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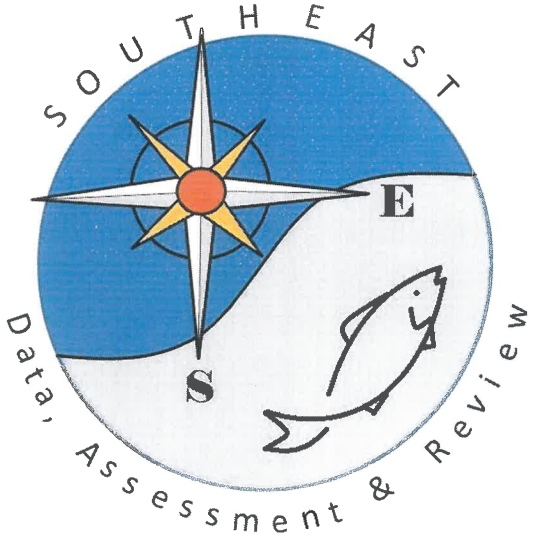
SEDAR33-DW12

8 May 2013



Please cite as:

Murie, D.J., D.C. Parkyn, and J. Austin. 2011. Seasonal movement and mixing rates of greater amberjack in the Gulf of Mexico and assessment of exchange with the South Atlantic spawning stock. SEDAR33-DW12. SEDAR, North Charleston, SC. 46 pp.

SEDAR33-DW12

Seasonal Movement and Mixing Rates of Greater Amberjack in the Gulf of Mexico and Assessment of Exchange with the South Atlantic Spawning Stock

Submitted by:

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Final Report for Cooperative Research Program (NA07NMF4540076)

28 December 2011

Acknowledgements

The study could not have been completed without the active collaboration of our associate investigators, including: Captain Myron Fischer (Cut-Off, LA; presently of the Louisiana Department of Wildlife and Fisheries), Captain Mark Hubbard (Madeira Beach, FL), Captain Ron Meyers (Little Torch Key, FL), and Captain Clay Bailey (Apalachicola, FL). We greatly appreciate them sharing their expertise in fishing for greater amberjack.

We are also grateful for the assistance of the Louisiana Department of Fisheries and Wildlife and the Gainesville Offshore Fishing Club for help in tagging fish. As with any tagging study, we were dependent on both commercial and recreational fishers returning tags and we are especially grateful to all of those that returned tags with information that could be used in this study.

This study required substantial field and laboratory support and we greatly appreciated the assistance of Geoff Smith, Doug Colle, John Hargrove, Felipe Carvalho, Chelsey Campbell, and Pat Gardner throughout this study. John Hargrove and Emily Saarinen also had a major contribution to the genetics portion of this study. We also thank the many other fishers that volunteered at one time or another to help tag amberjack.

1.0 INTRODUCTION

Greater amberjack is widely distributed throughout warm temperate and tropical waters and is an important recreational and commercial fishery in the Gulf of Mexico (Browder et al. 1978; Burch 1979; Parrack 1993a,b; Manooch and Potts 1997; Thompson et al. 1999). The recreational catch for amberjack in the Gulf of Mexico has historically exceeded commercial hand-line/longline and headboat landings on a Gulf-wide basis (Berry and Burch 1977; Manooch and Potts 1997; Cummings and McClellan 2000; SEDAR 2006). For example, in 2004 the private and charterboat catches represented 59.5% of the total catch, with the commercial handline fishery constituting a further 35%; headboat and commercial longline catches were relatively minor at 3% and 2.5%, respectively (Clarke 2006, SEDAR 9 Panel Review). Landings of greater amberjack peaked in 1986-89, declined through 1995 and remained at low levels until ~2000, after which landings increased again until 2003 but have since declined, especially in the recreational sectors (SEDAR 2006). Landings from the west coast of Florida and Louisiana have dominated commercial and recreational catches of amberjack in the Gulf (SEDAR 2006).

Based on trends in landings, Gulf of Mexico greater amberjack have been regulated since 1990 with a daily bag and minimum size limits. Increasing regulations in 1997-1998 included a reduction in the daily bag limit to one fish and a prohibition of commercial fishing and selling of amberjacks (greater, lesser, almaco, or banded rudderfish) from March to May during the spawning season. Increased regulations instituted in 2008 included an increase in the recreational minimum size limit (30 inches fork length), no bag limit allowed for captain and crew of for-hire vessels, and quotas. Recreational and commercial quotas have been exceeded since the 2009 fishing season, resulting in a temporary annual closure of the fisheries in Oct-Nov of each year.

The most recent stock assessment for greater amberjack was completed in 2006, using data up to and including 2004 (SEDAR 2006). As with the previous stock assessment in 2000 (Turner et al. 2000, using data up to and including 1998), the 2006 assessment concluded that Gulf of Mexico greater amberjack are overfished and experiencing overfishing. Under Secretarial Amendment 2, greater amberjack were already under a rebuilding plan as of 2003 with the purpose of ending overfishing and restoring the stock to the biomass level (B_{MSY}) capable of producing maximum sustainable yield (MSY) on a continuing basis. In the 2006 stock assessment, however, trends in catch rate data among the fishing sectors in 2004 (last year of data used) was inconsistent and the weighting of these indices changed the outcome and projections of the stock (SEDAR 2006). This led to a consensus by the SEDAR Stock Assessment Review Panel to recommend that Gulf of Mexico greater amberjack go through an update assessment, which was completed in 2010 (SEDAR 9 2010 Update, 2011). This 2010-11 update continued to designate greater amberjack as overfished and experiencing overfishing in the Gulf of Mexico.

Stock assessment of greater amberjack in the Gulf is complicated by a lack of basic biological information. A study of fishery-specific age, growth, and sexual maturity of

greater amberjack on a Gulf-wide basis has recently been completed (Murie and Parkyn 2008). However, unanswered questions pertaining to the distributional patterns, seasonal movements, spawning aggregations and stock-mixing of greater amberjack in the Gulf of Mexico have the potential to influence the outcome of the stock assessment and subsequent stock trajectory.

Currently, greater amberjack are managed as two, non-mixing resident stocks with separate stock assessments done for the Gulf of Mexico and the South Atlantic stocks. This distinction of Gulf versus Atlantic stocks has primarily been based on tag-recovery studies, rather than detailed genetic stock identification. Exchange rates between the Gulf and Atlantic (southeast U.S.) greater amberjack stocks based on tagging studies have been estimated to be very low, ~1.3-1.6% (Cummings and McClellan 1996; McClellan and Cummings 1997). In addition, 72.9% and 92.7% of Atlantic and Gulf fish, respectively, were recovered within 100 nm of their release site, with the majority of fish recovered within 25 NM of their release site (McClellan and Cummings 1997). McClellan and Cummings (1997) noted that temporal movement of amberjack was in part related to the area of release. Amberjack tagged and released in North Carolina were recaptured both off North Carolina and off southeast Florida, whereas amberjack tagged off the Florida east coast were only recaptured off eastern and southeastern Florida (i.e., not South Carolina, and similar to the observations from MARMAP unpubl. data). This directional movement of amberjack from North Carolina was suggested to be a spawning migration, whereas amberjack off the east coast of Florida were assumed to be residents. McClellan and Cummings (1997) observed that the vast majority (92.7%) of amberjack recovered from the Gulf had traveled <100 miles from their release point and therefore did not participate in the longer migrations observed in amberjack from the Atlantic. Burch (1979) summarized amberjack tag recoveries from the Cooperative Gamefish Tagging Program on the east coast of the U.S. and estimated that 71.5% of the recoveries indicated no large-scale migration (i.e., no movement >25 NM). Data from amberjack tagged in the Gulf of Mexico were not analyzed in his study due to small sample size.

In contrast to earlier studies, recent analysis of greater amberjack tagged on the east coast from North Carolina south to the Florida Keys showed substantial movement of fish into the Gulf of Mexico, with a few fish reaching the northeastern Gulf (off Mississippi and northern Florida) (MARMAP, preliminary unpub. data). These tagging studies raise the concern that with tagging efforts concentrated in the southern latitudes of Florida, where the amberjack may be resident (Burch 1979; McClellan and Cummings 1997), it would not be surprising that these fish are observed to have little movement. However, another large management concern is the degree of mixing between the presumed Gulf and the Atlantic stocks of amberjack on a seasonal basis, similar to that seen in the complex movement and mixing zone of king mackerel *(Scomberomorus cavalla)* (DeVries et al. 2002). To date, there is considerable information on the movements of greater amberjack in the South Atlantic Region of the U.S. but not for Gulf amberjack other than a possible "resident" subpopulation off south/southwest Florida. Studies of movement and migration patterns of greater amberjack in the Gulf of Mexico are needed to examine whether amberjack in the northeastern Gulf (west and east of the Mississippi) spawn in the northern Gulf or

undertake longer migrations to the south and spawn in mixed aggregations with the Atlantic stock. This latter scenario obviously has consequences to what would be considered the spawning stock supplying larvae and later recruits to the Gulf of Mexico fishery for greater amberjack.

Spawning of greater amberjack in the Gulf of Mexico is a fundamental measure of the potential productivity of the stock but is not well known. Information from the South Atlantic stock of greater amberjack has been provided by Harris (2004) and Harris et al. (2007). In sampling females in spawning condition from the North Carolina/South Carolina border south along the Atlantic coast and as far as the Florida Keys, Harris (2004) found females with hydrated oocytes (which are indicative of imminent spawning) only in the area around south Florida and the Florida Keys between March and May. They concluded that the further north a female greater amberjack is located on the east coast then the less likely she will be in spawning condition. They further speculated that the area of spawning located off of south Florida may represent a single spawning area for greater amberjack from both the South Atlantic and the Gulf of Mexico. Their idea is based on preliminary tag recapture data that show greater amberjack tagged in the South Atlantic (North Carolina/South Carolina) moving into the Gulf, including the northeastern Gulf (MARMAP, unpubl. data; P. Harris, pers. comm.).

Because the only known pelagic spawning ground for greater amberjack in the southeastern U.S. is off the southern tip of Florida (Pat Harris, unpublished data), identifying potential alternative spawning locations that may be feeding recruitment of the Gulf stock is critical for effective management of the overall fishery. As highly mobile fish, oceanographic regions used by individual amberjack during breeding and non-breeding seasons may vary greatly. Whether the Florida Keys region is an important spawning area primarily for the Atlantic stock or is used by a portion (or all) of the Gulf of Mexico stock is a critical question given that current management practices treat Gulf and Atlantic stocks separately, and given that the Gulf of Mexico greater amberjack stock is considered to be overfished and experiencing overfishing when the South Atlantic stock is not. For these reasons, it is desirable to not only identify, but also determine the level of connectivity between breeding and non-breeding areas for these fish, and the degree to which these potential stocks are mixing during spawning and non-spawning periods. Tagging studies focusing on seasonal movements and migration, especially in relation to spawning areas and season, combined with a complementary genetic assessment of mixing rates and temporal changes in regional genetic structure, can specifically address these important issues.

There has been limited research using genetics to estimate demographic connectivity or mixing among greater amberjack stocks. Gold and Richardson (1998) used mitochondrial DNA (mtDNA) restriction data to examine stock structure between South Atlantic and Gulf samples. Their results did not strongly support the established management stock-structure, although they did describe "significant heterogeneity" among samples from the Florida Keys and Atlantic pooled in comparison to Gulf samples. During this time, mtDNA was the primary genetic marker using in stock identification due to its ease of use and because it is typically variable within species. However, one limitation to using mtDNA is that it only

provides information on maternal gene flow. Given the significant mtDNA heterogeneity among the two recognized stocks, the application of highly variable, bi-parentally inherited, nuclear DNA markers like microsatellites may provide useful information on stock mixing.

The present management of Gulf and Atlantic greater amberjack as separate stocks could be supported if virtually no or very low levels of recent and historical mixing are detected, and potential spawning areas are identified in the Gulf. Conversely, if amberjack are determined to mix at a higher frequency throughout the year, and in particular during the spring spawning season off south Florida, then it would be necessary to consider a joint stock assessment for the Gulf and Atlantic stocks of greater amberjack.

The overall goal of the study was to examine the seasonal pattern and rates of movement of greater amberjack in the Gulf of Mexico and to determine the potential mixing rate of the Gulf of Mexico greater amberjack stock with the South Atlantic greater amberjack stock. The specific objectives necessary to accomplish this goal were:

1. Capture and externally tag greater amberjack, determine sexual status, and collect fin rays for aging and tissue samples for genetic analysis in four geographic regions: 1) in the northern Gulf of Mexico west of the Mississippi (Texas and Louisiana); 2) in the northern Gulf of Mexico east of the Mississippi (Mississippi, Alabama, and northwestern Florida); 3) in the eastern Gulf of Mexico (north-central to south-western coast of Florida); and off south Florida and the Florida Keys in known spawning areas of the South Atlantic greater amberjack stock.

2. Determine presence and timing of any seasonal dispersal or movement patterns of Gulf greater amberjack through analysis of tag recaptures.

3. Through tag recaptures, estimate potential mixing rate of Gulf greater amberjack with greater amberjack from known spring spawning areas of the South Atlantic stock off south Florida.

4. Determine the location(s) of potential spawning of greater amberjack in the Gulf by tagging large, sexually mature fish with pop-off archival transmitting tags.

5. Use genetic sampling via microsatellites of greater amberjack to identify stocks and mixing rates.

6. Integrate tagging and genetic analyses to estimate movement and mixing rates of Gulf greater amberjack in relation to current management practices.

2.0 MOVEMENT PATTERNS OF GREATER AMBERJACK

This section of the report combines Objectives 1 through 3 and is the basis for the general tagging and sampling of greater amberjack and the resulting analysis of dispersal, movements, and potential mixing rate based on tag returns.

2.1 METHODS

Tagging Areas: Greater amberjack were tagged in four major areas, including the northwestern Gulf (Louisiana, west of Mississippi) (NW-GULF), northeastern Gulf (east of Mississippi) (NE-GULF), west central Florida (FL-W), and Florida Keys (FL-KEY) (Fig. 2.1). Amberjack were tagged from December 2007 through to July 2011. Greater amberjack were tagged in the Florida Keys only in April during the spawning season of the South Atlantic stock (Harris et al. 2007).

Tagging: Greater amberjack were caught using a variety of hook-and-line gear, including recreational and charterboat bottom-fishing and jigging, commercial hook-and-line, and commercial bandit gear. Specific capture information was recorded for each fish, including: location (GPS latitude and longitude), bottom depth and estimated capture depth (ft), hook type (C-hook, J-hook, or jig), and bait type (live, dead, cut/species). Small fish (e.g., less than ~10 lbs) were boated using the fishing rod whereas larger fish were boated using a large landing net to avoid break-offs; fish were not gaffed in this study.

All captured fish were measured for fork length (nearest mm). The location of the hook (e.g., corner of the mouth, roof of mouth, etc.) and any signs of bleeding or trauma from either the hook or predators were recorded.

All fish caught were tagged with a heavy-duty dart tag (Hallprint PDA) using a stainless steel tag applicator. The tag was applied through the dorsal musculature under the second dorsal fin. Tags were anchored between the pterygiophores below the base of the second dorsal fin (Williams 1992) (www.dnr.sc.gov/marine/pub/ seascience/tagfish.html). Approximately 5% of the fish were double tagged to estimate tag loss (Gulland 1963; Seber and Felton 1981; Xiao 1999; Cadigan and Brattey 2003).

Tags were printed with the tag number, "Reward", and tag return information. Fishers returning tags chose from a tagging reward of either a baseball cap or a travel mug for each tag returned with a minimum of the date and general location of recapture. In addition to these individual smaller rewards, cash rewards of $100 were randomly selected from all tag returns during each quarter of the year, and an annual cash reward of $500 was selected from all tag returns during each year of the program. High, random cash rewards gave a potential for increased rate of tag returns (Pollack et al. 2001).

Tagged amberjack were recovered by recreational and commercial fisherman, as well as scientific fishing operations throughout the duration of the study. Fishers reporting tags were called back in most cases to request more specific information on fish length, location

of recapture, depth of capture, gear and bait used, and condition of the fish. GPS coordinates of tag recoveries were converted to NAD83 UTM format for analysis and comparison with release sites in ArcGis 9.1.

Non-lethal Aging: Finrays have been shown to be a reliable structure for the non-lethal aging of various fishes (Beamish 1981; Debicella 2005). A study of amberjack aging methodology (Murie and Parkyn 2008) suggested that pectoral finrays were an alternative non-lethal aging structure for amberjack. Therefore, two pectoral finrays were removed from the left pectoral fin of all tagged amberjack, placed on ice in the field, and later frozen until processed for aging.

Finrays were processed to obtain observed ages of tagged fish that were recaptured. Finrays were thawed and thoroughly dried prior to being mounted in epoxy resin. Finrays were then cut into 0.7-0.9 mm thick sections using a Buehler Isomet 2000 high speed saw and a diamond sectioning blade (Chilton and Beamish 1982; Debicella 2005). Multiple finray sections for each fish were mounted on a glass slide with Flotexx, dried, and then viewed using a stereomicroscope. A 540 nm interference filter was used when necessary to enhance visual contrast. The protocol for aging finrays was based on aging criteria set forth by Murie and Parkyn (2008).

Non-lethal Sexing and Gonadal Development: Sex of captured fish was also determined by examining the urogenital pores, as well as extrusion of gametes during the reproductive season. A subsample of these data was supplemented with non-lethal catheterization, which was used to take a small biopsy of the gonad tissue. To validate the non-lethal sexing method, a series of fish were first externally sexed using the urogenital pores followed by dissection to observe their gonads.

Catheter samples were kept cold (but not frozen) until viewed fresh under a dissecting scope, at which time the oocytes were classified following (Hunter and Goldberg 1980; Marte and Lacanilao 1986; Render and Wilson 1992). Catheter samples and samples from dissected gonads from sacrificed fish were preserved in chilled, 10% phosphate-buffered formalin (Humason 1979; Hinton 1990).

Genetic Sampling: Prior to freezing the pectoral fins, the distal tips of the fin rays were rinsed in double distilled deionized water and clipped using scissors rinsed in undenatured ethanol. The sample was placed into a sterile micro-centrifuge tube filled with 95% undenatured ethanol for later processing of the genetics of the fish (See Section 4.0).

Analysis of Tagged Fish and Recoveries: Fork lengths of tagged fish in the four sampling areas were compared using a one-way analysis of variance. Tag return data was analyzed by area, size and, where possible, sex and age of fish. Coordinates of capture-recapture data were recorded in WGS84 UTM data format and spatial data was projected using ArcGis 10.0.

Great circle distances moved by individual fish were calculated using Vincenty's inverse method which corrected for the ellipsoid shape of the earth's surface and provides bearings between the points of capture and return (Vincenty 1975). The ellipsoid model was based on the WGS84 format. Movement rates were calculated as the minimum great circle distance between individual release and recapture locations divided by the number of days at large. Directional statistics of movements were calculated for specific tagging areas, including mean vectors of directionality and circular standard deviation using Oriana (Version 3, Kovach Computing Services, Anglesey, Wales) and summarized with circular histograms with data grouped into 10° bins. Rayleigh tests were used to determine if angular distributions of data deviated from a null hypothesis of a uniform distribution (Batschelet 1981). A doubling of angles procedure was used for data with an axial distribution (Batschelet 1981; Parkyn et al. 2003).

2.2 RESULTS AND DISCUSSION

Tagging and Tag Recaptures

A total of 1,493 amberjack were captured and tagged in the four regions in the Gulf of Mexico (Figure 2.2). Most tagging trips originated from ports in Grand Isle/Port Fourchon, Louisiana (NW-GULF), Apalachicola and Suwannee, Florida (NE-GULF), Madeira Beach, Florida (FL-W), and Little Torch/Big Pine, Florida (FL-KEY).

Approximately 4.9% (74 out of a total of 1,493) of the fish were double-tagged to assess tag loss, and 7 out of 7 double-tagged fish that have been recovered had both tags attached (100% tag retention).

Fish size

Fish tagged and released ranged from 226 to 1412 mm fork length (FL) (Figure 2.3). Size of greater amberjack differed significantly among the four sampling regions ($F_{3df,,\ 0.05}$= 285.99, $p < 0.0001$) with FL-KEYS fish being significantly larger than amberjack caught in the other regions (Student-Newman-Keuls test: $\alpha = 0.05$) (Table 2.1).

Overall, the proportion of amberjack recaptured as a function of their release length was skewed towards larger fish (Figure 2.4A), most likely because of the minimum size limits. When the size of released fish was constrained to only fish >72 cm fork length (28" recreational size limit when tagging started), then the proportion of fish released and recapture by size interval was similar (Figure 2.4B). However, fish size did not appear to affect recapture rate as fish of all sizes that were released were also recaptured during the study.

Non-lethal Sexing and Gonadal Maturation through Catheterization

The methodology of non-lethally sexing greater amberjack and using catheterization to stage gonad maturation was developed for this study and formed the basis for the Master's

thesis of Geoff Smith (Smith 2011). He was able to show that the method was accurate for ~96-100% of the fish (Figure 2.5). Since that time, we have been able to sex 371 fish that were subsequently released. Of these fish, 149 were females from 502-1412 mm FL and 222 were males ranging from 366-1174 mm FL (Figure 2.6), with most fish <900 mm FL males whereas fish >1100 mm FL were females. During the spawning season, mature males and females were also identifiable through the release of milt or some eggs.

Recapture Rate

In total, 169 tags (11.3%) have been returned, with 3 fish with multiple tag returns (total of 172 recapture locations). Of these, 159 tags were returned with recapture location information. Size frequency distributions of non-lethally sexed and tagged fish that were later recaptured indicated that the sizes of female and male greater amberjack recaptured were skewed towards larger fish, especially for males (Figure 2.7).

Distances Moved, Days-at-Large and Directionality

Based on updated return information provided by fishers, distance travelled could be estimated from 172 tag returns (169 fish, with two multiple recaptures), with an average distance travelled from the tagging site of 69.54 ± 188.96 km (Table 2.2; Figure 2.8). However, the median distance of recaptures was only 8.0 km, indicating most fish were caught near where they were tagged. The maximum observed distance traversed was a straight-line distance by an amberjack tagged in Apalachicola, FL, on 7 March 2009 and recaptured 13 February, 2010, near Tampico, Mexico (1501 km), as well as another amberjack tagged in March 2008 and recaptured 10 months later in Jamaica (1231 km) (Figure 2.9).

The average number of days at large was 150.96 ± 224.41 days. To date, the maximum days-at-large was 1112 days (Table 2.2). The distance moved appeared to be not related to the number of days at large, at least for a significant number of tagged fish (Figure 2.10).

Eighty of 172 greater amberjack (46.5 %) were recaptured at distances greater than 10 km from the point of initial capture (Figures 2.11, A-D). Fish captured from the NW-GULF and FL-KEYS (Figures 2.11, A and B) displayed movements that were primarily east or west (78/258°), although four fish from the FL KEYS moved northward and were distributed significantly differently from uniform (Rayleigh test $Z = 16.188$, $p < 0.0001$, and $Z = 3.711$, $p = 0.022$, respectively). Similarly amberjack tagged in NE-GULF were observed to move mostly in a SW direction (243°) significantly different from uniform (Rayleigh test: $Z = 2.918$, $p = 0.052$) (Figure 2.11, C). The most extreme of these movements was a fish recaptured from Tampico, Mexico. In contrast, amberjack caught in FL-W were observed to move in all directions and were not distributed significantly from uniform (Rayleigh test: $Z = 0.405$, $p = 0.6720$) (Figure 2.11, D). Several of these fish moved within the range the range of the Atlantic greater amberjack stock and one exceptional fish was recaptured along the Northeast coast of Jamaica.

Potential Mixing Rates

Mixing rates varied by region but in general greater amberjack were recovered in the same region from which they were initially tagged, indicative of the low median distance of movement observed. FL-KEYS fish mixed with Gulf of Mexico fishes at a 1.5 % rate (1 of 66 recaptured fish) (Table 2.3). Similarly, Gulf of Mexico fish overall mixed with FL-KEYS fishes at 0.94 % (1 of 106 recaptured fish). Specifically, 1 of 37 fish moved from FL-W to FL-Keys (2.07 %). No fish moved from the NW-GULF area. In contrast, one amberjack tagged from NE-GULF moved into NW-GULF, while another moved to Tampico, Tamaulipas, Mexico. These reciprocal mixing rates were similar to that observed previously by McClellan and Cummings (1997), indicating no recent changes in patterns of exchange among the stocks.

Table 2.1. Mean (and S.E.) of forklength of greater amberjack tagged in the present study by region.

Region	Mean	Standard Error	N
NW-GULF	728	14.3	310
NE-GULF	713	5.1	418
FL-W	751	6.5	427
FL-KEYS	1039	7.1	276

Table 2.2. Updated summary statistics of the days-at-large and recapture distance (km) for 172 tagged and recaptured greater amberjack

	Days-at-Large	Recapture Distance (km)
Mean	150.96	69.54
Standard deviation	224.41	188.96
Median	30	8.0
Minimum	0	0.00
Maximum	1112	1500.66

Table 2.3. Inter-regional mixing of greater amberjack from 172 tag returns (169 fish, with 3 fish with multiple recaptures).

	Area Recovered					
	NE-GULF	NW-GULF	FL-W	FL-KEYS	Mexico	Jamaica
Area Tagged						
NE-GULF	20	1			1	
NW-GULF	47					
FL-W	34	1		1		1
FL-KEYS	65		1			

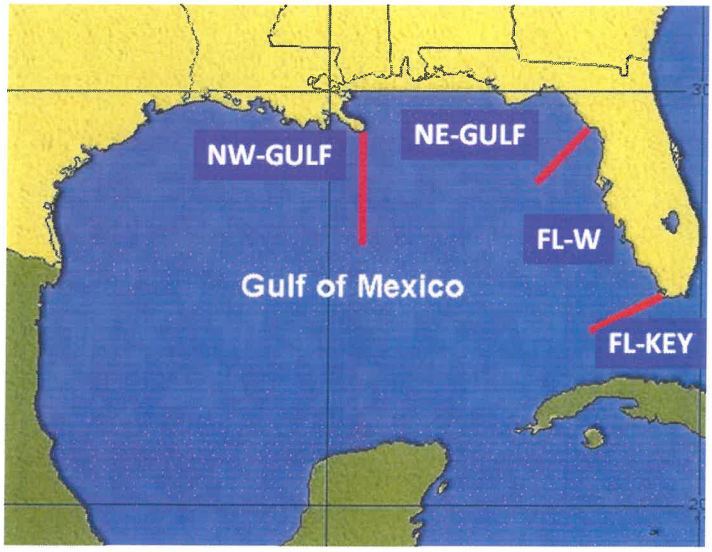


Figure 2.1. Location of tag and release areas for greater amberjack in the Gulf of Mexico. NW-GULF (Louisiana), NE-GULF (northeastern Gulf), FL-W (west-central coast of Florida), and FL-KEY (Florida Keys).

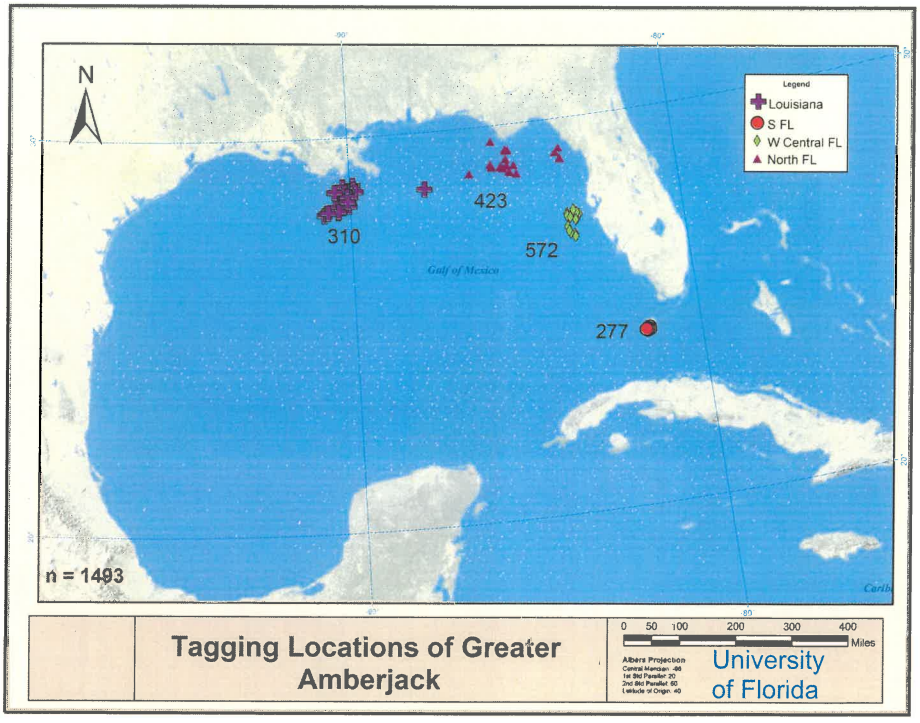


Figure 2.2. Tagging locations of greater amberjack (n=1,493) in the Gulf of Mexico.

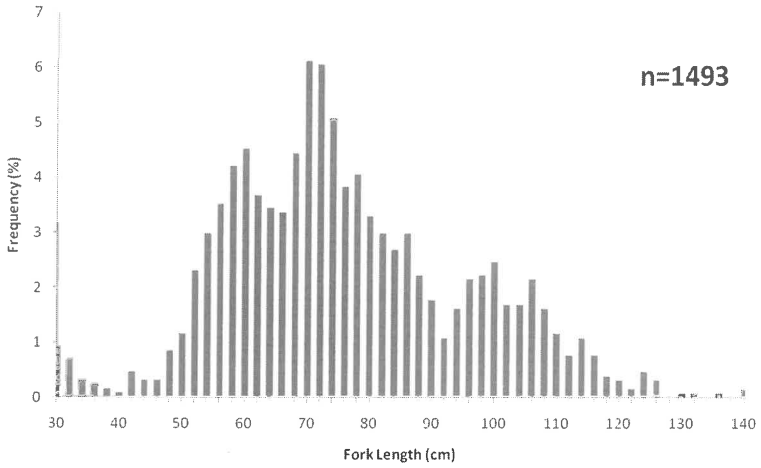


Figure 2.3. Length frequency distribution of all greater amberjack tagged and released.

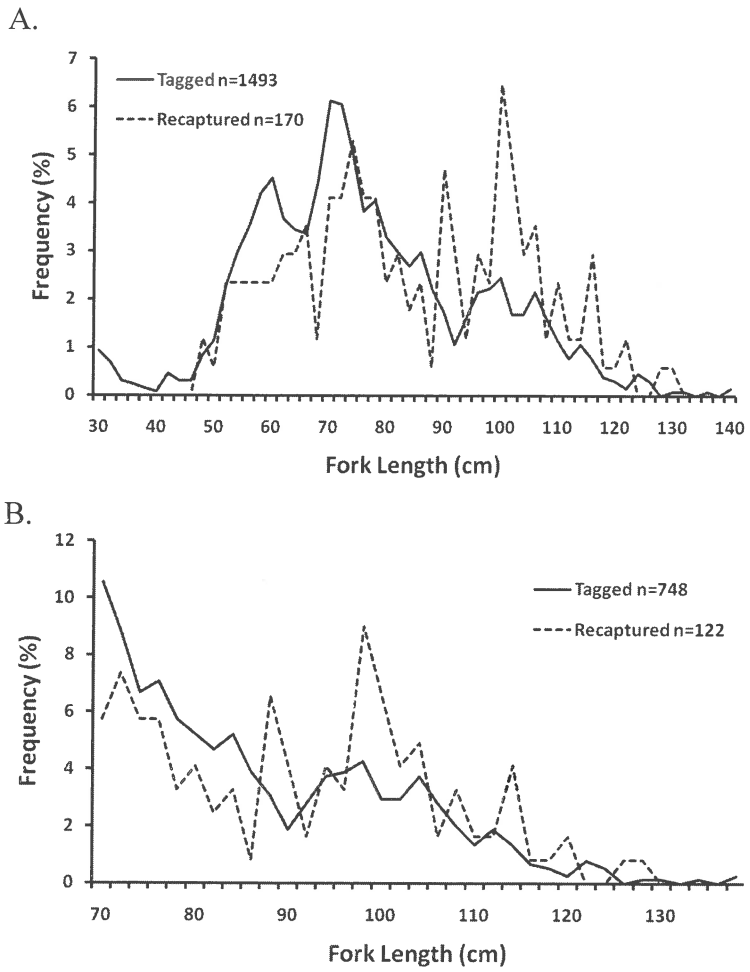


Figure 2.4. A) Length frequency distributions of all greater amberjack tagged, released, and later recaptured; and B) length frequency distribution of greater amberjack >72 cm fork length (28" legal-sized recreational fish) that were tagged, released, and later recaptured.

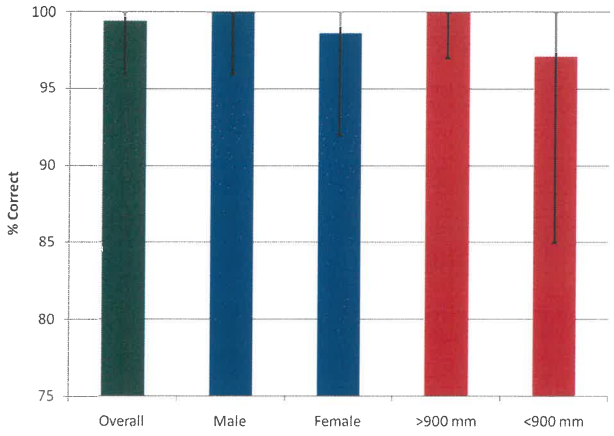


Figure 2.5. Accuracy of external and catheterization methods of non-lethally sexed greater amberjack.

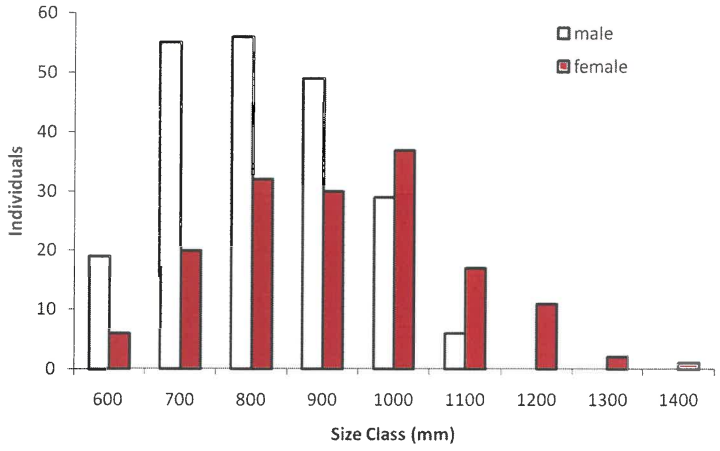


Figure 2.6. Frequency of male and female greater amberjack tagged as a function of their fork length. Fish were sexed using either external morphology or catheterization.

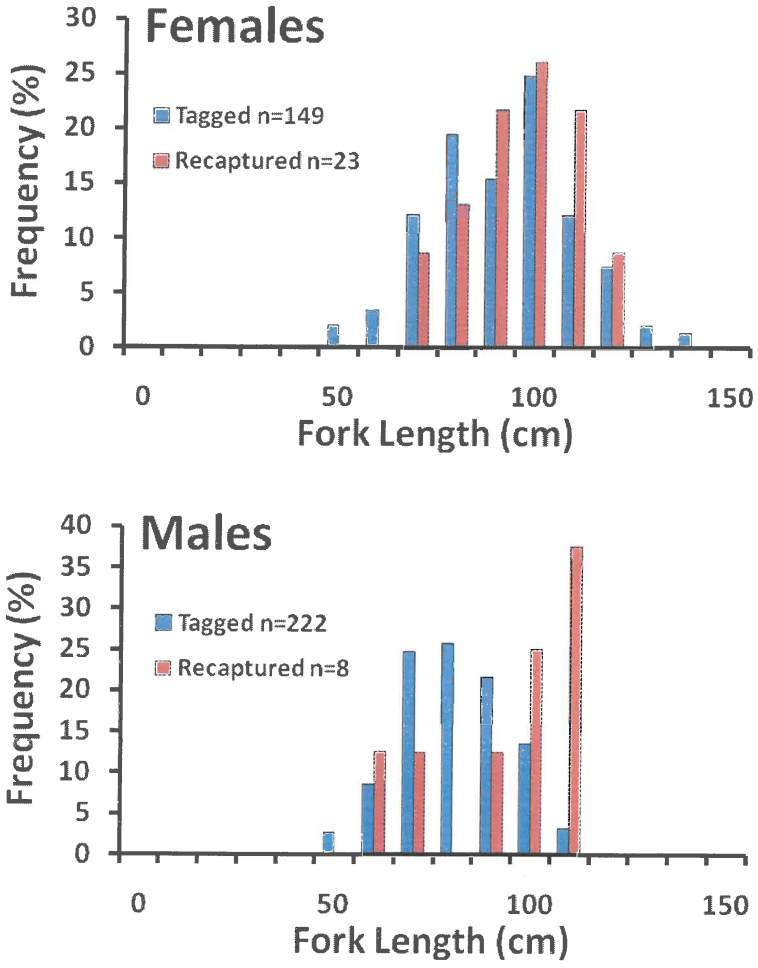


Figure 2.7. Length frequencies for tagged and released female and male greater amberjack in relation to lengths of fish that were later recaptured.

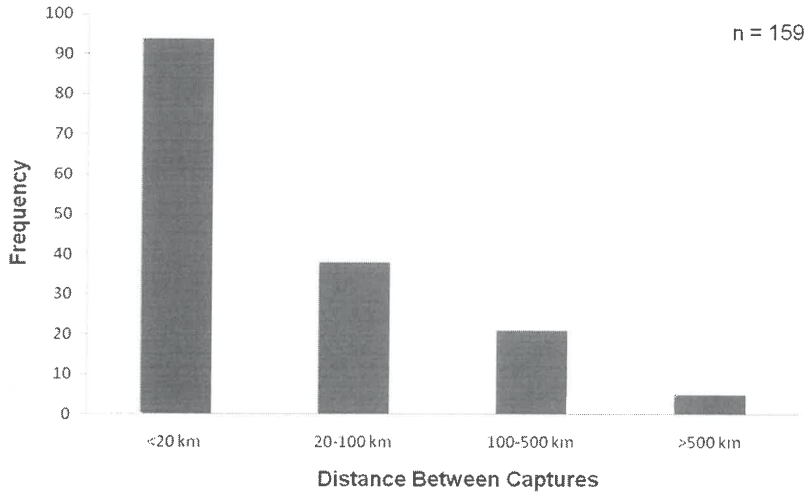


Figure 2.8. Frequency of greater amberjack recaptured as a function of observed distance travelled.

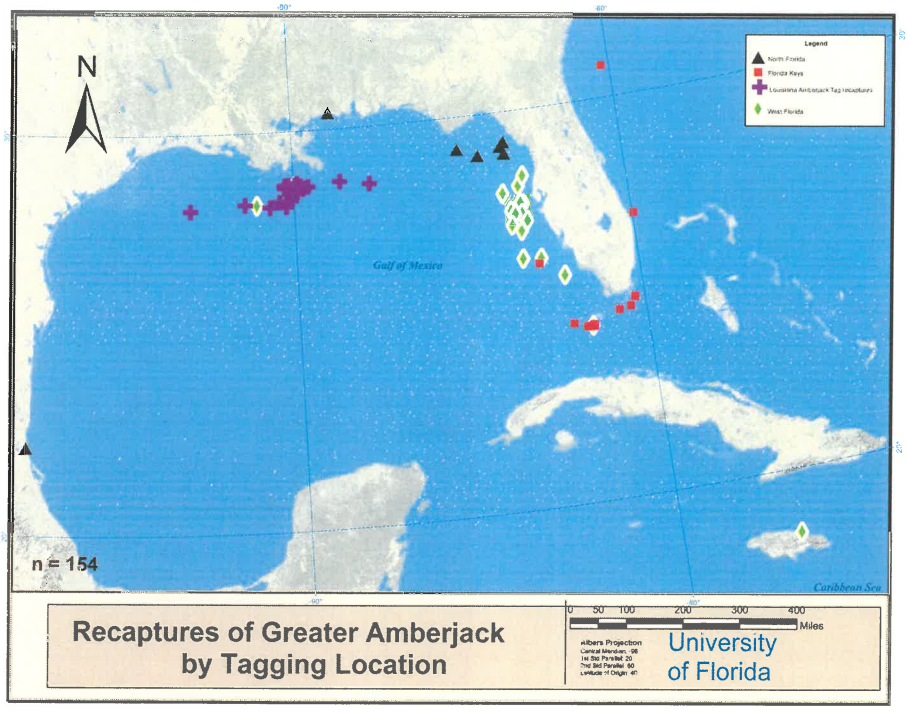


Figure 2.9. Locations of greater amberjack recaptured by recreational and commercial fishers in the Gulf of Mexico. Symbols denote originally tagging area of the recaptured fish: FL-KEY (red square), FL-W (green diamond), NE-GULF (black triangles), and NW-GULF (purple crosses). Note the individual fish recaptured off Vera Cruz, Mexico (black triangle), and Port Maria, Jamaica (green diamond).

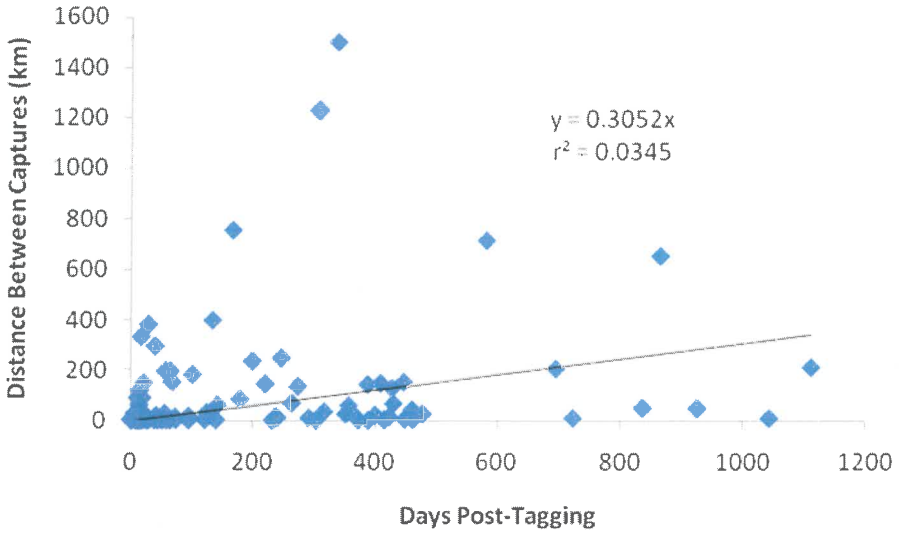


Figure 2.10. Distance moved by greater amberjack as a function of days post-tagging (days-at-large).

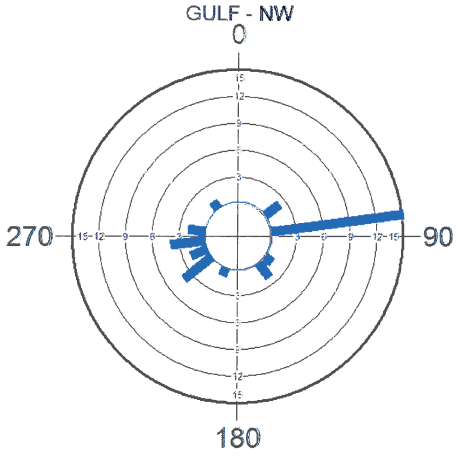


Figure 2.11A. Numbers of greater amberjack moving from point of capture and recapture in the northwest Gulf (Louisiana). Observations are grouped in bins of 10°. N = 34.

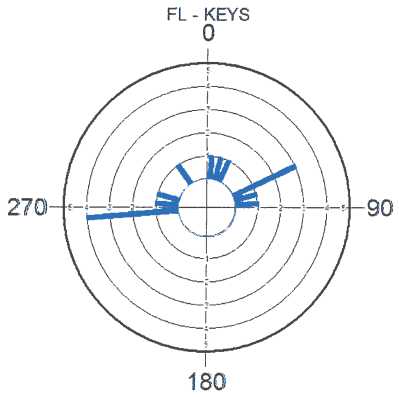


Figure 2.11B. Numbers of greater amberjack moving from point of capture and recapture in the Florida Keys. Observations are grouped in bins of 10°. N = 15.

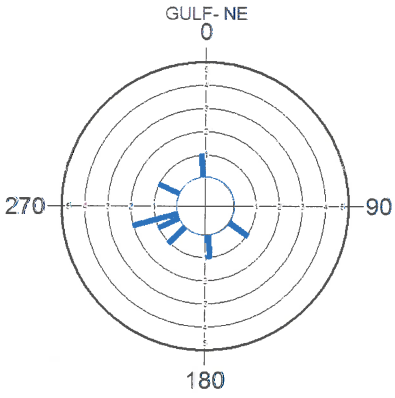


Figure 2.11C. Orientation of fishes moving between the capture and recapture in NE-GULF. N =8.

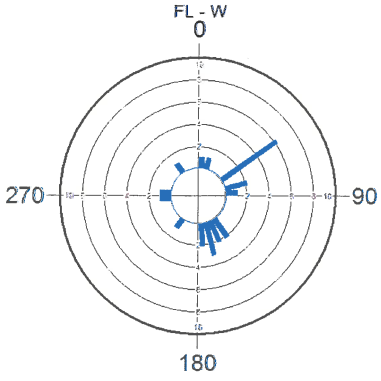


Figure 2.11D. Orientation of greater amberjack moving between the capture and recapture site for W-FL. N = 24.

3.0 TRACKING SPAWNING GULF OF MEXICO GREATER AMBERJACK THROUGH POP-OFF SATELLITE TAGS

Pop-up archival satellite tags (PSATs) were used to help identify potential spawning areas in the Gulf of Mexico or movement of spawning fish from the northern Gulf areas southward to known spawning sites in the Florida Keys (identified by Harris et al. 2007).

3.1 METHODS

Five PSATs (x-tag, Microwave Telemetry) were attached to amberjack behind the first dorsal fin through the epaxial musculature and between the pterygiophores of the second dorsal fin and the adjacent neural spines. Large mature fish were tagged in March of 2010 off the coast of Louisiana in the NW-GULF and their tags were programmed to release on 1 April 2010 during the peak of the spring spawning season. To insure that the fish were 100% reproductively mature, only fish >865 mm FL (Harris 2004, SEDAR 2006) were tagged. Reproductive status of each fish was confirmed by catheterization to ensure fish were mature and reproductively active when tagged in March.

Pop-up tags were labeled with "Cash Reward" along with return information to encourage reporting and recovery of the tags. Although the pop-up archival tags download information to the ARGOS satellite without having to be physically recovered, more detailed data records (uncompressed data with a finer scale) can be recovered from the tag if the tag is physically recovered.

The MK-10 PAT tags measure ambient pressure (depth: 0 to 1000 m, ± 0.5 m), temperature (-40°C to +60°C, ± 0.05°C), and light (5×10^{-12} W.cm^{-2} to 5×10^{-2} W.cm^{-2}), the latter permitting determination of dawn and dusk to 300 m depth. This information was used to calculate solar noon and longitude, while day length and satellite-derived sea surface temperatures were used to refine estimates of latitude (Block et al. 1998; Lutcavage et al. 1999; Teo et al. 2004). Once sea surface corrections for geolocations were undertaken, the data consisted of a continuous track of movements on each individually tagged amberjack, the depths the fish utilized, and the water temperatures encountered.

Pop-up tag data were examined for water depth and water temperature frequency distributions for each fish. Horizontal movement and directionality was examined using tests outlined in Section 2.0. Release and recapture positions of tagged fish were displayed using ArcGIS 9.1.

3.2 RESULTS AND DISCUSSION

Three mature female and two mature males (Table 3.1) were captured on 3 March 2010 between depths of 150 and 350 ft near oil rigs off the coast of Louisiana; maximum bottom depths at the sites were between 200 and 580 ft. These fish were selected because they were large mature fish that were certain to spawn in the upcoming spawning season. Based

on catheter samples, the male amberjack were flowing milt and the female fish had late stage vitellogenic oocytes.

Three of the tags popped up immediately on the scheduled pop-up date, while two more detached the same day but were temporarily trapped below an oil rig subsurface structure. Based on data obtained from the tags, the fish moved between 0.7 and 16.7 km from their initial tagging site (Table 3.1). Fish moved a mean of 7.60 ± 3.23 km in the 26 days prior to pop-off or 0.29 km/d. Four of the fish moved along a bi-directional plane (63° and 243°), while the fifth moved 90° to this direction (Fig. 3.1). This indicated that reproductively active fish remained off the coast of Louisiana during the spawning season (i.e., they did not travel south to the Florida Keys to spawn) (Figure 3.2).

From the depth and temperature data archived by the PSAT tags while the fish were at large, it was apparent that three of the tagged greater amberjack were relatively consistent in the depth and temperature they experienced, with the two other tagged fish showing more variability (Figure 3.3). Two fish appeared to utilize the water column at shallower depths, between 11-50 m, with a second smaller mode at deeper depths of 71-90 m (Figure 3.4). The three other fish consistently used deeper depths of 51-80 m (Figure 3.4). Regardless of their depth distribution, all fish consistently were in water that was 18-19°C for the duration of their tagged period (Figure 3.5). Although there was obviously some combination of depth and temperature selection by the tagged amberjack (i.e., most of the fish did not stay in shallow), this was also confounded by the mixing of the water during the winter months in the area. Spear et al. (2011) showed that the water off Louisiana was well mixed at 15-20°C to a depth of 150 m before it became cooler with increasing depth.

Table 3.1. Summary of greater amberjack tagged with satellite tags.

Satellite Tag No.	**96789**	**96790**	**96791**	**96792**	**96793**
Sex	M	F	M	F	F
Fork Length (mm)	1070	1165	963	1179	1061
Distance Moved (km)	11.7	7.8	16.7	0.7	0.9

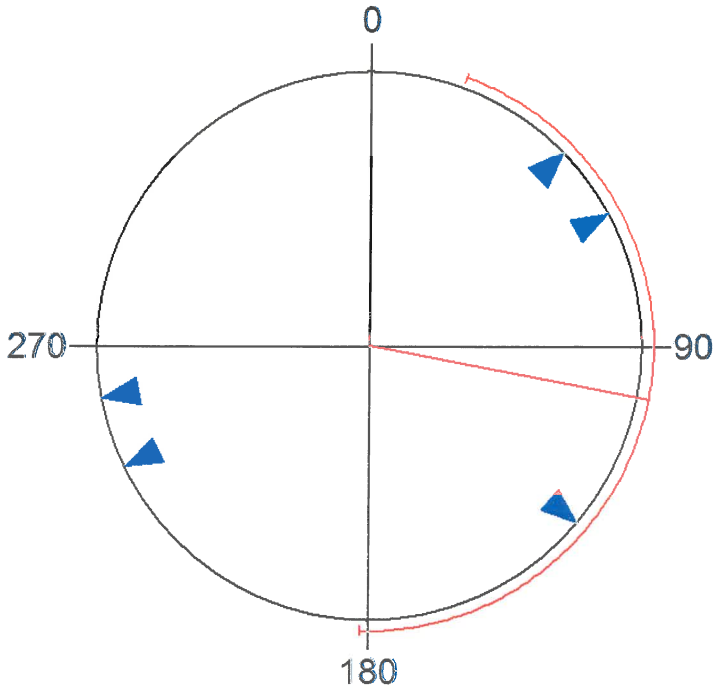


Figure 3.1. Angular movements of five reproductively mature greater amberjack tagged with PSAT tags off the coast of Louisiana (NW-GULF) during the spring spawning season. Red line indicates mean angular movement (±S.D.). Note that all of these fish travelled less than 20 km from their original release site.

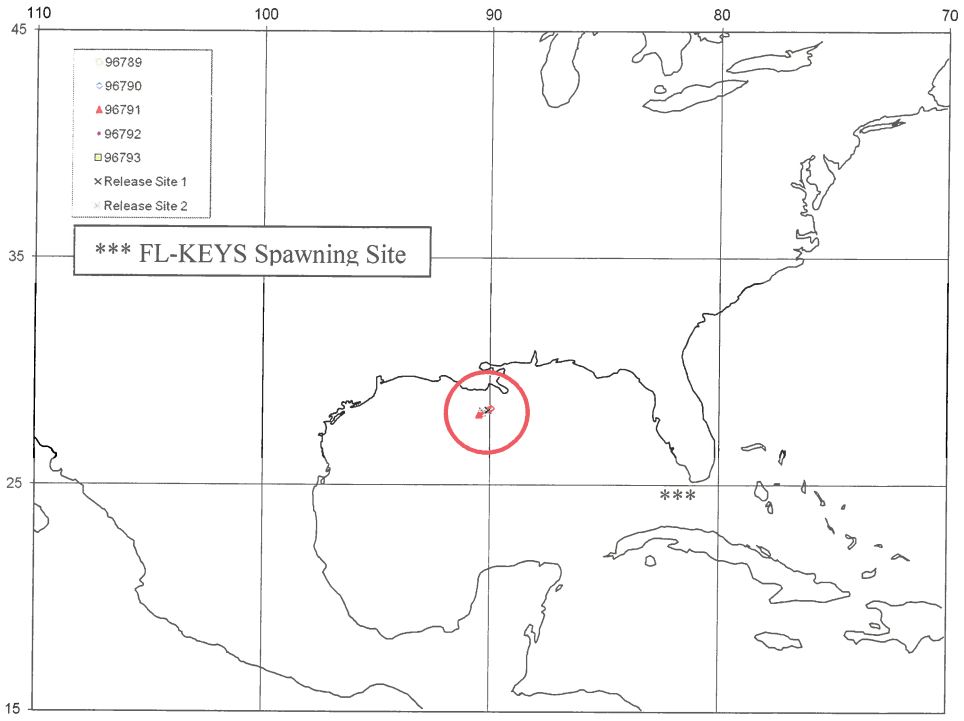


Figure 3.2. Release and recovery sites (area in red circle) for reproductively mature greater amberjack tagged with PSAT tags off the coast of Louisiana (NW-GULF). Note that none of the PSAT-tagged fish moved southward toward the known spawning area (***) of the Atlantic stock of greater amberjack..

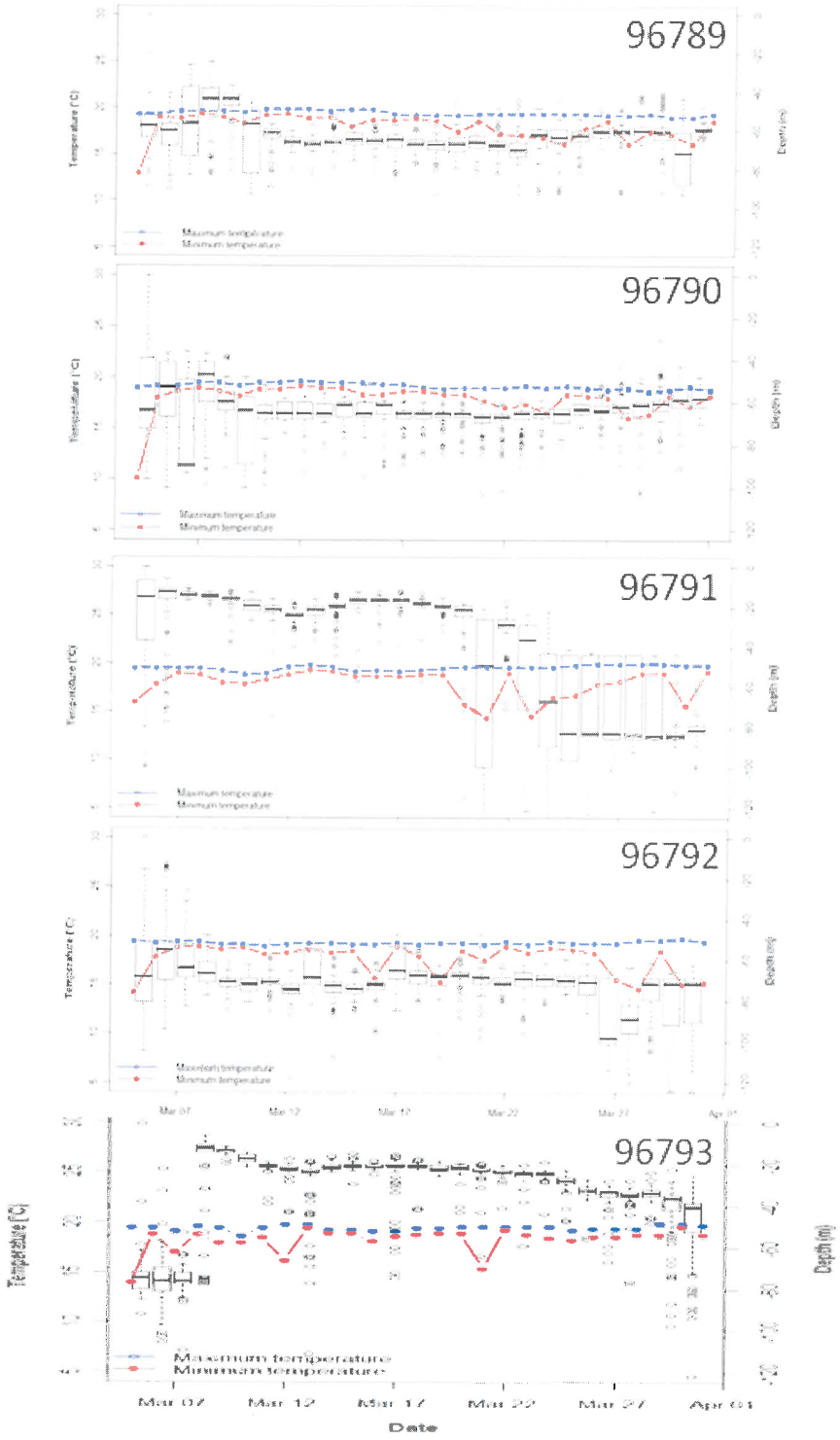


Figure 3.3. Water temperature and depth profiles experienced by PSAT-tagged greater amberjack in the NW-GULF. Water temperature is given by minimum and maximum temperatures whereas water depth is given by box plots where the solid bold line is the mean, and the top and bottom of the box are the 25% and 75% quartiles.

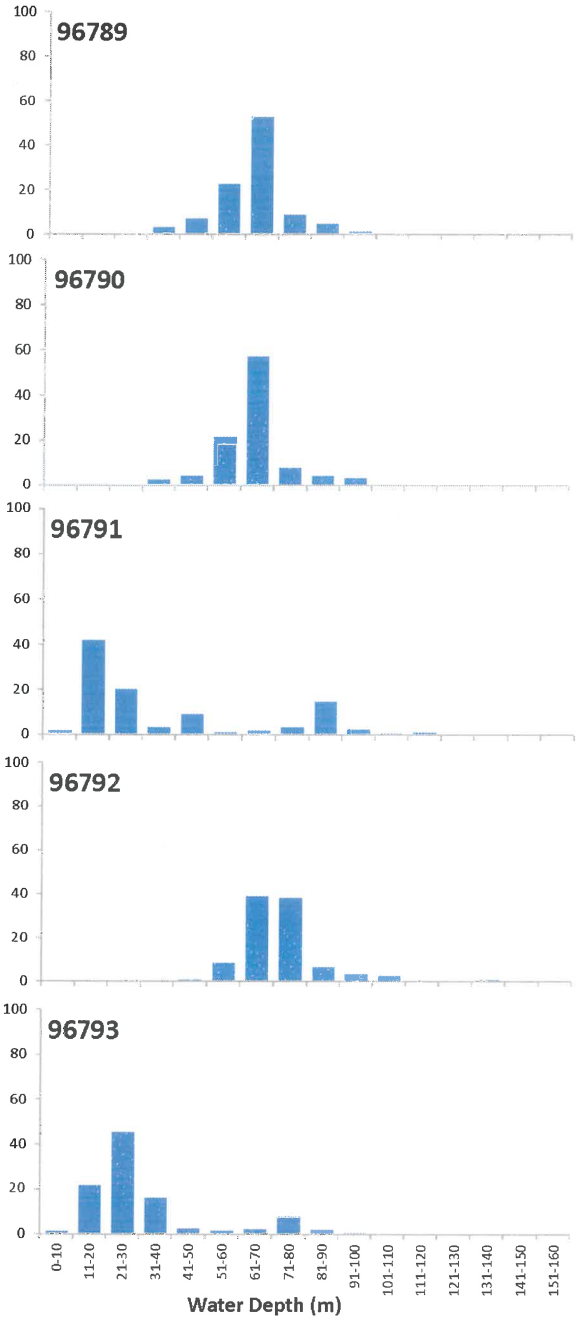


Figure 3.4. Water depth distribution frequencies for PSAT-tagged greater amberjack in the NW-GULF.

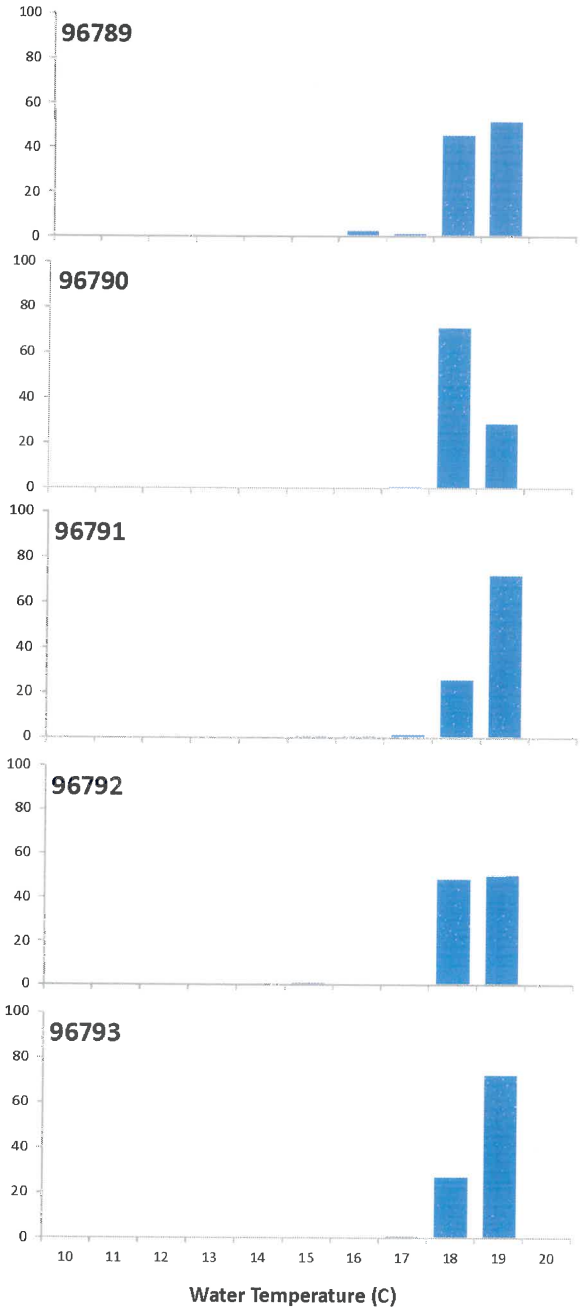


Figure 3.5. Water temperature distribution frequencies for PSAT-tagged greater amberjack in the NW-GULF.

4.0 STOCK IDENTIFICATION AND MIXING RATE BASED ON MICROSATELLITES

4.1 METHODS

Marker Choice and Evaluation

Genotypes were generated using 15 published greater amberjack microsatellite loci [Sdu1, Sdu3, Sdu5, Sdu10, Sdu12, Sdu16, Sdu21, Sdu22, Sdu23, Sdu27 (Renshaw et al. 2006), and Sdu 32, Sdu33, Sdu37, Sdu41, and Sdu46 (Renshaw et al. 2007)]. These included a range of di-, tri-, and tetranucleotide markers. Microsatellites were chosen over the original plan to use amplified fragment length polymorphisms (AFLPs) due to the publication of the microsatellite information by Renshaw et al. (2006, 2007) coincident with the start of this grant. Given that an objective was to utilize genetic markers with potential for high-resolution at low cost, developing new AFLP markers was uneconomical given the newly available microsatellites (AFLPs were initially planned due to their lower developmental cost, but at higher risk for detecting suitable variation).

A total of 543 samples were genotyped from the four sampling regions (NW-GULF, NE-GULF, FL-W, and FL-KEY; hereafter referred to as "populations"). Data were examined manually for outlier alleles, and reliability of genotype scoring was tested using MICRO-CHECKER 2.2.1 (van Oosterhout et al. 2004). This program tests for potential errors in scoring due to stuttering patterns erroneously interpreted as alleles, large allele drop-out (a failure to amplify larger alleles), or presence of null alleles (alleles not being amplified due to, for example, mutations in primer sequences). Deviations from Hardy Weinberg Equilibrium (HWE) were evaluated using GENODIVE (version 2.0; Meirmans and Van Tienderen 2004) with significance adjusted using sequential Bonferroni correction of *P*-values (Rice 1989).

Global genetic differentiation among populations was estimated by computing the fixation index (G_{ST}) (Nei 1987), the standardized fixation index (G'_{ST}) (Hedrick 2005) that controls for downward bias of G_{ST} in highly variable markers like microsatellites, and Jost's (2008) differentiation (D) that is independent of the amount of within-population diversity. Standard errors for differentiation estimates were obtained by jackknifing over loci. A permutation test (n=1,000) was also conducted to determine whether lower differentiation would be obtained under random mating (panmixia). Differentiation tests were performed in GENODIVE.

Potential for Detecting Stock Mixture

To attempt to estimate the rate of mixing between Atlantic and Gulf of Mexico stocks, mixture proportions of each of the regional populations that included non-reproductive individuals (NW-GULF, NE-GULF, FL-W) were estimated. In this sense, the reproductive individuals sampled at NW-GULF and FL-KEYS were used as reference populations (i.e.,

breeding stocks). This method assumes that the two reproductive reference populations are distinct, and consist of effectively randomly mating individuals within, and some limited gene flow between populations. This assumption can be contrasted with an assumption of panmixia, where each generation there are a large number of breeders exchanged between breeding stocks, effectively resulting in one randomly mating breeding stock.

Mixture proportions were estimated using a conditional maximum likelihood approach (Millar 1987) implemented in ONCOR (http://www.montana.edu/kalinowski/). When reference populations are not highly differentiated, the conditional maximum likelihood method can be biased toward 1/k, where k is the number of reference populations in the data set (ONCOR users manual, accessed October 19, 2011). With k=2 in the present study, the bias would be towards 0.5 mixture proportions. The leave-one-out assignment test implemented in ONCOR was also applied to evaluate how well fish could be assigned to the putative breeding population of origin. Using only fish from the two breeding populations, this test sequentially removes each fish from the baseline and its origin is estimated from the remainder of the baseline stock. Each fish genotype is tested in this manner.

Given the evidence for a single genetic stock in the Gulf (see below), the error decomposition that represents the percentage of the total error that is attributable to fishery sampling, genotypic sampling, and to baseline sampling was also examined. Fishery sampling is error introduced by sampling too few fish (genotypes) from a fishery. Genotyping error is due to sampling too few loci, and baseline sampling error is related to not knowing the true allele frequencies in a fishery. The latter is related to the first source of error (too few genotypes assessed to obtain an accurate picture of allele frequencies within loci) but the former (fishery sampling) could have limited power if samples are small, even if true allele frequencies can be assumed. This analysis required estimates of stock proportions (Gulf and Atlantic) in each sample. Because this was not known, a variety of proportions (0.1 to 0.9) were explored to determine the impact on error decomposition by simulating 10,000 genotypes based on the empirical allele frequencies, and randomly sampling 543 genotypes from the simulated fishery.

The program STRUCTURE version 2.3 (Pritchard et al. 2000) implements a Bayesian clustering method for inferring population structure using genotype data consisting of unlinked markers. This model-based approach permits the demonstration of the presence of distinct genetic groups, assigning individuals to delimited populations, and identifying migrants and admixed individuals. We used the admixture model that allows for portions of individuals genomes (q) to be probabilistically assigned to specific populations, K, where K is unknown. The admixture model reflects recent or current admixture at rates that are sufficient to suggest ancestry from more than one population. Our analyses applied the correlated allele model that assumes populations diverged from a common ancestor and that some of the differences in allele frequencies are due to genetic drift as well as possible gene flow. This approach assumes that allele frequencies in different populations may be similar and should increase the power of clustering weakly differentiated individuals. The model choice criterion implemented in STRUCTURE to detect the true K is an estimate of the

posterior probability of the data for a given K, Pr(X|K). Individuals in the sample are assigned (probabilistically) to K populations, or jointly to two or more populations if their genotypes indicate that they are admixed. It is assumed that within populations, the loci are at Hardy-Weinberg equilibrium, and linkage equilibrium.

Three approaches were taken to explore the data in STRUCTURE. First, a naïve analysis (no prior knowledge of breeding condition or sample location) was conducted to explore the possible number of genetic stocks and the level of admixture in the samples. Second, a sample identification was included as a prior that can help inform the search for the 'true' K when data are poorly informative. For both analyses a number of possible genetic clusters (K) were examined (K = 1 to K = 5). A total of 50,000 burn-in generations were run followed by 100,000 generations to estimate posterior distributions. Runtime plots of likelihood values were examined to ensure adequate chain exploration. For each value of K, 10 independent replicates (using different starting seeds) were run and the mean and variance across replicates were examined to determine whether independent runs were converging on similar results, and to examine the distribution and pattern of likelihood values across K values.

The third approach specifically examined the fit of the data to an admixture model between NW-GULF and FL-KEYS (Atlantic) spawning groups by using a USEPOPINFO model to pre-specify the stock origin of spawners (NW-GULF, FL-KEYS) and to assist in the ancestry estimation of unassigned genotypes (NW-GULF, NE-GULF, FL-W). K was set to 2 (to reflect the hypothesized breeding stocks contributing to a mixed fishery in the Gulf of Mexico) and included a 'popflag' that identified the reproductive individuals sampled at NW-GULF and FL-KEYS. By applying the PFROMPOPFLAGONLY option, STRUCTURE uses only allele frequencies from these two groups to update allele frequency estimates during the MCMC simulations.

Approximations of the Marginal Likelihoods of Competing Migration Models

Due to the lack of effective genetic mixing rate estimation that assumes genetic differentiation exists among stocks, we evaluated various migration models between the two sampled breeding populations (NW-GULF and FL-KEYS). Alternative genetic population models were evaluated through a Bayesian coalescent framework using MIGRATE vers. 3.2.6 (Beerli and Felsenstein 2001; Beerli 2006). Model examination was restricted to known reproductive individuals from the NW-GULF and FL-KEYS (the only two regions where reproductively mature individuals were sampled). A logical set of four models were chosen for investigation: 1) M_1, testing whether FL-KEYS and NW-GULF represent two distinct genetic populations of different sizes that exchange migrants at independent rates (a full migration model); 2) M_2, examining whether migration occurs unidirectionally from the FL-KEYS to the NW-GULF, (this is similar to a source-sink model where the NW-GULF breeders might represent a recently or continuously seeded breeding group from the Atlantic (FL-KEYS) stock); 3) M_3, a model where gene migration was forced to be symmetrical (an equal amount of migration in either direction); and

finally, 4) M_4, testing whether FL-KEYS and NW-GULF belong to the same panmictic population (gene migration is effectively random across both breeding stocks).

The Bayesian approach implemented in MIGRATE uses thermodynamic integration (Gelman and Meng 1998) of the marginal likelihood and performs well regardless of prior choice (though priors need to be the same among models compared). This type of full marginal likelihood model estimation is useful in that it allows for the comparison of nested *and* non-nested models (Beerli and Palczewski 2010). Initial exploratory runs were used to determine the required run length and priors to obtain good posterior distributions for all parameters in the full model (M_1 above). Once this was established each model was then run for three replicates using the same starting priors and conditions, and the results were summarized across runs. Analyses were run under default conditions with the following exceptions: Brownian motion mutation model for microsatellite data; uniform theta (scaled population size) priors {min. = 0.000, max. = 300.000, mean = 0.010}; uniform migration priors {min. = 0.000, max. = 200.000, mean = 10.000}; increment between sampled geneologies {100}; samples per replicate {50,000}; initial discarded samples per replicate (burn-in) {50,000}. We ran eight static heated chains {temperatures: 1.00, 1.77, 3.34, 6.46, 12.69, 25.17, 50.11, 100.00}. We calculated model probabilities by subtracting the highest marginal likelihood from each of the competing models', exponentiated each value, summing and using this summed value as the denominator. Each exponentiated value is divided by the sum to estimate the probability of each model (P. Beerli, personal communication).

4.2 RESULTS AND DISCUSSION

Though Renshaw et al. (2006, 2007) reported all loci conforming to Hardy-Weinberg equilibrium (HWE), results from our population samples revealed a large number of significant departures (33 of 75 total), though only one locus (Sdu37) departed across all five populations (i.e., NW-GULF-Reproductive, NW-GULF-Nonreproductive, NE-GULF, FL-W, FL-KEYS-Reproductive). The remaining loci had significant deviations from HWE at zero to four of the population samples. MICROCHECKER revealed possible deviations from HWE due to null alleles at four of five samples at Sdu37 (the exception being NW-GULF-Reproductive). Twenty-six of the remaining 28 departures from HWE were also inferred to be potentially caused by null alleles. No tests inferred large allele dropout or scoring error due to stuttering. The removal of Sdu37 did not qualitatively affect the results of our MIGRATE analyses, and therefore we assumed that it had a minimal effect on the remainder of our results. Furthermore, due to the lack of systematic deviation from HWE from other loci, it was assumed that these results were minor. Moreover, Bonin et al. (2004) suggest that genotyping errors resulting in deviations like these are more problematic for individual-based analyses (e.g., kinship, relatedness) rather than for population-structure questions such as the primary focus here.

Overall differentiation among populations in the Gulf of Mexico was low across 15 highly variable loci (G_{ST} = 0.007, S.E. = 0.003), even after correction for biases associated with highly variable markers (G'_{ST} = 0.037, S.E. = 0.014; D = 0.030, S.E. = 0.012) (Table 4.1).

Though differentiation was low overall, the permutated data sets were all smaller than the observed differentiation tests (all $P = 0.001$), suggestive of low though statistically significant differentiation overall. Comparison between the two reproductive population samples only (NW-GULF-Reproductive and FL-KEYS-Reproductive) was similarly low ($G_{ST} = 0.006$, S.E. = 0.004; $G'_{ST} = 0.043$, S.E. = 0.029; $D = 0.038$, S.E. = 0.026), with all empirical values significantly greater than zero (all $P = 0.001$).

Stock Mixture Analyses

The mixture proportions estimated in ONCOR reflected a large association of individuals with the Florida Keys (Table 4.2). Each sample (NW-GULF-Nonreproductive, NE-GULF and FL-W) was suggested to be approximately 70%-80% Atlantic stock (FL-KEYS), however, this may be biased downward due to the low differentiation among breeding samples (see methods). Similar proportions were estimated on all samples combined.

The assignment test (leave-one-out) performed poorly, with only 62.5% correct assignment for Louisiana spawning fish (NW-GULF-Reproductive), and 77.8% correct assignment for FL-KEYS. Examination of error decomposition based on varying proportions of baseline populations trended from ~90% baseline error for highly skewed proportion of baseline Atlantic or Gulf, to roughly 50% fishery error if populations are equally represented (Table 4.3).

Bayesian analysis of admixture performed using STRUCTURE functioned poorly in detecting multiple genetic clusters and admixed samples. This was due to the strong support for the existence of a single genetic population in the Gulf of Mexico including the Florida Keys. Under the naïve analysis, the posterior likelihood was highest for K = 1, with a gradual decrease in likelihood and a concomitant increase in variation among replicates with increasing K. While the increase in variance among replicates was very high at K = 3 to K = 5 (Fig. 5.1), it also increased between K=1 (mean –LnL = 34,209.71, S.D. = 1.2) and K=2 (mean –LnL = 34,408.90, S.D. = 49.1). When population priors were included the results were similar in that there was an increase in variance with increasing K (number of populations assumed). The likelihoods for both models were nearly identical for K = 1 (-LnL = 34,209.68, S.D. = 0.42 for population priors model). The likelihood values increased weakly from K = 1 to K = 3 before declining (Fig. 5.1). Results from the 'learning samples' approach where known reproductive individuals (NW-GULF and FL-KEYS) were used to update allele frequencies and K was set at 2 (assuming the genetic structure matches the current management of two separate stocks) resulted in an unresolved pattern where each of the 543 fish genotyped were assigned to both genetic clusters at approximately 50% (not shown). This result is common in STRUCTURE analyses where data are not informative.

The results from the model comparison using the thermodynamic integration method is shown in Table 4.4. Model 3, which allows for gene flow but constrains migration to be symmetrical between the FL-KEYS and the NW-GULF, had the highest marginal

likelihood. M_2 was the second best model; in it migration from NW-GULF to FL-KEYS was reduced to zero, but allowed for migration from FL-KEYS to the Gulf. The most parameter-rich model (M_1) was third (independent migration rates in either direction), while panmixia (M_4) was the least supported. The difference between the best model and the closest competitor was large; difference in model support between M_3 and M_2 (an subsequently between M_3 and all others) was effectively zero.

Interpretation

The methods employed herein to evaluate mixing rates, and previous genetic studies over similar scales (Gold and Richardson 1998), reveal limitations in traditional genetic methods to differentiate between Atlantic and Gulf of Mexico stocks of greater amberjack. This may reflect a true lack of differentiation over time scales of 10s of generations (i.e., high migration and, by extension, high mixing rates). Alternatively, the historical effective population size (N_e) of greater amberjack is considerably larger than our sample can differentiate. Both of these factors may be responsible, further creating difficulty in evaluating mixing rates in this and similarly mobile marine species. Our coefficients of genetic differentiation (FST and analogs) reflect low values (i.e., < 0.1) but are still statistically greater than zero (no differentiation). These methods can be downwardly biased when applied to highly variable markers, something our unbiased estimators (G'_{ST}, D) help to correct. However, the fishery management stocks have been assumed to reflect, to a considerable degree, independent demographic populations, an assumption that is not strongly supported by the genetic data.

Attempts to estimate rates of mixing, either through a traditional stock mixing algorithm (ONCOR), or by examining assignment of individuals to different stocks (assignment test and clustering algorithms) performed poorly. Regional samples (NW-GULF, NE-GULF, FL-W) typically had a larger proportion (~0.8) of membership to the Atlantic stock (FL-KEYS) (Table 4.2); a result that may be biased downward due to the low overall differentiation between the two breeding populations. Genotype approaches (assignment tests and clustering) can be more sensitive to fine-scale structuring than allele-based approaches (F_{ST} and stock mixing) (Garrick et al. 2010). However, these complementary approaches similarly failed to suggest strong differences between samples collected from reproductive fish from the putative Atlantic breeding grounds in the Florida Keys (FL-KEYS) and the Gulf breeding grounds off Louisiana (NW-GULF). Together, these data suggest that genetic estimates of mixing are unlikely to resolve the management question without a greater emphasis on geographic sampling (see below).

A Bayesian modeling approach was applied to attempt to inform the discussion of whether or not a two population model best reflects the current two stock model. Our results do not completely resolve this issue but they do provide a more informative picture of amberjack stock genetic mixing than traditional methods. For example, Gold and Richardson (1998) used tests for spatial homogeneity and differentiation (F_{ST}) of mitochondrial DNA (mtDNA) restriction fragment data to suggest that the two stocks represent subpopulations

corresponding to the Gulf of Mexico and Atlantic (latter including the Florida Keys). Our models included two that reflect this relationship; one that has independent rates of migration (M_1) and one with a symmetrical rate (M_3). The two models did not perform equally, with the model with the fewer parameters (M_3) performing the best. Of interest is that the model where gene flow was restricted to the Gulf from Atlantic (M_2) also out-performed M_1 (by a substantial margin). The panmixia model (M_4) was poorly supported, rejecting the possibility that the Gulf and Atlantic stocks are a single genetic population.

In general, these models together with the Bayesian clustering analysis (Fig. 5.1) strongly reflect a high rate of genetic mixing in this system. This is supported by previous mitochondrial work. Gold and Richardson (1998) did not find significant heterogeneity for all their samples pooled (8 Gulf, 2 Atlantic, plus the Keys) as might be expected if Gulf and Atlantic stocks were partially reproductively isolated. Similarly, they did not report testing genetic heterogeneity between Gulf versus Atlantic samples with the Florida Keys omitted.

Assuming the Florida Keys spawning fish represent the Atlantic stock and that the Gulf stock was represented by NW-GULF spawning fish, an interpretation that was argued in favor of based on mitochondrial data (Gold and Richardson 1998), we assumed that estimating mixing rates could be accomplished with some degree of support when employing high resolution nuclear markers. However, an interesting outcome of this effort is a well-supported pattern of weak genetic differentiation, suggesting that stocks do not correspond well to reproductive units. As a result, attempts at quantifying mixing performed poorly. An important consideration is that attempting to elucidate the patterns of mixing without considering other portions of the range (e.g., Caribbean and other South Atlantic "populations") may cloud our interpretation. It is possible that the unique heterogeneity represented by the Florida Keys may reflect its importance as a breeding area for other stocks.

Our error decomposition analysis suggests that considerably larger sample sizes (more so than greater numbers of loci, i.e., genotypic error) would be required to improve the possibility of accurately estimate mixing, assuming the two samples are truly demographically independent (i.e., not mixing at a high frequency within or between generations). An important assumption here is that two independent (though not necessarily isolated) breeding stocks do exist, which is not strongly supported by these data. Therefore doubling (for example) the sample sizes would potentially still perform poorly at estimating mixing rate. While panmixia can be rejected based on our Bayesian modeling and the non-zero estimates of differentiation, other analyses reflect a lack of structure (e.g. genetic clustering, Fig. 1).

Table 4.1. Population diversity measures based on 15 microsatellite loci.

	N	n	n_e	H_o	H_e	G_{is}
NW-GULF-Reproductive	76	15.13	6.13	0.689	0.779	0.115
NW-GULF-Non-reproductive	143	17.53	6.39	0.719	0.771	0.067
NE-GULF	109	16.20	6.11	0.729	0.745	0.021
FL-W	98	18.67	6.35	0.674	0.748	0.099
FL-KEYS	91	15.93	6.14	0.688	0.761	0.096

Number of alleles (n) and effective number of alleles (n_e) controlling for evenness of allele frequencies. Observed heterozygosity (H_o), expected (H_e) and inbreeding coefficient (G_{IS}) per sample population.

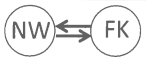
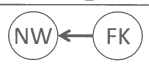
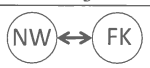
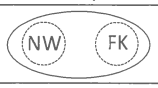
Table 4.2. Mixture estimates of Gulf of Mexico greater amberjack based on genotypes sampled from baseline stocks [spawning fish caught off Louisiana (NW-GULF) and the Florida Keys (FL-KEYS)] relative to non-reproductive fish sampled in the northwestern Gulf (NW-Gulf), northeastern Gulf (NE-GULF) and the west coast of Florida (FL-W).

	Area Sampled			
Baseline stock	NW-GULF	NE-GULF	FL-W	Combined
NW-GULF (Louisiana)	0.191	0.294	0.173	0.211
FL-KEYS (Florida Keys)	0.809	0.706	0.827	0.789

Table 4.3. Error decomposition of microsatellite data. Fishery proportions tested range from 0.1 Atlantic to 0.9 Atlantic (versus a Gulf breeding population). Estimates are based on 10,000 simulated genotypes and a random fishery sample of 543.

	Proportion Atlantic stock (Florida Keys)				
Baseline stock	0.1	0.3	0.5	0.7	0.9
Fishery	5.8%	31.8%	52.2%	27.7%	6.8%
Genotypic	2.1%	7.0%	9.9%	5.1%	2.0%
Baseline	92.1%	61.2%	38.0%	67.2%	91.2%

Table 4.4. Log marginal likelihoods (lmL) using thermodynamic integration of two different gene flow models: the model with the highest likelihood (lmL) and an alternative model (M_i). M_1, two genetically distinct breeding populations of varying size that are free to exchange migrants at different rates; M_2, two distinct population sizes with migration from the FL-KEYS (FK) to NW-GULF (NW); M_3, two unconstrained population sizes exchanging migrants at an equal (symmetrical) rate; and M_4, panmixia.

	M_1	M_2	M_3	M_4
				
lmL	-18,016.25	-13,303.41	-10,706.68	-26,194.54
Model rank	3	2	1	4
Difference from best model	-7,309.57	-2,596.73	0	-15,487.86
Model probability	~0	~0	~1.0	~0

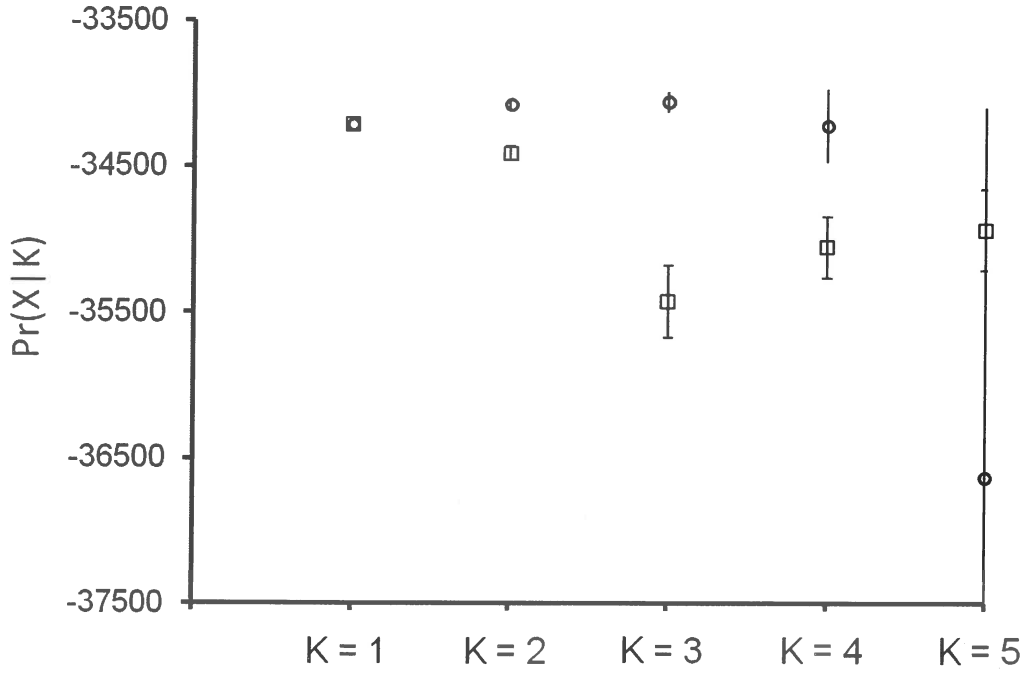


Figure 4.1. Graph of STRUCTURE *results with posterior probability for each of K putative genetic groups. Means and standard deviations for 10 replicate runs per K are presented. Naïve runs (no sample location prior) are represented by square symbols, informed runs (sample location used as prior) represented by open circles. Error bars are truncated for informed run at K = 5.*

5.0 INTEGRATION OF TAG-RECAPTURES AND MICROSATELLITE INFORMATION TO INFER MIXING RATE OF GOM GREATER AMBERJACK

Although a lower percentage of tagged fish were recovered (11.3%) relative to a recent study of Atlantic stock amberjack (~19%) (MARMAP 2007), tagging data in both studies suggest some low level movement of between Atlantic and Gulf of Mexico regions. The reciprocal mixing rates in the present study were similar to that observed previously by McClellan and Cummings (1997), indicating no recent changes in patterns of exchange between the stocks. The low but roughly similar observed levels of exchange between the two stocks based on tag returns in this study was also consistent with the genetic model with the marginal likelihood, Model 3, which allowed for gene flow but constrained migration to be symmetrical between the FL-KEYS and the NW-GULF. It is of particular interest that panmixia (Model 4) was the least supported model, likely due to levels of exchange not being high enough to eliminate genetic differences among the Gulf and Atlantic stocks. Thus although allele frequencies do not greatly differ between Gulf and Atlantic stocks, given the low level of exchange of individuals exacerbated by the relatively short movement distances of most fish, the two regions are continuing to function as essentially separate stocks.

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