



Cascading effects of climate change on recreational marine flats fishes and fisheries

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Abstract Tropical and subtropical coastal flats are shallow regions of the marine environment at the intersection of land and sea. These regions provide myriad ecological goods and services, including recreational fisheries focused on flats-inhabiting fishes such as bonefish, tarpon, and permit. The cascading effects of climate change have the potential to negatively impact coastal flats around the globe and to

reduce their ecological and economic value. In this paper, we consider how the combined effects of climate change, including extremes in temperature and precipitation regimes, sea level rise, and changes in nutrient dynamics, are causing rapid and potentially permanent changes to the structure and function of tropical and subtropical flats ecosystems. We then apply the available science on recreationally

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targeted fishes to reveal how these changes can cascade through layers of biological organization—from individuals, to populations, to communities—and ultimately impact the coastal systems that depend on them. We identify critical gaps in knowledge related to the extent and severity of these effects, and how such gaps influence the effectiveness of conservation, management, policy, and grassroots stewardship efforts.

Keywords Recreational fisheries · Flats fishing · Nearshore · Tropical · Subtropical · Climate change · Management

Introduction

Under current projections, climate change is expected to drastically alter the function and structure of ecosystems across the globe (Hoegh-Guldberg et al. 2019). In 2017, the global mean surface temperature reached 1 °C above the pre-industrial period (IPCC 2018), and unless deep reductions in greenhouse gas emissions occur, it is projected to exceed 1.5 °C and 2 °C during the twenty-first century (IPCC 2021). As global mean surface temperatures have continued to increase, widespread changes have already occurred at both global and regional scales (IPCC 2021), including increased frequency and/or duration of heatwaves across North America, Europe, and Australia, higher numbers of intense cyclones in many areas (Hoegh-Guldberg and Bruno 2010), increased precipitation rates during cyclones (Hoegh-Guldberg and Bruno 2010; Risser and Wehner 2017), and longer droughts in mid- and high-latitude regions (Gudmundsson et al. 2017; Mathbout et al. 2018).

Marine ecosystems and the many services they provide may be particularly vulnerable to climate change, specifically episodic climatic events (e.g., heatwaves, cyclones, storm-induced cold shock events), sea level rise, ocean acidification, deoxygenation, and feedback loops among these changes (Hoegh-Guldberg and Bruno 2010; Pörtner et al. 2014; Gattuso et al. 2015, IPCC 2021). Although these effects and their consequences differ from location to location, such as for sea level rise (Yin et al. 2010; Kopp et al. 2014, 2017; Marsooli et al. 2019) and cyclone frequency and intensity (Bender et al. 2010; Emanuel 2013; Knutson et al. 2015; Murakami et al. 2017), low lying tropical and subtropical coastal and island communities are some

of the most vulnerable to the threats of climate change (Hare et al. 2011; Connell 2015). For example, Pacific Island nations, such as The Republic of the Marshall Islands, are likely to become uninhabitable by the mid-twenty-first century due to sea-level rise, related flooding, and saltwater inundation of freshwater (Storlazzi et al. 2018). Similarly, coastal flooding from tropical cyclones, in combination with sea level rise, is expected to worsen in the southeastern USA Atlantic and Gulf of Mexico regions. These areas are predicted to experience 100-year historic level floods as frequently as every 1–30 years by the late twenty-first century (Marsooli et al. 2019). These factors interact with anthropogenic effects, such as overfishing, loss, and degradation of habitats that buffer coasts from sea level rise and erosion (especially wetlands), anthropogenic structures (e.g., seawalls), and water management practices (e.g., drainage and pollution run-off). As climate change continues to increase regional precipitation and flooding, seaward nutrient pulses, particularly of nitrogen and phosphorous, are expected to continue to occur along coastal regions (Paerl et al. 2016) leading to nutrient-over enrichment, harmful algal blooms, and ultimately eutrophication and “dead zones” (Paerl and Scott 2010; Moss et al. 2011).

In some coastal areas, differential heating of the water column may lead to stronger and deeper thermoclines, potentially preventing nutrient-rich waters from being upwelled (Roemmich and McGowan 1995) and thus dramatically altering coastal marine systems and the fisheries that depend on these ecological cycles (Harley et al. 2006; Hoegh-Guldberg et al. 2019). Overall, marine heatwave duration and intensity have increased by a factor of 3 since 1980 and are expected to increase even more (Smale et al. 2019). Moreover, storm-induced cold shock events could also harm fish assemblages (Szekeres et al. 2016), which occurred in 2010 causing widespread mortality of marine fishes in South Florida, including flats species (Adams et al. 2012; Stevens et al. 2016). As oceans continue to absorb large percentages of anthropogenic CO₂ emissions (Feely et al. 2004; Sabine et al. 2004; le Quéré et al. 2009), oceanic pH levels have dropped (Harley et al. 2006; Gattuso et al. 2015), with this acidification proving detrimental to calcifying organisms (e.g., shellfish, zooplankton, and coral reefs). Expected increases in ocean acidification exceed any observed pH changes over the past 200–300 million years (Caldeira and Wickett 2003;

Feely et al. 2004) making adaptation difficult for many marine species (Harley et al. 2006).

Shallow, nearshore areas of the marine environment are ecotones between the shoreline, the intertidal zone, and open coastal waters (Barbier et al. 2011; Alongi 2020). As such, nearshore coastal marine habitats are naturally prone to physiochemical extremes that, in turn, make these regions highly dynamic. For instance, intertidal water movement and peaks in the lunar cycle can leave the benthos of nearshore coastal marine zones exposed at low tides. The relatively shallow depth gradient of these areas also means that water movement can be easily accentuated by wind and waves. Furthermore, shallow depths of these regions can result in extremes in water temperature (Amos et al. 2013), depending on the extent of water movement and ambient conditions. The same is true for salinity gradients, subject to the extent of freshwater discharge from rivers, coastal precipitation regimes, and groundwater flow. Collectively, these factors contribute to nutrient loading and primary production that ultimately shape nearshore biotic communities, benthic habitats, and the fishes that rely on these regions (Lo-Yat et al. 2011).

Tropical and subtropical nearshore and estuarine ecosystems provide immense economic goods, services, and values to human societies, including extractive commercial fisheries, tourism, and recreation (reviewed in Barbier et al. 2011). For recreational anglers, shallow nearshore tropical and subtropical areas are easily accessible and able to be traversed on foot or in small boats, offering a diverse range of target species (Fig. 1, Table 1). This provides an experience where fish can be seen in the water and pursued selectively (i.e., “sight fishing”). Indeed, flats fishing contributes greatly to the economic well-being of coastal communities in developed and developing nations (Fedler 2010, 2013; Wood et al. 2013; Smith et al. In review; Perez et al. 2020).

Many books have been written specifically about flats fishing in tropical and subtropical waters (e.g., Sosin and Kreh 1988; Maizler 2007; Mill 2010; Olch 2017; Horn 2021), with angling strategies for particular target species ranging across spatial and temporal scales that often transcend the partitioning of benthic habitat types typically used by oceanographers. In other words, the spatial and temporal scales by which fish use these habitats may not match the way we have classically partitioned the nearshore coastal zone, and

some fish species may depend on a suite of flats habitats including seagrass beds, mangroves, coral reefs, and even pelagic waters throughout their life histories (Adams 2017). As such, treating these shallow, coastal habitat mosaics (Adams 2017) collectively as “flats” may permit an examination of how fishes in these areas respond to natural and anthropogenic disturbances through their ontogeny, as well as better reflect the way management agencies tend to structure their policies and regulations related to flats fisheries.

Despite overwhelming evidence that climate change is impacting marine ecosystems around the globe (Allison and Bassett 2015; Aswani et al. 2018; He and Silliman 2019), we are only beginning to understand the interactions between climate change and other anthropogenic impacts (e.g., dredging, pollution, overharvest) on marine ecosystems in general (Roessig et al. 2004; Harter et al. 2015; Jones and Cheung 2015) and nearshore coastal environments in particular (Breitburg and Riedel 2005; Crain et al. 2009; Hewitt et al. 2016). Fish that utilize these shallow, nearshore areas will certainly be impacted by climate change (Roessig et al. 2004); however, managing for predicted future scenarios remains difficult. Moreover, marine fisheries management is largely species-specific and does not typically incorporate habitat-related considerations, such that recognizing the broader defining framework of tropical and subtropical flats as a collective conservation and management unit may be prudent (Adams 2017).

Objectives

This paper provides an overview of the current knowledge of how climate change in the Anthropocene has impacted, and will likely continue to impact, recreationally targeted fishes that utilize tropical and subtropical coastal flats for most or all of their life history. The principles and evidence presented here could apply to many fisheries, but our aim is to examine the effects of climate change on tropical and subtropical flats fisheries and habitats across the individual, population, and ecosystem levels. We recognize that non-game fishes are also important and generate diverse ecosystem services, but these are beyond the scope of this review. Moreover, since flats fishes can be used as proxies for broader conservation and management (e.g., common snook used as a

Fig. 1 Images of commonly targeted fish species in the recreational subtropical and tropical flats fishery. **(a)** Bonefish (*Albula glossodonta*). **(b)** Common snook (*Centropomus undecimalis*). **(c)** Red drum/redfish (*Sciaenops ocellatus*). **(d)** Atlantic tarpon (*Megalops atlanticus*). **(e)** Permit (*Trachinotus falcatus*). **(f)** Giant trevally (*Caranx ignobilis*). Photo credits. **(a)** Brad Simpson/Alphonse Fishing Company. **(b)** Adrian Gray. **(c)** Steve Signberg. **(d)** Capt. Benny Blanco. **(e)** Capt. James Johnson. **(f)** Andy Danylchuk



flagship umbrella species, Wilson et al. 2022), focus on flats species should provide information relevant to these habitat systems as a whole. We also use current climate change models and projections to draw predictions of how further changes in factors such as water temperature, sea level rise, and nutrient dynamics will impact fish that use tropical and subtropical coastal flats and the associated recreational flats fisheries. Furthermore, we have attempted to combine

information and perspectives from academia, stakeholders, rightsholders, and managers, because such transdisciplinary perspectives greatly enhance studies attempting to understand the implications of environmental issues such as climate change (Kelly et al. 2019). Lastly, we discuss knowledge gaps that inhibit our understanding of how fish inhabiting coastal flats will respond to further physiochemical changes linked to climate change, as well as management challenges

Table 1 Subtropical and tropical species commonly targeted by recreational anglers in exemplar flats fisheries

| Common name | Genus species | Exemplar flats fisheries | Source |
|------------------------------------|---------------------------------------|----------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------|
| Bonefish | <i>Albula vulpes</i> | Florida Keys, Bahamas, Western and Northern Caribbean, Bermuda | Kaufmann 2000; Adams 2003, 2012; Danylchuk et al. 2007a, b, c; Fernandez and Adams 2017 |
| Bonefish (shortjaw) | <i>Albula glossodonta</i> | Indo-Pacific (Hawaii, Kiribati, French Polynesia) | Kaufmann 2000; Fernandez and Adams 2017 |
| Atlantic tarpon | <i>Megalops atlanticus</i> | Florida Keys, Gulf of Mexico, SE Florida-Carolinas, Bahamas, Caribbean, West Africa (Gabon, Congo) | Mill 2010; White and Brennen 2010; Horn 2021 |
| Permit (Atlantic) | <i>Trachinotus falcatus</i> | Florida Key, Eastern Gulf of Mexico, Bahamas, Caribbean | Olch 2017; Kaufmann 2000; Adams 2003, 2012 |
| Indo-Pacific permit/silver pompano | <i>Trachinotus blochii</i> | Indo-Pacific (Seychelles, Oman) | Olch 2017; Griffin et al. 2021 |
| Common snook | <i>Centropomus undecimalis</i> | SE Florida, Gulf of Mexico, Western Caribbean (Yucatan) | Sargeant 1990; Kaufmann 2000; Adams 2003, 2012 |
| Red drum/redfish | <i>Sciaenops ocellatus</i> | SE Florida-Carolinas, Gulf of Mexico | Sargeant 1991; Adams 2003, 2012; Fernandez and Adams 2015 |
| Speckled/spotted seatrout | <i>Cynoscion nebulosus</i> | South Florida-Carolinas, Gulf of Mexico | Maizler 2014 |
| Barramundi | <i>Lates calcarifer</i> | Northern Australia | Eussen 1999 |
| Giant trevally | <i>Caranx ignobilis</i> | Indo-Pacific (Seychelles, Kiribati, French Polynesia,) | Kaufmann 2000; McLeod 2017; Griffin et al. 2021 |
| Bluefin trevally | <i>Caranx melampygus</i> | Indo-Pacific (Seychelles, Kiribati, French Polynesia) | Kaufmann 2000; Griffin et al. 2021 |
| Milkfish | <i>Chanos chanos</i> | Indo-Pacific (Seychelles, Kiribati) | Kaufmann 2000; Griffin et al. 2021 |
| Yellow margin triggerfish | <i>Pseudobalistes flavimarginatus</i> | Indo-Pacific (Seychelles, Kiribati, French Polynesia) | Griffin et al. 2021 |
| Mustache triggerfish | <i>Balistoides viridescens</i> | Indo-Pacific (Seychelles, Kiribati, French Polynesia) | Griffin et al. 2021 |

as we work toward conserving coastal flats and their essential habitats in the face of growing anthropogenic disturbances.

Individual-level effects

Climate change is often viewed in terms of how it influences the distribution of animals and their persistence (Roesig et al. 2004), such as with the poleward shift of common snook (*Centropomus undecimalis*); Purtlebaugh et al. 2020). Yet, underpinning these ecological patterns is a physiological constraint of individual fish (Portner and Farrell 2008). It is individual fish and their relative performance that drive selection and related population-level processes (see next

section). Water temperature is considered the master environmental factor in fish (being ectotherms) given the manifold effects it has on individuals ranging from molecules, to cells, to organ systems, to the whole body (see Brett 1971; Fry 1971). Water temperature therefore is a key regulator and constraint on feeding, digestion, locomotion, growth, reproductive development, reproductive activities, and immune function (Brett and Groves 1979). Organisms in the tropics and subtropics, including many species of fish targeted by anglers, experience a relatively narrow range of temperatures during their lives compared with organisms in temperate regions. As such, they have adapted to these narrow thermal environments to minimize maintenance costs and thus thermal variation anticipated with climate change may be

particularly harmful to fish residing in such regions (Pörtner and Farrell 2008). As mentioned above, beyond water temperature, climate change is expected to alter the pH (Doney et al. 2009) and salinity (due to changes in precipitation, freshwater runoff, and evaporation; Scavia et al. 2002) of coastal flats ecosystems. Here, we review what is known about the effects of climate change on flats fishes at the individual-level. Our efforts in this section focus primarily on changes in water temperature given the relatively large body of research on the topic, but we also consider other climate change issues such as ocean acidification and salinity.

One of the most rudimentary ways of assessing the effects of water temperature on fish is to define basic thermal tolerances, including critical thermal maxima [CT_{max}] and optimal temperatures (Somero 2010; Bates and Morley 2020). Yet, for most fish species that reside in coastal flats, this basic information does not exist, or if it does, it is speculative and based on field observations where animals are observed relative to different thermal conditions. Shultz et al. (2016) assessed the CT_{max} for three flats species in The Bahamas, including the checkered puffer (*Sphoeroides testudineus*), yellowfin mojarra (*Gerres cinereus*), and bonefish (*Albula vulpes*), and found the CT_{max} for all three was almost 3 °C higher in summer (i.e., ~37 °C) compared to winter (34 °C). However, the maximum environmental temperature of 43 °C measured in the nearshore environment exceeded the summer CT_{max} of the species by more than 1 °C, 2 °C, and almost 5 °C, respectively (Shultz et al. 2016). Sudden or prolonged exposure to exceedingly high water temperatures could limit the distribution of fish residing in coastal flats, impact metabolic rates, and lead to mortality. Murchie et al. (2011) used an acoustic telemetry array to monitor bonefish (*A. vulpes*) movements coupled with hourly temperature data collected within tidal creeks, and found the majority of bonefish spent most of their time at the creek mouth where changes in water temperature are moderate compared to adjacent open ocean and backwater habitats. Bonefish avoided upper reaches of the tidal creeks when water temperatures approached CT_{max}. Subsequently, Murchie et al. (2011) then held bonefish in the laboratory after reaching CT_{max} temperatures which yielded a stress response that included an increase in blood lactate, glucose, and potassium. As flats fishes are pushed to

the edge of their thermal tolerance, sublethal effects become evident.

Warming waters may have dramatic effects on the bioenergetics of flats fishes that will influence respiration, other aspects of metabolism, and swimming performance. Fishes in general tend to exhibit metabolic traits that reflect the conditions of their ecosystem (Eliason et al. 2011), including flats fishes (Vetter 1982; Song et al. 2019), which raises concerns over impacts of rapidly warming waters. Despite living in coastal waters that can get quite warm, flats fishes exhibit relatively moderate metabolic rates that likely reflect adaptations to function in these systems (Vetter 1982; Tolley and Torres 2002; Nowell et al. 2015; Song et al. 2019). Nowell et al. (2015) found that bonefish (*A. vulpes*) in The Bahamas exhibit optimal metabolic and swimming performance around 27 °C, with sharp declines above 32 °C, at which they experience high energetic costs but limited capacity for swimming and digestion. Monitoring bonefish (*A. vulpes*) within a natural tidal creek system, Nowell et al. (2015) further noted that under potential temperature increases of 1 °C, 2 °C, 3 °C, and 4 °C, temperatures would exceed bonefish critical temperature threshold 1.48, 2.88, 5.40, and 9.58% of the time, respectively. Similarly, Brownscombe et al. (2017) found that bonefish (*A. vulpes*) in Puerto Rico selectively occupy shallow nearshore flats within a temperature window that corresponds to these optima, avoiding upper thermal extremes when their energetics are suboptimal. Examining seasonal variation in bonefish energy stores, Murchie et al. (2010) found that larger, reproductively active bonefish (*A. vulpes*) acquire energy stores in the warmer months and expend them in the winter when they spawn. This raises concerns for flats fishes over how warmer waters may exacerbate energetic costs during spawning periods, or limit energetic gains in the summer due to high costs of coastal foraging or higher rates of thermal exclusion as temperatures more frequently exceed those to which fish are physiologically adapted.

Although warming waters may have concerning impacts on the energetics of flats fishes, fish physiology can be flexible, as evidenced by the fact that bonefish (*A. vulpes*) CT_{max} values vary substantially among seasons depending on acclimation temperature (Shultz et al. 2016). Furthermore, since metabolic

rates are also heritable, phenotypic and genotypic variation may help fish adapt to long-term changes in climate (Brownscombe et al. 2022). For example, in spotted seatrout (*Cynoscion nebulosus*), upper thermal tolerances also appear to vary widely among populations and body sizes (Vetter 1982; MacDonald 2013; Song et al. 2019). Indeed, Song et al. (2019) compared two populations of spotted seatrout across a latitudinal gradient and found the southern population maintained significantly lower metabolic rates at relatively high water temperatures than the northern population, with potential implications for the impacts of climate change.

Coastal ecosystems are highly dynamic, and fish exhibit a range of behavioral and related physiological characteristics to utilize these systems (Vetter 1982; Brownscombe et al. 2017). The extent to which fish may be capable of adapting behaviorally and physiologically to the rate of changing water conditions due to climate change is generally not well known and a key determinant of the degree to which climate change will impact their energetics, and more broadly, their populations. There is also often a complex relationship between fish energetics and life history traits including maturation and reproductive output (e.g., Young et al. 2020), which will influence how changes in energetics may result in altered population dynamics for flats fishes. Although the degree to which changing ocean conditions will impact flats fishes is not totally clear, given they live in such thermally extreme shallow coastal habitats, often near thermal maxima, it certainly allows for potential to have negative impacts on their bioenergetics, which in turn may influence individual fitness and population dynamics.

Water temperatures or other environmental conditions (pH or salinity) that approach tolerances can impart physiological disturbances and lead to a glucocorticoid stress response. Using tissue samples, such as blood, muscle, and liver, and biochemical assays, it is possible to characterize how fish respond to different environmental challenges (Sopinka et al. 2016). Some experiments have been conducted on a number of intertidal species (see Lam et al. 2006) but relatively little is known about flats fishes. In one of the few exceptions, Shultz et al. (2014) exposed bonefish (*A. vulpes*) to a 30-min increase in salinity (50 ppt), acidity (decrease in pH by 0.5 units),

temperature (7–10 °C), or temperature and acidity combined. Fish were then held in these conditions for 6 h after which they were blood sampled. The experiments were repeated in summer and winter. Bonefish exposed to the environmental challenges in the summer experienced osmotic and ionic disturbances relative to fish held in ambient conditions. The thermal challenges were evidently the most challenging to fish, particularly during the summer months where thermal increases approached their CTmax. Because of strong tidal influence on coastal flats, thermal environmental variation is the norm and can vary widely across a 24-h period. Nonetheless, there are limits, as noted here, where fish must move or experience sublethal alterations that will presumably impact fitness. Sublethal physiological alterations could then, in turn, have impacts on other individual-level traits, such as growth. For example, Neuheimer et al. (2011) showed that increasing temperature initially increased fish growth rates, but ultimately reduced growth rates due to thermally induced metabolic stress for animals in the warmest portions of a species range. Considering some low-latitude fish species already live at or just above their thermal optima, increased temperatures from climate change could drastically affect individuals if unable to adapt (Rummer et al. 2014).

Although we have largely focused on the idea that water temperature will increase in the face of climate change, there is also an expectation of increased variation. As such, cold shock events may become more common, further challenging coastal fish. This has already been observed in recent decades with an increasing number of massive fish kill events documented in coastal waters. For example, in January 2010, Florida (USA) experienced a 12-day cold period leading to decreases in water temperature of over 10 °C (NOAA 2010; Adams et al. 2012). The massive fish kill that ensued included a variety of species resulting in a 60–80% decline in the common snook population (Adams et al. 2012; Muller and Taylor 2014; Stevens et al. 2016; Santos et al. 2020) and likely accelerating a long-term decline of bonefish (*A. vulpes*) (Santos et al. 2017; Brownscombe et al. 2019a). Other such fish kills of various scales have also been reported to occur around the globe when weather-driven cold shock occurs in tropical and sub-tropical zones (e.g., Bohnsack, 1983, Cyrus and McLean, 1996,

Lamadrid-Rose and Boehlert 1988; reviewed in Szekeres et al. 2016).

Although there is a rather large body of literature on cold shock (see Donaldson et al. 2008), comparatively little is known about its impacts on coastal flats fishes. One of the only studies on the topic focused on bonefish (*A. vulpes*; Szekeres et al. 2014). The authors assessed the sub-lethal physiological and behavioral consequences of cold shock on bonefish by exposing fish to 2-h cold shocks that were either 7 °C or 14 °C below ambient conditions. The bonefish exposed to the more extreme cold shock event (i.e., 14 °C below ambient) had elevated blood lactate concentrations and exhibited impaired reflexes. Cold shock also impaired swimming ability. Based on these findings, the authors concluded that abrupt declines in water temperature in coastal flats > 7 °C due to storm events or upwelling have the potential to cause physiological and behavioral impairment that could lead to mortality in bonefish (and presumably other flats fishes). More recently, Mace et al. (2017) studied the cold tolerance of juvenile Atlantic tarpon (*Megalops atlanticus*) with a focus on a population near the northern edge of the juvenile range (i.e., the South Atlantic Bight north of Florida). When they combined their data with all published information on the cold tolerance of juvenile Atlantic tarpon (see Moffett and Randall 1957; Howells 1985), the authors revealed an overall mean minimum lethal temperature of 12.0 °C. However, less is known about sublethal impacts of cold temperatures and about rapid temperature declines on Atlantic tarpon. Clearly, more work is needed to understand the resilience of flats fishes to extreme climate events including cold shock (Boucek et al. 2016).

Above we have focused largely on adults or juveniles, but climate change will also have dramatic effects on individuals in early life stages of fishes (e.g., fertilized eggs, larval growth). The impact of changing thermal regimes may have dramatic effects on larval growth and survival (reviewed in Pankhurst and Munday 2011), and influence recruitment into juvenile and adult populations. For example, larval Atlantic tarpon are transported by currents for 15–26 days post-spawning before settling (Shenker et al. 2002) in coastal marsh habitats. In the USA, juvenile Atlantic tarpon have been found in a wide array of natural and anthropogenically altered marshes (e.g., mosquito control and

rice agriculture impoundments, drainage ditches, restored wetlands) from the Florida Keys through peninsular and panhandle Florida, into Georgia and South Carolina, as well as northern Gulf of Mexico states. Wade (1962) found juvenile Atlantic tarpon in hurricane-overwash ponds, and Shenker et al. (2002) observed larval recruitment into the Indian River Lagoon on the east coast of Florida was dramatically enhanced by hurricane-driven cross-shelf transport. Altered hurricane regimes associated with climate change may thus affect the magnitude and location of pulses of larval Atlantic tarpon recruitment.

Once larval Atlantic tarpon enter their coastal marsh nurseries in summer or early fall, their euryhaline and eurythermal physiological capabilities enable them to withstand salinities from near zero to over 40 ppt, and temperatures up to at least 36 °C (Geiger et al. 2000). Their vascularized swim bladder enables them to gulp air from the surface even under virtually anoxic conditions (Geiger et al. 2000), suggesting that the effect of increasing temperature on dissolved oxygen concentrations in nursery habitats may have minimal impact on respiration and post-settlement survival. However, newly recruited juvenile Atlantic tarpon that are found within northern Gulf of Mexico and South Carolina marshes in summer and fall could be negatively impacted by extreme temperature swings indicative of climate change, with cold winter temperatures preventing their survival within shallow water habitats (Graham et al. 2017; Mace et al. 2017, 2018). Thermal refugia in deeper portions of a South Carolina impounded pond, however, appeared to allow some overwinter survival of juvenile Atlantic tarpon (Mace et al. 2020). This observation suggests that increasing temperatures may actually result in an expansion of nursery habitats along the southeastern US coastline. Examination of United States Geological Service water temperature records in several coastal regions show wide interannual variation in lowest winter temperature. For example, the lowest temperatures measured at Back Bay, Biloxi, MS, site (USGS station 02,481,270) from 2007 to 2021 included 5 years where temperatures dropped to or below 10 °C for only 1–2 days in a winter, reaching a level where local thermal refugia could potentially permit some overwinter survival. Conversely, six winters had temperatures below 7 °C, most likely preventing juvenile Atlantic tarpon survival in

those winters. As the frequency of warmer winters increases in coming decades, the potential Atlantic tarpon nursery function of marshes in the northern Gulf of Mexico and along the southeastern USA may thus increase.

Population-level effects

Individual-level physiological changes can have cascading effects on population dynamics (Louthan et al. 2021). Impacts, both positive and negative, on growth, reproduction, and survival resulting from climate change may be mechanisms through which climate change ultimately impacts the health and sustainability of flats fisheries (Chown et al. 2010). Given that our paper focuses on exploited fish species, we limit this section to discussions of productivity (somatic growth, survival, reproduction, and net migration) and capacity, with implications of fishing mortality and sub-lethal effects included under sections focused on management (below). We also recognize that the effects of climate change on populations can be compounded by other anthropogenic disturbances that have resulted in a progressive degradation of the near-shore environment, such as tidal flats (Murray et al. 2019), coral cover (De'ath et al. 2012; Bruno and Selig 2007), oyster reefs (Beck et al. 2011), seagrass (Oarth et al. 2006), mangroves (Polidoro et al. 2010), and salt marshes (Mcowen et al. 2017), which are covered later in this paper.

There are two components to productivity to consider beyond growth and fecundity—maximum productivity (i.e., productivity at low population densities) and mean average population density, in the absence of harvest removals (i.e., capacity). Maximum productivity rate is dependent upon factors that impact baseline mortality across life history stages: disease, factors that alter time spent acquiring resources, and changes to the per unit time mortality risk (i.e., predation). Capacity tends to be related to habitat quality and availability which determine the strength of competitive interactions via density-dependent relationships. There is, of course, interconnection between factors that affect these two components. Flats species may be particularly sensitive to climate impacts because of a bipartite life history that inexorably links them to nearshore environments for the juvenile component of their life history (see

Individual-level section above). Climate change could also enhance differences in regional individual growth rate because of countergradient variation (Conover 1990), and have cascading effects on population-level traits, such as mean size at age and age at maturity. For instance, growth of bonefish (*A. vulpes*) in the Florida Keys is significantly greater than growth rates in the Caribbean (Adams et al. 2008), and these differences may not be related to habitat-related drivers (Rennert et al. 2019).

A general pattern related to fisheries that emerge from climate modeling is increasing degradation of fisheries in the tropics and possible enhancement in more temperate areas (Lam et al. 2020; Blanchard et al. 2012). Within the tropics, reductions in primary productivity, habitat loss, and the compression of the suitability of species-specific envelopes will negatively impact both the maximum productivity and capacity of most tropical flats species. This is particularly true for populations around tropical islands which are the most vulnerable regions to climate impacts (Thompson et al. 2020). For tropical populations, the expectation is a reduction in productivity as well as capacity. Degradation of tropical populations will have spillover consequences in more temperate regions even if dispersal among areas is not disrupted. If source-sink dynamics maintain sub-tropical flats fish species, such as for bonefish (*A. vulpes*) in the Florida Keys, losses based on impacts to recruitment would directly impact the productivity (through reduced net migration) in sub-tropical regions even if capacity in these regions is not changed (Zeng et al. 2019).

Changes in temperature are expected to alter fish growth rates and longevity and ultimately could impact the sustainability of flats fishery resources. For example, rising temperatures are expected to increase growth rates to a point but also decrease longevity (Jensen 1996), so the levels at which fishing-induced mortalities are sustainable will be influenced by changes in expected natural mortality. Thus, increasing temperatures could ultimately result in negative population-level traits in areas where historically species flourished, causing a reduction in fish productivity. These changes are a direct threat to fish that spend all or most of their time in nearshore flats, especially since the cumulative effects of changes in physiochemical alterations caused by climate change could result in changes in fish abundance, distribution

patterns, and related association with flats habitats that are also being impacted by climate change. Slow progressive change in the underlying productivity of stocks is possible to track provided some form of monitoring is in place. However, there is also the possibility that change, particularly at the local scale, will be rapid and irreversible due to erosion of sub-stock structure or reaching a threshold that triggers population change (e.g., Boucek et al. 2022). These potential shifts in the underlying population dynamic will have immediate consequences, be difficult to anticipate, and require highly adaptable management.

Impacts to flats habitats, communities, and food webs

In recent decades, nearshore flats habitats have experienced widespread declines (Valiela et al. 2001; Alongi 2002; Green et al. 2003; Hughes 2004; Hughes et al. 2009; Polidoro et al. 2010; Waycott et al. 2011) that have led to reduced recruitment and survival of fish and impaired populations (Lotze et al. 2006). As temperatures continue to increase, range shifts in vegetated coastal habitats have been observed—vegetation that plays an important role in the structure and function of flats communities and food webs (Bates et al. 2014). Mangrove distribution is expected to continue to shift poleward (Duke et al. 1998) and replace salt marshes (Osland et al. 2013; Saintilan et al. 2014), fundamentally altering coastal ecosystems in all oceans. While mangrove species have begun to adapt with range expansion, they are vulnerable to the increased frequency of *Sargassum* spp. mats/blooms that come ashore in subtropical and tropical areas of the Caribbean, Gulf of Mexico, and southeastern coast of the USA. It has been suggested that these blooms are in-part attributed to higher sea surface temperatures and nutrient runoff in the central Atlantic (Wang et al. 2019), all of which are also in-part driven by weather patterns and climate variations (e.g., precipitation). The increasing frequency of *Sargassum* blooms or “*Sargassum* brown-tides” may have a major impact on the stability of nearshore habitats, including mangrove and seagrass habitats, and the associated flats fisheries they support (Rodríguez-Martínez et al. 2019).

With physiological thermal limits being reached, seagrass meadows are already being impacted by

warming sea surface temperatures in the Atlantic and Indo-Pacific. Increased temperatures are resulting in widespread seagrass mortality events driven by heat waves in the Mediterranean Sea (Marbà and Duarte 2010) and Australia (Rasheed and Unsworth 2011; Arias-Ortiz et al. 2018). In Florida (USA), a seagrass die-off event in 1987–1989 was driven by high summer temperatures with persistent drought conditions leading to over two decades of changes in vegetation, algal blooms, and associated declines in shrimp and sponges (Fourqurean and Robblee 1999; Zieman et al. 1999; Madden et al. 2008). In sub-tropical and tropical latitudes globally, many coastal flats rely on adjacent coral reefs to reduce wave action and, thus, provide sediment stability for seagrass meadows to flourish (Waycott et al. 2011). However, coral reefs are at risk from multiple climate stressors including increased sea surface temperatures, sea levels, storm intensity, and acidification (Kleypas et al. 1999; Keller et al. 2009; Hoegh-Guldberg and Bruno 2010; Field et al. 2011; Pandolfi et al. 2011; Lough et al. 2018). In turn, coral reefs may become bleached, vulnerable to disease, and ultimately shift to macroalgae-dominated states (Glynn 1993; Bruno et al. 2007; Hughes et al. 2018; Johns et al. 2018). Ultimately, the loss of coral reefs and seagrasses may provide cascading consequences for subtropical and tropical flats due to increased wave energy and loss of connected biological communities that support coastal flat and reef habitats (Nagelkerken et al. 2000; Dorenbosch et al. 2004, 2007; Berkström et al. 2013).

Extreme temperature events (hot and cold) result in punctuated mortalities of subtropical and tropical species that can also cause long-term and persistent habitat alterations. Extreme cold spells can cause long-term damage to mangrove forests through freeze stress. At the northern edge of their latitudinal range, extreme cold spells can change successional trajectories for coastal vegetation, where black mangroves are replaced by *Spartina* spp. Similarly, extreme heat waves can cause system wide mortalities to seagrass, an important habitat for flats fishes.

Common disturbance events that have helped naturally structure nearshore flats habitats and related communities are expected to be exacerbated by climate change in both frequency and intensity. For example, tropical cyclones are an important structuring force in the tropics and subtropics that can reset

succession in mangrove forests, increase shoreline structural complexity, increase freshwater discharges, and reduce water temperatures, all of which can have direct and indirect consequences on shallow water fisheries. Following catastrophic hurricanes, (category 4 and above), coastal ecosystems can undergo regime shifts that likely reduce the productivity of shallow water fisheries. The catastrophic 1935 Labor Day hurricane in South Florida resulted in the conversion of mangrove forests to mudflats, and an estimated elevation loss of approximately 75 cm. As hurricanes are expected to become more intense under climate change, we may expect significant alterations to nearshore habitats at such a frequency that their cascading effects on flats fishes and the food webs they are a part of are permanently altered.

The physical structure and function of flats habitats are tightly intertwined and support productive fish and invertebrate communities (Watanabe et al. 2018). For instance, mangroves and seagrass habitats offer abundant food sources and protection against predators (Nagelkerken et al. 2001, 2002; Adams et al. 2006). In these ecosystems, sharks, great barracuda (*Sphyraena barracuda*) (Cooke and Philipp 2004), osprey (*Pandion haliaetus*), and brown pelicans (*Pelecanus occidentalis*) prey on bonefish (*A. vulpes*) (Perez et al. 2020). In turn, adult bonefish (*A. vulpes*) prey on crabs, shrimps, molluscs, and occasionally on benthic fishes (Colton and Alevizon 1983; Crabtree et al. 1998) while juvenile bonefish feed on polychaetes, copepods, and amphipods (Snodgrass et al. 2008; Griffin et al. 2019). All of these flats feeding habitats are likely to change with water temperature increases and salinity variations produced by weather patterns. Once the structure and function of ecosystems and connectivity are affected, many other community level processes, including local movements and ontogenetic migrations between seagrass beds, mangroves, and coral reefs (Mumby 2005; Mumby and Hastings 2008; Perez et al. 2019), are also impacted. Indeed, flats fishes are likely already experiencing increased exposure to predators, like bull sharks (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*), whose ranges are shifting due to climate change, leading to expansion into new estuarine nursery areas (Bangley et al. 2018) and higher potential for competitive foraging among predator species as the ranges of tropical and temperate species increasingly overlap (Niella et al. 2022). With

species-specific variation in tolerances to physiochemical conditions in nearshore flats, we predict there will be differential responses to changes in these conditions caused by climate change that will have cascading effects on the foundational structure and function of nearshore flats habitats, as well as the biotic communities they support, including fishes targeted by recreational anglers.

Compounded anthropogenic effects

Changes in physiochemical properties associated with contemporary climate change are not happening in isolation from other anthropogenic disturbances and threats to nearshore flats habitats and their inhabitants (Fig. 2). Indeed, anthropogenic impacts decrease the resilience of ecosystems to disturbances (White and Jentsch 2001) and to climate change (IPCC 2022), so these interactions must be considered. When impacts related to climate change are combined with other anthropogenic non-climate-related impacts (e.g., dredging, pollution, overharvest), they impose multiple or even synergistic stressors and threats to the coastal marine environment (Breitburg and Riedel 2005; Crain et al. 2009; Hewitt et al. 2016). To adequately plan for maintaining or improving on flats habitat structure and function, it is prudent that our review considers the interrelated and potentially compounded effects of these other anthropogenic impacts and the accelerating impacts of climate change.

Physical habitat damage, alteration, and loss

Anthropogenic activities that physically damage, alter, and remove flats habitats can cause fragmentation and change patch dynamics that impact flats fishes (Jackson et al. 2017), reducing their resiliency to the additional stressors brought on by climate change. Dredging causes considerable loss of seagrass through direct removal and indirectly through siltation, resulting in a cascading effect on invertebrate and fish distribution and productivity (Erftemeijer and Lewis 2006). In Florida, major shifts of seagrass species composition and seascape structure have occurred and are compounded by changes to the hydrology of coastal watersheds

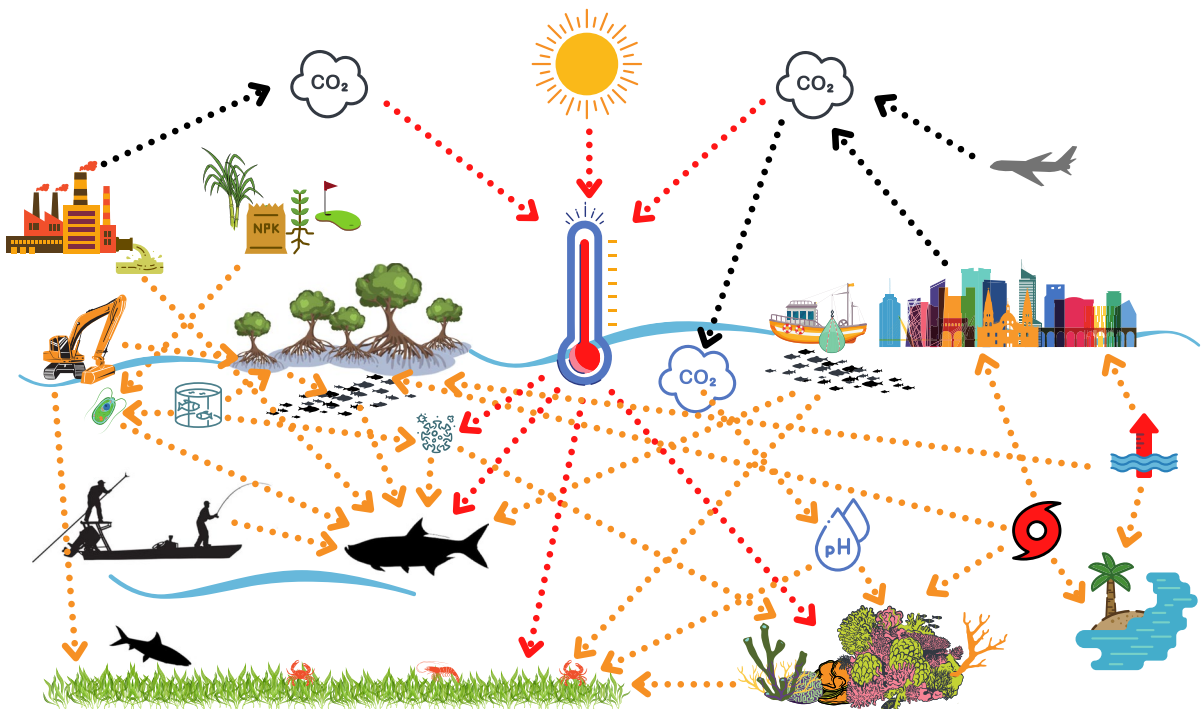


Fig. 2 Cascading effects of anthropogenic-derived climate change on sub-tropical and tropical flats fisheries and the coastal habitat mosaic. Arrows indicate the direction of the effect. Black dashed lines represent sources of CO_2 loading that are causing physiochemical changes in coastal systems, such as increasing water temperatures and ocean acidification.

Red dashed lines represent direct effects of increased CO_2 on temperature regimes, and direct effects of increasing water temperature on flats fishes species and their habitats. Orange dashed lines represent cascading, compound effects related to other human activities

induced by climate change and oscillations, as well as freshwater management activities (Fourqurean and Robblee 1999; Hall et al. 2016; Santos et al. 2020). For instance, in Biscayne Bay (Miami, Florida, USA), seagrass seascapes in nearshore environments have been transformed due to habitat loss and fragmentation processes associated with the variable salinity regimes created by freshwater canals (Lirman et al. 2014; Santos et al. 2020). Seagrass seascapes in Florida Bay basins have significantly transformed after die-off events since the summer of 2015, resulting from a combined effect of extreme drought conditions and chronic anthropogenically reduced freshwater inflows. The full extent and effects of this complex disturbance event are still unknown (with an estimated 40 km² seagrass affected; Hall et al. 2016); however, the potential for lasting effects on flats fisheries is concerning.

As sea level rise continues, anthropogenic introduced structures, such as sea walls and roads, will

prevent the inland migration of important intertidal coastal habitats such as mudflats, saltmarshes, mangroves, and sandy beaches. In North America, these intertidal habitats may be reduced by 20–70% within the next 100 years depending on if anthropogenic structures prevent the inland migration of such habitats (Galbraith et al. 2002). In The Bahamas, roads and culverts often fragment tidal flats habitats, which can result in significant reductions in secondary production for fishes in mangrove habitat (Valentine-Rose et al. 2007). A disproportionate loss or shift of habitats, particularly in coastal flats systems, may jeopardize the structure and function of entire coastal ecosystems, including coastal flats and their inhabitants. Physical damage to flats habitats reducing patch sizes could also increase sensitivity to other disturbances such as extreme weather conditions and sea level rise (Blanco-Libreros and Ramirez-Ruiz 2021), both of which are resulting because of climate change.

Coastal eutrophication

Nutrient loading leading to eutrophication is a frequent global consequence of human activities and a leading problem in coastal regions worldwide (Rabalais et al. 2009; Lefcheck et al. 2018). Eutrophication, the increased rate of primary production and accumulation of organic matter, stems from the increased land-based production and flux rates of reactive nitrogen and phosphorus into coastal waters exceeding natural production rates (Oelsner and Stets 2019). Changes in precipitation will affect land-based runoff, and thus nutrient loading to coastal habitats (Wei et al. 2020) in areas that already have sufficient impervious surface to alter estuarine ecology (Sklar and Browder 1998). Even if external loading is unaffected, microbial activity in sediments will accelerate at higher temperatures, increasing internal nutrient loading (Donald et al. 2002). Chemical and biological processes are temperature sensitive, and as temperatures increase, eutrophication will occur at lower nutrient concentrations (Moss et al. 2011). Effects of nutrient loading include noxious and harmful algal blooms (HABs; see below), reduced water quality (e.g., suspended sediment and associated increased turbidity and decreased light levels), and hypoxia (i.e., oxygen depletion as a result of decomposition of organic matter resulting from algal blooms; Donald et al. 2002; Rabalais et al. 2009; Howarth et al. 2011)—all of which have negative effects on flats habitats, flats species, and prey organisms. For instance, coastal nutrient loading can have a detrimental effect on seagrass habitats via its effects on algal overgrowth and associated light reduction, and on mangroves by lowering their resilience to environmental variability (Burkholder et al. 2007; Lovelock et al. 2009). Furthermore, in seagrass beds, sediment re-suspension resulting from the loss of cover can result in additional internal nutrient loading as fluxes of nutrients from sediments to the water column are enhanced in denuded areas (Burkeholder et al. 2007). Lastly, eutrophication will have profound effects on coastal food webs, which are dependent on the balance of enhanced production, shifts in foundational species (e.g., seagrass to algal dominated seascapes), and hypoxia (Valentine and Duffy 2006; Breitbart et al. 2009a, b).

Climate change will exacerbate the effects of eutrophication on marine ecosystems (Doney et al.

2012), including flats. In addition to episodic climatic disturbances, climate change may exacerbate the intensity, frequency, and the geographic range of HABs (Wells et al. 2015; Gobler et al. 2017; Pörtner et al. 2019; Gobler 2020). HABs, categorized by toxic algae, have been detrimental to animal, human, and ecosystem health (Hallegraeff 1993). For example, while the blooms of the photosynthetic dinoflagellate, *Karenia brevis*, are naturally occurring, in recent decades, blooms are occurring more frequently, are more widespread, often with higher potency in southwest Florida (Kusek et al. 1999; Brand and Compton 2007), which have been linked to anthropogenic nutrient inputs (Medina et al. 2022), and are responsible for the widespread mortality of fish and marine mammals (Landsberg 2002; Flewelling et al. 2005). Specifically, these blooms have been shown to repeatedly kill Atlantic tarpon and seriously affect the fishery (Griffin et al. 2022). In the St. Lucie Estuary and Indian River Lagoon on Florida's east coast, algal blooms continue to harm the estuaries and their fish communities due to a combination of increased hurricane and precipitation intensity coupled with mismanagement of freshwater flows (Phlips et al. 2020). In addition, coastal regions are experiencing macroalgal blooms that are becoming an increasing problem affecting both seagrass habitats and associated fisheries (Collado-Vides et al. 2013; van Tussenbroek et al. 2017; Santos et al. 2020). In Florida, a macroalgal bloom, associated with *Anadyomene* spp. (Cladophorales, Anadyomenaceae), affected nearshore seagrass seascapes by causing habitat fragmentation and the loss of turtlegrass (*Thalassia testudinum*) patches (Santos et al. 2020) with unknown consequences to local recreational fisheries. Considering Florida's notoriety for its recreational fisheries (Camp et al. 2018), increase in algal blooms is impacting both the ecosystem and the economy.

Freshwater flow regimes

Natural flow regimes are central to the structure and function of freshwater and coastal ecosystems and thus the services they provide. Unfortunately, anthropogenic activities worldwide have resulted in major alterations to the magnitude, frequency, timing, duration, and rate of change of freshwater flows (Poff et al. 1997; Lytle and Poff 2004; Palmer and Ruhi, 2019). Anthropogenic flow alterations

not only result in hydrologic change, but also geomorphic responses (e.g., floodplain deposition and erosion), effects on in-stream, floodplain, and watershed processes such as primary production, nutrient cycling, and ecosystem metabolism, and impacts on the life history, trophic, spatial ecology, and adaptations of riparian and aquatic biota (Palmer and Ruhi 2019). Grill et al. (2019) estimate that due to fragmentation, via dams and reservoirs, and flow regulation, only 23% of the world's large rivers flow uninterrupted to the coast. In coastal habitats, the timing and magnitude of freshwater flows, either via surface or ground discharges, are critical to coastal patterns and processes, including salinity, nutrient, temperature, oxygen, sediment, and submerged aquatic vegetation regimes, and to mediating pollution and eutrophication risks (Sklar and Browder 1998; Gillanders and Kingsford 2002; Luijendijk et al. 2020). Indeed, when > 10% of a watershed's acreage is converted to impervious surface, the water bodies can become seriously degraded and may be characterized by losses of faunal diversity, productivity, and overall stability (reviewed in Beach 2002). Climate change will affect all aspects of the water cycle, resulting in pronounced changes to hydrological regimes (Jimenez Cisneros et al. 2014), that will interact with present and future anthropogenic flow alterations (e.g., future dam construction). Anthropogenic infrastructure (e.g., dams) often results in decreases in freshwater influence to the coast (Grill et al. 2019) and/or changes to flow variability that either increases or decreases hydrological flashiness (frequency and rapidity of short-term changes; Lytle and Poff 2004) to coastal habitats. For example, alteration of freshwater flow patterns into mangrove creeks used by juvenile common snook as nursery habitat significantly reduced snook diet diversity in creeks with highly altered versus less-altered flows (Adams et al. 2009). Climate change, by altering the distribution, variability, and intensity of precipitation events, may exacerbate these effects, with an overall effect of global decreases in riverine flows to the coast (Shi et al. 2019). In contrast, higher discharges associated with extreme precipitation events will cause greater erosion and resuspension, and result in higher sediment, nutrient, and pollutant (e.g., pesticides; Delcour et al. 2015; Warne

et al. 2022) loads to the coast (e.g., Wei et al. 2020), further threatening the health of coastal ecosystems.

Resource exploitation

Nutrient enrichment and primary production typical of nearshore coastal waters can act as the foundation for fisheries production and the subsequent exploitation of desirable species (Nixon et al. 1986; Houde and Rutherford 1993; Breitburg et al. 2009a, b; Jordan and Peterson 2012). The mosaic of coastal vegetation and benthic habitats in these regions are prime nursery areas and foraging grounds for extractive fisheries resources. For example, Manson et al. (2005) demonstrated a direct connection between the extent of mangroves and coastal fisheries production in northeastern Australia. In addition, Turner (1977) showed that inshore commercial yields of penaeid shrimp were directly related to the overall area of estuarine, intertidal vegetation across multiple sites. In the Gulf of Mexico, over 50% of commercial finfish and shellfish harvest occurs within 3 miles from shore for some US states (Keithly and Roberts 2017). Traditional and subsistence fisheries tend to be in nearshore estuaries and flats habitats, and support food security and small-scale commerce in local communities (Zeller et al. 2006). Lastly, nearshore flats fish species also serve as the foundation for economically valuable recreational fisheries that can be extractive or non-extractive (i.e., catch-and-release) (Cooke and Cowx 2004).

Processes by which fisheries resources are extracted from nearshore flats can be impactful on the target species, bycatch, and the habitats where harvest is occurring (reviewed in Blaber et al. 2000). The direct loss of target and non-target species at excessive rates can create imbalances in food web structure and alter the resiliency of coastal ecosystems (Pauly et al. 1998). For example, destructive demersal fishing methods, such as bottom trawling, have contributed to the loss of seagrass worldwide (Grech et al. 2012), which has cascading effects on water quality, suspended sediments (Dellapenna et al. 2006), benthic community structure (Labropoulou and Papaconstantinou 2005), and the exploited species themselves. Physical disturbance to flats habitats caused by destructive fishing practices and land-based development (see Lewin et al. 2006) could make these regions less resilient to the already increasing

biophysical and chemical effects of climate change (He and Silliman 2019). There is already mounting evidence that the biophysical effects of climate change are impacting global fisheries production (Sumaila et al. 2011); however, the additional cumulative threats related to the fishing practices themselves could exacerbate the effects and reduce coastal resiliency.

As extractable resources decline, aquaculture in nearshore waters is increasing to help meet the demand for seafood (Ottinger et al. 2016; Clavelle et al. 2019). Whether shore-based or intertidal, the construction and operation of aquaculture can have negative impacts on nearshore waters, including habitat modification and loss (Holmer et al. 2008), nutrient discharge, and eutrophication (Olsen et al. 2008), changes in benthic communities (Simenstad and Fresh 1995), introduction of non-native, invasive species (Naylor et al. 2005; Molnar et al. 2008), and the introduction of pathogens and disease (Lafferty et al. 2015; Bouwmeester et al. 2021)—all of which could be compounded by climate change, and thus negative effects on flats fishes and associated fisheries.

Capture and the associated release mortality and/or harvest can dominate the dynamics of exploited species. Flats fisheries attract a diversity of participants across a spectrum of specialization with some species targeted for harvest and others release. How climate change impacts are integrated over the diverse spectrum of anglers is an important consideration for understanding its influences on the population dynamics of targeted flats species. While catch-related aspects are the dominant component of angler satisfaction and ultimately participation (Beardmore et al. 2015), non-catch dimensions are also significant, and may have a strong influence on flats fisheries.

A key driver to angler participation in flats fishing is access to fishing locations. The influence of climate change on access is likely to be mixed and dependent on changes in local conditions. The general pattern is a potential increase in access in cooler areas and a decrease in warmer areas (Dundas et al. 2020; Townhill et al. 2019; Whitehead et al. 2016), with decreases driven by less desire by anglers to fish in degraded habitats and disruption in the status of civic infrastructure. The magnitude of change, for US recreational fisheries, is estimated to range from –15 to 27%, with modeling results influenced by projected changes in temperature and precipitation. Assuming

that changes in environmental conditions allow for the persistence of target species in these areas, the expectation over time is a reduction in recreational fishing activity directed at flats species. These declines in recreational effort in tropical areas could be countered by potential increased targeting as species shift distributions to historically cooler areas.

The effort directed at flats species is not only recreation but, in many areas, has an artisanal and commercial component. Fishery production in the tropics is expected to decline by 40% due to climate change effects (Lam et al. 2020, Barange et al. 2018). Marine fisheries are an important source of nutrition, and reductions in harvest of some species will likely result in increasing pressure on flats species. Since recreational fishing pressure is catch-and-release for many flats species, this shift of focus to artisanal and commercial fisheries will increase fishing mortality. In addition, release mortality is expected to increase as temperatures warm (Gale et al. 2013; Kerr et al. 2009; Bartholomew and Bohnsack 2005), increasing the impact of non-consumptive fisheries on fishing mortality. Thus, within the current geographic range of the flats fishery, we might expect a shift toward consumptive use of flats species, and increased release mortality within the catch-and-release recreational fishery.

Disease regimes

The idea that climate change is a driver of the overarching health of nearshore marine ecosystems first gained broad recognition in the Millennial Ecosystem Assessment (Agardy et al. 2005). According to this assessment, marine wildlife such as turtles, crocodiles, marine mammals, and waterbirds are constituents of “healthy” (i.e., ecologically balanced) systems, and many of the habitats they currently occupy are “unhealthy” and imperiled by myriad anthropogenic stressors (Agardy et al. 2005). In 2007, the Intergovernmental Panel on Climate Change brought the link between climate change and health/disease (traditionally defined) to the forefront of scientific and public attention (Parry et al. 2007). Largely absent from such assessments to date, however, are flats species and the unique ecosystem services that they can provide—such as the provision of recreational opportunities for anglers and associated economic benefits for conservation and local communities (Adams et al.

2014; Adams and Cooke 2015; Brownscombe et al. 2019a).

Specific diseases of flats fishes are almost entirely unknown (Goldberg 2019). This is in part because of lack of research and in part because illness in flats fishes would likely go unobserved due to rapid predation of weak individuals (Danylchuk et al. 2007a, 2007b). Thus, inferences about how climate change might lead to ill health and population declines in flats sport fisheries are largely speculative. Direct effects of increased temperature and salinity and decreased pH and dissolved oxygen on flats fishes physiology would undoubtedly occur (Little et al. 2020). Fish species that inhabit or frequent flats habitats are adapted to extremes in these water chemistry parameters (Harborne 2013). However, experimental studies on checkered puffer (*Sphoeroides testudineus*), bonefish (*A. vulpes*), yellowfin mojarra, (*Gerres cinereus*), and schoolmaster snapper (*Lutjanus apodus*) from flats systems in The Bahamas showed that physiological thermal maxima of these species may be exceeded under near-future climate scenarios (Murchie et al. 2011; Shultz et al. 2016). Similarly, temperature and oxygen stress may interact with angling to cause mortality in cobia (*Rachycentron canadum*) as temperatures increase and hypoxic zones expand (Crear et al. 2020). On a population level, such effects would likely multiply as climate-driven changes cascade to various compartments of the flats ecosystem (e.g., mangroves, the benthos), affecting the health of flats fishes through decreased availability of prey and subsequent declines in nutritional status. Nutritional stress is widely known to exacerbate disease processes across a wide range of fish taxa (Lim and Webster 2001).

Infectious diseases in marine systems also respond acutely to climate change (Aalto et al. 2020, Burge and Hershberger 2020, Byers 2021). This topic is currently at the forefront of research due to the alarming rate with which infectious diseases are emerging worldwide, threatening human health directly when emerging pathogens are human-adapted or zoonotic, and indirectly when pathogens infect plant and animal populations essential for human well-being (Mora et al. 2018; Rohr and Cohen 2020). Infectious diseases of flats fishes are virtually unknown, for the reasons mentioned above. A recent study showed that the microbiota of Caribbean bonefish gills differed significantly between The Bahamas and the Florida Keys, and that microbes overabundant on the gills

of bonefish (*A. vulpes*) in the Florida Keys included taxa associated with diseases of marine fish and with coastal development processes such as agricultural runoff and sugar production (Dunn et al. 2020). Flats fishes such as bonefish can therefore be colonized by environmental bacteria, although with unknown health consequences. Furthermore, Campbell et al (2022) demonstrate infection of bonefish across their western Atlantic range with four previously unknown viruses, with patterns of viral load mirroring patterns of anthropogenic degradation, but again with unknown health consequences.

More is known about infectious diseases of other marine fishes and the effects of climate change on their distribution and severity, particularly in cultured species (Collins et al. 2020; Vollset et al. 2020). For example, sea lice increase their reproductive rate at elevated temperatures (Groner et al. 2014) and may spread to new geographic regions and new hosts (captive and wild) with altered pathogenic effects as ocean temperatures rise (Hemmingsen et al. 2020; Shephard and Gargan 2020). It is also worth noting that many diseases of corals have strong links to climate change (Burge and Hershberger 2020, Howells et al. 2020). Given the dependence of flats fishes on nearby coral reefs (Bayles et al. 2016; Brownscombe et al. 2020), the cascading negative effects of coral loss due to infection would be expected to extend to flats fishes. Generalities about the effects of climate change on host-parasite dynamics may therefore be extrapolatable to tropical flats based on studies of other estuarine and nearshore environments (Byers 2020).

Among potentially pathogenic microbes of marine fishes, the least is currently known about viruses. Intriguingly, recent metagenomic surveys have shown that marine fishes host divergent relatives of many important emerging mammalian viruses, including viruses of humans (Geoghegan et al. 2018, 2021). For example, distant relatives of the ebolaviruses have been found in various marine species (Shi et al. 2018; Geoghegan et al. 2021), as have distant relatives of influenza viruses (Geoghegan et al. 2021) and coronaviruses (Miller et al. 2021). Because samples and data for these studies have been obtained from seafood markets or similar sources, it remains unclear what effects, if any, these viruses have on the health of wild fish populations or whether flats fishes host similar viruses. Even if these viruses are benign, co-evolved commensals, climate change is known to

alter the physiological (e.g., immunological) balance between hosts and pathogens, such that a long history of benign coexistence may not predict the future state of such relationships (Aalto et al. 2020, Burge and Hershberger 2020, Byers 2021).

Implications for management and conservation

Some of the shortcomings that currently hinder management and conservation of flats fisheries and habitats must be addressed to enable an effective response to climate change. These shortcomings include an overall lack of habitat incorporation into fisheries management, insufficient recognition of coastal habitat mosaic connectivity, and communication gaps that inhibit integration of user groups, rightsholders, and stakeholders in research, conservation, and management efforts.

Fish and habitat management

Climate change is occurring in a scenario in which much of the coastal habitat mosaic that supports the flats fishery is already in decline. One extreme example is Florida (USA) where mangrove loss has been severe: Tampa Bay has lost > 50% of mangroves and Charlotte Harbor has lost > 60%. In the Indian River Lagoon on the east coast of Florida, over 16,000 ha of coastal marshes were impounded in the 1950s and 1960s for the control of mosquito breeding (Brockmeyer et al. 1996), and 85% of the mangrove habitats of the ecosystem are located within these impoundments (FWC 2021). Subsequent installation of culverts in many of the mangrove-filled impoundments, and seasonal control of hydrographic connectivity allowed some of the fish nursery functionality to be restored (Gilmore et al. 1982; Brockmeyer et al. 1996; Poulakis et al. 2002; Cianciotto et al. 2019). Since ecologically intact systems are more resilient to disturbances and the interaction between natural and anthropogenic disturbances are especially problematic for maintaining ecological integrity (White and Jentsch 2001), the compromised state of the coastal habitat mosaic will mean an even greater challenge to managing fish species that support flats fisheries. Moreover, human development of coastal areas will prevent landward migration of important habitats that transit

the terrestrial-marine margin like marshes and mangroves, which will likely shrink in extent—squeezed by sea level rise on one side and human development on the other (Valiela et al. 2018).

Although coastal ecosystems are threatened globally by habitat loss (Crain et al. 2009), habitat remains largely absent from fisheries management. Indeed, the importance of habitat to coastal fish populations has long been recognized—more than 60 years ago, Marshall (1958), a state fish biologist in Florida (USA), considered habitat alteration as the biggest culprit in common snook population declines in Florida. Marshall's lament on the impact of habitat alteration on snook was further shared by American state biologists nearly 30 years later (Bruger and Haddad 1986). More recently and more generally, Beck et al. (2001) proposed a framework for identifying and prioritizing fish nursery habitat for fisheries conservation. Although these efforts have resulted in habitat being recognized as an important factor in fish population productivity, they have not resulted in incorporating habitat into fisheries management. The US Federal Magnuson Stevens Fisheries Management Act, for example, states that managers should “consider” habitat in management strategies, far from a mandate.

Indeed, the Indian River Lagoon (Florida, USA) is an exemplar for the disconnect between habitat and fisheries management, which looms ever-greater with climate change. Beginning with extensive plankton blooms in 2011 caused by excessive nutrients, the Indian River Lagoon has lost > 58% of seagrasses, with no recovery due to negative feedbacks due to sediment resuspension and continuing high nutrient loads (Morris et al. 2022). The poor ecological state of the Indian River Lagoon has resulted in declines in flats fish populations, including snook (Boucek et al. 2022). Boucek et al. (2022) compared snook population recovery from an intense cold event in 2010 in four estuaries, and found that the northern Indian River Lagoon, which had suffered the greatest habitat loss and degradation of the studied estuaries, was the only estuary in which the snook population had not yet recovered. Also in the Indian River Lagoon, the red drum (*Sciaenops ocellatus*) population has declined to such an extent that the Florida Fish and Wildlife Conservation Commission (FWC) has designated red drum as catch and release only beginning September 1, 2022 (<https://myfwc.com/news/all-news/redfish-722/>). This decision was based on low

population size, stakeholder advocacy for the closure, and poor ecological health of the estuary. Using this situation to a positive advantage, FWC is embarking on a revision of red drum management that will include habitat and water quality metrics at the estuary level as a first step to including habitat in fisheries management (<https://myfwc.com/fishing/saltwater/recreational/red-drum/>).

The scientific literature is increasingly focused on the effects of sea level rise on coastal habitats, especially wetlands (e.g., Comeaux et al. 2012; Rogers et al. 2014; Valiela et al. 2018; Colombano et al. 2021), which is an essential first step toward formulating conservation and management responses to climate change. Considerably less research, however, has focused on the effects of fragmentation of the coastal habitat mosaic (but see Fulford et al. 2014)—whether by past and ongoing anthropogenic habitat loss and degradation or potential effects of sea level rise. This is especially concerning since connectivity in the coastal habitat mosaic is complex and multifaceted, expressed in many ways including ontogeny, migration, dispersal, trophic dynamics, and nutrient transport (Sheaves 2009). Common snook and Atlantic tarpon, for example, are obligate users of mangrove creeks and wetlands, yet habitat is not considered in management of the fisheries these species support (Adams and Murchie 2015).

The inability for standard fisheries management as currently practiced to adjust to climate change (Gaines et al. 2018), combined with the inability of fisheries management to adequately consider or incorporate the key role of habitat (Levin and Stunz 2005), requires a paradigm shift in coastal fisheries management. This new paradigm will integrate standard fisheries management with a focus on maintaining and restoring the most intact coastal habitat mosaic feasible—a spatial approach essential to enable effective adaptation of resource management to climate change. For example, at the local scale, many fish species undergo ontogenetic habitat shifts that are interrupted by habitat fragmentation (ontogenetic habitat shifters; Adams et al. 2006). Without active management efforts to account for these shifts through maintaining habitat mosaic connectivity, the likelihood of these species successfully adapting to climate change will be diminished. In contrast, species with less restrictive ontogenetic requirements

(habitat generalists; Adams et al. 2006) may be more adaptable to an increasingly fragmented habitat mosaic. Unfortunately, many of the fishes that support the flats fishery, e.g., bonefish (*Albula* spp.), Atlantic tarpon, permit (*Trachinotus falcatus*), and common snook, are ontogenetic habitat shifters, suggesting limited capacity to adapt to the combination of climate change and habitat fragmentation. In contrast, red drum and spotted seatrout have habitat generalist characteristics that may make them more adaptable. These scenarios are impossible to plan for without implementing a spatial management approach.

Habitat restoration strategies should also be adjusted to the spatial management approach in that prioritization of habitat restoration should be in the context of the coastal habitat mosaic and anthropogenic habitat alteration in a landscape approach (Peterson and Lipcius 2003). Wetland restoration and protection might prioritize upland areas where inland migration is predicted due to sea level rise (Rogers et al. 2014, Vinent 2019). The influence of location within an estuary should also be considered. In Charlotte Harbor, Florida, for example, the distance of mangrove creeks from the Gulf of Mexico influenced the degree to which they were viable juvenile common snook nursery habitats as well as fish assemblage species composition (Wilson et al. 2022). Restoration strategies need to be resilient to climate change (Simonson et al. 2021) which is currently an active area of research in coastal ecosystems (see Waltham et al. 2020).

On a larger scale, portions of the coastal habitat mosaic are connected by migration and larval dispersal. Many flats fishes are aggregate spawners with different larval dispersal abilities, different levels of migratory capacity and site fidelity, and thus different catchment areas for spawning aggregation locations (de Mitcheson 2016) and geographic ranges. This reality is already not considered in management of Atlantic tarpon, which undergo long-distance seasonal migrations (Griffin et al. 2018; Luo et al. 2020) across jurisdictional boundaries, and bonefish, with a larval stage of 41–71 days (Mojica et al. 1995) resulting in connectivity of separately regulated management regions (Zeng et al. 2019). The spatial, and perhaps temporal, dynamics of this connectivity will likely shift with climate change, but due to our lack of focus on spatial habitat management, we are unable to appropriately manage these species now and are ill

prepared for adjusting management to account for climate change.

The nature of the fisheries for many of the flats species, the regions in which they occur, and the focus on spatial and habitat management will require acceptance of some uncertainty (Johannes 1998) and a realistic outlook on data needs and availability. Many flats species (e.g., Atlantic tarpon, bonefish (*Albula* spp.), permit, and giant trevally (*Caranx ignobilis*)) are mostly catch-and-release, have never had a stock assessment, and occur in jurisdictions with very limited research capacity and financial resources. These species should be defined as data-limited (i.e., species/fisheries that lack data and for which the prospect of data being acquired are slim to none, thus data are permanently limited). In contrast, species that support harvest fisheries in the USA (e.g., common snook, red drum, spotted seatrout) or occur in jurisdictions with sufficient financial resources might have regular stock assessments, but some might be considered data-poor (i.e., species/fisheries that lack data and for which it is possible that additional data can be obtained, so the data-poor situation might improve). The data status of fisheries should be a consideration in both expectations of data availability and thus appropriate strategies to manage with different levels of uncertainty, especially with the added complexity of the multiple stressors of climate change.

Engagement, outreach, and science communication

The scientific community has unequivocally shown that anthropogenic greenhouse emissions drive climate change (IPCC 2021), yet awareness and acceptance of this fact in society are only slowly increasing (Whitmarsh and Capstick 2018). In developed countries, awareness is nearly ubiquitous, while elsewhere it is largely uneven (Lee et al. 2015). Data from the USA suggests that 13% of people think that climate change is not happening, and only 55% of people believe that it is mostly human induced (Leiserowitz et al. 2017). Views are similar in Germany and the UK where 16% and 12%, respectively, of people do not think that the climate is changing. Likewise, less than 50% of people in both Germany and the UK believe that it is caused primarily by humans (Steentjes et al. 2017). Furthermore, even those individuals who are well-informed and understand the causes and consequences of climate change often have a limited

understanding of how different activities contribute to climate change and tend to underestimate their own role in causing climate change (Whitmarsh and Capstick 2018).

Some studies have found that in places where there is more risk exposure to climate change, there is a higher level of awareness (Swim and Whitmarsh 2017). Brody et al. (2008) found that US respondents who were the most vulnerable to sea level rise perceived climate change as a greater personal risk. More recently, Brown et al. (2020) surveyed boaters in Everglades National Park who had participated in recreational fishing in the park at least once in the last 3 years and found that 68% of respondents believed that the risk of sea level rise and climate change was real. Furthermore, they supported mitigation actions and expressed a high degree of willingness to pay for mitigation (Brown et al. 2020).

Overall, the general lack of understanding and acknowledgement about the true drivers of climate change presents an impediment to creating mitigation and solution programs. However, more education is not necessarily the right remedy or even helpful (Clayton and Manning 2018; Markowitz and Guckian 2018). Viewing attitudes about climate change as formed by factors other than scientific information can help create better communication strategies (Clayton and Manning 2018). Markowitz and Guckian (2018) propose seven insights to improve climate change communication consisting of the following: (1) know what motivates the audience, (2) figure out what the audience already knows, (3) confront false information, do not reinforce it, (4) find frames that “fit” audiences’ needs, (5) highlight solutions, (6) tell stories, and (7) leverage the right messengers and communication channels. Collectively, embracing these seven steps may be useful for addressing the multiple threats of climate change on flats fishes and the habitats they depend on.

There has long been a disconnect between conservation efforts and fisheries-oriented user groups, but this disconnect must be corrected as part of a comprehensive approach to flats fishery conservation in the context of climate change. Recreational fisheries, for example, are supported by a large and growing community that is only beginning to engage in conservation, albeit with varying levels of success (Danylchuk and Cooke 2011). Indeed, the increasing participation

of recreational anglers is being manifested in the increase in non-profit organizations focused on fisheries and habitat conservation as this user group becomes more engaged with scientists and resource managers (Raynal et al. 2020). This is especially true for flats fisheries, which tend to be advanced anglers who understand the connection between the health of the environment and quality of the fishery (Oh and Ditton 2006), so are well positioned to advocate for conservation if given appropriate opportunity. Underpinning successes in this space will be a combination of engagement, outreach, and science communication efforts (Markowitz and Guckian 2018).

Communicating scientific knowledge with diverse audiences is increasingly recognized as an essential component of the scientific process (Weigold 2001; Jacobson et al. 2015). Science communication is often viewed as being unidirectional whereby the knowledge generator (scientist) pushes knowledge out to potential knowledge consumers and users. However, science communication done well is about bidirectional communication that more resembles a conversation than simply a proclamation (Cooke et al. 2017). The benefit of science communication is that it can serve as the basis for empowerment and changes in understanding and behavior (Jacobson et al. 2015). For example, in the context of flats fish conservation, there may be new knowledge that arises about catch-and-release air exposure thresholds for a given species and a particular location or setting, for instance bonefish in Florida. In turn, scientists publish a paper on the topic that is read largely by other scientists. However, the scientists also engage in a variety of science communication activities. First, they use social media to share their research on Twitter and Instagram while tagging key players in the recreational fishing sector. Next, they share their findings with an organization like Bonefish & Tarpon Trust (as an example of a trusted organization with communication expertise; Fiske and Dupree 2014) and work with them to prepare an accessible summary for their newsletter and website. They then deliver presentations on the topic to several fishing clubs and guide associations. Finally, they meet with the staff from the state's resource management agency (FWC) to ensure that findings are used to update guidance for catch-and-release. This example assumes the typical approach where science communication occurs on the back end after research is complete. However, there

is a growing body of research on science communication that suggests such approaches may not always work (Burns et al. 2003; Cooke et al. 2017).

The best place to begin science communication is before one does any research. The emerging paradigm for generating science that has impact involves co-production where researchers and various stakeholders, rights holders, and end users are engaged from the early stages of a project such as identification of research needs and priorities (Cooke et al. 2021). This level of engagement continues throughout the project such that science communication is not an afterthought but rather embedded in the project design and delivery. Co-production increases the relevance of the work and increases the likelihood that findings will be accepted by external parties even if those findings do not align with their preconceived notions or world views (Cooke et al. 2017). By involving these actors in research, they assume a level of ownership which increases trust in the scientists and the scientific process (Young et al. 2016). These same actors can then be the ones that communicate findings to their respective communities. Indeed, this approach is rather common in flats research where, for example, fishing guides and researchers work hand in hand to execute tagging studies (e.g., Murchie et al. 2015). In another example, a collaborative approach with recreational fishing guides in The Bahamas resulted in five new national parks and one park expansion to protect bonefish (*A. vulpes*) habitats (Adams et al. 2019; Boucek et al. 2019). The community engagement and coproduction approach is not limited to the recreational fishery but is also valuable for artisanal fisheries (Johannes 1998). In Anaa Atoll, for example, research, education, and community engagement were effectively used to improve an artisanal fishery for bonefish (*Albula glossodonta*) (Filous et al. 2021). Overall, a mixed method interdisciplinary approach that best encapsulates the complex social-ecological systems related to flats fisheries and that includes co-production of knowledge and embraces the rights of local user groups may produce the most effective conservation strategies (Kinnebrew et al. 2021).

Engagement of flats fishery user groups must also be at the local scale. Management actions must show local benefits and importance since the global scale approach to climate change that is standard is too abstract at the local scale. For example, engaging recreational or artisanal users of flats habitats

to support wetland conservation to increase carbon sequestration will find little local support because this concept is too far removed from fishery-related benefits. If instead the education and research focus is on the importance of wetlands to the juvenile life stages of species important to the fishery, fisher involvement is much more likely. This reflects the findings of Cowx et al. (2010) that users will advocate for habitat conservation that helps to protect their fishery, particularly when the scale of conservation efforts is local with local benefits. The value of wetland conservation in terms of climate change, via carbon sequestration, is an added global benefit of local conservation action.

No matter what approach one takes to science communication, it is important to be strategic and have a plan (Cooke et al. 2017) as well as be clear and concise, especially when communicating information on climate change (Townhill et al. 2020). The most effective science communication activities are done with careful thought rather than taking a more shotgun approach. It may be necessary to include external experts in the process such as those with expertise in graphic design (Murchie and Diomedea 2020), generating digital media content (Dickel and Franzen 2016), or social media campaigns (Claussen et al. 2013; Danylchuk et al. 2018). It may also be necessary to engage with individuals who span boundaries or knowledge brokers (see Goodrich et al. 2020) to assist with translating scientific findings to managers and policy makers. A good example of using the latter is a recent success story where telemetry data revealed that permit were moving from the flats to offshore spawning sites in Florida earlier than previous data indicated (Crabtree et al. 2002), and were not protected by existing fisheries regulations. Members of Bonefish & Tarpon Trust with expertise in science, advocacy, and policy worked with the state government to identify and enact new management strategies to benefit permit (reviewed in Brownscombe et al. 2019b).

With the great interest in flats fishes and the stunning imagery that is inherent with such species and systems, science communication is inherently advantaged relative to work on less iconic or visually stunning species and systems. That of course does not mean that science communication is easy or unimportant for flats fishes but that it should be relatively easy to tell good stories and connect with diverse

audiences (Wilson et al. 2016). If one looks globally, we submit that most science communication efforts related to flats and flats fisheries have focused on developed countries (mostly the USA), so there is much need for efforts to communicate more broadly and generate public and political will to conserve and manage flats ecosystems and fisheries around the globe, especially in the face of threats from climate change.

Acknowledging disparities and inequities

The Florida Keys are often touted as the ‘birthplace’ of flats fishing (Sosin and Kreh 1988; Maizler 2007; Horn 2021), so it is not surprising that many of the examples and discussions on the impacts of climate change and compounded anthropogenic disturbances center on this region. As the popularity of flats fishing has increased and demands have grown, recreational anglers now also pursue other flats species in the southeastern USA and Gulf of Mexico (e.g., red drum), and also on other relatively accessible and geographically proximate countries and regions, such as The Bahamas, Central America, and the Caribbean, as well as more remote destinations such as Kiritimati (Christmas Island), the South Pacific, and The Seychelles.

The global expansion of flats fishing also exposes recreational anglers to diverse human cultures that have benefited from and been impacted by the development of recreational fisheries (Barnett et al. 2016). Although recreational angling is often seen as something that can provide economic prosperity and alternative livelihoods to local communities, regions, and even entire countries (Smith et al. In Review), this activity, particularly catch-and-release, can be at odds with cultural norms (i.e., viewed as playing with food), while infrastructure development, employment strategies, and foreign investment can potentially create disparities related to who actually benefits, as well as new pressures on the environment that are not included in conservation and management strategies (Gibbs et al. 2021).

As we move toward a more comprehensive understanding of the impacts of climate change on flats fisheries, it would be remiss if we did not acknowledge the fact that developed nations, such as the USA, are playing a disproportionately greater role in the climate crisis in comparison to distant coastal

communities of developing nations (Roberts 2001), many of which are and will also face disproportionately greater impacts from climate change. When approaching these issues, it is important to unpack the colonialist tendencies related to broader climate change policy, as well as how the conservation and management of flats fisheries are discussed and solutions proposed (rather than imposed; Gibbs et al. 2021). In many tropical developing nations, marine-protected areas (MPAs) are often touted and used as low cost, simple solutions to the complex socioecological systems conservation problems (Green et al. 2014). However, in some situations, MPAs could not only be deemed as a form of “new colonialism” (Hart et al. 2021), but they may also bring into question of compatibility with catch-and-release recreational fisheries (Cooke et al. 2006; Danylchuk and Cooke 2011; but see Pina-Amargós et al. 2022). Although some cultures have traditionally used area closures to help protect fisheries resources (Filous et al. 2021), and the motivation for doing so is generally not related to competing demands tied to recreational fisheries. Before imposing conservation and management strategies related to flats fishes and their habitats, it will be imperative to better understand the rights and values of human communities and societies that have relied on these species for much longer than those who seek to participate in the relatively young activity of recreational flats fishing (Ruddle 2016). As with examples in The Bahamas, Belize, and Cuba, it will be imperative that lengthy engagement of local communities by local/regional management and conservation agencies be a precursor to any establishment of controls (e.g., MPAs) related to flats fisheries so that social and cultural values and identities are respected and preserved.

Knowledge gaps and calls to action

As we continue to try to keep up with and comprehend the cumulative effects of anthropogenic disturbances on marine ecosystems, including coastal flats (Roessig et al. 2004; Harter et al. 2015; Jones and Cheung 2015), it will be important to acknowledge that, because organisms have different tolerances to conditions and potential extremes brought about by climate change, there will be both biological and ecological winners and losers (Begon et al. 2006; Somero

2010). A prime example are three popular flats fishes in South Florida—Atlantic tarpon, common snook, and bonefish (*A. vulpes*). Because of a combination of their early life history, tolerances to abiotic conditions (salinity, dissolved oxygen) and habitat requirements, Atlantic tarpon and common snook are more likely to experience range shifts than bonefish. In fact, since 2007, the distribution of common snook has expanded about 150 km northward along the west coast of Florida, from the Tampa Bay region to north of Cedar Key (Purtlebaugh et al. 2020). Beginning with the range expansion of adult fish, local reproduction was observed in the northern-most regions in 2016–2018, and all size classes were collected. This species typically spawns in late summer near ocean inlets, with a pelagic larval duration of about 14–20 days (Peters et al. 1998). After entering an estuary, metamorphosing larvae settle in backwater habitats that are often also used by juvenile Atlantic tarpon. With feeding behavior and potential mortality occurring at an estimated 9–12 °C (Howells et al. 1990), the northern-most juvenile habitats may include thermal refuges such as near-freshwater springs. As with Atlantic tarpon, inclusion of nursery habitat requirements for common snook should be incorporated into management strategies in coming decades, including mitigation measures tied to the physiochemical changes predicted through climate change. However, bonefish (*A. vulpes*) depend on low energy sandy habitats for larval settlement (Haak et al. 2019), and such habitats are not expected to extend northward along the Florida coastline in the face of climate change and other anthropogenic disturbances. Thus, even with the potential for long distance larval transport that can provide connections among the adult populations and drive local population dynamics (Zeng et al. 2019), other limitations may constrain the capacity of bonefish to contend with the impacts of climate change. However, in some cases, the anthropogenic decline of ecological health of coastal waters may create more habitat required by bonefish. For example. The Indian River Lagoon, which spans much of Florida’s east coast, has lost >58% of seagrass coverage (Morris et al. 2022), leaving open sandy bottom in areas protected from wind energy. Catches of juvenile bonefish in the Indian River Lagoon via seine sampling have increased in recent years (Jon Shenker, Florida Institute of Technology, pers. com.), which may reflect this benthic habitat change.

Additional attention is needed to understand the physiological (e.g., related to temperature, dissolved oxygen) and ecological thresholds of fish targeted in the recreational flats fishery so that we do not inadvertently overlook threats related to compounding effects of climate change and other anthropogenic disturbances. How flats fishes respond to rapid onset changes, versus slower, chronic disturbances, will provide a lens into how resilient individual species are, and if mitigation measures are even possible (De Battisti 2021). The same is true for higher and lower levels of biological organization, from predators to prey (Bernhardt and Leslie 2013)—recognizing that resilience and adaptation of species to the complexities of climate change may be difficult to untangle; the future of flats fish populations and the fisheries that depend on them is uncertain.

Commercial extractive fisheries have traditionally drawn more attention from policy makers and resource managers, leaving recreational fisheries comparatively undervalued and unappreciated (Cooke and Cowx 2004). However, over the past 20 years, an understanding is emerging as to how recreational fisheries contribute to the economy and societal well-being (World Bank 2012; Arlinghaus and Cooke 2009), yet it remains uncertain as to how much recreational fisheries are being included in coastal climate action plans. Since recreational fisheries focused on flats species can play important roles in local and regional economies, management of local and regional scale climate stressors should include the interests of user groups, stakeholders, and rightsholders. Likewise, understanding the scope of effectiveness for local and regional management options in the face of climate change will help keep solutions transparent and realistic. For example, having recreational anglers included in conversations about MPAs is important (Danylchuk and Cooke 2011), yet the debate is still ongoing about how locally effective MPAs will be against certain physiochemical changes brought about by climate change (Green et al. 2014). Similarly, more widely communicating the conservation status of flats species (Adams et al. 2014) may provide ways to elevate the current vulnerability of species to anthropogenic disturbances that will only be amplified in the face of climate change. Such amplification could prove invaluable when advocating for policy changes focused on addressing flats habitat protection, stronger management actions to

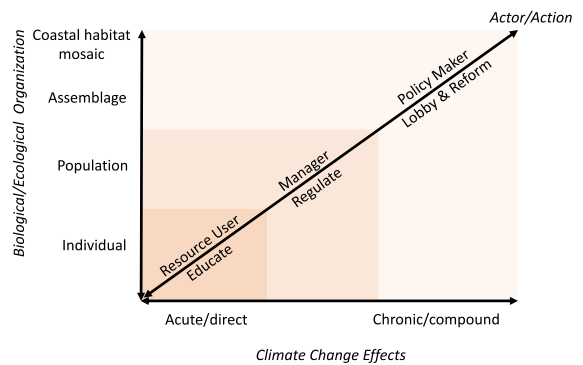


Fig. 3 Schematic diagram that integrates actors and actions with the effects of climate change on biological and ecological levels of organization that support flats fisheries. Bi-directional vectors imply cascading linkages up or down in scale/organization. Actor/actions vector reveals complementary needs that are necessary to promote positive action as it relates to the impacts of climate change of flats fisheries

reduce pressures on flats fish stocks, and promoting more robust grassroots efforts that also include advocating for actions against the growing threats of climate change.

It is essential that resource managers better engage the recreational fishing community to formulate and implement management strategies that account for habitat and climate change interactions (Fig. 3). For example, Wilson et al. (2022) suggest that managers in Florida engage the recreational fishing community to guide identification, protection, and restoration of nursery habitats for juvenile common snook to not only address threats to the snook fishery but also for broader conservation benefit. Wilson et al. (2022) borrow from the realm of terrestrial conservation to propose that common snook are a good flagship umbrella species. Flagship species are chosen to increase public awareness for conservation of habitats of concern upon which the flagship species depends (Smith and Sutton 2008). Common snook is a flagship species because it supports an economically important (Taylor et al. 2001; Young et al. 2014) and popular fishery in Florida, with an avid recreational angler population and extensive media attention within the fishing culture. Moreover, the fishing community is becoming increasingly focused on habitat conservation (Wilson et al. 2022). Common snook should also be considered an umbrella species that provides broader conservation benefits, especially valuable in response to climate change because

juvenile common snook rely upon mangrove wetlands (Adams and Murchie 2015). By engaging flats fishery stakeholders, resource managers will be better able to address any challenges brought by climate change and other anthropogenic activities summarized here.

Greater effort is needed to understand how user groups, stakeholders, and rightsholders in both developed and developing nations perceive the threats of climate change to tropical and subtropical flats species and habitats. Such information can help shape strategies related to communicating fundamental differences related to mitigation, adaptation, and resilience, as well as assessing political and societal will related to equitable strategies focused on climate change (van Putten et al. 2017). More broadly, it will be important to reflect on the future of recreational fisheries in the face of climate change and how cultural attachments to what is predominantly thought of as a leisure activity may either interfere with or help with any acknowledgement of the climate crisis that is facing our planet (van Putten et al. 2017).

Conclusion

Traditionally, given that fisheries management is largely species-specific and because many recreationally targeted species depend on the coastal habitat mosaic, recognizing the broader defining framework of flats as a collective conservation and management unit is prudent. Nearshore tropical and subtropical flats are dynamic and prone to natural extremes in physiochemical conditions, and even subtle changes in these conditions brought on by anthropogenic climate change can result in cascading effects on the structure and function of these regions, as well as the fishes they support. Since these habitats and fishes are at the ‘bulls eye’ for physiochemical impacts associated with climate change, it is critical to escalate efforts to highlight how climate change and compounded anthropogenic impacts (e.g., habitat alteration, invasive species, pollution) can permanently change these fish populations and the ecological and economic goods and services they provide. Given that many of the impacts to be felt on flats fishes will operate through changes in habitat, there is a dire need for engagement and co-production with the greater fishing community and research that identifies effective

ecological restoration practices that are resilient to environmental change.

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Author contribution Andy Danylchuk, Steven Cooke, Aaron Adams, and Lucas Griffin conceptualized the review. Andy Danylchuk and Lucas Griffin coordinated the organization of the content. All authors contributed to writing and commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Declarations

Ethics approval This article does not contain any studies involving animal subjects or human participants. It is a review paper.

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