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Bonefish in South Florida: status, threats and research needs

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Abstract Bonefish (*Albula vulpes*) support a world-renowned fishery in South Florida, USA. However, fishing guides and anglers have been reporting significant declines in bonefish angling quality over that past three decades. In the absence of any long-term bonefish stock and ecosystem assessments, the cause of this decline in the fishery is unclear. Here we summarize our current knowledge of bonefish ecology in Florida and discuss potential causes of fishery decline. Reductions and alterations in freshwater flows from the Everglades have caused major changes in bonefish habitat, including acute (anoxic conditions) and chronic (changes in benthic flora and fauna) effects in Florida Bay and Biscayne Bay. Various pollutants from agricultural and urban runoff may also be impacting bonefish population(s) directly and/or indirectly throughout their range. Efforts to locate juvenile *A. vulpes* in Florida have been largely unsuccessful to date, suggesting abundances may be low, and/or juveniles have unknown habitat requirements in Florida. Further, bonefish larvae

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may be sourced from adult individuals outside of Florida in areas such as Cuba or Mexico, in which case bonefish conservation in other regions is highly relevant to the Florida population. Extreme weather events may have also contributed to the decline; an extreme cold spell in 2010 caused significant bonefish mortality and coincided with documented declines in the fishery. The fishery may also be impacting the population. We outline research needs and potential approaches to better understand the causes of the bonefish decline in Florida and restore populations of this ecologically and socioeconomically important species.

Keywords Fisheries management · Catch-and-release · Recreational angling · Habitat loss · Exploitation · Pollution

Introduction

Bonefish (*Albula* spp.) are a group of marine teleost fishes found in shallow tropical and subtropical marine ecosystems worldwide where they occupy diverse habitats including sand, mud, marl flats, seagrass, macroalgae beds and mangrove lagoons (Alexander 1961; Adams et al. 2012; Wallace 2014). In many regions of the Caribbean Sea and western Atlantic Ocean, bonefish (*Albula vulpes*) make frequent movements into shallow water with tides to forage on benthic invertebrates and fish, and serve an important ecological role in nearshore habitat connectivity (Humston et al. 2005; Murchie et al. 2013; Brownscombe et al. 2017b). Bonefish populations are estimated to have declined by 20% based on rates of habitat loss throughout their range and are listed as Threatened on The International Union for Conservation of Nature Red List (Adams et al. 2012).

Bonefish can be sighted on shallow water flats, making this species popular for recreational anglers in many regions of their range (Adams 2017). Bonefish angling has historically been highly popular in South Florida, including Biscayne Bay, Florida Bay, and the Florida Keys (Fig. 1; Ault et al. 2008a). They are part of a flats fishery that has an estimated annual economic impact of $465 million on the Florida economy (Fedler 2013). However, bonefish fishing quality (i.e., number and size of bonefish observed and caught) has been declining since the 1950s (Sosin 2008; Larkin 2011), with significant reductions in angling quality reported by fishing guides and anglers since 1985 (Frezza and Clem 2015; Santos et al. 2017; Rehage et al. *In Review*; Santos et al. 2018a). No direct long-term scientific data on bonefish population dynamics in the South Florida exist [See Frezza and Clem 2015 for a list of shorter term data sets, mainly angler catch based]. Recreational angler reports, fishing guide log books and perceptions, and tournament catches are the only indication of their putative long-term decline. Nevertheless, changes in angling quality may serve as early indicators of changes in fish population dynamics (Post et al. 2002; Cooke and Cowx 2004; Brownscombe et al. 2014). There are many potential factors that may have singularly or in combination contributed to the apparent declines in bonefish abundance in the region. For example, altered hydrological regimes, habitat loss and degradation, increased contaminant and nutrient inputs, climate disturbances such as tropical cyclones and cold spells, and overexploitation of fish and crustaceans by fishers causing direct and indirect impacts on bonefish populations through trophic cascades (McIvor et al. 1994; Porter 2001; Abtew and Iricanin 2008; Santos et al. 2017).

Recognizing the growing number of threats to the region, the Everglades National Park was established in 1947, and Biscayne National Park in 1968. In 1990, the National Oceanic and Atmospheric Administration (NOAA) established the Florida Keys National Marine Sanctuary restricting human activities and providing special protection for fish, wildlife, and their habitats within an area of 2900 square nautical miles from south of Miami to the Dry Tortugas (NOAA 2016). The first bonefish harvest regulations were implemented in 1972, prohibiting commercial sale and limiting harvest to one fish per day over 46 cm (18 in.; Barbieri et al. 2008). While bonefish angling in South Florida has been culturally a catch-and-release (C&R) fishery for decades (Ault et al. 2008b), recreational harvest was banned in 2011, and retention in livewells for tournament weigh-ins was banned in 2013 (Florida Fish and Wildlife Conservation Commission 2013).

Although the above-mentioned regulations are important steps for conserving bonefish in the region, the declining trend in bonefish angling quality in South Florida has caused significant concern over population status and the future of this historically eminent fishery. Here we outline the current state of knowledge on bonefish ecology in South Florida, focusing on each life history stage. We then discuss the factors that may be responsible for their decline or impede their recovery,

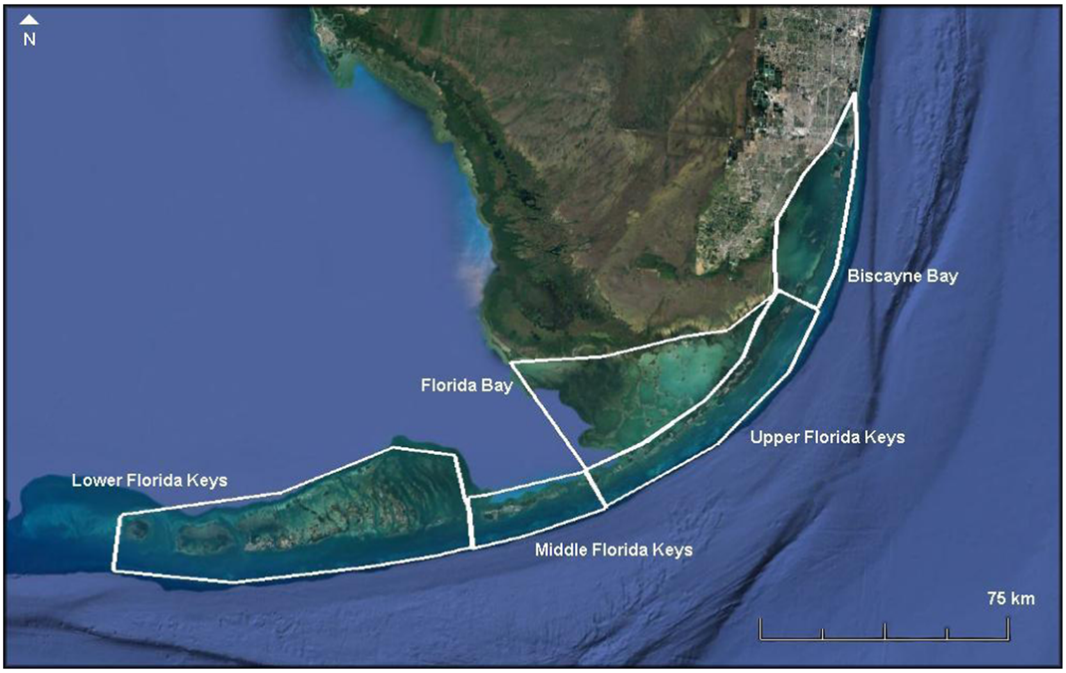

Fig. 1 Map of the regions in South Florida that support recreational bonefish flats fisheries, each of which has experienced a unique set of environmental stressors that may be impacting bonefish population(s), as well as unique chronology and degree of bonefish decline

followed by an outline of research needs to better manage and restore bonefish populations in Florida to ensure a sustainable bonefish fishery in the future.

Bonefish ecology, life history, and conservation

To characterize conservation threats to bonefish in Florida, it is important to consider their ecology across all life history stages. Due to their complex life history, involving an extended pelagic leptocephalus stage and distinct juvenile and adult habitats, many potential stressors could influence bonefish populations across broad geographical space. Here we briefly summarize our state of knowledge and research needs on bonefish ecology across all life history stages.

Adults and sub-adults

Historically adult and sub-adult bonefish (50% sexual maturity at 418 mm fork length, 3.6 years old for males; 488 mm fork length, 4.2 years old for females in Florida; Crabtree et al. 1997) were found throughout coastal regions of South Florida including Florida Bay, Biscayne Bay, and the Florida Keys in diverse habitat types, including sand, mud, seagrass, and macroalgae (Humston et al. 2005; Ault et al. 2008a). Visual surveys of bonefish in Biscayne Bay and the Florida Keys from 2003 to 2005 estimated a population size of roughly 290,000 adults, although this is based on limited observations with large error estimates (Ault et al. 2008b). In mark recapture studies, the majority of recaptures occurred in close proximity to the tagging location, with 88% of fish captured <20 km, and 51% of fish <2 km (Larkin et al. 2008). However, rare long-range movements indicate some population connectivity throughout their known range in South Florida, from Biscayne Bay to the Lower Florida Keys (~100–200 km), and there were two recaptures in The Bahamas. Notably, the majority of long-distance movements (>50 km) were observed in mature adult bonefish, and recaptures typically occurred in the spring or fall seasons. Given the majority of spawning activity tends to occur in the winter months (Danylchuk et al. 2011), these large-scale movements by mature individuals may be related to spawning activity.

Acoustic telemetry studies in Biscayne Bay found bonefish had a moderate degree of site fidelity, often returning to the same locations on the flats, although long-distance movements (>13 km) along shorelines over the course of 1 month were commonly observed (Humston et al. 2005; Larkin et al. 2008). Bonefish also frequently moved up to 6 km offshore into deeper water (>20 m). These findings are consistent with studies in other regions such as The Bahamas, where bonefish have high site fidelity, but traverse expansive sand flats as well, with larger scale movements associated with spawning (Danylchuk et al. 2011; Murchie et al. 2013). In Culebra, Puerto Rico, bonefish exhibit extremely high site fidelity to specific fringing reefs, rarely traveling >500 m (Brownscombe et al. 2017b; A.J. Danylchuk, unpublished data).

In tropical and subtropical shallow flats, water temperatures can be highly variable and often extreme (>40 °C; Murchie et al. 2011). Although we know little about the drivers of bonefish movement in Florida, research from other regions has found temperature is a major driver of spatial movements and activity levels in nearshore flats. For example, in Culebra, Puerto Rico, bonefish actively select for flats when water temperatures are near optimal (~26–29 °C) for their aerobic scope for activity (Brownscombe et al. 2017a, 2017b). On a broader scale, fishing charter data suggests that bonefish shift their habitat use in diverse regions of South Florida, occupying the Atlantic side more frequently in cool weather months (November to April), shifting to interior bay waters and Gulf of Mexico side flats more frequently in warmer months (Humston 2001). Long-term (multi-season) regional bonefish movement patterns have yet to be studied in Florida, and the drivers of movements (e.g., spawning, water temperature, predator and prey dynamics) are unknown (Table 1).

Bonefish spawning activity in Florida has been inferred from gonadal development, which peaks between November and May (Crabtree et al. 1997), but spawning locations have yet to be identified (Table 1). In The Bahamas, bonefish reproduction occurs in deep, offshore waters, most often near full and new moons (Danylchuk et al. 2011; Murchie et al. 2015). Bonefish travel from flats habitats, aggregating in nearshore locations prior to offshore movements for spawning at night. Putatively, spawning offshore occurs near regions of high current during periods of high tidal fluxes (i.e., full and new moons) that facilitate broad-scale advective larval transport (Alexander 1961; Crabtree et al. 1997). Pre-spawning sites are particularly important to identify, because they often occur in relatively deep-water nearshore regions that are popular for shoreline development and boat traffic (Adams et al. *In Review*). Adams et al. (*In Review*) describe a protocol for locating pre-spawning aggregation sites that has been highly successful in The Bahamas, which could be applied to Florida bonefish.

Bonefish diet in South Florida consists of mainly benthic invertebrates, predominantly crustaceans including portunid and xanthid crabs, penaeid, and alpheid shrimps, as well as small fishes, primarily gulf toadfish (*Opsanus beta*)(Bruger 1974; Crabtree et al. 1998). Crabtree et al. (1998) noted a significant ontogenetic shift in bonefish diet at 440 mm total length, from predominantly penaeid shrimp in smaller fish, to xanthid crabs, alpheid shrimp and gulf toadfish in larger size classes. A cursory study on bonefish prey abundance at select sites throughout the Florida Keys found no evidence of decadal changes in prey in the region (Liston et al. 2013). Yet, Liston et al. (2013) found bonefish prey abundances were higher in the Lower Keys than other sites, where bonefish populations have been less prone to decline.

Larvae

Bonefish have an extended leptocephalus larval stage, which in *A. vulpes* is typically lasts between 41 and 71 days (Mojica et al. 1995). Leptocephali have been found in coastal waters, within the top 50 m of the water column in pelagic zones the Caribbean Sea and the Gulf of Mexico (Pfeiler 2008; Vásquez-Yeomans et al. 2009). Bonefish larval transport may play a critical role in population dynamics and connectivity; however, we currently have limited knowledge of bonefish larval transport patterns or mechanisms (Table 1). Larval transport and spatial population connectivity have been examined in many other marine fish species, especially reef-associated fishes, which often exhibit high levels of local larval retention due to larval behavior (Paris and Cowen 2004; Cowen et al. 2006). Larval transport modeling of permit (*Trachinotus falcatus*) found a high level of local recruitment in Florida from spawning sites in the Dry Tortugas, with more limited inputs from other regions including Cuba and Belize (Bryan et al. 2015). Preliminary genetics research suggests there is a high level of connectivity between populations of *A. vulpes* throughout the Caribbean Sea and western Atlantic Ocean (Wallace 2014), however, more extensive, ongoing genetics research will shed better light on regional

Table 1 Information deficiencies for bonefish in Florida by life stage, and potential scientific approaches to addressing knowledge gaps

Life stage	Information deficiency	Potential approaches
Adult	Population dynamics (size, mortality rate, fecundity, recruitment)	• Mark recapture • Field surveys • Age and size structure analysis • Virtual population analysis • Angler/guide logbooks and interviews
	Long term, broad scale space use	• Acoustic telemetry • Mark recapture • Isotopes
	Spawning locations	• Acoustic telemetry • Sampling of seasonal reproductive status • Mark recapture • Behavioral observations • Guide interviews
	Fine scale habitat use and function	• Acoustic telemetry with a fine scale positioning system • Acceleration biologgers • Benthic prey sampling
	Presence of disease and epigenetic effects	• Virus sampling and analysis • Epigenetic sampling and analysis
	Overexploitation	• Population size estimates via mark recapture • Age and size structure analysis • Post release survival from catch-and-release • Angler surveys
	Vulnerability to extreme weather events	• Acoustic telemetry • Post-storm mortality estimates • laboratory tests of pressure sensitivity
	Prey population dynamics	• Spatiotemporal prey sampling • Gut content analysis • Stable isotopes
Larval	Regional movement via oceanic currents	• Ocean mixing models • Leptocephali behavior in relation to oceanic currents • Sampling spatiotemporal abundance • Genetic connectivity between regions
	Physiological ecology	• Laboratory tests for tolerance to ecologically relevant factors (e.g., temperature, salinity) • Sampling of larval ecology in the wild
	Factors influencing inshore movement and survival	• Spatiotemporal sampling and environmental monitoring • Otolith microchemistry
Juvenile	Habitat use	• Seine net sampling • Acoustic telemetry • Stable isotopes • Otolith microchemistry
	Regional and temporal abundance	• Seine net sampling • eDNA
	Physiological ecology	• Laboratory tests for tolerance to ecologically relevant factors (e.g., temperature, salinity)
	Interspecific interactions	• Seine net sampling • Laboratory behavioural observations • Experimental tests of schooling behaviour and advantages
	Prey population dynamics	• Spatiotemporal prey sampling • Gut content analysis • Stable isotopes

connectivity. It is possible that because bonefish spawn offshore and have an extended pelagic larval stage, passive transport of larvae may enable greater regional connectivity than is observed in many reef-associated fishes such as permit with shorter pelagic larval durations. Indeed, particle tracking simulations indicate the potential for high levels of larval bonefish connectivity between Cuba, Mexico and South Florida, in addition to some self-recruitment in Florida itself (Zeng et al. *In Review*). Knowledge of actual bonefish larval movement in relation to oceanic currents is limited (Table 1), with the latter likely having significant effect on the determination of larval transport patterns (Cowen et al. 2006), including the potential for the self-recruitment of locally sourced bonefish larvae in South Florida.

Larval bonefish move into nearshore habitats prior to metamorphosis. In South Florida, movement into sublittoral habitats is believed to occur predominantly during winter and early spring seasons (Snodgrass et al. 2008). However, most efforts to locate larvae in nearshore habitats of Florida have been unsuccessful, or have found them in very low densities (Dahlgren et al. 2008). Several studies employing channel-net sampling in shallow-water cuts of The Bahamas and Turks and Caicos Islands have documented large recruitment pulses of settlement-stage *Albula* leptocephali (Thorrold et al. 1994; Mojica et al. 1995; Maddox 2006), often capturing tens to hundreds of individuals in a single night. In contrast, extensive, year-long sampling efforts by two studies using similar methodologies in cuts connecting Biscayne Bay and Florida Bay to the Atlantic Ocean resulted in the collection of just two and six individual *Albula* larvae, respectively (Harnden et al. 1999; Maddox 2006).

The stark discrepancy in apparent levels of larval recruitment may be indicative of limited reproductive success due to diminished adult stocks, or may reflect reduced connectivity and/or exceptionally high mortality for settlement-stage larvae in Florida waters. The latter could be related to human activities, which can have sweeping negative consequences for larval orientation and survival (see Siebeck et al. 2015 for review). Anthropogenically sourced pollutants in the form of chemical compounds, suspended sediments, or boat noise can alter behaviors and impair the sensory abilities of settling larvae, interfering with environmental cues used to identify suitable settlement habitats (Holles et al. 2013; Lecchini et al. 2017). Ambient light pollution (Davies et al. 2014) may pose a particular threat to settlement-stage leptocephalus larvae. *Albula* settlement peaks typically coincide with periods of dark (moonless) flood tide, presumably an adaptation that minimizes predation (Shenker et al. 1993; Mojica et al. 1995). During settlement, *Albula* larvae display positive phototactic behavior; consequently, high levels of artificial illumination near routes of larval ingress or settlement corridors (i.e., cuts) may disorient settlers, while also increasing their visibility, and thus, their vulnerability to predators. Together, these impacts may have profound consequences for recruitment success in Florida, where coastal development is widespread. Alternatively, the low densities of recruiting larvae observed in Florida may be related to long-term, climate-related regime shifts in broad-scale oceanographic processes (Nye et al. 2014; Johnson et al. 2017), potentially resulting in unfavorable conditions for the advection and transport of bonefish larvae into Florida's coastal waters. For instance, Pfeiler (2000) linked drastic reductions in the abundance of settlement-stage *Albula* larvae in the Gulf of California to anomalously elevated water temperatures.

Due to challenges with collecting leptocephali, data on their physiological tolerances are scarce (but see Pfeiler 2008). During phase I (premetamorphic) bonefish larvae occupy offshore waters, in which environmental conditions are generally more stable than in adjacent coastal regions (Pfeiler 2008). Limited data suggest phase I larvae may have broad temperature and dissolved oxygen tolerance, but may also be limited by temperatures >20 °C. Phase II larvae transition into nearshore habitats and metamorphose into juveniles and during this phase they have a broad salinity tolerance range, higher metabolic requirements and an increased sensitivity to hypoxia (Pfeiler 1984, 2008). Their vulnerability to other potential environmental stressors such as chemical contaminants, increased turbidity, nutrient concentrations, or water temperatures is currently unknown (Table 1). Given that mortality rates are generally greatest for larval fishes (Chambers and Trippel 1997), settlement into ideal habitat conditions is critical.

Juveniles

Juvenile bonefish (post metamorphic, 18.6–141.8 mm standard length) have been found in South Florida on shallow sandy shorelines year round, but with peak abundances in the spring season (Adams et al. 2008; Snodgrass et al. 2008). However, the majority of specimens collected by these efforts were identified as *A. goreensis*, a cryptic species comprising a very small fraction of the recreational fishery (Wallace and Tringali 2016). These results stand in contrast to observations throughout much of The Bahamas archipelago, where *A. vulpes* have predominated collections in efforts to identify juvenile habitats in that region (Haak et al. 2018). Although very limited in scope, more recent efforts in the Florida Keys targeting habitats with characteristics similar to those utilized by *A. vulpes* juveniles in The Bahamas (i.e., sparsely vegetated shorelines experiencing low wave or tide-driven water velocities) have resulted in the collection of just several early juvenile *A. vulpes* from the waters of northeastern Florida Bay, certainly not in the frequencies of corresponding efforts in The Bahamas.

The comparatively low observed abundance of *A. vulpes* juveniles in South Florida waters may be attributed to several factors. The characteristics of shallow-water benthic habitats of the region are largely distinct from those of The Bahamas. In particular, the coverage of macroalgae and benthic epifauna such as *Cassiopeia* spp. that thrive in more eutrophic conditions is markedly greater in the coastal waters of the Florida Keys, and likely due to limited tidal flushing, this effect is often the most pronounced in the largely enclosed, sheltered, and shallow basins (CR Haak, personal observations) that are typical of habitats occupied by *A. vulpes* juveniles in The Bahamas. Accordingly, low-energy hydrodynamic environments and sparsely vegetated sediments with low canopy heights, the two key environmental characteristics of juvenile *A. vulpes* habitats in The Bahamas, do not frequently coincide in South Florida waters. The degree to which this is a naturally existing discrepancy related to the greater influence of terrestrial nutrient inputs in South Florida, as opposed to the result of vastly higher densities of anthropogenic nutrient inputs (See *Altered freshwater flow* and *Pollution* below), as well as and reduced water flow due to highway construction, is not entirely clear. Further, juvenile bonefish habitats in The Bahamas typically occur in water bodies characterized by fully marine salinities, whereas Florida Bay is an estuary with mesohaline and polyhaline salinity levels. Santos et al. (2018b) found with otolith microchemistry analysis that juvenile bonefish occupy more estuarine habitats with freshwater influence, moving to fully saline marine environments at a mean age of 4 years. Metamorphosing larvae are known to have broad salinity tolerances (Pfeiler 1984), and juvenile bonefishes, have been collected from more estuarine environments in The Bahamas (Layman and Silliman 2002) and Florida (J.M. Shenker, unpublished data) indicating some degree of euryhalinity. Nonetheless, the ability of juvenile bonefish to persist in diverse and increasingly variable salinity levels in Florida Bay is currently unknown, as is their general physiological ecology in relation to various relevant environmental factors such as water temperature and pH (Table 1). This information is valuable for predicting juvenile habitats, as well as the impacts of environmental changes and stressors, such as changes to freshwater inflows and associated salinity regimes and increases in water temperature due to climate change (see Conservation Threats below).

Extensive sampling throughout The Bahamas Archipelago indicates that post-metamorphic juvenile *A. vulpes* do not typically occur among large groups of conspecifics, but rather alone or in small groups, and in apparently obligate association with shoals of similarly sized mojarras (Eucinostomus spp.; Haak et al. 2018). Accordingly, the health of eucinostomid populations in coastal Florida may have important implications for the growth and survival *A. vulpes* juveniles. Anecdotal observations suggest that densities of eucinostomids in the littoral zones of Florida Bay are substantially lower than those observed in similar habitats in The Bahamas (C.R. Haak, personal observation). Between 1985 and 1996, Thayer et al. (1999) documented a nearly three-fold decline in eucinostomid abundance across Florida Bay, as part of a general shift in the structure of juvenile and small-adult ichthyofaunal communities away from bottom-associated species and towards pelagic planktivores. Such a rapid and pronounced decline in eucinostomid abundance may have serious negative implications for the survival of *A. vulpes* juveniles that depend directly or indirectly on eucinostomids, and may also reflect negative environmental changes that could be impacting juvenile bonefish as well. Yet, Flaherty et al. (2013) found eucinostomids are still a predominant component of the fish community in Florida Bay, which may indicate other factors have been impacting bonefish population recovery.

Spatiotemporal dynamics of bonefish decline

In the absence of standardized, long-term scientific monitoring of bonefish population sizes, population trends must be inferred from fisheries dependent data and local ecological knowledge. Although angler reports on fish catch and fishing quality are often biased, robust survey methods by multiple studies (i.e., Larkin et al. 2010; Frezza and Clem 2015; Santos et al. 2017; Rehage et al. *In Review*; Santos et al. 2018a) provide a strong indication of bonefish population trends using metrics including fishing guide and angler observations of bonefish abundance, size, catch, and fishing quality. Overall these studies indicate significant declines in bonefish fishing quality and catch rates throughout most regions of South Florida since the 1980s. Geographically, Frezza and Clem (2015) found the greatest declines in fishing quality occurred in Florida Bay, followed by the Upper Keys, Biscayne Bay, and the Middle Keys. However, fishing quality was more consistent over time in the Lower Florida Keys. Temporally, Frezza and Clem (2015) reported the greatest period of decline in the Florida Bay bonefish population from 2001 to 2012, as well as more specific periods of decline in the mid-1990s and 2006–08. More recently, Santos et al. (2017) reported declines in catch rates (42%), in Florida Bay since 1985, with the greatest rate of decline beginning in 1999–2000. Rehage et al. (*In Review*) reported a 56% decline in bonefish catch and 45% decline in bonefish size since 1975, with accelerated rates of decline in numbers from 2005 to 2010, and similar rates of decline amongst regions. Yet, unlike Frezza and Clem (2015), Rehage et al. (*In Review*) examined the Florida Keys in aggregate rather than by subregion. Santos et al. (2018a) reported the greatest declines in bonefish catch in Florida Bay (53%), followed by the Florida Keys (38%), and Biscayne Bay (26%), with varied temporal patterns in bonefish decline, suggesting both localized and regional stressors may be involved. The above-referenced studies obtained these data through fishing guide and angler logbooks, interviews, and surveys. In the absence of standardized sampling, these are valuable proxies for population trends.

Potential contributors to bonefish decline

To identify potential causes of bonefish decline in Florida, a group of experts in bonefish biology and Florida's coastal marine ecosystems convened at the 2014 and 2017 Bonefish and Tarpon Trust Symposiums. Here we report the potential causes identified in these sessions, which included altered freshwater flow, pollution, habitat loss, fish disease, overexploitation, extreme weather events, and changes in ecosystem structure (Table 2). These factors are fairly consistent with those previously rated by bonefish anglers and guides, which included water quality, habitat loss, weather, boating pressure, angling pressure, catch mortality, and commercial gill netting (Frezza and Clem 2015).

Altered freshwater flow

Due to efforts to dry the central Everglades for farming, estuarine regions of Florida Bay, Biscayne Bay, and Everglades National Park, receive 50–70% less freshwater relative to the natural state, as well as more variable and pulsed outflows (McIvor et al. 1994; Davis et al. 2005). Alterations to freshwater flows into estuarine ecosystems often have diverse impacts including altered salinity, nutrients export, landscape topography, sediment fertility, dissolved oxygen and xenobiotic concentrations, which in turn influences the abundance and diversity of marine organisms (Sklar and Browder 1998; Kimmerer 2002; Orth et al. 2006).

With major reductions in freshwater flow, Florida Bay is less resistant to ecological change from droughts, which have repeatedly caused hypersaline conditions (>75 ppt in locations) that have triggered over 50,000 acres of seagrass mortality in single events (Hall et al. 2016). From the decaying seagrass, heterotrophic respiration increases, creating hypoxia. Nutrients within the decaying seagrass tissue are mobilized, driving algal blooms with Chlorophyll α values exceeding 100 μg·L − 1. Further, sediments held by seagrass roots systems are released, increasing turbidity. Presumably, these die-offs have negative effects on recreational fisheries (Robblee et al. 1991; Rudnick et al. 2005, 2006; Hall et al. 2016). Frezza and Clem (2015) suggested the most significant periods of bonefish decline in Florida Bay corresponded to periods of sustained algae blooms in the mid-1990s and 2006–2008. Yet Santos et al. (2017) did not detect significant changes in the fishery in these

Table 2 Potential causes of bonefish population decline in South Florida

Cause	Source	Mechanism	Affected life stage
Altered freshwater flow	Agricultural, urban water demands, flood control	Chronic reductions in freshwater inflows have changed the character of coastal estuaries Reduced freshwater flow increases severity of drought effects (hypersalinity events involving seagrass mortality, algae blooms, and anoxic conditions)	All
Pollution	Industrial, agricultural, urban effluent and runoff	Habitat degradation. Increased disease, parasites, reduced growth and reproductive output, altered behaviour, epigenetic effects	All, particularly juvenile and adult
Habitat loss	Shoreline development, alterations to freshwater inputs, nutrient and pollution effluent	Less area to support bonefish (e.g., reduced food quantity or quality), reduced connectivity between habitats	Juvenile and adult
Disease	Eutrophication, pollution, acute stressors	Increased bacterial and virus loads in environment, reduced immune function in bonefish	Adult
Overexploitation	Recreational angling, illegal netting	Direct removal, unintended post-release mortality in adults reduces population size	Adult
Extreme weather events	Natural but increasing in frequency and intensity with climate change	Extreme, rapid temperature changes cause cold shock stress and mortality, displacement from habitats	Juvenile and adult
Changes to ecosystem structure	Changes in biotic and abiotic conditions due to reduced freshwater inflows, overexploitation, habitat destruction, and pollution	Altered prey and/or predator communities and habitat structure causes imbalances in bonefish populations	Juvenile and adult
Reductions in larval supply	Reductions in bonefish populations in other regions that supply bonefish larvae to Florida	Overexploitation, habitat loss, changes in ecosystem structure, alterations in oceanic current patterns	Larvae

periods, rather an increased rate in decline in bonefish catch rates starting in 1999–2000.

The more chronic effects of alterations in freshwater outflows involve alterations in seascape characteristics as well as the biotic conditions (i.e., aquatic vegetation). Historically Florida Bay was over 80% seagrass habitat; however, from 1984 to 1994 significant declines occurred, including *Thalassia testudinum*, (28% decline in standing crop), *Syringodium filiforme* (88%), and *Halodule wrightii* (92%) that resulted in patchy stands of primarily *Thalassia testudinum* and exposed mud substrate (Hall et al. 1999). As of 2012, *Thalassia testudinum* had returned to pre-die-off densities, however, an extreme drought in the summer of 2015, exacerbated by altered water flows, again resulted in mass seagrass mortalities and associated negative impacts on water quality and fish kills (Hall et al. 2016). The acute effects of hypersalinity events, as well as long term changes in ecosystem structure have resulted in substantial declines in the densities of diverse organisms at all trophic levels of the food web in Florida Bay (McIvor et al. 1994; Lorenz 2014), with changes that may have impacted bonefish directly (i.e., acute mortality) or indirectly (e.g., altered/reduced forage base). Similar issues exist in the central region of Biscayne Bay, where canals deliver sporadic pulses of freshwater into the Bay, causing highly variable salinity levels and fragmented seagrass beds compared to other regions of the Bay with more stable salinity regimes (Santos et al. 2011). However, effects on the food web in this region have not been well documented. This has likely had a considerable effect on the benthic fauna community, which would impact bonefish prey availability, although these effects are not well documented.

Pollution

The coastal marine habitats of South Florida are subject to diverse pollutants from urban, industrial, and agricultural sources. Documented pollutants include nutrients, suspended solids, pesticides, metals, pharmaceuticals, plastics and other debris, polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons (PAHs), and various other organic compounds (Lapointe and Clark 1992; Miles and Pfeuffer 1997; Derraik 2002; Heath and Frederick 2005; Johnson-Restrepo et al. 2005). There are many potential impacts of these pollutants on marine organisms directly (e.g., causing disease, reduced cognitive or immune function, reduced survival or recruitment), and indirectly through altered habitat or ecosystem structure (Islam and Tanaka 2004). There has been no research of potential impacts of any of these contaminants on bonefish.

Nutrient enrichment from anthropogenic activity in the watershed has long been recognized as an important issue for coastal ecosystems in many regions of South Florida, including bonefish habitats in nearshore regions of Florida Bay, Biscayne Bay and the Florida Keys (Lapointe and Clark 1992; Lapointe et al. 1994; Caccia and Boyer 2007). In Florida Bay and Biscayne Bay, the most prominent identified source of habitat degradation is related to alterations in freshwater flows, which results in seagrass die-off causing the release of nutrients from autochthonous sources including sediments and decaying plant material (Lapointe 1989; Boyer et al. 2009; See *Altered freshwater flow above).* Yet, land use in the watershed also generates agricultural and urban runoff of various pollutants into these systems (Caccia and Boyer 2007; Rehage et al. 2016). In particular, urban runoff from the Miami region is a major source of nutrient enrichment in Biscayne Bay (Caccia and Boyer 2007). This region has also received nutrient inputs from other sources, for example, Hurricane Katrina caused significant agricultural runoff in 2005 (Zhang et al. 2009).

In the Florida Keys, domestic wastewater contaminated by septic tanks, shallow injection wells, and cesspits, are sources of nutrient inputs to coastal waters in the region that have contributed to declining water quality (Lapointe et al. 1990). Nutrient loading has caused algae blooms, negatively affected seagrass meadows and coral reefs, with the greatest effects occurring in close proximity to shore (Lapointe et al. 1994; Lapointe 1997). Sewage was disposed into the ocean in the Florida Keys until 1976, when Key West built a treatment plant. However, the remainder of the Florida Keys continued with more primitive treatment methods until a state mandate implemented sewage treatment throughout the region in 1999 to combat coastal nutrient enrichment issues. Conversion to modern water treatment processes is still underway in some regions of the Florida Keys today, so sewage runoff remains a potential issue for bonefish habitat.

Aside from nutrients, many other pollutants are present in bonefish habitats throughout South Florida. Due to high levels of urbanization in the watershed, sediments in Biscayne Bay contain high levels of pollutants including metals such as arsenic and copper, PCBs, PAHs, and pesticides (Rehage et al. 2016). Sediments and water in Florida Bay also have potentially harmful concentrations of pesticides. Although few studies have been conducted in the region on other pollutants such as PCBs and metals, samples in the Florida Keys have tested low for hydrocarbons and pesticides (Rehage et al. 2016). These contaminants have the potential to negatively impact bonefish through reduced growth or mortality, acute or chronic physiological impairment, reduced immune response and increased disease, or epigenetic effects (Werner and Hitzfeld 2012; Palanikumar et al. 2013; Zeitoun et al. 2014; Burris and Baccarelli 2014; See ***Fish disease*** below). Given the large spatial area, and number of potential contaminants and impacts on bonefish, few studies have addressed this issue to date.

Habitat loss

Bonefish habitat requirements are tightly connected with seagrasses, mangroves, and coral reefs (Ault et al. 2008a; Larkin et al. 2008; Adams et al. 2012), each of which has experienced some level of decline in recent years. Habitat loss is cited as the major reason why bonefish are now listed as Threatened on The International Union for Conservation of Nature Red List (Adams et al. 2012). The most dominant changes in habitat are likely related to increased nutrient inputs in Biscayne Bay and the Florida Keys, and altered freshwater flow in Florida Bay and Biscayne Bay (discussed above in *Altered freshwater flow* and *Pollution*).

Shoreline development is another major cause of bonefish habitat loss, particularly in the Florida Keys and Biscayne Bay where large areas of natural vegetated shorelines and seagrass substrates have been replaced with dredged, man-made canals with concrete shoreline structures and soft sediment substrates (Fig. 2). For example, in the Upper Florida Keys, 41% of tropical forests and 15% of mangrove forests were replaced by human development by 1994 (Strong and Bancroft 1994). The occlusion of many passes in the Florida Keys due to highway construction likely caused the loss of bonefish habitat, as well as changes in water flow patterns impacting adjacent shallow water habitats (Rudnick et al. 2005). Shoreline modification may be of particular concern for the juvenile life stages of *A. vulpes*, for which shallow, low-energy littoral zones within sheltered basins are a fundamental habitat requirement (Haak et a. 2018). Unfortunately, these qualities are also highly desirable for human development (e.g., marinas), and few such natural locations remain unaltered.

Human activities in the marine environment have also impacted bonefish habitat. For example, boating has caused noticeable propeller scarring in seagrass beds throughout South Florida (Zieman 1976; Sargent et al. 1995; Dawes et al. 1997). Due to increased boating activities in the past 20 years, the number of seagrass flats that are classified as severely degraded has quadrupled (Kruer 2017). Overfishing of reef fishes (Ault et al. 2005), has contributed to declines in the health of coral reefs (Pandolfi et al. 2003). Although bonefish are not considered to be directly associated with coral reefs in Florida, shallow flats and reef habitats comprise complex, interconnected ecosystems (see *Changes in ecosystem structure and function* below).

Much of the bonefish habitat in Florida is covered by special regulations through the Everglades National Park, Biscayne National Park, and the Florida Keys National Marine Sanctuary. Yet, maintaining habitat integrity requires consideration of human activity in the ocean and in the adjacent watershed. Increased boater education and boating regulations such as poll/troll zones (Black et al. 2015) are potential measures for remedying this issue. In the watershed, restoring a more natural freshwater outflow regime from the Florida Everglades, along with strategic land planning to reduce pollutant effluents (Guardo et al. 1995; Sklar et al. 2005) would likely have a significant positive impact on bonefish habitat quality in many regions of South Florida.

Fish disease

Numerous anthropogenic stressors can cause pathological changes in fish (Wedemeyer and Goodyear 1984; Andersen 1990). Pollution can cause increased prevalence of fish disease, which often results from a combination of compromised physiological (e.g., immune) function, combined with increases in harmful bacterial and viral loads in the environment (Vethaak and ap Rheinallt 1992). Acute stressors such as those related to C&R angling (i.e., physiological stress, injury, slime loss from handling) may also cause increased susceptibility to disease (Arlinghaus et al. 2007). Although there is currently no evidence of disease issues with Florida bonefish (i.e., no mass fish kills with obvious signs of pathology), the conditions of the region, particularly the high levels of pollutants in nearshore regions of Biscayne Bay, are such that disease may be an issue worth exploring (Tables 1 and 2).

Overexploitation and discard mortality

Overexploitation is now considered the largest threat to marine fishes, particularly in coastal regions (Arthington et al. 2016), and there is evidence of overfishing in numerous fish species in coastal Florida (Ault et al. 2005; Heithaus et al. 2007; McClenachan 2009). Historically bonefish were impacted by commercial netting

Fig. 2 An aerial photograph of Marathon, Florida in 1987. Significant coastal development has occurred in many regions of South Florida, changing coastal habitats from natural vegetated shorelines to concrete seawalls. Both habitat loss and urban pollution may be playing a role in the decline of bonefish in Florida. Photograph taken by the Federal Government, sourced from the Wright Langley Collection. Source: www.keyslibraries.org

until it was banned in 1985 (Frezza and Clem 2015). Similarly, harvest by recreational anglers was also common (Fig. 3) until it became prohibited by law in 2011 (Ault et al. 2008a). Although it is unclear whether overexploitation had a significant effect on bonefish populations historically, given their life history characteristics (maximum age 21 years, age of maturity ~4 years; Crabtree et al. 1996, 1997), overexploitation via harvest is unlikely to be the major cause of low contemporary bonefish population sizes. Furthermore, Rehage et al. (*In Review*) found declines in bonefish abundance actually preceded declines in bonefish size. This is atypical of fisheries induced population declines observed in numerous other species, which usually involve declines in mean size prior to population crashes (Pauly et al. 1998; Rosenberg 2003).

From a regulatory perspective the recreational bonefish fishery is entirely catch-and-release, however, the practice may still have negative impacts on the bonefish population (Lewin et al. 2006) due to post release mortality, as well as sublethal effects from injury and stress (Cooke and Suski 2005; Brownscombe et al. 2015). Until 2013, bonefish fishing tournaments involved retention and transport of bonefish to a central weigh-in location, which may be highly detrimental due to unintended mortality and fish displacement (Wilde 1998). Furthermore, bonefish are particularly sensitive to angling stressors and vulnerable to post-release predation (Danylchuk et al. 2007). Post-release mortality rates due to predation are highly variable, ranging from 0 to 40% in The Bahamas (Cooke and Philipp 2004; Danylchuk et al. 2007; Brownscombe et al. 2013), to over 80% in French Polynesia (Lennox et al. 2017). There have been no studies quantifying post-release mortality of bonefish in Florida. The population-level effects of catch-and-release mortality are important in recreational fisheries because fishing mortality resulting from released fish can sometimes be a biologically significant mortality source (Kerns et al. 2012). Such information would be valuable to ensure the sustainability of this

Fig. 3 Fishing guide Harry Snow and angler Grace Tauck with the world record largest angled bonefish, captured in the Florida Keys in 1950. Historically bonefish were harvested until catch-and-release became mandatory by law in Florida in 2011. Historical and current angling practices may be playing a role in the decline of bonefish in Florida, although the extent to which is unclear. Photograph source: www.keyslibraries.org

fishery (Table 1). Predator densities can be high in some regions of South Florida, but are spatiotemporally variable (Heithaus et al. 2007). Knowledge and practice of conservation minded angling techniques and factors influencing survival have been increasing rapidly since the turn of the century (e.g., Danylchuk et al. 2007; Shultz et al. 2011; Brownscombe et al. 2013, 2015) and recreational angling tactics can be modified to minimize impacts, including retaining bonefish for a short recovery period prior to release in habitats with high predation risk (Brownscombe et al. 2013).

Extreme cold events

Extreme cold events are defined as abnormally low ocean water temperatures for an extended period of time (i.e., days to weeks), which can have negative impacts on aquatic biota through direct mortality or sublethal effects (Donaldson et al. 2008; Szekeres et al. 2016). In Florida, extreme cold events are a product of multiple climate anomalies, in particular the Pacific North American Anomaly (PNA), and the North Atlantic Oscillation (Boucek et al. 2016 and citations within). In the subtropical USA, upper airflows during the positive phase of the PNA coincide with 80% of the region's ecologically and economically impactful cold events (Downton and Miller 1993; Sheridan 2003). Historically, these have occurred in Florida once every 30 to 40 years (Boucek and Rehage 2014). Since the 1920s, 3 extreme cold events have affected South Florida, all occurred in the month of January in years 1940, 1981, and 2010. All three of these disturbances have reported fish kills associated with the events, but the January 2010 event was the most severe cold spell of the three extremes (Boucek et al. 2016). The event was the third coldest, but most influential was its duration. Minimum air temperatures remained <15 °C, which is stressful or lethal to many tropical fish species, for nearly twice as many days as the next most severe period (1940 event; Boucek and Rehage 2014). This extreme cold event resulted in up to 80% declines many of Florida's economically important tropical sportfishes, including bonefish *A. vulpes*, juvenile goliath grouper (*Epinephelus itajara*), and common snook (*Centropomus undecimalis*; Santos et al. 2016). The 2010 event led to closures of recreational fisheries and economic losses for those who rely on those resources. Following the 2010 event, Santos et al. (2016) documented the lowest bonefish catches in at least 30 years (duration of time series available). Similar to other species such as common snook, anecdotal reports indicated smaller bonefish were disproportionately affected (M. Larkin, personal observations; Adams et al. 2012).

These events can have lethal and sublethal effects depending on the intensity and duration of the cold event in relation to species physiological characteristics, as well as the spatial structuring and availability of thermal refuge (Donaldson et al. 2008). As for the thermal tolerances of bonefish, Szekeres et al. (2014) found a 14 °C decline from 25 °C caused significant physiological and behavioural impairment, but a 7 °C decline had no significant effects. Shultz et al. (2016) found when bonefish were acclimated to 24 °C, the minimum temperature they could tolerate was 11 °C, but when acclimated to 29 °C it was 14 °C. Therefore, both the absolute low temperatures and the degree of temperature change are relevant to the biological impacts of cold events. Research to date suggests that rapid absolute changes of >10 °C to absolute temperatures of <15 °C have the potential to negatively impact bonefish.

In the case of approaching storms, some fish are capable of sensing declines in pressure and transitioning out of nearshore areas (Heupel et al. 2003). Offshore bonefish movements have been observed to coincide with pressure declines (Larkin et al. 2008). Behavioural avoidance of the adverse storm conditions in shallow coastal regions may enable adult bonefish to avoid the potential negative consequences of storm events. However, given the rarity (average < 1 event per bonefish lifetime) and intensity of such extremes, it is uncertain if bonefish have the capacity to move at the appropriate scale to seek out the few habitats that serve as refuge during these events (Boucek et al. 2017). For instance, during the extreme 2010 cold event, acoustic tracking showed that common snook moved short distances, presumably to the nearest deep-water habitat. These nearby deepwaters would provide refuge during more frequent and less severe events. However, during the 2010 event, many of these nearby deep habitats became lethal (Stevens et al. 2016).

Whether extreme cold events will increase or decrease in frequency intensity, or duration is uncertain and varies geographically. Regardless, we should to continue to develop formal predictions for the bonefish fishery under various potential scenarios (Vavrus et al. 2006; Kodra et al. 2011). Cold events dictate the northern boundary of bonefishes and other tropical species range in Florida (Boucek et al. 2016). If these events decrease in frequency, we may expect bonefish populations to shift poleward, potentially creating new fishing opportunities elsewhere in the region. However, if these events increase in frequency, they may pose significant limitations on bonefish populations.

Changes in ecosystem structure and function

Ecosystems are complex networks with interconnected biological, chemical, and physical characteristics, which must be considered in fisheries management (Pikitch et al. 2004). Changes in environmental conditions related to freshwater inflows, water quality, habitat characteristics and connectivity, as well as the overfishing of top predators and invasive species can all cause significant alterations to fish communities and ecosystem structure. For example, overfishing on coral reefs has cascading effects on invertebrate abundance and reef health (Roberts 1995). Similarly, overfishing of top predators in coastal Florida (Heithaus et al. 2007) may have cascading effects on bonefish populations through altered predator or prey abundance. Well-documented declines of vertebrate and invertebrate species at all trophic levels in Florida Bay food webs, triggered by seagrass mortality and long-term changes in ecosystem conditions (Lorenz 2014; Hall et al. 2016) have undoubtedly impacted ecosystem function and species interactions. Liston et al. (2013) sampled bonefish prey abundance at sites throughout their range in South Florida and found it was generally highest in the Lower Florida Keys, where bonefish populations have been most stable, compared to the Florida Bay and Biscayne Bay where greater declines in fishing quality have been observed. However, examining decadal changes at two sites in Florida Bay, no significant changes in bonefish prey abundance were detected, leading Liston et al. (2013) to suggest changes in prey availability are unlikely to be the cause of bonefish decline in the region. Importantly, this is based on limited sampling locations, and more extensive long-term data would be necessary to determine bonefish prey availability has changed throughout their range in South Florida.

Consideration of such changes in the context of overall ecosystem dynamics, structure, and function using conceptual models such as that developed for Florida Bay (Rudnick et al. 2015) may place understanding of bonefish population dynamics in a broader perspective. To this end, knowledge of regional connectivity via movements of adults and larval settlement, as well as changes in predator and prey communities over time would provide valuable insight into the influence of ecosystem level factors on the abundance and distribution of bonefish (Table 1).

Synthesis

Above we describe an array of factors that may be impacting bonefish directly (e.g. extreme weather events) or indirectly through reduced habitat quality or changes in ecosystem structure. It is unlikely to be any one of these factors impacting the bonefish alone, rather, a combination thereof, which could very well have compounding effects. Indeed, the patterns revealed by Santos et al. (2018a), which include bonefish decline throughout South Florida, yet varied levels and timing of decline amongst regions, are suggestive of multiple stressors acting on a region specific basis. In Florida Bay, the acute hypoxia events and changes in ecosystem structure due to altered/reduced freshwater flow almost certainly have negative impacts on bonefish (along with diverse biota), particularly early life stages that are less mobile than adults. In Biscayne Bay, altered freshwater flow and anthropogenic contaminant inputs have also impacted ecosystem structure, and contaminants may be affecting bonefish directly as well. In the Florida Keys, nutrient effluents have caused more localized habitat degradation; yet evidence suggests bonefish in the Lower Florida Keys have experienced the least decline. This is perhaps not surprising given this area is the furthest geographically from large human populations and has experienced the least decline in habitat quality. Other stressors have been acting on the entire region, including extreme weather events, the most marked being that of 2010, which Santos et al. (2017) suggest was correlated with significant declines in the fishery. Lastly, there may have been significant historical impacts of the recreational fishery due to bonefish harvest and stressful handling practices. Bonefish angling is currently entirely catch-and-release, yet we still lack knowledge of bonefish post-release survival in the various regions of South Florida, which could be influenced significantly by post-release predation.

Where do we go from here?

To restore Florida's bonefish fishery to its historical quality, significant conservation actions and research are required. The foundation of healthy fisheries is healthy habitats, so restoring and maintaining habitat quality is a major priority, particularly reestablishing historical freshwater flow through the Everglades, with sufficient wetland filtration to remove contaminants that have aggregated from the watershed (Guardo et al. 1995) into Florida Bay. Reducing urban pollutants in Biscayne Bay and the Florida Keys is also paramount for improved habitat quality in these regions. These pollutants have the potential to impact bonefish directly through disease or other contaminant-related issues, which are worth investigation.

Perhaps the most essential knowledge gaps with Florida bonefish are currently in the early life stages. To date, efforts to locate juveniles in Florida have been largely unsuccessful, meaning there may be some combination of: 1) a lack of larval input. 2) major recruitment issues, and/or 3) we have yet to locate essential juvenile habitat. Regarding 1), recent particle tracking simulations suggest that a significant proportion of larval bonefish could be sourced from regions outside of Florida including Cuba and Mexico (Zeng et al. *In Review*). Further research should explore this potential connection, which could be accomplished with advanced genetic analyses. Regarding 2) and 3), South Florida consists of different habitat types from The Bahamas, which is our current basis of knowledge on juvenile habitats and the timing and locations of larval ingress. More extensive sampling for juveniles and larvae in Florida would inform their ecology, as well as whether larval inputs or juvenile recruitment are issues of concern. Further, collections of live juveniles or larvae would enable studies on their tolerance of ecologically relevant stressors such as thermal extremes (cold events) and hypoxia (Florida Bay seagrass mortality).

There are also major knowledge gaps in adult bonefish ecology in Florida. We currently lack knowledge of their movement patterns and regional connectivity, including spawning and pre-spawning aggregation sites. It is essential to understand whether, for example, bonefish in the Florida Keys and Florida Bay are distinct, or move between regions. In the case of the latter, any stressors impacting one region (e.g., acute hypoxia in Florida Bay) impact fish from the other. Knowledge of spawning sites would be valuable for forming a basis for understanding spatial larval recruitment patterns, and pre-spawning sites require particular protection from stressors such as boat traffic or angling pressure.

With a lack of a stock assessment for bonefish, continued monitoring of the fishery through guide and angler logbooks, surveys, and interviews forms an essential basis for population monitoring, which also serves to form links between population trends and potential environmental stressors such as extreme cold events. Specific to the fishery, it is also essential to continue to evolve catch-and-release practices to ensure the fishery is having a minimal impact on bonefish population(s). Knowledge of 'best handling practices' are already well established for bonefish (Cooke and Philipp 2008; Brownscombe et al. 2017c), nevertheless studies of actual bonefish survival in Florida's coastal habitats, particularly in relation to predation risk, would provide a valuable indication of the sustainability of the fishery.

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References

Abtew W, Iricanin N (2008) Hurricane effects on South Florida water management system: a case study of hurricane Wilma of October 2005. J Spat Hydrol 8:1–21

Adams AJ (2017) Guidelines for evaluating the suitability of catch and release fisheries: lessons learned from Caribbean flats fisheries. Fish Res 186:672–680

Adams AJ, Wolfe RK, Tringali MD et al (2008) Rethinking the status of Albula spp. biology in the Caribbean and western Atlantic. In: Ault JS (ed) Biology and management of the world tarpon and bonefish fisheries. CRC Press, Boca Raton, pp 203–216

Adams A, Guindon K, Horodysky A, et al (2012) The IUCN red list of threatened species 2012

Alexander ECDR (1961) A contribution to the life history, biology and geographical distribution of the bonefish *Albula vulpes* (Linnaeus). Danna-Rep 53:1–51

Andersen DP (1990) Immunological indicators: effects of environmental stress on immune protection and disease outbreaks. In: American Fisheries Society Symposium. pp 38–50

Arlinghaus R, Cooke SJ, Lyman J, Policansky D, Schwab A, Suski C, Sutton SG, Thorstad EB (2007) Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. Rev Fish Sci 15: 75–167

Arthington AH, Dulvy NK, Gladstone W, Winfield IJ (2016) Fish conservation in freshwater and marine realms: status, threats and management. Aquat Conserv Mar Freshwat Ecosyst 26: 838–857

Ault J, Smith S, Bohnsack J (2005) Evaluation of average length as an estimator of exploitation status for the Florida coral-reef fish community. ICES J Mar Sci 62:417–423

Ault JS, Humston R, Larkin MF et al (2008a) Population dynamics and resource ecology of Atlantic tarpon and bonefish. In: Ault JS (ed) Biology and management of the world tarpon and bonefish fisheries. CRC Press, Boca Raton, pp 131–146

Ault JS, Moret S, Luo J et al (2008b) Florida keys bonefish population census. In: Ault JS (ed) Biology and Management of the World Tarpon and Bonefish Fisheries. CRC Press, Boca Raton, pp 383–298

Barbieri LR, Ault JS, Crabtree RE (2008) Science in support of management decision making for bonefish and tarpon conservation in Florida. In: Ault JS (ed) Biology and Management of the World Tarpon and Bonefish Fisheries. CRC Press, Boca Raton, pp 399–404

Black BD, Adams AJ, Bergh C (2015) Mapping of stakeholder activities and habitats to inform conservation planning for a national marine sanctuary. Environ Biol Fish 98:2213–2221

Boucek RE, Rehage JS (2014) Climate extremes drive changes in functional community structure. Glob Chang Biol 20: 1821–1831

Boucek RE, Gaiser EE, Liu H, Rehage JS (2016) A review of subtropical community resistance and resilience to extreme cold spells. Ecosphere 7. https://doi.org/10.1002/ecs2.1455

Boucek RE, Heithaus MR, Santos R, Stevens P, Rehage JS (2017) Can animal habitat use patterns influence their vulnerability to extreme climate events? An estuarine sportfish case study. Glob Chang Biol 23:4045–4057

Boyer JN, Kelble CR, Ortner PB, Rudnick DT (2009) Phytoplankton bloom status: chlorophyll a biomass as an indicator of water quality condition in the southern estuaries of Florida, USA. Ecol Indic 9:S56–S67

Brownscombe JW, Thiem JD, Hatry C, Cull F, Haak CR, Danylchuk AJ, Cooke SJ (2013) Recovery bags reduce post-release impairments in locomotory activity and behavior of bonefish (*Albula* spp.) following exposure to angling-related stressors. J Exp Mar Biol Ecol 440:207–215

Brownscombe JW, Bower SD, Bowden W, Nowell L, Midwood JD, Johnson N, Cooke SJ (2014) Canadian recreational fisheries: 35 years of social, biological, and economic dynamics from a national survey. Fisheries 39:251–260

Brownscombe JW, Griffin LP, Gagne T, Haak CR, Cooke SJ, Danylchuk AJ (2015) Physiological stress and reflex impairment of recreationally angled bonefish in Puerto Rico. Environ Biol Fish 98:2287–2295

Brownscombe JW, Cooke SJ, Algera DA et al (2017a) Ecology of exercise in wild fish: integrating concepts of individual physiological capacity, behavior, and fitness through diverse case studies. Integr Comp Biol 139:437–449

Brownscombe JW, Cooke SJ, Danylchuk AJ (2017b) Spatiotemporal drivers of energy expenditure in a coastal marine fish. Oecologia 183:689–699

Brownscombe JW, Danylchuk AJ, Chapman JM, Gutowsky LFG, Cooke SJ (2017c) Best practices for catch-and-release recreational fisheries – angling tools and tactics. Fish Res 186:693–705

Bruger G (1974) Age, growth, food habits, and reproduction of bonefish, *Albula vulpes*, in South Florida waters. Florida Mar Res Publ 3:1–20

Bryan DR, Luo J, Ault JS, McClellan DB, Smith SG, Snodgrass D, Larkin MF (2015) Transport and connectivity modeling of larval permit from an observed spawning aggregation in the Dry Tortugas, Florida. Environ Biol Fish 98:2263–2276

Burris HH, Baccarelli AA (2014) Environmental epigenetics: from novelty to scientific discipline. J Appl Toxicol 34:113–116

Caccia VG, Boyer JN (2007) A nutrient loading budget for Biscayne Bay, Florida. Mar Pollut Bull 54:994–1008

Chambers RC, Trippel EA (1997) Early life history and recruitment: legacy and challenges. In: Early life history and recruitment in fish populations. Springer Netherlands, Dordrecht, pp 515–549

Colton DE, Alevizon WS (1983) Feeding ecology of bonefish in Bahamian waters. Trans Am Fish Soc 112:178–184

Cooke SJ, Cowx IG (2004) The role of recreational fishing in global fish crises. Bioscience 54:857–859

Cooke SJ, Philipp DP (2004) Behavior and mortality of caught-and-released bonefish (*Albula* spp.) in Bahamian waters with implications for a sustainable recreational fishery. Biol Conserv 118:599–607

Cooke SJ, Philipp DP (2008) Improving the sustainability of catch-and-release bonefish (*Albula* spp.) fisheries: insights for anglers, guides and fisheries managers. In: Ault JS (ed) Biology and management of the world tarpon and bonefish fisheries. CRC Press, Boca Raton, pp 359–381

Cooke SJ, Suski CD (2005) Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? Biodivers Conserv 14:1195–1209

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311:522–527

Crabtree RE, Harnden CW, Snodgrass D, Stevens C (1996) Age, growth, and mortality of bonefish, *A1bula vulpes*, from the waters of the Florida keys. Fish Bull 94:442–451

Crabtree RE, Snodgrass D, Harnden CW (1997) Maturation and reproductive seasonality in bonefish, *Albula vulpes*, from the waters of the Florida keys. Fish Bull 95:456–465

Crabtree R, Stevens C, Snodgrass D, Stengard F (1998) Feeding habits of bonefish, *Albula vulpes*, from the waters of the Florida keys. Fish Bull 96:754–766

Dahlgren C, Shenker JM, Mojica R (2008) Ecology of bonefish during the transition from late larvae to early juveniles. In: Ault JS (ed) Biology and management of the world tarpon and bonefish fisheries. CRC Press, Boca Raton, pp 155–178

Danylchuk SE, Danylchuk AJ, Cooke SJ, Goldberg TL, Koppelman J, Philipp DP (2007) Effects of recreational angling on the post-release behavior and predation of bonefish (*Albula vulpes*): the role of equilibrium status at the time of release. J Exp Mar Biol Ecol 346:127–133

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

Davies TW, Duffy JP, Bennie J, Gaston KJ (2014) The nature, extent, and ecological implications of marine light pollution. Front Ecol Environ 12:347–355

Davis SM, Childers DL, Lorenz JJ, Wanless HR, Hopkins TE (2005) A conceptual model of ecological interactions in the mangrove estuaries of the Florida Everglades. Wetlands 25:832–842

Dawes CJ, Andorfer J, Rose C, Uranowski C, Ehringer N (1997) Regrowth of the seagrass *Thalassia testudinum* into propeller scars. Aquat Bot 59:139–155

Derraik JG (2002) The pollution of the marine environment by plastic debris: a review. Mar Pollut Bull 44:842–852

Donaldson MR, Cooke SJ, Patterson DA, Macdonald JS (2008) Cold shock and fish. J Fish Biol 73:1491–1530

Downton MW, Miller KA (1993) The freeze risk to Florida citrus. Part II: Temperature variability and circulation patterns. J Clim 6:364–372

Fedler T (2013) Economic Impact of the Florida Keys Flats Fishery 32608:25

Flaherty KE, Matheson RE, McMichael RH, Perry WB (2013) The influence of freshwater on nekton community structure in hydrologically distinct basins in northeastern Florida bay, FL, USA. Estuar Coasts 36:918–939

Florida Fish and Wildlife Conservation Commission (2013) Bonefish *Albula vulpes*. http://myfwc.com/fishing/saltwater/recreational/bonefish/#

Frezza PE, Clem SE (2015) Using local fishers knowledge to characterize historical trends in the Florida bay bonefish population and fishery. Environ Biol Fish 98:2187–2202

Guardo M, Fink L, Fontaine TD, Newman S, Chimney M, Bearzotti R, Goforth G (1995) Large-scale constructed wetlands for nutrient removal from stormwater runoff: an everglades restoration project. Environ Manag 19:879–889

Haak CR, Cowles GW, Danylchuk AJ (2018) Wave and tide-driven flow act on multiple scales to shape the distribution of a juvenile fish (Albula vulpes) in shallow nearshore habitats. Limnol Oceanogr. https://doi.org/10.1002/lno.11063

Hall MO, Durako MJ, Fourqurean JW, Zieman JC (1999) Decadal changes in Seagrass distribution and abundance in Florida bay. Estuaries 22:445

Hall M, Furman B, Merello M, Durako M (2016) Recurrence of *Thalassia testudinum* seagrass die-off in Florida bay, USA: initial observations. Mar Ecol Prog Ser 560:243–249

Harnden CW, Crabtree RE, Shenker JM (1999) Onshore transport of elopomorph leptocephali and glass eels (Pisces: Osteichthyes) in the Florida keys. Gulf Mex Sci 17:17–26

Heath JA, Frederick PC (2005) Relationships among mercury concentrations, hormones, and nesting effort of white ibises (*eudocimus albus*) in the Florida Everglades. Auk 122:255

Heithaus MR, Burkholder D, Hueter RE, Heithaus LI, Pratt HL Jr, Carrier JC (2007) Spatial and temporal variation in shark communities of the lower Florida keys and evidence for historical population declines. Can J Fish Aquat Sci 64: 1302–1313

Heupel MR, Simpfendorfer CA, Hueter RE (2003) Running before the storm: Blacktip sharks respond to falling barometric pressure associated with tropical storm Gabrielle. J Fish Biol 63:1357–1363

Holles SH, Simpson SD, Radford AN, Berten L, Lecchini D (2013) Boat noise disrupts orientation behaviour n a coral reef fish. Mar Ecol Prog Ser 485:295–300

Humston R (2001) Development of movement models to assess the spatial dynamics of marine fish populations. Thesis dissertation, University of Miami

Humston R, Ault J, Larkin M, Luo J (2005) Movements and site fidelity of the bonefish *Albula vulpes* in northern Florida keys determined by acoustic telemetry. Mar Ecol Prog Ser 291: 237–248

Islam MS, Tanaka M (2004) Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: a review and synthesis. Mar Pollut Bull 48:624–649

Johnson DR, Perry H, Sanchez-Rubio G, Grace MA (2017) Loop current spin-off eddies, slope currents and dispersal of reef fish larvae from the flower gardens National Marine Sanctuary and the Florida middle grounds. Gulf Carib Res 28:29–39

Johnson-Restrepo B, Kannan K, Addink R, Adams DH (2005) Polybrominated diphenyl ethers and polychlorinated biphenyls in a marine foodweb of coastal Florida. Environ Sci Technol 39:8243–8250

Kimmerer WJ (2002) Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Mar Ecol Prog Ser 243:39–55

Kodra E, Steinhaeuser K, Ganguly AR (2011) Persisting cold extremes under 21st-century warming scenarios. Geophys Res Lett 38:L08705. https://doi.org/10.1029/2011GL047103

Kruer CR (2017) Florida keys shallow water boating impact analysis and trends assessment - mapping summary report

Lapointe BE (1989) Macroalgal production and nutrient relations in oligotrophic areas of Florida bay. Bull Mar Sci 44:312–323

Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and Southeast Florida. Limnol Oceanogr 42:1119–1131

Lapointe BE, Clark MW (1992) Nutrient inputs from the watershed and coastal eutrophication in the Florida keys. Estuaries 15:465

Lapointe BE, O'Connell JD, Garrett GS (1990) Nutrient couplings between on-site sewage disposal systems, groundwaters, and nearshore surface waters of the Florida keys. Biogeochemistry 10:289–307

Lapointe BE, Tomasko DA, Matzie WR (1994) Eutrophication and trophic state classification of Seagrass communities in the Florida keys. Bull Mar Sci 54:696–717

Larkin MF (2011) Assessment of South Florida' s bonefish stock. Thesis dissertation, University of Miami

Larkin MF, Ault JS, Humston R et al (2008) Tagging of bonefish in South Florida to study population movements and stock dynamics. In: Ault JS (ed) Biology and management of the world tarpon and bonefish fisheries. CRC Press, Boca Raton, pp 301–322

Larkin MF, Ault JS, Humston R, Luo J (2010) A mail survey to estimate the fishery dynamics of southern Florida's bonefish charter fleet. Fish Manag Ecol 17:254–261

Lecchini D, Dixson DL, Lecellier G, Roux N, Frédérich B, Besson M, Tanaka Y, Banaigs B, Nakamura Y (2017) Habitat selection by marine larvae in changing chemical environments. Mar Pollut Bull 114:210–217

Lennox R, Filous A, Danylchuk S et al (2017) Factors influencing post-release predation for a catch-and-release tropical flats fishery with a high predator burden. N Am J Fish Manag 37: 1045–1053

Lewin W-C, Arlinghaus R, Mehner T (2006) Documented and potential biological impacts of recreational fishing: insights for management and conservation. Rev Fish Sci 14:305–367

Liston SE, Frezza PE, Robinson M, Lorenz JJ (2013) Assessment of benthic Fauna communities on Florida keys' shallow banks as an Indicator of prey availability for bonefish (*Albula vulpes*). Vero Beach, Florida

Lorenz JJ (2014) A review of the effects of altered hydrology and salinity on vertebrate fauna and their habitats in northeastern Florida bay. Wetlands 34:189–200

Maddox E (2006) Temporal patterns in the ingress of settlement-stage gray snapper (*Lutjanus griseus*) and other fishes to Biscayne Bay, Florida, and the Caicos Bank, Turks and Caicos Islands. Thesis dissertation, University of Miami

McClenachan L (2009) Documenting loss of large trophy fish from the Florida keys with historical photographs. Conserv Biol 23:636–643

McIvor CC, Ley JA, Bjork RD (1994) Changes in freshwater inflow from the Everglades to Florida bay including effects on biota and biotic processes: a review. In: Davis S, Ogden JC (eds) Everglades: the ecosystem and its restoration. St Lucie Press, Boca Raton

Miles CJ, Pfeuffer RJ (1997) Pesticides in canals of South Florida. Arch Environ Contam Toxicol 32:337–345

Mojica R Jr, Shenker JM, Harnden CW, Wagner DE (1995) Recruitment of bonefish, *Albula vulpes*, around lee Stocking Island, Bahamas. Fish Bull 93:666–674

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

Murchie KJ, Cooke SJ, Danylchuk AJ, Danylchuk SE, Goldberg TL, Suski CD, Philipp DP (2013) Movement patterns of bonefish (*Albula vulpes*) in tidal creeks and coastal waters of Eleuthera, the Bahamas. Fish Res 147:404–412

Murchie KJ, Shultz AD, Stein JA, Cooke SJ, Lewis J, Franklin J, Vincent G, Brooks EJ, Claussen JE, Philipp DP (2015) Defining adult bonefish (*Albula vulpes*) movement corridors around Grand Bahama in the Bahamian archipelago. Environ Biol Fish 98:2203–2212

NOAA (2016) National Oceanic and Atmopheric Administration - Florida Keys National Marine Sanctuary. http://floridakeys.noaa.gov/about/welcome.html?s=about

Nye JA, Baker MR, Bell R, Kenny A, Kilbourne KH, Friedland KD, Martino E, Stachura MM, van Houtan KS, Wood R (2014) Ecosystem effects of the Atlantic multidecadal oscillation. J Mar Syst 133:103–116

Orth RJ, Carruthers TIMJB, Dennison WC, Duarte CM (2006) A global crisis for seagrass ecosystems 56:987–997

Palanikumar L, Kumaraguru AK, Ramakritinan CM, Anand M (2013) Toxicity, feeding rate and growth rate response to sub-lethal concentrations of Anthracene and Benzo [a] Pyrene in milkfish Chanos chanos (Forsskal). Bull Environ Contam Toxicol 90:60–68

Pandolfi JM, Bradbury RH, Sala E et al (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958

Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limnol Oceanogr 49:1964–1979

Pauly D, Christensen V, Dalsgaard J et al (1998) Fishing down marine food webs. Science 279:860–863

Pfeiler E (1984) Effect of salinity on water and salt balance in metamorphosing bonefish (*Albula*) leptocephali. J Exp Mar Biol Ecol 82:183–190

Pfeiler E (2000) Growth rate, age and size of bonefish from the Gulf of California. J Fish Biol 56:448–453

Pfeiler E (2008) Physiological ecology of developing bonefish larvae. In: Ault JS (ed) Biology and Management of the World Tarpon and Bonefish Fisheries. CRC Press, Boca Raton, pp 345–347

Pikitch EK, Santora C, Babcock EA et al (2004) Ecosystem-based fishery management. Science 305:346–347

Porter J (ed) (2001) The Everglades, Florida bay, and coral reefs of the Florida keys: an ecosystem sourcebook. CRC Press, Boca Raton

Post JR, Sullivan M, Cox S, Lester NP, Walters CJ, Parkinson EA, Paul AJ, Jackson L, Shuter BJ (2002) Canada's recreational fisheries : the invisible collapse? Fisheries 27:6–17

Rehage JS, Beck CP, Santos RO, Gardinali P (2016) The potential effects of chemical contaminants on South Florida bonefish *Albula vulpes*. Florida International University

Robblee MB, Barber TR, Jr PRC et al (1991) Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida bay (USA). Mar Ecol Prog Ser 71:297–299

Roberts CM (1995) Effects of fishing on the ecosystem structure of coral reefs. Conserv Biol 9:988–995

Rosenberg AA (2003) Managing to the margins: the overexploitation of fisheries. Front Ecol Environ 1:102–106

Rudnick DT, Ortner PB, Browder JA, Davis SM (2005) A conceptual ecological model of Florida Bay. Wetlands 25:870–883

Rudnick D, Madden C, Kelly S, et al (2006) Report on algae blooms in eastern Florida bay and southern Biscayne Bay. South Florida Water Management District

Santos RO, Lirman D, Serafy JE (2011) Quantifying freshwater-induced fragmentation of submerged aquatic vegetation communities using a multi-scale landscape ecology approach. Mar Ecol Prog Ser 427:233–246. https://doi.org/10.3354/meps08996

Santos RO, Rehage JS, Adams AJ, Black BD, Osborne J, Kroloff EK (2017) Quantitative assessment of a data-limited recreational bonefish fishery using a time-series of fishing guides reports. PLoS One 12:e0184776

Santos RO, Rehage JS, Kroloff EKN, Heinen JE, Adams AJ (2018a) Combining data sources to elucidate spatial patterns in recreational catch and effort: fisheries-dependent data and local ecological knowledge applied to the South Florida bonefish fishery. Environ Biol Fish

Santos RO, Schinbeckler R, Viadero N, Rehage JS, Larkin MF, Rennert J, Shenker J (2018b) Linking bonefish (*Albula vulpes*) populations to nearshore estuarine habitats using an otolith microchemistry approach. Environ Biol Fish

Sargent FJ, Leary TJ, Crewz DW, Kruer CR (1995) Scarring of Florida's seagrasses: assessment and management options. Florida Mar Res Inst Tech Reports 37

Shenker JM, Maddox ED, Wishinski E, Pearl A, Thorrold SR, Smith N (1993) Onshore transport of settlement-stage Nassau grouper Epinephelus striatus and other fishes in Exuma sound, Bahamas. Mar Ecol Prog Ser 98:31–43

Sheridan SC (2003) North American weather-type frequency and teleconnection indices. Int J Climatol 23:27–45

Shultz AD, Murchie KJ, Griffith C, Cooke SJ, Danylchuk AJ, Goldberg TL, Suski CD (2011) Impacts of dissolved oxygen on the behavior and physiology of bonefish: implications for live-release angling tournaments. J Exp Mar Biol Ecol 402: 19–26

Shultz AD, Zuckerman ZC, Suski CD (2016) Thermal tolerance of nearshore fishes across seasons: implications for coastal fish communities in a changing climate. Mar Biol 163:83

Siebeck UE, O'Connor J, Braun C, Leis JM (2015) Do human activities influence survival and orientation abilities of larval fishes in the ocean? Integr Zool 10:65–82

Sklar FH, Browder JA (1998) Coastal environmental impacts brought about by alterations to freshwater flow in the Gulf of Mexico. Environ Manag 22:547–562

Sklar FH, Chimney MJ, Newman S et al (2005) The ecological - societal underpinnings of Everglades restoration. Front Ecol Environ 3:161–169

Snodgrass D, Crabtree RE, Serafy JE (2008) Abundance, growth, and diet of young-of-the-year bonefish (*Albula* spp.) off the Florida keys, U.S.A. Bull Mar Sci 82:185–193

Sosin M (2008) Memories of the Florida keys. In: Ault JS (ed) Biology and Management of the World Tarpon and Bonefish Fisheries. CRC Press, Boca Raton, pp 345–347

Stevens PW, Blewett DA, Boucek RE, Rehage JS, Winner BL, Young JM, Whittington JA, Paperno R (2016) Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in southern Florida. Ecosphere 7. https://doi.org/10.1002/ecs2.1400

Strong AM, Bancroft GT (1994) Patterns of deforestation and fragmentation of mangrove and deciduous seasonal forests in the upper Florida keys. Bull Mar Sci 54:795–804

Szekeres P, Brownscombe JW, Cull F, Danylchuk AJ, Shultz AD, Suski CD, Murchie KJ, Cooke SJ (2014) Physiological and behavioural consequences of cold shock on bonefish (*Albula vulpes*) in the Bahamas. J Exp Mar Biol Ecol 459:1–7

Szekeres P, Eliason E, Lapointe D, Donaldson MR, Brownscombe JW, Cooke SJ (2016) On the neglected cold side of climate change and what it means to fish. Clim Res 69:239–245

Thayer GW, Powell AB, Hoss DE (1999) Composition of larval, juvenile, and small adult fishes relative to changes in environmental conditions in Florida bay. Estuaries 22:518–533

Thorrold SR, Shenker JM, Maddox ED, Mojica R, Wishinski E (1994) Larval supply of shorefishes to nursery habitats around lee Stocking Island, Bahamas. II. Lunar and oceanographic influences. Mar Biol 118:567–578

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

Vavrus S, Walsh JE, Chapman WL, Portis D (2006) The behavior of extreme cold air outbreaks under greenhouse warming. Int J Climatol 26:1133–1147

Vethaak AD, ap Rheinallt T (1992) Fish disease as a monitor for marine pollution: the case of the North Sea. Rev Fish Biol Fish 2:1–32

Wallace EM (2014) Assessing biodiversity, evolution, and biogeography in bonefishes (Albuliformes): resolving relationships and aiding management. Thesis dissertation, University of Minnesota

Wallace EM, Tringali MD (2016) Fishery composition and evidence of population structure and hybridization in the Atlantic bonefish species complex (*Albula* spp.). Mar Biol 163:142

Wedemeyer GA, Goodyear CP (1984) Disease caused by environmental stressors. In: diseases of marine animals. Volume IV, part 1: introduction, Pisces. John Wiley & Sons and the Biologische Anstalt Helgoland, pp 424–434

Werner I, Hitzfeld B (2012) 50 years of ecotoxicology since silent spring – a review. GAIA - Ecol Perspect Sci Soc 21:217–224

Wilde GR (1998) Tournament-associated mortality in black bass. Fisheries 23:12–22

Zeitoun MM, Sayed E, Mehana E (2014) Impact of water pollution with heavy metals on fish health: overview and updates. Glob Vet 12:219–231

Zhang J-Z, Kelble CR, Fischer CJ, Moore L (2009) Hurricane Katrina induced nutrient runoff from an agricultural area to coastal waters in Biscayne Bay, Florida. Estuar Coast Shelf Sci 84:209–218

Zieman JC (1976) The ecological effects of physical damage from motor boats on turtle grass beds in southern Florida. Aquat Bot 2:127–139