Global conservation status and research needs for tarpons (Megalopidae), ladyfishes (Elopidae) and bonefishes (Albulidae)

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Abstract

We assessed the taxonomic diversity, geographic distributions, life history, ecology and fisheries of tarpons, ladyfishes and bonefishes (members of the subdivision Elopomorpha), which share many life history and habitat use characteristics that make them vulnerable to environmental and anthropogenic stresses in coastal environments. This assessment of Red List status for the International Union for the Conservation of Nature reveals three species considered near threatened or vulnerable, three species of least concern, and 11 data-deficient species. Although the taxonomy of tarpons appears stable, it is less so for ladyfishes and bonefishes. In aggregate, these species are distributed circumtropically and foray into temperate zones. Although they spawn in marine habitats, larvae of many species disperse into estuarine habitats, which are declining in area or degrading in quality. Several species support high-value recreational fisheries, or culturally important small-scale commercial and artisanal fisheries. Nonetheless, no formal stock assessment exists for any species, so improved data collection, information sharing and assessment techniques should facilitate socio-economic development of individual fisheries. Catch-and-release recreational fisheries that promote conservation of tarpon and bonefishes in some regions are promising models to improve the conservation status of these fishes elsewhere, as well as the economic development of these fishing communities. Most tarpons, ladyfishes and bonefishes likely face significant challenges from anthropogenically mediated habitat loss and alteration, and several are vulnerable to both habitat degradation and overfishing. Broader protection and enhancements to fisheries habitat in all regions will benefit these as well as many other coastal fishery species.

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Keywords Albuliformes, Elopiformes, fisheries conservation, habitat degradation, habitat loss, overfishing

Introduction

Tarpons (Megalopidae), ladyfishes (Elopidae) and bonefishes (Albulidae) are distributed globally among all warm-water seas. Within the subdivision Elopomorpha, representing early stages in the basal radiation of teleost fishes (Nelson 2006), these fishes are of considerable phylogenic interest, yet several new species have been named only recently or are proposed. They have complex life cycles involving ontogenetic habitat shifts among geographically distinct marine and coastal habitats, the latter of which are vulnerable to destruction or alteration. Their dependence upon coastal and nearshore habitats, and their value in consumptive and recreational fisheries, has generated concern that harvest and habitat loss and degradation pose threats to tarpons, ladyfishes and bonefishes. Moreover, sympatric distributions and conservative morphology combine to make taxonomic identification difficult and create challenges for management and conservation for ladyfishes and bonefishes.

These general concerns are difficult to directly associate with specific species because no formal stock assessment exists for any elopomorph. As part of an assessment of the global status of tarpons, ladyfishes and bonefishes for the International Union for the Conservation of Nature (IUCN), we assemble the first comprehensive Red List classification of these taxa. Overall, biological and fisheries knowledge is lacking for the majority of these species, especially in the Pacific and Indian Oceans. Still, data for 6 of 17 species were sufficient for this assessment and recommendation of conservation actions, and for 3 of the 17 species, there is specific cause for concern due primarily to a combination of harvest and habitat loss or degradation (Table 1).

We report on our findings, anticipated threats to these species, and suggest future directions for data acquisition and conservation. This review is organized to first provide a summary on the general status of knowledge (biology, fisheries, threats) for each family, followed by a broader discussion of threats and recommended conservation measures that encompasses all species. Species-specific information on Red List status, major threats and conservation needs is available in Table 1, and on geographic range in Table 2; detailed species-specific accounts are available online (http://iucn.org).

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E. affinis DD Dams and reduced river flow; effects unknown	Ir Indexe	information regarding taxonomy, population status, fisheries interactions and potential threats

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Family	Binomial	Red List Status	Major threats	Research and conservation needs
Albulidae	A. nemoptera	DD	Unknown	Information regarding demographics, population status, fisherias interactions and notential threats
	A. oligolepis	DD	Likely targeted by commercial, recreational and subsistence fishers but there are no data specific to this species. It may occur as by-catch. Given its shallow water habitat, degradation and habitat loss, declines in water quality may adversely affect this species. Effects unknown	Information regarding demographics, population status, fisheries interactions and potential threats
	A. sp. B	DD	Habitat loss, degradation, fragmentation and declining water quality of juvenile habitats; effects unknown	Information regarding demographics, population status, fisheries interactions and potential threats
	A. sp. cf. <i>vulpes</i>	Not Evaluated	This species has been genetically identified, but not taxonomically described.	Taxonomic description. Information regarding demographics, population status, fisheries interactions and potential threats.
	A. vulpes	ΤN	Commercial, artisanal and recreational fisheries, habitat loss and fragmentation (particularly mangroves and seagrasses), declines in water quality, coastal development and urbanization	New information on population dynamics and resource ecology is critically needed to support fishery management strategies
	A. glossodonta	٨U	Commercial, artisanal, and recreational fisheries, habitat loss and fragmentation (particularly mangroves and seagrasses), declines in water quality, coastal development and urbanization	Uncertainties regarding taxonomy and population connectivity need resolution
	A. argentea	Not Evaluated	This species has also been referenced as <i>A. neoguinaca</i> and <i>A. forsteri.</i> As little information exists and the taxonomic designation remains unclear, this species was not evaluated.	Taxonomic description. Information regarding demographics, population status, fisheries interactions and potential threats
	P. belloci	DD	Although of minor commercial importance, it is often found in the by-catch of commercial vessels; effects unknown	Information regarding ecology, life history, fisheries impacts and potential threats
	P. gissu	DD	May occur as by-catch in deep trawl fisheries; effects unknown	Information regarding ecology, life history, fisheries impacts and potential threats

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Family	Binomial	Geographic range
Megalopidae	<i>Megalops atlanticus</i> (Valenciennes, 1847) <i>Megalops cyprinoides</i> (Broussonet, 1782)	W. Atlantic ¹ : VA to Gulf of Mexico, Caribbean Sea, C. and S. America E. Atlantic ² : Mauritania to Angola E. Pacific ³ : Panama and Costa Rica Indo-W. Pacific: East Africa to Society Isl., Japan to Australia
Elopidae	Elops saurus (Linnaeus 1766)	Western N. Atlantic ⁴ : New England to Florida, Gulf of Mexico, Yucatan Penninsula
	Elops smithi (McBride et al. 2010)	Western S Atlantic. ⁵ : Brazil through Caribbean Sea, Bahamas, SW Gulf of Mexico
	<i>Elops lacerta</i> (Valenciennes, 1847)	E. Atlantic ⁶ : W. Africa, Nigeria and Benin
	Elops senegalensis (Regan, 1909)	E. Atlantic ⁷ : W. Africa, Nigeria and Benin
	Elops hawaiiensis (Regan, 1909) Elops machnata (Forsskål, 1775)	Indo-W. Pacific ⁸ : Andaman Sea to Hawaii, S. Japan to NW Australia. Indian O. & W. Pacific ⁹ : Red Sea to E. Africa, Seychelles, Madagascar, Mascarenes. Phillipines. Hawaii
	<i>Elops affinis</i> (Regan, 1909)	E. Pacific ¹⁰ : S. California to Peru, including Cocos Isl.
Albulidae	Albula nemoptera (Fowler, 1911)	W. N. Atlantic: Caribbean Sea E. Pacific ¹¹ : Central American coast
	Albula oligolepis	Indian Ocean ¹⁸
	A. sp. B (description pending)	W. &. E Atlantic ¹² : Western North Atlantic and Caribbean Sea, W Africa
	A. sp. cf. <i>vulpes</i> (description pending)	W. Atlantic: Florida, US. Virgin Isl., Mexico
	Albula vulpes (Linnaeus, 1758)	W. Atlantic ¹³ : Caribbean Sea, The Bahamas, Florida Keys
	<i>Albula glossodonta</i> (Forsskål, 1775)	Indo-W. Pacific ¹⁴ : Seychelles to Hawaii, Japan to N. Australia
	Albula argentea (Bloch and Schneider, 1801)	W. Pacific ¹⁵ : Hawaii, Fiji, Northern Territory, Australia
	Pterothrissus belloci (Cadenat, 1937)	E. Atlantic ¹⁶ : Mauritania to Namibia
	<i>Pterothrissus gissu</i> (Hilgendorf, 1877)	NW Pacific ¹⁷ : Japan, China and Russia

 Table 2
 Geographic ranges for 17 species of the families Megalopidae, Elopidae and Albulidae.

¹Zale and Merrifield (1989), Crabtree et al. (1995).

²Migdalski and Fichter (1976), Anyanwu and Kusemiju (2008).

³Swanson (1946).

⁴Crabtree (2002), McBride and Horodysky (2004), McBride et al. (2010).

⁵McBride and Horodysky (2004).

⁶Ikomi (1994), Adite (2002), Agboola and Anetekhai (2008), Lawson and Aguda (2010).

⁷Adite (2002), Agboola and Anetekhai (2008), Abowei (2010).

⁸Fujita et al. (2002), Doupe et al. (2005), Eschmeyer and Fong (2008).

- ⁹Fraser (1973), Smith-Vaniz (1984), Eschmeyer and Fong (2008).
- ¹⁰Follett (1960), Lea and Rosenblatt (2000), Eschmeyer and Fong (2008).
- ¹¹Wallace and Tringali (2010).

¹⁴Colborn et al. (2001), Friedlander et al. (2008).

¹⁶Smith (1986), Hulet and Robins (1989).

¹⁷Masuda *et al.* (1984), Ueno (1984), Nelson (1994), Zhang (2001), Novikov *et al.* (2002).

¹⁸Hidaka *et al.* (2008).

Methods

An IUCN Red List Assessment Workshop was held at the Perry Institute for Marine Science on Lee Stocking Island, in Exuma, Bahamas, in March 2011, to synthesize existing species-specific data and apply IUCN Red List Categories and Criteria (IUCN 2001) to 17 species of the families Megalopidae, Elopidae and Albulidae. The IUCN Red List Categories and Criteria are the most widely

¹²Colborn et al. (2001), Wallace and Tringali (2010).

¹³Bowen *et al.* (2008).

¹⁵Colborn *et al.* (2001).

accepted system for classifying extinction risk at the species level (Butchart et al. 2005; Rodrigues et al. 2006; Hoffmann et al. 2008). The assessment process consolidates the most current, highquality data available and ensures peer-reviewed scientific consensus on the probability of extinction for each species. The conservation status of each species was independently evaluated during the 5-day workshop, utilizing verified species-specific information on taxonomy, distribution, population status and trends, life history, and ecology. Past, existing and potential future threats, and present conservation actions were included in these evaluations. Ouantitative information was then used to determine whether a species met the threshold for a threatened category.

The workshop participants represented scientists with extensive knowledge of species tarpons, ladyfishes and bonefishes through research of these species and collaboration with colleagues involved in research or fisheries management of these species. In addition, as part of the workshop and manuscript preparation process, workshop participants interacted with colleagues to gain additional information that was absent from the peer-reviewed and gray literature. Much of this information is referenced herein as 'personal communication'. For example, information from Australia, Nigeria, Brazil and Central America was gleaned from interactions with colleagues from those areas. Workshop participants also found that in many instances, there was no local or scientific knowledge of life history or fisheries landings (e.g. portions of the west coast of Africa). Finally, relevant sections of this manuscript were shared with colleagues in geographical regions of coverage during manuscript preparation. As is frequently noted in the body of this manuscript, there remains relatively little known about many of these species, the habitats upon which they depend, and the fisheries they support.

The IUCN Red List Categories are comprised of eight different levels of extinction risk: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) and Data Deficient (DD). A species qualifies for one of the three threatened categories (CR, EN or VU) by meeting the quantitative threshold for that category in at least one of the five different IUCN Criteria (A–E). The criteria are based on the highest quality data available regarding extinction risk theory (Mace *et al.* 2008) and provide a standardized methodology that is applied consistently to any species from any taxonomic group (Butchart *et al.* 2004; Stuart *et al.* 2004; Carpenter *et al.* 2008; Schipper *et al.* 2008; Polidoro *et al.* 2010; Collette *et al.* 2011; Knapp *et al.* 2011).

Tarpons, ladyfishes and bonefishes were assessed under Criterion A. A species qualifies for a threatened category under this criterion when it meets the threshold of population decline (30% for Vulnerable, 50% for Endangered and 80% for Critically Endangered): (i) over a time frame of three generation lengths, a measure of reproductive turnover rate; (ii) in the recent past; or (iii) if the species is expected to reach those thresholds in the near future. This decline can be based on any of the following: direct observation; an index of abundance appropriate to the taxon, such as catch per unit effort (CPUE): a decline in area of occupancy (AOO). extent of occurrence (EOO) and or/habitat quality; actual or potential levels of exploitation: or effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites. Under Criterion A, generation length is the average age of the reproducing adult (IUCN 2001) and was conservatively estimated using published estimates of age at first maturity and longevity. Global population reductions were inferred from declines in fisheries landings and habitat area and habitat quality.

A category of NT is assigned to species that come close to, but do not fully meet all requirements of a threatened category under any given criterion. A category of LC is assigned if available data on a species fall below any given criterion threshold, indicating a relatively low risk of extinction. A species is assessed as DD when extinction risk or population status cannot be evaluated because of insufficient available information. An assigned category of DD does not mean that a species is not threatened, merely that there are presently insufficient data for assessment. When data become available, DD species often prove to be at risk.

Overview of the Elopomorpha

The Elopomorpha is generally considered a monophyletic group (Greenwood *et al.* 1966; Forey *et al.* 1996), although there is some controversy surrounding the monophyly of the clade as well as inter- and intra-relationships among the taxa (Forey *et al.* 1996; Nelson 2006). Nelson (2006) recognizes three orders within the Elopomorpha,

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two of which are reviewed here: Elopiformes (including tarpons and ladyfishes) and Albuliformes (including bonefishes). Other researchers differ on the treatment of notacanthid and saccophangeoid fishes as separate orders (see Nelson 2006). Elopomorph fishes represent one of the earliest stages in the basal radiation of teleost fishes (Greenwood et al. 1966; Nelson 2006). One of the primary synapomorphic characteristics of the elopomorph fishes is the laterally compressed, transparent leptocephalus larval stage. Planktonic leptocephalus larvae may persist in the open ocean for months prior to metamorphosis to the juvenile stage in shallow coastal habitats (Greenwood et al. 1966; Pfeiler 1986). The potential for long-distance transport of the larvae can provide important genetic linkages among dispersed shallow water populations of adults (Reece et al. 2011), and add to the challenge of assessing local populations.

Status of knowledge

Tarpons, ladyfishes and bonefishes are distributed throughout the world's tropical and subtropical coastal waters, with some distributions extending to temperate waters. The vast majority of these fishes depend upon coastal habitats for all or portions of their life histories, which make them especially susceptible to harvest and habitat degradation or loss. Available data indicate that all species are offshore spawners. Nearly all species show some form of ontogenetic, seasonal and spawning movements: juveniles of most species are obligate inhabitants of shallow coastal or estuarine nursery habitats; adults use an expanded and diverse range of coastal habitats. The wide range of coastal habitats required for most species thus creates challenges for conservation. Figures 1 -5 summarize the geographic distribution of the species assessed herein, depict spatial distributions of species richness, and identify geographic locations of concern (areas which contain a high proportion of species designated as Threatened).

Elopiformes: Megalopidae: Megalops spp

Two tarpon species are distributed throughout tropical and subtropical habitats of the Atlantic, Pacific and Indian Oceans (Table 1). Megalops cyprinoides (Megalopidae) is widely distributed in the Indo-Pacific (Table 2) and is common in parts of its range. Megalops atlanticus (Megalopidae) is widely distributed in the North Atlantic Ocean (Table 2), Gulf of Mexico and Caribbean Sea. Adults have been observed as far north as Nova Scotia and Ireland (Twomey and Byrne 1985), but these likely represent vagrants. This species has recently become established on the Pacific coast of Panama and Costa Rica, presumably via the Panama Canal (Swanson 1946). The latitudinal distribution of Atlantic tarpon is limited by sensitivity to low temperature (Zale and Merrifield 1989); in the extremes of their range, tarpon experience winter thermal mortality circa 10 °C (Robins et al. 1977) and have an upper lethal thermal limit of 40 °C (Moffett and Randall 1957).

Although spawning of *Megalops* species has not been observed and specific locations have not yet



Figure 1 Species richness of tarpons.



Figure 2 Percentage of species of tarpons classified as Vulnerable (see text for explanation of classifications). The species depicted here is *M. atlanticus*. *M. cyprinoides* was classified as Data Deficient.



Figure 3 Species richness of the ladyfishes.

been identified, it is presumed to occur offshore based on collection of day old larvae (Leis and Reader 1991 as cited in Ley 2008; Crabtree *et al.* 1992; Shenker, unpub. data) and by following offshore movements of adult fish (Ault *et al.* 2008). Schools of gravid *M. atlanticus* migrate from nearshore and inshore habitats to form large pre-spawning aggregations approximately 2–5 km offshore before moving presumably up to 200– 250 km offshore where 3- to 6-day old larvae were collected (Crabtree *et al.* 1992). These spawning events relate to summer lunar phases in Florida (Crabtree 1995; Shenker *et al.* 2002), and spawning seasons are more protracted in tropical waters such as Costa Rica (Crabtree *et al.* 1997a) and Puerto Rico (Zerbi *et al.* 2001). In India, *M. cyprinoides* inhabit the estuary of the Waltair Coast as juveniles and mature in coastal areas where spawning may occur twice per year (Kulkarni 1983; Padmaja and Rao 2001). The collection of a single larva from the Great Barrier Reef approximately 25–45 km off the Australian mainland (Leis and Reader 1991) indicates offshore spawning of this species. *Megalops* spp. are iteroparous batch spawners (de Menezes and Paiva 1966; Smith 1980; Cyr 1991; Chacon-Chaverri 1993; Crabtree *et al.* 1997a; Ley 2008).

Larvae of both species swim or drift with tidal currents and recruit to shallow coastal nurseries in 20–40 days post-hatching (Tsukamoto and

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Figure 4 Species richness of bonefishes. As the taxonomy of bonefishes in the Indo-Pacific is still in a state of revision, depictions for that region should be viewed with caution.



Figure 5 Percentage of species of bonefishes classified as Vulnerable (see text for explanation of the classification).

Okiyama1997; Tzeng *et al.* 1998; Shenker *et al.* 2002). Post-metamorphic juveniles are euryhaline and have been collected in waters ranging from 0 to 45 PSU. The vascularized swim bladders of tarpon allow aerial respiration, permitting juveniles to inhabit hypoxic inshore waters where they presumably experience low predation rates and have little competition for prey (Schlaifer and Breder 1940; Geiger *et al.* 2000; Seymour *et al.* 2004). Juvenile *M. atlanticus* habitats include stagnant pools, back waters, ephemeral coastal ponds and hurricane and storm overwashes, swales, and mangrove swamps and marshes, as well as manmade habitats such as mosquito impoundments and artificial wetlands (Wade 1962; Dahl *et al.*

1965; Robins *et al.* 1977; Zerbi *et al.* 2001; Jud *et al.* 2011). In contrast, *M. cyprinoides* are more abundant in wave-dominated estuaries that are located in higher rainfall catchments, have more constricted mouths, less mangrove area, and sandy substrate (Ley 2005). As they grow, juveniles of both species spend significant time in larger rivers, bays and estuaries before exhibiting the more extensive movements of adults (Crabtree *et al.* 1995; Pusey *et al.* 2004). Adult *M. atlanticus* [>120 cm fork length (FL)] also inhabit inshore waters and bays, across a wide range of salinities (fresh to hypersaline) and temperatures (17–40°C) (Zale and Merrifield 1989; Crabtree *et al.* 1995). They are also capable of seasonal migrations along the south-east coastline of the United States and around the periphery of the Gulf of Mexico (Ault *et al.* 2008).

Juvenile *M. atlanticus* prey upon zooplankton, small crustaceans, polychaetes and insects that frequent inshore nurseries (Harrington 1958; Jud *et al.* 2011). As older juveniles and adults begin to inhabit deeper-water habitats such as lagoons, creeks, canals and sloughs for emigration to coastal bays, their diet transitions to larger crustaceans (penaeid shrimps, swimming crabs), polychaetes, and a suite of fishes (Whitehead and Vergara 1978; Boujard *et al.* 1997). The diet of *M. cyprinoides*, summarized from four trophic studies, is also highly diverse and consists of insects, fish, crustaceans, crabs and even plants, although they are classified as opportunistic, intermediate carnivores (Ley 2008).

Megalovs species are fairly long-lived compared to other elopomorphs, with M. atlanticus reaching maximum ages of 43–78 years (Crabtree et al. 1995: Andrews et al. 2001) and M. cyprinoides reaching 44 years (Kulkarni 1983). Adult M. atlanticus may exceed 2 m in length and 110-130 kg in mass (Crabtree et al. 1997a; J.S. Ault., personal communication), reaching substantially larger maximum sizes than M. cyprinoides (61 cm and 18 kg mass; Coates 1987; Lev 2008). Consequently, although there is considerable variation across its range, M. atlanticus reaches sexual maturity at larger body sizes (>130 cm) and later ages (7-12 years) (de Menezes and Paiva 1966; Chacon-Chaverri 1993; Crabtree et al. 1997a) than M. cyprinoides (30-40 cm, 2 years; Coates 1987; Padmaja and Rao 2001; Pusey et al. 2004; Ley 2008).

Elopiformes: Elopidae: Elops spp

Seven *Elops* species are distributed throughout much of the tropical and subtropical marine and estuarine habitats of the Atlantic, Pacific and Indian Oceans (Table 2). They may also be dispersed as larvae or venture as rare vagrant adults to temperate latitudes of the Atlantic and Pacific oceans. Two sympatric species, *Elops senegalensis* (Elopidae) and *Elops lacerta* (Elopidae), occur in the Eastern Atlantic and are often mistaken for one another in the western African estuaries of Benin and Nigeria (Adite 2002; Agboola and Anetekhai 2008; Abowei 2010). Two largely allopatric species are now recognized in the western Atlantic, *Elops saurus* (Elopidae) and the recently described *Elops smithi* (Elopidae). Although mostly geographically isolated, their distributions overlap in the Gulf of Mexico and south-east USA (McBride and Horodysky 2004; McBride *et al.* 2010). Two Indo-Pacific species, *Elops hawaiiensis* (Elopidae) and *Elops machnata* (Elopidae), may also occur sympatrically, but species identifications have been contested in some reports (e.g., Whitehead 1962; Sato and Yasuda 1980). The Eastern Pacific has a single species; *Elops affinis* (Elopidae).

Offshore spawning by *Elops* species is inferred from the distribution of specific life stages (e.g., Gehringer 1959; Ugwumba 1989; Tzeng and Wang 1992; Aceves-Medina *et al.* 2003; Tzeng *et al.* 2005) and the larval duration appears to extend up to several months. Larvae are transported to and metamorphose in shallow embayments (Sato and Yasuda 1980; Beckley 1984). Age-0 stages settle in low salinity areas in estuaries without entering fresh water (McBride *et al.* 2001), but juveniles are capable of surviving hypersaline conditions (>60 PSU; Bayly 1972).

In regions of sympatry, recruitment by multiple *Elops* species may occur over broad time scales but each species may be temporally specific. For example, the nearly year-round recruitment of *Elops* to Florida, USA, estuaries is now known to arise from *E. saurus* in the winter–spring and the recently recognized *E. smithi* in autumn (McBride and Horodysky 2004). There is little information on gonad development to confirm reproductive seasonality, except 'a nearly ripe female of 604 mm ...taken on October' (Hildebrand 1963) or females in spawning condition nearly year-round (Santos-Martínez and Arboleda 1993).

In estuaries, *Elops* species are almost exclusively carnivorous but sample sizes are typically low, so prey diversity or potential for prey switching is poorly known [but see Santos-Martínez and Arboleda (1993); who reported high taxonomic diversity in the diet]. Fishes, crustaceans and other aquatic invertebrates dominate the Elops diet, and insects and plant material are also reported in small quantities (Hiatt 1947; Odum and Heald 1972: Santos-Martínez and Arboleda 1993: Smith 1997). Ontogentic shifts in diet - from the larval to juvenile stages - are expected but have been reported in detail only by Harrington and Harrington (1960). Sportfish and marine mammals eat Elops species (Simmons 1957; Barros and Wells 1998), but the trophic value of Elops species to aquatic ecosystems has not been evaluated.

Age, growth and reproductive characteristics are poorly known for all Elops species. One report of planktonic larval duration indicates that larval transport can occur over several weeks (Wheeler 2000). No validated method to determine annual growth has been reported, but length-frequency analyses suggest that only three-year classes occupy estuaries and nearshore habitats (Ugwumba 1989; McBride et al. 2001; McBride and Horodysky 2004: Lawson and Aguda 2010). while examinations of scales and otoliths indicate that Elops species live at least 4-6 years (Blake and Blake 1981; Palko 1984). Gonad maturity occurs once fish leave the estuary, at sizes larger than 500 mm (Ugwumba 1989; Santos-Martínez and Arboleda 1993; McBride et al. 2001). The only report of fecundity - approximately 500 000 yolked eggs (Santos-Martínez and Arboleda 1993) does not account for the dynamics of oogenesis or spawning frequency, so reproductive potential is poorly known.

Albuliformes: Albulidae

The family Albulidae is comprised of two genera. Members of Albula are found throughout the world's shallow tropical seas, whereas Pterothrissus inhabit waters of the continental slope up to 1000 m in depth in subtropical and temperate regions of the Eastern Atlantic and North-west Pacific (Table 1). Bonefishes are currently in a state of revision, and this is especially true in the Pacific and Indian Oceans, where species delineation and geographic distributions remain unclear. Until recently, the genus Albula contained two species, the circumglobal Albula vulpes (Albulidae) and the western Atlantic and eastern Pacific Albula nemoptera (Albulidae). Recent morphometric and population genetic research indicates that there are at least 12 morphologically indistinguishable, but genetically distinct species (Colborn et al. 2001; Hidaka et al. 2008; Wallace and Tringali 2010; Kwun and Kim 2011; Pfeiler et al. 2011). In the Caribbean and western North Atlantic, there are two described species of Albula, A. vulpes and A. nemoptera, and we include here recent genetic work that documents two additional cryptic and presently unnamed species: Albula species B (Albulidae) and Albula sp. cf. vulpes (Albulidae) (Colborn et al. 2001; Adams et al. 2008; Bowen et al. 2008; Wallace and Tringali 2010; Albula sp. cf. vulpes referenced as Albula sp. F in Valdez-

Moreno et al. 2010; Pfeiler et al. 2011). In the Indo-West Pacific, Albula glossodonta (Albulidae) is broadly distributed, and in Hawaii, Fiji and northern Australia, it is sympatric with Albula argentea (Albulidae) (also referenced as Albula neoguinaca and Albula forsteri). Albula oligolevis (Albulidae) is recorded from the Indian Ocean (Hidaka et al. 2008), Albula virgata (Albulidae) from Hawaii (Jordan and Jordan 1922) and Albula koreana (Albulidae) has been recently described for Korea and Taiwan (Kwun and Kim 2011), but little is known about these species. Because Albula morphology has been conserved across species, taxonomic identification remains difficult, yet their different life history requirements necessitate focused conservation strategies for each species.

There are two deepwater *Pterothrissus* species: *Pterothrissus belloci* (Albulidae) in the eastern Atlantic and *Pterothrissus gissu* (Albulidae) in continental slope waters of the North-west Pacific (Masuda *et al.* 1984; Ueno 1984; Hulet and Robins 1989; Nelson 1994; Zhang 2001; Novikov *et al.* 2002).

Similar to the situation with other elopomorphs examined herein, offshore spawning in bonefishes is inferred from the movements of adults and the subsequent distribution of specific life stages. Spawning in Albula spp. is poorly known except for A. vulpes, but it is likely that other Albula spp. show similar patterns and behaviours. From October through April or May, schools of adult A. vulpes migrate from nearshore and inshore habitats to form large pre-spawning aggregations presumably before moving offshore for spawning in deep waters (>300 m) on the full moon (Danylchuk et al. 2011). Planktonic duration of A. vulpes and A. glossodonta leptocephali is 41-71 days, with recruitment to inshore nurseries from summer through winter, reflecting either a prolonged spawning season (Mojica et al. 1994; Friedlander et al. 2008) or similar seasonal spawning by cooccurring cryptic species. Spawning or larval dispersal by Pterothrissus species is unknown.

Juvenile and adult stage *Albula* spp. use a range of shallow, nearshore habitats, including seagrass beds, mangroves, sand flats, mud flats, marl flats, algae beds, coral reefs, beaches, and other shallow water subtidal and intertidal habitats (Shaklee and Tamaru 1981; Colton and Alevizon 1983; Kaufmann 2001; Layman and Silliman 2002; Layman *et al.* 2004; Nero and Sullivan-Sealey 2005; Adams *et al.* 2008; Friedlander *et al.* 2008). Bonefishes feed predominately on benthic invertebrates (bivalves, polychaetes, crustaceans) but also on small fishes; piscivory increases with size (Warmke and Erdman 1963; Friedlander *et al.* 1997; Crabtree *et al.* 1998; Snodgrass *et al.* 2010). *Pterothrissus* species appear to prey on polychaetes and benthic copepods, although a synoptic understanding of their diet is lacking (Macpherson and Roel 1987).

Growth rates of A. vulpes appear to differ geographically, with faster growth (up to 3x) occurring in the Florida Keys, and slower growth in the Bahamas, Central America and insular Caribbean (Adams et al. 2008; C. Haak, UMass, unpublished data); growth may vary even at the scale of the Bahamas archipelago (C. Haak, personal communication). Recent aging of large bonefish has revealed that A. vulpes live to at least 20 years in the Florida Keys (Larkin 2011) and 25 years in the Bahamas (C. Haak, personal communication), reaching sizes >70 cm (Crabtree et al. 1996). Pacific A. glossodonta can reach 8 kg in mass and 90 cm in length (Myers 1991). In contrast, deepwater Pterothrissus species have only been collected up to 47 cm in length, with size at maturity estimated circa 40 cm (Whitehead 1990). On average, A. vulpes and A. glossodonta mature between 3.5 and 4.5 years between 42 and 49 cm, with males maturing at smaller sizes and vounger ages than females (Crabtree et al. 1997b; Friedlander et al. 2008). Size and age at maturity and dimorphic growth patterns are unknown for most other bonefishes and may differ among regions. For example, smaller specimens of mature A. vulpes individuals have been sampled in the Caribbean (Adams et al. 2008), and intense fishing pressure has decreased the size-at-maturity by roughly 10 cm for A. glossodonta in Tarawa Lagoon in the Pacific (Beets 2000).

Global fisheries for Megalopidae, Elopidae and Albulidae

Many of the elopomorph species assessed herein are economically or culturally important, yet large gaps of knowledge persist regarding their basic biology and harvest (landings) which hampers effective management. In the United States, these species support important recreational fisheries and, with the exception of ladyfish (*Elops* spp.), have never been commercially harvested, so few landings data have been collected. Moreover, few landings data on these fisheries are available from other regions, inhibiting the examination of population status and trends.

Megalopidae

The two *Megalops* fisheries are very different. *Megalops cyprinoides* supports artisanal fisheries in India and Papua New Guinea (Coates 1987), whereas they are landed commercially in the Philippines and Malaysia, occur as bycatch throughout their range, and are the target of a directed sport fishery in northern Australia (Wells *et al.* 2003). In general, fishery and biological data are unavailable, which stymies stock assessments in countries where this species is exploited.

The economic value of M. atlanticus is better known; it is an economically important recreational species and occurs in cultural, subsistence, aquaculture and small commercial fisheries in portions of its range. The recreational fishery for this species developed in 1885 in Florida (White and Brennan 2010) and has expanded along the south-eastern United States, the Gulf of Mexico, and portions of the Caribbean. In some parts of its range outside of the United States, M. atlanticus have cultural, subsistence and commercial value: the scales are used for medicinal purposes in Brazil (B. Ferreira, personal communication); they are traditionally served at Christmas in Africa (P. Anyanwu, personal communication) and Central America: they are consumed readily in Cuba and Colombia (Garcia and Solano 1995); and subsistence and small scale commercial fisheries for roe and flesh occur in Mexico and some of the Caribbean Islands (A.J. Adams and K.Y. Guindon, personal communication). In Nigeria, tarpon are cultured for food from wild stocks of juveniles (P. Anyanwu unpublished data). They occur as incidental catch by purse seiners, long-liners and gill nets in Mexico and Belize, and are often brought to market (J.S. Ault, Univ. Miami, personal communication).

There has been no formal stock assessment of tarpon in any portion of the species' range; however, multiple lines of evidence suggest that populations of *M. atlanticus* appear to have declined from historical levels throughout their range. Although patchy, data on total commercial landings in Central and South America (Fig. 6) show large historical declines. Total global landings of *M. atlanticus* declined 84.5% between 1965 and



Figure 6 Annual reported or estimated landings (metric tons) of *M. atlanticus* from Brazil, Columbia, Mexico and other countries (Columbia, Dominican Republic, French Guiana, Puerto Rico and Suriname), from 1950–2006. (Data from FAO 2011).

2007, particularly in Brazil, and mostly during the early years of that time period, reflecting a drop in population size rather than change in fishery effort (FAO 2011). Using a generation time of 12.7 years for tarpon (Froese and Pauly 2010), the estimated decline in FAO landings over three generations (38 years) is $\geq 80\%$.

Most twentieth century data on the M. atlanticus recreational fishery in the USA is from Florida. Catches in the recreational tarpon fishery in south-west Florida appeared to decline after the mid-1930s with a notable decrease during World War II (1941–1945) (White and Brennan 2010). However, the fishery changed from harvest to catch-and-release during post-war years; this practice increased through the 1970s, contributing to a decline in recorded landings (White and Brennan 2010; Guindon 2011). Anglers perceive population declines in Florida waters since the 1960s, mirrored by a decline in average length in the catches as recorded by anglers on souvenir scales through 1980 (Bortone 2008). A similar population decline was observed in Texas in the 1960s and 1970s (Winemiller and Dailey 2002): however, length modes did not decline over time as observed in Florida (Holt et al. 2005). This may result from the selection of only large fish for display or acknowledgement, and/or a possible post-1960 reduction in recruitment of smaller juvenile tarpon into the fishery, especially from Mexico, resulting from a decline in nursery habitat and/or overfishing (Holt *et al.* 2005). In more recent years (1981–2010), most recreational catches of *M. atlanticus* in the USA occurred along the Gulf of Mexico coast (Fig. 7), with additional catches in Puerto Rico.

Currently, more than 95% of the catch in the USA is from Florida, where most tarpon are released. In fact, when data from the Floridaissued \$50USD harvest permits are used as a proxy for harvest over the last decade, it is estimated that less than 1% of the total recreational tarpon catch is harvested (Guindon 2011). Therefore, in this and other areas where M. atlanticus supports a catch-and-release fishery, post-release mortality likely has greater impact on abundance than does harvest. In the absence of predation, estimated post-release mortality is 5% for the Gulf of Mexico coast of Florida. However, predation by sharks increases post-release mortality to 13% [95% CI 6-21%, but upper 95% CI may reach 28% when analysed by individual estuarine systems (Guindon 2011)]. Estimates of post-release mortality of M. atlanticus in Florida (Guindon 2011) applied to USA catch data suggest annual recreational post-release mortality ranges from 8000 to 16 000 individuals (Fig. 8).

Recreational fishing regulations for *M. atlanticus* differ regionally. In the USA, for example: Alabama – minimum size 60" total length (TL), \$50 (USD) tag required for each harvested fish; Florida – catch-and-release only unless a special



Figure 7 Estimates of total annual catch from the recreational *M. atlanticus* fishery for the USA. Data presented are total catch (harvested + released) for the Gulf of Mexico and Atlantic coasts of the continental United States and Puerto Rico [Personal communication from the National Marine Fisheries Service, Fisheries Statistics Division (2011)]. All areas and modes of fishing were included.



Figure 8 Annual release mortality based on the estimated numbers of *M. atlanticus* released alive along the Atlantic and Gulf Coasts of the USA from 2000 to 2010. Catch data are available from the National Marine Fisheries Service, Fisheries Statistics Division (2011). Dotted lines represent the upper and lower 95% confidence limits based on proportional standard errors reported with the MRFSS data. Average mortality estimates were calculated using the short-term catch-and-release mortality rate of 13% representative of Florida's Gulf Coast recreational fishery that included post-release shark predation (Guindon 2011).

harvest tag (\$50 USD) is purchased; Georgia – open season March 16 through November 30, minimum size 173 cm FL, allowable harvest of 1 per person per day; Louisiana and Mississippi – not regulated; North Carolina and South Carolina – allowable harvest of 1 per person per day, no minimum size; Texas – minimum size 216 cm TL,

allowable harvest of one per person per day; Puerto Rico and United States Virgin Islands – catch-and-release only. There are no regulations in USA federal waters. Elsewhere, regulations are the following: Belize – catch-and-release only; Mexico – two per person per day, no minimum size; Cuba – catch-and-release only in recreational fishing protected areas, no regulations outside of these zones; no regulations in other locations.

Although more of the fishery appears to be trending toward catch and release, historically high levels of harvest (followed by dramatic declines) and continuing harvest in some areas, suggest cause for concern. In addition, *M. atlanticus* is a periodic species (Winemiller and Rose 1992), long-lived and late to mature, with correspondingly long generation length (>10 years), which may affect its resistance to and recovery from threats. Species with long generation lengths have correspondingly high population recovery time and are thus typically more susceptible to threats that cause population declines (Collette *et al.* 2011).

Elopidae

Of the seven Elops species, adequate fisheries information is published for only E. saurus and E. machnata. Nonetheless, where comparative information is available, the basic biology, fisheries and threats appear to be similar within the genus. Elops species are important components of global fisheries, in either commercial, recreational or subsistence sectors. Time series of landings, catch or effort exist in Florida, USA and South Africa (Mann et al. 2002; FWC 2008). In other locations, fisheries statistics are lacking, and as no formal stock assessment for any Elops species exists, the effect of fishing mortality on Elops populations is difficult to evaluate. In the better documented examples (E. saurus, E. machnata), populations appear stable, but in both cases, commercial effort restrictions are in place or no commercial sale is allowed. Other, likely more pressing threats to Elops species include coastal habitat degradation or loss.

Elops saurus is primarily harvested for bait in the USA (e.g. Simmons 1957), is taken for human consumption (K.Y. Guindon, personal communication) and serves as an important recreational game fish for light-tackle anglers (Fable and Saloman 1974; Harper *et al.* 2000; FWC 2008). There are historic time series data for commercial (fish meal, human consumption) and recreational catches as well as fishery-independent time series data of *E. saurus* in the southeast USA. The recent discovery of *E. smithi*, a sympatric congener with *E. saurus* in the southeast USA, does not influence the interpretation of these landings because the newly recognized species most likely comprises only 1-2% of the south-east U.S. catch (McBride and Horodysky 2004). Carles (1967) reported that *E. smithi* were used as bait in commercial fisheries in Cuba; this species is caught in subsistence fisheries elsewhere in its range (Zaneveld 1962; R.S. McBride, personal communication).

Most USA commercial landings of E. saurus occur along Florida's Gulf of Mexico coast, where landings rose steadily from the 1960s to peak at 2630 MT in 1990 (Fig. 9). Due to Florida's statewide prohibition of entangling nets in 1995, landings declined to 500 MT in 2009. Recently, the landings attributed to other Gulf of Mexico states have increased, and since 2000, landings attributed throughout the Gulf have averaged 625 MT (\pm 227 MT SD). These landings over the last decade are similar to landings from the 1960s, suggesting that the effect of Florida's net ban on restricting effort have contributed to relative stability in the commercial landings of E. saurus. Most USA recreational landings of E. saurus also occur in the Gulf of Mexico (Fig. 10). Recreational landings increased markedly following the late 1990s, in both Gulf of Mexico and Atlantic fishing regions, possibly due to Florida's net ban restricting the availability of commercial product. There are no recreational size or bag limits in place for E. saurus in Florida waters. Minor landings in the Caribbean have only been reported from Puerto Rico since 2000, and these should be attributed to E. smithi, because E. saurus does not occur there (Schmied and Burgess 1987; McBride et al. 2010).

Annual trends in abundance for *E. saurus* ($\geq 200 \text{ mm SL}$) collected by Florida's Fisheries-Independent Monitoring program's 183-m haul seine surveys in Atlantic and Gulf coast estuaries show an overall increasing trend in abundance between 1998 and 2010 (Fig. 11). CPUE has been 4.5 times greater in Florida's Gulf of Mexico estuaries than Atlantic estuaries.

Other *Elops* species also support important recreational, commercial and subsistence fisheries in other regions. *E. lacerta* and *E. senegalensis* are considered commercial species in Benin (Adite 2002), with *E. lacerta* comprising 5–6% of the artisanal fishery and 3–4% of the coastal trawl fishery (Ugwumba 1989; Ikomi 1994). *Elops machnata* is also an important component of recreational and subsistence fisheries in African estuaries. The



Figure 9 Commerical landings of ladyfish, nominally *E. saurus*, in the United States from 1950 to 2009. Data are available at http://www.st.nmfs.noaa.gov/st1/commercial (last accessed 10 December 2012), shown here by Florida coast (Gulf of Mexico coastal counties or Atlantic Ocean coastal counties) or other regions (Gulf of Mexico states or Atlantic Ocean states).



Figure 10 Recreational landings of ladyfish, nominally *E. saurus*, in the United States from 1981 to 2010. Data are available at http://www.st.nmfs.noaa.gov/st1/recreational (last accessed 10 December 2012), shown here by region: Gulf of Mexico states, South Atlantic states, and Caribbean (=Puerto Rico). All data are combined, by fishing modes, fishing areas and catch type (A + B1 + B2). Rare catches reported for Atlantic coastal states north of the Carolinas are not plotted here.

recreational fishery landings of *E. machmata* from the St. Lucia Estuary, South Africa, were ranked eighth by numbers and fifth by weight, although CPUE was stable from 1986 to 1999 (Mann *et al.* 2002). Recreational catch is by hook and line, and spear, whereas subsistence harvest is by fish traps and gillnets (Mann and Radebe 1999). There is no commercial fishery in South Africa, where *E. machnata* is not legal to sell (Crook and Mann 2002; Kemp *et al.* 2009). In the Sundays and Swartkops estuaries (South Africa), CPUE of *E. machnata* in gill nets increased between the late



Figure 11 Annual mean catch-per-unit-effort (fish per set) of ladyfish, nominally *E. saurus*, collected during 183-m haul seine surveys conducted by Florida's Fisheries-Independent Monitoring Program in Atlantic (Indian River Lagoon) and Gulf of Mexico (Apalachicola Bay, Cedar Key, Tampa Bay, and Charlotte Harbor) estuaries of Florida, 1998–2010.

1970s and the early 1990s, and the percentage composition of anglers' catches increased from 1.9% in 1972-1978 to 2.2% in 1988-1993 in Swartkops estuary (Mann and Radebe 1999). In the Pacific, minor commercial landings of E. hawaiiensis by spearing have been reported in Hawaii (Smith 1993), and it is targeted by recreational anglers throughout its range. Everson and Friedlander (2004) reported landings of E. hawaiensis in Kaneohe Bay for 1991 and 1992 of 814.5 and 997.3 kg, respectively (3.47% of the total landings, mostly from trolling, for all species). Elops hawaiensis also occurred in prehistoric and historic fish ponds (Kikuchi 1976; Hiatt 1947; referred to as E. machnata by Bond and Gmirkin 2003). The current population status of E. hawaiensis is unknown throughout its range, and fisheries information is greatly lacking. In the Eastern Pacific, E. affinis is reported from archeological sites (Gobalet and Wake 2000), Meso-American markets (Meek and Hildebrand 1923) and modern polyculture involving shrimp and fish (Hendricks et al. 1996).

There are likely small-scale subsistence fisheries for many *Elops* species across portions of their respective ranges; however, insufficient data exist to quantify the effects of these fisheries on *Elops* species. Accordingly, efforts to improve the knowledge of the fisheries prosecuted on some species are underway (Abowei 2010), and the expansion of these efforts across the ranges of various *Elops* species is recommended.

Albulidae

Globally, shallow-dwelling Albula species support popular and highly valuable directed recreational fisheries. In portions of their range, bonefishes occur as bycatch and are taken in directed subsistence and small-scale commercial fisheries that may strongly impact regional populations. Of the bonefishes considered in this review, adequate fisheries information to facilitate Red List assessment exists for only A. vulpes and A. glossodonta. There are no known fisheries for A. nemoptera, Albula sp. B. Albula, sp. cf. vulves, A. argentea, A. oligolepis, A. koreana, A. virgata, P. belloci, and P. gissu, although some of these species may comprise a proportion of total bonefish catch of fisheries targeted on other Albula species. For example, A. vulpes supports high-value, primarily catch-andrelease destination sportfisheries in the Florida Keys (USA), Cuba, Bahamas, Belize, Mexico, and Venezuela. Genetic analysis of samples from the recreational catch throughout the Caribbean indicate that the two presently undescribed cryptic species, Albula sp. B and Albula sp. cf. vulpes, contribute <2% to the recreational catch (Wallace and Tringali 2010).

Albula vulpes supports subsistence and recreational fisheries throughout its range, yet there has been no formal stock assessment to quantify the effect of these fisheries on the population in any region. In numerous locations throughout the Caribbean, the species is harvested for subsistence and occurs as bycatch in other fisheries, thereby entering the commercial market (A.J. Adams, personal communication). Fish are harvested with hook and line, gill nets, and seine nets. Regulations differ by location: in Florida (USA), Belize, Puerto Rico, and the United States Virgin Islands, bonefish are designated as catch-and-release only; capture with nets and commercial sale are illegal in the Bahamas, but there are no limits on harvest for personal consumption; in Mexico, there is no minimum size and a per person limit of five per day.

The bonefish recreational fishery is economically valuable. In 2009, the Bahamian recreational fishery had an economic impact of \$141 million USD (Fedler 2010a); in Belize, the flats fishery (including A. vulpes, M. atlanticus, and permit Trachinotus *falcatus*) was valued at > \$25 million USD annually (Fedler and Hayes 2008). Major factors affecting post-release survival involve the amount and type of handling by anglers, exposure to air, duration of the fight, and abundance of predators at the release location (Cooke and Philipp 2004; Danylchuk et al. 2007a,b). In areas with few predators, the postrelease survival of properly handled fish is > 95%(Cooke and Philipp 2004; Danylchuk et al. 2007a), but can drop to 61% if predatory sharks are abundant (Cooke and Philipp 2004).

Albula glossodonta presumably dominates the bonefish fisheries of the Pacific, although *A. argentea* may comprise some of the total bonefish catch in regions of Hawaii and northern Australia, and *A. oligolepis* along portions of the Australian coast. In portions of its range, the *A. glossodonta* population has experienced significant population declines presumably due to overharvest and/or habitat loss (Friedlander *et al.* 2008).

Commercial landings of *Albula* species (primarily *A. glossodonta*) in Hawaii have decreased dramatically over the past few decades from over 300 000 lbs in 1900 to less than 3000 lbs since 2002 (Friedlander *et al.* 2008). Bonefish were the most important species in the commercial seine fishery between 1966 and 1970, with average annual yields of nearly 18 000 pounds. The commercial seine catch now averages only 581 lbs per year, accounting for less than 8% of the total catch. Similarly, CPUE of *Albula* species recruits in Kahana, Hawaii, was highest in 1999 and has declined by 79% since that time (Friedlander *et al.* 2008). In response, state regulations in Hawaii recently raised minimum size for harvest from 23 cm TL to 36 cm FL, although there is neither a closed season nor bag limit (Friedlander *et al.* 2008). Illegal netting, however, appears to be an issue of concern (A.J. Adams, personal communication).

In the republic of Kiribati, heavy commercial and subsistence fishing pressure and degradation of habitats at Tarawa and Kiritimati Atolls have resulted in the loss of pre-spawning staging sites and spawning migration routes, which may be responsible for the observed declines in the catches, average size and sex ratios of A. glossodonta at these locations (Friedlander et al. 2008). The annual take of bonefish from Tarawa Lagoon is between one and five million fish per year, but no stock assessment has been conducted (Friedlander et al. 2008). In Tarawa, where spawning aggregations are often targeted, there have been dramatic declines in catch and changes in population characteristics (Beets 2000). In 1977, bonefish comprised 44.6% of the total catch; they declined to 7.5% of the total catch by 1992. When data are compared between 1977 and 1992-1993, there are notable impacts of harvest: the sex ratio (F:M) changed from 0.71:1 in 1977 to 0.15:1 by 1992-1993; mean length decreased from 46.4 cm to 37.6 cm; mean weight declined from 1.3 kg to 0.84 kg; size at maturity for both males and females decreased by roughly 10 cm; and by 1992, > 30% of total catch was non-reproductive (Beets 2000).

Fisheries for *A. glossodonta* also occur elsewhere in the south Pacific, but remain undocumented throughout much of the species' range. Comparative data from fished and protected locations at Palmyra Atoll show significant differences in population characteristics which may indicate that threats are expressed asymmetrically across its range (A. Friedlander, personal communication). Concern for the conservation status of the species is warranted given the dramatic declines in more data-rich portions of its range, the documented habitat loss, and the lack of data on fisheries and habitat throughout the large portions of its range where likely subsistence harvest occurs at unknown intensity.

Discussion

These Elopomorpha species exemplify the concerns for long-term conservation that apply to many fishes. For several of these species, the lack of knowledge, coupled with the reliance of the entire subdivision upon coastal habitats that are under threat worldwide, is a cause for concern. In fact, the species for which information is available (e.g., *A. glossodonta* at Tarawa Atoll, Beets 2000; historic *M. atlanticus* commercial landings in the Caribbean, FAO 2011) suggest that population declines due to fishing may be more widespread than currently assumed. Further, the loss or degradation of coastal habitats upon which early life stages of many species depend, such as mangroves, has likely impacted these life stages.

A challenge to an assessment as contained in this manuscript, and development of strategies to address data and conservation needs, is the relative paucity of data on many species (summarized in Mrosovsky and Godfrey 2008). This has been and will continue to be a challenge, especially in regions that lack the financial and personnel resources to conduct data-intensive stock assessments (Degnbol 2001), as is the case for many of the species addressed herein. However, rather than default to a position of not including reports that are not in peer-reviewed journals, an assessment such as this must rely upon the best data that are available. Therefore, the grey literature cited in this manuscript is available online at www.iucnredlist.org for independent reader review.

Threats

Worldwide, overharvest and habitat loss or degradation are major anthropogenic threats to fisheries (Halpern *et al.* 2007). This is especially true for coastal fishes, which are more proximate to coastal human populations. The collapse of estuarine and marine fisheries is increasingly acknowledged as one of the gravest global environmental crises (Worm *et al.* 2009). Moreover, species that reach large maximum size are late to mature or have low rates of population increase, characteristics that are shared by some of the species addressed herein, are more vulnerable to overfishing (Jennings *et al.* 1998).

Although the extent to which populations of tarpons, ladyfishes and bonefishes may be overfished is generally unknown for most species and over much of the globe, the life histories of these fishes may render them especially susceptible to overfishing. Bonefishes frequently school and form pre-spawning aggregations in nearshore habitats

that can be efficiently targeted with gill nets or purse seines. Both characteristics appear to have been at play in Kiribati, where abundance, size and size at maturity have declined precipitously due to overfishing (Beets 2000). Harvest from spawning aggregations of other tropical species has led to fisheries collapses, including the once ubiquitous Nassau grouper (e.g., Sala et al. 2001). In addition, the schooling nature of elopomorphs may make it more difficult to accurately assess population status due to hyperstability (Sadovy and Domeier 2005), whereby high catches of aggregating fishes persist and suggest inflated population sizes long after the true overall abundance may have declined (e.g., Gadus morhua, Rose and Kulka 1999).

The life-history strategy of tarpon (Winemiller and Dailey 2002) may render it especially vulnerable to overfishing. Tarpon reach sexual maturity fairly late in life (8-12 years; Crabtree et al. 1995), are slow growing, and are long-lived (Crabtree et al. 1995; Andrews et al. 2001). Regional losses of juvenile habitat or intense fishing of adults may have impacts that are not visible for years or decades. Moreover, adult tarpon undergo extensive regional migrations (e.g., Ault et al. 2008), which may temporarily mask the local impacts of nursery habitat loss due to influx of adults from other regions. Concurrently, intense fishing of adults may significantly reduce reproductive output, which may not become apparent for years until the lack of new recruits into the population becomes visible as the adult populations decline. For example, reduced reproductive output may result from tertiary stress effects caused by intense fishing pressure which can cause population-level effects (Guindon 2011). In contrast, large reductions in spawning biomass may have occurred in Brazil, where an intense fishery from 1960-1980s led to a severe decline in population and catch rates (FAO 2011).

The importance of habitat loss and degradation as causes of fish population declines is becoming increasingly apparent (Turner *et al.* 1999; Jones *et al.* 2004). In the 1990s, approximately 50% of the world human population lived within 100 km of the coastline (Coen *et al.* 1997), and global population projections indicate that by the year 2025, 75% of the world's population may reside in coastal areas (Hinrichsen 1998). Therefore, coastal ecosystems and the fisheries they support will likely face increasing habitat loss, habitat degradation, and overfishing (Hughes 1994; Lapointe *et al.* 1994). Potential sea level rise associated with global climate change will exacerbate the loss and degradation of coastal habitats that are vital to these fish species (e.g., Day *et al.* 1995; Duarte 2002; Fish *et al.* 2005; Gilman *et al.* 2007).

The juvenile life stages of tarpons and ladyfishes depend upon estuarine habitats, which make them highly susceptible to anthropogenic habitat degradation. For example, disruption of hydrologic connectivity (Pringle 2006) between freshwater and marine sources may alter the magnitude or dynamics of freshwater flow into estuaries (Sklar and Browder 1998; reviewed in Beach 2002; Layman et al. 2007). Elops affinis populations are sensitive to reduced river flow and dam operations on the Colorado and Gila rivers (Bettaso and Young 1999; Schooley and Marsh 2007): Elovs machnata displace from South African estuarine nurseries in favour of higher salinity waters when faced with high freshwater flow (Whitfield and Harrison 2003). Altered freshwater flows into estuaries can affect species composition (Sklar and Browder 1998), which can impact diet of predatory fishes (e.g., Adams et al. 2009a). Moreover, many species of bonefishes use the shallow seagrass, subtidal and intertidal flats, coral reef, and other habitats adjacent to estuaries that are themselves affected by alterations of freshwater flow. For example, the negative effects of freshwater flow alterations from the Florida Everglades on Florida Bay are well documented (e.g., Fourguran and Robblee 1999), and this has coincided with catch declines for A. vulpes in the recreational fishery (P. Frezza, Audubon Society, unpublished data).

Mangrove forests that serve as an essential component of coastal and estuarine nurseries for tarpons, ladyfishes and bonefishes are among the most threatened coastal habitats worldwide, decreasing an estimated 35% globally over the past 50 years, with continuing annual declines of 2% (Valiela et al. 2001; Alongi 2002). For example, four of the ten mangrove species present along the Pacific coasts of Costa Rica, Panama and Colombia are listed in one of the three threatened categories, and a fifth species Rhizophora samoensis is listed as NT by IUCN criteria (Polidoro et al. 2010). Ongoing and planned coastal development in Belize, Mexico, the Bahamas and other locations in the Caribbean and worldwide pose serious threats to mangroves.

Most tarpons, ladyfishes and bonefishes rely on mangrove habitats for some portion of their life history, or upon the productivity of mangroves as sources of prey. For example, juvenile tarpons and ladyfishes require shallow, protected mangrove swamps and similar saltmarsh habitats (Wade 1962; Dahl et al. 1965; Robins et al. 1977; Zerbi et al. 2001; Mwandya et al. 2009; Jud et al. 2011). As these habitats are lost, the amount of available essential nursery habitat declines, which may have implications for adult populations. Similarly, loss of mangroves for salt farms caused a decline in ladyfish abundance (Mwandya et al. 2009), which may have wider population-level implications. Although no bonefishes appear to rely on mangrove habitats as juveniles, they do use mangrove habitats for foraging and refuge as adults. Given the importance of mangroves to tarpons, ladyfishes, bonefishes and their prey, mangrove loss is likely having major negative consequences on population resilience.

The coverage of seagrasses has decreased in many estuaries and coastal areas worldwide in recent decades, due largely to anthropogenically induced declines in water clarity and other human impacts (Orth et al. 2006). Globally, there has been a 29% decline in seagrass coverage since original estimates in 1879, and seagrasses have continued to disappear at a rate of 110 km² per year since 1980 (Waycott et al. 2009). Seagrasses serve as important habitats for tarpons, ladyfishes and bonefishes. In Florida (USA), for example, the majority of bonefish prey resides in seagrass beds (Crabtree et al. 1998). Also in Florida, E. saurus obtains a significant portion of its diet from seagrass-associated prey (Jordan et al. 1996). Therefore, the continuing global loss of seagrass beds could have profoundly negative impacts on these species.

In addition to the threats of outright habitat loss and degradation, habitat fragmentation poses particular challenges. Habitat fragmentation occurs when portions of a continuous habitat, or of habitat mosaics, are destroyed or degraded, creating gaps in suitable habitat. For example, human-induced fragmentation of tidal creeks of the Bahamas drastically simplifies food webs (Layman *et al.* 2007), which can have populationand system-level implications when reductions in prey diversity cause sublethal losses in productivity, including reduced growth rates, lower fish condition and higher parasite loads of top predators (Rypel and Layman 2008). This is especially important for fishes that use multiple habitats through their life-history strategies, as do tarpons, ladyfishes and bonefishes.

The effects of natural disturbances to elopomorphs must also be addressed, as they may be positive or negative. On the one hand, tropical cyclones may be responsible for recruitment pulses of some species. Shenker et al. (2002), recorded more recruiting M. atlanticus larvae into a Florida estuary in association with a hurricane than during any previous sample period, and Wade (1962) reported that juvenile tarpon were often found in beach overwash swales following tropical cyclones and other major storm and flood events (although these ephemeral habitat types could be population sinks rather than sources of subadult fishes (Breder 1944; Kulkarni 1983). In contrast, data from other estuarine and coastal species suggest negative impacts due to weather disturbances. Tropical cyclones and hurricanes that occur during the settlement seasons cause high juvenile mortality of coral reef fishes (Lassig 1983), and reduce abundance of juvenile snook in mangrove creeks of a Florida estuary (A.J. Adams unpublished data), so may have similar effects on juvenile elopomorphs. In addition, as coastal systems potentially become less hospitable due to overfishing, habitat degradation and loss, and declines in water quality, diseases may become more prevalent and thus impact fish populations (e.g., Arkoosh et al. 1998).

Temperature fluctuations associated with climate change will likely affect mortality both directly and indirectly. For example, A. vulpes demonstrate compromised physiological response to stressors such as fishing at higher temperatures that already occur naturally on shallow flats during warm summer months (Murchie et al. 2011b). As water temperatures in these shallow habitats increase with climate change, a suite of lethal and sublethal physiological responses may further impact fitness (e.g., Harrison and Whitfield 2006). Climate change may also bring less stability to temperature regimes, changing the frequency of thermal events (e.g., Meehl et al. 2000) that can affect elopomorphs. For example, M. atlanticus and Elops species have long suffered mortality from hypothermal events in Florida (e.g., Willcox 1887). A more recent hypothermal event caused significant A. vulpes mortalities as well (A. Adams, personal communication). Although the population-level effects of these events are unclear, effects

of changes in the frequency of these events should be monitored.

Climate change is expected to change precipitation patterns in many regions, which will alter freshwater flows (and thus salinity structure) and delivery of nutrients, sediments and contaminants into estuaries and other coastal areas. This will further exacerbate anthropogenic alterations already occurring in many coastal regions. Likewise, changes in temperature and seasonal flow rates may change primary production, causing phenological mismatches between first-feeding post-larval elopomorphs and their zooplankton prev that may increase mortality and reduce recruitment to subsequent life-history stages (sensu Cushing 1990). Loss of sediments resulting from freshwater flow alteration may cause net coastal erosion as sediments are no longer delivered from terrestrial sources, thus decreasing the extent of coastal habitats such as wetlands, which are essential to these fishes: this is presently occurring in the coastal state of Louisiana (USA).

The accelerated rate of sea level rise resulting from climate change will further influence mangroves, seagrasses and marshes. For example, even in areas where mangroves have legal protection (e.g., Florida, USA), there is no landward buffer between development and mangrove habitat. Therefore, as sea level rises, mangroves will not be able to colonize developed coastal lands that are inundated by seawater, and the mangrove fringe will be lost. Similarly, possible increases in sedimentation may adversely affect seagrasses by decreasing irradiance and constraining the fringe buffer between existing shorelines and coastal development immediately landward (Orth et al. 2006). Finally, in island regions of the tropical south Pacific frequented by certain bonefish species, shoreline buffers are narrow fringes around steep volcanic islands, where even mild sea level rise can have dramatic impacts on the inundation and loss of limited critical habitats (Nichols et al. 1999).

As all elopomorphs spawn in offshore waters and have an extended planktonic larval duration, changes in coastal and oceanic wind and circulation patterns associated with climate change may impact larval success and recruitment to inshore juvenile habitats. Many species of marine fishes show high levels of fidelity to spawning locations [e.g., common snook, *Centropomus undecimalis* (Adams *et al.* 2009b, 2011); Atlantic cod, *Gadus* morhua (Robichaud and Rose 2001); Albula vulpes appears to demonstrate spawning site fidelity (Danylchuk *et al.* 2011)]. As recent work has shown that self-recruitment of marine fishes is common (reviewed in Swearer *et al.* 2002), changes in ocean circulation patterns may interrupt the connectivity between spawning locations, larval transport and nursery habitats that causes such self-recruitment. Climate-induced changes in currents that transport larvae to less suitable habitats could have population-level negative impacts, particularly if fewer habitats are available because of anthropogenic habitat loss and degradation.

Research and conservation needs

Successful conservation of bonefishes, tarpons and ladyfishes will require new approaches to gathering data on habitat ecology and habitat needs of these species, potential effects of habitat loss or degradation, and development of methods to track fisheries trends over time. Models that incorporate these factors can then be derived to provide a framework and guide research and conservation.

Given what is known about habitat requirements for most of these species, and the threats to these habitats, it is safe to assume that many of the species addressed herein have suffered from coastal habitat loss and will suffer to a greater extent in the future. What is less clear is the level at which threats occur at local scales. Thus, there exists an urgent need to formulate species-specific (genus-specific if species-level data are lacking) conceptual ecological frameworks that describe ecological requirements, such as habitat. These conceptual frameworks would then be used to estimate the likely effects of local- and regional-scale habitat loss and degradation. This has been addressed for some species (e.g., Nero and Sullivan-Sealey 2005; Harborne et al. 2006), but not for elopomorphs. The conceptual frameworks would be used to guide the focus of the habitat assessment, for example, the assessment would focus on habitat mosaics important to the species of interest. The assessment would evaluate local and regional habitat health using a matrix of: (i) habitat quality (areas with low, moderate or high levels of habitat loss and degradation); (ii) threat levels (low, medium or high) to habitat health. Factors to consider in developing this matrix include historical and current habitat distributions: trends in habitat coverage (increasing,

declining and the rates); habitat health (e.g., natural, partly degraded, highly degraded, contiguous or fragmented); sources of habitat loss or degradation; management status (e.g., protected, slated for development); restoration or protection efforts; predictions of future threats. This can be approached via a mixture of remote sensing (e.g., habitat maps) and on-the-ground assessment (e.g., water quality evaluation, habitat map ground-truthing), efforts that would be repeated at regular time intervals (e.g., every 5-10 years). The result would be regional maps that would allow prioritization of conservation and restoration efforts. The underlying assumption to this approach is that a healthy habitat mosaic equals a healthy fish population.

There is a similar need for better assessment of fisheries impacts on populations of tarpons, ladyfishes and bonefishes. As much of the range of these species is largely in developing nations that lack the resources for standard stock assessments. or are not on the priority list to receive the attention needed for a stock assessment (e.g., in the USA), we must use different approaches to monitor these fisheries. For example: Artigas et al. (2003) stated that 'Marine fish species are not systematically studied in French Guiana and it is difficult to quantify fluctuations in the populations': and in Venezuela, tarpon, bonefish and ladyfish are listed under 'miscellaneous marine fishes'. Moreover, the fishing effort in developing countries tends to be spatially dispersed (making data collection difficult), and the institutions in charge of resource management and data collection lack operational capacity. In addition, in countries that have the operational resources (e.g., USA), management priorities do not include stock assessments of elopomorphs. This is due largely to the difficulty in obtaining data appropriate for standard stock assessment because the fisheries are entirely catch and release (e.g., bonefish and tarpon), but also because commercially harvested species have historically received greater attention. Moreover, attempts to estimate stock size are not useful unless they are repeated over time; as management priorities in the USA are now set, resources will not be applied to do so with elopomorphs, and those resources will not be forthcoming in developing countries.

New strategies are needed to assess stocks. For example, the use of rapid, intensive sampling techniques to assess abundance and age structure adapted from approaches used for other species (e.g., Jones and Stockwell (1995) used electroshocking to sample salmonids, but nets could be used to sample Albula spp.). Models can be created based on more detailed assessments of similar species for which catch data are available (e.g., Porch et al. 2006) or species with similar life-history requirements (e.g., Jennings et al. 1998; Cortes 2008), but care must be taken with this approach. Adams et al. (2008), for example, found the growth rate of A. vulpes differed between Florida (fast growth rate) and numerous locations in the Caribbean and western North Atlantic (slower growth rates), which underscores the need for local-scale assessment. Absent this information, an assessment of a population in Belize, where growth rates are low, that used data from Florida, where growth rates are higher, would have concluded that the Belize fishery is growth overfished because the population is comprised of small fish, when in fact the age structure of each population does not suggest differences in mortality. In addition, application of data to an 'ecological risk assessment from effects of fishing' approach (as described in Walker 2007) would be appropriate to numerous species addressed here.

Alternatively, the development of indices for monitoring trends in abundance and age structure should be developed. In this scenario, precise estimates of abundance are not the goal, as in traditional stock assessment. Rather, monitoring of trends over time would be used to highlight changes in catch rate or size that would initiate more detailed examination. This type of assessment approach would require participation of people in the fishery as well as data collection by resource management staff, but would not require the collection of highly detailed data required for standard stock assessments. Given that the fisheries in developing nations tend to be spatially dispersed and culturally diverse, stakeholder participation will be critical regardless of the assessment method used, providing an advantage to an approach that uses moderate levels of data collection to derive indices. A similar approach may also be applicable to the catch-and-release fisheries in more developed nations. In fact, the use of stakeholders to collect effort, catch, and size data is already being tested in some regions for some fisheries and has been used to a limited extent in the past. For example, angler diaries have been used to assess effort, catch and size in some freshwater fisheries in Canada (e.g.,

Kerr 2007), and current efforts are under way to use 'smartphone' technology to increase angler participation. For these catch-and-release fisheries, studies must be carried out to provide reliable estimates of post-release mortality so that they can be incorporated into assessments (Coggins *et al.* 2007).

In contrast, visual surveys (e.g., aerial surveys) are not appropriate. For example, aerial surveys were attempted as a tool to monitor adult tarpon, but the numbers of fish in offshore schools could not be reliably estimated, and the distribution of the schools was not random – the latter a critical assumption of line transect methods for estimating abundance (Crabtree 1991). Although a transect visual census approach has been suggested for bonefish, they are also not randomly distributed, so the applicability of such data is unknown.

As the species addressed here are all high-level carnivores, declines in their populations due to overfishing may induce ecological cascades (sensu Polis et al. 2000). Bonefishes, for example, are major predators of benthic invertebrates, potentially exerting significant top-down effects. Significant declines in bonefish abundance may alter the dynamics of other predators and cause shifts in selected prey that may restructure benthic communities. Similar outcomes have occurred in other systems in which important predators have declined in abundance due to overfishing (e.g., Atlantic cod, Gadus morhua; Frank et al. 2005). Comparative study of community dynamics in locations in which target species are overfished (low abundance), fished as catch and release (moderate to high abundance) and not fished (high abundance) would enable a better understanding of the system-level effects of overfishing and allow predictions for areas in which overfishing is occurring or is expected to occur.

An additional challenge to designing research with application to long-term conservation understands how bonefish, tarpons and ladyfishes will respond to the environmental changes previously addressed, including climate change, habitat loss or degradation, and overfishing. These stressors will likely affect trophic pathways of the coastal systems in which these species live, as well as the bioenergetics of each species. For example, habitat fragmentation caused drastically simplified food webs and narrowing of trophic niche width in a predator important in coastal habitats used by elopomorphs in the Caribbean (Layman *et al.* 2007), and a decrease in diet diversity of a juvenile predator in mangrove habitats (Adams et al. 2009a). In addition, changes in water temperature affect the ability of fishes to pursue, consume and metabolize prey, migrate, as well as respond to stresses such as catch-and-release fishing and predator avoidance (e.g., Murchie et al. 2010, 2011a, 2011b). Conducting bioenergetic studies of bonefishes, tarpons and ladyfishes under varied environmental conditions that incorporate expected changes will help determine the extent that these system-level changes influence the ability of juveniles to recruit to adult populations and adults to successfully reproduce.

Economic incentives for conservation

Ecotourism is becoming recognized as an important component of sustainable economies, especially in the developing world where many of the species addressed herein occur. Recreational fishing, especially catch-and-release fishing, is an important component of ecotourism and can make a significant economic contribution while maintaining high abundance of targeted fishes if managed appropriately. In locations where it is established, the activity makes significant contributions to the local economies: A. vulpes in the Bahamas in 2009, \$141 USD million (Fedler 2010a); Megalops atlanticus in Charlotte Harbor, Florida (USA) in 2010, \$110 million (Fedler 2011); and M. atlanticus in the Florida Everglades = \$991 million annually (Fedler 2010b).

This activity occurs without any government support and could be increased to a greater level with appropriate incentives. In other areas such fisheries could be encouraged to develop; however, great care must be taken to avoid overcapitalization and overfishing of the resource, which has negatively impacted other fisheries. For example, too much fishing effort results in a decline in catch rates because fish may become 'educated' to anglers, thus reducing catchability, causing a decline in the quality of the fishery and a loss of clientele. This becomes increasingly important as developing countries realize the potential value of these fisheries, increasing the risk of overcapitalization.

An important factor in creating and sustaining these fisheries is the effect of post-release mortality on the target species. Fortunately, studies on *A. vulpes* and *M. atlanticus* indicate that survival may

exceed 90% when proper handling practices are used (e.g., Cooke and Philipp 2004; Danylchuk et al. 2007a,b; Guindon 2011). However, in areas with high densities of predators (e.g., sharks), survival can be significantly lower (Cooke and Philipp 2004: Guindon 2011), which highlights the need for an adaptive approach to creating and managing these catch-and-release fisheries (Cooke and Suski 2005; Cooke et al. 2006) including angler education. Marine-protected areas, for example, might be managed as 'catch-and-release zones' that allow recreational catch-and-release fisheries (Cooke et al. 2006) for tarpons and bonefishes that support local economically important fisheries. This effort must also include the dissemination of proper catch-and-release guidelines by management agencies (Pelletier et al. 2007), because education of recreational anglers on best handling practices and on ways to reduce predation will play an important role in the effectiveness of catch-and-release fishing as a management tool (Cooke et al. 2006).

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