The physiological ecology and behaviour of an apex marine predatory fish, the great barracuda (*Sphyraena barracuda*)

By

Amanda Christine O'Toole

B.Sc., Carleton University, 2008

A thesis submitted to the Faculty of Graduate Studies and Research

in partial fulfillment of the requirements for the degree of

Masters of Science
in
Biology

Carleton University
Ottawa, Ontario

©2010, Amanda C. O'Toole

Dedication

To my parents and grandparents for being the first to introduce me to the wonders of the natural world, outdoor living, and summer fishing trips. For Kyle, who has supported me through the rough moments and celebrated with me during the happy ones and for always believing in me. Thank you to the members of the Cooke lab, past and present, for their friendship, wise advice, and for sharing their experiences. To Andy for his advice and sense of humour. To my advisor Steve, for his constant guidance, enthusiasm, and for presenting me with endless opportunities over the past four years, all of which have led me to achieve goals that I would never have imagined previously.

Abstract

As a common nearshore predator in tropical and sub-tropical regions, great barracuda (*Sphyraena barracuda*) hold ecological, economic, and cultural importance, however, little is known about their basic biology. Fine-scale behaviour was assessed by tagging fish with acoustic transmitters equipped with pressure and tri-axial accelerometer sensors and tracking them with a hydrophone array in the The Bahamas. Although barracuda did not show differences in locomotory activity or depth use across habitat types and diel periods, some degree of movement repeatability and transience were apparent. The consequences of catch-and-release angling were also investigated showing some evidence of injury associated across lure types, that physiological disturbance was relatively minor, and initial mortality was negligible. Blood samples were examined for ciguatoxin, leading to the development of the first non-lethal approach for detecting ciguatera in fish. This thesis has increased the understanding of great barracuda biology and will promote conservation and management initiatives for this species.

Acknowledgments

I would like to acknowledge the staff and volunteers at Cape Eleuthera Institute and The Island School for use of facilities and assistance with fieldwork. Thank you to Edd Brooks, Jim Cooke, Chris Haak, Kyle Hanson, Caleb Hasler, Karen Murchie, Chris Pullen, Kristen Pullen, David Philipp, Aaron Shultz, and Mark Taylor for field and laboratory assistance. I would also like to acknowledge my co-authors Andy Danylchuk, Kyle Hanson, Karen Murchie, Chris Pullen, Cory Suski, and Steven Cooke who assisted in developing Chapters 2 and 3 and the preliminary work presented in the appendices. Ciguatoxin bioassays were performed by Marie-Yasmine Bottein Dechraoui and John Ramsdell of the Marine Biotoxin Program, Center for Coastal Environmental Health and Biomolecular Research, NOAA. Thank you to my committee members for providing comments during the final stages of preparing this thesis. The Bahamas Department of Marine Resources provided scientific collection permits and animal care approval was obtained from the Canadian Council on Animal Care through Carleton University. The receiver array was partially supported by grants from Bonefish and Tarpon Trust, the Charles A. and Anne Morrow Lindbergh Foundation, and the Baldwin Foundation. Additional financial support was provided by Ontario Ministry of Research and Innovation (through an Early Researcher Award to S.J.C.), the Canada Foundation for Innovation, the Canada Research Chairs Program, and Carleton University.

Co-Authorship

Chapter 2: Locomotory activity and depth distribution of adult great barracuda (*Sphyraena barracuda*) in Bahamian coastal habitats determined using accelerometer biotelemetry transmitters. A. C. O'Toole, K. J. Murchie, C. Pullen, K. C. Hanson, C. D. Suski, A. J. Danylchuk, and S. J. Cooke.

While this study is my own, the research was undertaken as part of a collaborative effort and each co-author played a valuable role in its completion. The project was conceived by O'Toole, Danylchuk, Suski, and Cooke. Fieldwork was completed by all authors and laboratory calibrations were conceived and performed by O'Toole, Murchie, Hanson, Danylchuk, and Cooke. All computer and data analysis was conducted by O'Toole and Hanson. Data were interpreted by O'Toole, Danylchuk, Hanson, and Cooke. All writing was conducted by O'Toole. All co-authors provided comments and feedback on the manuscript. This manuscript has been submitted to *Marine and Freshwater Research*.

Chapter 3: Consequences of catch-and-release angling on the physiological status and condition of great barracuda (*Sphyraena barracuda*) in The Bahamas. A. C. O'Toole, A. J. Danylchuk, C. D. Suski, and S. J. Cooke.

While this study is my own, the research was undertaken as part of a collaborative effort and each co-author played a valuable role in its completion. The project was conceived by O'Toole, Danylchuk, Suski, and Cooke. Fieldwork was completed by all authors. All computer and data analysis was conducted by O'Toole. Data were

interpreted by O'Toole, Danylchuk, Suski, and Cooke. All writing was conducted by O'Toole. All co-authors provided comments and feedback on the manuscript. This manuscript has been accepted for publication in *ICES Journal of Marine Science.*

Table of Contents

List of Tables

List of Figures

List of Appendices

Glossary

ANOVA: Analysis of variance

CFP: Ciguatera fish poisoning

CTX: Ciguatoxin

C-CTX-1: Caribbean ciguatoxin congener

eDNA: Environmental DNA

FL: Fork length

MDT: Median distance travelled

MLD: Minimum linear distance

MS222: 3-aminobenzoic acid ethyl ester

ODBA: Overall dynamic body acceleration

PCR: Polymerase chain reaction

SE: Standard error

SL: Standard length

TL: Total length

Chapter 1: General Introduction

As a common inhabitant in the warm, subtropical waters of the Caribbean and Western Atlantic Ocean, a lurking barracuda watching curiously from the edge of the reef is not an unusual sight for a dive tourist. It is surprising that, although common, there is a paucity of knowledge pertaining to the biology of great barracuda (*Sphyraena barracuda*). In fact, the most comprehensive body of literature on the natural history and basic biology of the great barracuda that currently exists emanates from a Ph.D. thesis written by Donald de Sylva in 1963 through the University of Miami; a body of work which was based largely on data obtained from commercial and recreational catches. Few other studies have focused exclusively on this species, concentrating mainly on crude behavioural observations and juvenile feeding habits (summarized in Table 1-1). Furthermore, a very small number of publications include *S. barracuda* observations as a part of an overall analysis of the Sphyraenidae family (Williams, 1959; Williams, 1965) and few papers document other species of Sphyraenidae (Barreiros et al., 2002; Rim et al., 2007; Pastore, 2009). Various researchers have also included barracuda as a component of ecological (Nagelkerken and van der Velde, 2004; Verweij et al., 2006; Serafy, 2007; Valentine et al., 2007; Faunce and Serafy, 2008), life history (Randall, 1967; Gero, 1952; Porter and Motta, 2004), or biotoxin (de Sylva, 1994; Dechraoui et al., 2005) studies. While many of these past studies are informative and provide some important basic knowledge of the species, much of the research is based on observations made by divers, catches from the recreational and commercial fishing sectors, or anecdotal evidence. This fragmented knowledge makes piecing together the overall picture of barracuda natural history and basic biology challenging. As such, there is a

need for more extensive research on this fascinating and dynamic species across its geographical range. In this chapter, I will provide a general overview of the barracuda biology and natural history including available information on reproduction, life cycle, spatial ecology, behavioural activity, and the ecological, economic, and cultural importance of this species.

Reproduction and Life Cycle

Currently, knowledge of reproductive behaviour and the life cycle of great barracuda and all Sphyraenidae are limited. It is believed that adult barracuda spawn in deeper, offshore areas at the intersection of coastal and oceanic circulation so that larvae may be dispersed to other regions by currents or carried inshore with tidal action (de Sylva, 1963). The peak reproductive period (inferred from annual trends in gonadal somatic indices) tends to occur in early summer (May-July), extending through to early autumn (based on data collected from the southern coast of Florida), with females having a narrower spawning time-range than males (de Sylva, 1963). In addition, larval and post-larval barracuda (<12 mm, SL) have been collected in plankton tows from offshore, pelagic waters throughout the year in the eastern Caribbean Sea and off the east coast of the United States (de Sylva, 1963; Figure 1-1). Juvenile barracuda are known to inhabit mangrove-dominated coastal habitats (i.e. tidal creeks) suggesting such areas may serve as nursery habitat (Serafy et al., 2007). Once the young barracuda attain a size of approximately 500 mm, it is believed that they move into deeper, reef dominated habitat as they grow to reach adulthood. Given that reproductive activity and growth rates may vary between geographic locations it remains uncertain whether global populations of great barracuda share similar spawning patterns and life history traits.

Spatial and Behavioural Ecology

Great barracuda have a circumtropical distribution within the western Atlantic Ocean, Caribbean Sea, and Indo-Pacific regions, and individuals are typically found inhabiting reef areas, seagrass beds and offshore pelagic waters (de Sylva, 1963). Current knowledge about the habitat utilization and movement of great barracuda has been presented at very coarse spatial scales. To date, only two studies have utilized anchor tags and mark-recapture methods to study barracuda spatial distribution and movement (Springer and McErlean, 1961; Villareal et al., 2007) and a third study has used natural body marks to observe local movement of individual barracuda (Wilson et al., 2006b). It has been suggested that barracuda migrate seasonally (de Sylva, 1963), in some cases, up to 1000 km (Villareal et al., 2007) and that larger individuals move greater distances than smaller fish (Springer and McErlean, 1961). By using natural body markings to identify individual barracuda, Wilson et al. (2006b) determined that barracuda exhibited a certain degree of site fidelity, although it was postulated that some individuals also migrated out of the immediate area.

Great barracuda are efficient predators, characterized as having slender, stream-lined bodies, well developed eyes, and strong jaws and teeth (Horn, 1998). As ambush predators, they exhibit ram-bite feeding behaviour, where they burst at high-speeds, impacting prey at the hinge of the mouth, severing it in half before swallowing (Porter and Motta, 2004; Grubich et al., 2008). Although prey items vary by geographic location (Blaber, 1982; Schmidt, 1989), stomach content analyses from barracuda caught near Florida and Bimini show that adults feed mainly on fast-swimming pelagic and surface-dwelling fish as well as tetraodontiform reef fish (de Sylva, 1963; Schmidt, 1989). de

Sylva (1963) observed that barracuda appear to depend heavily upon eyesight to locate prey, and may be predominately diurnal foragers. Adult great barracuda often exhibit solitary and sometimes territorial behaviour, although sometimes they are found in small schools of 3 or 4 individuals. In contrast, juveniles and young adults have been documented to aggregate in bigger groups compared to their larger conspecifics (de Sylva, 1963; Paterson, 1998). The reasons for this type behaviour in adult barracuda are unclear and it is postulated to be attributed to pre-spawn aggregations, forging groups, or predator avoidance (de Sylva, 1963; Paterson 1998).

Recent developments in acoustic telemetry technology have enhanced the ability to understand fish behaviour, energetics, and physiology in an undisturbed state within their natural environment (Cooke et al., 2004; Heupel et al., 2006a). These techniques have been applied in a variety of habitat-use, seasonal migration, diel activity studies, enhancing biological knowledge and potential management of top predators including reef-dwelling teleosts and elasmobranch species (Meyer and Holland, 2005; Heupel et al., 2006b; Meyer et al., 2007; Yeiser et al., 2008). Furthermore, information gained from telemetry transmitters equipped with biological sensors (for example, accelerometer and pressure sensors) may give a better indication of biological activity at a finer scale.

Importance of Great Barracuda

Great barracuda may play a significant ecological role as an apex predator in nearshore tropical marine systems, similar to that of many shark species (Myers et al., 2007) and large teleosts (Friedlander and DeMartini, 2002). Declines in top predators may contribute to changes in marine ecosystems through predation and risk effect processes (Myers and Worm, 2003; Heithaus et al., 2008). Because they are relatively

abundant and inhabit nearshore areas, barracuda are often targeted by anglers for recreation as well as by subsistence fishers for consumption (Springer and McErlean, 1961; de Sylva, 1963; Villareal et al., 2007). Recreational fishing and dive tourism often contribute to regional economies through income generated by tourism, especially in island nations such as The Bahamas where the tourism industry accounts for a considerable proportion of the Gross Domestic Product (Government of The Bahamas, 2005). Subsistence fishers rely heavily on locally available marine resources and often fish nearshore reefs and mangrove creeks as a source of income and food (Dunn et al., 2010).

Ciguatera fish poisoning is caused by the human consumption of contaminated reef fish and clinical cases are typically confined within distinct subtropical and tropical regions of the Caribbean Sea, Pacific Ocean, and Indian Ocean (Swift and Swift, 1993; Lewis, 2001; Bienfang et al., 2008). Since little is known about the behaviour and spatial ecology of barracuda, the origin of ciguatoxin concentrations found in the tissues of contaminated fish are difficult to identify. In addition, current techniques for evaluating ciguatera poisoning are lethal (Matta et al., 1999; Dechraoui et al., 2005), which thus far has made it impossible to attempt to determine how spatial ecology of individual fish influences ciguatoxin burden.

Research Objectives and Predictions

The overall objective of this thesis is to examine the physiological ecology and behaviour of the great barracuda. The field work for my Master's thesis research was conducted off the coast of Cape Eleuthera, The Bahamas, in conjunction with Cape Eleuthera Institute (CEI), taking advantage of a previously established fixed acoustic

telemetry array. Chapter 2 of this thesis examines the fine-scale behaviour of great barracuda across habitat types and diel periods using acoustic transmitters equipped with accelerometer and pressure sensors. I expected to observe differences in relative activity and depth utilization across habitat types and according to time of day. As the fish for this project were captured via standard angling techniques, it also provided an opportunity to evaluate species-specific injury and physiological consequences of catch-and-release practices for great barracuda. Similar to other popular marine gamefish, I predicted that great barracuda may be subject to increased physiological disturbance when exposed to long angling durations and excessive handling. In addition, I predicted that barracuda would be prone to injury as a result of lure and hook types commonly used in the recreational fishery of the western Atlantic and Caribbean regions. The findings from this catch-and-release study are presented in Chapter 3. Chapter 4 will integrate the findings of the previous two chapters and will present potential management recommendations, conservation implications, and future research directions. Appendix I contains preliminary results from a spatial ecology study regarding barracuda habitat use and temporal behaviour and Appendix II briefly summarizes an innovative project where in collaboration with scientists from the National Oceanic and Atmospheric Administration we developed a non-lethal technique for determining ciguatera burden in fish.

Tables

Table 1-1. Summary of available and current literature focused primarily on the biology and natural history of great barracuda (*S. barracuda*).

Author, year	Research summary	Comments
Blaber, 1982	Ecology and natural history of *S. barracuda* in South Africa.	Focused on juvenile life stage within an estuary and habitat and diet preferences of *S. barracuda*. Includes references to differences between global geographic locations.
de Sylva, 1963	General research devoted to the biology, natural history and systematics of *S. barracuda*.	Most comprehensive body of literature to date for *S. barracuda*. Presents broad range of information forming a basis of research for the species. Observations based mainly on anecdotal and fisheries catch data.
Grubich et al., 2008	Functional morphology of *S. barracuda* bite mechanics.	Showed barracuda feeding habits and prey capture mechanisms. Although experiments were performed with juveniles, findings can be applied to adults.
Paterson, 1998	Group occurrence and mobility of *S. barracuda* associated with habitat, size, and environmental factors.	Gives insight into behaviour and movement, however, data collected was solely from underwater visual observations.
Schmidt, 1989	Food habits, condition, length-weight relationship.	Quantitative feeding and growth data specific to juveniles in Florida. No information pertaining to adults.
Springer and McErlean, 1961	*S. barracuda* mark-recapture study.	Provides a rough estimation of *S. barracuda* movement and habitat use. The fish were at large for 4 – 348 days and 8.1% of the tags were returned. Larger individuals were estimated to move longer distances than small individuals.

Wilson et al., 2006b	Identification of individual *S. barracuda* using body markings.	Found that identification of individuals based on body markings to be effective and non-invasive method of monitoring movement and behaviour. However, long-term studies involving migrating or non-resident individuals would require the use of tagging or telemetry techniques.

Figures

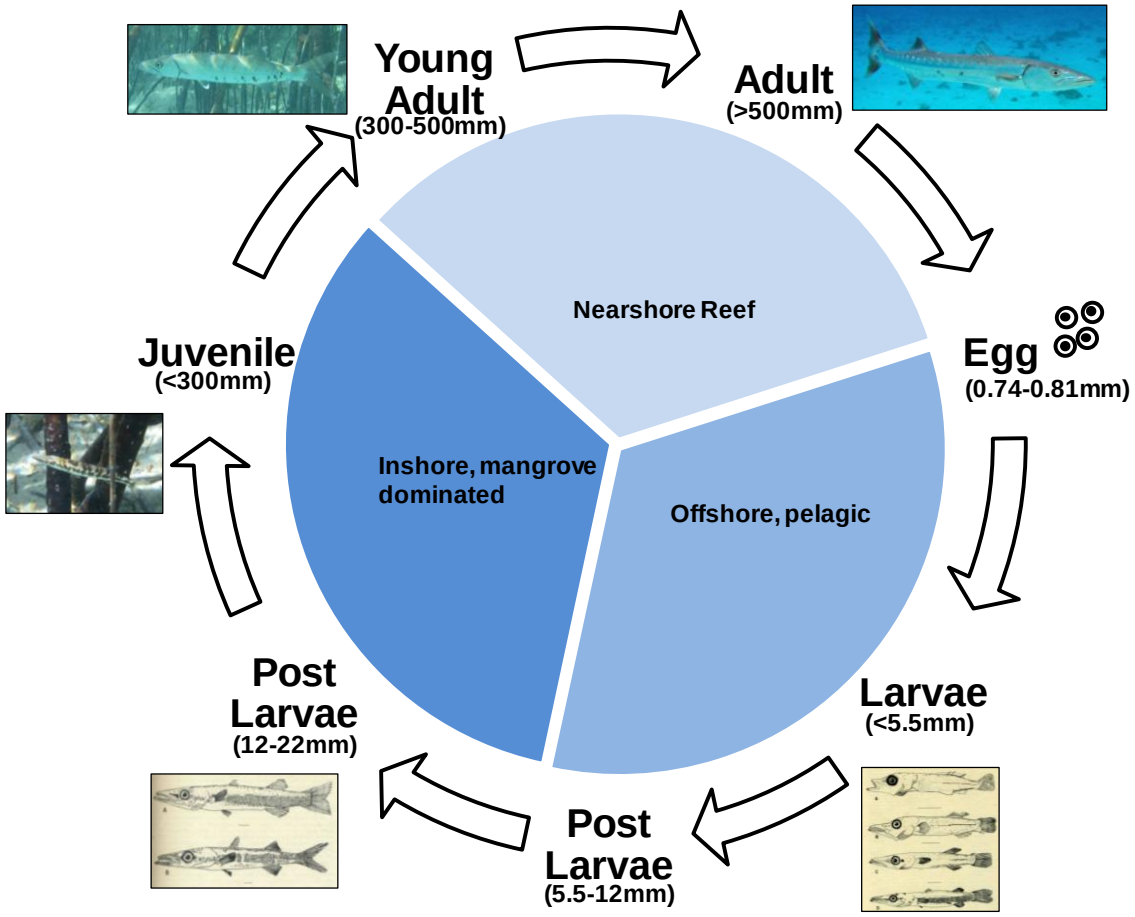

Figure 1-1. Diagram depicting the life cycle of *S. barracuda*. For each ontogenetic stage, the general size range (represented in standard length, SL) and habitat preference are illustrated.

Chapter 2: Locomotory activity and depth distribution of adult great barracuda (*Sphyraena barracuda*) in Bahamian coastal habitats determined using accelerometer biotelemetry transmitters

Abstract

Great barracuda (*Sphyraena barracuda*) are a common nearshore predator in tropical and sub-tropical regions that hold ecological, economic, and cultural importance, however, little is known about their behaviour. Fine-scale locomotory activity and depth utilization of adult great barracuda were monitored across habitat types and diel periods using acoustic transmitters equipped with tri-axial accelerometer and pressure sensors. An acoustic telemetry array (n = 53 receivers) was deployed near Cape Eleuthera, The Bahamas. Barracuda most frequently exhibited low levels of locomotory activity (0.10 - 0.74 m s^{-2}), representing 58% of total activity measurements for wild fish as they engaged in slow swimming or hovering in place. Occasionally, fish were more active, showing higher levels of bursting activity (>3.47 m s^{-2}). Barracuda were generally detected at depths < 5 m below the water surface, even while in deep, continental shelf habitat. There were no differences in acceleration or depth use across habitats or diel periods. On occasion, some fish moved into shelf habitat during mid-day (into depths >10 m) before moving back into nearshore waters around dusk, although the pattern was not consistent among all fish. Despite having an expansive array covering roughly 23,426 km^2, no fish remained within the array for the entire period and several fish were only detected for short periods suggesting that barracuda are transitory. This paper represents one of the

first reports of the use of telemetered accelerometer values from free-swimming fish and is also the first telemetry study on barracuda.

Introduction

Documenting the distribution of free-ranging marine animals in space and time is fundamental to understanding their basic natural history, intra- and inter-specific interactions, and habitat requirements (Cooke et al., 2004a; Ropert-Coudert and Wilson, 2005; Cooke, 2008). To that end, there have been hundreds of studies that have used different biotelemetry, biologging, and mark recapture techniques to document the spatial ecology of marine animals in habitats ranging from inshore coastal flats to the high seas (Kohler and Turner, 2001; Block et al., 2003; Cooke et al., 2004a; Block, 2005; Ropert-Coudert and Wilson, 2005). This information has improved our knowledge of the spatial ecology of marine animals, enabling managers and conservation practitioners to identify and protect critical habitats (Palumbi, 2004; Cooke, 2008; Hofmann and Gaines, 2008; Wilson et al., 2008).

Far fewer studies have evaluated the spatial ecology and mobility of marine animals at smaller temporal and spatial scales. Although some animals undertake large scale migrations, sometimes transiting oceanic basins (Block et al., 2005; Holdsworth et al., 2009), many animals also make localized small-scale movements as they engage in activities such as locating food and avoiding predators (Cooke and Philipp, 2004; Humston et al., 2005; Meyer and Holland, 2005; Wearmouth and Sims ,2009). Locomotory activity, on the scale of seconds to hours influences the activity costs which are a primary driver in the bioenergetics of fish (Boisclair and Leggett 1989; Webber et al., 1998; Cooke et al., 2004b). Another aspect of spatial ecology that is rarely

considered in marine animals is the third dimension of space - depth. Information on the depth distribution of marine fish is relevant to ecological processes such as foraging activity, refuge, and habitat preferences (Brill et al., 1999; González-Sansón et al., 2009; Wearmouth and Sims, 2009) and has implications for various management protocols (e.g. regulations concerning deployment position of fishing gear, Hoolihan and Luo, 2007; Cartamil and Lowe, 2004). In addition, daily movement patterns are also an important component of fish ecology, as many marine species exhibit diel changes in activity or diel vertical migrations (Cartamil and Lowe, 2004; Meyer and Holland, 2005; Wearmouth and Sims, 2009).

With recent advances in biotelemetry and biologging technology, researchers have been provided with new tools for studying the fine-scale activity and depth distribution of animals in the ocean (Cooke et al., 2004a; Wilson et al., 2008). Depth has been measured for more than 20 years using inexpensive and robust pressure transducer sensors on a range of taxa including diving birds, turtles, marine mammals and fish (*Makaira nigricans*, Block et al., 1992; *Thunnus albacores*, Brill et al., 1999; *Caretta caretta*, Houghton et al., 2002; *Mola mola*, Cartamil and Lowe, 2004; *Halichoerus grypus*, Austin et al., 2006; *Aptenodytes forsteri*, Zimmer et al., 2008). Depth information can easily be transmitted or logged, however, accelerometer sensors for estimating field activity level are a more recent development and the use of this type of technology is in its infancy. Early deployment of accelerometers has relied on archival loggers (e.g., *Pygoscelis adelaie*, Yoda et al., 2001; *Balaenoptera physalus*, Goldbogen et al., 2006; *Triaenodon obesus*, Whitney et al., 2007; *Negaprion brevirostris Rhincodon typus*, Gleiss et al., 2009a,b; Accipitridae, Halsey et al., 2009), however given that

accelerometer data can be collected on the order of milliseconds in multiple axes, it has not been, until recently, that such data can be transmitted in real time. Recent innovations in onboard processing have enabled acceleration data to be recorded and averaged in three dimensions, calculating a practical value such that it can be transmitted to a receiving device.

Great barracuda (*Sphyraena barracuda*) are a predatory fish found in tropical and subtropical nearshore systems worldwide (deSylva, 1963), and although a relatively common species, there is a paucity of knowledge pertaining to their behavioural ecology. Adult great barracuda have generally been regarded as diurnally active (de Sylva, 1963; Randall, 1967; Blaber, 1982) and observed in a broad range of water depths from shallow, coastal waters as well as at depths of over 50 m (de Sylva, 1963). However, these observations are largely anecdotal, emanating primarily from visual observations by divers, commercial fishers, and anglers. Differences in activity have been observed relative to water depth and position in the water column, and attributed to foraging activity, predator avoidance, and pre-spawning activity (de Sylva, 1963; Blaber, 1982; Paterson, 1998). To date, barracuda movement has only been studied using mark-recapture methods (Springer and McErlean, 1961; Villareal et al., 2007) and body markings to identify individuals in a localized area (Wilson et al., 2006b). With an increasing awareness of the ecological importance of apex marine predatory fish (Myers and Worm, 2003; Heithaus et al., 2008) as well as the economic and cultural significance of reef fish in tropical and subtropical regions (Sadovy, 2005), there is great value in understanding the behavioural ecology of top predators to facilitate management and conservation.

The objective of my study was to describe the localized, fine-scale behavioural activity and depth utilization of wild great barracuda across habitat types and diel periods. For the first time, commercially-available acoustic transmitters capable of transmitting both acceleration and depth were used on free-swimming fish in the ocean. Previous attempts to use accelerometers have relied on biologging techniques and typically have focused on larger animals that are capable of supporting large electronic tags (Wilson et al., 2008). Beyond discussing the biological data emanating from this study, I also discuss technological constraints and opportunities for applying this technology to other species and questions in marine biology.

Materials and methods

Study site

The study site was located off the coast of Cape Eleuthera, The Bahamas (24°54'N; 76°20'W). This marine environment in this region includes a unique variety of available habitat ranging from shallow tidal flats, nearshore reefs, and seagrass beds of the Grand Bahama Bank to deep, continental shelf environments along the Exuma Sound. An array consisting of 53 autonomous acoustic receivers (VR2 and VR2W; Vemco/Amirix Systems, Shad Bay, NS) was deployed along the ocean floor, each receiver attached to a short length of rebar cemented into a cinder block. The entire receiver array spanned an area of approximately 44 km^2, while the approximate area of coverage provided by the receivers within the array was 23,426 km^2, under the assumption that each receiver had an average detection range diameter of 750 m (due to fluctuation of acoustic detection efficiencies according to local biotic and abiotic variables). The receiver stations were positioned in three curtains projecting from Powell

Point on Cape Eleuthera, with additional receiver units placed in a net formation between the curtains and along the edge of the continental shelf (receiver detection ranges generally did not overlap). All barracuda were monitored until the transmitter batteries expired or until the individual fish left the detection range of the array.

Capture and tagging methods

All barracuda were captured and surgically implanted with acoustic transmitters during December 12 – 15, 2008 (n = 13). The fish ranged in total length from 62 – 120 cm. Individual barracuda were captured within the geographical confines of the array by trolling with heavy-action recreational angling gear (14 kg [30 lb] test fishing line) and artificial lures. Each fish was landed in a mesh cradle, lifted onboard the boat and placed into a 100 l cooler of seawater infused with 3-aminobenzoic acid ethyl ester (MS222) at a dosage that would render each barracuda unable to maintain equilibrium (approx. 100 mg l^{-1}). Once the fish were anaesthetized, they were held in a supine position with the head and gills completely submerged to ensure adequate irrigation of the gills throughout the surgical procedure. An incision approximately 1.5 cm long was made with a scalpel along the ventral midline of the fish midway between the pelvic and anal fin and the disinfected transmitter was placed into the abdominal cavity. The incision was closed with two to three simple interrupted PDS II 3/0 absorbable sutures (Ethicon Ltd, NJ; Cooke et al., 2003). Fresh seawater was added to the cooler partway through the surgery to dilute the anaesthetic concentration and begin reviving the fish. After the completion of the surgery, all fish were given ample time (approx 45 min, depending on size of the fish) to recover with frequent additions of fresh seawater to the recovery bath, and

released at a fixed point within the array. All surgeries were completed by the same trained surgeon. All surgery and handling procedures were performed in compliance with protocols put forth by the Canadian Council for Animal Care issued through Carleton University, Ottawa, Canada.

I implanted the fish with individually coded acoustic transmitters (V9AP; Vemco/Amirix systems, Shad Bay, NS) equipped with accelerometer and pressure sensors. The tag dimensions were 46 mm x 9 mm and weighed 3.3 g in water (6.3 g in air). The V9AP accelerometer calculates the root mean square (g) of acceleration from three axes (X, Y, Z) measured over a specified sampling period. For example, in my study, I used three groups of accelerometers with different settings, all of which measured five samples s^{-1} over a specified sampling period. Two groups of tags (n = 5 for each group) had an average delay of 45 s with an accelerometer sampling period of 19 or 37 s, so that the accelerometers were sampling for 21% or 41% of the time. These two groups of transmitters had an estimated tag life of 95 or 65 days respectively. The third group of transmitters (n = 3) had an average delay of 90 s with an accelerometer sampling period of 25 s and the accelerometer was sampling 14% of the time. The third group of transmitters had an estimated battery life of 160 days. The tag immediately begins to record acceleration measurements once an ID and pressure value are recorded and transmitted. Thus, the tags used in my study ran on 45 or 90 s cycles with acceleration and pressure measured intermittently. Acceleration data was later converted from g units into m s^{-2} (acceleration is defined as change in velocity over time). The maximum capability of the accelerometer sensor was 3.47 m s^{-2} (0.35 g) and the maximum depth capability of the pressure sensors were 50 m (Fish #149-153) or 100 m (Fish #203-253).

Accelerometer Calibration

As the V9AP transmitters are relatively new technology and have not been tested in great barracuda, I performed accelerometer calibration trials on six barracuda ranging 69 – 94 cm in total length from January 15 – 25, 2009. All fish were captured (via trolling, as described above), transported back to a seawater facility in large coolers, and implanted with transmitters using the same surgical methods outlined previously. Fish were placed in a large 13,180 l circular tank where they were held overnight to recover from any potential capture, transport, or surgical stress. Twelve hours later, the undisturbed activity of the barracuda in the holding tank was monitored using a manual tracking receiver (VR100; Vemco/Amirix systems, Shad Bay, NS) for 30 min (i.e. "Low" activity). Each fish was exposed to two bursting trials in two consecutive cycles of sensor logging, where the fish were forced to burst by chasing around a large tank for 30 s to quantify high acceleration activity, followed by a 120 s rest period and then another 30 s burst trial (i.e. "High" activity). Once both burst acceleration trials were run, the fish was left undisturbed and monitored for a further two cycles (i.e. "Low" activity). To quantify "still" or minimal movement (to represent readings of a dead fish in the wild), transmitters were placed undisturbed, on a table top and monitored with the manual tracking receiver for 60 min prior to implantation into barracuda for calibration trials. In addition, I placed a dead fish (implanted with a transmitter) at the bottom of a tank and monitored acceleration readings for 25 min. Values from both trials (undisturbed on table top and in the dead fish) were pooled to calibrate for a non-moving, dead fish.

Data Analysis

Only fish with more than 50 detections were used in the analysis, and detections collected within 24 h of tagging were excluded to account for potential behavioural changes associated with the surgery. Habitat type was divided into three categories: coastal, mosaic, and shelf. Coastal habitat was generally less than 5 m deep, within approximately 1 km from shore, typical characteristics included tidal flats, some seagrass, small patch reefs, and often exposed to some wave and tidal action due to nearness to shore and shallow depth. Man-made structures such as marinas or blasted rock cuts (regardless of deeper water) were also included in the coastal habitat due to the close proximity of these locations to other available coastal habitat. Mosaic habitat was generally less than 10 m deep, usually within 2 km from shore and characterized as having a mosaic of patch reefs, seagrass beds, and areas of sandy bottom. Shelf habitats were located along the continental shelf, at depths greater than 10 m deep (the greatest depth of a receiver station was over the edge of the shelf at 42 m), characterised by some patch reefs and exposure to currents. Some of the locations were somewhat closer to shore (<1 km) than other shelf habitat locations.

A one-way repeated measures ANOVA (Zar, 1999) was used to assess differences in acceleration across the three habitat types and between diel periods (according to local sunrise and sunset times). A log10 transformation was used to satisfy the assumption of residual normality and homogeneity of variances for both tests. Diel depth utilization was assessed for each habitat type separately using a one-way repeated measures ANOVA (Zar, 1999). All statistical analyses were performed using JMP v. 7.0 (SAS Institute, Raleigh, NC) software program and results were assessed at $\alpha = 0.05$.

Results

Of the 13 fish tagged, only six fish were detected on more than 50 occasions (ranging from 73 – 1230 hits, acceleration; 56 – 1184 hits, depth; Table 2-1), thus only these six individuals were included in the analysis. Of these six fish, two individuals were detected within the array region for less than 10 days, while the other four were present for 21 – 115 days, however, within these time frames, individual barracuda were only actually detected on 5 – 77 days across the four month period while the transmitters were active (Table 2-1). Over the course of the study period, barracuda were detected by 19 of the 53 receivers within the array (Table 2-1).

Acceleration

Lab calibration trials revealed that undisturbed or "still" transmitters had mean acceleration readings of 0.06 m s^{-2}, modal value of 0.05 m s^{-2} and ranged from 0.05 – 0.08 m s^{-2} (Table 2-2). Mean "low" locomotory activity was 0.22 m s^{-2} but most frequently 0.12 m s^{-2} (ranging, 0.010 – 0.74 m s^{-2}), which typically corresponded to a fish swimming in place or slow swimming around the tank (Table 2-2). "High" locomotory activity was measured while the barracuda burst constantly for 30 s and these values were consistently 3.47 m s^{-2} (the maximum capability of the V9AP transmitter).

I compared acceleration of wild great barracuda across three habitat types (repeated measures ANOVA model: $F = 43.37$, d.f. = 12, $P < 0.0001$) and found that acceleration values across all three habitats were similar ($P > 0.05$; coastal: 0.05 – 3.47 m s^{-2}, mosaic: 0.10 - 3.47 m s^{-2}, shelf: 0.12 - 3.47 m s^{-2}; Table 2-3, Figure 2-1). The modal acceleration value recorded for coastal habitat was 0.54 m s^{-2}, 0.42 m s^{-2} for mosaic

habitat, 0.52 m s^{-2} for shelf habitat, and 0.52 m s^{-2} when all observations were pooled (Table 2-3, Figure 2-1). Although there was not a difference in mean locomotory activity across habitat types, there were differences among individual barracuda (repeated measures ANOVA: $F = 21.32$, d.f. = 10, $P < 0.0001$; Figure 2-2a). Overall, wild fish primarily exhibited low locomotory activity, spending approximately 58% of the time swimming slowly or swimming in place, but also showed a range of values from very minimal movement to high, bursting activity (Figure 2-1a). Low activity was generally consistent across the three habitat types, while high activity or bursting behaviour was also evident but not frequently detected (Figure 2-1).

We also compared acceleration across time of day (repeated measures ANOVA model: $F = 47.46$, d.f. = 2,11, $P < 0.0001$), and there was no diel effect ($P > 0.05$). I did observe variation among individual fish across diel periods ($F = 50.37$, d.f. = 10, $P < 0.0001$; Figure 2-2b). Fish #153 and #205 were generally less active than other tagged individuals, while fish #229 and #253 were more active (Figure 2-2). Acceleration values were generally consistent across 24 h periods, as exemplified by fish #223 and #253 (Figure 2-5).

Depth

Barracuda depth-use values across the three habitat types ranged from 0 m – 32.22 m (coastal: 0.12 – 7.6 m; mosaic: 0 – 8.5 m; shelf: 1 – 32.2 m, Table 2-4, Figure 2-3). The fish were detected most frequently near the surface at depths less than 5 m (modal values across habitats: coastal, 1.00 m; mosaic, 4.62 m; shelf, 1.44 m, Table 2-4). There was also a lack of diel effect on depth of barracuda within each of the three habitat

types ($P > 0.05$), but I noted individual variation in depth use within the three habitat types (repeated measure ANOVA, coastal: $F = 29.61$, d.f. = 2, $P < 0.0001$; mosaic: $F = 13.76$, d.f. = 7, $P < 0.0001$; shelf: $F = 167.41$, d.f. = 6, $P = 0.0001$). To some extent, barracuda appear to use the entire available water column within each habitat type, but not all individuals used each habitat type (Figure 2-4).

Despite efforts to quantify how much of the available depth was actually utilized by the tagged barracuda, I was limited in my abilities to decipher where the fish was located in relation to a specific receiver. This was of particular concern in the deeper shelf habitats where the receiver was placed near the edge of the deep drop off of the Exuma Sound and the detection range of the transmitters reached depths greater than the depth of the closest receiver. Therefore, some fish were detected at depths greater than that of the receiver. The V9AP transmitters are equipped to measure up to a maximum depth of 50 or 100 m and according to my results, barracuda were only using up to approximately 20-30% of the capacity of the pressure sensor.

While there were no apparent trends in acceleration across 24 h time periods, fish #223 and #253 often moved from coastal and mosaic areas into shelf habitat, where they spent time deeper in the water column (>10m deep) during the middle of the day (approx 10:00-14:00 hrs), before returning to shallower, coastal or mosaic habitats in the late afternoon (Figure 2-5). This trend was not apparent with other individuals in the study as there were minimal or inconsistent detections over the 24hr period to draw conclusive results.

Discussion

This study was the first to use acoustic telemetry techniques to monitor fine-scale behavioural activity of great barracuda by focusing on acceleration and depth utilization across habitat types and diel periods. Overall, barracuda locomotory activity ranged from stationary holding to bursting activity, although most observations were on the lower end of the activity spectrum. This finding was consistent with anecdotal observations that suggested barracuda spend significant time swimming slowly or hovering in place (de Sylva, 1963; Paterson, 1998). Barracuda are ambush predators that lie-in-wait and burst at high speeds (burst velocities have been measured at 12.2 m s^{-1}; Gero, 1952) to capture a prey item (Grubich et al., 2008). Although not the most frequently seen behaviour in the present study, occasional burst activity was apparent (Figure 2-1), which may have been attributed to foraging events or predator avoidance (by sharks or larger conspecifics). Fast-start performance in northern pike (*Esox Lucius)*, a freshwater species that is morphologically and behaviourally similar to Sphyraenidae, has been shown to be energetically expensive (Frith and Blake, 1995). Like northern pike, barracuda are morphologically suited for high performance acceleration (fusiform body shape with high percentage of white muscle), so it may be advantageous for barracuda to spend the majority of time being less active (i.e. slow swimming/cruising or hovering) as a means to reserve energy for feeding or predator avoidance.

Energy expenditure in fish is largely driven by locomotion (Boisclair and Leggett, 1989; Webber et al., 1998; Cooke et al., 2004b). Unfortunately, there have been limitations to studying bioenergetics in wild marine fish due to the lag in development of acoustic activity sensor technology compared to available radio telemetry technology that

is more suited for freshwater applications (Gollock et al., 2009). Overall dynamic body acceleration (ODBA, measured using triaxial accelerometers) and rate of oxygen consumption have been shown to be positively correlated in avian species (*Phalacrocorax* spp., Wilson et al., 2006a; *Gallus gallus domesticus*, Halsey et al., 2009), indicating that accelerometers may potentially be a useful tool for estimation of energy expenditure in barracuda and other marine species. However, laboratory respirometry experiments must be performed in order to calibrate energy consumption and behaviour on a species-specific basis (Lucas et al., 1993; Butler et al., 2004).

Many animals show variation in diel activity levels, often associated with foraging (Meyer and Holland, 2005; Whitney et al., 2007). Based upon stomach content analyses, great barracuda have generally been regarded as diurnal foragers (dependant on sight to capture prey items), feeding in shallower habitats during the early morning and early evening, and spending time in surface waters over deeper habitats when not feeding (de Sylva, 1963; Blaber, 1982). In contrast to those previous anecdotal observations, I did not detect significant diel differences in activity and would require more complete monitoring of full diel cycles across multiple days to draw sound conclusions about daily barracuda feeding activity. Incomplete temporal sequence data is often a shortcoming of open, non-overlapping acoustic array designs (Heupel et al., 2006a). Moreover, the array boundaries did not cover all potential areas where the tagged barracuda could potentially swim (i.e., vast sections of the ocean). My findings actually indicate that barracuda may be quite transient and that techniques for monitoring movement on broader spatial scales will be necessary to fully document the spatial ecology and migrations of barracuda. My results did show a significant individual variation in activity levels (Figure 2-2), which

may have masked any potential differences in activity across diel periods and habitat types, suggesting that individual barracuda could exhibit behavioural variation suggestive of differing animal personalities (Sih et al., 2004).

Low locomotory activity for great barracuda across habitat types (Figure 2-1) may reflect consistencies in prey availability and foraging opportunities throughout the study region. Barracuda have been documented to inhabit a range of habitats including shallow, sand patches, seagrass borders, the halo zones around patch reefs and deeper coral wall regions (de Sylva, 1963; Paterson, 1998). Stomach content analyses have shown that adult barracuda feed on a range of prey types, including fast-swimming pelagic and surface-dwelling fish as well as tetraodontiform reef fish (de Sylva, 1963). The habitat structure in this region may perhaps offer similar resource availability and environmental conditions across all three habitat types.

To an extent, the fish in this study utilized the entire available water column within each habitat type with the deepest detection at 32 m below the surface (Figure 2-3). Blaber (1982) and Paterson (1998) documented that barracuda were typically found higher in the water column over deeper, shelf environments, often at depths of 5m below the surface. In the present study, most fish were generally observed in the top 5 – 10 m of the available water column (Figure 2-3). Although diel differences in depth utilization were not apparent, two individuals (#223 and #253) consistently moved into shelf habitat, spending time at greater depths during the middle of the day before heading back to coastal and mosaic habitat in the late afternoon, however, there were still not any significant trends in acceleration across the 24hr period (Figure 2-5). It is also important to note that fish #223 and #253 were also only detected for nine and 18 days respectively,

with few full days of complete data. It is uncertain whether some of the tagged individuals were resident to the area or were migrating through the array during the study period. A possible way to address this is through the use of other telemetry techniques, such as archival pop-up satellite tags (Block et al., 2003).

Our ability to decipher fine-scale behavioural occurrences (such as individual feeding events) was often impeded, since the accelerometer transmission intervals were infrequent (90 or 120 s) and the fish were not always within the detection range of the receivers in the array. Initially I had intended to make direct comparisons among the three different settings chosen for the transmitters in the study, however, due to resultant low sample sizes (non-detections due to tagged fish moving outside of the detection range of the array within days of release is a common occurrence in open array telemetry studies, Heupel et al., 2006a; Meyer et al., 2007), this was not possible. Nonetheless, the data still provide important insight into the biology of these animals. In addition, as the transmitters were highly sensitive, the full range of barracuda acceleration may not have been captured as the maximum accelerometer sensor capability was 3.47 m s^{-2} (0.35 g) and continuous bursting behaviour evident from lab calibration trials consistently resulted in maximum values. Due to the design of the accelerometers, even the slightest change in acceleration on a single axis will affect the overall calculation of the average acceleration value. Although these transmitters were effective in helping understand relative activity, a greater maximum sensor capability as well as potential disengagement of one or two of the axes on the accelerometer may present a clearer picture of locomotory activity. In future studies I encourage researchers to select transmitters that average over as short of a period as possible and transmit data as frequently as possible to

maximize resolution and ability to detect short-duration, but high intensity activity. In addition, potential exists to gain a greater overall understanding of barracuda biology and natural history, by recording additional parameters (such as light, temperature, and speed) combined on a single electronic tag. However, given problems with transmitting complex data, efforts to obtain more detailed information may need to rely on logger technology such as "daily diaries" (Wilson et al., 2008). Tools used in the present study as well as forthcoming acoustic technology would have far-reaching applications for studying behavioural ecology (e.g. spawning patterns or post-release behaviour) in other free-ranging marine species.

Currently, the basic biology and behaviour of great barracuda, and all Sphyraenidae, are poorly understood. However, these fish are popular game fish contributing to a large portion of the local tourism and culture of tropical nations that are within their range. Therefore, detailed knowledge of barracuda ecology is required to make informed management decisions to ensure sustainable fisheries that can balance both the continued economic growth for local communities and conservation of the species at large.

Tables

Table 2-1. Summary table of *S. barracuda* tagged with V9AP transmitters Dec 12-15, 2008 near Cape Eleuthera, The Bahamas (n = 13). Individuals with >50 hits were included in the analysis (n = 6) and are highlighted in bold. TL, total length.

Tag ID	Date tagged	TL (cm)	# Hits (acceleration)	# Hits (depth)	# Days in array	# Days detected	# Receivers
149	Dec-13-2008	81	15	15	116	7	1
151	Dec-13-2008	79	46	43	3	3	6
153	**Dec-12-2008**	**83**	**403**	**404**	**115**	**77**	**10**
203	Dec-14-2008	60	0	0	1	1	0
205	**Dec-13-2008**	**62**	**73**	**56**	**104**	**19**	**5**
207	Dec-13-2008	79	0	1	1	1	1
209	Dec-15-2008	85.5	35	36	3	3	10
221	**Dec-13-2008**	**92**	**1131**	**1166**	**74**	**46**	**12**
223	**Dec-12-2008**	**120**	**431**	**431**	**9**	**9**	**5**
225	Dec-14-2008	79	77	74	3	1	3
227	Dec-14-2008	99	0	0	1	0	0
229	**Dec-12-2008**	**94**	**207**	**189**	**3**	**5**	**7**
253	**Dec-15-2008**	**81**	**1230**	**1184**	**21**	**18**	**19**

Table 2-2. Summary of accelerometer lab calibration values for locomotory activity (low, high, still) of six *S. barracuda*. All individuals were captured off the coast of Cape Eleuthera, The Bahamas and transported back to a wet lab facility at Cape Eleuthera Institute.

Fish ID	Activity type	Mean acceleration ± SE ($m\ s^{-2}$)	Modal acceleration ($m\ s^{-2}$)	Min acceleration ($m\ s^{-2}$)	Max acceleration ($m\ s^{-2}$)
Acc1	Low	0.19 ± 0.02	0.18	0.11	0.41
	High	3.47 ± 0.00	3.47	3.47	3.47
Acc2	Low	0.33 ± 0.03	0.34	0.18	0.74
	High	3.47 ± 0.00	3.47	3.47	3.47
Acc3	Low	0.14 ± 0.01	0.11	0.10	0.20
	High	3.47 ± 0.00	3.47	3.47	3.47
Acc4	Low	0.22 ± 0.04	0.16	0.01	0.49
	High	3.47 ± 0.00	3.47	3.47	3.47
Acc5	Low	0.25 ± 0.03	0.15	0.12	0.55
	High	3.47 ± 0.00	3.47	3.47	3.47
Acc6	Low	0.15 ± 0.01	0.12	0.11	0.21
	High	3.47 ± 0.00	3.47	3.47	3.47
Total	Low	0.22 ± 0.01	0.12	0.10	0.74
	High	3.47 ± 0.00	3.47	3.47	3.47
	Still	0.06 ± 0.00	0.05	0.05	0.08

Table 2-3. Summary of field acceleration values (m s^{-2}) of six individual *S. barracuda* detected using acoustic telemetry off the coast of Cape Eleuthera, The Bahamas December, 2008 – April, 2009.

Habitat	Fish ID	N	Mean acceleration ± SE (m s^{-2})	Modal acceleration (m s^{-2})	Min acceleration (m s^{-2})	Max acceleration (m s^{-2})
Coastal	205	1	0.48 ± 0.00	0.48	0.48	0.48
	229	206	0.95 ± 0.03	0.54	0.34	3.47
	253	917	0.85 ± 0.01	0.69	0.05	3.47
Total coastal		1124	0.87 ± 0.01	0.54	0.05	3.47
Mosaic	153	375	0.52 ± 0.02	0.44	0.10	3.47
	205	72	0.45 ± 0.03	0.35	0.10	1.54
	221	103	0.88 ± 0.05	0.84	0.14	3.47
	223	18	0.87 ± 0.07	0.72	0.42	1.63
	253	20	1.11 ± 0.15	0.49	0.45	3.47
Total mosaic		588	0.60 ± 0.02	0.42	0.10	3.47
Shelf	153	28	0.66 ± 0.10	0.45	0.26	2.86
	221	1028	0.80 ± 0.01	0.52	0.12	3.47
	223	413	0.73 ± 0.02	0.56	0.25	2.89
	229	1	0.80 ± 0.00	0.80	0.80	0.80
	253	293	0.79 ± 0.02	0.52	0.30	2.21
Total shelf		1763	0.78 ± 0.01	0.52	0.12	3.47
Grand total		3475	0.78 ± 0.01	0.52	0.05	3.47

Table 2-4. Summary of field depth values of six individual *S. barracuda* detected using acoustic telemetry off the coast of Cape Eleuthera, The Bahamas December, 2008 – April, 2009.

Habitat	Fish ID	N	Mean depth ± SE (m)	Modal depth (m)	Min depth (m)	Max depth (m)
Coastal	229	189	1.47 ± 0.04	1.00	0.56	3.20
	253	870	2.02 ± 0.03	1.00	0.12	7.60
Total coastal		1059	1.92 ± 0.03	1.00	0.12	7.60
Mosaic	153	367	4.07 ± 0.06	4.62	0.00	6.15
	205	56	6.46 ± 0.12	6.72	3.64	7.60
	221	103	4.49 ± 0.26	1.88	1.00	8.48
	223	24	3.31 ± 0.17	3.64	1.00	4.52
	253	15	2.99 ± 0.45	1.00	0.56	6.72
Total mosaic		565	4.32 ± 0.07	4.62	0.00	8.48
Shelf	153	37	4.26 ± 0.26	3.96	1.54	9.89
	221	1063	5.76 ± 0.12	1.44	1.00	22.11
	223	407	14.02 ± 0.19	12.87	3.64	25.62
	253	299	13.90 ± 0.30	15.95	1.00	32.22
Total shelf		1806	8.94 ± 0.14	1.44	1.00	32.22
Grand total		3430	6.01 ± 0.09	1.44	0.00	32.22

Figures

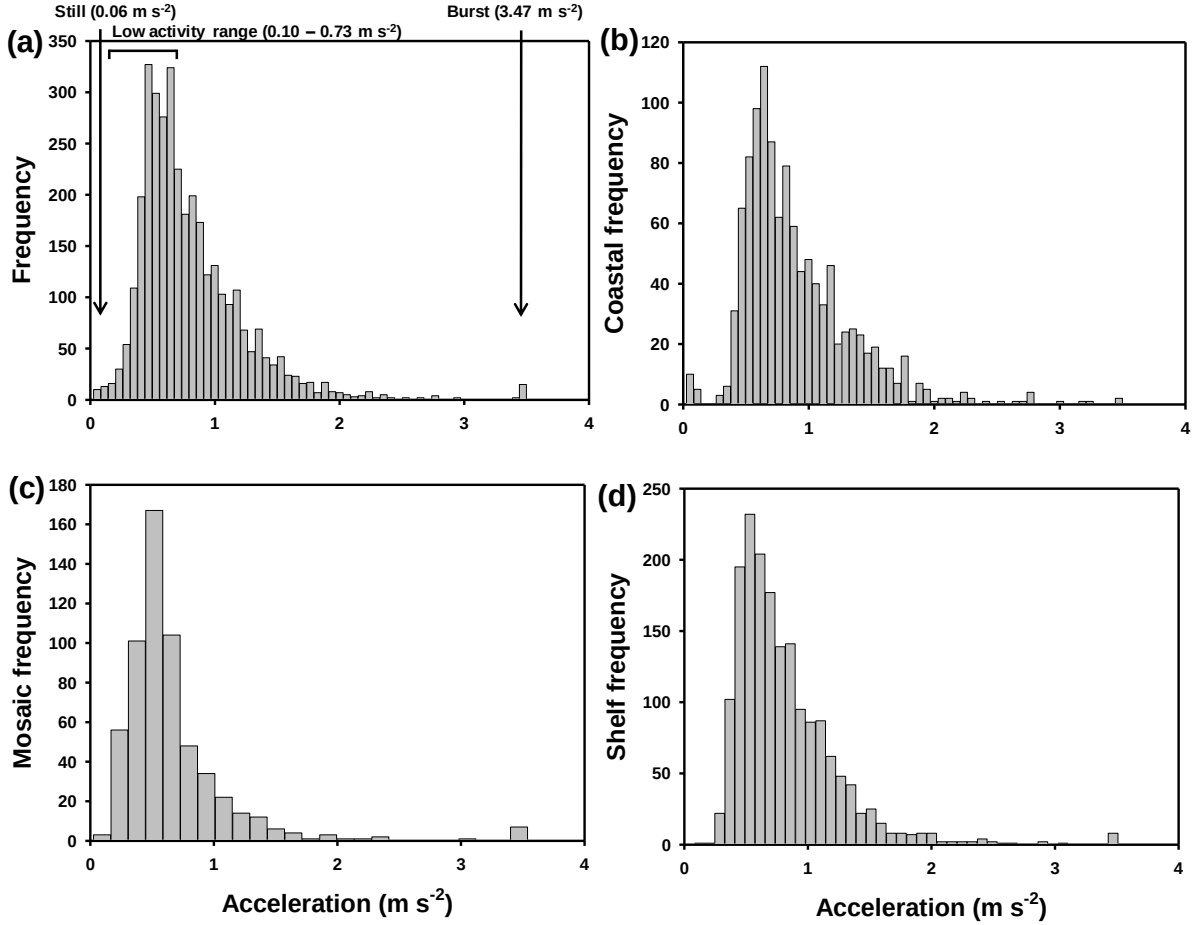

Figure 2-1. Frequency histograms of wild *S. barracuda* acceleration (m s^{-2}) in (a) all habitats combined, (b) coastal habitat, (c) mosaic habitat, and (d) shelf habitat. Lab calibration values of accelerometers is included in (a) for relative comparison with acceleration values collected from wild fish.

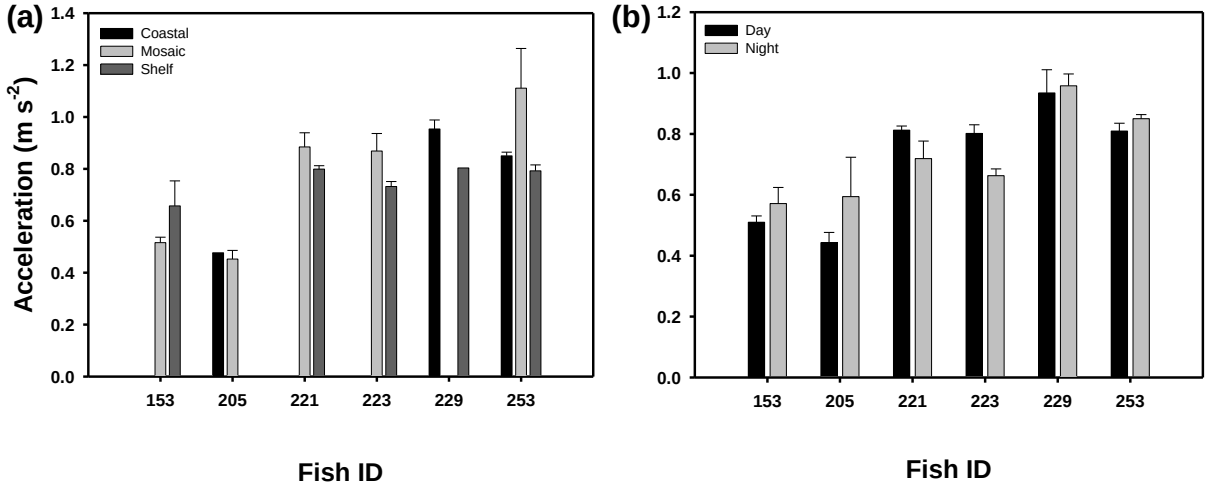

Figure 2-2. Mean (±SE) acceleration (m s^{-2}) of six *S. barracuda* across (a) three habitat types and (b) diel periods.

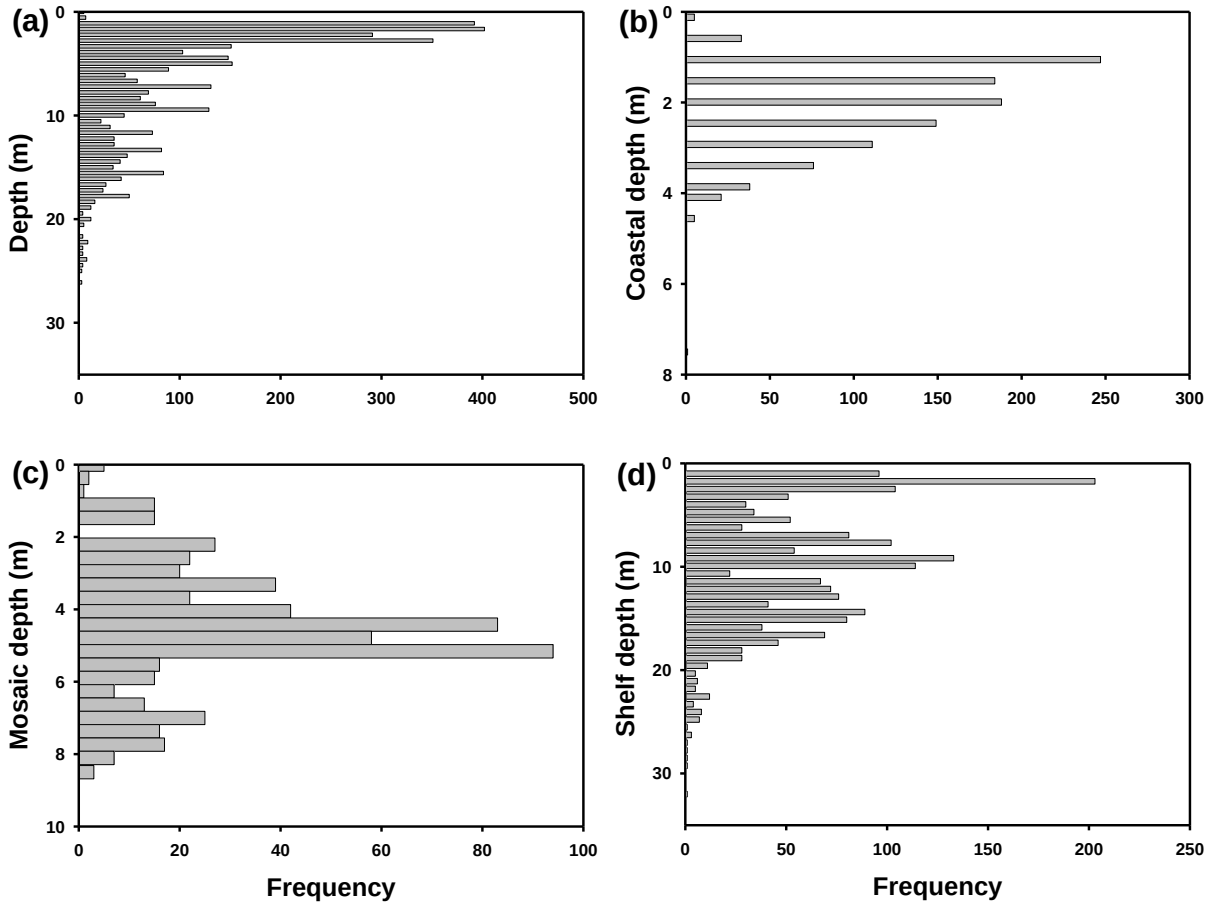

Figure 2-3. Frequency histogram of wild *S. barracuda* depth (m) utilization in (a) all habitats combined, (b) coastal habitat, (c) mosaic habitat, (d) shelf habitat.

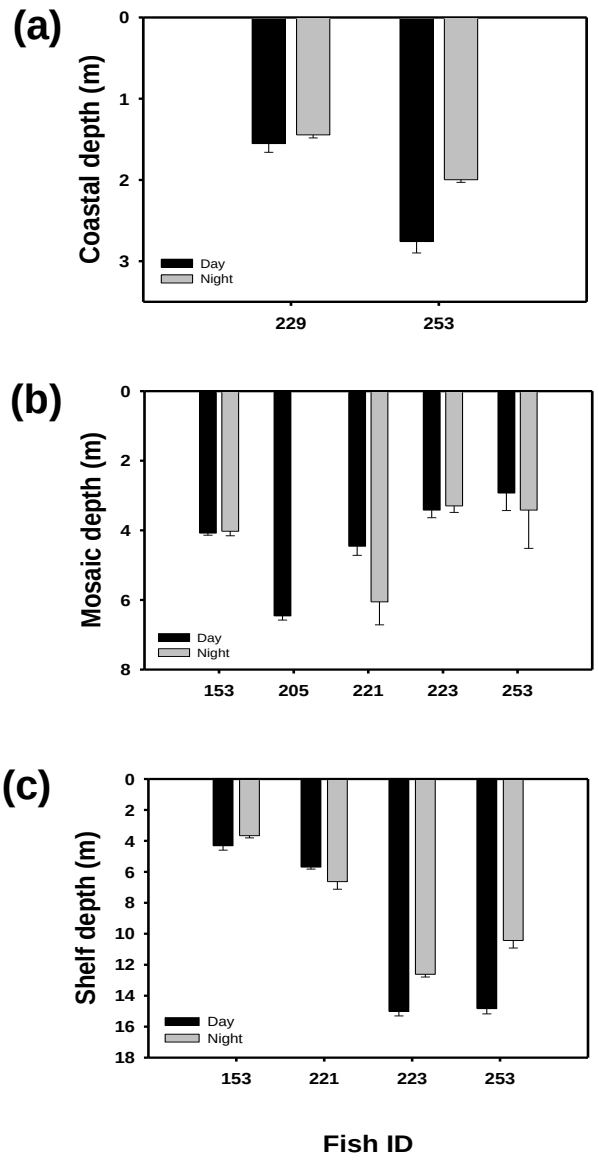

Figure 2-4. Mean (±SE) diel depth (m) of six wild *S. barracuda* in (a) coastal habitat, (b) mosaic habitat, and (c) shelf habitat.

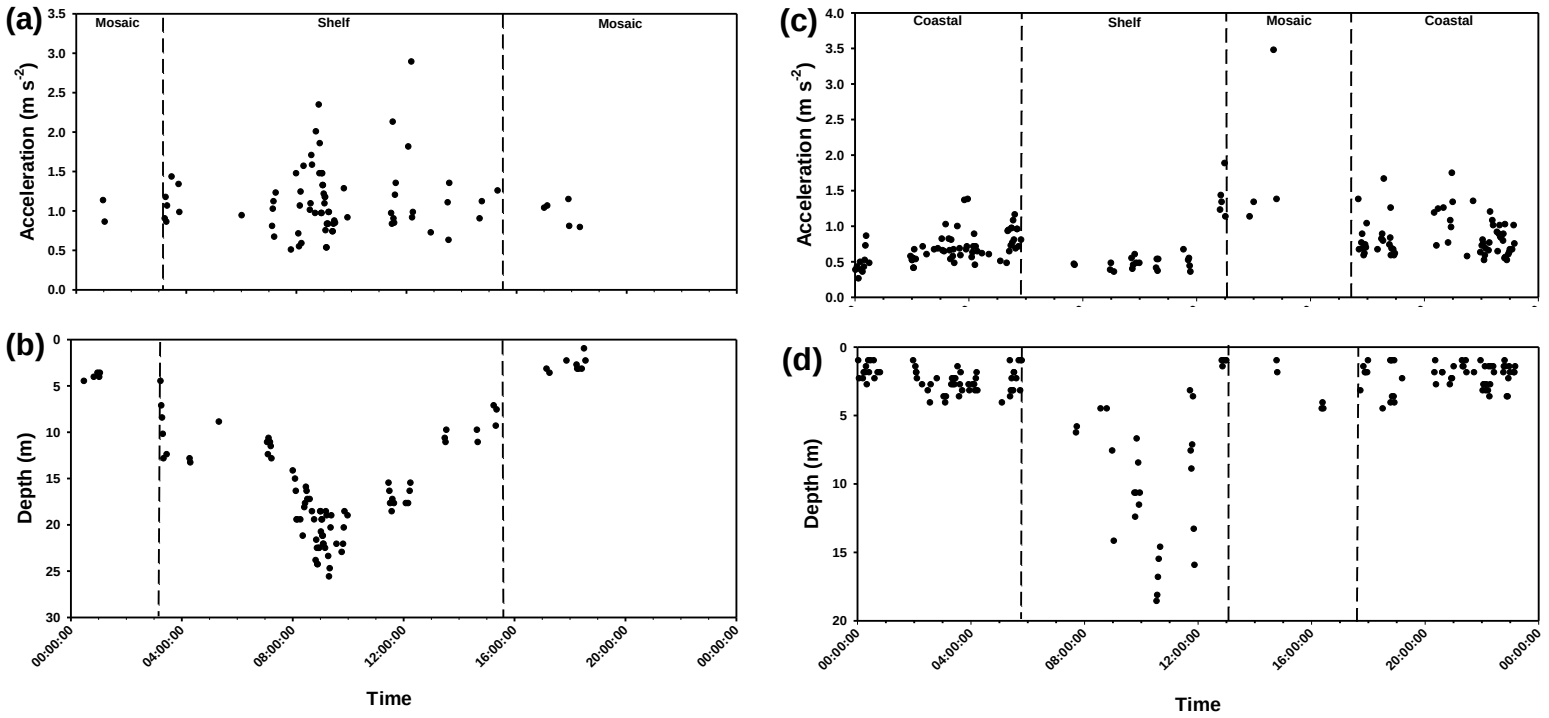

Figure 2-5. Examples of behavioural patterns across habitat types of two wild *S. barracuda* over two 24 h periods. (a) acceleration (m s^{-2}) and (b) depth (m) of fish #223 on December 16, 2008 and (c) acceleration (m s^{-2}) and (d) depth (m) of fish #253 on December 23, 2008. Dashed lines represent movement into a different habitat type.

Chapter 3: Consequences of catch-and-release angling on the physiological status and condition of great barracuda (*Sphyraena barracuda*) in The Bahamas

Abstract

Great barracuda (*Sphyraena barracuda*) are a common marine predatory fish readily captured by anglers, most frequently as incidental bycatch while pursuing other gamefish. I conducted a study in The Bahamas to evaluate how common angling techniques influence the physiological stress response in relation to fight and handling time duration, hooking injury, and initial mortality of barracuda. Post-angling blood glucose and plasma sodium levels increased with the duration of fight and handling, while lactate levels increased with longer handling times. Results showed that concentrations of plasma chloride and potassium were not influenced by angling duration or handling time. I did not observe any differences in injury, bleeding, hook removal, or hooking depth between three types of artificial lures tested. Only two fish were hooked in critical areas (i.e. eye, gills), while the rest (n=57) were shallowly hooked in non-critical anatomical locations (i.e., jaw). Most of the fish experienced minimal or no bleeding at the hook site and immediate mortality upon landing was negligible. Although great barracuda appear to be fairly resilient to physiological stress and injury associated with catch-and-release angling and initial mortality was insignificant, these fish typically reside in habitats where post-release predation is possible. As such, efforts should be made to promote careful handling to ensure high survival rates.

Introduction

Great barracuda (*Sphyraena barracuda*) have a circumtropical distribution within the western Atlantic Ocean, Caribbean Sea, and Indo-Pacific regions, and individuals are typically found inhabiting reef areas, seagrass beds and offshore pelagic waters (de Sylva, 1963). Great barracuda are a piscivorous species (exhibiting lie-in-wait predatory behaviour) and may hold a similar predatory position as Elasmobranchii and Carangidae in nearshore reef environments (de Sylva, 1963). However, to date, there is a relative dearth of information about barracuda biology and natural history. Because they are relatively abundant, occupy habitats that are accessible to fishers (Serafy et al., 2007), and readily strike a variety of different lure types, great barracuda can be easily targeted by anglers as well as by subsistence fishers using angling gear (Springer and McErlean, 1961; de Sylva, 1963; Villareal et al., 2007). According to creel survey data (Harper et al., 2000), approximately 80% of landed barracuda are released by skilled recreational anglers and 60% of barracuda are released by all other types of recreational parties combined. Recreational fishing is undertaken by anglers of all skill levels, for a range of species throughout the Caribbean and western Atlantic, so it is likely that great barracuda are often encountered as bycatch while anglers are in pursuit of other sportfish such as dolphin (*Coryphaena hippurus*), wahoo (*Acanthocybium solandri*), and billfish (Istiophoridae; Mike and Cowx, 1996; Harper et al, 2000). It is likely that most of those barracuda that are incidentally captured are released. Ciguatera, a biotoxin that can lead to neurological and gastrointestinal problems in humans, is often associated with larger barracuda (Lehan and Lewis, 2000) and thus may further promote discard (release) of barracuda in the recreational sector, although subsistence fisheries tend to largely ignore

this risk. In general, there is a paucity of information on the basic biology of this species and this is the first study that I am aware of to examine the effects of catch-and-release on great barracuda.

There is a growing body of literature documenting the sublethal impacts of catch-and-release fishing in terms of stress physiology and hooking injury (Cooke et al., 2002a; Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005), as well as more than several hundred studies that have documented the short term mortality associated with catch-and-release for a range of sportfish (Muoneke and Childress, 1994; Arlinghaus et al., 2007a). In general, relatively little knowledge of the consequences of catch-and-release fishing is available for marine game fish compared to the broad range of studies completed on freshwater game fish species (Cooke et al., 2002a; Cooke and Suski, 2005), although this is changing as catch-and-release studies in marine environments have been increasing since the 1990's (Arlinghaus et al., 2007a). Given that recreational fishing contributes to regional economies through revenue generated by tourism (Granek et al., 2008), there is a need to ensure long-term sustainability and high survival rates in fisheries that release a large proportion of their catch (Cooke et al., 2006). This is especially important in coastal communities or island nations such as The Bahamas where the tourism industry accounts for approximately 40% of the Gross Domestic Product (Government of The Bahamas, 2005). In addition, there is growing recognition of the importance of understanding the consequences of recreational fishing practices on fish welfare (Arlinghaus et al., 2007b) such that efforts can be taken by anglers and managers to ensure that the welfare status of angled fish is maintained (Davie and Kopf, 2006; Cooke and Sneddon, 2006).

Given that the ecological role of apex predators such as barracuda is unknown but presumably critical for structuring marine ecosystems (e.g. Myers and Worm, 2003; Myers et al., 2007; O'Connor and Bruno, 2007; Heithaus et al., 2008), and that even low levels of post-release mortality can lead to population declines in some marine fish (Schroeder and Love, 2002; Coleman et al., 2004), research on catch-and-release impacts (in terms of lethal and sublethal effects and injury) on barracuda and other large marine fish is needed to ensure the sustainability of the fisheries and to inform managers about potential conservation problems. In addition, a broad range of responses to catch-and-release angling exist between species, as there are often inter-specific differences in terms of morphology, physiology, and behaviour (reviewed in Cooke and Suski, 2005).

Numerous studies have revealed that fish experience some level of physiological disturbance (i.e. changes in glucose, lactate, and ionic concentrations) when exposed to catch-and-release angling events (summarized in Cooke and Suski, 2005; Arlinghaus et al., 2007a), including several studies that have been conducted on marine species (e.g., large pelagics, Wells et al., 1986; *Scorpis violaceus*, Lowe and Wells, 1996; *Albula vulpes*, Suski et al., 2007, Cooke et al., 2008). The duration of the angling event (i.e. exercise) and the degree of handling are two factors that contribute to a range of sublethal effects (behavioural alterations, fitness impacts, physiological disturbance) and post-release mortality (Cooke et al., 2002b; Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005).

Typically, investigators have quantified hooking injury due to catch-and-release fishing in terms of hooking location, degree of tissue damage, and hooking depth measurements (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005). Lure

type may influence hooking depth and severity of injury (Diggles and Ernst, 1997; Bartholomew and Bohnsack, 2005; Arlinghaus et al., 2008b) and hook design comparison studies (single hooks vs. treble hooks) have presented conflicting results in terms of the associated injury (Diodati and Richards, 1996; Ayvazian et al., 2002; Dubois and Dubielzig, 2004). Hook location has been shown to influence ease of hook removal (lengthening air exposure, contributing to physiological stress, and increasing risk of post-release mortality) and deeply hooked fish experience more bleeding than fish hooked in non-critical areas, as a fish that is excessively bleeding upon release may bleed to death or be more susceptible to predation (Diggles and Ernst, 1997; Cooke et al., 2001; Prince et al., 2002; Bartholomew and Bohnsack, 2005; Arlinghaus et al., 2008b).

We conducted a study to investigate the sublethal physiological consequences, injury, and immediate mortality of great barracuda captured and released in The Bahamas. The first objective of this study was to investigate the degree of physiological disturbance of captured great barracuda relative to angling. I predicted that I would observe increased levels of physiological disturbance in fish that were played and handled for longer periods of time. The second objective was to determine the types of injury and amount of immediate mortality arising from catch-and-release angling using a range of common lure types and hook configurations. I predicted that different types of artificial lures (particularly those with multiple treble hooks) would affect the severity of injury, bleeding, hooking depth, and ease of hook removal. I also predicted that hooking location would affect the ease of hook removal and the amount of bleeding experienced by the fish, both of which would influence mortality. This paper will contribute to the growing body of knowledge on the species-specific responses of fish to catch-and-release

angling (Cooke and Suski, 2005) enabling the opportunity to disseminate educational materials to anglers (Pelletier et al., 2007).

Methods

Study Site and Capture Method

The study was conducted off the coast of Cape Eleuthera, The Bahamas (24°54′N 76°20′W). Barracuda were captured between December 2007 and January 2009 (n = 63), ranging in total length from 50-120 cm. Individual barracuda were captured via typical angling techniques employed by anglers in the Caribbean and Western Atlantic Ocean. Such techniques include trolling at speeds between 6 and 9 knots with heavy-action recreational angling gear (e.g., 14 kg [30 lb] test fishing line). Three types of artificial lures were used: a) hard lure (crankbait or hard topwater lures with two treble hooks, size range of 130-170 mm, i.e. Rapala X-Rap Saltwater Lure), b) soft lure (soft rubber barracuda tube lure with two treble hooks, size range of 350-360 mm, i.e. Hook Up Barracuda Tube Lure), or c) single hook lure (plastic skirted lures such as a tuna candy and mahi popper, or a hard lure such as a cedar plug, size range of 110-180 mm, i.e. Offshore Angler Blue Water Trolling Bait; Figure 3-1). I chose to initially separate lures adorned with treble hooks into two categories as I wanted to distinguish potential differences between lures used to specifically target barracuda (i.e. soft barracuda tube lure) and lures used to target other species (which may consequently result in bycatch of barracuda). All hooks used in the study were barbed as per what I regard as typical angler behaviour in the fishery. Once hooked, each fish was fought until it could be safely landed in a mesh cradle (rubber coated knotless nylon to minimize dermal abrasion and fin fraying; Barthel et al., 2003). The length of time (s) elapsed from the initial strike

to landing the fish was recorded as fight time, where the fish was played until exhausted enough to be safely and efficiently handled (i.e. mimicking typical angling methods). During the fight I also recorded instances in which a predator attacked a known barracuda (evaluated either by visually confirming it was a barracuda prior to the attack or by the body parts [i.e., head] left on the lure upon landing). Handling time was defined as the time period (s) ranging from landing of the fish in the cradle until the blood sample was taken.

Physiological Assessment

Upon landing the fish in the mesh cradle, fish were held in a supine position for blood sampling. A 3 ml vacutainer (lithium heparin coated; B-D Inc, New Jersey) and 3.8 cm (1.5") 21 gauge needle was used to collect 2 ml of blood from the caudal vasculature. Once the blood sample was obtained it was immediately placed in a water-ice slurry. Blood was collected over the side of the boat before bringing the fish into the vessel. Fish that were sampled over the side of the boat were then transferred to the cooler following phlebotomy to enable hook removal and assessment. Once aboard the boat, fish were temporarily held in a 200 l cooler filled with fresh seawater. All handling and sampling was done with the fish held in water to minimize the amount of air exposure. I did not test for control physiological values mainly because the purpose of my study was to examine the relationship between stress physiology and factors directly related to angling, but also because of the difficulty associated with obtaining an accurate measure of undisturbed baseline data in wild fish. Even attempts to hold barracuda in the

laboratory failed due to their propensity to escape, attack conspecifics, or not survive the extended transportation to the lab.

Blood glucose, lactate, and ionic concentrations are physiological stress indicators commonly documented in catch-and-release studies, since they are relatively simple to obtain and measure in the field and changes in these concentrations may be associated with exhaustive exercise and handling (Lowe and Wells, 1996; Suski et al., 2007; Cooke et al., 2008). Lactate and glucose concentrations were obtained from whole blood using hand-held lactate (Lactate Pro LT-1710 portable lactate analyser; Arkray Inc., Kyoto, Japan) and glucose (ACCU-CHEK glucose meter; Roche Diagnostics, Basel, Switzerland) meters. The devices have previously been calibrated for use on fish (Morgan and Iwama, 1997; Wells and Pankhurst, 1999; Venn Beecham et al., 2006; Cooke et al., 2008). Blood was then centrifuged at 10,000 g for 6 min and plasma was frozen (-20°C) and shipped back to Carleton University where it was held in a -80°C ultracold freezer until analysis. Ion assays (sodium, potassium, chloride) were conducted on blood plasma using a Roche-Hitachi 917 analyzer (Basal, Switzerland) and based upon the International Federation of Clinical Chemistry and Laboratory Medicine (IFCC). To ensure that the integrity of the analysis was maintained, laboratory personnel followed the Veterinary Laboratory Association Quality Assurance Program, New York State Department of Health, College of American Pathologists, and the Canadian Food Inspection Agency External Proficiency Panel guidelines.

Injury Assessment

Once the barracuda were landed and placed in a cooler of water, hooking injury was assessed. Hooking depth (measured from the tip of the snout to the point of hook entry) was measured for each fish and corrected for the total length for comparison between fish of different sizes (documented as the proportion of hooking depth to total length of the fish as outlined by Cooke et al., [2001]; herein termed "length-corrected hooking depth"). Hooking location was categorized as critical (gills, gullet, eye) or as non-critical (jaw, hinge, roof of mouth, foul hooked in body) using similar criteria to those developed by Meka (2004) and Arlinghaus et al., (2008b). Angling-related injury was quantified as minor (minimal or no tissue damage and less than two cumulative injuries in non-critical areas) or severe (hooked in a critical location such as the gills, gullet, or eye and three or more cumulative injuries including tissue damage, foul hooking, and line wrap). Presence of bleeding (present or absent) and ease of hook removal (easy < 30 s to remove; difficult > 30 s to remove) were also recorded. Full injury assessments and hook removals were completed within two minutes after the blood sample was obtained by the same person, with the fish submerged to avoid unnecessary air exposure. Fish were also assessed for evidence of immediate mortality based on whether a fish had lost gill colour and fin perfusions and/or was unable to maintain equilibrium after 5 min of resuscitation. Once fish were able to maintain equilibrium independently (as many fish required resuscitation) they were released near the point of capture.

Statistical Analysis

Linear regressions were used to test the relationships of both fight time and handling time with physiological response variables (i.e. glucose, lactate, sodium, potassium, chloride; Zar, 1999). Where the assumption of residual normality was not met, any outliers were removed (assessed as being outside of the 95% confidence interval) and glucose data were log10 transformed. I was unsuccessful with obtaining blood from all fish, which explains the differing sample sizes between some analyses. Contingency table analysis was used to determine the relationships between categorical variables such as lure type or hook location and injury, ease of hook removal, and bleeding (Zar, 1999). Upon visualizing data, there was some evidence that hook type (i.e., two treble hooks vs. one single hook) could represent a more informative analysis for ease of hook removal and an additional contingency table analysis was performed to test this. The effect of lure type on the hooking depth was analysed using one-way Analysis of Variance (ANOVA). Hooking depth was corrected for the total length of the fish and log10 transformed to meet the assumptions of normality and homogeneity of variances. All statistical analyses were conducted using the statistical software program JMP v. 7.0 (SAS Institute, Raleigh, NC) and results were assessed for significance at $\alpha = 0.05$.

Results

Physiological parameters

Sixty-three great barracuda were angled near Cape Eleuthera, The Bahamas between December 2007 and January 2009. During the study, the water temperature ranged from 21-29 °C and mean water temperature was 24.2 ± 0.2°C. Fish ranged in size from 50-120 cm total length, with an average length (±SE) of 85.5 ± 1.8 cm. The mean

(±SE) fight time duration was 175 ± 9 s (range: 31 – 413 s) and mean handling time duration (±SE) was 190 ± 16 s (range: 31 – 468 s). I saw a positive relationship with blood glucose concentrations for both fight time and handling time (Table 3-1; Figure 3-2). A positive relationship also existed between plasma sodium and fight time duration as well as handling time (Table 3-1; Figure 3-3). There was not an effect of fight time on lactate concentration; however, there was a positive relationship between handling time and lactate (Table 3-1; Figure 3-2). I did not see any trends in plasma ion concentrations for either potassium or chloride according to fight time or handling time duration (Table 3-1; Figure 3-3). The mean (± S.E.) physiological values for barracuda (the first ever reported) were, 3.8 ± 0.2 mmol l^{-1}, blood glucose; 3.9 ± 0.2 mmol l^{-1} blood lactate; 199 ± 1.1 mmol l^{-1}, plasma sodium; 5.7 ± 0.2 mmol l^{-1}, plasma potassium; 177 ± 1.4 mmol l^{-1}, plasma chloride.

Injury

Contingency table analysis results did not reveal an association between the three lure types and degree of injury, presence of bleeding, or ease of hook removal (Table 3-2, Figure 3-4). One-way ANOVA also did not reveal differences between the three lure types and mean length-corrected hooking depth ($F = 1.21$; d.f. = 2; $P = 0.31$; Figure 3-4d). Although there was not a significant difference in ease of hook removal between lures with single and treble hooks (Table 3-2, Figure 3-4e), more than 28% treble hook lures required more than 30 s to remove compared to only 9% of the single j-style hooks. Only two individuals (3%) were hooked in critical locations (i.e. eye, gills), while all other fish were hooked in non-critical locations. Non-critical hooking locations occurred

mainly in the jaw (68%) and hinge (17%), while the remainder of non-critical hook locations occurred in the roof of the mouth and exterior of the body (6% and 9% respectively). Of the fish that were hooked in non-critical locations, 88% had hooks that were easily removed and experienced minimal or no bleeding. However, both individuals that were hooked in critical locations bled from the hook wound and the hooks were difficult to remove as these areas were in close proximity to delicate tissue (i.e. gills, stomach, eye) and often required the use of side cutters to facilitate removal. Of the two fish hooked in critical locations, the individual hooked the eye was caught with a single hook lure and the other was hooked in the gills with a treble hook. Upon hook removal some fish did appear to have significant tissue damage (i.e., flaps of skin and tissue hanging from the jaw; see Figure 3-5a) and it is unknown how barracuda heal post-release.

Mortality

Of the 63 barracuda landed throughout the study, none experienced immediate mortality however, five individuals (8%) lost equilibrium post capture. These fish appeared to expel gas from their vent when ventral pressure was applied. Within 5-10 min, the barracuda were able to independently maintain buoyancy and regain equilibrium. Two barracuda were killed during the angling event when they were attacked by unknown predators (either conspecifics or likely sharks; Figure 3-5b). Given these attacks, I observed that approximately 3% of fish (that were hooked securely enough to be played for long durations and successfully landed at the boat) were attacked and killed by predators.

Discussion

With the dearth of information about the basic biology of great barracuda as well as the general lack of catch-and-release studies published on marine species, there is great value in understanding the physiological response of barracuda to recreational angling. Understanding the effects of catch-and-release on barracuda will enhance awareness among anglers to reduce potential sublethal stress and mortality. Compared to other fish species that I regularly work with, great barracuda have proven to be relatively difficult to obtain a blood sample from (blood was relatively slow to draw; O'Toole and Cooke, Unpublished Data). This factor often increased handling time (at times doubling the time the fish was fought) and despite best efforts to minimize air exposure and handling, concentrations of glucose, lactate, and sodium increased from the time the fish was landed until the blood sample was obtained (Table 3-1). Many studies in marine and freshwater have documented increases in lactate and glucose in relation to exhaustive exercise (Gustaveson et al., 1991; Meka and McCormick, 2005; Wells et al., 1986; Lowe and Wells, 1996; Suski et al., 2007; Cooke et al., 2008). Burst swimming during an angling event can lead to depleted tissue energy stores, and an increase in plasma glucose levels (Frische and Anderson, 2000; Kieffer, 2000; Barton et al., 2002). Cumulative stressors may also result in elevated levels of physiological disturbance (Barton et al., 1986; Kieffer, 2000; Cooke and Suski, 2005) such as longer angling duration followed by long handling times, such as in the current study.

Although I did not observe changes in blood lactate concentrations with fight duration, it is common for angled fish to experience an accumulation of lactic acid due to

anaerobic metabolism associated with exhaustive exercise (Kieffer, 2000; Barton et al., 2002; Meka and McCormick, 2005; Cooke et al., 2008). However, with the positive relationship between blood lactate levels and handling time, it is possible that lactate values immediately post exercise had not yet peaked in the blood and were continuing to rise as the fish was handled and even after the blood sample was procured. I was unable to obtain control physiological values for barracuda as I had limited holding facilities and transporting such large fish to the laboratory proved difficult (a common limitation in catch-and-release studies; Cooke and Schramm, 2007) and unfortunately makes it difficult to determine the extent of physiological disturbance that arises from the angling event itself. In general, the blood lactate values that I recorded were relatively low (e.g., 3.9 ± 0.2 mmol l^{-1}) compared to values obtained for other fish angled for similar durations (e.g., 5-7 mmol l^{-1}, northern pike (*Esox lucius*), Schwalme and MacKay, 1985; 5-8 mmol l^{-1}, rainbow trout (*Oncorhynchus mykiss*), Meka and McCormick, 2005; 4-6 mmol l^{-1}, bonefish (*A. vulpes*), Cooke et al., 2008). In addition, a certain amount of variation around the regression lines was noted for the glucose and lactate relationship with fight and handling time (Figure 3-2), which may be attributed to individual variation and the relationship could possibly be strengthened with a larger sample size.

Ionic changes are also indicators of physiological stress caused by exhaustive exercise (Wells et al., 1986; Wood, 1991), although only a few studies have tested the relationship between angling duration and ionic imbalance in marine teleosts (e.g. Wells et al., 1986; Thompson et al., 2002; Cooke et al., 2008; Fabrizio et al., 2008). Wells et al. (1986) showed that K^+, Na^+, and Cl^- all increased in capture-stressed striped marlin (*Tetrapturus audax*), blue marlin (*Makaira nigricans*), black marlin (*Makaira indica*),

skipjack (*Katsuwonus pelamis*), and yellowfin tuna (*Thunnus albacares*), while bonefish (*A. vulpes*) did not experience any relationship between fight time and plasma ion levels (Suski et al., 2007; Cooke et al., 2008). The release of stress hormones in marine fish is associated with osmoregulatory difficulties, which may lead to hydromineral imbalance (Eddy, 1981; Barton et al., 2002). Stressors such as long fight durations or handling trigger the release of corticosteroids and catecholamines, which may increase gill permeability and alter ionic balance (Moyle and Cech, 2000). Thus, in marine teleosts, a stress response could include a loss of water and a gain of ions across the gills (Wells et al., 1986; Moyle and Cech, 2000). Although plasma sodium increased with fight and handling time, similar trends in plasma chloride concentrations were not apparent in the present study (Figure 3-3), despite expectations that increased NaCl uptake (from seawater) and loss of water across gills would result as a stress response in angled barracuda.

Anatomical hook location has often been considered the single most important mortality factor during catch-and-release events (Bartholomew and Bohnsack, 2005) and a broad array of studies have been completed to better understand the effect of angling on hooking injury, handling, and post-release survival (e.g. Diodati and Richards, 1996; Diggles and Ernst, 1997; Alós et al., 2008; Arlinghaus et al., 2008b). In the present study, lure type did not have an effect on relative hooking depth, severity of injury, bleeding, or ease of hook removal for captured great barracuda. I had predicted that lure type would influence severity of injury, particularly those lures with multiple treble hooks; however, my results showed uniform levels of injury among lure types, which may be due to the limitations of small sample sizes in some treatment groups and the lack

of fish that were severely injured or hooked in critical areas. Barracuda are ambush predators that strike their prey at high speeds, exhibiting ram-biting behaviour where prey is initially impacted at the corner of the mouth (Grubich et al., 2008). Striking a lure would happen in a similar fashion, so that the hook would likely penetrate in the mouth or jaw instead of deeply hooking the barracuda in the gullet or gills. The amount of bleeding present at the site of the hook wounds was minimal as great barracuda may have less perfused tissues in their jaw area, potentially as an adaptation to prevent excessive bleeding while preying on fish with spines and hard appendages. Muskellunge (*Esox masquinongy*) and northern pike (*E. lucius*), two freshwater species with similar morphology and feeding behaviour, also exhibit very little bleeding when hooked in the jaw (Ostrand et al., 2006; Arlinghaus et al., 2008b).

We did not observe any immediate mortality throughout my study, however, five of the fish noticeably lost equilibrium after landing and upon examination post capture they appeared to have air in their digestive tracts. The abdomens were compressed, expelling the air out of the vent, after which the fish quickly regained equilibrium. As the risk of predation in environments where barracuda inhabit may be very high (two individuals in the study were attacked while being reeled in, Figure 3-5b), all of the fish captured throughout the study underwent some degree of revival prior to being released to reduce the chance of post-release predation. Gamefish released in marine waters can experience post-release predation although this phenomenon has not received much attention (Jolley and Irby, 1979; Edwards, 1998; Cooke and Philipp, 2004; Danylchuk et al., 2007; Henderson, 2009) and I was unable to quantify post-release mortality in this study. On a few occasions, other large predatory fish (i.e. Carcharhinidae, Carangidae,

other barracuda) followed the hooked barracuda right up to the boat, likely attracted to the noise and movement produced by the angled fish or by olfaction (Moss, 1977, Bleckmann and Hofmann, 1999). Although not quantified in this study, many barracuda were lost when they cut or broke the line despite using a wire or heavy monofilament leader. I estimate that this occurred about 20% of the time a barracuda hit the line. The fate of barracuda that break-off and retain the lures is unknown. In fact, only two studies currently exist on the fate of gamefish released with lures in their mouth (i.e., northern pike (*E. lucius*); Arlinghaus et al., 2008a; smallmouth bass (*Micropterus dolomieu*); Henry et al., 2009), which showed that behavioural and physiological alterations may result from lure retention and would be an issue worthwhile examining in great barracuda.

While angled barracuda appear to be fairly robust and immediate mortality was negligible, I am uncertain as to the extent of delayed mortality, particularly associated with post-release predation, a topic worthy of study. Although I did not observe differences in the amount of injury caused by three common lure types, choosing lures with single hooks and having pliers or hemostats accessible will expedite quick hook removal, reduce handling, and decrease air exposure. When targeting great barracuda, I recommend running lines short when trolling to reduce fight duration, landing the fish in a knotless mesh net or cradle for ease of handling and hook removal over the side of the vessel without removing the fish from the water to reduce air exposure. Predictions of specific effects of angling on great barracuda will contribute to future management decisions (Cooke and Suski, 2005; Coggins et al., 2007) and given that barracuda are often encountered as bycatch while anglers are targeting other gamefish such, it may be

beneficial to educate anglers and guides on the importance of predators such as barracuda to promote better handling and release practices for what I believe many anglers regard as a nuisance fish.

Tables

Table 3-1. Summary results of linear regressions used to evaluate the effect of variables associated with catch-and-release angling (fight time and handling time) on physiological blood parameters of great barracuda. Statistically significant values are presented in italics ($\alpha = 0.05$).

Response Variable	Independent Variable	R^2	d.f.	F-value	P-value
Glucose	Fight time	0.14	1, 56	9.80	*0.003*
	Handling time	0.27	1, 46	17.12	*<0.001*
Lactate	Fight time	0.03	1, 57	2.06	0.16
	Handling time	0.12	1, 48	6.87	*0.01*
Sodium	Fight time	0.07	1, 49	4.25	*0.04*
	Handling time	0.16	1, 43	7.99	*0.007*
Potassium	Fight time	0.02	1, 48	1.22	0.27
	Handling time	0.03	1, 42	1.47	0.23
Chloride	Fight time	0.03	1, 49	1.45	0.23
	Handling time	0.04	1, 43	1.88	0.17

Table 3-2. Summary results of contingency analysis used to evaluate the effect of lure type, hook location, and hook type on severity of injury (minor, severe), bleeding (yes, no) and ease of hook removal (easy, difficult) for great barracuda. Statistical significance was evaluated at $\alpha = 0.05$.

Variable		**d.f.**	χ^2	**P-value**
Lure type	Injury	2	5.77	0.06
	Bleeding	2	2.60	0.27
	Ease of hook removal	2	2.79	0.25
Hook type	Ease of hook removal	1	3.08	0.08

Figures

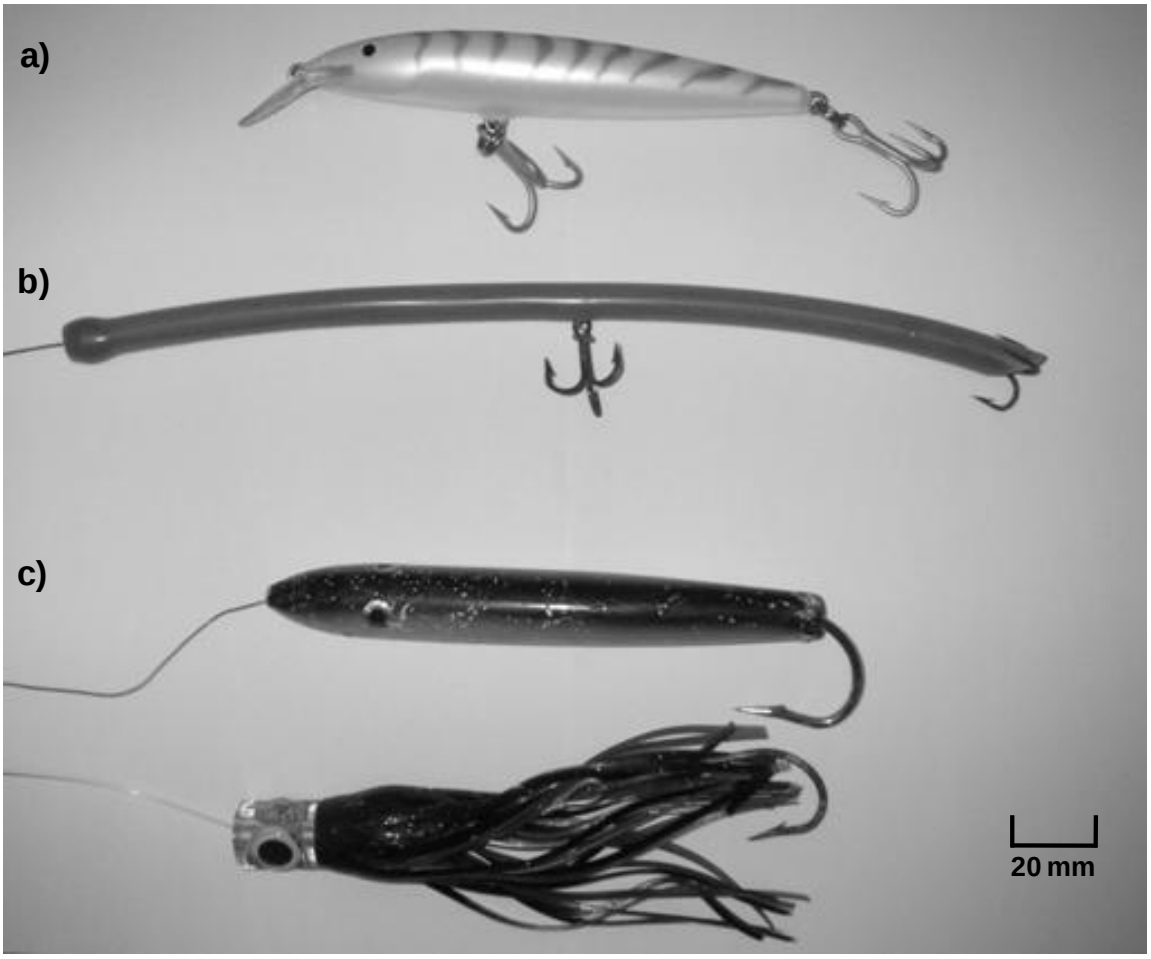

Figure 3-1. Photograph depicting examples of the three types of artificial lures used during the study to capture great barracuda, (a) hard lure with two treble hooks, (b) soft lure with two treble hooks, and(c) single hook lures.

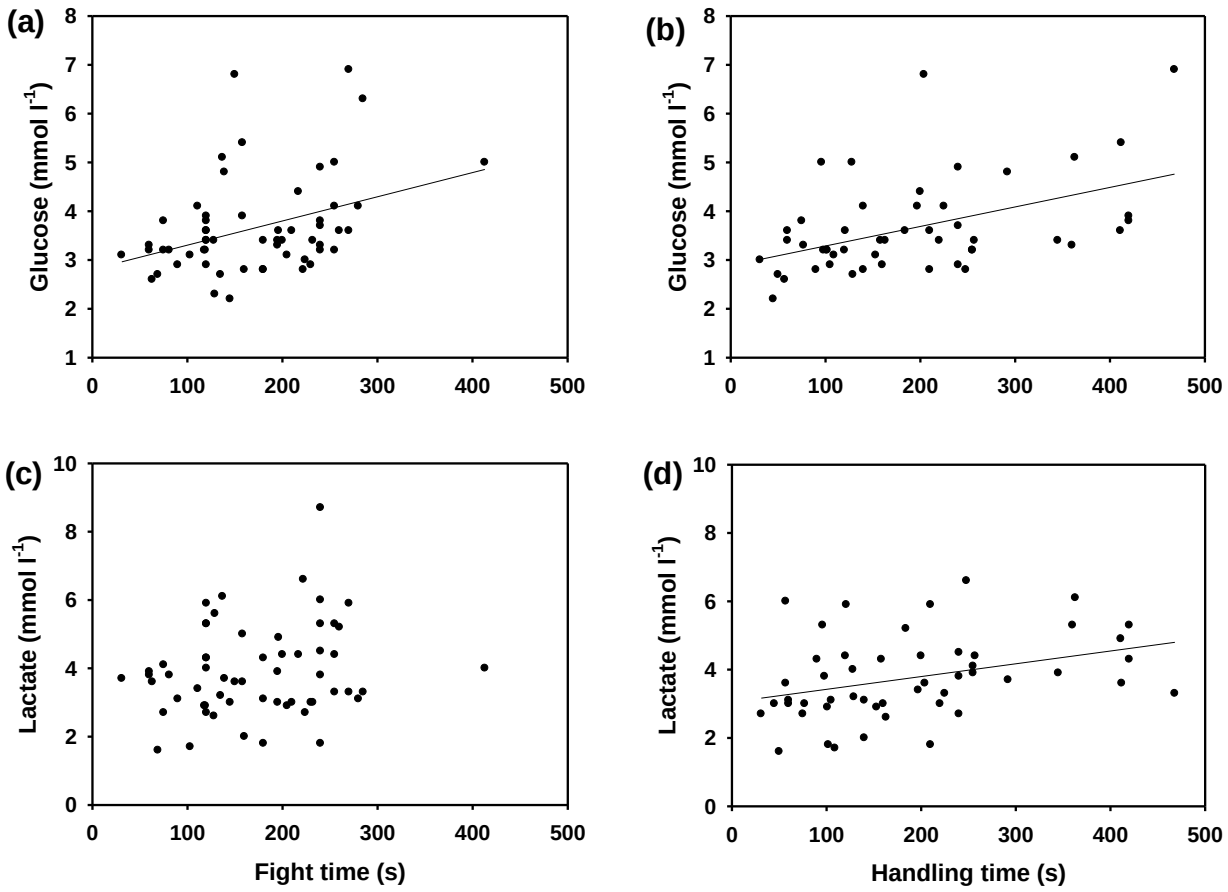

Figure 3-2. Relationships between blood glucose concentration (mmol l^{-1}) and (a) fight time and (b) handling time and blood lactate (mmol l^{-1}) concentration and (c) fight time and (d) handling time for great barracuda caught by hook-and-line angling.

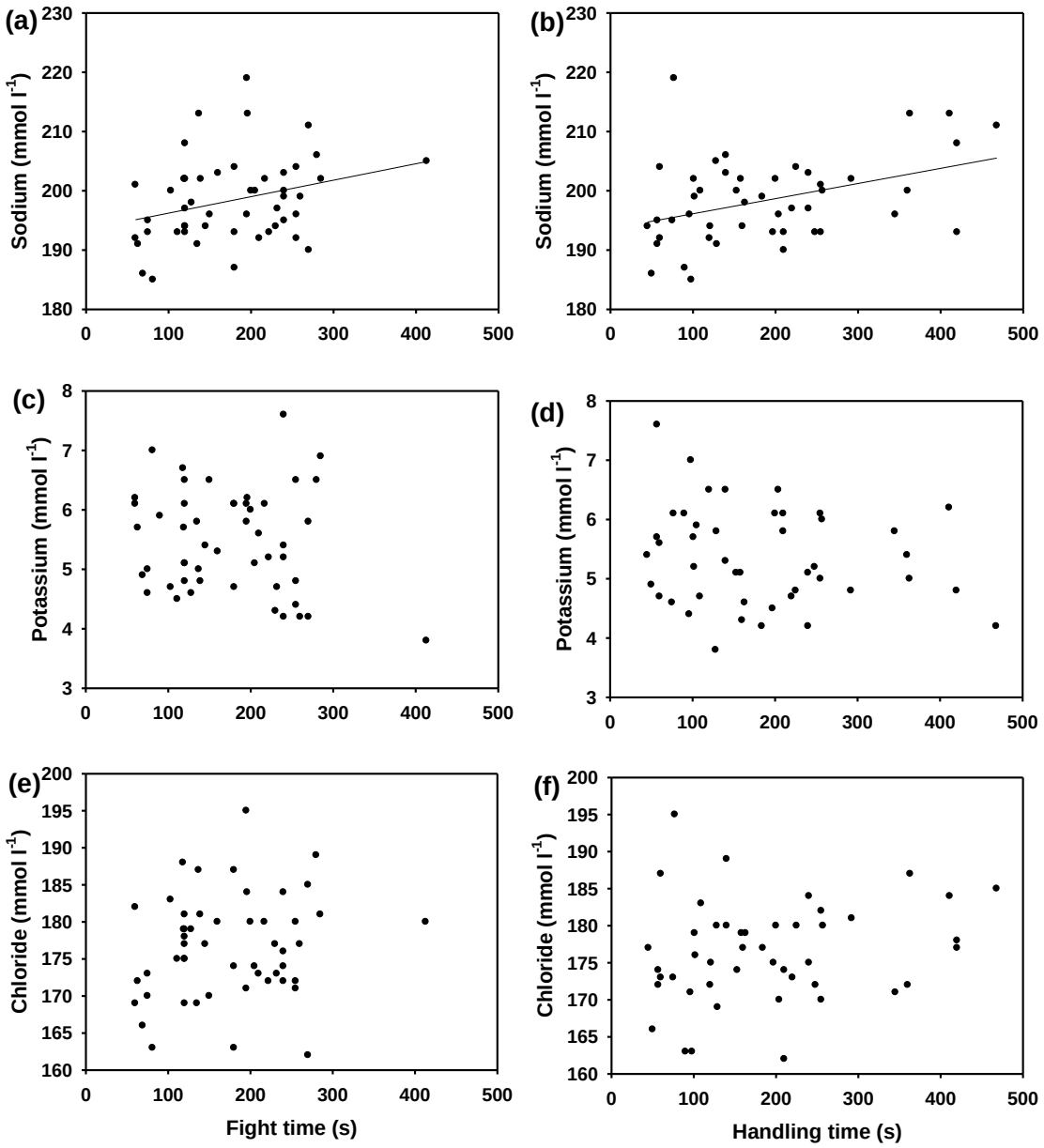

Figure 3-3. Ionic parameters measured in blood plasma of great barracuda caught by hook-and-line angling. Relationship between sodium concentration (mmol l^{-1}) and (a) fight time and (b) handling time; potassium concentration (mmol l^{-1}) and (c) fight time and (d) handling time; chloride concentration (mmol l^{-1}) and (e) fight time and (f) handling time.

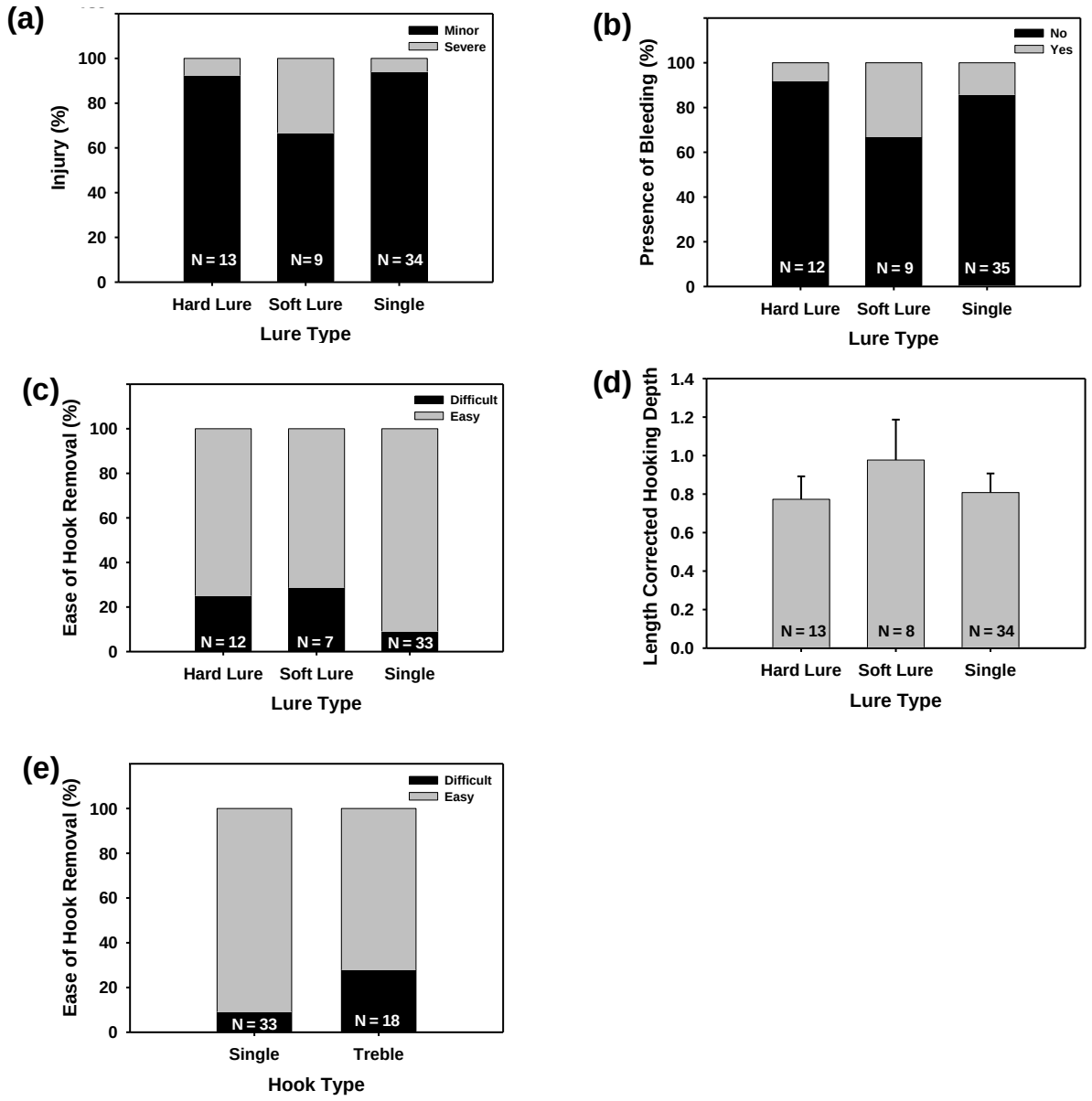

Figure 3-4. The effect of lure type (hard lure, soft lure, single hook lure) on (a) injury, (b) presence of bleeding, (c) ease of hook removal, (d) hooking depth, and (e) the effect of hook type (two treble hook or single j-style hook) on the ease of hook removal (easy, <30 s; difficult, >30 s) for angled great barracuda. Sample sizes are provided for each category.

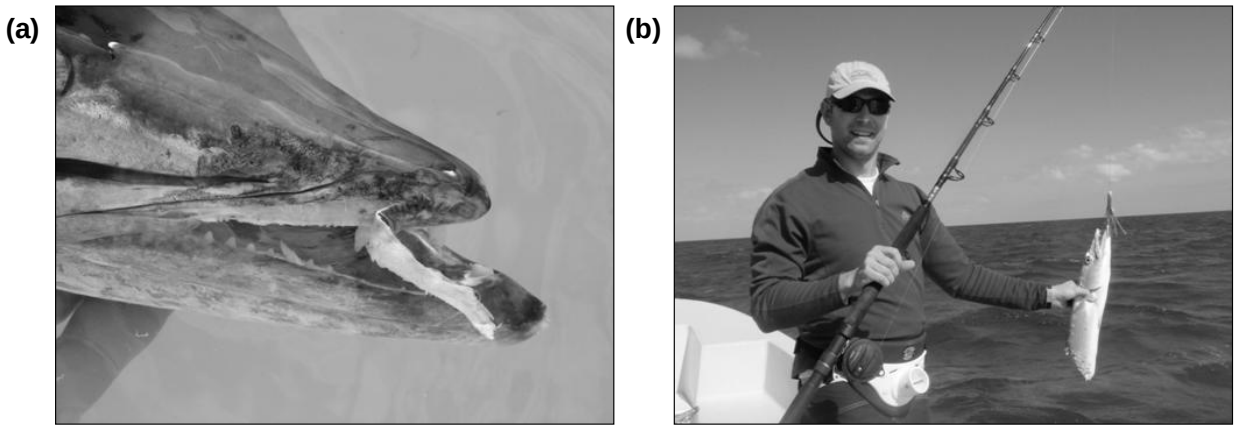

Figure 3-5. Photographs of (a) tissue damage to the jaw of an angled great barracuda and (b) a great barracuda attacked by a predator and killed during an angling event.

Chapter 4: General Discussion

Through the use of novel technology and applied techniques, this dissertation has increased the general knowledge concerning the basic biology of great barracuda. In Chapter 2, barracuda were implanted with acoustic telemetry transmitters equipped with accelerometer and pressure sensors to gain useful insight into fine scale behavioural patterns. Chapter 3 summarized the physiological consequences, injury, and immediate mortality attributed to catch-and-release of great barracuda. In Appendix I, I present preliminary results from a spatial ecology study and in Appendix II, I detail a novel approach for determining ciguatera levels in fish through non-lethal sampling. The overall objective of this dissertation was to explore and present the physiological and injury response to catch-and-release angling, as well as the behavioural ecology for great barracuda. Past research concerning the fundamental biology of great barracuda has been minimal, based predominately on visual observations and anecdotal evidence. The work presented in this thesis has built upon some of those past studies by applying experimental research elements to attain a more comprehensive ecological understanding of this species.

Findings and Implications

To date, only four studies have examined the behavioural ecology and spatial movement of great barracuda using mark-recapture methods, underwater visual surveys, and individual body markings for identification (Springer and McErlean, 1961; Paterson, 1998; Wilson et al., 2006b; Villareal et al., 2007). The research summarized in Chapter 2 is the first telemetry study performed to assess barracuda movement. There were no

apparent differences in relative activity or depth utilization across habitat types or diel periods, however, not all fish were detected within each of the designated habitats and many of the fish moved out of the detection range of the acoustic receiver array, suggesting that barracuda are somewhat transient. In general, barracuda spend much of the time engaged in low locomotory activity (slow swimming or hovering in place), with occasional bursts of high activity, often within the upper 5 m of the water column. There was also variation in behaviour between individual fish, as some showed distinct, regular movements into deeper water during midday, illustrating the need to conduct further telemetry analyses to better understand temporal movement patterns. Identifying the fine scale behaviour for large teleost species such as barracuda may contribute to future marine and coastal management practices. A more complete understanding of barracuda (and other large reef predators) spatial ecology, ontogeny, and response to disturbance may contribute to the conservation of the species and the ecosystem of which they are a part of. The behavioural results presented in my study, combined with knowledge of life history and marine community dynamics may provide valuable insight when applied to conservation strategies such as the design and management of marine protected areas (Kramer and Chapman, 1999).

Barracuda are a popular sportfish targeted worldwide by anglers, but are also frequently captured as a bycatch species while anglers are in pursuit of other species and are consequently released. This is the first catch-and-release study and also the first body of work to present physiological data for wild great barracuda. The physiological effects, associated injury, and immediate mortality of caught-and-released great barracuda are presented in Chapter 3. Blood glucose and plasma sodium concentrations increased with

fight time and handling duration, while blood lactate levels increased as a result of longer handling times. Injury, bleeding, hook removal, and hooking depth were not influenced by lure or hook design and immediate mortality was minimal. Anglers may reduce potential physiological disturbance by landing fish quickly and reducing the degree of handing prior to release. Physiological and morphological characteristics differ widely between species and may result in variable responses to environmental conditions and anthropogenically-induced stressors (Cooke and Suski, 2005), thus, species-specific angling guidelines are an important management and conservation tool.

In Appendix I, I continue to build on the research that I conducted in Chapter 2 by investigating the horizontal movements of great barracuda across habitat types and temporal periods. Some barracuda do indeed appear to be fairly transient, although other individuals are more resident to the waters adjacent to Cape Eleuthera. Studying barracuda movement may prove to have important implications for local artisanal fishers because knowledge of barracuda behaviour may contribute to a heightened understanding ciguatera fish poisoning distribution. In Appendix II, I present some preliminary results of a ciguatera study that attempts to link the occurrence of ciguatera fish poisoning to barracuda spatial ecology. Thus far, results have shown that detection of ciguatoxin (CTX) concentration in blood is comparable to that of other tissues (i.e. liver, muscle), indicating that, for the first time, CTX detection from a non-lethal sample is possible. These findings imply that non-lethal blood samples could provide an excellent marker of recent exposure or accumulation of CTX and will facilitate future research in coral reef health, fish biology, and biotoxin and human health issues.

Overall, my results have shown that great barracuda appear to be relatively resilient (physically and physiologically) and while they predominately exhibit low locomotory activity, they may be capable of transiting broad distances. Although presently a common and abundant species in nearshore systems worldwide, baseline information representing the ecology, behaviour, and natural history of barracuda would be valuable if, in the future, great barracuda become a species of concern. Already, considerable declines in top-level marine predators are apparent (Myers and Worm, 2003) and barracuda may represent a similar trophic position as other large teleosts and elasmobranchii species (de Sylva, 1963). Furthermore, although my results did not show differences in relative activity across habitat types, barracuda appear to be dependent upon particular habitats according to life cycle or temporal scales, which illustrate the importance for conservation of critical habitat. From an applied perspective, my research may contribute to efforts to better manage the recreational fishery and potentially provide insight into spatial distribution of fish that are contaminated with biotoxins such as ciguatera fish poisoning.

Future Research Directions

Results presented in Chapter 2 showed that great barracuda may be fairly transient beyond the confines of the array area, but also may exhibit movement into deeper habitats during certain time periods throughout the day. A general lack of continuous temporal detections for these fish has limited my ability to clearly decipher the general movements of barracuda. In addition to the 13 accelerometer tags used in Chapter 2, 42 acoustic transmitters have been deployed in order to answer questions pertaining to habitat use, home range tendencies, and temporal behaviour (preliminary results obtained

from this study are presented in Appendix I). In addition, a larger sample size combined with transmitters that have a longer-term battery life or by using pop-up satellite tag technology would allow for long-term monitoring over a much larger spatial region without the limitation of fish moving beyond the boundaries of an acoustic array.

Ciguatera fish poisoning (CPF) is a biotoxin issue originating from the naturally occurring ciguatoxin (CTX) in tropical and subtropical regions. CTX bioaccumulates in large, predatory reef fish such as barracuda and can cause CPF in humans who consume fish with high concentrations of the toxin in their tissues. Currently, determination of fishing areas that are more or less likely to produce fish with CTX is purely anecdotal and often based largely on local traditions (Bienfang et al., 2008). I would like to link the occurrence and severity of CTX with the spatial ecology of barracuda. In addition to transmitters deployed for the spatial ecology study described above and in Chapter 2, blood, liver, and muscle samples were obtained for most of the barracuda captured for this thesis project (See Appendix I). Investigation into the distribution of fish with detectable concentrations of CTX would benefit human health initiatives within local communities by advising local subsistence fishers about the risks involved with capture and consumption of potentially toxic fish in particular regions. Preliminary results obtained from this study are presented in Appendix II.

Environmental DNA (eDNA) is a new technique that uses polymerase chain reaction (PCR) to detect the presence of biological organisms (even at low concentrations) within a water sample (Ficetola et al., 2008; Mahon et al., 2009). eDNA could potentially be used to test various areas for the presence of *Gambierdiscus toxicus,*

the species of dinoflagellate that is commonly known to produce CTX. By running eDNA tests on water samples from areas where ciguatoxic barracuda are known to inhabit (based upon long-term telemetry data) and across seasons (*G. toxicus* are often associated with certain species of algal blooms), it may be possible to determine if barracuda are acquiring CTX locally or if the more transient fish are picking it up from another location.

The majority of the work completed on barracuda foraging ecology has been with stomach content analysis on juvenile fish, with little work completed on adult barracuda. A stable isotope study could advance some of the past stomach content studies by confirming where barracuda are positioned trophically. This information may be applied to further CFP research by comparing individual barracuda with and without CTX to see if larger or highly toxic fish are feeding at a higher trophic level.

Chapter 3 quantified some of the physiological effects of fight time and handling duration on great barracuda during catch-and-release (C&R) events. Past C&R research has shown that sustained air exposure and angling during seasonal water temperature extremes contribute to physiological disturbance in angled fish (Wilkie et al., 1996, 1997; Suski et al., 2007). Additionally, determining baseline physiological values for barracuda would be of great value to future experimental research initiatives. Artificial lure types did not affect the degree of injury; however, barracuda are also sometimes angled using live bait. Studies have shown that the use of natural or live bait is often related to deeply hooked fish causing greater injury and potentially decreasing post-release survival (Diggles and Ernst, 1997; Margenau, 2007). Immediate mortality in caught-and-released

barracuda is negligible, although, the long-term fate of released fish is still unknown. Monitoring of fish behaviour post-release with acoustic telemetry would provide insight into potential mortality as a result of physiological disturbance, injury, or predation. Additional research in this area, specific to barracuda, would contribute to the overall understanding of the effects of catch-and-release practices to ensure a sustainable recreational fishery across tropical and subtropical regions worldwide.

With limited knowledge of the habitat utilization at various stages of great barracuda life history warrants for behavioural research on juvenile barracuda. Juvenile barracuda are easily caught in nearshore habitats and could be implanted with small acoustic telemetry transmitters (for example, V7 coded transmitter, Vemco, Shad Bay, NS). Receivers could be placed inside and at mouths of mangrove creeks, along beaches, and within rocks cuts and marinas (or other anthropogenically-altered habitat). This will answer habitat use related questions such as which habitat types juvenile barracuda are using at a given ontogenetic stage, whether they move between habitats or locations (i.e. between mangrove creeks), and how they behave in accordance to temporal or tidal trends. Identifying potential nursery habitat and how barracuda use these areas is of particular importance when developing conservation strategies and predicting potential responses to human-based disturbances.

Afterword and Summary

The overall objective of this dissertation was to examine the physiological and behavioural ecology of the great barracuda (*S. barracuda*). My research has contributed

to past work completed on the ecology, behaviour, and natural history of this large, nearshore predator in the following ways:

1. Confirmation of anecdotal and observational behavioural activity characteristics in great barracuda. Barracuda spend much of the time exhibiting low level locomotory activity with occasional bursts of high level activity, across a range of habitat types, often within 5 m of the surface. In addition, barracuda may also engage in repeated movements during certain times of the day.

2. Continued research is required to assess great barracuda spatial ecology and habitat use. The barracuda studied in Chapter 2 showed considerable variation between individuals, some of which appeared to be fairly transient in nature. Thus, further telemetry work on this species is warranted to obtain a more complete understanding of temporal behaviour and habitat utilization.

3. Great barracuda are relatively resilient to some aspects associated with catch-and-release angling techniques. Some physiological disturbance occurs in response to longer fight and handling durations. Lure and hook type had a minimal effect on injury and immediate mortality was negligible. Regardless, barracuda should be landed quickly and appropriate handling procedures should be employed to ensure long-term survival post-release.

4. Non-lethal blood sampling is an effective way to detect CTX in wild great barracuda. This is the first report of CTX detection from a non-lethal biosample. The ability to detect CTX in live fish presents new opportunities to study the geographic

characteristics associated with the toxin and will allow researchers to monitor recent exposure of ciguatoxin in individual fish.

References

Alós, J., Palmer, M., Grau, A. M., and Deudero, S. 2008. Effects of hook size and barbless hooks on hooking injury, catch per unit effort, and fish size in a mixed-species recreational fishery in the western Mediterranean Sea. *ICES Journal of Marine Science* **65**: 899-905.

Arlinghaus, R., Cooke, S. J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S. G., and Thorstad, E. b. 2007a. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science* **15**: 75-167.

Arlinghaus, R., Cooke, S. J., Schwab, A., and Cowx, I. G. 2007b. Fish welfare: a challenge to the feelings-based approach, with implications for recreational fishing. *Fish and Fisheries* **8**: 57-71.

Arlinghaus, R., Klefoth, T., Gingerich, A. J., Donaldson, M. R., Hanson, K. C., and Cooke, S. J. 2008a. Behaviour and survival of pike, *Esox lucius*, with a retained lure in the lower jaw. *Fisheries Management and Ecology* **15**: 459-466.

Arlinghaus, R., Klefoth, T., Kobler, A., and Cooke, S. J. 2008b. Size selectivity, injury, handling time, and determinants of initial hooking mortality in recreational angling for northern pike: the influence of type and size of bait. *North American Journal of Fisheries Management* **28**: 123-134.

Austin, D., Bowen, W. D., McMillan, J. I., and Iverson, S. J. 2006. Linking movement, diving, and habitat to foraging success in a large marine predator. *Ecology* **87**: 3095-3108.

Ayvazian, S. G., Wise, B. S., and Young, G. C. 2002. Short-term hooking mortality of tailor (*Pomatomus saltatrix*) in Western Australia and the impact on yield per recruit. *Fisheries Research* **58**: 241-248.

Balkwill, D., Coad, B. W., Galvez, I., and Gilhen, J. 2006. First record of the great barracuda, *Sphyraena barracuda* from Canada. *Canadian Field Naturalist* **120**: 241-242.

Barreiros, J. P., Santos, R. S., and de Borba, A. E. 2002. Food habits, schooling and predatory behaviour of the yellowmouth barracuda, *Sphyraena viridensis* (Perciforms: Sphraenidae) in the Azores. *Cybium* **26**: 83-88.

Barthel, B. L., Cooke, S. J., Suski, C. D., and Philipp, D. P. 2003. Effects of landing net mesh type on injury and mortality in a freshwater recreational fishery. *Fisheries Research* **63**: 275-282.

Bartholomew, A., and Bohnsack, J. A. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries* **15**: 129-154.

Barton, B. A., Schreck, C. B., and Sigismondi, L. A. 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile Chinook salmon. *Transactions of the American Fisheries Society* **115**: 245-251.

Barton, B. A., Morgan, J. D., and Vijayan, M. M. 2002. Physiological and condition-related indicators of environmental stress in fish. *In* Biological Indicators of Ecosystem Stress. *Edited by* S. M. Adams. American Fisheries Society, Bethesda, Maryland. pp. 111-148

Bienfang, P.K., Parsons, M. L., Bidigare, R. R., Laws, E. A., Moeller, P. D. R. 2008. Ciguatera Fish Poisoning: A synopsis from Ecology to Toxicity. *In* Oceans and Human Health Risks and Remedies from the Seas. *Edited by* P. J. Walsh, S. L. Smith, L. E. Fleming, H. M. Solo-Gabriele, W. H. Gerwick. Academic Press, New York. pp 257-270

Blaber, S. J. M. 1982. The ecology of *Sphyraena barracuda* (Osteichthyes: Perciformes) in the Kosi system with notes on the Sphyraenidae of other Natal estuaries. *South African Journal of Zoology* **17**: 171-176.

Bleckmann, H., and Hofmann, M. H. 1999. Special senses. *In* Sharks, Skates and Rays: The Biology of Elasmobranchs. *Edited by* W. C. Hamlett. John Hopkins University Press, Baltimore, Maryland. pp. 300-328.

Block, B. A. 2005. Physiological Ecology in the 21st Century: Advancements in Biologging Science. *Integrative and Comparative Biology* **45**: 305-320.

Block, B. A., Booth, D. T., and Carey, F. G. 1992. Depth and temperature of the blue marlin, *Makaira nigricans*, observed by acoustic telemetry. *Marine Biology* **114**: 175-183.

Block, B. A., Costa, D. P., Boehlert, and G. W., Kochevar, R. E. 2003. Revealing pelagic habitat use: the tagging of Pacific pelagic program. *Oceanologica Acta* **25**: 255-266.

Block, B. A., Teo, S. L. H., Walli, A., Boustany, A., Stokesbury, M. J. W., Farwell, C. J., Weng, K. C., Dewar, H., and Williams, T. D. 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* **434**: 1121-1127.

Boisclair, D. and Leggett, W. C. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. *Canadian Journal of Aquatic Science* **46**: 1859-1867.

Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V., and Marcinek, D. J. 1999. Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Marine Biology* **133**: 395-408.

Butler, P. J., Green, J. A., Boyd, I. L., and Speakman, J. R. 2004. Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. *Functional Ecology* **18**: 168-183.

Cartamil, D. P. and Lowe, C. G. 2004. Diel movement patterns of ocean sunfish *Mola mola* off southern California. *Marine Ecology Progress Series* **266**: 245-253.

Coggins, L. G., Catalano, M. J., Allen, M. S., Pine III, W. E., and Walters, C. J. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries* **8**: 196-210.

Coleman, F. C., Figueira, W. F., Ueland, J. S., and Crowder, L. B. 2004. The impact of United States recreational fisheries on marine fish populations. *Science* **305**: 1958-1960.

Colman, J. R., Dechraoui, M. Y. B., Dickey, R. W., Ramsdell, J. S. 2004. Characterization of the developmental toxicity of Caribbean ciguatoxins in finfish embryos. *Toxicon* **44**: 59-66.

Cooke, S. J. 2008. Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endangered Species Research* **4**: 165-185.

Cooke, S. J., Danylchuk, A. J., Danylchuk, S. E., Suski, C. D., and Goldberg, T. L. 2006. Is catch-and-release recreational angling compatible with no-take marine protected areas? *Ocean and Coastal Management* **49**: 342-354.

Cooke, S. J., Graeb, B. D. S., Suski, D. C., and Ostrand, K. G. 2003. Effects of suture material on incision healing, growth and survival of juvenile largemouth bass implanted with miniature radio transmitters: case study of a novice and experienced fish surgeon. *Journal of Fish Biology* **62**: 1366-1380.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G., and Butler, P. J. 2004a. Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution* **19**: 334-343.

Cooke, S. J. and Philipp, D. P. 2004. Behaviour and mortality of caught-and-released bonefish (*Albula* spp.) in Bahamian waters with implications for a sustainable recreational fishery. *Biological Conservation* **118**: 599-607.

Cooke, S. J., Philipp, D. P., Dunmall, K. M., and Schreer, J. F. 2001. Influence of terminal tackle on handling time, and cardiac disturbance of rock bass. *North American Journal of Fisheries Management* **21**: 333-342.

Cooke, S. J. and Schramm, H. L. 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. *Fisheries Management and Ecology* **14**: 73-79.

Cooke, S. J., Schreer, J. F., Dunmall, K. D., and Philipp, D. P. 2002a. Strategies for quantifying sublethal effects of marine catch-and-release angling: insights from novel freshwater applications. *In* Catch-and-Release in Marine Recreational Fisheries. *Edited by* J. A. Lucy and A. L. Studholme. American Fisheries Society Symposium 30, Bethesda, Maryland. pp. 121-134.

Cooke, S. J., Schreer, J. F., Wahl, D. H., and Philipp, D. P. 2002b. Physiological impacts of catch-and-angling practices on largemouth bass and smallmouth bass. *In* Black Bass: ecology, conservation and management. *Edited by* D. P. Philipp, and M. S. Ridgway. American Fisheries Society Symposium 31, Bethesda, Maryland. pp 489-512.

Cooke, S. J. and Sneddon, L. U. 2006. Animal welfare perspectives on recreational angling. *Applied Animal Behaviour Science* **104**: 176-198.

Cooke, S. J. and Suski, C. D. 2005. Do I need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? *Biodiversity and Conservation* **14**: 1195-1209.

Cooke, S. J., Suski, C. D., Barthel, B. L., Ostrand, K. G., Tufts, B. L., and Philipp, D. P. 2003. Injury and mortality induced by four hook types on bluegill and pumpkinsee. *North American Journal of Fisheries Management* **23**: 883-893.

Cooke, S. J., Suski, C. D., Danylchuk, S. E., Danylchuk, A. J., Donaldson, M. R., Pullen, C., Bulté, G. O'Toole, A., Murchie, K. J., Koppelman, J. B., Shultz, A. D., Brooks, E., and Goldberg, T. L. 2008. Effects of different capture techniques on the physiological condition of bonefish *Albula vulpes* evaluated using field diagnostic tools. *Journal of Fish Biology* **73**: 1351-1375.

Cooke, S. J., Thorstad, E. B., Hinch, and S. G. 2004b. Activity and energetics of free-swimming fish: insights from electromyogram telemetry. *Fish and Fisheries* **5**: 21-52.

Danylchuk, S. E., Danylchuk , A. J., Cooke, S. J., Goldberg, T. L., Koppelman, J., and Philipp, D. P. 2007. Effects of recreational angling on the post-release behaviour and predation of bonefish (*Albula vulpes*): the role of equilibrium status at the time of release. *Journal of Experimental Marine Biology and Ecology* **346**: 127-133.

Davie, P. S. and Kopf, R. K. 2006. Physiology, behaviour and welfare of fish during recreational fishing and after release. *New Zealand Veterinary Journal* **54**: 161-172.

de Sylva, D. P. 1963. Systematics and life history of the great barracuda *Sphyraena barracuda*. University of Miami Press, Coral Gables, Florida.

de Sylva, D. P. 1994. Distribution and ecology of ciguatera fish poisoning in Florida, with emphasis on the Florida Keys. *Bulletin of Marine Science* **54**: 944-954.

Dechraoui, M. Y. B., Tiedeken, J. A., Persad, R., Wnag, Z., Granade, H. R., Dickey, R. W., and Ramsdell, J. S. 2005. Use of two detection methods to discriminate ciguatoxins from brevetoxins: application to great barracuda from Florida Keys. *Toxicon* **46**: 261-270.

Diggles, B. K. and Ernst, I. 1997. Hooking mortality of two species of shallow-water reef fish caught by recreational angling methods. *Marine and Freshwater Research* **48**: 479-483.

Diodati, P. J. and Richards, R. A. 1996. Mortality of striped bass hooked and released in salt water. *Transactions of the American Fisheries Society* **125**: 300-307.

DuBois, R. B. and Dubielzig, R. R. 2004. Effect of hook type on mortality, trauma, and capture efficiency of wild stream trout caught by angling with spinners. *North American Journal of Fisheries Management* **24**: 609-616.

Dunn, D. C., Stewart, K., Bjorkland, R. H., Haughton, M., Singh-Renton, S., Lewison, R., Thorne, L., Halpin, P. N. A regional analysis of coastal and domestic fishing effort in the wider Caribbean. *Fisheries Research* **102**: 60-68.

Eddy, F. B. 1981. Effects of stress on osmotic and ionic regulation in fish. *In* Stress and Fish. *Edited by* A. D. Pickering. Academic Press, London. pp. 77-102.

Edwards, R. E. 1998. Survival and movement patterns of released tarpon (*Megalops atlanticus*). *Gulf of Mexico Science* **16**: 1-7.

Fabrizio, M. C., Scharf, F. S., Shepherd, G. R., and Rosendale, J. E. 2008. Factors affecting catch-and-release mortality of bluefish. *North American Journal of Fisheries Management* **28**: 533-546.

Faunce, C. H. and Serafy, J. E. 2008. Selective use of mangrove shorelines by snappers, grunts, and great barracuda. *Marine Ecology Progress Series* **356**: 153-162.

Ficetola, G. F., Miaud, C., Pompanon, F., and Taberlet, P. 2008. Species detection using environmental DNA from water samples. *Biology Letters* **4**: 423-425.

Friedlander, A. M. and DeMartini, E. E. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Marine Ecology Progress Series* **230**: 253-264.

Frith, H. R. and Blake, R.W. 1995. The mechanical power output and hydromechanical efficiency of northern pike (*Esox lucius*) fast-starts. *The Journal of Experiemental Biology* **198**: 1863-1873.

Frisch, A. and Anderson T. 2005. Physiological stress responses of two species of coral trout (*Plectropomus leopardus* and *Plectropomus maculates*). *Comparative Biochemistry and Physiology A* **140**: 317-327.

Gero, D. R. 1952. The hydrodynamic aspects of fish propulsion. *American Museum Novitates* **1601**: 1-32.

Gillespie, N. C., Lewis, R. J., Pearn, J. H., Bourke, A. T. C., Holmes, M. J., Bourke, J. B., and Shields, W. J. 1989. Ciguatera in Australia – occurrence, clinical-features, pathophysiology and management. *Medical Journal of Australia* **145**: 584-590.

Gleiss, A. C., Gruber, S. H., and Wilson, R. P. 2009a. Multi-channel data-logging: towards determination of behaviour and metabolic rate in free-swimming sharks. *In* 'Tagging and Tracking of Marine Animals with Electronic Devices'. *Edited by* J. L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, J. Sibert. Springer, Netherlands. pp. 211-228.

Gleiss, A. C., Norman, B., Liebsch, N., Francis, C., and Wilson, R. P. 2009b. A new prospect for tagging large free-swimming sharks with motion-sensitive data-loggers. *Fisheries Research* **97**: 11-16.

Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A., and Hildebrand, J. A. 2006. Kinematics of foraging dives and lunge-feeding in fin whales. *The Journal of Experimental Biology* **209**: 1231-1244.

Gollock, M. J., Hunter, K. J., Syme, D. A., Freeman, M., McKinley, R. S., and Gamperl, A. K. 2009. Potential methods for measuring the activity patterns and energy use of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Science* **66**: 1095-1106.

González-Sansón, G., Aguilar, C., Hernández, I., and Cabrera, Y. 2009. Effects of depth and bottom communities on the distribution of highly territorial reef fish in the northwestern region of Cuba. *Journal of Applied Ichthyology* **25**: 652-660.

Government of the Bahamas. 2005. About the Bahamas. The Commonwealth of The Bahamas. Available: www.bahamas.gov.bs/bahamasweb2/home.nsf/vContentW/F1D7AA0803E7FFEF06256F02007F5607 (February 2009).

Granek, E. F., Madin, E. M. P., Brown, M. A., Figueira, W., Cameron, D. S., Hogan, Z., Kristianson, G., de Villiers, P., Williams, J. E., Post, J., Zahn, S., and Arlinghaus, R. 2008. Engaging recreational fishers in management and conservation: global case studies. *Conservation Biology* **22**: 1125-1134.

Grubich, J. R., Rice, A. N., and Westneat, M. W. 2008. Functional morphology of bite mechanics in the great barracuda (*Sphyraena barracuda*). *Zoology* **111**: 16-29.

Gustaveson, A. W. and Wydoski, R. S. 1991. Physiological response of largemouth bass to angling stress. *Transactions of the American Fisheries Society* **120**: 629-636.

Harper, D. E., Bohnsack, J. A. and Lockwood, B. R. 2000. Recreational fisheries in Biscayne National Park, Florida, 1976-1991. *Marine Fisheries Review* **62**: 8-26.

Hasley, L. G., Green, J. A., Wilson, R. P., and Frappel, P. B. 2009. Accelerometry to estimate energy expenditure during activity: best practice with data loggers. *Physiological and Biochemical Zoology* **82**: 396-404.

Heithaus, M. R., Frid, A., Wirsing, A. J., and Worm, B. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* **23**: 202-210.

Henderson, I. M. 2009. Optimising recreational harvests of blue cod: The effects of catch-and-release mortality and size selectivity. *Fisheries Research* **99**: 184-195.

Henry, N. A., Cooke, S. J., and Hanson, K. C. 2009. Consequences of lure retention on the behaviour and physiology of free-swimming smallmouth bass. *Fisheries Research* **100**: 178-182.

Heupel, M. R., Semmens, J. M., and Hobday, A. J. 2006a. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research* **57**: 1-13.

Heupel, M. R., Simpfendorfer, C. A., Collins, A. B., and Tyminski, J. P. 2006b. Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. *Environmental Biology of Fishes* **76**: 47-67.

Hofmann, G. E. and Gaines, S. D. 2008. New tools to meet new challenges: emerging technologies for managing marine ecosystems for resilience. *BioScience* **58**: 43-52.

Holdsworth, J. C., Sippel, T. J., and Block, B. A. 2009. Near real time satellite tracking of striped marlin (*Kajikia audax*) movements in the Pacific Ocean. *Marine Biology* **156**: 505-514.

Hoolihan, J. P. and Luo, J. 2007. Determining summer residence status and vertical habitat use of sailfish (*Istiophorus platypterus*) in the Arabian Gulf. *ICES Journal of Marine Science* **64**: 1791-1799.

Horn, M. H. 1998. Feeding and Digestion. *In* The Physiology of Fishes, 2nd ed. *Edited by* D.H. Evans. CRC Press, New York, NY. pp 43-64.

Houghton, J. D. R., Broderick, A. C., Godley, B. J., Metcalfe, J. D., and Hays, G. C. 2002. Diving behaviour during the interesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Marine Ecology Progress Series* **227**: 63-70.

Humston, R., Ault, J. S., Larkin, M. F., and Luo, J. 2005. Movements and site fidelity of the bonefish *Albula vulpes* in the northern Florida Keys determined by acoustic telemetry. *Marine Ecology Progress Series* **291**: 237-248.

Jolley, J. W. and Irby E. W. 1979. Survival of tagged and released Atlantic sailfish (*Istiophorus platypterus:* Istiophoridae) determined with acoustical telemetry. *Bulletin of Marine Science* **29**: 155-169.

Kieffer, J. D. 2000. Limits to exhaustive exercise in fish. *Comparative Biochemistry and Physiology A*, **126**: 161-179.

Kohler, N. E. and Turner, P. A. 2001. Shark tagging: a review of conventional methods and studies. *Environmental Biology of Fishes* **60**: 191-223.

Lehan, L. and Lewis, R. J. 2000. Ciguatera: recent advances but the risk remains. International *Journal of Food Microbiology* **61**: 91-125.

Lewis, N. D. 1986. Disease and development: ciguatera fish poisoning. *Social Science and Medicine* **23**: 983-993.

Lewis, R. 2001. The changing face of ciguatera. *Toxicon* **39**: 97-106

Lewis, R.J., Sellin, M., Poli, M. A., Norton, R. S., MacLeod, J. K., Sheil, M. M. 1991. Purification and characterization of ciguatoxins from moray eel (*Lycodontis javanicus, muraenidae*). *Toxicon* **29**: 1115-1127.

Lowe, T. E. and Wells, R. M. G. 1996. Primary and secondary stress responses to line capture in the blue mao mao. *Journal of Fish Biology* **49**: 287-300.

Lucas, M. C., Johnstone, A. D. F., and Priede, I. G. 1993. Use of physiological telemetry as a method of estimating metabolism of fish in the natural environment. *Transactions of the American Fisheries Society* **122**: 822-833.

Mahon, A. R., Senapati, S., Feder, J. L., Chang, H. C., and Lodge, D. M. 2009. Rapid detection of invasive species in ballast water using molecular methods. *Integrative and Comparative Biology* **49**: E105-E105.

Margenau, T. L. 2007. Effects of angling with a single-hook an dlive bait on muskellunge survival. *Environmental Biology of Fishes* **79**: 155-162.

Matta, J., Milad, M., Manger, R., and Tosteson, T. 1999. Heavy metals, lipid peroxidation, and ciguatera toxicity in the liver of the Caribbean barracuda (*Sphyraena barracuda*). *Biological Trace Element Research* **70**: 69-79.

Meka, J. M. 2004. The influence of hook type, angler experience, and fish size on injury rates and the duration of capture in an Alaskan catch-and-release rainbow trout fishery. *North American Journal of Fisheries Management* **24**: 1309-1321.

Meka, J. M. and McCormick, S. D. 2005. Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature. *Fisheries Research* **72**: 311-322.

Meyer, C. G. and Holland, K. N. 2005. Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. *Environmental Biology of Fishes* **73**: 201-210.

Meyer, C. G., Holland, K. N., and Papastamatiou, Y. P. 2007. Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of marine protected areas. *Marine Ecology Progress Series* **333**: 13-25.

Mike, A. and Cowx, I. G. 1996. A preliminary appraisal of the contribution of recreational fishing to the fisheries sector in north-west Trinidad. *Fisheries Management and Ecology* **3**: 219-228.

Morgan, J. D. and Iwama, G. K. 1997. Measurement of stressed states in the field. *In* Fish stress and health in aquaculture. *Edited by* G. K. Iwama, A. D. Pickering, J. P. Sumpter, and C. B. Schreck. Cambridge University Press, Cambridge, United Kingdom. pp 247-268.

Moss, S. A. 1977. Feeding mechanisms in sharks. *American Zoologist* **17**: 355-364.

Moyle, P. B. and Cech, J. J. 2002. Hydromineral Balance. *In* Fishes: an introduction to ichthyology. 4th ed. *Edited by* T. Ryu. Prentice-Hall, NJ. pp. 79-96.

Myers, R. A. and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* **423**: 280-283.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., and Peterson, C. H. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**: 1846-1850.

Muoneke, M. I. and Childress, W. M. 1994. Hooking mortality: a review for recreational fisheries. *Reviews in Fisheries Science* **2**: 123-156.

Nagelkerken, I. and van der Velde, G. 2004. Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds? *Marine Ecology Progress Series* **274**: 143-151.

O'Connor, N. E. and Bruno, J. F. 2007. Predatory fish loss affects the structure and functioning of a model marine food web. *Oikos* **116**: 2027–2038.

Ostrand, K. G., Siepker, M. J., and Cooke, S. J. 2006. Capture efficiencies of two hook types and associated injury and mortality of juvenile muskellunge angled with live baitfish. *North American Journal of Fisheries Management* **26**: 622-627.

Pastore, M. A. 2009. *Sphyraena intermedia* sp. nov. (Pisces: Sphyraenidae): a potential new species of barracuda identified from the central Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* **89**: 1299-1303.

Paterson, S. E. 1998. Group occurrence of great barracuda (*Sphyraena barracuda*) in the Turks and Caicos Islands. *Bulletin of Marine Science* **63**: 633-638.

Palumbi, S. R. 2004. Marine reserves and ocean neighbourhoods: the spatial scale of marine populations and their management. *Annual Reviews of Environment Resources* **29**: 31-68.

Pelletier, C., Hanson, K. C., and Cooke, S. J. 2007. Do catch-and-release guidelines from state and provincial fisheries agencies in North America conform to scientifically based best practices? *Environmental Management* **39**: 760-773.

Porter, H. T. and Motta, P. J. 2004. A comparison of strike and prey capture kinematics of three species of piscivorous fishes: Florida gar (*Lepisosteus platyrhincus*), redfin needlefish (*Strongylura notata*), and great barracuda (*Sphyraena barracuda*). *Marine Biology* **145**: 989-1000.

Prince, E. D., Ortiz, M., and Venizelos, A. 2002. A comparison of circle hook and "J" hook performance in recreational catch-and-release fisheries for billfish. *In* Catch-and-Release in Marine Recreational Fisheries. *Edited by* J. A. Lucy, and A. L. Studholme. American Fisheries Society Symposium 30, Bethesda, Maryland. pp. 121-134.

Randall, J. E. 1967. 'Food habits of reef fishes of the West Indies.' University of Miami Press: Coral Gables, FL.

Rim, Z. K., Samira, E., Mohamed-Nejmeddine, B., Mohamed, G., Abderrahmen, B. 2007. Age and growth of the Lessepsian Migrant *Sphyraena chrysotaenia* Klunzinger,1884 from the Gulf of Gabes (Eastern Mediterranean). *Reviews in Fisheries Science* **15**: 169-181.

Ropert-Coudert, Y. and Wilson, R. P. 2005. Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* **3**: 437-444.

Sadovy, Y. 2005. Trouble on the reef: the imperative for managing vulnerable and valuable fisheries. *Fish and Fisheries* **6**: 167-185.

Schmidt, T. W. 1989. Food habits, length-weight relationship and condition factor of young great barracuda, *Sphyraena barracuda* (Walbaum), from Florida Bay, Everglades National Park, Florida. *Bulletin of Marine Science* **44**: 163-170.

Schroeder, D. M. and Love, M. S. 2002. Recreational fishing and marine fish populations in California. *California Cooperative Oceanic Fisheries Investigations Reports* **43**: 182-190.

Schwalme, K. and MacKay, W. C. 1985. The influence of angling-induced exercise on the carbohydrate metabolism of northern pike (*Esox lucius L.*). *Journal of Comparative Physiology B* **156**: 67-75.

Serafy, J. E., Valle, M., Faunce, C. H., and Luo, J. 2007. Species-specific patterns of fish abundance and size along a subtropical mangrove shoreline: an application of the delta approach. *Bulletin of Marine Science* **80**: 609-624.

Sih, A., Bell, A. M., Johnson, J. C., and Ziemba, R. E. 2004. Behavioural syndromes: an integrative overview. *The Quarterly Review of Biology* **79:** 241-277.

Springer, V. G. and McErlean, A. J. 1961. Tagging of great barracuda *Sphyraena barracuda* (Walbaum). *Transactions of the American Fisheries Society* **90**: 497-500.

Suski, C. D., Cooke, S. J., Danylchuk, A. J., O'Connor, C. M., Gravel, M. A., Redpath, T., Hanson, K. C., Gingerich, A. J., Murchie, K. J., Danylchuk, S. E., Koppelman, J. B., and Goldberg, T. L. 2007. Physiological disturbance and recovery dynamics of bonefish (*Albula vulpes*), a tropical marine fish, in response to variable exercise and exposure to air. *Comparative Biochemistry and Physiology A* **148**: 664-673.

Swift A. E. B. and Swift, T. R. 1993. Ciguatera. *Clinical Toxicology* **31**: 1-29.

Thompson, J. A., Hughes, S. G., May, E. B., and Harrell, R. M. 2002. Effects of catch and release on physiological responses and acute mortality of striped bass. *In* Catch-and-Release in Marine Recreational Fisheries. *Edited by* J. A. Lucy and A. L. Studholme. American Fisheries Society Symposium 30, Bethesda, Maryland. pp 139-143.

Valentine, J. F. Kenneth, L. H. Jr., Blackmon, D., Goecker, M. E., Christian, J., Kroutil, R. M. Kirsch, K. D., Peterson, B. J., Beck, M., and Vanderklift, M. A. 2007. Food web interactions along seagrass-coral reef boundaries: effects of piscivore reductions on cross-habitat energy exchange. *Marine Ecology Progress Series* **333**: 37-50.

Venn Beecham, R., Small, B. C., and Minchew, C. D. 2006. Using portable lactate and glucose meters for catfish research: acceptable alternative to established laboratory methods? *North American Journal of Aquaculture* **68**: 291-295.

Verweij, M. C., Nagelkerken, I., de Graaff, D., Peeters, M., Bakker, E. J., and van der Velde, G. 2006. *Marine Ecology Progress Series* **306**: 257-268.

Villareal, T. A., Hanson, S., Qualia, S., Jester, E. L. E., Granade, H. R., and Dickey, R. W. 2007. Petroleum production platforms as sites for the expansion of ciguatera in the northwestern Gulf of Mexico. *Harmful Algae* **6**: 253-259.

Wearmouth, V. J. and Sims, D. W. 2009. Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging. *Journal of Experimental Marine Biology and Ecology* **380**: 77-87.

Webber, D. M., Boutilier, R. G., Kerr, S. R. (1998). Cardiac output as a predictor of metabolic rate in cod *Gadus morhua*. *The Journal of Experiemental Biology* **201**, 2779-2789.

Wells, R. M. G., McIntyre, R. H., Morgan, A. K., and Davie, P. S. 1986. Physiological stress responses in big gamefish after capture: observations on plasma chemistry and blood factors. *Comparative Biochemical Physiology A* **84**: 565-571.

Wells, R. M. G. and Pankhurst, N. W. 1999. Evaluation of simple instruments for the measurement of blood glucose and lactate, and plasma protein as stress indicators in fish. *Journal of the World Aquaculture Society* **30**: 276-284.

Whitney, N. M., Papastamatiou, Y. P., Holland, K. N., and Lowe, C. G. 2007. Use of an acceleration data logger to measure diel activity patterns in captive whitetip reef sharks, *Triaenodon obesus*. *Aquatic Living Resources* **20**: 299-305.

Wilson, R. P., Shepard, E. L. C., and Liebsch, N. 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* **4**: 139-146.

Williams, F. 1959. The barracudas (Genus Sphyraena) in British East African waters. *The Annals & Magazine of Natural History* **2**: 92-130.

Williams, F. 1965. Further notes on the biology of East African pelagic fishes of the families Carangidae and Sphyraenidae. *East African Agricultural and Forestry Journal*. **31**: 141-168.

Wilkie, M. P., Davidson, K., Brobbel, M. A., Kieffer, J. D., Booth, R. K., Bielak, A. T., and Tufts, B.L. 1996. Physiology and survival of wild Atlantic salmon following angling in warm summer waters. *Transactions of the American Fisheries Society* **125**:572-580.

Wilkie, M. P., Brobbel, M. A., Davidson, K., Forsyth, L., and Tufts, B. L. 1997. Influences of temperature upon the postexercise physiology of Atlantic salmon (*Salmon salar*). *Canadian Journal of Fisheries and Aquatics Science* **54**:503-511.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., and Butler, P. J. 2006a. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* **75**: 1081-1090.

Wilson, S. K., Wilson, D. T., Lamont, C., and Evans, M. 2006b. Identifying individual great barracuda *Sphyraena barracuda* using natural body marks. *Journal of Fish Biology* **69**: 928-932.

Wood, C. M. 1991. Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. *Journal of Experimental Biology* **160**: 285-308.

Yeiser, B. G., Heupel, M. R., and Simpfendorfer, C. A. 2008. Occurrence, home range and movement patterns of juvenile bull (*Carcharhinus leucas*) and lemon (*Negaprion*

brevirostris) sharks within a Florida estuary. *Marine and Freshwater Research* **59**: 489-501.

Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M., and Le Maho, Y. 2001. A new technique for monitoring the behaviour of free-ranging adélie penguins. *The Journal of Experimental Biology* **204**: 685-690.

Zar, J. H. 1999. Biostatistical Analysis, 4th edn. Prentice-Hall, Englewood Cliffs, New Jersey.

Zimmer, I., Wilson, R. P., Gilbert, C., Beaulieu, M., Ancel, A., and Plötz, J. 2008. Foraging movements of emperor penguins at Point Géologie, Antarctica. *Polar Biology* **31**: 229-243.

Appendix I: Spatial ecology and seasonal habitat utilization of great barracuda (*Sphyraena barracuda*) in the Bahamian Archipelago

Adult great barracuda are typically regarded as a nearshore reef predator in tropical and subtropical regions and are often observed in a range of habitat types, including nearshore reefs, tidal flats, and deeper pelagic environments (deSylva, 1963; Blaber, 1982; Paterson, 1998; Wilson et al., 2006). Presence in these areas may be a function of life history stage or environmental conditions, while seasonal migrations are presumed to be associated with spawning activity (May to October) or in response to variations in water temperatures (deSylva, 1963; Paterson, 1998). Basic tagging data have shown that larger individuals move greater distances and are more likely to inhabit offshore reefs (Springer and McErlean, 1961). In contrast, Wilson et al. (2006) found that larger barracuda exhibited a certain degree of site fidelity over a span of ten months near South Caicos. Great barracuda have also been documented to migrate over 1000 km across the Gulf of Mexico (Villareal et al., 2007) and one individual (carcass) was even found washed up on a beach in Nova Scotia, Canada (Balkwill et al., 2006). Thus, local residency, home range, and habitat use are poorly understood and warrant investigation. Apart from the fine scale behavioural study outlined in Chapter 2, there has not been sufficient quantification of barracuda movement and habitat use apart from two mark-recapture studies (Springer and McErlean, 1961; Villareal et al., 2007) and two behavioural studies based on underwater visual observations (Paterson, 1998; Wilson et al., 2006). The objective of this study is to quantify the temporal and seasonal horizontal movements and habitat use of great barracuda within an acoustic telemetry array in The Bahamas.

Between February 2007 and December 2008, 42 barracuda were implanted with acoustic telemetry transmitters (V13, V16, V9AP, Vemco/Amirix systems, Shad Bay, NS) and released within the confines of an established VR2 acoustic receiver array near Cape Eleuthera, The Bahamas (for surgery and tagging procedures, refer to Chapter 2 of this thesis). Barracuda were monitored from February 20, 2007 to October 27, 2009. Tagged barracuda ranged in size from 60 – 125 cm, TL (Table I-1). Ten fish were detected within the array for less than 24 hr, while other fish were detected on more than 400 days over the course of the study period (Table I-1). To estimate home range tendencies, I calculated median distance travelled (MDT, median distance travelled from receiver with greatest proportion of hits to all other receivers visited) and minimum linear distance (MLD, straight-line distance between the two farthest receivers on which the fish was detected). Barracuda exhibited MDT values that ranged from 449 – 7824 m and MLD values ranging 898 – 15950 m (not including fish that were detected for less than 24 hr, Table I-2). Some barracuda were detected by up to 21 receiver stations in a single day and the mean number of receivers detected on per day ranged from 1.0 ± 0.0 to 5.0 ± 0.2 receivers (Table I-2). Receiver stations were categorized into four habitat types, coastal, creek (including tidal flats), mosaic, and shelf. The three receivers with the most detections per days deployed were 4th Hole 1 (coastal), 4th Hole 2 (mosaic), and Noname Harbour (coastal; Table I-3). The barracuda in this study, at times, appear to move outside of the detection zone of the array for both shorter and longer time periods before returning, while some fish left and did not return again (Figure I-1). These movements out of, and then back into the array are particularly evident in 2008, where many of the fish were not detected between June and August, and could be associated with spawning

behaviour or migration to deeper habitats that are less susceptible to broad ranging water temperature fluctuations characteristic of coastal habitats during the summer months. Overall, the spatial tendencies of individual barracuda are variable, as some fish are fairly resident (i.e. #2606 was at large for 631 days and highly resident in coastal and creek habitats near Broad Creek, Table I-1 and I-2), while others are more transient (i.e. #2608 was tagged in February 2007 and was not detected again until September 2009, when the fish was detected six times over a two day period).

These summary statistics and preliminary results form the basis for further analysis of the spatial ecology of great barracuda. I will continue to analyse the data for patterns in seasonal and daily movement patterns across habitat types and examine potential associations with biological factors such as fish size. This study will contribute to increased ecological knowledge of this species, contribute to coastal marine management initiatives, and may be useful for novel applications such as determining local biotoxin distribution (see Appendix II for ciguatera fish poisoning applications).

Table I-1. Summary data for *S. barracuda* tagged with acoustic telemetry transmitters (n = 42) off the coast of Cape Eleuthera, The Bahamas between February 2007 and October 2009.

Tag ID	Date Tagged	TL (cm)	Total # Detections	# Days at large	# Days detected	% Time detected in array
930	Feb-20-2007	61	2988	348	50	14
2608	Feb-21-2007	96	6	942	2	0
2606	April-14-2007	125	63320	631	334	53
935	Dec-5-2007	70	0	1	0	0
2380	Dec-6-2007	84	1344	480	97	20
2607	Dec-6-2007	90	698	116	35	30
2610	Dec-6-2007	106	2756	454	134	30
2609	Dec-8-2007	91	13297	689	386	56
10010	Feb-14-2008	88	1999	468	125	27
9525	Feb-15-2008	97	2474	620	162	26
10009	Feb-15-2008	69	0	1	0	0
9526	Feb-15-2008	92	736	613	93	15
9524	Feb-16-2008	106	74174	619	410	66
9527	Feb-16-2008	109	4495	464	60	13
9533	Feb-17-2008	91	2406	44	38	86
9531	Feb-17-2008	86	0	0	0	0
9530	Feb-17-2008	77	20	33	4	12
9532	Feb-17-2008	88	0	0	0	0
9528	Feb-17-2008	101	0	1	0	0
10011	Feb-17-2008	72	53	5	4	80
10012	Feb-17-2008	75	9230	617	335	54
938	Feb-17-2008	62	3810	618	277	45
79	Dec-10-2008	101	161	8	6	75

222	Dec-12-2008	120	843	9	9	100
228	Dec-12-2008	94	355	3	5	167
152	Dec-12-2008	83	823	115	77	67
9523	Dec-13-2008	96	4568	318	49	15
204	Dec-13-2008	62	129	104	19	18
9529	Dec-13-2008	80	234	167	35	21
80	Dec-13-2008	94	2226	303	20	7
150	Dec-13-2008	79	88	3	3	100
148	Dec-13-2008	81	30	116	7	6
1440	Dec-13-2008	103	0	1	0	0
220	Dec-13-2008	92	2297	74	46	62
206	Dec-13-2008	79	1	1	1	100
1441	Dec-13-2008	99	13761	316	101	32
224	Dec-14-2008	79	151	3	1	33
202	Dec-14-2008	60	0	1	1	100
226	Dec-14-2008	99	0	1	0	0
9522	Dec-15-2008	112	0	1	0	0
254	Dec-15-2008	81	2447	21	18	86
208	Dec-15-2008	85.5	67	3	3	100

Table I-2. Summary of movement data for individual *S. barracuda* detected within the acoustic telemetry array between February 2007 and October 2009. Median distance travelled (MDT), minimum linear distance (MLD), minimum # of receivers visited daily, maximum # receivers visited daily, and mean # receivers visited daily (± SE) are reported for each fish.

Tag ID	# receivers	Receiver with highest # detections	MDT (m)	MLD (m)	Min # receivers daily	Max # receivers daily	Mean # receivers daily ± SE
930	19	WMB Out	1400	9005	1	18	2.58 ± 0.61
2608	1	7c	0	0	1	1	1.00 ± 0.00
2606	41	WMB Out	4634	15950	1	21	5.32 ± 0.20
935	0	n/a	0	0	0	0	0.00 ± 0.00
2380	8	W5 (Cage)	2487	5931	1	4	1.18 ± 0.05
2607	15	M6	2821	5931	1	8	2.58 ± 0.28
2610	8	M6	2291	3870	1	4	1.76 ± 0.07
2609	67	M6	3660	11849	1	18	2.07 ± 0.09
10010	29	West of IS Off	2602	15595	1	8	1.72 ± 0.10
9525	23	10a	2197	10277	1	6	2.29 ± 0.10
10009	0	n/a	0	0	0	0	0.00 ± 0.00
9526	45	M6	3660	14119	1	16	1.83 ± 0.21
9524	65	Noname	2154	13108	1	14	4.65 ± 0.13
9527	14	Poison In	7824	14703	1	9	1.98 ± 0.15
9533	3	W5 (Cage)	3037	5320	1	2	1.11 ± 0.05
9531	0	n/a	0	0	0	0	0.00
9530	3	W4	1420	2457	1	2	1.33 ± 0.29
9532	0	n/a	0	0	0	0	0.00
9528	0	n/a	0	0	0	0	0.00
10011	6	W4	2286	4801	1	5	3.00 ± 1.00

10012	43	W4	1561	9512	1	8	1.69 ± 0.06
938	33	W3	1455	8102	1	5	1.28 ± 0.04
79	9	W5 (Cage)	1926	5037	1	5	2.50 ± 0.67
222	5	WZ3 (Chub)	1870	2724	1	5	2.89 ± 0.35
228	7	MarNet SE	449	1331	1	5	3.25 ± 0.76
152	14	Cape Net 3	1173	2897	1	6	1.59 ± 0.11
9523	3	MarNet SE	563	898	1	2	1.10 ± 0.04
204	5	M4	1621	5318	1	1	1.00 ± 0.00
9529	1	SW2	0	0	1	1	1.00 ± 0.00
80	5	WZ1 (Deals)	1577	5711	1	3	1.15 ± 0.11
150	6	MarNet SE	449	1331	3	5	3.67 ± 0.67
148	1	M6	0	0	1	1	1.00 ± 0.00
1440	0	n/a	0	0	0	0	0.00
220	12	W5 (Cage)	2477	5949	1	6	1.98 ± 0.19
206	1	Kemps Out Mouth	0	0	1	1	1.00 ± 0.00
1441	37	4th Hole 2	1558	7384	1	10	4.71 ± 0.27
224	3	West of IS Off	4989	5729	1	3	2.00 ± 1.41
202	0	n/a	0	0	0	0	0.00
226	0	n/a	0	0	0	0	0.00
9522	0	n/a	0	0	0	0	0.00
254	20	M1	1392	4395	1	14	7.32 ± 1.00
208	10	MarNet SE	838	3730	1	8	4.67 ± 2.03

Table I-3. Summary of VR2 receiver stations (n = 105) deployed between 2007 and 2009 off Cape Eleuthera, The Bahamas. Habitat type, UTM coordinates and total # detections/days deployed are provided for each station.

Habitat type	Station name	Date deployed	X-Easting	Y-Northing	Total days deployed	# Detections per days deployed
Coastal	Kemps Off	20-Feb-07	18368465	2745239	626	3.49
	Red Point In	20-Feb-07	18371426	2743032	836	2.72
	Red Point Off	20-Feb-07	18371599	2743434	688	1.84
	West of IS In	20-Feb-07	18364898	2747390	980	0.23
	West of IS Off	20-Feb-07	18365028	2748038	836	1.61
	West Palm Off	20-Feb-07	18367891	2746016	836	3.20
	WMB Off	20-Feb-07	18369678	2744547	626	3.67
	E of EMB Off	2-Dec-07	18370431	2743793	342	3.43
	Marina Mouth	2-Dec-07	18364062	2747636	550	0.09
	M1	2-Dec-07	18364106	2748277	550	2.14
	Cow Pt	14-Jan-08	18365891	2747179	33	0.36
	In Marina	14-Jan-08	18364357	2747448	456	0.02
	MarNet NE	19-Feb-08	18363967	2747878	355	2.61
	MarNet NW	19-Feb-08	18363719	2747777	355	4.75
	MarNet SE	19-Feb-08	18363905	2747368	355	16.01
	MarNet SW	19-Feb-08	18363723	2747506	355	4.18
	Cape Net 1	8-Nov-08	18363523	2746627	208	38.03
	Noname	28-Nov-08	18364110	2746555	333	78.52
	4th Hole 1	8-Feb-09	18363900	2746137	116	190.88
	GuardHouse Cut	14-Apr-09	18364760	2747178	51	0.00
	4a	6-Jun-09	18363952	2744200	143	0.36
	5b	6-Jun-09	18363854	2745377	143	13.57

	6c	6-Jun-09	18363717	2746563	143	57.45
Creek	Broad Backwaters	20-Feb-07	18369719	2743300	281	1.59
	EMB In	20-Feb-07	18369525	2743509	626	3.09
	Kemps Backwaters	20-Feb-07	18368163	2744388	281	0.00
	Kemps In Mouth	20-Feb-07	18368118	2744691	836	0.29
	Kemps Out Mouth	20-Feb-07	18368248	2744887	835	3.69
	Page Mouth	20-Feb-07	18367203	2745362	626	0.06
	Poison In	20-Feb-07	18376913	2742032	980	4.45
	Poison Mid	20-Feb-07	18376734	2742269	836	4.27
	Poison Off	20-Feb-07	18376416	2742584	281	2.99
	West Palm In	20-Feb-07	18367592	2745659	856	3.84
	WMB Inshore	20-Feb-07	18369392	2744189	836	12.62
	WMB Inside	20-Feb-07	18369297	2743602	626	2.77
	WMB Outside	20-Feb-07	18369031	2743970	836	24.19
	E of EMB In	2-Dec-07	18370258	2743423	342	7.24
	EMB Out	2-Dec-07	18369630	2743734	551	9.94
	Broad In	6-Jun-09	18369486	2743451	143	0.79
Mosaic	E1	2-Dec-07	18365205	2748591	550	1.42
	E 2	2-Dec-07	18365418	2749163	550	0.04
	E3	2-Dec-07	18365602	2749890	550	0.24
	E4	2-Dec-07	18365841	2750444	550	0.23
	E5	2-Dec-07	18366026	2751013	550	0.58
	M2	2-Dec-07	18363716	2748716	550	0.09
	M3	2-Dec-07	18363306	2749177	550	0.28
	M4	2-Dec-07	18362880	2749613	550	5.17
	M5	2-Dec-07	18362467	2750030	550	3.90
	M6	2-Dec-07	18362001	2750409	550	9.29
	W1	2-Dec-07	18363344	2747693	550	1.27

	W2	2-Dec-07	18362763	2747876	550	0.12
	W3	2-Dec-07	18362168	2748033	550	6.49
	W4	2-Dec-07	18361534	2748166	550	13.83
	SW1	24-Jun-08	18363335	2747118	345	2.92
	SW2	24-Jun-08	18362947	2746784	345	4.01
	Cape Net 2	8-Nov-08	18362603	2747144	208	1.21
	Cape Net 3	8-Nov-08	18362383	2747592	208	1.42
	Cape Net 5	8-Nov-08	18362887	2748821	208	0.65
	Cape Net 6	8-Nov-08	18363949	2749173	103	0.03
	Cape Net 7	8-Nov-08	18364590	2749169	82	0.17
	Cape Net 4	10-Jan-09	18362513	2748402	145	0.05
	4th Hole 2	8-Feb-09	18363431	2745976	116	92.72
	4th Hole 3	8-Feb-09	18363062	2745818	116	1.81
	4th Hole 4	8-Feb-09	18363073	2746382	116	14.75
	4.5	6-Jun-09	18363961	2744821	143	3.41
	5.5	6-Jun-09	18363364	2745608	143	4.51
	10b	6-Jun-09	18360735	2749407	143	11.38
	6b	6-Jun-09	18363245	2746165	143	6.11
	7b	6-Jun-09	18362520	2746883	143	0.15
	7c	6-Jun-09	18363012	2747273	143	0.29
	7d	6-Jun-09	18363476	2747690	143	0.16
	8b	6-Jun-09	18361879	2747624	143	4.80
	8c	6-Jun-09	18362333	2748016	143	0.25
	8d	6-Jun-09	18362793	2748401	143	0.31
	9b	6-Jun-09	18361190	2748397	143	1.71
	9c	6-Jun-09	18361665	2748883	143	1.55
	9d	6-Jun-09	18362115	2749169	143	0.80
Shelf	WZ2 (Bamboo)	2-Dec-07	18364258	2744213	550	0.26

W5 (Cage)	14-Jan-08	18360783	2748241	507	12.54
WZ1 (Deals)	8-Jun-08	18365367	2741959	361	6.40
WZ3 (Chub)	8-Jun-08	18362464	2746422	361	3.48
WZ5	8-Jun-08	18359289	2750246	361	1.17
WZ6	8-Jun-08	18357327	2751850	361	0.00
WZ7	8-Jun-08	18354841	2752852	361	0.00
Cage Deep	2-Jul-08	18360637	2748227	337	1.01
WZ 3.5	29-Jul-08	18361577	2747322	310	5.36
WZ 2.5	19-Feb-09	18362779	2746128	105	0.52
WZ 3.25	19-Feb-09	18361966	2746767	105	0.35
WZ 3.75	19-Feb-09	18361154	2747803	62	2.34
1.5	6-Jun-09	18365292	2742127	143	0.59
2.5	6-Jun-09	18364826	2743043	143	0.49
3.5	6-Jun-09	18364298	2743878	143	0.33
6.5	6-Jun-09	18362677	2746335	143	0.09
7.5	6-Jun-09	18361984	2747076	143	0.03
8.5	6-Jun-09	18361265	2747799	143	0.97
9.5	6-Jun-09	18360768	2748717	143	9.53
10a	6-Jun-09	18360255	2748960	143	23.53
1a	6-Jun-09	18365407	2741528	143	0.59
2a	6-Jun-09	18364954	2742451	143	0.62
3a	6-Jun-09	18364526	2743401	143	0.43
5a	6-Jun-09	18363426	2745039	143	0.85
6a	6-Jun-09	18362807	2745775	143	0.21
7a	6-Jun-09	18362072	2746515	143	0.06
8a	6-Jun-09	18361414	2747218	143	0.36
9a	6-Jun-09	18360730	2748029	143	0.13

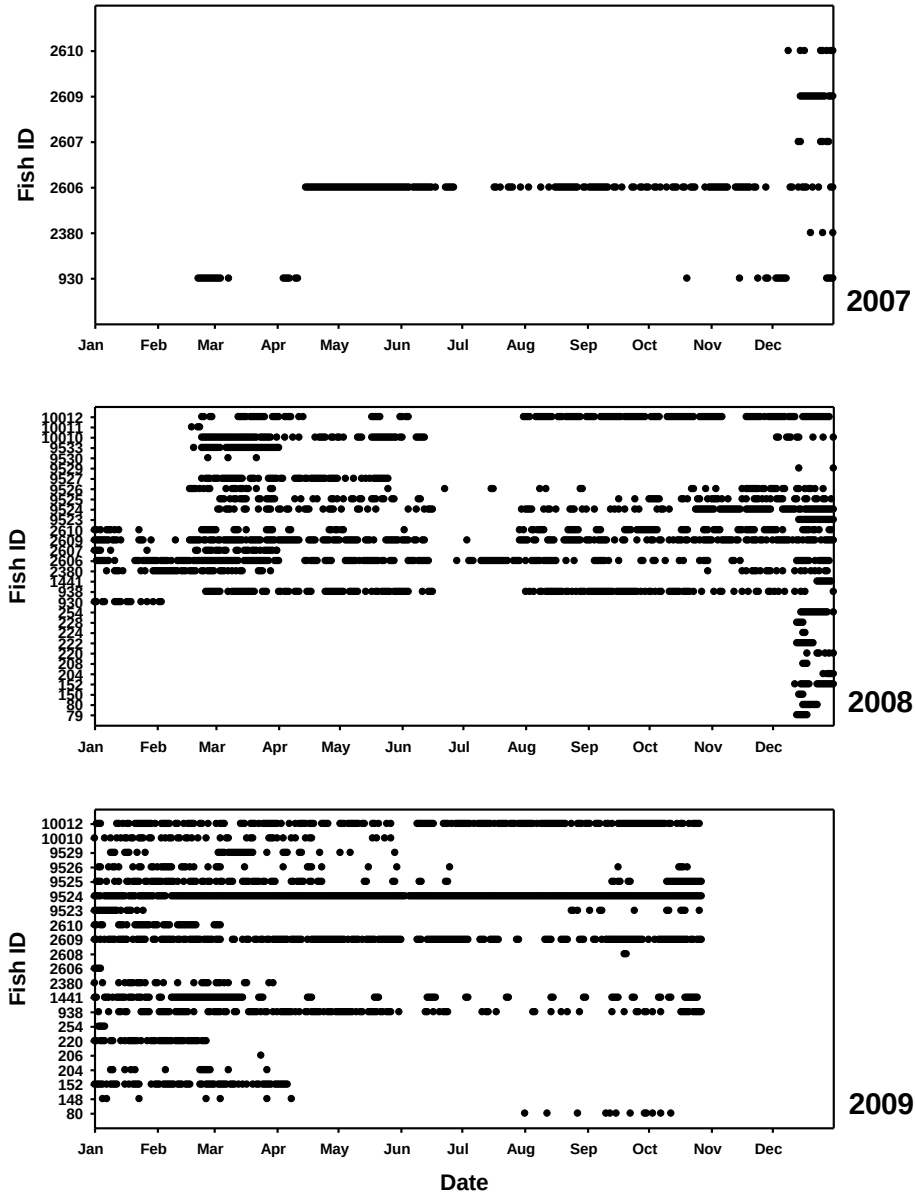

Figure I-1. Presence-absence data for each tagged S. barracuda detected within the VR2/VR2W acoustic telemetry array over three years (2007-2009) off the coast of Cape Eleuthera, The Bahamas. Each data point represents a day during which a barracuda was detected at any location within the array.

Appendix II: Linking ciguatera to spatial ecology: a novel approach to examining the distribution of biotoxin levels in an apex predatory reef fish, the great barracuda.

Ciguatera fish poisoning (CFP) is a type of marine fish poisoning caused by the human consumption of reef fish contaminated with ciguatoxin (CTX), that occurs in tropical and subtropical regions of the Caribbean Sea, Pacific Ocean, and Indian Ocean (Lewis, 2001). It is estimated that more than 25,000 cases of ciguatera fish poisoning are reported worldwide every year (Lewis, 2001) and has the potential to cause severe and potentially long-lasting human health effects (Swift and Swift, 1993; Lewis, 2001; Bienfang et al., 2008). CTX originates in a dinoflagellate (*Gambierdiscus toxicus*) often found in warm, shallow waters in association with various algae species, or in recently disturbed or altered marine habitats (Lewis, 1986; Bienfang et al., 2008). Ciguatoxin produced by *G. toxicus* biomagnifies through marine food chains reaching peak concentrations in apex predators such as great barracuda (*Sphyraena barracuda*), snappers (*Lutjanus* spp.), and jacks (*Caranx* spp.), with concentrations of ciguatoxin varying between species depending upon their trophic level (Lewis et al., 1991; Bienfang et al., 2008). The toxin is most concentrated in tissues such as the liver and viscera (Swift and Swift, 1993; Bienfang et al., 2008), however, muscle of the fish is eaten in larger quantities by humans and therefore presents more serious risks to human health (Lehane and Lewis, 2000). Ciguatera symptoms include a suite of gastrointestinal distress (predominant in the Caribbean), neurological disturbances (predominant in the Pacific Ocean), and occasional cardiovascular problems and hallucinations (predominant

in the Indian Ocean; Gillespie, 1986). These differences are a result of different congeners of the toxin found across various geographic regions (Lewis, 2001).

There are many challenges associated with the prediction, diagnosis, and treatment of ciguatera poisoning, especially within island communities that are most affected due to reliance on reef fish as a main protein source (Lewis, 2001). As there is often a lack of knowledge concerning the presence of ciguatoxin in fish, as well as the origin of a particular fish at the time of sale or ingestion, there is currently no readily available information that can be used to prevent consumption of contaminated fish leading to CFP. Very little is known about the behavioural ecology (i.e. spatial ecology and foraging habits) of great barracuda (could be subject to biomagnification of toxins, due to its role as a nearshore apex predator) and only one study has attempted to link spatial distribution of barracuda to the occurrence of ciguatera, however, the results were somewhat ambiguous (Villareal et al., 2007). Currently, there has not been any biotelemetry studies conducted on fish contaminated with ciguatoxin. Monitoring the behaviour of barracuda in the wild and, at the same time, determining if these particular fish have significant concentrations of ciguatoxin in their tissues will help improve the understanding of the occurrence and origin of ciguatera so that more rigorous prevention measures might be put into place. Various anecdotal reports have lead to the belief that barracuda caught in certain areas near Eleuthera are unsafe for consumption, whereas fish captured in other areas are considered safe. The objective of the study is to link the spatial ecology of the great barracuda to the occurrence and severity of ciguatera poisoning.

Whole blood samples were collected from all barracuda that were implanted with acoustic telemetry transmitters (see Chapter 2 and Appendix I for description of tracking and surgical procedures) for quantification of CTX. Due to the invasive nature of the surgical procedures required to extract samples from internal organs, I was concerned that taking additional tissue samples from telemetered fish would negatively influence survival. Therefore, 10 barracuda were lethally sampled to obtain tissue-specific (specifically liver and muscle) measures of ciguatoxin levels. All tissue samples were sent to the Marine Biotoxins Program at the NOAA Center for Coastal Environmental Health and Biomolecular Research specializes in biomonitoring methods for toxins and blood diagnostic tests for ciguatera.

Our results show that 92% of the liver samples tested positive for ciguatoxin, ranging between 5.0 - 168 pg ml^{-1} with a mean value of 32 pg ml^{-1} and 67% of muscle samples tested positive, ranging from 2.5 to 100 pg ml^{-1} with a mean value of 19 pg ml^{-1} (Table II-1, Figure II-1). Although blood is often tested for CTX levels, liver (Dechraoui et al., 2005), muscle (Colman et al., 2004), and gonads (Colman et al., 2004) have traditionally been regarded as having the highest concentrations of CTX and therefore the most suitable tissues for detecting ciguatoxin using the N2A cell based assay. However, my results show that blood is, in fact, comparable to the other tissues since 60% of barracuda blood samples contained detectable amounts of CTX, ranging from 3 to 211 pg ml^{-1} and had a mean value of 25 pg ml^{-1} (Table II-1, Figure II-1). The maximum concentration across all tissue types was 211.74 pg ml^{-1} in a blood sample taken from fish U70 (Figure II-2) and blood and liver concentrations were correlated ($P < 0.042$). Comparable detection of CTX concentrations indicates that blood may be an indicator of

recent exposure and accumulation to ciguatoxin. Twelve barracuda tagged with acoustic telemetry transmitters were also found to be ciguateric (Table II-2). The information gained from the movement data will provide insight into the residency and habitat use for each of these fish. This is the first report of CTX detection from a non-lethal sample, which will allow for future low-impact biosampling for the assessment of the spatial distribution of ciguatoxin and aid in identifying high-risk areas. Through further telemetry analyses and collaboration with Dr. John Ramsdell and Dr. Marie-Yasmine Bottein Dechraoui (NOAA Marine Biotoxins Program), I will be able to better understand the link between barracuda spatial ecology and the presence of ciguatera fish poisoning.

Table II-1. Summary of C-CTX-1 equivalents concentrations (pg ml^{-1}) for *S. barracuda* captured near Cape Eleuthera, The Bahamas between August 2008 – January 2009. Mean ± SE toxin concentration values are presented for liver, muscle, and blood where applicable (<dl: below detection limit) as detected by N2A bioassay.

Fish ID	Date	TL (cm)	Liver Mean ± SE (pg ml^{-1})	Muscle Mean ± SE (pg ml^{-1})	Blood Mean ± SE (pg ml^{-1})	Tagged?
U22	Aug-23-2008	74	N/A	21.74 ± 1.76	9.85 ± 1.7	N
U23	Aug-26-2008	86	N/A	N/A	16.36 ± 1.38	N
U24	Aug-26-2008	66	N/A	N/A	<dl	N
U25	Aug-26-2008	109	N/A	N/A	15 ± 0.84	N
U26	Aug-26-2008	92	N/A	N/A	<dl	N
U35	Aug-26-2008	84	N/A	98.83 ± 14.09	N/A	N
U37	Aug-25-2008	98	41.05 ± 7.46	11.43 ± 0.65	9.7 ± 1.63	N
U38	Dec-10-2008	101	N/A	N/A	<dl	Y
U40	Dec-12-2008	94	N/A	N/A	<dl	Y
U41	Dec-12-2008	83	N/A	N/A	<dl	Y
U42	Dec-12-2008	96	N/A	N/A	5.87 ± 0.33	Y
U43	Dec-13-2008	62	N/A	N/A	N/A	Y
U44	Dec-13-2008	80	N/A	N/A	14.87 ± 1.42	Y
U45	Dec-13-2008	94	N/A	N/A	12.7 ± 0.79	Y
U46	Dec-13-2008	79	N/A	N/A	9.84 ± 2.5	Y
U47	Dec-13-2008	81	N/A	N/A	15.96 ± 3.96	Y
U49	Dec-13-2008	92	N/A	N/A	<dl	Y
U50	Dec-13-2008	79	N/A	N/A	7.65 ± 1.3	Y

U51	Dec-13-2008	99	N/A	N/A	48.89 ± 0.48	Y
U52	Dec-13-2008	79	N/A	N/A	<dl	Y
U53	Dec-13-2008	60	N/A	N/A	<dl	Y
U54	Dec-14-2008	99	N/A	N/A	8.48 ± 1.32	Y
U57	Dec-14-2008	85.5	N/A	N/A	24.83 ± 2.81	Y
U58	Dec-14-2008	N/A	<dl	<dl	N/A	Eaten by shark
U69	Dec-15-2008	84	23.55 ± 3.09	2.6 ± 0.53	18.47 ± 4.16	N
U70	Dec-15-2008	94	27.86 ± 1.51	5.62 ± 1.43	211.74 ± 109.31	N
U71	Dec-15-2008	72	21.58 ± 4.17	<dl	6.6 ± 0.1	N
U72	Dec-13-2008	68.5	26.69 ± 1.93	2.51 ± 0.25	14.8 ± 3.32	N
U73	Jan-14-2009	80	5.22 ± 0.84	<dl	<dl	N
U74	Jan-14-2009	103	5.6 ± 0.59	<dl	<dl	N
U75	Jan-18-2009	85	4.96 ± 1.07	5.54 ± 1.42	<dl	N
U76	Jan-18-2009	71	6.25 ± 1.19	4.2 ± 0.35	3.07 ± 0.84	N
U77	Jan-22-2009	N/A	18.22 ± 2.89	N/A	N/A	From fisherman
U78	Jan-22-2009	N/A	167.77 ± 26.72	N/A	N/A	From fisherman

Table II-2. Behavioural summary of *S. barracuda* tagged with acoustic telemetry transmitters Dec 13-15, 2008 off the coast of Cape Eleuthera, The Bahamas. Only tagged barracuda with detectible (or <dl: below detection limit) concentrations of C-CTX-1 equivalents in their blood are included.

Fish ID	Tag ID	Date tagged	Mean CTX ± SE (pg ml^{-1})	Capture location	Total Detections	# Days at large	# Days detected	% Time in array
U42	9523	Dec-13-2008	5.87 ± 0.33	N/A	4568	318	49	15
U44	9529	Dec-13-2008	14.87 ± 1.42	W4	234	167	35	21
U45	80	Dec-13-2008	12.70 ± 0.79	W4	2226	303	20	7
U46	150	Dec-13-2008	9.84 ± 2.50	W4	88	3	3	100
U47	148	Dec-13-2008	15.96 ± 3.96	N/A	30	116	7	6
U49	220	Dec-13-2008	<dl	M4	2297	74	46	62
U50	206	Dec-13-2008	7.65 ± 1.30	WZ3 (Chub)	1	1	1	100
U51	1441	Dec-13-2008	48.89 ± 0.48	Tunnel Rock	13761	316	101	32
U52	224	Dec-14-2008	<dl	W5	151	3	1	33
U53	202	Dec-14-2008	<dl	WZ2 (Bamboo)	0	1	1	100
U54	226	Dec-14-2008	8.48 ± 1.32	4th Hole	0	1	0	0
U57	208	Dec-15-2008	24.83 ± 2.81	Schooner Keys	67	3	3	100

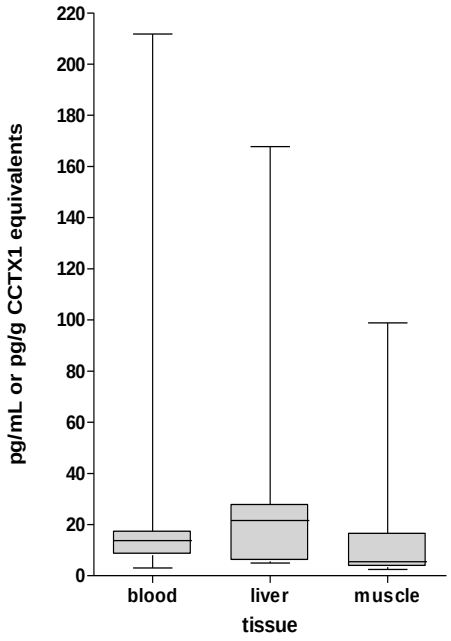

Figure II-1. Mean C-CTX-1 equivalents (pg ml^{-1}) for n = 34 *S. barracuda* blood, liver, and muscle samples analysed by N2A bioassay. Figure courtesy of M.Y. Bottein Dechraoui, NOAA Marine Biotoxins Program, Charleston, SC

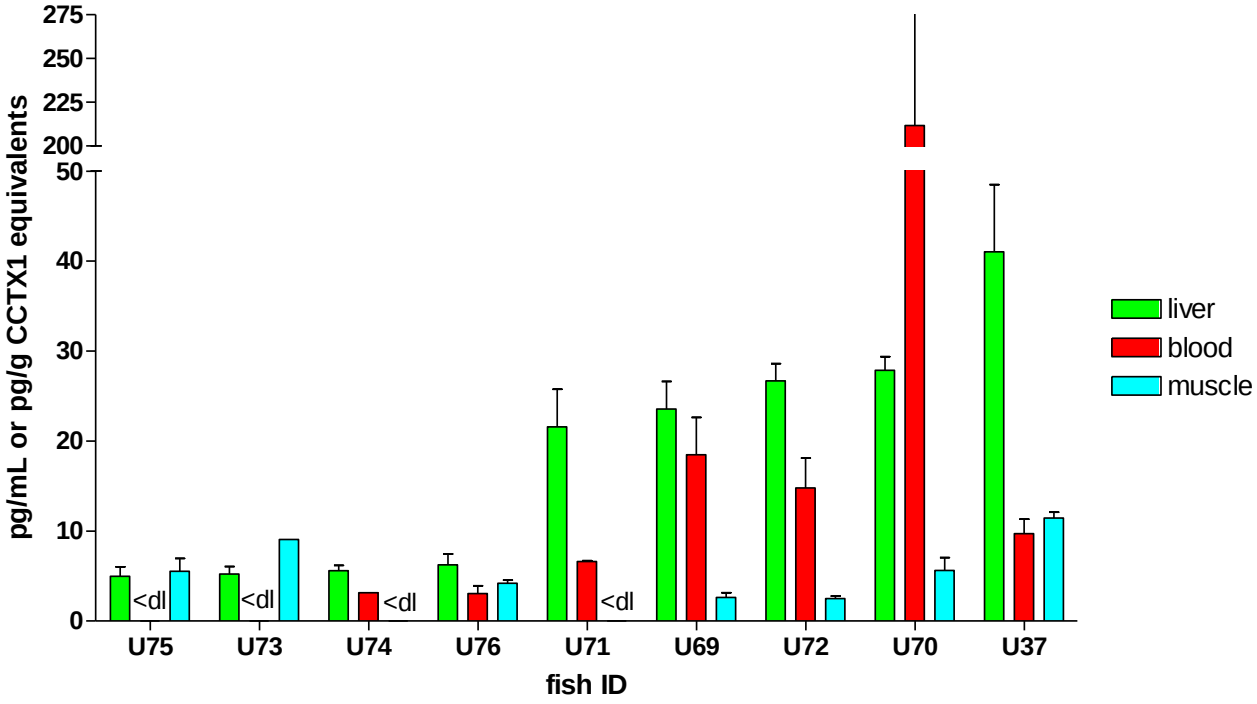

Figure II-2. C-CTX-1 (or equivalents) concentrations from a subset of *S. barracuda* blood, liver, and muscle samples analysed by N2A bioassay. Figure courtesy of M.Y. Bottein Dechraoui, NOAA Marine Biotoxins Program, Charleston, SC.