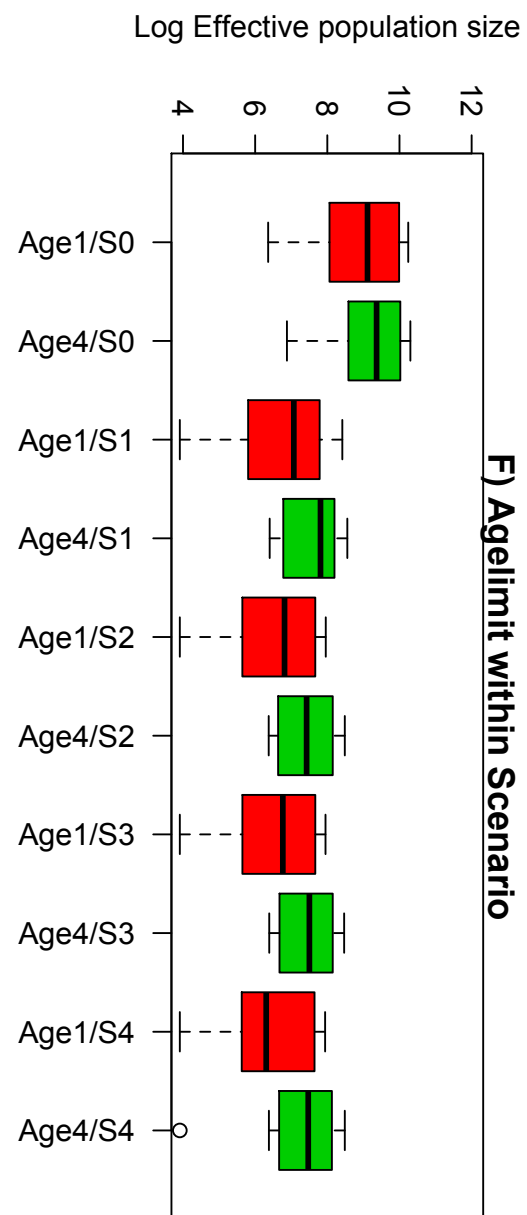


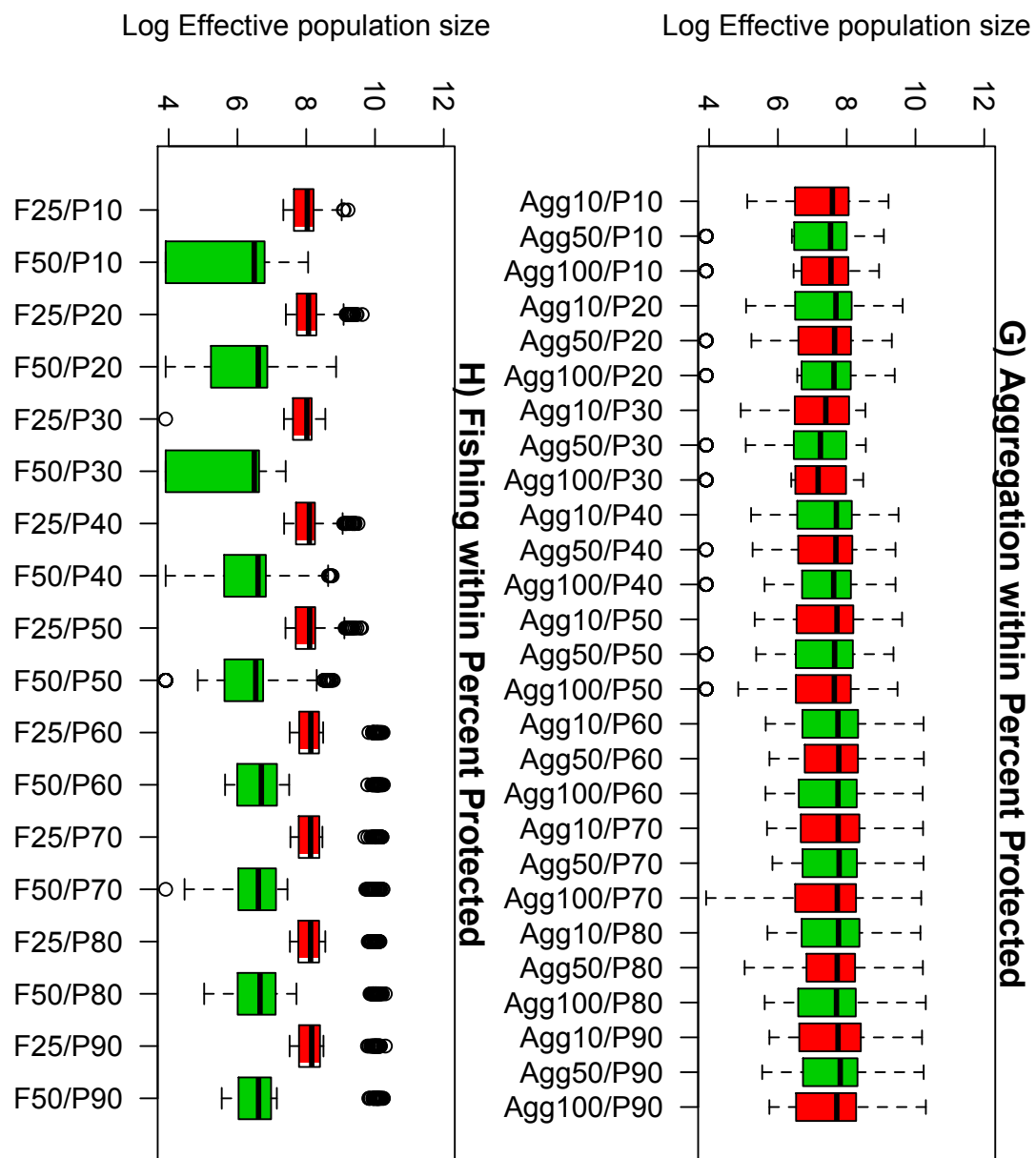
Figure 3.14 Main effects of aggregation, fishing, age limit, scenario, and percent protected on effective population size

*The y-axis is log abundance with 50 uniformly added to account for zeroes in the data. The range of the y-axis was also restricted in order to better show the effects of each treatment. It is important to note that there are some outliers that have been deleted only for ease of interpretation of these graphs, but not from the ANOVA results.









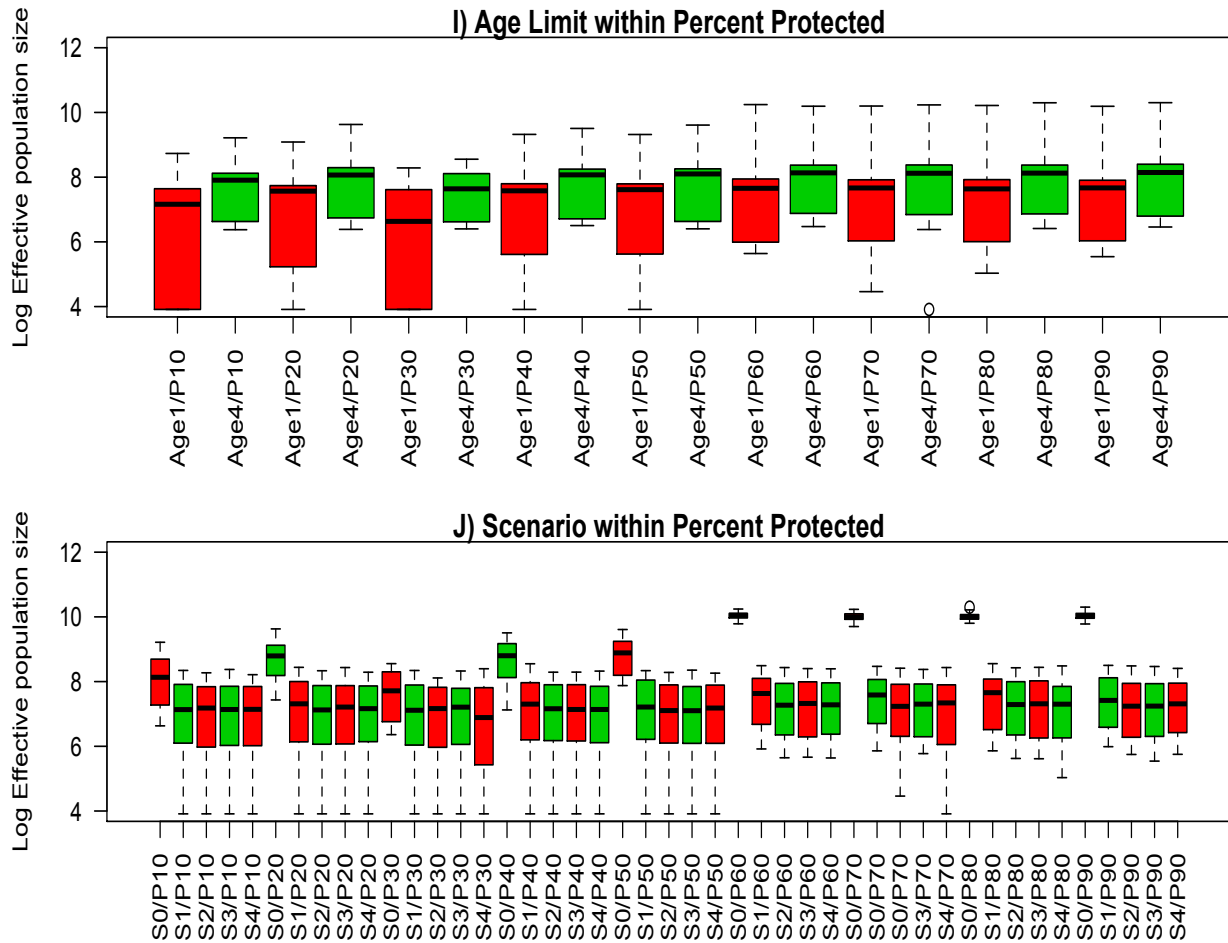


Figure 3.15 Interaction effects of aggregation, fishing, age limit, scenario, and percent protected on effective population size

*The y-axis is log abundance with 50 uniformly added to account for zeroes in the data. The range of the y-axis was also restricted in order to better show the effects of each treatment. It is important to note that there are some outliers that have been deleted only for ease of interpretation of these graphs, but not from the ANOVA results.

Table 3.3 Significant effects on effective population size when reserves are present
All non-significant effects have been deleted from the ANOVA results and only significant effects are shown. All parameters in the table have one degree of freedom.
Significance legend: <0.001 ‘***’ 0.001 ‘**’ 0.01 ‘*’

<u>Effect</u>	<u>F value</u>	<u>Pr(>F)</u>
aggregation	34.65	4.43e-09 ***
fishing	3497.45	< 2.2e-16 ***
agelimit	859.23	< 2.2e-16 ***
scenario	1992.43	< 2.2e-16 ***
percent	494.67	< 2.2e-16 ***
aggregation:fishing	15.23	9.74e-05 *
aggregation:agelimit	21.87	3.04e-06 ***
fishing:agelimit	199.02	< 2.2e-16 ***
aggregation:scenario	5.52	0.01 *
fishing:scenario	195.54	< 2.2e-16 ***
agelimit:scenario	63.73	2.09e-15 ***
aggregation:percent	10.75	0.001 **
fishing:percent	143.74	< 2.2e-16 ***
agelimit:percent	96.58	<2.2e-16 ***
scenario:percent	158.82	< 2.2e-16 ***
aggregation:fishing:agelimit	28.43	1.05e-07 ***
fishing:agelimit:scenario	13.89	0.0001 *
aggregation:fishing:percent	7.90	0.004 **
aggregation:agelimit:percent	12.23	< 2.2e-16 ***
fishing:agelimit:percent	72.73	3.576e-11 ***
fishing:scenario:percent	10.34	0.001 ***
aggregation:fishing:agelimit:percent	20.63	5.80e-06 ***
aggregation:agelimit:scenario:percent	5.78	0.01 *

3.3 Spatial Variation in Fishing Pressure

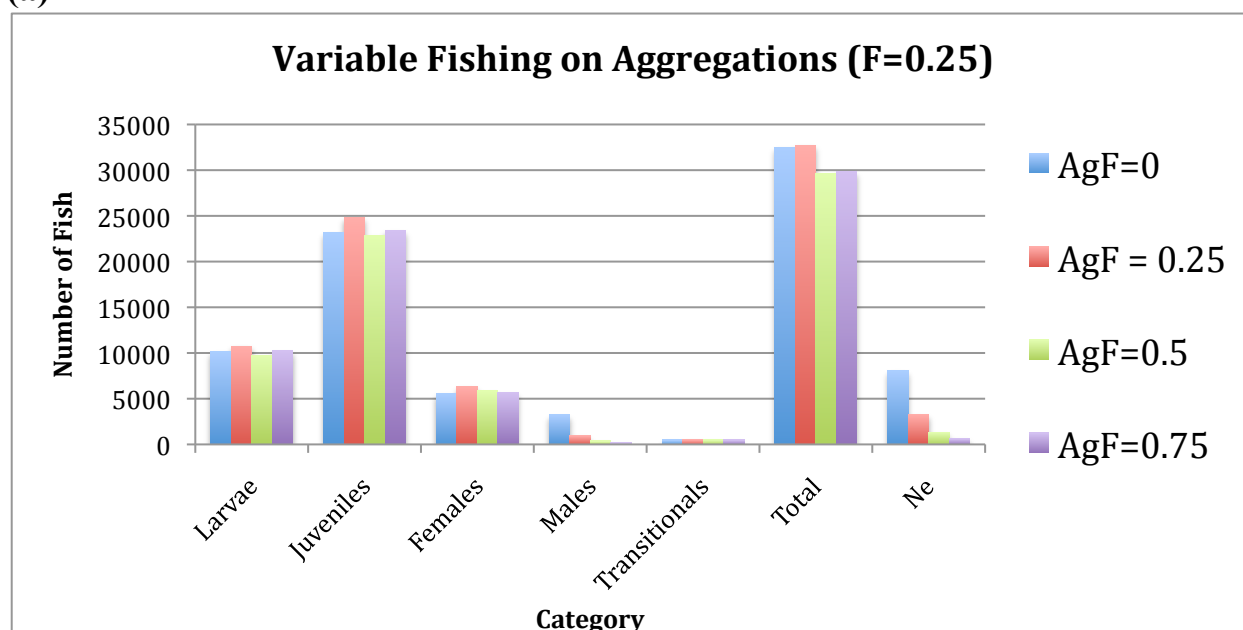
Variable fishing was imposed to answer the following questions: (1) Does the spatial distribution of the species affect its susceptibility to increased fishing pressure? and (2) What management strategy or suite of management strategies would be optimal for this species in terms of their effect on effective population size? For these scenarios, fishing is set for either low ($F=0.25$) or high ($F=0.5$) levels that are applied to the entire model space except for the spawning aggregations. The spawning aggregations are subject to an independent level of fishing pressure of 0, 0.25, 0.50, and 0.75. This allows fishing in aggregations to be set to be high or lower than surrounding areas, creating variation in pressure. Age limit was held constant at 4 years old (similar to current management levels) and neither female behavior nor the fertility function were manipulated. Since neither female behavior nor the fertility function were found to have significant effects, fertility function was not included and female behavior was set to the basic scenario where females are distributed to the closest aggregation. The number of mating aggregations was also varied, but had no significant effect; to simplify the presentation, only the results taken from runs with 50 aggregations are shown below.

Fishing pressure on these aggregations was set to be higher or lower than their surroundings. The surrounding fishing pressure was either low (Figure 3.16, Graph A) or high (Figure 3.16, Graph B). When fishing is low already ($F=0.25$), as shown in Graph A), the reducing fishing on aggregations treatment results in no fishing at all at these sites. This does not raise the total population size significantly; however, it does significantly increase the effective population size by approximately 30%, as compared to the aggregations that experience fishing at $F=0.75$, by protecting the males in the aggregations (Table 3.4). When fishing is high ($F=0.5$, Graph B), reducing fishing on aggregations results in aggregations that experience both low fishing ($F=0.25$) and no fishing ($F=0$). This scenario again allows more males to survive and results in an increase in effective population sizes. Fishing on aggregations was also increased to observe possible effects of fishermen targeting aggregations. While the total population sizes are not significantly different when this occurs (Table 3.5), the effective population sizes decline. Both the base fishing pressure and the aggregation fishing pressure are significant as main effects. The interaction between these variables also caused significant effects on the effective

population size (Figure 3.18), but not on the total population size. This trend holds true for all aggregations: as fishing levels in aggregations increase, the effective population size decreases.

Spatial distribution was therefore shown to have a significant effect on effective population size as a result of variation of fishing pressure spatially. Total population size, however, was not significantly affected by varying fishing pressure on aggregations, so no results are shown for total size. As a management technique, variable fishing was shown to significantly affect the effective population size when lower fishing pressure is applied to aggregations relative to their surroundings. The implications and feasibility of this technique will be discussed in the following chapter.

(a)



(b)

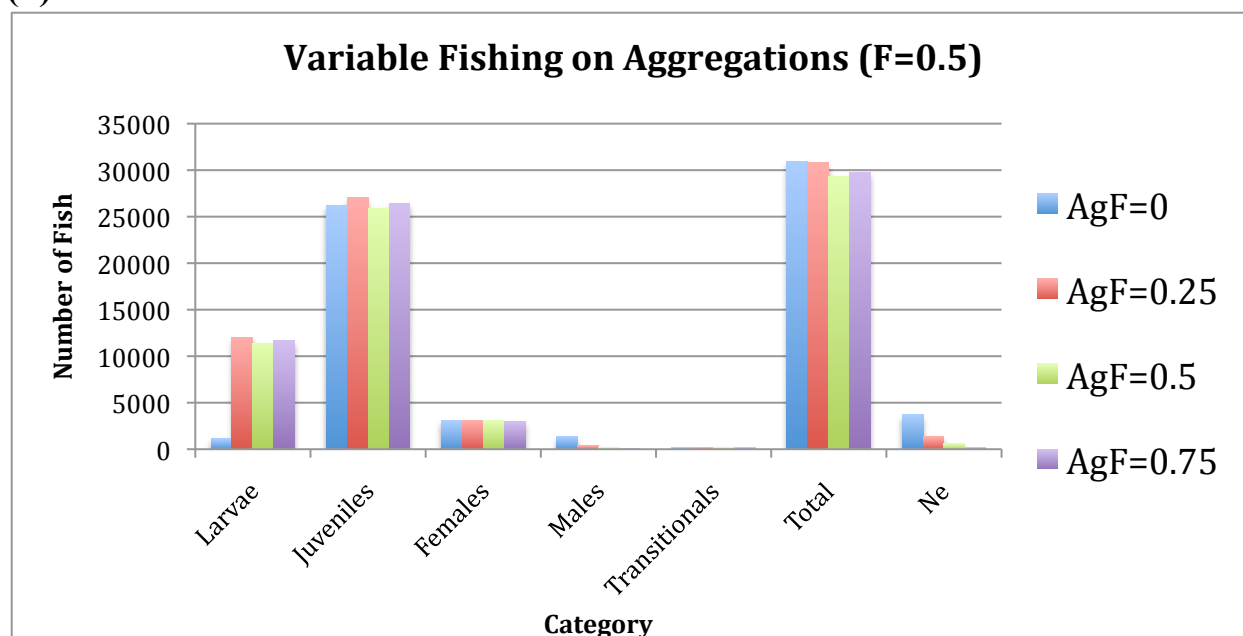


Figure 3.16 Population size with variable fishing on 50 aggregations with age limit of 4 years

Population size by stage, including total population size and effective population size, for varying levels of fishing pressures on aggregations, where (a) implements fishing pressures on aggregations both higher and lower than the low fishing ($F=0.25$) applied to the rest of the model space, and (b) implements fishing pressures on aggregations both higher and lower than the high fishing ($F=0.5$) applied to the rest of the model space.

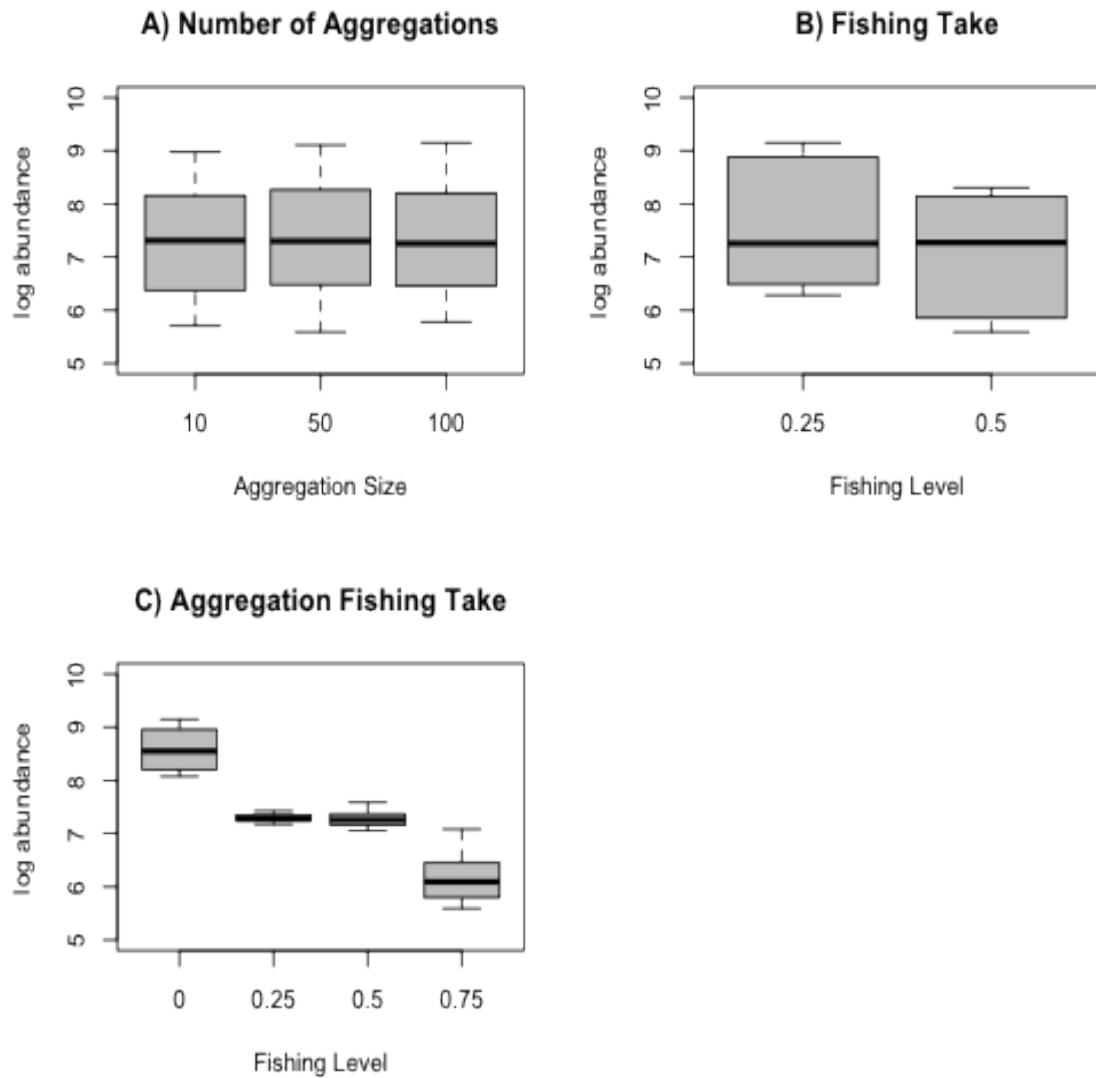


Figure 3.17 Main effects of aggregations, fishing, and aggregation fishing on effective population size for spatially variable fishing
 *The y-axis is log abundance with 100 uniformly added to account for zeroes in the data. The range of the y-axis was also restricted in order to better show the effects of each treatment. It is important to note that there are some outliers that have been deleted only for ease of interpretation of these graphs, but not from the ANOVA results.

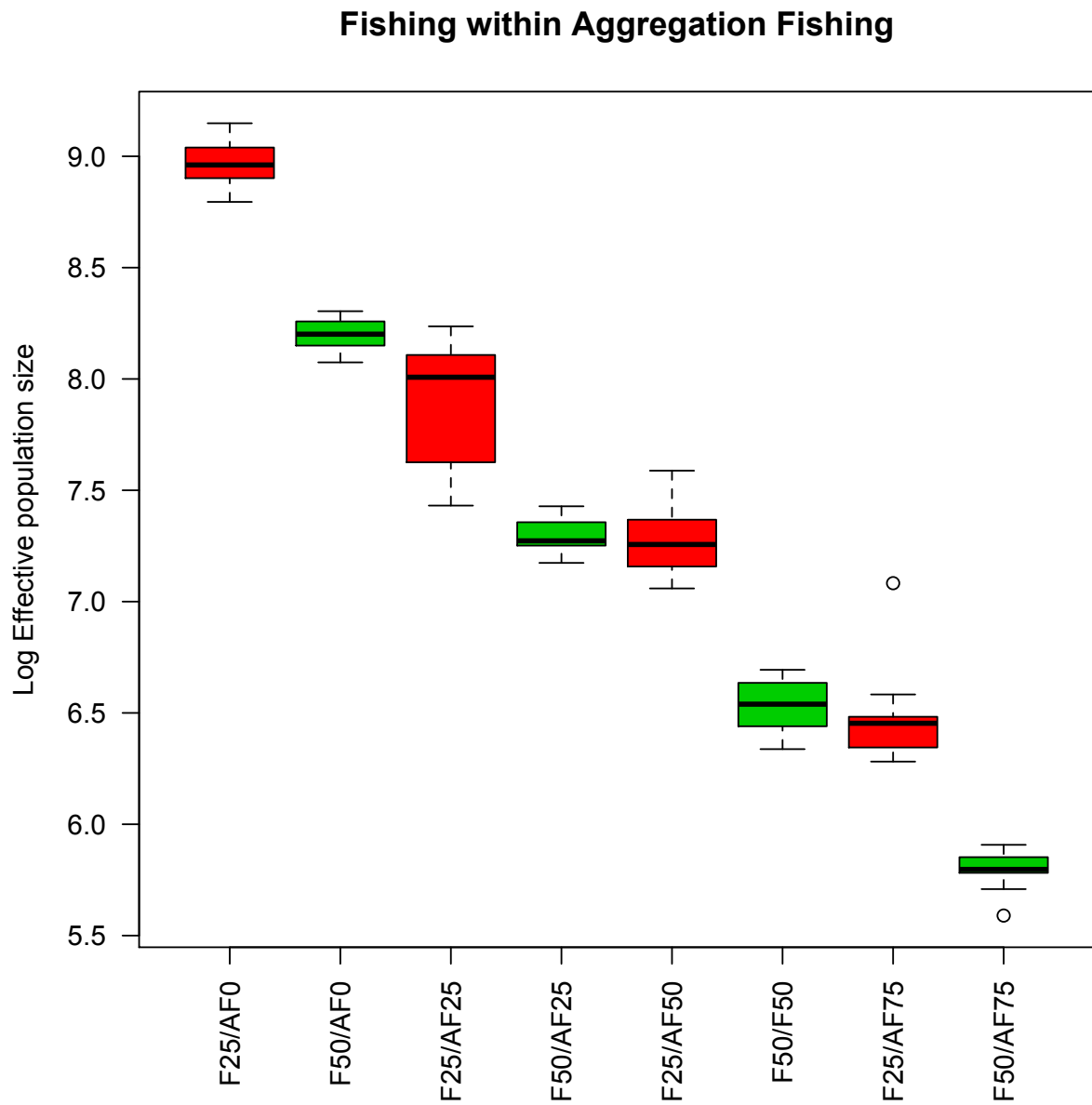


Figure 3.18 Interaction effects of fishing and aggregation fishing for spatially variable fishing

*The y-axis is log abundance with 100 uniformly added to account for zeroes in the data. All red boxes indicate low fishing ($F=0.25$) while green boxes indicate high fishing ($F=0.5$).

Table 3.4 Significant effects on effective population size with spatial variation of fishing
All non-significant effects have been deleted from the ANOVA results and only significant effects are shown. All parameters in the table have one degree of freedom.

Significance legend: < 0.001 ‘***’ 0.001 ‘**’ 0.01 ‘*’

<u>Effect</u>	<u>F value</u>	<u>Pr(>F)</u>
fishing	561.54	< 2e-16 ***
aggregation fishing	3762.38.16	< 2e-16 ***
fishing:aggregation fishing	4.60	0.03 *

Table 3.5 Effect on total population size with spatial variation of fishing

No significant main effects or interactions. All parameters in the table have one degree of freedom.

<u>Effect</u>	<u>F value</u>	<u>Pr(>F)</u>
aggregation	0.45	0.50
fishing	0.12	0.72
aggregation fishing	0.68	0.41
aggregation:fishing	0.63	0.42
aggregation:aggregation fishing	0.25	0.61
fishing:aggregation fishing	0.46	0.49
aggregation:fishing:aggregation fishing	0.26	0.61

3.4 Sensitivity Analysis

A sensitivity analysis was run using a Latin hypervolume approach (McKay et al. 2000, Megrey and Hinckley, 2001) to answer the following questions: (1) which model parameters have the most significant effect on the output variables of the model? and (2) Which output variables are most sensitive to changes in model parameters?

Sensitivity in three output variables was explored: effective population size (N_e), total population size, and sex ratio (SR). How each of the 17 model parameters affects these three output variables can be seen in Figures 3.25 to 3.27. Because the distributions were not easily transformed, Spearman rho rank correlations are shown in Table 3.5, along with estimated p values. Statistically significant values ($p < 0.05$) are highlighted in yellow; these values should be

interpreted cautiously since no corrections have been made for multiple comparisons. The equations pertaining to each parameter, as well as the range of values used in the sensitivity test and descriptions of each individual parameter, can be found in Table 2.1 and 2.2.

The effective population size, N_e , was significantly sensitive to five different parameters: fecundity (parameters 2 and 3), slope of the probability of sex change, natural mortality (parameter 2), and age limit. The second parameter of fecundity determines the rate at which fecundity increases with age and had the highest correlation with effective population size. Though the relationship is negative, the correlation between absolute fecundity at age (the third parameter of fecundity) and effective population size nearly matched the correlation with the second parameter. The probability of sex change was negatively correlated with the effective population size. The parameter controlling age specific mortality rates (natural mortality parameter 2) and age limit had the least significant effects on the effective size. The effective population size was most sensitive to change as it was affected most by the variation in parameters. All parameter correlations with effective population size can be seen in Figure 3.19.

The total population size showed significant correlations with three parameters: recruitment (parameter 2), fecundity (parameter 3), and natural mortality (parameter 2). The second parameter of recruitment represents stochasticity of yearly recruitment and had the greatest effect on total population size, exhibiting the most significance and the largest correlation coefficient. The third parameter of fecundity determines the absolute fecundity at age and was negatively correlated with total population size. The second parameter of natural mortality, which determines the steepness of the function, had the least significant effect on total population size. Total population size was not as sensitive to changes in model parameters in terms of number of significantly correlated parameters, but its correlation with recruitment is the strongest of all other parameters and any other output variable. All parameter correlations with total population size are shown in Figure 3.20.

Sex ratio was sensitive to three parameters: age limit, slope of the probability of sex change, and natural mortality (parameter 2). Sex ratio and effective population size are related, and as such are similarly affected by variations in parameters. Sex ratio, however, is not significantly affected by fecundity though all other correlated parameters are shared. Age limit, however, shows the second strongest correlation between all other parameters and output variables. Whereas effective population size was most highly correlated with fecundity

parameters, sex ratio is most highly correlated with the age limit at which fish can be removed from the population. The slope of the probability of sex change is again negatively correlated with the sex ratio, and the natural mortality parameter that determines age specific mortality shows the least significant correlation with sex ratio. Sex ratio was not as sensitive to changes in model parameters in terms of number of significantly correlated parameters. All parameter correlations with sex ratio are visualized in Figure 3.21.

Sensitivity of Effective Population Size to Model Parameters

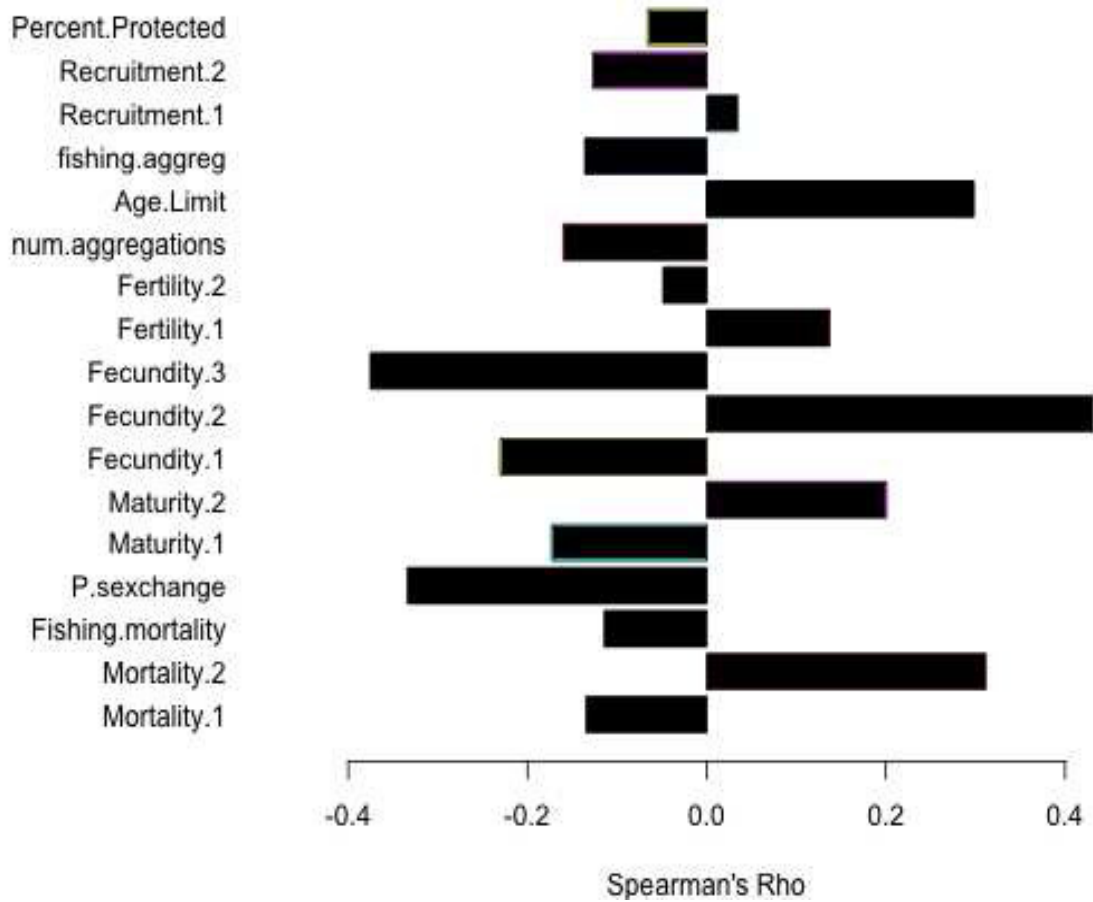


Figure 3.19 Sensitivity of effective population size to each model parameter
Magnitude and direction of coefficients of correlation between parameters and output variables as determined by Latin Hypercube Sampling

Sensitivity of Total Population Size to Model Parameters

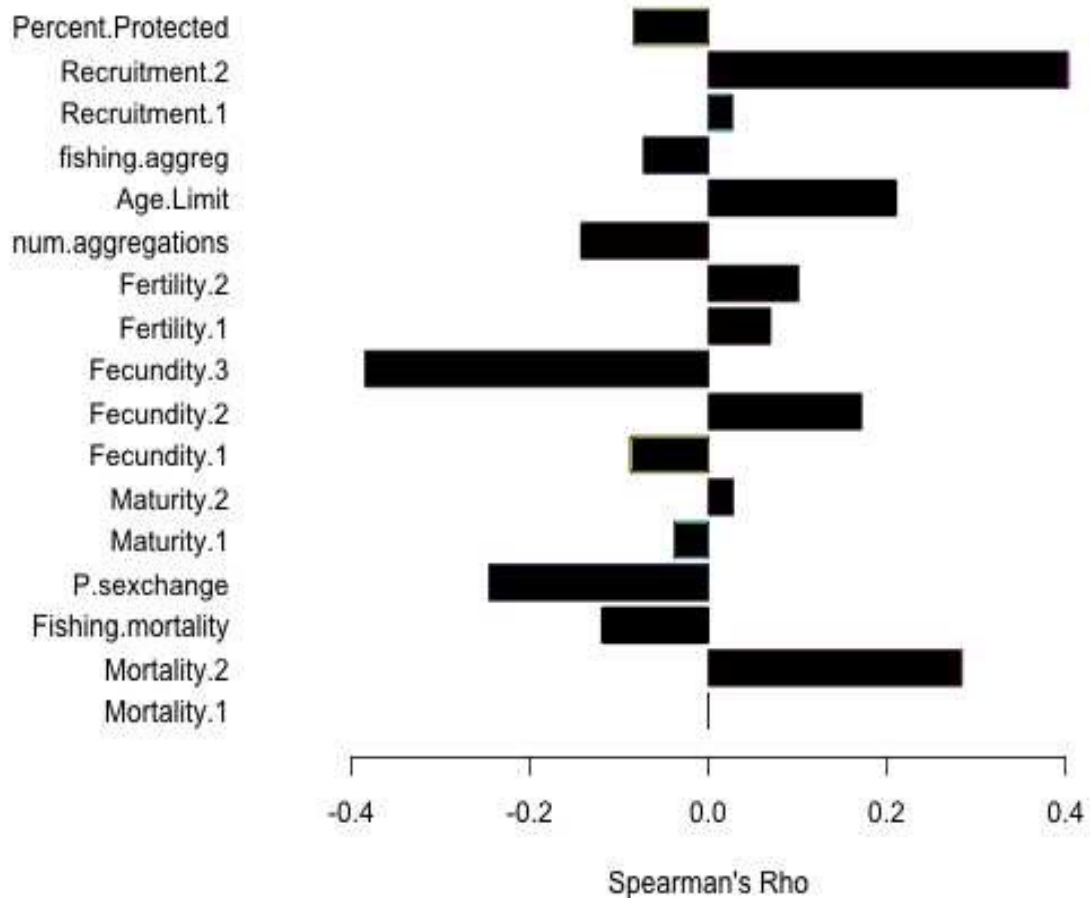


Figure 3.20 Sensitivity of total population size to each model parameter
Magnitude and direction of coefficients of correlation between parameters and output variables as determined by Latin Hypercube Sampling

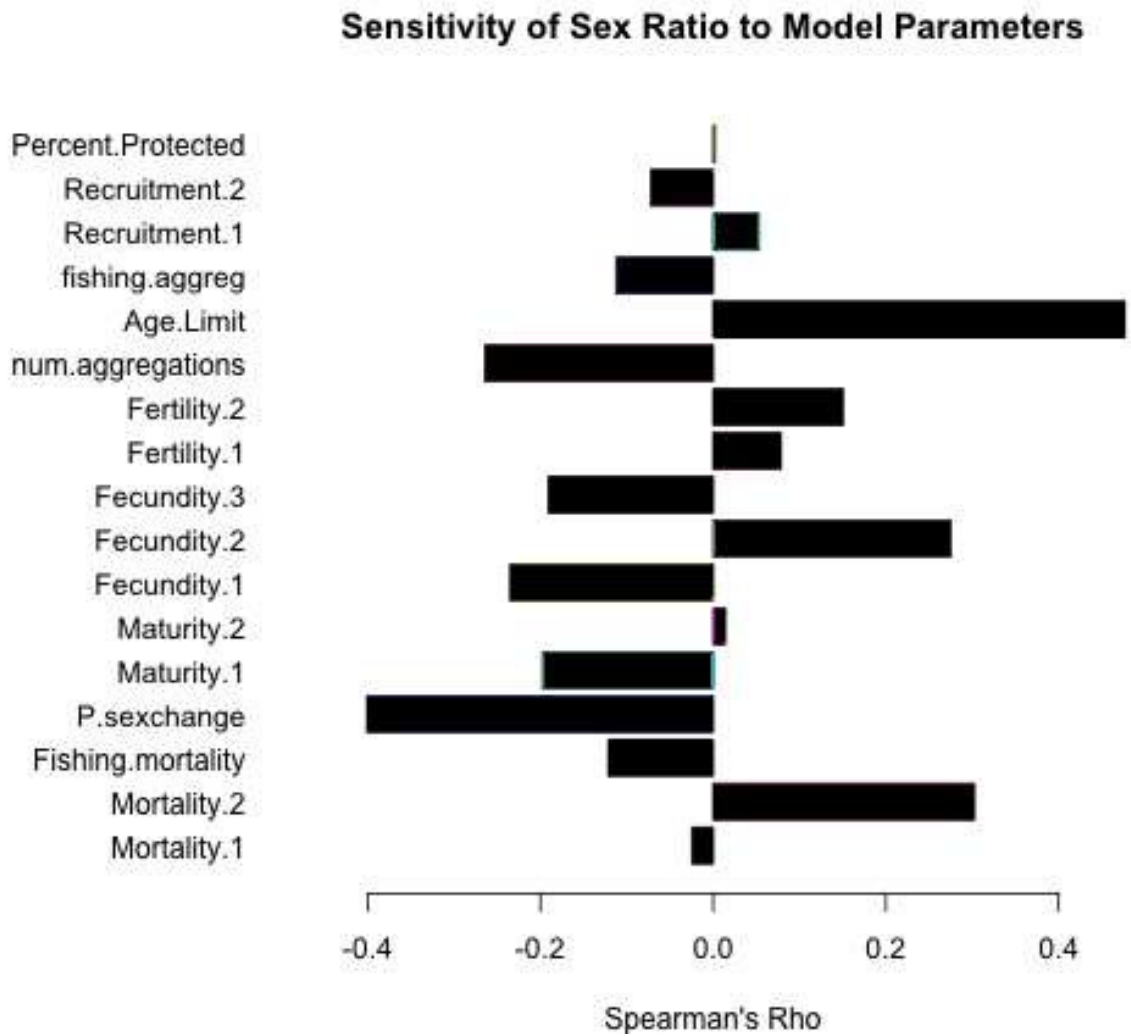


Figure 3.21 Sensitivity of sex ratio to each model parameter
 Magnitude and direction of coefficients of correlation between parameters and output variables as determined by Latin Hypercube Sampling

Table 3.6 Sensitivity of Effective Population Size, Total Population Size, and Sex Ratio to Model Parameters

*Highlighted cells represent significant correlation coefficients

	Ne		Tpop		SR	
	<u>P</u>	<u>Rho</u>	<u>P</u>	<u>Rho</u>	<u>P</u>	<u>rho</u>
Natural Mortality 1	-0.352	-0.134	1	0	0.866	-0.025
Natural Mortality 2	0.028	0.311	0.046	0.284	0.033	0.302
Fishing Mortality	0.429	-0.114	0.408	-0.120	0.401	-0.121
Sex change prob.	0.018	-0.334	0.08511	-0.246	0.004	-0.401
Maturity 1	0.230	-0.173	0.791	-0.039	0.169	-0.197
Maturity 2	0.163	0.2	0.849	0.028	0.923	0.014
Fecundity 1	0.107	-0.230	0.545	-0.088	0.1	-0.235
Fecundity 2	0.002	0.432	0.234	0.171	0.053	0.275
Fecundity 3	0.007	-0.375	0.006	-0.385	0.185	-0.191
Fertility Rate 1	0.341	0.137	0.633	0.069	0.589	0.078
Fertility Rate 2	0.737	-0.049	0.487	0.101	0.298	0.150
Number of Aggregations	0.267	-0.160	0.323	-0.143	0.063	-0.264
Age Limit	0.035	0.298	0.143	0.210	0.0005	0.476
Aggregation Fishing	0.347	-0.136	0.616	-0.073	0.438	-0.112
Recruitment 1	0.812	0.034	0.854	0.027	0.716	0.053
Recruitment 2	0.381	-0.127	0.004	0.618	0.403	-0.072

CHAPTER 4

DISCUSSION

4.1 Questions

The purpose of my model was to answer questions concerning the effects of fishing, marine reserves, and other management pertaining to gag, while attempting to overcome the assumptions of prior models that may have limited the scope and accuracy of their predictions (Gerber et al. 2003). I explored the sensitivity of gag to natural stresses in the form of natural mortality, female behavior, and spatial distributions as well as human-induced stresses in the form of fishing mortality. The specific questions asked are (1) How does fishing affect the population demography? (2) How does fishing affect the effective population size vs. the total population size? (3) How does sex ratio affect the population demography and effective population size? (4) Does the spatial distribution of the species increase its susceptibility to increased fishing pressure? (5) Which aspects of life history are most sensitive to increased fishing pressure? (6) Which output variables are most sensitive to changes in model parameters? and (7) What management strategy or suite of management strategies would be optimal for this species? In order to answer these questions, I ran my model to produce results in four different categories: (1) no reserves, (2) reserves, (3), variable fishing, and (4) sensitivity analysis. I will also briefly explore and discuss realistic management strategies for this species and potential marine policy implications on state and federal levels as they relate to gag and the results of the model.

4.2 No Reserves

The effects of both fishing and sex ratio were studied in a variety of scenarios without reserves. These scenarios varied a number of natural history and management aspects, including: number of aggregations, fishing pressure, size limits for fishing, inclusion of the

fertility function, and female behavior. In general, fishing pressure most influenced both total population size and effective population size. Size limit for fishing and aggregation size also affected these dependent variables to a lesser degree, and there were significant interactions among these three variables (Table 3.1). However, effects of fertility and female behavior, as well as any interaction terms with these variables, were generally not significant.

As a main effect, number of aggregations had a small but significant effect on the effective population size, with 10 aggregations producing the largest effective size (Figure 3.4). This suggests that, with only 10 aggregations, males and females are better spread throughout the aggregations when there are low numbers of established aggregations. While female behavior did not have an effect on total or effective population sizes, the distribution of females among certain numbers of aggregations did. Whether or not females went to the closest aggregation or the same aggregation had no effect but increasing the number of aggregations seems to stretch both the number of males and females thin. In this case, males are unable to fertilize females in some aggregations and females are unable to be fertilized in other aggregations because there are not enough males. The insignificance of imposing the fertility function may also have to do with having such a small population size that the fertility function causes such a low number of larvae to be produced so that the carrying capacity is not reached. This may, in turn, allow more juveniles to survive to become adults. It is interesting that female movement did not affect the effective population size since one would expect that females might clump together when migrating to the closest aggregations. One would also expect that effective size would be higher when females return to the same aggregation each year and therefore may have a higher chance of spawning. However, there is high variability and stochasticity in both scenarios that seem to average out over time, causing neither to affect total or effective population sizes.

Age limit is shown to be an important factor by significantly increasing the effective population size when fishing is implemented. This suggests that manipulating the size limits (inferred from the age limit proxy) may be an important management tool for this species. A higher size limit may allow for a more stable population in the face of not only fishing pressure but also its interaction with certain life history aspects such as naturally skewed sex ratio and numbers of aggregations. When both fishing and numbers of aggregations were high, the population was only viable when the age limit at which fish can be removed from the population

by fishing was increased to 4 years old, further supporting the importance of age limit, and thus, the importance of using size limits as a management tool, when fishing occurs.

The most significant effect of fishing can be seen when it is increased to $F = 0.5$ and the age limit is reduced to 1 year. When there are 10 aggregations in place, this results in a severely depleted population of breeding age individuals and an effective population size of less than 1% of the total population size. However, only the scenario with 10 aggregations produced viable populations at all: at both 50 and 100 aggregations, the population crashes under the same conditions, leading to the significant interaction between number of aggregations, fishing take, and age limit. Increasing the age limit to 4 years, however, helps to offset the negative effects of heavy fishing and too many aggregations. When the age limit is set higher, high fishing not only reduces the total population size, but more importantly reduces the effective population size to less than 2% of the total population size. Fishing causes breeding age individuals to be taken out of the population even when the age limit is increased to 4 years old, since it is approximately at this age that they reach maturity. Even without fishing, the effective population size is approximately half of the total population size, as might be expected for a protogynous hermaphrodite such as gag. In such species, the total population size may not be a good indicator of the health of the population and the effective size may be more important in determining whether a population is in danger of extinction or overfishing. Therefore, effective population size, not total size, should be used as a measure of effectiveness of management for this fishery.

I expected population demography to be more highly skewed away from breeding adults with the inclusion of fishing and my hypothesis was supported. When there was no fishing, breeding age individuals (males, females, and transitionals) made up between 43% and 45% of the population. As fishing increased, however, they made up only 3-18% of the population. While increasing the age limit allows younger fish to make it into the breeding population, fishing is still extremely effective at removing these breeding individuals from the population both at low and high fishing levels.

My hypothesis as to the effects fishing has on total vs. effective population size was also supported: total population size was indeed misleading, and high fishing could cause a severe depletion of breeding age individuals that led to a very small effective population size as

compared to the total. It is, therefore, important to estimate effective population size instead of relying on the total population size as a measure when determining management techniques.

I expected that the sex ratio in the form of the fertility function would have a significant negative impact on both the total and effective population sizes due to the exaggeration of the skewed sex ratio. However, the fertility function only operates by adjusting fertility to determine the number of eggs that are ultimately produced based on the sex ratio of the population. This would only have an effect on the total population size by reducing the number of juveniles but not significantly affecting effective population size. While a previous model that did not include space showed an effect of the fertility function on total population size, this model does not. Fertility, or sex ratio, never has a significant or consistent effect on total or effective population size. Therefore, my hypothesis was not supported.

Testing these variables at different numbers of aggregations partly answered my question of how spatial distribution affects the susceptibility of the species to fishing pressure, as did testing female behavior. The manner in which females distribute themselves among aggregations (e.g. female behavior) did not have a significant effect on either total or effective population sizes. However, the number of mating aggregations by themselves did have a small but significant effect on both total and effective size but not on population demography. Further, there were significant interactive effects of fishing levels, minimum age limits, and aggregation on the population size. As pointed out previously, the scenarios where aggregations were greater than 10 and fishing was high with a low age limit (1 year), the model was unable to run because males were fished out. Population demography was thus affected by the interaction between fishing, aggregation number, and age limit. This partially supports my hypothesis, however, it will also be discussed in the section on variable fishing.

4.3 Reserves

Implementing reserves addressed the question of how spatial distributions affected the susceptibility of the species to fishing pressure. In addition, reserve scenarios explored different management strategies in order to determine which combination of strategies might be most

effective. The five reserve scenarios varied amount of model space protected and which habitat was placed under protection.

All main effects in the reserve scenario were significant as were many of the interactions between the dependent variables: number of aggregations, fishing level, size/age limit, reserve scenario, and percent protected (Table 3.3). These many significant factors highlight the complexity of imposing reserves as well as other management strategies to a marine species with a complex life cycle. Applying protection over all types of habitats (Scenario 0) was significantly more effective at increasing the effective population size than any other scenario (Figure 3.14, Graph D). This scenario also best exhibits a threshold pattern of protection found with several of the scenarios, in which 60% of the area must be protected to get these results. An interaction between age limit and protection was also seen (Figure 3.15, Graph F), indicating that a combination of low level of protection and a higher age limit (i.e., 4 years old) will increase the effective population size without having to reserve over 60% of the model space. Even still, the largest effect is seen when 60% or more of the habitat tested is protected.

The protection of shelf edge aggregation habitat in Scenario 1 also yields somewhat higher effective population sizes and generally exhibits the 60% threshold of increased protection (Figure 3.13, Graph B, Figure 3.14, Graph D, also see Appendix). This suggests that protecting the aggregation habitat is the most important reserve strategy apart from protecting 60% of the entire model space. By focusing on this one habitat, the effective population size is increased without taking drastic measures such as the current closure of the entire gag fishery. Shelf edge aggregations are usually in deeper waters and further from shore, so while protection of this habitat in a marine reserve may be easier to establish, it will also be harder to enforce.

The remaining reserve scenarios do not consistently exhibit the 60% threshold and do not always show a trend of increasing effective population size as protection increases. This makes sense since protecting these other habitats does nothing to increase the number of males in the population, which would in turn increase the effective population size. These scenarios do, however, increase the effective population size as compared to the non-reserve scenarios suggesting that even some moderate levels of protection, even if not in optimal habitat, can help to increase the effective population size. For example, protection of the offshore reefs allows breeding age females to be protected so that they can reach an age that they will be more likely to switch to become a male, increasing effective population size. Females, both mature and

immature, are also commonly found on the nearshore reefs at certain times of the year. Protecting the seagrass beds also keeps juveniles from being caught when the age limit is set to 1 year. This effect, combined with the fact that Scenario 0 was the most effective reserve scenario, suggests that a shore to aggregation reserve would perhaps be the most effective because it protects all stages of the species.

Reserves are also important to offset the effects seen in non-reserve scenarios when fishing was high ($F=0.5$), age limit was set to 1 year, and aggregations were 50 or 100. If the entire model space or the shelf edge aggregations were protected, the population crash was avoided. At lower levels of protection in reserve scenarios 2, 3, and 4, the population still crashed (Appendix, 3.2). If more than 40-60% of the area in each scenario was protected, the population was able to remain viable, suggesting that reserves can be effective when both fishing and bycatch (where bycatch is represented by using an age limit of 1 since much bycatch includes undersized juveniles) are high and many aggregations are present. Since we know this to be the case for gag, reserves should help the population to remain viable even if protected at low levels in key habitats.

My hypothesis that reserves would best protect the males of the population was partially supported. Scenario 1 was most effective of all the specialized habitat protection scenarios, which protects the male aggregations, however, the scenario that varied protection over the entire model space (Scenario 0) was even more effective than just protecting spawning aggregation habitat. My hypothesis that size and placement of reserves would be crucial to their effectiveness was therefore supported. Not only was a threshold apparent in many scenarios, but there were clearly habitats that were more responsive to the establishment of a reserve than others. I also hypothesized that suites of management techniques would be more effective, and including age limit as well as reserves did in fact increase effective population size. These strategies will be compared with variable fishing in the next section.

4.4 Spatial Variation in Fishing Pressure

Creating variation in fishing pressure between aggregation sites and other areas was used to answer the question of whether or not the spatial distribution of fishing affects the

susceptibility of gag to increased fishing pressure. Variable fishing was also used as a management strategy by lowering the fishing pressure on aggregations compared to the surrounding model space. This was done for high and low fishing levels but age limit, fertility, and female behavior were held constant.

Both levels of fishing (surrounding aggregations and inside aggregations) were found to be significant as main effects as well as an interaction between them. Variable fishing has a significant effect on the effective population size but not on the total population size. Since variable fishing changes only the fishing pressure on fish within a minimum distance of each spawning aggregation where the males are typically found, the effective population size is affected the most. Males are already a small fraction of the population, so increasing their numbers does not add much to the total population size. It does, however, contribute significantly to the effective population size by affecting the sex ratio. When fishing was low, effective population size was kept at 25% of the total population size (Figure 3.16, Graph A), suggesting that reducing fishing on aggregations while keeping fishing pressure the same elsewhere can be quite effective at maintaining the effective population size. With no fishing at all, the effective population size was still only 50% of the total (Figure 3.1), so keeping aggregations off limits to fishing seems to be a good way to keep the highest possible effective size whether the surrounding area is fished sustainably or heavily. When fishing is raised to $F = 0.5$, the effective population size becomes approximately 12% of the total size (Figure 3.16, Graph B), also suggesting that fishing on aggregations may be inversely proportional to the percent of the population that contributes to the effective size.

Increasing the fishing pressure in aggregations was done to observe the severity of the effect of selective fishing on aggregations. It has been previously proposed that the sedentary lifestyle of males makes them an easy target for fishermen. Not only can the aggregations be found time after time by marking them on a GPS, but, if desired, a fisherman could completely fish out an aggregation all at one time. The results obtained from the model show that this could have devastating consequences on the effective size of the population, reducing it as low as $< 1\%$ of the total population size in some cases with a range between less than 1% and 5%.

Aggregation number in this case did not have any main effect nor did it interact with other variables to create a significant effect on the total or effective population sizes. This is likely because all aggregations are protected. Unlike previous scenarios that showed a decrease

in population sizes as the number of aggregations increased, these scenarios show no such effect, suggesting that protection of aggregations could be able to offset the crash of the population if fishing level is high and the number of aggregations is high.

My hypothesis that spatial distribution would be integral to a management plan was supported. While aggregation numbers in this case had no effect on the population size, varying fishing on aggregations had a significant effect on the effective population size that was negatively correlated with increasing fishing pressure on aggregations or positively correlated with reduction of fishing pressure on aggregations. Spatial variation in fishing pressure was also found to be important in offsetting negative effects of some spatial distributions when combined with other life history aspects and lax management. Spatial variation that increased fishing pressure, however, was also found to be important and warrants attention from managers. The mapping of existing aggregations as well as additional catch data from these aggregations are needed to determine the extent to which this problem occurs.

My hypothesis that reserves would be the optimal management strategy was supported in general. Since reduction of fishing pressure within spawning aggregations is essentially creating a reserve specifically around the spawning aggregations, reserves are maintained as an optimal management tool for increasing the effective population size. Ways in which reserves could be set up and determined will be discussed in the management section. My hypothesis that suites of management techniques would best benefit gag populations was also supported: including an age limit of 4 years in addition to variable fishing had a significant positive effect on the effective population size. Previously, reserves paired with an age limit of 4 years also had a significant positive effect.

Finally, this section also helped to answer the question of how fishing affects total vs. effective population size. For variation of fishing pressure on aggregations, the total population size is not significantly affected by either main effects or interactions of the variables tested (Table 3.5). Effective size, however, is significantly affected by both surrounding fishing levels and aggregation fishing levels, as well as their interactions. This result further supports the hypothesis that total population size is not the optimal metric by which to evaluate fisheries' viability.

4.5 Sensitivity Analysis

The sensitivity analysis was performed in order to determine which parameters had the most significant effect on the output variables. In addition to knowing which parameters had the most influence on the model, it is also important to know which output variables were most easily influenced by changes in model parameters.

The effective population size was most sensitive to two terms associated with the equation determining fecundity (F2 and F3). The second term controls the rate at which fecundity increases with age, while the third controls the absolute fecundity at each age. The effective population size was also significantly sensitive to the probability of changing sex, natural mortality, and the age limit for fishing. Besides age limit, these are all life history aspects that are driving the model outcome. For gag, then, natural mortality, sex change, fecundity, and recruitment are the most influential characteristics in their life cycle. In terms of management, the effective population size was sensitive only to the size limit for allowing catch. This means that managers and scientists should be paying close attention to these parameters when collecting data and developing predictions from models. Special attention should be paid to the accuracy of the data collected for these life history parameters in order to best be able to predict outcomes of manipulating other parameters such as any management parameter. The model also identifies age limit, as used in the model, as an important factor for determining effective population size, which is consistent with the currently popular use of size limits as a management tool. While it is good that this tool is already in place, the model has shown that multiple protections may also need to be utilized in addition to size limits in order to optimize management.

Total population size was found to be most sensitive to natural mortality, fecundity, and recruitment. Total population size was sensitive to the second parameter of natural mortality, which determines the steepness of the function and, therefore, the age at which natural mortality plateaus as well as the mortality rate at which it plateaus. Total size was also sensitive to the third parameter of fecundity, which controls the absolute fecundity at age. Finally, total population size was found to be sensitive to the stochasticity associated with recruitment (parameter R3). Many aquatic species have high year-to-year variation in recruitment, which has been shown to be a driving factor of population dynamics. Though somewhat obvious, these life

history aspects are what drive the total population size. No management tools were significantly correlated with total population size, again supporting the hypothesis that effective population size is a better measure for the health of the population.

The sex ratio was most sensitive to parameters associated with natural mortality, sex change, and age limit. Varying natural mortality may have an effect because it allows more or less individuals to make it to breeding age by determining age-specific natural mortality rates. Sex change and age limit, however, have a more direct effect on the sex ratio itself. Changing the slope of the sex change function will directly affect the ratio between males and females. Size/age limit has also been shown to affect the numbers of breeding age individuals, thus also having an important effect on sex ratio. As with the effective population size, this also supports the idea that size limits may be an important management tool.

I hypothesized that certain life history aspects would be more sensitive to change, and that hypothesis was supported by the fact that natural mortality, sex change, fecundity, and recruitment were all correlated with multiple output variables. These are the crucial life history aspects for this species and management may thus require very accurate estimates of these parameters. I also hypothesized that effective population size would in general be most sensitive to variation in the input parameters, whereas total population size would be more apt to mask these variations. The estimate of total population size does not take into account the numbers of females compared to the numbers of males, so even though a population size may be high, the population may still not be viable. In the case of gag, the viability of the population is limited by the number of males because it is a protogynous species. Therefore, looking at the total number of fish is uninformative. The effective population size gives a much better description of the true population dynamics by taking into account the number of females and males to yield size of the population that is essential to its health, genetic viability, and survival. This hypothesis was supported by the sensitivity of effective population size to effects such as fishing, life history, and management. Variation of these parameters did not always have an effect on total population size, but almost always significantly affected effective size, supporting the hypothesis that total size may not be the best measure of population health.

4.6 Management Strategies

Current management strategies include a daily bag limit, a size limit, yearly commercial fishing quotas, and seasonal closures. Daily bag limits are not likely to be effective due to the ease with which enforcement of these limits are eluded. It is not uncommon for recreational fishermen to catch their limit, bring it back to shore, and go out and catch another limit. This problem is only exacerbated by the fact that the numbers of recreational fishermen continue to grow and are not limited (Coleman et al. 2004, Figueira and Coleman, 2010). This can, and does, happen multiple times a day. While this limit may do some small good for the fishery for those fishermen that do abide by the law and by bringing the state revenue from fines collected by those that don't, the overall effectiveness of this management tool is minimal.

The size limit (which correlates with the model parameter "age limit") in the Gulf is commonly set to 22 inches (with some exceptions of larger limits in the Florida Keys). Based on the correlation between age and size, this works out to be approximately the same as the 4-year-old age limit used in the model. The results of the model support the use of size limit as an effective management tool (Tables 3.1, 3.2, 3.3, 3.5) and it is somewhat easier to enforce as compared to reserves. One problem with this is when undersized fish are caught by both commercial and recreational fishers and are thrown back dead. Even though such fish are not kept, they are nevertheless removed from the population and are considered part of the overall catch. The recreational dead discards often comprise the highest catch category for gag, indicating that while age/size limit may be an optimal management tool when perfectly executed, the reality is that many fish under the age/size limit will still be removed from the population by fishing. Barotrauma is also important to note as a problem since fish caught in deeper waters have a lower chance of survival (Coleman citation). In this case, regardless of age/size limit, they will still experience a high rate of mortality when caught in deep water whether they are thrown back due to small size or kept.

Seasonal closures were not explicitly defined in the model since fishing pressure was only applied yearly. Seasonal closures can be likened to a temporary reserve or variable fishing, however, both of which were shown to have positive effects on the effective population size. Seasonal closures are likely the easiest management tool to enforce, because they make fishing for and keeping gag completely off limits. There is little gray area to be exploited in this case,

since anyone found with any size gag is automatically in violation of the regulation. There is no need to measure, observe coordinates, etc. Breeding age individuals are also protected while they are most vulnerable. Currently, there is an emergency, temporary closure for gag because of the results of the last stock assessment. Until better management techniques are developed, the fishery will remain completely closed before and after their spawning season (through May).

While there are some reserves established, most of these are not species-specific. The model suggests that, in order to best manage gag, reserves would either need to cover greater than 60% of the Gulf or 60% of the shelf-edge habitat (Figure 3.19, Graph A). The first option, covering greater than 60% of the Gulf, is not feasible, though it would not only help gag, but many other species as well. Covering 60% of the shelf edge aggregation (Figure 3.19, Graph B) is somewhat more feasible because of the distance from shore of the aggregations, but public resistance would likely be strong and enforcement more difficult. The model results showed that combining age limit with reserves (Figure 3.21, Graph D, F) or variable fishing (Figure 3.22, Figure 3.23) were effective ways of increasing the effective population size. Establishing low levels of protection of critical habitat, such as over specific aggregations or along the shelf edge in general, combined with the current size limits should be effective. While establishing reserves around the many aggregations would be optimal, it would not be feasible as many aggregation locations are unknown and enforcement would be next to impossible. Establishment of reserves over a certain percent of the shelf edge habitat would not only benefit gag, but also other species found in such habitat.

Imposing TURFs, or territorial use rights in fisheries, may be a good management tool for gag. Commonly used for sedentary species, there are many variations that would allow TURFs to be modified for gag. Since males are sedentary, each zone could encompass one or more aggregations. In this case, the fishermen that owned the rights to that “turf” is more likely to be a good steward and “self-manage” in order to maintain the population for future personal use. A common attitude is to want to get all the fish before someone else does, but if the fisherman knows that he is the only one fishing that spot and he has gone through some process or payment to procure that spot for himself, he is not likely to fish it out (Castilla, 2000 and 2010). A terrestrial example of this would be deer hunting: on land that is state-owned and open for hunting, mature deer are sparse, however, on privately-owned, high-fenced hunt leases, the owner will better manage those deer so that they are abundant. Such landowners set rules and

restrictions for those that hunt on their land so that too many deer are not removed from the population. A TURF is essentially the same principle but in an aquatic environment, the only difference and problem being that there is no “high-fence”. If certain fishermen or commercial fishing companies are essentially given ownership of select areas, they would not be tempted to completely fish out the aggregation that has been placed in their care. Ownership could be bid out or randomly selected from a pool of applicants each year or for a specified lease period. Since this would cause fishermen to be territorial, they would enforce fishing within their zones, leaving less work for law enforcement. Aquatic animals are free to move throughout their continuous environment, which makes sedentary species preferred. Since male gag are essentially sedentary, TURFs may work well for this species and should be seriously considered.

4.7 Future Questions and Directions

In the future, the model developed in this paper could be expanded to include the following:

1. Explicit genetic variation using allele data collected from gag in the Gulf of Mexico.

This will increase the level of complexity of the model and allow for more accurate genetic analyses and predictions above and beyond effective population size.

2. Combine this model with a hydrodynamic model of currents and depths in the NE Gulf of Mexico. Since gag are aggregating fish, the spatial component of their life history has been shown to be essential in determining their optimal management strategy, including the maintenance of biodiversity. Thus, determining exact spatial position based on depths and hydrodynamics would add further complexity and accuracy to the model. The coupling of a hydrodynamic model with the species model would also allow for highly sophisticated modeling of larval dispersal from specific point sources. This would allow for the most detailed reserve model possible.

3. Model larval dispersal out of these patches to the seagrass beds as well as the recruitment back into the patches in a metapopulation-like system. This step will help (1) to determine the extent of the gene flow between patches and (2) to determine the connectivity between patches when it comes to larval recruitment. This second part has a direct application to the possible establishment of marine reserves: it should determine if reserves are a good management technique from a metapopulation standpoint and if so, the appropriate number and spacing of these reserves.

4. Develop a method to assign a certain “dominance index” to each female that will determine how often a female gets a mate. Since the sex ratio of gag is so skewed, females must compete to get a mate. As previously mentioned, some females show atretic bodies as a result of not being able to mate. When females are in a group they may establish a scale of aggressiveness; this method would take this into account to determine which females will get a preference to mate. This scale of aggressiveness could also be factored into the probability of sex change from female to male. This mode of sex change could be compared to the two different modes used in the current model to see if different results are obtained.

5. Make mortality seasonally variable (imposed monthly) to more accurately reflect the natural conditions. This will also enable further exploration of another management technique: seasonal closures.

6. Incorporate spatial distributions of fisherman in addition to spatial distributions of the species. This will enable exploration of the differences between different types of fishing methods, with the most important being the distinction between commercial and recreational fishing.

7. An economic model could also be incorporated to pair economic patterns with the species model in order to determine the optimal management strategies for both the species and the economic fishery.

8. Include a method to measure the total weight of the population in addition to total number of fish in order to account for the high numbers of larvae and juveniles.

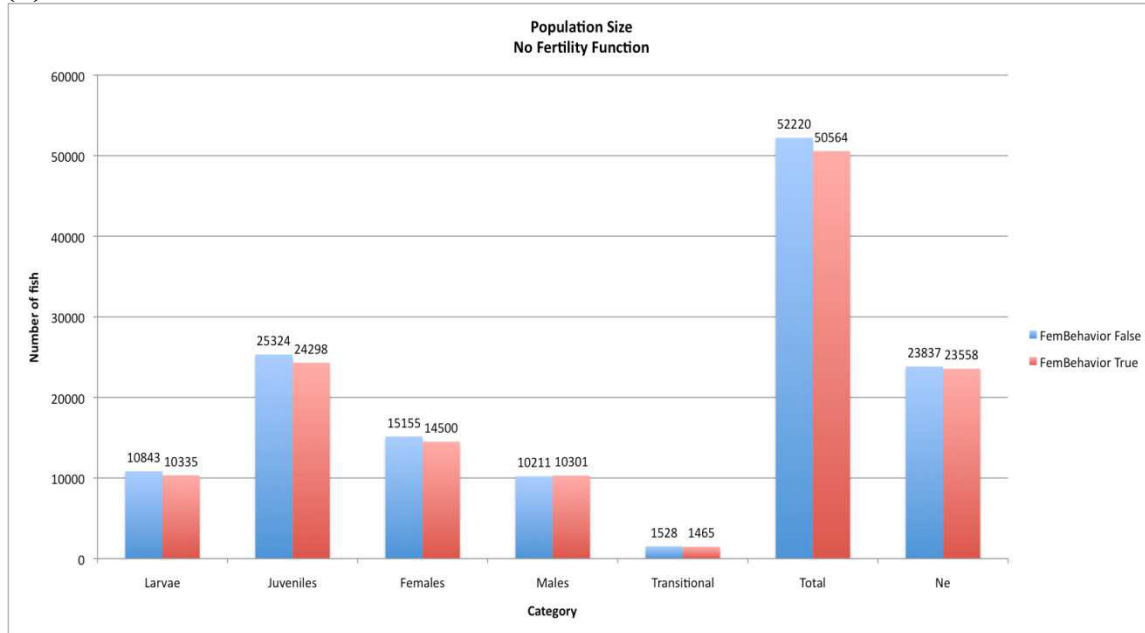
4.8 Final Summary

In conclusion, gag have a unique life history that does in fact make them susceptible to higher fishing pressures. Fishing negatively affects the demography, total population size, and effective population size of the species. While fishing has a noticeable effect on total population size, the real impact is seen on effective population size. Thus, managers and scientists (especially stock assessment scientists) alike should use effective population size and/or other measures of genetic variation and diversity to make statements about or judgments on the health and viability of the population. While sex ratio may be thought to have a significant effect on this effective population size, imposing fertility constraints based on the sex ratio of the population in fact does not have a significant effect. Instead, spatial distributions and controlling the age at which fish can be caught contribute most to the maintenance of a high effective population size. Males can be managed effectively by protecting aggregations (spatial variation in fishing pressure), increasing the breeding age population and thus, the effective population size. Reserves are also effective when placed in critical habitat or at a protection level above the 60% threshold. Reserves allow for a higher effective population size and act as a buffer against spatial distribution effects and little management. Traditional management including bag limit, size limit, and seasonal closures may be more effective when paired with non-traditional reserves that are selectively placed based on habitat and percent protected. Other non-traditional management such as TURFs yield themselves to closer study for such a species as gag. The current federal, temporary closure based on the status of the population has shed light on the seriousness of the condition of the population. It is time to think outside the box and apply management techniques that are outside of tradition. After all, it is better to be limited in *where* one is able to fish than to be banned from fishing gag in its entirety.

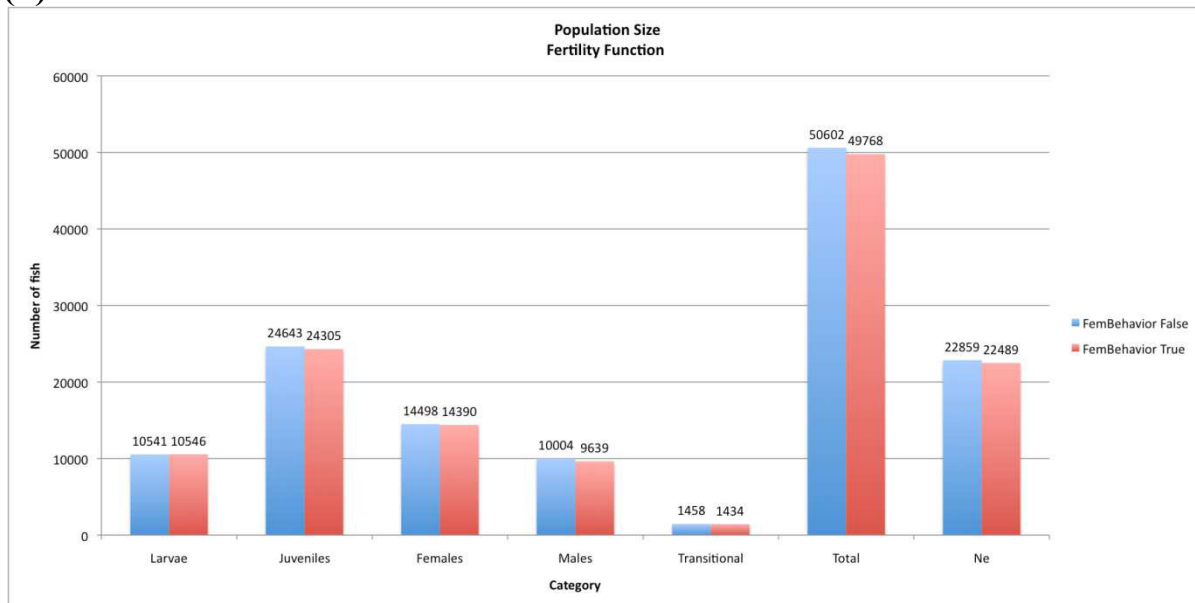
APPENDIX A

No Reserves

(a)



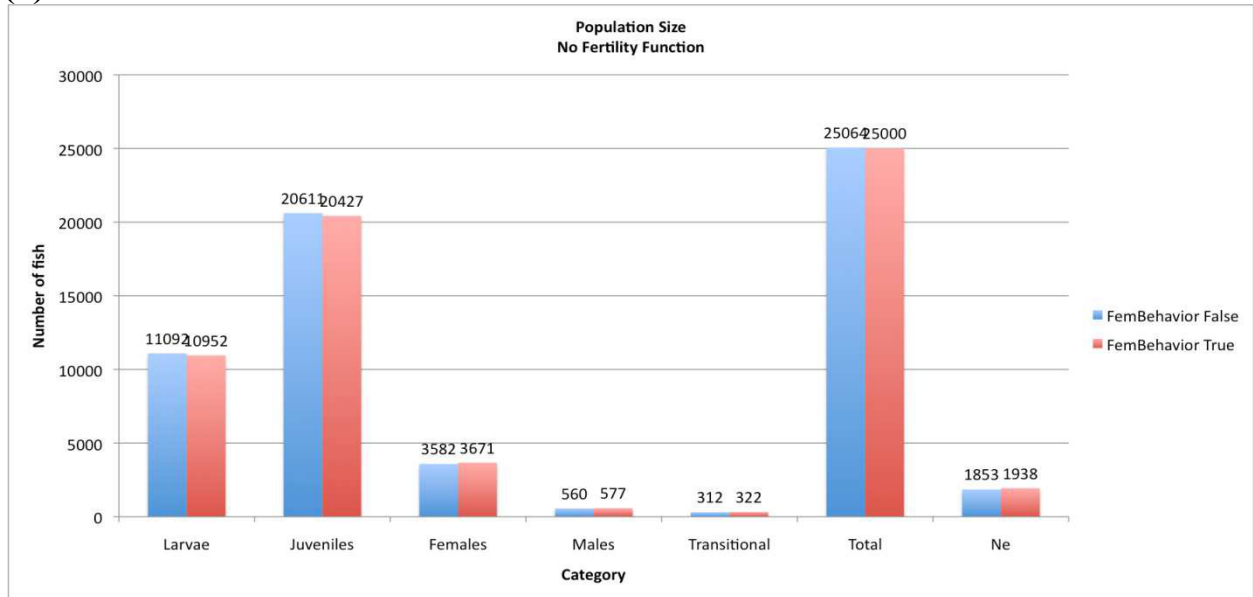
(b)



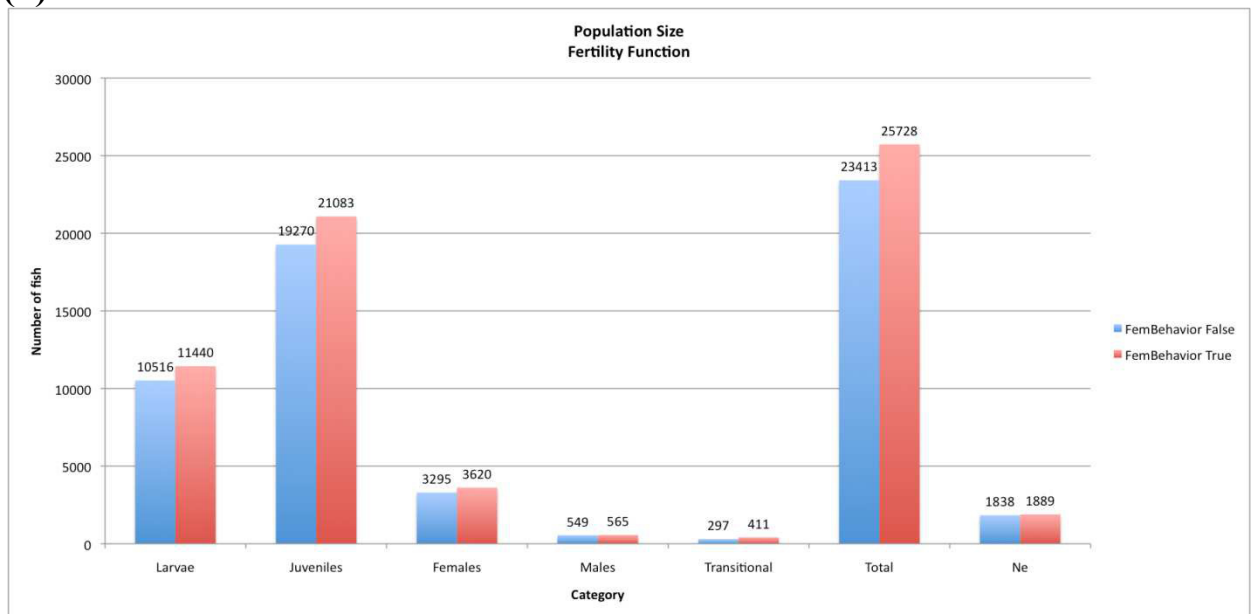
Population size with no fishing ($F=0$) at 10 aggregations

Population size by stage, including total population size and effective population size, where (a) fertility function is not included, (b) fertility function is included.

(a)

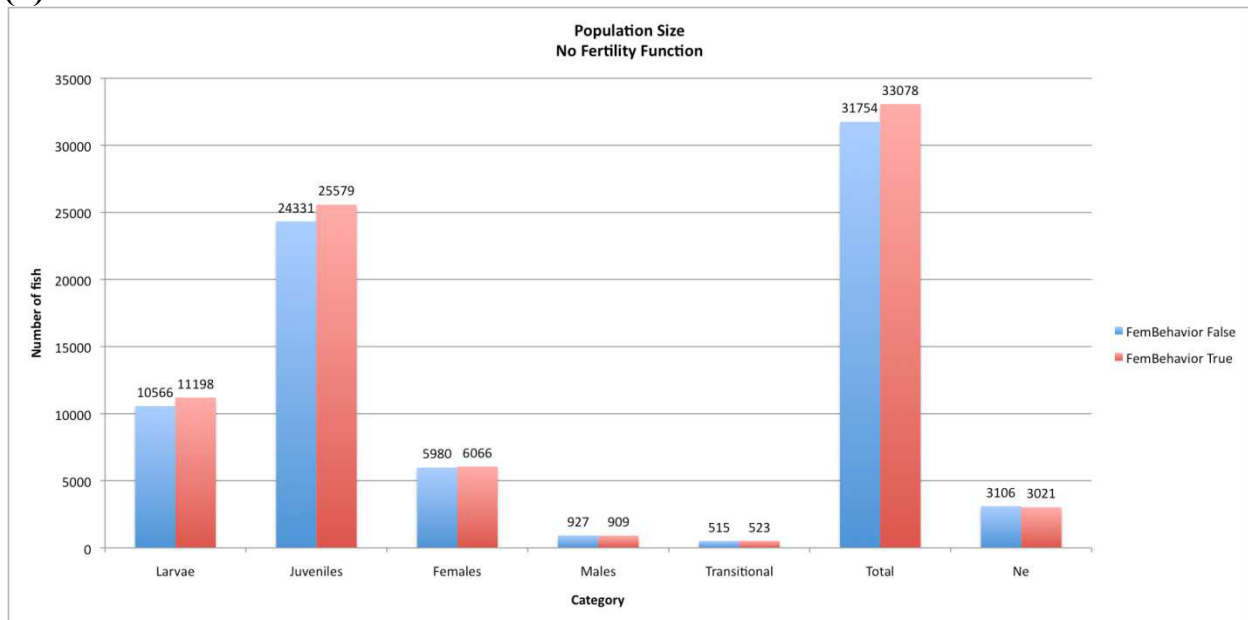


(b)

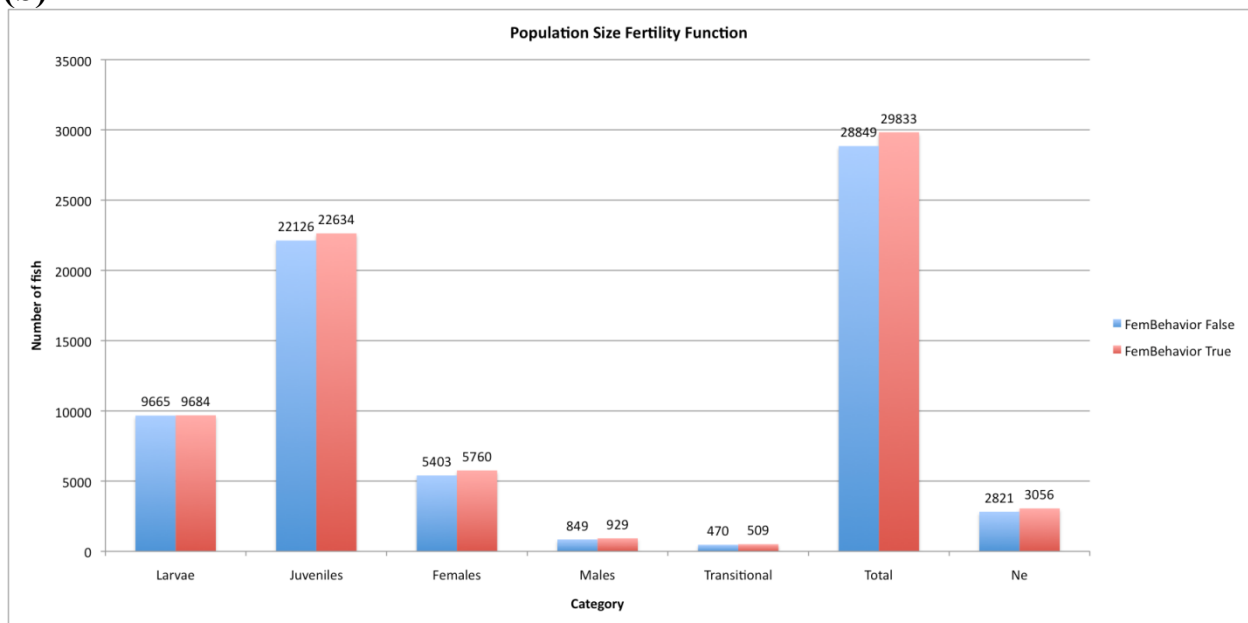


Population size with low fishing ($F=0.25$) and age limit of 1 year at 10 aggregations
Population size by stage, including total population size and effective population size, where (a) fertility function is not included, (b) fertility function is included.

(a)

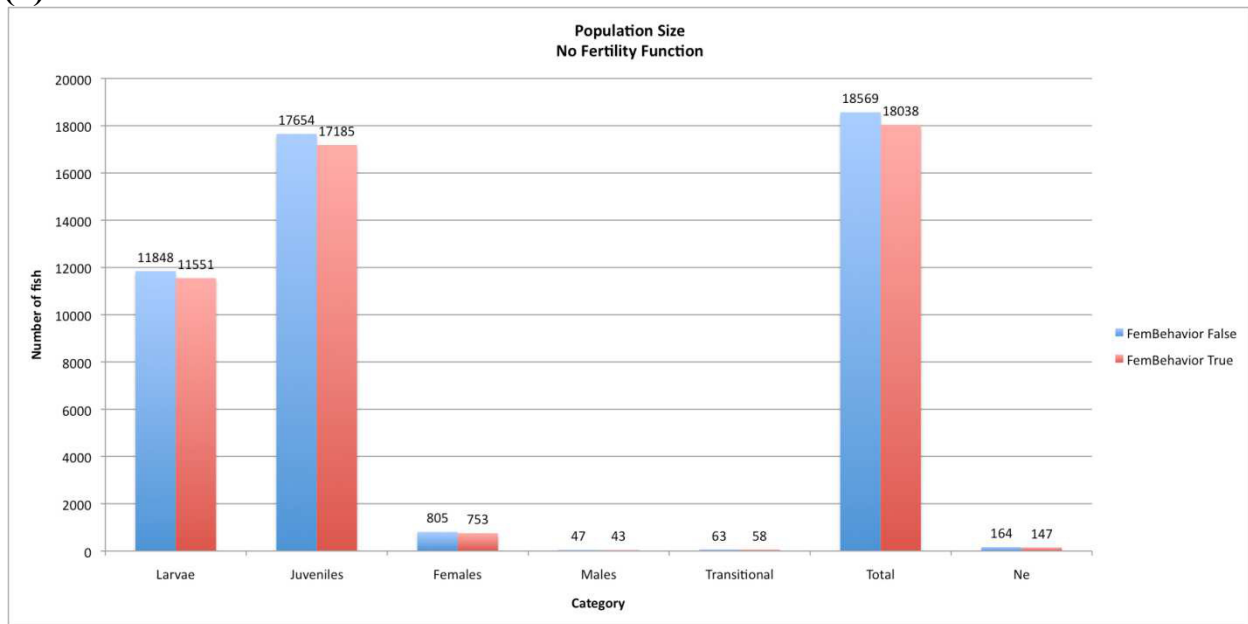


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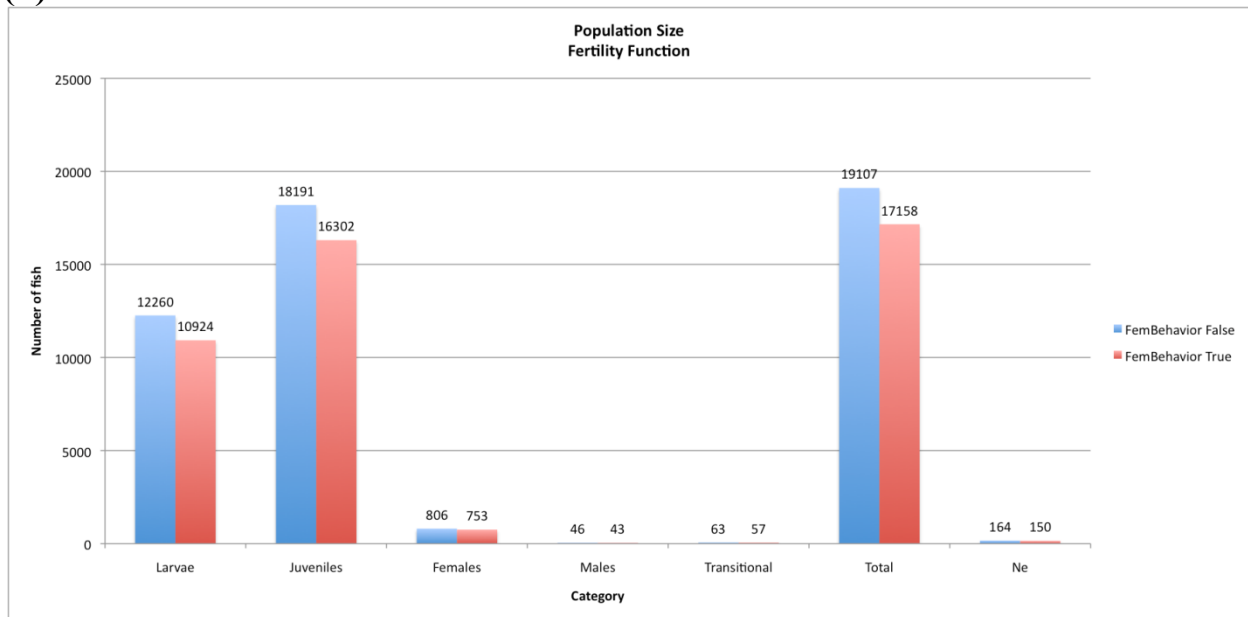


Population size with low fishing (0.25) and age limit of 4 years at 10 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

(a)

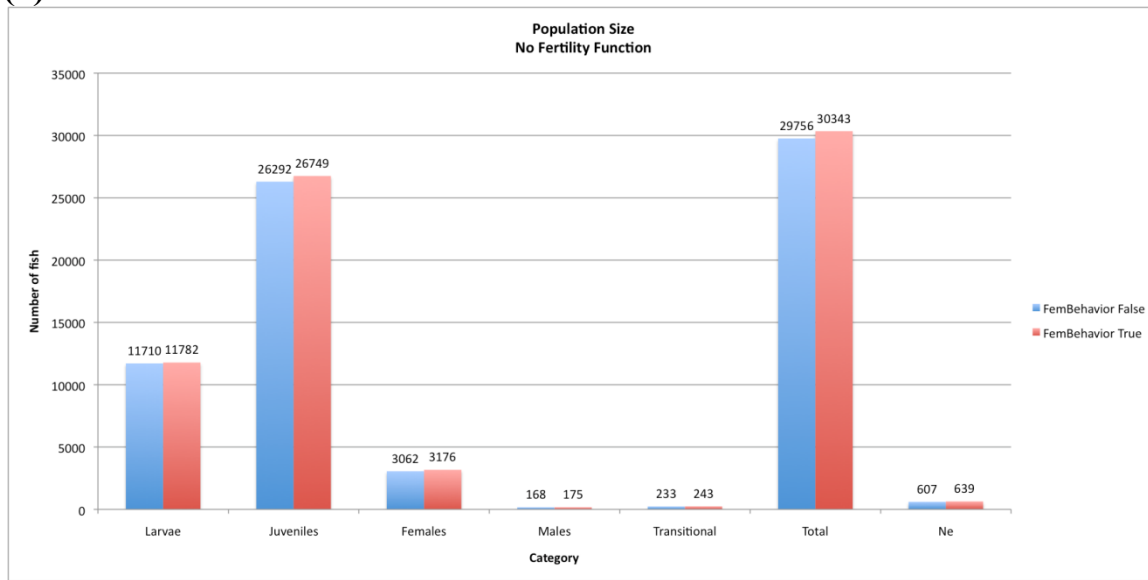


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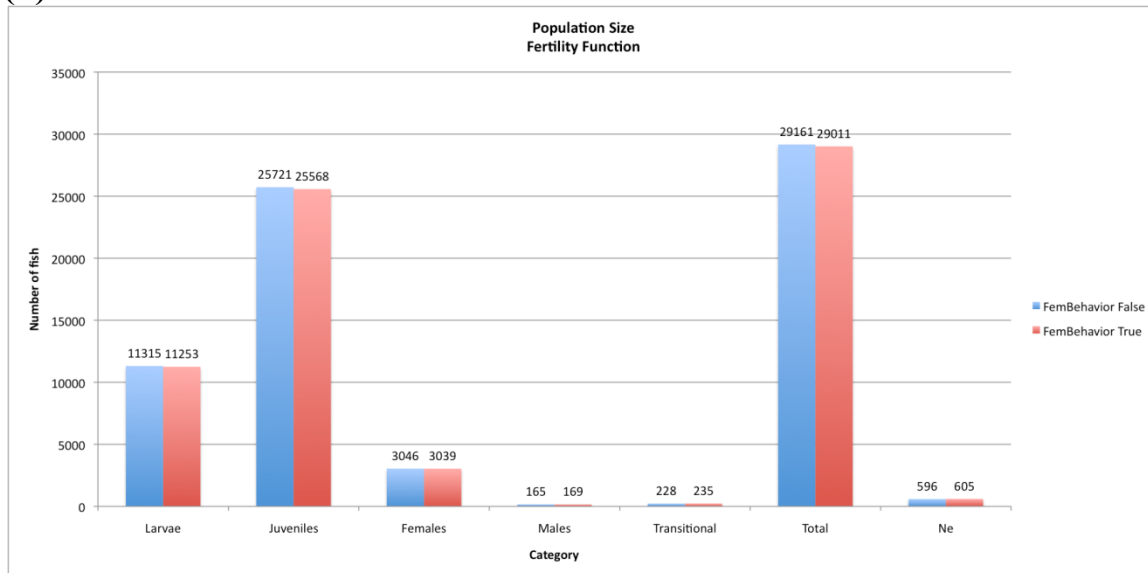


Population size with high fishing ($F=0.5$) and age limit of 1 year at 10 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

(a)

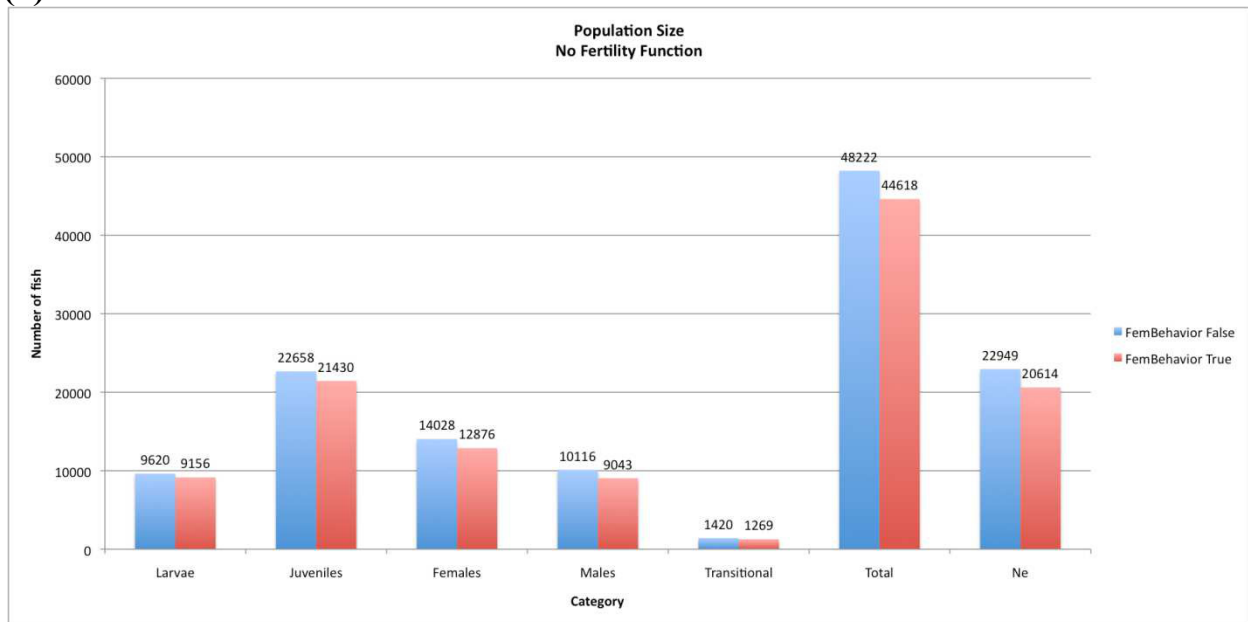


(b)

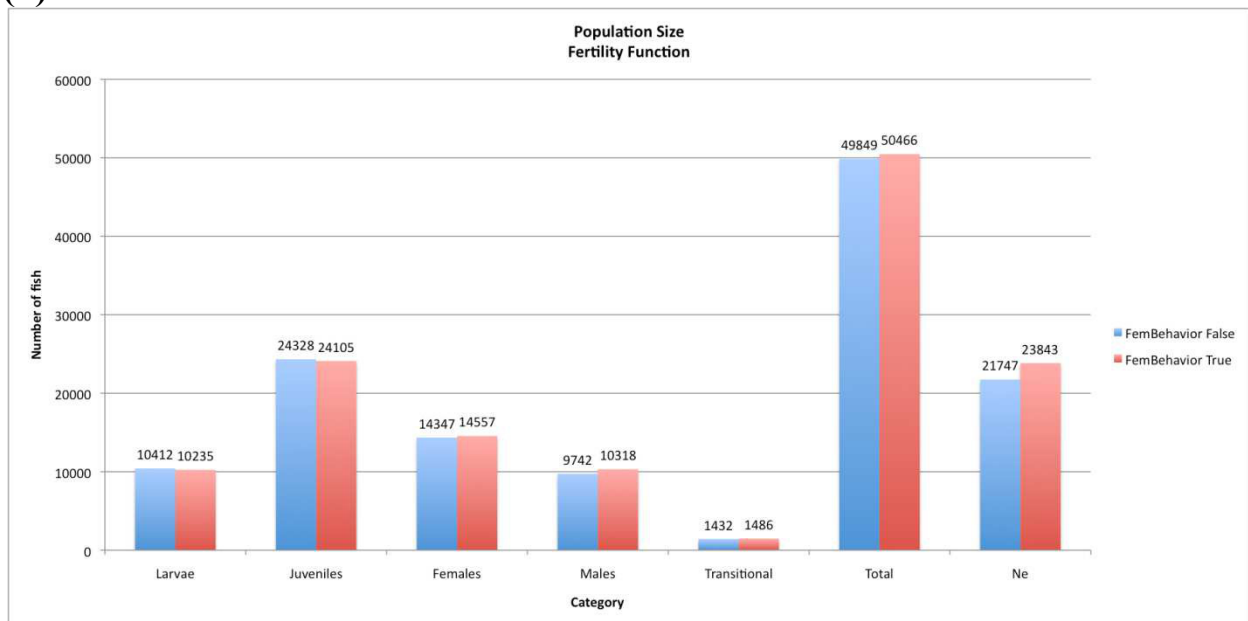


Population size with high fishing ($F=0.5$) and age limit of 4 years at 10 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

(a)

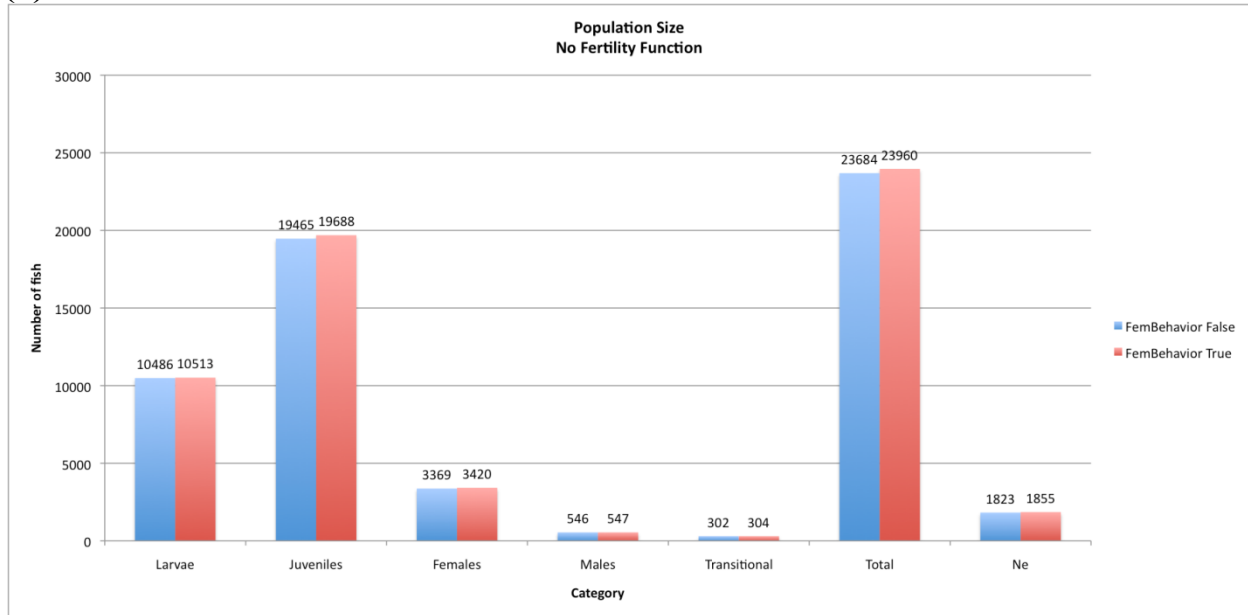


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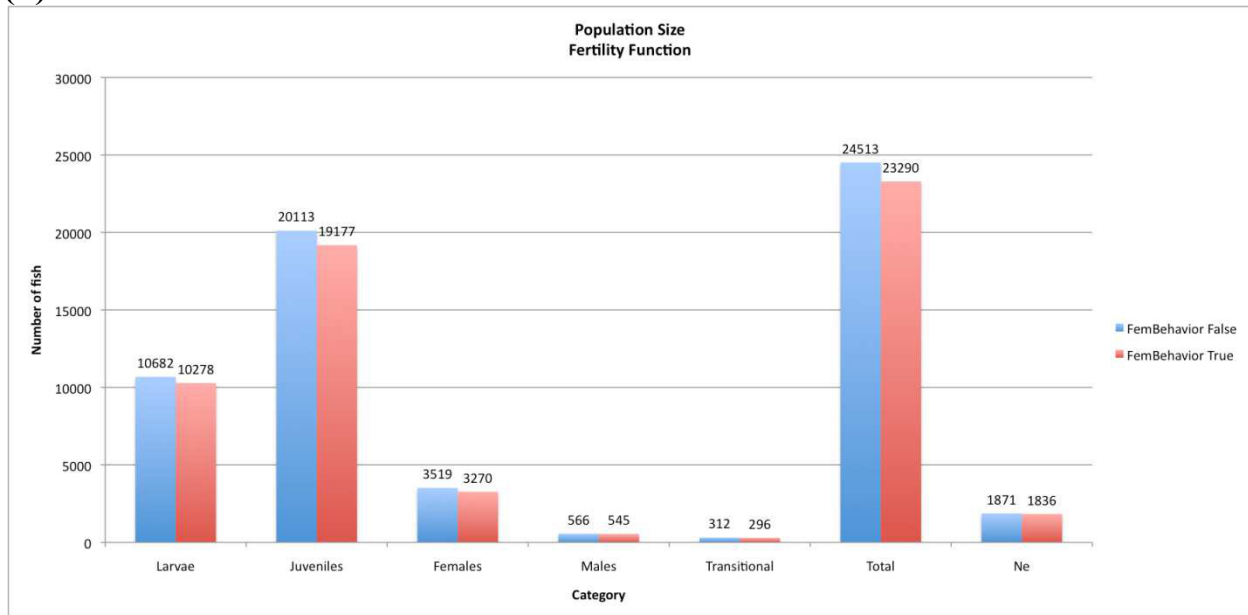


Population size with no fishing ($F = 0$) at 50 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

(a)

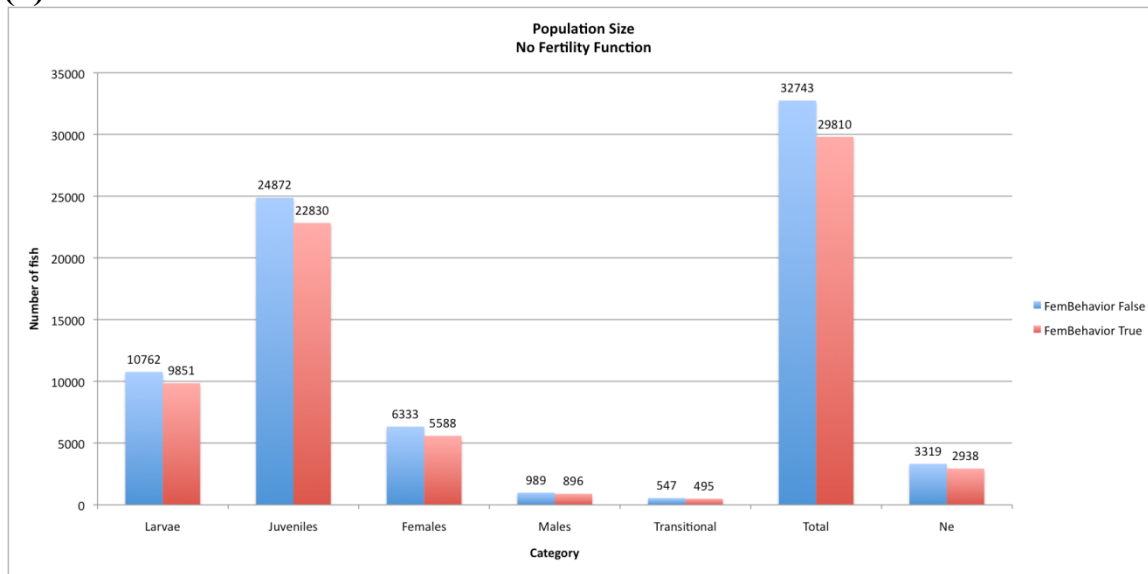


(b)

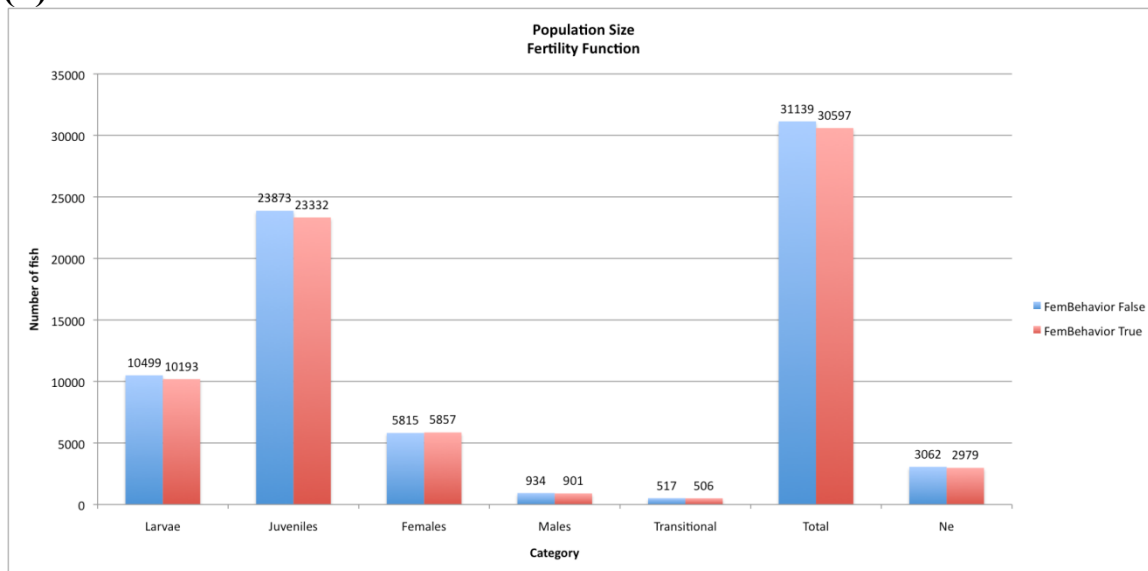


Population size with low fishing ($F=0.25$) and age limit of 1 year at 50 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

(a)

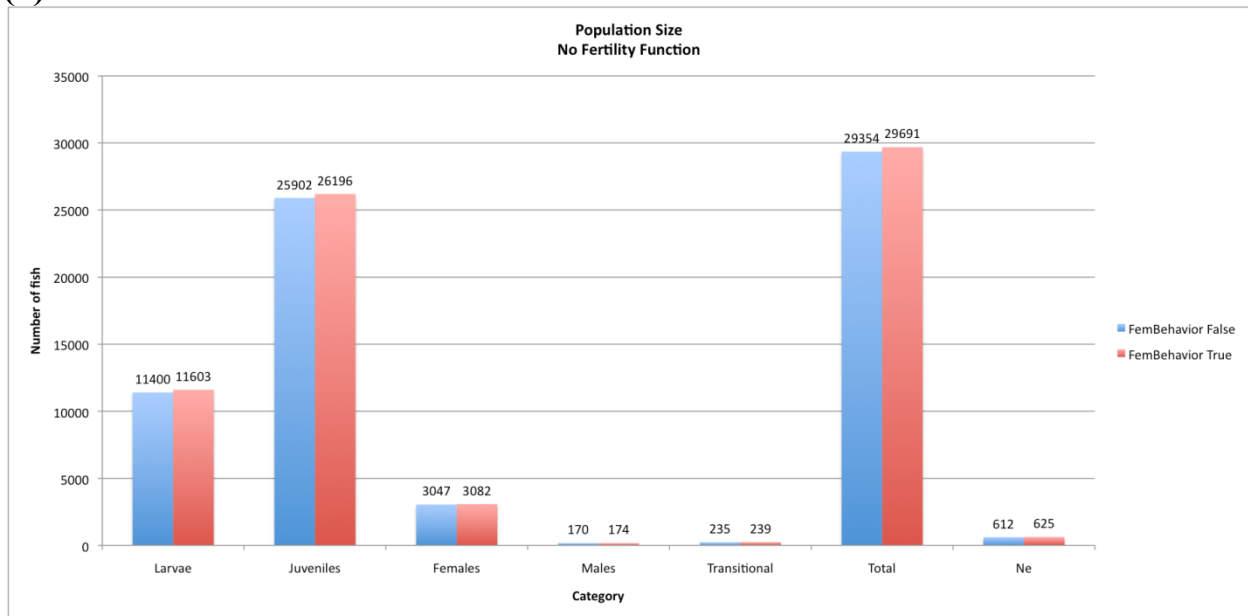


(b)

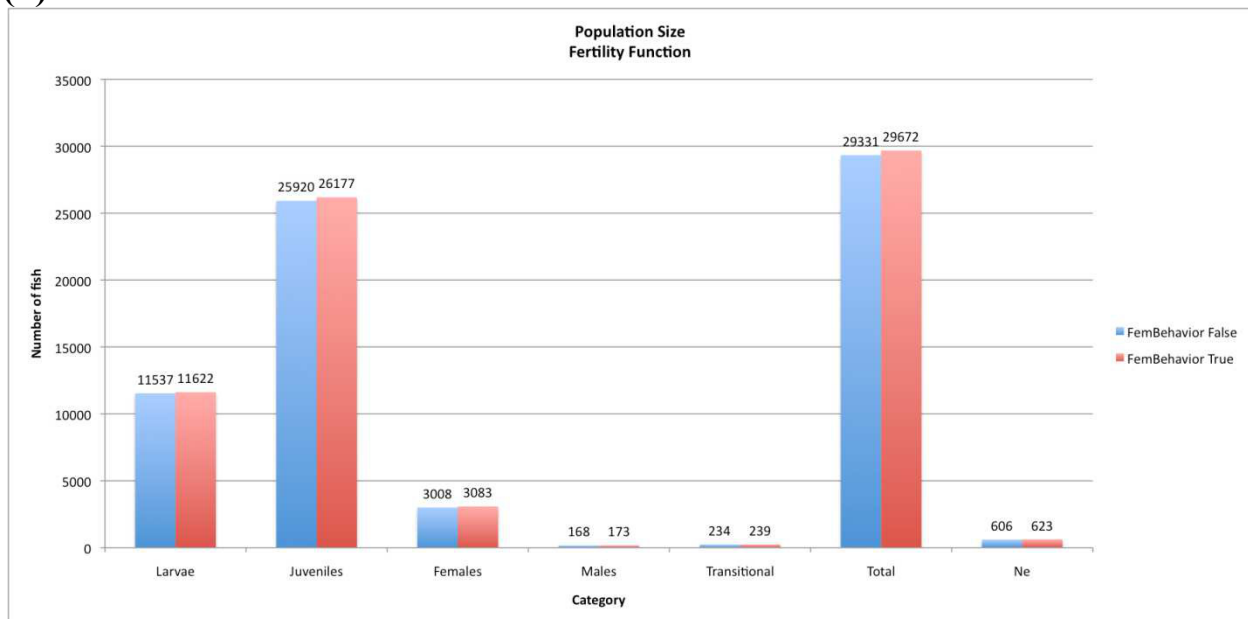


Population size with low fishing ($F=0.25$) and age limit of 4 years at 50 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

(a)



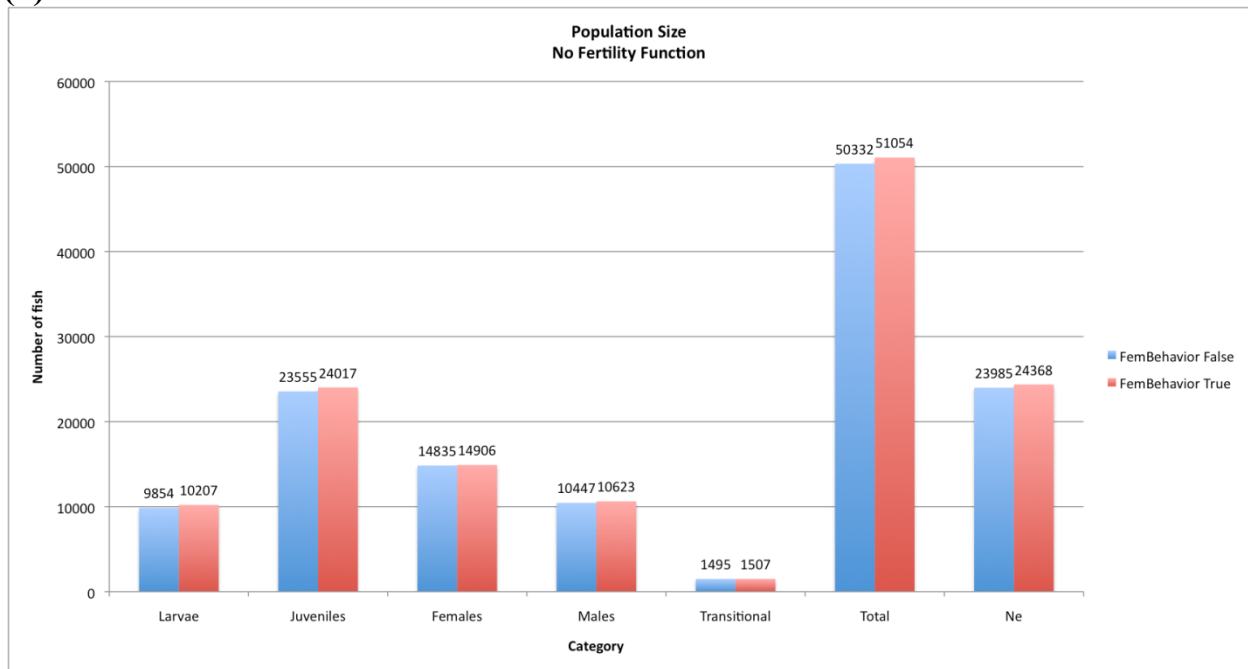
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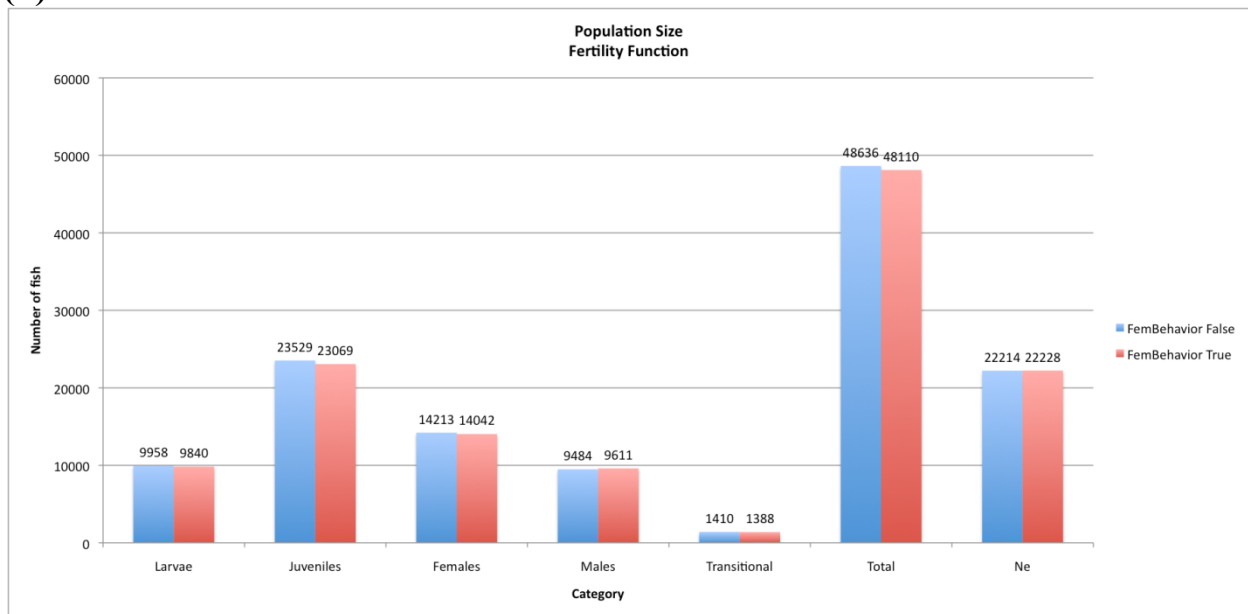
Population size with high Fishing ($F=0.5$) and age limit of 4 years at 50 aggregations*
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

*Age Limit of 1 is not pictured here since the population crashed repeatedly and no data could be obtained for this scenario.

(a)

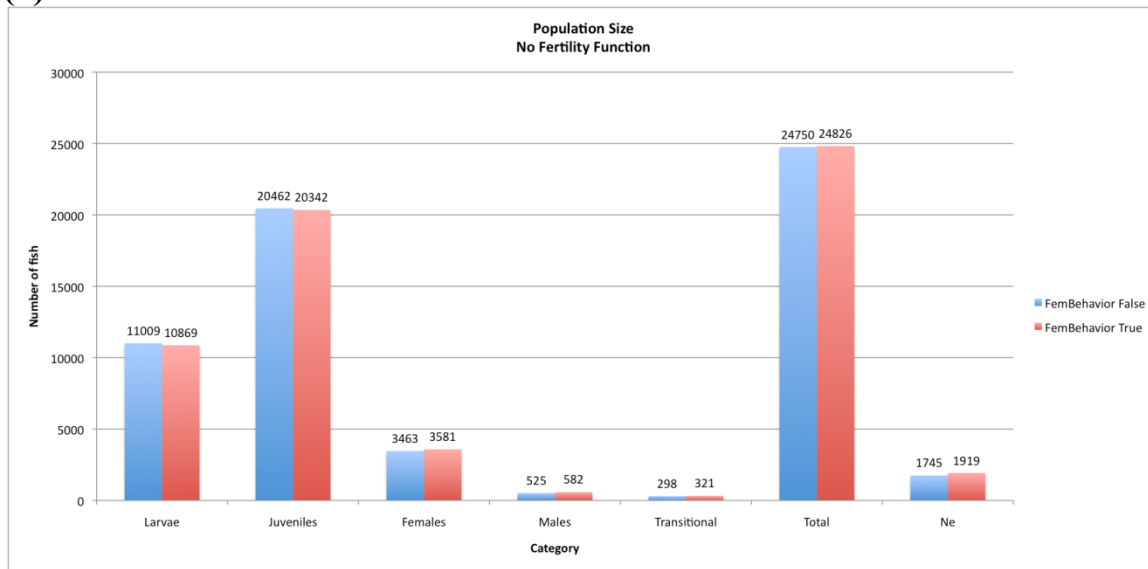


(b)

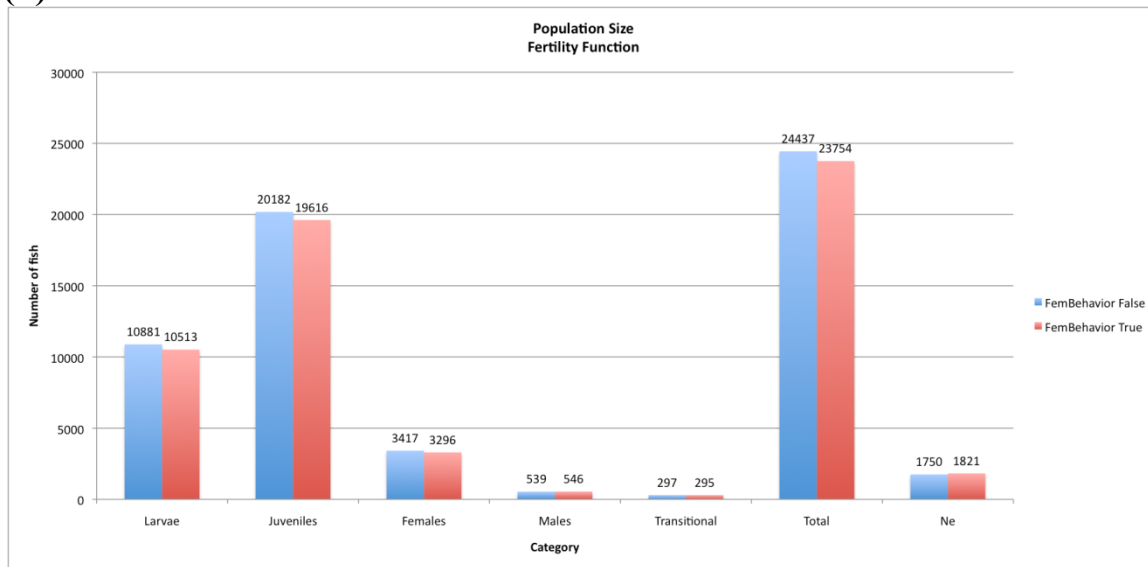


Population size with no fishing ($F=0$) at 100 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

(a)

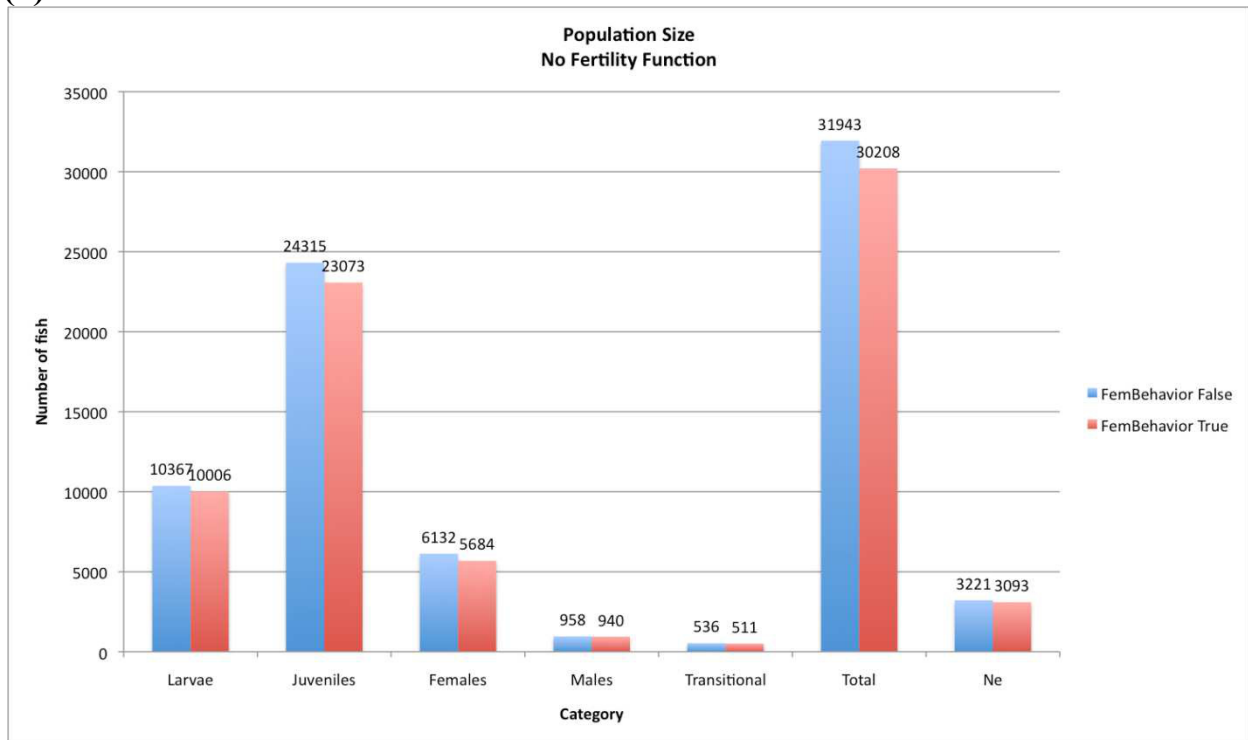


(b)

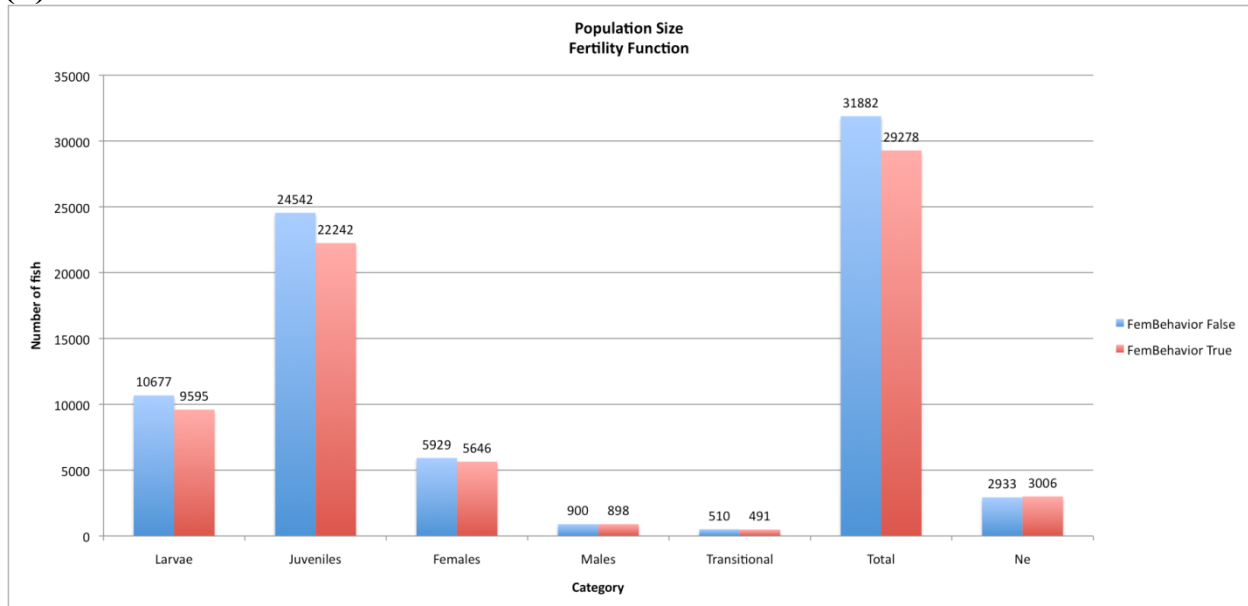


Population size with low fishing ($F=0.25$) and age limit of 1 year at 100 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

(a)

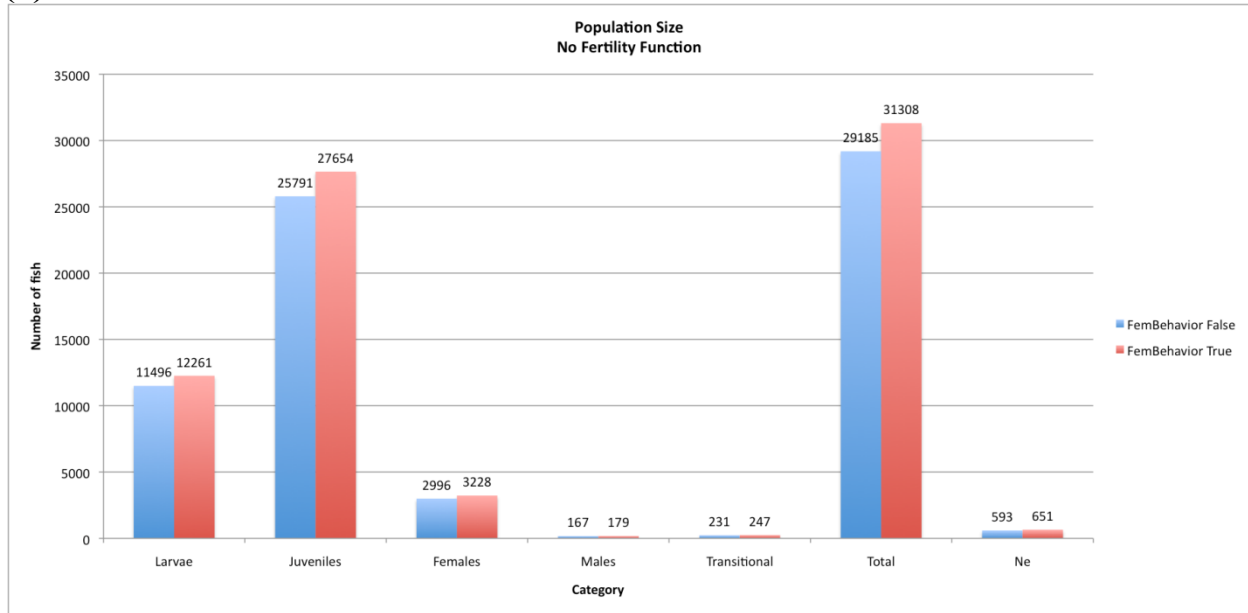


(b)

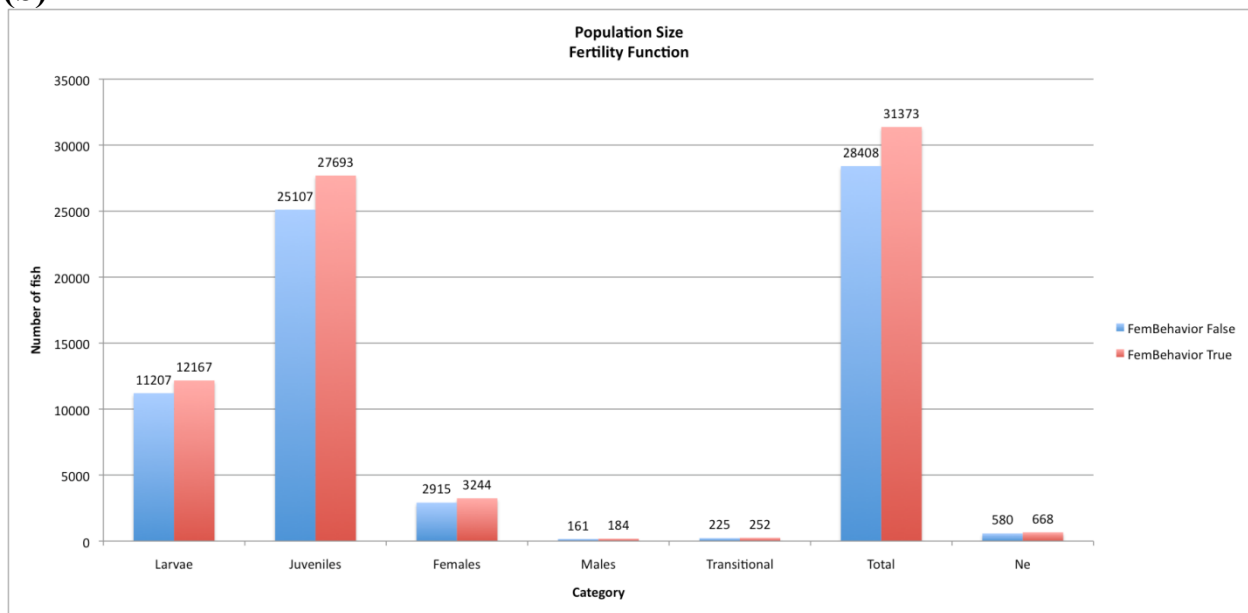


Population size with low fishing ($F=0.25$) and age limit of 4 years at 100 aggregations
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

(a)



(b)



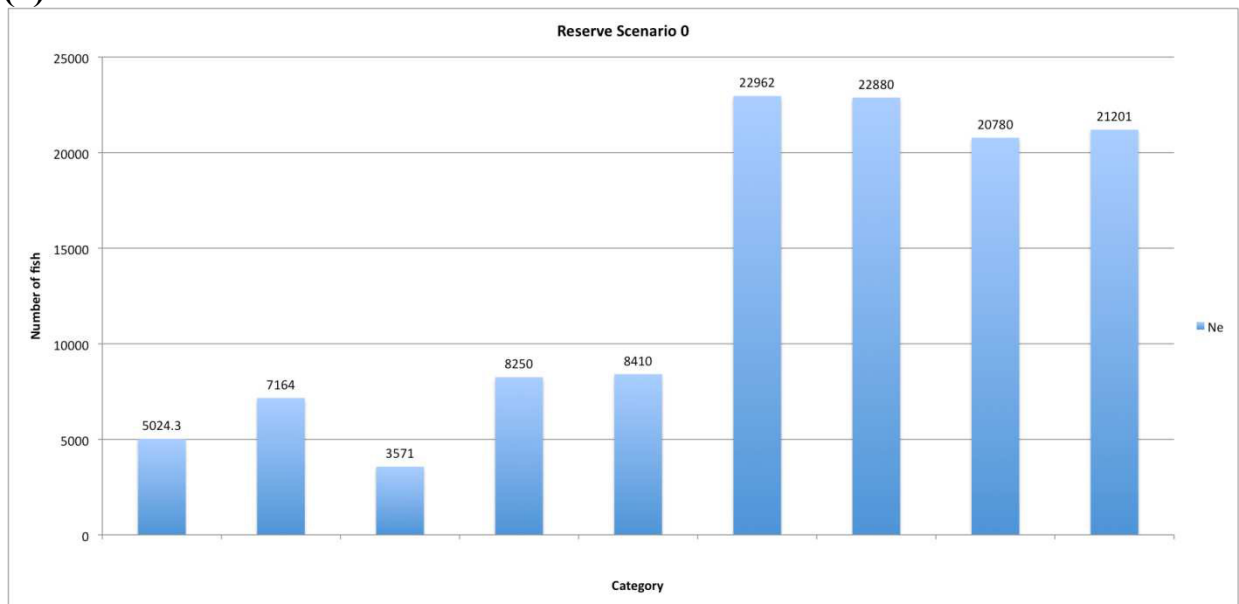
Population size with high fishing ($F=0.5$) and age limit of 4 years at 100 aggregations*
Population size by stage, including total population size and effective population size,
where (a) fertility function is not included, (b) fertility function is included.

*Age Limit of 1 is not pictured here since the population crashed repeatedly and no data could be obtained for this scenario.

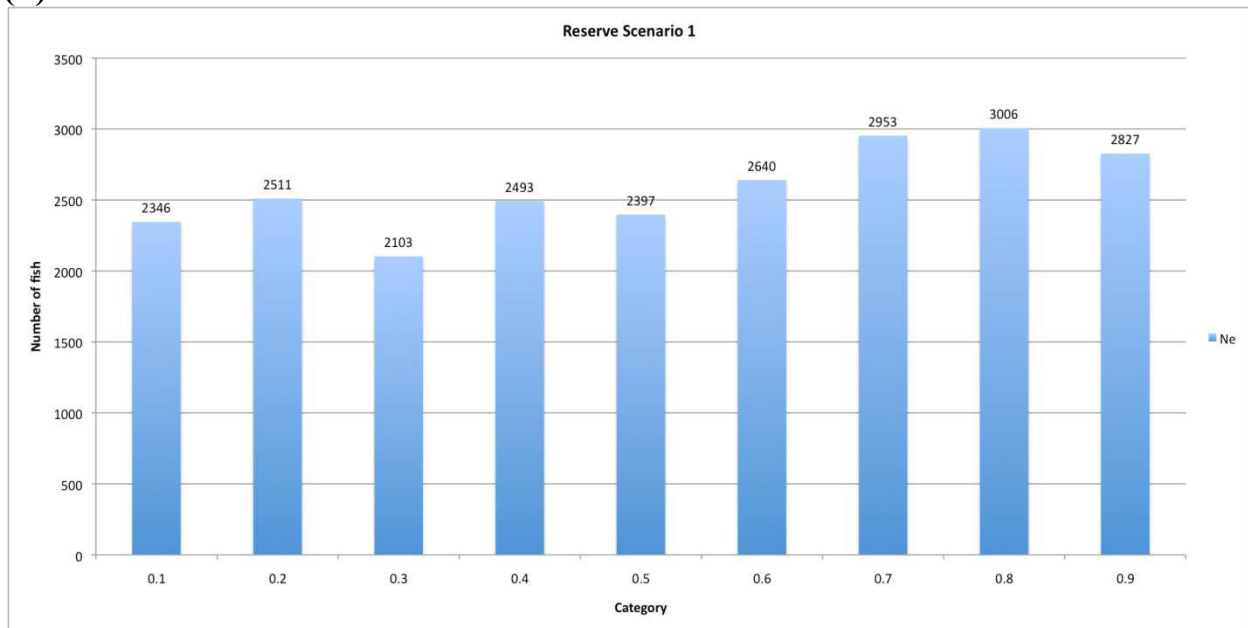
Reserves

Population size is graphed by stage in each reserve figure, including total population size and effective population size, for varying levels of protection, where (a) implements Reserve Scenario 0, or protection of the entire model space, (b) implements Reserve Scenario 1, or protection of the aggregation habitat of the model space, (c) implements Reserve Scenario 2, or protection of the offshore reef habitat of the model space, (d) implements Reserve Scenario 3, or protection of the nearshore reef habitat of the model space, and (e) implements Reserve Scenario 4, or protection of the seagrass bed habitat of the model space.

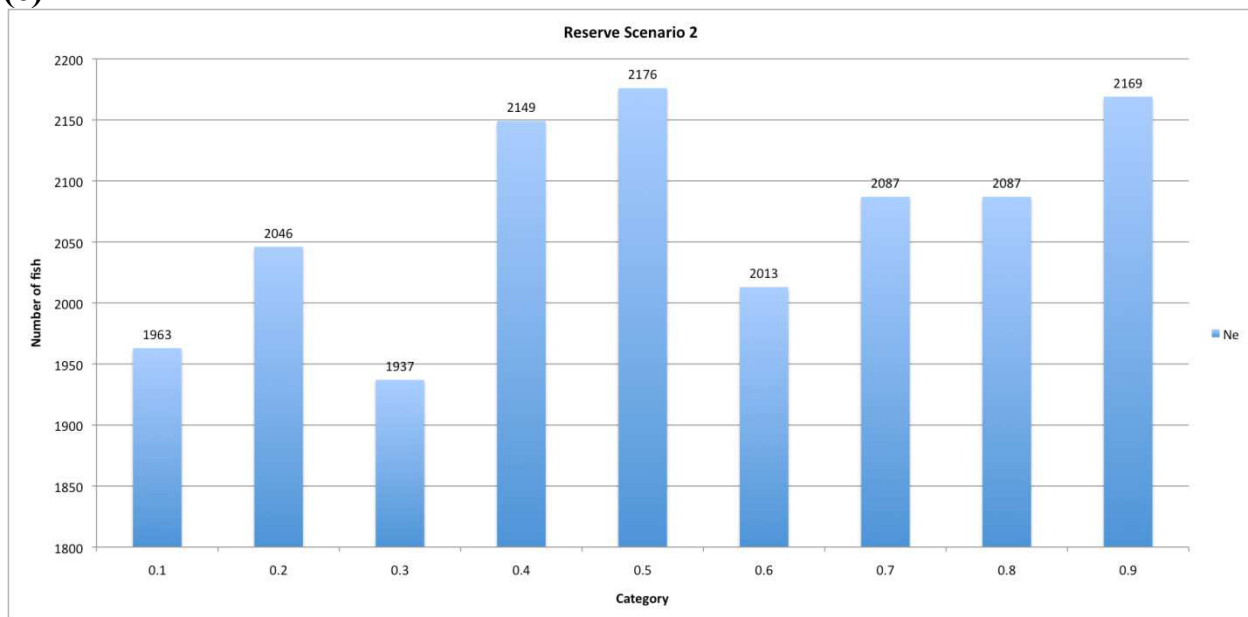
(a)



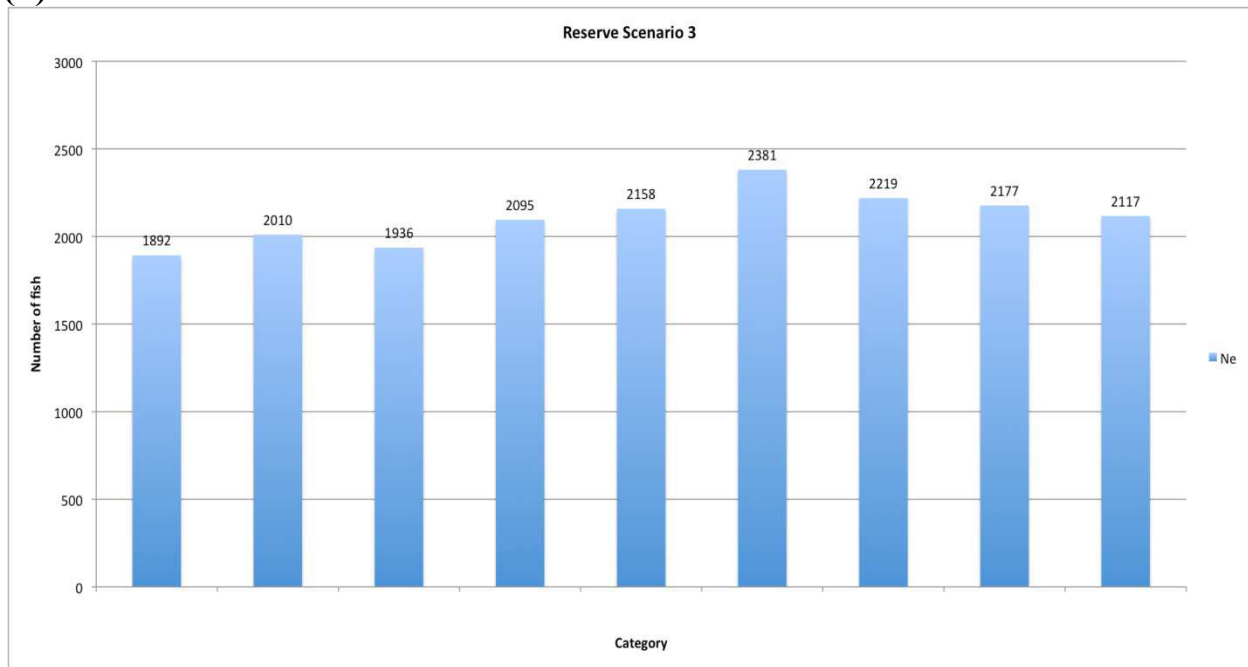
(b)



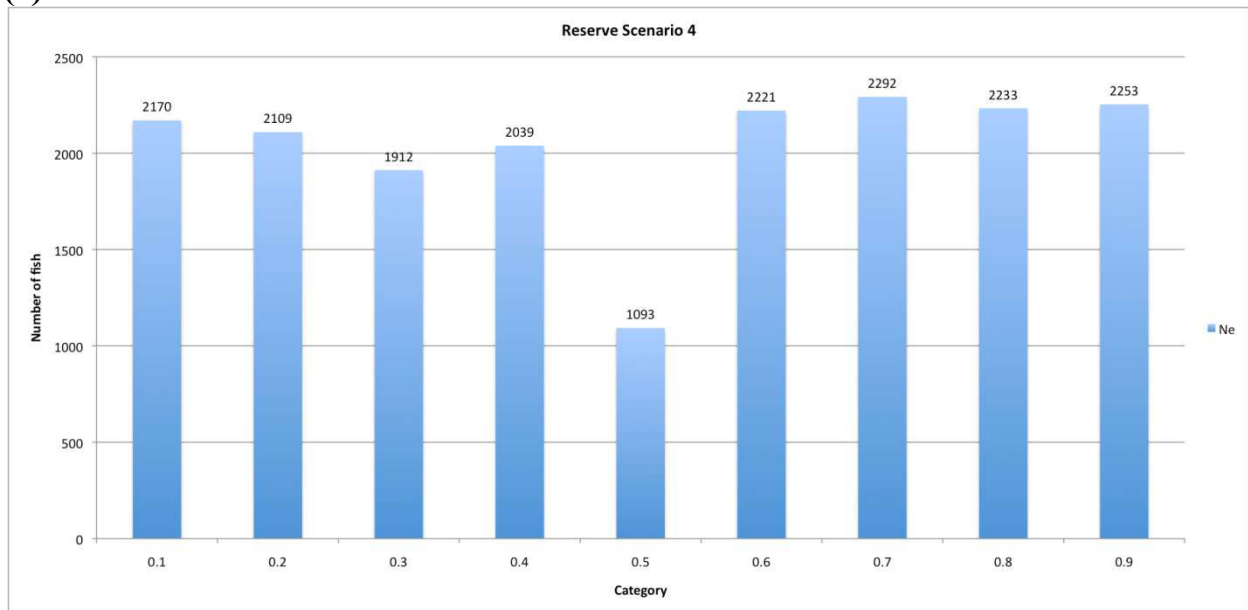
(c)



(d)

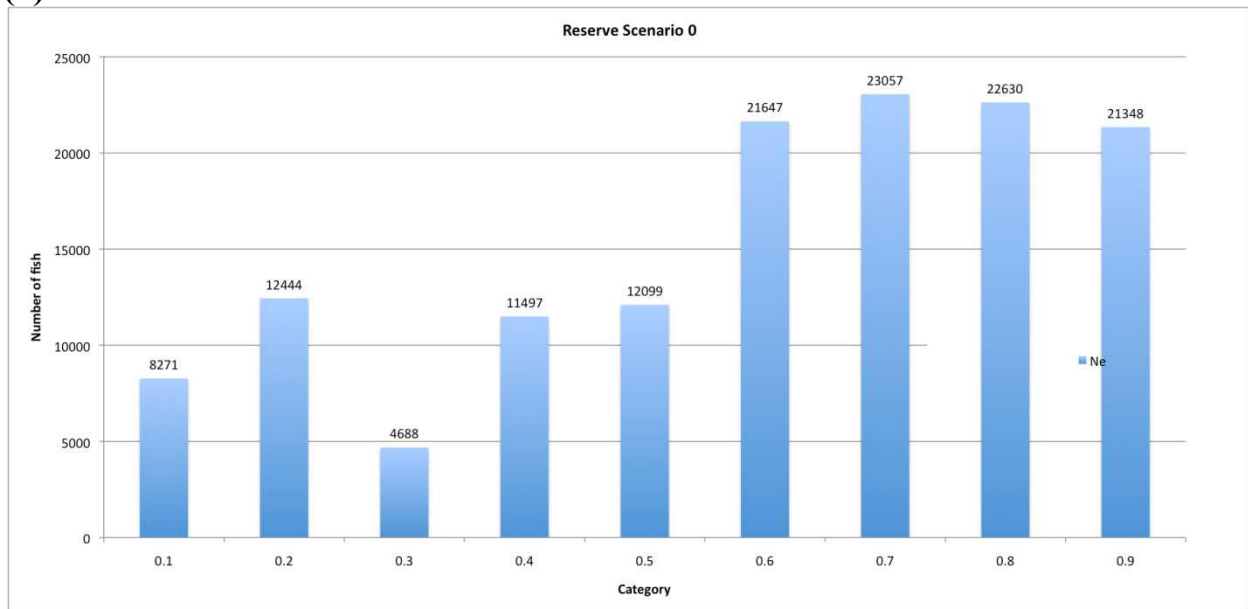


(e)

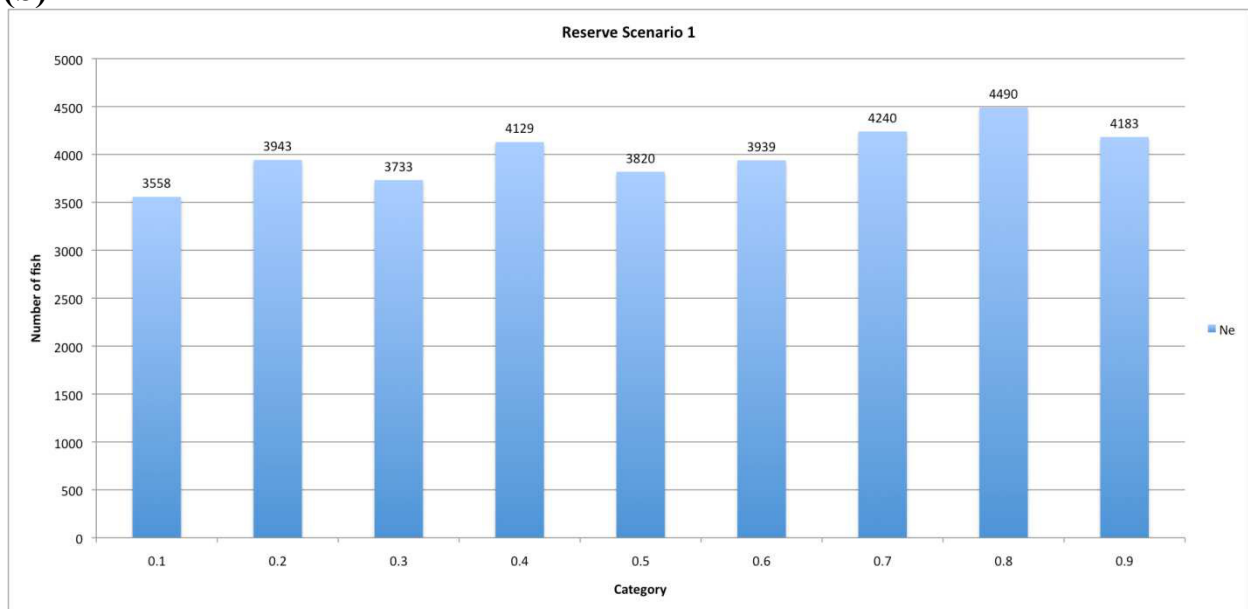


Population size with reserves and low fishing ($F=0.25$), and age limit of 1 year at 10 aggregations

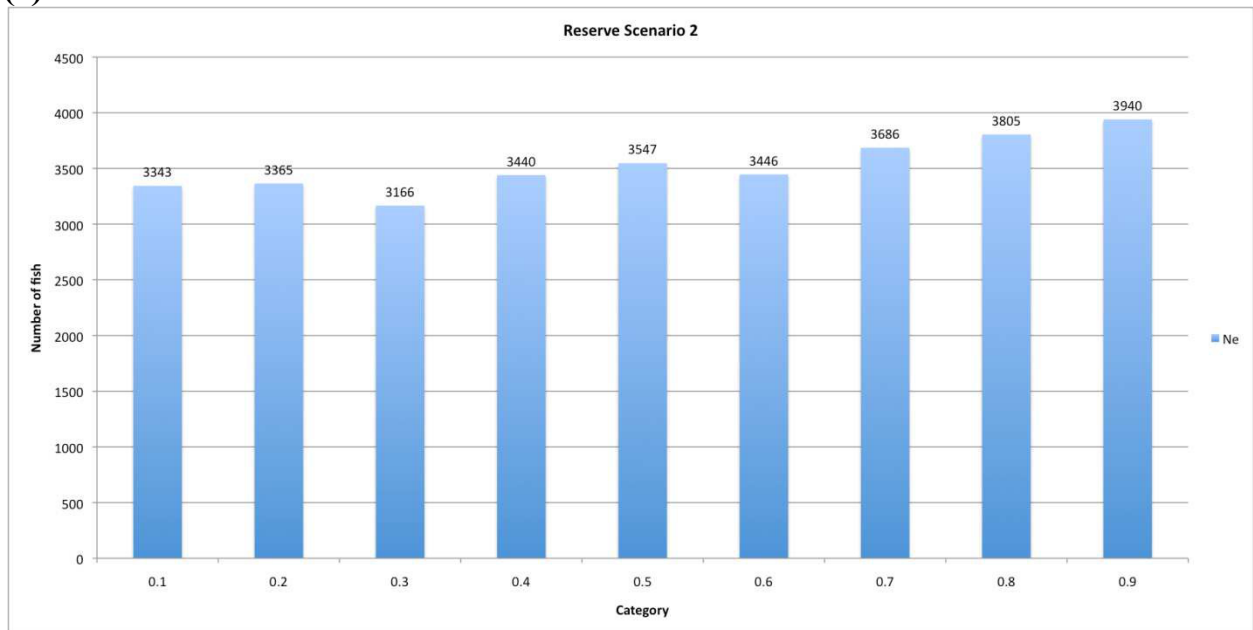
(a)



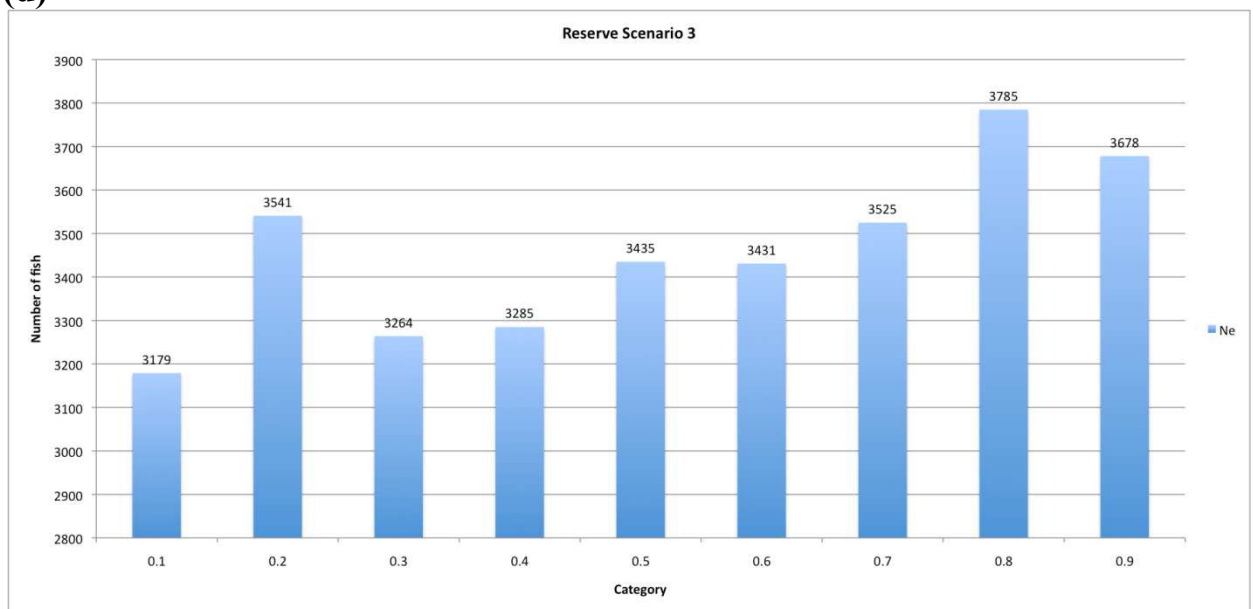
(b)



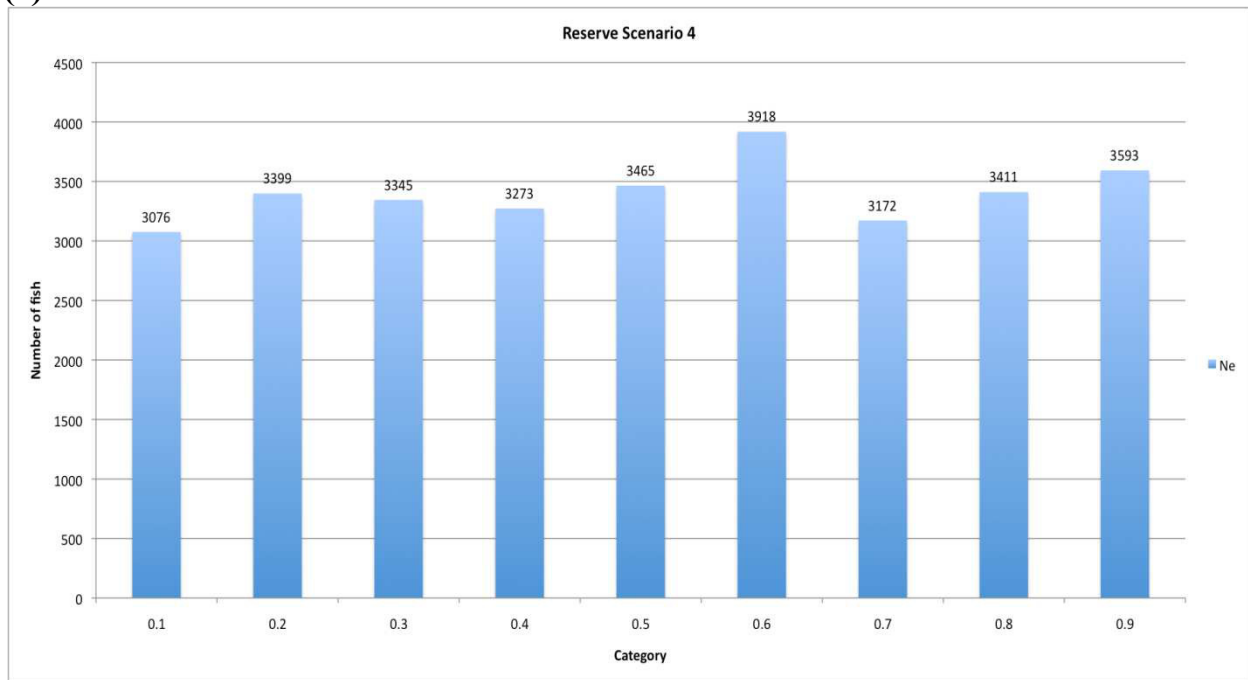
(c)



(d)

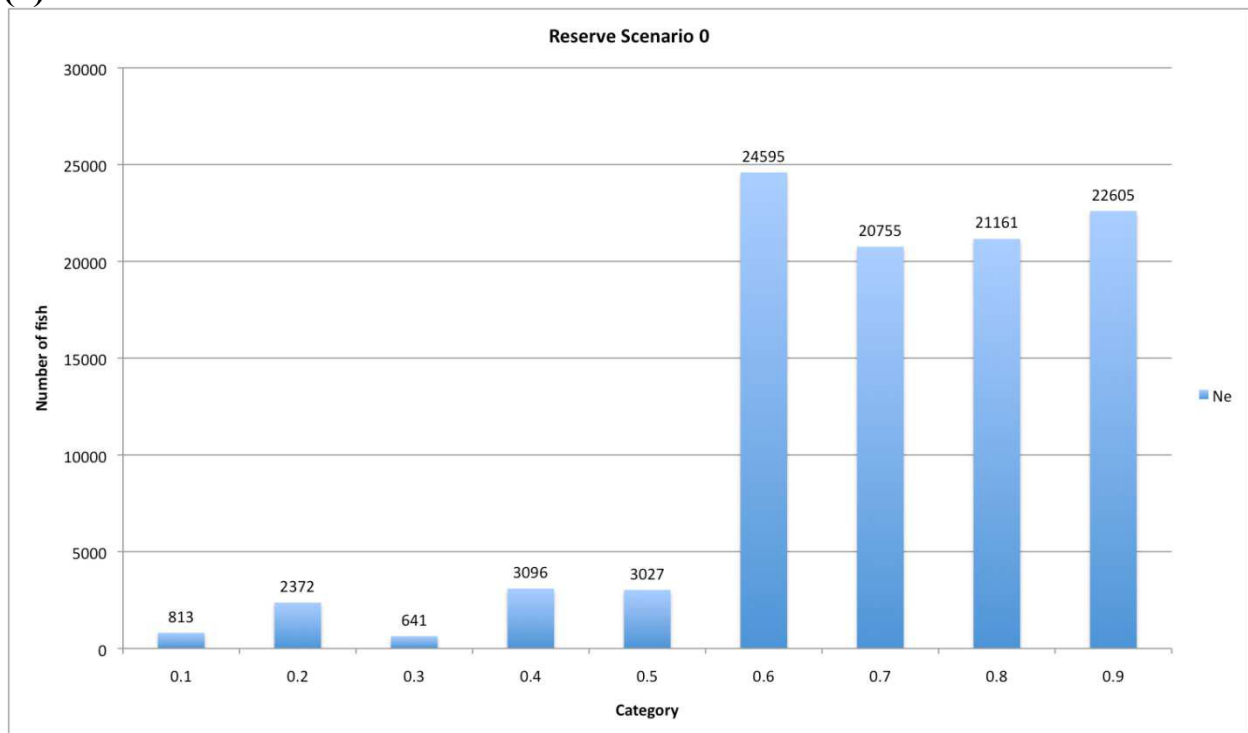


(e)

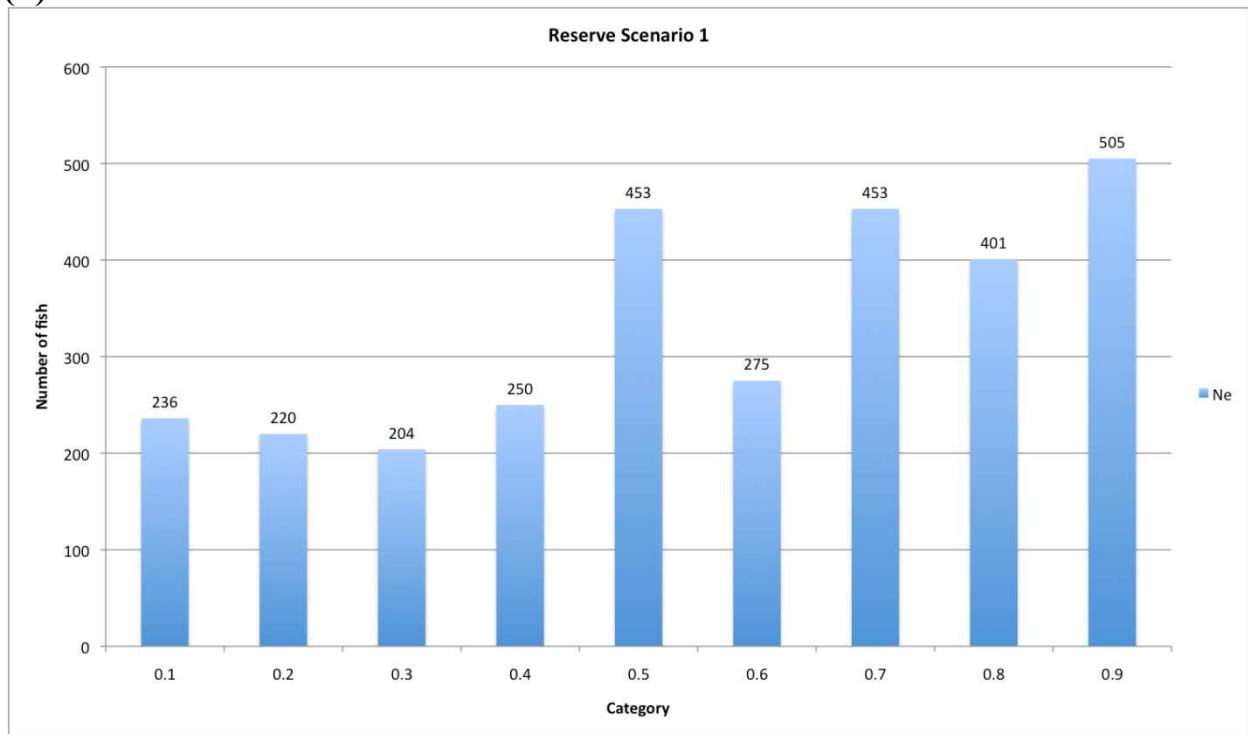


Population size with reserves and low fishing ($F=0.25$), and age limit of 4 years at 10 aggregations

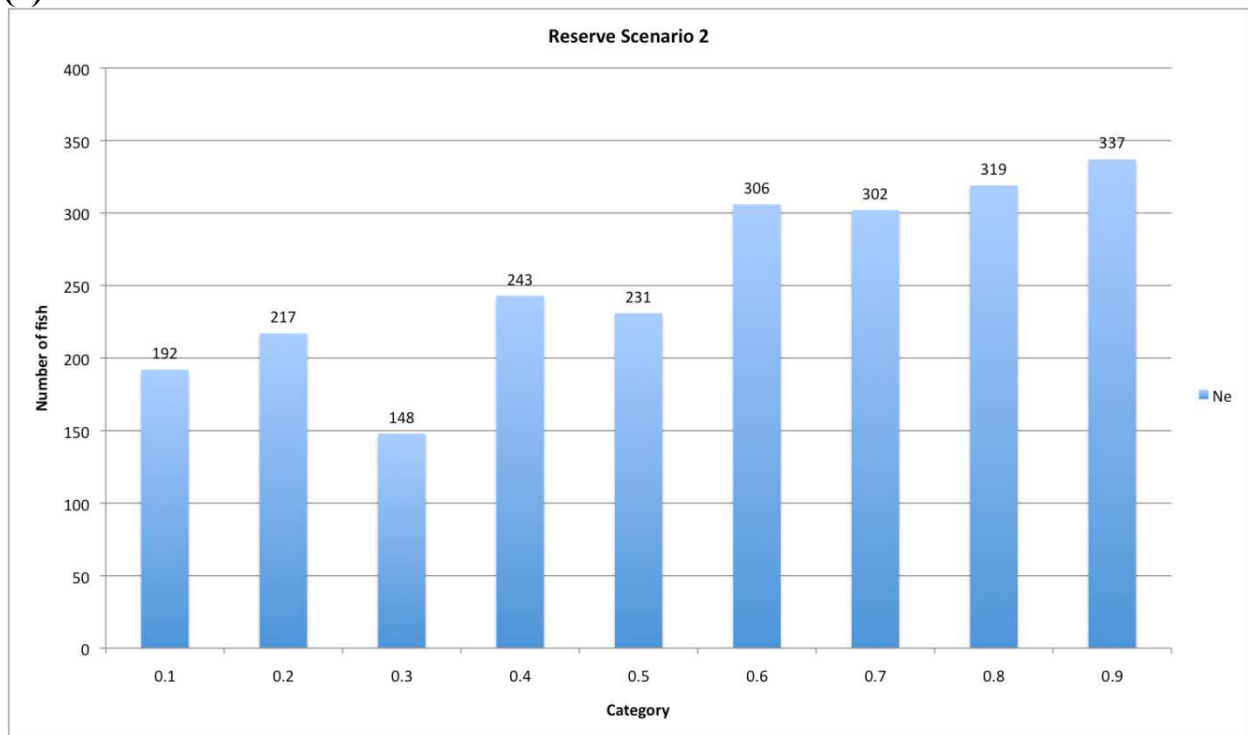
(a)



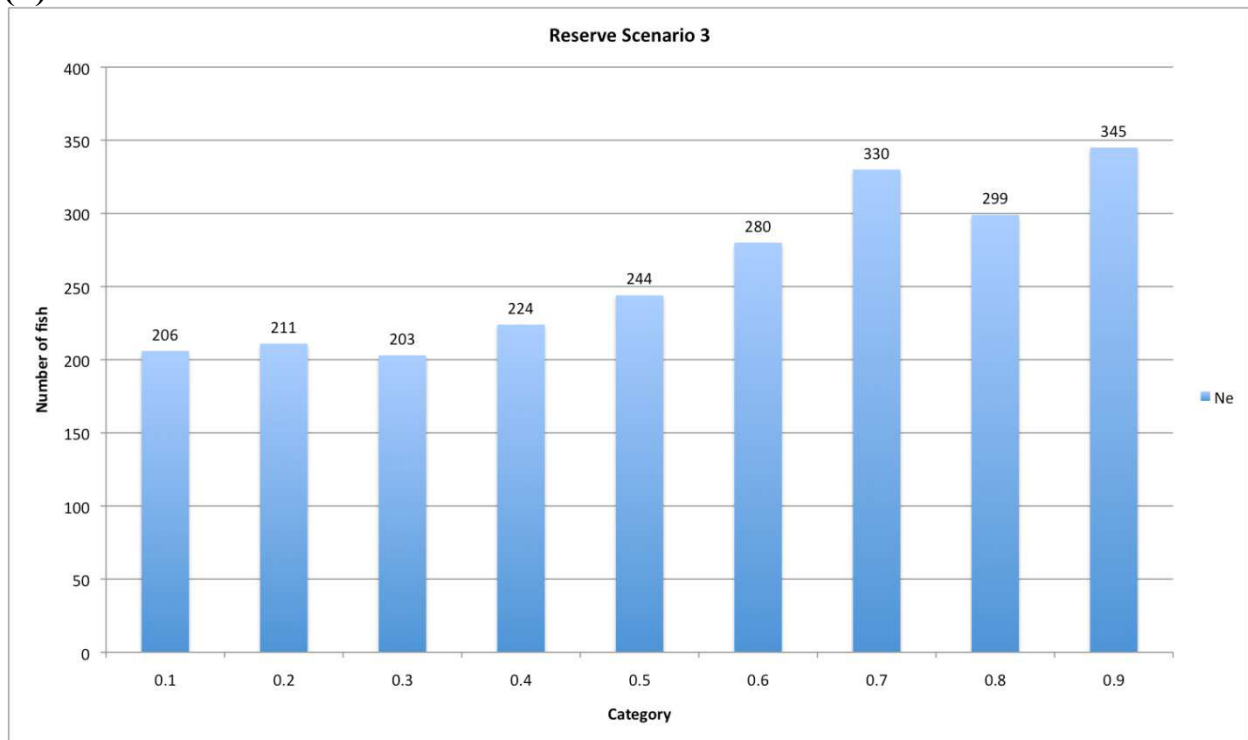
(b)



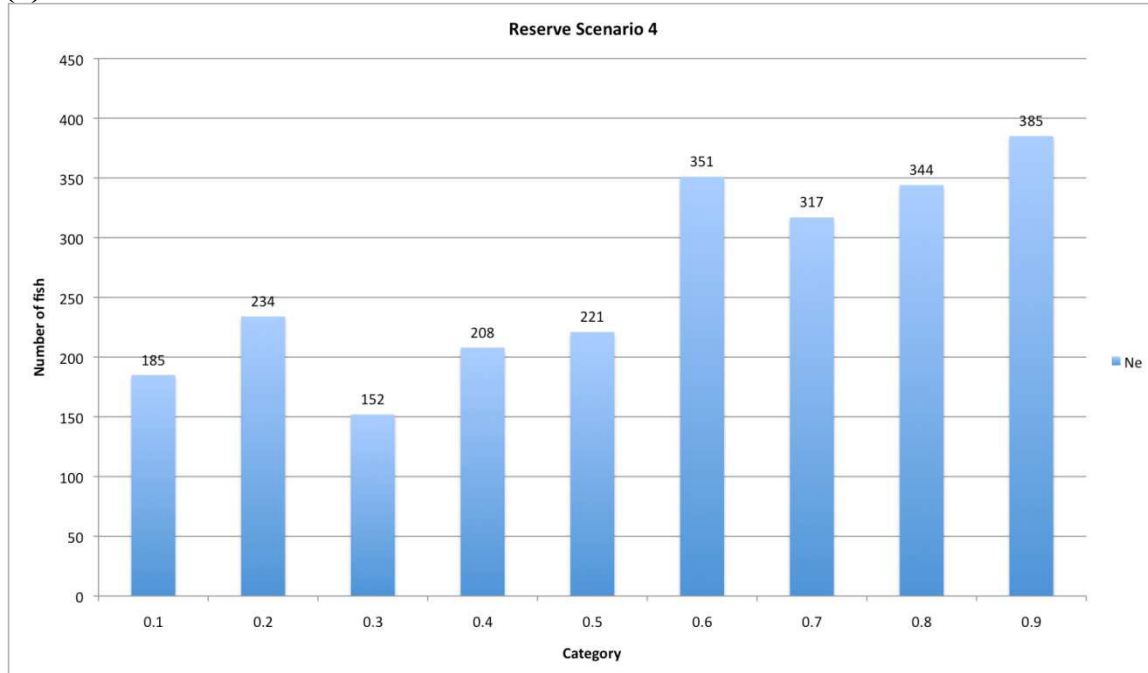
(c)



(d)

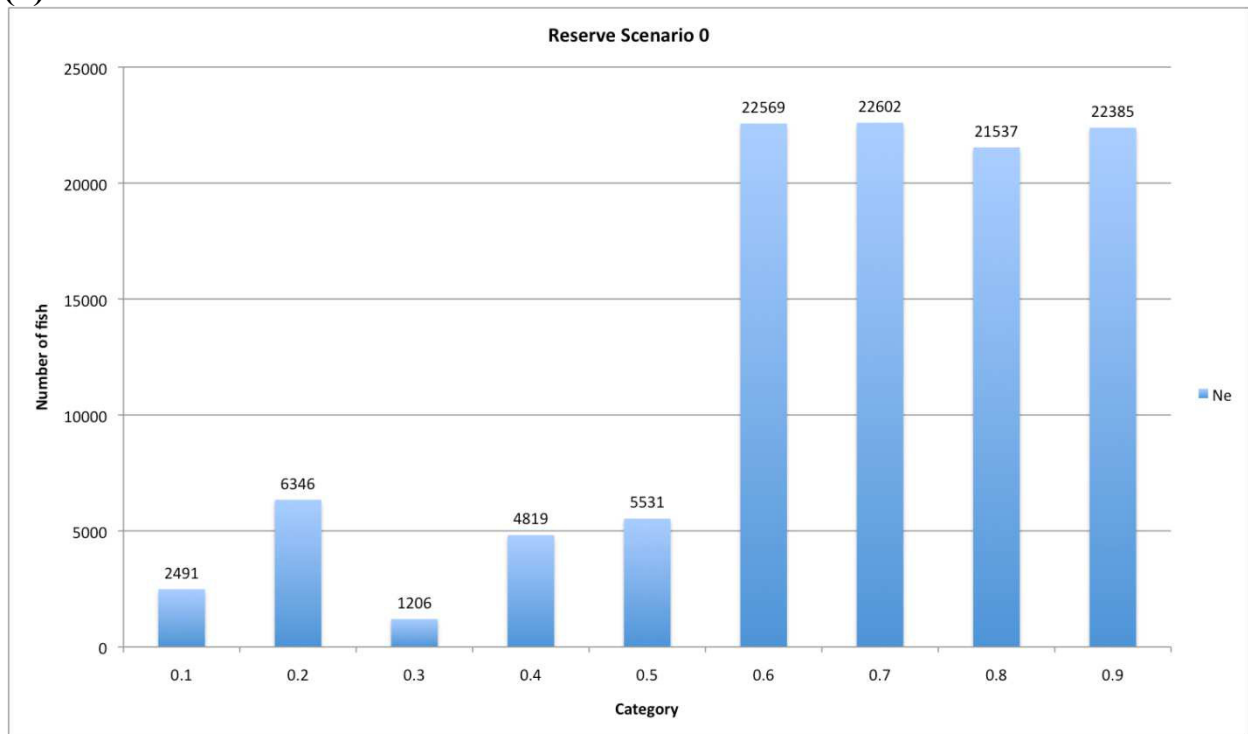


(e)

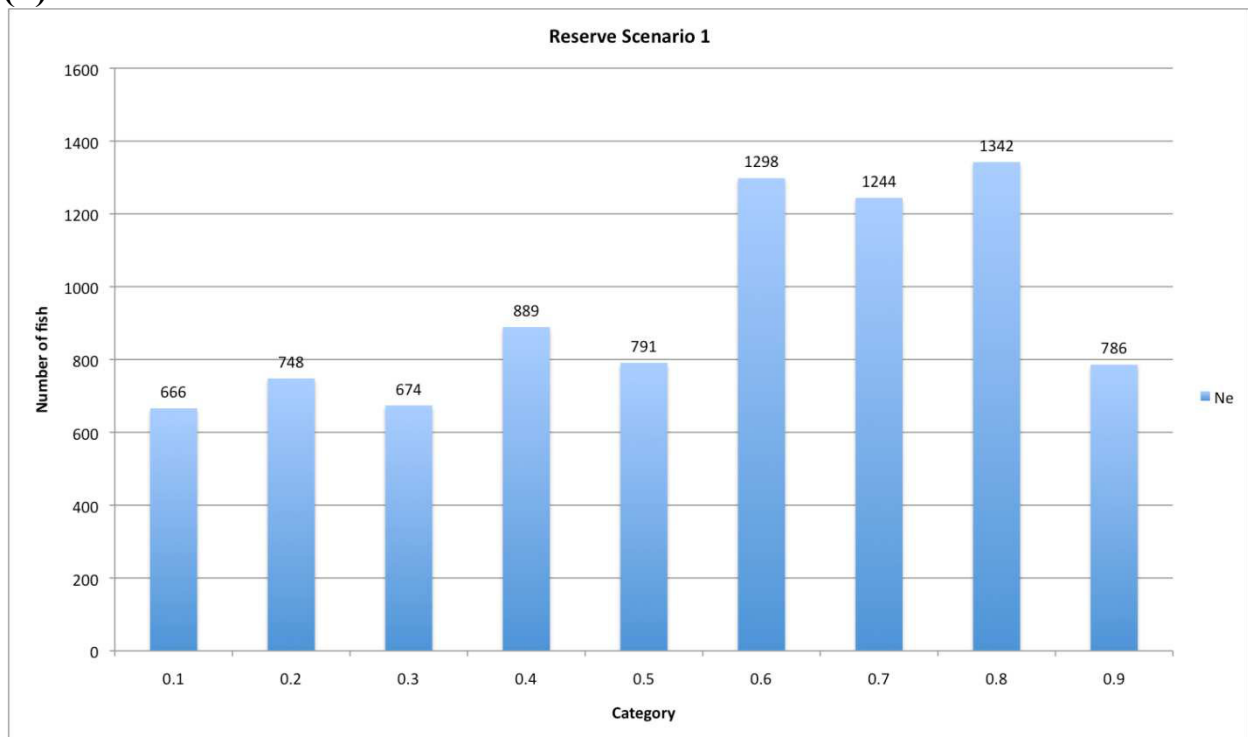


Population size with reserves and high fishing ($F=0.5$), and age limit of 1 year at 10 aggregations

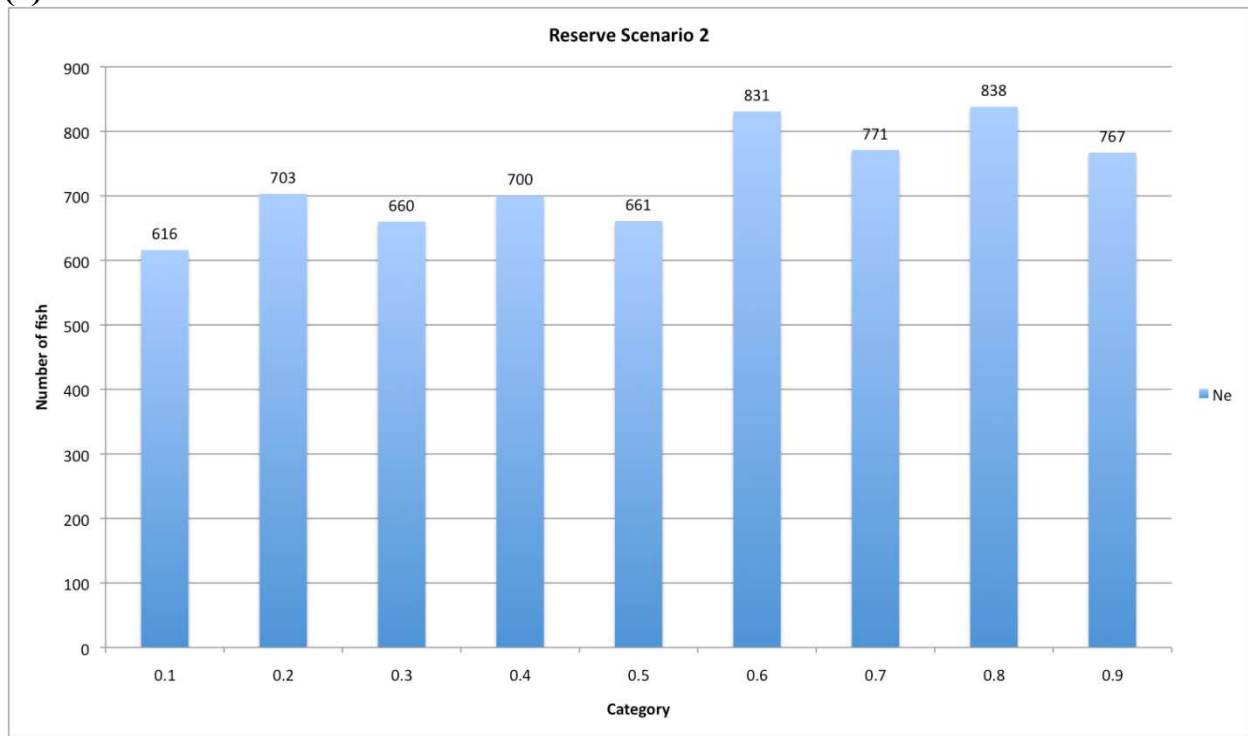
(a)



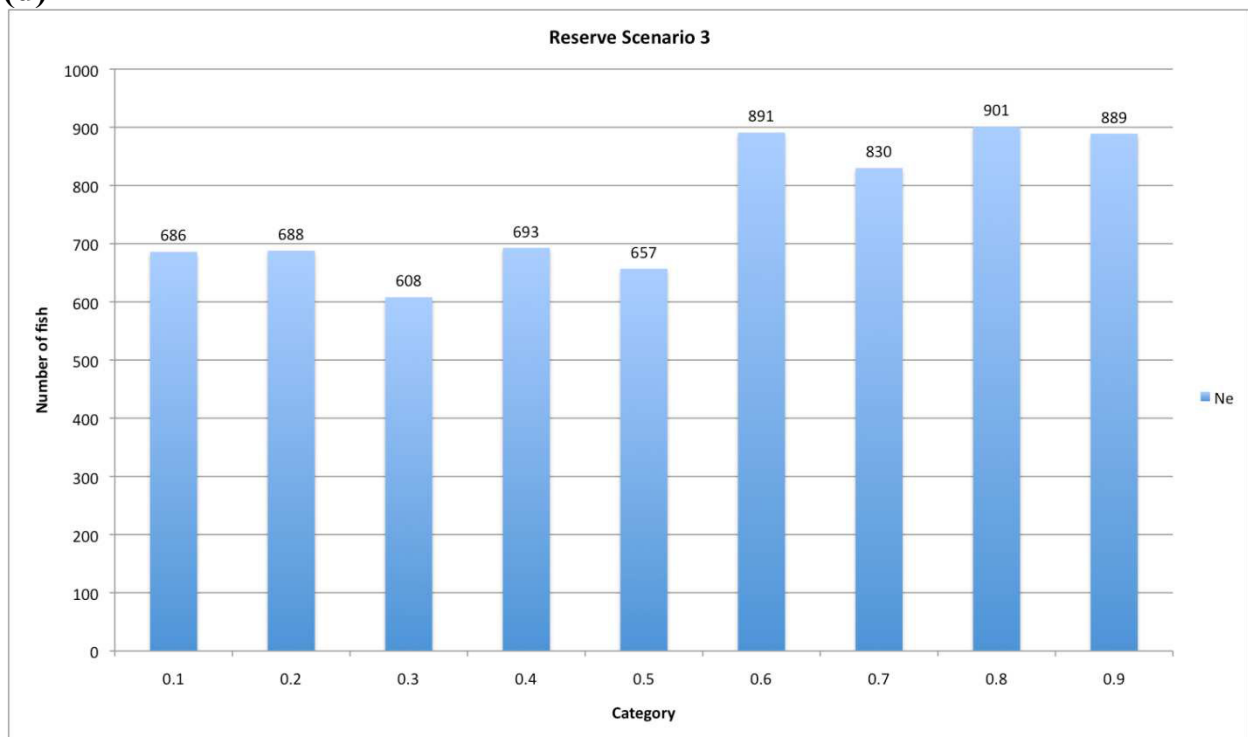
(b)



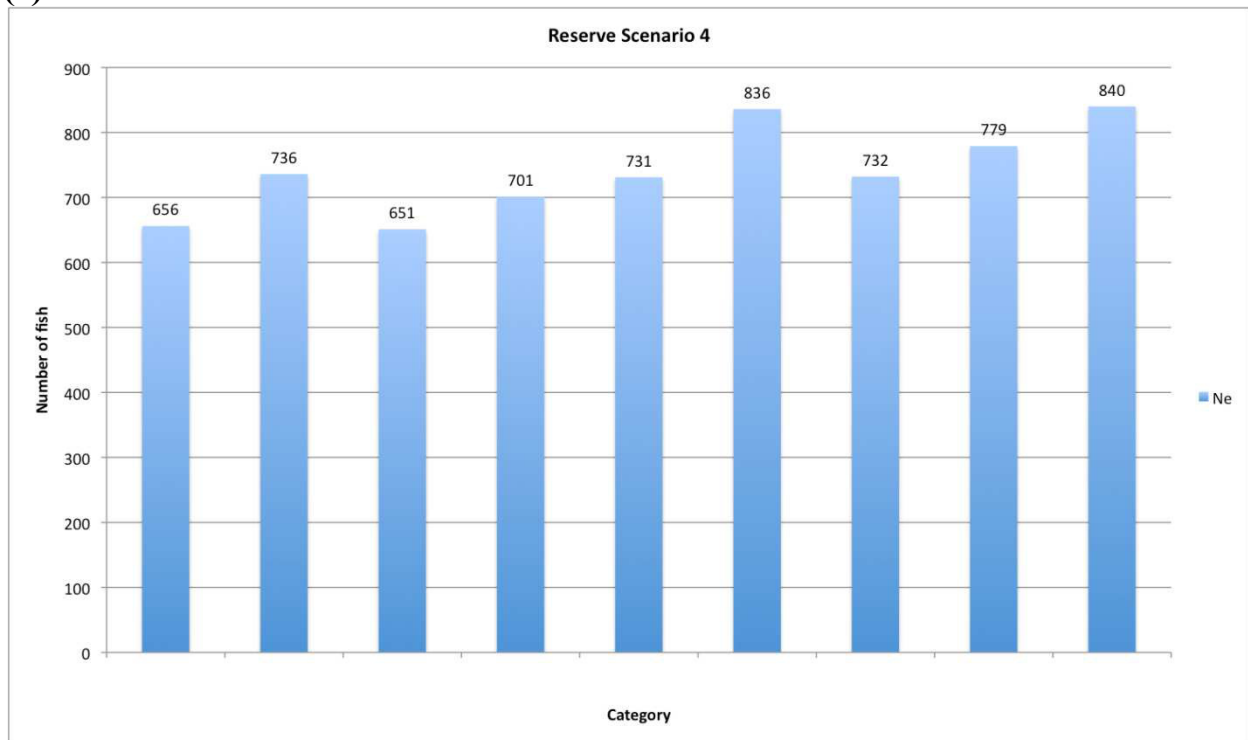
(c)



(d)

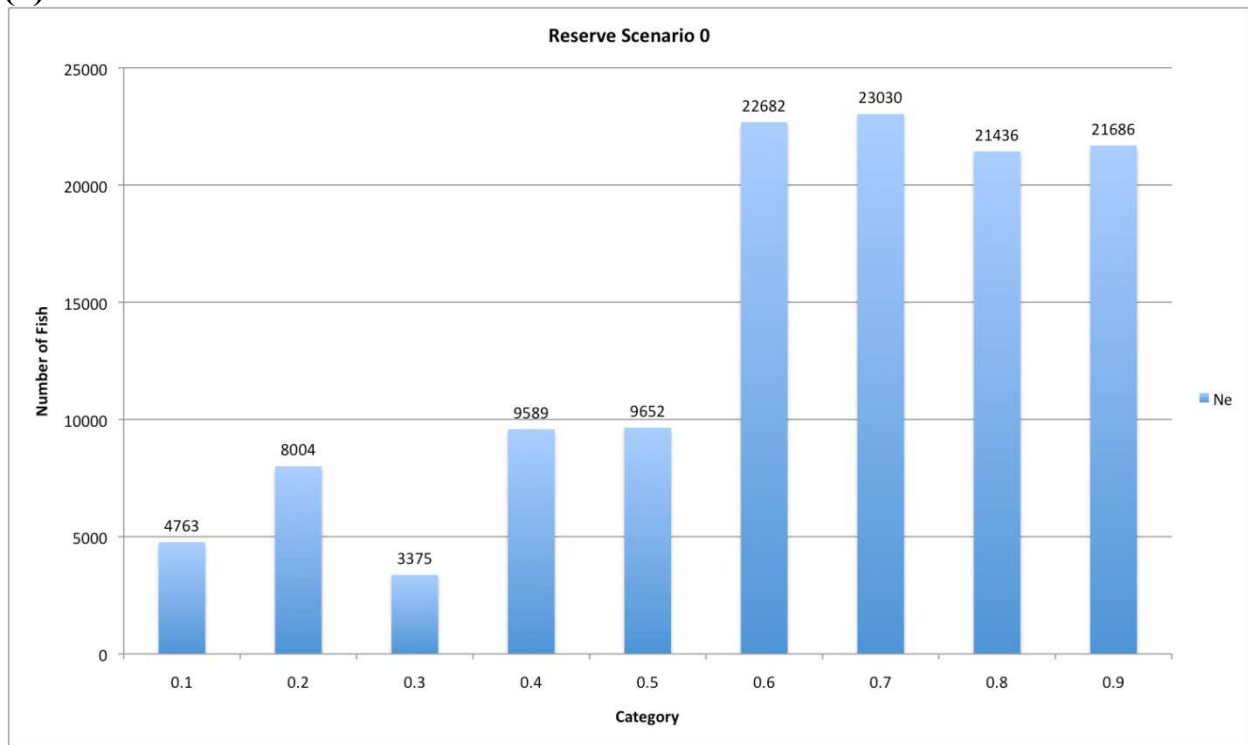


(e)

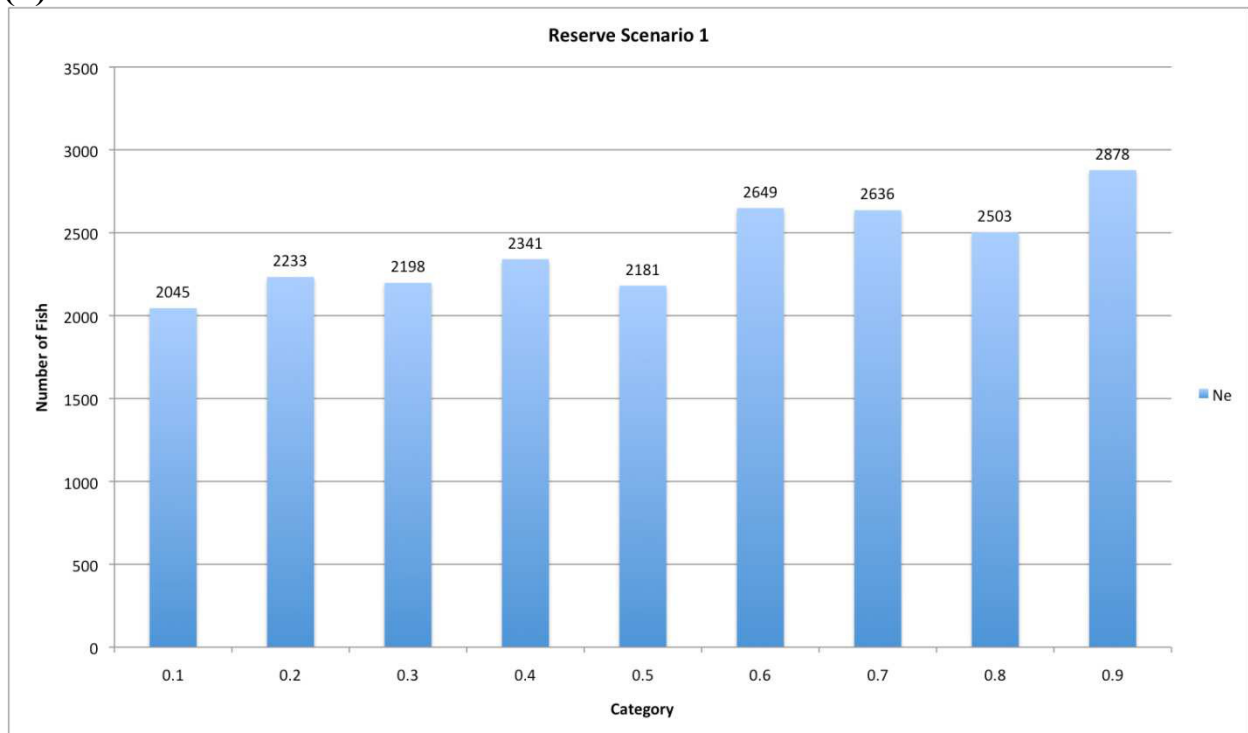


Population size with reserves and high fishing ($F=0.5$), and age limit of 4 years at 10 aggregations

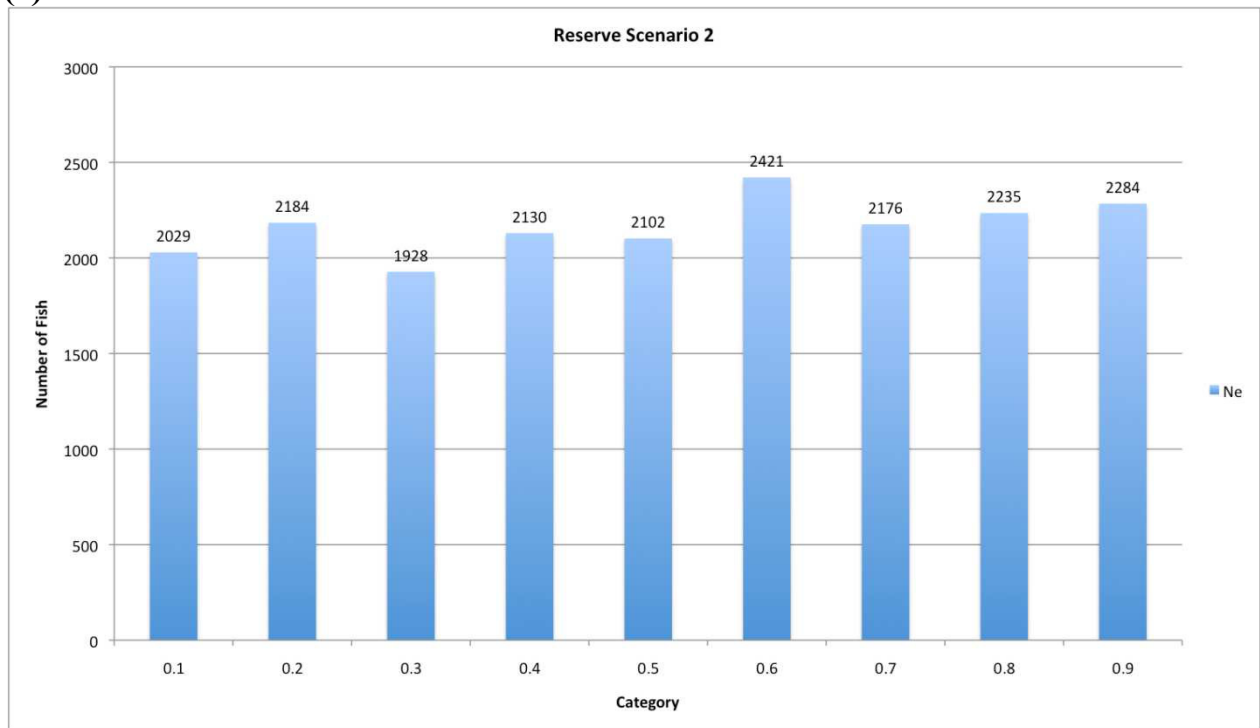
(a)



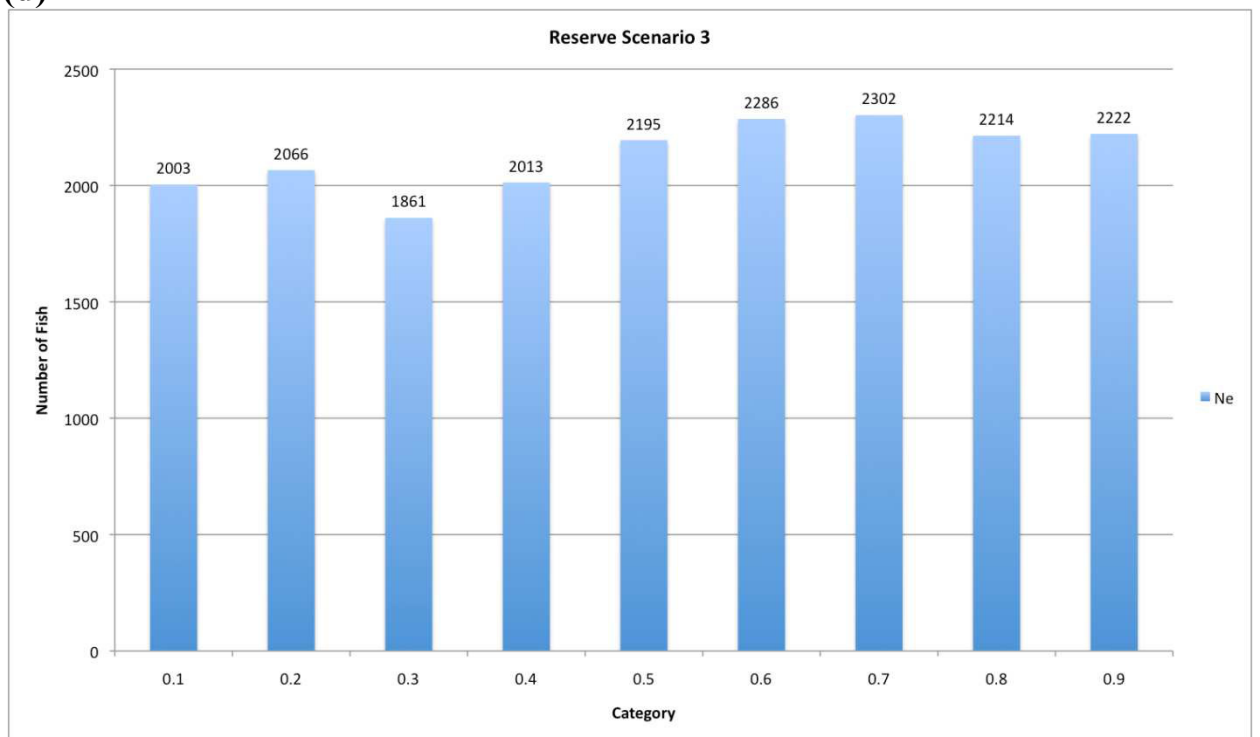
(b)



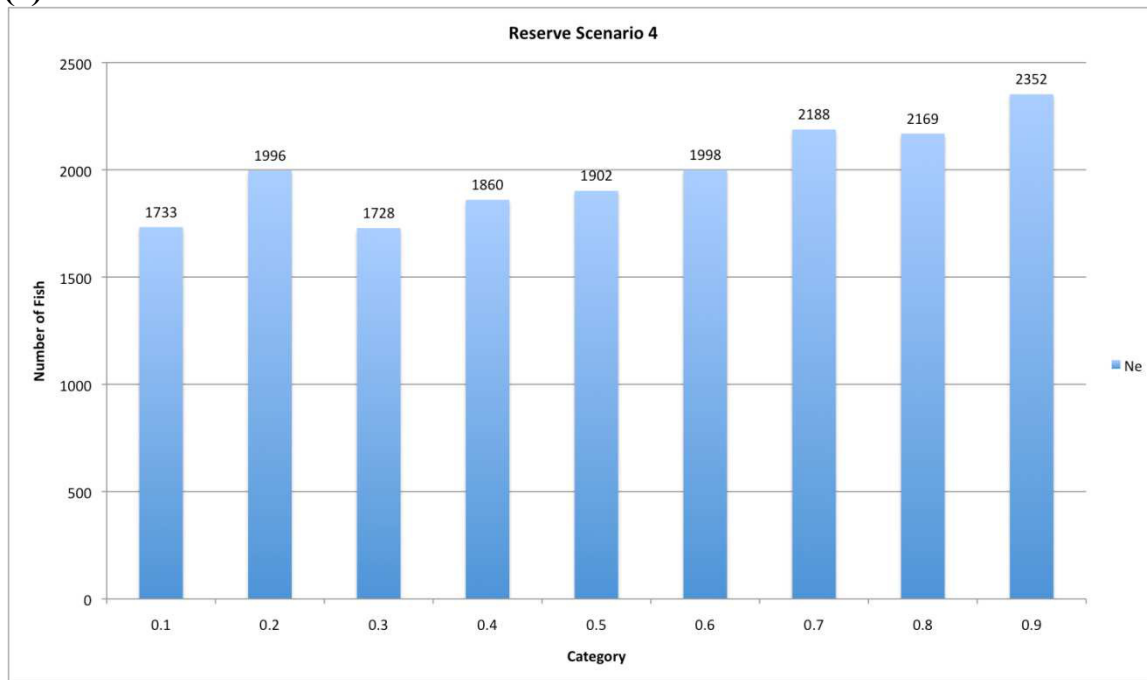
(c)



(d)

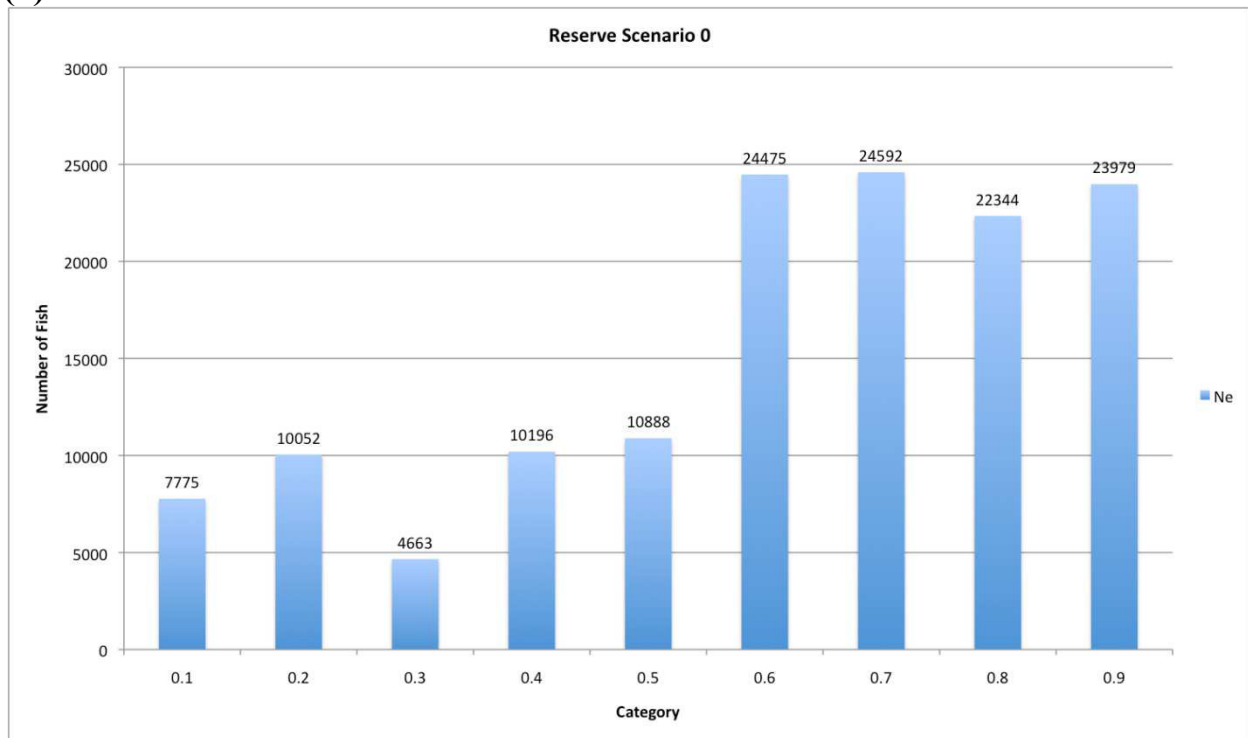


(e)

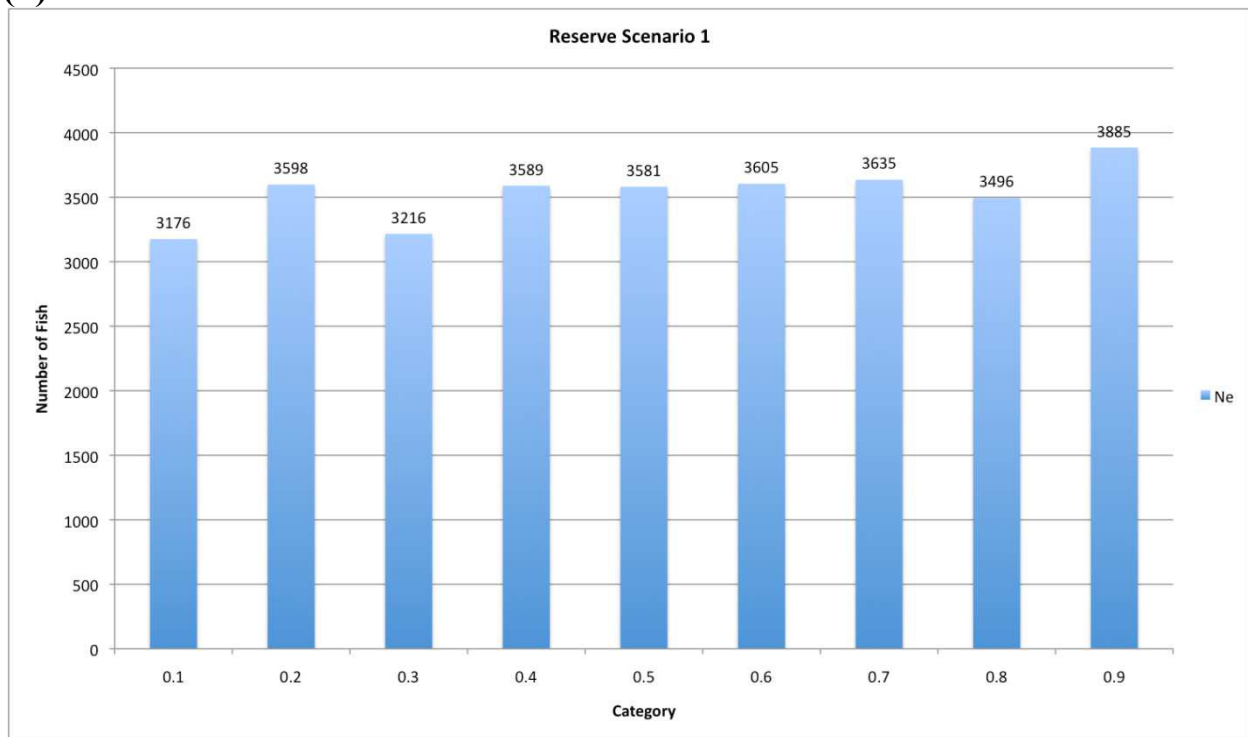


Population size with reserves and low fishing ($F=0.25$), and age limit of 1 year at 50 aggregations

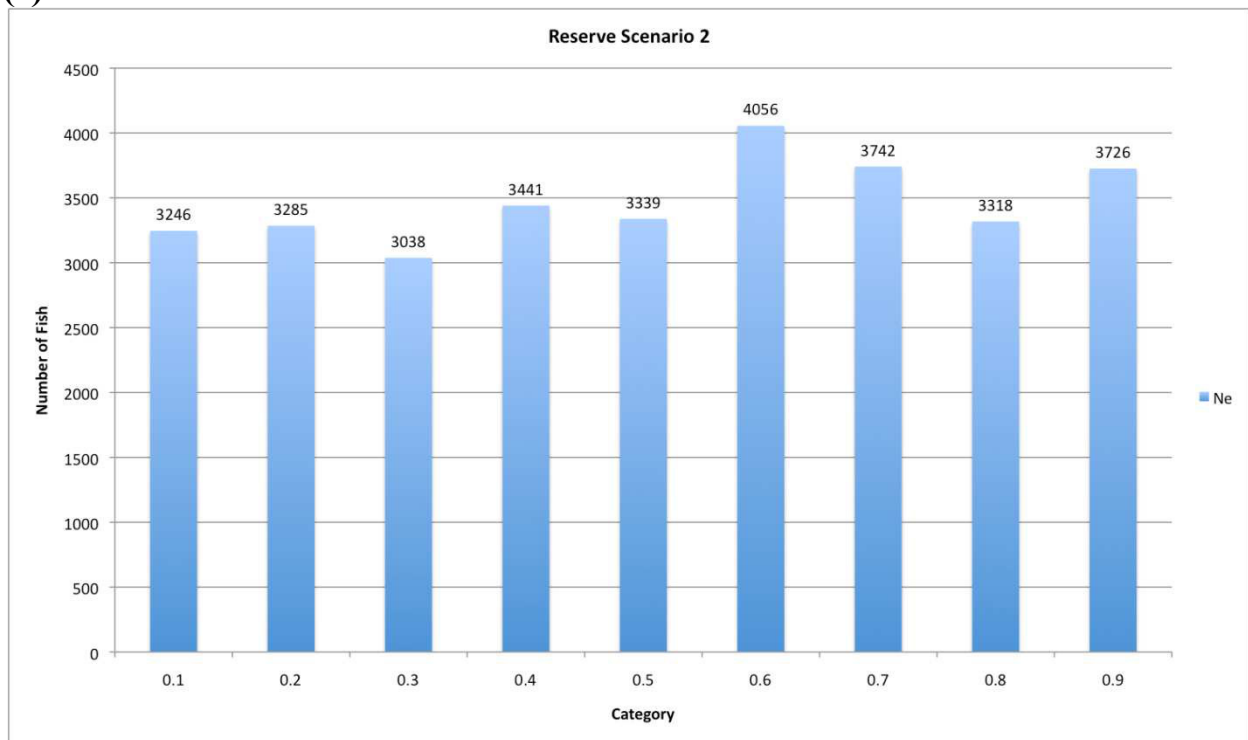
(a)



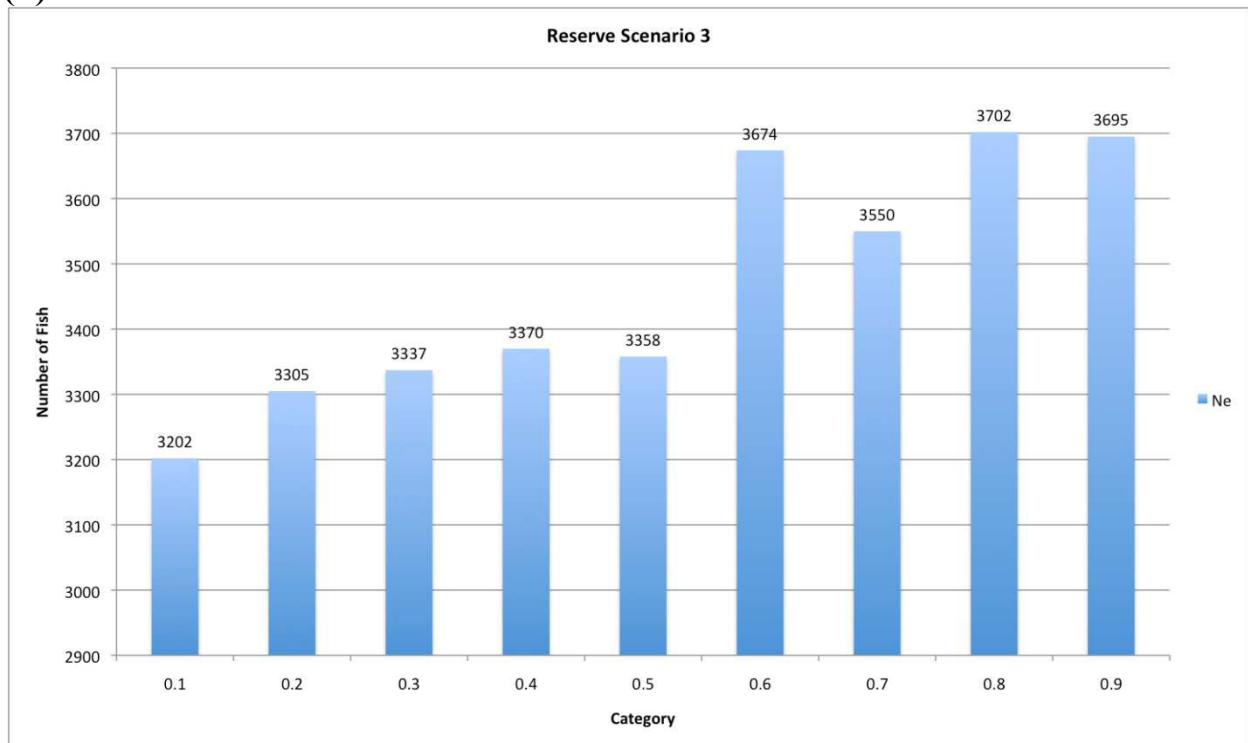
(b)



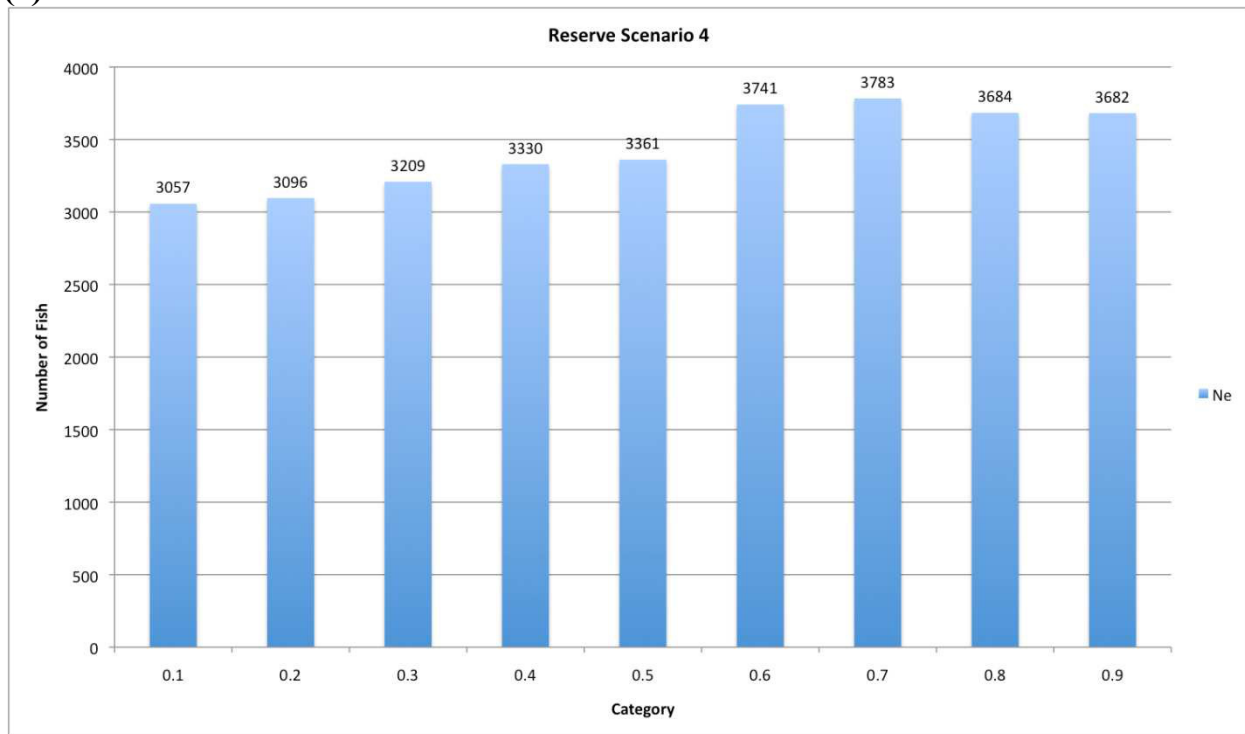
(c)



(d)

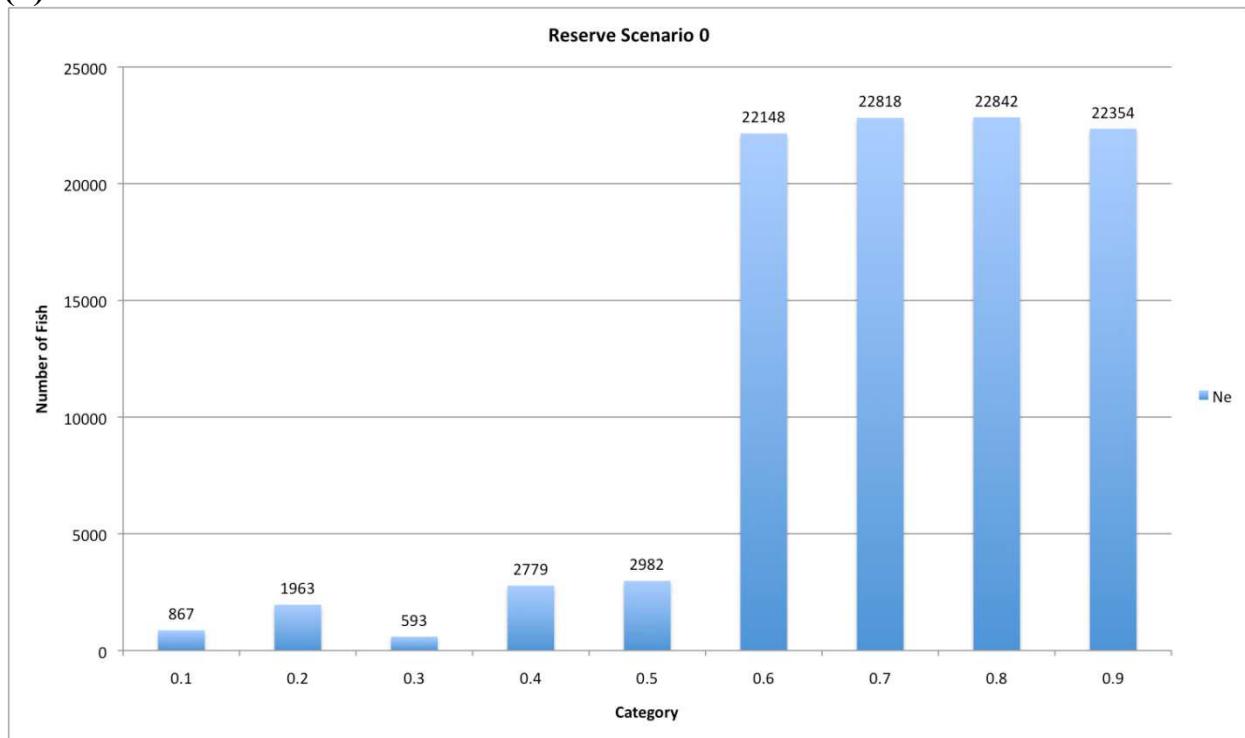


(e)

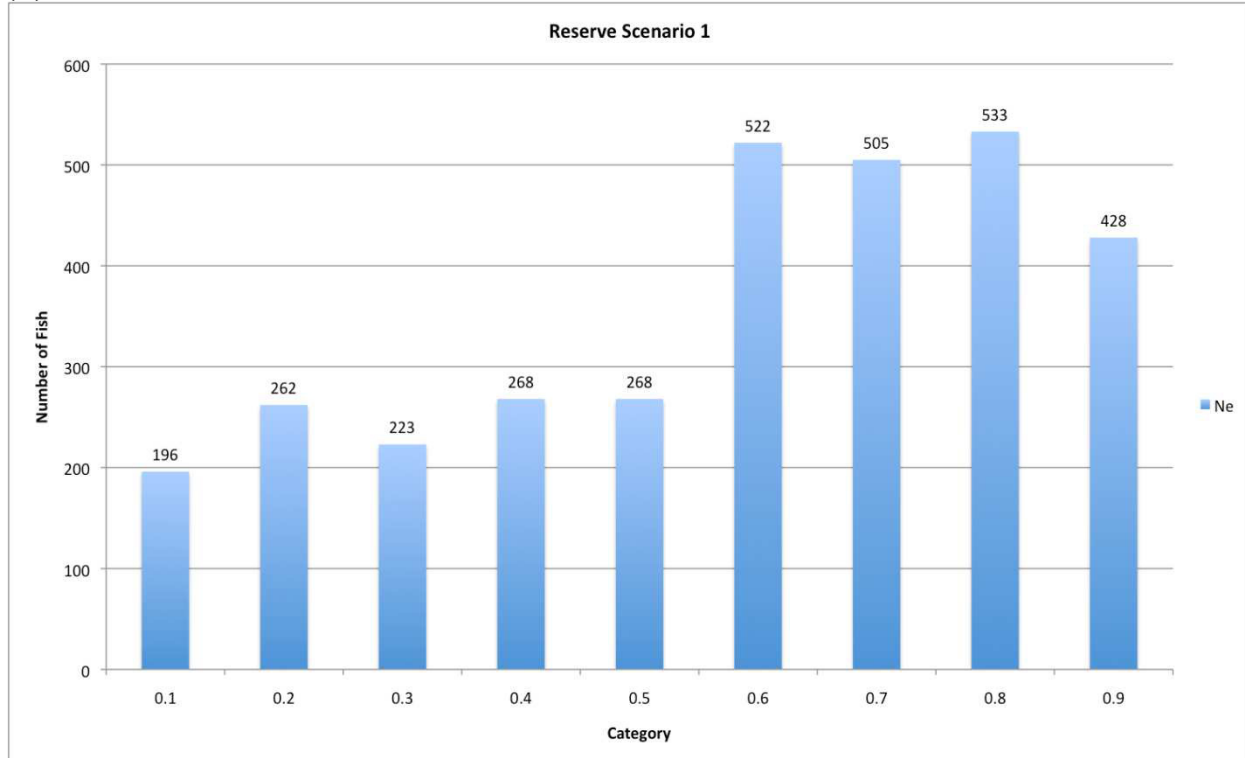


Population size with reserves and low fishing ($F=0.25$), and age limit of 4 years at 50 aggregations

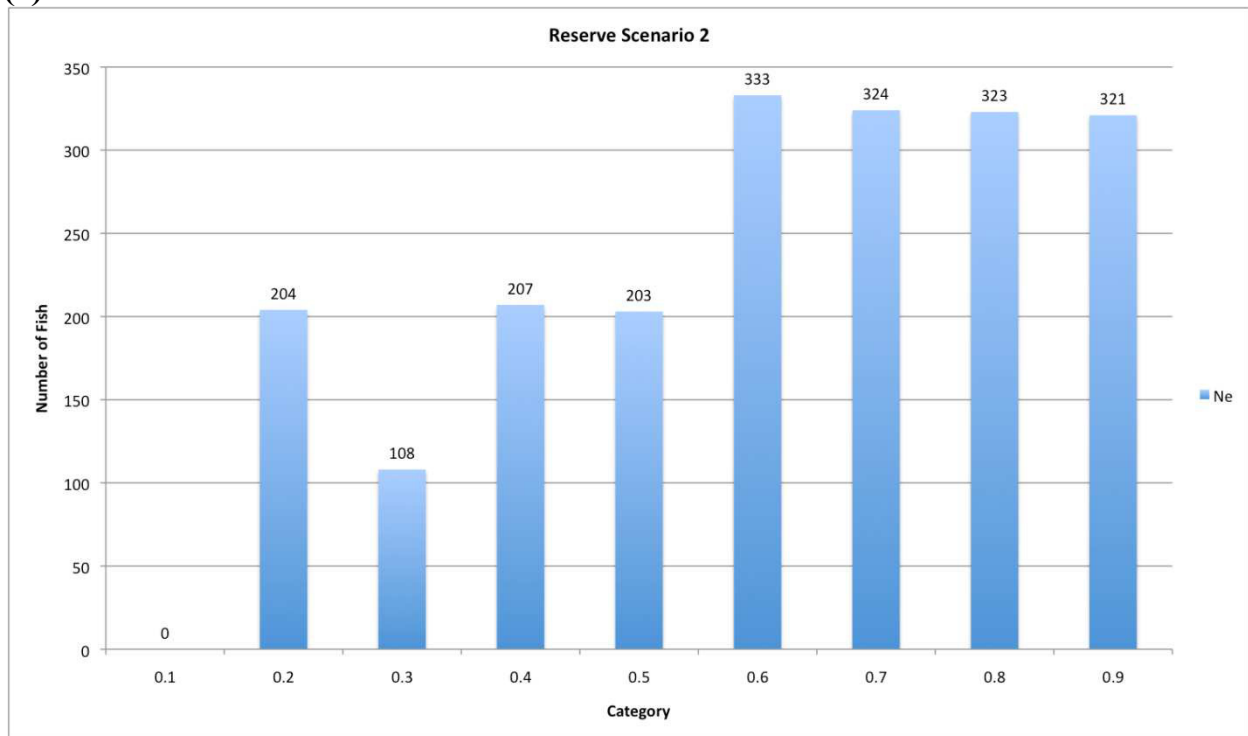
(a)



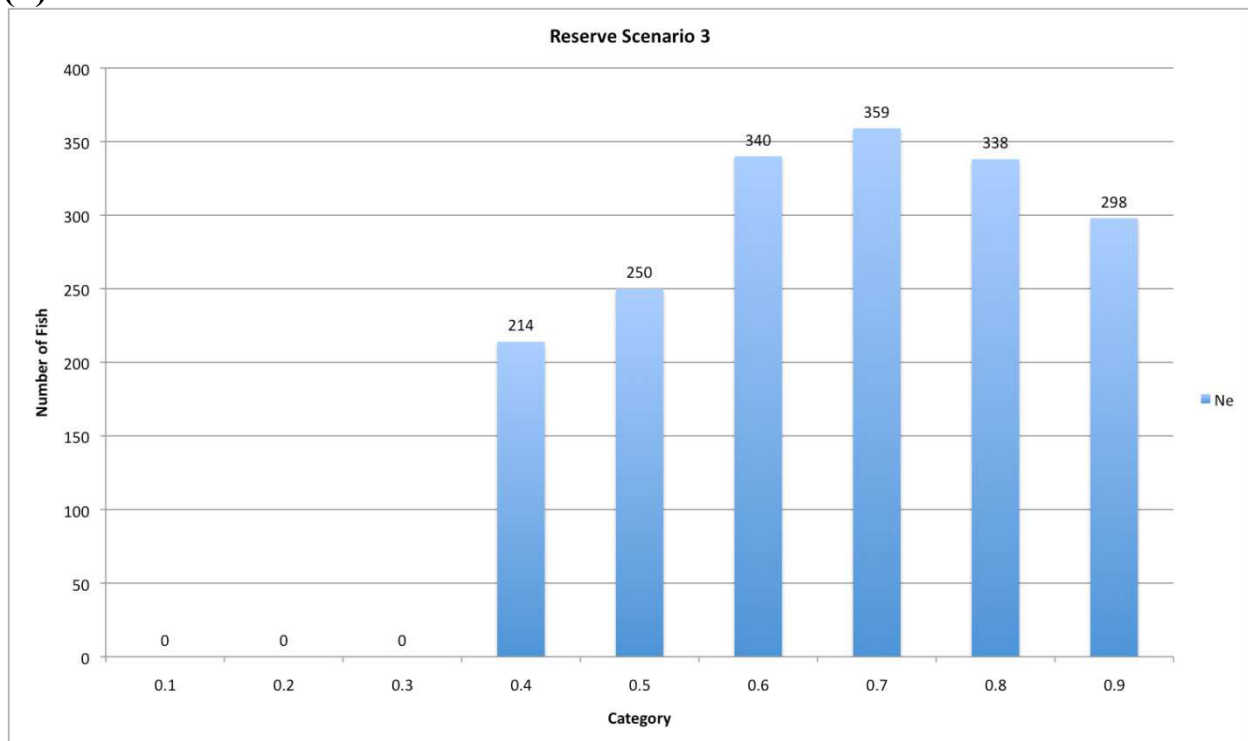
(b)



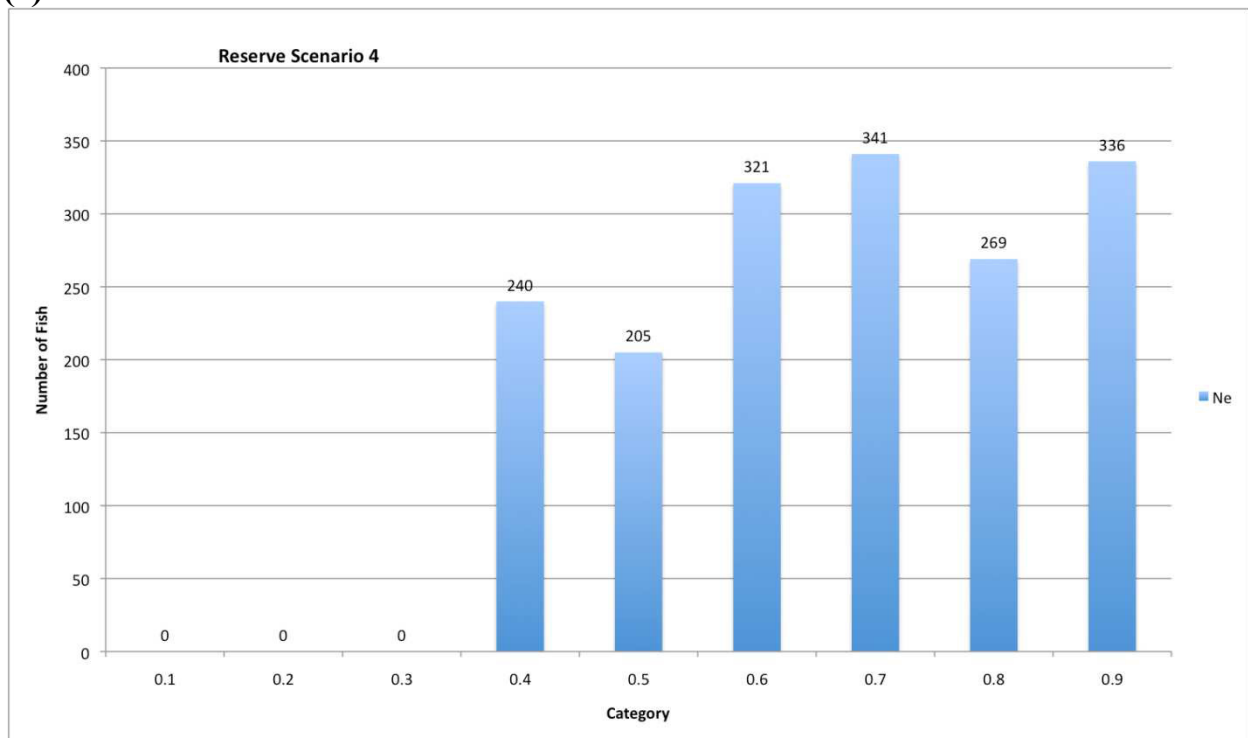
(c)



(d)

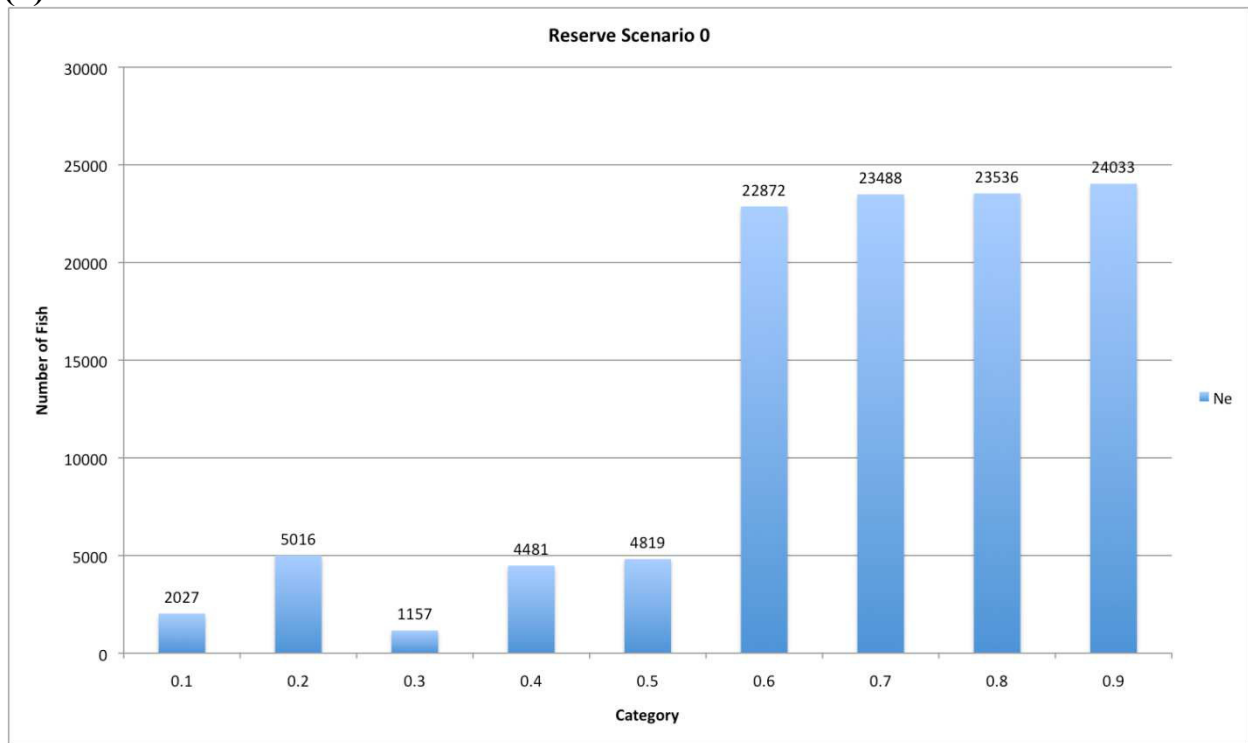


(e)

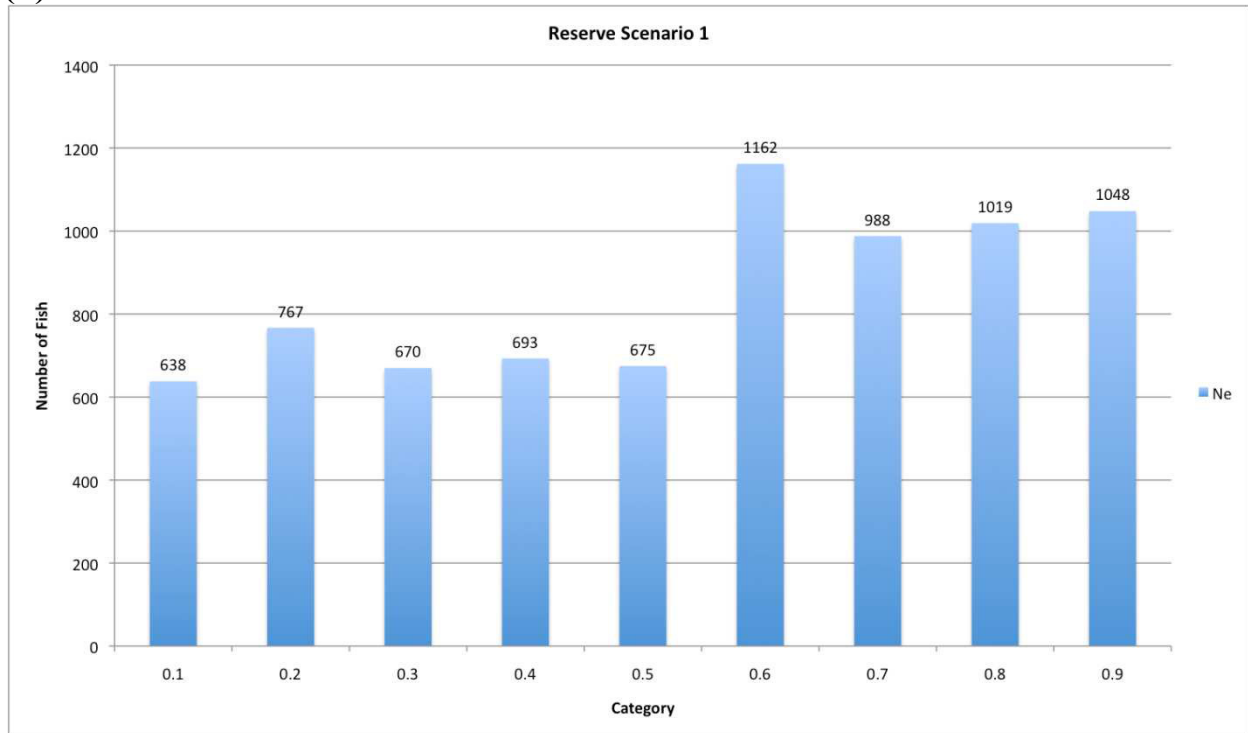


Population size with reserves and high fishing ($F=0.5$), and age limit of 1 year at 50 aggregations

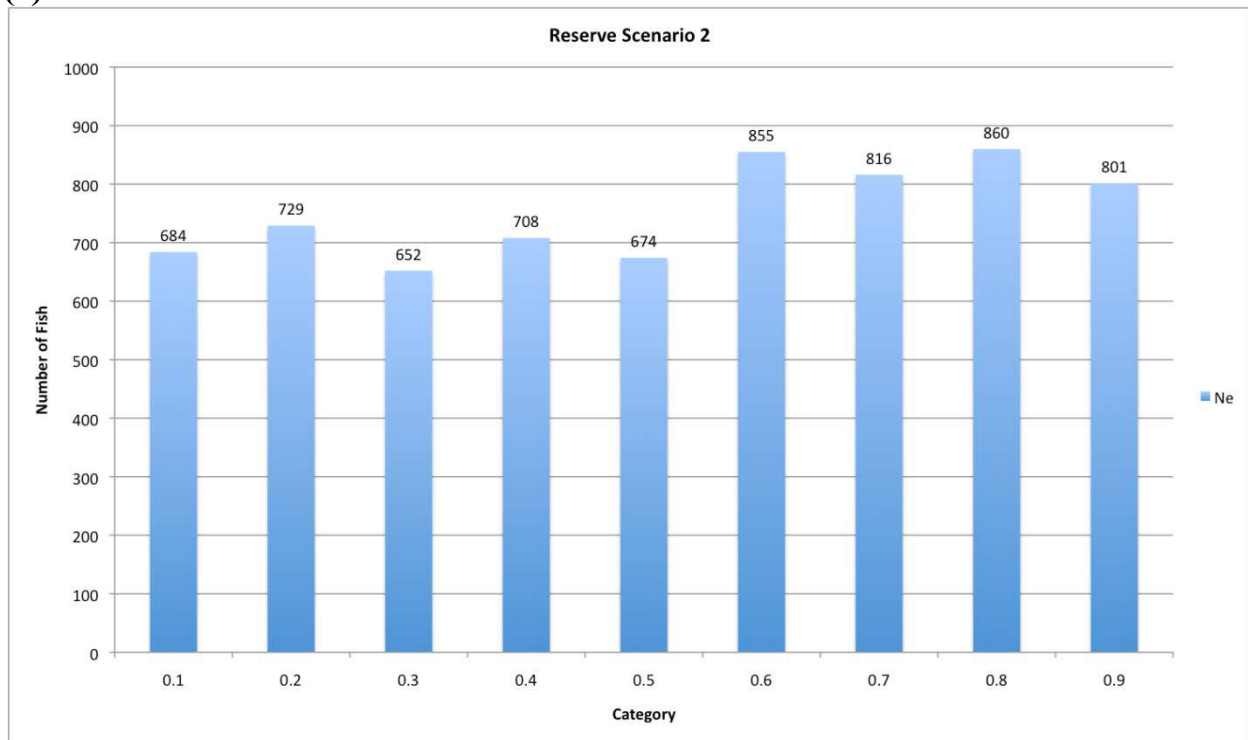
(a)



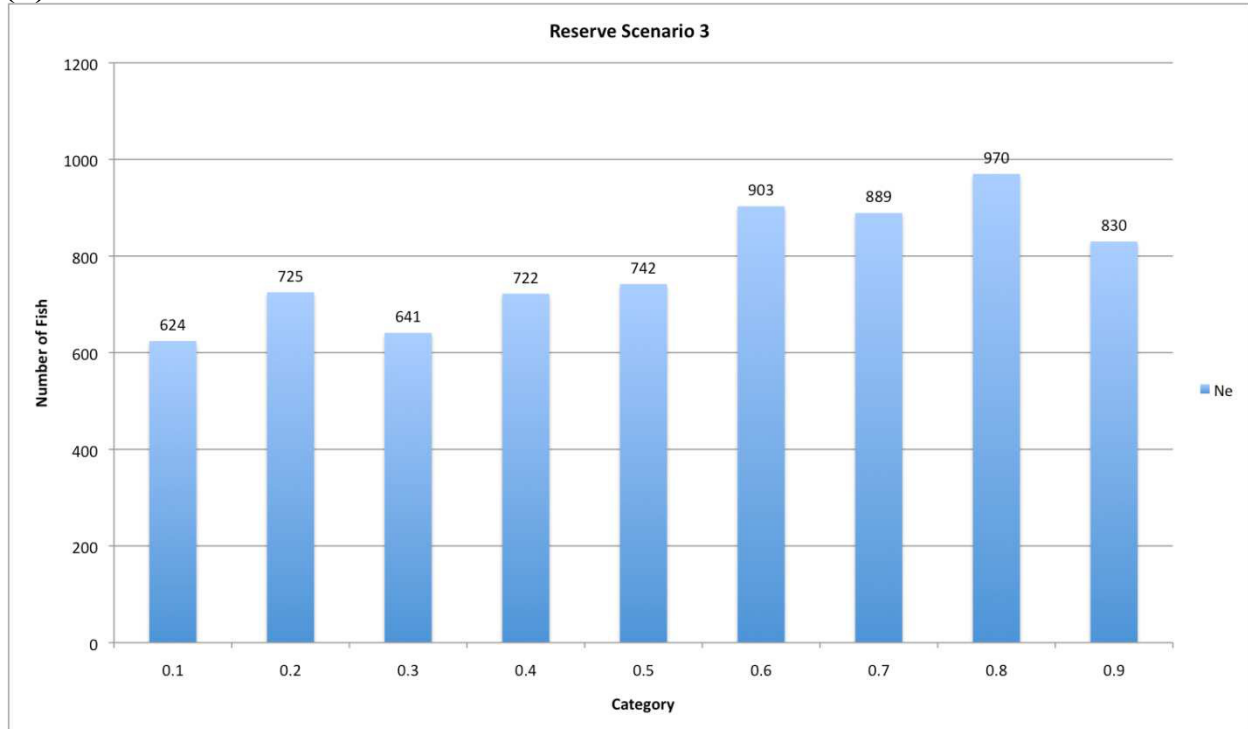
(b)



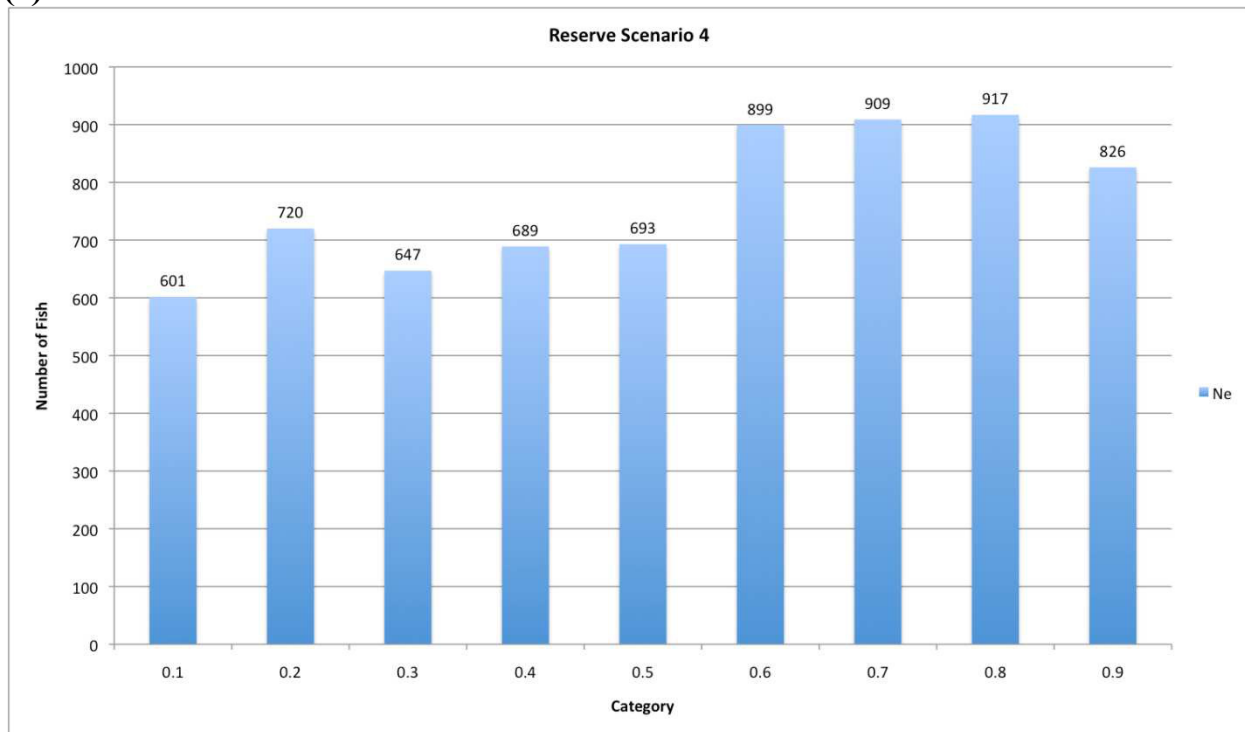
(c)



(d)

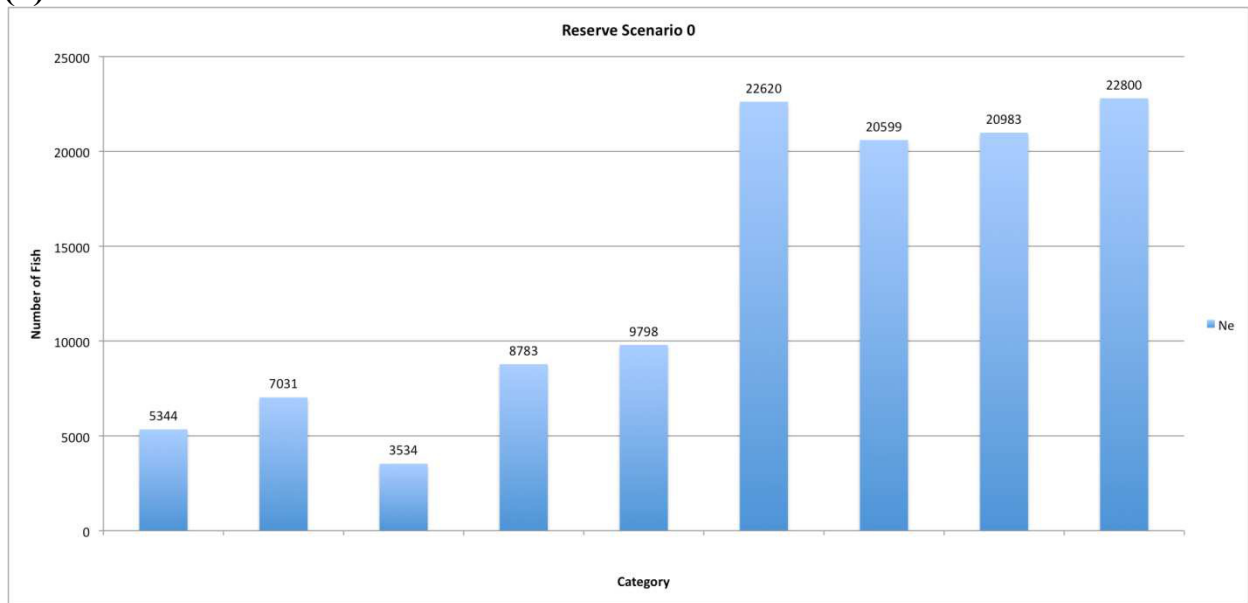


(e)

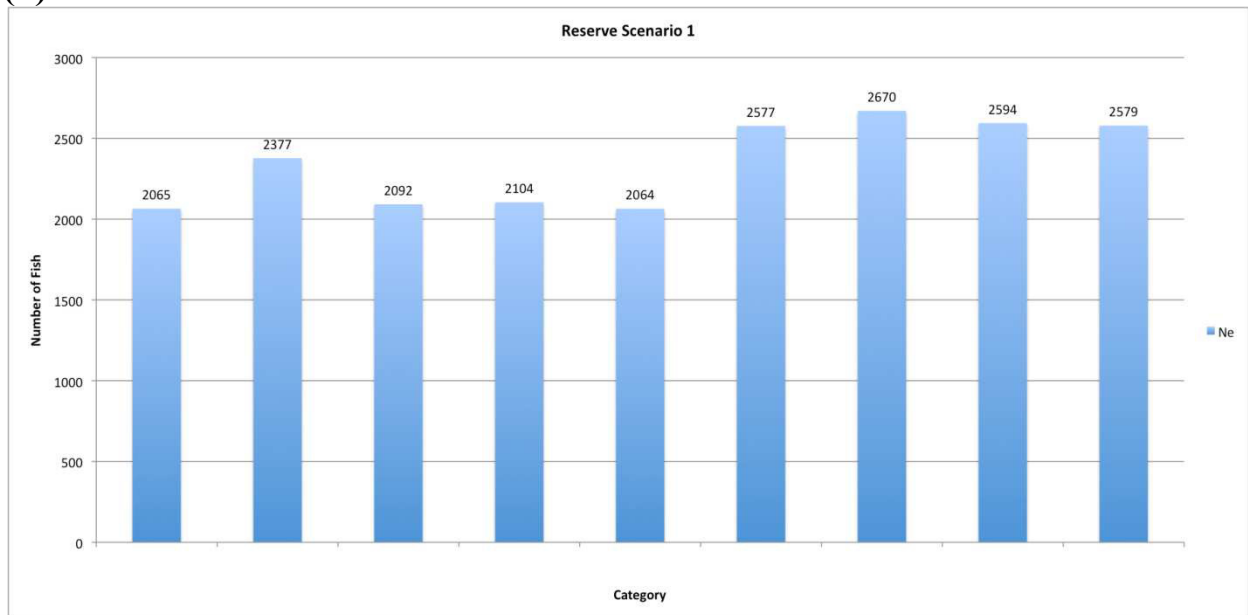


Population size with reserves and high fishing ($F=0.5$), and age limit of 4 years at 50 aggregations

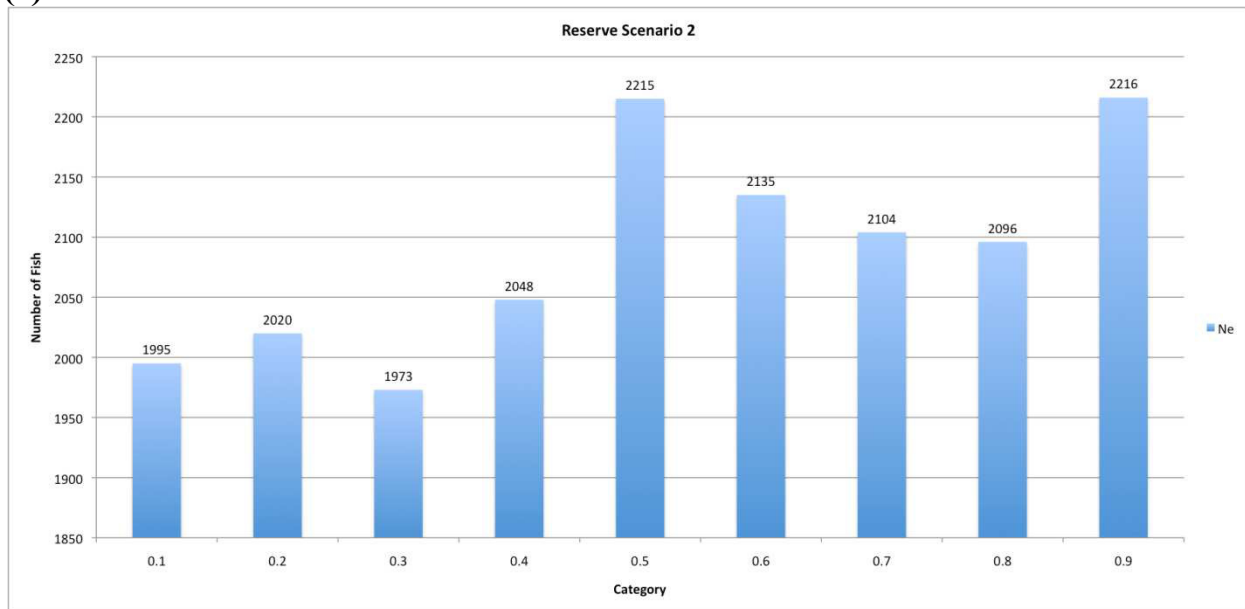
(a)



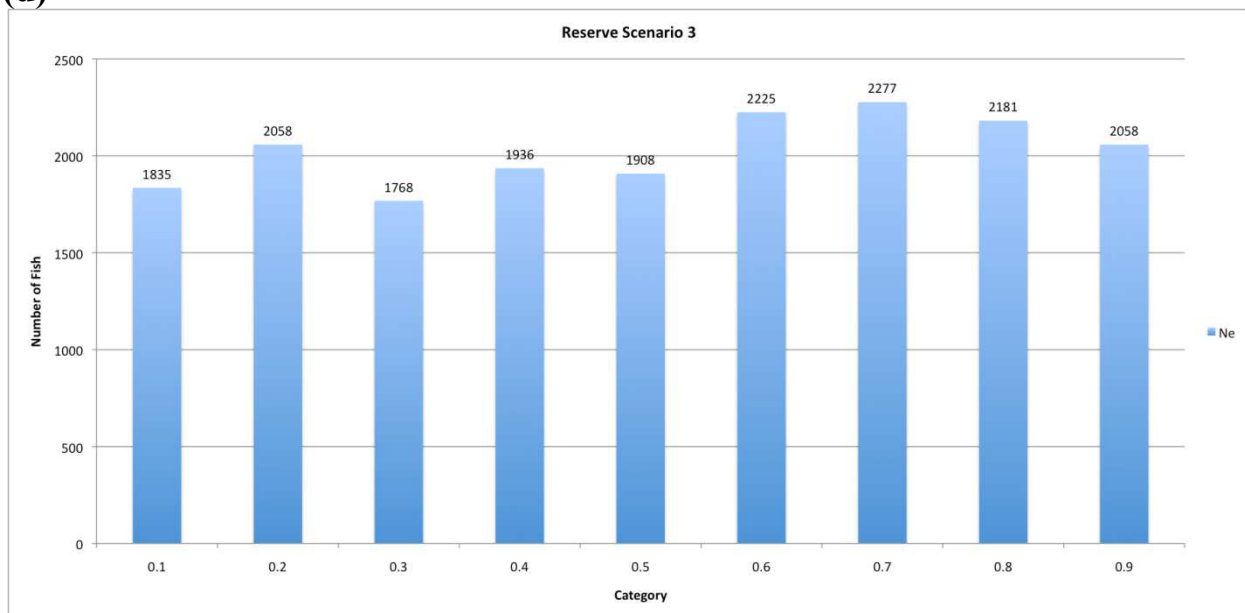
(b)



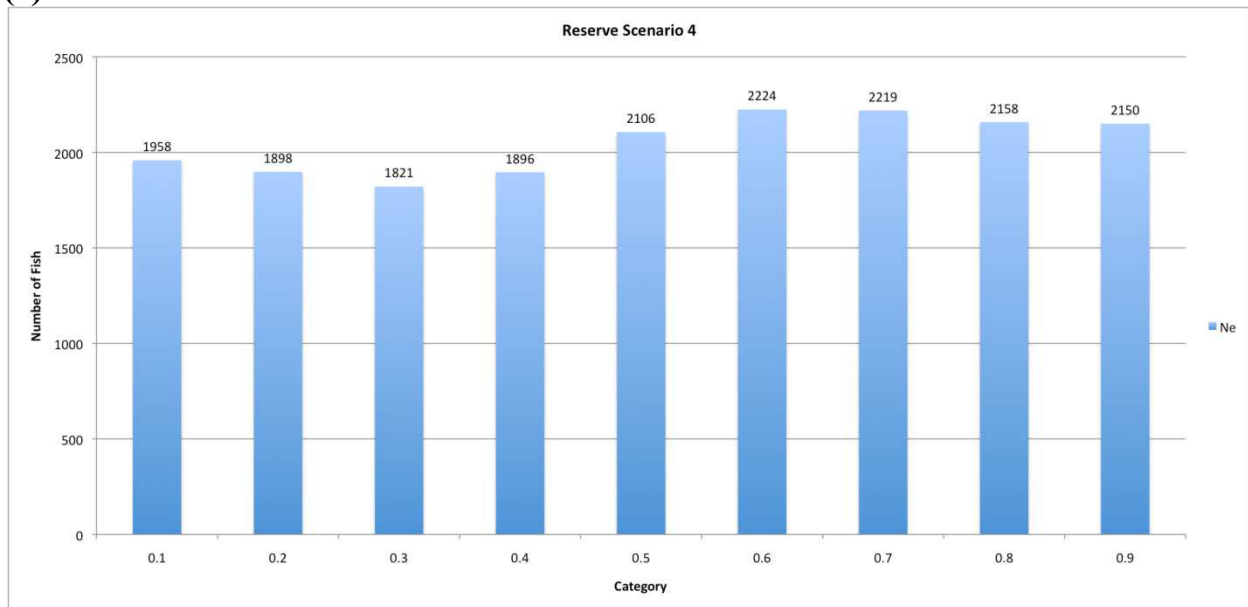
(c)



(d)

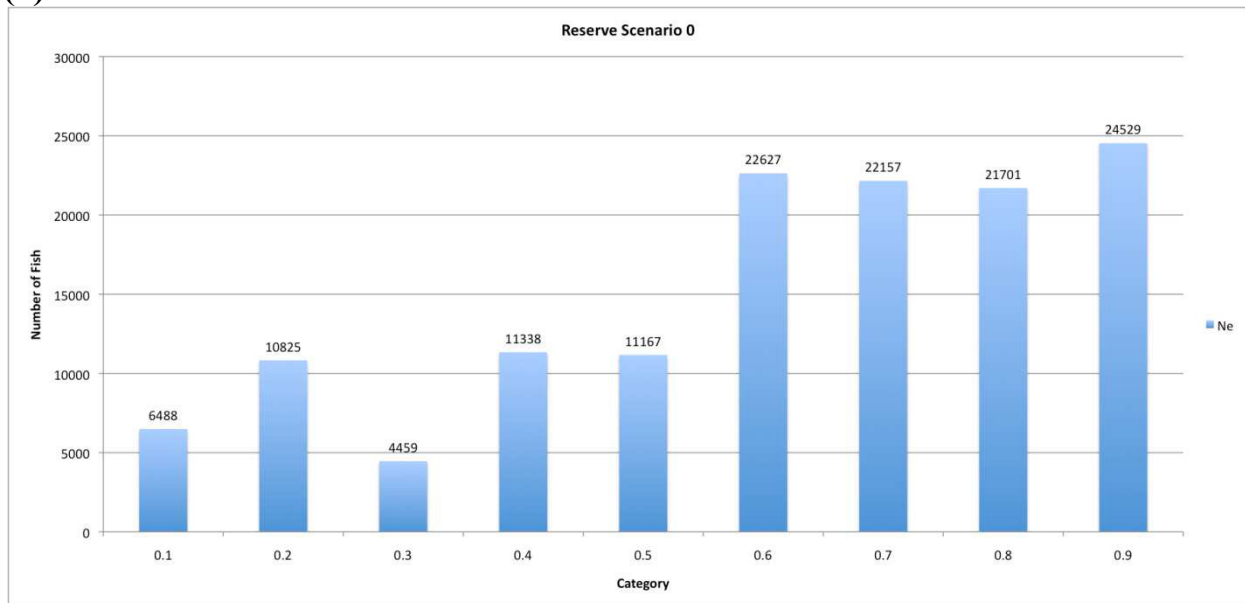


(e)

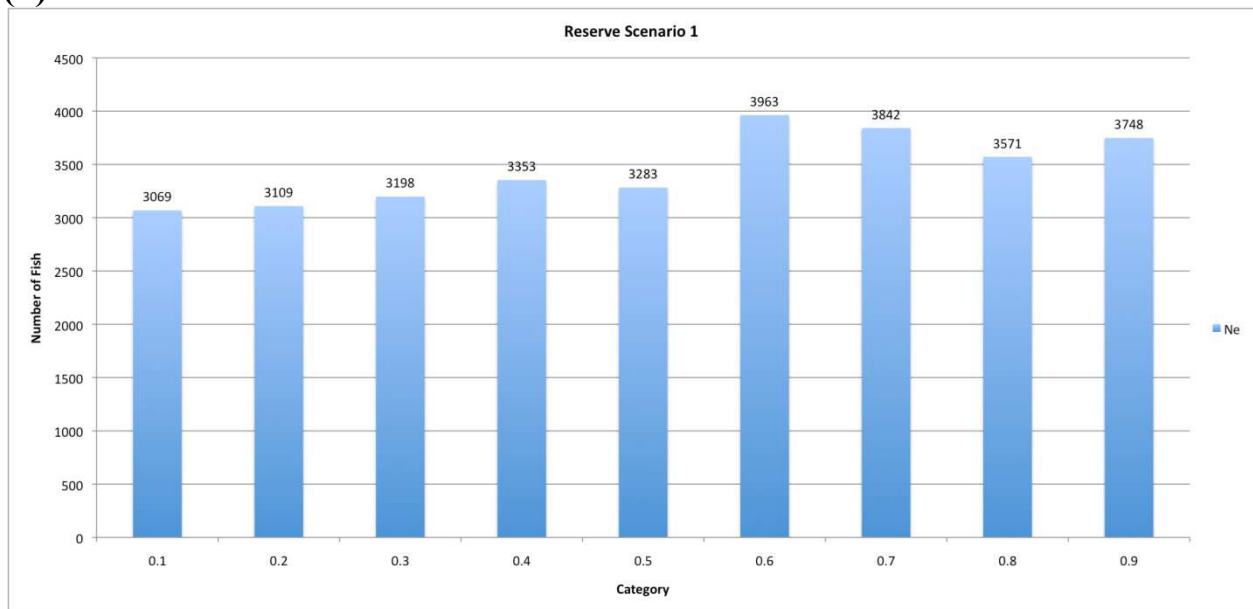


Population size with reserves and low fishing ($F=0.25$), and age limit of 1 year at 100 aggregations

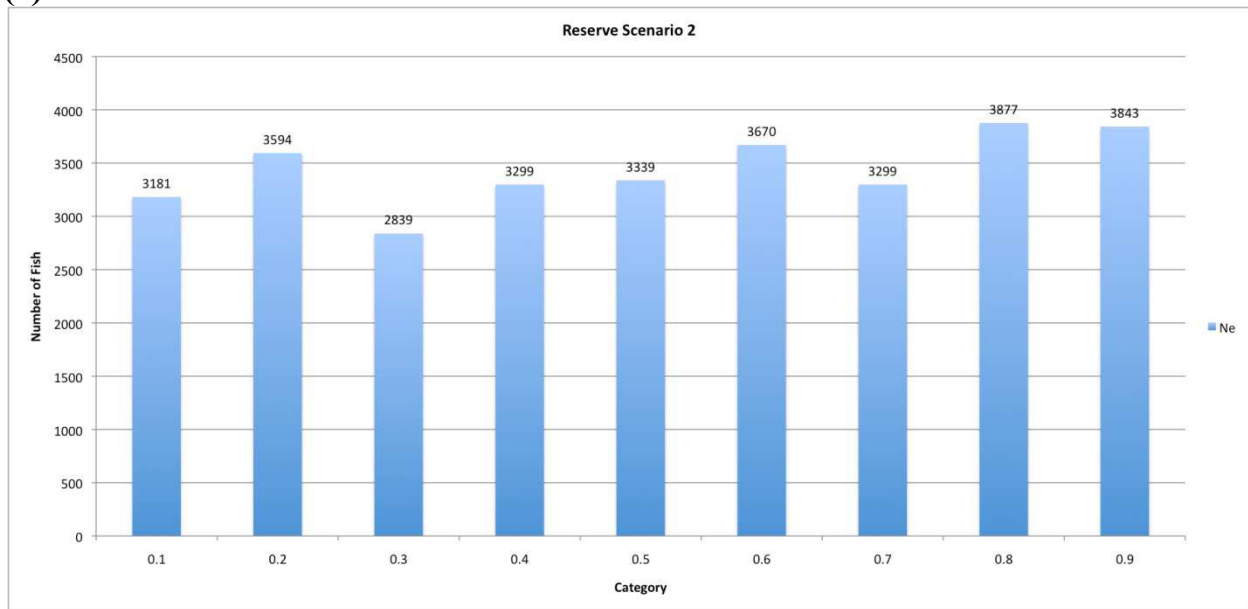
(a)



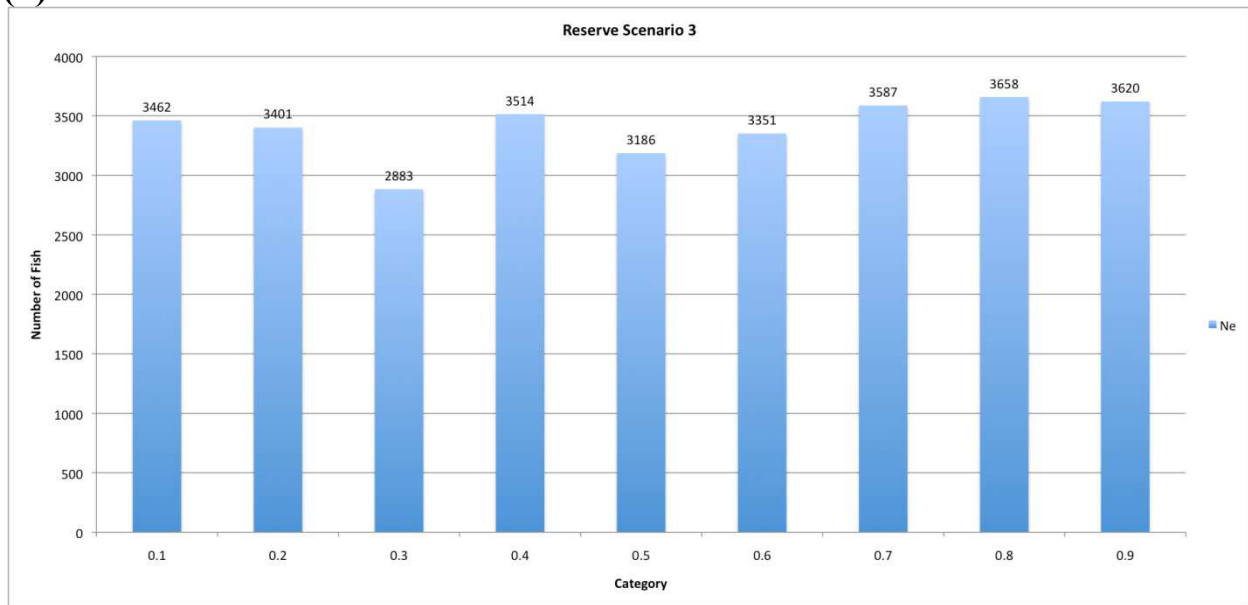
(b)



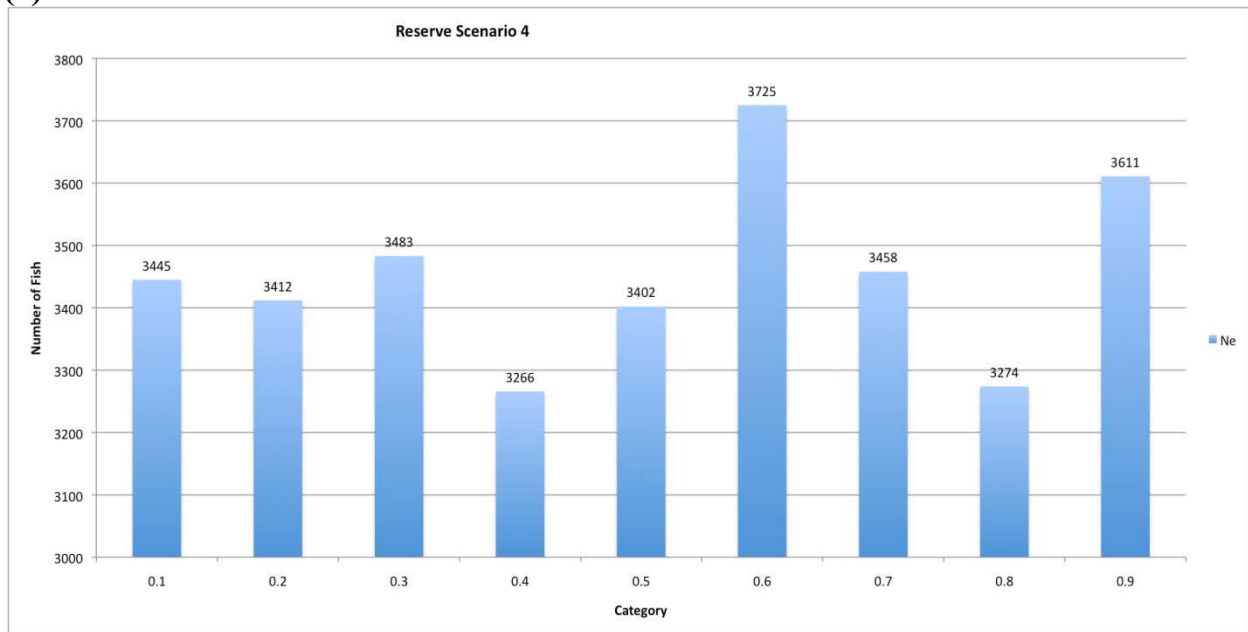
(c)



(d)

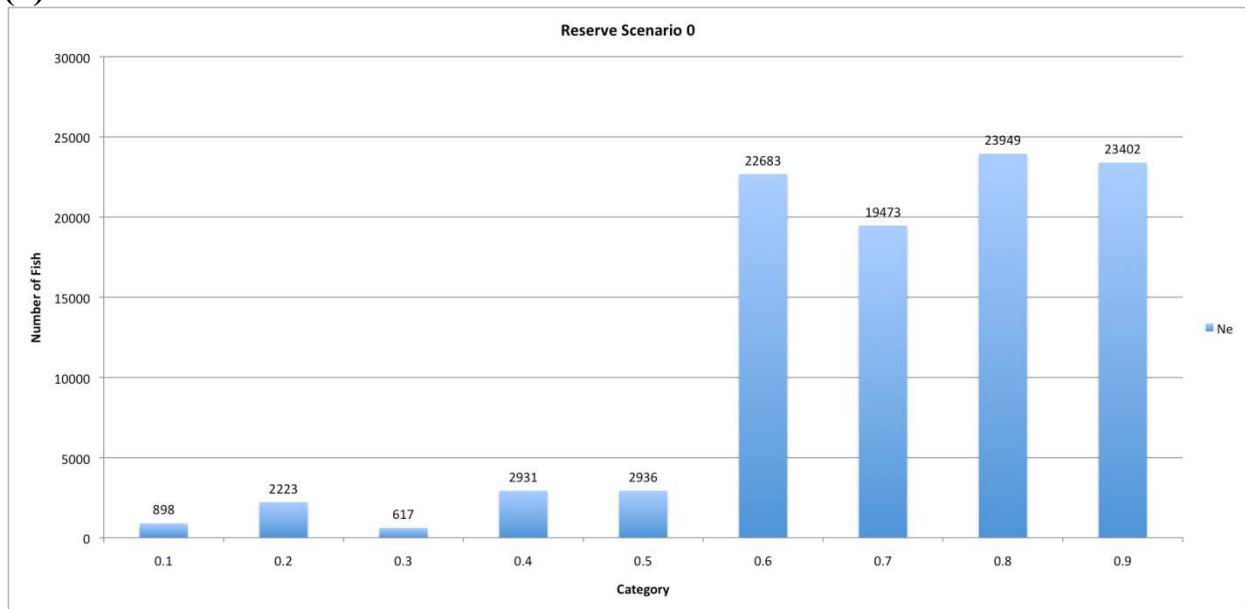


(e)

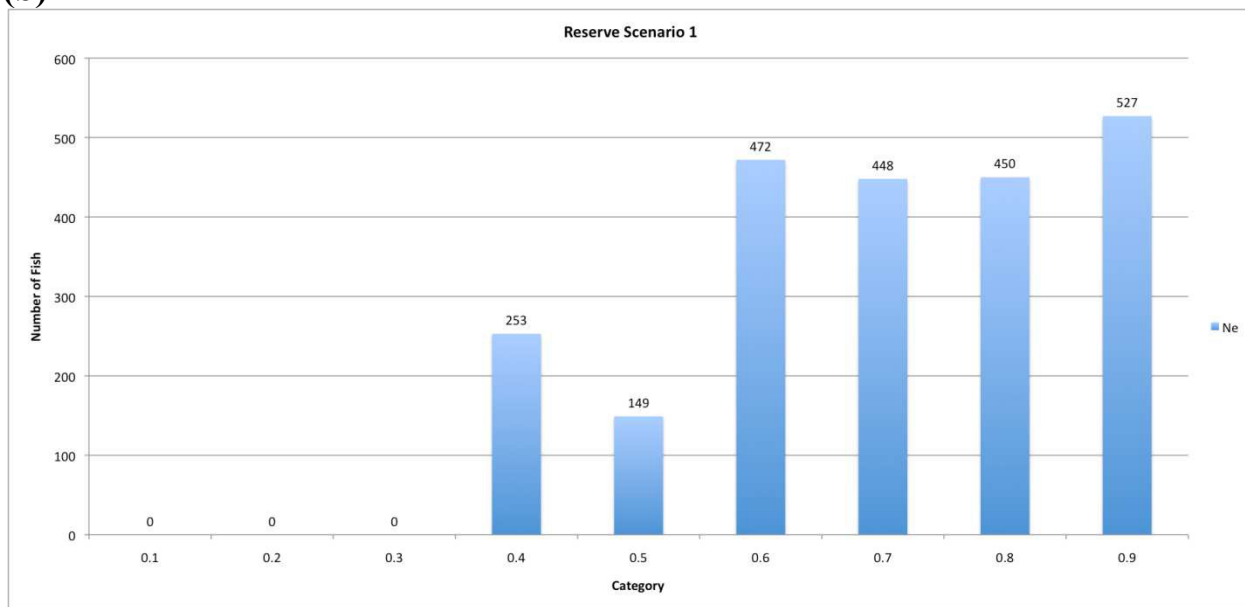


Population size with reserves and low fishing ($F=0.25$), and age limit of 4 years at 100 aggregations

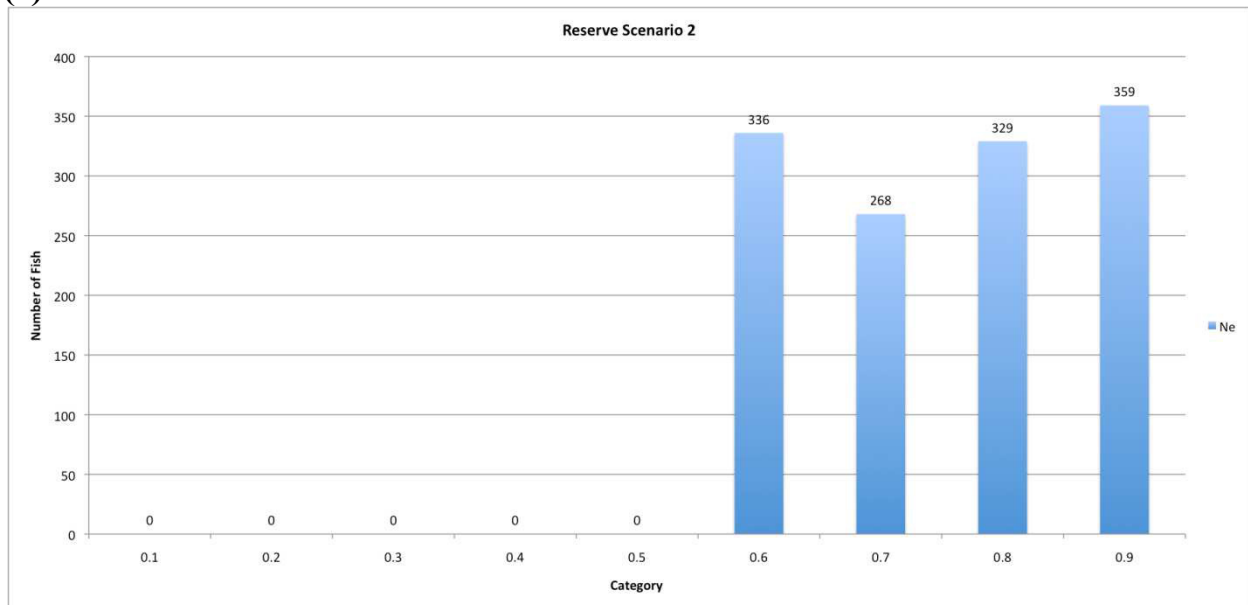
(a)



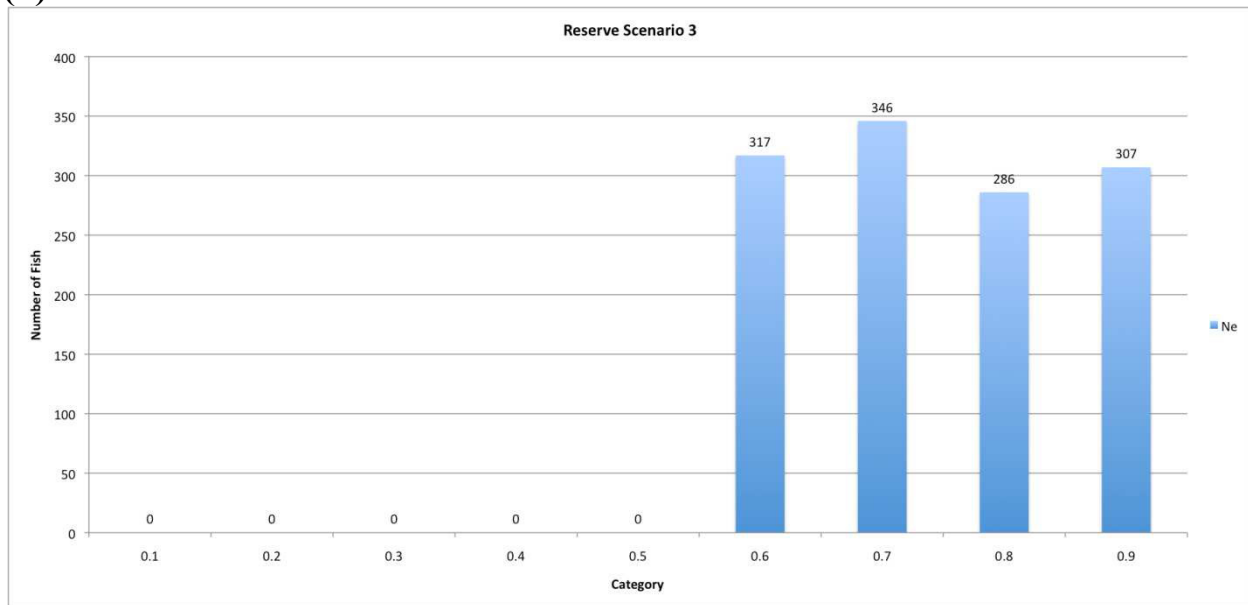
(b)



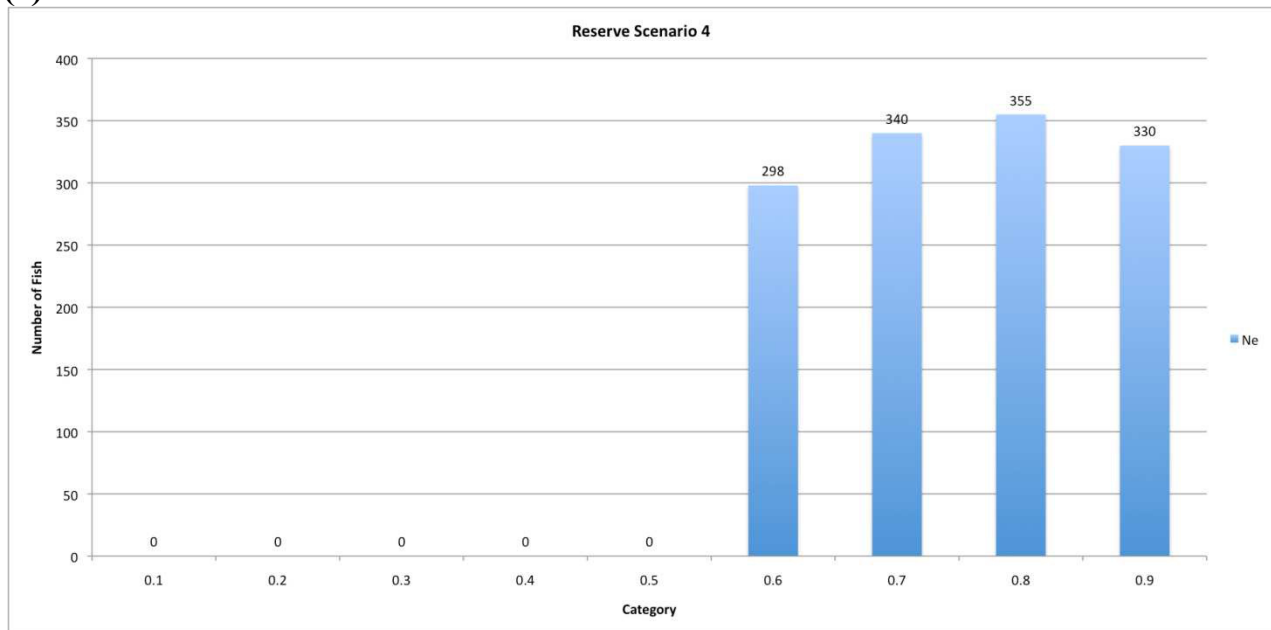
(c)



(d)

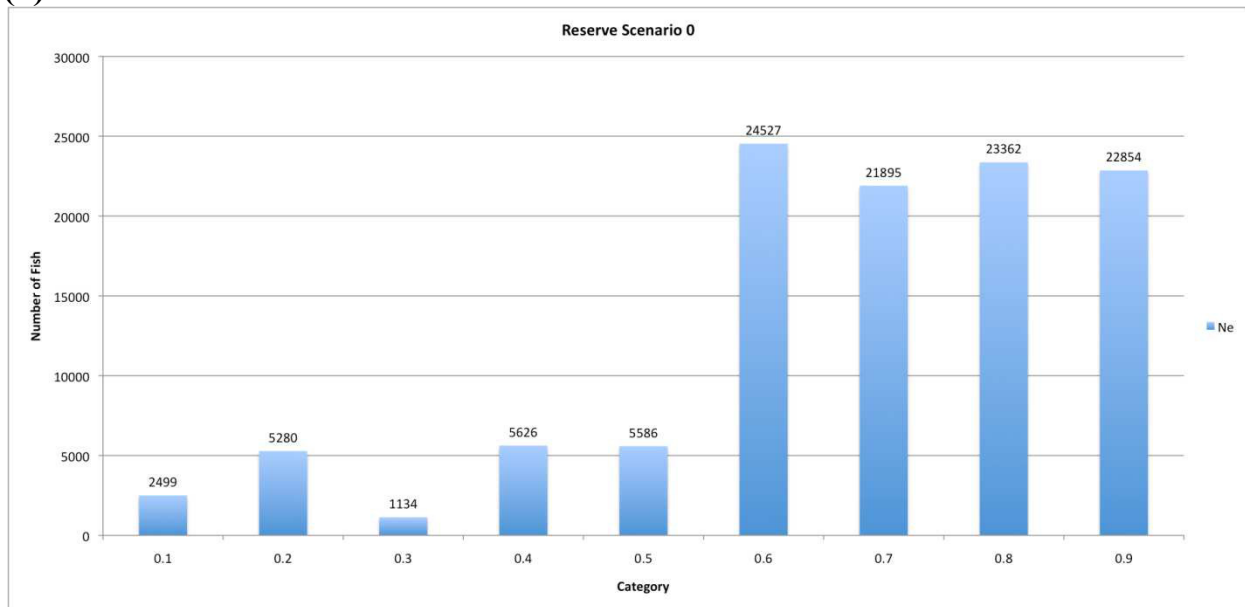


(e)

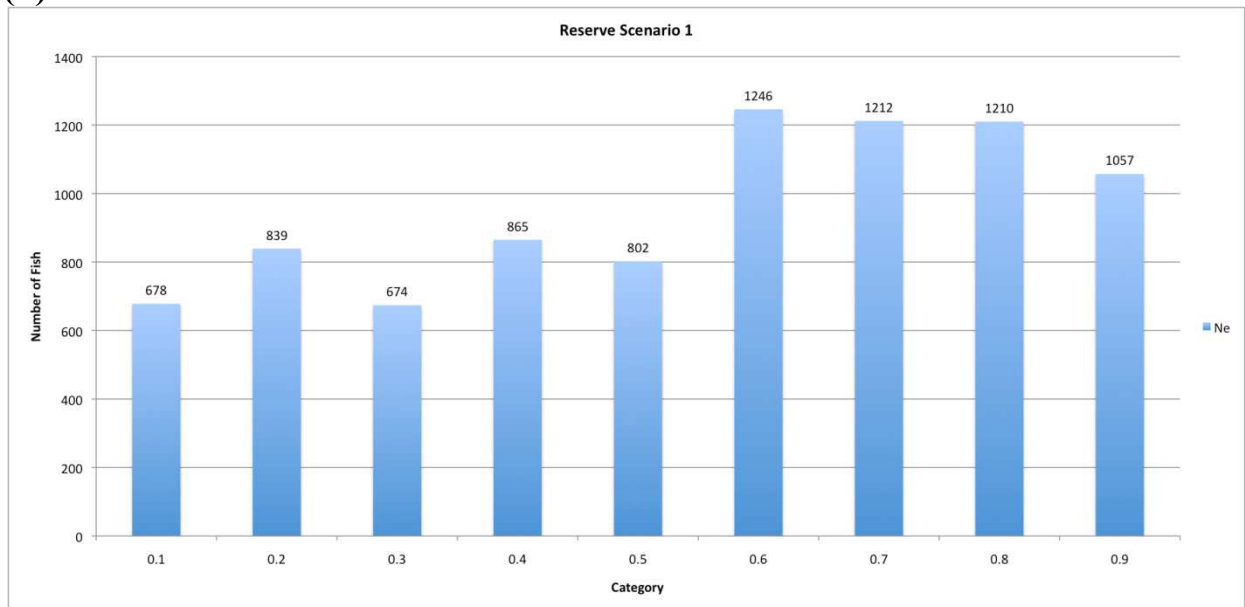


Population size with reserves and high fishing ($F=0.5$), and age limit of 1 years at 100 aggregations

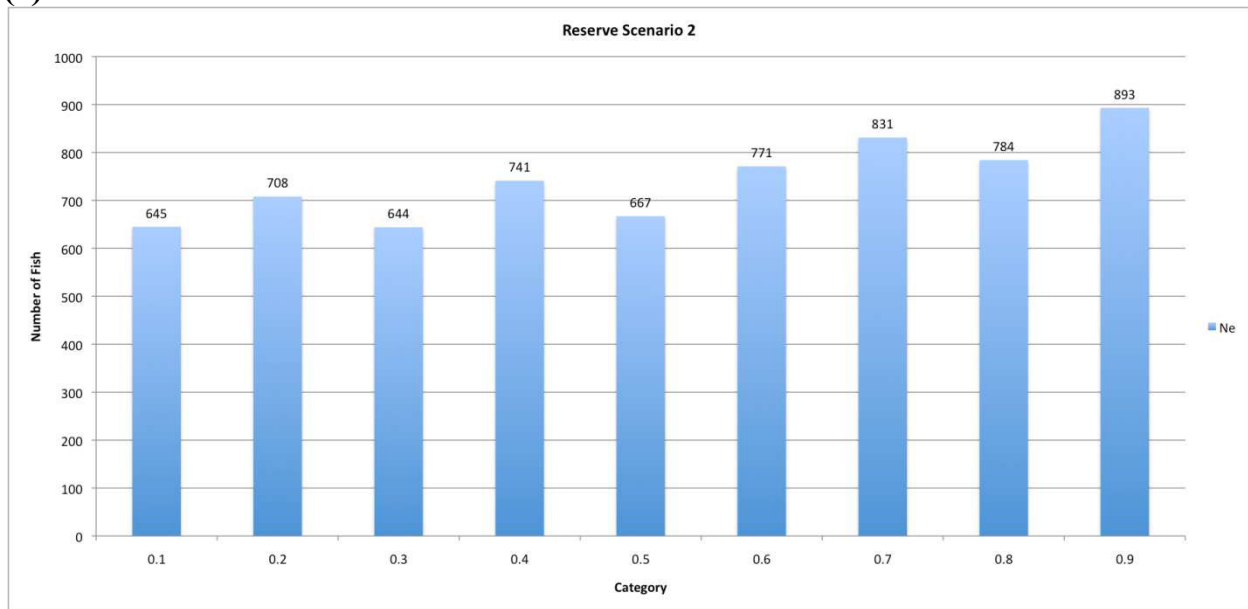
(a)



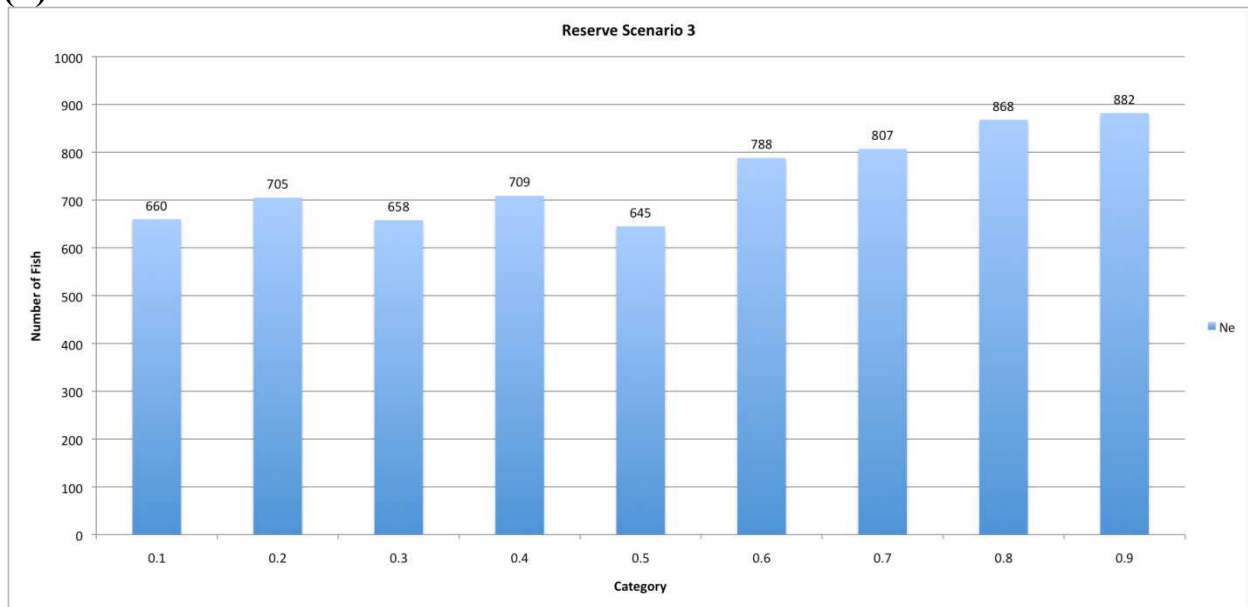
(b)



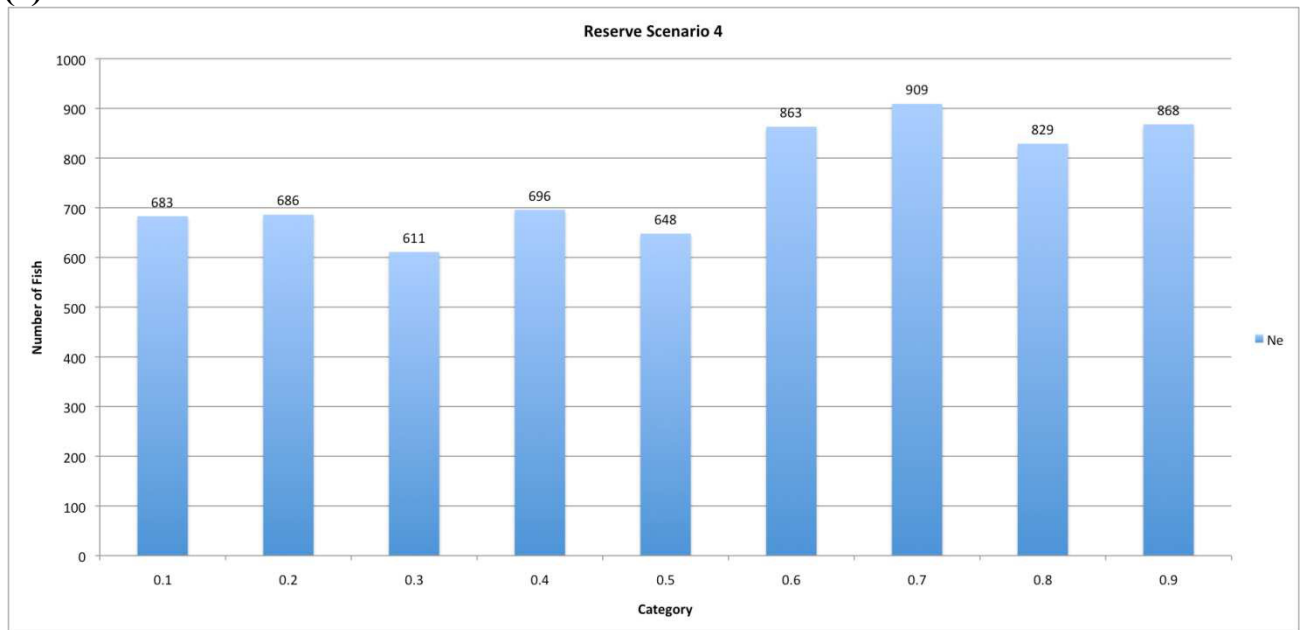
(c)



(d)



(e)

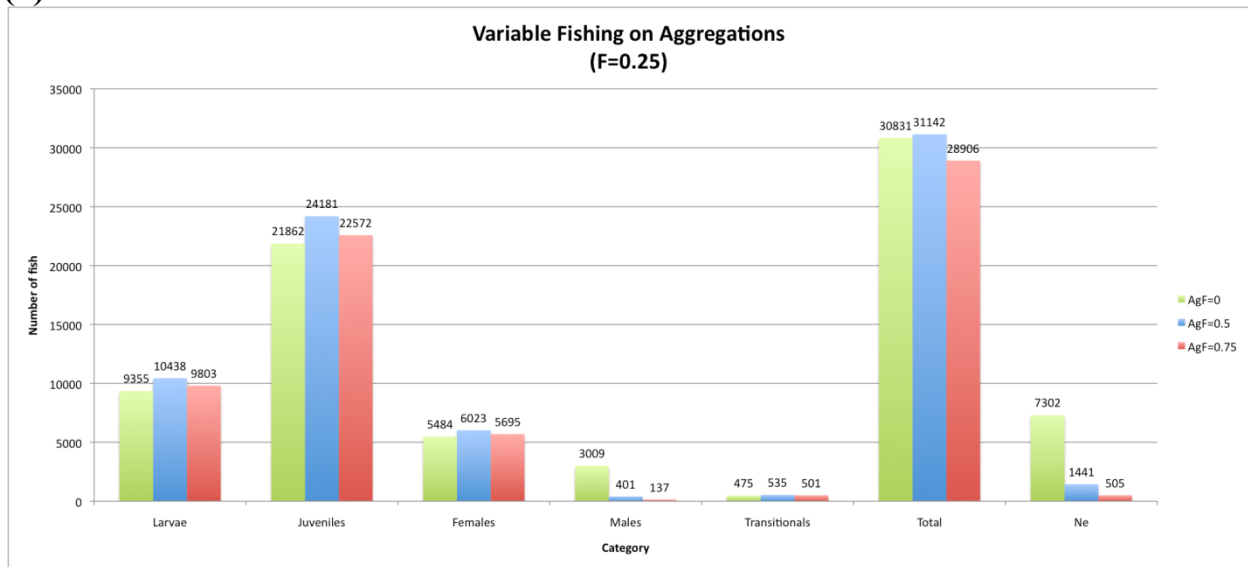


Population size with reserves and high fishing ($F=0.5$), and age limit of 4 years at 100 aggregations

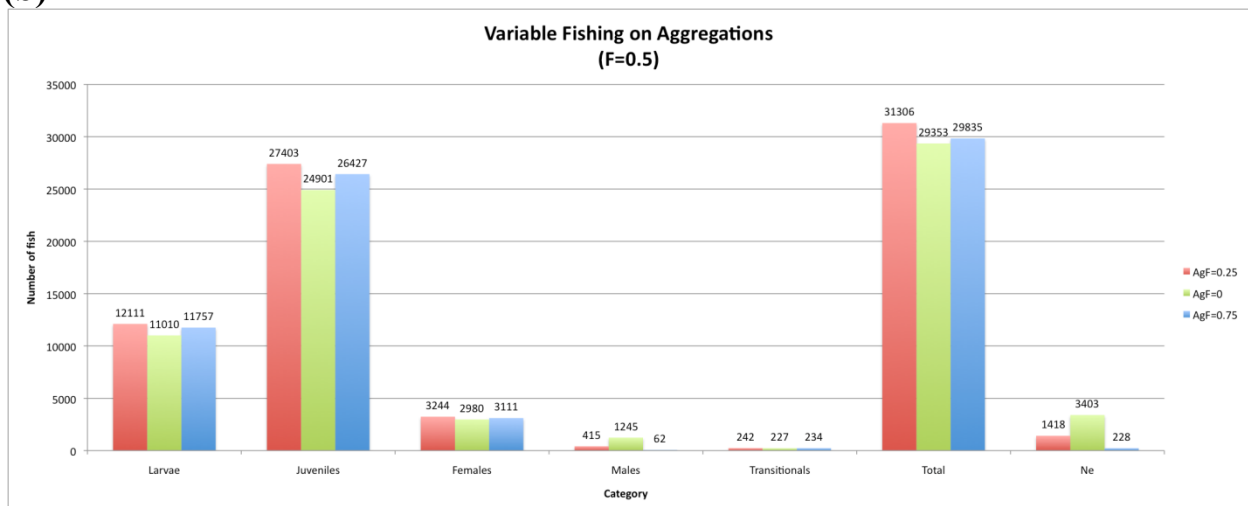
Variable Fishing

Population size is graphed by stage for each figure, including total population size and effective population size, for varying levels of fishing pressures on aggregations, where (a) implements fishing pressures on aggregations both higher and lower than the low fishing ($F=0.25$) applied to the rest of the model space, and (b) implements fishing pressures on aggregations both higher and lower than the high fishing ($F=0.5$) applied to the rest of the model space.

(a)

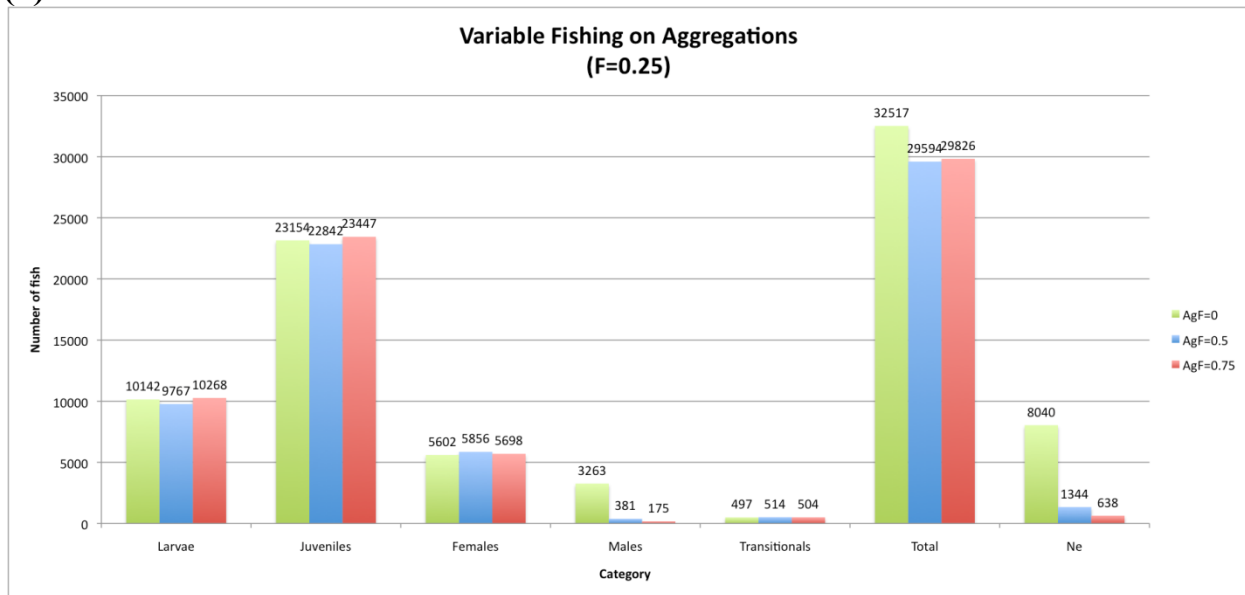


(b)

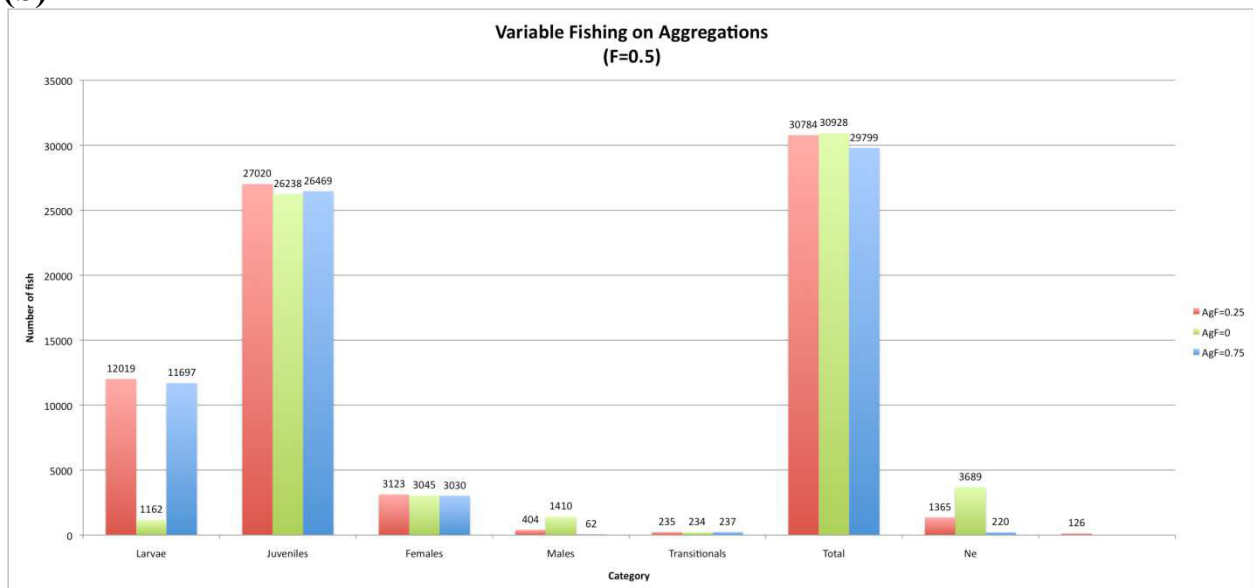


Population size with variable fishing on 10 aggregations with age limit of 4 years

(a)

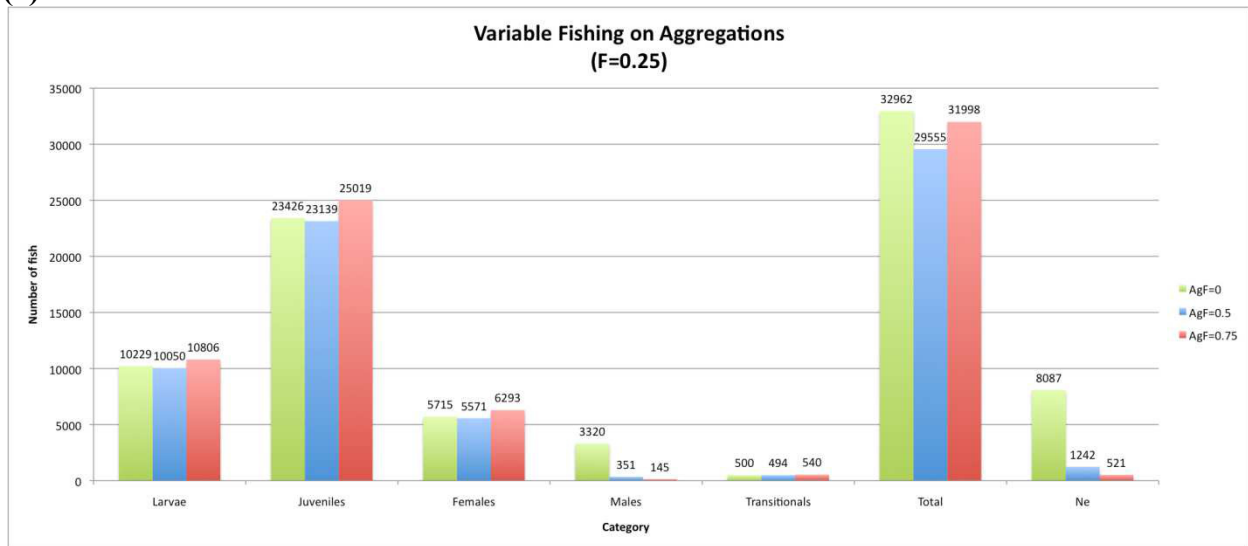


(b)

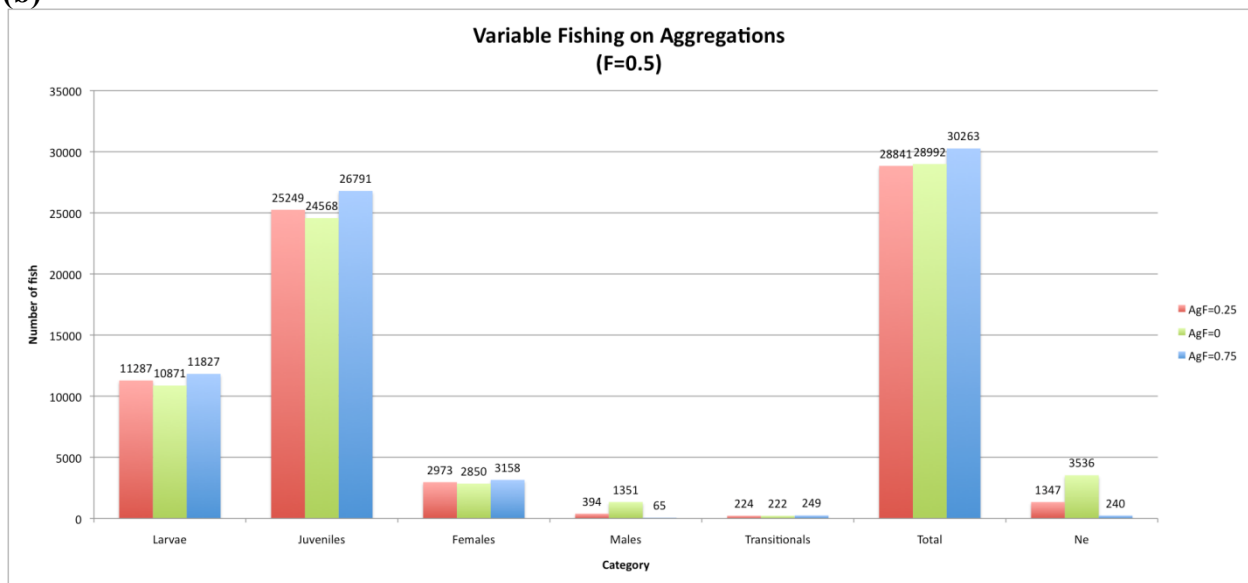


Population size with variable fishing on 50 aggregations with age limit of 4 years

(a)

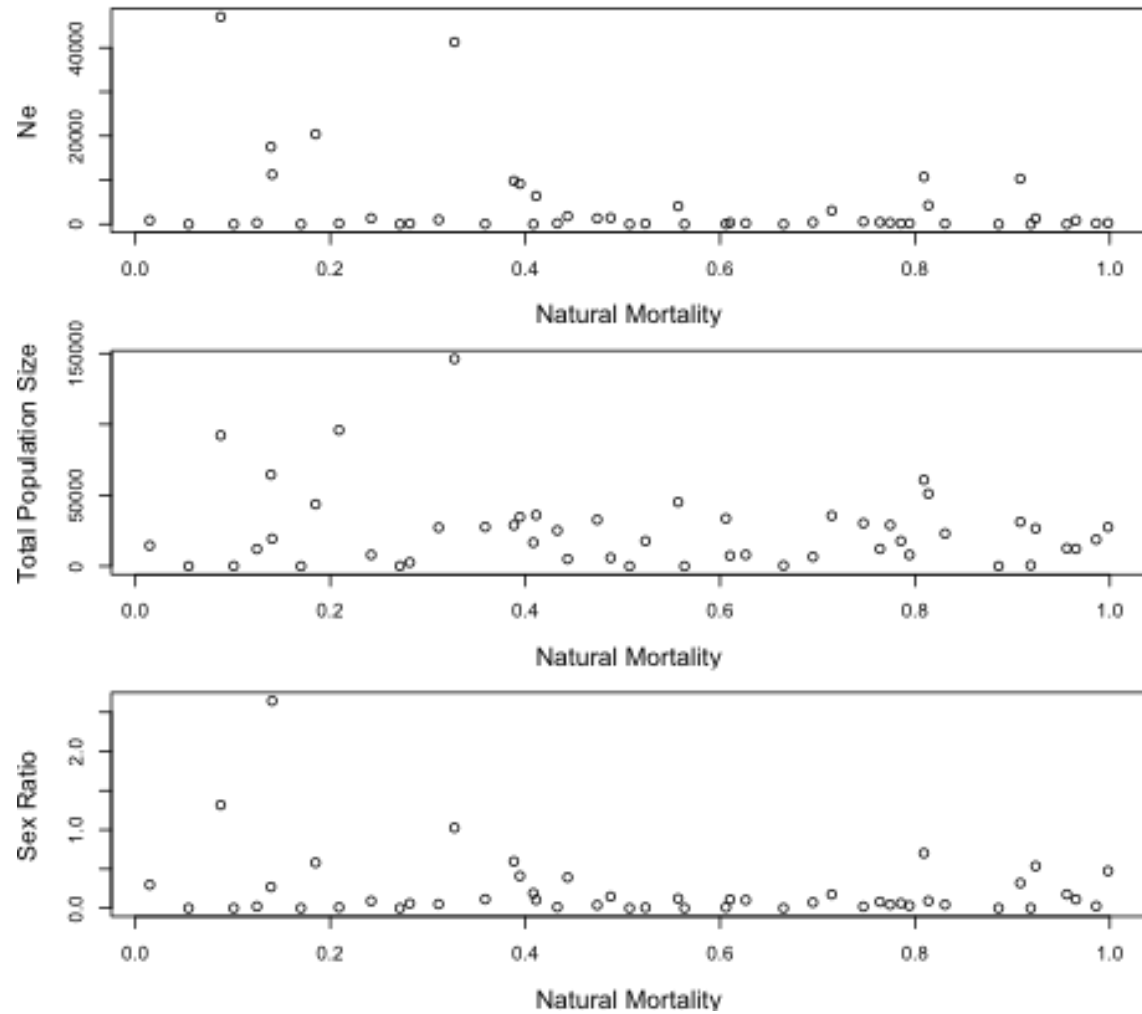


(b)

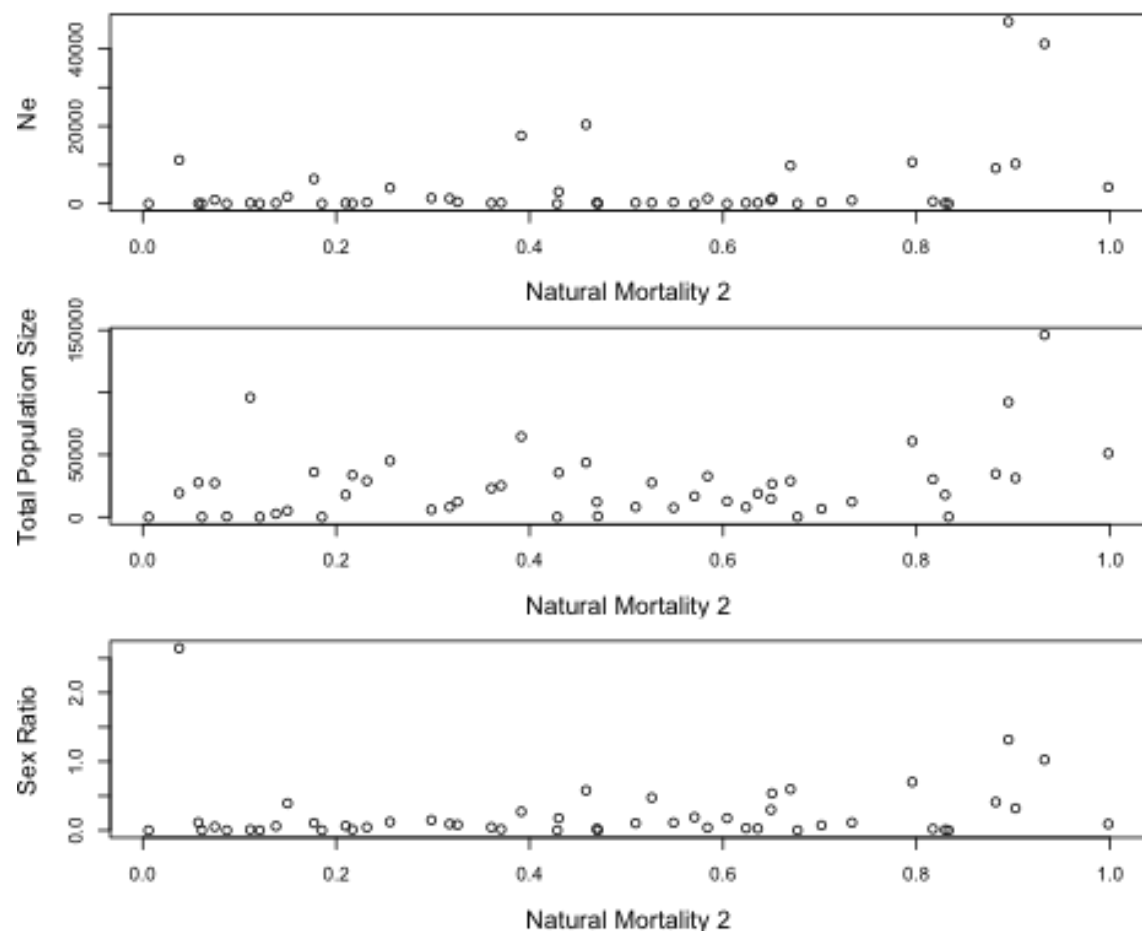


Population size with variable fishing on 100 aggregations with age limit of 4 years

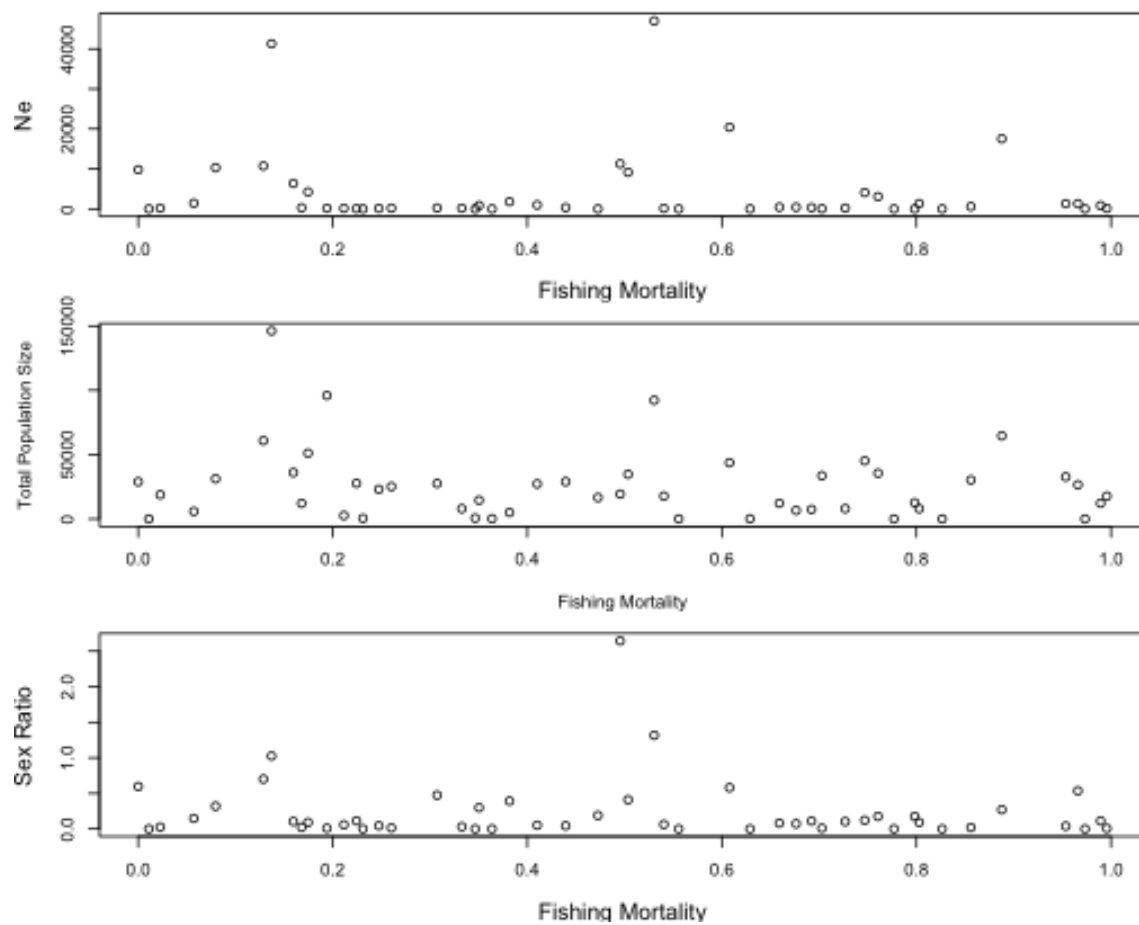
Sensitivity Analysis



Correlation between natural mortality parameter 1 and output variables
From top to bottom, natural mortality parameter 1 correlated with effective population size, total population size, and sex ratio, respectively

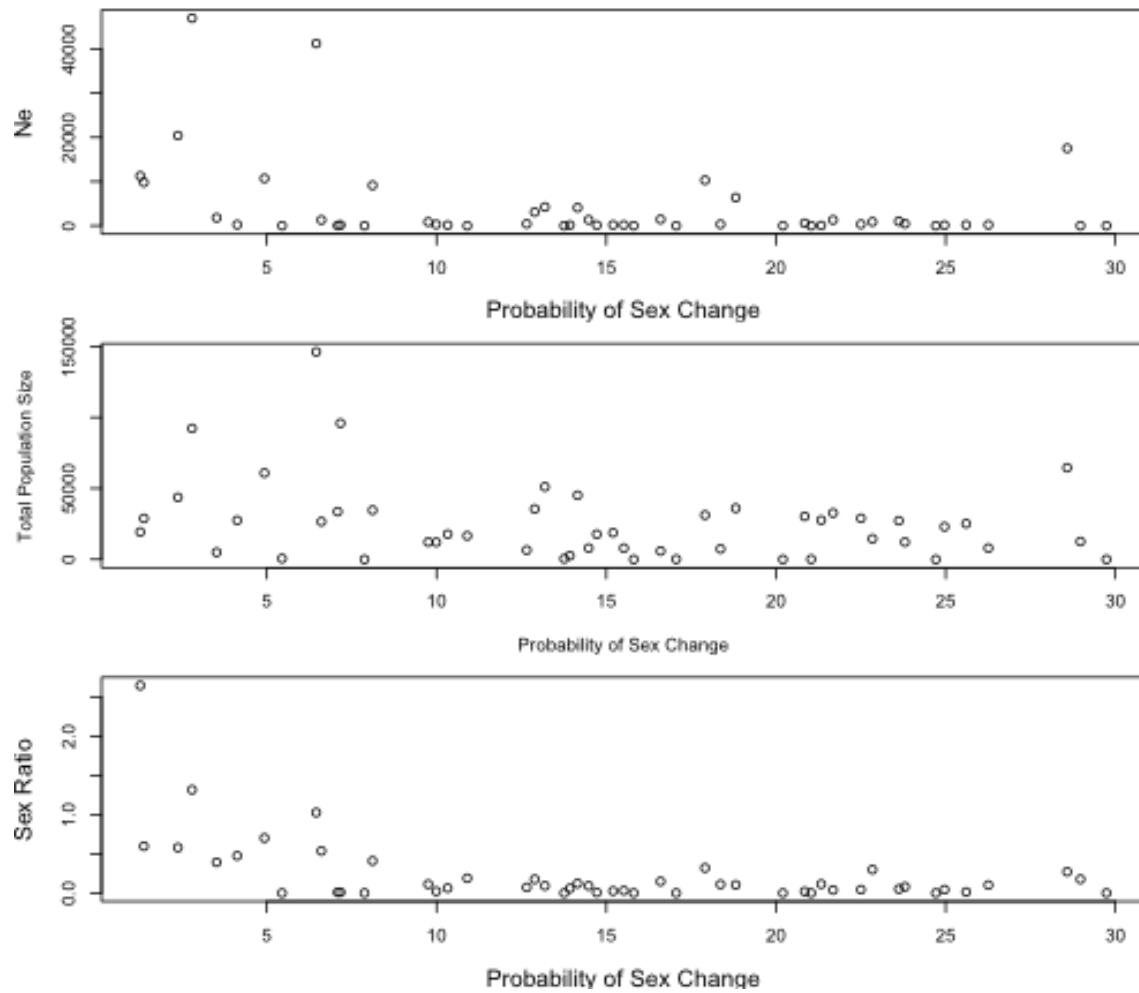


Correlation between natural mortality parameter 2 and output variables
From top to bottom, natural mortality parameter 2 correlated with effective population size, total population size, and sex ratio, respectively

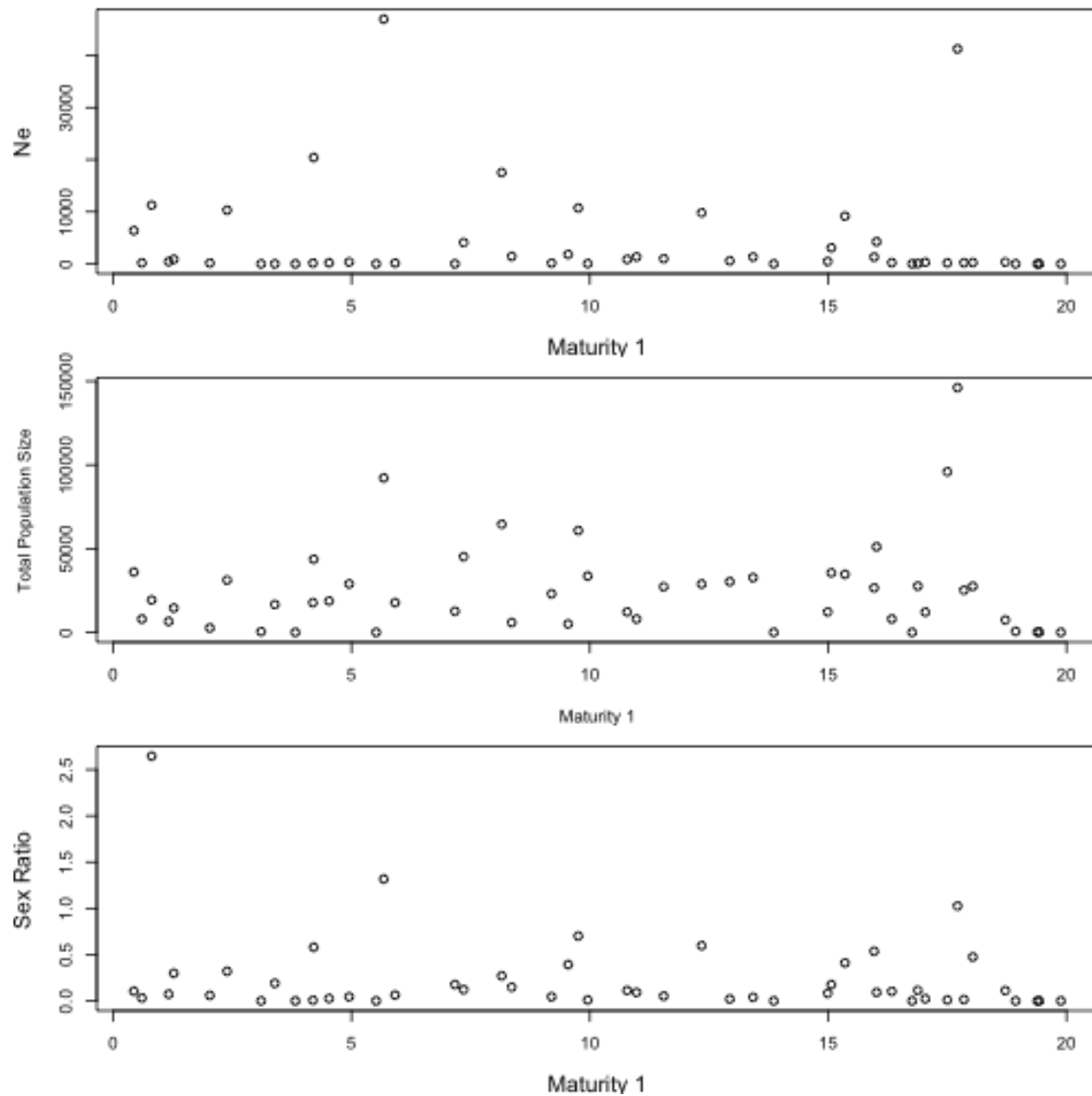


Correlation between fishing mortality and output variables

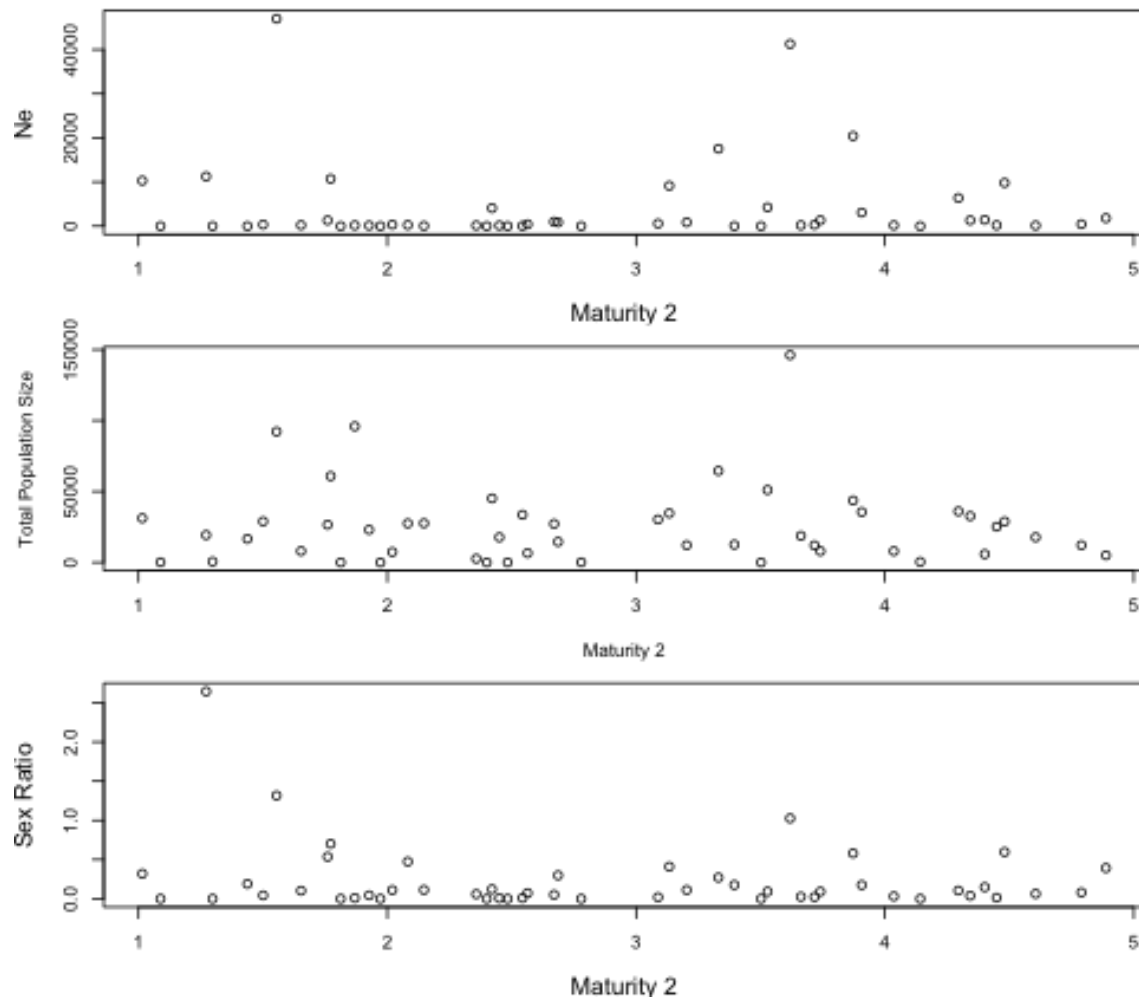
From top to bottom, fishing mortality correlated with effective population size, total population size, and sex ratio, respectively



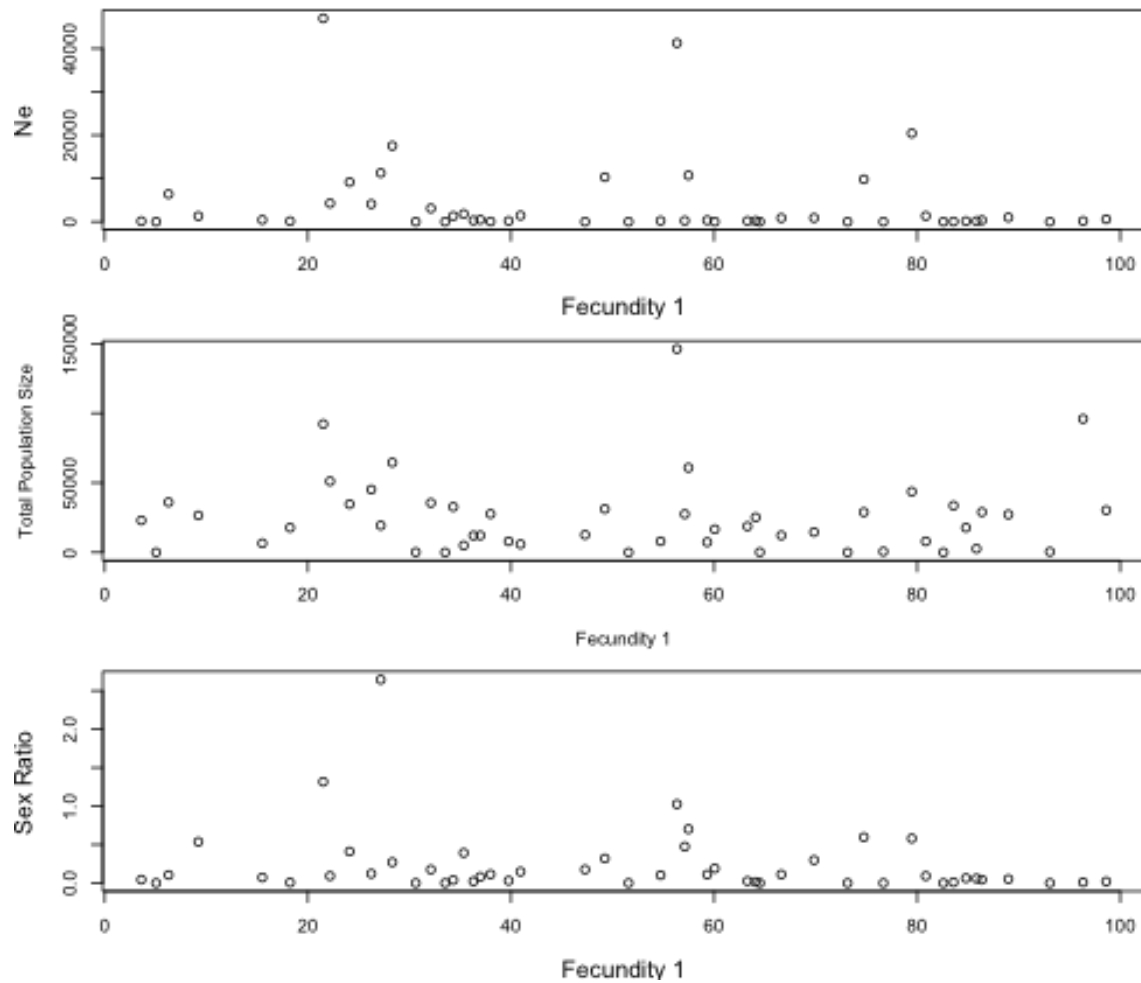
Correlation between probability of sex change and output variables
 From top to bottom, probability of sex change (pfslope) correlated with effective population size, total population size, and sex ratio, respectively.



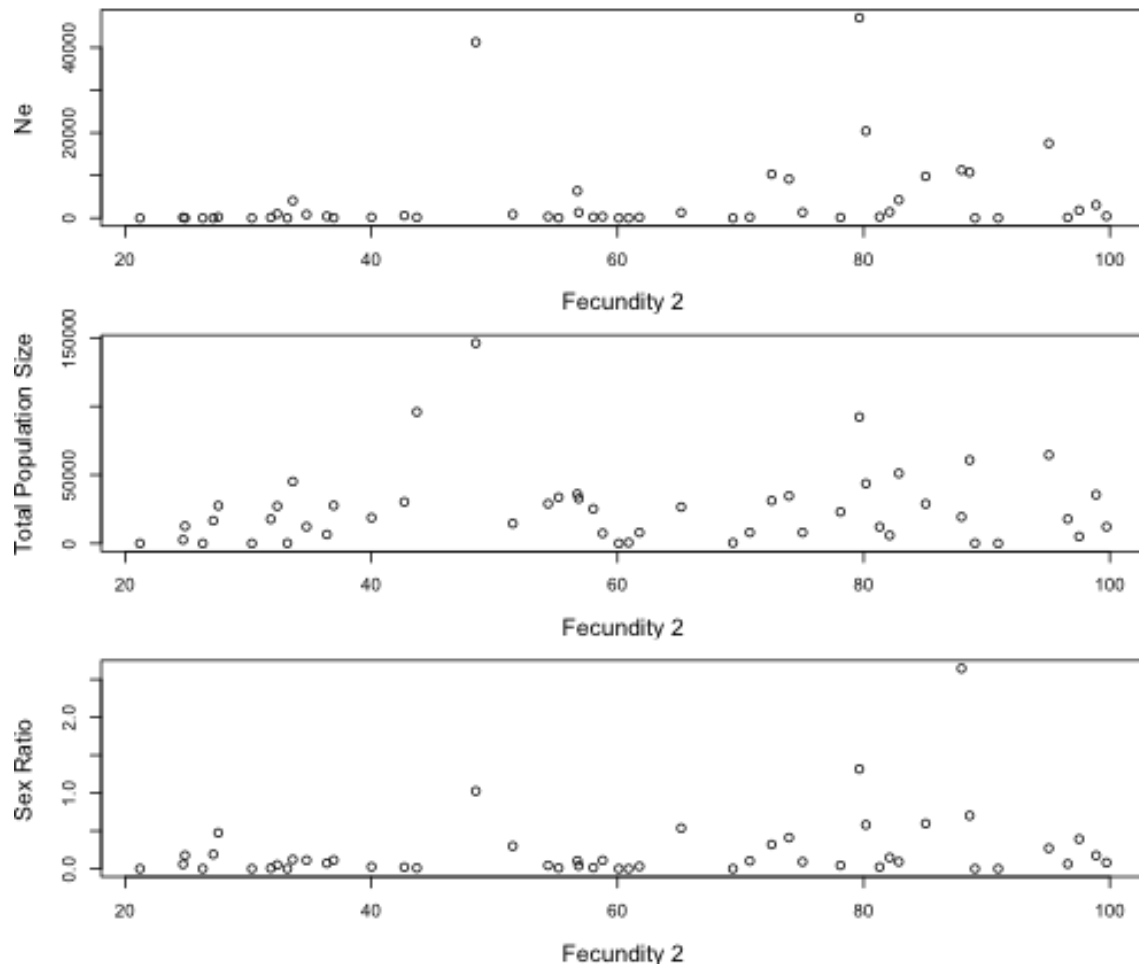
Correlation between maturity parameter 1 and output variables
 From top to bottom, maturity parameter 1 correlated with effective population size, total population size, and sex ratio, respectively



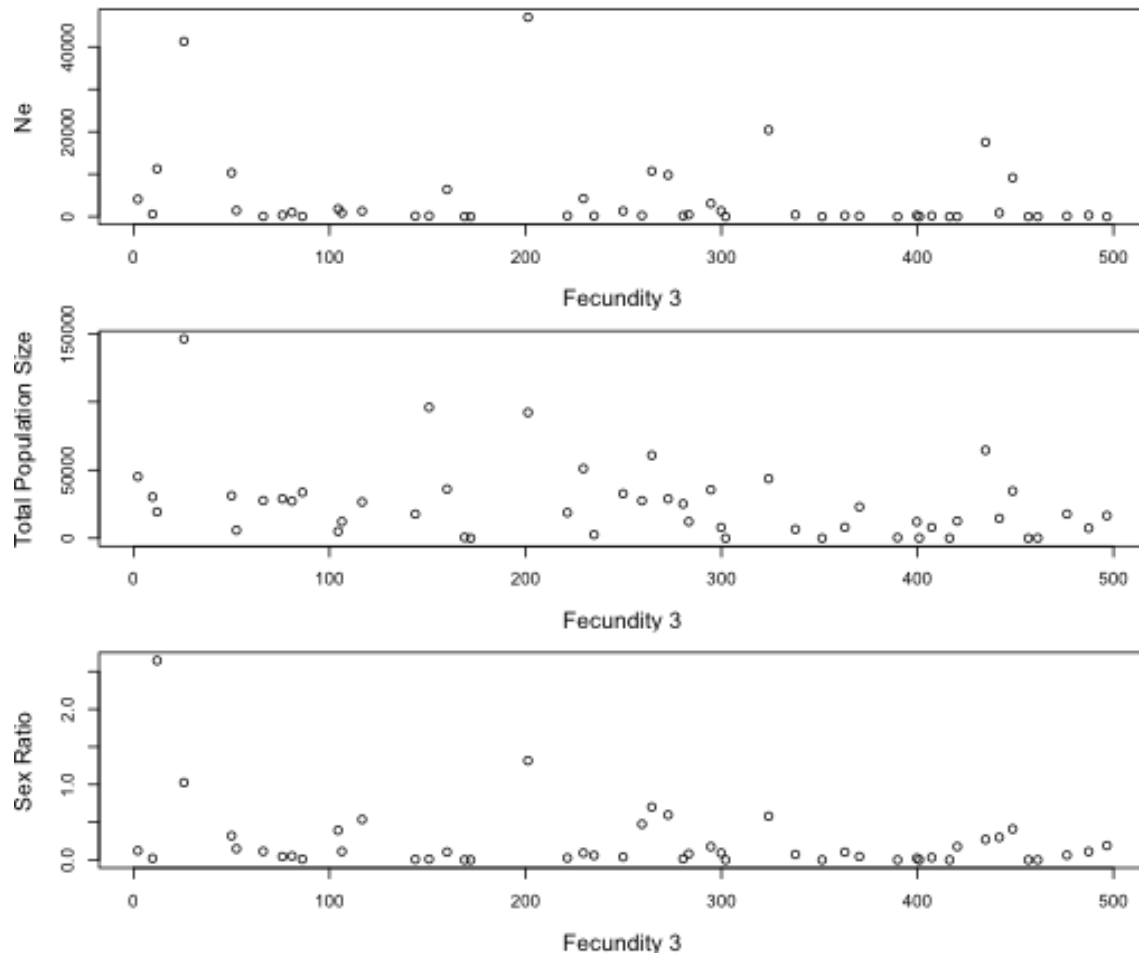
Correlation between maturity parameter 2 and output variables
From top to bottom, maturity parameter 2 correlated with effective population size, total population size, and sex ratio, respectively



Correlation between fecundity parameter 1 and output variables
 From top to bottom, fecundity parameter 1 correlated with effective population size, total population size, and sex ratio, respectively

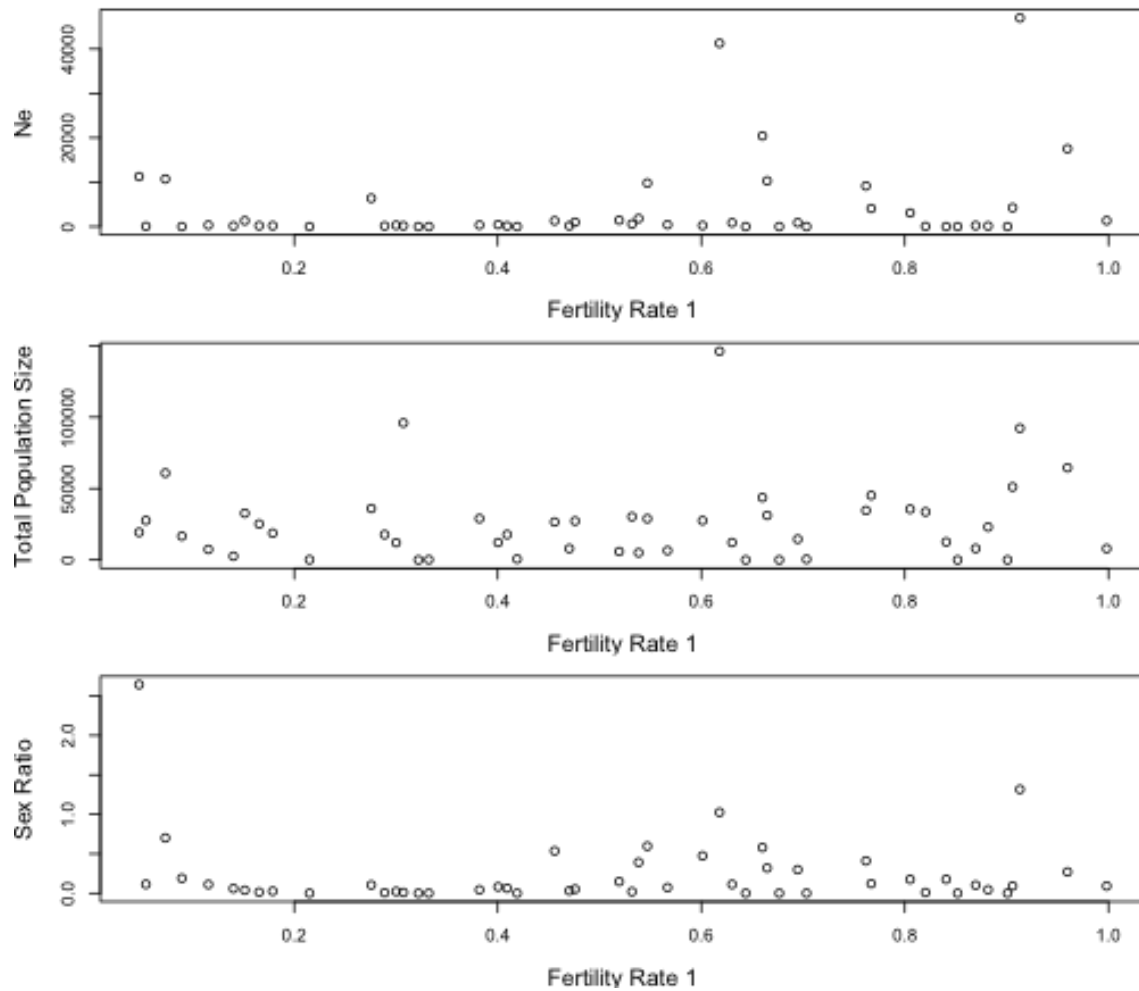


Correlation between fecundity parameter 2 and output variables
From top to bottom, fecundity parameter 2 correlated with effective population size, total population size, and sex ratio, respectively

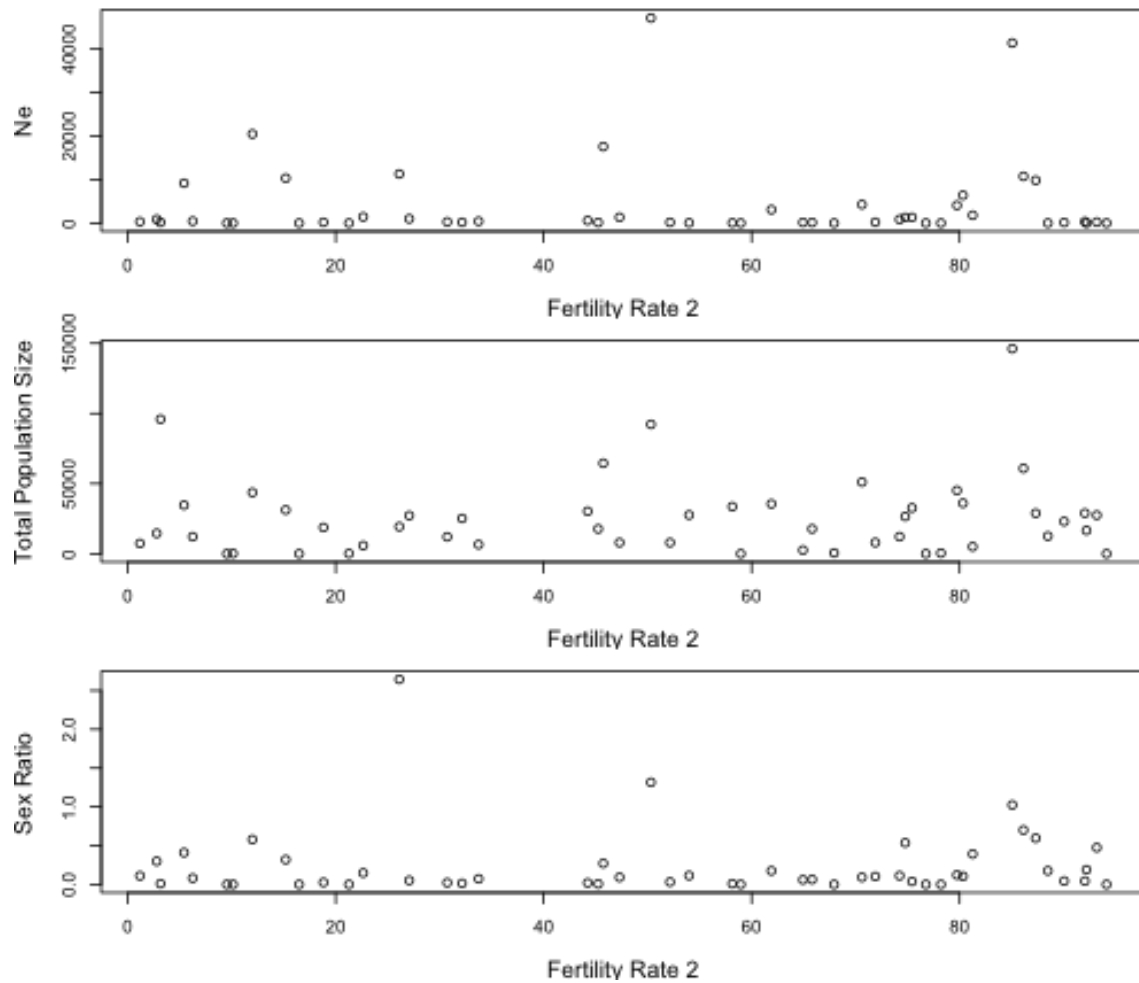


Correlation between fecundity parameter 3 and output variables

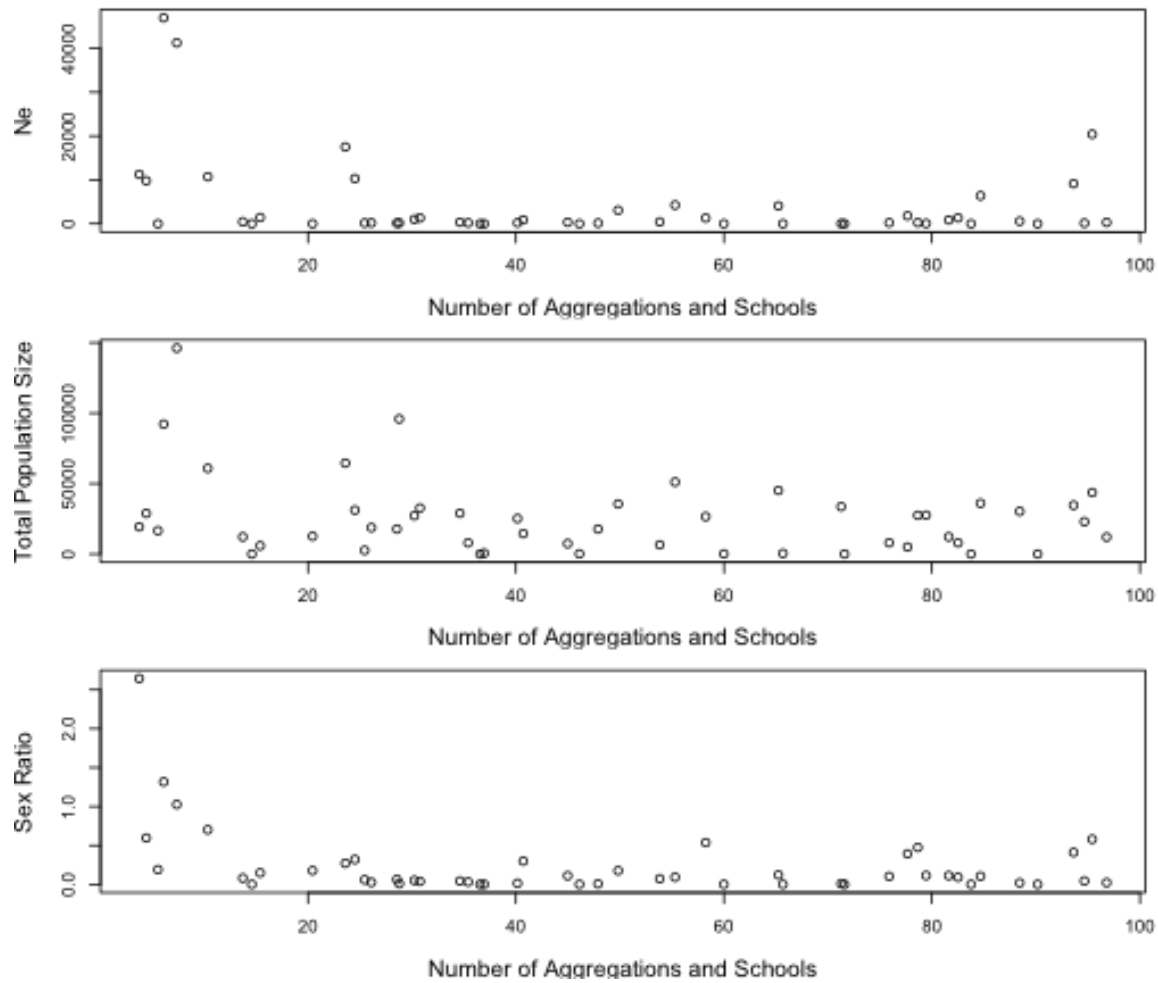
From top to bottom, fecundity parameter 3 correlated with effective population size, total population size, and sex ratio, respectively



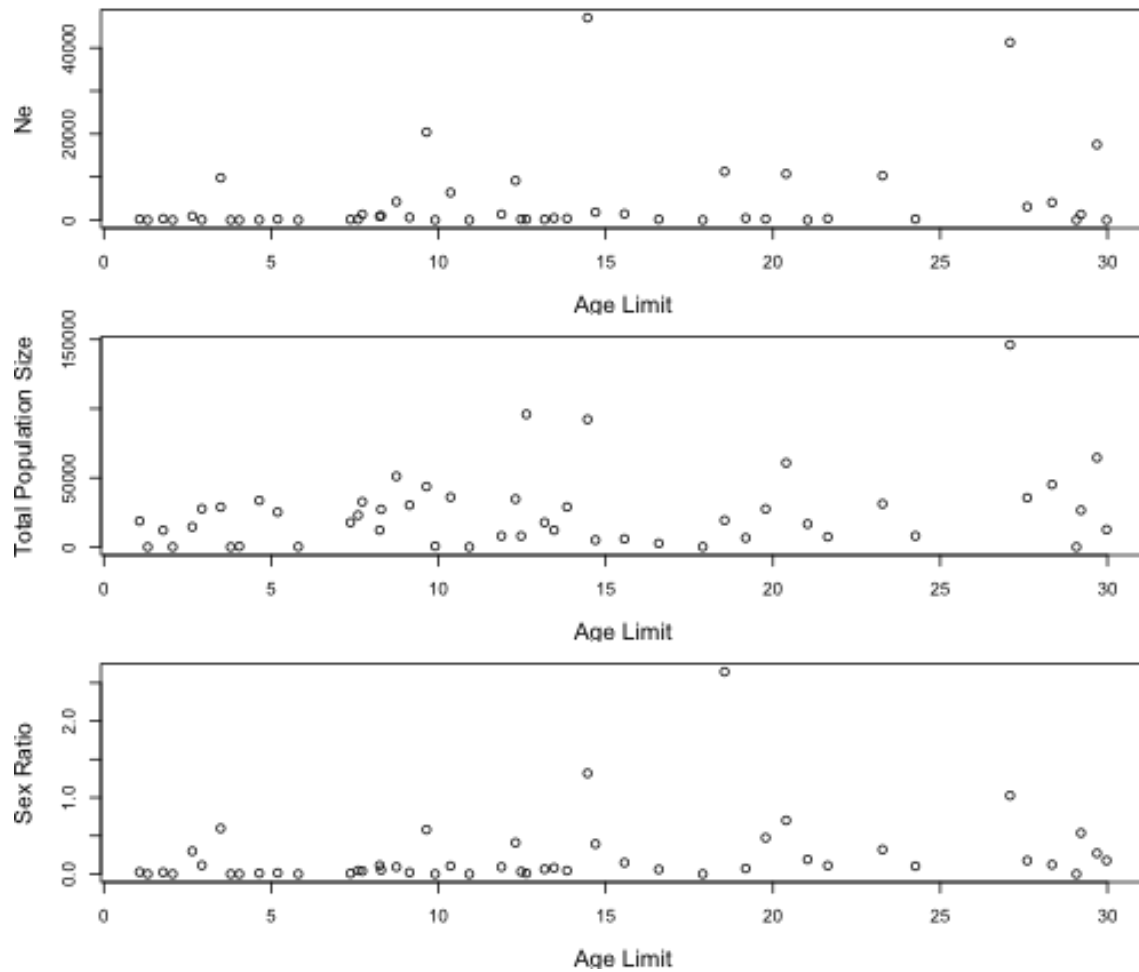
Correlation between fertility rate parameter 1 and output variables
From top to bottom, fertility rate parameter 1 correlated with effective population size, total population size, and sex ratio, respectively



Correlation between fertility rate parameter 2 and output variables
 From top to bottom, fertility rate parameter 2 correlated with effective population size,
 total population size, and sex ratio, respectively

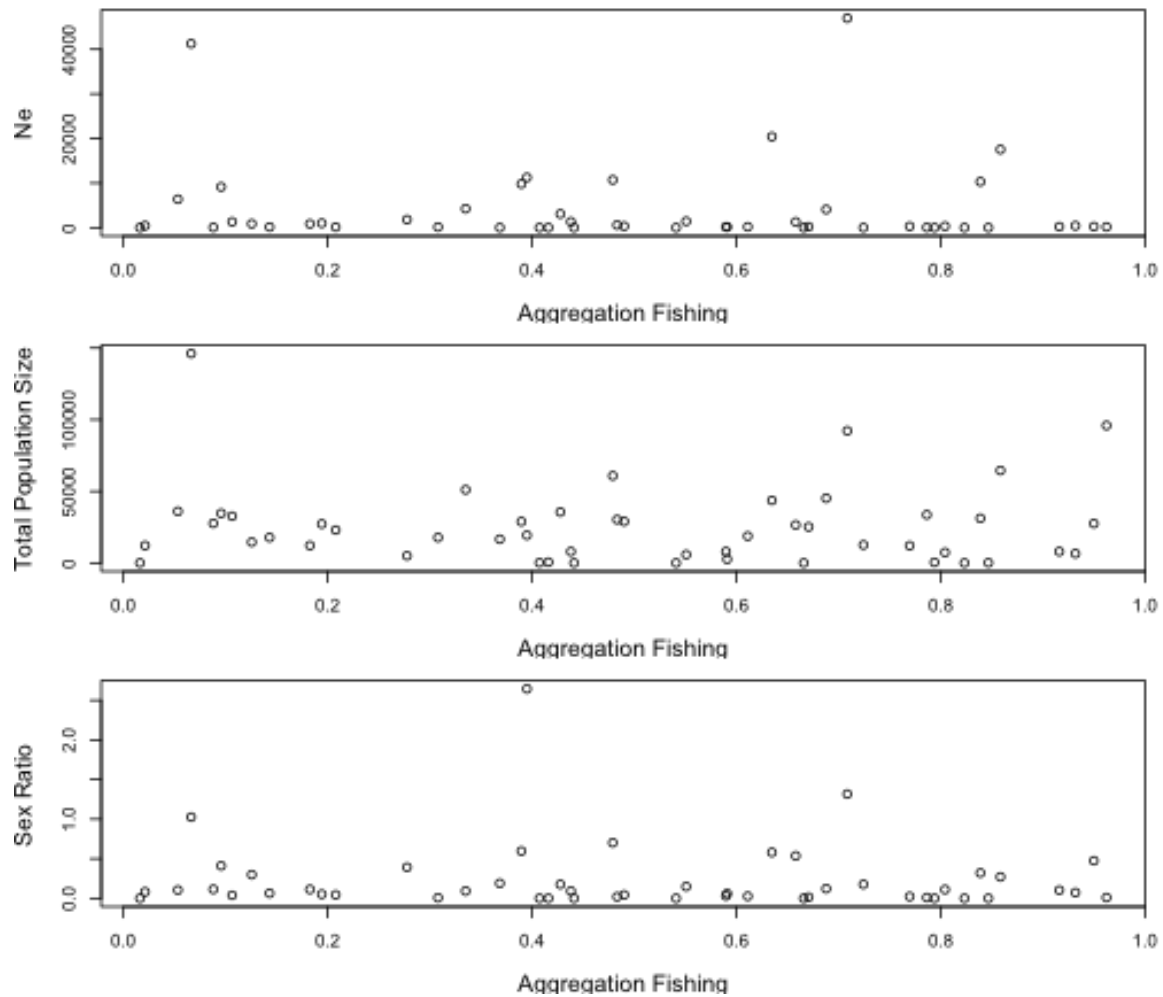


Correlation between number of aggregations and schools, and output variables
 From top to bottom, number of aggregations and schools correlated with effective population size, total population size, and sex ratio, respectively



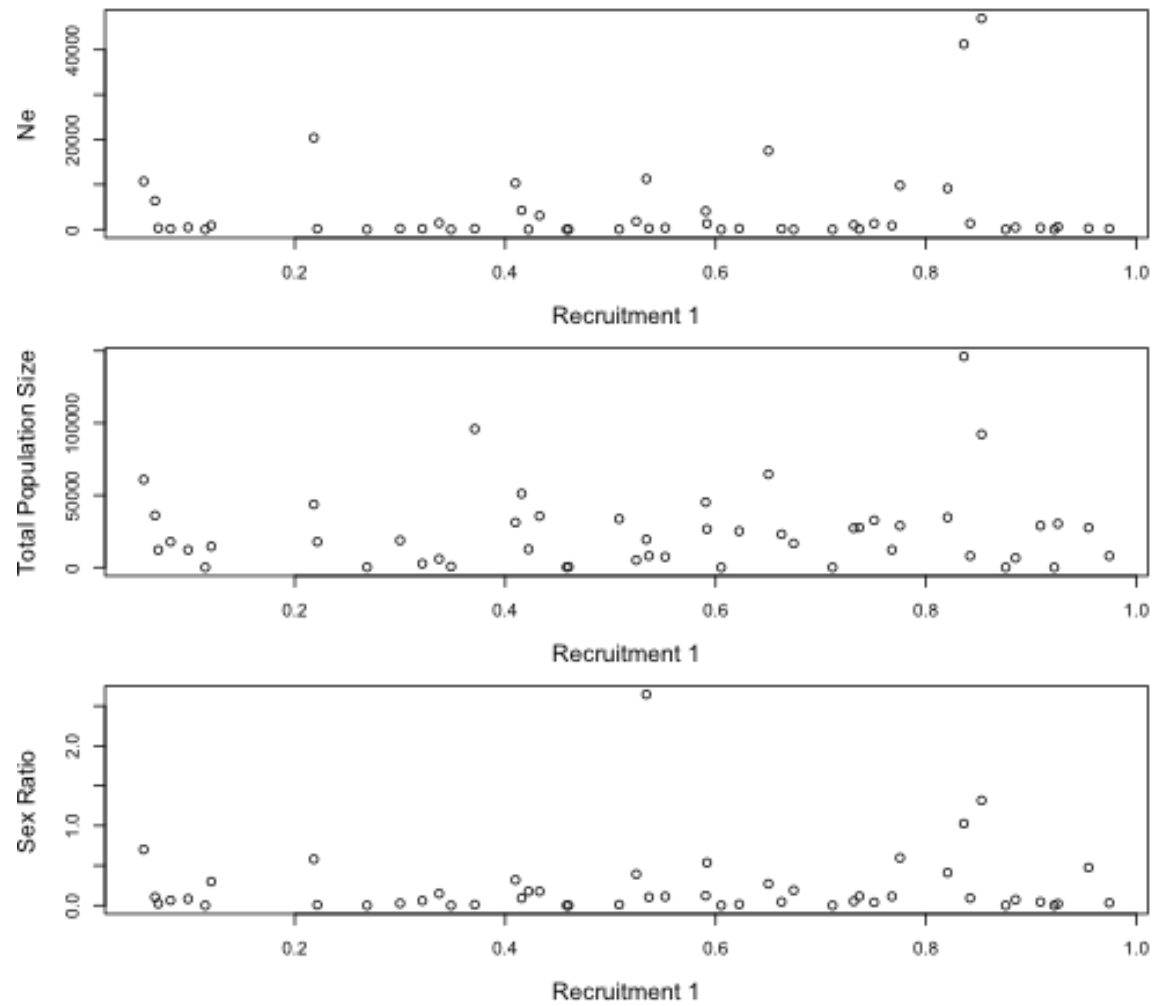
Correlation between age limit and output variables

From top to bottom, age limit correlated with effective population size, total population size, and sex ratio, respectively

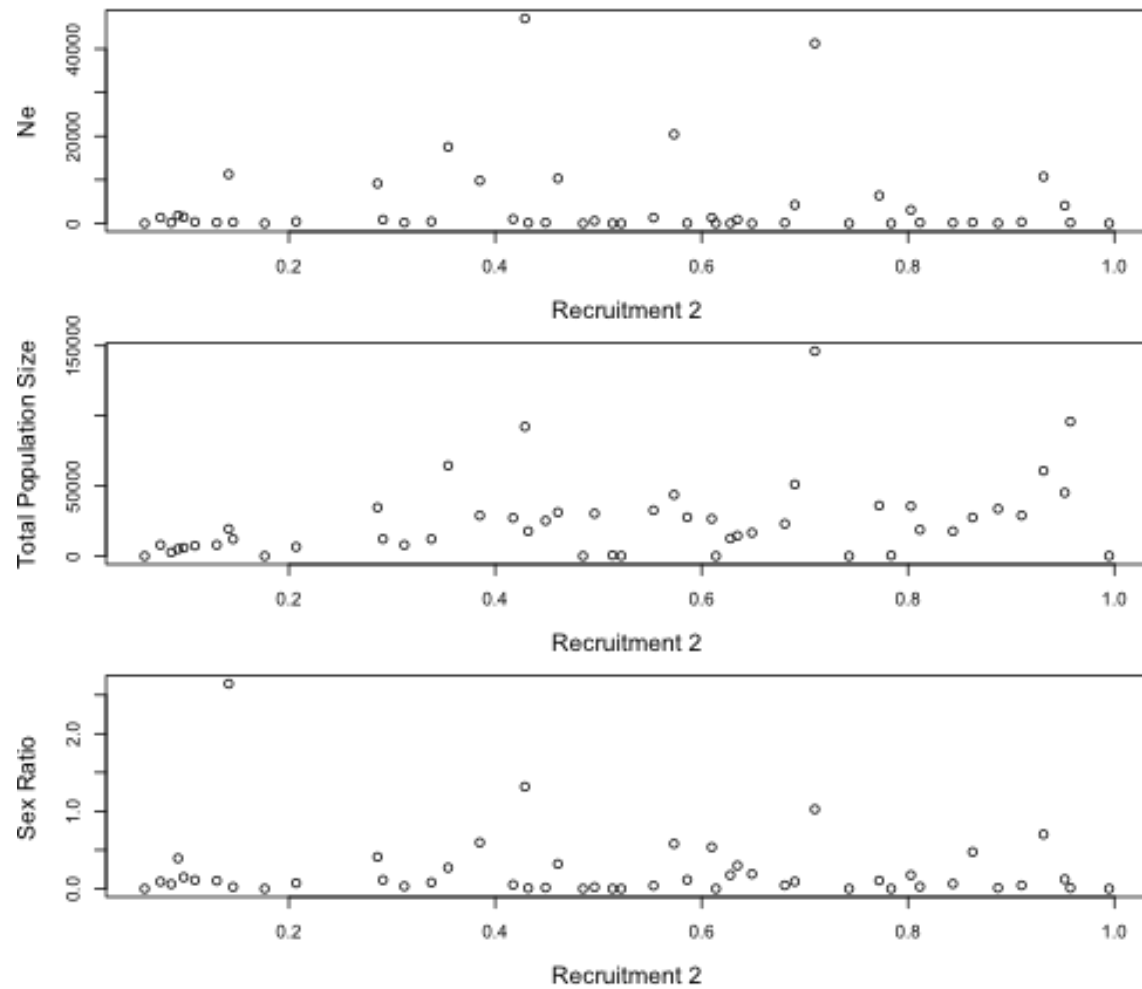


Correlation between aggregation fishing and output variables

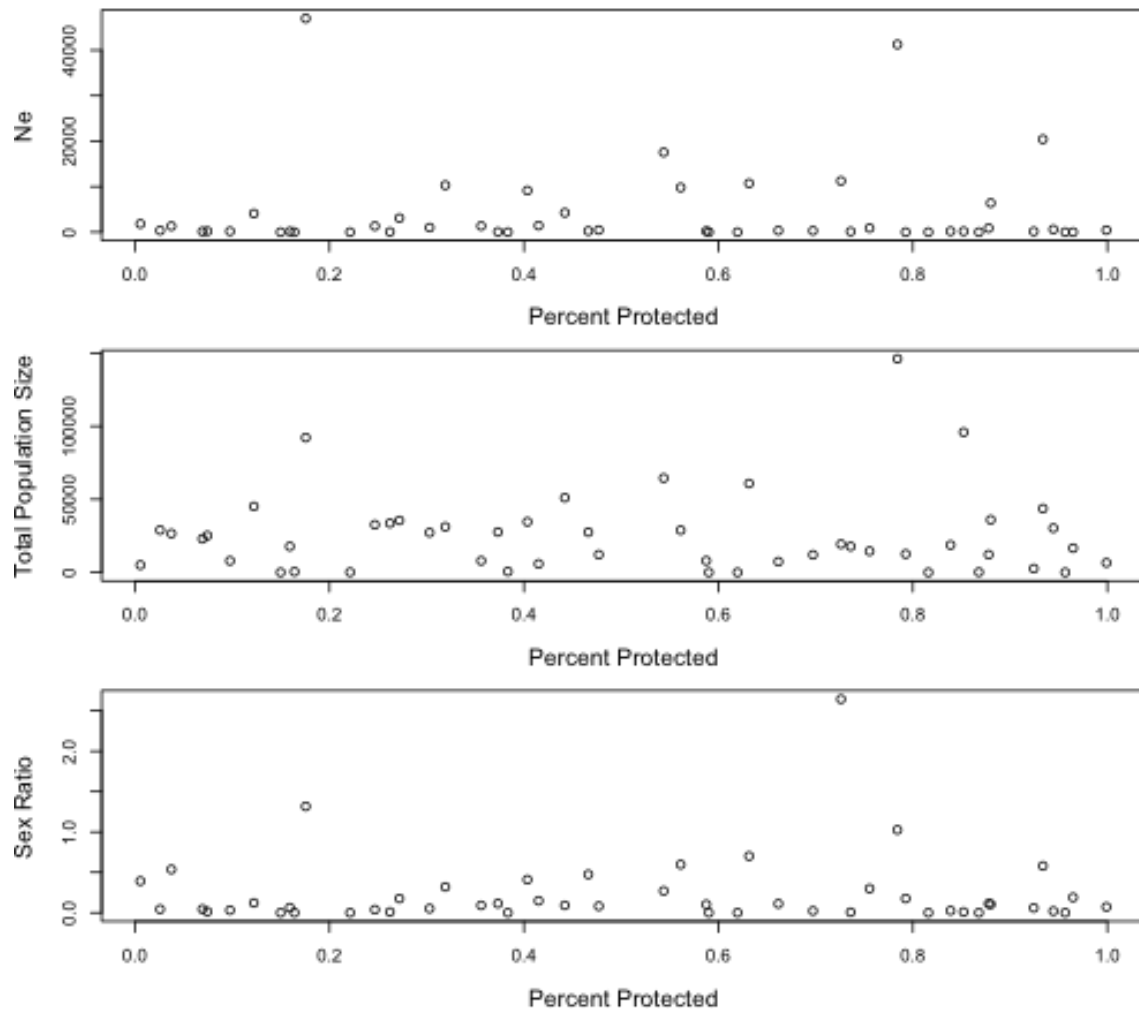
From top to bottom, fishing pressure on aggregations correlated with effective population size, total population size, and sex ratio, respectively



Correlation between recruitment parameter 1 and output variables
From top to bottom, recruitment parameter 1 correlated with effective population size, total population size, and sex ratio, respectively



Correlation between recruitment parameter 2 and output variables
From top to bottom, recruitment parameter 2 correlated with effective population size, total population size, and sex ratio, respectively



Correlation between percent protected and output variables
From top to bottom, percent of the model space protected correlated with effective population size, total population size, and sex ratio, respectively

APPENDIX B

Main Class

```
package gag;

import java.util.*;

public class Main {

    public static void main(String[] args) {

        Random rng = new Random ();

        int xloci = 3;

        int xalleles = 4;

        double larmort = 0.99;

        double natmort = 0.15;

        //VARIABLES TO CHANGE FOR VARIOUS SCENARIOS//

        int initsize = 50000;           //size of starting population

        double fishmort = 0;           //mortality from fishing

        double ageLimit = 1;           //age at which fish can be kept by fishermen

        int numAggs = 10;              //number of spawning aggregations

        int numSchools = numAggs;       //number of schools is equal to the number of
        aggregations

        boolean femBehavior = false;    //females behavior: true = return to same agg, false =
        go to closest agg

        boolean popFert = false;        //if pop fertility is imposed, then true

        boolean varFishMort = false;    //if variable fishing mortality is used, then true

        double agF = 0;                //value of fishing mortality inside an aggregation
```



```

boolean reserves = false;          //if reserves are implemented then true

int scenario = 0;                   //scenario refers to the protected area scenario in place, where
0 = percent protection of the entire model space

double percentProtected = 0.1;      //percent of area protected

int years = 35;                     //years to run program

int time = 12;                      //months in the year

int outputPeriod = 30;              //years to output

double avgJuvPop = 20000;

double k = 2;

double theta = 2;

double pfslope = 7;                 //steepness of probability fxn of switching sex (from
retrofitting data)

double maxDist = 10;                //maximum male distance

double sampleDist = 10;             //radius distance for spatial sample

int OSRx = 40;                      //Off shore reef coordinate on x axis = 40;

int NSRx = 80;                      //Near Shore Reef coordinate on x axis = 80;

int SGBx = 120;                     //Sea Grass Bed coordinates on x axis = 120

int coords = 2;                     //x and y coordinates

```

Population pop = new Population (xloci, xalleles, coords, SGBx, numAggs, numSchools, outputPeriod);

```
//-----//
```

```
//initialize//
```

```
//-----//
```

```
pop.initializeVector(initsize);
```

```

pop.initProportions(initsize);

pop.initializeAggregations(numAggs);

pop.setInitAgeGend();

pop.initPopGeno(xloci);

pop.Fecundity(pop.v);

pop.countPop(pop.v);

pop.setCurrentPop();

if(reserves == true)
{
    pop.fillReserve_Matrix(pop.createReserves(rng, percentProtected), scenario);

    pop.createReserves(rng, percentProtected);

    System.out.println("percent protected = " + percentProtected);
}
    //System.out.println("fishmort = " + fishmort + " ; agFish = " + agF);

for (int j=1; j<=years; j++)
{
    pop.clearVectors();

    pop.changeSex();

    pop.countPop(pop.v);

    pop.buildPopArray(pop.totalPopArray);

    pop.buildPopArray(pop.subPopArray);

    pop.natMortality();

    if(varFishMort == false)
    {
        pop.fishingMortality(fishmort, ageLimit, reserves);
    }

    else if(varFishMort == true)
    {

```

```

    pop.varfishMortality(fishmort, ageLimit, agF, maxDist);
}

pop.countPop(pop.v);

pop.setCurrentPop();

pop.Fecundity(pop.v);

pop.getVectors();
    //System.out.println("females.size = " + pop.Females.size());

//loop over months//

    for(int i = 1; i<=time; i++)

    {

        pop.countTime(i);

        int cm = pop.getTime();

        //-----//

        //switch gender//

        //-----//

        if(i==2)

        {

            pop.switchGender(pfslope);

        }

        //-----//

        //movement//

        //-----//

        pop.maleMove(rng, maxDist);

        pop.femaleMove(rng, OSRx, NSRx, pop.SEAx, pop.SEAy, i, femBehavior);    //true
        means females behavior = returning to same agg each year

```

```

    pop.juvMove(rng, SGBx, NSRx, femBehavior);

//-----//

//reproduction//

//-----//

    if(i==3)
    {
        pop.countPop(pop.v);

        pop.setCurrentPop();

        pop.sexRatio();

        if(pop.sexRatio > 0 || pop.countTrans > 0)
        {
            pop.countPop(pop.v);

            int femSampSize = (int)(pFem*(double)pop.countFem);

            int[]femsamp = new int[femSampSize];

            pop.initializeFemSamp(femSampSize);

            pop.getFemSamp(femsamp);

            //pop.Fecundity(pop.F);

            pop.Spawn(femBehavior);

            pop.Recruitment(k, theta, larmort, avgJuvPop);

            if(popFert == true)
            {
                pop.popFertility(pop.sexRatio);
            }

            for (int z=0; z<pop.PL; z++)
            {
                pop.eggtoPL(xloci, xalleles);
            }
        }
    }

```

```

        }

        pop.countPop(pop.v);

        pop.setCurrentPop();
    }

    else

    {
        System.out.println("no males at generation " + j);

        System.out.println("pop size (no males) = " + pop.currentpop);

        pop.countPop(pop.v);

        pop.fillPopArray();

        break;
    }

}

pop.PLMove(rng);

pop.PLtoBJ(SGBx);

pop.juvMove(rng, SGBx, NSRx, femBehavior);

}

//-----//

//output population//

//-----//

int startOutput = years - outputPeriod;

pop.countPop(pop.v);

pop.fillPopArray();

```

```

    if(j >= startOutput)
    {
        pop.addNe(j - startOutput, pop.calcEffectPopSize());

        if(j == years)
        {
            pop.calcHarmonicMean();
        }
    }

//-----//

//aging//

//-----//
    pop.Aging();
}

}

}

```

Population Class

```
package gag;
import java.util.*;
public class Population {
    Random rng = new Random(); //random number generator
    int countFem;           //keeps track of number of females
    int countJuv;           //keeps track of number of juveniles
    int countNew;           //keeps track of surviving newborn larval stage individuals
    int countMal;           //keeps track of number of males
    int countTrans;         //keeps track of number of transitionals
    int totalPopArray[];     //displays the population by age class
    int subPopArray[];       //displays the population by age class of subsample
    double []myF_Array;
    double []myA_Array;
    int femsamp[];
    double EPSArray[];      //effective population size array for last years of sampling
    double larmort;          //larval mortality rate
    double juvmort;          //juvenile mortality rate
    double natmort;          //natural mortality rate
    double fishmort;         //mortality rate due to fishing
    int countnatDead;        //counts fish dead from natural mortality
    int countjuvNatDead;     //counts dead juveniles from DD in seagrass
    int countfishDead;       //counts fish dead from fishing mortality
    int samplesize;          //gives sample size
    Vector u;                //subsample pop vector
}
```

```

Vector v;           //population vector

Vector F;           //female subsample for reproduction vector

Vector Females;     //total female pop to use for subsampling

Vector Males;

Vector PLarvae;

Vector Juvs;

int currentpop;      //method to set and output current population

double prSwitch;     //probability of female individual changing sex

int possiblenew;     //possible number of newborns based on fecundity

int PL;             //total number of Pelagic Larvae spawned after larval mortality

Individual fish, fish2; //labels each individual as a fish

int initsize;        //given initial size

double fecund;       //fecundity of individual

int xalleles;        //number of alleles at each locus

int xloci;

int mi;             //mom index

int pi;             //dad index

int[] mh;           //mom haplotype

int[] dh;           //dad haplotype

double fertRate;

double sexRatio;

int initjuv;

int initfem;

```



```
int initmal;  
int initM;  
int initF;  
double alpha;  
double maxDist;  
double currDist;  
int OSRx;  
int OSRy;  
int SGBx;  
int SGBy;  
int NSRx;  
int NSRy;  
int[] SEAx;  
int[] SEAy;  
int[][] reserveMatrix;  
int time;  
int outputPeriod;  
int SLeft;  
int CLeft;  
int numAggs;  
int numSchools;  
int newx;  
int newy;
```

```

int coords;

int month = 0;

int year = 0;

double[][] pFreqs;

//:default constructor://

public Population (int xloci,int xalleles, int coords, int SGBx, int numAggs, int numSchools, int
outputPeriod)
{

    this.xloci=xloci;

    this.xalleles=xalleles;

    this.coords = coords;

    this.SGBx = SGBx;

    this.SGBy = SGBy;

    this.OSRx = OSRx;

    this.OSRy = OSRy;

    this.NSRx = NSRx;

    this.NSRy = NSRy;

    this.numAggs = numAggs;

    this.numSchools = numSchools;

    this.outputPeriod = outputPeriod;

    SEAx = new int[numAggs];

    SEAy = new int[numAggs];

    for(int i =0; i<numAggs; i++)
    {
        SEAx[i] = 0;

```

```

        SEAy[i] = 0;
    }

    totalPopArray = new int[5];

    subPopArray = new int[5];

    reserveMatrix = new int[121][121];

    v= new Vector ();                //why commented out?

    u = new Vector ();

    F = new Vector();

    Males = new Vector();

    Females = new Vector();

    PLarvae = new Vector();

    Juvs = new Vector();

    dh = new int[xloci];

    mh = new int[xloci];

    for(int i=0; i<xloci; i++)

    {
        mh[i]=0;

        dh[i]=0;
    }

    EPSArray = new double[outputPeriod];
}

//:initializes total population array://

public int [] buildPopArray(int[] array)

{
    for (int i=0; i<5; i++)

    {

```

```

        array [i] = 0;
    }

    return array;
}

//:initialize vector of individuals://
public void initializeVector(int initsize)
{
    v = new Vector(initsize);
    for(int i=0; i<initsize; i++)
    {
        fish = new Individual();
        fish.createHaplo(xloci);
        v.add(i, fish);
    }
}

public void countTime(int time)
{
    month = time;
    if(time == 12)
    {
        year++;
    }
}

```

```

public int getTime()
{
    return month;
}

public void initProportions(int initsize)
{
    initjuv = (int)Math.round(0.6*initsize);
    initfem = (int)Math.round(0.3*initsize);
    initmal = (int)Math.round(0.1*initsize);
}

//:assign initial age classes in vector://

public void setInitAgeGend ()
{
    for(int i=0; i<initjuv; i++)
    {
        fish = (Individual) v.get(i);
        fish.setNumAlleles(xalleles);
        fish.setAge(rng.nextInt(6)+1); //1-5yrs
        fish.setGender(0);
        fish.setPosition(120, rng.nextInt(120));
    }

    for(int i=initjuv; i<(initjuv + initfem); i++)
    {
        fish = (Individual) v.get(i);

```

```

        fish.setNumAlleles(xalleles);

        fish.setAge(rng.nextInt(5)+6); //6-10yrs

        fish.setGender(0);

        fish.setPosition(rng.nextInt(120), rng.nextInt(120));

        fish.setSchool(rng.nextInt(numSchools));

    }

    for(int i=(initjuv + initfem); i<v.size(); i++)
    {

        fish = (Individual) v.get(i);

        fish.setNumAlleles(xalleles);

        fish.setAge(rng.nextInt(21)+11); //11-31yrs

        fish.setGender(1);

        int randAgg = rng.nextInt(numAggs);

        fish.setAgg(randAgg);

        fish.setPosition(SEAx[randAgg], SEAy[randAgg]);

    }

}

public void initializeAggregations(int numAggs)
{
    for(int i = 0; i < numAggs; i++)
    {
        SEAx[i] = 5;
        SEAy[i] = rng.nextInt(120);

    }

    for(int i = 0; i < numAggs; i++)
    {
        System.out.println("SEAx" + "\t" + "SEAy");
    }
}

```

```

        System.out.println(SEAx[i] + "\t" + SEAy[i]);
    }

}

public void clearVectors()
{
    PLarvae.setSize(0);
    Juvs.setSize(0);
    Females.setSize(0);
    Males.setSize(0);
}

public double sexRatio()
{
    sexRatio = ((double)countMal/((double)countFem));
    return sexRatio;
}

public void Fecundity(Vector v)
{
    possiblenew = 0;
    for (int i=0; i<v.size(); i++)
    {
        fish = (Individual) v.get(i);
        fish.getFecundity(rng);
        possiblenew += fish.fecund;
    }
}

```

```

    }
}

//:method to get actual fertility rates://
public void popFertility(double sexRatio)
{
    possiblenew = 0;
    for (int i=0; i<v.size(); i++)
    {
        fish = (Individual) v.get(i);
        fish.getFecundity(rng);
        fertRate = fish.fecund * (0.8 * (1 - Math.exp(-80*sexRatio)));
        possiblenew += (int)Math.round(fertRate);
    }
}

//:increases age by one year and removes individuals over age 30://
public void Aging()
{
    for (int i=0; i<v.size(); i++)
    {
        fish = (Individual) v.get(i);
        fish.Older();
        if (fish.getAge()>=30)
            v.remove(i);
    }
}

```



```

    }
}

//:removes individuals by natural mortality://

public void natMortality ()
{
    countnatDead = 0;
    for (int i=v.size()-1; i>=0; i--)
    {
        fish = (Individual) v.get(i);
        if (fish.age > 1)
        {
            double die = rng.nextDouble();
            double mort = 0.4298*Math.pow(fish.age, -0.488);
            if(die <= mort)
            {
                v.remove(i);
                countnatDead++;
                // System.out.println("Fish " + i + " = dead");
                // System.out.println("Current pop size = " + v.size());
            }
        }
    }
}

```

```

//:removes individuals by fishing mortality://

public void fishingMortality (double fishmort, double ageLimit, boolean reserves)
{
    countfishDead = 0;
    for (int i=v.size()-1; i>=0; i--)
    {
        fish = (Individual) v.get(i);

        if (fish.age >= ageLimit)
        {
            double die = rng.nextDouble();

            if(reserves == true)
            {
                if(die < fishmort*reserveMatrix[fish.x][fish.y])
                {
                    v.remove(i);

                    countfishDead++;
                }
            }
            else if (reserves == false)
            {
                if(die < fishmort)
                {
                    v.remove(i);

                    countfishDead++;
                }
            }
        }
    }
}

```

```

    }
}

//:removes individuals by variable fishing mortality://

public void varfishMortality (double fishmort, double ageLimit, double agFishing, double
agDist)

{
    countfishDead = 0;

    for (int i=v.size()-1; i>=0; i--)
    {
        fish = (Individual) v.get(i);

        fish.getPosition();

        if (fish.age >= ageLimit)
        {
            double minDist = 10000;

            for(int j = 0; j < numAggs; j++)
            {
                currDist = Math.sqrt(Math.pow((fish.getX() - SEAx[j]),2) +
                Math.pow((fish.getY() - SEAy[j]),2));

                if (currDist < minDist)
                {
                    minDist = currDist;
                }
            }

            if(minDist <= agDist)
            {
                double test = rng.nextDouble();

                if(test <= agFishing)

```

```

        {
            v.remove(i);

            countfishDead++;
        }

    }

    else if(rng.nextDouble() <= fishmort)

    {

        v.remove(i);

        countfishDead++;

    }

}

}

}

public void fillReserve_Matrix(int[] reserveCoords, int scenario)
{
    for(int i = 0; i < reserveMatrix.length; i++)
    {
        for(int j = 0; j < reserveMatrix[0].length; j++)
        {
            reserveMatrix[i][j] = 1;
        }
    }

    int start = 0;
    int stop = 0;

    if(scenario ==0)        //total area of model space
    {
        start = 0;
        stop = 120;
    }

    else if(scenario ==1)    //area of SEA only
    {
        start = 0;
        stop = 10;
    }

```

```

    }

    else if(scenario ==2)          //area of OSR only
    {
        start = 35;
        stop = 45;
    }

    else if(scenario ==3)          //area of NSR only
    {
        start = 75;
        stop = 85;
    }

    else if(scenario ==4)          //area of SGB only
    {
        start = 110;
        stop = 120;
    }

    for(int i = 0; i < reserveCoords.length; i++)
    {
        for(int j = start; j < stop; j++)
        {
            reserveMatrix[reserveCoords[i]][j] = 0;
        }
    }
}

public int[] createReserves(Random rng, double percentProtected)
{
    Vector v1 = new Vector();
    Vector v2 = new Vector();
    int pick = 0;
    int increment = (int)(1.0/percentProtected);

    int i = 0;
    while (i < 120)
    {
        v1.add(i);
        i=i+increment;
    }
    i=0;
    while (i < v1.size())
    {
        pick = rng.nextInt(v1.size());

```

```

        v2.add(v1.get(pick));
        v1.removeElementAt(pick);
    }

    int reserveCoords[] = new int [v2.size()];

    for(int j = 0; j < reserveCoords.length; j++)
    {

        reserveCoords[j] = (Integer)v2.get(j);

    }

    return reserveCoords;
}
public void maleMove(Random rng, double maxDist)

{

    for(int i = 0; i<Males.size(); i++)

    {

        fish = (Individual) Males.get(i);

        fish.getPosition();

        currDist = 0;

        int newDist = 0;

        currDist = Math.sqrt(Math.pow((fish.getX() - SEAx[fish.getAgg()]),2) +
        Math.pow((fish.getY() - SEAy[fish.getAgg()]),2));

        newDist = (int)Math.round(maxDist - currDist);

        fish.newMalePosition(rng, newDist);

    }

}

public void femaleMove(Random rng, int OSRx, int NSRx, int[] SEAx, int[] SEAy, int month,
boolean behavior)

```

```

{
    int a1, a2, a3, a4, a5;
    a1 = 0;
    a2 = 0;
    a3 = 0;
    a4 = 0;
    a5 = 0;

    for(int i = 0; i<Females.size(); i++)
    {

        fish = (Individual) Females.get(i);

        if (year == 0 && month == 1)    //OFFSHORE REEF//
        {

            fish.setPosition(OSRx, rng.nextInt(120));    //OFFSHORE REEF COORDS: OSRX
= 40, OSRY B/N 0,119

        }

        if(month==2||month==3)    //SPAWN//

        {
            double minDist = 10000;
            int myAgg = 100;

            for(int j = 0; j < numAggs; j++)
            {
                if (behavior == false)
                {
                    //for females going to closest aggregation each year

                    currDist = Math.sqrt(Math.pow((fish.getX() - SEAx[j]),2) +
                    Math.pow((fish.getY() - SEAy[j]),2));
                    if (currDist < minDist)
                    {
                        minDist = currDist;
                        myAgg = j;
                    }
                }

            }

            else if (behavior == true)

```

```

    {
        //for females returning to same aggregation each year
        if(fish.school == j)
        {
            myAgg = j;
        }
    }
    fish.setPosition(SEAx[myAgg], SEAy[myAgg]);

    //count how many are in each agg//
    if(myAgg == 0)
        a1++;

    else if(myAgg == 1)
        a2++;

    else if(myAgg == 2)
        a3++;

    else if(myAgg == 3)
        a4++;

    else if(myAgg == 4)
        a5++;

}

else if (month == 9 || month == 10 || month == 11)    //NEARSHORE REEF//
{

    fish.setPosition(NSRx, rng.nextInt(120));          //COORDS: NSRX = 60, NSRY B/N
    0,159

}

else if (month == 12)    //OFFSHORE REEF//
{
    fish.setPosition(OSRx, rng.nextInt(120));          //OFFSHORE REEF COORDS: OSRX
    = 60, OSRY B/N 0,159

}

else    //MOVE RANDOMLY//

{
    fish.newFemalePosition(rng);
}

```



```

    }
}

public void juvMove(Random rng, int SGBx, int NSRx, boolean behavior)
{
    for(int i = 0; i<Juvs.size(); i++)
    {
        fish = (Individual) Juvs.get(i);
        if(fish.age <= 1 && month < 9)
        {
            int juvdist = SGBx - fish.getX();
        }

        else if (fish.age == 1 && month == 9)
        {
            fish.setPosition(NSRx, rng.nextInt(120));
            fish.setSchool(rng.nextInt(numSchools));
        }

        else
        {
            int juvdist = NSRx - fish.getX();
            fish.newJuvPosition(rng, juvdist);
        }
    }
}

public void PLMove(Random rng)
{
    for(int i = 0; i<PLarvae.size(); i++)
    {

```

```

        fish = (Individual) PLarvae.get(i);

        fish.newPLPosition(rng);

        if(time == 4)

        {

            fish.setPosition(SGBx, rng.nextInt(120));

        }

    }

}

public void setAFArraySize()

{

    myF_Array = new double[v.size()];

    myA_Array = new double[v.size()];

    for(int i=0; i<myF_Array.length; i++)

    {

        myF_Array[i] = 0.0;

        myA_Array[i] = 0.0;

    }

}

//:calculates probability of females becoming transitionals based on frequency of younger
females://

public void switchGender(double pfslope)

{

    double countSwitch = 0;

    double FC = .95;

```

```

double F = 0;

setAFArraySize();
for (int i=0; i<v.size(); i++)

{
    double countYoungerFems = 0;
    double a = fish.age;

    fish = (Individual) v.get(i);

    if (fish.getGender()==0 && fish.getFecundity(rng)>0)
    {
        int S_fish1 = fish.getSchool();

        for(int j = 0; j < Females.size(); j++)
        {

            fish2 = (Individual) Females.get(j);

            int S_fish2 = fish.getSchool();

            if (S_fish1 == S_fish2 && fish2.age < a)
            {
                countYoungerFems++;
            }
        }

        F = countYoungerFems/Females.size();

        prSwitch = 1/(1 + Math.exp(-(pfslope*(F-FC))));

        if(rng.nextDouble() <= prSwitch)

        {

            fish.setGender(2);

            countSwitch ++;

            fillFarray(i,F);

            fillAarray(i,(double) fish.age);

        }
    }
}

```

```

    }

}

}

//:calculates probability of females becoming transitionals based on age://
public void switchGender()

{

    if(month==2)

    {
        double countSwitch = 0;

        setAFArraySize();
        for (int i=0; i<v.size(); i++)

        {

            fish = (Individual) v.get(i);

            double countYoungerFems = 0;

            double F = 0;

            double a = fish.age;

            if (fish.getGender()==0 && fish.getFecundity(rng)>0)

            {

                for(int j = 0; j < Females.size(); j++)

                {

                    fish2 = (Individual) v.get(j);

                    if(fish2.age < a)

                    {

                        countYoungerFems++;

```

```

    }
}

F = countYoungerFems/Females.size();

prSwitch = 1/(1+Math.exp(-(6.89 - 0.637*fish.getAge())));
if(rng.nextDouble() >= prSwitch)
{
    fish.setGender(2);
    countSwitch ++;
    fillFarray(i,F);
    fillAarray(i,(double) fish.age);
}
}
}
}

public void fillFarray(int index, double a)
{
    myF_Array[index]=a;
}

public void fillAarray(int index, double a)
{

```

```

    myA_Array[index]=a;
}

//:calculates mean of an array://
public double calcMean(double[]a)
{
    double mean = 0;
    int counter = 0;
    for(int i = 0; i < a.length; i++)
    {
        if(a[i]>0)
        {
            mean += a[i];
            counter++;
        }
    }
    mean/=counter;

    return mean;
}

//:calculates variance of an array://
public double calcVar(double[]a)
{
    double var = 0;
    int counter = 0;
    double mean = calcMean(a);

```

```

for(int i = 0; i<a.length; i++)
{
    if(a[i]>0)
    {
        var += Math.pow((a[i] - mean),2);

        counter++;
    }
}
var/=counter;

return var;
}

//:changes sex of transitional to male://
public void changeSex()
{
    for(int i=0; i<v.size(); i++)
    {
        fish = (Individual) v.get(i);

        if(fish.gend ==2)
        {
            fish.setGender(1);
            int randAgg = rng.nextInt(numAggs);
            fish.setAgg(randAgg);
            fish.setPosition(SEAx[randAgg], SEAy[randAgg]);
        }
    }
}

```

```

}

//:counts the number of individuals in each category://
public void countPop(Vector v)
{
    countJuv = 0;
    countFem = 0;
    countMal = 0;
    countTrans = 0;
    countNew = 0;
    for(int i=0; i<v.size(); i++)
    {
        fish = (Individual) v.get(i);
        if(fish.gend==0)
        {
            if(fish.age >=1)
            {
                if(fish.fecund>0)
                {
                    countFem++;
                }
                else if(fish.fecund == 0)
                {

```



```

        countJuv++;
    }
}
else
    countNew++;
}
else if(fish.gend==1)
{
    countMal++;
}
else if(fish.gend == 2)
{
    countTrans++;
}

}
setCurrentPop();
}

```

//:counts the total population://

```
public void setCurrentPop()
```

```
{
```

```
    currentpop = 0;
```

```
    currentpop = countJuv + countFem + countMal + countTrans + countNew;
```

```

public void fillPopArray()
{
    int [] array = new int[5];

    array[0] = PL;

    array[1] = countJuv;

    array[2] = countFem;

    array[3] = countMal;

    array[4] = countTrans;

    //    System.out.println("Categories");
    //    System.out.println("0\t1\t2\t3\t4");

    for(int i=0; i<array.length; i++)
    {
        //        System.out.println("Category" + i + " = " + array[i]);

        System.out.print(array[i] + "\t");

    }

    System.out.print(currentpop);

    System.out.println()

}

//density-dependent recruitment function

public void Recruitment(double k, double theta, double larMort, double avgJuvPop)
{
    double gamma = 0.0;

    gamma = (GammaSampler2.sampleGamma(k, theta))/8;

```

```

        //System.out.println("possible new inside recruitment method: " + possiblenew);

        PL = (int) Math.round(possiblenew*(1-larMort)*(gamma));

        //System.out.println("PL before avgJuvPop = " + PL);

        if(PL>avgJuvPop)

        {

            PL = (int)(avgJuvPop*gamma);

        }

        //System.out.println("gamma = \t" + gamma + "\tPL after avgJuvPop = " + PL);

    }

    public int newRecruitment(double k, double theta, double larMort, double K)

    {

        double gamma = 0.0;

        gamma = (GammaSampler2.sampleGamma(k, theta))/8;

        //System.out.println("possible new inside recruitment method: " + possiblenew);

        PL = (int) Math.round(possiblenew*(1-larMort)*(gamma));
        //System.out.println("gamma\t" + gamma + "\tPL\t" + PL);

        return PL;

    }

    public void Spawn(boolean femBehavior)
    {
        possiblenew = 0;

        for(int i = 0; i<numAggs; i++)
        {
            int countSpawningMales = 0;

            for(int j = 0; j<v.size(); j++)
            {
                fish = (Individual) v.get(j);

```

```

        //System.out.println("fish " + j + " and fish gend = " + fish.gend + ", agg = " + fish.agg
+ " or school = " + fish.school);

        if(fish.gend==1 && fish.agg==i)
        {
            countSpawningMales++;
            //System.out.println("male fish " + j);
        }
    }

    //System.out.println("Spawning Males = " + countSpawningMales);

    if(countSpawningMales > 0)
    {
        //System.out.println("agg " + i + " has\t" + countSpawningMales + "\tmales");

        for(int l = 0; l<Females.size(); l++)
        {
            fish = (Individual) Females.get(l);

            if(femBehavior == true)
            {
                //System.out.println("femBehavior = true and fish goes to same aggregation as
school");

                if(fish.getSchool()== i)
                {
                    fish.getFecundity(rng);

                    //System.out.println("fish " + l + ": age = " + fish.age + " gend = " + fish.gend +
" fecund = " + fish.fecund + " MATCH: school = " + fish.getSchool() + "agg = " + i);

                    possiblenew += fish.fecund;

                }

            }

            else if(femBehavior == false)
            {
                // System.out.println("femBehavior = false and fish goes to closest aggregation");

                if(fish.y == SEAy[i])
                {
                    fish.getFecundity(rng);

```

```

        //System.out.println("fish " + l + ": age = " + fish.age + " gend = " + fish.gend +
" fecund = " + fish.fecund + " position = x " + fish.x + " y " + fish.y);
        //System.out.println("MATCH: Female y = " + fish.y + "AGG y = " + SEAy[i]
    );

        possiblenew += fish.fecund;
    }
}

}

else
{
    //System.out.println("agg " + i + " has no males: NO SPAWNING");
    //System.out.println();
}
}

//:adds newborns to the population as juveniles://

public void eggtoPL(int xloci, int xalleles)

{

    if(month==3)

    {

        fish = new Individual();

        fish.setNumAlleles(xalleles);

        fish.iGeno(xloci);

        fish.createHaplo(xloci);

        fish.setAge(0);

        fish.setPosition(0, rng.nextInt(120));

        v.add(fish);

```

```

        PLarvae.add(fish);

        //System.out.println("YOY position = " + fish.getX() + "\t" + fish.getY());

    }

}

//pelagic larvae (PL) to benthic juveniles (BJ)

//benthic juveniles to seagrass beds//

public void PLtoBJ(int SGBx)

{

    fish = new Individual();

    int j = 0;

    //System.out.println(YOY.size());
    if (month == 5)

    {

        for (int i=0; i<v.size(); i++)

        {

            fish = (Individual) v.get(i);

            if (fish.age ==0)

            {

                //System.out.println("init age (yoy) = " + fish.getAge());

                Juvs.add(j, fish);

                PLarvae.remove(fish);

                fish.setAge(1);

                //System.out.println("age after set to 1 (juv)= " + fish.getAge());

                fish.setPosition(SGBx, 0);

```

```

    }

    }

}

public void spatialSample(double sampleDist)
{
    int countFish = 0;
    int randX = 0;
    int randY = 0;
    randX = rng.nextInt(120);
    randY = rng.nextInt(160);

    for(int i = 0; i<v.size(); i++)
    {
        fish = (Individual) v.get(i);
        if(fish.x <= randX + sampleDist && fish.x >= randX - sampleDist)
        {
            if(fish.y <= randY + sampleDist && fish.y >= randY - sampleDist)
            {
                countFish++;
            }
        }
    }

    int []subsample = new int[countFish];
    //System.out.println("number of Fish sampled" + subsample.length);

}

public void initializeSubPop(int samplesize)
{
    u = new Vector (samplesize);

}

public static boolean noResample(int[] s, int pick, int spot)
{

```

```

        boolean nores = false;

        if(spot != 0)
        {
            for(int i=0; i<s.length; i++)
            {
                if(i != spot)
                {
                    if(s[i] == pick)
                    {
                        nores = true;
                        break;
                    }
                }
            }
        }

        return nores;
    }
    public static void checkResample(int[] array)
    {
        for(int i=1; i<array.length; i++)
        {
            if(array[i-1]==array[i])
            {

```



```

        System.out.println("=====");

        System.out.println("attention there has been a");

        System.out.println("sample resampled");

        System.out.println("=====");

        System.exit(0);

    }

}

}

public void doSample(int[] subsample)
{
    Random rng = new Random();

    int vectorsize = v.size();

    int pick = 0;
    for(int i=0; i<subsample.length; i++)
    {
        do
        {
            pick = rng.nextInt(vectorsize);

            while(noResample(subsample, pick,i) == true);
            subsample[i] = pick;

        }

        for(int i=0; i<subsample.length; i++)
        {

```

```

        //System.out.println(subsample[i]);
    }

    //System.out.println("v.size = " + v.size());
    for (int i=0; i<subsample.length; i++)
    {
        fish = (Individual) v.get(subsample[i]);

        u.add(i, fish);
    }

    for (int i=0; i<u.size(); i++)
    {
        fish = (Individual) u.get(i);

        //System.out.println("subsample size = " + u.size());

        //System.out.println("fish = " + fish.age);
    }
}

//:sets individual genotypes based on pop frequencies://
public void initPopGeno(int xloci)
{
    for(int i=0; i<v.size(); i++)
    {
        fish = (Individual) v.get(i);

        fish.iGeno(xloci);

        for(int j=0; j<xloci; j++)
        {

```

```

for (int k=0; k<2; k++)

    {

        double test1 = rng.nextDouble();

        if (j==0)

            {

                if (test1 <= a)

                    {

                        fish.geno[j][k]=0;

                    }

                else if (test1 > a && test1 <= b)

                    {

                        fish.geno[j][k]=1;

                    }

                else if (test1 >b && test1 <= c)

                    {

                        fish.geno[j][k]=2;

                    }

                else

                    fish.geno[j][k]=3;

            }

        else if(j==1)

            {

                if (test1 <= e)

```

```

    {
        fish.geno[j][k]=0;
    }
else if (test1 > e && test1 <= a)
    {
        fish.geno[j][k]=1;
    }
else if (test1 >a && test1 <= f)
    {
        fish.geno[j][k]=2;
    }
else
    fish.geno[j][k]=3;
}
else if(j==2)
    {
        if (test1 <=g)
            {
                fish.geno[j][k]=0;
            }
        else if (test1 >g && test1 <= h)
            {
                fish.geno[j][k]=1;
            }
    }

```

```

        }
        else if (test1>h && test1 <= m)
        {
            fish.geno[j][k]=2;
        }
        else
            fish.geno[j][k]=3;
    }

    //System.out.println("Fish" + i + ":" + "(" + fish.geno[j][k] + ")");
}
}
}

}

//:selects male fish for reproduction://
public int getDad(Vector v)
{
    int dadIndx = 0;
    int dadGend = 0;
    do
    {
        dadIndx = rng.nextInt(v.size());
        fish = (Individual) v.get(dadIndx);
        dadGend = fish.getGender();
    }

```

```

        // System.out.println(dadIndx);

    }

    while(dadGend != 1);

    //System.out.println("dadIndx = " + dadIndx);

    return dadIndx;

}
public void initializeFemSamp(int samplesize)
{
    F = new Vector (samplesize);

    //Females = new Vector(samplesize);
}

public void initializeFemales()
{
    //F = new Vector (100);

    Females = new Vector(100);
}

public void getVectors()
{
    fish = new Individual();

    int cf,cm,cj;

    cf = cm = cj = 0;
    for(int i=0; i<v.size(); i++)
    {
        fish = (Individual) v.get(i);
    }
}

```

```

if(fish.gend == 0)
{
    //System.out.println("fecundity =\t" + fish.fecund + "\tgender=\t" + fish.gend);
    if(fish.fecund > 0)
    {
        Females.add(fish);
        cf++;
    }
    else if(fish.fecund==0)
    {
        Juvs.add(fish);
//        System.out.println("I am a juvenile");
        cj++;
    }
//    System.out.println("females vector size is=\t" + Females.size());
}

else if(fish.gend == 1)
{
    Males.add(fish);
    cm++;
}
}

//System.out.println("females =\t" + cf + "\tmales=\t" + cm + "\tjuvs=\t" + cj);

```

```

//System.out.println("new = " + countNew + "\t" +
//
//          "juvs =" + countJuv + "\t" +
//
//          "trans =" + countTrans + "\t" +
//
//          "fems =" + countFem + "\t" +
//
//          "males =" + countMal);
}

public void getFemSamp(int[]femsamp)
{
    Random rng = new Random();
    int vectorsize = Females.size();
    int pick = 0;
    for(int i=0; i<femsamp.length; i++)
    {
        do
        {
            pick = rng.nextInt(vectorsize);
        }

        while(noResample(femsamp, pick,i) == true);
        femsamp[i] = pick;
    }

    for(int i=0; i<femsamp.length; i++)
    {
// System.out.println(femsamp[i]);
    }
}

```



```

        //System.out.println("v.size = " + v.size());
        for (int i=0; i<femsamp.length; i++)

        {

            fish = (Individual) Females.get(femsamp[i]);

            F.add(i, fish);

        }

        for (int i=0; i<F.size(); i++)

        {

            fish = (Individual) F.get(i);

            //System.out.println("fish = " + fish.gend);

        }

        //System.out.println("subsample size = " + F.size());
    }

    //:selects female fish for reproduction://

    public int getMom(Vector v)

    {

        int momIndx = 0;

        int momGend = 0;

        //countPop();

        //setCurrentPop();

        if(v.size()>0)
        {
        do

        {

            momIndx = rng.nextInt(v.size());

```

```

        fish = (Individual) v.get(momIndx);

        momGend = fish.getGender();

    }

    while (fish.gend!= 0 && fish.fecund==0);
}

return momIndx;

}

```

//:selects parents' haplotypes://

```
public void getHaplotypes(Vector v, Vector F)
```

```

{

    mi = getMom(F);

    //System.out.println(getMom());

    pi = getDad(v);

    //System.out.println(getDad());

    fish = (Individual) v.get(mi);

    fish.setNumAlleles(xalleles);

    fish.createHaplo(xloci);

    fish.setHaplotype(rng);

    //System.out.println(fish.getHaplotype()[0]);

    for(int i=0; i<mh.length; i++)

    {

        mh[i]=fish.haplo[i];

        //System.out.println("mom locus " + i + ": " + fish.haplo[i]);
    }
}

```

```

    }

    fish = (Individual) v.get(pi);

    fish.setNumAlleles(xalleles);

    fish.createHaplo(xloci);

    fish.setHaplotype(rng);

    for(int i=0; i<dh.length; i++)

    {

        dh[i]=fish.haplo[i];

        //System.out.println("dad locus " + i + ": " + fish.haplo[i]);

    }

}

double total = 0.0;

for(int i=0; i < pFreqs1.length; i ++)

{

    double t = 0.0;

    for (int j=0; j <pFreqs1[i].length; j++)

    {

        //System.out.println("Juv Allele Freq Locus"+i+" Allele"+j+" = " + pFreqs1[i][j]);

        t = pFreqs1[i][j] + t;

    }

    //System.out.println("Total Locus"+i+" = " + t);

}

for(int i=0; i < pFreqs1.length; i ++)

```

```

    {
        double t = 0.0;

        for (int j=0; j <pFreqs1[i].length; j++)
        {
            //System.out.println("Adult Allele FreqLocus"+i+" Allele"+j+" = " + pFreqs2[i][j]);

            t = pFreqs2[i][j] + t;
        }

        //System.out.println("Total Locus"+i+" = " + t);
    }

    public double calcEffectPopSize()
    {
        double EPS = 0;
        int Nm = countMal;
        int Nf = countFem;
        int N = countMal + countFem;

        // System.out.println("Males before EPS calc = " + Nm);
        // System.out.println("Females before EPS calc = " + Nf);
        // System.out.println("N before EPS calc = " + N);

        // double EPSArray[] = new double[outputPeriod];

        EPS = (4.0*Nm*Nf)/N;

        return EPS;

        //System.out.println("EPS = " + EPS);

    }

    public void addNe(int gen, double EPS)
    {
        if(gen<EPSArray.length)
        {
            EPSArray[gen] = EPS;
        }
    }
}

```

```

public void calcHarmonicMean()
{
    double sum = 0;

    double harmonicMean = 0;

    for(int i=0; i < EPSArray.length; i++)
    {
        sum += (1/EPSArray[i]);

        //System.out.println(EPSArray[i]);
    }

    harmonicMean = EPSArray.length*(1/sum);

    System.out.println("Harmonic Mean of Effective Population Size = " + harmonicMean);
}

}

```

Individual

```
package gag;
import java.util.*;
public class Individual {
int gend;      //gender of individual
double age;    //age of individual
double fecund; //fecundity of an individual
double maturity; //measure of how mature individual
double tester; //random number
int [][] geno; //genotype array of alleles and loci
int xloci;     //number of loci
int xalleles;  //number of alleles at each locus
int newgend;   //new gender after an individual has changed gender
int[] haplo;
int[] position;
int school;
int agg;
int coords;
int x;
int y;
int swimrate = 16; //female swimrate
int jswimrate = 2; //juvenile swimrate
int current = 60;  //strength of current carrying YOY

//:constructor://
public Individual (int gend, int xloci, int coords, int school, int agg)
{
    this.gend=gend;
    this.xloci=xloci;
    this.coords = coords;
```

```

    this.school = school;
    this.agg = agg;
    haplo = new int[xloci];
    position = new int[coords];
}

//:default constructor://
public Individual()
{
    gend=0;
    age=0;
}

public void setNumAlleles(int xalleles)
{
    this.xalleles=xalleles;
}

public void createHaplo(int xloci)
{
    this.xloci=xloci;
    haplo = new int[xloci];
}

//:initializes age://
public void setAge(int a)
{
    age=a;
}

//:returns age://
public double getAge ()
{
    return age;
}

//:adds one year to age://
public void Older()
{
    age++;
}

//:sets gender to a new gender://
public void setGender (int newgend)

```

```

{
    gend=newgend;
}

//:returns gender://
public int getGender()
{
    return gend;
}

public void setSchool(int b)
{
    school = b;
}

public int getSchool()
{
    return school;
}

public void setAgg(int c)
{
    agg = c;
}

public int getAgg()
{
    return agg;
}

//:assigns fecundity based on age://
public double getFecundity(Random rng)
{
    tester = rng.nextDouble();
    maturity = Math.exp(-Math.exp(-(-6.42 + 1.81*age)));

    if(tester > maturity || age<2 || gend==1 || gend==2)
    {
        fecund=0;
    }
    else
    {
        fecund=25*((80.997*age) - 151.2);
    }
    // System.out.println(fecund);
}

```



```

    return fecund;
}

public void createPosition(int coords)
{
    this.coords = coords;
    position = new int[coords];
    for(int i = 0; i < position.length; i++)
    {
        position[i]=0;
    }
}

public void setPosition(int x,int y)
{
    // position[0]=x;
    // position[1]=y;

    this.x = x;
    this.y = y;
}

public void newMalePosition(Random rng, int newD)
{
    int tx = 0;
    int ty = 0;

    if (newD<=0)
    {
        if (x<0 && y<0)
        {
            tx = rng.nextInt(2);
            ty = rng.nextInt(2);

            if (tx==0)
            {
                x += 0;
            }
            else if (tx==1)
            {
                x += (int)Math.round((2*rng.nextDouble()));
            }
            if (ty==0)
            {
                y +=0;
            }
        }
    }
}

```

```

        else if (ty==1)
        {
            y += (int)Math.round((2*rng.nextDouble()));
        }
    }
    else if (x<0 && y>0)
    {
        tx = rng.nextInt(2);
        ty = rng.nextInt(2);

        if (tx==0)
        {
            x += 0;
        }
        else if (tx==1)
        {
            x += (int)Math.round((2*rng.nextDouble()));
        }
        if (ty==0)
        {
            y +=0;
        }
        else if (ty==1)
        {
            y -= (int)Math.round((2*rng.nextDouble()));
        }
    }
    else if (x<0 && y==0)
    {
        tx = rng.nextInt(2);
        ty = rng.nextInt(3);

        if (tx==0)
        {
            x += 0;
        }
        else if (tx==1)
        {
            x += (int)Math.round((2*rng.nextDouble()));
        }
        if (ty==0)
        {
            y +=0;
        }
        else if (ty==1)
        {

```

```

        y += (int)Math.round((2*rng.nextDouble()));
    }
    else if (ty==2)
    {
        y -= (int)Math.round((2*rng.nextDouble()));
    }
}
else if (x>0 && y<0)
{
    tx = rng.nextInt(2);
    ty = rng.nextInt(2);

    if (tx==0)
    {
        x += 0;
    }
    else if (tx==1)
    {
        x -= (int)Math.round((2*rng.nextDouble()));
    }
    if (ty==0)
    {
        y +=0;
    }
    else if (ty==1)
    {
        y += (int)Math.round((2*rng.nextDouble()));
    }
}
else if (x>0 && y>0)
{
    tx = rng.nextInt(2);
    ty = rng.nextInt(2);

    if (tx==0)
    {
        x += 0;
    }
    else if (tx==1)
    {
        x -= (int)Math.round((2*rng.nextDouble()));
    }
    if (ty==0)
    {
        y +=0;
    }
}

```

```

    else if (ty==1)
    {
        y -= (int)Math.round((2*rng.nextDouble()));
    }
}
else if (x>0 && y==0)
{
    tx = rng.nextInt(2);
    ty = rng.nextInt(3);

    if (tx==0)
    {
        x += 0;
    }
    else if (tx==1)
    {
        x -= (int)Math.round((2*rng.nextDouble()));
    }
    if (ty==0)
    {
        y +=0;
    }
    else if (ty==1)
    {
        y += (int)Math.round((2*rng.nextDouble()));
    }
    else if (ty==2)
    {
        y -= (int)Math.round((2*rng.nextDouble()));
    }
}
else if (x==0 && y<0)
{
    tx = rng.nextInt(3);
    ty = rng.nextInt(2);

    if (tx==0)
    {
        x += 0;
    }
    else if (tx==1)
    {
        x += (int)Math.round((2*rng.nextDouble()));
    }
    else if (tx==2)
    {

```

```

        x -= (int)Math.round((2*rng.nextDouble()));
    }
    if (ty==0)
    {
        y +=0;
    }
    else if (ty==1)
    {
        y += (int)Math.round((2*rng.nextDouble()));
    }
}
else if (x==0 && y>0)
{
    tx = rng.nextInt(3);
    ty = rng.nextInt(2);

    if (tx==0)
    {
        x += 0;
    }
    else if (tx==1)
    {
        x += (int)Math.round((2*rng.nextDouble()));
    }
    else if (tx==2)
    {
        x -= (int)Math.round((2*rng.nextDouble()));
    }
    if (ty==0)
    {
        y +=0;
    }
    else if (ty==1)
    {
        y -= (int)Math.round((2*rng.nextDouble()));
    }
}
}

else if(newD>0)
{
    tx = rng.nextInt(3);
    ty = rng.nextInt(3);

    if (tx==0)
    {

```

```

        x += 0;
    }
    else if (tx==1)
    {
        x += (int)Math.round((2*rng.nextDouble()));
    }
    else if (tx==2)
    {
        x -= (int)Math.round((2*rng.nextDouble()));
    }
    if (ty==0)
    {
        y += 0;
    }
    else if (ty==1)
    {
        y+= (int)Math.round((2*rng.nextDouble()));
    }
    else
    {
        y -= (int)Math.round((2*rng.nextDouble()));
    }
}

if(x>120)
{
    x=120;
}
if(x<0)
{
    x=0;
}
if(y>120)
{
    y=120;
}
if(y<0)
{
    y=0;
}

}

public void newFemalePosition(Random rng)
{
    int t2 = 0;

```

```

int t3 = 0;
t2 = rng.nextInt(3);
if(t2 == 0)
{
    x += (int)Math.round((swimrate*rng.nextDouble()));
}
else if (t2 == 1)
{
    x -= (int)Math.round((swimrate*rng.nextDouble()));
}
else
{
    x +=0;
}
t3 = rng.nextInt(3);
//System.out.println("y rng = " + t3);
if(t3 == 0)
{
    y += (int)Math.round((swimrate*rng.nextDouble()));
}
else if (t3 == 1)
{
    y -= (int)Math.round((swimrate*rng.nextDouble()));
}
else
{
    y +=0;
}
if(x>120)
{
    x=120;
}
if(x<0)
{
    x=0;
}
if(y>120)
{
    y=120;
}
if(y<0)
{
    y=0;
}
}

```

```

public void newPLPosition(Random rng)
{
    x += (int)Math.round((current*rng.nextDouble()));
    int t3 = 0;
    t3 = rng.nextInt(3);
    //System.out.println("y rng = " + t3);
    if(t3 == 0)
    {
        y += (int)Math.round((current*rng.nextDouble()));
    }
    else if (t3 == 1)
    {
        y -= (int)Math.round((current*rng.nextDouble()));
    }
    else
    {
        y +=0;
    }
    if(x>120)
    {
        x=120;
    }
    if(x<0)
    {
        x=0;
    }
    if(y>120)
    {
        y=120;
    }
    if(y<0)
    {
        y=0;
    }
}

```

```

public void newJuvPosition(Random rng, int juvdist)
{

    int t2 = 0;

    if (juvdist<-5)
    {
        t2 = rng.nextInt(2);
        if(t2 ==0)

```



```

        {
            x -= (int)Math.round((jswimrate*rng.nextDouble()));
        }
        else
        {
            x+=0;
        }
    }
    else if (juvdist>5)
    {
        int t3 = rng.nextInt(2);
        if(t3 ==0)
        {
            x += (int)Math.round((jswimrate*rng.nextDouble()));
        }
        else
        {
            x+=0;
        }
    }

    else
    {
        int t4 = rng.nextInt(3);
        if(t4 ==0)
        {
            x += (int)Math.round((jswimrate*rng.nextDouble()));
        }
        else if(t4==1)
        {
            x -= (int)Math.round((jswimrate*rng.nextDouble()));
        }
        else
        {
            x+=0;
        }
    }

    int t3 = 0;
    t3 = rng.nextInt(3);
    //System.out.println("y rng = " + t3);
    if(t3 == 0)
    {
        y += (int)Math.round((jswimrate*rng.nextDouble()));
    }
    else if (t3 == 1)

```

```

        {
            y -= (int)Math.round((jswimrate*rng.nextDouble()));
        }
    else
    {
        y +=0;
    }
    if(x>120)
    {
        x=120;
    }
    if(x<0)
    {
        x=0;
    }
    if(y>120)
    {
        y=120;
    }
    if(y<0)
    {
        y=0;
    }
}
public int getY()
{
    return y;
}

public int getX()
{
    return x;
}

public int[] getPosition()
{
    return position;
}

//:initialized genotype array://
public void iGeno(int xloci)
{
    //xloci = loci;
    //xalleles = alleles;

    geno = new int[xloci][2];
}

```

```

        for (int i=0; i < xloci; i++)
        {
            for (int j=0; j < 2; j++)
            {
                geno[i][j]= 0;
            }
        }
    }

    public void setGeno(int[] mh, int[] dh)
    {
        //System.out.println("mh length" + mh.length);
        for(int i=0; i<mh.length; i++)
        {
            geno[i][0]= mh[i];
            geno[i][1]= dh[i];
        }
    }

    public int[][] getGeno()
    {
        return geno;
    }

    //:gets the haplotype from genotype array://
    public void setHaplotype(Random rng)
    {
        int myAllele = 0;

        //System.out.println(haplo.length);
        //System.out.println(xalleles);

        for(int i=0; i<haplo.length; i++)
        {
            if(rng.nextInt(xalleles)==0)
                myAllele = geno[i][0];

            else
                myAllele = geno[i][1];

            haplo[i] = myAllele;
        }

        //System.out.println("geno " + geno[0][0]);
    }

```

```

    //System.out.println("haplo " + haplo[0]);
}

public int[] getHaploType()
{
    return haplo;
}
}

```

Gamma Sampler

```

/*
 * To change this template, choose Tools | Templates
 * and open the template in the editor.
 */

package gag;

/**
 *
 * @author erinelizabeth6
 */
import java.util.Random;

public class GammaSampler2 {

    private static Random rng = new Random();

    public static double sampleGamma(double k, double theta)
    {
        boolean accept = false;
        if (k < 1) { // Weibull algorithm
            double c = (1 / k);
            double d = ((1 - k) * Math.pow(k, (k / (1 - k))));
            double u, v, z, e, x;
            do
            {
                u = rng.nextDouble();
                v = rng.nextDouble();
                z = -Math.log(u);
                e = -Math.log(v);
            }
        }
    }
}

```

```

        x = Math.pow(z, c);
        if ((z + e) >= (d + x))
        {   accept = true;   } }
        while (!accept);

        return (x * theta);
    }

else
{ // Cheng's algorithm
    double b = (k - Math.log(4));
    double c = (k + Math.sqrt(2 * k - 1));
    double lam = Math.sqrt(2 * k - 1);
    double cheng = (1 + Math.log(4.5));
    double u, v, x, y, z, r;
    do {
        u = rng.nextDouble();
        v = rng.nextDouble();
        y = ((1 / lam) * Math.log(v / (1 - v)));
        x = (k * Math.exp(y));
        z = (u * v * v);
        r = (b + (c * y) - x);
        if ((r >= ((4.5 * z) - cheng)) || (r >= Math.log(z)))
        {   accept = true;   } }
        while (!accept);
        return (x * theta);
    }
}
}

```

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BIOGRAPHICAL SKETCH

In the summer of 2008, Erin Simmons completed her Bachelor's of Science degree in Biological Science with a certificate in Marine Biology and Living Resource Ecology and minors in mathematics and chemistry at The Florida State University. Under the advisement of Dr. Thomas E. Miller, she began her Master's of Science degree in the Department of Ecology and Evolution at The Florida State University in the fall of 2008. Erin's research interests include marine reserve theory, fisheries management, population modeling, and marine population ecology. She is currently a Florida Gubernatorial Fellow spending time at both the Florida Capitol and the Department of Environmental Protection in order to gain firsthand knowledge of policymaking and public service. Her career interests also include marine science outreach as well as marine policy. She enjoys all activities associated with the water including SCUBA diving, free diving, scalloping, swimming, and maintaining multiple aquariums in her own personal zoo. Upon completion of her master's, Erin will take a position with the Naval Experimental Dive Unit in Panama City, Florida, studying human performance under extreme diving conditions.