The spatial ecology of *Albula glossodonta* in the St. Joseph Atoll, Seychelles

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By

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Abstract

Bonefish (*Albula* spp.) support valuable recreational and artisanal fisheries worldwide. Declining stocks have been reported at multiple localities, potentially jeopardising numerous multimillion-dollar industries. In particular, tourism generated through bonefish fly fishing contributes considerably to the economies of many isolated tropical islands and atolls. However, despite their economic value, little is known about bonefish in the Indian Ocean. This study aimed to contribute to the understanding of bonefish ecology in the Indian Ocean by (1) reviewing the bonefish literature to identify knowledge gaps; (2) evaluating the post-release survival of acoustically tagged bonefish and; (3) quantifying the spatial and temporal movements of bonefish at a near-pristine and predator rich atoll in the Seychelles. A review of published literature on bonefish indicated that despite considerable biological and ecological research in the Pacific and Atlantic oceans, virtually no research has been conducted in the Indian Ocean. To help address this research gap, an acoustic telemetry study was initiated at the remote St. Joseph Atoll, within an existing array of 88 automated data-logging acoustic receivers. Thirty *Albula glossodonta* were surgically implanted with Vemco V13 acoustic transmitters in May 2015 and tracked for a period of one year. Only 10% of the tagged bonefish were detected for more than two weeks. A comparison of the final 100 hours of movement data from fish that were detected for less than two weeks to fish detected for longer periods revealed distinct differences. These included differences in area use patterns and significant differences in the average daily distance moved, speed of movement and residency index. This suggested that mortality in the form of post-release predation was high (90%) with tagged fish detected for less than two weeks being preyed upon by sharks. The three surviving bonefish were tracked for 210 to 367 days. These individuals remained in the atoll and showed high use of the marginal habitats between the shallow sand flats and the deeper lagoon. Water temperature, diel cycle and tide were significant predictors of bonefish presence in the lagoon. The high post-release predation of bonefish has implications for the management of this and other *Albula* species. Despite these fisheries being catch-and-release, bonefish fishing may be unsustainable due to the high post-release mortality, particularly in areas that are rich in predators. Therefore, protected areas or limitations on fishing effort need to be considered.

Keywords: Acoustic telemetry; catch-and-release; Indian Ocean; marine; predation bias

Contents

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Dedicated to William John Moxham (dad)

I wish I could have had the chance to share with you what I chose to study and see that brilliant mind of yours ticking away at some new crazy idea.

Chapter 1

General introduction

Photo Credit: Rainer von Brandis, Save Our Seas Foundation, D'Arros Research Centre

"In the end, we will conserve only what we love, we will love only what we understand, and will understand only what we are taught" ~ Baba Dioum

Bonefish (*Albula* spp.) occur around the world in tropical and subtropical habitats (Colborn *et al.* 2001). Due to the morphological similarities found within the *Albula* genus, it was believed that only two species of bonefish occurred throughout the world (Shaklee and Tamaru 1981). Consequently, the majority of the research to date has been based on a single species (*Albula vulpes*) and limited to the Atlantic Ocean (Murchie *et al.* 2013; Wallace 2015). However, recent studies have identified 12 different species within the *Albula* genus, many of which are poorly understood (Hidaka *et al.* 2008; Wallace and Tringali 2016). Therefore, further research into the *Albula* genus is recommended.

Bonefish are an environmentally and economically valuable species that require conservation. Environmentally, bonefish act as an indicator species (Larkin 2011). Indicator species are used to monitor the state of an ecosystem (Kremen 1992; Ogden *et al.* 2014). The presence of a viable bonefish population indicates a balance in the food chain between benthic organisms and predator species (Murchie *et al.* 2010; Adams *et al.* 2014). Economically, bonefish support valuable recreational fisheries (Danylchuk *et al.* 2008a, 2008b). Their agility, strength and speed has given bonefish the reputation as a highly prized sport fish (Murchie *et al.* 2009). Anglers targeting bonefish generally practice catch-and-release (Danylchuk *et al.* 2011a), a practice that is regarded as a profitable and sustainable form of ecotourism (Humston *et al.* 2005). Ecotourism aims to create a sustainable tourism industry, which focuses on wildlife and conservation initiatives (Cisneros-Montemayor and Sumaila 2010). The success and popularity of ecotourism would benefit from a healthy ecosystem and an abundance of the target species (Hickley and Tompkins 1998). The tourism generated through catch-and-release angling for bonefish contributes significantly to the economy of tropical areas such as those in the Pacific (e.g. Christmas Island, Kirimbiti and Hawaii), Atlantic (Bahamas, Cuba, Mexico and the Florida Keys) and the Indian Ocean (Seychelles) (Cooke *et al.* 2008; Ram-Bidesi 2011; Kamikawa *et al.* 2015). However, this industry is threatened by evident declines in bonefish stocks in several areas (Larkin 2011; Ram-Bidesi 2011).

The decline in bonefish stocks may be due to habitat destruction, pollution, coastal urbanisation and overexploitation by the fishing industry (Larkin 2011; Adams *et al.* 2014; Murchie *et al.* 2015). Bonefish rely on coastal sand flats, clear water and a healthy environment all of which is threatened due to environmental negligence and coastal development (Szekeres *et al.* 2014). However, even in protected areas such as Los Roques Archipelago National Park, a decline in bonefish has been noted (Debrot and Posada 2005). This may be due to the negative effects associated with catch-and-release fishing (Debrot and Posada 2005). Research has indicated that not all bonefish survive post-capture release and that survival rate varies depending on the location and handling practices (Danylchuk *et al.* 2007a). When stressed, bonefish release chemicals (namely ammonia, cortisol, lactate and urea) into the water which may act as an olfactory cue for sharks (Dallas *et al.* 2010). Furthermore, when targeting bonefish, poor handling techniques such as excessive fight times, too much air exposure and rough handling can lead to the fish losing equilibrium and becoming prone to predation (Danylchuk *et al.* 2007a). The combined result of an influx of predators and a decrease in locomotive ability, can lead to an increased probability of mortality upon release (Raby *et al.* 2014). A better understanding and improved management of these catch-and-release fisheries are vital to conserve bonefish stocks and ensure sustainable ecosystems.

Effective fisheries management policies relies on information such as habitat use, home range and vulnerable life stages (e.g. spawning migrations) (Allen and Singh 2016). By assessing aspects such as rhythmic cycles in a species' movement, movement behaviour and habitat use, we gain an improved understanding of their spatial ecology (Hindell *et al.* 2008; Bacheler *et al.* 2009; Biesinger *et al.* 2013). Movement studies, which are one of the key tools used by fisheries managers, further aid in identifying which management methods may be most effective in the conservation of a species (Dresser and Knieb 2007; Cowley *et al.* 2008; Revuelta *et al.* 2015). Closed seasons and conservation areas are only effective conservation tools if they are established in appropriate areas (Ruiz-Frau *et al.* 2015). For example, if a species is resident within a marine protected area (MPA), the protection offered to the species can be extremely beneficial and aid in the recovery of the stock in that area (Kerwath *et al.* 2009). For highly mobile species, MPAs may be advantageous as a refuge site, however they are seldom able to cover the entire range of a species (Pendoley *et al.* 2014). Therefore, to effectively conserve bonefish, an increased understanding of their movements, residency, home range and habitat use is required (Adams *et al.* 2014; Wallace 2015).

Movement studies have enabled further understanding of the spatial use by aquatic animals (Hussey *et al.* 2015). This knowledge ranges from snapshots of movement to in-depth spatial analyses of habitat use and the effects of cyclical variables on movement, depending on the technological capabilities of the specific research approach (Voegeli *et al.* 2001). Using advanced technologies such as acoustic telemetry and satellite tagging, fisheries managers can begin to discern a species' home range, residency and movement patterns within a particular area (Zeller and Russ 2000; Stein *et al.* 2012). Acoustic telemetry has increased in popularity in recent years as it provides accurate long-term positional data and is relatively easy to use in offshore environments (Biesinger *et al.* 2013). Acoustic telemetry enables effective management based on the understanding of a species' spatial (specific locations) and temporal (seasons) patterns (Ackerman *et al.* 2000). Movement studies can further explain behavioural changes, which may occur over time due to events such as spawning aggregations and other mechanisms affecting individual and population-level processes (Finn *et al.* 2014). The information generated from movement studies, combined with the knowledge of the landscape ecology, aids in the identification of critical habitats (Hartill *et al.* 2003).

The overall aim of this project was to contribute to the understanding of bonefish *Albula glossodonta* in the Indian Ocean. The specific objectives were to (1) assess the current knowledge of bonefish and identify research gaps, (2) evaluate the post-release survival of acoustically tagged bonefish, and (3) quantify the spatial and temporal movements of bonefish within and around the St. Joseph Atoll, Seychelles.

Chapter 2

General methods

Photo Credit: Rainer von Brandis, Save Our Seas Foundation, D'Arros Research Centre

"It is by acts and not ideas that people live" ~ Harry Emerson Fosdick

2.1 Study site

The Republic of Seychelles falls between 4° and 10° south of the equator and comprises about 150 islands distributed throughout its 1 400 000 km^2 exclusive economic zone (Friedlander *et al.* 2014). The Seychelles is divided into three main regions namely the inner Islands, Southern Islands and the Amirantes Group. The St. Joseph Atoll and neighbouring D'Arros Island (5.43° S, 53.35° E) are part of the Amirantes group of islands, situated approximately 240 km south-west of the capital Island of Mahe, Seychelles (Figure 2.1). Surrounding the Amirantes Bank is a basin and a trough with water depths of about 3 500 m and 5 000 m respectively (Mart 1988). The Amirantes Bank is a submerged plateau roughly 3 220 km^2 in size with a series of more than 20 islands consisting of both coral atolls and sand cays (Mortimer *et al.* 2011).

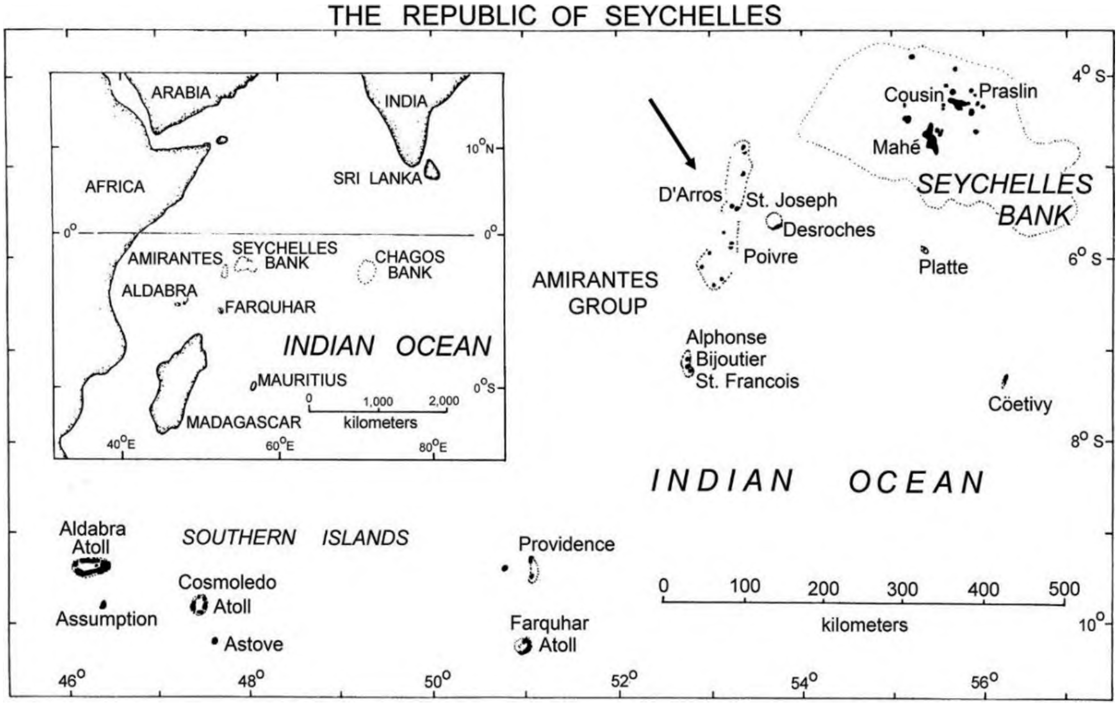

Figure 2.1: Map of the Seychelles indicating the location of the main island groups. The arrow indicates the position of D'Arros Island and the St. Joseph Atoll (after Mortimer *et al.* 2011).

The unpopulated St. Joseph Atoll is separated from the populated (< 50 inhabitants) D'Arros Island by a 1.1-km wide channel, which reaches a maximum depth of 72 m (Figure 2.2). The St. Joseph Atoll has a total area of about 21.8 km^2. The atoll is made up of a circle of 16 small islands (1.6 km^2; 7%), surrounded by 15.3 km^2 of reef flats (70%), encircling a central lagoon of about 4.9 km^2 (23%) (Filmalter *et al.* 2013). Ribbon reef and seagrass beds are intermittently dispersed throughout the atoll, particularly along the western and northern edges (Figure 2.2). The atoll is surrounded by steep sloping coral reef, with an incline of 45° to 70°, which, in parts (particularly on the north-eastern side of the atoll), descends to greater than 2 000 m within 4 km of the shore (Selin *et al.* 1992).

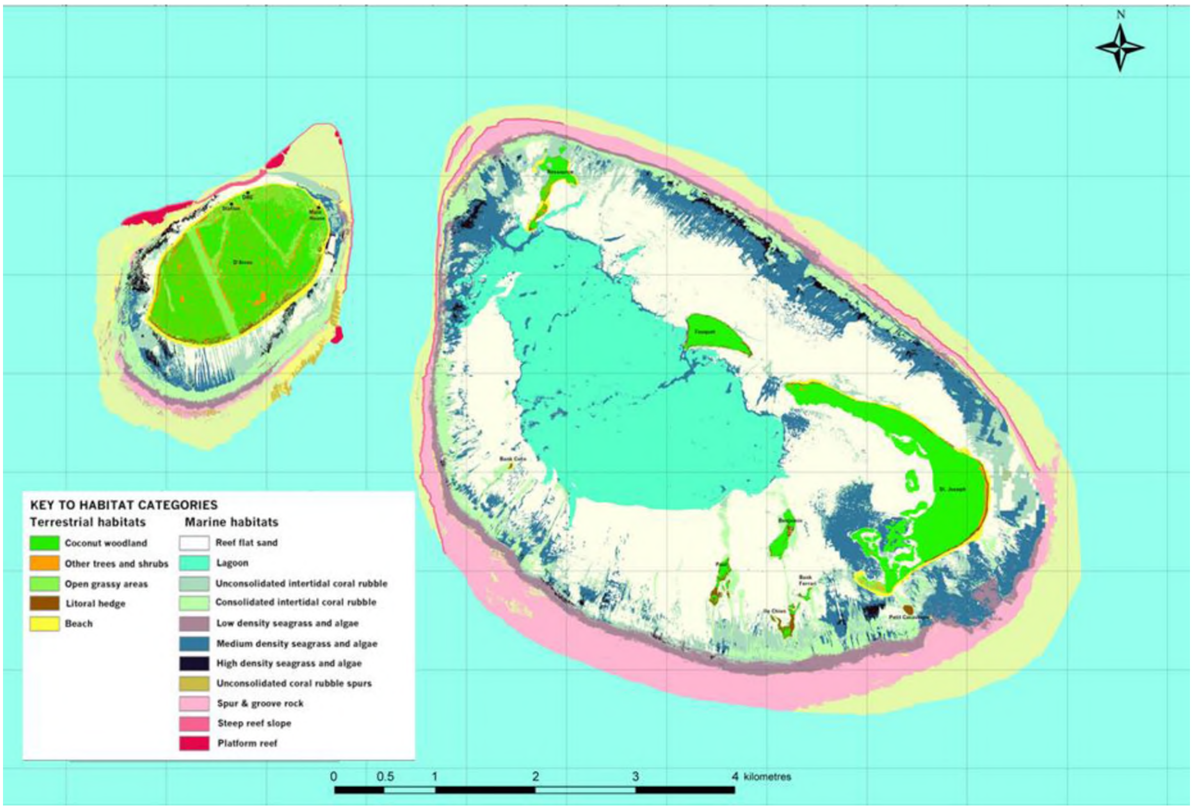

Figure 2.2: Map of D'Arros Island and the St. Joseph Atoll indicating the dominant islands, habitat coverage and layout of the area (base map courtesy of Spencer *et al.* 2008).

2.1.1 Seasons

The Seychelles, like most other tropical regions, is dominated by two seasons. From December to May (summer), there is a north-west monsoon characterised by light winds (0 to 15 kn) and the majority of the annual precipitation (annual mean = 1 490 mm). From June to November (winter), a strong (15 to 30 kn) south-east wind dominates with relatively dry weather. The average minimum air temperatures vary from 23°C (winter) to 31°C (summer) and the sea water temperatures vary from 26°C (winter) to 30°C (summer) (von Brandis 2012). A weather station (Davis Vantage Pro2) situated on D'Arros Island enables accurate monitoring of the environmental variables such as air temperature, wind speed and rainfall.

2.1.2 Temperature

Temperature is an important environmental variable which can fluctuate depending on the air temperature, water depth, tide and currents (Figure 2.3). Water temperature loggers (HOBO U22-001) were deployed at various locations in and around the St. Joseph Atoll, permitting accurate monitoring of water temperature at 10-minute intervals. Water temperature inside the atoll (22.7°C to 38.8°C) is generally warmer than the surrounding ocean (19.8°C to 31°C) and can fluctuate by as much as 8°C in 30 minutes (von Brandis 2012). The tidal fluctuations contribute to the extreme variation in temperature as the incoming tide brings an influx of cooler water from the open ocean. Within the atoll, temperature varies between the shallow water sand flats and the deeper lagoon (by as much as 8°C). This temperature difference within the atoll is due to a combination of factors such as water depth, the tropical solar radiation and the direction of the tide (Filmalter 2011; von Brandis 2012).

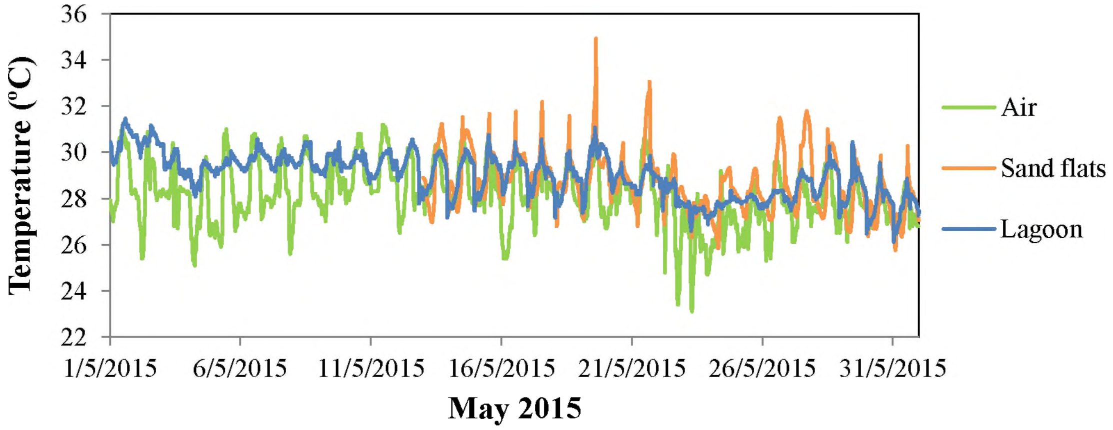

Figure 2.3: Air temperatures; water temperatures in the lagoon; and water temperatures on the sand flats (receiver 17) at the St. Joseph Atoll for the month of May 2015.

2.1.3 Tides

Due to the rotation of the Earth and the moon, and the resulting centrifugal force, there are two high and low tides each lunar day (24.8 h); with two 14-day semi-lunar spring/neap tides every lunar month (29.5 d) (Morgan 2001). Tides in the Seychelles are asymmetrical, meaning that the first and second high and low tides of each day do not reach the same level (Figure 2.4). In the St. Joseph Atoll, the lagoon has a maximum depth of about 6.5 m, and the maximum tidal range is approximately 2 m (Stoddart *et al.* 1979). As there is no dominant channel into the atoll, water spills over the encircling reef flat as the tides rise and fall (Filmalter 2011). To monitor the tidal fluctuations in the St. Joseph Atoll accurately, a tidal logger (HOBO U20-001-01-TI) was positioned in the lagoon at a depth of 3 m.

Most of the ecological processes in the atoll are in some way governed by the tides. At low tide, a large portion of the sand flats is exposed, as well as some reef outcrops. This affects both the amount of tidal flats habitat available for animals during low tide and the vegetation growth that can be sustained on the exposed reef (von Brandis 2012). Strong tidal flow (0.43 m.s^{-1} during a rising spring tide) in silty areas results in turbid water, which reduces visibility (Filmalter 2011). Animals that remain on the sand flats during low tides must therefore be able to withstand high levels of turbidity, turbulent conditions and fluctuating temperatures (von Brandis 2012).

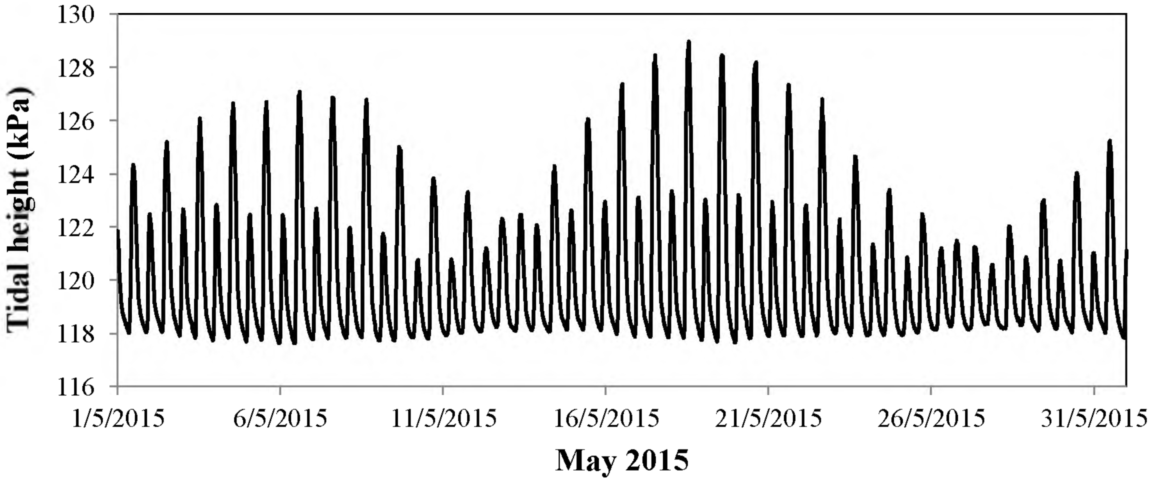

Figure 2.4: Tidal regime over the course of one month, showing the mixed semi-diurnal tidal cycles (different tidal height of the first and second high tide during a lunar day). The two spring tides (greater tidal range) and two neap tides (lower tidal range) are clearly evident.

2.2 Acoustic telemetry

Acoustic telemetry is a tool for monitoring animal movements. It has the ability to detect long-term and fine-scale movements of aquatic animals and is suitable for use in a range of environments (Biesinger *et al.* 2013). Acoustic telemetry enables researchers to discern a species' home range, residency and movement patterns within a particular area (Zeller and Russ 2000; Stein *et al.* 2012). Acoustic telemetry uses sound (acoustic) waves, which are emitted by the transmitter attached to or implanted inside the study animal (Campbell *et al.* 2012). If a receiver is within the vicinity of the transmitted signal, it is able to detect (receive and interpret) the sound wave signal, and log the date, time and unique tag identification (ID) number (Espinoza *et al.* 2011). The range and accuracy of the telemetry system depend on outside (ambient) noise (e.g. boat noise and noise generated by biological organisms and wind generated wave action noise) and environmental factors (e.g. temperature, salinity and turbidity) (Humston *et al.* 2005; Kerwath 2005; Webber 2009). Range testing trials at the St. Joseph Atoll indicated a detection range of between 100 m and 300 m in the sand flats and the lagoon environments (Elston 2015).

2.2.1 Acoustic receivers

The St. Joseph Atoll and surrounding area has been equipped with an array of 88 acoustic receivers (model VR2W, Vemco Ltd., Halifax, Canada) (Figure 2.5 A, C). The receivers in the atoll were deployed both on the shallow water reef flats and within the lagoon (Figure 2.5 C). The depth of deployment ranged from 0.2 m to 6 m, depending on the location and tidal phase. Receivers in shallow areas (< 3 m at low tide) were fixed directly to a concrete block on the sea floor while those in deeper waters were suspended in the water column between a concrete block and a buoy. Each receiver was an independent, omnidirectional single channel tracking unit, which monitors its surroundings continually for transmitters (Simpfendorfer *et al.* 2002). Certain areas, particularly on the sand flats, were unable to host a receiver due to the lack of water during low tides, thus limiting acoustic coverage on the sand flats (Humston *et al.* 2005).

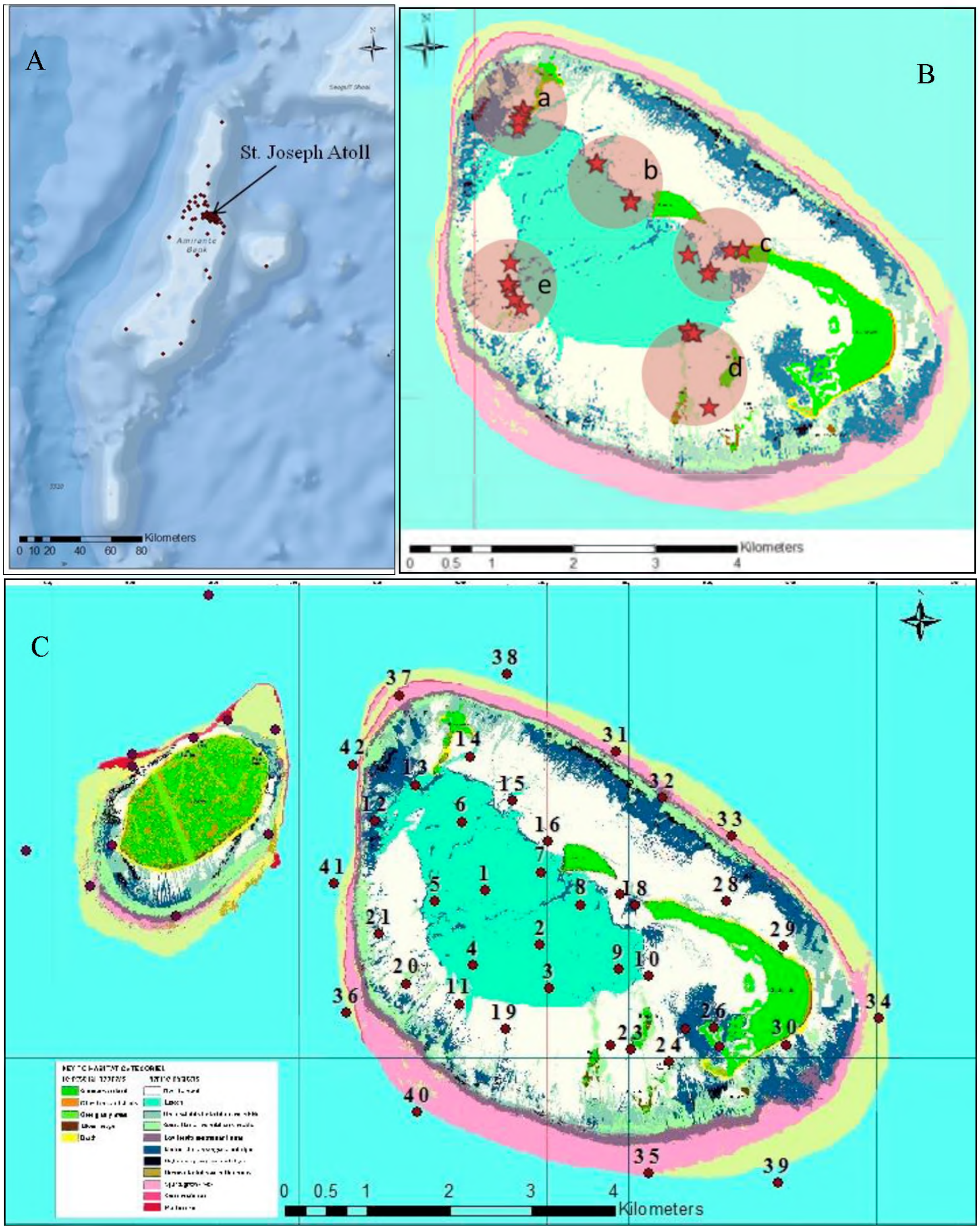

Figure 2.5: Study site of the acoustically tagged bonefish in the St. Joseph Atoll. (A) View of the Amirantes Bank showing the location of the 88 acoustic receivers, with a concentration of receivers in and around the St. Joseph Atoll. (B) Shaded red circles display the five different tagging areas, with the red stars showing the location of the 30 acoustically tagged bonefish (n = 6 per location). (C) Location of the acoustic receivers stationed in and around the St. Joseph Atoll. Base map (A) taken from ESRI online resources, www.arcgis.com/home/webmap/viewer.html?useExisting=1, accessed 10/01/2016. Base maps (B and C) adapted from Spencer *et al.* (2008).

2.2.2 Field methods

Thirty bonefish were captured using conventional angling methods (rod and reel) and surgically equipped with V13 transmitters (Vemco Ltd., Halifax, Canada). These transmitters transmitted a unique signal every 80 to 160 seconds, at 69 kHz with a power output of 153 dB, had an estimated battery life of 1 118 days, weighed 6 g in water and were 13 mm in diameter and 36 mm in length. Care was taken to ensure that the samples were collected from a range of locations around the atoll. Six specimens were tagged at each of the five selected locations around the atoll (Figure 2.5 B). A soft mesh, knotless dip net was used to land the fish. The hook was then removed, and the fish was transferred to an isolated keep-pen filled with fresh sea water (Figure 2.6). In the keep-pen, a wet cloth was placed over the fish's head and eyes. The fork length (FL) was measured and a photograph of the inferior side of the jaw was taken for morphometric comparisons. A fin clip was taken from the pectoral fin and placed in a vial containing 99% ethanol, for genetic analysis.

During the surgical procedure to insert the acoustic tag, the fish was inverted, allowing access to the abdomen. Care was taken to ensure that air exposure was kept to a minimum during the entire procedure. An incision of one to two centimetres was made halfway between the pectoral and anal fins, and slightly to one side of the ventral midline. The acoustic transmitter was sterilised in a 15% ammonia solution before being inserted into the peritoneal cavity. The incision was closed with two to three individual sutures (Clinisilk black braided Silk sutures 3/0). After this, an anti-bacterial gel was placed over the area to minimise infection. For the release procedure, the surrounding waters were assessed for the presence of predators and once deemed 'safe' the fish was released from the keep-pen. If the area was deemed 'unsafe', meaning there was an abundance of predators, the fish was moved while contained in the keep-pen to an area nearby. Once the fish was released, visual observations were made for about three minutes to assess if a shark attack occurred. The fight time, duration of the surgical procedure and release time were recorded. To reduce the risk of contamination during the surgical procedure, all surgical tools were cleaned in a 15% ammonia solution prior to each surgical procedure.

Figure 2.6: Bonefish placed in an isolated keep-pen filled with fresh sea water prior to and during the implantation of an acoustic transmitter. Photo: Copyright Rainer von Brandis, Save Our Seas Foundation, D'Arros Research Centre.

2.2.3 Filtering of detection data

In acoustic telemetry studies, additional stress is placed on the fish due to the capture myopathy (Cooke and Schramm 2007; Cooke *et al.* 2013). Residual stress from handling and surgery may influence the behaviour or survival of an animal after release into the wild (Mulcahy 2003). During the tagging process, cortisol levels, blood glucose, packed cell volume (PCV), haemoglobin, lactate and ions (Sodium and Potassium) increase as a response to the stress of capture and surgery (Lower *et al.* 2005; Cooke *et al.* 2008; Murchie *et al.* 2011a). Thus the use of movement data from the first 12 hours to 15 days has been cautioned (Robichaud and Rose 2002; Lower *et al.* 2005; Masters *et al.* 2005). In bonefish movement studies, post-release mortality usually occurs between one hour and one week after release, suggesting that data from this period must be treated with caution (Humston *et al.* 2005, Danylchuk *et al.* 2007b, Murchie *et al.* 2013). In bonefish, the recovery period after an angling event is unknown; therefore, the first 48 hours of data after release were excluded before analysing the results of this study.

2.2.3.1 False detections

At the time of this study, passive acoustic telemetry studies were underway in and around the atoll on several species, including porcupine *Urogymnus asperrimus*, mangrove *Himantura granulate* and feather tail *Pastinachus sephen* stingrays, lemon sharks *Negaprion acutidens*, black tip reef sharks *Carcharhinus melanopterus*, hawksbill turtles *Eretmochelys imbricata* and green turtles *Chelonia mydas* (von Brandis 2015). False detections may arise due to the collision of detections from two or more transmitters transmitting signals simultaneously (Pincock 2012) or due to external biotic (e.g. snapping prawns) or abiotic (e.g. boats) acoustic factors affecting the frequency of the transmission signal (Heupel *et al.* 2006, Pincock 2012). To identify false detections in this study, results were manually screened for single detections (Clements *et al.* 2005). If the single detection was accompanied by a second detection on the same receiver or a different receiver directly adjacent to it within 30 minutes, the detection was retained; if not, the single detection was considered a possible collision and thus excluded.

2.2.4 Analyses

Passive acoustic tracking of the fish took place for a period of 12 months. Data were downloaded from the acoustic receivers in November 2015 (six-month receiver download) and again in May 2016 (one-year receiver download). The data obtained from the six-month download were analysed for abnormal behaviour which may represent predation bias. This analysis is presented in Chapter 4. The data obtained from the 12-month download were analysed to identify habitat use and home range size, and to assess the effects of cyclical variables (e.g. lunar cycles and diel patterns) on bonefish movement patterns. These analyses are presented in Chapter 5.

Chapter 3

Review of scientific literature on bonefish (Albulidae)

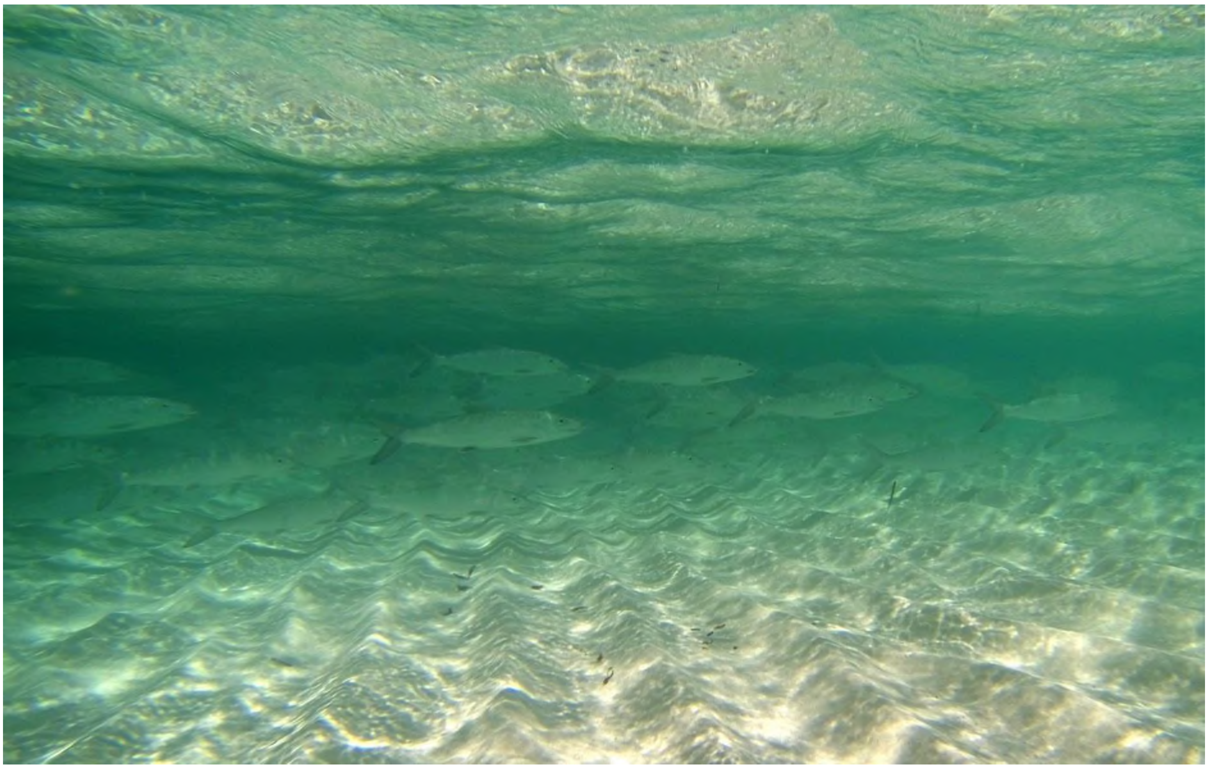

Photo Credit: Paul Cowley, South African Institute for Aquatic Biodiversity

“The more that you read, the more things you will know. The more that you learn, the more places you'll go.” ~ Dr Seuss

3.1 Introduction

The bonefish (Albulidae: *Albula*) is one of the most primitive forms of the living teleosts, with fossil deposits found worldwide (Fitch 1950). Present day fish of the *Albula* genus can be found in both tropical and sub-tropical seas (Fitch 1950; Shaklee and Tamaru 1981; Randall and Bauchot 1999). Due to their powerful fighting ability and their elusive nature, bonefish have become a popular target in recreational fisheries and form part of a valuable tourism industry (Danylchuk *et al.* 2007b; Wallace 2015). For example, bonefish contribute more than US$ 141 million annually to the Bahamian economy (Fedler 2010; Murchie *et al.* 2015). Many developing countries, in particular small island countries such as the Seychelles, rely on the revenue generated through tourism, of which fishing tourism is an important contributing sector (Wallace 2015). Economic, social and technological changes have all impacted on the focus of bonefish studies and a shift in research trends over the last 70 years.

Responsible management of a particular fishery relies on research for informed decision making (Humston *et al.* 2005; Weinberger and Posada 2005). The purpose of this review was to identify areas where bonefish research was lacking, thus enabling future research to contribute to the pool of bonefish knowledge in a meaningful way. Specific objectives were to (1) assess regional trends in bonefish research and how they have changed over the past seven decades, and (2) identify knowledge gaps to prioritise future research needs.

3.2 Literature review methods

3.2.1 Online literature search

An extensive literature search was conducted from August to September 2015. Common (bonefish) and scientific (*Albula*) names were used as keywords for several search engines; namely (1) Google Scholar (www.scholar.google.co.za), the first 30 pages, (2) Web of Science (www.webofknowledge.com) and (3) Catalogue of Fishes (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp).

The search conducted using the Google Scholar search engine included all valid names and synonyms within the genus *Albula* (*argentea, esuncula, gilbert, glossodonta, goreensis,* *koreana, nemoptera, oligolepis, pacifica, virgata, vulpes*). However to reduce the number of unrelated journal articles in the search results, the Genus names *Coregonus* (Alps) and *Spodoptera* (Germany), which carry the species name *albula* were omitted from the search results using the "-" function available in Google Scholar, as these refer to species in unrelated families and phyla, respectively.

3.2.2 Criteria for selecting eligible journal articles

For the purpose of this review, only English, peer-reviewed journal articles since 1946 (spanning the last seven decades) with the keywords *Albula* or bonefish in the title[1] were considered. Conference abstracts, posters, academic theses, books, biodiversity or biogeography lists and other grey literature were not included.

3.2.3 Themes and focus areas used for the categorisation of publications

Each article was classified according to five main themes, and then further into focus areas (outlined below, adapted from Palmer *et al.* (2008)). Owing to the considerable potential for overlap of research focus areas, in order to avoid duplication, each article was assigned to a single theme and focus area based on either the primary study objective or the main findings.

I. Taxonomy and systematics

Bonefish species descriptions using molecular or non-molecular techniques.

a. *Genetics*: molecular techniques to investigate aspects such as phylogeny, phylogeography and population genetics
b. *New records and descriptions:* for example new species descriptions, taxonomic revisions, new distribution records or clarifications
c. *Taxonomy and systematics:* non-molecular classification of fish including relationships between species or stocks within a single species.

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[1] Certain studies that had the keyword in the abstract were also included, provided the article predominantly studied bonefish and fitted into one of the focus areas.

II. Biology

The biology of bonefish, with non-management related results.

a. *Physiology:* such as measuring and assessing metabolic rates, temperature preference, food conversion ratios, salinity tolerance and body structure (e.g. teeth, eyes, brain)
b. *Life history:* descriptions of different life history strategies, e.g. descriptions of fish growth and ontogenetic changes in metabolic processes
c. *Age and growth:* age evaluation; for example, scales and/or otoliths
d. *Reproduction:* reproductive processes of bonefish such as gonosomatic index (GSI), age at maturation and reproductive seasonality
e. *Diet and feeding*: assessments and descriptions of diet and feeding
f. *Tagging and movement:* different tagging methods or descriptions of movement patterns
g. *Eggs and larvae:* biology of eggs and larvae

III. Ecology

Ecology of bonefish with non-management related results, where research emphasis was placed on the ecosystem rather than the biology of the species.

a. *Habitat:* study of the habitat and habitat use
b. *Oceanography:* the effects of ocean events and currents on bonefish (e.g. El Niño and La Niña)
c. *Spatial and temporal distribution:* dispersal, seasonal patterns, spatial use, biomass and density, in relation to habitat and ecology
d. *Trophic relationship:* the trophic relationship within the environment, such as food webs, nutrient cycle and stable isotope analysis

IV. Management & fisheries

Publications focusing predominantly on the management of bonefish.

a. *Stock assessments:* stock assessment techniques such as data modelling and catch statistics
b. *Research programs or objectives*: the focus was on objectives of a study or research program rather than results
c. *Status report:* reports on the status of a fishery or fish stock

d. *Fisheries, resource use and economics:* focusing on economics, including social economics and resource use
e. *Policy and regulations*: the development of regulations, legislation, quotas, fishing rights and conservation strategies (e.g. marine protected areas). Or, focus on the rationale and application of management strategies, including aspects such as best handling techniques and recreational fishing
f. *Biology, ecology and age and growth*: management decisions or strategies based on biological, ecological and age and growth data

V. Other

Publications that did not fall into any of the above categories.

a. *Parasites and bacteria*: focusing on parasites or bacteria of bonefish rather than the taxon itself
b. *Mariculture and aquaculture:* for example, the farming of bonefish

3.2.4 Decadal trend in research publications

To assess how bonefish research has changed over time, publications were sorted chronologically within each research theme. Themes were then grouped into seven decadal increments from 1946 to 2015. Owing to the complex nature of the *biology* theme and the high volume of publications over time, publications within the *biology* theme were further categorised according to the focus area, into decadal bins.

3.2.5 Geographic location

To present a geographical view of where bonefish research has taken place, the general location of the research was mapped according to the ocean region in which the research was conducted.

3.3 Findings

The search revealed 99 peer-reviewed articles on the *Albula* genus, published from 1946 to 2015 (see Appendix I). In general, the frequency of publications on bonefish has increased over the last 70 years, with the majority (68%) published in the last 20 years (1996 to 2015). The discussion of this review follows the order of (1) decadal trends in bonefish research, (2) the locations of research according to the ocean in which the research was conducted, and (3) further discussion of dominant themes and elaboration on individual focus areas where relevant.

3.3.1 Decadal trends in bonefish research

Of the papers reviewed, 54% of the articles focused on the *biology* theme, 21% on *taxonomy and systematics*, 20% on *management and fisheries*, 3% on *ecology* and 2% *other* (Figure 3.1). Biological research dominated the research field for the first 60 years (1945 to 2006) of the review period, with the *taxonomy and systematics*, and *management and fisheries* themes surpassing it in the last 10 years. Taxonomic research was the second most common research theme overall, with 43% of articles published from 1956 to 2005, and 57% in the last 10 years. *Management and fisheries* represented a new field of research for bonefish, with articles first published in 1996, but has become the most dominant topic of research in the last 10 years, surpassing both *biology* and *taxonomy and systematics*. Finally, *ecology* is a relatively new theme within bonefish research, with the first ecological paper published in 1995, but no growth in this research field has occurred over time.

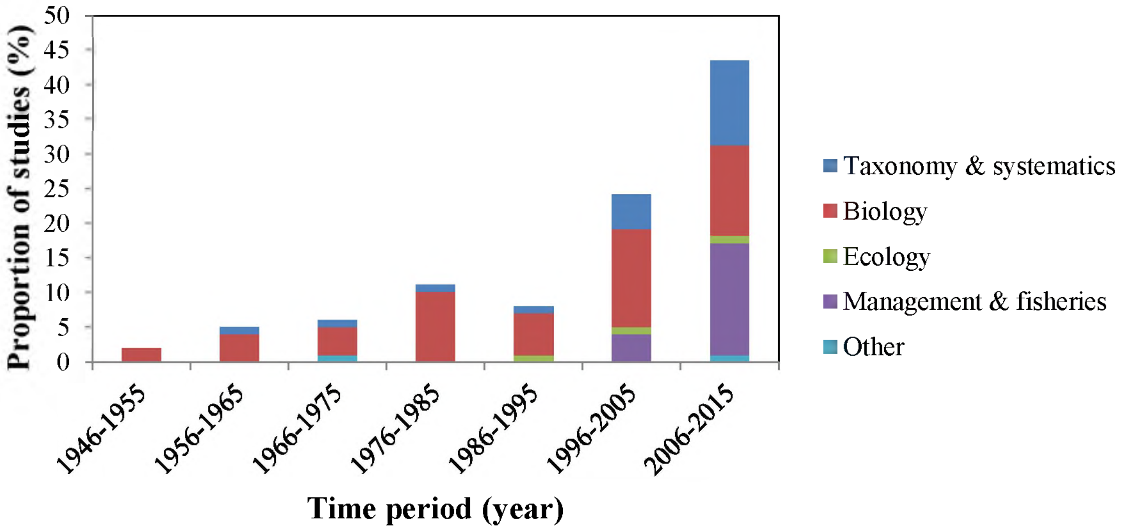

Figure 3.1: Proportion of bonefish publications within each research theme over seven decadal periods between 1946 and 2015.

3.3.2 Geographical distribution of bonefish research

Based on the number of publications, the majority of bonefish research has taken place in the Atlantic (56%) and Pacific (41%) oceans, with no research conducted exclusively in the Indian Ocean, but some conducted in the Indo-Pacific (3%) (Figure 3.2). Within the Atlantic Ocean, all studies were confined to the Western Atlantic, particularly the North-Western Atlantic, namely the Caribbean and the Gulf of Mexico. Within the Pacific Ocean, 73% of the studies were conducted along the western Mexican coastline, 14% around the Hawaiian Islands, 8% around the region of Korea and Taiwan and 5% at the Republic of Kiribati.

The contrast between the level of knowledge in the Indian Ocean in comparison with the Atlantic and Pacific oceans was stark. The literature review revealed just three studies which presented data on bonefish within the Indo-Pacific, all of which focused on taxonomy and systematics (Randall and Bauchot 1999; Hidaka *et al.* 2008; Wallace 2015). Although more research in the Indian Ocean is required, due to the isolation of many of the islands, the expense involved in research in this area is high. This is likely the reason for the current lack of research in this area, and particularly the lack of baseline research on the biology and ecology of bonefish. Simultaneously, however, the isolation and associated ecological condition of these islands provides a unique opportunity to develop baseline information on bonefish in a relatively pristine environment. This could further the understanding of bonefish biology and ecology and enable comparisons with areas that have been affected by development.

Without information on aspects of biology and ecology, effective management of bonefish is difficult. This knowledge is vital as many areas within the Indian Ocean are popular tourist destinations for recreational anglers targeting bonefish (e.g. Seychelles and Mauritius). Therefore, stable bonefish stocks are essential for the continued success of this tourism industry, thus highlighting the urgency for further assessments.

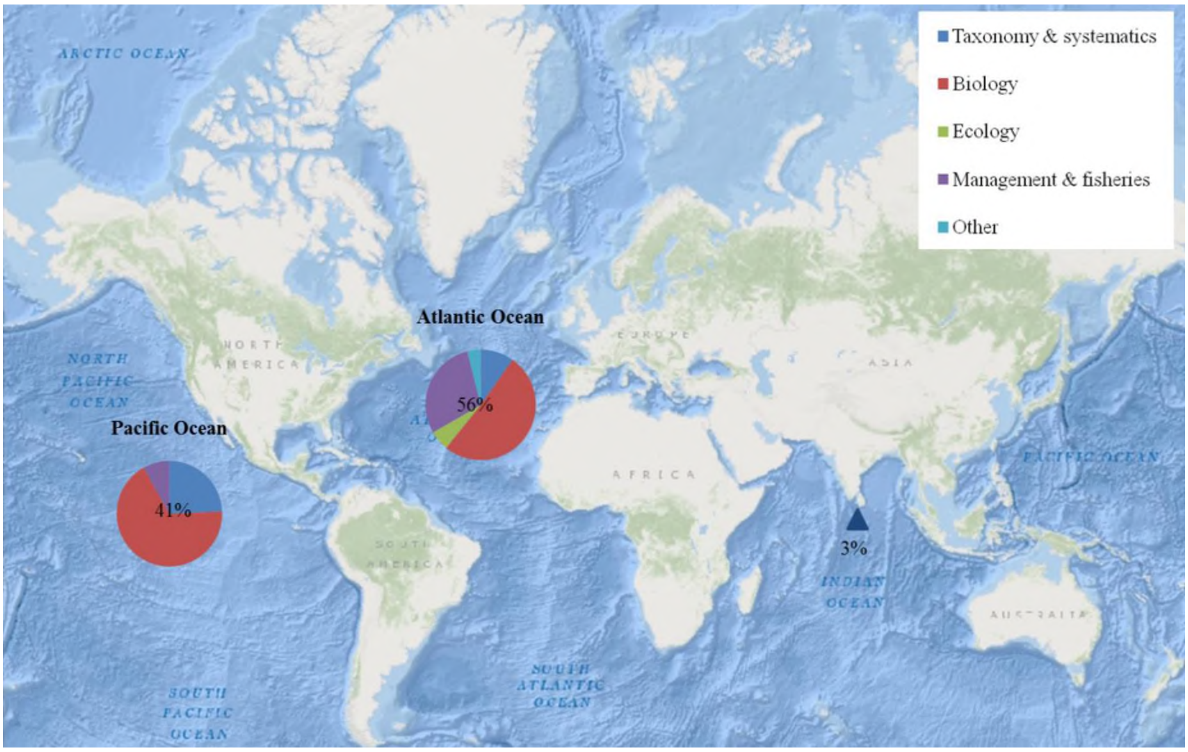

Figure 3.2: Distribution of bonefish research across the world's oceans, with pie charts indicating the research themes conducted in each area. The triangle represents three taxonomy studies which took samples from the Indian and Pacific oceans (base map taken from ESRI online resources, www.arcgis.com/home/webmap/viewer.html?useExisting=1, accessed 10/01/2016).

3.3.3 Research themes and focus areas

3.3.3.1 Aspects and focus areas within the biology theme

Biology studies of bonefish were the most dominant form of research until 2005, with few other themes being investigated historically (1946 to 1995). From 1946 to 1975, bonefish research was limited to *eggs and larvae, physiology* and *life history* (Figure 3.3). The high proportion of *eggs and larval* (32%) and *life history* (13%) research was predominantly due to the research efforts of Dr Edward Pfeiler (Monterey Institute of Technology and Higher Education) and his team. They were responsible for a considerable increase in bonefish research from 1984 to 2011, particularly within the focus area *eggs and larvae*, in the Gulf of California. Research on *eggs and larvae* of bonefish was popular between 1980 and 2000, during which time Pfeiler and his team authored more than three quarters (76%) of the research outputs on *eggs and larvae*. This can be observed in the noticeable increase in biological research based in the Pacific Ocean, with particular focus on the Gulf of California (Figure 3.2). While there has been considerable research on *eggs and larvae* in the Pacific, further research needs to be conducted on the early development of bonefish species in other areas.

Within the *physiology* theme (26% of all *biology* publications on bonefish) a broad range of topics was examined. Examples of these include salinity tolerance (Pfeiler 1981; Thompson and Deegan 1982), thermal tolerance (Murchie *et al.* 2011a), body composition (Murchie *et al.* 2010), visual acuity (Taylor and Grace 2005) and energy use (Murchie *et al.* 2011c; Brownscombe *et al.* 2014). The relatively primitive taxonomic characteristics of *Albula* make certain aspects of its physiology important for comparative purposes (Fridberg *et al.* 1966). Aspects such as the neurosecretory cells, which show both primitive and advanced features (Nishioka and Bern 1964; Fridberg *et al.* 1966), the caudal skeleton (Nybelin 1973) and jaw morphology (Nybelin 1976) have been explored for comparative purposes.

The increase in studies from 1996 onwards may also be attributed to the founding of The Bonefish and Tarpon Trust (BTT) (www.btt.org) in 1988, with the research focus becoming more dynamic across all themes. The BTT is a non-profit organisation that began as a response to the decline in bonefish and tarpon and the lack of biology research on these taxa (Adams and Cooke 2015). This institution has been vital in the development and funding of research and scientific knowledge relating to bonefish, tarpon (*Megalops atlanticus*) and permit (*Trachinotus falcatus*), particularly within and around the Caribbean.

Tagging and movement studies are generally viewed as a more ethical approach to fisheries research as study animals are not sacrificed. A movement to more sustainable research methods has been noted from the increase in *tagging and movement* studies in both the *biology* theme (Humston *et al.* 2005; Danylchuk *et al.* 2011b) and as a research method when developing best handling practices in the *management* theme (Danylchuk *et al.* 2007a; Kamikawa *et al.* 2015) (Figure 3.3). The increased use and technological advancements in tag types, such as dart tags (Colton and Alevizon 1983a; Kamikawa *et al.* 2015), tri-axial accelerometer biologgers (Brownscombe *et al.* 2014) and acoustic telemetry (Cooke and Philipp 2004; Murchie *et al.* 2011a, 2015), have enabled researchers to further investigate aspects such as thermal biology (Murchie *et al.* 2011a), bioenergetics (Murchie *et al.* 2011c), spawning locations (Danylchuk *et al.* 2011b) and the long term movement of bonefish

(Colton and Alevizon 1983a). These studies have furthered our understanding of bonefish movement, in relation to environmental cycles such as tidal cycles, lunar cycles and seasonal changes, spawning seasons and areas, as well as aspects pertaining to home range, site fidelity and habitat use (Colton and Alevizon 1983a; Humston *et al.* 2005; Murchie *et al.* 2015). All of this information enables more informed conservation and fisheries management decisions.

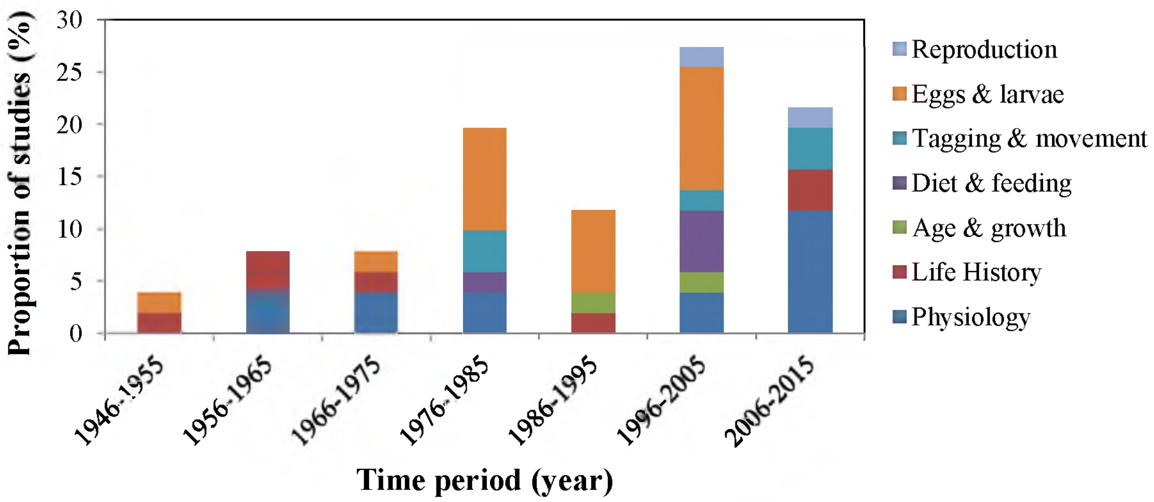

Figure 3.3: Proportion of bonefish publications over time according to each focus area within the theme *biology*.

3.3.3.2 An overview of taxonomy and systematics studies

In order to adequately conserve a fishery, knowledge on the species distribution is vital. Despite the global distribution of bonefish, *taxonomic* research of the *Albula* genus has only recently discerned more than two species (Shaklee and Tamaru 1981). Yet genetic evidence indicates that certain speciation events occurred as much as 20 to 30 million years ago (Shaklee and Tamaru 1981). Although nucleotide divergence among bonefish species took place at a ‘normal’ rate, morphological divergence has occurred extremely slowly, possibly due to their habitat use patterns (Colborn *et al.* 2001). This has resulted in limited morphological differences among bonefish species (Shaklee and Tamaru 1981; Hidaka *et al.* 2008). The lack of morphological differences has presented challenges when describing species using basal morphological and physiological techniques such as morphology and meristics (Rivas and Warlen 1967; Whitehead 1986). This was the likely reason for the species complex remaining undetected until recently. The progress on taxonomic and systematics research among bonefish species can be attributed mainly to advances in genetic technology. The field of taxonomy has grown substantially, allowing access to new methods of analysing species variation (such as DNA taxonomy, DNA barcoding and molecular operational taxonomic units) (Vogler and Monaghan 2007).

Worldwide, 12 different bonefish species have been identified, although, only 11 have been named (Hidaka *et al.* 2008; Wallace and Tringali 2010; Wallace 2015). The discovery of multiple bonefish species was surprising as bonefish display a leptocephalus larval stage (an extended pelagic larval period) which would reduce the likelihood for allopatric speciation (Thompson and Deegan 1982; Hidaka *et al.* 2008). Recent taxonomic work, such as the work conducted by Colborn *et al.* (2001), Hidaka *et al.* (2008), Wallace and Tringali (2010), Kwun and Kim (2011), Pfeiler *et al.* (2011) and Wallace (2015) has proven helpful in discerning the confusion of the *Albula* species and their distributions. Adams *et al.* (2014) and Wallace (2015) provide comprehensive summaries on the current state of knowledge about the global distribution of the *Albula* genus.

This review revealed that *taxonomy and systematics* studies accounted for 21% of published bonefish research, of which most was conducted in the last 20 years. Due to the lack of knowledge about the species complex, most of the *biology, ecological* and *management and fisheries* research did not consider species-specific research as part of the studies. Many bonefish studies either assumed that the study species was *A. vulpes* or did not refer to the species name in the article (e.g. Peña *et al.* 1998; Pfeiler and Vrijenhoek 2005; Danylchuk *et al.* 2008a; Vásquez-Yeomans *et al.* 2009). However, such assumptions can generate confusion and create the impression that information on bonefish species is interchangeable among species and areas. Indeed, even within a small area, different bonefish species can display variation in diet, reproductive strategies, growth and habitat preferences, as was observed between two species that occur in Hawaiian waters, *A. glossodonta* and *A. virgata* (Donovan *et al.* 2015).

An example of a possible species complex is apparent when considering literature on spawning seasons. For example, in the Bahamas, spawning reportedly takes place from autumn to early winter (October to January), and can also occur through to spring (May) (Mojica *et al.* 1995; Murchie *et al.* 2013). Western Caribbean and Florida report year-round spawning (Burger 1974; Vásquez-Yeomans *et al.* 2009). Late spring to summer spawning months were reported for the Gulf of California (Pfeiler *et al.* 1988), and in Hawaii, a peak in spawning was recorded in winter (November to April) for both species present in the area, namely *A. glossodonta* and *A. virgata* (Donovan *et al.* 2015). When comparing different localities, variations in spawning seasons become apparent. This could be due to the location-specific environmental cues for spawning, such as sea temperature, current and photoperiod (Pankhurst and Porter 2003); or it could be due to the species complex and differences in life history strategies found among species (Donovan *et al.* 2015).

Due to the progress made within *taxonomy and systematics* research, inclusion of or reference to species-specific information is becoming standard, with more recent studies generally identifying their study species, or referring to genetic analyses from the same area (Danylchuk *et al.* 2007a; Murchie *et al.* 2009). However, further studies are essential as little information is available for most bonefish species, particularly with regards to their range and distribution. Such information is critical when developing management strategies for different species.

3.3.3.3 Management

Management and fisheries publications (20% of all publications on bonefish) have dominated bonefish research in the last decade, with no previous studies prior to 1996. In the last 20 years, a new trend in bonefish research, investigating potential reasons for an observed decline in bonefish, has begun. A number of reasons have been noted to account for the declines in bonefish stocks including: (1) fishing and targeting of the spawning migration in places such as the Hawaiian Islands and the Republic of Kiribati (Beets 2000; Friedlander *et al.* 2008), (2) a breakdown of social structures of people in places like the Republic of Kiribati (Johannes and Yeeting 2000), (3) by-catch of bonefish in commercial fishery operations in the Caribbean and other areas (Crabtree *et al.* 1996; Adams *et al.* 2014) and (4) uncontrolled touristic recreational fisheries occurring throughout most of their distribution, including protected areas such as the Florida Keys, United States of America and Los Roques Archipelago National Park, located off the coast of Venezuela (Debrot and Posada 2005; Frezza and Clem 2015). The supposed 'impact free' catch-and-release of bonefish as an explanation for the decline in stocks has received the most research attention. The observation that this decline has been noted in areas that only permit catch-and-release fishing, suggests that catch-and-release of bonefish is probably not a benign form of tourism, and has greater impacts than previously thought.

Given the concern of high post-release mortality following catch-and-release fishing of bonefish, much of the literature in the last decade has focused on improved handling techniques (Danylchuk *et al.* 2007a, 2007b; Hannan *et al.* 2015). Tagging and movement analyses are often used in studies focusing on *management and fisheries*. These studies typically assess the survival rate of released fish in relation to particular handling techniques, proximity to shelter and relative abundance of predators (Cooke and Philipp 2004; Danylchuk *et al.* 2007b; Brownscombe *et al.* 2013).

Unfortunately, formal stock assessments of bonefish are minimal due to the fishery being largely recreational (Beets 2000; Humston *et al.* 2005; Adams *et al.* 2014). However, angler-based science has been used to collect genetic samples and length data, assist in tagging studies and provide information on historical changes in the fishery (Larkin *et al.* 2010; Frezza and Clem 2015; Kamikawa *et al.* 2015). For example, results from a mail survey of 322 bonefish charter captains suggest that bonefish stocks in the Caribbean declined between 2000 and 2010. In a similar survey, commercial landings were shown to have declined by 99% over the last century in Hawaii (Larkin *et al.* 2010; Kamikawa *et al.* 2015). Angler based science can be a cost-effective method to assess the status of bonefish fisheries. The fishery may even benefit from an increased drive towards citizen science where anglers have the opportunity to report their catch rates and observations.

3.3.3.4 Ecology

Ecological studies are relatively new to bonefish research, with the earliest ecological paper published in 1995 (Mojica *et al.* 1995). Ecological investigations comprise only 3% of the total research output. Reasons for the apparent paucity of ecological research may be the broad scope of ecology transgressing into secondary themes within this review. Many of the topics within this review were closely interlinked with one another, often complicating the classification of papers into broad themes. The *ecological* theme was a good example, as a great deal of overlap was noted in some studies (for example: Murchie *et al.* 2013, 2015). This may have led to *ecology* studies being under-represented in this review. Furthermore, given the strict criteria for accepting articles into this review, *ecological* studies pertaining to areas where bonefish occur (rather than bonefish specifically) were likely filtered out. Examples of filtered out articles include Lea and Rosenblatt (2000) and Sielfeld *et al.* (2010) who discussed the impact of the 1998 El Nino event on ichthyofaunal communities (including bonefish) in California and Northern Chile respectively. The paucity of studies within the focus areas: *habitat, oceanography,* and *trophic relationship* indicate vast gaps in knowledge. This information contributes to data on energy flow, species diversity and population density (Layman *et al.* 2005). Although other articles have touched on these aspects, dedicated studies would prove beneficial.

Owing to the shallow water and near shore habitat preferences of bonefish, it is likely that they form part of a complex food web and are vulnerable to habitat degradation (Gupta 2002; Layman *et al.* 2005). Based on this, the conservation of bonefish habitats including shallow water flats, estuaries and mangroves and other nearshore environments has been suggested (Debrot and Posada 2005; Adams *et al.* 2014; Adams and Cooke 2015). Further studies to understand their trophic position in the food web such as body size analysis and stable isotope analysis, are also required. Due to rapidly changing marine habitats (coral bleaching, mangrove deforestation, death of seagrass beds, etc.) information pertaining to the importance of different habitat types for bonefish is essential for future research (Gratwicke and Speight 2005).

3.3.3.5 Other

Two bonefish articles (2%) could not be classified into the four main themes and were therefore listed as '*other*': one focused on bonefish aquaculture (Murchie *et al.* 2009) and the second on bonefish parasites (Overstreet 1970). Knowledge on the aquaculture of bonefish has already proved useful for conducting laboratory-based studies on physiological parameters such as critical temperature and metabolic rate (Murchie *et al.* 2011a, 2011c). Furthermore, this knowledge may prove useful in future research studies, which may require the culture of bonefish.

3.4 Conclusion

Bonefish support an important recreational fishery, yet a dearth of knowledge has been noted. This review detailed the current state of knowledge on bonefish, highlighting areas where research is lacking. The findings reveal a relatively biased literature on bonefish, heavily weighted toward the *biology* theme and more recently, *taxonomy and systematics* and *management*. The review indicated an increasing trend in bonefish research, yet it is still very geographically restricted and generally relates to only one species, namely *A. vulpes*. The lack of research in the Indian Ocean is problematic given the economic importance of the recreational bonefish fisheries in this region. Furthermore, managers in other parts of the world that may have misidentified the *Albula* species which occur in their area, may be utilising inappropriate information and may thus potentially prevent the effective protection of their particular bonefish species.

Owing to rapid global development, it is important to understand the mechanisms behind previous or current bonefish declines so that these may be mitigated. Bonefish are vulnerable to urbanisation, environmental change and post-release predation; all of which are likely to increase in the near future. Island communities in the Indian Ocean and other remote areas of the world are an example of where bonefish need to be conserved before development and fisheries grow to unsustainable levels. However, without fundamental information, such as species-specific *biology*, *ecological*, *management* and *taxonomic* research on bonefish, such conservation is difficult. Therefore, research focusing on those bonefish species and areas that have received little research attention to date is paramount. Aspects such as home range, niche separation and life history traits (e.g. spawning migrations) should be further investigated, thus enabling effective protection and management decisions based on the specific bonefish species of a particular area.

Chapter 4

Evaluation of post-release survival of tagged bonefish (*Albula glossodonta*)

Photo Credit: Paul Cowley, South African Institute of Aquatic Biodiversity

"The capacity to be puzzled is the premise of all creation, be it in art or science" ~ Erich Fromm

4.1 Introduction

Bonefish occur worldwide in tropical and subtropical areas and support valuable recreational fisheries (Pfeiler *et al*. 2006; Levesque 2011). These fisheries are usually characterised by catch-and-release fishing and are therefore considered to be a sustainable form of ecotourism (Holt and Holt 2005). Such tourism is essential as it contributes to the economic standing of many small tropical islands and atolls (Hickley 1998; Cisneros-Montemayor and Sumaila 2010). However, several studies have found that catch-and-release fishing for certain species is not as sustainable as previously believed (Cooke and Cowx 2004; Bartholomew and Bohnsack 2005; Danylchuk *et al*. 2007b).

Questions regarding the sustainability of bonefish fisheries have arisen, due to reported declines in fish stocks by charter captains in Florida and an investigation conducted at Tarawa Lagoon, Republic of Kiribati (Beets 2000; Larkin *et al.* 2010). Possible reasons for the decline of bonefish stocks include pollution, habitat destruction and uncontrolled tourism (specifically recreational angling) (Debrot and Posada 2005; Adams *et al.* 2014; Murchie *et al.* 2015). Bonefish are dependent on coastal sand flats and are therefore vulnerable to pollution and urban development along the coastline (Szekeres *et al.* 2014). However, their vulnerability to catch-and-release fishing requires further exploration. Catch-and-release does not always ensure the survival of a fish post release (Brownscombe *et al.* 2017). Post-release survival of bonefish depends on factors such as the capture environment (e.g. temperature), capture method (e.g. fishing gear and fight time) and handling practices (such as air exposure time) (Bartholomew and Bohnsack 2005; Cooke *et al.* 2013). Bonefish are particularly susceptible to post-release predation, especially in areas with a high density of sharks (Humston *et al*. 2005; Danylchuk *et al*. 2007b). Poor handling practices have been found to increase the likelihood of post-release predation; however, even with best handling practices, mortality estimates in bonefish studies range from 15% to 100% (Colton and Alevizon 1983; Humston *et al*. 2005; Friedlander *et al*. 2008).

The St. Joseph Atoll is characterised by a high density of sharks, mostly juvenile sicklefin lemon sharks *Negaprion acutidens* and blacktip reef sharks *Carcharhinus melanopterus* (von Brandis 2012; Filmalter *et al.* 2013). Due to the remoteness of the atoll, low density of human inhabitants and lack of commercial shark fisheries in and around the St. Joseph Atoll, a high density of sharks may be expected (DeMartini *et al*. 2008; Graham *et al*. 2010; Salinas de León *et al*. 2016). This study aimed to assess the movement of bonefish at this remote atoll. However, given the large body of knowledge documenting bonefish vulnerability to shark predation (Brownscombe *et al*. 2013; Murchie *et al*. 2013), and the richness of predators in the St. Joseph Atoll, a predation event on tagged bonefish was likely during this study. This study was, therefore, susceptible to predation bias.

Predation bias occurs when a tagged animal is preyed upon and the acoustic tag is ingested by the predator, resulting in the transmitter representing the predator's movements as opposed to the original study animal (Gibson *et al.* 2015). Examples of predation bias in the literature include a noticeable change in temperature and depth range of a satellite-tagged silver eel (*Anguilla rostrata*) consistent with the known behaviour of porbeagle sharks (*Lamna nasus*) (Béguer-Pon *et al*. 2012); and a tagged Atlantic salmon (*Salmo salar*) displaying movements correlating to the known behaviour of a striped bass (*Morone saxatilis*) (Gibson *et al.* 2015). In this study, if a predation event occurred, then a behavioural change should have been noticeable and quantifiable when compared with the movement patterns of bonefish.

Before the movement analysis of bonefish could begin, data were examined for predation bias. If predation bias occurred, then abnormal behaviour should be evident during the period of gastric tracking (while the transmitter is retained in the gastric tract of the predator). Literature suggests that gastric retention of acoustic transmitters ingested by sharks ranges from 24 h (bull shark *Carcharhinus leucas*) to 34 days (tiger shark *Galeocerdo cuvier*) (Brunnschweiler 2009; Murchie *et al*. 2012), with an average retention time of three to six days (Mc Kibben and Nelson 1986; Economakis and Lobel 1998). By assessing tag retention time and comparing the movement behaviour from the last 100 h of tracking for those fish that appear to have suffered predation bias to the behaviour of fishes considered to be surviving bonefish (i.e. long-term retention of transmitters), we could quantify the level of possible predation bias.

The aim of this chapter was to evaluate the post-release survival of acoustically tagged bonefish and to determine the prevalence of predation events on tagged individuals. This was achieved through a comparison of multiple movement metrics, including residency index, the daily distance moved among receivers, average movement speed and diel area use, in order to categorise behaviour patterns and thus identify whether predation events had occurred.

4.2 Methods

4.2.1 Rapid assessment of the raw acoustic detections

Tagging of thirty bonefish with acoustic transmitters took place from the 4th to the 9th May 2015 in the St. Joseph Atoll (see Chapter 2). Acoustic receiver data were downloaded from the 21st to the 25th November 2015 (six-month download). Initial screening and analysis of detection data revealed that the number of tracking days varied considerably among individuals, ranging from zero to 204 (Table 4.1). This variation required further analyses. Of the 30 fish tagged, 14 fish (47%) were excluded from the analyses. Of these, ten fish (33%) were excluded as they were never detected (13%), or were detected exclusively (17%) or almost exclusively (3%)[2] on one receiver. Four fish (14%) were excluded as they were detected less than 75 times (the minimum detection number set for this experiment) over their tracking period. Therefore, the evaluation of predation bias was conducted on 16 individuals (Table 4.1).

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[2] Fish 21 was considered as part of this group "detected almost exclusively on one receiver" as 98% of the detections were detected on one receiver.

Table 4.1: Raw (non-filtered) metadata of bonefish (n = 30), tagged at St. Joseph Atoll between the 4th and the 9th May 2015. Tagged fish that were never detected are marked with ND (not detected). Star symbols refer to fish removed from further analysis: * = fish not detected or detected exclusively or almost exclusively on one receiver, ** = fish with fewer than 75 detections. Tagging location refers to Figure 2.5 B.

Fish ID	Date and time tagged	Fork length (mm)	Tagging location	Total receivers visited	Receiver detections	Total monitoring days	Days Detected
1 *	5/5/2015 9:27	550	c	ND	ND	ND	ND
2 *	5/5/2015 15:48	470	d	ND	ND	ND	ND
3 *	6/5/2015 9:20	500	e	1	21	2	2
4	4/5/2015 17:26	465	c	10	102	5	5
5	4/5/2015 18:10	494	c	9	417	12	12
6	5/5/2015 8:47	525	c	21	375	12	10
7 *	5/5/2015 9:51	472	c	1	1	1	1
8 *	5/5/2015 14:56	499	d	ND	ND	ND	ND
9	5/5/2015 15:19	499	d	6	396	5	5
10 **	6/5/2015 9:15	519	e	6	64	2	2
11 **	6/5/2015 9:49	487	e	2	7	1	1
12 *	6/5/2015 10:07	452	e	ND	ND	ND	ND
13	8/5/2015 9:04	518	a	14	4860	124	124
14	6/5/2015 14:31	515	b	17	2969	204	115
15	6/5/2015 14:45	450	b	9	109	4	4
16 **	6/5/2015 15:05	470	b	7	58	3	3
17	8/5/2015 9:20	553	a	11	388	7	7
18 *	8/5/2015 9:38	525	a	1	35	2	2
19	6/5/2015 10:22	506	e	11	697	202	77
20	6/5/2015 10:57	551	e	11	83	4	4
21 *	6/5/2015 13:05	528	b	8	6387	105	100
22 **	6/5/2015 13:22	502	b	4	34	5	4
23	8/5/2015 5:58	495	a	12	185	39	4
24 *	8/5/2015 10:19	518	a	1	2402	25	24
25 *	5/5/2015 12:10	477	a	1	64848	198	198
26	8/5/2015 16:28	532	d	6	268	42	9
27	9/5/2015 15:45	528	b	15	2358	196	106
28	8/5/2015 15:57	478	d	4	568	26	20
29	8/5/2015 16:11	462	d	10	109	4	4
30	5/5/2015 9:10	467	c	6	127	3	3

The results from the 16 individuals were then filtered (see Chapter 2), and each individual was allocated to one of two categories. Categories were assigned based on the tracking duration of individual fish (once filtered), Category 1 (13 fish; fish 4, 5, 6, 9, 13, 15, 17, 20, 23, 26, 28, 29 and 30) included fish with less than two weeks of tracking data and Category 2 (three fish; fish 14, 19 and 27) included fish with more than two weeks of tracking data. To test for a difference in movement behaviour, the final 100 h (or part thereof) from Category 1 fish were used. Fish in Category 2 were tracked for the entire six months and were therefore assumed to represent bonefish movement behaviour. To avoid bias, detections only after the first 48 hours and up to the final 100 h from Category 2 fish were used.

4.2.2 Spatial distribution

Bonefish area use was plotted in ArcView 10.2 (Environmental Systems Research Institute Inc., Redlands, California). Movement trajectories were approximated using lines to connect the receivers visited. Circles were used to identify the receivers on which each fish was detected, and these were scaled to the frequency of detections. Depending on the region of the atoll in which the majority of the detections took place (namely the lagoon or the sand flats), the movement trajectories were classified into three groups (a) predominantly detected on the sand flats, (b) predominantly detected in the lagoon and (c) detections approximately evenly distributed between the lagoon and the sand flats.

4.2.3 Metrics for the assessment of behavioural differences (predation events)

4.2.3.1 Average daily distance travelled per day detected

The total distance between consecutive receivers on which each fish was detected was calculated for each day (0:00 to 23:59). These daily distances (km) were then averaged across the total number of days that each fish was detected within the array. This value provided an index of average daily distance travelled (km.day^{-1}).

4.2.3.2 Movement speed

Where multiple receivers were visited within a 30-minute time frame, the velocity ($m.s^{-1}$) of movement was estimated by dividing the distance (m) between the two receiver locations by the time (s) between detections on the two receivers.

4.2.3.3 Residency to the atoll

Calculations were conducted to determine the residency index (RI) for each tagged fish. Residency index was determined by dividing the total number of days that each transmitter was detected at any receiver within the array by the total number of monitored days (Abecasis and Erzini 2008). Residency index was expressed as a proportion from 0 (lowest, completely absent) to 1 (highest, detected every day).

4.2.3.4 Multivariate analyses

The clustering of the movement data (RI, average daily distance and average speed) was analysed in Primer-E (Ltd; 7.0.10) using non-metric multidimensional scaling (nMDS) (Shepard 1962; Kruskal 1964). Non-metric MDS plots configure data into a 2-dimensional ordination plot in a way that best represents the relationship amongst samples (Clarke and Warwick 2001). Similarities between metrics were identified through MDS ordination and cluster analysis (Bray-Curtis similarity coefficient). The stress value indicated the goodness-of-fit of the model to the observed data. Stress values less than 0.1 were considered good, 0.1 to 0.2 as potentially useful, and greater than 0.2 as arbitrary (after Clarke and Warwick 2001).

4.2.3.5 Statistical analyses

A series of statistical tests was conducted to compare the three metrics between Category 1 and Category 2 fish. Tests for normality and homogeneity of variance (normal distribution of residuals) (Shapiro and Wilk 1965; $p < 0.05$), standard error skewness ($-1.96 < x < 1.96$) (Doane and Seward 2011) and a visual inspection of probability plots and histograms) showed that the data were not normally distributed. Therefore, a non-parametric test, namely a Mann-Whitney U test, was used to test for a statistical difference between Category 1 and Category 2 (Wilcoxon 1945; Mann and Whitney 1947). Analyses were conducted in Statistica™ (DellTM StatisticaTM, StatSoft. Inc., USA). Alpha was set at 0.05.

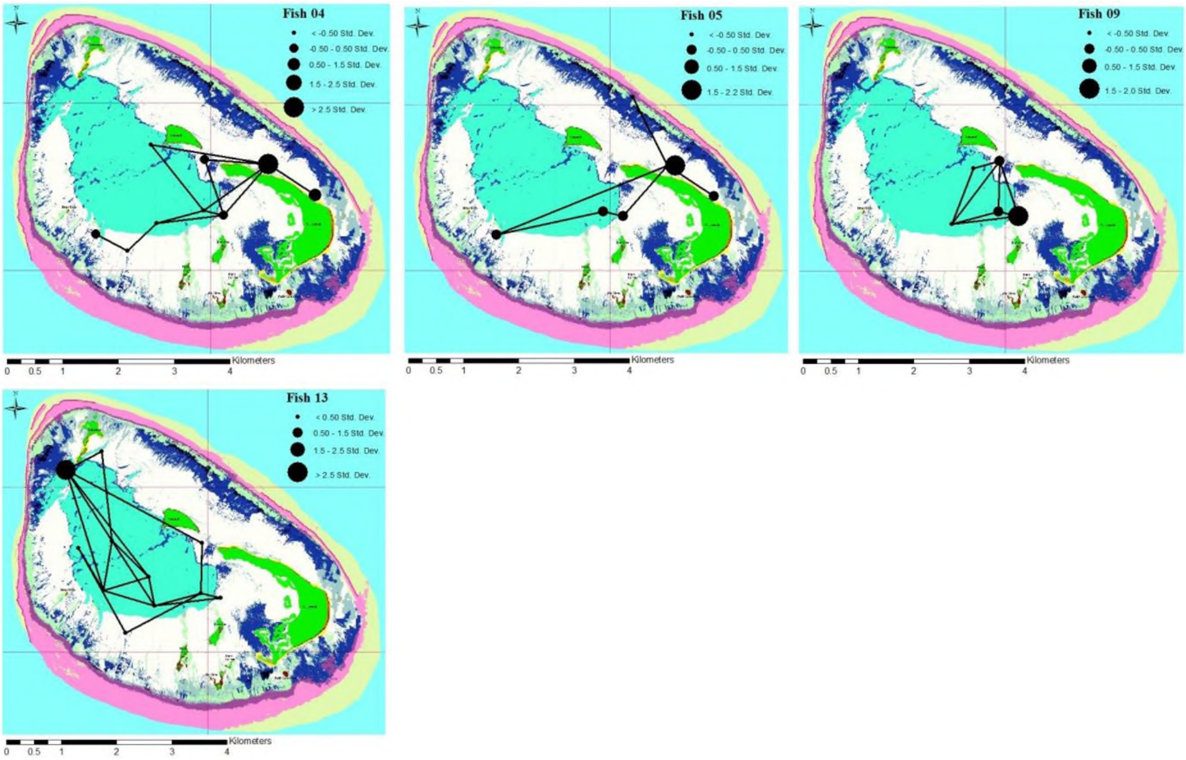
4.3 Results

A total of 30 bonefish were surgically implanted with acoustic transmitters at five different locations within the St. Joseph Atoll. Of the 30 fish tagged, 16 (53%) were considered eligible for further analyses (due to having more than 75 detections on multiple receivers).

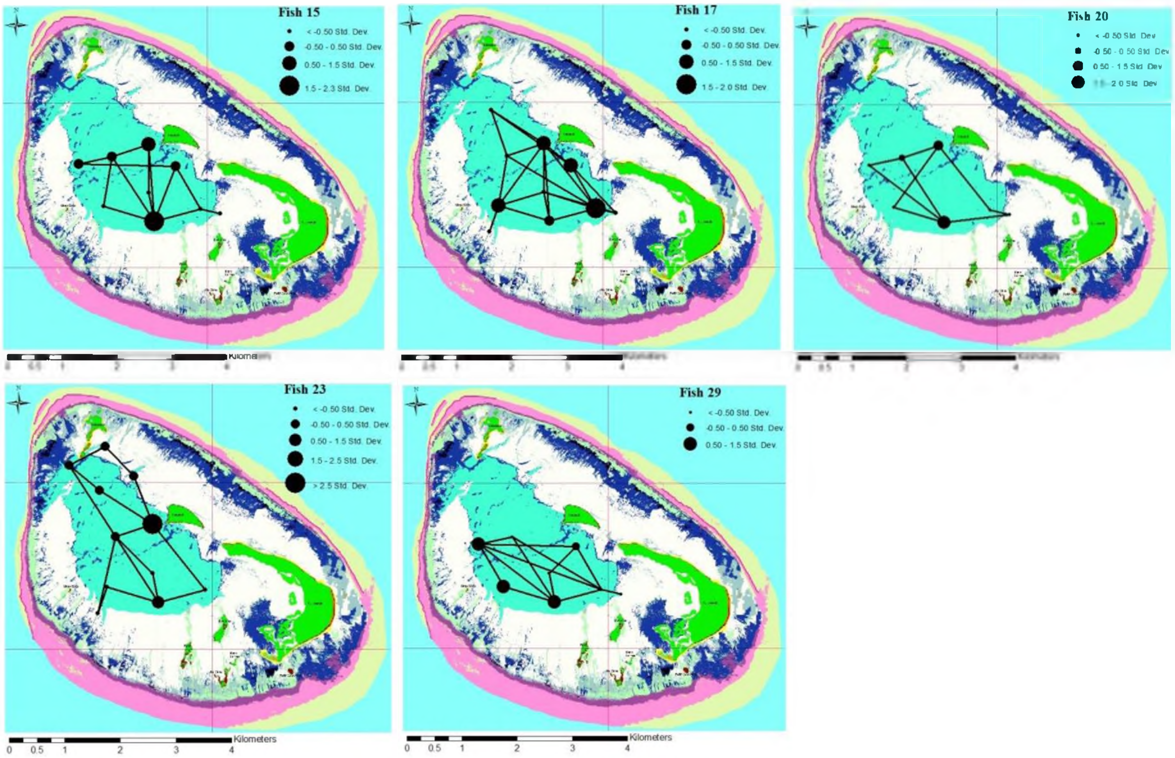
4.3.1 Spatial use of the St. Joseph Atoll

A visual assessment of space use was based on plotted maps of the St. Joseph Atoll, showing the proportion (%) of detections for individual transmitters at each receiver (Figure 4.1). Plots were separated into three groups, (A) majority of the detections found on the sand flats (average ± standard deviation; SD, 89% ± 5% of detections on the sand flats and 11% ± 5% of detections in the lagoon), (B) majority of the detections found in the lagoon (average = 94% ± 7% of detections in the lagoon and, 6% ± 7% of detections on the sand flats) and (C) approximate even spread of detections on the sand flats and in the lagoon (average = 51% ± 8% of detections on the sand flats and 48% ± 9% of detections in the lagoon) (Figure 4.1). Fish that fell into Category 1 (detections for less than two weeks) were found within all three groups. Fish that fell into Category 2 (detected for more than two weeks; fish 14, 19 and 27) were all placed into group C, as the distribution of detections was approximately even (average = 45% ± 3% of detections on the sand flats and 55% ± 3% of detections in the lagoon). Almost all fish, except fish 5, 14, 19 and 27, were detected on one or more of the most centrally located receivers in the lagoon.

(A) Predominantly detected on the sand flats



(B) Predominantly detected in the lagoon



(C) Detections approximately evenly distributed between the lagoon and sand flats

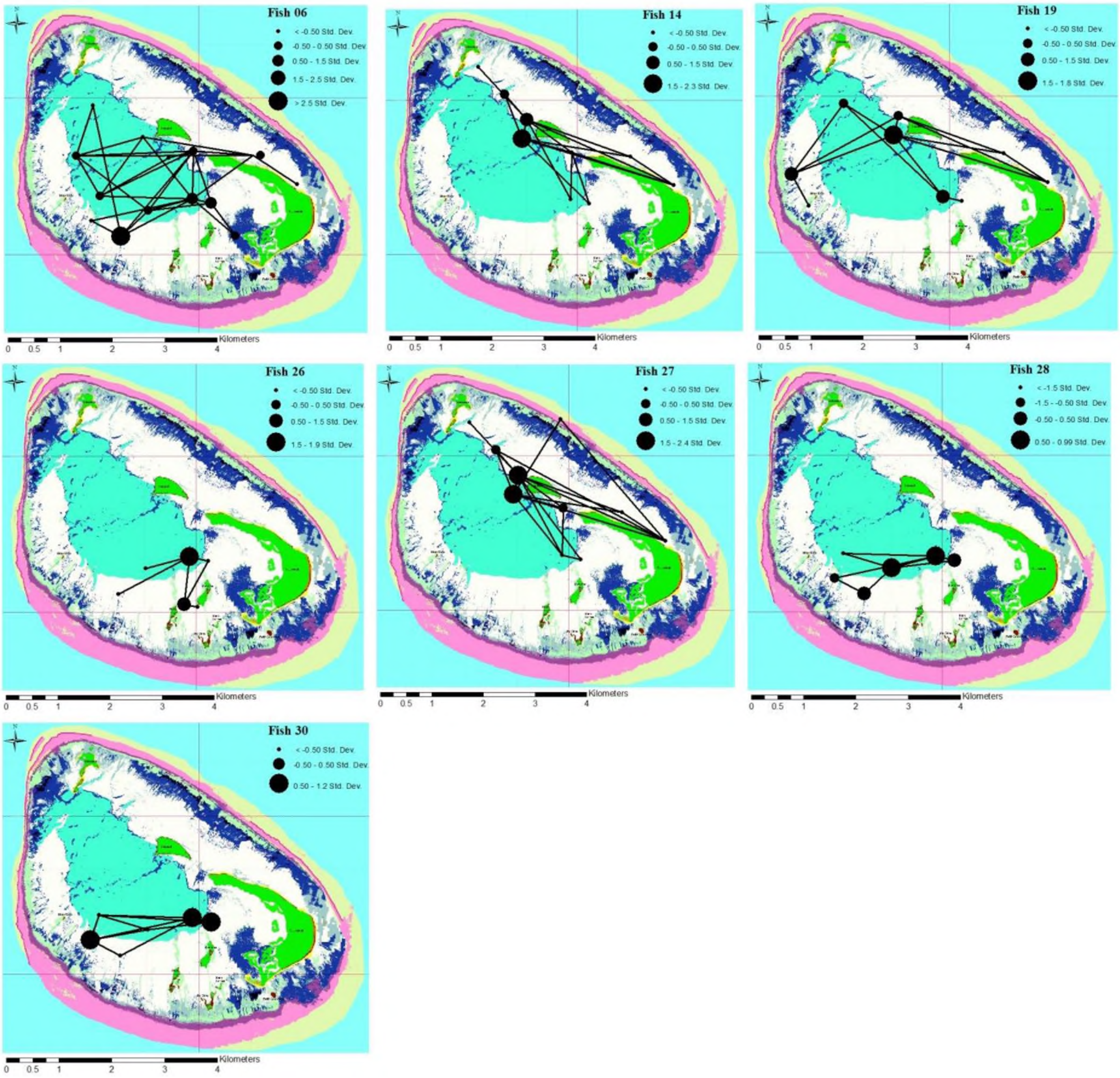


Figure 4.1: Movement trajectories representing the spatial distributions of transmitter detections, with circles scaled to the frequency of detections for each fish at each receiver. Groups display the spatial distributions of the frequency of detections: (A) a greater proportion of detections on the sand flats, (B) a greater proportion of detections in the lagoon and (C) proportion of detections approximately evenly distributed between the lagoon and the sand flats. Base maps adapted from Spencer *et al.* (2008).

4.3.2 Metrics for the assessment of behavioural differences

Three fish in Category 2 (14, 19 and 27) had consistently lower values for their average daily distance (km.day^{-1}), their average speed (m.s^{-1}) and their residency index. Values for the remaining fish in Category 2 were highly variable (Figure 4.2).

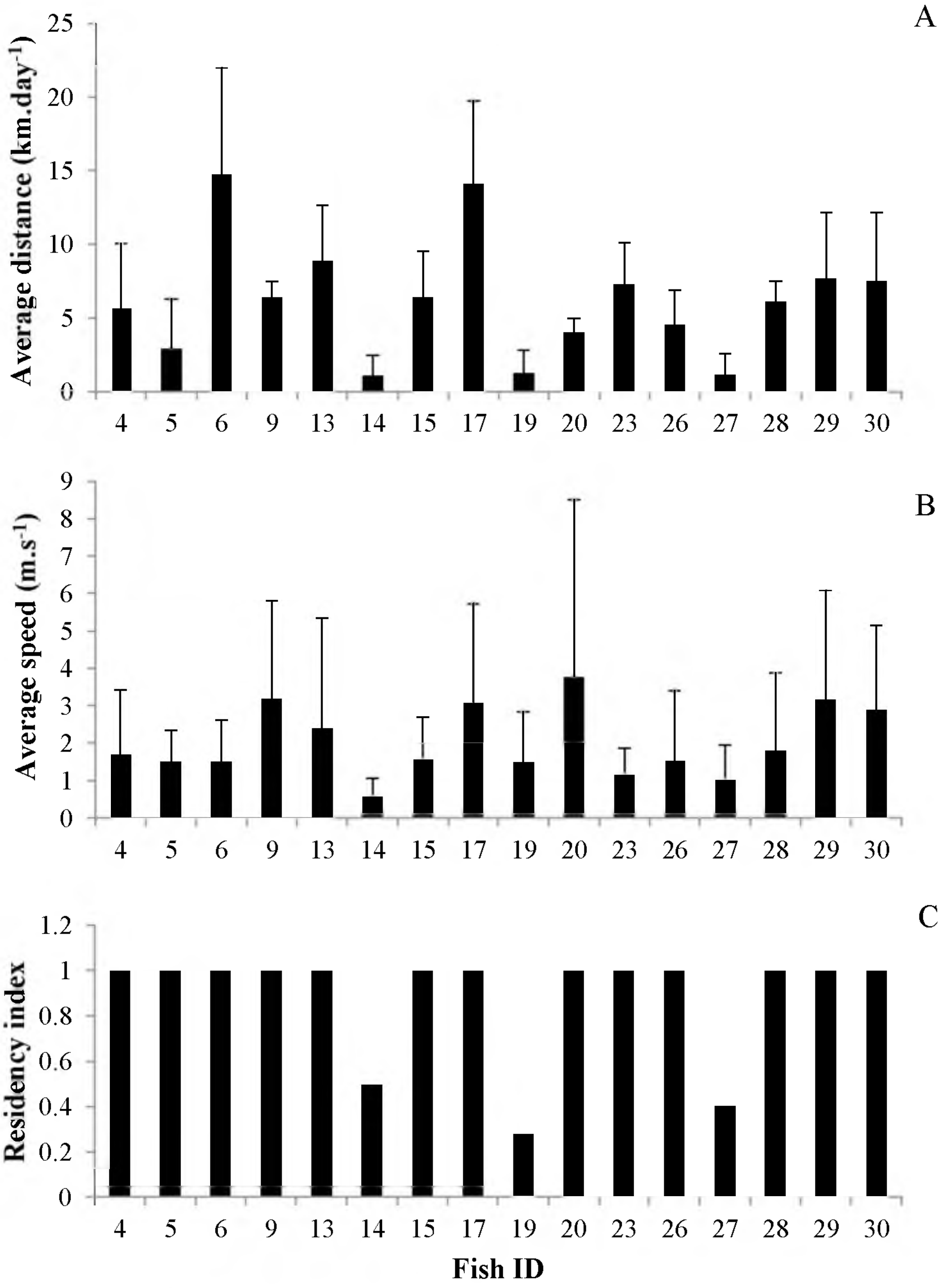


Figure 4.2: Rapid assessment metrics for analysing fish behaviour (A) average daily distance between receivers visited (km.day^{-1}) (± standard deviation; SD), (B) the average speed (m.s^{-1}) between detections at two different receivers (± SD) and (C) residency index (RI).

4.3.2.1 Non-metric multidimensional scaling

Multidimensional scaling (nMDS) of a Bray-Curtis similarity matrix revealed a clear clustering of fish IDs, based on average distance, average speed and RI (Figure 4.3). The cluster analysis separated individuals into five groups with the greatest separation found between Category 1 and Category 2 fish.

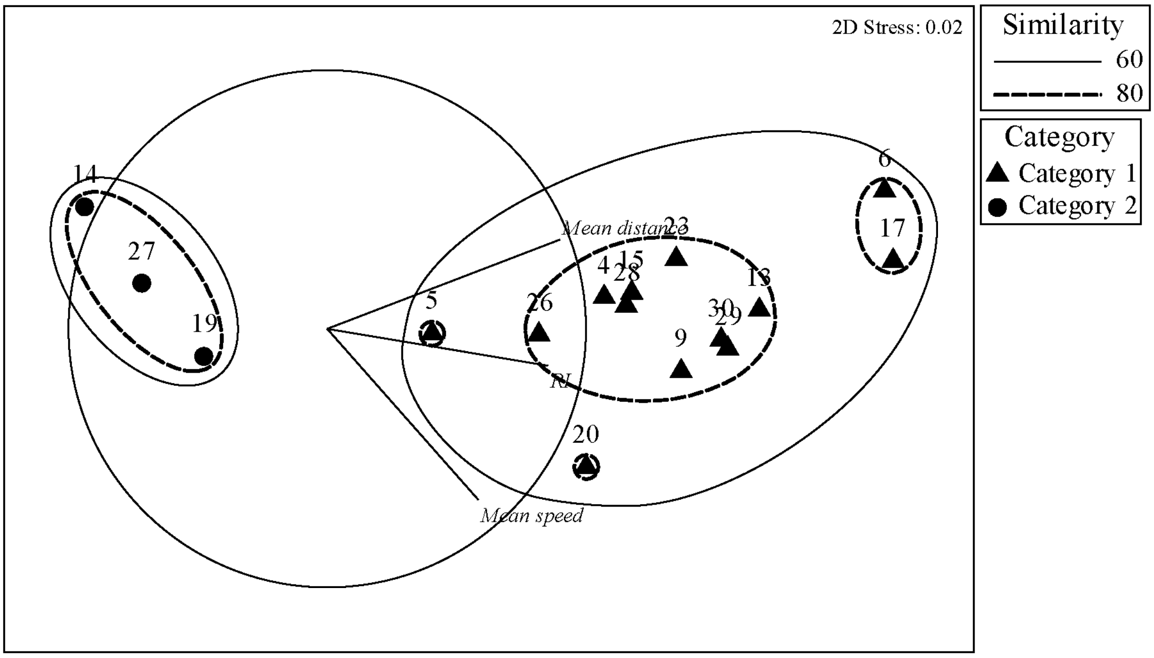


Figure 4.3: Ordination by non-metric multidimensional scaling with a Bray-Curtis similarity matrix based on the effect of average daily distance between receivers per day detected (km.day^{-1}), average speed (m.s^{-1}) and residency index (RI) on the ordinal distribution of 16 tagged fish.

4.3.2.2 Movement characteristics

Comparison of Category 1 and Category 2 movement metrics revealed significant differences in movement distance (km.day^{-1}), speed (m.s^{-1}) and RI between the two groups (Mann-Whitney U test, $Z = 2.56$, $p = 0.011$; $Z = 2.42$, $p = 0.015$ and $Z = -2.56$, $p = 0.011$ respectively). Category 2 fish (average = 1.15 km.day^{-1}, ± 0.095) moved less than Category 1 fish (average = 7.39 km.day^{-1}, ± 3.51) and at a lower average speed (Category 1: 2.25 m.s^{-1}, ± 0.86; Category 2: 1.02 m.s^{-1} ± 0.46). Category 1 fish had significantly higher RI, being present on a daily basis (average = 1 ± 0), than Category 2 fish (average = 0.39 ± 0.11).

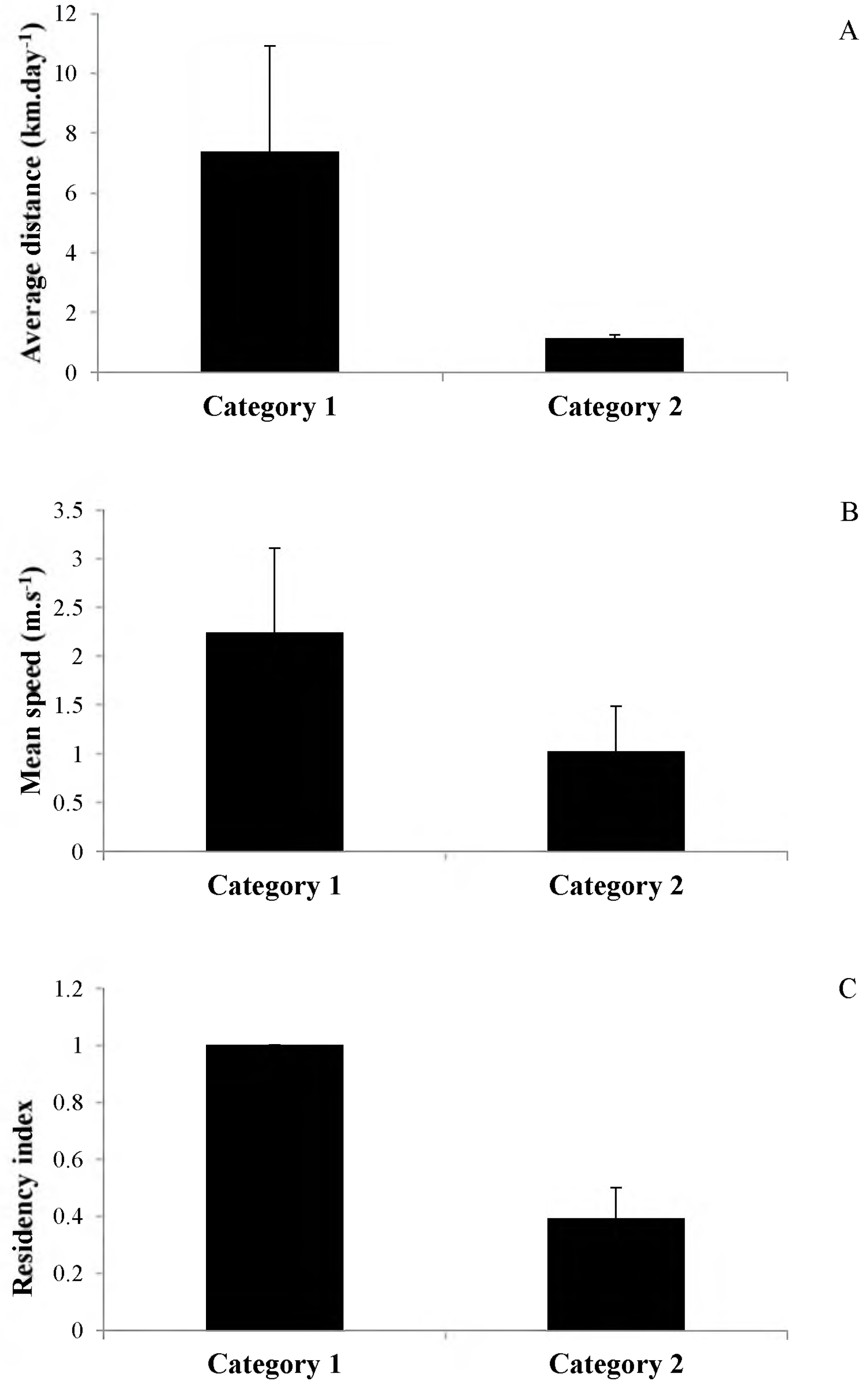


Figure 4.4: Comparisons of movement metrics (average ± standard deviation; SD) (A) average daily distance (km.day^{-1}), (B) average speed (m.s^{-1}) and (C) residency index, between Category 1 and 2 fish.

4.4 Discussion

The transmitters implanted into the bonefish were manufactured to last approximately three years. Therefore, the short duration of tracking (less than two weeks) for the majority of tagged fish raised concerns regarding the probability of predation. From numerous bonefish studies, a high post-release predation rate has been documented (Colton and Alevizon 1983a; Humston *et al.* 2005; Danylchuk *et al.* 2007a, 2007b; Friedlander *et al.* 2008; Murchie *et al.* 2013). However, it was difficult to identify the reason for the short tracking durations as predation cannot be proved unless the predation event was directly observed (Brownscombe *et al.* 2013). In previous studies, the identification of abnormal behaviour was assumed indicative of a predation event (Morrissey and Gruber 1993; Melnychuk *et al.* 2013; Gibson *et al.* 2015). As the St. Joseph Atoll is a predator rich area, data needed to be examined for predation bias before assuming that the observed movements were representative of bonefish. If movement data were analysed without the prior scrutiny of predation events, then the results generated may have provided inaccurate information.

Spatial use and general movement behaviour of marine vertebrates play an important role as movements to certain areas often serve a particular purpose and relate to alternative states of behaviour (Jonsen *et al.* 2007). For instance, the bonefish's use of the sand flats has been associated with feeding and shelter, and their use of the lagoon as a temperature refuge (Humston *et al.* 2005). Furthermore, the movements of large shoals of bonefish between habitats have been linked to nutrient transport among different environments (Murchie *et al.* 2013). Movement trajectories representing tagged bonefish enabled comparison of observed movements with those published for bonefish and other species. High spatial use of the atoll was noted from the movement trajectories, particularly for fish 6, 15, 17, 20, 23 and 29. These fish are all from the short-term movement analysis group (Category 1) and displayed high utilisation of different areas of the atoll, particularly the lagoon environment. This information is contrary to long-term movement patterns (fish 14, 19 and 27) and bonefish literature, which identify the predominant use of the sand flats and margins of the lagoon (Humston *et al.* 2005). Therefore the high use of the lagoon environment indicates abnormal movement behaviour for bonefish. The abnormal movement seen in some Category 1 individuals correlates closely with blacktip and lemon shark movement from the

St. Joseph Atoll (Filmalter *et al.* 2013; Lea *et al.* 2016) (Figure 4.6). The results from the movement trajectories are the first form of evidence suggesting that predation occurred on tagged bonefish and that some acoustic telemetry data likely represent blacktip reef shark or lemon shark movement (the dominant predator in the St. Joseph Atoll) instead of bonefish movement.

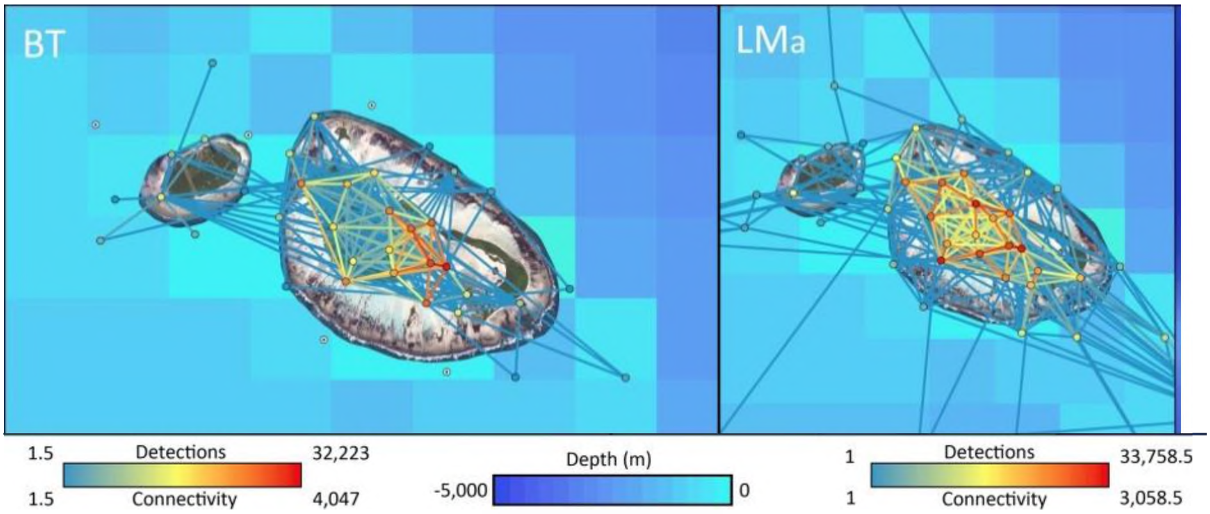


Figure 4.6: Fine-scale movement trajectories of blacktip reef sharks (BT) and lemon shark (LMa) movement in the St. Joseph Atoll (map from Lea *et al.* (2016)).

In addition to the alternative area use, differences in average daily distance moved and the average speed of movement were also observed, between Category 1 and Category 2 fish. In general, a lower average daily distance and a lower average speed of movement were noted for the three long-term surviving fish (fish 14, 19 and 27). The speed and distance that an animal moves can reveal information pertaining to their feeding behaviour, for instance, animals (such as sharks) that feed on mobile species (e.g. bonefish) would need to cover greater distances and move at greater speeds, while fish (such as bonefish) feeding on small benthic organisms (e.g. crustaceans and molluscs) would move slowly across areas where these prey items may occur. In general, sharks feed on larger, more energy-rich meals and therefore need to sustain increased energy demands such as greater speed of movement and increased daily distance travelled in order to find food (Wetherbee *et al.* 1990; Pethybridge *et al.* 2014). Bonefish feed more regularly on smaller and less energy-rich food sources (Colton and Alevizon 1983b). Therefore, while bonefish can achieve high bursting speeds (possibly for predator avoidance (Nowell *et al.* 2015)), their average movements need to be slower in order to find food (e.g. crustaceans and molluscs) within the sand. The different area use of the atoll in combination with differences in behavioural tendencies (speed and distance) while traversing the atoll, suggests that different species, with different needs and ecological roles, were being tracked during this acoustic telemetry study, thus providing evidence of predation bias.

Residency Index showed two distinct patterns: daily detections (average = 1 ± 0) for individuals tracked for short periods (Category 1) and detections within the array on fewer than half the tracking days (average = 0.39 ± 0.11) for individuals tracked for more than two weeks (Category 2). The results from the movement trajectories, average daily distance and average speed reinforce the results of the RI calculations. Greater movement (daily distance and higher average speed) within the atoll, with particular use of the lagoon (which has a greater receiver coverage), increases the possibility of being detected and therefore explains the daily detections noted by Category 1 individuals. In contrast, the long-term surviving fish (Category 2) showed lower average daily distance and speed and less use of the lagoon environment and were, therefore, less active within the array, explaining the lower frequency of detections. The literature on juvenile sharks reports high residency and almost daily detections (Filmalter *et al.* 2013; Lea *et al.* 2016), while the literature on bonefish reports variable RI values, ranging from high to low (Murchie *et al.* 2013). This provides further support that the behaviour observed during this study for Category 1 fish is incongruent with known bonefish behaviour.

When calculating the distance moved per day detected and the average speed, results are subject to bias. The speed of movement for sharks is on average less than 1 $m.s^{-1}$ (Gruber et al. 1988; Papastamatiou 2008; Chin et al. 2013), with a bursting speed of 5.57 $m.s^{-1}$ reported for lemon sharks (Sundström *et al.* 2001), while bonefish velocity has been shown to range from 0.18 to 6.4 $m.s^{-1}$ (Larkin 2011; Brownscombe et al. 2014). Speed estimates in this current study may be an underestimation or an overestimation as they assume that (1) the fish movement was in a straight line and (2) the fish moved from the base of one receiver to the base of the next, therefore not accounting for alternative movement pathways or detection range (Gruber *et al.* 1988; Hedger *et al.* 2010). In the St. Joseph Atoll, detection range varies between 100 m and more than 300 m depending on the location (sand flats or lagoon), tide, weather and time of day (Elston 2016). However, the stark contrasts between the tracks considered to represent bonefish and those considered to represent sharks, in terms of speed and distance, suggest that these estimates were sufficiently accurate in the context of this study. The average daily distance and average speed therefore give only relative estimates, suitable for comparison within this study; however the results do not represent the actual speed or distance moved by a fish.

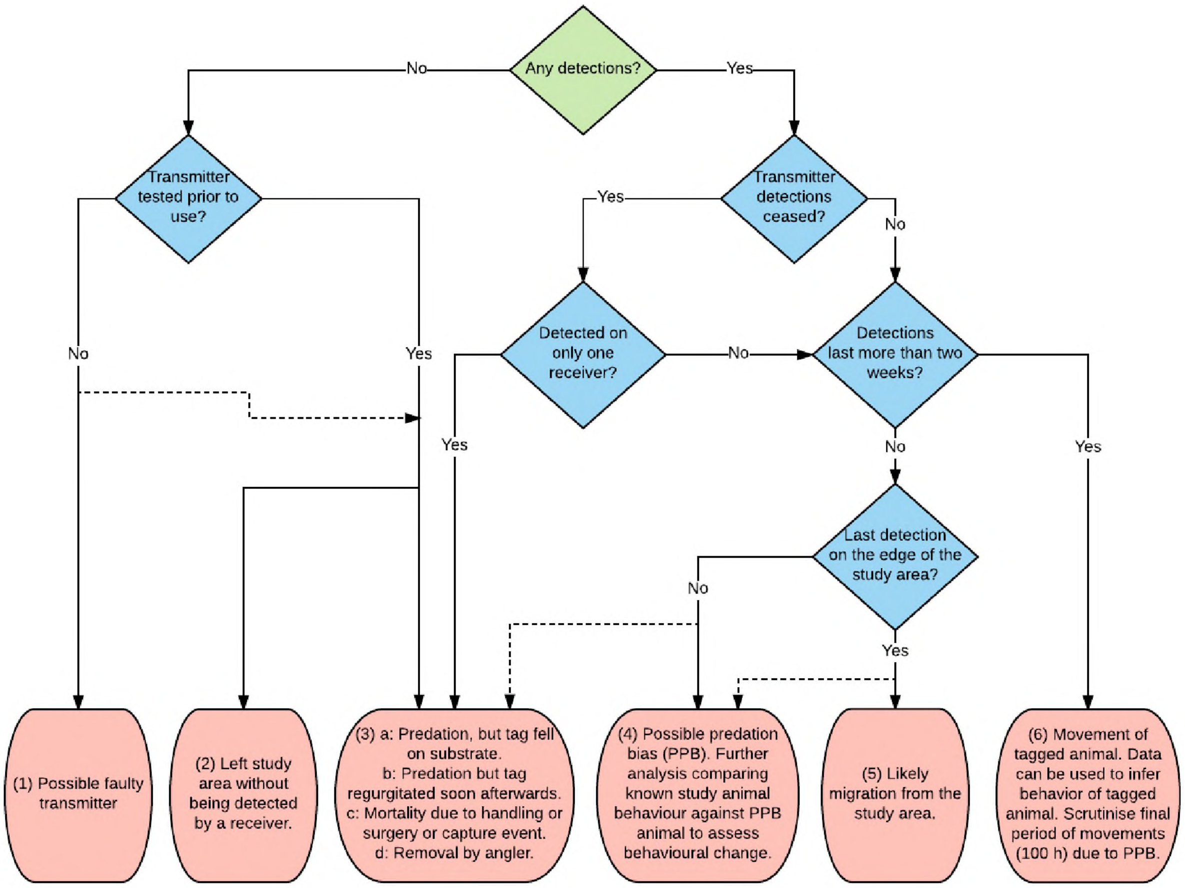
Using the metrics average distance, average speed and RI, non-metric multidimensional scaling confirmed the separate grouping of individuals into two categories based on short term and long term tracking periods (Categories 1 and 2 respectively). Non-metric MDS plots and the parametric principal component analysis (PCA) can be used in a variety of circumstances and have been commonly used by taxonomists to test for speciation, with the clustering of different criteria serving as supporting evidence of different species (Hedgecock *et al.* 1988; Olavo *et al.* 2011). Similarly, the nMDS used in this analysis provided supporting evidence for two categories, namely bonefish (Category 2) and other (Category 1). The separation of the individuals within the nMDS is further evidence of abnormal behaviour and therefore predation bias within this study.

Within the nMDS, the cluster of Category 1 displays high variability. This variability was possibly due to the different predators (black tip reef sharks and lemon sharks) present within the atoll or due to the uncertain retention time of the transmitters ingested by the predators. Some of the Category 1 individuals may thus be displaying partial bonefish and shark movement behaviour. However, the standard deviation accounts for this variation, for example, Category 1 had a high standard deviation indicating that the movement seen shows high variability among and within individuals. Within Category 1, before extracting the final 100 h of movement data, some fish were tracked for as long as 12 days. It is possible, although unlikely that this was shark movement the entire time. A more probable explanation was that the bonefish survived for a few days before predation occurred. The possible survival time of more than two days was contrary to the literature, which often states that bonefish are preyed upon within the first 48 hours post-release, with the majority of events occurring within the first few minutes post-release (Danylchuk *et al.* 2007a). Therefore, considering the longer tracking periods relative to the short retention time of transmitters ingested by sharks, it is unlikely that all the fish were preyed upon within the first 48 hours. Therefore, the predation event would have taken place after blood cortisol levels had returned to normal (Dallas *et al.* 2010; Shultz *et al.* 2011; Szekeres *et al.* 2014). The increased survival time of bonefish post-release suggests that alternative factors to post-release stress need to be considered. Factors that could have increased bonefish vulnerability to predation include prolonged recovery from surgery and decreased camouflage due to the wound gel powder used in this study (which can remain on the fish for a period and sets as a blue colour).

From the results of the nMDS, the initial categorisation was confirmed and individuals were grouped and the two groups were compared using the median of the average daily distance, average speed and RI. Significant differences were noted, with Category 1 fish (which likely display shark behaviour) exhibiting significantly greater daily distance, speed and RI, confirming the presence of abnormal behaviour within this category and therefore predation bias in this study. The abnormal behaviour observed was due to the gastric ingestion of the transmitter by predators (most likely either blacktip reef sharks or lemon sharks) and therefore the tracking of the predator's movements as opposed to bonefish movement. From the evidence presented above, predation in this study may also account for the 14 fish that could not be analysed due to insufficient detections on multiple receivers, and therefore predation may have accounted for up to 90% of post-release mortality of bonefish in this study.

4.4.1 Future acoustic telemetry data analysis recommendations

In this study, evidence of predation was strong and demonstrated the need for scrutiny of telemetry data for predation bias before analyses. However, alternative scenarios such as faulty transmitters (Dresser and Knieb 2007), migration from the study site (Childs 2005; Danylchuk *et al.* 2011b), angling (Cowley *et al.* 2008) and mortality due to the tagging process (Jepsen *et al.* 2008) may also result in loss of tagged animals (most of which were ruled out in this study). A simple flow chart is proposed, which will enable future telemetry studies to rapidly assess their data for predation bias before analysis (Figure 4.7).



	Legend
🟩	Starting question
🔷	Question
🟥	Final
→	Leads to
⇢	Possible alternative

Figure 4.7: Flow diagram for a rapid assessment of survival estimates and possible alternatives such as a faulty transmitter, migration from the study area, angling, natural mortality and possible predation bias (PPB) in telemetry data.

4.5 Conclusion

In an attempt to reduce mortality of tagged bonefish post release, the development of best handling practices has been documented within the literature. The most widely accepted methods for improving survival rate were to reduce air exposure and handling time and keep bonefish in an isolated area where they are free from predators and can recover to a state of equilibrium before release (Cooke and Philipp 2004; Humston *et al.* 2005). However, despite following best handling guidelines, the discontinuation of tracking data (within a two week period) in areas with medium to high predator abundance has been observed in this study and several others (Danylchuk *et al.* 2007b; Murchie *et al.* 2013). Conversely, bonefish studies in isolated areas, or areas with very low predator abundance, report multiple recapture events of the same fish, poor handling and releasing the fish before it has fully recovered; yet mortality events are negligible (Crabtree *et al.* 1988; Danylchuk *et al.* 2007a). High predator abundance may, therefore, be the greatest reason for a high mortality rate (Cooke and Philipp 2004).

The results of this study indicate that mortality due to predation is an important factor, and consideration of post-release predation when implementing management strategies for catch-and-release fisheries is important. Post-release survival estimates and studies are usually conducted in controlled laboratory environments and therefore do not take predation into account (Crabtree *et al.* 1988; Raby *et al.* 2014). These results are then used to advise management of the sustainability of fisheries in the wild. The results of this study and many others indicate that management protocols for sustainable and effective management approaches need to take potential predation into account, as the effects can be exceptionally high.

Chapter 5

Spatial and temporal movements and habitat use patterns of *Albula glossodonta*

Photo Credit: Thomas Peschak

“Not all those who wander are lost.” ~ JRR Tolkien

5.1 Introduction

Understanding the movement of an animal elucidates population processes, habitat use and fine-scale environmental influences (Hussey *et al.* 2015). This can aid in further identification of essential areas for feeding, spawning and shelter of a multitude of species (Welsh and Bellwood 2012). Such information can inform managers of the most effective methods for the conservation of a species (e.g. marine protected areas), which can differ depending on the species' home range, habitat use and economic importance (Grüss *et al.* 2011).

Understanding the movement of aquatic animals is further complicated by the many factors that influence their movement on a daily, monthly and annual basis, as well as how each life stage may respond to such changes (Palmer 1973). Fish movement may be affected by the gravitational pull from the movement of the moon around the earth, and the earth around the sun, which affects patterns such as diel (24 h), tidal (12.4 and 24.8 h) and lunar (28 day) cycles (Morgan 2001). Light-dark cycles determine diel patterns and affect fish movement and area use. For example, goatfish *Parupeneus porphyreus* migrate to different feeding habitats depending on the diel cycle (Meyer *et al.* 2000). Tidal cycles can affect fish movements in that the rise and fall of water may change the accessibility that fish have to different habitats for feeding and shelter (Gratwicke and Speight 2005).

In this study, the movement of bonefish in the Seychelles was investigated. There have been several bonefish movement studies, however, based on the extensive review (Chapter 3), this study was the first acoustic telemetry study on bonefish in the Indian Ocean and the first account of long-term acoustic tracking (> 24 days) of *Albula glossodonta*. The movements of other bonefish species have been related to cyclical patterns such as diel, tidal and lunar phases (Colton and Alevizon 1983a). During high tide, bonefish move from the deeper lagoon onto the shallow sand flats to feed and take shelter from predators (Humston *et al.* 2005). Furthermore, bonefish have also been shown to move into deeper water in response to elevated temperatures in the shallows (Murchie *et al.* 2011a, 2013).

Spawning patterns have been linked to lunar cycles, with sexually mature bonefish (50% maturity for *A. glossodonta* at 410 mm FL and 437 mm FL for males and females, respectively) moving offshore during the full moon of the lunar phase (Friedlander *et al.*

2008; Donovan *et al.* 2015). Offshore spawning during spring high tides has been related to an increase in larval dispersal (Doherty *et al.* 1985; Domeier and Colin 1997). However, many of these spawning aggregations have been negatively affected by fisheries and industrial or urban development (Johannes and Yeeting 2000; Friedlander *et al.* 2008; Murchie *et al.* 2015).

Many coastlines around the world are becoming increasingly urbanised and it is essential that the biodiversity of these ecosystems are preserved (Hickley 1998; Halpern *et al.* 2015). To date, all successful acoustic telemetry studies on bonefish have been conducted in coastal areas that have been affected by human development and fisheries (recreational, subsistence or small-scale commercial) (Ault *et al.* 2005; Humston *et al.* 2005). Impacts of urbanisation and overfishing on predator-prey relationships have been reported, with apex predators usually being the first to disappear from populated areas (Salinas de León *et al.* 2016). The once pristine bonefish environments of Florida, the Bahamas and Kiritimati Atoll (the Republic of Kiribati, Central Pacific), have all undergone substantial changes due to overfishing, ineffective management guidelines, urban development and pollution (Cooke and Philipp 2004; Friedlander *et al.* 2008; Murchie *et al.* 2015). In contrast, the St. Joseph Atoll in the Indian Ocean offers the opportunity to study bonefish in a near-pristine environment. Thus, by studying bonefish movements in the predator rich St. Joseph Atoll, this study will be able to contribute knowledge towards the development of baseline information on bonefish movement in a near-pristine habitat.

The aim of this study was to assess the spatial and temporal movements and habitat use patterns of bonefish in the St. Joseph Atoll. The specific objectives of this chapter were (1) to identify the habitat use of bonefish and to classify areas of high use, (2) to determine home range size relative to total area use of the atoll and the surrounding environments, and (3) to identify the effects of cyclical patterns (diel, tidal and lunar) on bonefish movement and habitat use.

5.2 Methods

Details of the study site, research approach and filtering of detections were described in Chapter 2. Data generated from the acoustic tags were screened and assessed for predation bias (see Chapter 4). Due to high levels of predation only long term surviving fish (ID codes 14, 19 and 27) were used in this chapter. Data from the one year download was used in this chapter. The final days of receiver detections for each of the three fish were examined for abnormal behaviour (as described in Chapter 4). Fish 14 had a sudden increase in mean daily distance moved from day 197 onwards (possible predation by a shark) and thus subsequent detections were excluded from the analysis.

5.2.1 Habitat use

To facilitate this study, the atoll was divided into two habitats namely the lagoon environment (receivers 1 to 9) and the sand flats (receivers 10 to 32). According to the location of daily detections, an abacus plot was constructed in R 3.2.1 (R Core Team 2015), with colour coded bands representing the spatial use of the atoll (lagoon, sand flats or both) on a daily scale over the tracking period.

5.2.2 Residency Index

A residency index (RI) was calculated for each of the three tagged fish by dividing the total number of days that each transmitter was detected by a receiver by the total number of monitored days (Abecasis and Erzini 2008). Residency index was expressed as a proportion from 0 (lowest, completely absent) to 1 (highest, detected every day).

5.2.3 Space use

The minimum convex polygon (MCP) is the area that encompasses all the known location points of a given animal for a particular period (Papastamatiou *et al.* 2009). The MCP for each of the three individuals was calculated in ArcView 10.2 (Environmental Systems Research Institute Inc., Redlands, California). The area of overlap for all three fish was calculated and represented graphically.

5.2.4 Temporal patterns

5.2.4.1 Daily presence in the St. Joseph Atoll in relation to lunar cycles

The locations of bonefish were assessed in relation to lunar cycles, using Oriana software (version 4.1, Kovach Computing Services, Anglesey, Wales). Data obtained from two areas in the atoll were used in this analysis: (1) areas of high use, based on receivers with the highest proportion of detections (namely receivers 6, 7, 15 and 16) and (2) receivers at the north-eastern edge of the atoll (receivers 28 and 29) based on the preliminary analysis of data revealing a possible pattern. Data were inserted as dates of positive detections for each fish. Results were represented as circular rose diagrams (expressed as angles), divided into eight sections (45° each) with each section representing and centred on a different phase of the moon. Lunar phases included new moon (0°), waxing crescent (45°), first quarter (90°), waxing gibbous (135°), full moon (180°), waning gibbous (225°), third quarter (270°) and waning crescent (315°).

The mean lunar phase for days that fish were positively detected was calculated as mu (μ) indicating the mean angle, "r" the mean vector length and "n" the numbers of times that the fish was detected at the receivers (Batschelet 1981). The mean angle of positive detections for the three fish was then calculated on Oriana, using the mean angle of positive detections from each fish. Mean vector length ranged from zero (no significant clustering of data points) to one (indicating that the data were closely clustered around the mean). The Rayleigh's Test of Randomness assessed the unimodal distribution and the probability that the data were not randomly distributed (Batschelet 1981). The Rayleigh's Test was displayed visually on the plots in the form of an arrow (Kovach 2011). The Rao's Spacing Test assessed the bimodal distribution and the probability that the data were not normally distributed (Batschelet 1981; Rao 1976).

5.2.4.2 Hourly presence in the St. Joseph Atoll in relation to tidal and diel patterns

Cyclical patterns of bonefish movement were assessed using Fast Fourier Transform (FFT) in R 3.2.1 (R Core Team 2015). Fast Fourier Transform decomposes time series data and constructs visual peaks of cyclical data in the form of spectral density plots in the frequency domain (Papastamatiou *et al.* 2015). The presence or absence of each fish per habitat category (lagoon, sand flats or both) was placed into hourly bins for analyses using a FFT. No smoothing factor was applied to the FFT.

5.2.4.3 Diel area use

To assess the effects of time of day (day or night) and habitat type (lagoon or sand flats) on area use, the proportions of detections for each fish occurring within each time of day and habitat type combination were compared using the parametric one-way analysis of variance (ANOVA) and a Tukey post-hoc multiple comparison test (Dell™ Statistica™, StatSoft. Inc., USA)(Alpha was set at 0.05). Transmitter detections were classified as day (06:00-17:59) or night (18:00 to 05:59) and detection location: lagoon or flats receivers. Numbers of detections in each category were log-transformed prior to analysis.

5.2.4.4 Effects of environmental variables on presence in the lagoon

A generalised linear mixed model (GLMM) with a binomial distribution and a log-link function was fitted to the presence-absence data and was used to determine if environmental variables had an effect on the presence of bonefish in the lagoon. The GLMM method was originally chosen due to its ability to incorporate random effects (such as individual fish) and compute binomial and non-normal data or data that is subjected to autocorrelation (Bolker *et al.* 2009; Zuur *et al.* 2009). Presence/absence in the lagoon was used as the response variable, water temperature (°C) on the sand flats (measured on receiver 15), tide and diel period (day (06:00 to 17:59) or night (18:00 to 05:59)) were included as fixed effects and individual fish ID was included as a random effect. As the response variable was of the form of presence (1) or absence (0), the binomial family was used when computing the data (Zuur *et al.* 2009).

The model selection process was run for all factors (independent and combined), and the best fit model (the model with the lowest Akaike Information Criterion (AIC)) was selected for representation. The 'Wald' chi-square statistic and p-value were then used to test the level of significance of the fixed effects (Alpha was set to 0.05). Models were computed in R 3.2.1 (R Core Team 2015), using the *lmer* function from the package *lme4* (Bates *et al.* 2015).

5.3 Results

Analyses of the 30 bonefish tagged with acoustic transmitters revealed that only three were eligible for further analyses as the remaining 27 had either insufficient detections or were suspected of displaying predation bias (see Chapter 4). Three fish (ID codes 14, 19 and 27) accounted for a total of 9310 detections on 12 different receivers from the 08/05/2015 to the 08/05/2016. Analyses were limited to these three fish.

5.3.1 Spatial patterns

5.3.1.1 Habitat use

The tagged bonefish were detected for an average (± standard deviation; SD) of 45% (± 10%) of the total number of days of their respective monitoring periods (188, 363 and 303 days for fish 14, 19 and 27 respectively). Residency indices for fish 14, 19 and 27 were 0.48, 0.34 and 0.54 respectively. Absence periods ranged from 1 to 26 consecutive days during their respective monitoring periods. The mean percentage of days (± SD) (of the 45% of the days detected) that a fish spent at each habitat type was 18% (± 2%) on the flats, 9% (± 3%) in the lagoon and 18% (± 12%) in both habitats (Figure 5.1).

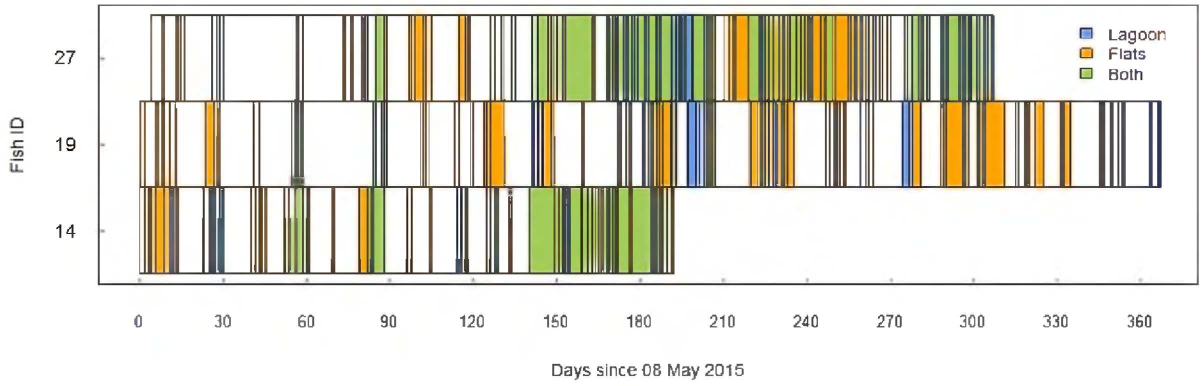


Figure 5.1: Daily habitat use of bonefish (fish 14, 19 and 27) over the tracking period. Habitats include lagoon (blue), sand flats (orange) and daily detections on both the lagoon and sand flats receivers (green). White spaces represents periods of absence.

5.3.1.2 Home range

The total area of the St. Joseph Atoll is 21.8 km^2. Average area usage of the three bonefish, as calculated by MCP, was 5.42 km^2 (± 1.85 km^2; 27% of the atoll). Fish 14 used an area of 3.36 km^2 (15% of the atoll) over six months, fish 19 used an area of 5.96 km^2 (27% of the atoll) over 12 months and fish 27 utilised an area of 6.95 km^2 (32% of the atoll) over 10 months (Figure 5.2). The MCP showed that bonefish remained primarily within the atoll boundaries, using a variety of habitats including reef flat sand (sand flats), lagoon, medium density seagrass and algae and spur and groove rock (Figure 5.2). The margin of the lagoon and the sand flats along the northern side of the atoll were utilised most frequently by the fish (Figure 5.2), which also represents the area of overlap in home ranges of the three fish (Figure 5.2A).

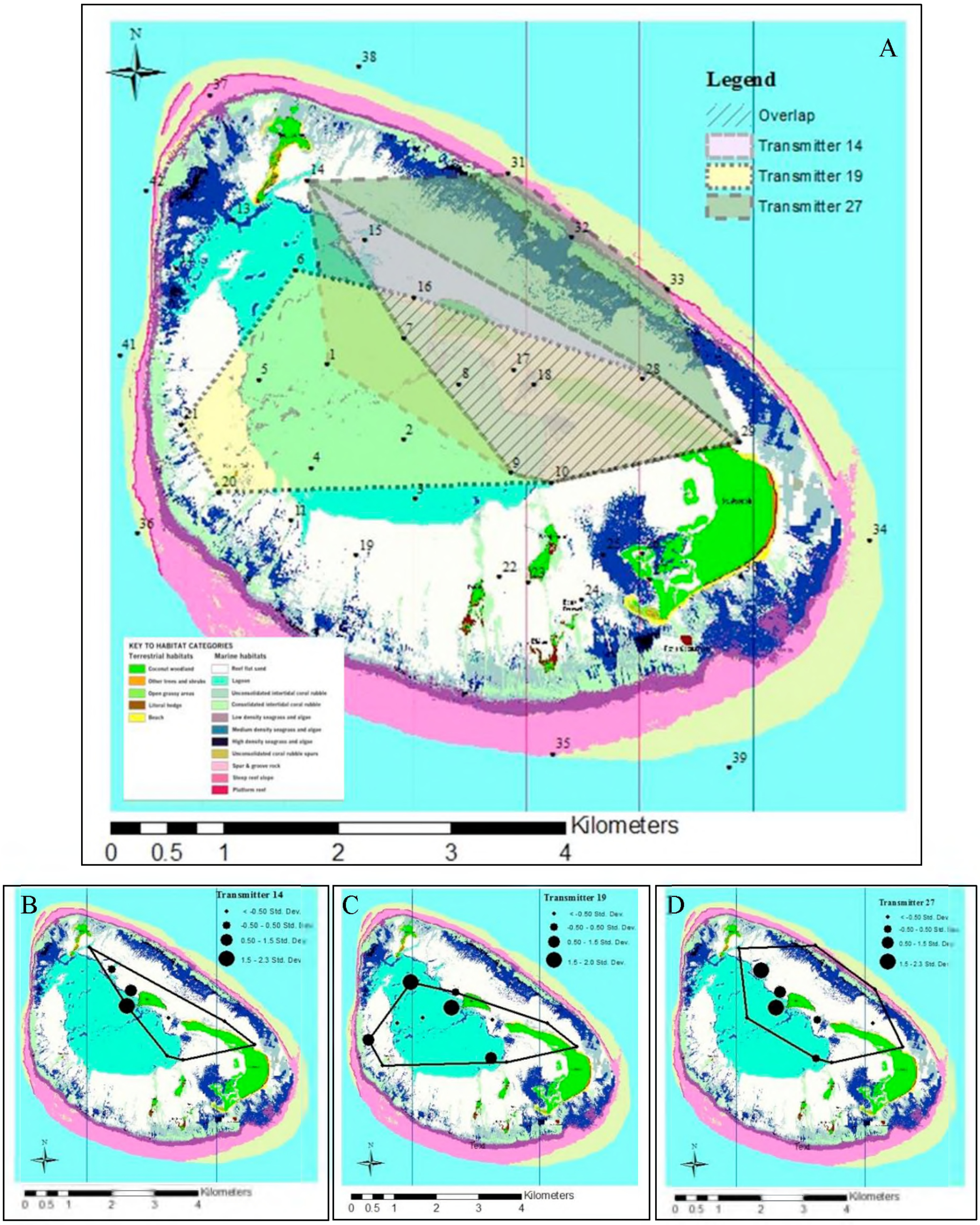


Figure 5.2: Minimum convex polygon delineating the home ranges of the three bonefish tracked over a period of six months to one year fish 14 (purple; 3.36 km^2), fish 19 (yellow; 5.96 km^2) and fish 27 (green; 6.95 km^2) (colours refer to Figure 5.2A). Diagonal line shading denotes the area of overlap (2.44 km^2) of all three fish. Circles sizes in Figure 5.2B, C and D are proportional to the number of detections at each receiver and display the individual MCP plots for fish 14, 19 and 27 respectively.

5.3.2 Temporal patterns

5.3.2.1 Effects of lunar cycles

Lunar phase had a significant influence on the presence of fish at receivers bordering the lagoon and the sand flats on the north-eastern side of the lagoon (receivers 6, 7, 15 and 16, Roa's Spacing Test, Figure 5.4). For fish 14 (mean lunar phase = waning gibbous, $\mu = 238.95° \pm 113.39°$, $r = 0.14$, $n = 87$, $p < 0.01$), fish 19 (mean lunar phase = waning gibbous, $\mu = 192.02° \pm 127.06°$, $r = 0.09$, $n = 125$, $p < 0.01$) and fish 27 (mean lunar phase = waxing crescent, $\mu = 47.6° \pm 186.03°$, $r = 0.01$, $n = 150$, $p < 0.01$) standard deviations were high, and data were not closely correlated around the mean vector angle for the average of the mean of the three fish (mean vector angle ± SD; 201.72 ° ± 89.64°; Figure 5.3). However, Roa's Spacing Test indicated a bimodal distribution, particularly with the uniformity of detections surrounding full and new moon (spring tide) and the absence (or reduction) of detections at the 1st and 3rd quarters (neap tides). No significant unimodal directional lunar trend was noted for fish 14, 19 and 27 ($p = 0.177$, $p = 0.401$ and $p = 0.996$ respectively; Rayleigh's Test of Randomness).

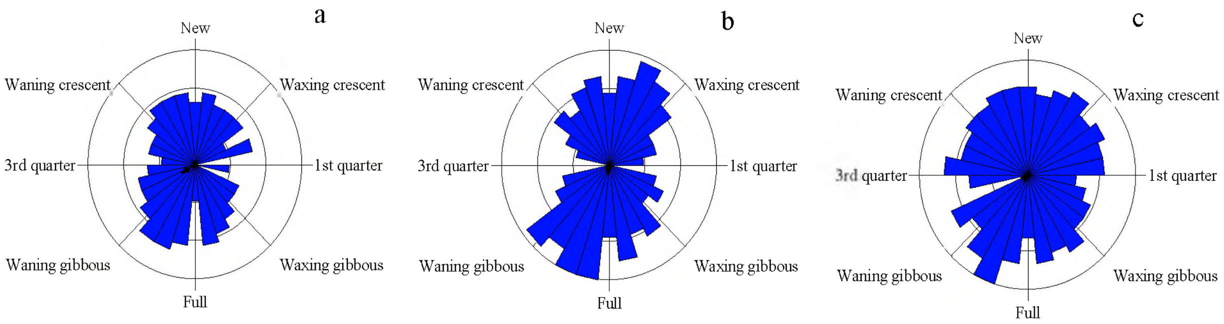


Figure 5.3: Rose diagram showing the effect of lunar phase on the presence of fish 14 (a), 19 (b) and 27 (c) at receivers with the greatest proportion of detections (6, 7, 15 and 16) at the St. Joseph Atoll.

Detections at receivers 28 and 29, on the north-eastern rim of the atoll, were recorded for multiple months over the tracking period (from 04/06/2015 to 31/12/2015). Trips to the north-eastern rim of the atoll always took place when the tidal range was above the 90th percentile, indicating the influence of the spring tidal phase. Lunar phase had a significant influence on the presence of fish at the north-eastern rim of the atoll, with presence at receivers 28 and 29 occurring predominantly during the waning gibbous lunar phase (mean vector angle for the three fish was 221° ± 4°, Rayleigh Test of Randomness). Dates of individual trips for fish 14 (mean lunar phase = waning gibbous, $\mu = 216° \pm 7°$, $r = 0.991$, $n = 7$, $p < 0.01$), 19 (mean lunar phase = waning gibbous, $\mu = 225° \pm 9°$, $r = 0.988$, $n = 5$, $p < 0.01$) and 27 (mean lunar phase = waning gibbous, $\mu = 222° \pm 11°$, $r = 0.982$, $n = 13$, $p < 0.01$) displayed a strong correlation around the mean and had low standard deviations (Figure 5.4). A significant bimodal distribution was noted for fish 14, 19 and 27 ($p < 0.01$, $p < 0.01$ and $p < 0.01$ respectively; Rao's Spacing Test).

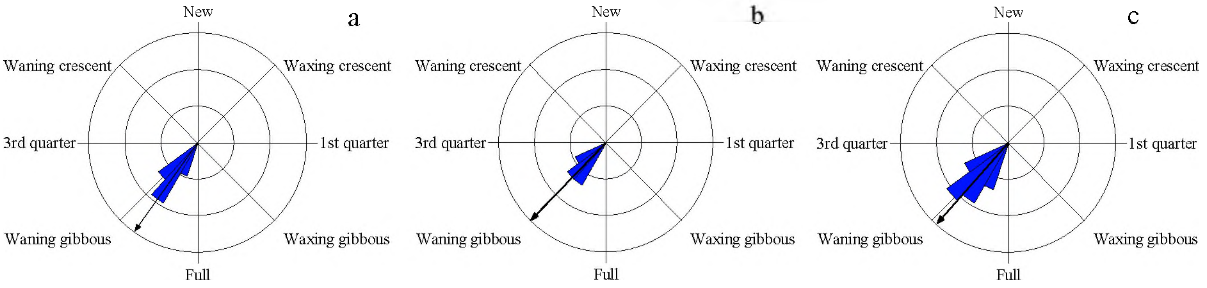


Figure 5.4: Rose diagrams of the effect of lunar phase on the presence of fish 14 (a), 19 (b) and 27 (c) at receivers 28 and 29 on the outer north-eastern rim of the St. Joseph Atoll.

5.3.2.2 Effects of tidal and diel cycles

Spectral analysis using FFT data obtained from hourly detections (presence/absence) of the three bonefish at the St. Joseph Atoll revealed diel (24 h) cyclical patterns, but no tidal (12.4 h) or lunar day (24.8 h) patterns. Fish 14 and 27 displayed diel peaks for all atoll (graphs a and g) and lagoon (c and i) detections, however, no peaks were observed for the detections on the sand flats (b and h). Fish 19 (graphs d, e and f) showed no cyclical peaks in presence/absence data in any habitats (Figure 5.5).

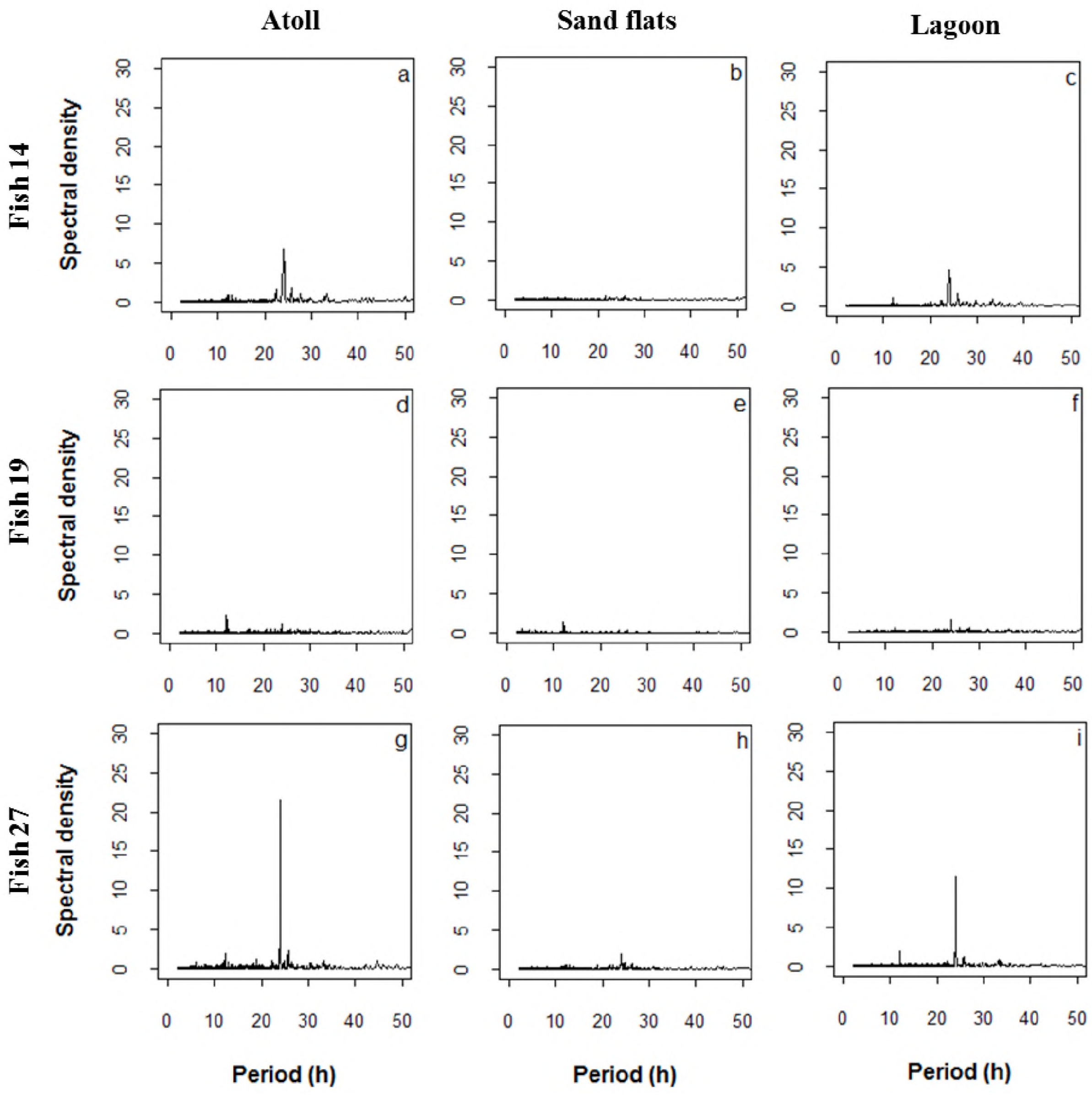


Figure 5.5: Spectral density plots of the presence-absence data collected from the three surviving bonefish, fish 14 (a, b and c), 19 (d, e and f) and 27 (g, h and i), from the atoll, sand flats and lagoon (left to right).

5.3.2.3 Diel Area Use

Significant differences in area use were observed (ANOVA, $F_{(3,8)} = 13.27$, $p = 0.0018$). The greatest proportion of detections was logged in the lagoon during the day (50.34% ± 9.32%) and the least in the lagoon at night (6.00% ± 2.75%). From the Post hoc test, the significant differences were found to occur between the lagoon (day) and the lagoon (night), lagoon (day) and the flats (night) and, lagoon (night) and the flats (day) (Tukey HSD, df = 8, p = 0.0022, p = 0.0138 and p = 0.0116 respectively) (Figure 5.6).

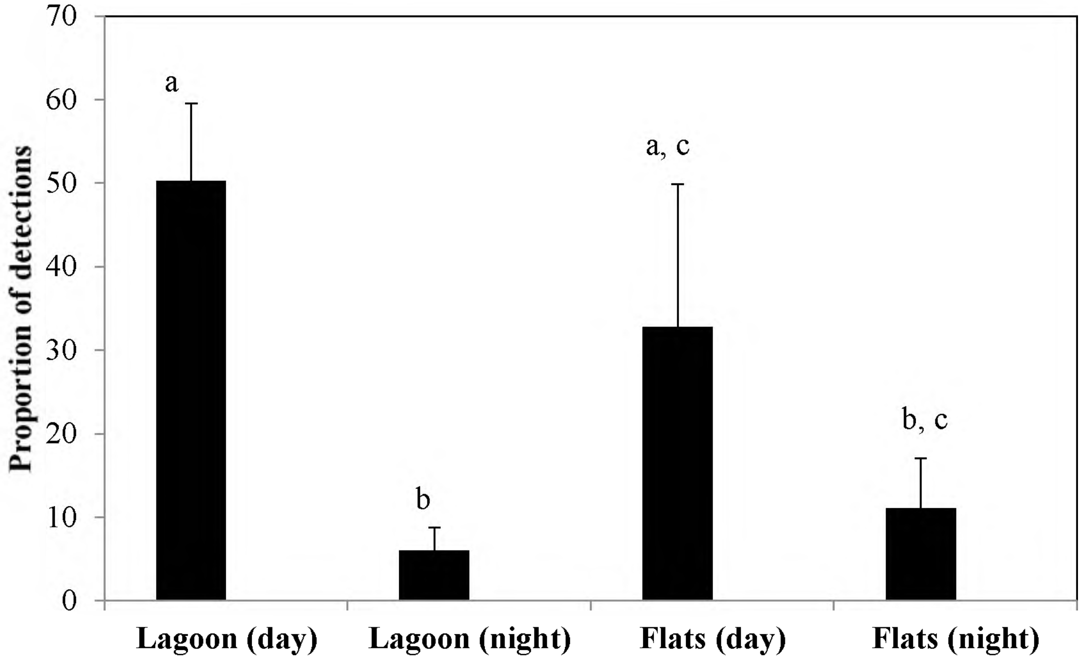


Figure 5.6: Mean proportions (%) (± SD) of day and night detections recorded on the sand flats and in the lagoon of the atoll for bonefish. Different letters indicate significant differences.

5.3.2.4 Effect of environmental variables on presence of bonefish in the lagoon

The probability of fish being present in the lagoon increased significantly with increased water temperature on the sand flats (W = 368.24, $p < 0.0001$) and decreased tidal height (W = 5.5303, p = 0.01869), but was significantly reduced at night (W = 22.87, $p < 0.0001$) (Table 5.1). This indicates that fish were most likely to be present in the lagoon during the day when the temperature on the sand flats was high and the tide was low.

Table 5.1: Coefficients of a generalised linear mixed model, showing the effect of water temperature (°C) on the sand flats, tidal height and diel period on the presence of bonefish in the lagoon. Using Wald chi-square statistics (Wald Chisq), standard error (SE), and degrees of freedom (df). Stars denote significance.

	Estimate	SE	Wald Chisq	df	Pr (>Chisq)	
Intercept	-23.5492	3.4134				
Temperature	0.9323	0.0486	368.2414	1	<0.0001	*
Tide	-0.5899	0.0251	5.5303	1	0.01869	*
Diel (night)	-1.7615	0.2250	22.8674	1	<0.0001	*

5.4 Discussion

Bonefish movements have been well studied in many parts of the world. Knowledge of the spatial movement of bonefish is important for identifying areas vital to the support of bonefish stocks. Shallow sand flats are important to bonefish in atolls and coastal habitats (Johannes and Yeeting 2000; Cooke and Philipp 2004); however, movements to nearby deeper waters have also been recorded (Danylchuk *et al.* 2011b). Their movements have been related to lunar cycles, tidal fluctuations, water temperature change and predator avoidance (Colton and Alevizon 1983a, 1983b). The sand flats are considered to be an important feeding site, yet they also offer protection from predators given the limited ability of larger animals to move in the shallow water (Humston *et al.* 2005). However, during low tide the sand flats may not be covered by enough water and water temperatures may rise to critical levels, thus bonefish may seek refuge in the lagoon (Murchie *et al.* 2011a).

In this study, bonefish were not detected beyond the confines of the St. Joseph Atoll, despite the receiver array covering adjacent deeper waters. Tagged fish made use of both habitats (the lagoon and sand flats) and their movements were dependent on temperature, tide and diel period.

5.4.1 Spatial patterns

The MCP plots suggested that bonefish showed fidelity to the atoll environment. Despite being criticised for overestimating area use and habitat range (Anderson 1982; van der Lingen *et al.* 2001), the MCP plots suggest that bonefish use a relatively small portion of the atoll (5.42 km^2 ± 1.85 km^2; 27% of the atoll). This finding is supported by studies elsewhere, for example, Humston *et al.* (2005) and Kamikawa *et al.* (2015) found that individuals or groups of bonefish are highly resident, with fish frequently using an area of about 1.5 km^2. However, some studies have also reported movements away from the study area for long periods (up to 339 days) or across great distances (> 100 km) (Colton and Alevizon 1983; Larkin *et al.* 2008; Murchie *et al.* 2013).

Atolls generally exhibit high biological productivity and have a broad range of habitats (Pugh and Rayner 1981; Acosta and Robertson 2003; Friedlander *et al.* 2014). The high frequency of detections at the northern margin of the lagoon and sand flats could be due to the advantageous location within the atoll. This area has a diversity of habitats, thereby providing access to food resources and shelter from predators on the sand flats and refuge from high temperatures in deeper waters (Pugh and Rayner 1981; Acosta and Robertson 2003; Friedlander *et al.* 2014). Furthermore, the use of one area offers the benefit of familiarity which can optimise feeding, movement efficiency and predator avoidance (Hansler and Wisby 1958; Jadot *et al.* 2006).

5.4.2 Temporal patterns

5.4.2.1 Effects of the lunar cycle

Fish movements often coincide with temporal patterns such as lunar phase and seasonal patterns (Erisman *et al.* 2012; Taylor and Mills 2013; Dadswell *et al.* 2016). This study showed that the presence of bonefish at the northern margin of the lagoon and sand flats (receivers 6, 7, 15 and 16; receivers with the greatest proportion of detections) had no directional lunar trend (Rayleigh's Test of Randomness) with bonefish detected almost consistently throughout the lunar cycle. However, a significant bimodal relationship between periods of decreased and increased detections was noted (Rao's Spacing Test), with a decrease in detections during the 1st and 3rd quarters of the moon, and an increase in detections during the new and full moon periods for all three fish (particularly fish 19).

The decrease in detections coincided with neap tides, while an increase in detections coincided with spring tides. Unlike neap tides, spring tides provide periods of increased water depth on the sand flats providing better access to the shallower regions of the sand flats, which may allow for periods of high activity (thus increasing the chance of detections) during high tide. Furthermore, the tidal current of a neap tide is not as intense as that of spring tides. Fish movement has been found to follow strong flooding tides, yet neap tides do not exert a strong directional force (Krumme 2004). Therefore, the increased movement prompted by the flooding tide during new and full moon most likely increased the possibility of detection during these periods.

If bonefish did leave the atoll, for example for the purpose of foraging or spawning, their movements would likely be predictable (Erisman *et al.* 2012; Taylor and Mills 2013; Dadswell *et al.* 2016). One predictable movement pattern was noted during the waning gibbous (shortly after full moon) in a north-easterly direction towards the outer rim of the reef flat (receivers 28 and 29). Because detections were relatively few at these locations, these trips were difficult to discern and at times it was not possible to distinguish a genuine detection from a false detection. All single detections were regarded as false and subsequently excluded. Despite this, a discernible pattern remained. The infrequent detections at each receiver suggest that fish did not stay in the area for extended periods and the detections were probably due to transient movement to another location, possibly towards the outer edge of the reef flat or further offshore to greater depths (the eastern side of the atoll descends to depths greater than 2 000 m within 4 km of the shore (Selin *et al.* 1992)). These trips always occurred during the waning gibbous moon at tidal heights above the 90th percentile. All of the three surviving tagged bonefish were greater than 500 mm FL and were therefore likely sexually mature (Friedlander *et al.* 2008; Donovan *et al.* 2015). The timing (two days after full moon) and movement trajectories (to offshore drop off points) of bonefish to receivers 28 and 29 can be linked to reports on bonefish spawning behaviour. Previous studies have recorded spawning trips which contain large groups of mature bonefish (100 s to 1 000 s) (Johannes and Yeeting 2000; Friedlander *et al.* 2008; Danylchuk *et al.* 2011b) to oceanic drop off points (Colton and Alevizon 1983a; Vásquez-Yeomans *et al.* 2009; Murchie *et al.* 2015). These trips occur at a particular stage in the lunar cycle and during a specific season (Pfeiler *et al.* 1988; Donovan *et al.* 2015). For example, Johannes and Yeeting (2000) and Friedlander *et al.* (2008) reported spawning aggregations of *A. glossodonta* shortly after or around full moon at the sand flat and reef interface. The location and periodicity of a possible spawning ground has management implications as spawning migrations are typically vulnerable to overfishing and habitat alterations (Robinson *et al.* 2015). However, the low sample size and lack of further evidence such as visual observations and gonadal dissections means that further investigation is required before spawning can be confirmed.

5.4.2.2 Tidal and diel patterns

Predictability of fish movement makes fish more vulnerable to fishing pressure, but also easier to manage (Grigg 1994; Meyer *et al.* 2000). Fish movement is strongly influenced by temporal patterns such as the lunar phase (outlined above), tides, water temperature and photoperiod (Kessel *et al.* 2014). From the literature, it was expected that bonefish movement would be affected by the tidal phase, photoperiod and temperature (Colton and Alevizon 1983a; Brownscombe *et al.* 2014; Nowell *et al.* 2015). In this study, the GLMM indicated that bonefish movement was affected by the above factors. However, the FFT analyses, aimed at detecting tidal, diel and lunar day effects, identified only diel patterns in the tagged bonefish's movement.

Daily patterns in habitat use show that bonefish were detected for an average of 45% (± 10%) of all the days of the study period and that bonefish total area use was divided between the lagoon (9% ± 3%), sand flats (18% ± 2%) and both habitats on the same day (18% ± 12%). The high use of the sand flats was consistent with the literature, which commonly reported bonefish (particularly *A. glossodonta* and *A. vulpes*) on the sand flats and other shallow water habitats (Donovan *et al.* 2015; Kamikawa *et al.* 2015). High use of the sand flats may be due to their dietary preference of crabs, molluscs, shrimps, polychaetes, etc. which are commonly found in this habitat (Friedlander *et al.* 2008; Donovan *et al.* 2015) and predator avoidance as the sand flats are often too shallow for large-bodied fish and sharks (Humston *et al.* 2005). However, the lagoon environment is essential as a temperature refuge as bonefish are sensitive to extreme temperatures. According to Murchie *et al.* (2011a), the critical thermal maximum of *A. vulpes* was 36.4 ± 0.5°C and 37.9 ± 0.5°C for fish acclimated to 27.3 ± 1.3°C and 30.2 ± 1.4°C, respectively. Temperatures recorded on the shallow water sand flats at the St. Josephs Atoll sometimes exceed these values. Furthermore, most mobile large-bodied organisms have been found to retreat into deeper water during the extreme low tide, as the shallow water reduces their ability to move (von Brandis 2012). The isolated daily use of either the lagoon or sand flats is contrary to the tidal movement of bonefish between the two habitats as reported in the literature (Colton and Alevizon 1983a; Humston *et al.* 2005; Murchie *et al.* 2011a). If bonefish movements in the current study were related to tidal phase, then detections on both the lagoon and sand flats would be expected on a daily scale.

A lack of tidal movement was also noted in the FFT analysis. The FFT decomposes time series data and constructs visual peaks which can be used to discern the temporal patterns driving fish movements, namely tidal (24.8 h), diel (24 h) and lunar (28 days) (Morgan 2001; Papastamatiou *et al.* 2015). However, the FFT only revealed a diel cyclical period for bonefish movement in the lagoon, but no tidal patterns, as may be expected from the literature. These diel patterns appeared to be related to two main factors, namely photoperiod and temperature change (Meyer *et al.* 2007).

Diel patterns in detections can be caused by an increase or decrease in movement. For example, species such as the cow bream (*Sarpa salpa*) were less mobile during the day (Jadot *et al.* 2002). Furthermore, the decrease in activity is often periodical and location-specific, as has been identified in multiple species (Jadot *et al.* 2006). Diel changes in depth or use of refuges can also affect the ability to detect a species, as was the case for the sixgill shark (*Hexanchus griseus*) and the ballan wrasse (*Labrus bergylta*) (Andrews *et al.* 2009; Morel *et al.* 2013). The diel peaks in the FFT of the two bonefish were associated with a decrease in night time detections, particularly in the lagoon. This may be due to a reduction in night time activity, use of alternative habitats, or a combination of these. Literature on diel changes in bonefish movement is not consistent. Humston *et al.* (2005) and Brownscombe *et al.* (2014) reported that diel patterns were a predictor of bonefish behaviour (e.g. resting, swimming, bursting, coasting and foraging). They found an increase in swimming activity during daylight hours (particularly dawn) and foraging on the sand flats at night. However, Murchie *et al.* (2011b) found no diel change in acceleration values or activity patterns for bonefish. Furthermore, bonefish may make more extensive use of the sand flats at night as they do not require the use of the lagoon as a temperature refuge. As predators are known to influence the habitat selection of fish (Brown *et al.* 1999), the use of the sand flats at night by bonefish may also reduce their contact with predators, especially during low tide and thus reduce their chance of predation.

Although tide was not a predictor of bonefish movement according to the FFT, the GLMM identified water temperature on the sand flats, diel period and tidal height, to be significant predictors of bonefish movement into the lagoon. An increase in water temperature, coinciding with a decrease in tidal height during daylight hours positively influenced bonefish presence in the lagoon. Solar heating occurs during the day, and to a greater extent at low tide, resulting in bonefish being more likely to move into the lagoon during the low tidal phase during the day. This reflects the findings of the previous bonefish movement studies which have shown that water temperature on the sand flats and tide have a significant influence on bonefish movement (Humston *et al.* 2005), with bonefish using the lagoon environment when water depth is insufficient on the sand flats and/or when the water temperature exceeds optimal (Murchie *et al.* 2013). Since global sea surface temperatures are predicted to rise (Klein *et al.* 1999), this may have implications for bonefish populations worldwide. An increase in water temperature may force bonefish to use the lagoon environment more regularly, which may increase their vulnerability to predators and decrease their ability to feed.

5.4.3 Absence periods

The findings of this study suggest that bonefish make consistent use the atoll environment; however, daily detection frequencies were low. Despite the comprehensive array of acoustic receivers, gaps in detections (absence periods; no detections for a day or an hour) accounted for an average of 55% (± 10%) of time on a daily scale, and 92% (± 4%) on an hourly scale. The presence/absence of transmitters over a period of time (more than two weeks) and the movement of bonefish among receivers indicate that the bonefish were alive; however, for the majority of the tracking period, the fish were located in areas of limited detection range. The acoustic telemetry array in and around the St. Joseph Atoll comprises 88 receivers spread across a large portion of the Amirantes Bank, spanning an area of 6 213.3 km^2 (MCP). Given the comprehensive array of acoustic receivers covering portions of the surrounding islands and marine area and the absence of detections on receivers outside the atoll, migration from the atoll was unlikely.

This study has revealed high use of the sand flats habitat, most likely due to food availability and predator avoidance. Calculations of receiver coverage, assuming a 300 m radius, in the two different habitats revealed that the sand flats had less coverage (40%) compared to the lagoon habitat (53%). Therefore, bonefish were likely to be present within the atoll (possibly on the sand flats) for the majority of the study period, but undetected due to decreased coverage. Humston *et al.* (2005) reported a similar finding in their study and predicted that bonefish were located on the sand flats during this period. These results highlight the importance of the sand flats for bonefish, yet receiver coverage in this area is evidently lacking. Increased coverage of the sand flats would enable an improved temporal analysis. However, due to the low water depth during spring low tide, an increase in the number of receivers on the sand flats was not feasible.

5.5 Conclusion

The results of this study suggest that bonefish are resident to the atoll and highlights the importance of the sand flats and the lagoon habitat to bonefish. Low tide in combination with high water temperature on the sand flats during the day accounted for bonefish movement into the lagoon habitat. The lack of tidal patterns in the FFT may be related to a combination of decreased movement on the sand flats and/or the reduced detection range in this area. Bonefish movement followed a diel pattern. Bonefish tended to use the lagoon to a greater extent during the day, when temperatures were higher on the flats and tidal height was low. Yet, during the night a decrease in detections was noted (particularly in the lagoon). This decrease in night time detections could be due to a reduction in night time activity, occupying the sand flats for night time foraging and/or a possible decrease in detection range.

A series of fixed sentinel tags stationed around the atoll at a few key sites would provide a better understanding of the coverage in the different areas of the atoll. These range tests would further be able to assess if individual receivers were subject to diel variability. Additional bonefish studies, particularly investigating the spawning migration, would be highly beneficial as the St. Joseph Atoll is an important refuge for bonefish.

Chapter 6

General discussion

Photo Credit: Chantel Elston

"Life is either a great adventure or nothing at all" ~ Helen Keller

Several species of bonefish *Albula* spp. are targeted in major ecotourism-based fisheries around the world. The economic importance of bonefish has generated considerable research interest in places such as Florida, Bahamas and Hawaii. Conversely, bonefish *Albula glossodonta* in the Indian Ocean has received no research attention despite a well established and growing recreational fly fishing tourism industry. Therefore, this study aimed to contribute to the knowledge of *A. glossodonta* in the Indian Ocean, by (1) conducting a literature review on the *Albula* genus, to identify the global distribution and themes of research interest and allow for the identification of research gaps (Chapter 3); (2) conducting an acoustic telemetry study to investigate movement behaviour, which initially involved an evaluation of post-release mortality and an investigation into the possibility of predation bias (Chapter 4); and (3) evaluating habitat use patterns and movement behaviour of acoustically tagged bonefish, thus contributing new biological information on *A. glossodonta* in the Indian Ocean (Chapter 5).

6.1 Literature review

The review of scientific literature on the *Albula* genus indicated that bonefish research has increased over time; however much of the research has been concentrated around the United States of America, Mexico and Central America, with focus on only one species (*Albula vulpes*). Published accounts were categorised into five research themes including (in order of dominance): biology; taxonomy; management; ecology and finally a category including all other studies.

In the first 60 years (1946 – 2006), research was almost completely dominated by biological studies, however the focus within these biological studies has changed over time. Early research was dominated by early life history studies (eggs and larvae studies) and physiology with a recent shift to behavioural (movement) studies. Taxonomy and systematics research increased considerably over the last 20 years given the recognition of a worldwide species complex of the *Albula* genus. Increased research attention in certain disciplines is likely to relate to technological advancements, such as acoustic telemetry (movement studies) and improved molecular application for genetic studies.

In the last decade, management became the most dominant theme. This was possibly due to the reported decline of bonefish stocks in many parts of the world (Frezza and Clem 2015). Due to the economic value of bonefish a decline could have negative social impacts, thus spurring research to investigate the cause and possible mitigation effects to curb the observed declines. In comparison to biology, taxonomy and systematics and management, dedicated ecological studies have been poorly represented. Consequently, the conservation of bonefish would benefit from further ecological investigations.

The literature review revealed an alarming dearth of knowledge on bonefish in the Indian Ocean. As such, extending the geographical range of bonefish research should become the primary focus for future studies. The current study was the first to address this research gap.

6.2 Tagging impacts and the consideration of predation bias

To address the lack of knowledge of bonefish in the Indian Ocean and to address the second and third research objectives, an acoustic telemetry study was conducted at the St. Joseph Atoll (Amirantes Bank, Seychelles). Post-capture mortality of bonefish, mostly accredited to predation, has been frequently reported in the literature. In Chapter 4, movement patterns of bonefish from data downloaded from the acoustic receivers after a period of six months were assessed for abnormal behaviour. A comparison of the movement patterns of long-term surviving fish (fish detected for more than two weeks) against short-term survivors revealed differences in area use, daily distance moved, speed of movement and residency. The behaviour of the short-term surviving bonefish matched existing information on shark movement behaviour and served as evidence for predation of tagged bonefish. The results of this study demonstrated the high susceptibility of bonefish to post-release mortality in predator-rich areas such as the St. Joseph Atoll. In contrast to previous studies, it is unlikely that all predation events occurred within minutes after release (Danylchuk *et al.* 2007a), rather, some of the events likely occurred within a period of days. These results may bias movement studies that assume that fish surviving this time frame survive in general (Cooke and Philipp 2004; Brownscombe *et al.* 2013). The high mortality rate (of up to 100% reported by Friedlander *et al.* (2008)) may be a combination of post-release stress in the short term and bonefish serving as an important food source for sharks in the long term. Future research to assess the importance and prevalence of bonefish in the diet of sharks is recommended to generate information of relevance to these discussions.

The high mortality rate (90%) found in the current study has important management implications as it suggests that catch-and-release bonefish fisheries in predator-rich areas are not benign. Accordingly, it is recommended that sustainable management interventions are developed in such instances.

6.3 Spatial and temporal movements of bonefish

The aim of this study was to provide baseline information on the ecology of *A. glossodonta* in the Indian Ocean, specifically in relation to their spatial and temporal movements. Although bonefish predominantly used the sand flats and lagoon environment; extended periods of absence from these habitats were also noted. While these periods of absence may have been as a consequence of fish departing the atoll, bonefish were never detected on the extensive array of receivers outside of the atoll. The periods of no detections are likely due to the high use of the sand flats, which are intertidal and often exposed thus limiting acoustic receiver coverage. Therefore, bonefish possibly used the sand flats more than the data suggested. This information is consistent with the literature, which suggests that bonefish use the sand flats for feeding and as a refuge from sharks (particularly during high tide) (Humston *et al.* 2005). During low tide, bonefish increase their use of the lagoon, particularly when there is insufficient water on the sand flats during the day or when water temperatures on the sand flats exceed the thermal optimum (Murchie *et al.* 2013).

Cyclical patterns such as tide, hour and lunar phase are important factors in predicting bonefish movements. Tidal movement of bonefish from the sand flats into the lagoon at low tide has been noted in previous studies (Murchie *et al.* 2013). However, the current study only found partial evidence to support this pattern. The Fast Fourier Transform (FFT) identified no cyclical movement patterns in relation to tides, yet the effects of tidal height, water temperature on the sand flats and time of day in the generalised linear mixed model (GLMM) were significant predictors of bonefish presence in the lagoon. This supports the hypothesis that bonefish use the lagoon environment as a temperature refuge during midday high water temperatures (Humston *et al.* 2005), although further studies are needed to fully understand the effects of tide on the behaviour of *A. glossodonta*.

Lunar cycles are related to tidal fluctuations and are the cause of spring tides during new and full moon every 14 days (Morgan 2001). The lunar cycle was a significant predictor of bonefish location within the atoll. In general, bonefish were present at the margin of the sand flats and the lagoon, but during the waning gibbous they tended to move towards the north-eastern edge of the atoll. This movement links closely with previous descriptions of bonefish movement for the purpose of spawning. Danylchuk *et al.* (2011) identified spawning migrations of thousands of bonefish over certain seasons and lunar cycles. Spawning migrations are an extremely vulnerable life history stage that can be severely impacted by development and fisheries (Friedlander *et al.* 2008). Thus, locating and protecting the spawning site and/or period is fundamental to bonefish conservation.

To my knowledge, this was the first successful acoustic telemetry study conducted on *Albula* spp. in a near-pristine environment, the first long-term acoustic monitoring of *A. glossodonta* and the first bonefish study to be conducted in the Indian Ocean. The primary research aim was most comprehensively addressed in Chapter 5. Unfortunately, the low sample size due to the high levels of predation, as explained in Chapter 4, limits the power of the study. Despite these confines, the study reflects pioneering research on bonefish in the Indian Ocean and provides vital information that can serve as a guideline for management considerations and future studies.

6.4 Future studies

The literature review highlighted that almost nothing is known about bonefish in the Indian Ocean; therefore, an extension of this study would be beneficial. One way to improve management of a fishery is to provide an evaluation of the economic income generated through the fishery and thus its value to local economies (Fedler 2013). Like other areas of the world, bonefish fishing in the Seychelles attracts a large number of tourists and generates substantial revenue per annum (Wallace 2015). However, no studies have been conducted on this topic. To support the continued research of bonefish in the Indian Ocean, an assessment of the intensity, locality, seasonality and economic value of bonefish fishing in the Seychelles is recommended.

Unfortunately, in the Seychelles there are no formal management strategies in place for protecting bonefish stocks. The Seychelles does not have a recreational fishing permit system nor an effective method of monitoring the fishery and, consequently, quantifying the fishing intensity in the Seychelles is difficult (Hutton and Pitcher 1998). However, as much of the fishing is conducted through tour companies and resorts, a survey method could be used to form a baseline assessment of fishing pressure. Bonefish surveys have been successfully conducted in Florida, Belize and the Bahamas, which have provided a more realistic impression of the economic value, fishing effort and stock status (Browder *et al.* 1981; Frezza and Clem 2015). For example, future studies that focus on assessing whether the fisheries predominantly retain or release the fish, the main target species, the number of fish caught and the catch per unit effort would provide a good baseline for impact assessments.

Once the intensity of the fisheries has been established, a map of the important fishing areas could be developed. The location of fishing grounds is an important consideration as it allows the prediction of potential primary and secondary effects or impacts, which may result from a high concentration of fishing in one area. For example, on Grand Récif of Toliara, Madagascar, substantial damage to the reef has been caused through gleaning by fishers (a traditional activity where invertebrates and small fish are collected from the reef flats at low tide). This activity has resulted in the destruction of corals, resulting in habitat loss for coral reef species and a reduction of water quality (Andréfouët *et al.* 2013). If such an activity occurred in areas inhabited by bonefish, it could affect the clarity of water and impact on their food sources (Taylor and Grace 2005; Weinberger and Posada 2005). Furthermore, questions regarding the dominant type of fishing methods used (e.g. boat- or land-based) could form part of spatial planning assessments and further the understanding of key fishing areas. This information could be used in the design and spatial planning of areas in a participatory and cost-effective way (Aswani and Lauer 2006). Acknowledging that bonefish represent only one of the many important species, such exercises could provide management agencies with vital information required for a marine spatial planning exercise for protected areas in the Seychelles (Tirant 2016).

In addition to knowing the distribution of fishing effort, understanding the timing is extremely important, particularly when the timing of fishing results in the targeting of a vulnerable life stage of a species (e.g. spawning). Due to the windy south-east monsoon season in the Seychelles (particularly between May and September) (von Brandis 2012), bonefish fishing may be seasonal. Such a period of reduced fishing pressure could form a natural 'closed season' to allow fish stocks and habitats to recover. Closed seasons are commonly used to reduce fishing pressure, protect spawning populations and maximise yield (Watson *et al.* 1993; Arendse *et al.* 2007). Furthermore, fish have been found to be more vulnerable to the adverse effects of fishing when they are reproductively ripe (Cooke and Suski 2005). Future studies investigating the seasonality and timing of bonefish spawning in the Seychelles would be beneficial to formulate fishing regulations. If spawning of bonefish in the Seychelles correlates with the monsoon season, then a formal closed season during this period would be beneficial to the maintenance of healthy stocks and would have limited implications on the recreational fishery.

Economically, the recreational fishery in the Seychelles may be underutilised. Recreational fishers typically generate income through boat hire, fishing tackle, fishing guides, accommodation, shopping and other activities (Fedler and Hayes 2008). If recreational fishing is correctly targeted and marketed it has the potential to create more jobs and attract more tourists (Ditton *et al.* 2002). In Los Roques Archipelago National Park, Venezuela, economic benefits are created through tourism (generating 40% employment), which provides substantial revenue from entrance fees and recreational fishing fees (Debrot and Posada 2005) - a fee that is not charged in the Seychelles. The introduction of a recreational fishing permit system in the Seychelles, particularly for international visitors, would provide a way of monitoring the fishing industry and of generating income. This, in turn, would generate income that could be re-invested into the fishing sector to facilitate job creation, research and the protection of this resource.

The life history of bonefish makes them relatively robust to some fishing pressure. However, when overexploited (as has been noted in other parts of the world) a stark decline in stocks occurs (Frezza and Clem 2015). Thus, the potential economic benefits depend on the availability of the resource and access to good fishing grounds. This highlights the importance of corrective management as, with relatively little infrastructure, bonefish have the potential to produce a substantial income for small island communities.

6.5 Conservation and threats

Albula glossodonta is listed as vulnerable on the IUCN redlist of threatened species, and may experience increased fishing pressure due to their extensive range (Indian and Pacific Ocean) and inshore habitat use. Bonefish occurring in the Indo-Pacific may therefore need both local and regional protection to prevent further declines and a localised collapse. Yet, bonefish fisheries remain unregulated in many areas, including the Seychelles (Wallace 2015).

Common threats to coastal fisheries include coastal habitat loss, urbanisation, declines in water quality and overharvesting (Adams *et al.* 2014). Vulnerable species are characterised by certain life history traits such as slower growth, late maturity, low fecundity, longer lifespan, low natural mortality and restricted geographical range (Cheung *et al.* 2005; Morato *et al.* 2006). Shoaling fish are typically vulnerable as they provide hyperstability of catch rates and are therefore often targeted (Morato *et al.* 2006). While bonefish are shoaling species, they mature at between one and four years (for *A. glossodonta* and *A. vulpes* respectively), have high fecundity (0.4 to 1.7 million oocytes), a high natural mortality (although literature on natural mortality in bonefish is conflicting), live for a maximum of 19 years and the species are widely dispersed (Crabtree *et al.* 1996; Friedlander *et al.* 2008; Donovan *et al.* 2015; Kamikawa *et al.* 2015). Therefore, if bonefish populations are correctly managed, their life history patterns make them a relatively resilient species.

Spawning migrations appear to be the most vulnerable life history stage for bonefish, as they were traditionally targeted by fisheries and are negatively affected by development, which may affect their traditional spawning migration route (Beets 2000; Friedlander *et al.* 2008). However, the current study was only able to suggest a possible location of where spawning aggregations may occur. Based on the literature, it is possible that the observed monthly movement to the north-east of the atoll was likely to represent a spawning behaviour. Bonefish fishing in the Seychelles is mostly recreational; therefore, their spawning aggregations are relatively safe from over harvesting (provided fishing pressure remains reasonable). However, the development of coastal areas has the potential to negatively influence spawning aggregations, as was shown in Florida, USA and Tarawa Lagoon, Republic of Kiribati (Beets 2000; Murchie *et al.* 2015). Development would also increase turbidity, thus affecting the environmental optical qualities which may have negative effects for recruitment and survival of larvae (Taylor and Grace 2005). Therefore, with an increase in tourism and accessibility, a balance between increased fishing, development of coastal areas and protection of fish stocks is required.

6.5.1 Catch-and-release as a management strategy

Catch-and-release is often viewed as a form of ecotourism and is the main management strategy for bonefish in Florida (Ault *et al.* 2008). Due to the perceived low impact of catch-and-release fishing, this activity has even been allowed in some no-take marine reserves (Cooke *et al.* 2006). However, the negative effects of catch-and-release have been widely documented and several studies have attributed the reported declines in bonefish stocks to uncontrolled recreational catch-and-release fishing (Debrot and Posada 2005; Dallas *et al.* 2010).

In areas where predator abundance is lower than witnessed in the current study, catch-and-release may still be feasible as a form of conservation, provided best handling practices are followed (Cooke and Philipp 2004). However, for predator-rich areas, best handling practices may not be enough. Studies aimed at decreasing post-release mortality have provided additional suggestions, over and above the general ‘best handling practice’ guidelines. These suggestions include retaining the fish in a live well until the fish has fully recovered and subsequently moving the fish to a site away from predators (Suski *et al.* 2007; Dallas *et al.* 2010). To implement these suggested best-handling-practices, a considerable amount of time and resources would be required; furthermore, these actions may have implications that have not been accounted for. For example, physiological recovery after air exposure takes approximately two to four hours (Suski *et al.* 2007) and the effect of releasing the fish away from its capture site could have further implications such as negative impacts on the shoaling behaviour (Dallas *et al.* 2010). Furthermore, for the average recreational fisher, these suggested best-handling-practices are also likely to be impractical and expensive (e.g. equipment to hold fish, as well as fuel and time for moving the fish to a new location). The 90% mortality rate witnessed during this study (despite following best handling guidelines and ensuring a healthy fish was released each time) suggests that bonefish in areas with high predator biomass are extremely vulnerable to post-release mortality. Methods of protection such as effort limits and no-take marine protected areas (MPAs) may, therefore, offer greater protection to the bonefish stocks.

Catch-and-release fishing needs to be regulated as, even with education of best handling practices, it is possible that post-release mortality will be high. In areas with high predator densities, it would be beneficial to calculate an average mortality rate given a certain area and species, so that a catch limit taking this mortality rate into consideration could be implemented. Catch limits and bag limits are not a new form of conservation and have been used as a management tool for fish species around the world. Bag limits restrict a number of animals that can be kept per unit of time, which allows for managers to restrict fishing mortality and allocate the use of a stock more equitably (Porch and Fox 1990). Similarly, a catch limit could be implemented in a catch-and-release fishery, where, instead of a limit on the number of fish an angler is allowed to keep, there is a limit on the total number of fish the angler is allowed to catch, thus taking into account the effect of post-release predation. Although this method could be enforced by the fishing guides and charter companies, formally, this method requires considerable resources and law enforcement, which is absent in the remote bonefish fishing destinations in the Seychelles.

6.5.2 Marine protected areas as a management strategy

Marine protected areas (MPAs) are an additional management strategy that deserves consideration. Although MPAs require law enforcement and monitoring, they are one of the most simplistic concepts of resource management available, so are often advocated as a management tool (Bohnsack 1998). In the Indo-Pacific, protection of marine resources is often achieved by means of MPAs (Wallace 2015). Allen and Singh (2016) designed a framework of advised conservation planning based on the movement patterns of fish. Five strategic steps of evaluation were proposed (1) identify species movement and characteristics, (2) evaluate ecosystem effects, (3) designing management guidelines based on this information (e.g. protected areas, ecological networks, time-area closures and threat management), (4) action and implementation, and (5) feedback on success of the management strategy. Looking at the movement results from this study in conjunction with the first three steps proposed by Allen and Singh (2016): (1) bonefish movement attributes are “sedentary” (or resident) with dispersal characteristics during particular life stages (i.e. spawning migrations and as lephtocephalus larvae). (2) They act as indicator species, provide ecosystem services in the form of nutrient transport and play an important part in predator prey interactions where they control benthic invertebrate populations and act as a food source to apex predators (Murchie *et al.* 2010; Adams *et al.* 2014). (3) Based on these findings, the scale of management that Allen and Singh (2016) recommended for bonefish is localised protection through protected areas and reserves, while taking the following implications into account: cost, manpower, stakeholder interest, monitoring effort, human-wildlife conflicts and policy and law enforcement.

Marine protected areas are defined as “Clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means to achieve the long term conservation of nature with associated ecosystem services and cultural values.” (Day *et al.* 2012, p 11). In 2013, only 2.8% of the world’s oceans had MPA status. The aim set by the convention on biological diversity is to have 10% of the world’s oceans declared as MPAs by 2020 (Costello and Ballantine 2015). Full protection of an area has been shown to yield the most comprehensive protection for both the ecosystem and biodiversity by minimising human impacts on a range of species and protecting ecosystems, thus best allowing the provision of ecosystem services (Mouillot *et al.* 2016).

The implementation of an MPA requires careful consideration of secondary impacts for commercial, social and recreational users. For example, an MPA may alter the location of fishing effort that may contribute to a concentration of fishing pressure on a different ecosystem (Brown *et al.* 2015). Socially, MPAs often fall under high dispute from local communities. The complaints are often due to perceived socio-economic costs from loss of fishing grounds and increased travel to new areas (da Silva *et al.* 2015). Such complaints are difficult to resolve, especially if the resource was used for subsistence fishing by impoverished local communities (Mouillot *et al.* 2016). The St. Joseph Atoll is fairly remote, has no human inhabitants, no subsistence fishing and limited recreational fishing activities (e.g. tourism). Despite this, the proposed declaration of this area as an MPA has fallen under considerable dispute from interested and affected parties (Tirant 2016).

Protected areas and reserves can be zoned for different levels of protection, from partial protection to fully protected no-take, and restricted use in between. Partially protected areas are often considered to be a balance between two goals, namely biodiversity conservation and socio-economic viability (Sciberras *et al.* 2015). Partially protected MPAs generally have a higher biodiversity value than open access areas, yet well-enforced no-take areas have significantly greater density of organisms relative to adjacent exploited areas (Lester and Halpern 2008). Partial protection can be in the form of closed seasons or partial access. Closed seasons were discussed previously and are beneficial if implemented during spawning seasons (or other important life history events) as they provide protection to the stock at a time when they are aggregated and particularly vulnerable to overfishing. It is conjectured that this would likely be very beneficial for bonefish stocks, especially if the spawning season and the peak of tourism activities fall over different time periods, however this requires further investigation.

Partial access, or zonation, is an additional consideration where certain activities are restricted. For example, commercial fisheries may be prohibited, but activities such as recreational fishing, tourism activities and subsistence fishing would still be allowed. However, based on the high post-release mortality of bonefish, uncontrolled recreational fishing is not recommended as evidence of declining bonefish stocks has been seen in other areas of the world where catch-and-release bonefish fishing went unregulated (Larkin *et al.* 2010). A third possible option is partial protection, where part of the St. Joseph Atoll is restricted. If the areas of high use of a bonefish stock were protected (as seen in the MCP, chapter 5), then a partial reserve that only allows fishing in a portion of the atoll may provide sufficient fishing grounds and refuges for bonefish. A possible negative implication, as noted by fishing guides, is site specific fishing could result in bonefish abandoning their regular feeding areas (Debrot and Posada 2005). To address this potential concern, within the open area it is important that rotational fishing takes place with different areas and species targeted over time. Rotational fishing limits the effort placed on a resource, thereby limiting the impact of overfishing. However, rotational fishing is only effective as a conservation measure if enough time between areas and/or species is allocated to enable the species to sufficiently recuperate (Kaplan *et al.* 2010).

Currently, despite their economic importance to many small island communities, bonefish in the Indo-Pacific have no formal management plans, regulations or conservation practices (Wallace 2015). The only formal protection for bonefish in the Indian Ocean is through the already developed MPAs around the Seychelles such as Aldabra, Cousin and Aride. To date, no bonefish research has been conducted in the Seychelles, therefore the extent of bonefish stocks on these islands is unknown and further assessments are recommended.

The protection of the St. Joseph Atoll (along with the islands currently conserved) could potentially facilitate a spillover effect, where stocks in other areas are replenished through larval recruitment (da Silva *et al.* 2015). This could ensure the continued larval recruitment at neighbouring islands, despite potentially unsustainable fishing pressure. However, further studies investigating the range of recruitment and accurately determining the dispersal potential of *A. glossodonta* from the St. Joseph Atoll (and other protected islands) are recommended. Evidence of ongoing gene flow of *A. glossodonta* between Seychelles and Kiribati has been found which suggests weak separation between the Indian and Pacific Oceans. This information implies that larval dispersal across these oceans may occur (Wallace 2015; Wallace and Tringali 2016).

The design of MPAs or conservation laws are often developed based on species that represent public interest and concern, yet this may not adequately protect other species (Lea *et al.* 2016). One, therefore, needs to consider specifics of a whole range of species when designing an MPA. The current discussion has focused on the protection of bonefish, yet the St. Joseph Atoll is home to a multitude of species that are extremely vulnerable to exploitation and require different considerations for conservation. Fortunately, a considerable amount of research, particularly movement research, has taken place at the St. Joseph Atoll. This will enable managers to make sound decisions on the best methods of protection to safeguard the ecosystem and the species in the most effective way. Research studies using movement data from multiple species to support a protected area that covers the greatest combined habitat use are becoming more common (Pendoley *et al.* 2014; Lea *et al.* 2016). This multi-species approach serves the aim of protected areas more fully as they are better able to protect a range of species and their habitats. The implementation of a specific MPA would require further discussion, as deciding on the correct level of protection for different areas and species requires a balance of resource use, management and conservation priorities (Lester and Halpern 2008).

6.6 Conclusion

The current study has provided information on the potential impacts of catch and release fishing (i.e. post-release mortality), and also provided information on bonefish movement. This study has shown that catch-and-release of bonefish in a predator-rich ecosystem can result in high mortality. It is therefore recommended that some protection of bonefish in Seychelles waters is necessary, as unregulated fishing pressure could potentially severely impact isolated bonefish populations. While the results may differ from one region to the next, and be dependent on several factors such as fishing pressure, human habitation, development, distance to other islands/atolls, predator density and level of protection, this study contributes valuable information that can be used towards the development of management plans for bonefish. Further research into the extent and economic value of this fishery is recommended. With an inevitable increase in the demand for exclusive ecotourism fishing, conservation efforts are essential to sustain the unique opportunities on offer in the Seychelles.

References

Abecasis, D, & Erzini, K. 2008. Site fidelity and movements of gilthead sea bream (*Sparus aurata*) in a coastal lagoon (Ria Formosa, Portugal). *Estuarine, Coastal and Shelf Science* 79: 758–763.

Ackerman, JT, Kondratieff, MC, Matern, SA, & Cech, JJ. 2000. Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. *Environmental Biology of Fishes* 58: 33–43.

Acosta, C, & Robertson, D. 2003. Comparative spatial ecology of fished spiny lobsters *Panulirus argus* and an unfished congener *P. guttatus* in an isolated marine reserve at Glover's Reef atoll, Belize. *Coral Reefs* 22: 1–9.

Adams, AJ, & Cooke, SJ. 2015. Advancing the science and management of flats fisheries for bonefish, tarpon, and permit. *Environmental Biology of Fishes* 98: 2123–2131.

Adams, AJ, Horodysky, AZ, Mcbride, RS, Guindon, K, Shenker, J, MacDonald, TC, Harwell, HD, Ward, R, & Carpenter, K. 2014. Global conservation status and research needs for tarpons (Megalopidae), ladyfishes (Elopidae) and bonefishes (Albulidae). *Fish and Fisheries* 15: 280–311.

Allen, AM, & Singh, NJ. 2016. Linking Movement Ecology with Wildlife Management and Conservation. *Frontiers in Ecology and Evolution* 3.

Anderson, J. 1982. The Home Range: A New Nonparametric Estimation Technique. *Ecology* 63: 103–112.

Andréfouët, S, Guillaume, MMM, Delval, A, Rasoamanendrika, FMA, Blanchot, J, & Bruggemann, JH. 2013. Fifty years of changes in reef flat habitats of the Grand Récif of Toliara (SW Madagascar) and the impact of gleaning. *Coral Reefs* 32: 757–768.

Andrews, KS, Williams, GD, Farrer, D, Tolimieri, N, Harvey, CJ, Bargmann, G, & Levin, PS. 2009. Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator. *Animal Behaviour* 78: 525–536. Elsevier Ltd.

Arendse, CJ, Govender, A, & Branch, GM. 2007. Are closed fishing seasons an effective means of increasing reproductive output? A per-recruit simulation using the limpet *Cymbula granatina* as a case history. *Fisheries Research* 85: 93–100.

Aswani, S, & Lauer, M. 2006. Incorporating Fishers' Local Knowledge and Behavior into Geographical Information Systems (GIS) for Designing Marine Protected Areas in Oceania. *Human Organization* 65: 81–102.

Ault, JS, Moret, S, Luo, J, Larkin, M, Zurcher, N, & Smith, S. 2008. Florida Keys Bonefish Population Census. *In* Biology and Management of the World Tarpon and Bonefish Fisheries, pp 383–398. Ault, JS. (eds). CRC Press, Boca Raton.

Ault, JS, Smith, SG, & Bohnsack, JA. 2005. Evaluation of average length as an estimator of exploitation status for the Florida coral-reef fish community. *ICES Journal of Marine Science* 62: 417–423.

Bacheler, NM, Paramore, LM, Buckel, JA, & Hightower, JE. 2009. Abiotic and biotic factors influence the habitat use of an estuarine fish. *Marine Ecology Progress Series* 377: 263–277.

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

Batschelet E. 1981. Circular statistics in biology. Academic Press: London

Bates, D, Machler, M, Bolker, B, & Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1–48.

Beets, J. 2000. Declines in finfish resources in Tarawa Lagoon, Kiribati, emphasize the need for increased conservation effort. *Atoll Research Bulletin* 490: 1–14.

Béguer-Pon, M, Benchetrit, J, Castonguay, M, Aarestrup, K, Campana, SE, Stokesbury, MJW, & Dodson, JJ. 2012. Shark Predation on Migrating Adult American Eels (*Anguilla rostrata*) in the Gulf of St. Lawrence. *PLoS ONE* 7.

Biesinger, Z, Bolker, BM, Marcinek, D, Grothues, TM, Dobarro, JA, & Lindberg, WJ. 2013. Testing an autonomous acoustic telemetry positioning system for fine-scale space use in marine animals. *Journal of Experimental Marine Biology and Ecology* 448: 46–56. Elsevier B.V.

Bohnsack, JA. 1998. Application of marine reserves to reef fisheries management. *Australian Journal of Ecology* 23: 298–304.

Bolker, BM, Brooks, ME, Clark, CJ, Geange, SW, Poulsen, JR, Stevens, MHH, & White, JSS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127–135.

Browder, JA, Davis, JC, & Sullivan, E. 1981. Paying-Passenger Recreational Fisheries of the Florida Gulf Coast and Keys. *Marine Fisheries Review* 43: 12–20.

Brown, CJ, White, C, Beger, M, Grantham, HS, Halpern, BS, Klein, CJ, Mumby, PJ, Tulloch, VJD, Ruckelshaus, M, & Possingham, HP. 2015. Fisheries and biodiversity benefits of using static versus dynamic models for designing marine reserve networks. *Ecosphere* 6: 1–14.

Brown, JS, Laundre, JW, & Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80: 385–399.

Brownscombe, JW, Danylchuk, AJ, Chapman, JM, Gutowsky, LFG, & Cooke, SJ. 2017. Best practices for catch-and-release recreational fisheries – angling tools and tactics. *Fisheries Research* 186: 693–705.

Brownscombe, JW, Gutowsky, LFG, Danylchuk, AJ, & Cooke, SJ. 2014. Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. *Marine Ecology Progress Series* 505: 241–251.

Brownscombe, JW, Thiem, JD, Hatry, C, Cull, F, Haak, CR, Danylchuk, AJ, & Cooke, SJ. 2013. Recovery bags reduce post-release impairments in locomotory activity and behavior of bonefish (*Albula* spp.) following exposure to angling-related stressors. *Journal of Experimental Marine Biology and Ecology* 440: 207–215. Elsevier B.V.

Brunnschweiler, JM. 2009. Tracking free-ranging sharks with hand-fed intra-gastric acoustic transmitters. *Marine and Freshwater Behaviour and Physiology* 42: 201–209.

Burger, G. 1974. Age, Growth, Food Habits, and Reproduction of Bonefish, *Albula vulpes*, in South Florida Waters. *Florida Marine Research Publications* 3: 1–20.

Campbell, HA, Watts, ME, Dwyer, RG, & Franklin, CE. 2012. V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. *Marine and Freshwater Research* 63: 815–820.

Cheung, WWL, Pitcher, TJ, & Pauly, D. 2005. A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation* 124: 97–111.

Childs, A-R. 2005. Movement patterns of spotted grunter, *Pomadasys commersonnii* (Haemulidae), in a highly turbid South African estuary. MSc thesis. Rhodes University. South Africa

Chin, A, Heupel, M, Simpfendorfer, C, & Tobin, A. 2013. Ontogenetic movements of juvenile blacktip reef sharks: evidence of dispersal and connectivity between coastal habitats and coral reefs. *Aquatic Conservation: Marine and Freshwater Ecosystems* 23: 468–474.

Cisneros-Montemayor, AM, & Sumaila, UR. 2010. A global estimate of benefits from ecosystem-based marine recreation: potential impacts and implications for management. *Journal of Bioeconomics* 12: 245–268.

Clarke, KR, & Warwick, RM. 2001. Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth. pp 1–172.

Clements, S, Jepsen, D, Karnowski, M, & Schreck, CB. 2005. Optimization of an Acoustic Telemetry Array for Detecting Transmitter-Implanted Fish. *North American Journal of Fisheries Management* 25: 429–436.

Colborn, J, Crabtree, RE, Shaklee, JB, Pfeiler, E, & Bowen, BW. 2001. The evolutionary enigma of bonefishes (*Albula* spp.): cryptic species and ancient separations in a globally distributed shorefish. *Evolution* 55: 807–820.

Colton, D, & Alevizon, W. 1983a. Movement Patterns of Bonefish *Albula vulpes*, in Bahamian waters. *Fishery Bulletin* 81: 148–154.

Colton, D, & Alevizon, W. 1983b. Feeding ecology of bonefish in Bahamian waters. *Transactions of the American Fisheries Society* 112: 178–184.

Cooke, SJ, & Cowx, IG. 2004. The Role of Recreational Fishing in Global Fish Crises. *BioScience* 54: 857–859.

Cooke, SJ, Danylchuk, AJ, Danylchuk, SE, Suski, CD, & Goldberg, TL. 2006. Is catch-and-release recreational angling compatible with no-take marine protected areas? *Ocean and Coastal Management* 49: 342–354.

Cooke, SJ, Donaldson, MR, O'connor, CM, Raby, GD, Arlinghaus, R, Danylchuk, AJ, Hanson, KC, Hinch, SG, Clark, TD, Patterson, DA, & Suski, CD. 2013. The physiological consequences of catch-and-release angling: perspectives on experimental design, interpretation, extrapolation and relevance to stakeholders. *Fisheries Management and Ecology* 20: 268–287.

Cooke, SJ, & Philipp, DP. 2004. Behavior 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, SJ, & Schramm, HL. 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. *Fisheries Management and Ecology* 14: 73–79.

Cooke, SJ, & Suski, CD. 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? *Biodiversity and Conservation* 14: 1195–1209.

Cooke, SJ, Suski, CD, Danylchuk, SE, Danylchuk, AJ, Donaldson, MR, Pullen, C, Bulté, G, O'toole, A, Murchie, KJ, Koppelman, JB, Shultz, AD, Brooks, E, & Goldberg, TL. 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.

Costello, MJ, & Ballantine, B. 2015. Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. *Trends in Ecology and Evolution* 30: 507–509. Elsevier Ltd.

Cowley, PD, Kerwath, SE, Childs, A-R, Thorstad, EB, Økland, F, & Næsje, TF. 2008. Estuarine habitat use by juvenile dusky kob *Argyrosomus japonicus* (Sciaenidae), with implications for management. *African Journal of Marine Science* 30: 247–253.

Crabtree, R, Snodgrass, D, & Harnden, C. 1988. Survival rates of bonefish, *Albula vulpes*, caught on hook-and-line gear and released based on capture and release of captive bonefish in a pond in the Florida Keys. 252–254.

Crabtree, RE, Harnden, CW, & Stevens, C. 1996. Age, growth, and mortality of bonefish, *Albula vulpes*, from the waters of the Florida Keys. *Fishery Bulletin* 94: 442–451.

da Silva, IM, Hill, N, Shimadzu, H, Soares, AMVM, & Dornelas, M. 2015. Spillover Effects of a Community-Managed Marine Reserve. *PLoS ONE* 10: 1–18.

Dadswell, MJ, Wehrell, SA, Spares, AD, Mclean, MF, Beardsall, JW, Logan-Chesney, LM, Nau, GS, Ceapa, C, Redden, AM, & Stokesbury, MJW. 2016. The annual marine feeding aggregation of Atlantic sturgeon *Acipenser oxyrinchus* in the inner Bay of Fundy: population characteristics and movement. *Journal of Fish Biology* 89: 2107–2132.

Dallas, LJ, Shultz, AD, Moody, AJ, Sloman, KA, & Danylchuk, AJ. 2010. Chemical excretions of angled bonefish *Albula vulpes* and their potential use as predation cues by juvenile lemon sharks *Negaprion brevirostris*. *Journal of Fish Biology* 77: 947–962.

Danylchuk, A, Cooke, S, Goldberg, T, Petersen, D, & Danylchuk, S. 2011a. Involving Recreational Anglers in Developing Best Handling Practices for Catch-and-Release Fishing of Bonefish: Using Citizen Science to Further Stewardship. *American Fisheries Society* 75: 1–18.

Danylchuk, AJ, Adams, A, Cooke, SJ, & Suski, CD. 2008a. An evaluation of the injury and short-term survival of bonefish (*Albula* spp.) as influenced by a mechanical lip-gripping device used by recreational anglers. *Fisheries Research* 93: 248–252.

Danylchuk, AJ, Cooke, SJ, Goldberg, TL, Suski, CD, Murchie, KJ, Danylchuk, SE, Shultz, AD, Haak, CR, Brooks, EJ, Oronti, A, Koppelman, JB, & Philipp, DP. 2011b. Aggregations and offshore movements as indicators of spawning activity of bonefish (*Albula vulpes*) in The Bahamas. *Marine Biology* 158: 1981–1999.

Danylchuk, AJ, Danylchuk, SE, Cooke, SJ, Goldberg, TL, Koppelman, J, & Philipp, DP. 2008b. Ecology and Management of Bonefish (*Albula* spp) in the Bahamian Archipelago. *In* The world biology of tarpon and bonefish, pp 73–92. Ault, J, & Humston, R. (eds). CRC Press, Boca Raton, Florida.

Danylchuk, AJ, Danylchuk, SE, Cooke, SJ, Goldberg, TL, Koppelman, JB, & Philipp, DP. 2007a. Post-release mortality of bonefish, *Albula vulpes*, exposed to different handling practices during catch-and-release angling in Eleuthera, The Bahamas. *Fisheries Management and Ecology* 14: 149–154.

Danylchuk, SE, Danylchuk, AJ, Cooke, SJ, Goldberg, TL, Koppelman, J, & Philipp, DP. 2007b. Effects of recreational angling on the post-release behavior 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.

Day, J, Dudley, N, Hockings, M, Holmes, G, Laffoley, D, Stolton, S, & Wells, S. 2012. *Guidelines for applying the IUCN Protected Area Management Categories to Marine Protected Areas*. Gland, Switzerland: IUCN. pp 36.

Debrot, D, & Posada, J. 2005. A brief description of the bonefish recreational fishery in Los Roques Archipelago National Park, Venezuela. *Contributions in Marine Science* 37: 61–65.

DeMartini, EE, Friedlander, AM, Sandin, SA, & Sala, E. 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology Progress Series* 365: 199–215.

Ditton, RB, Holland, SM, & Anderson, DK. 2002. Recreational Fishing as Tourism. *Fisheries* 27: 17–24.

Doane, DP, & Seward, LE. 2011. Measuring Skewness: A Forgotten Statistic? *Journal of Statistics Education* 19: 1–18.

Doherty, PJ, Williams, DM, & Sale, PF. 1985. The adaptive significance of larval dispersal in coral reef fishes. *Environmental Biology of Fishes* 12: 81–90.

Domeier, ML, & Colin, PL. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* 60: 698–726.

Donovan, MK, Friedlander, AM, Harding, KK, Schemmel, EM, Filous, A, Kamikawa, K, & Torkelson, N. 2015. Ecology and niche specialization of two bonefish species in Hawai'i. *Environmental Biology of Fishes*.

Dresser, BK, & Knieb, RT. 2007. Site fidelity and movement patterns of wild subadult red drum, *Sciaenops ocellatus* (Linneaus), within a salt marsh-dominated easturine landscape. *Fisheries Management and Ecology* 14: 183–190.

Economakis, AE, & Lobel, PS. 1998. Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhychos*, at Johnston Atoll, Central Pacific Ocean. *Environmental Biology of Fishes* 51: 129–139.

Elston, C. 2016. The trophic and spatial ecology of juvenile porcupine rays *Urogymnus asperrimus* at the remote St. Joseph Atoll. Rhodes University.

Erisman, B, Aburto-Oropeza, O, Gonzalez-Abraham, C, Mascareñas-Osorio, I, Moreno-Báez, M, & Hastings, PA. 2012. Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the Gulf of California. *Scientific reports* 2: 1–11.

Espinoza, M, Farrugia, TJ, Webber, DM, Smith, F, & Lowe, CG. 2011. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fisheries Research* 108: 364–371. Elsevier B.V.

Fedler, J, & Hayes, C. 2008. Economic Impact of Recreational Fishing for Bonefish, Permit and Tarpon in Belize for 2007. pp 20.

Fedler, T. 2010. The Economic Impact of Flats Fishing in The Bahamas. pp 20.

Fedler, T. 2013. Economic Impact of the Florida Keys Flats Fishery. pp 25.

Filmalter, J. 2011. Movements of sub-adult sicklefin lemon sharks *Negaprion acuyidens* in a remote Indian Ocean atoll. MSc thesis, Rhodes University, South Africa.

Filmalter, JD, Dagorn, L, & Cowley, PD. 2013. Spatial behaviour and site fidelity of the sicklefin lemon shark *Negaprion acutidens* in a remote Indian Ocean atoll. *Marine Biology* 160: 2425–2436.

Finn, JT, Brownscombe, JW, Haak, CR, Cooke, SJ, Cormier, R, Gagne, T, & Danylchuk, AJ. 2014. Applying network methods to acoustic telemetry data: Modeling the movements of tropical marine fishes. *Ecological Modelling* 293: 139–149. Elsevier B.V.

Fitch, J. 1950. Life history notes and the early development of the bonefish *Albula vulpes* (Linnaeus). *California Fish and Game* 36: 2–6.

Frezza, PE, & Clem, SE. 2015. Using local fisher's knowledge to characterize historical trends in the Florida Bay bonefish population and fishery. *Environmental Biology of Fishes* 98: 2187–2202.

Fridberg, G, Bern, HA, & Nishioka, RS. 1966. The caudal neurosecretory system of the isospondylous teleost, *Albula vulpes*, from different habitats. *General and comparative endocrinology* 6: 195–212.

Friedlander, AM, Caselle, JE, Beets, J, Lowe, CG, Bowen, BW, Ogawa, TK, Kelley, KM, Calitri, T, Lange, M, & Anderson, BS. 2008. Biology and Ecology of the Recreational Bonefish Fishery at Palmyra Atoll National Wildlife Refuge with Comparisons to Other Pacific Islands. CRC Press, Boca Raton. 27-56.

Friedlander, AM, Obura, D, Aumeeruddy, R, Ballesteros, E, Church, J, Cebrian, E, & Sala, E. 2014. Coexistence of Low Coral Cover and High Fish Biomass at Farquhar Atoll, Seychelles. *PLoS ONE* 9: e87359.

Gibson, AJF, Halfyard, EA, Bradford, RG, Stokesbury, MJW, & Redden, AM. 2015. Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. *Canadian Journal of Fisheries and Aquatic Sciences* 72: 728–741.

Graham, NAJ, Spalding, MD, & Sheppard, CRC. 2010. Reef shark declines in remote atolls highlight the need for multi-faceted conservation action. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20: 543–548.

Gratwicke, B, & Speight, MR. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* 66: 650–667.

Grigg, RW. 1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Marine Ecology Progress Series* 103: 25–34.

Gruber, SH, Nelson, DR, & Morrissey, JF. 1988. Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. *Bulletin of Marine Science* 43: 61–76.

Grüss, A, Kaplan, DM, Guénette, S, Roberts, CM, & Botsford, LW. 2011. Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation* 144: 692–702.

Gupta, A. 2002. Geoindicators for tropical urbanization. *Environmental Geology* 42: 736–742.

Halpern, BS, Frazier, M, Potapenko, J, Casey, KS, Koenig, K, Longo, C, Lowndes, JS, Rockwood, RC, Selig, ER, Selkoe, KA, & Walbridge, S. 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications* 6: 7615. Nature Publishing Group.

Hannan, KD, Zuckerman, ZC, Haak, CR, & Shultz, AD. 2015. Impacts of sun protection on feeding behavior and mucus removal of bonefish, *Albula vulpes*. *Environmental Biology of Fishes*: 1–8.

Hansler, D, & Wisby, J. 1958. The Return of Displaced Largemouth Bass and Green Sunfish to a 'Home' Area. *Wiley* 39: 289–293.

Hartill, BW, Morrison, MA, Smith, MD, Boubée, J, & Parsons, DM. 2003. Diurnal and tidal movements of snapper (*Pagrus auratus*, Sparidae) in an estuarine environment. *Marine and Freshwater Research* 54: 931–940.

Hedgecock, D, Nelson, K, & López-Lemus, LG. 1988. Biochemical genetic and morphological divergence among three species of thread herring (*Opisthonema*) in northwest Mexico. *CalCOFI Reports* 29: 110–121.

Hedger, RD, Næsje, TF, Cowley, PD, Thorstad, EB, Attwood, C, Økland, F, Wilke, CG, & Kerwath, S. 2010. Residency and migratory behaviour by adult *Pomatomus saltatrix* in a South African coastal embayment. *Estuarine, Coastal and Shelf Science* 89: 12–20. Elsevier Ltd.

Heupel, MR, Semmens, JM, & Hobday, AJ. 2006. Automated acoustic tracking of aquatic animals: Scales, design and deployment of listening station arrays. *Marine and Freshwater Research* 57: 1–13.

Hickley, P. 1998. Recreational fisheries - Social, economic and management aspects. *In* Fish, sustainability and development, pp 137–157. Blackwell Science, Oxford, UK.

Hidaka, K, Iwatsuki, Y, & Randall, J. 2008. A review of the Indo-Pacific bonefishes of the *Albula argentea* complex, with a description of a new species. *Ichthyology Research* 55: 53–64.

Hindell, JS, Jenkins, GP, & Womersley, B. 2008. Habitat utilisation and movement of black bream *Acanthopagrus butcheri* (Sparidae) in an Australian estuary. *Marine Ecology Progress Series* 366: 219–229.

Holt, G, & Holt, S. 2005. Tarpon and Other Fishes of the Western Gulf of Mexico: Proceedings from the Third International Tarpon Forum. Marine Science Institute, University of Texas, Austin, Texas.

Humston, R, Ault, JS, Larkin, MF, & 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.

Hussey, NE, Kessel, ST, Aarestrup, K, Cooke, SJ, Cowley, PD, Fisk, AT, Harcourt, RG, Holland, KN, Iverson, SJ, Kocik, JF, Flemming, JEM, & Whoriskey, FG. 2015. Aquatic animal telemetry: A panoramic window into the underwater world. *Science* 348: 1221–1233.

Hutton, T, & Pitcher, TJ. 1998. Current directions in fisheries management policy: a perspective on co-management and its application to South African fisheries. *South African Journal of Marine Science* 19: 471–486.

Jadot, C, Donnay, A, Acolas, ML, Cornet, Y, & Begout Anras, ML. 2006. Activity patterns, home-range size, and habitat utilization of *Sarpa salpa* (Teleostei: Sparidae) in the Mediterranean Sea. *ICES Journal of Marine Science* 63: 128–139.

Jadot, C, Ovidio, M, & Voss, J. 2002. Diel activity of *Sarpa salpa* (Sparidae) by ultrasonic telemetry in a *Posidonia oceanica* meadow of Corsica (Mediterranean Sea). *Aquatic Living Resources* 15: 343–350.

Jepsen, N, Mikkelsen, JS, & Koed, A. 2008. Effects of tag and suture type on survival and growth of brown trout with surgically implanted telemetry tags in the wild. *Journal of Fish Biology* 72: 594–602.

Johannes, R, & Yeeting, B. 2000. I-Kiribati knowledge and management of Tarawa's lagoon resources. *Atoll Research Bulletin* 489: 1–24.

Jonsen, ID, Myers, RA, & James, MC. 2007. Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series* 337: 255–264.

Kamikawa, KT, Friedlander, AM, Harding, KK, Filous, A, Donovan, MK, & Schemmel, E. 2015. Bonefishes in Hawai'i and the importance of angler-based data to inform fisheries management. *Environmental Biology of Fishes*.

Kaplan, DM, Hart, DR, & Botsford, LW. 2010. Rotating spatial harvests and fishing effort displacement: A comment on Game *et al.* (2009). *Ecology Letters* 13: E10–E12.

Kerwath, SE. 2005. Empirical studies of fish movement behaviour and their application in spatially explicit models for marine conservation. Rhodes University. pp 227.

Kerwath, SE, Thorstad, EB, NÆsje, TF, Cowley, PD, Økland, F, Wilke, C, & Attwood, CG. 2009. Crossing Invisible Boundaries: The Effectiveness of the Langebaan Lagoon Marine Protected Area as a Harvest Refuge for a Migratory Fish Species in South Africa. *Conservation Biology* 23: 653–661.

Kessel, ST, Chapman, DD, Franks, BR, Gedamke, T, Gruber, SH, Newman, JM, White, ER, & Perkins, RG. 2014. Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris*). *Marine Ecology Progress Series* 514: 175–190.

Klein, SA, Soden, BJ, & Lau, NC. 1999. Remote Sea Surface Temperature Variations during ENSO: Evidence for a Tropical Atmospheric Bridge. *Journal of Climate* 12: 917–932.

Kovach, WL. 2011. *Oriana – Circular Statistics for Windows, ver.4*. Kovach Computing Services, Pentraeth, Wales, UK.

Kremen, C. 1992. Assessing the indicator porperties of species assemblages for natural areas monitoring. *Ecological Applications* 2: 203–217.

Krumme, U. 2004. Patterns in tidal migration of fish in a Brazilian mangrove channel as revealed by a split-beam echosounder. *Fisheries Research* 70: 1–15.

Kruskal, JB. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1–27.

Kwun, HJ, & Kim, JK. 2011. A new species of bonefish, Albula koreana (Albuliformes: Albulidae) from Korea and Taiwan. *Zootaxa* 2903: 57–63.

Larkin, MF. 2011. Assessment of South Florida's Bonefish Stock. University of Miami. pp 1–214.

Larkin, MF, Ault, JS, Humston, R, & Luo, J. 2010. A mail survey to estimate the fishery dynamics of southern Florida's bonefish charter fleet. *Fisheries Management and Ecology* 17: 254–261.

Larkin, MF, Ault, JS, Humston, R, Luo, J, & Zurcher, N. 2008. Tagging of Bonefish in South Florida to Study Population Movements and Stock Dynamics. *Biology and Management of the World Tarpon and Bonefish Fisheries*: 301–320.

Layman, C, Winemiller, K, Arrington, D, & Jepsen, D. 2005. Body Size and Trophic Position in a Diverse Tropical Food Web. *Ecology* 86: 2530–2535.

Lea, JSE, Humphries, NE, von Brandis, RG, Clarke, CR, Sims, DW, & Lea, JSE. 2016. Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. *Proceedings of the Royal Society B* 283: 1–8.

Lea, RN, & Rosenblatt, RH. 2000. Observations on fishes associated with the 1997–98 El Nino off California. *California Cooperative Oceanic Fisheries Investigations Reports* 41: 117–129.

Lester, SE, & Halpern, BS. 2008. Biological responses in marine no-take reserves versus partially protected areas. *Marine Ecology Progress Series* 367: 49–56.

Levesque, JC. 2011. Is Today's Fisheries Research Driven by the Economic Value of a Species? A Case Study Using an Updated Review of Ladyfish (*Elops saurus*) Biology and Ecology. *Reviews in Fisheries Science* 19: 137–149.

Lower, N, Moore, A, Scott, AP, Ellis, T, James, JD, & Russell, IC. 2005. A non-invasive method to assess the impact of electronic tag insertion on stress levels in fishes. *Journal of Fish Biology* 67: 1202–1212.

Mann, H, & Whitney, D. 1947. On a Test of Whether one of Two Random Variables is Stochastically Larger than the Other. *The Annals of Mathematical Statistics* 18: 50–60.

Mart, Y. 1988. The tectonic setting of the Seychelles, Mascarene and Amirante plateaus in the western equatorial Indian Ocean. *Marine Geology* 79: 261–274.

Masters, JEG, Hodder, KH, Beaumont, WRC, Gozlan, RE, Pinder, AC, Kenward, R, & Welton, J. 2005. Spatial behaviour of pike *Esox lucius* L. in the River Frome, UK. *In* Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe., pp 179–190. Spedicato, M, Lembo, G, & Marmulla, G. (eds). FAO/COISPA, Rome.

Mc Kibben, J, & Nelson, D. 1986. Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bulletin of Marine Science* 38: 89–110.

Melnychuk, MC, Christensen, V, & Walters, CJ. 2013. Meso-scale movement and mortality patterns of juvenile coho salmon and steelhead trout migrating through a coastal fjord. *Environmental Biology of Fishes* 96: 325–339.

Meyer, CG, Holland, KN, Wetherbee, BM, & Lowe, CG. 2000. Movement patterns, habitat utilization, home range size and site fidelity of witesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. *Environmental Biology of Fishes* 59: 235–242.

Meyer, CG, Papastamatiou, YP, & Holland, KN. 2007. Seasonal, diel, and tidal movements of green jobfish (*Aprion virescens*, Lutjanidae) at remote Hawaiian atolls: Implications for marine protected area design. *Marine Biology* 151: 2133–2143.

Mojica, R, Shenker, JM, Harnden, CW, & Wagner, DE. 1995. Recruitment of bonefish, *Albula vulpes*, around Lee Stocking Island, Bahamas. *Fishery Bulletin* 93: 666–674.

Morato, T, Cheung, WWL, & Pitcher, TJ. 2006. Vulnerability of seamount fish to fishing: Fuzzy analysis of life-history attributes. *Journal of Fish Biology* 68: 209–221.

Morel, GM, Shrives, J, Bossy, SF, & Meyer, CG. 2013. Residency and behavioural rhythmicity of ballan wrasse (*Labrus bergylta*) and rays (*Raja* spp.) captured in Portelet Bay, Jersey: implications for Marine Protected Area design. *Journal of the Marine Biological Association of the United Kingdom* 93: 1407–1414.

Morgan, E. 2001. The moon and life on earth. *Earth, Moon and Planets* 85–86: 279–290.

Morrissey, JF, & Gruber, SH. 1993. Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. *Environmental Biology of Fishes* 38: 311–319.

Mortimer, JA, Camille, J-C, & Boniface, N. 2011. Seasonality and Status of Nesting Hawksbill (*Eretmochelys imbricata*) and Green Turtles (*Chelonia mydas*) at D'Arros Island, Amirantes Group, Seychelles. *Chelonian Conservation and Biology* 10: 26–33.

Mouillot, D, Parravicini, V, Bellwood, DR, Leprieur, F, Huang, D, Cowman, PF, Albouy, C, Hughes, TP, Thuiller, W, & Guilhaumon, F. 2016. Global marine protected areas do not secure the evolutionary history of tropical corals and fishes. *Nature Communications*: 1–8. Nature Publishing Group.

Mulcahy, DM. 2003. Surgical implantation of transmitters into fish. *Ilar Journal* 44: 295–306.

Murchie, KJ, Danylchuk, AJ, Cooke, SJ, O'Toole, AC, Shultz, A, Haak, C, Brooks, E, & Suski, CD. 2012. Considerations for tagging and tracking fish in tropical coastal habitats: lessons from bonefish, barracuda and sharks tagged with acoustic transmitters. In: Adams, NS, Beeman, JW, & Eiler, JH. (eds). Telemetry Techniques: A User Guide for Fisheries Research. American Fisheries Society, Bethesda, Maryland, pp 389–412

Murchie, KJ, Cooke, SJ, & Danylchuk, AJ. 2010. Seasonal Energetics and Condition of Bonefish from Different Subtropical Tidal Creeks in Eleuthera, the Bahamas. *Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science* 2: 249–262.

Murchie, KJ, Cooke, SJ, Danylchuk, AJ, Danylchuk, SE, Goldberg, TL, Suski, CD, & Philipp, DP. 2011a. Thermal biology of bonefish (*Albula vulpes*) in Bahamian coastal waters and tidal creeks: An integrated laboratory and field study. *Journal of Thermal Biology* 36: 38–48. Elsevier.

Murchie, KJ, Cooke, SJ, Danylchuk, AJ, Danylchuk, SE, Goldberg, TL, Suski, CD, & Philipp, DP. 2013. Movement patterns of bonefish (*Albula vulpes*) in tidal creeks and coastal waters of Eleuthera, The Bahamas. *Fisheries Research* 147: 404–412. Elsevier B.V.

Murchie, KJ, Cooke, SJ, Danylchuk, AJ, & Suski, CD. 2011b. Estimates of field activity and metabolic rates of bonefish (Albula vulpes) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry. *Journal of Experimental Marine Biology and Ecology* 396: 147–155.

Murchie, KJ, Cooke, SJ, Danylchuk, AJ, & Suski, CD. 2011c. Estimates of field activity and metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry. *Journal of Experimental Marine Biology and Ecology* 396: 147–155. Elsevier B.V.

Murchie, KJ, Danylchuk, SE, Pullen, CE, Brooks, E, Shultz, AD, Suski, CD, Danylchuk, AJ, & Cooke, SJ. 2009. Strategies for the capture and transport of bonefish, *Albula vulpes*, from tidal creeks to a marine research laboratory for long-term holding. *Aquaculture Research* 40: 1538–1550.

Murchie, KJ, Shultz, AD, Stein, JA, Cooke, SJ, Lewis, J, Franklin, J, Vincent, G, Brooks, EJ, Claussen, JE, & Philipp, DP. 2015. Defining adult bonefish (*Albula vulpes*) movement corridors around Grand Bahama in the Bahamian Archipelago. *Environmental Biology of Fishes*.

Nishioka, R, & Bern, H. 1964. Secreation Masses in the Nuclei of the Caudal Neurosecretory Cells of the Teleost *Albula vulpes*. *Nature* 203: 1191–1192.

Nowell, LB, Brownscombe, JW, Gutowsky, LFG, Murchie, KJ, Suski, CD, Danylchuk, AJ, Shultz, A, & Cooke, SJ. 2015. Swimming energetics and thermal ecology of adult bonefish (*Albula vulpes*): a combined laboratory and field study in Eleuthera, The Bahamas. *Environmental Biology of Fishes*.

Nybelin, O. 1973. On the Caudal Skeleton of *Albula vulpes* (L.) (Pisces, Teleostei). *Zoologica Scripta* 2: 251–256.

Nybelin, O. 1976. Note on the osteology of the lower jaw in *Albula vulpes* (L.) (Pisces, Teleostei). *Zoologica Scripta* 5: 235–237.

Ogden, JC, Baldwin, JD, Bass, OL, Browder, JA, Cook, MI, Frederick, PC, Frezza, PE, Galvez, RA, Hodgson, AB, Meyer, KD, Oberhofer, LD, Paul, AF, Fletcher, PJ, Davis, SM, & Lorenz, JJ. 2014. Waterbirds as indicators of ecosystem health in the coastal marine habitats of Southern Florida: 2. Conceptual ecological models. *Ecological Indicators* 44: 128–147.

Olavo, G, Costa, PAS, Martins, AS, & Ferreira, BP. 2011. Shelf-edge reefs as priority areas for conservation of reef fish diversity in the tropical Atlantic. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21: 199–209.

Overstreet, R. 1970. Spinitectus beaveri sp. n. (Nematoda: Spiruroidea) from the bonefish, *Albula vulpes* (Linnaeus), in Florida. *Journal of Parasitology* 56: 128–130.

Palmer, JD. 1973. Tidal rhythms: The clock control of the rhythmic physiology of marine organisms. *Biological Review* 48: 377–418.

Palmer, RM, Cowley, PD, & Mann, BQ (eds). 2008. A Century of Linefish Research in South Africa: Bibliography and review of research trends. South African Network for Coastal and Oceanic Research Occasional Report No. 6: 108.

Pankhurst, NW, & Porter, MJR. 2003. Cold and dark or warm and light: Variations on the theme of environmental control of reproduction. *Fish Physiology and Biochemistry* 28: 385–389.

Papastamatiou, Y. 2008. Movement patterns, foraging ecology and digestive physiology of blacktip reef sharks, *Carcharhinus melanopterus*, at Plamyra atoll: a predator dominated ecosystem. University of Hawai'i.

Papastamatiou, YP, Dean Grubbs, R, Imhoff, JL, Gulak, SJB, Carlson, JK, & Burgess, GH. 2015. A subtropical embayment serves as essential habitat for sub-adults and adults of the critically endangered smalltooth sawfish. *Global Ecology and Conservation* 3: 764–775. Elsevier BV.

Papastamatiou, YP, Lowe, CG, Caselle, JE, & Friedlander, AM. 2009. Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. *Ecology* 90: 996–1008.

Peña, M, Williams, C, & Pfeiler, E. 1998. Structure of keratan sulfate from bonefish (*Albula* sp.) larvae deduced from NMR spectroscopy of keratanase-derived oligosaccharides. *Carbohydrate Research* 309: 117–124.

Pendoley, KL, Schofield, G, Whittock, PA, Ierodiaconou, D, & Hays, GC. 2014. Protected species use of a coastal marine migratory corridor connecting marine protected areas. *Marine Biology* 161: 1455–1466.

Pethybridge, HR, Parrish, CC, Bruce, BD, Young, JW, & Nichols, PD. 2014. Lipid, Fatty Acid and Energy Density Profiles of White Sharks: Insights into the Feeding Ecology and Ecophysiology of a Complex Top Predator. *PLoS ONE* 9.

Pfeiler, E. 1981. Salinity tolerance of leptocephalous larvae and juveniles of the bonefish (Albulae: *Albula*) from the gulf of California. *Journal of Experimental Marine Biology and Ecology* 52: 37–45.

Pfeiler, E, Bitler, B, & Ulloa, R. 2006. Phylogenetic Relationships of the Shafted Bonefish *Albula nemoptera* (Albuliformes: Albulidae) from the Eastern Pacific Based on Cytochrome *b* Sequence Analyses. *Copeia* 4: 778–784.

Pfeiler, E, Mendoza, MA, & Manrique, FA. 1988. Premetamorphic bonefish (*Albula* sp.) leptocephali from the Gulf of California with comments on life history. *Environmental Biology of Fishes* 21: 241–249.

Pfeiler, E, Van Der Heiden, AM, Ruboyianes, RS, & Watts, T. 2011. *Albula gilberti*, a new species of bonefish (Albuliformes: Albulidae) from the eastern Pacific, and a description of adults of the parapatric *A. esuncula*. *Zootaxa* 14: 1–14.

Pfeiler, E, & Vrijenhoek, RC. 1988. Differential Expression of the C_4 Isozyme of lactate Dehydrogenase ($LDHC_4$) in Developing Bonefish (*Albula* sp.). *Journal of Experimental Zoology* 246: 324–327.

Pincock, DG. 2012. False detections: What They Are and How to Remove Them from Detection Data. pp 1–11.

Porch, CE, & Fox, WW. 1990. Simulating the Dynamic Trends of Fisheries Regulated by Small Daily Bag Limits. *Transactions of the American Fisheries Society* 119: 836–849.

Pugh, DT, & Rayner, RF. 1981. The Tidal Regimes of Three Indian-Ocean Atolls and Some Ecological Implications. *Estuarine, Coastal and Shelf Science* 13: 389–407.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raby, GD, Packer, JR, Danylchuk, AJ, & Cooke, SJ. 2014. The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. *Fish and Fisheries* 15: 489–505.

Ram-Bidesi, V. 2011. An economic assessment of destructive fishing methods in Kiribati: A case study of *te ororo* fishing in Tarawa. pp 21–27.

Randall, J, & Bauchot, M. 1999. Clarification of the two indo-pacific species of bonefishes, *Albula glossodonta* and *A. forsteri*. *Cynium* 23: 79–83.

Rao, JS. 1976. Some tests based on arc-lengths for the circle. *Sankhya: The Indian Journal of Statistics, Series B (1960–2002)* 38: 329–338.

Revuelta, O, Hawkes, L, León, YM, Godley, BJ, Raga, JA, & Tomás, J. 2015. Evaluating the importance of Marine Protected Areas for the conservation of hawksbill turtles *Eretmochelys imbricata* nesting in the Dominican Republic. *Endangered Species Research* 27: 169–180.

Rivas, L, & Warlen, S. 1967. Systematics and biology of the bonefish *Albula Nemoptera* (Fowler). *Fishery Bulletin* 66: 251–258.

Robichaud, D, & Rose, G. 2002. The return of cod transplanted from a spawning ground in southern Newfoundland. *ICES Journal of Marine Science* 59: 1285–1293.

Robinson, J, Graham, NAJ, Cinner, JE, Almany, GR, & Waldie, P. 2015. Fish and fisher behaviour influence the vulnerability of groupers (Epinephelidae) to fishing at a multispecies spawning aggregation site. *Coral Reefs* 34: 371–382. Springer Berlin Heidelberg.

Ruiz-Frau, A, Possingham, HP, Edwards-Jones, G, Klein, CJ, Segan, D, & Kaiser, MJ. 2015. A multidisciplinary approach in the design of marine protected areas: Integration of science and stakeholder based methods. *Ocean & Coastal Management* 103: 86–93. Elsevier Ltd.

Salinas de León, P, Acuña-Marrero, D, Rastoin, E, Friedlander, AM, Donovan, MK, & Sala, E. 2016. Largest global shark biomass found in the northern Galápagos Islands of Darwin and Wolf. *PeerJ* 4.

Sattar, SA. 2009. Reef fish tagging programme – Baa Atoll pilot project, Marine Research Centre/ Atoll Ecosystem Conservation Project, Malé, Maldives, pp 39.

Sciberras, M, Jenkins, SR, Mant, R, Kaiser, MJ, Hawkins, SJ, & Pullin, AS. 2015. Evaluating the relative conservation value of fully and partially protected marine areas. *Fish and Fisheries* 16: 58–77.

Selin, N, Latypov, Y, Malyutin, A, & Bolshakova, L. 1992. Species composition and abundance of corals and other invertebrates on the reefs of the Seychelles Islands. *Atoll Research Bulletin*: 1–9.

Shaklee, JB, & Tamaru, CS. 1981. Biochemical and Morphological Evolution of Hawaiian Bonefishes (*Albula*). *Systematic Zoology* 30: 125–146.

Shapiro, SS, & Wilk, MB. 1965. An Analysis of Variance Test for Normality (Complete Samples). *Biometrika* 52: 591–611.

Shepard, RN. 1962. The analysis of proximities: Multidimensional scaling with an unknown distance function. I. *Psychometrika* 27: 125–140.

Shultz, AD, Murchie, KJ, Griffith, C, Cooke, SJ, Danylchuk, AJ, Goldberg, TL, & Suski, CD. 2011. Impacts of dissolved oxygen on the behavior and physiology of bonefish: Implications for live-release angling tournaments. *Journal of Experimental Marine Biology and Ecology* 402: 19–26.

Sielfeld, W, Laudien, J, Vargas, M, & Villegas, M. 2010. El Niño induced changes of the coastal fish fauna off northern Chile and implications for ichthyogeography. *Revista de Biología Marina y Oceanografía* 45: 705–722.

Simpfendorfer, CA, Heupel, MR, & Hueter, RE. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 23–32.

Spencer, T, Hagan, AB, Hamylton, SM, & Renaud, P. 2008. The Atlas of the Amirantes. Cambridge Coastal Research Unit, University of Cambridge: Cambridge, UK.

Stein, JA, Shultz, AD, Cooke, SJ, Danylchuk, AJ, Hayward, K, & Suski, CD. 2012. The influence of hook size, type, and location on hook retention and survival of angled bonefish (*Albula vulpes*). *Fisheries Research* 113: 147–152. Elsevier B.V.

Stoddart, DR, Coe, MJ, & Fosberg, FR. 1979. D'Arros and St Joseph, Amirante Islands. *Atoll Research Bulletin* 223: 1–48.

Sundström, LF, Gruber, SH, Clermont, SM, Correia, JPS, De Marignac, JRC, Morrissey, JF, Lowrance, CR, Thomassen, L, & Oliveira, MT. 2001. Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Environmental Biology of Fishes* 60: 225–250.

Suski, CD, Cooke, SJ, Danylchuk, AJ, O'Connor, CM, Gravel, MA, Redpath, T, Hanson, KC, Gingerich, AJ, Murchie, KJ, Danylchuk, SE, Koppelman, JB, & Goldberg, TL. 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* 148: 664–673.

Szekeres, P, Brownscombe, JW, Cull, F, Danylchuk, AJ, Shultz, AD, Suski, CD, Murchie, KJ, & Cooke, SJ. 2014. Physiological and behavioural consequences of cold shock on bonefish (*Albula vulpes*) in The Bahamas. *Journal of Experimental Marine Biology and Ecology* 459: 1–7. Elsevier B.V.

Taylor, BM, & Mills, JS. 2013. Movement and spawning migration patterns suggest small marine reserves can offer adequate protection for exploited emperorfishes. *Coral Reefs* 32: 1077–1087.

Taylor, S, & Grace, M. 2005. Development of retinal architecture in the elopomorph species *Megalops atlanticus*, *Elops saurus* and *Albula vulpes* (Elopomorpha: Teleostei). *Contributions in Marine Science* 37: 1–29.

Thompson, B, & Deegan, L. 1982. Distribution of Ladyfish (*Elops Saurus*) and Bonefish (*Albula vulpes*) Leptocephali in Louisiana. *Bulletin of Marine Science* 32: 936–939.

Tirant, N. 2016. D'Arros Island: Seychellois demand answes! *Todays Newspaper*.

van der Lingen, CD, Hutchings, L, Merkle, D, van der Westhuizen, JJ, & Nelson, J. 2001. Comparitive spawning habitats of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) in the Southern Benguela Upwelling Ecosystem. In: Kruse, GH, Bez, N, Booth, A, Dorn, MW, Hills, S, Lipcius, RN, Pelletier, D, Roy, C, Smith, SJ, & Witherell, D (eds). *Proceedings of the International Symposium on Spatial Processes and Management of Marine Populations, 27–30 October, Anchorage, Alaska.* University of Alaska Sea Grant, AK-SG-01-02, Fairbanks. pp 185–209.

Vásquez-Yeomans, L, Sosa-Cordero, E, Lara, MR, Adams, AJ, & Cohuo, JA. 2009. Patterns of distribution and abundance of bonefish larvae *Albula* spp. (Albulidae) in the western Caribbean and adjacent areas. *Ichthyological Research* 56: 266–275.

Voegeli, FA, Smale, MJ, Webber, DM, Andrade, Y, & O'dor, RK. 2001. Ultrasonic telemetry, tracking and automated monitoring technology for sharks. *Environmental Biology of Fishes* 60: 267–281.

Vogler, AP & Monaghan, MT. 2007. Recent advances in DNA taxonomy. *Journal of Zoological Systematics and Evolutionary Research* 45: 1–10.

von Brandis, R. 2012. D'Arros Research Centre - annual report. pp 77.

von Brandis, R. 2015. Annual public report. pp 1–32.

Wallace, E, & Tringali, M. 2010. Identification of a novel member in the family Albulidae (bonefishes). *Journal of Fish Biology* 76: 1972–1983.

Wallace, EM. 2015. High intraspecific genetic connectivity in the Indo-Pacific bonefishes: implications for conservation and management. *Environmental Biology of Fishes*: 1–25.

Wallace, EM, & Tringali, MD. 2016. Fishery composition and evidence of population structure and hybridization in the Atlantic bonefish species complex (*Albula* spp.). *Marine Biology* 163: 1–15. Springer Berlin Heidelberg.

Watson, RA, Die, DJ, & Restrepo, VR. 1993. Closed Seasons and Tropical Penaeid Fisheries: A Simulation Including Fleet Dynamics and Uncertainty. *North American Journal of Fisheries Management* 13: 326–336.

Webber, D. 2009. VEMCO Acoustic Telemetry New User Guide. Vemco, Halifax. pp 1–26.

Weinberger, C, & Posada, J. 2005. Analysis on the diet of bonefish, *Albula vulpes*, in Los Roques Archipelago National Park, Venezuela. *Contributions in Marine Science* 37: 30–45.

Welsh, JQ, & Bellwood, DR. 2012. Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): An evaluation using acoustic telemetry. *Coral Reefs* 31: 55–65.

Wetherbee, BM, Gruber, HS, & Cortes, E. 1990. Diet, feeding habitat, digestion, and consumption in sharks, with special reference to the lemon shark, *Negaprion brevirostris*. Miami. pp 29–47.

Whitehead, P. 1986. The synonymy of *Albula vulpes* (Linnaeus, 1758) (Teleostei, Albulidae). *Cybium* 10: 211–230.

Wilcoxon, F. 1945. Individual Comparisons by Ranking Methods. *Biometrics Bulletin* 1: 80–83.

Zeller, D, & Russ, G. 2000. Population estimates and size structure of *Plectropomus leopardus* (Pisces: Serrainidae) in relation to no-fishing zones: mark-release-resighting and underwater visual census. *Marine and Freshwater Research* 51: 221–228.

Zuur, A, Ieno, E, Walker, N, Saveliev, A, & Smith, G. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science & Business Media, New York. pp 1–549.

Appendix I

	Category	Sub-category	Author	Year	Title	Journal	Ocean
1	Biology	Age & growth	Crabtree, RE, Harnden, CW, & Stevens, C	1994	Age, growth, and mortality of bonefish, *Albula vulpes*, from the waters of the Florida Keys	Fishery Bulletin	Atlantic
2	Biology	Age & growth	Pfeiler, E, Padron, D, & Crabtree, RE	2000	Growth rate, age and size of bonefish from the Gulf of California	Journal of Fish Biology	Pacific
3	Biology	Age & growth	Debrot, D, Posada, JM & Antczak, A	2007	What can archaeological otoliths of bonefish (*Albula vulpes*) tell us?	Gulf and Carribbean Fisheries Institute	Atlantic
4	Biology	Diet & feeding	Colton, DE & Alevizon, WS	1983	Feeding ecology of bonefish in Bahamian waters	Transactions of the American Fisheries Society	Atlantic
5	Biology	Diet & feeding	Crabtree, RE, Stevens, C, Snodgrass, D, & Stengard, FJ	1998	Feeding habits of bonefish, *Albula vulpes*, from the waters of the Florida Keys	Fishery Bulletin	Atlantic
6	Biology	Diet & feeding	Pfeiler, E, Mendoza, MA, & Manrique, FA	1998	Elemental (C, N and P) analysis of metamorphosing bonefish (*Albula sp.*) leptocephali : relationship to catabolism of endogenous organic compounds, tissue remodeling, and feeding ecology	Marine Biology	Pacific
7	Biology	Diet & feeding	Weinberger, CS & Posada, JM	2005	Analysis on the diet of bonefish, *Albula vulpes*, in the Los Roques Archipelago national park, Venezuela	Contributions in Marine Science	Atlantic
8	Biology	Eggs & Larvae	Rasquin, P	1955	Observations on the metamorphosis of the bonefish, *Albula vulpes* (Linnaeus)	Journal of Morphology	Atlantic
9	Biology	Eggs & Larvae	Eldred, B	1967	Larval bonefish, *Albula vulpes* (Linnaeus, 1758), (Albulidae) in Florida and adjacent waters	Immature vertebrates	Atlantic
10	Biology	Eggs & Larvae	Thompson, BA & Deegan, LA	1982	Distribution of Ladyfish (*Elops Saurus*) and Bonefish (*Albula vulpes*) Leptocephali in Louisiana	Bulletin of Marine Science	Atlantic
11	Biology	Eggs & Larvae	Pfeiler, E	1984	Changes in Water and Salt Content during Metamorphosis of Larval Bonefish (*Albula*)	Bulletin of Marine Science	Pacific
12	Biology	Eggs & Larvae	Pfeiler, E	1984	Effect of salinity on water and salt balance in metamorphosing bonefish (*Albula*) leptocephali	Journal of Experimemtal Marine Biology and Ecology	Pacific
13	Biology	Eggs & Larvae	Pfeiler, E	1984	Glycosaminoglycan Breakdown during Metamophosis of Larval Bonefish *Albula*	Marine Biology Letters	Pacific
14	Biology	Eggs & Larvae	Pfeiler, E & Luna, A	1984	Changes in biochemical composition and energy utilization during meta- morphosis of leptocephalous larvae of the bonefish (*Albula*)	Enviromental Biology of Fishes	Pacific
15	Biology	Eggs & Larvae	Pfeiler, E	1987	Free amino acids in metamorphosing bonefish (*Albula sp*.) leptocephali	Fish Physiology and Biochemistary	Pacific
16	Biology	Eggs & Larvae	Pfeiler, E & Lindley, V	1989	Chloride-Type Cells in the Skin of the Metamorhposing Bonefish (*Albula sp.*) Leptocephalus	Journal of Experimental Biology	Pacific
17	Biology	Eggs & Larvae	Pfeiler, E, Almada, E, & Vrijenhoek, RC	1990	Ontogenetic changes in proteins and isozyme expression in larval and juvenile bonefish (*Albula*)	Journal of Experimental Zoology	Pacific
18	Biology	Eggs & Larvae	Diaz, RE & Pfeiler, E	1993	Glycosidase and sulfatase activities and their possible role in keratan sulfate degradation in metamorphosing bonefish (*Albula sp.*) leptocephali	Fish Physiology and Biochemistary	Pacific
19	Biology	Eggs & Larvae	Padron, D, Lindley, VA, & Pfeiler, E	1996	Changes in lipid composition during metamorphosis of bonefish (*Albula sp.*) leptocephali	Lipids	Pacific
20	Biology	Eggs & Larvae	Pfeiler, E	1996	Energetics of metamorphosis in bonefish (*Albula sp*.) leptocephali: Role of keratan sulfate glycosaminoglycan	Fish Physiology and Biochemistary	Pacific
21	Biology	Eggs & Larvae	Pfeiler, E	1997	Effect of Ca^{2+} on survival and development of metamorphosing bonefish (*Albula sp.*) leptocephali	Marine Biology	Pacific
22	Biology	Eggs & Larvae	Pfeiler, E	1998	Isolation and partial characterization of a novel keratan sulfate proteoglycan from metamorphosing bonefish (*Albula*) larvae	Fish Physiology and Biochemistary	Pacific
23	Biology	Eggs & Larvae	Pfeiler, E	2001	Changes in hypoxia tolerance during metamorphosis of bonefish leptocephali	Enviromental Biology of Fishes	Pacific
24	Biology	Eggs & Larvae	Pfeiler, E & Vrijenhoek, RC	2005	Differential expression of the C4 isozyme of lactate dehydrogenase (LDHC4) in developing bonefish (*Albula sp.*)	Journal of Experimental Biology	Pacific
25	Biology	Life history	Fitch, JE	1950	Life history notes and the early development of the bonefish *Albula vulpes* (Linnaeus)	California Fish and Game	Pacific
26	Biology	Life history	Alperin, IM & Schaefer, RH	1964	Juvenile bonefish (*Albula vulpes*) in Great South Bay, New York	New York Fish and Game Journal	Atlantic
27	Biology	Life history	Shen, SC	1964	Notes on the leptocephali and juveniles of Elops saurus Linnaeus and *Albula vulpes* (Linnaeus) collected from the estuary of Tam-sui river in Taiwan	Quarterly Journal of the Taiwan Museum	Pacific
28	Biology	Life history	Burger, GE	1974	Age, Growth, Food Habits, and Reproduction of Bonefish, *Albula vulpes*, in South Florida Waters	Florida Marine Research Publications	Atlantic

29	Biology	Life history	Pfeiler, E, Mendoza, MA, & Manrique, F a	1988	Premetamorphic bonefish (*Albula sp.*) leptocephali from the Gulf of California with comments on life history	Enviromental Biology of Fishes	Pacific
30	Biology	Life history	Snodgrass, D, Crabtree, RE, & Serafy, JE	2008	Abundance, growth, and diet of young-of-the-year bonefish (*Albula spp.*) off the Florida Keys, U.S.A.	Bulletin of Marine Science	Atlantic
31	Biology	Life history	Donovan, MK, Friedlander, AM, Harding, KK, Schemmel, EM, Filous, A, Kamikawa, K, & Torkelson, N	2015	Ecology and niche specialization of two bonefish species in Hawai'i	Enviromental Biology of Fishes	Pacific
32	Biology	Physiology	Nybelin, O	1960	A gular plate in *Albula vulpes* (L.)	Nature	Atlantic
33	Biology	Physiology	Nishioka, RS & Bern, HA	1964	Secreation Masses in the Nuclei of the Caudal Neurosecretory Cells of the Teleost *Albula vulpes*	Nature	Pacific
34	Biology	Physiology	Fridberg, G, Bern, H a, & Nishioka, RS	1966	The caudal neurosecretory system of the isospondylous teleost, *Albula vulpes*, from different habitats	General and comparative endocrinology	Pacific
35	Biology	Physiology	Nybelin, O	1973	On the Caudal Skeleton of *Albula vulpes* (L.) (Pisces, Teleostei)	Zoologica Scripta	Atlantic
36	Biology	Physiology	Nybelin, O	1976	Note on the osteology of the lower jaw in *Albula vulpes* (L.) (Pisces, Teleostei)	Zoologica Scripta	Atlantic
37	Biology	Physiology	Pfeiler, E	1981	Salinity tolerance of leptocephalous larvae and juveniles of the bonefish (Albulae: *Albula*) from the gulf of California	Journal of Experimental Marine Biology and Ecology	Pacific
38	Biology	Physiology	Pena, M, Williams, C, & Pfeiler, E	1998	Structure of keratan sulfate from bonefish (*Albula sp* .) larvae deduced from NMR spectroscopy of keratanase-derived oligosaccharides	Carbohydrate research	Unknown
39	Biology	Physiology	Taylor, S & Grace, MS	2005	Development of retinal architecture in the elopomorph species *Megalops atlanticus, Elops saurus* and *Albula vulpes* (Elopomorpha: Teleostei)	Contributions in Marine Science	Pacific
40	Biology	Physiology	Murchie, KJ, Cooke, SJ, & Danylchuk, AJ	2010	Seasonal Energetics and Condition of Bonefish from Different Subtropical Tidal Creeks in Eleuthera, the Bahamas	Marine and Coastal Fishes	Atlantic
41	Biology	Physiology	Murchie, KJ, Cooke, SJ, Danylchuk, AJ, Danylchuk, SE, Goldberg, TL, Suski, CD, & Philipp, DP	2011	Thermal biology of bonefish (*Albula vulpes*) in Bahamian coastal waters and tidal creeks: An integrated laboratory and field study	Journal of Thermal Biology	Atlantic
42	Biology	Physiology	Murchie, KJ, Cooke, SJ, Danylchuk, AJ, & Suski, CD	2011	Estimates of field activity and metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry	Journal of Experimental Marine Biology and Ecology	Atlantic
43	Biology	Physiology	Brownscombe, JW, Gutowsky, LFG, Danylchuk, AJ, & Cooke, SJ	2014	Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers	Marine Ecology Progress Series	Atlantic
44	Biology	Physiology	Szekeres, P, Brownscombe, JW, Cull, F, Danylchuk, AJ, Shultz, AD, Suski, CD, Murchie, KJ, & Cooke, SJ	2014	Physiological and behavioural consequences of cold shock on bonefish (*Albula vulpes*) in the Bahamas	Journal of Experimental Marine Biology and Ecology	Atlantic
45	Biology	Physiology	Nowell, LB, Brownscombe, JW, Gutowsky, LFG, Murchie, KJ, Suski, CD, Danylchuk, AJ, Shultz, A, & Cooke, SJ	2015	Swimming energetics and thermal ecology of adult bonefish (*Albula vulpes*): a combined laboratory and field study in Eleuthera, The Bahamas	Environmental Biology of Fishes	Atlantic
46	Biology	Reproduction	Crabtree, RE, Snodgrass, D, & Harnden, CW	1997	Maturation and reproductive seasonality in bonefish, *Albula vulpes*, from the waters of the Florida keys	Fishery Bulletin	Atlantic
47	Biology	Reproduction	Danylchuk, AJ, Cooke, SJ, Goldberg, TL, Suski, CD, Murchie, KJ, Danylchuk, SE, Shultz, AD, Haak, CR, Brooks, EJ, Oronti, A, Koppelman, JB, & Philipp, DP	2011	Aggregations and offshore movements as indicators of spawning activity of bonefish (*Albula vulpes*) in The Bahamas	Marine Biology	Atlantic
48	Biology	Tagging & movement	Colton, DE & Alevizon, WS	1983	Movement Patterns of Bonefish *Albula vulpes*, in Bahamian waters	Fishery Bulletin	Atlantic
49	Biology	Tagging & movement	Pfeiler, E	1984	Inshore migration, seasonal distribution and size of larval bonefish, *Albula*, in the Gulf of California	Enviromental Biology of Fishes	Pacific
50	Biology	Tagging & movement	Humston, R, Ault, JS, Larkin, MF, & 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	Atlantic
51	Biology	Tagging & movement	Murchie, KJ, Cooke, SJ, Danylchuk, AJ, Danylchuk, SE, Goldberg, TL, Suski, CD, & Philipp, DP	2013	Movement patterns of bonefish (*Albula vulpes*) in tidal creeks and coastal waters of Eleuthera, The Bahamas	Fisheries research	Atlantic
52	Biology	Tagging & movement	Finn, JT, Brownscombe, JW, Haak, CR, Cooke, SJ, Cormier, R, Gagne, T, Danylchuck, AJ	2014	Applying network methods to acoustic telemetry data: Modeling the movements of tropical marine fishes	Ecological Modelling	Atlantic
53	Biology	Tagging & movement	Murchie, KJ, Shultz, AD, Stein, JA, Cooke, SJ, Lewis, J, Franklin, J, Vincent, G, Brooks, EJ, Claussen, JE, & Philipp, DP	2015	Defining adult bonefish (*Albula vulpes*) movement corridors around Grand Bahama in the Bahamian Archipelago	Enviromental Biology of Fishes	Atlantic
54	Ecology	Spatial & temporal distribution	Mojica, R, Shenker, JM, Harnden, CW, & Wagner, DE	1995	Recruitment of bonefish, *Albula vulpes*, around Lee Stocking Island, Bahamas	Fishery Bulletin	Atlantic
55	Ecology	Spatial & temporal distribution	Vasquez-Yeomans, L, Sosa-Cordero, E, Lara, MR, Adams, AJ, & Cohuo, JA	2009	Patterns of distribution and abundance of bonefish larvae *Albula spp*. (Albulidae) in the western Caribbean and adjacent areas	Ichthyological Research	Atlantic

56	Ecology	Trophic relationship	Amin, OM & Dailey MD	1996	Redescription of *Dollfusentis heteracanthus* (Acanthocephala: Illiosentidae) from Bonefish, *Albula vulpes*, in the West Indies	Journal of the Helminthological Society of Washington	Atlantic
57	Management & fisheries	Biology, ecology, age & growth	Adams, AJ, Horodysky, AZ, Mcbride, RS, Guindon, K, Shenker, J, Macdonald, TC, Harwell, HD, Ward, R, & Carpenter, K	2014	Global conservation status and research needs for tarpons (Megalopidae), ladyfishes (Elopidae) and bonefishes (Albulidae)	Fish and Fisheries	Global
58	Management & fisheries	Fisheries, resource use & economics	Johannes, RE & Yeeting, B	2000	I-Kiribati knowledge and management of Tarawa's lagoon resources	Atoll research bulliten	Pacific
59	Management & fisheries	Fisheries, resource use & economics	Debrot, D & Posada, J	2005	A brief description of the bonefish recreational fishery in Los Roques archipelago national park, Venezuela	Contributions in Marine Science	Atlantic
60	Management & fisheries	Fisheries, resource use & economics	Larkin, MF, Ault, JS, Humston, R, & Luo, J	2010	A mail survey to estimate the fishery dynamics of southern Florida's bonefish charter fleet	Fisheries management and Ecology	Atlantic
61	Management & fisheries	Fisheries, resource use & economics	Adams, AJ & Cooke, SJ	2015	Advancing the science and management of flats fisheries for bonefish, tarpon, and permit	Environmental Biology of Fishes	Global
62	Management & fisheries	Fisheries, resource use & economics	Frezza, PE & Clem, SE	2015	Using local fisher's knowledge to characterize historical trends in the Florida Bay bonefish population and fishery	Environmental Biology of Fishes	Atlantc
63	Management & fisheries	Policy & regulation	Cooke, SJ & Philipp, DP	2004	Behavior and mortality of caught-and-released bonefish (*Albula spp.*) in Bahamian waters with implications for a sustainable recreational fishery	Biological conservation	Atlantic
64	Management & fisheries	Policy & regulation	Danylchuk, AJ, Danylchuk, SE, Cooke, SJ, Goldberg, TL, Koppelman, JB, & Philipp, DP	2007	Post-release mortality of bonefish, *Albula vulpes* , exposed to different handling practices during catch-and-release angling in Eleuthera, the Bahamas	Fisheries management and Ecology	Atlantic
65	Management & fisheries	Policy & regulation	Danylchuk, SE, Danylchuk, AJ, Cooke, SJ, Goldberg, TL, Koppelman, J, & Philipp, DP	2007	Effects of recreational angling on the post-release behavior and predation of bonefish (*Albula vulpes*): The role of equilibrium status at the time of release	Journal of Experimental Marine Biology and Ecology	Atlantic
66	Management & fisheries	Policy & regulation	Suski, CD, Cooke, SJ, Danylchuk, AJ, O'Connor, CM, Gravel, MA, Redpath, T, Hanson, KC, Gingerich, AJ, Murchie, KJ, Danylchuk, SE, Koppelman, JB, & Goldberg, TL	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	Atlantic
67	Management & fisheries	Policy & regulation	Cooke, SJ, Suski, CD, Danylchuk, SE, Danylchuk, AJ, Donaldson, MR, Pullen, C, Bulté, G, O'toole, A, Murchie, KJ, Koppelman, JB, Shultz, AD, Brooks, E, & Goldberg, TL	2008	Effects of different capture techniques on the physiological condition of bonefish *Albula vulpes* evaluated using field diagnostic tools	Journal of Fish Biology	Atlantic
68	Management & fisheries	Policy & regulation	Danylchuk, AJ, Adams, A, Cooke, SJ, & Suski, CD	2008	An evaluation of the injury and short-term survival of bonefish (*Albula spp* .) as influenced by a mechanical lip-gripping device used by recreational anglers	Fisheries research	Atlantic
69	Management & fisheries	Policy & regulation	Dallas, LJ, Shultz, a. D, Moody, a. J, Sloman, K a., & Danylchuk, a. J	2010	Chemical excretions of angled bonefish *Albula vulpes* and their potential use as predation cues by juvenile lemon sharks Negaprion brevirostris	Journal of Fish Biology	Atlantic
70	Management & fisheries	Policy & regulation	Shultz, AD, Murchie, KJ, Griffith, C, Cooke, SJ, Danylchuk, AJ, Goldberg, TL, & Suski, CD	2011	Impacts of dissolved oxygen on the behavior and physiology of bonefish: Implications for live-release angling tournaments	Journal of Experimental Marine Biology and Ecology	Atlantic
71	Management & fisheries	Policy & regulation	Stein, JA, Shultz, AD, Cooke, SJ, Danylchuk, AJ, Hayward, K, & Suski, CD	2012	The influence of hook size, type, and location on hook retention and survival of angled bonefish (*Albula vulpes*)	Fisheries research	Atlantic
72	Management & fisheries	Policy & regulation	Brownscombe, JW, Thiem, JD, Hatry, C, Cull, F, Haak, CR, Danylchuk, AJ, & Cooke, SJ	2013	Recovery bags reduce post-release impairments in locomotory activity and behavior of bonefish (*Albula spp.*) following exposure to angling-related stressors	Journal of Experimental Marine Biology and Ecology	Atlantic
73	Management & fisheries	Policy & regulation	Brownscombe, JW, Griffin, LP, Gagne, T, Haak, CR, Cooke, SJ, & Danylchuk, AJ	2015	Physiological stress and reflex impairment of recreationally angled bonefish in Puerto Rico	Enviromental Biology of Fishes	Atlantic
74	Management & fisheries	Policy & regulation	Hannan, KD, Zuckerman, ZC, Haak, CR, & Shultz, AD	2015	Impacts of sun protection on feeding behavior and mucus removal of bonefish, *Albula vulpes*	Environmental Biology of Fishes	Atlantic
75	Management & fisheries	Research programs or objectives	Kamikawa, KT, Friedlander, AM, Harding, KK, Filous, A, Donovan, MK, & Schemmel, E	2015	Bonefishes in Hawai'i and the importance of angler-based data to inform fisheries management	Enviromental Biology of Fishes	Pacific
76	Management & fisheries	Stock assesment	Beets, J	2000	Declines in finfish resources in Tarawa Lagoon, Kiribati, emphasize the need for increased conservation effort	Atoll research bulliten	Pacific
77	Other	Mariculture & aquaculture	Murchie, KJ, Danylchuk, SE, Pullen, CE, Brooks, E, Shultz, AD, Suski, CD, Danylchuk, AJ, & Cooke, SJ	2009	Strategies for the capture and transport of bonefish, *Albula vulpes* , from tidal creeks to a marine research laboratory for long-term holding	Aquaculture Research	Atlantic

78	Other	Parasites	Overstreet, RM	1970	*Spinitectus beaveri* sp. n.(Nematoda: Spiruroidea) from the bonefish, *Albula vulpes* (Linnaeus), in Florida	Journal of Parisitology	Atlantic
79	Taxonomy & systematics	Genetic	Pfeiler, E, Bitler, BG, & Ulloa, R	2006	Phylogenetic Relationships of the Shafted Bonefish *Albula nemoptera* (Albuliformes: Albulidae) from the Eastern Pacific Based on Cytochrome b Sequence Analyses	Copeia	Pacific
80	Taxonomy & systematics	Genetic	Pfeiler, E, Watts, T, Pugh, J, & van der Heiden, AM	2008	Speciation and demographic history of the Cortez bonefish, *Albula sp. a* (Albuliformes: Albulidae), in the Gulf of California inferred from mitochondrial DNA	Journal of Fish Biology	Pacific
81	Taxonomy & systematics	Genetics	Shaklee, JB & Tamaru, CS	1981	Biochemical and Morphological Evolution of Hawaiian Bonefishes (*Albula*)	Systematic Biology	Pacific
82	Taxonomy & systematics	Genetics	Pfeiler, E	1996	Allozyme differences in Caribbean and Gulf of California populations of bonefishes (*Albula*)	Copeia	Pacific & Atlantic
83	Taxonomy & systematics	Genetics	Colborn, J, Crabtree, RE, Shaklee, JB, Pfeiler, E, & Bowen, BW	2001	The evolutionary enigma of bonefishes (*Albula spp.*): cryptic species and ancient separations in a globally distributed shorefish	Evolution	Global
84	Taxonomy & systematics	Genetics	Pfeiler, E, Colborn, J, Douglas, MR, & Douglas, ME	2002	Systematic status of bonefishes (*Albula spp*.) from the eastern Pacific Ocean inferred from analyses of allozymes and mitochondrial DNA	Enviromental Biology of Fishes	Pacific
85	Taxonomy & systematics	Genetics	Pfeiler, E, Bitler, BG, Ulloa, R, van der Heiden, AM, & Hastings, PA	2008	Molecular Identification of the Bonefish *Albula esuncula* (Albuliformes: Albulidae) from the Tropical Eastern Pacific, with Comments on Distribution and Morphology	Copeia	Pacific
86	Taxonomy & systematics	Genetics	Seyoum, S, Wallace, EM, & Tringali, MD	2008	Twelve polymorphic microsatellite markers for the bonefish, *Albula vulpes* and two congeners	Molecular Ecology Resources	Atlantic
87	Taxonomy & systematics	Genetics	Wallace, EM & Tringali, MD	2010	Identification of a novel member in the family Albulidae (bonefishes)	Journal of Fish Biology	Atlantic
88	Taxonomy & systematics	Genetics	Kwun, HJ & Kim, JK	2011	A new species of bonefish, *Albula koreana* (Albuliformes: Albulidae) from Korea and Taiwan	Zootaxa	Pacific
89	Taxonomy & systematics	Genetics	Kwun, HJ, Kim, JK, Doiuchi, R, & Nakabo, T	2011	Molecular and morphological evidence for the taxonomic status of a newly reported spacies of *Albula* (Albuliformes: Albulidae) from Korea and Taiwan	Animal Cells and Systems	Pacific
90	Taxonomy & systematics	Genetics	Pfeiler, E, Van Der Heiden, AM, Ruboyianes, RS, & Watts, T	2011	*Albula gilberti*, a new species of bonefish (Albuliformes: Albulidae) from the eastern Pacific, and a description of adults of the parapatric A. esuncula	Zootaxa	Pacific
91	Taxonomy & systematics	Genetics	Wallace, EM	2015	High intraspecific genetic connectivity in the Indo-Pacific bonefishes: implications for conservation and management	Enviromental Biology of Fishes	Indo-Pacific
92	Taxonomy & systematics	New records & descriptions	Leary, TR	1957	The Bonefish, *Albula vulpes*, in Texas	Copeia	Atlantic
93	Taxonomy & systematics	New records & descriptions	Rivas, LR & Warlen, SM	1967	Systematics and biology of the bonefish *Albula nemoptera* (Fowler)	Fishery	Atlantic and Pacific
94	Taxonomy & systematics	New records & descriptions	Randall, JE & Bauchot, ML	1999	Clarification of the two indo-pacific species of bonefishes, *Albula glossodonta* and *A. forsteri*	Cynium	Indo-Pacific
95	Taxonomy & systematics	New records & descriptions	Cuevas, KJ, Franks, JS, & Buchanan, M	2004	First Record of Bonefish, *Albula vulpes*, from Mississippi Coastal Waters	Gulf and Caribbean research	Atlantic
96	Taxonomy & systematics	New records & descriptions	Hidaka, K, Iwatsuki, Y, & Randall, JE	2008	A review of the Indo-Pacific bonefishes of the *Albula argentea* complex, with a description of a new species	Ichthyological Research	Indo-Pacific
97	Taxonomy & systematics	New records & descriptions	Pfeiler, E	2008	Resurrection of the name *Albula pacifica* (Beebe, 1942) for the shafted bonefish (Albuliformes: Albulidae) from the eastern Pacific	Revista de Biologia Tropical	Pacific
98	Taxonomy & systematics	New records & descriptions	De Lucena, CAS & Neto, PC	2012	Elopomorpha leptocephali from Southern Brazil: a new report of *Albula sp*. (Albulidae) and first record of *Elops smithi* (Elopidae) in Brazilian waters	Biotemas	Atlantic
99	Taxonomy & systematics	Taxonomy & systematics	Whitehead, PJP	1986	The synonymy of *Albula vulpes* (Linnaeus, 1758) (Teleostei, Albulidae)	Cybium	Global