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Survival of the blacktip shark, Carcharhinus limbatus

William A. Swinsburg
University of Rhode Island, billswinsburg@gmail.com

SURVIVAL OF THE BLACKTIP SHARK,

CARCHARHINUS LIMBATUS

BY

WILLIAM A. SWINSBURG

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OF

WILLIAM A. SWINSBURG

APPROVED:

Thesis Committee:

Major Professor   David Bengtson

Nancy Kohler

Jeremy Collie

Graham Forrester

Nasser H. Zawia
DEAN OF THE GRADUATE SCHOOL

UNIVERSITY OF RHODE ISLAND
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ABSTRACT

Proportional survival (*S*) is a crucial life-history parameter in population dynamics, natural selection, and management of harvested stocks; variations in survival due to age, sex, or geographic region may have large effects on the success of managing fish stocks. The blacktip shark, *Carcharhinus limbatus,* is the most abundantly harvested shark species in American fisheries. Direct estimates of survival are preferred, but all current survival estimates for this species are either focused on young-of-the-year (YOY) or based on indirect methods. The objectives of this study were to determine whether age, sex, or geographic grouping affects survival and to generate direct survival estimates based on tag-recovery data. As a byproduct of this analysis, distribution maps and descriptive data summarizing captures were included. The U.S. National Marine Fisheries Service has been collecting tag-recovery data since 1962 through the Cooperative Shark Tagging Program (CSTP). Models were generated from this database with program MARK, ranked in order of parsimony according to Akaike's Information Criterion, and tested for significance of effects with likelihood ratio tests. No movement has been observed to date between the west Gulf of Mexico, east Gulf of Mexico, and U.S. Atlantic, but 2 sharks tagged in the U.S. Virgin Islands were recaptured off Florida and Georgia (displacement= 1049 and 1183 n. mi., respectively). Survival did not differ significantly for males vs. females (*P*=0.761), east vs. west Gulf of Mexico (*P*=0.654), or U.S. Atlantic vs. Gulf of Mexico (*P*=0.243). However, significant differences were found for survival of YOY (0.580) and post-YOY (0.725) within the Gulf of Mexico (*P*=0.0003). These results demonstrate that survival can be modeled effectively for species in the CSTP with

relatively small sample sizes. Future analyses may benefit from a length-based model,

due to the difficulty in assigning life stages based on size.

ACKNOWLEDGMENTS

DEDICATION

I dedicate this thesis to my inspiring parents Robin and Joan, my kind-hearted sisters

Becky and Laura, and my breathtaking fiancée Barbara. *Soli Deo gloria*.

PREFACE

This thesis is presented in Manuscript Format. This paper is formatted according to the guidelines for submission to *Fishery Bulletin.* The paper has not yet been submitted for publication. All the pages have been formatted in the accepted font and margin alignment.

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"Survival of the blacktip shark, *Carcharhinus limbatus*"

by

William Swinsburg[1]; Nancy Kohler[2]; Jeremy Collie[3]; Patricia Turner[4]; Camilla McCandless[5]

is in preparation to Fishery Bulletin

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[1] M.S. Candidate, Department of Fisheries, Animal, and Veterinary Science, The University of Rhode Island, Kingston, RI 02881. Email: billswinsburg@gmail.com

[2] NOAA/NMFS/NEFSC, Narragansett, RI 02882. Email:Nancy.Kohler@noaa.gov

[3] Professor, Graduate School of Oceanography, The University of Rhode Island, Narragansett, RI 02882. Email: jcollie@mail.uri.edu

[4] NOAA/NMFS/NEFSC, Narragansett, RI 02882. Email: pat.turner@noaa.gov

[5] NOAA/NMFS/NEFSC, Narragansett, RI 02882. Email: cami.mccandless@noaa.gov

ABSTRACT

Proportional survival (*S*) is a crucial life-history parameter in population dynamics, natural selection, and management of harvested stocks; variations in survival due to age, sex, or geographic region may have large effects on the success of managing fish stocks. The blacktip shark, *Carcharhinus limbatus,* is the most abundantly harvested shark species in American fisheries. Direct estimates of survival are preferred, but all current survival estimates for this species are either focused on young-of-the-year (YOY) or based on indirect methods. The objectives of this study were to determine whether age, sex, and geographic grouping affect survival and to generate direct survival estimates based on tag-recovery data. As a byproduct of this analysis, distribution maps and descriptive data summarizing captures were included. No movement has been observed to date between the west Gulf of Mexico, east Gulf of Mexico, and U.S. Atlantic, but 2 sharks tagged in the U.S. Virgin Islands were recaptured off Florida and Georgia (displacement= 1049 and 1183 n. mi., respectively). Survival did not differ significantly for males vs. females (*P*=0.761), east vs. west Gulf of Mexico (*P*=0.654), or U.S. Atlantic vs. Gulf of Mexico (*P*=0.243). However, significant differences were found for survival of YOY (0.580) and post-YOY (0.725) within the Gulf of Mexico (*P*=0.0003). Future analyses may benefit from a length-based model, due to the difficulty in assigning life stages based on size.

INTRODUCTION

Proportional survival (*S*) is a crucial life-history parameter in population dynamics, natural selection, and management of harvested stocks (Lebreton et al.,

1992). Variation in survival, fecundity, and growth rate can interact to influence

adaptive fitness (Endler, 1986; Hutchings, 1993). Accurate estimates of survival are

a key component of demographic analysis and stock assessment of marine

species (Cortés, 1998; Mollet & Cailliet, 2002), and they determine which levels of

exploitation are sustainable (Simpfendorfer et al., 2005a).

Vetter (1988) suggested that survival in fish stocks can vary due to a

number of factors, including changing levels of fishing effort (Quinn and Deriso,

1999). Gear selectivity, predation pressure, or other factors may result in survival

probabilities that vary with age (Deriso et al., 1985; Quinn and Deriso, 1999). These

variations in survival could also have large effects on the success of fisheries

management (Deriso et al., 1985; Cortés, 1998; Quinn and Deriso, 1999). In either of

the cases above, stock assessments that assume constant survival may greatly

overestimate or underestimate a stock's capacity to handle intensive fishing pressure.

This lack of information may lead to fishing limits that are too high for sustainable

harvest. In a broader sense, determining whether survival varies with time or age is

the first step in understanding how anthropogenic causes may be affecting the life-

history of a species.

Proportional survival over a finite interval is related to total instantaneous

mortality rate (Z) by

$$S = e^{-Z}$$

where Z is the sum of instantaneous natural mortality (M) and instantaneous

fishing mortality (F) (Quinn and Deriso, 1999). Converting between

instantaneous mortality and finite survival assumes that the instantaneous

mortality rate is constant during the finite time interval. Many methods of

estimating survival were described by Ricker (1975) and Seber (2002). Direct

methods of calculating survival (i.e., mark-recapture) are preferable over indirect

methods that involve the use of life-history parameters (Brownie et al., 1985; Lebreton

et al., 1992; Quinn & Deriso, 1999; Simpfendorfer et al., 2005b). Recent advances in

computer modeling technology allow powerful hypothesis testing related to variations

in survival (Lebreton et al., 1992). New models allow the user to separate the effects

of recovery probability from the probability of death using mark-recapture histories

(White & Burnham, 1999; Cooch & White[1]).

Elasmobranchs are slow-growing fish with late maturity and small litter size

(Hoenig and Gruber, 1990). This K-type strategy (sensu MacArthur & Wilson, 1967)

represents a significant challenge for managing these populations (Hoenig & Gruber,

1990; Pratt and Casey, 1990; Walker, 1998). In addition, large predatory fishes like

sharks may be much more sensitive to overexploitation (and ultimately, extinction)

than previously anticipated (Myers and Worm, 2005).   In order to assist stock

assessment and management, more information about shark populations and biological

variables is needed (Walker, 1998; ICCAT[2]). In particular, proportional survival is a

critical factor in stock assessment and demographic analysis (Mollet & Calliet, 2002).

The blacktip shark, *Carcharhinus limbatus* (Müller and Henle, 1839)*,* is the

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[1]Cooch, E. and G. White. 2004. *Program MARK*. "A Gentle Introduction", 5th edn.

[http://www.phidot.org/software/mark/docs/book/, accessed November 2011.]

[2]ICCAT. 2005. Report of the 2004 inter-sessional meeting of the ICCAT subcommittee on bycatches: shark stock

assessment. Collect. Vol. Sci. Pap. ICCAT 54:799–890.

most abundantly harvested shark species in American fisheries; investigations of survival are appropriate for such an ecologically and economically important species (Castro, 1996; Grace and Henwood, 1997; Cortés[3]; NOAA/NMFS[4]; NOAA/NMFS[5]). Blacktip sharks inhabit tropical, subtropical, and temperate waters throughout the world (Garrick, 1982; Castro, 1996). This species has an annual migration cycle that corresponds with a biennial ovulation cycle (Branstetter, 1981; Castro, 1996). Females either breed or give birth in May to June; post-parturition females are not able to mate again until the following spring. It is believed that the entire population migrates to more southern waters in the fall; in the following spring, the sharks return to their northern breeding and pupping grounds (Branstetter, 1981; Killam[6]; Castro, 1993; Castro, 1996).

Indirect methods have provided survival probabilities for blacktip sharks that range from 0.66-0.88 (Cortés, 1998) and 0.70-0.82 (Cortés and Brooks[7]). However, all of these methods are based on life history parameters like longevity and age at maturity; no one has estimated adult blacktip shark survival based on

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[3]Cortés, E. 2000. 2000 shark evaluation annual report. Document SFD-00/01-119. *NOAA/NMFS Southeast Fisheries Science Center*, Panama City, Fla. 24 p.

[4]NOAA/NMFS. 2006. SEDAR 11 Stock Assessment Report. Large Coastal Shark Complex, Blacktip, and Sandbar Shark. 387 p.

[5]NOAA/NMFS. 2012. SEDAR 29 Stock Assessment Report. HMS Gulf of Mexico Blacktip Shark. 197 p.

[6]Killam, K. 1987. The reproductive biology, age, and growth of the blacktip shark, *Carcharhinus limbatus* (Valenciennes) near Tampa Bay, Florida. M.S. Thesis, University of South Florida, Tampa, FL.

[7]Cortés, E and E. Brooks. 2005. Indirect estimates of natural mortality for sandbar (*Carcharhinus plumbeus*) and blacktip (*Carcharhinus limbatus*) sharks in the western North Atlantic. SEDAR 11 LCS05/06-DW-15 14 p.

empirical tag-recovery data from the population itself. As a result, survival

estimates based on direct methods were unavailable for the 2005 SouthEast Data

Assessment and Review (SEDAR) on large coastal sharks (Cortés and Brooks[7]).

Similarly, no one has tested for significant differences in survival based on time,

age, sex, and location in blacktip sharks. Therefore, the primary objectives of this

research were to estimate survival in blacktip sharks based on tag-recovery data and

determine if significant differences in survival exist based on time, age, sex, and

location.

Information on size, distribution, and movement were provided as a byproduct

of this survival analysis. Blacktip sharks in the Gulf of Mexico (GOM) are currently

managed by the National Marine Fisheries Service (NMFS) as a single stock, but the

degree of exchange between the east GOM, west GOM, and U.S. Atlantic is unknown

(Kohler et al., 1998; Keeney et al., 2003; Kohler et al.[8]; NOAA/NMFS[4]). According

to recent SEDAR stock assessment reports, there is a great need for conventional

mark-recapture studies that describe the exchange (or lack thereof) of this stock

between the East and West GOM (NOAA/NMFS[4]; NOAA/NMFS[5]). No exchange

has been observed between these regions to date. Therefore, it is desirable to

determine whether survival differs significantly among sharks from these 3 regions.

The NMFS Cooperative Shark Tagging Program (CSTP) is one of the largest

mark-recapture databases for sharks in the world. It currently includes over 227,000

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[8]Kohler N. E., P. A. Turner, and R. Briggs. 2005. Preliminary Tag and Recapture Data for the Sandbar Shark,

Carcharhinus plumbeus, and the Blacktip Shark, *Carcharhinus limbatus*, in the Western North Atlantic. SEDAR

11 LCS05-06-DW-29. 40p.

tagged sharks of over 50 species and 13,000 recaptures. NMFS has been collecting mark-recapture data since 1962 through the CSTP. Recreational and commercial fishermen tag sharks, providing information on size, sex, condition, location, and date of capture. If a tagged shark is recaptured, corresponding information is sent to NMFS, allowing for the calculation of time at large and displacement (calculated as the shortest distance between mark and recapture locations). Displacement values are presented in nautical miles, n. mi, where 1 n. mi=1.852 km.

Blacktip sharks were predominantly caught by rod and reel, longline, and gill net. The body length of some sharks was measured by biologists, but some were recorded as "estimates." The effect of this uncertainty was minimized by collapsing length data into life stage categories. This database was fishery-dependent, but the large sample size (n>9000 blacktip shark captures) presented a unique opportunity to map distribution and analyze survival in the geographic areas that are most important to fisheries. The CSTP database represented extensive spatial coverage of U.S. waters, so spatial bias in distribution was minimized (Kohler et al., 1998). For the purposes of this analysis, all shark landings were defined as "captures", including both tags and recaptures. Shark recaptures were "dead" recoveries; the sharks were not re-released and recaptured after initial recapture.

MATERIALS AND METHODS

In the CSTP, length and weight were reported with varying units of measure. Fork length was used whenever provided and converted to cm when applicable. Total length was converted to fork length using the formula:

$$TL(cm)=(1.1955)FL(cm)+1.13$$ (NMFS SEFSC unpublished data).

When neither fork length nor total length was provided, weight in kilograms was converted to FL according to the formula:

$$\text{Weight (kg)}=(1*10^{-5})\text{FL(cm)}^{3.0549} \text{ (NMFS SEFSC unpublished data)}.$$

Sharks were categorized into life stages according to length. The boundary between young-of-the-year (YOY) and juveniles was set to 56.6 cm FL, the maximum embryo size plus 10% TL (cm) according to Garrick (1982). Sharks measuring less than 56.6 cm FL were classified as YOY. Males and females in the Gulf of Mexico were considered mature when FL was greater than the median length at maturity, 103.4 cm and 117.3 cm, respectively (Carlson et al., 2006). Males and females between 56.6 cm FL and the median length at maturity were considered to be juveniles for the purposes of this study. Sharks of unknown sex that were between 56.6 cm FL and 103.4 cm FL were categorized as juveniles. Sharks without a size estimate or sharks of unknown sex that were between 103.4 cm FL and 117.3 cm FL were categorized as "unknown maturity." Sharks of unknown sex that were larger than 117.3 cm FL were categorized as mature. Sharks were classified as embryos when they were taken from pregnant females. A similar methodology was used for Atlantic sharks, substituting 116.7 and 126.6 cm FL as the median length at maturity for males and females, respectively (Carlson et al., 2006). Data were plotted as points for distribution maps with *MapInfo Professional 7.0* (MapInfo Professional, vers. 7.0, Pitney Bowes Software, Inc., Troy, NY).

In the CSTP database, blacktip sharks have been reported along the east coast of the United States from Texas to Delaware; a limited amount of data were also available from Mexico and the Caribbean, as far south as French Guiana. NMFS

manages 2 stocks of blacktip sharks, 1 in the U.S. Atlantic Ocean and 1 in the GOM.

The U.S. Atlantic region was defined as the geographic area within the U.S. Exclusive

Economic Zone (EEZ) from Delaware to the Straits of Florida (NOAA/NMFS[4]). The

Gulf of Mexico was defined as the geographic region from the Florida Keys

throughout the Gulf of Mexico (NOAA/NMFS[4]).   For the purposes of these analyses,

the boundary between the Gulf of Mexico and the U.S. Atlantic region was a line

beginning on the east coast of Florida at 25º10.4'N latitude, proceeding due east to the

U.S. EEZ. The "International Atlantic" was defined as the region of the northwest

Atlantic not included in the aforementioned regions. For certain analyses, the Gulf of

Mexico was further divided into 3 sub-regions: the east U.S. GOM, west U.S. GOM,

and the Mexican GOM. The U.S. EEZ and the meridian at 89°W longitude were the

boundaries to separate these sub-regions (Figure 1).

Direct estimates of survival were calculated with the freely available

program MARK (Program MARK, vers. 6.2, Gary C. White, Fort Collins, CO),

loosely following the procedure of Wood et al. (2007). The 4 survival analyses

conducted were: 1) YOY vs. post-YOY, 2) male vs. female, 3) west vs. east GOM,

and 4) GOM vs. Atlantic. Survival was modeled with the reduced (Seber)

parameterization (Seber, 1970; Anderson et al., 1985). In this parameterization, *S* was

the probability that the fish survives the year, and *r* was the probability that the fish

was recovered and reported (Fig. A-1). Model names describe the parameters

included in the model. For example, *S*(g*t) *r*(g+t) indicates that survival was

modeled with an interaction between group and time, and recovery probability

was modeled with group and time effects, but no interaction. A period (.)

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indicates that either group or time effects were not included in the model. Data were entered in the classic recovery (triangular) matrix format (Fig. A-2). *S* and *r* were solved numerically for the maximum likelihood estimate, and the profile likelihood method generated confidence intervals. A parametric bootstrap procedure (Cooch and White[1]) for the most general model (group- and time-dependent survival and recovery probabilities) assessed goodness of fit. The quasi-likelihood parameter, ĉ was estimated as the average of the mean ĉ and mean deviance estimates. Models were ranked according to the quasi-likelihood adjusted AIC (White and Burnham, 1999). Likelihood ratio tests (LRT) determined whether survival and recovery probabilities were time-dependent, age-dependent, sex-dependent, region-dependent or constant.

In addition to the predictive variables of group and time, models were fit with an external index to account for changing levels of yearly fishing effort. It is known that

$$F=qf$$

where *F*=fishing mortality rate, *q*=catchability coefficient, and *f*=fishing effort (Quinn and Deriso, 1999). The catchability coefficient was assumed to be constant over time, so that *F* could be used as proxy for effort. Values of *F* were available specifically for Gulf of Mexico and U.S. Atlantic blacktip sharks from 1986-2004 from the SEDAR 11 Stock Assessment Report (Fig. A-3). Therefore, the analysis was constrained to this time period. A more detailed explanation of survival analysis procedures is provided in Appendix II.

The first blacktip sharks in the CSTP were tagged in 1964, but the tagging rates remained below 100 sharks per year until 1988 in the GOM and 1999 in the U.S. Atlantic (Figs. A-4-A-5). Tagging rate in the International Atlantic reached a maximum of 69 sharks per year in 2005 (Fig. A-6). A total of 8871 blacktip sharks were tagged within the CSTP. From 1964 through 2011, 230 of these sharks were recaptured, leading to 9101 captures, total (Table 1). The fate of these tagged sharks is displayed by region in Table 2. Notably, 1 shark tagged in U.S. waters of the Atlantic Ocean was recaptured in the International Atlantic, 3 sharks tagged in the International Atlantic were recaptured in the U.S. Atlantic, and 35 sharks tagged in the U.S. waters of the western GOM were recaptured in Mexican waters of the GOM.

Information on these captures by sex and life stage is provided in Tables 3-5. Females were caught more often than males, resulting in a male to female sex ratio of 1:1.2 in the U.S. Atlantic, 1:1.8 in the GOM and 1:1.6 in the International Atlantic. Juveniles were the most commonly caught life stage for both males and females.

Mean time at liberty ranged from 242.3 days in the eastern U.S. GOM to 506.9 days in the International Atlantic (Table 6). During the period of study, 35 blacktip sharks were recaptured in Mexican waters, but no blacktip sharks were tagged there. For this reason, the final destination of sharks in the southern GOM was unknown.

Recapture statistics by sex are provided in Tables A-1-3 (excluding the 4 sharks that crossed between the U.S. Atlantic and the International Atlantic, as described in Table 7). In the U.S. Atlantic, 3959 sharks were tagged, and 81 of these tagged sharks were recaptured in the same region (2.0%), yielding a total of 4040

captures. The highest values for maximum displacement (616 n. mi.), maximum speed (15.3 n. mi./day), and maximum time at liberty (5.9 years) were from a male, female, and a shark of unknown sex, respectively. In the GOM, 4415 sharks were tagged, and 130 of these tagged sharks were recaptured (2.9%), yielding a total of 4545 blacktip shark captures. The highest values for maximum displacement (632 n. mi.), maximum speed (16.4 n. mi./day), and maximum time at liberty (7.8 years) were from female sharks. In the International Atlantic, 493 sharks were tagged, and 15 of these tagged sharks were recaptured in the same region (3.0%), yielding a total of 508 captures. The highest values for maximum displacement (215 n. mi.) and maximum speed (0.5 n. mi./day) were from females, but the maximum time at liberty (2.6 years) was from a male.

Distribution of recaptures by time at liberty, displacement, and speed is displayed in Figure 3. The shark with the longest time at liberty (7.8 years) was a juvenile female tagged near Galveston, Texas that was recaptured 632 nautical miles away in the waters off Veracruz, Mexico. The fastest moving shark was a YOY female that was tagged off Padre Island, Texas and recaptured near Veracruz, Mexico, traveling 459 nautical miles in 28 days (16.4 n. mi./day). The 2 sharks with the largest displacement were YOY males tagged by a NMFS biologist at the British Virgin Islands and recaptured 1043 and 1089 n. mi. away off Cape Canaveral, FL and Jekyll Sound, GA, respectively. Mean displacement of blacktip sharks at liberty for less than 1 year are displayed by region in Figure A-7. Sharks tagged as juveniles had the largest mean displacement in all 3 regions.

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Blacktip sharks measuring approximately 50-60 cm FL were the most frequently caught size group, corresponding to the boundary between YOY and juvenile categories (Figs. 2-4 and Figs. A-8-10). The smallest shark categorized as a YOY was caught in the GOM, and was measured as 32 cm FL. The largest measured male and female were 160 and 166 cm FL in the GOM, 179.6 and 176.5 cm FL in the U.S. Atlantic, and 134 and 166cm FL in the International Atlantic, respectively. The largest 2 sharks with "estimated" lengths were females estimated at 190 cm FL (1 from the GOM and 1 from the U.S. Atlantic).

The CSTP database included a combination of effort from recreational fishermen, biologists, and commercial fishermen. Recreational landings were more common than those specifically identified as "commercial". Biologists also tagged many sharks in the GOM, but most of the tagging was done by recreational fishermen (Table A-4). The number of sharks tagged by biologists increased dramatically in the 2000s (Figs. A-11-12).

The temporal trends in the fishing industry (Figs. A-11-12) were mirrored by temporal trends in gear (Figs. A-13-14). In the U.S. Atlantic, the 3 most common sets of gear for captures were rod and reel (n=2144), longline (n=1659), and gill net (n=216) (Table A-5). Rod and reel captures increased moderately through the 1990s and 2000s, whereas longline captures increased dramatically in the 2000s (Fig. A-13). Blacktip sharks in the GOM were also predominantly caught by rod and reel (n=3278), longline (n=1110), and gill net (n=134). The 1980s and 1990s were dominated by rod and reel captures, whereas longline captures increased in the 2000s.

Sharks were also caught in smaller numbers (n<20) with handline, otter trawl, beach seine, set line, and hand landing net.

Male blacktip sharks have not yet been tagged in certain areas off Florida, Tamaulipas and Veracruz (Figs. 5-7 and Figs. A-15-20). Blacktip sharks seemed to remain strictly within the 200m depth contour. Larger sharks have been tagged in both nearshore and continental shelf waters within this range, but YOY were almost exclusively found close to shore (Figs. 8-10 and Figs. A-21-26).

YOY were present along most of the U. S. Gulf of Mexico coastline, with exceptions in parts of Florida and Louisiana (Figs. A-27-35). This trend may have simply reflected reduced effort in these areas. Almost all of these sharks were caught near the shore.

No movement was observed between the west GOM, east GOM, and U.S. Atlantic (Figs. 11-13 and Figs. A-36-41). However, sharks of all 3 life stages migrated from U. S. to Mexican waters in the Gulf of Mexico (Fig. A-39). Of the 130 sharks that were tagged and recaptured in the GOM, only 32 were recaptured in an older life stage than tagged (25%); the majority of sharks were recaptured within the same life stage. Similarly, of the 81 sharks tagged and recaptured in the U.S. Atlantic, 19 were recaptured in an older life stage (23%). In the International Atlantic, 3 of the 15 recaptured sharks were recaptured in an older life stage (20%).

Survival

In analysis 1, survival models were constructed with an age effect, differentiating between YOY and post-YOY groups (designated by a "g" in the model structure). The most parsimonious model $S(..)$ $r(g+effort)$ had 2.38 times more weight

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than the next best model $S(g.)$ $r(g+\text{effort})$ and 29.73 times more weight than $S(g.)$

$r(.\text{effort})$ (Table A-6). Likelihood ratio tests determined the significance of various

effects in the GOM YOY vs. post-YOY analysis (Tables A-7-8). No tests were

significant for the interaction of age group and time for recovery probability, $r(g*t)$, or

survival, $S(g*t)$. However, 7 out of 14 possible tests were significant for $S(g)$, 5 out of

14 for $S(t)$, 8 out of 10 for $r(\text{effort})$, and 5 out of 10 for $r(t)$. All LRT's were

significant for $r(g)$. The first comparison in each section of Tables A-7-8 displays the

simplest model that contains the parameter of interest. These comparisons are

particularly useful in hypothesis testing. By only considering the simplest LRT's,

$r(\text{effort})$, $r(g)$, and $S(g)$ were significant effects. Therefore, survival and recovery

probabilities were significantly different for YOY and post-YOY, and effort is a

significant factor in recovery probability in this analysis.

In analysis 2, post-YOY data were modeled with male and female groups. The

most parsimonious model $S(..)$ $r(.\text{effort})$ had 2.64 times more weight than the next best

model, $S(g.)$ $r(.\text{effort})$ and 2.67 times more weight than $S(..)$ $r(g+\text{effort})$ (Table A-9).

The relevant likelihood ratio tests are given in Tables A-10-11. No tests were

significant for $S(g)$, $S(g*t)$, $r(t)$ and $r(g*t)$. However, 1 out of 14 tests was significant

for $S(t)$, 7 out of 10 for $r(\text{effort})$, and 4 out of 15 for $r(g)$. By only considering the

simplest LRT's, only $r(\text{effort})$ was a significant effect. Therefore, survival was not

significantly different for male vs. female sharks, and effort is a significant factor in

recovery probability in this analysis.

In analysis 3, post-YOY data were modeled with groups representing the west

GOM and east GOM. The most parsimonious model $S(..)$ $r(.\text{effort})$ had 2.64 times

more weight than the next best model $S(g.)$ $r(.effort)$ and 2.67 times more weight than $S(..)$ $r(g+effort)$ (Table A-12). The relevant likelihood ratio tests are shown in Tables A-13-14. No tests were significant for $S(g)$, $S(g*t)$, $r(t)$, or $r(g*t)$. However, 3 out of 14 tests were significant for $S(t)$, 8 out of 10 tests were significant for $r(effort)$, 6 out of 15 tests were significant for $r(g)$. By only considering the simplest LRT's, only $r(effort)$ was a significant effect. Therefore, survival was not significantly different for post-YOY sharks from the west GOM vs. those from the west GOM. Effort was a significant factor in recovery probability in this analysis.

In analysis 4, post-YOY data were then modeled with groups in the Atlantic and GOM. The most parsimonious model $S(..)$ $r(g+effort)$ had 1.53 times more weight than the next best model, $S(g.)$ $r(g+effort)$, and 149.90 times more weight than $S(..)$ $r(..)$ (Table A-15). The relevant likelihood ratio tests are displayed in Tables A-16-17. No tests were significant for $S(g)$. However, 7 out of 12 tests were significant for $S(t)$, 1 out of 6 for $S(g*t)$, 4 out of 5 for $r(effort)$, 3 out of 10 for $r(g)$, 4 out of 10 for $r(t)$, and 1 out of 5 for $r(g*t)$. By only considering the simplest LRT's, $S(g*t)$, $r(effort)$, and $r(t)$ were significant effects. Therefore, there was no evidence that survival was significantly different for post-YOY sharks from the GOM vs. those from the U.S. Atlantic. However, effort and time significantly affected recovery probability in this analysis. The interaction between group and time on survival is significant, but it cannot be easily interpreted.

The average ĉ values generated from the deviance ĉ and mean ĉ are provided in Table 8. All average ĉ values were less than 3, indicating that the models fit the

data adequately. Recovery probability ranges for the most parsimonious models are also given in Table 8.

DISCUSSION

The extensive spatial and temporal span of data in the CSTP provides a unique opportunity to describe the biology and ecology of the species within the program. Specifically, the data gathered provide unique insights into size, spatial distribution, movement, and changes in fishing industry and gear over time. Of course, one of the most substantial contributions of this database is its ability to provide direct estimates of survival.

Size

With the large sample size of the CSTP, it was possible to observe a wide range of size estimates. In the GOM, 2.4% of males and 1.2% of females in the CSTP were larger than the largest sharks observed by Clark and Von Schmidt (1965). Similarly, in the U.S. Atlantic, 4.2% of males and 3.8% of females in the CSTP were larger than the largest sharks observed by Castro (1996). Excluding the 7 sharks specifically listed as embryos, 40 of the YOY tagged in the CSTP were smaller than the smallest neonate size observed by Branstetter (1981) and Castillo-Géniz et al. (1998) (range: 32-37.5 cm FL). These 40 YOY were evenly distributed throughout the east and west Gulf coasts, and 22 of these 40 (including the smallest) were "measured," not "estimated" lengths. These authors sampled sharks with the same types of gear (gillnet, longline, and rod and reel) as the CSTP. We are therefore encouraged to expand the perceived size range of this species.

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Spatial Distribution

Some have reported the presence of blacktip sharks in water over 800 m deep (Garrick, 1982; Russell, 1993). However, the Gulf of Mexico blacktip sharks in the CSTP seemed to remain strictly within the 200 m depth contour (Figs. 5-6). There was extensive fishing effort from the CSTP in deeper waters; other species were commonly reported in mid-Gulf waters in the CSTP (Kohler et al., 1998). It is therefore likely that blacktip sharks rarely venture into water deeper than 200m. Accounts of blacktip shark in water deeper than 800m seem to be the exception, not the rule, to their behavior.

The location of YOY and pregnant females can be useful for the identification of nurseries. In the CSTP, YOY were almost exclusively found close to shore (Figs. A-27-35). These data further support the idea that blacktip shark juveniles spend the first few months of their lives in nurseries close to shore (Castro, 1993; Heupel and Simpfendorfer, 2002; Heupel et al., 2007). While pregnant and embryo blacktip sharks were generally found close to shore, there were also exceptions to this behavior. A mother of 3 embryos (each measuring 41 cm FL) off Louisiana was caught very close to the 200 m depth contour (Fig. A-32). The date of capture for this event was January 3rd, several months before the expected time of parturition. Similarly, 2 YOY were found very close to the 200 m depth contour off the Florida Keys (Fig. A-31). However, these YOY were still relatively close (<15 nautical miles) to land.

Movement

For the purposes of effective population management, it is desirable to determine the extent of exchange within and among water bodies in the northwest Atlantic. Genetic work by Keeney et al. (2003) implied that the U.S. Atlantic waters and the Gulf of Mexico represented 2 distinct populations, while Ryburn[9] suggested that sharks from the 2 areas interbreed. None of the Gulf of Mexico blacktip sharks migrated out of the Gulf to the Caribbean or Atlantic (Figs. 11-12). By comparison, CSTP data indicated that other sharks have well-established exchange patterns between Gulf and Atlantic waters (Kohler et al., 1998). However, the CSTP data currently suggest that the Gulf blacktip sharks do not mix with those from the Atlantic. This data set continues to support the decision to manage the Gulf of Mexico and Atlantic blacktip sharks as 2 separate stocks (NOAA/NMFS[4]).

Exchange was also not observed between the west and east Gulf of Mexico in the CSTP. Limited genetic data suggest that the east and west Gulf of Mexico are 2 separate populations of blacktip sharks, although they are currently managed as 1 population (Keeney et al., 2005; NOAA/NMFS[4]). If the Gulf truly contains 2 stocks, the CSTP data suggest that eastern Louisiana (approximately 89°W longitude) may be the location of this natural boundary; no recaptures have been observed across this line.

An exchange of blacktip sharks was observed between Mexican and U.S. waters within the Gulf of Mexico (Fig. 12). Blacktip sharks of all ages (n=35)

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[9]Ryburn J.A. 2003. Inter-oceanic divergence and speciation in *Carcharhinus plumbeus, Carcharhinus limbatus* and *Carcharhinus falciformis* inferred from mitochondrial DNA sequence. Master's thesis. Iowa State University.

migrated south from the waters of Texas and Louisiana to Tamaulipas, Veracruz, Tabasco, and Campeche. Most (n=33) of these recaptures occurred within a time at liberty of less than 1 year, and the shortest such migration was 103 nautical miles in 11 days. Interestingly, 3 sharks that were born off Texas arrived in southern Veracruz as YOY (i.e., less than 56.6cm FL). One male also made a remarkable journey from Louisiana to Campeche. If this shark remained within the 200m depth contour for the entire journey, he would have traveled 1,090 nautical miles (over a maximum time period of 4.4 years).

While exchange between the GOM and Atlantic was not observed, 4 sharks crossed the U.S. EEZ between U.S. and International waters of the Atlantic Ocean (Table 7). Two of these sharks were recaptured over 1000 nautical miles away from their tagging location (Fig. 13). These recaptures are the first documented evidence that blacktip sharks can travel this far, and that exchange exists for blacktip sharks between the U.S. coastal waters and those of the Caribbean. A NMFS biologist identified the 2 males as blacktip sharks, ensuring positive identification.

Migration Research Integration and Synthesis

On the eastern U.S. coast, blacktip sharks spend the winter in the waters of southern Florida, migrate to the Carolinas and Georgia in the spring to breed and give birth, and return to their wintering grounds in the fall (Castro, 1996). The seasonal movement of blacktip sharks within the GOM, however, is not fully understood. Sharks in the western and eastern GOM may have separate yearly north-south migration cycles, similar to those in the U.S. Atlantic waters (Branstetter, 1981; Killam[6]; Castillo-Géniz et al., 1998; Heupel and Simpfendorfer, 2002). Genetic work

suggests that females are philopatric for their natal nurseries, but it is possible that males contribute to genetic exchange between regions (Hueter et al., 2005; Keeney et al., 2005).

The migration cycle in the western GOM is especially interesting because the CSTP provides strong evidence of exchange with Mexican waters. It is believed that blacktip sharks in the western GOM spend the spring and summer months in the northern coastal waters for mating and breeding (Branstetter[10]). Nursery habitat can be found from Sabine Lake to Lower Laguna Madre, Texas (McCandless et al., 2002; Keeney et al., 2005).   Gravid females have also been caught from April to September in the waters of Matamoros, near the Texas-Mexico border (Castillo-Géniz et al., 1998). Therefore, the entire coast of Texas represents the starting point for these newly born blacktip sharks.

In the fall, blacktip sharks of all ages are believed to move south to warmer water (Branstetter[10]). Castillo-Géniz et al. (1998) note increased catches in Mexican waters late in the year, due to annual southward migration. Blacktip sharks are most common in Tamaulipas in October-December, and Veracruz in November-May (Castillo-Géniz et al., 1998). It may be inferred that the sharks pass through Tamaulipas and spend winter in the warmer waters of Veracruz, Tabasco, and Campeche. This hypothesis is consistent with the observation that blacktip sharks are generally rare in Tamaulipas, but very common in Veracruz (Bonfil, 1997).

Despite the observation that US-born YOY migrate to Mexican waters, not all

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[10]Branstetter, S. G. 1986. Biological parameters of the sharks of the northwestern Gulf of Mexico in relation to their potential as a commercial fishery resource. PhD Dissertation. Texas A&M University, Corpus Christi, TX.

blacktip sharks in Mexican waters are originally born U.S. waters. Nurseries have been documented in Campeche and Quintana Roo, Mexico (Bonfil, 1997; Castillo-Géniz et al., 1998). One can infer that blacktip sharks caught in Mexican waters during the winter represent a mixture of Mexican-born and US-born sharks.

Tagging data are lacking in southern Gulf waters. Very few sharks have been tagged in Mexican waters in the CSTP, so the sharks' movements after arriving in Mexico are unknown. Researchers at Mote Marine Laboratory reported westward movement of blacktip sharks from the northeast Yucatan Peninsula (Tyminski et al.[11]). This may further suggest that western Gulf blacktip sharks stay in the western Gulf, instead of crossing into eastern waters.

This analysis of Gulf of Mexico blacktip sharks is not without limitations. Movement data are only based on 2 points of reference (i.e., mark and recapture). GPS tags would provide a more continuous record of animal movement. In addition, the life stages assigned in the CSTP are approximated bins based on the shark's fork length. Biological indicators of life stage (e.g., healing of the umbilical scar, condition of the clasper, etc…) are not recorded by CSTP volunteers. These life stages are not intended to serve as absolute descriptions of life stage.

Change in Effort Over Time

Blacktip shark landings in the U.S. Atlantic were dominated by recreational fishing from 1981 through 1990 (Fig. A-42). Commercial landings increased dramatically in 1991, and dominated the catch until 1998. Both sources have

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[11]Tyminski, J., C. Simpfendorfer and R. Hueter. 2006. Results of Mote Marine Laboratory Shark Tagging Program for blacktip (*Carcharhinus limbatus*) and sandbar (*C. plumbeus*) sharks. SEDAR 11 LCS05/06-DW-44. 7 p.

contributed more or less evenly since 1999 (NOAA/NMFS[4]). In the GOM, fishing

effort has been a combination of Mexican, recreational, and commercial sources, with

the highest contributor varying from year to year (Fig. A-42). Mexico was the greatest

contributor of blacktip shark landings in the GOM in 1984. Recreational landings

exceeded commercial landings from 1981 through 1987, with a maximum in 1986.

Commercial landings reached a maximum in 1988 to 1989. Landings in all categories

have shown an overall decline from 1990 through the present (NOAA/NMFS[5]). By

2010, recreational fishing had become the greatest source of fishing mortality in the

GOM (NOAA/NMFS[5]). The temporal trend of fishing industry in the CSTP (Fig. A-

11) roughly matches that listed in the SEDAR SAR (Fig. A-42). Comparing the east

and west GOM, similar trends in capture history were observed. Recreational captures

were more common in the 1990s, whereas biologist captures were the most substantial

contributor in the early 2000s (Fig. A-12).

During the period of study, fishing mortality rate was much lower in the

Atlantic (average F=0.003) compared with that in the GOM (average F=0.047). In the

GOM, F was highest in the 1990s, but never reached F_{MSY} of 0.084 (Fig. A-3). Effort

and catches decreased through the early 2000s, so that $F_{current}$ is 0.03-0.04

(NOAA/NMFS[5]). As of 2006, only about 8-23% of the virgin stock size was depleted

in the GOM (NOAA/NMFS[4]). The SEDAR SAR concluded on the basis of these data

that neither the Atlantic nor GOM stock was overfished (NOAA/NMFS[4]).

Survival

The 4 assumptions of the Seber parameterization are: (1) all marked animals

present at time (i) have the same probability of surviving to time (i+1) and the same

recapture probability, (2) sampling is an instantaneous processes, relative to the time interval between occasions (i) and (i+1), (3) tagged cohorts are thoroughly mixed, and (4) tags are not lost or missed. If there were a difference in survival probability or recapture probability due to age (assumption 1), this difference needed to be addressed (Simpfendorfer et al., 2005b). Therefore, the data were first modeled with YOY vs. post-YOY groups, to determine if such a difference existed.

Assumption 3 (mixing of cohorts) was investigated because genetic work has suggested that the east GOM, west GOM, and U.S. Atlantic may represent distinct populations of blacktip sharks (Keeney et al., 2003; Keeney et al., 2005). No exchange of blacktip sharks has been observed to date between these 3 areas. Recaptures in these 3 regions were analyzed for nonmixing with a χ^2 contingency table (Latour et al., 2001). This test did not require evidence of exchange between geographic areas; it simply determined if the number of recaptures in each region differed significantly from what would be expected if cohorts were thoroughly mixed. Due to the sparseness of the data, recapture cohorts were binned into 5-year groups (1980-1984, 1985-1989, etc..). With 2 degrees of freedom, 5 out of 6 tests did not indicated significant evidence of nonmixing (P=0.36, 0.52, 0.58, 0.54, and 0.31). However, the final test (2005-2009) was marginally significant (P=0.05), indicating some evidence for a lack of mixing in those years. The number of recaptures was small (n<20) for every combination of region and cohort, so these results may be affected by the sparseness of the data.

Regardless of χ^2 test results, it is possible to determine post-facto whether survival in these geographic areas is significantly different. According to the simplest

likelihood ratio tests, geographic grouping had no effect on either survival or recovery probability (Table 9). Satellite tags would be necessary to definitively determine if tagged cohorts are thoroughly mixed. Nevertheless, the CSTP data demonstrate that the survival is not significantly different among the east GOM, west Gulf of Mexico, and U.S. Atlantic.

In order to correct for assumption (4), the final true survival estimate is given by the equation

$$S_T = S(1-\Lambda)^{-1}$$

where S_T is the true survival estimate, S is the apparent survival probability, and Λ is the instantaneous tag-shedding rate. A double-tagging experiment is ongoing in the NMFS CSTP, but the results of this experiment are not yet available. There are several different types of tags used in mark-recapture research; tag-shedding rates should be based on the type of tag under consideration (Xiao et al., 1999). Wood et al. (2007) developed a proxy tag-shedding rate (an instantaneous rate of 0.259 yr^{-1}) specifically designed for the type of tag used in the CSTP. This proxy was calculated as weighted mean tag-shedding rate based on tuna-tagging experiments. Due to the slower cruising speed and thicker skin of blacktip sharks (compared to tuna), the proxy tag-shedding rate likely represents a maximum value for blacktip sharks. Therefore, corrected survival estimates are likely maximum estimates as well. Aires-da-Silva et al. (2009) investigated alternative values of Λ to be used with data from the CSTP; the S_T estimates generated from varying Λ are given in Table 10.

This survival analysis provided two useful types of information: tests of significance for various effects on survival and recovery, and direct estimates of

survival. Likelihood ratio tests supported the conclusion that YOY and post-YOY have different survival probabilities (Table 9). There was no evidence for significant differences in survival based on sex or geographic region within the GOM. These findings were encouraging, because they were consistent with current NMFS policy to manage the entire GOM as 1 stock (NOAA/NMFS[4]; NOAA/NMFS[5]). However, genetic work suggested that the Atlantic and GOM are 2 distinct populations (Keeney et al., 2003; Keeney et al., 2005). Therefore, it was interesting that there was no significant difference in survival between the Atlantic and GOM. It is possible that the small sample size of recaptures only permits the detection of large differences in survival.

Likelihood ratio tests were also used to investigate the significance of different effects on recovery probability (Table 9). Recovery probability was different for YOY vs. post-YOY, but not significantly affected by other grouping schemes. In every analysis, recovery probability was significantly affected by fishing effort. These results underscore the need to account for changes in fishing effort in any future studies in the CSTP.

True survival estimates were generated after correcting for tag-shedding rate (Table 8). In analysis 1 (YOY vs. post-YOY), the model $S(..)$ $r(g+effort)$ was the most parsimonious model with a corrected age-constant survival of 0.711. Likelihood ratio tests determined that there was a significant age effect on survival and recovery probability in this analysis, and that fishing effort had a significant effect on recovery probability (Table 9). Therefore, the second most parsimonious model $S(g.)$ $r(g+effort)$ was also found to be valuable for management purposes. In this model,

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corrected post-YOY survival was 0.725, whereas YOY survival was 0.580. Time did

not have an effect on survival or recovery probability, on the basis of LRT. Similarly,

there was no significant interaction between group and time for either survival or

recovery probability.

The estimate of survival for GOM post-YOY in analysis 1 (0.725) did not

exactly match the corresponding estimates from analyses 2, 3, and 4 (0.814, 0.781, and

0.781, respectively) (Table 8). Differences between these estimates were caused by

differences in data input. Analysis 2 did not include any sharks of unknown sex,

resulting in a slightly different estimate of survival. Analyses 3 and 4 only included

sharks that were tagged as post-YOY, and they both yielded the same estimate.

Analysis 1 included YOY that were assumed to mature into post-YOY after 1 year;

this additional source of data resulted in the narrowest of the 4 confidence intervals.

For this reason, 0.725 is the preferred estimate of post-YOY survival.

Several authors have suggested that survival is lowest in the first year of life

for fish in general, and elasmobranchs specifically (Caley, 2006; Hoenig and Gruber,

1990; Manire and Gruber, 1993; Simpfendorfer 1999). Manire and Gruber (1993)

provided an empirical estimate of YOY survival as low as 0.36 to 0.55 for lemon

sharks in Bimini, Bahamas. Why does survival appear to be so low for YOY? It is

possible that inexperienced young sharks are more vulnerable to predation or less

effective at foraging (Branstetter, 1990; Simpfendorfer et al., 2005b). Alternatively,

survival of YOY may appear to be low due to emigration from the studied area. If

juvenile sharks are dispersing from the Gulf of Mexico, it would be impossible to

determine whether those sharks died or emigrated.

Survival estimates can only take values from 0 to 1. Confidence intervals for all original survival estimates fell within these limits. However, when confidence intervals were corrected for tag-shedding rate, some values were inflated to impossibly high values (≥ 1). It is possible that the true tag-shedding rate in blacktip sharks is lower than the proxy value of 0.259 (Table 10). A larger sample size would also ensure that confidence interval boundaries were between 0 and 1.

The effects of sex and geographic location were intentionally tested for post-YOY only. Combining YOY and post-YOY in these analyses would have confounded the effects that were being investigated. Because direct estimates of YOY survival have already been conducted with robust methods (Heupel and Simpfendorfer, 2002), it was more appropriate to test these group differences in post-YOY sharks. This experimental design allowed a more definitive investigation of the significance of group effects through LRT.

The corrected survival estimates provided were consistent with those already published. The survival for age 0 blacktip sharks used in management is 0.52, based on the direct estimate by Heupel and Simpfendorfer (2002) (NOAA/NMFS[4]). The YOY survival estimate from analysis 1 (0.580) was slightly higher than this value. Whereas the CSTP included a full size range of YOY, Heupel and Simpfendorfer (2002) studied a narrower subset of smaller "neonate" sharks (i.e., those with an open umbilical scar and a mean TL of 62 cm). This difference in data source likely caused the small apparent discrepancy between these 2 estimates.

Prior to this paper, the only estimates of adult survival for blacktip sharks have been from indirect methods based on life history parameters. Cortés (1998) reported a

survival of 0.66-0.88. Cortés and Brooks[7] calculated average survival for blacktip

sharks based on 11 indirect methods. The average survival ranged from 0.70 to 0.78

for the GOM and 0.75 to 0.82 for the Atlantic (Cortés and Brooks[7]). A more realistic

average *S* (based on age-specific methods only) ranged from 0.71 to 0.81 for the GOM

and 0.75 to 0.85 for the Atlantic. The CSTP estimate of post-YOY survival in the

GOM (0.725) fits within these all of these ranges, but the Atlantic estimate (0.933)

was slightly higher than that given by Cortés and Brooks[7].

In 2006, NMFS tentatively accepted the average mortalities from Chen and

Watanabe (1989) and Lorenzen (1996) weight-based indirect methods as developed by

Cortés and Brooks[7] for post-YOY sharks. These mortalities were 0.198-0.358

(*S*=0.699-0.820) for the GOM and 0.157-0.654 (*S*=0.520-0.855) for the Atlantic

(NOAA/NMFS[4]). These mortalities were judged to be unrealistic by the SEDAR 11

review panel, because they were too high to maintain a self-sustaining population. As

a result, the age 0 survival was increased from 0.52 to 0.75 and the post-YOY natural

mortalities were decreased to a range of 0.102-0.263 (*S*=0.769-0.903) for the GOM

and 0.089-0.219 (*S*=0.803-0.915) for the Atlantic (NOAA/NMFS[4]).

In 2012, life history and natural mortality values were updated for the GOM

using a combined dataset from Carlson et al. (2006) and Passerotti and Baremore[12]

(NOAA/NMFS[5]). Age-specific values of instantaneous natural mortality were

calculated from the methods of Hoenig (1983), Chen and Watanabe (1989), Peterson

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[12]Passerotti, M. S. and I. E. Baremore. 2012. Updates to age and growth parameters for blacktip shark,

Carcharhinus limbatus, in the Gulf of Mexico. SEDAR29-WP-18. SEDAR, North Charleston, SC. 12 p.

and Wroblewski (1984) and Lorenzen (1996). To ensure that calculated *M* values allowed for positive population growth, the minimum of these 4 estimates was used. Values of instantaneous *M* for ages 1 through 18 ranged from 0.226 to 0.134, respectively (*S*=0.798-0.875).

Total instantaneous mortality (*Z*) is the sum of natural mortality (*M*) and fishing mortality (*F*). Proportional survival is related to *Z* by $S=e^{-z}$ (Quinn and Deriso 1999). If post-YOY survival was 0.725 in the GOM, *Z* was 0.322. Given a fishing mortality ranging from 0.023 to 0.073, natural mortality was relatively high (0.249-0.299). Similarly, in the Atlantic, a survival of 0.933 yielded a total mortality of 0.069. If fishing mortality rate ranged from 0.001 to 0.006 in the Atlantic, natural mortality would be 0.063-0.068. It appears that fishing mortality made up a very small proportion of overall mortality in these stocks. Given the relatively high rate of natural mortality, future studies may be able to determine the relative contribution of cannibalism, predation from other sharks, disease, old age, and other factors in this natural mortality. It is known that adult blacktip sharks (up to 180 cm TL) have been attacked by even larger sharks (Dodrill[13]). It is likely, therefore, that predation continues to contribute to natural mortality into older age.

Recent studies have investigated the evolutionary impact of size-selective fisheries (Conover and Munch, 2002; Olsen et al., 2004; Heino and Dieckmann[14]).

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[13]Dodrill, J. W. 1977. A hook and line survey of the sharks of Melbourne Beach, Brevard County, FL. M.S. Thesis, Florida Institute of Technology, Melbourne, FL. 304 pp.

[14]Heino, M., and U. Dieckmann. Fisheries-induced selection as a driver of biodiversity change in exploited populations. ICES. CM 2007/E:17. 5 p.

These changes often resulted in decreasing length at maturity; evidence has suggested

that this phenomenon has also occurred in elasmobranchs (Sminkey and Musick,

1995; Carlson and Baremore, 2003; Cassoff et al. 2007). Carlson et al. (2006)

suggested that size at maturity has decreased for blacktip sharks in the Gulf of Mexico

in a span of 11-14 years (Carlson et al., 2006). If there was a real decrease in size-at-

maturity in blacktip sharks, some juvenile sharks from the early years of the program

were categorized as "mature" according to the modern size at maturity. If future

survival analyses differentiate between juvenile and mature sharks, this potential life

history change may negatively affect the results. Because specific data on the

magnitude of these changes is limited, it would be beneficial to analyze survival based

on length, instead of life stage.

The usefulness of this survival analysis is limited by the broad categorization

of sharks into groups such as "YOY" and "post-YOY." Unfortunately, it is not

possible to further refine post-YOY estimates into juvenile vs. mature groups, due to

ambiguity in the coding of juvenile shark parameters. It was assumed that YOY

became post-YOY after 1 year's time, but juvenile sharks may take 1-4 years to

become mature (Carlson et al., 2006). Because of the inherent variation in size and

maturity at age (and because estimates of age in the CSTP are originally based on

length measurements), a length-based model may be more appropriate for future work.

Program MARK has already been used to calculate survival directly in some

elasmobranchs (Rodríguez-Cabello and Sánchez, 2005; Wood et al., 2007). Despite

the relatively low sample size for blacktip sharks, it was possible to effectively model

survival. As a result, survival estimates for YOY and post-YOY blacktip sharks were

calculated from direct methods, and likelihood ratio tests determined that there is a significant effect of age group on survival and recovery probability.

CONCLUSIONS

No movement has been observed to date between the west Gulf of Mexico, east Gulf of Mexico, and U.S. Atlantic in the CSTP. However, 2 sharks tagged in the U.S. Virgin Islands were recaptured off Florida and Georgia, traveling over 1000 nautical miles. This paper provides evidence that finite survival differs between YOY and post-YOY blacktip sharks. There is no evidence that survival varies between males and females, or among the west GOM, east GOM, or U.S. Atlantic. However, it is possible that only relatively large differences in survival would be detectable with the sample size in the CSTP. Corrected direct estimates of survival were consistent with indirect estimates for YOY (S=0.580) and post-YOY (S=0.725). This positive result demonstrates that direct estimates of survival (and related analysis) can be successfully performed for species with smaller sample size in the CSTP.

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TABLES

Table 1. Summary of all tags and recaptures of blacktip sharks by region.

	U.S. Atlantic	International Atlantic	Western US. GOM	Eastern U.S. GOM	Mexican GOM	Total
Tags	3960	496	2178	2237	0	8871
Recaptures	84	16	29	66	35	230
Total Captures	4044	512	2207	2303	35	9101

Table 2. Summary of tagging fate of blacktip sharks for each region.

Tagging Region	No. Tagged	No. Recaptured	No. Recaptured in:				
			U.S. Atlantic	International Atlantic	Western U.S. GOM	Eastern U.S. GOM	Mexican GOM
U.S. Atlantic	3960	82	81	1	0	0	0
International Atlantic	496	18	3	15	0	0	0
Western U.S. GOM	2178	64	0	0	29	0	35
Eastern U.S. GOM	2237	66	0	0	0	66	0
Mexican GOM	0	0	0	0	0	0	0
Total	8871	230	84	16	29	66	35

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Table 3. CSTP capture distribution by sex and life stage for blacktip sharks tagged and recaptured in the U.S. Atlantic Ocean.

Key
Frequency
Percent
Row Percent
Column Percent

Sex	Tagged and Recaptured in U.S. Atlantic						Fork Length (cm)				
	Mature	Juveniles	YOY	Embryos	Unknown Maturity	Total	Min	Max	Median	Mean	SD
Male	**407** *10.07* *24.85* *43.53*	**866** *21.44* *52.87* *38.78*	**359** *8.89* *21.92* *43.73*	**3** *0.07* *0.18* *60.00*	**3** *0.07* *0.18* *6.52*	**1638** *40.54*	33	180	101	101.2	33.8
Female	**431** *10.67* *21.06* *46.10*	**1178** *29.16* *57.55* *52.75*	**427** *10.57* *20.86* *52.01*	**2** *0.05* *0.10* *40.00*	**9** *0.22* *0.44* *19.57*	**2047** *50.67*	38	180	84	88.8	32.4
Unknown Sex	**97** *2.40* *27.32* *10.37*	**189** *4.68* *53.24* *8.46*	**35** *0.87* *9.86* *4.26*	**0** *0.00* *0.00* *0.00*	**34** *0.84* *9.58* *73.91*	**355** *8.79*	33	190	85	92.2	35.9
Total	**935** *23.14*	**2233** *55.27*	**821** *20.32*	**5** *0.12*	**46** *1.14*	**4040** *100*	33	190	86	91.6	34.5

Sex Ratio (M:F)
1:1.2

41

Table 4. CSTP capture distribution by sex and life stage for blacktip sharks tagged and recaptured in the Gulf of Mexico.

Sex	Mature	Juveniles	YOY	Embryos	Unknown Maturity	Total	Min	Max	Median	Mean	SD
		Tagged and Recaptured in the GOM					Fork Length (cm)				
Male	**363** 7.99 25.30 27.65	**640** 14.08 44.60 29.14	**427** 9.39 29.76 44.25	**1** 0.02 0.07 14.29	**4** 0.09 0.28 6.25	**1435** 31.57	33	183	74	80.4	29.5
Female	**838** 18.43 32.13 63.82	**1330** 29.26 51.00 60.56	**431** 9.48 16.53 44.66	**4** 0.09 0.15 57.14	**4** 0.09 0.15 6.25	**2607** 57.35	29	191	99	96.1	34.1
Unknown Sex	**112** 2.46 22.27 8.53	**226** 4.97 44.93 10.29	**107** 2.35 21.27 11.09	**2** 0.04 0.40 28.57	**56** 1.23 11.13 87.50	**503** 11.06	32	166	88	88.8	33.4
Total	**1313** 28.88	**2196** 48.31	**965** 21.23	**7** 0.15	**64** 1.41	**4545** 100	29	191	89	90.4	33.4

Sex Ratio (M:F)
1:1.8

Key
Frequency
Percent
Row Percent
Column Percent

Table 5. CSTP capture distribution by sex and life stage for blacktip sharks tagged and recaptured in the International Atlantic Ocean.

Key
Frequency
Percent
Row Percent
Column Percent

Sex	Tagged and Recaptured in International Atlantic						Fork Length (cm)				
	Mature	Juveniles	YOY	Embryos	Unknown Maturity	Total	Min	Max	Median	Mean	SD
Male	**57** / 11.22 / 30.32 / 35.63	**84** / 16.54 / 44.68 / 32.68	**46** / 9.06 / 24.47 / 52.87	**0** / 0.00 / 0.00 / N/A	**1** / 0.20 / 0.53 / 25.00	**188** / 37.01	42	152	101	99.6	33.7
Female	**96** / 18.90 / 32.54 / 60.00	**159** / 31.30 / 53.90 / 61.87	**40** / 7.87 / 13.56 / 45.98	**0** / 0.00 / 0.00 / N/A	**0** / 0.00 / 0.00 / 0.00	**295** / 58.07	43	177	104	90.9	31.9
Unknown Sex	**7** / 1.38 / 28.00 / 4.38	**14** / 2.76 / 56.00 / 5.45	**1** / 0.20 / 4.00 / 1.15	**0** / 0.00 / 0.00 / N/A	**3** / 0.59 / 12.00 / 75.00	**25** / 4.92	50	177	115	108.9	30.6
Total	**160** / 31.50	**257** / 50.59	**87** / 17.13	**0** / 0.00	**4** / 0.79	**508** / 100	42	177	111	101.4	32.4

Sex Ratio (M:F) 1:1.6

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Table 6. Summary statistics for recaptures of all regions.

	Mean Displacement (n. mi.)	Max Displacement (n. mi.)	Mean Time at Liberty (days)	Max Time at Liberty (days)	Mean Speed (n. mi./day)	Max Speed (n. mi./day)
U.S. Atlantic	114.7	616	351.8	2146	1.2	15.3
International Atlantic	147.2	1183	506.9	2471	0.2	1.4
Western U.S. GOM	227.3	632	264.0	2845	3.4	16.4
Eastern U.S. GOM	23.0	180	242.3	2050	0.4	6.6
Mexican GOM	N/A	N/A	N/A	N/A	N/A	N/A
Total	122.3	1183	308	2845	1.5	16.4

Table 7. Tag and recapture information for four sharks that crossed between U.S. and International Atlantic waters.

Sex	Type	Industry	Gear	Year	Region	FL (cm)	Life Stage	Displacement (n. mi.)	Time at Liberty (days)	Speed (n. mi./day)
Male	Tag	Unknown	Rod and Reel	1976	U.S. Atlantic	69	Juvenile	45	34	1.3
	Recapture	Unknown	Longline	1977	International Atlantic	N/A	Unknown			
Female	Tag	Biologist	Longline	2008	International Atlantic	150	Mature	157	740	0.2
	Recapture	Recreational	Rod and Reel	2010	U.S. Atlantic	76	Mature			
Male	Tag	Biologist	Longline	2004	International Atlantic	48	YOY	1049	760	1.4
	Recapture	Commercial	Gill Net	2006	U.S. Atlantic	N/A	Unknown			
Male	Tag	Biologist	Longline	2004	International Atlantic	48	YOY	1183	2471	0.5
	Recapture	Recreational	Rod and Reel	2011	U.S. Atlantic	148	Mature			

Table 8. Final results for ĉ, r, and S_T for select models. Recovery estimates are given for the most parsimonious model. Survival estimates are bold when the simplest LRT revealed a significant group effect on survival. Note that the 95% CI must between 0 and 1. Cases in which the upper boundary of the CI exceeded 1 are marked by *.

Analysis	Average ĉ / Deviance ĉ / Mean ĉ	r	Model	Group	S	S_T	95%CI
1) GOM: YOY vs. Post-YOY	**1.2751**	0.013-0.166	S(..) r(g+effort)	-	0.527	0.711	(0.551, 0.867)
	1.2615		S(g.) r(g+effort)	YOY	0.430	**0.580**	(0.206, 1.000)*
	1.2888			Post-YOY	0.537	**0.725**	(0.557, 0.887)
2) Post-YOY GOM: Male vs. Female	**2.2422**	0.012-0.069	S(..) r(.effort)	-	0.603	0.814	(0.551, 1.000)*
	1.4177		S(g.) r(.effort)	Male	0.572	0.772	(0.374, 1.000)*
	3.0666			Female	0.620	0.837	(0.514, 1.000)*
3) Post YOY GOM: West vs. East	**1.9528**	0.012-0.061	S(..) r(.effort)	-	0.579	0.781	(0.552, 0.988)
	1.496		S(g.) r(.effort)	West	0.586	0.791	(0.483, 1.056)
	2.4096			East	0.571	0.771	(0.452, 1.000)*
4) Post-YOY: Atlantic vs. GOM	**1.2496**	0.012-0.063	S(..) r(g+effort)	-	0.627	0.846	(0.702, 0.974)
	1.285		S(g.) r(g+effort)	Atlantic	0.691	0.933	(0.703, 1.000)*
	1.2142			GOM	0.579	0.781	(0.597, 0.950)

Table 9. P values for the simplest likelihood ratio tests of each effect. † indicates that the effect is significant according to the simplest LRT at the α=0.05 level.

Analysis	S(g)	S(t)	S(g*t)	r(effort)	r(g)	r(t)	r(g*t)
1) GOM: YOY vs. Post-YOY	0.0003†	1.0000	0.6638	<0.0001†	<0.0001†	0.7900	0.4372
2) Post-YOY GOM: Male vs. Female	0.7607	0.3024	0.9444	0.0067†	0.8057	0.9371	0.9008
3) Post YOY GOM: West vs. East	0.6540	0.9254	0.978	0.0028†	0.6180	1.0000	0.8053
4) Post-YOY: Atlantic vs. GOM	0.2433	0.9997	0.0004†	0.0002†	0.9379	0.015†	0.4754

Table 10. Sensitivity analysis for S_T as a function of varying Λ.

Analysis	Model	Group	Λ 0	0.11	0.22	.259	0.36
1	S(..) r(g+effort)	-	0.527	0.592	0.676	0.711	0.820
	S(g.) r(g+effort)	YOY	0.430	0.483	0.551	0.580	0.669
		Post-YOY	0.537	0.604	0.689	0.725	0.836
2	S(..) r(.effort)	-	0.603	0.678	0.773	0.814	0.938
	S(g.) r(.effort)	Male	0.572	0.643	0.734	0.772	0.890
		Female	0.620	0.697	0.795	0.837	0.965
3	S(..) r(.effort)	-	0.579	0.651	0.742	0.781	0.901
	S(g.) r(.effort)	West GOM	0.586	0.658	0.751	0.791	0.911
		East GOM	0.571	0.642	0.732	0.771	0.888
4	S(..) r(g+effort)	-	0.627	0.704	0.803	0.846	0.975
	S(g.) r(g+effort)	Atlantic	0.691	0.777	0.886	0.933	1.075
		GOM	0.579	0.650	0.742	0.781	0.900

Figure 1. Geographic regions used in analysis.
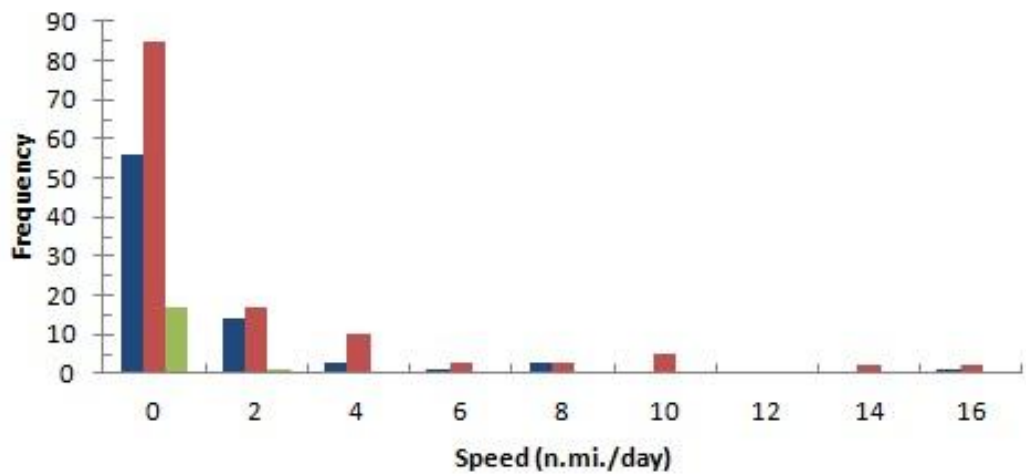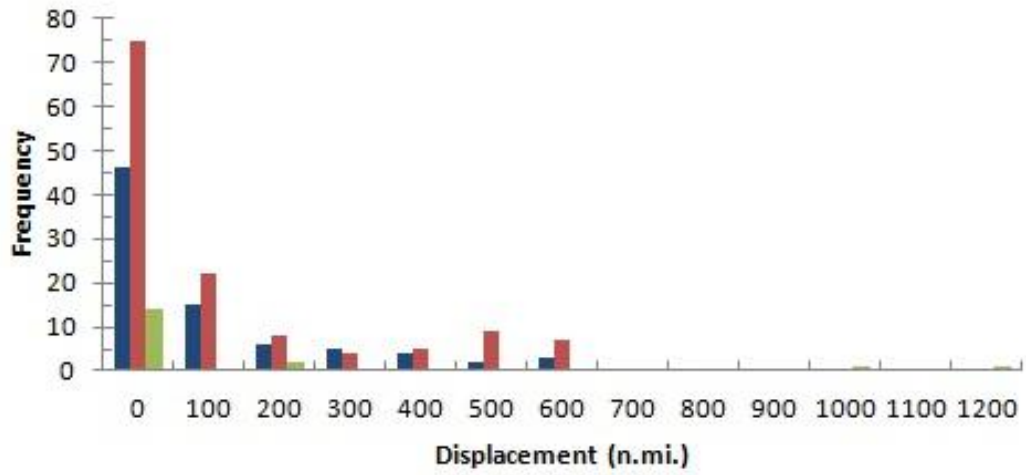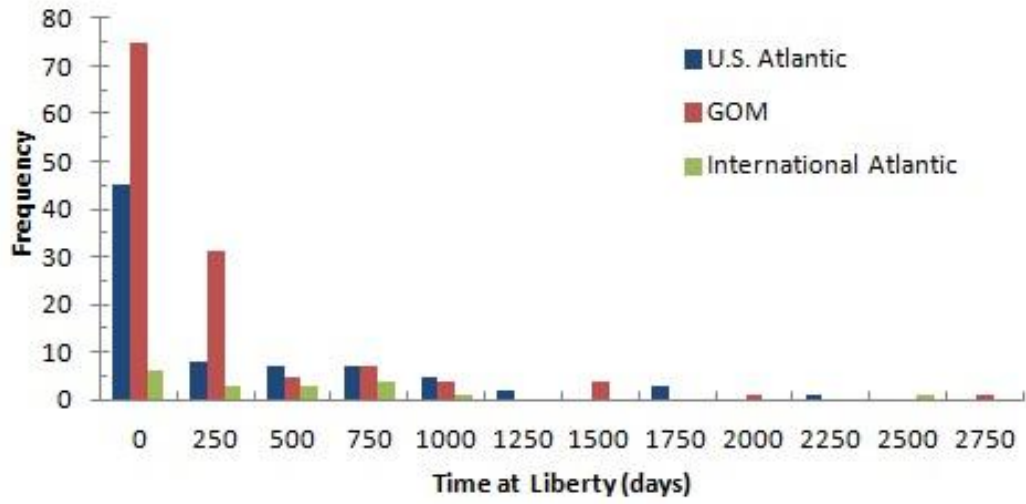
Figure 2. Distribution of recaptures according to time at liberty, displacement, and speed.
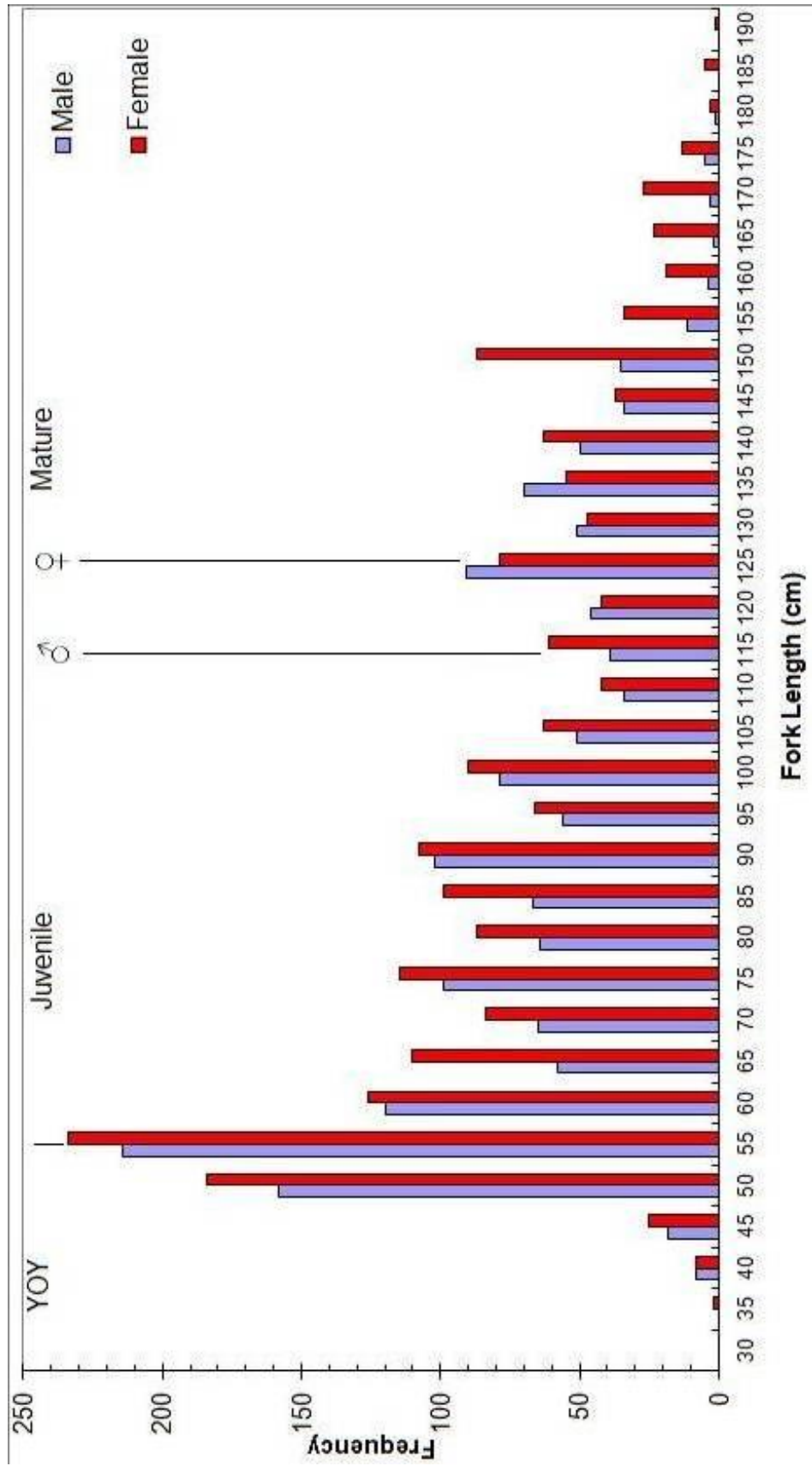
Figure 3. Length frequency by sex for blacktip shark captures in the U.S. Atlantic Ocean.
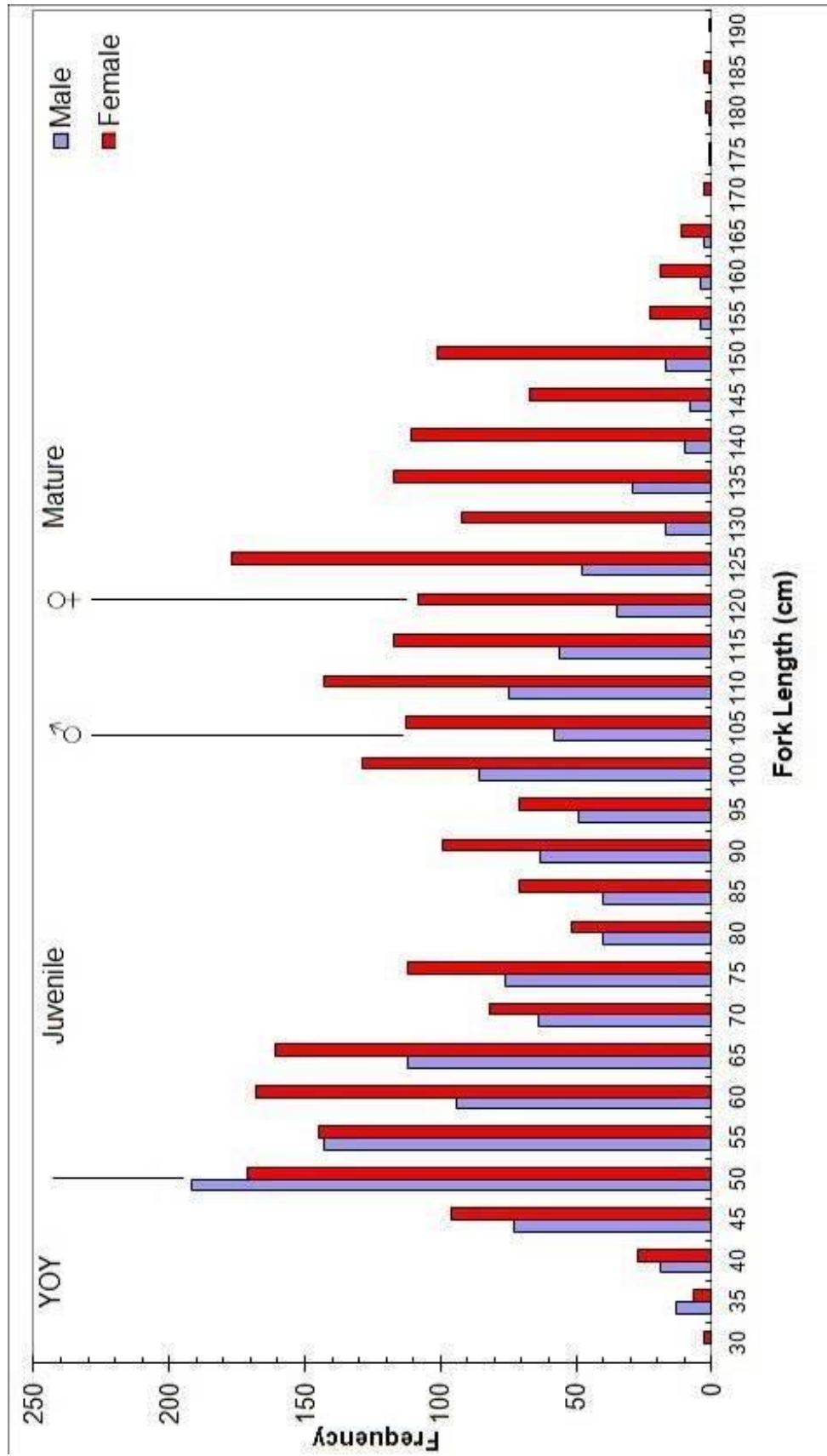
50

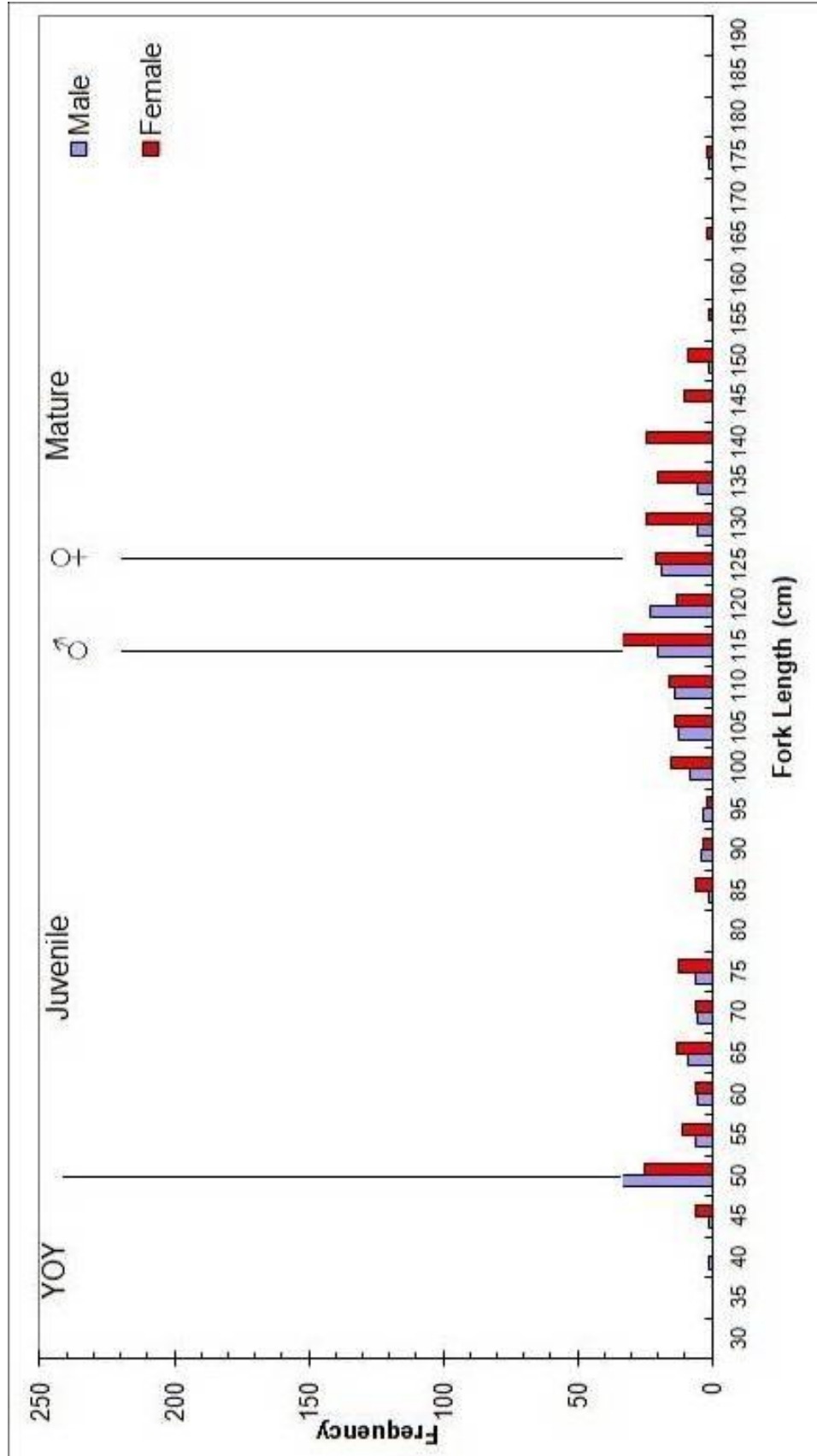Figure 4. Length frequency by sex for blacktip shark captures in the Gulf of Mexico.

51

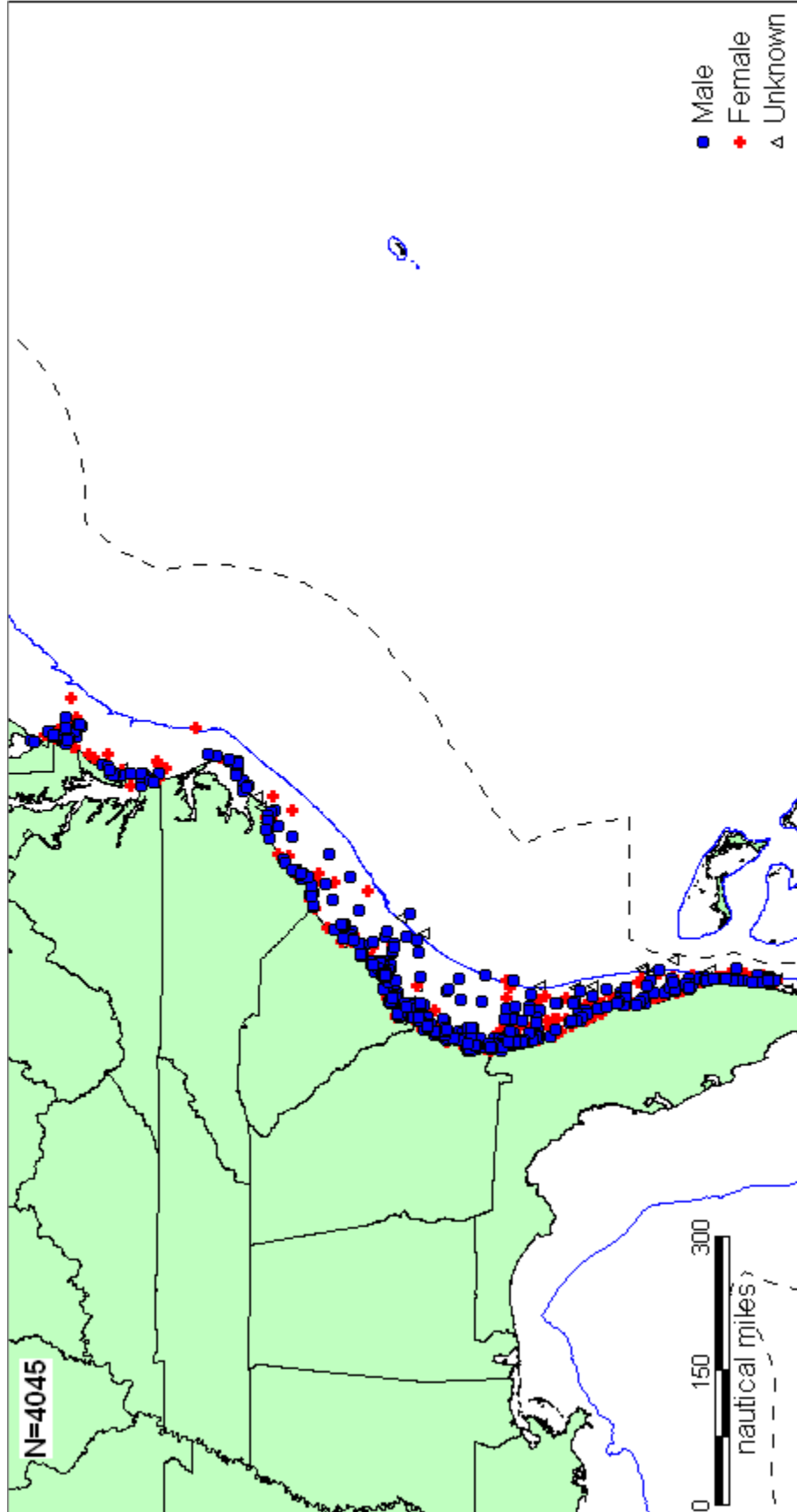Figure 5. Length frequency by sex for blacktip shark captures in the International Atlantic Ocean.

Figure 6. Blacktip shark captures by sex in the U.S. Atlantic. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
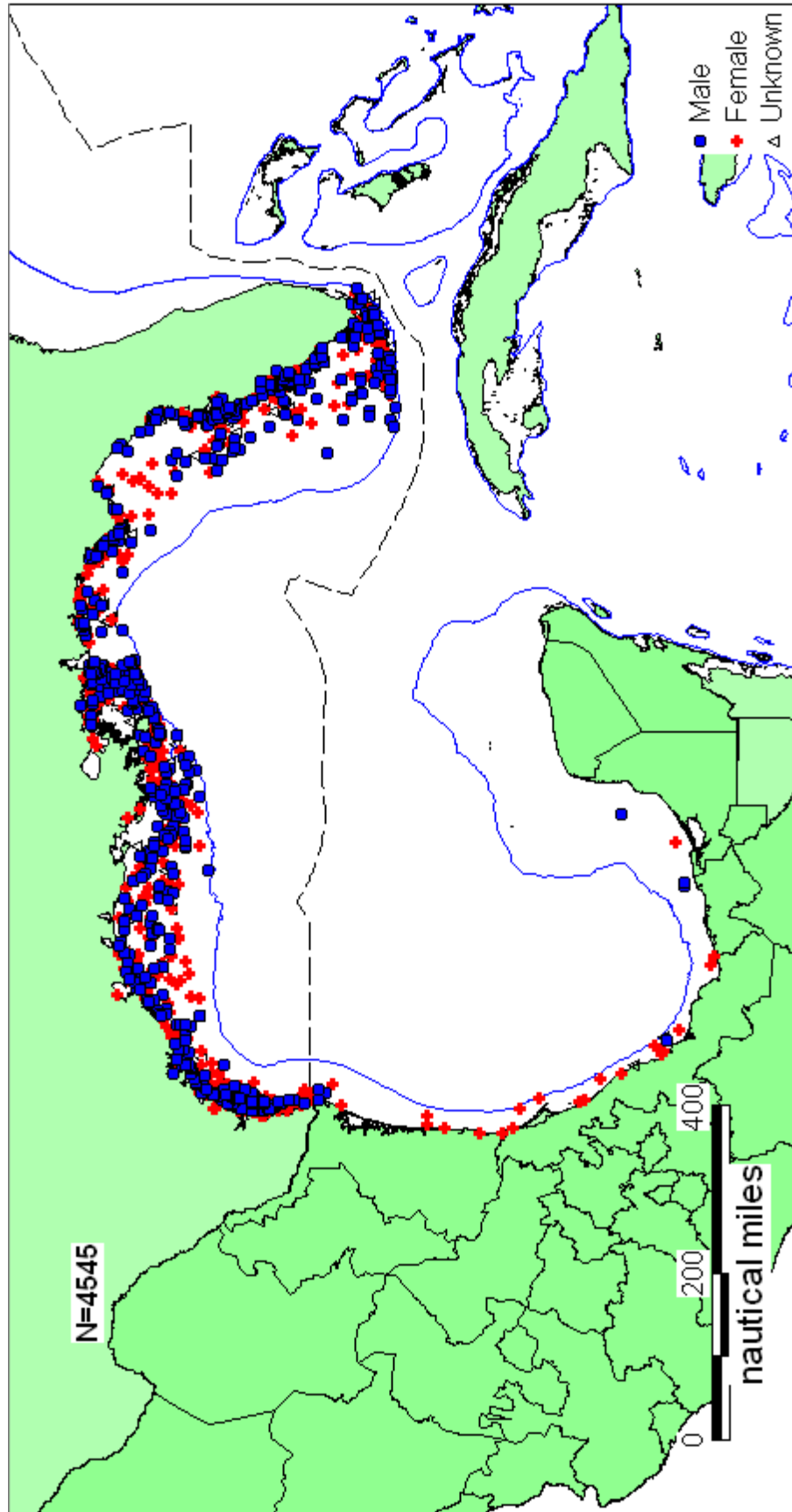
Figure 7. Blacktip shark captures by sex in the GOM. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
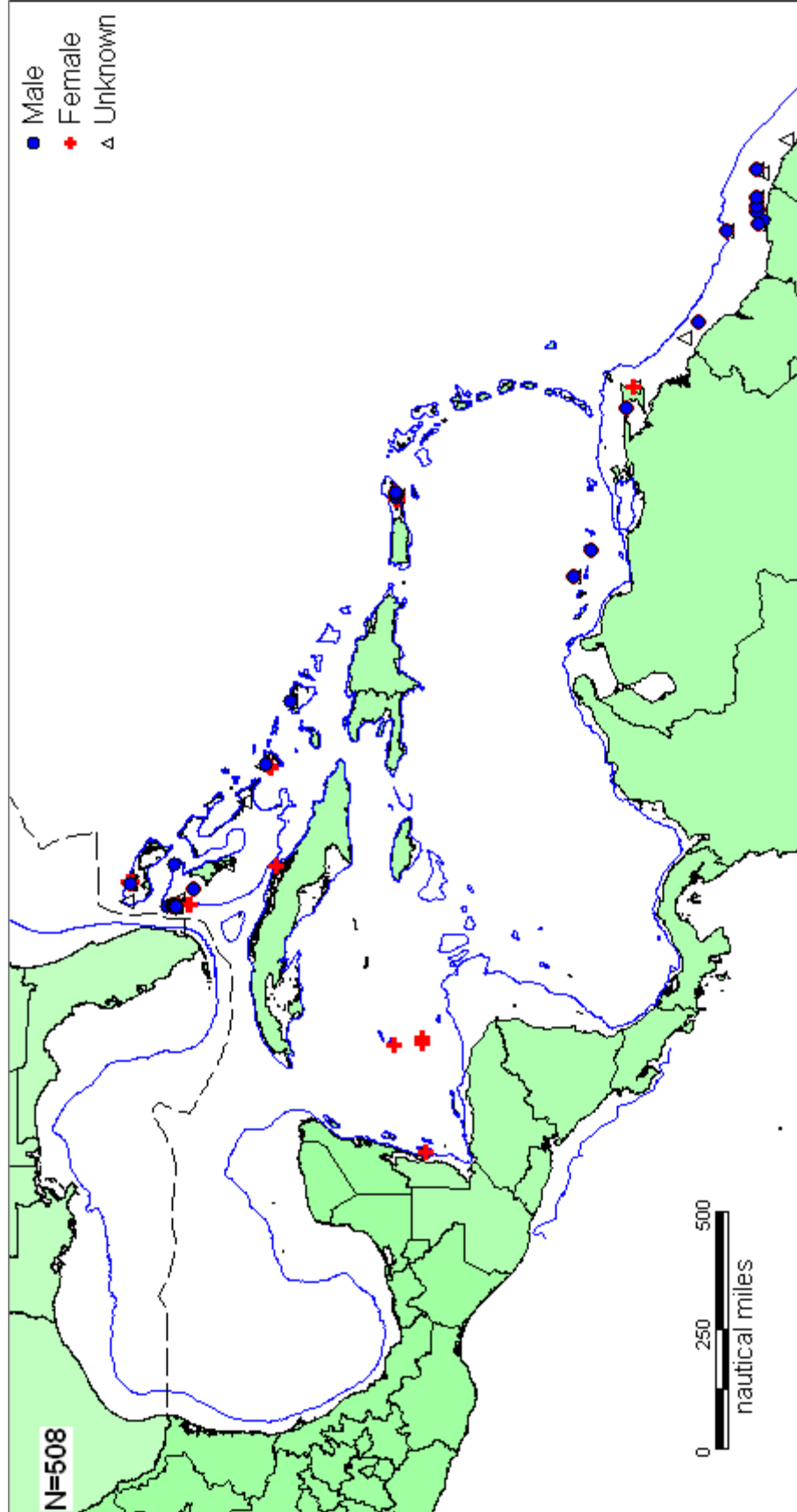
Figure 8. Blacktip shark captures by sex in the International Atlantic. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
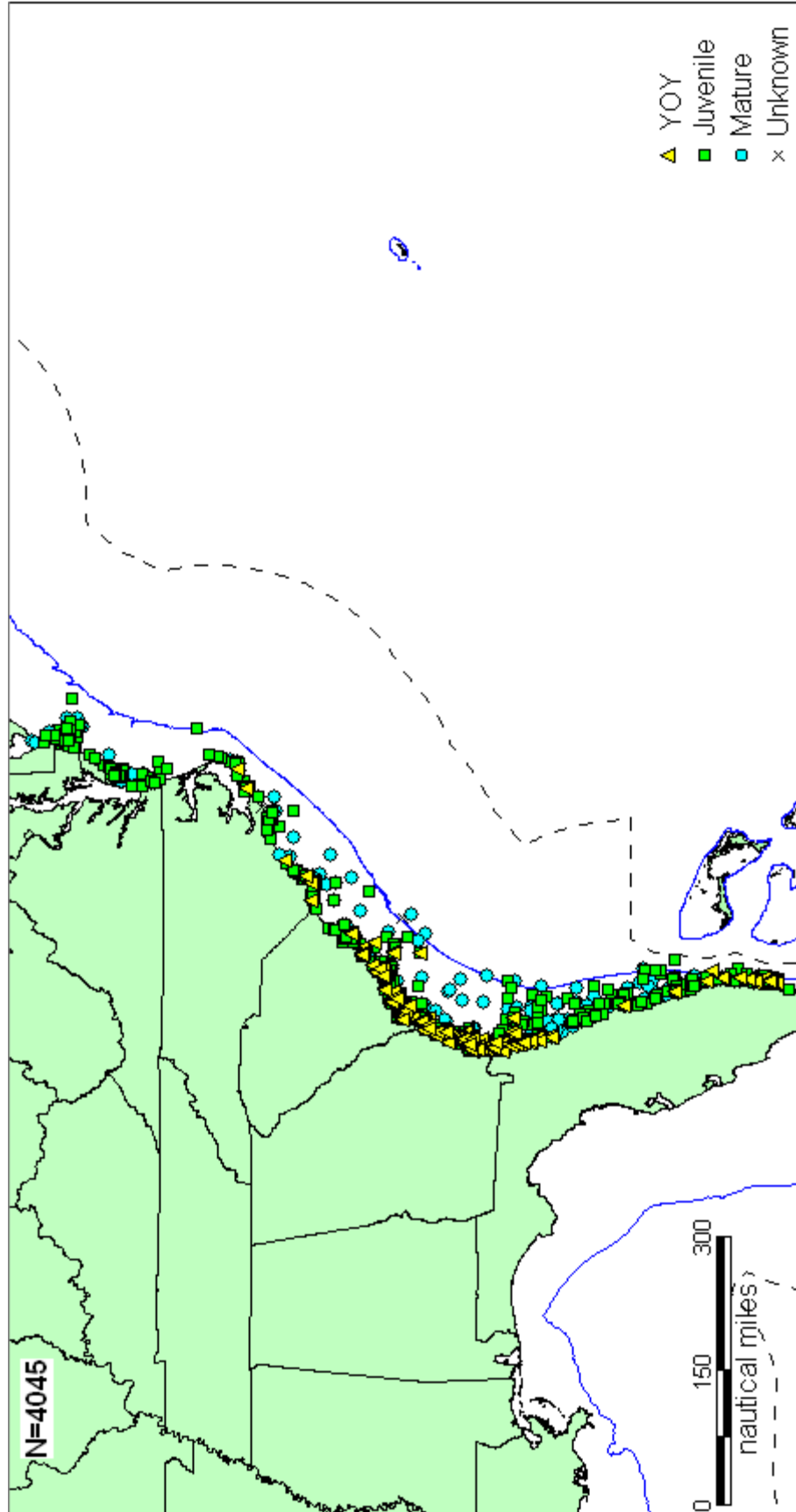
55

Figure 9. Blacktip shark captures by life stage in the U.S. Atlantic. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

N=4045

YOY
Juvenile
Mature
× Unknown
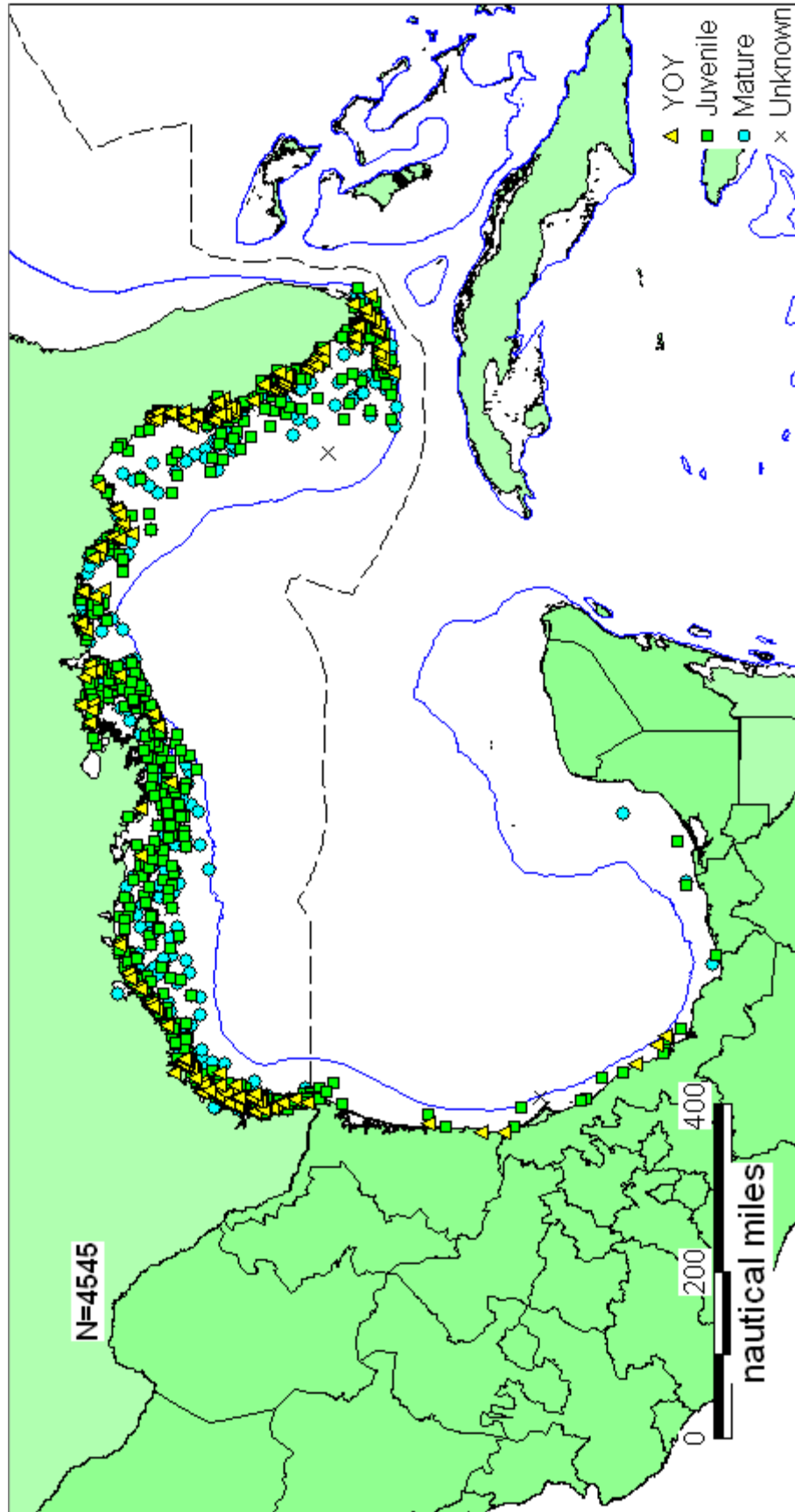
nautical miles

0   150   300

56

Figure 10. Blacktip shark captures by life stage in the Gulf of Mexico. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

N=4545

YOY
Juvenile
Mature
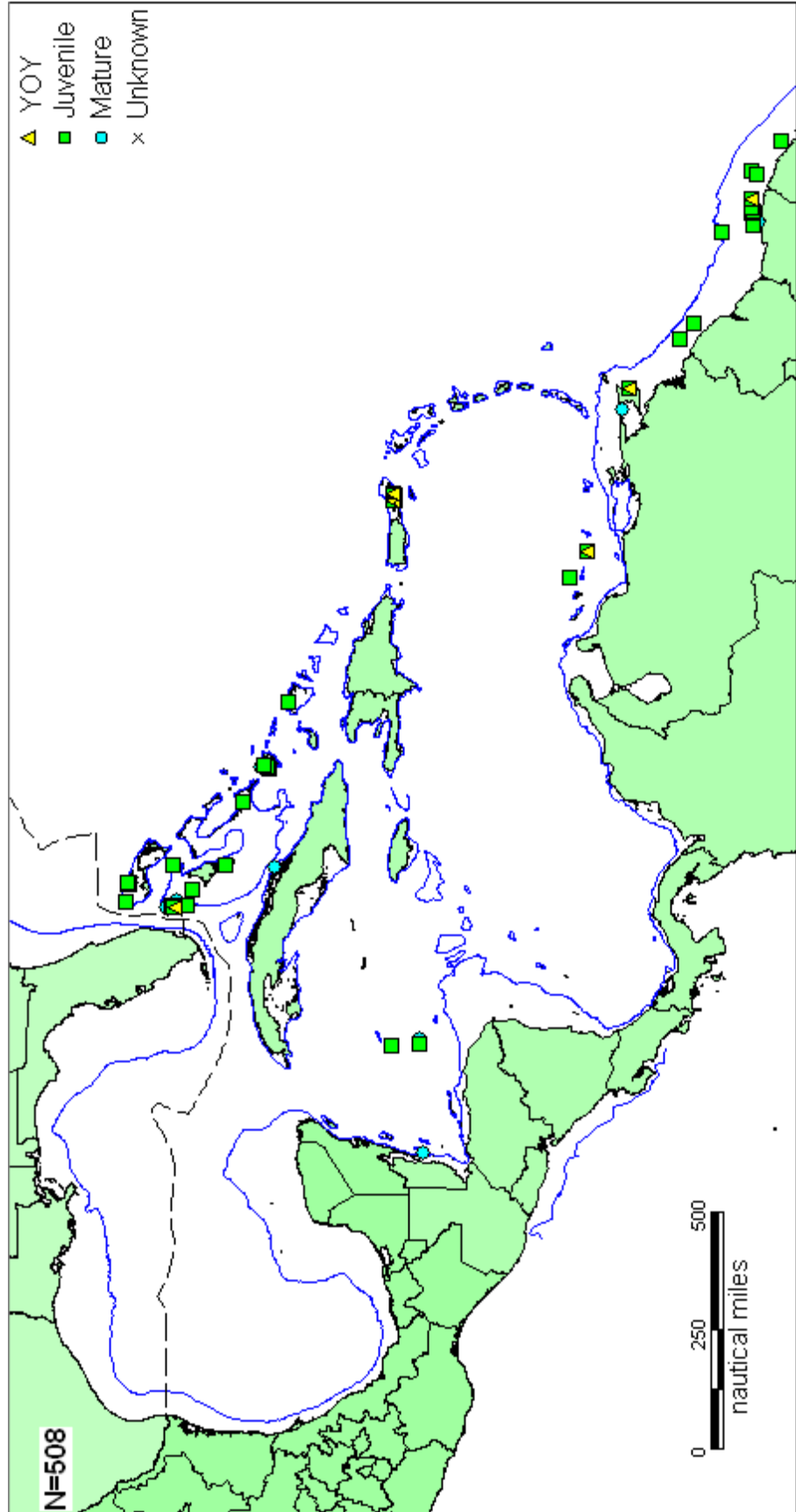Unknown

0   200   400
nautical miles

Figure 11. Blacktip shark captures by life stage in the International Atlantic. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
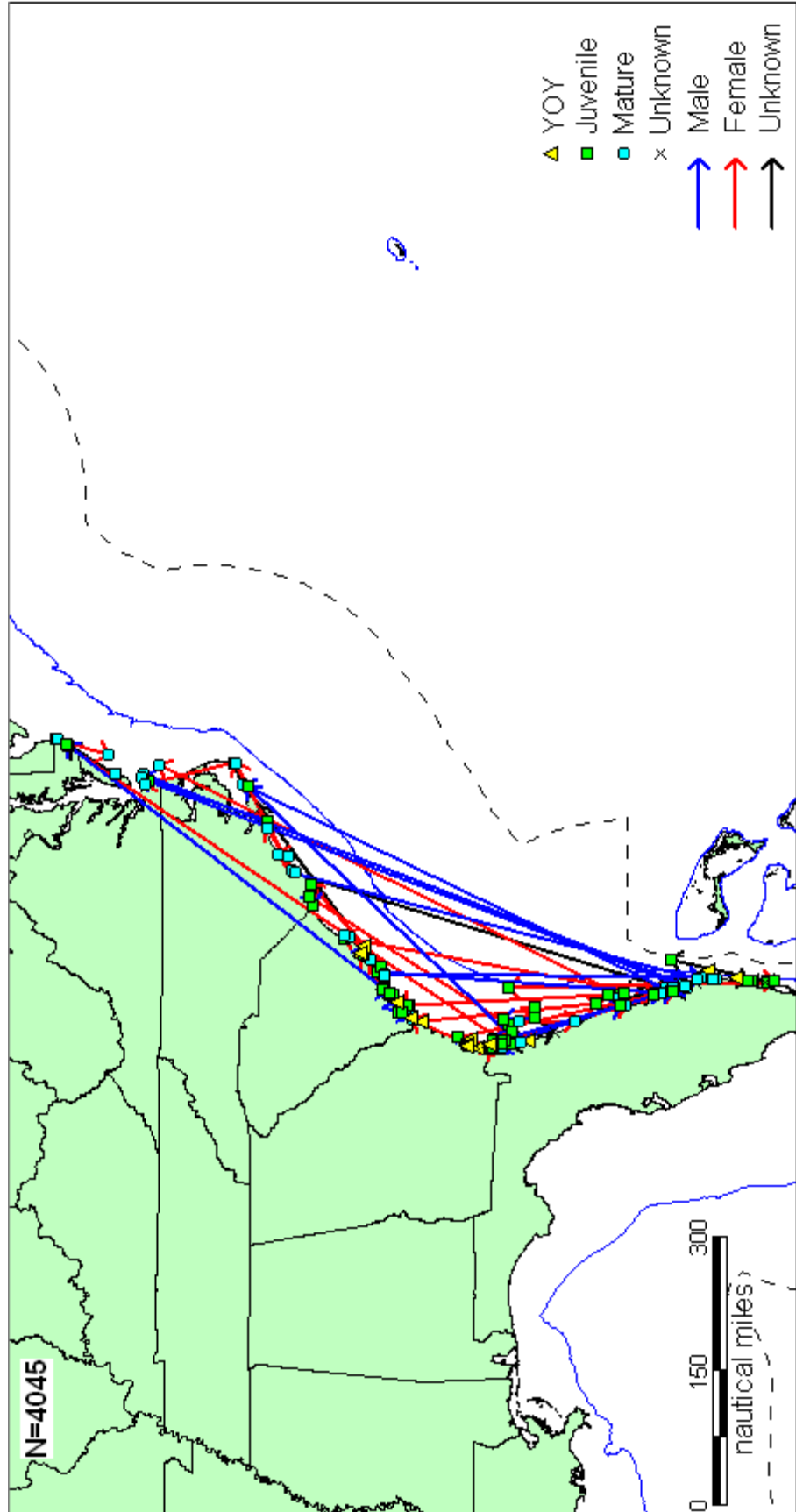
Figure 12. Blacktip shark recaptures by sex and life stage in the U.S. Atlantic. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
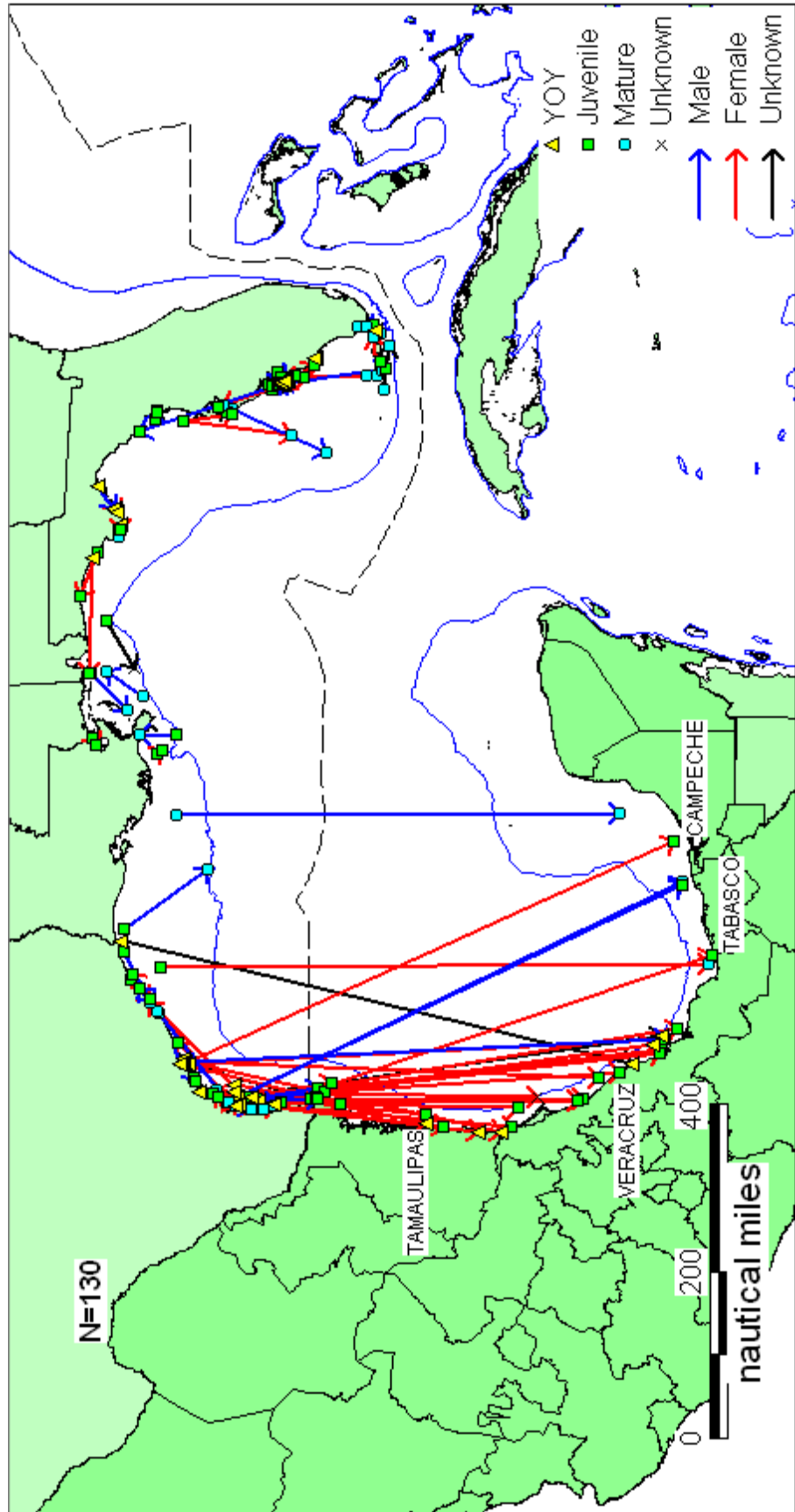
Figure 13. Blacktip shark recaptures by sex and life stage in the Gulf of Mexico. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
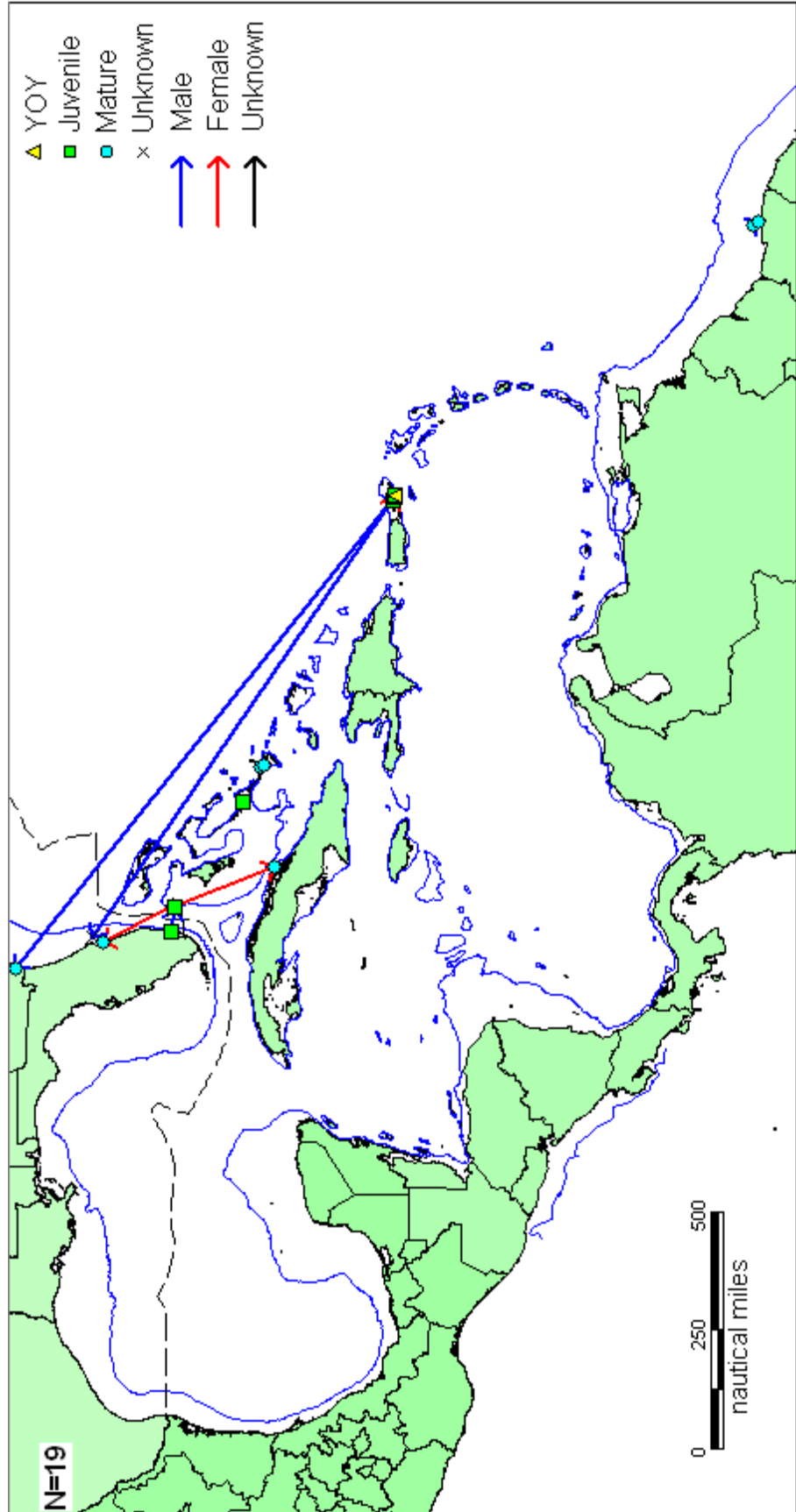
Figure 14. Blacktip shark recaptures by sex and life stage in the International Atlantic. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

APPENDICES

APPENDIX I: Definition of Terms

AIC: Akaike's information criterion, used for determining relative parsimony of a model, balancing overall fit with the number of parameters involved. AIC= -2ln(L) +2K, where K is the number of parameters

Ĉ: the variance inflation factor, which indicates the degree of overdispersion (lack of fit) in the most general model

Capture: any landing event, including both tags and recaptures

CSTP: Cooperative Shark Tagging Program

F: instantaneous fishing mortality rate

Likelihood ratio test: a statistical significance test for estimates made under the maximum likelihood approach. Determined by comparing [deviance of reduced model-deviance of general model] with a χ^2 distribution with n degrees of freedom, where n is the difference in number of parameters

M: instantaneous natural mortality rate

Nested models: a reduced model is considered nested if it can be created by constricting a more general model (e.g., fixing a time-dependent parameter to become time-independent)

NMFS: National Marine Fisheries Service

Parametric bootstrap: a resampling technique used to determine Goodness of Fit (GOF). A model is created from the original data, and is used to simulate data.

Proportional Survival (*S*): the probability of surviving from year (i) to year (i+1). $S=N_{t+1}/N_t= e^{-Z}$

QAIC$_c$: quasi-likelihood adjusted AIC. The AIC value that has been adjusted by ĉ

Recovery probability (*r*): probability that a dead animal is both recovered and reported

Recapture rate: the percent of tagged sharks that are recaptured

S$_T$: true survival estimate, corrected for tag-shedding rate. $S_T = S(1-\Lambda)^{-1}$

Tagging rate: the number of sharks that are tagged per year

Tag-shedding rate (Λ)**:** the instantaneous rate of tag shedding from year (i) to year (i+1)

YOY: young of the year

Z: instantaneous total mortality rate (Z=M+F)

Reduced (Seber) Parameterization

Survival was modeled with the reduced (Seber) parameterization (Seber, 1970; Anderson et al., 1985). Animals are tagged once, released, and recovered once; they are not re-released alive after recovery. In this model, S is the probability that the fish survives a time interval, and r is the probability that a dead fish is recovered and reported (Fig. A-1). If the number of animals released and recovered during each occasion is known, one can calculate estimates of these parameters based on the probability associated with each specific fate (Fig. A-1).

The simplicity of the reduced parameterization is advantageous for the calculation of parameters. The disadvantage of the reduced parameterization is that S does not consider the source of mortality (natural vs. hunting/fishing). As a result, a fish that avoids natural mortality – but is caught and reported – has the probability $(1-S)r$. Therefore, survival from the Seber parameterization represents survival from *all* sources of mortality, including natural and fishing mortality.

The probabilities S and r can be used to calculate expressions for the expected number of fish recovered in a given occasion. In the sample diagram in Figure A-43, three rows represent three years of marking, and three columns represent three years of recovery. In this diagram, N_i is the number of individuals tagged in year i (i=1,2,…, I), r_i is the recovery probability in year i, and S_i is the survival probability in year i.

Estimates of S and r can also be modeled separately for young-of-the-year (YOY) and post-YOY. When investigating models with an age effect, S and r represent the post-YOY survival and recovery probability, respectively, while S^* and

r^* represent YOY survival and recovery probability, respectively. An animal that is marked and released as YOY is assumed to acquire the post-YOY parameters by the second year of its life. Therefore, probability expressions for sharks tagged as YOY include both YOY and post-YOY parameters (Fig. A-44).

The triangular matrix of probability expressions corresponds to a triangular matrix of fish recovered in each element of that matrix. Recovery data are entered into program MARK using this classic recovery matrix format (Fig. A-2). In this format, n represents the number of fish recaptured, rows represent years of tagging (up to I years), and columns represent years of recovery (up to J years). A sample input file that was used in the analysis is shown in Figure A-45.

Models were also fit with an external index of effort. It is known that $F=qf$, where F=fishing mortality rate, q=catchability coefficient, and f=fishing effort. If the catchability coefficient is assumed to be constant over time, fishing mortality rate (F) can be used as proxy for effort. Values of F are available specifically for Gulf of Mexico and U.S. Atlantic blacktip sharks from 1986-2004 from the SEDAR 11 Stock Assessment Report (Fig. A-3). Therefore, the analysis was constrained to this time period. From 1986 to 2004, 3240 blacktip sharks were tagged in the CSTP in the GOM, and 96 of these were recaptured (2.96%). During the same time period, 1589 sharks were tagged in the U.S. Atlantic, and 38 were recaptured (2.39%).

Calculation of Parameters

To calculate parameter estimates, the observed recovery matrix is compared to matrix of probability expressions. Program MARK solves for the maximum likelihood estimates of S and r numerically (not algebraically). In maximum

likelihood methods, the true value of the parameter is unknown. However, there is a likelihood (probability) distribution for the value of the true parameter, given the observed data (Fig. A-46). Program MARK solves for the maximum likelihood, and its corresponding parameter value. The maximum likelihood estimate (MLE) of the parameter is the point where the likelihood distribution's first derivative is 0.

The variance associated with a given parameter depends on the shape of the likelihood distribution. For example, two likelihood distributions may have the same MLE of survival, but different variances (Fig. A-46). A greater spread in the likelihood function implies greater variance. The profile likelihood method generates confidence intervals that are 0,1 bounded. In this method, possible parameter values are plotted on the x axis, and log-likelihood is plotted on the y axis. When $\alpha = 5\%$, the χ^2 value with 1 degree of freedom is 3.84. With the profile likelihood approach, a y value is calculated by adding 1.92 (half of 3.84) to the log-likelihood at the maximum of the log-likelihood distribution (Fig. A-47). This y value intersects with the log-likelihood function at two points, and the x values at these intersections represent the 95% CI. The confidence interval in this method is not symmetrical around the MLE for the parameter, but it is always 0,1 bounded.

Goodness of Fit (GOF)

Models can only be successfully analyzed if they adequately fit the data. Deviance (difference in fit) is defined by the equation: deviance= -2(log-likelihood of model) – [-2(log-likelihood of saturated model)], where the saturated model is the model with all possible parameters included. Considering the saturated model itself, the ratio of model deviance over the model's degrees of freedom is a measure of

overdispersion (lack of fit) in the model. This ratio is known as the variance inflation factor or quasi-likelihood parameter, ĉ (Cooch and White, 2004). Perfect fit is achieved when ĉ=1, whereas overdispersion or lack of fit occurs when ĉ>1. A parametric bootstrap approach can be used to estimate ĉ. In this method, the most general model is used to simulate data (capture histories) that fit all the assumptions of model. The model is then fit to each set of simulated data, and the model deviance and ĉ are calculated for each simulation.

There are two ways to use bootstrap simulations to estimate ĉ. One method of calculating ĉ is based on deviance. The mean of all the simulated deviances represents the expected deviance when no assumptions are violated (and fit is perfect). Therefore, the estimate of ĉ is the ratio of the observed model deviance over the mean of all the simulated deviances. A ratio higher than 1.0 suggests a certain amount of overdispersion. Figure A-48 shows a visual representation of how this method was applied to the general model S(g*t) r(g*t) in the analysis of YOY vs. post-YOY. The second method of calculating ĉ is based on the simulated values of ĉ in the bootstrap. The mean of all the simulated ĉ represents the expected value of ĉ when fit is perfect. Therefore, the ratio of the observed model ĉ over the mean of all the simulated ĉ provides a similar measurement of overdispersion. Estimates from both methods were averaged to calculate the final value of ĉ in the analysis. The model fits the data adequately if ĉ≤3 (Lebreton et al., 1992).

Ranking

Various models can be ranked using Akaike's Information Criterion, AIC. This metric is used for determining relative parsimony of a model, balancing overall fit

with the number of parameters involved (Akaike, 1973). AIC is defined by: AIC= -2ln(L) +2K, where K is the number of parameters and L is the likelihood of the model, given the data. High likelihood results in a lower AIC; more parameters results in a higher AIC. As a result, a more parsimonious model has a lower AIC.

AIC_c is a variation of AIC that corrects for sample size (Sugiura, 1978; Hurvich & Tsai, 1989). AIC_c is defined by: AIC_c= -2ln(L) +2K + [2K(K+1)]/[n-K-1], where n is sample size The extra term in this definition creates a higher penalty for small sample size. $QAIC_c$ is another variation, known as the quasi-likelihood adjusted AIC (White and Burnham, 1999). $QAIC_c$ is defined by: $QAIC_c$= [-2ln(L)]/ ĉ +2K + [2K(K+1)]/[n-K-1]. If ĉ >1, the contribution of the model likelihood term decreases, and the K penalty is relatively more powerful. Therefore, when ĉ >1, simpler models with fewer parameters become more favored. All models in the candidate set are ranked by $QAIC_c$ to identify the most parsimonious model.

Any two models can be directly compared through $\Delta QAIC_c$, the difference in $QAIC_c$ between two models. If $\Delta QAIC_c$ >7, there is strong support for a difference in the two models. If 2<$\Delta QAIC_c$ <7, there is moderate support for a difference in the two models. If $\Delta QAIC_c$ <2, there is very little support for a difference in the two models (Anderson and Burnham, 1999). The normalized Akaike weights are used to quantify and standardize the difference in support between two models. By definition, w_i=($e^{-\Delta AIC(2)^{-1}}$)($\Sigma e^{-\Delta AIC(2)^{-1}}$)$^{-1}$, where w_i is the normalized Akaike weight (Buckland et al. 1997). The ratio of two normalized Akaike weights shows the relative support of one model over another. For example, if model A has a weight of 0.6 and model B has a weight of 0.2, model A is 3 times more supported than model B. Program MARK also

provides an index called "model likelihood," which is simply the weight of a model divided by weight of most parsimonious model.

Likelihood Ratio Tests

QAIC is one useful method of comparing two models, but it also possible to use classic statistical hypothesis testing between nested models using the likelihood ratio test (LRT). Two models are nested if one (known as the general model) can be transformed into the other (known as the reduced model) by a linear restriction (Cooch and White, 2004). In other words, the two models differ only by the presence or absence of a term. In most cases, the general model contains a certain parameter (e.g., $S(t)$), whereas the reduced model does not (e.g., $S(.)$) (Fig. A-49). The difference in deviance between nested models is approximately Chi-square distributed, and the difference in the number of parameters is the degrees of freedom. The Chi-square statistic is calculated as: $\chi^2 = \text{Dev}_r - \text{Dev}_g$ where χ^2 is the Chi-square statistic, Dev_r is the reduced model deviance, and Dev_g is the general model deviance. Equivalently, LRT is determined by comparing $-2 \ln(L_r/L_f)$ with a χ^2 distribution, where L_f is the likelihood of the full model, and L_r is the likelihood of the reduced model.

In a LRT, a significant difference (probability<0.05) means that there is a significant increase in deviance with the reduction in the number of parameters. In other words, there is a significant increase in deviance when you remove the parameter of interest; the model that includes the added parameter fits the data significantly better. A non-significant difference (probability>0.05) means that the two models both fit the data equally well, but the reduced model is preferred, since it has fewer parameters. The deviance is not statistically different between the two

models, but the reduced model is more parsimonious. If probability>0.05, there is not

a significant difference between the models; adding the parameter (e.g., time-

dependency in survival) does not significantly improve the model fit.

APPENDIX III: Additional Tables and Figures

Table A-1. CSTP recapture statistics by sex for blacktip sharks tagged and recaptured in the U.S. Atlantic Ocean. Displacement and speed values are calculated using the straight line distance from the tagging location to the recapture location.

Sex	Tagged	Recaptured	Recapture Rate (%)	Mean Displacement (n.mi)	Max Displacement (n. mi.)	Mean Time at Liberty (days)	Max time at Liberty (days)	Mean Speed (n.mi./day)	Max Speed (n.mi./day)
Male	1609	29	1.8	151.0	616	397.4	1769	0.9	8.5
Female	2009	38	1.9	99.7	567	296.5	1141	1.3	15.3
Unknown	341	14	4.1	83.2	416	439.2	2146	1.2	7.5
Total	3959	81	2.0	115.6	616	355.9	2146	1.2	15.3

Table A-2. CSTP recapture statistics by sex for blacktip sharks tagged and recaptured in the Gulf of Mexico. Displacement and speed values are calculated using the straight line distance from the tagging location to the recapture location.

Sex	Tagged	Recaptured	Recapture Rate (%)	Mean Displacement (n.mi.)	Max Displacement (n. mi.)	Mean Time at Liberty (days)	Max Time at Liberty (days)	Mean Speed (n.mi./day)	Max Speed (n.mi./day)
Male	1386	49	3.5	86.6	584	255.2	1591	1.0	14.2
Female	2539	68	2.7	155.2	632	256.2	2845	2.6	16.4
Unknown	490	13	2.7	109.5	607	249.6	2050	1.5	9.1
Total	4415	130	2.9	123.6	632	253.1	2845	1.9	16.4

Table A-3. CSTP recapture statistics by sex for blacktip sharks tagged and recaptured in the International Atlantic. Displacement and speed values are calculated using the straight line distance from the tagging location to the recapture location.

Sex	Tagged	Recaptured	Recapture Rate (%)	Mean Displacement (n.mi.)	Max Displacement (n.mi.)	Mean Time at Liberty (days)	Max time at Liberty (days)	Mean Speed (n.mi./day)	Max Speed (n.mi./day)
Male	182	6	3.3	2.7	12.0	331.0	959.0	0.0	0.0
Female	289	6	2.1	38.8	217.0	489.5	865.0	0.1	0.5
Unknown	22	3	13.6	3.7	9.0	76.7	91.0	0.0	0.1
Total	493	15	3.0	17.3	217.0	343.5	959.0	0.0	0.5

Table A-4. Captures by industry (including all tags and recaptures).

Industry	U.S. Atlantic	Western US. GOM	Eastern U.S. GOM	Mexican GOM	International Atlantic	Total
Recreational	**2121**	**1555**	**1708**	**3**	**92**	**5479**
	23.31	17.09	18.77	0.03	1.01	60.20
	38.71	28.38	31.17	0.05	1.68	
	52.45	70.46	74.16	8.57	17.97	
Biologist	**1758**	**614**	**496**	**0**	**414**	**3282**
	19.32	6.75	5.45	0.00	4.55	36.06
	53.56	18.71	15.11	0.00	12.61	
	43.47	27.82	21.54	0.00	80.86	
Commercial	**122**	**34**	**38**	**32**	**0**	**226**
	1.34	0.37	0.42	0.35	0.00	2.48
	53.98	15.04	16.81	14.16	0.00	
	3.02	1.54	1.65	91.43	0.00	
Fishery Observer	**13**	**1**	**45**	**0**	**0**	**59**
	0.14	0.01	0.49	0.00	0.00	0.65
	22.03	1.69	76.27	0.00	0.00	
	0.32	0.05	1.95	0.00	0.00	
Other	**30**	**3**	**16**	**0**	**6**	**55**
	0.33	0.03	0.18	0.00	0.07	0.60
	54.55	5.45	29.09	0.00	10.91	
	0.74	0.14	0.69	0.00	1.17	
Total	**4044**	**2207**	**2303**	**35**	**512**	**9101**
	44.43	24.25	25.30	0.38	5.63	100

Key

Frequency
Percent
Row Percent
Column Percent

Table A-5. Captures by gear (including all tags and recaptures).

Gear	U.S. Atlantic	Western US. GOM	Eastern U.S. GOM	Mexican GOM	International Atlantic	Total
Rod and Reel	**2144**	**1546**	**1719**	**3**	**98**	**5510**
	23.56	16.99	18.89	0.03	1.08	60.54
	38.91	28.06	31.20	0.05	1.78	
	53.02	70.05	74.64	8.57	19.14	
Longline	**1659**	**633**	**463**	**14**	**363**	**3132**
	18.23	6.96	5.09	0.15	3.99	34.41
	52.97	20.21	14.78	0.45	11.59	
	41.02	28.68	20.10	40.00	70.90	
Gill Net	**216**	**13**	**106**	**15**	**2**	**352**
	2.37	0.14	1.16	0.16	0.02	3.87
	61.36	3.69	30.11	4.26	0.57	
	5.34	0.59	4.60	42.86	0.39	
Other	**25**	**15**	**15**	**3**	**49**	**107**
	0.27	0.16	0.16	0.03	0.54	1.18
	23.36	14.02	14.02	2.80	45.79	
	0.62	0.68	0.65	8.57	9.57	
Total	**4044**	**2207**	**2303**	**35**	**512**	**9101**
	44.43	24.25	25.30	0.38	5.63	100

Key

Frequency
Percent
Row Percent
Column Percent

Table A-6. The 7 most parsimonious models (those with model likelihood ≥0.0001) tested with YOY and post-YOY groups.

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
S(..) r(g+effort)	796.8661	0	0.68734	1	4	101.411
S(g.) r(g+effort)	798.604	1.7379	0.28826	0.4194	5	101.142
S(g.) r(.effort)	803.6501	6.784	0.02312	0.0336	4	108.195
S(..) r(g.)	810.6105	13.7444	0.00071	0.001	3	117.16
S(g.) r(g.)	812.6154	15.7493	0.00026	0.0004	4	117.16
S(..) r(.effort)	813.3228	16.4567	0.00018	0.0003	3	119.872
S(g+t) r(g.)	816.1102	19.2441	0.00005	0.0001	22	84.3519

Table A-7. Survival likelihood ratio tests for YOY vs. post-YOY sharks in the GOM. ** indicates that models are nested, but sparseness in data does not allow for calculation of probability.

Effect	Reduced Model	General Model	Chi-sq.	Df	Prob.	Significant
S(g)	S(..) r(..)	S(g.) r(..)	13.127	1	0.0003	†
	S(..) r(.effort)	S(g.) r(.effort)	11.678	1	0.0006	†
	S(..) r(.t)	S(g.) r(.t)	8.418	1	0.0037	†
	S(..) r(g*t)	S(g.) r(g*t)	-22.333	1	**	
	S(..) r(g.)	S(g.) r(g.)	0	1	0.9911	
	S(..) r(g+effort)	S(g.) r(g+effort)	0.268	1	0.6045	
	S(..) r(g+t)	S(g.) r(g+t)	1.837	1	0.1753	
	S(.t) r(..)	S(g+t) r(..)	9.212	1	0.0024	†
	S(.t) r(.effort)	S(g+t) r(.effort)	11.304	1	0.0008	†
	S(.t) r(.t)	S(g+t) r(.t)	19.013	1	<.0001	†
	S(.t) r(g*t)	S(g+t) r(g*t)	-1.71	1	**	
	S(.t) r(g.)	S(g+t) r(g.)	3.754	1	0.0527	
	S(.t) r(g+effort)	S(g+t) r(g+effort)	3.063	1	0.0801	
	S(.t) r(g+t)	S(g+t) r(g+t)	3.901	1	0.0483	†
S(t)	S(..) r(..)	S(.t) r(..)	0.811	18	1	
	S(..) r(.effort)	S(.t) r(.effort)	8.654	18	0.9672	
	S(..) r(.t)	S(.t) r(.t)	40.898	17	0.001	†
	S(..) r(g*t)	S(.t) r(g*t)	9.992	17	0.9039	
	S(..) r(g.)	S(.t) r(g.)	29.054	18	0.0477	†
	S(..) r(g+effort)	S(.t) r(g+effort)	14.345	18	0.7064	
	S(..) r(g+t)	S(.t) r(g+t)	15.879	17	0.5325	
	S(g.) r(..)	S(g+t) r(..)	-3.104	18	**	
	S(g.) r(.effort)	S(g+t) r(.effort)	8.28	18	0.9742	
	S(g.) r(.t)	S(g+t) r(.t)	51.493	17	<.0001	†
	S(g.) r(g*t)	S(g+t) r(g*t)	30.616	17	0.0222	†
	S(g.) r(g.)	S(g+t) r(g.)	32.808	18	0.0176	†
	S(g.) r(g+effort)	S(g+t) r(g+effort)	17.139	18	0.5136	
	S(g.) r(g+t)	S(g+t) r(g+t)	17.943	17	0.3925	
S(g*t)	S(g+t) r(..)	S(g*t) r(..)	14.973	18	0.6638	
	S(g+t) r(.effort)	S(g*t) r(.effort)	15.951	18	0.5959	
	S(g+t) r(.t)	S(g*t) r(.t)	16.265	18	0.574	
	S(g+t) r(g*t)	S(g*t) r(g*t)	11.289	18	0.8817	
	S(g+t) r(g.)	S(g*t) r(g.)	-14.014	18	**	
	S(g+t) r(g+effort)	S(g*t) r(g+effort)	8.443	18	0.9713	
	S(g+t) r(g+t)	S(g*t) r(g+t)	16.395	18	0.565	

Table A-8. Recovery probability likelihood ratio tests for YOY vs. post-YOY sharks in the GOM. ** indicates that models are nested, but sparseness in data does not allow for calculation of probability.

Effect	Reduced Model	General Model	Chi-sq.	Df	Prob.	Significant
r(effort)	S(..) r(..)	S(..) r(.effort)	27.091	1	<.0001	†
	S(..) r(g.)	S(..) r(g+effort)	15.749	1	0.0001	†
	S(.t) r(..)	S(.t) r(.effort)	34.933	1	<.0001	†
	S(.t) r(g.)	S(.t) r(g+effort)	1.04	1	0.3079	
	S(g*t) r(..)	S(g*t) r(.effort)	38.004	1	<.0001	†
	S(g*t) r(g.)	S(g*t) r(g+effort)	22.806	1	<.0001	†
	S(g.) r(..)	S(g.) r(.effort)	25.642	1	<.0001	†
	S(g.) r(g.)	S(g.) r(g+effort)	16.018	1	0.0001	†
	S(g+t) r(..)	S(g+t) r(.effort)	37.026	1	<.0001	†
	S(g+t) r(g.)	S(g+t) r(g+effort)	0.349	1	0.5549	
r(g)	S(..) r(..)	S(..) r(g.)	29.803	1	<.0001	†
	S(..) r(.effort)	S(..) r(g+effort)	18.462	1	<.0001	†
	S(..) r(.t)	S(..) r(g+t)	44.498	1	<.0001	†
	S(.t) r(..)	S(.t) r(g.)	58.046	1	<.0001	†
	S(.t) r(.effort)	S(.t) r(g+effort)	24.152	1	<.0001	†
	S(.t) r(.t)	S(.t) r(g+t)	19.478	1	<.0001	†
	S(g*t) r(..)	S(g*t) r(g.)	23.601	1	<.0001	†
	S(g*t) r(.effort)	S(g*t) r(g+effort)	8.403	1	0.0037	†
	S(g*t) r(.t)	S(g*t) r(g+t)	4.495	1	0.034	†
	S(g.) r(..)	S(g.) r(g.)	16.676	1	<.0001	†
	S(g.) r(.effort)	S(g.) r(g+effort)	7.052	1	0.0079	†
	S(g.) r(.t)	S(g.) r(g+t)	37.916	1	<.0001	†
	S(g+t) r(..)	S(g+t) r(g.)	52.588	1	<.0001	†
	S(g+t) r(.effort)	S(g+t) r(g+effort)	15.911	1	0.0001	†
	S(g+t) r(.t)	S(g+t) r(g+t)	4.366	1	0.0367	†
r(t)	S(..) r(..)	S(..) r(.t)	13.026	18	0.79	
	S(..) r(g.)	S(..) r(g+t)	27.721	18	0.0664	
	S(.t) r(..)	S(.t) r(.t)	53.113	17	<.0001	†
	S(.t) r(g.)	S(.t) r(g+t)	14.545	17	0.6282	
	S(g*t) r(..)	S(g*t) r(.t)	64.207	17	<.0001	†
	S(g*t) r(g.)	S(g*t) r(g+t)	45.101	17	0.0002	†
	S(g.) r(..)	S(g.) r(.t)	8.318	18	0.9735	
	S(g.) r(g.)	S(g.) r(g+t)	29.557	18	0.042	†
	S(g+t) r(..)	S(g+t) r(.t)	62.914	17	<.0001	†
	S(g+t) r(g.)	S(g+t) r(g+t)	14.692	17	0.6177	
r(g*t)	S(..) r(g+t)	S(..) r(g*t)	18.283	18	0.4372	
	S(.t) r(g+t)	S(.t) r(g*t)	12.396	18	0.8261	
	S(g*t) r(g+t)	S(g*t) r(g*t)	1.68	18	1	
	S(g.) r(g+t)	S(g.) r(g*t)	-5.887	18	**	
	S(g+t) r(g+t)	S(g+t) r(g*t)	6.786	18	0.9918	

Table A-9. The 8 most parsimonious models (those with model likelihood ≥0.0001) tested with male and female groups.

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
S(..) *r*(.effort)	240.284	0	0.49438	1	3	55.824
S(g.) *r*(.effort)	242.227	1.9431	0.18712	0.3785	4	55.7599
S(..) *r*(g+effort)	242.252	1.9677	0.18483	0.3739	4	55.7844
S(g.) *r*(g+effort)	244.221	3.9368	0.06905	0.1397	5	55.7446
S(..) *r*(..)	245.644	5.3598	0.0339	0.0686	2	63.1892
S(g.) *r*(..)	247.556	7.2724	0.01303	0.0264	3	63.0964
S(..) *r*(g.)	247.589	7.3047	0.01282	0.0259	3	63.1287
S(g.) *r*(g.)	249.535	9.2509	0.00484	0.0098	4	63.0677

Table A-10. Survival likelihood ratio tests for male vs. female post-YOY sharks in the GOM. ** indicates that models are nested, but sparseness in data does not allow for calculation of probability.

Effect	Reduced Model	General Model	Chi-sq.	Df	Prob.	Significant
$S(g)$	$S(..)\ r(..)$	$S(g.)\ r(..)$	0.093	1	0.7607	
	$S(..)\ r(.effort)$	$S(g.)\ r(.effort)$	0.064	1	0.8	
	$S(..)\ r(.t)$	$S(g.)\ r(.t)$	-11.661	1	**	
	$S(..)\ r(g*t)$	$S(g.)\ r(g*t)$	-14.877	1	**	
	$S(..)\ r(g.)$	$S(g.)\ r(g.)$	0.061	1	0.8049	
	$S(..)\ r(g+effort)$	$S(g.)\ r(g+effort)$	0.04	1	0.8417	
	$S(..)\ r(g+t)$	$S(g.)\ r(g+t)$	-18.222	1	**	
	$S(.t)\ r(..)$	$S(g+t)\ r(..)$	-13.671	1	**	
	$S(.t)\ r(.effort)$	$S(g+t)\ r(.effort)$	0.014	1	0.9044	
	$S(.t)\ r(.t)$	$S(g+t)\ r(.t)$	0.112	1	0.7377	
	$S(.t)\ r(g*t)$	$S(g+t)\ r(g*t)$	1.24	1	0.2655	
	$S(.t)\ r(g.)$	$S(g+t)\ r(g.)$	0.12	1	0.7292	
	$S(.t)\ r(g+effort)$	$S(g+t)\ r(g+effort)$	0.163	1	0.6861	
	$S(.t)\ r(g+t)$	$S(g+t)\ r(g+t)$	0.891	1	0.3452	
$S(t)$	$S(..)\ r(..)$	$S(.t)\ r(..)$	20.555	18	0.3024	
	$S(..)\ r(.effort)$	$S(.t)\ r(.effort)$	8.081	18	0.9774	
	$S(..)\ r(.t)$	$S(.t)\ r(.t)$	14.839	17	0.6071	
	$S(..)\ r(g*t)$	$S(.t)\ r(g*t)$	8.067	17	0.9651	
	$S(..)\ r(g.)$	$S(.t)\ r(g.)$	20.523	18	0.3042	
	$S(..)\ r(g+effort)$	$S(.t)\ r(g+effort)$	13.185	18	0.7805	
	$S(..)\ r(g+t)$	$S(.t)\ r(g+t)$	9.273	17	0.9313	
	$S(g.)\ r(..)$	$S(g+t)\ r(..)$	6.791	18	0.9918	
	$S(g.)\ r(.effort)$	$S(g+t)\ r(.effort)$	8.031	18	0.9782	
	$S(g.)\ r(.t)$	$S(g+t)\ r(.t)$	26.612	17	0.064	
	$S(g.)\ r(g*t)$	$S(g+t)\ r(g*t)$	24.184	17	0.1145	
	$S(g.)\ r(g.)$	$S(g+t)\ r(g.)$	20.582	18	0.301	
	$S(g.)\ r(g+effort)$	$S(g+t)\ r(g+effort)$	13.309	18	0.7729	
	$S(g.)\ r(g+t)$	$S(g+t)\ r(g+t)$	28.387	17	0.0406	†
$S(g*t)$	$S(g+t)\ r(..)$	$S(g*t)\ r(..)$	9.592	18	0.9444	
	$S(g+t)\ r(.effort)$	$S(g*t)\ r(.effort)$	11.39	18	0.8771	
	$S(g+t)\ r(.t)$	$S(g*t)\ r(.t)$	9.508	18	0.9468	
	$S(g+t)\ r(g*t)$	$S(g*t)\ r(g*t)$	2.418	18	1	
	$S(g+t)\ r(g.)$	$S(g*t)\ r(g.)$	-8.322	18	**	
	$S(g+t)\ r(g+effort)$	$S(g*t)\ r(g+effort)$	6.236	18	0.9951	
	$S(g+t)\ r(g+t)$	$S(g*t)\ r(g+t)$	8.28	18	0.9742	

Table A-11. Recovery probability likelihood ratio tests for male vs. female post-YOY sharks in the GOM. ** indicates that models are nested, but sparseness in data does not allow for calculation of probability.

Effect	Reduced Model	General Model	Chi-sq.	Df	Prob.	Significant
r(effort)	*S*(..) *r*(..)	*S*(..) *r*(.effort)	7.365	1	0.0067	†
	S(..) *r*(g.)	*S*(..) *r*(g+effort)	7.344	1	0.0067	†
	S(.t) *r*(..)	*S*(.t) *r*(.effort)	-5.11	1	**	
	S(.t) *r*(g.)	*S*(.t) *r*(g+effort)	0.006	1	0.9366	
	S(g*t) *r*(..)	*S*(g*t) *r*(.effort)	10.373	1	0.0013	†
	S(g*t) *r*(g.)	*S*(g*t) *r*(g+effort)	14.608	1	0.0001	†
	S(g.) *r*(..)	*S*(g.) *r*(.effort)	7.337	1	0.0068	†
	S(g.) *r*(g.)	*S*(g.) *r*(g+effort)	7.323	1	0.0068	†
	S(g+t) *r*(..)	*S*(g+t) *r*(.effort)	8.576	1	0.0034	†
	S(g+t) *r*(g.)	*S*(g+t) *r*(g+effort)	0.05	1	0.8233	
r(g)	*S*(..) *r*(..)	*S*(..) *r*(g.)	0.061	1	0.8057	
	S(..) *r*(.effort)	*S*(..) *r*(g+effort)	0.04	1	0.8423	
	S(..) *r*(.t)	*S*(..) *r*(g+t)	6.062	1	0.0138	†
	S(.t) *r*(..)	*S*(.t) *r*(g.)	0.028	1	0.867	
	S(.t) *r*(.effort)	*S*(.t) *r*(g+effort)	5.144	1	0.0233	†
	S(.t) *r*(.t)	*S*(.t) *r*(g+t)	0.497	1	0.4809	
	S(g*t) *r*(..)	*S*(g*t) *r*(g.)	-4.095	1	**	
	S(g*t) *r*(.effort)	*S*(g*t) *r*(g+effort)	0.14	1	0.7087	
	S(g*t) *r*(.t)	*S*(g*t) *r*(g+t)	0.048	1	0.8263	
	S(g.) *r*(..)	*S*(g.) *r*(g.)	0.029	1	0.8654	
	S(g.) *r*(.effort)	*S*(g.) *r*(g+effort)	0.015	1	0.9016	
	S(g.) *r*(.t)	*S*(g.) *r*(g+t)	-0.499	1	**	
	S(g+t) *r*(..)	*S*(g+t) *r*(g.)	13.819	1	0.0002	†
	S(g+t) *r*(.effort)	*S*(g+t) *r*(g+effort)	5.293	1	0.0214	†
	S(g+t) *r*(.t)	*S*(g+t) *r*(g+t)	1.276	1	0.2587	
r(t)	*S*(..) *r*(..)	*S*(..) *r*(.t)	9.838	18	0.9371	
	S(..) *r*(g.)	*S*(..) *r*(g+t)	15.84	18	0.6037	
	S(.t) *r*(..)	*S*(.t) *r*(.t)	4.122	17	0.9994	
	S(.t) *r*(g.)	*S*(.t) *r*(g+t)	4.59	17	0.9987	
	S(g*t) *r*(..)	*S*(g*t) *r*(.t)	17.821	17	0.4002	
	S(g*t) *r*(g.)	*S*(g*t) *r*(g+t)	21.964	17	0.1861	
	S(g.) *r*(..)	*S*(g.) *r*(.t)	-1.916	18	**	
	S(g.) *r*(g.)	*S*(g.) *r*(g+t)	-2.443	18	**	
	S(g+t) *r*(..)	*S*(g+t) *r*(.t)	17.905	17	0.3949	
	S(g+t) *r*(g.)	*S*(g+t) *r*(g+t)	5.362	17	0.9965	
r(g*t)	*S*(..) *r*(g+t)	*S*(..) *r*(g*t)	10.844	18	0.9008	
	S(.t) *r*(g+t)	*S*(.t) *r*(g*t)	9.638	18	0.9431	
	S(g*t) *r*(g+t)	*S*(g*t) *r*(g*t)	4.124	18	0.9997	
	S(g.) *r*(g+t)	*S*(g.) *r*(g*t)	14.19	18	0.7166	
	S(g+t) *r*(g+t)	*S*(g+t) *r*(g*t)	9.987	18	0.9323	

Table A-12. The 9 most parsimonious models (those with model likelihood ≥0.0001) tested with west and east GOM groups.

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
S(..) *r*(.effort)	305.504	0	0.51722	1	3	69.0311
S(g.) *r*(.effort)	307.502	1.9983	0.19044	0.3682	4	69.023
S(..) *r*(g+effort)	307.505	2.0015	0.19013	0.3676	4	69.0262
S(g.) *r*(g+effort)	309.5	3.9965	0.07012	0.1356	5	69.0133
S(..) *r*(..)	312.438	6.9338	0.01614	0.0312	2	77.9696
S(..) *r*(g.)	314.194	8.6899	0.00671	0.013	3	77.721
S(g.) *r*(..)	314.241	8.7377	0.00655	0.0127	3	77.7688
S(g.) *r*(g.)	316.087	10.5832	0.0026	0.005	4	77.6079
S(.t) *r*(g.)	324.394	18.8901	0.00004	0.0001	21	51.5613

Table A-13. Survival likelihood ratio tests for post-YOY sharks in the west GOM vs. those in the east GOM. ** indicates that models are nested, but sparseness in data does not allow for calculation of probability.

Effect	Reduced Model	General Model	Chi-sq.	Df	Prob.	Significant
$S(g)$	$S(..) \, r(..)$	$S(g.) \, r(..)$	0.201	1	0.654	
	$S(..) \, r(.effort)$	$S(g.) \, r(.effort)$	0.008	1	0.9284	
	$S(..) \, r(.t)$	$S(g.) \, r(.t)$	-5.329	1	**	
	$S(..) \, r(g*t)$	$S(g.) \, r(g*t)$	-17.64	1	**	
	$S(..) \, r(g.)$	$S(g.) \, r(g.)$	0.113	1	0.7366	
	$S(..) \, r(g+effort)$	$S(g.) \, r(g+effort)$	0.013	1	0.9095	
	$S(..) \, r(g+t)$	$S(g.) \, r(g+t)$	0.066	1	0.798	
	$S(.t) \, r(..)$	$S(g+t) \, r(..)$	0.642	1	0.4231	
	$S(.t) \, r(.effort)$	$S(g+t) \, r(.effort)$	0.062	1	0.803	
	$S(.t) \, r(.t)$	$S(g+t) \, r(.t)$	1.092	1	0.296	
	$S(.t) \, r(g*t)$	$S(g+t) \, r(g*t)$	-0.154	1	**	
	$S(.t) \, r(g.)$	$S(g+t) \, r(g.)$	0.198	1	0.6564	
	$S(.t) \, r(g+effort)$	$S(g+t) \, r(g+effort)$	0.382	1	0.5366	
	$S(.t) \, r(g+t)$	$S(g+t) \, r(g+t)$	3.622	1	0.057	
$S(t)$	$S(..) \, r(..)$	$S(.t) \, r(..)$	10.194	18	0.9254	
	$S(..) \, r(.effort)$	$S(.t) \, r(.effort)$	11.134	18	0.8886	
	$S(..) \, r(.t)$	$S(.t) \, r(.t)$	29.564	17	0.0297	†
	$S(..) \, r(g*t)$	$S(.t) \, r(g*t)$	11.397	17	0.8352	
	$S(..) \, r(g.)$	$S(.t) \, r(g.)$	26.16	18	0.0962	
	$S(..) \, r(g+effort)$	$S(.t) \, r(g+effort)$	17.478	18	0.4905	
	$S(..) \, r(g+t)$	$S(.t) \, r(g+t)$	11.608	17	0.8233	
	$S(g.) \, r(..)$	$S(g+t) \, r(..)$	10.634	18	0.9092	
	$S(g.) \, r(.effort)$	$S(g+t) \, r(.effort)$	11.188	18	0.8862	
	$S(g.) \, r(.t)$	$S(g+t) \, r(.t)$	35.985	17	0.0046	†
	$S(g.) \, r(g*t)$	$S(g+t) \, r(g*t)$	28.883	17	0.0356	†
	$S(g.) \, r(g.)$	$S(g+t) \, r(g.)$	26.245	18	0.0943	
	$S(g.) \, r(g+effort)$	$S(g+t) \, r(g+effort)$	17.847	18	0.4657	
	$S(g.) \, r(g+t)$	$S(g+t) \, r(g+t)$	15.165	17	0.5836	
$S(g*t)$	$S(g+t) \, r(..)$	$S(g*t) \, r(..)$	8.04	18	0.978	
	$S(g+t) \, r(.effort)$	$S(g*t) \, r(.effort)$	8.838	18	0.9634	
	$S(g+t) \, r(.t)$	$S(g*t) \, r(.t)$	8.871	18	0.9627	
	$S(g+t) \, r(g*t)$	$S(g*t) \, r(g*t)$	4.968	18	0.9989	
	$S(g+t) \, r(g.)$	$S(g*t) \, r(g.)$	-4.874	18	**	
	$S(g+t) \, r(g+effort)$	$S(g*t) \, r(g+effort)$	2.04	18	1	
	$S(g+t) \, r(g+t)$	$S(g*t) \, r(g+t)$	7.051	18	0.9897	

Table A-14. Recovery probability likelihood ratio tests for post-YOY sharks in the west GOM vs. those in the east GOM. ** indicates that models are nested, but sparseness in data does not allow for calculation of probability.

Effect	Reduced Model	General Model	Chi-sq.	Df	Prob.	Significant
r(effort)	S(..) r(..)	S(..) r(.effort)	8.939	1	0.0028	†
	S(..) r(g.)	S(..) r(g+effort)	8.695	1	0.0032	†
	S(.t) r(..)	S(.t) r(.effort)	9.878	1	0.0017	†
	S(.t) r(g.)	S(.t) r(g+effort)	0.013	1	0.9077	
	S(g*t) r(..)	S(g*t) r(.effort)	10.097	1	0.0015	†
	S(g*t) r(g.)	S(g*t) r(g+effort)	7.112	1	0.0077	†
	S(g.) r(..)	S(g.) r(.effort)	8.746	1	0.0031	†
	S(g.) r(g.)	S(g.) r(g+effort)	8.595	1	0.0034	†
	S(g+t) r(..)	S(g+t) r(.effort)	9.299	1	0.0023	†
	S(g+t) r(g.)	S(g+t) r(g+effort)	0.197	1	0.6568	
r(g)	S(..) r(..)	S(..) r(g.)	0.249	1	0.618	
	S(..) r(.effort)	S(..) r(g+effort)	0.005	1	0.9445	
	S(..) r(.t)	S(..) r(g+t)	18.337	1	<.0001	†
	S(.t) r(..)	S(.t) r(g.)	16.215	1	0.0001	†
	S(.t) r(.effort)	S(.t) r(g+effort)	6.35	1	0.0117	†
	S(.t) r(.t)	S(.t) r(g+t)	0.382	1	0.5366	
	S(g*t) r(..)	S(g*t) r(g.)	2.857	1	0.091	
	S(g*t) r(.effort)	S(g*t) r(g+effort)	-0.129	1	**	
	S(g*t) r(.t)	S(g*t) r(g+t)	1.092	1	0.2959	
	S(g.) r(..)	S(g.) r(g.)	0.161	1	0.6883	
	S(g.) r(.effort)	S(g.) r(g+effort)	0.01	1	0.9215	
	S(g.) r(.t)	S(g.) r(g+t)	23.732	1	<.0001	†
	S(g+t) r(..)	S(g+t) r(g.)	15.771	1	0.0001	†
	S(g+t) r(.effort)	S(g+t) r(g+effort)	6.669	1	0.0098	†
	S(g+t) r(.t)	S(g+t) r(g+t)	2.912	1	0.0879	
r(t)	S(..) r(..)	S(..) r(.t)	1.652	18	1	
	S(..) r(g.)	S(..) r(g+t)	19.74	18	0.3476	
	S(.t) r(..)	S(.t) r(.t)	21.022	17	0.2253	
	S(.t) r(g.)	S(.t) r(g+t)	5.189	17	0.9972	
	S(g*t) r(..)	S(g*t) r(.t)	22.303	17	0.1734	
	S(g*t) r(g.)	S(g*t) r(g+t)	20.538	17	0.2476	
	S(g.) r(..)	S(g.) r(.t)	-3.878	18	**	
	S(g.) r(g.)	S(g.) r(g+t)	19.693	18	0.3504	
	S(g+t) r(..)	S(g+t) r(.t)	21.472	17	0.2059	
	S(g+t) r(g.)	S(g+t) r(g+t)	8.613	17	0.9516	
r(g*t)	S(..) r(g+t)	S(..) r(g*t)	12.766	18	0.8053	
	S(.t) r(g+t)	S(.t) r(g*t)	12.555	18	0.8173	
	S(g*t) r(g+t)	S(g*t) r(g*t)	6.695	18	0.9925	
	S(g.) r(g+t)	S(g.) r(g*t)	-4.94	18	**	
	S(g+t) r(g+t)	S(g+t) r(g*t)	8.779	18	0.9646	

Table A-15. The 11 most parsimonious models (those with model likelihood ≥0.0001) tested with Atlantic and GOM groups.

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
S(..) *r*(g+effort)	735.205	0	0.59659	1	4	132.894
S(g.) *r*(g+effort)	736.061	0.8556	0.38894	0.6519	5	131.744
S(..) *r*(..)	745.224	10.0192	0.00398	0.0067	2	146.921
S(g.) *r*(..)	745.866	10.6608	0.00289	0.0048	3	145.559
S(.t) *r*(g+effort)	746.84	11.6348	0.00178	0.003	22	108.271
S(g+t) *r*(g+effort)	747.196	11.9911	0.00149	0.0025	23	106.602
S(..) *r*(g.)	747.221	12.0163	0.00147	0.0025	3	146.915
S(g.) *r*(g.)	747.808	12.6029	0.00109	0.0018	4	145.497
S(.t) *r*(g.)	747.986	12.7807	0.001	0.0017	21	111.44
S(g+t) *r*(g.)	749.745	14.5396	0.00042	0.0007	22	111.175
S(..) *r*(g+t)	750.071	14.8654	0.00035	0.0006	21	113.525

Table A-16. Survival likelihood ratio tests for post-YOY sharks in the Atlantic vs. those in the GOM. ** indicates that models are nested, but sparseness in data does not allow for calculation of probability.

Effect	Reduced Model	General Model	Chi-sq.	Df	Prob.	Significant
S(g)	S(..) r(..)	S(g.) r(..)	1.361	1	0.2433	
	S(..) r(.t)	S(g.) r(.t)	1.384	1	0.2395	
	S(..) r(g*t)	S(g.) r(g*t)	-2.946	1	**	
	S(..) r(g.)	S(g.) r(g.)	1.418	1	0.2338	
	S(..) r(g+effort)	S(g.) r(g+effort)	1.15	1	0.2836	
	S(..) r(g+t)	S(g.) r(g+t)	-51.305	1	**	
	S(.t) r(..)	S(g+t) r(..)	2.813	1	0.0935	
	S(.t) r(.t)	S(g+t) r(.t)	1.008	1	0.3155	
	S(.t) r(g*t)	S(g+t) r(g*t)	1.771	1	0.1833	
	S(.t) r(g.)	S(g+t) r(g.)	0.265	1	0.607	
	S(.t) r(g+effort)	S(g+t) r(g+effort)	1.668	1	0.1965	
	S(.t) r(g+t)	S(g+t) r(g+t)	2.602	1	0.1068	
S(t)	S(..) r(..)	S(.t) r(..)	4.061	18	0.9997	
	S(..) r(.t)	S(.t) r(.t)	51.14	17	<.0001	†
	S(..) r(g*t)	S(.t) r(g*t)	42.795	17	0.0005	†
	S(..) r(g.)	S(.t) r(g.)	35.475	18	0.0082	†
	S(..) r(g+effort)	S(.t) r(g+effort)	24.624	18	0.1356	
	S(..) r(g+t)	S(.t) r(g+t)	10.654	17	0.874	
	S(g.) r(..)	S(g+t) r(..)	5.513	18	0.9978	
	S(g.) r(.t)	S(g+t) r(.t)	50.764	17	<.0001	†
	S(g.) r(g*t)	S(g+t) r(g*t)	47.512	17	0.0001	†
	S(g.) r(g.)	S(g+t) r(g.)	34.322	18	0.0115	†
	S(g.) r(g+effort)	S(g+t) r(g+effort)	25.142	18	0.1211	
	S(g.) r(g+t)	S(g+t) r(g+t)	64.561	17	<.0001	†
S(g*t)	S(g+t) r(..)	S(g*t) r(..)	44.88	18	0.0004	†
	S(g+t) r(.t)	S(g*t) r(.t)	23.498	18	0.1722	
	S(g+t) r(g*t)	S(g*t) r(g*t)	14.511	18	0.6952	
	S(g+t) r(g.)	S(g*t) r(g.)	-9.751	18	**	
	S(g+t) r(g+effort)	S(g*t) r(g+effort)	16.71	18	0.5432	
	S(g+t) r(g+t)	S(g*t) r(g+t)	23.483	18	0.1727	

Table A-17. Recovery probability likelihood ratio tests for post-YOY sharks in the Atlantic vs. those in the GOM. ** indicates that models are nested, but sparseness in data does not allow for calculation of probability.

Effect	Reduced Model	General Model	Chi-sq.	Df	Prob.	Significant
r(effort)	S(..) r(g.)	S(..) r(g+effort)	14.02	1	0.0002	†
	S(.t) r(g.)	S(.t) r(g+effort)	3.169	1	0.075	
	S(g*t) r(g.)	S(g*t) r(g+effort)	31.034	1	<.0001	†
	S(g.) r(g.)	S(g.) r(g+effort)	13.753	1	0.0002	†
	S(g+t) r(g.)	S(g+t) r(g+effort)	4.573	1	0.0325	†
r(g)	S(..) r(..)	S(..) r(g.)	0.006	1	0.9379	
	S(..) r(.t)	S(..) r(g+t)	39.88	1	<.0001	†
	S(.t) r(..)	S(.t) r(g.)	31.419	1	<.0001	†
	S(.t) r(.t)	S(.t) r(g+t)	-0.606	1	**	
	S(g*t) r(..)	S(g*t) r(g.)	-25.761	1	**	
	S(g*t) r(.t)	S(g*t) r(g+t)	0.974	1	0.3238	
	S(g.) r(..)	S(g.) r(g.)	0.062	1	0.8031	
	S(g.) r(.t)	S(g.) r(g+t)	-12.809	1	**	
	S(g+t) r(..)	S(g+t) r(g.)	28.871	1	<.0001	†
	S(g+t) r(.t)	S(g+t) r(g+t)	0.988	1	0.3202	
r(t)	S(..) r(..)	S(..) r(.t)	-6.484	18	**	
	S(..) r(g.)	S(..) r(g+t)	33.39	18	0.015	†
	S(.t) r(..)	S(.t) r(.t)	40.595	17	0.0011	†
	S(.t) r(g.)	S(.t) r(g+t)	8.569	17	0.9528	
	S(g*t) r(..)	S(g*t) r(.t)	17.407	17	0.4272	
	S(g*t) r(g.)	S(g*t) r(g+t)	44.141	17	0.0003	†
	S(g.) r(..)	S(g.) r(.t)	-6.462	18	**	
	S(g.) r(g.)	S(g.) r(g+t)	-19.333	18	**	
	S(g+t) r(..)	S(g+t) r(.t)	38.789	17	0.0019	†
	S(g+t) r(g.)	S(g+t) r(g+t)	10.906	17	0.8614	
r(g*t)	S(..) r(g+t)	S(..) r(g*t)	-14.438	18	**	
	S(.t) r(g+t)	S(.t) r(g*t)	17.702	18	0.4754	
	S(g*t) r(g+t)	S(g*t) r(g*t)	7.9	18	0.9801	
	S(g.) r(g+t)	S(g.) r(g*t)	33.92	18	0.0129	†
	S(g+t) r(g+t)	S(g+t) r(g*t)	16.872	18	0.5319	
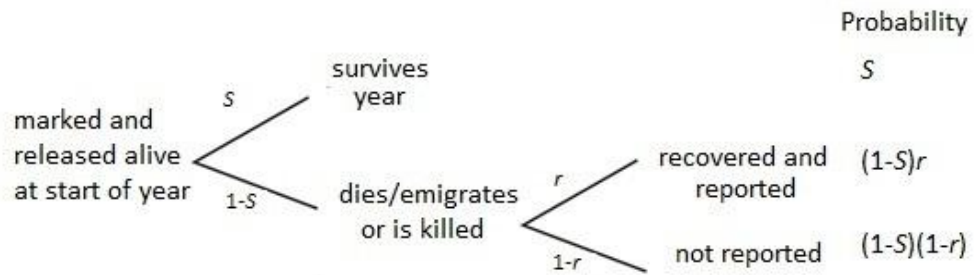
Figure A-1. Possible encounter histories and associated probabilities for the reduced (Seber) parameterization (adapted from Cooch and White 2004).

$$n= \begin{bmatrix} n_{11} & n_{12} & \cdots & n_{1J} \\ & n_{22} & \cdots & n_{2J} \\ & & \ddots & \vdots \\ & & & n_{IJ} \end{bmatrix}$$

Figure A-2. Recovery matrix format.
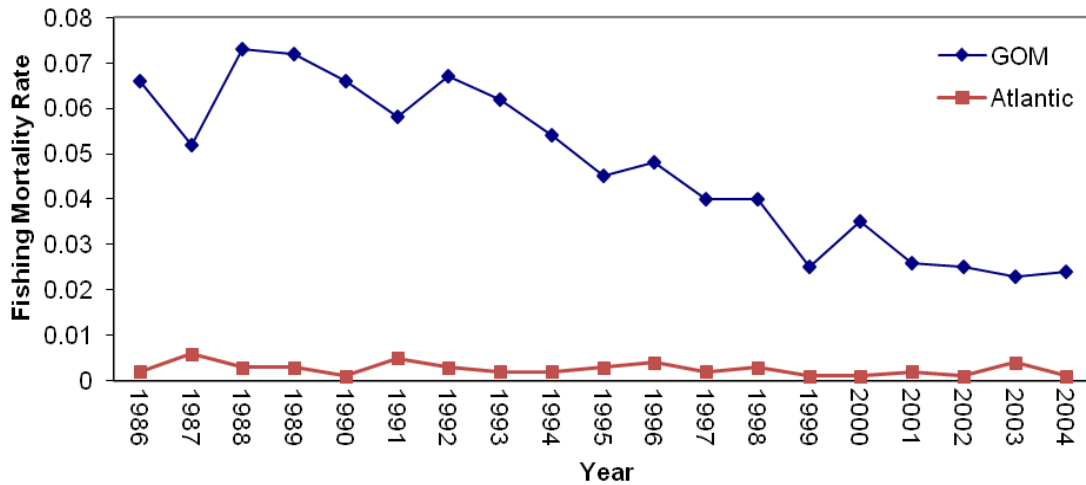
Figure A-3. Fishing mortality rate of blacktip sharks in the Gulf of Mexico and Atlantic from 1986 through 2004 (NOAA/NMFS 2006).
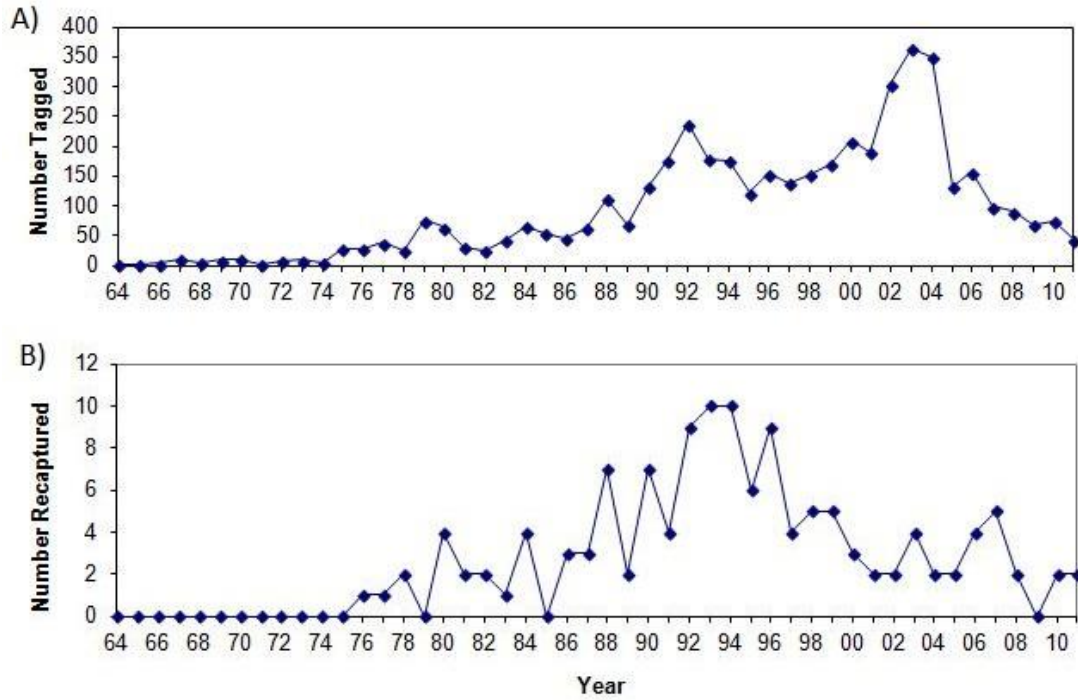
Figure A-4. Distribution of blacktip sharks tagged (a) and recaptured (b) in the Gulf of Mexico from 1964 through 2011.
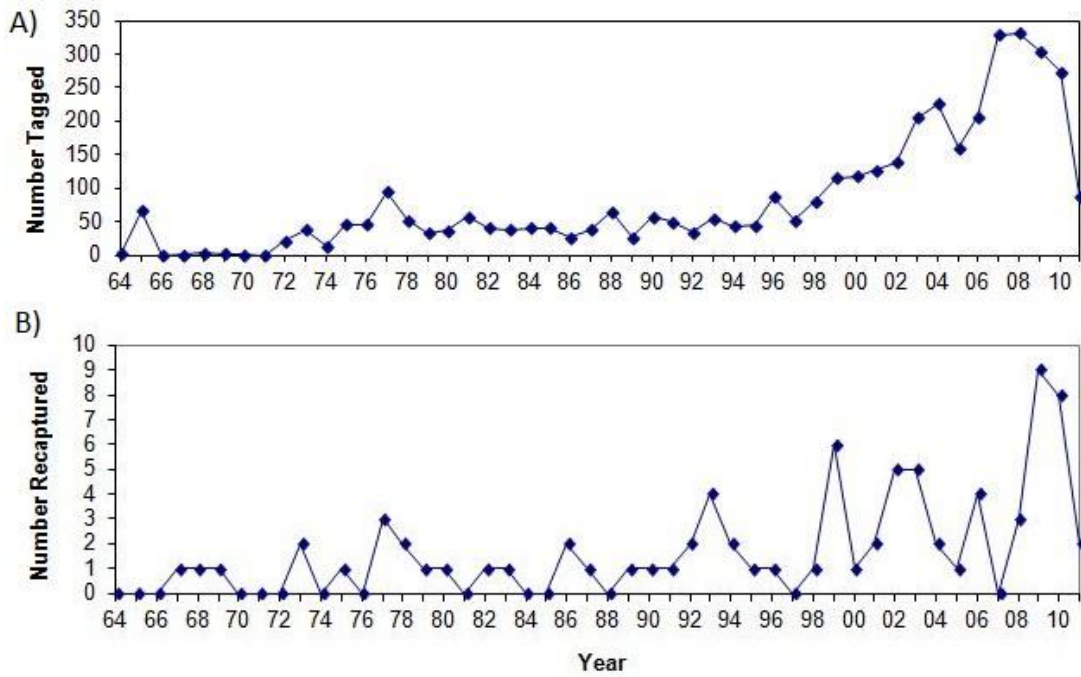
Figure A-5. Distribution of blacktip sharks tagged (a) and recaptured (b) in the U.S. Atlantic waters from 1964 through 2011.

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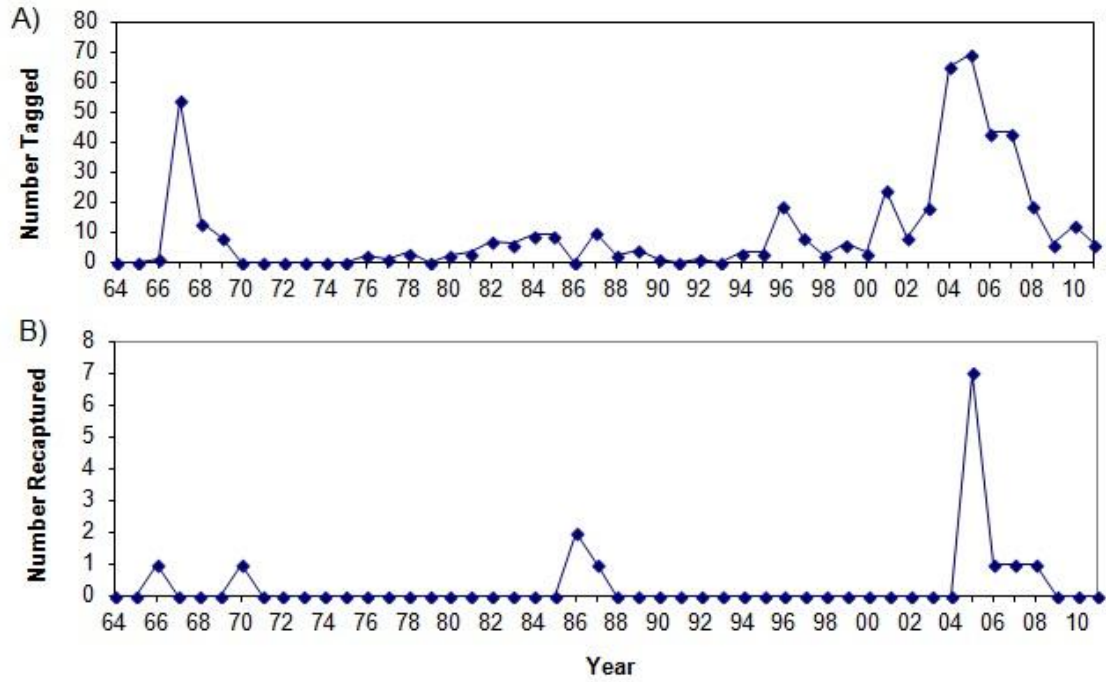
Figure A-6. Distribution of blacktip sharks tagged (a) and recaptured (b) in
International Atlantic waters from 1964 through 2011.
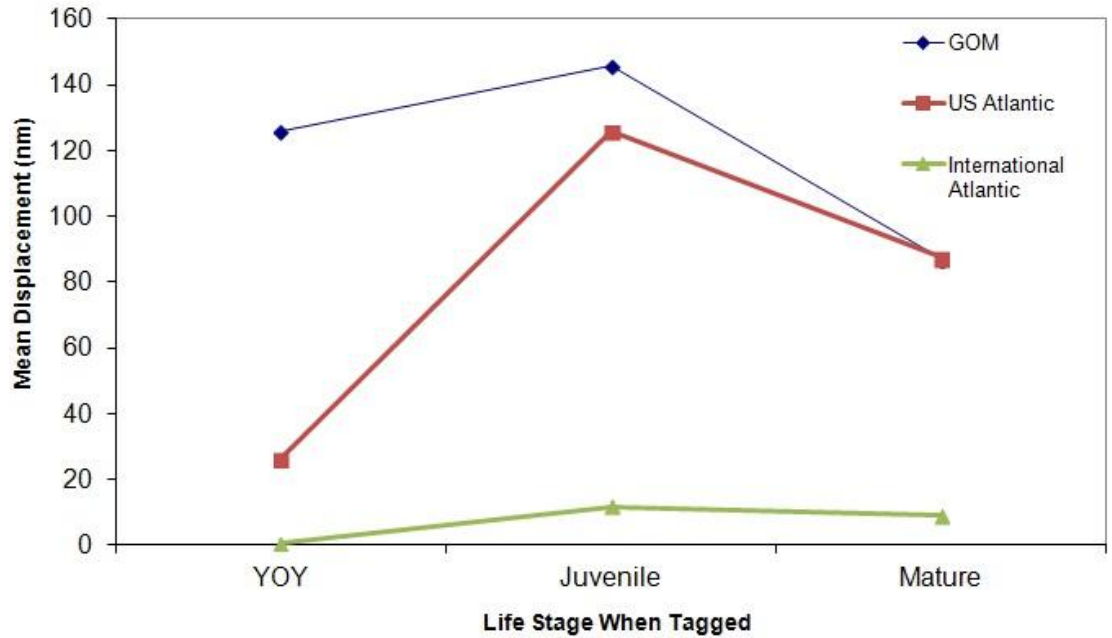
Figure A-7. Mean displacement of blacktip sharks at large for less than 1 year. N= 53, 43, and 12, for YOY, juveniles, and mature sharks, respectively, in the GOM. N= 16, 18, and 16 for YOY, juveniles, and mature sharks in the U.S. Atlantic. N=5,4, and 1 for YOY, juveniles, and mature sharks, respectively, in the International Atlantic.
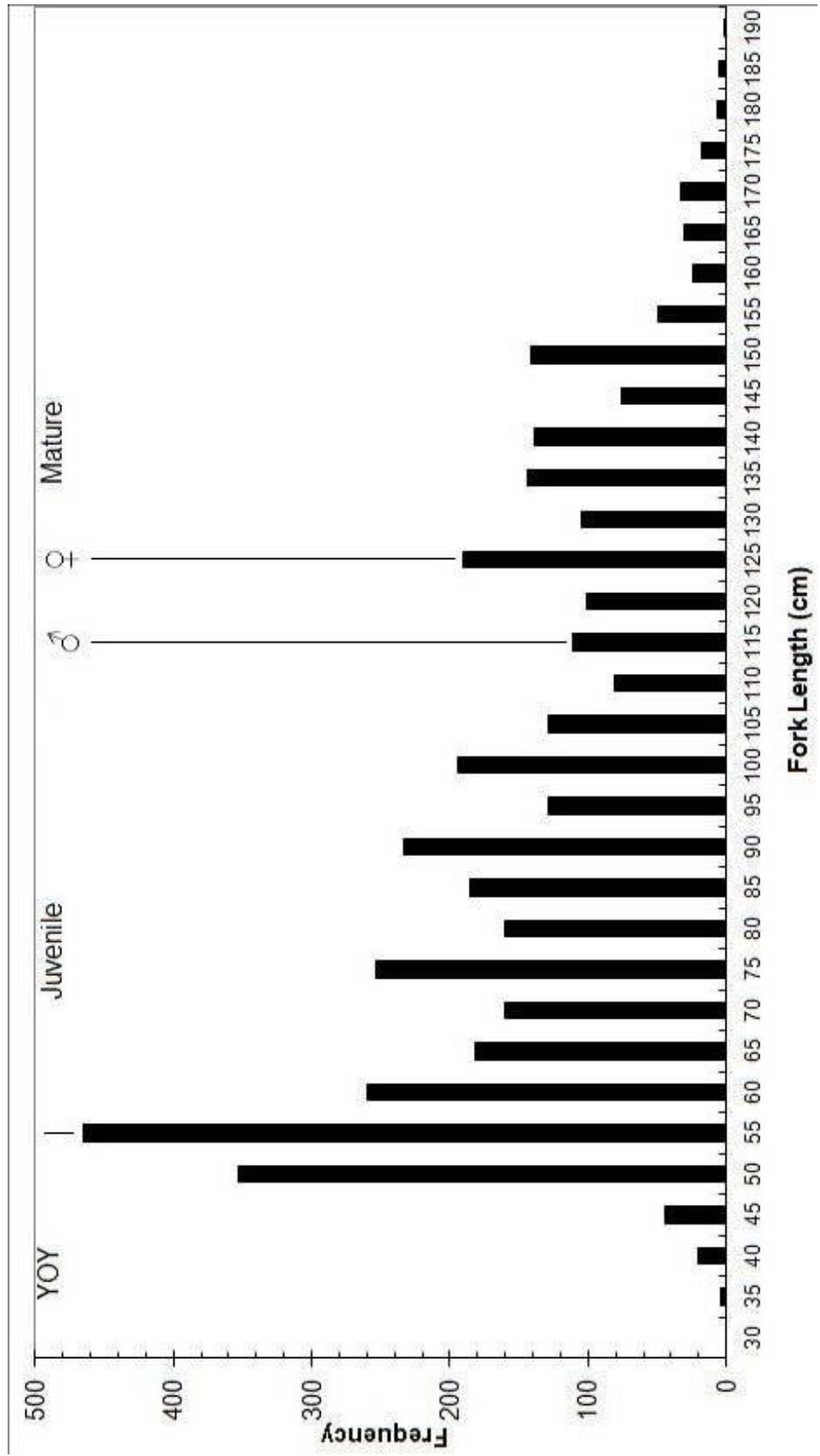
Figure A-8. Length frequency for blacktip shark captures in the U.S. Atlantic Ocean.
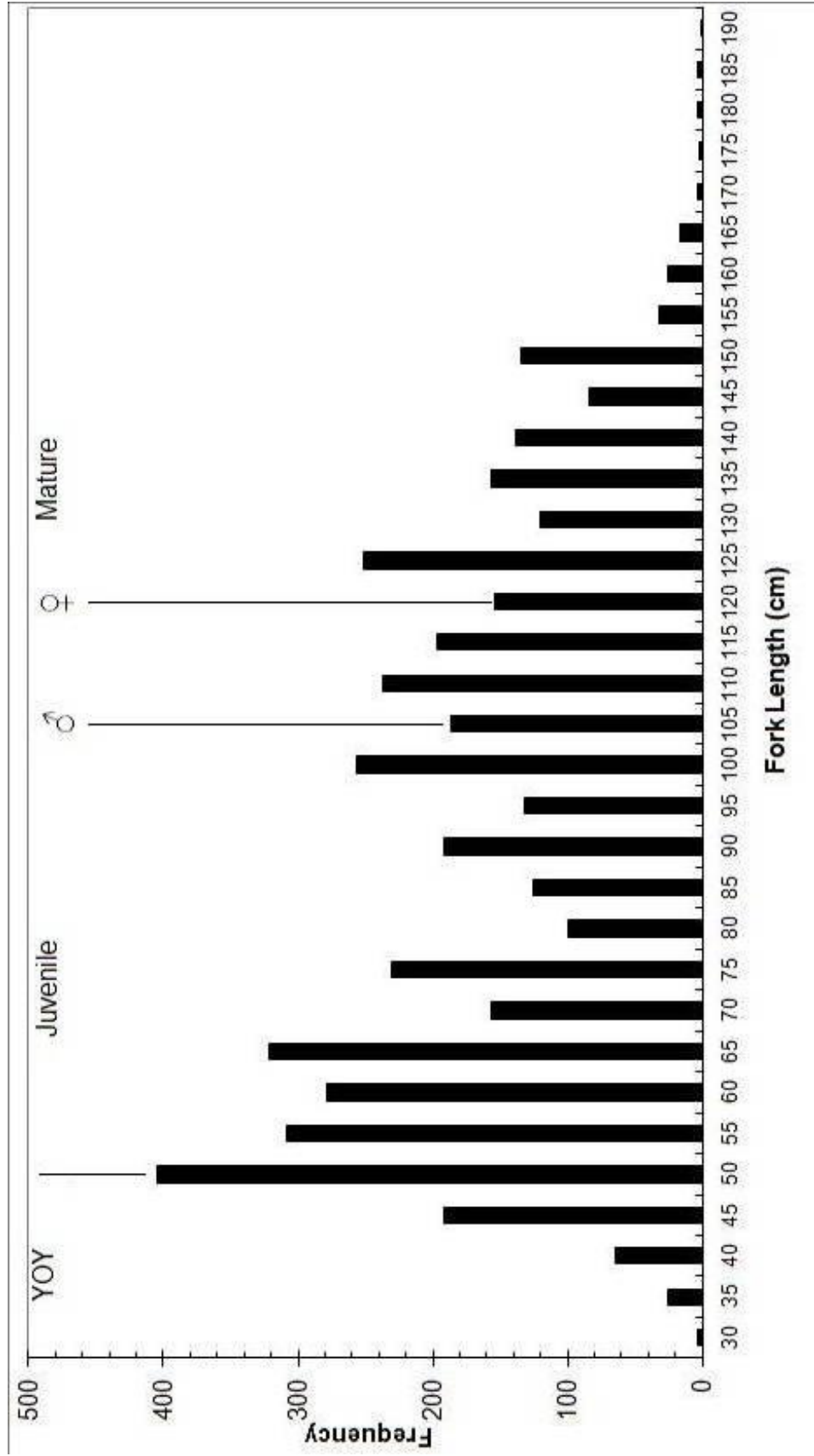
Figure A-9. Length frequency for blacktip shark captures in the Gulf of Mexico.
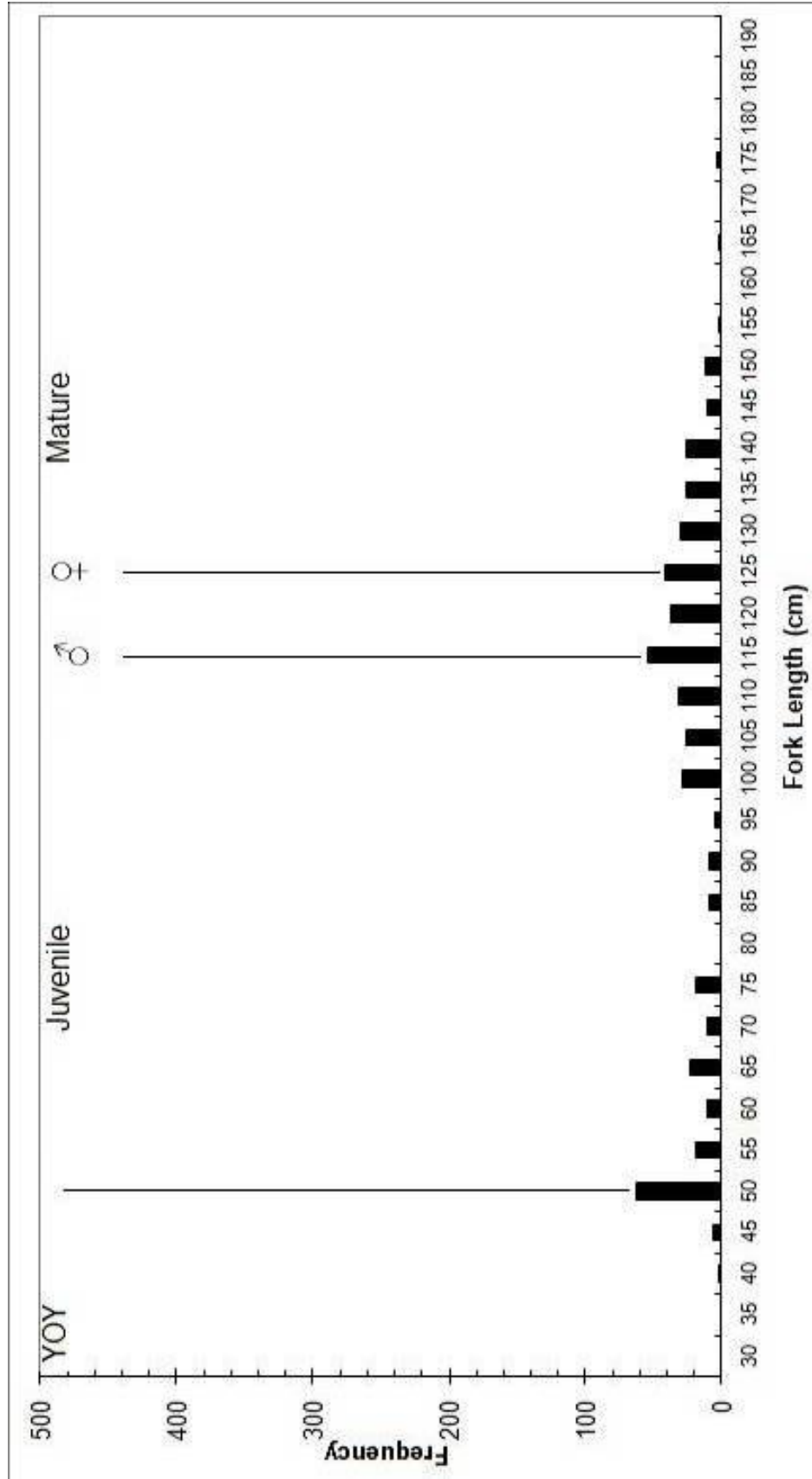
Figure A-10. Length frequency for blacktip shark captures in the International Atlantic Ocean.

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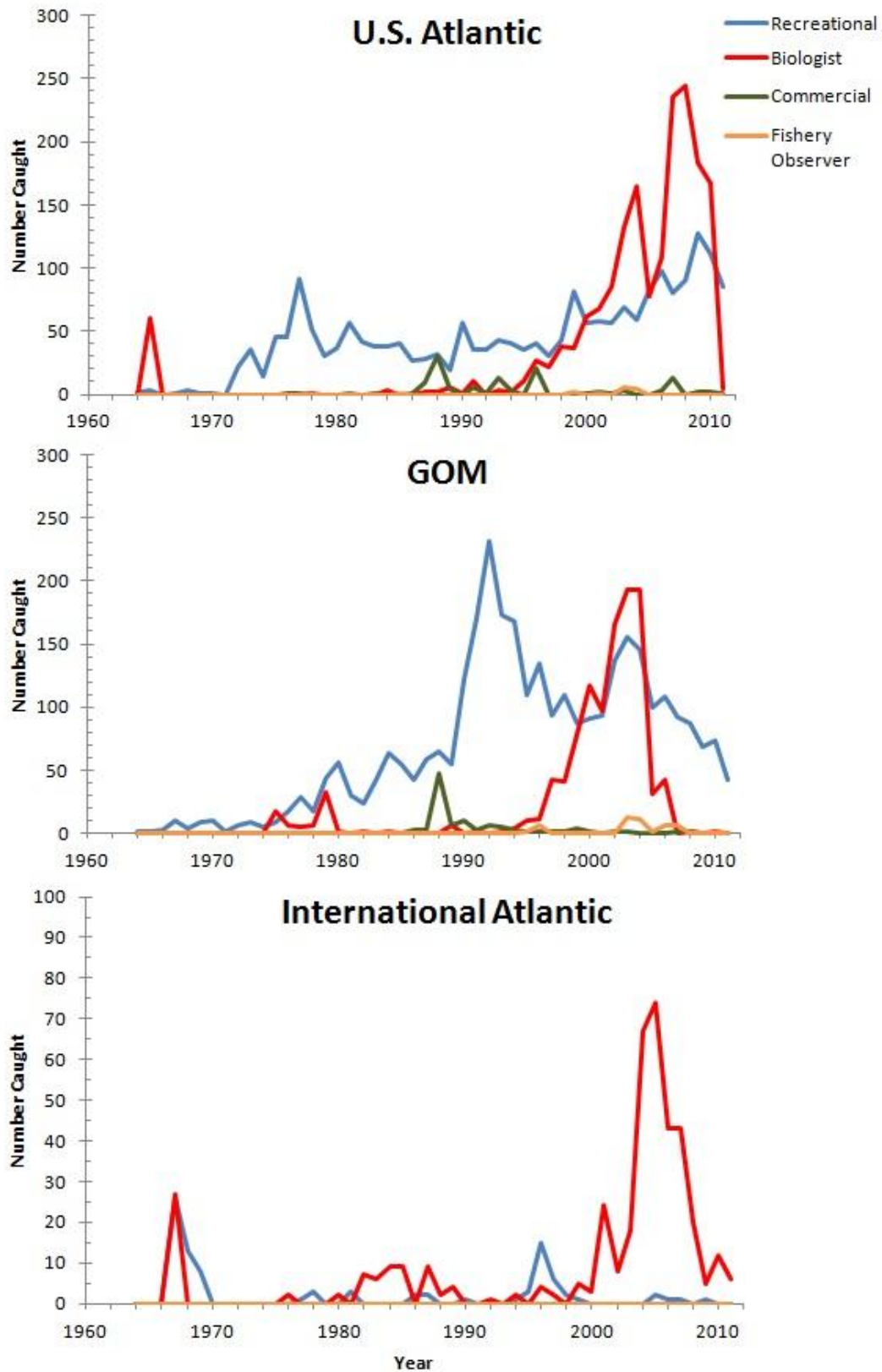
Figure A-11. Blacktip shark captures in the CSTP by industry.
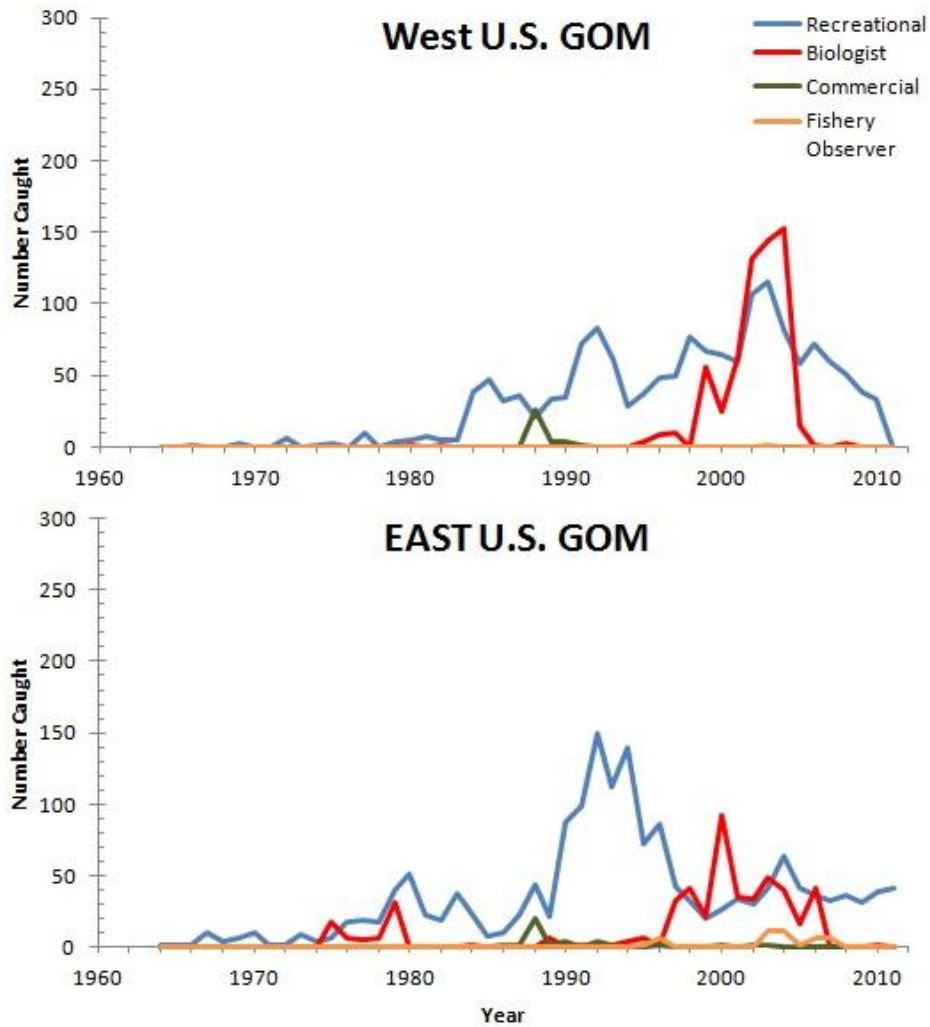
Figure A-12. Blacktip shark captures in the CSTP by industry in the west and east U.S. GOM.
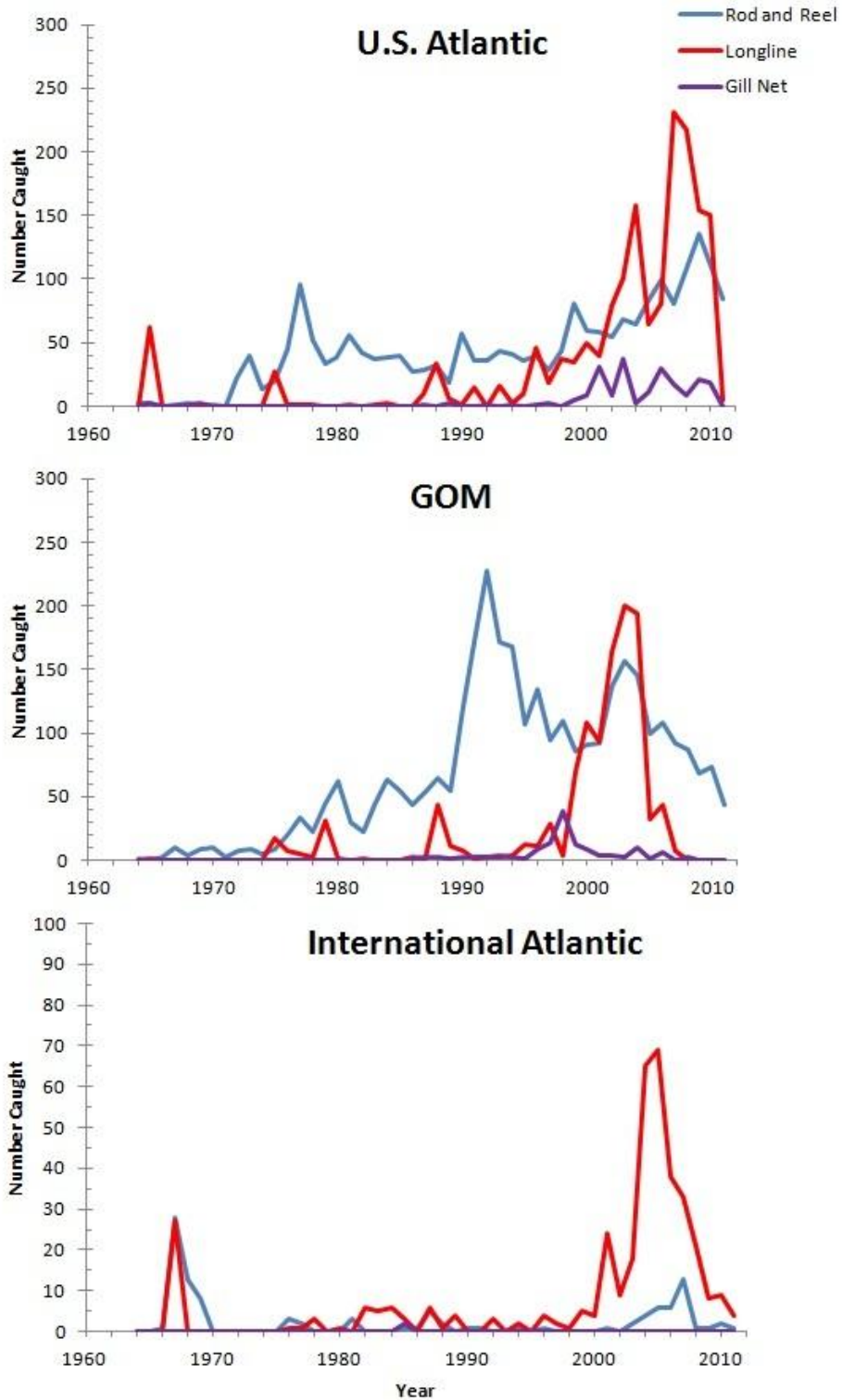
Figure A-13. Blacktip shark captures in the CSTP by gear.
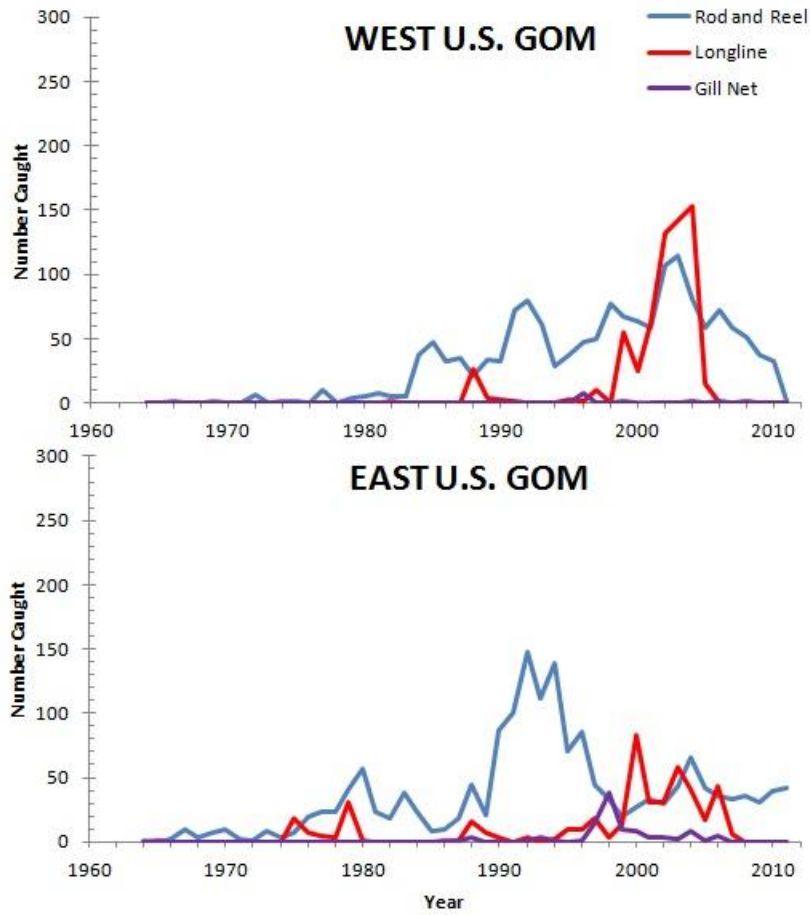
Figure A-14. Blacktip shark captures in the CSTP by gear in the west and east U.S. GOM.
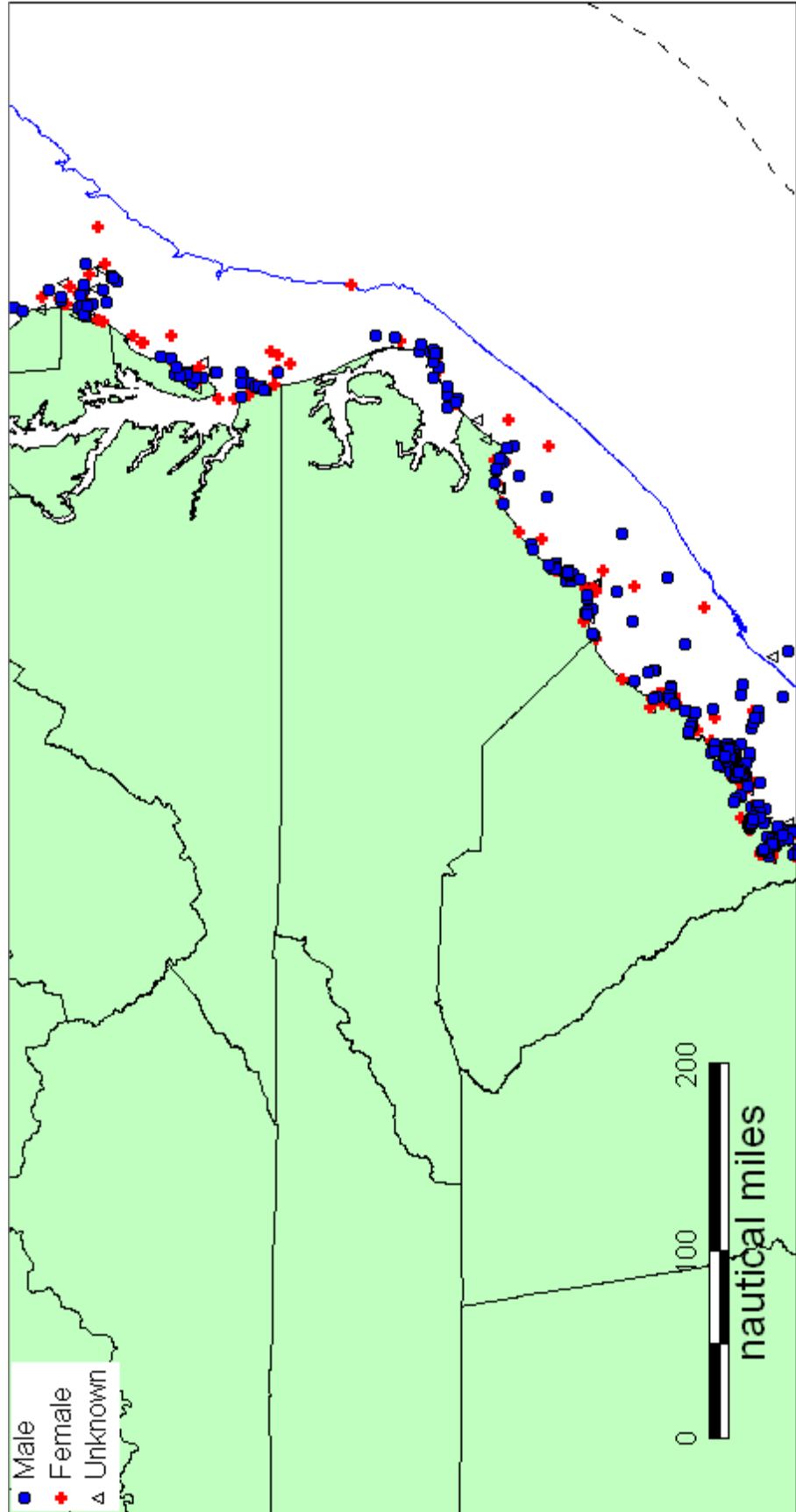
Figure A-15. Blacktip shark captures by sex off the north U.S. Atlantic coast. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
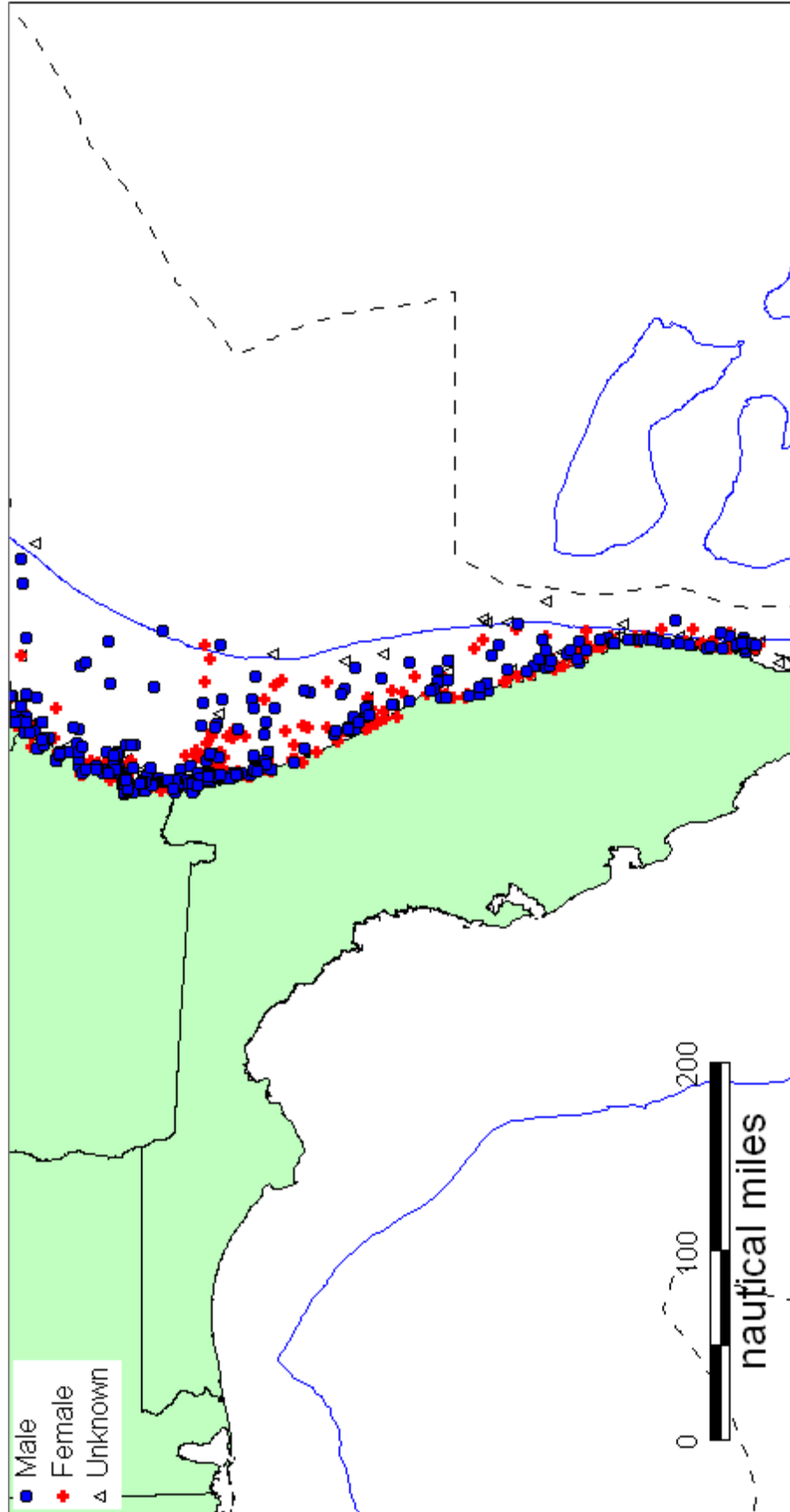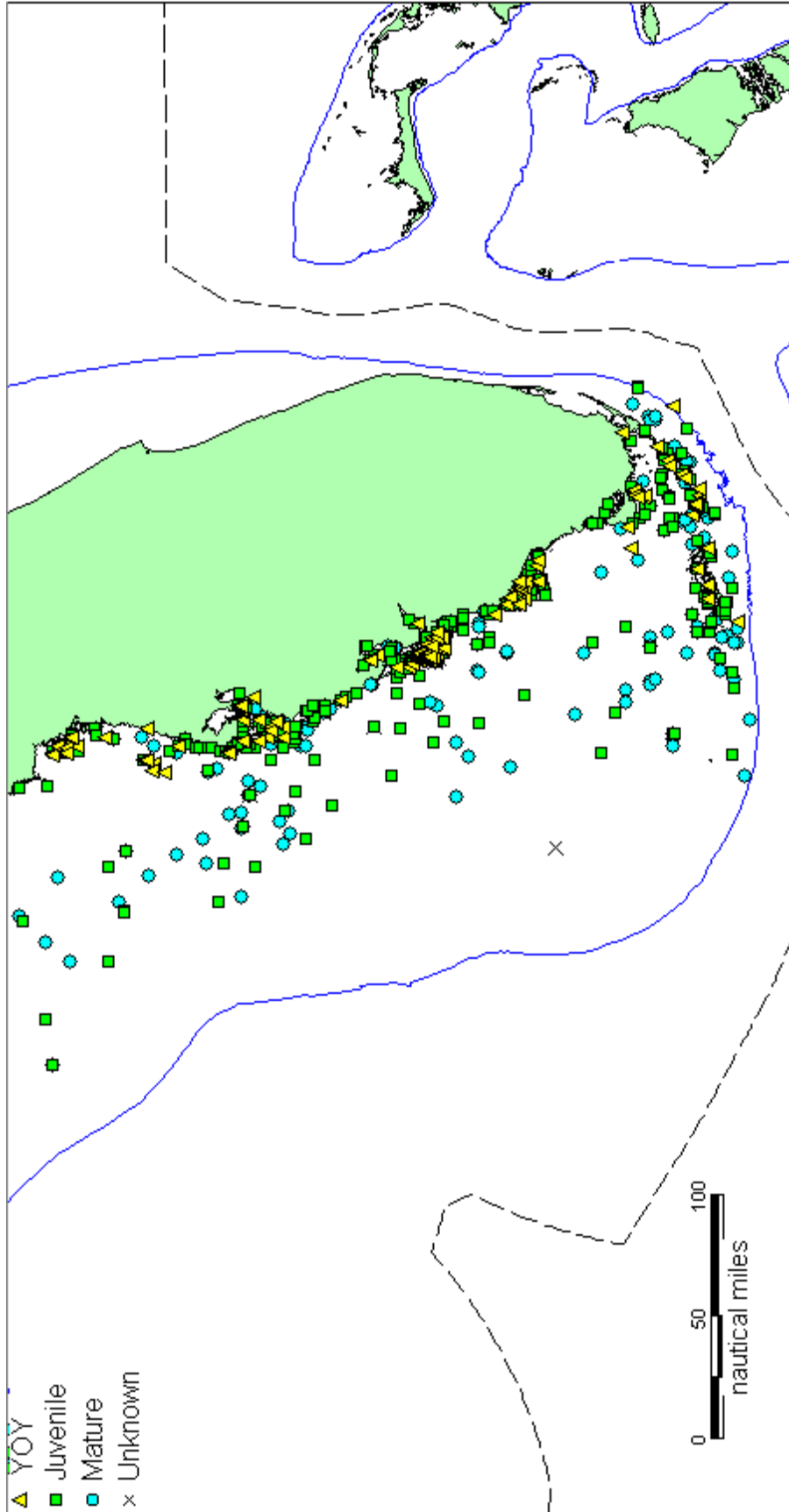
Figure A-16. Blacktip shark captures by sex off the south U.S. Atlantic coast. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ

Male
Female
Unknown

0   100   200
nautical miles
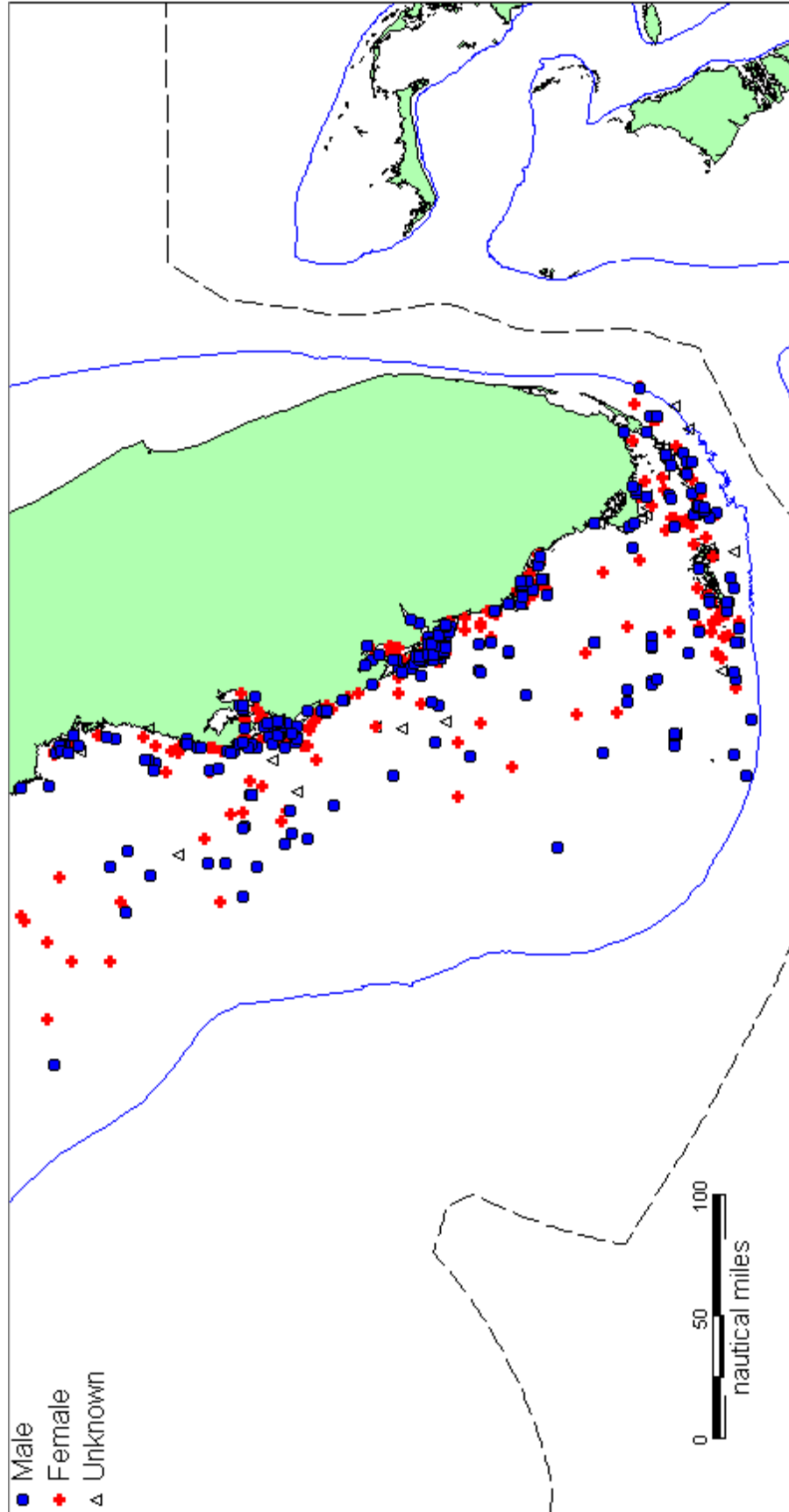
Figure A-17. Blacktip shark captures by sex off the west coast of Florida. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
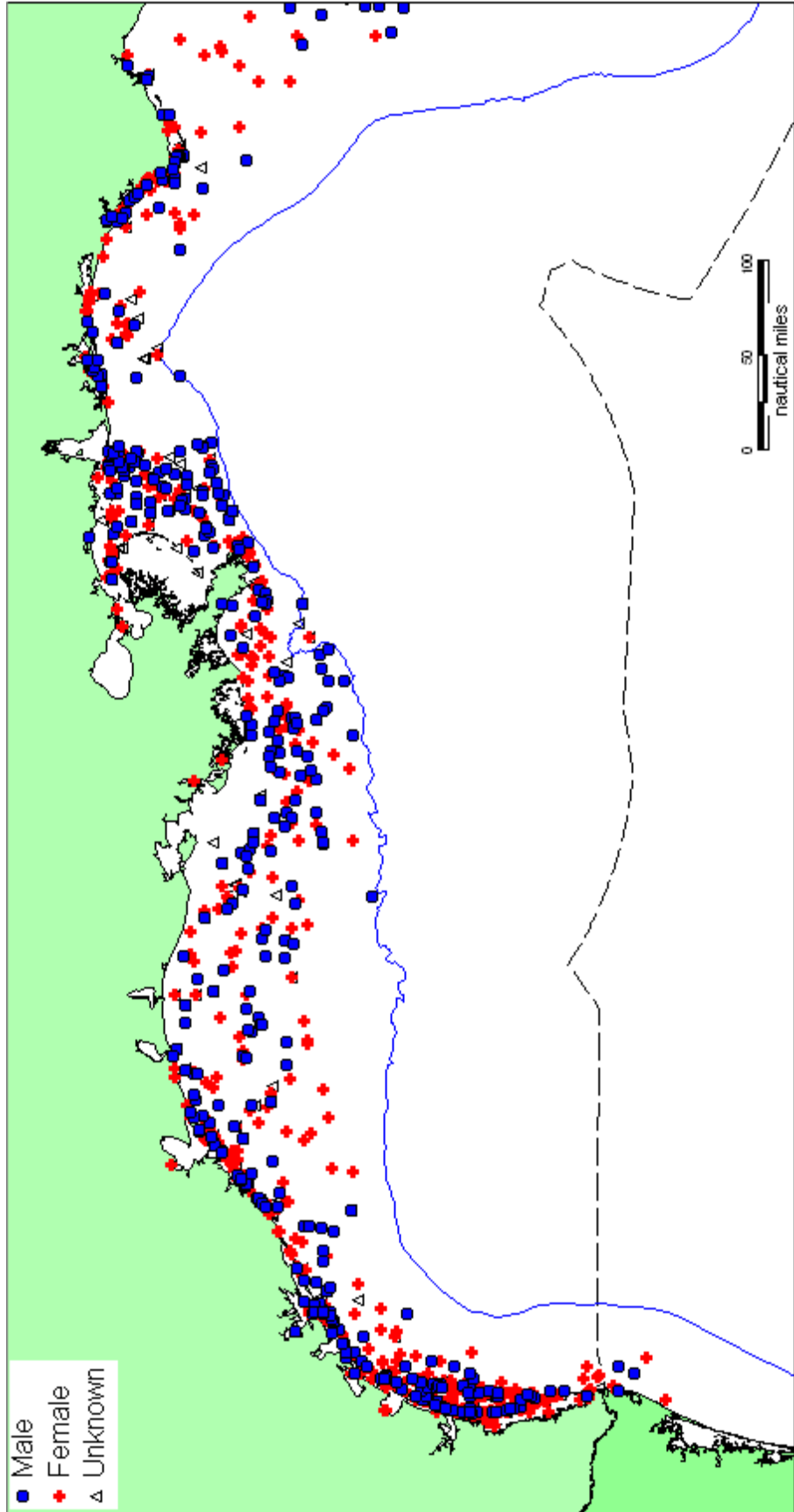
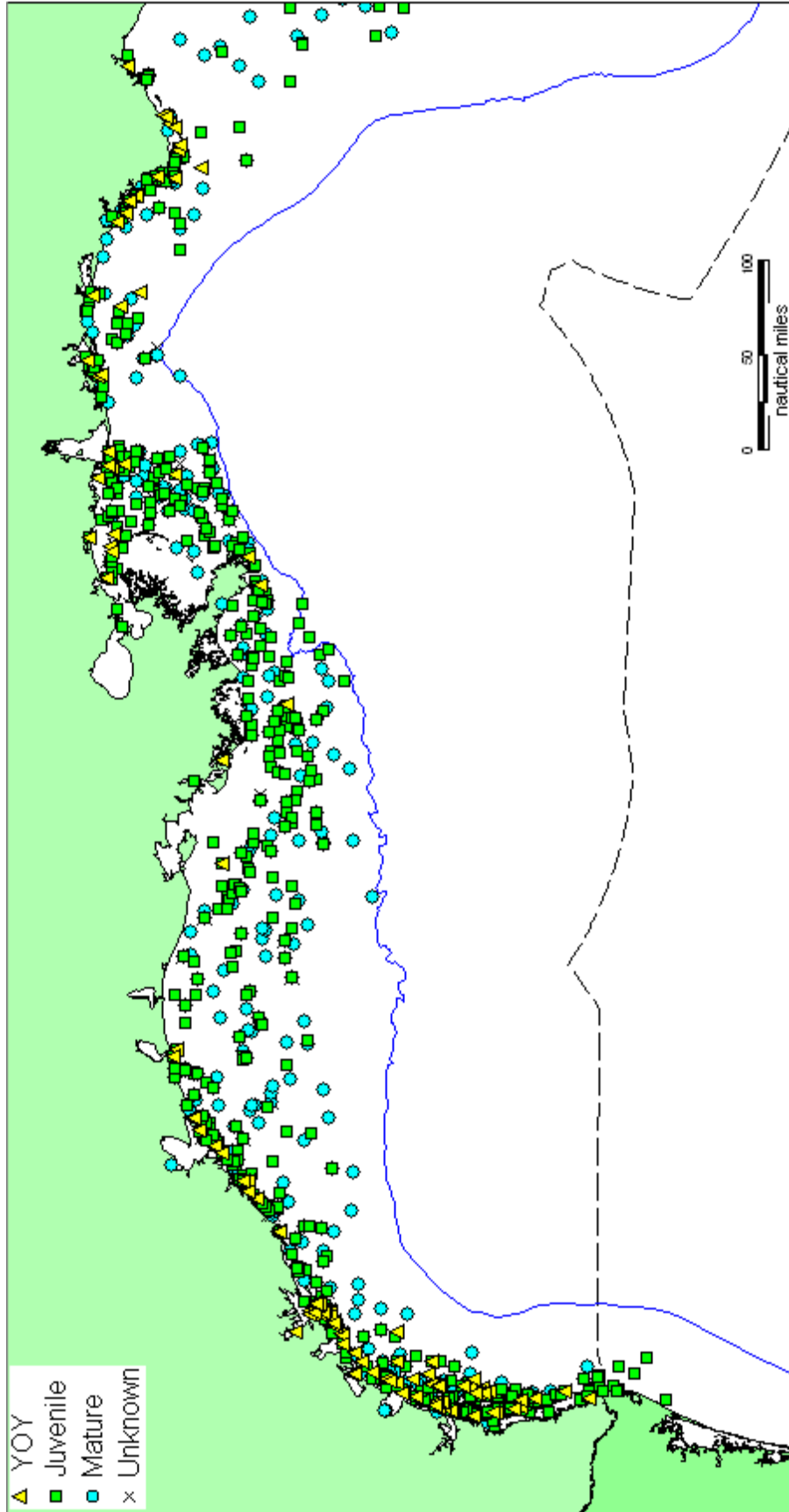Figure A-18. Blacktip shark captures by sex in the northwestern Gulf of Mexico. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

Legend:
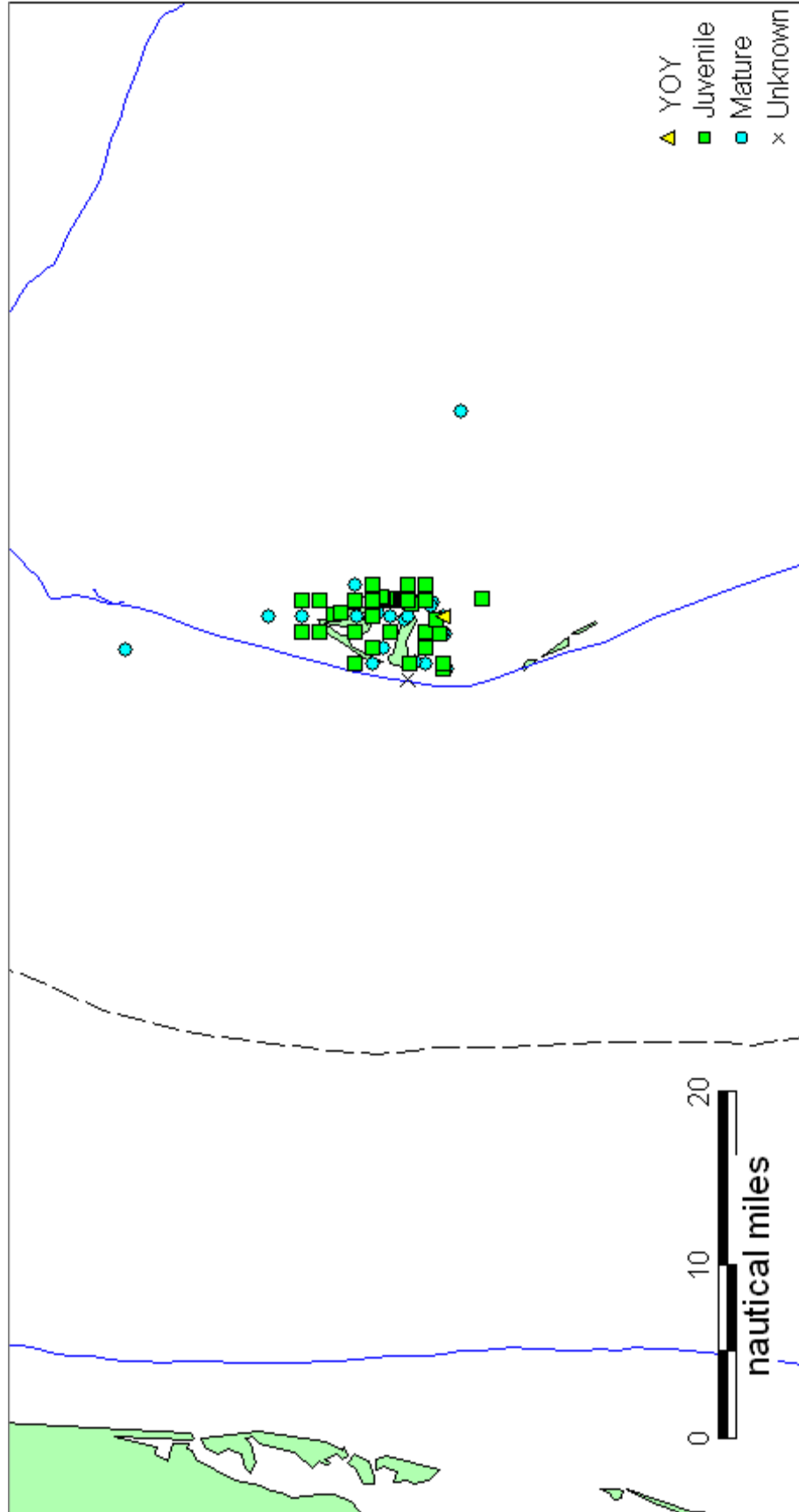■ Male
✛ Female
△ Unknown

0   50   100
nautical miles
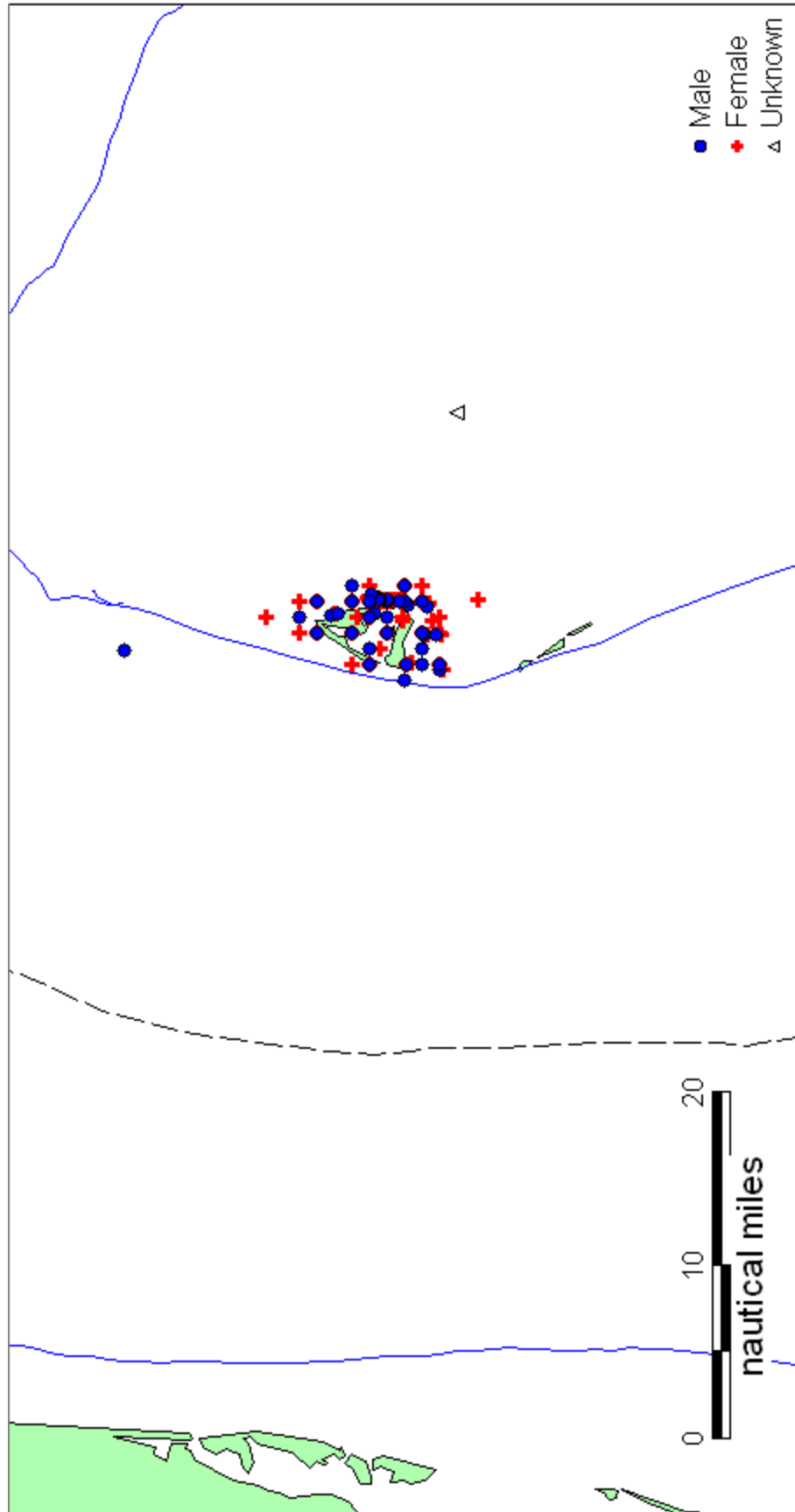
Figure A-19. Blacktip shark captures by sex in the Bahamas. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
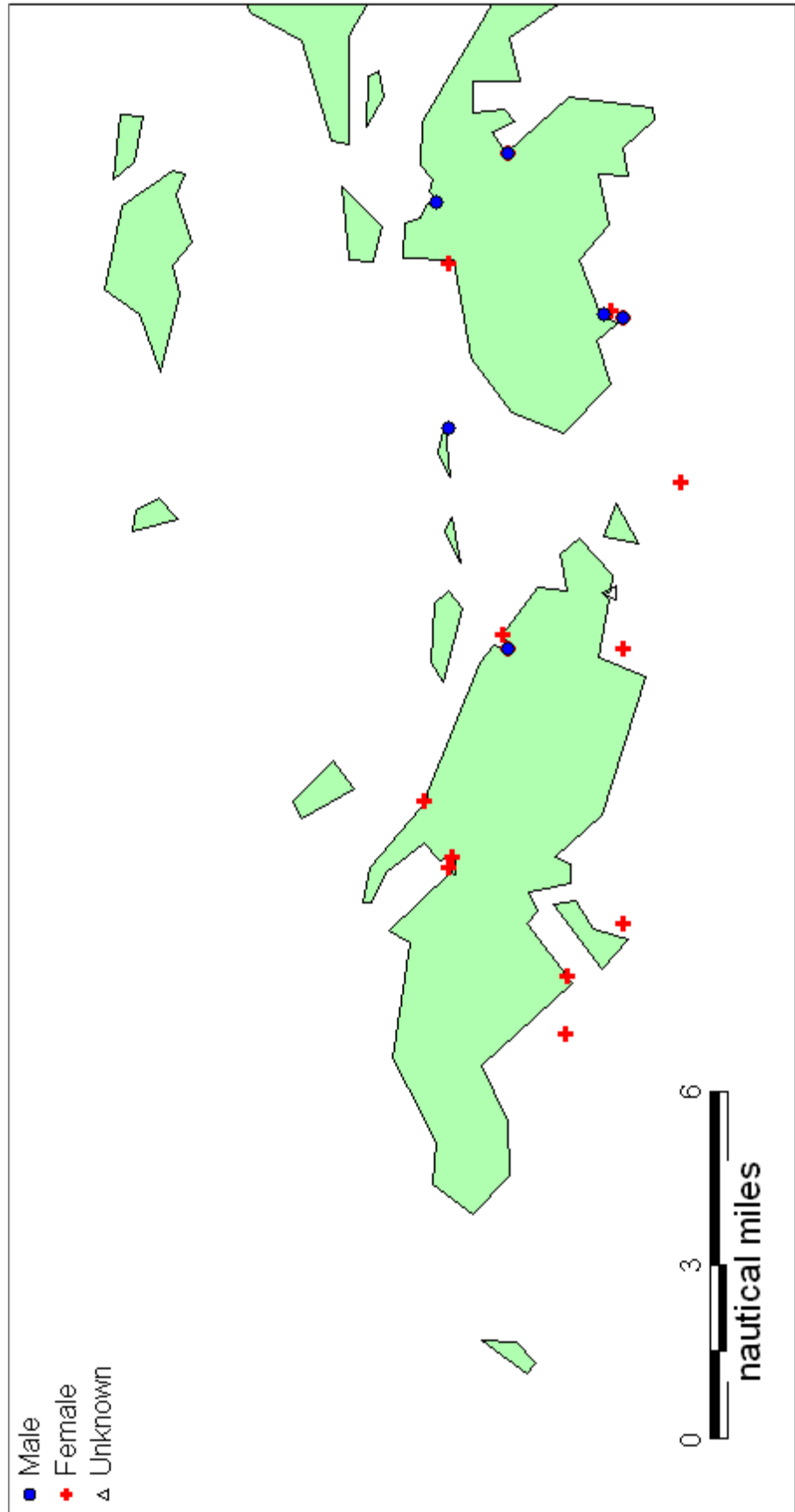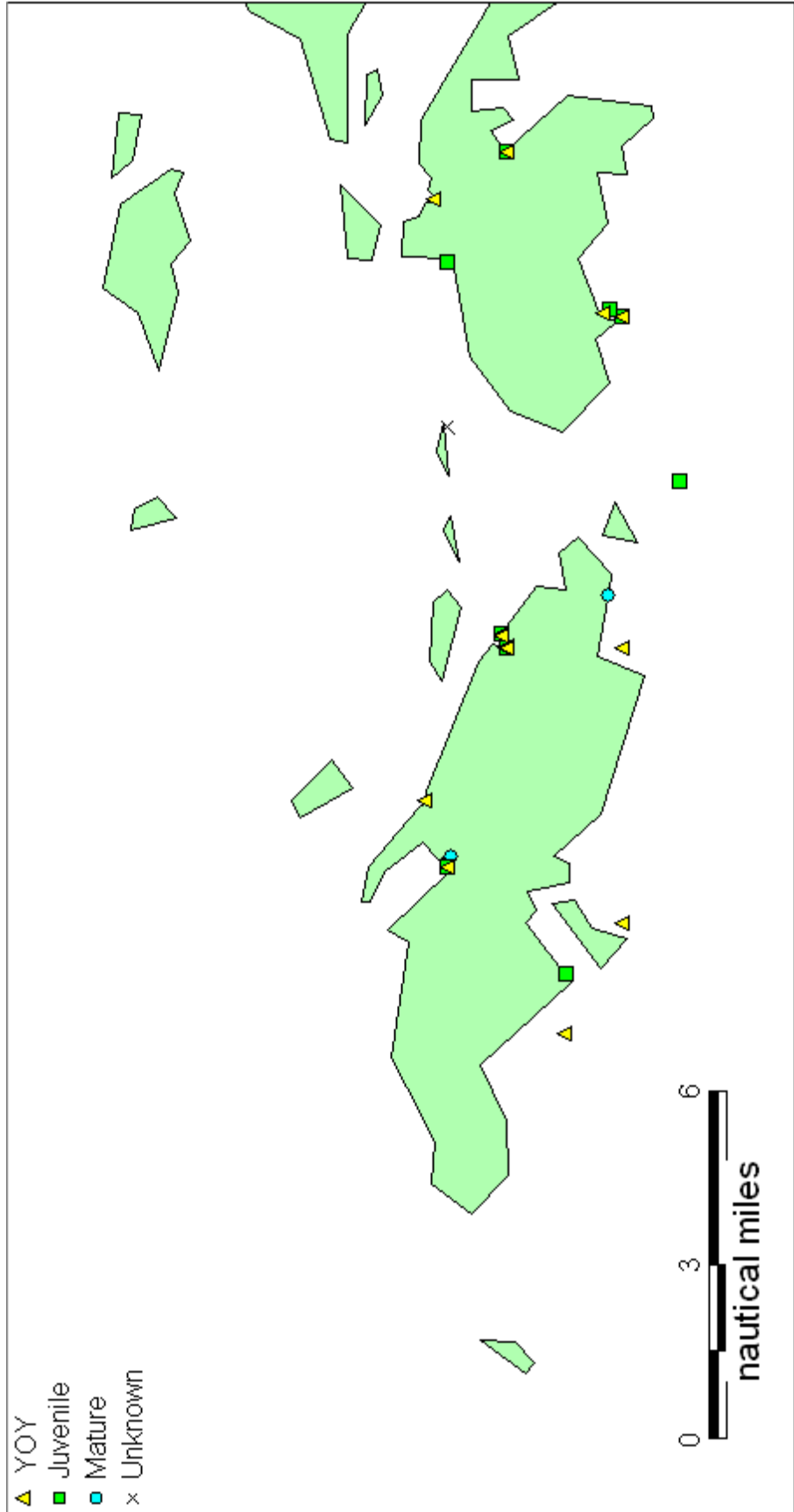
Figure A-20. Blacktip shark captures by sex in the U.S. Virgin Islands. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
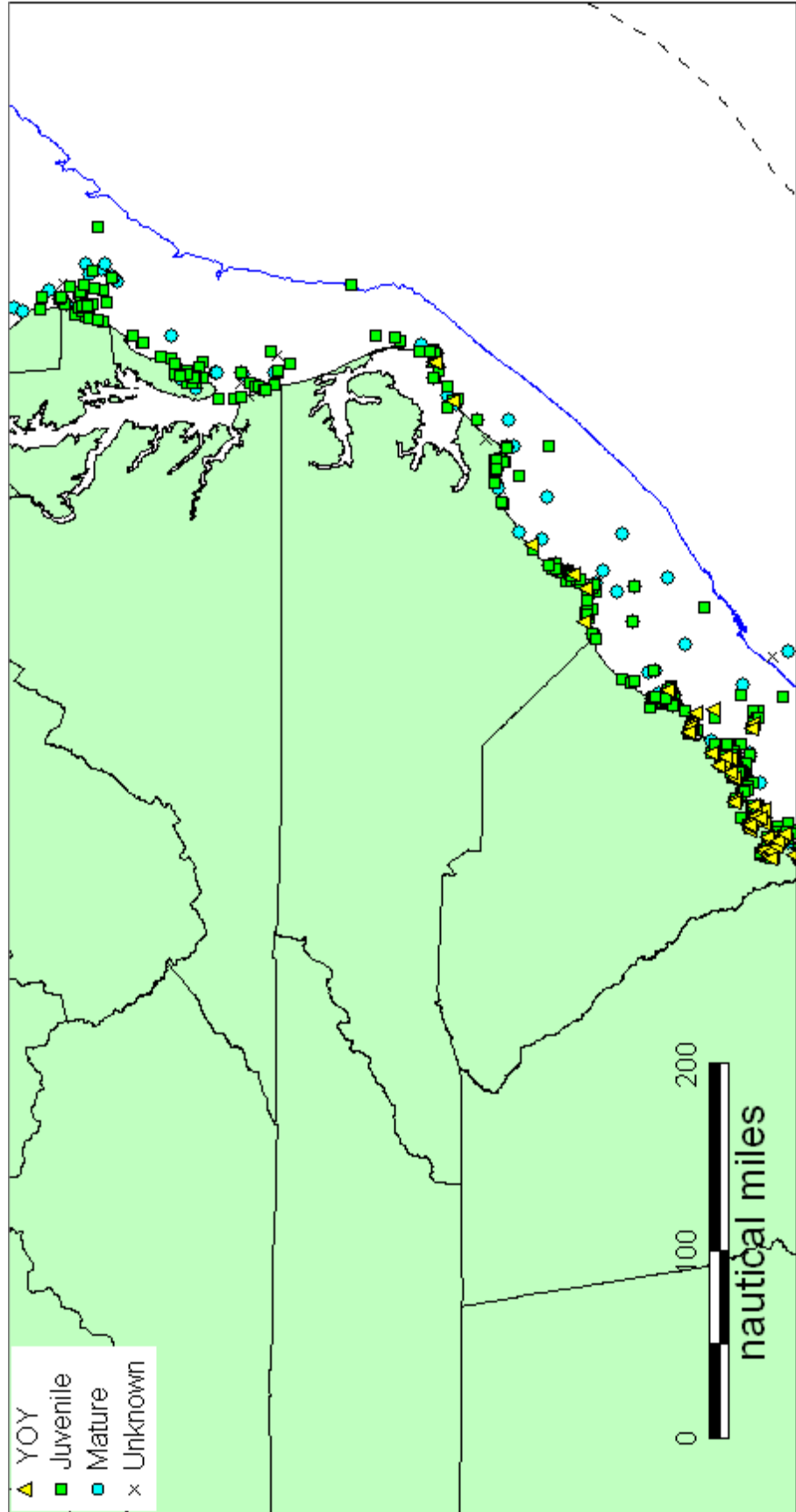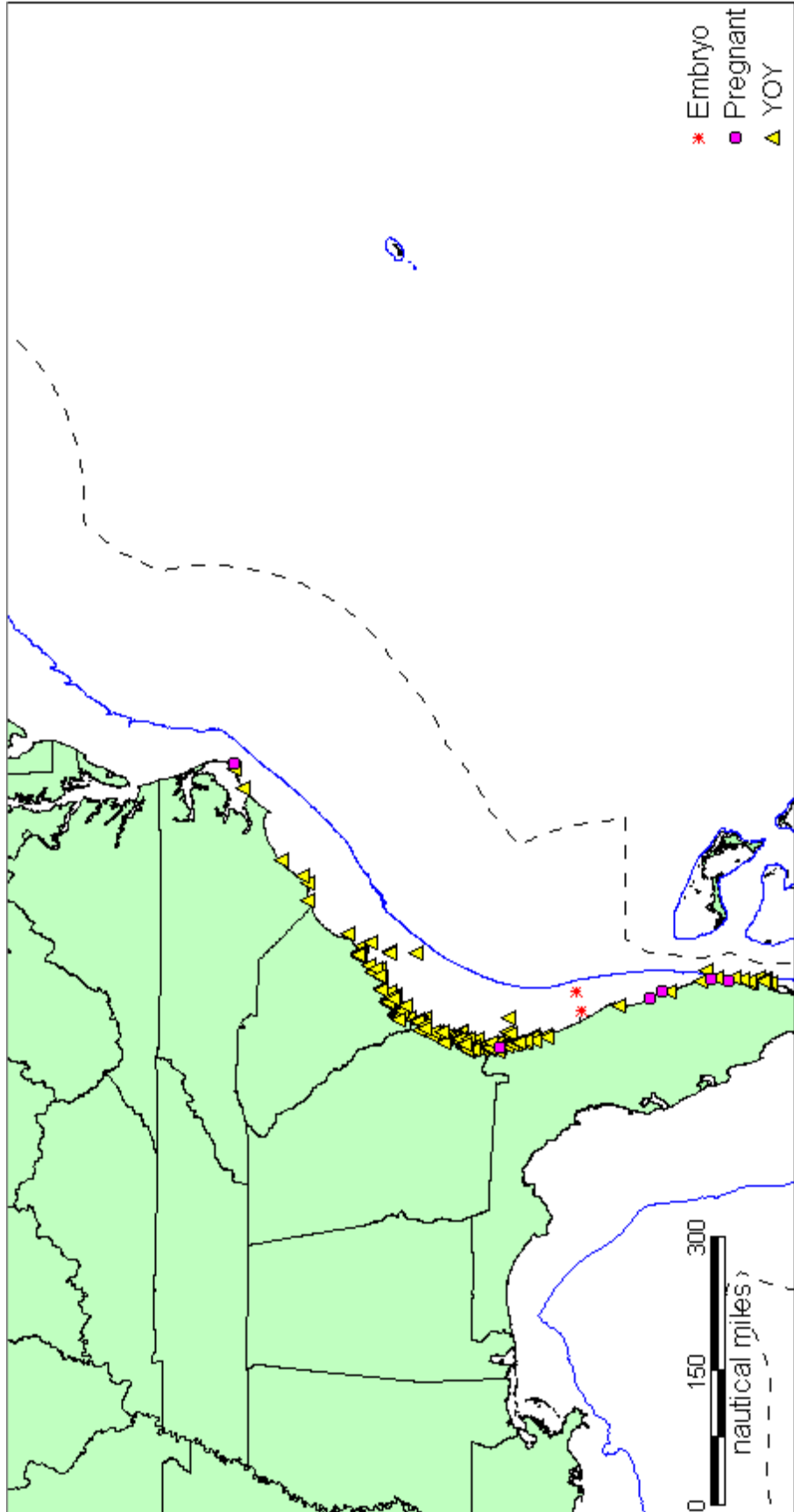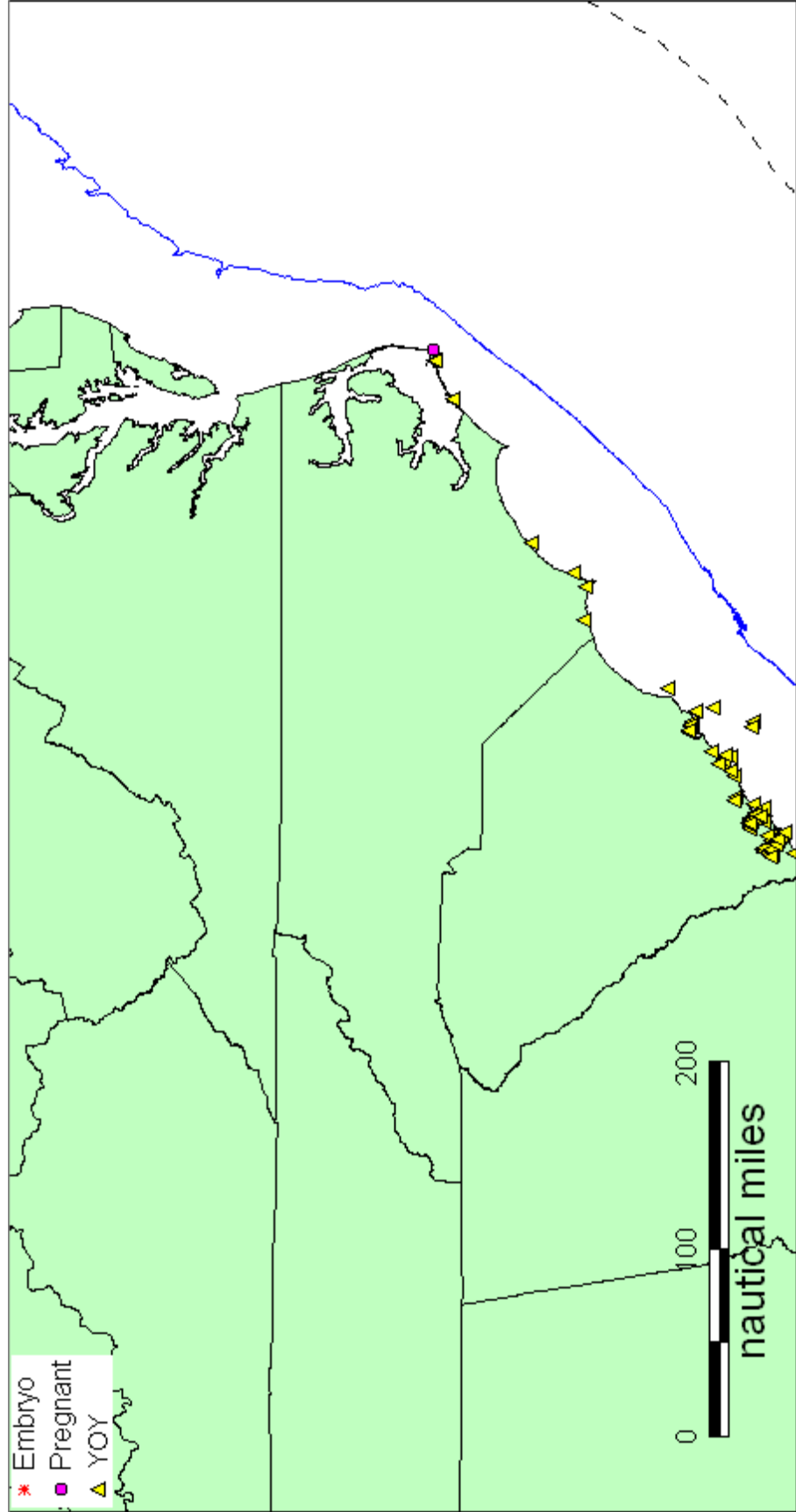
Figure A-21. Blacktip shark captures by life stage off the north U.S. Atlantic coast. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
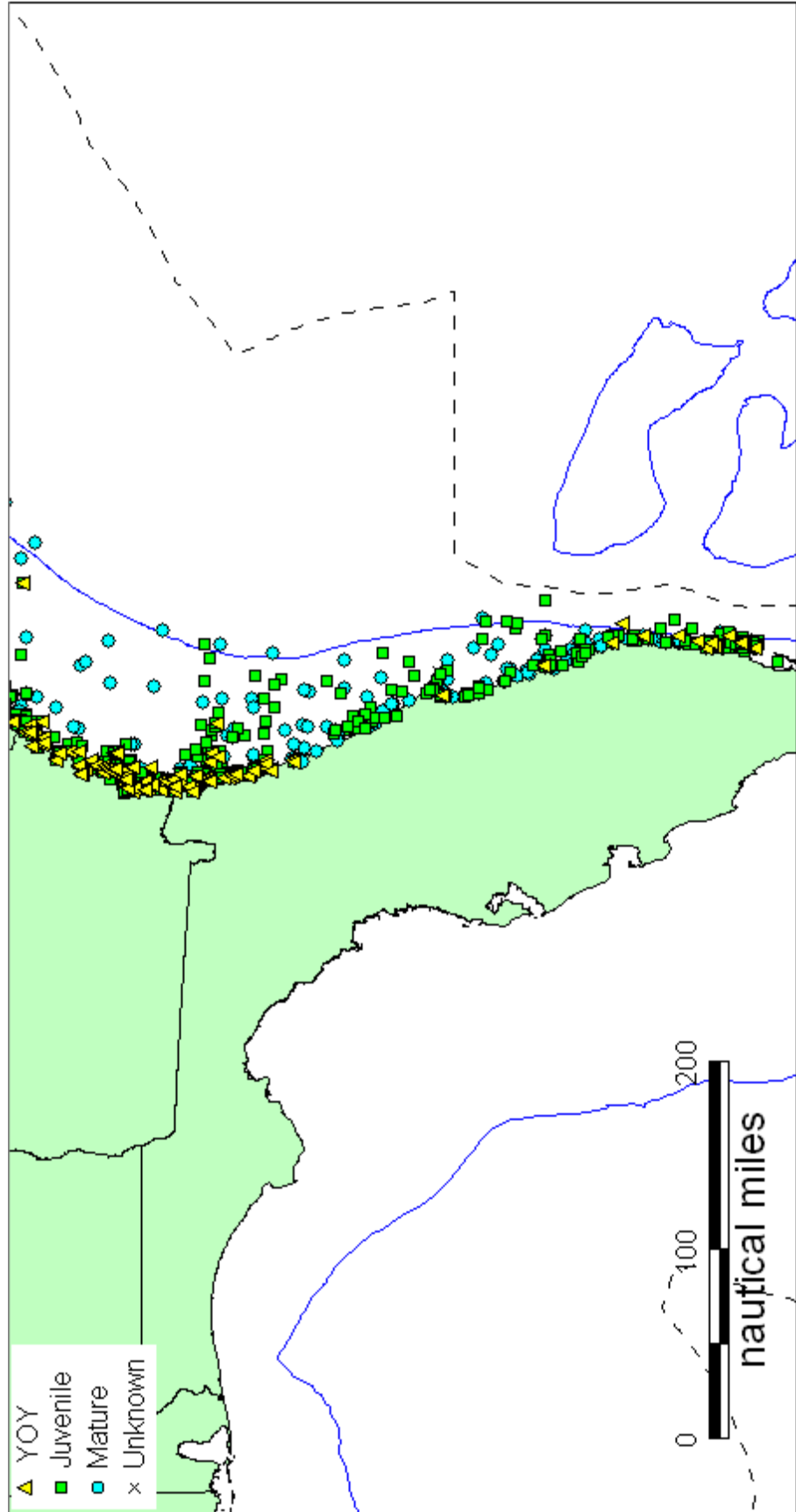
Figure A-22. Blacktip shark captures by life stage off the south U.S. Atlantic coast. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

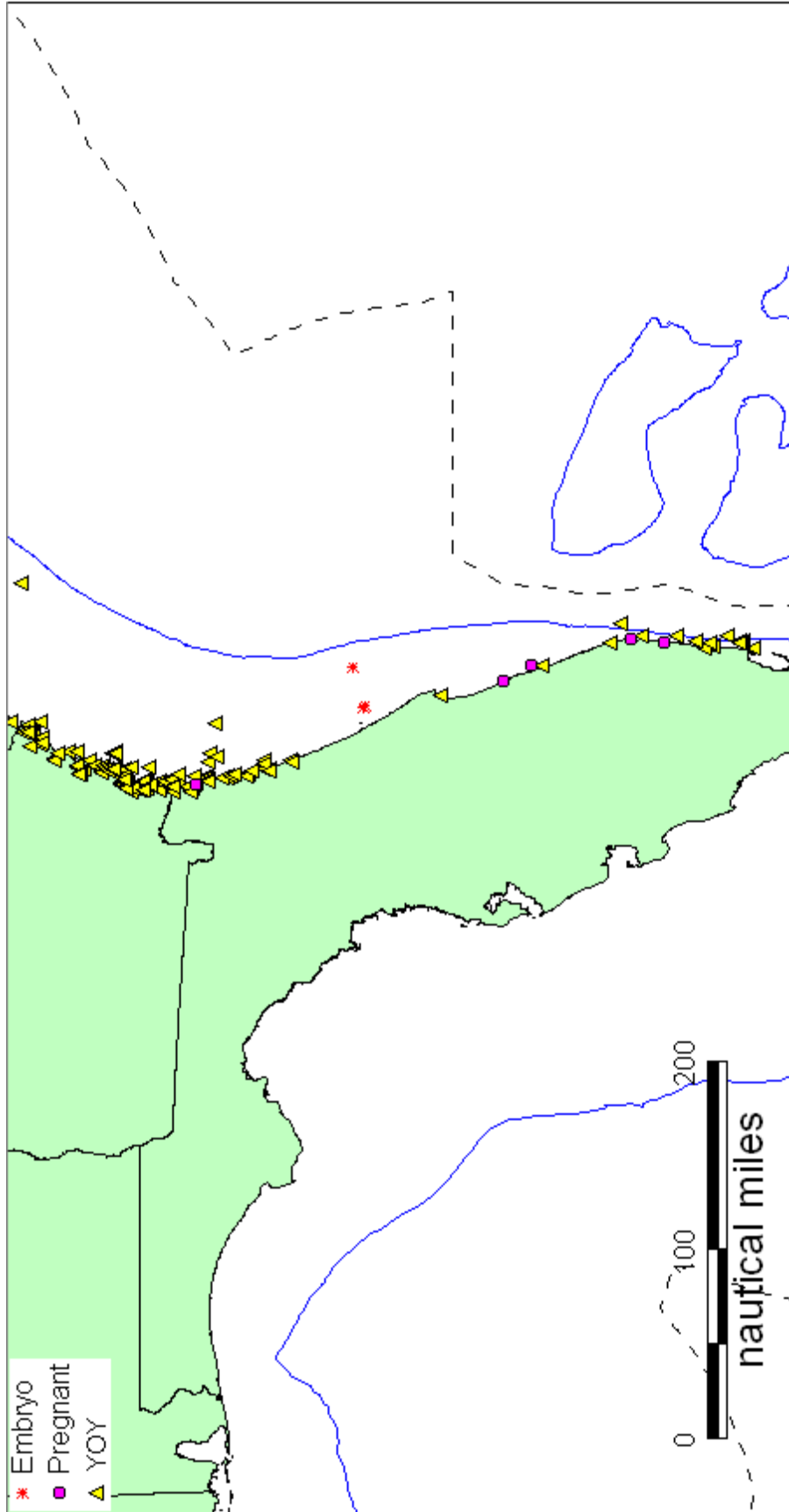Figure A-23. Blacktip shark captures by life stage off the west coast of Florida. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

Figure A-24. Blacktip shark captures by life stage in the northwestern Gulf of Mexico. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

Figure A-25. Blacktip shark captures by life stage in the Bahamas. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

Figure A-26. Blacktip shark captures by life stage in the U.S. Virgin Islands. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

YOY
Juvenile
Mature
Unknown

nautical miles

0   3   6

Figure A-27. Embryo, YOY and pregnant blacktip shark captures in the U.S. Atlantic. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

Figure A-28. Embryo, YOY and pregnant blacktip shark captures off the north U.S. Atlantic coast. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
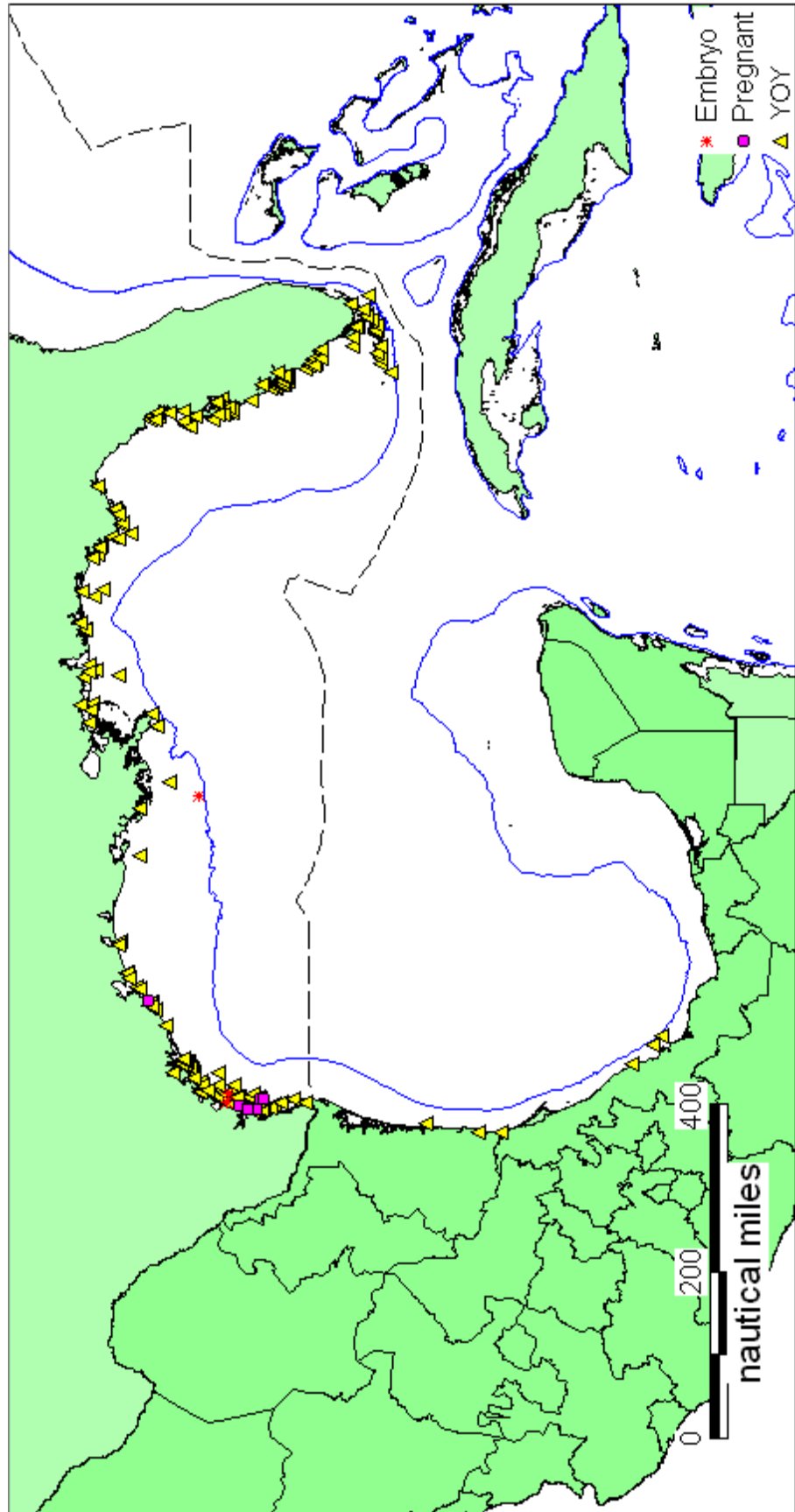
Figure A-29. Embryo, YOY and pregnant blacktip shark captures in the south U.S. Atlantic coast. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

Figure A-30. Embryo, YOY and pregnant blacktip shark captures in the Gulf of Mexico. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
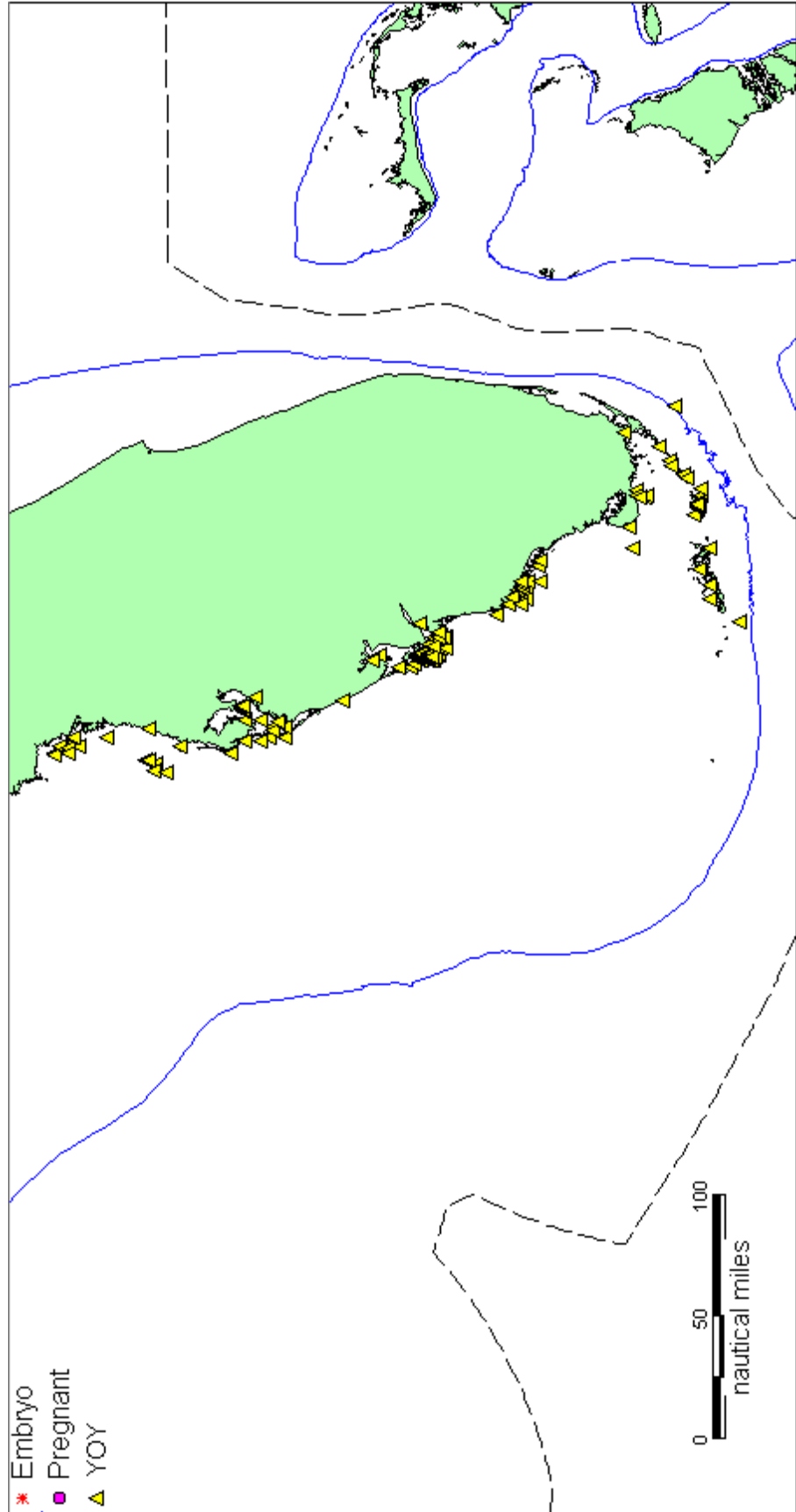
Figure A-31. Embryo, YOY and pregnant blacktip shark captures off the west coast of Florida. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
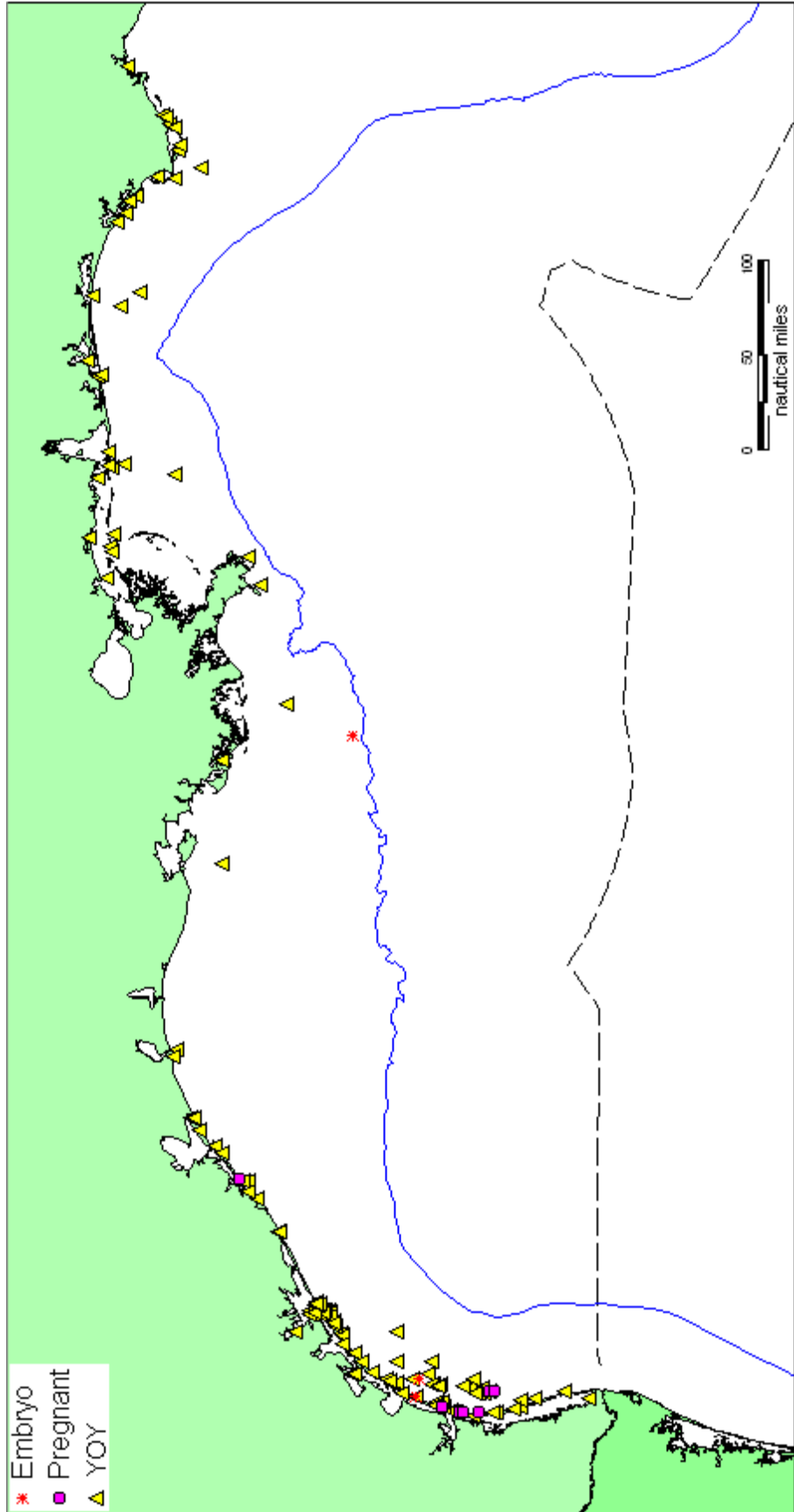
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Figure A-32. Embryo, YOY and pregnant blacktip shark captures in the northwestern Gulf of Mexico. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
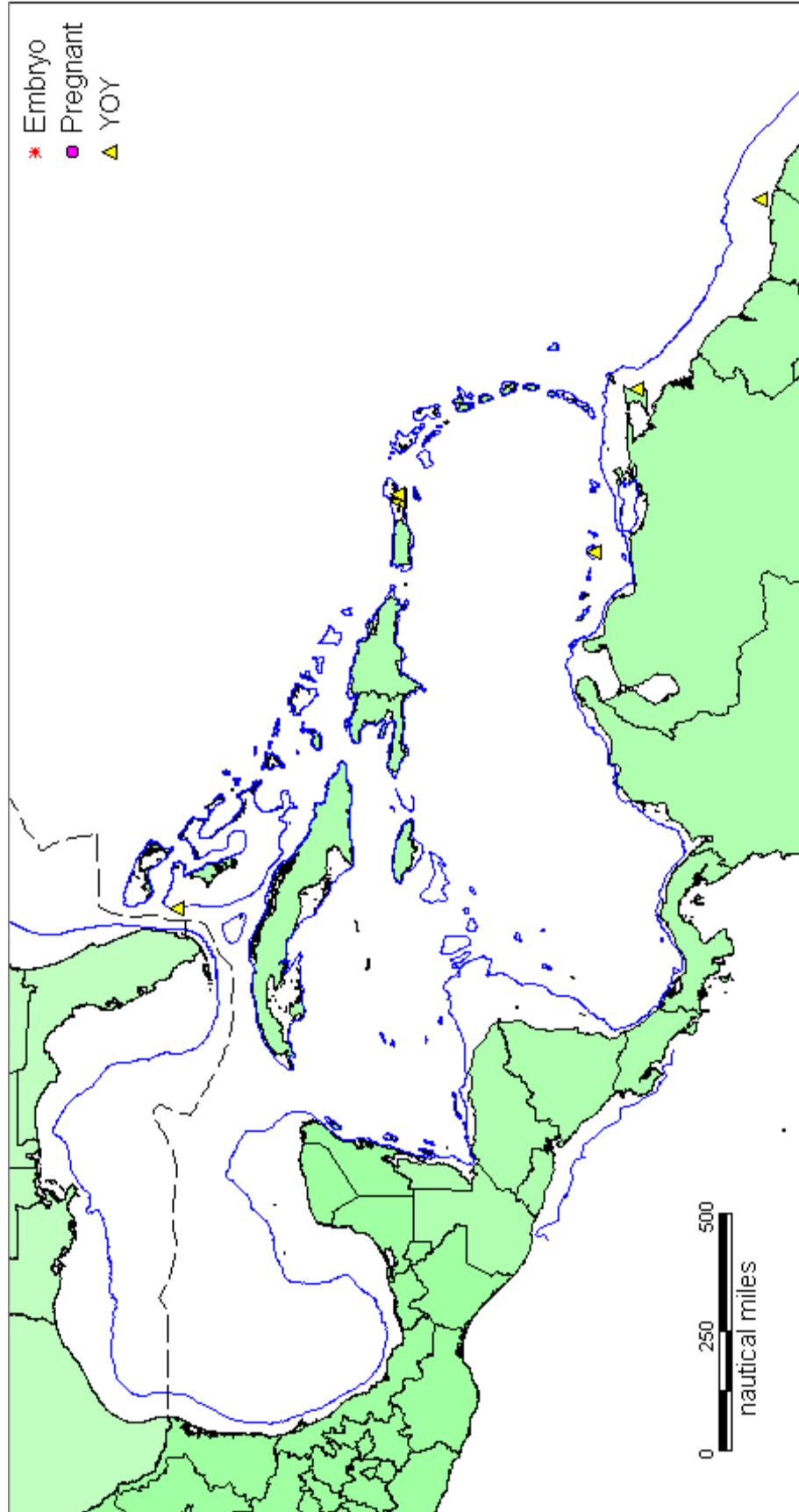
113

Figure A-33. Embryo, YOY and pregnant blacktip shark captures in the International Atlantic. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
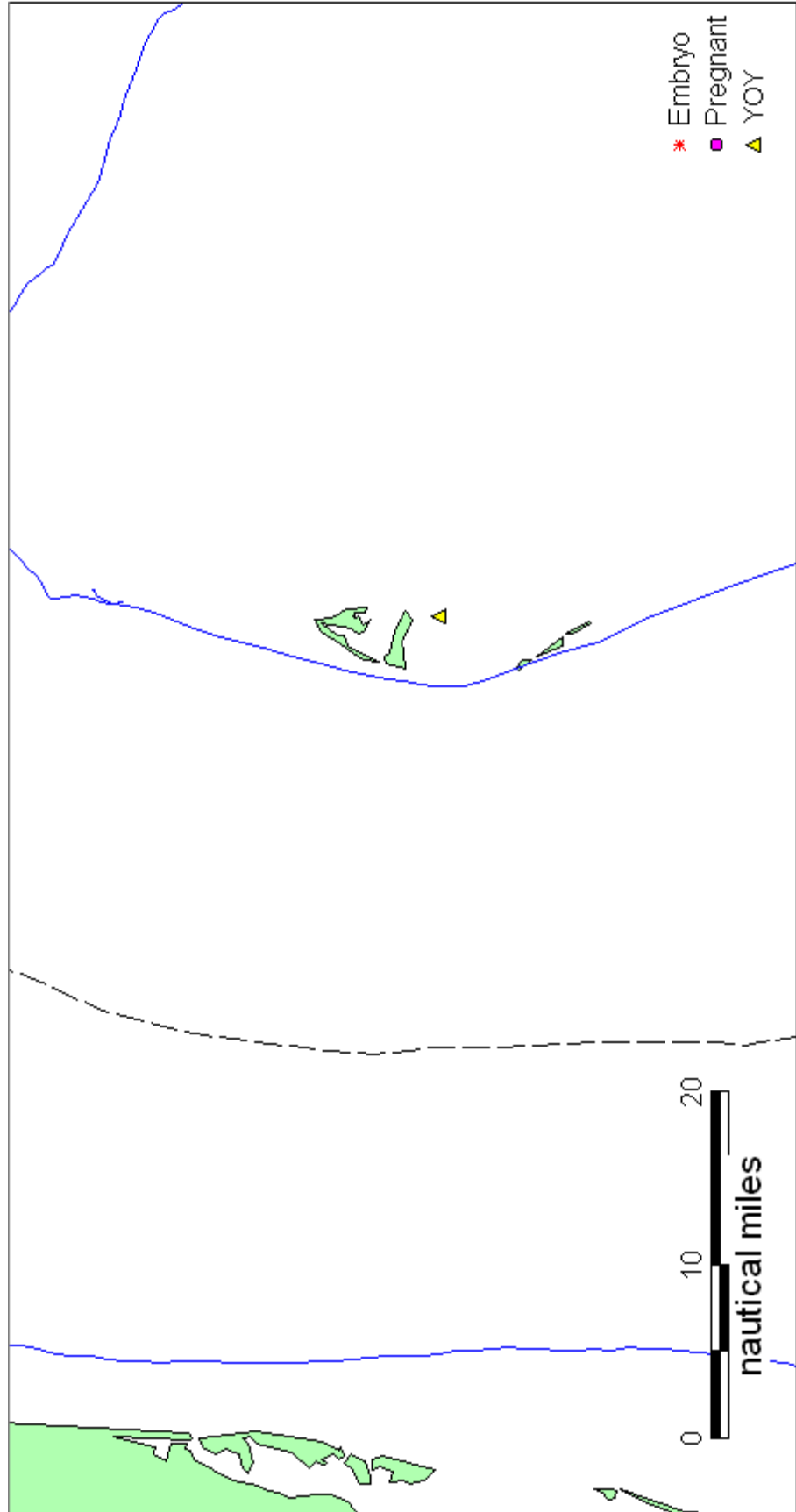
Figure A-34. Embryo, YOY and pregnant blacktip shark captures in the Bahamas. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
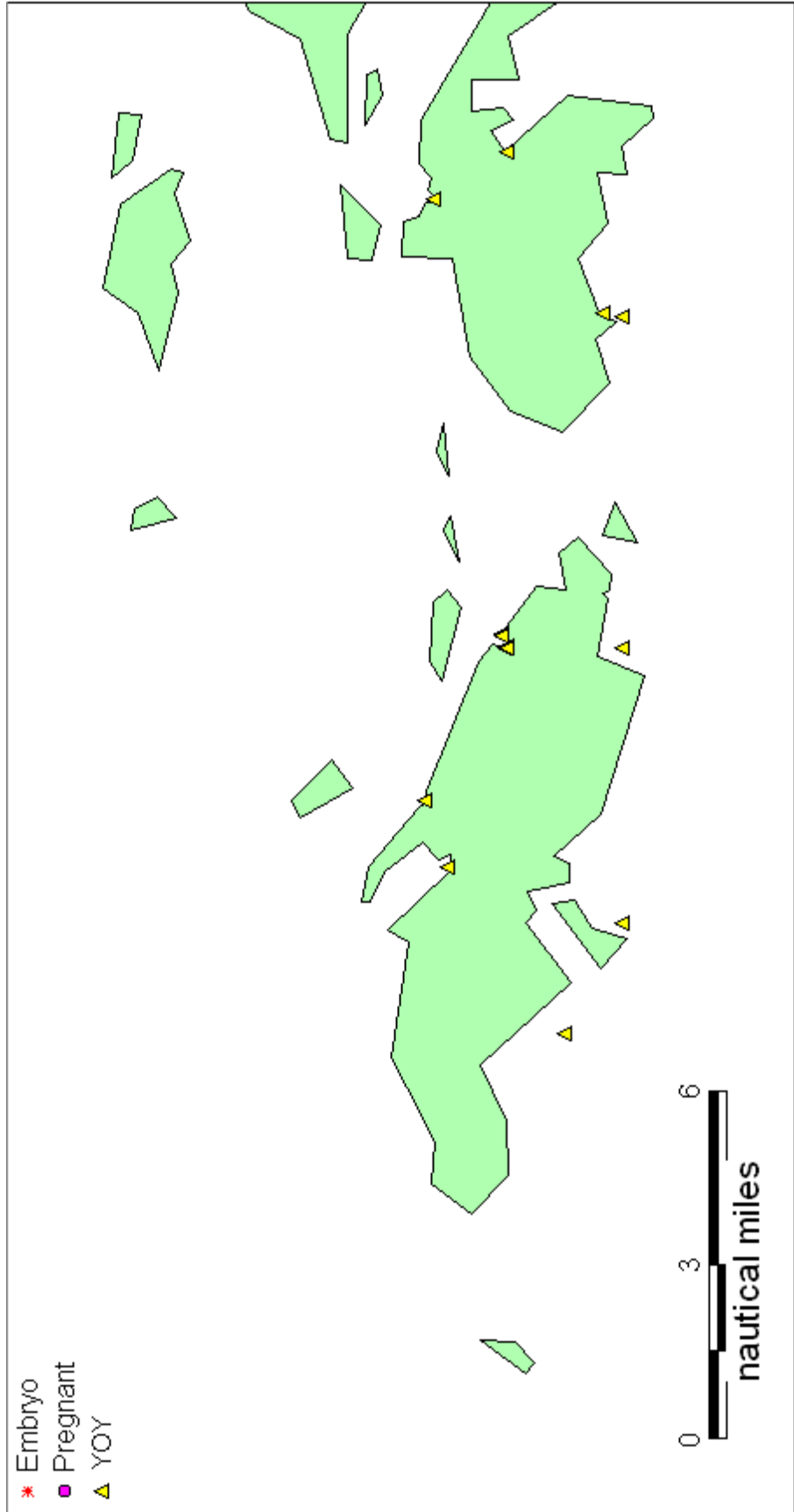
Figure A-35. Embryo, YOY and pregnant blacktip shark captures in the U.S. Virgin Islands. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
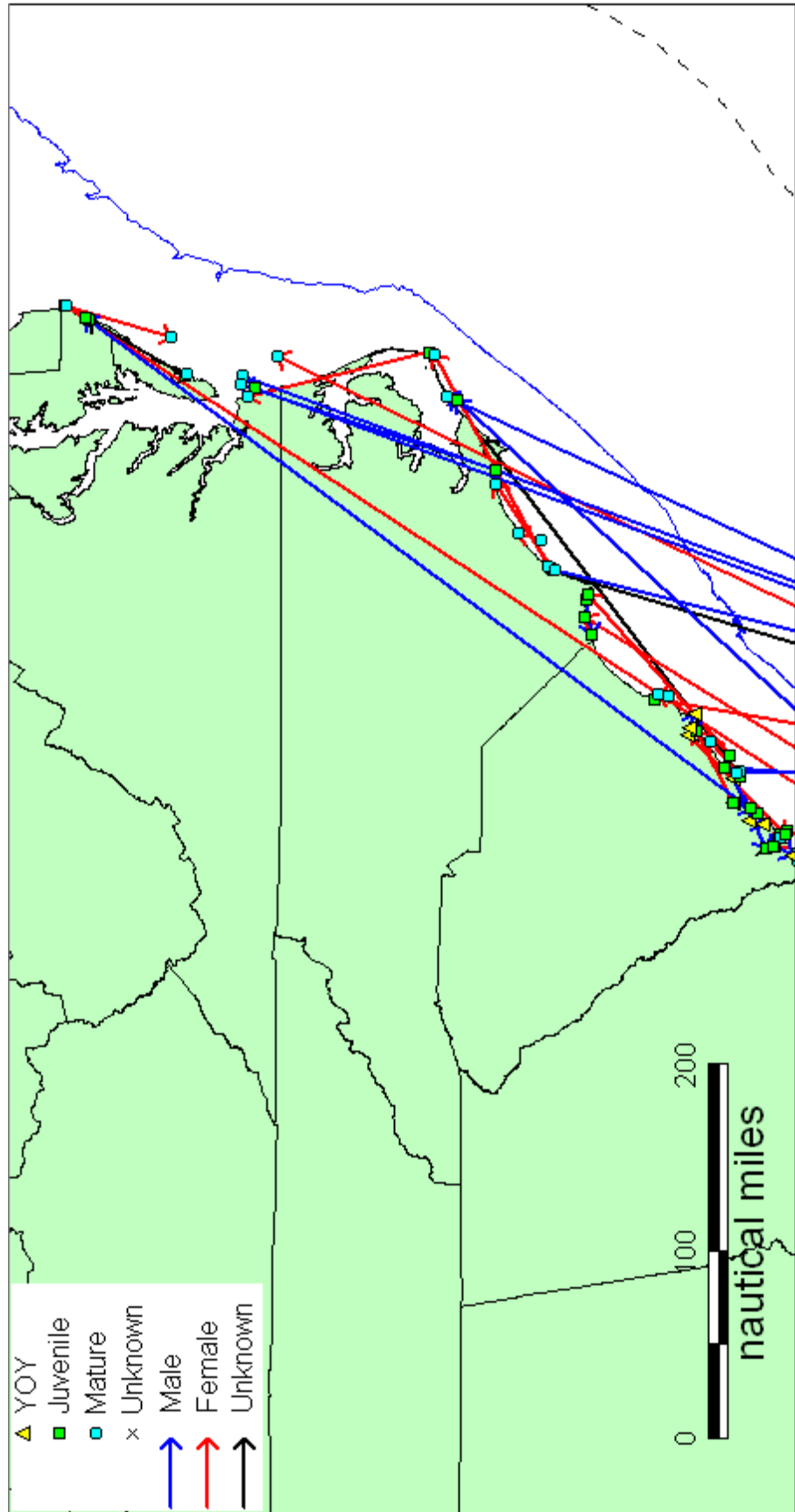
Figure A-36. Blacktip shark recaptures by sex and life stage off the north U.S. Atlantic coast. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
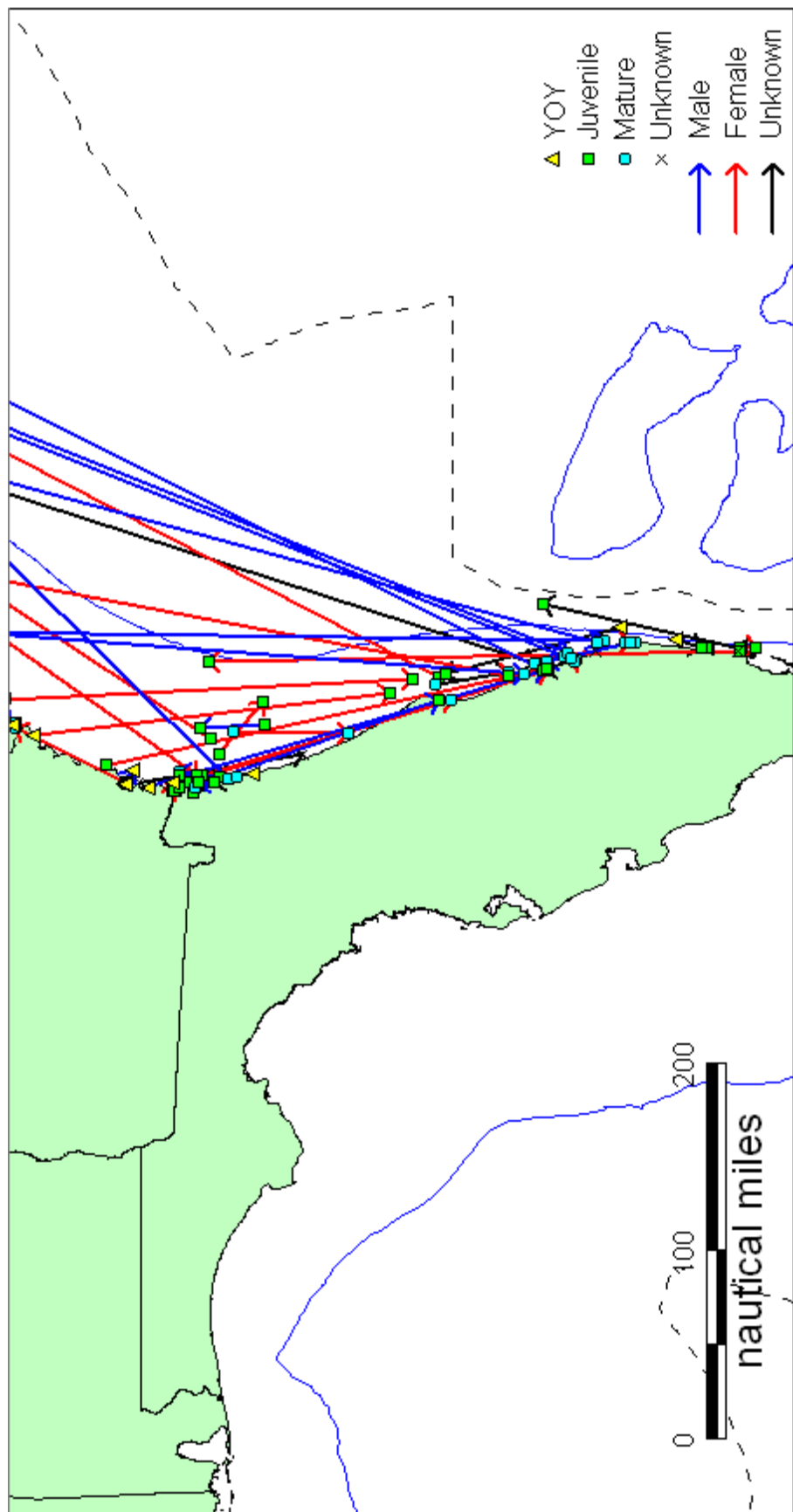
Figure A-37. Blacktip shark recaptures by sex and life stage off the south U.S. Atlantic coast. The solid line represents the 200m depth contour. The dotted-dashed line represents the U.S. EEZ.
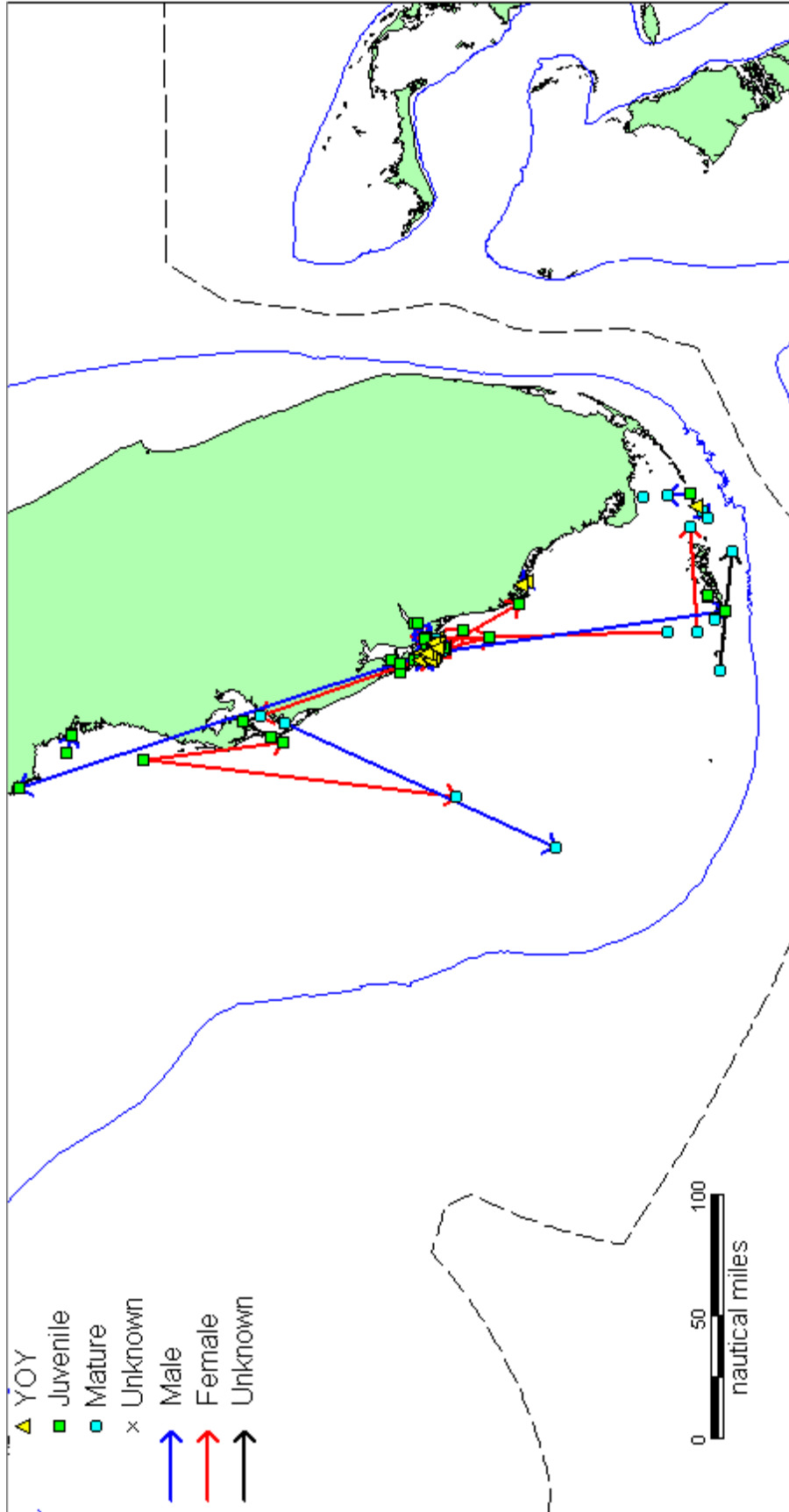
Figure A-38. Blacktip shark recaptures by sex and life stage off the west coast of Florida. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.

Figure A-39. Blacktip shark recaptures by sex and life stage in the northwestern Gulf of Mexico. The solid line represents the 200m depth contour. The dotted-dashed line represents the U.S. EEZ.

Figure A-40. Blacktip shark recaptures by sex and life stage in the Bahamas. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
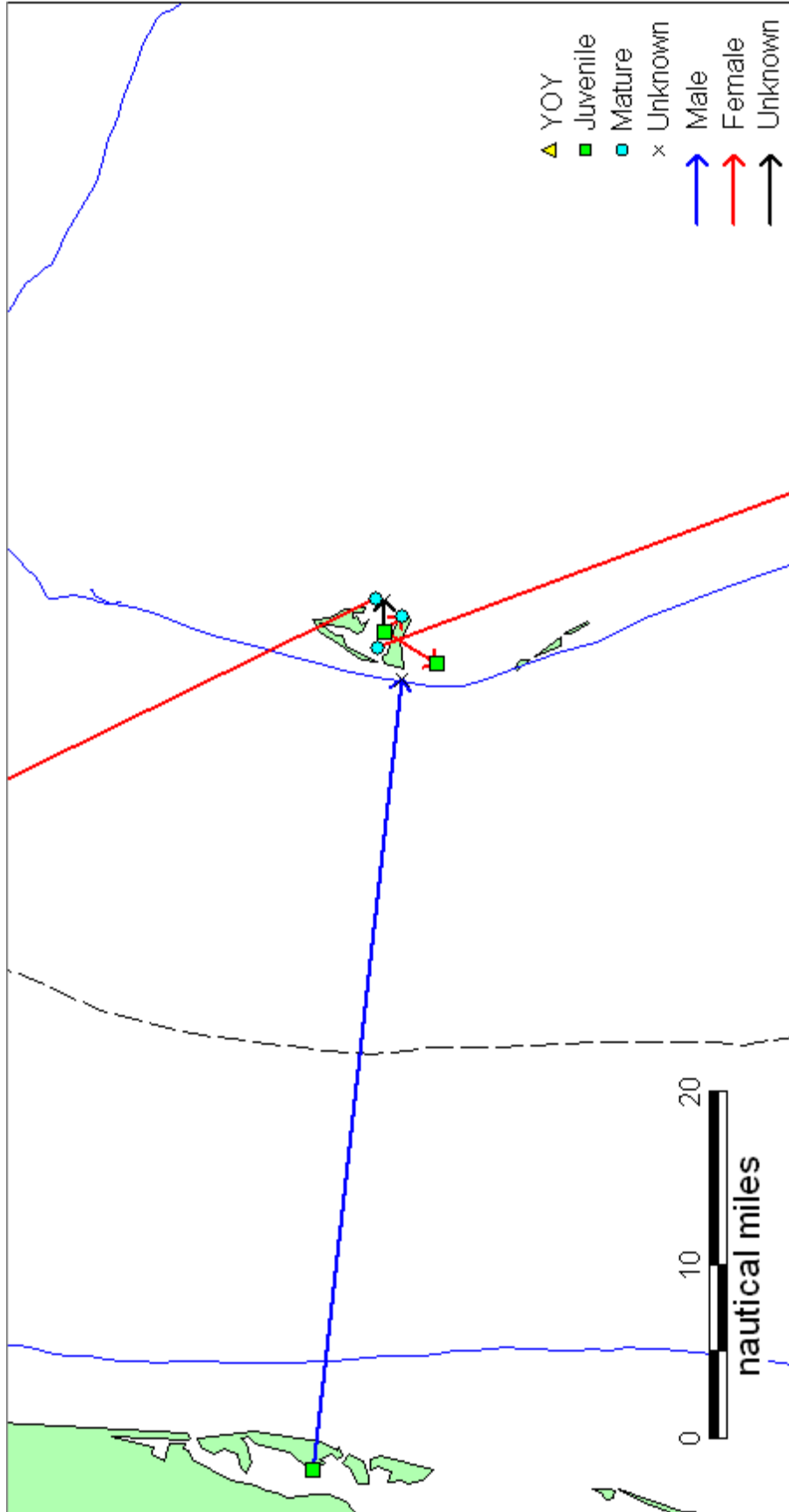
Figure A-41. Blacktip shark recaptures by sex and life stage in the U.S. Virgin Islands. The solid line represents the 200 m depth contour. The dashed line represents the U.S. EEZ.
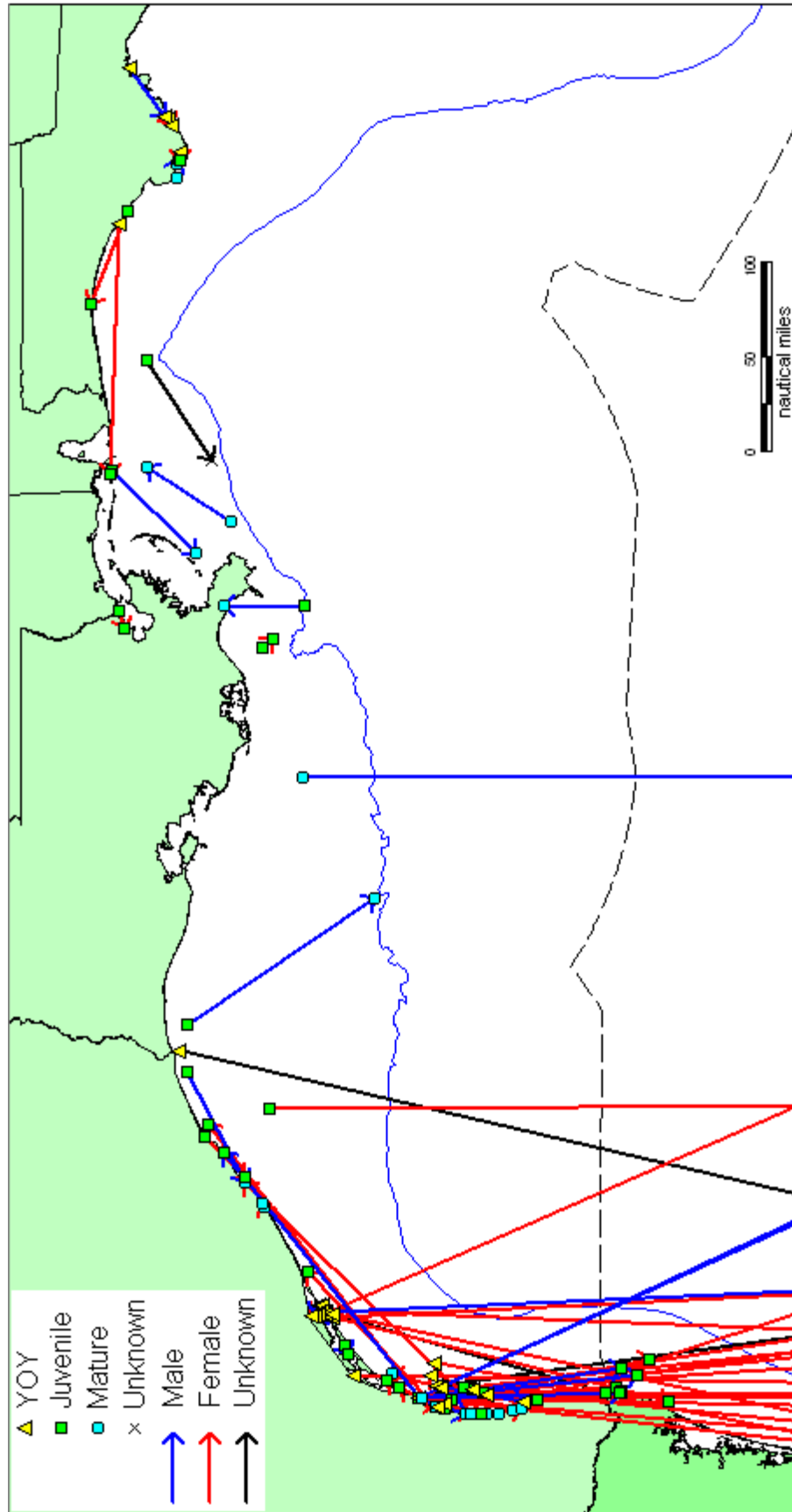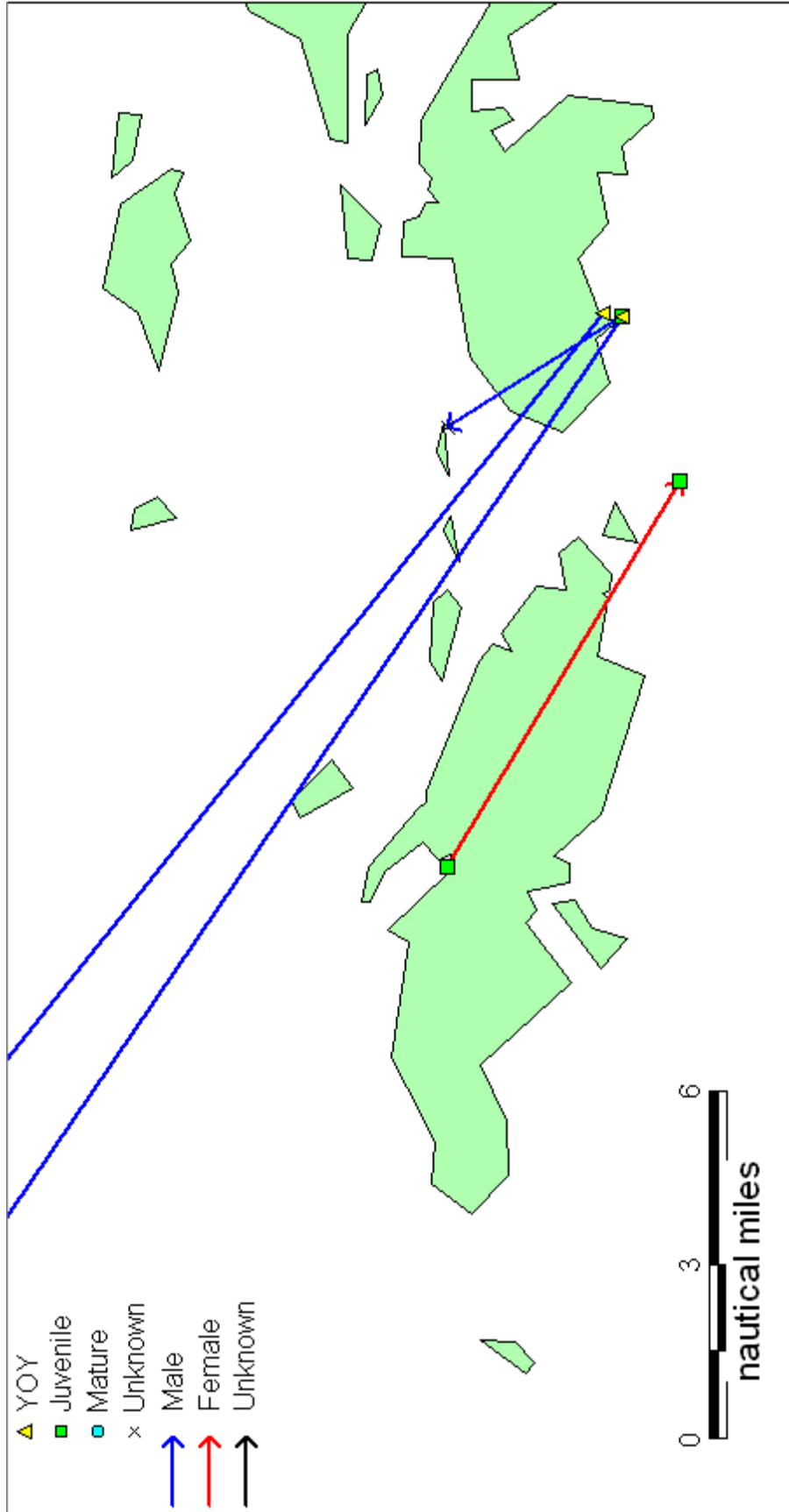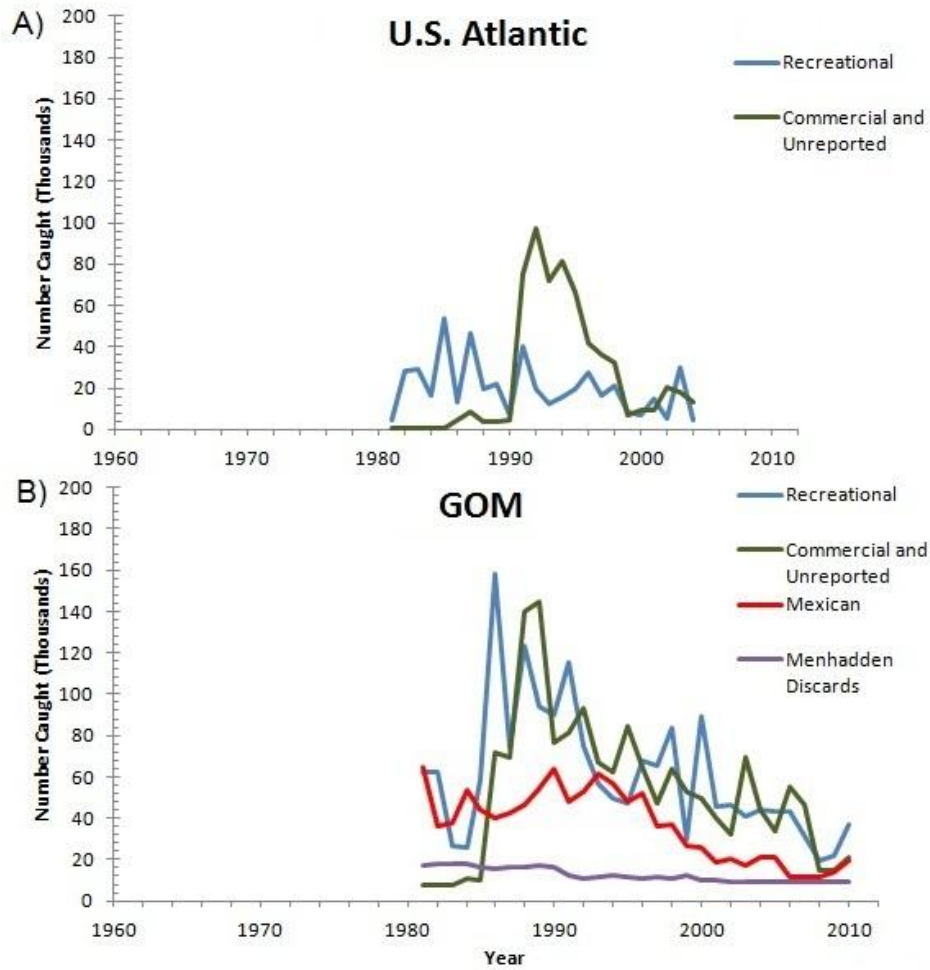
Figure A-42. Blacktip shark landings in the Gulf of Mexico by fleet (NOAA/NMFS 2012).

		Year of Recovery		
Year Marked	Number Marked	1	2	3
1	N_1	$N_1(1-S_1)r_1$	$N_1S_1(1-S_2)r_2$	$N_1S_1S_2(1-S_3)r_3$
2	N_2		$N_2(1-S_2)r_2$	$N_2S_2(1-S_3)r_3$
3	N_3			$N_3(1-S_3)r_3$

Figure A-43. Probability expressions for number of sharks marked and recovered in a given year, with no age grouping. (Cooch and White 2004).

Year Marked	Number Marked	Year of Recovery		
		1	2	3
		Marked as Post-YOY		
1	N_1	$N_1(1-S_1)r_1$	$N_1S_1(1-S_2)r_2$	$N_1S_1S_2(1-S_3)r_3$
2	N_2		$N_2(1-S_2)r_2$	$N_2S_2(1-S_3)r_3$
3	N_3			$N_3(1-S_3)r_3$
		Marked as YOY		
1	N_1	$N_1(1-S_1^{*})r_1^{*}$	$N_1S_1^{*}(1-S_2)r_2$	$N_1S_1^{*}S_2(1-S_3)r_3$
2	N_2		$N_2(1-S_2^{*})r_2^{*}$	$N_2S_2^{*}(1-S_3)r_3$
3	N_3			$N_3(1-S_3^{*})r_3^{*}$

Figure A-44. Probability expressions for number of sharks marked and recovered in a given year, including an age effect. (Cooch and White 2004). An asterisk (*) indicates parameters that are specific to young-of-the-year.

```
/* CSTP Blacktip shark
encounter occasions=19, groups=2
glabel(1)=post-YOY
glabel(2)=YOY   */
recovery matrix group=1;
1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0;
  1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0;
    3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0;
      2 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0;
        2 0 0 1 0 0 0 0 0 0 0 0 0 0 0;
          0 1 0 0 0 1 0 0 1 0 0 0 0 0;
            2 1 0 0 0 0 0 0 0 0 0 0 0;
              2 3 0 1 0 0 0 0 0 0 0 0;
                2 1 0 0 0 0 0 0 0 0 0;
                  3 1 0 1 0 0 0 0 0 0;
                    1 2 0 0 0 0 0 0 0;
                      2 1 0 0 1 0 0 0;
                        0 1 0 0 0 0 0;
                          1 0 0 0 0 0;
                            1 0 1 0 0;
                              0 1 0 0;
                                0 1 1;
                                  2 0;
                                    0;
25 34 80 62 73 94 116 83 78 71 88 118 103 142 171 167 288 338 321;
recovery matrix group=2;
2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0;
  1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0;
    2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0;
      0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0;
        1 0 0 1 0 0 0 0 0 0 0 0 0 0 0;
          4 0 0 0 0 0 0 0 0 0 0 0 0 0;
            6 1 0 0 0 0 0 0 0 0 0 0 0;
              5 1 1 0 0 0 0 0 0 0 0 0;
                4 1 0 0 0 0 0 0 0 0 0;
                  0 0 0 0 0 0 0 0 0 0;
                    5 1 0 0 0 0 0 0 0;
                      1 0 0 0 0 0 0 0;
                        2 0 0 0 0 0 0;
                          1 0 0 0 0 0;
                            2 1 0 0 0;
                              0 0 0 0;
                                0 0 0;
                                  1 0;
                                    1;
16 25 25 4 49 77 113 86 87 45 57 16 44 22 35 20 15 19 26;
```

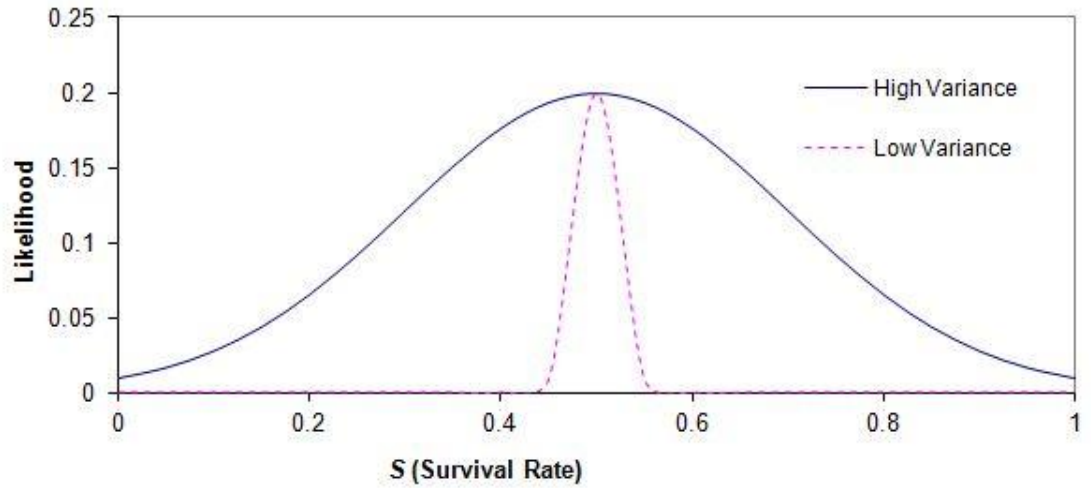Figure A-45. Data input file for analysis with an age grouping.

Figure A-46. Sample likelihood distributions with different variances.
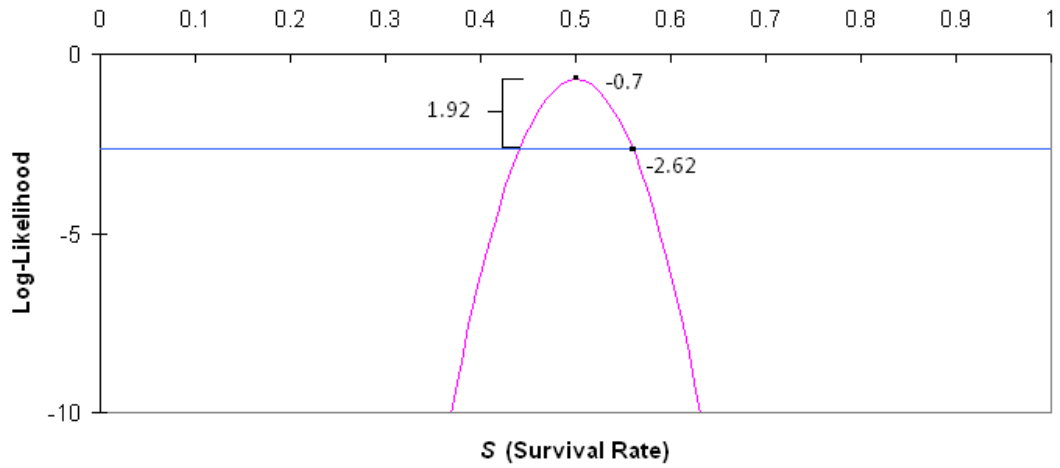

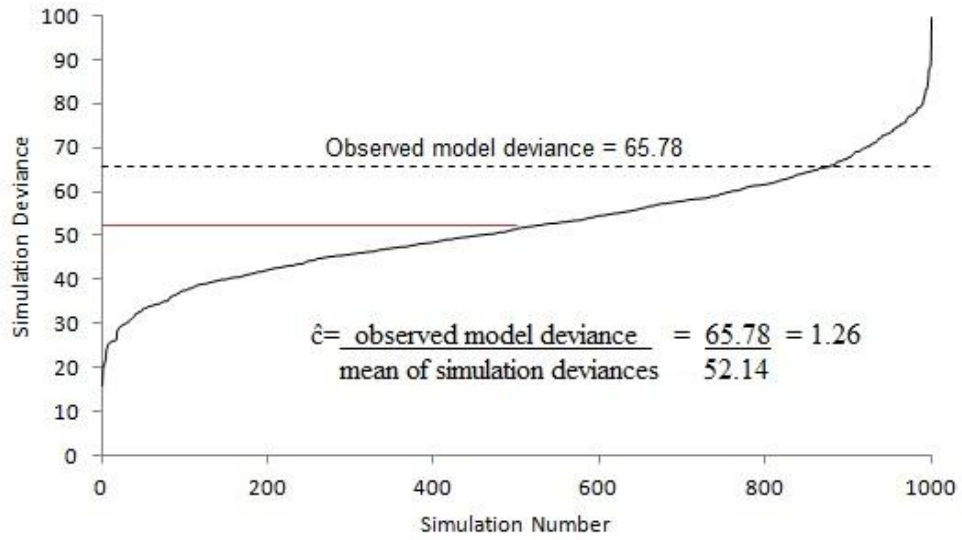Figure A-47. Sample calculation of variance with profile likelihood method.

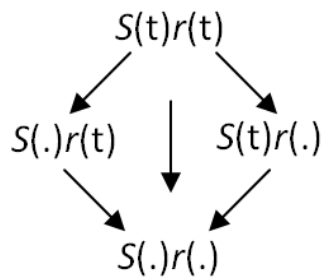Figure A-48. Calculation of observed model deviance over mean deviance.

Figure A-49. Visual representation of nesting. Arrows point from general model to reduced model.

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