

Abstract—Reproductive data collected from porbeagle, shortfin mako, and blue sharks caught around New Zealand were used to estimate the median length at maturity. Data on clasper development, presence or absence of spermatophores or spermatozoogmata, uterus width, and pregnancy were collected by observers aboard tuna longline vessels. Direct maturity estimates were made for smaller numbers of sharks sampled at recreational fishing competitions. Some data sets were sparse, particularly over the vital maturation length range, but the availability of multiple indicators of maturity made it possible to develop estimates for both sexes of all three species.

Porbeagle shark males matured at 140–150 cm fork length and females at about 170–180 cm. New Zealand porbeagles therefore mature at shorter lengths than they do in the North Atlantic Ocean. Shortfin mako males matured at 180–185 cm and females at 275–285 cm. Blue shark males matured at about 190–195 cm and females at 170–190 cm; however these estimates were hampered by small sample sizes, difficulty obtaining representative samples from a population segregated by sex and maturity stage, and maturation that occurred over a wide length range. It is not yet clear whether regional differences in median maturity exist for shortfin mako and blue sharks.

Length at maturity in three pelagic sharks (*Lamna nasus*, *Isurus oxyrinchus*, and *Prionace glauca*) from New Zealand

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The attainment of sexual maturity in sharks is a major developmental milestone which has a large impact on their distribution, behavior, and biology. Immature sharks often associate with each other regardless of sex, but after maturity sexual segregation is the norm. Mature males and females may come together only to mate, resulting in movements that may range from small-scale aggregation of dispersed individuals to long-range migrations over thousands of kilometers.

The process of maturation, and the subsequent need to channel energy into reproduction, affect the growth rate of at least some shark species. Immature male and female porbeagles grow at the same rate, and the growth rate of both sexes slows at maturity; however females mature at a greater age than males and therefore their period of fast immature growth lasts longer and they grow larger than males (Natanson et al., 2002).

The maximum reproductive lifespan of a shark species is the time elapsed between the age at maturity and the maximum age. In conjunction with the duration of the reproductive cycle, the reproductive lifespan determines the maximum number of litters a female shark can produce in her lifetime. Population modeling indicates that shark species that mature at a young age have a greater capacity to recover from exploitation than

sharks that mature later (Smith et al., 1998). Thus age at maturity is a crucial factor influencing the productivity of a species.

Age at maturity can be estimated directly from paired age-and-maturity estimates taken from the same shark, but often such data are not available, or are too few to provide precise estimates. Consequently it is often necessary to estimate age at maturity indirectly from length at maturity and a growth curve.

In the present study we estimate the length at maturity for three species of large pelagic sharks in New Zealand waters: porbeagle (*Lamna nasus* (Bonnaterre, 1788)), shortfin mako (*Isurus oxyrinchus* Rafinesque, 1810), and blue (*Prionace glauca* (Linnaeus, 1758)) sharks. These species are commonly caught by tuna longliners fishing around New Zealand (Francis et al., 2001). Longline fishing effort declined from a high of over 25 million hooks per year in the early 1980s, to a low of 2–4 million hooks in 1995–98, largely because of a reduction in the number of foreign licensed vessels (Francis et al., 2001). Since then, the domestic longline fleet has expanded, and fishing effort exceeded 10 million hooks in 2001–02 (Ayers et al., 2004). Because of concern over the sustainability of the catches of both target and nontarget species in this fishery, the New Zealand Ministry

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of Fisheries introduced individual transferable quotas for a number of pelagic species, including the three sharks, in October 2004.

Despite the panglobal distributions of porbeagle, shortfin mako, and blue sharks, and their importance in the catches of pelagic longline fisheries worldwide, comparatively little effort has been devoted to estimating their length (or age) at maturity. In the northwest Atlantic Ocean, the length at maturity of male and female porbeagles has been well determined (Jensen et al., 2002), but preliminary data from the southwest Pacific Ocean indicate that females mature at a much smaller length there (Francis and Stevens, 2000). Mollet et al. (2000) found significant differences in the length at maturity of female shortfin makos between the Northern and Southern hemispheres; however there is little information on the length at maturity of male makos (Stevens, 1983). Blue sharks have been studied in a number of regions worldwide (Pratt, 1979; Stevens, 1984; Hazin et al., 1994; Nakano, 1994; Castro and Mejuto, 1995), but size and sex segregation have made it difficult to obtain representative samples of both sexes from which to determine length at maturity.

In the southwest Pacific Ocean, estimates of length at maturity are lacking or uncertain for at least one sex of all three species. Although all species make long distance movements, and presumably have wide-ranging stocks, the interhemispheric differences in length at maturity reported for female porbeagles and shortfin makos indicate that it is not safe to transfer estimates from one region to another. The aim of the present study is to develop region-specific estimates of length at maturity for male and female porbeagle, blue and shortfin mako sharks, and to determine whether this parameter varies globally. These results will contribute to efforts to determine the productivity and stock status of pelagic sharks in New Zealand waters.

Materials and methods

Data sources

Reproductive data were collected from two main sources. The first consisted of sharks sampled by the authors at recreational fishing competitions, or occasionally sharks retained by commercial fisheries or research vessels. The second source consisted of data and occasionally embryos and female reproductive tracts collected by Ministry of

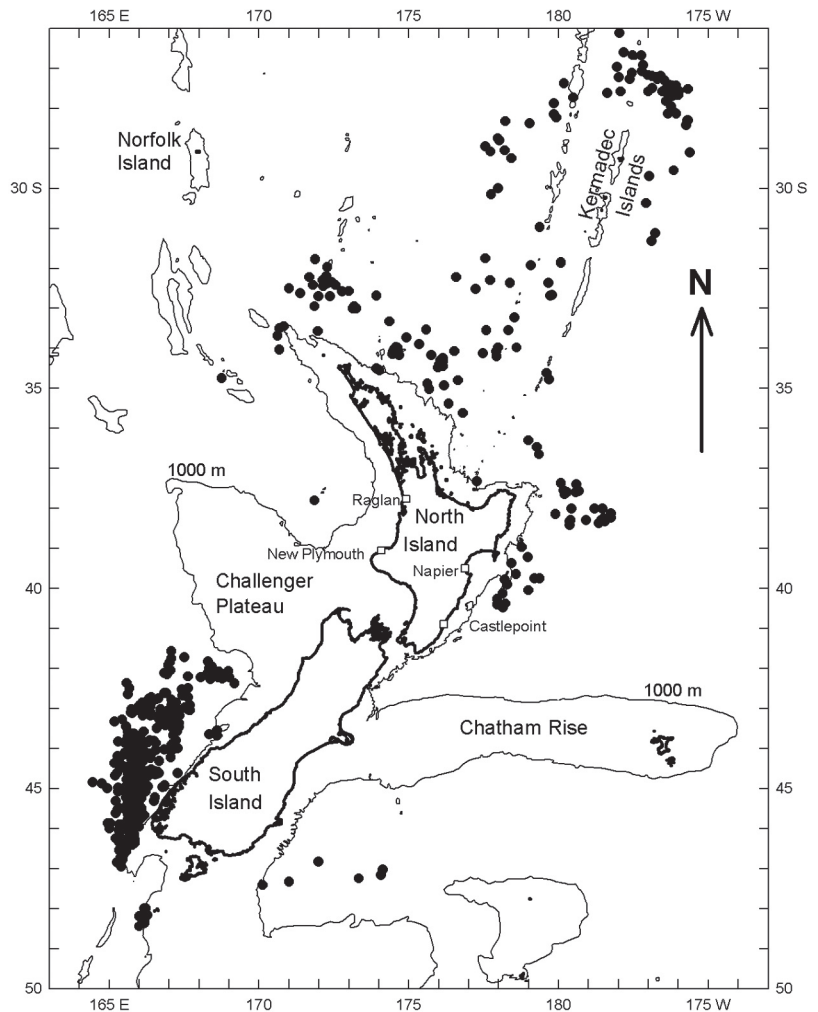


Figure 1

Start-of-set positions of tuna longline sets during which observers sampled porbeagle (*Lamna nasus*), shortfin mako (*Isurus oxyrinchus*), and blue (*Prionace glauca*) sharks. Also shown are the North Island ports where sharks landed during fishing competitions were sampled.

Fisheries observers aboard commercial tuna longline vessels (Fig. 1). Sharks obtained from fishing competitions provided the opportunity to measure a wide range of reproductive parameters on relatively small samples, whereas sharks observed on tuna longline vessels provided large samples but limited reproductive data.

Sharks obtained from fishing competitions

Competition sharks consisted mainly of makos and blue sharks sampled at fishing competitions around the North Island (Fig. 1). Most sharks were sampled from the Hawke Bay competition held annually in February or March from the port of Napier. Other significant competitions were sampled at Castlepoint, Raglan, and New Plymouth. All except two of the competition sharks were collected in summer (January–March) and samples

spanned the period from 1986 to 2004. In the early years, only data on length, sex, weight, and maturity were collected. In later years, detailed reproductive data were also collected. The following length measurements were made as point-to-point straight line distances to the whole centimeter below actual length:

- Total length (TL_{nat}): tip of snout to a perpendicular dropped from the tip of tail to the midline (with the tail in the natural position);
- Total length (TL_{flex}): tip of snout to tip of tail (with the tail flexed towards the midline to provide maximum extension);
- Fork length (FL): tip of snout to fork in the tail;
- Precaudal length (PCL): tip of snout to the upper precaudal pit (mako and porbeagle sharks) or the origin of the upper caudal lobe (blue sharks).

Total weight was measured on accurate scales provided at the fishing competitions, on research vessels, or in commercial fish processing sheds.

In males, inner clasper length was measured between the anterior margin of the cloaca and the posterior clasper tip, and expressed as a percentage of fork length:

$$\text{Clasper length index (CLI)} = 100 (\text{clasper length}/FL).$$

The degree of clasper calcification and development was determined and included an assessment of whether the terminal cartilages could be splayed open, whether a spur was present and erupted, and whether the entire clasper could be rotated. In some males sampled in later years, the degree of development of the testes, epididymis, and ampulla at the posterior end of the epididymis was also recorded, and occasionally testes were weighed and measured (following dissection from the epigonal organ if necessary). The presence or absence of spermatophores or spermatozeugmata in the ampulla epididymis was noted. (Spermatophores are masses of encapsulated sperm, and they are found in porbeagle and mako sharks; spermatozeugmata are unencapsulated masses of naked sperm that are found in blue sharks [Pratt and Tanaka, 1994]).

In females, the reproductive system was examined, and in later years a number of measurements were taken. Uterus width was measured near the middle of the body cavity and expressed as a percentage of fork length:

$$\text{Uterine width index (UWI)} = 100 (\text{uterus width}/FL).$$

The maximum diameter of ova, where they were sufficiently developed to be visible in the ovary, was recorded, and the diameter of the oviducal gland was measured. Ovarian dimensions and weight were mea-

sured after dissection (if necessary) from the epigonal organ. Any contents of the uteri were noted; embryos were measured and sex was determined. The presence or absence of a hymen (cloacal membrane occluding the vaginal opening) was recorded.

For both males and females, a direct assessment of maturity (hereafter called direct maturity) was made by using all the available reproductive data. A three-stage classification scheme was used: immature, maturing, and mature. Mature sharks were defined as those in which the reproductive system was judged to be fully functional and capable of delivering reproductive products. For analysis purposes, maturing sharks were grouped with immature sharks.

Sharks sampled by observers

Observers sampled tuna longline sets from around the New Zealand region (Fig. 1). Data from blue and mako sharks were obtained throughout the sampled area, but porbeagles came mainly from the southwestern South Island. Most sharks were sampled in autumn–winter (April–July) over the period 2001–2003. The “standard” length measurement for sharks was FL, but frequently observers also recorded TL_{nat} or PCL.

Observers were provided with instructions and photographs indicating the reproductive data they needed to collect, but they were not provided with any practical training. The main data they collected were the following: inner clasper lengths, presence or absence of spermatophores or spermatozeugmata in the ampulla epididymis (for males); uterus width, maximum ovum diameter, and whether the shark was pregnant or not (for females).

Examination of observer pregnancy records for blue sharks indicated numerous probable errors: uterus widths from sharks scored as pregnant were frequently less than 18 mm, which seems implausible considering that ova are ovulated at about 18 mm, and pregnant sharks are unlikely to have such small uteri (Pratt, 1979; Natanson¹). This problem was apparent for several observers, some of whom were very experienced (although they had no previous experience examining shark reproductive systems). We suspect that they may have scored some female blue sharks as pregnant if the ovary contained large yolky ova (this problem did not occur for mako and porbeagle sharks, which have much smaller ovarian ova). We therefore used observer blue shark pregnancy records only if they were supported by appropriate comments on the data sheet (e.g., mention of embryos or ovulated eggs in uteri), or if the observers retained embryos or intact uteri for us to examine.

Observers did not assess direct maturity; therefore we were unable to derive direct maturity ogives for observer sharks.

¹ Natanson, L. 2004. Unpubl. data. National Marine Fisheries Service, 28 Tarzwell Drive, Narragansett, Rhode Island 02882-1152.

Table 1

Regression equations used to convert shark lengths reported in the literature. r^2 =the coefficient of determination; n =sample size. Measurement method acronyms are defined in the "Materials and methods" section, except that CFL = curved fork length and CTL = curved total length (both measured over the curve of the body).

Species	Regression equation	r^2	n	Data range (cm)	Source
Porbeagle	$FL = -6.943 + 0.893 TL_{nat}$	0.997	103	61–181 FL	This study
	$FL = 0.90 + 0.95 CFL$	0.997	172	83–253 FL	S. Campana ¹
Mako	$CFL = -1.7101 + 0.9286 CTL$	0.997	199	65–338 CFL	Kohler et al., 1995
	$FL = 0.973 + 0.968 CFL$	0.999	30	113–287 FL	This study
	$FL = 0.766 + 1.100 PCL$	0.997	999	61–346 FL	This study
	$FL = 0.821 + 0.911 TL_{nat}$	0.993	399	70–346 FL	This study
Blue	$FL = -0.90 + 0.98 CFL$	0.99	789	123–286 FL	S. Campana ¹
	$FL = -1.615 + 0.838 TL_{nat}$	0.990	273	50–270 FL	This study
	$FL = 0.745 + 1.092 PCL$	0.998	12,657	34–326 FL	This study

¹ Refers to footnote 2 in the general text.

Data analysis

For each shark species and sex, we were interested in determining the length at which 50% of the individuals in a population reached full sexual maturity. That length is the median length at maturity, hereafter referred to as "median maturity."

Many shark species show abrupt transitions in the sizes of reproductive organs near length at maturity. To locate such transitions in clasper length, we fitted "split" linear regressions to CLI data plotted against FL. Split regressions consist of two simple linear regressions fitted to different nonoverlapping data ranges that meet at a point called the breakpoint (Kováč et al., 1999). A split regression has the form

$$\begin{aligned} CLI &= f(FL - p) + h \text{ for } FL < p \\ CLI &= g(FL - p) + h \text{ for } FL \geq p, \end{aligned}$$

where f and g are slope parameters for the two limbs of the regression, and h and p are the y -axis and x -axis coordinates of the breakpoint, respectively. The parameters f , g , h , and p were estimated by least squares by using the curve fitting routine in the Sigmaplot statistical and graphing package (Sigmaplot, vers. 9.01, Systat Software Inc., Richmond, CA). The length at the breakpoint was corrected for downward rounding of FL by adding 0.5 cm.

Maturity ogives were fitted to the direct maturity data separately by sex by using probit analysis (Pearson and Hartley, 1962). The analyses were performed on individual FL measurements, but we also calculated the proportions of mature individuals in 10-cm length classes to illustrate the trends. Probit analysis assumes that the length at which a randomly selected fish reaches maturity is normally distributed. Two pa-

rameters, the mean and standard deviation of the normal distribution, were fitted. Each maturity ogive is the cumulative distribution function for the associated normal distribution. The probit function was fitted by maximum likelihood, and 95% confidence limits were estimated by the bootstrap method. The mean of the normal distribution is an estimate of the median maturity, and it was corrected for downward rounding of FL by adding 0.5 cm.

All shark length measurements provided in the present study are FL, unless otherwise stated. For comparison with our results, we converted measurements from the literature to FL where necessary using the regression equations in Table 1. Literature reports of total length were assumed to be TL_{nat} unless otherwise stated. Scientists working on sharks in the northeastern United States, and eastern Canada have typically measured lengths over the curve of the body rather than as straight line distances (Natanson¹; Campana²; Pratt³), notwithstanding some published statements to the contrary (Pratt, 1979; Kohler et al., 1995).

Results

Porbeagle shark

In male porbeagles, CLI showed two strong inflection points: the first at about 110 cm, and the second, esti-

² Campana, S. E. 2004. Personal commun. Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

³ Pratt, H. L. 2004. Personal commun. Mote Marine Laboratory, 24244 Overseas Highway, Summerland Key, FL 33042.

mated by split linear regression fitted to sharks longer than 110 cm, at 142.7 cm (95% confidence interval (CI) 140.7–144.7 cm) (Fig. 2). Thus rapid elongation of the claspers began at about 110 cm and was completed by 143 cm. Spermatophores first appeared in the posterior reproductive tract at 135 cm and by about 152 cm 50% of males contained spermatophores. The percentage of sharks with spermatophores peaked at 165 cm (82% of males) and then declined to about 50%, although sample sizes were small in the longer length groups (Table 2).

In females, UWI began increasing at a length of about 145 cm, but many larger, nonpregnant sharks showed no expansion of the uteri (Fig. 3). Three females with UWI of about 4–5% were postpartum, and two with UWI about 11% and one with UWI of about 4% were pregnant. Pregnant females measured 167–202 cm (mean 184 cm, $n=55$). Of 19 females longer than 175 cm that were scored by observers for pregnancy, 10 (53%) were pregnant, two (11%) were postpartum, and seven (37%) were resting (or possibly immature).

Apart from a 185-cm pregnant female, all whole porbeagles examined by us were immature; therefore no attempt was made to estimate maturity directly.

Shortfin mako shark

CLI showed two strong inflection points in male makos; the first at about 140 cm and the second (estimated by split linear regression) at 185.1 cm (CI 182.5–187.7 cm) (Fig. 4). The smallest male with spermatophores was 136 cm, but this measurement was an outlier and may have been an error; the next smallest was 156 cm. Fifty percent of males contained spermatophores by 178 cm, and 100% by about 235 cm. Sample sizes were reasonable over the transition range but small above 230 cm (Table 2).

Male makos examined by us showed little overlap in length between immature and mature sharks (Fig. 4), but sample sizes were small in all length classes (Table 2). The smallest mature male was 182 cm and the largest immature male was 183 cm long. The median maturity estimated by probit analysis was 182.9 cm (CI 180.7–185.1 cm) (Fig. 4).

In females, UWI began increasing at a length of about 275 cm, and all larger sharks had expanded uteri (Fig. 5). Only one pregnant female mako has been recorded from New Zealand waters, and it was 290 cm FL (Duffy and

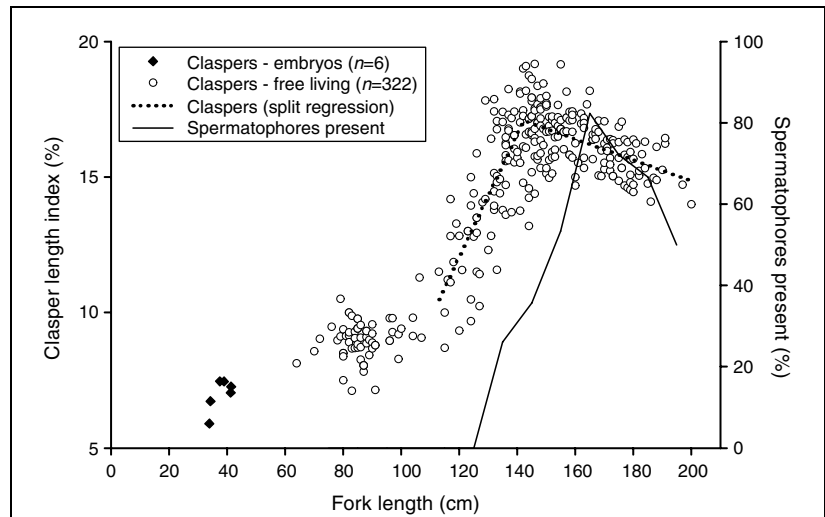


Figure 2

Maturation of male porbeagle sharks (*Lamna nasus*): variation in clasper development and presence of spermatophores in the reproductive tract.

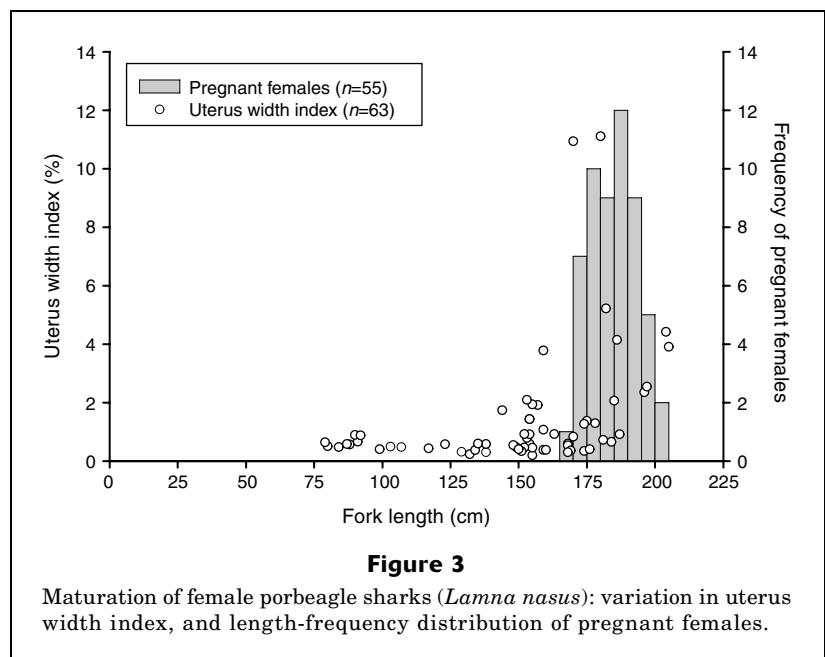


Figure 3

Maturation of female porbeagle sharks (*Lamna nasus*): variation in uterus width index, and length-frequency distribution of pregnant females.

Francis, 2001); no uterus width measurement was available for that shark. The remaining makos over 275 cm were either postpartum or resting. The maximum ovum diameter began increasing in sharks longer than 250 cm (in shorter sharks, ova were barely visible or were invisible) (Fig. 6). The diameter of the oviducal gland increased abruptly between 250 and 270 cm, but ovary dimensions showed no abrupt change in size (Fig. 6).

Median maturity was estimated directly from a sample of 88 females (Table 3). The smallest mature female

Table 2

Sample sizes by 10-cm length class for the assessment of maturity in male porbeagle, mako, and blue sharks.

Length class midpoint (cm)	Porbeagle shark	Shortfin mako shark		Blue shark	
	Spermatophores	Spermatophores	Direct maturity	Spermatozeugmata	Direct maturity
45	0	0	0	0	1
55	0	0	0	0	3
65	0	0	0	0	2
75	2	0	0	0	0
85	15	0	1	1	0
95	4	0	0	2	1
105	0	3	1	2	0
115	2	3	3	0	0
125	8	3	0	1	0
135	23	4	8	1	0
145	28	4	11	3	1
155	30	9	4	6	5
165	17	10	6	13	3
175	18	19	3	4	6
185	6	16	7	20	4
195	4	15	1	21	6
205	1	27	1	18	6
215	0	19	4	15	4
225	0	14	1	12	1
235	0	8	0	20	8
245	0	5	1	26	2
255	0	3	0	19	1
265	0	0	0	11	1
275	0	1	0	6	2
285	0	0	0	2	0
295	0	0	0	1	1
Total	158	163	52	204	58

Table 3

Sample sizes by 10-cm length class for the assessment of maturity in female mako and blue sharks.

Length class midpoint (cm)	Shortfin mako shark	Blue shark	Length class midpoint (cm)	Shortfin mako shark	Blue shark
	Direct maturity	Direct maturity		Direct maturity	Direct maturity
55	0	6	215	10	2
65	0	3	225	10	0
75	0	1	235	6	0
85	0	2	245	9	0
95	0	0	255	4	0
105	0	0	265	3	0
115	2	0	275	1	0
125	2	0	285	2	0
135	2	0	295	3	0
145	10	1	305	1	0
155	6	1	315	0	0
165	3	0	325	3	0
175	1	3	335	2	0
185	3	5	345	1	0
195	0	0	Total	88	26
205	4	2			

was 274 cm and the longest immature female was 300 cm. Median maturity was estimated by probit analysis to be 280.1 cm (CI 267.5–292.9 cm), but sample sizes were very small over the transitional range (Fig 5). The nonoverlap of the CIs between males and females showed that median maturity differs significantly between the sexes.

Blue shark

The relationship between CLI and FL was essentially linear in blue sharks, and no apparent inflections were evident (Fig. 7). The smallest male with spermatozeugmata was 164 cm; 50% of males contained spermatozeugmata by 194 cm, and 100% by about 260 cm.

Samples of male blue sharks examined by us were small (Table 2). Maturation occurred over a wide length range: the smallest mature male was 157 cm and the largest immature male was 237 cm long. The direct estimate of median maturity was correspondingly variable (192.1 cm, CI 178.1–206.3 cm) (Fig. 7).

The UWI increased abruptly above about 170 cm in some sharks, all of which were pregnant (Fig. 8). Other non-pregnant sharks up to about 220 cm FL, which were presumably subadults, had UWIs less than 2%. Pregnant females ranged from 166 to 252 cm (mean 203 cm) (Fig. 8).

Only 26 females were available for direct maturity estimation (Table 3). The smallest recorded mature female was 142 cm, but this seems exceptional; the next smallest was 172 cm. The longest immature female was 185 cm. The number of sharks in the maturation length range was inadequate for determining median maturity (Table 3), although we have shown the probit analysis ogive in Figure 8.

Discussion

Maturity estimates

To be sexually mature, a male shark must be able to produce viable sperm and have the means to deliver them to a female. Similarly, females must be able to produce viable eggs and nourish the developing embryos through to parturition. An assessment of the degree of development of all parts of the reproductive system and the presence or absence of reproductive products is the best way to determine sexual maturity. We used

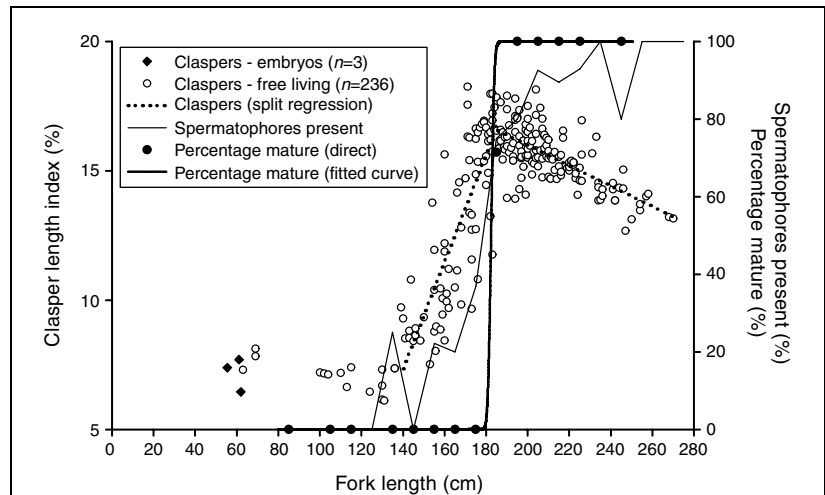


Figure 4

Maturation of male shortfin mako sharks (*Isurus oxyrinchus*): variation in clasper development, presence of spermatophores in the reproductive tract, and direct maturity estimation determined from a suite of maturity indicators.

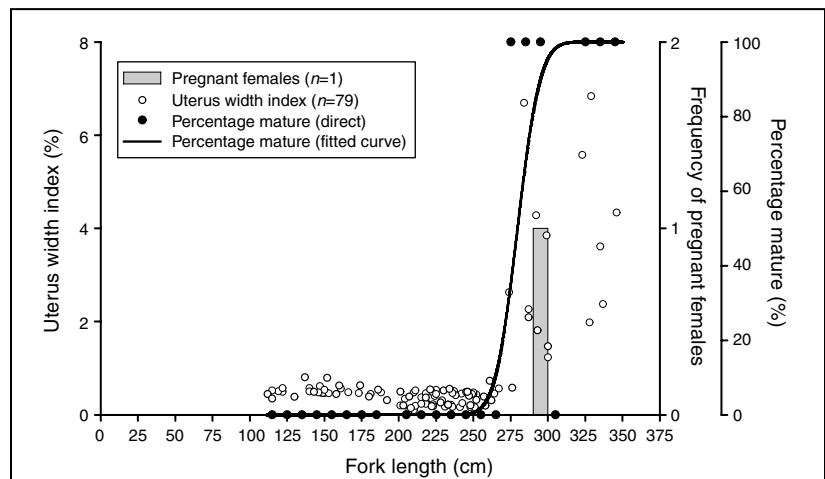


Figure 5

Maturation of female shortfin mako sharks (*Isurus oxyrinchus*): variation in uterus width index, and direct maturity estimation from a suite of maturity indicators. The only pregnant female recorded from New Zealand waters is also indicated.

this approach to score the maturity status of individual sharks and thereby derive direct median maturity estimates. However, the sample sizes available for this approach were sometimes small, and confidence limits ranged from unrealistically low (because of lack of overlap of immature and mature sharks) to high; therefore it was not possible to rely entirely on these estimates.

We supplemented our direct maturity estimates with measurements or assessments (made by observers) of some key components and products of the reproductive

system. The presence or absence of spermatophores or spermatozeugmata is a good indicator of the ability of a male to produce viable sperm, but it is not infallible: such structures sometimes lack viable sperm (Pratt and Tanaka, 1994). Furthermore, male reproductive products may not be present year-round: blue sharks appear to have a seasonal cycle of spermatozeugmata production in the western central Atlantic (Hazin et al., 1994), although Pratt (1979) found no evidence of a cycle in the western North Atlantic. Thus the presence of spermatophores and spermatozeugmata does not

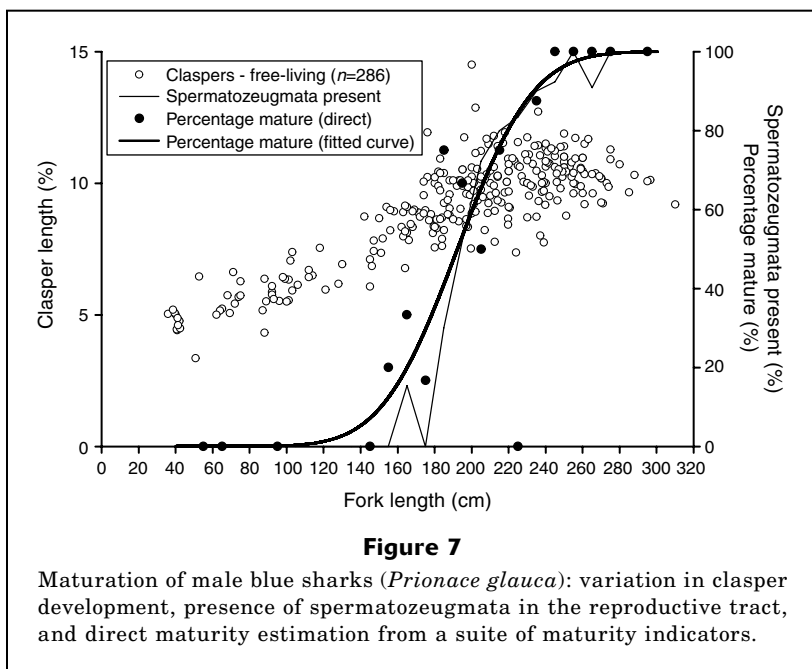
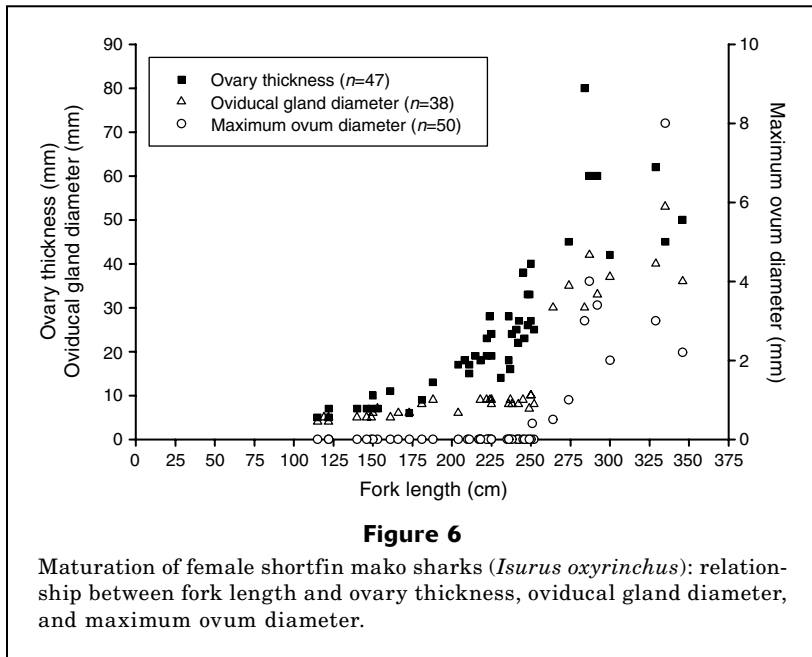
necessarily confirm reproductive viability, and their absence does not confirm immaturity. Similarly, fully calcified claspers that can be rotated, splayed open, and possess an anchoring mechanism may confer an ability to mate, but they do not necessarily confirm an ability to deliver viable products; however the lack of fully developed claspers presumably does prevent successful copulation.

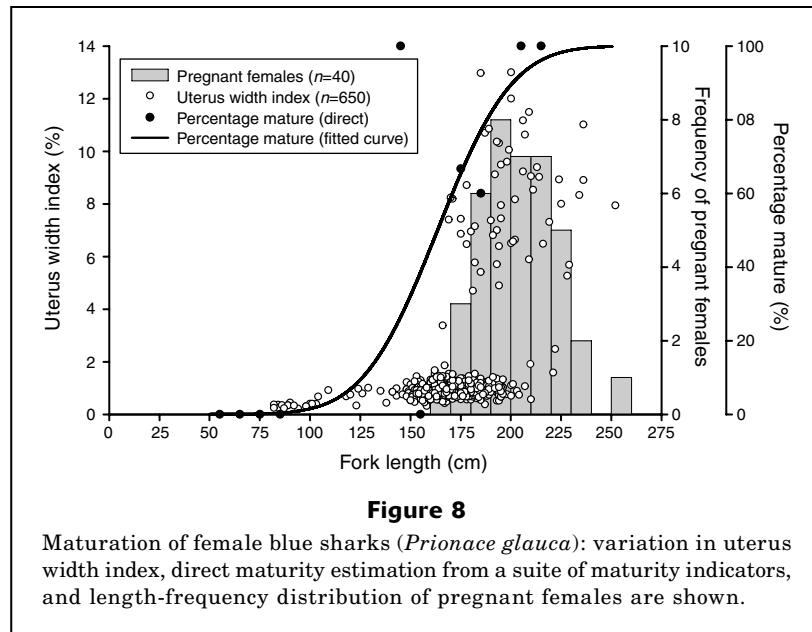
In the present study, either the length at which clasper development was completed in half the male population, or the length at which 50% of males possessed spermatophores or spermatozeugmata, whichever was higher, provided an estimate of the lower bound of the median maturity. The actual median maturity may be higher than this estimate if some males had reproductive products that lacked viable sperm, or if some other feature of the reproductive system (e.g., the siphon system) was insufficiently developed to enable delivery of sperm to the female.

An analogous argument applies to female sharks. Full development of the uterus and oviducal gland, and production of vitellogenic ovarian ova, are all required for successful reproduction. Expansion of the uterus, as measured here by UWI, may not be a sufficient condition by itself. Thus the length at which half the female population had expanded uteri places a lower bound on the median maturity.

The smallest length at which females were pregnant, and the length-frequency distributions of pregnant females, are not by themselves good indicators of median maturity. A better indicator would be the length at which half the females in a population first become pregnant, but this is impossible to determine. Furthermore, pregnancy estimates could be confounded by unrepresentative sampling of a population that may be segregated by reproductive status and by nonparticipation of some females during breeding because they are "resting" between pregnancies. Nevertheless, pregnancy absolutely confirms maturity; therefore it is a useful adjunct to other measures of maturity.

The presence or absence of a hymen has been used in some studies to indicate maturity. However it should not be used for that purpose because adolescent (premature) mating occurs in at least some species of sharks, including blue sharks (Pratt, 1979). Furthermore, the absence of a hymen may not even be a good indicator of mating: we observed



**Table 4**

Summary of length at maturity indicators in porbeagle, shortfin mako, and blue sharks, and estimates of median length at maturity. Table entries are fork lengths in centimeters. Direct maturity estimates were derived by examination of a suite of maturity indicators. Italics indicate estimates based on small sample sizes over the maturation length range. “—” indicates that an estimate was not possible.

Sex	Maturity indicator	Porbeagle shark	Shortfin mako shark	Blue shark
Males	50% with spermatophores	152	178	194
	Rapid clasper elongation complete	143	185	—
	Direct maturity estimate	—	<i>183</i>	192
	Median length at maturity	140–150	180–185	190–195
Females	Rapid expansion of uterus begins	145	275	170
	First females pregnant	167	<i>—</i> ¹	166
	Direct maturity estimate	—	<i>280</i>	—
	Median length at maturity	170–180	275–285	170–190

¹ Only one pregnant female (290 cm FL) has been recorded from New Zealand.

some female shortfin makos in which the membrane was very thin and partially perforated, but had clearly not been damaged by copulation. We believe that the hymen disintegrates naturally with growth in makos; the same possibility was proposed for blue sharks by Pratt (1979).

Using a combination of our direct maturity estimates, and other indicators of maturity based on larger samples of sharks, we generated overall estimates of median maturity for both sexes of the three pelagic sharks (Table 4).

Porbeagle shark

In male porbeagles, the length at which 50% of sharks had spermatophores (152 cm) was longer than the length

at which clasper elongation was complete (143 cm) (Table 4). However the percentage of males having spermatophores did not reach 100% in the longer length groups (Fig. 2), indicating that some mature males were reproductively inactive. This finding is consistent with reports from the western North Atlantic that male porbeagles have a seasonal cycle of spermatophore production, with a minimum in winter–spring (Jensen et al., 2002). If some mature males lacked spermatophores, the length at which 50% of males had spermatophores in our study was probably greater than the median maturity. The lack of a direct maturity estimate limits our ability to estimate the median maturity, but it is likely in the range 140–150 cm.

Similarly, we have no direct estimate of female porbeagle maturity. There was a considerable gap between

the length at which rapid expansion of the uterus began (145 cm) and the length of the smallest pregnant female (167 cm). UWI values less than 2% occurred for females up to about 185 cm (Fig. 3), but this does not mean that a high proportion of females in this length group had narrow uteri; uterus width measurements were not available for most of our pregnant females and therefore large UWI values are underrepresented in Figure 3. Most pregnant females were 170–200 cm long. We estimate that median maturity in females is about 170–180 cm, but this estimate requires confirmation. It is essentially the same as that provided by Francis and Stevens (2000) for New Zealand and Australian porbeagles (their New Zealand data were a smaller subset of the data used in the present study).

Although our estimates of median maturity for both males and females are uncertain, it is clear that porbeagles from New Zealand mature at considerably smaller lengths than they do in the North Atlantic. In the western North Atlantic, males mature at about 166 cm and females at 208 cm (Jensen et al., 2002). Data from the eastern North Atlantic (Gauld, 1989; Ellis and Shackley, 1995) are insufficient to estimate length at maturity, but the pregnant females reported by Gauld (1989) were considerably longer (199–248 cm) than those from New Zealand.

Porbeagles from the North Atlantic also grow larger than those from New Zealand: in the North Atlantic, sharks longer than 200 cm are common (Gauld, 1989; Campana et al., 2001), whereas around New Zealand and Australia they are very rare (Francis et al., 2001; Stevens and Wayte⁴). Differences in length at maturity between the North Atlantic and New Zealand and the proportion of sharks in the longer length classes indicate the existence of separate populations in the two regions—a conclusion that is supported by the disjunct distribution of porbeagles in the Northern and Southern Hemispheres (Compagno, 2001).

Shortfin mako shark

Our direct maturity estimate for male makos (183 cm) was based on a small sample size, and the small overlap between the lengths of immature and mature sharks is implausible. However, the lengths at which clasper development was completed, and at which 50% of males had spermatophores, were similar to the direct estimate (Table 4). Median maturity for males is therefore about 180–185 cm.

Our direct maturity estimate for female makos (280 cm) was based on few sharks over the maturation length range but was consistent with the length at which rapid uterus expansion began (275 cm). Our best estimate of median maturity in females is 275–285 cm.

Stevens (1983) used the degree of clasper calcification and an inflection in clasper length to estimate the length at maturity of males from New South Wales as 176 cm. In South Africa, males were estimated to mature at 177–188 cm (Cliff et al., 1990), but very few immature sharks were available. Our estimate of median maturity in New Zealand males (180–185 cm) is therefore similar to those from elsewhere.

Mollet et al. (2000) reported lengths at maturity for female makos of 298 cm total length in the Northern Hemisphere and 273 cm total length in the Southern Hemisphere. However, some of the 25 cm difference was due to Northern Hemisphere measurements having been taken over the curve of the body and Southern Hemisphere measurements having been taken in a straight line. Using appropriate conversion regressions, their Northern Hemisphere median maturity is equivalent to 267 cm FL, and their Southern Hemisphere median maturity is equivalent to 248 cm FL. When Mollet et al.'s Southern Hemisphere data are analysed separately for two subregions, South Africa and Australia, the estimated lengths at maturity are 244 cm ($n=50$) and 254 cm ($n=32$) respectively (Mollet⁵). The former is consistent with Cliff et al.'s (1990) estimate of 243 cm for South Africa, and the latter is consistent with Stevens's (1983) estimate of 255 cm for eastern Australia (both those estimates were made from subsets of the data used by Mollet et al. [2000]).

Our estimate of median maturity in New Zealand females (275–285 cm) is substantially higher than Mollet's⁵ estimate for Australia (254 cm). Because tagged makos have moved between New Zealand and eastern Australia in both directions (Chan, 2001; Hartill and Davies, 2001; Holdsworth and Saul, 2003), we think it is unlikely that the difference is due to the presence of distinct populations in the two regions. We suspect that the difference is a result of possible length estimation errors (some of the Australian shark lengths were calculated from recorded weights, with a length-weight regression [Stevens, 1983; Mollet et al., 2000]), and the result of small sample sizes over the length range at maturation. For our direct maturity estimate, we had only 19 New Zealand sharks over the length range 240–290 cm, and Mollet⁵ had 15 sharks.

Interestingly, our estimate of median maturity in New Zealand females is also greater than Mollet et al.'s (2000) estimate for the western North Atlantic, thus removing the reported between-hemisphere difference. We believe that larger, accurately measured samples of female makos are required before definitive statements can be made about length at maturity in the various regions.

Blue shark

In male blue sharks from New Zealand, CLI lacked an inflection near the length of maturity—a feature that

⁴ Stevens, J. D., and S. E. Wayte. 1999. A review of Australia's pelagic shark resources. FRDC Proj. Rep. 98/107, 64 p. [Available from CSIRO Marine Research, PO Box 1538, Hobart, Tasmania 7001, Australia.]

⁵ Mollet, H. 2004. Personal commun. Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039.

has also been reported elsewhere (Pratt, 1979; Hazin et al., 1994). Thus clasper length was not useful in estimating length at maturity. Our direct maturity estimate was similar to the length at which 50% of sharks had spermatozeugmata and indicated that median maturity occurs at about 190–195 cm (Table 4).

In females, maturation occurred over a wide length range, as reported elsewhere (Hazin et al., 1994). Taking into account the length distributions of pregnant females and females with low UWI values (Fig. 8), we believe median maturity is likely in the range 170–190 cm.

In other blue shark studies, estimation of the length at maturity has also been hindered by small sample sizes, or even a complete absence of immature or mature sharks. In the western North Atlantic, males mature at about 178 cm, and females at around the same length, although few mature females have been available (Pratt, 1979). In the Gulf of Guinea, Atlantic Ocean, 50% of females were pregnant at 180 cm (Castro and Mejuto, 1995). In Australian studies, a lack of immature sharks made it impossible to estimate maturity adequately (Stevens, 1984; Stevens and McLoughlin, 1991). In the North Pacific Ocean, 50% of males had spermatozeugmata at 166 cm and 50% of females were pregnant at 174 cm (Nakano, 1994). Thus worldwide estimates of maturity in blue sharks are similar to ours from New Zealand, except perhaps for a smaller length at maturity of males in the North Pacific. Unlike females in most species of sharks, female blue sharks do not appear to mature at a length greater than that for mature males.

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Literature cited

- Ayers, D., M. P. Francis, L. H. Griggs, and S. J. Baird.
2004. Fish bycatch in New Zealand tuna longline fisheries, 2000–01 and 2001–02. N.Z. Fish. Assess. Rep. 2004/46, 47 p.
- Campana, S. E., L. Marks, W. Joyce, and S. Harley.
2001. Analytical assessment of the porbeagle shark (*Lamna nasus*) population in the Northwest Atlantic, with estimates of long-term sustainable yield. Can. Sci. Advisory Secretariat Res. Doc. 2001/067, 59 p.
- Castro, J. A., and J. Mejuto.
1995. Reproductive parameters of blue shark, *Prionace glauca*, and other sharks in the Gulf of Guinea. Mar. Freshw. Res. 46:967–973.
- Chan, R. W. K.
2001. Biological studies on sharks caught off the coast of New South Wales. Ph.D. diss., 323 p. Univ. New South Wales, Sydney, New South Wales, Australia.
- Cliff, G., S. F. J. Dudley, and B. Davis.
1990. Sharks caught in the protective gill nets off Natal, South Africa. 3. The shortfin mako shark *Isurus oxyrinchus* (Rafinesque). Sth Afr. J. Mar. Sci. 9:115–126.
- Compagno, L. J. V.
2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO Species Cat. Fishery Purposes 1, vol. 2, 269 p. FAO, Rome.
- Duffy, C., and M. P. Francis.
2001. Evidence of summer parturition in shortfin mako (*Isurus oxyrinchus*) sharks from New Zealand waters. N. Z. J. Mar. Freshw. Res. 35:319–324.
- Ellis, J. R., and S. E. Shackley.
1995. Notes on porbeagle sharks, *Lamna nasus*, from the Bristol Channel. J. Fish Biol. 46:368–370.
- Francis, M. P., L. H. Griggs, and S. J. Baird.
2001. Pelagic shark bycatch in the New Zealand tuna longline fishery. Mar. Freshw. Res. 52:165–178.
- Francis, M. P., and J. D. Stevens.
2000. Reproduction, embryonic development and growth of the porbeagle shark, *Lamna nasus*, in the south-west Pacific Ocean. Fish. Bull. 98:41–63.
- Gauld, J. A.
1989. Records of porbeagles landed in Scotland, with observations on the biology, distribution and exploitation of the species. Scot. Fish. Res. Rep. 45, 16 p.
- Hartill, B., and N. M. Davies.
2001. New Zealand billfish and gamefish tagging, 1999–2000. NIWA Tech. Rep. 106, 29 p.
- Hazin, F. H. V., K. Kihara, K. Otsuka, C. E. Boeckman, and E. C. Leal.
1994. Reproduction of the blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean. Fish. Sci. 60:487–491.
- Holdsworth, J., and P. Saul.
2003. New Zealand billfish and gamefish tagging 2001–02. N.Z. Fish. Assess. Rep. 2003/15, 39 p.
- Jensen, C. F., L. J. Natanson, H. L. Pratt, N. E. Kohler, and S. E. Campana.
2002. The reproductive biology of the porbeagle shark, *Lamna nasus*, in the western North Atlantic Ocean. Fish. Bull. 100:727–738.
- Kohler, N. E., J. G. Casey, and P. A. Turner.
1995. Length-weight relationships for 13 species of sharks from the western North Atlantic. Fish. Bull. 93:412–418.
- Kováč, V., G. H. Copp, and M. P. Francis.
1999. Morphometry of the stone loach, *Barbatula barbatula*: do mensural characters reflect the species' life history thresholds? Environ. Biol. Fish. 56:105–115.
- Mollet, H. F., G. Cliff, H. L. Pratt, and J. D. Stevens.
2000. Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. Fish. Bull. 98:299–318.
- Nakano, H.
1994. Age, reproduction and migration of blue shark in the North Pacific Ocean. Bull. Nat. Res. Inst. Far Seas Fish. 31:141–256.
- Natanson, L. J., J. J. Mello, and S. E. Campana.
2002. Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. Fish. Bull. 100:266–278.

- Pearson, E. S., and H. O. Hartley.
1962. Biometrika tables for statisticians. Vol. 1, 2nd ed., 240 p. Cambridge Univ. Press, Cambridge, UK.
- Pratt, H. L.
1979. Reproduction in the blue shark, *Prionace glauca*. Fish. Bull. 77:445-470.
- Pratt, H. L., and S. Tanaka.
1994. Sperm storage in male elasmobranchs: a description and survey. J. Morph. 219:297-308.
- Smith, S. E., D. W. Au, and C. Show.
1998. Intrinsic rebound potentials of 26 species of Pacific sharks. Mar. Freshw. Res. 49:663-678.
- Stevens, J. D.
1983. Observations on reproduction in the shortfin mako *Isurus oxyrinchus*. Copeia 1983:126-130.
1984. Biological observations on sharks caught by sport fishermen off New South Wales. Aust. J. Mar. Freshw. Res. 35:573-590.
- Stevens, J. D., and K. J. McLoughlin.
1991. Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. Aust. J. Mar. Freshw. Res. 42:151-199.