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Observation to Action: A Stakeholder Driven Analysis and Assessment of a Data-Limited Fishery

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

OBSERVATION TO ACTION: A STAKEHOLDER DRIVEN ANALYSIS AND ASSESSMENT OF A DATA-LIMITED FISHERY

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

EARTH SYSTEMS SCIENCE

by

Carissa L. Gervasi Bloom

To: Dean Michael R. Heithaus College of Arts, Sciences and Education

This dissertation, written by Carissa L. Gervasi Bloom, and entitled Observation to Action: A Stakeholder Driven Analysis and Assessment of a Data-Limited Fishery, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

Elizabeth Anderson

Mahadev Bhat

Alastair Harborne

Mandy Karnauskas

Jennifer Rehage, Major Professor

Date of Defense: March 10, 2022

The dissertation of Carissa L. Gervasi Bloom is approved.

 Dean Michael R. Heithaus College of Arts, Sciences and Education

Andrés G. Gil Vice President for Research and Economic Development and Dean of the University Graduate School

Florida International University, 2022

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DEDICATION

To my incredibly supportive husband Jeff, without whom this dissertation may not have been finished. And to my parents Dan and Lynn, who worked hard every day so that I could pursue my dreams.

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This dissertation research would not have been possible without the support and encouragement of my advisor Jennifer Rehage. Jenn supported my decision to change research projects and pursue a path more in line with my career goals. She's pushed me to do things beyond the limits of what I thought I was capable of and for that I will forever be grateful. I want to thank Ross Boucek for bringing the concerns of stakeholders in the Florida Keys to our lab's attention, sparking my dissertation project. I especially want to thank the many Florida Keys fishing guides and anglers without whom this research would not have been possible. Specifically, Nathaniel Linville and Doug Kilpatrick went above and beyond to support this project and provide invaluable advice. Many thanks go to the members of the Lower Keys Guides Association and the Florida Keys Fishing Guides Association. This research was entirely stakeholder driven, and I am so grateful that I had the opportunity to work with such a fantastic and dedicated group of anglers. I especially want to thank captains Doug Kilpatrick, Nick LaBadie, Steve Lamp, Zach Routman, Diego Rouylle, and Justin Rousey, fishing guides who volunteered their time and resources to help me tag fish. Their efforts are incredibly appreciated. I also appreciate the many other anglers who provided their knowledge and expertise via interviews and who assisted with sample collection.

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OBSERVATION TO ACTION: A STAKEHOLDER DRIVEN ANALYSIS AND ASSESSMENT OF A DATA-LIMITED FISHERY

ABSTRACT OF THE DISSERTATION

by

Carissa L. Gervasi Bloom

Florida International University, 2022

Miami, Florida

Professor Jennifer Rehage, Major Professor

Translational ecology defines a collaborative effort among scientists and stakeholders with the goal of rapidly translating environmental problems into action. This approach can be applied in a fisheries management context when information needed to inform regulations is unavailable, yet conservation concerns exist. My dissertation research uses a translational ecology framework to assess the stock status and develop research priorities for the Crevalle Jack (*Caranx hippos*), an unregulated and data-poor fish species, by collaborating with recreational fishing guides in the Florida Keys, U.S.A. In chapter II, I used interview data that compiled veteran fishing guide knowledge to develop hypotheses about Crevalle Jack stock status that I then tested using existing fisheries-dependent datasets. The results of this chapter revealed that Crevalle Jack populations in the Florida Keys appear to be in decline since at least the 1990s, that the decline has been gradual, and that Crevalle Jack are seasonal residents, inhabiting the Florida Keys mainly in the winter months. For chapters III and IV I used two complementary techniques to describe the daily, seasonal, and lifetime movement and migration patterns of Crevalle Jack in Florida and the northern Gulf of Mexico. The

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DECLARATION STATEMENT

I, Carissa L. Gervasi Bloom, declare that the dissertation entitled Observation to Action: A Stakeholder Driven Analysis and Assessment of a Data-Limited Fishery is the result of my original research work, and it has been written by myself under the supervision of my advisor, Jennifer Rehage. Reference to the literature, and acknowledgement of collaborative research and discussions are made, and appropriate credit has been given within this dissertation. I confirm that this work has not been submitted for any other degree qualification.

CHAPTER I

GENERAL INTRODUCTION

Ecosystems provide fundamental life-support services that are necessary for human survival (Daily et al., 1997), and these services depend upon the maintenance of ecosystem structure and function (IPBES, 2019; Truchy et al., 2015). Currently, global ecosystem services are threatened as climate change and other anthropogenic disturbances result in unprecedented changes across ecosystems (Chambers et al., 2019; Ellis et al., 2021; IPBES, 2018; IPCC, 2014). These changes have been shown to alter and degrade ecosystem structure and function, leading to a host of critical conservation issues that need to be proactively addressed (Chapin, 2017; Ingrisch and Bahn, 2018). However, ecology remains predominantly a reactive field, with conservation practice occurring piecemeal and differing across ecological systems (Brooks et al., 2006; Cook et al., 2014; Crotty et al., 2019; Sutherland et al., 2011). In this era of global anthropogenic and climatic changes, new methods of proactive environmental planning and management are necessary to ensure sustainable use and conservation of natural resources (Lipsman, 2019).

Recreational fisheries are one example of an important ecosystem service that would greatly benefit from improved management. Recreational fishing is defined as the fishing of aquatic animals that are not generally sold or traded on markets and do not constitute an individual's primary resource to meet basic nutritional needs (FAO, 2012). Approximately one in ten people fish recreationally in developed countries (Arlinghaus et al., 2015), enjoying many benefits ranging from supplemental dietary protein (Cooke et al., 2018) to an increase in quality of life (Arlinghaus et al., 2002). Recreational fisheries contribute substantially to many regional economies and job markets. In the United States alone, saltwater recreational fishing supports 472,000 jobs, and contributes \$39 billion to

the GDP (NMFS, 2018). These fisheries are also vital to coastal conservation because not only do they create revenue for resource management, but they also connect society with nature, increasing the public's awareness of environmental processes (Arlinghaus et al., 2019; Griffiths et al., 2017). Although recreational fisheries provide many benefits to individuals and communities, they can also have substantial impacts on wild fish populations (Cooke and Cowx, 2004; Lewin et al., 2006). Furthermore, recreational fisheries are challenging to manage due to the diffuse nature of fishing effort and high incidence of unreported and unregulated fishing, which makes data collection difficult (Arlinghaus et al., 2016). Many recreational fisheries have no quotas or limits on angler entry to the fishery, so it is difficult to accurately determine effects on fish stocks and ecosystems. Angler behavior also plays an important role, as recreational fisheries are socio-ecological systems. Anglers alter their behavior in response to fish availability, and their behavior, in turn, impacts fish stocks (Hunt et al., 2013).

Traditional fisheries management uses stock assessments to set fishing quotas and limits (Gulland, 1983). However, these traditional assessments require extensive timeseries data of catch and effort, knowledge of the biology and ecology of the species of interest, and information about angler behavior, all of which is typically lacking for recreational species (Arlinghaus et al., 2019). Due to the difficulties associated with data collection and assessment, stock assessments for recreationally targeted species are often not conducted or are based on insufficient data (Griffiths and Fay, 2015; Holder et al., 2020). Holder et al. (2020) presented a detailed list of pressing issues currently hindering effective recreational fisheries management that need to be pro-actively addressed. One main issue the authors identified was the fact that most recreational fisheries are data-

poor, meaning there is either a lack of historical baseline data (Rick and Lockwood, 2013), or a lack of sufficient information to conduct stock assessments (Pilling et al., 2008). Furthermore, stock assessments for species targeted by both commercial and recreational anglers are often only based on commercial landings data, ignoring effects by the recreational sector. How to assess the status of these data-poor fisheries and develop effective management plans is a critical question.

In a 2010 editorial in Science, William Schlesinger coined the term "translational ecology" which is a concept he used to define a collaborative effort between scientists and stakeholders (i.e., resource users) with the goal of rapidly translating scientific results into action (Schlesinger, 2010). Schlesinger argued that too often scientists fail to share their research with the public and policy-makers, which means policy decisions are often made without the best available scientific information. Since Schlesinger's editorial, many prominent ecologists have recognized the importance of translational ecology to modern society, and the journal Frontiers in Ecology and the Environment even published a special issue on the topic in 2017 (volume 15, issue 10). Beyond opportunistic applied research, translational ecology deliberately addresses issues that are important to resource managers and decision makers, and is essentially scientific research conducted to address a specific management need (Enquist et al., 2017). In today's world of anthropogenic global change and urgent ecological crises, clear pathways for translating science to action are more important than ever (Chapin, 2017). Although the term "translational ecology" is recent, it stems from the much older concepts of translational sociology, which describes collaborative research aimed at solving realworld problems (Callon, 1986). Examples of scientists, policymakers, stakeholders, and

the general public working in multidisciplinary teams to tackle applied issues are abundant in the literature across many disciplines (e.g., Picou 2009; Wethington 2015; Eisenhauer et al. 2021). However, the application of translational ecology has thus far been limited in environmental research (Adler, 2020; Crotty et al., 2019). Translational ecology has the potential to help tackle pressing issues facing recreational fisheries management, such as the assessment and management of data-poor fisheries.

In the United States, nearly 60% of fish stocks are considered data-poor (Newman et al., 2015). This number is even higher in biodiverse areas like the southeastern U.S., where it is estimated that over 75% of stocks are data-poor (Berkson and Thorson, 2015; Newman et al., 2015). This high percentage of data-poor stocks is especially alarming considering the high economic value of commercial and recreational fisheries in the region. Marine fisheries are particularly vital to the state of Florida. In 2011, Florida saltwater recreational anglers accounted for 27% of all U.S. saltwater anglers, the largest percentage of any state (USFWS and USCB, 2011). Additionally, commercial landings for Florida in 2019 were valued at about \$250 million (NMFS, 2021). Intense levels of fishing pressure and an abundance of data-poor and unregulated species in Florida have resulted in a pressing need for alternative approaches to data collection and fisheries management.

My dissertation research uses a translational ecology approach to specifically address an ecological concern expressed by recreational fishing guides in the Florida Keys. In recent years, fishing guides have observed an alarming decline in catch rates of the Crevalle Jack (*Caranx hippos*), a popular sportfish in the region. The Crevalle Jack is a large marine fish native to the eastern and western coasts of the Atlantic Ocean, the

Gulf of Mexico, and the Mediterranean Sea (Smith-Vaniz and Carpenter, 2007). In the western Atlantic, the species is found from Nova Scotia to Uruguay, and is targeted by both commercial and recreational fisheries mainly in the southeastern U.S. (Kwei, 1978). Crevalle Jack are also large, predatory fish that play important ecological roles in coastal communities (Douglass et al., 2018; Rudnick et al., 2005). Despite their economic and ecological importance, Crevalle Jack are currently unregulated in every coastal U.S. state within the species' range. This means that little to no restrictions on fishing effort or harvest exist, and that trends in catch and abundance over time are not being monitored. Additionally, little is known about the species biology or ecology (McBride and McKown, 2000). The unregulated and data-poor status of the Crevalle Jack makes traditional stock assessment and management difficult. The translational ecology approach outlined in my dissertation is ideally suited to studying the status and trends of such a species.

Specifically, my dissertation depicts a collaborative research effort between scientists and stakeholders to assess the status and trends of the Crevalle Jack fishery in south Florida, fill in critical knowledge gaps regarding the ecology of the species, and present suggestions for management and future research priorities. In Chapter II, I developed a framework for applying the concepts of translational ecology to recreational fisheries management that begins with stakeholder knowledge. Veteran anglers and recreational fishing guides have an in-depth knowledge of the environments in which they fish, and a vested interest in conservation, making them exceptional translational ecology partners (Adkins, 2020; Kroloff et al., 2019; Santos et al., 2017; Silvano and Valbo-Jørgensen, 2008). By routinely and actively listening to angler concerns, scientists

can quickly identify emerging environmental issues, and therefore prioritize research to address pressing needs. Angler knowledge can also be used to develop hypotheses about the conservation concern, especially in situations where little prior knowledge exists (Silvano and Valbo-Jørgensen, 2008). In this chapter, I collected angler knowledge via in-depth interviews and used the interview data to develop hypotheses concerning Crevalle Jack status and trends in the Florida Keys. Testing these hypotheses with existing long-term data provided confidence in observed patterns and highlighted critical future research needs.

Chapter II revealed a major gap in knowledge of Crevalle Jack ecology important for managing the species. This gap concerned Crevalle Jack movement behavior and population connectivity. When management actions do not match the spatial distribution of a species, it can have severe consequences, leading to overfishing and localized depletion (Berger et al., 2021; Ying et al., 2011). Knowledge of movement and migration patterns and population connectivity of fishes is therefore critical. Chapters III and IV aimed to address this knowledge gap by using two complementary methods, otolith microchemistry and acoustic telemetry, to examine the daily, seasonal, and lifetime movements and migrations of Crevalle Jack. Migratory fishes have always been difficult to study in the wild due to their complex movement patterns and irregular distribution (Griffin et al., 2018; Miles et al., 2018). However, recent advances in technology have increased our ability to monitor fish migration patterns and habitat use, examine what drives movement, and assess connectivity among populations. Otoliths are hard calcium carbonate structures found directly behind the brain in all bony fishes. These structures aid in balance and hearing, and because they grow as a fish grows, certain trace elements

and isotopes are incorporated in proportion with ambient water concentrations. If a fish resides in a certain body of water for a portion of its life, the chemical signature of that waterbody will be retained in the section of the otolith corresponding with that time in the fish's life. Because of these attributes, otoliths have often been used in fisheries science to reconstruct environmental histories (Campana, 1999; Walther and Limburg, 2012). Otolith chemistry can reveal individual movement history across lifetimes but cannot be used to determine detailed intra-annual movement patterns or exact locations where fish migrate to, feed, and spawn. For this reason, I additionally used acoustic telemetry and existing networks of acoustic receivers to passively track the movements and migrations of tagged individuals. The information gleaned from these chapters will give managers important information about Crevalle Jack movement and migration patterns that can help determine population connectivity and determine which spatial management actions will be most appropriate for this species.

In, chapter V, I compiled the information gleaned from chapters II-IV to conduct a data-limited stock assessment for Crevalle Jack in Florida and provide management recommendations. Fisheries management currently relies on stock assessments, and specifically estimated management reference points (i.e., exploitation and stock size benchmarks), to set targets and limits on both commercial and recreational fisheries (Caddy and Mahon, 1995; Gulland, 1983). However, traditional stock assessment models require more data than are available for data-limited fisheries (Dowling et al., 2015). In this chapter, I outlined a stock assessment approach that uses angler local ecological knowledge (Anadón et al., 2009) combined with a series of data-limited assessment tools to provide an initial stock assessment for the Crevalle Jack. Finally, in chapter VI I

discuss the implications of my research for the Crevalle Jack fishery and recreational fisheries management in general. I conclude this chapter with future research directions that will continue to improve recreational fisheries management and conservation in the South Florida region and beyond.

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CHAPTER II

BOTTOM-UP CONSERVATION: USING TRANSLATIONAL ECOLOGY TO INFORM CONSERVATION PRIORITIES FOR A RECREATIONAL FISHERY

Abstract: Translational ecology defines a collaborative effort among scientists and stakeholders to rapidly translate environmental problems into action. This approach can be applied in a fisheries management context when information needed to inform regulations is unavailable, yet conservation concerns exist. Our research uses a translational ecology framework to assess the stock status and develop research priorities for the Crevalle Jack (*Caranx hippos*) in the Florida Keys, U.S.A., a currently unregulated species. Interview data that compiled expert fishing guide knowledge were used to develop hypotheses tested using existing fisheries-dependent datasets to check for agreement among sources and assess the consistency of observed patterns. Six hypotheses were developed concerning the status and trends of the Crevalle Jack population in the Florida Keys, and four of these hypotheses received clear support, with agreement between guide observations and one or more of the fisheries-dependent datasets. The results of our study outline an effective translational ecology approach for recreational fisheries management designed to rapidly recognize potential management needs as identified by fishing guides, which allows for actionable science and proactive management.
1. Introduction

In today's world of anthropogenic global change and urgent ecological crises, clear pathways for actionable science are more important than ever (Chapin, 2017). Translational ecology (TE) is a developing field aimed at addressing such urgent ecological issues that stems from the broader concepts of translational sociology (Callon, 1986). TE describes collaborative efforts among scientists and stakeholders with the goal of rapidly translating environmental problems into action (Schlesinger, 2010), and TE frameworks have successfully been used to address conservation issues within various complex social-ecological systems (Angeoletto et al., 2019; Chen and Jin, 2019; Ward et al., 2020). For instance, Allison and Arnold (2018) highlight how TE has been used in the wind energy industry for decades to assess, avoid, and mitigate risks to wildlife. Yet, ecology remains predominantly a reactive field, with conservation practice occurring piecemeal and differing across ecological systems (Brooks et al., 2006; Cook et al., 2014; Crotty et al., 2019; Sutherland et al., 2011). Thus, the application of TE remains limited in key disciplines such as community ecology (Crotty et al., 2019) and environmental law (Adler, 2020).

One field that would greatly benefit from the application of TE is recreational fisheries management. Recreational fishing is one of the most popular leisure activities worldwide, with five times more recreational than commercial anglers, generating US \$190 billion in expenditures annually (Arlinghaus et al., 2019, 2015; The World Bank, 2012). Today's recreational anglers can contribute to a large proportion of total fisheries landings in certain areas (Arlinghaus et al., 2019; Coleman et al., 2004; Felizola Freire et al., 2020). Thus, recreational fishing can negatively impact fish populations and their

habitats through a myriad of direct and indirect means (Cooke and Cowx, 2004; Lewin et al., 2006; O'Toole et al., 2009; Post et al., 2002), including the interaction of anthropogenic and climatic factors (Townhill et al., 2019). Further, due to the rapid growth in popularity and efficiency of recreational fishing, the stock assessment process is struggling to keep pace with evaluating fishery status, necessitating more rapid interim assessments and management actions. Translational ecology has the potential to help overcome many challenges currently hindering effective recreational fisheries management, such as assessment of data-poor fisheries (i.e., fisheries with insufficient information for estimating relative stock status and appropriate reference points), where most fishing effort is unreported, landings data are not available (i.e., for catch and release), and fisheries-independent monitoring is absent (Holder et al., 2020; Lester et al., 2003).

Our study aimed to apply a rapid, low-cost TE approach for assessing the stock status and developing research priorities for an unregulated and data-poor recreational fishery species (Figure 1). Recreational fishing guide knowledge was used to generate six testable hypotheses concerning the stock status of the Crevalle Jack (*Caranx hippos*) in the Florida Keys. This species is highly valued by many recreational fishing guides and is an important predator in coastal environments (Kwei, 1978; Saloman and Naughton, 1984). Hypotheses were subsequently tested using fisheries-dependent time series (including commercial landings and recreational surveys). TE methods have been used to develop hypotheses concerning marine resources in the context of small-scale artisanal fisheries (Aswani and Hamilton, 2004; Cardoso da Silva et al., 2020; Poizat and Baran, 1997; Silvano and Valbo-Jørgensen, 2008). However, to our knowledge, such a

collaborative TE approach to hypothesis generation has yet to be applied to a large-scale recreational fishery. The research outlined herein entails the hypothesis generation and testing component (Panel A in Figure 1) of our broader TE framework for Crevalle Jack conservation, which we are confident will serve as a model for the use of TE in the coproduction of fisheries science with stakeholders, bridging the science to management gap.

2. Methods

2.1 Study species

The Crevalle Jack was chosen as a study species for this research because it is a popular recreational fishery species throughout Florida but is currently unregulated and data-poor. In recent years, reports from recreational fishing guides in the Florida Keys suggest a decline in Crevalle Jack catches (Lower Keys Guides Association, personal communication, 2018), indicating management action may be warranted to conserve the population. Our translational ecology approach is ideally suited to studying the status and trends of such a species.

The Crevalle Jack is a large marine fish found throughout the tropical and temperate waters of the North Atlantic, from Nova Scotia to Uruguay in the west Atlantic and Portugal to Angola in the east Atlantic (Smith-Vaniz and Carpenter 2007). Crevalle Jack grow rapidly, reaching about 200 mm FL within one year (Snelson 1992). Length at 50% maturity for Crevalle Jack in the Caribbean is 636 mm FL (Caiafa et al., 2011), and maximum size throughout the species range often meets or exceeds 22.7 kg (50 lbs.; Smith-Vaniz and Carpenter 2007). Crevalle Jack spawn in tropical offshore waters in the

spring/summer (Heyman and Kjerfve, 2008), and larvae are distributed via ocean currents throughout the Gulf of Mexico and Atlantic coast (Berry, 1959; Ditty et al., 2004). Juveniles are known to occur in inshore and estuarine habitats (Berry 1959; McBride and McKown 2000), while mature adults are found in various habitats, including coastal waters, canals, and offshore reefs (Smith-Vaniz and Carpenter, 2007). A voracious carnivore, the Crevalle Jack is a major predator of small schooling fishes in coastal areas (Saloman and Naughton, 1984), and it is caught in both commercial and recreational fisheries (Kwei, 1978).

Though considered poor quality as a food fish, Crevalle Jack are valued by recreational anglers for their strength, speed, and voracity and are considered a "superb light tackle species" by the International Game Fish Association (IGFA 2006). Throughout Gulf of Mexico coastal waters, Crevalle Jack was the $10th$ most popular fishery species in 2017, with about 2.4 million lbs. (1089 metric tons) landed by recreational anglers and 423 000 lbs. (192 metric tons) landed by the commercial fishery (NMFS 2018). In Everglades National Park, where recreational fishing is a key economic activity (an estimated one in five Florida recreational anglers fish in the Everglades region; Fedler 2009), Crevalle Jack is the second most captured species behind only Spotted Seatrout (*Cynoscion nebulosus*), with 462 288 fish caught according to dockside angler surveys between 1980 and 2019 (NPS 2015). Recreational fishing guides often refer to Crevalle Jack as "trip savers" on guided trips when other targeted species are unobtainable.

Despite its importance to Florida's commercial and recreational fisheries and its role as a predator in coastal environments, the Crevalle Jack is currently an unregulated

species, meaning there are no specific regulations regarding size limits, gear restrictions, bag limits, or closed seasons (FWC 2021b). In Florida, a default bag limit for recreational species of two fish or 100 lbs. per person, per day (whichever is greater) applies to all unregulated species. Due to its unregulated status, little research has been done to assess Crevalle Jack life history, track abundance patterns, or determine mortality rates (McBride and Mckown 2000). Reports from Florida Keys fishing guides of a decline in Crevalle Jack catch rates may indicate a decline in abundance. If so, management efforts may need to be enacted to restore and ensure sustainable catch for the population in Florida (and potentially elsewhere in the U.S., where it remains unregulated in all 18 coastal states where the species occurs). Thus, our study has the potential to inform management throughout a large portion of the species range. However, though Crevalle Jack occur in the fishery throughout Florida and in other states, this study focused solely on the Florida Keys where our fishing guide collaborators observed a decline.

2.2 Hypothesis generation

Translational ecology comprises a diverse spectrum of approaches for tackling various research questions (Lawson et al., 2017). One such approach is local ecological knowledge (LEK), defined as the often place-based knowledge, beliefs, and practices concerning the natural environment that individuals or groups of people gain via observations, practical experience, or community dialogue (Anadón et al. 2009). To assess guide perceptions of Crevalle Jack population dynamics, key informant interviews with knowledgeable Florida Keys fishing guides were conducted between January and March 2019 (Figure 2a). Key informant interviews have become a cornerstone technique

for extracting local ecological knowledge and involve in-depth interviews with a nonrandom group of people who demonstrate expert knowledge about a particular topic gained via experience, participation, and/or position (e.g., Dongol and Heinen, 2012; Heinen and Shrestha-Acharya, 2011). Key informant interviews have been used successfully to study Bonefish (*Albula vulpes*) populations in South Florida for example, and the authors were able to identify periods of population decline, spatial patterns in decline, and the most likely factors contributing to the decline (Kroloff et al., 2019; Santos et al., 2019).

Saltwater recreational fishing guides in South Florida are typically individual, small business owners who have either a charter captain or charter boat license issued to them by the Florida Fish and Wildlife Conservation Commission (FWC). This license allows them to carry paying customers for the purpose of taking or possessing saltwater fish or organisms. In the Florida Keys, charter operations are a large component of the tourism industry. In 2012, Florida Keys fishing guides had a total economic impact of over \$111 million (Fedler, 2013). Only guides who reported spending a minimum of 100 days/year on Florida water and regularly guiding for at least 5 years were interviewed for this study. Interviewees were selected using the "snowball" method - i.e., word-of-mouth referrals by other guides and/or guide associations (Atkinson and Flint, 2001). By using a snowball sampling approach, we identified as many key informants as possible, focusing on charter captains with a lot of experience fishing in the Florida Keys. We interviewed everyone who was recommended to us as having expert knowledge of inshore fisheries, including Crevalle Jack, and was willing to be interviewed, for a total sample size of 18 guides. In key informant studies, saturation is typically used to determine appropriate

sample size. Hennink et al. (2017) examined 25 in-depth interviews and determined that code saturation was reached after nine interviews, where the range of thematic issues was identified. Similarly, Guest et al. (2006) examined 60 interviews and found that saturation occurred within 12 interviews. Muellmann et al. (2021) observed no change in results with an increase from 4-6 key informants to 12-15. Based on this literature we deemed 18 key informants a suitable sample size for our study.

From our interviews, we determined that guides typically operate within two broad regions of the Florida Keys, either from Marathon south to the Marquesas or the Florida Keys region north of Marathon and including Florida Bay and Biscayne Bay. So, we split interviewees into "Lower Keys" guides (Marathon and points south) and "Upper Keys" guides (north of Marathon). A semi-structured interview format was used with all key informants, and the interviews were recorded on an audio recording device with the guide's permission. Guides were asked four open-ended questions to direct conversations: (1) what is your general background and experience fishing and guiding? (2) what do you know about Crevalle Jack? (3) have you noticed any changes in Crevalle Jack fishing over time? and (4) is fishing for Crevalle Jack important to you? More specific follow-up questions were asked if guides did not provide specific answers during the interview or if clarification was warranted (Figure S1). This semi-structured interview format allowed us to gain as much information from guides as possible while ensuring specific questions were addressed (e.g., when did you start noticing a change in your Crevalle Jack catches?) Audio data were later transcribed, and common topics were compiled and developed into testable hypotheses about where Crevalle Jack are in decline, when the decline began, and what factors might be responsible for the decline.

Topics were developed into hypotheses if more than 50% of guides interviewed agreed about a particular observation. This 50% cutoff was used because we aimed to develop one hypothesis per topic rather than employing a multiple hypothesis framework. All protocols for human subject research were approved by Florida International University's Institutional Review Board and all participants gave consent before being interviewed.

2.3 Fisheries-dependent datasets

Since the Crevalle Jack is an unregulated species and the species lacks a formal stock assessment process, abundance trends in South Florida are unknown. Furthermore, there are no existing fisheries-independent surveys in the region that frequently encounter Crevalle Jack, so our hypotheses were tested using existing fisheries-dependent datasets (Table 1). The three datasets used for hypothesis testing were (1) the NOAA Marine Recreational Information Program (MRIP) survey (NOAA 2021), (2) the Everglades National Park (ENP) creel survey (NPS 2015), and (3) the state of Florida commercial landings data (FWC 2021a). Each dataset provided independent information that was appropriate for addressing one or more of the LEK-derived hypotheses. For the MRIP and ENP surveys, Crevalle Jack catch-per-unit effort (CPUE) time series were standardized using generalized linear models (GLMs) to generate estimated annual indices of abundance that could be used to test hypotheses about changes in abundance over time. Commercial landings data and records of recreational landings were used to assess the extent of fishing harvest (i.e., a potential cause of decline) in the Florida Keys region, while sizes of landed fish from the MRIP dataset were used to assess changes in fish size. All datasets were subset to the Florida Keys region such that the data would be

reflective of where the interviewed guides regularly fish and could be used to test the LEK-derived hypotheses (Figure 2).

A Florida saltwater fishing license is required to land any saltwater species in Florida, in state or federal waters. Recreational licenses (including charter captain or charter boat licenses) do not allow the commercialization of catch. Harvest of more than 100 lbs. or two fish (whichever is greater) is considered commercial quantity and requires a commercial license (FWC 2021b). Recreational fisheries throughout the state of Florida are surveyed by the Marine Recreational Information Program (MRIP) conducted by NOAA Fisheries (formerly the Marine Recreational Fisheries Statistics Survey, MRFSS). This survey has monitored shore-based, private, and charter fishing modes since 1981, and recently underwent a substantial modification and peer review in 2018 following a three-year transition period (Papacostas and Foster, 2018). MRIP data have been used to assess the status and trends and develop standardized indices of abundance to inform stock assessments for several fish species throughout the Western Atlantic and Gulf of Mexico, including Sailfish (*Istiophorus platypterus*), Vermilion Snapper (*Rhomboplites aurorubens*), Red Grouper (*Epinephelus morio*), Shortfin Mako (*Isurus oxyrinchus*), and many others (Babcock, 2013; Ortiz and Brown, 2002; Rios, 2015; Sagarese, 2019).

Everglades National Park (ENP) was established in 1947 and voluntary dockside interviews have been conducted within park boundaries since 1958 (Davis and Thue, 1979; Schmidt et al., 2002). Commercial fishing has been prohibited within the park since 1985 (Osborne et al., 2006), but recreational fishing is allowed and bag and size limits follow freshwater and saltwater recreational fishing regulations established by FWC. A sample of recreational anglers are interviewed by ENP personnel upon arrival

post-fishing at either of two popular public ramps in the park. Recorded data include trip origin, area fished, number of anglers, hours fished, numbers of fish caught and released by species, etc. Creel survey data have been used to examine the impacts of coastal protected areas on recreational world records (Bohnsack, 2011), to monitor the recovery of an endangered species (Smalltooth Sawfish, *Pristis pectinata*, Carlson et al. 2007), and to track trends in abundance for other data-poor species such as Bonefish (*Albula vulpes*, Santos et al. 2017) and Atlantic Goliath Grouper (*Epinephelus itajara*, Cass-Calay and Schmidt 2009).

Commercial landings data for the state of Florida are collected by FWC. These fisheries include all species that are harvested for profit, including those sold for human consumption, aquariums, and medical use. Florida began a mandatory trip ticket program in 1984, and the first official year of landings is 1986. Commercial landings data have been used for several applications. These applications include the development of regulations to prevent overexploitation of shark species in Florida (Brown, 1999), informing stock assessment of important species such as the Caribbean Spiny Lobster (*Panulirus argus*, SEDAR 2010) and Red Grouper (Wrege and Orhun 2019), and evaluating the sustainability of coral reef fisheries in the Florida Keys (McClenachan and Kittinger, 2013).

2.4 Development of abundance indices

Catch-per-unit-effort (CPUE) is often assumed to be proportional to stock abundance and is therefore commonly used as a relative abundance index when fisheriesindependent data are unavailable (Maunder and Punt, 2004). However, many factors can

influence fisheries catch rates (e.g., spatial, temporal, or environmental variability). It is, therefore, necessary to standardize CPUE data to remove the influence of factors other than stock abundance before CPUE data can be used as an index of abundance (Maunder et al., 2006). Generalized linear models (GLMs; Nelder and Wedderburn 1972) are commonly used to standardize CPUE data (Maunder and Punt, 2004; Venables and Dichmont, 2004). The delta-lognormal GLM approach (Lo et al., 1992) has specifically been used to standardize CPUE for several species using the MRIP and ENP datasets (e.g., Carlson et al. 2007; Cass-Calay and Schmidt 2009; Cass-Calay 2012; Rios 2015; Sagarese 2019), and was thus used in this study. The delta-lognormal method combines separate GLM analyses on the positive trips (trips that captured the species of interest) and the proportion of positive trips (trips that captured the species of interest/total trips) to create a single index. Prior to model fitting, data exploration and filtering following the methods of Zuur et al. (2010) were conducted on all three datasets (MRIP, ENP, and commercial landings), including assessing the data for outliers, collinearity, zeroinflation, and balanced categorical covariates, and filtering the data as appropriate (see data filtering specifics below). The commercial landings dataset was deemed unsuitable for developing a standardized index of abundance because very few Crevalle Jack were captured on commercial trips in the Florida Keys (only 1% of trips captured Crevalle Jack). The commercial data were instead used to assess other hypotheses concerning fishing harvest (see hypothesis testing section below).

2.4.1 Data filtering

The MRIP data were subset to include only trips from Monroe County, which encompasses the Florida Keys (Figure 2b), and several categorical variables were constructed from the data prior to analysis. These included Year (1991-2019), Month (1- 12), Season (spring – March, April, May; summer – June, July, August; fall – September, October, November; and winter – December, January, February), Area fished (inshore – less than 10 miles from shore, or offshore – greater than 10 miles from shore), and Fishing mode (shore, charter, or private). Gear type was also recorded in the data, but since 97% of Monroe County trips used hook and line gear, the data were subset to only include hook and line trips. Party code was defined as a single trip and catches for every individual within the party were summed, such that in our analyses we were examining the trip catch for every trip in the data set. Since the party code was not recorded until 1991, the data were truncated so that only data from 1991 to 2019 were analyzed. Fishing effort for the MRIP data was defined as the number of people in the party who were interviewed multiplied by the reported hours fishing. Size information was available for a subset of landed Crevalle Jack, and fork lengths differed significantly between inshore $(M = 378$ mm, $SD = 151$ mm) and offshore $(M = 590$ mm, $SD = 184$ mm) trips. A Welch 2-sample t-test between inshore and offshore fish showed a significant difference in fish size between the two groups ($p < 0.0001$), suggesting that these areas capture different size classes of the population, matching the presumed life history in South Florida consisting of inshore recruitment and juvenile habitat use and offshore habitat use and reproduction by larger adults (Smith-Vaniz and Carpenter, 2007). Therefore, trips that occurred offshore were modeled separately from trips that occurred inshore, with

offshore trips used to assess abundance trends of large adult and subadult Crevalle Jack. In contrast, inshore trips were used to assess abundance trends of smaller juvenile Crevalle Jack. Length at 50% maturity for Crevalle Jack in the Caribbean is 636 mm FL (Caiafa et al., 2011), suggesting that the majority of inshore and even some of the offshore Crevalle Jack were likely immature.

The ENP angler data were analyzed for the period 1980 to 2019 because in 1980 the survey was expanded to include routine surveys at both Flamingo and Everglades City boat ramps, where anglers continue to be interviewed presently (Carlson and Osborne, 2013; Osborne et al., 2006; Schmidt et al., 2002). Categorical variables were also constructed from the ENP dataset and included Year (1980-2019), Month (1-12), Season (spring – Mar, Apr, May; summer – Jun, Jul, Aug; fall – Sep, Oct, Nov; and winter – Dec, Jan, Feb), and Area fished (6 fishing areas defined by Schmidt et al. 2002). The entire ENP region was analyzed since Upper Keys anglers typically fish throughout ENP coastal waters (Figure 2c), so we did not subset the data further.

2.4.2 Accounting for catchability

The use of CPUE as an index of abundance assumes that catchability for the species of interest is constant; however, with multispecies fisheries, different fishing tactics employed to target focal fish species can influence catchability. Anglers do report the primary and secondary species targeted on each trip in the MRIP data, but Crevalle Jack were rarely reported as the main species targeted (less than 1% of trips). This matched the guide perspectives captured from interviews, which described Crevalle Jack were more a species of opportunity and not as targeted as other species. Since Crevalle

Jack are often captured opportunistically, we wanted to ensure that we only included trips in our analysis that occurred in areas where Crevalle Jack were likely to be. Accounting for catchability in abundance models is regularly employed for species with low catch rates (Carlson et al., 2007). The MRIP data do not include specific fishing location information (e.g., habitat type), so we performed a hierarchical clustering analysis following the methods of Shertzer and Williams (2008) that clusters species based on how often they are captured together. We then assumed that any trip where a species in the Crevalle Jack cluster was captured was a trip that was also likely to capture Crevalle Jack (whether Crevalle Jack were captured or not). This allowed us to use the species composition of the catch as a proxy for habitat. To perform the clustering analysis, the data were formatted into a CPUE matrix with rows representing species and columns a combination of month, area, and mode of fishing, which are factors that may represent different fishing tactics and therefore influence catchability. Species were removed if they appeared in fewer than 1% of trips since rare species can distort inferred patterns (Koch, 1987; Mueter and Norcross, 2000). The data were transformed using a $4th$ root transformation, and a matrix of dissimilarities between species was computed with the Bray-Curtis measure of distance (Bray and Curtis, 1957). Hierarchical cluster analysis was then used to partition species into groups. Trips were removed if they did not catch at least one of the species in the cluster with Crevalle Jack, and trips where no fish were caught were also excluded. Clustering and subsequent data filtering and model fitting were performed separately for offshore and inshore MRIP trips because smaller, inshore Crevalle Jack associated with different species than larger, offshore Crevalle Jack, and trends in abundance over time may differ between the groups. Since Crevalle Jack were

the second most captured species in the ENP dataset and the park encompasses a relatively small inshore only area, there was no need to employ a clustering analysis to account for catchability with the ENP data.

2.4.3 Statistical analyses

For both the MRIP and ENP data, a logit link function with a binomial error distribution was fitted to the proportion of positive trips (i.e., presence or absence of Crevalle Jack in a trip) following the delta-lognormal model approach. For the positive trips (i), total catch was defined as the sum of landed and released Crevalle Jack and the natural log of catch-per-unit effort $(lnCPUE_i)$ was used as the response variable, where:

(1)
$$
\ln CPUE_i = \ln((total catch_i) / (number of angles_i * hours fished_i)),
$$

and a log link function with a lognormal error distribution was fitted to the data. A backward stepwise regression procedure was used to determine the set of fixed factors included in the final models among Year, Season, and Fishing mode for the MRIP data (offshore and inshore) and Year, Season, and Area fished for the ENP data. Deviance tables were constructed for each GLM to determine the percent of total reduction in deviance $(\% \text{rd}_t)$ due to the addition of each factor:

(2) $% \text{rd}_t = 100 * (\text{rd}_f) / (\text{rd}_{nm} - \text{rd}_{fm}),$

where rd_f is residual deviance attributed to the addition of a given factor, rd_{nm} is the residual deviance of the null model, and rd_{fm} is the residual deviance of the full model (Cass-Calay and Schmidt, 2009). Factors were selected for inclusion in final models if the addition of the factor explained more than 5% of the deviance and the χ^2 test was significant ($p \leq 0.05$). However, factors Year and Season were kept in final models even if they explained less than 5% of the deviance because our goals were to assess both annual and seasonal differences in Crevalle Jack abundance.

For each model, CUSUM plots were used to assess breakpoints in the time series. CUSUM control methods were developed by Page (1954) for industrial quality control applications and are designed to detect persistent changes in observed processes. Recently, the method has been used in ecological applications to assess underlying features of time series data and for environmental modeling (Keatley and Hudson, 2012; Mac Nally and Hart, 1997; Manly and Mackenzie, 2000; Regier et al., 2019). The method entails a cumulative sum of the deviation of observations from a global mean, and the slope and direction of the line in a CUSUM plot enables identification of periods that are above average (positive slope), below average (negative slope), or are not changing (no slope) (Hawkins and Olwell, 1998; Scandol, 2003). A change from a positive slope to a negative slope (dome shape) would indicate a decline in the index over time. All statistical analyses were performed in R version 3.6 (R Core Team, 2019).

2.5 Hypothesis testing

Each LEK-derived hypothesis (Table 2) was tested using one or more of the fisheries-dependent datasets (Commercial, MRIP, and ENP). Comparisons between the LEK data and fisheries-dependent data were possible because expert interviewee duration of experience was on the same time scale as the examined catch data (both covering approximately the 1980-2019 period). Standardized indices of abundance derived from the MRIP and ENP datasets were used to assess whether Crevalle Jack populations in the Florida Keys have declined (Hypotheses 1, 2). Plots of cumulative sums of z-scored indices (CUSUM) were used to visually assess any breakpoints in the time series and determine when the decline began (Hypothesis 3). To assess whether fishing harvest (commercial and/or recreational harvest) might have contributed to the Crevalle Jack decline (Hypothesis 4), total commercial landings over time for all gear types combined were assessed for both the Lower Florida Keys and the Upper Florida Keys for the period of record from 1986 to 2019 as a proxy of fishing mortality due to commercial harvest. As a proxy of fishing mortality due to recreational harvest, the proportion of Crevalle Jack landed (kept) by recreational anglers in ENP and MRIP data were calculated annually for 1980-2019 (ENP) and 1991-2019 (MRIP). We assessed whether the decline was specific to a certain size/age class of Crevalle Jack (Hypothesis 5) by creating separate indices of abundance for MRIP offshore and MRIP inshore trips, and the addition of Season as a fixed factor in our GLM models allowed us to assess seasonality of Crevalle Jack abundance in the Florida Keys (Hypothesis 6). Hypotheses that received support from multiple data sources were considered highly likely, while hypotheses with no support from long-term datasets were considered as priorities for additional research.

3. Results

3.1 Guide local ecological knowledge

Recreational fishing guide interviewees ($n = 17$, all male participants) had been full-time guides in the Florida Keys between 5 and 49 years, with an average of 26 years of experience guiding. One additional angler interviewed was not a guide but had been fishing in the Florida Keys for 14 years and was considered an expert angler. Of these anglers (hereafter referred to as guides), 12 operated in the Lower Florida Keys (from Marathon south), and 6 operated in the Upper Florida Keys (north of Marathon including Florida Bay and Biscayne Bay; Figure 2a). All the guides interviewed at least occasionally fished for Crevalle Jack, and eight guides reported regularly targeting Crevalle Jack on guided trips. Five of these guides operated in the Lower Keys while three operated in the Upper Keys, so about half of the guides in each population regularly targeted Crevalle Jack. Of the 12 Lower Keys guides, 11 described a decline in Crevalle Jack catch over time while only three of the six Upper Keys guides noticed a decline. The remaining four guides (one from the Lower Keys and three from the Upper Keys) did not report any change in the Crevalle Jack population. Of the guides who did report a decline in catch, the average estimate for when the decline began was 2005, with a range from 1985 to 2014 (Figure 3a). There was a relationship between years angling and estimated year the interviewees perceived the decline began, with more seasoned guides typically noting an earlier decline than newer guides (linear regression $p < 0.05$; Figure 3b).

Guides who reported a decline described between a 30-100% decline in Crevalle Jack populations where they fish, with certain areas and size classes declining more so than others. For example, one guide estimated that catches had declined over 50% in

offshore areas, but less than 50% in inshore areas. Another guide observed a 90-100% decline in catches on the shallow water flats and about a 50% decline elsewhere. 10 of the 14 guides who reported a decline in Crevalle Jack catches also noticed a size decline, with fewer fish over 10 lbs. being observed. Most guides (13) agreed that Crevalle Jack in the Florida Keys are most abundant in the winter months and likely migrate out of the Keys region in spring or summer following changes in temperature and/or migrating bait.

Guides who observed a decline in Crevalle Jack catches were asked to speculate on the reasons for the decline (Figure 4). The most common explanation was a loss of prey, mentioned by 12 guides. Recreational and commercial harvest were the next most common explanations (7 and 6 guides, respectively), followed by poor water quality (5 guides) and increased predator abundance (4 guides). All the guides interviewed reported releasing at least 90% of the Crevalle Jack they captured while guiding or fishing recreationally. However, some reporting keeping a few a year to use as shark bait. When asked if they knew of anyone keeping Crevalle Jack for consumption or other purposes, most guides agreed that they rarely see the species brought into the docks. However, several guides mentioned that there might be populations of Florida residents who regularly capture Crevalle Jack for consumption.

All the guides expressed being pro-regulation of Crevalle Jack, and they all placed high quantitative and qualitative value on the species. Several guides referred to Crevalle Jack as "trip savers", because when more commonly targeted species like Bonefish or Permit were nowhere to be found, guides could typically count on fishing a school of Crevalle Jack to keep their customers happy. One guide specifically stated: "I probably make more money putting smiles on people's faces because the fight is 2-3

times better than any species of fish we have inshore." Another guide referred to Crevalle Jack in South Florida as the "bread and butter of the flats fishing industry".

3.2 Hypothesis generation

Collected key informant data were used to develop six hypotheses (Table 2). Hypothesis 1 was that Crevalle Jack populations in the Florida Keys have declined, which received the support of 14 of the 18 guides interviewed. Hypothesis 2 was that Crevalle Jack populations have declined more so in the Lower Florida Keys than in the Upper Florida Keys. This hypothesis was generated based on the observation that while 11 guides operating in the Lower Keys observed a decline in Crevalle Jack catch, only three guides operating in the Upper Keys noticed any sort of decline. Hypothesis 3 concerned the timing of the decline. Nine guides estimated that the decline began sometime after 2005, but there was no clear consensus among guides, with two guides estimating the decline began as early as the late 1980s to early 1990s and three guides pinpointing the late 1990s to early 2000s (Figure 3a). Hypothesis 4 was that fishing harvest (commercial and/or recreational) at least in part contributed to the Crevalle Jack decline. Either commercial harvest, recreational harvest, or both were mentioned by 12 guides (Figure 4). Hypothesis 5 suggests that the decline was size-selective, with larger fish having declined more than smaller fish. This hypothesis received support from 10 guides. The final hypothesis (Hypothesis 6) derived from fishing guide LEK was that Crevalle Jack are migratory with the highest abundances in the Florida Keys being observed in the winter months, an observation shared by 13 guides.

3.3 Hypothesis testing

One or more of the three fisheries-dependent datasets were used to test each of our six hypotheses. Filtered and cleaned MRIP data included 5 687 inshore trips and 2 330 offshore trips from 1991-2019 (29 years). Of these, Crevalle Jack were caught on 1 122 inshore trips (20%) and 496 offshore trips (21%). Based on model selection via backward stepwise regression and deviance tables, the final inshore model for both the proportion positive and positive trip GLMs included Year, Fishing mode, and Season as fixed factors (Tables S1, S2), whereas the final offshore model for both the proportion positive and positive trip GLMs included Year and Season as fixed factors (Tables S3, S4). The filtered and cleaned ENP database consisted of 192 728 trips occurring from 1980-2019 (40 years), with 85 849 of those trips capturing Crevalle Jack (45%). After stepwise regression and deviance table selection, the final model was the same for both the proportion positive and positive trip GLMs and included Year, Area, and Season as fixed factors (Tables S5, S6). The cleaned commercial landings data consisted of over one million total trips in Monroe County from 1986-2019. Crevalle Jack were landed on only 10 755 (\sim 1%) of those trips. Of the trips where Crevalle Jack were landed, 6 487 (60%) occurred in the Lower Keys (Tortugas, Key West, and Marathon regions), and 4 268 (40%) occurred in the Upper Keys (Everglades National Park and Miami regions; Levesque 2009). The most common gear type used on commercial trips where Crevalle Jack were landed was hook and line gear (48% of trips), followed by gillnets (10%), rod and reel (10%), and cast nets (6%). Most remaining trips were of unknown/other gear types (14%) with minor gear types comprising the remaining 12% of trips (including combinations of traps, nets, spears, etc.).

3.3.1 Hypothesis 1: Crevalle Jack populations in the Florida Keys have declined

Our first hypothesis was that Crevalle Jack populations in the Florida Keys have declined, which had the support of 78% of the guides interviewed. This hypothesis was tested using the MRIP and ENP standardized indices of abundance. Some evidence of a decline in CPUE over time was observed in the fisheries-dependent data, but only in certain regions. In the MRIP data, standardized CPUE for inshore trips (less than 10 miles from shore) remained relatively constant from 1991 to 2019, but standardized CPUE for offshore trips (greater than 10 miles from shore) declined steadily over the same period (Figs. 5a, c). A decline in the standardized abundance index was also apparent in ENP, though less pronounced than the MRIP offshore decline (Figure 6a). For the MRIP offshore data, the maximum standardized abundance of the time series (in fish per unit effort) was 0.47 in 1991, while the minimum was 0.01 in 2017, which represents a 98% decline. For the ENP data, the maximum standardized abundance was 0.39 in 1991 and the minimum was 0.11 in 2018, a 72% decline. CUSUM plots for the zscored MRIP offshore index and ENP index both show dome shapes indicative of declines in the time series starting around the early 1990s. Additionally, the negative slopes in the CUSUM plots reveal that abundance has been below the average of the time series almost every year since the early 2000s (Figs. 5b, d, 6b). The agreement among LEK, MRIP offshore, and ENP data lends support to this hypothesis.

3.3.2 Hypothesis 2: Populations have declined more in the Lower Keys than Upper Keys

Our second hypothesis was that populations have declined more so in the Lower Keys than the Upper Keys because most Lower Keys guides interviewed observed a decline (92%) while only 50% of Upper Keys guides observed a decline. We would expect that in regions where the population declined substantially, a higher proportion of guides would have noticed the decline, while in regions where the population decline was minimal, it would have been noticed by fewer guides. The MRIP dataset does not provide low enough resolution to assess differences in the Lower Keys vs. the Upper Keys, and we have no other information on Crevalle Jack abundance in the Lower Keys only. However, the ENP dataset mostly covers the Upper Keys region and is entirely inshore. A decline over time was apparent in the ENP data, though not as dramatic as the decline in the offshore MRIP data. Also, there is much more interannual variability in the ENP index, which could explain why some Upper Keys guides did not notice a decline. There was also no apparent decline in the MRIP inshore data. Generally, the Upper Keys guides reported mostly fishing inshore, while the Lower Keys guides reported fishing both inshore and offshore. Therefore, the discrepancy between the two guide groups may be more attributable to the habitats where they fish than the spatial domain where they fish. While fisheries-dependent data suggest declines in Crevalle Jack abundance in both regions, we do not have the spatial resolution in the data to assess differences in abundance between the Lower and Upper Keys, so our support for this hypothesis is limited.

3.3.3 Hypothesis 3: The decline started sometime after 2005

Our third hypothesis was that the decline began sometime after 2005, which was when 64% of guides started noticing fewer encounters with Crevalle Jack and fewer individuals when they were encountered (Figure 3a). One caveat of this hypothesis was that the interviewees who have been guiding the longest generally were the ones who reported the decline began the earliest (Figure 3b), suggesting that recollection as to when the decline began depended on fishing experience. Our hypothesis as to when the decline began may therefore be different had we interviewed guides with more or less fishing experience. However, the guides who reported noticing the decline after 2005 had a wide range of experience, with two of them guiding since the 1980s. This lends support to our hypothesis and suggests that something might have happened around 2005 that caused anglers to observe a change in Crevalle Jack catches. Both the MRIP offshore and ENP datasets showed a decline in standardized abundance after a peak in 1991. Only two guides reported the decline beginning during this period. However, although no dramatic change in abundance on or after 2005 was apparent in the data, both MRIP offshore and ENP CUSUM plots showed that Crevalle Jack abundance has been below average almost every year since the early 2000s (i.e., negative slopes, Figs. 5b, d, 6b), which approximately aligns with when most guides noticed the decline (Figure 3a). Both fisheries-dependent datasets revealed that there has been no sudden change in Crevalle Jack abundance at a particular point in time, but that the decline has instead been gradual. Guides also reported that the observed decline has been gradual and were unable to point to a particular event that prompted the decline.

3.3.4 Hypothesis 4: Fishing harvest in the Florida Keys is a contributor to the decline

Our fourth hypothesis was that fishing harvest in the Florida Keys region above the capacity of fish stock recovery contributed to the decline, based on 86% of guides suggesting either commercial or recreational fishing pressure as likely contributors. This hypothesis did not receive support from fisheries-dependent data (Commercial, MRIP, or ENP). Crevalle Jack commercial landings in the Upper Keys were relatively high from the mid-1990s to mid-2000s, but then dropped considerably and have been below 10 000 lbs. annually since 2006 (Figure 7a). In the Lower Keys, commercial landings were relatively high for a short period in the late 1980s but have since declined and been below 15 000 lbs. per year since 1990 (Figure 7b). In 1995, commercial entanglement nets were banned in the state of Florida (Smith et al., 2003), which could explain some of the relatively high landings early in the time series. In ENP, the most Crevalle Jack landed by recreational anglers in a year was 1 497 fish in 1984 (just prior to the ban on commercial fishing in ENP in 1985; Osborne et al. 2006), which accounted for 12% of the catch (the remaining 88% of captured Crevalle Jack were released). Since 1990, landed Crevalle Jack have only accounted for 5% or less of the total catch reported by recreational anglers (Figure 7c). Similarly, landed Crevalle Jack have accounted for less than 20% of reported catch in the MRIP dataset since 1991 (Figure 7d). Additionally, the proportion of landed Crevalle Jack in the MRIP data has declined slightly over time. Data showing low commercial landings and high release rates for recreationally captured fish do not support the suggestion by guides that fishing harvest in the Florida Keys has contributed to the decline in Crevalle Jack catch over time.

3.3.5 Hypothesis 5: Larger fish have declined more than smaller fish

Our fifth hypothesis was that larger fish have declined more so than smaller fish (observed by 71% of the guides who reported a decline in Crevalle Jack catches). Since Crevalle Jack captured in the offshore MRIP dataset were significantly larger than Crevalle Jack captured inshore, inshore fish could be considered a smaller, younger population than offshore fish. This observation aligns with the life history of the species, since juveniles typically inhabit estuarine nursery habitats before presumably migrating to more offshore adult habitats (Smith-Vaniz and Carpenter, 2007). Since a decline in CPUE over time was only observed for offshore trips, this lends evidence to the hypothesis that larger, older Crevalle Jack have declined in abundance more so than smaller, younger fish. However, a decline was also apparent in the ENP dataset, which consists of mostly inshore trips. Since the ENP data did not include size information for Crevalle Jack, it is unknown whether the decline observed in ENP was specific to larger fish, so this hypothesis may warrant additional research. Again, the MRIP offshore data showed a more dramatic decline over the time series than the ENP data, which lends some additional support to this hypothesis.

3.3.6 Hypothesis 6: Crevalle Jack are most abundant in the Keys in the winter

Our final hypothesis was that Crevalle Jack are migratory, with abundance in the Keys region being highest in the winter months, as observed by 72% of guides. This hypothesis was tested by including Season as a fixed factor in the MRIP and ENP standardization models. In the MRIP data, both the probability of encountering Crevalle Jack (proportion positive model) and the abundance of Crevalle Jack when caught

(positive trips model) were significantly higher in the winter than in the summer inshore (*p* < 0.001; Tables S1, S2). Offshore, both the probability of encountering Crevalle Jack and abundance when caught were significantly higher in the winter than in spring or summer ($p < 0.01$; Tables S3, S4). In the ENP data, the probability of encountering Crevalle Jack was significantly higher in the winter than in the summer $(p < 0.0001)$; Table S5), and the abundance of Crevalle Jack when caught was significantly higher in the winter than in the spring, summer, or fall $(p < 0.0001$; Table S6). These results support the hypothesis that Crevalle Jack are most abundant in the Florida Keys in the winter months and appear to display seasonal migration patterns.

4. Discussion

Translational ecology provides an intentional approach to collaborative, actionable science that can inform and improve decision-making for environmental conservation and management (Enquist et al., 2017). Although the terminology is recent, the concepts and ideas behind translational ecology are not new. In Michel Callon's seminal article on the "sociology of translation" published in 1986, he tells the story of scientists and scallop fishermen in France working together to find solutions to dwindling scallop populations (Callon, 1986). Other examples of collaborative research that includes scientists, stakeholders, policymakers, and consumers working in multidisciplinary teams to solve real-world problems appear across numerous disciplines (e.g., Picou 2009; Wethington 2015; Eisenhauer et al. 2021). In fisheries, stakeholder involvement and recognition of fisheries as coupled social-ecological systems are key principles of Ecosystem-Based Management (Long et al., 2015). Many countries are

actively working to shift environmental management to a more ecosystem-based approach, recognizing that environmental issues are often too complex and dynamic for conventional management to succeed (Long et al., 2015; O'Higgins et al., 2020). Translational approaches (including LEK and traditional ecological knowledge, or TEK) often provide vital insight when incorporated into Ecosystem-Based Management (Cinner and Aswani, 2007; Ruiz-Mallén and Corbera, 2013; Stori et al., 2019).

The use of TE in fisheries management is particularly well suited to partnerships with recreational fishing guides. In Florida, where saltwater recreational fishing is diverse and abundant, a 9.2 billion-dollar industry, and a vital aspect of the state's culture (FWC 2018; NMFS 2018), recreational fishing guides can be ideal key informants and translational ecology partners (Kroloff et al., 2019; Santos et al., 2017). Due to frequent interactions with fishes and their environments and a vested interest in fisheries conservation, fishing guide knowledge can be used as a low-cost monitoring program. Developing state or federal fisheries-independent surveys for every unregulated species is not feasible given budgetary and personnel constraints, and even regularly analyzing existing data to ensure stocks are sustainably harvested is beyond the scope of most fishery management programs (Harford and Carruthers, 2017; Sagarese et al., 2019). However, by working with the resource users/stakeholders to co-produce actionable science, scientists and managers can rapidly develop research priorities and effective management plans that can promote the sustainability of important fisheries resources.

The results of this study provide evidence of the utility of translational ecology to recreational fisheries management. Collaborating with experienced recreational fishing guides and accessing their local ecological knowledge via semi-structured interviews

allowed us to rapidly generate six testable hypotheses concerning the status and trends of the Crevalle Jack fishery in the Florida Keys. By subsequently analyzing existing fisheries-dependent data, we provided multiple lines of evidence to support acceptance of four of these hypotheses, revealing that Crevalle Jack populations in the Florida Keys appear to be in decline, and that the decline has been gradual with below-average abundance since the early to mid-2000s. Large, adult fish mainly captured offshore appear to have declined the most, while a less dramatic decline was also observed in the Everglades National Park region. Crevalle Jack also appeared to be seasonal residents in the Florida Keys, with the highest abundances observed in the winter months. Unsupported hypotheses helped identify several priorities for future research. These include determining the lifetime movement and migration patterns of the Crevalle Jack and examining possible factors that contributed to its decline, such as commercial and recreational fishing harvest in other areas throughout the population range.

4.1 Biases in LEK and fisheries-dependent data

Our study contributes to ongoing investigations into the utility of LEK and fisheries-dependent data for assessing fish population dynamics (Aylesworth et al., 2017; Hind, 2015; Santos et al., 2019; Zukowski et al., 2011). Despite increasing acceptance of these types of data as reliable sources, they nevertheless suffer from several biases and limitations. Fisheries-dependent data are inherently affected by fishing dynamics and angler behavior, altering the relationship between CPUE and abundance (Maunder and Punt, 2004). By standardizing the MRIP and ENP data prior to analysis, we accounted for various temporal and spatial dynamics that may influence catch. However, the choice of

model used to standardize CPUE data may also influence the resulting abundance index. During preliminary analysis, we fit a series of additional models, including several generalized additive models (GAMs; Hastie & Tibshirani 1990) to the MRIP and ENP datasets. Regardless of the model used, the overall trends in abundance over time remained the same. Since the goal of our study was not to develop standardized indices of abundance for use in stock assessment, but instead to assess overall shifts in abundance over time, the relatively simpler delta lognormal models were chosen for easier interpretation, and for consistency with other studies that have analyzed these datasets (e.g., Cass-Calay and Schmidt 2003; Rios 2015; Sagarese 2019). Further, because the Crevalle Jack is a large, pelagic species with a distribution spanning the Western Atlantic, Caribbean, and the Gulf of Mexico regions, an index of abundance using data only compiled from the Florida Keys region would not be suitable for stock assessment nor management outside of the Florida Keys.

In this study, we observed a mismatch between the ENP data and the guide observations that could be attributed to limitations of the data. Although a decline in Crevalle Jack abundance was apparent in the ENP data, 50% of Upper Keys guides did not observe a decline. A limitation specific to recreational angler-reported data is that the accuracy of the data is dependent upon angler recall and willingness to report everything that was released. Since the majority of Crevalle Jack caught by recreational anglers in the Florida Keys are released, it is possible that the MRIP and ENP datasets are conservative estimates of the Crevalle Jack catch. It is also possible that the decline in standardized abundance over time represents a decline in angler willingness to report catches for this species or a bias in reporting, rather than representing a true decline in

population abundance. Alternatively, the Upper Keys guides may have failed to perceive the decline because it was gradual and there was substantial interannual variability in abundance, as previously mentioned. Otherwise, our small sample size may have simply given us a biased view of the perceptions of Upper Keys guides.

A common criticism of LEK is that resource users are subject to the shifting baseline syndrome (SBS), a well-known phenomenon describing how human perception and memory are subject to how much experience an individual has with historic reference conditions (Pauly, 1995). Numerous studies have shown that changing perceptions over time can lead to acceptance of degraded environmental conditions as normal, thus making target setting for species and habitat recovery difficult (Beaudreau and Levin, 2014). For example, Barbosa-Filho et al. (2020) interviewed Lane Snapper (*Lutjanus synagris*) anglers in Brazil and found that older anglers were significantly more likely to report a decline in abundance over time than younger anglers. This shifting baseline contributed to disagreement among anglers as to whether specific management rules for Lane Snapper were necessary. SBS may explain why some guides we interviewed did not observe a decline in Crevalle Jack catches or why most guides did not notice the start of the decline (circa 1991 according to the MRIP offshore and ENP data) but noticed when abundance started dipping below average (early 2000s). This is supported by our observation that some of the anglers who have been guiding the longest suggested the decline began the earliest (Figure 3b). Also, the three Upper Keys guides who did not observe a decline have only been guiding full time since the early 2000s. Since these anglers were not guiding during the period of relatively high abundance observed in the ENP data (1990-2000; Figure 6a), it is possible they have not been fishing for Crevalle

Jack long enough to notice the decline. Other LEK studies have found similar patterns, with older or more experienced anglers being more likely to report changes in abundance over time for a given species than younger or less experienced anglers (Beaudreau and Levin, 2014; Frezza and Clem, 2015).

4.2 Supported hypotheses

When rigorous fisheries-independent data are lacking, consistency in ecological patterns among multiple, independent yet imperfect datasets (e.g., fisheries-dependent data, LEK or expert opinion, gear selective data) can provide confidence in observed patterns and bolster the reliability and credibility of LEK-based research (Rehage et al., 2019). Several studies have demonstrated such consistencies between LEK and other data sources in a variety of applications (e.g., Poizat and Baran 1997; Aswani and Hamilton 2004; Zukowski et al. 2011; Santos et al. 2019; Bourdouxhe et al. 2020) and even shown that LEK data can provide better insights with less effort and lower costs than traditional data sources (e.g., fisheries-independent surveys; Aylesworth et al. 2017). In our study, four of our six LEK-derived hypotheses received clear support from fisheries-dependent data and provide critical information that can be used to develop management recommendations. The agreement among guides, MRIP data, and ENP data concerning the timing (below average abundance since the mid-2000s) and pattern of decline (gradual decrease mainly affecting large, adult offshore fish) provides confidence in these observed patterns and demonstrates the utility of our translational ecology approach. Although the exact cause of the Crevalle Jack decline remains unknown, declines in large, old fish are often indicative of overfishing and can have severe consequences for

fish populations and ecosystems (Heino and Godø, 2002). Disproportionate removal of large fish truncates age and size distributions, leaving only younger spawners that typically produce lower quality eggs and larvae than older spawners (Green, 2008). Large, old female fish in particular contribute substantially to stock productivity and sustainability by ensuring reproductive success (Hixon et al., 2014). Removal of large fish from an ecosystem can also lead to cascading effects on other species and the environment, such as increasing abundance and altering behavior of prey fish (Baum and Worm, 2009). Our analysis of fisheries-dependent data supported fishing guide concerns about the status and trends of Crevalle Jack in the Florida Keys, which suggests that implementing regulations to restore the population may be warranted. Since our results revealed that larger adults appear to be more at risk and Crevalle Jack make seasonal migrations into the Florida Keys, such management regulations could include a size or slot limit to protect large fish or a rotational closure. Slot limits have been particularly successful at preventing significant truncation of age or size structure while maintaining high fishery yields (Gwinn et al., 2015; Kasper et al., 2020). Rotational closures can be beneficial for preserving spatial heterogeneity in populations, especially when the closures protect vital spawning areas or seasons (Brownscombe et al., 2019a; Hsieh et al., 2010). If movement data reveals regular Crevalle Jack migrations to spawning grounds either in the Florida Keys or elsewhere, closure of these areas during the spawning season could aid in population recovery.

4.3 Unsupported hypotheses

While consistency among LEK and biological datasets provides confidence in observed ecological patterns, disagreement among data sources provides focal areas for future research that can elucidate patterns and mechanisms driving the discrepancies originally observed (Silvano and Valbo-Jørgensen, 2008). Out of our six hypotheses, two had limited support from fisheries-dependent data and may serve as priorities for future research. These hypotheses concerned the spatial extent of the decline and the causes of the decline. The hypothesis that Crevalle Jack populations have declined more in the Lower Keys than the Upper Keys (Hypothesis 2) did not have much support from fisheries-dependent data, but we also lacked the spatial resolution to accurately assess this hypothesis (MRIP data encompassed the entire Keys region and ENP data only partially encompassed the Upper Keys). Furthermore, the extent of mixing between fish in the Lower and Upper keys is unknown, which makes pinpointing the extent of the decline difficult. Preliminary results of an acoustic telemetry study in South Florida showed several Crevalle Jack detected on both Upper Keys and Lower Keys receivers (Gervasi et al. unpublished data), suggesting that there may be at least some mixing between the two regions. To fully determine the extent of the decline, research into the spatial distribution of Crevalle Jack (including seasonal and lifetime movement and migration patterns) will be necessary. Many marine fishes are known to exhibit complex movement patterns which have important implications for fisheries management (Zemeckis et al., 2017). For example, knowledge of fish movements is necessary for elucidating stock structure, and accurate stock identification is crucial for developing biologically relevant management unit boundaries (Cadrin, 2020; Pita et al., 2016).

Fish movements can also affect their vulnerability to fishing pressure (Olsen et al., 2012), which could help explain the disagreement among datasets concerning Hypothesis 4. Most guides speculated that commercial and/or recreational fishing harvest may have contributed to the Crevalle Jack decline, but fisheries-dependent data showed that commercial harvest of Crevalle Jack in the Florida Keys region is limited, and the majority of fish captured by recreational anglers are released. Furthermore, most recreational anglers use hook and line gear to capture Crevalle Jack (97% of MRIP trips and 100% of ENP trips that captured Crevalle Jack were hook and line). Although discard mortality rates have not been estimated for Crevalle Jack specifically, studies on other recreationally captured species in the region show that hook and line discard mortality is generally low (Flaherty-Walia et al., 2016). So, it seems unlikely that fishing pressure in the Florida Keys (either commercial or recreational) has contributed to the decline in Crevalle Jack abundance. We cannot, however, exclude the possibility of unreported bycatch discard mortality in the commercial fishery or higher harvest than reported in the recreational fishery. Gillnets were the second most common gear type used on commercial trips that landed Crevalle Jack. Dotson et al. (2009) examined bycatch of Black Crappie (*Pomoxis nigromaculatus*) in a Florida commercial gillnet fishery and found that bycatch mortality exceeded 30% in both years of the study. However, commercial gillnets were banned throughout most of Florida's coastal waters in 1995 (Smith et al., 2003), so bycatch mortality from this gear type would have only affected the earlier years of the time series. Nonetheless, investigating the extent of commercial bycatch mortality for Crevalle Jack may be needed before we can exclude the Monroe County commercial fishery as a contributor to the decline. As previously

noted, Crevalle Jack are most abundant in the Keys region in the winter months, which agreed with guide observations and suggests that the species migrates elsewhere during the summer months. Preliminary acoustic telemetry results (Gervasi et al. unpublished data) have revealed that Crevalle Jack make regular long-range movements into and out of the Florida Keys, moving northward along both the east and west coasts of Florida and occasionally migrating from one coast to another. It is therefore also possible that Crevalle Jack are being overfished somewhere else within the population range, like central Florida, where most of the Crevalle Jack commercial landings have been from over the past five years (C. Bradshaw pers. obs.).

Other factors may also be contributing to the Crevalle Jack decline, such as loss of prey, poor water quality, or increased predator abundance, as several guides suggested. Loss of prey was the most common suggestion by guides, many of whom mentioned changes in Ballyhoo (*Hemiramphus brasiliensis*) abundance as a possible factor. Pelagic schooling fishes are common prey for adult Crevalle Jack (Correia et al., 2017; Kwei, 1978). Changes in the abundance or distribution of Ballyhoo populations may therefore explain why larger, offshore Crevalle Jack appear to have declined more so than smaller, inshore Crevalle Jack. Additionally, regional climate variability has been linked to changes in the distribution and productivity of several fish species (Brander, 2007), and continued temperature increases and declines in primary production due to climate change are anticipated to cause global decreases in marine animal biomass (Lotze et al., 2019). Research on Bonefish in South Florida (another economically important recreational fishery species) has revealed that several factors likely contributed to a population decline that began in the 1950s (Frezza and Clem, 2015; Santos et al., 2017),
including habitat loss and modification, extreme weather events, and fishing mortality (Brownscombe et al., 2019b). In Florida Bay specifically, shifts in both recruit and adult survivorship of Bonefish may have been caused by increased fishing effort, changes in abiotic factors, and/or habitat changes (Klarenberg et al., 2019). Therefore, in addition to examining the spatial distribution of Crevalle Jack, another future research priority is to examine the varying factors operating at several spatial scales that affect Crevalle Jack populations.

5. Conclusions

In an era of global anthropogenic and climatic changes, new methods of environmental planning and management are necessary to ensure sustainable use and conservation of natural resources (Lipsman, 2019). Combining multiple data sources and including stakeholders in science co-production under a translational ecology framework provides opportunities for rapid, proactive, and adaptive management (Chapin, 2017; Zipkin and Saunders, 2018). In our study, LEK-derived hypotheses supported by multiple data sources supplied key information that fisheries managers can use immediately to aid in the conservation of Crevalle Jack. These hypotheses suggest that: (1) populations in the Florida Keys have been declining gradually with below-average abundance since the early 2000s, (2) large, old fish have declined more than small fish, and (3) Crevalle Jack are most abundant in the Keys region in the winter months. Additionally, our unsupported hypotheses led us to two main priorities for future research: (1) analysis of the seasonal and lifetime movement and migration patterns of Florida Keys Crevalle Jack, and (2) examination into the anthropogenic and environmental dynamics and

drivers occurring throughout the population range that may be responsible for the decline. These two hypotheses were most likely unsupported because of limitations in the available fisheries-dependent data, not because the guides we interviewed were incorrect in their observations. In fact, the general agreement among guides and the different data sources reveals that recreational fishing guide knowledge is an excellent source of information that has the potential to substantially improve fisheries management.

The results of our study outline an effective translational ecology approach that can be progressed by including fishing guides in future research efforts and in developing management recommendations via transdisciplinary research (Klenk, 2018; Pohl, 2008). Furthermore, our framework (Figure 1) can be easily applied to other species and areas, as fishing guides typically encounter a wide variety of fishes as they tailor their charter trips to diverse clients. Most saltwater fish species native to Florida currently have no specific recreational regulations and are listed as unregulated species (FWC 2021c), including several species often targeted by recreational anglers. Formal stock assessments have not been conducted for most of these species and are not expected to be conducted in the future. Therefore, trends in abundance patterns are not being monitored, and the effects of fishing pressure on these populations remain unknown. Through collaborative efforts, there are a few instances where scientific results have successfully informed management changes for important recreational fisheries (e.g., Brownscombe et al., 2019a). However, knowledge-action gaps are still common (Cook et al., 2013) and there is ample room for increased collaboration among guides, angler associations, fisheries scientists, conservation groups, and managers. The translational ecology approach

outlined herein provides an additional tool for the fishery scientist's toolbox that can help better develop conservation priorities and effective management.

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Table 1. Fisheries-dependent datasets used to test angler-derived hypotheses. Source denotes the agency responsible for data collection and dissemination, Years are the years of data analyzed in this study, and Area is the region each dataset covers.

Table 2. List of hypotheses derived from LEK interviews, number (percent) of guides interviewed who agreed with each hypothesis, and proposed method for testing each hypothesis including the datasets used. $LK =$ Lower Keys, $UK =$ Upper Keys.

Translational Ecology for Recreational Fishery Management

Figure 1. Conceptual diagram of the translational ecology framework applied in this study to a recreational fishery: Crevalle Jack in the Florida Keys. Panel A outlines a rapid approach to developing hypotheses concerning fishery resources via fishing guide local ecological knowledge and using existing data to test the hypotheses. Hypotheses without clear support from existing data serve as priorities for additional research (Panel B), which can provide missing support for existing hypotheses or lead to additional hypotheses. Finally, information from Panels A and B are used to produce management recommendations supported by both fishery scientists and stakeholders (Panel C). Results from panel A are presented in this paper, while panels B and C outline future directions.

Figure 2. Map of the study area. The state of Florida, U.S.A. highlighting the South Florida region (inset map), approximate fishing range of the anglers interviewed, split into the Lower and Upper keys (a), extent of the MRIP survey subset to Monroe County, split into inshore and offshore (b), extent of the ENP creel survey (c), and extent of the commercial landings data subset to Monroe County, split into the Lower and Upper keys (d). Boundary lines are approximate and for illustrative purposes only. Commercial fishing was prohibited within ENP boundaries after 1985 (Osborne et al 2006). Maps created using the ESRI light gray canvas basemap (ESRI 2011) with ArcGIS desktop (ESRI 2020).

Reported year decline began

Figure 3. Time frame in 5-year blocks when anglers first reported noticing a decline in crevalle jack catches in the Florida Keys (a) and reported year decline began compared to the year anglers began guiding or fishing full time (b). Black line in panel (b) denotes fitted linear regression.

Figure 4. Reasons for the decline in Crevalle Jack abundance as speculated by interviewed anglers. X-axis denotes the number of anglers who mentioned each reason.

Figure 5. Nominal and standardized (modeled) Crevalle Jack CPUE (scaled to mean of 1) for MRIP inshore (a) and offshore (c) data, and CUSUM plots for z-scored MRIP inshore (b) and offshore (d) indices. Nominal CPUE is the average annual CPUE before standardization. Positive slopes on CUSUM plots denote periods where standardized CPUE was above the average of the time series while negative slopes denote periods where standardized CPUE was below average. Red dotted lines denote model 95% confidence intervals. Horizontal black dashed lines lie at the averages of each time series (scaled to 1).

Figure 6. Nominal and standardized (modeled) Crevalle Jack CPUE (scaled to mean of 1) for the ENP data (a) and CUSUM plot for the z-scored ENP index (b). Nominal CPUE is the average annual CPUE before standardization. Positive slopes on the CUSUM plot denote periods where standardized CPUE was above the average of the time series while negative slopes denote periods where standardized CPUE was below average. Red dotted lines denote model 95% confidence intervals. The horizontal black dashed line lies at the average of the time series (scaled to 1).

Figure 7. Total annual commercial landings of Crevalle Jack by all gear types for the Upper Keys (a) and Lower Keys (b), proportion of Crevalle Jack landed by year in ENP data (c), and proportion of Crevalle Jack landed by year in MRIP data (d). Vertical dashed lines on (a) and (b) denote when commercial entanglement nets were banned in Florida (1995; Smith et al. 2003) and the dashed line in (c) denotes when commercial fishing was banned within Everglades National Park (1985; Osborne et al. 2006).

Coefficient	Estimate	Standard Error	z-value	p-value
Intercept	-1.892	0.245	-7.717	0.001
Year1992	-1.216	0.358	-3.398	0.001
Year1993	-1.079	0.300	-3.602	0.001
Year1994	-1.786	0.355	-5.027	< 0.001
Year1995	-1.130	0.327	-3.454	0.001
Year1996	-0.777	0.319	-2.436	< 0.05
Year1997	-0.071	0.274	-0.261	0.794
Year1998	-0.062	0.279	-0.223	0.824
Year1999	-0.537	0.280	-1.914	0.056
Year2000	-0.384	0.312	-1.232	0.218
Year2001	-1.630	0.368	-4.434	0.001
Year2002	-0.492	0.345	-1.428	0.153
Year2003	-0.538	0.313	-1.721	0.085
Year2004	-0.709	0.353	-2.006	< 0.05
Year2005	-0.836	0.437	-1.911	0.056
Year2006	-0.796	0.403	-1.977	< 0.05
Year2007	-0.679	0.341	-1.990	< 0.05
Year2008	-0.609	0.314	-1.941	0.052
Year2009	-0.382	0.336	-1.135	0.256
Year2010	-1.486	0.355	-4.183	0.001
Year2011	-0.605	0.302	-2.004	< 0.05
Year2012	-0.085	0.279	-0.306	0.759
Year2013	-0.413	0.289	-1.431	0.152
Year2014	-0.081	0.260	-0.312	0.755
Year2015	-0.489	0.267	-1.835	0.067
Year2016	-1.251	0.323	-3.878	0.001
Year2017	-2.239	0.421	-5.316	0.001
Year2018	-1.075	0.309	-3.484	0.001
Year2019	-0.951	0.295	-3.230	0.01
ModeCharter	2.012	0.119	16.941	0.001
ModePrivate	1.263	0.114	11.050	0.001
SeasonSpring	-0.143	0.094	-1.524	0.128
SeasonSummer	-0.438	0.111	-3.945	0.001
SeasonAutumn	0.132	0.104	1.272	0.203

Table S1. Coefficients, estimates, standard errors, z-values, and p-values for the MRIP inshore binomial model on proportion positive data.

Coefficient	Estimate	Standard Error	z-value	p-value
(Intercept)	-0.503	0.214	-2.348	< 0.05
Year1992	-0.424	0.333	-1.272	0.204
Year1993	-0.402	0.276	-1.456	0.146
Year1994	0.091	0.339	0.269	0.788
Year1995	-0.361	0.307	-1.176	0.240
Year1996	-0.383	0.293	-1.305	0.192
Year1997	-0.267	0.240	-1.111	0.267
Year1998	-0.071	0.243	-0.294	0.769
Year1999	-0.061	0.244	-0.248	0.804
Year2000	-0.433	0.270	-1.603	0.109
Year2001	-0.468	0.341	-1.371	0.171
Year2002	-0.322	0.298	-1.080	0.280
Year2003	-0.635	0.272	-2.334	< 0.05
Year2004	-0.406	0.310	-1.312	0.190
Year2005	-0.063	0.389	-0.163	0.871
Year2006	-0.614	0.356	-1.727	0.085
Year2007	-0.588	0.301	-1.955	0.051
Year2008	-0.546	0.278	-1.965	< 0.05
Year2009	-0.114	0.291	-0.390	0.697
Year2010	0.042	0.328	0.127	0.899
Year2011	-0.167	0.262	-0.639	0.523
Year2012	0.040	0.242	0.165	0.869
Year2013	0.238	0.254	0.937	0.349
Year2014	-0.329	0.229	-1.436	0.151
Year2015	-0.457	0.237	-1.930	0.054
Year2016	0.005	0.296	0.016	0.987
Year2017	-0.424	0.404	-1.050	0.294
Year2018	-0.204	0.280	-0.731	0.465
Year2019	-0.039	0.266	-0.146	0.884
ModeCharter	-0.019	0.112	-0.168	0.867
ModePrivate	-0.182	0.112	-1.622	0.105
SeasonSpring	-0.392	0.082	-4.790	0.001
SeasonSummer	-0.378	0.104	-3.643	0.001
SeasonAutumn	-0.079	0.089	-0.888	0.374

Table S2. Coefficients, estimates, standard errors, z-values, and p-values for the MRIP inshore lognormal model on positive trips data.

Coefficient	Estimate	Standard Error	z-value	p-value
(Intercept)	0.304	0.586	0.518	0.604
Year1992	-0.217	0.889	-0.244	0.807
Year1993	0.166	0.796	0.208	0.835
Year1994	-1.274	0.773	-1.648	0.099
Year1995	-0.755	0.857	-0.880	0.379
Year1996	0.056	0.666	0.085	0.933
Year1997	-0.827	0.680	-1.217	0.223
Year1998	-0.694	0.648	-1.070	0.284
Year1999	-0.574	0.612	-0.937	0.349
Year2000	-1.395	0.630	-2.215	< 0.05
Year2001	-1.567	0.618	-2.537	< 0.05
Year2002	-1.301	0.622	-2.093	< 0.05
Year2003	-1.023	0.604	-1.694	0.090
Year2004	-1.689	0.625	-2.704	0.01
Year2005	-1.346	0.633	-2.126	< 0.05
Year2006	-1.225	0.629	-1.949	0.051
Year2007	-1.820	0.633	-2.874	0.01
Year2008	-1.566	0.615	-2.546	< 0.05
Year2009	-1.612	0.640	-2.517	< 0.05
Year2010	-1.358	0.621	-2.185	< 0.05
Year2011	-1.904	0.655	-2.908	0.01
Year2012	-1.995	0.645	-3.090	0.01
Year2013	-2.477	0.723	-3.425	0.001
Year2014	-1.502	0.642	-2.341	< 0.05
Year2015	-2.027	0.682	-2.971	0.01
Year2016	-1.909	0.694	-2.751	0.01
Year2017	-2.728	0.780	-3.497	0.001
Year2018	-2.191	0.706	-3.105	0.01
Year2019	-3.219	0.928	-3.467	0.001
SeasonSpring	-0.386	0.129	-3.004	0.01
SeasonSummer	-0.469	0.173	-2.703	0.01
SeasonAutumn	-0.006	0.156	-0.037	0.970

Table S3. Coefficients, estimates, standard errors, z-values, and p-values for the MRIP offshore binomial model on proportion positive data.

Coefficient	Estimate	Standard Error	z-value	p-value
Intercept	-0.797	0.503	-1.584	0.114
Year1992	-0.214	0.782	-0.274	0.784
Year1993	-1.159	0.654	-1.772	0.077
Year1994	-1.066	0.733	-1.454	0.147
Year1995	-0.739	0.781	-0.946	0.345
Year1996	-0.655	0.564	-1.163	0.246
Year1997	-0.174	0.599	-0.290	0.772
Year1998	-0.311	0.567	-0.548	0.584
Year1999	-0.272	0.527	-0.517	0.606
Year2000	-0.593	0.557	-1.065	0.287
Year2001	-0.544	0.546	-0.997	0.319
Year2002	-0.558	0.546	-1.021	0.308
Year2003	-0.640	0.521	-1.229	0.220
Year2004	-0.395	0.556	-0.710	0.478
Year2005	-0.154	0.562	-0.273	0.785
Year2006	-0.056	0.555	-0.101	0.919
Year2007	-0.309	0.567	-0.544	0.587
Year2008	-0.059	0.540	-0.110	0.912
Year2009	-0.750	0.575	-1.305	0.193
Year2010	-0.539	0.549	-0.981	0.327
Year2011	-0.824	0.600	-1.373	0.171
Year2012	-0.415	0.587	-0.708	0.480
Year2013	-0.826	0.701	-1.178	0.239
Year2014	-0.204	0.577	-0.353	0.724
Year2015	-0.873	0.635	-1.375	0.170
Year2016	-0.577	0.655	-0.881	0.379
Year2017	-1.788	0.783	-2.284	< 0.05
Year2018	-0.701	0.673	-1.041	0.298
Year2019	-0.521	0.984	-0.529	0.597
SeasonSpring	-0.408	0.138	-2.958	< 0.001
SeasonSummer	-0.570	0.194	-2.936	0.001
SeasonAutumn	-0.187	0.166	-1.129	0.259

Table S4. Coefficients, estimates, standard errors, z-values, and p-values for the MRIP offshore lognormal model on positive trips data.

Coefficient	Estimate	Standard Error	z-value	p-value
Intercept	-0.321	0.035	-9.069	< 0.001
Year1981	-0.518	0.045	-11.506	0.001
Year1982	-0.277	0.044	-6.283	0.001
Year1983	-0.129	0.043	-3.021	0.01
Year1984	-0.164	0.040	-4.073	0.001
Year1985	-0.536	0.043	-12.401	0.001
Year1986	-0.259	0.041	-6.302	0.001
Year1987	-0.167	0.042	-3.967	0.001
Year1988	0.186	0.046	4.040	0.001
Year1989	0.200	0.046	4.305	0.001
Year1990	0.757	0.041	18.258	0.001
Year1991	0.807	0.043	18.923	0.001
Year1992	0.754	0.042	17.937	0.001
Year1993	0.458	0.044	10.391	0.001
Year1994	0.650	0.040	16.186	0.001
Year1995	0.632	0.042	14.885	0.001
Year1996	0.728	0.040	18.151	0.001
Year1997	0.978	0.040	24.676	0.001
Year1998	0.828	0.041	20.160	0.001
Year1999	0.907	0.042	21.676	0.001
Year2000	0.986	0.042	23.246	0.001
Year2002	0.570	0.044	13.061	0.001
Year2003	0.530	0.045	11.903	0.001
Year2004	0.510	0.044	11.509	0.001
Year2005	0.146	0.048	3.069	0.01
Year2006	0.359	0.047	7.681	0.001
Year2007	0.551	0.046	12.006	0.001
Year2008	0.387	0.048	8.103	0.001
Year2009	0.229	0.049	4.653	< 0.001
Year2010	-0.192	0.054	-3.551	0.001
Year2011	-0.036	0.051	-0.699	0.485
Year2012	0.481	0.050	9.616	0.001
Year2013	0.653	0.050	13.171	0.001
Year2014	0.120	0.051	2.346	< 0.05
Year2015	-0.038	0.052	-0.727	0.467
Year2016	0.055	0.053	1.043	0.297
Year2017	-0.234	0.056	-4.155	0.001
Year2018	-0.192	0.054	-3.556	0.001
Year2019	0.433	0.052	8.281	0.001

Table S5. Coefficients, estimates, standard errors, z-values, and p-values for the ENP binomial model on proportion positive data.

Coefficient	Estimate	Standard Error	z-value	p-value
Intercept	-0.865	0.027	-32.265	< 0.001
Year1981	-0.035	0.036	-0.972	0.331
Year1982	0.101	0.035	2.915	0.01
Year1983	-0.034	0.033	-1.017	0.309
Year1984	-0.155	0.031	-4.938	0.001
Year1985	-0.225	0.034	-6.534	< 0.001
Year1986	-0.145	0.032	-4.527	0.001
Year1987	-0.170	0.033	-5.172	0.001
Year1988	-0.110	0.035	-3.131	0.01
Year1989	-0.128	0.035	-3.657	0.001
Year1990	0.015	0.030	0.496	0.620
Year1991	0.303	0.031	9.820	0.001
Year1992	0.084	0.031	2.743	0.01
Year1993	-0.089	0.033	-2.714	0.01
Year1994	-0.318	0.030	-10.666	< 0.001
Year1995	-0.213	0.031	-6.836	0.001
Year1996	-0.323	0.030	-10.891	0.001
Year1997	-0.145	0.029	-5.027	0.001
Year1998	-0.226	0.030	-7.545	0.001
Year1999	-0.092	0.030	-3.039	0.01
Year2000	-0.050	0.030	-1.669	0.095
Year2002	-0.353	0.032	-10.975	0.001
Year2003	-0.367	0.033	-11.160	0.001
Year2004	-0.348	0.033	-10.589	0.001
Year2005	-0.400	0.036	-10.965	0.001
Year2006	-0.309	0.035	-8.822	0.001
Year2007	-0.289	0.034	-8.570	< 0.001
Year2008	-0.374	0.036	-10.521	0.001
Year2009	-0.333	0.037	-8.964	< 0.001
Year2010	-0.337	0.043	-7.881	< 0.001
Year2011	-0.300	0.040	-7.522	0.001
Year2012	-0.144	0.037	-3.918	0.001
Year2013	-0.064	0.036	-1.803	0.071
Year2014	-0.337	0.039	-8.630	0.001
Year2015	-0.392	0.040	-9.736	0.001
Year2016	-0.310	0.041	-7.615	0.001
Year2017	-0.286	0.045	-6.364	0.001
Year2018	-0.378	0.043	-8.811	0.001
Year2019	-0.275	0.039	-7.122	0.001

Table S6. Coefficients, estimates, standard errors, z-values, and p-values for the ENP lognormal model on positive trips data.

Figure S1. List of key informant interview questions. Four open-ended questions were used to guide conversations while sub-questions were asked if the angler did not cover a specific topic during conversation.

- 1. What is your general background and experience fishing and guiding?
	- a. How long have you been fishing/guiding?
	- b. Where do you typically guide? Is that different from where you fish?
	- c. How often do you guide?
	- d. How often do you fish recreationally apart from guiding?
	- e. What kind of boat do you use for guiding / fishing?
	- f. What habitats do you target?
	- g. Are there particular species that you target?
- 2. What do you know about Crevalle Jack?
	- h. What time of year do you see them?
	- i. Where do you catch them?
	- j. Where don't you catch them?
	- k. Do you see them with certain other species?
- 3. Have you noticed any changes in Crevalle Jack fishing over time?
	- l. Do you see fewer Crevalle Jack than you used to?
	- m. Can you estimate how much they have declined?
	- n. When did you first notice a decline in your Crevalle Jack catches?
	- o. Have you seen a change in size?
	- p. Have you seen a shift in where you find Crevalle Jack?
	- q. Do you think this decline is happening elsewhere?
- 4. Is fishing for Crevalle Jack important to you?
	- r. Do you ever specifically target Crevalle Jack?
	- s. If you catch Crevalle Jack, what do you do with them? (Release, harvest, use as bait, etc.)
	- t. What do you think we can do to protect Crevalle Jack?
	- u. Do you have any ideas why they are declining?
	- v. Do you believe a Crevalle Jack management plan is necessary or would be beneficial?

CHAPTER III

OTOLITH STABLE ISOTOPE MICRO-SAMPLING TO DISCRIMINATE POORLY STUDIED STOCKS: CREVALLE JACK IN THE EASTERN GULF OF MEXICO

Abstract: Developing conservation and management strategies for species with complex life histories, broad spatial distributions, and long lifespans is notoriously difficult. Too often managers cannot identify critical habitats nor vulnerable life stages because of the sheer scale of migration or uncertainty about connectivity among populations. Advancements in otolith stable isotope analyses, and specifically sampling of discrete otolith layers, have provided opportunities to assess lifetime migrations and connectivity without extensive, long-term field sampling. Here, we compared carbon and oxygen stable isotope values in discrete otolith layers for Crevalle Jack (an unregulated and datapoor species) captured in two isotopically distinct regions (Alabama and the Florida Keys). Our goal was to address vital questions about how juvenile recruitment, ontogenetic migration, and adult large-scale movement patterns differ between the two regions and whether connectivity occurs throughout the life history. Our results revealed that Crevalle Jack appear to inhabit inshore nursery areas at age-0, before migrating to coastal/offshore habitats between age-1 and age-2. Comparisons between fish collected in northeastern and southeastern Gulf of Mexico regions revealed significant differences in stable isotope values throughout the life history. These results provide evidence that on average, Crevalle Jack likely exhibited local recruitment from age-0 nursery habitats throughout the eastern GOM to nearby coastal habitats. However, overlap in stable isotope profiles between individuals from the two regions suggested that some connectivity between the two populations may occur. Our research illustrates the value of otolith stable isotope micro-sampling for answering critical questions about fish populations that can inform management and conservation.
1. Introduction

The understanding of population connectivity and dispersal pathways is essential to effective fisheries management. Knowledge of connectivity patterns in particular is crucial for delineating appropriate spatial scales of management and for specifying vital subareas to protect from exploitation (Fogarty and Botsford, 2007). Misaligned stock assessment and population boundaries can have severe consequences, including overexploitation and localized depletion (Berger et al., 2021; Ying et al., 2011). Additionally, successful implementation of marine protected areas requires that the size and location match the spatial distribution and habitat use of the species of interest (Kramer and Chapman, 1999; Moffitt et al., 2009). However, population connectivity (specifically ecological connectivity) can occur over multiple spatiotemporal scales and can therefore be challenging to assess. Ecological connectivity is defined as the exchange of individuals among local populations that can affect population dynamics and demographics (Sale et al., 2010). This exchange can occur over multiple life history stages, and includes larval dispersal, juvenile recruitment and retention, and large-scale movements of sub-adults and adults. Ecological connectivity is the basis of metapopulation ecology (Levins, 1968) and contingent theory (Hjort, 1914; Secor, 1999), paradigms that are increasingly being used to explain empirical observations of fisheries dynamics (Cadrin and Secor, 2009).

Despite increasing recognition of the importance of ecological connectivity and metapopulation processes in fisheries, many stock assessments are unable to account for complex population structures, often assuming that a fish stock is a single, spatially homogeneous population stemming from a single larval pool (Archambault et al., 2016).

Spatially-explicit population models are becoming increasingly common, but studies of population connectivity mainly focus on early life history stages (e.g., Hinrichsen et al., 2011; Miller, 2007). Juvenile and adult-mediated connectivity is largely understudied, despite research showing that adult movements can significantly affect metapopulation structure and dynamics (Frisk et al., 2014). It is therefore crucial that population connectivity of exploited fishes is assessed at all life history stages, and that this spatial structure is incorporated into population models and stock assessments.

Assessment of population connectivity throughout the life history of a species is challenging, often requiring extensive, long-term field studies (e.g., routine fisheriesindependent sampling or tag-recapture/animal tracking projects) to examine movement/dispersal patterns of the different life stages. However, advances in otolith microchemistry provide opportunities to rapidly examine movement patterns over the entire life history of an individual. Otoliths remain the most common structure used to age fishes, since clear growth bands are evident for most species (Campana, 2001). Additionally, because otoliths are inert, trace elements and isotope ratios are incorporated into otoliths as a fish grows in proportion with ambient water concentrations. If a fish resides in a certain body of water for a portion of its life, the chemical signature of that water body will be retained in the section of the otolith corresponding with that period of the fish's life (Walther and Limburg, 2012). Because of these attributes, otoliths have been used in fisheries science to reconstruct environmental histories (Campana, 1999; Walther and Limburg, 2012).

The applications of otolith chemical composition are numerous and include identifying nursery areas or natal origin (Gerard and Muhling, 2010; Thorrold et al.,

2001), reconstructing migration patterns (Avigliano et al., 2021; Sturrock et al., 2012; Walther and Limburg, 2012), retrospectively assigning adults to areas of origin (Gerard et al., 2015), and determining stock structure (Tanner et al., 2016). Furthermore, changes in chemical composition over the lifetime of an individual fish can be discerned via sampling of discrete otolith layers (i.e., micro-sampling; Jamieson et al., 2004). Stable isotope micro-sampling throughout the entire otolith is a relatively recent approach that has distinct advantages, including establishing environmental histories of individual fish, examining partial migration, and comparing life history patterns among populations (Høie et al., 2004; Jamieson et al., 2004; Kawazu et al., 2020; Wang et al., 2021; Weidman and Millner, 2000). More often though, studies concentrate on broad regions of the otolith (e.g., core vs. edge) corresponding to different life history stages (e.g., birth vs. age at collection), potentially missing critical transition periods or periods of connectivity throughout the entire life history.

The purpose of this study was to examine lifetime migration patterns of Crevalle Jack (*Caranx hippos*) captured from two distinct regions of the eastern Gulf of Mexico (the Florida Keys and Alabama). The Crevalle Jack is an important part of the recreational fishery in both these areas, yet is currently unregulated and there is evidence that population abundance may be declining (Gervasi et al., 2022). Specifically, our study aimed to determine whether otolith micro-sampling could be used to distinguish between fish from each region based on differences in stable isotope values throughout otoliths. If separation in isotope values is evident throughout the life history, it would suggest a lack of mixing between the two areas, which has implications for stock assessment and management. By comparing stable isotope chemistry in discrete otolith layers between

the two groups, our research addresses vital questions about how juvenile recruitment, ontogenetic migration, and adult movement patterns differ between the two regions and when/if during the life history of the species connectivity occurs. We hypothesized that Crevalle Jack in the Florida Keys and Alabama may represent separate stocks, which is vital information for management as the two states would be able to manage local populations separately without having to engage in multi-state management efforts. In addition to aiding in conservation and management, our results demonstrate the applicability of otolith stable isotope micro-sampling as a tool for assessing lifetime population connectivity of fishes that can better inform future population models and stock assessments.

2. Methods

2.1 Study species

The Crevalle Jack is a large marine fish native to the Atlantic coast of North America and the Gulf of Mexico (GOM; Smith-Vaniz & Carpenter, 2007). The species is targeted by both commercial and recreational anglers (Kwei, 1978) but is unregulated in all coastal U.S. states within the species range and is considered data-poor (i.e., there is not enough information available to estimate relative stock status and appropriate reference points). In recent years, a decline in population abundance has been observed in the Florida Keys region (Gervasi et al., 2022) but the extent of the decline is unknown. Knowledge of migration patterns and population connectivity is, therefore, crucial for conservation and management of the species. However, little research has been

conducted to date on Crevalle Jack biology and ecology, and critical questions remain about stock structure and life history.

Spawning is suspected to occur in subtropical and tropical waters, but in the Western Atlantic, it has only been observed at Gladden Spit, Belize, a promontory reef that serves as a multi-species spawning aggregation site (Heyman and Kjerfve, 2008). Although other species in the Carangidae family have been observed spawning in continental shelf edge habitats throughout the GOM (Heyman et al., 2019), only indirect evidence (courtship behavior and color changes) of Crevalle Jack spawning has been observed at a marine sanctuary in the northwestern GOM (Helies et al., 2016). However, Crevalle Jack larvae have been observed throughout the GOM, mostly in the spring and summer months (Ditty et al., 2004; Flores-Coto and Sanchez-Ramirez, 1989). Post-larval fish have also been observed in offshore waters in the summer and fall (Mohan et al., 2017). Young-of-the-year Crevalle Jack are found in coastal estuaries throughout the Atlantic and GOM (Flaherty et al., 2013; McBride and McKown, 2000; Nelson, 1992), but the linkages between these juvenile nursery habitats and adult populations are unknown. McBride and McKown (2000) examined seasonal abundance and size structure of Crevalle Jack from New York to Florida. Their findings suggested that larvae spawning at subtropical and tropical latitudes are dispersed via ocean currents up the Atlantic coast and into temperate estuarine habitats, and at least some individuals can migrate back down to the tropics and return to the spawning sites. This suggests that Crevalle Jack throughout the Atlantic coast of the U.S. may represent a single stock, but evidence is limited and connectivity with Gulf of Mexico, Caribbean, and South American populations is unknown. Veteran fishing guides in the Florida Keys have

observed that large, adult Crevalle Jack appear to migrate seasonally into and out of the south Florida region, but where these individuals go is unknown (Gervasi et al., 2022). Previous research estimates that Crevalle Jack age at 50% maturity is about 3-4 years, but maturation data comes from a single population in the Caribbean (Caiafa et al., 2011). Adult Crevalle Jack are found in a variety of habitats, including coastal flats, coral reefs, artificial reefs, channels, and canals (Smith-Vaniz and Carpenter, 2007), but again, movement and migration patterns of adults is currently unknown.

2.2 Focal populations and alternative hypotheses

Adult Crevalle Jack were collected from two coastal regions: the Florida Keys (FK) and coastal Alabama (AL; Figure 1). These regions were selected for several reasons. First, there is evidence that several ecological and faunal divides exist in the northern GOM. Studies have suggested that zoogeographic breaks occur at Mobile Bay (Drymon et al., 2020), the DeSoto Canyon at the eastern edge of the Mississippi River basin (Defenbaugh, 1976; Gallaway, 1981; Ward, 2017), and at Cape San Blas at the eastern end of the Florida panhandle (Estes, 2016; Zieman and Zieman, 1989). Fish and invertebrate assemblages have been shown to differ on either side of these boundaries, suggesting that AL and FK Crevalle Jack may represent distinct populations. Secondly, according to Marine Recreational Information Program data (MRIP; NOAA, 2021), out of all coastal Atlantic and GOM states, recreational catch of Crevalle Jack from 2000- 2021 was highest in Florida, followed by Alabama. Total catch from Alabama was more than twice the next highest-ranking state (North Carolina). Assuming recreational landings are a proxy for fish abundance, the MRIP data suggest that the Florida and

Alabama regions may encompass centers of abundance for the species within the U.S. The Florida Keys was specifically chosen because previous research found evidence of a decline in Crevalle Jack abundance in the area, prompting management concerns (Gervasi et al., 2022). To successfully manage the population in Florida, it is important to understand if connectivity between Florida and other management jurisdictions exists. Finally, AL and FK represent two isotopically distinct regions, with both $\delta^{13}C_{water}$ and $\delta^{18}O_{\text{water}}$ values varying substantially. Coastal areas near the large rivers of the northcentral GOM receive substantial inputs of freshwater depleted in ¹⁸O, with average $\delta^{18}O$ of river samples ranging from -2.2‰ to as low as -6.6‰ in the Mississippi River (Wagner and Slowey, 2011), and terrestrial carbon depleted in ${}^{13}C$, with values near -27‰ (Fry, 1983). In the Florida Keys, limited freshwater input combined with high rates of evaporation lead to ¹⁸O-enriched waters $(1.7\%$ in the Upper Florida Keys; Sternberg and Swart, 1987), and abundant ¹³C-enriched seagrasses and macroalgae (δ^{13} C ~ -10 to -15‰) grow in nearshore areas and are exported offshore (Fry, 1983). Therefore, we expected that FK Crevalle Jack would have higher $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values than AL Crevalle Jack at least in the otolith edge region. Furthermore, if juveniles exhibited local recruitment (i.e., if the two populations represented separate, self-recruiting stocks), we expected the $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values of FK fish to be significantly different than the values for AL fish throughout the otoliths (H1; Figure 2). Alternatively, if recruitment to both adult locations was from common nursery grounds, we would expect an overlap in the $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values in the juvenile regions, followed by a divergence to either the FK or AL adult habitats (H2; Figure 2). Adult connectivity would be evidenced by an overlap in the isotope values throughout adult ages (H3; Figure 2). Otolith micro-

chemistry has been previously used to test similar hypotheses about migratory patterns and connectivity of other fish species (Avigliano et al., 2021).

All FK fish were collected opportunistically in cooperation with local charter boat captains and recreational fishermen between 2019 and 2021. Otoliths from AL fish were collected by Mississippi State University (MSU) scientists from fish harvested by recreational anglers during the annual Alabama Deep Sea Fishing Rodeo from 2017- 2019. Exact coordinates of capture locations were not recorded for most fish, but the broad area of capture was documented in all cases (Figure 1). We aimed to analyze otoliths from the oldest fish possible so we could capture the full time series of movements for each population. However, in Florida, fish over 4-years old were rarely encountered by charter boat captains, so we limited our analyses to fish 4-5 years old. A total of 12 otolith samples were collected for analysis per population ($n = 24$ total; Supplementary, Table S1), with multiple transects milled per otolith for stable isotope analysis ($n = 426$ total transects).

2.3 Otolith sectioning and aging

The left and right otoliths from each fish were embedded, sectioned, and mounted to microscope slides for further analysis, with the left otoliths used for aging and the right otoliths used for stable isotope analysis. We first embedded both otoliths in epoxy using a silicone mold and a two-part epoxy resin. Once solidified, embedded otoliths were sectioned through the nucleus using an Isomet low-speed diamond bladed saw with four blades separated by spacers to produce three thin sections per otolith. For the left otoliths, a 0.5 mm spacer was used, such that resulting thin sections were approximately 0.5 mm

thick for aging. For the right otoliths, a 0.6 mm spacer was used to produce thin sections approximately 0.6 mm thick. These thicker sections were used for stable isotope analysis as they provided a bit more otolith material for analysis. All thin sections were rinsed with water or 95% ethanol and adhered to clear microscope slides using a toluene-based mounting medium. Slides were allowed to dry for a minimum of 48 hours before further analysis.

Using the left otolith, opaque zones were counted from the core to the edge using a stereomicroscope following standard aging protocols (VanderKooy et al., 2020). Age class was determined based on the number of opaque zones and summer annulus deposition (Snelson, 1992), i.e., age was determined as the number of opaque zones unless the fish was collected between January 1 and July 31 and the margin code was 3 or 4. In this case, age was assigned as the number of opaque zones plus one. Each fish from the Florida Keys was read with at least two blind reads at the Florida Fish and Wildlife Conservation Commission Fish and Wildlife Research Institute (FWRI) in St. Petersburg, FL. If the two reads disagreed, then a third read was conducted, and the final age was determined from the consensus age of the three reads. Each fish from Alabama was aged by two readers at MSU. If the two readers disagreed on an age assignment, a third reader aged the otolith and final age was assigned if two out of the three readers agreed. If all three readers disagreed, then the first two readers consulted with each other and either reached an agreement or deemed the otolith unreadable.

2.4 Stable isotope analysis

Oxygen and carbon stable isotopes can be used to examine spatial connectivity since stable isotope values vary predictably across the Gulf of Mexico as a function of climate and nutrient regimes (McMahon et al., 2013; Trueman et al., 2012). Sectioned otoliths not used for aging (right sagittal) were first photographed using a high-resolution camera affixed to a stereomicroscope. Using ImageJ software (Abràmoff et al., 2004), the approximate width of each growth band in mm was measured. Otoliths were then sampled using a New-Wave micromill in the University of Miami Stable Isotope Laboratory (Figure 3). With the micromill system used in this study, the user manually traces transects across the sample region of interest on an image of the otolith on the computer screen. The computer then interpolates between two transects at a fixed distance with the material from each pass being milled on the advancing edge of the cutting blade. Transects were milled starting from the otolith edge and moving in towards the core in 0.05 mm increments for a maximum of 21 transects per otolith (range $= 16$ -21). Increments of 0.05 mm between transects were chosen to maximize temporal resolution while ensuring enough material was available for analysis (at least 0.04 mg of powder per transect was required). Powdered material was collected in glass vials for subsequent analysis. The $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values of the multiple transects of each analyzed otolith were measured using a ThermoQuest Finnigan Delta Plus Mass Spectrometer (Thermo Fisher Scientific, Inc., Bremen, Germany) attached to a Kiel III automated carbonate device. Internal standards (six within each run) calibrated to NBS-19 (National Bureau of Standards) were processed along with a batch of 40 samples. The measured values were corrected for the usual isobaric interferences and are reported

relative to Vienna Pee Dee Belemnite (V-PDB) using the conventional notation. Standard deviations determined on the standards were less than 0.05‰ for $\delta^{13}C$ and less than 0.1‰ for $\delta^{18}O$.

2.5 Statistical analysis

According to independent 2-group *t*-tests for each growth band, there were no significant differences in growth band widths between the two groups of Crevalle Jack (*p* > 0.05 for all *t*-tests). We therefore assumed growth rates were approximately the same between AL and FK and transect numbers corresponded to the same time in each fish's life. A series of regression models were fit to the carbon and oxygen data, with $\delta^{18}O_{\text{oto}}$ or δ^{13} C_{oto} values as the response variable and transect number (proxy for fish age) and population (FK or AL) as explanatory variables. The goal of the regression modeling was to examine the typical trends in $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values throughout the life history of Crevalle Jack and determine if isotopic profiles differed significantly between fish captured in isotopically distinct regions. The regression models fit to the isotope data included linear, logarithmic, quadratic, cubic, and restricted cubic spline models. Residuals and q-q plots were used to assess normality and homogeneity of variance assumptions for the linear models (linear, logarithmic, quadratic, cubic). For all models, the normality assumption was not met, so we subsequently fit restricted cubic spline models using the rms package in R (Harrell Jr, 2021). Restricted cubic splines are flexible models that can fit many types of non-linearities by joining a series of polynomial functions together at knots (Durrleman and Simon, 1989). Simplified models with $\delta^{18}O_{\text{oto}}$ or $\delta^{13}C_{\text{oto}}$ values as the response variable and transect number as the only explanatory

variable were fit with 3, 4, and 5 knots and compared using AIC (Akaike Information Criterion; Akaike, 1973) and BIC (Bayesian Information Criterion; Schwarz, 1978). The model with the lowest AIC and BIC was then selected and named model 1. This model was the simplest model with only transect as the sole source of variance, and its fit was compared with models that incorporated population information. Two additional models were fit to the data, model 2 with transect and location as explanatory variables, and model 3 with transect, location, and a transect by location interaction term. All three models were compared using AIC/BIC and the model with the lowest AIC/BIC was selected as the best fitting model.

Once the best fitting models were selected for both carbon and oxygen, we computed contrasts of the estimated regression coefficients between the two locations for each transect using the contrast.rms function in the rms package. Within a linear model, contrasts can be used to make specific comparisons between treatments and test various hypotheses. We wanted to test whether the difference between the model coefficients for AL and FK fish was significantly greater than zero at each transect. Significant differences $(p < 0.05)$ provided evidence that on average, AL and FK fish inhabited isotopically distinct areas during a given point of the life history. Average measured growth band widths of all samples were used to assign each transect to an approximate age to assist with interpreting the isotope data. All analyses were conducted using R version 4.0 (R Core Team, 2021).

3. Results

A total of 24 Crevalle Jack otoliths were analyzed, 12 from coastal Alabama and 12 from the Florida Keys. All fish were collected between 2017 and 2021 and ranged in age from 4-5 years old, with 16 fish age-4 and 8 fish age-5 (Supplementary, Table S1). The number of transects milled per otolith ranged from 16 to 21, depending on the age of the fish and timing of collection. The average number of transects milled per otolith was 19.3, and the total sample size was 426 transects. As there were no significant differences in growth band widths between the two groups, the average estimated growth band widths from all fish were used to assign the following approximate ages to each transect: Transects-1-3 were assigned to age-0, transects-4-7 to age-1, transects-8-11 to age-2, transects-12-15 to age-3, transects-16-19 to age-4, and transects-20-21 to age-5 (Table 1).

3.1 Model selection

For the $\delta^{18}O_{\text{oto}}$ values, a 3-knot restricted cubic spline was the best fitting model according to BIC, but a 5-knot spline was the best fitting model according to AIC. Since the 3-knot spline was only four AIC points higher than the 5-knot spline, the 3-knot spline was chosen as the best fitting model based on parsimony (Burnham and Anderson, 2002; Table 2). For $\delta^{13}C_{\text{oto}}$ values, the 3-knot restricted cubic spline model fit the data best according to both AIC and BIC (Table 2). For both $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values, the most complex model including transect, location, and a transect by location interaction was the best fitting model (Table 3).

3.2 Average lifetime stable isotope patterns

The regression models revealed that the typical life history stable isotope profile of a Crevalle Jack in the eastern GOM begins with relatively low $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values at age-0 followed by an increase in both $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values between ages-1 and -2. Model predicted $\delta^{13}C_{\text{oto}}$ values increased by 2.78% from transect-1 to transect-11 for AL fish and by 3.82‰ from transect-1 to transect-12 for FK fish, while predicted $\delta^{18}O_{\text{oto}}$ values increased by 2.99% from transect-1 to transect-13 for AL fish and by 5.78‰ from transect-1 to transect-14 for FK fish (Figure 4). The observed peaks for both isotope ratios were between transects-12 and -14, which approximately corresponds to age-3. The timing of the peak in isotope values was similar between AL and FK fish. Across both groups, $\delta^{13}C_{\text{oto}}$ values remained relatively stable throughout the remainder of the transects, decreasing by less than 1‰ after the peak for both AL and FK fish. $\delta^{18}O_{oto}$ values however, decreased gradually after the transect-12 peak by 2.06‰ for AL fish and by 1.73‰ for FK fish.

3.3 Individual variability

Although regression models showed a general pattern of increasing $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values from age-0 to age-3 followed by a slight decline from age-3 to age-5 among all Crevalle Jack, individual variability in stable isotope profiles was evident (Figs. 5, 6; Supplementary, Table S2). For AL fish, the $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values for fish #AL 2, AL 7, AL 8, and AL 12 did not increase from age-0 to age-3, instead remaining relatively constant throughout the life history. Additionally, fish #AL 4 and #AL 6 showed much more variability in isotope values over time, with several peaks and

valleys. FK fish showed slightly less individual variability than AL fish, with the general pattern revealed by the regression models being evident for each fish except fish #FK 12. There was instead a substantial dip in both $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values at age-3 for this individual.

3.4 Geographic variation

Initially, both $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values were lower on average for FK fish than AL fish, from about transect-1 to transect-6. After transect-6, the average $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values for FK fish increased more than for AL fish and remained higher for the rest of the life-history (Figure 4). For each transect value, contrasts of the estimated regression coefficients from the best fitting models were assessed. For $\delta^{18}O_{\text{oto}}$ values, contrasts were significant at the $\alpha = 0.5$ level for transect-1 and transects-10-21 (Supplementary, Table S3). For $\delta^{13}C_{\text{oto}}$ values, contrasts were significant for transects-1-4 and transects-8-21 (Supplementary, Table S4). Despite location being a significant factor in the regression models, individual variability led to some overlap in $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values throughout the otolith transects between the two populations.

4. Discussion

Stable isotope micro-sampling of fish otoliths can provide a wealth of information about habitat use throughout the life-history of a species, which is critical information for fisheries management and conservation (Compton et al., 2012; Galaiduk et al., 2017; Nagelkerken et al., 2015). Our research showed the applicability of this approach for assessing lifetime migration patterns and connectivity of data-poor populations with

wide-ranging distributions. In the eastern GOM, there is a substantial difference in environmental stable isotope values of carbon and oxygen between northern and southern coastal aquatic habitats (Fry, 1983; Vander Zanden et al., 2015). The main goal of our research was to determine whether otolith stable isotope micro-sampling could be used to distinguish between individual fish captured from both regions of the GOM (northeastern and southeastern), and whether fish from the two regions exhibited similar lifetime migration patterns. Our model results suggested that on average, isotopic profiles of Crevalle Jack from Alabama and the Florida Keys were significantly different, but that both groups underwent ontogenetic migrations from nursery to sub-adult/adult habitats at the same age and seemed to follow the same migration patterns post-ontogeny. However, there was overlap in stable isotope values between some individuals from the two regions, suggesting that some connectivity may occur. In other words, the overlap in ranges of both $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values suggests that some level of mixing between contingents of the AL and FK populations, and thus the northeastern and southeastern GOM, may occur. Our results did not appear to support any of our original hypotheses (Figure 2), but instead supported a fourth hypothesis, that there is a separation between age-0 to age-5 Crevalle Jack from the two areas, but that some level of connectivity may occur due to individual variability. This information will help guide spatial management of the Crevalle Jack in the GOM.

4.1 Lifetime migration patterns

In our study, most Crevalle Jack otoliths displayed the same trend of increasing $\delta^{18}O_{\text{oto}}$ values from age-0 to about age-3 regardless of the region where they were

collected (AL or FK). The minimum measured $\delta^{18}O_{\text{oto}}$ value was -9.32% for fish #AL 6 and the maximum was 1.20‰ for fish #FK 2 (Supplementary, Table S2). Oxygen stable isotope values in the ocean are influenced by evaporation and freshwater input, and correlate with salinity (Epstein and Mayeda, 1953). During incorporation into biominerals (i.e., aragonite and calcite in shells and otoliths), stable isotopes of oxygen are fractionated and the magnitude of fractionation is directly related to water temperature (Trueman and St. John Glew, 2019). Under conditions where the $\delta^{18}O_{\text{water}}$ value is constant, an increase in $\delta^{18}O_{\text{oto}}$ value is indicative of a decrease in water temperature. Research has shown that temperature-induced $\delta^{18}O_{\text{oto}}$ varies by approximately 1‰ per 4°C (Høie et al., 2004). According to NOAA sea surface temperature satellite data, water temperature varies by less than 10°C seasonally in the Florida Keys region and by less than 15°C seasonally in the Alabama region (Huang et al., 2015). These seasonal temperature ranges are not enough to explain the full range of $\delta^{18}O_{\text{oto}}$ values measured in Crevalle Jack otoliths. However, fish migrating among seawater, brackish estuaries, and freshwater environments can display much larger variations in $\delta^{18}O_{\text{oto}}$ values (Hsieh et al., 2019). Open ocean seawater has measured δ^{18} O_{water} values close to 0‰, while freshwater is typically depleted in ¹⁸O, with δ^{18} O_{water} values as low as -10‰ (Kendall and Coplen, 2001; Lin et al., 2011). The increase in $\delta^{18}O_{\text{oto}}$ values from age-0 to age-3 observed in Crevalle Jack otoliths likely reflects some combination of a decrease in water temperature and increase in salinity, which could be explained by a transition from warm, shallow water inshore habitats to cooler, higher salinity coastal habitats.

Measured $\delta^{13}C_{\text{oto}}$ values also increased from age-0 to age-3 for most fish. The minimum measured $\delta^{13}C_{\text{oto}}$ value was -15.63% for fish #AL10 and the maximum was -1.58‰ for fish #FK 4 (Supplementary, Table S2). The carbon isotope composition of fish otoliths is much more complex than the oxygen isotope composition, and is deposited in disequilibrium with the surrounding environment (Martino et al., 2020). Carbon isotopes in otoliths are a combination of dissolved inorganic carbon (DIC) in the aquatic environment and oxidized organic carbon derived from the diet of the fish (Høie et al., 2003; Solomon et al., 2006). Studies have estimated that the majority of otolith isotope composition is derived from DIC $(-80%)$ with the remaining 20% derived from the diet (Høie et al., 2003; Nelson et al., 2011; Solomon et al., 2006; Tohse and Mugiya, 2007; Weidman and Millner, 2000). However, δ^{13} C_{DIC} values in coastal waters exhibit a fairly limited range (approximately -2‰ to 2‰), with 13 C often more depleted in estuarine and freshwater systems than in marine systems (Bouillon et al., 2011). The increase we observed in Crevalle Jack $\delta^{13}C_{\text{oto}}$ values over time therefore could reflect a combination of an ontogenetic migration between habitats with distinct $\delta^{13}C_{\text{DIC}}$ values, a shift in diet, possibly from a more terrestrial source (low δ^{13} C values) to a more marine source (high δ^{13} C values; Peterson and Fry, 1987), a shift in trophic position, as δ^{13} C values typically increase by 1‰ for every increase in trophic level (Peterson and Fry, 1987), and/or a decrease in size-specific metabolism, which causes an increase in $\delta^{13}C_{\text{oto}}$ values (Chung et al., 2019; Høie et al., 2004). Additionally, there is an inverse relationship between δ^{13} C_{oto} values and temperature, as temperature is a primary driver of metabolic rate (Martino et al., 2020).

Our ontogenetic migration hypothesis aligns with previous observations of Crevalle Jack habitat use as well as previous literature. The Florida Fish and Wildlife Conservation Commission (FWC) conducts regular 183-m seine fisheries-independent monitoring (FIM) surveys in shallow, coastal estuaries. In all Gulf coast estuaries sampled between 1996 and 2018, length-frequency distributions of the catch showed that age-0 Crevalle Jack were most abundant, with few fish captured older than age-1 (FWC, 2021). Previous otolith micro-sampling research also attributed similar increases in both $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values over time observed in Chum Salmon (*Oncorhynchus keta*) to ontogenetic movement from inshore nurseries to more marine habitats (Wang et al., 2021). Ontogenetic migrations from inshore, estuarine nursery habitats to coastal and offshore subadult/adult habitats have been observed for several sportfish species in the GOM, including Red Drum (*Sciaenops ocellatus*; Winner et al., 2014) and Atlantic Tarpon (*Megalops atlanticus*; Kurth et al., 2019). Morphology and behavior change as fish grow, which often necessitates a change in habitat to meet energetic requirements and resource needs (Huijbers et al., 2015). Movement from juvenile to adult habitats may specifically be associated with reproduction or habitat shifts reflecting changing ratios of mortality risk and growth rates (Gillanders et al., 2003). Typically, individuals will reside in areas of low mortality risk as juveniles, when they are most susceptible to predation, and move to areas with higher mortality risk but better access to food resources as they grow and become less susceptible to predation. These ontogenetic habitat shifts therefore often involve trade-offs between fitness and survival that can impact physiological processes like growth (Higgins et al., 2015). Knowledge of these changes in habitat niche requirements over the life history of a species is crucial for understanding how

community composition is structured across a mosaic of habitats (Compton et al., 2012; Nagelkerken et al., 2015). This in turn aids in multispecies spatial management (Galaiduk et al., 2017).

Although most Crevalle Jack otoliths exhibited an increase in $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values from age-0 to age-3, there were a few individuals (all AL fish), for which isotope values did not increase (Figure 5). Fish #AL 2, AL 7, AL 8, and AL 12 had relatively constant $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values from age-0 to age-3. This result does not necessarily preclude ontogenetic migration, as it is possible these individuals simply moved between nursery and adult habitats that had similar isotopic profiles. The influence of the large river systems in the northern GOM extends out into the coastal environment, leading to substantial mixing between inshore and coastal areas that varies seasonally and annually (Sanial et al., 2019). This mixing could explain the relatively homogeneous stable isotope profiles of some AL Crevalle Jack even if they engaged in migration behavior. However, we also noted individual variability in the range of $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values present throughout the otoliths of fish from both regions. Research has shown that variability in intrinsic factors such as body condition and sex can influence animal behavior and lead to substantial individual variability in lifetime movement and migration patterns within populations (Bolnick et al., 2011; Sih et al., 2004). Understanding the drivers and consequences of individual variability in movement patterns through ontogeny is important for understanding how environmental changes affect individual fitness of valuable species (Matich and Heithaus, 2015).

By age-3, Crevalle Jack appeared to have completed their ontogenetic migration, which coincides with estimated age at sexual maturity in the Caribbean (Caiafa et al.,

2011), though age at maturation has been shown to vary significantly between populations of the same species, e.g., for Bonefish (*Albula vulpes*; Rennert et al., 2019). $\delta^{18}O_{\text{oto}}$ values then decreased gradually after age-3 by about 2‰ while $\delta^{13}C_{\text{oto}}$ values remained relatively constant, declining only slightly. It is difficult to make any conclusions regarding movement patterns from age-3 to age-5 based solely on the $\delta^{13}C_{\text{oto}}$ values due to the variety of factors that influence carbon fractionation in fish otoliths. The decline in $\delta^{18}O_{\text{oto}}$ values, however, suggests movement to an isotopically distinct habitat, perhaps lower salinity and/or warmer waters. The observed decrease in $\delta^{18}O_{\text{oto}}$ values from age-3 to age-4 could feasibly represent a gradual movement towards the species preferred temperature (Fry, 1947). Adult Crevalle Jack occupy a range of habitats, including canals, deep-water reefs, and shallow-water flats (Smith-Vaniz and Carpenter, 2007). High-resolution stable isotope analysis of the older bands of the otoliths coupled with oceanographic data and other methods like acoustic telemetry (Ajemian et al., 2020), could increase our understanding of these fine-scale movement patterns postontogeny.

4.2 Geographic variation

Overlap in individual stable isotope profiles between AL and FK fish precludes concluding that fish from the two regions represent distinct, self-recruiting populations with no mixing. However, there was a distinction on average between the otolith stable isotope values of AL and FK Crevalle Jack, with location of capture being a significant factor in both the oxygen and carbon cubic spline models. At the point of capture (age-4 or age-5) contrasts of the estimated regression coefficients revealed that the predicted

 $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values were significantly higher in FK otoliths than AL otoliths, with about a 0.5 to 0.9‰ difference in $\delta^{18}O_{\text{oto}}$ values between regions on average and about a 0.6 to 1.5‰ difference in $\delta^{13}C_{\text{oto}}$ values between regions on average (Supplementary, Tables S3, S4). In the GOM, numerous studies have examined spatial heterogeneity of δ^{18} O and δ^{13} C values in coastal water, primary producers, fish muscle tissue, and fish otoliths. Compared to the southeastern GOM (Florida Keys), where $\delta^{18}O_{water}$ values in marine environments are relatively high $({\sim} 1.7%)$ due to high rates of evaporation (Sternberg and Swart, 1987), in the northeastern GOM (Alabama), influxes of freshwater from large river systems lead to relatively low $\delta^{18}O_{\text{water}}$ values ranging from -2.2 to -6.6‰ (Wagner and Slowey, 2011). This pattern has also been observed in fish otoliths. Gerard & Muhling (2010) examined $\delta^{18}O_{\text{oto}}$ values for juvenile Gray Snapper (*Lutjanus griseus*) in the Florida Keys region, with mean values around 0‰. Similarly, Patterson et al. (2014) examined $\delta^{18}O_{\text{oto}}$ values in juvenile Red Snapper (*Lutjanus campechanus*) and Lane Snapper (*Lutjanus synagris*) in coastal Alabama waters, and mean $\delta^{18}O_{\text{oto}}$ values were about -1.8‰ and -1.2‰, respectively.

Vander Zanden et al. (2015) created a δ^{13} C value isoscape for the Eastern Gulf of Mexico region using loggerhead scute tissue that showed clear $\delta^{13}C_{\text{scute}}$ value enrichment in south Florida coastal waters $({\sim}$ -13 to -8‰) compared to the northern GOM $({\sim}$ -20 to -15‰). Fry (1983) compared δ^{13} C_{muscle} values in several species of shrimp throughout coastal GOM waters and had similar findings as Vander Zanden et al. (2015). The authors found a significant difference between the south Florida coast and the Louisiana and North Texas coasts, with lower $\delta^{13}C_{\text{muscle}}$ values in shrimp from the latter regions (\sim -13 to -11‰ in Florida compared to ~ -19 to -16‰ in Louisiana). As metabolic carbon

comprises about 20% of fish otoliths, this difference of around 5 to 10‰ between $\delta^{13}C$ values of loggerhead scute tissue and shrimp muscle tissue in the northeastern and southeastern GOM could explain the approximate 0.6 to 1.5% difference between $\delta^{13}C_{\text{oto}}$ values of AL and FK Crevalle Jack post-ontogeny. Since $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values for FK fish remained significantly higher than for AL fish from age-3 to age-5, it suggests most fish in this age range remained in their respective regions (northeastern or southeastern GOM), but some individuals may have moved between regions.

The significant difference in $\delta^{13}C_{\text{oto}}$ values between AL and FK fish at age-0 (Supplementary, Tables S3, S4) suggests that these two groups of fish may have utilized geographically distinct nursery habitats. The difference in $\delta^{13}C_{\text{oto}}$ values between nurseries could be due to differences in estuarine vegetation. In the GOM, salt marshes and mangroves are the predominant intertidal habitats, and there is a north-south transition with salt marshes ranging from 25 to 45°N (IFAS, 2016), and mangrove habitats dominating latitudes 30°N to 30°S (Giri et al., 2011). Therefore, south Florida mainly consists of mangrove intertidal habitats while Alabama is dominated by salt marsh habitats. Mangroves are predominantly C_3 plants and salt marshes contain predominantly C₄ plants (Baker et al., 2021). Numerous studies have shown that $\delta^{13}C$ values are significantly higher in C_4 plants than C_3 plants (Baker et al., 2013; Bouillon et al., 2008; Cerling et al., 1997; Currin et al., 1995), with δ^{13} C values of C₄ plants being around -12‰ and $\delta^{13}C$ values of C_3 plants being around -24‰ to -30‰ (Bouillon et al., 2011). This regional difference in the base of the estuarine food web could explain why the $\delta^{13}C_{\text{oto}}$ values were lower on average in age-0 FK fish than in age-0 AL fish and

suggests most fish may have exhibited local recruitment from inshore juvenile habitats to nearby coastal habitats.

4.3 Study limitations

An assumption of our study was that growth rates did not vary significantly among all the sampled Crevalle Jack, and therefore each transect corresponded to the same region of the otolith. There were slight differences in measured growth band widths among otoliths (Table 1), but the differences were minor, suggesting that growth rates were similar among the individuals. Furthermore, there were no significant differences in growth band widths between the two populations (AL and FK) based on independent 2 group t-tests for each growth band. Nevertheless, the slight differences in growth band widths likely explain some of the variance in $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values per transect among fish from the same region, and this variation also means that the groups of transects assigned to each age are approximate. Another potential source of variation is due to sampling of Crevalle Jack otoliths over multiple years (2017-2021). Carbon stable isotope values in the ocean can vary annually due to changes in productivity, and oxygen stable isotope values can vary with changes in runoff, evaporation, and precipitation. This variability can thus effect $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values (Trueman et al., 2012). Finally, while lifetime isotopic profiles were only examined through age-5, the Crevalle Jack is a relatively long lived species with a maximum recorded age of 19 years (Snelson, 1992). Therefore, movements beyond age-5 remain unknown. However, a challenge with micromilling otoliths from very old fish is that growth band width decreases with age as somatic growth slows. Transects at these older bands would therefore likely reflect the

combined isotopic environment experienced over an entire year, or even multiple years, possibly obscuring migrations. Studies that combine otolith stable isotope analysis with other techniques like acoustic telemetry (Crossin et al., 2017) or genetics (Ovenden, 2013) can help further elucidate lifetime movement and migration patterns and connectivity of important species.

5. Conclusions

The results of our research provide detailed information about Crevalle Jack migration patterns through ontogeny and a distinction on average between individuals captured in the Florida Keys and coastal Alabama that aligns with known isotopic variations between the two regions. These findings suggest that some Crevalle Jack may exhibit local recruitment from inshore estuaries to nearby coastal habitats and remain in either the northeastern or southeastern GOM regions through to at least age-5. However, there was substantial individual variability, suggesting that some individuals may move between regions during ontogeny (i.e., recruit to inshore nurseries at age-0 in one region but migrate to sub-adult habitats in the other region). This information is critical for spatial management of the species and will aid in future conservation efforts. Microsampling of otoliths allowed us to assess changes in movement and migration throughout the life history quickly and easily, with only a limited number of samples collected over a short time. Even though we had little *a priori* knowledge of Crevalle Jack migration patterns and population connectivity, well-known isotopic gradients in the Gulf of Mexico afforded us the opportunity to examine migration and connectivity without extensive, long-term sampling. As scientists continue to map isoscapes of marine and

coastal environments and assess seasonal and annual variability, stable isotope research will further aid in understanding and managing important fish stocks. Our research serves as a case study for the applications of otolith stable isotope micro-analysis to assessing species ecology, population dynamics, and connectivity. Future work analyzing stable isotopes of Crevalle Jack juvenile otoliths from a range of nursery habitats could help identify linkages between juvenile and adult habitats, further elucidating stock structure. Furthermore, the methods outlined in this manuscript can be applied to any fish species and may be especially useful for future studies on migration and connectivity of datapoor species with broad spatial distributions.

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Table 1. Mean and standard error of growth band widths measured using ImageJ, approximate number of transects milled within each age band (each transect was 0.05 mm), and transect numbers assigned to each age. Age-4 growth bands were only measured for fish aged to be 5 years old since the entire age-4 band may not have been present at the time of collection for 4-year-old fish. Growth band widths were not measured for age 5, since age-5 fish were culled at varying times during year 5, and thus remaining transects were assigned to age-5.

$\delta^{18}O_{oto}$	Knots	Adjusted \mathbb{R}^2	AIC -	BIC
	3	0.327	1477	1493
	4	0.332	1474	1495
		0.337	1473	1497
$\delta^{13}C_0$ \mathbf{C}_{oto}	Knots	Adjusted \mathbb{R}^2	AIC	BIC
	3	0.385	1677	1693
	4	0.385	1678	1698
		0.383	1680	1704

Table 2. Adjusted \mathbb{R}^2 , AIC, and BIC for each base restricted cubic spline model (isotope \sim transect) with 3, 4, and 5 knots fit to the $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ data. Bolded terms indicate the best model selected.

$\sqrt{$}^{18}O_{\text{oto}}$	Variables	Adjusted \mathbb{R}^2	AIC	BIC
	Transect	0.327	1477	1493
	Transect, Location	0.335	1473	1493
	Transect, Location, Transect x Location	0.353	1463	1491
s13 _C \sim oto	Variables	Adjusted \mathbb{R}^2	AIC	BIC
	Transect	0.385	1677	1693
	Transect, Location	0.405	1664	1684
	Transect, Location, Transect x Location	0.449	1633	1661

Table 3. Adjusted \mathbb{R}^2 , AIC, and BIC for each 3-knot restricted cubic spline model fit to the $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ data. Bolded terms indicate the best model selected.

Figure 1. Approximate capture locations of Crevalle Jack in Alabama (red hashed box) and Florida (blue hashed box) sampled for otolith stable isotope analysis. Exact GPS coordinates of capture locations were not recorded. Yellow arrows point to Mobile Bay, the DeSoto canyon, and Cape San Blas, areas that may serve as zoogeographic divides in the northern Gulf of Mexico. Inset map highlights study area in the southeastern United States. Map credit Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors.

Figure 2. Hypotheses concerning population connectivity between Florida Keys (blue lines) and Alabama (red lines) Crevalle Jack. Diagrams show simplified expected otolith stable isotope results corresponding to each hypothesis, with shaded regions denoting expected ranges of individual transects. If the two populations represent distinct, selfrecruiting stocks (H1), we would expect $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values to differ between populations throughout the otolith, regardless of the actual isotope ratio values, with no overlap between individuals from the distinct regions. If there are common nursery habitats but distinct habitats post-ontogeny (H2), we would expect overlap in the $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\alpha}$ values at earlier ages, with potentially substantial individual variability indicative of random distribution amongst juvenile habitats, followed by a divergence to different values post-ontogeny. If mixing between populations occurs throughout the life history (H3), we would expect overlap in $\delta^{18}O_{\text{oto}}$ and $\delta^{13}C_{\text{oto}}$ values everywhere except the otolith edge (point of capture), with substantial variability amongst individual fish.

Figure 3. Simplified schematic diagram of the micromilling system used in this study. The initial drill path runs parallel to the edge of the otolith section (A). Powdered sample is collected, and the drill is moved up the sample towards the core in increments of 0.05 mm until the entire otolith has been sampled. Drill path partway through the otolith (B). Image of the user-drawn initial and final drill paths (yellow lines) and computer interpolated drill paths (green lines) (C). Image of the otolith sample with the initial drill path completed (D).

Figure 4. Three-knot cubic spline regression model predictions (black lines) for $\delta^{18}O_{\text{oto}}$ (top) and $\delta^{13}C_{\text{oto}}$ (bottom). Red dots are raw data points and shaded red regions are 95% confidence intervals corresponding to Alabama Crevalle Jack (AL). Blue dots and shaded blue regions are 95% confidence intervals corresponding to Florida Crevalle Jack (FK). Gray dotted vertical lines are estimated age transition points, and numbers 0-5 across the top are estimated ages corresponding to each range of transects.

Figure 5. Individual $\delta^{18}O_{\text{oto}}$ (oxygen) and $\delta^{13}C_{\text{oto}}$ (carbon) transects for each Crevalle Jack from Alabama (AL). Some transects have missing values due to instrument error or small sample size.

Figure 6. Individual $\delta^{18}O_{\text{oto}}$ (oxygen) and $\delta^{13}C_{\text{oto}}$ (carbon) transects for each Crevalle Jack from the Florida Keys (FK). Some transects have missing values due to instrument error or small sample size.

Fish number	Population	Capture date	Fork length (mm)	Assigned age (years)
AL ₁	Alabama	7/21/2017	690	4
AL ₂	Alabama	7/21/2017	821	5
AL ₃	Alabama	7/21/2017	751	5
AL ₄	Alabama	7/22/2017	750	4
AL ₅	Alabama	7/23/2017	711	5
AL ₆	Alabama	7/20/2018	703	$\overline{4}$
AL ₇	Alabama	7/20/2018	771	5
AL ₈	Alabama	7/20/2018	849	5
AL ₉	Alabama	7/22/2018	745	$\overline{4}$
AL 10	Alabama	7/19/2019	797	5
AL 11	Alabama	7/20/2019	785	5
AL 12	Alabama	7/21/2019	750	$\overline{4}$
FK ₁	Florida	11/9/2018	600	4
FK ₂	Florida	11/9/2018	524	4
FK ₃	Florida	11/9/2018	570	4
FK4	Florida	11/9/2018	615	$\overline{4}$
FK ₅	Florida	11/9/2018	553	$\overline{4}$
FK ₆	Florida	11/9/2018	615	$\overline{4}$
FK7	Florida	2/18/2019	645	$\overline{4}$
FK ₈	Florida	2/18/2019	790	4
FK ₉	Florida	2/18/2019	642	$\overline{4}$
FK10	Florida	2/18/2019	640	5
FK11	Florida	1/3/2021	660	4
FK12	Florida	1/4/2021	620	$\overline{4}$

Table S1. Capture location (Alabama = Mobile Bay, Florida = Florida Keys), capture date, fork length, and otolith assigned age for each of the Crevalle Jack assessed in this study.

Fish		Max.		Avg.	Max.	
number	Avg. $\delta^{13}C_{\text{oto}}$	$\delta^{13}C_{\text{oto}}$	Min. $\delta^{13}C_{\text{oto}}$	$\delta^{18}O_{o\underline{t}\underline{o}}$	$\delta^{18}O_{\text{oto}}$	Min. $\delta^{18}O_{\text{oto}}$
AL ₁	-7.95	-6.37	-10.25	-1.70	-0.55	-4.59
AL ₂	-6.19	-5.38	-6.79	-0.71	-0.19	-2.30
AL ₃	-6.08	-4.69	-13.90	-1.56	-0.42	-7.98
AL ₄	-7.45	-6.04	-10.75	-2.11	-0.08	-8.69
AL ₅	-7.64	-6.38	-9.40	-0.92	-0.07	-3.26
AL ₆	-7.03	-4.52	-11.00	-3.01	-0.25	-9.32
AL ₇	-5.33	-4.31	-6.26	-0.38	0.22	-1.83
AL ₈	-5.88	-4.98	-7.23	-1.10	-0.45	-2.45
AL ₉	-6.15	-4.55	-9.21	-2.32	0.26	-8.56
AL 10	-9.19	-6.39	-15.63	-1.72	0.04	-5.61
AL11	-7.16	-5.37	-11.82	-0.46	0.44	-4.78
AL 12	-5.97	-4.55	-7.39	-0.88	0.26	-4.66
FK ₁	-6.05	-4.27	-10.07	-0.71	0.25	-2.09
FK ₂	-4.98	-2.47	-9.35	-0.91	1.20	-3.31
FK ₃	-5.75	-4.15	-9.05	-0.86	0.56	-3.47
FK4	-5.06	-1.58	-10.73	-0.95	0.08	-3.19
FK ₅	-6.13	-1.75	-11.78	-0.92	0.41	-3.29
FK ₆	-6.94	-4.69	-11.12	-1.23	0.20	-3.83
FK7	-5.93	-4.29	-9.73	-0.99	0.18	-4.49
FK 8	-6.90	-4.70	-11.86	-1.41	-0.02	-7.40
FK ₉	-6.33	-4.50	-10.58	-1.14	-0.17	-4.99
FK10	-6.60	-4.65	-9.26	-1.04	0.20	-3.16
FK11	-6.23	-4.63	-9.79	-0.44	0.81	-5.09
FK12	-8.33	-6.06	-11.73	-1.75	0.06	-5.93

Table S2. Average, maximum, and minimum $\delta^{13}C_{\text{oto}}$ and $\delta^{18}O_{\text{oto}}$ values throughout the otolith for each Crevalle Jack.

Table S3. Contrasts of regression coefficients between Alabama and Florida for each transect number from the best fitting $\delta^{18}O_{\text{oto}}$ model, including standard errors, lower and upper confidence limits, t-values, and p-values (α = 0.05). Confidence intervals are 0.95 individual intervals. Estimated ages are based on measured growth band widths (Table 2).

Transect	Estimated age	Contrast	S.E.	Lower	Upper	t-value	p-value
1	$\overline{0}$	0.66	0.33	0.01	1.31	1.98	< 0.05
$\overline{2}$	θ	0.52	0.28	-0.04	1.08	1.84	0.07
3	0	0.38	0.24	-0.09	0.85	1.61	0.11
4	1	0.25	0.20	-0.15	0.64	1.22	0.22
5	$\mathbf 1$	0.11	0.18	-0.24	0.46	0.63	0.53
6	1	-0.02	0.17	-0.35	0.32	-0.10	0.92
7	1	-0.14	0.17	-0.48	0.20	-0.81	0.42
8	$\overline{2}$	-0.26	0.19	-0.62	0.11	-1.38	0.17
9	$\overline{2}$	-0.36	0.20	-0.75	0.02	-1.84	0.07
10	$\overline{2}$	-0.46	0.20	-0.86	-0.06	-2.25	< 0.05
11	$\overline{2}$	-0.54	0.20	-0.94	-0.14	-2.65	0.01
12	3	-0.61	0.20	-1.00	-0.22	-3.09	0.01
13	3	-0.67	0.19	-1.03	-0.30	-3.60	0.01
14	3	-0.71	0.17	-1.06	-0.37	-4.08	0.01
15	3	-0.75	0.17	-1.09	-0.41	-4.35	0.01
16	4	-0.78	0.19	-1.15	-0.42	-4.21	0.01
17	4	-0.81	0.21	-1.23	-0.39	-3.77	0.01
18	4	-0.84	0.26	-1.34	-0.33	-3.26	0.01
19	4	-0.86	0.31	-1.46	-0.26	-2.82	0.01
20	5	-0.89	0.36	-1.59	-0.18	-2.47	< 0.05
21	5	-0.91	0.41	-1.72	-0.10	-2.20	< 0.05

Table S4. Contrasts of regression coefficients between Alabama and Florida for each transect number from the best fitting $\delta^{13}C_{\text{oto}}$ model, including standard errors, lower and upper confidence limits, t-values, and p-values (α = 0.05). Confidence intervals are 0.95 individual intervals. Estimated ages are based on measured growth band widths (Table 2).

Transect	Estimated age	Contrast	S.E.	Lower	Upper	t-value	p-value
1	$\boldsymbol{0}$	1.40	0.40	0.60	2.19	3.45	0.01
$\overline{2}$	$\overline{0}$	1.09	0.34	0.42	1.77	3.17	0.01
3	Ω	0.79	0.29	0.22	1.36	2.71	0.01
$\overline{4}$	1	0.49	0.25	0.00	0.97	1.97	< 0.05
5	1	0.19	0.22	-0.24	0.62	0.88	0.38
6	1	-0.09	0.21	-0.50	0.32	-0.44	0.66
$\overline{7}$	1	-0.36	0.21	-0.78	0.06	-1.68	0.09
8	$\overline{2}$	-0.60	0.23	-1.05	-0.16	-2.67	0.01
9	$\overline{2}$	-0.82	0.24	-1.30	-0.35	-3.44	0.01
10	$\overline{2}$	-1.02	0.25	-1.51	-0.53	-4.08	0.01
11	$\overline{2}$	-1.17	0.25	-1.66	-0.68	-4.69	0.01
12	3	-1.29	0.24	-1.76	-0.82	-5.36	0.01
13	3	-1.37	0.23	-1.82	-0.93	-6.08	0.01
14	3	-1.43	0.21	-1.85	-1.01	-6.72	0.01
15	3	-1.47	0.21	-1.88	-1.05	-6.96	0.01
16	4	-1.48	0.23	-1.93	-1.04	-6.54	0.01
17	4	-1.49	0.26	-2.00	-0.97	-5.68	0.01
18	$\overline{4}$	-1.49	0.31	-2.10	-0.87	-4.76	0.01
19	$\overline{\mathcal{A}}$	-1.49	0.37	-2.22	-0.76	-4.00	0.01
20	5	-1.49	0.44	-2.35	-0.63	-3.40	0.01
21	5	-1.49	0.51	-2.48	-0.49	-2.94	0.01

CHAPTER IV

COLLABORATIVE ACOUSTIC TELEMETRY RESEARCH REVEALS MANAGEMENT-RELEVANT INFORMATION ABOUT AN UNREGULATED MIGRATORY FISH SPECIES

Abstract: The Crevalle Jack (*Caranx hippos*) is an economically and ecologically important marine fish species in Florida, U.S.A., but there is evidence the population may be in decline, potentially due to overfishing. As an unregulated species, little is known about Crevalle Jack biology and ecology, including movement and migration behavior. As the species is found throughout the western Atlantic and Gulf of Mexico, knowledge of stock structure, habitat use, and population connectivity are vital for developing effective conservation and management plans. In this study, we conducted collaborative acoustic telemetry research aimed at revealing management-relevant information about Crevalle Jack movement behavior in south Florida. By soliciting the aid of experienced recreational fishing guides to tag fish and partnering with the FACT and iTAG acoustic telemetry networks, we were able to tag 73 juvenile and adult Crevalle Jack and track their movements over three years. Our results showed connectivity between south Florida and the northern Gulf of Mexico, with five individuals being detected as far as coastal Louisiana. There was also a clear seasonality to movement patterns, with Crevalle Jack mainly residing in the south Florida region for the winter months before migrating north in the spring and inhabiting the northern GOM in the summer and fall. Whether individual fish engaged in these migrations appeared to be size-dependent, with smaller fish residing in south Florida year-round. Continued monitoring will determine if these long-range movements represent a bidirectional seasonal migration or a unidirectional ontogenetic migration. Our findings will aid in developing an appropriate management plan for the Crevalle Jack and illustrate the benefits of collaborative acoustic telemetry research.

1. Introduction

Animals move throughout their environments for various reasons, including foraging, predator avoidance, and spawning (Nathan et al., 2008). These movements, while vital, can affect how vulnerable species are to exploitation, climate change, or other anthropogenic stressors (Miller et al., 2014; Nash et al., 2013; Sawyer et al., 2009). Tracking animal movements and understanding habitat use are therefore critical for conservation and management (Hansson and Åkesson, 2014; Lédée et al., 2021). Movement information helps determine stock boundaries, identify important areas like spawning aggregations and nursery habitats, and assess the timing of seasonal migrations, all of which aid in understanding possible threats to the species of interest and managing populations accordingly (Cooke et al., 2004; Crossin et al., 2017). Tracking movements of marine and coastal fishes is particularly important but especially challenging. Many coastal fish species support both recreational and commercial fisheries and are at risk of overexploitation as fishing pressure increases and fishing technology continues to improve (Arlinghaus et al., 2007; Cooke and Cowx, 2004). Fisheries management is also typically based on stock structure and productivity, which depend on movement patterns and site fidelity (Lowerre-Barbieri et al., 2017, 2015). Furthermore, when management does not match the spatial distribution of a species it can have severe consequences, leading to overfishing or localized depletion (Berger et al., 2021; Ying et al., 2011). However, movements of aquatic animals are much more difficult to discern than movements of terrestrial animals (Sibert and Nielsen, 2001).

Advancements in tracking technology have substantially increased our ability to monitor movement and migration patterns of mobile fish species (Crossin et al., 2014;

Hockersmith and Beeman, 2012; Matley et al., 2021). Acoustic telemetry is a relatively affordable tracking method with widespread use that can operate in both marine and freshwater environments (Hussey et al., 2015; Matley et al., 2021). By attaching acoustic transmitters to individuals, their movements can be tracked by hydrophones and receivers that detect the sonic pulses emitted by the transmitters (Donaldson et al., 2014; Stasko and Pincock, 1977; Voegeli and Pincock, 1996). This method has many benefits and applications, and has been used to assess core habitat use, migratory pathways, home ranges, and individual and population level variations in movement behavior (Crossin et al., 2017). Furthermore, researchers have taken advantage in recent years of the crosscompatibility of acoustic telemetry technology to create collaborative networks of receiver arrays and share detection data among users (Crossin et al., 2017; Ellis et al., 2019). In the Gulf of Mexico and western Atlantic alone, thousands of receivers are currently deployed, owned by numerous research groups. Detection data from these receivers are shared through collaborative institutional networks including the Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) network (1,118 receivers; FWC, 2022), the FACT network (2,100+ receivers; FACT Network - SECOORA, 2021), which includes partners from the Carolinas to the Bahamas, and the Atlantic Cooperative Telemetry (ACT) network (~5,000 receivers; ACT, 2020), with receiver coverage from the Carolinas to Canada (Currier et al., 2015; Hussey et al., 2015; Whoriskey and Hindell, 2016). The Ocean Tracking Network (OTN) facilitates sharing of detection data, provides additional receivers to increase detection coverage in key areas, and works to improve researcher collaboration and marine monitoring (Cooke et al., 2011).

Research has demonstrated that acoustic telemetry can directly inform fisheries conservation and management, as characterization of spatiotemporal movements, habitat use, and interactions among individuals are key to conservation and management planning (Cooke et al., 2016; Crossin et al., 2017). For example, habitat management via protected areas is a common fisheries management tool (Goodchild, 2004; Jamieson and Levings, 2001; Mesnildrey et al., 2013). Identification of critical habitat (e.g., spawning grounds, juvenile nurseries, and overwintering sites; Rosenfeld and Hatfield, 2006; Schmitten, 1999) is key to designing protected areas that will adequately safeguard important habitats and the pathways between them. Many studies have used acoustic telemetry to characterize habitat use and preference of exploited fishes to inform habitat management (Crossin et al., 2017; Donaldson et al., 2014; Hussey et al., 2015). Once protected areas are established, acoustic telemetry can also be used to monitor habitat use and movements in and out of protected area boundaries (e.g., Bonnin et al., 2021; Chapman et al., 2005; Espinoza et al., 2015). Acoustic telemetry is also increasingly being used to estimate parameters for stock assessment (Sippel et al., 2015). Stock assessments are based on the concept of a unit stock, which is a closed, geographic region where a population is self-sustaining (Gulland, 1983). Estimates of stock size and how it changes over time are used to determine fisheries catch rates and quotas (Hilborn and Walters, 1992). Studies have demonstrated that acoustic telemetry is an excellent tool for determining stock structure and geographic boundaries, a key initial step to estimating stock size (Lédée et al., 2021; Lowerre-Barbieri et al., 2014; Zemeckis et al., 2017).

In this study, we examined the extent and timing of movement and migration patterns of Crevalle Jack (*Caranx hippos*) via a collaborative acoustic telemetry effort.

Our main goal was to determine if Crevalle Jack make regular, long-distance movements out of the south Florida region, where a decline in catch rates observed by recreational anglers has led to conservation concerns (Gervasi et al., 2022). Effective management of the species in south Florida will depend on knowledge of stock structure, connectivity, and habitat use. The Crevalle Jack is a large marine species with a distribution ranging from Nova Scotia to Uruguay in the western Atlantic (Smith-Vaniz and Carpenter, 2007). The species is an important component of commercial and recreational fisheries (Kwei, 1978), but previous research has shown that Crevalle Jack populations in south Florida are in decline, likely due to several years of overfishing since the 1990s (Gervasi et al., 2021). Management action is therefore warranted, but little is known about the species home range and distribution. To-date, the only information on Crevalle Jack movement and migration patterns in the U.S. is from a single study that examined seasonal abundance and size structure of juvenile fish from New York to Florida (McBride and McKown, 2000). Young-of-the-year Crevalle Jack were found to occur in temperate and subtropical estuaries from New York to Florida from June to November. When juveniles disappeared from temperate estuaries in the fall, similar sized fish appeared on the continental shelf, leading the authors to postulate that a least some Crevalle Jack migrate from temperate estuaries in the fall to overwinter at subtropical latitudes. This study suggested possible connectivity among Crevalle Jack along the western Atlantic coast but provided no information on Crevalle Jack movements in the Gulf of Mexico (GOM) nor on movements of adult fish.

Our study aimed to provide vital information about Crevalle Jack movement behavior that will aid in future restoration and conservation efforts. Specifically, our

research addresses three main questions about the long-range movement patterns of south Florida Crevalle Jack: (1) Where do fish that leave the south Florida region move to? (2) Do these long-range movements constitute a seasonal migration? And (3) are long-range movements size-dependent? Our results will help determine the spatial scale and type of management that will be best suited to restoring and conserving south Florida Crevalle Jack. Additionally, information gleaned about the scale of movement will aid in determining stock boundaries for future stock assessment. Finally, our research illustrates the benefits of collaborative telemetry research for addressing management-relevant questions concerning data-limited fish species.

2. Methods

2.1 Migration hypotheses

Based on the local ecological knowledge of recreational fishing guides in the Florida Keys, Crevalle Jack in south Florida are presumed to be coastal migrants, with abundance increasing in the winter months and decreasing in the summer months (Gervasi et al., 2022). Guides observed that Crevalle Jack are most abundant in south Florida from approximately November to April, with peak abundance from January to March. Based on these observations, we set an expected migration window of May $1st$ to November 1st when we hypothesized that Crevalle Jack would leave the south Florida region before returning to overwinter in south Florida. We then developed a total of four hypotheses concerning the migration patterns of south Florida Crevalle Jack (Figure 1). These hypotheses were based both on angler observations and on the migration behavior of other coastal fish species in the region (Friess et al., 2021; McBride, 2014). Our first

hypothesis was that Crevalle Jack migrate throughout the Atlantic and Gulf coasts, with population connectivity throughout the species range in the U.S. Detections of south Florida fish in both the northern Atlantic and northern Gulf regions in the summer months with movement back to south Florida in the winter months would provide support for this hypothesis. Our second and third hypotheses were that south Florida Crevalle Jack only engage in either Atlantic coast or Gulf coast migrations. This movement behavior could indicate that the Gulf and Atlantic populations of Crevalle Jack represent separate stocks. Finally, our fourth hypothesis was that south Florida serves as a juvenile and sub-adult source population with fish migrating to either Gulf or Atlantic adult habitats after reaching a certain size or age. This movement pattern would be evidenced by an exit of individuals out of the south Florida region but no returns, with individuals only leaving south Florida once they reach a certain size. The range, seasonality, and timing of movements of acoustically tagged Crevalle Jack were used to test these hypotheses.

2.2 Crevalle Jack capture and tagging

Crevalle Jack were captured and surgically implanted with acoustic tags in three broad areas of south Florida (Figure 2): the Florida Keys, southeast Florida (Fort Lauderdale), and southwest Florida (Fort Myers, Rookery Bay). All fish were captured using hook and line with conventional fishing gear. Most fish were captured with the assistance of recreational fishing guides, who provided their boats, fishing rods and reels, bait, and experience targeting Crevalle Jack. Most fish were tagged in the winter/spring (January through March) as Crevalle Jack are most abundant in the Florida Keys during

those months based on guide observations. Guide assistance allowed us to substantially increase sample size and increased our targeting efficiency. The largest individuals available were targeted using live baitfish, as recreational anglers typically target larger individuals for sportfishing, and we aimed to assess the movements and migrations of individuals subject to fishing pressure. Previous research has shown that Crevalle Jack captured by anglers in south Florida waters are typically smaller than Crevalle Jack captured elsewhere (e.g., the northern GOM), with individuals older than age-4 being rarely encountered (Jefferson et al., *in review*; Snelson, 1992). Additional research has estimated Crevalle Jack age at 50% maturity is approximately 3-4 years or 636 mm fork length (FL; Caiafa et al., 2011). We therefore expected that most Crevalle Jack tagged in south Florida would be juvenile or sub-adult fish. At each capture location, a 120-quart cooler was partially filled with ocean water and a sling constructed of PVC piping and silicone netting was placed inside. The sling allowed us to immobilize fish for surgery while ensuring their gills remained underwater throughout the procedure. Immediately after capture, fish were placed in the cooler and standard length (SL), total length (TL), and girth (mm) were measured. Weight (kg) was also measured by placing fish briefly in a soft bucket attached to a hanging scale.

Acoustic tags (Vemco V16-4H, 69kHz, 17.3 g in air, 16 mm diameter, 98 mm length, min and max delay times 60-120 s, estimated battery life 1897 days; Vemco Inc., Halifax, NS, Canada) were surgically implanted in Crevalle Jack between January 2019 and February 2021. Previous research examined the minimum sample size of acoustically tagged individuals to determine the full range of movements for several migratory species (Lédée et al., 2021). The authors found that a minimum of 45, 65, and 50 tagged

individuals were needed to produce the full network of movements for blacktip reef sharks, pink snapper, and white sharks, respectively. We therefore aimed to tag a minimum of 65 individual Crevalle Jack in south Florida. It is standard practice in telemetry studies to ensure acoustic tags weigh no more than 2% the total body weight of the tagged fish (Smircich and Kelly, 2014). Fish weighing less than 1 kg were therefore not tagged. To implant tags, a 3 cm incision was made posterior to the pelvic fin with a sterilized scalpel. A transmitter was inserted into the coelomic cavity, and the incision was closed using 2-3 surgical staples (Conmed Reflex One skin stapler 35W, Medex Supply). Research has shown that surgeries with staples can be performed faster than with sutures and can lead to lower incidence of local and systemic infection (Swanberg et al., 1999). A Floy tag (FT-4 lock on tag, Floy Tag and Mfg. Inc., Seattle, WA) with a unique tag number and a contact phone number was also externally attached in the dorsal muscle behind the second dorsal spine to identify tagged fish should they be subsequently encountered by anglers. Total surgery time was less than 5 min. Crevalle Jack were held over the side of the boat while idling forward to allow water to pass over the gills and were released once fully revived. All protocols for fish collection and surgery were approved by the Florida International University Institutional Animal Care and Use Committee.

2.3 Tracking via collaborative networks

Acoustically tagged Crevalle Jack were tracked via the existing arrays within the FACT and iTAG networks for about three years from January $7th$, 2019, to November $24th$, 2021 (Figs. 2, 3). The FACT network conducts regular data pushes where members

are encouraged to upload any new tag and detection data by the deadline and the FACT administrators compile the data and match orphan tags to their owners. The last data push before these data were analyzed was October $13th$, 2021, and the detection data were received on November $30th$, 2021. The latest FACT detections were from August $29th$, 2021. iTAG orphan detections are matched and sent to tag owners asynchronously as the data are uploaded by receiver owners. Detection data received from iTAG after December $1st$, 2021, were not considered for this manuscript, and the latest iTAG detections occurred on November $24th$, 2021. Since acoustic arrays are downloaded by array owners at different frequencies and over different time periods, it is possible that additional detections prior to December $1st$, 2021, will be received in the future. Additionally, since the acoustic tags used in this study have an approximate 5-year battery life, detection data will continue to be collected until the tags reach their end-oflife. This manuscript therefore serves as an initial assessment of preliminary detection data, and future research will examine the full time series of detections over the course of the tag lives.

2.4 Statistical analysis

Accumulated detection data were cleaned, filtered to remove false detections, and summarized using the glatos package (Holbrook et al., 2021) in R version 4.1 (R Core Team, 2021). Data were additionally filtered to remove any individuals with less than a 2-week detection history, since these limited detections provided no information on longrange movements. To test our hypothesis of a seasonal migration, we first examined whether any fish were detected outside of south Florida during the expected migration

window and then returned to south Florida for the remainder of the year. The Animal Tracking Toolbox (ATT; Udyawer et al., 2018) within the VTrack R package (Campbell et al., 2012) was used to calculate dispersal distances between the point of tagging and each receiver where an individual fish was detected. Maximum dispersal distances and bearings were used to examine the extent and direction of long-range movements. Dispersal distance kernels using a gamma distribution were generated from the distribution of maximum dispersal distances for all fish by season, with detections during March, April, and May assigned as spring, detections in June, July, and August assigned as summer, detections in September, October, and November assigned as fall, and detections in December, January, and February assigned as winter. Monthly centers of activity for each fish over the three years were also calculated using the COA function in VTrack with a timestep of 43,800 minutes (one month) to examine where most fish were during each season. Generalized linear models (GLMs) with a gamma distribution were used to examine whether season influenced maximum dispersal distance and COA latitude. Multiple comparisons of means using Tukey contrasts were used to compare maximum dispersal distance and COA latitude between seasons. QGIS version 2.18 (QGIS Development Team, 2016) was used to visualize movement tracks of all individuals and examine the timing and seasonality of movements.

Since most of the Crevalle Jack tagged were likely immature, we also wanted to examine whether the expected seasonal migration was size-dependent. Partial migration is common among several fish taxa, and whether individuals partake in migrations or remain resident is often related to size (Chapman et al., 2012). Additionally, many species engage in ontogenetic migrations, as biotic and abiotic requirements can change

from one life stage to another (Dahlgren and Eggleston, 2000), necessitating movement to a new habitat (Barbeaux and Hollowed, 2018; Nakamura et al., 2008; Vecchio and Peebles, 2022; Wilbur, 1980). To examine size-dependence, we used linear models to assess the relationship between size at tagging (SL) and maximum dispersal distance separately for fish tagged in 2019 and in 2020. We hypothesized that larger fish would have greater maximum dispersal distances than smaller fish, because fishing guides in the Florida Keys observed that smaller Crevalle Jack are typically encountered year-round, while larger Crevalle Jack appear to be only seasonally available (Gervasi et al., 2022). Since tracking occurred over a three-year period with three potential migration windows, we additionally assigned each fish to one of three migration categories. A migration was defined as any directed coastal movement away from the area of tagging during the hypothesized migration window (May $1st$ to November $1st$), regardless of whether the individual returned to south Florida. A year-1 migrant was defined as any fish that migrated during the first migration window in the same year the fish was tagged. A year-2 migrant was defined as any fish that was detected in south Florida during the first migration window in the year the fish was tagged, but then migrated during the second window a year after tagging. Undermined fish were those with no detections outside of south Florida to-date. These fish may have engaged in seasonal migrations, but since acoustic telemetry is limited to positive observations, the fate of undetected fish can be difficult to discern (Kraus et al., 2018). A Welsh two sample t-test was used to test whether there was a significant difference in size at tagging (SL) between year-1 migrants and year-2 migrants. A binomial GLM was additionally used to examine the probability of year-1 migration as a function of size at tagging. Year-2 migrants were

coded as "0", as they did not engage in migrations within the first year. Year-1 migrants were coded as "1".

3. Results

A total of 73 Crevalle Jack were acoustically tagged throughout south Florida from January 2019 to February 2021. Of these fish, 57 (78%) were detected on 457 acoustic receivers within the FACT and iTAG networks between January $7th$, 2019, and November 24th, 2021. The acoustic arrays where Crevalle Jack were detected ranged from the Florida Keys to Louisiana (Figure 2). Of the 271,527 total detections, the false_detections function in the glatos package identified 952 (0.35%) as potentially false. These false detections were removed for a resulting 270,575 Crevalle Jack detections. The detection data were further filtered by removing 16 fish that had detection histories less than 2 weeks. The movement patterns of 41 tagged Crevalle Jack based on 208,161 detections on 433 receivers were therefore assessed in this study (Table 1). These fish ranged in size from 380 to 640 mm standard length (SL) at tagging with an average length of 475 mm. Weight ranged from 1.25 to 6.45 kg with an average weight of 3.04 kg. Published maturity-at-size information for Crevalle Jack estimates length at 50% maturity is 636 mm FL (approximately 591 mm SL; Snelson, 1992) for both sexes (Caiafa et al., 2011). Most tagged fish were therefore likely immature sub-adults. For the filtered, detected individuals, total number of detections per fish ranged from 30 to 38,031 with an average of 5,077 detections per fish. Individual Crevalle Jack were detected on 19 receivers on average, with a range from 1 to 55 receivers.

3.1 Movement patterns

Tagged Crevalle Jack made regular movements throughout south and central Florida on the east and west coasts (Figure 2). Additional movements to north Florida on the west coast were also observed, with five fish crossing state boundaries into coastal Louisiana waters (Table 2). Fish tagged in all three areas of south Florida (Florida Keys, southeast Florida, and southwest Florida) were detected north of Tampa in the GOM. However, thus far only fish that were tagged in southeast Florida made any northbound movements along the Atlantic coast. Six individuals moved north from the tagging area (Fort Lauderdale) to as far as the St. Lucie River before moving back south, with southbound movements extending past the tagging area and into the Florida Keys (Supplemental Figure S1). There were no detections further north on the Atlantic coast despite extensive receiver coverage (Griffin et al., 2018). The average maximum dispersal distance among all Crevalle Jack was 225.07 km from the point of tagging to the furthest receiver. Maximum dispersal distance ranged from 0.35 km to 990.59 km. Fish were detected on receivers throughout a range of habitats, from shallow-water nearshore areas to deep-water reefs and wrecks. Receiver depth information was available for a subset of receivers $(n = 195)$, and ranged from 0.4 m to 38 m, with an average depth of 7.8 m.

Many of the tagged individuals remained in the south Florida region for at least one full year before either ceasing to be detected or moving north out of south Florida and into the northern GOM (Figure 3). The fish with the longest detection history (Fish ID #24) was first detected on April $11th$, 2019, and last detected on October 30th, 2021, with a total of 7,606 detections on 31 receivers. The five fish that moved the furthest, crossing into Louisiana waters, displayed remarkably similar movement patterns

regardless of whether they were tagged in 2019 or 2020 (Table 2). They were all tagged between March and April and remained in the south Florida region for about one year after tagging. All fish were then detected in either west central (Tampa) or northwest (Apalachicola) Florida between March and May a year after tagging, and in Louisiana between July and October 2021. The Louisiana coastal receiver array was not deployed until July $11th$ and $12th$ 2021, so it is possible the fish arrived in Louisiana earlier than July 2021.

3.2 Seasonality

From the detection data collected to date, only one Crevalle Jack (Fish ID #3) appeared to make a clear seasonal migration, moving north from the Florida Keys (last detection on May $7th$, 2019) to receivers off the coast of central Florida (first detection on June $15th$, 2019). There was then a gap in detections from June $15th$, 2019, to November 18th, 2019, when the individual was once again detected off the coast of central Florida. Later that same day, the fish was again detected in south Florida, where it remained until November $27th$, 2019, before ceasing to be detected. This migration aligns with the hypothesized migration window of May $1st$ to November $1st$. None of the other fish that left south Florida during the migration window appeared to return, but continued monitoring will hopefully confirm the fate of these potential migrants. Despite a lack of returns, dispersal distance kernels revealed a clear seasonality, with tagged Crevalle Jack remaining in the south Florida region in the winter months, while all long-distance movements out of south Florida were made in the spring, summer, or fall (Figure 4). Average maximum dispersal distance was 31.34 km (range = 0 to 138.11 km) in the

winter months, 147.03 km (range = 0 to 716.44 km) in the spring months, 253.68 km (range $= 0.35$ to 990.59 km) in the summer months, and 227.56 km (range $= 0.35$ to 990.59 km) in the fall months. A GLM with a gamma distribution fitted to the maximum dispersal distance for all individuals revealed that season was a significant predictor. A multiple comparisons test showed that maximum dispersal distance was significantly lower in the winter than in the spring, summer, or fall (Table 3). Monthly center of activity plots revealed similar seasonal patterns (Figure 5). Crevalle Jack movements were mainly centered around the south Florida region from November to February, with COAs shifting northward for a few fish beginning in March and April. COAs then shifted even further north for several fish beginning in May, and movements were centered in Louisiana for a few fish from July to at least October. Season was also a significant predictor in a gamma GLM fitted to the monthly COA latitude of each individual. A multiple comparisons test revealed that COA latitude was significantly lower in the winter than in spring, summer, or fall, and was also significantly lower in the spring than in the summer (Table 4). However, several Crevalle Jack were continuously detected in south Florida throughout the year, suggesting that some individuals might have remained in south Florida during the detection period.

3.3 Migration and size

According to linear models fit to the maximum dispersal distance data, size at tagging did not have a significant effect on maximum dispersal distance for fish tagged in 2019 or 2020 (adjusted \mathbb{R}^2 values for both models were less than 0.01). However, size at tagging did appear to affect the timing of migration. In total, 20 of the 41 detected

Crevalle Jack (49%) were categorized as migrants, with a migration defined as any directed coastal movement away from the area of tagging during the hypothesized migration window (May $1st$ to November $1st$). Five of these fish were categorized as year-1 migrants, while 15 were categorized as year-2 migrants. The remaining 21 individuals were unable to be categorized. There was a significant difference between size at tagging (SL) for year-1 and year-2 migrants (Welch two sample t-test $p < 0.001$), with the average size of year-1 migrants (608 mm SL , sd = 32.71 mm) being larger than the average size of year-2 migrants $(459 \text{ mm} \text{ SL}, \text{ sd} = 63.26 \text{ mm}$; Figure 6a). A binomial model was used to examine the probability of year-1 migration as a function of size at tagging (Figure 6b). The model revealed that size at tagging was not a significant predictor at the α = 0.05 level (p = 0.06), but the model predictions suggest that migrations generally do not occur until fish reaches a particular size. 50% probability of year-1 migration occurred at 513 mm SL, close to the estimated size at 50% maturity from previous research (591 mm SL; Caiafa et al., 2011). Limited information on size at maturation exists for Crevalle Jack in the U.S., but to-date, observed minimum size at maturity is 511 mm SL for males and 614 mm SL for females (Thompson and Munro, 1983).

4. Discussion

The results of our acoustic telemetry research fill an important gap in knowledge about movement behavior of Crevalle Jack in south Florida, where the population appears to be in decline (Gervasi et al., 2022). The detection histories of 41 tagged individuals revealed broad-scale, heterogeneous movement behavior. Our results align

with recreational fishing guide observations, and suggest that Crevalle Jack may be coastal migrants, overwintering in the south Florida region and migrating to habitats in the northern GOM in the spring and summer. Limited movements north along the Atlantic coast were made by a few individuals, but these movements did not extend far beyond the south Florida region. These results provide some evidence that south Florida Crevalle Jack may engage in Gulf coast migrations only (Hypothesis 3, Figure 1). However, coastal migration appears to be size-selective, with smaller (likely immature) fish remaining in south Florida year-round, not engaging in coastal migrations until they presumably reach a certain age or size (possibly at sexual maturity). From the detection data collected to date, one individual made a clear seasonal migration, moving north out of south Florida in the spring and back to south Florida in the fall. However, 19 other individuals made springtime movements out of south Florida but did not return. Continued monitoring will help determine if most Crevalle Jack return to south Florida, or if most movements out of the region are unidirectional. It is also possible that longdistance movements of Crevalle Jack out of the south Florida region represent a unidirectional ontogenetic migration from juvenile to adult habitat instead of a bidirectional seasonal migration (Hypothesis 4, Figure 1). Regardless of the reason Crevalle Jack engage in coastal migrations, which will be examined in future research, detection data collected to-date revealed that the movements of south Florida Crevalle Jack cross state boundaries, confirming multi-state stock connectivity.

4.1 Crevalle Jack movement patterns and pathways

Previous acoustic telemetry research has shown that several fish species make regular seasonal migrations between the Florida Keys and the northern GOM, including several shark species, Cobia (*Rachycentron canadum*), Atlantic Tarpon (*Megalops atlanticus*), and Smalltooth Sawfish (*Pristis pectinata*; Friess et al., 2021). For all these species, northbound movements were generally made in the spring while southbound movements were made in the fall. This commonality in large-scale seasonal movement patterns among species suggests shared biophysical movement drivers (Friess et al., 2021). These drivers may include abiotic factors such as changes in temperature (Lear et al., 2019), or biotic drivers like reproduction, predation, or foraging (Friess et al., 2021; Furey et al., 2018). From the Crevalle Jack detection data collected to date, one individual made a clear seasonal migration that aligned with the hypothesized migration window derived from fishing guide observations as well as the migration patterns exhibited by other coastal fish species. Several other individuals made springtime movements out of south Florida but did not return. The lack of return detections could be attributed to several factors. First, mortality rates along migratory routes may be high, which could explain why some of the individuals stopped being detected after leaving the south Florida region. Secondly, receiver coverage in the GOM is mostly limited to relatively shallow inshore and nearshore habitats (Friess et al., 2021). Crevalle Jack may use deeper waters with little receiver coverage when migrating from north to south, making it possible for the migrations to occur undetected. Finally, it is possible that the movement of these Crevalle Jack north out of the south Florida region represents a

unidirectional ontogenetic migration from juvenile and sub-adult habitat to adult habitat, rather than a bidirectional seasonal migration.

Continued monitoring will help determine if most Crevalle Jack return to south Florida, or if movements out of the region are unidirectional. Size distributions of Crevalle Jack throughout the GOM may support the hypothesis that movements north out of south Florida are unidirectional (Hypothesis 4). Jefferson et al. (*in review*) examined the size structure of Crevalle Jack captured by recreational anglers year-round throughout the GOM and found that 62% of Crevalle Jack caught in Mississippi and Alabama measured greater than 620 mm FL, with only 28.4% measuring between 230- and 620 mm FL. Conversely, 85.9% of Crevalle Jack caught in Florida were small (230 – 620 mm FL), with only 1.5% measuring over 620 mm FL. Previous research has also determined that Crevalle Jack older than age-4 are rarely encountered in Florida (Snelson, 1992). The Crevalle Jack is a fast-growing, relatively long-lived species (maximum recorded age = 19 years; Snelson, 1992). Previous research on Crevalle Jack in the Colombian Caribbean estimated that length at 50% maturity is 591 mm SL for both sexes and corresponding age at 50% maturity is about 3-4 years (Caiafa et al., 2011). Most fish inhabiting the south Florida region are therefore likely immature. Our tagging efforts supported this, as the average size of tagged fish was only 475 mm SL, below estimated size at 50% maturity. This heterogeneity in size structure between the northeastern and southeastern GOM coupled with the lack of return detections for tagged fish supports the possibility of a unilateral movement of fish from southern juvenile habitats to northern adult habitats. South Florida may therefore represent an important juvenile and sub-adult habitat for the Crevalle Jack, potentially serving as a nursery area (Beck et al., 2001). Juvenile nursery

habitats are incredibly important, as they support high density, survivorship, or productivity of recruits and support export of individuals to adult habitats (Nagelkerken et al., 2015). The mangrove and seagrass habitats of the south Florida region have been shown to serve as important juvenile habitats for several economically and ecologically important fish and invertebrate species (Acosta et al., 2007; Adams et al., 2006; Butler IV et al., 2005; Koenig et al., 2007; Saville et al., 2002).

Previous otolith microchemistry research revealed that GOM Crevalle Jack reside in inshore nursery habitats at age-0 (young-of-the-year, YOY), before engaging in an ontogenetic migration to more coastal habitats through at least age-4 or 5 (Chapter II). Our tagging results suggest that coastal south Florida habitats may serve as intermediate habitat for juveniles once they leave inshore YOY nurseries through to the sub-adult stage. Red Grouper (*Epinephelus morio*) and Gag Grouper (*Mycteroperca microlepis*), two other economically important coastal fish species in the GOM, exhibit similar dual ontogenetic migrations. Both species inhabit inshore shallow habitats as YOY fish and undergo a first ontogenetic migration to nearshore reefs after about one year (Coleman et al., 2010; Mullaney, 1994; Saul et al., 2012; Switzer et al., 2015). A second ontogenetic migration to offshore reefs then occurs once individuals reach sexual maturity at approximately three years of age (Coleman et al., 2010; Grüss et al., 2017) Furthermore, research has shown that GOM Red Grouper sub-adults are mainly found in coastal areas along the west coast of Florida, but that adults are found throughout the northern GOM (Grüss et al., 2017). Crevalle Jack may exhibit a similar life-history strategy, moving from inshore YOY habitats, to nearshore south Florida juvenile habitats, to northern GOM adult habitats. Throughout the GOM, the only evidence of Crevalle Jack spawning

(courtship behavior and color changes) has been observed in the Flower Garden Banks National Marine Sanctuary off the western coast of Louisiana (Helies et al., 2016; Heyman et al., 2019). It is possible that south Florida Crevalle Jack are spawned at this location, and that adults return to spawn there after reaching sexual maturity. Our results have helped fill key gaps in knowledge concerning the life history of the Crevalle Jack and identified potential key juvenile and sub-adult habitat. Our research also provided evidence of connectivity between south Florida Crevalle Jack and the greater eastern GOM region. Continued monitoring of tagged individuals will increase our understanding of these movement patterns and allow us to identify individual variability.

4.2 Management implications

As fisheries management is based on the concept of a unit stock, understanding stock structure and boundaries is vital (Crossin et al., 2017). The preliminary acoustic telemetry results presented herein showed that the movements of south Florida Crevalle Jack cross state boundaries, revealing multi-state stock connectivity. This information suggests that conservation of the south Florida population will necessitate multi-state management, with any harvest regulations extending throughout Florida and the eastern GOM to account for individuals that move across jurisdictional boundaries. The lack of movements north beyond south and central Florida on the Atlantic coast suggest that south Florida may be part of a GOM Crevalle Jack stock, with Crevalle Jack on the Atlantic coast potentially representing a separate stock. Continued monitoring of tagged individuals and additional tagging of Crevalle Jack along the Atlantic coast will aid in determining exactly where stock boundaries exist. Tagged Crevalle Jack were detected on
a range of receivers in inshore, nearshore, and offshore habitats, suggesting that a multitude of different habitat types are utilized by juvenile and adult fish over their lifetimes. Any strategies for habitat restoration or protection aimed at improving Crevalle Jack population status will therefore need to consider multiple scales and regions (e.g., the Florida Keys reef tract, Florida coastal embayments, and offshore reefs). Future research will more closely examine how and why Crevalle Jack utilize different habitat types, which will further aid in habitat management. Our results also revealed that a substantial proportion of south Florida Crevalle Jack (at least 20 out of 41 tagged individuals) left the south Florida region, engaging in northbound migrations. The timing of these long-range movements was very consistent, occurring mainly in the spring months from March to May. Additionally, migrating individuals appeared to be larger than individuals that did not partake in migrations. If these movements represent migrations of adult Crevalle Jack to spawning sites, protection of these migrating individuals could be critical for ensuring population persistence. Management may consider instituting a size limit or seasonal closure that protects these larger, migratory fish from exploitation. Continued monitoring of tagged Crevalle Jack will reveal more indepth information about habitat use, residency, and connectivity, all of which will aid in future management efforts.

4.3 Collaborative acoustic telemetry

Despite the many examples of acoustic telemetry informing fisheries conservation and management, tracking via acoustic telemetry remains challenging for highly mobile species with broad spatial distributions (Brownscombe et al., 2019). For example,

receiver coverage must encompass the home range of the species of interest but deploying and maintaining receivers throughout a vast spatial area is often not feasible for a single research group. Fortunately, acoustic telemetry is a method that naturally lends itself to collaboration, as the receivers used by most researchers can generally detect any fish tagged with an acoustic transmitter (Brownscombe et al., 2019). This cross-compatibility makes tracking fish that move long distances possible without having to resort to much more costly and laborious techniques such as satellite tagging. Networks like FACT, iTAG, ACT, and OTN make long-distance tracking feasible, as they facilitate sharing of detection data among researchers. However, these networks currently consist of individually owned receiver arrays designed to address various research questions, and changes in array configurations are frequently made that can confound temporal comparisons of movement patterns and space use for species that move between multiple arrays. Care therefore needs to be taken when analyzing the results of networked telemetry studies (Friess et al., 2021).

Another limitation of acoustic telemetry research is that the sample size of tagged individuals must be sufficiently large to account for tag loss, mortality, movement of animals outside of areas covered by receivers, and individual variability in movement behavior (Brownscombe et al., 2019). This is particularly important for data-limited species where movement and migration patterns are largely unknown. As with receiver networks, collaborative tagging efforts can increase sample size and spatial coverage. Specifically, partnerships with stakeholders can help get tags deployed rapidly and in multiple areas. Experienced recreational fishing guides have an in-depth knowledge of the areas where they fish (Cardoso da Silva et al., 2020; Gervasi et al., 2022; Kroloff et

al., 2019) and can help target and capture species of interest efficiently while minimizing bycatch. Involving experienced anglers in fieldwork enhances their understanding of the scientific process and allows them to contribute to conservation efforts. Previous research has shown that anglers are highly motivated to participate in fisheries research by a desire to enhance data collection, help scientists, contribute to research, and improve fisheries (Crandall et al., 2018). Research has also shown that angler participation in sampling efforts can be extremely beneficial, especially in animal tracking studies. Pierce et al. (2021) conducted a capture-mark-recapture study in south Florida to estimate Florida Largemouth Bass (*Micropterus salmoides floridanus*) survival in relation to hydrologic variability. The authors recruited 27 local anglers to collect recapture data, which greatly increased sample size. Furthermore, anglers produced similar recapture probabilities for the same effort. Numerous other examples in the literature have shown that citizen science is a low-cost method for collecting high-quality data to supplement existing research efforts (e.g., Bonney et al., 2021; Hughes et al., 2022; Potts et al., 2021).

The Crevalle Jack is just one example of many data-poor and unregulated fish species in critical need of assessment and management (Costello et al., 2012). However, managing fish stocks like the Crevalle Jack with wide-ranging spatial distributions requires knowledge of stock boundaries and migration patterns (Chapman et al., 2012; Crossin et al., 2017). The collaborative nature of this research, both among scientists from different institutions and between scientists and anglers, enabled us to discover vital information about the movement behavior of south Florida Crevalle Jack that would not otherwise have been possible. Continued efforts by scientists to collaborate with stakeholders, increase membership in collaborative telemetry networks, and improve

consistency in networked telemetry infrastructure will enhance our understanding of the movement and migration patterns of aquatic animals and allow us to monitor how movement behaviors may change in the future under multiple scenarios of climate change and other anthropogenic threats.

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Table 1. Fish ID, transmitter ID, date tagged, standard length (mm), and weight (kg) at tagging, total number of detections, and number of receiver locations detected at for all Crevalle Jack acoustically tagged in south Florida with detection histories longer than 2 weeks.

Fish ID	Transmitter	Date	Standard	Weight	#Detections	#Locations
	ID	tagged	length (mm)	(kg)		
$\mathbf{1}$	9341	2/17/2019	410	1.93	1222	25
\overline{c}	9331	3/15/2019	420	2.16	6952	34
3	7587	3/15/2019	630	6.45	4209	14
4	7575	3/15/2019	405	1.92	8055	20
5	7578	3/15/2019	510	3.30	168	21
6	6581	3/22/2020	620	5.94	6557	34
$\overline{7}$	6593	3/22/2020	590	5.43	156	17
8	6590	3/22/2020	510	3.76	65	$\mathbf{1}$
9	6587	3/22/2020	560	5.41	40	$\boldsymbol{7}$
10	7582	3/22/2020	520	3.91	460	17
11	6591	3/22/2020	640	6.25	194	42
12	9328	1/7/2019	520	3.11	1231	8
13	9338	1/7/2019	440	2.19	8069	17
14	9357	1/7/2019	430	2.39	86	$\overline{4}$
15	9327	1/7/2019	390	1.77	451	16
16	9358	1/7/2019	550	3.42	13149	39
17	9344	1/8/2019	380	1.34	30	$\overline{2}$
18	9339	1/8/2019	420	2.00	7086	21
19	9355	1/8/2019	390	1.69	58	$\overline{4}$
20	9330	1/8/2019	400	1.86	4391	16
21	9336	1/8/2019	430	1.94	2970	11
22	9329	1/8/2019	390	1.64	38031	16
23	9354	1/8/2019	410	1.93	30350	23
24	7577	3/28/2019	480	3.02	7606	31
25	7583	3/28/2019	450	2.54	2872	20
26	7576	3/28/2019	520	4.08	4265	14
27	9337	3/28/2019	400	1.80	526	12
28	7586	3/28/2019	450	2.25	826	10
29	7585	3/28/2019	410	1.87	86	$\overline{3}$
30	8585	5/1/2019	560	4.85	5465	40
31	7488	3/26/2020	600	5.71	6140	10
32	7485	3/26/2020	460	2.62	7461	6
33	6585	3/26/2020	560	4.84	10261	20
34	7470	4/24/2019	450	2.20	767	30
35	7482	4/24/2019	395	1.71	904	55
36	7469	4/14/2020	495	2.26	21223	31
37	7484	4/29/2020	380	1.25	2078	11
38	7479	4/29/2020	450	2.51	224	$\mathbf{1}$
39	6589	4/29/2020	450	2.39	40	$\overline{4}$
40	7476	4/29/2020	550	4.31	921	33
41	7480	4/29/2020	460	2.51	2521	35

Fish ID	Date tagged	SFL	CFL	NFL	LA
24	3/28/2019	$4/11/19-$	4/10/20	NA	$7/26/21 -$
		3/18/20			10/30/21
25	3/28/2019	$4/8/19-$	$4/4/20 -$	NA	8/6/21
		3/2/20	4/5/20		
31	3/26/2020	$5/8/20 -$	NA	NA	$7/16/21 -$
		2/14/21			10/29/21
32	3/26/2020	$11/15/20 -$	NA	$5/22/21 -$	$7/17/21 -$
		4/5/21		5/27/21	10/14/21
40	4/29/2020	$5/4/20 -$	3/28/21	NA	$7/22/21 -$
		2/15/21			10/12/21

Table 2. Fish ID, date tagged, and dates fish were detected in each of four regions, south Florida (SFL), west central Florida (CFL), northwest Florida (NFL) and eastern Louisiana (LA), for the five Crevalle Jack detected outside the state of Florida.

Linear hypotheses	Estimate	Std. Error	z-value	p-value
$Spring - winter == 0$	-0.0241	0.0078	-3.0970	< 0.01
Summer – winter $== 0$	-0.0267	0.0077	-3.4700	< 0.01
$Fall - winter == 0$	-0.0263	0.0077	-3.3930	< 0.01
Summer – spring $== 0$	-0.0027	0.0016	-1.6300	0.3263
$Fall - spring == 0$	-0.0022	0.0018	-1.2190	0.5810
$Fall - summer == 0$	0.0005	0.0015	0.2940	0.9898

Table 3. Multiple comparisons of means (Tukey contrasts) between seasons for the gamma GLM fitted to the maximum dispersal distance data.

Table 4. Multiple comparisons of means (Tukey contrasts) between seasons for the gamma GLM fitted to the monthly COA latitude data.

Linear hypotheses	Estimate	Std. Error	z-value	p-value
$Spring - winter == 0$	-0.0010	0.0003	-3.1340	< 0.01
Summer – winter $== 0$	-0.0019	0.0003	-5.6640	< 0.01
$Fall - winter == 0$	-0.0017	0.0004	-4.6870	< 0.01
Summer – spring $== 0$	-0.0009	0.0003	-3.3150	< 0.01
$Fall - spring == 0$	-0.0008	0.0003	-2.3940	0.0772
$Fall - summer == 0$	0.0002	0.0003	0.4520	0.9690

Figure 1. Hypotheses concerning the movement and migration patterns of south Florida Crevalle Jack, including expected detection results and management implications of each hypothesis. Base map credit Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community.

Figure 2. Map of all deployments (top) and detections (bottom) for Crevalle Jack tagged in south Florida and tracked from January 2019 to November 2021. Deployments, detections, and paths between receivers are colored by the broad area where fish were tagged. Inset map highlights area of interest in the southeastern United States. Base map credit Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community.

Figure 3. Abacus plot of Crevalle Jack acoustic detections for each of the 41 tagged fish detected by receivers from January 2019 to November 2021 (filtered to exclude fish with detection histories less than 2 weeks). Red triangles denote tag deployment date. Detections are colored by latitude. Gray shading denotes hypothesized migration periods for each year as estimated by recreational fishing guides.

Figure 4. Dispersal distance kernel plots with a gamma distribution depicting the distribution of maximum dispersal distances for all Crevalle Jack over all years, separated by season.

Figure 5. Maps of monthly centers of activity (COA) for each Crevalle Jack from January 2019 to November 2021. COAs are split by season and colored by month. The size of each point represents the natural log of the number of detections informing each monthly COA. Base map credit Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community.

Figure 6. Violin and boxplots displaying the mean size at tagging (SL) for Crevalle Jack categorized into one of three migration groups, with gray dots displaying raw data points (A). Binomial model (blue line) fitted to the probability of year-1 migration as a function of size at tagging (SL), with "0" representing year-2 migrants (did not migrate in year-1) and "1" representing year-1 migrants (B). The dotted lines in panel B represent estimated size at maturation for males (511 mm SL) and females (614 mm SL) from Thompson and Munro (1983).

Figure S1. Northward movements along the Atlantic coast of Florida made by six individual Crevalle Jack tagged in southeast Florida (Fort Lauderdale, black circle). All fish that moved north along the Atlantic coast subsequently moved back south. Base map credit Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community.

CHAPTER V

RAPID APPROACH FOR ASSESSING AN UNREGULATED FISHERY USING A

SERIES OF DATA-LIMITED TOOLS

Abstract: Fisheries provide countless benefits to human populations but face many threats from climate change to overfishing. Despite these threats and an increase in fishing pressure globally, most stocks remain unassessed and data-limited. An abundance of data-limited assessment methods exists, but each have different data requirements, caveats, and limitations. Furthermore, developing informative model priors can be difficult when little is known about the stock, and uncertain model parameters could create misleading results about stock status. Our research illustrates an approach for rapidly creating robust initial assessments for unregulated and data-limited fisheries. Our method uses stakeholder knowledge combined with a series of data-limited tools to identify an appropriate stock assessment method, conduct an assessment, and examine how model uncertainty influences the results. Our approach was applied to the unregulated and data-limited Crevalle Jack fishery in Florida, U.S.A. Results suggest a steady increase in exploitation and decline in stock biomass over time, with the stock currently overfished and fully exploited. These findings highlight a need for management action to prevent continued stock depletion. Our approach can help streamline the initial assessment and management process for unregulated and data-limited stocks and serves as an additional tool for combating the many threats facing global fisheries.

1. Introduction

Despite their importance, the status of many global fisheries remains unknown or poorly estimated due to a lack of sufficient data required to conduct stock assessments. Fisheries lacking formal assessment comprise over 80% of global catch, and studies have estimated that these unassessed fisheries may be in significantly worse condition than assessed fisheries (Costello et al., 2012). Furthermore, due to increasing fishing pressure and constraints on fisheries management programs, developing monitoring and assessment plans for all harvested fish species is an unattainable goal (Harford and Carruthers, 2017; Sagarese et al., 2019). While researchers are working to improve data collection for several data-limited stocks (e.g., Bryan et al., 2016), there will likely continue to be a need for alternative, data-limited approaches to stock assessment in the future (Sagarese et al., 2019). This is particularly true for areas like the southeastern United States, a highly biodiverse region where fisheries are dominated by the recreational sector (Shertzer et al., 2019), and over 75% of stocks are considered datalimited (i.e., lacking sufficient data to conduct traditional assessments; Berkson and Thorson, 2015; Newman et al., 2015). There is an urgent need for rapid assessment and management action that can keep pace with increasing fishing pressure and methods that can identify unregulated and data-limited fisheries at risk of overexploitation and depletion (Sun et al., 2020).

Over the past few decades, numerous data-limited assessment methods have emerged to tackle this issue (Dowling et al., 2015). Rather than relying on traditional quantitative, model-based stock assessments, these methods estimate the status of fish stocks using a range of approaches from expert judgment to multiple indicator models

(Dowling et al., 2019). However, methods differ greatly in their data requirements, caveats, and context, making it difficult to determine which assessment method is the best choice for a particular fishery. Blanket application of generic models can lead to an inaccurate portrayal of fishery status and trends, hindering effective management (Dowling et al., 2019). This is because using generic methods without first assessing whether they are suitable to the fishery of interest increases the likelihood of violating model assumptions and overlooking biases or other data quality issues. Fortunately, several decision-support tools have been developed in recent years that aim to assist fisheries scientists, managers, and stakeholders in determining the appropriate methods for assessing and managing a given fishery (McDonald et al., 2018). One example is the FishPath tool, which was developed in 2016 and is a decision-support tool that helps guide users through the selection of appropriate methods for monitoring, assessment, and management of data-limited fisheries (Dowling et al., 2016). The FishPath online assessment tool contains a repository of data requirements and assumptions for over 50 stock assessment methods, with a focus on data-limited options (Dichmont et al., 2021; Fitzgerald et al., 2018). Users first characterize their fishery via a series of multiplechoice questions concerning biological and life history attributes, fishery operational characteristics, data availability, socioeconomic factors, and governance context. The answers to these questions are then used to identify possible assessment and management options that are best suited to the fishery.

Despite the many benefits provided by the FishPath tool, it has to date been rarely mentioned in the peer-reviewed literature (though additional applications exist in the gray literature). A Web of Science search for the term "FishPath" conducted on 31-01-2022,

six years after the tool was developed in 2016, had only three pertinent results. One publication presented a website (the Stock Assessment Toolbox) that collates available stock assessment packages from data-limited to data-rich (Dichmont et al., 2021). FishPath was used in this study simply as a resource of available data-limited methods. The authors did state that FishPath would be a valuable tool used in conjunction with their website to guide a user to an appropriate assessment method, the package for which could then be found in the Stock Assessment Toolbox. The second study was a field experiment testing the influence of FishPath on stakeholder buy-in to management (Crosman et al., 2020). Here, participants were provided a hypothetical fishery and explored management options using FishPath. The only published study that used the FishPath tool to identify a stock assessment method for a real fishery was Fitzgerald et al. (2018). The authors used FishPath to select an assessment method for the southern California rock crab fishery, and they noted that the tool helped avoid overlooking important information when selecting an assessment method. Using a standardized tool like FishPath can provide consistency and objectivity to data-limited fisheries management, and it has the potential to become a key resource for the assessment and management of unregulated species.

In addition to the development of numerous alternative approaches to traditional stock assessment, fisheries science is increasingly using stakeholder local ecological knowledge (LEK) to help identify conservation concerns (Gervasi et al., 2022; Silvano and Valbo-Jørgensen, 2008), estimate trends in stock status over time (Beaudreau and Levin, 2014; Kroloff et al., 2019), improve fisheries models (Bélisle et al., 2018), and fill in critical knowledge gaps about species biology and ecology (Anadón et al., 2010). LEK

is the in-depth knowledge of the local natural environment obtained by individuals or groups of people through personal observations, practical experience, and community dialog (Anadón et al., 2009). Research has shown that angler LEK can complement biological data and provide new insights (Cardoso da Silva et al., 2020; Silvano et al., 2008). There are several examples of angler LEK being used to directly inform fisheries management, including developing management options with a high probability of success and compliance (Heyman and Granados-Dieseldorff, 2012), understanding causes of disagreement with existing management measures (Hill et al., 2010), developing fishery surveillance indicators that can be used to continually monitor fisheries (Shephard et al., 2021), and providing estimates of model parameters used in stock assessments (Ainsworth and Pitcher, 2005; Beaudreau and Levin, 2014; Friedlander et al., 2015). Although these studies demonstrate clear benefits to incorporating angler LEK into fisheries management, there remains a lack of standardized protocols and methods for doing so (Hind, 2015).

The goal of this study was to develop an approach for conducting rapid initial assessments of unregulated and data-limited fisheries that could be applied to the Crevalle Jack (*Caranx hippos*) fishery in Florida, U.S.A. The Crevalle Jack is a large marine species targeted by both commercial and recreational anglers, but the fishery in Florida is currently unregulated and data-limited. Furthermore, research has suggested the population may be in decline (Gervasi et al., 2022). Our approach uses angler LEK in conjunction with a series of data-limited assessment tools to assess the current status of the Florida Crevalle Jack stock, examine trends in stock status and exploitation over time, and develop initial management reference points, which are benchmarks that scientists

and managers use to set targets or limits on fishing effort and monitor the success of management strategies (Caddy and Mahon, 1995). Our approach first uses information gathered from LEK and other sources to fill out the FishPath assessment questionnaire and choose a data-limited stock assessment method suited to the fishery of interest. Second, a stock assessment is conducted using the chosen method, with LEK informing unknown model parameters and filling in data gaps. Finally, simple sensitivity analyses are run to test how uncertain or unknown parameters (including those estimated by LEK) affect estimates of stock status (Figure 1). Sensitivity analysis is a common approach stock assessment scientists use to understand aspects of model uncertainty (Privitera-Johnson and Punt, 2020). Applying this series of strategies is a rapid, low-cost method that can help to minimize uncertainty, highlight critical research needs, and inform management for previously unassessed species.

2. Methods

2.1 The FishPath tool

In this study, the FishPath assessment questionnaire was filled out by C. Gervasi for Florida Crevalle Jack using information compiled from various sources, including LEK, published literature, and fisheries-dependent data. LEK was accessed via in-depth, semi-structured interviews with 19 expert recreational fishing guides in the Florida Keys (see Gervasi et al., 2022 for details on interview methods). The FishPath assessment questionnaire includes five categories of questions concerning the biology and life history of the species, data availability, governance, management, and operational characteristics. Previous literature on the Crevalle Jack was used to inform questions about biology and

life history (e.g., Saloman and Naughton, 1984; Snelson, 1992; Smith-Vaniz and Carpenter, 2007; Caiafa et al., 2011). LEK data included information on relative stock status and the nature of fishery operations, i.e., gear, selectivity, targeting, current rules and regulations, and fishing areas. All available fisheries-dependent and -independent surveys that operate in Florida and regularly encounter Crevalle Jack were compiled to answer questions about data availability (e.g., Gervasi et al., 2022).

The FishPath assessment tool does not rank the possible assessment methods but does filter out any methods where the minimum data requirements or criteria are not met based on the questionnaire responses. The tool also displays traffic light caveats that highlight each possible assessment method's major assumptions and data requirements as they relate to the fishery of interest. Caveats that are red are important assumptions that might not be met according to the questionnaire responses, so those methods should be used with caution. All options with one or more red caveats were eliminated. FishPath also ranks each method by assessment tier (i.e., model complexity), with tiers ranging from simple, extremely data-limited methods to robust, data-rich methods. Options that were only one assessment tier were eliminated, as these options are less robust and require very little data inputs. Each remaining option was subsequently narrowed down by model assumptions as they relate to the fishery, reliability of available data, and the amount of management-relevant information the assessment provides. We narrowed down to a few plausible options, including production models (e.g., Schaefer, Fox, Pella-Tomlinson models; Hilborn and Walters, 1992), the qR method (McGarvey et al., 1997), and the CMSY (Catch-MSY) method (Froese et al., 2017). Production models and the CMSY model are related in that they both require a continuous timeseries of fishery

removals and the two major parameters in the models are intrinsic population growth rate, *r*, and carrying capacity, *k*. These parameters are used to estimate maximum sustainable yield (*MSY*). Production models are slightly more complex than the CMSY method because they additionally require at least one index of abundance. The qR method uses timeseries of catch by weight and in numbers, an estimate of natural mortality (*M*), and an average of weight-at-age to estimate biomass, catchability, exploitation rate, and yearly recruitment. We thoroughly reviewed each of these methods in the scientific literature to select the best option for the assessment of the Crevalle Jack fishery. The qR method was eliminated as an option because catch by numbers is not recorded for Crevalle Jack in the commercial fishery. Furthermore, natural mortality for Florida Crevalle Jack is currently unknown and unable to be estimated with any certainty. The production models and CMSY model required fewer inputs of uncertain parameters.

2.2 Stock assessment method

Out of the possible assessment options presented by the FishPath tool, we chose the CMSY-BSM method created by Froese et al. (2017) and further updated by Froese et al. (2019). This method includes both the CMSY model and a production model (BSM), two of the top options narrowed down by FishPath. This method was chosen because the model estimates biomass, exploitation rate, *MSY*, and related fisheries reference points with the only data requirements being catch and productivity (Froese et al., 2017). The CMSY model is an updated version of the Catch-MSY method originally proposed by Martell and Froese (2013), which reviews of data-limited assessment methods have found to be a promising approach (ICES, 2014; Rosenberg et al., 2014). The predictions of the

CMSY-BSM method have been validated against 48 simulated stocks and evaluated against 159 fully or partially assessed real stocks, and estimates of *r*, *k*, and *MSY* were not significantly different from the actual values for 90% of simulated stocks and 76% of real stocks (Froese et al., 2017). Furthermore, a detailed user manual and R code last updated in 2019 are available for download from [https://oceanrep.geomar.de/33076/,](https://oceanrep.geomar.de/33076/) making the method easily accessible and reproducible. The updated version of the model (CMSY+ and BSM; Froese et al., 2019) was used in this study but will be referred to below as simply the CMSY-BSM model.

Species resilience in the model is defined as species productivity or resilience to fishing and depends on several factors including maximum population growth, von Bertalanffy growth rates, fecundity, age of maturity, and maximum age (Demirel et al., 2020; Holling, 1973). Species with low intrinsic growth rates and low fecundities (e.g., many sharks, rays, and large teleosts) tend to have low resilience and are thus particularly vulnerable to exploitation (Musick, 1999). In the CMSY-BSM model, classification of resilience based on previous literature or expert knowledge is used to set prior ranges for the maximum intrinsic rate of population increase (*r*). A Monte Carlo approach is used by the model to filter probable ranges for carrying capacity (*k*) and *r* to detect "viable" *r-k* pairs. When biomass or CPUE data are available, as is the case in our study, the CMSY model incorporates a Bayesian state-space implementation of the Schaefer surplus production model (BSM). The main benefit of the BSM compared to other versions of the surplus production model are that the timeseries of CPUE data can be incomplete (fragmented) and shorter than the catch timeseries, as is the case in our study (Froese et al., 2019).

2.3 Model inputs

2.3.1 Model priors

The CMSY-BSM model requires a timeseries of total fishery removals (hereafter referred to as catch), priors for species resilience and for biomass relative to carrying capacity (*B/k*) at the beginning, middle, and end of the catch timeseries, and an optional biomass timeseries. For Crevalle Jack, prior estimates for *r* were extracted from the "Estimates based on models" section of FishBase, based on a species resilience category of "medium" (Froese and Pauly, 2021; Smith-Vaniz et al., 1990). A prior range for *k* was derived by the model from the maximum catch. Fishing guide LEK was used to derive prior ranges for *B/k* at the beginning, middle, and end of the timeseries. Fishing guides reported in interviews that Crevalle Jack populations have declined steadily over time, with the lowest abundance in recent years (Gervasi et al., 2022). This observation was used to set prior B/k as high at the beginning of the timeseries (nearly unexploited), moderate in the middle of the timeseries (low depletion), and relatively low at the end of the timeseries (medium depletion). The default *B/k* ranges corresponding to these categories from Table 3 in Froese et al. (2017) were used in the model (Table 1).

2.3.2 Catch timeseries

The following formula was used to create a timeseries of total fishery removals (catch timeseries) for Crevalle Jack in Florida from 1950-2020: *commercial landings^t + recreational landings_t* + (*recreational discards_t* $*$ *discard mortality*), where *t* is year, and discard mortality is an estimated discard mortality rate (Figure 2). Discard mortality occurs when fish are caught and released alive but die post-release due to injuries

suffered from the angling encounter or from an increased susceptibility to predation (Rudershausen et al., 2007). The discard mortality rate is defined as the proportion of individuals that suffer from discard mortality and can therefore be considered a component of fishery removals. Preliminary acoustic telemetry research has revealed population connectivity of Crevalle Jack throughout the state of Florida (C.L. Gervasi, unpublished data). We, therefore, assumed that state-level boundaries are a reasonable approximation of the stock unit. All catch data were therefore collected for the entire state.

2.3.2.1 Commercial landings

In Florida, recreational and commercial catch data for Crevalle Jack are available from the National Oceanic and Atmospheric Administration (NOAA). Commercial landings data were obtained from the National Marine Fisheries Service (NMFS) Accumulated Landings System (NOAA, 2021a). Landings data for Crevalle Jack were downloaded for all of Florida from the beginning of the timeseries (1950) to the last available year (2020). Discards from the commercial fishery are not recorded for Crevalle Jack but are expected to be low because there is a market for Crevalle Jack for use as food fish, animal food, or as bait, with average price per pound increasing from about \$0.20 to \$1.00 from 1986 to 2019. Commercial anglers do not typically discard anything that has a market value (C. Bradshaw pers. comm.).
2.3.2.2 Recreational landings and discards

Recreational fisheries in the U.S. are surveyed by the NOAA Fisheries Marine Recreational Information Program (MRIP). Dockside surveys have been conducted since 1981 covering shore-based, private, and charter fishing modes (Papacostas and Foster, 2018). Crevalle Jack recreational landings (fish brought back to shore) and discards (fish caught and released either dead or alive) for the state of Florida were downloaded from the MRIP online query tool for the period of record from 1981-2020 (NOAA, 2021b). With MRIP, catch is reported for three categories: harvest based on observed harvest (type A; harvest physically observed by MRIP observers), harvest based on reported harvest (type B1; dead discards that were not brought back to shore), and fish released alive (type $B2$). Data were downloaded separately for harvested fish (types $A+B1$) and released fish (type B2).

Stock assessment models ideally include a catch timeseries that goes back to the beginning of exploitation for the fishery (Froese et al., 2017). The early 1950s mark the beginning of rapid growth in fishing pressure, prior to this, biomass for most stocks is assumed to be relatively high (Pauly et al., 2002). Commercial landings data for Crevalle Jack in Florida date back to 1950, but recreational landings data only date back to 1981, the beginning of the MRIP survey. We, therefore, were missing data on Crevalle Jack recreational landings from 1950-1980. In fisheries assessments, it is common practice to back-calculate missing recreational landings data using historical angling sources (i.e., estimates of fishing activity from census surveys or similar; Brennan, 2020; Rios, 2013). The U.S. Fish and Wildlife Service National Survey of Fishing, Hunting, and Wildlife-Associated Recreation (FHWAR) is one of the oldest comprehensive recreational census

surveys that exists and has been conducted every 5 years since 1955, with the latest report being for 2016 (USFWS, 2018). The FHWAR back-calculation method uses estimates of U.S. saltwater angling days from the FHWAR surveys to estimate historic recreational landings for species of interest in the U.S. (Brennan and Fitzpatrick, 2012).

Within the FHWAR reports, the number of U.S. saltwater angling days is estimated for each report year (1955-2016 every five years). However, state-level estimates of saltwater angling days are only available in the reports for 1991, 1996, 2001, 2006, and 2011. The most recent FHWAR publication (2016) did not collect data at the state level. For the purposes of our study, we were interested in estimates of saltwater angling days from 1950-1980 in Florida only. We, therefore, calculated the average proportion of saltwater angling days in Florida out of all U.S. saltwater angling days per year from the 1991-2011 reports. We assumed that this average was a reasonable estimate of the proportion of saltwater angling days that occur in Florida each year. We then multiplied this average proportion of saltwater angling days in Florida by the total U.S. saltwater angling days reported for 1955-1980 to estimate how many saltwater angling days occurred in Florida during those years. Next, we needed to convert estimates of fishing days into total fishing trips. This was done by comparing estimated Florida saltwater angling days from the FHWAR census survey to the total number of Florida angler trips from the MRIP dockside survey. The 1985 FHWAR survey is the earliest survey that overlaps with the MRIP survey. To adjust for interannual variability we took the average of the total number of angler trips for Florida from the years 1984-1986 from the MRIP online query tool and divided that number by the estimated FHWAR Florida saltwater fishing days for 1985. This gave us an estimated number of trips per angling

day (1.32 trips per day). The estimated Florida saltwater angling days for each year from 1955-1980 were then multiplied by this number to estimate total historical Florida saltwater fishing trips.

We then needed to estimate Crevalle Jack CPUE for the years 1955-1980, so we could multiply CPUE by the estimated number of angler trips to get estimated Crevalle Jack landings. We calculated Crevalle Jack CPUE (total kg of fish divided by total number of angler trips) for Florida for the entire MRIP timeseries (1981 to 2020) using the MRIP query tool. To examine whether CPUE had changed over time, linear models were fit to the CPUE data as a function of year separately for harvested fish (types $A+B1$) and released fish (type B2). Year was not a significant predictor in the CPUE harvest model ($p = 0.23$), but it was significant for the CPUE releases model ($p < 0.001$), showing that CPUE for released fish has increased significantly over time (Supplementary Figs. S1, S2). We therefore only used the first 5 years of the MRIP timeseries (1981-1985) to estimate CPUE during the historical years, as CPUE for these years was likely to be the most like CPUE for the historical years. We then calculated the average CPUE for years 1982-1985 for harvested and released fish. We excluded the CPUE for 1981 due to high proportional standard error (PSE) in catch totals for that year. These average CPUEs were multiplied by our adjusted Florida saltwater trips to estimate recreational harvest and live releases of Crevalle Jack in 5-year increments from 1955- 1980. To fill in the gaps for missing years and create a timeseries of recreational harvest and releases from 1955-1980, linear interpolation was used between each 5-year data point. The last step was to estimate landings for 1950-1954. To do so, we fit linear models to the timeseries of harvest and releases from 1955-1980. Linear models fit the

data well, as both harvest and releases increased rather linearly over time (adjusted $R^2 =$ 0.95 for both timeseries). The linear model predictions were therefore used to estimate harvest and releases for 1950-1954. Total timeseries of recreational harvest and live discards were created by piecing together the historical estimates from 1950-1980 with the MRIP data from 1981-2020.

2.3.2.3 Discard mortality

Discard mortality has not been assessed for Crevalle Jack, but studies have empirically derived discard mortality rates for several other hook and line fisheries. Rudershausen et al. (2007) evaluated release mortality of eight commercially caught snapper and grouper species in North Carolina, U.S.A., and mortality rates ranged from 0% for Gag Grouper (*Mycteroperca microlepis*) to 23% for Scamp (*Mycteroperca phenax*). To get a better approximation of Crevalle Jack discard mortality, recreational fishing guides were asked to estimate post-release survival rates. All guides estimated that post-release survival was high, with individual estimates ranging from 85-95%. Average guide-estimated survival rate was 91%, so we applied a discard mortality rate of 10% to the Crevalle Jack data, such that 10% of the recreational discards were included in the timeseries of total fishery removals (Figure 2).

2.3.3 Abundance timeseries

No fisheries-independent surveys are operating in the region that regularly encounter adult Crevalle Jack, but relative abundance trends can be inferred from CPUE data (Maunder and Punt, 2004). For the purposes of this study, we used MRIP CPUE data subset to Florida to create an index of Crevalle Jack abundance for the entire state. Numerous factors besides stock abundance can influence fisheries catch rates (e.g., spatial, temporal, and environmental variability), so we standardized the CPUE data for Crevalle Jack in Florida using generalized linear models (Matthews, 2014). Specifically, a delta-lognormal GLM approach (Lo et al., 1992) was applied with the categorical factors Year (1991-2020), Season (spring — March, April, May; summer — June, July, August; fall — September, October, November; and winter — December, January, February), Fishing mode (shore, charter, and private), and Day (weekday or weekend) included in the model. Additional details on standardization methods can be found in Gervasi et al. (2022). Filtered and cleaned MRIP data included 233,408 trips from 1991– 2020 (30 years). Of these, crevalle jack were caught on 37,803 trips (16%). Based on model selection via backward stepwise regression and deviance tables, the final model for the proportion positive GLM included Year and Season as fixed factors and the final model for the positive trip GLM included Year, Season, and Fishing mode as fixed factors (Supplementary Tables S1, S2).

2.4 Sensitivity analyses

To examine the sensitivity of our Crevalle Jack CMSY-BSM model to unknown or poorly estimated parameters, we conducted a series of sensitivity analyses and compared stock status and biomass and exploitation trends to our base model (Table 1). We explored six different scenarios that tested the model sensitivity to potential uncertainty by varying the estimated discard mortality rate instead of using the LEKderived value (analysis 1), ignoring the CPUE data and using only the CMSY model

without the surplus production model (BSM; analysis 2), subsetting the catch timeseries to begin at 1981 (the beginning of the MRIP timeseries), thereby ignoring the estimated historic recreational catch and historic commercial catch (analysis 3), removing potential outlier data points from the MRIP timeseries with high proportional standard error $($ 50%) and replacing them with interpolated values based on adjacent years (analysis 4), using uninformed biomass priors instead of the LEK-derived priors (analysis 5), and using an alternative standardized CPUE timeseries (developed by Gervasi et al., 2022) using the Everglades National Park (ENP) creel survey (Osborne et al., 2006) and updated to include data from 2020, as an index of abundance (analysis 6).

3. Results

3.1 Base model run

Our base stock assessment model run for Crevalle Jack revealed a gradual increase in exploitation and corresponding gradual decline in stock size from 1950 to 2020 (Table 1; Figure 3). Total catch was below *MSY* (3,170 tonnes year -1) from 1950 to 1988 and fluctuated around *MSY* for the remaining years, with catch being above *MSY* for 18 out of the 32 years from 1989 to 2020. Several definitions for the terms "overfished" and "overfishing" exist in the literature, but generally a stock is considered "overfished" if biomass is below *BMSY* by some degree and undergoing "overfishing" if fishing mortality is above *FMSY* by some degree (Froese and Proelss, 2013, 2012; Hilborn, 2020; Langseth et al., 2019). For the purposes of this study, we refer to the Crevalle Jack stock as "overfished" whenever model estimated biomass was below *BMSY* (*B/BMSY* < 1) and undergoing "overfishing" whenever model estimated fishing mortality was above *FMSY*

(*F/FMSY* > 1). These definitions do not account for fluctuations around the thresholds due to inherent variability. A stock managed at maximum sustainable yield could be expected to fluctuate around *BMSY*. However, the Crevalle Jack stock is unmanaged and stock size has continually declined, suggesting that the stock is not being sustainably harvested. According to the base model, fishing mortality (*F*), was above *FMSY* for 11 out of the 21 years since 2000, revealing that overfishing has been occurring regularly since 2000. Biomass (*B*) was above *BMSY* from 1950 to 2002 but was below *BMSY* for every year from 2003 to 2011 and then again from 2017 to 2020, with biomass being the lowest in 2019. It appears that high levels of catch above *MSY* starting in 1989 led to overfishing beginning in 2000 and the stock becoming overfished starting in 2003. According to the assessment, the current status of the stock is overfished and fully exploited, with estimated $F_{2020}/F_{MSY} = 0.99$ and $B_{2020}/B_{MSY} = 0.90$ (Table 2).

3.2 Model sensitivity runs

Our first set of sensitivity runs examined the impact of selecting various discard mortality rates for the recreational fishery by running a series of models with recreational discard mortality ranging from $0 - 50\%$ at 5% increments (Table 1; Figure 4). Discard mortality rates above 50% were not considered because they were deemed highly unrealistic by fishing guides. For all model runs, exploitation (*F2020/FMSY*) in 2020 ranged from 0.94 at 0% mortality to 1.03 at 50% mortality. Stock size (*B2020/BMSY*) in 2020 ranged from 0.85 at 0% mortality to 0.96 at 50% mortality (Table 2; Figure 4b). Regardless of the discard mortality rate used, the models revealed the same trend of gradually increasing exploitation and gradually decreasing stock size over time. The

status of the stock in 2020 was overfished regardless of the mortality rate used but was only overexploited if the natural mortality rate was set above 10%. Choice of discard mortality rate had little effect on the estimate of *r* in the model, but greatly affected the estimate of *k*, with *k* increasing linearly as the discard mortality rate increased (Figs. 4c, 4d). Since *k* directly affects the estimate of *MSY*, estimated *MSY* also increased linearly as the discard mortality rate increased. At a mortality rate of 0%, estimated *MSY* was 2,340 tonnes, and at a mortality rate of 50% estimated *MSY* was 6,800 tonnes (Table 2).

The remaining sensitivity analyses (2-6) examined the effects of excluding the abundance timeseries (using the CMSY model only), excluding historical catch data, excluding high PSE data points from the MRIP data, using uniformed priors vs. LEK priors, and using an alternative abundance dataset (Table 1). Except for sensitivity analyses 5 (uninformed priors) and 6 (alternative abundance dataset), each of the sensitivity model runs revealed the same pattern of gradually decreasing stock size over time (Figure 5a). Furthermore, estimated biomass in 2020 was below *BMSY* for all models except sensitivity analysis 5 (Table 2; Figure 5b). For all model runs, biomass was below *BMSY* for at least 3 years and fishing mortality was above *FMSY* for at least 4 years out of the 70-year timeseries (Supplementary Figs. S2-S6).

Using uninformed biomass priors (analysis 5) had the greatest impact on the model results, leading to a much more optimistic depiction of current stock status than the base model. For this analysis, starting and ending biomass priors (1950 and 2020) were set to a wide range (0.01 to 1), which tells the model we have no information about stock status at the beginning nor end of the timeseries (Froese et al., 2019). The intermediate biomass level was set to NA which allowed the model to estimate it from

maximum or minimum catch according to some simple rules (Froese et al., 2017). This version of the model showed the same trajectory of gradually increasing exploitation over time as the base model, but it estimated that stock size in 1950 was below *BMSY*, rapidly increased to high levels in the 1960s, and then gradually declined (Supplementary Figure S5). The most important difference between this model and the initial model was that using uninformed priors painted a much more optimistic picture of stock status, with the stock in 2020 being above *BMSY* and below *FMSY* (Table 2; Figure 5b). Additionally, exploitation was above *FMSY* for only 6 years out of the 70-year timeseries (2009, 2010, 2015, 2016, 2017, and 2018).

The most pessimistic model was sensitivity analysis 4, excluding high PSE data points (Supplementary Figure S4). Two data points had PSEs above 50%, 1986 and 2009. The catch estimate for 1986 was similar to the average of the timeseries at 3,107 tonnes. However, the catch estimate for 2009 was anomalously high compared to the rest of the timeseries at 7,116 tonnes, compared to a mean catch of 2,078 tonnes before 2009 (Figure 2b). Removing that data point and replacing it with an interpolated value brought the total catch for 2009 down to 2,787 tonnes. This decrease in total catch for 2009 had a negative effect on *r*, with estimated *r* decreasing from 0.54 to 0.49. This resulted in a lower estimated *MSY* and *FMSY* and a more pessimistic stock status, with the stock being overfished and undergoing overfishing in 2020 (Table 2; Figure 5). For this model, the Crevalle Jack stock was undergoing overfishing for 15 years out of the 70-year timeseries (Supplementary Figure S4).

Using an alternative abundance timeseries (sensitivity analysis 6), had little effect on estimated management reference points. However, the ENP timeseries went back

farther in time than the MRIP timeseries, and the trajectory of stock status over time differed slightly between the two models. With the ENP timeseries as an index of abundance, stock size declined rapidly from 1970 to 1985 before increasing back to historic levels and then gradually declining from 1990 to 2020 in the same fashion as the base model (Supplementary Figure S6). Where the two abundance timeseries overlapped (1991-2020), model results were very similar.

4. Discussion

In the United States, the Magnuson-Stevens Reauthorization Act mandates that federal fishery management plans prescribe annual catch limits to prevent overfishing while achieving optimum yields for each stock (MSFCMA, 2007). It is recognized that preventing overfishing leads to maximum beneficial use of fisheries resources. Improvements in data-collection are being made for several fisheries (e.g., Bryan et al., 2016), but for many stocks, data-limited assessment approaches may be required as longterm solutions (Harford and Carruthers, 2017), especially in areas like the southeastern United States where over 75% of stocks remain data-limited (Berkson and Thorson, 2015; Newman et al., 2015). Studies have shown that combining multiple data sources and different data-limited tools and techniques can help create the most robust and accurate assessments possible, decreasing bias and uncertainty (e.g., Chrysafi et al., 2019; Michielsens et al., 2008; Pinto et al., 2019; Roux et al., 2019).

In this paper, we demonstrated how a variety of data-limited tools, when used in combination, can aid in developing rapid yet robust assessments for data-limited, unregulated fisheries that provide a basis for initial management. Our approach takes

advantage of local ecological knowledge to inform both model selection and analysis. LEK and other existing data sources are used to fill out the FishPath assessment questionnaire, which is a currently underutilized program that provides a transparent, standardized approach for selecting an appropriate stock assessment model. LEK is then again used to parameterize the chosen model where parameter estimates are unavailable, which is the case for many data-limited fisheries. Finally, by identifying unknown and uncertain parameters and running sensitivity analyses to test their effects on estimates of stock status, we can develop clear goals and priorities for future research, thus ensuring funding and effort are put towards the greatest needs. The results of applying our framework to assessing stock status of the Crevalle Jack in Florida suggest that biomass has been below *BMSY* for 13 out of the past 18 years and the stock is currently fully exploited (with fishing mortality rates roughly equaling the fishing mortality at *MSY*). Any increase in fishing pressure will likely lead to a continued decline in stock size. Fishing guides in the Florida Keys have observed a gradual decline in Crevalle Jack catch rates, beginning as early as 1985, with very low catch rates observed since the early 2000s (Gervasi et al., 2022). Our stock assessment results align with the timing of this observation and further highlight the need to develop a management plan for this important fishery.

4.1 Crevalle Jack stock status and trends

Our base CMSY-BMS model revealed that catch of Florida Crevalle Jack has been at or above *MSY* almost every year since 1989 with several years of overfishing occurring, and the stock has been in an overfished state almost every year since 2003. Stock size has been gradually declining over time while recreational fishing effort appears to be continually increasing. Commercial landings were relatively low throughout the timeseries compared to recreational landings, and commercial landings dropped considerably in the mid-1990s (coincident with the commercial gillnet ban in Florida; Smith et al., 2003). The increasing recreational fishing effort is somewhat surprising, as fishing guides reported that the Crevalle Jack fishery is largely opportunistic and catch-and-release in the Florida Keys (Gervasi et al., 2022). However, in the statewide MRIP data, recreational anglers report which species were primarily targeted on each fishing trip, and out of all Florida trips Crevalle Jack were reported as the 46th most targeted species out of 318 species listed as primary targets. Crevalle Jack are therefore in the top 15% of recreationally targeted species throughout the state.

Studies have shown that recreational landings exceed commercial landings for many fisheries (Coleman et al., 2004; Lewin et al., 2019; Radford et al., 2018; Shertzer et al., 2019), and there is growing evidence that recreational fisheries can be responsible for declines in fish populations and have other biological impacts (Brownscombe et al., 2019; Lewin et al., 2006). Worldwide, the number of recreational anglers (Kearney, 2002; Pawson et al., 2008), magnitude of catches (Coleman et al., 2004; Felizola Freire et al., 2020), and economic impact (Arlinghaus et al., 2019) of recreational fishing is increasing. Although recreational fisheries provide funding for conservation efforts and connect society with nature, increasing public awareness and appreciation of conservation concerns (Arlinghaus et al., 2019; Brownscombe et al., 2019; Griffiths et al., 2017), these fisheries are prone to high uncertainty, which undermines sustainable

management (Shertzer et al., 2019). Appropriate management action that balances the social-ecological dimensions of these fisheries is therefore vital.

The timing and trajectory of Crevalle Jack exploitation matches the observations of recreational fishing guides in Florida, some of whom began noticing a decline in Crevalle Jack catch rates as early as 1985 (Gervasi et al., 2022). Most guides, however, noticed the decline in the early to mid-2000s, which corresponds with when stock size began dipping below *BMSY* (2003). Additionally, guides reported that the decline had been gradual, which again matches the model results (even for the analysis using uninformed priors, stock size declined gradually from 1970 to 2020). This agreement between fishing guide observations and model results provides confidence in the stock assessment and highlights the benefits of incorporating LEK into fisheries research. Consistency between LEK and other data sources has been observed in many studies (e.g., Aswani and Hamilton, 2004; Bourdouxhe et al., 2020; Poizat and Baran, 1997; Rehage et al., 2019; Santos et al., 2019; Zukowski et al., 2011), and the use of LEK in fisheries research and management has increased substantially over the years (Beaudreau and Levin, 2014). A recent study by Shephard et al. (2021) showed that angler LEK matched stock assessment results for four recreational fisheries in Ireland, further demonstrating that LEK can provide valuable, robust information about fisheries stock status and trends.

The CMSY-BSM model approach has been successfully applied to several other data-limited fisheries, including five exploited tuna fisheries in India (Nisar et al., 2021) and 54 commercial fish and invertebrate stocks in the Mediterranean and Black sea (Demirel et al., 2020). Anderson et al. (2017) evaluated the performance of several individual models and superensemble models combining multiple data-limited

assessment methods with 5,760 simulation stocks and 249 real stock assessments. The original Catch-MSY model (Martell and Froese, 2013) was one of the models evaluated. This model was shown to be the best performing individual model. Furthermore, the individual Catch-MSY model performed just as well as some of the superensemble models in the performance metrics assessed (accuracy, bias, and rank-order correlation). Since the CMSY-BSM model is an advanced version of the original Catch-MSY model, the high model performance of the Catch-MSY model in comparison to other methods provides confidence that the CMSY-BSM model is robust and well suited for assessment of data-limited fish stocks like the Crevalle Jack.

Despite the demonstrated accuracy of the CMSY-BSM model approach, there are limitations to the method. According to simulation studies, the CMSY model is not as efficient when used for less-captured or very low-resilience fisheries such as sharks, rays, and some large teleosts (ICES, 2014). Since the Crevalle Jack is categorized as a species with medium resilience according to FishBase, this limitation should not apply to our study. The method also tends to underestimate *MSY* and *k* if only landings data are used and discards are substantial (Froese et al., 2017). Again, since our CMSY-BSM model used a full timeseries of fishery removals that included recreational discards, this limitation should not apply to our study. However, we did see that the choice of discard mortality rate in sensitivity analysis 1 greatly affected estimates of *MSY* and *k*. Finally, the BSM model can provide unrealistic results if any major changes in the system such as environmental regime shifts, or major changes in catchability, productivity, or sizestructure over time violate model assumptions (Froese et al., 2017). In our study, fishing guides did not identify any substantial environmental changes over time that might

influence our model results. The fact that the model's inherent limitations did not appear to apply to this study further demonstrates that the FishPath tool helped identify a stock assessment method that was well-suited to initial assessment of the Florida Crevalle Jack fishery.

4.2 Sensitivity analyses

Fisheries management is commonly based on setting target quotas or catch limits based on fisheries reference points from stock assessments (Newman et al., 2015). Uncertainty in model parameters that greatly affect the estimation of reference points can lead to target setting based on inaccurate estimations of stock status, increasing the risk for either overfishing or underutilizing the resource (Cadrin et al., 2015; Dankel et al., 2012; Privitera-Johnson and Punt, 2020). Compared to our initial CMSY-BSM model, none of the sensitivity analyses dramatically altered the overall pattern of exploitation and stock size over time, nor the estimated current stock status. In all models, exploitation increased over time with harvest increasing to levels at or above *MSY* at some point during the timeseries. Stock size also generally decreased over time, with overfishing occurring in all models, though the number of years the stock was in an overfished state varied depending on the model. Exploitation in 2020 was high for all models, with *F2020/FMSY* ranging from 0.85 to 1.17 (Table 2). All models except analysis 5 (uninformed priors) also showed that the stock in 2020 was overfished $(B_{2020}/B_{MST} < 1)$. This model consistency reveals high model precision and provides some additional confidence in our stock assessment results. However, there still may be unaccounted for

sources of uncertainty (i.e., unknown unknowns; Drouineau et al., 2016) that could affect model accuracy.

Despite the consistency in overall trends among model runs, estimated management reference points deviated from the initial model for some of the sensitivity analyses. Changing the discard mortality rate for our first analysis had the greatest effect on reference points, with *k* increasing dramatically with an increase in the discard mortality rate. This change in *k* led to a substantial impact on estimated *MSY* and *BMSY*, which are important values needed to determine fisheries quotas. This analysis highlights the importance of estimating an accurate discard mortality rate for fisheries that are predominantly catch-and-release. When angling effort is high, catch-and-release fishing is often applied as a management solution for reducing angling impacts on important fisheries (Cooke and Schramm, 2007). Although catch-and-release fishing can provide many benefits to fisheries when used appropriately (Arlinghaus et al., 2007, 2002), it can also have unintended and unaccounted for consequences (Cooke et al., 2002; Cooke and Suski, 2005). Several studies have shown that angling can have a multitude of physiological effects on fish, resulting in morbidity and mortality after release (Campbell et al., 2010; Cooke et al., 2002), and can increase vulnerability to predation (Holder et al., 2020). Accurately accounting for discard mortality in assessments for largely catch-andrelease fisheries is therefore vital.

Of the remaining sensitivity analyses, using uninformed priors had the greatest effect on estimates of *k* and *BMSY*, resulting in a much more optimistic view of available biomass and stock status. According to this version of the model, the stock was not overfished nor was it undergoing overfishing in 2020. Failure to provide informed priors

could therefore prevent management action from being taken, potentially leading to continued overfishing and even stock collapse. Previous research has shown that Bayesian methods (such as BSM) are highly sensitive to mis-specified priors, and that well-thought-out informative priors can considerably reduce uncertainty (Punt and Hilborn, 1997). Expert anglers have been shown to provide accurate estimates of biomass trends in many studies (Beaudreau and Levin, 2014; Shephard et al., 2021), and thus serve as a useful resource for developing informative priors. In fact, research has shown that synthesizing expert knowledge can be the most powerful approach for selecting informative model priors (Punt and Hilborn, 1997). Previous studies employing the CMSY-BSM method specifically, have used expert knowledge to inform the relative biomass priors required by the model (Demirel et al., 2020). The results of this sensitivity analysis highlight the importance of the LEK component of our assessment framework (Figure 1).

Excluding or changing the source of the CPUE data (analyses 2 and 6) had some effect on the trajectory of stock status and exploitation over time (Supplementary Figs. S2, S6). The timeseries of stock size when the CPUE dataset was ignored showed a slightly less dramatic decline than the base model, with biomass only dipping below *BMSY* at the very end of the timeseries (2018-2020). Estimated management reference points, however, were similar to the base model, with the main difference being a slightly higher estimate of *MSY* (Table 2). Studies have shown that accurate estimates of stock abundance lead to better stock assessment models and perform better than catch-only methods (Carruthers et al., 2014). Our analysis showed that excluding CPUE or

abundance data could lead to more optimistic estimates of stock status, potentially preventing management action.

When estimated abundance from fisheries-independent surveys is not available, abundance trends can be inferred from CPUE data (Maunder and Punt, 2004). However, it is important that the chosen fisheries-dependent data accurately reflect actual stock abundance trends. The purpose of sensitivity analysis 6 was to determine if choosing a different CPUE dataset (ENP vs. MRIP), significantly altered model results. Both the MRIP and ENP datasets have specific pros and cons that should be taken into consideration when they are used to develop indices of abundance. The main benefit of the MRIP survey is that it is a national survey program that has undergone substantial review and modification, and has been used to provide essential stock assessment information for management of numerous fish species (National Academies of Science Engineering and Medicine, 2017). However, the data remains susceptible to several inherent limitations of dockside intercept survey methods. Mainly, it can be difficult to estimate the species, number, and fates of fish released rather than landed, and privateaccess sites cannot be sampled, which can lead to bias (National Academies of Science Engineering and Medicine, 2017). The ENP dataset is also susceptible to the same limitations of dockside intercept survey methods, and it is furthermore restricted to a small spatial area in south Florida (Osborne et al., 2006). Regional variations in catch rates can occur due to differences in habitat, environmental variables, etc. (e.g., Bigelow et al., 1999; Briand et al., 2011; Ochwada-Doyle et al., 2021). Recreational catch and effort in ENP therefore may or may not be representative of catch and effort trends for the state. However, Crevalle Jack are more commonly captured in the ENP dataset than

in the MRIP dataset (Gervasi et al., 2022). So, it is possible that the ENP dataset provides a more precise estimate of Crevalle Jack abundance trends than the MRIP data. The standardized index developed from the ENP dataset also goes back farther in time than the MRIP dataset, to 1980 vs. 1991.

Standardized indices of abundance developed from both surveys showed similar temporal trends where the timeseries overlapped (Figure 2), and estimated management reference points were similar between the base model and analysis 6, but the analysis using the ENP dataset revealed a slightly more pessimistic estimate of current stock status (Table 2). The main difference between the two models was in the timeseries of exploitation and stock size. With the ENP dataset used as an index of abundance, the model showed a general increase in exploitation from 1950 to 1980, followed by a plateau from 1980 to 2005 before exploitation again increased. Stock size was relatively constant from 1950 to 1970, then dramatically declined to below *BMSY* in 1985 before quickly rebounding and then once again declining following a similar pattern as the base model (Supplementary Figure S6). Ideally, abundance indices should be developed using fisheries-independent data, but that is not always available, especially for unregulated stocks. In these cases, collection of quality fisheries-dependent data or reliable LEK data on CPUE trends is crucial (Sagarese et al., 2019). Regardless of the dataset used to develop an index of abundance for Crevalle Jack, estimated management reference points were very similar, as were trends in exploitation and stock size during the years the MRIP and ENP datasets overlapped. Agreement between these datasets provides confidence in the inferred abundance trends.

Removing data points from the catch timeseries with high PSE (analysis 4) did not affect the trajectory of exploitation and stock status over time but led to a more pessimistic view of stock status (Table 2; Supplementary Figure S4). Outliers in the catch timeseries can therefore influence estimated stock status and management reference points, which further highlights the need for accurate and robust collection of fisheriesdependent data. The MRIP survey underwent substantial peer review and modification in 2018 after a three-year transition period (Papacostas and Foster, 2018). Continued improvements to this survey and a focus on improving statistically unreliable estimates will aid in developing more accurate assessments for many data-limited fisheries (National Academies of Science Engineering and Medicine, 2017).

The sensitivity analysis that provided the most similar results to the initial model was analysis 3, excluding historic catch (Table 2; Supplementary Figure S3). Removing the first 31 years from the catch timeseries did not alter the trajectory of exploitation or stock status over time and resulted in almost identical estimates of management reference points as the initial model. This result shows that the historical fishery removals had little influence on current stock status, with more recent removals being more influential. However, historical recreational catches were estimated using a relatively simple method (FHWAR) and may therefore be over- or under-estimations of actual catches. Continued research into the accuracy of back-calculation methods for estimating historical catches will help improve stock assessments for fisheries with relatively short available timeseries data on fishery removals (Brennan and Fitzpatrick, 2012).

4.3 Implications for management

According to our base model and five out of the six sensitivity analyses, the current status of the Florida Crevalle Jack stock is overfished (*B* < *BMSY*), and overfishing has been occurring for several years over the past 2 decades (*F* > *FMSY*). Our sensitivity analyses revealed some uncertainty in the extent of overfishing that has occurred since 1950, but all models showed stock size trending in a negative direction, suggesting management action is needed to halt the decline in stock size. The current exploitation rate is also right at or slightly above *MSY*. Since the Crevalle Jack is currently an unregulated species in Florida (FWC, 2021), and recreational fishing in the region is continually increasing (Hanson and Sauls, 2011; Shertzer et al., 2019), it is likely that exploitation rates will continue to increase to unsustainable levels if the fishery remains unregulated. Importantly, with recreational fisheries, the goal is not always to maximize yield. Fishing guides in the Florida Keys have observed that catch rates of Crevalle Jack have declined below a desirable level in recent years (Gervasi et al., 2022). So, although our models revealed that fishing mortality is currently right at *MSY* and biomass is only slightly below *BMSY*, management regulations that bring catch rates back up to desirable levels may be more beneficial to the fishery than managing for *MSY*. As the Crevalle Jack is an unregulated species in all U.S. Gulf and Atlantic states within the species range, additional research into Crevalle Jack stock structure and stock status in other areas are also critical next steps.

Although the overall trends in exploitation and estimated status of the Crevalle Jack stock did not vary much amongst the different model variations, there was considerable disparity in some of the estimated management reference points. This

uncertainty makes it difficult to provide recommendations for setting a target quota. However, the result that the Crevalle Jack fishery is fully exploited and overfished does suggest that management efforts are warranted. Our suggested next steps for management include engaging in cooperative research and co-management (Johnson and Van Densen, 2007; Kaplan and McCay, 2004) and setting regulations on the Crevalle Jack recreational fishery that are both acceptable to the stakeholders and follow a precautionary approach. Beyond that, additional research can aid in reducing uncertainty and providing more concrete management recommendations. The results of our sensitivity analyses revealed the importance of estimating an accurate discard mortality rate, since the vast majority of Crevalle Jack captured by recreational anglers in Florida are released. Tagging studies that assess how factors such as handling time, hooking location, depth, predator abundance, etc. influence post-release survival will aid in getting a better estimate of the survival rate (e.g., Flaherty-Walia et al., 2016; Jiang et al., 2007; Rudershausen et al., 2007). Our results also highlighted the importance of using an accurate and appropriate timeseries of abundance in the CMSY-BSM model. Developing a fisheries-independent survey to monitor Crevalle Jack populations would be the best way to improve the relative abundance timeseries. However, continued improvements to fisheries-dependent surveys like the NOAA MRIP and ENP creel survey programs can also increase the reliability of CPUE data as an index of relative abundance. Finally, accurately delineating stock boundaries is an important part of stock assessment (Berger et al., 2021; Ying et al., 2011). Preliminary acoustic telemetry research in Florida has revealed that Crevalle Jack make regular long-range movements throughout the state, and that some individuals even cross state boundaries into other states within the Gulf of Mexico (C.L. Gervasi,

unpublished data). These results suggest that the catch and abundance timeseries may need to be expanded to include data from other states to encompass the entire stock. As the acoustic telemetry data continue to reveal patterns of Crevalle Jack movements and migrations, the CMSY-BSM model can be re-run to account for changes in estimated stock boundaries. As new data about the species and fishery are collected, the FishPath assessment questionnaire can also be updated, and other data-limited assessment methods can be explored and compared. The LEK-driven, three-prong assessment approach outlined herein can easily be included as part of an adaptive management plan and can be applied to other unregulated species and in other regions.

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	Base model	Sensitivity analysis 1	Sensitivity analysis 2	Sensitivity analysis 3	Sensitivity analysis 4	Sensitivity analysis 5	Sensitivity analysis 6
Description of sensitivity analysis	\blacksquare	Varying the discard mortality rate	Excluding CPUE data (CMSY model <i>only</i>)	Excluding historical catch	Excluding high PSE points in MRIP data	Using uninformed priors vs. LEK priors	Using an alternative abundance dataset
Catch start year	1950	1950	1950	1981	1950	1950	1950
Catch end year	2020	2020	2020	2020	2020	2020	2020
Abundance timeseries	MRIP	MRIP	N/A	MRIP	MRIP	MRIP	ENP
Resilience category [†]	Medium	Medium	Medium	Medium	Medium	Medium	Medium
Prior ranges for r^{\dagger}	$0.35 - 0.8$	$0.35 - 0.8$	$0.35 - 0.8$	$0.35 - 0.8$	$0.35 - 0.8$	$0.35 - 0.8$	$0.35 - 0.8$
Relative biomass category $(beginning)*$	Nearly unexploited	Nearly unexploited	Nearly unexploited	Low depletion	Nearly unexploited	Uninformed	Nearly unexploited
Prior range for B/k (beginning)*	$0.75 - 1.0$	$0.75 - 1.0$	$0.75 - 1.0$	$0.4 - 0.8$	$0.75 - 1.0$	$0.01 - 1$	$0.75 - 1.0$
Relative biomass category $(middle)*$	Low depletion	Low depletion	Low depletion	Low depletion	Low depletion	Uninformed	Low depletion
Prior range for B/k (middle)*	$0.4 - 0.8$	$0.4 - 0.8$	$0.4 - 0.8$	$0.4 - 0.8$	$0.4 - 0.8$	N/A	$0.4 - 0.8$
Relative biomass category (end)*	Medium depletion	Medium depletion	Medium depletion	Medium depletion	Medium depletion	Uninformed	Medium depletion
Prior range for B/k (end)*	$0.2 - 0.6$	$0.2 - 0.6$	$0.2 - 0.6$	$0.2 - 0.6$	$0.2 - 0.6$	$0.01 - 1$	$0.2 - 0.6$
Discard mortality rate*	0.1	Range from $0 - 0.5$	0.1	0.1	0.1	0.1	0.1

Table 1. Model inputs and parameters for the base Crevalle Jack stock assessment model, and for the 6 sensitivity analyses.

Changes to model inputs and parameters from the base model for each sensitivity analysis are bolded

*Values derived from angler LEK except for in sensitivity analyses 1 (discard mortality not informed by LEK) and 5 (priors not informed by LEK) †Derived from FishBase (Froese and Pauly 2021)

	Base model	Sensitivity analysis 1	Sensitivity analysis 2	Sensitivity analysis 3	Sensitivity analysis 4	Sensitivity analysis 5	Sensitivity analysis 6
Description of sensitivity analysis	$\overline{}$	Varying the discard mortality rate	Excluding CPUE data (CMSY model <i>only</i>)	Excluding historical catch	Excluding high PSE <i>points in</i> MRIP data	Using uninformed <i>priors vs. LEK</i> priors	Using an alternative abundance dataset
r (year $^{-1}$)	0.54	$0.50 - 0.55$	0.55	0.56	0.49	0.47	0.50
$k(1000 \text{ tonnes})$	23.4	17.6-54.6	23.2	23.0	24.3	28.5	25.1
$MSY(1000 \text{ tonnes})$	3.17	2.34-6.79	3.47	3.23	2.96	3.32	3.14
F_{MSY} (year $^{-1}$)	0.27	$0.25 - 0.28$	0.30	0.28	0.24	0.23	0.25
B_{MSY} (1000 tonnes)	11.7	8.78-27.3	11.4	11.5	12.2	14.3	12.6
F_{2020}/F_{MSY}	0.99	$0.95 - 1.04$	0.96	0.96	1.17	0.85	1.04
B_{2020}/B_{MSY}	0.90	0.84-0.96	0.98	0.92	0.81	1.01	0.87
F_{2020} (year ⁻¹)	0.27	$0.25 - 0.27$	0.29	0.27	0.28	0.20	0.26

Table 2. Estimated management reference points from the base Crevalle Jack stock assessment model, and for the 6 sensitivity analyses.
3-Prong Approach for Rapid Assessment of Data-Limited Fisheries **Using Local Ecological Knowledge**

Figure 1. Framework presented in this paper for conducting rapid initial assessments of unregulated and data-limited fisheries using a 3-prong approach with angler local ecological knowledge (LEK) permeating each step. First, data from LEK and other sources are used to fill out the FishPath assessment questionnaire and choose a datalimited stock assessment method suited to the fishery of interest. Second, a stock assessment is conducted for the species of interest using the chosen method, with LEK informing unknown model parameters. Finally, simple sensitivity analyses are run to test how uncertain or unknown parameters (including those estimated by LEK) affect estimates of stock status. Highly influential parameters highlight critical future research needs.

Figure 2. Time series of crevalle jack catch (total fishery removals) used in the initial CMSY-BSM model (A) and breakdown of fishery removals by fleet (B). In both panels (A) and (B) an estimated discard mortality rate of 10% was applied to the recreational live releases to get an estimate of recreational dead discards. Panel (C) is the MRIP standardized abundance index used in the base model and sensitivity analyses 1, 3, 4, and 5 as the biomass time series. Panel (D) is the ENP standardized abundance index used in sensitivity analysis 6 as the biomass time series.

Figure 3. Summary of information relevant for management of Florida Crevalle Jack from the base CMSY-BSM model. Panel (A) shows catches (total fishery removals) relative to *MSY* (dashed line). Panel (B) shows the development of predicted relative total biomass (*B/BMSY*). Panel (C) shows relative exploitation (*F/FMSY*). Panel (D) shows the trajectory of relative stock size (*B/BMSY*) as a function of fishing pressure (*F/FMSY*). Gray shading in panels (A-C) denote 95% confidence limits for *MSY*, relative biomass, and relative exploitation, respectively. The oval shape around the assessment of the final year triangle indicates uncertainty with yellow for 50%, gray for 80%, and dark gray for 95% confidence levels.

Figure 4. Results of the recreational discard mortality sensitivity analysis (sensitivity analysis 1). Panel (A) shows the time series of catch with discard mortality set at 0, 10, 20, 30, 40, and 50%. Panel (B) shows the time series of exploitation (*F/FMSY*) on the yaxis and of stock size (*B/BMSY*) on the x-axis in the final year (2020) for the range of discard mortality rates assessed (0-50%). Panel (C) shows the effect of discard morality rate on estimated resilience (*r*) and panel (D) shows the effect of discard mortality rate on estimated unexploited stock size (*k*).

Figure 5. Results of the base model in comparison to sensitivity analyses 2-6. Panel (A) shows the development of predicted relative total biomass (*B/BMSY*) for each model run. Panel (B) shows the time series of exploitation (*F/FMSY*) on the y-axis and of stock size (*B/BMSY*) on the x-axis in the final year (2020) for each model run.

Coefficient	Estimate	Standard Error	z-value	p-value
Intercept	-1.418	0.052	-27.442	0.001
Year1992	0.028	0.062	0.450	0.653
Year1993	-0.252	0.062	-4.049	0.001
Year1994	-0.160	0.060	-2.669	0.01
Year1995	-0.032	0.060	-0.542	0.588
Year1996	0.153	0.060	2.560	< 0.05
Year1997	0.141	0.059	2.381	< 0.05
Year1998	0.212	0.057	3.704	0.001
Year1999	0.221	0.055	3.997	0.001
Year2000	0.054	0.057	0.956	0.339
Year2001	-0.125	0.057	-2.183	< 0.05
Year2002	-0.113	0.056	-1.998	< 0.05
Year2003	-0.039	0.056	-0.686	0.492
Year2004	-0.267	0.059	-4.522	0.001
Year2005	-0.226	0.059	-3.831	0.001
Year2006	-0.212	0.059	-3.591	0.001
Year2007	-0.353	0.060	-5.922	0.001
Year2008	-0.507	0.060	-8.382	0.001
Year2009	-0.435	0.060	-7.277	0.001
Year2010	-0.540	0.060	-8.985	0.001
Year2011	-0.693	0.061	-11.262	0.001
Year2012	-0.360	0.058	-6.191	0.001
Year2013	0.068	0.058	1.164	0.244
Year2014	0.048	0.057	0.842	0.400
Year2015	-0.081	0.058	-1.404	0.160
Year2016	-0.285	0.059	-4.816	0.001
Year2017	-0.314	0.061	-5.174	0.001
Year2018	-0.408	0.064	-6.357	0.001
Year2019	-0.419	0.065	-6.497	0.001
Year2020	-0.425	0.063	-6.717	0.001
SeasonSpring	-0.192	0.017	-11.017	0.001
SeasonSummer	-0.294	0.017	-16.843	0.001
SeasonAutumn	0.195	0.016	11.894	0.001

Table S1. Coefficients, estimates, standard errors, z-values, and p-values for the MRIP binomial model on proportion positive data.

Coefficient	Estimate	Standard Error	z-value	p-value
Intercept	-0.392	0.047	-8.369	< 0.001
Year1992	0.018	0.056	0.319	0.750
Year1993	-0.055	0.056	-0.973	0.330
Year1994	-0.096	0.054	-1.781	0.075
Year1995	0.025	0.054	0.471	0.638
Year1996	0.030	0.053	0.564	0.572
Year1997	0.059	0.053	1.123	0.262
Year1998	0.037	0.051	0.727	0.467
Year1999	0.028	0.049	0.576	0.565
Year2000	-0.118	0.051	-2.318	< 0.05
Year2001	-0.135	0.051	-2.644	0.01
Year2002	-0.129	0.051	-2.558	< 0.05
Year2003	-0.074	0.051	-1.454	0.146
Year2004	-0.157	0.053	-2.952	0.01
Year2005	-0.121	0.053	-2.273	< 0.05
Year2006	-0.086	0.053	-1.624	0.104
Year2007	-0.074	0.054	-1.382	0.167
Year2008	-0.109	0.055	-1.989	< 0.05
Year2009	-0.112	0.054	-2.081	< 0.05
Year2010	0.003	0.054	0.048	0.962
Year2011	-0.047	0.056	-0.839	0.401
Year2012	0.054	0.052	1.022	0.307
Year2013	0.094	0.052	1.812	0.070
Year2014	-0.050	0.051	-0.981	0.327
Year2015	-0.095	0.052	-1.825	0.068
Year2016	-0.062	0.053	-1.158	0.247
Year2017	-0.108	0.055	-1.962	< 0.05
Year2018	0.010	0.058	0.176	0.860
Year2019	-0.010	0.059	-0.173	0.862
Year2020	0.050	0.057	0.877	0.380
SeasonSpring	-0.341	0.016	-21.506	< 0.001
SeasonSummer	-0.451	0.016	-28.219	< 0.001
SeasonAutumn	-0.143	0.015	-9.668	< 0.001
ModeCharter	-0.680	0.021	-32.212	< 0.001
ModePrivate	-0.616	0.012	-52.723	< 0.001

Table S2. Coefficients, estimates, standard errors, z-values, and p-values for the MRIP lognormal model on positive trips data.

Figure S1. Crevalle Jack recreational CPUE for all fish harvested (A) and released alive (B) from the MRIP data for each year from 1981 to 2020. Blue lines are linear model predictions, gray shading denotes 95% confidence intervals.

Figure S2. Summary of information relevant for management of Florida Crevalle Jack from sensitivity analysis 2 (excluding CPUE data). Panel (A) shows catches (total fishery removals) relative to *MSY* (dashed line). Panel (B) shows the development of predicted relative total biomass (*B/BMSY*). Panel (C) shows relative exploitation (*F/FMSY*). Panel (D) shows the trajectory of relative stock size (*B/BMSY*) as a function of fishing pressure (*F/FMSY*). Gray shading in panels (A-C) denote 95% confidence limits for *MSY*, relative biomass, and relative exploitation, respectively. The oval shape around the assessment of the final year triangle indicates uncertainty with yellow for 50%, gray for 80%, and dark gray for 95% confidence levels.

Figure S3. Summary of information relevant for management of Florida Crevalle Jack from sensitivity analysis 3 (excluding historic catch). Panel (A) shows catches (total fishery removals) relative to *MSY* (dashed line). Panel (B) shows the development of predicted relative total biomass (*B/BMSY*). Panel (C) shows relative exploitation (*F/FMSY*). Panel (D) shows the trajectory of relative stock size (*B/BMSY*) as a function of fishing pressure (*F/FMSY*). Gray shading in panels (A-C) denote 95% confidence limits for *MSY*, relative biomass, and relative exploitation, respectively. The oval shape around the assessment of the final year triangle indicates uncertainty with yellow for 50%, gray for 80%, and dark gray for 95% confidence levels.

Figure S4. Summary of information relevant for management of Florida Crevalle Jack from sensitivity analysis 4 (excluding high PSE points). Panel (A) shows catches (total fishery removals) relative to *MSY* (dashed line). Panel (B) shows the development of predicted relative total biomass (*B/BMSY*). Panel (C) shows relative exploitation (*F/FMSY*). Panel (D) shows the trajectory of relative stock size (*B/BMSY*) as a function of fishing pressure (*F/FMSY*). Gray shading in panels (A-C) denote 95% confidence limits for *MSY*, relative biomass, and relative exploitation, respectively. The oval shape around the assessment of the final year triangle indicates uncertainty with yellow for 50%, gray for 80%, and dark gray for 95% confidence levels.

Figure S5. Summary of information relevant for management of Florida Crevalle Jack from sensitivity analysis 5 (using uninformed priors). Panel (A) shows catches (total fishery removals) relative to *MSY* (dashed line). Panel (B) shows the development of predicted relative total biomass (*B/BMSY*). Panel (C) shows relative exploitation (*F/FMSY*). Panel (D) shows the trajectory of relative stock size (*B/BMSY*) as a function of fishing pressure (*F/FMSY*). Gray shading in panels (A-C) denote 95% confidence limits for *MSY*, relative biomass, and relative exploitation, respectively. The oval shape around the assessment of the final year triangle indicates uncertainty with yellow for 50%, gray for 80%, and dark gray for 95% confidence levels.

Figure S6. Summary of information relevant for management of Florida Crevalle Jack from sensitivity analysis 6 (using an alternative abundance dataset). Panel (A) shows catches (total fishery removals) relative to *MSY* (dashed line). Panel (B) shows the development of predicted relative total biomass (*B/BMSY*). Panel (C) shows relative exploitation (*F/FMSY*). Panel (D) shows the trajectory of relative stock size (*B/BMSY*) as a function of fishing pressure (*F/FMSY*). Gray shading in panels (A-C) denote 95% confidence limits for *MSY*, relative biomass, and relative exploitation, respectively. The oval shape around the assessment of the final year triangle indicates uncertainty with yellow for 50%, gray for 80%, and dark gray for 95% confidence levels.

CHAPTER VI

GENERAL CONCLUSION

Marine fisheries are a source of food, recreation, and jobs to human populations across the globe, and they are a vital component of the economy in many coastal communities (Sumaila et al., 2016). However, over 80% of global catches are comprised of fisheries that lack formal assessment, and research suggests these unassessed fisheries may be in significantly worse condition than assessed fisheries (Costello et al., 2012). There is therefore a pressing need to develop stock assessments that can rapidly identify fisheries at risk of overexploitation and depletion, and will result in proactive, effective management. However, since most unassessed fisheries are unregulated and data-poor, traditional data collection and assessment methods are too difficult, costly, and time consuming for widespread application (Harford and Carruthers, 2017). This is particularly an issue for recreational fisheries, where fishing effort is difficult to quantify and the effects of fishing on exploited species are largely unknown (Arlinghaus et al., 2019). Rapid, low-cost methods for monitoring fishery status and trends, recognizing critical data gaps, and developing robust, adaptive management can help tackle these issues.

My dissertation followed a translational ecology approach to assess the status and trends and fill in critical knowledge gaps to inform conservation and management of the Crevalle Jack in Florida. The Crevalle Jack is an unregulated and data-poor species, yet is targeted by both commercial and recreational fisheries and is an important predator in coastal environments (Kwei, 1978). In Chapter I, I introduced the concepts underlying translational ecology and how they can be applied to recreational fisheries management. I also introduced the concern of declining catch rates of Crevalle Jack in the Florida Keys

observed by recreational fishing guides. In chapter II, I developed a framework for applying translational ecology to the assessment and management of the Crevalle Jack fishery that began with stakeholder observations. By interviewing veteran fishing guides and synthesizing their local ecological knowledge (LEK), I was able to develop informed hypotheses about Crevalle Jack status and trends. When rigorous data collection and analysis are not possible, numerous studies have shown how LEK can fill in knowledge gaps and provide new insights (Dongol and Heinen, 2012; Heinen and Shrestha-Acharya, 2011; Kroloff et al., 2019; Silvano and Valbo-Jørgensen, 2008). I then tested these hypotheses using existing long-term datasets. The multiple data sources all suggested that Crevalle Jack populations in the Florida Keys have declined steadily since at least the 1990s with below average abundance since the mid-2000s, and larger fish appear to have declined more so than smaller fish. Furthermore, Crevalle Jack appear to be seasonal residents of the Florida Keys with highest abundance in the winter months. Two hypotheses concerned the spatial distribution and population connectivity of Crevalle Jack and the causes of the decline, but existing long-term data were not well suited for testing these hypotheses. This chapter showed how recreational fishing guide knowledge can be used to identify a conservation concern and develop hypotheses about trends, causes, and fish behavior quickly and inexpensively. The agreement between guide observations and long-term data further highlighted the benefits of incorporating angler knowledge into fisheries research. A bottom-up conservation approach that begins with observations of stakeholders on the ground can help scientists conduct better applied research that can lead to more proactive management.

In chapters III and IV, I expanded upon the priorities for future research that were identified in chapter II. For future Crevalle Jack management to be successful, it is necessary to know where the population needs to be managed. Depending on the spatial scale of movement and migration patterns, management based only in the Florida Keys may or may not be sufficient. In chapter III, I used a relatively novel otolith microsampling approach to assess the lifetime migration patterns of sub-adult Crevalle Jack from two regions of the Gulf of Mexico, the Florida Keys and coastal Alabama. Changes in stable isotope values throughout otoliths revealed that Crevalle Jack from both regions inhabited inshore, warm water habitats as young-of-the-year fish (age-0), and engaged in an ontogenetic migration to cooler, more offshore habitats between ages-1 and -2, where they appeared to remain through at least age-5. Comparison of stable isotope transects between Florida Keys and Alabama fish suggested that most individuals exhibited local recruitment from nursery habitats throughout the eastern GOM to nearby coastal areas. However, overlap between individual transects of AL and FL fish suggested some level of population connectivity between the two regions may occur. This chapter revealed the potential of otolith stable isotope micro-sampling for examining lifetime migration patterns and stock structure of highly mobile fish species with large spatial distributions. Future research that pairs otolith micro-sampling with other techniques like genetics or acoustic telemetry has the potential to greatly enhance our understanding of stock structure and population connectivity of fishes, which will inform better stock assessments and management.

In chapter IV, I conducted a collaborative acoustic telemetry study to complement the otolith microchemistry work and more closely examine Crevalle Jack movement and

migration patterns at both daily and seasonal scales. Acoustic telemetry is a powerful tool for assessing stock structure, home range, and seasonal distribution, as well as identifying hotspots of activity, all critical information for fisheries management (Crossin et al., 2017). However, tracking highly mobile species with wide-ranging distributions remains challenging (Brownscombe et al., 2019). Fortunately, the cross-compatibility of acoustic telemetry technology has made it possible for research groups to form collaborative telemetry networks where data are shared among users (Ellis et al., 2019). By partnering with the FACT and iTAG acoustic telemetry networks, we were able to track the movement patterns of tagged juvenile and adult Crevalle Jack on receiver arrays throughout the Atlantic coast of Florida and the Gulf of Mexico. We additionally partnered with recreational fishing guides in south Florida to help deploy acoustic tags, which greatly increased our sampling efficiency. Thus far we have collected almost three years of preliminary tracking data and determined that Crevalle Jack tagged in south Florida made regular, long-distance movements north out of the south Florida region and into the northern Gulf of Mexico. The movements of five individuals into coastal Louisiana waters confirmed multi-state stock connectivity, which is critical information for management. Results additionally revealed a clear seasonality to long-range movements, with most movements out of the south Florida region occurring in the spring and summer months, while most individuals appeared to remain in south Florida for the winter months. The exact reasons for these long-range migrations are not yet clear, but future detection data will continue to reveal migration patterns and trends. This chapter highlighted the benefits of collaborative acoustic telemetry research for determining management-relevant information about the movements of data-poor fish species. By

pairing the complementary techniques of otolith microchemistry and acoustic telemetry, I was able to fill in critical knowledge gaps about the life history of the Crevalle Jack, revealing what may be a dual ontogenetic migration strategy. Understanding where fish reside during different life history stages is key to developing effective conservation and management plans (Nathan et al., 2008).

In chapter V, I synthesized the information gleaned from chapters II-IV to develop the first stock assessment for Crevalle Jack in the U.S. I applied a series of datalimited tools to conduct the assessment, including stakeholder knowledge throughout the assessment process. Fishing guide local ecological knowledge and existing data from the literature were first used to fill out the assessment questionnaire within the FishPath tool (Dowling et al., 2016). This tool helped to identity a stock assessment model ideally suited to the Crevalle Jack fishery based on species biology and ecology, existing data, and fishery characteristics. Fishing guide knowledge was again used to inform parameters of the stock assessment model, including prior biomass estimates and discard mortality. Finally, model sensitivity to uncertainty in several parameters was assessed to examine which parameter estimates had the greatest influence on the model results. The stock assessment revealed that the Crevalle Jack fishery in Florida has been routinely overfished and fully exploited for the past two decades, and that stock size has been gradually declining since 1950. Conducting data-limited stock assessments can be incredibly challenging, as assessment methods are not one-size-fits-all solutions (Dowling et al., 2019). By pairing the FishPath Tool with stakeholder knowledge I was able to identify an assessment method best suited to the Crevalle Jack fishery. The

combination of data-limited tools used in this chapter could be used to inform stock assessment of other data-limited species in the future.

The overarching goal of my dissertation was to apply translational ecology methods to identify a pressing recreational fishery concern, assess status and trends, fill in critical knowledge gaps, and provide initial management recommendations. Translational ecology is an action-oriented approach that draws on the ideas and expertise of both scientists and stakeholders, with the goal of rapidly addressing critical conservation issues (Enquist et al., 2017). This method is ideally suited for studying and managing recreational fisheries, as they are complex social-ecological systems that are highly affected by human behavior. Including stakeholders in conversations about appropriate management and drawing on their knowledge and expertise is therefore highly beneficial. Stakeholder knowledge can also be used to identify potential conservation concerns and fill in critical knowledge gaps concerning data-poor and unregulated fisheries, which describes many recreational fisheries.

In my dissertation, I used a translational ecology approach to examine the perceived decline in catch rates of Crevalle Jack in the Florida Keys by experienced recreational fishing guides. As the Crevalle Jack is an unregulated and data-poor species, catch rates and population trends had not previously been monitored and little was known about the species biology and ecology. My dissertation research filled in critical knowledge gaps about Crevalle Jack life history and revealed that the population is fully exploited and in need of management action. This information will aid in developing initial conservation and management plans. The fishery would greatly benefit from future research into the main drivers of Crevalle Jack abundance throughout the GOM and

western Atlantic regions and continued monitoring of movement and migration patterns. Human dimensions research that examines the effects of potential management options on recreational and commercial anglers would also help to limit any negative effects on the angling community when possible and ensure that compliance with regulations is high.

If fishing guides had not expressed their concerns, the assessment and management of the Crevalle Jack would likely not have begun until the population level was dangerously low. Reactive management after a fishery is critically depleted often needs to be severe, which can cause major disturbances to fisheries, affecting jobs, incomes, and livelihoods (Pauly et al., 2005). Proactive management that occurs as soon as warning signs that a fishery may need management action are observed can prevent major, abrupt changes to the fishery. Constant communication and collaboration between scientists and stakeholders following the principles of translational ecology can help transition recreational fisheries management from predominantly reactive to more proactive, increasing fishery stability, improving fishery yields, and maintaining the health and productivity of important aquatic ecosystems.

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