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Assessment of South Florida's Bonefish Stock

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UNIVERSITY OF MIAMI

ASSESSMENT OF SOUTH FLORIDA'S BONEFISH STOCK

By

Michael F. Larkin

A DISSERTATION

Submitted to the Faculty
of the University of Miami
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the requirements for the degree of
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ASSESSMENT OF SOUTH FLORIDA'S BONEFISH STOCK

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Florida's recreational bonefish fishery generates substantial economic benefits to the region; however, the resource has never been adequately assessed to determine standard benchmarks for sustainability. The situation offered a unique opportunity to address unresolved issues in sustainability for a valuable recreational fishery that is almost exclusively catch and release. The goal of this dissertation was three-fold: (1) to develop a comprehensive framework for conducting rigorous stock assessments on recreational catch-and-release fisheries; (2) to apply these methods to the Florida bonefish fishery to compare results against internationally-recognized sustainable fishery benchmarks; and, (3) provide recommendations for longer-term assessment strategies and management efforts. Due to the dearth of available bonefish information, existing literature were synthesized and new quantitative data and models concerning bonefish demographics (i.e. growth, survivorship) and population dynamics were developed. Data for age-and-growth were collected with a focus on both small (< 100 mm FL) and large (>650 mm FL) bonefish which had been under-sampled in previous research. A two-stage growth model was developed that allowed predictions of size-at-age over the complete life history of the species. Evidence from multiple analyses suggested a single species of bonefish in the Florida fishery. A mail survey of bonefish captains (guides) acquired baseline statistics on the south Florida bonefish fishery. Fleet fishing effort is mostly concentrated in the northern Florida Keys (Biscayne Bay to Islamorada) and reflects to some extent bonefish spatial population abundance. The majority of the respondents indicated the stock had declined over the past few decades. A sized-based mortality estimator was used to determine mortality. Changes in current population size from 2003-2010 were determined from a visual survey. Historical stock size was inferred from a relative abundance index from standardized tournament catch rates. Annual trends of the mortality estimates implied a stable population that is not declining which contrasts with the index of abundance and visual survey results. Both the index of abundance and visual survey displayed overall declining trends in recent years. Bonefish movements were determined from anchor tag and acoustic telemetry. Anchor tagging data were analyzed to evaluate movements, stock size structure and mortality. Results revealed no significant relationships between distance moved and days at large or days at large and length at tagging; however, significant individual movements (>100 kilometers) were recorded. Use of acoustic telemetry showed frequent movements around the barrier islands, schooling behavior, and a possible spawning effect with movements to offshore reef habitats.

Stock status was addressed with two different classes of assessment models: REEFS, a length-based model which estimated the stock as moderately exploited with the current fishing mortality rate less than the maximum sustainable yield fishing mortality rate; and a “catch-free” age-structured model which indicated a large stock decline over the past 40 years with the stock currently bordering an overfished benchmark. The age-structured model was assumed to be the most robust method because it incorporated the

majority of the research data (age and growth, selectivity, mortality, visual survey, CPUE standardization, vessel effort). In conclusion, the stock's productivity has been significantly reduced over the past 50 years due to fishing, but also degradation of key prey populations, habitats, and water quality, resulting in a current bonefish population that is bordering an overfished state. Recommendations are provided for improving future stock assessments and management approaches. The assessment framework and quantitative methods and models developed here are broadly applicable to bonefish stocks around the world.

DEDICATION

To Mom, Dad, Alison, and Jeff.

You always believed in me, even when I didn’t believe in myself.

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I have frequently heard the proverb “It takes a village to raise a child.” Based on my graduate school experience, I think a new proverb would be more appropriate: “It takes a village to complete a dissertation.” I had a lot of help along the way, and I am forever grateful for the help I received.

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Chapter 1

Introduction

South Florida boasts a productive coastal ecosystem that supports a world-renown recreational bonefish fishery, hallmarked by the availability of large bonefish (i.e., average fish caught is > 4 kg and > 563 mm FL) (Larkin et al. 2008). Notably, more than 68% of the saltwater fly rod and saltwater line class world records for bonefish listed by the International Game Fish Association were caught in south Florida coastal waters (International Game Fish Association 2011). This fishery supports a fleet of over 300 professional captains (Larkin et al. 2010) and has an contribution of $1 billion per annum to Florida's economy (Ault et al. 2008b). Despite the fisheries popularity, the resource has never been adequately evaluated.

In addition to being a valuable resource to the economy, bonefish are also good indicators of the ecosystem's health. They are an important link in the food chain because they feed on benthic organisms (e.g., shrimp, snails, crabs, small fish; Crabtree et al. 1998b) and, in turn, are prey for large predators (e.g., sharks, groupers, barracuda, bottlenosed dolphin; Ault et al. 2008a). The habitats supporting the bonefish stock over its complex life history have experienced many changes over the last forty years. Starting in the 1960s, levees were installed to control freshwater flow to key bonefish habitats of Biscayne Bay and Florida Bay causing saltwater inclusion to coastal areas (Grunwald 2006). This caused a reduction in freshwater flow and resulted in increased nutrients (phosphorus and other pollutants) which degraded water quality and ecosystem health. This led to many problems: seagrass mortality, mangrove die-offs, algae blooms, and declines in sponges and pink shrimp (Boesch et al. 1993).

Coastal habitats may dramatically change in the future from the Comprehensive Everglades Restoration Plan. This is a multiagency project to restore water flow to historical levels in south Florida. The impact of this plan on south Florida's bonefish stock is largely unknown, making an assessment of the resource even more significant.

Pink shrimp abundance relates to the bonefish stock because they are the primary prey item for juvenile bonefish (Crabtree et al. 1998b). South Florida pink shrimp populations have been reduced from both changes in water quality (Boesch et al. 1993) and by two distinct fisheries: live-bait and food-shrimp. Shrimp removal has the potential to impact the entire ecosystem (Ault et al. 1999, 2003; Diaz 2001).

Another factor influencing the bonefish stock is the large increase in south Florida's human population. The region has experienced rapid and substantial growth of both regional human populations and exploitation pressures from recreational fishing fleets over the past several decades (Ault et al. 2005c, 2009), as well as abrupt environmental changes due to massive coastal development (Porter and Porter 2001).

The impact of the many changes the bonefish stock has experienced, the economic and ecological relevance, and concern for future changes warrants a stock assessment to determine the current status of the stock relative to management targets. The first step was collection of all relevant information with a literature review. Then additional research was conducted to build upon past work and close additional knowledge gaps.

A review of bonefish literature revealed the stock has received scant attention from the scientific community. Bonefish reproduction, stomach contents, age and growth, and mortality have been examined (Crabtree et al. 1996, 1997, 1998a, and

1998b), but many questions still exist. One area that needs further work is age and growth of bonefish. Crabtree et al. (1996) aged 451 bonefish from the Florida Keys and found a maximum age of 19 years; their largest fish sampled was 679 mm fork length (FL). University of Miami's bonefish tagging database contains 292 bonefish (or about 5% of the bonefish tagged) larger than Crabtree et al.'s (1996) largest fish, suggesting the maximum age is greater than 19 years. Maximum age has implications for fishery sustainability with respect to exploitation and environmental changes. Fish stocks with greater maximum ages tend to be more susceptible to declines from relatively small reductions in survivorship (Beverton and Holt 1959; Adams 1980; Kirkwood et al. 1994; Ault et al. 2005b); thus, additional ageing of large fish from the fishery is warranted to better estimate maximum age. Another reason the age and growth of bonefish needs further exploration is the fact that Crabtree et al. (1996) failed to allocate equal sampling for each age class in the bonefish stock. This created two problems in their analysis: (1) over-sampling of the most common age classes of 3 to 9 years old, and (2) under-sampling of the youngest (<2 years old) and oldest (>12 years old) age classes. These discrepancies affected their growth curve and maximum age estimations and caused speculation as to whether their growth curve truly reflected the dynamics of the south Florida's bonefish population. Additional work was done to address maximum age and provide a more thorough assessment of bonefish growth.

There is a paucity of information available for bonefish movements. Past bonefish tagging projects have produced limited results. Four previous conventional anchor tagging studies have been conducted but were largely unsuccessful. Bruger (Florida Marine Research Institute, pers. comm.) initiated an anchor tagging program in the Florida Keys in the 1970s, but crude anchor-tag technology in that era resulted in no recaptures despite the tag-and-release of several hundred bonefish. Colton and Alevizon (1983) anchor-tagged 214 bonefish in the Bahamas but had only one recapture of a fish that remained at liberty for only a few days post-release. Clark and Danylchuck (2003) tagged 120 bonefish in the Turks and Caicos with only one recapture. Friedlander et al. (2008) tagged 861 bonefish at Palmyra Atoll and had 2 recaptures. These studies led to much concern about tagging mortality and a general lack of confidence in anchor-tag methodologies. However, the conventional anchor tagging project run by University of Miami personnel has proved to be highly successful. To date, almost 8,000 bonefish have been tagged with just under 300 recaptures. This provided information on movements throughout the fishery. The 8,000 tagged fish reflected the length frequency distribution of the catch, thus, providing detail on selectivity.

Acoustic telemetry (AT) methods provide high resolution information on fish movements and habitat utilization, and this method has been applied to bonefish. Colton and Alevizon (1983) tracked 13 AT tagged bonefish using a boat-mounted directional hydrophone. They stated that bonefish movements ranged widely through available habitats. However, their conclusions were equivocal as they were only able to detect and track three fish after 24 hours, and two of these for a 5 day maximum. Friedlander et al. (2008) AT tagged 40 bonefish and recorded them moving between three lagoons. However, Friedlander et al. (2008) had very short durations for their detections which ranged from 1 to 24 days with a mean of 5 days. A more thorough AT tagging project was conducted with a larger number of fish AT tagged and a larger array to illustrate high resolution bonefish movements and habitat utilization.

Movements of bonefish are not the only research area that needs further attention. It is unknown how the bonefish stock has changed over the past 30 years. Analysis of the catch rates of tournament results revealed changes in the stock over time. This is critical information to address the current stock condition.

The stock condition is impacted by the fishing mortality imposed on it and needs to be examined to determine sustainability. Crabtree et al. (1996) estimated mortality rates for Florida's bonefish stock using a catch curve for total mortality and Pauly's (1980) formula for natural mortality. However, more robust estimates and further separation of fishing mortality and natural mortality are needed. Despite being a catch-and-release fishery, there is fishing mortality (Ault et al. 2002a; Larkin et al. 2008, 2010) and an increase in fishing effort can lead to a decline in the bonefish stock. This occurred in Florida's snook (*Centropomus spp.)* fishery where despite being primarily a catch and release fishery (96% of snook are released; Muller and Taylor, 2006), with no commercial harvest, the large increase in recreational fishing effort combined with a 3% postrelease mortality pushed the stock toward an overfished condition (Nelson 2002). The bonefish stock could follow the same fate as the snook stock because south Florida has experienced growth of regional human populations and exploitation pressures from recreational fishing fleets (Ault et al. 2005c). The number of registered recreational vessels in south Florida has increased by almost five times between the 1960's and 2000 (Ault et al. 2009).

The ultimate goal of the dissertation is to determine the stock status of this ecologically and economically significant resource. To accomplish this goal, the objectives were to synthesize and integrate quantitative information on bonefish population and fishery dynamics so that these could then be applied to two different, but highly complementary, stock assessment methods: (1) a “length-based” estimation employing a stochastic age-independent continuous model to determine population numbers and biomass for given lengths; and, (2) an age-structured “catch-free” production model recast in terms of relative to pre-exploitation levels. Once stock status was determined, management recommendations to ensure sustainability were provided.

Chapter 2

Bonefish age, growth and species definition

Summary

Information on bonefish population dynamics is critically needed to support fishery management strategies for habitat preservation, stock management, and conservation. In this chapter, existing literature concerning the population dynamics of south Florida's bonefish stock is synthesized with additional work on modeling growth and population structure.

Three different datasets and three different methods were used to model bonefish growth. The datasets were observed age-length, back-calculated length-at-age, and size increment versus time-at-large from tag-recapture data. The observed age-length data revealed a shift in growth rate which lead to a Double Exponential growth model having a better fit than other growth models. The Double Exponential growth model fitted to the observed length-data estimated the parameters of A = 365.4 (5.905 SE), B = 2.905 (0.2060 SE), and C =-2.625 (0.1306 SE) for the small bonefish (<440 mm FL) before the diet shift and L_∞ = 703.8 (12.09 SE), K = 0.2942 (0.0417 SE), t_0 = -0.5583 (0.5485 SE) for the larger fish. The modified Fry back-calculation model was applied to otolith measurement data and von Bertalanffy growth parameters were estimated with a non-linear mixed effects model. The estimated von Bertalanffy parameters are L_∞ = 712.8 (9.48 SE), K = 0.2239 (0.0080 SE), and t_0 = -1.391 (0.0674 SE). The tag-recapture database estimates were L_∞ = 694.1 (16.07 SE) and K = 0.3868 (0.0603 SE) using the Fabens method. The tag-recapture dataset has potential for being problematic and the

parameter estimates were not compared to the other two methods. Comparison of the parameter confidence intervals for the large bonefish (>440 mm FL) produced overlapping intervals for the age-length and back-calculated modeling results. Modeling growth from the age-length dataset allowed predictions of size at age for the complete growth history of the species (i.e. both the young and old age classes). Therefore, the growth model derived from the age-length dataset will be used in future applications and simulations.

There is evidence against the claim of two species of bonefish in Florida waters: (1) misclassification of the discriminant function when the two species are of similar lengths; (2) PCA results show bonefish morphometrics are not independent by species; (3) no dramatically different age-length relationships; and, (4) both species are frequently caught together. Until additional genetic work, such as looking at more than one gene, is conducted it will be assumed that Florida's bonefish stock comprises of one bonefish species.

2.1 Species Distribution and Unit Stock

Bonefish, *Albula vulpes* (Linnaeus), support important recreational fisheries throughout the tropical central western Atlantic Ocean (Colborn, et al. 2001; Ault 2008). In south Florida, which includes the Florida Keys, bonefish are primarily found in nearshore waters (<1 km from land) from Key Biscayne to the Marquesas, with catches rarely made outside this range (Larkin et al. 2010). Bonefish were not previously believed to be ocean migrants, but recent results of conventional anchor tagging studies in Florida have documented movement of mature bonefish between the Florida Keys and the Bahamas (Larkin et al. 2008; Chapter 5 of this dissertation).

2.2 Reproduction

Studies by Bruger (1974) and Crabtree et al. (1997) provided information on bonefish reproductive seasonality in south Florida. Bruger (1974) suggested that spawning occurred year-round off the Florida Keys based upon finding ripe females in all months. A more extensive study by Crabtree et al. (1997) concluded that gonadal activity showed seasonal periodicity that peaked during November to May. No fully hydrated ovaries or postovulatory follicles were found; therefore spawning periodicity and batch fecundity are unknown. Crabtree et al. (1997) suggested that bonefish spawn outside of the fishing grounds, which is also suggested by Colton and Alevizon (1983) and Mojica et al. (1995). Crabtree et al. (1997) reported south Florida bonefish reach sexual maturity at about age 4.2 and 488 mm FL, and total fecundity ranged from 0.4 to 1.7 million oocytes and had a positive relation to weight. Crabtree et al. (1997) reported a fecundity-weight relationship of:

$$log_{10}FEC = 1.936 + 1.131WT \tag{2.1}$$

where *FEC* is fecundity in million oocytes and *WT* is weight in grams. This equation was derived from a sample size of 33 and had an r-squared value of 0.706. The range of weight values was 1,790 to 5,790 grams.

2.3 Recruitment

The location of juvenile bonefish habitats remains an enigma. Crabtree et al. (1996) conducted limited seine collections in sand and seagrass benthic habitats of the Florida Keys and produced 56 young-of-the-year (YOY) bonefish that ranged from 21-116 mm FL. They did not comment on the spatial distribution of abundance. A comprehensive rollerframe trawl survey to assess the fish and macroinvertebrates of

Biscayne Bay revealed that a large number of fish species utilize its various benthic habitats as YOY nursery grounds (Ault et al. 1999). However, despite exhaustive sampling over four seasons and two years that included areas that adult bonefish frequent, no YOY bonefish were ever observed. YOY bonefish were caught with trawl gear by Florida's Fish and Wildlife Institute's fisheries independent monitoring program in Florida Bay, but only 2 bonefish were caught in 180 trawl samples and 2 bonefish were caught in 192 seine samples (Florida Fish and Wildlife Research Institute 1996). Most likely YOY bonefish are residing in south Florida waters but have yet to be captured in large numbers. Surprisingly, the cold weather event of January 2010 caused over 100 YOY bonefish to be washed on the shores of the Upper Florida Keys (Key Largo, Islamorada). It is unknown where these bonefish came from but additional sampling effort is needed in these areas to discover the primary habitat of YOY bonefish.

Harnden et al. (1999) deployed two channel nets in Hawk Channel in the Florida Keys in 1993 for over 160 nights throughout the year. They captured nearly 35,000 larval fishes but only 6 of them were bonefish. A channel net deployed in Lee Stocking Island in the Bahamas averaged over 1,000 bonefish larvae in a similar time period (Mojica et al. 1995). The near absence of bonefish larvae from Harnden et al's (1999) sampling may be indicative of low recruitment to the Florida Keys or not effectively targeting peak settlement months or settlement areas.

Since 1998, a conventional tagging program in south Florida (www.bonefishresearch.com; Humston 2001; Ault et al. 2005a, Larkin et al. 2008) has caught and tagged more than 200 bonefish in the 200-350 mm FL size classes (ages 1 to 2 years old) along the coastline near Jupiter Inlet (about 150 km north of Miami).

Surprisingly, no bonefish larger than 350 mm FL were caught in this region despite the fishermen using the same gear (hook size and crustaceans for bait) as used in the Florida Keys region. The presence of immature fish to the north suggests that primary areas of stock recruitment and nursery grounds could be north of the principal area of the Florida Keys fishery. This is supported by the discovery by Alperin and Schaefer (1964) of over 100 juvenile bonefish in Great South Bay, New York.

2.4 Movements and Migrations

The movements and migrations of bonefish are discussed thoroughly in chapter 5 of this dissertation.

2.5 Mortality

Predators of bonefish must be fast enough to capture and large enough to consume this wary species. Sharks, groupers, barracuda, and bottlenosed dolphin are known predators of bonefish (Ault et al. 2008a). Cooke and Phillip (2004) described sharks in the Bahamas as significant predators of bonefish following angling release. In various regions (Bahamas, Belize, wider Caribbean Sea) bonefish are often employed as bait for catching large pelagic or reef fishes (marlin, grouper, etc.). This may indicate that bonefish represent familiar "prey of opportunity" to these deep water species, perhaps intercepted on occasion as bonefish migrate to offshore spawning grounds.

Mortality estimates have been generated for south Florida's bonefish stock (**Table 2.1**). Crabtree et al. (1996) estimated total mortality with a catch curve analysis and natural mortality with Pauly's (1980) formula. They found that the total and natural mortality estimates were similar and argued that little fishing mortality exists. More recent literature states that fishing mortality in bonefish fisheries can be quite significant. Cooke and Phillip (2004) reported 40% fishing mortality for a Bahamian bonefish fishery. A more recent estimate of total mortality was done by Larkin et al. (2008) using a length based mortality estimate (Ault and Ehrhardt 1991; Ehrhardt and Ault 1992). Ault et al. (2008a) estimated natural mortality from the Alagaraga (1984) method, and the new estimate was lower than Crabtree et al.'s (1996) estimate. The reduced M suggests that fishing mortality may have a more prominent role in the survivorship of the stock. New estimates of natural, fishing, and total mortality are discussed in chapter 4 of this dissertation.

Table 2.1- Estimates for instantaneous rates of natural mortality (M) and total mortality (Z) for south Florida's bonefish stock.

Source	Method	M
Crabtree et al. (1996)	Pauly's formula	0.31
Ault et al. (2008a)	Alagaraga (1984)	0.1498
Source	Method	Z
Crabtree et al. (1996)	Catch curve analysis	0.21
Larkin et al. (2008)	Length based mortality estimation	0.208

2.6 Population size

Ault et al. (2008b) developed and implemented a novel visual survey in south Florida to estimate bonefish population size. The survey was conducted during one day each year over eight consecutive years. Professional bonefish guides and experienced anglers were recruited to the field effort at specific survey locations between Miami and the Marquesas, and enumerated the numbers of bonefish seen in the sampling area. Statistical sampling techniques were used to estimate adult stock size at approximately 300,000 individuals with relatively good precision. Chapter 4 of this dissertation adds an additional estimate of population size by combining a logbook program with tag-recapture data.

2.7 Length-Length and Length-Weight relationships

Length-length (i.e., total length *TL*, standard length *SL*, and fork length *FL*) and allometric weight-length relationships for south Florida bonefish have been reported by Bruger (1974) and Crabtree et al. (1996). New length-length and weight-length regressions were created from Crabtree et al.'s (1996) (n=451) data with additional data for their un-aged samples (n=405) and new data collected for this dissertation (n=280). The relationship between lengths and allometric weight-length are presented in **Table 2.2**.

Table 2.2- Fork length-total length, fork length-standard length, and weight-fork length regressions for bonefish from south Florida waters. FL= fork length (mm), TL = total length (mm), and WT=weight (g). Sample fork length range was from 21-740 mm. Values in parentheses are standard errors.

			$Y=a+bX$		
Y	X	n	a (1 SE)	b (1 SE)	r^2
FL	TL	1,130	-1.3813 (0.3627)	0.8619 (0.0007602)	0.999
FL	SL	1,136	4.5153 (0.5923)	1.0411 (0.001514)	0.998
			$Y=aX^b$		
Y	X	n	a (1 SE)	b (1 SE)	
WT	FL	1,127	5.2658E-6 (1.025)	3.1696 (0.004557)	

2.8 Age and Growth

Background

The production of a stock, in terms of biomass and abundance, is determined by immigration, emigration, recruitment, and growth of individuals already in the population. Additionally, growth information can be used to determine age- and length-specific mortality rates, age at maturity and life span (Ricker 1975; Gulland 1983). Growth was assessed from multiple data sources: age-length, back-calculation, and tag-recapture data. Age-length data provide an estimated age of the individual fish at one point in time. Back-calculation of the fish's length from the measured distances between the annuli deposited on a body structure of the fish provides estimated growth trajectories for each fish.

2.8A Observed Age-Length

Many different body structures are frequently used to determine the age of fish (i.e. otoliths, vertebrae, spines, opercle). Otoliths are one of the most commonly used body structures for ageing. Crabtree et al. (1996) used otoliths to age 451 bonefish in the Florida Keys but failed to sample equal numbers of fish from each age class. Specifically, they: (1) over-sampled the most common age classes of 3 to 9 years old; and, (2) under-sampled the youngest (< 3 years old) and oldest (> 12 years old) age classes. To adequately sample all age classes, a sampling design should focus on securing a good size representation. Since different sampling gears will have different selectivity of sizes multiple sampling gears must be used.

Another reason to reexamine the age-length study of Crabtree et al. (1996) is the fact that the size distribution data from the bonefish tag-recapture study suggested that bonefish may live longer than previously estimated. Crabtree et al. (1996) found a maximum age of 19 years with a 679 mm FL bonefish. The bonefish tag-recapture database contained 449 bonefish (or about 5% of the bonefish tagged) larger than

Crabtree et al.'s (1996) largest fish (**Figure 2.1**). Since fish have indeterminate growth (Helfman et al. 1999) the possibility exists that bonefish live longer than 19 years.

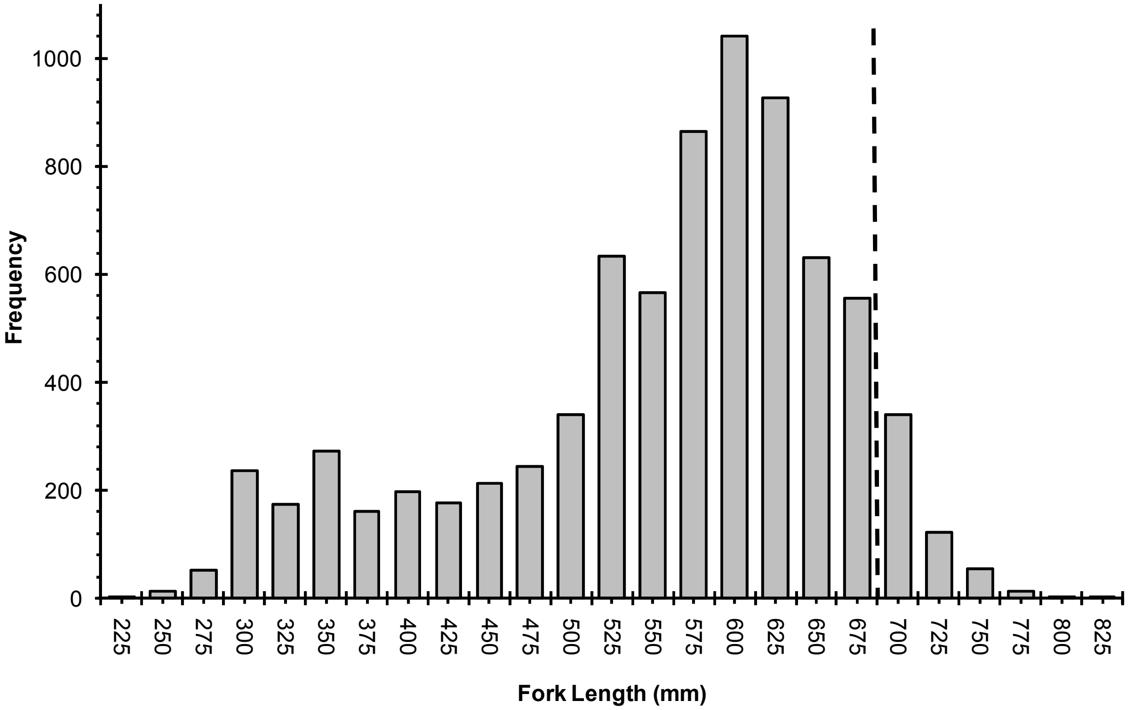

Figure 2.1- Length frequency distribution for 7,961 bonefish tagged-and-released during 1998 to 2010 for which length information was available. The dashed line represents the largest bonefish collected by the age and growth study of Crabtree et al. (1996).

Missing age classes and lack of data available for younger and older individuals is common for age and growth studies. The underrepresentation of smaller individuals in the younger age classes is usually due to gear selectivity and lower availability, and underrepresentation of the larger individuals among the older age classes is usually due to the fact that old fish are less abundant due to mortality, especially for depleted stocks (Ehrhardt and Deleveaux 2006). This problem can lead to selection of an inappropriate growth model, biased parameter estimates and incorrect estimates of precision. Campana (2001) stated that the youngest and oldest age classes are the most influential in estimates of growth, mortality, and longevity. I overcame the problems of underrepresented age classes by using multiple gears and many different fishermen. This provided complete information over the entire life span of the species and created a much improved growth curve for bonefish.

Methods

Age-length data was collected through selective sampling. The sampling design focused on fish sizes that correspond to the young age classes (<3 years old) and the oldest age classes (>12 years old) by targeting small (<300 mm FL) and large (>300 mm FL) bonefish.

The fish in the dataset of Crabtree et al. (1996) were caught with hook-and-line gear mostly by a single professional bonefish captain. My dataset has a total of 281 bonefish collected with several sampling gears from over 20 fishermen. Large bonefish (>650 mm FL, n=30) were selectively culled from tournaments and juvenile (<300 mm FL) bonefish were collected from the beaches of Key Biscayne and Key West (n=44) using 21.4 m seine with 6.35-mm mesh. Additional samples were collected from the middle age classes (300 to 650 mm FL) (n=63) from hook-and-line fishermen. A large number of dead bonefish (n=144) were collected from the shorelines in the Florida Keys during the cold weather event in January 2010. Of the total collection of 281 bonefish the daily age was estimated for the small bonefish (<300 mm FL, n=163) and annual age was estimated for the large bonefish (>300 mm FL, n=118).

The daily age of the young (<300 mm FL, age<500 days) age classes was estimated from otoliths to allow the growth model to be fitted to data near the origin. Mojica et al. (1995) determined the daily age of bonefish leptocephali in the Bahamas, but the formation of daily otolith increments for bonefish has yet to be confirmed.

However, the daily formation of increments in many species of eel leptocephalus has been verified (Tsukamoto 1989; Umezawa et al. 1989, Martin 1995; Arai et al. 2000; Cieri & McCleave, 2001; Sugeha et al. 2001; Shinoda et al. 2004). Daily otolith increments have also been verified by the close relative species tarpon (*Megalops spp.*) for the young-of-the-year phase in the Pacific (Chen and Tzeng 2006) and the Caribbean (Zerbi et al. 2001).

For both large and small fish, standard length, fork length, and total length were measured to the nearest millimeter and fish were weighed to the nearest gram. Sagittae otoliths were removed, rinsed with water, and stored dry until sectioned. The sex of all mature fish was recorded. The left sagitta was used for age estimation; however, in cases where the left otolith was broken, lost, or damaged during processing, the right otolith was substituted.

Otolith preparation differed between the small (<300 mm FL) and large bonefish (>300 mm FL) because one was used to determine daily increments and the other to determine annual increments. The juvenile bonefish otoliths were mounted with epoxy resin then polished with various wet sandpapers (600 to 2,000 grits per sheet) and Buehler Micropolish II alumina suspension until the primordium was revealed. A Leica DMLB microscope with oil immersion magnification (40-100x) with an Infinity 2 microscopy camera was used to capture images of each otolith. Image Pro Plus 7.0 software was used to read the otolith increments. The increments were assumed to be daily because daily increments have been validated by injection of oxytetracycline hydrochloride from many species of closely related eels (Tsukamoto 1989; Umezawa et al. 1989; Martin 1995; Arai et al. 2000; Cieri and McCleave 2001; Sugeha et al. 2001;

Shinoda et al. 2004) and tarpon (Tzeng et al. 1998; Zerbi et al. 2001). Enumeration of otolith increments was done following the method of Reveillac et al. (2009) which counted from the first feeding check and stopped at the last increment near the sagitta's edge (**Figure 2.2**). Otoliths do not grow symmetrically but instead different axes grow at different rates resulting in some compressed and some long axes. Increments were read along the ventral ridge, which is the longest axis and was recommended by Zerbi et al. (2001). The reading criterion of D'Alessandro et al. (2010) was used where two counts of the increments were taken per otolith. If the two counts were less than 5% different from each other then the first count was kept. If the counts were greater than 5% different than a third count was conducted. If the third count was less than 5% different from one of the original two counts then it was kept. If the third count was greater than 5% different from both of the first two counts then the otolith was removed from further analysis. Daily ages were converted to decimal ages by dividing by 365.25.

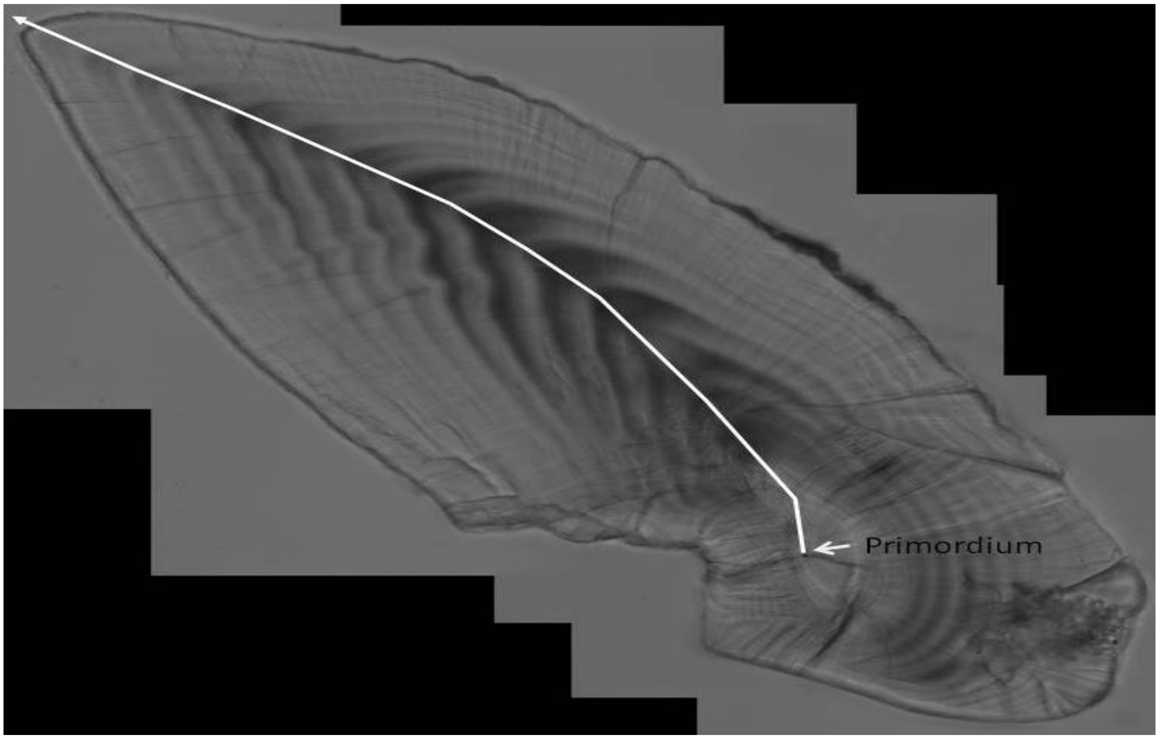

Figure 2.2- Sagitta of juvenile bonefish (Fork Length = 31 mm, age =102 days) at 100x magnification showing the primordium and ventral axis for counting otoliths.

The otoliths of large bonefish were prepared by cutting three thin sections approximately 0.5 mm thick, one of which was through the otolith core, using a Beuhler Isomet low-speed saw with a diamond blade. Sections were then mounted on a microscope slide with Flo-texx mounting media. Annuli were counted using a dissection microscope equipped with reflected light at magnifications of 8-25x. Following the procedure of Crabtree et al. (1996), annuli were counted three times by each of two independent reviewers and it was noted if the otolith had an annulus on the margin. Any otoliths that caused disagreements between the readers were re-examined. In most cases the readers were able to reconcile these disagreements and determine the number of annuli, however, if an agreement could not be made then the otolith was removed from further analysis.

Marginal-increment analysis and an annuli validation experiment were done for bonefish in south Florida by Crabtree et al. (1996). Their results reveal that bonefish otoliths formed one annulus per year, which was deposited in the months of March-June. The cohort ages of bonefish in my collections were determined by evaluating the collection date relative to the marginal formation period and birth date. The birth date of all fish was assumed to be February 15, because this is in the middle of the spawning season (Crabtree et al. 1997) and February was the peak month for birth from back calculation of birthdates from the daily ages. The age of the bonefish collected between January 1st and February 15 were equal to the number of annuli counted on the otolith. The age of a bonefish collected between February 16 and February 28 was equal to the number of annuli plus one. The age of the bonefish collected between March 1 and June 30 was equal to the number of annuli plus one, unless there was an annulus on the margin in which case no adjustments were made. Bonefish collected between July 1 and December 31 did not have any adjustments to the annuli counts and the age of a bonefish was equal to the number of annuli. The decimal age values that were added to the cohort age came from dividing the number of days since the previous birth date by 365.25. For example a fish with a cohort age of 10 that was collected on January 2, 2006 is 321 days since February 15, 2005 so the decimal age was 10.879.

The dataset of Crabtree et al. (1996) and mine were collected in two different time periods: 1989 to 1995 and 2003 to 2010. Therefore, the possibility exists for changes in the age-length relationship over time. This was addressed by comparing the average size-at-age for each age class from each dataset with a t-test (alpha level of 0.05). Each dataset was divided into half-year bins (i.e. age class 5 becomes age 5.0 to 5.5 and 5.51 to

5.99) before testing. In cases where the sample sizes were not large enough for comparison (n<3) then entire year classes were compared, and if that did not provide enough samples then age classes were combined until the minimum sample size was accomplished. If no different size at age relationships existed, then both datasets were pooled together for modeling growth.

A requirement for nonlinear fitting procedures is normally distributed data. The distribution of sizes for each age class was tested for normality with the Shapiro-Wilk test with an alpha level of 0.05. Once this requirement was satisfied non-linear regression procedures were used to fit growth models.

Crabtree et al. (1996) used the von Bertalanffy growth model; however, since the current dataset has a larger age-range many different candidate growth models were pursued using nonlinear fitting procedures in R software (www.r-project.org). The eight candidate models were: von Bertalanffy, generalized von Bertalanffy, Gompertz, Logistic, Schnute-Richards, double von Bertalanffy, Chapman-Richards, and a Double Exponential model. The von Bertalanffy growth function model (1938) was applied to fisheries by Beverton and Holt (1957). This model is the most commonly applied and studied growth model (Laslett et al. 2002, Katsanevakis 2006). The model is

$$L(t) = L_\infty(1 + e^{-k_1(t-to)}) \tag{2.2}$$

where $L_{(t)}$ is fork length for age t, L_∞ is the asymptotic maximum length, k_1 is the growth coefficient that determines how quickly the maximum is attained, and t_0 is the hypothetical age at which the fish has zero length. The generalized von Bertalanffy growth model (Pauly 1979) is given by the equation

$$L(t) = L_\infty(1 - e^{-k_2(t-t_1)})^p \tag{2.3}$$

where the parameters have the same interpretation as the von Bertalanffy growth model with the extra *p* parameter representing a dimensionless factor. The Gompertz growth model (Quinn and Deriso 1999) is a sigmoidal growth curve that assumes exponential decrease of the growth rate with size.

$$L(t) = L_\infty exp(-\frac{1}{k_3} e^{-k_3(t-t_2)}) \qquad (2.4)$$

where k_3 is the rate of exponential decrease of the relative growth rate with age, and $t_2 = \frac{1}{k_3} ln\lambda$ (Quinn and Deriso, 1999). The logistic model (Ricker 1975), given by the equation

$$L(t) = L_\infty(1 + e^{-k_4(t-t_3)})^{-1} \qquad (2.5)$$

where k_4 is a relative growth rate parameter and t_3 corresponds to the inflection point of the sigmoidal curve. The Schnute-Richards model (Schnute and Richards 1990) is a 5-parameter model, given by the equation

$$L(t) = L_\infty(1 + \delta e^{-k_5 t^{\nu}})^{1\backslash\gamma} \qquad (2.6)$$

where the parameter k_5 is the rate of decrease of the relative growth with age, and δ, ν, γ are dimensionless parameters.

Some fish exhibit dramatic changes in growth rates with age that are not adequately captured by standard growth models. This phenomenon has been explained by ontogenetic changes, especially the abrupt shift in growth rate from juveniles to adults. Red drum (*Sciaenops ocellatus*) (Vaughan and Helser 1990) and southern bluefin tuna (*Thunnus maccoyii*) (Hearn and Polacheck 2003) have required growth curves that accommodate this shift. To evaluate the possibility of bonefish displaying a similar shift alternative growth models were developed. One of the models is the double von

Bertalanffy curve (Vaughan and Helser 1990) which allows the rate an animal approaches the asymptotic length to change after some pivotal age, t_p:

$$L(t) = \begin{cases} L_\infty\left(1 - e^{-k_6(t-t_5)}\right) & \text{if } t < t_p \\ L_\infty\left(1 - e^{-k_7(t-t_6)}\right) & \text{if } t \geq t_p \end{cases} \tag{2.7}$$

$$t_p = (k_7t_6 - k_6t_5)/(k_7 - k_6)$$

where the parameters have the same interpretation as the von Bertalanffy growth model but the parameters, except for L_∞, are different before and after the pivotal age. This model accommodates the possibility that older, larger fish might grow more slowly in proportion to their length than younger, smaller fish.

Another model that adjusts for a shift in growth rate is the Chapman-Richards growth model:

$$L(t) = L_\infty(1 - Be^{-k_8t})^{\frac{1}{1-m}}, \qquad 0<m<1 \tag{2.8}$$

$$L(t) = L_\infty(1 - Be^{-k_9t})^{\frac{1}{1-m}}, \qquad m>1$$

where L_∞ is the asymptote, m determines the shape and inflection point of the growth function, and the *k* parameters relate to the growth rate.

An adjustment was made to the double von Bertalanffy model to allow two different growth curves to be modeled due to a shift in diet. Ontogenetic shifts in diet, specifically a shift from invertebrates to fish, have been shown to increase the growth rate of several species of fish (Olson 1996; Pazzia 2001; Sherwood et al. 2002; Govoni et al. 2003; Graeb et al. 2006). To accommodate this phenomenon, two different growth curves were fitted, a logistic model to fish below the size of the diet shift (L_d) and a von Bertalanffy model to fish above L_d. This is called the Double Exponential model and is:

$$L(t) = Aexp\left(-Bexp\left(C(t)\right)\right) \quad \text{if } L < L_d \tag{2.9}$$

$$L(t) = L_{\infty b}(1 - exp^{-k_{10}(t-t_9)}) \quad \text{if } L \geq L_d.$$

The first step is a logistic model where A is the asymptote, and parameters A and B determine the growth rate. After the diet shift the von Bertalanffy model parameters have the same interpretation of equation 2.2. Bonefish display a distinct diet shift where they eat mostly penaeid shrimp when they are less than 440 mm FL, then start feeding on toadfish (*Opsanus beta*) and increase the feeding frequency and size of ingested xanthid crabs, alpheid shrimp, and *Callinectes spp*. (Crabtree et al. 1998b). A likely explanation for the diet shift is an increase in gape size once the size of the diet shift is reached (Crabtree et al. 1998b). Magnhagen and Heibo (2001) describe how both predator gape size and prey size are the main factors deciding whether a gape-limited piscivore can ingest a potential prey fish.

Mimimum, maximum, and best guess parameter values to start the non-linear optimization routine were determined from the bonefish growth modeling work of Crabtree et al. (1996). Once convergence was accomplished, model selection was based on Akaike's Information Criteria (AIC) (Akaike 1973). This was calculated for least squares with

$$AIC = nlog(\sigma^2) + 2k,\ \sigma^2 = RSS/n \qquad (2.10)$$

where RSS is the residual sum of squares, n is the number of observations, and k is the number of estimated parameters. The model with the smallest AIC value (AIC_{min}) was selected as the best among the models tested. Following the method of Katsanevakis (2006), the AIC differences $\Delta_i = AIC_i - AIC_{min}$ were computed for all the candidate models. To quantify the plausibility of each model, given the data and the set of eight models, the Akaike weight (w_i) of each model was calculated, where

$$w_i = \frac{\exp\,(-0.5\Delta_i)}{\sum_{k=1}^{8} exp(-0.5\Delta_i)} \tag{2.11}$$

Akaike weight was considered the weight of evidence in favor of model *i* being the best model of the available set of models (Burnham and Anderson 2002; Katsanevakis 2006). Once the best model was chosen likelihood ratio tests (Kimura 1980; Cerrato 1990) were used to compare growth curves and parameter estimates between sexes (the 8 growth models were fit for both sexes combined).

There is a possibility that small samples of certain size ranges could influence the growth curve selection process. This was tested by breaking the age-length data into 50 mm size bins and then randomly selecting with replacement 10 samples from each bin. Then, the eight models were applied and model selection was based on AIC and Akaike weight.

Results

Of the 281 bonefish collected for this study, daily age was estimated for 163 (58%) of the sample collections. Of these otoliths 10.4% did not pass the reading criteria and were removed from further analysis. The fish ranged in size from 28 to 319 mm FL and ages from 42 to 501 days. Back-calculated birthdates occurred in every month but 70% took place in the months of January to April with a peak in February.

Of the 281 fish sampled, 118 were large bonefish (>300 mm FL) where annuli increments were read. The ages of these fish ranged from 1 to 21 years. Six (5%) of these sub-adult and adult otoliths were rejected because of disagreements among readings due to irregular and poorly defined annuli. Shapiro-Wilk test for normality could only be applied to 12 of the 21 age classes that had three or more samples. None of the age classes failed the normality test with *P* values ranging from 0.064 to 0.867.

Comparison of average size at age for my data and the data of Crabtree et al. (1996) did not show significant differences for the majority of the comparisons. The *P* values for the t-tests ranged from 0.0854 to 0.6605. However, the t-test results for the age classes of 11 and 15 produced *P* values of 0.0256 and 0.0199. Since only two of the twenty-four comparisons produced significantly different means it was assumed that the two datasets were similar and they were pooled for modeling growth.

A plot of both age-length datasets combined revealed overlap (**Figure 2.3**). The large dataset of Crabtree et al. (1996) had higher variance for the ages but overall the two datasets are very similar.

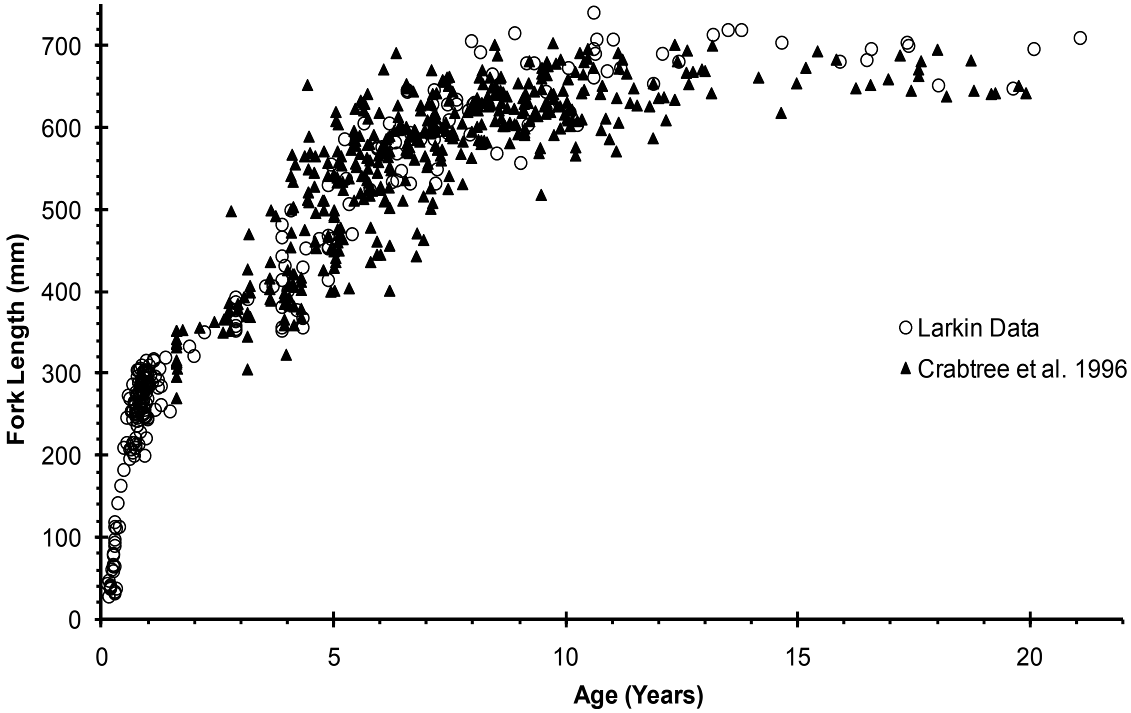

Figure 2.3-Observed age-length data from Crabtree et al. (1996) (n=451) and data collected for this dissertation (Larkin Data, n=258).

For each candidate model the corresponding AIC, Δ_i, and percent w_i are given in **Table 2.3**. The Double Exponential model was found to be the best among the candidate models with the lowest AIC value and accounted for 99% of the Akaike weight. This model produced the parameter estimates of A = 365.4 (5.905 SE), B = 2.905 (0.2060 SE), and C =-2.625 (0.1306 SE) for the small bonefish (<440 mm FL) before the diet shift and L_∞ = 703.8 (12.09 SE), K = 0.2942 (0.0417 SE), t_0 = -0.5583 (0.5485 SE) for the larger fish. Overall this model fits the data well except that the model underpredicted lengths for the ages from 101 to 227 days and again from ages 2 to 3 (**Figures 2.4** and **2.5**).

Table 2.3- Equation number, number of parameters, sum of squares (S.O.S.), Akaike information criterion (AIC), and Akaike differences (Δ_i), for each candidate model. The models are sorted by increasing number of parameters.

Model	Equation	Parameters	S.O.S.	AIC	Δ_i
Logistic	2.5	4	831452	2120	279
von Bertalanffy	2.2	4	710977	2079	238
Gompertz	2.4	4	788526	2107	266
Generalized von Bertalanffy	2.3	5	710977	2081	240
Chapman-Richards	2.8	5	788743	2109	268
Schnute-Richards	2.6	6	534927	2009	168
double von Bertalanffy	2.7	6	641053	2056	215
Double Exponential	2.9	7	279398	1841	0

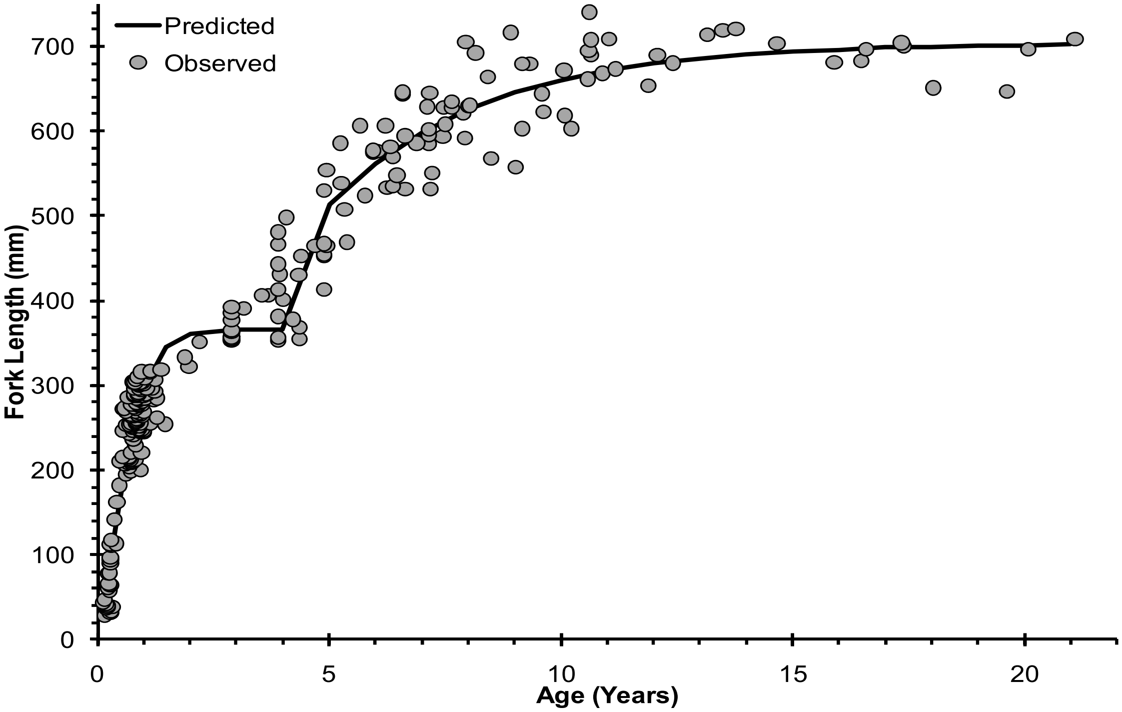

Figure 2.4-The predicted Double Exponential growth model plotted with the observed data (n=262).

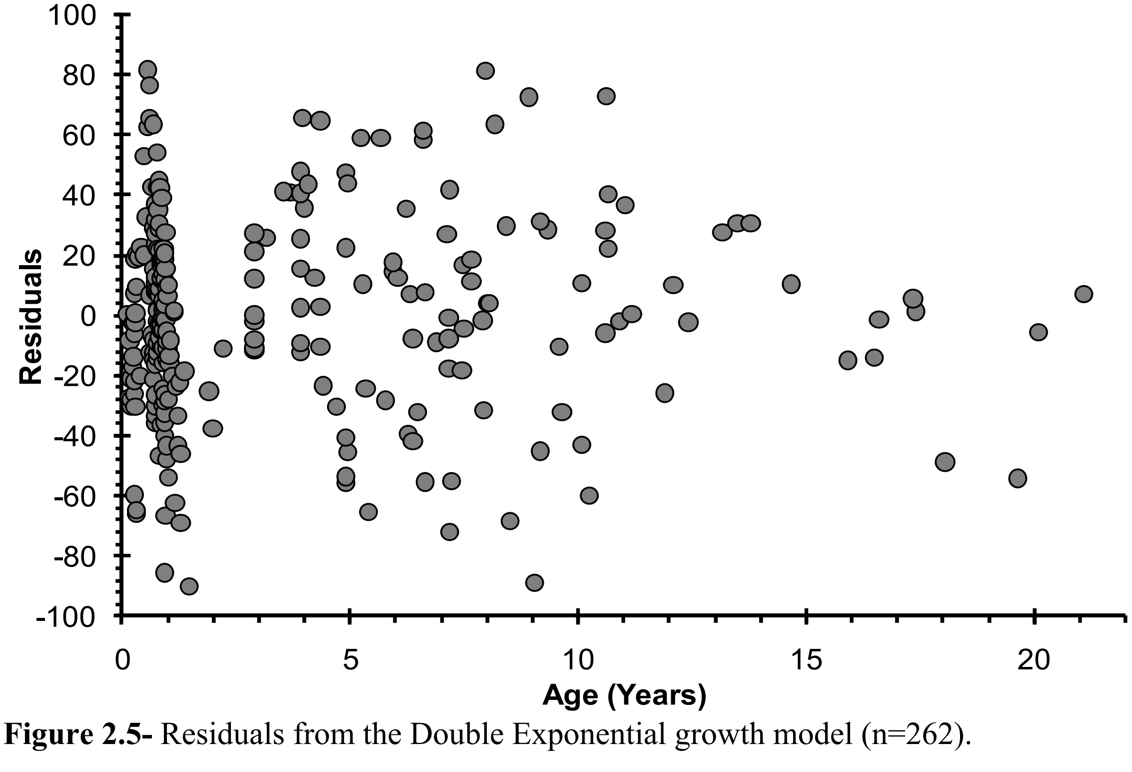

Figure 2.5- Residuals from the Double Exponential growth model (n=262).

The eight candidate models were fitted to the dataset of randomly selected age-length data from each size bin. Again, the double exponential model was found to be the best among the candidate models due to the lowest AIC value and highest w_i percentage.

The overall male and female double exponential models were statistically different ($X^2 = 22.8$, df=3, $P<0.001$). However, no differences were detected for the individual parameters.

Discussion

Sampling the large bonefish in the fishery resulted in two more age classes (ages 20 and 21) than Crabtree et al. (1996) and a new maximum age (21 years). Maximum age can have implications for fishery sustainability with respect to exploitation and environmental changes. Fish stocks with greater maximum ages tend to be more susceptible to declines from relatively small reductions in survivorship (Beverton and Holt 1957, Ricker 1975, Ault et al. 2005b). Thus, these data may imply that bonefish may be more vulnerable than was previously believed. Bonefish in south Florida have a larger maximum age then bonefish in other areas. Bonefish in Palmyra atoll in the central Pacific ocean have a maximum age of 11 years (Friedlander et al. 2008), and bonefish in Los Roques, Venezuela have a max age of 17 years (Posada et al. 2008). Assuming the low maximum ages of the other regions is not due to higher exploitation or lower sampling effort, the large maximum age of south Florida bonefish may make them more susceptible to declines from fishing mortality.

Sampling the young age classes revealed new insight into the growth of bonefish. Biphasic growth in fishes has been known for nearly a century, with some of the early work reviewed by Illes (1974). However, biphasic growth models are still relatively rarely applied. One explanation for the scarcity of biphasic growth models is that age-length data commonly come from harvested fish, which are dominated by older individuals (Ricker 1975). The juveniles are usually not harvested, and thus sampled, due to selectivity or ontogenetic habitat shifts.

Recent literature has provided both theoretical arguments and empirical evidence for biphasic growth (Lester et al. 2004, Quince et al. 2008a, Quince et al. 2008b). However these papers described allocation of energy to reproduction as the driving force for biphasic growth. Bonefish length at maturity occurs at older ages (4.2 years) and lengths (488 mm FL, Crabtree et al. 1997) then the shift location.

Beverton and Holt (1957) discussed how shifts in growth rates can be caused by fish feeding on a different prey types. This shift in diet occurs from fish reaching a certain size where they attain the capability and gap size to capture and consume both larger prey and new prey items. Bonefish display this behavior at about 3.6 years and 440 mm FL where they shift from eating mostly penaeid shrimp to eating more and larger xanthid crabs, alpheid shrimp, and *Callinectes spp.* (Crabtree et al. 1998b). The greatest difference in the diet shift was the absence of toadfish (*Opsansus beta*) in the young bonefish, but after the shift toadfish become the second most abundant prey item. Examples in the literature show that when a fish makes a diet shift from invertebrates to fish the result is an increase in growth rate (Keast and Eadie 1985; Jones et al. 1994; Olson 1996; Pazzia 2001; Graeb et al. 2006). The strong shift observed in bonefish growth can be explained by the strong diet shift. This growth increase can be explained by the relative energy costs and gains of different prey types. A rough comparison of the small penaeid shrimp consumed before the diet shift with large toadfish after the shift can illustrate the energetic costs and gains. The average weight of a penaeid shrimp consumed by the young bonefish was 1.56 grams (Crabtree et al. 1998b) which produces 826 calories/gram wet weight (Cortez 1987). The average weight of a toadfish consumed after the diet shift was 6.39 grams which produce 885 calories/gram wet weight (Cummings 1987). Therefore, a bonefish would have to consume 9 penaeid shrimp to equal the caloric value of 2 toadfish. The energy spent to capture toadfish is presumably relatively low since toadfish are mostly sedentary animals that burrow in 5–10 cm of sediment often leaving only their eyes exposed (Barimo et al. 2007). Additionally, finding toadfish should be relatively easy since they are one of the most abundant fish in south Florida waters (Sogard et al. 1987; Serafy et al. 1997). This strategy can also increase survival because eating fewer but larger prey requires less effort to be spent of foraging so that more time can be spent avoiding predation (Sherwood et al. 2002).

The mathematics of the growth model can be explained by the fish's biology. At the young ages growth displays exponential behavior. Then growth approaches the first asymptote which is likely a function of prey availability due to the fish's gape size. Once the gape size is reached the fish's growth increases dramatically and follows the commonly applied von Bertalanffy growth model.

Additional evidence to support bonefish biphasic growth was the observed data reported by Crabtree et al. (1996). Despite their sample collection occurring more than a decade from the current collection, Crabtree et al's (1996) observed age-length data displayed the shift (ages 2 through 5; **Figure 2.3**). However, Crabtree et al's (1996) samples did not contain the daily aged fish which likely prevented them from detecting and reporting this unique growth behavior.

A potential problem with the observed age-length data was relatively low number of samples for the age classes of 2 and 3. This may be a result of selectivity. Bonefish in these ages may have been too large to be captured in a seine net or killed in the January cold weather event. However, they may have been too small to be commonly caught in the fishery. Sampling efforts targeted these age classes and some collections were made but the end result was a relatively small sample size. This small sample size could have influenced the predicted growth model.

The January cold weather event provided a record of natural mortality. A large sample of bonefish (n=144) were collected, and **Figure 2.6** shows the sizes and ages of bonefish impacted by the event. Bonefish ranging in age from <1 to 16 years were killed in the event, and there was evidence of selectivity. Most of the bonefish (83%) killed were <2 years in age. It was possible that the majority of the dead bonefish were young fish because they were more abundant. Another option is the result demonstrated that natural mortality events, such as cold weather, selectively remove the younger fish from the stock. Trexler and McManus (1992) placed juvenile and adult sailfin mollies (*Poecilia latipinna*) in field cages to exclude predators, and found that winter conditions caused higher mortality rates for the juveniles.

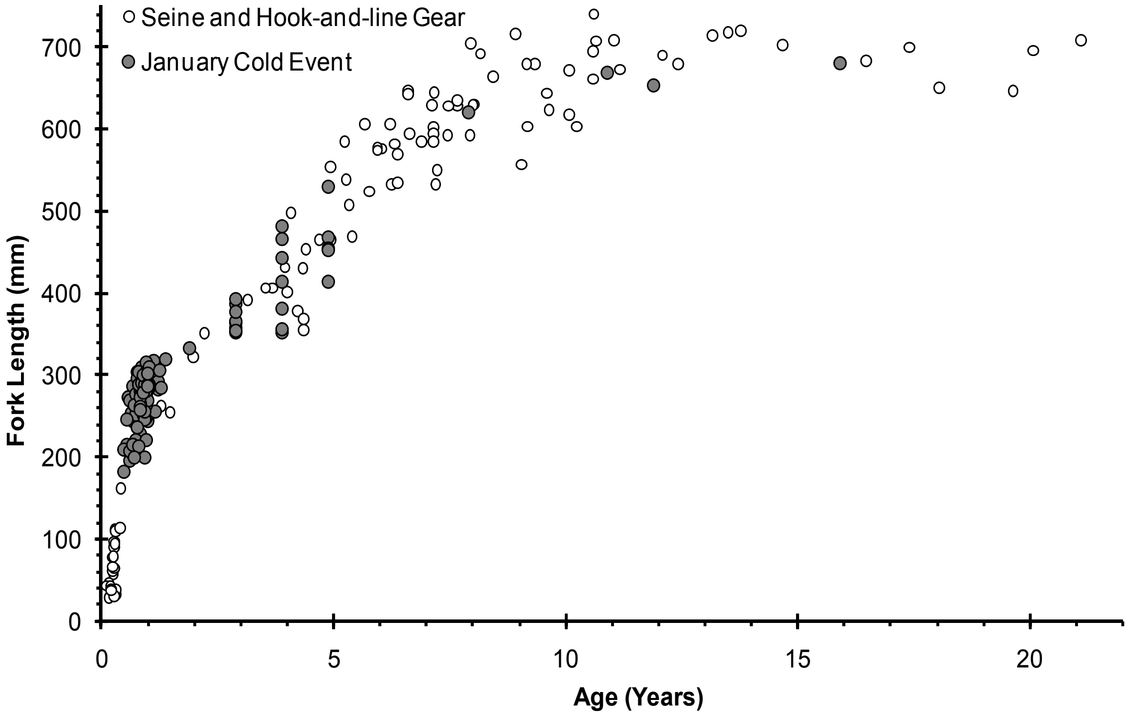

Figure 2.6- Observed data for bonefish culled from a seine net (n=44), hook-and-line gear (n=93), and a January cold weather event (n=144).

2.8B Back-calculation

Background

Back-calculation techniques are used to fill in the gaps in size-age life history information at earlier ages. The technique is frequently used to create individual growth trajectories to estimate fish growth when sample sizes are small. This increases sample sizes and fills in the gaps in life history information at earlier ages. It has proven to be an invaluable tool for fisheries scientists and fish ecologists.

There are requirements of the data for the back-calculation of size at age technique to work successfully. First, annual growth from otoliths must have a rate of deposition that does not vary and that creates annual increments. Experimental studies have validated this assumption for numerous species (Geffen 1992) including bonefish

(Crabtree et al. 1996). Second, all back-calculation models assume a relationship between the growth of the otolith (increment width) and somatic growth, usually length, of the fish. For bonefish, Crabtree et al. (1996) reported a significant relationship between otolith weight and fish age. Third, the technique assumes that these increments can be read with accuracy and precision (Campana 1992). Bonefish otoliths are relatively easy to read (**Figure 2.7)**. Crabtree et al. (1996) had a 4.2% rejection rate and I recorded a 5.9% rejection rate due to differences among readings of annuli. This percent rejection rate is low when compared to other Florida fish (tarpon *Megalops atlanticus*, 20.6% rejection rate from Crabtree et al. 1995; gag grouper *Mycteroperca microlepis*, 18.1% rejection rate from Hood and Schlieder 1992; scamp *Mycteroperca phenax*, 18% rejection rate from Harris et al. 2002)

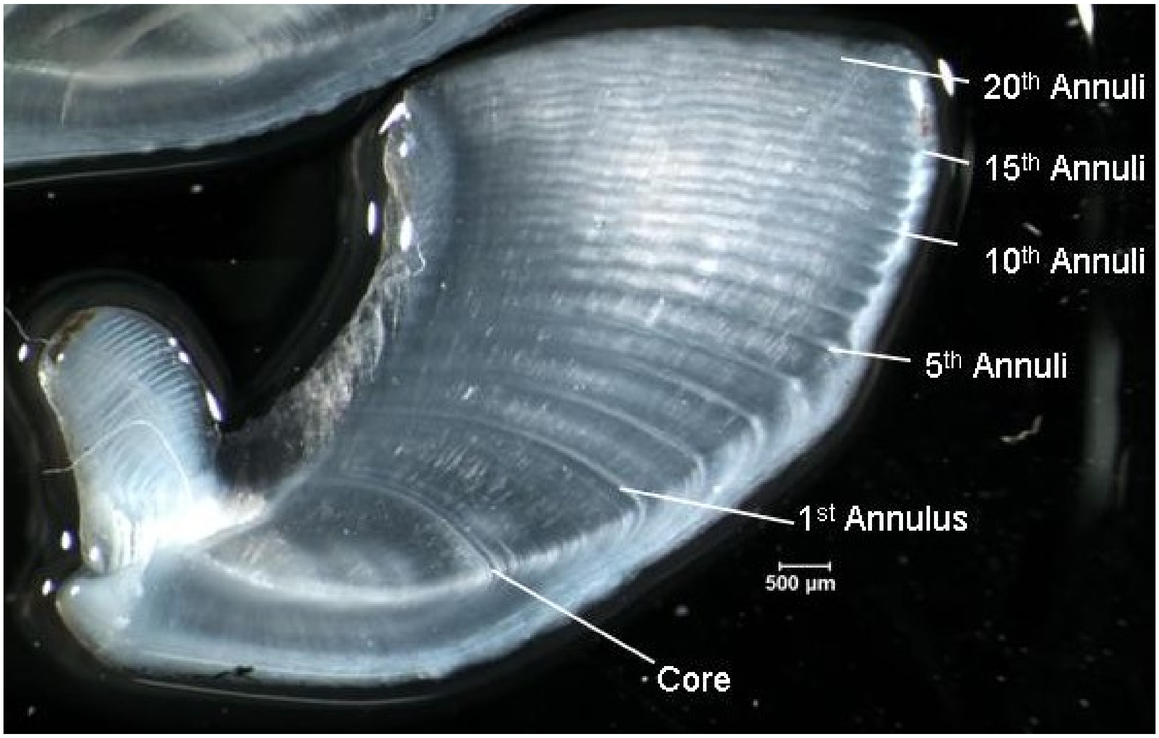

Figure 2.7- Otolith of a 700 mm fork length bonefish showing the core and the annuli counted for age estimation.

Numerous back-calculation models have been developed and were reviewed by Francis (1990, 1995). Vigliola and Meekan (2009) updated the list of back-calculation models and examined the theoretical and experimental evidence for and against the models. The Modified Fry back-calculation model created by Vigliola et al. (2000) produced growth curves that were most similar to those derived from direct observations and created the most precise estimates of size-at-age for two goby species (*Elacatinus evelynae* and *E. prochilos*) (Wilson et al. 2008) that share the Caribbean Sea with bonefish. These comparisons were made with both newly settled fish in the field and fish of known ages kept in aquariums.

The dataset generated from growth back-calculations are longitudinal and autocorrelated which makes them unsuitable for many statistical analyses (Chambers and Miller 1995, Vigliola and Meekan 2009). Specifically, data that originate from multiple observations per otolith cannot be assumed to be independent. The lack of independence of longitudinal data implies that analysis should occur at the level of individuals, rather than the population. However, this causes problems of there not being enough data for each fish to fit a growth model, and it’s unclear how to translate individual growth models to a population growth model. Vigliola and Meekan (2009) found that ad-hoc methods such as averaging the parameters estimated for each individual, or pooling the back-calculated size-at-age data and fitting a growth curve produced biased results. They recommended non-linear mixed effects models (NLME) (Vigliola and Meekan 2009). This method fits any non-linear model to longitudinal data with great flexibility. The models are mixed because they have both fixed and random effects. For the back-calculation case, fixed effects correspond to population level estimate of parameters, while random effects correspond to variability of parameters among individuals relative to the population. Thus, mixed-effects models generate estimates of model parameters at both the individual and population level.

Methods

Measurements of the fish and otolith preparation were described in the age-length section of this chapter. The back-calculation method was only applied to the eighty-six large bonefish (>440 mm FL) due to the shift in growth at 440 mm FL and annuli visual distinction for bonefish >300 mm FL.

A Leica MZ12 microscope equipped with reflected light at magnifications of 8-25x was used with a Media Cybernetics Cool SNAP-Pro cf video camera to capture images of each otolith. The radius of the otolith was measured from the core to each annulus and to the outer edge following the ventral ridge using Image Pro Plus 7.0 software. The ventral ridge was chosen because it's the longest axis which facilitates annuli counting.

The Modified Fry back-calculation model was applied to the annual increment data for the large bonefish (>300 mm FL). The assumption of this model is that there is proportionality between relative growth rates of the fish and the otolith. Following Vigliola and Meekan (2009), an estimate of fish size at first annulus (L_{0p}) was determined from the average size of one year old bonefish. The otolith radius at the first annulus (R_{0p}) came from the mean radius at the first annuli across all sampled fish. Non-linear regression was used to estimate parameter d with the equation of

$$L_{cpt,j} = L_{0p} - dR_{0p} + dR_{cpt,j} \qquad (2.12)$$

where $L_{cpt,j}$ is fish length at capture for fish j and $R_{cpt,j}$ is otolith radius at capture for fish j. The parameter *a* is the body length of an average fish at otolith formation (Fraser 1916; Lee 1920, Vigliola et al. 2000), and was calculated with

$$a = L_{op} - dR_{op} \qquad (2.13)$$

The back-calculated fish size at age for fish j ($L_{i,j}$) was calculated using the equation of

$$L_{i,j} = a + \exp\left(\ln\left(L_{0p} - a\right) + \frac{[\ln(L_{cpt,j} - a) - \ln(L_{op} - a)][\ln(R_{i,j}) - \ln(R_{op})]}{[\ln(R_{cpt,j}) - \ln(R_{op})]}\right) \qquad (2.14)$$

where R_i is the measured radius at age for fish j.

The seven covariance patterns of unstructured, toeplitz, compound symmetry, heterogeneous compound symmetry, first-order autoregressive, heterogeneous first-order autoregressive, and first-order autoregressive moving average were explored. The choice of covariance pattern incorporated into the NLME model fitting procedure was based on model fit criteria of AIC and Bayesian Information Criteria (BIC) with the lower value representing the better fit.

A von Bertalanffy growth model was fitted to the Modified Fry back-calculation estimated fish lengths using a NLME method in R software. The fixed part of the model was the global von Bertalanffy growth model parameter estimates, and the random part was von Bertalanffy growth model parameters for each individual fish.

Results

A collection of 86 bonefish from south Florida waters were used for the back-calculation method. The sizes ranged from 443 to 740 mm FL and the number of annuli counted for each otolith ranged from 3 to 20. The majority of the fish were female (n=55) which produced 485 otolith measurements. The remaining fish were 27 males (198 measurements), 3 immature fish (10 measurements), and 1 was unknown sex (6 measurements). **Figure 2.8** shows the back-calculated length at age from the Modified Fry model for all of the fish.

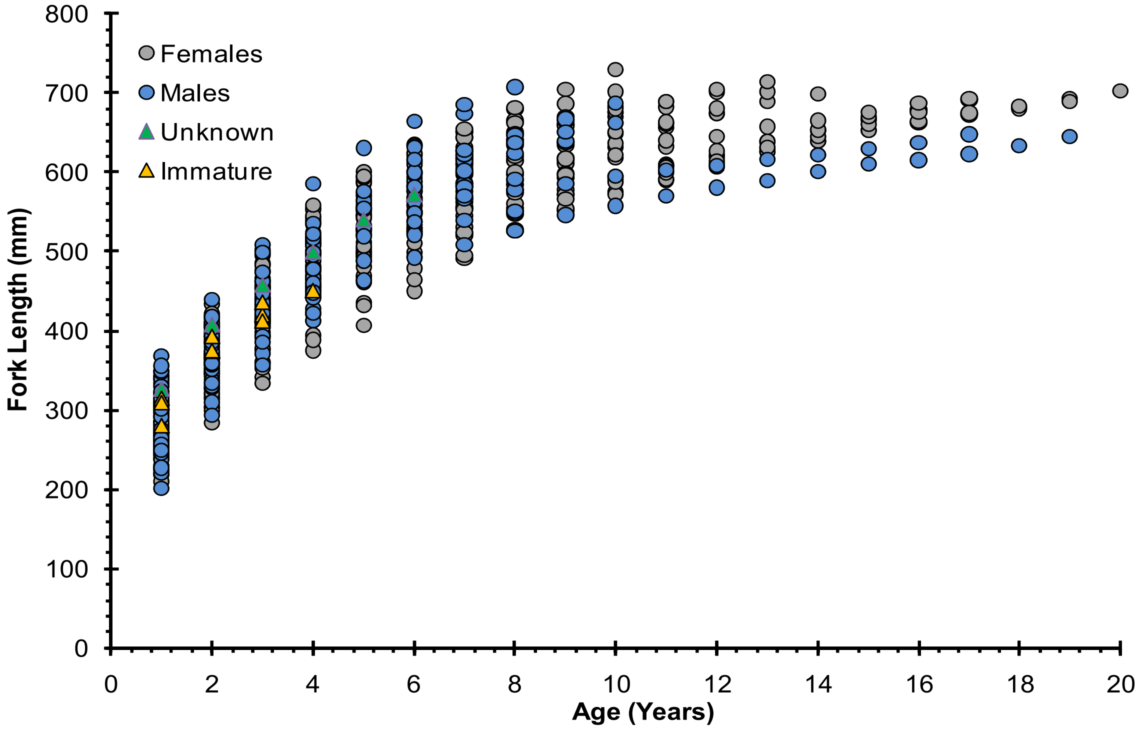

Figure 2.8- Back-calculated bonefish fork length at age from the Modified Fry model plotted against age. The model predictions came from 699 measurements taken from 86 bonefish otoliths.

The covariance patterns were explored (**Table 2.4**). AIC and BIC values were not available for the covariance patterns of unstructured and toeplitz, likely because there was not enough data to support estimation of the additional parameter required. The first order autoregressive moving average was the best fit and was incorporated into the NLME model fitting procedure.

Table 2.4- Akaike information criterion (AIC), and Bayesian Information Criteria (BIC) for each covariance pattern.

Model	AIC	BIC
Compound Symmetry	6358.7	6363.6
Heterogeneous compound symmetry	6379.2	6430.7
First Order Autoregressive	5605.5	5610.5
Heterogeneous First-Order Autoregressive	5557.3	5608.9
First-Order Autoregressive Moving Average	5508.2	5515.6

NLME was applied to the back-calculated results to generate parameter estimates for the von Bertalanffy growth equation. The model was run for each sex and also for all the data combined. **Table 2.5** provides the parameter estimates. Histograms of individual parameter estimates are shown in **Figures 2.9** (t_0), **2.10** (K), and **2.11** (L_∞). **Figure 2.12** plots the residuals of the model fit of all available data.

Table 2.5- Sex, sample size, number of back-calculated measurements, and parameter estimates for the von Bertalanffy growth model fitted to the Modified Fry model using a NLME method. "All Data" refers to both sexes combined and the data from unknown and immature fish. Values in parentheses are standard errors.

Sex	n	Measurements	L_∞ (mm)	K	t_0
Males	27	198	689.4 (22.23)	0.2501(0.0157)	-1.378 (0.1258)
Females	55	485	724.6 (9.875)	0.2160 (0.0094)	-1.344 (0.0802)
All Data	86	699	712.8 (9.48)	0.2239 (0.0080)	-1.391 (0.0674)

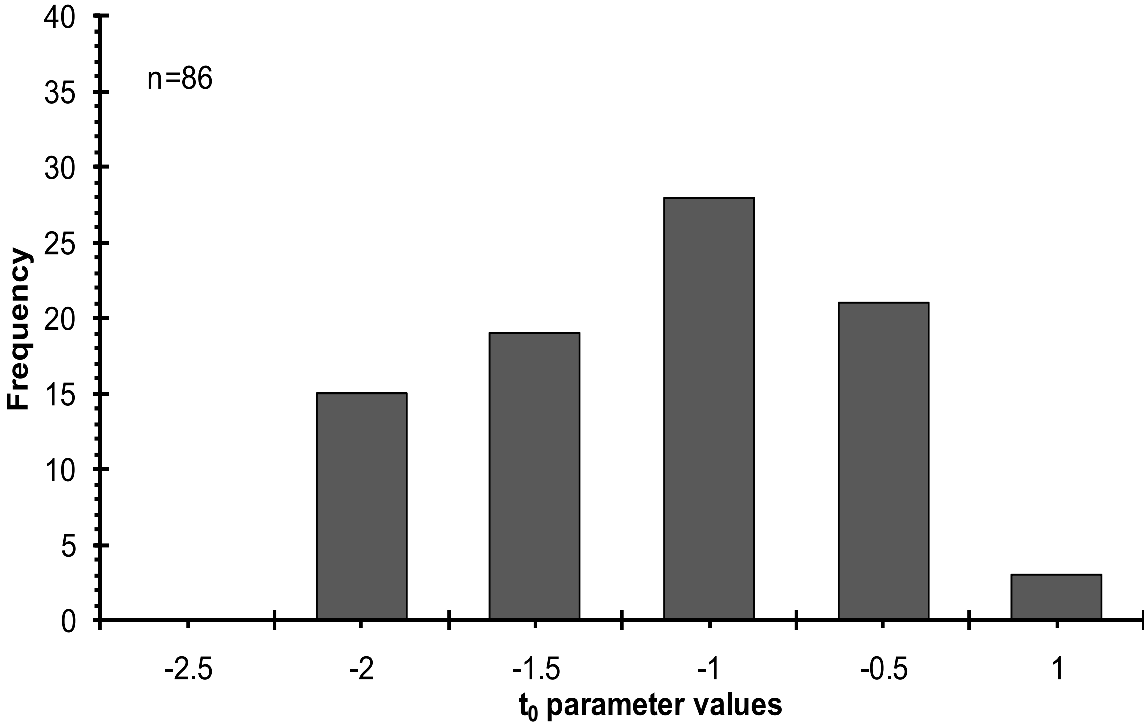

Figure 2.9- Individual t_0 parameter estimates of the von Bertalanffy growth model generated from the NLME method.

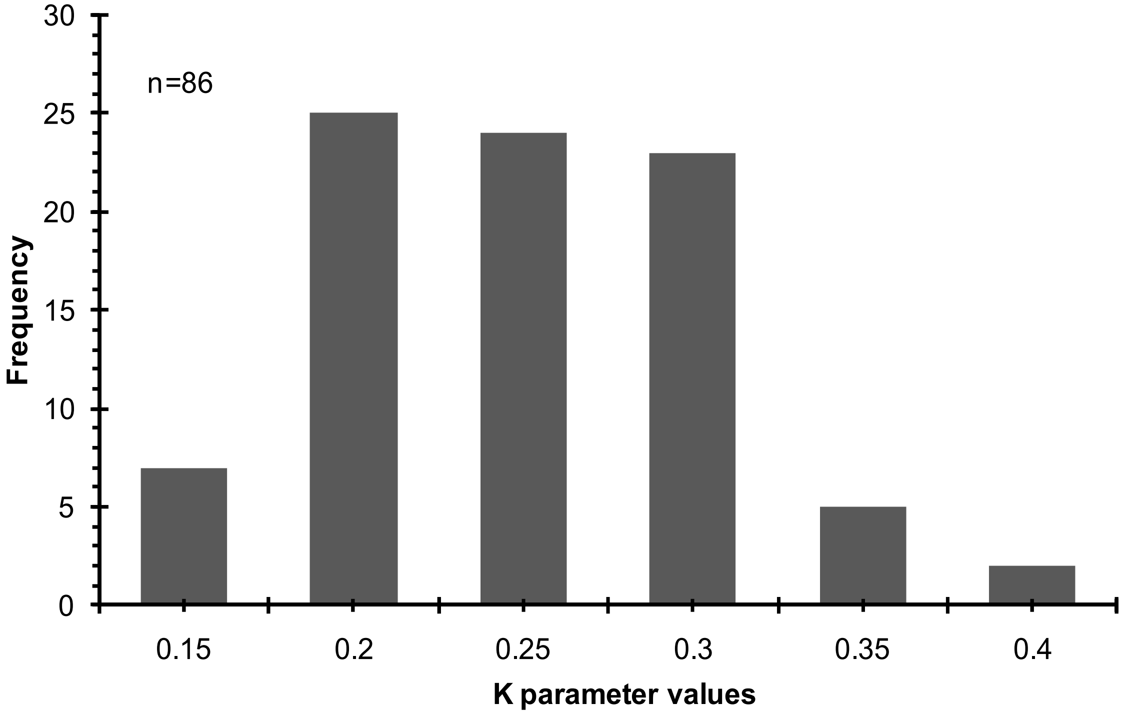

Figure 2.10- Individual K parameter estimates of the von Bertalanffy growth model generated from the NLME method.

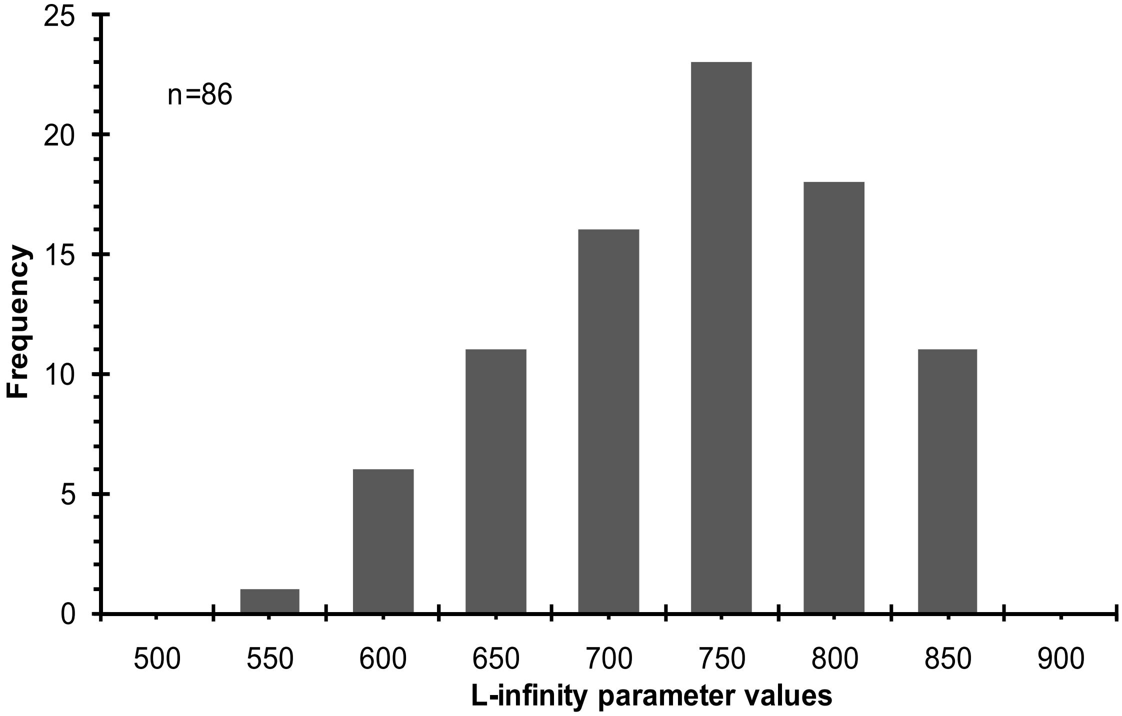

Figure 2.11- Individual L_∞ parameter estimates of the von Bertalanffy growth model generated from the NLME method.

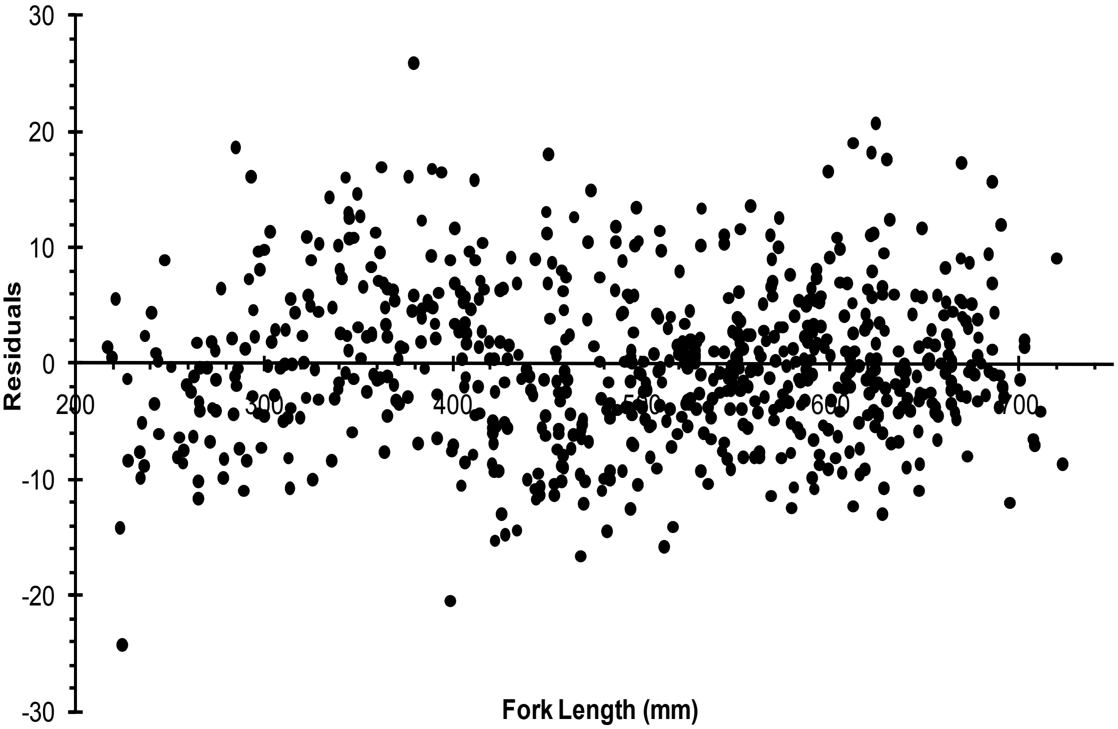

Figure 2.12- Residuals from a von Bertalanffy growth model fitted to Modified Fry back-calculation model results using a NLME method. Measurements from 86 bonefish provided 699 measurements.

Discussion

The NLME generated estimates of model parameters from a longitudinal, unbalanced, and auto-correlated dataset. The residual plot shows a good model fit throughout the entire data range (**Figure 2.12**). Thus, it was a useful method which provided parameter estimates at both the individual and population levels which can now be compared to parameter estimates from other methods.

2.8C Tag-recapture

Background

One of the primary sources of information used for estimating growth rates of fish is tagging studies. The length of a fish is measured and recorded when the fish is released and again when it is recaptured. The dates of release and recapture are also recorded so that the time at liberty is known. Tagging studies provide more than one observation per fish because a tagged fish is released to be recaptured at a later date and, thus, they provide valuable information about how individuals grow. A common method for estimating von Bertalanffy growth parameters is Fabens (1965) method which models the changes in length over the specified time.

Methods

The bonefish tag-recapture program began in 1998. Experienced bonefish anglers and professional bonefish guides were given tags and tagging supplies (tag applicator, datasheet, pencils, and a plastic container). Tags were placed in the dorsal area of the fish; the unique tag number was recorded along with the fork length and location, and then the fish was released.

Originally the project used Floy FD-94 T-bar anchor tags but in February of 2008 the project switched to Hallprint PDL dart tags. We switched to dart tags because a bonefish tag-recapture project in Hawaii using dart tags was getting tag retentions of more than 4 years (Harding 2010) while our study with T-bar anchor tags was not. In the 10+ years of the project the longest recapture was only 815 days (2.2 years). Since tagging does not cause mortality in bonefish (Baeza and Basurto. 1999) and estimates of bonefish natural mortality are low (Crabtree et al. 1996) it was assumed that tag shedding was the primary reason for the lack long-term tag recoveries (3 years or greater).

Fabens (1965) method was used to generate von Bertalanffy growth model parameters. This method models change in length of the fish over the time at liberty. The model is:

$$\Delta L = (L_{\infty} - L_t)(1 - e^{-K\Delta t}) \tag{2.15}$$

where ΔL is the change in length through the time period of Δt, L_∞ and K are same parameters as the von Bertalanffy growth model, and L_t is the initial length of the fish. The t_0 parameter cannot be estimated unless the absolute ages are known (Wang et al. 1995). Estimates of K and L_∞ are generated from minimizing the sum of squared difference between the observed ΔL and the expected ΔL.

Measurement error was quantified by evaluating the change in length between tag and recapture over short periods of time (10, 20, 30, 40, and 50 days). The distributions of change in length created for these time periods were evaluated to see if they captured measurement error without displaying growth, which would cause a right skewed distribution. The time period that provided the largest sample size and a non-skewed distribution was used to calculate the distribution of measurement error. To assess the impact of measurement error on the parameter estimates two different simulated tag-recapture datasets were created. The first dataset was 1,000 bootstrap draws of the tag-recapture data. The second dataset came from a Monte Carlo method where random values from the measurement error distribution were added to the initial length at release and a new size increment was estimated and then 1,000 random draws of the data were conducted. Fabens method (1965) was applied to each simulation to produce 1,000 estimates of the L_∞ and K parameters for each of the two datasets. All of the analysis was done in R software.

Results

A total of 8,340 anchor tags were deployed to produce 331 recaptures. The recaptured bonefish ranged from 327 mm to 750 mm FL (mean=590 mm FL). Only 7,840 of the total tagged fish had length data available and of the 331 recaptures length data was available at both tagging and recapture for 220 of them. Measurement error was estimated from the distribution of the change in size between tag and recapture for 30 days. This distribution was chosen because it appeared to follow a normal distribution, did not show any right skewed behavior, (**Figure 2.13**) which would suggest fish growth, and provided a sufficient sample size (n=29). The 30 days recaptures had a mean of 0.55 and a standard deviation of 9.248. The size-frequency distributions of released and recaptured bonefish (**Figure 2.14**) were not significantly different (Kolmogorov-Smirnov two-sample test, D=0.075, P=0.08). **Figure 2.15** displays the range of growth increments plotted against days at liberty.

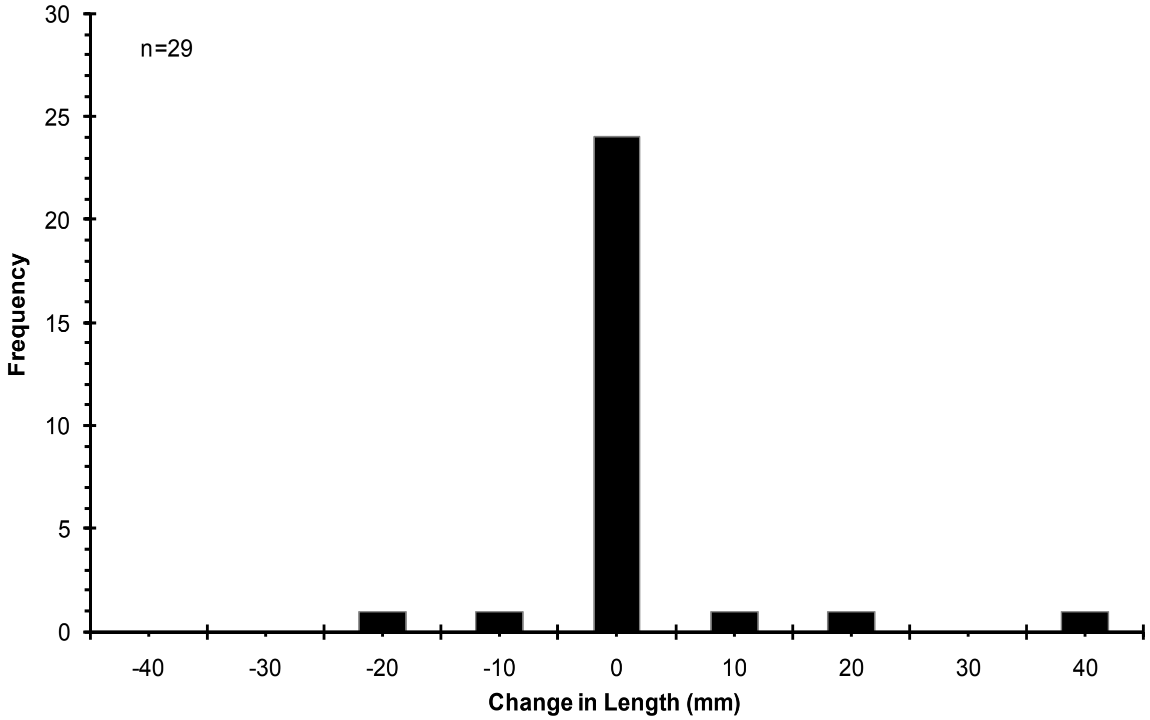

Figure 2.13-Distribution of change in length between tag and recapture for recaptures 30 days or less.

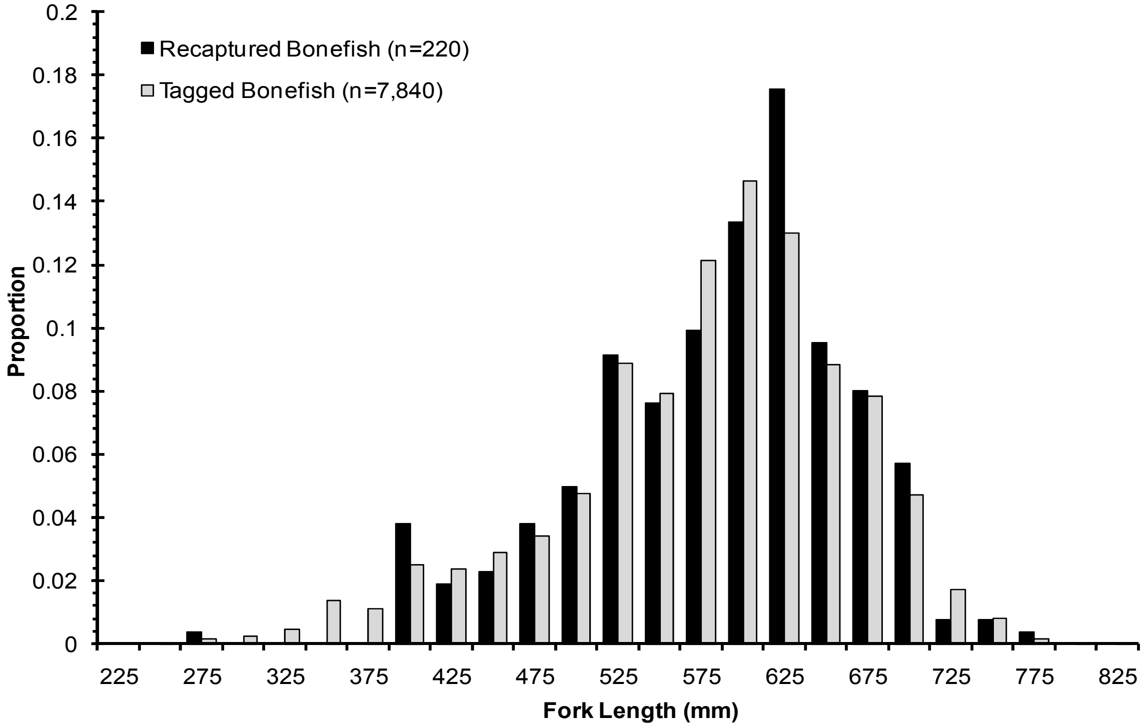

Figure 2.14- The proportion of bonefish separated into size bins for length at tagging (black bars) and at recapture (grey bars).

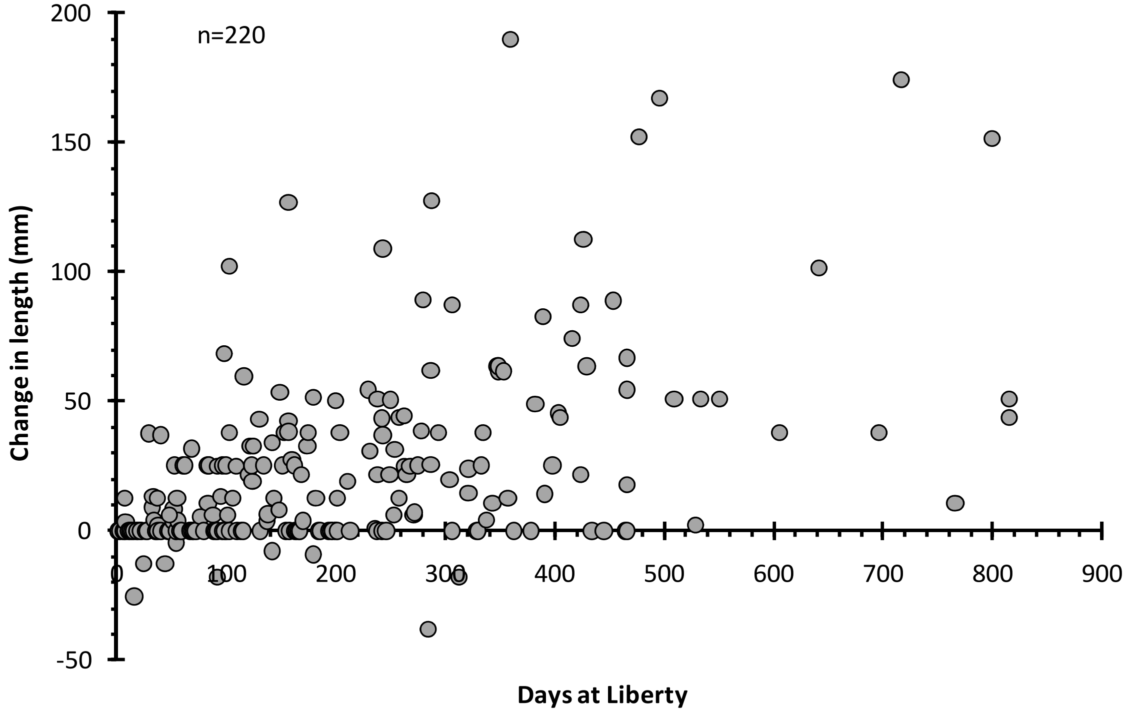

Figure 2.15- Change in length between tagging and recapture dependent on days at liberty.

The age-length section of this chapter found different growth rates between small (<440 mm FL) and large bonefish. Since only 8% (n=19) of the recaptured bonefish were in the small bonefish size range they were removed from the analysis. This was done to facilitate parameter comparison to the age-length and back-calculation estimates.

Fabens (1965) method was run on the large bonefish (>440 mm FL) and produced the parameter estimates of L_∞ = 694.1 (16.07 SE) and K = 0.3868 (0.0603 SE). The 95% confidence intervals for the parameters are L = 669.86 to 735 and K = 0.274 to 0.5002. **Figure 2.16** plots the residuals from the model fit.

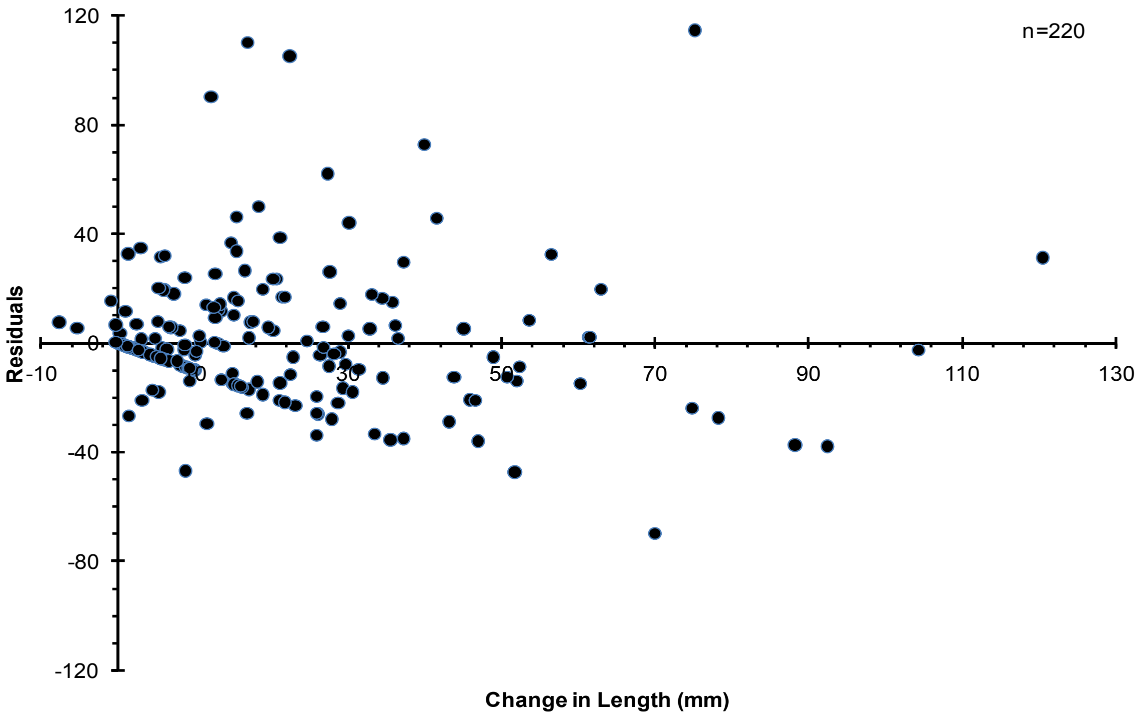

Figure 2.16- Residuals from fitting the tag data with Fabens (1965) method.

Incorporating measurement error into Fabens (1965) method provided different parameter estimates (L_∞ = 686.9 (0.5111 SE) and K = 0.4233(0.0022 SE)) than the unmodified bootstrapped tag data (L_∞ = 696.4 (0.5394 SE) and K = 0.3853 (0.00182 SE)). **Figure 2.17** shows the distributions for the parameter estimates from the bootstrapped tag-recapture data and the parameter estimates that incorporated measurement error.

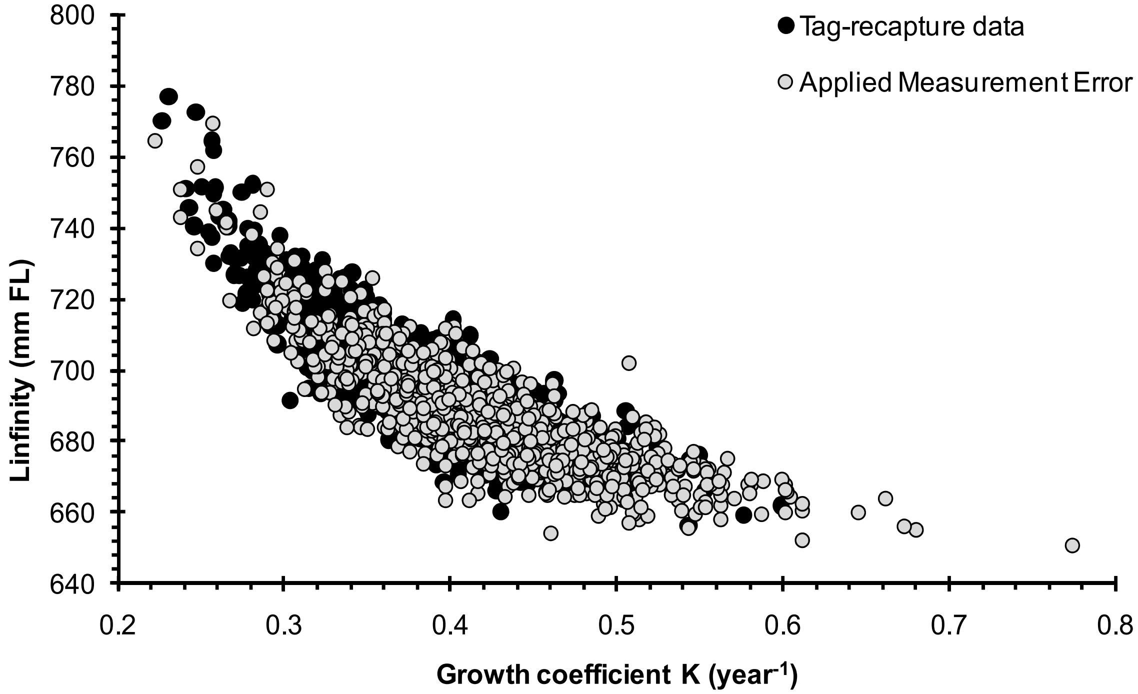

Figure 2.17- Growth curve parameter estimates derived from the Fabens (1965) method from 1000 simulations of two datasets. The black circles were generated from bootstrapped tag-recapture data with the overall parameter estimates. The grey circles are Monte Carlo simulation of the tag-recapture data that incorporated measurement error with the overall parameter estimates.

Discussion

The method of Fabens (1965) produced L_∞ growth model parameter estimates that were relatively similar to the estimates generated in the age-length and back-calculation sections. However, the K parameter values were much larger.

A problem with the fitted model was the residuals were not equally distributed among positive and negative values (**Figure 2.16**). Most (62%) of the residuals were negative. There were fewer positive residual values and they had a larger range of values (max positive residual = 114, max negative residual = -70). Therefore, the model fitting was biased. In addition to Fabens (1965) method, the models of Francis (1988) was also applied and resulted in implausible parameter values of K = 0.598 and L_∞ = 740.4. They were not plausible because the K value is more than twice the value estimated by Crabtree et al. (1996), section 2.8A, and section 2.8B, and the L_∞ parameter is greater than 5% larger than the L_∞ parameter generated from the other studies.

The tag-recapture dataset was problematic. One of the key assumptions when using tagging data to determine growth is the length of the fish is measured without bias and with a reasonable amount of precision, both at release and recapture. Measurement error tends to be large for fish measured alive at sea, especially in this case since the data was collected by volunteer fishermen. Evidence of this measurement error is the fact that 4% of the recaptures reported negative growth and 35% of the recaptures reported no change in length despite days at liberty greater than 400 days (**Figure 2.15**).

Another potential source for measurement error may have been rounding bias since the volunteers used imperial units (i.e. inches) and could have rounded the fish length to the nearest inch or 1/2 inch. The incorporation of measurement error into the data altered the parameter estimates. It caused the L_∞ values to decrease and the K values to increase (**Figure 2.17**). Both Wang et al. (1995) and Laslett et al. (2002) showed when measurement error is substantial it causes decreases in L_∞ and increases in K values.

A data requirement of using tag data to estimate growth is a wide range of recaptured fish sizes. **Figure 2.14** shows a wide range of bonefish that were recaptured but the majority of the recaptures (66%) are above 580 mm FL where growth slows down considerably and approaches the asymptote (**Figure 2.4**). The predicted growth model only changes 91 mm from age 7 (580 mm FL) to age 21. The relatively large variance of the measurement error (s.d. = 9.25) suggests it is greater than the reported change in length for most of the recaptures.

A significant problem with the tag-recapture data was the low recapture rate (3.9%). Many possibilities can explain this result such as a large stock size, high mortality rate, and/or shedding of the tags. These topics are addressed further in chapter 3.

Due to the potential flaws and biases of estimating growth from the tag-recapture data the parameter estimates will not be used or discussed further. More recaptures in the future could potentially increase the precision of parameter estimates; however, currently the potential problems outweigh the benefits.

2.8D Discussion of parameter estimation from different data and models

A comparison of the predicted Double Exponential growth curve and the back-calculated data provided an interesting result. The back-calculation results could falsely lead to the application of the von Bertalanffy growth model for all ages. This is because the back-calculated data is a good fit to the predicted curve for ages 1 to 2 and 5 to 20, however, ages 3 and 4 do not fit the predicted curve very well (**Figure 2.18**). Length-frequency distributions of ages 1, 3, and 6 from the age-length and back-calculated data were compared visually and statistically with Chi-squared goodness of fit tests with significance at the 5% level. The visual comparison of the ages (**Figure 2.19)** and the statistical test showed similarity in ages 1 (X^2=48, df=42, *P*=0.2426) and 6 (X^2=12.86, df=12, *P*=0.3795) but revealed a significant difference for age 3 (X^2=30, df=18, *P*=0.0375).

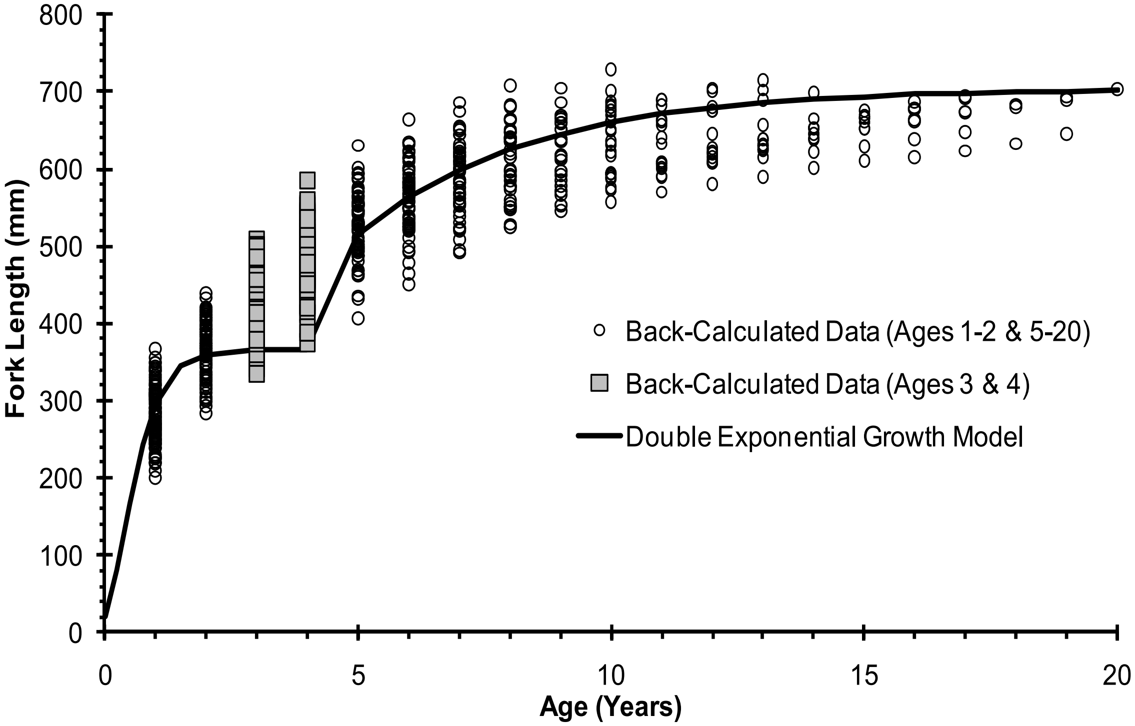

Figure 2.18- The predicted Double Exponential growth model plotted with the predicted lengths at age generated from back-calculation. Ages 3 and 4 (gray squares) of the back-calculated data were plotted separately from the other ages (open black circles) to show their separation from the predicted model.

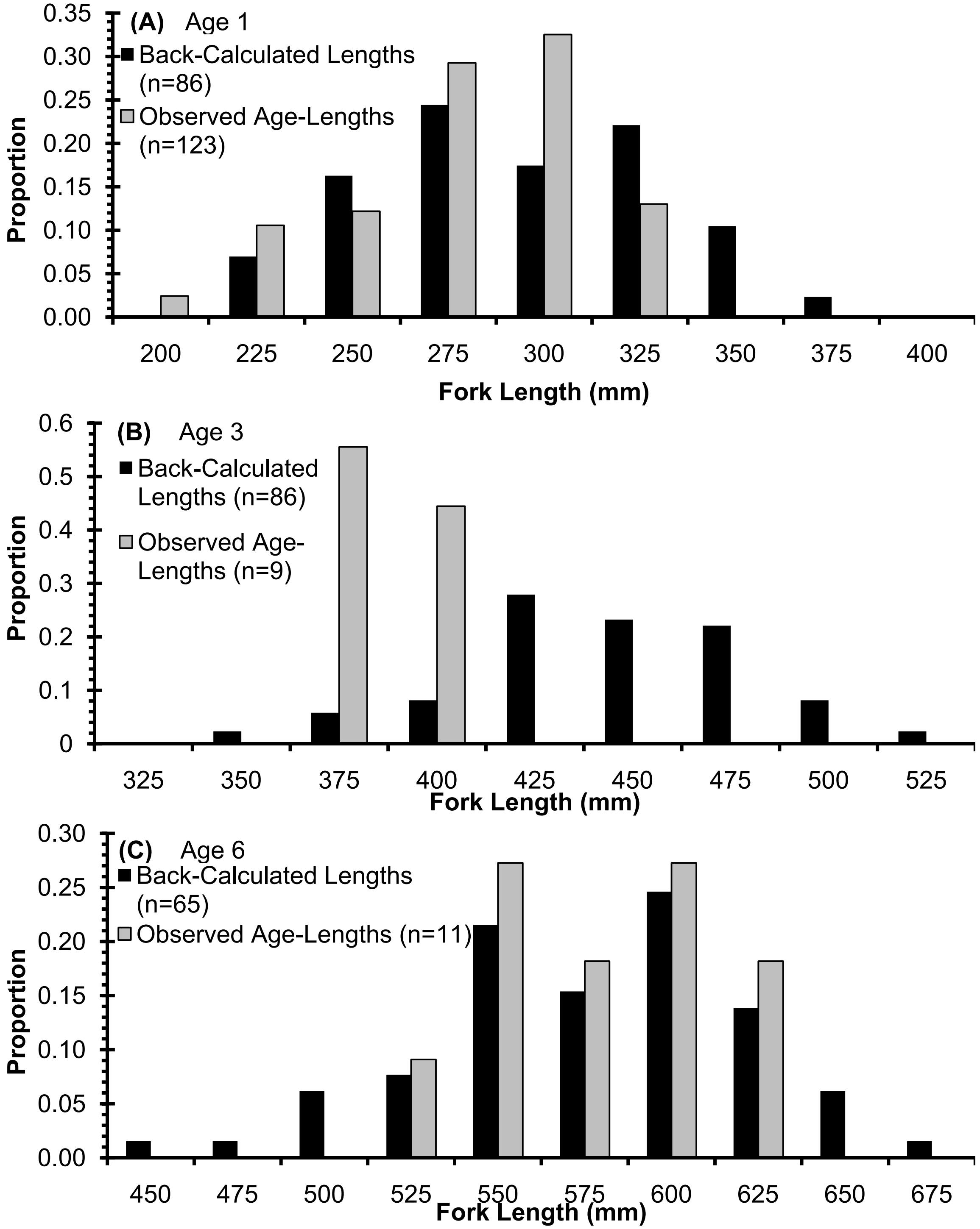

Figure 2.19- Length-frequency distributions of both back-calculated lengths and observed age-lengths for three age groups: (A) age 1; (B) age 3; and (C) age 6.

The age-length section of this chapter revealed different growth curves for small bonefish (<440 mm FL) than large bonefish. Since only the age-length database has a sufficient sample size of small fish, comparisons of the parameter estimates were only made for bonefish greater than 440 mm FL. These large bonefish produced similar von Bertalanffy parameters because the age-length and back-calculated databases had overlapping confidence intervals (**Figures 2.20, 2.21,** and **2.22**).

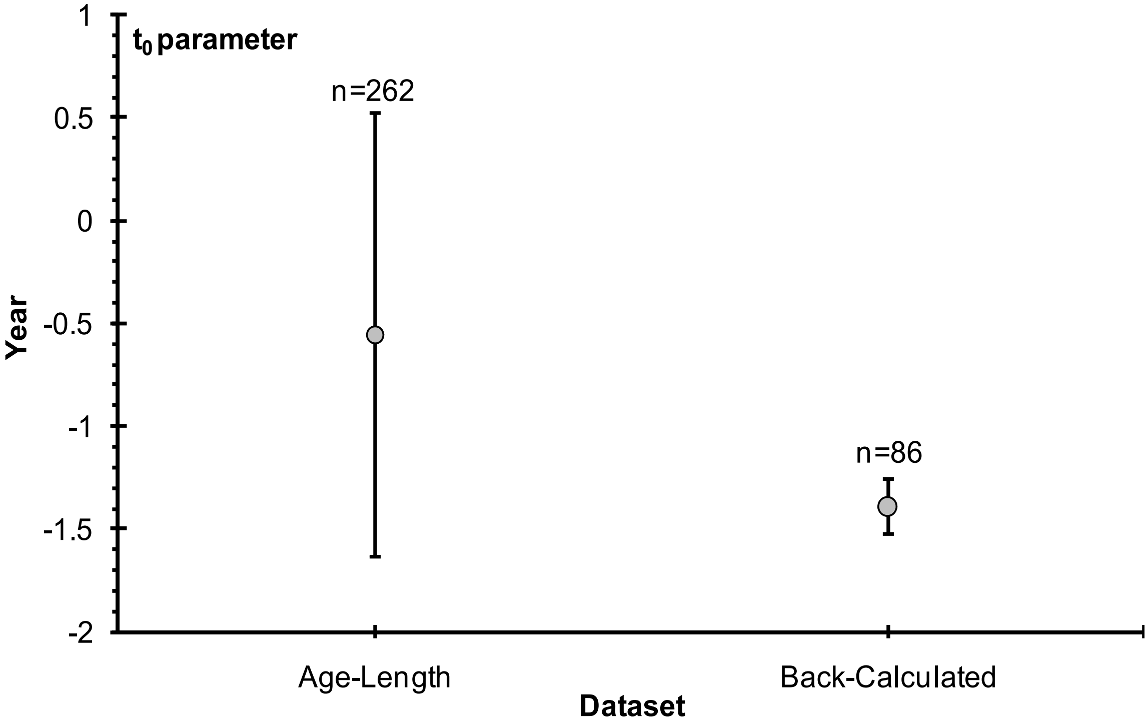

Figure 2.20- Comparison of the estimated t_0 parameter of the von Bertalanffy growth model from modeling growth from the age-length and back-calculated datasets. Bars denote 95% confidence intervals with sample sizes list on the top cap.

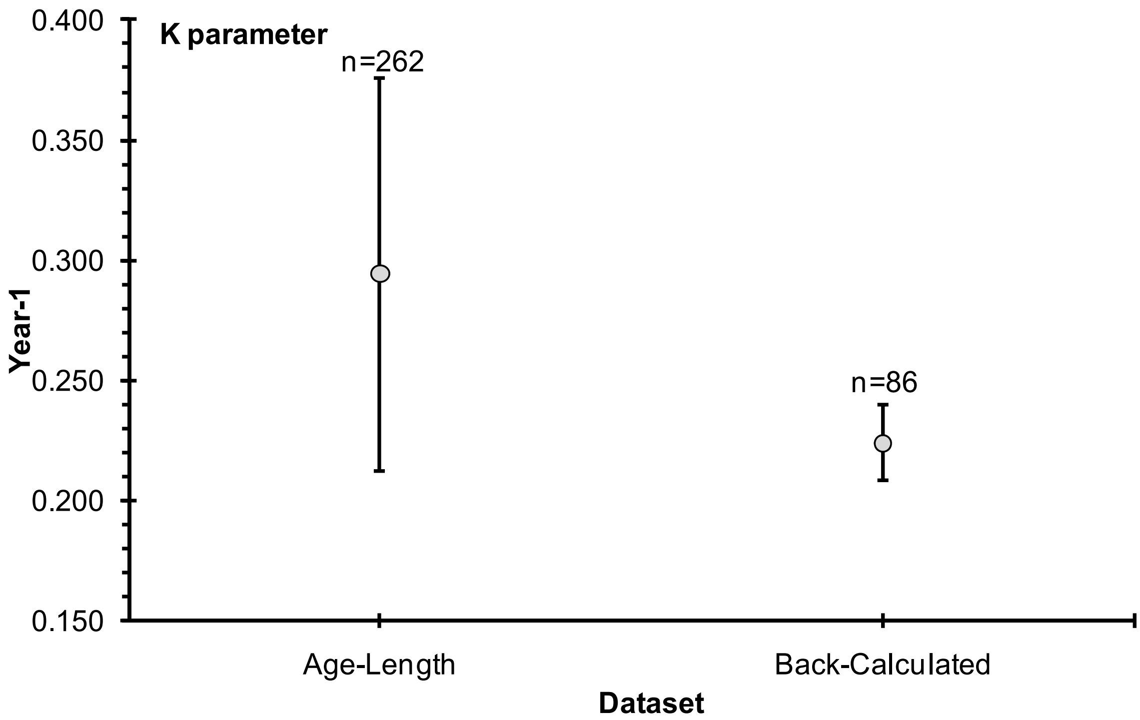

Figure 2.21- Comparison of the estimated K parameter of the von Bertalanffy growth model from modeling growth from the age-length and back-calculated datasets. Bars denote 95% confidence intervals with sample sizes list on the top cap.

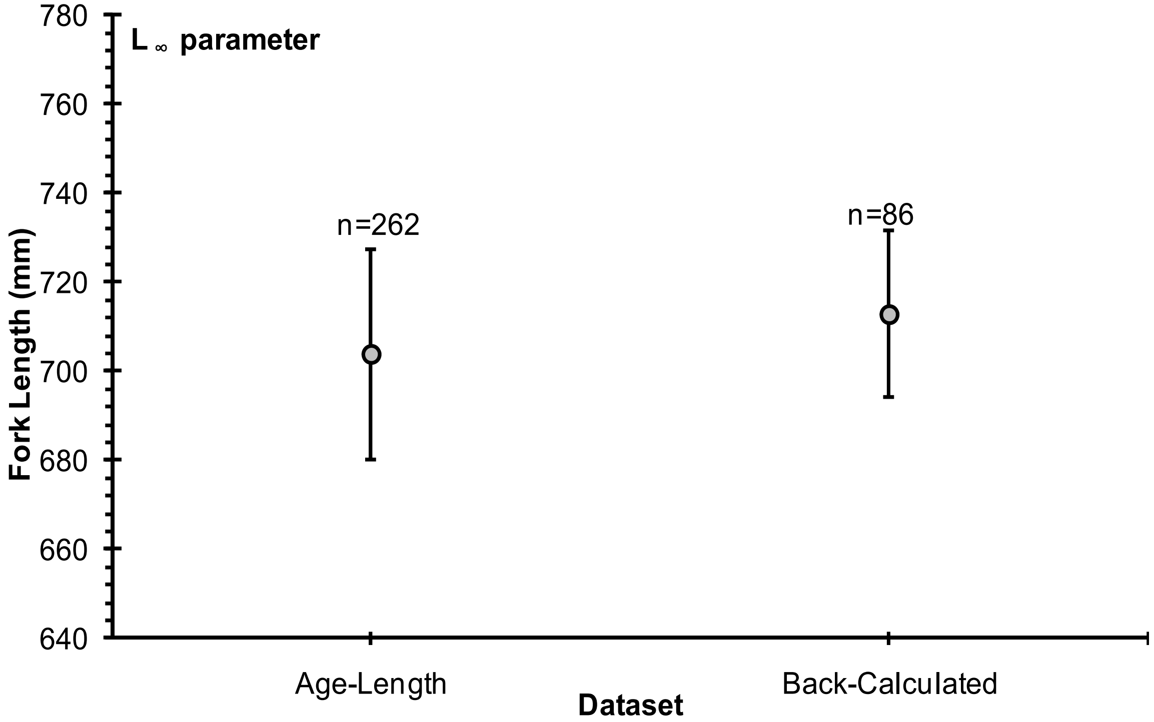

Figure 2.22- Comparison of the estimated L_∞ parameter of the von Bertalanffy growth model from modeling growth of the three different datasets. Bars denote 95% confidence intervals with sample sizes list on the top cap.

The observed age-length dataset provided robust parameter estimates relatively similar to estimates generated from back-calculation. The age-length data included the daily age of the juvenile bonefish which was not available in the other datasets. This created a more complex von Bertalanffy growth equation that modeled the entire bonefish lifespan, and provided insight into the biology of the fish that was previously unknown. Therefore, the Double Exponential growth model from the age-length dataset will be used to model bonefish growth in future applications.

2.9 Selectivity

Selectivity was addressed by first creating an age-length key from the otolith derived ages and length data of this chapter (section 2.8A) following the method of Isermann and Knight (2005). The age-length key was applied to the anchor tagging length frequency dataset when length data were available (n=7,961) (**Figure 2.1**). This led to conversion of lengths to ages. Selectivity of bonefish for each age (s_a) was modeled as a sigmoid-shaped logistic curve

$$s_a = \frac{1}{1+e^{-(a-a_{50})/d}} \tag{2.16}$$

where the parameters a_{50} and d were obtained by fitting the curve to the relative frequency of ages. The a_{50} parameter is the age of 50% selectivity.

Full selectivity was at 6 years (72 months) (**Figure 2.23**). The logistic curve representing selectivity vector by monthly age was created by first creating an age-length key from the age The sigmoid-shaped logistic curve representing vulnerability had the parameter values of a_{50} = 3.713 and d = 0.183.

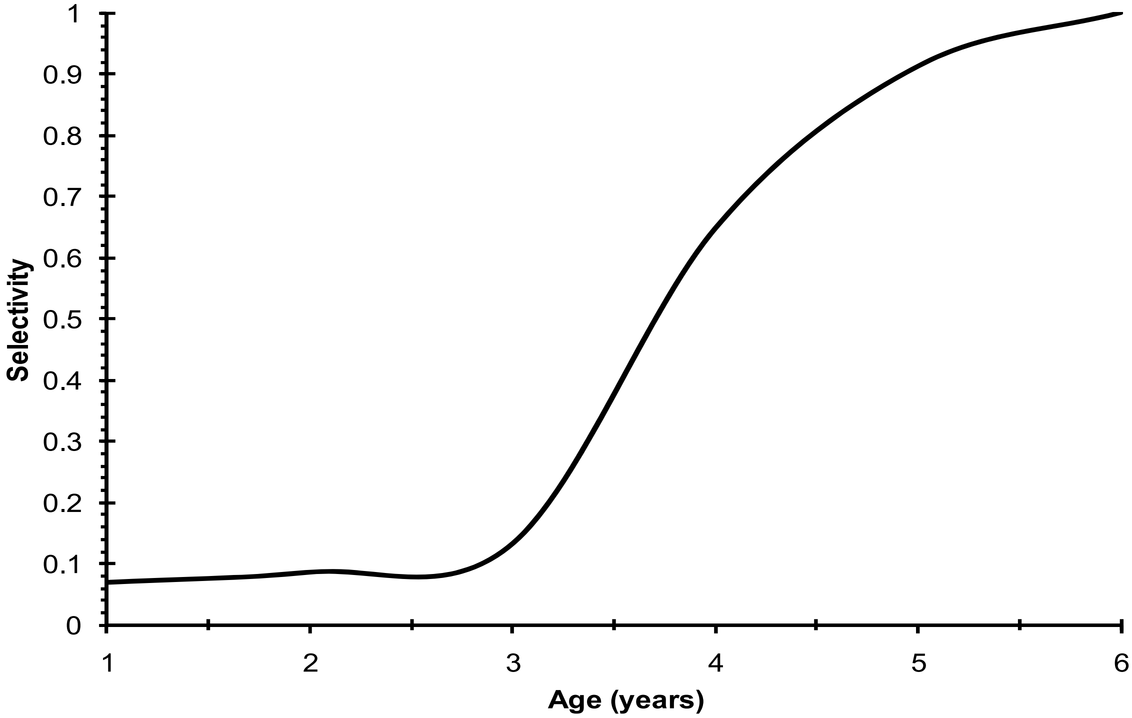

Figure 2.23- Selectivity curve created from application of an age-length key to the anchor tagging length frequency dataset.

2.10 Bonefish population structure in south Florida waters

Background

The population structure of the bonefish stock of the Western Atlantic has received some attention. Robins et al. (1986) described two species of bonefish in the Atlantic: *Albula nemoptera* and *Albula vulpes,* and separated them by the shape of the dorsal fin, anal fin, and the number of lateral line scales. *A. nemoptera* is found in the northern South America waters (Columbia to Brazil), whereas, *A. vulpes* is found in the entire Caribbean Sea, including Florida. Colborn et al. (2001), Bowen et al. (2008), and Adams et al. (2008) examined the nucleotide differences occurring in the mitochondrial DNA cytochrome-b gene and reported an additional bonefish species (*A. species B*) in south Florida waters.

The problem with the genetic identification of *A. species B* is that it is only based on one gene in the mitochondrial DNA, and ignored other factors. Smith et al. (1995), Seberg et al. (2003), and Will et al. (2005) argue that species should not be determined by one factor or gene but by assessment of morphological, ecological, behavioral, genetic and reproductive independence. Morphology was chosen to evaluate bonefish speciation because: (1) it has been used as a powerful tool for determining differences within and among species (Ihssen et al. 1981; Melvin et al. 1992); (2) historically, phenotypic traits such as morphology were the basis for determining speciation in fishes (Hanne et al. 2008); (3) the body shape of fishes has ecological and evolutionary relevance (Klingenberg et al. 2003); and (4) different species will possess different anatomical characteristics (Campbell 1993).

Historically a discriminant function was applied to morphometric data to determine differences within and among species (Amos et al. 1963; Messieh 1975). Recently principal components analysis (PCA) techniques have become more prevalent (Trapani 2003; Quilang et al. 2007). Both methods will be applied to investigate the combination of morphology and speciation.

Methods

A range of bonefish sizes were collected in south Florida waters. Twelve different morphometric measurements and weight were recorded. Standard morphometric measurements of total length, fork length, standard length, and girth were collected along with the body morphometric measurements of pectoral-fin-to-fork, anal-fin-to-fork, dorsal-fin-to-fork, and caudal peduncle (**Figure 2.24**) as used by Banerji (1981). The head morphometric measurements of head length, snout length, eye diameter, and post-orbital head length (**Figure 2.25**) were recorded following Serafy et al. (1996). Measurements were taken to the nearest mm and weight was measured to the nearest gram.

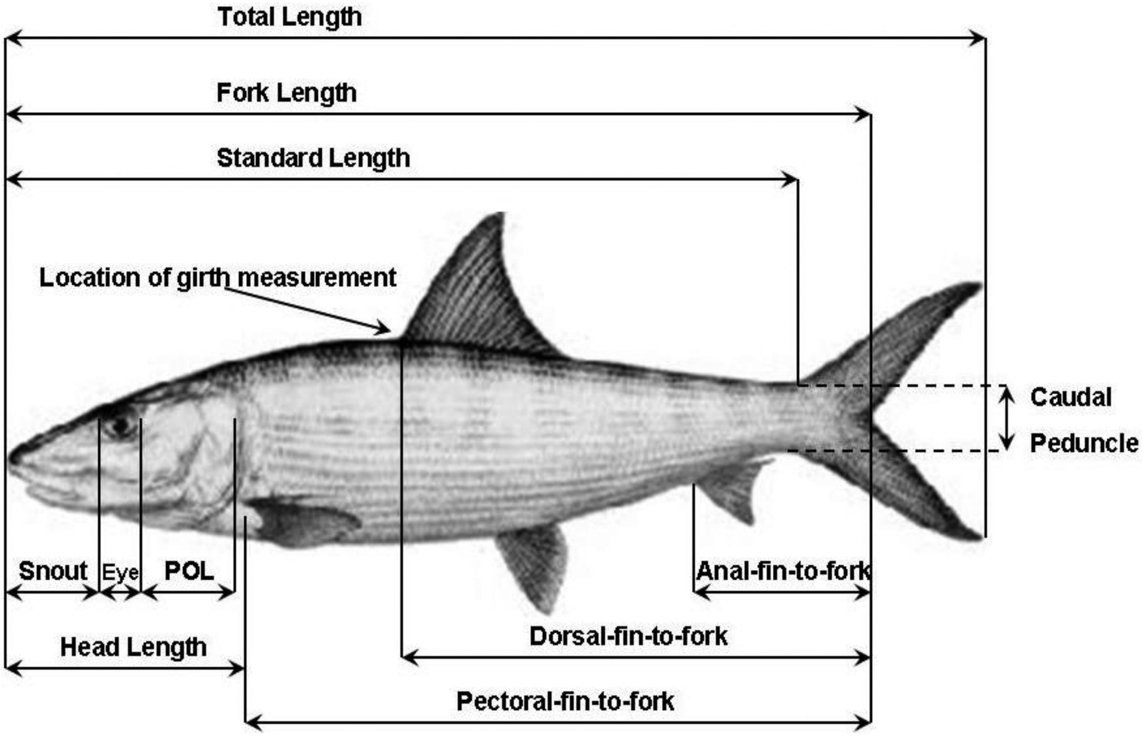

Figure 2.24- Diagram depicting body morphology measurements made in the bonefish population structure analyses.

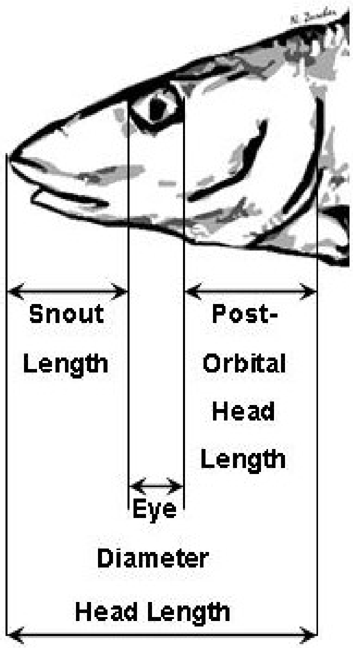

Figure 2.25- Diagram of the four head morphology measurements used in bonefish population structure analysis.

Every fish had a small triangular piece (10mm x 10mm x 10mm) cut from the soft ray tissue at the rear of the dorsal fin and stored in 95% ethanol. The tissue samples were sent to the Florida Fish and Wildlife Research Institute (FWRI) in Saint Petersburg, Florida (http:research.myfwc.com) where genetic assays were run on the mitochondrial DNA cytochrome-b gene. Details of the assays can be found at Adams et al. (2008).

Multivariate methods were applied to the data and compared to the genetic results. Discriminant analysis was done in SAS statistical software (1997) to classify individual fish into putative species. A stepwise variable selection procedure based on calculated F values and F-test significance at P=0.05. Principal components analysis was conducted with Matlab software (Mathworks Inc. 2000) to evaluate the structure of the morphometric data.

Genetic results were combined with the age and growth data from section 2.8A. This allowed evaluation of the age-length relationship for each species.

Results

Morphometric measurements and weights were collected from 268 bonefish collected from south Florida waters. The bonefish ranged from 28 to 740 mm FL with an average of 371 mm, and were collected from March 2003 to January 2010. The genetic results were available for 201 (75%) of the samples, and determined 61 are *A. Species B* and 140 are *A. vulpes*. There was a strong size component with most of the small fish identified as *A. Species B* and most of the large fish as *A. vulpes* (**Figure 2.26**). *A. Species B* ranged from 28to 285 mm FL and *A. vulpes* ranged from 38 to 740 mm FL.

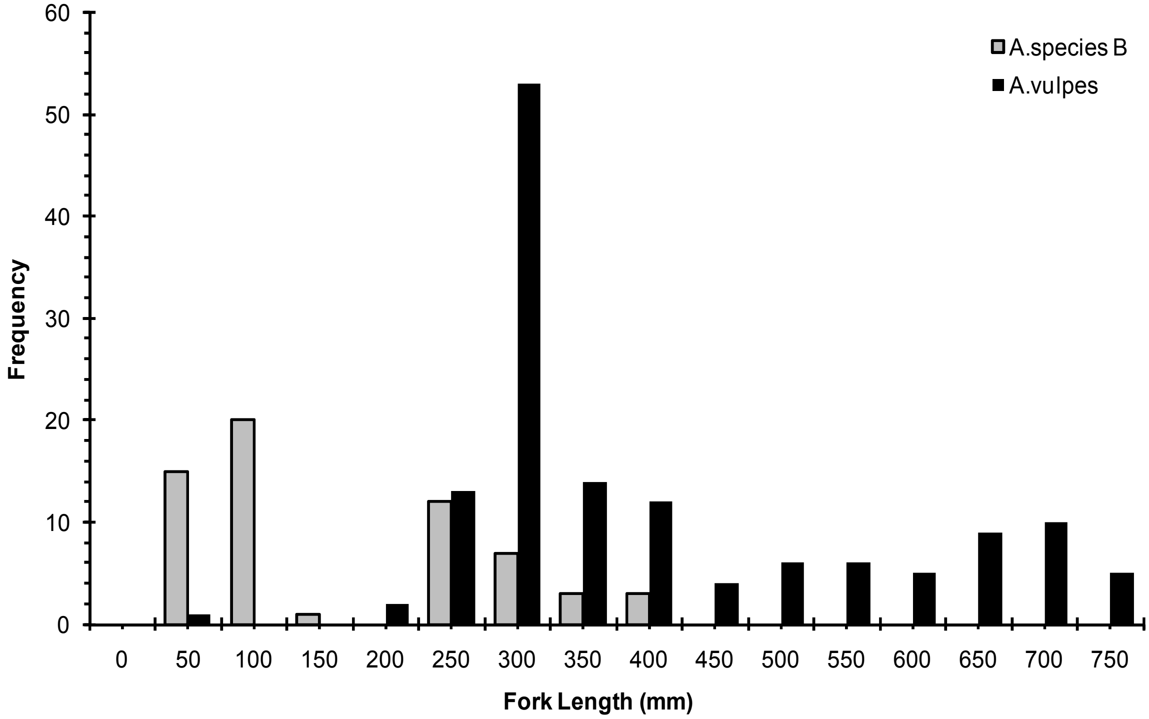

Figure 2.26- Length frequency of bonefish collected for population structure analysis. Gray bars were identified by genetic analysis as *A. Species B* (n=61) and black bars are *A. vulpes* (n=140).

The morphometric data was corrected for body size by dividing each variable by total length. The discriminant function analysis determined 7 significant variables between the species: fork length, standard length, head length, post orbital head length, snout length, eye diameter, and weight, each divided by total length. The three most dominant variables were post-orbital head length (F-value = 269.85, F-test P<0.0001), eye diameter (F-value = 13.60, F-test P=0.0003), and standard length divided by total length (F-value = 42.22, F-test P=0.0001) (**Figure 2.27**). The discriminant function is:

$$D = \frac{65FL}{TL} + \frac{74SL}{TL} - \frac{177.6HL}{TL} - \frac{212PO}{TL} - \frac{251ST}{TL} + \frac{580ED}{TL} - \frac{1.33WT}{TL} \tag{2.17}$$

where if D>60 then the classification is *A. Species B*, otherwise it's *A. vulpes*. The cross validation classification results were 93.44% of *A. Species B* classified correctly and 99.29% of *A. vulpes* were classified correctly. A close examination of the function revealed that bonefish less than 300 mm FL were classified as *A. Species B*, the function switched to classifying the fish as *A. vulpes* around 300 mm FL. A closer look at the three most dominant variables in the function shows overlap between species when bonefish are of similar sizes (**Figure 2.27**).

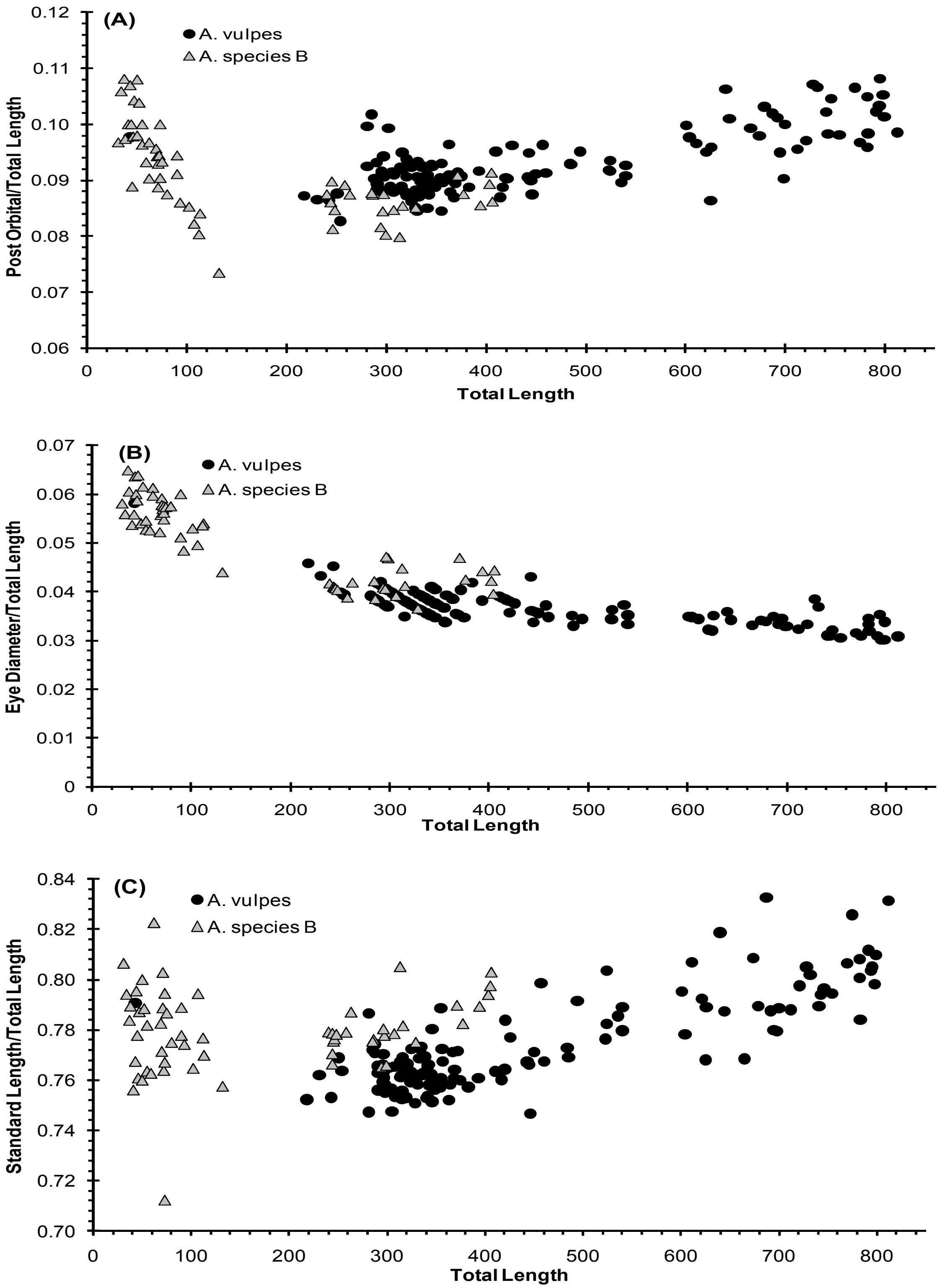

Figure 2.27- The three most dominant variables of the discriminant function plotted by species. The three variables are (A) post orbital, (B) eye diameter, and (C) standard length divided by total length. Gray triangles are identified as *A. Species B* (n=61) and black circles are *A. vulpes* (n=140). All variables were measured in mm.

The first and second axes of the PCA show that putative species is highly correlated with size (**Figure 2.28**). Individuals clustered together following a curve in PC space. There was a great degree of overlap for bonefish species when fish of similar sizes were available.

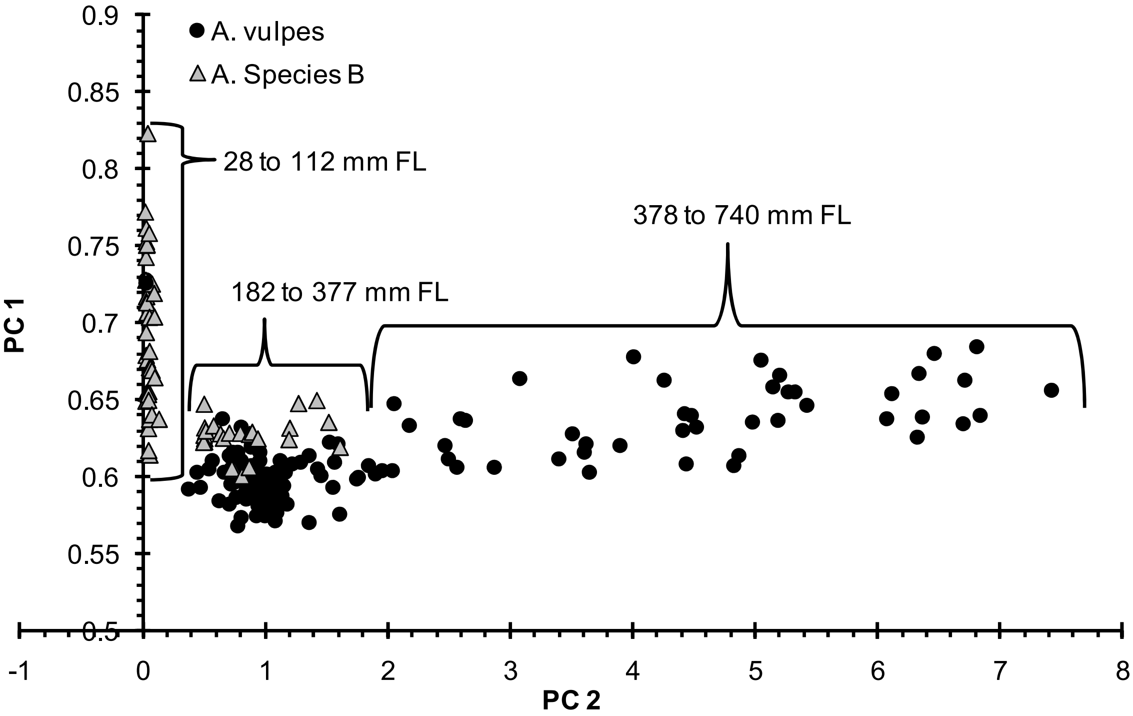

Figure 2.28- Principal component analysis results from morphometric measurements plotted with the genetics species identification for 201 bonefish from Florida waters. Data points were labeled with three fork length ranges.

Both genetic results and age-length information were available for 190 samples (*A. species B*, n = 39; *A. vulpes*, n = 151). A plot of data (**Figure 2.29**) for sizes that overlap (28 mm to 300 mm FL) shows similar age-length relationship between species. Unfortunately, only one *A. vulpes* sample was available at a very small size (age = 0.208, FL=38) and no age-length data was available for *A. species B* larger than 285 mm FL. These gaps in the data hindered model fitting and prevented a valid comparison.

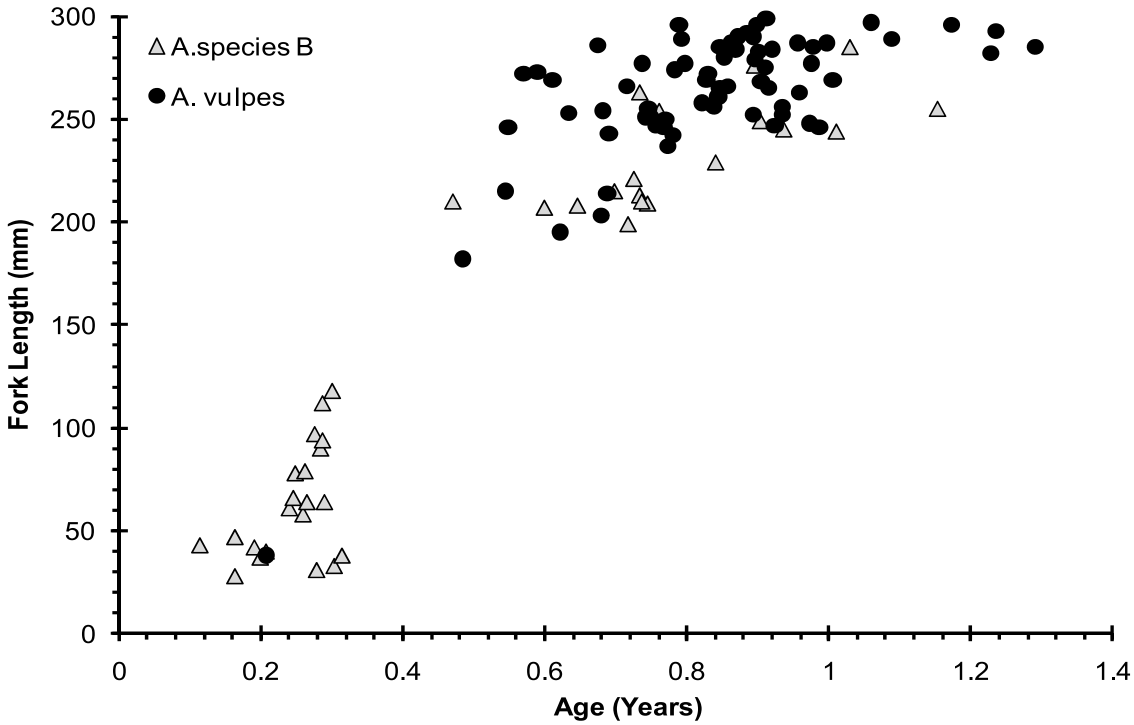

Figure 2.29- Observed age-length data less than 300 mm FL for *A. Species B* (n=39) and *A. vulpes* (n=151).

Discussion

The discriminant function analysis found a difference that reflected the genetic results, however, this was misleading because it simply predicted the small fish as one species and the larger fish as another. When the species overlapped in size (around 300 mm FL) the function misclassified the species. This was further illustrated in **Figure 2.27** showing overlap in species when fish were of similar lengths. The PCA did not show any distinct groupings, which is in contrast to the PCA results run on other fish species (i.e. cichlid morphometrics, Trapani 2003). Instead, Florida's bonefish clustered together following a curve in PC space relating to length despite the fact that each variable was adjusted with total length. The curve suggests that the body dimensions undergo some transformation with ontogenetic development (i.e., ageing) as the fish grows larger which supports both the observed data and growth model shown in **Figure**

2.4. Crabtree et al. (2003) analyzed a wide array of eleven morphometric and eleven meristic characters of the two species but did not determine any differences. The combination of my species project with the work of Crabtree et al.'s (2003) resulted in thirty-five measurements that did not produce clear and consistent differences between species for all lengths.

Wallace and Tringali (2010) looked at the same meristics that Crabtree et al. (2003) examined and declared a distinction among species. However, Wallace and Tringali (2010) only examined seven fish and failed to review and reference the previous work of Crabtree et al. (2003). In contrast, Crabtree et al. (2003) had a sample size of 64 and found overlap in all their morphometric and meristic results.

Morphometrics are not the only feature these two presumptive species share. Similar age-length relationships are shown in **Figure 2.29**. Also, Bowen et al. (2008) found that the two species overlap in space and occupy the same habitats. Evolutionary theory implies that when similar species overlap in space and time one of two outcomes is inevitable: (1) either they will diverge in ecological traits; or, (2) one species will out-compete the other to point of exclusion or extinction. A possible explanation of coexistence is that these presumptive species may occupy cryptic and distinct, but unrecognized, ecological niches. However, the two species of bonefish coexisting in Hawaiian waters show very little mixing based on beach seining and catch data (Shaklee and Tamaru 1981; Friendlander et al. 2008). The coexistence of two bonefish species with identical growth curves in the same habitat in Florida therefore seems unlikely.

Additional evidence to contradict the Florida bonefish speciation results are that bonefish are highly mobile with recorded movements greater than 300 km (Larkin et al.

2008). The marine environment, in contrast to terrestrial and freshwater environments, often lack physical barriers that restrict mixing of populations. This leads to mixing of organisms, primarily eggs and larvae, over appreciable distances (Palumbi 2001, Knutsen et al. 2003).

It is likely that the south Florida's bonefish stock is comprised of only one species. This is supported by: (1) misclassification of the disciminant function when the two species are of similar lengths; (2) PCA results showing bonefish morphometrics are not independent by species; (3) similar age-length relationships; and, (4) the fact that both species are frequently caught together. The evidence suggesting two bonefish species in south Florida waters are differences in the cytochrome-b gene of the mitochondrial DNA. Future work should utilize more than one gene because most contemporary speciation analyses are using both multiple mitochondrial and nuclear genes (Gonzalez and Labarere 2000). Will et al. (2005) argues that multiple genes are needed to reliably identify clades, and a single mitochondrial DNA gene approach will fail to recover phylogenetically and biologically units. Moritz and Cicero (2004) state that mitochondrial DNA is not sufficient as a criterion for delineating species without biological evidence. This project depended on the geneticist of the FWRI. Attempts were made to get FWRI staff to explore more than one gene and to apply the same genetic methods used to determine bonefish species in the Pacific ocean (protein electrophoreses, Shaklee and Tamaru 1981). However, budget constraints and staff limitations prevented them from pursuing further genetic work.

Additional work is warranted because at the present time the bonefish speciation issue is unresolved. Since the majority of the research results suggested one species I will make this assumption for the remainder of the project.

2.10 Population Dynamics Discussion

Key life history and demographic data are needed to assess the risks of increasing and intensifying exploitation effects on bonefish resources. This chapter provided an overview of available population dynamics literature, and a summary of population dynamic parameters are described in **Table 2.6** and given in **Table 2.7**. Lifetime growth and life span was addressed. This information is needed to define lifetime expectation of survivorship and determine the stock's sensitivity to exploitation. Thus it is critical for a robust assessment of the bonefish stock.

Table 2.6- Parameters, definitions, and units for population dynamics variables for bonefish in south Florida.

Parameter	Definition	Units
M	Instantaneous natural mortality	per year
t_λ	Maximum age	years
A	Double Exponential Parameter A	dimensionless
B	Double Exponential Parameter B	dimensionless
C	Double Exponential Parameter C	dimensionless
L_∞^L	Ultimate Length	mm FL
K^L	Brody growth coefficient	per year
t_0^L	Age at which length equals 0	years
W_∞	Ultimate Weight	grams
L_m	Length at 50% maturity	mm FL
t_m	Age at 50% maturity	years
α_{WL}	Weight-length parameter	dimensionless
β_{WL}	Weight-length parameter	dimensionless
FEC_a	Fecundity parameter a	dimensionless
FEC_b	Fecundity parameter b	dimensionless

Table 2.7- Population dynamics parameters for bonefish in south Florida.

Population parameters														
M	t_λ	A	B	C	L_∞	K	t_0	W_∞	L_m	t_m	α_{WL}	β_{WL}	FEC_a	FEC_b
0.1498	21	365.4	2.905	-2.625	703.8	0.294	-0.558	5,580	488	4.2	5.27E-06	3.1696	1.936	1.131

Chapter 3

A mail survey to estimate the fishery dynamics of southern Florida's bonefish charter fleet[1]

Summary

Bonefish, *Albula vulpes* (L.), support an economically important recreational fishery in southern Florida, USA that has received little scientific study and has never been adequately assessed. A mail survey of 322 captains that comprise the southern Florida bonefish charter fleet was conducted to acquire a baseline understanding of the primary fishery statistics. The response rate was 59%, and a follow-up telephone survey of nonrespondents indicated no non-response bias. Experience in the fishery ranged from 3 to 61 years. The annual fishing effort was 30,875 boat days. The majority of the fleet fishing effort occurred in the northern Florida Keys and is presumed to reflect bonefish abundance. The instantaneous mortality rate of released fish was 0.11 year^{-1}. The majority of the respondents indicated that the bonefish stock had declined over the past decade.

Background

Bonefish, *Albula vulpes* (L.), support important recreational fisheries throughout the tropical central western Atlantic Ocean (Colborn et al. 2001; Ault 2008). In southern Florida, which includes the Florida Keys, bonefish are primarily found in nearshore waters from Key Biscayne to the Marquesas (**Figure 3.1**), with catches rarely made outside this range. Southern Florida is home to the world's most popular recreational

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[1] Fisheries Management and Ecology, 2010. Vol. 17, pp.254-261.

bonefish fishery because of the availability of large bonefish [i.e. >760 mm total length, > 4 kg; average fish caught is > 563 mm fork length (Larkin et al. 2008)]. More than 68% of the saltwater fly rod and saltwater line class world records for bonefish listed by the International Game Fish Association were caught in southern Florida coastal waters (International Game Fish Association 2009).

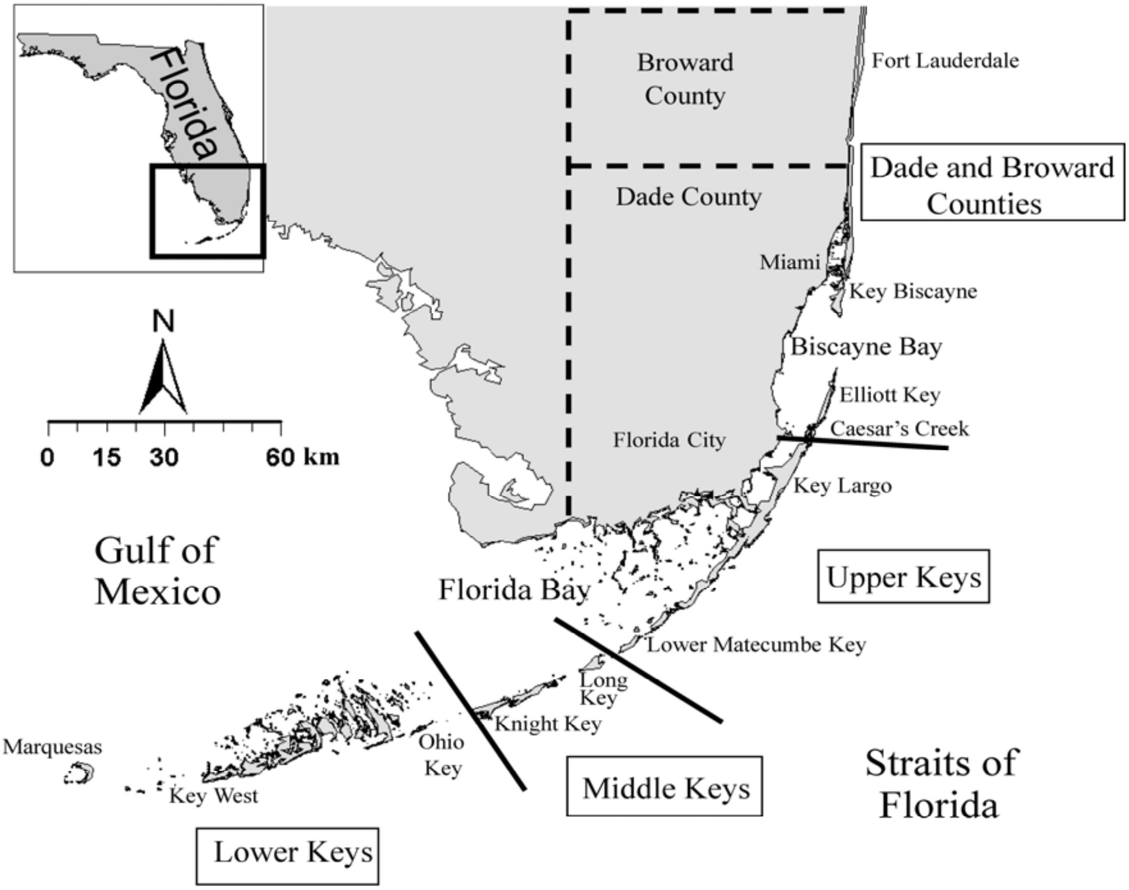

Figure 3.1- Map of southern Florida illustrating the area over which the bonefish fishery occurs and the geographic regions defined for purpose of analysis.

Southern Florida has experienced some drastic changes over the years. There have been rapid and substantial growth of both human populations and exploitation from recreational fishing fleets during the past several decades, as well as abrupt environmental changes due to extensive coastal development (Porter and Porter 2001; Ault et al. 2005c). Evidence of resource declines and overfishing of important coral reef snapper-grouper fisheries in the Florida Keys has already become apparent (Ault et al. 1998; Ault et al. 2005b). Understanding the dynamics of the bonefish population and its southern Florida fishery is paramount to management and conservation of this fishery.

The bonefish fishery is not only experiencing drastic changes but there is also a dearth of scientific knowledge on bonefish biology, ecology and population dynamics; in addition, very little is known about the dynamics of the southern Florida fishery to guide management strategies (Ault et al. 2008a). Because few data on fishery catches and landings have been recorded, interviewing experienced captains about the history and status of the fishery can be an important source of information (Matlock 1991). A survey of the captains was designed to elicit key information on critical issues concerning stock status and fishery dynamics such as number of captains in the bonefish fishery, years in the fishery, fishing effort, annual release mortality rate and changes in stock abundance.

Methods

Survey design

To collect data on southern Florida's bonefish stock and its fishery, a mail survey was designed for captains participating in the bonefish charter fleet who had extensive knowledge of the fish and the fishery. A mail survey was chosen over other survey methods because, on balance, the advantages and disadvantages of mail surveys were the best match for the information sought. Mail surveys are cost-effective, allow anonymity that increases the likelihood of receiving honest responses, allow longer and more complex questions and provide respondents more time to consider questions and provide accurate answers. Disadvantages of mail surveys are that the questionnaire must be easy to understand, they have relatively long completion times, and they have the potential for non-response and recall bias. The survey instrument was designed to benefit from the advantages and reduce the disadvantages. This was done while eliciting information on critical issues such as number of captains in the bonefish fishery, years in the fishery, fishing effort reflecting the total effort units exerted on a stock in a given time period, bonefish mortality rate and perceived changes in stock abundance.

The survey instrument was mailed to individuals that were licensed bonefish captains in southern Florida. The comprehensive sampling frame was compiled from various lists that included: (1) captains that participated in bonefish tournaments held throughout southern Florida; (2) captains with permits to operate charters in Everglades National Park; (3) volunteer captains in the University of Miami's bonefish tagging program (Humston 2001; Ault et al. 2002a; Larkin et al. 2008; www.bonefishresearch.com); and (4) interviews with bonefish captains and tackle vendors throughout southern Florida that subsequently referred us to other bonefish captains. This was considered to be close to a comprehensive sampling frame.

The survey asked respondents to provide information for an entire year. To reduce recall bias, the survey was mailed at the beginning of the 2002 calendar year (January), which corresponded to the end of the seasonal peak in bonefish fishing effort. Data from an earlier pilot survey suggested a bimodal distribution of annual fishing effort with peaks in the spring (April) and autumn (November) (Humston 2001). To increase response rate, the survey sampling procedure included a three-phased mailing following the “total design method” outlined by Dillman (1978) and included a raffle with monetary rewards (Goodstadt et al. 1977; Pollock et al. 1994).

Study site

The southern Florida bonefish charter fleet operates from Key Biscayne in the Upper Florida Keys near Miami, southwestward about 270 km through the Florida Keys, including the eastern side of Florida Bay, to the Marquesas located some 30 km west of Key West (**Figure 3.1**). Except for nonresidents, the captains usually maintained primary residence near the location fished. Using primary residence information, the captains were grouped into five regions: (1) Lower Keys (Key West to Ohio Key); (2) Middle Keys (Knight Key to Long Key); (3) Upper Keys (Lower Matecumbe Key to north Key Largo); (4) Dade and Broward Counties (Florida City to Fort Lauderdale); and (5) nonresident, which included captains who did not maintain a primary residence in southern Florida.

Survey instrument

The captains were asked to provide the number of years they had been a captain in southern Florida’s bonefish fishery and the number of days in calendar year 2001 spent fishing for bonefish. Previous discussions with captains made it clear that 1 day fishing for bonefish was an 8-h fishing trip. To generate an estimate of total annual effort for the fishery (days yr^{-1}) for 2001, mean annual effort and corresponding 95% confidence intervals (CI) were calculated for each regional stratum, then multiplied by the total number of charter captains for each region to account for nonrespondents. Means and confidence intervals were then summed over all strata to obtain total annual effort.

To assess the spatial distribution of fishing effort, the survey included a map of southern Florida waters (Biscayne Bay, Florida Bay, and Florida Keys) overlain with a grid of 8 km^2 cells. Respondents were asked to shade in the cells where $\geq$90% or more of their fishing effort occurred and mark an X in cells that contained <10% (low-effort areas) of their fishing effort for the 2001 calendar year. This information for all the respondents was combined with the responses for total number of days spent fishing for bonefish in calendar year 2001 (TDF_{2001}). This allowed computation of total annual effort for a grid cell (E_i) as

$$E_i = \sum_{i=1}^{n} \left(\frac{0.90}{C_i} * TDF_{2001} \right) + \left(\frac{0.10}{D_i} * TDF_{2001} \right) \tag{3.1}$$

where, C_i is the number of grid cells shaded by respondent *i* and D_i is the number of grid cells marked with an X by respondent *i*. The total effort values calculated for each cell were then mapped with a geographic information system (ArcGIS software, Environmental Systems Research Institute, Redlands, CA) to assess the spatial distribution of the bonefish charter fleet for the 2001 calendar year.

Captains were asked to characterise the general physical condition at release of bonefish captured in 2001 as excellent, partially impaired, or not likely to survive. Fish in excellent condition displayed no obvious injuries or incapacitation at release. Partially impaired fish were those that sustained minor injury (gut or deep hooking, fin damage, etc.) or required extensive resuscitation (>5 minutes) before release. Fish judged not likely to survive were either unable to swim away or were injured or consumed by a predator during capture or after release. Median response values were reported to accommodate the asymmetrical distributions in responses. The captains were asked to rank six factors that affected the likelihood of mortality after release: (1) water temperature; (2) time elapsed in capture; (3) water depth; (4) predator abundance in the area of release; (5) lure or bait used; and (6) hook location.

Non-response bias

Non-response bias was assessed by conducting a phone survey of a randomly selected subsample of mail survey nonrespondents. The phone survey used the same questionnaire as the mail survey. Interviews were conducted 3 weeks after the last mailing.

Non-response bias was evaluated in two different ways. For quantitative responses, mean response values were compared between respondent and nonrespondent samples using *t*-tests; while multiple choice questions were tested using the likelihood ratio G-statistic (Sokal and Rohlf 1995). Statistical significance was assessed at $\alpha = 0.05$.

Results

Survey questionnaires were mailed to 322 captains in southern Florida. A total of 190 captains (59 %) responded to the mail survey. Captains from the Lower Keys region had the lowest response rate (**Table 3.1**). Each respondent answered most of the questions, and every question was answered by at least 95% of the respondents.

Table 3.1- Survey response details for the five regions of southern Florida.

Location	Sample size	Responded	% Response
Lower Keys	51	26	51
Middle Keys	37	24	65
Upper Keys	172	95	55
Dade & Broward Counties	53	36	68
Nonresident	9	9	100
Total	322	190	59

The fishery

The number of years in the bonefish fishery as a captain ranged from 3 to 61 years (n = 171) with a mean ± SE of 22.7 ± 1.0 yr. The number of days spent fishing for bonefish during calendar year 2001 ranged from 13 to 250 d with a mean of 97.9 ± 5.1 d. The majority (61%) of the 190 responding captains fished 100 to 150 days yr^{-1}. About 8% of the captains in the fishery focused exclusively on bonefish ($\geq$250 days yr^{-1}), and 31% of the captains fished part-time for bonefish (25 to 50 days yr^{-1}). The 95% CI for days spent fishing for bonefish for the five regions were 65 to 117 d in the Lower Keys, 112 to 168 d in the Middle Keys, 83 to 110 d in the Upper Keys, 52 to 103 d in Dade and Broward Counties and 0 to 79 d for Nonresidents. The 95% CI for total number of days fishing ranged from 24,520 to 37,262 d, with a mean of 30,875 d. Although captains in the Middle Keys expended greater annual effort on average than those from other regions, the majority (53%) of captains resided in the Upper Keys. Therefore, total effort (as number of captains multiplied by average annual effort per captain) was highest overall in the Upper Keys region. This was reflected in spatial distribution of effort over the fishing grounds as indicated by captains (**Figure 3.2**).

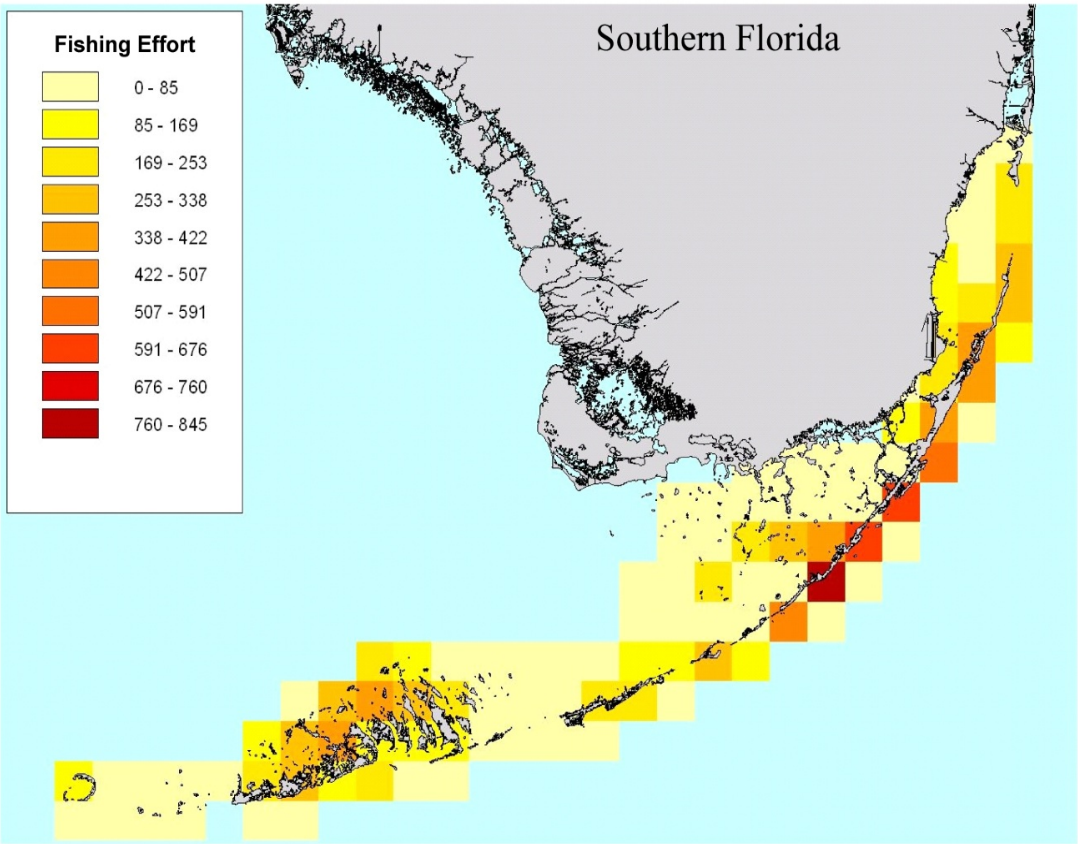

Figure 3.2- Spatial distribution (8 km^2 cells) of fishing effort for bonefish in 2001 reported by captains of the fishery. Fishing effort was defined as days spent targeting bonefish.

Captains reported median values of 90% for bonefish caught in excellent condition, 5% were partially impaired, and 0% died (*n* = 172). Median values are reported instead of means because responses were asymmetrically distributed. Because the captains were asked to provide an annual estimate of release condition and assuming that the 90% median response represents the expected annual survivorship rate from the fishing event ($S_{release}$), annual release mortality rate ($F_{release}$; $S_{release} = e^{-F_{release}}$) was 0.11.

Although captains indicated that most bonefish were in excellent condition upon release, they suggested that the principal factor contributing to release mortality was predator abundance (mean rank = 2.43, range of 1 to 6). The next two most important factors were time elapsed during capture (mean rank = 2.64) and hook location (i.e. lip hooked vs. gut hooked) (mean rank = 2.84). Seventeen percent of the respondents provided an additional response that indicated that handling time during release was a significant contributor to mortality.

Perceived population abundance changes and anthropogenic impacts

Almost half of the respondents (n = 83) indicated the population had declined, and 30% of the respondents (n = 53) indicated no change in abundance. The respondents that reported a decline most frequently stated that it took place druing the past decade. The three most common reasons given for decreased bonefish abundance were increased fishing pressure, increased boating pressure and deteriorating water quality. Seventeen percent of the captains reported increasing bonefish abundance, and most stated the trend began about 5 yr before 2001. There were differences in responses between captains that had been in the fishery for $\leq$ 10 years compared to those with >10 years experience (G-test, $P < 0.001$). Captains with less experience responded equally between increased and decreased bonefish abundance. The principal reason given for increased abundance was elimination of entangling (gill) nets in Florida coastal waters commencing in 1995.

Non-response bias

Sixteen non-responding captains were contacted by phone and consented to interviews. Responses of respondents and nonrespondents did not differ for years in the fishery ($P = 0.622$), annual days fished for bonefish ($P = 0.731$), condition of bonefish when released (*P* = 0.470) or mean size of bonefish caught in the previous year (*P* = 0.093). Respondents and nonrespondents did not differ in their perception of changes in bonefish abundance (*P* = 0.062) or factors affecting mortality (*P* = 0.488). There was no evidence of non-response bias.

Discussion

Information on southern Florida's bonefish fishery was nonexistent before this survey. A great amount of research effort was expended to develop a sampling frame for the survey. With a sampling frame established, the next step was to determine the best method to survey the captains. A mail survey was chosen over other methods due to funding constraints and contact method. A telephone survey of the entire fleet could have been completed faster but would have been expensive (>US$1000) and time-consuming compared to a mail survey (<$200). An on-site survey would not have been practical due to the cost and the multiple access sites of the fishery. A mail survey, despite being the most economical survey method in this case, has limitations. Mail surveys tend to have lower response rates and increase the potential for non-response bias (Pollock et al. 1994); this was addressed here with a follow-up telephone survey of nonrespondents. Cost and time demands limited the sample size of the phone survey and may have restricted the ability to detect differences between respondents and nonrespondents. Nevertheless, no non-response bias was detected. Another potential problem with any after-the-fact survey is recall bias. Recall bias of the responses was considered during development of the questionnaire and limited the number and type of questions asked. For example, despite the importance of determining the annual catch of the fishery, this question was not asked because of the likelihood of recall bias. Instead, the survey focused on collecting information that minimised recall bias. The two results that had the greatest potential for recall bias were the condition of bonefish at release and fishing effort for the previous year. Recall bias for these two questions was assumed to be low for several reasons: (1) the captains are attentive to the survival of bonefish during release because their future income depends on the availability of bonefish; (2) they can provide a reliable estimate of the distribution of their fishing effort because they are very familiar with the fishing grounds; and (3) they track the number of days fished for bonefish because it related to their income. Anglers asked to recall fishing activity tend to overestimate the number of days fished (Hiett and Worrall 1977; Gems et al. 1982; Chu et al. 1992). Although the bonefish captains surveyed were expected to keep records of fishing activity and to have used those records to complete the survey, the accuracy of this information remains unknown.

Annual fishing effort for bonefish appeared to be focused from Biscayne Bay to the Upper Keys. The highest numbers of bonefish captains also resided close to these areas suggesting that the captains lived close to best fishing locations. If fishing effort was assumed to be concentrated in areas of high stock abundance, then the majority of Florida’s bonefish stock is likely located in the northern Florida Keys (Dade County and Upper Keys). The fishing effort could have been influenced by spatial variation in the size of bonefish available in the different areas instead of bonefish abundance, but three annual bonefish visual surveys in southern Florida (Ault et al. 2008b) revealed that the fishing effort values significantly related to bonefish abundance.

Captains stated that 90% of the bonefish were released in excellent condition. Thus, the 10% in less than excellent condition were assumed mortalities. This mortality estimate was lower than the mean mortality rate presented in a compilation of marine catch-and-release fisheries by Bartholomew and Bohnsack (2005) and the 39% and 42% reported for bonefish caught and released at two sites in the Bahamas by Cooke and Philipp (2004). Fishing mortality in the south Florida bonefish fishery is relatively low, but bonefish are relatively long lived (19 years; Crabtree et al. 1996). Thus, even relatively low mortality in this catch-and-release fishery may reduce stock abundance.

The captains ranked predator abundance, duration of capture and hook location as the three most important variables contributing to bonefish mortality. This suggests that post-release survival can be increased if captains are willing to: (1) avoid fishing in locations with high predator abundance (as suggested by Cooke and Phillip 2004); (2) use high-breaking strength fishing lines (> 4.5 kg) to reduce capture time; and, (3) use hooks that decrease the probability of "gut-hooking" fish (e.g. circle hooks).

The 322 charter captains targeted bonefish for about 30,875 days a year at a fee of $400 a day. This produced a direct expenditure of US$12 million for 2001. Despite the economic impact of the charter-based recreational fishery, there are no survey programs in place to adequately monitor it. Landings and catch statistics of southern Florida's bonefish fishery have been recorded by the Marine Recreational Fisheries Statistics Survey (MRFSS), but this survey did not effectively sample bonefish fishery participants. For example, our mail survey results indicate that annual effort among charter captains in 2001 was approximately 30,875 days targeting bonefish. However, the MRFSS results for 2001 estimated the number of days (angler trips in their database) fishing for bonefish from the charter fleet was 14,334 for Dade and Monroe (Florida Keys) counties (unpublished data from the National Marine Fisheries Service, Fisheries Statistics Division, www.st.nmfs.noaa.gov). Also, MRFSS reported no bonefish catches in the years of 2002, 2004, 2005, and 2006, despite a bonefish tagging project in southern Florida having at least 500 bonefish tagged in each of those years (Larkin et al. 2008). The erroneous estimates of fishing effort and catch by the MRFSS method could be due to the bonefish fishery having many access locations, and the high likelihood that the limited sampling locations of the MRFSS survey method would have failed to intercept the bonefish captains. Flaws in the MRFSS sampling, such as those discussed above, were noted in a recent National Research Council (2006) study.

Our survey collected information only from the bonefish charter captain fleet. The fishing effort of the bonefish recreational fleet should be addressed. Leeworthy (1996) and Leeworthy and Wiley (1997) estimated effort of all the recreational activities (fishing, diving, boating, etc.) in the Florida Keys. These surveys were very broad in scope and grouped the nearshore fishing fleet into one. This fleet is composed of fisherman not only targeting bonefish but several other species such as red drum, *Sciaenops occelatus* (L.), snook, *Centropomus undecimalis* Bloch, spotted seatrout, *Cynoscion nebulosus* Cuvier, and many more species. The proportion of fishing effort in the nearshore fishery targeting bonefish relative to other species is unknown. Therefore, recreational (non-captain) fishing effort in the bonefish fishery cannot be reliably determined.

This mail survey was the first to mine the extensive knowledge of experienced charter captains and gather substantial information on the southern Florida bonefish fishery. This group of fishermen probably spends more time on the water in bonefish habitats then any other fishermen or even scientists. Their knowledge has helped to fill important knowledge gaps for this fishery. This survey also documents that the majority of the anecdotal evidence suggests a decline in the Florida bonefish stock. These survey results need to be validated with other data sources and can be used to trigger a scientifically valid assessment of the resource. To date, the only fishery regulations in place prohibit commercial harvests and limit recreational harvests to one fish greater than 457 mm TL per angler per day (Florida Fish and Wildlife Conservation Commission 2009). These limited regulations may be inadequate to ensure future sustainability of the fishery given the increases in angling effort and regional environmental changes.

The survey not only provided useful information for fishery management, but also allowed researchers to develop a trusted presence and rapport within the community of bonefish captains. This relationship has paved the way for further cooperative scientist-captain efforts on other bonefish research including mark-recapture, acoustic telemetry, and visual surveys of bonefish in southern Florida (Ault et al. 2005a; Ault et al. 2008b; Humston et al. 2008; Larkin et al. 2008). Knowledge gained from working collaboratively with bonefish captains may help facilitate development of cooperative management strategies to conserve and sustain southern Florida's ecologically and economically important bonefish resource.

Chapter 4

Estimating mortality and abundance of bonefish in south Florida

Summary

An anchor tag project was conducted for bonefish from 1998 to 2010. The project provided a large dataset of bonefish lengths to which a length based mortality function was applied to estimate instantaneous rates of total mortality (0.269 y^{-1}), natural mortality (0.143 y^{-1}), and fishing mortality (0.126 y^{-1}). The fishing mortality rate was less than the natural mortality rate suggesting fishing mortality may be at a level that promotes a sustainable fishery. Since bonefish harvest levels are low the majority of the fishing mortality estimate is likely release mortality.

An annual 1-day visual survey was implemented using the volunteered services of professional bonefish guides and avid anglers throughout the Florida Keys. The surveys were conducted in early fall (September and October) for eight consecutive years (2003-2010). The population size for each year ranged from 238,083 to 382,535 with an 8-year average of 306,964. The population size estimates changed from year to year with an overall decline in 2010.

To evaluate changes in the bonefish population over a longer period, catch-per-unit-effort data from tournaments were analyzed to create an index of abundance for bonefish. The tournament CPUE data were standardized in two ways. For the period 1968 to 2010 CPUE was standardized using the factors of year, gear, and season. For the period 1991 to 2010 the additional variables of tide phase, wind speed, cloud cover, and moon phase were available and could be used for standardization. Changes in these two

variations of the CPUE index may reflect changes in fishing regulations such as banning of commercial fishing in Everglades National Park in 1985. There has been an overall decrease in CPUE from 1997 to 2010 potentially caused by an increase in fishing effort.

4.1 Estimating Mortality

Background

Mortality is a key piece of information needed to successfully manage a stock for sustainability. In fisheries, total mortality (*Z*) is composed of two types: natural and fishing mortality. Natural mortality (*M*) denotes death from natural causes such as predation and cannibalism. Fishing mortality (*F*) is death from fishing or activities related to fishing. The comparison of natural mortality to fishing mortality reflects stock status and future sustainability.

Methods

A bonefish tag-recapture program was run from 1998 to 2010. Experienced bonefish anglers and professional bonefish guides were given tags and tagging supplies (tag applicator, datasheet, pencils, and a plastic container). Anchor tags were placed in the dorsal area of the fish; the unique tag number was recorded along with the location and fork length.

Locations of the anchor-tagged releases were grouped into two regions because of differences in size distributions (Larkin et al. 2008, Chapter 5). The regions are: (1) south Florida – extending from Key Biscayne south to the Marquesas; and, (2) Palm Beaches – extending north of Key Biscayne into the Palm Beaches (**Figure 4.1**).

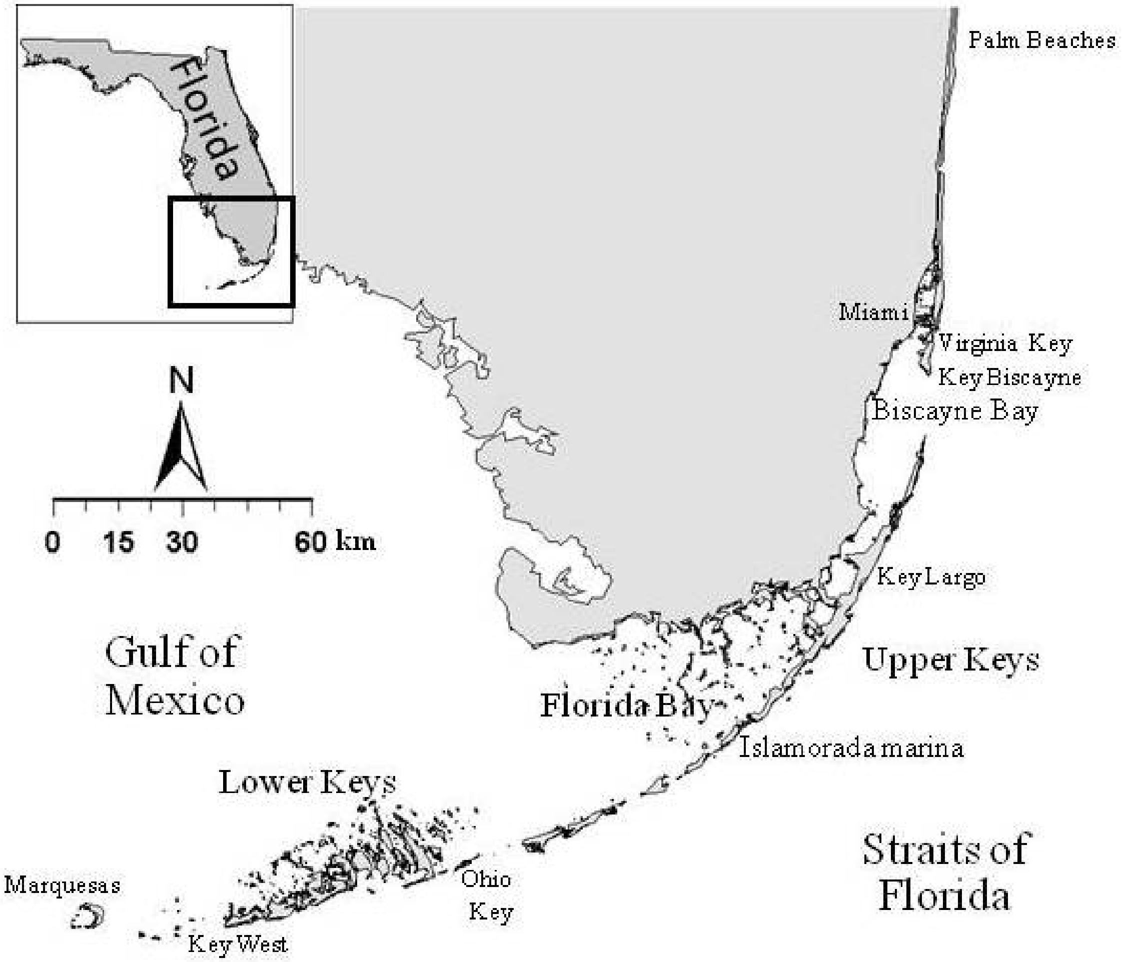

Figure 4.1- Map of Florida showing the bonefish tagging study region running from the St. Lucie Inlet to the Marquesas.

Instantaneous mortality rate (Z) was estimated with a length based mortality function using the length at release for bonefish in the south Florida region. The function is

$$\left(\frac{L_\infty - L_\lambda}{L_\infty - L_C}\right)^{Z/K} = \frac{Z(L_C - \bar{L}) + K(L_\infty - \bar{L})}{Z(L_\infty - \bar{L}) + K(L_\infty - \bar{L})} \qquad (4.1)$$

where L_∞ and K are von Bertalanffy growth parameters, L_λ is the maximum length in the catch, L_C is the length at first capture, and $\bar{L}$ is the mean length of the sample from L_C to L_λ (Ault and Ehrhardt 1991; Ehrhardt and Ault 1992). The algorithm was declared the name LBAR in Ault et al. (1996). L_∞, K, and L_λ values are from modeling growth of bonefish larger than 440 mm FL (Chapter 2). L_C came from the size class that reached full recruitment in annual length-frequency diagrams (i.e. the mode of the histogram) created from the smallest length increments available in the data (i.e. 13 mm, half inch). $\bar{L}$ was calculated for each year of the tagging project. Annual total mortality rates (Z) were obtained by solving equation 4.9 iteratively. A geometric mean was calculated from the annual Z values to approximate the true Z value.

Natural mortality is difficult to quantify because natural deaths often go unseen. Alagaraga (1984) estimates natural mortality from the fraction of the population (P) that survives to the oldest age class. The equation is

$$M = \frac{-\ln{(P)}}{t_{max}} \tag{4.2}$$

where it was assumed 5% of a cohort survives to the maximum age ($P=0.05$). Instantaneous fishing mortality rate (F) was obtained by subtracting M from Z.

Results

Length was available for 7,840 of the tagged bonefish. Length-frequency diagrams for each year displayed a range of length-at-first-capture from 530-620 mm FL and a mean of 587 mm FL. An example is **Figure 4.2** which shows an L_c of 584 for the length-frequency diagram of bonefish tagged in 2005. Annual estimates of average length of bonefish in the exploitable phase (>587 mm FL) for the south Florida region were fairly constant throughout the project years (**Table 4.1**). Growth parameters used in the model were $L_\infty = 703.8$ and $K = 0.2942$. The length-based mortality estimation procedures resulted in estimates of total annual instantaneous mortality rates that ranged from 0.140 to 0.937 and had a geometric average of 0.269 y^{-1} (**Table 4.1**).

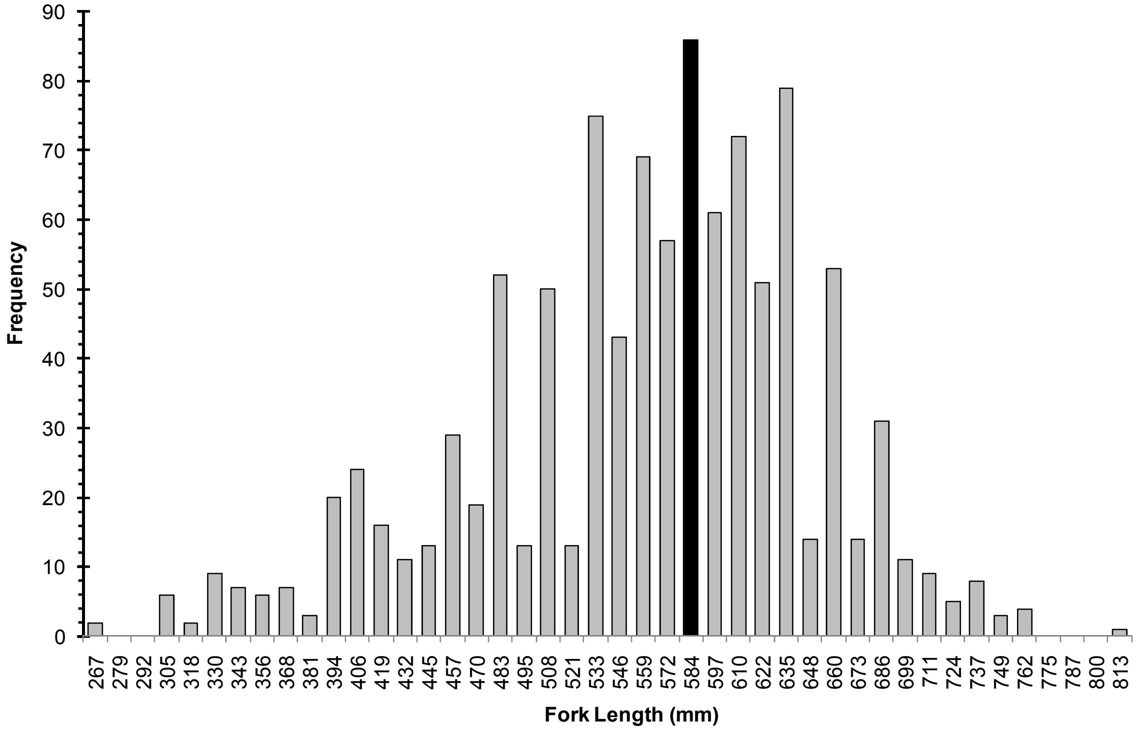

Figure 4.2- Length frequency distribution for 1,048 bonefish tagged-and-released during 2005 for which length information was available. The black bar denotes the length-at-first-capture of 584 mm FL.

Table 4.1- Estimates of average size from the bonefish tagging program: (A) mean length (mm FL), sample size, standard error, and size range for all bonefish tagged from 1998-2010; and (B) annual mean length in the exploitable phase $\overline{L}$, sample size, and estimated total instantaneous mortality rate $\hat{Z}$ of tagged bonefish in south Florida (L_c=587; L_∞=703.8; K=0.2942).

(A)

Region	Mean	N	SE	Size Range
South Florida	564.5	7,127	1.03	[248, 813]
Palm Beaches	319.0	713	1.49	[223, 533]

(B)

Year	$\int_{L_c}^{L_\lambda} \overline{L}$	N	$\hat{Z}$
1998	614.5	75	0.937
1999	626.3	76	0.500
2000	636.0	39	0.243
2001	634.0	127	0.293
2002	638.7	266	0.178
2003	636.9	288	0.221
2004	636.9	348	0.221
2005	637.2	415	0.214
2006	637.1	495	0.217
2007	637.2	450	0.214
2008	640.3	304	0.140
2009	637.8	295	0.199
2010	627.3	113	0.471

Instantaneous natural mortality rate (M) was estimated using a t_{max} of 21 years and produced a rate of 0.143 y^{-1}. The M value was subtracted from the instantaneous total mortality (Z) value to estimate the instantaneous fishing mortality rate (F). When the sample sizes of fish in the exploitable phase was greater than 200 the range of Z values ranged from 0.140 to 0.221 y^{-1} which resulted in F values from 0 to 0.078 y^{-1}. The overall *Z* value (0.269 y^{-1}) had M subtracted to produce an overall F value of F= 0.126 y^{-1}.

Discussion

Friedlander et al. (2008) used similar methods to estimate total mortality and natural mortality for bonefish at Palymra atoll, central Pacific. They did not estimate fishing mortality because they assumed the area was lightly exploited due to the region's isolation from human development and its status as a national wildlife refuge. Their total mortality estimate (0.2686 y^{-1}) was very similar to the present study; however, their natural mortality estimate (0.270 y^{-1}) was very different. This difference can be explained by the dissimilar maximum ages attained for bonefish between the two areas. Palmyra atoll bonefish reach a maximum age of only 11 years (Friedlander et al. 2008), whereas, south Florida bonefish reach a maximum age of 21 years (Chapter 2).

The fishing mortality rate was less than the natural mortality rate. This suggests fishing mortality may be at a level that promotes a sustainable fishery. The fishing mortality rate is also relatively low compared to the harvested fish species in south Florida. Ault et al. (2001) estimated fishing mortality rates for 35 species of reef fish in Biscayne National Park, and all of them had higher fishing mortality rates.

In years where there was a sufficient sample size ($n > 200$) to estimate total mortality from the length-based mortality function, similar total mortality estimates were generated for each year (**Table 4.1**). This trend displays stabilizing of the average size which is in contrast to reductions of average size seen in other south Florida fisheries which displayed large declines in average size over the years (Ault et al. 1998). The stable average length implies a population that is not declining. However, the time series is only for a recent period (1998 to 2010) and relatively short (13 years). The population may have declined substantially before this time.

Crabtree et al. (1996) estimated total mortality of south Florida bonefish with a catch curve analysis and estimated natural mortality with Pauly's (1980) formula. The present study's estimate of Z (0.269 y^{-1}) is similar and falls within the confidence interval of Crabtree et al.'s (1996) total mortality estimate (0.25 y^{-1}). Crabtree et al. (1996) concluded that there was little fishing mortality because their natural mortality estimate (0.29 y^{-1}) was similar to their total mortality estimates. In the current analysis, fishing mortality was non-zero, because a lower M was estimated than by Crabtree et al. (1996), in part because of the discovery of a higher maximum age. Furthermore, Larkin et al. (2010) reported 10% release mortality for Florida's bonefish fishery implying that fishing mortality is greater than zero.

Florida's bonefish fishery is primarily a catch-and-release fishery. Harper et al. (2000) conducted a creel survey (28,923 interviews) in Biscayne National Park from 1976 to 1991 and only reported one bonefish harvest. With such low harvest levels the fishing mortality estimate of 0.126 y^{-1} is likely to be primarily release mortality (i.e. mortality after released alive).

4.2 Visual survey to estimate population size

Background

Bonefish habitat frequently contains structure (i.e. mangroves) and soft seagrass beds. The habitat attributes combined with the bonefish's elusive nature makes sampling with nets problematic. However, the clear and shallow water they frequent makes them a good candidate for visual surveys. A survey was conducted on the stock using experienced guides and avid anglers.

Methods

Study Location and Sampling Domain

South Florida's bonefish fishery extends about 400 km from Key Biscayne to the Marquesas (**Figure 4.3**). Due to lack of any initial estimates of population size or stock spatial distribution, expert knowledge of several key professional guides and experienced anglers were employed to design the initial pilot survey. This produced a survey domain comprised of 19 geographical zones (**Figure 4.3**). For statistical reporting and analysis, these zones were grouped into 4 regions or statistical strata (i.e., Biscayne, Upper Keys, Middle Keys, and Lower Keys) circumscribing geological and hydrographic features of the seascape (Marszalek et al. 1977; Shinn et al. 1977; Wolanksi 2000; Porter and Porter 2001).

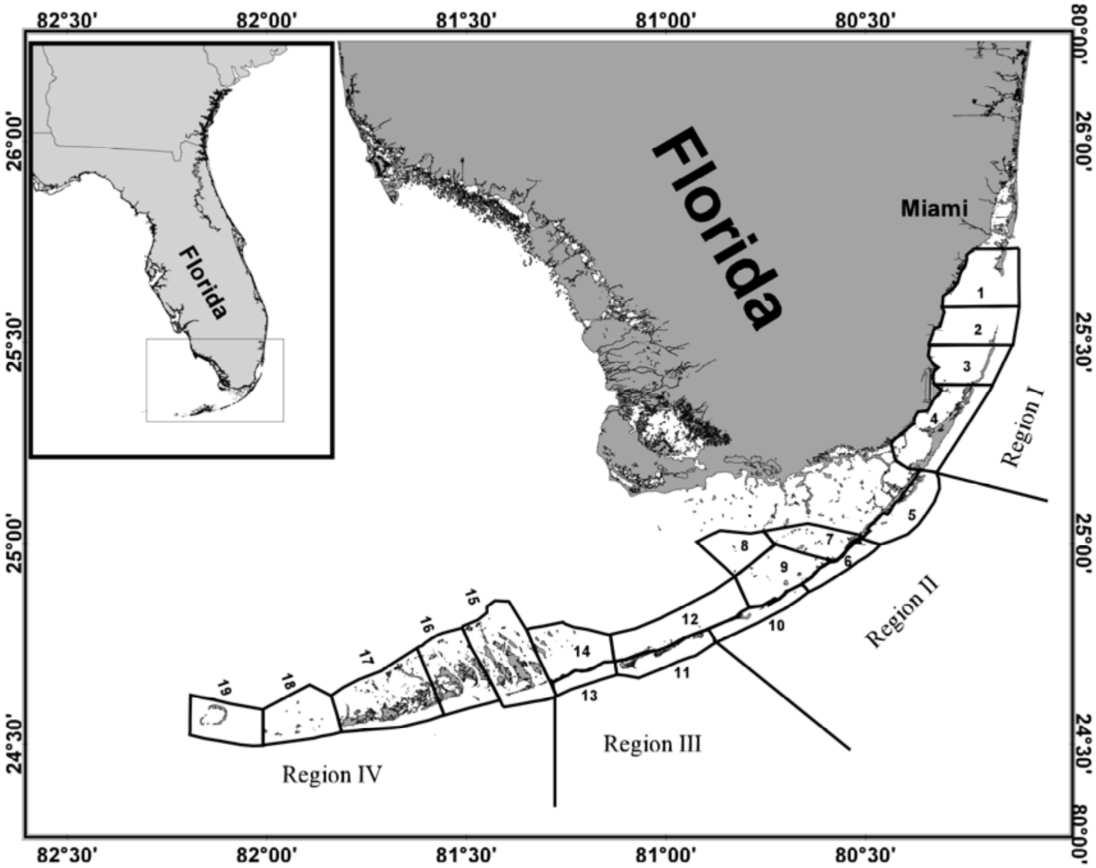

Figure 4.3- Map of the south Florida showing the 19 geographical zones from Miami to the Marquesas for the annual bonefish visual survey. Also shown are the 4 regions: region I is Biscayne, region II is Upper Keys, Region III is Middle Keys, and region IV is Lower Keys.

Field Survey and Data Collection

An annual 1-day survey was implemented using the volunteered services of professional guides and expert anglers. The surveys were conducted in early fall (September and October) for eight consecutive years (2003-2010).

Survey assessment methodology was based on Ault et al. (2008b). A standard line transect of known distance was utilized during the visual estimation procedure as described by Gunderson (1993). The transect was the distance the boat was poled in shallow water while two observers counted the bonefish in a width of 100 meters.

Generally, the two observers consisted of a professional bonefish guide and an experienced angler stationed at the bow. Each observer wore polarized sunglasses. The boat generally moved in the direction of the prevailing tides and winds, and to the extent possible, with the sun behind the observers to further highlight the bonefish against the coral-sand and seagrass covered bottoms. To ensure adequate coverage of the fishery area during a survey, 2 to 8 boats were assigned to each of the 19 geographic zones. The well-lit portion of the entire day (0800 to 1600) was spent looking and fishing for bonefish. Survey participants recorded where they fished, the distance poled, and how many bonefish were seen.

Statistical Sampling Design

Each one-day survey employed a stratified random sampling design. Statistical sampling design procedures are described in Cochran (1977) and Ault et al. (1999, 2002b, 2006, 2008b). The total area (A) of the survey sampling domain was divided into 19 geographical zones to ensure that effort was distributed across the ecosystem. A geographical information system (GIS) was used to compute total area of each zone. **Table 4.2** provides the two different estimates of stratum area.

Table 4.2- Area (km^2) for the 19 zones of the four geographical regions.

Region	Zone	Area (km^2)
Biscayne	1	245
	2	211
	3	196
	4	319
Upper Keys	5	177
	6	84
	7	146
	8	140
	9	102
	10	224
Middle Keys	11	133
	12	295
	13	66
	14	235
Lower Keys	15	384
	16	288
	17	398
	18	231
	19	200

Following Ault et al. (2008b), the 19 zones were subsequently grouped into 4 regions (h = 4) or statistical strata of area A_h for reporting and analysis (**Figure 4.3**). The basic statistical observation of density was the number of bonefish observed per area searched for a single vessel-day. Mean density $\overline{D}$ and associated sample variance s^2 of bonefish in stratum h were respectively computed as

$$\overline{D}_h = \frac{1}{n_h} \sum_{j=1}^{n_h} D_{hj} \tag{4.3}$$

and

$$s_h^2 = \frac{\sum_j [D_{hj} - \overline{D}_h]^2}{n_h - 1}, \tag{4.4}$$

where n_h was the number of samples obtained in stratum h, and D_{hj} was observed density by vessel j in stratum h. Mean bonefish density for the survey domain, i.e., all strata combined, was estimated by

$$\overline{D}_{str} = \sum_h w_h \, \overline{D}_h \tag{4.5}$$

with stratum weighting factor w_h defined as

$$w_h = \frac{N_h}{N} \ , \tag{4.6}$$

where N_h was the total possible sample units in a stratum, and N was the total possible sample units in all strata combined. We estimated N_h by dividing stratum area A_h by average searched (fished) area $\overline{T}_h$ of vessels in stratum h,

$$N_h = \frac{A_h}{\overline{T}_h} \tag{4.7}$$

Variance of $\overline{D}_{str}$ was estimated by

$$\text{var}[\overline{D}_{str}] = \sum_h w_h^2 \left(1 - \frac{n_h}{N_h}\right)\left(\frac{s_h^2}{n_h}\right) \ . \tag{4.8}$$

Bonefish population size P_h (numbers of fish) in stratum h was obtained by multiplying stratum mean density by stratum area

$$P_h = \overline{D}_h A_h \, . \tag{4.9}$$

Variance of P_h was estimated as

$$\text{var}[P_h] = A_h^2 \left(1 - \frac{n_h}{N_h}\right)\left(\frac{s_h^2}{n_h}\right) \ . \tag{4.10}$$

Total bonefish population size, P , in the survey domain was obtained by summing (9) over all strata,

$$P = \sum_{h} P_h \ . \qquad (4.11)$$

The associated variance, $\mathrm{var}[P]$, was obtained in a similar manner,

$$\mathrm{var}[P] = \sum_{h} \mathrm{var}[P_h] \quad . \qquad (4.12)$$

The standard error of P was computed as

$$SE[P] = \sqrt{\mathrm{var}[P]} \quad . \qquad (4.13)$$

To evaluate a measure of relative precision of the sampling designs for survey years, coefficient of variation (CV) of population size was computed as

$$CV[P] = \frac{SE[P]}{P} \quad . \qquad (4.14)$$

The 95% confidence interval of the population size estimate was calculated as

$$95\% CI[P] = P \pm t_{\alpha, n-1} SE[P] \ , \qquad (4.15)$$

where t is the critical value of Student's t-distribution with $\alpha=0.05$.

Results

The annual one-day bonefish surveys were conducted in early fall in consecutive years from 2003 to 2010. The number of volunteers ranged from 25 boats to 72, and the area covered ranged from 8.4 km^2 to 33.9 km^2 (**Table 4.3**). The population size for each year ranged from 238,083 to 382,535 with an 8-year average of 306,964 (**Figure 4.4**). The population size estimates changed from year to year but were not statistically different. The calculated coefficient of variation (CV) ranged from 13% to 36% with an average of 20%.

Table 4.3- Sample size (n) and area covered for each year.

Year	n	Area(km^2)
2003	40	33.9
2004	55	33.5
2005	50	18.6
2006	59	23.5
2007	72	31.0
2008	30	12.1
2009	37	14.3
2010	25	8.4

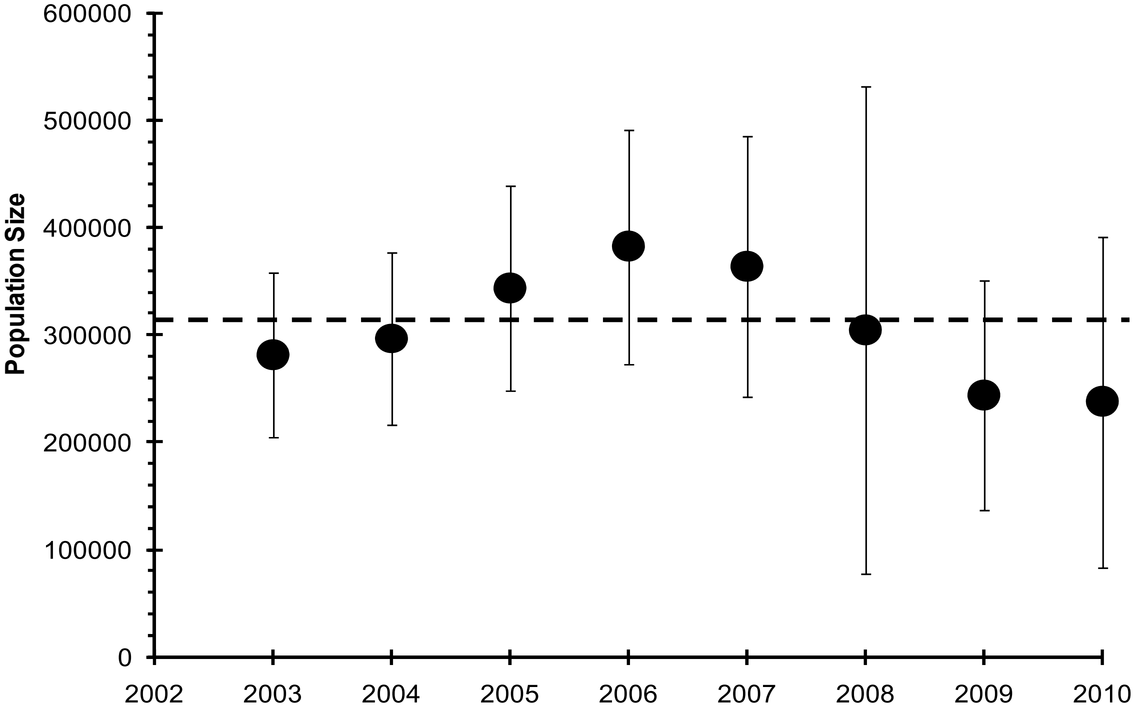

Figure 4.4- Comparison of population size estimates by years with the entire zone area. Bars denote 95% confidence intervals and the horizontal dashed line represents the mean population size (82,403).

Discussion

Bonefish appear to be excellent candidates for assessing ecological changes in the Florida Keys ecosystem. Bonefish rely on and are sensitive to changes in prey whose populations are not as easy to assess. Bonefish also inhabit shallow, clear inshore waters on grass and sand flats that are highly susceptible to human impacts. These attributes also make them ideal candidates for a visual census in that, to the trained eye, they are easy to spot and count. Every year of the project produced estimates of the population size that were statistically similar. In one year (2008) there were suboptimal conditions (cold, windy, and mostly cloudy) but yet the population estimate was statistically similar to previous years.

The survey population estimates are a quantitative measure for assessing future change. For the current bonefish population, there could be cause for considerable concern if the survey estimate of abundance population were to drop from 300,000 to 200,000. Also, this fishery-independent estimate of abundance would facilitate regional assessments of bonefish populations and provide a quantitative basis for comparing ecosystems that support bonefish fisheries.

4.3 Standardized catch rates from recreational bonefish tournaments

Background

The bonefish fishery in south Florida uses hook-and-line gear and is closed to commercial fishing. The fishery is primarily catch-and-release; a creel survey with 28,923 interviews from 1976 to 1991 only reported the harvest of one bonefish (Harper et al. 2000). As a result of the catch-and-release practice of the fishery, no catch statistics from markets (i.e. landings data) are available for use in assessing stock status. The Marine Recreational Fisheries Statistics Survey (MRFSS) collects catch records for the fishery, albeit not effectively. Larkin et al. (2010) revealed how the MRFSS survey does not effectively sample bonefish fishery participants, and additional flaws in the MRFSS sampling design were noted in a National Research Council (2006) study.

The bonefish tournaments of Islamorada, Florida, have taken place over the past forty-two years and have records of the number of bonefish caught, dates of each tournament, hours of fishing, number of participants, and gear, making an excellent resource to analyze the catch-per-unit-effort (CPUE) data as has been done for other tournament results (Farber 1994; Ortiz and Brown 2002; Hoolihan et al. 2008; Hoolihan et al. 2010). CPUE data are frequency analyzed to create indices of abundance under the assumption that catch per unit effort is proportional to stock size. These indices are used for monitoring a large number of fisheries worldwide (Harley et al. 2001). However, before CPUE data can be used as an effective index of abundance, it must be standardized to remove, or explain, variation in the data that is not related to changes in abundance. Factors such as gear and fishing conditions can influence the raw CPUE and can be removed from standardized measures of relative abundance (Maunder and Punt 2004).

A delta-lognormal modeling approach, following Lo *et al*. 1992 and Ortiz 2006, is commonly used to standardize CPUE data and provide an estimate of relative abundance. This method combines separate general linear model (GLM) analyses of the proportion of successful tournament catches (at least one bonefish was caught) and the catch rates on successful trips to construct a single standardized CPUE index. The main advantage of using this approach was allowance for the possibility of zero catches (Ortiz et al 2000). Porch and Scott (1994) found that using the delta-lognormal model yielded the most accurate abundance estimates when a large number of zeros are present.

Methods

The Islamorada bonefish tournaments are comprised of four annual events: the spring and fall fly fishing and spring and fall multi-gear tournaments. Each type of tournament took place during the same week every year. For example, the spring fly tournament was always the third week of April. The multi-gear tournaments allotted different points for using the different gears and baits: pink shrimp (*Penaeus duorarum*) with a spinning reel, artificial lures with a spinning reel, artificial lures with a bait casting reel, and flies with a fly reel. Only fly fishing was allowed in the fly fishing tournaments. Each tournament record contained the dates, hours of fishing, number of participants, and total number of bonefish caught by each team for the entire event. A team was comprised of a professional bonefish guide and one angler. Bonefish tournament participants and organizers were contacted to provide tournament records.

The rules and calculation of points between tournaments were sufficiently similar to allow comparisons among tournaments. All boats were required to leave and return to the marina specified by the tournament (**Figure 4.1**, Islamorada marina, 24° 55.17 N, 80° 37.59 W). The participants were given an hour and a half travel time before and after fishing hours. The majority of the tournaments allowed 8 fishing hours each day, but some tournament years allowed 8.5 hours. Three of the tournaments were three consecutive days, and one of the tournaments (spring multi-gear) was five consecutive days.

All tournament results were combined, and CPUE was calculated as bonefish caught per hour for each individual team at each tournament event. Hour was used instead of days because the hours of fishing often changed between 8 and 8.5 hours a day over the years. A delta-lognormal method was used to estimate relative abundance indices for bonefish. The final model was built on the two submodels of the proportion of records with a positive catch (i.e., where at least one bonefish was caught) and catch rates with positive catches. The proportion of records with a positive catch submodel assumed a binomial error distribution with a logit link function, whereas the catch rates of positive catches submodel assumed a lognormal distribution with a log link function.

Two types of factors, class and continuous, were tested for significance in the two submodels. Class factors were Year, Gear, Season, and Hour. Gear was the four categories of bait, fly, artificial lure with a spinning reel, and artificial lure with a bait-casting reel. Season was either spring or fall. Hour was the number of fishing hours permitted in the tournament. Interviews of six tournament participants (3 anglers and 3 guides) identified additional variables that influenced catch rates: Moon, Tide, Wind, and Cloud. Moon was a class variable of the primary moon phase that took place during the tournament, and consisted of the eight moon phases (i.e. full moon, waning crescent). Tide was a continuous variable generated from the times of rising and falling tides recorded at the tide station at Shell Key (24° 54.47 N, 80° 39.35 W, http://tbone.biol.sc.edu). This tide station was chosen because of the proximity to the tournament marina and because it is a common fishing area of the participants. The Tide variable was the proportion of time spent during a rising tide during the fishing hours. Wind was a continuous variable generated from the recorded wind speed during the fishing hours at Molasses Reef Weather Buoy (25° 00.36 N, 80° 22.48 W; www.ndbc.noaa.gov) which is close to the declared tournament marina. Interviews with tournament participants stated that catch rates were substantially different when the wind was greater than 20 knots (10.28 meters/second). The Wind variable was the proportion of fishing time with the wind speed 20 knots or less. Cloud was a continuous variable relating to cloud cover taken during the fishing hours at the airport in Marathon, Florida (available from National Climatic Data Center http://www.ncdc.noaa.gov). The Cloud variable was the proportion of time spent during clear or partly cloudy skies (less than 50% cloud cover). Continuous variables were calculated as proportions instead of means. This was necessary because the tournament records were pooled results for the entire tournament making individual day records unavailable. Proportions better represent the continuous variables because the mean could be heavily influenced by the weather event from one day. For example, the mean wind from a three day tournament could be very high from one extremely windy day and two calm days. A multicollinearity analysis was run on all factors by plotting each factor against one another and evaluating correlation.

Following the methods of Hoolihan et al. (2008), Pollack (2009), and Arocha and Ortiz (2010), the significance of the factors and their interaction terms were determined using a forward step-wise regression procedure with SAS GENMOD procedure (SAS Institute Inc. 2007). First, a null model was run through the GENMOD procedure that contained only the Year factor. Year was included because the objective was to determine changes in CPUE by year. From the null model, a base deviance per degree of freedom was obtained. Explanatory factors were then entered into the submodels one at a time, and a deviance per degree of freedom was calculated for each factor. The factor with the greatest reduction in deviance per degree of freedom was then included in the submodel only if two conditions were met: 1) at least a 1% reduction in the deviance per degree of freedom and 2) the chi-square test of significance at the 5% level. The chi-square test statistic was used to test for significance of additional factors in the final model because the difference in deviance between two consecutive nested models follows a chi-square distribution (Ortiz 2006). The submodel was then rerun with the other factors to see if they should be included. This process continued until no terms that reduced the deviance per degree of freedom by more than 1% or significant chi-squared values were found.

Once a set of individual factors were found for each submodel, first level interactions were evaluated using the same procedure as the solitary factors. Interaction terms were built from the determined significant factors present in their respective submodel. The interactions were further analyzed using PROC GLIMMIX and PROC MIXED (SAS Institute Inc. 2007) with significance evaluated using three criteria: (1) likelihood ratio test of residual log likelihoods with significance at the 5% level; (2) Akaike's Information Criteria (AIC); and, (3) Schwarz's Bayesian Criteria (BIC). AIC and BIC are measures of goodness of fit relative to the number of calculated model parameters where lower values indicated a better model.

After determination of the selection of the final set of factors, the delta-lognormal index of relative abundance (I_y) as described by Lo *et al.* (1992) was estimated as:

$$I_y = c_y p_y \tag{4.16}$$

where c_y is the estimate of mean CPUE for positive catches for year y, and p_y is the estimate of mean probability of capture during year y. Both c_y and p_y were estimated with general linear models using the GENMOD procedure (SAS Institute Inc. 2007). Data used to estimate abundance for positive catches (c) were assumed to have a lognormal distribution, approximately, and modeled using the following equation:

$$\ln(c) = X\beta + \varepsilon \quad (4.17)$$

where c is a vector of the positive catch data, X is the design matrix for main effects, β is the parameter vector for main effects, and ε is a vector of independent normally distributed errors with expectation zero and variance σ^2. The probability of having at least one bonefish caught in a record (p) was assumed to have a binomial distribution and modeled using the following equation:

$$p = \frac{e^{X\beta+\varepsilon}}{1+e^{X\beta+\varepsilon}} \quad (4.18)$$

where p is a vector of the capture/no capture data. Both c_y and p_y were estimated as least-squares means for each year along with their corresponding standard errors, SE(c_y) and SE(p_y). From these estimates, I_y was calculated, as in equation 3.1, and its variance calculated as:

$$V(I_y) = V(c_y)p_y^2 + c_y^2V(p_y) + 2c_yp_yCov(c,p) \quad (4.19)$$

where

$$Cov(c,p) = \rho_{c,p}[SE(c_y)SE(p_y)] \quad (4.20)$$

and $\rho_{c,p}$ denotes correlation of c and p among years.

Results

CPUE data were collected from 98 tournament scoresheets (spring multi-gear n=14, spring fly n=30, fall multi-gear n=28, and fall fly n=26) from the years 1968 to 2010. Not all of the tournament records were available for every year due to lost scoresheets and tournament cancelations. No scoresheets were available for the years of

1969, 1971-1974, and 1978. The majority of the scoresheets (67%) obtained are from 1991 to 2010.

The tournament scoresheets produced 1,861 individual team catch records, and 7,920 bonefish were caught. No catch was recorded in 408 (22%) of the records. The CPUE ranged from 0 to 1.46 with an average of 0.137 (0.00354 SE). The fly fishing tournaments had higher participation and produced the majority of the catch records (64%, n=1,189). The multi-gear tournaments had about 4% of the participants use fly fishing gear with the rest primarily using bait. Catch records using artificial lures with a spinning reel (n=17) and bait casting reel (n=12) accounted for only 1% of the records, and were excluded from the standardization procedure because of the small sample size.

The variables of Year, Gear, and Season, were available for all of the catch records. The variables of Tide, Wind, Cloud, and Moon phase were not consistently available until 1991. The two standardized indices were based on different time series and availability of data for the variables. One index, including all records and the variables of Year, Gear, Season, is referred to as the complete index. Another index, referred to as the truncated index, was calculated from 1991 to 2010 using all of the explanatory variables.

The multicollinearity analysis of the variables only found a relatively small correlation between Wind and Hour. A closer evaluation of the relationship determined a low coefficient of correlation (R^2 =0.0057). The relationship between CPUE and the continuous variables were explored. All three of the continuous variables had linear relationships with CPUE. Wind was the only variable that had a direct relationship (slope = 0.13) (**Figures 4.5** and **4.6**). No strong direct or inverse relationship existed between CPUE against tide (slope = 0.00004) or CPUE against cloud (slope = -0.087).

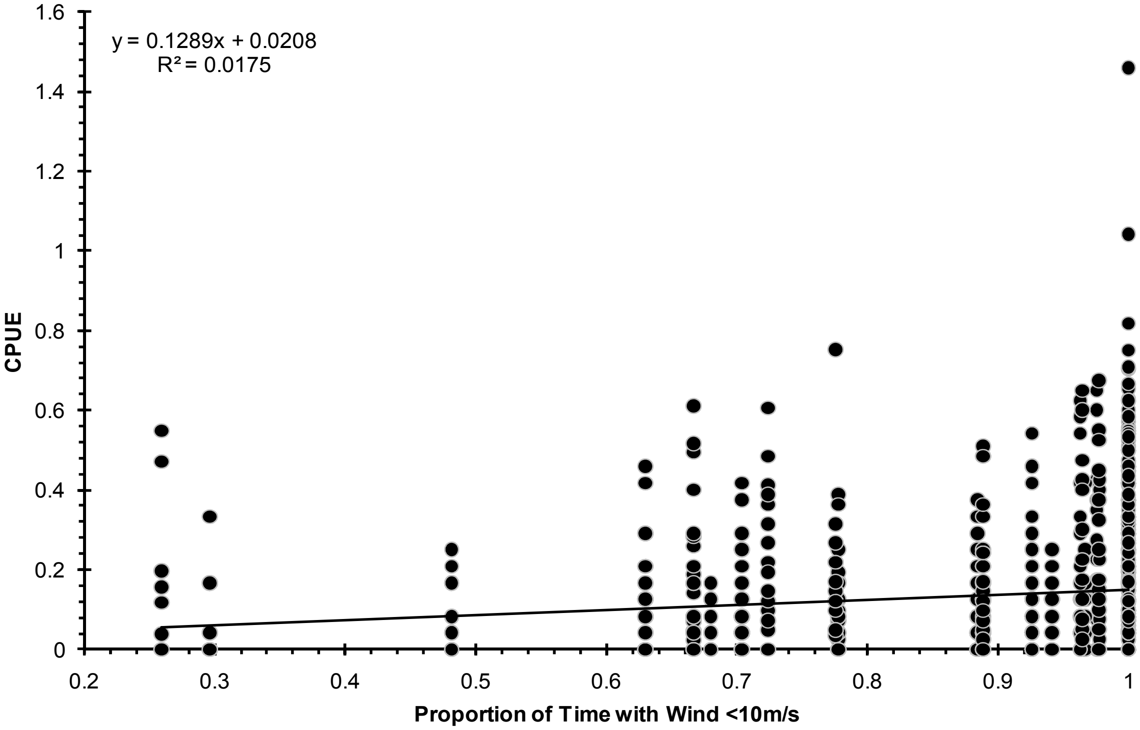

Figure 4.5- Catch-per-unit-effort (bonefish/hour) plotted against proportion of time spent in a tournament with wind <10 meter per second (n = 1,408).

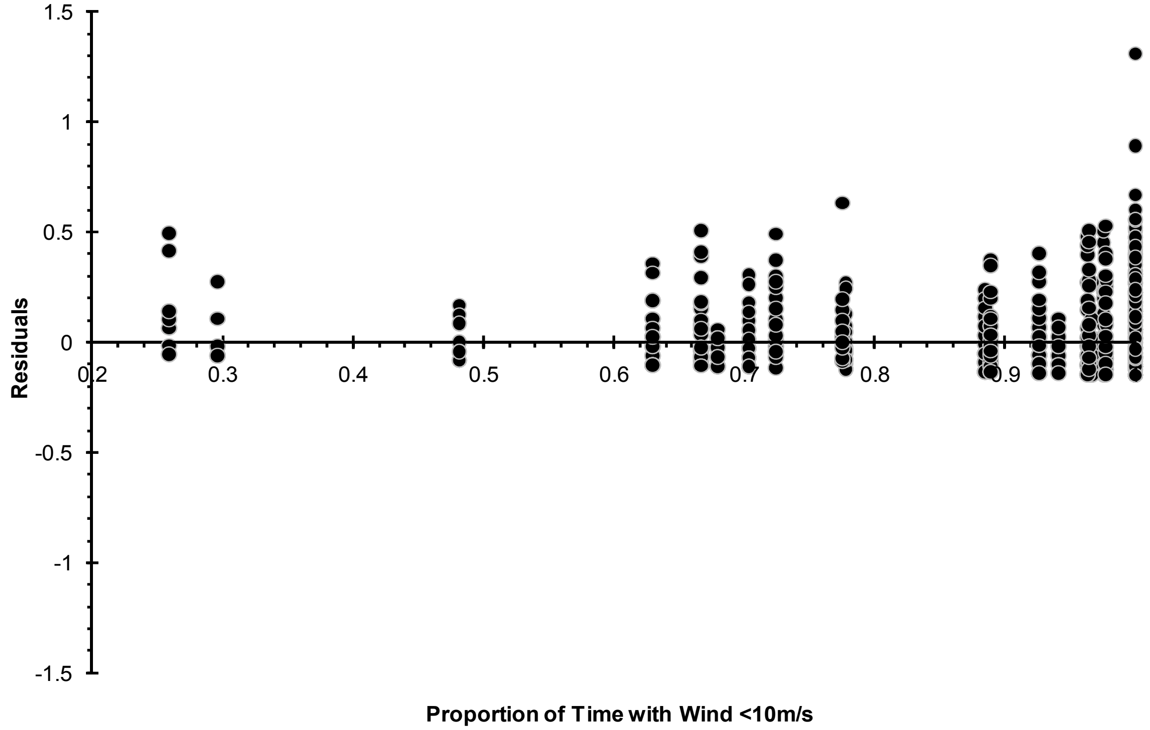

Figure 4.6- Residuals from fitting a linear model to catch-per-unit-effort (bonefish/hour) plotted against proportion of time spent in a tournament with wind <10 meter per second (n = 1,408).

The log-transformed frequency distribution of positive catch rates was approximately normally distributed (**Figure 4.7)**. The step-wise analysis of deviance (**Table 4.4**) for the complete index indicated that Gear, Season, and Year*Season were the significant explanatory variables for the positive catch, and only the Hour factor was significant for the proportion of positive trip-records. The Year*Season interaction of the positive catches was significant (**Table 4.5**) (likelihood ratio tests: $\chi^2 = 5.9$, df = 1, $P = 0.0151$) and improved the model fit (lower AIC and BIC values).

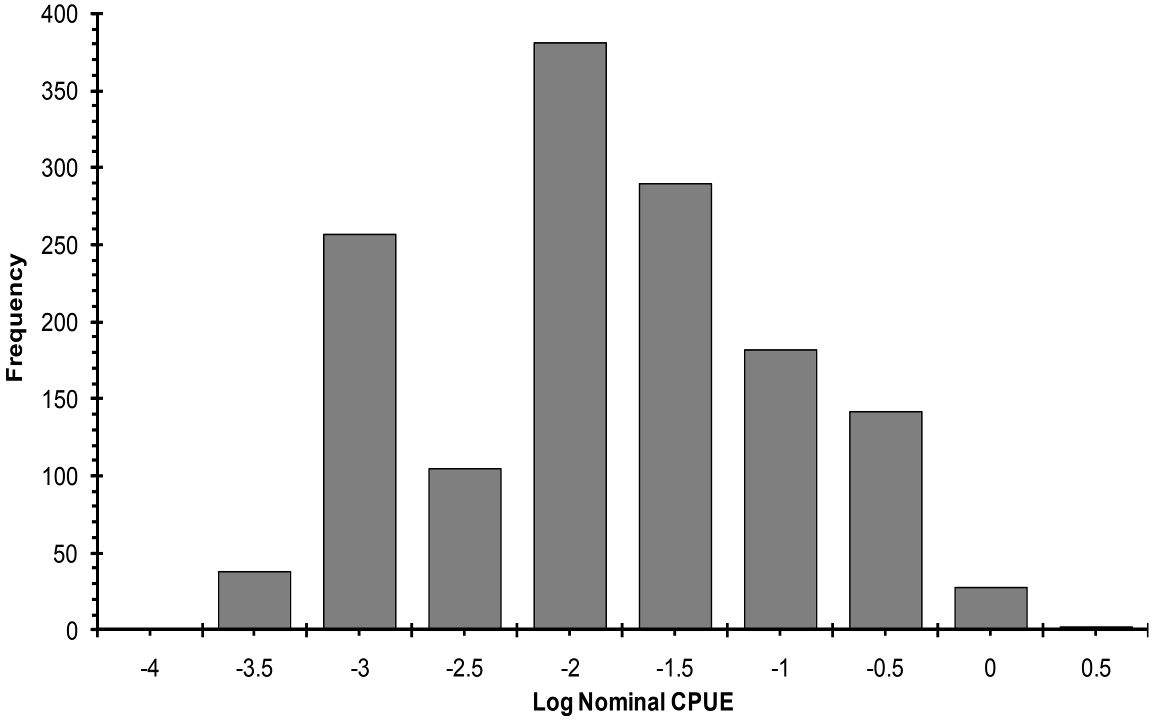

Figure 4.7- Frequency distribution for log transformed positive catch rates (bonefish per hour) from south Florida bonefish tournaments (1968-2010).

Table 4.4- Deviance analysis table showing the stepwise addition of explanatory factors for the delta lognormal model for complete bonefish tournament catch rates (bonefish per hour) from 1968 to 2010. Percentage difference refers to the total percentage of difference between the model with the explanatory variables and the null model. *P* value refers to the Chi-square probability between consecutive models.

Factors for Positive Catch	Degrees of Freedom	Deviance	Deviance per degrees of freedom	Percentage difference	*P*
Null Model with Year	1387	937.7	0.6760		
Year + Gear	1386	906.4	0.6540	3.27	<0.0001
Year + Gear + Season	1385	891.6	0.6437	1.51	<0.0001
Year + Gear + Season + Year*Season	1357	859.8	0.6336	1.49	<0.0001
Factors for Proportion Positive	Degrees of Freedom	Deviance	Deviance per degrees of freedom	Percentage difference	*P*
Null Model with Year	1795	1872.8	1.0434		
Year + Hour	1794	1768.4	0.9857	5.5	<0.0001

Table 4.5- Analysis of an interaction for inclusion in the positive catch submodel for the complete bonefish tournament catch rates (bonefish per hour) from 1968 to 2010. Likelihood ratio tests the differences of -2* residual log likelihoods (-2 REM log likelihood) between two nested models, while *P* represents the Chi-squared probability for the likelihood ratio tests. Akaike's Information Criteria and Schwartz's Bayesian Criterion represent goodness of fit criteria to assess how the interaction affected the overall model.

Positive Catch	-2 REM Log likelihood	Akaike's Information Criterion	Schwartz's Bayesian Criterion	*P*
Year + Gear + Season	3462.6	3464.6	3469.9	
Year + Gear + Season + Season*Year	3456.7	3460.7	3465.0	0.0151

The step-wise analysis of deviance (**Table 4.6**) for the truncated index indicated the factors Gear, Moon, and Year*Moon were the significant explanatory variables for the positive catch, and the factors Hour and Wind were the significant exploratory variables for the proportion of positive trip-records. The Year*Moon interaction of the positive catches was significant (**Table 4.7**) (likelihood ratio tests: $\chi^2 = 8.9$, df = 1, $P = 0.0029$) and improved the model fit (lower AIC and BIC values).

Table 4.6- Deviance analysis table showing the stepwise addition of explanatory factors for the delta lognormal model for the truncated bonefish tournament catch rates (bonefish per hour) from 1991 to 2010. Percentage difference refers to the total percentage of difference between the model with the explanatory variables and the null model. *P* value refers to the Chi-square probability between consecutive models.

Factors for Positive Catch	Degrees of Freedom	Deviance	Deviance per degrees of freedom	Percentage difference	*P*
Null Model with Year	947	636.7	0.6723		
Year + Gear	946	619.3	0.6547	2.63	<0.0001
Year + Gear + Moon	939	605.0	0.6443	1.54	0.0020
Year + Gear + Moon + Year*Moon	911	571.7	0.6276	2.49	0.0018
Factors for Proportion Positive	**Degrees of Freedom**	**Deviance**	**Deviance per degrees of freedom**	**Percentage difference**	***P***
Null Model with Year	1242	1308.6	1.0536		
Year + Hour	1241	1250.9	1.0080	4.33	<0.0001
Year + Hour + Wind	1240	1231.0	0.9928	1.44	<0.0001

Table 4.7- Analysis of an interaction for inclusion in the positive catch submodel for the truncated bonefish tournament catch rates (bonefish per hour) from 1991 to 2010. Likelihood ratio tests the differences of -2* residual log likelihoods (-2 REM log likelihood) between two nested models, while *P* represents the Chi-squared probability for the likelihood ratio tests. Akaike's Information Criteria and Schwartz's Bayesian Criterion represent goodness of fit criteria to assess how the interaction affected the overall model.

Positive Catch	-2 REM Log likelihood	Akaike's Information Criterion	Schwartz's Bayesian Criterion	*P*
Year + Gear + Moon	2369.4	2409.4	2507.1	-
Year + Gear + Moon + Year*Moon	2360.5	2402.5	2445.1	0.0029

Delta-lognormal indices of relative abundance were created for the complete and truncated indices. Diagnostic plots for the complete index's fit of proportion of positive model component (**Figure 4.8**), and the fit of the positive observations model (qq plot) (**Figure 4.9**) corroborate the final model selection. **Table 4.8** displays the complete index and **Table 4.9** provides the coefficients. Comparison between the standardized CPUE and the observed CPUE for the complete index (**Figure 4.10**) shows similar patterns in changes in catch rates. **Table 4.10** displays the truncated index and **Table 4.11** provides the coefficients. The truncated index is more variable from year to year then the complete index (**Figure 4.11**). The two indices are not statistically different as shown by their overlapping confidence intervals. The truncated index had a higher standardized CPUE value in 1995 and 1997 and a lower value in 2005.

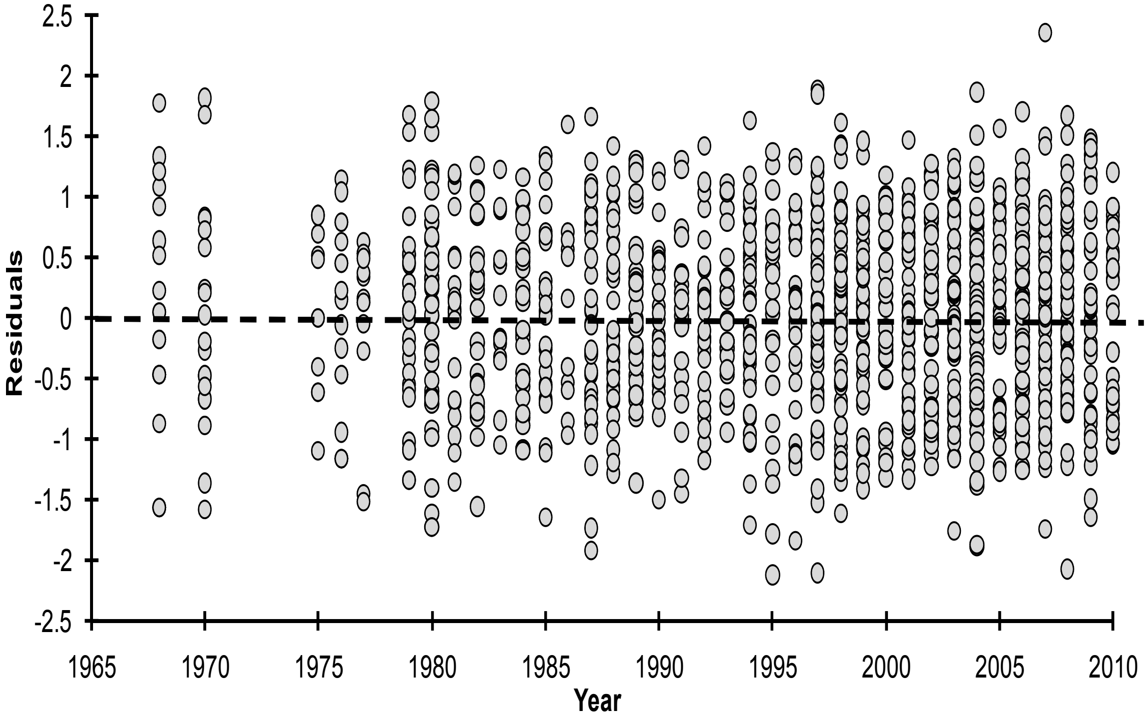

Figure 4.8- Residual distribution, by year, from the proportion of positive observations of the complete index model fit for bonefish tournament catch rates (bonefish per hour) from 1968 to 2010. The dashed line represents zero values.

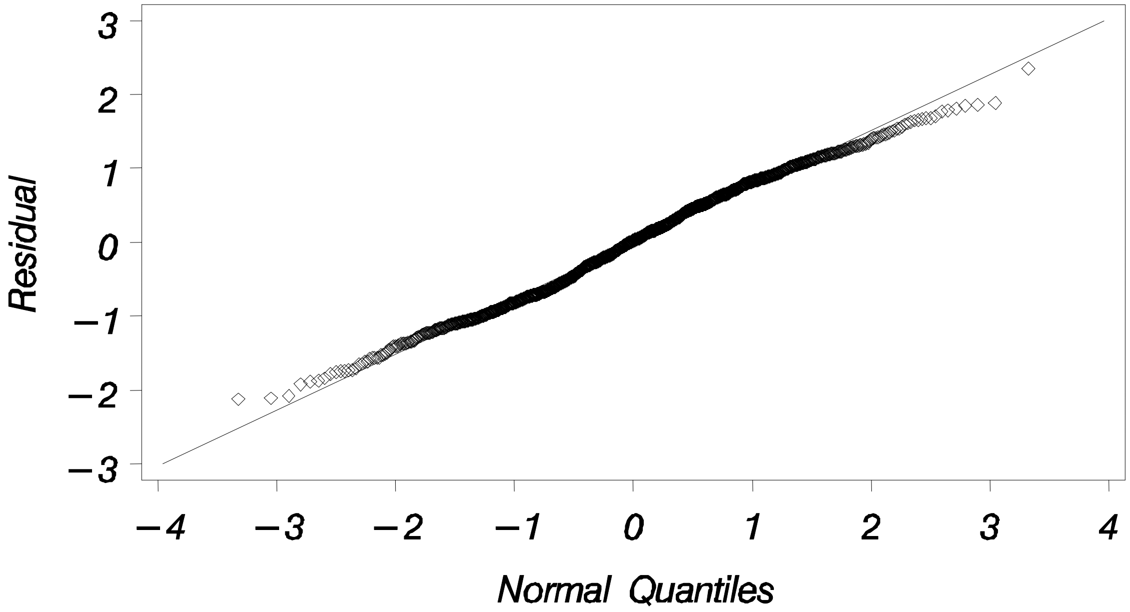

Figure 4.9- Normalized predicted plot (qq-plot) of residual fit of the positive observations of the complete index model fit for bonefish tournament catch rates (bonefish per hour) from 1991 to 2010.

Table 4.8- Delta-lognormal indices of relative abundance (I_y) (bonefish per hour) for the complete bonefish tournament catch rates from 1968 to 2010. Total number of catch records (n), total number of catch records where a bonefish was caught (S), and the nominal frequency of occurrence of a bonefish catch for each year. Coefficient of variation (CV) and the upper (UCL) and lower (LCL) 95% confidence intervals are also provided for each year.

Year	n	S	Frequency	I_y	CV	LCL	UCL
1968	23	21	0.9130	1.0227	0.2715	0.5999	1.7433
1970	23	20	0.8696	0.7540	0.2855	0.4308	1.3198
1975	19	12	0.6316	0.6089	0.3786	0.2928	1.2662
1976	19	17	0.8947	0.6898	0.3042	0.3805	1.2507
1977	20	13	0.6500	0.6533	0.3810	0.3128	1.3644
1979	44	38	0.8636	0.7331	0.2450	0.4523	1.1881
1980	52	46	0.8846	0.7956	0.2362	0.4992	1.2679
1981	37	25	0.6757	1.1968	0.2307	0.7591	1.8870
1982	31	27	0.8710	1.1041	0.2072	0.7326	1.6638
1983	24	16	0.6667	1.2218	0.2517	0.7443	2.0055
1984	44	30	0.6818	0.7390	0.2124	0.4854	1.1250
1985	35	26	0.7429	1.3720	0.2109	0.9039	2.0824
1986	21	13	0.6191	1.0387	0.2845	0.5945	1.8149
1987	45	40	0.8889	1.0945	0.1917	0.7485	1.6005
1988	44	34	0.7727	1.4843	0.2027	0.9936	2.2173
1989	50	40	0.8000	1.2553	0.1894	0.8623	1.8274
1990	39	29	0.7436	1.1549	0.2124	0.7587	1.7580
1991	28	21	0.7500	0.8528	0.2249	0.5469	1.3298
1992	48	33	0.6875	0.9930	0.2064	0.6600	1.4940
1993	37	27	0.7297	1.0127	0.2079	0.6711	1.5282
1994	56	45	0.8036	1.1611	0.1847	0.8050	1.6746
1995	34	28	0.8235	1.3463	0.2053	0.8966	2.0213
1996	43	34	0.7907	1.3240	0.1954	0.8991	1.9498
1997	72	64	0.8889	1.3714	0.1706	0.9774	1.9242
1998	77	61	0.7922	1.0183	0.1737	0.7214	1.4375
1999	61	50	0.8197	1.0087	0.1808	0.7046	1.4438
2000	80	59	0.7375	1.3137	0.1946	0.8934	1.9318
2001	67	51	0.7612	0.9310	0.1792	0.6524	1.3285
2002	69	58	0.8406	0.9545	0.1755	0.6738	1.3522
2003	86	76	0.8837	1.1242	0.1666	0.8075	1.5650
2004	90	65	0.7222	0.8448	0.1731	0.5991	1.1911
2005	60	48	0.8000	0.9250	0.1821	0.6445	1.3275
2006	80	63	0.7875	0.9312	0.1725	0.6612	1.3114
2007	77	63	0.8182	0.7802	0.1722	0.5543	1.0981
2008	74	52	0.7027	0.6783	0.1810	0.4736	0.9714
2009	60	44	0.7333	0.9305	0.1912	0.6369	1.3594
2010	63	35	0.5556	0.5796	0.2066	0.3851	0.8724

Table 4.9- Summary of coefficients for the complete bonefish tournament catch rates from 1968 to 2010. "RC" is the reference category and "NA" is not applicable.

Positive Catch	Estimate	Standard Error	Proportion Positive	Estimate	Standard Error
Intercept	-2.572	0.180	Intercept	2.201	0.409
Year 1968	-0.152	0.296	Year 1968	0.150	0.969
Year 1970	-0.170	0.298	Year 1970	-0.304	0.841
Year 1975	0.051	0.332	Year 1975	-1.662	0.697
Year 1976	-0.222	0.307	Year 1976	-0.061	0.977
Year 1977	0.251	0.325	Year 1977	-1.582	0.691
Year 1979	-0.185	0.271	Year 1979	-0.356	0.663
Year 1980	-0.029	0.265	Year 1980	-0.165	0.658
Year 1981	0.286	0.263	Year 1981	-0.214	0.551
Year 1982	0.188	0.260	Year 1982	0.952	0.732
Year 1983	0.404	0.289	Year 1983	-0.176	0.637
Year 1984	-0.053	0.256	Year 1984	-0.217	0.523
Year 1985	0.521	0.262	Year 1985	0.376	0.570
Year 1986	0.261	0.326	Year 1986	0.262	0.613
Year 1987	0.289	0.245	Year 1987	1.036	0.664
Year 1988	0.690	0.250	Year 1988	0.186	0.556
Year 1989	0.416	0.244	Year 1989	0.824	0.528
Year 1990	0.441	0.256	Year 1990	0.120	0.562
Year 1991	0.143	0.271	Year 1991	0.334	0.628
Year 1992	0.285	0.254	Year 1992	0.159	0.493
Year 1993	0.260	0.260	Year 1993	0.770	0.533
Year 1994	0.340	0.241	Year 1994	0.840	0.511
Year 1995	0.488	0.257	Year 1995	0.689	0.639
Year 1996	0.509	0.250	Year 1996	0.660	0.554
Year 1997	0.421	0.231	Year 1997	1.586	0.543
Year 1998	0.229	0.232	Year 1998	0.837	0.456
Year 1999	0.233	0.239	Year 1999	0.915	0.507
Year 2000	0.299	0.233	Year 2000	0.544	0.433
Year 2001	0.183	0.237	Year 2001	0.936	0.455
Year 2002	0.184	0.235	Year 2002	1.439	0.493
Year 2003	0.371	0.228	Year 2003	1.569	0.505
Year 2004	0.184	0.231	Year 2004	0.495	0.417
Year 2005	0.196	0.240	Year 2005	0.843	0.497
Year 2006	0.282	0.231	Year 2006	0.946	0.446
Year 2007	0.078	0.231	Year 2007	1.109	0.466
Year 2008	0.054	0.236	Year 2008	0.432	0.432
Year 2009	0.351	0.243	Year 2009	0.789	0.459
Year 2010	RC	NA	Year 2010	RC	NA
Gear - Bait	0.298	0.050	24 Hour	-1.978	0.276
Gear - Fly	RC	NA	40 Hour	RC	NA
Fall	0.227	0.064			
Spring	RC	NA			

Table 4.10- Delta-lognormal indices of relative abundance (I_y) (bonefish per hour) for the truncated bonefish tournament catch rates from 1991 to 2010. Total number of catch records (n), total number of catch records where a bonefish was caught (S), and the nominal frequency of occurrence of a bonefish catch for each year. Coefficient of variation (CV) and the upper (UCL) and lower (LCL) 95% confidence intervals are also provided for each year.

Year	n	S	Frequency	I_y	CV	LCL	UCL
1991	28	21	0.7500	0.7793	0.2700	0.4584	1.3247
1992	48	33	0.6875	1.0061	0.2030	0.6732	1.5036
1993	37	27	0.7297	0.8188	0.2228	0.5272	1.2717
1994	56	45	0.8036	1.1080	0.2125	0.7278	1.6868
1995	34	28	0.8235	1.6112	0.2640	0.9588	2.7077
1996	43	34	0.7907	1.3543	0.2317	0.8573	2.1395
1997	72	64	0.8889	1.5331	0.2072	1.0174	2.3102
1998	77	61	0.7922	0.9515	0.2021	0.6377	1.4197
1999	61	50	0.8197	0.9262	0.1956	0.6286	1.3645
2000	80	59	0.7375	0.9464	0.1872	0.6529	1.3717
2001	67	51	0.7612	0.8465	0.2151	0.5532	1.2953
2002	69	58	0.8406	1.0203	0.1887	0.7019	1.4832
2003	86	76	0.8837	1.0682	0.1851	0.7400	1.5419
2004	90	65	0.7222	0.8521	0.1992	0.5743	1.2642
2005	60	48	0.8000	0.8163	0.2087	0.5402	1.2337
2006	80	63	0.7875	0.9389	0.1887	0.6458	1.3649
2007	77	63	0.8182	0.8557	0.1808	0.5978	1.2250
2008	74	52	0.7027	0.7560	0.2138	0.4953	1.1538
2009	60	44	0.7333	1.1026	0.2160	0.7194	1.6899
2010	63	35	0.5556	0.7087	0.1936	0.4828	1.0401

Table 4.11- Summary of coefficients for the truncated bonefish tournament catch rates from 1991 to 2010. “RC” is the reference category and “NA” is not applicable.

Positive Catch	Estimate	Standard Error	Proportion Positive	Estimate	Standard Error
Intercept	0.688	0.623	Intercept	-2.670	0.222
Year 1991	-0.341	0.494	Year 1991	0.121	0.279
Year 1992	-0.011	0.404	Year 1992	0.338	0.256
Year 1993	0.621	0.480	Year 1993	0.105	0.269
Year 1994	0.196	0.502	Year 1994	0.316	0.244
Year 1995	0.882	0.470	Year 1995	0.549	0.312
Year 1996	0.103	0.491	Year 1996	0.491	0.255
Year 1997	1.321	0.440	Year 1997	0.504	0.265
Year 1998	0.881	0.505	Year 1998	0.126	0.244
Year 1999	0.378	0.680	Year 1999	0.231	0.225
Year 2000	0.317	0.369	Year 2000	0.225	0.246
Year 2001	0.982	0.398	Year 2001	0.054	0.255
Year 2002	0.828	0.450	Year 2002	0.218	0.234
Year 2003	0.971	0.476	Year 2003	0.271	0.253
Year 2004	-0.095	0.391	Year 2004	0.110	0.229
Year 2005	0.291	0.420	Year 2005	0.109	0.256
Year 2006	0.384	0.442	Year 2006	0.203	0.244
Year 2007	0.758	0.411	Year 2007	0.046	0.232
Year 2008	0.124	0.421	Year 2008	-0.036	0.264
Year 2009	0.209	0.422	Year 2009	0.285	0.251
Year 2010	RC	NA	Year 2010	RC	NA
24 Hours	-2.439	0.396	Gear - Bait	0.235	0.066
40 Hours	RC	NA	Gear - Fly	RC	NA
Wind	2.586	0.511	Full Moon	0.360	0.174
			First Quarter Moon	0.399	0.166
			New Moon	0.330	0.177
			Last Quarter Moon	0.339	0.208
			Waning Crescent	0.234	0.225
			Waning Gibbous	0.488	0.201
			Waxing Crescent	0.129	0.200
			Waxing Gibbous	RC	NA

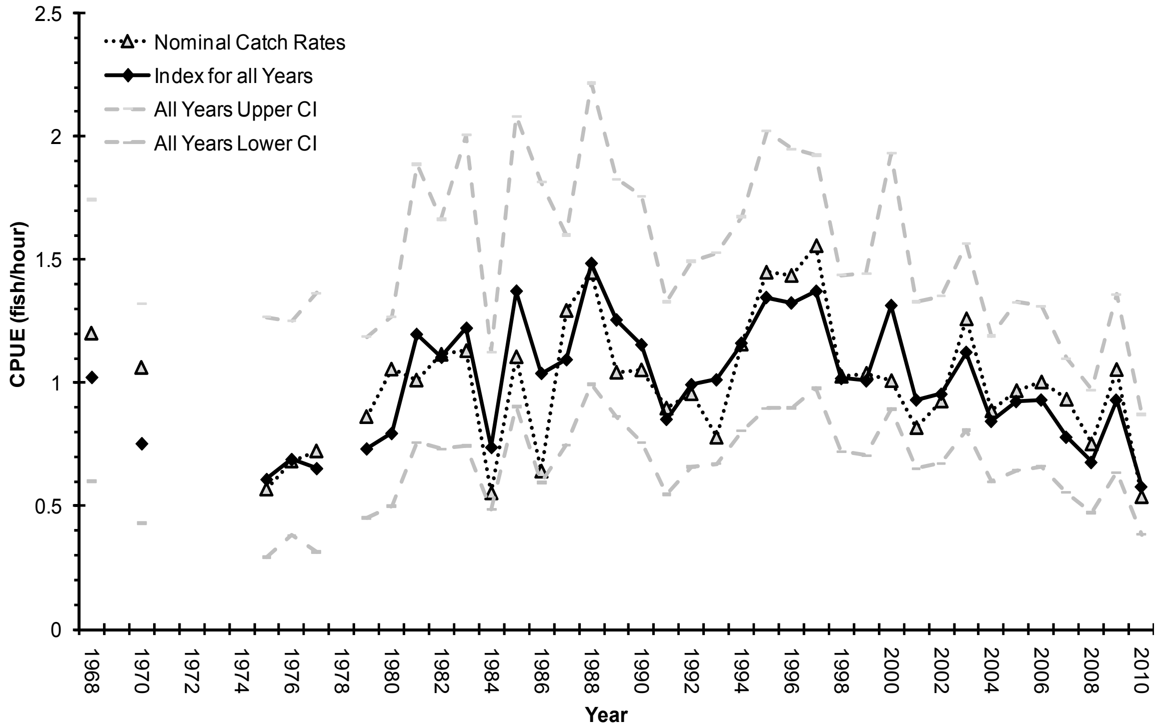

Figure 4.10- Standardized CPUE from the complete index (black dotted line) and nominal catch rates (black line) for bonefish tournament catch rates (bonefish per hour) from 1968 to 2010. Dashed gray lines indicate the estimated 95% confidence intervals for the standardized CPUE.

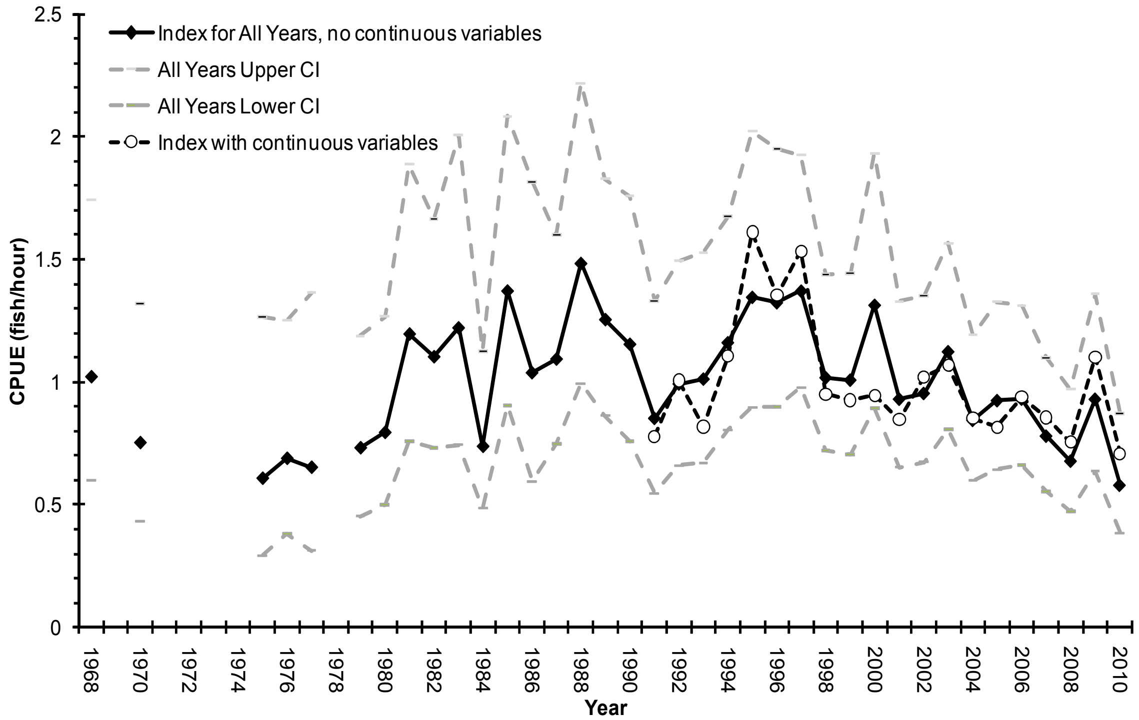

Figure 4.11- Complete standardized CPUE (black dotted line) and truncated standardized CPUE (black dashed line) for bonefish tournament catch rates from 1968 to 2010. Dashed gray lines indicate the estimated 95% confidence intervals for the complete standardized CPUE.

Discussion

The tournament CPUE data do not cover the entire spatial range of the bonefish population. All of the boats left and returned from the same marina which restricted the areas they fished. However, the marina used is located in the area of highest bonefish fishing effort (Larkin et al. 2010) and bonefish densities (Ault et al. 2008b). Also, the location of the marina and the one and a half hour travel time provided the opportunity for the fishermen to reach other areas of high fishing effort and bonefish densities (i.e. Key Largo, Biscayne Bay). Thus, the location of the tournament is in a prime location to capture trends in bonefish abundance.

The movements of the fish provide addition support of the tournaments capturing trends in bonefish abundance. A tagging project (Larkin et al. 2008) discovered that bonefish move throughout the entire south Florida fishery (i.e. Biscayne Bay to Lower Keys, Upper Keys to Biscayne Bay) throughout the year. The combination of both the movements of the fish and the tournament participants make it likely that the index is fairly representative of the entire south Florida bonefish stock.

The removal of the insignificant season factor and the addition of the two significant factors of moon phase and wind caused the truncated index to show greater changes in each year (**Figure 4.11**). The truncated index removed variation in the data that was not specifically attributed to changes in abundance. This may have caused a more accurate reflection of abundance; however, it is still within the confidence intervals of the index without those variables in the model (complete index). Therefore, there are no statistical differences between them.

The standardized index shows changes in abundance that may reflect fishing regulations. In 1985 commercial fishing was banned in Everglades National Park. This could have affected bonefish population size because the mullet netting fishery, the largest commercial fishery operating in the park in the early 1980's, reported bonefish as bycatch (Tilmant 1989). After 1985 the bonefish CPUE indices increased to the highest levels in the time series.

An interesting trend in the predicted indices values was the decline from 1997 to 2010. A potential explanation for this decline may be an increase in fishing effort. This possibility was discussed in Chapter 3 where increased fishing pressure was the most common factor reported by fishers as contributing to stock decline. The addition of new fishery participants may be deleterious to the bonefish stock despite the fact that it is a no-harvest fishery, because there is apparently a 10% release mortality rate (Larkin et al.

2010). Pollock and Pine (2007) discussed how low mortality per angling capture event could result in substantial population impacts if effort and release rates are high. Cogging et al. (2007) simulated the impacts from a catch-and-release fishery by evaluating the combination of a size limit and release mortality. They found that even low release mortality rates (0.05) can cause significant declines in the population, especially for long-lived, low-productivity fish. Nelson (2002) demonstrated that the large increase in recreational snook fishing effort combined with a 3% post-release mortality is pushing the stock towards an overfished condition.

To date, there are no reliable estimates of total effort for the bonefish fishery. The recreational fishery survey of MRFSS is very broad scale and probably does not adequately monitor the bonefish fishery. The MRFSS survey has well documented shortcomings (NRC 2006), including a low number of intercepts with bonefish anglers (Crabtree et al. 1998a). A proxy for annual bonefish effort is the number of for-hire fishing permits of Everglades National Park (ENP). The mail survey revealed over one-third of the bonefish captains resided in the Florida Keys close to ENP, and the highest fishing effort values were inside the park boundaries (Chapter 3). A plot of Everglades National Parks annual for-hire fishing permits (acquired from Jason Osborne, Everglades National Park; only available for 1999 to 2010) against the standardized values for the truncated index shows divergence from 2004 to 2010 (**Figure 4.12**). The divergence suggests an increase in fishing effort may have caused the stock to decline.

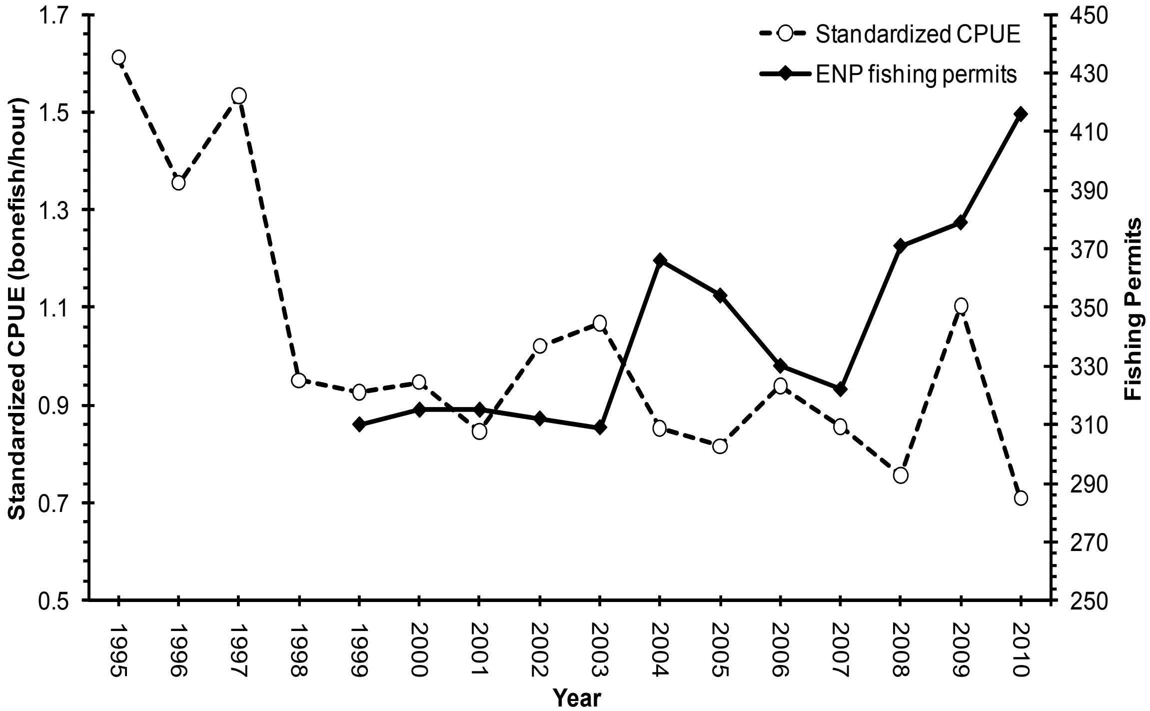

Figure 4.12- Truncated standardized CPUE (black dashed line) plotted with the number of for-hire fishing permits (black line) for Everglades National Park from 1995 to 2010.

4.6 Overall discussion

The majority of the mail survey respondents reported the decade of 1992 to 2002 as the most common time period of bonefish population decline. This is not consistent with the index of abundance from 1992 to 2001 which shows an increase then a decrease to about the same level. However, the fishermen's response may have been influenced by the large decrease in abundance seen from 1995 to 2002 (**Figures 4.10** and **4.11**).

The length-based mortality function provided similar total mortality estimates for each year when there was a sufficient sample size (n > 200). This trend implies a population that is not declining which contrasts the index of abundance and visual survey results. Both the index of abundance and visual survey display overall declining trends in recent years (**Figure 4.13**). However, the two results displayed inconsistent trends for the majority of the years.

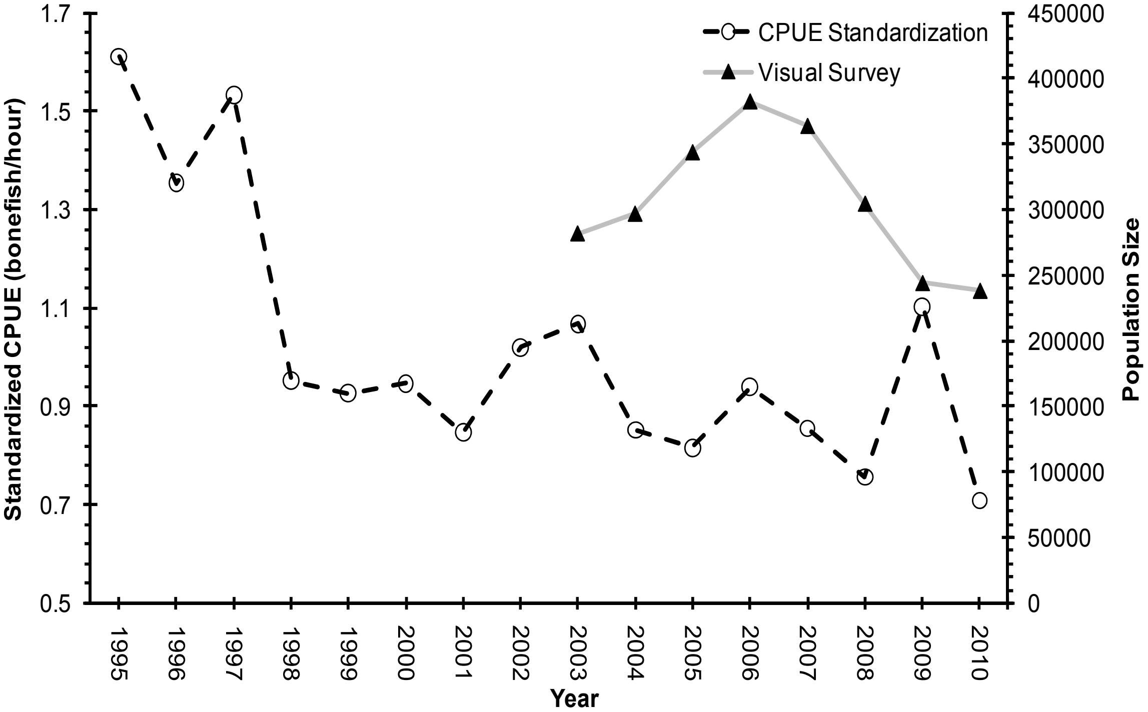

Figure 4.13- Truncated standardized CPUE (black dashed line) plotted with the population size generated from the visual survey (gray line) from 1995 to 2010.

Chapter 5

Tagging of bonefish in south Florida to determine movements[2]

Summary

Anchor tag and acoustic telemetry methods were used to determine bonefish movements. A total of 8,340 bonefish were fitted with anchor tags to produce 331 recaptures. The majority of the recaptures (45%) occurred at the location where the fish was tagged, demonstrating a high level of site fidelity. In contrast, thirty-seven bonefish (13%) were observed to have moved >20 km with substantial distances that ranged up to 340 km. Analysis of anchor tagging results revealed no significant relationships between distance moved and days at large, distance moved and length at tagging, and days at large and length at tagging. Results also demonstrated no significant effects of age and spawning season on movements. The acoustic telemetry (AT) project deployed forty AT-tagged bonefish into an array of forty hydrophone receivers to produce 57,070 detections. Results showed frequent movements around the barrier islands, schooling behavior, and, in contrast to the anchor tagging, showed a possible spawning effect with unique movements to the reef habitats.

Background

Despite the importance of bonefish as a premier game fish, there is little known about the stock's spatial distribution, spawning migrations or movements between fishing areas (Ault et al. 2008a). A lack of this kind of vital information hinders development of management practices to ensure sustainability of bonefish fisheries. The bonefish fishery

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[2] The majority of this chapter was published in Larkin et al. (2008).

is atypical in fact that fish are caught but not harvested (catch-and-release). Thus, controls placed on harvest would have little impact on fishery sustainability. One management option are spatial closures which are becoming more prevalent (Pauly et al. 2002, Lubchenco et al. 2003) and are currently practiced in south Florida (Ault et al. 2006). Understanding movement patterns are critical for effective spatial closures (Weatherbee et al. 2004). Thus, anchor tag and acoustic telemetry methods were used to evaluate and quantify bonefish movements and aspects of population dynamics.

Methods

Two complimentary methods, anchor tags and acoustic telemetry, each with its own advantages and disadvantages, were used to study movements, migrations, stock structure and population dynamics. Deployment of anchor tags broadly over the range of the fishery requires little training on how to tag bonefish and record necessary information. However, such mark-recapture data can only provide information on the time and location of tagging / release and, with luck, subsequent recapture. No inference is gained on the whereabouts or behavior of fish during the intervening period at liberty. Use of acoustic telemetry methods for monitoring bonefish movements – while labor intensive and requiring substantial technical expertise to deploy – provides high-resolution spatial and temporal data on fish movements and apparent responses to environmental cues.

Anchor Tagging

Initiated in 1998 in consultation with professional fishing captains and concerned anglers who ply the waters of the Florida Keys year-round, a bonefish anchor tagging program was developed that used volunteered expert efforts and well-tested quantitative methods in fishery science (Humston 2001; Ault et al. 2002a). Initially, volunteers received a tagging kit consisting of a Mark II pistol grip gun, Floy FD-94 T-bars tags (www.floytag.com), a document containing tagging instructions and guidelines, mechanical pencils, and a waterproof data sheet. In February of 2008 the project switched to Hallprint PDL dart tags (www.hallprint.com) and stainless steel Hallprint PDS applicators in an attempt to decrease tag shedding. After volunteers caught a bonefish on hook-and-line gear, they used the tag-gun or applicators to insert a relatively thin, high-grade polymer plastic tag into an "anchored" position between the dorsal musculature and pterygiophore bone structures of the fish. At the time of each tag deployment, the date, location, fork length (FL) and weight (W) was recorded.

Spatial differences in bonefish size were tested among regions using ANOVAs with statistical significance assessed at $\alpha = 0.05$. If differences were detected, Tukey's post-hoc test was run to define the differences. The regions were: A) Palm Beaches to north of Key Biscayne, B) Key Biscayne to north of Key Largo, C) Key Largo to Lower Matecumbe Key, D) Long Key to Pigeon Key, and E) Ohio Key to the Marquesas (**Figure 5.1**). The regions were defined by circumscribing geological and hydrographic features of the seascape (Marszalek et al. 1977; Shinn et al. 1977; Wolanksi 2000; Porter and Porter 2001) and distribution of bonefish fishing effort (**Figure 3.2**).

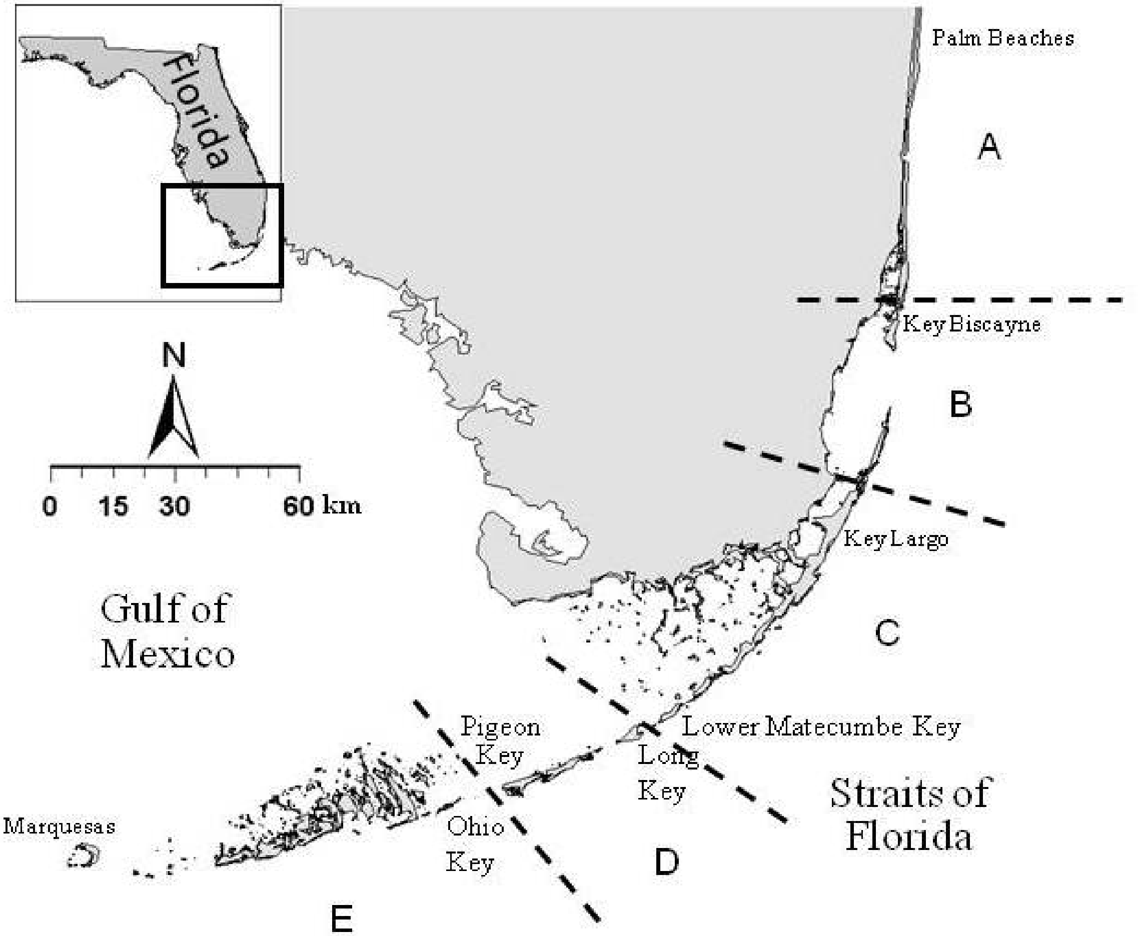

Figure 5.1- Map of south Florida illustrating the geographic regions defined for purpose of analysis. The regions are: A) Palm Beaches to north of Key Biscayne, B) Key Biscayne to north of Key Largo, C) Key Largo to Lower Matecumbe Key, D) Long Key to Pigeon Key, E) Ohio Key to the Marquesas.

The three relationships of: 1) distance and days at large, 2) distance and length at tagging, and 3) days at large and length at tagging were tested using a F-test with statistical significance assessed at $\alpha = 0.05$. In addition, the effect of age on movements was tested with distance moved and days at liberty data using ANOVAs with statistical significance assessed at $\alpha = 0.05$. Distance moved between tag and recapture was the shortest distance over water using ArcGIS software (ESRI, Redlands, CA). Both distance moved and days at liberty were log-transformed to cause approximately normally distributed data. Three age bins were defined by bonefish biology and adequate samples sizes. Juvenile bonefish were defined as a single bin < age 5 ($\leq$488 mm FL) based on the reproductive work of Crabtree et al. (1997). Bonefish ages 5 to 9 (>488 and $\leq$600 mm FL) were a middle age-bin chosen based on growth rate. In this age range, growth starts to slow down and approach an asymptote (**Figure 2.4**). The final age-bin was comprised of the oldest fish (> 9 years, >600 mm FL). During this period, growth reaches an asymptote causing a large degree of overlap in sizes for different ages (**Figure 2.4**).

The effect of spawning season on movements was tested by comparing movements within the season against movements outside the season, again using ANOVAs. Only bonefish tagged and recaptured within the spawning and non-spawning seasons were included in this analysis to allow accurate classification. Crabtree et al. (1997) defined bonefish spawning season as November to May. Since the spawning season is a longer duration (211 days) than the non-spawning season (186 days), days at large was not included in the spawning movement analysis.

Acoustic Telemetry

An automated acoustic telemetry (AT) system was deployed to continuously monitor movements of bonefish among the shallow flats, channels, and reefs extending from the Ragged Keys to Caesar Creek (**Figure 5.2**). Forty VEMCO (www.vemco.com) VR2 hydrophone receivers and data logging stations were deployed in an array that maximized the likelihood of tag detection whenever bonefish accessed or entered the flats, passed through telemetered channels, or cruised along the bayside or oceanside receiver array. To facilitate the evaluation of potential spawning migrations, two transects of receivers were oriented cross-shelf extending from the barrier island to the reef tract (roughly east-west) to increase the likelihood of capturing north-south migrations along the “outside” flats. This configuration also presented the possibility of documenting offshore movements if they occurred near either transect. The array had a spatial coverage of about 20 km running north to south and 8 km from east to west. VEMCO Model V16 coded acoustic transmitting pinger tags were employed on 69 kHz frequency with 158 dB (1 μPa at 1 m) power output, to maximize transmission power and receiver detection range. Tag transmissions were separated by 30 to 79 s (random) delays, providing battery life of at least 62 days post-activation. Acoustic tags were 58 mm long and 16 mm in diameter and were surgically implanted into the peritoneal cavity of bonefish using field procedures described in Humston et al. (2005). All AT-tagged fish were also identified with conventional T-bar anchor tags (Floy Tag) prior to release into the array of hydrophone receivers. Tagging efforts were focused around the spawning season, defined as November to May by Crabtree et al. (1997), to capture migrations and movements relative to frontal passages.

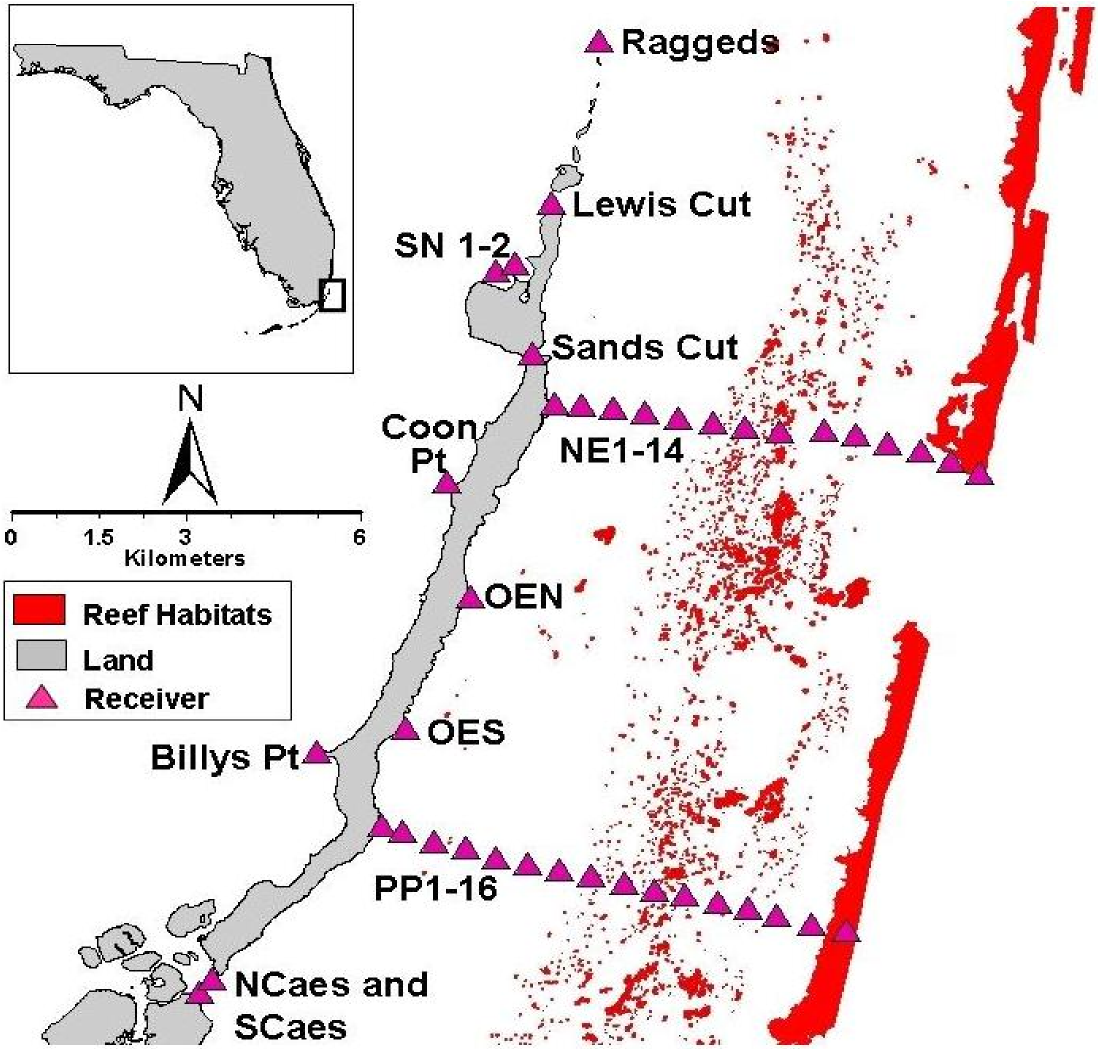

Figure 5.2- Location of the forty VR2 hydrophone receiver array (magenta triangles) used in the bonefish acoustic telemetry study extending from the Ragged Keys (RK) to southern Biscayne Bay at Caesar Creek (NCaes and SCaes).

Due to the difficulty of obtaining bonefish, a professional bonefish fishing guide was employed to help catch bonefish and then bring them to holding pens with recirculating seawater at the University of Miami's Rosenstiel School near Key Biscayne. At the facility, AT-tagging procedures were conducted, and fish were then released back into the ocean within 1 to 3 days. Most tagged bonefish placed in holding pens were released close to or within the VR2 array. Bonefish tagged in the field were released near their capture location, which was typically ≤ 1 km from one of the hydrophone receivers.

Assessment of hydrophone reception ranges were conducted following the procedure described in Humston et al. (2005). Results of range-testing of acoustic telemetry tags by hydrophone receivers revealed that detections were limited to 200 to 450 m at relatively shallow (<2 m) sites; while at deep ($\geq$2 m) receivers, AT tag detections ranged from 500 to 700 m. Tag range-testing results were used to guide configuration of the receiver array.

Swimming speed relates to maturation, diet, growth, and feeding (Videler 1993). Bonefish speed was calculated by the distance moved over time between receivers. Speed was calculated both as distance and fish body length (fork length) moved per second. Only receivers deployed in a linear format could be reliably used to calculate speed. Therefore, only movements between Sands Cut, NE1, OEN, OES, PP1, North Caesar were used (**Figure 5.2**).

Results

Anchor Tagging

From 1998 through 2010 a total of 8,340 bonefish were captured by about 100 volunteer captains and experienced anglers, fitted with anchor tags and then released into south Florida coastal waters ranging from the Palm Beaches down through the Florida Keys and west to the Marquesas (**Figure 5.1**). Both the number of bonefish released with tags, and those subsequently recaptured, increased until 2006 then experienced an overall decline until 2010 (**Figure 5.3**).

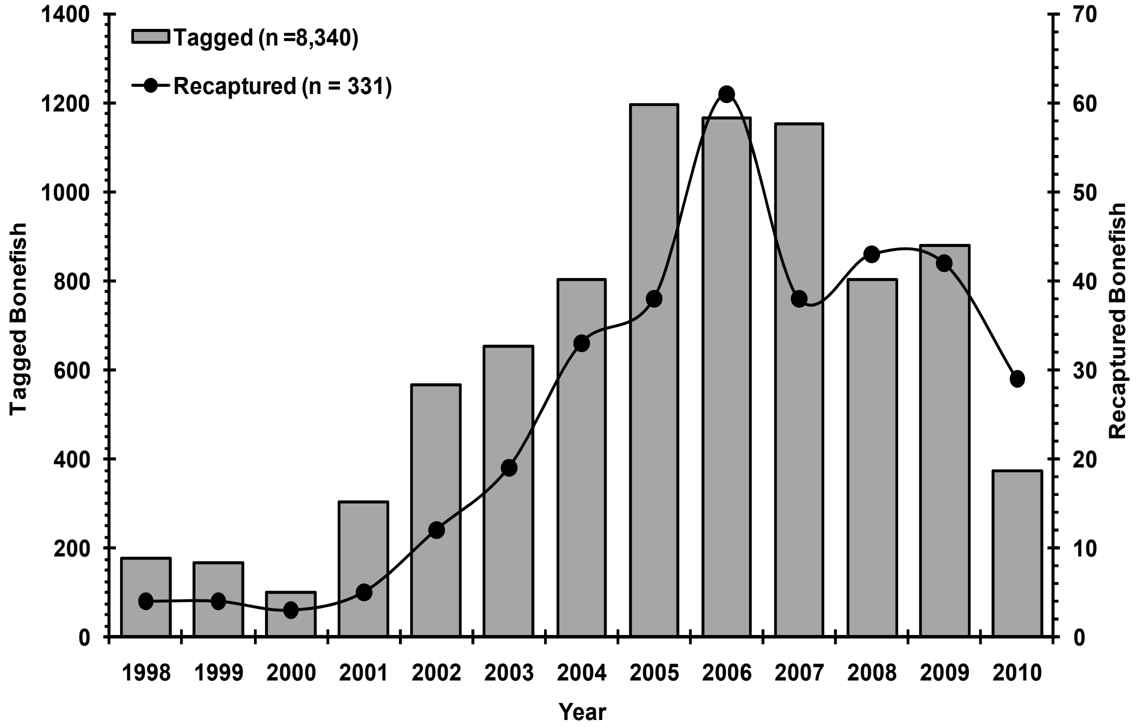

Figure 5.3- Numbers of bonefish anchor tagged (histograms) and recaptured (dark circles and black line) by year from 1998 to 2010.

The anchor tags were not evenly distributed throughout south Florida. The majority of the tagging effort took place in the Upper Keys (regions B and C) with relatively few fish tagged in regions D and E (**Table 5.1**). This same trend was reflected in the number of recaptures in each region.

Table 5.1–Bonefish tagged and recaptured by region. The regions are: A) Palm Beaches to north of Key Biscayne, B) Key Biscayne to north of Key Largo, C) Key Largo to Lower Matecumbe Key, D) Long Key to Pigeon Key, E) Ohio Key to the Marquesas.

Region of tagging	Total Tagged	Total Recaptured
A	730	0
B	5156	204
C	2080	80
D	105	1
E	269	2

The comparison of mean size at tagging from the five regions shows significant differences (**Figure 5.4**, ANOVA: F=1482, df=4, P<0.001). All of the means were statistically different from each other (Tukey test, P<0.001) except for the means from regions D and E (Tukey's test, P=0.997). The largest mean sizes came from the Upper Keys (regions B and C), and an extremely small average size came from the Palm Beaches (region A).

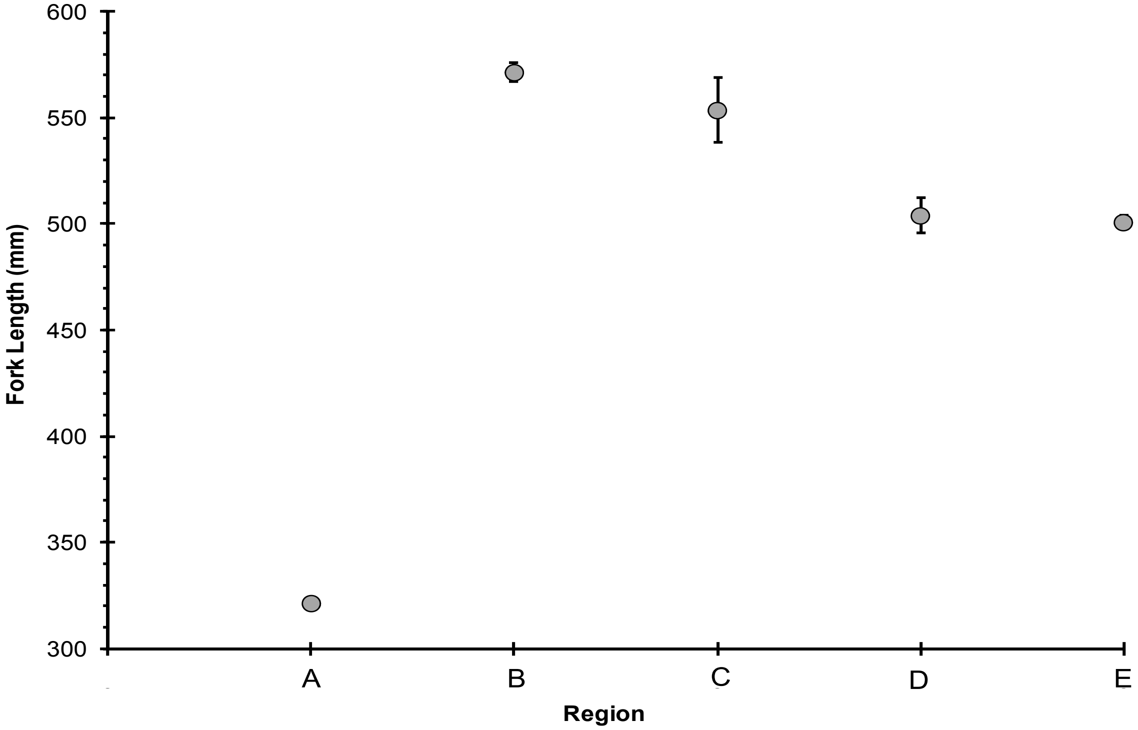

Figure 5.4- Average size at tagging and 95% confidence intervals for each region (n=8,210). The confidence intervals for regions A, B, and E are small and difficult to see on the figure. The regions are: A) Palm Beaches to north of Key Biscayne, B) Key Biscayne to north of Key Largo, C) Key Largo to Lower Matecumbe Key, D) Long Key to Pigeon Key, E) Ohio Key to the Marquesas.

A total of 331 (4.0%) tagged bonefish have been recaptured. All of the relevant information (i.e. size, date, location) were available for ~280 of the recaptures. Patterns documented from recaptured anchor-tagged bonefish revealed individual movements and stock mixing throughout the Florida Keys (**Figure 5.5**). The majority (87.1%) of observed bonefish movements were < 20 km, with 45% of those fish being recaptured at the same location where they were tagged (i.e. zero movement). In contrast, thirty-seven bonefish (13%) were observed to have moved >20 km, and some for substantial distances that ranged up to 340 km. Two bonefish tagged in south Florida were recaptured at Andros Island, Bahamas, traveling a least-linear distance of >300 km.

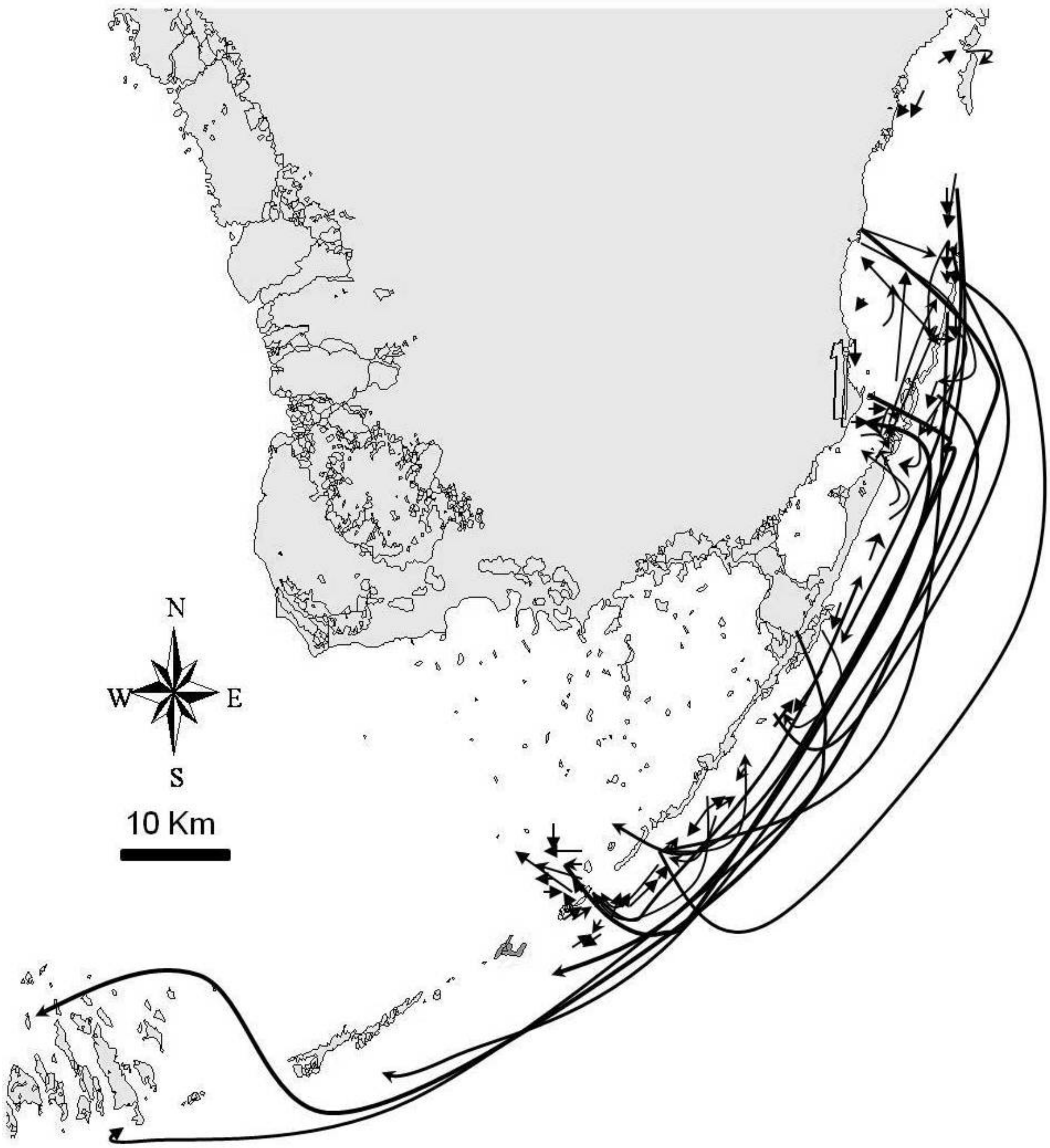

Figure 5.5- Summary of bonefish movements from recaptured anchor-tagged bonefish for which both release and recapture locations were known.

No apparent relationship existed between the distances moved and days at liberty for recaptured bonefish (**Figure 5.6A**) (F-statistic=2.07, df=282, *P*=0.1514). Bonefish moved substantial distances (>100 km) in periods that ranged from 15 to >400 days. Some bonefish appeared to have only moved a few km, even after two years at liberty. Bonefish size and days at liberty were not correlated (**Figure 5.6B**) (F-statistic=0.6429, df=279, *P*=0.4233), suggesting no differential mortality by size due to tagging. Almost the entire size range showed long distance movements (>20 km) with the majority being large, sexually mature (>488 mm FL from Crabtree et al. 1997) bonefish **(Figure 5.6C**). However, there was no significant relationship between distance moved and bonefish size (F-statistic=0.5977, df=280, P=0.4401).

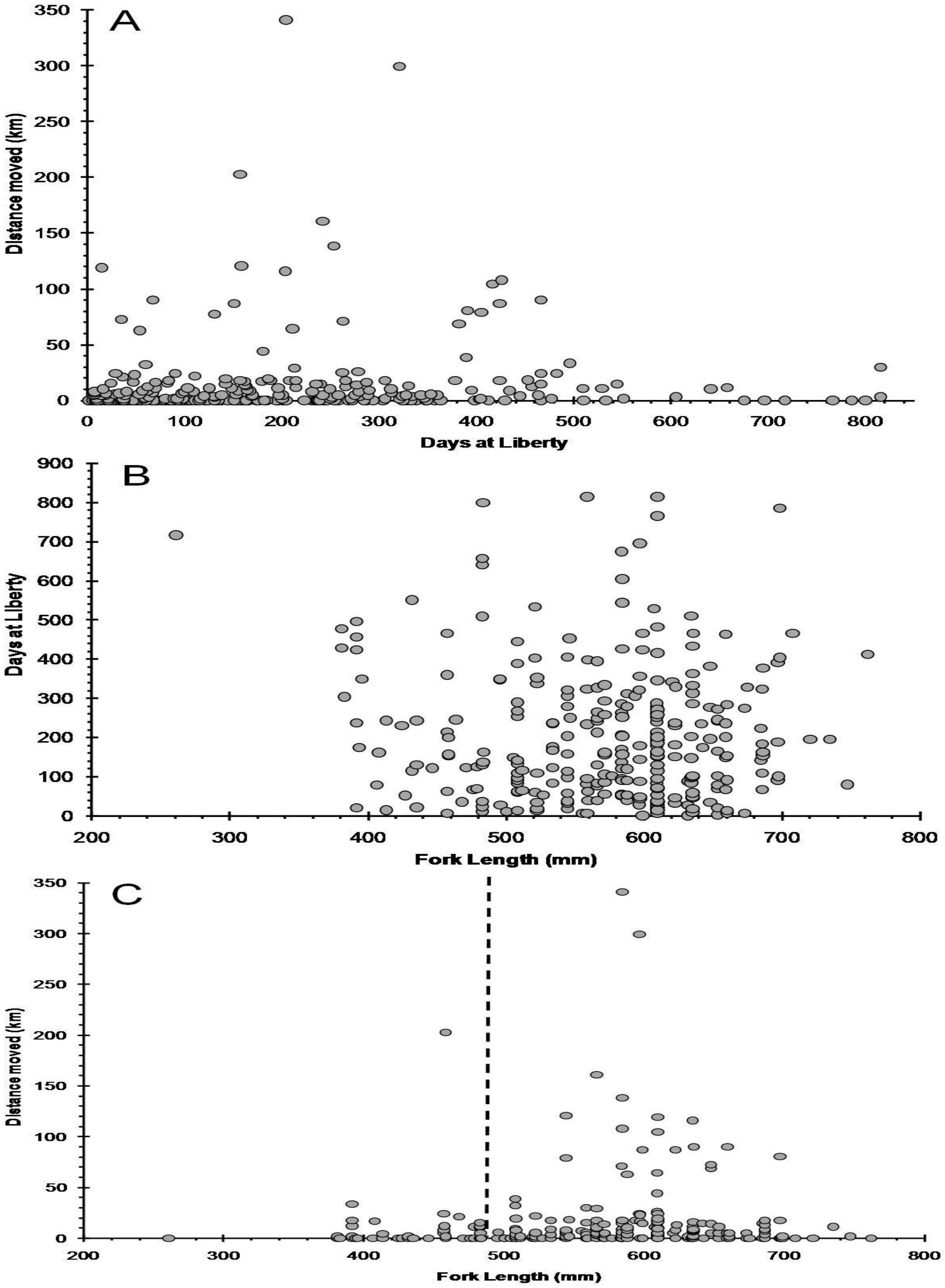

Figure 5.6- Results from recaptured anchor-tagged bonefish: (A) least-linear distance moved dependent on days at liberty (n=287); (B) days at liberty dependent on size (mm FL) at release (n=284); and, (C) least-linear distance moved dependent on size at release (n=285). Dashed vertical line shows minimum size at 50% sexual maturity (488 mm FL from Crabtree et al. 1997).

The majority (45%) of the distance records had zero movement. This prevented log-transformation of distances to reduce skewdness and to homogenize variability. Additionally, these zero movement results did not provide any evidence of movement which limited comparisons. To pursue the movement analyses, the zero movement results were removed which allowed comparison of movements between ages and within and among spawning season.

A summary of movements of each age-bin resulted in the "middle" age bin with the largest mean distance moved (**Table 5.2**). However, movements by age bin did not have any significant differences for log-transformed mean days at large (ANOVA: F=0.0489, df=2, P=0.9523) and log-transformed mean distance moved (ANOVA: F=0.1175, df=2, P=0.8893).

Table 5.2- Summary of movement information for the three age-bins. "Juveniles" were $\leq$488 mm FL, and $\leq$age 5, "Middle" was ages 5 to 9 (>488 and $\leq$600 mm FL), and "Oldest" was ages 9 and older (>600 mm FL). Standard errors (SE) are shown in parentheses. Shortest distance in water was used for all distances.

	Total Recoveries	Mean (SE) days at large	Maximum days at large	Mean distance moved (km)	Maximum distance (km)	Proportion recaptured same spot	Proportion moving >20 km
Juvenile	47	243.6 (30.6)	800	5.9 (2.7)	203	0.52	0.04
Middle	119	198 (14.9)	815	10.9 (2.8)	341	0.42	0.1
Oldest	118	195 (15.1)	815	7.5 (1.4)	119	0.46	0.1

A summary of movements in and outside the spawning season had similar statistics (**Table 5.3**). There was no apparent trend in movements due to spawning for the log-transformed mean distance moved (ANOVA: F=0.0101, df=1, P=0.9205).

Table 5.3- Summary of movements in and outside of spawning season. Bonefish spawning season was defined by Crabtree et al. (1997) as October to May. Standard errors (SE) are shown in parentheses. Shortest distance in water was used for all distances.

	Total Recaptures	Mean (SE) distance moved (km)	Proportion recaptured same spot	Proportion moving >20 km
Non-Spawning	25	7.10 (4.75)	0.64	0.08
Spawning	69	7.85 (1.82)	0.52	0.09

Acoustic Telemetry

From March 2004 to July 2005 a total of 40 bonefish were implanted with AT transmitter tags and released. Individual data on fish sizes, dates of release, days in the study area, field-tagged or holding-pen bonefish, and day of last recorded transmission are provided in **Table 5.4**. The size range of bonefish tagged with AT transmitters was similar to those from the anchor tag study (**Figure 5.7**). Of the 40 fish AT tagged and released, 31 (78%) of these were subsequently detected at least once, producing 57,070 unique tag detections within the 40 receiver array (**Table 5.5**). Nine AT tags were never detected by any of the receivers; 5 of these were in bonefish released north of the array. Field-tagged bonefish had higher tag detection rates than lab-tagged fish; however, by and large, these fish were captured in foraging habitats north of the array and released south within the array. Lower tag detection rates by lab-tagged fish may have been biased as these fish likely returned to their original capture locations after release. Receivers with greatest number of different tag detections were those placed at unique geographic features like bay-to-ocean passes and oceanside points (i.e., NE1, PP1, LC, and OES) (**Figure 5.8A**). There were no apparent trends in receiver detections by size of fish (**Figure 5.8B**).

Table 5.4- Summary of acoustic telemetry data for 40 tagged bonefish between March 2004 and July 2005. Type is if the fish was tagged at the University of Miami facility (R) or in the field (F). W is weight and FL is fork length. Bayside and Oceanside for release locations refer to the side of a specific barrier island. NR indicates there were no recorded transmissions by the array.

Tag ID	Type	W kg	FL mm	Release Date	Release Location	Last Transmission	Days Detected
188	F	2.95	594	7/14/2005	Boca Chita	8/16/2005	29
192	F	1.81	489	6/12/2005	Caesars Creek	NR	0
193	F	2.04	511	6/12/2005	Caesars Creek	9/17/2005	96
195	F	4.42	654	2/1/2005	Caesars Creek	5/6/2005	94
196	R	1.13	445	1/22/2005	Lewis Cut	1/23/2005	1
197	F	1.47	478	2/3/2005	Elliott Key	5/4/2005	90
198	R	2.72	566	2/9/2005	Soldier Key	NR	0
199	F	1.81	500	2/1/2005	Elliott Key	4/28/2005	86
200	F	2.04	533	3/24/2005	Sands Cut, Bayside	6/24/2005	84
201	F	3.18	588	5/9/2005	Sands Cut, Bayside	6/7/2005	19
202	R	2.72	566	5/5/2005	Soldier Key	NR	0
203	R	1.81	522	5/18/2005	Elliott Key	NR	0
204	R	4.65	643	5/2/2005	Soldier Key	NR	0
205	R	3.18	599	5/13/2005	Soldier Key	5/14/2005	1
206	R	2.83	522	5/18/2005	Elliott Key	5/18/2005	1
207	F	4.20	588	3/3/2005	Sands Cut, Bayside	4/6/2005	34
208	F	2.61	572	5/14/2005	Cutter Bank	5/21/2005	6
209	F	3.97	632	4/5/2005	Sands Cut, Bayside	5/29/2005	54
210	F	2.72	566	3/24/2005	Sands Cut, Bayside	6/14/2005	79
221	R	5.33	643	03/06/04	Sands Key, Oceanside	NR	0
222	R	3.52	588	03/06/04	Sands Key, Oceanside	03/06/04	1
223	R	2.04	500	10/5/2004	North Elliott Key	10/10/04	5
224	R	3.29	610	03/27/04	Sands Cut, Bayside	03/27/04	1
225	R	2.95	566	05/21/04	Elliott Key	05/21/04	1
226	R	2.15	522	05/21/04	Elliott Key	05/27/04	6
227	R	4.31	632	03/27/04	Sands Cut, Bayside	04/02/04	6
228	F	1.81	511	03/17/04	Elliott Key	04/14/04	28
229	F	2.61	566	03/17/04	Elliott Key	03/28/04	10
230	F	3.63	594	04/21/04	Caesars Creek	05/04/04	13
231	R	2.27	544	05/21/04	Elliott Key	06/15/04	25
232	R	4.54	632	05/20/04	Elliott Key	NR	0
233	F	2.72	555	12/14/2004	Caesar's Creek	12/26/2004	12
234	R	2.38	522	12/14/2004	Elliott Key	12/14/2004	1
235	R	2.95	561	10/26/2004	Lewis Cut	NR	0
236	R	1.81	478	12/14/2004	Elliott Key	12/18/2004	4
237	F	4.65	632	06/04/04	Lewis Cut	08/22/04	78
238	R	4.88	654	04/24/04	Elliott Key	04/24/04	1
239	F	0.79	357	12/19/2004	Elliott Key	01/05/05	17
240	R	3.40	555	06/04/04	Elliott Key	06/07/04	3
861	R	1.36	522	05/20/05	Soldier Key	NR	0

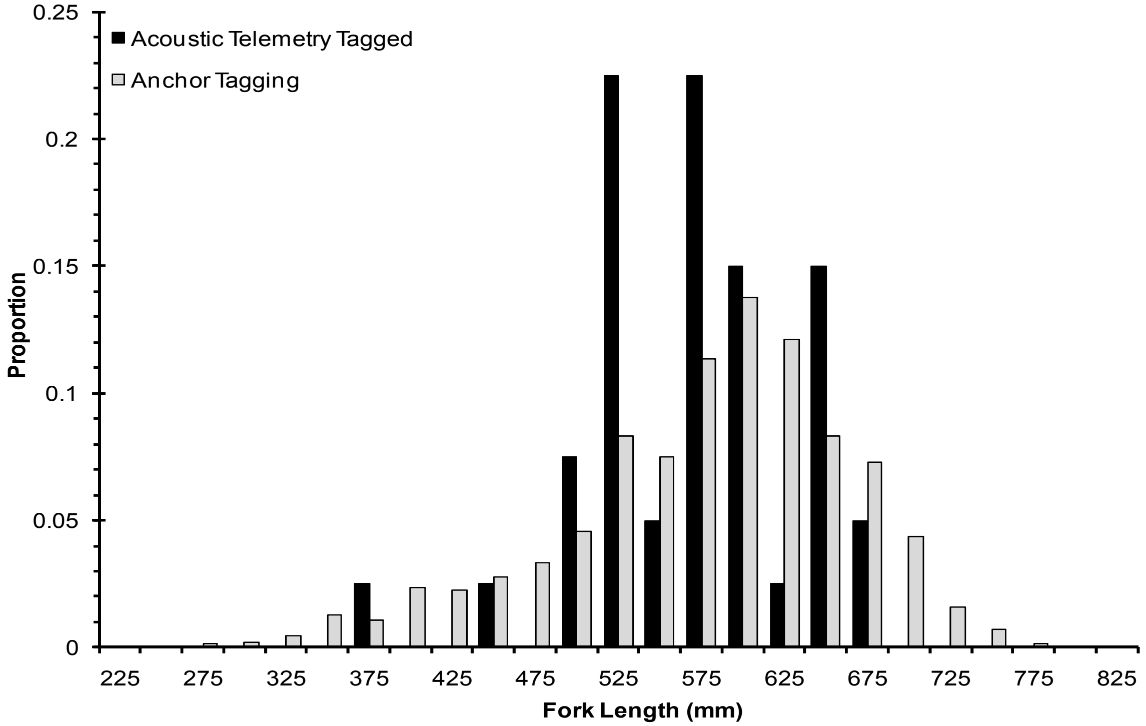

Figure 5.7- Comparison of length frequency distributions for anchor-tagged bonefish (grey columns; n=7,961) and acoustic telemetry tagged bonefish (black columns; n=40).

Table 5.5- Tag detections at specific receivers for individually acoustic telemetry tagged bonefish.

Receiver	Tag Identification Number																														
Location	188	193	195	196	197	199	200	201	205	206	207	208	209	210	222	223	224	225	226	227	228	229	230	231	233	234	236	237	238	239	240	Total
Bayside																																
SN2								71			6		41	144																	6	268
SN1								103			164		134	101																	10	512
CPt																																0
BPt																																0
Oceanside																																
RK	4			1	228	6					6			4					7	7								90				353
LC	225	1143			1455	2309		123					89	63	1	142				89			65	53				2233				7990
SC		8	107		540	244	20				14			24			153			29	1774	29	37						21	66	3	3069
NE1		67	498		4029	3064	36	55		2						488		79	12	98	7130	35	368	241		279	141		15	594	29	17260
NE2			16		218	94										5			29	49	1016		3			5	55			1		1491
NE3																			3	17											1	21
NE4																			25							52	28				3	108
NE5																				2						208	107					317
NE6																			24	38						39	4					105
NE7																				21							6					27
NE8																			5				12			72						89
NE9																			28	6			307			226	9					576
NE10																			10	1			37			71						119
NE11																										25						25
NE12																										7						7
NE13																																0
NE14																																0
OEN		30	9		13	38	9	23												1	1614	229	50	11			17					2044
OES		236	17		27	2003	733	430																			11					3457
PP1		1663	10			3856	279	226														105	39	8098								14276
PP2		318				166	28	33											14				2	616			2					1179
PP3		2				3													12					8								25
PP4						1													11													12
PP5																			7													7
PP6																			1													1
PP7																			47								15					62
PP8																			80								3					83
PP9																			92													92
PP10																			1													1
PP11																																0
PP12																			18							114						132
PP13																			23							491						514
PP14									8										2							489						499
PP15																										90						90
PP16																																0
NCA		744	58			5						1										30	733	10	103							1684
SCA		30	301			2						35											13	6	188							575
Total	229	4241	1016	1	6510	11791	1105	1064	8	2	190	36	264	336	1	635	153	79	451	358	11534	428	1666	9043	291	2168	398	2323	36	661	52	57070

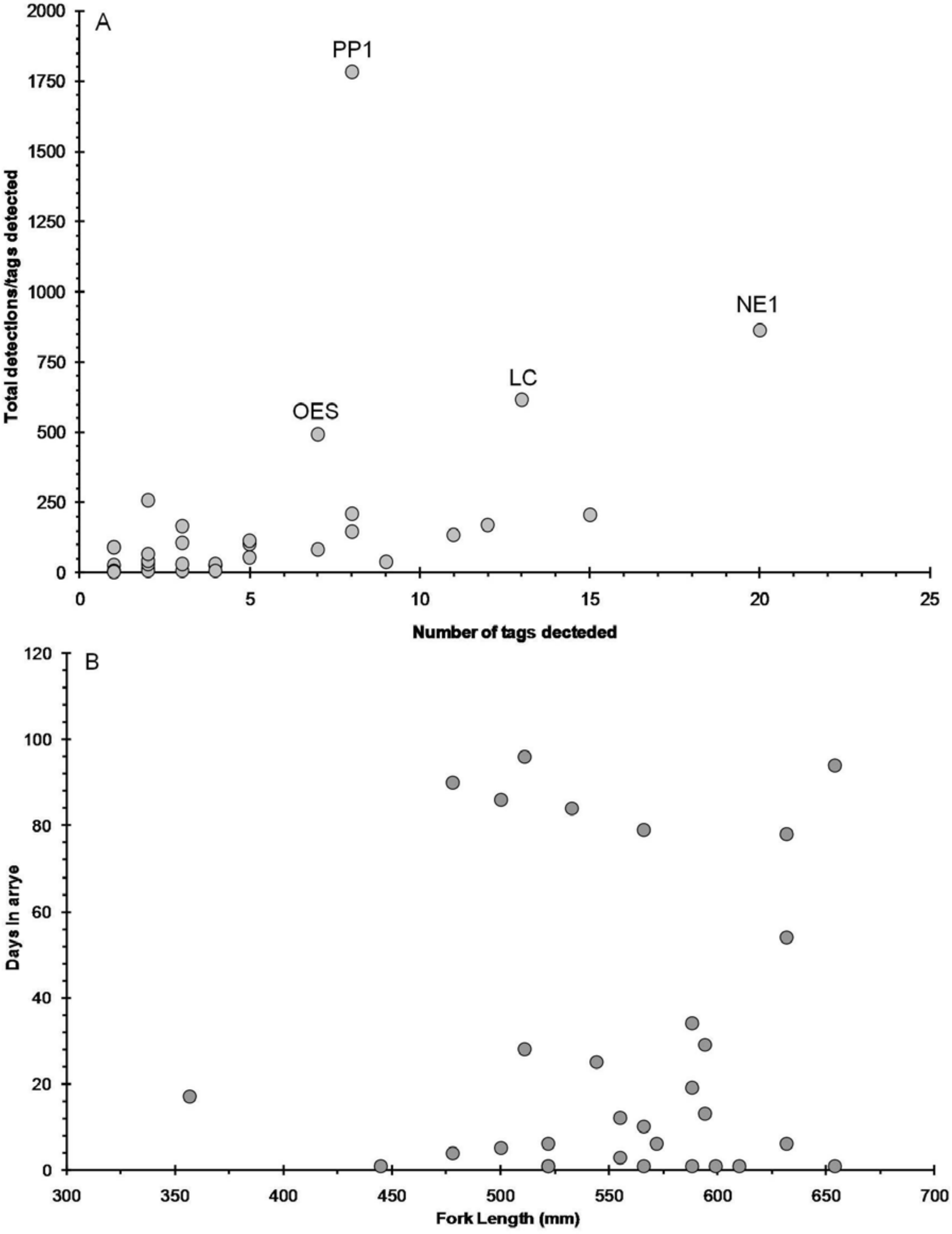

Figure 5.8- Bonefish acoustic telemetry results: (A) total detections at a given receiver divided by individual tags detected dependent on individual tags detected at receiver; and, (B) days detected in array dependent on bonefish size.

Bonefish exhibited substantial variation in patterns of movement (**Figure 5.9A**), at times moving rapidly alongshore either north to south or vice versa. Five bonefish covered the entire eastern shore of Elliott Key, a distance of approximately 13 km in ≤ 3.5 hr. In several other cases, bonefish moved seaward in apparent response to drops in barometric pressure (**Figure 5.9B**). A total of 5 large mature bonefish were detected at receivers NE2-NE10 and PP2-PP15 located in water depths to 20 m and distances ranging from >0.5 to 6 km east of the barrier island flats of Elliott Key **(Table 5.5, Figure 5.9B**). Often fish returned to the same areas they had previously frequented. Not surprising for fish that are known to school, several AT tagged bonefish were simultaneously detected at the same receivers (**Figure 5.9C**). Due to the relatively large detection ranges of receivers, it is assumed that these fish displayed similar spatio-temporal patterns in movements and habitat selection, but aggregation behaviors cannot be ruled out. This occurred among similar-sized bonefish (i.e., IDs 197 and 199), and for bonefish of different sizes (IDs 195 and 199). Bonefish IDs 197 and 199 stayed in the same proximal area over several days before departure.

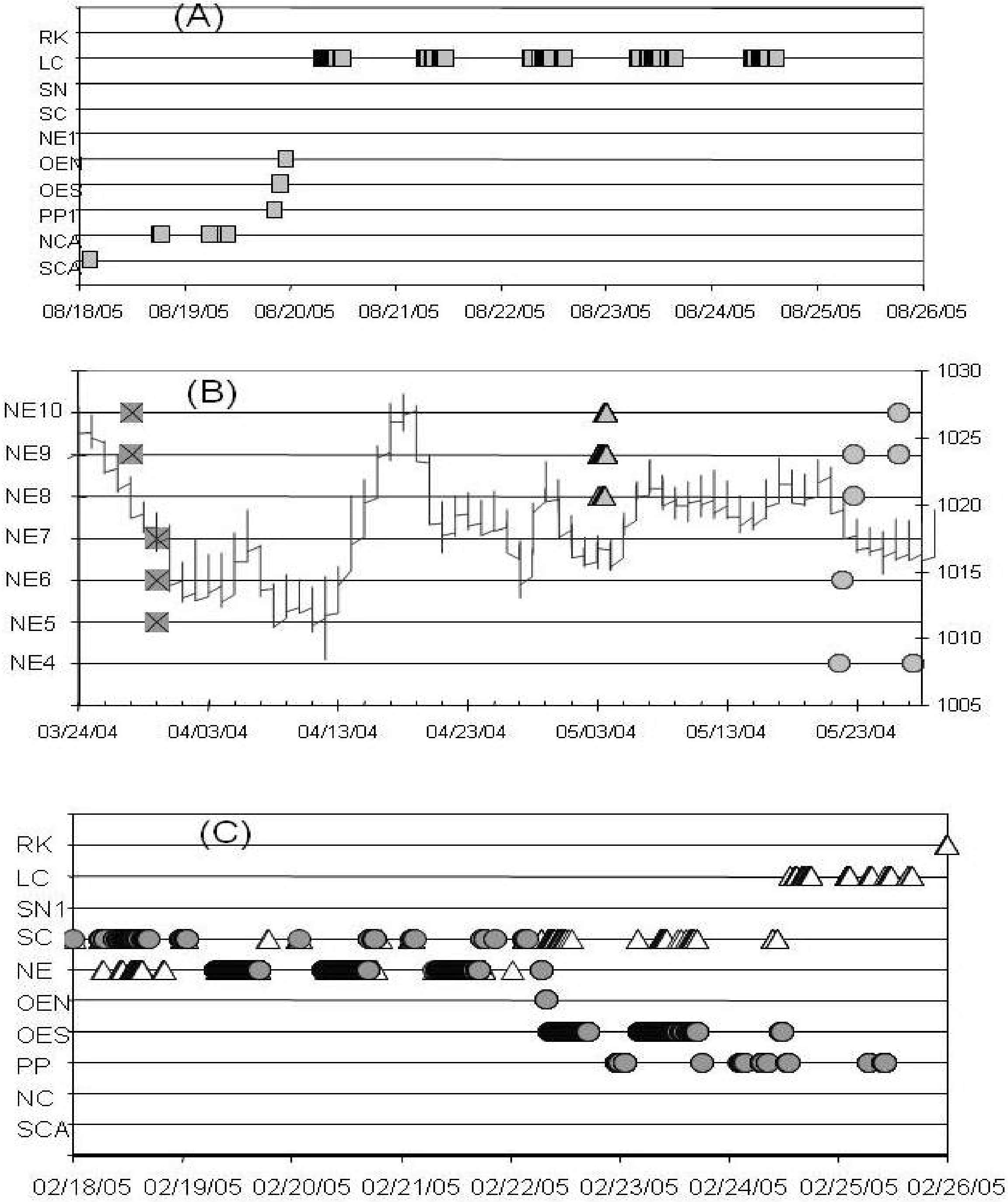

Figure 5.9- Bonefish acoustic tag detections by date with receiver location listed on the y-axis. (A) Fish ID 193 showing northward movement in the array during August 2005; (B) Fish IDs 227 (squares), 230 (triangles), and 226 (circles) from March to May 2004 showing movements east of the barrier islands in deepwater habitats near the barrier coral reef in relationship to barometric pressure (line); and, (C) apparent aggregation behaviors of fish IDs 197 (triangles) and 199 (circles) at receiver locations during February 2005.

A total of 243 movements from 12 fish were available for speed calculations. Distance between receivers ranged from 327 to 7,493 meters. Time between detections ranged from 6 minutes to just under 12 hours. Speeds were calculated for each individual fish. The average swimming speed ranged from 0.103 to 0.827 m s^{-1} and from 0.369 to 1.39 body-lengths s^{-1} (**Table 5.6**).

Table 5.6- Minimum, mean, and maximum speed for each fish defined as distance per second and body length per second. Rows are arranged by fish size. Standard errors (SE) are shown in parentheses.

			Distance (m)/Second			Body Length/Second		
Tag ID	FL (mm)	n	Min	Mean	Max	Min	Mean	Max
239	357	4	0.045	0.103 (0.055)	0.267	0.125	0.290 (0.153)	0.747
197	478	29	0.032	0.405 (0.125)	3.386	0.066	0.847 (0.262)	7.081
199	500	54	0.036	0.564 (0.070)	1.701	0.073	1.13 (0.139)	3.401
193	511	22	0.078	0.462 (0.056)	1.034	0.153	0.903 (0.110)	2.023
228	511	57	0.031	0.403 (0.053)	1.864	0.062	0.789 (0.104)	3.648
200	533	17	0.043	0.476 (0.084)	1.201	0.081	0.893 (0.158)	2.252
233	555	2	0.041	0.339 (0.298)	0.638	0.074	0.612 (0.538)	1.149
229	566	14	0.110	0.416 (0.051)	0.643	0.194	0.736 (0.091)	1.136
201	588	15	0.091	0.524 (0.091)	1.086	0.154	0.891 (0.155)	1.847
207	588	1	0.217	0.217 (NA)	0.217	0.369	0.369 (NA)	0.369
230	594	13	0.185	0.827 (0.193)	2.158	0.312	1.39 (0.325)	3.637
195	654	15	0.028	0.474 (0.124)	1.344	0.042	0.726 (0.189)	2.055

Discussion

Recovered anchor tag sample size was a limitation to these analyses. Despite over 8,000+ bonefish tagged, there were only about 300 recaptures reported. Reporting rate of tag recaptures was likely influenced by some fishermen's anti-research attitude. The beginning of the project experienced significant resistance, but this resistance was translated to cooperation in later years once communication with the fishermen was well established.

Tagging projects of other species have analyzed movements relative to month, season, and region (Bacheler et al. 2009), but separation of the 300 recaptures caused either very small or no samples for the appropriate category. Thus, the current data available did not allow analysis of movements by month, season, and regions.

Another limitation was the distribution of anchor tagging effort. The majority of the tagging effort took place in regions B and C which resulted in the majority of the recaptures. There were relatively few or no recaptures in the other regions which prevented analysis movements by region. Therefore, the movement results may reflect only the northern regions instead of the entire south Florida bonefish stock.

The lack of tagging effort in the southern regions is a source of frustration. There were many phone calls and field trips to regions D and E to recruit new tagging volunteers and motivate current ones. Unfortunately, these communication efforts were almost fruitless. Reduced interest in the bonefish tagging may be attributed to their lower bonefish abundance (Ault et al. 2008b) and/or the popularity of other target species (i.e. permit, *Trachinotus falcatus*) (Stu Apte, personal communication) in these regions.

There was a reduction in tagging effort from 2008 to 2010 (**Figure 5.3**) despite an increase in tagging volunteers during this period. There are numerous possible reasons to explain the reduction. One reasons reported by the volunteers was the recession period in America's economy. The majority of the volunteers are professional fishing guides with incomes dependent on charter payments. Reductions in disposable incomes due to the recession could have influenced their charters and reduced the time fishing and tagging bonefish. Another reason the volunteers reported the decline in tagging effort was observed declines in bonefish abundance. For example, one of the dedicated volunteers greatly reduced his bonefish fishing effort because of the present difficulty of finding and catching bonefish (David Denkert, personal communication).

Prior to this study, conventional wisdom in south Florida amongst knowledgeable fishing guides and experienced anglers was that bonefish inhabited a limited home range, often frequenting the same foraging areas, and that bonefish rarely, if ever, moved even more than a few km. These perceptions and the noted resource declines (Larkin et al. 2010) motivated the need for additional study. However, there was little empirical or scientific guidance concerning the most effective methods to track bonefish movements. Two previous anchor tagging studies, one in Florida and one in the Bahamas, were largely unsuccessful. Bruger (Florida Marine Research Institute, pers. comm.) initiated an anchor tagging program in the Florida Keys in the 1970s. However in that era anchor-tag technology was crude, and none of his tagged fish were ever recaptured, despite the tag-and-release of several hundred bonefish. Colton and Alevizon (1983) anchor-tagged 214 bonefish in the Bahamas but had only one recapture of a fish that remained at liberty for only a few days post-release. These studies led to much skepticism by fishing guides concerning potential mortality from tagging and a general lack of confidence in anchor-tag methodologies. Colton and Alevizon (1983), tracked a small number (i.e., 13) of AT tagged fish using a boat-mounted directional hydrophone. They stated that bonefish movements ranged widely through available habitats; however, their conclusions were equivocal as they were only able to detect and track three fish after 24 hours, and two of these for a 5 day maximum.

The dearth of successful anchor-tagging studies made the unprecedented number of tagged-releases (8,340) and subsequent recaptures (331) even more remarkable. This research has revealed that bonefish do move, and frequently for substantially long distances. While most of the anchor tagged bonefish were recaptured within 20 km of their release locations, about 13% of these moved long distances that ranged up to 340 km.

Some bonefish moved great distances (>100 km) in relatively short periods (15 days). About 45% of recaptured bonefish were caught from the same location where they were originally tagged, and the majority of them (85%) were above the size of sexual maturity (488 mm FL, Crabtree et al. 1997). There is evidence suggesting that bonefish do not spawn in nearshore waters (<1km from land). Crabtree et al. (1997) sampled over 500 bonefish gonads collected in nearshore waters and never found evidence of recent or future spawning activity (i.e. hydrated gonads, postovulatory follicles**)**. This suggests that either: (1) these mature bonefish had migrated to spawning sites and then returned to the same foraging areas; or (2) some of these mature bonefish may not have participated in spawning migrations. Reasons for lack of participation in spawning migrations for mature fish is generally unknown, but such behavior has been documented in other fishes (Harden Jones 1968; Pollock 1982).

A combination of both the anchor tagging and AT-tagging results provided insight into bonefish movements. The anchor tagging revealed the majority of the recaptures occurred in the same tagging location, suggesting that bonefish do not move from the foraging grounds where they were caught. However, AT-tagging shows quite an opposite result with bonefish moving frequently. A closer look at the AT-tagging reveals individual fish were frequently detected by the same receivers (**Table 5.5**, **Figure 5.9**). In conclusion, bonefish move frequently but have a high degree of site fidelity.

Two anchor-tagged bonefish were documented to have migrated >300 km across the Straits of Florida to the inshore waters of Andros Island, Bahamas. The cross Florida

Straits movement to Bahamian waters raises the question of the appropriate scale of unit stock that defines the Florida bonefish fishery. It is possible that exchange of mature adult bonefish between Florida and the Bahamas could be an important factor for consideration by an international management regime if this kind of observed movement is a common occurrence. It also suggests that new attention should be given to the degree of genetic differentiation between Florida and Bahamas bonefish, with inference for stock mixing based on gene flow (e.g. Gharett and Zhivotovsky 2003). In addition, since bonefish are schooling fish (Robins et al. 1986; Crabtree et al. 1996), the recaptured fish likely traveled with others.

Because information was lacking concerning how far offshore bonefish would travel, in the design phase of the acoustic telemetry study, a risk adverse position was taken. Instead of creating an array of known bonefish habitats, two cross-shelf lines of receivers that extended several km eastward of the shallow inshore waters were deployed. This resulted in AT-tagged bonefish detected at substantial distances offshore and at times close to the barrier coral reefs. The observed offshore movements may have possibly been bonefish on spawning migrations because those fish were generally well above the minimum size of sexual maturity and moved during peak reproductive months according to gonadosomatic indices reported by Crabtree et al. (1997).

Johannes (1978) reported an apparent bonefish spawning migration to sandy areas adjacent to Micronesian reefs and also suggested a strong lunar connection with bonefish spawning behavior. In the present study, offshore movements of some bonefish corresponded directly with or slightly lagged drops in barometric pressure, at times coinciding with cold front passage. Cold fronts are seasonally intensive in south Florida during periods of peak bonefish reproductive activity and may be natural physical cues for offshore movements. This type of physical-biological behavior has been documented for striped mullet, *Mugil cephalus*, (Behzad Mahmoudi, Florida Marine Research Institute, personal communication) in the region.

Bonefish spawning may coincide with spring ebb tides that maximize tidal transport of eggs and pelagic leptocephalus larvae, and presumably favors survivorship. The relatively close proximity of the Gulf Stream current in the Straits of Florida to the deep seaward edges of the barrier coral reefs could greatly facilitate retention or northward transport (Stommel 1976). Northward dispersal of bonefish larvae is suggested by the presence of substantially smaller bonefish in the Palm Beaches region than in the Florida Keys. The Palm Beaches may be an important recruitment and natal development area for post-larval bonefish. Small immature bonefish from the Palm Beaches region may ultimately recruit to the exploited phase of the stock by southward migration to the Florida Keys after reaching sexual maturity. It is of interest to note that 108 young-of-the-year bonefish were collected in a seine net in Great South Bay, New York (Alperin and Schaefer 1964).

Potential mortality from either the anchor- or AT-tagging process was a concern amplified by the fishing community. This concern has been generally assuaged by the indications of no size-selective mortality. The majority of the anchor tags were the same tags (Floy T-bar) used by Baeza and Basurto (1999) who reported no mortality associated with tagging. Further evidence was the fact that bonefish in the present study carried external anchor tags for significant periods of time (i.e., >2 years). The acoustic telemetry study also supported the notion of minimal mortality associated with tagging.

One bonefish fitted with a transmitter was caught by a fisherman several months after release, and while the fishermen dutifully noted and reported the external anchor tag, he was unaware that the same bonefish also carried an internal AT transmitter. Humston et al. (2005), using the same tagging procedure also had an AT-tagged bonefish recaptured by a fisherman several months after release.

These results have been encouraging, but much work is still required to better integrate the capabilities of the two tagging methodologies and to facilitate better understanding of the timing and location of spawning migrations, behavioral responses to environmental cues, and key aspects of population dynamics. Such integrated studies will require higher intensity tagging efforts and expansion of acoustic arrays to cover more inshore and cross-shelf habitats. Greater anchor tagging efforts need to be spread proportionally across the range of the unit stock and be linked to a systematic coverage of guide- and tournament-based catch-and-effort logbook data to facilitate improved estimates of stock size, growth and survivorship. Limiting steps will always be equipment costs and manpower requirements. Anchor tagging studies bear minimal fiscal costs to supply participants with the necessary equipment (i.e., tag guns, anchor tags, and data sheets), but they require significant human costs in volunteer participation to meet program goals. On the other hand, AT-tagging requires substantial fiscal and manpower costs to deploy and maintain receivers and tag fish and to conduct computer-intensive data analyses. However, costs were minimal relative to several important benefits achieved by this tagging research: it provided a means to address gaps in understanding basic bonefish biology and movement patterns needed for better management practices; it provided a partnership between scientists and the recreational angling community to work together for the goal of more fish in the water; and, it was a means to educate the angling public about the importance of catch and release fishing. The methodology of this study could be easily replicated for other bonefish fisheries in a way that would allow effective comparison of results to those obtained from Florida, and such studies could serve as important mechanisms to build sustainable bonefish fisheries.

Chapter 6

Application of Modern Stock Assessment Models

Summary

South Florida’s bonefish fishery generates substantial economic benefits to the region, but the resource has never been adequately assessed to determine standard benchmarks for sustainability. Stock status was evaluated using two contemporary assessment models: (1) REEFS, a length-based algorithm employing a stochastic age-independent continuous population model that allows estimation of population numbers and biomass at given lengths (Ault et al. 1996, 1998, 2008c); and, (2) an age-structured production model (catch-free assessment model) recast in terms relative to pre-exploitation levels (Porch et al. 2006). Using the current instantaneous fishing mortality rate of 0.126 y^{-1} in the length-based model generated estimates of yield-in-weight per recruit (Y_w/R) at 1.003 kg and spawning potential ratio (SPR) of 49%, suggesting that Florida’s bonefish stock is moderately exploited. However, the age-structured model indicated a relatively large stock decline had occurred over the past 60 years, and the current stock size is now bordering an overfished benchmark.

Background

The use of quantitative assessment models is standard practice in contemporaneous fishery management to assess the impacts of exploitation and environmental changes on resource sustainability (Quinn and Deriso 1999; Haddon 2001; Walters and Martell 2004; Ault et al. 2005c). Up to now, little data and few assessment models have been applied to specifically address the situation of a primarily recreational catch and release fishery. To address these issues, complimentary modern assessment models were used to evaluate a range of fishing scenarios to better understand the stock's vulnerability and prospects for sustainability.

Methods

Length-based model

Following Ault et al. (1998, 2008c), a suite of length-based computer algorithms (REEFS - Reef Ecosystem Exploited Fishery Simulator) that employed a stochastic age-independent continuous population model was used to determine population numbers and biomass at given lengths over time. The algorithm begins with determining the average number of fish at a given length, $\overline{N}(L)$, with

$$\overline{N}(L) = \int_{L_r}^{L_\lambda} R(\tau - a)S(a)P(L|a)da. \qquad (6.1)$$

The equation is integrated from size at recruitment (L_r) to the largest size (L_λ). $R(\tau\text{-}a)$ is cohort recruitment lagged back to birth date, $S(a)$ is survivorship to age a, and $P(L|a)$ is the conditional probability of being length L given the fish is age a. The total mortality rate Z for a given average size in the exploitable phase of the stock was estimated using the LBAR algorithm (Ault et al. 1996; equation 4.1). Fishing mortality rate F was estimated from subtracting the natural mortality rate (M) from the total mortality rate

Population biomass, $B(L|a,t)$, is the product of numbers-at-age, $N(L|a,t)$, times weight-at-age, $W(L|a,t)$, where $(L|a,t)$ represents the age a at time t for a given length (L). Yield in weight (Y_w) was calculated as the fishing mortality rate at time t, $F(t)$, multiplied to biomass of the fishery represented by

$$Y_W = F(t)\int_{L_c}^{L_\lambda} B(L|a,t)dL = F(t)\int_{L_c}^{L_\lambda} N(L|a,t)W(L|a,t)dL \qquad (6.2)$$

where $F(t)$ is the fishing mortality rate applied to the exploited phase (L_c to L_λ) in year t. Yield-per-recruit in weight (Y_w/R) or number (Y_n/R) was calculated by dividing the yield by the initial number of recruits. Spawning stock biomass (SSB), a measure of stock reproductive potential, was integrated between the minimum size of sexual maturity (L_m) and the maximum size (L_λ),

$$SSB(t) = \int_{L_m}^{L_\lambda} B(L|a,t)dL. \tag{6.3}$$

Spawning stock potential ratio (SPR) is a management benchmark that measures the stock's current reproductive potential to produce optimum yields on a sustainable basis. SPR is calculated as

$$SPR = \frac{SSB_{exploited}}{SSB_{unexploited}} \tag{6.4}$$

where $SSB_{exploited}$ is the spawning stock biomass with a fishing mortality rate and $SSB_{unexploited}$ is the spawning stock biomass with no fishing.

Estimated SPRs were compared to U.S. federal standards which define 30% SPR as overfished threshold (Rosenburg et al. 1996). REEFS model inputs came from the literature or research conducted for this dissertation (**Table 6.1**).

Three different model scenarios were conducted to compute fishery sustainability benchmarks such as stock yield-per-recruit and SPR. The first scenario assumed the current length/age at first capture with no exploitation (i.e., F=0). The second assumed the fishing mortality rate equaled the natural mortality rate which is a proxy for maximum sustainable yield (Smith et al. 1993). The third scenario assumed current age/size at first capture and fishing mortality rate equal to the current estimate of F. These scenarios were evaluated in the context of all possible states of age/size of capture and fishing mortality rates to determine an optimum and the stock consequences estimated current exploitation levels on Y_w/R and SPR.

Table 6.1- REEFS model input values for bonefish life history parameter estimates and the source of the information. The parameters are longevity (t_{max}), weight-length parameters (α,β), von Bertalanffy model parameters (t_0, K, L_∞,W_∞), logistic selectivity curve parameters (a_{50}, d), length and age at first maturity (Lm, tm), and mortality rates (M, F). All lengths are in mm fork length and all weight is in kilograms.

Parameter	Estimate	Unit	Source
t_λ	21	Years	Chapter 2
α	5.27E-06	Dimensionless	Chapter 2
β	3.170	Dimensionless	Chapter 2
t_0	-0.558	Years	Chapter 2
K	0.294	per year	Chapter 2
L_∞	703.8	mm FL	Chapter 2
W_∞	5.58	Kilograms	Chapter 2
a_{50}	3.713	Years	Chapter 2
d	0.183	Dimensionless	Chapter 2
L_m	497.1	mm FL	Crabtree et al. (1997a)
t_m	4	Years	Crabtree et al. (1997a)
M	0.143	per year	Chapter 4
F	0.126	per year	Chapter 4

Age-structured assessment model

The “catch-free” age-structured assessment model of Porch et al (2006) was applied to evaluate potential changes in stock productivity over time. The model was parameterized using known biological information from **Table 6.1**, but also incorporated the indices of relative abundance from Chapter 4, and a new index of fleet fishing effort (Florida vessel registrations), and some auxiliary information on recruitment from a meta-analysis of stocks with similar life history characteristics. The model’s Bayesian structure allows informative priors on parameters such as fishing and natural mortality rates, growth curve, and selectivity.

The period of analysis begins when the stock is believed to be near virgin levels (i.e., unexploited, F=0). Relative abundance of each age (N_a) at the beginning of the first year of analysis is given by

$$N_{a,1} \begin{cases} 1 & a = a_r \\ N_{a-1,1} e^{-M_{a-1}} & a_r < a \end{cases} \tag{6.5}$$

where a_r is the youngest age class in the fishery and M is the natural mortality rate. The rate of instantaneous natural mortality was estimated by the method of Alagaraga (1984) by assuming that 5% of the recruits survive to the maximum age (see Chapter 4). To reflect uncertainty in this estimated value, a lognormal prior was specified with mean 0.143 and coefficient of variation of 0.3.

Relative abundance at the beginning of subsequent years (y) is modeled by the recursion

$$N_{a,y} \begin{cases} r_y & a = a_r \\ N_{a-1,y-1} e^{-F_{y-1} v_{a-1} - M_{a-1}} & a_r < a \end{cases} \tag{6.6}$$

where r_y is the annual recruitment to age class a_r relative to virgin levels, F is the fishing mortality rate on the most vulnerable age class, and v_a is the relative selectivity of the remaining age classes (which implicitly includes factors such as gear selectivity and the fraction of the stock exposed to the fishery).

Relative recruitment (r) is modeled as a first-order lognormal autoregressive process,

$$r_y = \mu_r e^{\varepsilon_y} \tag{6.7}$$

$$\varepsilon_y = \rho_r \varepsilon_{y-1} + n_{r,y},$$

where μ_r is the median expectation of recruitment, ε_y are annual deviations in recruitment, ρ_r is the correlation coefficient, and η is the normal-distributed random variates having a mean 0 and standard deviation σ_r (ostensibly representing the effect on recruitment of fluctuations in the environment).

The median expectation of recruitment was modeled by the Beverton-Holt spawner-recruit function recast in terms of the maximum lifetime reproductive rate α and relative spawning biomass s:

$$\mu_r = \frac{\alpha s_{y-a_r}}{1+(\alpha-1)s_{y-a_r}} \tag{6.8}$$

$$s_y = \sum_{a=a_r}^{A} E_a e^{-(F_y v_a - M_a)t_s} N_{a,y} / \sum_{a=a_r}^{A} E_a e^{-M_a t_s} N_{a-1}$$

where E is an index of the per-capita number of eggs produced by each age class, and t_s is the fraction of the year elapsed at the end of the spawning season.

There is no information on the spawning stock-recruit relationship of any bonefish stocks. Following Porch et al. (2006), a Beverton and Holt spawning stock-recruit model was used where a prior for the steepness parameter (α) was constructed using data from the periodic life history strategist species of Rose et al. (2001). Rose et al. (2001) conducted a meta-analysis of the life history data from Myers et al. (1999) and defined periodic life history strategists as larger, highly fecund fishes with long life spans and variable recruitment. Examples included striped bass (*Morone saxatilis*) and red snapper (*Lutjanus campechanus*).

The fishing mortality rate of the most vulnerable age class F is also modeled as a first-order lognormal autoregressive process,

$$F_y = \mu_F e^{\delta_y} \tag{6.9}$$

$$\delta_y = \rho_F \delta_{y-1} + \eta_{F,y},$$

where μ_F is the median level fishing mortality rate, δ_F is the annual deviations in fishing mortality rate, ρ_F is the correlation coefficient, and η is the normal-distributed random variates having mean of 0 and standard deviation σ_F.

The median annual fishing mortality rate is generally assumed to be proportional to an index of fishing effort *f*:

$$\mu_F = \Phi f_y, \tag{6.10}$$

where Φ can vary among three eras of exploitation: a "prehistoric" period, during which little data are available; a "modern" period, when presumable there are some data on abundance or mortality rates; and a "future" period, when fishing mortality rates are controlled (input). The absence of data during the "prehistoric era" generally precludes the estimation of annual deviations in recruitment (ε) or fishing mortality rate (δ) during that period.

Two indices were inputted into the model to provide a time series of changes in abundance. The first is the standardized bonefish tournaments catch rates and the second index was the visual survey estimates of population size. The indices were modeled as

$$c_{i,y} = q_i \textstyle\sum_a v_{i,a} N_{a,y} e^{-(F_y v_a + M_a) t_i} e^{\Upsilon i} \tag{6.11}$$

where *i* indexes the survey time series, q is the proportionality coefficient scaling the time series to the relative abundance of the population, t_i is the fraction of the year elapsed at the time of the survey, $\sigma_{c,i}$ is the standard deviation of the fluctuations owing to changes in the distribution of the stock, and v_a is the relative selectivity of each age class to the fishery.

The fishing mortality rate on the most vulnerable age classes were modeled as

$$F_y = \begin{cases} \Phi_1 f_y & 1900 \leq y \leq 1968 \\ \Phi_2 \overline{F} & 1969 \leq y \end{cases} \tag{6.12}$$

where f_y is a time series of historical effort, and Φ_1 and Φ_2 were estimated. Historical effort was modeled with the number of registered recreational vessels in the counties of Broward, Dade, and Monroe (www.flhsmv.gov/dmv/vslfacts.html). After 1968 the fishing mortality rate no longer needs to track historical effort because the standardized catch rates from the bonefish tournaments are available. Then in 2002 the additional index of the visual survey is added to the model.

A reference point to determine stock status is the equilibrium spawning potential ratio (Goodyear 1993) defined as the expected lifetime fecundity per recruit at a given F (Ψ_F) divided by the expected lifetime fecundity in the absence of fishing (Ψ_0). This is defined as

$$p = \frac{\Psi_F}{\Psi_0} \tag{6.13}$$

$$\Psi_F = \sum_{a=0}^{A} E_a e^{-(F_a+M_a)t_s} e^{-\sum_{i=0}^{a-1} Fvi+M}$$

The model was implemented with the nonlinear optimization package AD Model Builder (version 9.1, University of California, Santa Barbara, USA) which allowed estimation of mode and shape of posterior distributions. Model code was provided by Clay Porch.

Results

Length-based model

The first model trials estimated yield in weight per recruit of 1.003 kg and spawning potential ratio of 49% for current conditions (**Table 6.2**). At F_{msy} yield in weight per recruit would be 1.056 kg and spawning potential ratio would be 46%. Model predicted length frequency distributions implied declining abundance of larger bonefish with increase in fishing mortality (**Figure 6.1**). The average length generated from all of the REEFS simulations generated the same corresponding total mortality rate in the LBAR algorithm. The current fishing mortality rate is just below F_{msy} suggesting the stock is close to the maximum sustainable yield.

Table 6.2- REEFS model estimation of yield-in-weight per recruit (kg), spawning stock biomass, and spawning potential biomass ratio for: (A) unexploited (F=0); (B) current fishing mortality rate (F=0.126 y^{-1}); and, (C) maximum sustainable yield (F_{msy}=0.143y^{-1}).

Fishing Mortality Rate (y^{-1})	Yield in weight per Recruit (kg)	Spawning Potential Biomass Ratio (%)
0	-	100
0.126	1.003	49
0.143	1.056	46

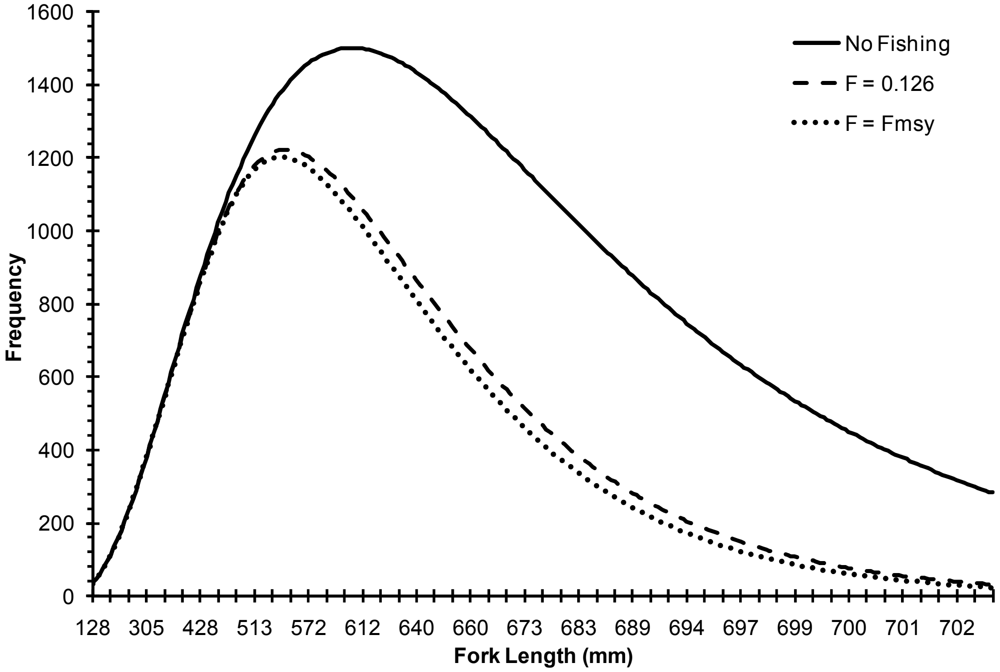

Figure 6.1- Bonefish size-structured relative abundance generated by the REEFS model for three levels of fishing mortality rates: no exploitation (F=0); current estimated fishing mortality rate (F=0.126 y^{-1}); and, maximum sustainable yield (F_{msy} = M).

The second model trials produced isopleths of equilibrium contours in yield in weight per recruit and spawning stock biomass ratio determined by the relationship between age/size of first capture and fishing mortality rate (**Figure 6.2** to **6.5**). Stars were plotted on the isopleths to show current conditions.

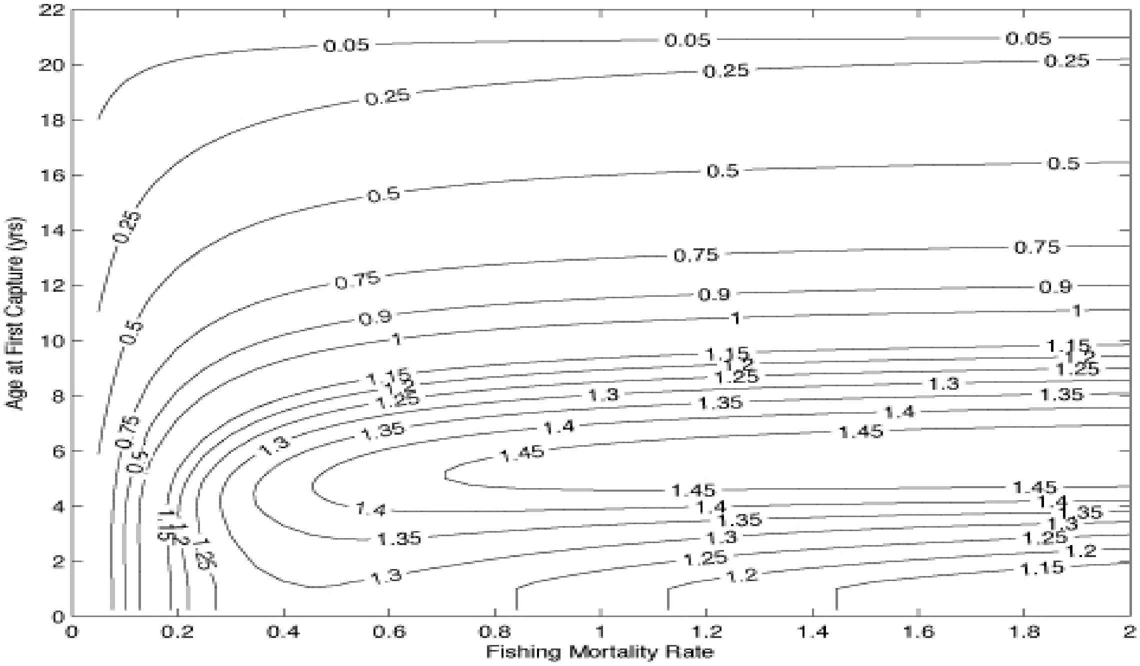

Figure 6.2- Yield in weight per recruit isopleths as functions of fishing mortality rate and age at first capture.

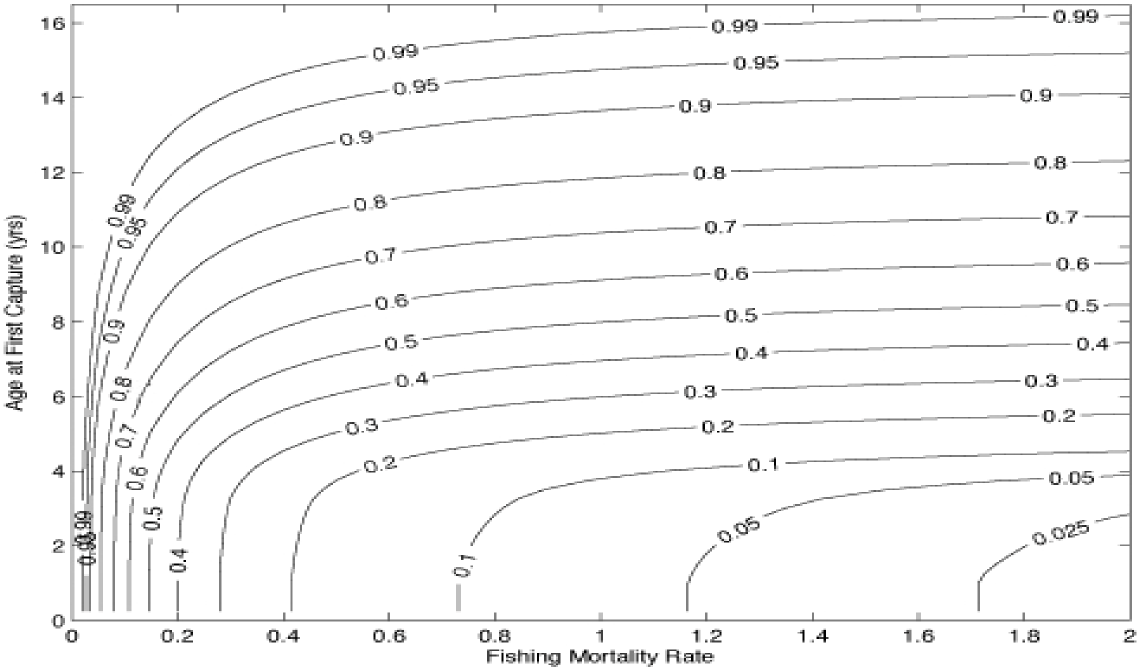

Figure 6.3- Spawning stock biomass ratio isopleths as functions of fishing mortality rate and age at first capture.

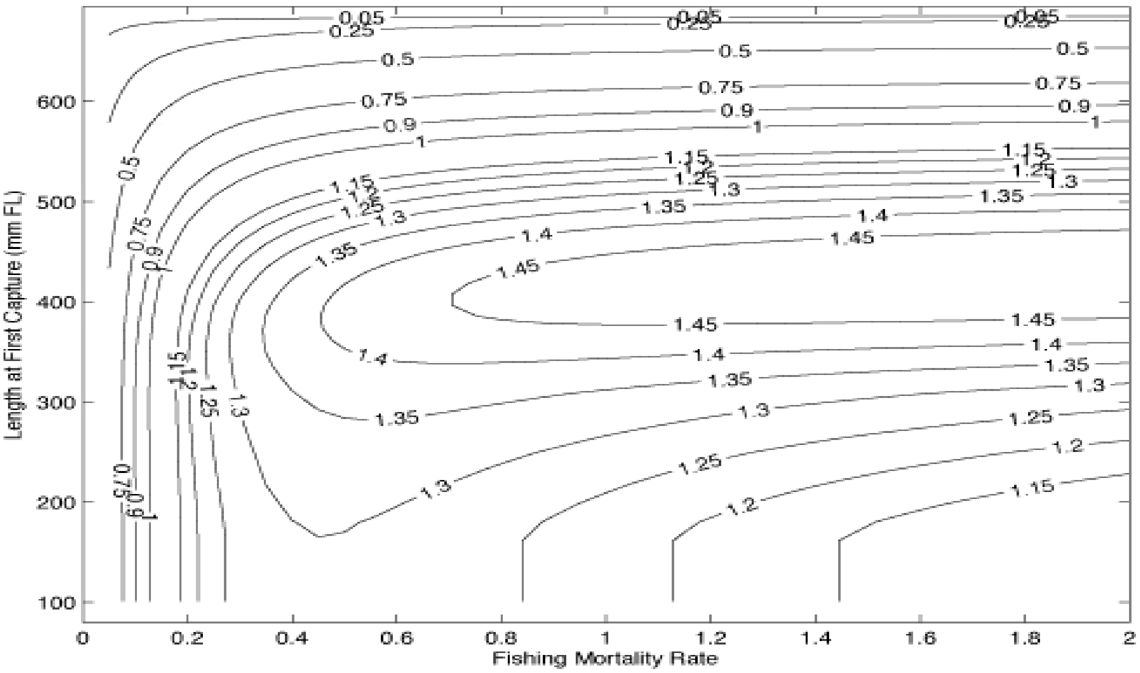

Figure 6.4- Yield in weight per recruit isopleths as functions of fishing mortality rate and length at first capture.

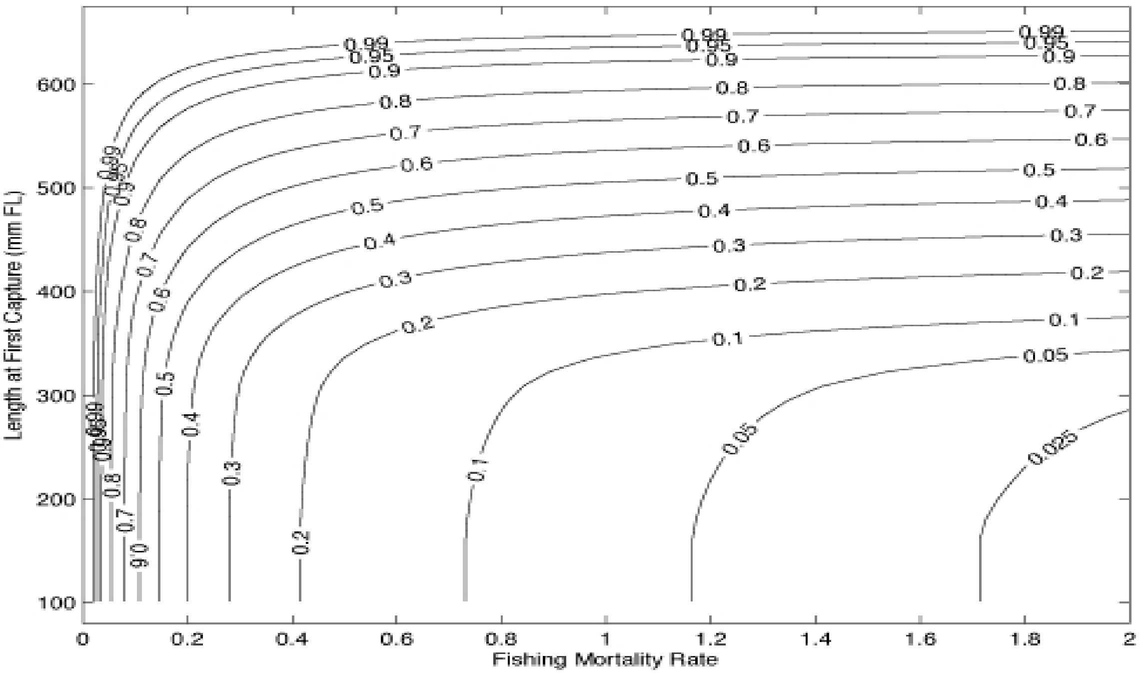

Figure 6.5- Spawning stock biomass ratio isopleths as functions of fishing mortality rate and length at first capture.

Catch-Free assessment model

The model fit the indices fairly well (**Figure 6.6**) and the two indices showed similar trends. The model displayed a large drop in bonefish population relative abundance from 1950 until 1975 followed by a somewhat level trend through 2010.

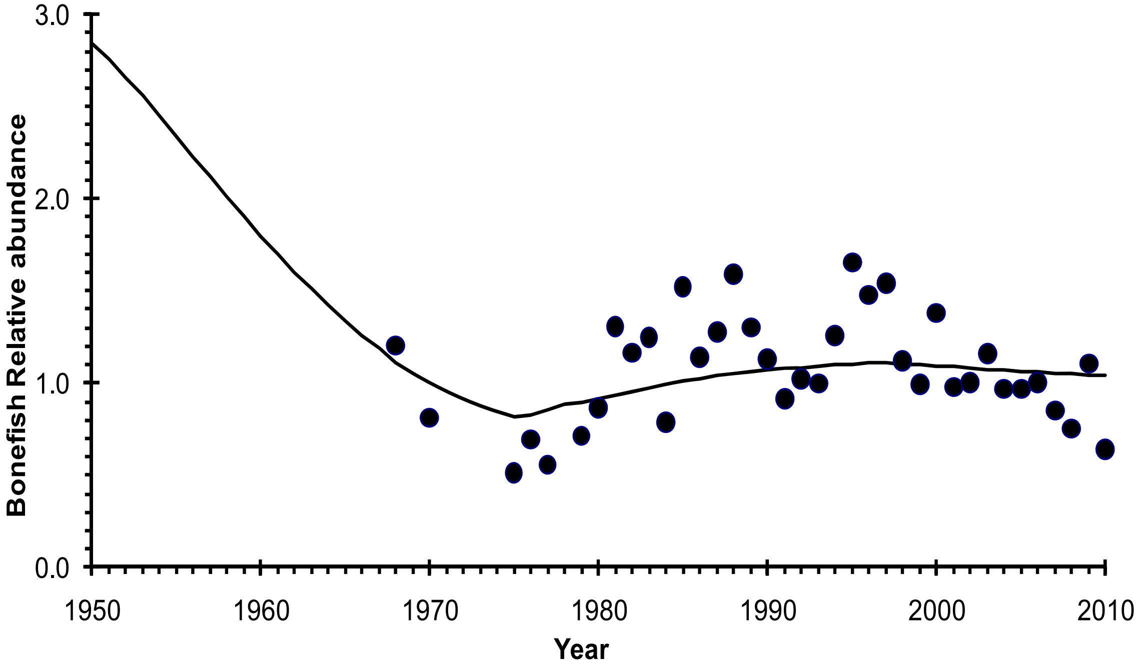

Figure 6.6- Indices fits for the catch-free assessment model.

Fishing mortality rates reached a peak in 1970, then dipped down and again increased in the most current year 2010 (**Figure 6.7**). The estimated fishing mortality rate for the most current year (2010) was 0.210 y^{-1}. The fishing mortality trend had an impact in reduction of stock spawning biomass (**Figure 6.8**). Spawning potential ratio (SPR) for the most current year was estimated at 30.1%.

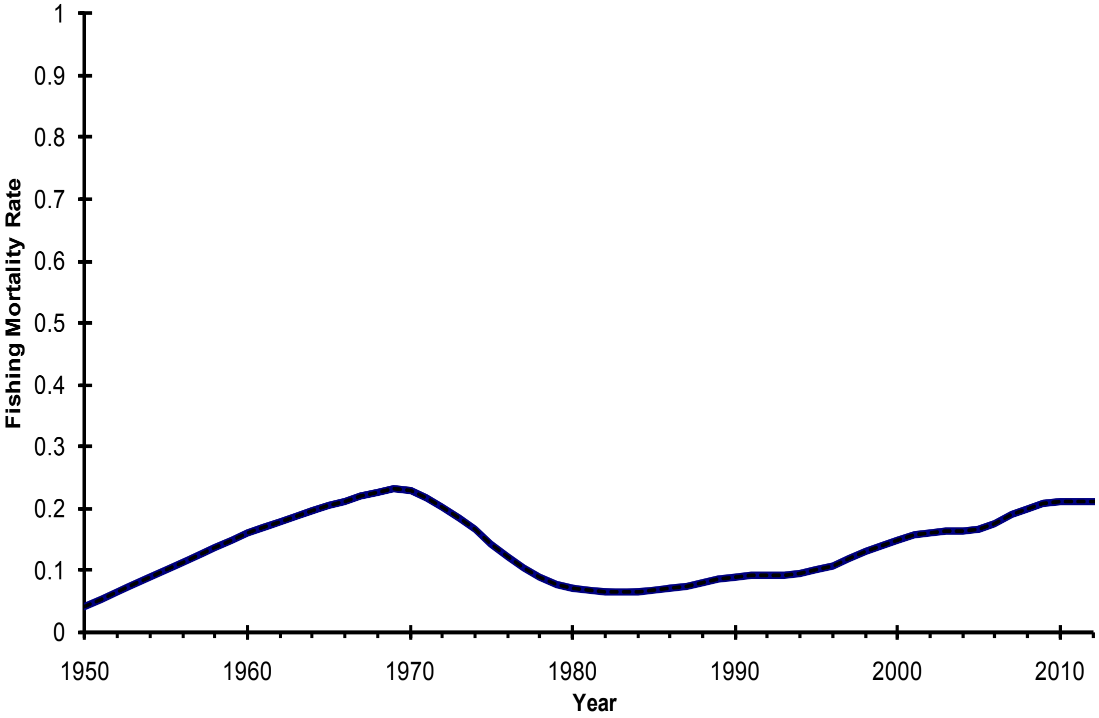

Figure 6.7- Predicted changes in fishing mortality rates from the catch-assessment model.

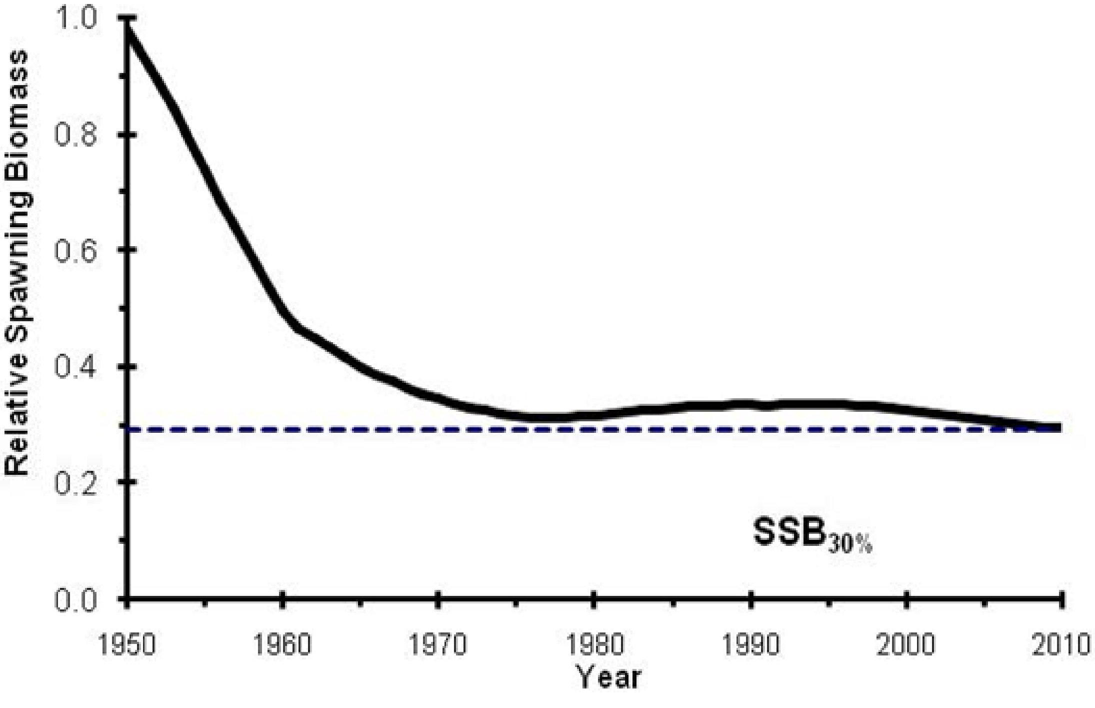

Figure 6.8- Predicted changes in the spawning biomass by year from the catch-free assessment model.

Discussion

Both stock assessment models employed here made the assumption that the bonefish was one unit of stock with no immigration or emigration. This assumption was likely violated because two bonefish tagged in Florida waters were subsequently recovered in the Bahamas. However, the overall population emigration rate is likely low, and here we assumed the immigration rates from other areas to also be low. If these rates are significantly altering the stock size then emigration will decrease SPR, conversely, immigration will increase SPR values.

The yield and SPR isopleths showed the impact of length at first capture on fishery sustainability. Length at first capture is heavily influenced by gear selectivity. Currently, length at first capture is relatively high (587 mm FL) but could be increased by changes in selectivity. Since the fishery is catch and release the only practical gear selectivity option is to increase hook size.

Figure 6.1 implied that large bonefish are still present under the current fishing mortality rate, but are less abundant than they were historically (e.g., no fishing). If fishing mortality rates were to increase the decline in larger fish could reduce the fishery's "large bonefish" reputation and lead to decline in popularity. Thus, the economic benefit of the fishery would be reduced.

A data limitation of the catch-free assessment model was that the two indices did not include juveniles so that the model could not effectively estimate recruitment. The current model trials cannot distinguish changes in the population productivity from differences in annual recruitment and fishing mortality rates. Therefore, it's not possible to determine which of the factors (e.g. habitat degradation, prey loss, or fishing mortality) may have had the greatest impact on the stock.

The catch-free assessment model implied that the stock's productivity had been greatly reduced (**Figure 6.8**). This could be a result of the mullet fishery (gillnet) which was the largest operating fishery of the Florida Keys from 1960's to the 1980's, and bonefish were reported as bycatch (Tillmant 1989). The stock's productivity showed a slight increase from 1980 to 1990 which may be a result of two things: (1) bonefish tournaments in the Florida Keys switched from "kill" to "release" tournaments in 1978 (Bert Scherb, personal communication); and, (2) commercial fishing was banned inside Everglades National Park in 1985 (Tilmant 1989).

The most recent estimates of the status of the stock's productivity is close to an overfishing management benchmark (**Figure 6.8**). In the past the stock was likely subjected to both growth overfishing from the fishing mortality rate (**Figure 6.1**) and recruitment overfishing from both high spawning stock mortality and concomitant habitat degradation. Any future impacts on the stock, such as an increase in fishing mortality or decrease in recruitment, could potentially reduce the stock's productivity into the overfished state. Considering the ecological and economic relevance of the resource the Florida bonefish stock needs to be closely monitored.

Summary and Conclusions

Summary of Analysis Results

Six different methods were employed to address, compare and contrast the status of south Florida's bonefish stock (**Table 7.1**); but, each method had limitations. The mail survey reported a stock decline but was anecdotal information. The estimation-simulation length-based mortality modeling revealed a stable stock, but model results were sensitive to sample size of the relatively short data time-series (1998-2010). The visual survey reported an overall decline in recent years, but also had a relatively small time series of data (2003-2010). The CPUE standardization also reported an overall stock decline in recent years, but never had more than 100 records in a given year. The length based model reported the stock as moderately exploited with the current fishing mortality rate less than the maximum sustainable yield fishing mortality rate, however, the method provided stock status at an assumed equilibrium instead of dynamic changes in recruitment through time. The catch-free assessment model indicated the stock bordering an overfished benchmark. However, due to a lack of an index for juvenile bonefish, it could not be conclusively determined if the stock was mostly impacted from a decline in recruitment or from increases in fishing mortality rates.

Table 7.1- Summary of the six different methods to evaluate the status of south Florida's bonefish stock.

Method	Status	Comments
Mail Survey of Captains	Declined	Population declined over past decade
Length Based Mortality Function	Stable	Similar mortality estimates when there was a sufficient sample size (n > 200)
Visual Survey	Declined	Overall declining trends in recent years
CPUE Standardization	Declined	Overall declining trends in recent years
Length Based Model	Moderately Exploited	Current F is less than F_{MSY}
Catch-Free Assessment Model	Declined	Stock is on the border of management benchmark

The catch-free assessment model was assumed to be the most robust method because it incorporated the majority of the research results (age and growth, selectivity, mortality, visual survey, CPUE standardization). In conclusion, the stock's productivity has been significantly reduced over the past 50 years and is bordering an overfished state.

Future Research

Despite the research accomplishments of this study, addition bonefish research is needed. Lack of information on both bonefish spawning locations and frequency are significant knowledge gaps in understanding larval production and subsequent recruitment. Identifying locations and essential conditions for spawning has significant implications for studying larval dispersal and recruitment exchange. Determining spawning frequency allows predictions of recruitment to potentially determine future population growth.

A greater understanding is needed of the bonefish stock-recruitment relationship. This is a difficult topic to address since it requires accurate and precise estimates of recruitment and spawning stock size over an adequate number of years. However, the relationship will allow analysis of impacts of exploitation.

Essential nursery habitat for bonefish is presently an enigma. Loss of nursery habitat is a significant concern for conservation of coastal species (Adams et al. 2006) and can undermine even the most restrictive management strategies for adult stocks. Quantifying the extent of available nursery habitat and any spatial variability in their contribution to adult recruitment would also support conservation efforts for this species. The present study showed bonefish first entering the Keys fishery (Regions B through E, **Figure 5.1**) in significant numbers at 400 mm FL (~4.4 years). Where are these bonefish located for the first 4 years of their life? A year-round seining project of over 120 deployments only collected 44 young-of-the-year bonefish. A large number of bonefish less than 4 years in age were available during the January cold weather event of 2010, but the origin of the dead bonefish on the shorelines was not determined. A possible explanation is the Gulf Stream transporting the majority of bonefish larvae north of the primary fishery location and then the fish migrate south at older ages. This is supported by the small size and age of bonefish in region A. There were directed tagging efforts with over 700 bonefish tagged to address connectivity of bonefish from region A to the other regions. Unfortunately, none of the bonefish tagged in region A were recaptured. The location of juvenile bonefish before they enter the bonefish fishery (regions B-E) is still unanswered, but future research should pursue otolith chemistry analyses (Dorval et al. 2005; Brown and Severin 2008).

Once juveniles are discovered a survey should be implemented to develop an index of juvenile abundance. This would could be used to forecast changes in the fishery and can be combined with an index of adults to evaluate the stock-recruit relationship.

A better understanding of connectivity between regional fisheries needs to be developed, especially since bonefish populations span international boundaries. The present study provided evidence of adult bonefish connectivity between Florida and the Bahamas. Harding (2010) tagged bonefish in Hawaii and also recorded bonefish moving large distances (>200 km) over deep water (>100 m). These results suggest adult bonefish connectivity between countries (i.e. between Florida, Bahamas and Cuba; between Kiribati and Western Samoa) is possible. Study of connectivity can be accomplished with anchor tags, large-scale acoustic telemetry arrays, and satellite communicating tags when they become available in smaller sizes. Quantifying adult movement between fisheries will allow management decisions to account for variable fishing mortality rates between regions.

Connectivity can also occur during the planktonic larval phase when animals are transported by ocean currents via passive or behaviorally-mediated dispersal (Cowen et al. 2006). The relatively long larval duration of bonefish (~55 days, Mojica et al. 1995) facilitates the exchange of larva from other areas. Genetic analyses can provide inferences on connectivity between populations. However, detectable genetic differences occur on much longer time scales, and these analyses cannot generally discern between contributions of the two life stages. Additionally, otolith chemistry investigations may be useful for documenting larval dispersal or ontogenetic movements (e.g. Sandin et al.

2005; Brown and Severin 2008). Directed studies on both larvae and adults are therefore essential to precisely quantify exchange.

The present study produced an intensive age-and-growth study of bonefish and documented biphasic bonefish growth which was previously unknown. Age-and-growth studies need to be done for other bonefish stocks to allow age-structured modeling and to compare and contrast different stocks.

The present growth study suggested a link between bonefish prey selection and growth. Additional work is needed to further assess the status of prey species populations, determine the impacts of directed harvest on these species, and define trophodynamic links. Ware and Thompson (2005) linked phytoplankton abundance to fish catches, revealing the link of prey to productivity. Applying the link of prey to predator for bonefish suggests anthropogenic nutrient inputs, pollution and habitat destruction in coastal waters could lead to a decline in bonefish abundance. Future bonefish assessments need an ecosystem-based perspective in management as discussed by Pikitch et al. (2004).

The recreational fishery survey of MRFSS is very broad scale and probably does not adequately monitor the bonefish fishery. The MRFSS survey has well documented shortcomings (NRC 2006), and the primary shortcoming leading to flawed data on the bonefish fishery was the extremely low number of intercepts with bonefish anglers (Crabtree et al. 1998a). This dissertation determined both the tournament CPUE standardization and visual surveys were effective monitoring methods and should be continued into the future.

An alternative method to monitor a primarily catch-and-release fishery, such as the bonefish fishery, is to conduct a tagging project. The tagging project presented in this dissertation is not without problems and limitations. However, the combination of a tagging project with auxiliary studies to estimate tag shedding, tag reporting rate, tag mortality, and natural mortality can provide robust estimates of critical population parameters that could guide management of economically significant fisheries. I suggest abandoning the MRFSS survey for the bonefish fishery. Instead focus efforts on continuation of the tagging project, CPUE standardization, and visual surveys, coupled with the addition of new projects (e.g. logbooks) to collect data on effort and catch. This is already occurring at Palmyra Atoll where they are rigorously monitoring their bonefish fishery through logbook records and tagging studies (Friedlander et al. 2008). Walters and Martell (2004) recommend focusing efforts on tagging methods to estimate exploitation rate. Martell and Walters (2002) discuss a common ground where information from tagging is combined with traditional assessment information for cross-validation and improvement of estimation performance. Specifically, a tagging project is used to monitor exploitation rates and changes in catchability which is then incorporated into an assessment.

Bonefish prey densities also need to be monitored. Pink shrimp are one of the primary prey items for bonefish (Crabtree et al. 1998b) and shrimp populations have been reduced from both changes in water quality (Boesch et al. 1993) and by two distinct fisheries: live-bait and food-shrimp fisheries. Shrimp removal has potential to reduce the carrying capacity of the bonefish stock.

Management

In recreational fisheries around the globe, managers are faced with overfished stocks and increasing numbers of fishermen which leads to reduced bag limits and restrictive size limits. Therefore, catch-and-release will take a more prominent role in management. This study aimed at addressing the status of a fishery that is primarily catch-and-release.

A synthesis of the current work provided cause for concern for the future of the bonefish resource. The visual survey and CPUE standardization results had inconsistencies among them, but did reveal overall declines (**Figure 4.13**). The catch-free assessment model revealed a dramatic decline in stock abundance over the last fifty years (**Figure 6.8**). A possible explanation for this decline could be an increase in fishing effort since this was the most significant factor reported by the captains for the decline in bonefish abundance. Over 300 tagged bonefish were recaptured, proving that bonefish are caught more than once, especially since they have a live span of 21 years. Bartholomew and Bohnsack (2005) modeled cumulative mortality from increased catch-and-release encounters and found increase in mortality. Crabtree et al. (1998a) provide evidence to support this in their catch-and-release study observing mortality for bonefish that were caught multiple times. Therefore, an increase in fishing effort could lead to a bonefish decline from the cumulative effect of repeated captures causing mortality.

A positive sign was the stock assessment using either the length-based or the catch free assessment model did not reveal an overfished state. However, given the economic contribution of the fishery and the fact that bonefish have a high maximum age

(21 years) making them susceptible to declines from fishing mortality, management options need to be pursued to prevent overfishing.

The bonefish fishery presents an interesting management case since it is primarily a catch-and-release fishery. In fact, in July of 2011 new fishery regulations eliminate the bag limit and make it a catch-and-release only fishery. How do you manage a fishery without controlling harvest? One of the management actions employed by the Florida Fish and Wildlife Conservation commission for a popular catch-and-release fishery (red drum, *Sciaenops ocellatus*) is stock enhancement. They rear larval redfish then release them into natural waters to augment the population. This is not a viable option for bonefish at this time due to fragile and complicated leptocephalus larvae (Lieby 1989) and sensitivity to changes in salinity (Hulet and Robins 1989). There have been advances in rearing leptocephali in the past decade (Pederson et al. 2003; Chen et al. 2008; Govoni 2010), but much work is needed before a successful bonefish stock enhancement program can be created. Other potential problems with stock enhancement are wild stock declines and negative ecological and genetic impacts (Evans and Wilcox 1991, Hilborn 1992).

Gear restrictions for south Florida's bonefish fishery could be feasible. In Palmyra Atoll only barbless hooks can be used for bonefish to facilitate faster hook removal, shorter air exposure, and reduced tissue damage (Friedlander et al. 2008). Barbless hooks could be enforced in Florida's bonefish fishery. Another, potential gear restriction in Florida's fishery is hook size which can increase the size/age at first capture. However, enforcement of barbless hooks and hook size regulations would be difficult. Also, the fly fishing community would likely oppose hook size regulations because their gears are more effective at casting smaller and lighter hook sizes.

Another option is reducing fishing effort through temporal or spatial closures. Temporal closures would be difficult to enforce due to the many access sites for the fishery. However, spatial closures are a common management tool in south Florida and have been successful at improving stock status (Ault et al. 2006). Spatial closures have the extra benefit of minimizing damage to the ecosystem from fishing gear but are difficult to accomplish due to political and economic pressures (Walters and Martell 2004).

A third way to manage the fishery is to control effort. Controlling effort has been discussed in other recreational fisheries using a lottery-access system of limited entry management similar to the ones used to manage big-game hunters (Walters and Cox 1999, Post et al. 2002). A lottery based system would be difficult to enforce due to the multiple access points of the fishery. Individual transferable quotas (IFQ) are being implemented in U.S. commercial fisheries to control fishing landings, increase fishing efficiency, and promote safety at sea. Nyeon et al. (2009) proposed an application of IFQ's for recreational fisheries where anglers and for-hire charters bid for access days to a fishery, and these access days are transferable. This management action has the potential to greatly reduce fishing effort; however, enforcement would not be practical due to the multiple access sites and many fishing grounds in the bonefish fishery.

Controlling effort in a bonefish fishery is not a novel idea. Palmyra Atoll's fishery has limits on the number of anglers and fishing seasons (Friedlander et al. 2008). Cuba's Peninsula de Zapata National Park restricts the bonefish fishery by limiting the areas, number of boats, number of anglers, and number of days.

If management options are unable to be implemented, a public outreach campaign can educate fishermen on how to improve their fishing practices and reduce discard mortality. There are factors that can minimize bonefish discard mortality. Cooke and Philipp (2004) found higher bonefish release mortality in areas with high shark densities, suggesting survivorship can be increased by ensuring bonefish are released in habitats with low shark densities. Cooke et al. (2008) found a positive relation between the increases in lactate and duration of the angling event, implying that anglers can reduce stress by minimizing fight duration. Suski et al. (2007) found metabolic disturbances (lactate production, hyperglycemia) increased following air exposure, and mortality occurred in bonefish exposed to air 3 minutes or longer. Anglers can decrease mortality by minimizing air exposure to 3 minutes or less.

Bonefish are important ecologically and economically to south Florida. This dissertation was the first assessment of this resource. As discussed earlier in this chapter, there is still a lot of work to be done. Although the stock is currently not overfished, it needs to be closely monitored and assessed to ensure its sustainability. Especially since ecosystem changes are expected if Florida’s human population continuous to increase and the ecosystem impacted from the Comprehensive Everglades Restoration Plan.

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