Biological observations on lamnoid sharks (Lamniformes) caught by fisheries in eastern Indonesia

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Fish landing site surveys in eastern Indonesia, conducted between April 2001 and March 2006, recorded seven species of lamnoid sharks (order Lamniformes) belonging to four families. Of these, Alopiidae were most abundant in the landings, with *Alopias pelagicus* contributing ~13% to the total biomass of all sharks recorded. Single specimens of both *Carcharias taurus* and *Odontaspis ferox* represent the first confirmed records of these two odontaspid species from Indonesian waters. The length at first maturity (L_{50}) of females and males of *Alopias pelagicus* were 2853 and 2468 mm total length (TL), respectively, and size at birth was 1300–1440 mm TL. Pregnant females of both *A. pelagicus* and *A. superciliosus* had litters of only two embryos (one per uterus) that were confirmed to be oophagous, but not adelphophagous. Females and males of *Pseudocarcharias kamoharai* matured at 870–1030 and ~725 mm TL, respectively, and size at birth was 360–450 mm TL. Pregnant females of *Isurus oxyrinchus* and *I. paucus* matured at ~1860 and 2050–2281 mm TL, respectively. These are the first biological data reported on lamnoid sharks in Indonesian waters.

INTRODUCTION

The order Lamniformes comprises 15 species belonging to seven families, and has a worldwide distribution in a variety of marine habitats (Compagno et al., 2005). They are mostly large, active and pelagic sharks with all species, except the crocodile shark *Pseudocarcharias kamoharai* (Matsubara), attaining more than three metres in length. Several lamnoids are important in commercial and recreational fisheries and the white shark *Carcharodon carcharias* (L.) and the basking shark *Cetorhinus maximus* (Gunnerus) are important for ecotourism in some regions (Compagno et al., 2005). Pelagic longline fisheries, that operate in all major oceans, account for most of the catch of shortfin mako *Isurus oxyrinchus* Rafinesque, thresher *Alopias* spp. and porbeagle *Lamna nasus* (Bonnaterre) sharks (see e.g. Marin et al., 1998; Matsunaga & Nakano, 1999).

Lamnoid sharks are viviparous, with oophagy and occasionally adelphophagy (Compagno et al., 2005). Adelphophagy has only been definitively reported in *Carcharias taurus* Rafinesque (Bass et al., 1975; Gilmore et al., 1983), but further research is required on those species reported to typically have a single embryo per uterus, e.g. *Alopias* spp. (Gilmore, 1993).

Despite Indonesia having the largest chondrichthyan fishery in the world (Stevens et al., 2000), studies on the species and size compositions of the landings and biology of the species involved have been limited (but see White et al., 2006a,b; White & Dharmadi, in press). Although White et al. (2006b) provides details of lamnoids present in the fisheries' landings in eastern Indonesia, there are currently no published data on the relative contributions of each of the species to the total number and biomass of

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all sharks recorded. This paper presents data on the species and size compositions of the lamnoid sharks landed in eastern Indonesia, together with aspects of their biology such as size at maturity and litter size.

MATERIALS AND METHODS

Lamnoid sharks were recorded at various fish landing sites in Indonesia: Muara Baru and Muara Angke (Jakarta), Pelabuhanratu (West Java), Cilacap (central Java), Kedonganan (Bali) and Tanjung Luar (Lombok) (see Figure 1 in White et al., 2006b for locations). A total of 21 survey trips were undertaken between April 2001 and March 2006. The number of individuals of each lamnoid species landed, their sex and the fishing gear used to capture them were recorded.

Whenever possible, the total length (TL) of each individual at the landing site was recorded. In *Alopias pelagicus* and *A. superciliosus* (Lowe), the caudal fin was frequently removed or damaged and so fork (FL) and/or precaudal (PCL) length was recorded. Total, fork and precaudal lengths for these species were obtained from a subsample of individuals with intact caudal fins to derive relationships between these lengths. The outer length of the clasper (CL), measured from the lateral junction of pelvic-fin inner margin to apex of clasper, and its level of calcification (non-calcified, partially calcified or fully calcified) were recorded, where possible, for males.

The reproductive condition of females could only be recorded for a subsample of several of the species at the Tanjung Luar (Lombok) and Kedonganan (Bali) landing sites due to processing practices. The maturity status of these females (immature, mature but not pregnant or

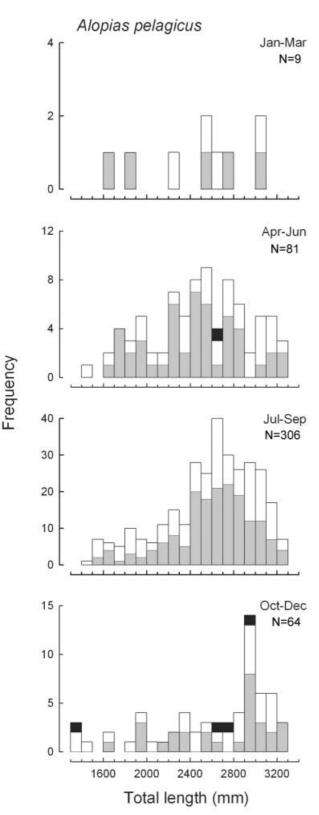


Figure 1. Quarterly length-frequency histograms for females and males of *Alopias pelagicus* caught in Indonesian waters. Grey bars, females; white bars, males; black bars, unsexed individuals.

pregnant) was recorded. For pregnant females, the TL (to nearest 1 mm) and sex of all embryos were recorded.

Total weights (TW) were recorded to the nearest gram, but most could not be weighed due to time constraints. A length-weight relationship for *A. pelagicus* was obtained by

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fitting a power curve of the form $y=ax^{b}$ using MicrosoftTM Excel. Weights of individuals measured but not weighed were calculated using the above equation. For those species where a TL vs TW equation was not determined, estimated weights were obtained using a TL vs TW equation from a morphologically-similar shark species which would yield appropriate weight estimations. For each species, the weights of individuals which were counted but not measured were estimated by obtaining an average weight of individuals for that species using the above methodology. Total biomass was then determined for each species.

The length at maturity of males was calculated for the two species for which there were adequate numbers of individuals with non-calcified, partially-calcified and fully-calcified claspers, i.e. *A. pelagicus* and *Isurus oxyrinchus*. Individuals with either non- or partially-calcified claspers were considered immature, while those with fully-calcified claspers were considered mature. The length, at which 50% of males of each species attain maturity (i.e. the L_{50} at maturity) was derived from the following logistic regression, where the proportion, $p_{\rm L}$, of those sharks that were mature at length *L* was calculated as:

$$p_L = \frac{1}{1 + \exp\left[-\ln(19)\frac{(L-L_{50})}{(L_{95}-L_{50})}\right]},$$
(1)

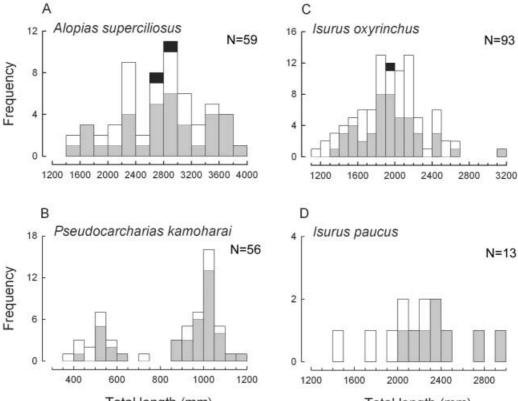
and where L_{50} and L_{95} are constants and ln is the natural logarithm. Maximum likelihood estimates of the parameters were obtained using the routine SOLVER in MicrosoftTM Excel and calculating the likelihood of immature and mature individuals as $1 - p_L$ and p_L , respectively. The reported estimates of the parameters were determined as the median values derived from 200 sets of randomlyresampled data, with the same sample size, drawn from the data on the observed maturity status at length for males. The approximate 95% confidence intervals were estimated as the 2.5 and 97.5 percentiles of the 200 estimates resulting from these resampled data. The length at maturity (L_{50}) of females of A. pelagicus was determined using the same methodology described above for males with mature, but not pregnant and pregnant females considered as mature for the analysis.

The relationships between clasper length (*CL*) and length (*L*) of the males of those species for which there were sufficient data, i.e. *A. pelagicus* and *I. oxyrinchus*, were each described using the modified logistic function, $CL=b+\{(a-b)[1+\exp(-\ln(19)(L-L_{50})(L_{95}-L_{50})^{-1})]^{-1}\}$, where *CL* is the estimated *CL* at length *L*, *a* is the estimated maximum length attained by the claspers (mm) and *b* is the estimated minimum value attained by the claspers (mm). It was not appropriate to use this logistic function for those species with insufficient data points throughout the whole size-range or when the data points do not follow the typical sigmoidal pattern.

RESULTS

Species composition

The most abundant lamnoid family recorded in Indonesia was the Alopiidae, which constituted 3.0 and 14.9% to the total number and biomass, respectively, of



Total length (mm)

Total length (mm)

Figure 2. Number of females and males in sequential length classes of: (A) *Alopias superciliosus*; (B) *Pseudocarcharias kamoharai*; (C) *Isurus oxyrinchus*; and (D) *Isurus paucus*, caught in Indonesian waters. Grey bars, females; white bars, males; black bars, unsexed individuals.

all sharks recorded (Table 1). The Lamnidae were the second most abundant family recorded, constituting 0.6 and 3.8% to the total number and biomass, respectively, of all sharks. *Alopias pelagicus* was the most abundant lamnoid observed in the landings (12.7% of total biomass of sharks) followed by *Isurus oxyrinchus* (3.4%) and *Alopias superciliosus* (2.2%) (Table 1).

Size and weight relationships

The parameters for the linear regression equations for the TL and FL, and TL and PCL relationships for females and males of *A. pelagicus* and *A. superciliosus* are shown in Table 2. The relationship between TW and TL of both sexes combined of *A. pelagicus* is expressed by the following equation:

Both sexes :
$$TW = 4.0 \times 10^{-7} \times TL^{3.217}$$

($r^2 = 0.976$; n = 9). (2)

Size and sex compositions

Only a single, unsexed individual of both *Carcharias* taurus and *Odontaspis ferox* (Risso), which had lengths of >2500 and ~ 1200 mm, respectively, were recorded in this study.

Table 1. The contribution by number and biomass and minimum and maximum sizes of each of the species of lamnoids recorded in eastern Indonesia.

Scientific name	Common name	% by number	% by biomass	Minimum size (mm)	Maximum size (mm)
ODONTASPIDIDAE		< 0.1	<0.1		
Carcharias taurus	grey nurse shark	< 0.1	< 0.1	>2500	>2500
Odontaspis ferox	sandtiger shark	< 0.1	< 0.1	~ 1200	~ 1200
ALOPIIDAE	0	3.0	14.9		
Alopias pelagicus	pelagic thresher	2.6	12.7	1309	3260
Alopias superciliosus	bigeye thresher	0.4	2.2	1530	3820
PSEUDOCARCHARIIDAE	0,	0.4	0.1		
Pseudocarcharias kamoharai	crocodile shark	0.4	0.1	363	1181
LAMNIDAE		0.6	3.8		
Isurus oxyrinchus	shortfin mako	0.6	3.4	1167	3100
Isurus paucus	longfin mako	0.1	0.3	1490	2980
TOTAL (of all sharks recorded)		21 651	$184268~\mathrm{kg}$		

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Table 2. Total length vs fork and precaudal lengths parameters for females and males of Alopias pelagicus and A. superciliosus, where $TL=(a \times FL \text{ or } PCL) + b$.

Species		а	b	r^2	Ν
Alopias pelagio	cus				
Females:	\mathbf{FL}	1.72	333.36	0.873	95
	PCL	1.98	195.58	0.943	105
Males:	\mathbf{FL}	1.85	123.12	0.968	62
	PCL	2.05	101.71	0.980	85
Alopias superci	liosus				
Females:	\mathbf{FL}	1.75	-3.20	0.984	13
	PCL	1.92	-4.96	0.991	16
Males:	\mathbf{FL}	1.62	164.74	0.909	13
	PCL	1.70	192.31	0.939	16

N, number.

A total of 570 *A. pelagicus* was recorded, consisting of 287 females, 217 males and 66 unsexed individuals. The landings consisted of significantly more females than males (χ^2 -test P < 0.05). The 252 females, 203 males and five unsexed individuals that were measured ranged from 1521 to 3260, 1309 to 3240 and 1338 to 2935 mm TL, respectively. A wide size-range of individuals were recorded in each of the quarters of the year, despite the sample size varying greatly (Figure 1). Neonates of < 1700 mm TL were present in each of the quarters of the year. In the quarter with the largest sample size (July–September) individuals in the 2400–3199 mm length classes dominated the landings (Figure 1).

A total of 76 *A. superciliosus* was recorded, consisting of 46 females, 24 males and six unsexed individuals. The landings consisted of significantly more females than males (χ^2 -test P < 0.05). The 36 females, 22 males and one unsexed individual that were measured ranged from 1530 to 3820, 1539 to 3550 and 2675 mm TL, respectively. No distinct size cohorts were apparent in the landings of this species, but a large number of individuals recorded were in the 2200–2999 mm length classes (Figure 2A).

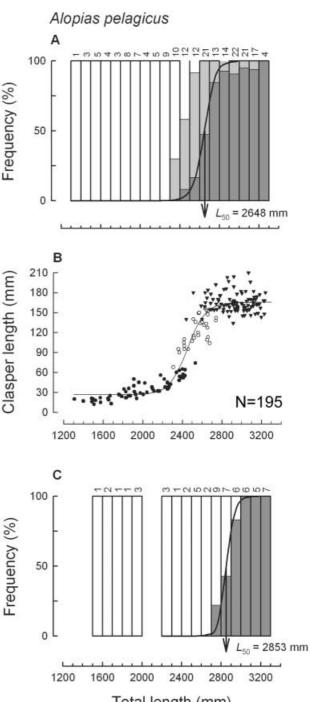
A total of 77 *Pseudocarcharias kamoharai* was recorded, of which 40 were females (434–1181 mm TL), 16 were males (363–1068 mm TL) and 21 were counted but not sexed (Figure 2B). The landings consisted of significantly more females than males (χ^2 -test P < 0.05). Two distinct size cohorts were observed in the landings, one of which consisted of neonates and juveniles in the 350–649 mm length classes and the other of sub-adults and adults in the 850–1199 mm length classes (Figure 2B).

A total of 120 *I. oxyrinchus* was recorded, of which 51 were females, 51 were males and 18 were counted but not sexed. The 47 females and 45 males that were measured ranged from 1308 to 3100 and 1167 to 2644 mm TL, respectively. The size-classes that were best represented in the landings were the 1800–2199 mm length classes, with only one individual present in the length classes > 2500 mm (Figure 2C).

A total of 13 *Isurus paucus* Guitart Manday was recorded, of which eight were females (2031–2980 mm TL) and five were males (1490–2281 mm TL), with no distinct size cohorts apparent in the landings (Figure 2D).

Length at maturity

All males of *A. pelagicus* < 2400 mm TL possessed either non- or partially-calcified claspers, whereas all males



Total length (mm)

Figure 3. (A) Percentage frequencies of occurrence of immature (white bars), maturing (light grey bars) and mature (dark grey bars) males in sequential length classes; (B) clasper length vs total length relationship; and (C) percentage frequencies of occurrence of immature (white bars) and mature (grey bars) females in sequential length classes for *Alopias pelagicus*. In (A) and (C), arrows indicate position of the L_{50} . Sample sizes are given above each bar. In (B) closed circles, non-calcified claspers; open circles, partially-calcified claspers; closed triangles, fully-calcified claspers.

>2750 mm TL possessed fully-calcified claspers (Figure 3A,B). The L_{50} and L_{95} (95% confidence intervals) of males at maturity were 2648 (2601–2685) mm and 2802 (2773–2870) mm, respectively (Figure 3A). The point of inflection (95% confidence intervals) for the clasper length vs total length curve occurs at 2451 (2428–

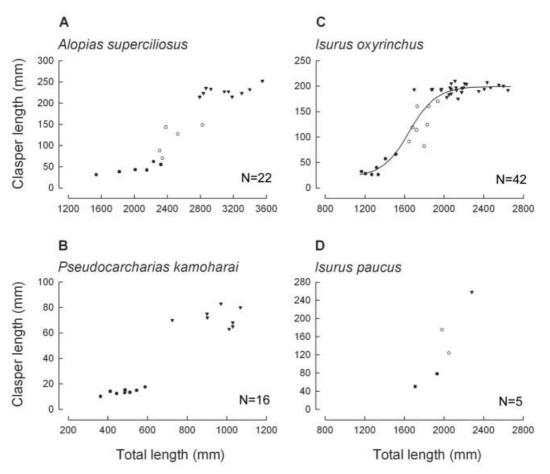


Figure 4. Relationship between clasper length and total length of males of: (A) *Alopias superciliosus;* (B) *Pseudocarcharias kamoharai;* (C) *Isurus oxyrinchus;* and (D) *Isurus paucus.* Closed circles, non-calcified claspers; open circles, partially-calcified claspers; closed triangles, fully-calcified claspers.

2476) mm TL. All females of *A. pelagicus* < 2780 mm TL were immature, while all females > 2900 mm TL were mature. The L_{50} and L_{95} (95% confidence intervals) of females at maturity were 2853 (2764–2900) mm and 2976 (2795–3045) mm, respectively (Figure 3C)

All males of *A. superciliosus* <2790 mm TL possessed non- or partially-calcified claspers, whereas all males >2830 mm TL possessed fully-calcified claspers (Figure 4A), indicating that males are attaining maturity between 2790 and 2830 mm TL. A size at maturity for females could not be determined, except that it is less than the size of the smallest pregnant females of 3501 mm TL.

All males of *P. kamoharai* < 590 mm TL possessed noncalcified claspers, whereas all males > 725 mm TL possessed fully-calcified claspers (Figure 4B), indicating that males are attaining maturity between these sizes. Since no males with partially-calcified claspers were recorded, the size at maturity is presumably closer to 725 mm TL. The maturity status of only four females of *P. kamoharai* was recorded, one of which was immature (871 mm TL) and three were pregnant (1032–1067 mm TL). Thus, females are becoming mature between 870 and 1030 mm TL.

All males of *I. oxyrinchus* <1690 mm TL possessed nonor partially-calcified claspers, whereas all of those >1970 mm TL possessed fully-calcified claspers (Figure 4C). However, although one male of 1698 mm TL possessed fully-calcified claspers, all other males <1850 mm TL were immature. The L_{50} and L_{95} (95% confidence intervals) of males at maturity were 1857

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(1768–1917) mm and 2014 (1858–2148) mm, respectively (Figure 4C). A logistic curve provided a good fit to the clasper length vs total length data, with the point of inflection (95% confidence intervals) occurring at 1648 (1397–1765) mm TL (Figure 4C). There was only limited data collected on maturity status of females. Six females examined (1452–2417 mm TL) were immature, while a single female (2485 mm TL) was mature.

Only a single mature male (2281 mm TL) of *I. paucus* was recorded, with the remaining four males (1710–2050 mm TL) possessing non- or partially-calcified claspers (Figure 4D). This provides some indication that males are becoming mature between 2050 and 2280 mm TL. No maturity data was collected for females.

Reproductive biology

A total of 22 pregnant female *A. pelagicus*, ranging from 2780 to 3252 mm TL, was recorded. All pregnant females contained only a single embryo in each of the two uteri. The sex ratio of the 44 embryos, which ranged from 15 to 1440 mm TL, did not differ significantly from parity, i.e. 22 females, 14 males and eight unsexed embryos. In each of the four months that embryos were recorded, a wide range of embryo developmental stages and sizes were observed (Figure 5), indicating that this species does not have a seasonal reproductive cycle. For example, in July, embryo sizes ranged from 86 mm TL in one litter to 1382 mm TL in another litter (Figure 5). All pregnant

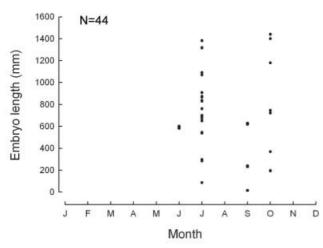


Figure 5. Monthly total lengths of embryos of *Alopias pelagicus*.

females possessed enlarged ovaries with large quantities of small yolked oocytes (\sim 45 mm diameter), which are presumably continually ovulated during gestation as a source of embryonic nutrition. Since the smallest neonate recorded was 1309 mm TL, the size at birth in *A. pelagicus* in Indonesian waters is about 1300–1440 mm TL.

Two pregnant females of *A. superciliosus* (3508 and 3786 mm TL) were recorded, one of which contained a single embryo in each uterus (785 and 742 mm TL) and the other contained two presumably fertilized *in utero* eggs. Since the smallest neonate recorded was 1540 mm TL, an accurate size at birth could not be determined, but lies between 742 and 1540 mm TL.

Three pregnant females of *P. kamoharai* (1032–1067 mm TL) were recorded, each of which contained four late-term embryos (two per uterus) ranging in length from 298–450 mm. No evidence of any reproductive seasonality could be determined since late-term embryos were observed in March, April and October and neonates were recorded mostly in July and December. Since the smallest neonate recorded was 363 mm TL, the size at birth in this species is 360–450 mm TL.

DISCUSSION

Alopias pelagicus

There is very little published information on the biology of Alopias pelagicus (but see Liu et al., 1999), despite the fact that it is found throughout the tropical IndoPacific region and is a common by-catch of pelagic tuna fisheries (Matsunaga & Nakano, 1999; White et al., 2006b). The landings of A. pelagicus in eastern Indonesia consisted of significantly more females than males, which is consistent with the findings of Liu et al. (1999) for this species off Taiwan. This indicates some form of sex segregation in this species, which is similar to that recorded for the scalloped hammerhead Sphyrna lewini (Rüppell) in the same two locations (Chen et al., 1988; W.T. White, unpublished. data), and may be related to individuals of one sex moving further offshore than the other. The sex ratio of embryos was close to parity in both this and the Taiwan studies. Although the maximum size recorded for females off Taiwan was substantially larger than recorded in this study, i.e. ~ 3630 vs 3260 mm TL, respectively, the

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maximum size of males were similar in both studies, i.e. $\sim 3200~\rm{mm\,TL}$ (Liu et al., 1999).

Although there were only nine data points in the length-weight relationship provided for this species, the resulting equation provides better calculations of total weights of the majority of individuals than that provided by Liu et al. (1999).

The L_{50} s at maturity of females and males of A. pelagicus recorded in Indonesia (2648 and 2853 mm TL, respectively) lie within the ranges of maturity reported off Taiwan (2820–2920 and 2670–2760 mm TL, respectively) (Liu et al., 1999). All pregnant females recorded contained two embryos, one in each uterus, as reported previously (Nakamura, 1935; Otake & Mizue, 1981; Liu et al., 1999). These results also indicate that this species has a nonseasonal reproductive cycle, as was also reported by Liu et al. (1999). The presence of vast quantities (>100) of small, yolked oocytes in the right (functional) ovary of all pregnant females provides further confirmation that this species is viviparous, with oophagy (see Gilmore, 1993). The presence of only a single embryo, at various development stages, in each uterus also provides further confirmation that adelphophagy does not occur in this species. The size of birth of 1300-1440 mmTL recorded in Indonesia is considerably smaller than the 1590-1900 mm TL recorded off Taiwan (Liu et al., 1999).

Alopias superciliosus

Aspects of the biology of A. superciliosus have been reported previously (Gilmore, 1993; Chen et al., 1997). As was reported for Alopias pelagicus, significantly more females of this species were present in the landings in Indonesia (this paper) and off Taiwan (Chen et al., 1997). The maximum size of A. superciliosus recorded in Indonesia of 3786 mm TL is considerably less than the known maximum size of this species of 4840 mm TL (Thorpe, 1997). The size at maturity of males recorded, i.e. 2790-2830 mm TL, is similar to that reported for north-eastern Atlantic and north-western Pacific populations, i.e. 2760 and 2701-2876 mm TL, respectively (Moreno & Morün, 1992; Chen et al., 1997). Although an accurate size at maturity for females could not be determined, the size of the smallest pregnant female (3508 mm TL) is close to the size at maturity reported previously, i.e. 3410 and 3320-3411 mm TL (Moreno & Morün, 1992; Chen et al., 1997). An accurate size at birth could not be determined, but since the smallest neonate recorded was 1540 mm TL, the size at birth of this species in Indonesian waters is likely to be close to the 1350–1400 mm TL reported by Chen et al. (1997). The two pregnant females contained two embryos (one per uterus) with evidence of oophagy in both cases.

Pseudocarcharias kamoharai

There are few published studies on the reproductive biology of *Pseudocarcharias kamoharai* (Abe, 1969; Bass et al., 1975; Fujita, 1981), which probably reflects the fact that pelagic fisheries which catch this species are discarding it due to its small size and limited value. The maximum size of 1181 mm TL recorded for a female in this study is slightly larger than the previously reported maximum size of 1100 mm TL (Last & Stevens, 1994; Compagno et al., 2005). Although an accurate size at maturity for males could not be determined, it is likely that they are attaining maturity at around 725 mm TL. This is similar to that previously reported by Compagno et al. (2005), i.e. \sim 740 mm TL. The broad size-range for maturity in females recorded in Indonesia, i.e. 870–1030 mm TL, is similar to those previously reported for this species, i.e. \sim 980–990 mm TL (Abe, 1969; Fujita, 1981).

Pregnant females of P. kamoharai are reported to have litters of only four pups (two per uterus), (Bass et al., 1975; Fujita, 1981), which was also the case for the three pregnant females examined in this study. The size-range at birth found in Indonesia, i.e. 360-450 mm TL, is wider than previously reported for this species, i.e. 40-43 (Fujita, 1981; Compagno et al., 2005). The lack of seasonality in the reproductive cycle found in the Indonesian populations has also been previously reported for this species by Fujita (1981). The functional ovary of the three pregnant females recorded contained numerous small, yolked ova, indicating that this species is oophagous as has been previously reported (Bass et al., 1975; Fujita, 1981). Although Compagno et al. (2005) reports that adelphophagy is possible in this species, the fact that litters always contain two embryos provides strong indication that this species is oophagous but not adelphophagous.

Isurus oxyrinchus

Although there have been numerous studies on the biology of Isurus oxyrinchus throughout its range (e.g. Stevens, 1983; Cliff et al., 1990; Mollet et al., 2000), there has been no such studies on this species in the tropical Indo-Australian region. The L_{50} at maturity of males recorded in Indonesia, i.e. 1857 mm TL, is slightly less than the size at maturity previously reported for this species off eastern Australia and southern Africa, i.e. 1950 and 1940-2060 mm TL, respectively (Stevens, 1983; Cliff et al., 1990), but similar to the 1800-1850 mm TL reported off New Zealand (Francis & Duffy, 2005). The approximate size at maturity for females in this study, i.e. 2400-2500 mmTL, is less than that reported in other studies, i.e. 2750-3000 mm TL (Stevens, 1983; Mollet et al., 2000; Francis & Duffy, 2005). However, as this estimate was based on only one mature female, further data from this region is required to determine a more accurate size at maturity for females.

Isurus paucus

The biology of *Isurus paucus* is very poorly known (but see Gilmore, 1983, 1993) which is largely due to its apparent rarity through most of its circumtropical range (Compagno et al., 2005). The approximate size at maturity of males recorded in this study, i.e. 2050– 2280 mm TL, represents the most reliable estimate of male maturity in this species throughout its range. No maturity data for females could be collected in this study, but one female *I. paucus* of 2450 mm TL is reported as being the smallest mature specimen (Gilmore, 1993).

Carcharias taurus and Odontaspis ferox

The single specimens of both *Carcharias taurus* and *Odontaspis ferox* observed in this study represent the first confirmed records of these two species in Indonesian waters.

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A special thanks go to Fahmi and Dharmadi for there assistance in the field throughout the project. Thanks are also expressed to Ashlee Jones, Mike Travers, Claire Bartron and Simon de Lestang for their assistance on field trips and to Steve Blaber, Jenny Giles, Ian Potter, Norm Hall, Peter Last, John Stevens, John Salini, Richard Pillans, Alastair Graham, Cathy Dichmont, Malcolm Tull, Simon Vieira, Ono Kurnaen Sumadhiharga and Subhat Nurhakim for help in this project. This five year project was funded by the Australian Centre for Agricultural Research (ACIAR).

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Submitted 4 November 2006. Accepted 15 February 2007.