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Chapter 9

The Biology and Ecology of the Porbeagle Shark, *Lamna nasus*

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Abstract

Information on the biology, ecology, and fisheries of porbeagle sharks (*Lamna nasus*) is reviewed to assess biological and population parameters that are relevant to stock assessment, and to identify gaps in our knowledge. Separate porbeagle stocks occur in the Northwest and Northeast Atlantic, but stock identity is poorly understood in the Southern Hemisphere. Porbeagles are born at 58–67 cm fork length (FL). Length at maturity is lower for Southwest Pacific males and females (about 140–150 and 170–180 cm FL, respectively) than for North Atlantic males and females (166 and 208 cm FL). Ages at 50% maturity for North Atlantic males and females are 8 and 13 years, respectively. Porbeagles recruit to commercial fisheries in both hemispheres during their first year. North Atlantic males and females reach at least 253 and 302 cm FL, respectively, and longevity exceeds 26 years. Age at maturity and longevity in the Southwest Pacific are unknown. Growth is almost linear, and similar for both sexes, for about 8 years, after which females grow faster. The rate of natural mortality for the Northwest Atlantic is 0.10 for immature sharks, rising to 0.15–0.20 for mature sharks. The gestation period is 8–9 months and the length of the female reproductive cycle may be about 1 year. Mean litter size is 3.7–4.0 embryos, and the embryonic sex ratio is 1:1. Porbeagle sharks are vulnerable to overfishing. Directed fisheries in the Northwest Atlantic are now restricted by catch quotas, but stock biomass declined to about 10–20% of virgin biomass before restrictive quotas were introduced. In the Southern Hemisphere, porbeagles are taken mainly as bycatch in tuna longline fisheries; no biomass estimates or stock assessments are available. The low productivity of porbeagles and their history of overfishing indicate that sustainable yields will be low.

Key words: porbeagle, *Lamna nasus*, Lamnidae, growth, maturity, longevity, mortality, reproduction, stock status.

Introduction

Porbeagles (*Lamna nasus*, Lamnidae) are thermoregulating sharks that inhabit temperate, subarctic, and subantarctic waters. They live mainly in the open ocean and over continental shelves, but also enter coastal waters. Porbeagles have proven to be vulnerable to overfishing in the Northwest Atlantic: A target longline fishery in the 1960s lasted only 6 years before collapsing. This fishery was revived by Canadian and US vessels in the 1990s, but catch levels during the last decade appear to be unsustainable (Campana *et al.*, 2002a, 2008). In the Southern Hemisphere, porbeagles have not been targeted, but they are frequently taken as bycatch in tuna longline fisheries (Francis *et al.*, 2001; Ayers *et al.*, 2004). The history of the Northwest Atlantic fishery demonstrates a need for cautious, assessment-based management of porbeagles.

Until recently, information on the biology of porbeagles was sparse. Aasen (1961, 1963) conducted pioneering studies on porbeagle biology in the Northwest Atlantic, but there was little increase in knowledge until dedicated studies were made in the North Atlantic and Southwest Pacific Oceans beginning in the late 1980s (Gauld, 1989; Francis and Stevens, 2000; Francis *et al.*, 2001; Campana *et al.*, 2002a, b; Jensen *et al.*, 2002; Joyce *et al.*, 2002; Natanson *et al.*, 2002; Francis and Duffy, 2005).

This chapter reviews the available biological and fishery information on porbeagles, presents the best available estimates of biological and population parameters that are relevant to stock assessment, and identifies data gaps that need to be addressed before detailed assessment is possible.

Distribution, movements, and stock structure

Porbeagles live mainly in the latitudinal bands 30–50°S and 30–70°N (Last and Stevens, 1994; Yatsu, 1995; Francis and Stevens, 2000). They occur in the North Atlantic Ocean and in a circumglobal band in the Southern Hemisphere. Porbeagles are absent from the North Pacific Ocean, where they are replaced by the closely related salmon shark (*Lamna ditropis*, Lamnidae).

In the South Pacific Ocean, porbeagles are caught north of 30°S only in winter–spring; in summer they are not found north of about 35°S (Yatsu, 1995). Off the east coast of Australia, porbeagles enter subtropical waters (to 23°44′S) in winter. They appear to penetrate farther south during summer and autumn (Yatsu, 1995), and are found near many of the subantarctic islands in the Indian and Southwest Pacific Oceans (Francis and Stevens, 2000). The temperature range inhabited by porbeagles in the Southern Hemisphere is about 1–23°C, with abundance declining above about 19°C (Svetlov, 1978; Stevens *et al.*, 1983; Yatsu, 1995; Francis and Stevens, 2000). Most Northwest Atlantic porbeagles are caught at temperatures between −1°C and 15°C, with a mean of 7–8°C at the depth of the fishing gear (Campana and Joyce, 2004).

In the North Atlantic, porbeagle abundance varies seasonally and spatially (Aasen, 1961, 1963; Templeman, 1963; Mejuto and Garcés, 1984; Mejuto, 1985; Gauld, 1989). Off North America, porbeagles move north along the coast in spring and early summer and spend late summer and fall at about 46–48°N; the return migration occurs in the late fall (Campana *et al.*, 1999).

In the Northwest Atlantic, several studies found that most tagged sharks move short to moderate distances (up to 1,500 km) along continental shelves, though one moved about 1,800 km off the shelf into the mid-Atlantic Ocean (Kohler *et al.*, 1998; O'Boyle *et al.*, 1998; Campana *et al.*, 1999). Sharks tagged off southern England were mainly recaptured between Denmark and France, with one shark moving 2,370 km to northern Norway (Stevens, 1976, 1990). Only one tagged shark has crossed the Atlantic: It traveled 4,260 km from southwest Ireland to 52°W off eastern Canada (Kohler and Turner, 2001; P. Green, personal communication). Thus porbeagles from the Northwest and Northeast Atlantic appear to form two distinct stocks (Campana *et al.*, 1999). Stock structure in the Southern Hemisphere is unknown, but if movements are similar in scale to those in the North Atlantic, there would be several stocks.

There have been no genetic studies to determine the number of porbeagle stocks, but based on the disjunct (antitropical) geographic distribution, North Atlantic porbeagles are probably reproductively isolated from Southern Hemisphere porbeagles.

Biology and ecology

Length–length and length–weight relationships

In this chapter, we use straight-line fork length (FL) for all measurements except where otherwise stated. Literature reports based on other measurement methods (mainly FL measured over the body and total length, TL) were converted to straight-line FL. Length–length and length–weight relationships are given in Table 9.1. Other length–length regressions were provided by Aasen (1963) and Campana *et al.* (1999). Gauld (1989) found significant differences in weight between males and females longer than 180 cm. Other length–weight relationships based on smaller sample sizes have been published for the North Atlantic (Aasen, 1961; Mejuto and Garcés, 1984; Stevens, 1990; Ellis and Shackley, 1995; Kohler *et al.*, 1995).

Length at birth and maturity

The length at birth is 58–67 cm in the Southwest Pacific (Francis and Stevens, 2000) and is probably similar in the North Atlantic (Gauld, 1989; Jensen *et al.*, 2002).

In the Northwest Atlantic, females mature at 200–219 cm, and 50% are mature by 208 cm (Jensen *et al.*, 2002). Males mature at 155–177 cm, and the length at 50% maturity is 166 cm (Jensen *et al.*, 2002). Off New Zealand, males mature at about 140–150 cm and females at 170–180 cm (Francis and Duffy, 2005). Thus both sexes mature at substantially smaller lengths in the Southwest Pacific than in the Northwest Atlantic.

Growth, maturity, and recruitment

Age and growth have been comprehensively studied in the Northwest Atlantic, and age estimation has been validated up to 26 years (Campana *et al.*, 2002b; Natanson *et al.*, 2002). Growth in both sexes is similar up to the age of maturity, whereupon growth slows. Because females mature later than males, the growth curves diverge (Table 9.1). Males mature at 6–10 years, with 50% mature at 8 years, and females mature at 12–16 years,

Table 9.1 Summary of porbeagle biological parameters.*

Parameter	Southwest Pacific Ocean		North Atlantic Ocean	
	Value	Source	Value	Source
Stock structure	?		NW Atlantic, NE Atlantic	4
Length–length relationships (cm)	FL = −0.567 + 0.881 TL	1	CFL = 0.99 + 0.885 CTL	4
	TL = 4.165 + 1.098 FL		CTL = 1.12 CFL	
	PL = −1.366 + 0.907 FL		CPL = −1.36 + 0.89 CFL	
	FL = 1.990 + 1.098 PL		CFL = 1.7 + 1.12 CPL	
			FL = 0.90 + 0.95 CFL	9
Length–weight relationship (kg, cm)	F + M: $W = 8.91 \times 10^{-6}\ FL^{3.128}$	1	F + M: $W = 5 \times 10^{-5}\ CFL^{2.713}$	4
	(juveniles < 150 cm)		F: $W = 3 \times 10^{-4}\ TL^{2.357}$	5
			M: $W = 1.9 \times 10^{-3}\ TL^{2.008}$	5
Length at birth (cm)	58–67 FL	1, 2	Similar to SW Pacific	1, 6
Length at maturity (cm)	F: 170–180 FL	3	F: 200–219 FL; 50% 208 FL	6
	M: 140–150 FL		M: 155–177 FL; 50% 166 FL	6
Growth	NZ: FL = 66.5 + 19.8 age	1	F + M: $CFL = 289.4(1-e^{-0.066(t+6.06)})$	7
	Australia: FL = 65.4 + 16.1 age		F: $CFL = 309.8(1-e^{-0.061(t+5.90)})$	
	(juveniles < 150 cm)		M: $CFL = 257.7(1-e^{-0.080(t+5.78)})$	
Median age at maturity (year)	F: ?		F: 13	6, 7
	M: ?		M: 8	6, 7
Age at recruitment (year)	0–1	1	0–1	8
Maximum length (cm)	F: 208 FL	1, 2	F: 278 FL; M: 253 FL	5
	M: 204 FL		F: 302 FL; M: 250 FL	9
Longevity (years)	?		>26	10
Natural mortality ($year^{-1}$)	?		0.10–0.20	4, 8
Gestation period (months)	8–9	1, 2	8–9	1, 6
Reproductive cycle (year)	≥1	1	1?	1, 6
Mean litter size	3.75	1, 2	3.7–4.0	5, 6
Annual fecundity	≤3.75	1, 2	~3.7–4.0?	5, 6
Embryonic sex ratio	F = M	1, 2	F = M	6

*?: unknown; FL: fork length; TL: total length; PL: precaudal length; CFL: curved fork length (over the curve of the body); CTL: curved total length; CPL: curved precaudal length; W: weight; M: males; F: females.

Sources: 1: Francis and Stevens (2000); 2: M. P. Francis, unpublished data; 3: Francis and Duffy (2005); 4: Campana *et al.* (1999); 5: Gauld (1989); 6: Jensen *et al.* (2002); 7: Natanson *et al.* (2002); 8: Campana *et al.* (2001); 9: S. E. Campana, unpublished data; 10: Campana *et al.* (2002a).

with 50% mature by 13 years (Jensen *et al.*, 2002; Natanson *et al.*, 2002). In the Southwest Pacific, juveniles grow 16–20 cm/year for 4–5 years and reach 110–125 cm after 3 years (Francis and Stevens, 2000). Porbeagles recruit to commercial fisheries during their first year, and much of the commercial catch is immature (Campana *et al.*, 2001; Francis *et al.*, 2001; Ayers *et al.*, 2004).

Maximum length, longevity, and natural mortality

Lengths of 253 and 278 cm for males and females, respectively, are the largest reliable measurements from the Northeast Atlantic (Gauld, 1989). In the Northwest Atlantic, the greatest known lengths are 250 cm (males) and 302 cm (females) (S. E. Campana, unpublished data). Thus females grow larger than males, and the maximum reported length is 302 cm (=335 cm TL).

In the Southwest Pacific, the largest male and female porbeagles recorded were 236 and 208 cm, respectively (Francis and Stevens, 2000; Ayers *et al.*, 2004; M. Francis, unpublished data). However, only four males exceeding 204 cm have been recorded in the region and they were 220–236 cm long, so these outliers may have been incorrectly measured or identified. If so, the maximum known lengths for males and females are 204 and 208 cm, respectively. Thus Southwest Pacific porbeagles appear to reach considerably smaller maximum lengths than North Atlantic porbeagles, and there is little difference between the sexes.

The greatest known age is 26 years for a 251-cm porbeagle (Campana *et al.*, 2002a), but this likely underestimates longevity because the population had been fished. Indirect methods based on the von Bertalanffy growth curve and estimates of natural mortality indicate they may live for more than 40 years (Natanson *et al.*, 2002). The natural mortality rate has been estimated as 0.10 for immature porbeagles of both sexes, rising to 0.15 for mature males and about 0.20 for mature females (Campana *et al.*, 1999, 2001).

Length, age, and sex composition

Porbeagles appear to segregate by size and sex. Off Spain, twice as many males as females are caught (Mejuto, 1985), whereas 30% more females are caught off Scotland (Gauld, 1989). In the Bristol Channel, United Kingdom, the size composition is skewed toward smaller, presumably immature individuals and the population is dominated by males (Ellis and Shackley, 1995). In the Northwest Atlantic there is a marked segregation by sex in individual catches, but the overall sex ratio is balanced (Aasen, 1963; O'Boyle *et al.*, 1998). There is a strong seasonal shift in size composition: Spring catches are dominated by small, immature sharks, while the fall fishery farther to the north takes mainly larger, mature sharks (Campana *et al.*, 1999).

In the Southwest Pacific, catches are dominated by immature sharks (Francis *et al.*, 2001; Ayers *et al.*, 2004). The size and sex distributions of both sexes are comparable up to about 150 cm, but larger individuals are predominantly male; few mature females are caught. Regional differences in length composition suggest segregation by size (Francis and Stevens, 2000).

Reproduction

Porbeagles are aplacental viviparous and oophagous (Francis and Stevens, 2000; Jensen *et al.*, 2002). The embryonic growth rate is 8 cm per month, and the gestation period is about 8–9 months, though the high variability and uneven temporal distribution of the data mean that the latter estimate is uncertain (Francis and Stevens, 2000; Jensen *et al.*, 2002). In the Northwest Atlantic, all females sampled in winter were pregnant, suggesting that there is no extended resting period between pregnancies, and that the female reproductive cycle lasts for 1 year (Jensen *et al.*, 2002).

Litter size is usually four embryos, but ranges from one to five (Bigelow and Schroeder, 1948; Gauld, 1989; Francis and Stevens, 2000; Jensen *et al.*, 2002). Mean litter sizes in the Southwest Pacific, Northeast Atlantic, and Northwest Atlantic were 3.75, 3.70, and 4.0, respectively (Gauld, 1989; Francis and Stevens, 2000; Jensen *et al.*, 2002; M. P. Francis, unpublished data). If the reproductive cycle lasts for 1 year, annual fecundity would be about 3.7–4.0 young per female. The sex ratio of embryos is not significantly different from one (Francis and Stevens, 2000; Jensen *et al.*, 2002).

Diet

Porbeagles are active predators of fish and cephalopods (Gauld, 1989; Ellis and Shackley, 1995). In the Northwest Atlantic, pelagic fish and squid dominate the diet in deep water, and pelagic and demersal fish are consumed in shallow water (Joyce *et al.*, 2002). Gastropods, crabs, and debris have also been observed in stomachs.

Threats and status

Fisheries

Porbeagles have been fished since at least the 1920s to supply markets with fresh and dried flesh, oil, fish meal, and fins. Global catches peaked at more than 9,000 metric tons (t) in the 1960s, declining to 1,300–2,600 t in the 1990s as both sides of the Atlantic became overfished (Myklevoll, 1989; O'Boyle *et al.*, 1998; Campana *et al.*, 1999, 2001, 2008). Porbeagles are taken in the Atlantic primarily by a directed pelagic longline fishery, although there is some bycatch from bottom trawls, handlines, and gill nets (Gauld, 1989; Myklevoll, 1989; Campana *et al.*, 1999). In contrast, most of the catch in the Southern Hemisphere is bycatch from tuna longline fleets operating in the South Pacific and southern Indian Oceans (Francis *et al.*, 2001; Ayers *et al.*, 2004; J. D. Stevens, personal communication).

Management restrictions on porbeagle catches vary depending on the area and regulating country. Total catches by the European Union in the Northeast Atlantic are now regulated, and strict quotas have been implemented in the Northwest Atlantic. In addition, the mating aggregations in the Canadian portion of the Northwest Atlantic have been protected by a time and area closure. Catch quotas were introduced in New Zealand in 2004, and there is a general finning ban in Australia. There is a recreational fishery for porbeagles on both sides of the North Atlantic, but catches are small. The US recreational fishery is regulated by a bag limit.

Stock status

With the exception of the Northwest Atlantic stock, little is known about stock status. Myklevoll (1989) reported that directed catch rates by the Norwegian fleet in European waters were poor after 1960, prompting the shift of the fishery to the then-unexploited population in the Northwest Atlantic. No trends in abundance were noted in Scottish waters, although Gauld (1989) concluded that only a small portion of the stock area was fished by Scottish vessels. Reported catches from the Northeast Atlantic were low in the 1990s compared to earlier years (Campana *et al.*, 1999, 2001, 2008), suggesting that relative abundance was low.

In the Northwest Atlantic, stock status has been assessed using annual trends in length composition, total mortality, and commercial catch per unit effort (CPUE), and Petersen analysis of tag recaptures (Campana *et al.*, 1999, 2001, 2002a). The median length of sharks in the offshore commercial fishery has declined from more than 200 cm to about 140 cm since 1960. By 2000, the standardized CPUE of mature porbeagles had declined to 10% of its 1992 level. Three independent measures of fishing mortality were all above a level that would maintain the stock size at current levels, or allow it to recover. The 2000 biomass was 10–20% of estimated virgin biomass. In 2002 the Canadian quota was reduced to 25% of recent quotas in an attempt to make the catch sustainable. In 1999, the United States separated porbeagles from the general pelagic shark quota in an effort to manage this species independently.

In the South Pacific, the likelihood of unreported landings, the absence of adequate CPUE data, and the presumably large geographic range of the stock complicate any attempt at assessing population status (Francis *et al.*, 2001; Ayers *et al.*, 2004). Unstandardized CPUE indices from 1993 are available for New Zealand waters, but the relative rarity of mature individuals in the catch suggests that they are not reliable measures of overall stock abundance (Ayers *et al.*, 2004).

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References

Aasen, O. (1961) *Some Observations on the Biology of the Porbeagle Shark* (*Lamna nasus* L.). ICES C.M. 1961: 109. International Council for the Exploration of the Sea, Copenhagen, Denmark, 7 pp.

Aasen, O. (1963) Length and growth of the porbeagle (*Lamna nasus*, Bonnaterre) in the North West Atlantic. *Fiskerdirektoratets Skrifter, Serie Havundersøkelser* **13**(6), 20–37.

Ayers, D., Francis, M. P., Griggs, L. H. and Baird, S. J. (2004) *Fish Bycatch in New Zealand Tuna Longline Fisheries, 2000–01 and 2001–02*. New Zealand Fisheries Assessment Report No. 2004/46. Ministry of Fisheries, Wellington, New Zealand, 47 pp.

Bigelow, H. B. and Schroeder, W. C. (1948) Sharks. In: *Fishes of the Western North Atlantic. Part 1. Lancelets, Cyclostomes, Sharks* (eds. A. E. Parr and Y. H. Olsen). Sears Foundation for Marine Research, New Haven, CT, pp. 59–546.

Campana, S. E. and Joyce, W. N. (2004) Temperature and depth associations of porbeagle shark (*Lamna nasus*) in the Northwest Atlantic. *Fisheries Oceanography* **13**, 52–64.

Campana, S. E., Marks, L., Joyce, W., Hurley, P., Showell, M. and Kulka, D. (1999) *An Analytical Assessment of the Porbeagle Shark (Lamna nasus) Population in the Northwest Atlantic*. Document No. 99/158. Canadian Science Advisory Secretariat, Fisheries and Oceans, Ottawa, Ontario, Canada, 57 pp.

Campana, S. E., Marks, L., Joyce, W. and Harley, S. (2001) *Analytical Assessment of the Porbeagle Shark (Lamna nasus) Population in the Northwest Atlantic, with Estimates of Long-Term Sustainable Yield*. Document No. 2001/067. Canadian Science Advisory Secretariat, Fisheries and Oceans, Ottawa, Ontario, Canada, 59 pp.

Campana, S. E., Joyce, W., Marks, L., Natanson, L. J., Kohler, N. E., Jensen, C. F., Mello, J. J., Pratt, H. L. and Myklevoll, S. (2002a) Population dynamics of the porbeagle in the Northwest Atlantic Ocean. *North American Journal of Fisheries Management* **22**, 106–121.

Campana, S. E., Natanson, L. J. and Myklevoll, S. (2002b) Bomb dating and age determination of large pelagic sharks. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 450–455.

Campana, S. E., Joyce, W., Marks, L., Hurley, P., Natanson, L. J., Kohler, N. E., Jensen, C. F., Mello, J. J., Pratt Jr., H. L., Myklevoll, S. and Harley, S. (2008) The rise and fall (again) of the porbeagle shark population in the Northwest Atlantic. In: *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (eds. M. D. Camhi, E. K. Pikitch and E. A. Babcock). Blackwell Publishing, Oxford, UK.

Ellis, J. R. and Shackley, S. E. (1995) Notes on porbeagle sharks, *Lamna nasus*, from the Bristol Channel. *Journal of Fish Biology* **46**, 368–370.

Francis, M. P. and Duffy, C. (2005) Length at maturity in three pelagic sharks (*Lamna nasus*, *Isurus oxyrinchus*, and *Prionace glauca*) from New Zealand. *Fishery Bulletin* **103**, 489–500.

Francis, M. P. and Stevens, J. D. (2000) Reproduction, embryonic development and growth of the porbeagle shark, *Lamna nasus*, in the South-west Pacific Ocean. *Fishery Bulletin* **98**, 41–63.

Francis, M. P., Griggs, L. H. and Baird, S. J. (2001) Pelagic shark bycatch in the New Zealand tuna longline fishery. *Marine and Freshwater Research* **52**, 165–178.

Gauld, J. A. (1989) *Records of Porbeagles Landed in Scotland, with Observations on the Biology, Distribution and Exploitation of the Species*. Report No. 45. Fisheries Research Services, Aberdeen, Scotland, 15 pp.

Jensen, C. F., Natanson, L. J., Pratt, H. L., Kohler, N. E. and Campana, S. E. (2002) The reproductive biology of the porbeagle shark, *Lamna nasus*, in the western North Atlantic Ocean. *Fishery Bulletin* **100**, 727–738.

Joyce, W., Campana, S. E., Natanson, L. J., Kohler, N. E., Pratt, H. L. and Jensen, C. F. (2002) Analysis of stomach contents of the porbeagle shark in the Northwest Atlantic Ocean. *ICES Journal of Marine Science* **59**, 1263–1269.

Kohler, N. E. and Turner, P. A. (2001) Shark tagging: A review of conventional methods and studies. *Environmental Biology of Fishes* **60**, 191–223.

Kohler, N. E., Casey, J. G. and Turner, P. A. (1995) Length–weight relationships for 13 species of sharks from the western North Atlantic. *Fishery Bulletin* **93**, 412–418.

Kohler, N. E., Casey, J. G. and Turner, P. A. (1998) NMFS Cooperative Shark Tagging Program, 1962–93: An atlas of shark tag and recapture data. *Marine Fisheries Review* **60**(2), 1–87.

Last, P. R. and Stevens, J. D. (1994) *Sharks and Rays of Australia*. CSIRO, Collingwood, Victoria, Australia.

Mejuto, J. (1985) *Associated Catches of Sharks, Prionace glauca, Isurus oxyrinchus, and Lamna nasus, with NW and N Spanish Swordfish Fishery, in 1984*. ICES C.M. 1985: H42. International Council for the Exploration of the Sea, Copenhagen, Denmark, 16 pp.

Mejuto, J. and Garcés, A. G. (1984) *Shortfin Mako, Isurus oxyrinchus, and Porbeagle, Lamna nasus, Associated with Longline Swordfish Fishery in NW and N Spain*. ICES C.M. 1984: G72. International Council for the Exploration of the Sea, Copenhagen, Denmark, 9 pp.

Myklevoll, S. (1989) *Norway's Porbeagle Fishery*. ICES C.M. 1989: H. International Council for the Exploration of the Sea, Copenhagen, Denmark, 16 pp.

Natanson, L. J., Mello, J. J. and Campana, S. E. (2002) Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. *Fishery Bulletin* **100**, 266–278.

O'Boyle, R. N., Fowler, G. M., Hurley, P. C. F., Joyce, W. and Showell, M. A. (1998) *Update on the Status of NAFO SA 3-6 Porbeagle Shark (Lamna nasus)*. Document No. 98/41. Canadian Science Advisory Secretariat, Fisheries and Oceans, Ottawa, Ontario, Canada, 58 pp.

Stevens, J. D. (1976) First results of shark tagging in the North-east Atlantic, 1972–1975. *Journal of the Marine Biological Association of the United Kingdom* **56**, 929–937.

Stevens, J. D. (1990) Further results from a tagging study of pelagic sharks in the North-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **70**, 707–720.

Stevens, J. D., Dunning, M. C. and Machida, S. (1983) Occurrences of the porbeagle shark, *Lamna nasus*, in the Tasman Sea. *Japanese Journal of Ichthyology* **30**, 301–307.

Svetlov, M. F. (1978) The porbeagle, *Lamna nasus*, in Antarctic waters. *Journal of Ichthyology* **18**, 850–851.

Templeman, W. (1963) *Distribution of Sharks in the Canadian Atlantic (with Special Reference to Newfoundland Waters)*. Bulletin No. 140. Fisheries Research Board of Canada, Ottawa, Ontario, Canada, 77 pp.

Yatsu, A. (1995) *Zoogeography of the Epipelagic Fishes in the South Pacific Ocean and the Pacific Sector of the Subantarctic, with Special Reference to the Ecological Role of Slender Tuna, Allothunnus fallai*. Bulletin No. 32. National Research Institute of Far Seas Fisheries, Shimizu, Japan, 145 pp.