Heritable Risk Sensitive Foraging in Juvenile Fish: Potential Implications for the Dynamics of Harvested Populations

by

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Abstract

Walters and Juanes (1993) proposed that heritable risk sensitive foraging behavior in juvenile fish could cause substantial delays in the recovery of a population if selection has favored individuals with reduced foraging times while population abundance is low. They predict that such selection may occur in a over-exploited stock given the following conditions i.) spawning stock abundance has been eroded to a point where there is a reduction in juvenile density, ii.) reduction in juvenile density reduces competition between juveniles, iii.) predation risk forces juveniles to forage in small volumes near predation refuges, iv.) food availability in these small volumes is affected by juvenile density, v.) juvenile density remains low long enough for selection to occur. Low juvenile density could favor individuals with reduced foraging times, due to improved survival resulting from less exposure to predation risk, while high juvenile density could favor extended foraging time, in spite of predation risk, due to relatively better growth resulting from increased consumption during foraging bouts. If juvenile density remains low long enough for selection to occur, the proportion of individuals with reduced foraging time as juveniles will increase. When harvesting is halted, allowing spawning and juvenile densities to increase, there may be a substantial delay in stock recovery as a result of poor survival in the juvenile stage due to a predominance of individuals with reduced foraging time.

I attempted to select for reduced and extended foraging time in populations of guppies (*Poecilia reticulata*) by maintaining high (non-harvested) and low (harvested) density adult populations over a number of generations. These populations were then reduced to the same abundance and the resulting population recoveries were monitored.

Although there appeared to be a decrease in the amount of time juveniles spent foraging in low density populations, changes could not be attributed to selection for reduced foraging time. The observed reduction in juvenile foraging time during the experiment was attributed to a substantial increase in predation risk caused by cannibalism from large adult females. When the populations were reduced to the same abundance after the selection experiment, one low density population recovered more slowly and to a lower abundance than the high density population. The low equilibrium abundance observed in tanks that were held at low density was attributed to a substantial reduction in juvenile survival as a result of cannibalism.

Heritable, risk-sensitive foraging was incorporated into an age-structured genetic model of the northern cod fishery to see if selection for individuals with reduced foraging time could explain the observed decline in mean weight-at-age in the catch as well as the impact that such selection would have on the recovery of the northern cod population after the 1992 fishery closure. A genetic model containing heritable differences in juvenile foraging behavior reproduced the observed trend in mean weight-at-age in the catch. When the recovery time of the genetic model was compared to a model where all juveniles had the same average foraging behavior, the genetic model population recovered to a pre-1962 abundance faster. However, the resulting stock was less productive and composed of smaller individuals than the historical pre-1962 stock. Stock productivity and size structure did not return to pre-1962 levels until the genetic composition of the stock recovered. Genetic composition of the simulated stock did not recover to pre-1962 levels until approximately 200 simulated years after the fishery closure.

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Dedication

This work is dedicated to my grandfather Norman Cowdell who gave me adventures and stories that truly enriched my life.

Acknowledgments

There are many individuals who helped and provided encouragement during my thesis. I would like to thank Dr. Carl Walters for giving me the opportunity to undertake this masters as well as for his encouragement, insight, enthusiasm and pointing me in the right direction. Many thanks to my committee members, Dolph Schluter, Don McPhail and Robin Liley for their advice and criticism. A huge muchas gracias to my office mate Leonardo Huato for his assistance with modeling and putting up with my love of entropy in the office. Thanks to Sean Cox for venturing into the world of Bayesian statistics with me as well as the opportunity to "squeeze" a real fish while doing some fabulous fishing. Many thanks to Steve Martell for his enthusiasm and suggestions. Thanks to Joel Sawada for a fine set of clubs and all his help. I thank my parent for maintaining their faith that one day I would finish. I am forever in debt to Nancy Lee for her unwavering love, support and encouragement.

Chapter 1. General Introduction

Fisheries data covers a wide range of spawning stock abundance and often shows recruitment to be highly variable and on average independent of spawning stock. Figure 1.0 shows a typical stock-recruitment relationship for the northern cod with no clear positive correlation between spawning stock and the resulting recruitment. Lack of positive correlation between spawning stock and average recruitment is commonly attributed to strong density dependent changes in survival during early life stages (Ricker 1954, Houde 1987, Anderson 1988, Wooster and Bailey 1989, Hilborn and Walters 1992, Walters and Juanes 1993). In particular a number or researchers have stressed that the dynamics of such interaction may be particularly important in determining year class strength during the later stages of early life (Houde 1987, Bradford 1992, de Lafontaine et al. 1992). Such arguments do not imply that density independent or density dependent survival in egg or larval stages are not important in determining recruitment. Such processes can roughly determine year class strength (Houde 1989, Bailey and Spring 1992, Myers and Cadigan 1993). However, in many cases, correlation between year class strength and subsequent recruitment is stronger when post larval or juvenile stages abundance indexes are used (Nielsen 1980, van der Veer 1986, Peterman et al. 1988, Wooster and Bailey 1989, van der Veer et al. 1990, and Bradford 1992). The improvement in the correlation between recruitment and later juvenile stages indicated that density dependent changes in survival during these stages is important in determining year class strength.

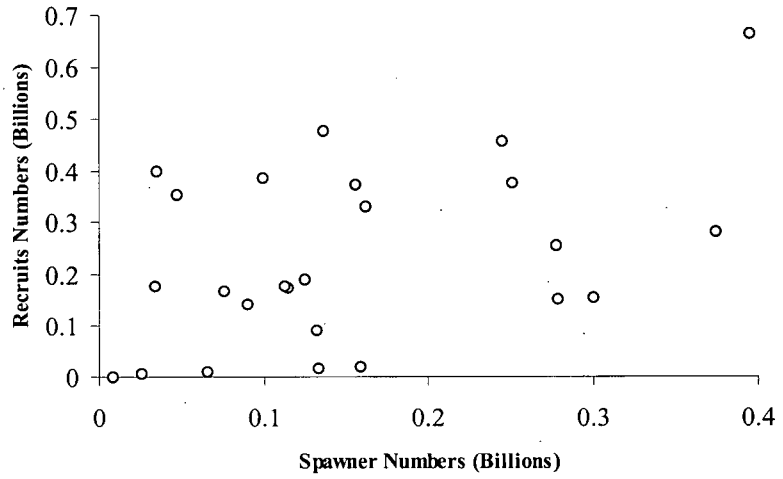

Figure 1.0. Spawning stock numbers and resulting age two recruitment for the northern cod stock (NAFO divisions 2J3KL) for 1970 to 1995. Calculated from VPA stock reconstruction.

Predation and competition for food during early life stages are suspected to limit recruitment through density dependent changes in survival but, correlating recruitment with food density or predator abundance has proven uninformative (Anderson 1988, Heath 1992 and Leggett and Deblois 1994). Walters and Juanes (1993) proposed that a lack of correlation between food, predators and recruitment could result from natural selection for restriction of juvenile foraging time in habitats with high predation risk. Focusing on the early juvenile stage where juveniles have some control over movement, allowing habitat choice, but are still small enough to face potentially high predation risk, the authors argue that high predation risk forces juvenile fish to foraging in limited areas or "arenas" that surround predation refuges. The size of these foraging arenas and the time spent foraging must be restricted because moving too far or spending more time outside the refuge increases predation risk. Food densities within these arenas can depend strongly on juvenile density even when juvenile density is not high enough to

affect large-scale regional food densities. As juvenile density increases, natural selection should favor increased foraging time and hence increased predation mortality, resulting in strong density dependent changes in mortality with no apparent change in regional food densities, growth or predator levels.

It is not unrealistic to assume that juvenile fish restrict their movements to refuge areas when there is risk of predation from visual predators. Numerous authors have reported a reduction in activity levels of juvenile fish when predators are present, indicating a trade-off between predation risk and potential consumption (Milinski and Heller 1978, Dill 1983, Lima 1985, Weissburg 1986, Huntingford et al. 1988, Abrahams and Dill 1989, Lima and Dill 1990, Moore 1994, Skelly 1994, Healey and Rienhardt 1995). Juvenile reef fishes spend most of the day in refuges with low food densities but reduced predation risk and move out to feed during short periods at dawn and dusk (Helfman 1993). Juvenile sockeye salmon (*Onchorhynchus nerka*) reduce predation risk by migrating vertically at dawn and dusk to feed (Clark and Levy 1988). Juvenile cod migrate inshore to feed at night (Keats 1990, Keats and Steele 1992). Other individuals group together in schools (Murphy and Pitcher 1991, Pitcher and Parrish 1993), which reduces each individual's risk of predation by spreading the risk over a number of individuals. Guppies (*Poecilia reticulata*) form more cohesive schools when predation risk is high (Breden et al. 1987, Magurran et al. 1993). Such a wide variation in behaviors to reduce predation risk indicates that natural selection for restricting foraging time in the presence of predators must be strong.

Restricting foraging activities places tight limits on the volume or area searched by juveniles during foraging bouts. Moving long distances or spending extended periods

of time outside refuge areas would greatly increase predation risk providing predation risk is constant per unit time spent foraging. Food densities in these restricted volumes can be depleted rapidly in spite of being replenished by (1) physical mixing processes between the arena and a larger production environment, and (2) biological processes such as insect emergence and prey reproduction. If juveniles forage randomly during foraging bouts and food densities are low enough to prevent satiation (or substantial prey handling times), then as juvenile density increases, food availability, within these restricted volumes, decreases rapidly being most sensitive to juvenile density when juvenile density is low (Walters and Juanes 1993).

Providing that juveniles require a certain amount of food to obtain some minimum threshold size, such as a minimum size needed to escape predation risk or a size dependent shift in to some more favorable habitat (Werner and Hall 1988 and Ludwig and Rowe 1990), natural selection should favor an increase in foraging time, resulting in an increase in exposure to predation, as juvenile density increases. Thus one should observe density dependent changes in juvenile survival with little change in food densities (densities in the volume of water outside foraging arenas) or increases in predator densities.

Walters and Juanes (1993) explored stock-recruitment relationships resulting from their foraging arena model, as juveniles adjusted their foraging behavior. If juveniles adopt a foraging time strategy based on the initial juvenile densities in a foraging habitat, (i.e., there is no change in foraging behavior as juvenile density declines due to mortality over time) the stock-recruitment relationship will be dome-shaped as in the Ricker recruitment curve. If juveniles are continually adjusting their foraging

behavior in response to changes in juvenile density and growth, the recruitment relationship becomes asymptotic as in the Beverton-Holt curve. Perhaps the most interesting possibility, and the focus of this thesis, is what happens if juvenile foraging behavior is genetically determined and does not adjust to changing competitive conditions. In this case, at high juvenile densities competition for resources in the foraging arenas is high, and selection should favor those individuals with longer foraging times. Individuals with longer foraging times can maintain enough food intake, due to longer foraging excursions, to eventually escape predation through growth. It is not unreasonable to assume that size dependent cutoffs in predation risk exist. Dill (1983) noted that large bluegill sunfish move out into the open water of lakes, an area with high predation risk from large mouth bass, when larger than 100mm because at this size they are less vulnerable to predation. At low juvenile densities selection should favor individuals with lower foraging times. A reduction in juvenile density reduces competition for resources, allowing individuals with short foraging times to acquire sufficient resources during foraging excursions. These individuals will have higher survival relative to individuals with longer foraging times due to less exposure to predation. The authors noted that given such tradeoffs it is meaningless to talk of a single stock-recruitment curve; recruitment will depend on the genetic composition of the stock that is changing with abundance (Fig. 1.1).

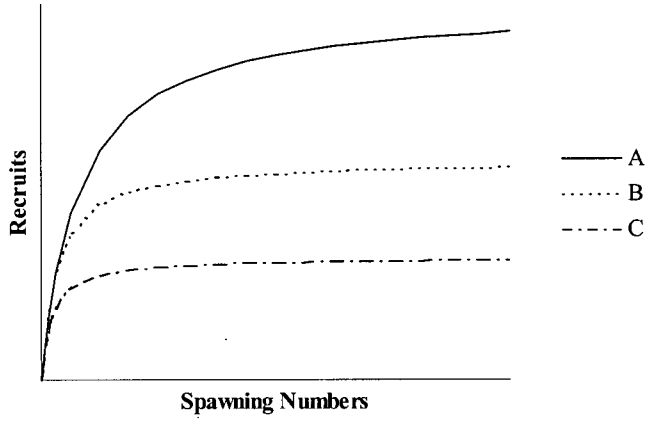

Figure 1.1. Theoretical average recruitment curves resulting from genetically determined juvenile foraging behavior. Recruitment curve A would result if a large proportion of the population had longer foraging times. As the proportion of individuals with longer foraging times decreased the recruitment curve shifts towards B. When the majority of individuals in the population have low foraging times the recruitment curve resembles C.

Consider a population with heritable variation in juvenile foraging time that has been at a high abundance for a long time. Egg deposition is high resulting in high densities of juveniles. If juvenile predation risk is high enough to cause juveniles to express risk sensitive foraging behavior and juvenile predation risk is size dependent then one might expect natural selection to favor individuals with longer foraging times. A population where the majority of individuals had longer juvenile foraging times might have an average recruitment curve similar to curve A in figure 1.1. If the population is then subject to exploitation depleting the spawning stock to a point where egg and juvenile production decrease, there will be a substantial reduction in juvenile competition. Since the population is composed mainly of individuals with longer juvenile foraging times one might observe an increase in the juvenile growth rate due to reduced food competition. However, because many juveniles spend much time feeding, survival will still be low due to predation mortality. If harvesting continues, keeping

juvenile densities low, conditions will begin to favor individuals with reduced foraging times. Reduced foraging time is favored under low juvenile density because individuals with reduced foraging times can still acquire sufficient resources for growth due to reduced competition. Low foraging time individuals also spend less time exposed to predation that results in lower mortality. As the proportion of reduced foraging time individuals increases in the population the growth rate should decrease to levels observed before the exploitation. Juvenile survival improves since a greater proportion of juveniles spends less time exposed to predation risk. If one could "freeze" the genetic structure of such a population at some equal mix of behavioral genotypes , and then vary the spawning abundance, the resulting average recruitment curve would resemble curve B (Fig. 1.1).

We now ask what could happen if fishing stopped and the population was allowed to recover. If the scenario presented above is correct, and selection for individuals with reduced foraging times has gone on long enough, a greater proportion of the population will have reduced foraging times. As the population increases there will be an increase in juvenile density. The increase in juvenile density will result in increased competition among the juvenile fish. The individuals with reduced foraging time will find themselves in conditions that favor longer foraging times. This will result in reduced growth in the individuals with reduced foraging time due to increased food competition. Slower growth rates may also result in a decrease in survival since juveniles will remain smaller for longer. The increase in juvenile density will result in selection favoring individuals with longer foraging times. However, there may be a considerable delay before individuals with longer foraging times become abundant enough to result in higher total

recruitment rates. It is entirely possible that the recruitment curve that results, before the abundance of individuals with longer foraging times increased, is similar to curve C (Fig. 1.1).

The whole notion that populations could be composed of individuals with short and long foraging time may seem unrealistic. Surely individuals would have evolved plasticity (Lima and Dill 1990, Stearns 1992) in their foraging behavior, adjusting their foraging time optimally depending on competitive conditions. However, plasticity may not always be favored. Consider a species that has been abundant for a long time. In this case one might expect selection to favor individuals that develop specialized behaviors to take advantage of spatial heterogeneity (Real 1980, Van Tienderen 1991). Heritable differences in foraging behavior have been seen in juvenile steelhead (Johnsson and Adrahams 1991). Domestic steelhead, reared at high densities, were more willing to forage in the presence of a predator than wild steelhead that usually occur at much lower densities. Hybrids between the wild and domestic strains had intermediate foraging behaviors. Murphy and Pitcher (1991) found individual differences in feeding rate of minnows when confronted with a pike. Many researchers have reported that behavioral differences within the same species have a genetic basis (Reznick and Endler 1982, Breden et al. 1987, Ehlinger 1990, Skulason et al. 1993, Magurran et al. 1993, Magurran 1993, Reznick 1996 and Reznick and Bryga 1996).

In this thesis I examine the possibility that population recovery may be delayed because different juvenile foraging time have been selected for. Chapter 2 focuses on a laboratory experiment in which I attempted to indirectly select for individuals with short and long juvenile foraging times in populations of guppies (*Poecillia reticulata*). I

outline the methods and present the results of the selection experiment. I then discuss if the results indicate differences in juvenile foraging times and if selection has an effect on population dynamics. In chapter 3, I develop an age-structured genetic model of the northern cod (*Gadus moruah*) fishery off the east coast of Canada. I use this model to determine if selection for juveniles with reduced foraging times could explain some of the patterns observed during the northern cod stock decline. I then compare the genetic model to a model that no genetic differences in juvenile behavior to determine whether selection for reduced juvenile foraging time would cause a delay in the stock recovery. In chapter 4, I summarize the findings from both the laboratory experiments and modeling exercise and discuss some criticisms of the methods.

Chapter 2: Attempting to Select for High and Low Juvenile Foraging Times in Laboratory Populations of Guppies

Introduction

I set out to test Walters and Juanes' prediction in the lab using populations of guppies (*Poecilia reticulata*). By establishing the conditions outlined in the Walters and Juanes prediction, one should be able to select for juveniles with reduced foraging times when population density is low. If this selection process is allowed to proceed for a number of generations, increasing the proportion of reduced foraging time individuals in the population, such a population will increase at a slower rate than it would without selection.

There are however, a number of conditions required for the experimental set up for selection, as proposed by Walters and Juanes, to occur. A critical condition of the prediction is that juvenile predation risk is high enough to cause juveniles to utilize predation refuges. Thus, any predator must be sufficiently inefficient to not remove all the juveniles but, to provide enough mortality to induce risk sensitive behaviors in the juveniles. It was also important to find a predator that would not simply sit in front of the refuge and wait for juveniles to exit. Such a predator would violate the assumption that juvenile mortality was proportional to foraging time.

Another key feature of the experimental design was the refuge structure. The refuge had to be designed so that juveniles could move in and out freely, but the predator and adults could not. The amount of food entering the refuge had to be controlled such that food within or close to the refuge could be depleted quickly forcing juveniles to leave the refuge to forage. It was assumed that establishing high and low density

populations of guppies would result in high and low densities of juveniles necessary to create the competitive conditions for selection of high and low juvenile foraging times. The key assumption of the Walters and Juanes prediction is that foraging behavior of individual juveniles within a population is genetically determined and varies according to genotype but does not change depending on competitive conditions or food availability.

If I am able to select over a number of generations for juveniles with long and short foraging times by establishing the necessary juvenile densities, competitive conditions and predation risk outlined by Walters and Juanes, there will be a number of indicators that selection for reduced foraging time individuals has occurred. These are i.) a greater proportion of the juveniles will be found in the refuges, ii.) juvenile survival rate will increase, iii.) the population will recover from a low abundance more slowly than non-selected populations. The last prediction is expected because as juvenile density increases in a growing population, juvenile growth and survival will decrease more in populations that are genetically prone to reduced foraging times.

Experimental Methods

The Guppy is a viviparous species that prefers slightly hard (1 gm sea salt per liter), alkaline water at temperatures between 20-30°C. Sexual maturity is reached at two to three months. Mature male guppies can reach a standard length of 3.5 cm and are distinguished by their bright coloration and gonopodium. Mature females, usually larger than males of the same age, are distinguished by their drab olive or silver-gray color and dark gravid spot. Females typically produce broods of approximately 20 fry.

Guppies were raised in an environmental chamber maintaining a water temperature of 27 °C and a 12 hour photoperiod. Aquariums (100L) with slightly hard

(1gm sea salt per liter) , alkaline water were placed on a three tiered shelving unit each having its own light source in addition to the general lab lighting. Six populations of feeder guppies were established from an aquarium wholesaler. It was not known how long the populations had been removed from the wild. Therefore, it was possible that inbreeding occurred in the population. I attempted to compensate for this by acquiring the guppies in three separate batches when new shipments arrived at the wholesaler. Populations of 100 individuals with a 50:50 sex ratio were allowed to acclimate to the laboratory conditions for two weeks. Individuals that appeared stressed from transport or those individuals that could not acclimatize were sacrificed. Three populations were selected at random and all but eight individuals were removed while maintaining a sex ratio of 50:50. Tanks with eight individuals are the "low density tanks" and tanks with >8 individuals are the "high density tanks". Eight individuals were used for the low density tanks because it represented approximately 10% of the high density populations and this was considered to be representative of heavily exploited population.

Guppies were fed twice a day with approximately 0.5g of fish flakes supplied by an automatic feeder. Although the amount of food dispensed by each feeder was similar, the feeders were rotated between the tanks each day so that over the course of the experiment there would be no feeder effect. It seemed that the amount of food provided was sufficient to satiate the adult populations. Adults were considered satiated if, after five minutes of feeding, there was still food in the aquarium. It was important to keep food levels in the high density tanks high enough to prevent competition between the adults. Food from the feeder distributed evenly over the water surface, eventually dispersing throughout the aquarium and finally settling on the bottom.

Food from the previous day was siphoned up five days per week to prevent waste food build up. Aquaria water was topped up every two days and a one-third water change was performed every month. Replacement water used in topping up and in the water changes was treated with a dechlorinator. Sea salt was added to match the salinity of the aquaria and sodium bicarbonate was added to make the water slightly alkaline. The water was allowed to sit with aeration for one week before being used. The sides of the aquaria were kept clean so that observations would not be obscured. Algae was scraped off using the edge of a glass strip. Filter floss was changed once a week, and the charcoal cartridges were replaced every two weeks.

Refuges (0.5L) were placed in each tank near the top and off to one side (Fig. 2.0). Refuges were made of a hard plastic frame covered with small plastic mesh (0.5mm) on the sides and back. The top, front and bottom of refuges were covered with larger green mesh (3mm) and the front panel was covered in light green plastic plants (approximately 7cm long). The top of the refuges were always above the water line. The front and bottom panels allowed juvenile guppies to move in and out but prevented the predator and adult guppies from entering. Refuge construction allowed very little food to enter during feedings, but a small amount of food could collect on the plants.

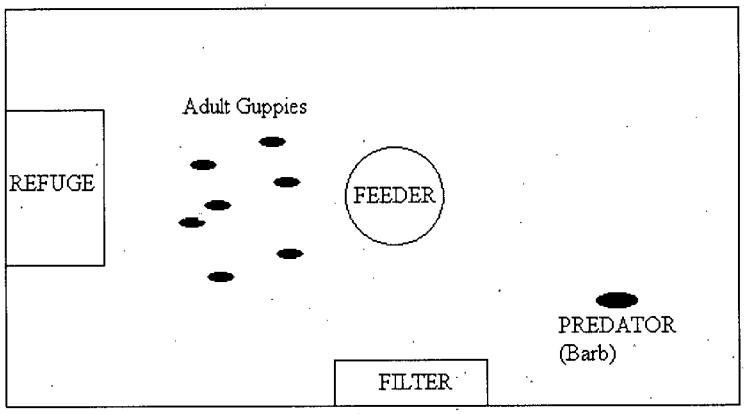

Figure 2.0. Experimental tank setup.

All tanks contained a Green Tiger Barb (*Barbus tetrayona*) as a predator. All barbs were selected to be approximately the same size (4cm) to prevent any large difference in prey size-selection. Tiger Barbs were used because they are gape limited and relatively inefficient predators. Initial efficiency tests of the predator indicated that a single barb would eat approximately 1 juvenile (<0.5cm) per day out of 20 when juveniles were not provided a refuge. I found that juvenile guppies more than two weeks old (>0.5cm) had little risk of predation from the barbs. This apparent size threshold for juvenile vulnerability to predation was used to classify juveniles. Any individual smaller than 0.5cm was considered to be a juvenile and vulnerable to predation. Individuals larger than 0.5cm, although still juveniles, were assumed to have grown large enough to avoid predation. A population of barbs was maintained in the lab so that individuals could be replaced if there was a mortality or when a barb grew larger than 4.5cm in order to keep the size of the barbs constant throughout the experiment. It was important to maintain a fairly constant size of predator throughout the experiment so that mortality rates and size at vulnerability in the juvenile guppies did not fluctuate.

Low density tanks were harvested every two months to prevent juvenile density from increasing to that of the high density tanks. A period of two months was chosen because juvenile guppies take 6-8 weeks to mature. Harvesting a low density tank consisted of removing all the adults with a large dip net that had been sterilized in weak bleach. Each tank had its own dip net to prevent cross contamination. Any immature

individuals that were inadvertently removed were returned to the tank. Mature individuals were recognized by fully developed gonopodia (males) and dark gravid spots (females). Four females and four males were randomly chosen from the harvested adult pool and returned to the tank. Although this harvesting process potentially reduces the number of generations that occurred during the experiment, randomly returning individuals from the harvested adult pool should prevent selection for early maturity. Abrams and Rowe (1996) and Reznick and Endler (1982) point out that increased predation on adults i.e., harvesting, will normally result in selection for a younger age at maturity. Because I was only interested in selection for reduced foraging time, I felt that this harvesting method was required to avoid selection for a younger age at maturity.

High density tanks were not harvested during the experiment. The tanks were however disturbed at the same time the low density tanks were harvested in order to mimic the handling effects associated with harvest. The adults were held out of the tank in the same holding containers used in the low density tank harvesting before they were returned to the aquarium. It was assumed that these tanks would maintain densities equal to the carrying capacity of the aquaria. Carrying capacity was estimated to be approximately 60 individuals assuming an average individual (1.5 cm standard length) needs a tank surface area approximately 30 cm^2 per cm standard length (Scott 1987).

After each harvesting, propensity of newly produced juveniles (<0.5cm length) to use refuge habitat and survival rate of new juveniles was determined in each of the high and low density tanks. The length of juveniles in both assessments was determined by eye. Juvenile size was not measured at these times because it was found that the measuring process was highly stressful and resulted in high juvenile mortality. Juveniles

that were large enough (>0.5cm length) to have little predation risk were not counted. Assessing juvenile refuge use and survival in the low density tanks was done by monitoring specific cohorts (when a specific cohort could be monitored). During the two month period between harvests I watch for brood production twice a day (in the morning and afternoon). Most of the time broods were produced when I was not present in the lab and I assumed, for these cases, that there was no predation loss between the time of production and my initial count of the brood. Each day for two weeks I counted juveniles three times for each measurement and used the average integer of the three counts. During each counting I noted if a juvenile was inside or outside of the juvenile refuge. For the first week of this monitoring, the proportion of juveniles inside and outside of the refuge was calculated. The mean of these proportion was used as an indicator of the propensity of juveniles to use the refuge habitat. I assumed that after two weeks juveniles had grown large enough avoid predation. In many cases, after two weeks the remaining juveniles from a brood would be found outside the refuge. This seemed to confirm my previous observation that after two weeks of growth juveniles were large enough to avoid predation from the barb. Juvenile survival rate was calculated as the total number of juveniles remaining from a brood after two weeks divided by the initial number of juveniles produced. If a second brood of juveniles was produced while the first was being monitored I used the following criteria to decide whether or not the monitoring could continue. If the brood was produced a day after the monitoring began, the additional number of juveniles was noted and the monitoring continued as though the juveniles were from a single brood. If a second brood was produced a week or so later, I determined if I could tell the individuals from each brood

apart. If there was a large enough size difference between the juveniles of each brood such that individuals could be traced back to there original brood then the broods were monitored separately. If I was unable to distinguish between the two broods and the second brood was produced more than one day later, the initial increase in juveniles was noted for brood size measurements but, the other data could not be used. Overlapping broods was not a common problem in the low density tanks. However, it was a common occurrence in the high density tanks. Many times data from the high density tanks could not be used. Counts for measurements of brood size, juvenile refuge use and juvenile survival in the high density tanks were done five times with the average integer of the five counts being used. The number of counts done for each measure was increased in the high density tanks because juvenile densities were higher. Higher overall population densities made it difficult to see juveniles making it easier to double count or miss juveniles.

After 21 months, eight adults (4 males and 4 females) were randomly selected from each tank and placed in a new identically treated tank that contained a refuge and a barb. The new tanks were prepared two weeks earlier and allowed to sit with the filter running. The recovery of each of the new populations was then monitored for six months.

Experimental Results

Over 21 months of harvesting there was a declining trend in the adult population size that low density tanks reached after two months (Fig. 2.1). After each successive harvesting, all low density adult populations recovered to lower levels. There was no apparent mortality of adults (mortality within the first few weeks) caused by the

harvesting technique. Low density tank one (LD1) declined from an initial adult population recovery of 35 individuals to an apparent stable recovery level of approximately 23 individuals after 6 harvesting events. LD2 declined from an initial adult population recovery of 32 individuals to an apparent stable recovery level of approximately 15 individuals after 7 harvesting events. LD3 adult population recovery declined continuously over the 21 month period. This decline in adult population during the experiment resulted in an increase in the probability that an adult from a previous generation would be returned to the tank after harvest. This resulted in the adult populations near the end of the experiment being composed of much larger, older individuals. There was however no significant change in the size of broods these females produced even though they were larger (two-tailed t-test $p=0.606$, $t=0.559$, $df=4$). The initial mean number of juveniles produced in a brood at the beginning of the experiment was 12.99 compared to 11.22 at the end. The apparent decline in fecundity of females in the low density tanks and the declining trend in the overall adult populations over the course of the experiment indicated that there may have been some inbreeding depression. Assuming there was no inbreeding already in the population at the start of the experiment, an effective population size of 8 and at least six generations breeding, the calculated inbreeding coefficient is quite high and optimistic ($F=0.32$). Such a high inbreeding coefficient indicated that inbreeding depression was likely to have occurred (Falconer 1989). LD2 and LD3 showed some signs of the onset of disease near the end of 21 months. Older individuals exhibited fin rot and hollow belly, that increased adult mortality and could account for the difference between the total population sizes in LD2

and LD3 compared to LD1. Mean juvenile density for low density tanks during the experiment was approximately 8 (Table 2.0).

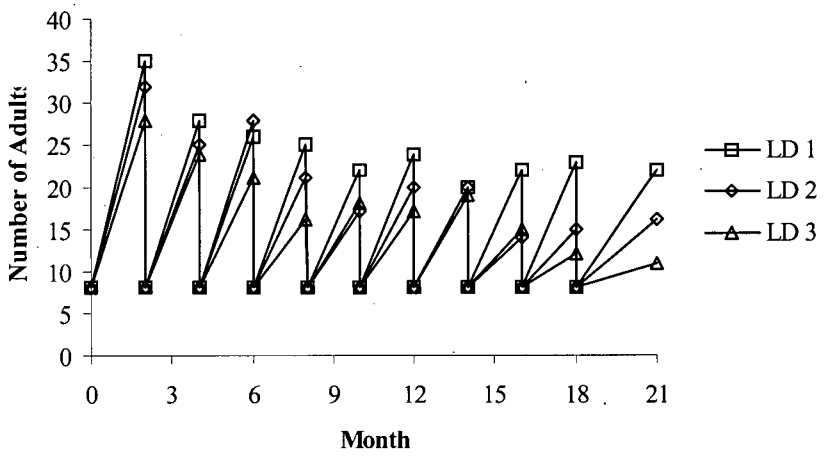

Figure 2.1. Adult population abundance for low density (LD) treatment tanks over 21 months of harvesting. Low points on the graph indicate the month in that harvesting occurred.

High density tank populations behaved as expected (Fig. 2.2). I observed slight decreases in abundance during the early months of the experiment, but stable abundance later at what was assumed to be the carrying capacity. High density tank one (HD1) maintained the highest average density of approximately 60 adults. Lower average densities in HD2 and HD3 could not be directly attributed to any obvious factors. There was a slight difference in the light levels in each of the tanks due to the structure of the shelving units used in the lab. Tank one had the highest light level, that may have resulted in better water quality. There was a slightly higher adult mortality in HD2 and HD3, but it could not be attributed to obvious factors like disease.

Inbreeding was not a problem in the high density tanks. Assuming an effective population size of 30 and 6 generations of breeding the computed F (F=0.096) does not indicate any inbreeding depression in the populations (Falconer 1989).

Table 2.0. Mean juvenile density (individuals <5 mm) during the 21 month experiment for high (HD) and low (LD) tanks.

	Tank Type					
	HD1	HD2	HD3	LD1	LD2	LD3
Mean Juvenile abundance	16.87	19.47	17.02	8.77	9.75	5.82
Std. Deviation	9.3	6.55	3.819	4.38	4.35	3.86

As in the low density tanks, brood size in high density tanks did not change significantly during the experiment (two-tailed t-test p=0.691, t=0.427, df=4). The initial mean number of juveniles produced in a brood at the beginning of the experiment was 12.67 compared to 12.04 at the end. Juvenile density was significantly higher on average in the high density tanks (Table 2.0) (two-tailed t-test p=0.001, t=6.67, df=4).

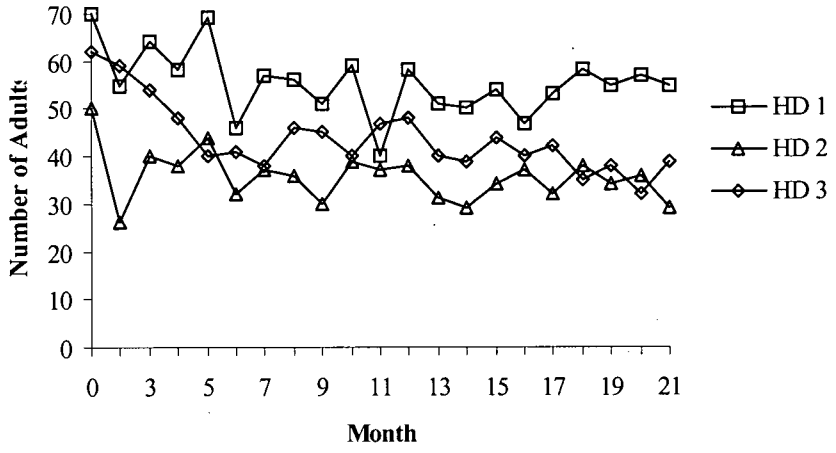

Figure 2.2. Adult population abundance for high density (HD) tanks over 21 months.

After 21 months (an estimated six generations) of maintaining the high and low density tanks, all tanks were reduced to eight individuals and allowed to grow in the presence of a predator (Fig. 2.3). All high density tanks had higher numbers of adults after the first month. HD1 increased to near the level observed before the reduction by the end of the six months. Adult fish in the tank were healthy and it appeared the population would recover to the same level as before the reduction. HD2 and HD3 initially increased but, after the first month in HD3 and the second month in HD2, signs of disease were evident. The tanks were given antibiotics and the water was changed as frequently as possible but, the disease had apparently spread to all fish. Populations in both tanks declined resulting in extinction of HD3 and a reduction to two individuals in HD2. Reproduction in both tanks stopped with the onset of disease. LD1 increased after the reduction, but abundance stabilized at around 15 adults with reproduction continuing. There was a large problem in LD3. A day after the population was reduced to eight individuals only one female remained in the tanks. It was discovered that all other individuals had jumped out of the tank. This jumping behavior had not been observed over the previous 21 months. It was assumed that aggressive behavior from the barb, having been initially placed in the tank a few days before, caused this unexpected behavior. The remaining female in the tank reproduced once but none of the juveniles survived to maturity. The decline to extinction in HD2 was a result of disease. The outbreak of disease in three of the tanks may have been due to stress resulting from the transfer of individuals to new tanks. Physical removal and transplant of the guppies should not have caused enough stress to initiate the disease outbreak. Guppies had been

removed throughout the experiment during harvesting with no deleterious effects. Water in the new tanks had been acclimatizing for three weeks, and no change was made to salinity or alkalinity; still, the switch to "cleaner" water may have caused the outbreak.

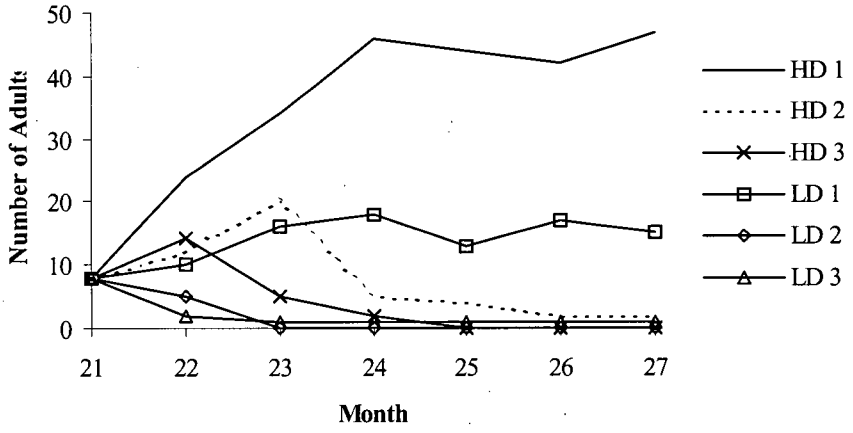

Figure 2.3. Time series of population abundance for low density (LD) treatment and high density (HD) tanks after population reduction.

Trends in mean juvenile survival (individuals <0.5cm) were monitored over the first 21 months of the experiment (Fig. 2.4). Mean survival for the high and low density tanks did not differ significantly at the beginning of the experiment ($p=0.527$, $t=-0.69$, $df=4$ two-tailed t-test on the logit transformed data) but, as the experiment progressed survival in the low density tanks decreased. There was no significant change in mean survival of juveniles in the high density tanks during the experiment ($p=0.49$, $t=-0.783$, $df=4$ two-tailed t-test on the logit transformed data). Initial mean survival in the low density tanks was approximately 70% but declined steadily over the course of the experiment to approximately 30%. There was a significant difference in the mean survival rate between the high and low density tanks by the end of 21 months ($p = 0.035$, $t=3.13$, $df=4$ two tailed t-test on the logit transformed data).

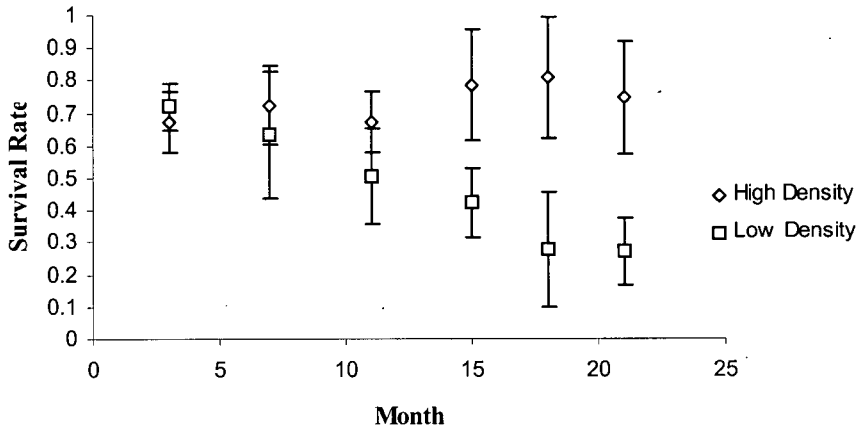

Figure 2.4. Trend in mean survival for high and low density tanks during the experiment.

Mean proportion of juveniles less than approximately 0.5 cm standard length using the refuge habitat was monitored over the first 21 months of the experiment (Fig. 2.5). No significant difference in the mean proportion of juveniles utilizing the refuge at the beginning of the experiment was found between the high and low density tanks ($p=0.434$, $t=-0.868$, $df=4$ two-tailed t-test on the logit transformed data). Refuge use in the high density tanks was variable during the experiment but there was no significant change in refuge use from the start to the end of the 21 months ($p=0.817$, $t=0.247$, $df=4$ two-tailed t-test on the logit transformed data) . A clear trend in refuge use in the low density tanks emerged over the course of the experiment. The mean proportion of juveniles using the refuge increased from approximately 30% to over 80%. There was a significant difference in the observed means between the high and low density tanks by the end of 21 months ($p=0.003$, $t=-6.36$, $df=4$ two-tailed t-test on the logit transformed data).

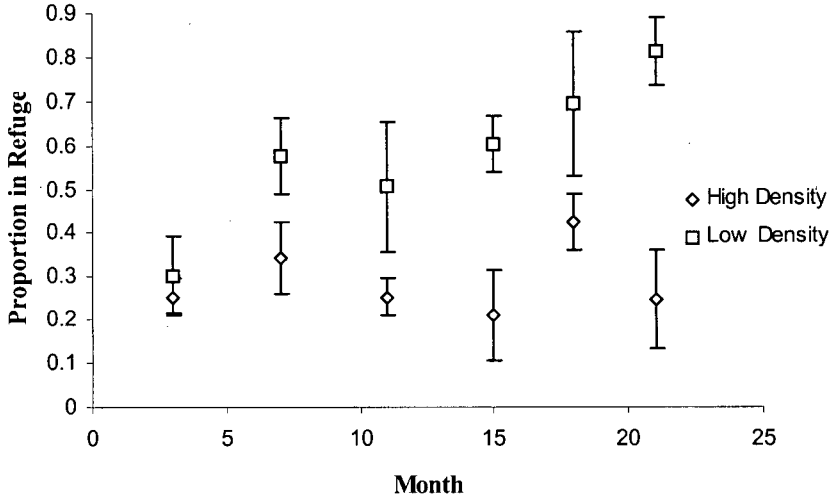

Figure 2.5. Mean proportion of juveniles observed in the tank refuge over 21 months of experimental manipulation.

There was no significant difference in mean weight of adult male at the start of the experiment (p=0.352, t=0.94, df=47 two-tailed t-test). There was also no significant difference in the mean weight if adult females at the start of the experiment (p=0.752, t=0.317, df=47 two-tailed t-test). After 21 months of selection there was significant differences in mean weight of males between the high and low density tanks experiment (p=0.007, t=3.31, df=11 two-tailed t-test). There was also a significant difference in mean weight of females between the high and low density tanks after 21 months of selection (Fig. 2.6) (p=0.001, t=4.26, df=11 two-tailed t-test). The difference in the mean weight of males and females is likely due to reduced adult competitive conditions and a high proportion of older adults in the low density tanks. The decline in adult population size over 21 month in the low density tanks resulted in an increase in the probability that older adults would be returned to the tanks after harvesting. It is likely that some of the adults remaining in the low density tanks were at least four months old.

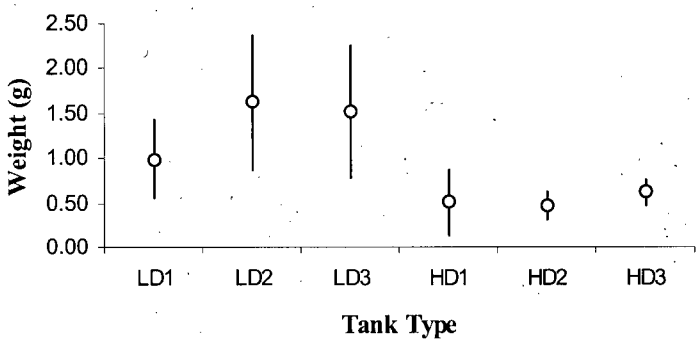

Figure 2.6. Mean weight of females in low density (LD) treatment tanks and high density (HD) tanks after 21 months of selection. Four females were weighed from each tank.

A larger mean weight of females in the low density tanks was also apparent after month 28 (Fig. 2.7). Some of the females weighed were still from the initial four individuals in month 21. A t-test on the mean weight of females from LD1 and HD1 indicated a significant size difference ($p = 0.008$, $t=3.85$, $df=6$). The other tanks were excluded from the analysis due to the extinction of the populations.

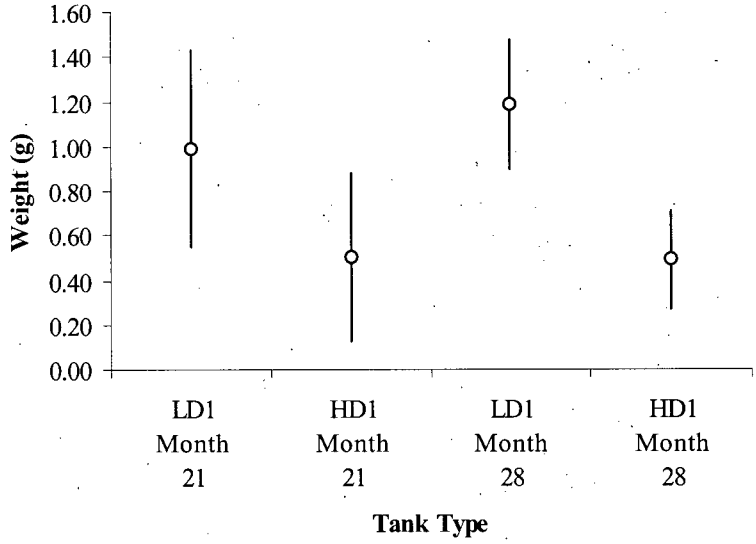

Figure 2.7. Mean weight of females in low density tank(LD1) and high density tank (HD1) after month 28. Eight females were weighed from each tank.

Discussion

The goal of the experiment was to select for individuals with reduced foraging times as juveniles and to see if selection had the same impact on the recovery dynamics of a population as predicted by Walters and Juanes. According to Walters and Juanes, one could imply that selection for reduced foraging time in juveniles had occurred if a population, that had been maintained at low densities for a number of generations, did not increase in abundance as quickly when compared to a population that had been at high densities. The slower population recovery in the low density populations would result from slower growth in the juveniles as population density increase. Slower juvenile growth results in an increase in juvenile mortality and increase in the time needed to reach maturity. A slow population recovery after a number of generation of selection was not the only indicator that selection for reduced foraging time in juveniles had occurred. Walters and Juanes also indicated that as the proportion of individuals with reduced foraging times as juveniles increases in a population over time there should be an increase in the observed juvenile survival rate assuming predation risk remained constant. Juveniles with reduced foraging times should have a relatively better survival because they spend less time exposed to predation. The proportion of juveniles utilizing refuge areas should also increase as selection for reduced foraging times occurs.

Given the experimental results and the criteria laid out by Walters and Juanes, can selection for reduced foraging times as juveniles be implied? There was a noticeable

difference between the recovery dynamics of LD1 and HD1 (Fig 2.3). LD1 recovered more slowly and to a lower abundance than HD1. There was also an increase in the proportion of juveniles observed in the refuge areas in the low density tanks over the 21 months (Fig. 2.5). This increase in refuge use suggests a decrease in the amount of time juveniles spent foraging. It is also possible to imply from this that selection for reduced foraging times had occurred. Unfortunately, there were a number of other trends that were contrary to the predictions of Walters and Juanes. Decreasing juvenile survival (Fig. 2.4) in the low density tanks over the 21 months is contrary to what selection for reduced foraging times would produce. If selection for reduced foraging times had occurred, there should have been an increase in juvenile survival.

As the low density populations were allowed to recover, there should have been a decrease in the size of individuals in the population. This decrease in adult size should have resulted from a decrease in the growth rate of juveniles as population densities increases. Figure 2.7 indicates no decrease in the size of adult females after six months of population recovery. Therefore, there is no clear evidence that allowed me to imply that selection for reduced foraging time as juveniles had occurred and was responsible for the slower recovery and lower abundance in low density tank one after harvesting was removed. Without a clear indication that selection for reduced foraging time had occurred in the low density tanks the slower recovery of the low density tank compared to the high density tank is unexplained and it remains a question whether selection for reduced foraging times occurred at all.

There is another reasonable explanation as to why LD1 recovered more slowly and to a lower abundance than HD1. It is likely that the slow growth rate and low

population abundance in LD1 resulted from an increase in juvenile mortality caused by cannibalism from large adults. Decreases in juvenile survival (Fig 2.4) were the result of a substantial increase in the predation mortality faced by juveniles when outside the refuge. Reduction in foraging time (as indicated by increasing refuge use) and a decrease in survival indicates that an additional source of mortality increased over the course of the experiment. It is unlikely that the increase in mortality resulted from the barbs. There was no difference in the size or behavior of the barbs during the experiment. A reasonable explanation for the progressive increase in mortality is cannibalism from adult guppies. Incidents of cannibalism were observed in low density tanks as mean adult body size increased over the experimental period. More cannibalism events were observed than barb attacks near the end of the experiments. Increased size in adult guppies increased the number of effective predators in the low density tanks, creating a higher risk of predation per foraging excursion by juveniles.

The increase in adult size in the low density tanks as the experiment progressed was due to an increase in the age of adults as a result of the harvesting process. The decline in adult abundance after successive harvest in the low density tanks increased the probability that older individuals would be returned to the tank. Therefore, it is likely that as the experiment progressed the number of older adults in each low density population increased. The increase in age and larger body size resulted in an adult population that was cannibalistic. An increase in juvenile mortality due to cannibalism did not occur in the high density tanks because adults were not large enough. It is probable that there were a number of older adults in the high density tanks, since adults were not removed by harvesting. However, these older adults could not achieve larger body sizes due to the

competitive conditions. Although the adults in the high density tanks were fed ample food, it is likely that being at high densities increased their energy expenditure. Adult guppies are known to display aggressive behavior when there is competition for resources and predation risk is low (Magurran et al. 1993). I noted that the level of aggressive interactions was higher in the high density tanks. Males and females spent more time chasing each other. There was a higher frequency of mating displays by males that usually involved a number of males chasing a female around the tank. The increase in aggressive behavior and activity in the high density tanks likely resulted in a higher energy expenditure reducing the amount of resources available for growth.

When the populations were reduced to eight individuals after 21 months, the larger size females persisted until month 28 (Fig. 2.7). Therefore, in low density tanks, predation risk for juveniles remained high resulting in higher juvenile mortality. Higher mortality resulted in reduced population growth rate a lower equilibrium abundance. It is also possible that poor juvenile production as a result of inbreeding aided in the poor recover rate of the low density population. An inbreeding coefficient of 0.32 was calculated for the low density tanks. Falconer (1989) noted that with an inbreeding coefficient of 0.32 there is likely to be a reduction in fecundity. There was no change in the brood size produced in the low density tanks during the experiment but, there was an increase in the size of females in the low density tanks. One would have expected there to be an increase in the number of juveniles each female produced. A lower juvenile production and a high juvenile mortality due to cannibalism would certainly result in a slow population growth rate and a decrease in the equilibrium abundance of a population.

Botsford (1981) argued that an increase in the mean body size of adult individuals in a population, as a result of reduced resource competition when a population is at low densities, can maintain the population at low densities through increased juvenile mortality from cannibalism. As competition for resources between adults decreases, a greater proportion of the population will grow above a size where they become cannibalistic. This increase in cannibalism increases juvenile mortality rate and causes reduced recruitment into the adult population, keeping adult densities low and maintaining the improvement in growth . Botsford's hypothesis is a reasonable explanation for observed increases in juvenile mortality of low density tanks during the 21 months of harvesting as well as an apparent lower equilibrium density when harvesting was removed. Larger females were observed to be cannibalistic and this resulted in increasing juvenile mortality. A low density equilibrium did not occur in the high density tanks after a reduction to low abundance because increases in adult size were not immediate. All of the fish were already adults and did not increase their body size. There was also a rapid increase in the adult population shortly after reduction, due to higher juvenile survival (Fig. 2.3). Increasing densities would have increased aggressive behavior limiting the size of individuals.

It seems reasonable to conclude that an increase in juvenile mortality caused by cannibalism resulted in the differences in the recovery dynamics of the high and low density tanks not selection for individuals with reduced foraging time as juveniles. It is questionable if selection had occurred at all during the experiment or if selection did occur it may not have been strong enough or for long enough. Reznick (1996) reported noticeable changes in life history traits in guppies in six generations. If six generations

are required to see changes in life history traits that have estimated heritabilities of approximately 0.27 (Roff 1992) one would expect a change in a behavioral trait, like foraging behavior, that have higher estimated heritabilities of approximately 0.37 (Roff 1992). With the overlapping generations in the low density tanks as well as female guppies ability to store sperm for six months, it is questionable if there were six generations over the course of the experiment.

Most of the conditions required by Walters and Juanes to cause selection for reduced foraging time were met in the experimental set up, although it is questionable if there were enough generations of selection. The increase in juvenile mortality in the low density tanks would have resulted in stronger selection for reduced foraging times. There was however no clear evidence that selection for reduced foraging times had occurred. Although there was an increase in the proportion of juveniles in the refuge areas in the low density tanks that might indicate selection for individuals with reduced foraging time, there was also a declining trend in juvenile survival. It is likely that the increase in refuge use in the low density tanks was a behavioral response to an increase in predation risk. One of the key indicators that selection for reduce foraging time as juveniles had occurred would have been a reduction in the size of adults as the low density populations were allowed to recover. Unfortunately, the low density tank that did recover, reached a low population abundance due to high juvenile mortality cased by cannibalism. This low population abundance and possible inbreeding depression prevented the juvenile density from increasing high enough to cause an increase in resource competition in the juveniles. Without an increase in juvenile density the effects of reduced foraging times

could not be seen and, according to Walters and Juanes, selection for individuals with reduced foraging times can not be implied.

It does not seem that the experimental results lend support to Walters and Juanes' prediction. One could not conclude from the experimental results that selection for reduced foraging time individuals occurs when a population is held at low abundance. It is also unclear if such selection would cause the population to recover more slowly than a population were selection had not occurred. However, the experimental results do point to another problem that may arise if a population is held at low densities and then allowed to recover. Decreasing the adult abundance in the population may allow the remaining adults to grow to larger sizes. As Botsford (1981) pointed out if adults grow large enough to be cannibalistic there can be a substantial increase in juvenile mortality. The increased juvenile mortality will result in a reduction in the population growth rate and the population will recover to a lower abundance once harvesting is stopped.

Chapter 3. Modeling the Northern Cod Fishery and Genetically Determined Juvenile Foraging Behavior.

Introduction

The Atlantic cod fishery located in NAFO divisions 2J, 3K, 3L (hereafter, northern cod; Fig. 3.0) produced catches of 100,000 to 150,000 t. from 1805 to 1850. Catches rose to around 200,000 t. in the later half of the nineteenth century (Hutchings and Myers 1994). The fishery developed further in the early 1900's, producing catches up to 250,000 t. With the development of "factory freezer" (stern otter) trawlers, catches continued to grow to a maximum of 810,000 t. in 1968. In 1977, when Canada extended its jurisdiction to 200 miles, the annual harvest declined to approximately 80% of the 1968 level. During the first 11 years of Canadian management (1978-1988) commercial landings increased from 140,000 t. to 270,000 t. with the development of an offshore fishing fleet. By 1992 the spawning stock biomass had declined to its lowest level, the oldest age class observed in the catch had dropped from twenty to nine, and in July of 1992 the Canadian government imposed a moratorium on the fishery. Total catch in 1992 was estimated at approximately 41,000 metric tones resulting from a estimated harvest rate of approximately 95% on fully vulnerable age classes. There was a sizable catch in 1993 of approximately11,400 metric tones, an estimated harvest rate of approximately 86%. Catch was taken in 1994 and 1995 as a result of bycatch, food fisheries and sentinel survey fishing. Estimated harvest in 1994 was approximately1400 metric tones and approximately 300 metric tones in 1995.

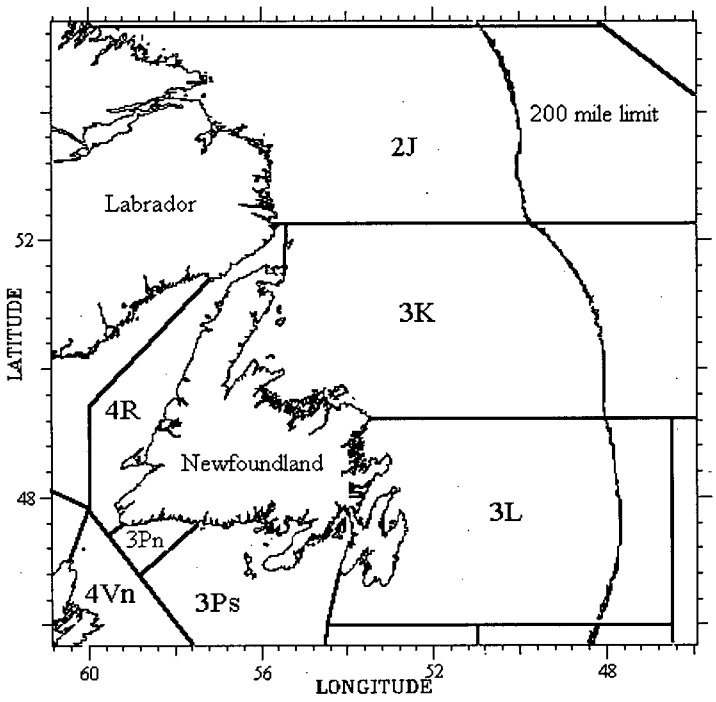

Figure 3.0 Map of the northern cod fishery in NAFO divisions 2J, 3K, 3L.

There is general consensus that unsustainable harvest levels caused the collapse of the northern cod fishery (Hutchings 1996, Myers and Cadigan 1995 and Hutchings and Myers 1994). Erosion of the spawning stock biomass to 13% of its estimated historical levels by 1992 (Fig. 3.1) resulted in an estimated 94% decrease in recruitment (abundance of age three individuals) (Hutchings 1996). There is no indication that the stock has recovered to an exploitable abundance (Myers et al 1997 and Hutchings et al 1997) since the moratorium. Recruitment to the population has been poor since 1992 (Shelton et al 1996 and deYoung and Rose 1993). Between 1980 and 1995 there was a noticeable decline in the mean weight-at-age observed in the catch (Shelton et al 1996).

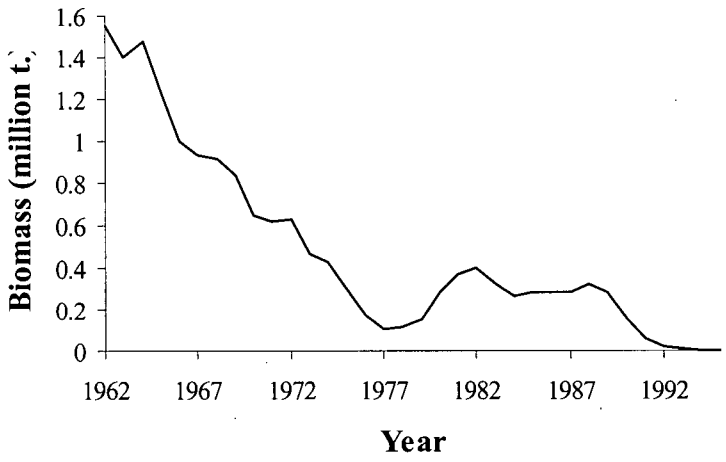

Figure 3.1. Northern cod spawning biomass (individuals age 7+) for 1962-1995 estimated from VPA reconstruction.

Certain trends in the northern cod data as well as some behavioral characteristics of juvenile (age 0+) cod give some indication that the selection process proposed by Walters and Juanes (1993) may have occurred in the northern cod stock. Juvenile cod (age 0+ post settlement) are know to associate with substrate that provides refuge from predation, as well as altering their foraging behavior in the presence of predators (Gotceitas and Brown 1993). Declines in mean weight-at-age of all age classes, observed in the commercial catch from 1980-1995, indicates that selection for reduced foraging times may have occurred. Erosion of spawning biomass from 1962 to 1995 and subsequent reduction in recruitment may have created the condition for low juvenile density under which selection for reduced foraging times could have occurred (Walters and Juanes 1993). There has been poor juvenile production and recruitment into the population since the fishery closure in 1992 (Shelton et al 1996) indicating that the delay in stock recovery predicted by Walters and Juanes may be occurring.

In this chapter I develop a model of the northern cod fishery that incorporates the fundamentals of Walters and Juanes' prediction, to see if such a model could fit the estimated abundance for 1962 to 1995 as well as produce the observed trend in mean weight-at-age. I then use the model to explore the impact that selection for reduced juvenile foraging time might have on the recovery of the northern cod fishery and how this recovery time compares the predictions of a model that assumes all juveniles have the same average foraging behavior.

Model Structure

Introduction

Modeling the northern cod stock with genetically determined juvenile foraging behavior and exploring the resulting population dynamics that selection for reduced foraging time individuals might have on recovery of the population after closure of the fishery requires an age and genetically structured population dynamics model. Basic biology of the cod (survival, fecundity, size-at-age and the relationship between foraging time and juvenile survival) had to be represented as genotype-specific. Simulation from 1901 to 1995 of harvesting of northern cod, and resulting changes in stock structure, had to be altered to account for genetic differences. Probability distributions of leading parameters need to be calculated for two scenarios: (1) juvenile foraging behavior is genetically determined and (2) all juveniles have the same average foraging behavior. Parameter probability distributions can then be used in Monte Carlo simulations of the fishery, to estimate probability distributions for recovery time to pre 1962 abundance.

Data used for stock reconstruction and in the genetic model came from the 1996 northern cod stock status report by the Department of Fisheries and Oceans (Shelton et al. 1996). Virtual population analysis (VPA), an age structured stock reconstruction method, used the measured catch-at-age history to reconstruct historical stock abundance. Methodology used in the VPA is outlined by Hilborn and Walters (1992). The catch-at-age and weight-at-age data for 1962-1995 came from DFO statistics, and the VPA was tuned using abundance indices from research trawl done by DFO for 1981-1995 corrected for sample bias by Hutchings (1996) for 1981-1992. From the reconstruction, yearly spawning biomass (Fig. 3.1) of age seven and older cod, biomass of cod age three years and older (Fig 3.2), harvest rates (Fig 3.7), vulnerability at age schedules and recruitment anomalies (Fig. 3.6) were estimated. Recruitment anomalies were calculated as deviations between expected recruitment based on spawning stock biomass and a fecundity per kilogram of spawning individual, versus the VPA estimated recruitment. Recruitment anomalies were used to account for density-independent changes in juvenile survival rate as a result of environmental conditions (Taggart et al. 1994).

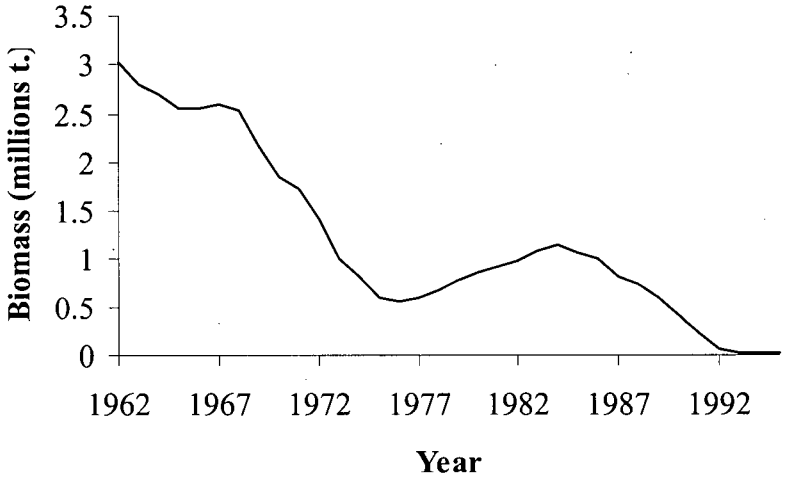

Figure 3.2. Time series of age 3+ northern cod from 1962 to 1995 estimated using VPA

Genetics, Biology and Fishery Impacts.

At the heart of the model is the relationship between genetically determined juvenile foraging times and the impact of foraging time and competition on juvenile (age 0+ post settlement) survival. Inheritance and variation in genetically determined foraging time were modeled as a diploid two locus system with additive foraging time effects, resulting in nine genotypes and five phenotypes. It was assumed that this representation would provide enough complexity to simulate realistic variation in individual behavior as well as inheritance of such behavior. Trait loci (QTL) studies on the foraging behavior of the honey bee (Lynch and Walsh 1998) indicated that two model QTL were sufficient to explain the observed variation in foraging behavior in subsequent generations.

Amount of time spent foraging as a juvenile was assumed to be additive depending on whether a locus had a value of 1 (additive effect on foraging time) or 0

("no effect" on foraging time). Thus an individual with the genotype 1111 (homozygous additive at both loci), was assigned a foraging time score of four, and the genotype 0000 (homozygous "no effect" at both loci), was given a score of zero. The amount of time spent foraging by a phenotype was modeled using the linear equation:

$$ft_i = 0.1 + 0.2*\text{score} \quad (3.0)$$

where ft_i is an index of relative foraging time for genotype i and score is the previously mentioned additive effect of a loci on foraging time. Predation risk per unit of time spent foraging was assumed constant, implying decline in survival with increasing foraging time (when juvenile density is low) can be modeled using the equation:

$$pr_i = e^{-risk*ft_i} \quad (3.1)$$

where pr_i is the genotype-specific relative survival rate for genotype i, risk is the predation risk per unit time foraging and ft_i is the genotype-specific foraging time from equation 3.0. Equation 3.1 is reasonable if predation mortality results from random encounters with predators during feeding times. Thus, low foraging times results in higher survival due to fewer encounters with predators.

Food density within cod foraging arenas was modeled as a hyperbolic decrease in available food density with increasing juvenile density, with food density being most sensitive to juvenile density when juvenile density is low. Food densities in these restricted volumes, as mentioned earlier, can be depleted rapidly in spite of being replenished by physical mixing processes and biological processes. The relationship between juvenile density and food density was modeled using the equation:

$$food = Fo / (1 + N / Nh) \quad (3.2)$$

Where food is the mean food density seen by an individual fish during a foraging bout, Fo is food density in the absence of juveniles, N is the total number of juveniles and Nh is the density of juveniles needed to drop food density to half the Fo level. Nh was set so that mean juvenile survival would maintain equilibrium abundance given a historical harvest. Juvenile growth was assumed proportional to consumption and mortality was assumed to be size dependent such that when food density is low, juveniles that forage for less time remain susceptible to predation longer, resulting in higher mortality. Equations 3.0, 3.1 and 3.2 can be combined to predict genotype-specific juvenile survival over the first year of life (post settlement):

$$s_i = \frac{pr_i * (ft_i * food)^m}{0.005^m + (ft_i * food)^m} \quad (3.3)$$

Where s_i is the survival of genotype i. Setting the risk and Fo parameters from equations 3.1 and 3.2 to specific values describes the desired genotype survival curve. For the northern cod model, the risk parameter was set to 3.0 and the Fo parameter was set to 2.0 resulting in the set of phenotype specific survival curves seen in figure 3.3. Note that equation 3.3 predicts both genetic and density effects on juvenile survival, given the "food" term in 3.3 is assumed to depend on overall juvenile density (via eq. 3.2).

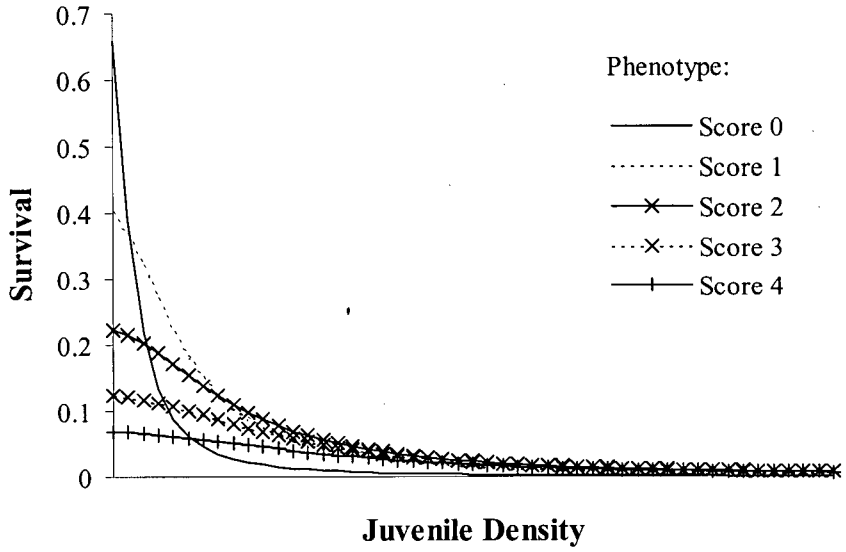

Figure 3.3. Phenotype-specific survival rates as a function of juvenile density

Risk and Fo parameters were set so that the set of survival curves (Fig. 3.3) would represent higher fitness for individuals with lower foraging time, at lower juvenile density. As juvenile density decreases, individuals with reduced foraging time gain a survival advantage (Fig 3.3) resulting from a reduction in predation risk due to less time spent foraging, but sufficient consumption during foraging bouts for growth. As density increases individuals with higher foraging time are favored due to a relative improvement in survival resulting from acquiring sufficient resources for growth. Instantaneous mortality rate for fish one year and older was set at 0.2 (Myers and Cadigan 1994).

The genetic foraging model assumes that individuals with lower foraging times will not grow as quickly during the juvenile stage, resulting in a genotype-specific size at age 1. It is unreasonable to assume that individuals with reduced foraging times as juveniles (age 0+) would continue to grow at a slower rate once they have grown large

enough to escape size dependent predation and leave the juvenile rearing areas. Dalley and Anderson (1997) noted that age 0+ cod were found to be distributed almost exclusively in inshore rearing areas, but age 1 juveniles were found further onto the shelf indicating an ontogenetic pattern in juvenile distribution. Thus one would expect there to be differences in the initial size of individuals age one as a result of different growth rates resulting from foraging behavior while in the rearing areas, but there should be no behavioral difference in the growth rate in older ages as juveniles move onto the shelf and display less risk adverse behavior. These arguments result in the growth curves used in the model (figure 3.4).

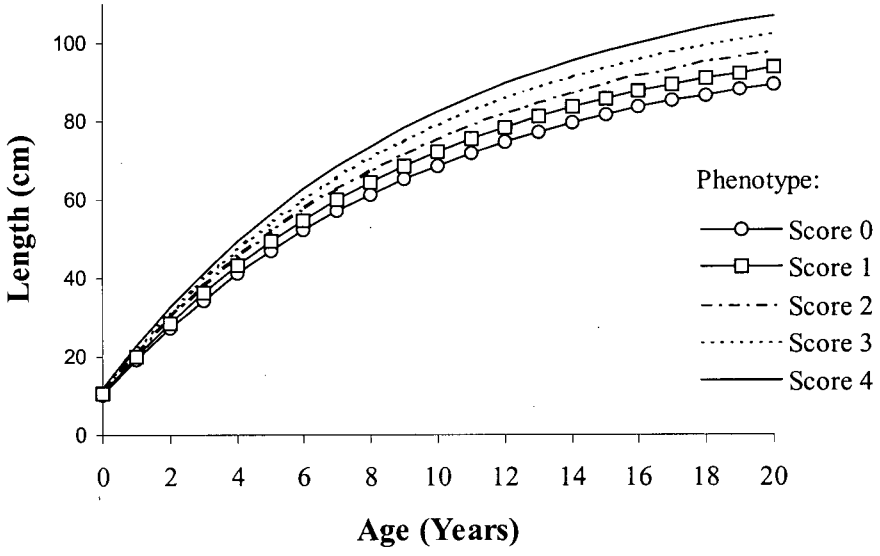

Figure 3.4. Phenotype specific growth curves assuming von Bertalanffy growth with constant growth rate after age one.

Genotype-specific mean size at age one was estimated by taking the observed range of size at age one (Dalley and Anderson 1997), dividing this range into five intervals and using the midpoint of each interval as the genotype-specific size. Growth rate after age

one was calculated from length-at-age data from the fishery. Length at age was then converted to weight at age using equation 3.4 taken from Shelton et al.(1996).

$$\ln(weight) = 3.0879 * \ln(length) - 5.2106 \quad (3.4)$$

Population age and genotype-specific abundance were initialized assuming that early in the 1900's the population was at equilibrium with respect to some constant historical harvest rate. According to the Walters and Juanes prediction a high density equilibrium population should be mainly composed of individuals with high foraging times as a result of high juvenile densities. The initial frequencies of the positive effect allele at both loci were set to 0.8 that was the equilibrium value given the constant historical harvest rate. Genotype frequencies for the initial population were then calculated using the Hardy-Weinberg equilibrium assumption (Falconer 1989). Catches in the early 1900's were fairly constant (Fig. 3.5), and as a result it was assumed that the historical harvest rate was constant.

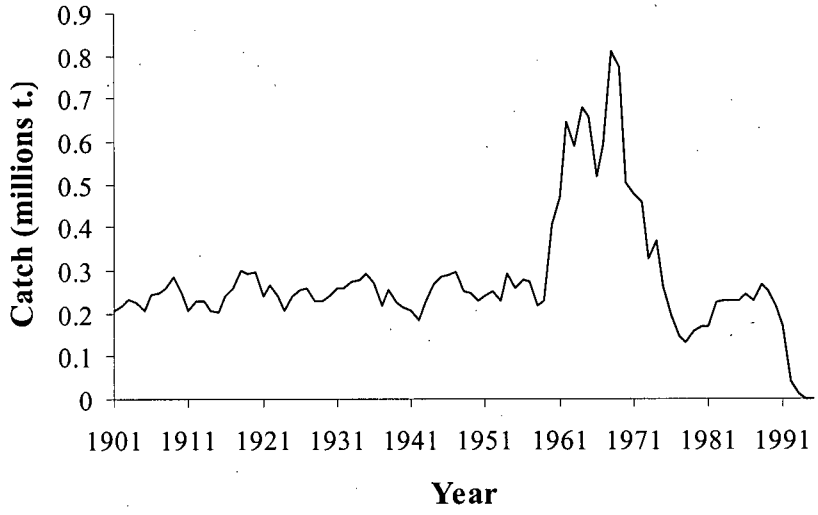

Figure 3.5. Historical catches from the northern cod fishery 1901-1995 in million tonnes.

If equilibrium is assumed then the recruitment needed to maintain the population at equilibrium can be calculated as:

$$R_{eq} = \frac{c}{\Phi_c} \qquad (3.5)$$

$$\Phi_c = \sum_{g=1}^{9} \Phi_{cg} p_g \qquad (3.6)$$

$$\Phi_{cg} = \sum_{i=1}^{a\max} u l_{ig} v_{ig} w_{ig} \qquad (3.7)$$

Where R_{eq} is the equilibrium recruitment, c is the mean historical catch, u the historical harvest rate parameter, amax the oldest age class in the population (20 for northern cod), g the number of genotypes, p_g the genotype frequency, w_{ig} the mean weight at age, v_{ig} vulnerability to harvest at age and l_{ig} the survivorship to age. Given the equilibrium recruitment the age specific abundance of a genotype can be calculated as the product of equilibrium recruitment, the survivorship to age, and the genotype frequency at high density equilibrium.

Fecundity was assumed to be proportional to body weight (May 1966). It is important to note that fecundity in the model is not a measure of egg production but the number of settled (demersal) juveniles produced per kilogram of spawner. Age at full maturity was set at seven as indicated by data presented by Shelton et al.(1996). Although a change in the mean length at 50 % maturity was seen in the last few years of the fishery (Taggart et al. 1994) it was assumed that selection for smaller-sized individuals was the cause, rather than a change in age at maturity. Total juvenile production was then calculated as the sum across mature ages and genotypes as the

product of fecundity per kilogram times age, genotype specific body weight, and (when available) a recruitment anomaly (years 1964 to 1994; Fig.3.6), as shown in equation 3.8.

$$TJ = \left(\sum_{a=7}^{20} \sum_{g=1}^{9} fec \cdot w_{a,g} \right) \cdot e^{r_t} \qquad (3.8)$$

Where TJ is the total juvenile production, fec is the fecundity per kilogram parameter, $w_{a,g}$ is the genotype-specific weight at age and r_t is the recruitment anomaly in year t. The proportion of juveniles of each genotype was calculated each year using the Hardy-Weinberg equilibrium accounting for changes in frequency of the positive foraging time effect allele at each locus as a result of selection on juveniles in the spawning population. Note that all the recruitment anomalies shown in fig. 3.6 are small, and even the negative anomalies since 1989 are not large enough to cause a population decline absent other mortality factors.

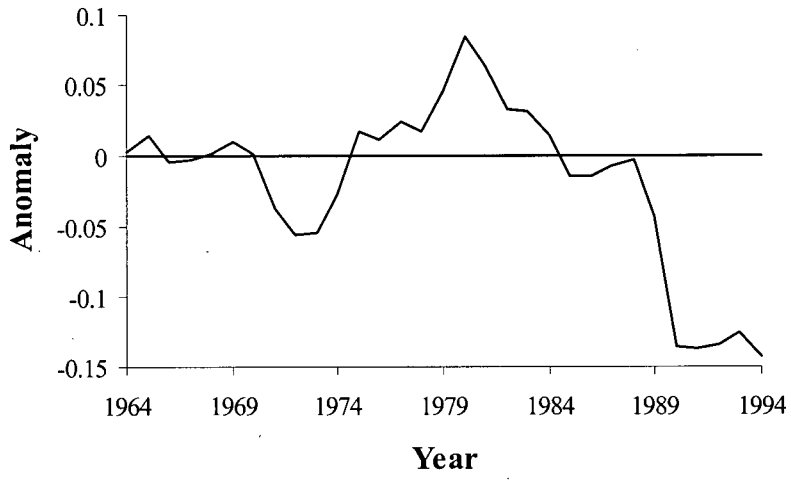

Figure 3.6. Recruitment anomalies for years 1964-1994 calculated from VPA stock reconstruction.

Yearly change in abundance of a given age and genotype was calculated using a simple balance model:

$$N_{g,a+1,t+1} = N_{g,a,t} \cdot s(1 - u_t \cdot v_{g,a,t}) \qquad (3.9)$$

where $N_{g,a,t}$ is the number of individuals of a genotype in a year at an age, s is the natural survival rate or the genotype specific juvenile survival rate, u is the harvest rate in a given year, and $v_{g,a,t}$ is a genotype-specific vulnerability to harvest based on weight for a given age in a given year. The harvest rate for each year was calculated either as the model predicted vulnerable biomass divided by observed total catch in that year (years 1901-1961), or a harvest rate estimated from the VPA (years 1962-1995, Fig. 3.7).

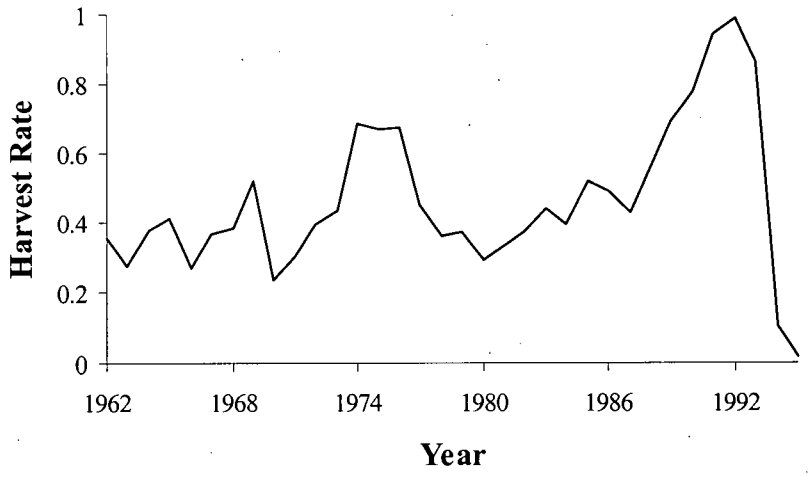

Figure 3.7. Yearly harvest rates for the northern cod from 1962-1995, estimated from VPA.

To account for differences in vulnerability to harvest at a specific age due to the resulting genetic differences in weight at age, an age- and genotype-specific vulnerability schedule was created from the vulnerability at age schedule estimated from the VPA

and the observed mean weight at age in the catch. This was accomplished by fitting a power model of the form:

$$v_{g,a,t} = 0.001 + \left(\frac{w_{g,a}{}^{m_t}}{wh_t{}^{m_t} + w_{g,a}{}^{m_t}} \right) \qquad (3.10)$$

where $v_{g,a,t}$ is the age and genotype-specific vulnerability in a given year, $w_{g,a}$ is the weight of the individual in kilograms, wh_t is the weight when vulnerability is .5 and m_t is a power parameter describing the slope at wh_t. For each year between 1962 - 95, wh and m were estimated, given the VPA trend in age-specific vulnerability and the observed mean weights at age from the catch (Fig. 3.8). For years before 1962, the 1962 schedule was used.

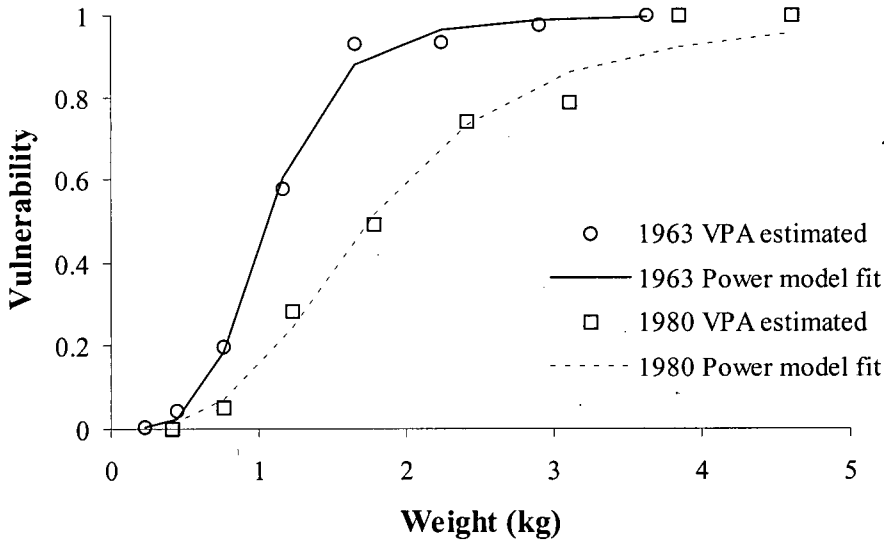

Figure 3.8. 1963 and 1980, VPA estimated vulnerability at weight and Power model fit to the data.

Estimation of Parameters and Recovery Time.

Probability distributions for two parameters, historical harvest rate and fecundity per kilogram of spawner, were estimated for two scenarios: (1) juvenile foraging behavior was genetically determined (hereafter the genetic model) and (2) all juveniles have the same average foraging behavior (hereafter the average behavior model). Historical harvest rate determines the equilibrium historical stock abundance, while the fecundity per kilogram spawner parameter determines the productivity of the stock; thus, historical harvest rate and fecundity are leading parameters in the model and are the parameters of primary interest.

A number of authors have pointed out the importance of evaluating uncertainty in parameter estimation (Punt and Hilborn 1997, Walters and Ludwig 1994, Ludwig et al 1993) by reporting key uncertainties in terms of a few such leading parameters. Evaluating uncertainty around parameters for the scenarios mentioned above is more desirable than simply finding parameter values that provide the best fit to the VPA estimated biomasses, because distributions of recovery time can be calculated and compared per uncertainty in the leading parameter estimates.

Bayesian statistics allow one to make probability statements about parameters from data using probability models (Gelman et al 1996). Bayes' rule states that the probability of a parameter given the data is equal to the probability of the data given the parameter times the prior probability of the parameter, divided by the total probability of the data:

$$p(\theta|y) = \frac{p(y|\theta)\,p_o(\theta)}{p(y)} \qquad (3.11)$$

For the northern cod model θ is the vector of leading parameters (historical harvest rate and fecundity). The data are the VPA biomass estimates of age three and older cod for 1962-95. Each data point y is assumed to be from a log normal distribution (Walters and Ludwig 1994) with mean a function of θ's and some equal variance σ^2. The posterior distribution can then be written, up to a normalizing constant, as:

$$p(\theta|y) \propto e^{\left(-\frac{1}{2\sigma^2}\sum_{i=1}^{n}(\ln(y_i)-\ln(f(\theta)_i))^2\right)} \; p_o(\theta) \qquad (3.12)$$

where y_i are the VPA age 3+ biomass estimates and $f(\theta)_i$ are the model generated age 3+ biomasses for the years 1962-95. If a uniform prior is used, ($p_o(\theta)$ constant) and the probability density is integrated over the nuisance parameter σ^2, the posterior distribution for θ is proportional to the following simple marginal kernel (Walters and Ludwig 1994):

$$p(\theta|y) \propto ss^{\frac{n-1}{2}} \qquad (3.13)$$

$$\text{where:} \quad ss = \sum_{i=1}^{n}\left(\ln(y_i) - \ln(f(\theta)_i)\right)^2$$

In equation 3.13 n is the number of data points. One can use Markov chain simulations to draw samples form the joint posterior distributions. Markov chain algorithms simulate a random walk in the p(θ/y) space, where θ converges to a stationary distribution that is

the joint posterior distribution. A Metropolis-Hastings algorithm was used for this task (Gelman et al 1996, Punt and Hilborn 1997).

If the joint posterior distribution can be computed up to a normalizing constant the Metropolis-Hastings algorithm creates a sequence of points whose stationary distribution is the joint posterior distribution. The Metropolis-Hastings algorithm was implemented as follows. A candidate θ^* for each θ is selected using a jumping distribution. It is convenient to make the jumping distribution (J_t) symmetrical, although this is not necessary. The jumping distribution used was normal with mean 0 and a standard deviation set for each parameter. The product of the posterior density of the candidate θ^* and the jumping distribution density is then calculated and the ratio (r) of the candidate value and the value determined in the previous iteration is calculated (eq. 3.14):

$$r = \frac{p(\theta^* | y) | J_t(\theta^* | \theta^{t-1})}{p(\theta^{t-1} | y) | J_t(\theta^{t-1} | \theta^*)} \qquad (3.14)$$

This ratio is then evaluated and the new θ^* value of the parameter accepted if r is greater than a random(0,1) value and rejected if not. Standard deviations in the jumping distributions were set so acceptance of parameters was approximately 20%. According to Gelman et al. (1996) this acceptance rate allows the algorithm to "walk" about the stationary distribution at an efficient rate. Metropolis-Hastings algorithms are designed to perform a random walk around the space of the stationary distribution; therefore, it is necessary to have an idea of when the algorithm is drawing samples from the stationary

distribution. It is common to run a number of chains that start from different initial values of θ and to assess the within and between chain variance as a measure of convergence. Gelman et al (1986) propose that if a potential scale reduction value is below 1.2 that the chains have converged and the algorithm is drawing points from the stationary distribution. The potential scale reduction value R is calculated as:

$$\sqrt{\hat{R}} = \sqrt{\frac{\frac{n-1}{n}W + \frac{1}{n}B}{W}} \qquad (3.15)$$

where W is the within chain variance for a parameter and B is the between chain variance for the parameter. When estimating the posterior distributions of historical harvest rate for both scenarios, four chains were run for each parameter and 25,000 data points were drawn from the stationary distribution of each parameter.

Posterior distribution of each parameter from each scenario were utilized in Monte Carlo simulations of the northern cod stock from 1901 to 2100 to calculate recovery time distributions. Harvest rate after 1995 was set to zero. 30,000 simulations were done for each scenario, drawing a value for historical harvest rate and fecundity from the posterior distribution. Initial stock structure for each parameter combination was calculated and the population was simulated forward in time as outlined in the previous section. Recovery time was measured as the number of years after 1995 the simulated population age 3+ biomass took to grow as large as the average age 3+ biomass for years 1952 to 1962 for that simulation. The average 3+ biomass for 1952 to 1962 was used as an indicator of stock recovery since prior to 1962 catches were fairly constant indicating that exploitation was sustainable. It was not until after 1962, when exploitation rates increased, that the stock began to collapse.

Modeling Results

Walters and Juanes predicted that if there was selection for reduced foraging time behaviors when a population is harvested to a low abundance, the resulting population would be dominated by individuals who are slower growing as juveniles and hence smaller as adults. Smaller size at age will result in reduced reproductive capacity. When fishing is stopped and the population is allowed to recover there will also be a decline in juvenile survival. The decline in juvenile survival is a result of juveniles with reduced foraging times experiencing an increase in competitive conditions. Since food availability decreases juveniles will receive less food resulting in slower growth. Slower growth causes the juvenile to be vulnerable to predation for longer increasing mortality. The combined effect of reduced reproductive potential and reduced juvenile survival results in a recovery rate that is slower than would be predicted using a simple stationary stock recruitment curve. This section will present the results from the northern cod fishery model that incorporated genetically determined juvenile foraging time and compare it to a model where all juveniles had the same average juvenile foraging behavior.

Posterior probability densities from the Metropolis-Hastings algorithm of historical harvest rate and fecundity from the genetic model and the average behavior model are summarized in figures 3.9 and 3.10. The "most probable" estimate of each parameter is the mode of the marginal posterior distribution for that parameter.

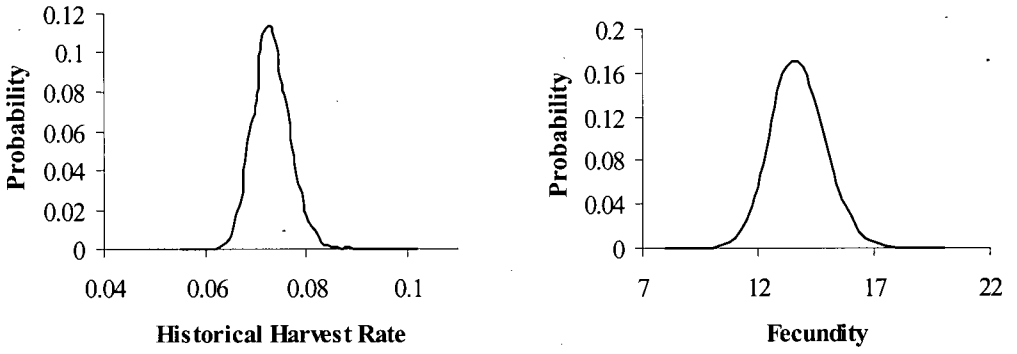

Figure 3.9. Marginal posterior distribution of historical harvest rate and fecundity parameters from the genetic model.

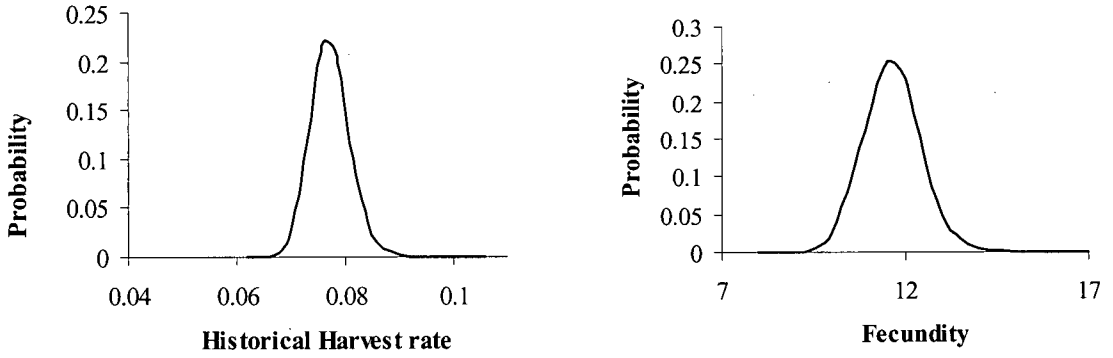

Figure 3.10. Marginal posterior distribution of historical harvest rate and fecundity parameters from the average behavior model.

When the posterior distributions for the parameters were used in Monte Carlo simulations to determine recovery time, the two scenarios produce quantitatively and qualitatively different distributions (Fig. 3.11). Recovery time distribution for the genetic model was bimodal, the first mode fell at 2023 with the first part of the distribution falling mainly between 2018 and 2029. There was a large gap and a much smaller second mode at 2050 with a distribution between 2049 and 2051. The bimodality of the recovery time distribution is a result of the stock recovery criterion used. If a

lower target stock abundance was chosen the second mode would disappear. If a target level closer to the population equilibrium had been chosen the first mode would disappear. The average behavior model produced a unimodal distribution with a mode at 2031 and a distribution between 2027 and 2040.

To explore the mechanism causing the difference in the two distributions, a forward simulation for each scenario was run using the best estimates of the respective parameters (Fig. 3.9). Both the genetic and average behavior models fit the VPA 3+ biomass estimates well. There is a discrepancy in the 3+ biomass between the models and the VPA during 1965 and 1970. After 1995 the best fitting genetic model recovered to the pre 1962 average biomass of approximately four million metric tones in 2023 while the mean genotype model recovers in 2032.

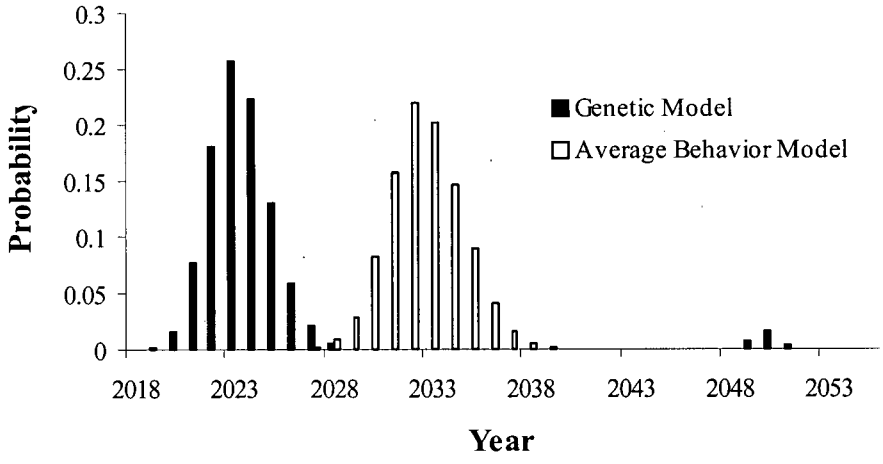

Figure 3.11. Distribution of year of recovery of the northern cod stock to pre 1962 3+ biomass levels for the simulation using the genetic model and the simulation using the average behavior model.

Genetic model biomass however, fell below the target biomass almost immediately and did not recover again until 2049. Biomass then slowly built toward the equilibrium level

of approximately five million metric tones in the absence of harvest but not until after 2100. The average behavior model provided a different picture after reaching the target abundance. Population abundance overshot the equilibrium level up to a maximum of approximately six and a half million metric tones, passing the equilibrium value in a few year after reaching the target abundance, then fell back down to the equilibrium value. The cyclic fluctuation in both models are a result of biomass accumulation in older age classes. This increase in biomass in the older age classes causes much higher juvenile production. Higher densities of juveniles results in a decline in juvenile survival causing a decline in cohort size. Lower recruitment persists until there is a decline in the biomass of older individuals that is caused by the smaller cohorts reaching older ages.

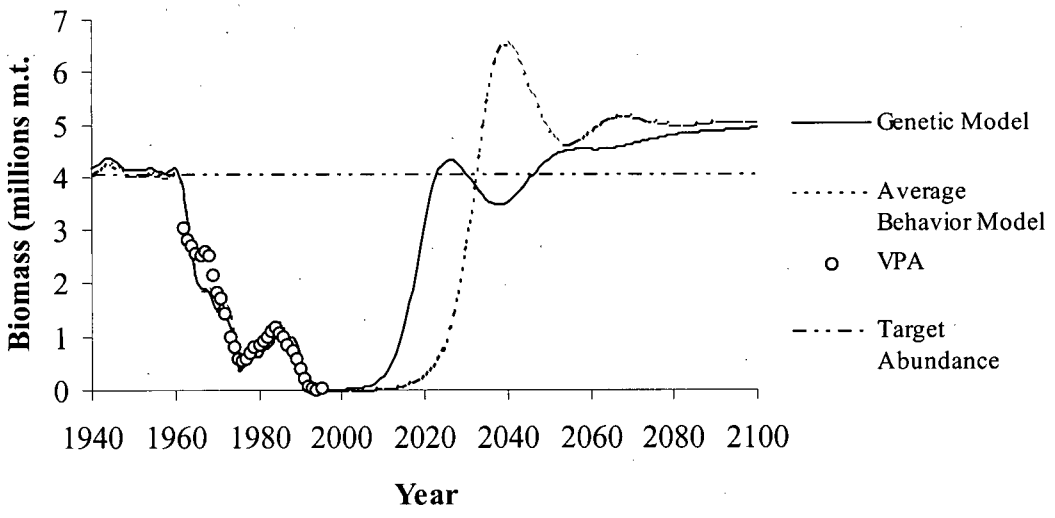

Figure 3.12. Time series of from 1940 to 2100 for 3+ biomass for the northern cod stock compared to the VPA estimated 3+ biomass using the maximum likelihood estimates of the mean historical harvest rate and fecundity parameter for the genetic model scenario and the mean genotype scenario.

Selection was evident for reduced foraging time juveniles in the best fitting genetic model. Figure 3.13 shows the shift in the frequency of the additive foraging effect allele at each locus in the simulated population. As the harvest rate increased after 1962, there was strong simulated selection for individuals with reduced foraging times. The frequency of alleles that had a positive effect on foraging time at each locus continued to decline well past 1992, the period of highest exploitation. By 2021 the decline stopped and the frequency of alleles that had a positive effect on foraging time slowly began to recover back to the initial equilibrium levels but not until the year 2200.

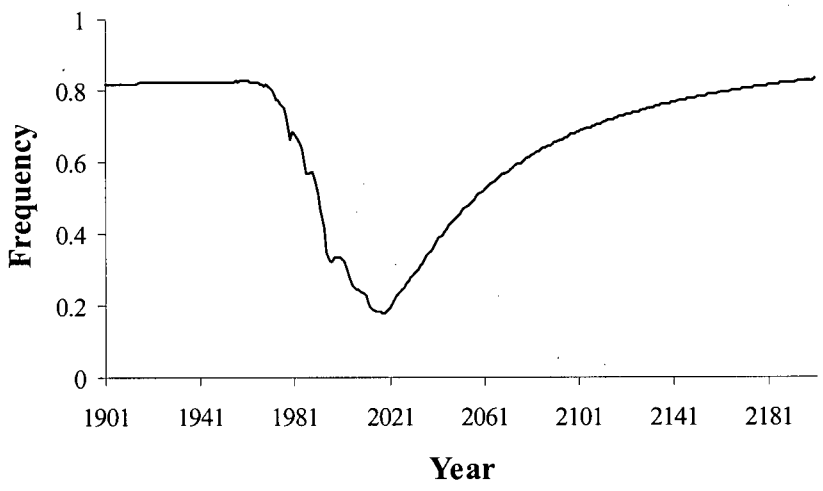

Figure 3.13. Trend in the frequency of the additive foraging effect allele at both loci from 1901 to 2200 from the genetic model scenario evaluated using the maximum likelihood estimates of the historical harvest rate and fecundity parameters.

Another prediction of Walters and Juanes is that mean body weight at age in the population should decline as selection favors juveniles with reduced foraging times. Figure 3.14 shows the observed trend in mean weight-at-age for age three, seven and ten fish in the catch (from DFO statistics) and the trends predicted by the best fitting genetic

and mean genotype models. Note that mean weight at age was not used in the fitting procedure. However, mean weight at age did have an indirect effect on the estimates of historical biomass. Trends in mean weight-at-age observed in the catch and those produced from both scenarios (for age three, seven and ten individuals) are similar to the trends observed and predicted for all age classes. Although there are discrepancies between the genetic model and observed weight-at-age, the general trend is described quite well by the genetic model.

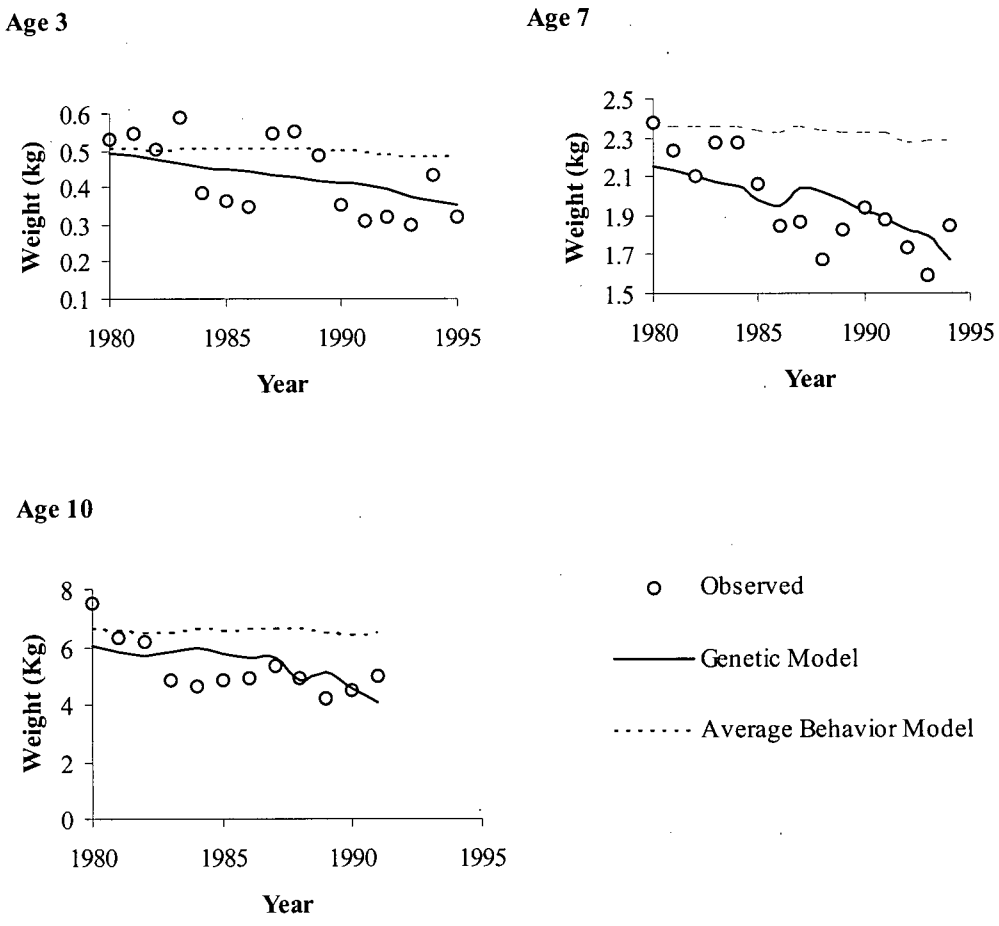

Figure 3.14. Observed trend in mean weight at age three, seven and ten from years 1980 to 1995 from DFO statistics compared to the trend in mean weight at age three, seven and ten estimated from the genetic model scenario and the average behavior

scenario. Both scenarios were evaluated using the maximum likelihood estimates of the model parameters.

Discussion

Decline in mean weight-at-age observed in the catch (Fig. 3.14) from 1980 to 1995 can be explained by the genetic foraging model. The progressive decline in the abundance of juveniles during the fishery may have favored individuals with reduced foraging times. As the proportion of these individuals increased, the mean weight at age in the population would have decreased as a result of increase in proportion of smaller individuals that had spent less time foraging as juveniles. The genetic model predicts that the proportion of these individual will continue to increase well after 1995 (Fig. 3.13). One would expect to see the mean weight of individuals remain low and decline until there is a positive increase in the proportion of individuals with higher foraging times in the population. Hanson and Chouinard (1992) argued that such changes in mean weight at age in Atlantic cod are a result of size selective fishing. They argue that the fishery removes faster growing animals from the population, and as a result there is greater proportion of slower growing fish. Patterns that would be observed if the decline in mean weight at age were a result of size selective fishing were explored using the average behavior model. The average behavior model was initialized, as mentioned earlier in this chapter, with the same size at age distribution except that juveniles had the same foraging behavior so that smaller juveniles survived at the same rate as larger juveniles. The same vulnerability at size schedule was used in both scenarios; therefore, there would be a greater proportion of the larger fish in each age class removed as a result of increased vulnerability. Although there is a slight decline in the predicted mean

weight at age from the average behavior model (Fig.3.14) configured this way, the change is not as dramatic as observed in the fishery. Comparing model simulations, change in mean weight at age is mainly a result of selection for slower growing juveniles and only a small part of the change is a result of size selective fishing mortality.

Walters and Juanes proposed that if juvenile foraging behavior is genetically determined and selection for individuals with reduced foraging time as juveniles occurs when a population is held at low densities, there could be a delay in recovery of such a population. Once harvesting is stopped, increasing spawner abundance would produce a greater juvenile density resulting in a decline in juvenile survival. This decline in the observed juvenile survival results because a greater proportion of the population has the reduced juvenile foraging time genotypes. As juvenile density increases, reduced foraging time juveniles acquire less resources resulting in starvation or slower growth. Slower growth would result in the juveniles being susceptible to predation for longer increasing their mortality. A rapid decline in the juvenile survival would result in poor recruitment and slower stock rebuilding. Simulations of the northern cod fishery indicated that selection for individuals with reduced foraging time does not in fact cause an initial delay cod stock recovery (Fig. 3.9), but rather a delay later in the recovery. Selection for individuals with reduced foraging time improves the initial growth rate of the population when compared to a population composed of individuals with the same average foraging behavior (Fig. 3.15).

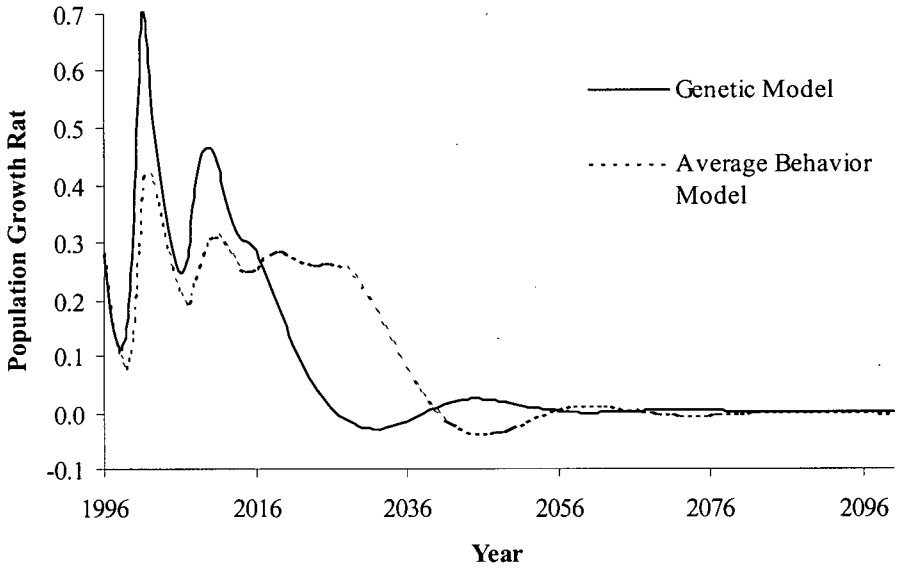

Figure 3.15. Population growth rate over time evaluated using the maximum likelihood parameter estimates for the genetic model scenario and the average behavior scenario.

The delay predicted by Walters and Juanes did not occur initially in the cod model because juvenile density was not high enough during the initial recovery to cause a reduction in juvenile survival. Relatively high juvenile survival during initial recovery was not considered by Walters and Juanes when they initially developed their prediction; however, a closer examination of conditions required for selection to occur shows that improvement in population growth rate should be expected in general. In order for selection for reduced foraging times to occur there has to a reduction in the juvenile density. Such a reduction can only occur when there is a substantial reduction in the spawning stock biomass to the point where recruitment becomes proportional to spawning stock density. As with the northern cod, selection for reduced foraging time is increased as the spawning stock is further eroded. When harvesting is stopped, spawning stock must first rebuild to a biomass that can produce juvenile density sufficient to cause

competition resulting in the decline of juvenile survival proposed in the prediction. Rebuilding of spawning biomass may require a substantial length of time particularly if selection has favored a reduction in the size of spawners. Spawning stock in the northern cod model does not build up sufficiently until 2016, at that time there is a substantial increase in the juvenile density (Fig. 3.16).

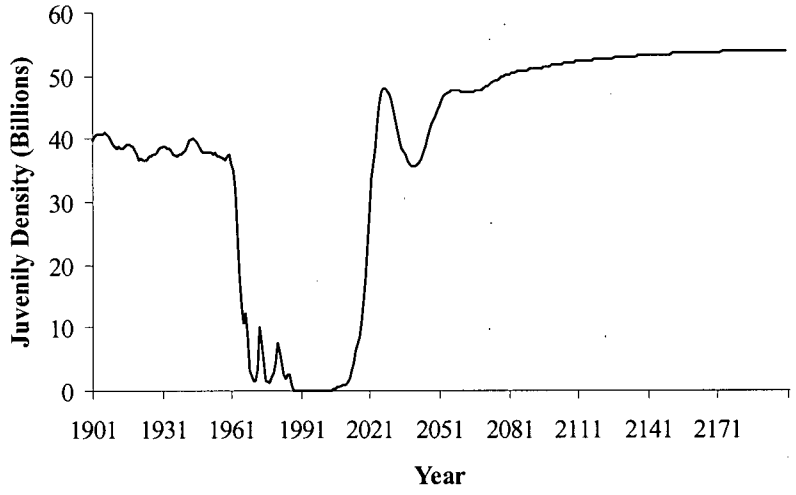

Figure 3.16. Juvenile density prior to survival from the genetic model evaluated using the maximum likelihood estimates of the parameters.

Model simulations have shown that the initial recovery of the population is not affected by selection for reduced foraging time. However, this does not imply that there is not a detrimental effect of such selection on the recovery dynamics of the population. Once juvenile densities increase after 2016 there is rapid decline in the growth rate of the population (Fig. 3.15). It is at this point where the delay predicted by Walters and Juanes occurs. Once juvenile density increases enough to cause competition there is a dramatic reduction in the mean juvenile survival rate since the majority of the population have low juvenile foraging times. Although selection for increased foraging time begins at this

point, that eventually results in improved juvenile survival, selection is slow (Fig. 3.13) and declining survival causes a substantial reduction in the population growth rate (Fig. 3.15).

Although stock abundance recovers in the genetic model to pre-1962 abundance by 2023, its composition and productivity are quite different than would have been observed prior to 1962. By 2023 the frequency of alleles with positive foraging effects at both loci has only increased to approximately 0.3 thus, there is still a greater proportion of low-foraging time individuals in the population. Such a distribution would result in a lower mean weight-at-age than would have been observed in the pre-1962 population, resulting in a decrease in potential egg production. Mean juvenile survival would also be lower resulting from a substantial reduction in the survival of juveniles with reduced foraging times hence lowering the productivity of the population further. Figure 3.17 displays the recruitment curves that would result if the genetic composition of the population did not change during the stock recovery, as well as the continually changing recruitment curve that results from the genetic model. A population composed of mainly reduced foraging time individuals (Curve B) has the greatest initial rate of increase. However, due to the rapid reduction in juvenile survival as abundance increases and the lower egg production due to smaller body size in the spawning population, the productivity of such a population at higher abundance is the poorest. In contrast, Curve E results from a population dominated by high foraging time individuals. Such a population has the best productivity at high abundance due to better juvenile survival and increased juvenile production from larger spawning individuals. However, due to poor juvenile survival at low juvenile densities, productivity is the lowest at low

abundance. As the northern cod stock recovers in the genetic model and gene frequencies change, there is a transition between the various recruitment curves depending on the gene frequencies (Fig. 3.17, Curve A). However, change in the gene frequencies is slow (Fig 3.13). The genetic structure of the stock, pre- 1962, is not recovered until the year 2200. Although the population abundance recovers by 2023 the stock has a much lower productivity until the genetic structure recovers.

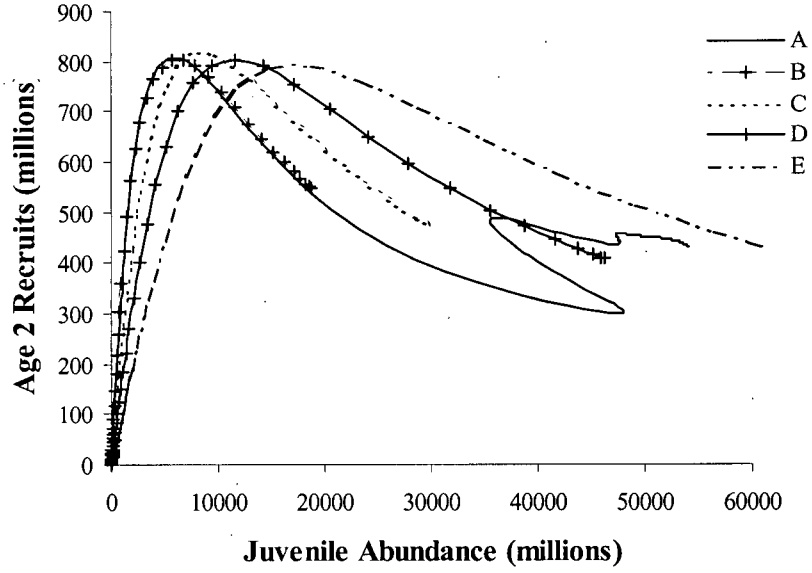

Figure 3.17. Recruitment curves resulting from model simulations during stock recovery depending on gene frequencies in the population. A) genetic model, continuous change in gene frequency as stock rebuilds. B) Frequency of additive effect on foraging time alleles at both loci are 0.2. C) Frequency of additive effect on foraging time alleles at both loci are 0.4 D) Frequency of additive effect on foraging time alleles at both loci are 0.6. E) Frequency of additive effect on foraging time alleles at both loci are 0.8

Modeling the collapse of the northern cod fishery indicates that if juvenile foraging behavior is heritable, selection for reduced foraging time may have occurred as spawning stock abundance was reduced to the point where juvenile density declined. A

decline in mean weight-at-age observed in the catch may be an indicator that selection for more individuals with reduced foraging time has indeed occurred. If the genetic model is correct we should observe a greater initial increase in the population than would be expected given the observed stock recruitment relationship. It is important to note that such an increase will not occur until the spawning stock begins to rebuild. The initial improvement in growth will decline rapidly as increases in spawning stock abundance results in increased juvenile density and competition. This rapid decline in growth rate does occur until after the genetic model population has reached a pre-1962 abundance. Although the genetic model population recovers to pre-1962 biomass levels faster than the average behavior model population, the genetic model population still has a high proportion of reduced foraging time individual. The high proportion of reduced foraging time individuals results in a stock that has a lower productivity than would have been seen in the pre-1962 population. The historical productivity of the genetic model stock does not recover until the genetic composition of the stock recovers. Genetic composition does not recover until approximately 200 years after the closure of the fishery.

Although the models have shown that selection for individuals with reduced foraging times does not delay the recovery of a stock when compared to a population where there is no heritable variation in juvenile behavior, they have shown that such selection does have an impact on the productivity of a stock and the size of individuals in the population. Having a less productive stock composed of individuals with a smaller weight at age would certainly have an impact on harvest management plans. A manager would not be able to set optimal harvest rates, once the stock biomass has recovered,

based on the stock recruitment curve observed before the closure. Such harvest rates would be too high because the stock is less productive as a result of the selection for individuals with reduced juvenile foraging time. Therefore, if selection for individuals with reduced foraging times occurs when a population is harvested to low abundance, it would be important for managers to have a clear early indication that such selection had occurred.

Unfortunately, there is no convenient indicator of selection having occurred. Walters and Juanes argue that a decline in weight at age is an indicator that selection for individuals with reduced juvenile foraging time has occurred. The genetic model also indicated that a decline in mean weight at age can be explained by an increase in the proportion of individuals with reduced juvenile foraging time. Not only did mean weight at age, in the genetic model, decline during the fishery but, it continued to decline after the fishery closure. Perhaps, if mean weight at age continued to decline after the closure of the fishery, a manager could imply that selection for reduced foraging times had occurred. However, a decline in the mean weight at age could also be explained if there had been selection for younger age at maturity. A number of authors (Reznick and Endler 1982, Abrams and Rowe 1996) have pointed out that increased predation on adults, as would be caused by harvesting selects for a younger age at maturity. A decrease in the age at maturity reduces size at age. Shelton et al (1996) noted that there was a decline in the age at maturity in the northern cod stock. Therefore, one could not discern if the decline in mean weight at age was from the selection process proposed by Walters and Juanes or selection for a younger age at maturity. Declines in mean weight at age could also be a result of poor environmental conditions. Shelton et al (1996) also

reported that during the decline in the northern cod stock environmental conditions were not favorable for cod growth.

Walters and Juanes argued that poor recruitment may be a result of selection for individuals with reduced juvenile foraging times. Unfortunately, the genetic model showed that there was no reduction in recruitment during the initial recovery of the stock and that the decline in recruitment predicted by Walters and Juanes did not occur until the population had recovered to the target biomass. Even if the model is wrong and selection for reduced foraging times does reduce the initial recruitment to a population, it would be difficult to prove if the poor recruitment was a result of selection. Poor environmental condition or and increase in juvenile predators could also produce the same effect.

The modeling exercise has shown that the selection process proposed by Walters and Juanes would not delay the recovery rate of a stock. However, selection for individuals with reduced juvenile foraging times could reduce the productivity of a stock. The reduction in stock productivity could have consequences for management until the genetic structure of the population recovers. Unfortunately, there is no clear indicator in conventional fisheries data that selection for individuals with reduced juvenile foraging time has occurred.

Chapter 4. Summary and Conclusions

Although the outcome of the low density selection experiment is the same as what Walters and Juanes predict, the cause of the reduced equilibrium population abundance was different. During the experiment there was an increase in the size of adults in the low density tank. Larger female guppies grew to a size where they became cannibalistic, increasing the total risk of predation in the low density tanks resulting in much higher juvenile mortality. The increase in juvenile mortality resulted in lower recruitment to the adult population keeping the population at a lower abundance. If there had been selection for reduced foraging time in the juveniles, low juvenile production, possibly the result of inbreeding depression as well as high juvenile mortality from cannibalism prevented juvenile density from building to a point where juvenile growth would have declined. There was no clear indication in the laboratory experiment that selection for reduced juvenile foraging time occurred in the low density tanks. The only consequence for the dynamics of harvested populations that could be implied by the experiments was that a low density population equilibrium could result if adults grew to a size where they became cannibalistic.

If the experiment were to be repeated there would need to be a number of changes to the design. The most problematic part of the experiment was maintaining a low density adult population. The low density population was needed so that juvenile density would also be low. However, it is likely that such a low density of adults resulted in inbreeding depression over the course of the experiment. Harvesting the adult population to maintain low densities also caused problems. To avoid selecting for a reduction in the age at maturity adults were returned at random to the tank. This resulted in older larger

adults being present in the population over the course of the experiment. Larger adult size resulted in increasing juvenile mortality as a result of cannibalism. One could argue that the increased mortality would have only selected harder for individuals with reduced foraging times. Unfortunately, when the resulting population dynamics were explored, such an effect was masked because high mortality from cannibalism prevented the population density from increasing to the point were juvenile density would have increased. Harvesting the low density population in this way also decrease the number of generations over that selection occurred. It is not clear how many generations there were during the 21 months of selection in either of the tanks. Separating the adult and juvenile populations would provide direct control over the juvenile density as well as the number of generations of selection. Separation of the juveniles and adults would also allow for better control of the amount of food available. Juveniles could be reared at high and low densities in the presence of a predator without the concern that different adult densities were affecting the availability of food. Adults could be reared at the same densities so that any difference in size could be attributed to the effect of juvenile foraging behavior and not to differences in competitive conditions. The only drawback to the separation of adults and juveniles is that it may not be a reasonable representation of what occurs in nature. Abrams and Rowe (1996) have pointed out that increased predation on adults, as harvesting is, results in selection for a younger age at maturity. Although selection for individuals with reduced foraging times as juveniles may result in slower growth and poor survival as juvenile densities increase resulting in delayed population growth, selection for younger age at maturity may counter this effect resulting in little change in population growth rate. This effect that may occur in nature when adult densities are low

would not bee seen if adult densities were kept equal in the experimental design. Therefore, although such an experiment would give a clearer indication that selection for individuals with reduced foraging times had occurred, it would be difficult to speculate how such selection might affect dynamics at the population level since all possible selective factors were not considered.

Simulations of the northern cod fishery, incorporating genetically determined juvenile foraging behavior, provide a good fit to the estimated abundance of cod from 1962 to 1995. Declines in mean weight-at-age observed during the fishery could be reproduced by the genetic model. Initial recovery rate of the stock after 1995 were not suppressed as anticipated by Walters and Juanes. The lags anticipated by Walters and Juanes did not occur until the spawning stock had grown large enough to substantially increase juvenile density. The slow recovery of spawning stock biomass and the higher juvenile survival during this time in the genetic model resulted in a population that recovered to pre 1962 abundance faster than a model where all individual had the same average juvenile foraging behavior. However, the composition of the recovered stock was substantially different from the pre-1962 stock resulting in lower productivity. The productivity of the stock did not increase to pre 1962 levels until the gene frequencies had returned to pre 1962 levels. Genetic recovery of the stock did not occur until the year 2200.

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