The Habitat, Movements, and Management of Dolphin, *Coryphaena hippurus*, in the Western North Atlantic, Caribbean, and Gulf of Mexico

by

Edward R. Farrell
Dr. Patrick Halpin, Advisor
May 2009

Masters project submitted in partial fulfillment of the requirements for the Master of Environmental Management degree in the Nicholas School of the Environment of Duke University
2009
ABSTRACT

Dolphin, *Coryphaena hippurus*, is a highly migratory cosmopolitan pelagic fish that is found seasonally in the Caribbean, Gulf of Mexico, and along the Atlantic coast of the United States. Dolphin are considered as one unit stock throughout the study area. This study used release-recapture data from a long-term tagging project to investigate baseline environmental preferences, habitat suitability based on dynamic eco-geographical variables, spatio-temporal movement through marine cadastral zones, and related policy implications. The data was collected from hundreds of recreational fishermen that tagged dolphin and also recaptured dolphin. A combination of *in situ* observations from recreational taggers and remotely sampled physical and biological variables (depth, bathymetric slope, distance to shore, distance to continental shelf, sea surface temperature, and sea surface chlorophyll-*a*) were used to establish an updated and novel baseline of environmental characteristics. A presence-only spatially explicit multivariate modeling approach was used to reveal the bio-physical seasonal preferences of dolphin that define the ecological niche. The results of the models show strong spatial sensitivity to sea surface temperature and surface chlorophyll-*a* concentration. The tag-recapture analysis showed that dolphin are capable of crossing multiple national and international marine jurisdictional zones throughout their lives. These movements bring the current management insufficiencies to light. Recommendations based on this multifaceted analysis focus on horizontal domestic and international fisheries integration.
ACKNOWLEDGEMENTS

I would like to thank my wife, Daira, for providing unending support. I would also like to thank my advisor, Pat Halpin, for providing the opportunity to work on this project. Thanks to Andre Boustany for guidance throughout the project. Jason Roberts provided crucial technical support. I would also like to thank the people at the Duke Marine Lab that provided helpful discussions and technical support; Erin Labrecque, Caroline Goode, all of the other Coastal Environmental Management Students, and the Marine Lab IT Department. Special thanks to Don Hammond of the Dolphin Research Program in Charleston, SC. Don’s dedication and expertise are invaluable to the future of dolphin research, and his comments and support were valued throughout the project. The project would not be possible if not for the voluntary efforts of the hundreds of fishermen who tagged thousands of dolphin. I would also like to especially acknowledge the continued love and support from my family.
# TABLE OF CONTENTS

1.0 Introduction .......................................................................................................................... 1

2.0 Methods .................................................................................................................................. 8
   2.1 Description of Tagging Project ......................................................................................... 8
   2.2 Study Area ...................................................................................................................... 10
   2.3 Oceanographic Sampling ............................................................................................... 11
       2.3.1 Bathymetry and Slope ......................................................................................... 11
       2.3.2 Distance to Continental Shelf and Shoreline ...................................................... 12
       2.3.3 Sea Surface Temperature .................................................................................. 12
       2.3.4 Surface Chlorophyll ......................................................................................... 13
   2.4 Data Filtering .................................................................................................................. 13
   2.5 Sargassum Presence vs. Absence .................................................................................. 14
   2.6 Movement ...................................................................................................................... 14
   2.7 Habitat Modeling .......................................................................................................... 15
       2.7.1 Presence Only Modeling .................................................................................. 15

3.0 Results .................................................................................................................................... 21
   3.1 Oceanographic Sampling .............................................................................................. 21
   3.2 Sargassum Presence vs. Absence .................................................................................. 25
   3.3 Movement ...................................................................................................................... 25
   3.4 Ecological Niche Factor Analysis .................................................................................. 27
       3.4.1 Season One ......................................................................................................... 28
       3.4.2 Season Two ........................................................................................................ 31
       3.4.3 Season Three ..................................................................................................... 33
       3.4.4 Season Four ....................................................................................................... 37
   3.5 Management and Policy in the Caribbean ..................................................................... 37
   3.6 Management and Policy in the U.S. ............................................................................ 40

4.0 Discussion ............................................................................................................................... 43

5.0 Conclusion ............................................................................................................................. 51
1.0 INTRODUCTION

The dolphin, *Coryphaena hippurus*, is a highly migratory circum-tropical pelagic fish (Oxenford 1999). In the Atlantic, they are found as far north as Nova Scotia, Canada (Vladykov & McKenzie 1935), and as far south as South Africa (Barnard 1927). However, dolphin are generally considered common throughout the Caribbean, Gulf of Mexico, and from the Straits of Florida to North Carolina (Oxenford 1999). Due to their migratory nature, they are only seasonally abundant in these areas. Dolphin are valued in the western central Atlantic (Oxenford & Hunte 1986) by sport, commercial, and artisanal fishermen.

Although the life cycle of the dolphin is short (≤ 4 years, Beardsley 1967), it is cosmopolitan throughout its range. Dolphin have been recorded to regularly move hundreds and sometimes thousands of miles through multiple marine jurisdictional boundaries. They spend most of their time in surface waters (< 60 meters) and have been primarily observed in waters above 20° C (Potthoff 1971, Palko et al. 1982). A Recent study using popup satellite archival tags (PAT) has shown that dolphin can inhabit temperatures as low as 16° C, and spend a majority of their time in warmer surface waters (27.2°C – 28.9°C) in the upper 10 meters of the water column (Hammond 2008). Both sexes reach maturity during their first year of life (between the lengths of 35-55cm, fork length), and spawning primarily occurs in waters above 24° C (Beardsley 1967).

Dolphin are voracious predators and are considered feeding generalists due to the wide range of prey species. Primary prey for adult dolphin are fish (Gibbs & Collette

---

1 The term “fishermen” will be used throughout as a general term to describe a person who captures fish, regardless of gender.
2 Maps showing movement and distance are available at http://dolphintagging.homestead.com/.
1959, Shcherbachev 1973, Rose & Hassler 1974, Massutí et al. 1998), although squid and crustaceans are also taken. Rose and Hassler (1974) found that five fish families accounted for 74% of the prey weight, and that Sargassum was present in 28% of the stomachs. These were; Exocoetidae (26%), Scombridae (22%), Carningidae (12%), Balistidae (9%), and Coryphaenidae (5%).

The occurrence of dolphin seems to be closely tied to the presence of Sargassum (Sargassum fluitans and Sargassum natans) mats (Gibbs & Collette 1959, Beardsley 1967, Palko et al. 1982). It is suggested that the dolphin use the floating Sargassum mats for shelter from predators (tuna, sharks, marlin, sailfish, and swordfish) and for the abundant prey species available within the mats. Many stomach content studies show the presence of Sargassum in the stomach, as well as numerous species of vertebrates and invertebrates that inhabit the mats (Gibbs & Collette 1959, Shcherbachev 1973, Palko et al. 1982). Sargassum circulates between 20° and 40° N latitude and 30° W longitude, with an apparent center between 28°N and 34°N (Butler et al. 1983, Dooley 1972). While speculation exists, the relationship with Sargassum warrants increased investigation.

Most dolphins are observed over continental shelf/slope waters. However, they do occur over the deeper waters of the abyssal plain (Gibbs & Collette 1959, Shcherbachev 1973). Ditty (1994) inferred from the distribution of very small (<7 mm) larvae in the Gulf of Mexico that spawning occurs in the oceanic waters here, rather than over shelf waters.

Dolphin in the western central Atlantic have a protracted spawning season, and may spawn multiple times during the season (Palko et al. 1982). Known spawning
locations are; North Carolina (late spring through the summer) (Schuck 1951), the Florida Current (year round) (Gibbs & Collette 1959, Beardsley 1967, Shcherbachev 1973, Fahay 1975, Powles & Stender 1976), Puerto Rico (March – June) (Perez & Sadovy 1992), Barbados (year round) (Oxenford & Hunte 1986), and in the Gulf of Mexico (year round) (Ditty et al. 1994).

There has been some disagreement about the stock structure of the dolphin. Oxenford and Hunte (1986) suggested a two stock hypothesis based on information recorded in previous studies, seasonal catch statistics from various countries, genetic techniques (gel electrophoresis), and life history characteristics. The two stock hypothesis proposes one northern stock and one southern stock. The northern stock occupies the waters north and west of Puerto Rico and exhibits a clockwise annual migration pattern. They suggest that this stock winters off the northwest coast of Puerto Rico, migrates through the Bahamas in spring, moves north (using the Gulf Stream) through the Straits of Florida up to North Carolina in the late spring/early summer, resides in the Carolina and northern waters throughout the summer, then migrates out towards Bermuda and the Sargasso Sea in the fall, eventually making their way back to Puerto Rican waters in the Winter. The southern stock occupies the waters around Barbados in the winter, migrates north to southern Puerto Rican waters for the summer, then takes a clockwise route around the Lesser Antilles in the fall leading back to Barbadian waters for the winter.

Since the 1986 study, the idea that there are two stocks within the western central Atlantic and Caribbean has been discredited. This is largely based on the contentions of Mahon and Mahon (1987) and the genetic study by Robin Wingrove (2000). The
Wingrove study showed no genetic differences between dolphin from North Carolina, South Carolina, Georgia, Florida, Gulf of Mexico, Puerto Rico, Bermuda, The Azores, Martinique, Barbados, Tobago, and Brazil.

While Oxenford and Hunte’s two stock hypothesis may be unproven, the seasonal abundance of dolphin in these areas is readily observed. While the explicit movements of dolphin throughout the Caribbean region are largely unknown, the south to north movement along the Atlantic coast of the United States is indeed observed (Hammond 2006). The generalized seasonal movement of dolphin is shown in figure 1.

**Figure 1.** Map showing the generalized seasonal movement and distribution of *C. hippurus*. Red arrows indicate northern movement. Blue arrows indicate southern movement. This representation is based Oxenford and Hunte (1986).
Dolphin distribution in relation to the environment is essential for ecological understanding. Many traditional habitat distributional studies have relied on approaches that require presence-absence data (Guisan & Zimmermann 2000). This requires data where the species is known to occur as well as data where it does not occur. In many cases the presence locations and absence locations are given equal weight. In these models it is essential that occurrence data is as accurate as the absence data, and that there are no ‘false’ absences. These ‘false’ absences are locations where a species occurs but for some reason was not detected (Hirzel et al. 2002). In the marine environment, accurate absence data may all but be impossible to collect, particularly for species that occur far from shore and are very mobile (MacLeod et al. 2008). Comparative analysis has shown that presence-only models have a high level of accuracy in comparison to presence-absence methods and are sufficient for modeling distribution (Elith et al. 2006).

Ecological niche factor analysis (ENFA) uses presence only data to compute suitability functions by comparing the species distribution in the eco-geographic variable (EGV) space with that of the whole set of cells in the study area (Hirzel et al. 2002). This method is based on Hutchinson’s (1957) concept of the ecological niche being the hyper-volume in the multidimensional space of ecological variables with which a species can maintain a viable population. Hirzel (2002) applies this definition in the same sense; the ecological niche is the subset of cells in the eco-geographical space where the focal species has a reasonable probability of occurrence. The ENFA converts the multiple correlated variables into multiple non-correlated factors. The first factor that is extracted for analysis is the marginality (M), which is the maximal difference between environmental conditions in the available habitat and the used habitat. Marginality is a
measure of distance in ecological space of average environmental conditions of available and used habitat. The second factor that is extracted is the specialization (S), which is the maximal difference in variation between the available habitat and the used habitat. Specialization is a measure of tolerance of the ecological niche. The higher the specialization the less tolerant the species is to deviations to average environmental conditions. ENFA will be used to analyze the habitat preferences for dolphin in this study.

The habitat preferences are based on the multiyear efforts of the Dolphinfish Research Program\(^3\) (DRP). The main goal of the DRP is “to establish the temporal and spatial occurrence and movement patterns of the common dolphinfish in the United States territorial waters of the Atlantic and Gulf of Mexico”. The program has deployed over 8,500 conventional tags between the start of the program in 2002 through the present using recreational anglers. Approximately 250 tags have been returned to date. This program also uses satellite tagging technology to analyze and track the movements of dolphin. This program is the largest scale tagging program for *C. hippurus* and continues to provide valuable data.

Currently, In the United States *C. hippurus* is managed by the South Atlantic Fishery Management Council (SAFMC), in cooperation with the New England Fishery Management Council (NEFMC) and the Mid-Atlantic Fishery Management Council (MAFMC). The most recent (and first) fishery management plan (FMP) for dolphin was intended to encompass the entire Atlantic region, the Caribbean region, and the Gulf of Mexico region. However, this joint plan was never achieved because of the additional

\(^3\) The Dolphinfish Research Program is operated by Cooperative Science Services L.L.C. Detailed description can be found at http://dolphintagging.homestead.com/about.html
time needed to address the Caribbean and Gulf areas. Instead, the SAFMC constructed an
Atlantic-wide plan with guidance from the NEFMC and MAFMC that could be
implemented in a timely manner ((SAFMC) 2003). The plan was written in 2003 and
was approved in 2004. Fishery data from the Gulf of Mexico and Caribbean region are
ignored in the FMP. Only fisheries data that is within the jurisdiction of the SAFMC,
NEFMC, and MAFMC are included. Dolphin are considered as one unit stock throughout
the western central Atlantic, Caribbean and Gulf of Mexico based on the study by R.
Wingrove (2000), and the DRP tagging results showing large scale movements
throughout the regions (Hammond 2006). The U.S. fishery is dominated by recreational
fishermen, with a fractional contribution of catch from the commercial sector (SAFMC
2003).

There are at least 37 non-U.S. countries that are fishing for dolphin in the wider
Caribbean region. In contrast to the U.S., the major stakeholders in these fisheries are
commercial and artisanal/small-scale (Mahon & Oxenford 1999). Since there is no
regional fishery management organization that requires standardized statistical reporting,
the records that exist are scattered and are often inaccurate.

Distribution of dolphin is clearly influenced by the physical and biological
oceanographic environment. Although dolphin have shown patterns in where they were
observed (e.g. warm water, tropical/sub-tropical areas, Sargassum mats), a more precise
evaluation is needed. One focus of this study is to evaluate which environmental factors
contribute to the distribution and their relative importance. Based on the historic
observations of dolphin it seems plausible that they will be found in waters warmer than
20° C, will commonly be associated with Sargassum, may be found over waters of any
depth, and will travel long distances through multiple jurisdictional boundaries. The most effective way to investigate is to use spatially explicit analytical techniques that will quantify environmental preferences, and will have the ability to predict suitable habitat. Also, remote sampling using a geographic information system (GIS) will provide insight to environmental preferences. The goal is not only to characterize where dolphin are able to occur, but to also discover what they search for in their environment. Another focus is to evaluate the movements of individual dolphin in terms of jurisdictional boundaries and current policy. Effectiveness of the current management regime concerning *C. hippurus* will be evaluated, and recommendations will be made based on the results and conclusions of this study.

2.0 METHODS

2.1 South Carolina Division of Natural Resources (SCDNR) /Cooperative Science Services L.L.C. Dolphin Tagging Project (Dolphinfish Research Program)

The marine division of the SCDNR initiated a dolphin tagging project in order to better understand dolphin distribution and movements. The project was started in 2002 and approximately 430 conventional\(^4\) tags were deployed during the first year. The tags were Hallprint PDAT nylon dart tags with an external 15.2 cm yellow or orange polyethylene streamer. The project was operated by the SCDNR through 2005 because the project was slated to end. Instead, the Dolphinfish Research Program (Cooperative Science Services L.L.C.) was established in 2006 by Don Hammond along with many

---

\(^4\) A “conventional” tag is any tag that is affixed to a fish by humans. Usually location and biological parameters are recorded, and the tag will contain contact/reward information upon recapture.
sponsors and the project was kept alive. Since 2002, over 8500 tags have been deployed and about 250 have been recaptured.

Printed on the tags is the tag number, the address of the DRP, the project website (www.dolphintagging.com), the parameters that should be measured, and reward amount. Initially the reward was $20 cash or a dolphin tagging project t-shirt. Currently, the reward is a t-shirt along with entrance into a raffle to win a rod/reel combination\(^5\). Participating taggers are instructed to implant the tag in the back musculature approximately ½ - ¼ the fish’s body length behind the head. Also, the tag should be placed at a 45° angle toward the rear of the fish with the implanted barb facing down inside of the fish\(^6\). The corresponding data cards were filled out appropriately and mailed back to the DRP. The data card has a variety of information including; location, date, Sargassum presence/absence, Sargassum form, Sargassum, density, water temperature, length of the fish (fork length), and the sex of the fish.

The fish that were released in this study fall within the years of 2002 through 2007. The number of dolphin released was 8,492. Of these, 4751 included water temperature, 3096 included measured fork length (FL), and 3290 had recorded Sargassum presence/absence.

The fish that were recaptured fall within the years of 2002 through 2008. The total number of dolphin recaptured during this time was 257 (~ 3.03%). Of these; 36 were sexed (male/female), 102 included water temperature, 116 recorded fork length, 108 included Sargassum presence or absence.

\(^5\) The rod/reel combination is a stand-up custom built rod by Star Rods, and a Shimano TLD-50. Approximate value ~$700

\(^6\) More specific instructions are found at www.dolphintagging.com. Anglers are instructed to read this prior to participating in the project and acquiring tags.
This study relies on the honesty and cooperation of recreational anglers in a variety of different regions. The accuracy of data that was reported by the anglers is assumed to be accurate. It was also assumed that the behavior of the tagged fish was not significantly influenced by the tag implantation. The anglers that deployed and recaptured the tags can be quantified into two categories of effort; anglers that were targeting dolphin, anglers that were targeting other pelagic species. It is unknown how many anglers fall into either category.

2.2 Study Area

In order to properly assess environmental variables and encompass a representative area of possible occurrence for the dolphin, a study area was chosen (figure 2). The northern extent of the study area is 41° N latitude, which is approximately 24km south of Nantucket Island, Massachusetts. Gibbs and Collette (1959) considers 45° N latitude the extreme northern extent of *C. hippurus*, noting that few have been observed north of Cape Cod. Oxenford (1999) considers the dolphin common from North Carolina (~33° - 36° N latitude) to the northeast coast of Brazil (~ 4°N - 5°S latitude). Since there are consistent catches of dolphin off the coast of New York to southern Massachusetts and a dearth of catches north of Cape Code (SAFMC 2003), 41° N is a plausible northern extent for the study area.

The southern extent of the study area is 0° latitude. The southern extent is noted to be the northeastern coast of Brazil (4°N - 5°S latitude). This effectively excludes the extreme southern portion (as was done with the northern portion) of occurrence, a central location was chosen on the northeastern coast of Brazil, the equator (0°). Hence, the extreme 5° of latitude are excluded, in order to encompass the habitat that the dolphin
The eastern extent of the study area is 49° W longitude. This coincides with the point that the equator meets the northeastern coast of Brazil. The western extent of the study area is the western most portion of the Gulf of Mexico, or approximately 98° W longitude.

2.3 Oceanographic Sampling of Conventional Tags

2.3.1 Bathymetry and Slope
Coastal Digital Elevation Model (DEM) grids (3 arc second) were downloaded from the NOAA Geophysical Data System (GEODAS), National Geophysical Data Center (NGDC) website (Divins & Metzger). Volume 1-5, and 9 were used, which encompasses the coastal ocean from Maine to Texas, and Puerto Rico. For the remaining oceanic study area, the S2004 grid\(^7\) (1 arc minute, \(\sim\) 1.86-km) was used based on evaluation by Marks and Smith (2006). Slope grids were then created in ArcGIS 9.3 using a 3x3 focal window. The slope grid represents the highest range of vertical relief for the focal area. Locations of the released and recaptured dolphin were sampled for depth and slope values using ArcGIS 9.3. Values taken from the more precise coastal DEM grids were retained over values from the S2004 grid.

2.3.2 Distance to Continental Shelf and Shoreline

Location of the continental shelf was calculated as the 200 meter isobaths throughout the study area, using the S2004 grid. Euclidean distance was calculated from the continental shelf throughout the study area. Release and recapture locations were then sampled using ArcGIS 9.3 to obtain distance values. Location of shorelines in the study area were downloaded from the NOAA National Geophysical Data Center (NGDC) website\(^8\). Euclidean distance was calculated, and release/recapture points were sampled using ArcGIS 9.3.

2.3.3 Sea Surface Temperature (SST) Sampling

Only 56\% of the total release locations and 40\% of the recapture locations included in situ temperature measurements. Sea surface temperature values were

---

\(^7\) The S2004 grid is unpublished, but is available online: ftp://falcon.grdl.noaa.gov/pub/walter/Gebco_Sands_S_blend.bi2.

\(^8\) http://www.ngdc.noaa.gov/mgg/shorelines/data/gshhs/
obtained\footnote{SST and chlorophyll data was downloaded and maintained by the Marine Geospatial Ecology Laboratory (MGEL) at Duke University. http://www.mgel.env.duke.edu} using Advanced Very High Resolution Radiometer (AVHRR) sensors (Pathfinder SST, http://www.podaac.jpl.nasa.gov). The data grids consisted of daily and 8-day averaged SSTs on a 4-km equal angle grid. The values were sampled based on date using the Marine Geospatial Ecology Tools (MGET)\cite{Roberts}. The \textit{in situ} values were retained over the daily values, which were retained preferentially to the 8-day values. Data from 2002-2006 were used, and the total number of release locations with corresponding SST values is 7,432 (86%). The total number of recapture locations with SST values is 138 (54%).

\textbf{2.3.4 Chlorophyll Concentration Sampling}

Surface chlorophyll concentration data\footnote{SST and chlorophyll data was downloaded and maintained by the Marine Geospatial Ecology Laboratory (MGEL) at Duke University. http://www.mgel.env.duke.edu} from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and the Moderate Resolution Imaging Spectroradiometer (MODIS/Aqua) was used (http://www.oceans.gsfc.nasa.gov). Data from 2002-2006 was used, and consisted of daily and 8-day averaged chlorophyll concentration values on a 9-km equal angle grid. Similar to the SST filtering process, daily measurement were given priority over 8-day values. Sampling was also done using MGET. A total of 4,965 release locations (58.5\%) chlorophyll values were retrieved, and total of 133 (52\%) chlorophyll values at recapture locations were retrieved.

\textbf{2.4 Data Filtering}

After close evaluation, it was determined that many of the data points were not correctly reported by the program participants. It was apparent that many reported geographic locations were located at docks, rather than release or recapture locations. Also, many dates were misreported so that release/recapture could no longer be
corroborated. A total of 58 release locations and a total of 6 recapture locations were excluded from the analysis.

2.5 Sargassum Presence vs. Absence

To determine if there was a difference between dolphin captured where *Sargassum* was present versus dolphin captured where there was no observed *Sargassum*, pairwise significance tests were used. The variables tested were: depth, slope, sea surface temperature, surface chlorophyll content, distance to shoreline, distance to continental shelf, and fork length.

The Kolmogorov-Smirnov (K-S) test is a goodness of fit test for continuous distributions that are independent (Verzani 2005). The distribution for presence and absence of each variable has a cumulative distribution function (c.d.f), which describes the probability distribution for the variable X. The presence distribution for each variable has a c.d.f. described by $F_p(x)$, and the absence distribution has a c.d.f described by $F_A(x)$. The two sample K-S significance test was used using the following formulas:

$$H_O: F_p(x) = F_A(x), \quad H_A: F_p(x) \neq F_A(x)$$

Where $H_O$ is the null hypothesis and $H_A$ is the alternative hypothesis. Initially, a two-sided test was performed in order to reject the null hypothesis. If the null hypothesis was rejected, then a one sided test was used to explore if one distribution was larger than the other.

2.6 Movement

Analysis of movement was done for the 215 dolphin with matching release and
recapture locations. Days at liberty and straight line distances were calculated, and movement through political and jurisdictional zones were analyzed. Marine cadastre boundaries that were downloaded included; (1) exclusive economic zones\textsuperscript{10} (EEZ) for the study area, (2) the Food and Agricultural Organization (FAO) fisheries statistical boundaries\textsuperscript{11}, (3) U.S. fishery management council (FMC) boundaries\textsuperscript{12}, (4) U.S. National Marine Fisheries Service (NMFS) boundaries\textsuperscript{13}, and (5) state boundaries which were calculated as the area between the EEZ and the shoreline.

2.7 Habitat Modelling

2.7.1 Presence Only Habitat Model — Ecological Niche Factor Analysis

The basic tenet of ecological niche factor analysis (ENFA) is to define the realized niche of the species by comparing its observed habitat to its available habitat. In this study, the observed habitat for dolphin is based on field observations of captured dolphin. The available habitat is the area encompassed in the study area (figure 2). The static features (discussed in the previous sections) of the available habitat are bathymetry, bathymetric slope, distance to shore, and distance to the continental slope. The variable features are sea surface temperature (SST) and sea surface chlorophyll-\textit{a} content. SST and chlorophyll-\textit{a} are continuously changing, thus presenting a temporal challenge to this type of analysis. A model approach was chosen that encompasses all of the locations over the entire study period. Each of these variables are considered eco-geographical variables (EGVs)

Since \textit{C. hippurus} shows seasonal movement patterns within the study area, the

\textsuperscript{10} Flanders Marine Institute (http://www.vliz.be/vmdcdata/marbound/)
\textsuperscript{11} http://www.fao.org/geonetwork/srv/en/main.home
\textsuperscript{12} http://www.csc.noaa.gov/legislativeatlas/html/summary/fmc.htm
\textsuperscript{13} http://www.csc.noaa.gov/legislativeatlas/html/summary/nmfslink.htm
most appropriate technique is create four individual seasonal models. Season one consists of the first three months of the year (January, February, and March), season two is the next three months (April, May, and June), season three is the next three months (July, August, and September), and the fourth season consists of the final three months of the
year (October, November, December). The static variables are consistent throughout the
seasonal models, but SST and chlorophyll are different in each season.

The best representation for SST and chlorophyll for each season was to create
seasonal climatologic grids. Average sea surface temperature was calculated for each
month (2002-2006), then temperature averages were calculated across years (2002-2006).
These monthly climatology grids were then averaged by season. The end result was four
seasonal climatology grids representing average sea surface temperature from 2002-2006.
The same process was used for chlorophyll-\(a\), but only from 2002-2005.

It became apparent that the frequencies of depth values throughout the study area
were either large (deep) or small (shallow). The large values are indicative of areas
deeper than 200m, and the small values indicate areas that are shallower than 200m
(continental shelf). This variable was coded as 0 (deep) or 1 (continental shelf) before
being imported into the ENFA.

The factorial analysis is robust to non-normal distributions, but it is ideal to have
unimodal and roughly symmetric variables (Hirzel et al. 2002, Basille et al. 2008). The
variables with asymmetric distributions were transformed to as close to normal as
possible. A natural logarithmic transformation was used on the bathymetric slope
variable. A square root transformation was used on distance to shore and distance to
continental shelf break variables.

The analytical specifics of the ecological niche factor analysis are given in Basille
(2008), and Hirzel (2002). For the purposes of this analysis the available habitat is
described by \(P\) environmental variables (6 isometric grids for each season) in \(N\) pixels. \(Z\)
is the \(N \times P\) matrix with the values of \(P\) variables. \(Z\) defines a cloud of points in the \(P\)-
dimensional ecological space. The $Z$ matrix is column centered and scaled so that the centroid of the scatterpoint plot corresponds to the origin $O$ of the ecological space and represents the average available habitat (figure 4). Each available pixel in the study area has equal “availability weight”. These weights sum to 1, and are $1/N$ for all pixels.

**Figure 4.** Stylized representation of the ecological niche and available space from (Basille 2008). A) Representation the available habitat (small dots) and the used habitat (large spheres) in $P$-dimensional space. The centroid $O$ of available space is centered on the origin, and the centroid of used space $G$ is separated from $O$. The vector $q$ is the marginality vector normed to 1. The distance between $O$ and $G$ in ecological space is the marginality. The vector $u_1$ is the first vector of specialization. The $Z$ vectors are three theoretical eco-geographical variables. B) The biplot. This is a two dimensional representation of $P$-dimensional space. The vectors $u_1$ and $q$ are orthogonal and define the plane on which the points are projected.

The locations within the available habitat area of grid cells were the dolphin were observed defines the used habitat. The vector $p$ of length $N$ provides the proportion of locations in each cell and defines the utilization weights (the utilization weights sum to 1). The points in the available space for which the corresponding utilization weights are larger than zero defines the used space. This used space is the ecological niche. The centroid of this used space is referred to as $G$ and represents the average combination of environmental conditions (EGVs) experienced by *C. hippurus*. 
Figure 4 shows that the marginality (M) is measured as the ecological distance between O and G. The model maximizes this distance. The higher the marginality value, the more the niche deviates from the average conditions of the available habitat (Basille et al. 2008).

The specialization (S) is defined as the ratio of the standard deviation of the available habitat to the used habitat; this ratio is also maximized in the model. The higher the specialization, the more restricted the niche is in that dimension, which indicates that the species does not tolerate large variation in habitat features that determine that dimension (Basille et al. 2008).

The ENFA was done using the R-package “adehabitat” (Calenge 2006). The R software is freely available on the internet at http://www.r-project.org/ and was designed by the R Development Core Team (2005). All data inputs were first converted to the match the study area, had a cell size of 0.0439 (~ 4-km), had 32-bit floating point values, had 933 rows and 1112 columns. These grids were then converted to ASCII grids for input into R. Once the data was properly formatted in R, the ENFA function produced statistical summaries, plots, and habitat suitability maps.
Figure 5. Histograms of combined in situ and remotely sampled variables for released and recaptured dolphin. Distributions that are unimodal have mean, bimodal or multimodal distributions do not. Red line is a smoothed frequency line for visual purposes.
3.0 RESULTS

3.1 Remote Sampling and in situ Sampling

After the release and recapture data were filtered for spatial and temporal inconsistencies, a total of 8434 release locations and 215 recapture locations were retained. The 215 recapture locations were locations that matched release tags from 2002-2007. Figure 5 shows the overall frequency distributions of the measured environmental variables. All locations were sampled for depth, bathymetric slope, distance to shore, and distance to the 200 meters isobaths (continental shelf).

The depth at which dolphin were observed varied widely. The values in figure 5 reflect combined in situ and remotely sampled values. The maximum depth was 4810 meters, which is clearly located above the abyssal ocean. The mean depth was 232.4 meters, while the median was 188 meters. Figure 5A shows that the majority of dolphin were captured at depths less than ~800 meters. There are two peaks in the 0-300 meter range at approximately ~100 meters and ~ 200 meters. Average bathymetric slope (fig. 5B) was 6.524 meters. The possible range of slope areas was 0-4039 meters, which indicates that most dolphin occurrences are in low slope areas. Distance to the 200 meter isobaths (continental shelf break) throughout the study area ranged from 0 km to 150 km. The majority of dolphin observations occurred less than 50 km from the shelf continental break (fig. 5C). Distance to shoreline shows a
strong bimodal distribution (fig. 5D) with peaks at ~25km and ~95km. The closest to shore that dolphin were captured was ~0.75km, and the furthest from shore was ~259km.

A total of 7,430 locations were sampled for sea surface temperature (fig. 5E). The lowest observed temperature was ~10° C, but the majority ranged from 20.0°C to 34.9°C. The mean observed SST was 27.62°C. A total of 4,965 locations were sampled for sea surface chlorophyll-α concentration (mg m⁻³), shown in figure 5F. The lowest observed value was 0.00 mg m⁻³, and the highest observed value was 5.20 mg m⁻³. The mean chlorophyll-α concentration was 0.1824 mg m⁻³, and the majority of dolphin were captured in low concentration waters (below 0.5 mg m⁻³).

Fork length was measured at a total of 3088 tag locations (figure 6). The shortest measured dolphin was 25.4 cm, and the longest was 121.9 cm. The mean measured length was 50.66 cm.
3.2 Sargassum Presence vs. Absence

The Kolmogorov-Smirnov (K-S) significance tests showed that the distributions for all variables differed significantly when *Sargassum* was present versus when it was absent. The cumulative distribution functions (c.d.f) for each variable are shown in figure 7. A two sample one sided K-S test was used to assess whether the dolphins found associated with *Sargassum* had higher or lower values than dolphin where no *Sargassum* was present. In all cases, the null hypothesis was rejected. Figure 7 shows the results of the one sided test using greater than or less than symbols. Depth, slope, distance to shelf, chlorophyll, and fork length are generally lower when *Sargassum* is present. Distance to shore and sea surface temperature are generally higher when *Sargassum* is present.

3.3 Movement

A total of 215 released/recaptured dolphin were used in this study. The fish were released from 2002 through 2007, and recaptured from 2002 through 2008. All fish were released within an exclusive economic zone (EEZ) area. 15 fish were released in the Bahamas EEZ, and 200 were released within the United States EEZ (four of which were within Florida state waters). All of the recaptured fish were taken from EEZ waters as well. Of the 215 recaptures; 204 were within U.S. waters (of these; 10 within Florida waters, 1 Puerto Rico), and 11 were from other countries (Mexico, Antigua and Barbuda, Venezuela, Bahamas, and Cuba). Within U.S. waters 45% of dolphin moved from one fishery management council (FMC) area to another FMC area.

The average distance traveled in straight line distance (figure 8) was 406.6 km. The longest distance was 2512.5 km. The average days at liberty (days between release and recapture) was 40.77, with the longest being 373 days.
The complexity of the movements of *C. hippurus* is shown in figure 8. This map shows some of the most prominent marine jurisdictional boundaries that the dolphin may swim through. Dolphin move throughout management zones within the U.S. (state, fishery management council, National Marine Fisheries Service) and cross international EEZ boundaries. It is apparent that dolphin can cross these boundaries in a short amount of time.

**Figure 8.** Map showing the complexity of the multiple cadastral zones that *C. hippurus* swims through. This exemplifies the challenges faced by managers and scientists. FAO = Food and Agricultural Organization, EEZ = Exclusive Economic Zone, FMC = U.S. Fishery Management Council Area, NMFS = U.S. National Marine Fisheries Service Area.
of time because of their close proximity and overlap (figure 8). It should be noted that FAO area 31 encompasses the majority of dolphin observations in this study. The FAO zones are strictly used for fishery statistical coverage; requiring member countries to report catch statistics.

3.4 Ecological Niche Factor Analysis

Assessment of the ecological niche was done using the eco-geographic variables (EGVs); sea surface temperature, sea surface chlorophyll-$a$, distance to shore, distance to the continental shelf break, depth, and bathymetric slope (table 1). As mentioned, four seasonal models were constructed to properly capture the seasonal behavior of dolphin within the study area. Table 1 shows the six EGV names that were used in the ENFA and their meaning. The $sst$ and $chl$ variables were different for each season, but were given the same code name in the models.

<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$sst$</td>
<td>Sea Surface Temperature (°C)</td>
</tr>
<tr>
<td>$chl$</td>
<td>Chlorophyll-a concentration (mg m$^{-3}$)</td>
</tr>
<tr>
<td>slope</td>
<td>Bathymetric slope (meters)</td>
</tr>
<tr>
<td>shore</td>
<td>Distance to shore (km)</td>
</tr>
<tr>
<td>shelf</td>
<td>Distance to continental shelf (km)</td>
</tr>
<tr>
<td>shallow</td>
<td>Depth values. High value = shallow depth, low value = high depth.</td>
</tr>
</tbody>
</table>

For each season, the marginality axis and one specialization axis (as opposed to multiple) were produced from the models. The results for each season are best described by showing the eigenvalues of specialization barplot, the biplot, and the habitat suitability map. The eigenvalues of specialization barplot shows the specialization values of each EGV relative to one another. Multiple specialization axes can be retained if more than one EGV is of high importance (high eigenvalue). However, each seasonal analysis produced one specialization axis that accounted for the majority of the specialization. The
biplot is a two dimensional representation of multi-dimensional ecological space. It contains information about the available habitat, the used habitat, and the relationship of eco-geographic variables within the model. The habitat suitability model is a geographic representation of preferred vs. non-preferred habitat. The ENFA model produces scores for each cell in the study area. These scores are used to evaluate distance from the centroid of the ecological niche. This is an evaluation of whether or not the cell has the desired combination of environmental conditions.

3.4.1 Season One – January, February, and March

Seasonal climatology of sea surface temperature and surface chlorophyll-a content were used along with the static variables shown in figure 3. Figure 9 shows the average temperatures and chlorophyll content of surface waters during January, February and March (2002-2006). These are representations of available habitat for the study area.

![Figure 9. Maps showing the seasonal climatology of sea surface temperature (left) and chlorophyll-a content (right). Sea surface temperature values are in degrees Celsius. Black areas were not included in the analysis.](image-url)
Figure 10. Graphical outputs from the ecological niche factor analysis for season one. The biplot (top) for season one. Light grey polygon is the available habitat, and dark grey is the used habitat. The biplot shows that sst is the dominant specialization factor (y-axis), and the rest of the EGVs combine to account for the marginality (x-axis). The eigenvalue barplot showing specialization values for the EGVs is within the biplot (top). The first specialization value was 101, and corresponds to the sst variable. The habitat suitability map (bottom) shows areas of high suitability (green) and low suitability (blue). The white areas are areas of no data, but represent continental land masses and islands in the study area. N = 221.
The ecological niche factor analysis was performed and revealed some interesting results. Figure 10 shows the eigenvalues of specialization within the biplot, the largest being 101.2 for sea surface temperature. Since one variable accounts for the majority of specialization, only one specialization axis was retained. The large specialization value for sea surface temperature means that the available habitat has a variance that is 101.2 times larger than the used habitat. The large marginality value (6.24) for the model indicates that the average available habitat is substantially different than the used habitat.

To evaluate the accuracy of the model a randomization test was performed using Monte-Carlo methods. Specifically, 1000 permutations of 221 random locations were dispersed throughout the study area. At each permutation the ecological niche factor analysis was performed on the random locations and evaluated against the observed locations. The results of the randomization test were that the observed locations were significantly different than the randomizations (p-value < 0.001).

Figure 10 shows the biplot for season one. Instead of showing a scatterplot of points like figure 4, the used and available habitats are depicted as polygons. The x-axis is the axis of marginality and the y-axis is the axis of specialization. The arrows for each EGV are vectors in $P$-dimensional space projecting from the centroid the available habitat. Arrows that parallel the marginality axis are variables that contribute to the marginality, while arrows that parallel the specialization axis influence the specialization. Arrows projecting in the positive x or y direction indicate that the used habitat variables have higher relative values, while arrows in the negative x and y direction indicate lower relative values. The biplot indicates that the preferred (used) habitat that dolphin occupy has higher bathymetric slope values, low depth values, short distances to the shoreline
and continental shelf, slightly lower chlorophyll values, and much higher sea surface
temperature values.

The results of the ENFA model were used to create a habitat suitability map (fig. 10, bottom). The blue areas indicate high suitability habitat for season one, while the
green values represent low suitability area. This map used the ENFA results to depict
suitability based on the combination of all six EGVs. Visual inspection of the map
indicates that SST may play a large role in predicted suitability because of the large area
in the north that has low suitability, which can be corroborated with the SST map in
figure 8. Since SST is the dominant specialization variable, it is intuitive that dolphin will
not inhabit the colder areas based on the biplot results. Since the study area is large, it is
difficult to interpret habitat suitability in local areas but major trends can be seen.

3.4.2 Season Two – April, May, and June

The ecological niche factor analysis for season two revealed more interesting
results. A high marginality value of 5.62 indicates that the difference between average
and available habitat is significant. Again, one variable accounted for the majority of

![Figure 11](image1.png)

Figure 11. Maps showing the seasonal climatology of sea surface temperature (left) and chlorophyll-a
content (right) for season two. Sea surface temperature values are in degrees Celsius. Black areas were not
included in the analysis.
Figure 12. The biplot for season two (top), and the habitat suitability map (bottom). The eigenvalues of specialization barplot is captured in the bottom right corner of the biplot. N= 5576
specialization (figure 12) and only one specialization axis was retained. The
corresponding variable was sea surface temperature with a specialization value of 11.34,
indicating a low variance in temperature range for the used habitat. The model indicates
that dolphin not only prefer warmer waters but areas that are shallow, have a low slope,
are close to shore and continental shelf, and have slightly higher chlorophyll values. The
habitat suitability map in figure 12 shows that the northeastern United States is still
unsuitable habitat because of low temperatures. The randomization test for the accuracy
of the niche was significant (p-value < 0.001).

3.4.3 Season Three – July, August, and September

Season three encompasses the late summer months of the year. The sea surface
temperature map in figure 13 shows that the lowest temperature available to dolphin is
9.34 °C. The marginality value is 5.23 for this season, indicating a stark difference
between average available and used habitat. The eigenvalues of specialization barplot
(figure 14) shows that one variable explains the majority of specialization. The
specialization value for season three is 12.43, and is explained by the chlorophyll-a

![Figure 13](image)

**Figure 13.** Maps showing the seasonal climatology of sea surface temperature (left) and chlorophyll-a content (right) for season three. Sea surface temperature values are in degrees Celsius. Black areas were not included in the analysis.
Figure 14. The biplot for season three (top), and the habitat suitability map (bottom). The eigenvalues of specialization barplot is captured in the bottom right corner of the biplot. N= 2323
variable (biplot, figure 14). The preferred habitat of dolphin in season three is characterized by low distance to the continental shelf and shoreline, and low bathymetric slope. Dolphin show preference for areas that are warmer than average, and are in shallower waters above the continental shelf (figure 14).

The major difference in this seasonal model is that surface chlorophyll-\(a\) content is the dominant specialization factor. The biplot in figure 14 shows that dolphin prefer habitat that has higher chlorophyll content than the available habitat. Also, the northeastern United States is now considered suitable habitat (figure 14, map). Although the model shows that the dolphin prefer habitat that has higher than average chlorophyll values, there is a tolerance range on the high end of the range as well. This can be seen by comparing the habitat suitability map in figure 14 to the chlorophyll-\(a\) map in figure 13. Visual inspection reveals that dolphin prefer habitat with higher surface chlorophyll values, but will avoid areas where it is too high like the U.S. Gulf Coast, and the northeast coast of South America. Again, the randomization test was highly significant (p-value < 0.001).

Figure 15. Maps showing the seasonal climatology of sea surface temperature (left) and chlorophyll-a content (right) for season four. Sea surface temperature values are in degrees Celsius. Black areas were not included in the analysis.
Figure 16. The biplot for season four (top), and the habitat suitability map (bottom). The eigenvalues of specialization barplot is captured in the bottom right corner of the biplot. N= 286
3.4.4 Season Four – October, November, and December

Season four encompasses the late fall/early winter time of the year. The marginality value for the model is 5.87. The eigenvalue barplot shown in figure 16 indicates that one variable accounts for the majority of the specialization. Chlorophyll is the dominant variable that explains the majority of the specialization, with an eigenvalue of 7.23. The biplot of the model (figure 16) indicates that dolphin prefer low distances to the shoreline and continental shelf, along with low bathymetric slope values. Dolphin also prefer shallow waters above the continental shelf, and warmer than average sea surface temperature values. The biplot also indicates that dolphin prefer higher surface chlorophyll habitat in relation to the available habitat. The Monte-Carlo randomization test for accuracy of the niche model was significant (p-value < 0.015).

3.5 Management and Policy in the Caribbean Region

The ecological complexity of *C. hippurus* in the study area is rivaled by the complexity of the regional fisheries and multitude of local jurisdictions. While regulation and enforcement of dolphin fisheries is the responsibility of individual countries in the Caribbean (Chakalall et al. 1998), there are international agreements that guide governance of shared resources. Some of the relevant organizations include; the FAO Western Central Atlantic Fishery Commission (WECAFC) was established in 1973, the UN Convention on the Law of the Sea (1982), the UN conference on straddling and highly migratory fish stocks (1995), and the FAO Code of Conduct for Responsible Fisheries (1995). Within the Caribbean, there are a variety of overlapping regional organizations that operate with the intention of cooperation for trading, resources, and a variety of other reasons. The membership of all regional and international organizations
with responsibility for fisheries management and development of dolphin in the wider Caribbean area is shown in figure 17. These organizations all operate at different capacities with respect to dolphin. The best suited regional organization that is involved with management of dolphin is the WEFAFC.

The WECAFC is a part of the FAO Fisheries and Aquaculture Department and was established in 1973. It is responsible for managing fisheries in statistical area 31 (figure 8). The goal of WECAFC is to “promote effective conservation, management, and development of the living marine resources” (FAO 2008) by promoting the application of the FAO Code of Conduct for Responsible Fisheries (FAO 1995), ensuring attention to
small-scale, artisanal, and subsistence fisheries, and improving the cooperation of institutional fisheries governance organizations. WECAFC encompasses almost all Caribbean and Gulf of Mexico stakeholder countries, as well as Japan (figure 17). The FAO Code of Conduct “sets out principles and international standards of behavior for responsible practices with a view to ensuring the effective conservation, management and development of living aquatic resources, with due respect for the ecosystem and biodiversity” (FAO 1995) which are used to guide WECAFC and other FAO regional fisheries bodies. Also, the code is designed to work in unison with UNCLOS (Article 1.1) and is generally thought of as a global guide for fisheries management and intergovernmental cooperation.

The third conference of the United Nations Convention on the Law of the Sea (UNCLOS) in 1982 (U.N. 1982) established guidelines for managing shared resources. UNCLOS does not have regulatory power over nations; rather it acts as a common worldwide standard for managing marine resources. Annex XI designates *Coryphaena hippurus* as highly migratory. Since the dolphinfish is highly migratory and occurs within exclusive economic zones (EEZ) of two or more coastal states as well as on the high seas adjacent to these areas, UNCLOS recommends “...agreement upon measures necessary to ensure the conservation and development of such stocks...” (Article 63.1) through “…appropriate international organizations with a view to ensuring conservation...” (Article 64.1).

In addition to the general text of UNCLOS, the 1995 United Nations Conference on Straddling and Highly Migratory Fish Stocks, or the “Fish Agreement”, is a supplement for management of shared fishery resources. The Fish Agreement uses more
strict language about promoting conservation of marine resources (Article 7, (U.N. 1995)), establishes a variety of guidelines for intergovernmental cooperation mechanisms for current organizations and for new organizations (Articles 8-14), and urges states to take a precautionary approach to management (Article 6).

Although membership and coherence with its recommendations are voluntary, WECAFC establishes a vehicle for collecting fisheries statistics (FAO database), provides a forum for mitigating resource disputes, and participates in an internationally accepted *modus operandi*. WECAFC also provides the most thorough investigations and recommendations for dolphinfish on a regional scale. The 2008 WECAFC report states that dolphin are a single stock throughout the Western Central Atlantic, that the biomass is above maximum sustainable yield (MSY), and that overfishing is not occurring (WECAFC 2008).

### 3.6 Management and Policy: United States Atlantic and Gulf Coasts

The institutional framework within U.S. waters is a “top-down” federal approach to management. Since *C. hippurus* primarily exists beyond state waters and above the continental shelf, the federal government is responsible for regulation. The domestic legislature that mandates the current management structure is the Magnuson-Stevens Fishery Conservation and Management Act of 1976 (MSA)\(^\text{14}\). This statute created the eight regional fishery management councils (§ 301, MSA). The fishery management councils that are involved in the management of the dolphinfish are; New England (NEFMC), Mid-Atlantic (NEFMC), South Atlantic (SAFMC), Gulf of Mexico (GMFMC), and Caribbean (CFMC). The management councils are responsible for submitting fisheries management plans (FMP) (§303, MSA) to the secretary of commerce.

\(^{14}\) As amended through January 12\(^{\text{th}}, 2007\).
for approval in accordance with the national standards for fishery conservation and management (§ 301, MSA).

The first fishery management plan for dolphinfish was approved in 2004, and is bound by the language of the MSA as well as other environmental statutes. The National Environmental Policy Act (1970) creates the structure of the FMP because each plan constitutes a “major federal action significantly affecting the quality of the human environment” (42 U.S.C. §4332 (C)). As such, the FMP must provide a detailed statement on; the environmental impact of the FMP actions, any adverse environmental impacts, a list of alternatives to the proposed actions, consideration of long term effects, and any irreversible or irretrievable commitments of resources (42 U.S.C. §4332 (2)(C)). This detailed statement is known as an environmental impact statement (EIS). Since NEPA is strictly procedural in nature, not substantive, plans can be turned down by the Secretary for not following NEPA, but there are no sanctions for making perverse decisions.

The United States is a member of WECAFC and actively reports fisheries statistics to the FAO. Since WECAFC only issues recommendations and status reports, the federal government is solely responsible for implementation of regulations, much like the Caribbean nations.

The story of the dolphinfish FMP is an example of inter-commission success and failure. Currently, the SAFMC published the first dolphinfish FMP in cooperation with the New England and Mid-Atlantic councils in 2004. Originally, The New England, Mid-Atlantic, South Atlantic, Gulf of Mexico, and Caribbean Councils were supposed to create a joint FMP that covered all regions. Before the joint FMP could be drafted, the
South Atlantic Council broke away from the group and took the lead in creating an Atlantic-wide FMP. As a result of this breakdown in cooperation, the current FMP only considers the Atlantic coast of the United States. There is no mention of catch statistics, biological impacts, social impacts, or any other issues in the Caribbean or Gulf of Mexico regions in the 2004 FMP. Despite this, the SAFMC recognized that there is one united stock throughout the Western Central Atlantic Ocean that is shared by all nations within its range.

The dolphinfish FMP was established in response to record high recreational catches (1995, 1997), uncertainty about the health of the stock, conflict/competition between commercial and recreational fishermen, localized depletion of dolphinfish, and was an effort to better characterize the biological and ecological information of the dolphinfish (§ 1.0 (SAFMC)). The FMP addressed these concerns in a number of

<table>
<thead>
<tr>
<th>ACTION</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Management unit is U.S. Atlantic Coast</td>
</tr>
<tr>
<td>3</td>
<td>Requires dolphinfish dealers to have a valid permit for purchase and sale. Mandatory reporting of sale statistics</td>
</tr>
<tr>
<td>4/5/6</td>
<td>Requires that the owner of a for-hire or commercial vessel obtain a permit to harvest or possess dolphin. Mandatory reporting in accordance with the Atlantic Coastal Cooperative Statistics program.</td>
</tr>
<tr>
<td>7/8</td>
<td>Maximum sustainable yield (MSY) is between 18.8 and 46.5 million pounds. Optimal yield (OY) is 75% of MSY.</td>
</tr>
<tr>
<td>10</td>
<td>Establishes a framework for an adaptive management mechanism</td>
</tr>
<tr>
<td>11</td>
<td>Recreational sale of dolphin is prohibited</td>
</tr>
<tr>
<td>12</td>
<td>1.5 million pound cap of commercial fisheries</td>
</tr>
<tr>
<td>13</td>
<td>Daily bag limit of 10 dolphin/person/day. Maximum of 60 dolphin/boat (doesn’t apply to headboats).</td>
</tr>
<tr>
<td>14</td>
<td>No transfer of fish at sea</td>
</tr>
<tr>
<td>15</td>
<td>Minimum size limit of 20 inches fork length</td>
</tr>
<tr>
<td>22</td>
<td>Essential fish habitat (EFH); Gulf Stream, Charleston Gyre, Florida Current, and Sargassum.</td>
</tr>
</tbody>
</table>

Table 2. Summary of selected actions under the 2004 Dolphin/Wahoo fishery management plan.
different actions, the most important of which are shown in table 2. Previous to the 2004 FMP, there were no regulations concerning the dolphinfish.

The SAFMC is only responsible for creating a FMP for submission to the Secretary of Commerce. Implementation of the prescribed actions is the responsibility of federal and state agencies. The federal agency that is primarily responsible for regulation is the National Marine Fisheries Service (NMFS) Southeast Regional Office. NMFS relies on coordination the various state agencies for implementation as well. Instead of making separate regulations for the dolphin that are caught within state waters, the states have adopted the regulations established by the SAFMC and NMFS.

4.0 DISCUSSION

Conventional tags were used to track the movements of *C. hippurus* throughout the study area. The observations during the release and subsequent re-capture were used to characterize their habitat preferences. A presence-only seasonal model was used to analyze the ecological niche that is occupied by dolphin throughout the study area. The results of the mark-recapture study and the ecological niche factor analysis supports a new approach to policy and management of dolphinfish in the western central Atlantic, Caribbean, and Gulf of Mexico.

The remote sampling combined with the *in situ* observations at tag locations produced much useful information. The results show that dolphin will inhabit shallow waters as well as deep waters, but a higher frequency of observations occurred in the shallow portions that are less than 500 meters (figure 5). The distance from the shoreline to the continental shelf varies throughout the study area, but is generally no more than
120 km from land. Areas deeper than the 200 meter isobath are considered continental slope and abyssal plain. The continental slope is an area of rapidly increasing depth, while the abyssal plain is an area of constant high depth. While recreational fishing effort is constrained to a certain proximity to shore, many dolphin are caught in the deep waters (> 200 meters).

It was expected that dolphin would be primarily observed in areas of high bathymetric slope. The mean observed slope value was 6.5 meters (figure 5B). A 3x3 focal window was used that encompasses approximately 31 km². For an area to have a slope value of 6.5 meters means that the maximum range of relief was 6.5 meters for the surrounding 31 km². It can then be concluded that dolphin are generally found in areas of lower slope. However, many dolphin were found in higher slope areas, they were just less frequently observed. When compared with the average distance to continental shelf (figure 5C), it can be seen that dolphin are usually found within 40 km of the shelf. Also, the frequency of occurrence increases with decreasing distance. This means that while dolphin are generally found in areas of low slope, they are usually near areas of high slope (the continental shelf).

It was expected that sea surface temperature observations would generally fall above the 20° C isotherm. Only two observations out of 7,570 locations had temperatures lower than 20° C. Figure 5E shows the distribution of sea surface temperature observations, with a mean of 27.62° C. This supports the general scientific consensus that the lower range of dolphin temperature tolerance is 20° C.

The mean chlorophyll-α value observed was 0.1824 mg m⁻³, which is a low value. Chlorophyll content is a measure of primary productivity and consequently water clarity.
Generally, highly productive (high chlorophyll) waters have low clarity due to the high concentration of phytoplankton inhabiting the surface waters. These low chlorophyll values indicate that dolphin generally inhabit waters with high clarity.

When considered together, the warm surface temperatures along with low chlorophyll values correspond to what is generally observed in warm oceans worldwide. In general, warm surface waters have low primary productivity because they are nutrient deficient. It is the cold surface waters in the high latitudes that support a higher level of primary productivity because of the influx of nutrients.

To test the possible difference between dolphin that were captured in association with *Sargassum* to the dolphin that were captured outside the *Sargassum*, a series of pairwise Kolmogorov-Smirnov tests were used. The results showed that there were differences between the distributions of *Sargassum* presence and absence. The most notable result is that dolphin found within *Sargassum* habitat are generally smaller in length. This partially corroborates the idea that smaller female dolphin are found associated with *Sargassum*, while larger males are found outside the *Sargassum*. This idea is untested but is common pattern observed by fishermen. The results certainly show that larger dolphin were taken outside of the *Sargassum*, but sex attributes are unknown at this point.

The seasonal ecological niche factor analysis (ENFA) models showed that habitat preferences change during different seasons. The multivariate models showed that preferred habitat in all seasons were; preference for areas of low distance to shore and continental shelf, and low depth (< 200 meters). During season one, dolphin showed preference to higher slope areas. However, the next three seasons showed a preference
for low slope areas. Sea surface temperature and surface chlorophyll-a concentration had the largest effect on the models. Suitable habitat in seasons one and two were limited by low temperature, further corroborating the influence of the 20° C lower tolerance range.

Chlorophyll-a became the prominent variable during seasons three and four. The change in dominant eco-geographic variables (EGVs) from temperature to chlorophyll creates habitat suitability maps that capture the seasonal south to north movement of dolphin. During season one the waters north of the Gulf Stream are cold (~1.4° C - 18°C) and unsuitable. This corroborates the general observations (Oxenford & Hunte 1986, Oxenford 1999) and catch data (SAFMC 2003) that show no dolphin north of North Carolina during season one. The biplot (fig. 10) shows that dolphin prefer habitat with higher than average temperatures and lower than average chlorophyll concentration.

Surface temperature is the dominant factor during season two as well. The habitat suitability map (fig. 12) shows similar features to season one, but more coastal habitat along the southeastern U.S. is now available as well as areas north of Cape Hatteras, NC. This is the time when dolphin are moving north during the spring months. The water temperatures north of the Gulf Stream are still too cold for dolphin to inhabit.

The general oceanographic features as well as the suitable habitat change drastically during season three. While dolphin still prefer warm waters, they are more influenced by surface chlorophyll levels. The model indicates that dolphin prefer areas with higher surface chlorophyll concentration. Since the surface waters north of the Gulf Stream are now at high enough temperatures for dolphin to exist, the next most important factor is chlorophyll level. This means that one temperature is no longer limiting, dolphin
will readily inhabit areas will lower clarity. This is most likely due to food availability. The habitat suitability map in figure 14 shows that preferred habitat now ranges the entire length of the U.S. Atlantic coast in the study area. This is what is seen in reality during the south to north migration. Catch data show that dolphin are taken in the mid-Atlantic and northeast states during the summer months (SAFMC 2003, NMFS).

Chlorophyll remains the dominant factor in season four. Dolphin still prefer areas of warm water. The habitat suitability model shows that most of the Atlantic coast of the U.S. is still preferred, but many localized areas are no longer preferred. The southern winter habitats off the coasts of the Caribbean islands are suitable areas as well.

The presence-only modeling approach applied to Coryphaena hippurus is a scientifically useful way to evaluate habitat using basic observations. While the Monte-Carlo methods provide an accuracy evaluation method, the results adequately captured the hypothesized seasonal movements along the U.S. Atlantic coast. Since the ENFA method is a comparison of available habitat to used habitat, it is sensitive to changes in study area (available habitat). The study area for this analysis attempted to include all available habitats for the stock of fish, even in data poor areas. The seasonal suitability of habitat can be more robustly modeled with a broader inclusion of catch data from more regions of the study area. Rigidity of the temporal component of the ENFA models are also a hindrance to accuracy. This study used seasonal climatology to account for this that used average conditions as a proxy for instantaneous conditions. While further temporal accuracy would improve the models, applications on this scale in the marine environment remain rare throughout the literature.
The tag-recapture analysis showed that dolphin are capable of travelling long distances over short time periods. While only 215 individuals were recaptured, many of them travelled through major marine jurisdictional boundaries. The estimates of boundary crossings are conservative because it was only assumed that each fish travelled in a straight line to where they were recaptured (not including the boundaries crossed on the way to the final destination). The map shown in figure 8 is a depiction of the complicated array of marine cadastre encompassed within the study area, overlaid with dolphin movement.

This study only solidifies the need for more horizontal integration of management for *C. hippurus* within the U.S. structure and international community. Unlike many stocks of fish that have become commercially and recreationally extinct, the current healthy state of the dolphin fishery presents the opportunity to create a regional management scheme that will protect the fish and its human dependants far into the future. It is apparent that while managing dolphin on a localized scale is the current mode of operation, a regional scheme is needed for proper management.

The current method of using localized regulations (or no regulations) with poor enforcement and non-reporting in the Caribbean region is ultimately doomed to failure. The WECAFC and the FAO are collecting fisheries statistics for the region, but many nations do not participate or heed their recommendations. This reduces the WECAFC assessments to an exercise of speculation. The WECAFC describes the fishery as “healthy”, but there is no baseline for comparison because of non-participation and lack of adequate monitoring resources.
In order to secure this fishery for the future, the Wider Caribbean region needs a centralized organization that not only conducts research and produces recommendations, but has the authority to allocate regulations to member countries. This presents two choices; create a new fishery organization in the Wider Caribbean region, or strengthen the Western Central Atlantic Fishery Commission. While strengthening the WECAFC would be the most efficient way to manage the fishery, it will be more politically feasible to create a new organization, a “Caribbean Fishery Council”, which operates in accordance with the same international agreements as the WECAFC and is tailored for the Wider Caribbean region. The political repercussions of using a U.N. body to decide resource allocation may hinder membership and create international discord. Structural changes to the Caribbean Council would include; allocation of fishery quotas to member countries based on updated stock assessments, regulatory mechanisms (time/area limits, catch limits, effort limits), mandatory monitoring and reporting, and increased enforcement. Member countries would have the right to use economic sanctions in response to non-compliance with WECAFC recommendations (in accordance with other international agreements). Of course, this will depend on voluntary participation of member countries and would ideally include other pelagic species. These measures will not only ensure the health of the fishery, but the health of local communities and economies that depend on it.

The current U.S. institutional structure is seemingly effective in terms of dolphin. However, the manner in which the SAFMC and other regional councils are operating is not. The creation of an FMP for dolphin is an improvement in and of itself. The proposed actions (table 2) that define the plan define a precautionary approach to
management. The SAFMC acknowledges that there is only one stock of dolphinfish throughout the entire Western Central Atlantic Ocean, which is crucial to any other decision that is made under the plan. Also, the implementation of dealers and fishermen reporting catch statistics is crucial to gauging the health of the stock, and whether the stock is being overfished. The commercial and recreational limits on catch quantity and size are sensible.

The current situation presented by the 2004 dolphinfish FMP (action 1) elucidates the need for regional cooperation. The five regional councils that are responsible have already recognized the need for cooperation and creation of a joint plan. The breakdown of cooperation is detrimental to the fishery and its stakeholders. It is irresponsible to allow an FMP that attempts to protect and sustain the fishery while simultaneously ignoring thousands of square kilometers of habitat in the Gulf of Mexico and Caribbean. The answer to this problem is simple – create a new plan that includes all regions that is led by the SAFMC. This will enable quantitative analysis of the Gulf and Caribbean fisheries in the context of the FMP, and will set a precedent for managing highly dynamic migratory species within the EEZ of the United States.

The ultimate goal of integrated regional management of dolphinfish in the Western Central Atlantic Ocean is improved coordination between the United States and the Caribbean countries. To ensure horizontal integration, the United States should participate in the Caribbean Council. The U.S. should not initially be part of an organization that is geared towards Caribbean nations. However, since the U.S. fishery encompasses a much larger area and has a higher economic stake, they should coordinate with the regional organization but should not be a full member. Limited membership
would mean that the U.S. would contribute scientific support staff, science, and other resources. Also, the U.S. would be mandated incorporate the findings of the regional council into its own management structure in conjunction with domestic management. This would vastly improve the institutional structure in the study area and would create a legitimate structure for managing dolphinfish as one unit stock.

**5.0 CONCLUSION**

This study effectively characterized the habitat preferences of *Coryphaena hippurus* in the study area. The large scale remote sampling in combination with *in situ* measurements produced a new baseline of oceanographic features for the dolphin. The ENFA models further elucidated the variables that were most important in terms of predictive ability of habitat suitability. Despite the drawbacks of the modeling approach, the use of powerful geographic information systems coupled with statistical software packages enables scientists and managers the ability to investigate the relationships between animals and their environment. Also, the method of using recreational fishermen as field scientists can be applied in a variety of situations, especially in the U.S.

Based on the results of this study, horizontal integration throughout the United States and the Caribbean region must be established. Movement of dolphin throughout the multitude of complex cadastral zones warrants a more streamlined management and monitoring framework. The U.S. has vastly improved its management of dolphin with the creation of the 2004 fishery management plan. However, horizontal integration among regional councils is crucial to the success of this plan, and the fishery. Hopefully, this
study will be an impetus for international cooperation between nations to ensure the future of the fishery as a whole. All estimates indicate that the dolphinfish is a healthy fishery, but creating an integrated management structure will ensure the sustainability of this species. If progress is not made, this may be a species that “slips through the cracks” of fishery management.
REFERENCES


DIVINS, D. L. and D. METZGER. National Geophysical Data Center (NGDC) coastal relief model.


