Following bonefishes in Hawai‘i: Connecting the dots from ocean to table

A DISSERTATION SUBITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAI‘I AT MĀNOA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

MARINE BIOLOGY

May 2023

By

Keith T. Kamikawa

Dissertation Committee:
Brian Bowen, Chairperson
Robert Humphreys
Donald Kobayashi
Kirsten Oleson
Kim Peyton

Keywords: bonefish, life history, leptocephalus, recruitment, population genetics, preferences, disposition

Acknowledgements

Thank you very much to my committee for all of their time, expertise, and patience throughout my academic journey. Many thanks to the Bonefish Tarpon Trust and the UH Mānoa Graduate Student Organization for funding this research. Thank you to Allan Yoshimoto, Christopher Haak, and Matthew Ramsey for assistance with light trap design, deployment recommendations, and participating in sampling. Thanks to Keliʻi Kotubetey and the Department of Forestry and Wildlife for granting me access to Heʻeia Fish Pond and Paiko Lagoon for sampling, respectively. Thanks to Jeffrey Sampaga and Ryan Nichols for teaching otolith extraction and processing techniques. Thank you to all the anglers who collected bonefish fin clips and/or participated in my survey. Thanks to T.J. Breshears for assistance with generating maps and Liz Wallace for assisting with the population genetics chapter. Lastly, thanks to all who provided comments and edits on this dissertation.

Abstract

Hawai‘i is home to the Indo-Pacific round jaw (*Albula glossodonta*) and the endemic sharp jaw (*A. virgata*). These species’ hold cultural, recreational, and commercial value in Hawai‘i and it is important to fill various data gaps in their life history. Our understanding of bonefish site fidelity, habitat use, population structure and effective conservation measures is based on limited information in Hawai‘i. First, leptocephalus larvae were captured by light trap in Kāne‘ohe and Maunalua Bays and aged through otolith analyses. Leptocephali ranged from 28-72 days old and 54-66 mm. The mean age of the larvae was 48.8 days, indicating high dispersal ability. Tissue samples from larvae and over 300 fin clips, collected by volunteer anglers from O‘ahu, Maui, Kiritimati and Anaa Atoll, were used to determine population structure within the Pacific Ocean. Results showed Anaa and Hawai‘i exhibiting distinct genetic stocks and Kiritimati with admixed individuals. Lastly, a survey was conducted of bonefish anglers to understand their motivations and preferences. Of the anglers that keep bonefish for food, they prefer fish over a four-pound threshold. Comments also revealed anglers’ attitudes towards current management and competing demands. Aligning biological and social information regarding bonefish life history is critical to update fisheries management tools and promote responsible fishing practices.

Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction

Bonefishes (*Albula* spp.) are recognized around the world as a sport fish prized for their incredible speed, fighting strength on rod-and-reel, and cunning elusiveness. Bonefish systematics is quite complex with relatively recent studies revising the classification and revealing cryptic species (Colborn *et al*., 2001; Adams & Cooke, 2015; Wallace & Tringali, 2016). Current research suggests that there are at least 12 species distributed throughout tropical and sub-tropical waters, and several of them are still undescribed (Bowen *et al*., 2008). They are usually characterized as a "flats" species, which is generalized as a shallow habitat usually consisting of mangroves, sand, mud, rubble, and benthic algae (Adams & Cooke, 2015). This makes them a target for fly-fishing anglers, but also makes them susceptible to many other types of shallow harvest techniques. However, several species reside mainly in deeper habitats and are targeted by a different set of fishing methods.

The International Game Fish Association (IGFA) compiled a list of the seven top destinations to target trophy sized bonefishes, and Hawaiʻi is on this reputable list for producing several world records over past decades. Hawaiʻi hosts two bonefish species, the Indo-Pacific round jaw (*Albula glossodonta*) and the endemic sharp jaw (*Albula virgata*) (Shaklee & Tamaru, 1981; Randall & Bauchot, 1999; Hidaka *et al*. 2008). The importance of these bonefishes in Hawaiʻi extends further than providing a top destination in the world for catching a trophy caliber fish. Bonefishes were culturally significant and an important food source for early Hawaiians (Titcomb, 1972; Allen, 2014). They are still valued table fare and usually prepared raw as "lomi ʻōʻio" or in a cooked fishcake form. Many of the *Albula* species in developed regions are not readily consumed or considered a delicacy as they are in Hawaiʻi. These fishes support a rapidly expanding fly-fishing industry and are one of the top species targeted during year-around shoreline fishing tournaments. The recreational fishery continues to expand, whereas commercial landings have decreased by 99% in the past century (Friedlander *et al*., 2007; 2015).

Despite the economic, cultural, recreational, and commercial value of bonefishes in Hawaiʻi, there is scant life history information available. Compounding this problem, there is often a communication "gap" between resource users, policy makers, and scientists in Hawaiʻi. A bonefish tagging project was established in Hawaiʻi in 2003 to engage anglers in citizen science and provide reliable information for proper management and sustainable use of near shore resources. As a result, there is a growing conservation ethic for these species and new information was recently published about their basic biology and ecology (Donovan *et al*., 2015; Kamikawa *et al*., 2015). There are still important knowledge gaps that need to be filled to provide a holistic picture of bonefish life history and fisheries in Hawaiʻi.

The bonefish life cycle begins with spawning in the pelagic realm. Bonefish spawning events have not been formally documented in Hawaiʻi, however, it could be expected that they form spawning aggregations and spawn offshore as their sister species do in Florida and the Bahamas (Crabtree *et al*., 1997; Larkin *et al*., 2007). Leptocephali, bonefish larvae, can have a pelagic larval duration (PLD) ranging from 42-70 days (Friedlander *et al*., 2007). These larvae seek inshore, calm habitats to undergo metamorphosis (Pfeiler, 1984; Mojica *et al*., 1995). Few anecdotes and grey literature reports allude to leptocephali in near shore waters around Oʻahu and Hawaiʻi Island. A few confirmed bonefish leptocephalus larva were captured during beach seining during NOAA Pacific Island Fisheries Science Center (PIFSC) and Hawaiʻi Division of Aquatic Resources sampling projects. Overall, the bonefish larval stage is still not clearly understood in Hawaiʻi.

This unique larval stage has the ability to travel long distances and contribute to gene flow throughout its Indo-Pacific range (Wallace, 2015). Previous *A. glossodonta* mtDNA studies have shown population structure between the Line and Hawaiian Islands, but some studies have been limited by small sample sizes (Friedlander *et al*. 2008; Wallace, 2015). Genetic breaks are also seen between Hawaiian Islands in various fish species (Rivera *et al*., 2011; Toonen *et al*., 2011; Tenggardjaja *et al*., 2016). A genomic approach would be able to illuminate any bonefish structure existing within Hawaiʻi. Bonefish population structure would have important management implications, as different countries and different Hawaiian Islands have varied regulations.

In Hawaiʻi, there is only marginally more information for the juvenile life stage. *A. vulpes* and (undescribed) Sp. B in the Atlantic and Caribbean show alternate use of habitat, where adult *A. vulpes* use the shallow flats and the juveniles reside in the deep and Sp. B adults are mainly found in the deeper waters and the juveniles are found in shallower coastal habitats. A similar pattern is suspected in Hawaiʻi between *A. glossodonta* and *A. virgata*. Beach seining has revealed that most of the juvenile bonefishes caught in the shallow nearshore environment are *A.*

virgata and catch data from fishers clearly show that adult *A. virgata* use deep water habitats (Donovan *et al*., 2015; 2016). In contrast, adult *A. glossodonta* use shallow flats and the juveniles are residing in deeper areas (Donovan *et al*., 2015). This niche partitioning may allow for reduced competition between related species.

Most of the information existing for Hawaiʻi's bonefishes apply to the adult stage, targeted in Hawaiʻi's diverse fishery. Baseline data for diet, spawning, habitat preference, sight fidelity, and growth for both *A. glossodonta* and *A. virgata* are provided in Kamikawa *et al*., 2015 and Donovan *et al*., 2015. Fishery related data is only available from commercial landing reports and the Marine Recreational Information Program (McCoy *et al.*, 2018). Bonefish sell for <$3/pound on average, making these species not very lucrative (WPacFIN). Most of the bonefishes' value is through the non-commercial or recreational fishery, which also happens to be extremely data limited from a fishery-dependent data perspective. Therefore, little is known regarding how many fish are caught in the non-commercial fishery and what importance these fishes have post hooking (i.e. cultural, sustenance, bait, etc.).

This dissertation intends to fill the information and data gaps described above, through a multi-disciplinary project to complete the holistic picture of a bonefishes' life cycle. This also presents an opportunity to incorporate members of the fishing community and create a collaborative effort among agencies. Chapter 2 focuses on using underwater light traps to locate and obtain life history information for bonefish leptocephali larvae. Chapter 3 utilizes genomic methods to identify population structure of Hawaiʻi's bonefishes at an island, state, and Pacific-basin scale. Chapter 4 characterizes the fishery's social dynamics by understanding angler attitudes and preferences and fish disposition.

Chapter 2: Presence of bonefish leptocephalus in estuarine habitats on O‘ahu

Abstract

Bonefishes and other elopomorphs have a unique, transparent leptocephalus larval stage that is challenging to study due to its cryptic nature. Understanding life history is important especially considering adult bonefishes in Hawai‘i are highly sought gamefish valued for their tenacious fight on rod-a-reel and delicate taste. In this study light traps were used to capture leptocephali at three nearshore locations around O‘ahu, Hawai‘i. Otolith analyses revealed ages from 28-72 days with an average age of about 48 days. Genetic species identification on a subset of the larvae showed that one of 28 specimens was *Albula virgata*, which is endemic to Hawai‘i, and the remaining were the Indo-Pacific *A. glossodonta*. Leptocephali lengths ranged from 54-66 mm and most were caught during 8:00-9:00 pm on rising tides. Along with calm inshore waters, estuarine habitat appears to be a critical element for leptocephali recruitment success. Reducing impacts to these estuarine habitats and protecting and restoring freshwater input may have positive impacts on leptocephali recruitment, the essential starting point for thriving bonefish fisheries in Hawai‘i.

Introduction

Most marine fish species spend the first portion of their life as larvae in the pelagic environment (Almany & Webster, 2006). Shape, size, behavior, and duration of this larval stage varies greatly among species, and this often creates obstacles to studying larvae. However, identifying the characteristics and processes that determine fluctuations in recruitment can provide critical information for managing fish stocks (Bergenius *et al*., 2002). Larval fish also hold valuable chronological information, because pelagic larval duration (PLD) and age provide indicators of when spawning occurs (Campana & Thorrold, 2001; Begg *et al*., 2005). Simply documenting the presence or absence of larval fish offers insight into essential habitat preferences, potentially identifying critical nursery habitat for growth, feeding, and protection (Dahlgren *et al*., 2006).

Fishes in the superorder Elopomorpha, including bonefishes (*Albula* spp.), have a unique thin, transparent larval stage known as a leptocephalus (Miller & Tsukamoto, 2004). Although the fundamental shape of these larvae differs between taxonomic orders of fishes, the families Albulidae, Elopidae, and Megalopidae can be distinguished by the presence of a distinct forked caudal fin (Miller & Tsukamoto, 2004). The adult stage of the fishes from these families are also distinctly fish-like compared to other families that are more eel-like in adult body design. The number of muscle segments and the number of vertebrae are the only morphological traits universally maintained through metamorphosis, providing a useful method to distinguish some species (Smith, 1979). Bonefish leptocephali attain lengths ranging from 50-100mm before decreasing in length prior to metamorphosis and settlement (Alexander, 1961). *Albula* leptocephali attain lengths up to ~70mm and subsequently decline in length by 50% during metamorphosis (Mojica *et al*., 1995).

Bonefish leptocephali research has been conducted primarily in Western Atlantic regions focusing on distributions, abundances, and growth (Mojica *et al*., 1995; Adams *et al*., 2008; Snodgrass *et al*., 2008). In the Pacific, leptocephali have pelagic larval durations ranging from 42-70 days (Friedlander *et al*., 2007), and apparently disperse over long distances, contributing to basin-scale gene flow (Wallace, 2015). Bonefish spawning events have not been scientifically documented in Hawaiʻi, however, they may form offshore spawning aggregations similar to congeneric species in Florida and the Bahamas (Danylchuk *et al*., 2011; Adams & Cooke, 2015).

Leptocephali recruitment to nearshore habitat has been linked to dark moonless conditions and flood tides in the Bahamas (Mojica *et al*., 1995). In the central Pacific, recruitment appeared to have a seasonal pattern at Palmyra Atoll with leptocephali captured mainly during March and August (Friedlander *et al*., 2007). Both the Bahamas and Palmyra studies utilized channel nets to passively capture leptocephali in the water column. Limited information exists for bonefish leptocephali in the Pacific with no published information for leptocephali in Hawaiʻi (Friedlander *et al*., 2007), although grey literature reports and anecdotal observations allude to leptocephali in near shore waters around Oʻahu and Hawaiʻi Island. One preserved specimen exists at the Inouye Regional Center in the Pacific Island Fisheries Science Center (PIFSC).

Unlike the Bahamas and Palmyra studies, the use of fixed channel nets is not feasible in densely populated areas with high traffic, such as Hawaiʻi. Alternately, bonefish leptocephali can be captured in light traps set at night (Vasquez-Yeomans *et al*., 2009). Light traps are also a less invasive sampling strategy, especially when targeting fragile fish larvae (Doherty, 1987; Meekan *et al*., 2001). There are many different designs of light traps, and they can be used to sample in areas where net sampling is infeasible, in habitats that are too shallow, rugged, or vulnerable to coral damage (Rooker *et al*., 1996). These attributes make light traps the optimal sampling tool for the capture of delicate larvae in Hawaiian reef-associated waters.

The goal of this study was to locate and obtain life history information from bonefish leptocephali larvae around Hawaiʻi. Although adult bonefish are highly prized by the fishers and an important food source for local communities, their early life stages, particularly the cryptic leptocephalus stage and its subsequent metamorphosis, has been scantly studied and remains largely unknown. Through the application of otolith analysis on leptocephalus larvae, estimates of age and pelagic larval duration (PLD) can be derived. When the latter estimates are combined with capture date, time of spawning (hatch date) can also be estimated. This information can be combined with ovarian histological analyses to resolve spawning seasons. PLD can also be an indicator of dispersal potential, connecting populations of fish from different islands or regions. Furthermore, site-specific captures of leptocephali reveal their preferred environments and habitats. Bonefish leptocephali are expected to seek calm inshore waters, such as estuaries, before undergoing metamorphosis (pers. comm. with C. Haak). Their presence highlights the combination of habitat and environmental conditions associated with recruitment.

The life history information collated in this paper can inform future management decisions. Identifying bonefish spawning peaks can be used to promote responsible fishing practices during these times, and protect them from mass harvest techniques such as gill nets. Reducing runoff, development, groundwater pollution, freshwater diversion, or other anthropogenic impacts to critical recruitment habitat would safeguard the areas that serve as incubators for healthy fisheries.

Methods

Sampling

Light traps were constructed using plastic three-gallon buckets with inverted funnels epoxied into the side of the bucket body (Figure 1). An LED light hanging from a screw-on cover inside the top of the body acts as the attractant. Large PVC fittings were attached to a hole at the bottom of the body by a cylindrical neck of fine mesh netting. Lastly, a float is attached to the bucket handle and a tether line is tied to the float. Two traps were typically deployed at a time and they were tethered on dry land to ensure ease of recovery and loss prevention.

Figure 1. Image of light trap made from a three-gallon bucket and inverted funnels.

Various locations were tested for sampling, but only three locations were continuously visited throughout the duration of this study. Sampling sites were located in Kāne‘ohe Bay (the sluice gates of He‘eia fish pond) and two locations within Maunalua Bay (the mouth of Paiko Lagoon and the western mouth of Kuapa Pond at Maunalua Bay Beach Park) (Figure 2). Traps were deployed within and following the bonefish peak spawning season, which is generally from October through June in Hawai‘i. The ideal sampling conditions were after dusk, on rising tides, and during the week before and during the new moon (Mojica *et al*., 1995). They were checked regularly at intervals of 30-45 minutes, with salinity and temperature recorded from the surrounding water via thermometer and refractometer. A two-sample *t*-test was used to compare average salinity and temperature between sampling sessions that yielded larvae and those that did not. Leptocephali were carefully removed from the trap’s holding well and the trap was redeployed in the same location. Fork length (mm) and weight (g) of each leptocephali was logged prior to preservation in 90% ethanol, along with date and time of collection.

Figure 2. Light trap sampling locations for bonefish (*Albula* spp.) on O‘ahu He‘eia fish pond in Kāne‘ohe Bay (left) and Paiko Lagoon and Maunalua Bay Beach park in Maunalua Bay (right).

Otolith processing and analysis

Sagittal otoliths were isolated and removed from leptocephalus larvae after the braincase was dissolved in a dilute solution of sodium hypochlorite (Clorox bleach). Sagittal otoliths of juveniles were distinct and directly extracted from the braincase using fine-tipped forceps and fine-tipped art brushes. All otoliths were placed concave side down on glass slides and mounted in thermoplastic resin (Crystal Bond 509, Electron Microscopy Sciences, Hatfield PA). Each otolith was photographed with a microscope mounted camera. Digital images were enhanced using NIH ImageJ software. An initial count of daily growth increments (DGI) was conducted for each fish followed by a second count no less than a month later. Age determination was based on the average of the two counts. Otolith counts with age deviations >10% were removed from further analysis. For each fish aged, a back-calculation was used to estimate time (month) of spawning. Length and weight data from the juveniles was fit to the length-weight relationship in Froese (2006) and Froese *et al*. (2011).

DNA barcoding

A tissue sample from a subset of the bonefish leptocephalus larvae (n = 28) was sent to the Fish and Wildlife Research Institute (FWRI) in St. Petersburg, Florida. The subset was haphazardly chosen based on the leptocephali available at the time. Genetic species identification was conducted using the screening methodology of Wallace & Tringali (2010), and the allelic outputs were compared to verified genotypes of *Albula* species in the Pacific Ocean in Genetix 4.05 (Belkhir *et al*., 2000).

Results

Sampling

Over 130 hours of nighttime light trap sampling occurred during the winter and spring months of 2017-2021. Trap soak time ranged from 0.33h to 4h with a mean of 2h per trap deployment. Twenty-eight of the 63 total sampling sessions yielded 59 bonefish leptocephalus larvae. Two of the ten sessions at He‘eia fishpond yielded a total of five larvae, four of 18 Paiko Lagoon sessions yielded seven larvae, and 20 of 35 Maunalua Bay Beach Park yielded 47 larvae. Of the 20 successful sampling sessions at Maunalua Bay Beach Park, two nights yielded a total of 18 larvae. Other sampling sites 4,300 m east of He‘eia fishpond and 600 m east of Maunalua Bay Beach Park did not yield any larvae. Length and weight metrics were obtained from 39 larvae, with a fork length range of 54-66 mm (m=60.9 mm ± 3.2 SD) and weight range of 0.23-0.45 g (m=0.30 g ± 0.04 SD) (Figure 3). Their morphology and length range indicate these larvae are late Phase I, reaching their maximum length before metamorphosis (Figure 4). Water temperatures and salinity at the sampling sites ranged from 19.3-28 C (m=24.2 C ± 1.8 SD) and 15-34 ppm (m=29.6 ppm ± 3.8 SD). There was no significant difference in water temperature or salinity between successful sampling sessions and the nights that yielded no larvae, based on a two-sample *t*-test.

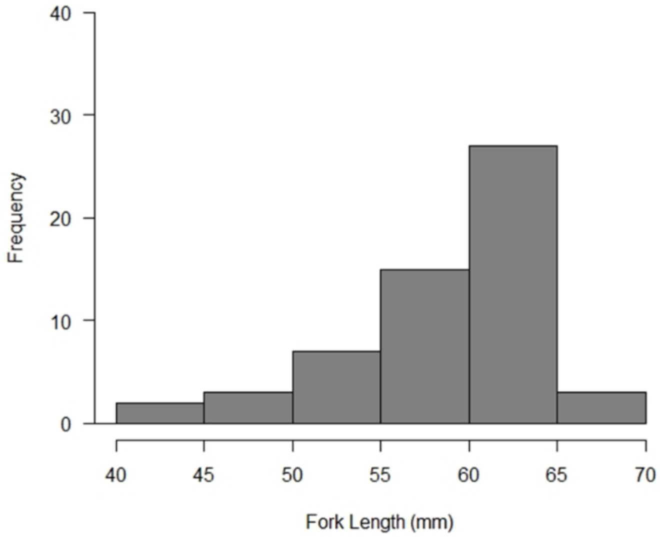


Figure 3. Length frequencies of *Albula* leptocephali captured from O‘ahu locations during winter and spring months from 2017-2020.

Figure 4. Stage I bonefish (*Albula* spp.) leptocephali caught at Maunalua Bay Beach Park.

A variety of bycatch species were also captured in the light traps, but they were not counted consistently or identified to species level. Crab megalops (larvae) were caught during each sampling session, but the magnitude differed greatly among sampling. The following are some of the bycatches by frequency: crab megalops, arrow worms (chaetognatha), mantis shrimp (stomatopod) larvae, pistol shrimp (Alpheidae) larvae, balloon fish (Tetradontidae) larvae, one Hawaiian bobtail squid (*Euprymna scolopes*), one juvenile jack (*Scomberoides lysan*), and one box jellyfish.

Otolith processing and analysis

Total DGI counts were successfully obtained for 26 leptocephali with an age range of 28-73 presumed days post-hatch (m=48.8 DGI ± 11.72 SD) (Figure 5). One leptocephalus was removed from the analysis because it had a DGI deviation >10% between the first and second count. Back-calculated hatch dates were distributed between December and April with a peak during March (n = 10).

DNA barcoding

Of the 28 Oʻahu leptocephali samples sent to FWRI, all were identified as *A. glossodonta* except for one Oʻahu sample that was identified as *A. virgata*. *A. glossodonta* larvae were caught at each of the three main sampling locations. The one *A. virgata* larvae was captured at Maunalua Bay Beach Park and no other larvae were captured during that sampling session.

Discussion

The presence of bonefish leptocephali around Oʻahu reveals important nearshore habitat preferred by bonefish leptocephalus larvae. Bonefish leptocephalus larvae are known to move onshore prior to undergoing metamorphosis (Friedlander *et al*., 2007; Snodgrass *et al*., 2008). Freshwater input is likely an attractive environmental component as all three locations have freshwater input through direct stream discharge or underground springs. These larvae are capable swimmers and likely choosing these areas as opposed to being passively carried there. This information is critical when considering future bonefish conservation measures that intersect with coastal development planning, runoff mitigation, and invasive species management. A stronger, healthier larval supply may help foster recruitment and ultimately more adult bonefish in Hawaiʻi waters (Milicich *et al*., 1992; Meekan *et al*., 1993).

The basic light trap design used during this research was able to successfully capture leptocephali, despite other studies showing success with channel nets. The extremely variable capture success of bonefish leptocephali is consistent with studies in less populated areas of the

Bahamas and Palmyra, where channel nets were used (Mojica *et al*., 1995; Friedlander *et al*., 2007). Anderson *et al*., (2002) showed that light traps can be effective in low current sites and the Maunalua Bay Beach Park sampling location, where most of the leptocephali were caught, was typically a slow current area. Paiko Lagoon and Heʻeia Fish Pond have calm interior waters, however, physical bottlenecks at the entrances cause swift waters during flood tides. The relatively few larvae collected at Heʻeia fishpond and Paiko Lagoon is likely due to sub-optimal light trap effectiveness during high flow conditions. Therefore, when light traps were placed at these bottlenecks, the ability to attract and capture leptocephali is likely less optimal compared to the Maunalua Bay Beach Park sampling site. However, these areas are still known to be productive estuarine environments for bonefishes (pers. comm. Kim Peyton) and the low larvae count does not represent a lower priority for bonefish management.

The leptocephali length and age ranges were similar to those captured in other regions, suggesting that *A. glossodonta* in Hawaiʻi migrate inshore at the same developmental stage (Pfeiler, 1984; Friedlander *et al*., 2007; Snodgrass *et al*., 2008; Vasquez-Yeomans *et al*., 2009). Exact PLD is technically not known since these have not yet settled and it is not clear whether they are still growing or beginning to decrease in length before metamorphosis. However, we can assume that their time offshore is equal to or less than their DGI-based age.

Donovan *et al*., (2015) found *A. glossodonta* spawning peaks in December and April on Oʻahu, Hawaiʻi, which coincides with the spawning months found in this study based on back calculated hatch dates. The sampling in this study was not year-round, therefore, there may have been other peaks throughout the year not revealed through this sampling effort. Regardless, these back calculations provide a reliable method to ground truth and compliment previous work (Donovan *et al*., 2015).

These nearshore habitats are vulnerable to a variety of anthropogenic impacts and have many competing uses. Areas in Maunalua Bay have undergone tremendous changes. In particular, restoring freshwater input, such as the effort to restore Lucas Spring, might generate conditions for bonefish recruitment (pers. comm. Kim Peyton; NOAA ONMS 2010). The efforts by PaePae o Heʻeia in Heʻeia Stream may not only enhance the overall habitat of the area, but similarly make it more attractive for leptocephali recruitment. Maintaining healthy recruitment habitat will help ensure anglers will continue to have the opportunity to target these popular species and cultural traditions that use bonefish can be perpetuated.

Chapter 3: Genetic Connectivity of Roundjaw bonefish *Albula glossodonta* (Elopomorpha, Albulidae) in the central North-South Pacific Ocean Resolved Through ddRAD-based Population Genomics

Abstract

Bonefishes are a nearshore species targeted by non-commercial anglers and subsistence fishers in Central and South Pacific islands. Of the bonefish species in the Indo-Pacific region, *Albula glossodonta* is known to have one of the widest geographic ranges, from the Red Sea to the Central Pacific and it is unknown how dispersive *A. glossodonta* are between geographically isolated islands. Volunteer anglers collected *A. glossodonta* fin clips from the main Hawaiian Islands in the North Pacific, Anaa Atoll in the South Pacific, and intermediate Kiritimati Island (Line Islands) to assess the inter-island population structure within the Pacific Ocean. Population genomics was conducted based on 208 individuals and 7225 SNPs. Although adult *A. glossodonta* exhibit strong site fidelity, genomic results show no difference between Oahu and Maui in Hawaiʻi. Bonefishes exhibit significant population structure between Anaa and Hawaii (F_{ST}=0.096), with intermediate Kiritimati comprising admixed fishes. A lengthy larval duration and long-distance spawning movements likely promote connectivity between Pacific islands. Regional management regimes may be most appropriate for a species with this level of gene flow.

Introduction

Bonefishes have highly conserved ecology and morphology, which can present challenges for distinguishing species in the field. This is reflected in a volatile taxonomy that has undergone many revisions and greater clarification is still needed. There were originally thought to be 23 species of bonefishes, but these were synonymized into two species by Hildebrand (1963). More recent research indicates that there are at least 12 bonefish lineages that may correspond to distinct species (Bowen *et al*., 2008; Hidaka *et al*., 2008; Wallace & Tringali, 2010). Eight species are known to occur in the Indo-Pacific region, and four in the Atlantic-Caribbean region (Wallace, 2015; Wallace & Tringali, 2016). Much of the research effort has been in the Atlantic-Caribbean region because of the substantial contribution bonefish fisheries make to local economies (Adams & Cooke, 2015; Wallace & Tringali, 2016). However, bonefish research in the Pacific has increased over the past decade (e.g., Donovan *et al*., 2015; Kamikawa *et al*., 2015; Filous *et al*., 2019a; 2019b).

Shaklee & Tamaru (1981) discovered a genetic distinction of two bonefishes in Hawaiʻi, which resulted in recognition of the round jaw bonefish (*Albula glossodonta*) and the sharp jaw bonefish (*A. virgata*). *Albula virgata* is endemic to Hawaiʻi, and *A. glossodonta* occurs from the Red Sea to the Central Pacific Ocean (Pickett *et al*., 2020). Very slight morphological differences are coupled with pronounced divergence in life history characteristics, leading to niche separation. *A. glossodonta* have rounded lower jaws, exhibit a specialized diet, prefer shallow flats habitat, and have a spawning peak from March to June and November to December (Donovan *et al*., 2015). *A. virgata* have a pointed lower jaw, exhibit a more generalized diet, prefer deep water habitats, and have one spawning peak from November to April (Donovan *et al*., 2015).

In the main Hawaiian Islands, *A. glossodonta* are targeted by a minor commercial fishery plus a very diverse non-commercial fishery with a multitude of gear types and differing motivations (Kamikawa *et al*., 2015). These fishes are also heavily targeted in other locales in the Pacific such as Kiritimati Island (Line Islands, Republic of Kiribati) and Anaa Atoll, (Tuamotu Archipelago, French Polynesia). However, those *A. glossodonta* fisheries are mostly catch-and-release in Kiritimati and for subsistence in Anaa (Allen, 2014; Filous *et al*., 2019b). The International Union for Conservation of Nature (IUCN) assessed *A. glossodonta* as vulnerable with a decreasing population trend and *A. virgata* as data deficient (Adams *et al*., 2012a; 2012b). Both species require updates, as these assessments were conducted in 2011.

The presence in Hawaiʻi of the range-restricted *A. virgata* and a widespread Indo-Pacific species invokes questions about dispersal and population structure; geographically widespread species accomplish gene flow through mechanisms such as adult fish movement or a highly dispersive larval stage (e.g., Gaither *et al*., 2011; Graves & McDowell, 2015; Wallace, 2015). There is no available data on the pelagic larval duration of *A. virgata,* but *A. glossodonta* pelagic larval duration is 57 days on average (Friedlander *et al*., 2008). The presence of an endemic bonefish species, and the genetic isolation of widespread Indo-Pacific fishes in Hawaiʻi (e.g., Gaither *et al*., 2011) may indicate that the *A. glossodonta* in Hawaiʻi are genetically distinct from cohorts at other Indo-Pacific locations. Adult *A. glossodonta* in Hawaiʻi show site fidelity at a fine scale and anecdotes from anglers suggest there may be distinct populations due to this key life history trait (Kamikawa *et al*., 2015). Comparing the genetic makeup of *A. glossodonta* from regions around the Indo-Pacific would reveal patterns of connectivity and aid in developing management decisions. In this regard, microsatellite data in Wallace (2015) show wide-spread genetic connectivity of *A. glossodonta* across its vast range, potentially indicating that populations in Hawaiʻi are seeded from other locations. If that is the case, the Line Islands (including Kiritimati) and Johnston Atoll (865 km south of Hawaiʻi) are postulated to be biodiversity gateways into Hawaiʻi (Hourigan & Reece, 1987; Craig *et al*., 2010; Hodge *et al*., 2014).

Reduced costs and increased capacity of DNA sequencing make genomes accessible and an excellent tool to understand distribution patterns and resolving evolutionary relationships (Peterson *et al*., 2012). Previous genetic methods have proven particularly useful for bonefish, as species often have very similar morphology and overlapping habitats, coupled with deep divergence in allozyme and mtDNA surveys (Bowen *et al*., 2008). Double Digest Restriction Associated DNA (ddRAD) sequencing has the throughput and precision to reveal differences that may exist within a species distributed across far-flung oceanic islands (e.g., Gaither *et al*., 2015).

Understanding the potential connectivity, or lack thereof, between populations of bonefishes has implications for the management of the species and their habitat. Hawaiʻi is comprised of eight inhabited islands, and place-based management throughout the archipelago has become a popular conservation tool. One example of this management challenge is Tarpon (*Megalops atlanticus*) in the Caribbean, Gulf of Mexico, and south-eastern United States. Tarpon regulations and available habitat vary among jurisdictions, and fishers in these regions target tarpon for a combination of recreation, subsistence, cultural, and commercial reasons (Adams *et al*., 2013; Wilson *et al*., 2019). In this complex network of habitats and fisheries, unregulated harvest in one location may nullify conservation-based fisheries or habitat management in another region. Determining geographic barriers to gene flow may indicate that management regimes would be effective at finer scales. This type of information would be important in establishing place-based management such as minimum sizes or seasonal catch restrictions.

The overall goal of this paper is to identify genetic population structure of *A. glossodonta* around Hawaiʻi at an island, archipelago, and Pacific-basin scale. Here we evaluate gene flow and genetic structure along a roughly linear path from French Polynesia in the South Pacific

Ocean through Kiribati in the Central Pacific to Hawaiʻi in the North. This type of work also presents an opportunity to engage members of the fishing community and create a collaborative effort toward understanding bonefish life history characteristics. Combining the traditional knowledge of anglers with modern science processes leads to successful research outcomes (Yochum *et al*., 2011; Schemmel *et al*., 2016; Filous *et al*., 2019a, 2019b).

Methods

2.1 Field collection methods

Hawaiʻi is located in the central North Pacific Ocean with Kiritimati located 2,000 km south and Anaa another 2,500 km further south (Figure 5). All sampling locations have shallow flats or accessible beaches, allowing bonefish to be targeted with conventional spinning or fly-fishing gear. All regions are known to have *A. glossodonta*, but anecdote suggests they exhibit slightly different morphology and behavior. There was an opportunity to collaborate with anglers from all locations and the fishing community was engaged to assist with collecting fin clips. The authors and volunteer anglers collected a cm^2 fin clip from the tip of bonefish caudal fin. Anglers on Oʻahu were equipped with 2mL vials with 90% ethanol, a small scissors, and basic instructions regarding best bonefish handling practices. Anglers on Maui, Kiritimati, and Anaa were provided vials containing saturated salt (NaCl) DMSO solution, which is more amenable than ethanol for air transport.

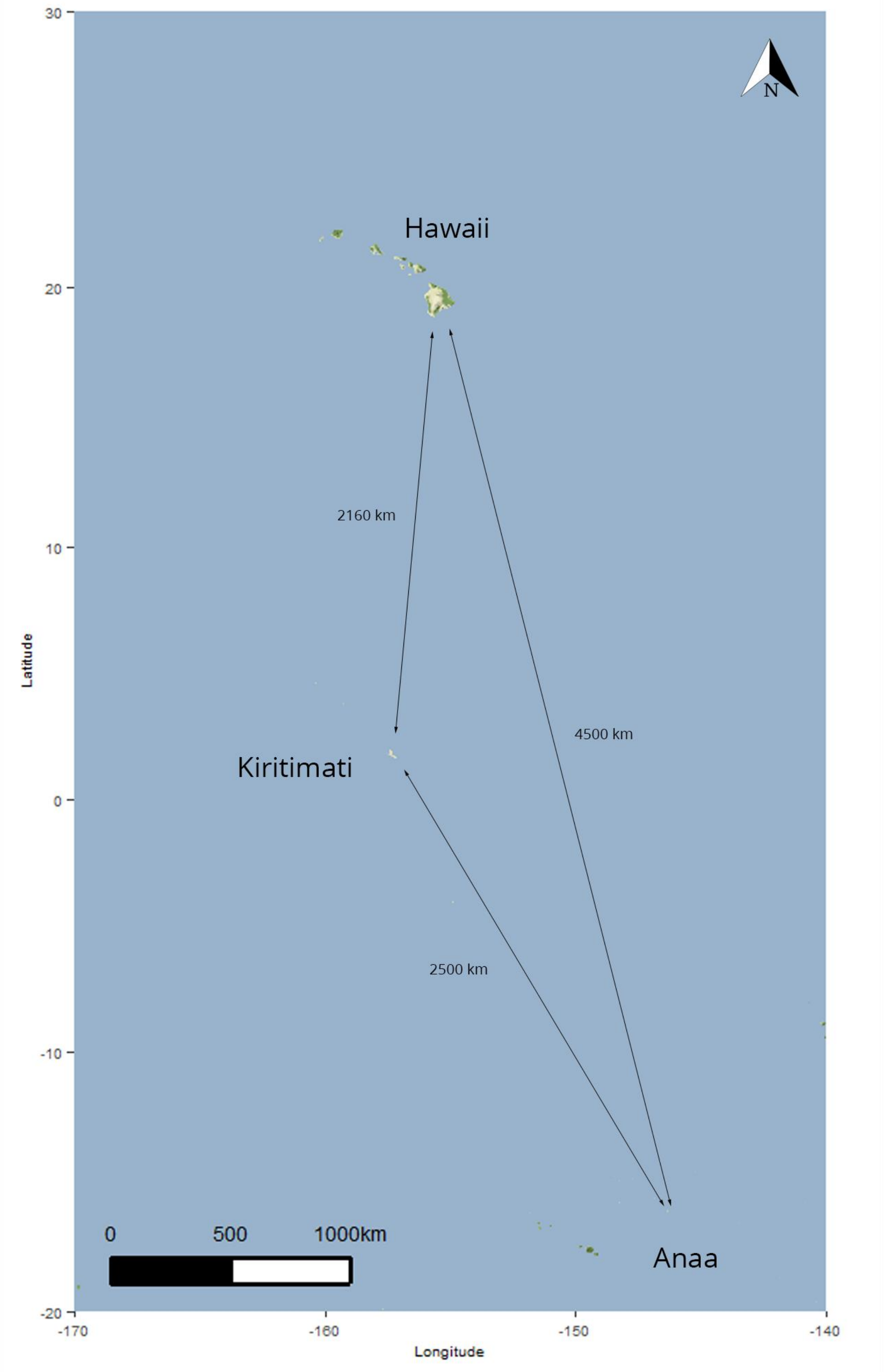


Figure 5. Map of three *Albula glossodonta* sampling regions in the Central Pacific.

2.2 Laboratory methods

Genomic DNA was purified from fin clips using the Puregene® tissue kit and a standardized protocol. Due to the presence of other *Albula* species in the study region, specimens were first screened using a four-locus microsatellite panel (Avu11, Avu12, Avu18, & Avu25) for genetic species identification (GSI) as previously characterized in Seyoum *et al*., (2008) and Wallace & Tringali (2010). The microsatellite fragments were PCR amplified in 12.5μl reactions consisting of: 0.5μl DNA, 0.07μl GoTaq® polymerase, 0.01-0.04μl combined forward and reverse 100uM primers, 0.3 μM each dNTPs, 2.32 mM MgCl2, 2.33μl 5X GoTaq® buffer, 0.06μl BSA, and 7.42μl sterile distilled water. Amplification was conducted on an Eppendorf mastercycler under the following thermal cycling conditions: 1X 94°C for 2min., 32X 94°C for 40s, 55°C for 40s, 72°C for 45s, followed by a final extension of 72°C for 7min. The PCR products were screened on an Applied Biosystems 3130XL genetic analyzer and scored with Genemapper®. The allelic data was compared to the previously GSI verified genotypes of all Pacific Ocean *Albula* species in Genetix v4.05 (Belkhir *et al*., 2000).

For genomic library preparation, the purified DNA was fluorometrically quantified using the broad range Qubit kit (Thermo Fisher Scientific) to ensure sufficient quality and quantity. The double digest restriction-site associated (ddRAD) libraries were prepared following a modified Peterson *et al*., (2012) protocol. Specimens were first digested at 37°C for 3 hours using the MspI and PstI restriction enzymes, bead cleaned following the Faircloth & Glenn (2011) protocol and quantified via Qubit with the high sensitivity kit. The cleaned digest products were ligated with adapters containing a set of eight unique 5bp barcodes under the following thermal conditions: 23°C for 30 min., 65°C for 10 min., then cooled at 2°C per 90 sec until reaching 23°C. Equal volumes of ligation products were pooled into sets of eight, bead cleaned, and libraries were size selected (200-300 bp) on a Pippin Prep. The Pippin size selected libraries were PCR amplified (98°C for 30s, 12X 98°C for 10s, 87.7°C for 30s, 72°C for 30s, and a final extension of 72°C for 10 min., then a 4°C hold) using the Phusion® kit (New England Biolabs) and a set of 12 unique indices. The PCR products were pooled by index and bead cleaned prior to final library quantitation via qPCR using the NEBnext® library quant kit. The final pooled libraries were sequenced on three 1x100 lanes on an Illumina HiSeq 2500 at the Brigham Young University genomics core facility.

2.3 Data Analysis

The ddRAD generated libraries were demultiplexed, quality filtered, and SNP genotyped using the Stacks v2.55 denovo pipeline and vcftools on the BYU Fulton HPC (Catchen *et al*., 2013; Danecek *et al*., 2011). Raw Illumina reads were demultiplexed with *process_radtags* then individual loci assembled with *ustacks*. A subset of specimens was used to build the SNP catalog in *cstacks*, then all specimens were matched to the catalog in *sstacks*. Data was converted to per-locus using *tsv2bam* and SNPs were re-called using all individuals with *gstacks*. A vcf file was obtained using *populations* with a minimum of 30% individuals per population set for each locus (populations were set to collection island). Quality filtering was completed in vcftools under the following criteria: removed 5 low scoring individuals, then genotype filtering with max-missing level of 0.8. HDPlot in the R package vcfR was used to further filter loci displaying non-conformance to Hardy-Weinberg equilibrium (HWE) while maintaining the site frequency spectrum (McKinney *et al*., 2017). The HDPlot outlier loci were pruned and the dataset further filtered (mac 3) in vcftools. Finally, a custom python script retained the single highest minor allele frequency SNP per locus to avoid linkage issues.

The R packages poppr was used to assess standard diversity indices and identify private alleles in the SNP dataset (Kamvar *et al*., 2014; Winter *et al*., 2017). Several analytical approaches were used to explore genetic population clustering. Pairwise metrics F_{ST} and G_{ST} (Hedrick, 2011) were calculated among the four collection islands, as *a priori* populations, in the R package diveRsity (Keenan *et al*., 2013). These metrics range from zero (no genetic differentiation) to 1 (complete differentiation). A multivariate discriminant analysis of principal components (DAPC) with cross validation was performed in the R package adegenet v2.1.0 (Jombart & Ahmed, 2011). Spatial partitioning was then evaluated via the Bayesian method in fastStructure using the simple model and visualized with Distruct v1.1 (Raj *et al*., 2014; Rosenberg, 2004). Lastly, genetic clustering was assessed through the maximum likelihood model implemented in Admixture v1.3 using the cross-validation procedure (--cv=10) (Alexander *et al*., 2009).

Results

3.1 GSI assays

Anglers collected over 300 fin clips from O‘ahu (n = 119), Maui (n = 30), Anaa (n = 58), and Kiritimati (n = 37) from 2016-2020 (Table 1). Leptocephalus larvae (N= 59) were collected from

Oʻahu from 2017-2020. A subset of 254 tissue samples were sent to the Fish and Wildlife Research Institute (FWRI) for processing and analysis. The GSI assays identified 14 *A. virgata* collected from Maui and Oʻahu. These were included in the Illumina sequencing lanes but were removed prior to quality filtering of the *A. glossodonta* SNP dataset for downstream population analyses. For the subadult/adult *A. glossodonta* specimens, fork length ranged from 8.5 – 31 inches (n = 146) and weight from 4.1 – 11.7 pounds (n = 8). Therefore, these fishes include multiple generations based on length and weight.

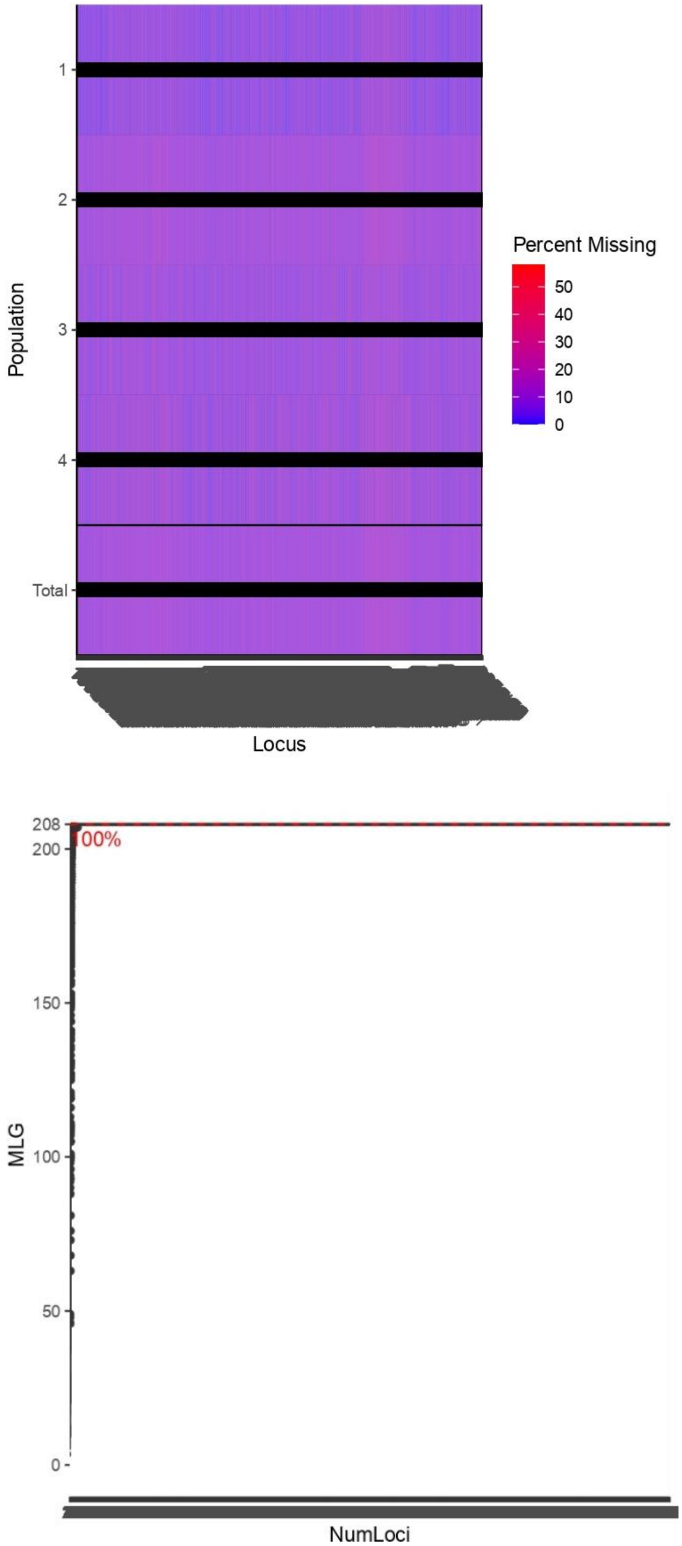
Table 1. Number of *Albula* specimens collected and processed from each location.

Location	**Samples collected**	**Samples processed**
Oʻahu (adults)	150	108
Oʻahu (leptocephalus)	28	23
Maui	30	30
Kiritimati	37	36
Anaa	58	57
Total	303	254*

* There were 14 *A. virgata* identified and these were removed from the analysis. Of the 240 GSI verified *Albula glossodonta*, 208 were retained for analyses after data quality filtering.

3.2 Genomic Libraries

The three Illumina sequencing lanes which included 254 total *Albula* specimens (240 *A.* glossodonta and 14 *A. virgata*) yielded 358,805,000 raw reads. After quality filtering, the final *A. glossodonta* SNP dataset consisted of 208 individuals and 7225 SNPs. The average depth of coverage was 20.2X across individuals (5.6-162.5X) and 20.7X across loci (9.5-236.3X). Overall data missing across loci and collection islands was low and the genotype accumulation curve reveals saturation was rapidly achieved (Figure 6). Genotypic richness (measured as MLG) was higher than expected for all locations (Table 2). Nei’s unbiased gene diversity (Hexp) was relatively low and similar across locations (0.23-0.24), and evenness (E)= 1. The three diversity indices evaluated, Shannon-Weiner (H), Stoddart & Taylor (G), and Simpson’s (λ), were similar across islands though highest for Oʻahu (which had the highest sample size).



Figures 6. The level of data missingness across *Albula glossodonta* individuals and collection locations (top), and a genotype accumulation curve of the 7,225 SNP dataset (bottom). Abbreviation: NumLoci = number of loci.

Table 2. Genetic diversity estimates for the 7225 SNP *Albula glossodonta* dataset collected from four islands in the Central-South Pacific Ocean. Indices were calculated in the R package poppr. Abbreviations: N = sample size, MLG = multilocus genotypes, eMLG = rarefaction corrected MLG, SE = standard error based on eMLG, H = Shannon-Weiner index, G = Stoddart & Taylor's index, λ = Simpson's index, E = allelic evenness, Hexp = Nei's unbiased gene diversity.

Location	**N**	**MLG**	**eMLG**	**SE**	**H**	**G**	**λ**	**E**	**Hexp**
Anaa	31	31	20	0.00	3.43	31	0.97	1	0.23
O'ahu	122	122	20	0.00	4.80	122	0.99	1	0.24
Kiritimati	35	35	20	0.00	3.56	35	0.97	1	0.24
Maui	20	20	20	0.00	3.00	20	0.95	1	0.24

The majority of private alleles occurred in individuals from Maui (N=682) and O'ahu (N=593), fewer were identified from Anaa and Kiritimati (N=287 & 234 respectively).
The *ad hoc* pairwise comparisons, G_{ST} and F_{ST}, reflected similar patterns among collection locations (Table 3). Differentiation was moderate between Anaa and both Hawaiian Islands, but moderate-low for pairs including Kiritimati and slight between O'ahu and Maui. The DAPC analysis retained 3 discriminant functions and 60 principal components after cross validation, which yielded 0.475 proportion of conserved variance. Strong assignment proportions to each collection island were observed (0.85-0.975), yet the DAPC plot displayed three clusters with O'ahu and Maui individuals overlapping (Figure 7). Two outlier individuals halfway between the Kiritimati and Hawai'i groups indicate occasional genetic connectivity. The individual assignment plots identified other admixed specimens (1 Anaa: O'ahu, 2 Kiritimati: O'ahu, and 5 O'ahu: Maui). Two of the admixed specimens were leptocephalus, both collected on O'ahu, with one assigned to Maui and the other to Kiritimati. Two genetic populations were identified under the simple model in fastStructure. One group consisted of individuals from Anaa while the second group contained Hawai'i specimens (O'ahu and Maui). The Kiritimati individuals all reflected admixture- displaying posterior mean of admixture proportions ~60-75% Anaa group and ~25-35% Hawai'i group membership. Two other individuals reflected ~50:50 admixture between the Anaa and Hawai'i populations. Similarly, the Admixture maximum-likelihood model results also supported two populations: Anaa and Hawai'i, displaying moderate genetic differentiation between them (F_{ST}=0.096) (Figure 9). The Kiritimati individuals were identified as admixed, with very similar proportions to those assigned by fastStructure. Further, the same

two individuals (one from Anaa and the other from O‘ahu) reflected ~50:50 admixture between the two genetic populations.

Table 3. Pairwise genetic differentiation of *Albula glossodonta* among four Pacific Ocean islands, measured as G_{ST} (Hedrick, 2011) (lower triangle) and F_{ST} (upper triangle).

	Anaa	**O‘ahu**	**Kiritimati**	**Maui**
Anaa	~	0.0998	0.0416	0.1066
O‘ahu	0.0847	~	0.0509	0.005
Kiritimati	0.0325	0.0415	~	0.0537
Maui	0.0872	0.0016	0.043	~

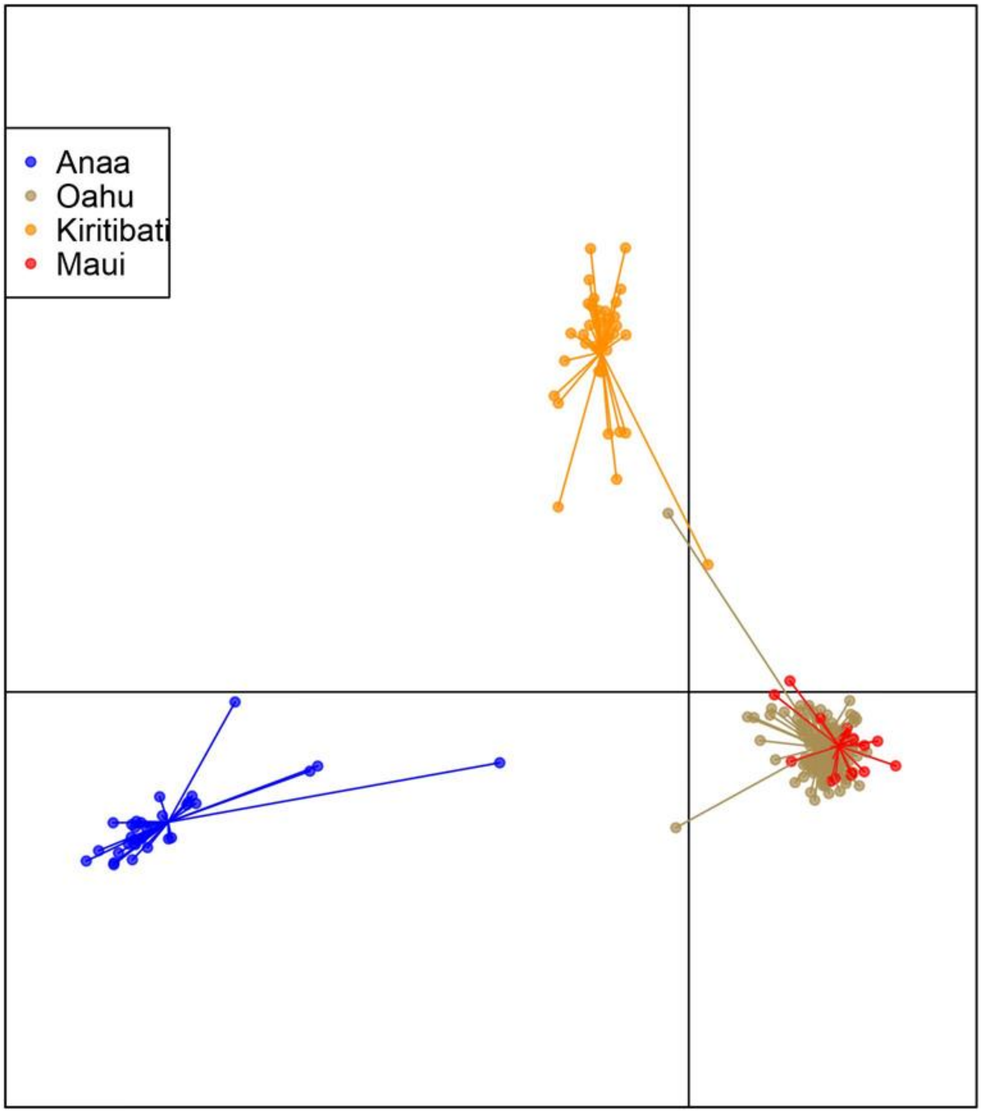


Figure 7. *Albula glossodonta* DAPC spatial clustering among four islands in the Central-South Pacific Ocean

Discussion

This project showcased a successful, collaborative effort between researchers and the fishing community. Anglers from the Hawaiian Islands, Kiritimati, and Anaa assisted in data collection to answer a question that both stakeholders were interested in understanding. Involving anglers in a project's progress aids in understanding and building trust for the science behind the fisheries management processes.

The population structure results were largely concordant across analyses, displaying strong support for two distinct genetic stocks - Anaa and Hawaiʻi, with Kiritimati containing admixed individuals. Notably a previous mtDNA comparison of *A. glossodonta* between Hawaiʻi and Kiritimati indicated significant population structure ($\phi_{ST} = 0.215$; Friedlander *et al*., 2008). Overall, these data indicate a low level of ongoing gene flow most frequently between Anaa and Kiritimati, and less frequently between Kiritimati and Hawaiʻi. Individual population assignments were identical in the fastStructure and Admixture analyses. It is important to acknowledge that of the genetic population structure methods used to evaluate *A. glossodonta*, fastStructure and Admixture are based on genetic models while the DAPC analysis is not model based. Even so, the differences in geographic clustering among them were slight, dealing exclusively with Kiritimati, the middle location among the islands sampled for this study spanning >4500km.

Leptocephalus larvae dispersal is likely aided by prevailing currents in the western and southern Pacific. The main Hawaiian Islands are subject to the North Hawaiian Ridge Current, moving from southeast to northwest above the archipelago, and the Hawaiian Lee Countercurrent moving from west to east below the archipelago (Toonen *et al*., 2011). These currents likely provide dispersal between Maui and Oʻahu. Larger-scale currents such as the North Equatorial Current, Equatorial Countercurrent, and South Equatorial Current, and the gyres they produce, can provide the connectivity observed between Hawaiʻi, Kiritimati, and Anaa.

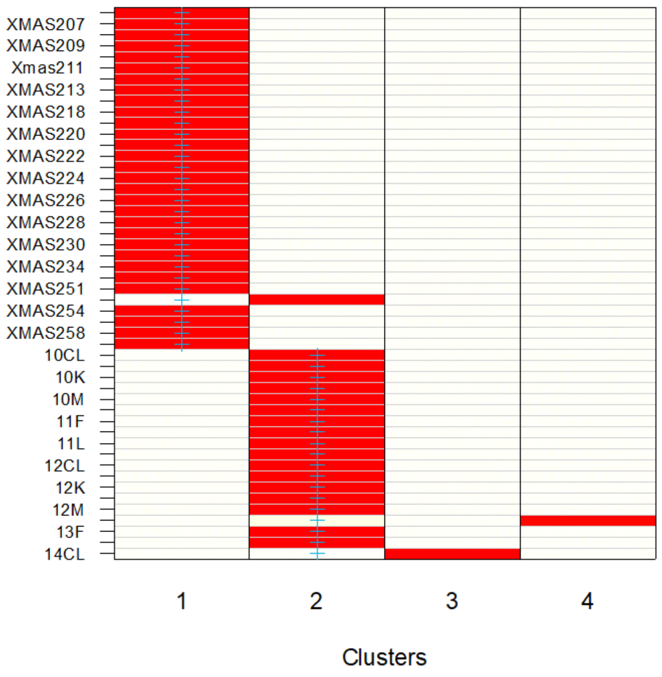
Genetic breaks have been found throughout the Hawaiian archipelago for some fish species (Rivera *et al*., 2011; Toonen *et al*., 2011; Tenggardjaja *et al*., 2016, Coleman & Bowen, 2022). However, bonefish larval life history is unique and *A. glossodonta* have the greatest range of all bonefishes, covering a vast expanse of the Indo-Pacific, including the Red Sea (Williams *et al*., 2020). The Sunda Shelf, a well-known marine biogeographic barrier, surprisingly does not affect population connectivity in this shallow flat inhabiting species (Husson *et al*., 2019). Gene flow across the broad range of *A. glossodonta* is likely maintained through a functional metapopulation, with higher connectivity for nearby neighbors through larval dispersal and/or adult spawning migrations. Bonefishes are known to travel offshore, away from inshore flats, and make deep dives during spawning activity (Danylchuk *et al*., 2011; Wills *et al*., 2022).

This study represents the first application of an intensive population genomic approach to evaluate inter-island scale bonefish population structure within the Pacific Ocean. Bonefishes have an extended pelagic stage and are potentially capable of long-distance oceanic dispersal. A recent ddRAD study of *A. glossodonta* in the southwest Indian Ocean identified weak genetic structure between the Seychelles and Mauritius, a distance of about 1,100 km (Talma, 2021). Another fine-scale population genomic study on *A. vulpes* in the Bahamas found an asymmetric pattern of inter-island geneflow (Douglas *et al*., 2021). Future studies should include gathering *A. glossodonta* from throughout the Hawaiian archipelago, especially from Hawaiʻi Island and the Northwestern Hawaiian Islands. A deep water grouper and snapper in Hawaiʻi have shown genetic structure at the scale of the Hawaiian archipelago range (Rivera *et al*., 2004; Rivera *et al*., 2011; Gaither *et al*., 2011).

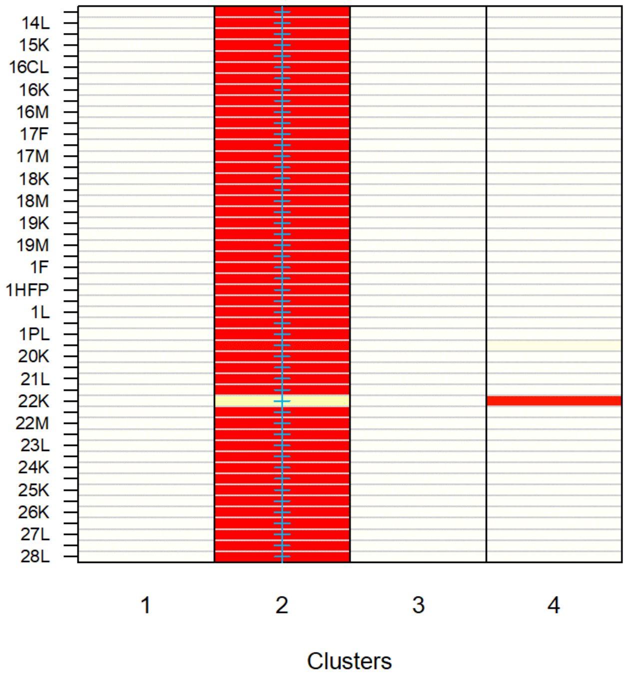
Given the volcanic origin of the Hawaiian Archipelago in the middle of the North Pacific, researchers have long speculated on the origins of the coastal marine fauna, with a focus on colonization from the south (Maragos & Jokiel, 1986; Kosaki *et al*., 1991; Randall, 1998). More recent phylogeographic studies have indicated the intriguing possibility that the flow of biodiversity is bidirectional, with some larvae colonizing from Hawaiʻi to Johnson Atoll and the Line Islands (DiBattista *et al*., 2011; Skillings *et al*., 2011). The present study clearly supports the latter scenario with DAPC analyses (Figure 8), as Kiritimati in the Line Islands seems to receive input from both the Hawaiian Archipelago and Polynesia (Anaa).

The observed long-distance connectivity indicates a regional management approach is needed for *A. glossodonta* and may aid restoration measures in areas that have experienced population declines. Islands with adequate protection of juvenile habitat and proactive management of the fishery (including protection of spawning migrations) may replenish local stocks through immigration via larval dispersal. The results from this study clarify local anecdote that although the adult bonefish in Hawaiʻi exhibit strong site fidelity, their larval stage and spawning habits lead to gene flow among regions.

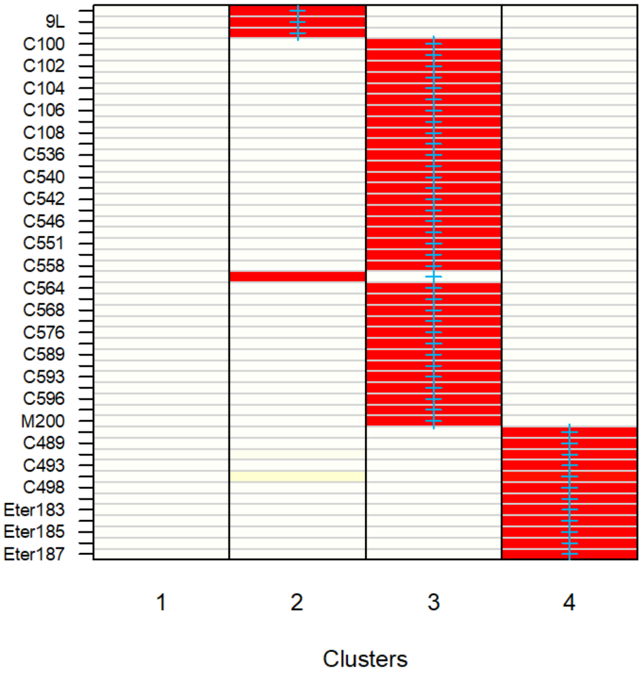
A)


XMAS207
XMAS209
Xmas211
XMAS213
XMAS218
XMAS220
XMAS222
XMAS224
XMAS226
XMAS228
XMAS230
XMAS234
XMAS251
XMAS254
XMAS258
10CL
10K
10M
11F
11L
12CL
12K
12M
13F
14CL
1
2
3
4
Clusters

B)


14L
15K
16CL
16K
16M
17F
17M
18K
18M
19K
19M
1F
1HFP
1L
1PL
20K
21L
22K
22M
23L
24K
25K
26K
27L
28L
1
2
3
4
Clusters

C)



D)

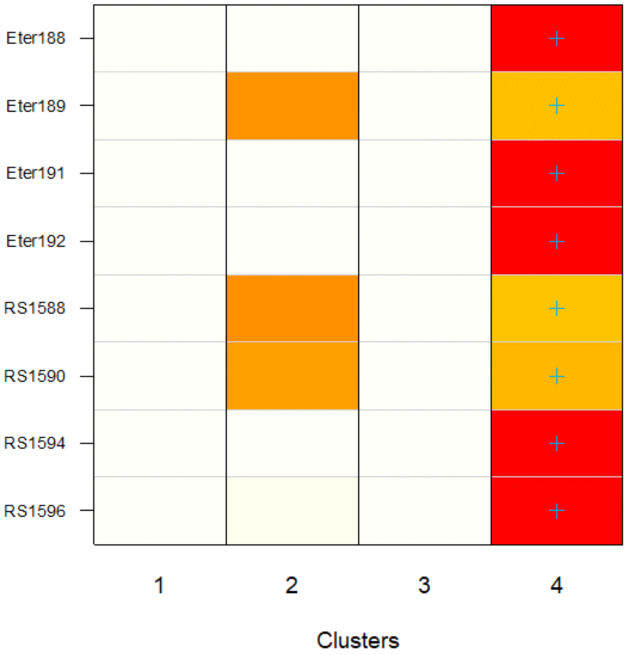


Figure 8. Group assignments for specimens 1-50 from *Albula glossodonta* (A) from the DAPC analysis. B) specimens 51-100, C) specimens 151-200, and D) specimens 201-208. Blue crosses indicate collection location, while heatmap colors represent post-analysis group (hotter colors = stronger assignment). 1 = Anaa, 2 = O‘ahu, 3 = Kiritimati, 4 = Maui.

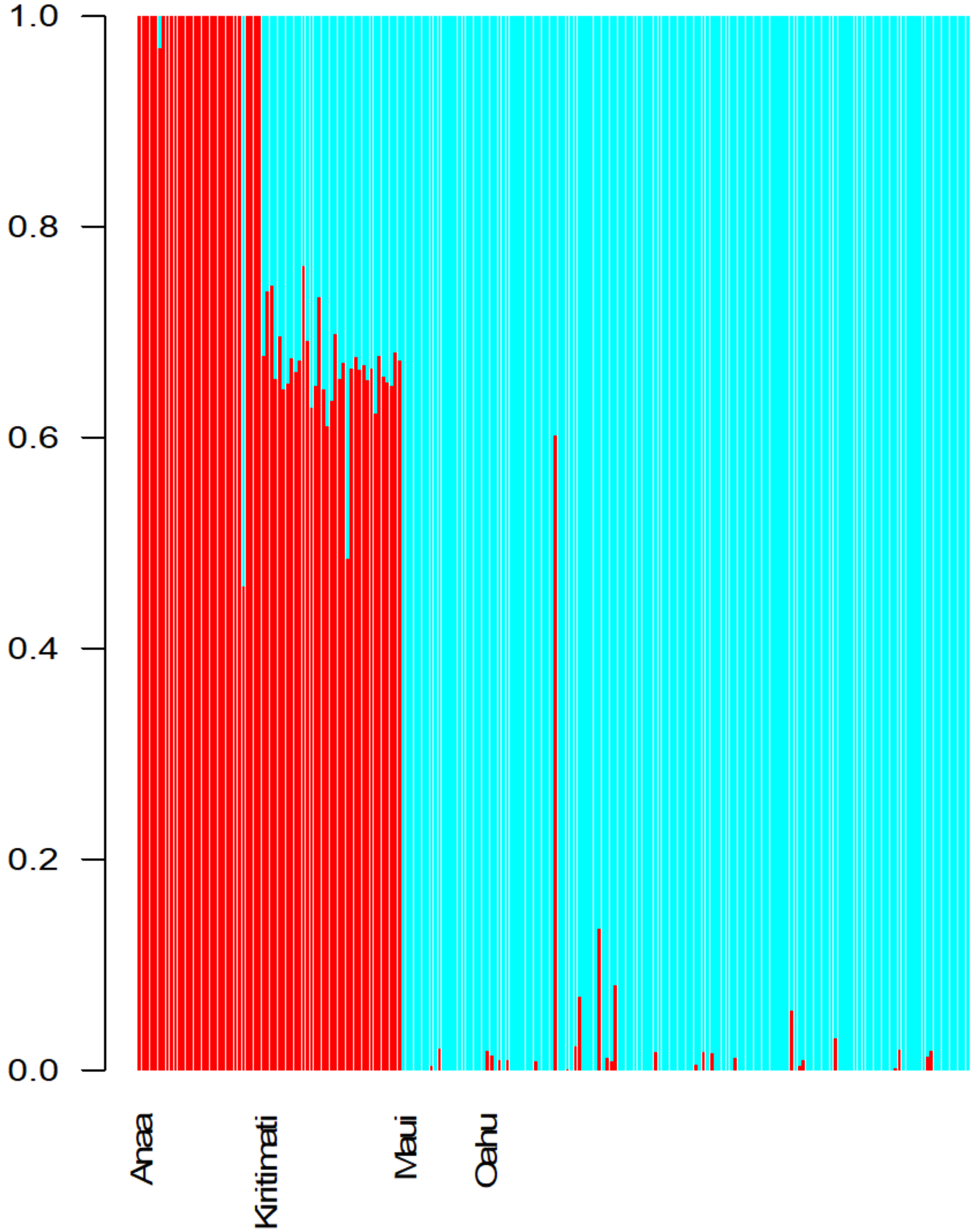


Figure 9. Maximum likelihood genetic clustering of *Albula glossodonta* from four Pacific Ocean islands assessed in Admixture based on 7,225 SNPs.

Chapter 4: Angler motivations and preferences when targeting bonefishes in Hawaiʻi

Abstract

Bonefishes in Hawaiʻi are highly valued for their subsistence value and are targeted by both non-commercial and commercial fisheries. Non-commercial fisheries data in Hawaiʻi is often sparse and disparate compared to commercial datasets and non-commercial data around the nation. The shortage of this data makes fisheries management challenging and reinforces the disconnect between stakeholders and natural resource managers. We surveyed 277 local fishers to characterize the non-commercial fishery and highlight the preferences and motivations of anglers who catch bonefish. A majority of respondents who choose to keep bonefish for food prefer to keep fish that are at least four to five pounds, often due to the unique preparation required before consumption. This size class is larger than the L_{50} for bonefish in Hawaiʻi and 86% of anglers prefer fish larger than the L_{50}. Bonefish are also sought after for their sport value, creating competing demands. However, 92% of anglers indicated they will release at some of their catch. Including the fishing community in the fisheries management process can help account for values and preferences. Information on fish disposition and angler preferences are critical in updating management tools, such as minimum sizes.

Introduction

Hawaiʻi hosts two bonefish species, the Indo-Pacific round jaw (*Albula glossodonta*) and the endemic sharp jaw (*Albula virgata*) (Shaklee & Tamaru, 1981; Randall & Bauchot, 1999; Hidaka *et al.,* 2008). These fishes, known as ʻōʻio in Hawaiʻi, are among the species targeted during year-around shoreline fishing tournaments hosted by local fishing clubs. A growing fly-fishing charter industry also targets them through guided fishing excursions. In Hawaiʻi, unlike many other places, the importance of these bonefishes extends beyond their value to sportfishing. Bonefishes were culturally significant and an important food for early Hawaiians (Titcomb, 1972; Allen, 2014), and they are still valued today as table fare, usually prepared raw as “lomi ʻōʻio” or in a cooked fishcake.

The largest and most diverse fishery that targets bonefish falls under the umbrella of non-commercial fishing. Non-commercial fishing effort and landings for nearshore species often has been many magnitudes higher than the commercial fishery in Hawaiʻi (McCoy *et al*., 2018).

Non-commercial comprises fishing activities that do not generate money from fish caught, and encompass motivations such as fishing for food, recreation, or social/cultural purposes (Titcomb, 1972; Kamikawa *et al.*, 2015). The bonefish non-commercial fishery in Hawaiʻi continues to expand, whereas commercial landings have decreased by 99% in the past century (Friedlander *et al.*, 2007; 2015). There is also a growing fly-fishing charter sector that is distinct from the commercial and non-commercial sectors. These fisheries are relatively unrestricted except for a minimum size of 14-inch (31.4 cm) fork length (DAR, 2012) (Figure 10).

Figure 10. A bonefish (*Albula glossodonta*) with roughly a 20-inch fork length. The minimum size for taking a bonefish in Hawaiʻi requires the fork length to be 14 inches or greater.

Despite the economic, cultural, recreational, and commercial value of bonefishes in Hawaiʻi, we do not have a holistic picture of bonefish life history and fisheries. To address this gap, a bonefish tagging project was established in Hawaiʻi in 2003, connecting scientists, managers, and anglers. The tagging program succeeded in bolstering scientific understanding about the fish's basic biology and ecology, as well as the fishery dynamics, by tapping into the wealth of stakeholder knowledge (Donovan *et al*., 2015; Kamikawa *et al*., 2015). As a result, we have basic data on fish habitat preference, diet, growth, and spawning season. This tagging project showcased how incorporating the fishing community advances sound science with stakeholders also achieving a better understanding of the scientific and management process. Biological and ecological data are important in fisheries management, but they should not be the sole pieces when considering management tools.

Human dimensions of fisheries can be just as important as biological data in management planning. Studying the human dimensions of fisheries can reveal how fishers' behavior reflects the value they place on the fish they target (Stevenson *et al.*, 2011; Kittinger *et al.*, 2013; Grafeld *et al.*, 2017). Tapping into stakeholder knowledge can illuminate fishery dynamics and highlight the human dimension of bonefish fisheries (Fedler, 2009; Larkin *et al.*, 2010; Frezza & Clem, 2015). Fishers' behavior and fish disposition in Hawai'i can be obscured by the diffuse and non-market nature of the bonefish fishery. Fish flow (i.e., path from fisher to final consumer; see Hixon *et al*., 2022) can be different by gear type, fishing motivation, etc. In many popular bonefish destinations, such as Florida, recreational and charter fisheries have relatively simple fish flows because fisheries are predominately catch-and-release (Adams & Cooke, 2015). Moreover, saltwater anglers must be licensed, resulting in readily available data about a fishery with a $465 million-dollar economic impact (Fedler, 2013). In Hawai'i, anglers are not required to have a non-commercial fishing license and limited landings data are available from commercial fishery reports (WPRFMC, 2016; McCoy *et al*., 2018). Therefore, accessing the non-commercial fishing community is challenging, especially because participants are diverse and engage in fishing for a range of cultural, subsistence, and recreational reasons. It will require a deliberate effort to understand these stakeholders and investment in an improved understanding of angler behavior and preferences.

The overall goal of this research is to develop an understanding of the bonefish fishery in Hawai'i and describe the anglers and their fish disposition preferences. The information collected can provide an example of how management tools can be aligned with both the biological traits as well as the social preferences of the anglers that target that species. Combining bonefish size at maturity with angler fish size preferences can provide managers with an informed minimum size regulation that would enhance bonefish populations and lessen difficulties with compliance. Direct engagement with anglers can build relationships with managers while improving data quality and anglers' understanding of fisheries management processes (Ayers & Leong, 2020).

Methods

A Google Forms survey posed 14 questions related to anglers' preferences and decision-making processes when they target or catch bonefish (located in appendix A). The survey was accompanied by a consent form, following University of Hawaiʻi IRB protocols (Protocol Number 2018-01100). The survey contained questions regarding angler demographics, fishing habitats, and transitioned to questions directly related to preferences around keeping or releasing bonefishes. An open-ended comment section allowed respondents to submit additional thoughts. Sampling followed a non-random (convenience and purposive) sampling technique. The survey was distributed to non-commercial anglers via 1) email: the survey was sent directly to personal contacts who fish and to local fisheries organizations, 2) hard copy: printed surveys were distributed at a fishing club meeting for participants to complete, and 3) social media: the survey link was advertised on Facebook pages, "808 Shore Casters" and "Whipping & Dunking Hawaiʻi" and distributed by the page Administrators.

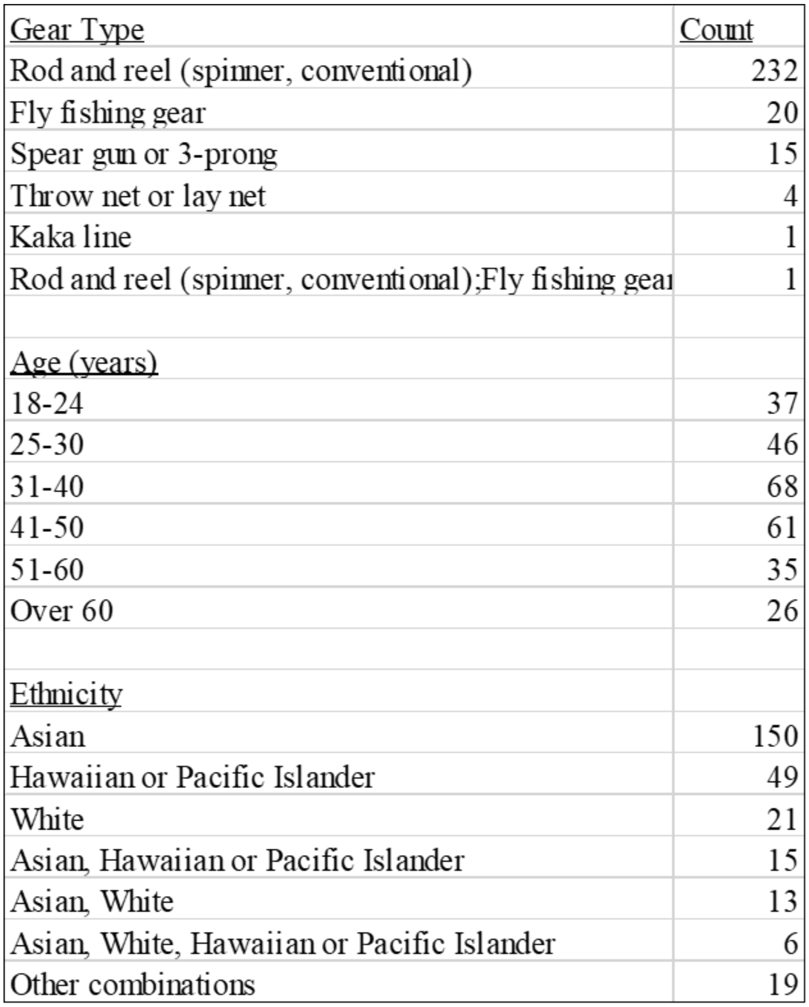
The distribution of the Hawaiʻi Bonefish Survey started in the summer of 2019 and the survey was closed to responses in December 2020. Survey responses were exported to Excel from Google Forms and manually keypunched from printed surveys. Patterns and emerging themes were explored through pivot tables. Data was analyzed and depicted for separating information by gear type. A theme was assigned to each open-ended comment based on the content and these themes were grouped together to reveal issues most concerning or important to respondents. Themes from all comments were then grouped together by commonalities.

Results

The survey effort yielded a total of 277 responses, with all but 22 anglers not originally from Hawaiʻi. The majority (67%) of the respondents were from Oʻahu and 25% were from Hawaiʻi Island, Maui, Kauaʻi, Molokaʻi, and Lanaʻi. A majority of the participants completed the survey virtually, with fewer than 20 participants filling out a hard copy of the survey. Only three surveys had missing responses, all of which were for the question prompting respondents for their motivations for releasing a bonefish. A total of 68 (~24.5%) anglers provided comments at the end of the survey. The main themes that emerged were related to changing state regulations, why bonefish should or should not be designated as a sportfish, and preference on what size bonefish to keep.

Four respondents self-identified as commercial fishers, so their data were removed from further analysis. The vast majority of participants were male, with only six female respondents and one respondent that did not specify their gender. Gear type used to catch bonefish was heavily skewed toward rod and reel (spinner, conventional) anglers and fly-fishers composing 84.1% and 7.6% respectively. Ethnicity was unevenly distributed with 56% Asian, 18% Hawaiian or Pacific Islander, and 8% white, accounting for 82% of respondents. Age was distributed more evenly with 47.3% of participants between 31-50 years old. Table 4 displays the gear, ethnicity, and age distributions.

Table 4. Demographics of non-commercial survey participants of the bonefish fishery in Hawai‘i



Gear Type	Count
Rod and reel (spinner, conventional)	232
Fly fishing gear	20
Spear gun or 3-prong	15
Throw net or lay net	4
Kaka line	1
Rod and reel (spinner, conventional);Fly fishing gea	1
Age (years)	
18-24	37
25-30	46
31-40	68
41-50	61
51-60	35
Over 60	26
Ethnicity	
Asian	150
Hawaiian or Pacific Islander	49
White	21
Asian, Hawaiian or Pacific Islander	15
Asian, White	13
Asian, White, Hawaiian or Pacific Islander	6
Other combinations	19

Overall, only 8% of respondents said they keep 100% of their bonefish catch. The remaining anglers (92%) will release all or at least some of their bonefish catch. When asked why, the single most frequent reason was because the bonefish was “too small” (32%). This response was not one of the selections given in the survey, but deliberately written in the “other” blank.

There were no fly-fishers that kept all bonefish they caught and 74% released all of their catch. Of the remaining fly-fishers, 11% estimate they keep a quarter and 5% keep half of their catch. All but one of these anglers reported their motivation for releasing bonefish was because they generally practice catch and release or enjoy catching them for sport. This fishery is predominantly catch-and-release, due primarily to guides’ employment being heavily dependent on the availability of bonefish on shallow flats (pers. comm. with local guides). The few that do keep bonefish, give it away or share it for special occasions like birthdays, parties, or holidays.

The keep versus release breakdown among rod and reel users was much more diverse. Anglers that either release (10%) or keep (5%) all the bonefish they catch comprised the smallest fraction of rod and reel users. A majority of these anglers responded somewhere in the middle, with 35% keeping a quarter, 29% keeping half, and 19% keeping three-quarters of the bonefish they land. Of these bonefish kept, the four-to-five-pound size class is clearly the most preferred weight. Anglers’ most prominent motives for keeping bonefish were to use it as food for themselves and their family (82%) and to give away and share with others (41%) (Figure 12). When a rod-and-reel angler released a bonefish, 41% said they generally practice catch-and-release or enjoy catching them for sport. A third of all survey participants added a response explaining that they release bonefish when “too small”.

Eighteen of the 68 people who provided feedback in the comments section spoke about a need for updated or renewed regulations for bonefish in Hawaiʻi. Five comments expressed dissatisfaction with the current regulations and call for an increase in the minimum size a bonefish can be taken or implementation of a slot limit.

Discussion

The results of this project illustrated the motivations and preferences by anglers that catch bonefish in Hawaiʻi. Although the survey does not represent a formal census of bonefish anglers in Hawaiʻi, results provide some fundamental insights. Angler preferences can be combined with bonefish life history to create science-informed conservation actions that are better understood by the fishing community and other bonefish consumers (Bennet *et al*., 2017; Ayers & Leong, 2020). Analyses revealed various trends related to fish size and disposition preferences by gear type (Figures 11 & 12).

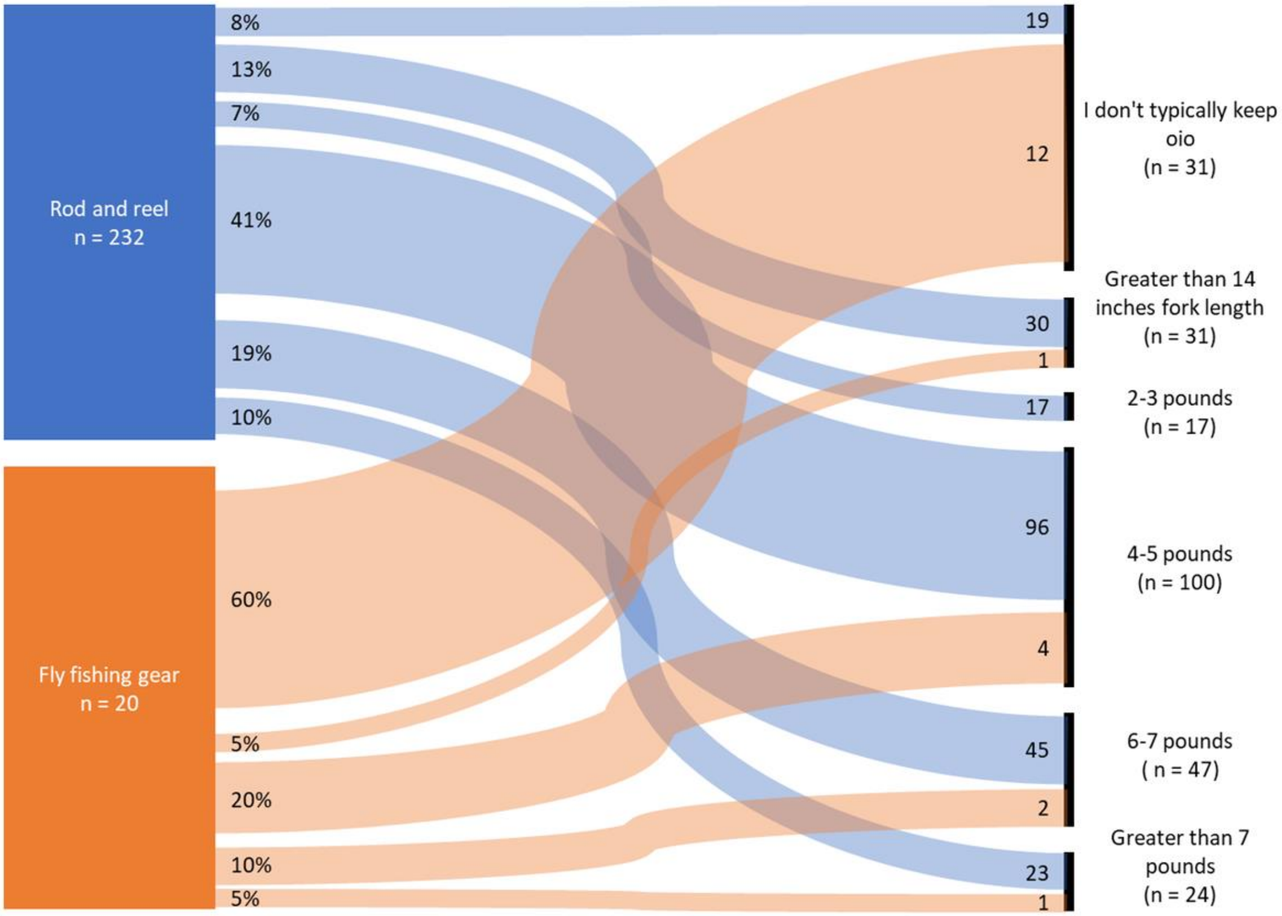


Figure 11. This Sankey Diagram depicts responses from the question: At what size do you prefer to keep an oio? The majority of anglers using fly-fishing gear do not keep bonefish. Rod and reel anglers have a much wider diversity of size preferences, with the majority of these anglers preferring to keep bonefish that are in the 4-5 pound size class.

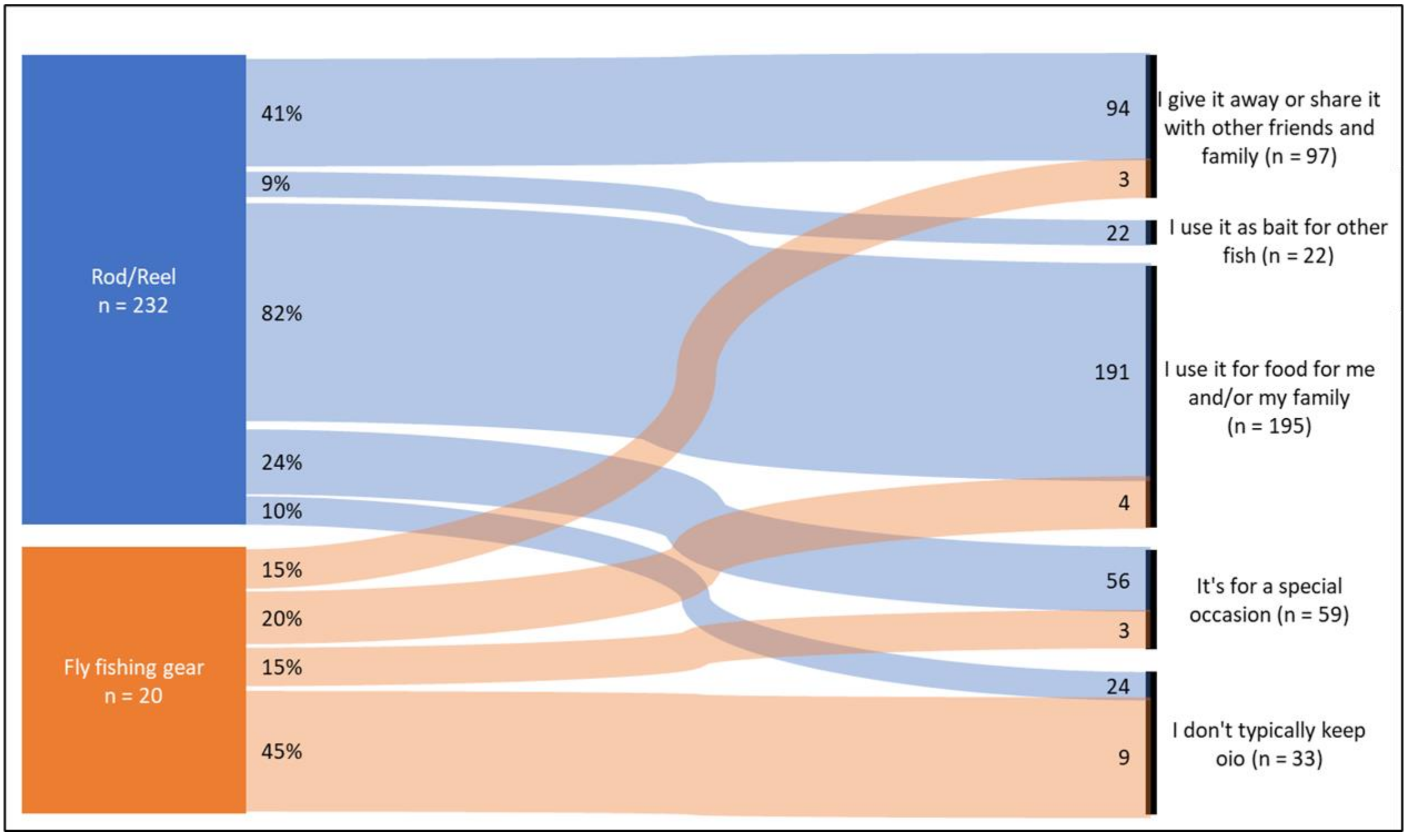


Figure 12. This Sankey Diagram depicts responses from the statement: If I keep an oio it's because… (select all that apply). As seen in Figure 11, anglers using fly-fishing gear do not typically keep bonefish. Rod and reel anglers are mostly keeping bonefish for food or sharing it with friends and family. Responses are not mutually exclusive, therefore, an angler can choose more than one reason why they keep their bonefish catch.

The Hawai‘i Division of Aquatic Resources (DAR) is currently undertaking a planning initiative to create island-specific management plans with input from the fishing community, that may include updating regulations to promote responsible fishing practices. As stated earlier, the only restriction for bonefish harvest is a 14-inch (31.4 cm) fork length minimum size (DAR, 2012). In contrast to a fork length minimum, a slot limit sets a length range (i.e., a minimum and maximum length) a fish can be legally taken. This protects juvenile fish that have not had the chance to spawn and larger fish that may be some of the most prolific spawners. Slot limits have successfully been used in fisheries from halibut in Alaska to snook in Florida (FWC, 1999; NOAA Fisheries, 2021). Complying with a minimum size is less burdensome, as it only requires a fish to be above a designated length, but a slot limit requires anglers to ensure a fish is above the minimum size and below the maximum size.

In the event that DAR increases the minimum size, the L_{50}, i.e., the length when 50% of bonefishes are able to spawn, could be an appropriate choice because it ensures some of the bonefish taken have reproduced. The L_{50} for bonefish in Hawaiʻi is roughly 17 inches and varies between species and sex, which equates to fish in the 2–3-pound range (Donovan *et al*., 2015). An increase in the minimum size to the L_{50} has the potential to impact anglers that prefer smaller (i.e., <4lb) bonefish, though the survey indicates this represents a small number of anglers (n = 30, 11%). Bonefish in the 4–5-pound range (equivalent to 20-22 inches length (Donovan *et al*., 2015)) exceed the L_{50}, and were the most desired size class, with 41% of anglers preferring this size. Another 29% prefer to keep bonefish only when they are at least 6 pounds, meaning an overwhelming majority (~70%) keep bonefish four pounds and bigger. Therefore, survey results suggest that 86% of responding anglers would not be heavily impacted by a minimum size increase to the L_{50} because they either do not prefer to keep bonefish or prefer sizes above the L_{50}.

The bonefish fishery in Hawaiʻi is predominantly catch-and-release. The low retention of bonefish by anglers and the preference for larger (≥4 pounds) fish when retained is likely due to the labor-intensive effort in its preparation. Furthermore, the effort to prepare a small bonefish (under 2-3 pounds) is not worth it given the low meat yield. As suggested in their name, bonefish are very bony. Bonefish are not typically filleted and prepared like more mainstream species (e.g., tunas, snappers, etc.). Bonefish meat is scraped out or rolled out prepared in a variety of ways. The meat is often prepared raw as lomi ʻōʻio, or mixed with various ingredients to make dishes such as burgers and fish cake. Awa (milkfish, *Chanos chanos*) and awaʻawa (lady fish, *Elops hawaiiensis*) are prepared similarly, although these species are not nearly as abundant and targeted as bonefish.

Controversial issues surrounding bonefishes have surfaced in recent years due to competing interests. Interest groups have tried to designate bonefish as a gamefish, which would lead to rules ranging from restricting the use of nets to banning the take of bonefish completely, regardless of gear type. Comments from the survey expressed support for both viewpoints, i.e., making bonefish a gamefish and keeping the status quo of not having gamefish status. Bonefish harvested from fishponds as well as wild-caught fish were a valuable food item in early Hawaiʻi (Titcomb, 1972). The results of this survey suggest that they are still valued as a food fish for non-commercial anglers, especially from rod and reel users (Figure 11).

Management plans in Hawaiʻi must balance the use of bonefish as a food source and their gamefish value that predominates in other locations. Bonefish account for 25% of Anaa Atoll's fisheries catch and they are traditionally an important food source (Filous *et al.*, 2019a). This locale must also balance a traditional subsistence fishery with a developing recreational fly-fishing industry (Filous *et al.*, 2019a). Locations such as Kiritimati have established a lucrative recreational fishery for bonefish (*A. glossodonta*) and prohibit taking or possessing bonefishes (Campbell & Hanich, 2014). Bonefishes also support economically significant recreational fisheries in the Caribbean (e.g., Belize, Bahamas, Venezuela, etc.) and southern Florida (Adams *et al.*, 2008). Arguably, the bonefish fishery in Hawaiʻi has a hybrid set of competing demands seen in all the regions mentioned above, ranging from subsistence fishing and recreational take to fly-fishing charters and commercial fishing.

Balancing contrasting values in a fishery is challenging, especially when there is no streamlined way to access the fishing community (i.e., a registry, permit, or license). Resource management is most effective when the fishing community is engaged and included in decision-making processes (Hospital & Beavers, 2011; Friedlander *et al.*, 2013; Schemmel *et al.*, 2016). There are a growing number of Hawaiʻi-specific examples that have shown how direct angler engagement leads to increased understanding of trevally, bottomfish, and shark fisheries (Iwai & Tagawa, 2008; Yau & Oram, 2016; Iwane *et al.*, 2021). These are inherently different fisheries compared to the bonefish fishery in Hawaiʻi. However, an underlying value of this project showed how a survey can give the fishing community an opportunity to voice their opinions and share their preferences related to a species they target. Successful management requires a foundation of local commitment and traditional knowledge, highlighting the importance of incorporating angler preferences and expertise into the management process (Honneland, 1999; Yochum *et al.*, 2011). Hawaiʻi is a small state and it is critically important to maintain meaningful connections between managers, scientists, and the fishers.

Chapter 5: Conclusion

This research brought together multiple disciplines to fill data gaps in the life history of *A. glossodonta* in Hawaiʻi. Modern fisheries management requires an understanding of a fish's biological and ecological characteristics as well as an understanding of how the environment and people interact with a species or fishery. Collecting leptocephalus data, population genetic connectivity, and fish disposition information, helped complete a holistic image of the bonefish life cycle in Hawaiʻi. The three chapters above appear to be disparate and unconnected, but combined with previous research, they show the path of a bonefish's life from the early larval stage, through juvenile and adult stages, to potential capture by an angler.

A bonefish begins its life in the deep, pelagic environment where gametes are dispersed during spawning events. Although, this habitat has not been documented in Hawaiʻi, in other locations the bonefishes form spawning aggregations offshore, away from the shallow flats where they feed as adults (Crabtree *et al*., 1997; Larkin *et al*., 2007; Wills *et al*., 2022). Eggs hatch within a couple of days and larvae begin to grow, where they can reach a fork length around 60-70 mm (Smith, 1979; Pfeiler, 1984). This research saw a maximum fork length of 66 mm, suggesting they were close to the maximum size before metamorphosis or had just begun to undergo the transformation. Leptocephali were not sampled every month throughout the year, but otolith analyses were still able to corroborate a spawning season previously determined through gonad histology analyses (Donovan *et al*., 2015). This was particularly useful because counting fewer otolith daily growth increments of young larvae is less challenging than otolith preparation and increment enumeration of older (<1 year old) juvenile bonefishes.

Bonefish leptocephalus migrate inshore, particularly during flood tides and dark moons (Mojica *et al*., 1995). Oʻahu leptocephalus recruited to estuarine areas in this study, suggesting the importance of preventing anthropogenic impacts to these habitats and ensuring freshwater input is not impeded. These recruitment areas also serve as the first habitat for early juveniles. Leptocephalus lose 50% of their lipids and decrease about 50% in fork length when they become a recognizable juvenile bonefish (Alexander, 1961; Padron *et al*., 1996). Local beach seine studies and angler anecdote show that juvenile *A. glossodonta* occupy deeper habitats and juvenile *A. virgata* utilize shallower habitats (e.g., nearshore beaches) (Kamikawa *et al*., 2015; Donovan *et al*., 2016). Then as adults, these species transition to opposite depths; *A. glossodonta* frequenting shallow flats and *A. virgata* reside in deeper channels and offshore areas.

Once past the juvenile stage, *A. glossodonta* recruit to the fishery in Hawaiʻi around 41-48 cm fork length (Kamikawa *et al*., 2015). The strong site fidelity shown through recaptures have led some to believe that distinct populations may exist at a regional (i.e., north vs. south side of a particular island) or island scale (i.e., Oʻahu vs. Maui). High levels of site fidelity are seen by sister species in other regions as well (Boucek *et* al., 2018; Griffin *et al*., 2022). Genetic results from Chapter 3 and age analyses from Chapter 2 disprove these notions as the dispersal potential of leptocephali connect populations not only at a state-wide scale, but at a Pacific-basin level (Wallace, 2015). It is less likely that the gene flow is caused by adults transiting regularly between islands and throughout the Pacific. More advanced kinship studies requiring larger sampling would be capable of distinguishing fine scale relatedness of bonefishes between islands.

If a bonefish does not encounter natural mortality (i.e., predation, disease, etc.) it may encounter fishing mortality (i.e., capture by an angler). The Hawaiʻi Bonefish Survey was able to provide more detail regarding fishing mortality, or the last stage in a bonefish's life cycle. *Albula glossodonta* can live to at least 14 years old, which can be over 70 cm long, providing many opportunities to be caught once it has recruited to the fishery (Donovan *et al*., 2015). The recreational, commercial, and cultural value of bonefishes in Hawaiʻi, create a variety of motivations and preferences whether to keep or release a bonefish that has been caught. As shown in Chapter 4, bonefish size is a major factor whether an angler keeps their catch. Hawaiʻi typically uses minimum sizes as a management tool for nearshore species and if minimum sizes were updated, this type of research provides insight into how changes in minimum size could impact anglers. The survey was not an exhaustive effort of all fishing stakeholders in Hawaiʻi, but it provided clear preferences from anglers that target bonefish. Combining this type of disposition information with biological characteristics such as size at maturity, can help align effective and accepted management tools.

A final highlight of this research is the angler involvement with collecting fin clips in Chapter 3 and participating in the survey in Chapter 4. This research provided a great framework on how to include stakeholders in the scientific data collection process. Direct engagement with the fishing community helps to build communication, trust, improved data, and ideally higher level of compliance with management (Ayers & Leong, 2020). Without an inventory of non-commercial anglers, it takes focused effort from managers and scientists to connect with resource users. The results from this work will be disseminated back to the anglers that contributed to this research via oral communication, manuscript, or visual presentation. This feedback is critically important in fostering trust in the scientific research process and reinforcing lines of communication between scientists & managers and their constituent community of fishers.

Appendix

Hawaiʻi Bonefish Survey

What is your age?

- ○ 18 – 24
- ○ 25 – 30
- ○ 31 – 40
- ○ 41 – 50
- ○ 51 – 60
- ○ Over 60

Please specify your ethnicity?

- ○ Asian
- ○ Black or African American
- ○ Hawaiian or Pacific Islander
- ○ Hispanic or Latino
- ○ White
- ○ Other

What is your sex?

- ○ Female
- ○ Male
- ○ Prefer not to say

What city are you from?

Email address (if you would like feedback on results)

How would you describe yourself as a fisher?

- ○ Commercial (own a commercial license and sell fish)
- ○ Non-commercial (do not sell fish)

On average, how many times a month do you go fishing?

- ○ I don’t fish
- ○ less than once a month
- ○ Once
- ○ Twice
- ○ Three times

- Four or more

On average, how many oio (bonefish, *Albula glossodonta*, *Albula virgata*) do you catch per fishing session?

- I don’t catch oio
- 1
- 2
- 3
- 4 or more

Do you target oio?

- Yes
- No

What gear type best characterizes how you catch oio?

- Rod and reel (spinner, conventional)
- Fly fishing gear
- Spear gun or 3-prong
- Throw net or lay net
- Other

When you catch oio, how often do you keep or release? Please choose answer closest to your keep and release percentages

- Keep 100%, Release 0%
- Keep 75%, Release 25%
- Keep 50%, Release 50%
- Keep 25%, Release 75%
- Keep 0%, Release 100%
- Other

If I keep an oio it’s because… (select all that apply)

- I use it for food for me and/or my family
- It’s for a special occasion (ex: birthday, party, etc)
- I give it away or share it with other friends and family
- I sell it
- I use it as bait for other fish

- I don’t typically keep oio
- Other

At what size do you prefer to keep an oio?

- Greater than 14 inches fork length
- 2 – 3 pounds
- 4 – 5 pounds
- 6 – 7 pounds
- Greater than 7 pounds
- I don’t typically keep oio
- Other

If I release an oio it’s because… (select all that apply)

- I don’t like to eat oio, or know anyone that does
- I generally practice catch and release
- I participate in tag and release programs
- I enjoy catching them for sport
- I don’t usually release oio I catch
- Other

We encourage you to leave any other comments or opinions that were not covered in this survey here.

Literature Cited

Adams, A.J., Wolfe, R.K., Tringali, M.D., Wallace, E.M. & Kellison, G.T. (2008). Rethinking the status of *Albula* spp. biology in the Caribbean and Western Atlantic. In: J.S. Ault (ed.), Biology and management of the world tarpon and bonefish fisheries, pp. 203-214. CRC Press, Boca Raton.

Adams, A., Guindon, K., Horodysky, A., MacDonald, T., McBride, R., Shenker, J. & Ward, R. (2012a). *Albula glossodonta. The IUCN Red List of Threatened Species 2012*: e.T194299A2310398.

Adams, A., Guindon, K., Horodysky, A., MacDonald, T., McBride, R., Shenker, J. & Ward, R. (2012b). *Albula virgata*. The IUCN Red List of Threatened Species 2012: e.T194302A2310633.

Adams, A. J., Horodysky, A. Z., Mcbride, R. S., Guindon, K., Shenker, J., Macdonald, T.C., et al. (2013). Global conservation status and research needs for tarpons (Megalopidae), ladyfishes (Elopidae) and bonefishes (Albulidae). *Fish and Fisheries*, 15, 280–311. https :// doi.org/10.1111/faf.12017.

Adams, A. J. & Cooke, S. J. (2015). Advancing the science and management of flats fisheries for bonefish, tarpon, and permit. *Environmental Biology of Fishes* 98, 2123-2131.

Alexander, D. H., Novembre, J., & Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Research*, 19(9), 1655-1664.

Alexander, E.C. (1961). A contribution to the life history, biology and geographical distribution of the bonefish, *Albula vulpes* (Linnaeus). Carlsberg Foundation Dana Report 53:1 - 51.

Allen, M. (2014). The historical role of bonefishes (*Albula* spp.) in Polynesian fisheries. Hawaiian Archaeology 4, 51-72.

Almany, G.R. & Wesbster, M.S. (2006). The predation gauntlet: early post-settlement mortality in reef fishes. *Coral Reefs* 25, 19-22.

Anderson, T.W., Bartels, C.T., Hixon, M.A., Bartels, E., Carr, M.H., & Shenker, J.M. (2002). Current velocity and catch efficiency in sampling settlement-stage larvae of coral-reef fishes. *Fishery Bulletin* 100, 404-413.

Ayers, A.L. & Leong, K. (2020). Examining the seascape of compliance in U.S. Pacific island fisheries. *Marine Policy* 115, 13 pp.

Begg, G. A., Campana, S. E., Fowler, A. J. & Suthers, I. M. (2005). Otolith research and application: current directions in innovation and implementation. *Marine and Freshwater Research* 56, 477-483.

Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N., & Bonhomme, F. (2000). GENETIX, logiciel sousWindowsTM pour la génétique des populations. Laboratoire Génome, Populations, Interactions CNRS UMR 5000. Université deMontpellier II, Montpellier.

Bennet, N.J., Roth, R., Klain, S.C., Chan, K., Christie, P., Clark, D.A., et al. (2017). Conservation social science: Understanding and integrating human dimensions to improve conservation. *Biological Conservation* 205, 93-108.

Bergenius, M.A.J., Meekan, M.G., Robertson, D.R. & McCormick, M.I. (2002). Larval growth predicts the recruitment success of a coral reef fish. *Oecologia* 131, 521-525.

Boucek, R.E., Lewis, J.P., Stewart, B.D., Jud, Z.R., Carey, E., & Adams, A.J. (2018) Measuring site fidelity and homesite-to-pre-spawning site connectivity of bonefish (*Albula vulpes*): using mark-recapture to inform habitat conservation. *Environmental Biology of Fishes* 102, 185-195.

Bowen, B., Karl, S.A., & Pfeiler, E. (2008). Resolving evolutionary lineages and taxonomy of bonefishes (*Albula* spp.). In: J.S. Ault (ed.), *Biology and management of the world tarpon and bonefish fisheries*, pp. 147-154. CRC Press, Boca Raton.

Campana, S.E. & Thorrold, S.R. (2001). Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 30-38.

Campbell, B. & Hanich, Q. (2014). Fish for the future: Fisheries development and food security for Kiribati in an era of global climate change. WorldFish, Penang, Malaysia. Project Report: 2014-47.

Catchen, J., Hohenlohe, P.A., Bassham, S., Amores, A., & Cresko, W.A. (2013). Stacks: an analysis tool set for population genomics. *Molecular Ecology* 22, 3124-3140.

Colborn, J., Crabtree, R.E., Shaklee, J.B., Pfeiler, E. & Bowen, B.W. (2001). The evolutionary enigma of bonefishes (*Albula* spp.): Cryptic species and ancient separations in a globally distributed shorefish. *Evolution* 55, 807-820.

Coleman, R.R. & Bowen, B.W. (2022). Genomic assessment of an endemic Hawaiian surgeonfish, *Acanthurus triostegus sandvicensis* reveals high levels of connectivity and fine-scale population structure. *Coral Reefs* 41:687 – 697.

Craig, M.T., Eble, J., & Bowen, B.W. (2010). Origins, ages, and populations histories: Comparative phylogeography of endemic Hawaiian butterfly fishes (genus *Chaetodon*). *Journal of Biogeography* 37, 2125–2136.

Dahlgren, C.P., Kellison, G.T., Adams, A.J., Gillanders, B.M., Kendall, M.S., Layman, C.A., Ley, J.A., Nagelkerken, I. & Serafy, J.E. (2006). Marine nurseries and effective juvenile habitats: concepts and applications. *Marine Ecology Progress Series* 312, 291-295.

Danecek, P.A. Auton, G. Abecasis, C.A., Albers, E., Banks, M.A., DePristo, R.E., Handsaker, G., Lunter, G.T., Marth, S.T., Sherry, G. McVean & R. Durbin. (2011). 1000 Genomes Project Analysis Group. The variant call format and VCFtools. *Bioinformatics* 27: 2156-2158.

Danylchuk, A. J., Cooke, S. J., Goldberg, T. L., Suski, C.D., Murchie, K.J., Danylchuk, et al. (2011). Aggregations and offshore movements as indicators of spawning activity of bonefish (*Albula vulpes*) in The Bahamas. *Marine Biology* 158, 1981-1999.

DiBattista, J.D., Wilcox, C., Craig, M.T., Rocha, L.A., & Bowen, B.W. (2011). Phylogeography of the Pacific Blueline Surgeonfish *Acanthurus nigroris* reveals a cryptic species in the Hawaiian Archipelago. *Journal of Marine Biology* Article ID 839134.

Division of Aquatic Resources (DAR). (2012). Marine fishes and other invertebrates. (dlnr.hawaii.gov/dar/fishing/fishing-regulations/marine-fishes-and-vertebrates/).

Doherty, P.J. (1987). Light-traps: Selective but useful devices for quantifying the distributions and abundances of larval fishes. *Bulletin of Marine Science* 41, 423-431.

Donovan, M. K., Friedlander, A. M., Harding, K. K., Schemmel, E. M., Filous, A., Kamikawa, K. & Torkelson, N. (2015). Ecology and niche specialization of two bonefish species in Hawai'i. *Environmental Biology of Fishes* 98, 2159-2171.

Donovan, M.K., Friedlander, A.M., Usseglio, P., Goodell, W., Iglesias, I., Schemmel, E.M., et al. (2016). Effects of gear restriction on the abundance of juvenile fishes along sandy beaches in Hawaii. *PLoS ONE* DOI:10.1371/journal.pone.0155221.

Douglas, M.R., Chafin, T., Claussen, J.A., & Philipp, D.P. (2021). Are populations of economically important bonefish and queen conch ‘open’ or ‘closed’ in the northern Caribbean basin? *Marine Ecology* 42, e12639. https://doi.org/10.1111/maec.12639.

Faircloth, B., & Glenn, T. (2011). Homemade AMPure XP beads. Department of Ecology and Evolutionary Biology. University of California, Los Angeles.

Fedler, T. (2009). The economic impact of recreational fishing the Everglades Region. Palmetto Bay, FL: The Everglades Foundation. 13pp.

Fedler, T. (2013). Economic impact of the Florida Keys flats fishery. Report to Bonefish & Tarpon Trust, FL 30p. https://lkga.org/wp-content/uploads/2017/05/btt-keys-economic-report.pdf.

Filous, A., Lennox, R.J., Coleman, R.R., Friedlander, A.M., Clua, E.E.G., & Danylchuk, A.J. (2019a). Life-history characteristics of an exploited bonefish *Albula glossodonta* population in a remote South Pacific atoll. *Journal of Fish Biology* 95, 562-574.

Filous, A., Lennox, R.J., Eveson, P., Raveino, R., Clua, E.E.G., Cooke, S.J., & Danychuk, A.J. (2019b). Population dynamics of roundjaw bonefish *Albula glossodonta* at a remote coralline Atoll inform community-based management in an artisanal fishery. *Fisheries Management and Ecology* 27, 200-2014.

Florida Fish and Wildlife Conservation Commission (FWC). (1999). Snook. https://myfwc.com/fishing/saltwater/recreational/snook/.

Frezza, P.E. & Clem, S.E. (2015). Using local fishers' knowledge to characterize historical trends in the Florida Bay bonefish population and fishery. *Environmental Biology of Fishes* 98, 2187-2202.

Friedlander, A. M., Brown, E. & Monaco, M. E. (2007). Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. *Marine Ecology Progress Series* 351, 221-233.

Friedlander, A.M., Caselle, J.E., Beets, J., Lowe, C.G., Bowen, B.W., Ogawa, T.K., et al. (2008). Biology and ecology of the recreational bonefish fishery at Palmyra Atoll National Wildlife Refuge with comparisons to other Pacific Islands. In J.S. Ault (ed.) *Biology and management of the world tarpon and bonefish fisheries*. Pp. 28-56, CRC Press, Boca Raton, FL

Friedlander, A.M., Shackeroff, J.M., & Kittinger, J.N. (2013). Customary marine resource knowledge and use in contemporary Hawaii. *Pacific Science* 67, 441-460.

Friedlander, A.M., Nowlis, J. & Koike, H. (2015). Improving fisheries assessments using historical data. In: Pauly, D. (ed.) *Marine Historical Ecology in Conservation*, pp. 91-118. University of California Press.

Froese, R. (2006). Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* 22, 241–253.

Froese, R., Tsikliras, A. C., & Stergiou, K. I. (2011) Editorial note on weight-length relations of fishes. *Acta Ichthyologica et Piscatoria* 41, 261– 263.

Gaither, M.R., Jones, S.A., Kelley, C., Newman, S.J., Sorenson, L., & Bowen, B.W. (2011). High connectivity in the deepwater snapper *Pristipomoides filamentosus* (Lutjanidae) across the Indo-Pacific with isolation of the Hawaiian Archipelago. *PLoS ONE* 6(12): e28913. doi:10.1371/journal.pone.0028913.

Gaither, M.R., Bernal, M.A., Coleman, R.R., Bowen, B.W., Jones, S.A., Simison, W.B., & Rocha, L.A. (2015). Genomic signatures of geographic isolation and natural selection in coral reef fishes. *Molecular Ecology* 24:1543-1557.

Grafeld, S., Oleson, K.L.L., Teneva, L., & Kittinger, J.N. (2017). Follow that fish: Uncovering the hidden blue economy in coral reef fisheries. *PLoS ONE* 12, 25pp.

Graves, J.E., & McDowell, J.R. (2015). Population structure of Istiophorid billfishes. *Fisheries Research* 166, 21-28.

Griffin, L.P., Brownscombe, J.W., Gagne, T.O., Haak, C.R., Cormier, R., Becker, S.L., et al. (2022). There's no place like home: high site fidelity and small home range of bonefish (*Albula vulpes*) inhabiting fringing reef flats in Culebra, Puerto Rico. *Environmental Biology of Fishes.* https://doi.org/10.1007/s10641-022-01312-x

Hedrick, P.H. (2011) *Genetics of populations, fourth edition*. James and Bartlett Publishers, Subury MA.

Hidaka, K., Iwatsuki, Y. & Randall, J.E. (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.

Hildebrand, S. F. (1963). Family Albulidae. Pages 132–147 in H. B. Bigelow, editor. *Fishes of the western North Atlantic*. Sears Foundation for Marine Research, Bingham Oceanographic Laboratory, Yale University, New Haven, Connecticut.

Hixon, M.A., Bowen, B.W., Coleman, R.R., Counsell, C.W., Donahue, M.J., Franklin, et al. (2022). Fish Flow: Following fisheries from spawning to supper. *Frontiers in Ecology and the Environment* 20, 247 – 254. doi:10.1002/fee.2449.

Hodge, J.R., van Herwerden, L., & Bellwood, D.R. (2014). Temporal evolution of coral reef fishes: global patterns and disparity in isolated locations. *Journal of Biogeography* 41, 2115–2127.

Honneland, G. (1999). A model of compliance in fisheries: theoretical foundations and practical application. *Ocean & Coastal Management* 42, 699-716.

Hospital, J., & C. Beavers. (2011). Management of the main Hawaiian Islands bottomfish fishery: fishers' attitudes, perceptions, and comments. *Pacific Islands Fisheries Science Center administrative report*. H-11-06, 46 p. + Appendices, Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.

Hourigan, T.F., & Reese, E.S. (1987). Mid-ocean isolation and the evolution of Hawaiian reef fishes. *Trends in Ecology and Evolution* 2, 187–191.

Husson, L., Boucher, F.C., Sarr, A.C., Sepulchre, P., and Cahyarini, S.Y. (2019). Evidence of Sundaland's subsidence requires revisiting its biogeography. *Journal of Biogeography* 47, 843-853.

Iwai, T. & Tagawa, A. (2008). Ulua tagging project & moi tagging program fishing survey summary. Honolulu, Hawaii. Special edition 14pp.

Iwane, M.A., Leong, K.M., Vaughan, M., & Oleson, K.L.L. (2021). When a shark is more than a shark: a sociopolitical problem-solving approach to fisher-shark interactions. *Frontiers in Conservation Science* 2, 669105.

Jombart, T., & Ahmend, I. (2011). Adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics* 27, 3070-3071.

Kamikawa, K. T., Friedlander, A. M., Harding, K. K., Filous, A., Donovan, M. K. & Schemmel, E. (2015). Bonefishes in Hawai'i and the importance of angler-based data to inform fisheries management. *Environmental Biology of Fishes* 98, 2147-2157.

Kamvar, Z. N., Tabima, J. F., & Grünwald, N. J. (2014). Poppr: an R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. *PeerJ* 2, e281.

Keenan, K., P. McGinnity, T. F. Cross, W. W. Crozier, & P. A. Prodöhl. (2013). diveRsity: An R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods in Ecology and Evolution* l4, 782-788.

Kittinger, J.N., Finkbeiner, E.M., Ban, N.C., Broad, K., Carr, M.H., Cinner, J.E., et al. (2013). Emerging frontiers in social-ecological systems research for sustainability of small-scale fisheries. *Environmental Sustainability* 5, 1-6.

Kosaki, R.K., Pyle, R.L., Randall, J.E., & Irons, D.K. (1991). New records of fishes from Johnston Atoll with notes on biogeography. *Pacific Science* 45, 186–203.

Larkin, M.F., Ault, J.S., Humston, R., Luo, J., & Zurcher, N. (2007). Tagging of bonefish in south Florida to study population movements and stock dynamics. In: J.S. Ault (ed.), *Biology and management of the world tarpon and bonefish fisheries,* pp. 301-320. CRC Press, Boca Raton.

Larkin, M.F., Ault, J.S., 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.

Maragos, J.E. & Jokiel, P.L. (1986). Reef corals of Johnston Atoll: one of the world's most isolated reefs. *Coral Reefs* 4, 141–150.

McCoy, K.S., Williams, I.D., Friedlander, A.M., Ma, H., Teneva, L., & Kittinger, J.N. (2018). Estimating nearshore coral reef-associated fisheries production from the main Hawaiian Islands. *PLoS ONE* 13(4) e0195840. https://doi.org/10.1371/journal.one.0195840.

McKinney, G. J., R. K. Waples, L. W. Seeb, & J. E. Seeb. (2017). Paralogs are revealed by proportion of heterozygotes and deviations in read ratios in genotyping-by-sequencing data from natural populations. *Molecular Ecology Resources* 17, 656-669.

Meekan, M.G., Milicich, M.J., & Doherty, P.J. (1993). Larval supply drives temporal patterns of larval supply and recruitment of a coral reef damselfish. *Marine Ecology Progress Series* 93, 217-225.

Meekan, M.G., Wilson S.G., Halford, A., & Retzel, A. (2001). A comparison of catches of fishes and invertebrates by two light trap designs, in tropical NW Australia. *Marine Biology* 139, 373-381.

Milicich, M.J., Meekan, M.G, & Doherty, P.J. (1992). Larval supply: a good predictor of recruitment of three species of reef fish (Pomacentridae). *Marine Ecology Progress Series* 86, 153-166.

Miller, M.J. & Tsukamoto, K. (2004). *An introduction to leptocephali: Biology and Identification*. Ocean Research Institute, The University of Tokyo, viii+96pp, 3plates.

Mojica Jr, R., Shenker, J.M., Harnden, C.W. & Wagner, D.E. (1995). Recruitment of bonefish, *Albula vulpes*, around Lee Stocking Island, Bahamas. *Fishery Bulletin* 93, 666-674.

NOAA Fisheries Alaska Region (2021). New 2021 regulations for charter halibut anglers. (https://media.fisheries.noaa.gov/2021-02/AK-charter-halibut-regulations-fact-sheet-akro.pdf?null).

NOAA Office of National Marine Sanctuaries Pacific Islands Region (ONMS). (2010). Action plan for the Kalauihai (Lucas Spring) Fishpond Restoration Project. Facility Programming and Consulting with Fraser and Fogle Architects and Leeway Enterprise. 66p.

Padrón, D., Lindley, V.F., & Pfeiler, E. (1996). Changes in lipid composition during metamorphosis of bonefish (*Albula* sp.) leptocephali. *Lipids* 31(5), 513–519

Peterson, B.K, Weber, J.N., Kay, E.H., Fisher, H.S., & Hoekstra, H.E. (2012). Double Digest RADseq: An inexpensive method for de novo SNP discovery and genotyping in model and non-model species. *PLoS ONE* 7(5), e37135. doi:10.1371/journal.pone.0037135

Pfeiler, E. (1984). Inshore migration, seasonal distribution and sizes of larval bonefish, *Albula*, in the Gulf of California. *Environmental Biology of Fishes* 10, 117-122.

Pickett, B.D., Wallace, E.M., Ridge, P.G., & Kauwe, J.S.K. (2020). Lingering taxonomic challenges hinder conservation and management of global bonefishes. *Fisheries* 45(7), 347–358. doi: 10.1002/fsh.10438.

Raj, A., Stephens, M., & J. K. Pritchard. (2014). fastSTRUCTURE: variational inference of population structure in large SNP data sets. *Genetics* 197, 573-589.

Randall, J.E. (1998). Zoogeography of shore fishes of the Indo-Pacific region. *Zoological Studies* 37, 227–268.

Randall, J. E. & Bauchot, M. L. (1999). Clarification of the two Indo-Pacific species of bonefishes, *Albula glossodonta* and *A. forsteri*. *Cybium* 23, 79-83.

Rivera, M.A.J., Kelley, C.D., & Roderick, G.K. (2004). Subtle population genetic structure in the Hawaiian Grouper, *Epinephelus quernus* (Serranidae) as revealed by mitochondrial DNA analyses. *Biological Journal of the Linnean Society* 81, 449–468.

Rivera, M.A.J., Andrews, K.R., Kobayashi, D.R., Wren, J.L.K., Kelley, C., Roderick, G.K. et al. (2011). Genetic analyses and simulations of larval dispersal reveal distinct populations and directional connectivity across the range of the Hawaiian Grouper (*Epinephelus quernus*). *Journal of Marine Biology* Article ID 765353 https://doi.org/10.1155/2011/765353

Rooker, J.R., Dennis, G.D., & Goulet, D. (1996). Sampling larval fishes with a nightlight lift-net in tropical inshore waters. *Fisheries Research* 26, 1-15.

Rosenberg, N. A. (2004). Distruct: a program for the graphical display of population structure. *Molecular Ecology Notes* 4, 137-138.

Schemmel, E., A. M. Friedlander, P. Andrade, K. Keakealani, L. M. Castro, C. Wiggins, B. A. Wilcox, Y. Yasutake, & J. N. Kittinger. (2016). The codevelopment of coastal fisheries monitoring methods to support local management. *Ecology and Society* 21(4), 34. https://doi.org/10.5751/ES-08818-210434.

Seyoum, S., Wallace, E.M., & Tringali, M.D. (2008). Twelve polymorphic microsatellite markers for the bonefish, *Albula vulpes* and two congeners. *Molecular Ecology Resources* 8, 354–356.

Shaklee, J. B. & Tamaru, C. S. (1981). Biochemical and morphological evolution of Hawaiian bonefishes (*Albula*). *Systematic Zoology* 30, 125-146.

Skillings, D.J., Bird, C.E., & Toonen, R.J. (2011). Gateway to Hawai’i: Genetic population structure of the tropical sea cucumber *Holothuria atra*. *Journal of Marine Biology,* Article ID 783030.

Smith, D.G. (1979). Guide to the leptocephali (Elopiformes, Anguilliformes, and Notacanthiformes). NOAA Technical Report NMFS Cicrular 424, 39 pp.

Snodgrass, D., Crabtree, R.E. & Serafy, J. (2008). Abundance, growth, and diet of young-of-the-year bonefish (*Albula* spp.) off the Florida Keys, U.S.A. *Bulletin of Marine Science* 82, 185-193.

Stevenson, T.C., Tissot, B.N., & Dierking, J. (2011). Fisher behaviour influences catch productivity and selectivity in West Hawaii's aquarium fishery. *ICES Journal of Marine Science* 68, 813-822.

Talma, S.C.A.L. (2021). *Genetic connectivity of the roundjaw bonefish (Albula glossodonta) in the Southwest Indian Ocean*. Thesis, Master of Science at Rhodes University. http://hdl.handle.net/10962/192174.

Tenggardjaja, K.A., Bowen, B.W., & Bernardi G. (2016). Reef fish dispersal in the Hawaiian Archipelago: Comparative phylogeography of three endemic damselfishes. *Journal of Marine Biology* Article ID 3251814.

Titcomb, M. (1972). *Native use of fish in Hawaii*. The University Press of Hawaii, Honolulu, Hawaii.

Toonen, R.J., Andrews, K.R., Baums, I.B., Bird, C.E., Concepcion, G.T., Daly-Engel, T.S., et al. (2011). Defining boundaries for ecosystem-based management: A multispecies case study of marine connectivity across the Hawaiian Archipelago. *Journal of Marine Biology* Article ID 460173. https://doi.org/10.1155/2011/460173.

Vasquez-Yeomans, L., Sosa-Cordero, E., Lara, M.R., Adams, A.J., & Cohuo, J.A. (2009). Patterns of distribution and abundance of bonefish larvae *Albula* spp. (Albulidae) in the western Caribbean and adjacent areas. *Ichthyological Research* 56, 266-275.

Wallace, E.M. (2015). High intraspecific genetic connectivity in the Indo-Pacific bonefishes: implications for conservation and management. *Environmental Biology of Fishes* 98, 2173-2186.

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

Wallace, E. M. & Tringali, M. D. (2016). Fishery composition and evidence of population structure and hybridization in the Atlantic bonefish species complex (*Albula* spp.). *Marine Biology* 163, 142.

Western Pacific Regional Fishery Management Council (WPRFMC). (2016). Feasibility of a non-commercial marine fishing registry, permit, or licensing system in Hawaii. (https://www.wpcouncil.org/wp-content/uploads/2016/12/NCMF_final_report.pdf).

Williams, C.T., Mclvor, A.J., Wallace, E.M., Lin, Y.J., & Berumen, M.L. (2020). Genetic diversity and life-history traits of bonefish *Albula* spp. from the Red Sea. *Journal of Fish Biology* 98, 855-864.

Wills, P.S., Shenker, J., Ajemian, M.J., Mejri, S., & Adams, A. (2022). Bonefish reproduction research project: March 2016-February 2022 Final Report. 189 pp. https://www.bonefishtarpontrust.org/downloads/research-reports/stories/brrp-btt-final%20report.pdf.

Wilson, J.K., Adams, A.J., & Ahrens, R.N.M. (2019). Atlantic tarpon (*Megalops atlanticus*) nursery habitats: evaluation of habitat quality and broad-scale habitat identification. *Environmental Biology of Fishes* 102, 383-402.

Winter, D., Green, P., Kamvar, Z., & Gosselin, T. (2017). mmod: modern measures of population differentiation (Version 1.3. 3). https://github.com/dwinter/mmod.

Western Pacific Fisheries Information Network (WPacFIN). Island Comparison. https://apps-pifsc.fisheries.noaa.gov/wpacfin/chart-island-comparison.php.

Yau, A. & Oram, R. (2016). Summary of 2013 and 2015 Main Hawaiian Islands Bottomfish Research Coordination Workshops. *Pacific Islands Fisheries Science Center administrative report*. H-16-04, 53 p. Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96818.

Yochum, N., Starr, R.M., & Wendt, D.E. (2011). Utilizing fishermen knowledge and expertise: Keys to success for collaborative fisheries research. *Fisheries* 36, 593-605.