ICES Journal of Marine Science, 59: 1263–1269. 2002
doi:10.1006/jmsc.2002.1286, available online at http://www.idealibrary.com on IDEAL®

Analysis of stomach contents of the porbeagle shark (*Lamna nasus* Bonnaterre) in the northwest Atlantic

W. N. Joyce, S. E. Campana, L. J. Natanson,
N. E. Kohler, H. L. Pratt Jr, and C. F. Jensen

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

Stomachs of 1022 porbeagle sharks (*Lamna nasus*) ranging in size from 85–264 cm were examined from the Canadian porbeagle shark fishery and a scientific cruise in the northwest Atlantic between February 1999 and January 2001. Teleosts occurred in the majority of stomachs and constituted 91% of the diet by weight. Cephalopods occurred in 12% and were the second most important food category consumed. Pelagic fish and cephalopods comprised the largest portion of the diet in the spring while groundfish dominated the diet in the fall. Diet did not differ significantly between the sexes. Stomach fullness differed slightly but significantly across months and declined slightly with fork length. The porbeagle is primarily an opportunistic piscivore with a diet characterized by a wide range of species. Diet composition changed seasonally following a migration from deep to shallow water.

Keywords: diet, elasmobranchs, Lamnidae, porbeagle, sharks, stomach content.

Received 4 September 2001; accepted 8 February 2002.

W. N. Joyce (corresponding author) and S. E. Campana: Marine Fish Division, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada; tel: +1902 426 6382; fax: +1902 426 9710; e-mail: JoyceW@mar.dfo-mpo.gc.ca; L. J. Natanson, N. E. Kohler and H. L. Pratt: National Marine Fisheries Service, 28 Tarzwell Drive, Narragansett, RI 02882, USA. C. F. Jensen: NC Division of Marine Fisheries, PO Box 769, Morehead City, NC 28557, USA.

Introduction

The porbeagle shark, *Lamna nasus* Bonnaterre, is a large cold-temperate pelagic shark commonly found in continental waters of the North Atlantic, South Atlantic and South Pacific oceans (Castro, 1983; Scott and Scott, 1988; Campana *et al.*, 2002). However, its size, high swimming speed, and its offshore distribution in deep water has made it a difficult species to study. As with other members of its family (Lamnidae), the porbeagle is able to maintain its body temperature 7–10°C higher than the surrounding water temperature (Carey and Teal, 1969) giving it the power needed for high-speed swimming activities.

Little is known about feeding behaviour and diet of porbeagle. Previous studies have included detailed but largely anecdotal information on stomach contents. Aasen (1961) made no systematic investigations of stomach contents collected in the northwest Atlantic, but noted that stomachs were mostly empty. Prey species observed included mackerel, herring, cod, hake, dogfish, lumpfish, and squid. Stevens (1973) found herring and mackerel in four individuals taken from SW United Kingdom waters. Stevens *et al.* (1983) noted squid beaks and epipelagic teleosts in two stomachs sampled in the Tasman Sea. Gauld (1989) found 20 species of benthic, epibenthic and pelagic teleosts and squid in samples from Scottish waters, while Ellis and Shackley (1995) found mackerel, herring and squid in 24 stomachs from the Bristol Channel. Stomachs from the Bay of Fundy contained herring, gaspereau, mackerel, redfish, and squid (Scott and Scott, 1988).

As part of intensive onboard sampling of all aspects of the biology of the porbeagle (Campana *et al.*, 1999; Natanson *et al.*, 2002), a large number of stomachs were collected from specimens taken in the Canadian commercial porbeagle shark fishery and on a US research cruise. We provide a quantitative description of the diet and investigate dietary changes in relation to season, size, and sex.

1054–3139/02/061263+07 $35.00/0

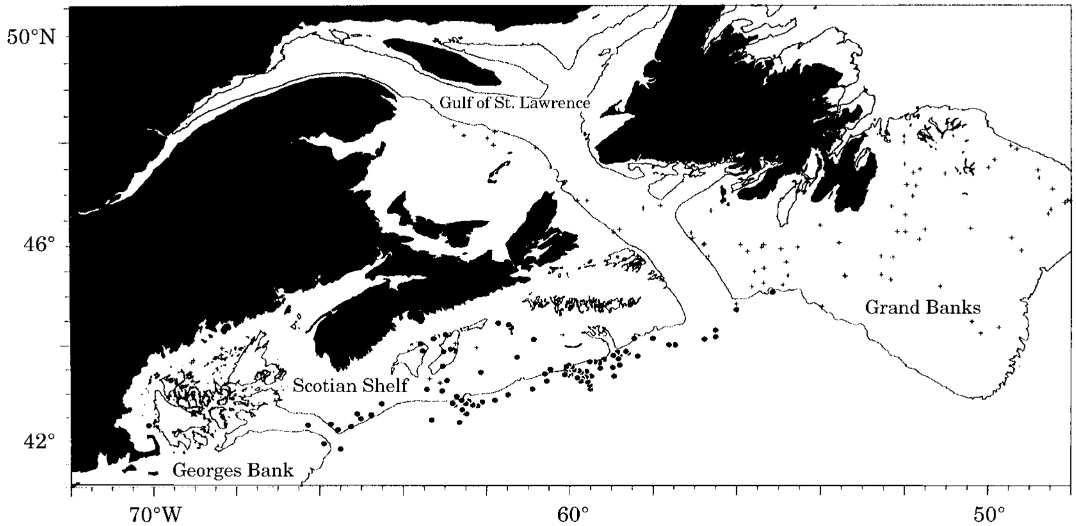

Figure 1. Bathymetric map (contour: 200 m depth) of eastern Canada showing start positions of fishing sets for porbeagles sampled in the Canadian Atlantic fishery (dots: spring; +: autumn).

Materials and methods

Stomachs were collected between February 1999 and January 2001 from two sources: (a) Canadian commercial longline vessels (11–33 m in length) directing for porbeagle (Campana *et al.*, 2002; n=1012) and (b) a United States commercial vessel chartered by the National Marine Fisheries Service for research purposes (n=10). Canadian catches extended from the northeast end of George's Bank, along the Scotian Shelf, in the Gulf of St Lawrence and on the Grand Banks of Newfoundland, while US catches took place in the Gulf of Maine (Figure 1). Gear used in all instances consisted of pelagic longline gear. Gear configuration varied slightly between vessels depending on weather, time of day, fishing area and individual preferences of the captain. However, the basic gear consisted of 900 lb – test monofilament mainline to which a number of gangions were attached by clip. Gangions were typically constructed of rope with wire leaders or monofilament with a clip on one end to attach to the mainline and a baited Mustad shark hook (usually number 9) on the other. Squid, herring or mackerel was typically used as bait. Gear would be strung out in 3–8 "sections" and each would consist of a highflyer or radio buoy followed by 7–20 gangions and then a float; this would continue until 3–5 floats were attached and then the section was completed with another highflyer or radio buoy. Number of hooks per buoy depended on the depth desired. Fishing took place at all times of the day. Typically, one set would be completed per fishing day.

A total of 1022 sharks ranging in size from 85–264 cm were examined (554 males, 465 females, 3 unknown) immediately after capture. Stomachs were first felt by hand through the stomach wall from within the abdominal cavity to determine if any contents were present. If contents could be felt then the stomach was excised (n=533). Of these, 497 actually contained food. Stomachs containing only a few eyes, otoliths or small bits of material were considered empty. The stomach was removed by cutting the pyloric sphincter and connective tissue as well as the oesophagus above the oesophageal sphincter. The stomach was then placed in a labelled bag and frozen directly on board ship for later analysis in the lab. In cases where smaller commercial vessels were unequipped with blast freezers, stomachs were kept on ice in the hold (usually 3–5 days) and then frozen immediately upon landing. Stomachs were stored at -20°C. Stomachs containing food items were taken from 268 males (85–241 cm) and 226 females (94–264 cm; fork length taken along the curve of the body). Of these, 339 were from immature or sub-adult sharks and 155 from mature sharks. Three additional stomachs for which sex and size were not recorded were included as well.

Stomachs were emptied onto a 425-µ sieve and contents separated and weighed to the nearest 50 g. Contents were identified to the lowest possible taxon by use of keys and field guides (Scott and Scott, 1988; Vecchione *et al.*, 1989). In cases where a prey item was largely digested, identification was sometimes possible by removing otoliths from the skull. These were then compared to an otolith reference collection. If identification failed, the prey item was included in the category "unidentified teleost". Contents identified as bait items by prominent hook marks and knife cuts were excluded from the analysis. Most bait could be quickly identified as the line was hauled back every 8 h.

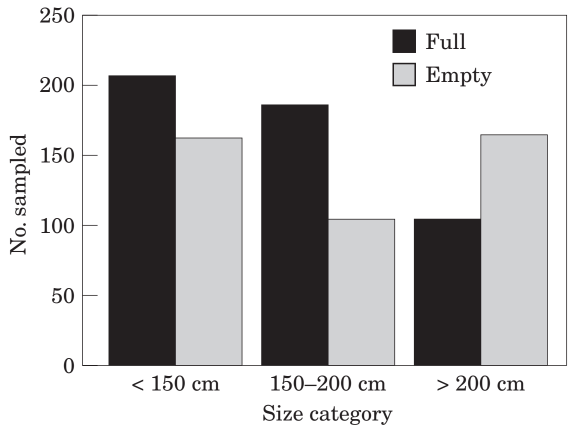

Figure 2. Number of full and empty porbeagle stomachs by size category.

Frequency of occurrence (percentage of stomachs containing a specific prey group, Fo), percent weight (weight of prey category in all stomachs as a percentage of total stomach content weights, %wt), and mean weight per stomach were recorded for major forage categories (Hyslop, 1980) and compared among different size groupings, sex and season. Fo and %wt were examined for three size groups that corresponded roughly to juveniles (<150 cm), sub-adult sharks (150–200 cm), and adults (>200 cm). The commercial fishery takes place mainly around Georges Bank and on the Scotian Shelf in spring, and in the Gulf of St. Lawrence and on the Grand Banks in autumn (Campana *et al.*, 1999; Figure 1). Accordingly, data were broken down into two seasonal groupings, spring (January–June) and autumn (July–December) to reflect the geographical shift in the fishery.

Volume of each stomach (stomach capacity) was determined, after contents were emptied and the pyloric sphincter was tied off, by filling it with water through a hose until it became distended and water flowed over. The water was then poured into a graduated cylinder and measured to the nearest 10 ml. The degree of stomach fullness was calculated by dividing the total stomach content weight (kg) by stomach capacity (kg).

Results

Of all porbeagle sharks examined, 51% were empty and 49% contained food items (Figure 2). A total of 20 different families and 21 species could be positively identified (Table 1). After grouping all food items into one of eight categories, teleosts were the main prey observed in stomachs, followed by cephalopods. Squid beaks occurred in 19.7% of stomachs but most were not accompanied by identifiable cephalopods. Unidentified teleosts comprised the bulk of the observed prey items (Fo=19.2) followed by pelagic teleosts (Fo=13.4) while groundfish were the major food group consumed by weight. Among the identified teleosts, lancetfish, unknown flounders, lumpfish and Atlantic cod occurred most frequently and contributed mostly to the weight. Frequencies of occurrence of the major food categories did not differ appreciably between juvenile and sub-adults in spring (Table 2), although more fish were observed in the latter. Pelagic fish formed the majority of the diet by weight and frequency for all sharks <200 cm (Figure 3). Cephalopods also constituted a substantial portion of the diet. A relatively small proportion of the weight was groundfish. Adult sharks contained more groundfish and less cephalopods and pelagic fish than the smaller size categories, and the %wt was similar among pelagic fish, elasmobranchs, groundfish and unidentified fish. In the fall, the %wt of pelagic fish was noticeably reduced, while groundfish constituted an increasing portion of the diet with increasing size. In contrast, sharks >150 cm had apparently eaten fewer cephalopods than smaller sharks. Very little weight was contributed by the other forage categories.

Unidentified teleosts formed generally an important part of the diet by weight, particularly in autumn. These items represent heavily digested and therefore unrecognizable parts and their interpretation is slightly different. Assuming that these items have the same distribution as the identifiable component, the importance of groundfish would be even more pronounced.

Stomach content weight increased slightly with stomach size (Figure 4a). Average stomach content weight for all stomachs (n=1022) was 121 g, 0.2% of the average body weight (61 kg). For stomachs containing food (n=497) average stomach content weight was 249 g, 0.4% of the average body weight. Mean prey species weight per stomach (g) was relatively low for most prey species (Table 1). Males had a slightly higher percentage of stomachs with food than females, 54% and 46% respectively. There were no appreciable dietary differences between males and females in any size category.

In addition to the prey species recorded in stomachs examined, two additional species were observed falling out of stomachs as fishers dressed sharks on deck: an Atlantic salmon (*Salmo salar*; family Salmonidae) and a filefish (*Monocanthus* sp.; Balistidae).

Free otoliths were found in 210 (39%) of the 533 excised stomachs investigated. Most free otoliths were eroded making identification difficult, and thus were not included in the analysis. However, white barracudina and pollock were prey species represented only by free otoliths.

A small number of items of unknown dietary significance were found associated with digested fish remains (i.e. bones and tissue). Most were small benthic invertebrates (<3cm) and were either found individually or in

Table 1. Prey items observed in 1022 porbeagle shark stomachs from the northwest Atlantic, grouped by major prey categories (N: number of organisms; W: total weight; %wt: percentage weight in g; n: number of stomachs with prey item; Fo: frequency of occurrence; w: weight per stomach sampled in g).

Prey category	N	W	%Wt	n	Fo	w
Crustaceans[1]	3	150	0.12	2	0.20	0.15
Cephalopods[2]	186	6 700	5.41	121	11.84	6.56
(excluding free squid beaks	2362			201	19.67	
Unidentified invertebrates	45	250	0.20	3	0.29	0.24
Elasmobranchs[3]	14	4 475	3.61	6	0.59	4.38
Pelagic teleosts	196	31 927	26.18	218	13.41	21.45
Alepisaurus ferox	97	20 400	16.47	82	8.02	19.96
Clupea harengus	42	7 677	6.20	35	3.42	7.51
Scomberesox saurus	3	500	0.40	2	0.20	0.49
Scomber scombrus	54	3 850	3.11	25	2.45	3.77
Groundfish	466	52 726	42.56	117	11.45	15.59
Ammodytes dubius	267	1 600	1.29	34	3.33	1.57
Anarhichas lupus	3	4 050	3.27	3	0.29	3.96
Hemitripterus americanus	1	1 100	0.89	1	0.10	1.08
Myoxocephalus scorpius	4	110	0.09	1	0.10	0.11
Cyclopterus lumpus	51	14 566	11.76	32	3.13	14.25
Gadus morhua	15	10 000	8.07	12	1.17	9.78
Melanogrammus aeglefinus	8	2 400	1.94	7	0.68	2.35
Merluccius albidus	4	1 050	0.85	3	0.29	1.03
Merluccius bilinearis	16	1 150	0.93	2	0.20	1.13
Unknown flounders	88	15 400	12.43	27	2.64	15.07
Sebastes fasciatus	9	1 300	1.05	6	0.59	1.27
Teleosts	19	1 225	0.99	12	1.17	1.20
Anguilla rostrata	3	950	0.77	3	0.29	0.93
Arotopteus pharao	1	150	0.12	1	0.10	0.15
Unknown dragon fish	1	100	0.08	1	0.10	0.10
Unknown myctophid	1			1	0.10	
Nemichthys scolopaceus	1			1	0.10	
Petromyzon marinus	12	25	0.02	5	0.49	0.02
Unidentified teleosts	526	26 029	21.01	196	19.18	25.47
Totals	3817	123 982	100	497	48.63	121.31

[1]Only *Chionectes opilio*.
[2]Only *Illex illecebrosus*.
[3]Only *Squalus acanthias*.

small quantities. These items may have represented incidental ingestion or the stomach contents of the target prey. Therefore, these items were not included in the overall analysis. Examples include mollusc shells (e.g. *Yolida* sp., Icelandic scallop), amphipods, small sand dollars, small brittle stars, nematode worms, flatworm, small pieces of seaweed, small crab carapaces (family Majidae*)*, digenetic trematodes and pelagic salps. While most of these organisms are common prey of at least some teleosts consumed by porbeagle, others are more likely parasites of either predator or prey (Scott and Scott, 1988).

Finally, pieces of inorganic debris were also observed. The most common items included pieces of small shiny plastic, small rocks and feathers. Other items found were various types of fishing line, twine, wrappers, rope, wire, a plastic bottle cap, a drinking straw, a balloon, a small ziploc bag, a circle hook and several lobster bands.

Stomach volumes ranged from 0.29 l in the smallest shark sampled to more than 8 l in the largest specimen (Figure 4b). Ratios of food content to stomach volume were available for 290 stomachs (range 1–63%) and averaged 12% (Figure 4c).

Discussion

About half of the porbeagle stomachs were found to be empty. The percentage was higher than in some studies on other shark species (Stevens, 1973; Stillwell and Kohler, 1982; Lowe *et al*., 1996) but lower than the 75% empty observed by Lessa and Almeida (1997). However, the proportion of empty stomachs is often variable in

Table 2. Number of items observed (N) and frequency of occurrence (Fo) by major prey categories, porbeagle size group and season.

	Porbeagle size group					
	<150 cm		150–200 cm		>200 cm	
Prey	N	Fo	N	Fo	N	Fo
Spring (January–June)						
Crustaceans	0	0.0	0	0.0	0	0.0
Cephalopods	44	31.0	42	35.0	7	19.4
Unid. invertebrates	1	0.7	1	0.8	1	2.8
Elasmobranchs	0	0.0	1	0.8	3	8.3
Pelagics	59	41.6	59	49.2	7	19.4
Groundfish	11	7.8	15	12.5	9	25.0
Teleosts	4	2.8	3	2.5	1	2.8
Unid. teleosts	62	43.7	39	32.5	17	47.2
Stomachs with food	142		120		36	
Autumn (July–December)						
Crustaceans	0	0.0	0	0.0	2	3.0
Cephalopods	15	23.1	8	12.5	5	7.6
Unid. invertebrates	0	0.0	0	0.0	0	0.0
Elasmobranchs	0	0.0	0	0.0	2	3.0
Pelagics	5	7.7	5	7.8	2	3.0
Groundfish	16	24.6	27	42.2	35	53.0
Teleosts	0	0.0	3	4.7	1	1.5
Unid. teleosts	33	50.8	22	34.4	22	33.3
Stomachs with food	65		64		66	

commercial shark catches (Lineweaver and Backus, 1984). Because there was no evidence of stomach eversion at capture, the high percentage of empty stomachs may reflect short periods of feeding followed by periods of rapid digestion. The elevated body temperature found in the porbeagle should help to digest large volumes of food more rapidly (Magnuson, 1969). Quick digestion can complicate dietary analysis in several ways. Firstly, a smaller proportion of certain prey species may be identifiable. We observed that otoliths become quickly eroded making identification difficult. Also, with high rates of digestion, bait fish may be difficult to identify if a shark has been hooked for several hours, while digestion during this time should also reduce stomach fullness. Another possibility is that the fraction of empty stomachs observed may be biased upward owing to sampling with passive gear (baited hooks) as opposed to active gear because hungry animals are more likely to take bait from a baited hook than satiated animals.

Most shark species appear to be opportunistic feeders consuming a large diversity of prey (Cortés, 1999). According to our results, porbeagle sharks in the Northwest Atlantic feed primarily on teleosts (i.e. alepisaurids, gadids, pleuronectids). Cephalopods also constituted a major portion of the diet but were more important in the diet of the smaller individuals. Juveniles tended to consume a less diverse range of prey species, comprising mostly of small pelagic fish and cephalopods. Larger sharks appear to become more piscivorous capable of capturing large teleosts and even small elasmobranchs but favour groundfish based on their percentage contribution to stomach content weight. These differences could be attributed to the size of the shark. Other shark species such as the lemon shark have been found to be selective at times, favouring certain prey items (e.g. elasmobranchs, adult jacks, and lobster) over others when food is abundant (Wetherbee *et al*., 1990). This may be the case with the porbeagle as well during its migration up the coast from deeper to shallow waters.

Blue sharks (*Prionace glauca*) appear to have a diet similar to that of porbeagle with a few exceptions. Stevens (1973) found that blue sharks sampled in European waters consumed mainly pelagic fish such as clupeids and mackerel and cephalopods, but some had been feeding on benthic species. In addition, larger specimens have been found with remains of marine mammals in their stomachs (Stevens, 1973; Cortés, 1999). Other carcharhinid sharks (galapagos shark *Carcharhinus galapagensis*, sandbar shark *Carcharhinus plumbus*, and tiger shark *Galeocerdo cuvier*) have diets comprised mostly of teleosts and squid, but have a higher occurrence of crustaceans, other elasmobranchs, birds, and reptiles in their food (Stillwell and Kohler, 1993; Lowe *et al*., 1996; Wetherbee *et al*., 1996; Cortés, 1999).

In comparison to other Lamnidae, the diet of the porbeagle most closely resembles that of the shortfin mako (Stillwell and Kohler, 1982), both species feeding primarily on teleosts. There are also notable differences: cephalopods are more important to the porbeagle and

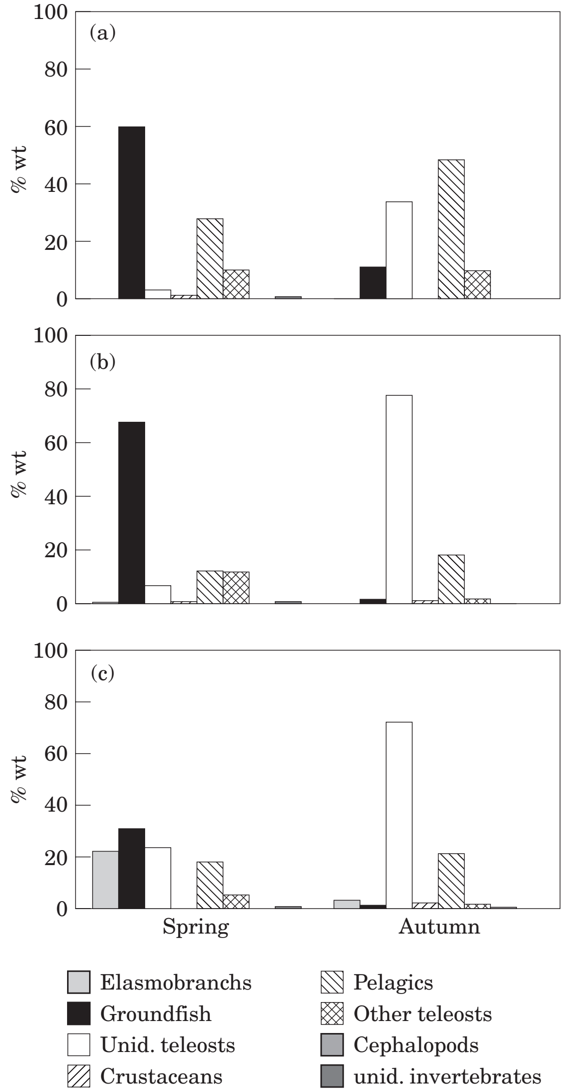

Figure 3. Percentage weight of major food categories by porbeagle size category and season. (a) <150 cm; (b) 150–200 cm; (c) >200 cm.

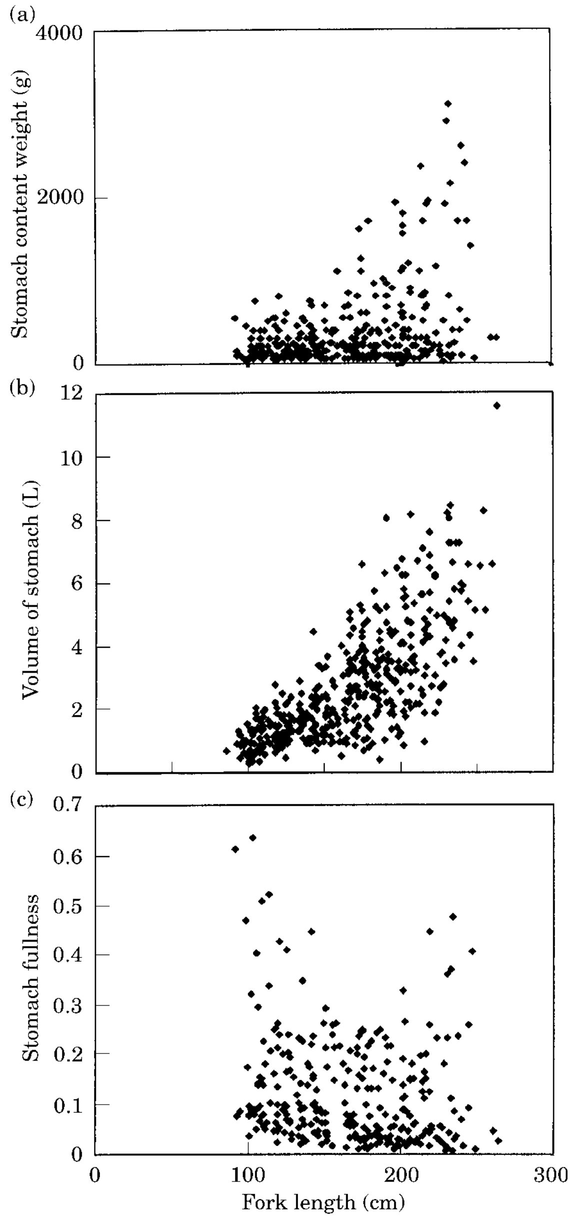

Figure 4. Stomach content weight (a), stomach volume (b) and stomach fullness (content/volume; c) plotted against porbeagle fork length (a and c excluding empty stomachs).

the mako is able to feed on larger prey items, such as swordfish, other elasmobranchs, and possibly even marine mammals when they attain a size >150 kg (Stillwell and Kohler, 1982; Cortés, 1999). Studies on white sharks have also shown prominent size-related shifts in diet (Klimley, 1994; Bruce, 1992; Dudley *et al.*, 2000; Cortés, 1999). Teleost remains dominated the stomach contents of white sharks <220 cm total length, while those >220 cm began feeding on large marine mammals and other elasmobranchs while consumption of teleosts decreased sharply. Although the porbeagle does attain weights and lengths comparable to those at which major diet shifts were observed in mako and white sharks (largest porbeagle in our sample was 278 kg and 260 cm), there was no evidence of feeding on marine mammals, while spiny dogfish was the only elasmobranch observed as prey.

Diet often changes with geographic area and this was observed for the porbeagle as well. Diet changes were noted as the season progressed and samples were derived from different locations. In spring, most of the population was found on the Scotian Shelf (Campana *et al.*, 2002) feeding on pelagic fish and squid. In the fall, the amount of groundfish in the diet increased, particularly among sharks >150 cm. This diet change can be attributed to the migration into the shallow waters of the Grand Banks and the Gulf of St Lawrence where the available prey spectrum includes more benthic fish species. So far, there is no obvious sign of high prey selection.

Pelagic sharks are opportunistic feeders that typically consume items of no importance (Strasburg, 1958). Inorganic items were found infrequently and in small amounts in stomachs. Shiny plastic wrapping may attract predators by resembling a prey. This may also apply to the feathers that were observed without any indication of other seabird remains. Stones have been found in mako (Stillwell and Kohler, 1982) and blue sharks (Stevens, 1973) and are believed to have been accidentally ingested or as part of the stomach contents of their prey.

Our results indicate that the porbeagle is an opportunistic fish feeder and that the diet may include a diverse prey spectrum of pelagic, epipelagic and benthic species, depending on what is available. The strong seasonal diet change observed is linked to changes in distribution, while the high incidence of empty stomachs may suggest that the porbeagle feeds intermittently and/or a high rate of digestion.

Acknowledgements

We thank Clearwater Fine Foods, Karlsen Shipping, and The Atlantic Shark Association for providing unpublished data and access to their fishing vessels in support of the porbeagle research programme.

References

Aasen, O. 1961. Some observations on the biology of the porbeagle shark (*Lamna nasus* L.). ICES CM 1961/Northern Seas Committee: 109, 7 pp.

Bruce, B. D. 1992. Preliminary observations on the biology of the white shark, *Carcharodon carcharias*, in south Australian waters. Australian Journal of Marine and Freshwater Research, 43: 1–11.

Campana, S. E., Marks, L., Joyce, W. N., Hurley, P. C. F., Showell, M., and Kulka, D. 1999. An analytical assessment of the porbeagle shark (*Lamna nasus*) population in the northwest Atlantic. Department of Fisheries and Oceans Atlantic Fisheries Research Document, 96/24.

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 shark in the Northwest Atlantic. North American Journal of Fisheries Management, 22: 106–121.

Carey, F. G., and Teal, J. M. 1969. Mako and porbeagle: warm-bodied sharks. Comparative Biochemical Physiology, 28: 199–204.

Castro, J. I. 1983. The Sharks of North American Waters. Texas A&M University Press, College Station. Texas. 180 pp.

Cortés, E. 1999. Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science, 56: 707–717.

Dudley, S. F. J., Anderson-Reade, M. D., Thompson, G. S., and McMullen, P. B. 2000. Concurrent scavenging off a whale carcass by great white sharks, *Carcharodon carcharias*, and tiger sharks, *Galeocerdo cuvier*. Fisheries Bulletin, 98: 646–649.

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

Gauld, J. A. 1989. Records of porbeagles landed in Scotland, with observations on the biology, distribution and exploitation of the species. DAFS Scottish Fisheries Research Report, 4: 1–15.

Hyslop, E. J. 1980. Stomach contents analysis—a review of methods and their application. Journal of Fish Biology, 17: 411–429.

Klimley, A. P. 1994. The predatory behavior of the white shark. American Scientist, 82: 122–133.

Lessa, R., and Almeida, Z. 1997. Analysis of stomach contents of the smalltail shark *Carcharhinus porosus* from northern Brazil. Cybium, 21: 123–133.

Lineaweaver, T. H., and Backus, R. H. 1984. The Natural History of Sharks. Nick Lyons Books, New York. 256 pp.

Lowe, C. G., Wetherbee, B. M., Crow, G. L., and Tester, A. L. 1996. Ontogenetic shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environmental Biology of Fishes, 47: 203–211.

Magnuson, J. J. 1969. Digestion and food consumption by skipjack tuna (*Katsuwonus pelamis*). Transactions of the American Fisheries Society, 98: 379–392.

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. Fisheries Bulletin, 100: 266–278.

Scott, W. B., and Scott, M. G. 1988. Atlantic Fishes of Canada. University of Toronto Press. Canadian Bulletin of Fisheries and Aquatic Sciences, 219: 731 pp.

Stevens, J. D. 1973. Stomach contents of the blue shark (*Prionace glauca* L.) off south-west England. Journal of the Marine Biological Association of the United Kingdom, 53: 357–361.

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

Stillwell, C. E., and Kohler, N. E. 1982. Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 39: 407–414.

Stillwell, C. E., and Kohler, N. E. 1993. Food habits of the sandbar shark *Carcharhinus plumbeus* off the U.S. northeast coast, with estimates of daily ration. Fishery Bulletin, 91: 138–150.

Strasburg, D. W. 1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. U.S. Fish and Wildlife Service Fisheries Bulletin, 58: 335–361.

Wetherbee, B. M., Gruber, S. H., and Cortés, E. 1990. Diet, feeding habits, digestion, and consumption in sharks, with special reference to the lemon shark, *Negaprion brevirostris*. NOAA Technical Report NMFS, 90: 29–47.

Wetherbee, B. M., Crow, G. L., and Lowe, C. G. 1996. Biology of the galapagos shark, *Carcharhinus galapagensis*, in Hawai'i. Environmental Biology of Fishes, 45: 299–310.

Vecchione, M., Roper, C. F. E., and Sweeney, M. J. 1989. Marine flora and fauna of the eastern United States Mollusca: Cephalopoda. NOAA Tehnical Report NMFS, 73: 1–21.