HOOKING MORTALITY OF REEF FISHES IN THE SNAPPER-GROUPER COMMERCIAL FISHERY OF THE SOUTHEAST UNITED STATES

David V. Guccione Jr.

A Thesis Submitted to the
University of North Carolina Wilmington in Partial Fulfilment
Of the Requirements for the Degree of
Master of Science

Department of Biological Sciences

University of North Carolina Wilmington

2005

Approved by

Advisory Committee

_____ _____

_____ _____

_____
Chair

Accepted by

_____
Dean Graduate School

TABLE OF CONTENTS

ABSTRACT……..…….iii

ACKNOWLEDGMENTS…….…….iv

LIST OF TABLES……..……v

LIST OF FIGURES……...….vi

LIST OF APPENDICES……...vii

INTRODUCTION……..…….1

METHODS……..……7

RESULTS……..…..…11

DISCUSSION …...……....20

REFERENCES CITED……..29

APPENDIX……35

ABSTRACT

A widely used management regulation in the grouper-snapper fishery of the Southeast United States is the use of minimum size limits. This approach assumes that under the size limit fish caught and returned experience minimal post-release mortality. However visible signs of decompression injury due to the expansion of gas within the swim bladder when fish are hooked and reeled quickly to the surface suggest potential mortality. Mortality rates of fishes that are caught and released are unknown. This study examined mortality rates and decompression injury in below or just legal sized red porgy (*Pagrus pagrus),* vermilion snapper (*Rhomboplites aurorubens),* red grouper (*Epinephelus morio*) and scamp grouper (*Mycteroperca phenax)* caught on hook and line then caged and returned to the water. The major objective was to determine mortality of these fishes on release. Secondary objectives were to look at the relationships between depth and mortality and size and mortality. The project was done in federal marine waters offshore of North Carolina in 1999 and 2000 in depths ranging from 33.6 – 54.8 m. Mean mortality rates were conservatively estimated as 33% for *E. morio*, 39.5% for *M. phenax*, 30.35% for *R. aurorubens*, and 42.9% for *P. pagrus*. There were positive trends between depth and mortality in *P. pagrus* and *M. phenax* and depth caught was a significant factor in the mortality for *R. aurorubens*. Length was found to have a marginally significant positive correlation with mortality in *P. pagrus.* These results cast doubts on the use of size limits as an effective management tool for the snapper/grouper fishery. Various species-specific regulations and techniques are discussed as well as an ecosystem-based approach as an alternative to size limits for management of the snapper-grouper complex.

ACKNOWLEDGMENTS

My deepest thanks go out to all of the commercial fishermen who were full-on partners in the fieldwork of this project. Ed McCabe and John Wasterval were available with ideas and time when I asked for it, but I would like to especially thank my good friend Captain Matt Tierney. He made the conclusion of the fieldwork for this project possible by his consistent efforts to work together as a team and patience under some occasionally trying circumstances. Being on the water was always more fun with Matt.

I thank my Committee Chair and advisor Dr. Ileana Clavijo who showed faith in me to take me on as a graduate student and then patiently allowed me to take my time as life became very busy.

I thank my committee for their guidance and ideas from beginning to end. Thanks also to Dr. Larry Cahoon from whom I learned a great deal and for whom I have the deepest respect.

I thank the excellent North Carolina Sea Grant Program who funded my project and gave me support throughout.

Finally I would like to thank my wife Judith for believing in me and encouraging me to finish when it was the most difficult to do so.

LIST OF TABLES

Table Page

1. Mortality rates, n observed, means, standard deviations and ranges of length and depth caught for species sampled in the experimental group.……10

2. Mortality rates, n observed, means, standard deviations and ranges of length and depth caught for species sampled in the experimental group.……16

LIST OF FIGURES

Figure Page

1. Number of fish of all species caught by depth……..……11

2. Logistic regression of probability of mortality vs. depth caught for *R. aurorubens*……..12

3. Logistic regression of probability of mortality vs. length in *P. pagrus*……..16

LIST OF APPENDICES

Appendix Page

1. Individual experimental group observations in the order the fishes were sampled……..…29

2. Individual control group observations in the order the fishes were sampled. ……...35

INTRODUCTION

The snapper grouper complex is an important fishery extending from New York State to Florida along the eastern coast of the United States, the Gulf of Mexico, and California coastal waters. Some shared characteristics of these fishes have made them susceptible to overfishing. Typically fish of this complex are reef-associated and easy to find, particularly with the advancement of GPS and bottom imaging technology. They tend to be slow growing so populations do not quickly replace lost biomass. Life spans of some typical reef fishes are as high as 15 years in damselfishes (Kohda, 1996), 17 years in red porgy (*Pagrus pagrus*) (Hood and Johnson 2000), 40 years for wreckfish, (*Polyprion americanus*) (Sedberry et al. 1999), and 53 years in red snapper (*Lutjanus campechanus*). They also tend to be late maturing. Ages at first maturity range from less than 2 years in red porgy and vermilion snapper (*Rhomboplites aurorubens*) (Hood and Johnson 2000, Hood and Johnson 1999) to 5-7 years in red snapper (Goodyear 1995). Fishing effort tends to be focused on the larger individuals, which are the more prodigious breeders in the population (Hood and Johnson 1999, Collins et al. 1998). At least some of these fishes aggregate to spawn (Coleman et al. 1996, Colin 1992, Luckhurst 1998), which makes them easy to target when the location of the aggregations are known. There are numerous commercially valuable species at any given location targeted by fishers so it is virtually impossible to attempt to target or exclude only one species. Finally, distributions of most of these fishes cross borders of neighboring management areas.

Management of snapper-grouper complex stocks has not been effective in keeping the resource from over-exploitation. In the southeastern U.S. alone, for example,

species currently either over-fished or in danger of being so include red porgy (*Pagrus pagrus*) (Harris and McGovern 1997), black sea bass (*Centropristis striata*) (Vaughan et al. 1995), gag (*Mycteroperca microlepis*) (McGovern et al. 1998), scamp (*M. phenax*), snowy grouper (*Epinephelus niveatus*) (Wyanski et al. 2000), red grouper (*Epinephelus. morio*) (Schirripa et al. 1999), Warsaw grouper (*Epinephelus. nigritus*), Nassau grouper (*Epinephelus striatus*) (Carter et al. 1994), speckled hind (*Epinephelus drummondhayi*), Goliath grouper (*Epinephelus itajara*) (Sadovy and Eklund 1999), red snapper (*Lutjanus campechanus*), vermilion snapper (*Rhomboplites aurorubens*) (Zhao and McGovern 1997), white grunt (*Haemulon plumieri*), and tilefish (*Lopholatilus chamaeleonticeps*) (SAMFC 1993). Goliath and Nassau groupers have been so heavily overfished in the southeast U.S. that they are protected and are candidates for the Endangered Species List (Sadovy and Eklund 1999). Warsaw grouper and speckled hind are also protected with a limit of one per vessel per trip and are not legal to sell. The fishery for red porgy in the U.S. Atlantic was closed in 1999 because of extremely low spawning potential. The economic value of landings for the snapper-grouper fishery in 2002 was approximately 21,000 metric tons at an estimated value of U.S. $76 million (NMFS) making the sustainability of the fishery a critical consideration for this region.

The type of gear used in the snapper-grouper fishery is consistent over the southeast U.S. Since the 1992 banning of long lines in depths less than 50 fathoms, the gear used by southeast U.S. fishers has consisted of either a hand-held rod and electric reel commonly known as an electro-mate, or a motorized spool mounted to the gunwale, known as a “Bandit” or “Miami”. Boats typically will anchor over a hard bottom reef area and fish from two to eight of these devices at once, with generally at least two hooks

per line, thus the name bandit boats. Because the feeding habits and habitats of many reef fishes overlap, this gear is effective for many different species and it is difficult or impossible to target only one species of fish. Generally, a bandit boat will bring in from 8 - 15 different species on each trip. Because of the nature of the gear, regulation of a single overfished species is difficult or impossible, without infringing on the ability of commercial and recreational fishers to target less stressed species.

The main regulatory control of the snapper-grouper complex in federal waters off the coast of North Carolina has been the use of size limits to return immature fish to the population, in order to maintain a sustainable population of breeding adults. The goal is that all fish harvested would have reached maturity for at least one spawning season before being removed from the population by fishing. In 1992, amendment 4 to the Fishery Management Plan for the snapper-grouper fishery established minimum size limits for 22 species of reef fishes. These size limits were based on establishing a spawning stock biomass ratio of 30%, which the South Atlantic Fishery Management Council defined as the minimum necessary level for a sustainable fishery. Waters and Huntsman (1986) modeled yield per recruit for red snapper and showed that release mortality and minimum size limits were important parameters for achieving the 30% spawning stock biomass target. The size limits established for the species in this study were 50.8cm total length for *E. morio* and *M. phenax*, 35.6cm fork length for *P. pagrus* and 27.9cm fork length for *R. aurorubens*. This management practice assumes that below legal sized fish bycatch will survive after release and be subject to only natural mortality until they are of legal size. Because the mortality rates of fish that are caught and released are not known, it is possible they have been underestimated in calculating

sustainable fishing effort levels. This information is essential to determine the efficacy of size limits as a management tool for the snapper-grouper complex fishery.

Most reef fishes are physoclistous, meaning that they lack a duct leading from the swim bladder to the esophagus. This evolutionary development of the swim bladder has allowed otherwise negatively buoyant fishes to regulate their buoyancy. The main advantage is that they do not therefore need to be in motion in order to remain in the water column. The cost of this advantage is that due to changes of the volume of gas within the swim bladder as pressure changes with depth, the fish has a limited depth range within which it can quickly move. When physoclistous fishes are reeled from the bottom to the surface the gas within the swim bladder cannot be expelled as rapidly as it expands. Although there are variations among species in rates at which gas can be secreted into the swim bladder (Bently and Wiley, 1982) the speed at which the volume can be decreased in all species is limited by the rate at which the gas can diffuse back into the vasculature of the swim bladder wall. Almost certainly there are differences between species in resiliency of the gas bladder to expansion as life strategies vary, but the depth range through which these fishes move quickly during foraging or other activities is not fully documented. The following studies suggest that it may be quite narrow in shallower depths. Shasteen and Sheehan (1997) used an aquarium in which they could control the ambient pressure and found a mortality rate as high as 78% in a test group of largemouth bass (*Micropterus salmoides*) subjected to rapid depressurization from only 3.5m. This mortality was observed despite the fact that these fish were not subjected to hooking trauma. Depressurization was found to contribute to mortality in *E. morio* (Render and Wilson 1996, Wilson and Burns 1996) and yellow perch, *Perca flavescens* (Keniry et

al.1996). Tytler and Blaxter (1973) found that cod (*Gadus morhua*) were only able to fully adapt to a pressure change from 2 atm. to 1 atm. after nearly 5 hrs.

The amount of expansion of the gas contained in the swim bladder upon being brought to the surface is a function of the depth from which the fish are caught. Effects of this expansion include: the stomach everted through the mouth, the intestine prolapsed through the anus, bulging eyes, ruptured swim bladder, and inflated abdomens (personal observations). Often the fish will float on the surface upon release, unable to overcome the increased buoyancy. Methods for deflating the swim bladder with a hypodermic needle, or other sharp tube, have been developed (Cribb 1994; Render and Wilson, 1996; Keniry et al. 1996; Shasteen and Sheehan 1997). Unfortunately, although most fishermen have heard of these methods, few if any practice them. Valid concerns about sterility of the instrument used and the safety of handling a hypodermic needle and a lively fish on a pitching deck limit the practicality of this technique among fishers.

Neritic waters offshore of North Carolina's east coast range in depth from 0 m to roughly 200 m. The effects of rapid depressurization in reef fishes caught on commercial fishing gear may have lethal consequences, especially as depth increases, further complicating management strategies. Wilson and Burns (1996) found that *E. morio* caught and released in waters shallower than 44 m had survival rates of 86-100%. A sample of 23 fish caught at a depth of 44 m had a 91% survival rate, but there were no survivors from the three fish caught in 54m and 75m. Render and Wilson (1996) found that survival of released *L. campechanus* caught at 21m was 80.3%. A possible bias towards high survival rates in these studies was the use of hand cranked recreational fishing reels, which may produce less extreme physiological effects from

depressurization than the electric reels used on commercial fishing vessels. The latter bring a hooked fish to the surface much more quickly.

In this study, hooking mortality of commercial reef-associated fishes was assessed. The hypotheses tested were; that hook-and-line caught fish experience higher than natural mortality when subjected to rapid depressurization, that depth caught has an effect on mortality rates, and that fish length has an effect on mortality rates. The study concentrated on bycatch of species targeted in the North Carolina snapper-grouper fishery. The objectives were to develop and implement a method for determining mortality of reef fishes caught and released within the depth range of the fishery, to determine mortality rates for each species targeted, and to analyze whether depth caught or size had a significant influence on mortality of released fishes. These data were then used to evaluate the efficacy of using size limits for the fishery.

METHODS

Trips were conducted in Onslow Bay, North Carolina on the 9.75m commercial fishing vessel "Becky Sue". We sampled on 32 days from May to August in 1998, and 8 days in May and June of 1999, for a total of 40 days. Trip lengths ranged from one to four days, with trip lengths depending on weather conditions. All fishes were caught on a "Miami rig", commonly used on reef fishing vessels. Two #10 sized J-hooks were attached by a 59 kg test monofilament leader less than 3m in length to a two-way barrel swivel. The barrel swivel was attached with a bungee cord to one point of a stainless steel triangle. A 2 kg lead weight was attached to the lowest point of the triangle. The wire leading to the reel was attached to the highest point of the triangle. The reel was an electrically powered plastic spool with a diameter of 0.5m. The hooks were fished directly under the boat within two meters of the bottom. When a fish was hooked, a toggle switch was pushed, and the fish was reeled to the surface by the electric motor. The retrieval speed ranged from 0.9 to 1.9m per second but was not recorded for individual fish caught.

Four commonly caught reef species were sampled including: red porgy (*P. pagrus),* vermilion snapper *(R. aurorubens),* red grouper (*E. morio),* and scamp grouper *(M. phenax).* Fish caught measuring less than or close to ($\pm$ 8cm) the legal limit, as defined by federal fisheries regulations, were de-hooked, measured using either fork length or total length to the nearest 0.1cm, examined for any obvious signs of decompression (everted stomach, prolapsed anus, etc.), placed individually in a cage and lowered to the bottom. In order to decrease the variables confounding a depth/mortality relationship, only mouth-hooked fish were used in this study. Mortality has been found to

be higher for gill- or throat-hooked fish than mouth-hooked fish in brook trout *Salvelinus fontinalus* (Nufer and Alexander 1992) and spotted sea trout, *Cynoscion nebulosis* (Murphy et al. 1995).

Cages were constructed by modifying commercial traps for black sea bass *(Centropristus striata)*. These traps measured 0.61m x 0.61m x 0.61m, and were constructed with plastic-coated chicken wire with mesh size of approximately 5 cm, and a framework of 16 mm diameter steel re-bar on the bottom side. The modifications included the removal of the bait cage and interior divider, and the closure of all entrances. One seam along the top edge of the cage was left unattached to allow the caging and removal of a fish. After caging a fish, this entrance could be effectively sealed by a bungee cord attached to the top of the cage, stretched over the opening and hooked to the side. A 92 m rope was attached to each cage, leading to a Carlon MB8XX float (15cm x 36cm). The float had a 1.5m long section of 25mm diameter PVC pipe through its center, with a nylon flag attached. This apparatus was used as a marking buoy. The weight of the cage was augmented by approximately 5 kg of lead weights, attached to the outside of the cage with plastic cable ties. The depth in meters, time of capture and location in latitude and longitude was noted. Sampling efforts were in a depth range of 33.6 – 70 m as measured by several models of Furuno depth sounders.

Cages were left filled for a target time of 24 h. The actual mean time was 26.07 h with a standard deviation of 7.8 h, after which cages were hand retrieved by the rope attached to the marker buoy. Some cages were left with fish between trips for periods ranging from 48 - 336 h. Inter-trip time lengths depended on weather conditions and occasional boat maintenance. The length of time each fish had been caged and its

condition (whether alive or dead) was recorded. If alive, the fish was released. If dead, the fish was examined to determine whether the swim bladder was intact or ruptured. Cages were lost on several occasions due to current dragging on the marker buoy ropes either moving the cages or submerging the buoys. Adding weight to the cages solved this problem. One cage was destroyed by a 3.5m tiger shark (*Galeocerdo cuvieri*), which attacked the caged fish during retrieval.

A control group of 49 fishes was subjected to the same caging conditions as the experimental group, but without the rapid depressurization experienced when reeled to the surface. These fishes were caught on three two-day trips in May 2000 using a chevron style fish trap with dimensions 1.5 m length x 1.5 m width x 0.7 m height. Species caught were *M. phenax, R aurorubens* and *P. pagrus.* No *E. morio* were caught for the control portion of this study.

The trap was baited with Atlantic menhaden (*Brevoortia tyrannus*), dropped near a hard-bottom area, and allowed to soak for 120 min. The trap was then vertically retrieved at a rate of roughly 1.7 m per min. in order to avoid the trauma associated with rapid depressurization at faster retrieval rates. We conducted a trial test with an 18 min retrieval time using fish not included in the control sample, collected at roughly 31 m. All 21 fish in this trial were able to swim to the bottom of a 1 m deep live well and orient themselves normally within the water column. None of these trial fish exhibited any signs of rapid depressurization, such as everted stomach or prolapsed intestine. This suggested that a retrieval rate of 1.7 m per min. avoided the effects of decompression and could be used for the caging control group. Fishes of the target species were caged and returned to the bottom for 24 h soak periods as in the non-control portion of this study. Some cages

were left with fish for the two between trip periods of 48 h and 55 h. Caging times ranged from 21 - 57 h. To insure exposure to the same predators and conditions, the shallowest control samples were in at least the depth of the shallowest experimental samples. Control sampling efforts were in depths ranging from 33-46 m.

All statistical analyses were carried out with the SAS software program JmpIN version 3.2.1. A two sided t-test was used to test variance of mean depth between the control and experimental treatment groups. Contingency tables were used to test whether the mean mortality of these groups differed for each species. Logistic regressions were used to predict the probability of; mortality vs. depth caught, time in cage vs. depth caught and length vs. depth caught and interactive effects of these variables for each species. *E. morio* was excluded from statistical analysis as there were only 3 fish caught. Significance levels were set at 0.05.

RESULTS

Sampling resulted in 179 fishes of four species caged and retrieved (Table 1). Appendix 1 shows the individual observational data for all fishes caged and retrieved. Of the total fish sampled, 77 were dead upon cage retrieval, yielding an overall mortality of 43% (Table 1). On examination, 29 fish, or 37.7%, of the dead fish were found to have ruptured swim bladders. For all fish sampled 16.2% had everted stomachs and 5.0% had distended eyes when initially caught.

The number of fish sampled at each depth varied from 1 to 25. Most sampling time was spent targeting fishes at depths greater than 45 m in an attempt to obtain a more normally distributed sample (see discussion). The majority of fish were caught in the shallower range of depths sampled (Figure 1).

The relationship between depth and mortality differed for each species. Logistic regression including a depth-time interaction term showed that there was no significant interaction between depth caught and time in cage when testing for their effect on mortality (*P.pagrus* p=0.4597, *M. phenax* p=0.3226, *R. aurorubens* p=0.2995). Therefore, these variables were tested independently for their effect on mortality. The sample size of only 3 *E. morio* less than or near to the legal size limit was considered too small for individual group analysis in this and all subsequent analyses. There was a statistically significant relationship between depth and mortality in *R. aurorubens* ($p = 0.0075$, Figure 2). This data set predicts that for *R. aurorubens* as depth increases, the mortality rate of caught and released fish increases. There were positive non-significant relationships between depth and mortality for *P. pagrus* ($p = 0.6961$) and for *M. phenax* ($p = 0.4166$).

Table 1. – Mortality rates, n observed, means, standard deviations and ranges of length and depth caught for species sampled in the experimental group.

			Length in cm			Depth caught in m		
Species	n observed	% mortality	Mean	SD	range	Mean	SD	range
			Total Length					
E. morio	3	33	53.3	5.1	48.2 - 58.4	39.75	4.23	35.4 - 43.9
M. phenax	38	39.5	49.07	4.01	43.1 - 58.4	41.53	4.26	33.6 - 54.8
			Fork length					
R. aurorubens	31	48.4	30.35	4.45	17.8 - 35.6	40.06	2.38	34.2 - 42.1
P. pagrus	107	42.9	31.12	4.28	20.3 - 40.2	40.16	3.23	34.2 - 50.2
Total	179	43				40.42	3.39	33.6 -54.8

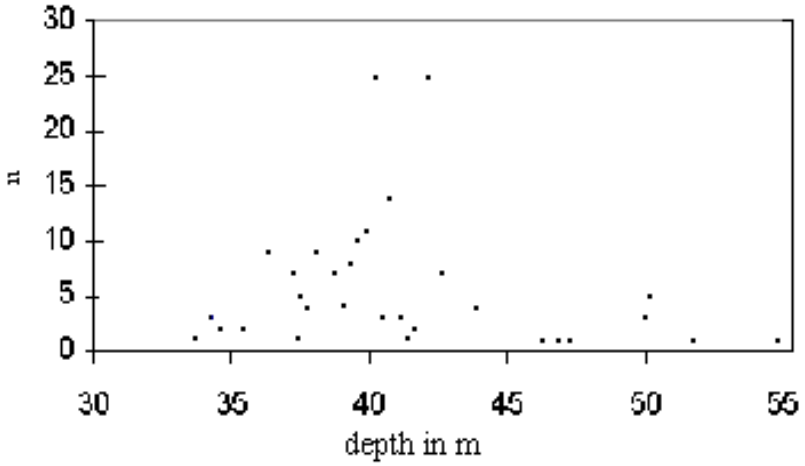


Figure 1. - Number of fish (n) of all species caught by depth.

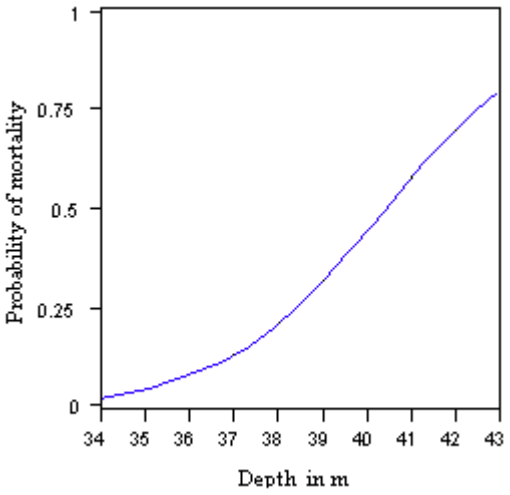


Figure 2. - Logistic regression of probability of mortality vs. depth caught for *R. aurorubens.* The line is a representation of the probability of mortality predicted by the data set. The probability of mortality (P) at any depth is the distance from the x-axis to the plotted line.

The null hypothesis, that depth caught will have no effect on mortality rates, could not be rejected for *P. pagrus* or *M. phenax*, but was rejected for *R. aurorubens*.

Length vs. mortality was tested for *P. pagrus, R. aurorubens*, and *M. phenax* to determine whether larger fish may be more resilient to hooking and depressurization. Logistic regression analysis showed a marginally significant positive correlation between length in *P. pagrus* and observed mortality ($p = 0.0555$, Figure 3). Due to this marginal significance, the null hypothesis, that length of the fish caught will have no effect on mortality, could not be rejected. Resiliency to hooking and decompression actually decreased as the size increased. Length was not a good predictor of mortality for *R. aurorubens* ($p = 0.9789$) or for *M. phenax* ($p = 0.8305$).

In order to test whether there was longer term mortality to released fishes as time since release increased, time caged vs. mortality was analyzed for each species group. There was a positive trend but not a statistically significant relationship between mortality and the length of time a fish is caged for each species group (*M. phenax* $p=0.27$, *P. pagrus* $p=0.2025$, *R. aurorubens* $p=0.527$). Between trip times were scheduled to be for no more than two days. There were several mechanical problems and weather events though which kept the vessel in port for longer periods. There were 148 fish left caged for less than 51 hours, no fish left caged for between 51 and 192 hours and 31 fish left caged for longer than 192 hours. The mean mortality rate of fishes caged less than 50 h was 40.2% and 54.8% for fish caged longer than 192 h. The overall mean mortality rate was 43% for all fishes sampled (Table 1). This suggests that initial mortality rates were high but continued to rise over time, or that a potential long term caging affect such as starvation may have occurred.

None of the fish in the control group showed physical signs of stress due to depressurization. Appendix 2 shows the individual observational data for the control group. Only one instance of mortality was recorded during the control portion of this study (Table 2). The fish was a *P. pagrus* trapped at 39 m depth. Upon retrieval it showed some scale loss, frayed dorsal and pectoral fins and had been partially consumed just anterior to the 1st dorsal spine. It had very cloudy eyes and a strong rotten smell indicating it had been dead for the majority of its 21 h caging time. Its swim bladder was intact suggesting death was probably caused by predation rather than decompression injury. This equates to a mortality rate of 2.04% from caging. However, two sampled t-test showed that the means of caging time for the control group and experimental group differed significantly ($p=0.0059$), so the more conservative, "deaths per hour caging time", was used for overall caging mortality. In the control group there was a rate of one death for 1499.5 h of caging time. Fish in the experimental group were caged for a total of 11,519.35 h. Extrapolating the control results indicated that caging could have caused 7.7 deaths or 10% of all deaths seen in the experimental group. Therefore we found that the range of mortality likely to have resulted from caging was from 0 - 10%.

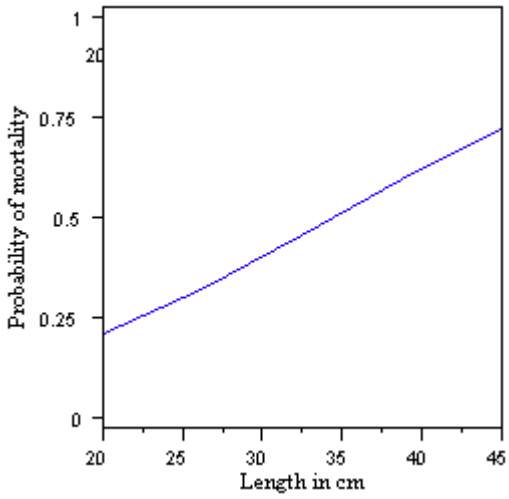


Figure 3. - Logistic regression comparing probability of mortality vs. length in *P. pagrus*. The line is a representation of the probability of mortality predicted by the data set. The probability of mortality (P) at any depth is the distance from the x-axis to the plotted line.

Table 2. – Mortality rates, n observed, means, standard deviations and ranges of length and depth caught for species sampled in the control group.

			Length in cm			Depth caught in m		
Species	n observed	% mortality	Mean	SD	range	Mean	SD	range
			Fork length					
P. pagrus	36	2.86	30.9	6.3	19.6 - 35.8	38.4	4.13	33 - 46
R. aurorubens	11	0	30.01	6.6	20.3 - 33	38.4	4.55	33 - 46
			Total Length					
M. phenax	2	0	48.8	3.2	46.5 -51	43.5	0	43.5 only
Total	49	2.04				38.4	4.1	33 - 46

A two tailed t-test showed that there was also a significant difference in means of depths of the experimental and control groups ($p=0.0006$). The mean depth was shallower for the control group than the experimental group. However, the depth at which the control fish were obtained should be irrelevant, considering that they were not subjected to a depressurization event, but were rather tested to determine whether caging was a factor in the mortality rate of the experimental sample. A chi-square test of contingency tables showed a strong significant relationship between the mortality rates of the experimental and control groups ($p<0.0001$). Mortality was higher for the experimental group ($m=0.43$) than the control group ($m=0.02$). The null hypothesis that fishes subjected to hooking and rapid depressurization showed no higher than natural mortality could not be supported.

DISCUSSION

A mean mortality rate of 43% was found for all fish that were mouth hooked. A potential caging mortality of up to 10% was factored in, thus the mortality rate due to hooking and rapid decompression was determined to be at least 33%. It is important to note, and relevant to the implications for fisheries management that the overall mortality rate of 33% is the most conservative estimate that these findings suggest. For example, this result could have been skewed by those fishes caged for short time periods which would have died had they been observed for a longer time period. If the 54.8% mortality seen in fishes caged longer than 192 h was the true mortality of the whole sample set, then more than half of all returned fishes may be lost to recruitment. Moreover, the number of gut-, gill- and esophagus-hooked fish that were caught were not incorporated in this study. Approximately 10% of fish caught were so hooked, and had these fish been used, the observed mortality rate would have been substantially higher.

Two caging effects, as well, may have caused the estimated mortality rate seen in this study to be lower than the true mortality rate of fishes subjected to hooking and rapid depressurization. The first effect is due to the expansion of gases within the swim bladder. Fishes that are returned to the water are sometimes unable to overcome the increased buoyancy in order to swim back down to the bottom. In the jargon of fishers, they are called “floaters”, because they simply float away from the boat drifting with the prevailing current. Shasteen and Sheehan (1997) found that largemouth bass were unable to swim down after depressurization from only 8.4 meters. Until these fish can regain negative or neutral buoyancy, they are subject to predation by pelagic predators, such as sharks or barracudas, and from birds. We observed both of these types of predators kill

released “floaters” of non-target species. There may be temperature stress as well, due to thermal stratification or to direct exposure to sunlight. Shasteen and Sheehan (1997) found that mortality of largemouth bass subjected to a depressurization event went from 0% in 14^{o} C water to 78% when held at 28^{o} C. Anecdotal evidence from conversations with commercial long line fishers is that roughly half of the targeted tunas, swordfish and sharks are alive during retrieval while fishing the colder Grand Banks area of the Northeast but virtually no hooked fish of the same species are alive in the warmer waters around the Bahamas and Caribbean. Fishes with expanded swim bladders were placed in a weighted cage, which was then lowered to the bottom, thereby repressurizing and decreasing the volume of the gasses within their body cavity. By eliminating “floaters”, observed mortality was probably lower than true mortality of released fishes. The second effect that may help to increase survival of caged fishes is protection from predators that the cage provides to released fish during their return to the bottom. When a fish is released and is able to swim back to the bottom, it is probably stressed and exhausted. Under these circumstances, the released fishes are easy prey for mackerels, barracudas, and other pelagic predators, that inhabit the water column above the reef. Protection provided by cages used in this study could have also caused the observed mortality to be lower than the actual mortality of released fishes.

There was a very significant difference in the mortality rates of fishes caught in the experimental and control groups. Control group fishes were subjected to the same caging conditions as the experimental group but were not subjected to hooking or rapid depressurization. None of the fishes in the control group exhibited signs of depressurization stress, compared to 16.2% with everted stomachs and 5.0% with

distended eyes in the experimental group. The 37.7% swim bladder rupture rate in fish that did not survive the caging period indicates that rapid depressurization causes physical trauma to fishes caught with high-speed electric reels.

This study shows that there is a statistically significant relationship between depth caught and mortality in *R. aurorubens.* For this species at least, the deeper fish are caught using standard commercial fishing gear, the more likely they are to die upon being released. This cannot be definitively said for other species, but positive trends between depth and mortality for *M. phenax, P. pagrus* indicate this is possible for those fish as well. The relationship between depth and mortality shown in *R. aurorubens*, and suggested in the other species tested, is a factor that complicates the already difficult job of determining the amount of sustainable fishing effort. A reasonable discard mortality figure for sustainable yield models would be difficult to determine, unless the modeler knew the amount of time each boat was spending targeting each depth, and the rate at which each of these boats catch below legal sized fish of each species and for each depth. Without this information, the proportion of recruitment lost due to mortality of caught and released fishes of various species can only be inaccurately estimated. Changing fishing conditions and techniques may even make discard mortality a dynamic factor. Log data on time spent fishing at various depths by fishers would help to determine actual mortality rates. This information, combined with a verified depth vs. mortality equation and catch history totals, may predict throwback mortality of a fleet. Also, future mortality studies using the methods of this experiment could be designed to concentrate on the range of depths most fished if this information was known.

The positive trend between time in the cage and mortality that was suggested may be due to the trauma of hooking and decompression, or from some effect caused by enclosure in the cage such as food limitation, or the inability to escape from predators able to enter the cage. Hooking trauma no doubt leads to some mortality and some injuries may take longer to kill a fish than others. A study by Warner (1978) and a review paper by Muoneke and Childress (1994) found that the majority of hooking mortality occurs within 24 h. Muoneke and Childress (1994) also concluded that observations over longer time periods provided a more complete picture of total mortality. Francesconi (personal communication) subjected fishes to depressurization and they appeared to swim normally, but died within two weeks if the swim bladder had been torn. Injuries from depressurization may include trauma to the swim bladder or trauma to any organ that is everted or prolapsed such as eyes, stomach or anus. Hook damage may occur to the jaw or other organs, making it difficult or impossible for a fish to feed. In this case the mortality is attributable to hooking but not immediately observable. Future studies of hooking mortality should include time from hooking to mortality, rather than simply whether the fish died or not. If cumulative effects from trauma do not cause more than short-term death, the correlation between increased time in cages and increased mortality is either due to random chance or due to caging effects discussed above.

An unexpected problem encountered in this study was the scarcity of below or just over legal sized fish caught in the deeper depths (>45m) sampled. Also, gag grouper (*M. microlepis*) was not included in this project, because not a single fish shorter than the legal size limit of 61 cm was caught. Yet, as anyone with commercial dayboat grouper/snapper experience will tell you, there are many below legal sized *M. microlepis*

caught in shallower depths. Below legal sized fish also make up a large percentage of the individuals of *E. morio* caught in depths up to roughly 40 m, but fewer are caught in deeper waters. Most fish in this study were from shallower depths, despite the fact that a majority of time was spent fishing in water deeper than 42 meters in an attempt to obtain a sample from a more normally distributed depth range. Currents and generally larger wave sizes also affected sampling effort in these depth ranges, but also there were fewer below or just legal sized fish caught. This could indicate that larger fish inhabit deeper water, or that larger fish are out-competing the smaller fish for bait, and may tend to be fished faster, whereas in shallower water closer to shore, those larger more aggressive fish would have already been removed due to heavier fishing pressure. Anecdotally, in 40 sampling days no gag were caught measuring smaller than the legal limit of 60.9 cm. North Carolina commercial day-boat fishers generally stay in water shallower than 36 m and can expect to catch at least several below legal sized gag every trip. This size-depth relationship may not be a naturally occurring phenomenon, but is more likely caused by the greater fishing pressure on those populations that are more easily accessed. If this relationship is true, discard mortality will be exacerbated by size limits on heavily fished populations as fishers must spend more time fishing and consequently produce more below legal sized bycatch in order to take their recreational limit or for the same commercial take. Also rates at which below legal sized fish are caught will be different for different depths and for heavily vs. non-heavily fished populations. Future studies may have greater success by focusing on obtaining larger data sets in the 25 – 45 m range, or by expanding the study to include larger than discard sized fishes, in order to increase sample size.

The results of this study cast doubts on the use of size limits as an efficient management tool for the exploitation of the snapper/grouper resource. The goal of size limits is to return juvenile, non-breeding fishes to the population, in order that they may grow large enough to contribute recruitment to the fishery. However if these released fishes, or a significant proportion of them, do not survive the post-release period then the effectiveness of the management tool is diminished or lost. If a size limit-based management strategy is to work, then either fishing effort must be further limited, or below legal target species catch rates must be reduced. The former of these solutions, reduction in fishing effort, would necessarily mean either reduction of the number of vessels allowed to partake in the fishery, or the closing of the snapper/grouper fishery for at least part of the year. The goal would be to reduce the amount of incidental bycatch to a point where mortality, with known hooking mortality rates factored in, is reduced to an acceptable and sustainable level. The latter of these two solutions, bycatch reduction, would be difficult or impossible to realize without a significant reduction in catches of legal sized fishes. If for example, hooks small enough to fit into the mouth of a juvenile red grouper were banned, then the hook and line fishery for vermilion snapper, grunt and black sea bass would be lost or greatly diminished. With current fishing techniques, disallowing the retention of a single species would not keep it from being caught and subjected to hooking mortality as fishers target other species that utilize the same habitat. Also, fishers rely on each of these species for part of their catch return, and in general would have difficulty making a profit targeting one or two species.

Size limits may be especially ineffective in species that have a size dependent mortality as seen in *P. pagrus*. By mandating an increased size limit for this species an

unwanted effect is that discard mortality is actually increased. There was no length dependent mortality noted in *M. phenax* or *R. aurorubens.* It would be surprising to find caging effects only in *P. pagrus*, which has a median life strategy, relative to the other sampled species. Here the life strategy is defined by, how far away from the reef and how high into the water column the fish forage, and presumably therefore how resilient they are to quick depth changes. *M. phenax's* life strategy is more reef associated than *P. pagrus*, while *R. aurorubens'* is more pelagic than *P. pagrus* (Hood and Johnson 1999, 2000, Bullock and Murphy 1994).

The findings of this study suggest that there may be enough waste of target species due to throwback mortality that a change to a more efficient management scheme should be considered. Disallowing the retention of a single over-fished species or size class does not keep it from being caught and subjected to hooking mortality as fishers target other species that utilize the same habitat. Given this fact, it is difficult to conceive of any species-specific management practice that mitigates the waste of throwback mortality, yet allows the achievement of harvesting the maximum sustainable yield of other species. For example, individual quotas would allow for the retention of undersized fishes, but once the quota for one species was filled, the fisher would continue to catch that species while working to reach his quota of other species using the same habitat. Seasonal closures for a single species are inefficient in that they either stop the fishers ability to target other healthier stocks using the same habitat, or the target species is caught and subjected to throwback mortality as other species are targeted. Gear restrictions likewise would be inefficient or ineffective as the hook sizes and bait selections for these fishes overlap. Possibly the use of fish traps with restrictions on

retrieval speed would mean that decompression injury could be mitigated as unwanted or undersized fishes could be graded out. Fish traps may have serious deleterious consequences on populations though, as they continue to be effective killing machines long after they are lost. The fish that are unable to escape the trap and die become the bait for the next victims in a cycle that only ends when the trap decays. (Breen 1990)

An ecosystem-based approach to management of the snapper-grouper complex may be a better option than the current size limit-based approach. Marine protected areas (MPA), could remove the complications of trying to micro-manage individual species in a multi-species fishery by eliminating size limits or quotas. A secondary benefit is that an MPA eliminates bycatch and hooking mortality of target species by allowing the fisher to retain everything caught. The economic gain in keeping small fishes may offset the loss of access to protected areas. Whether MPAs would protect these populations is by no means proven and depends upon both larval settlement patterns and whether brood stocks of a protected species are site specific enough to remain within the no-take area. Nassau groupers, *E. striatus*, gag grouper, *M. microlepis*, and *E. morio* migrate to spawning areas (Colin 1992, Coleman et al. 1996) and during their movement would be exposed to fishing pressure outside the protected areas. Bohnsack, 1996, and Fogarty et al., 2000 both argue that red snapper, *Lutjanus campechanus* are sedentary and might benefit from MPAs. However, tagging studies indicate that red snappers move away from tagging sites especially during extreme weather events (Watterson et al., 1998, Patterson et al. 2001). Information is lacking concerning the movements of vermilion snapper, red porgy or scamp. Not enough information on site specificity exists to predict the proportion of any population that would be protected by an MPA of a given size. MPAs as management

tools rely on some outflow of fishes into the harvestable population outside the protected area through both larval recruitment and migration of larger individuals as population within the MPA reaches carrying capacity. Even though gag grouper are known to migrate to spawning areas, not all mature individuals do this as gag can be caught year-round in other areas. Perhaps enough individuals either spawn locally or remain site specific enough to make a properly placed MPA an effective conservation and fisheries tool. The implications of this study are that size limits may not be the best management strategy for exploiting the snapper/grouper complex stocks. In economic terms, the fish that is released and dies is both taken out of the breeding population, as well as out of the sum received from sale of the catch. The consequence is anthropogenic destruction of a resource with no economic gain.

REFERENCES CITED

1. Bently, T.B. and M.L. Wiley. 1982. Intra- and inter- specific variation in buoyancy of some estuarine fishes. Environmental Biology of Fishes. 7(1): 77-81
2. Bohnsack, J.A. 1996. Marine reserves, zoning, and the future of management fisheries. Fisheries 21(9): 14-16.
3. Breen, P.A. 1990. A review of ghost fishing by traps and gillnets. Proceedings of the Second International Conference on Marine Debris. NOAA. Tech. Memo NOAA-TM-NMFS-SWFSC-154: 571-599
4. Bullock, L.H. and M.D. Murphy. 1994 Aspects of the life history of the yellowmouth grouper, *Mycteroperca interstitialis* in the eastern Gulf of Mexico. Bulletin of Marine Science. 55(1): 30-45.
5. Carter, J.G., G. Marrow and V. Pryor. 1994 Aspects of the ecology and reproduction of the Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. Proceedings of the Gulf and Carribean Fisheries Institute 43: 65-111
6. Coleman, F.C., C.C. Koenig, and L.A. Collins. 1996 Reproductive styles of the shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of spawning aggregations. Environmental Biology of Fishes. 47: 129-141.
7. Colin, P.L. 1992. Reproduction of the Naussau grouper, *Epinephelus striatus*, (Pisces: Serranidae) and its relationship to environmental conditions. Environmental Biology of Fishes. 34: 357-377.
8. Collins, L.A., A.G. Johnson, C.C. Koenig and M.S. Baker Jr. 1998. Reproductive patterns, sex ratio, and fecundity in the gag, a protogynous grouper (Serranidae:

Mycteroperca microlepis) from the northeast Gulf of Mexico. Fisheries Bulletin 96: 415-427.

9. Cribb, A. 1994. Returned believed alive. Western Fisheries 46-51
10. Fogarty, M.J., J.A. Bohnsack, and P.K. Dayton. 2000. Marine reserves and resource management. In: Sheppard, C (ed.) Seas at the Millenium. Elsevier Science Ltd. London.
11. Francesconi, J. Artificial Reef Coordinator. North Carolina Division of Marine Fisheries. 3441 Arendell St., Morehead City.
12. Goodyear, C.P. 1995. Red snapper in U.S. waters of the Gulf of Mexico: report for 1990. National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL.
13. Harris, P.J. and J.C. McGovern. 1997. Changes in the life history of red porgy *Pagrus pagrus*, from the southeastern United States, 1972-1994. Fishery Bulletin 95(4): 732-747.

14. Hood, P.B. and A.K. Johnson. 1999. Age, growth, mortality, and reproduction of vermilion snapper, *Rhomboplites aurorubens*, from the eastern Gulf of Mexico. Fishery Bulletin 97: 828-841.

15. Hood, P.B. and A.K. Johnson. 2000. Age, growth, mortality, and reproduction of red porgy, *Pagrus pagrus*, from the eastern Gulf of Mexico. Fishery Bulletin 98(4): 723-735.

16. Keniry, M.J., W.A. Brofka, W.H. Horns and J.E. Mardsen. 1996. Effects of decompression and puncturing the gas bladder on survival of tagged yellow perch. North American Journal of Fisheries Management 16(1): 201-206

17. Kohda, M.A. 1996. A damselfish living for more than 15 years: a longevity record for small reef fishes. Ichthyology Resources 43: 459-462

18. Luckhurst, B.E. 1998. Site fidelity and return migration of tagged red hinds (*Epinephelus guttatus*) to a spawning aggregation site in Bermuda. Proceedings of the Gulf and Caribbean Fisheries Institute. 50: 750-763.

19. McGovern, J.C., D.M. Wyanski, O. Pashuk, C.S. Manooch II and G.R. Sedberry. 1998. Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic Coast of the Southeastern United States during 1976-1995. Fisheries Bulletin 96(4): 797-807.

20. Muoneke, M.I. and W.M. Childress. 1994. Hooking mortality: a review for recreational fisheries. Reviews in Fisheries Science 2(2): 123-156 .

21. Murphy, M.D., R.F. Heagey, V.H. Neugebauer, M.D. Gordon and J.L. Hintz. 1995. Mortality of spotted seatrout released from gill net or hook and line gear in Florida. North American Journal of Fisheries Management 15(4): 748-753.

22. Nufer, A.J. and G.R. Alexander, 1992. Hooking mortality of trophy sized wild brook trout caught on artificial lures. North American Journal of Fisheries Management 12(3): 634-644

23. Patterson III, W.F., J.C. Watterson, R.L. Shipp, and J.H. Cowan. 2001 Movement of tagged red snapper in the northern Gulf of Mexico. Transactions of the American Fisheries Society. 130: 533-545.

24. Render, J.H. and C.A. Wilson. 1996. Effects of gas bladder deflation on mortality of hook and line caught and released red snappers: implications for management. Biology, fisheries and culture of tropical groupers and snappers - ICLARM conference proceedings 48: 244–253.

25. Render, J.H. and C.A. Wilson. 1996. Hook and Line mortality of caught and released red snapper around oil and gas platform structural habitat. Fifth International Conference on Aquatic Habitat Enhancement, Bulletin of Marine Science 55(2-3): 1106-1111.

26. Sadovy,Y. and A.M. Eklund. 1999. Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1972), and the Jewfish, *Epinephelus itajara* (Lichtenstien, 1822). NOAA Technical Report NMFS 146.

27. SAFMC (South Atlantic Fisheries Management Council). 1993. Amendment number 6, regulatory impact review and final environmental impact statement for the snapper-grouper fishery of the South Atlantic region. SAFMC Charleston S.C.

28. Schirripa, M.J. 1999. Management trade-off between the directed and undirected fisheries of red snapper, *Lutjanus campechanus,* in the U.S. Gulf of Mexico.

Proceedings of the International Conference on Integrated Fisheries Monitering 223-230.

29. Schirripa, M..J., K..M. Burns, and J.A. Bohnsack. 1993. Reef fish survival based on tag and recovery data. (Manuscript)

30. Sedberry, G.R., C.A.P Andrade, J.L. Carlin, R.W. Chapman, B.E. Luckhurst, C.S. Manooch, II, G. Menezes, B. Thomsen, and G.F. Ulrich. 1999. Wreckfish Polyprion americanus in the North Atlantic: fisheries, biology, and management of a widely distributed and long-lived fish. American Fisheries Society Symposium 23: 27-50.

31. Shasteen, S.P. and R.J. Sheehan. 1997. Laboratory evaluation of artificial swim bladder deflation in largemouth bass: potential benefits for catch and release fisheries. North American Journal of Fisheries Management 17(1): 32-37.

32. Tytler, P. and J.H.S. Blaxter. 1973. Adaptation by cod and saithe to pressure changes. Netherlands Journal of Sea Research 7: 31-45.

33. Vaughn, D.S., M.R. Collins and D.J. Schmidt. 1995. Population characteristics of the black sea bass, *Centropristus stiata*, from the southeastern U. S. Bulletin of Marine Science 56(1): 250-267.

34. Warner, K. 1978. Hooking mortality of lake dwelling landlocked Atlantic salmon, *Salmo salar* Transactions of the American Fisheries Society 107(4): 518–522.

35. Waters J.R. and G.R. Huntsman. 1986. Incorporating mortality from catch and release into yield-per-recruit analysis of minimum size limits. North American Journal of Fisheries Management 6(4) 463-471.

36. Watterson, J.C. W.F. Patterson III, R.L. Shipp, and J.H. Cowan Jr. 1998. Movement of Red Snapper, Lutjanus campechanus, in the north central Gulf of Mexico: Potential effects of hurricanes. Gulf of Mexico Science 1998(1): 92-104.

37. Wilson, R.R. and K.M. Burns. 1996. Potential survival of released groupers caught deeper than 40m based on shipboard and in-situ observation, and tag recapture data. Bulletin of Marine Science. 58(1): 234-247.

38. Wyanski, D.M., D.B. White and C.A. Barans. 2000. Growth, population age structure, and aspects of the reproductive biology of the snowy grouper, *Epinephelus niveatus*, off North Carolina and South Carolina. Fisheries Bulletin 98(1): 199-218.

39. Zhao, B. and J.C. McGovern. 1997. Temporal variation in sexual maturity and gear specific sex ratio of the vermilion snapper, *Rhomboplites aurorubens*, in the South Atlantic Bight. Fisheries Bulletin 95(4): 837-848.

APPENDIX

Appendix 1. - Individual experimental group observations in the order the fishes were sampled. Recorded for each observation was the species, length of the fish in centimeters, depth caught in meters, the time in hours the fish was caged, and whether the fish was alive or dead (y = alive, n = dead).

Species	length	depth caught	time in cage	alive
E.morio	48.2	35.44	21.5	y
M.phenax	45.7	35.44	21.5	y
R.aurorubens	25.4	34.53	18	y
P.pagrus	29.2	34.53	17.5	y
P.pagrus	26.2	34.2	24	y
R.aurorubens	27.9	34.2	24	y
R.aurorubens	29.2	34.2	24	y
M.phenax	51.4	33.63	23.75	y
P.pagrus	33	37.8	24.5	y
P.pagrus	35.5	37.8	24.5	y
P.pagrus	26.2	37.8	24.5	y
P.pagrus	35.5	37.8	24.5	y
P.pagrus	31.7	39.6	192	n
M.phenax	49.5	40.2	192	y
M.phenax	49.5	36.3	24	y
P.pagrus	34.3	36.3	24	y
P.pagrus	33	36.3	23.5	n
P.pagrus	31.8	36.3	23.5	y
R.aurorubens	31.8	42.1	22	y
R.aurorubens	34.3	42.1	22	y
R.aurorubens	34.3	42.1	22	y
R.aurorubens	33	42.1	22	n
R.aurorubens	31.8	42.1	22	n
R.aurorubens	33	42.1	22	n
R.aurorubens	30.5	42.1	22	n
P.pagrus	33	42.1	22	n
M.phenax	55.9	46.3	37	y
R.aurorubens	31.8	42.1	22	n
R.aurorubens	35.6	42.1	22	n
R.aurorubens	30.5	42.1	22	n
R.aurorubens	33	42.1	22	n
R.aurorubens	31.8	42.1	22	n
R.aurorubens	29.2	42.1	22	n

Appendix 1 - continued

M.phenax	49.5	46.9	51	y
P.pagrus	33	40.2	48	n
P.pagrus	36.8	40.2	48	n
P.pagrus	34.3	40.2	48	n
P.pagrus	38.1	40.2	48	n
P.pagrus	30.5	40.2	48	n
P.pagrus	22.9	40.2	48	y
P.pagrus	30.5	40.2	47.5	y
P.pagrus	40.6	40.2	47.5	n
M.phenax	51.1	37.5	21.5	y
P.pagrus	31.8	38.7	20.5	n
P.pagrus	33	38.1	216	n
P.pagrus	29.2	38.1	216	n
P.pagrus	29.2	38.1	216	n
R.aurorubens	22.9	37.5	216	n
P.pagrus	29.2	37.5	216	n
P.pagrus	30.5	37.5	22.5	n
P.pagrus	40.6	37.5	22.5	y
P.pagrus	25.4	40.8	22.5	y
P.pagrus	25.4	40.8	22.5	y
P.pagrus	25.4	40.8	22.5	y
P.pagrus	28	40.8	22.5	n
P.pagrus	28	40.8	22.5	y
P.pagrus	25.4	40.8	22.5	y
P.pagrus	28	40.8	22.5	y
P.pagrus	29.2	40.8	22.5	y
P.pagrus	28	40.8	22.5	y
P.pagrus	28	40.8	22.5	n
P.pagrus	25.4	40.8	22.5	n
P.pagrus	28	40.8	22.5	n
P.pagrus	29.2	40.8	22.5	n

Appendix 1 - continued

P.pagrus	29.2	40.8	22.5	y
P.pagrus	33	42.1	22	n
P.pagrus	33	42.1	22	y
P.pagrus	33	42.1	22	y
P.pagrus	30.5	42.1	22	y
P.pagrus	30.5	42.1	22	y
P.pagrus	33	42.1	22	y
P.pagrus	30.5	42.1	22	n
P.pagrus	30.5	42.1	22	y
P.pagrus	30.5	42.1	22	y
P.pagrus	33	42.1	22	n
M.phenax	50.8	39.3	264	n
M.phenax	49.5	39.3	264	n
M.phenax	49.5	39.3	264	y
M.phenax	48.3	39.3	264	y
M.phenax	48.3	39.3	264	n
M.phenax	43.2	39.3	264	y
M.phenax	49.5	39.3	264	n
M.phenax	48.3	39.3	264	y
M.phenax	48.3	42.7	23	y
M.phenax	47	42.7	23	n
M.phenax	43.2	42.7	20	y
M.phenax	43.2	42.7	20	y
P.pagrus	38.1	43.9	19.5	n
P.pagrus	34.3	38.7	20.1	n
R.aurorubens	28	38.7	20.1	y
P.pagrus	25.4	38.7	216	n
R.aurorubens	33	38.7	216	y
R.aurorubens	17.8	38.1	216	n
P.pagrus	43.2	39.9	21	n
P.pagrus	30.5	39.9	21	y
M.phenax	49.5	39.9	21	y
P.pagrus	29.2	36.6	25	y
P.pagrus	29.2	36.6	27.5	y
P.pagrus	28	36.6	25.4	n

Appendix 1 - continued

P.pagrus	29.2	36.6	25.4	y
P.pagrus	30.5	36.6	25.5	y
P.pagrus	25.4	37.2	39	y
P.pagrus	26.7	37.2	39	n
P.pagrus	28	37.2	39	n
P.pagrus	28	37.2	39	n
P.pagrus	28	37.2	39	n
P.pagrus	28	37.2	39	n
P.pagrus	28	37.2	39	n
P.pagrus	35.6	39.6	30.5	y
P.pagrus	25.4	39.6	30.5	y
R.aurorubens	33	39.6	30.5	y
P.pagrus	33	39.6	30.5	n
P.pagrus	33	39.6	28	y
M.phenax	49.5	39.6	27	y
P.pagrus	30.5	40.2	27	y
P.pagrus	28	40.2	27	y
P.pagrus	29.2	40.2	27	y
P.pagrus	26.7	40.2	27	y
P.pagrus	26.7	40.2	27	y
R.aurorubens	26.7	40.2	27	y
R.aurorubens	29.8	40.2	27	y
M.phenax	52.1	41.1	21	y
M.phenax	52.1	41.1	20.5	y
M.phenax	55.9	47.2	20.1	y
M.phenax	58.4	40.2	20	y
P.pagrus	30.5	40.2	20	n
P.pagrus	38.1	40.2	220	y
P.pagrus	33	39.6	19.5	y
P.pagrus	33	41.1	216	n
P.pagrus	30.5	39	216	y
P.pagrus	35.6	40.2	216	y
P.pagrus	35.6	40.2	216	y
P.pagrus	33	40.2	216	n
E.morio	58.4	43.9	19	n
P.pagrus	38.1	43.9	19.5	y

Appendix 1 - continued

M.phenax	58.4	43.9	19	n
P.pagrus	22.9	40.5	23.5	y
R.aurorubens	22.9	40.5	23.5	n
R.aurorubens	22.9	40.5	23.5	y
P.pagrus	35.6	39.6	216	y
P.pagrus	35.6	39.6	216	y
P.pagrus	33	38.1	21	n
P.pagrus	36.8	38.1	21	n
P.pagrus	38.1	38.1	21	y
R.aurorubens	35.6	39.9	20	n
R.aurorubens	35.6	39.9	20	y
P.pagrus	29.2	39.9	20	y
R.aurorubens	35.6	39.9	20	n
R.aurorubens	35.6	39.9	20	y
M.phenax	45.8	42.7	38	y
M.phenax	44.5	42.7	38	n
M.phenax	43.2	42.7	39.5	y
R.aurorubens	30.5	39	17	y
R.aurorubens	28	39	17	y
P.pagrus	33	39	17	y
E.morio	53.3	39.9	15.5	y
P.pagrus	35.6	39.9	15.5	y
P.pagrus	34.3	39.9	15.5	y
M.phenax	49.5	41.4	41	n
P.pagrus	26.6	41.7	40.5	y
M.phenax	44.4	41.7	38	n
M.phenax	48.2	40.2	31	n
M.phenax	48.2	40.2	31	n
M.phenax	43.1	40.2	31	n
P.pagrus	35.5	50.2	27.5	n
P.pagrus	36.8	50.2	27.5	n
P.pagrus	38.1	50.2	27.5	n
P.pagrus	30.5	50.2	27.5	y
P.pagrus	31.7	50	28	y

Appendix 1 - continued

P.pagrus	33	50	28	n
P.pagrus	33	50	28	y
P.pagrus	20.3	38.1	336	y
P.pagrus	20.3	38.1	336	y
M.phenax	48.2	37.4	336	n
P.pagrus	33	38.7	336	n
P.pagrus	33	38.7	336	n
M.phenax	55.8	51.8	35	n
M.phenax	48.2	50.2	36	y
M.phenax	48.2	54.8	36	n

Appendix 2. - Individual control group observations in the order the fishes were sampled. y = survived caging period, n = died during caging period.

Species	Length	depth caught	time caged in h	survived
P. pagrus	35.6	41	24	y
P. pagrus	34.3	41	24	y
R. aurorubens	20.3	41	24	y
R. aurorubens	28.1	41	24	y
R. aurorubens	28.3	43.5	25.5	y
P. pagrus	35.5	43.5	25.5	y
P. pagrus	30.5	43.5	25.5	y
M. phenax	46.5	43.5	25.5	y
M. phenax	51	43.5	26	y
R. aurorubens	33	43.5	26	y
P. pagrus	19.6	36	42	y
P. pagrus	20.3	36	42	y
P. pagrus	33	36	42.5	y
P. pagrus	19.6	36	42.5	y
P. pagrus	19.3	36	44	y
P. pagrus	31.7	36	44	y
P. pagrus	26.6	36	45	y
R. aurorubens	32.1	36	48	y
R. aurorubens	33	33	24	y
R. aurorubens	33	33	24	y
P. pagrus	36.8	33	24.5	y
P. pagrus	29.2	33	24.5	y
P. pagrus	25.6	33	25.5	y
P. pagrus	30.2	33	25.5	y
P. pagrus	38.1	33	26.5	y
P. pagrus	36	39	21	n
P. pagrus	33	39	21.5	y
R. aurorubens	28.4	39	23	y
R. aurorubens	28.4	39	23	y
P. pagrus	33	39	23	y
P. pagrus	26.2	39	23.5	y
P. pagrus	26.2	46	24	y
P. pagrus	25.9	46	24	y
P. pagrus	31.7	46	24	y
P. pagrus	31.8	46	24.5	y

Appendix 2 - continued

R. aurorubens	33	46	26	y
R.aurorubens	26.2	34	53	y
P. pagrus	33	34	55	y
P. pagrus	33	34	55	y
P. pagrus	26.2	34	55.5	y
P. pagrus	21.2	34	57	y
R. aurorubens	25.9	38	23	y
P. pagrus	35.5	38	23	y
P. pagrus	35.5	38	23.5	y
P. pagrus	35.5	38	23.5	y
P. pagrus	34.3	38	24	Y
P. pagrus	35.8	38	24	Y
P. pagrus	34.9	38	25.5	Y
P. pagrus	32.1	38	25.5	Y