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# A multi-methods approach supports the effective management and conservation of coastal marine recreational flats fisheries

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**Abstract** The recreational, catch and release fishery for fishes that inhabit shallow-water, coastal marine habitats in tropical and sub-tropical regions (called the flats fishery) is economically valuable and increasingly perceived as a sustainable ecotourism pursuit. However, knowledge of many aspects of target species (such as bonefish, tarpon and permit) ecology is incomplete, and fishery- and non-fishery-related threats to the fish and habitats are numerous and often poorly understood. The International Bonefish and Tarpon Symposium is convened every three years to share new knowledge and to chart directions for future research, with a focus on research that informs conservation and management. Most of the articles in this Special Issue focus on the flats fishery in the Caribbean Sea, Gulf of Mexico, and western North Atlantic ocean, but the findings presented here provide guidance for similar work in other regions. Conservation and management of flats fisheries present a challenge because the fisheries are typically data poor; they occur in locations that lack resources and there are scant data on the target species and their habitats. Since earlier symposia, much has been accomplished to fill knowledge gaps and contribute actionable knowledge to conservation. Studies are being replicated across a wider geographic range, and connectivity is being studied at local and regional scales. Citizen science and local ecological knowledge have contributed to a better understanding of historical trends and ongoing processes. In some instances, data have been applied to proactive habitat protections, as in the Bahamas, and to habitat restoration, as in Florida. In other instances, though much data have been gathered, additional information is needed before a comprehensive conservation strategy is possible, as in the Florida Keys. As the articles contained in this Special Issue demonstrate, a mixed-methods approach that uses complementary sources of information to construct a broad understanding of the flats fishery is necessary to guide research and inform conservation and management.

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## Introduction

The coastal habitat mosaic of marine tropical and sub-tropical regions is comprised of seagrass, mangroves, coral reefs, sand and mud bottom, limestone hardbottom, and benthic algae that support a diverse community of resident and transient fishes and invertebrates, as well as juveniles that use these habitats as nurseries. These habitats are typically shallow (<2 m) and are collectively referred to as *flats*. In the Caribbean Sea and western North Atlantic Ocean, bonefish (*Albula vulpes*), Atlantic tarpon (*Megalops atlanticus*), permit (*Trachinotus falcatus*) and numerous other species that depend upon flats habitats support economically and culturally important fisheries that are primarily the focus of recreational fishers that practice catch and release – called the *flats fishery*. The economic and cultural value of the fishery provides leverage for conservation and management, and since bonefish, tarpon, and permit use the entire coastal habitat mosaic during their life cycles, they are valuable umbrella species for broad-scale conservation. This manuscript summarizes the challenges posed by a chronic data-poor situation to conservation and management, the progress in filling knowledge gaps for these species that will improve conservation and management efforts, and outlines future needs to continue progress.

## Science to support conservation and management

One of the great challenges to conservation and management of bonefish, tarpon, permit and other tropical fish species that aggregate to spawn is that most exist in data poor situations. These species are either part of recreational catch and release fisheries or inhabit regions that lack resources for management; in both cases, data to inform standard fisheries management are not available. Indeed, there has never been a proper stock assessment of bonefish, tarpon, or permit, and for bonefish (the most well-studied species) only recently have data on age and growth (Crabtree et al. 1996; Rennert et al. 2019), and movements (e.g., Humston et al. 2005; Murchie et al. 2013) been reported. Indeed, the first scientific documentation of a bonefish pre-spawning aggregation was published less than a decade ago (Danylchuk et al. 2011) and only recently have these telemetric observations been extended to other regions (Brownscombe et al. 2017; Perez et al. 2019) and supplemented with behavioral observations (Danylchuk et al. 2011; Danylchuk et al. 2019). Moreover, most research has occurred in a small portion of the species' geographic range: The Bahamas and Florida Keys for bonefish; Florida and Belize for permit; the geographic coverage of tarpon research is more widespread but most has been in Florida. In addition to lacking data on the present-day fishery, historical data are lacking entirely, thus assessment of trends in the fishery or fish population size and demographics depend solely upon mostly qualitative reports from fishers and guides which are rarely codified (but see Santos et al. 2017; Black et al. 2015). Thus, it is unlikely the 'data poor' status of the flats fishery is going to improve substantially. It is therefore essential to develop fisheries and habitat management strategies that allow conservation despite limited data (Johannes 1998; Pilling et al. 2008). A multi-methods approach toward obtaining actionable knowledge [actionable knowledge is defined as "the creative intersection between what we know and putting what we know into everyday practice" (Blood 2006)] is therefore required to provide sufficient guidance to ensure ecosystems and species are able to function sustainably. In this context, multi-methods means using research from multiple approaches – including oceanography, telemetry, economics, genetics, habitat mapping, sociology – to obtain sufficient information to inform management, conservation, and in some instances restoration. This manuscript summarizes recent progress.

## Fishery characteristics

The recreational flats fishery is primarily catch and release, and fishing effort is frequently via a method known as sight fishing. For sight fishing, a recreational fisher, alone or with a professional fishing guide, wades or uses a pole to push a small skiff across the flats searching for fish. Once a bonefish, tarpon, or permit is sighted, the angler casts a lure or bait to the fish. Because this method requires large areas of flats to search for fish, overfishing can occur even though it is a catch and release fishery by exceeding the fishing capacity, where fishing capacity is defined as the amount of fishing effort that a catch and release fishery can support while maintaining a high-quality fishery (high catch rates, large fish size, intact habitats) (Adams 2017). Mortality arising from catch-and-release is often not considered fully in estimates of fishing mortality, and as such mortality is often cryptic (Coggins et al. 2007).

The recreational flats fishery is economically valuable in the Caribbean Sea, Gulf of Mexico, and western North Atlantic Ocean. For example, the estimated annual economic impact of the recreational fishery for bonefish in the Bahamas, exceeds $141 million USD

(Fedler 2010). The flats fishery generates an annual economic impact of approximately $465 million in the Florida Keys (Fedler 2013) and $50 million in Belize (Fedler 2014). The economic importance of the fishery has led to the creation of strict regulations in some countries: bonefish, tarpon and permit are catch and release only in Belize; bonefish and tarpon are catch and release only in Florida, Puerto Rico, and the U.S. Virgin Islands. In other locations, the flats fishery coexists with consumptive fisheries that are subject to varying levels of management. For example, in the Bahamas, capture of bonefish with nets and commercial sale are illegal, but harvest with hook and line for personal consumption is allowed. The recreational flats fishery in Cuba occurs within marine protected areas designated as recreational catch and release zones, outside of these zones there are no regulations on what appears to be an intensive harvest fishery (Rennert et al. 2019; J. Angulo, Univ. Florida, pers. com.).

## Species descriptions

Members of the Albula genus (family Albulidae) are found throughout the world's shallow tropical seas (Wallace and Tringali 2010; Wallace 2014). Four Albula species occur in the Caribbean Sea and western North Atlantic Ocean (Colborn et al. 2001; Adams et al. 2008; Bowen et al. 2008; Wallace and Tringali 2010) with one species, *Albula vulpes*, supporting the flats fishery (Wallace and Tringali 2016). For the remainder of this manuscript *bonefish* will describe *A. vulpes*. Bonefish feed predominately on benthic invertebrates (bivalves, polychaetes, crustaceans) but also on small fishes (Warmke and Erdman 1963; Colton and Alevizon 1983; Crabtree et al. 1998). Juvenile bonefish inhabit shallow sandy or sandy-mud bottoms (Haak et al. 2019), and adults inhabit sand, mud, algae, seagrass, and mangrove habitats. Recent research documented migrations from foraging areas to pre-spawning sites between October and April, with purported spawning occurring offshore at night (Danylchuk et al. 2011). The planktonic larval duration is 41–71 days (Mojica et al. 1995). Bonefish live to at least 20 years in the Florida Keys (Larkin 2011) and 25 years in the Bahamas (C. Haak, unpubl. data), reaching sizes >70 cm (Crabtree et al. 1996). In the Florida Keys, bonefish mature between 3.5 and 4.5 years between 42 and 49 cm, with males maturing at smaller sizes and younger ages than females (Crabtree et al. 1997a). Size and age at maturity and dimorphic growth patterns appear to differ among regions. For example, bonefish in the Bahamas, Central America and insular Caribbean (Adams et al. 2008; C. Haak, UMass, unpubl. data) may grow three times slower than in the Florida Keys (Crabtree et al. 1996), and growth may vary even at the scale of the Bahamas archipelago (C. Haak, pers. comm.). An International Union for the Conservation of Nature assessment classified bonefish as Near Threatened due to habitat loss and fragmentation (particularly mangroves and seagrasses), coastal development and urbanization, declines in water quality, and harvest by commercial, artisanal and recreational fisheries (Adams et al. 2013).

The geographic range of Atlantic tarpon includes the western Atlantic Ocean, Gulf of Mexico, and Caribbean Sea. Tarpon also inhabit coastal waters of the African continent in the western Atlantic Ocean. Little is published about tarpon in the eastern Atlantic Ocean, all information presented here applies to tarpon in the western Atlantic Ocean. Adults have been observed as far north as Nova Scotia and Ireland (Twomey and Byrne 1985), but these likely represent vagrants. Spawning occurs in summer months in the Gulf of Mexico and southeastern North American coast, with possibly a more protracted spawning season in tropical waters such as Costa Rica (Crabtree et al. 1997b). Spawning is presumed to occur offshore based on collection of larvae <3 days old (Crabtree et al. 1992; J. Shenker, Florida Institute of Technology, unpubl. data) and by following offshore movements of adult fish (Crabtree et al. 1992; Ault et al. 2008). The planktonic leptocephalus stage is 20–40 days (Shenker et al. 2002). Post-metamorphic juveniles are euryhaline and have been collected in waters ranging from 0 to 45 PSU. The vascularized swim bladders of tarpon allow aerial respiration, permitting juveniles to inhabit hypoxic inshore waters where they presumably experience low predation rates and have little competition for prey (Schlaifer and Breder 1940; Geiger et al. 2000). Juvenile habitats include stagnant pools, backwaters, ephemeral coastal ponds and hurricane and storm overwashes, swales, and mangrove swamps and marshes, as well as manmade habitats such as mosquito impoundments and artificial wetlands (Wade 1962; Dahl 1965; Zerbi et al. 2001; Jud et al. 2011). As they grow, juveniles spend significant time in larger rivers, bays and estuaries before exhibiting the more extensive movements of adults (Crabtree et al. 1995). Adults >120 cm fork length (FL) also inhabit inshore waters and bays across a wide range of salinities (fresh to hypersaline) and temperatures (17–40 °C) (Zale and Merrifield 1989; Crabtree et al. 1995), and are capable of seasonal migrations along the southeast coastline of the United States and the Gulf of Mexico (Ault et al. 2008; Griffin et al. 2018).

Permit inhabit coastal areas of the eastern North Atlantic as far north as Massachusetts, throughout the Gulf of Mexico, and the Caribbean Sea. Their presence in subtropical and warm-temperate waters is generally limited to warmer months. Permit spawn at reef promontories (Graham and Castellanos 2005) and offshore structures (e.g., artificial reefs; Crabtree et al. 2002). Spawning occurs during summer months in Florida (Crabtree et al. 2002), but for longer durations at lower latitudes (Graham and Castellanos 2005). There is disagreement on the planktonic larval duration (PLD) of permit: Adams et al. (2006) determined the PLD was 15–18 days, but Bryan et al. (2015) used a time period of 20 to 30 days for models of planktonic larval transport. Settlement and early juvenile habitat is windward sandy beaches (Adams et al. 2006). Adult permit inhabit a variety of coastal habitats, including seagrass, sand, and hardbottom flats to coral reefs.

## Scientific progress

The introductory article for the Proceedings of the 2014 Bonefish and Tarpon Symposium (Adams and Cooke 2015) summarized the status of knowledge for bonefish, tarpon, and permit biology, and placed the research presented in the Proceedings articles in that broader context. Based on the status of knowledge and new information presented in the Proceedings, Adams and Cooke (2015) outlined research needs. Many of those needs have been addressed in the ensuing years. In this Special Issue that includes articles from the 2018 Bonefish and Tarpon Symposium, 23 papers detail knowledge gained in several fronts for flats fishery species and with key relevance to ongoing and future conservation and management efforts.

A limited geographic scope of research was an important shortcoming in 2015. In many instances, this has been addressed. Research on bonefish, for example, previously limited to the Bahamas and Florida Keys, has been conducted in Belize and Mexico (Perez et al. 2019), and Cuba (Rennert et al. 2019). In combination with mark-recapture research in the Bahamas (Boucek et al. 2019), mark-recapture in Belize and Mexico (Perez et al. 2019) demonstrates a pattern of localized bonefish movements during much of the year, interrupted by migrations to pre-spawning sites, a pattern consistent among locations. The work by Rennert et al. (2019) expands the information on age and growth that previously was only available in detail from the Florida Keys (Crabtree et al. 1996), and more generally the wider Caribbean (Adams et al. 2008) to include Cuba – data that may reflect the influence of high levels of harvest of spawning migrations on population demographics. Expanding the geographic scope further, research presented in this issue addresses, for the first time, region-scale connectivity of bonefish via larval transport (Zeng et al. 2019). The likelihood of connectivity among bonefish populations that are managed independently emphasizes the need for attention to regional conservation.

Adams and Cooke (2015) also noted the need to increase partnerships to maximize data return on research investment. This is especially the case for fisheries that lack the resources allocated to managed species in a relatively data-rich environment. In data-poor fisheries, the local or traditional knowledge of fishery participants can be encyclopedic (Johannes 1998), and not only helps to characterize the fishery, past and present, but also assist and guide research (Hind 2015). Importantly in terms of conservation, inclusion of fishers, fishing guides, and others involved in the fishery into research increases their understanding and engagement in conservation efforts and ecosystem stewardship. Adams et al. (2019) report that fishing guides who participated in research to identify bonefish pre-spawning aggregations became advocates for protections that resulted in national parks. Indeed, fisheries and locations that are data-poor often also lack enforcement. Therefore, voluntary participation in conservation measures is often needed for the measures to be successful (Cooke et al. 2013).

Of the studies presented in this Special Issue, seven incorporated citizen science, whereby scientists collaborated with fishers and guides on research (Adams et al. 2019; Wilson et al. 2019; Rennert et al. 2019; Boucek et al. 2019) or worked with fishers and guides to obtain traditional ecological knowledge to describe fishery trends (Rehage et al. 2019; Santos et al. 2019a; Kroloff et al. 2019). The bonefish fishery in the Florida Keys has declined significantly in recent decades, but there were no data to document this decline. Rehage et al. (2019) and Kroloff et al. (2019) used surveys and interviews with fishers and fishing guides to establish trends in the fishery over time to determine the extent and temporal characteristics of the decline. Further, given that traditional stock assessment data are not anticipated for the fishery, Santos et al. (2019a) combined interviews, survey and fishery-dependent data to characterize spatial changes in catch and effort distribution. Combined, these studies place the current fishery in historical context, and help guide additional research and conservation measures. Finally, Klarenberg et al. (2019) incorporated fishery-dependent population trends to model the dynamics of the bonefish fishery to identify the role of adult vs. juvenile survivorship in driving trends, and good and bad survival years that might indicate important events in the historical population decline. This model will be updated as new information is available with the goal of helping to understand the responses of the bonefish population to real and predicted natural and anthropogenic stresses, and informing future research and conservation.

An important component of research on flats fishes and other species that rely on the coastal habitat mosaic is that research results inform actionable knowledge that addresses conservation and management priorities. For example, globally, overfishing and habitat loss/degradation are the greatest threats to coastal fisheries (Jackson et al. 2001; Coverdale et al. 2013). Since the flats fishery is primarily catch and release, or typically at the artisanal scale if harvest occurs (there are exceptions including poaching), the greatest threats to flats species and the fisheries they support are habitat loss and degradation. Thus, research that addresses habitat and spatial components of the flats species has the greatest potential to inform conservation. Moreover, since enforcement of fisheries regulations in locations where the flats fishery occurs is lacking, and since habitat loss/degradation is the top threat to the fisheries, spatial management, whereby important habitats are protected, is arguably the best conservation approach.

Following this theme, numerous studies in the Special Issue provided information directly applicable to conservation. In the Bahamas, a combination of mark-recapture, acoustic telemetry, and behavioral observations informed the creation of national parks to protect bonefish home range and pre-spawning habitats (Adams et al. 2019; Boucek et al. 2019; Danylchuk et al. 2019). Perez et al. (2019) used a similar approach in Belize and Mexico. Identification and characterization of juvenile habitats can inform prioritization for protection and restoration (Wilson et al. 2019), and a better understanding of how juveniles use habitats can inform modification of altered habitats to improve habitat function (Cianciotto et al. 2019; Santos et al. 2019b). Identification of juvenile habitats, the ecological processes at play within them (Griffin et al. 2019; Haak et al. 2019), and their ontogenetic context within the coastal habitat mosaic (Murchie et al. 2019; Santos et al. 2019b) develops a better understanding of fish-habitat dynamics that helps to further prioritize conservation actions.

Frequently missing from fisheries conservation discussions are data that are not fish-specific. Yet data that address abiotic factors that are important to fishes – such as habitat coverage or water quality – are essential to conservation. It is well documented, for example, that tarpon and other species depend upon mangrove habitat, and bonefish and other species are frequently associated with mangrove habitat (reviewed in Adams and Murchie 2015). Therefore, data on mangrove habitat coverage and the extent that mangrove coverage changes over time are essential for conservation, even if patterns of fish habitat use are not available for the study. This is the case for quantification of mangrove cover within a national park in Cuba, a protected area that supports a catch and release flats fishery (Cissel and Steinberg 2019). The fact that overall mangrove cover did not change appreciably over time, and that a short-term decline in mangrove cover was due to a hurricane (natural disturbance) in the context of extensive global mangrove decline (Atwood et al. 2017) underscores the importance of such protections. Similarly, Sweetman et al. (2019) describe water quality parameters in a marine reserve in southern Belize that supports an economically valuable catch and release flats fishery. The marine reserve is well-maintained and enforced, but to what extent will activities in the upland watershed influence water quality in the reserve, and thus the abundance and health of fishes that support the fishery? Baseline data as summarized in Sweetman et al. (2019) are essential to evaluating changes in habitats and fisheries in the reserve and adjusting conservation measures – information that in most locations is lacking entirely.

Although not anticipated by Adams and Cooke (2015), numerous ongoing projects are focusing on better understanding reproductive activities in bonefish. The examination of hormone levels (Luck et al. 2019) and fatty acids in eggs (Mejri et al. 2019) in bonefish shows that not all bonefish spawn synchronously even though they migrate long distances from home ranges to pre-spawning sites (Danylchuk et al. 2011; Adams et al. 2019; Boucek et al. 2019). Many other coastal tropical species that migrate long distances to spawn do so synchronously (e.g., Nassau grouper; Sadovy de Mitcheson 2013), which makes sense given that individuals that are spatially separated must follow common cues (e.g., lunar phase and day length), and then exhibit traditional reproductive behaviors once at the spawning location. In contrast, bonefish apparently are capable of spawning between October and April, often but not always near the full or new moon. Clearly, future research should build on these findings to identify the physiological processes that control the timing of reproductive migrations and behaviors. Although Danylchuk et al. (2019) were able to observe pre-spawning behavior, to our knowledge the actual spawning event, which occurs offshore at night, has never been observed nor described.

## Future needs

It is encouraging to see the volume of research that has been done on the top needs identified in Adams and Cooke (2015), and that much of the results are being applied to conservation. Even so, additional work in these themes is needed and should continue.

The two themes highlighted in Adams and Cooke (2015) that did not receive attention are studies on the economic impacts of flats fisheries and fishery capacity. Data on the economic impact of the flats fishery in the Florida Keys, Bahamas, and Belize provided leverage for the inclusion of scientific data in conservation measures: improved fishery regulations in the Florida Keys and Belize, and national parks in the Bahamas. Economic studies have not been conducted in Mexico, Cuba, and many locations throughout the region, and some studies are dated (e.g., the Bahamas study was in 2009). Fishery capacity is also an item of concern. A catch and release fishery can be overcapitalized, which results in a fishery that exceeds its capacity (Zwirn et al. 2005). Too much fishing effort results in a decline in catch rates because fish may become 'educated' to angler activities, thus reducing catchability (Post et al. 2002). A decline in catchability reduces the quality of the fishery from the perspective of anglers (Arlinghaus and Mehner 2005; Arlinghaus 2006), and thus a loss of clientele, even if the abundance of the target species does not decline. Given that catch and release fisheries are receiving more attention as part of a larger trend toward eco-tourism activities, the potential to exceed fishery capacity for flats fisheries is high and should receive attention.

Although considerable research has previously been conducted on the effects of catch and release, more work is required. By far, bonefish is the most studied, with over ten published articles (e.g., Cooke and Philipp 2004; Danylchuk et al. 2007a, b). However, nearly all studies were conducted in the Bahamas. Given that natural (e.g., predator field) and anthropogenic (e.g., water and habitat quality) stressors differ among locations, replication of studies over a wider geographic range is warranted. In contrast to the extensive work on catch and release effects on bonefish in the Bahamas, there are few data for tarpon (a single study – Guindon 2011) and permit (no studies). Given that the premise of catch and release as a conservation and management tool is that post-release survival is high (Cooke and Schramm 2007), studies must be conducted, especially given increasing interactions between predators and gamefish as the catch and release fishery expands and interacts with new threats and unrelated conservation measures. For example, anecdotal reports from fishing guides in the Florida Keys suggest that a potential secondary effect of recent shark conservation measures in Florida is increased depredation of flats species.

The review of the status of research and conservation of the Florida Keys bonefish fishery by Brownscombe et al. (2019) is an excellent synopsis of the challenges to understanding causes to the fishery's dramatic decline, and to formulate research to inform the conservation and restoration work required to restore the fishery. The synopsis touches on all of the themes summarized in Adams and Cooke (2015) and this Special Issue. Of emerging concern are what might be considered the secondary effects of habitat and water quality degradation – the incorporation of metals, pharmaceuticals and other contaminants into trophic pathways – all the while trying to better understand the impacts of freshwater flow alterations and increasing nutrient loads. Further, following on research on other fish species and other ecosystems, there are likely secondary effects from these many anthropogenic stressors, chief among them disease and sublethal physiological stress. A clear summary of status of knowledge and a framework for future research and conservation is essential to addressing these challenges.

Although the conservation attention to the Florida Keys fishery came about because of the dramatic bonefish population decline, similar synopses should be done for other flats fishery locations to guide how research and conservation are prioritized. The synopsis by Brownscombe et al. (2019) focuses in part on habitat loss and degradation and water quality as likely having negative impacts on the bonefish population in the Florida Keys. These threats are prevalent throughout the geographic ranges of bonefish, tarpon, and permit. In some locations, such as the Bahamas and Cuba, proactive steps toward habitat conservation are being taken, whereas in other locations, such as Belize, habitat loss and degradation continue at an alarming rate (Steinberg 2015). More work is required to further assemble available data (e.g., Cissel and Steinberg 2019; Sweetman et al. 2019) that will contribute to conservation strategies, as well as reveal data gaps. Similarly, emerging (or existing) flats fisheries in areas such as the Seychelles and Australia require study.

Recent and ongoing research is better addressing the geographic scope of the flats fishery, but should only be considered the foundation for additional work. Larval transport models that indicate high likelihood of connectivity (Zeng et al. 2019) are the foundation for additional studies to test and quantify these linkages. To what extent is connectivity due to adult migrations (e.g., Griffin et al. 2018) versus larval transport? Are some locations population sinks, thus more dependent on external sources of larvae than others, and if so how should this influence management strategy? Do locations that receive larvae from external sources contain suitable nursery habitat in sufficient amount and quality to support a local population, and to what extent are these habitats under threat (e.g., Santos et al. 2019b)? Are locations that rely mostly on local sources of larvae more or less susceptible to threats such as habitat loss or overfishing? What is the relative importance of local vs regional stressors for each location/fishery? At a smaller spatial scale, is the coastal habitat mosaic sufficiently intact to support the ontogenetic processes necessary for sustainable flats fisheries?

Little has been done on the possible effects of climate change on flats species and habitats. Given the lack of historical data, understanding changes in geographic distribution will be challenging but should nonetheless be examined. Research has explored the effects of cold shock (Szekeres et al. 2014) and warming temperatures (Shultz et al. 2016) on bonefish but this is just scratching the surface. Will shifts in the geographic range of flats species mirror changes in habitats, or will flats species need to adapt to new habitats as conditions become too stressful in flats habitats (e.g., high temperature)? For instance, how will predator-prey dynamics shift if mediated by new temperature regimes? Will climatic changes cause physiological stress with population-level consequences? Development of bioenergetics models for flats fish could be useful for modeling the effects of climate change and drivers of food quality and quantity on growth and reproduction (e.g., Brownscombe et al. 2017). Sufficient empirical data now exist to enable such model development for bonefish.

## Conclusion

Overall, the data-poor status of the flats fishery is not going to improve substantially for two reasons. First, to the extent that the fishery is catch and release, it doesn't receive the same level of management attention as species that are harvested. There has never been a stock assessment of bonefish, tarpon, or permit, for example, in any location throughout their geographic ranges. Second, a significant portion of the regional flats fishery occurs in Low- and Middle-Income Countries with limited financial and infrastructure resources required to obtain data required for standard fisheries management. Instead, limited scientific resources should focus on obtaining data that structure a conservation framework in data-poor situations (Johannes 1998; Pilling et al. 2008) in an iterative process whereby the framework is revised as new data become available.

Although great progress has been made, none of the knowledge gaps addressed in this manuscript have been completely filled, and therefore all require additional attention. For example, the new knowledge on bonefish pre-spawning sites (PSAs) (Adams et al. 2019; Danylchuk et al. 2019) should be used to identify more PSA sites so that these locations can be protected, even as research of bonefish behaviors and physiology in spawning migrations, the PSAs, and in the act of spawning continues. The decline of Nassau grouper due to targeted harvest from spawning migrations and spawning aggregations (Sadovy and Domeier 2005) is a fate that can be avoided. Indeed, given that reproductive mode influences genetic population structure (Ma et al. 2018), and the importance of larval connectivity (e.g., Zeng et al. 2019) this type of research should be conducted for all flats species and in conjunction with genetic and oceanographic approaches that benefit from technological advances and new data on the focal species. Given the leverage provided by economic data to conservation efforts, past studies should be repeated and studies should be conducted in areas not yet addressed. The economic studies would be improved by incorporating traditional ecological knowledge so that current economic values are placed within a historical context. Given the growing popularity of using catch and release fisheries as part of ecotourism (reviewed in Adams 2017), traditional ecological knowledge, in conjunction with science-based estimates of fish abundance, distribution, size, behavior, and catch and release effects, might be the best approach to addressing the challenge of fishery capacity. Finally, the greatest knowledge gap is on the impact of anthropogenic stresses on flats species, especially habitat loss and degradation, water quality declines, contaminant exposure, and climate change.

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