Journal of FISH BIOLOGY
Published for the Fisheries Society of the British Isles

Journal of Fish Biology (2012) **80**, 1844–1869
doi:10.1111/j.1095-8649.2012.03246.x, available online at wileyonlinelibrary.com

Recovery potential and conservation options for elasmobranchs

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Many elasmobranchs have experienced strong population declines, which have been largely attributed to the direct and indirect effects of exploitation. Recently, however, live elasmobranchs are being increasingly valued for their role in marine ecosystems, dive tourism and intrinsic worth. Thus, management plans have been implemented to slow and ultimately reverse negative trends, including shark-specific (*e.g.* anti-finning laws) to ecosystem-based (*e.g.* no-take marine reserves) strategies. Yet it is unclear how successful these measures are, or will be, given the degree of depletion and slow recovery potential of most elasmobranchs. Here, current understanding of elasmobranch population recoveries is reviewed. The potential and realized extent of population increases, including rates of increase, timelines and drivers are evaluated. Across 40 increasing populations, only 25% were attributed to decreased anthropogenic mortality, while the majority was attributed to predation release. It is also shown that even low exploitation rates (2–6% per year) can halt or reverse positive population trends in six populations currently managed under recovery plans. Management measures that help restore elasmobranch populations include enforcement or near-zero fishing mortality, protection of critical habitats, monitoring and education. These measures are highlighted in a case study from the south-eastern U.S.A., where some evidence of recovery is seen in *Pristis pectinata*, *Galeocerdo cuvier* and *Sphyrna lewini* populations. It is concluded that recovery of elasmobranchs is certainly possible but requires time and a combination of strong and dedicated management actions to be successful.

Key words: fisheries management; habitat restoration; population abundance; sanctuaries; shark conservation.

INTRODUCTION

Many elasmobranch populations are threatened primarily by high rates of directed fishing and by-catch mortality in global fisheries (Stevens *et al.*, 2000; Dulvy *et al.*, 2008), but also by marine pollution (Seitz & Poulakis, 2006), habitat destruction (Knip *et al.*, 2010) and potentially climate change (Chin *et al.,* 2007). As such, dramatic declines in abundance have been reported from many parts of the world's oceans (Baum *et al.*, 2003; Ferretti *et al.*, 2008, 2010; Ward-Paige *et al.*, 2010; Nance *et al.*, 2011, Reid *et al.*, 2011). To date, 67 species of elasmobranchs are considered critically endangered or endangered by the International Union for the Conservation of Nature (IUCN; http://www.nmfs.noaa.gov/sfa/magact/) (Simpfendorfer *et al.*,

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2011). These negative trends, combined with the importance of elasmobranchs in marine ecosystems (Baum & Worm, 2009; Ferretti *et al*., 2010; Heithaus *et al*., 2010) and their high value for tourism (Davis *et al*., 1997; Dobson, 2006; Clua *et al*., 2011; Gallagher & Hammerschlag, 2011), have prompted attention from scientists, conservation and management organizations, media and the general public (Camhi *et al*., 2009; Cavanagh *et al*., 2009; Lucifora *et al*., 2011). As a result, initiatives to halt and ultimately reverse these negative trends are underway (Camhi *et al*., 2009; Erickson & Berkeley, 2009; Koldewey *et al*., 2010).

Since the 1950s, legally and non-legally binding international fisheries legislation has existed to protect elasmobranchs along with other fishes, *e.g.* 1958 Convention on Fishing and Conservation of the Living Resources of the High Seas, 1994 (http://untreaty.un.org/ilc/texts/instruments/english/conventions/8_1_1958_fishing.pdf) United Nations Convention on the Law of the Sea (UNCLOS; http://www.un.org/depts/los/convention_agreements/convention_overview_convention.htm) and 1995 Food and Agriculture Organization (FAO) Code of Conduct for Responsible Fisheries (http://www.fao.org/docrep/005/v9878e/v9878e00.HTM). In recognition of the particular threats facing elasmobranchs, however, some pre-existing laws have been altered to address concerns around elasmobranchs specifically, *e.g.* 2001 UNCLOS Fish Stock Agreement, and new legislation has been devised that requires the conservation of elasmobranchs, *e.g.* 1999 FAO International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks; http://www.fao.org/fishery/ipoa-sharks/en) and 2011 U.S. Shark Conservation Act (http://www.gpo.gov/fdsys/pkg/PLAW-111publ348/pdf/PLAW-111publ348.pdf). Given the low recovery potential of most elasmobranchs (Smith *et al*., 1998; Garcia *et al*., 2008) it could take decades to reveal whether legislative and management tools are successful in achieving recovery.

Despite the fact that populations could take decades to rebuild even under stringent conservation efforts (Simpfendorfer, 2000) and that some populations are already at very low abundance, recoveries might still be possible. Marine mammal populations share similar life-history traits with elasmobranchs and experienced similar population declines, yet marked recovery has been observed in some populations as a result of strong national and international management actions (Lotze & Worm, 2009; Lotze *et al*., 2011; Magera, 2011). These conservation successes should provide guidance and hope for rebuilding other long-lived species like elasmobranchs.

Here, current knowledge on the recovery potential and conservation options for elasmobranchs is reviewed. First, elasmobranch populations with positive abundance trends are reviewed, and the rates, timelines and drivers of increase evaluated. Successful management and conservation initiatives require a clear understanding of acceptable mortality rates and timelines required for rebuilding, thus a population viability analysis is then used to explore the recovery potential of species where recovery plans are in place. Finally, strategies being used for elasmobranch management and conservation are reviewed, patterns and drivers of recovery in the south-eastern U.S.A. as a case study are discussed, and important knowledge gaps with respect to elasmobranch conservation and recovery are highlighted.

DEFINING RECOVERY FOR ELASMOBRANCHS

Although there is no standard definition of recovery, it is typically considered to be a return to a 'normal state' (http://oxforddictionaries.com/; Lotze *et al*., 2011) or to an alternative target that supports a certain management objective such as maximum sustainable yield (Worm *et al*., 2009). In wildlife populations, however, with natural fluctuations and anthropogenic disturbances that began long before ecological records were kept (Pauly, 1995), obtaining an accurate description of a normal state or historical reference point against which the current state can be compared can be difficult (Lotze & Worm, 2009; Magera, 2011). Recent studies that have managed to reconstruct historical baselines have revealed significantly more abundant populations than originally thought (Jackson *et al*., 2001; Lotze & Worm, 2009) thus changing the perception of what the normal state is and consequently the potential degree of recovery.

For elasmobranchs, determining historical reference points can be even more challenging than for other marine animals. Because elasmobranchs generally stay below the water surface, they are not easily observed and are therefore mentioned only occasionally in historical narratives (Sandin *et al*., 2008; Ward-Paige *et al*., 2010). Moreover, as cartilaginous fishes they are not readily preserved in archaeological samples and their presence is probably underrepresented in the fossil record (Marcus *et al*., 1999). Finally, fisheries organizations have not routinely kept species-specific information on elasmobranch catches. The common practice of lumping all elasmobranchs as shark makes it difficult to determine species-specific trends (Hayes *et al*., 2009; Ferretti *et al*., 2010). Even the largest extant fish, the whale shark *Rhincodon typus* Smith 1828, was still considered data deficient by the IUCN in 1996 (IUCN, 2011). Therefore, obtaining good historical reference points, especially for coastal populations that might have been affected for hundreds of years (Marcus *et al*., 1999; Ferretti *et al*., 2008, 2010; Ward-Paige *et al*., 2010; Nance *et al*., 2011), is often unrealistic for most elasmobranch populations.

Another option for defining recovery is to measure some metric of population increase. This requires records on population abundance proxies from research surveys, catch-per-unit-effort data (CPUE), or other standardized observations. Recovery could then be analysed over a certain time period, for example after a low point of abundance, after exploitation has ceased, or after a specific management measure has been implemented (Hutchings & Reynolds, 2004; Lotze *et al*., 2011; Magera, 2011). In the following, increases in abundance since a low point were modelled, regardless of the attributed driver, to explore recovery potential for elasmobranchs. Then, the recovery potential of populations with national recovery strategies were modelled based on their life-history characteristics under different anthropogenic mortality.

RECOVERY POTENTIAL FOR ELASMOBRANCHS

CASES OF POPULATION INCREASE

Drivers, timelines, rates of increase and increasing abundance trends can provide important insight into the recovery potential for elasmobranch populations. Information was assembled on elasmobranch populations from the scientific literature, including both fisheries dependent and independent data that were described as increasing, rebuilding or recovering. Various indices of relative abundance were used, including CPUE, numbers or biomass, some of which reported an intrinsic rate of population increase (Table I). These data were complemented with populations showing increasing abundance trends in a recently compiled stock recruitment database (RAM

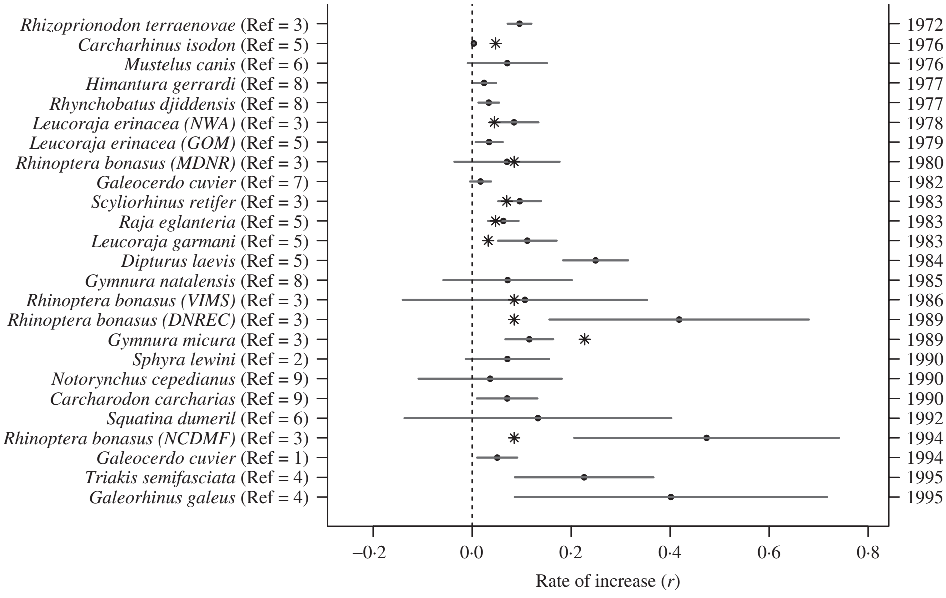

FIG. 1. Estimated annual rates of population increase for all populations marked as * in Table I (▬, 95% C.I.). Year (on secondary axis) is the low year from which the increase was computed. *The intrinsic rates of increase provided in the literature and reported in Table I. Numbered references (Ref) are provided in Table I. NWA, North-west Atlantic; GOM, Gulf of Mexico; MDNR, Maryland Department of Natural Resources; VIMS, Virginia Institute of Marine Science; DNREC, Delaware Department of Natural Resources and Environmental Control; NCDMF, North Carolina Division of Marine Fisheries.

Legacy; http://ramlegacy.marinebiodiversity.ca/srdb/updated-srdb; Ricard *et al*., 2011) (Table I, and Appendix SI). Although an attempt was made to be thorough by strategically searching the scientific literature and querying researchers in different regions, the present list may not be exhaustive.

The search yielded information on 35 increasing populations from the scientific literature. In addition, five of 14 elasmobranch populations represented in the RAM Legacy database were increasing (Table I). One population, the barndoor skate *Dipturus laevis* (Mitchill 1818), was documented in Gedamke *et al*. (2009) but here the same data in its raw version from the RAM Legacy database was used in Table 1 and Fig. 1. Eighteen (45%) of these increasing populations were sharks and the remaining were skates and rays. The majority of these increases (73%) were from the north-west Atlantic Ocean and Gulf of Mexico region. Although there was some ambiguity regarding the cause of increase, most (53%) of the increases were smaller-bodied species, which were attributed to predation release as a result of declines in larger shark populations (Shepherd & Myers, 2005; Myers *et al*., 2007; Ward-Paige *et al*., 2010). Twenty five per cent of increases, however, were at least partially attributed to improved management (McAuley, 2008; Hayes *et al*., 2009; Reid *et al*., 2011), gear restrictions (Pondella & Allen, 2008) and reduced mortality stemming from changes in targeting or market demand (Campana *et al*., 2008).

Each study used a different timeframe, sampling method and analysis to calculate a rate of population increase. Hence, in order to compare across populations this review focused only on the period of increase after a low point and calculated a

Table I. Elasmobranch populations with increasing, rebuilding or recovering trends from the literature or the RAM Legacy database (Ricard *et al.*, 2011) with stock location, reported intrinsic rates of increase or other indicators of recovery (Increase), data timelines (Timeline), and the key reported driver (Reported driver) attributed to the increase

Species	Scientific name	Location	Increase	Timeline	Reported driver	Reference
Florida smoothound	*Mustelus norrisi*	Gulf of Mexico	0·005	1972–2002	Predation release	Shepherd & Myers, 2005 (6)
Bullnose eagle ray	*Myliobatus freminvilli*	North-west Atlantic Ocean	0·013	1970–2005	Predation release	Myers *et al.*, 2007 (3)
Roundel skate	*Raja texana*	Gulf of Mexico	0·015	1972–2002	Predation release	Shepherd & Myers, 2005 (6)
Spiny butterfly ray	*Gymnura altavela*	North-west Atlantic Ocean	0·028	1970–2005	Predation release	Myers *et al.*, 2007 (3)
Bonnethead shark	*Sphyrna tiburo*	North-west Atlantic Ocean	0·028	1970–2005	Predation release	Myers *et al.*, 2007 (3)
Rosette skate	*Leucoraja garmani*	North-west Atlantic Ocean	0·033	1970–2005	Predation release	Myers *et al.*, 2007 (3)
Tiger shark*	*Galeocerdo cuvier*	North-west Atlantic Ocean	0·040	1992–2005	Productive, post-release survival, management	Baum & Blanchard, 2010 (1)
Clearnose skate	*Raja eglanteria*	Gulf of Mexico	0·040	1972–2002	Predation release	Shepherd & Myers, 2005 (6)
Little skate*	*Leucoraja erinacea*	North-west Atlantic Ocean	0·045	1970–2005	Predation release	Myers *et al.*, 2007 (3)
Finetooth shark	*Carcharhinus isodon*	North-west Atlantic Ocean	0·048	1970–2005	Predation release	Myers *et al.*, 2007 (3)
Clearnose skate	*Raja eglanteria*	North-west Atlantic Ocean	0·048	1970–2005	Predation release	Myers *et al.*, 2007 (3)

TABLE I. Continued

Species	Scientific name	Location	Increase	Timeline	Reported driver	Reference
Atlantic stingray	*Dasyatis sabina*	Gulf of Mexico	0·050	1972–2002	Predation release	Shepherd & Myers, 2005 (6)
Smalltooth sawfish	*Pristis pectinata*	Everglades National Park, U.S.A.	0·050	1972–2004		Carlson *et al*., 2007
Atlantic sharpnose shark*	*Rhizoprionodon terraenovae*	North-west Atlantic Ocean	0·060	1970–2005	Predation release	Myers *et al*., 2007 (3)
Sand devil angel shark*	*Squatina dumeril*	Gulf of Mexico	0·065	1972–2002	Predation release	Shepherd & Myers, 2005 (6)
Chain catshark*	*Scyliorhinus retifer*	North-west Atlantic Ocean	0·070	1970–2005	Predation release	Myers *et al*., 2007 (3)
Spreadfin skate*	*Dipturus olseni*	Gulf of Mexico	0·080	1972–2002	Predation release	Shepherd & Myers, 2005 (6)
Cownose ray*†	*Rhinoptera bonasus*	North-west Atlantic Ocean	0·085	1970–2005	Predation release	Myers *et al*., 2007 (3)
Smooth dogfish*	*Mustelus canis*	Gulf of Mexico	0·090	1972–2002	Predation release	Shepherd & Myers, 2005 (6)
Lesser devil ray	*Mobula hypostoma*	North-west Atlantic Ocean	0·105	1970–2005	Predation release	Myers *et al*., 2007 (3)
Bullnose eagle ray	*Myliobatis freminvillii*	Gulf of Mexico	0·115	1972–2002	Predation release	Shepherd & Myers, 2005 (6)
Smooth butterfly ray*	*Gymnura micura*	North-west Atlantic Ocean	0·228	1970–2005	Predation release	Myers *et al*., 2007 (3)
Yellow stingray	*Urobatis jamaicensis*	Jamaica	0·370	1994–2007	Predation release	Ward-Paige *et al*., 2010
White shark	*Carcharodon carcharias*	Australia	CPUE	1990–2010	Management	Reid *et al*., 2011 (9)

TABLE I. Continued

Species	Scientific name	Location	Increase	Timeline	Reported driver	Reference
Barndoor skate*	*Dipturus laevis*	North-West Atlantic Ocean	CPUE	1963–2005		Ricard *et al.*, 2011 (5)
Tiger shark*	*Galeocerdo cuvier*	South Africa	CPUE	1978–2003	Competition release, increased survivorship	Dudley & Simpfendorfer, 2006 (7)
Tope, school or soupfin shark*	*Galeorhinus galeus*	East Pacific Ocean	CPUE	1995–2004	Management (gillnet ban)	Pondella & Allen, 2008 (4)
Diamond ray*	*Gymnura natalensis*	South Africa	CPUE	1977–2002	Management, fishery changes	Pradervand *et al.*, 2007 (8)
Brown ray*	*Himantura gerrardi*	South Africa	CPUE	1977–2000	Management, fishery changes	Pradervand *et al.*, 2007 (8)
Little skate*	*Leucoraja erinacea*	North-West Atlantic Ocean	CPUE	1968–2005		Ricard *et al.*, 2011 (5)
Rosette skate*	*Leucoraja garmani*	North-West Atlantic Ocean	CPUE	1967–2005		Ricard *et al.*, 2011 (5)
Gummy shark	*Mustelus antarcticus*	West Australia	CPUE		Management	McAuley, 2008
Sevengill shark*	*Notorynchus cepedianus*	Australia	CPUE	1950–2010	Competition release	Reid *et al.*, 2011 (9)
Clearnose skate*	*Raja eglanteria*	North-West Atlantic Ocean	CPUE	1975–2005		Ricard *et al.*, 2011 (5)
Giant guitarfish*	*Rhynchobatus djiddensis*	South Africa	CPUE	1977–2001	Management, fishery changes	Pradervand *et al.*, 2007 (8)

TABLE I. Continued

Species	Scientific name	Location	Increase	Timeline	Reported driver	Reference
Leopard shark*	*Triakis semifasciata*	East Pacific Ocean	CPUE	1995–2004	Management (gillnet ban)	Pondella & Allen, 2008 (4)
Finetooth shark*	*Carcharhinus isodon*	Atlantic Ocean	Increase total	1976–2005		Ricard *et al*., 2011 (5)
Porbeagle shark	*Lamna nasus*	North-west Atlantic Ocean	Partial recovery	1960–2000	Reduced availability and profitability	Campana *et al*., 2008
Scalloped hammerhead shark*	*Sphyrna lewini*	North-west Atlantic, Ocean Gulf of Mexico	Rebuilding	1981–2005	Management	Hayes *et al*., 2009 (2)
Whiskery shark	*Furgaleus macki*	West Australia	Recovery		Management	McAuley, 2008

†A combined intrinsic rate of change was provided for the *Rhinoptera bonasus*, but four abundance trends were published in Myers *et al*., (2007).
CPUE, catch-per-unit-effort.
*, reference numbers shown in parenthease relate to populations shown in Fig. 1.

standard rate of increase from there (Appendix SI). This method tested for a long-term population trend (≥10 years) since the last low point in abundance assuming an exponential rate of increase: $N_t = N_0 e^{rt}$, where N is the population index (here assumed to be proportional to the CPUE) at time t, r is the intrinsic rate of growth and t is the time in years. For each time series, the ln-transformed population abundance indices were described by the linear model: $\ln N_t = \ln N_0 + rt$. From the available data, it was possible to calculate standardized rates of increase for 25 elasmobranch populations (Fig. 1). As expected, rates of increase, that only covered the period since the last low point in abundance, were generally higher than those reported in the literature using the entire time series (Table I). The estimated rates of increase were as high as 0·5 for one cownose ray *Rhinoptera bonasus* (Mitchill 1815) population (Fig. 1; Myers *et al.*, 2007). Periods of population increase began in the 1970s for eight populations, the 1980s for 10 populations and the 1990s for seven populations (Table 1 and Fig. 1). Although the majority of these species could be considered smaller elasmobranchs (mesopredators), a few large sharks that have been heavily targeted in the past, including the tope, school or soupfin shark *Galeorhinus galeus* (L. 1758), tiger shark *Galeocerdo cuvier* (Péron & LeSueur 1822), white shark *Carcharodon carcharias* (L. 1758), sevengill shark *Notorynchus cepedianus* (Péron 1807) and scalloped hammerhead *Sphyrna lewini* (Griffith & Smith 1834), also showed signs of increase.

MODELLED RECOVERY POTENTIAL FOR DEPLETED POPULATIONS

Species-specific conservation initiatives, such as national recovery strategies, are intended to secure the long-term survival of species that have undergone significant declines. The success of these strategies for elasmobranchs, however, is still unclear, given the recent nature of these plans. Trends and timelines of recovery for six populations (five species) were modelled, two of which have recovery strategies under the Canadian Species at Risk Act (SARA; http://www.sararegistry.gc.ca/approach/act/sara_e.pdf) [Pacific coast basking shark *Cetorhinus maximus* (Gunnerus 1765); Atlantic coast *C. carcharias*], one protected in the U.S. under the Endangered Species Act (ESA; http://www.nmfs.noaa.gov/pr/pdfs/laws/esa.pdf) [smalltooth sawfish *Pristis pectinata* Latham 1794] and three in Australia that are managed under the Commonwealth Environment Protection and Biodiversity Conservation Act (EPBC; http://www.environment.gov.au/epbc/index.html) (grey nurse shark *Carcharias taurus* Rafinesque 1810, *R. typus* and *C. carcharias*) (Table II). First, the intrinsic rate of population growth (r_V) was calculated for each species based on its life-history characteristics following the methods outlined in Smith *et al.* (1998) (Table II and Appendix SI), and then population trends were modelled under different levels of anthropogenic mortality rates, A (Fig. 2). This provides an estimate of the maximum anthropogenic mortality rates, *e.g.* fishing mortality plus additional mortality from entanglement and boat strikes, allowable for a population to recover and the time needed to meet recovery targets under different mortality scenarios.

Under zero anthropogenic mortality, all five species doubled their population size in <50 years [Fig. 2(a)]. Even under low mortality scenarios, however, population-doubling time greatly increased. Mortality rates between $0{\cdot}02 \leq A \leq 0{\cdot}06$ were chosen, which covered the range between increasing and decreasing population

TABLE II. Life-history attributes used to calculate intrinsic rate of population increase (r_V) of shark species with specific recovery plans and strategies. Life-history data from www.iucnredlist.org

Species	Scientific name	IUCN status	CITES list	Country	Year	F_{min}	F_{max}	F_{per}	b	w	α	r_V
Grey nurse shark	*Carcharias taurus*	Vulnerable		Australia	2002	2	2	2	0·5	25	6	0·058
White shark	*Carcharodon carcharias*	Vulnerable	Appendix II, 2004	Australia, Canada	2002, 2011	2	10	2	1·5	30	10	0·039
Basking shark	*Cetorhinus maximus*	Vulnerable	Appendix II, 2003	Canada	2011	6	6	3	0·8	50	16	0·025
Smalltooth sawfish	*Pristis pectinata*	Critically Endangered	Appendix I, 2007*	U.S.A.	2009	15	20	1	8·8	70	17	0·022
Whale shark	*Rhincodon typus*	Vulnerable	Appendix II, 2003	Australia	2002	300	300	1	150	100	21	0·017

IUCN, International Union for the Conservation of Nature; CITES, U.N. Convention on International Trade in Endangered Species.

*The most fecund values were used (*e.g.* earliest maturity, 1 year reproductive period when value was unknown), therefore likely to be more vulnerable than stated here; *Pristis pectinata* α is unknown, the average value was used from Simpfendorfer (2000).

F_{min} and F_{max}, the minimum and maximum number of pups produced per year; F_{per}, the fecundity period in years; b, the number of pups per female per year; w, longevity in years; α, age at maturity.

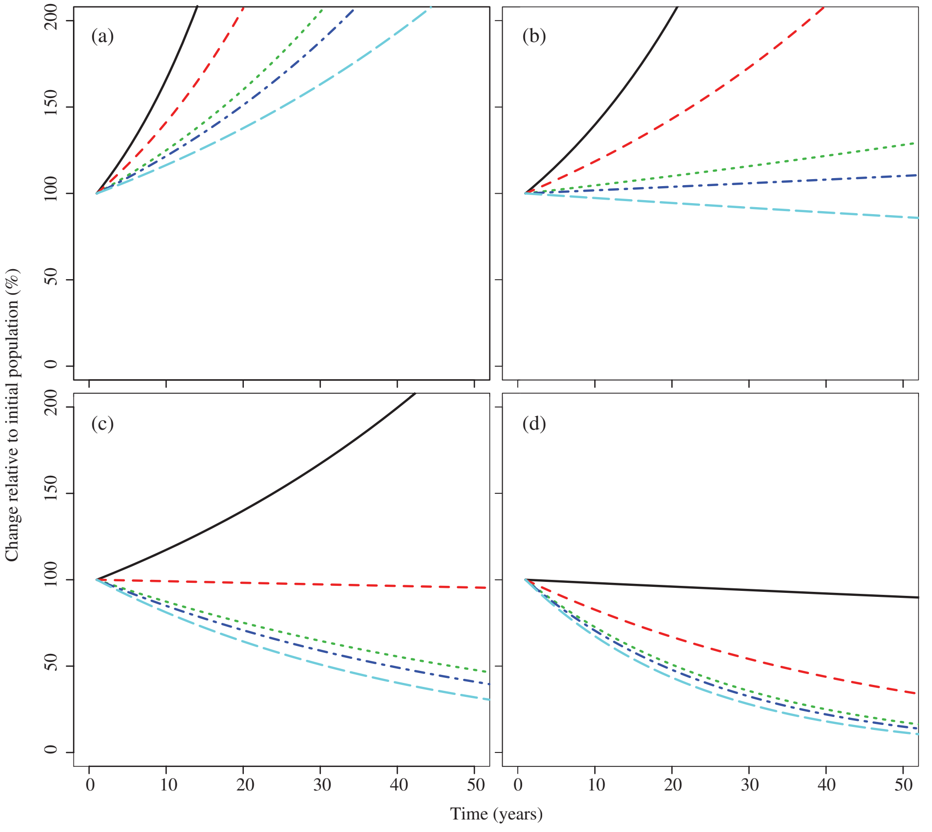

FIG. 2. Absolute changes in population abundance of five shark species (——, *Carcharias taurus*; - - - -, *Carcharodon carcharias*; ......, *Cetorhinus maximus*; -.-.-, *Pristis pectinata*; — —, *Rhincodon typus*) across a range of anthropogenic mortalities (A), (a) $A = 0{\cdot}00$, (b) $A = 0{\cdot}02$, (c) $A = 0{\cdot}04$ and (d) $A = 0{\cdot}06$ under density independent scenarios.

sizes. Actual mortality rates vary, but the mortality rates used here are fairly low for sharks, given that reported instantaneous fishing mortality rates can be as high as 0·2 [porbeagle *Lamna nasus* (Bonnaterre 1788); Campana *et al*., 2002] or 0·46 for species with a higher capacity for increase [Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Richardson 1836); Marquez-Farias & Castillo-Geniz, 1998]. With $A = 0{\cdot}02$, the population doubling time for *C. maximus* and *P. pectinata* increased to 139 and 353 years, respectively, and *R. typus* decreased in abundance [Fig. 2(b)]. Under $A = 0{\cdot}06$, all species declined [Fig. 2(d)]. In some of these cases, the rates are based on poorly resolved life-history data, often only based on a few individuals, *e.g.* for *R. typus*, and therefore, considerable uncertainty remains (Simpfendorfer *et al*., 2008). Ward-Paige *et al*. (2010) presents a similar analysis for more thoroughly understood elasmobranch species. Similarly, other studies have predicted recovery times of depleted elasmobranchs on the order of decades to centuries, even under low fishing mortality (Simpfendorfer, 2000; McFarlane *et al*., 2009). Although these models may not fully capture changes in age and size structure in a recovering population, they do highlight the strong negative effect of even low levels of anthropogenic mortality (2–6% of the population per year) and thus the risk inherent in delayed or lenient recovery strategies. They also provide important consideration for the potential detrimental effects to populations that might result from slight increases in natural mortality caused, for example, by climate change or changes in habitat quality, food supply or predators.

The results here also provide perspective on the potential for success of existing recovery strategies. For example, the recovery strategy for *C. maximus* has deemed that 10–17 mortalities per year across the entire population of 321–523 individuals to be acceptable (McFarlane *et al*., 2009). This equates to an anthropogenic mortality rate of $A \approx 0{\cdot}03$, which would cause the population to decline according to present results ($A > 0{\cdot}023$ caused a decline); however, McFarlane *et al*. (2009) used the maximum r_v values (0·032–0·040) from the range of known life-history characteristics, while that used here ($r_v = 0{\cdot}025$, Table II) is more conservative. Even with an anthropogenic mortality rate of $A = 0{\cdot}02$, the population would take *c*. 139 years to double, and even longer to recover to pre-exploitation levels. Similarly, *C. taurus* in New South Wales, Australia, has failed to increase despite being legally protected from fishing since 1984 (Otway *et al*., 2004). Because this population consists of only *c*. 300 individuals (Otway *et al*., 2004), an anthropogenic mortality rate of $A < 0{\cdot}05$ or less than 15 individuals per year is required to allow for the population to increase, fewer than the estimated 14–20 per year that are killed by fishing and beach netting (Dulvy & Forrest, 2010). *Carcharodon carcharias* in New South Wales, Australia, is the only population with a legal recovery strategy that has shown signs of increase since the early 1990's (Reid *et al*., 2011; Fig. 1). Considering, however, that legal protection and recovery strategies were not implemented for this species until 1998 and 2002, respectively, the long generation times and the highly migratory behaviour of this species, caution is urged in attributing all of the increase to protection measures (Reid *et al*., 2011). Due to inadequate age-specific data in these populations, the models here do not include age-specific selectivity, which may be an important factor in population growth. Despite these limitations, the results demonstrate the importance of removing all sources of anthropogenic mortality, and possibly increasing juvenile survival where possible, when abundance is so low that a recovery strategy is deemed necessary.

CONSERVATION OPTIONS FOR ELASMOBRANCH RECOVERY

Recently, a number of tools have been proposed and implemented to promote recovery of elasmobranch populations, especially sharks. Here an overview of these options is provided and the potential and limitations of each for enabling recovery is discussed.

RESTRICTING FISHING MORTALITY

Given that most elasmobranchs have low productivity and many have poor or collapsed stock status, successful recovery may require restriction of fishing mortality to near zero, for example through a moratorium and incidental by-catch mitigation (Caddy & Agnew, 2004; Cosandey Godin & Worm, 2010). Traditional fisheries management tools, including quotas, total allowable catches, size restrictions, bag limits, effort limits, gear restrictions and seasonal closures, are currently being used to reduce fishing mortality for depleted elasmobranch populations in various jurisdictions. In some regions, there is evidence that several populations have stabilized or started to recover as a result. For example, although the gummy shark *Mustelus antarcticus* Günther 1870 in southern Australia has been markedly reduced, harvest rates are thought to be sustainable at a level that is close to maximum sustainable yield (Walker, 2007*a*). In the southern and low western Australian demersal gillnet and longline fisheries, the catch rate of whiskery shark *Furgaleus macki* (Whitley 1943) has recently increased by 46%, to its highest level in 15 years, indicating that the stock has begun to recover after being depleted in the 1980s, a result of seasonal closures and constrained catches (McAuley, 2008). In the south-eastern U.S.A., *S. lewini* has also shown signs of recent rebuilding in response to fisheries management. Changes in allowable fishing gear, such as the removal of gillnets, have also allowed for increases in some shark populations within a few years off the coast of California (Pondella & Allen, 2008). On the scale of the greater-Caribbean, higher abundances of reef-associated sharks were found only in places like the Bahamas and Florida where management strategies with restricted catches, prohibited gear types, and protected species and areas were implemented (Ward-Paige *et al.*, 2010). Recently, this was further formalized with the declaration of a nation-wide shark sanctuary in the Bahamas. Despite these apparent successes, there remains a paucity of science-based management for targeted and by-catch elasmobranch species in many regions (Walker, 1998, 2007*b*). Even 12 years after the FAO recommended that fishing nations develop and adopt a National Plan of Action for Sharks (NPOA-Shark), only 13 countries have submitted such plans (http://www.fao.org/fishery/ipoa-sharks/npoa/en), and none has adequately addressed the recommendations in the International Plan of Action for Sharks (IPOA-Sharks) or is properly implemented so far (Lack & Sant, 2011).

SHARK-FINNING PROHIBITIONS

Shark-finning, where fins are removed at sea and the body is discarded, occurs because of the divergence in value of fins for shark-fin soup compared to the meat. This practice promotes unsustainable mortality rates, is inhumane and wasteful (Gilman *et al.*, 2008). Although prohibitions on shark-finning have existed since 1980 (Camhi *et al.*, 2009) this strategy has gained momentum as a tool for shark conservation more recently, given widespread evidence of population declines (Dulvy *et al.*, 2008, Ferretti *et al.*, 2010) and evidence that millions of fins enter the trade without being reported (Clarke *et al.*, 2006). Yet many countries lack proper enforcement and fin-retention policies that are often ineffective due to loopholes that allow finning to occur (Camhi *et al.*, 2009). As such, there has been a push towards regulations that mandate sharks be landed with their fins naturally attached, thereby closing the loopholes. For example, in 2011 the U.S. passed the Shark Conservation Act, which implements a fins-attached policy throughout the U.S. Exclusive Economic Zone (EEZ). In addition, a number of U.S. states and territories, *e.g.* California, Hawaii, Guam, Northern Marianas Islands, have further banned the possession, trade, distribution and sale of sharks and shark products (Pew, 2011). Despite being a useful conservation tool, shark-finning prohibition and retention policies without proper enforcement may not necessarily reduce mortality rates enough to sustain healthy populations (*e.g.* for reef sharks, Robbins *et al.*, 2006, Graham *et al.*, 2010).

SHARK SANCTUARIES

Recently, shark sanctuaries have been adopted by a number of countries including the entire EEZ of Palau (2009), Maldives (2010) and Honduras (2010), the Regent of Raja Ampat, Indonesia (2011), the Bahamas (2011), the Republic of the Marshall Islands (2011) as well as other smaller reserves such as the Shark Reef Marine Reserve in Fiji (Brunnschweiler, 2010; Pew, 2011; Shark Savers, 2011). These sanctuaries often cover relatively large areas, up to 1·99 million km^2 in the case of the Republic of the Marshall Islands, and include a range of habitats that are critical for different life stages of elasmobranch species. Although these targeted shark sanctuaries are too recent to have had any observable effects on elasmobranch populations so far, the success of other marine protected areas (MPA) might provide important insight.

Although no studies of MPAs have specifically documented the recovery of elasmobranchs, increases in other large predators (Micheli *et al*., 2004; McClanahan *et al*., 2007; McClanahan, 2011) and the sheer abundance of elasmobranchs in remote and protected regions (Friedlander & DeMartini, 2002; Stevenson *et al*., 2007; Sandin *et al*., 2008; Koldewey *et al*., 2010) might provide support for their potential for recovery of elasmobranchs. There is evidence that even relatively small MPAs can be effective for maintaining higher shark abundances (Heupel *et al*., 2009). Some inaccessible regions that are relatively close to human settlements, however, can be devoid of large predators, despite maintaining a high biomass of target fishes (Williams *et al*., 2008; McClanahan, 2011), which indicates that even modest levels of fishing effort can have significant effects on the abundance of wide-ranging predators (DeMartini *et al*., 2008). Some elasmobranchs are highly migratory and can easily move beyond the distances covered by even the largest sanctuaries (Skomal *et al*., 2009; Block *et al.,* 2011), leaving them vulnerable to exploitation. In these cases, the effectiveness of a sanctuary probably depends on what is and is not protected (portion of the population, critical life stages and duration) and the level of risk when outside the sanctuary (fishing pressure, habitat use and time of year). Furthermore, the success of sanctuaries may be increased by the inclusion of nursery areas and other essential fish habitat (Speed *et al*., 2010). As well, there is evidence of poaching and population declines in protected areas that are open to vessels (Graham *et al*., 2010), compared to higher shark abundances in no-entry zones (Robbins *et al*., 2006), which highlights the importance of enforcement for the success of sanctuaries in protecting elasmobranch populations.

HABITAT RESTORATION

The importance of identifying, describing and conserving critical habitat for the conservation and recovery of elasmobranchs is only recently being recognized, *e.g.* the Bonn Convention on Migratory Species of Wild Animals 2010 (CMS; www.cms.int), U.S. Magnuson-Stevens Fishery Conservation and Management Act 1996 (http://www.nmfs.noaa.gov/sfa/magact/). Habitat type, water temperature, freshwater input and ocean circulation influence elasmobranch behaviour, distribution patterns and prey availability (Bradshaw *et al*., 2007; Chin *et al*., 2007; Heupel *et al*., 2007; Kinney & Simpfendorfer, 2009; Froeschke *et al*., 2010; de la Parra Venegas *et al*., 2011). For many elasmobranchs, critical habitats for reproduction, nursery, and juvenile survival include a variety of coastal habitats (Heupel *et al*., 2004; Carraro

& Gladstone, 2006; Wiley & Simpfendorfer, 2007; Knip *et al*., 2010; Espinoza *et al*., 2011), which have been especially altered and deteriorated in highly human-affected zones (Pandolfi *et al*., 2005; Lotze *et al*., 2006). There are cases, however, in which habitat restoration appears to have benefited elasmobranch populations. For example, restored estuaries in California now provide a suitable environment for feeding and growth of gray smooth-hound sharks *Mustelus californicus* Gill 1864 (Espinoza *et al*., 2011). As well, habitat restoration of the Everglades National Park (ENP) might have been instrumental in preventing the extinction of *P. pectinata* since other factors such as management and protected status, *e.g.* U.S. Endangered Species Act (ESA) listings, came after the population began rebuilding in 1989 (Carlson *et al*., 2007) and follows the declaration of the ENP wilderness area in 1978 and the ENP Protection and Expansion Act (http://thomas.loc.gov/cgi-bin/query/z?c101:H.R.1727:) in 1989 when water flow was restored to improve ENP ecosystems.

SPECIES-SPECIFIC CONSERVATION

Species-specific international and national instruments exist as a last resort to conserve individual species by identifying and listing those species at risk of extinction and implementing strategies to secure their long-term survival (Camhi *et al*., 2009). The International Union for Conservation of Nature (IUCN), which provides species-specific conservation status at the global scale, has identified 67 elasmobranch species as critically endangered or endangered (Simpfendorfer *et al*., 2011). Other international instruments that aim to conserve threatened species, such as the Convention on International Trade in Endangered Species (CITES; http://www.cites.org/eng/disc/text.php) and the CMS have recently listed a number of elasmobranch species, including *C. carcharias*, *R. typus* and *C. maximus* on both instruments, and *L. nasus*, spiny dogfish *Squalus acanthias* L. 1758, longfin mako *Isurus paucus* Guitart 1966 and shortfin mako *Isurus oxyrinchus* Rafinesque 1810 on CMS (CMS, 2005). All *Pristis* spp. are listed under CITES Appendix I or II. Some elasmobranchs are also included on national instruments, including the *C. taurus*, *C. carcharias* and *R. typus* on the Australian EPBC, *C. maximus* on the Canadian SARA and *P. pectinata* on the U.S. ESA.

Despite progress in providing legal protection to some species at risk of extinction, there are limitations that can prevent the success of these strategies. These include: the challenge of establishing the extent of population decline and thus a proper assessment of the risk status (Marcus *et al*., 1999; Ferretti *et al*., 2008, 2010; Ward-Paige *et al*., 2010; Nance *et al*., 2011), hesitation to list species (Camhi *et al*., 2009, Lack & Sant, 2011), enforcement complexities such as distinguishing prohibited species from look-a-like species (Shivji *et al*., 2005) and monitoring remote areas (Graham *et al*., 2010), limited use of non-lethal monitoring techniques that inform about protected species (Domeier & Nasby-Lucas, 2007; Rowat *et al*., 2009; Bansemer & Bennett, 2010; Ward-Paige *et al*., 2010; Ward-Paige & Lotze, 2011), and a lack of information about life history, critical habitat and population dynamics at low abundance (Simpfendorfer, 2000, Kinney & Simpfendorfer, 2009; de la Parra Venegas *et al*., 2011). Due to elasmobranchs' low rate of recovery, the success of species-specific conservation initiatives might take decades to be fully revealed. Based on the first decade(s) of legal protection for elasmobranchs the success of these initiatives is not encouraging. For example, *C. taurus* in southern Australia have been legally protected from fishing since 1984, but incidental hooking rates remain high (Bansemer & Bennett, 2010) and populations continue to decline (Otway *et al*., 2004). *Rhincodon typus* in Australia also continue to decline in both abundance and size (Bradshaw *et al*., 2007) despite being protected by CMS, CITES and EPBC. While the success of these species-specific instruments for elasmobranchs remains to be seen, they almost certainly require long-term commitments, *e.g.* beyond species' generation times, and should be combined with other conservation strategies such as no-take areas, habitat restoration and by-catch mitigation.

RAISING AWARENESS AND EDUCATION

In recent years, there has been a shift in the public's perception of elasmobranchs, especially sharks, with momentum shifting towards conservation rather than exploitation. For example, scuba divers motivations have changed from 'adventure-seeking hunters' to 'nature-seeking observers' (Whatmough *et al*., 2011) and their 'willingness to pay' has increased the value of living sharks orders of magnitude above what can be earned from fishing that same individual (Rowat & Engelhardt, 2007; Dicken & Hosking, 2009; Brunschweiller, 2010; Clua *et al*., 2011). In areas where diving tourism is less of an economic incentive, some tour companies run shark watching trips (Southall *et al*., 2005) and catch-and-release shark fishing activities (Lynch *et al*., 2010). These activities provide the opportunity for public participation in scientific monitoring (Southall *et al*., 2005; Theberge & Dearden, 2006; Meyer *et al*., 2009; Ward-Paige *et al*., 2010; Ward-Paige & Lotze, 2011) and provide access to the public for education to dispel the myth of sharks as man-eaters and the belief that shark fins grow back after being cut off (C. Li, pers. comm.; C. A. Ward-page, pers. obs.), an issue that may be supported by field observations of *R. typus* with severed fins (Riley *et al*., 2009). These educational opportunities probably increase support for broader marine conservation initiatives such as MPAs (Bookbinder *et al*., 1998; Green & Donnelly, 2003) and shark-free marinas (www.sharkfreemarinas.com). As well, general awareness of the status of elasmobranchs among the general public can help curb demand for unsustainable products such as shark-fin soup (www.SharkTruth.org). Finally, increased awareness of the conservation concern of elasmobranchs should increase resources and the number of people willing to undertake the necessary research (Simpfendorfer *et al*., 2011).

CASE STUDY: PRELIMINARY SUCCESSES IN THE SOUTH-EASTERN U.S.A.

In the south-eastern U.S.A., several recovery strategies have been implemented that are designed to benefit the recovery of depleted elasmobranch populations: (1) shark fisheries management now includes recreational and commercial bag limits, gear restrictions, closed seasons, licensing and prohibiting the harvest of many shark species as well as shark-finning. These measures originally developed from the 1978 Preliminary Fisheries Management Plan (FMP), which was primarily concerned with foreign fishing vessels and the availability of sharks to the expanding U.S. fleet. Today, shark management regimes have become more conservation-oriented.

There is regular monitoring, assessment and evaluation of the status and threats to western Atlantic Ocean and Gulf of Mexico shark populations. Currently, 18 and 26 shark species are now completely prohibited in recreational and commercial fisheries, respectively (SEDAR, 2011). For other species, time and area closures have been implemented according to the recommendations by the South Atlantic Fishery Management Council, *e.g.* from January to July in coastal North Carolina (Conrath & Musick, 2008). For commercial fisheries, maximum sustainable yield is used as a basis for setting catch quotas. Recreational trip limits have been set at four large coastal or pelagic sharks per vessel and a daily bag limit of five small coastal sharks per person. Sharks not landed as part of the commercial or recreational fishery are required to be released uninjured; new protocols for counting dead discards are in place. Shark-finning has been prohibited since the 1993 FMP and has been enforced by requiring that sharks be landed with their fins naturally attached since 2008. Moreover, permits are required to sell all shark products. For more details on management measures see SEDAR (2011). (2) Established protected areas and habitat restoration zones that cover land, coast and sea ecosystems help conserve a variety of elasmobranchs. These include Everglades National Park (established 1947; *c*. 6000 km^2), Biscayne National Park (established 1968, *c*. 700 km^2), Big Cypress National Preserve (established 1974; *c*. 2900 km^2), Florida Keys National Marine Sanctuary (established 1990; 9600 km^2), and Dry Tortugas National Park (established 1992; 262 km^2). For example, the Everglades National Park (ENP) contains neonates, juveniles and adults of 27 elasmobranch species (Wiley & Simpfendorfer, 2007), including 10 species listed in Table I. The ENP protects primary nurseries for numerous elasmobranch species, has provided refuge from commercial fishing since 1985, and may have helped prevent the extirpation of *P. pectinata* before legal protection was afforded (Wiley & Simpfendorfer, 2007). (3) Enforcement by the NOAA Office for Law Enforcement has resulted in arrests of commercial and recreational fishers illegally possessing and selling elasmobranch parts. Through direct monitoring and collaboration with the U.S. Coast Guard a number of individuals have also been prosecuted for illegal shark finning, exceeding catch limits and unauthorized shark feeding (NMFS, 2010). (4) Fisheries-independent monitoring and assessment has helped to more accurately determine the status of elasmobranch populations. Prior to 1995, abundance indices were mostly derived from fishery-dependent sources (Morgan *et al.,* 2009). After discovering, however, that many shark populations declined by up to 75% between the 1970s and mid 1980s, the 1993 Fisheries Management Plan for sharks stressed the need for additional monitoring and assessment (Grace & Henwood, 1997; Carlson & Brusher, 1999). As such, fishery observer coverage (Hale *et al.,* 2011) and fisheries–independent indices of abundance were implemented (Grace & Henwood, 1997; Carlson and Brusher, 1999; Wiley & Simpfendorfer, 2007); (5) education and outreach efforts through universities, governmental and non-governmental organizations and conservation campaigns have greatly increased public awareness on the status of sharks and threats to their populations, thus enhancing the willingness to protect elasmobranchs, *e.g.* www.sharkfreemarinas.com and http://www.rsmas.miami.edu/users/fmg/research/sfssp.html.

Given these multi-faceted conservation and management strategies, it is expected that elasmobranchs will respond positively and increase in abundance. So far, some previously depleted populations have shown modest increases such as *P. pectinata* (Carlson *et al.,* 2007), *S. lewini* (Hayes *et al.,* 2009), *G. cuvier* (Baum & Blanchard,

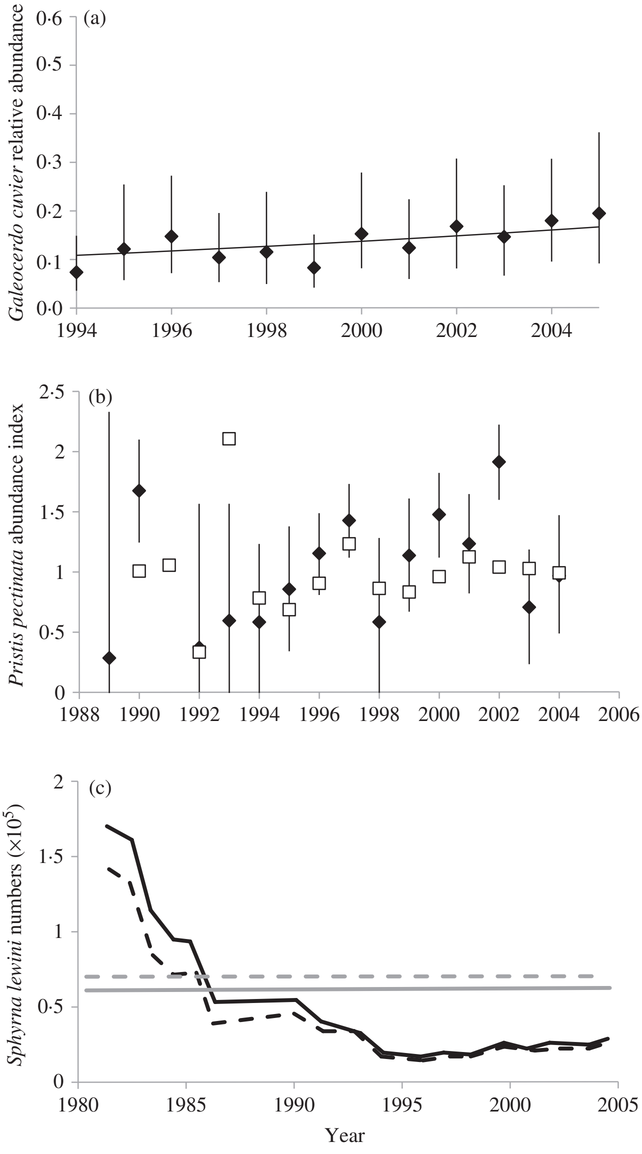

FIG. 3. Examples of population increase in the south-eastern U.S.A: (a) estimated change in relative abundance (standardized catch per 1000 hooks) in *Galeocerdo cuvier*, with 95% C.I. and overall trend (___) from generalized linear mixed model, (b) standardized relative index of abundance with coefficient of variation in *Pristis pectinata* (◆) and unstandardized relative catch-per-unit-effort (□) and (c) abundance estimates from Fox (___) and surplus population (_ _) models for *Sphyrna lewini*. Redrawn with permission from (a) Baum & Blanchard (2010), (b) Carlson *et al*. (2007) and (c) Hayes *et al*. (2009).

2010) (Fig. 3) and others are not considered to be overfished with overfishing not occurring [blacktip shark *Carcharhinus limbatus* (Müller & Henle 1839); (SEDAR, 2006)]. Increases in several other elasmobranchs such as *R. bonasus*, *R. terraenovae*, and the bullnose eagle ray *Myliobatis freminvillii* LeSueur 1824, all species with higher recovery potential, were attributed to predation release (Shepherd & Myers, 2005; Myers *et al.,* 2007); however, given the high realized rates of increase (up to 0·09 for *R. bonasus* Myers *et al.,* 2007;), conservation measures might have contributed to these positive population trends. Despite these positive examples, many populations are still overfished (below management targets) with overfishing still occurring, *e.g.* dusky shark *Carcharhinus obscurus* (LeSueur 1818) (SEDAR, 2011), and some are still declining (Baum & Blanchard, 2010); therefore, perseverance and a precautionary approach that includes species-specific monitoring, assessment and management is needed to establish recovery and restore the role of elasmobranchs in marine ecosystems.

IMPROVING THE ODDS FOR ELASMOBRANCH RECOVERY

Although several elasmobranch species have been extirpated throughout large parts of their natural range, none are considered extinct in the wild (Simpfendorfer *et al*., 2011). This review provides evidence for the recovery potential of depleted elasmobranch populations, but shows that actual recovery is still rare, and requires enforcement of very low levels of mortality. It also illustrates the complicated matter of rebuilding predators and their (small elasmobranch) prey simultaneously. If both were historically depressed by fishing, it should be possible to rebuild both over the long-term by reducing anthropogenic mortality. If fishing, however, does not directly affect small elasmobranchs, their abundance will mainly respond to changes in natural mortality, which will increase as large sharks recover from overexploitation. While the majority of increases discussed in this paper have been attributed, at least in part, to the loss of large sharks, a number were attributed to successful management (Table I) or a decrease in demand (*e.g. L. nasus*). This review and population viability analysis indicate, however, that population recovery for larger species in particular is expected to be slow, and sensitive to even low levels of mortality. This means that successful recovery of elasmobranch populations requires a long-term commitment with strong, dedicated management. The best strategy for elasmobranch recovery might be a multi-faceted conservation approach that includes (1) science-based management and near-zero fishing mortality, (2) clear and enforced anti-finning prohibitions and novel approaches (*e.g.* fin possession bans) to curb finning in unmanaged fisheries, (3) enforced MPAs or shark sanctuaries that cover a range of habitat types used by elasmobranchs in different life stages, (4) strong conservation and restoration initiatives for critical habitats and aggregation sites such as nurseries, breeding grounds and migration routes, (5) legally binding legislation with a more rapid response that gives species the protection they need before population abundances decline to dangerously low levels and (6) raised public and political awareness to reduce demand and increase support for conservation initiatives.

Since 2000, knowledge of elasmobranch biology and their population status have drastically improved, but there is still only localized evidence of rebuilding populations. Proper management needs appropriate recovery targets, good life-history information, accurate population assessments and precise taxonomic descriptions. Development and implementation of cost-efficient, long-term and broad-scale monitoring of different conservation strategies, *e.g.* shark sanctuaries, is needed. Because a large portion of the shark trade is illegal, unregulated and unreported, it cannot be the sole responsibility of conservation and management agencies, but also that of fishermen and the general public to raise awareness, promote good practices and curb demand for shark products.

We would like to thank A. Magera, G. Britten and J. K. Carlson for sharing their thoughts on the subject, and D. Ricard as well as contributors to the RAM Legacy database for data sharing. Financial support was provided by Natural Sciences and Engineering Research Council of Canada with a grant to H.K.L. and and scholarship to D.M.K., and the Lenfest Ocean Program with a grant to B.W.

SUPPORTING INFORMATION

Supporting Information may be found in the online version of this paper:

Appendix SI. Details of standardizing and modelling the recovery potential of elasmobranchs shown in Table 1 and Figure 1.

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