



Conservation connections: incorporating connectivity into management and conservation of flats fishes and their habitats in a multi-stressor world

Aaron Adams  · Andy J. Danylchuk · Steven J. Cooke

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Abstract Coastal marine fisheries and the habitats that support them are under extensive and increasing pressures from numerous anthropogenic stressors that occur at multiple spatial and temporal scales and often intersect in unexpected ways. Frequently, the scales at which these fisheries are managed do not match the scales of the stressors, much less the geographic scale of species biology. In general, fishery management is ill prepared to address these stressors, as underscored by the continuing lack of integration of fisheries and habitat management. However, research of these fisheries is increasingly being conducted at spatial and temporal scales that incorporate biology and ecological connectivity of target species, with growing attention to the foundational role of

habitat. These efforts are also increasingly engaging stakeholders and rights holders in research, education, and conservation. This multi-method approach is essential for addressing pressing conservation challenges that are common to flats ecosystems. Flats fisheries occur in the shallow, coastal habitat mosaic that supports fish species that are accessible to and desirable to target by recreational fishers. Because these species rely upon coastal habitats, the anthropogenic stressors can be especially intense—habitat alteration (loss and degradation) and water quality declines are being exacerbated by climate change and increasing direct human impacts (e.g., fishing effort, boat traffic, depredation, pollution). The connections necessary for effective flats conservation are of many modes and include ontogenetic habitat connectivity; connections between stressors and impacts to fishes; connections between research and management, such as research informing spawning area protections; and engagement of stakeholders and rights holders in research, education, and management. The articles included in this Special Issue build upon a growing literature that is filling knowledge gaps for flats fishes and their habitats and increasingly providing the evidence to inform resource management. Indeed, numerous articles in this issue propose or summarize direct application of research findings to management with a focus on current and future conservation challenges. As with many other fisheries, a revised approach to management and conservation is needed in the Anthropocene.

A. Adams (✉)
Bonefish & Tarpon Trust, 2937 SW 27Th Avenue, Suite 203, Miami, FL 33133, USA
e-mail: aaron@bonefishtarpontrust.org

A. Adams
Florida Atlantic University Harbor Branch Oceanographic Institute, 5600 US 1 North, Fort Pierce, FL 34946, USA

A. J. Danylchuk
Department of Environmental Conservation, University of Massachusetts Amherst, 160 Holdsworth Way, Amherst, MA 01003, USA

S. J. Cooke
Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada

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Overview of the flats fishery

The flats fishery occurs where the shallow, coastal marine habitat mosaic supports fish species that are accessible to and desirable to target by fishers. The term flats fishery typically applies to the recreational fishery, often with a significant portion that is catch-and-release, though in many regions the flats species also support artisanal subsistence-commercial (ASC) fisheries. Due to the geographic focus of the articles contained in this Special Issue, here we focus on the flats fishery in the Caribbean Sea and western North Atlantic, though flats fisheries occur globally. The flats fishery has traditionally occurred in tropical and subtropical regions, but increasing interest by fishers and expanding geographic distributions of the focal species have also increased the spatial scale of the flats fishery.

The flats are a complex habitat mosaic comprised of mangroves, sea grass, benthic algae, sand, coral rubble, limestone, and mud bottom that supports an inherently diverse community that includes resident species and species that use these habitats as nurseries (Barbier et al. 2011). Bonefish (*Albula vulpes*), Atlantic tarpon (*Megalops atlanticus*), permit (*Trachinotus falcatus*), and common snook (*Centropomus undecimalis*) are the top focal species in the region of focus for this Special Issue. The species in the flats fishery are mesopredators, so they have important ecological roles. They are also socially and economically important—for example, the estimated economic impact of the flats fishery focusing on bonefish in The Bahamas exceeds \$169 million annually (Smith et al. 2023, this issue) and supports thousands of jobs in areas with limited alternative employment (Smith et al. 2023, this issue).

A common theme with flats fisheries is the concept of connectivity. Connectivity manifests itself in diverse ways on the flats. For example, many flats fishes occupy different habitats over their lives (Adams 2017) such that physical habitat connectivity is essential for ecological processes (Grober-Dunsmore et al. 2009; Sheaves 2009). Moreover, coastal flats serve as a connection point between offshore

areas and riparian or other upland habitats (Fang et al. 2018). Therefore, human activities on shore (e.g., land use change, runoff) have the potential to influence flats and the fishes they support. Connectivity also exists between people and flats. Flats fisheries are a good example of a coupled social-ecological system (Ostrom 2009) where there are inherent interconnections and feedbacks (Ward et al. 2016). When flats fisheries are healthy and well-managed, local communities (and their economies) benefit. Yet, those same communities are negatively impacted if there is poor management or low compliance with regulations such that fisheries are over-exploited or habitats are degraded. There are also connections between levels of biological organization. From molecules to cells to individuals to populations to ecosystems, the connections between these hierarchical levels serve to influence the overall productivity of a system (Cooke et al. 2014). There is also a temporal component to connectivity where ecological and geological histories can influence or constrain current conditions. Knowing about the past is critical to identifying restoration targets (Hughes 2009). Finally, there are connections among management bodies—or should be—given that flats fishes often transcend management jurisdictions during their lives (Jay et al. 2016). Connectivity is therefore a logical construct to think about the current and future status of flats fisheries and their habitats.

Connectivity was therefore selected as a theme for a series of papers arising from an ongoing series of conferences led by Bonefish and Tarpon Trust and their partners. Previous conference outputs have been published in *Environmental Biology of Fishes* (Volume 98/Issue 11, November 2015; Volume 102/Issue 2, February 2019), after the conferences. Because of the COVID-19 pandemic which delayed the most recent symposium, this Special Issue of *Environmental Biology of Fishes* was constructed in parallel. The connectivity theme was emphasized by the symposium organizers, yet it also became apparent from the submissions that such a theme was obvious given how connectivity “connected” all of the papers. Here, we provide an overview of key subthemes that emerged from this series of contributions. We preface that with a brief overview of the natural history of some key flats fishes (i.e., bonefish, tarpon, permit, common snook) to orient the reader to the diverse ways in which flats fishes exemplify ecological

connectivity. We conclude with a candid perspective on what is needed to ensure that connectivity is maintained, enhanced, or restored for the benefit of flats fishes, flats ecosystems, and the communities that depend upon them.

Species descriptions

Bonefish (*Albula vulpes*)

Members of the *Albula* genus (family Albulidae) are found throughout the world's shallow tropical seas (Wallace and Tringali 2010; Wallace 2014), where they support fisheries in many locations (e.g., Beets 2001; Filous et al. 2019; Pina-Amargós et al. 2023, this issue). In the Caribbean Sea and western North Atlantic Ocean, four species have been genetically identified (Colborn et al. 2001; Adams et al. 2008; Bowen et al. 2008; Wallace and Tringali 2010), though just one species, *Albula vulpes*, supports the flats fishery (Wallace and Tringali 2016). The habitat ontogeny of *A. vulpes* is generally as follows: juveniles inhabit shallow sandy or sandy-mud bottoms protected from wave action (Haak et al. 2019); adults inhabit shallow sand, mud, algae, seagrass, and mangrove habitats; adults show fidelity to relatively small home ranges (e.g., Murchie et al. 2013; Boucek et al. 2019; Perez et al. 2019) and undergo long-distance migrations to pre-spawning aggregation (PSA) sites during spawning season (October through April) (Danylchuk et al. 2011; Adams et al. 2019; Boucek et al. 2019); spawning occurs offshore at night (Danylchuk et al. 2011; Lombardo et al. 2020), with spawning descent to 137 m (Lombardo et al. 2020); the planktonic larval duration is 41–71 days (Mojica et al. 1994), and this extended larval duration results in high levels of connectivity at medium (Lombardo et al. 2022) and regional (Zeng et al. 2019) scales.

Bonefish are important mesopredators in that they feed predominantly on benthic invertebrates (bivalves, polychaetes, crustaceans) but also on small fishes (Warmke and Erdman 1963; Colton and Alevizon 1983; Crabtree et al. 1998; Griffin et al. 2019). They are prey for larger piscivores, including barracudas and sharks (Cooke and Philipp 2004; Danylchuk et al. 2007). Bonefish also transfer flats-derived energy to offshore environments as part of the spawning process in two ways: (1) as prey for offshore

predators when spawning offshore (as evidenced by angler reports of bonefish in stomachs of blue marlin (*Makaira nigricans*) and swordfish (*Xiphias gladius*) and sightings of Caribbean reef sharks (*Carcharhinus perezi*) and tiger sharks (*Galeocerdo cuvier*) following bonefish spawning schools in offshore waters; A. Adams pers. obs.); and (2) broadcasting of eggs and sperm during spawning (Lombardo et al. 2020).

Bonefish in the Florida Keys live beyond 19 years and become sexually mature at 3.3 to 4.6 years of age (Crabtree et al. 1996). Bonefish in the Florida Keys grow significantly faster than in other parts of their range (Adams et al. 2008; Rennert et al. 2019).

Albula vulpes is listed as Near Threatened by the International Union for the Conservation of Nature (IUCN) Red List due to harvest and habitat loss in parts of their range (Adams et al. 2014). For example, the bonefish population in the Florida Keys declined significantly, particularly from the 1990s into the 2000s (Rehage et al. 2019; Santos et al. 2017), likely due to a combination of anthropogenic and natural stressors including habitat alteration, water quality decline, fishing pressure, and recruitment failure (Brownscombe et al. 2019). In recent years, the Florida Keys bonefish population appears to be rebounding, as yet with no explanation. In Cuba, the flats fishery occurs in marine protected areas in which only catch-and-release fishing is allowed (Ostrega et al. 2023, this issue), but bonefish are targeted for harvest outside of the protected areas. For example, ASC fishers target bonefish on their spawning migrations, resulting in tons harvested annually (Rennert et al. 2019; Ostrega et al. 2023, this issue). Bonefish populations in Belize and Mexico appear to be stable, though legal and illegal harvest by nets is a concern.

Tarpon (*Megalops atlanticus*)

Atlantic tarpon are widely distributed in the North Atlantic Ocean, Gulf of Mexico, and Caribbean Sea, with geographic range limited by water temperature tolerances (Zale and Merrifield 1989). The lower lethal limit is 10 °C (Robins et al. 1977), and upper lethal thermal limit is 40 °C (Moffett and Randall 1957). Although adults have been observed as far north as Nova Scotia and Ireland (Twomey and Byrne 1985), these were considered vagrants, but in recent years, reports of Atlantic tarpon in the northern edges of their possible range have increased, likely due to

increasing water temperatures associated with climate change.

Adult Atlantic tarpon inhabit coastal, estuarine, riverine, and offshore waters, the latter likely mostly associated with spawning. Spawning occurs in offshore waters, as evidenced by collection of day-old larvae (Crabtree et al. 1992; J. Shenker, Florida Institute of Technology, unpubl. data), following offshore movements of adult fish using satellite tags (Ault et al. 2008), and satellite tag-based observations of dives to > 130 m at night in offshore waters (Luo et al. 2020). This spawning behavior (offshore, deep dives) is common in the Elopiformes (Adams et al. 2014) and has been documented for bonefish (Lombardo et al. 2020). During spawning season and prior to spawning, adult Atlantic tarpon gather in what appear to be traditional pre-spawning aggregation regions (e.g., Florida Keys) and migrate offshore in schools of varying size near full and new moons. In Florida, peak spawning occurs during summer lunar phases (Crabtree 1995; Shenker et al. 2002), but the spawning season is more protracted in tropical waters such as Costa Rica (Crabtree et al. 1997) and Puerto Rico (Zerbi et al. 2001), and spawning occurs in northern areas of the range (e.g., northern Gulf of Mexico) in late summer.

The planktonic larval duration is 20–40 days (Shenker et al. 2002). The vascularized swim bladders of Atlantic tarpon allow aerial respiration, permitting juveniles to inhabit hypoxic wetland waters where they presumably experience low predation rates (Schlaifer and Breder 1940; Geiger et al. 2000). Juvenile habitats include stagnant pools, back waters, ephemeral coastal ponds and hurricane and storm over washes, swales, and mangrove swamps and marshes, as well as manmade impoundments and wetlands (Wade 1962; Dahl 1965; Zerbi et al. 2001; Jud et al. 2011). After 1–2 years, individuals emigrate from backcountry areas to rivers, bays, and estuaries (Crabtree et al. 1995). Many adults undergo seasonal migrations during summer to the northern Gulf of Mexico and Mid-Atlantic region of the eastern USA (Ault et al. 2008; Griffin et al. 2018; Luo et al. 2020).

Juvenile Atlantic tarpon prey upon zooplankton, small crustaceans, polychaetes, and insects that frequent inshore nurseries (Harrington 1958; Jud et al. 2011). Sub-adults and adults feed on larger crustaceans (penaeid shrimps, swimming crabs), polychaetes, and many species of fish (Whitehead and

Vergara 1978; Boujard et al. 1997). Atlantic tarpon reach maximum ages of 43–78 years (Crabtree et al. 1995; Andrews et al. 2001) and may exceed 2 m in length and 110–130 kg in mass (Crabtree et al. 1997). Atlantic tarpon reach sexual maturity at > 130 cm and 7–12 years (Chacon-Chaverri 1993; Crabtree et al. 1997), though there is considerable variation across their geographic range.

Atlantic tarpon are IUCN-listed as vulnerable due to past and ongoing harvest and loss of juvenile habitats (Adams et al. 2014). Juvenile habitat loss and alteration are especially concerning. For example, Florida has lost 50% of its mangroves and > 2 million acres of wetlands, which are essential juvenile habitats for tarpon (and snook, see below). Additional concerns are potentially high post-release mortality in some locations; for example, Florida regulates that tarpon > 40" total length should not be removed from the water (<https://myfwc.com/fishing/saltwater/recreational/tarpon/>) because handling stress greatly increases post-release mortality (Guindon 2011).

Permit (*Trachinotus falcatus*)

Permit are common year-round in coastal waters of the Caribbean Sea and south Florida and seasonally inhabit coastal habitats of the North Atlantic as far north as Massachusetts and throughout the Gulf of Mexico (GOM) (Crabtree et al. 2002; Graham and Castellanos 2005). 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 that the PLD was 15–18 days, but Bryan et al. (2015) used a time period of 20–30 days for models of planktonic larval transport.

Settlement and early juvenile habitat for permit is windward sandy beaches (Adams et al. 2006). Permit ontogenetically shift from beaches to sand and seagrass flats, with adults ranging from shallow seagrass beds to offshore reefs. Permit diet changes with ontogeny. The diet of juveniles 15–20 mm standard length (SL) is dominated by small fish and mysids. Permit 61–70 mm eat mostly crabs and gastropods (Carr and Adams 1973). Larger crustaceans and mollusks dominate the diet of 50–100 mm permit, and mollusks are the predominant food of

permit 100–138 mm (Finucane 1969). Adult permit (> 48 cm) prey on crabs, shrimp, bivalves, echinoderms, and small fish.

Acoustic tracking and dart-tag recaptures in Florida show that adult permit largely have limited regional movements, with relatively strong fidelity. For example, Brownscombe et al. (2020) using acoustic tracking, and Boucek et al. (2023a, this issue) using mark-recapture, found that a regional Special Permit Zone (<https://myfwc.com/fishing/saltwater/recreational/permit/>) that encompasses the Florida Keys to protect permit that support the flats fishery is appropriate because few permit cross the management zone boundaries. Similarly, acoustic tracking found fidelity to spawning sites by flats permit (Brownscombe et al. 2020). Combined with data that showed that depredation of permit by sharks at spawning sites sometimes exceeded 30% (Holder et al. 2020); the tracking data justified a seasonal fishing closure at an important spawning site (<https://myfwc.com/fishing/saltwater/recreational/wdr/>). Little information is available to evaluate the permit flats fishery in other locations.

Common snook (*Centropomus undecimalis*)

Common snook (hereafter referred to as snook) inhabit estuarine, riverine, and coastal habitats in the tropical and subtropical Caribbean Sea, Gulf of Mexico, and eastern Florida, though due to climate change, they are undergoing a northward range expansion (e.g., Purtlebaugh et al. 2020). Snook are protandrous hermaphrodites (Muller and Taylor 2006) that spawn in aggregations in high-salinity, coastal habitats (Peters et al. 1998; Taylor et al. 1998). Planktonic larval duration is approximately 2 weeks (Peters et al. 1998). Recruitment occurs in tidal mangrove wetlands (Peters et al. 1998). Juveniles use these habitats until age 2 (Stevens et al. 2007; Barbour and Adams 2012) but undergo annual emigrations and return at age 1 and age 2 (Barbour et al. 2014). Adults use estuarine, coastal, and riverine habitats.

The snook fishery in Florida is highly regulated, resulting in 98% of fish released after capture (Adams 2017). However, despite these strict regulations, the snook population appears to be stressed by anthropogenic actions. For example, habitat loss and water quality declines contributed to the loss of resilience of the snook population in the northern Indian River

Lagoon to a severe cold event in 2010 (Boucek et al. 2023b, this issue). Similarly, the snook fishery was closed in the southwest region of the Gulf of Mexico coast of Florida due to fish mortality from red tide (*Karenia brevis*) (<https://www.news-press.com/story/news/2021/08/30/florida-snook-season-2021-wont-open-tampa-bay-areas-south-collier-county-red-tide/5649493001/>), a harmful algal bloom that is naturally occurring but greatly enhanced by anthropogenic nutrient inputs (Medina et al. 2022). Information on snook populations in other locations is sparse.

Toward a paradigm shift in flats fishery management

Flats fisheries are subject to many stressors throughout their ranges, although the rank of relative importance of stressors may differ by location. For example, past habitat loss and ongoing water quality declines are among the top stressors in Florida, whereas in The Bahamas, the top concerns are preventing habitat loss and responding to the effects of climate change-enhanced natural disturbances like hurricanes. But perhaps the top big-picture stressor to the flats fishery is one that is common to many other fisheries and systems—a management approach that is not prepared for the challenges of the Anthropocene (Aswani et al. 2018).

Anthropogenic habitat loss and degradation (collectively habitat alteration) is a threat to biodiversity worldwide (McKee et al. 2003). For example, mangrove forests are among the most threatened coastal habitats worldwide, decreasing an estimated 35% globally over the past 50 years, with continuing annual declines of 2% (Valiela et al. 2001; Alongi 2002). Sixteen percent of mangrove species examined in an IUCN analysis were classified as either critically endangered, endangered, or vulnerable (Polidoro et al. 2010). In Florida, where nearly 80% of the human population live in the coastal zone (Rappaport and Sachs 2003), removal of mangroves for residential, commercial, and industrial purposes has arguably had the biggest impact on these habitats (Duke 1997). These habitats are crucial to the future of the flats fishery—Atlantic tarpon and snook, for example, depend upon mangrove wetlands as nurseries (Adams and Murchie 2015), and Atlantic tarpon are classified as vulnerable by IUCN in large part

due to loss of nursery habitats (Adams et al. 2014). In this Special Issue, we see that habitat loss (and water quality decline) in the northern Indian River Lagoon has reduced the resilience of snook to such an extent that the northern Indian River Lagoon snook population took many years to recover from a cold-induced mortality event, even as snook populations in other Florida estuaries similarly impacted by the cold event quickly recovered (Boucek et al. 2023b, this issue). Similarly, the snook population on the southwestern coast of Florida was considered vulnerable enough that the state fisheries agency closed the fishery to harvest in response to mortalities from a red tide event (<https://www.news-press.com/story/news/2021/08/30/florida-snook-season-2021-wont-open-tampa-bay-areas-south-collier-county-red-tide/5649493001/>). Red tide events have become more frequent, spatially widespread, intense, and longer-lasting due to anthropogenic nutrient inputs (Medina et al. 2022). Thus, although the snook fishery is so highly regulated (based on a stock assessment approach) that more than 98% of captured snook are released, habitat and water quality problems—which are not included in fishery management—have clearly impacted the ability of the fish population to respond to disturbances.

Habitat alteration is also a challenge in Belize and Mexico, where coastal development (often to support mass tourism) is degrading flats habitats. And though habitat alteration is not currently widespread in flats fishing areas in The Bahamas, concerns are substantial; thus, numerous national parks have been designated to proactively protect habitats important to bonefish (e.g., Adams et al. 2019). In Belize, the flats fishery benefits from a network of protected areas that are co-managed by local non-governmental organizations (NGOs) and government agencies, but more work is needed to better integrate flats fisheries into this spatial/habitat approach. This is why habitat assessment mapping efforts are so important. In many cases, we lack both historical and current habitat data and thus are unable to assess trends in habitats. For example, Williams et al. (2023, this issue) recently completed the first spatiotemporal habitat assessment in a protected area in southern Belize, information that will be critical for the protected area managers to assess the current status and address what appear to be habitat declines.

An important conclusion from Boucek et al. (2023b, this issue) is that the effects of habitat alteration do not occur gradually, as many assume, but instead become evident as a threshold is reached. From a conservation perspective, achieving the threshold signals that the damage has been done, and that restoration is the last option. Although restoration can be effective, sufficient information on the habitats and system in question is essential to properly design and place restoration. This was the approach of Stevens et al. (2023, this issue), who surveyed an estuarine system in southeast Florida to identify priority locations for habitat restoration, with a focus on habitat requirements for economically important flats species like snook. Borrowing from the terrestrial conservation realm, Wilson et al. (2023, this issue) propose using juvenile snook as a flagship umbrella species to identify and prioritize habitats for conservation and restoration in the context of addressing challenges from coastal development. Protecting or restoring habitats important to juvenile snook also protects more than 50 other species (the umbrella), but importantly Wilson et al. (2023, this issue) propose that snook is a flagship species because it is so important to the recreational fishing community. This codifies the necessity of connecting stakeholders and resource managers in a new, habitat-focused approach to flats fishery management.

Griffin et al. (2023a, this issue) incorporated stakeholders in a multi-method examination of the effect of red tide on Atlantic tarpon along the Gulf Coast of Florida. Using multiple data sources, including Local Ecological Knowledge (LEK), they determined that Atlantic tarpon appear somewhat resistant to red tide, in part based on their ability to move to avoid red tide hotspots. However, the fishing guides interviewed for the LEK information indicated that red tides are becoming more frequent, intense, widespread, and of longer duration; moreover, that red tides previously did not occur during tarpon season. Thus, Griffin et al. (2023a, this issue) concluded that future effects of red tides on tarpon mortality and reproduction (tarpon fishing season coincides with tarpon spawning season) are a concern and proposed that a more robust, multi-method, collaborative red tide and fishery monitoring program is designed to provide data that will enable assessment of the impacts of future red tides on Atlantic tarpon.

Boucek et al. (2023c, this issue) highlighted the value of LEK-type information as an additional source of data for assessing fishery trends. They analyzed decades worth of tournament data, compared it to previous independent assessments of the bonefish fishery, and showed that quality tournament catch and effort records provided an accurate assessment of the bonefish fishery in the Florida Keys. Such data should be a component of a multi-method approach that includes broad collaboration for future flats fishery management.

Much of the research being conducted on flats species is aimed at learning enough about a species' function and interaction with its environment to inform conservation. For example, Mejri et al. (2023, this issue) build upon recent work to further understanding of the physiology of bonefish *leptocephalus* larvae. Understanding larval physiology is an important component for assessing reproductive success when used in combination with understanding reproductive physiology of adults (Luck et al. 2019) and will help inform larval transport models (e.g., Zeng et al. 2019) that are essential to understanding regional population connectivity. A greater understanding of connectivity may well, in turn, help to predict the effects of climate change on connectivity and possible range expansion.

Understanding the processes by which anthropogenic environmental alterations affect flats fish is often nuanced. Effects may not be as direct as red tide-induced fish kills, for example. Campbell et al. (2023a, b, this issue) began to explore these indirect effects by examining the occurrence of viruses in bonefish. As it was the first study to do so, definitive conclusions on viral impacts are not yet known, but that viral loads were highest in bonefish from locations with the greater stressors (e.g., poor water quality) and greatest population declines (Florida Keys, in both instances) is a cause for concern and should be further examined. High viral loads due to degraded environments have caused population-level issues in other species (Snieszko 1974; Inendino et al. 2005; Moser et al. 2012; Richard et al. 2020).

Also important to flats fishery management is developing a better understanding of the full species assemblage and interactions between flats species and potential prey, predators, and competitors. Previous work demonstrated the importance of predator considerations for catch-and-release fishing, with

post-release mortality increasing from zero when no sharks were present to nearly 40% when sharks were present (Cooke and Philipp 2004). Holder et al. (2020) found similar results—post-release mortality of permit captured on the flats, where predator abundance was low, was near zero, whereas depredation at spawning sites exceeded 30%. Similarly, Atlantic tarpon post-release mortality and depredation rates were significantly higher in locations with high shark abundance (Guindon 2011). Such information is essential to formulating management strategies, such as the spawning season fishing closure at Western Dry Rocks to protect spawning permit.

In this Special Issue, Szekeres et al. (2023, this issue) further contribute to flats ecological knowledge by showing proof of concept for acoustic telemetry of small-bodied flats fishes. Such information can be used in combination with information on flats fish movements and habitat use to evaluate the effects of environmental variables such as water temperature—an increasingly important consideration due to climate change. Campbell et al. (2023a, b, this issue) devised a new and easy method for examining bonefish diet, providing another tool for evaluating the overall health of a flats system. Importantly, the method is non-lethal, which is important when studying a catch-and-release fishery in which stakeholders can become very protective of the target species.

Continuing on this theme, James et al. (2023, this issue) and Rezek et al. (2023, this issue) conducted extensive literature and data reviews, and found no likely direct effects of commercial shrimp fisheries on the flats species, particularly bonefish, in Biscayne Bay, Florida. They found that the shrimp fisheries only harvested ~10% of the shrimp population and that no flats species occurred as bycatch. This work addressed a perception of potential conflict between the flats fishery and commercial shrimp fisheries. Although bycatch of potential bonefish prey was relatively low, future research should directly examine indirect effects of possible prey-reduction due to bycatch on bonefish diet.

What is apparent when the full amount of available information of flats species and their habitats is viewed is that this information does not fulfill the information requirements for fishery management based on stock assessment. In this sense, flats fisheries are chronically data-poor. Here we differentiate data-poor from data-limited fisheries. Data-poor

fisheries not only currently lack data necessary for standard fishery management (e.g., stock assessments); it is extremely unlikely that such data will be obtained. In contrast, data-limited fisheries will often have gaps in data necessary for a full stock assessment but have reasonable expectations that additional data are obtainable. Given the lack of financial and expert personnel resources in most locations where flats fisheries occur, a different approach to management is needed. Moreover, it is clear that the standard stock assessment approach to fisheries management is insufficient given the historical and increasing anthropogenic impacts on habitat, water quality, and other factors that lie outside of standard fishery management. Thus, even locations with more resources are challenged to manage fisheries based on stock assessments: Boucek et al. (2023b, this issue) highlight such a case with snook; the tarpon IUCN vulnerable classification is mostly based on juvenile habitat loss; the bonefish fishery in the Florida Keys declined precipitously even though it was catch-and-release (Brownscombe et al. 2019); and the situation with redfish (*Sciaenops ocellatus*) in the Indian River Lagoon of Florida is so dire due to habitat and water quality declines that the fishery has now been declared catch-and-release only (<https://myfwc.com/news/all-news/redfish-722/>)—with the support of most stakeholders.

Much of the research described in the articles in this Special Issue, which builds upon previous work on flats species and habitats, points toward a new approach to flats fishery management. A new approach that explicitly incorporates spatial and habitat dynamics is essential, especially in the context of climate change (Danylchuk et al. 2023, this issue). For example, Pina-Amargós et al. (2023, this issue) provide the first examination of the effectiveness of protected areas as management tools for sustainable flats fisheries. In Cuba, the flats fishery occurs to a great extent in protected areas, where only catch-and-release fishing is allowed (a highly regulated commercial fishery for lobster also occurs in some areas). Pina-Amargós et al. (2023, this issue) used mark-recapture to determine if the protected areas provided sufficient protection to the flats species. They found that the study areas provided a large degree of protection for bonefish but that bonefish were susceptible to harvest when they migrated to likely pre-spawning sites outside of the protected areas. In contrast, Atlantic tarpon were considerably less protected by the

protected areas (especially fish older than juveniles) because of their ontogenetic habitat shifts and migratory patterns. Thus, for both species, protected areas provided important protections but must be applied as part of a broader management approach. Ostrega et al. (2023, this issue) picked up on this theme as they interviewed researchers, resource managers, and fishing guides to inform a framework for better management of bonefish in Cuba, with a particular focus on protection of spawning migrations and pre-spawning aggregation sites. In addition to the limits of protected areas revealed by Pina-Amargós et al. (2023, this issue), Ostrega et al. (2023, this issue) recommended a multi-method research and management approach that includes (1) initiating information exchange between Cuban management agencies and third party institutions related to bonefish management; (2) utilizing LEK to gather information, formulate management strategies, and enforce regulations; (3) implementing spatial and temporal management measures for bonefish spawning sites; (4) using what is already in place, by protecting spawning sites in the context of existing marine protected areas; (5) collaborating with all stakeholders to manage bonefish spawning sites; and (6) reducing the commercial harvest of the species.

Research in the Florida Keys (Brownscombe et al. 2023, this issue), south Florida (Boucek et al. 2023a, this issue), and Puerto Rico (Griffin et al. 2023b, this issue) similarly examine the application of a spatial approach to flats fishery management. Brownscombe et al. (2023, this issue) used acoustic telemetry to understand fine-scale permit habitat use, which should be used to better manage habitats and spatially integrate fisheries regulations, such as the Western Dry Rocks spawning season fishing closure. Boucek et al. (2023a, this issue) used mark-recapture and acoustic telemetry to examine whether the Special Permit Zone (SPZ) that encompasses the Florida Keys is of sufficient size and location to protect the Florida Keys flats fishery. They found that permit movement across the SPZ boundary was rare; thus, the SPZ is an effective spatial management tool. Studying more isolated habitats in Puerto Rico (reef flats rather than the expansive sand/seagrass flats of other locations previously studied), Griffin et al. (2023b, this issue) found a high level of site fidelity. While such behavior may confer an advantage to fish in undisturbed ecosystems, it may increase their

vulnerability to localized impacts. Indeed, the rapid rate of changes induced by climate change may make site fidelity a disadvantage (Abrahms et al. 2018; Krelling et al. 2021).

We now have an extra layer of concern from climate change and its many impacts on all aspects of the flats fishery (Danylchuk et al. 2023, this issue). Climate change is causing and will continue to cause stresses to the flats fishery due to increases in water temperature (e.g., exceeding species lethal maximum), alteration and loss of habitat (e.g., sea level rise will inundate wetlands that are already threatened by coastal development and pollution), changes in ocean currents (which may alter larval transport pathways), and acidification (which may affect flats species larval survival and that of their prey). While some of the impacts from climate change are relatively well reasoned, we continue to have extensive knowledge gaps. These knowledge gaps hinder a comprehensive management response, which is exacerbated by the current flats fishery management paradigm that does not incorporate habitat and other factors that are of most concern from climate change issues. Danylchuk et al. (2023, this issue) highlight the need to increase the rate of change of devising a new management paradigm.

Connecting the pieces with a new management paradigm

As outlined above and as evidence from the diverse contributions in this Special Issue, the concept of connectivity is highly salient to management in several ways. Although the term “connectivity” has different meanings (Worboys 2010), we embrace it in a holistic manner, whereby we consider it to include the interconnectivity of systems, matter, and processes across various spatial, temporal, biological, and institutional scales. Given the centrality of the concept of connectivity to flats fisheries, we propose that there is urgent need for a new management paradigm. Specifically, we envision a future where different tools, actors, jurisdictions, habitats, and ecosystem components are considered holistically and where efforts to establish, maintain, or enhance connections represent specific management actions or opportunities.

Consider a flats system in a coastal environment. From a management perspective, a key step is to

identify relevant fishery management and ecosystem management objectives. Objectives should be established in a collaborative manner, with input from diverse stakeholders and rights holders (Selin and Chevez 1995; Stephenson et al. 2019). This is the approach taken by Fernandes et al. (2023, this issue) in Brazil, where they are working collaboratively with stakeholders, scientists, and resource managers to collect data for direct application to a new management strategy for tarpon. Stock assessment or other forms of monitoring are then needed to assess the state of the system relative to the objectives. This has typically meant routine stock assessment, yet we know there is nothing routine about attempting stock assessment for most flats fisheries. Nonetheless, there are methods for doing so even in data poor situations, such as LEK-based approaches to examine temporal trends (e.g., Santos et al. 2017). Moreover, new developments in environmental DNA and use of drones could be applied to flats fisheries to supplement other fishery-dependent and fishery-independent sampling (Bradley et al. 2019). Given that healthy, interconnected habitat mosaics are the foundation for healthy and productive fish populations (Armstrong and Falk-Petersen 2008), assessment and monitoring can incorporate habitat which is comparatively easy to do relative to stock assessment. Knowledge of habitat can inform potential productive capacity and identify areas that are degraded (Schmittgen 1999). Establishing and understanding connections between habitat and fish populations for flats fisheries (something common for many inland and coastal fish populations) will help to identify where habitat enhancement, restoration, or protection could be worthwhile. Mapping habitats can also be useful for understanding fragmented habitats and documenting where movement corridors may exist providing additional opportunities for maintaining or re-establishing connections among habitats (Crook et al. 2015). Such habitat assessment and mapping can be done at a variety of scales to also consider range-wide habitat needs. Given that flats fishes often move across management boundaries (and jurisdictions), efforts at range-wide scales can be helpful for ensuring fisheries are managed in a coordinated manner across jurisdictions (e.g., Griffin et al. 2018).

Also relevant is thinking about flats fisheries as coupled complex social-ecological systems where people and institutions are considered part of a

biophysical system with recognition of connections and interdependencies (Ostrom 2009). Understanding how the various components of the system interact and how different pressures can impact both biota and people is a powerful approach for generating support for management and conservation initiatives (Stephenson et al. 2018). Moreover, a social-ecological framework that considers the cumulative effects of interacting pressures (e.g., nutrient pollution, changes in water management, human development) can be useful for identifying management levers (Gonçalves et al. 2020). Connectivity is increasingly recognized as an approach for managing for resilience in the face of climate change (Krosby et al. 2010) which needs to be considered for flats fishes given the manifold ways in which climate change will impact such systems (Danylchuk et al. 2023, this issue). In summary, there is much to be gained by considering how the concept of “connectivity” can be embraced to enhance the science-based collaborative management of flats fisheries today and in the future. The concept is not new (see Roberts 1997 for discussion of connectivity and management for coral reefs), yet it has still not been fully embraced in marine ecosystem management including for flats fishes and ecosystems.

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