

Developing Methodologies for Studying Elasmobranchs and Other Data-Poor Species

A Thesis

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Master of Science

by

Kristen L. Omori

2015

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Science

Kristen Omori

Approved, by the Committee, August 2015

John M. Hoenig, Ph.D.
Committee Chairman/ Advisor

Robert A. Fisher,
Marine Advisory Services

Jan R. McDowell, Ph.D.

Leah B. Shaw, Ph.D.

Jeffrey D. Shields, Ph.D.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS.....	v
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
THESIS ABSTRACT.....	viii
CHAPTER 1: INTRODUCTION.....	2
LITERATURE CITED.....	9
CHAPTER 2: SUMMER AND FALL MOVEMENT OF COWNOSE RAY, <i>RHINOPTERA BONASUS</i> (MITCHILL 1815), ALONG THE EAST COAST OF UNITED STATES OBSERVED WITH POP-UP SATELLITE TAGS.....	11
ABSTRACT.....	12
INTRODUCTION.....	13
METHODS.....	17
Tagging Process and Deployment.....	17
Tag Analysis.....	18
RESULTS.....	23
Deployment Duration and Data Retrieval.....	23
Horizontal Movement Patterns.....	23
Vertical Movement and Habitat Preferences.....	27
DISCUSSION.....	30
LITERATURE CITED.....	36
TABLES AND FIGURES.....	40

CHAPTER 3: EFFECTS OF UNDERESTIMATING CATCH AND EFFORT ON SURPLUS PRODUCTION MODELS.....	48
ABSTRACT.....	49
INTRODUCTION.....	50
CASE STUDY FISHERIES.....	53
SIMULATION METHODS.....	55
RESULTS.....	57
DISCUSSION.....	60
LITERATURE CITED.....	65
TABLES AND FIGURES.....	68
CONCLUSION.....	77
LITERATURE CITED.....	82
VITA.....	83

ACKNOWLEDGEMENTS

First, I want to extend my gratitude to Dr. John Hoenig, my advisor and mentor. For the past three years he has helped guide and challenge me to become a better scientist. John has provided the mentorship and support for these master's projects and as well as all my side projects that have helped me grow in the scientific realm. I greatly appreciate his dedication to his students and his patience when explaining concepts.

I also would like to thank my academic committee, Bob Fisher, Jan McDowell, Leah Shaw and Jeff Shields, for all their support and helpful comments as well as friendly faces to chat with throughout my thesis work. I want to extend a special thanks to Bob Fisher, who let me help with the cownose ray tagging project when I first arrived at VIMS. I was very fortunate to have Bob's enthusiasm, vast knowledge, and expertise on cownose rays and someone to share in the excitement when learning more about this species.

Funding was provided by Southeast Fisheries Science Center (NMFS) and University of Miami Cooperative Institute for Marine Atmospheric Studies along with VIMS Council. I also thank Dr. Linda Schaffner and the Office of Academic Studies for supporting my quantitative endeavors and financially. Grace Tisdale and Cindy Forrester also deserve thanks for their hard work and making our lives easier.

A special thanks to Heather Baer, from Wildlife Computers, for helping me greatly with the PSAT programming questions, Dr. Kevin Weng and Ben Galuardi for their tag analysis assistance for geolocations, Deb Gauthier for her ArcGIS mapping skills and Emily Loose and Ben Marcek for their help and support with the general PSAT data analysis.

The Hoenig lab past and present, Dan Gonzales, Phil Sadler, Lydia Goins, Amy Then, Matt Smith, Lisa Ailloud, Quang Huynh and Liese Carlton, has been a wonderful family. Amy provided so much comfort and friendship ever since I first arrived in Virginia. Lisa has always been there in full support and I truly would not have been this successful without her. Not only does she provide the thoughtful discussions, distractions and laughs in our office, but she also often serves as my memory.

The VIMS community is full of wonderful, supportive people who really have made my transition from West Coast to East Coast easy. I have made so many great, lifelong friends here at VIMS. I particularly thank my entering class, my roommates and friends in FSL for all the great memories and friendship.

Lastly, I would like to thank my family and Dan Goethel for all their support. My parents have always been very supportive of all my endeavors. I could not have made it to where I am today without them. To my sisters, Marisa and Lindsey, and brother-in-law, Jason, for their endless memories and pretending to care about my research. Dan Goethel for all his support and willingness to listen to my complaints. And to my extended family for their love and support.

LIST OF TABLES

Page

CHAPTER 2

Table 1. Summary of data on cownose rays tagged with pop-up satellite archival tags...41

CHAPTER 3

Table 1. Top 10 cases with the largest % error for all estimated parameters in swordfish and pike production models..... 69

LIST OF FIGURES

	Page
CHAPTER 2	
Figure 1. Estimated geolocations and most probable tracks for tagged cownose rays....	41
Figure 2. Longitude tracks from programs compared to coastline longitudes	43
Figure 3. Distribution of temperature and depth for each month by sex.....	44
Figure 4. Depth-temperature observations from tagged rays during night and day.....	45
Figure 5. Percentage of time rays spent at each depth during night and day.....	46
Figure 6. Percentage of time rays spent at each temperature during night and day.....	47
CHAPTER 3	
Figure 1. Depiction of simulated scenarios of underestimation of catch and effort.....	70
Figure 2. Production model parameter and ratio estimates for constant underestimation of catch and effort scenarios	71
Figure 3. Biomass estimates of North Atlantic swordfish, queen conch and northern pike under each family of scenarios of underreporting of catch and effort	72
Figure 4. Production model parameter and ratio estimates for increasing trends in underestimation of catch and effort	73
Figure 5. Production model parameter and ratio estimates for decreasing trends in underestimation of catch and effort	75

ABSTRACT

Fisheries have become increasingly important to manage and conserve, and this is particularly challenging for data-poor species. Elasmobranchs are commonly considered data-poor or data-limited species. Their life history characteristics make their populations susceptible to depletion from fishing pressures and habitat degradation. Thus, it is important to understand the movement patterns and habitat use of the targeted species as well as the models used in the stock assessment for the species. This thesis involves developing techniques and information for data-poor species, such as elasmobranchs. The objectives of this research were to 1) identify the wintering grounds for the cownose rays (*Rhinoptera bonasus*) from Chesapeake Bay, 2) determine summer and fall movement patterns for this species, and 3) understand how changes in the data input (i.e., catch and effort) affect the parameter estimates from a simple surplus production model.

Cownose rays have received negative attention in Chesapeake Bay for presumably heavy predation on commercial shellfish. Although the population size is unknown, there are concerns about the increase in abundance of this species, resulting in the need for management to control its population size. However, there are many questions regarding the movement patterns and habitat use for cownose rays, particularly for males. A total of 16 cownose rays in Chesapeake Bay were tagged with pop-up satellite archival tags (PSATs) to determine their wintering grounds and summer and fall movement patterns. Six tags (3 on females and 3 on males) were released on the programmed date and contained data on temperature, pressure (for depths) and light-level (for geolocations). The end locations from the satellite tags indicated that both sexes migrated to the coastal waters of central Florida for the winter. Females were exited Chesapeake Bay at the end of September and early October and migrated south to Florida. Males left the bay at the end of July and traveled northward to a second feeding ground in the coastal waters of southern New England. At the end of summer and early fall, the males made the southerly migration down the coast to Florida. There were no diel differences detected; however, male rays occupied a wider depth and temperature range compared to females.

Data-poor stocks are often regulated based on surplus production models when only catch and effort data are available. However, reported catch and effort rarely equal the true values. Reported data may not include bycatch, illegal fishing or local consumption, resulting in higher true catch and effort values than that reported. I used ASPIC (A Surplus Production Model Incorporating Covariates) software to examine the

effects of underestimated catch and effort on parameter and ratio estimates (e.g., MSY, F/F_{msy} and B/B_{msy}) in a production model. Using three example fisheries, I determined that a fishery with constant underestimation of catch and effort over time can be managed based on the parameter estimates from the production model. The parameter estimates either yielded no errors or were underestimated by the same percentage as the underreported data; however, the ratios of parameter estimates were free of error due to cancellation of errors. Trends in underestimation of catch and effort (e.g., improved reporting rates or increased illegal fishing) caused the errors in the estimates from the production model to be highly variable and scenario-dependent. Consequently, if underreporting of catch and effort is suspected, I would recommend conducting additional simulations specific to the fishery.

DEVELOPING METHODOLOGIES FOR STUDYING ELASMOBRANCHS
AND OTHER DATA-POOR SPECIES

CHAPTER 1
INTRODUCTION

With increasing demand for seafood, it is increasingly important to manage fisheries sustainably. Poor management can lead to population crashes as well as have negative effects on the livelihood of fishermen (e.g., Georges Bank cod fishery, Fogarty and Murawski 1998). However, well-managed fisheries generally require knowing the migration patterns, habitat utilization and the population structure and size of the targeted species. Such information can be difficult to obtain for many species for a variety of reasons including: 1) lack of management or surveys in smaller fisheries (e.g., artisanal fisheries), 2) low economic value, resulting from being a bycatch species, 3) habitat use that is challenging to assess (e.g., for highly migratory species and deep sea organisms). Often these animals are considered to be data-poor species because they lack the necessary information to conduct a detailed stock assessment. Data-poor species may be subjected to sources of fishing pressure that are either unknown or unaccounted for when assessing the health of the stock.

Elasmobranchs are in the subclass of Chondrichthyes, or cartilaginous fishes, which include sharks, skates and rays. Many elasmobranchs are intermediate ('meso') or top predators. This subclass plays an important role in the food web having both direct and indirect effects on the community (Stevens *et al.* 2000; Myers *et al.* 2007; Pennino *et al.* 2013). Although they show considerable variation in life history traits, elasmobranchs tend to be K-selected species. Life history characteristics of K-selected species include relatively late maturity, slow growth, large maximum size, low fecundity, long gestation periods and long longevity (Hoenig and Gruber 1990). As a result of these characteristics, elasmobranch populations have a slow intrinsic rate of growth (r), meaning the populations are slow to rebound if depleted. Population declines can be a consequence of

direct or indirect fishing as well as habitat degradation. Shark fisheries, as well as many other fisheries on similar K-selected species, are known to have a “boom and bust” fishing pattern if not properly managed, causing either local or widespread population depletion. This “boom and bust” pattern became apparent in the 1940-1970 period when shark fisheries expanded (Compagno 1990), followed by a rapid decline due to overharvesting. Large-bodied and shallow-water elasmobranch populations tend to be at the highest risk of depletion due to their slower population growth and higher fishing pressures near shore (Dulvy *et al.* 2014). They are often considered data-poor species because information about their life history, habitat use and/or population size are unknown. It is imperative to understand all these attributes for a species that is targeted by a fishery in order for their population to maintain a sustainable size.

The cownose ray, *Rhinoptera bonasus* (Mitchill 1815), is a common elasmobranch species in Chesapeake Bay. Although there is speculation that the abundance of this ray has increased in the past few decades (Merriner and Smith 1979; Smith and Merriner 1985), the true population size is unknown. Soft-shelled clams (*Mya arenaria*) are a preferred prey item of cownose rays (Merriner and Smith 1979; Smith and Merriner 1985; Fisher 2010). In the 1950's, the soft-shelled clam fishery was developed in the Chesapeake Bay along with an increase in oyster farming; however Tropical Storm Agnes in 1972 decimated this clam stock, causing a dietary shift to oysters (Merriner and Smith 1979). After shellfish stocks declined due to environmental and biological factors, their continued stasis was blamed on cownose rays (Merriner and Smith 1979; Smith and Merriner 1985; Peterson *et al.* 2001; Myers *et al.* 2007; Fisher

2009). As a result, more attention has been brought to studying the movements, biology and methods of determent of this elasmobranch species (Fisher 2009).

Several options have been explored to reduce the impact of rays on shellfish including the initiation of a commercial fishery. One possible fishery option was to target the male rays at a sustainable level, leaving a sufficient number of males so the reproductive output of the stock is not affected. For every gravid female ray fished, two rays are removed from the population, therefore decreasing the male population after mating would theoretically ensure that the number of pups produced each year would remain the same. This would subsequently reduce pressure on oyster predation if the males were feeding on the same shellfish stocks as females. However, it is unknown where males migrate after mating season because they are not seen in shallow waters of Chesapeake Bay during the remaining part of summer. If adult female cownose rays were targeted, it would be best to fish the rays after pupping. In addition, managers need to carefully regulate the fishery to ensure that the female population size stays above a viable abundance. We need to understand the habitat use and migration patterns for both sexes in order to create a sustainable fishery.

Pop-up satellite archival tags (PSATs) are commonly used to assess large scale movements of aquatic animals (e.g., Lutcavage *et al.* 1999; Musyl *et al.* 2011). PSATs are electronic tags that can internally store data and transmit messages to a satellite. The satellite tags record temperature, pressure (to calculate depth) and light-levels (to estimate location) and store the data at pre-set intervals. These tags have the ability to be released from the animals at a pre-programmed date; thus, it is not necessary to recapture the animals to retrieve information from the tags. PSATs can also be programmed to be

released from animals prior to the automated pop-off date based on two scenarios: 1) if the tag is at a constant depth for a programmed amount of days (e.g., 3 days), as a lack of vertical movement likely indicates a mortality, or 2) if the tag falls below a specified depth to prevent sensor failure from high pressure, which may also indicate that the tagged animal died. Once the tag surfaces, it will begin transmitting signals to the passing Argos satellites in which the geographical location (geolocation) of the tag can be calculated. The Argos locations are calculated based on the Doppler effect and require 4+ transmitted messages for accuracy between 250- 1500 m (Argos 2015). In addition, when the tag is at the surface it will transmit short, compressed messages of the archived data to passing Argos satellites. More detailed records of the archived data on temperatures, depths and light-levels are available if the tag is recovered.

Geolocations of the tagged animal are calculated based on civil twilight (when the center of the sun is 6° below the horizon). This is also better known as dawn (first light) and dusk (last light). The light-level curves are the steepest during these times, and therefore are used to estimate the longitude and latitude (Hill 1994). The halfway point between dawn and dusk is used to obtain the local noon or local midnight, which is then used to estimate the longitude. The latitude is then estimated based on the observed dawn and dusk times compared to the predicted dawn and dusk from the longitude calculation (Hill 1994).

In 2007, a targeted, subsidized fishery for cownose rays in Chesapeake Bay was launched by the Virginia Marine Resources Commission. The goal of promoting the new fishery was to reduce the total number of this species in the bay with the intention of lessening predation on the commercial bivalve species, eastern oysters (*Crassostrea*

virginica) and hard-shelled clams (*Mercenaria mercenaria*). Because cownose rays are a typical elasmobranch species, careful monitoring and assessments should be completed to ensure the population in the Chesapeake Bay is not overharvested. However, the movement and migration patterns of the cownose rays who mate and pup in the Chesapeake Bay are only partially known. My objectives for this chapter are to: 1) verify the wintering grounds for the cownose rays from Chesapeake Bay and 2) determine movement patterns of the male cownose rays after mating in the bay.

One simple model used to provide advice for the management of data-poor species is a surplus production model. A surplus production model requires a time series of two out of the three: catch, effort and catch rate. The simplest form of a production model is the Schaefer model (1957). This model is based on the logistic population growth function, and when integrated, returns the symmetric surplus production model.

$$\frac{dB}{dt} = rB \left(1 - \frac{B}{k} \right) - C \quad (1)$$

Here r is the intrinsic rate of population increase, B is the biomass of the stock, k is the carrying capacity of the population and C is the catch (as a rate), where

$$C = qEB \quad (2)$$

Here, q is the catchability coefficient (the fraction of fish caught per one unit of effort) and E is the fishing effort. The difference equation for the logistic Schaefer model is similar to the differential equation and is usually discretized into annual time steps:

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{k}\right) - C_t \quad (3)$$

$$C_t = qE_t B_t \quad (4)$$

The terms in this model are the same as in equation (1) except t represents time, thus B_t , C_t and E_t are the biomass, catch and effort at time, t . These equations can be rearranged to solve for catch-per-unit-effort (CPUE _{t}), which results in a linear equation. From the linear equation, the maximum sustainable yield (MSY) and fishing effort that gives MSY (E_{msy}) can be obtained. Because the Schaefer model assumes that the population is at equilibrium, which is rarely true, the equations can be transformed into a linear format or fit using a time series analysis with error terms to adjust for non-equilibrium (*see* Hilborn and Walters 1992).

Such production models are still used in assessments for data-poor species. However, there is the possibility of inaccurate data input; the catch and effort throughout the time series rarely reflect the true values. The reported catch and effort can be underestimated compared to the true catch and effort because the reported data may not include bycatch mortality, local consumption or illegal fishing. Thus, it is important to understand how the production model will respond to inaccurate catch and effort data because fishery benchmarks are often based on the parameters estimated by this model for data-poor fisheries. The objective for this chapter is to determine how underestimation of catch and effort affects the parameter estimates from the surplus production model.

LITERATURE CITED

- Argos. 2015. Argos user's manual. Available: <http://www.argos-system.org/manual/>. Accessed 2015 February.
- Compagno, L.J.V. 1990. Shark exploitation and conservation. *In* Elasmobranch as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries (H.L. Pratt Jr., S.H. Gruber, and T. Taniuchi, eds.). NOAA Technical Report NMFS 90: 391-414.
- Dulvy, N.K., S.L. Fowler, J.A. Musick, R.D. Cavanagh, P.M. Kyne, L.R. Harrison, J.K. Carlson, L.N.D. Davidson, S.V. Fordham, M.P. Francis, et al. 2014. Extinction risk and conservation of the world's sharks and rays. *eLife* 3: e00590.
- Fisher, R.A. 2009. Regional workshop on cownose ray issues identifying research and extension needs (proceedings). VIMS Marine Resource Report 2009-6. VSG-09-06. <http://web.vims.edu/GreyLit/VIMS/mrr09-06.pdf>
- Fisher, R.A. 2010. Life history, trophic ecology & prey handling by cownose ray, *Rhinoptera bonasus*, from Chesapeake Bay. NOAA final report (NA07NMF4570324) Grant No. 713031. VIMS Marine Resource Report No. 2010-20, VSG-10-25.
- Fogarty, M.J. and S.A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecological Applications* 8(1, suppl): S6-S22.
- Hilborn, R. and C.J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, London.
- Hill, R. D. 1994. Theory of geolocation by light levels. *In* Elephant Seals: Population Ecology, Behavior, and Physiology. Le Boeuf, Burney J., and Richard M. Laws (eds). Berkeley: University of California Press, pp. 227-236.
- Hoenig, J.M. and S.H. Gruber. 1990. Life-history patterns in the elasmobranchs: implications for fisheries management. *In* Elasmobranch as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries (H.L. Pratt Jr., S.H. Gruber, and T. Taniuchi, eds.). NOAA Technical Report NMFS 90: 1-16.
- Lutcavage, M.E., R.W. Brill, G.B. Skomal, B.C. Chase and P.W. Howey. 1999. Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries and Aquatic Sciences* 56: 173-177.

- Merriner, J.V. and J.W. Smith. 1979. A report to the oyster industry of Virginia on the biology and management of the Cownose Ray (*Rhinoptera bonasus*, Mitchill) in lower Chesapeake Bay. Virginia Institute of Marine Science, Special Report in Applied Marine Science and Ocean Engineering 216, Gloucester Point.
- Musyl, M.K., M.L. Domeier, N. Nasby-Lucas, R.W. Brill, L.M. McNaughton, J.Y. Swimmer, M.S. Lutcavage, S.G. Wilson, B. Galuardi and J.B. Liddle. 2011. Performance of pop-up satellite archival tags. *Marine Ecology Progress Series* 433: 1-28.
- Myers, R.A., J.K. Baum, T.D. Shepherd, S.P. Powers and C.H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315: 1846-1850.
- Pennino, M.G., F. Munoz, D. Conesa, A. Lopez-Quilez, and J. M. Bellido. 2013. Modeling sensitive elasmobranch habitats. *Journal of Sea Research* 83: 209-218.
- Peterson, C.H., F.J. Fodrie, H.C. Summerson and S.P. Powers. 2001. Site-specific and density-dependent extinction of prey by schooling rays: generation of a population sink in top-quality habitat for bay scallops. *Oecologia* 129: 349-356.
- Schaefer, M.B. 1957. Some considerations of population dynamics and economics in relation to the management of the commercial marine fisheries. *Journal of Fisheries Research Board of Canada* 14: 669-681.
- Smith, J.W. and J.V. Merriner. 1985. Food habits and feeding behavior of the Cownose Ray, *Rhinoptera bonasus*, in lower Chesapeake Bay. *Estuaries* 8: 305-310.
- Stevens, J.D., R. Bonfil, N.K. Dulvy and P.A. Walker. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, 57: 476-494.

CHAPTER 2

SUMMER AND FALL MOVEMENT OF COWNOSE RAY, *RHINOPTERA BONASUS* (MITCHILL 1815), ALONG THE EAST COAST OF THE USA OBSERVED WITH POP-UP SATELLITE TAGS

ABSTRACT

The cownose ray, *Rhinoptera bonasus*, is a common elasmobranch species along the southeast United States coast that has received negative attention in recent years. These rays are voracious predators on commercial shellfish beds raising concerns regarding their control and need for effective management. Although several life history characteristics have been documented for this species, we know little regarding its population abundance and migration patterns. I addressed the latter by reviewing 16 tagged cownose rays in Chesapeake Bay with pop-up satellite archival tags (PSATs) to study their movement patterns during the summer and fall and identify wintering grounds. Six tags (3 on males and 3 on females) were released at a predetermined time and provided archived data on temperature, pressure (depth) and light level. The migration tracks were deciphered through geolocation based on light levels, sea surface temperatures and depth constraints. PSAT end locations indicate the possibility of southern wintering grounds in the coastal waters of central Florida. Female cownose rays were found to migrate out of Chesapeake Bay at the end of September to October and continue their southerly migration to Florida. The predicted movement tracks from male rays indicated that the males exit the bay in July and migrate northward. The male rays appear to have a second summer feeding ground off the coast of southern New England. In the fall, males migrate south from New England to the same wintering grounds as the females in central Florida. No diel differences in habitat use were detected; however, male rays occupied a wider depth and temperature range compared to the females. Information on the movement patterns and habitat use for male and female cownose rays will assist in determining a more effective management plan for this species.

INTRODUCTION

Cownose rays (*Rhinoptera bonasus*) are a native, seasonal inhabitant in Chesapeake Bay. This highly migratory, coastal species is abundant in the bay during the summer months and uses the ecosystem for mating and nursery grounds. Cownose rays feed on a wide range of benthic organisms including molluscs, crustaceans, benthic polychaetes, but primarily bivalves (Smith and Merriner 1985, Collins *et al.* 2007, Fisher 2010). These rays are durophagous feeders. In the past, top prey items for this species in Chesapeake Bay were soft-shell clams (*Mya arenaria*) and Baltic macomas (*Macoma balthica*), whereas hard-shelled bivalves were not as common in their natural diets (Merriner and Smith 1979; Smith and Merriner 1985; Fisher 2010). Cownose rays prefer softer-shelled bivalves (Fisher *et al.* 2011), such as bay scallops (*Argopecten irradians*) and soft-shelled clams. However, the rays appear to be opportunistic feeders and tend to target areas with higher prey density (Smith and Merriner 1985; Collins *et al.* 2007; Fisher *et al.* 2011).

Since the decline of wild shellfish populations in Chesapeake Bay, there has been an increase in aquaculture and habitat restoration efforts for eastern oysters (*Crassostrea virginica*; Luckenbach *et al.* 2005; Murray and Hudson 2015) and hard-shell clams (*Mercenaria mercenaria*; Murray and Hudson 2015). However, for the past four decades, there have been increasing concerns and accusations regarding predation by cownose rays on the declining commercial shellfish populations in Chesapeake Bay (Merriner and Smith 1979; Smith and Merriner 1985; Fisher 2009). Peterson *et al.* (2001) blamed the

ray for the decline of bay scallop (*Argopecten irradians*) populations in North Carolina, proclaiming that schools of rays can exploit and effectively reduce dense areas of scallops. Claims have been made that the cownose ray population in Chesapeake Bay has increased dramatically and consequently is putting significant pressure on shellfish aquaculture and habitat restoration in the bay (Merriner and Smith 1979).

Only one study has attempted to estimate the cownose ray abundance in Chesapeake Bay. The aerial surveys from Blaylock (1993) indicated a wide variation in the average abundance of cownose rays throughout the summer. The counts ranged from no rays to a high monthly average estimated at 9.3 million in September from 1986-1989. This high variation likely reflects measurement error because of the patchy distribution of the rays. Unfortunately, because there is a lack of historical or present data to compare to Blaylock's abundance estimates of cownose rays in Chesapeake Bay, the estimated stock size of this population and trends in its abundance are unknown. In 2007, despite the lack of abundance surveys and to ameliorate potential pressure of predation on shellfish, a fishery for cownose rays was launched and subsidized by the Virginia Marine Resources Commission. Because this fishery is unregulated and unmanaged and because rays have life history characteristics that make them susceptible to fishing pressures, these factors may lead to a "boom and bust" situation as has been observed in similar fisheries (e.g., orange roughy, *Hoplostethus atlanticus*, fishery; Clark 2001).

The life history characteristics of the cownose ray follows the "K-selected" traits similar to other elasmobranchs (Hoenig and Gruber 1990; Musick 1999), which makes it vulnerable to overexploitation. These "K-selected" characteristics include late maturity, low fecundity, slower growth, larger maximum size and higher maximum age. Studies

have shown that cownose rays do not become fully mature until reaching ~70% of their maximum size, which equates to around seven to eight years for females (85-88 cm disc width) and six to seven years for males (>85 cm disc width) (Smith and Merriner 1987; Fisher *et al.* 2013). Females generally have one offspring per year, pupping in late June or July after an 11-12 month gestation period (Smith and Merriner 1986; Fisher *et al.* 2013). However, there have been a few documented cases of twins (Fisher *et al.* 2014). Immediately following parturition, mating occurs and females become gravid. The oldest individual female observed was estimated to be age 21 years and the oldest estimated age for males was 18 years (Fisher *et al.* 2013). These life history characteristics generally indicate a slow growing population.

Partial migration patterns of cownose rays in Chesapeake Bay have been identified in several studies. Both males and gravid females are observed off the coast of North Carolina in mid-spring (April) and enter Chesapeake Bay in the beginning of May (Smith and Merriner 1987; Blaylock 1993; Fisher 2010). This species is abundant throughout the summer in the bay with high variation in school size. The rays exit the bay in October (Merriner and Smith 1979; Blaylock 1993; Fisher 2010) for the start of their fall migration to their wintering grounds. This is also consistent with their seasonal patterns in North Carolina waters (Goodman *et al.* 2011). However, only the females and pups occupy the shallow estuarine waters of Chesapeake Bay from late July through October (Merriner and Smith 1979; Fisher 2010). Grusha (2005) suggested that the wintering nursery habitat for female cownose rays is off the coast of Florida. However, the male residency time inside Chesapeake Bay, subsequent movements in the summer, and the fall migration track are poorly known.

Habitat utilization and migration routes for both sexes of rays are important features to understand in order to provide appropriate management advice for cownose rays in the Chesapeake Bay. If cownose ray abundance in Chesapeake Bay were to decline dramatically from overexploitation, it may take years for the population to rebound. Thus, if a fishery is to continue, it may be more favorable to target males sustainably (i.e., allowing an adequate number of adult males for reproduction) so the population would be less prone to overexploitation.

The goals of this study are: 1) to verify the wintering grounds for rays that summer in Chesapeake Bay with results from Grusha (2005), and 2) to determine the timing and migration route for both male and female cownose rays that summer in Chesapeake Bay. The rays were tagged with pop-up satellite archival tags (PSATs), and the data on temperature, depth and light levels for geolocation information were analyzed to address these goals. The tagged rays used in this work were a part of an overall cownose ray tagging program at Virginia Institute of Marine Science (R. Fisher).

METHODS

Tagging and Deployment

A total of 16 mature cownose rays were captured, tagged and released in the Chesapeake Bay during the summers of 2011 and 2013. The rays were caught by local fishermen by haul seines in the Back River Inlet, which is a part of the Poquoson River in Virginia and transported to a large holding tank (4.3m x 6.4m x depth 0.71m) at the Virginia Institute of Marine Science (VIMS). The animals were acclimated for 72 hours in the tank with fresh circulating seawater before being subjected to handling and tagging under established Institutional Animal Care and Use Committee (IACUC) protocols (IACUC-2012-07-09-8040-rafish). Female rays were targeted in mid-September 2011 (n=5), and in 2013, male cownose rays were targeted mid-June through early July (n=11).

Only healthy rays were selected to be tagged with mini PSATs (MiniPAT, Wildlife Computers, Redmond, WA). The tagged female ranged from 95.0 cm to 100 cm in disc width (DW) and males ranged from 89.0 to 94.5 cm DW. Each ray selected for tagging was first anesthetized with tricaine methanesulfonate (MS-222), and then transferred to the tagging station. The PSAT was attached to each animal by suturing a loop of 200 lb. nylon fishing line through and around the base of the muscular part of the tail just forward of the small second dorsal fin (as described in Le Port *et al.* 2008). This method provided a central placement of the tag and minimized drag and has been performed successfully on a variety of batiod species (e.g., short-tailed stingray, Le Port

et al. 2008). After the tagging procedure, the ray was placed in a recovery pool and then returned to the large holding tank. Tagged rays were held in the holding tank for 24 hours to ensure the tagging process was successful and the health of the ray appeared normal before individuals were released into the York River off the VIMS beach (37.247°N, 76.505°W).

Most of the satellite tags were programmed to be released from the ray after the end of the fall migration in mid-December. For example, the tags deployed on the female rays were programmed to be released after 90 days in 2011 and the tags on males were set to detach between 100 to 150 days. If a PSAT was released early in Chesapeake Bay, attempts to recover the tag were made. The satellite tags were programmed to be released prematurely if the animal stayed at a constant depth (constant pressure) ± 2.5 m for 72 hours or went below 4000 m depth for 2011 tags and 1700 m depth for 2013 tags. The sensors were set to record every 3 or 5 seconds. The compressed, transmitted information to the satellites was stored as a 24 hour summary period with 12 temperature and depth bins, along with one set of dawn-dusk light curves when available. If the tag was recovered, the complete archive was accessible.

Tag Analysis

In this study, I used a variety of methods and programs to solve for the geolocations and the best estimated migration track, which is referred to as the most probable track. Geolocations are calculated based on light levels estimated from dawn and dusk of the local area, which then can be used to delimit latitude and longitude. Latitude is estimated from the time of the local dawn and dusk and can have many

sources of error (Hill 1994; Musyl *et al.* 2001). Latitudes during the solstices and at high latitudes can be estimated with much better accuracy compared to during the equinoxes and at lower latitudes. Longitude can be estimated more accurately than latitude because it is determined by the local noon and is not influenced by the latitude and time-of-year (Hill 1994; Musyl *et al.* 2001). The tag pop-up location (end location) is generally known with much more precision from the passing Argos satellites established by the first transmission with an Argos location class of 3, 2 or 1 (Argos 2015). The tag also transmits its compressed, archived information to the passing satellites. I downloaded and decoded the archived information on light-level, temperature and depth as well as the end location in the manufacturer's software program (WC- DAP 3.0, Wildlife Computers, Redmond, WA).

I calculated the geolocations and migration tracks for tags deployed for over 45 days, which included three females and three males (Table 1). The time interval ensured that a long distance could have been traveled. Wildlife Computers' global estimation program (WC-GPE2) was used to obtain estimated geolocations with and without matching sea surface temperatures (SST). I used the state-space Kalman filter (Harvey 1990), which is a linear quadratic estimation model used to describe the transition from one state to the next for the geolocation estimation. This statistical model uses recursive functions and is based on a biased random walk to determine the most probable track given in coordinate pairs (Sibert *et al.* 2003). I used this model, as described by Sibert *et al.* (2003), in the KFTRACK package, which is an add-on package for the statistical environment R (R Core Team 2012). I also used an improved version of the model, unscented Kalman filter with sea surface temperatures (UKFSST), described by Lam *et*

al. (2008). This updated model can handle non-linearities and uses sea surface temperature to estimate the most probable track. A third program was used, TRACKIT without SST (Nielsen and Sibert 2007) and with SST (Lam *et al.* 2010) through R (R Core Team 2012), that also is based on a state-space model with the unscented Kalman filter. This program estimates the most probable track from the raw measurements of light levels. In addition, TRACKIT does not limit the movement of the tag based on dawn and dusk nor assume thresholds for the light-levels. The last program I used to analyze the geolocations is WC-GPE version 3 (WC-GPE3). The WC-GPE3 model uses a gridded hidden Markov model using the forward-backward algorithm (H. Baer, *personal communication*). The model computes the posterior probability distributions to estimate the most likely state at a given time using the light-levels to calculate observed locations with error (Pedersen *et al.* 2011). This model can also exclude locations by setting their probabilities to zero (e.g., land for aquatic animals) to better estimate the most probable track. A secondary bathymetric correction based on maximum depths was used on all converged tracks from the different models to verify or reject the estimated geolocations (Hoolihan 2005; Teo *et al.* 2007; Galuardi *et al.* 2010).

In addition to using state-space modeling to delineate the most probable track for cownose rays in Chesapeake Bay, I also examined longitudes alone. I used the estimated longitudes throughout the tag deployment from each program (UKFSST, TRACKIT and WC-GPE3) and compared them to the longitudes along the east coast of the United States (coastline longitudes). Thus, if the rays were assumed to follow the east coast of the United States as they traveled to their wintering grounds, the longitudes of the coastline should match the longitudinal tracks from the programs.

Environmental preferences and daily movement patterns were inferred from the temperature and depth measurements for rays at liberty for more than 45 days. To assess any possible diel differences in habitat utilization and behavior through the depth and temperature records, two diel periods, day and night, were generated. The day captured a six hour period from 0800 to 1600 hours and the six hour period from 2100 to 0500 was designated as night.

To assess potential differences in mean depth and temperature between the two diel periods, night and day, and the sex of the ray, a general linear mixed effects model with repeated measures was used. The repeated measures analysis was used to account for the correlation of the replicates in the dataset due to the multiple observations for each individual ray. The linear mixed effects model is as follows:

$$Y_{ijk} = \mu + \delta_i + \tau + \omega_j + \rho_k + \varepsilon_{ijk}$$

Here, the mean depth and temperature, Y_{ijk} , were a function of the overall mean depth (logged) or temperature for each time period, i , for sex, j , and for the individual ray, k , the time period, δ_i , where i = day or night, Julian date, τ , the sex of the ray, ω_j , where j = female or male, the effect of the k th individual ray, ρ_k , and the random error, ε_{ijk} . All factors except the effect of the individual ray and error term were treated as fixed effects. Each factor was added to the model to determine the amount of influence it has on the mean temperature and depth. The depth data were log transformed (\log_e) to meet the assumptions of the model. The error terms for the mean depth (after the transformation) and mean temperature were normally distributed ($\varepsilon_{ijk} \sim N(0, \sigma_\varepsilon^2)$). There were no interactions found between any of the variables. Because the time period (night and day)

both occur in each day, the time period was nested in the Julian date. The repeated measures were addressed by specifying a covariance structure that allowed for correlation among the error terms. Akaike's information criterion (*AIC*, Akaike 1973) was used to select the most appropriate covariance structure (autoregressive 1, compound symmetry, unstructured, Toeplitz and variance components).

RESULTS

Deployment Duration and Data Retrieval

From the 16 PSATs deployed, 6 tags were successfully detached on the scheduled date (3 females and 3 males), ranging from 89 to 147 days at liberty (Table 1). One of these successful tags did not transmit any messages after the scheduled release, but was found a year later by a beachcomber. Only one tag was never heard from after the ray was tagged and released. The remaining nine PSATs were released early inside Chesapeake Bay after 5 to 32 days at liberty (Table 1).

Horizontal Movement Patterns

Based on the successful PSATs, the three female cownose rays migrated to the coast of central Florida, between Palm Bay, FL and Daytona, FL, around mid-December. Two tags that detached successfully from male rays in late November and early December were also found on the coast of central Florida. The third satellite tag attached to a male ray was deployed for a shorter time period, ending midway through the fall migration near the Virginia and North Carolina border.

The end locations of tags that successfully detached when programmed were known accurately to within 1.5 km (Argos 2015). In contrast, the migration tracks based on the geolocations from light-levels had large errors. With the secondary bathymetry correction, most of the estimated latitude and longitude coordinate pairs from the state-space Kalman filter models with and without sea surface temperature (programs:

KFTRACK, UKFSST and TRACKIT) were invalid. The WC-GPE3 program, which is based on the forward-backward algorithm, provided plausible most probable tracks.

Female ray number 1 (Ray 1) appeared to have exited Chesapeake Bay immediately after her release. Based on the WC-GPE3 track, she migrated to Cape Hatteras, North Carolina, in early October and stayed between the North Carolina and Virginia coast until early November. She then continued her southerly, fall migration following the coastline of southeastern USA (Figure 1a). The tag was released near Satellite Beach, FL (28.08°N -80.561°W) on December 13, 2011.

The estimated most probable track for the second female (Ray 2) was not as detailed or as plausible as the track from Ray 1. However, the WC-GPE3 program did return highly probable areas visited that were similar to the track from Ray 1. Ray 2 appeared to have stayed inside Chesapeake Bay until early October and possibly migrated south past the Cape Hatteras area in mid-October. In late October and November, this ray was likely off the coasts of South Carolina, Georgia, and the northern part of Florida (Figure 1b). The tag was released on schedule on December 13, 2011 near the end location of the first tag (on Ray 1) off Satellite Beach, FL (28.13°N -80.579°W).

The third female ray (Ray 3) also most likely stayed inside and around the mouth of Chesapeake Bay until early October before she began her southerly migration. Similar to Ray 1, Ray 3 migrated past Cape Hatteras around mid-October. However, as Ray 3 approached the North and South Carolina border area, she traveled northward again and possibly off the continental shelf (Figure 1c). In early December, it appears that this ray continued her migration along the coast to central Florida, where the tag was released on schedule north of Cape Canaveral by Mosquito Lagoon, FL (28.83°N -80.761°W).

Ray 9 was a male cownose ray tagged in early July 2013. Based on the WC-GPE3 track, this ray migrated out of the Chesapeake Bay soon after being released. In late July, he started a northerly migration following the general coastline (Figure 1d). By early August the ray was off the New Jersey coast and appeared to have stayed off the coast of Long Island, New York and Rhode Island through September. Ray 9 never appeared to travel farther north past Cape Cod or George's Bank (Figure 1d). In October, this male ray remained off the New Jersey coastal area generally staying within the continental shelf. At the end of October, the ray was around the Cape Hatteras region and continued the southerly migration similar to the tagged female rays. By mid-November, he appeared to be around the South Carolina coast and in early December around the coast of central Florida. The tag from this male was released on schedule (December 2, 2013), but never reached the surface to transmit any messages. The tag was found by a beachcomber a year later on the beach at Blowing Rock Conservatory on Jupiter Island, Florida. Thus, an assumption was made that the end location was near Jupiter Island (27.03°N -80.095°W).

The tag on the other male ray with a other full migration track (Ray 16) was only able to transmit 18 messages over a 9 hour period before all transmissions stopped. Based on the limited messages received by the Argos satellites, this ray, tagged in early July, appeared to have two highly probable locations (Figure 1e). One location was along the coast of North Carolina just south of Cape Hatteras in October. The other area was along the coast by the South Carolina and Georgia border in November. The tag end location was November 30, 2013 by Melbourne Beach, FL (28.15°N -80.584°W).

Ray 12, a male ray tagged on June 13, 2013, had a partial migration track ending in October 11, 2013. This ray migrated out of the bay soon after he was tagged; however

Ray 12 traveled south below Cape Hatteras in June and early July. By mid-July, it appeared that the ray changed to a northward course along the coast. In August, Ray 12 was most likely off the coast of Long Island, New York, and Rhode Island, similar to Ray 9. Ray 12 appeared to travel farther north by the Cape Cod coast and possibly to the George's Bank area (Figure 1d) for a few weeks in September. This ray then made the migration back south, where the end location was off the coast of the Virginia and North Carolina border (36.45°N -75.723°W).

Although the coordinate pairs for the other programs (i.e., TRACKIT and UKFSST) did not yield plausible geolocations for tagging location data, the estimated longitude is known to be more accurate than latitude (Hill 1994; Musyl *et al.* 2001). For the female rays, the coastline longitudinal track began in Chesapeake Bay and continued south to central Florida. The coastline longitudinal track for male rays started in the bay, demarcated the east coast longitudes in a northward direction to Rhode Island and then traced back down the coastline to central Florida. Based on the longitudes predicted by each of the programs that produced a converged track, female rays, Ray 1 and 3, appeared to have followed the east United States coastline pattern for their fall migration down to the coastal waters of central Florida (Figure 2a,b). The longitude tracks for male rays, Rays 9 and 12, also followed the general pattern of the longitude of the east coast of the United States (Figure 2c,d). Two rays, female Ray 2 and male Ray 16, were excluded from the longitudinal analysis because not enough geolocations were predicted to complete a full track. Generally, the longitudes predicted by WC-GPE3 more closely followed the coastline longitudes than the longitudinal tracks from TRACKIT or UKFSST.

Vertical Movement and Habitat Preferences

Temperature and depth records were examined from tags that were deployed for greater than 45 days. In general, male rays occupied a wider range of depths (0-51 m) compared to females (0-26 m) (Figures 3, 4, 5). According to the geolocation data, male rays occupied areas that had deeper depths available, especially in August, September and October. In September and October, the depth ranges for Ray 9 were from the surface waters to 50.9 m and 50.3 m, respectively. This male ray also showed frequent dives throughout the summer and fall. When Ray 9 was in Chesapeake Bay, he generally stayed closer to the surface, but made repeated dives. This ray also made frequent dives (5-8 dives per hour) often returning to the surface between each descent when he was in the north where the water was deeper. In contrast, this male ray stayed closer to the substrate and did not return to the surface as often when on the wintering grounds. Rays 12 and 16 demonstrated similar diving patterns, but dove less frequently compared to Ray 9. The male rays spent 50% of their time during both the day and night at the surface and ~ 85% of the time in depths between 0 and 15 m (Figure 5a). The males tended to prefer shallower waters (0-10m) from June through September and slightly deeper water in November and December (Figure 3c).

Female rays, similar to the males, occupied shallower depths during September and October, but were found at deeper depths (10-25 m) a higher percentage of the time during November and December (Figure 3d). The average depths (± 1 sd) in November and December (11.4 ± 4.8 and 11.5 ± 3.9 m, respectively) were deeper than the average overall depth (10.2 ± 10.4). However, compared to males, the female cownose rays tended to spend more time throughout the entire water column (Figure 5b). In particular,

Ray 1 spent a greater proportion of time at deeper depths compared to the other females and males. In December, Ray 3 always stayed within a 15-30 m depth range. Female rays do not appear to stay at constant depths for long periods of time when migrating or when occupying their summer or winter nursery habitats. There was no diel difference in the distribution of depth for the rays in this study according to the mixed effects model ($F_{1,27}=0.68$, $p=0.416$); however, sex of the ray was significant ($F_{1,33.2}=9.76$, $p=0.004$). The estimated parameters for sex and time period in the depth model were as follows: Females= 1.41 ± 0.13 , Males= 1.89 ± 0.07 , Day= 1.70 ± 0.09 , Night= 1.60 ± 0.09 . The autoregressive 1 (AR(1)) covariance structure was best for both depth and temperature models.

Similar to the depth model, there were no diel differences in water temperature distribution for the rays in this study ($F_{1,22.8}=0.45$, $p=0.511$), but the sex factor was significant ($F_{1,23.4}=10.61$, $p=0.003$). The estimated parameters were as follows: Females= 23.27 ± 0.35 , Males= 21.76 ± 0.23 , Day= 22.4 ± 0.26 , Night= 22.6 ± 0.25 . Male cownose rays occupied a wider temperature range (mean: 22.75 ± 2.34 °C) compared to the females in this study (mean: 22.6 ± 1.65 °C). This is directly related to the deeper depths to which the male rays were able to dive. From June to September, the temperature averages decreased, but the range was still large (Figure 3a). The minimum and maximum temperatures recorded were from male rays: Ray 9 at 11.6 °C in September, and Ray 12 at 30.1 °C in July. In November and December, the male cownose rays stayed in slightly warmer water, which corresponded to the shallower depth profiles (Figure 3c). The female cownose rays in this study stayed in warmer water from September through November, but preferred colder water in December compared to the males (Figure 3).

Overall, the temperature range for the females (18.6- 27.2 °C) was narrower than males (11.6- 30.1°C), particularly in September and October. In both the day and night time periods, the males spend about 40-45% of their time at 21-23 °C, whereas the females spend about 35-40% of their time at that temperature range (Figure 6). The average temperature was 21.8°C and the majority of the recorded temperatures were from 20 to 24°C for all rays.

DISCUSSION

Based on the PSAT data, I can confirm the location of the wintering grounds for cownose rays from Chesapeake Bay. Both sexes appear to aggregate around the coastal areas of central Florida between Daytona Beach and West Palm Beach, Florida. Three of the tags (from 2 females and 1 male) were released within an 8.5 km area of one another according to the Argos satellites. Grusha (2005) also identified central Florida as the wintering grounds for female cownose rays from Chesapeake Bay. This information reveals part of the migration pattern and overwintering grounds along the east coast of Florida as an important ecosystem for cownose rays.

Although cownose rays are known to swim at the surface, the rays are strongly associated with the benthic substrate for feeding. Female and male rays may not likely migrate off the continental shelf for extended periods of time based on their depth profiles. The general track gave reasonable large-scale movement patterns, despite the model estimating a few geolocations past the continental shelf. All in all, the underlying track produced by WC-GPE3 indicates that the females migrate from the Chesapeake Bay along the coastline to their wintering grounds in central Florida during the fall. Results from the male tracks suggest that the cownose rays that inhabit the Chesapeake Bay in early summer have a longer migration than anticipated. The tracks from Rays 9 and 12 suggest a second summer feeding area for males off the coast of southern New England.

The adult females continue to utilize the productive Chesapeake Bay estuary, but the males leave after mating. The question remains as to why the males choose to leave and expend more energy for the long migration northward. I hypothesize that the male cownose rays migrate out of the bay to reduce competition for the food and habitat resources for the females and pups. Fisher (2010) suggests sex-specific differences in cownose ray foraging tactics in the Chesapeake Bay during mixed sex schooling prior to mating. Females were observed to target a larger array and more nutrient rich prey than males. Chesapeake Bay has nutrient rich and easily accessible prey and offers protection from most large predators (i.e., sharks). Thus, it is more advantageous for the overall population to allow females and young to stay inside the nursery grounds within Chesapeake Bay where it is safer and to reduce the competition for the ideal feeding habitat. Although males are subjected to more extensive migratory movement than females, post-mating habitats off New Jersey through southern New England is productive and supports a large and diverse community of marine life (Georges Bank; Garrison and Link 2000).

The high seasonal occurrences of rays in the coastal waters of North Carolina align with the timing when tagged rays in this study were migrating along the coast of North Carolina. Goodman *et al.* (2011) found higher abundances of cownose rays in the spring time and late autumn in the coastal waters during known migration periods compared to the lower group sizes inside the North Carolina estuaries in the summer. The differences in abundance during the different seasons may suggest that the spring and fall migrations include cownose rays from the entire Atlantic population. Grusha (2005) and this study also suggest that the Atlantic populations of cownose rays (*R. bonasus*) do not

migrate around the southern part of Florida to the Gulf of Mexico. This finding supports the premise that the cownose rays in the Atlantic area are a separate stock from the *R. bonasus* in the Gulf of Mexico. Recent genetic work determined the presence of at least two distinct stocks of *R. bonasus* in Chesapeake Bay and Gulf of Mexico (McDowell and Fisher 2013). Likewise, cownose rays in the Gulf of Mexico are found to mature at an earlier age (age 4-5) (Neer and Thompson 2005) compared to age 6-7 and 7-8 for males and females, respectively, in Chesapeake Bay (Smith and Merriner 1987; Fisher *et al.* 2013). Neer and Thompson (2005) also showed that pupping occurs in mid-April through possibly November, which is much earlier and longer than in the Chesapeake Bay (Fisher 2010). The differences in the pupping season are likely a result of the warmer waters in the Gulf of Mexico compared to the Atlantic. However, maturity and pupping season could potentially be confounded because there are two species of cownose rays, *R. bonasus* and *R. brasiliensis*, in the Gulf of Mexico that are difficult to distinguish from one another (J. McDowell, *pers. comm.*).

The behavior of the cownose rays showed no differences with depth and temperature preferences during the two diel periods. However, there were differences between sexes in their profiles for mean temperature and depth throughout the seasons. Male rays occupied a broader depth range compared to females, but this was influenced by their longer migration and feeding habitat. The northern second feeding habitat for males is deeper (up to 100 m), whereas the depth in the Chesapeake Bay ranges from 0 to 53 m with an average of 6.5 m. Although this batoid species is associated with benthic feeding, they are considered epipelagic (e.g., Rogers *et al.* 1990; Blaylock 1993). My results support their epipelagic habit; the rays spend most of their time at the surface. The

male rays in this study spent half of their time at the surface (0-5 m) and 90% of their time at depths from 0-15 m. The females were not as associated with the surface as the males spending only about 30% of their time between 0-5 m. Females were found throughout 0-20 m from September to December.

The cownose rays from Chesapeake Bay were tolerant of a wide range of temperatures, particularly the males (recorded range: 11.6- 30.1°C). According to Schwartz (1964), the lethal minimum temperature for cownose rays is about 12°C. However, a sudden drop in temperature to 3.4°C did not appear to distress two of the captive specimens for a short time period (Schwartz 1964). Schwartz's study and results from this study suggest that the rays can tolerate colder waters for a short amount of time, for example, for episodic diving and feeding. In addition, tags from this study rarely recorded temperatures above 29°C, which supports the finding that cownose rays avoided temperatures greater than 30°C (Neer *et al.* 2007). Temperature and depth had no effect on the distribution of cownose rays in the Caloosahatchee River, FL (Collins *et al.* 2008) and along the northwestern part of the Gulf of Mexico (Craig *et al.* 2010). The rays in Craig *et al.* (2010) were most abundant around highly productive, riverine-influenced areas. Perhaps the cownose rays from Chesapeake Bay also seek areas that are highly productive with little regard for temperatures within a certain range. In conclusion, the rays appear to be fairly tolerant of temperature changes within a range from 18-28°C and can handle more extreme temperatures for short periods of time.

Unfortunately, one of the tags on a male ray was only able to transmit a few messages, which resulted in little and low resolution light-level, temperature and depth data. In contrast, one of my failed tags was found a year later yielding high resolution

data. Out of 16 PSATs deployed, only 5 were released and transmitted messages on schedule (31.25%). The non-reporting rate of the satellite tags in this study was 12.5% (2 out of 16 tags) and the percent of premature detachment was 56.25% (9 tags). These percentages align with those in the literature (Musyl *et al.* 2011). The reporting rate for Wildlife Computer pop-up satellite tags was calculated to be about 86% (all PSATs=79%) with only about 18% of the reporting tags remaining attached until the programmed release (Musyl *et al.* 2011).

Non-reporting and premature release is a common issue for PSATs. These tag failures arise from either issues with the tag or animal. Problems originating from the tag may include: battery failure, tag damage (e.g., antenna damage), mechanical failure (e.g., tethers) and biofouling of the tag (e.g., Hays *et al.* 2007, Musyl *et al.* 2011). The tag could fail to report or be released early due to problems with the location of the tag attachment on the animal (i.e., infections or tissue necrosis; Hoolihan *et al.* 2011), entanglement with substrate or other animals, social or mating behaviors (e.g., Swimmer *et al.* 2006), predation from sharks, natural mortality or mortality induced from the tagging event (e.g., Musyl *et al.* 2009). It is difficult to determine the reason behind the tag failures.

The tag in my study that was found one year later was released on schedule. The beachcomber who found the PSAT had to scrape away the biofouling in order to read the numbers on the tag. I hypothesized that the PSAT had too much biofouling, which caused the tag to sink to the bottom until the battery power expired. One theory for the 18 message tag was that the PSAT was washed up and buried on shore because of the close proximity of the end location to the shoreline. It is reasonable to believe that the tags that

were all released prematurely in the Chesapeake Bay were due to the social behavior of the rays (mating behavior), mortality induced from tagging or entanglement with the substrate. Yet, the tag success rate was similar to other studies.

From the pop-up satellite tags, I have provided greater insight on the movement patterns and habitat use of adult male and female rays from the Chesapeake Bay. The rays appear to be adaptable to changes in temperatures and utilize a wide range of habitats including estuaries with low salinity and coastal waters of depths up to 50 m. There are still many unanswered questions that need to be resolved for the appropriate management of the cownose rays on the Atlantic coast of the United States. For example, do male cownose rays that mate in bays other than Chesapeake Bay mix with Chesapeake rays off Long Island and Rhode Island? If the cownose rays continue to draw the attention of commercial shellfish farmers, we would need to consider the implications of a fishery on this elasmobranch species.

LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrova BN, Csaki F (eds) Proceedings of the 2nd international symposium on information theory. Publishing House of the Hungarian Academy of Sciences, Budapest: 268-281.
- Argos. 2015. Argos user's manual. Available: <http://www.argos-system.org/manual/>. Accessed 2015 February.
- Blaylock, R.A. 1993. Distribution and abundance of cownose rays, *Rhinoptera bonasus* (Rhinopteridae), in lower Chesapeake Bay, Virginia. *Estuaries* 16: 253-263.
- Clark, M. 2001. Are deepwater fisheries sustainable?- the example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fisheries Research* 51: 123-135.
- Collins, A.B., M.R. Huepel, R.E. Hueter and P.J. Motta. 2007. Hard prey specialists or opportunistic generalists? An examination of the diet of the cownose ray, *Rhinoptera bonasus*. *Marine and Freshwater Research* 58: 135-144.
- Collins, A.B., M.R. Huepel and C.A. Simpfendorfer. 2008. Spatial distribution and long-term movement patterns of cownose rays *Rhinoptera bonasus* within an estuarine river. *Estuaries and Coasts* 31: 1174-1183.
- Craig, J.K., P.C. Gillikin, M.A. Magelnicki and L.N. May. 2010. Habitat use of cownose rays (*Rhinoptera bonasus*) in a highly productive, hypoxic continental shelf ecosystem. *Fisheries Oceanography* 19: 301-317.
- Fisher, R.A. 2009. Regional workshop on cownose ray issues identifying research and extension needs (proceedings). VIMS Marine Resource Report 2009-6. VSG-09-06. <http://web.vims.edu/GreyLit/VIMS/mrr09-06.pdf>
- Fisher, R.A. 2010. Life history, trophic ecology & prey handling by cownose ray, *Rhinoptera bonasus*, from Chesapeake Bay. NOAA final report (NA07NMF4570324) Grant No. 713031. VIMS Marine Resource Report No. 2010-20, VSG-10-25.
- Fisher, R.A., G.C. Call and R.D. Grubbs. 2011. Cownose Ray (*Rhinoptera bonasus*) predation relative to bivalve ontogeny. *Journal of Shellfish Research* 30: 187- 196.
- Fisher, R.A., G.C. Call and R.D. Grubbs. 2013. Age, growth, and reproductive biology of cownose rays in Chesapeake Bay. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 5: 224-235.

- Fisher, R.A., G.C. Call and J.M. McDowel. 2014. Reproductive variations in cownose rays (*Rhinoptera bonasus*) from Chesapeake Bay. *Environmental Biology of Fishes* 97: 1031-1038.
- Galuardi, B., F. Royer, W. Golet, J. Logan, J. Neilson, and M. Lutcavage. 2010. Complex migration routes of Atlantic bluefin tuna (*Thunnus thynnus*) question current population structure paradigm. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 966-976.
- Garrison, L.P. and J.S. Link. 2000. Fishing effects on spatial distribution and trophic guild structure of the fish community in the Georges Bank region. *ICES Journal of Marine Sciences* 57: 723-730.
- Goodman, M.A., P.B. Conn, and E. Fitzpatrick. 2011. Seasonal occurrence of Cownose Rays (*Rhinoptera bonasus*) in North Carolina's estuarine and coastal waters. *Estuaries and Coasts* 34: 640-651.
- Grusha, R.D. 2005. Investigations into the life history of the Cownose Ray, *Rhinoptera bonasus*, (Mitchill, 1815). Master's thesis. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point.
- Harvey, A.C. 1990. Forecasting, structural time series models, and the Kalman filter. Cambridge University Press.
- Hays, G.C., C.J.A. Bradshaw, M.C. James, P. Lovell and D.W. Sims. 2007. Why do Argos satellite tags deployed on marine animals stop transmitting? *Journal of Experimental Marine Biology and Ecology* 349: 52-60.
- Hill, R. D. 1994. Theory of geolocation by light levels. *In* Elephant Seals: Population Ecology, Behavior, and Physiology. Le Boeuf, Burney J., and Richard M. Laws (eds). Berkeley: University of California Press, pp. 227-236.
- Hoenig, J.M. and S.H. Gruber. 1990. Life-history patterns in the elasmobranchs: implications for fisheries management. *In* Elasmobranch as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries. H.L. Pratt Jr., S.H. Gruber, and T. Taniuchi (eds). NOAA Technical Report 90.
- Hoolihan, J. P. 2005. Horizontal and vertical movements of sailfish (*Istiophorus platypterus*) in the Arabian Gulf, determined by ultrasonic and pop-up satellite tagging. *Marine Biology* 146: 1015-1029.
- Hoolihan, J. P., J. Luo, F.J. Abascal., S.E. Campana, G. De Metro, H. Dewar *et al.* 2011. Evaluating post-release behaviour modification in large pelagic fish deployed with pop-up satellite archival tags. *ICES Journal of Marine Science: Journal du Conseil* 68: 880-889.
- Lam, C.H., A. Nielsen and J.R. Sibert. 2008. Improving light and temperature based geolocation by unscented Kalman filtering. *Fisheries Research* 91: 15-25.

- Lam, C.H., A. Nielsen and J.R. Sibert. 2010. Incorporating sea-surface temperature to the light-based geolocation model Trackit. *Marine Ecology Progress Series* 419: 71-84.
- Le Port, A., T. Sippel and J.C. Montgomery. 2008. Observation of mesoscale movements in the short-tailed stingray, *Dasyatis brevicaudata*, from New Zealand using a novel PSAT tag attachment method. *Journal of Experimental Marine Biology and Ecology* 359: 110-117.
- Luckenbach, M.W., L.D. Coen, P.G. Ross, Jr. and J.A. Stephen. 2005. Oyster reef habitat restoration: relationships between oyster abundance and community development based on two studies in Virginia and South Carolina. *Journal of Coastal Research* 40: 64-78.
- McDowell, J. R. and R.A. Fisher. 2013. Discrimination of cownose ray, *Rhinoptera bonasus*, stocks based on microsatellite DNA markers. VIMS Marine Resource Report No. 2013-8.
- Merriner, J.V. and J.W. Smith. 1979. A report to the oyster industry of Virginia on the biology and management of the Cownose Ray (*Rhinoptera bonasus*, Mitchill) in lower Chesapeake Bay. Virginia Institute of Marine Science, Special Report in Applied Marine Science and Ocean Engineering 216, Gloucester Point.
- Murray, T.J. and K. Hudson. 2015. Virginia shellfish aquaculture situation and outlook report: Results of the 2014 Virginia shellfish aquaculture crop reporting survey. VIMS Marine Resource Report 2015-3. VSG-15-01.
- Musick, J.A, editor. 1999. Ecology and conservation of long-lived marine animals. In: Musick JA (ed) Life in the slow lane: ecology and conservation of long-lived marine animals, American Fisheries Society Symposium 23. Bethesda, MD.
- Musyl, M. K., R.W. Brill, D.S. Curran, J.S. Gunn, J.R. Hartog, R.D. Hill, *et al.* 2001. Ability of archival tags to provide estimates of geographical position based on light intensity. In Electronic tagging and tracking in marine fisheries reviews: Methods and technology in fish and biology and fisheries. J. Sibert and J. Nielsen (eds). Kluwer, Dordrecht, pp. 343-367.
- Musyl, M.K., C.D. Moyes, R.W. Brill and N.M. Fragoso. 2009. Factors influencing mortality estimates in post-release survival studies. *Marine Ecology Progress Series* 396: 157-159.
- Musyl, M.K., M.L. Domeier, N. Nasby-Lucas, R.W. Brill, L.M. McNaughton, J.Y. Swimmer, M.S. Lutcavage, S.G. Wilson, B. Galuardi and J.B. Liddle. 2011. Performance of pop-up satellite archival tags. *Marine Ecology Progress Series* 433: 1-28.
- Myers, R.A., J.K. Baum, T.D. Shepherd, S.P. Powers and C.H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315: 1846-1850.
- Neer, J.A. and B.A. Thompson. 2005. Life history of the cownose ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. *Environmental Biology of Fishes* 73: 321-331.

- Neer, J.A., K.A. Rose and E. Cortes. 2007. Simulating the effects of temperature on individual and population growth of *Rhinoptera bonasus*: a coupled bioenergetics and matrix modeling approach. *Marine Ecology Progress Series* 329: 211-223.
- Nielsen, A. and J.R. Sibert. 2007. State-space model for light-based tracking of marine animals. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 1005-1068.
- Pedersen, M.W., T.A. Patterson, U.H. Thygesen and H. Madsen. 2011. Estimating animal behavior and residency from movement data. *Oikos* 120: 1281-1290.
- Peterson, C.H., F.J. Fodrie, H.C. Summerson and S.P. Powers. 2001. Site-specific and density-dependent extinction of prey by schooling rays: generation of a population sink in top-quality habitat for bay scallops. *Oecologia* 129: 349-356.
- R Core Team 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-08-9, URL: <http://www.R-project.org/>.
- Rogers, C., C. Roden, R. Lohoefer, K. Mullin and W. Hoggard. 1990. Behavior, distribution, and relative abundance of cownose ray schools *Rhinoptera bonasus* in the northern Gulf of Mexico. *Northeast Gulf Science* 11: 69-76.
- Schwartz, F.J. 1964. Effects of winter water conditions on fifteen species of captive marine fishes. *American Midland Naturalist* 71: 434-444.
- Sibert, J. R., M.K. Musyl and R.W. Brill. 2003. Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging data. *Fisheries Oceanography* 12: 141-151.
- Smith, J.W. and J.V. Merriner. 1985. Food habits and feeding behavior of the Cownose Ray, *Rhinoptera bonasus*, in lower Chesapeake Bay. *Estuaries* 8: 305-310.
- Smith, J.W., and J.V. Merriner. 1986. Observations on the reproductive biology of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay. *Fisheries Bulletin* 84: 871-877.
- Smith, J.W. and J.V. Merriner. 1987. Age and growth, movements and distribution of the Cownose Ray, *Rhinoptera bonasus*, in Chesapeake Bay. *Estuaries* 10: 153-164.
- Swimmer Y, R. Arauz, M. McCracken, L. McNaughton, J. Ballester, M. Musyl, *et al.* 2006. Diving behavior and delayed mortality of olive ridged sea turtles *Lepidochelys olivacea* after their release from longline fishing gear. *Marine Ecology Progress Series* 323: 253-261.
- Teo, S. L., A.M. Boustany and B.A. Block. 2007. Oceanographic preferences of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. *Marine Biology* 152: 1105-1119.

TABLES AND FIGURES

Table 1. Summary of the cownose rays (*Rhinoptera bonasus*) in Chesapeake Bay that were tagged with pop-up satellite tags in 2011 and 2013. **Boldface** type indicates tags that were used for geolocation analysis. All rays were released at 37.247 °N latitude, 76.505 °W longitude. **estimated latitude and longitude because the tag was found by a beachcomber at Blowing Rock Conservatory, Jupiter, FL.

Ray ID	Sex (DW in cm)	Release Date	Report Date	Report Latitude (°N)	Report Longitude (°W)	Days at Liberty
1	F (97.0)	9/15/2011	12/13/2011	28.08	-80.561	89
2	F (96.0)	9/15/2011	12/13/2011	28.13	-80.579	89
3	F (100.0)	9/16/2011	12/15/2011	28.83	-80.761	90
4	F (98.0)	9/15/2011	9/19/2011	NA	NA	5
5	F (95.0)	9/15/2011	9/19/2011	NA	NA	5
6	M (92.5)	6/13/2013	6/25/2013	31.5	-78.661	13
7	M (90.5)	6/14/2013	7/15/2013	37.5	-74.578	32
8	M (90.0)	6/14/2013	6/18/2013	34.5	-77.157	5
9	M (93.0)	7/6/2013	12/2/2013	**27.03	** -80.095	147
10	M (93.5)	6/13/2013	6/18/2013	NA	NA	6
11	M (91.0)	6/14/2013	7/9/2013	38.29	-76.107	26
12	M (89.0)	6/13/2013	10/11/2013	36.45	-75.723	119
13	M (94.5)	7/5/2013	7/11/2013	32.5	-78.515	7
14	M (90.5)	6/14/2013	NA	NA	NA	NA
15	M (93.5)	7/6/2013	7/25/2013	37	-76.118	20
16	M (93.0)	7/6/2013	11/30/2013	28.15	-80.584	145

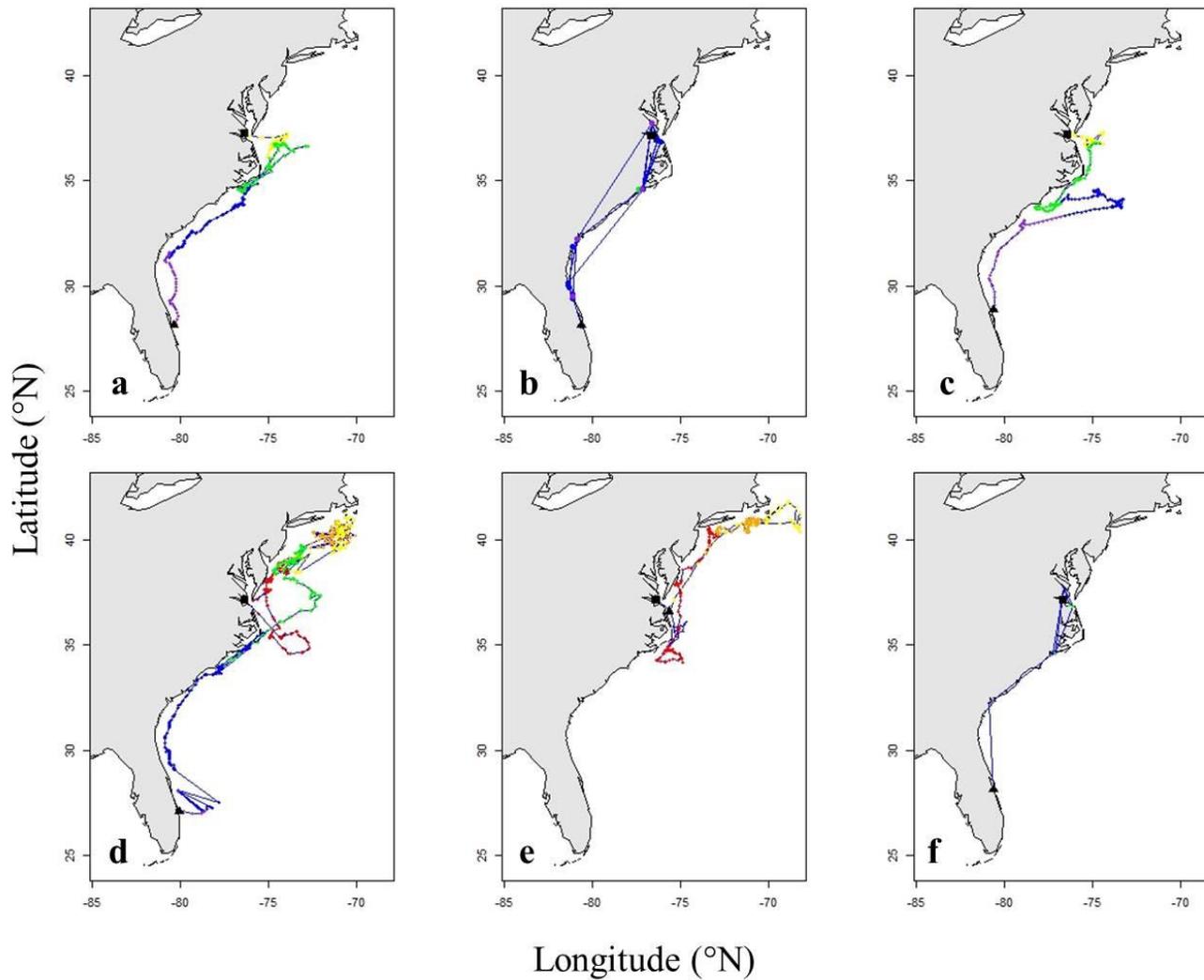


Figure 1. Geolocations and most probable tracks estimated by WC-GPE3 for the three female (Ray 1, 2 and 3: a, b and c, respectively) and three male (Ray 9, 12, 16: d, e, and f, respectively) cownose rays. Colors indicate the month of the estimated geolocation: red=June and July, orange=August, yellow=September, green=October, blue=November and purple= December

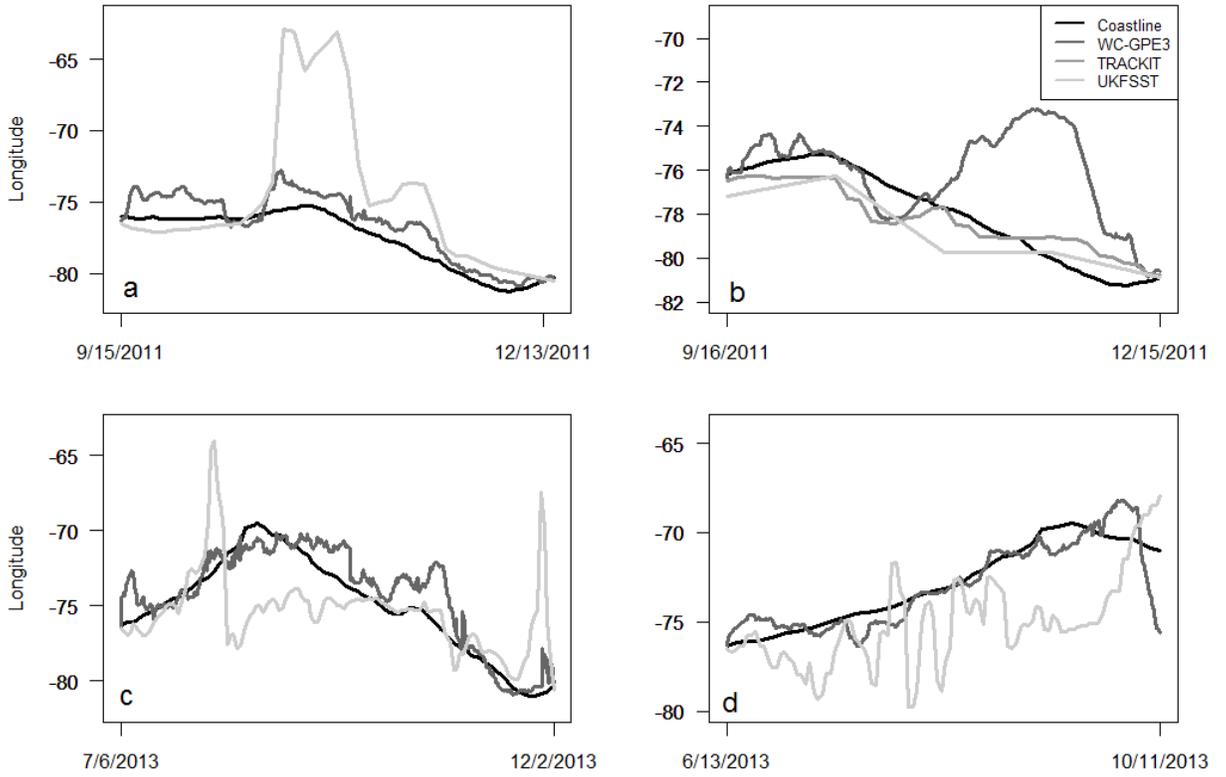


Figure 2. Longitude tracks from the WC-GPE3, TRACKIT and UKFSST programs for female rays, Ray 1 (a) and Ray 3 (b) and male rays, Ray 9 (c) and Ray 12 (d) overlaid on longitudes of the United States eastern seaboard coastline.

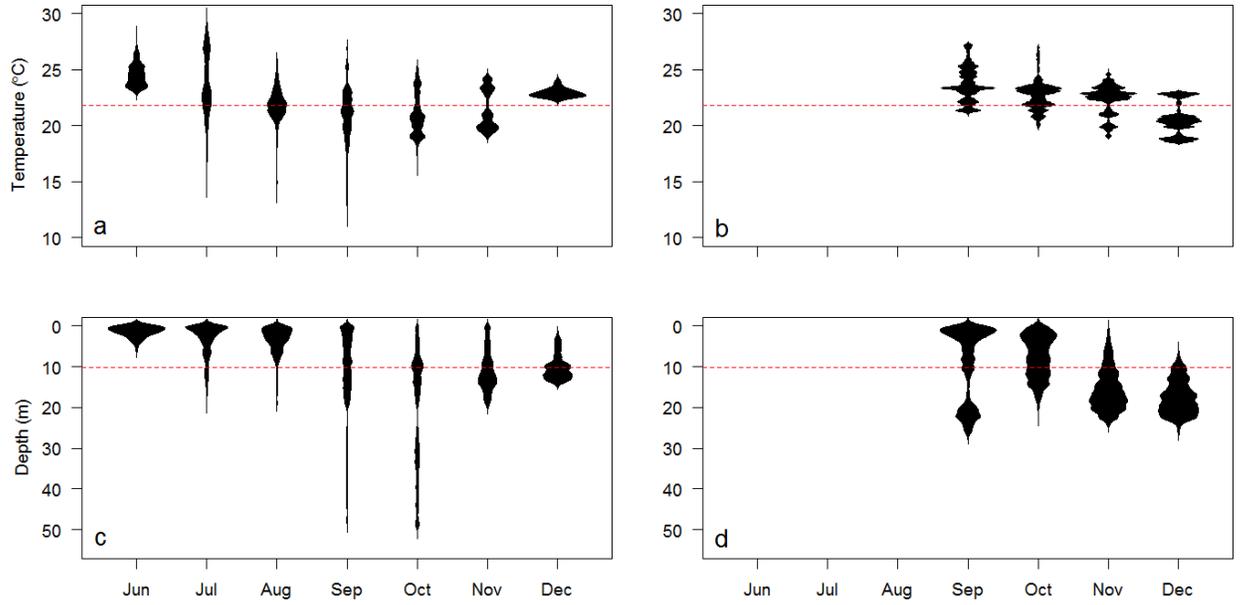


Figure 3. Plots of the distribution of temperature and depth for each month for male (a & c) and female (b & d) cownose rays. Dashed red line indicates the average temperature or depth for all rays combined.

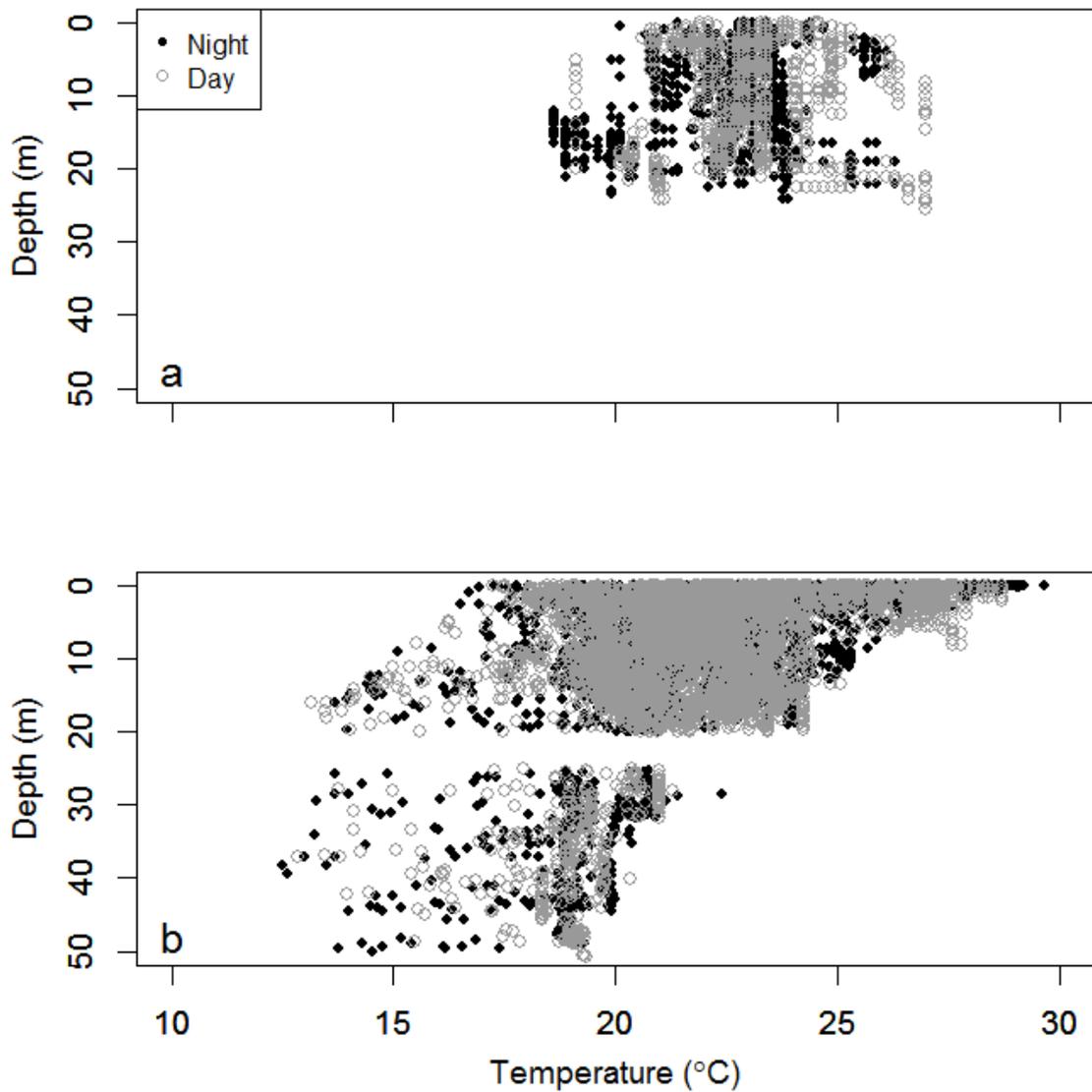


Figure 4. Depth-temperature observations for female (a) and male (b) cownose rays during night (2100-0500, black dots), and day (0800-1600, grey open circles) time periods throughout the entire deployment of PSATs (June-December).

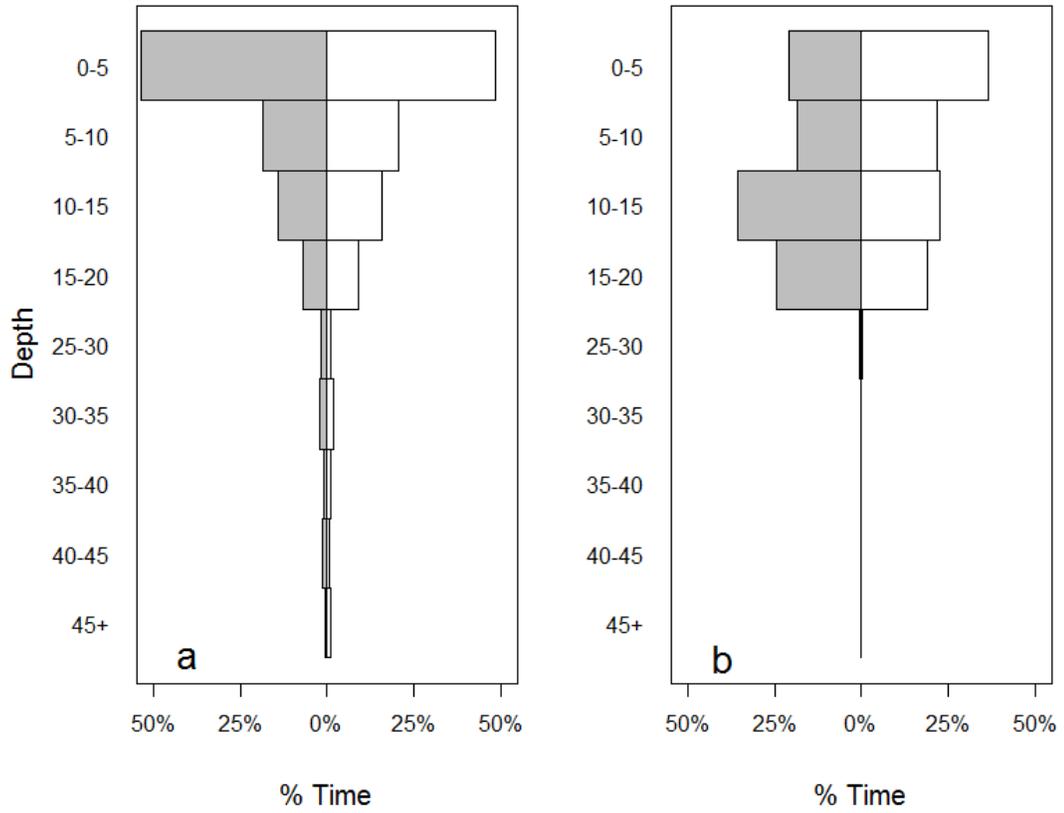


Figure 5. The percentage of total time cownose rays spent at each depth (5m bin-size) during night (grey) and day (white) time periods for male (a) and female (b) tagged rays at liberty for more than 45 days.

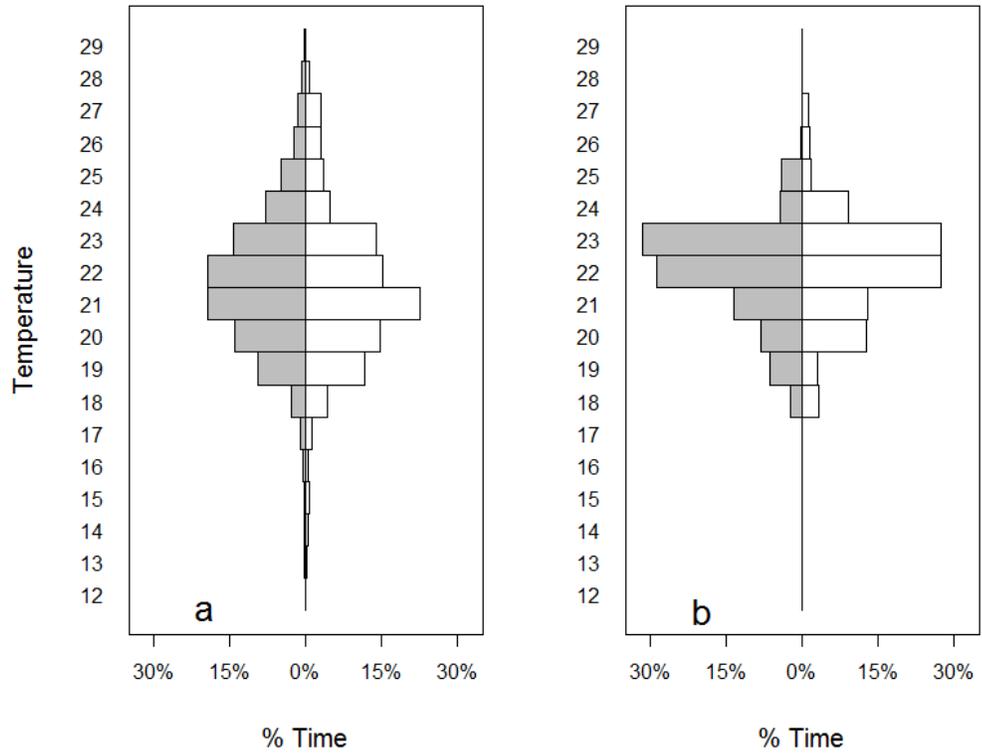


Figure 6. Percentage total time cownose rays spent at each temperature during night (grey) and day (white) time periods for male (a) and female (b) tagged rays at liberty for more than 45 days.

CHAPTER 3

EFFECTS OF UNDERESTIMATING CATCH AND EFFORT ON SURPLUS PRODUCTION MODELS

ABSTRACT

Stocks are often managed based on surplus production models when only catch and effort data are available. However, reported catch and effort rarely equal the true values. I studied the effects of underestimated catch and effort on surplus production model parameter estimates (e.g., MSY, B_{msy} and F_{msy}) as well as key ratios of parameters. I used ASPIC software to examine different scenarios of underreporting to compare to the original dataset for three example fisheries, North Atlantic swordfish, northern pike in Minnesota and queen conch in the Turks and Caicos Islands. Our results suggest that with constant underestimation of catch and effort throughout the time series the biomass parameters (MSY, B_{msy} , B_{next} , B_1 , and K) are all underestimated by the same percentage, and F_{msy} , F_{last} and the ratios, F/F_{msy} and B/B_{msy} , are not affected. This result is safe in the sense that when one thinks the harvest is MSY with $F=F_{msy}$, one is achieving MSY and F_{msy} even though the catch is actually larger than it appears. However, increasing or decreasing trends in underreporting of catch and effort cause errors in the parameter and ratio estimates whose direction is case specific and whose magnitude can be high or low. Each fishery model responded differently to the simulated scenarios, which may be a result of different exploitation histories or the quality of the fit of the production model to the data. If catch and effort are believed to be underestimated, I highly recommend conducting simulations of a variety of possible scenarios similar to the methods in this study to determine how the surplus production model responds.

INTRODUCTION

Surplus production models, also referred to as biomass dynamic models (Ricker 1975; Hilborn and Walters 1992), are one of the simplest methods of assessment with the only required inputs being a time series of catch and effort. Production models provide estimates of biomass throughout the time series, as well as estimates of four fundamental parameters: maximum population size (K), intrinsic rate of population growth (r), catchability coefficient (q) and population biomass at year 1 (B_1). In addition, other important parameters, notably maximum sustainable yield (MSY), biomass at which MSY is obtained (B_{msy}), and fishing mortality which produces MSY (F_{msy}), can be derived from the four fundamental parameters. These are commonly used to determine reference points for harvest regulations.

More complex models have been developed such as integrated size- or age-structured models (e.g., Methot and Wetzel 2013). However, the advanced methods require additional data which are not available for many stocks. For example, age composition is often difficult to obtain in tropical species, invertebrates (Punt *et al.* 2013), and highly migratory species (Kopf *et al.* 2010; Chang and Maunder 2012). Data-poor stocks, such as those in artisanal fisheries (e.g., Jamaican reef fisheries; Koslow *et al.* 1994), shark fisheries, or caught as bycatch (e.g., hammerhead species, *Sphyrna spp.*; Jiao *et al.* 2011), also require use of simple assessment methods such as production models. Moreover, there is a tradeoff between using recent, short time series with higher

quality data with less dynamic range versus utilizing a longer time series with less precise data, but more contrast (e.g., Georges Bank yellowtail flounder; Jacobson *et al.* 2002).

One problem with catch and effort data, particularly from historical records, is that the information may not have been accurately recorded. A major issue today in fisheries management is illegal, unreported, and unregulated (IUU) fisheries (Lodge *et al.* 2007). With high value species, such as eastern Atlantic bluefin tuna, there have been problems with misreported catches (Gagern *et al.* 2013) and fishing locations. This stems from concerns over the validity of logbooks (Polacheck 2012). An extreme case of unreported catch is the South African abalone (*Haliotis midae*) fishery; this species is in high demand which leads to poaching and illegal export (Hauck and Sweijd 1999) of up to 10 times the total allowable catch in one year (Plagányi *et al.* 2011). Another issue of underestimating catch and effort is bycatch mortality, which has only been considered as a source of mortality in the past few decades (Alverson *et al.* 1994). Bycatch mortality is a particularly a contentious problem for long-lived species with low reproductive rates (Hall *et al.* 2000). This additional mortality should always be included in the fishing mortality (Chopin *et al.* 1996; Hall *et al.* 2000). An additional source of non-recorded catch and effort is artisanal fisheries, which often lack fishery reporting regulations (Koslow *et al.* 1994) or even appropriate data.

The degree of underestimation of catch and effort may stay constant or may change through time. Unreported catch and effort in artisanal fisheries may increase as the local population grows. Alternatively, increased monitoring or enforcement efforts might result in reduced problems of unreported catch and effort.

With the possibility of inaccurate catch and effort data, it is necessary to understand the robustness of the production models because there is an increasing demand for stock assessments for data-poor species. The objective of this study was to address the reliability and robustness of the surplus production model, as estimated by Pella and Tomlinson (1969) and Prager (1994), to estimate parameters such as MSY , B_{MSY} and F_{MSY} when catch and effort are underestimated. I used three managed fisheries to represent realistic issues regarding underreported data. These species, North Atlantic swordfish (*Xiphias gladius*), northern pike (*Esox lucius*) and queen conch (*Strombus gigas*), were selected because they have different life histories and have probable underestimation of catch and effort. I underestimated data inputs to simulate how the underreported catch and effort influence estimated production parameters.

CASE STUDY FISHERIES

Three managed fisheries were selected for this study to represent a range of life history characteristics and fishery types (i.e., commercial, mixed commercial-artisanal and mixed recreational-artisanal). These fisheries also vary in the length of the time series and information content (contrast) in the data providing a spectrum of model fits (good to poor). Each of the assessments for these fisheries has used or currently incorporates surplus production models.

The North Atlantic swordfish is a highly migratory, fast-growing fish with longevity of 15 years (Arocha *et al.* 2003; DeMartini *et al.* 2006). This stock is managed by the International Commission for Conservation of Atlantic Tunas (ICCAT) and supports a valuable commercial fishery. Pelagic longlines are the primary gear type, and this target fishery has been operating since the 1950's. The tuna longline fishery, which catches swordfish opportunistically, started in 1956 (Anon. 2010). A combined, standardized catch-per-unit-effort (CPUE) index from 1950 to 2011 from all country participants in the swordfish fishery was used in the 2013 stock assessment (Anon. 2013) as well as in this study. The North Atlantic swordfish fishery was a prime example of a fishery that depended on a multitude of factors that could result in underestimated catch and effort, such as underestimating mortality associated with bycatch and underreported fishing (e.g., IUU).

The northern pike is a temperate, boreal freshwater fish with a longevity of around 17 years (R. Bruesewitz, Minnesota Department of Natural Resources, *pers.*

comm.). The northern pike fishery in Mille Lacs Lake, Minnesota, was selected because it supports a recreational and tribal subsistence fishery. It is jointly regulated by the Great Lakes Indian Fish and Wildlife Commission and Minnesota Department of Natural Resources. The recreational fishery is based on hook and line with catch and effort records starting in 1985. The tribal fishery primarily targets walleye (*Sander vitreus*) using gillnets, with northern pike occurring as a bycatch species. The records for tribal catch for northern pike began in 1997 when the tribal right to fish was affirmed by a court ruling. Although the tribal catch was initially small compared to the recreational fishery, it surpassed the recreational catch from 2003 to 2012. Surplus production models are currently used to determine the status of the northern pike population. Years used for this time series are 1985 to 2011.

The queen conch is a highly valued commercial species that is collected by free diving (Medley and Ninnes 1999). The queen conch fishery in the Turks and Caicos Islands, British West Indies, is an example of a commercial and artisanal fishery. Historically, queen conch was a staple food for the local inhabitants with landing data recorded from 1904 with minimal export. Throughout the century, the conch fishery went through several high and low periods of catch due to commercial and economic demands. It is now the second most important fishery in the Turks and Caicos Islands (Appeldoorn 1996; Ninnes 1994). Because there are only 5-6 processing plants (Medley and Ninnes 1999) for commercial export for all islands, the landings and effort were recorded for all commercial landings. Recorded catch and effort used for this study span from 1974 to 2011. However, the recorded catch and effort did not account for the local consumption from both locals and tourists, and led to an underestimate of the catch and effort.

SIMULATION METHODS

I treated the reported catch and effort as if they were recorded without error (true values). I decreased each by fixed percentages throughout the time series to simulate realistic scenarios of underestimation and observed how the assessment results changed. The scenarios encompassed eight groups (Figure 1): 1) a constant lower percentage of catch and effort by 10%, 20%, 30%, 40% and 50% (Constant), 2) an increase in the underestimation of catch and effort gradually by 1%, 2%, or 3% each year for the first 15 years followed by continued underestimation at 15%, 30% or 45%, respectively (IncreaseBeginCont), 3) the same increase in underestimation for the first 15 years as in (2) followed by no underreporting for all subsequent years (IncreaseBeginStop), 4) no underestimation initially followed by a continual increase in underreporting for the last 15 years as in (2) (IncreaseEnd), 5) a decrease in underestimation gradually by 1%, 2% or 3% each year starting at 15%, 30% and 45% underestimation at the beginning, respectively (DecreaseBegin), 6) same as in (5) but at the end of the time series (DecreaseEnd), 7) an exponential increase (1.01^y , 1.02^y or 1.03^y , where y = year number from 1, 2, ...15) with continued underestimation after year 15 similar to (2) (ExpIncreaseBegin) and 8) the same exponential increase as in (7), but for the last 15 years (ExpIncreaseEnd). All scenarios were created for each of the three species.

I used the non-equilibrium logistic model of Pella and Tomlinson (1969) as described in Prager (1994) because this model is the best to use when the shape of the surplus production curve is unknown, particularly for swordfish-like species (Prager

2002). I ran each of the scenarios and the base (the original, “true” catch and effort) datasets through the ASPICv5 software (A Stock Production Model Incorporating Covariates Version 5; Prager 1994) to obtain biomass and parameter estimates. ASPICv5 uses a lognormal observation error in fishing effort, which is found to provide the least biased and most precise parameter estimates (Polacheck *et al.* 1993, Prager 2002). All parameter estimates were bootstrapped 1000 times, the maximum number allowed in ASPICv5, using residual bootstrapping (Efron and Tibshirani 1986). I compared each of the outputs from the different scenarios to the base by calculating the percentage of change for each parameter and ratio estimate. For convenience, I referred to the percent change as percent error (% error) because I treated the base case as having the correct catch and effort and wanted to determine the error induced by observing false levels of catch and effort. Using estimates of MSY as an example:

$$\% \text{ error} = \frac{\widehat{MSY}_{\text{scenario}} - \widehat{MSY}_{\text{base}}}{\widehat{MSY}_{\text{base}}} * 100$$

I examined the percent error for MSY, Bmsy, Bnext (the starting biomass for the next year), Bnext/Bmsy, Fmsy, Flast (fishing mortality in the last year), and Flast/Fmsy.

RESULTS

Under a constant percentage of underestimation of catch and effort throughout a time series, the B_{next}/B_{msy} and F_{last}/F_{msy} ratios estimated by a surplus production model correctly matched the known ratios, whereas the catch and effort underestimation was reflected in some, but not all individual parameter estimates (Figure 2). For example, if the reported catch and effort were X% lower than the true values, B_{next} , B_{msy} and MSY estimates would also show the same X% error. Because B_{next} and B_{msy} are both underestimated by the same percentage, the ratio B_{next}/B_{msy} remains unchanged because the errors cancel. In contrast, F_{last} and F_{msy} were not affected by the constant underestimation of catch and effort, thus the F_{last}/F_{msy} was also unchanged (Figure 2). Likewise, when catch and effort are constantly underestimated throughout the time series, the estimated biomass is also underestimated by the same percentage (Figure 3 a, d, g). These patterns for constant underestimation were consistent for all three species.

Although scenarios with a constant lower percentage of catch and effort demonstrated clear results, the trends in underestimation throughout the time series produced different patterns among species (Figures 3, 4, 5). No major differences between an increasing underestimation by 1%, 2% and 3% each year ($IncreaseBeginCont$ and $IncreaseEnd$) and the corresponding exponential increase ($ExpIncreaseBegin$ and $ExpIncreaseEnd$, respectively) were discerned. Therefore, results from the exponential increase are not shown.

The errors in the swordfish production model were generally intuitive for all scenarios. For example, the increasing underestimation trend at the beginning of the time series (1%, 2%, or 3% increase per year), followed by a constant underestimation (at 15%, 30% or 45%, respectively, IncreaseBeginCont) resulted in about 15%, 30% or 45% error for the parameter estimates MSY, Bnext and Bmsy (Figure 4). Bnext/Bmsy, Flast, Fmsy and Flast/Fmsy had close to no error from the base (-0.65 to 0.88 % error). This pattern was the same for the constant percentage of underestimation. In addition, the decreasing underestimation trend at the beginning of the time series did not appear to affect the parameter and ratio estimates for the swordfish production model (Figure 5).

Both the pike and conch production models did not have intuitively obvious errors for the parameter and ratio estimates for increasing and decreasing trends in underestimation as in the swordfish model (Figures 4, 5). The trends in the errors were case and scenario specific. For example, with an increasing underestimation of catch and effort at the beginning of the time series followed by no underestimation for the remaining years (IncreaseBeginStop), the swordfish models had no errors for Flast/Fmsy. In contrast for the same scenario group, pike models had negative errors and conch models had positive errors. However, similar to the swordfish model, a 1% increase or decrease in underestimation of catch and effort during the pike time series generally corresponded to the smallest errors. Estimated parameters for the increasing trends (IncreaseBeginCont, IncreaseBeginStop and IncreaseEnd) for the pike production model all fell within 50.65% error (Figure 4).

The conch dataset produced the majority of the extreme percent errors, representing fourteen of the largest twenty errors overall. The largest percent error from a

conch production model was 701%. All of the percent errors that were greater than 100% were associated with biomass parameter estimates, B_{next} and B_{msy} . Despite conch having the majority of large errors, the pike dataset yielded the two largest errors observed.

In general, decreasing underestimation (improved reporting rates) during the time series appeared to generate the greatest range of errors for the swordfish and pike production models (Table 1). The ten largest errors were associated with both 2% and 3% decrease in underestimation of catch and effort at the beginning or end of the time series (Table 1). Estimated parameters in the pike production models associated with biomass, e.g. B_{msy} and MSY , appeared to yield more extreme errors compared to the fishing mortality parameters. In the swordfish production models, decreasing trends in underestimation tended to have a greater effect and more variability on the estimated fishing mortality parameters, e.g. F_{last} , compared to the biomass parameters. In general, each production model responded differently to underestimation of catch and effort.

DISCUSSION

Constant underestimation of catch and effort throughout the time series was manageable because the conclusions remain correct about the harvest rate and the relative biomass level. The biomass estimates and MSY are incorrect, but the production models return the correct biomass ratio. This is due to catch and effort being both underestimated by the same percentage and the errors in B_{next} and B_{msy} estimates are also lower by that same percentage. This results in the ratio B_{next}/B_{msy} being identical to the original data analysis. Thus, a fishery that is estimated as being fished at a certain rate from these data is in fact being fished at that level. Consequently, management efforts can be based on the fishing mortality parameter estimates or ratios, B_{next}/B_{msy} and F_{last}/F_{msy} , from the production models if catch and effort are constantly lower by an unknown percentage. This scenario of constant underestimation of catch and effort is not common, but in situations when this does occur, management can proceed without knowing the level of underreporting.

More common situations are trends in underestimation of catch and effort over time. However, these scenarios resulted in a wide range of positive and negative errors in the parameter estimates making it difficult to determine how the production model will respond to each case. For example, the swordfish production models performed in a manner that seemed intuitive, whereas the pike often displayed the opposite signs in the errors for the same corresponding scenarios. Small problems in underestimation in the swordfish models led to smaller, damped errors in the parameter and ratio estimates for

IncreaseBeginStop, DecreaseBegin and most of IncreaseBeginCont. Small changes in catch and effort in the pike model generally translated into small errors for IncreaseBeginCont and IncreaseBeginStop and for the biomass parameter estimates for IncreaseEnd. Conch models generally had the greatest range of errors and the least distinct patterns in parameter and ratio estimates. The biomass parameter estimates had the largest errors for the conch models. Small problems of underestimation in the conch data were magnified into large errors in most production model estimates. Not all parameter estimates were affected equally by underreporting, similar to the results from Zhang (2013) that showed that the accuracy of one parameter estimate is not reflected in another.

In general, decreasing trends in the underestimation of catch and effort at the beginning or end of the time series for the pike models and decreasing trend at the end for the swordfish models appeared to cause the simulations to perform the poorest. Small changes in catch and effort for the decreasing trends, particularly for DecreaseEnd, were magnified into large errors. A decreasing trend may become more common in fisheries because underreporting can continue to improve. This finding is disconcerting given these efforts. For example, decreased bycatch mortality and unaccounted fishing effort, better reporting rates due to increased observer coverage, or improved log book recordings, and decreased illegal fishing can help improve the accuracy of catch and effort data.

Positive and negative errors in parameter and ratio estimates can have different implications depending on the fishery. In general, a negative percent error for F_{msy} is safe for management because the supposed F_{msy} is smaller than the true F_{msy} , resulting

in under fishing. Similarly, a positive percent error for B_{msy} is not risky because fishery management would be aiming for a higher stock biomass than the true B_{msy} . General patterns are more difficult to describe for the ratios, B/B_{msy} and F/F_{msy} , and are explained case by case based on results from this study.

Case 1: Overall, in a fishery with a lightly exploited stock, for example northern pike in Mille Lacs Lake, a positive or negative error may not drastically change the perceived status of the stock. If the true F/F_{msy} is always less than one (overfishing is not occurring), then a negative error in F/F_{msy} means the fishery is obtaining a higher fishing mortality ratio than what is supposed. However, in this case as previously stated, fishing mortality will still be lower than F_{msy} . This is also true for B/B_{msy} ratio when B/B_{msy} is always greater than one. A negative or positive error in B/B_{msy} results in safe cases because the biomass is always higher than the targeted biomass. As a result, trends in underestimation of catch and effort may not be detrimental to the fishery, but potential yield will be foregone.

Case 2: For constantly heavily exploited stocks, underestimation of catch and effort results in a poor situation for the fishery. When the true F/F_{msy} is always greater than one, a negative error gives rise to risk because the true F/F_{msy} is higher than supposed. In contrast, a positive error in the estimate of F/F_{msy} suggests that the fishing mortality is not quite as high compared to F_{msy} as calculated, alleviating a little fishing pressure. When B/B_{msy} is always less than one, the opposing cases are true. A positive error results in a more severe situation because the true B_{msy} is actually lower than the predicted. A negative error for B/B_{msy} implies that fishery managers believe the biomass

of the stock is worse than the actual true biomass compared to the relative B_{msy} , yet the biomass is still lower than the optimal level.

Case 3: In well-managed fisheries, such as the North Atlantic swordfish fishery, where catch is close to targeted MSY levels, the direction of error is difficult to predict for F/F_{msy} and B/B_{msy} when catch and effort are underestimated. Each situation is unique. For example, if the scenario F/F_{msy} is less than one, but the true F/F_{msy} is greater than one, the percent error is negative. This would result in an unfavorable situation because fishery managers would conclude the stock is doing well when in reality overfishing is occurring. In summary, with a well-managed stock the significance of a positive or negative error for the parameter and ratio estimates is case specific.

Each species responded differently to the various trend scenarios. Swordfish models appeared to be more robust to changes in catch and effort based on the smaller and more intuitive errors, whereas pike models had some different trends in errors from the swordfish depending on the scenario. Conch models had large errors as well as unclear patterns in the errors. A possible explanation for the different results could be differences in exploitation history of each fishery. For example, the original Turks and Caicos queen conch production model has low contrast in fishing effort and was unstable possibly due to the lack of contrast in catch and effort. It appeared that better fitting models with high contrast (i.e., swordfish production models) are more robust to changes in catch and effort compared to poorly fitting models (i.e., queen conch). Examination of additional examples would help to establish the validity of this hypothesis. In addition, North Atlantic swordfish has the longest time series, totaling 62 years, which starts prior to the heavy exploitation of this species (Anon. 2010). As a result, the relatively long

time series begins close to the carrying capacity, K , of the stock and goes through periods of high and low catch and effort. In contrast, the northern pike in Mille Lacs Lake supports a recreational fishery as well as a secondary fishery to the local tribes with a shorter time series totaling 27 years. Regulations on size and bag limits for the recreational fishery were also added over time (M. Luehring, Minnesota Department of Natural Resources, *pers. comm.*). Thus, a number of possibilities could have influenced the model outcomes for each species when catch and effort are underestimated.

Consistent higher or lower parameter and ratio estimates compared to the true MSY-based targets can lead to misguided management strategies. In particular at low abundance levels, overestimating biomass or underestimating fishing mortality due to underestimated catch and effort can potentially lead to severe consequences such as hyperstability followed by stock depletion (Hilborn and Walters 1992; Roa-Ureta 2012). Although this situation may be rare, managing when there are trends in the underestimation of catch and effort can lead to problems and could potentially lead to hyperstability situation.

For data-poor species, I recommend conducting simulations of a variety of possible scenarios when catch and effort are believed to be underestimated in a surplus production model. Each model may respond differently to changes in catch and effort, and as a result these simulations can provide insight on how specific parameter and ratio estimates may be affected by underreporting. Simulations can help determine which estimates are robust to underestimation of catch and effort. Thus, changes in the parameter and ratio estimates from the simulations can potentially be used as precautionary benchmarks for the management of a specific stock.

LITERATURE CITED

- Alverson, D.L., M.H. Freeberg, S.A. Murawski and J.G.A. Pope. 1994. *Global assessment of fisheries bycatch and discards*. Fisheries Technical Paper No. 339. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Anon. 2010. Report of the 2009 Atlantic Swordfish Stock Assessment Session. Collective Volume of Scientific Papers ICCAT, 65: 1-123.
- Anon. 2013. Report of the 2013 Atlantic Swordfish Stock Assessment Session. Collective Volume of Scientific Papers ICCAT, 70: 1484-1678.
- Appeldoorn, R.S. 1996. Status of Queen Conch fishery in the Caribbean Sea. In: J.M. Posada and G. Garcia-Moliner (Eds.), *International Queen Conch Conference*. San Juan, Puerto Rico. 29-31 July: 40-49.
- Arocha, F., Moreno, C., Beerkircher, L., Lee, D.W., Marcano, L. 2003. Update on growth estimates for Swordfish, *Xiphias gladius*, in the northwestern Atlantic. Col. Vol. Sci. Pap. ICCAT 55(4): 1416-1429.
- Chang, S. K., & Maunder, M. N. 2012. Aging material matters in the estimation of von Bertalanffy growth parameters for dolphinfish (*Coryphaena hippurus*). *Fisheries Research*, 119: 147-153.
- Chopin, F., Inoue, Y., Matsushita, Y. and Arimoto, T. 1996. Sources of accounted and unaccounted fishing mortality. In *Solving Bycatch: Considerations for Today and Tomorrow*, eds. Alaska Sea Grant College Program, pp. 41-47. Alaska Sea Grant College Program Report No. 96-03, University of Alaska, Fairbanks.
- DeMartini, E.E., Uchiyama, J.H., Humphreys, R.L.Jr., Sampaga, J.D., Williams, H.A. 2006. Age and growth of Swordfish (*Xiphias gladius*) caught by the Hawaii-based pelagic longline fishery. *Fisheries Bulletin*, 105: 356-367.
- Efron, B. and R. Tibshirani. 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical Science*, 1: 54-75.
- Gagern, A., J. van den Bergh and U.R. Sumaila. 2013. Trade-based estimation of Bluefin Tuna catches in the eastern Atlantic and Mediterranean, 2005-2011. *PLoS ONE*, 8: e69959.
- Hall, M.A., D.L. Alverson and K.I. Metuzals. 2000. By-catch: Problems and solutions. *Marine Pollution Bulletin*, 41: 204-219.

- Hauck, M., and N.A. Sweijd. 1999. A case study of abalone poaching in South Africa and its impact on fisheries management. *ICES Journal of Marine Science: Journal du Conseil*, 56: 1024-1032.
- Hilborn, R. and C.J. Walters. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. Chapman and Hall, London.
- Jacobson, L.D., S.X. Cadrin and J.R. Weinberg. 2002. Tools for estimating surplus production and F_{MSY} in any stock assessment model. *North American Journal of Fisheries Management*, 22: 326-338.
- Jiao, Y., E. Cortes, K. Andrews and F. Guo. 2011. Poor-data and data-poor species stock assessment using a Bayesian hierarchical approach. *Ecological Applications*, 21: 2691-2708.
- Kopf, R.K, K. Drew and R.L. Humphreys Jr. 2010. Age estimation of billfishes (*Kajikia* spp.) using fin spine cross-sections: the need for an international code of practice. *Aquatic Living Resources*, 23: 13-23.
- Koslow, J.A., K. Aiken, S. Auil and A. Clementson. 1994. Catch and effort analysis of the reef fisheries of Jamaica and Belize. *Fishery Bulletin*, 92: 737-747.
- Lodge, M.W., D. Anderson, T. Lobach, G. Munro, K. Sainsbury and A. Wilock. 2007. *Recommended best practices for regional fisheries management organizations, Report of an independent panel to develop a model for improved governance by Regional Fisheries Management Organizations*. Chatham House, London.
- Medley, P. and C. Ninnes. 1999. A stock assessment for the conch (*Strombus gigas*) fishery in the Turks and Caicos Islands. *Bulletin of Marine Science*, 64: 399-406.
- Methot, R. D., & Wetzel, C. R. 2013. Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research*, 142: 86-99.
- Ninnes, C. 1994. A Review on Turks and Caicos Islands Fisheries for *Strombus gigas* L. In: R.S. Appeldoorn and B. Rodriguez Q. (Eds.) *Queen Conch Biology, Fisheries and Mariculture* Fundacion Cientifica Los Roques, Caracas Venezuela: 67-72.
- Pella, J.J. and P.K. Tomlinson. 1969. A generalized stock production model. *Bulletin of the Inter-American Tropical Tuna Commission Bulletin*, 13: 419-496.
- Plagányi, É., D. Butterworth, & M. Burgener. 2011. Illegal and unreported fishing on abalone—Quantifying the extent using a fully integrated assessment model. *Fisheries Research*, 107: 221-232.
- Polacheck, T. 2012. Assessment of IUU fishing for Southern Bluefin Tuna. *Marine Policy*, 36: 1150-1165.

- Polacheck, T., R. Hilborn and A.E. Punt. 1993. Fitting surplus production models: comparing methods and measuring uncertainty. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2597- 2607.
- Prager, M.H. 1994. A suite of extensions to a nonequilibrium surplus-production model. *Fishery Bulletin*, 92: 374-389.
- Prager, M.H. 2002. Comparison of logistic and generalized surplus-production models applied to swordfish, *Xiphias gladius*, in the North Atlantic Ocean. *Fisheries Research* 58: 41-57.
- Punt, A.E., T. Huang and M.N. Maunder. 2013. Review of integrated size-structured models for stock assessment of hard-to-age crustacean and mollusk species. *ICES Journal of Marine Science*, 70: 16-33.
- Ricker, W.E. 1975. Computer and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*, 191: 382.
- Roa-Ureta, R. H. 2012. Modelling in-season pulses of recruitment and hyperstability-hyperdepletion in the *Loligo gahi* fishery around the Falkland Islands with generalized depletion models. *ICES Journal of Marine Science: Journal du Conseil*, 69: 1403-1415.
- Zhang, Z. 2013. Evaluation of logistic surplus production model through simulations. *Fisheries Research*, 140: 36-45.

TABLES AND FIGURES

Table 1. Top 10 cases with the largest % error for all estimated parameters and ratios from swordfish and pike production models (**bold typeface**) and compared to the corresponding swordfish or northern pike model estimates. Decreasing trend at the beginning of the time series is denoted as DecreaseBegin, and decreasing trend at the end of time series as DecreaseEnd followed by the percent of increase or decrease each year (% Inc or Dec).

	Scenario	% Inc or Dec	% Error	
			Swordfish	Pike
1	DecreaseBeg	3 %	0.07	5732
2	DecreaseBeg	3 %	0.02	2348
3	DecreaseBeg	2 %	0.05	505
4	DecreaseEnd	2 %	193	38
5	DecreaseBeg	2 %	0.01	189
6	DecreaseEnd	3 %	126	145
7	DecreaseEnd	3 %	126	145
8	DecreaseEnd	3 %	-20	98
9	DecreaseBeg	3 %	0.34	-98
10	DecreaseBeg	3 %	-0.04	89

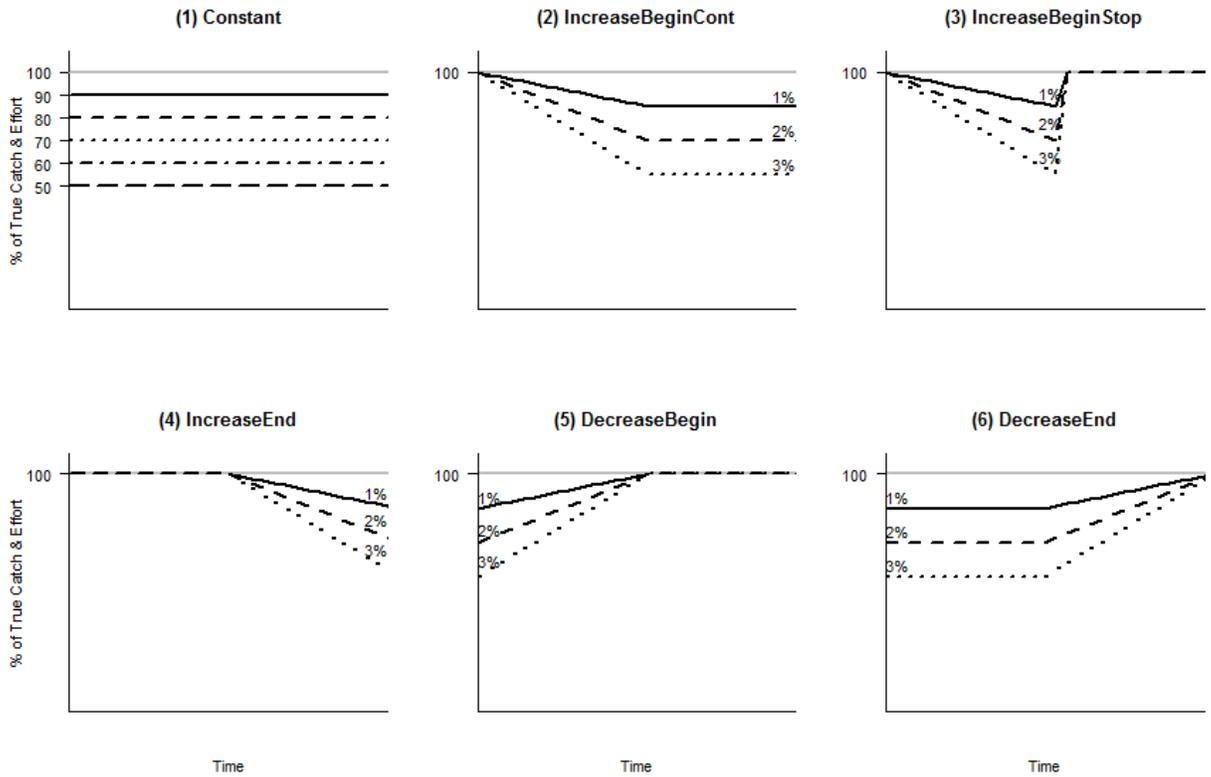


Figure 1. Changes in the simulation runs with the datasets. The percent of the underestimation of catch and effort for compared to the “true” catch and effort at 100% (grey line) for each of the eight groups. Note: The trends of (7) ExpIncreaseBegin and (8) ExpIncreaseEnd are similar to (2) IncreaseBeginCont and (4) IncreaseEnd respectively, and were not plotted.

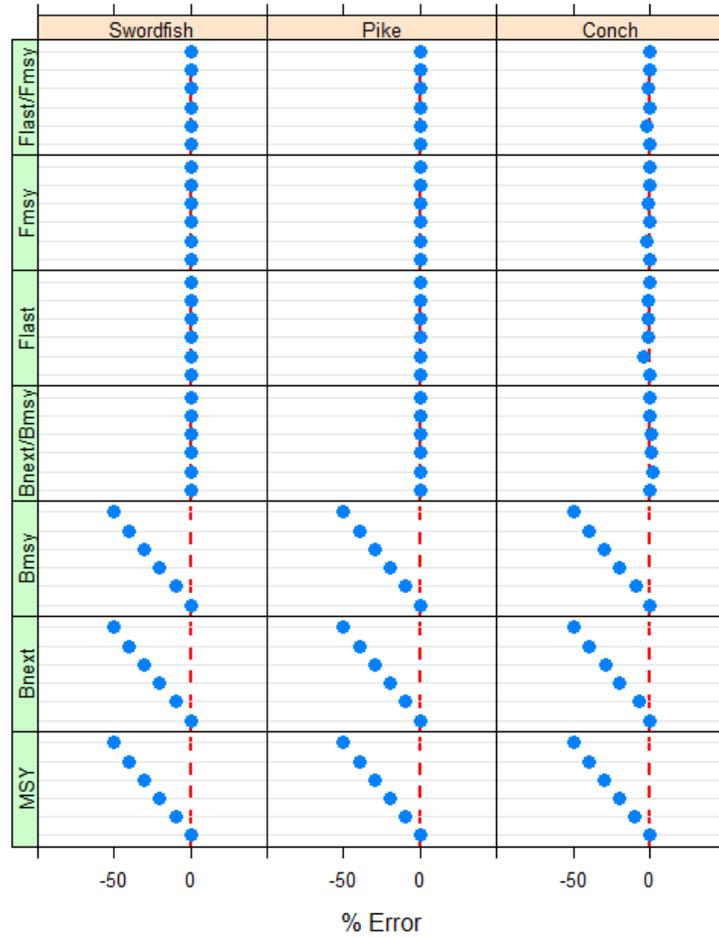


Figure 2. Estimates from the production models of individual parameters and parameter ratios for scenarios of constant percent underestimation of catch and effort for North Atlantic swordfish, northern pike and queen conch. For each panel, the scenarios from bottom to top are: 0%, 10%, 20%, 30%, 40% and 50% underestimation of catch and effort throughout the time series.

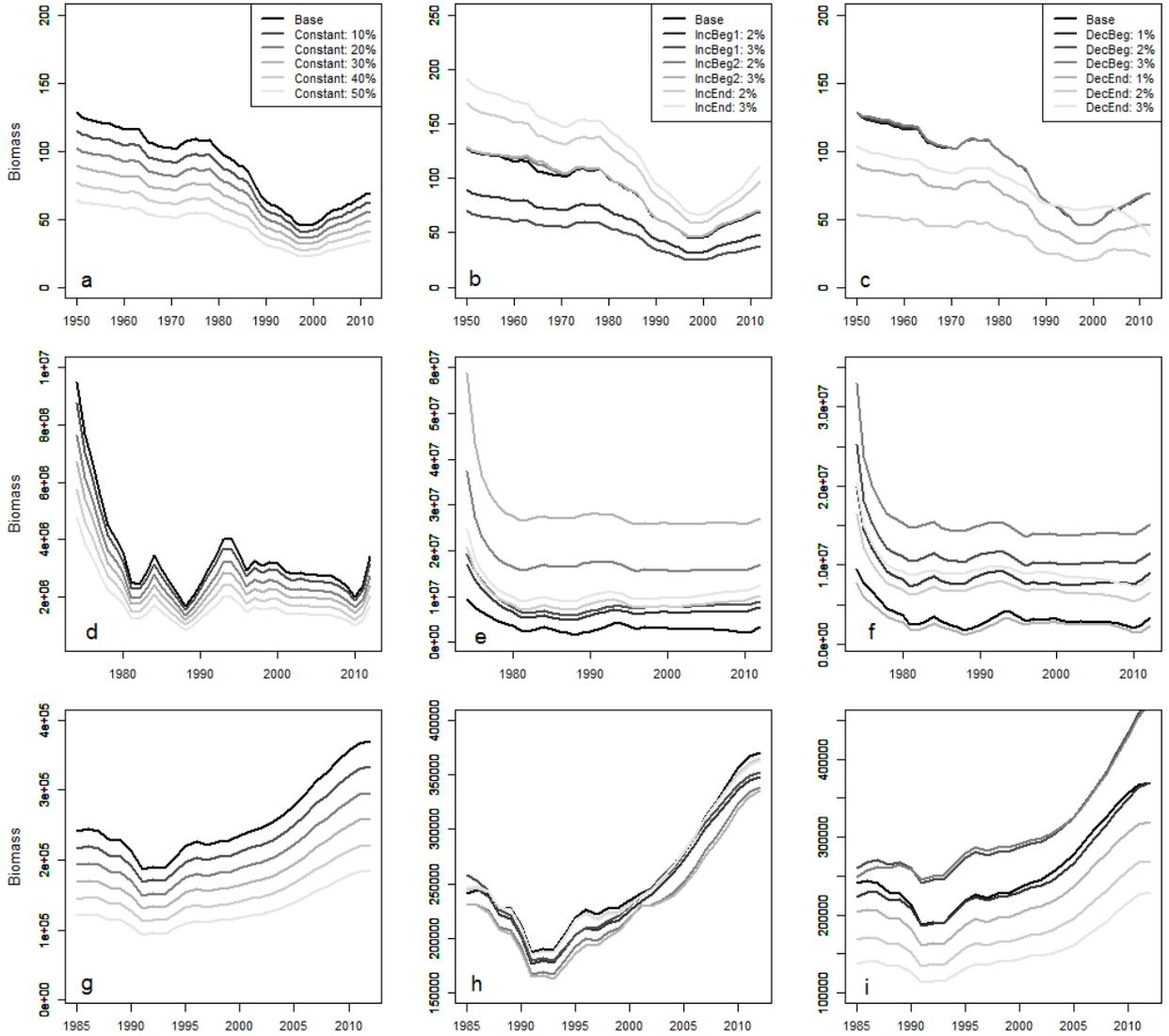


Figure 3. Biomass estimates from the production models for swordfish (row 1), queen conch (row 2) and northern pike (row 3), where each column presents a family of scenarios of underestimation of catch and effort. The first column is for constant underestimation throughout the time series (a, d, g). Second column is increasing trend of underestimation (b, e, h). Third column is decreasing trend of underestimation (c, f, i). Grey line in each panel indicates the base or “true” biomass estimate.

Figure 4. Parameter and ratio estimates from the production models for constant and increasing trends in underestimation of catch and effort for North Atlantic swordfish, northern pike and queen conch. Constant percent underestimation scenarios (10%, 20%...50% from top to bottom in each panel) are represented by open circles. Increasing trends at the beginning of the time series (1%, 2% and 3% from top to bottom) with constant underestimation for the rest of the time series (IncreaseBeginCont) are the filled circles. Increasing trends at the beginning of the time series (1%, 2%, 3% from top to bottom) with no underestimation of catch and effort after the first 15 years (IncBDeginStop) are the open squares. Filled squares are the increasing trend at the end of the time series (IncreaseEnd) for 1%, 2%, and 3%. The X's mark % error greater than 100% error.

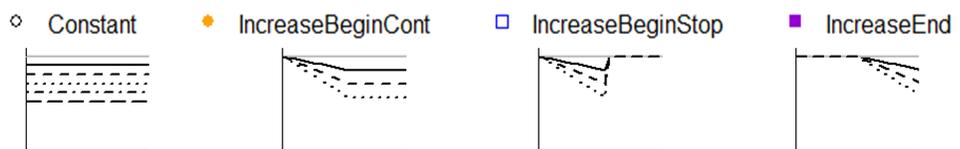
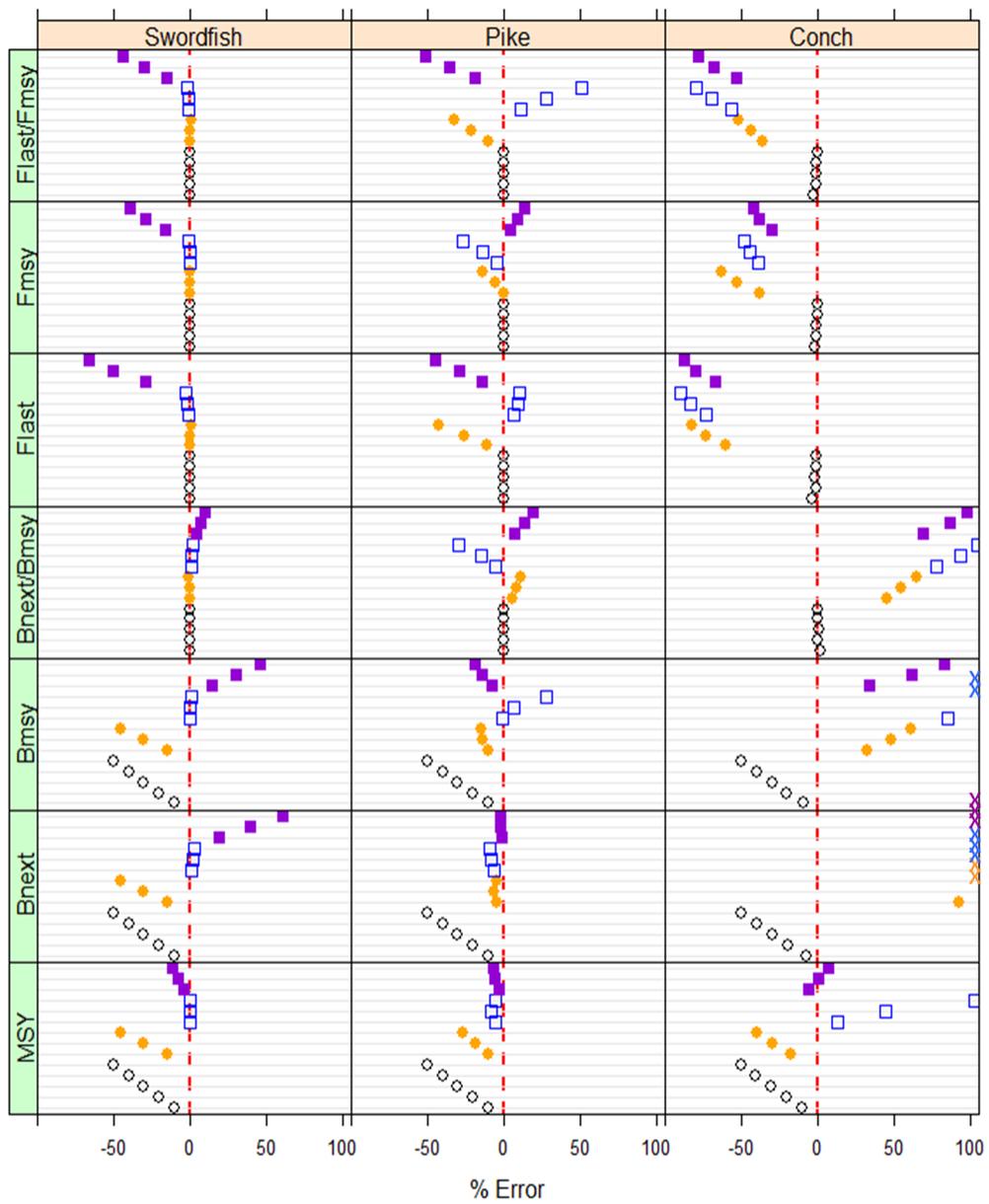
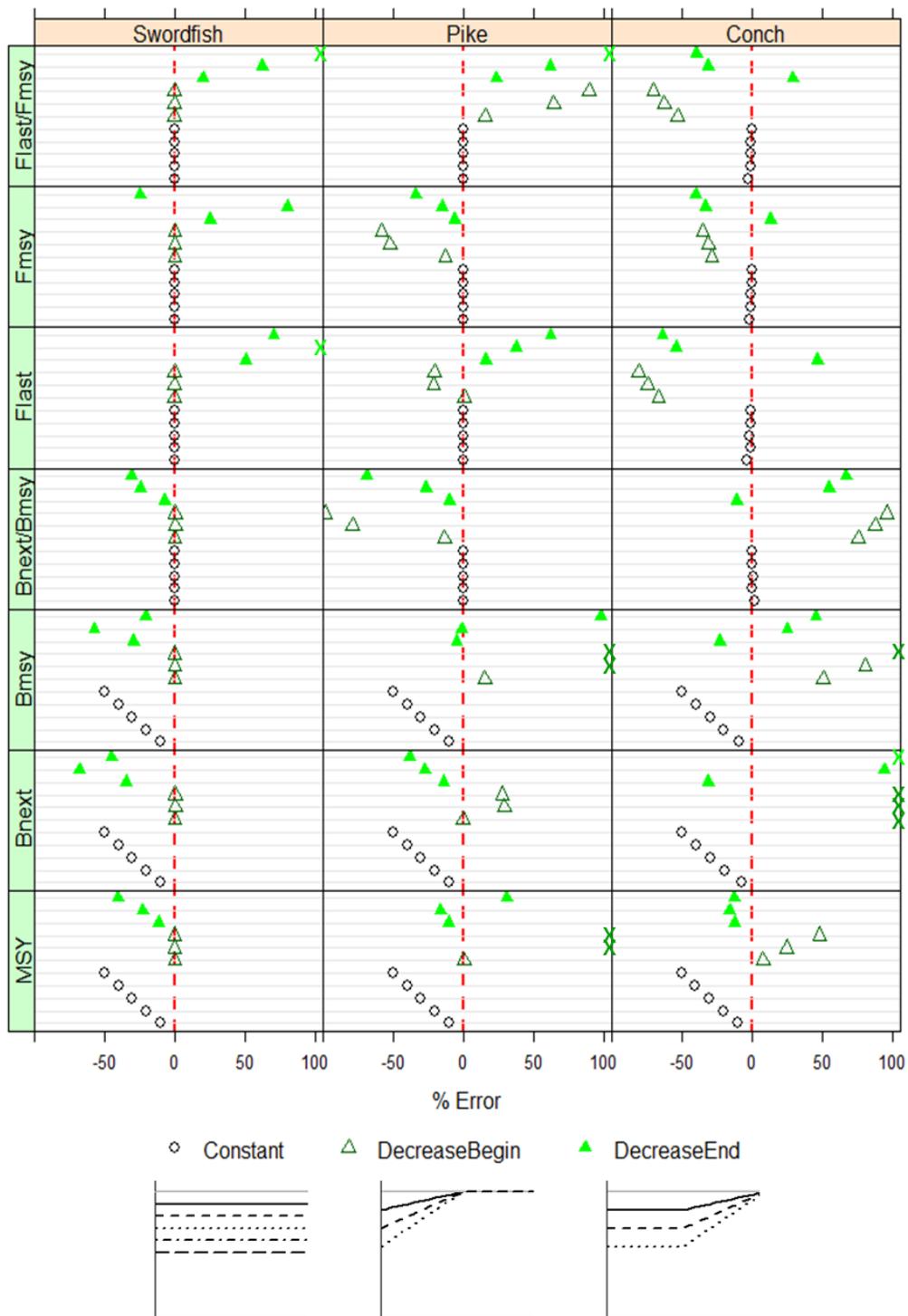


Figure 5. The production model parameter and ratio estimates for North Atlantic swordfish, northern pike and queen conch for increasing and decreasing trends in underestimation of catch and effort throughout the time series. Open circles are constant underestimation (Constant). Decreasing trend at the beginning of the time series for 1%, 2% and 3% (DecreaseBegin) are represented by open triangles from top to bottom. Decreasing trend at the end of the time series for 1%, 2% and 3% (DecreaseEnd) are filled triangles from top to bottom.



CONCLUSION

The goals of this thesis were to 1) provide further information on the movement and behavior of cownose rays from the Chesapeake Bay, and 2) understand how surplus production models respond to underestimation of catch and effort. It is important to understand movement patterns, behavior patterns and the basic biology of a species in order to make the best informed management decisions. Similarly, knowing how assessment models may perform under suboptimal conditions is vital for fish populations at sustainable levels.

In Chapter 2, I verified the wintering grounds for the female and male cownose rays as well as provided insight on the movements of male rays who mate in Chesapeake Bay. Both sexes of rays are found off the coast of central Florida in December, similar to the location discovered by Grusha (2005). However, it appears that this population of rays did not migrate farther south, around Florida, and into the Gulf of Mexico. This could suggest a physical barrier that prevents movement into the gulf area. Previous genetic work demonstrated that the Atlantic and Gulf of Mexico cownose rays are at least two distinct stocks (McDowell and Fisher 2013). Neer and Thompson (2005) also found differences in life history characteristics suggesting little mixing between the two populations. However, recent genetic work distinguished two separate species in the Gulf of Mexico, *R. bonasus* and *R. brasiliensis* (J. McDowell, *pers. l. comm.*), which may account for some of the differences in the life history characteristics.

Although the Atlantic cownose rays are seen farther north, around Cape Cod, it was surprising to discover that male cownose rays that mate in the Chesapeake Bay continue north to off the coast of Rhode Island and Long Island, New York. With this new finding, there is more work that needs to be completed to better understand male

cownose ray movements and behavior, and whether males from other bays along the Atlantic coast follow a similar summer movement pattern. In addition, rays tagged in this study were fairly tolerant to a wide range of temperatures and were able to endure colder temperatures for short periods of time.

The amount of data I was able to recover from each of the satellite archival tags varied. The tags that were prematurely released inside Chesapeake Bay were not included in the analysis because the main objectives were large scale movements and behavior. Moreover, I could not retrieve any useful light level data when the ray was inside of the bay. PSATs were originally designed for large pelagic fish in the open ocean where there are fewer factors that can influence the light-level curves. Although the light levels were recorded when the tag was near the surface, there were many factors in the coastal waters that could have caused errors in the light level readings. Some factors that could have affected the light level readings include turbidity, subaquatic vegetation, such as sea grass, shadows from land and docks, and weather.

Pop-up satellite tags are best used for long movement patterns with pelagic species and generally are not the most useful electronic tagging tool for fine scale movements of nearshore species. Exact timing of movements and movement inside the Chesapeake Bay would be better estimated by another device such as acoustic tagging. The most probable tracks from the WC-GPE3 program did suggest that tagged rays occasionally went farther offshore, past the continental shelf. Based on the rays diving patterns and assuming that many of the dives were to feed on benthic organisms, the geolocations estimated off the continental shelf area seem unlikely. Nevertheless, the overall most probable tracks appeared to capture the general movements of the rays.

Ultimately, movement patterns of the cownose rays from the Chesapeake Bay will aid in the management of this species to help determine whether and where a fishery could be sustainable.

In Chapter 3, I discussed the need to understand problems with the data input and the effect on a basic surplus production models. I determined that constant underestimation of catch and effort is manageable. The parameter estimated by the production model either produced no error (i.e., F_{msy} , F_{last} , F_{last}/F_{msy} , and B_{next}/B_{msy}) or the error was the same percentage lower as the underreporting (i.e., B_{msy} , B_{next} and MSY). In contrast, trends in underestimation of catch and effort throughout the time series, which is a more likely scenario than constant underreporting, resulted in little to no pattern and the outcomes were fishery dependent. Each scenario produced different results, thus trends in underestimation can lead to problems when management is only based on the production model parameter estimates. In particular, decreasing trends over time (improved reporting rates) produced the largest errors. As a result, I would suggest taking precautions when underestimation of catch and effort are thought to occur.

The results from this study will improve the knowledge on how surplus production models are affected when there are changes to the data input. In addition, two of the fishery examples used in this study, Northern pike from Mille Lacs Lake, Minnesota, and queen conch from the Turks and Caicos Islands have benefitted from these results. In Mille Lacs Lake, it was thought that additional bycatch mortality may change the parameter estimates from the production model. In the queen conch fishery, the catch and effort from local consumption was not included in the original assessment.

Thus, in both cases, it was originally believed that the catch and effort from the bycatch and local consumption were excluded by the same percentage throughout the time series representing a constant underestimation of catch and effort scenario. There are many data-poor fisheries that potentially have underreporting of catch and effort that can benefit from the simulations conducted in Chapter 3.

LITERATURE CITED

- Grusha, R.D. 2005. Investigations into the life history of the Cownose Ray, *Rhinoptera bonasus*, (Mitchill, 1815). Master's thesis. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point.
- McDowell, J. R. and R.A. Fisher. 2013. Discrimination of cownose ray, *Rhinoptera bonasus*, stocks based on microsatellite DNA markers. VIMS Marine Resource Report No. 2013-8.
- Neer, J.A. and B.A. Thompson. 2005. Life history of the cownose ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. *Environmental Biology of Fishes* 73: 321-331.

VITA

Kristen L. Omori

Born in Seattle, Washington, on July 4, 1987. Graduated from Juanita High School in Kirkland, Washington, in 2005. Earned two B.S. degrees in Aquatic and Fishery Sciences and Environmental Sciences and Resource Management from the University of Washington in 2010. Worked as a fisheries research technician for the Alaska Salmon Program in remote areas of Alaska. Worked as an assistant researcher in the Comoros Islands on coral reef surveys in artisanal fisheries. Worked for U.S. Geological Survey on Elwha River Restoration project in the Olympic Peninsula, Washington. Entered the Master's program in Fisheries Science at Virginia Institute of Marine Science, College of William & Mary in 2012.