Life history of the Critically Endangered largetooth sawfish: a compilation of data for population assessment and demographic modelling

P. M. Kyne[1],*, M. Oetinger[2], M. I. Grant[3], P. Feutry[4]

[1]Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory 0909, Australia
[2]Argus-Mariner Consulting Scientists, Owensboro, Kentucky 42301, USA
[3]Centre for Sustainable Tropical Fisheries and Aquaculture and College of Science and Engineering, James Cook University, Townsville, Queensland 4811, Australia
[4]CSIRO Oceans and Atmosphere, Hobart, Tasmania 7000, Australia

ABSTRACT: The largetooth sawfish *Pristis pristis* is a Critically Endangered, once widespread shark-like ray. The species is now extinct or severely depleted in many former parts of its range and is protected in some other range states where populations persist. The likelihood of collecting substantial new biological information is now low. Here, we review all available life history information on size, age and growth, reproductive biology, and demography as a resource for population assessment and demographic modelling. We also revisit a subset of historical data from the 1970s to examine the maternal size–litter size relationship. All available information on life history is derived from the Indo-West Pacific (i.e. northern Australia) and the Western Atlantic (i.e. Lake Nicaragua-Río San Juan system in Central America) subpopulations. *P. pristis* reaches a maximum size of at least 705 cm total length (TL), size-at-birth is 72–90 cm TL, female size-at-maturity is reached by 300 cm TL, male size-at-maturity is 280–300 cm TL, age-at-maturity is 8–10 yr, longevity is 30–36 yr, litter size range is 1–20 (mean of 7.3 in Lake Nicaragua), and reproductive periodicity is suspected to be biennial in Lake Nicaragua (Western Atlantic) but annual in Australia (Indo-West Pacific). There was a weak relationship between litter size and maternal size in Lake Nicaragua, and lifetime reproductive output for an individual female from Lake Nicaragua was estimated as 73 pups. Future demographic models should aim to capture the variability and uncertainty in life history parameters for *P. pristis* and we encourage a conservative approach to any application for conservation and management.

KEY WORDS: *Pristis pristis* · Threatened species · Age and growth · Reproductive biology · Demography

1. INTRODUCTION

Life history parameters form the foundation of species population assessments, demographic modelling, and fisheries management, yet even the most basic biological information is lacking for most of the world's chondrichthyan fishes (sharks, rays, and ghost sharks) (Heupel & Simpfendorfer 2010, Dulvy et al. 2014). A lack of data on life history parameters such as length- and age-at-maturity, litter size (LS)/fecundity, natural mortality (*M*), and longevity inhibits the accurate assessment of population status and productivity. Close to half of all chondrichthyans are Data Deficient on the IUCN Red List of Threatened Species (Dulvy et al. 2014); that is, they are so poorly known that their extinction risk status cannot be evaluated. Therefore, the collection of life history data remains a major research priority (Heupel & Simpfendorfer 2010, Simpfendorfer et al. 2011). Ensuring such data are

available to conservation biologists, fishery managers, and policy makers is even more urgent in the face of this data deficiency and the recognised global conservation status of chondrichthyans; an estimated 24% of all species are threatened with extinction (Dulvy et al. 2014).

The sawfishes (family Pristidae) are considered one of the most threatened fish families, with all 5 extant species assessed as Critically Endangered or Endangered on the IUCN Red List (Dulvy et al. 2016). Global declines and local and regional extinctions have resulted from targeted catch and bycatch in commercial and artisanal fisheries. Sawfishes occur in inshore, estuarine, and (for some species) freshwater habitats easily accessible to humans, which, along with their toothed rostrum, makes them highly susceptible to capture in fishing gear such as gill and trawl nets (Stobutzki et al. 2002, Peverell 2005). Of 90 historical range countries, 43 have lost one or more sawfish species, while sawfishes (all species) are now extinct in at least 20 former range states (Dulvy et al. 2016).

The largetooth sawfish *Pristis pristis* is the most wide-ranging of the sawfishes, with distinct, geographically separated subpopulations in the tropical Western Atlantic, Eastern Atlantic, Eastern Pacific, and Indo-West Pacific (see Fig. 1). It is a euryhaline species, with juveniles occupying freshwater habitats and adults occurring in estuarine and marine waters (Thorburn et al. 2007, Peverell 2009, Whitty et al. 2009). This species has previously been referred to as *P. microdon* (common name: freshwater sawfish) in the Indo-West Pacific, *P. perotteti* in the Atlantic, and *P. zephyreus* in the Eastern Pacific, but these taxonomic concepts are synonyms of *P. pristis* (Faria et al. 2013). The global population of *P. pristis*, as well as each of the 4 subpopulations, are assessed as Critically Endangered on the IUCN Red List (Kyne et al. 2013).

Lethal examination of individuals is the most effective method to assess many aspects of chondrichthyan life history, including age and growth (by examining growth bands on vertebrae) and fecundity (by examining uterine or ovarian contents) (Heupel & Simpfendorfer 2010). This is typically impractical in rare species where it is difficult to obtain sufficient specimens and may be prohibited in threatened species that are protected under national or sub-national legislation. For example, sawfish, including *P. pristis,* are protected to some degree in several range states (Dulvy et al. 2016). *P. pristis* has declined across their range, and aside from a few remaining hotspots (e.g. northern Australia, Papua New Guinea), the species

is now rarely encountered. Its threatened status, contracted distribution, and legislative protection across several range states where populations are persisting limits the future possibilities of obtaining significant new life history data.

The purpose of this study was to summarise available life history information on *P. pristis* as a resource for population assessment and demographic modelling. We also revisited a historical data set from the 1970s (Thorson 1976), the only comprehensive study on the species' reproductive biology, to examine the relationship between maternal size and LS. Additionally, we used available data to calculate a simple measure of generation length and lifetime reproductive output.

2. MATERIALS AND METHODS

Primary and secondary literature sources were reviewed for any information relating to the life history of *Pristis pristis* (including literature published under the synonyms *P. microdon* and *P. perotteti*). Parameters are reported by subpopulation with all available information coming from the Indo-West Pacific (primarily northern Australia) or the Western Atlantic (primarily Lake Nicaragua-Río San Juan system in Central America, hereafter referred to as 'Lake Nicaragua'); there are no data available from the Eastern Atlantic or Eastern Pacific subpopulations (Fig. 1). Analysis was performed using Microsoft Excel and SigmaPlot 14.0.

2.1. Age and growth

All previous age and growth studies on *P. pristis* have applied a 3 parameter von Bertalanffy growth function (VBGF) to length-at-age data incorporating the following parameters: t_0: theoretical time-at-length 0; k: growth coefficient; and L_∞: asymptotic length. These growth parameters from each study were used to calculate values for an alternative parameterisation of the VBGF that incorporates L_0 (size-at-age 0) in place of t_0:

$$L_t = L_0 + (L_\infty - L_0)(1 - \exp^{(-kt)}) \qquad (1)$$

where L_t is length-at-age t and L_0 was calculated from t_0 as:

$$L_0 = L_\infty(1 - \exp^{(kt_0)}) \qquad (2)$$

This parameterisation of the VBGF is more informative, as t_0 has no biological relevance while L_0 can
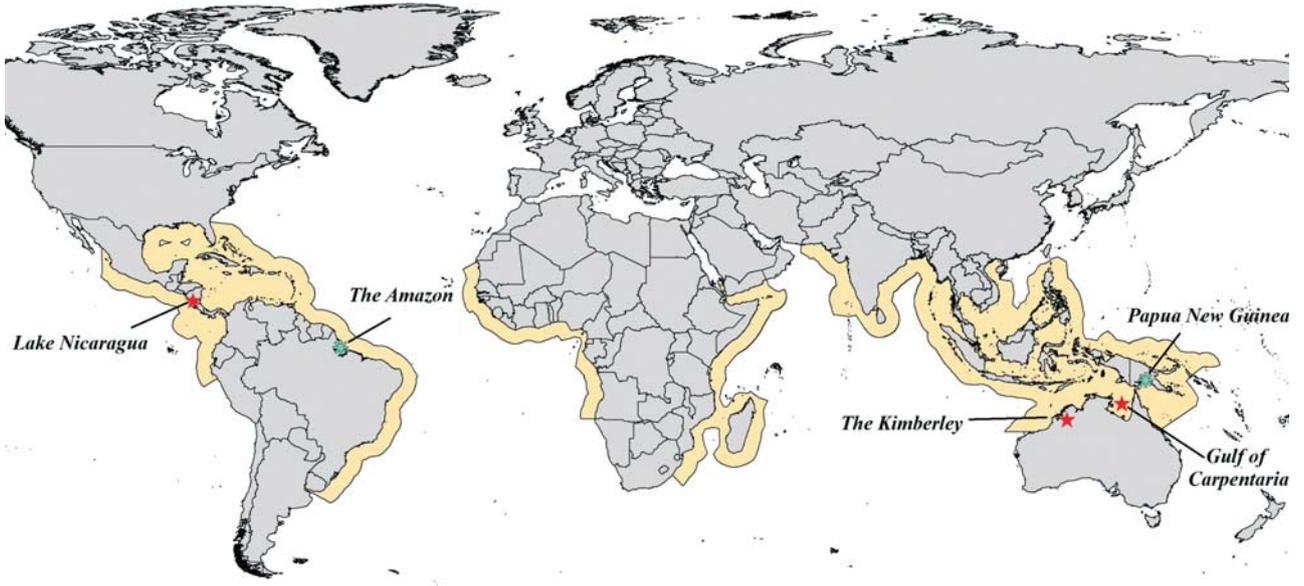
Fig. 1. Generalised historic distribution of largetooth sawfish *Pristis pristis* showing source locations for life history data. Red stars: major sources; green asterisks: minor sources. Distribution modified from that shown in Dulvy et al. (2016)

serve as a proxy for size-at-birth. Additionally, L_0 can be used to compare size-at-birth parameter estimates between a range of other growth models commonly applied to elasmobranchs (e.g. logistic and Gompertz growth functions) (Cailliet et al. 2006, Smart et al. 2016).

Longevity was estimated as the age corresponding to 95 % of L_∞ by solving the VBGF for t following Natanson et al. (2006):

$$\text{Longevity} = \left(\frac{1}{k}\right)\ln\left(\frac{L_\infty - L_0}{L_\infty(1 - x)}\right) \quad (3)$$

where $x = 0.95$ (i.e. $L_{Longevity} / L_\infty$).

2.2. Reproductive biology

A historical data set from Lake Nicaragua (Thorson 1976) was revisited to examine if there was a relationship between maternal size and LS. Such a relationship has been regularly reported in the order Rhinopristiformes (see for example, Schluessel et al. 2015). Linear regression was used to examine the relationship between maternal size (as total length; TL) and the number of embryos recorded in a litter (i.e. LS). Although Thorson (1976) reported on 67 gravid females, maternal size and LS data could only be located for 16 of these individuals (Oetinger 1978). A sawfish of 364 cm TL with a LS of 1 pup was removed from

analysis due to suspicion that it had aborted embryos (see Section 4).

2.3. Demography

Available data were used to calculate a simple measure of generation length that requires only female age-at-maturity and longevity. Theoretical lifetime reproductive output of an individual female was estimated for Lake Nicaragua using age and LS data. Generation length was calculated as the median age of parents of the current cohort as:

$$[(\text{maximum age} - \text{age-at-maturity})/2)] + \text{age-at-maturity} \quad (4)$$

Lifetime reproductive output was calculated as:

$$[(\text{maximum age} - \text{age-at-maturity})/ \text{reproductive periodicity}] \times \text{mean LS} \quad (5)$$

3. RESULTS

Available *Pristis pristis* life history parameters are presented here, commencing with size (size-at-birth, size-at-maturity, maximum size), followed by age and growth, reproductive biology, and concluding with demography. Life history parameters and demographic estimates are summarised in Table 1, and age-related data are summarised in Table 2.

Table 1. Largetooth sawfish *Pristis pristis* life history parameters and demographic estimates (see Table 2 for age data). See Section 3.4 for natural mortality estimation methods used by various authors. Note that parameters from the Western Atlantic are largely from Lake Nicaragua, which may not be representative of the wider ocean region. Indo-W Pac: Indo West-Pacific; W Atl: Western Atlantic; TL: total length

Parameter	Region	Value	Reference
Size-at-birth	W Atl	76 cm TL	Astorqui (1967)
		73–80 cm TL	Thorson (1976)
	Indo-W Pac	72–90 cm TL	Peverell (2009)
Size-at-maturity	W Atl	♀: 300 cm TL	Thorson (1976)
		♂: 300 cm TL	
	Indo-W Pac	♀: 300 cm TL	Thorburn et al. (2007), Whitty et al. (2008), Peverell (2009)
		♂: 280–300 cm TL	
Maximum size	W Atl	429 cm TL	Thorson (1982b)
	Indo-W Pac	705 cm TL	Devadoss et al. (1989)
Litter size	W Atl	4–12 (n = 7)	Astorqui (1967)
		1–13 (mean 7.3) (n = 67)	Thorson (1976)
		20 (n = 1)	Nunes et al. (2016)
	Indo-W Pac	4 (n = 1)	Peverell (2005, 2009)
Gestation period	W Atl	5 mo	Thorson (1976)
Reproductive periodicity	W Atl	Biennial?	Thorson (1976)
	Indo-W Pac	Annual?	Peverell (2009)
Natural mortality (age-independent)	W Atl	0.139–0.155 yr^{-1}	Simpfendorfer (2000)
	Indo-W Pac	0.119–0.145 yr^{-1}	Moreno Iturria (2012)
Natural mortality (age-dependent)	W Atl	First year: 0.27 Last year: 0.09	Simpfendorfer (2000)
	W Atl	First year: 0.55 Last year: 0.09	Moreno Iturria (2012)
	Indo-W Pac	First year: 0.68 Last year: 0.09	Moreno Iturria (2012)
Intrinsic rate of population increase	W Atl	0.05–0.07 yr^{-1}	Simpfendorfer (2000)
		0.03 yr^{-1}	Moreno Iturria (2012)
	Indo-W Pac	0.12 yr^{-1}	Moreno Iturria (2012)
Population doubling time	W Atl	10.3–13.6 yr	Simpfendorfer (2000)
		23.3 yr	Moreno Iturria (2012)
	Indo-W Pac	5.8 yr	Moreno Iturria (2012)
Generation length	W Atl	17.2 yr	Moreno Iturria (2012)
		20 yr	This study; calculated from Thorson (1982b)
	Indo-W Pac	14.6 yr	Moreno Iturria (2012)
		22 yr	This study; calculated from Peverell (2009)

3.1. Size

Estimates of size-at-birth are broadly similar between the Western Atlantic: 76 cm TL (Astorqui 1967) or 73–80 cm TL (Thorson 1976) and the Indo-West Pacific: 72–90 cm TL (Peverell 2009).

From the Western Atlantic, near-term embryos have been reported at ~76 cm TL (Astorqui 1967) and 75.5–80 cm TL (Nunes et al. 2016). In the Indo-West Pacific, the smallest sizes (free-living individuals) reported include 76.5 cm TL (Australian museum records; Pogonoski et al. 2002), 77.8 cm TL (Sepik

River, Papua New Guinea; Taniuchi et al. 1991), 78.9 cm TL (Betsiboka River, Madagascar; Taniuchi et al. 2003), 81.5 cm TL (Fitzroy River, Australia; Thorburn et al. 2004, 2007), 83 cm TL (Laloki River system, Papua New Guinea; Berra et al. 1975), and 87 cm TL (central Sumatra; Tan and Lim 1998). The size-at-birth of 50 cm TL reported by Wilson (1999) for Australia/New Guinea seems unlikely.

In the Western Atlantic (Lake Nicaragua), size-at-maturity is reached by 300 cm TL for both males and females, with the onset of maturity reported at ~240 cm TL by Thorson (1976), and subsequently by

Table 2. Largetooth sawfish *Pristis pristis* age-related data. TL: total length

Region	Method	Age-at-maturity (yr)	Asymptotic length (cm TL)	95% asymptotic length (cm TL)	Maximum observed age (yr)	Longevity (yr)	Reference
Western Atlantic	Tag–recapture	~10	456	433	–	30	Thorson (1982b)[a]
Indo-West Pacific	Vertebral band counts (observed)	20+	363	345	44	41	Tanaka (1991)
	Vertebral band counts (back-calculated)	20+	398	378	44	58	
Indo-West Pacific	Vertebral band counts (observed)	8	638	606	28	36	Peverell (2009)[b]
	Vertebral band counts (back-calculated)	8	589	560	28	36	

[a]Asymptotic length calculated by Simpfendorfer (2000); [b]Asymptotic length from observed data

other sources (e.g. Compagno & Last 1999). How-ever, Thorson (1976) sampled very few sawfish in the size class 240–299 cm TL (no females were sampled in that size class), and therefore the true size-at-maturity may fall somewhere between 240 and 300 cm TL. The smallest gravid female reported by Thorson (1976) was 305 cm TL. In the Indo-West Pacific, size-at-maturity is ~300 cm TL for females, and ~280–300 cm TL for males (Thorburn et al. 2007, Whitty et al. 2008, Peverell 2009).

Maximum reported size is 705 cm TL (Devadoss et al. 1989). The largest recorded size in Australia is 582 cm TL (Peverell 2009). For Lake Nicaragua, Thorson (1982b) recorded a maximum size of 429 cm TL, suggesting that this population may not reach the same maximum lengths as conspecifics elsewhere.

3.2. Age and growth

Vertebral ageing has been undertaken by Tanaka (1991; Australia and New Guinea) (n = 36; 77.8–361.1 cm TL), and Peverell (2009; Gulf of Carpentaria, Australia) (n = 41; 83–528 cm TL). Additional age and growth data are available from a tagging study by Thorson (1982b; Lake Nicaragua).

The growth rate of juvenile *P. pristis* is high, although estimates are variable. Peverell (2009; Gulf of Carpentaria, Australia) reported 52 cm during the first year, and 17 cm during the fifth year. Tanaka (1991; Australia and New Guinea) reported 18 cm in the first year and 10 cm in the tenth year. Thorson (1982b; Lake Nicaragua) reported 35–40 cm in the first year, 12 cm in the tenth year, and an average of 4.4 cm yr^{-1} for larger individuals (size at time of tagging: 361–394 cm TL).

Peverell (2009; Gulf of Carpentaria, Australia) esti-mated that *P. pristis* of 83–101, 119–140, 143–180, 170–219, 229–253, and 234–277 cm TL were of the age classes (years) 0+, 1+, 2+, 3+, 4+, and 5+, respec-tively. In northwest Australia, Thorburn et al. (2007) estimated that *P. pristis* of 100, 140–160, 180–220, and 230–280 cm TL were approximately of age 1, 2, 3, and 4 yr, respectively.

From tag–recapture data, an individual in the Fitzroy River, northwest Australia grew 3 cm in 4 mo (215–218 cm TL), equating to a growth rate of ~0.025 cm d^{-1} (Thorburn et al. 2004). In the Gulf of Carpentaria, a 153 cm TL individual grew 41 cm in 224 d (0.183 cm d^{-1}; erroneously reported as 0.107 cm d^{-1} in Table 8 of Peverell 2009), a 191 cm TL individual grew 25 cm in 187 d (0.134 cm d^{-1}), and a 231 cm TL individual grew 10 cm in 232 d (0.043 cm d^{-1}) (Peverell 2009). The average growth rate (4.4 cm yr^{-1}) for Lake Nicaragua was based on tag–recapture data from 8 mature females, but growth was highly variable among individuals, ranging from –16.2 to 25.0 cm yr^{-1} (negative values are likely the result of measurement error) (Thorson 1982b).

The following VBGF parameters (L_∞, k, L_0) have been estimated: Tanaka (1991) (vertebral ageing; Australia and Papua New Guinea): L_∞ = 363 cm, k = 0.066 yr^{-1}, L_0 = 85.51 cm (observed data); L_∞ = 398 cm, k = 0.047 yr^{-1}, L_0 = 91.24 cm (back-calculated data); Peverell (2009) (vertebral ageing; Gulf of Carpentaria): L_∞ = 638 cm, k = 0.08 yr^{-1}, L_0 = 74.4 cm (observed data); L_∞ = 589 cm, k = 0.08 yr^{-1}, L_0 = 80.62 cm (back-calculated data); and Simpfendorfer (2000) based on data in Thorson (1982b) (tag–recapture; Lake Nicaragua): L_∞ = 456 cm, k = 0.089 yr^{-1}, L_0 = 73.67.

Thorson (1982b) estimated an age-at-maturity of ~10 yr for Lake Nicaragua (this was a generic estimate and not specific to a sex), and Peverell (2009) estimated 8 yr in the Gulf of Carpentaria (from a single pupping 303 cm TL female). Tanaka (1991) reported an age of 16 yr for a 247 cm TL individual that was still immature and suggested that age-at-maturity may be 20+ yr (although this seems high based on the data of Thorson 1982b and Peverell 2009). The observed maximum age from Peverell (2009) was 28 yr for a 582 cm TL specimen, and from Tanaka (1991) it was 44 yr for a 361 cm TL individual. A longevity of 30 yr was suggested by Thorson (1982b) for Lake Nicaragua.

Longevity estimated using observed ($L_{Longevity}$ = 606.1 cm TL) and back-calculated ($L_{Longevity}$ = 559.6 cm TL) data from Peverell (2009) resulted in longevity estimates of 35.6 and 35.9 yr (hereafter 36 yr), respectively. This longevity estimate for observed data was previously erroneously reported as 35 yr by Peverell (2009). Longevity estimated using observed ($L_{Longevity}$ = 344.9 cm TL) and back-calculated ($L_{Longevity}$ = 378.1 cm TL) data from Tanaka (1991) resulted in longevity estimates of 41.3 and 58.2 yr, respectively (Table 2). Peverell (2009) also suggested a longevity of 80 yr based on a minimum growth rate threshold of 8 cm yr^{-1} derived from k in the VBGF (observed data), for an $L_∞$ = 638.0 cm TL.

3.3. Reproductive biology

Sawfishes appear to be lecithotrophic viviparous with 2 functional ovaries (Thorson 1976), although any matrotrophic contribution to embryonic growth has not been examined. In terms of LS, Thorson (1976) examined 67 gravid females captured in Lake Nicaragua with litters ranging from 1–13 (mean: 7.3). The embryonic sex ratio was 0.86:1 (males:females) (Thorson 1976). Astorqui (1967) examined 7 gravid females, with LS ranging from 4–12 with an approximately equal sex ratio. A large (~500 cm TL) *P. pristis* caught in Brazil contained 20 near-term embryos (sex ratio undetermined) (Nunes et al. 2016).

Although Wilson (1999) cited a likely LS of 1–12, and Moreno Iturria (2012) attributed a LS of 6–12 to Peverell (2005), the origins of these values could not be confirmed from the original literature. Peverell (2005, 2009) examined 2 gravid individuals but specifies the LS for only one which was carrying 4 near-term embryos.

There was a weak relationship between LS and maternal TL (in cm) in a subset of data from Lake Nicaragua (R^2 = 0.294, p = 0.037, n = 15) (Fig. 2). The relationship is given by the equation: LS = −11.951 + (0.0542TL).

Gestation period in Lake Nicaragua is estimated to be ~5 mo (Thorson 1976). Reproductive periodicity is uncertain; Thorson (1976, p. 649) states that 'breeding probably occurs every other year' in Lake Nicaragua (i.e. biennial; a female is gravid one year and presumed to 'rest' the next). This was based on the fact that of 52 mature females examined, 33 were gravid and 19 were not (Thorson 1976). In the Gulf of Carpentaria, Peverell (2009) suggested that the reproductive cycle is annual since the ovarian cycle and gestation occur concurrently.

In Lake Nicaragua, both mating and parturition seemed to occur in freshwater, at the beginning and the end of the wet season, respectively (i.e. May to July for mating, and October to December for parturition) (Astorqui 1967, Thorson 1976). A gravid female with large near-term embryos was caught in Maranhão State, north-eastern Brazil in May (Nunes et al. 2016), which is the latter part of the equatorial wet season. In northwest Australia, parturition is also reported to take place in the wet season (i.e. January to April) and is suspected to occur in brackish or saltwater (Whitty et al. 2008, 2009). In the Gulf of Carpentaria, Peverell (2005, p. 399) suggested that parturition occurs late in the wet season, and that the species 'appears to pup in freshwater'. After parturition, juveniles have been reported to spend 4–5 yr in freshwater before migrating to estuarine and coastal marine waters (Thorburn et al. 2007), although in Lake Nicaragua, Thorson (1976, 1982b) suggested that individuals may spend their entire life in freshwater.

Using the results from Thorson (1976, 1982b), an estimated lifetime reproductive output for *P. pristis* from Lake Nicaragua can be calculated. An age-at-maturity of 10 yr and a maximum age of 30 yr gives a potential reproductive lifespan of 20 yr. Assuming a biennial reproductive cycle and a mean LS of 7.3, lifetime reproductive output would have been 73 pups. Applying estimated first year natural mortalities (M) of 0.27 (Simpfendorfer 2000) or 0.55 (Moreno Iturria 2012), survivorship (calculated as $S = \exp^{-M}$) from 0 to age 1 is estimated to be 56 and 42 pups, respectively.

3.4. Demography

Applying age-independent M estimation methods, Simpfendorfer (2000) estimated M = 0.139 yr^{-1} (assuming a maximum age of 30 yr; Thorson 1982b)
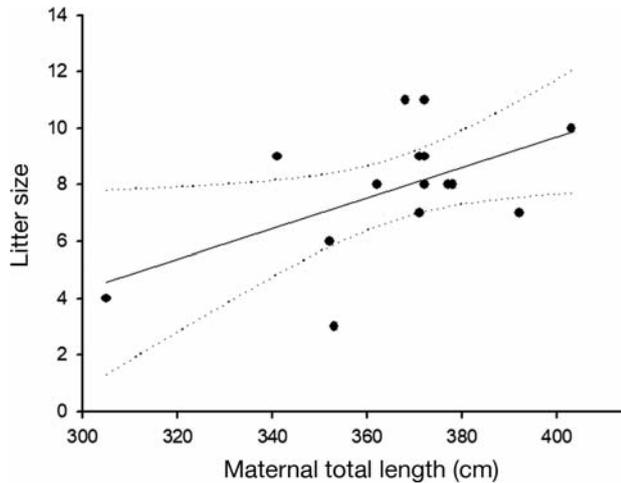
Fig. 2. Relationship between litter size and maternal total length for largetooth sawfish *Pristis pristis* from Lake Nicaragua, determined by linear regression analysis (R^2 = 0.294, p = 0.037, n = 15). Dotted lines: 95% confidence intervals

and M = 0.069 yr^{-1} (assuming 60 yr) for *P. pristis* using the method of Hoenig (1983), M = 0.142 yr^{-1} using the growth coefficient method of Jensen (1996), and M = 0.155 yr^{-1} using the method of Pauly (1980) (the latter 2 methods used the VBGF parameter k, derived from age and growth data in Thorson 1982b). Using a length–weight relationship derived from historical records and the age-dependent M estimation method of Peterson & Wroblewski (1984), Simpfendorfer (2000) estimated mortalities ranging from M = 0.27 yr^{-1} in the first year to M = 0.09 yr^{-1} for a 30 yr old individual (Simpfendorfer 2000, C. Simpfendorfer pers comm). Using the same methods, Moreno Iturria (2012) estimated similar values, but also applied the age-dependent method of Chen & Watanabe (1989), which estimated mortalities ranging from M = 0.55 yr^{-1} in the first year and M = 0.09 yr^{-1} in the last year (i.e. 30 yr).

For the Indo-West Pacific (using the VBGF and maximum age estimates in Peverell 2009), Moreno Iturria (2012) estimated age-independent mortalities of M = 0.119 yr^{-1} (Hoenig 1983), M = 0.128 yr^{-1} (Jensen 1996), and M = 0.145 yr^{-1} (Pauly 1980), and age-dependent mortalities of M = 0.68 yr^{-1} in the first year and 0.09 yr^{-1} in the last year (i.e. 35 yr, as previously reported by Peverell 2009) (Chen & Watanabe 1989).

Simpfendorfer (2000), using aged-based demographic models on life history information from Thorson (1976, 1982b) (Lake Nicaragua, Western Atlantic), estimated the most likely range of intrinsic rate of population increase to be 0.05–0.07 yr^{-1} and population doubling times to be 10.3–13.6 yr. These

rates were estimated under ideal conditions (i.e. no fisheries, no population fragmentation, no habitat modification, and no inbreeding depression). Moreno Iturria (2012), also using data from Thorson (1976, 1982b), estimated an intrinsic rate of population increase of 0.03 yr^{-1}, a population doubling time of 23.3 yr, and a generation length of 17.2 yr for the Western Atlantic (under a 'baseline' scenario; varying the mortality estimate or the reproductive periodicity produced differing results). For the Indo-West Pacific, Moreno Iturria (2012) estimated an intrinsic rate of population increase of 0.12 yr^{-1}, a population doubling time of 5.8 yr, and a generation length of 14.6 yr. For these models, Moreno Iturria (2012) used VBGF parameters and longevity (35 yr) from Peverell (2009) but used an age-at-maturity of 6 yr, a biennial reproductive periodicity, and a LS of 12. These parameters contrast with those reported by Peverell (2009): age-at-maturity of 8 yr, an annual reproductive cycle, and a LS of 4 (LS based on n = 1 so not likely to be representative of the subpopulation).

An alternative method of calculating generation length as the median age of parents of the current cohort yielded 20 yr for the Western Atlantic (age-at-maturity: 10 yr; longevity: 30 yr; Thorson 1982b) and 22 yr for the Indo-West Pacific (age-at-maturity: 8 yr; longevity: 36 yr; Peverell 2009).

4. DISCUSSION

Pristis pristis is locally extinct or has declined to very low levels across its historic range (Kyne et al. 2013, Dulvy et al. 2016). For such a large, wide-ranging, and charismatic species, its life history is poorly understood, and available information is patchy. Much of the available life history data comes either from the Lake Nicaragua-Río San Juan system in Central America (including the only dedicated reproductive study; Thorson 1976) or from northern Australia in the Indo-West Pacific, in particular from the Kimberley region of northwest Western Australia and the Queensland Gulf of Carpentaria (e.g. Tanaka 1991, Peverell 2005, 2009, Thorburn et al. 2007, Whitty et al. 2008, 2009). The species collapsed soon after the onset of targeted commercial fishing in Lake Nicaragua (Thorson 1982a,b) and remained in a depleted state 2 decades later (McDavitt 2002). Despite protection and a ban on targeted fishing in Lake Nicaragua, ongoing fishing activities are likely inhibiting recovery (McDavitt 2002). With estimated population doubling times of ~10–23 yr (Simpfendorfer 2000, Moreno Iturria 2012), recovery would take

many decades. In Australia, sawfishes are protected under federal and state/territory legislation. Therefore, the collection of new life history data, apart from opportunistic sampling of individual animals, is now unlikely to occur (a conclusion that Thorson 1976 had already made for Lake Nicaragua in the 1970s).

The life history of *P. pristis* is characterised by late age-at-maturity (8–10 yr), long lifespan (30–36 yr), and low fecundity (max. LS: 20) with a suspected annual or biennial reproductive cycle; these parameters result in a low intrinsic rate of population increase (Simpfendorfer 2000, Moreno Iturria 2012). Estimated rates of population increase for *P. pristis* (0.03–0.12 yr^{-1}) fall within the 'low' (0.05–0.15) or 'very low' (<0.05) categories of Musick et al. (2000), highlighting susceptibility to population depletion. These values for *P. pristis* sit within the range of coastal and pelagic sharks (e.g. Smith et al. 1998) but are generally higher than those of deep-sea chondrichthyans (Simpfendorfer & Kyne 2009).

Many life history parameter estimations reviewed here are based on small sample sizes, or a lack of individuals from certain size classes, especially larger ones. For example, age-at-maturity for the Indo-West Pacific (8 yr) was based on a single pupping female (Peverell 2009). Regional variation in life history parameters is evident, and it is likely that the Lake Nicaragua population may not have been representative of the wider Western Atlantic due to the fact that individuals from this population may have spent much, or all, of their life cycle in freshwater (Thorson 1976, 1982b). However, some parameters align well between the Western Atlantic (e.g. Thorson 1976, 1982b) and the Indo-West Pacific (e.g. Peverell 2009), although age data of Tanaka (1991) appears to have been overestimated.

The very large maximum size of *P. pristis* has likely resulted in difficulties with sampling a wide range of size classes and, in turn, has possibly resulted in inaccuracies for age and growth parameter estimations. Reported growth rates are variable, but generally high in juvenile *P. pristis*. The faster growth rates of Peverell (2009) compared to Tanaka (1991) (52 vs. 18 cm in the first year, respectively), both of which were based on ageing of sectioned vertebral centra, are supported by tag−recapture data from Peverell (2009), suggesting that these data are more reliable. Rapid juvenile growth rates of 65–85 cm in the first year and 48–68 cm in the second year have been reported from the congener smalltooth sawfish *P. pectinata*, which is among the highest for any elasmobranch (Simpfendorfer et al. 2008).

VBGF parameter estimates for L_0 and L_∞ in the Western Atlantic (Simpfendorfer et al. 2008) and Indo-West Pacific (Peverell 2009) paired well with observations of size-at-birth and maximum observed size in each of these regions. It remains unclear if the VBGF parameters estimated from observed or back-calculated data by Peverell (2009) provide more realistic growth estimates. Until new information is available, it is recommended that both are equally considered for use in demographic modelling. Meanwhile, other estimates reported in the Indo-West Pacific by Tanaka (1991) for L_0 and L_∞ appear to be over- and underestimated, respectively, likely due to inaccuracies in band pair interpretation during ageing of specimens. This was evidenced by the longevity estimate for observed data being lower than the oldest aged specimen. Longevity estimates suggest that *P. pristis* is a long-lived species, reaching 30 yr in the Western Atlantic (Thorson 1982b), and 36 yr in the Indo-West Pacific (Peverell 2009). These estimates are presently considered more realistic than those obtained from Tanaka (1991), and also the estimate of 80 yr obtained from growth rates by Peverell (2009). It is important to note, however, that these longevity estimates are based on VBGFs with limited large size classes. They may be prone to error due to the uncertainty in L_∞ estimation (and subsequently k and L_0) that arises when data from large size classes are lacking (Thorson & Simpfendorfer 2009). Furthermore, none of the ageing studies validated the temporal periodicity of vertebral band deposition, and growth parameters and maximum ages estimated from counting band pairs in sectioned vertebral centra may have been underestimated (Harry 2018).

Across the sawfishes, reproductive parameters are generally poorly defined. For example, both LS and reproductive periodicity is unknown in the dwarf sawfish *P. clavata* and the green sawfish *P. zijsron* (Dulvy et al. 2016). Both annual (Peverell 2009) and biennial (Thorson 1976) reproductive periodicity has been postulated for *P. pristis.* Peverell (2009) suspected an annual cycle based on the presence of large oocytes in the ovary of post-partum females, while Thorson (1976) suggests a biennial cycle for Lake Nicaragua based on the ratio of gravid and nongravid mature females observed concurrently. Understanding reproductive periodicity has significant implications for demographic modelling, and in the case of *P. pristis*, maximum annual fecundity would vary between 10 (biennial cycle) to 20 (annual cycle). A biennial cycle has been reported in *P. pectinata* (Poulakis et al. 2014), and a presumed annual cycle

in the smaller, more biologically productive narrow sawfish *Anoxypristis cuspidata* (Peverell 2009).

A positive relationship between LS and maternal size in elasmobranchs may indicate that larger individuals have more uterine space available to carry an increased LS over smaller individuals. Such a relationship has been shown in various species of guitarfishes (family Rhinobatidae), another group of rhinopristoid rays (see Schluessel et al. 2015). There was, however, only a weak relationship between these parameters in gravid female *P. pristis* from Lake Nicaragua. Detection of this relationship may be influenced by sample size and the size range of gravid females examined, although in the case of *P. pristis*, the available size range (305–403 cm TL) was from close to the reported size-at-maturity (300 cm TL) and maximum size (429 cm TL) sampled in Lake Nicaragua (Thorson 1976). Batoids are known to prematurely abort embryos under stress (e.g. capture in fishing gear) (Adams et al. 2018) and this can result in the underestimation of LS, which in turn can influence maternal size–LS relationships. For example, Marshall et al. (2007) reported abortion in the rhinopristiform southern fiddler ray *Trygonorrhina dumerilii*, and it is suspected that a 364 cm TL *P. pristis* with a recorded LS of 1 pup had aborted embryos during capture or was possibly even in the process of pupping (this data point was excluded from analysis for this reason).

This synthesis of life history parameters of *P. pristis* aims to provide a resource for demographic modelling, given that the collection of new biological information is now unlikely. As a range of values exist in the literature for some parameters, demographic models should capture this variability and explore the uncertainty around life history parameters. We encourage a conservative approach to demographic model interpretations based on these data, as such models will be important to understand productivity, recovery potential, and population growth under different natality and mortality schedules, which ultimately can lead to more informed implementation of future management options for this species (e.g. Carlson & Simpfendorfer 2015).

LITERATURE CITED

Adams KR, Fetterplace LC, Davis AR, Taylor MD (2018) Sharks, rays and abortion: the prevalence of capture-induced parturition in elasmobranchs. Biol Conserv 217: 11–27

Astorqui I (1967) Investigaciones de un Jesuita en aguas de Nicaragua. 5. Nuestro pez sierra. Rev Conservadora 16: 71–75

Berra TM, Moore R, Reynolds LF (1975) The freshwater fishes of the Laloki River system of New Guinea. Copeia 1975:316–326

Cailliet GM, Smith WD, Mollet HF, Goldman KJ (2006) Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. Environ Biol Fish 77:211–228

Carlson JK, Simpfendorfer CA (2015) Recovery potential of smalltooth sawfish, *Pristis pectinata*, in the United States determined using population viability models. Aquat Conserv 25:187–200

Chen S, Watanabe S (1989) Age dependence of natural mortality coefficient in fish population dynamics. B Jpn Soc Sci Fish 55:205–208

Compagno LJV, Last PR (1999) Family Pristidae. Sawfishes. In: Carpenter KE, Niem VH (eds) The living marine resources of the Western Central Pacific, Vol 3. Batoid fishes, chimaeras and bony fishes, Part 1 (Elopidae to Linophrynidae). FAO Species Identification Guide for Fishery Purposes. FAO, Rome, p 1410–1417

Devadoss P, Gnanamuttu JC, Srinivasarangan S, Subramani S (1989) On the landing of a large saw fish at Madras. Mar Fish Infor Serv 98:13

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD and others (2014) Extinction risk and conservation of the world's sharks and rays. eLife 3:e00590

Dulvy NK, Davidson LNK, Kyne PM, Simpfendorfer CA, Harrison LR, Carlson JK, Fordham SV (2016) Ghosts of the coast: global extinction risk and conservation of sawfishes. Aquat Conserv 26:134–153

Faria VV, McDavitt MT, Charvet P, Wiley TR, Simpfendorfer CA, Naylor GJP (2013) Species delineation and global population structure of Critically Endangered sawfishes (Pristidae). Zool J Linn Soc 167:136–164

Harry AV (2018) Evidence for systemic age underestimation in shark and ray ageing studies. Fish Fish 19:185–200

Heupel MR, Simpfendorfer CA (2010) Science or slaughter: need for lethal sampling of sharks. Conserv Biol 24: 1212–1218

Hoenig JM (1983) Empirical use of longevity data to estimate mortality rates. Fish Bull (Wash DC) 82:898–903

Jensen AL (1996) Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can J Fish Aquat Sci 53:820–822

Kyne PM, Carlson J, Smith K (2013) *Pristis pristis*. The IUCN Red List of Threatened Species 2013:e.T18584848A 18620395. https://dx.doi.org/10.2305/IUCN.UK.2013-1. RLTS.T18584848A141788242.en (accessed 13 April 2016)

Marshall LJ, White WT, Potter IC (2007) Reproductive biology and diet of the southern fiddler ray, *Trygonorrhina fasciata* (Batoidea: Rhinobatidae), an important trawl bycatch species. Mar Freshw Res 58:104–115

McDavitt MT (2002) Lake Nicaragua revisited: conversations with a former sawfish fisherman. Shark News. Newsletter of the IUCN Shark Specialist Group 14:5

Moreno Iturria DA (2012) Demography of the family Pristidae as an aid to conservation and management. BSc (Honours) dissertation, James Cook University, Townsville

Musick JA, Harbin MM, Berkeley SA, Burgess GH and others (2000) Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). Fisheries (Bethesda, Md) 25:6–30

Natanson LJ, Kohler NE, Ardizzone D, Cailliet GM, Wintner SP, Mollet HF (2006) Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean. Environ Biol Fish 77:367–383

Nunes JLS, Rincon G, Piorski NM, Martins APB (2016) Near-term embryos in a *Pristis pristis* (Elasmobranchii: Pristidae) from Brazil. J Fish Biol 89:1112–1120

Oetinger MI (1978) Post-embryonic development of the sawfish *Pristis perotteti* Müller and Henle, 1841. MSc dissertation, University of Nebraska, Lincoln, NE

Pauly D (1980) On the interrelationship between natural mortality, growth parameters, and mean environmental temperatures in 175 fish stocks. ICES J Mar Sci 39: 175–192

Peterson I, Wroblewski JS (1984) Mortality rates of fishes in the pelagic ecosystem. Can J Fish Aquat Sci 41: 1117–1120

Peverell SC (2005) Distribution of sawfishes (Pristidae) in the Queensland Gulf of Carpentaria, Australia, with notes on sawfish ecology. Environ Biol Fishes 73:391–402

Peverell SC (2009) Sawfish (Pristidae) of the Gulf of Carpentaria, Queensland, Australia. MSc dissertation, James Cook University, Townsville

Pogonoski JJ, Pollard DA, Paxton JR (2002) Conservation overview and action plan for Australian threatened and potentially threatened marine and estuarine fishes. Environment Australia, Canberra

Poulakis GR, Stevens PW, Grubbs RD, Chapman DD and others (2014) Smalltooth sawfish (*Pristis pectinata*) research and outreach: an interdisciplinary collaborative program. Final report to the National Marine Fisheries Service for award NA10NMF4720032. FWRI File-code F2858-10-14-F. https://f50006a.eos-intl.net/ELIBSQL12_F50006A_Documents/F2858-10-14-F.pdf (accessed 13 July 2017)

Schluessel V, Giles J, Kyne PM (2015) Notes on female reproductive biology and embryos of the brown guitarfish *Rhinobatos schlegelii* from the Penghu Islands, Taiwan. Ichthyol Res 62:347–350

Simpfendorfer CA (2000) Predicting population recovery rates for endangered western Atlantic sawfishes using demographic analysis. Environ Biol Fishes 58:371–377

Simpfendorfer CA, Kyne PM (2009) Limited potential to recover from overfishing raises concerns for deep-sea sharks, rays and chimaeras. Environ Conserv 36:97–103

Simpfendorfer CA, Poulakis GR, O'Donnell PM, Wiley TR (2008) Growth rates of juvenile smalltooth sawfish *Pristis pectinata* Latham in the western Atlantic. J Fish Biol 72: 711–723

Simpfendorfer CA, Heupel MR, White WT, Dulvy NK (2011) The importance of research and public opinion to conservation management of sharks and rays: a synthesis. Mar Freshw Res 62:518–527

Smart JJ, Chin A, Tobin AJ, Simpfendorfer CA (2016) Multimodel approaches in shark and ray growth studies: strengths, weaknesses and the future. Fish Fish 17: 955–971

Smith SE, Au DW, Show C (1998) Intrinsic rebound potentials for 26 species of Pacific sharks. Mar Freshw Res 49: 663–678

Stobutzki IC, Miller MJ, Heales DS, Brewer DT (2002) Sustainability of elasmobranchs caught as bycatch in a tropical prawn (shrimp) trawl fishery. Fish Bull 100:800–821

Tan HH, Lim KKP (1998) Freshwater elasmobranchs from the Batang Hari Basin of central Sumatra, Indonesia. Raffles Bull Zool 46:425–429

Tanaka S (1991) Age estimation of freshwater sawfish and sharks in northern Australia and Papua New Guinea. In: Shimizu M, Taniuchi T (eds) Studies on elasmobranchs collected from seven river systems in northern Australia and Papua New Guinea. Univ Mus Univ Tokyo Nat Cult 3:71–82

Taniuchi T, Kan TT, Tanaka S, Otake T (1991) Collection and measurement data and diagnostic characters of elasmobranchs collected from three river systems in Papua New Guinea. In: Shimizu M, Taniuchi T (eds) Studies on elasmobranchs collected from seven river systems in northern Australia and Papua New Guinea. Univ Mus Univ Tokyo Nat Cult 3:27–41

Taniuchi T, Ishihara H, Tanaka S, Hyodo S, Murakami M, Séret B (2003) Occurrence of two species of elasmobranchs, *Carcharhinus leucas* and *Pristis microdon*, in Betsiboka River, West Madagascar. Cybium 27:237–241

Thorburn DC, Morgan DL, Rowland AJ, Gill H (2004) Elasmobranchs in the Fitzroy River, Western Australia. Report to the Natural Heritage Trust. Murdoch University, Perth

Thorburn DC, Morgan DL, Rowland AJ, Gill HS (2007) Freshwater sawfish *Pristis microdon* Latham, 1794 (Chondrichthyes: Pristidae) in the Kimberley region of Western Australia. Zootaxa 1471:27–41

Thorson TB (1976) Observations on the reproduction of the sawfish, *Pristis perotteti*, in Lake Nicaragua, with recommendations for its conservation. In: Thorson TB (ed) Investigations of the ichthyofauna of Nicaraguan lakes. University of Nebraska, Lincoln, NE, p 641–650

Thorson TB (1982a) The impact of commercial exploitation on sawfish and shark populations in Lake Nicaragua. Fisheries (Bethesda, Md) 7:2–10

Thorson TB (1982b) Life history implications of a tagging study of largetooth sawfish, *Pristis perotetti*, in the Lake Nicaragua-Río San Juan System. Environ Biol Fishes 7: 207–228

Thorson JT, Simpfendorfer CA (2009) Gear selectivity and sample size effects on growth curve selection in shark age and growth studies. Fish Res 98:75–84

Whitty JM, Phillips NM, Morgan DL, Chaplin JA, Thorburn DC, Peverell SC (2008) Habitat associations of freshwater sawfish (*Pristis microdon*) and northern river sharks (*Glyphis* sp. C): including genetic analysis of *P. microdon* across northern Australia. Report to Department of the Environment, Water, Heritage and the Arts. Centre for Fish and Fisheries Research, Murdoch University, Perth

Whitty JM, Morgan DL, Peverell SC, Thorburn DC, Beatty SJ (2009) Ontogenetic depth partitioning by juvenile freshwater sawfish (*Pristis microdon*: Pristidae) in a riverine environment. Mar Freshw Res 60:306–316

Wilson D (1999) Freshwater sawfish *Pristis microdon*. Australian New Guinea Fishes Association's A–Z notebook of native freshwater fish. ANGFA Bull 41