



## OVERVIEW

# Biology and ecology of sawfishes: global status of research and future outlook

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**ABSTRACT:** Globally, sawfishes are threatened with extinction because they occur in coastal habitats, which are disproportionately affected by human activities. In particular, sawfishes are susceptible to myriad fisheries that operate in the same regions. Unfortunately, these well-documented threats can be only partly mitigated because of ongoing human resource needs. However, the outlook for sawfishes is optimistic if we build on 5 successful research and conservation approaches developed over the past 2 decades: (1) local ecological knowledge, (2) identification of nurseries, (3) state-of-the-art techniques, (4) tagging studies, and (5) threat mitigation. If appreciation of healthy ecosystems that contain top predators like sawfishes can be fostered by healthy human populations where sawfishes occur (e.g. ecosystem management, promotion of sustainable livelihoods), and if local knowledge can be used to influence scientific studies that inform customized management decisions, this group of iconic species will have a chance to recover. In addition, promoting sample collection, sample archiving, and collaboration, especially in instances of sawfish mortality, will maximize the knowledge gained, despite often limited funding and limited samples. The first 2 decades of the 21st century have seen the first steps taken toward sawfish recovery, but there is more to do. Ultimately, translation of research results into conservation actions that include enforcement and fisher behavior change will be the key to sustained recovery. This Overview provides a context for the papers in the Theme Section 'Biology and ecology of sawfishes', and we incorporate them as part of a mini-review of research on this threatened group to provide a future outlook.

**KEY WORDS:** Conservation · Local ecological knowledge · Behavior change · Ecosystem management · Nursery · Acoustic tagging and monitoring · Genetics · Environmental DNA

## 1. INTRODUCTION

Sawfishes belong to a family of large, shark-like rays that occur at low latitudes, and populations of all 5 species have declined to the point that they are among the most threatened fishes in the world (Dulvy et al. 2014). Most species were not studied prior to population declines and so are poorly understood biologically and ecologically; however, conservation-focused research efforts have expanded over

the past decade. Globally, these research efforts have provided (1) new insights into the current distribution, biology, and ecology of sawfishes, and (2) guidance toward achieving species' recoveries (e.g. NMFS 2009, Fordham et al. 2018).

From its inception in 1985 at its first meeting in Knoxville, Tennessee, at which Dr. Thomas Thorson was the keynote speaker, the American Elasmobranch Society has played a key role in sawfish research and conservation. As part of a large work

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focused on the ichthyofauna of Nicaraguan lakes, Dr. Thorson was the first researcher to study the biology of a sawfish in detail (Thorson 1976). At that time, the connectivity of Lake Nicaragua to the Atlantic Ocean was not well understood, but he documented sawfish movements within the lake and between the lake and the ocean through his tagging research (Thorson 1982a). He took advantage of a sawfish and shark fishery in Lake Nicaragua to document the reproductive biology of the largetooth sawfish *Pristis pristis*, while sounding the alarm about the unsustainability of the fishery (Thorson 1976, 1982b).

Not surprisingly, the fishery in Lake Nicaragua collapsed by the mid-1980s, and concurrently, global declines in sawfish populations began to be noticed by a variety of regional organizations. It was too late for Lake Nicaragua, but multiple conservation actions followed in developed parts of the world. Early protections and listings included prohibition of sawfish harvest by the State of Florida, USA, in 1992, protection in Western Australia state waters by the Fish Resources Management Act in 1994, and the listing of 4 sawfish 'species' as Endangered or Critically Endangered on the IUCN Red List of Threatened Species by the IUCN Species Survival Commission Shark Specialist Group (SSG) in 1996 (IUCN 1996, FWC 1999). At that time, so little research had been conducted on sawfishes that the taxonomy of the family was poorly understood, but 5 extant species are now recognized (Faria et al. 2013). Taxonomic resolution allowed species-specific assessments and research to proceed and be published (e.g. Chapman et al. 2011, Carlson et al. 2013, Kyne et al. 2013, Simpfendorfer 2013), including updates to large ichthyofaunal works that helped clarify some of the historical literature on topics such as species ranges and life-history traits (e.g. Last & Stevens 2009).

Efforts to champion the plight of sawfishes and bring researchers together began at about the time the smalltooth sawfish *Pristis pectinata* was added to the US Endangered Species List, which occurred on 1 April 2003 (NMFS 2003). That year, a symposium titled 'Sawfish: threats, biology, and conservation in the 21st century' was organized for the 19th annual meeting of the American Elasmobranch Society in Manaus, Brazil. The symposium featured 8 presentations: 1 on their global status, 5 from the USA, and 2 from Australia, reflecting the 2 countries where most sawfish research and recovery efforts were underway. A 2012 meeting organized by the IUCN SSG led to the production of a global conservation strategy for sawfishes (Harrison & Dulvy 2014). Another sawfish-

focused symposium featuring 9 presentations was held in 2014 at the 2nd Sharks International meeting in Durban, South Africa. Since those symposia, research has increased and many collaborations have developed, an ongoing online issue of the journal *Aquatic Conservation* began, and the Sawfish Conservation Society (<http://sawfishconservationsociety.org>) was founded. In 2017, the IUCN SSG organized a meeting to evaluate conservation progress in the 5 yr since the meeting that produced the global conservation strategy. One of the main findings was that sawfish research was underway in at least 35 of the 78 countries where sawfishes historically occurred and they are specifically protected in 19 of the 36 countries where sawfish populations are known to still occur (Fordham et al. 2018).

In 2016, a symposium at the 32nd annual meeting of the American Elasmobranch Society in New Orleans, Louisiana, brought together many of the world's sawfish researchers to share their latest findings and promote future collaborations. The symposium included nearly 40 presentations representing 14 countries and all 5 species. Based on this symposium, we compiled a Theme Section for *Endangered Species Research* titled 'Biology and ecology of sawfishes'. Topics ranged broadly from summaries of the knowledge of local fishers in under-studied regions (e.g. Africa, the Middle East, Papua New Guinea, South America) and the role of public aquaria in sawfish conservation, to research on sawfish ecology, physiology, and population genetics. As an overview of this body of research papers, we incorporate them as part of a mini-review of research on this threatened group to provide a future outlook.

## 2. STATUS OF RESEARCH AND FUTURE OUTLOOK ON THE BIOLOGY, ECOLOGY, AND CONSERVATION OF SAWFISHES

### 2.1. Local ecological knowledge and identification of nurseries

Often, besides scouring the literature and museum collections for reliable records (e.g. White et al. 2017 this Theme Section), a first step toward assessing the status of sawfishes involves collecting historical and contemporary data from fishers in an area of interest, usually with a standardized questionnaire. These data have been referred to by several names, such as local ecological knowledge (LEK), traditional ecological knowledge (TEK), and public encounter reports (Sáenz-Arroyo et al. 2005, Pinnegar & Engelhard

2008). Since artisanal, commercial, and recreational fishing activities occur in almost all coastal waters, people who engage in these activities are often a good source of information on fishes, especially easily recognizable species like sawfishes, because there are many more fishers than scientists. In the past 2 decades, this approach has been used in many regions where sawfishes are found, or were thought to historically occur, and has helped (1) determine areas of historical occurrence, (2) avoid erroneous designation of local extinctions, (3) determine areas in which they still occur, (4) determine areas in which they are locally extinct or never occurred, (5) prioritize where to focus scientific research and management efforts, and (6) in the USA, as required by the Endangered Species Act, establish recovery criteria and juvenile critical habitat areas, which are purely management designations and spatially broader than documented nurseries (e.g. Seitz & Poulakis 2002, NMFS 2009, Norton et al. 2012, Hossain et al. 2015). Most recently, this approach has been used in Argentina, Brazil, Mexico, Papua New Guinea, Sudan, Gambia, UAE, and Uruguay (e.g. Reis-Filho et al. 2016, Jabado et al. 2017, Manir Feitosa et al. 2017, Bonfil et al. 2018, Elhassan 2018, Leeney et al. 2018, Cuevas et al. 2019, all in this Theme Section, and Leeney & Downing 2016, Bonfil et al. 2017). Use of data obtained from fishers is ongoing and will be a rich resource for protecting remaining sawfish populations and promoting recovery. Environmental DNA (eDNA) studies have emerged in recent years and may be able to build on encounter-derived data, especially in remote locations, if important methods details can be adequately addressed *a priori* (see Section 2.2.2).

Sawfish-reporting phone numbers, email addresses, signage at boat ramps and fishing piers, websites, and social media networks help establish, promote, and maintain communication between the public, scientists, and managers. Sawfish records provided by fishers can be plotted on maps to help identify and protect important habitats such as nursery areas, an important step in research and conservation. Often, these data will be the first of multiple lines of evidence used to document areas of occurrence that can be used for specific management actions, such as the establishment of juvenile critical habitats in the USA (Norton et al. 2012), and perhaps locate the last-remaining nurseries associated with some populations. The encounter data have been used to direct scientific research and allow local authorities to make informed decisions about development projects and habitat restoration opportunities

(Poulakis et al. 2011, National Marine Fisheries Service [NMFS] pers. comm., The Nature Conservancy pers. comm.). For example, intra-nursery areas of high use, i.e. the most productive habitat patches within the nursery (Nagelkerken et al. 2015), that is nursery hotspots (Poulakis et al. 2011, 2016) have been identified in multiple smalltooth sawfish *Pristis pectinata* nurseries, some of which have already been, and will continue to be, protected from habitat loss, thanks in large part to initial clues in fisher-derived data (Huston et al. 2017, Scharer et al. 2017, Hollensead et al. 2018, all in this Theme section, and Poulakis et al. 2011, 2013, Hollensead et al. 2016, NMFS pers. comm.).

It is noteworthy that smalltooth sawfish nursery hotspots are small areas within the broader nurseries where young-of-the-year and age-1 juveniles commonly occur over many years (i.e. the most productive habitat patches within the nursery; Nagelkerken et al. 2015). Regardless of terminology (Heupel et al. 2018), it is our hope that readers will understand that all portions of smalltooth sawfish nurseries are not used equally and that the distinct areas of most intense use (Poulakis et al. 2011, 2016, Scharer et al. 2017) are the highest priority for management actions (NMFS pers. comm.). It is important to be clear that the existence of these hotspots does not restrict nursery designations to these areas of most intense use. In fact, the broader nurseries that were identified for the smalltooth sawfish by applying the Heupel et al. (2007) criteria seem to be adequate (Norton et al. 2012), so the hotspot concept and nursery criteria are complementary.

Interdisciplinary, collaborative, habitat-use studies and detailed biological and ecological questions have been answered as part of research published in this Theme Section as a result of long-term surveys conducted within nurseries, especially regarding the smalltooth sawfish (Feldheim et al. 2017, Huston et al. 2017, Morgan et al. 2017, Poulakis et al. 2017, Scharer et al. 2017, Whitty et al. 2017, Bakenhaster et al. 2018, Hollensead et al. 2018, Prohaska et al. 2018, all in this Theme Section). In addition to identifying geographic regions in which nurseries still exist, near-real-time, fisher-derived data have also been used to maximize tagging efforts, because juveniles exhibit high degrees of site fidelity. It is hoped that similar studies can be conducted in all places where sawfishes need protection, like Papua New Guinea, that have emerged as potential strongholds for remaining populations of the other 4 sawfish species, but currently have no protective measures in place (White et al. 2017, Green et al. 2018, Leeney et

al. 2018, all in this Theme Section). A preliminary roadmap exists from the public-research-management approach that is working for the smalltooth sawfish, and this model may be able to be modified to fit the needs of other species.

## 2.2. Demography and use of state-of-the-art techniques

### 2.2.1. Modern techniques

Modern techniques, especially those in genetics, have been instrumental in answering questions about sawfishes related to biology, ecology, and recovery potential. Sources of DNA generally include thumbnail-size fin clips taken during research encounters or dried rostra that are common curios in private collections and museums (Phillips et al. 2009, Seitz & Hoover 2017 this Theme Section). For example, because most sawfish populations have declined dramatically, one of the first questions that needs to be answered about a population is whether there is or was a genetic bottleneck. Sometimes, when populations of organisms decline severely, genetic diversity is compromised and populations can become inbred, which is problematic for recovery. Studies in the USA and Australia have shown generally high genetic diversity despite precipitous declines (Chapman et al. 2011, Phillips et al. 2017 this Theme Section), which should provide optimism for recovery, although in Australia, some assemblages of *Pristis* and *Anoxypristis* sawfishes may have experienced population bottlenecks or founder effects at some time (Phillips et al. 2017, Green et al. 2018).

Collecting and archiving DNA from all sawfishes encountered, and preserving their parts (e.g. organs, vertebrae), is recommended, and using subsamples in future studies will maximize what can be learned from the original samples. These samples can be used to answer a variety of questions related to biology and ecology, and archiving is important because it may take many years to collect enough samples to conduct research. High-quality, 95% ethanol is recommended for long-term storage of thumbnail-size samples for genetic analyses, and care should be taken to avoid desiccation of samples due to the volatility of ethanol and to avoid cross-contamination during the subsampling process (e.g. rinse the scissors with bleach, then with autoclaved deionized water between samples). If available and possible, larger samples from necropsies should be preserved in 10% buffered formaldehyde as quickly as possible, or as a last resort, frozen

for archiving. Because of the large size that can be attained by sawfishes, care should be taken to ensure adequate fixation by using small enough subsamples and large enough containers. Developing a necropsy datasheet that linked samples, including preservation techniques, to collaborators has maximized what has been learned from smalltooth sawfish necropsies in Florida, USA, on topics such as age and growth, reproduction, and parasitology (e.g. Scharer et al. 2012, Kritsky et al. 2017, Poulakis et al. 2017, Bakenhaster et al. 2018).

Little is known about the biology of most sawfish species. For example, how often do females reproduce and how many offspring are born in each reproductive cycle? Answering these basic questions is vital for estimating recovery time, and DNA analyses can be used instead of traditional examinations of the reproductive tracts of many individuals, which is impractical when studying rare species. Feldheim et al. (2017) reconstructed parental genotypes using smalltooth sawfish DNA from the fin clips of juveniles collected over 12 consecutive years. This technique allowed construction of a time series whereby a biennial maternal reproductive cycle was documented even though young were captured every year. If sample collection is robust, these techniques can even be used to estimate brood size, as has been done for some elasmobranchs, including the smalltooth sawfish (Feldheim et al. 2004, DiBattista et al. 2008, Feldheim et al. 2017).

Little is known about the ecology of most sawfishes, including their feeding habits. Knowing what organisms sawfishes rely on as prey is an important part of the recovery process, especially since their growth rates can be fast during early life history (Scharer et al. 2012). Because of the small sample size, traditional stomach content analyses are difficult to conduct on endangered species (e.g. necropsies, gastric lavage), but analyses of stable isotopes of carbon and nitrogen from tissue or blood samples and DNA analyses of opportunistically collected fecal samples have been used to gain insights into diet (Thorburn et al. 2014, Poulakis et al. 2017). Stable isotope analyses are useful for learning about what the sawfishes are assimilating into their bodies, and stomach contents, feces, and other opportunistic samples (e.g. scales attached to rostral teeth) can be used to validate the stable isotope results (Poulakis et al. 2017). Further, general characterizations of prey assemblages at relatively low taxonomic resolution can be determined using 18S rRNA techniques, and, to better elucidate trophic ecology, higher resolution can be attained using analyses of other genes (Poulakis et al. 2017). Similar

to eDNA methods (see Section 2.2.2), some of these techniques require extensive knowledge of the local fauna so samples can be collected to make useful comparisons between better-understood proxy species or across trophic levels (Poulakis et al. 2017). Care should be taken when planning these research projects to ensure realistic timelines and budgets, adequate access to necessary samples, adequate expertise for sample processing, an understanding of any effects of preservation techniques on samples, especially if the study area is remote (Olin et al. 2014), and acquisition of any associated permits (e.g. field sampling, sample shipping).

Other state-of-the-art techniques such as use of time-synchronized acoustic receivers to collect continuous estimates of sawfish positions with accuracies of a few meters and use of accelerometers to link behaviors and physiology to ecology have been initiated on sawfishes (see Section 2.3). These technologies can be used to improve our understanding of habitat use, especially when used simultaneously. For example, knowing where individuals are and what they are doing (e.g. resting, swimming slowly, swimming rapidly) may provide insight on specific habitats being used and when feeding or predator avoidance could be occurring (Whitney et al. 2012).

### 2.2.2. eDNA

Studies of eDNA can build on encounter-derived data (see Section 2.1), or act as a proxy for them in regions where fisheries data are scarce, to foster scientific data collection on sawfishes, especially in remote locations. The relatively new field of eDNA stands to revolutionize our understanding of many species, including sawfishes. Simply put, a water or sediment sample is tested for the presence of DNA from a species of interest. Conceptually, the approach is simple, but practically, many details related to methods must be addressed, well in advance, before any reliable eDNA data can be collected and analyzed. For example, a major requirement for any species-specific eDNA study is development of species-specific primers, or a primer set, that has been thoroughly tested to eliminate the possibility of false positives, such as those from cross-amplification of non-target species (note: biodiversity assessments would use a different approach, see Bakker et al. 2017). False positives are important to avoid so that conservation efforts and research funds are not directed where sawfishes do not exist. Development of a primer set requires extensive knowledge of the

local ichthyofauna, especially the most closely related species, which for the purposes of this Theme Section are other sawfishes, guitarfishes, wedgefishes, and stingrays (Last et al. 2016). Primers that work in one study area may not be appropriate for another study area, depending on the related taxa found there, which themselves may have to be sampled for DNA if archived samples are unavailable (e.g. fin clip collections, GenBank records). Problems can arise if the local ichthyofauna is not well known or includes closely related taxa that are rare or are becoming so (Moore 2017 this Theme Section). In addition, obtaining the required state, federal, and international permits can add substantially to the time required to complete the process if samples of protected species such as sawfishes need to be shipped across borders. Permit acquisition and maintenance are sometimes underappreciated aspects of working with protected species because they can take months or years to secure. Even though water or sediment samples for eDNA research may not themselves require permits, necessary supporting work usually does. Collaborations with other researchers can help with local knowledge and permitting-related aspects of research, but the indirect requirements of conducting reliable eDNA research can be expensive and time-consuming, especially because field and laboratory work is involved. Thus, we recommend that researchers and funding entities consider these factors when developing project timelines and budgets.

Contamination must also be addressed from multiple perspectives (e.g. between samples or from external sources) before eDNA samples can be collected (Goldberg et al. 2016). Because the latest techniques are so sensitive, false positives could result if water samples are collected on a vessel on which a sawfish has been collected or if water samples are filtered in a laboratory in which sawfish parts or tissues have been processed. Simpfendorfer et al. (2016 this Theme Section) conducted the first eDNA study that applied this fast-evolving field to a sawfish species—the largemouth sawfish *Pristis pristis*. They filtered surface water and analyzed samples using conventional PCR techniques. Since that study was published about 3 yr ago, the field of eDNA has moved from using PCR, to quantitative PCR (qPCR), and now into highly sensitive droplet digital (ddPCR) techniques for quantifying results (Baker et al. 2018). The importance of eliminating contamination cannot be overstated, as some ddPCR assays can detect <1 pg of target DNA (Doi et al. 2015). It is imperative to establish protocols to reduce the risk of contamination, such as cleaning all field and laboratory equip-

ment with 10% bleach, ultraviolet light, and autoclaves. Globally, several sawfish eDNA studies are being planned or are underway, and we hope investigators will collaborate as much as possible so that the results of these studies are valid, comparable, and minimize duplication of effort.

Once reliable methods have been established (e.g. vetted species-specific primer set developed, decontamination protocols established) and adequate numbers and volumes of water samples have been collected (to minimize false negatives), eDNA sampling can be used to establish the presence of a target species in a study area and to potentially direct field research. Ideally, these eDNA data would be used as part of multiple lines of evidence used to document the presence of the target species and establishing occupied habitat. For example, eDNA could be used to measure recovery of a sawfish species if encounter reports were received from, or were suspected in, a new area; eDNA sampling becomes the next step in a sawfish-targeted monitoring program. The use of robust eDNA methods could be used for 'early detection' of presence to help researchers and managers foster recovery. Knowing whether these species are present and having estimates of the spatial extent where they occur would inform conservation and management actions. Field surveys and acoustic tagging studies would still be necessary to answer more detailed questions regarding demography, habitat use, site fidelity, and population status, but future improvements in eDNA techniques may provide insight into some of those questions as well. Regardless, we stress the need for careful experimental planning and quality control for any eDNA study, especially if the results might be a primary basis for conservation and management actions.

### 2.3. Tagging studies and habitat use

In general, sawfishes inhabit shallow (<10 m) coastal waters, including estuaries and rivers of the tropics and subtropics (Dulvy et al. 2016), though they have been shown to occur to about 100 m depth (Poulakis & Seitz 2004, Carlson et al. 2014). Encounters with the species from public and research sources have provided insight into habitat use by all life stages. Associations with shallow-water habitats such as mangrove shorelines have been documented, and encounters have most often been reported over muddy or sandy bottoms (Poulakis & Seitz 2004, Thorburn et al. 2008, Whitty et al. 2009, Wiley & Simpfendorfer 2010, Morgan et al. 2015, 2017).

For the 2 species that have been studied the most, the smalltooth sawfish and largetooth sawfish, habitat use changes with ontogeny, and smaller animals are found in shallower water and larger animals in deeper water (Poulakis & Seitz 2004, Whitty et al. 2009, 2017, Simpfendorfer et al. 2010, 2011, Poulakis et al. 2013, Carlson et al. 2014). The smallest juveniles have had the most specific habitat associations in nearshore areas, and these have been targeted relatively easily with recovery efforts (e.g. critical habitat designation, fishery-independent gill-net surveys in shallow water). Larger juveniles and adults, however, have more varied habitat associations (Poulakis & Seitz 2004, Carlson et al. 2014, Waters et al. 2014). For other species, future research and recovery efforts may need to be more broadly based or targeted at specific areas (e.g. aggregation sites), depending on the goals of those efforts.

Combined with local ecological knowledge and fisheries-independent data, when available, use of long-lasting acoustic tags, especially when placed internally, will likely be the most informative way to improve our understanding of large-scale migrations, smaller-scale localized movements, and habitat use of all life stages. Pop-up satellite archival tags (PSATs) have been used on smalltooth sawfish and have indicated relatively small-scale movements (i.e. within Florida state waters) over ~5 mo time periods and have provided insight concerning patterns of depth use (Carlson et al. 2014). Thus, in areas where sawfish are rarely encountered and little is known about their habitat use patterns, PSATs are likely the most useful tracking method. However, given cost-benefit considerations and light-based location error estimates of PSATs, acoustic transmitters and subsequent monitoring by acoustic receivers may be a better investment for sawfishes, provided the infrastructure is available for deployment and long-term maintenance of receiver arrays of ecologically meaningful size. Smart position and temperature (SPOT) tags (satellite tags that provide real-time locations when they break the surface) have shown some promise, but are useful only for sawfish using shallow habitats over relatively short time periods (i.e. months, R. D. Grubbs unpubl. data). Some studies have already provided much-needed, longer-term information on sawfishes using internal acoustic tags (Whitty et al. 2017), but permit requirements and cautious approaches to conducting research on these threatened species have resulted in the use of external tags until relatively recently. As a result, most studies have focused on habitat use by small juveniles because of their high site fidelity (e.g. Whitty et

al. 2009, Poulakis et al. 2013, Morgan et al. 2015, 2017, Scharer et al. 2017). The short retention times of externally attached tags limit their utility in understanding the ecology of long-lived species such as sawfishes. The expanded use of internally placed acoustic tags, especially appealing now that recaptures have shown that the incisions made for implantation heal completely, are proving instrumental for filling data gaps within and beyond the nurseries (Whitty et al. 2017, R. D. Grubbs & G. R. Poulakis unpubl. data). With battery lives up to 10 yr, internally implanted acoustic tags may provide information about movements and habitat use over large portions of the lives of these long-lived species.

Sawfishes spend their first few years within nurseries and eventually move into a broader range of coastal habitats. Use of acoustic tags has improved our understanding of the early life history of 3 species: the smalltooth sawfish, largetooth sawfish, and green sawfish *Pristis zijsron*. General movement patterns (e.g. on the scale of an entire river) have been documented with regular acoustic tags and receivers, but use of time-synchronized acoustic receivers to continuously estimate sawfish positions within meters (G. R. Poulakis & R. A. May unpubl. data) and use of accelerometers to link behaviors and physiology to ecology (Gleiss et al. 2017, N. M. Whitney, K. O. Lear, & G. R. Poulakis unpubl. data) have been conducted or initiated on sawfishes, and these technologies have great potential to improve our understanding of finer-scale habitat use, especially within the nurseries. For example, accelerometers have documented seasonal patterns of depth use by the largetooth sawfish and diel patterns of activity by the smalltooth sawfish (Gleiss et al. 2017). Some of these approaches may be useful outside the nurseries, such as in adult aggregation sites, but because of high site fidelity, relatively small activity spaces, and hotspot use within the broader nurseries (e.g. Poulakis et al. 2011, 2013, 2016, Morgan et al. 2015, 2017, Nagelkerken et al. 2015, Hollensead et al. 2016), data collection has been maximized and, in the case of accelerometers, tag recovery has been optimized in nursery habitats.

Improving our understanding of ontogenetic shifts in habitat use after age-0, such as critical habitats for large juveniles and adults, as well as associations of adult females with specific nurseries, will need to be a focus of future research for all sawfish species. Progress has been made in this regard for some species, such as the smalltooth sawfish and narrow sawfish *Anoxypristis cuspidata*, but gaps remain. For example, Feldheim et al. (2017) reconstructed adult

female genotypes from DNA collected from young smalltooth sawfish captured in 2 of at least 5 unique nurseries (Norton et al. 2012), and showed strong, decade-scale, biennial parturition site fidelity, which is often a precursor to establishing maternal natal philopatry (Chapman et al. 2015). Similarly, Green et al. (2018) examined larger-scale population structure of the narrow sawfish and found evidence of regional parturition site fidelity. Using these or similar approaches to study the relationship between the migrations of adult females and their nurseries range-wide for all sawfishes where long time series of DNA samples exist will improve our understanding of their life histories and may help prioritize conservation and management actions.

Like for many marine species, temperature has emerged as a driver of habitat use on a variety of temporal and spatial scales for some sawfishes. For example, during normal daily or seasonal fluctuations, small-scale movements of juvenile largetooth sawfish and all life stages of the smalltooth sawfish have been influenced by temperature (Papastamatiou et al. 2015, Gleiss et al. 2017, Whitty et al. 2017). These studies have shown that the timing of shifts in habitat use, such as moving from the shallows to deeper water (or vice versa) in the same river or moving from canals into the open waters of an embayment, may be cued by temperature. In addition, atypical cold events have been shown to influence smalltooth sawfish habitat use in nurseries as juveniles look for refuge before succumbing in cases where their lower temperature tolerance limit was exceeded (Poulakis et al. 2011, Scharer et al. 2017). Learning more about species-specific tolerances and how temperature influences habitat use will be important as we continue to assess ranges and project how they might change on a variety of temporal scales related to climate change.

#### 2.4. Anthropogenic threats and mitigation

Historically, anthropogenic threats to sawfishes have included targeted catch and bycatch in myriad fisheries (biggest threat), habitat loss and degradation (e.g. destruction of mangrove shorelines), commercial trade in sawfish parts (e.g. highly valued rostra and fins), and entanglement in marine debris (Seitz & Poulakis 2006, Dulvy et al. 2016, Brame et al. 2019 this Theme Section). These threats have reduced species ranges and caused sawfishes to be eliminated from more than 20%, and perhaps even up to 50%, of the countries in whose waters they

once existed (Dulvy et al. 2016, Fordham et al. 2018). Due to a variety of conservation actions (e.g. all sawfish species are listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora [CITES], so international trade should not occur), threats such as legal harvest and trade in live animals have been theoretically eliminated from 24% of countries in their collective ranges (Fordham et al. 2018). However, implementation of conservation actions, especially their enforcement (Hossain et al. 2015), and fostering of fisher behavioral changes (Battista et al. 2018), and ongoing threats such as fisheries bycatch and habitat loss remain problematic for these species. Establishing effective, ongoing, public outreach and education programs that are catered to the needs of local people (e.g. promoting a shift to ecosystem management, see Section 2.4.1) will be imperative if we hope to mitigate the effects of these threats.

#### 2.4.1. Fisheries catch and bycatch

Mortality resulting from artisanal, commercial, and recreational fisheries, intentional or not, has been the primary cause of sawfish population declines worldwide (Seitz & Poulakis 2006, Dulvy et al. 2016, Brame et al. 2019). The extended, toothed rostrum of sawfishes makes them vulnerable to capture in net fisheries, especially gill nets and trawls, and efforts such as shark control programs that use similar nets. Capture of sawfishes in such efforts has been well documented (e.g. Hossain et al. 2015, Dulvy et al. 2016, Wueringer 2017 this Theme Section). Gill-net fisheries have been eliminated in some portions of the smalltooth sawfish range, such as most US states, including Florida, but more reductions are needed. For example, high-density artisanal gill-net fisheries (e.g. Senegal has over 90 000 fishers and 12 000 canoes along a 700 km coastline) in the western Indian and eastern Atlantic oceans still exist off Africa and Bangladesh (Pinnegar & Engelhard 2008, Hossain et al. 2015). Similarly, in some regions such as India and the USA, trawl fisheries remain a concern, as interactions with them generally result in the death of larger individuals; however, some progress has been made, as trawl fisheries have been banned in waters off the UAE, and there are seasonal closures in other countries such as Kuwait and Bahrain (Brame et al. 2019, R. Jabado pers. comm.).

Sawfish conservation in low-income countries is especially complex because it involves issues of poverty and human welfare in marginalized commu-

nities. In these situations, assuming there is a willingness on the part of all involved (i.e. the public, scientists, and management) to make changes and the capacity exists for these changes, one realistic way forward could involve identifying nurseries, migration corridors, and large juvenile and adult critical habitats which would provide guidance in establishing additional time-area closures to minimize interactions with sawfishes and related overfished species, while supporting the original fisheries. As the species become better understood, areas of consistent, intense use may emerge and these may help prioritize spatial and temporal aspects of conservation actions, as has occurred for the smalltooth sawfish (see Section 2.1). Some of these changes may not be very disruptive to the overall fisheries because the same gear could be used (e.g. avoiding ~2 km portions of a river) and may be easier to implement compared to establishment of large protected areas that tend to be focused on biodiversity (Devitt et al. 2015). Another more expensive possibility that may be an option in some communities could involve integrating hooked gears like modestly sized longlines or drumlines into the fishery, as capture using these techniques likely results in limited physiological stress compared to capture in trawls and gill nets, because large sawfish caught in bottom longline fisheries in the USA are typically released alive (Prohaska et al. 2018, R. D. Grubbs & G. R. Poulakis unpubl. data).

In the USA and Australia, sawfishes continue to be captured in recreational fisheries, sometimes in large numbers, though the risk of mortality is likely low when they are handled and released properly (Peeverell 2005, Waters et al. 2014, Prohaska et al. 2018). Unfortunately, reports of sawfish being retained or released after the removal of their rostra are still received, even in regions with adequate protections and extensive outreach efforts (Seitz & Poulakis 2006, Morgan et al. 2016). These reports highlight the ongoing need for outreach wherever sawfishes are found, so that coastal residents from all user groups that might encounter sawfish will be aware of the laws and can appreciate the multiplicative value (e.g. through ecotourism and ecosystem management) of live sawfishes as part of healthy ecosystems.

#### 2.4.2. Habitat loss

Because sawfishes are found in coastal habitats at all life stages, habitat loss has been and will continue to be a threat, because humans tend to live along the

coast. Remote regions and large parks have acted as 'life boats' for sawfishes in some parts of the world (e.g. Everglades National Park, Florida; West Side National Park, Andros Island, Bahamas; northern Australia; Papua New Guinea), but in highly developed portions of southwest Florida such as the Charlotte Harbor estuarine system, which contains 2 distinct smalltooth sawfish nurseries (Feldheim et al. 2017, Scharer et al. 2017), many mangrove-lined shorelines have been replaced by concrete seawalls or other armored shorelines to protect waterfront property (Poulakis et al. 2011, 2013, 2016, Norton et al. 2012, Scharer et al. 2017). Although the species is physiologically resilient, Prohaska et al. (2018) showed that juvenile smalltooth sawfish in Charlotte Harbor nurseries had higher metabolic stress than juveniles from more pristine nurseries. These results suggest that living in human-altered or fragmented habitats may cause chronic stress in juveniles, though any effects on body condition, behavior, or survival are unknown.

Mangroves have been demonstrated to serve as important foundation habitats supporting most, if not all, sawfishes and their ecosystems, yet mangrove deforestation due to urban development, aquaculture, agriculture, tourism, and lumber acquisition continues to result in global loss of this habitat (Duke et al. 2007, Friess & Webb 2014). The effects of mangrove loss in countries that remain strongholds for 1 or more species (e.g. Papua New Guinea, Australia, USA), or those where recent data suggest that viable populations may still exist (e.g. Sundarbans region of Bangladesh, India [R. Jabado pers. comm.], Pakistan, Cuba, Bahamas), could be a major impediment to recovery. It is encouraging, however, that research results have been, and will continue to be, used to influence habitat-modification projects to avoid and minimize loss of mangroves and other habitats in both units of official juvenile smalltooth sawfish critical habitat in Florida (Norton et al. 2012, NMFS pers. comm.). Hopefully, emerging research results in other parts of the world can be used to safeguard habitats similarly, even on small spatial scales (see Section 2.4.1), and a message of how these actions benefit the entire ecosystem, not just sawfishes, can be disseminated to affected parties as part of the process.

#### 2.4.3. Marine debris and other threats

Although currently a relatively minor threat, especially compared to fishing catch and bycatch (see Section 2.4.1), marine debris is an ongoing threat

to sawfishes, especially juveniles, whose elongate, toothed rostra are easily entangled or encircled. This threat could be more important than currently thought if affected sawfish are trapped at depth (e.g. in discarded monofilament longline, G. R. Poulakis unpubl. data) or in the future if populations begin to recover, which would increase the chances of interactions and counteract recovery progress. For sawfishes, marine debris includes a range of human-made materials that are found wherever sawfishes are found, including monofilament fishing line of all strengths, non-monofilament line, and other refuse, especially if it is or can become cylindrical (Seitz & Poulakis 2006). A wide range of cylindrical objects have been found on rostra and heads of sawfishes because their rostra pass through the center of the object, and the object either gets stuck on the rostral teeth or passes beyond the rostrum and stops at the broader head. Objects that have been found on sawfish include loops of various types of rope (e.g. from commercial traps), a section of polyvinyl chloride (PVC) pipe, loops of monofilament fishing line, a dog's plastic ball, and rubber bands (Seitz & Poulakis 2006, G. R. Poulakis unpubl. data).

The severity of debris-related injuries and their effects on individual fitness varies. Objects that have been on sawfish for a long time—months or even years—have caused serious injuries or healed such that the objects have become incorporated into the body (Seitz & Poulakis 2006). Rostral damage has included broken or lost rostral teeth and damage to the rostral cartilage. These injuries can have lasting effects because lost rostral teeth do not regrow (Slaughter & Springer 1968), and damaged cartilage can result in weakening or breaking of the rostrum. Monofilament lines do not have to be wrapped tightly around the rostrum to cause damage because of the normal lateral slashing behavior sawfishes employ for feeding and defense. In recent years, rubber bands have become a relatively common occurrence on juvenile smalltooth sawfish, especially in the Caloosahatchee River, Florida (G. R. Poulakis pers. obs.). Apparently, the estuarine salinities in this nursery preserve the rubber's elasticity, causing open wounds in multiple individuals, and impeding spiracle function in one instance. Incorporating these threats into outreach presentations and encouraging fishers to untangle unintentionally caught sawfishes as much as possible before release is recommended and will help lessen these effects.

Natural threats such as disease, parasites, and stochastic events (e.g. extreme cold weather events, hurricanes, algal blooms) to sawfishes are largely

unknown, but they clearly stand to impede recovery. In Australia and the Bahamas, juvenile sawfishes sometimes get trapped on drying floodplains or sand flats and need to be rescued by researchers or indigenous rangers (R. D. Grubbs & P. M. Kyne unpubl. data.). Making local people aware of the weather conditions (e.g. onset of dry season, short-term blowdown events) that increase the possibility of this happening may prevent mortality events. Some natural threats might be related and provide early warnings of future problems. For example, parasites are part of healthy ecosystems, but excessive ecto- or endoparasite loads could indicate compromised health of an individual or group, or disruptions in the overall health of the ecosystem. Identifying metazoan parasites that affect sawfishes, especially since many are infection site- and host-specific, and establishing baseline infection rates, may help determine indicator species that could assess the severity of future imbalances in the ecosystem (Kritsky et al. 2017, Bakenhaster et al. 2018).

In general, sawfishes seem to be a resilient group (Prohaska et al. 2018), but monitoring the effects of these threats, especially if they occur near occupied habitats, is recommended. In addition, promoting sample collection, especially when mortalities occur, will maximize the knowledge gained from these unfortunate events (see Sections 2.2.1 and 2.3).

### 2.5. Related species

Globally, sawfishes have received considerable research and conservation attention in recent years because they are among the elasmobranch taxa most at risk of extinction (Dulvy et al. 2014, 2016). Yet many other species with similar life-history traits are just as susceptible to overfishing and could be in the same situation as sawfishes now or soon. Wedgefishes and guitarfishes (especially the Rhinidae and Glaucostegidae), for example, are vulnerable groups that are closely related to sawfishes in the Order Rhinopristiformes and inhabit similar habitats as sawfishes (Last et al. 2016, Moore 2017). We recommend incorporating these taxa into sawfish-focused conservation and outreach efforts and promoting healthy ecosystems while maximizing biodiversity. In addition, understanding the biology, ecology, and status of these related species may be critical in informing research on sawfishes, such as studies on trophic ecology (see Section 2.2.1) and development of species-specific primers for eDNA research (see Section 2.2.2).

### 3. CONCLUSIONS

It is our hope that this Theme Section will serve as a resource for research ideas and aid in informing responses to conservation and management issues that arise for sawfishes and related taxa worldwide. In addition, we encourage researchers to collaborate as much as possible on research projects. The benefits of collaborative science are not unique to studies of sawfishes, but this group of threatened fishes will have the best chance for survival if researchers work together and make decisions with the species as the priority. As a field-based example, funding for acoustic tags and receivers can sometimes be scarce when needed for many reasons, but sharing tags and unused receivers between researchers (i.e. items that have already been purchased and can be mobilized quickly) may allow researchers to take advantage of time-sensitive tagging and data collection opportunities. Further, participating in existing acoustic detection sharing networks, or developing new ones, will be instrumental in advancing our understanding of sawfishes, as the benefits of this approach have been realized for many large, mobile species, including the smalltooth sawfish (e.g. Hussey et al. 2015, Pratt et al. 2018, Ellis et al. 2019). In the laboratory, communicating about successes and failures regarding sampling protocols and species-specific primer development, well in advance of scheduled eDNA sampling, will reduce costs and maximize efficiency, while minimizing delays. Streamlining research as much as possible will maximize recovery benefits because these species need our collective help as soon as possible.

Ultimately, effective and timely translation of the results of scientific research into conservation and management actions that include enforcement and efforts to change fisher behavior will be important in the future, especially in countries outside the USA and Australia. Ongoing local ecological knowledge reports highlight the ongoing need for outreach and behavior change efforts wherever sawfishes are found, so that coastal residents from all user groups that might encounter sawfishes will be aware of existing laws and can appreciate the multiplicative value of live sawfishes as part of healthy ecosystems (e.g. Battista et al. 2018). Successful conservation is certainly a complicated issue, especially in impoverished coastal communities in low-income countries. Effective management and conservation will require addressing socioeconomic issues that lead to overfishing. Solutions must include human behavior change, development and promotion of alternative

livelihoods, and food security through sources of sustainable protein, exclusion of industrial fishing fleets, and approaches such as theory of change (e.g. Mayne 2015). If an appreciation of healthy ecosystems that contain top predators like sawfishes can be fostered by healthy human populations where sawfishes occur, and local knowledge can be used to inform scientific studies that subsequently inform customized management decisions, this group of iconic species will have a chance to recover.

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