RAPID COMMUNICATION / COMMUNICATION RAPIDE

Subtropical pupping ground for a cold-water shark

Steven E. Campana, Warren Joyce, and Mark Fowler

Abstract: Porbeagle sharks (*Lamna nasus*) are large pelagic sharks apparently restricted to the cold temperate waters of the northern and southern hemispheres. Despite considerable knowledge of their biology, their pupping (birthing) grounds have never been identified. Pop-up archival transmission tags applied to 21 sharks off eastern Canada indicated that males and immature sharks of both sexes remained primarily on the continental shelf for periods of up to 348 days after tagging. However, mature female porbeagles migrated up to 2356 km through the winter, at depths down to 1360 m beneath the Gulf Stream, to a subtropical pupping ground in the Sargasso Sea. In addition to this pupping ground being well south of their documented range, the placement of such a key life history stage in international, largely unregulated waters poses problems for the conservation and management of a species that is largely fished in Canadian waters.

Résumé : Les maraîches (*Lamna nasus*) sont de grands requins pélagiques apparemment restreints aux eaux tempérées froides des hémisphères nord et sud. Bien que leur biologie soit bien connue, leurs sites de mise bas n'ont jamais été identifiés. Des étiquettes enregistreuses émettrices à déploiement automatique fixées à 21 requins au large de la côte est du Canada indiquent que les requins mâles et les immatures de deux sexes demeurent principalement sur la plateau continental pour des périodes pouvant atteindre 348 jours après le marquage. Cependant, les maraîches femelles matures migrent sur des distances de jusqu'à 2356 km au cours de l'hiver à des profondeurs atteignant 1360 m sous le Gulf Stream jusqu'à un site subtropical de mise bas dans la mer des Sargasses. En plus d'être nettement au sud de l'aire de répartition connue, la position du site de mise bas, une étape essentielle du cycle biologique, dans des eaux en grande partie non règlementées pose des problèmes pour la conservation de cette espèce qui est surtout pêchée dans les eaux canadiennes.

[Traduit par la Rédaction]

Introduction

Porbeagle sharks (*Lamna nasus*) are large pelagic sharks apparently restricted to the cold temperate waters of the northern and southern hemispheres (Francis et al. 2008). The population abundance in the Northwest Atlantic is at a stable but depleted level and is largely confined to the continental shelf of eastern Canada and the northeastern US (Campana et al. 2002). Experimental pelagic longline fishing in the 1960s, during a period when the population abundance was high, demonstrated that the species range extended as far south as latitude 37°N, but that most of the population was concentrated in Canadian waters north of latitude 41°N (Cassoff et al. 2007). All life history stages, from young-of-the-year to sexually mature adults, are most abundant on or near the continental shelf, despite the presence of some individuals in international waters to the east (Campana et al. 2010). Summer–fall mating grounds have been documented on the continental shelf south of Newfoundland (Jensen et al. 2002) and on Georges Bank (Campana et al. 2010). However, the pupping (birthing) grounds have never been identified. Here we report a seasonal 2000 km migration of mature female porbeagles from eastern Canada, at depths down to 1360 m beneath the Gulf Stream, to a pupping ground in the Sargasso Sea, well south of their previously known distribution.

Materials and methods

Porbeagle sharks were captured with pelagic longlines onboard commercial shark fishing vessels and then tagged with pop-up archival transmission tags (PATs) (2001–2002, model PTT-100, Microwave Telemetry, Inc., Columbia, Maryland; 2005–2008, model 4 (2005) and model Mk-10 (2006–2008), Wildlife Computers, Redmond, Washington). Tagged sharks were on deck for 5–10 min for tagging and measurement and showed no obvious stress above and beyond that of capture. PATs were attached to porbeagles by darting a nylon umbrella tip about 8 cm into the dorsal musculature of the shark just lateral to the posterior end of the first dorsal fin. The angle of dart insertion was such that the tip engaged the pterygiophores immediately underneath the dorsal fin, thus reducing the possibility of premature release. The umbrella tip was attached to the PAT with a monofilament leader of 400-pound test, sheathed to reduce trauma to the shark near the point of insertion. Each PAT was also fit-

Received 16 November 2009. Accepted 1 March 2010. Published on the NRC Research Press Web site at cjfas.nrc.ca on 30 March 2010. J21521

S.E. Campana,[1] W. Joyce, and M. Fowler. Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.

[1]Corresponding author (e-mail: steven.campana@dfo-mpo.gc.ca).

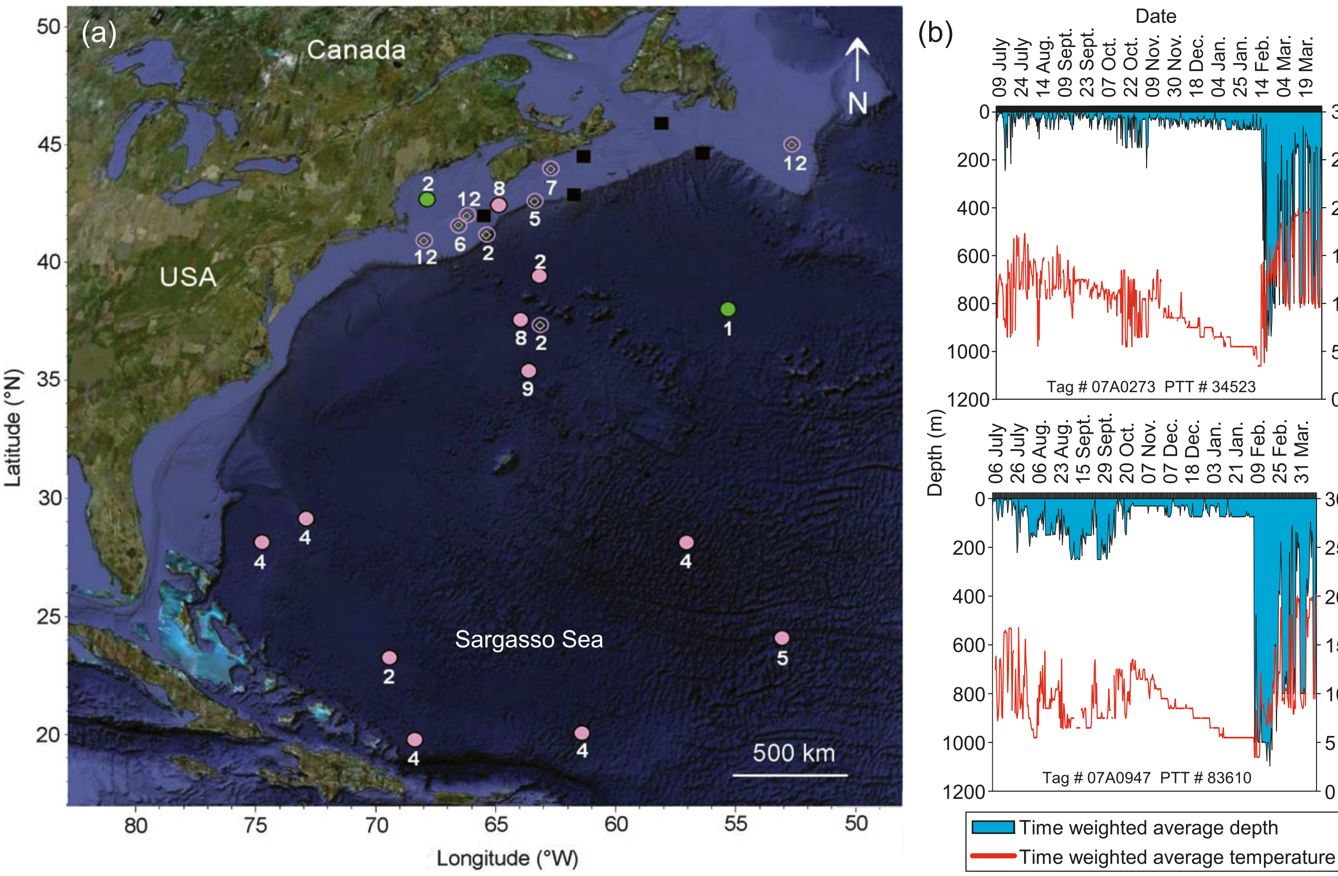
Table 1. Tag and release data from porbeagles with pop-up archival transmission tags (PTTs).

Argos PTT No.	Date deployed	FL (cm)	Sex	Release lat. (N)	Release long. (W)	Pop-up date	Pop-up lat. (N)	Pop-up long. (W)	Days at liberty	Distance travelled (km)
13701	8 May 2001	130	Female	43°54′	62°52′	23 July 2001	44°07′	63°03′	76	28
13702	5 June 2002	145	Female	44°01′	62°52′	21 June 2002	41°40′	67°29′	16	460
13702	27 April 2005	150	Female	42°45′	62°42′	16 May 2005	42°44′	63°49′	19	91
66396	24 July 2007	220	Female	42°06′	66°50′	20 August 2007	37°57′	64°20′	27	507
66397	11 June 2007	189	Female	44°51′	55°09′	10 February 2008	41°18′	66°06′	244	973
67735	28 September 2006	181	Male	45°53′	56°49′	19 January 2007	38°14′	54°46′	113	865
70158	1 October 2006	191	Male	44°40′	61°54′	2 February 2007	42°39′	69°13′	124	630
70161	19 June 2007	198	Female	41°56′	65°53′	10 December 2007	40°56′	69°05′	174	289
70241	7 August 2007	235	Female	42°06′	66°36′	12 September 2007	35°54′	63°55′	36	726
70243	20 June 2007	192	Female	42°54′	62°15′	12 December 2007	42°03′	67°07′	175	411
70246	20 June 2007	203	Female	42°58′	61°42′	14 December 2007	44°57′	50°16′	177	942
75373	6 August 2007	215	Female	42°05′	66°37′	10 April 2008	29°24′	56°58′	248	1652
34520	14 March 2008	188	Female	42°50′	62°51′	25 February 2009	37°42′	63°24′	348	571
34521	6 July 2008	238	Female	42°05′	66°31′	13 February 2009	39°41′	63°33′	287	365
34522	3 May 2008	249	Female	42°27′	64°00′	28 February 2009	24°17′	68°39′	302	2058
34523	6 July 2008	235	Female	42°05′	66°30′	8 April 2009	21°57′	68°50′	276	2241
83609	6 July 2008	217	Female	42°05′	66°31′	15 April 2009	28°18′	74°51′	283	1703
83610	6 July 2008	229	Female	42°05′	66°31′	22 April 2009	21°14′	61°32′	290	2356
83611	6 July 2008	221	Female	42°05′	66°30′	6 May 2009	25°04′	53°20′	304	2240
83612	6 July 2008	240	Female	42°05′	66°28′	1 April 2009	29°42′	72°51′	269	1487
83613	6 July 2008	233	Female	42°05′	66°30′	15 August 2008	42°24′	65°37′	40	81

Note: FL, fork length; lat, latitude; long, longitude; distance travelled (km), a straight-line measure between the tagging and pop-up locations.

Published by NRC Research Press

Fig. 1. (*a*) Map showing tagging (black squares) and pop-up locations for 21 porbeagles tagged off the eastern coast of Canada. Male (solid green circles) and immature female (open pink circles with centres) sharks stayed north of latitude 37°N, whereas all mature females (solid pink circles) with spring pop-up dates migrated to the Sargasso Sea by April. Month of pop-up is indicated by the number. (*b*) Time-weighted depth and temperature of two mature female porbeagles, representative of other mature females. Geolocation estimates indicate that entry into the Gulf Stream coincided with the abrupt increase in depth and water temperature recorded by the pop-up archival transmission tag.



ted with an emergency cutoff device, which physically released the tag if it went below 1800 m (which is the maximum nominal safe depth for tag operation).

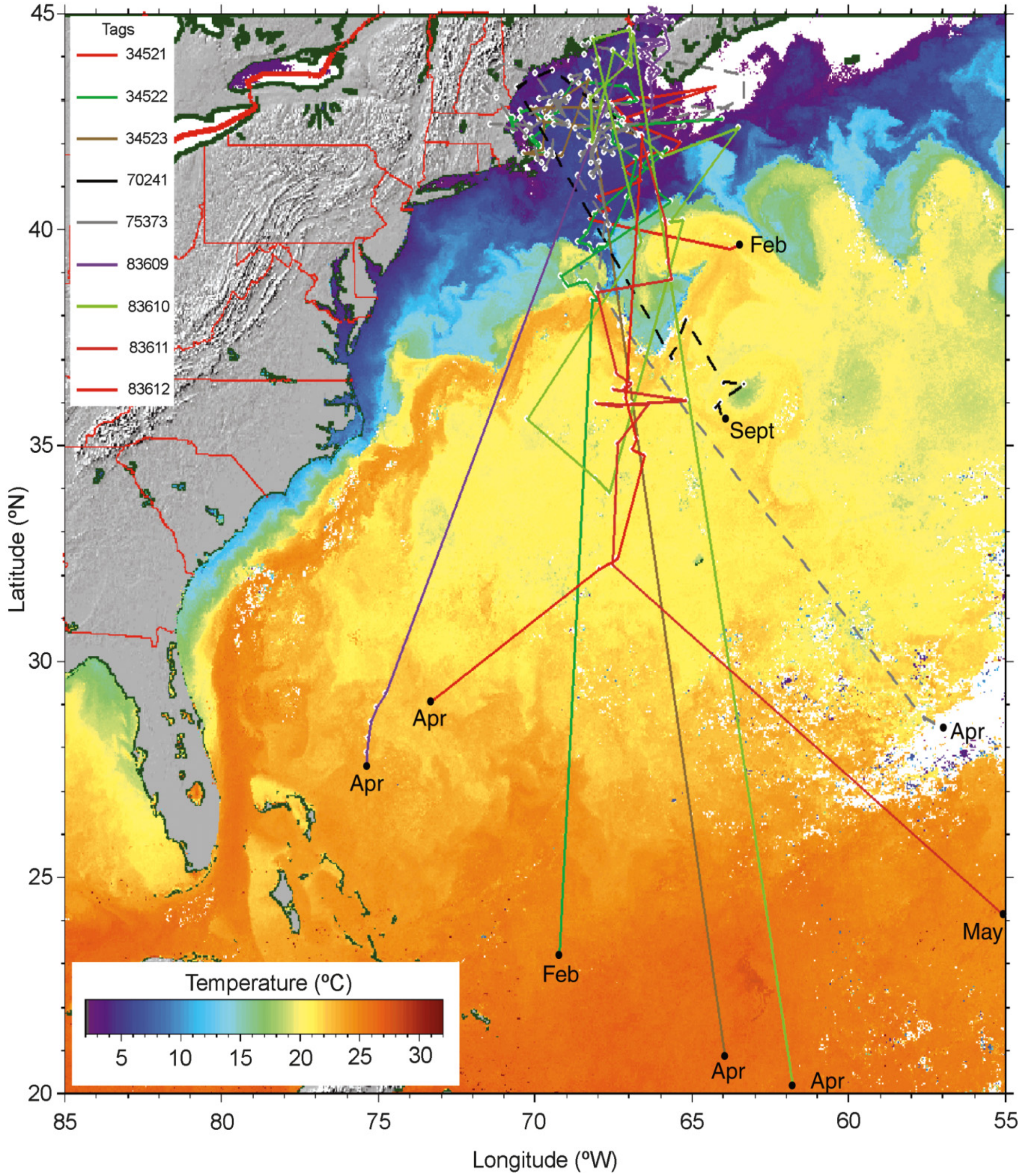
PAT tags were programmed to record depth (±0.5 m), temperature (±0.1 °C), and light intensity at 1 min (model 4) or 10 s (model Mk-10) intervals for up to 12 months after release. The tag data were internally binned by 6 h intervals, and the summarized data were transmitted to an Argos satellite after release of the PAT from the shark. One tag was physically recovered after pop-up, allowing a full download of all stored data. More than 92% of the tags transmitted successfully after release from the shark. Tags that popped up less than two weeks after tagging were excluded from subsequent analysis. All PATs were programmed to release from the shark if a constant depth was maintained for a period of four days, as a constant depth equal to that of the water depth at that location would be indicative of death in an actively swimming, pelagic shark such as a porbeagle. One shark appears to have died shortly after tagging.

Shark location at the time of pop-up was determined with an accuracy of <1 km through Doppler-shift calculations provided by the Argos Data Collection and Location Service. The reconstruction of the migration pathway between the time of tagging and pop-up was based on sea surface temperature and ambient light at depth measurements recorded by the PAT, analyzed with the state–space model "ukfsst" described by Nielsen and Sibert (2007). The requirement for PAT temperature measurements near the surface limited the availability of geolocation estimates during periods when the shark was deep in the water column, e.g., the majority of the time in the Gulf Stream and Sargasso Sea.

Results and discussion

Transmissions were received from 21 PATs applied in the summer to porbeagles off the eastern coast of Canada between 2001 and 2008 (Table 1). Males and immature sharks of both sexes remained primarily in cool temperate waters on the continental shelf, always north of latitude 38°N, for periods of up to 348 days after tagging. In contrast, all mature female porbeagles exited the continental shelf by December, swimming distances of up to 2356 km into the Sargasso Sea (south of latitude 35°N) before the PAT released from the shark (Fig. 1*a*). All seven of the mature females with PATs programmed for a spring release encountered the Gulf Stream between 22 December and 9 March (Fig. 2); the date and location of entry into the Gulf

Fig. 2. Reconstructed migration pathways of mature female porbeagles tagged with pop-up archival transmission tags (PATs), overlaid on the sea surface temperature (SST) satellite imagery of 1 March 2009 showing the Gulf Stream and the Sargasso Sea. Solid lines show tracks of sharks entering the Gulf Stream within two weeks of 1 March 2009 for which the satellite imagery would be a good match. Broken lines show tracks of sharks in 2007 and 2008 for which the temperature field would only be approximate. Tag pop-up month is indicated.



Stream was readily distinguished on the PAT record by the abrupt temperature discontinuity and the almost instantaneous initiation of deep diving behaviour (daily maximum depth of <248 m before entry and a mean of 845 m after entry) (Fig. 1*b*). Entry into the Gulf Stream was also accompanied by a shift from a weakly diurnal diving behaviour (75 m and 10.5 °C during night to 129 m and 9.5 °C during day) to a strongly diurnal vertical movement (243 m and 18.3 °C during night to 614 m and 13.1 °C during day). Both the current flow and the temperature of the Gulf Stream is greatly minimized at depths greater than 400 m (Johns et al. 1995), suggesting that the porbeagles are diving underneath the main flow of the Gulf Stream during their migration, both to maximize their net swimming speed and to minimize their ambient temperature. Although all lamnid sharks are capable of thermoregulation (Carey and Teal 1969), no porbeagles were recorded in waters with a 6 h mean temperature greater than 21.9 °C, suggesting that the warm surface waters (22–29 °C) of the Gulf Stream and Sargasso Sea were uninhabitable for the overwintering females.

Porbeagles have not previously been reported south of latitude 37°N (Cassoff et al. 2007), presumably because their time-weighted mean migratory depth of 489 m is too deep for detection by fishing fleets or other observers. One shark dove to 1360 m during its migration, which is among the deepest dives recorded for a pelagic shark species.

The Sargasso Sea is well known for being the spawning area for European and American eels but has not previously been suggested as a pupping ground for any species of shark. Porbeagle pupping was strongly inferred based on the observation that the southward migration was only made by sexually mature females (mean fork length (FL) of 230 ± 12 cm compared with mature FL_{50} of 218 cm; Jensen et al. 2002) and that every mature female monitored into the spring made the migration. Previous work has demonstrated that every mature female (87 of 88 examined) is gravid after November (Jensen et al. 2002). In addition, the residency period in the Sargasso Sea overlapped the known pupping period of early April to early June (Jensen et al. 2002). Given the strong likelihood of porbeagle pupping in the Sargasso Sea, the possibility that other pelagic sharks also give birth in this region of the Atlantic cannot be dismissed lightly.

Although pupping has never been observed in a lamnid shark, and thus the pupping environment is unknown, no obvious birthing events were visible in the PAT records; each shark undertook multiple ascents and descents between about 50 and 850 m in waters between about 8 and 23 °C (maximum recorded temperature of 25.4 °C) during the April–May period. Mean daily depth and temperature during April and May was 480 m and 14.8 °C, respectively, indicating that most of the pupping period was spent at depth. Porbeagle young-of-the-year are first captured off the eastern coast of Canada in July (Natanson et al. 2002), suggesting that the Gulf Stream aids in the return transport of the young sharks much as it does squid and other North Atlantic organisms (Dawe and Beck 1985). The question of the evolutionary advantage of a 2000 km pupping migration to an unproductive region of the ocean, followed by a return migration within several months by both females and pups, remains unanswered.

Porbeagles are fished commercially, in both Canadian domestic and international waters. Although not considered a species at risk, the abundance of the Northwest Atlantic population is currently at about 25% of virgin levels and thus is under strict regulation and cautious management in Canadian waters to promote recovery (Campana et al. 2010). Porbeagle mating grounds have been closed to shark fishing to aid in conservation efforts. Although the International Commission for the Conservation of Atlantic Tunas (ICCAT) supports Canadian conservation efforts and has recommended that there be no directed porbeagle fishery in international waters, high seas catches of porbeagles have been reported by numerous countries (Campana et al. 2010). The Sargasso Sea is currently not considered by ICCAT to be a key area for porbeagle, and it is also not considered to be essential fish habitat by the US (NOAA Office of Sustainable Fisheries, http://www.nmfs.noaa.gov/sfa/hms/EFH/index.htm). The discovery of a key life history stage in relatively unprotected international waters raises the possibility that stock recovery efforts in Canada and elsewhere could be compromised.

Acknowledgements

We thank Brin Jones, Jonathan Monaham, and Ben Zisserson for applying the tags and fishermen Paul Drew, Patrick Gray, Frank Reyno, and Gus Reyno for their assistance and expertise in catching and tagging the sharks. John Carlson and Ken Goldman provided helpful comments on the manuscript. Funding was provided by the International Governance Strategy Program of Fisheries and Oceans Canada.

References

Campana, S.E., Joyce, W., Marks, L., Natanson, L.J., Kohler, N.E., Jensen, C.F., Mello, J.J., Pratt, H.L., Jr., and Myklevoll, S. 2002. Population dynamics of the porbeagle in the Northwest Atlantic Ocean. N. Am. J. Fish. Manage. **22**(1): 106–121. doi:10.1577/1548-8675(2002)022<0106:PDOTPI>2.0.CO;2.

Campana, S.E., Gibson, A.J.F., Fowler, M., Dorey, A., and Joyce, W. 2010. Population dynamics of porbeagle in the Northwest Atlantic, with an assessment of status to 2009 and projections for recovery. SCRS/2009/095. Collect. Vol. Sci. Pap. International Commission for the Conservation of Atlantic Tunas (ICCAT). In press.

Carey, F.G., and Teal, J.M. 1969. Mako and porbeagle: warm-bodied sharks. Comp. Biochem. Physiol. **28**(1): 199–204. doi:10.1016/0010-406X(69)91335-8. PMID:5777366.

Cassoff, R.M., Campana, S.E., and Myklevoll, S. 2007. Changes in baseline growth and maturation parameters of Northwest Atlantic porbeagle, *Lamna nasus*, following heavy exploitation. Can. J. Fish. Aquat. Sci. **64**(1): 19–29. doi:10.1139/F06-167.

Dawe, E.G., and Beck, P.C. 1985. Distribution and size of juvenile short-finned squid (*Illex illecebrosus*) (Mollusca: Cephalopoda) south of Newfoundland during winter. Vie Milieu, **35**: 139–147.

Francis, M.P., Natanson, L.J., and Campana, S.E. 2008. The biology and ecology of the porbeagle shark, *Lamna nasus*. *In* Sharks of the open ocean: biology, fisheries and conservation. *Edited by* M.D. Camhi, E.K. Pikitch, and E.A. Babcock. Blackwell Publishing, Oxford, UK. pp.105–113.

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. Fish. Bull. (U.S.), **100**: 727–738.

Johns, W.E., Shay, T.J., Bane, J.M., and Watts, D.R. 1995. Gulf Stream structure, transport, and recirculation near 68°W. J. Geophys. Res. **100**(C1): 817–838. doi:10.1029/94JC02497.

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. Fish. Bull. (U.S.), **100**: 266–278.

Nielsen, A., and Sibert, J.R. 2007. State–space model for light-based tracking of marine animals. Can. J. Fish. Aquat. Sci. **64**(8): 1055–1068. doi:10.1139/F07-064.