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Population Dynamics of the Porbeagle in the Northwest Atlantic Ocean

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Abstract.—A virgin population of porbeagles *Lamna nasus* in the northwest Atlantic Ocean supported annual catches of up to 9,000 metric tons (mt) in the early 1960s before the fishery collapsed in 1967. Low and apparently sustainable catches of about 350 mt in the 1970s and 1980s allowed the stock to partially rebuild before a new fishery arose in the early 1990s. The response of the population to this renewed fishing pressure has been unclear until now. However, a new population dynamics analysis suggests that population abundance has once again declined. On the basis of more than 140,000 length measurements, an extensive catch rate index, a confirmed growth model, and a catch-at-age matrix, it appears that at least 90% of the sexually mature population has been lost as fishing mortality has increased. Independent measures of fishing mortality (F) based on Petersen analysis of tag-recaptures, Paloheimo Zs, and a population model all suggest that fishing mortality was about 0.20 in 2000. Biological reference points based on life table analysis indicate that fishing at $F_{0.1}$ = 0.18 will result in population collapse, that F = 0.08 corresponds to zero population growth, and that fishing mortality at maximum sustainable yield is about 0.04. Porbeagles have a low pup production rate and mature considerably after the age at which they first appear in the fishery. In light of the very low numbers of mature females now found in the population, it is unlikely that even the strict quota management now in place will allow the population to rebuild quickly. However, the shark fishing industry has actively supported scientific research and conservation practices in recent years, suggesting that long-term sustainability may still be possible.

The porbeagle *Lamna nasus* is a large cold–temperate pelagic shark species of the family Lamnidae that occurs on both sides of the North Atlantic Ocean, as well as in the South Atlantic and South Pacific oceans. In the northwest Atlantic, the species ranges from Newfoundland to New Jersey and possibly to South Carolina, but it is most abundant off the eastern coast of Canada between the Gulf of Maine and Newfoundland (Templeman 1963). It is the only large shark species for which a directed commercial fishery exists in Canadian coastal waters (Hurley 1998).

Despite the fact that surprisingly little is known of the biology of this species (Aasen 1963; Francis and Stevens 2000), and almost nothing is known of its population dynamics, the porbeagle population in the northwest Atlantic has often been cited as a clear example of stock collapse in an elasmobranch (Anderson 1990; Walker 1998; Stevens et al. 2000). The basis for this widely accepted conclusion is the detailed catch records of the Norwegian long-liners who first arrived in the northwest Atlantic to fish the virgin (previously unfished) population in 1961. By 1967, the fishery had almost disappeared, due to low catch rates and unprofitable sizes. Thus it is clear that the fishery

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TABLE 1.—Number of porbeagle fork length measurements available from each data source; LPRT = large pelagic research tally sheet; SF IOP = Scotia-Fundy International Observer Program; and NF IOP = Newfoundland International Observer Program.

	Source						
Year	Norway	Industry	LPRT	NF IOP	SF IOP	Research	Total
1961	1,971						1,971
1980				810			810
1981				1,984			1,984
1987				1,521	359		1,880
1988				1,541	5,512		7,053
1989				2,132	58		2,190
1990				1,705	8,552		10,257
1991				26	16,474		16,500
1992				13	14,619		14,632
1993				886	9,175		10,061
1994				116	2,764		2,880
1995		3,640		3,409	3,006		10,055
1996		2,057	4,092	5	3,824		9,978
1997		1,228	4,643	3	1,483		7,357
1998		10,441		21	17		10,479
1999		16,989				735	17,724
2000		15,931				357	16,288
Total	1,971	50,286	8,735	14,172	65,843	1,092	142,099

had suffered an economic collapse. What is not so clear is whether there had been a corresponding population collapse. To this point, there has been no analysis of population trends, abundance indices, size or age structure, biological indicators of population health, or mortality rates to confirm suspicions of population collapse. Nor have any estimates of sustainable yield been made. Without these measures of population status, it is difficult to see how any meaningful conclusions could have been drawn.

Recent years have seen an increasing number of countries discuss legislation to protect endangered elasmobranch stocks, highlighted by the United Nations Food and Agriculture Organization's recently released *International Plan of Action for the Conservation and Management of Sharks* (FAO 1998). The FAO plan is based on the conclusion that many of the world's shark species are severely depleted (FAO 1998). Numerous authors have noted the low productivity of elasmobranchs compared with teleosts, which is largely a result of their low fecundity and late age at sexual maturation, and have suggested that only a handful of fast-growing, fecund species are able to sustain a fishery (Cortés 1998; Walker 1998; Musick 1999; Stevens 1999). Because many of the above conclusions are based in part on published reports of the porbeagle fishery collapse, it is important that the collapse and any subsequent recovery be both documented and understood. This paper presents the first detailed analysis of the past and present status of porbeagle population dynamics in the northwest Atlantic. Included in the study are new results pertaining to porbeagle catch history, trends in catch rate, size composition, population abundance, fishing mortality, and sustainable yield. The analysis concludes with an estimate of recent fishing mortality rate in relation to the sustainable catch targets commonly used in teleost fisheries and their applicability to a sustainable porbeagle fishery.

Methods

Biological data.—Measures of porbeagle size and sex were available from both scientific and industry sources (Table 1). Samples from the virgin 1961 population were reported by Aasen (1963), using dorsal length and a nonstandard measure of total length. The International Observer Program (IOP) monitored the size composition of the catch on randomly selected fishing vessels before 1987 and on all foreign vessels from 1987 onwards, recording either total length (Scotia-Fundy IOP) or fork length (Newfoundland IOP). Individual carcass weights were recorded by dockside monitors for a substantial proportion of the Canadian catch between 1995 and 1997. In addition, the shark fishing industry recorded the interdorsal length of more than 75% of the catch between 1998 and 2000 as part of an industry-supported research project. Altogether, more than 142,000 porbeagle measurements were collated

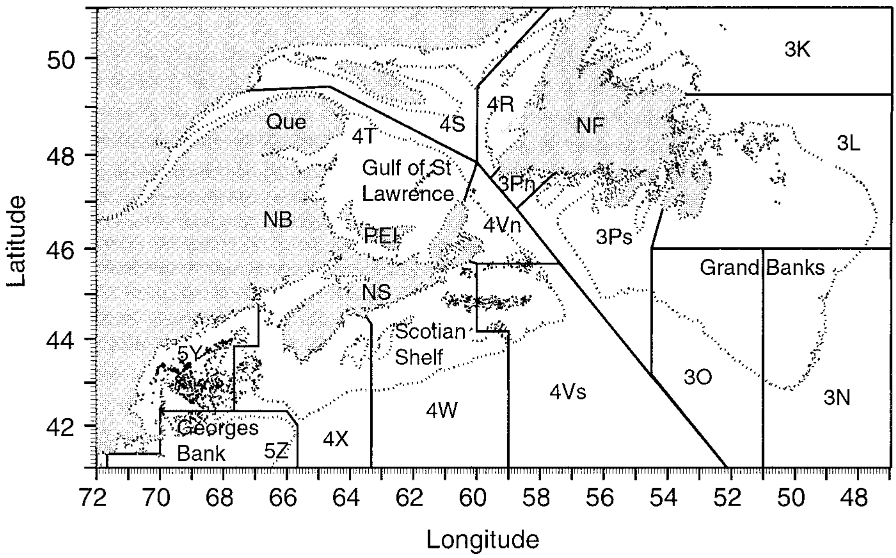

FIGURE 1.—Map of the eastern coast of Canada, showing major fishing grounds and North Atlantic Fisheries Organization divisions. The 200-m contour is shown.

from a variety of sources for this study (Table 1). To convert all of these measurements into a common size measurement (fork length, measured over the curve of the body), a series of inter-conversion factors were developed through matched measurements made by scientific staff (Campana et al. 2001).

Commercial data.—Commercial catch and effort statistics were available for the years 1961 to the present, with the landings from 1987 onward considered to be very reliable (Campana et al. 1999, 2001). Canadian landings data were extracted from North Atlantic Fisheries Organization (NAFO) files between 1961 and 1990 and from Canadian Department of Fisheries and Oceans (DFO) zonal statistics files from 1991 to the present. Foreign landings for 1961–1963 (other than those from Norway) were extracted from the International Commission for the Conservation of Atlantic Tunas (ICCAT) *Report of the Shark Working Group* (Miami, 26–28 February 1996) and from NAFO files thereafter. The NAFO files were also the source of Norwegian catch data between 1961 and 1986. Foreign catches (including discards) from 1987 onward (from 1981 onward in the case of Japanese and USSR catches) were available from Scotia-Fundy and Newfoundland IOPs. The U.S. landings were extracted from U.S. nominal catch statistics (J. Brodziak, National Marine Fisheries Service, unpublished data). Landings data from the northeast Atlantic are from FAO statistics (FAO 2000).

Inconsistencies in the conversion factor applied by the Canadian Department of Fisheries and Oceans to convert landed dressed weight to live equivalent (round) weight have resulted in some errors in previously reported landings. This source of error was eliminated by applying a standardized conversion factor of 1.5 (kg–kg) to all landing statistics and catches used in catch rate calculations (Campana et al. 1999, 2001).

Calculations of commercial catch rate were based on directed longline catches, which account for virtually all historical catches. Most of the directed effort has traditionally come from the offshore fleet, both foreign and Canadian. However, effort from the inshore fleet became substantial in 1996 when exploratory licenses first became available. In the same year, one of the three offshore vessels was removed from the fishery. Effort trends and the balance between inshore and offshore have been relatively stable since then (Campana et al. 2001).

Catch rate measures were disaggregated into those for immature and those for mature porbeagles: both were calculated in terms of $\log_e$-transformed numbers per hook (Campana et al. 2001). A fork length (FL) equal to 200 cm is approximately midway between the lengths corresponding to 50% maturity in males and females (C. F. Jen-

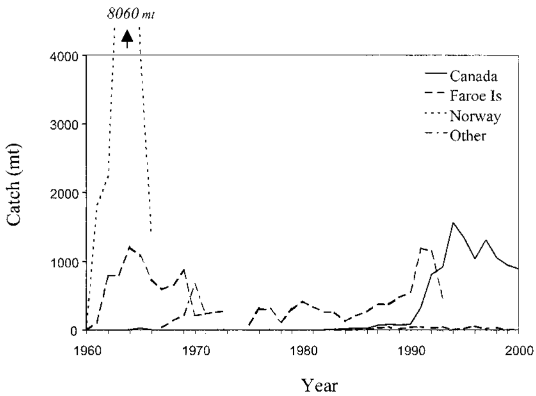

FIGURE 2.—Reported landings in metric tons (mt) of porbeagles in the northwest Atlantic by country.

sen, unpublished data), and was therefore used as a proxy for the size of a sexually mature porbeagle.

Standardized catch rate was determined by the linear model approach of Gavaris (1980). The terms subarea, month, fishing vessel, and year were treated as factors. Subareas were defined as indicated in the next section. Interaction terms were evaluated but not included in the final model.

Age composition.—Age determinations are an important component of a population analysis because ages form the basis for both growth and mortality rates. Natanson et al. (in press) presented a validated growth model for northwest Atlantic porbeagles based on counts of growth bands visible in 576 vertebral cross sections. The accuracy of the age interpretations was validated to an age of at least 11 years (Natanson et al., in press). Although there was evidence of sexually dimorphic growth after the onset of sexual maturity, the difference in size at age was small. Therefore, a sex-combined growth curve was used to convert catch at length to catch at age.

To calculate catch at length, length composition by sex was determined for each of three subareas (southern Scotian Shelf, eastern Scotian Shelf, and Newfoundland–Gulf; Figure 1) in each of three seasons (January–March, April–June, and July–December) for each year based on available measurements (Table 1). Lengths were aggregated into 5-cm categories corresponding to measurement precision prior to 1990. Sampled catches were subsequently scaled to the total catch of each aggregation cell. Catch at length in each cell was converted to catch at age (excluding age 0) using maximum likelihood estimators characteristic of the fitted growth model (Campana et al. 2001). Normal variability and a constant standard deviation of length at age (SD, ~12) were assumed based on the sharks aged by Natanson et al. (in press). This approach would be expected to yield estimates of proportion at age that are considerably more accurate than the cohort slicing used by Campana et al. (1999), particularly for ages less than 15 years.

Paloheimo Zs.—The total instantaneous mortality rate (Z) in the most recent years was estimated through use of Paloheimo Zs, based on the reduction in catch at age along a cohort between adjacent years (Ricker 1975). The catch at age for each of the two major fishing grounds was first standardized to a common fishing effort by using the observed number of hooks for each fishing ground for each year. Age-groups 3–5 years and 7–9 years were used on the Scotian Shelf, since those age-groups were fully recruited to the fishery. Age-group 9–12 was analyzed in the Newfoundland–Gulf fishery, an age range that includes many sexually mature porbeagles. Paloheimo Zs were not calculated for young sharks on the Scotian Shelf between 1998 and 1999; since April 1998 was the first month in which detailed length measurements were collected as part of the science–industry collaboration, the month with the highest proportion of small sharks (March) was not represented in the catch at age. The absence of small sharks would be expected to distort the catch at age and artifactually produce a low estimate of Z.

Petersen analysis.—Petersen calculations of recent exploitation rate were based on a subset of the data from two independent and unpublished tag–recapture studies. Although Campana et al. (2001) presented a Petersen analysis of the complete data set, more than 80% of the tags were applied to porbeagles tagged at age 0 or 1 (<125 cm FL). Therefore, the current analysis was restricted to these younger sharks in order to improve the accuracy and precision of the exploitation rate estimates for these cohorts. The U.S. tags were applied each year between 1993 and 1997, while Canadian tagging was carried out between 1994 and 1997. The total number of releases at size was not available for the Norwegian tagging program and thus could not be included in the analysis. The number of tags applied to age-0 and age-1 sharks since 1993 was 1,177, of which 86 were subsequently recaptured.

The Petersen calculations were described by Ricker (1975):

$$\text{Exploitation rate} = \text{number recaptured/tags remaining},$$

where

$$\text{tags remaining} = \text{Numtag} \cdot e^{(-\text{Prloss} \cdot \text{Interval})} \cdot (1 - \text{Prmort}) \cdot \text{Prreport},$$

and Numtag = number tagged in a given year, Interval = interval between tagging and recapture (year), Prloss = Probability of tag loss, Prmort = Probability of tagging mortality, and Prreport = Probability of reporting. Tag recaptures from a given tagging year but prior to the calculated exploitation year were subtracted from ''tags remaining'' before adjustment for reporting rate and tag loss. Note that the exploitation rate is calculated for the year of recapture.

While the Petersen calculations are straightforward, certain assumptions must be made concerning rates of tag loss, tag-induced mortality, and the probability of nonreporting. Published estimates were not available for these rates in sharks tagged with steel dart tags, so approximate values based on teleosts were used. The probability of nonreporting was very low through the 1990s, given the few vessels in the fishery and the high level of motivation to tag and recapture. Sensitivity analysis indicated that mean exploitation rate did not differ by more than 25% with alternative but reasonable estimates for tag loss and mortality.

Life table analysis.—Life table analysis is well suited for use in sharks given their well-defined reproductive cycle and high rates of survival (Cortés 1998). The method uses age-structured estimates of survival rate, sexual maturation, and fecundity to project population growth under various scenarios. Survival-rate-at-age estimates were based on the natural mortality (M) estimates of Campana et al. (2001): $M = 0.2$ for first-year sharks, $M = 0.1$ for other immature age-groups, increasing to 0.2 for mature females. A scenario in which M remained at 0.1 after maturity was also evaluated. Fecundity was set at 3.9 pups per year, half of which were female (Jensen, unpublished data). The age-specific female maturity ogive was presented by C. F. Jensen (unpublished data), as was the evidence that reproduction occurred annually. Maximum longevity was set at 29 years or 45 years, depending on the postmaturity mortality rate selected (Natanson et al., in press). Area-specific selectivity curves were derived from an age- and sex-structured population model (Campana et al. 2001).

Results

The Fishery

The fishery for porbeagle sharks in the northwest Atlantic Ocean (NAFO areas 3–6) (Figure 1) started in 1961 when Norwegian vessels began exploratory fishing on what was then a virgin population (Table 2; Figure 2). These vessels had previously fished for porbeagles in the northeast Atlantic. They were joined by vessels from the Faroe Islands during the next few years. Reported landings in the northwest Atlantic rose from about 1,900 metric tons (mt) in 1961 to over 9,000 mt in 1964 and then fell to less than 1,000 mt in 1970 as a result of a collapse of the fishery (Table 2; Figure 2). Although the fishery was unrestricted, reported landings were less than 500 mt until 1989. Reported landings rose to about 2,000 mt in 1992 as a result of increased effort by Faroese vessels and the entry of Canadian interests into this fishery. Faroese participation was phased out of the directed fishery by 1994, at which time total landings by three Canadian offshore pelagic longline vessels and a number of inshore vessels was about 1,600 mt. Since that time, the fishery has been almost exclusively Canadian, with landings declining gradually to 1,066 mt in 1998. Landings from 1998 onwards have been restricted by quota control to between 900 and 1,000 mt.

Efforts to develop a fisheries management plan for any of the pelagic shark species in Atlantic Canada did not come into force until 1994. The management plan made provision for the collection of catch and effort data through completion and submission of logbooks and for collection of sampling data (species, sex, length, weight) for each shark landed through a dockside monitoring program (DMP). In 1997, a more comprehensive plan was released to govern the exploitation of all large pelagic shark species through the maintenance of a biologically sustainable resource and a self-reliant fishery. Conservation was not to be compromised and a precautionary approach was to guide decision making. All licenses issued under the plan were to be considered exploratory while scientific information was collected and the sustainability of the resource was evaluated. The management plan of 2000–2001 was the first to be based on the new scientific data and the accompanying analytical stock assessment for the porbeagle (Campana et al. 1999). In addition to a reduced quota, the plan restricted access to the porbeagle mating grounds off of southern Newfoundland. Based on additional scientific infor-

TABLE 2.—Reported porbeagle landings (metric tons) by country.

	Northwest Atlantic (NAFO areas 3–6)										
Year	Canada	Faroe Islands	France	Iceland	Japan	Norway	Spain	USSR	USA	Total	Northeast Atlantic
1961	0	100				1,824				1,924	1,600
1962	0	800				2,216				3,016	500
1963	0	800				5,763				6,563	300
1964	0	1,214		7		8,060				9,281	400
1965	28	1,078				4,045				5,151	500
1966	0	741				1,373				2,114	500
1967	0	589			36					625	600
1968	0	662			137	269				1,068	1,000
1969	0	865			208					1,073	1,000
1970	0	205			674					879	4,300
1971	0	231			221					452	4,400
1972	0	260				87				347	3,500
1973	0	269								269	400
1974	0									0	343
1975	0	80								80	577
1976	0	307								307	497
1977	0	295								295	374
1978	1	121								122	3,120
1979	2	299								301	1,295
1980	1	425								426	1,172
1981	0	344			3					347	1,031
1982	1	259			1					261	341
1983	9	256			0					265	886
1984	20	126			1	17				164	556
1985	26	210			0					236	440
1986	24	270			5			1		300	425
1987	59	381			16			0	12	468	404
1988	83	373			9			3	32	500	523
1989	73	477			9			3	4	566	444
1990	78	550			8			9	19	664	684
1991	329	1,189			20			12	17	1,567	450
1992	814	1,149			7			8	13	1,991	643
1993	920	465			6			2	39	1,432	840
1994	1,573				2				3	1,578	1,023
1995	1,348		7		4				5	1,364	730
1996	1,043		40		9				8	1,100	411
1997	1,317		13		2				2	1,334	539
1998	1,054		20		0				12	1,086	465
1999	955				6					961	
2000	899				0					899	

mation and an improved stock assessment, the management plan of 2002 reduced allowable catches of porbeagles by a further 70% and eliminated access to the mating grounds (Campana et al. 2001). Further details of the shark management plan and porbeagle management history are presented in Campana et al. (1999, 2001).

Porbeagles are taken almost exclusively by a Canadian directed longline fishery which focuses its effort on largely immature porbeagles on the Scotian Shelf (Shelf) in spring and on larger, primarily mature animals off Newfoundland and in the Gulf of St. Lawrence (NF–Gulf) in the fall (Figure 3). Both inshore and offshore fleets fished the Shelf in the spring of recent years, although the offshore fleet tended to fish near the edge of the continental shelf while the inshore fleet fished well onto the Shelf. Fishing by both fleets was minimal in the summer. In the fall, the small amount of catch taken by the inshore fleet was mainly from the Scotian Shelf, while the much larger offshore catches were made in the Gulf of St. Lawrence, off southern Newfoundland, and on the Grand Banks (NF–Gulf; Figure 3).

Porbeagle bycatch in the Canadian longline fishery for swordfish *Xiphias gladius*, the Japanese longline fishery for tuna *Thunnus* spp., and various inshore fisheries is minimal, seldom exceeding 40 mt in recent years (Table 3). While the reported catches of shortfin makos *Isurus oxyrinchus* and unspecified sharks prior to 1996 are likely to have been mainly porbeagles, the effect on the overall

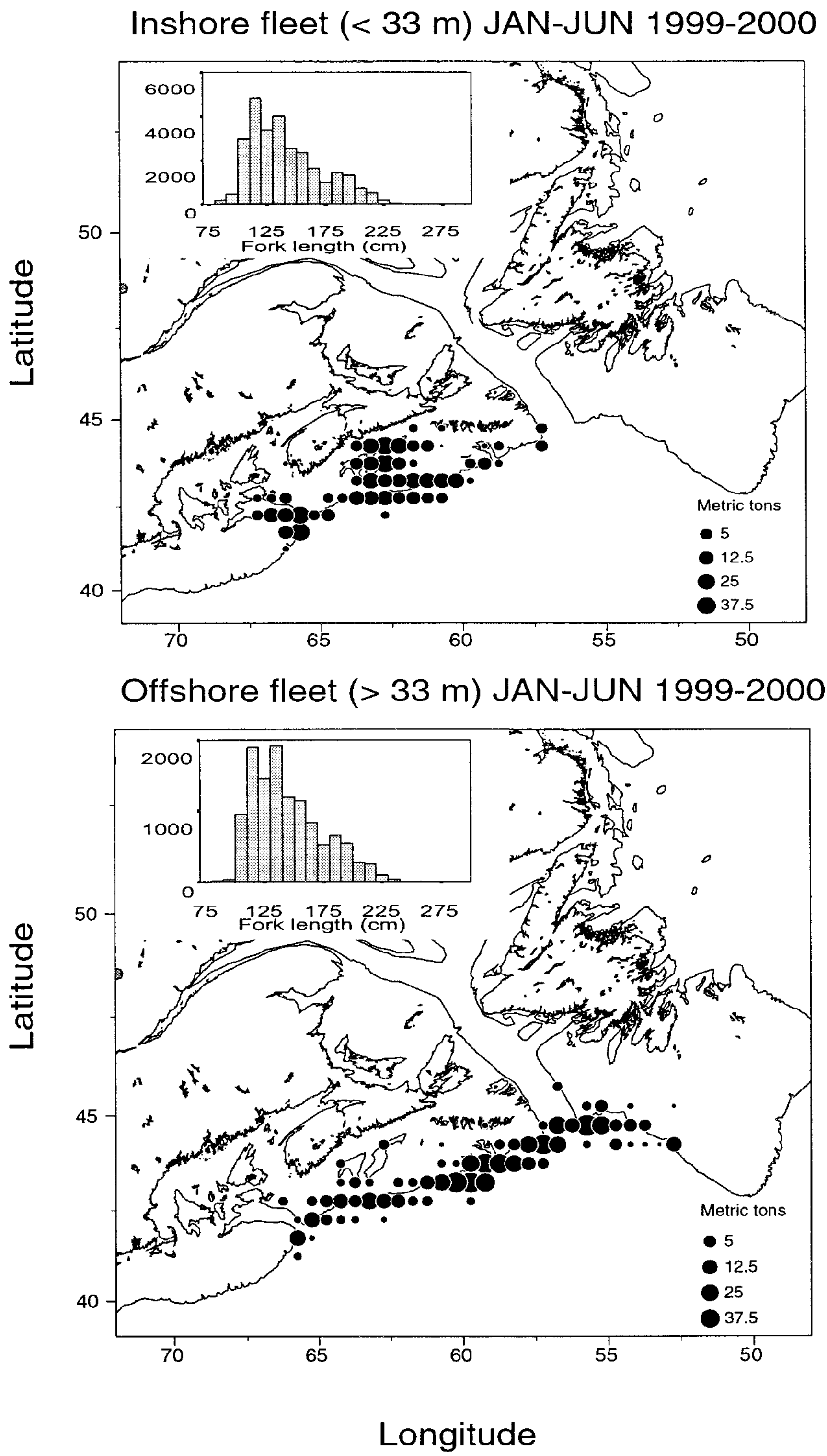

FIGURE 3.—Catch location and associated length composition for Canadian inshore (<33 m) and offshore (>33 m) vessels in spring (January–June) and fall (July–December) of 1999–2000.

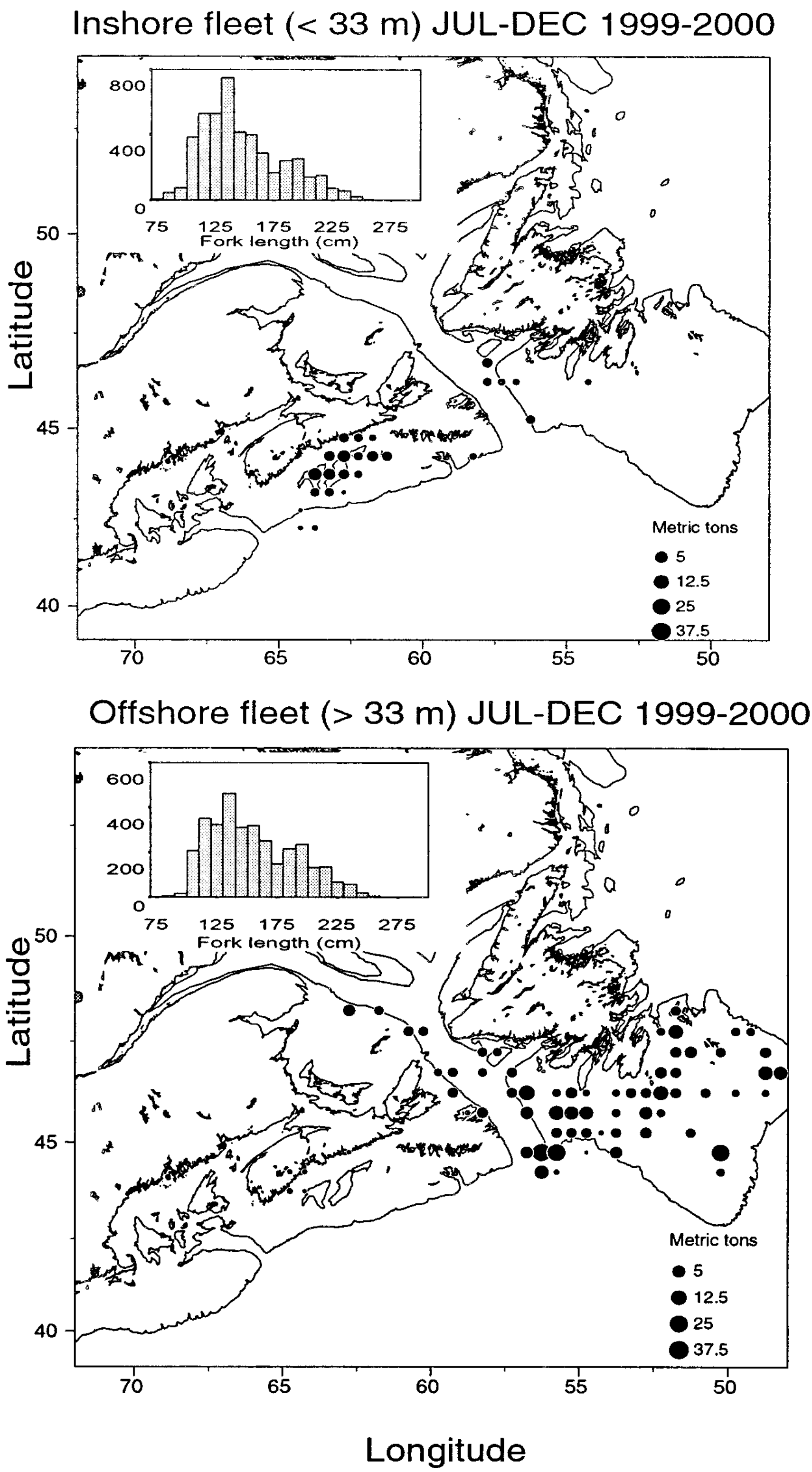

FIGURE 3.—Continued.

TABLE 3.—Canadian porbeagle, mako, and unspecified shark landings (metric tons) by fishery; TAC = total allowable catch.

Year	Directed longline	Swordfish bycatch	Tuna bycatch	Other bycatch	Reported as mako	Reported as unspecified shark	Total shark	TAC
1991	329	0	0	0	0	185	514	NA
1992	805	0	0	9	0	171	985	NA
1993	912	0	0	8	4	174	1,098	NA
1994	1,552	9	2	18	142	121	1,844	NA
1995	1,313	21	0	15	111	40	1,500	1,500
1996	1,024	6	1	24	67	20	1,142	1,500
1997	1,295	6	0	40	86	43	1,470	1,000
1998	1,020	8	0	28	71	37	1,164	1,000
1999	930	2	1	23	64	16	1,036	1,000
2000	888	2	1	8	62	13	974	850

catch trend is minimal. The International Observer Program has maintained 100% coverage of foreign catches in the Canadian zone since 1987, thus ensuring the accuracy of the foreign catches since that time. The recreational fishery for porbeagles is minimal.

In contrast with many other pelagic and groundfish fisheries, the directed fishery for porbeagles is highly species specific. An analysis of IOP-observed, porbeagle-directed sets between 1990 and 2000 demonstrated that 92% of the catch was porbeagles (Table 4). Most of the 8% bycatch consisted of blue sharks, and less than 1% consisted of large pelagic species other than sharks. Both Canadian and Faroese vessels experienced similarly low levels of bycatch in the porbeagle fishery.

Trends in Length and Age Composition

A biological indicator of a high exploitation rate is a long-term decline in fork length in the catch. A plot of median fork length against year of collection showed a long-term decline on the NF–Gulf mating ground in early fall (Figure 4). The median lengths for the years prior to 1980 are most representative of the length composition of a lightly fished population. In contrast, 1999 and 2000 were characterized by very low median sizes, indicating the loss of many sharks of mature size. There were no consistent long-term trends in size composition on the Scotian Shelf, an area dominated by smaller, primarily immature porbeagles.

The age composition of past and present landings is shown in Table 5. In recent years, the age of full recruitment to the fishery has dropped to only 2–3 years in all areas. Before 1993, the age of full recruitment was usually 6–7 years. The age composition of individual subareas more clearly showed the change in age structure. Before 1991, the most abundant age-class off southern Newfoundland in the fall was 10–15 years, which is consistent with the use of this area as a mating ground by a lightly fished population. In contrast, porbeagles less than age 3 were the most abundant age-classes in the NF–Gulf catch of 1998–2000.

Commercial Catch Rates

The overall trend in catch rate was analyzed with a linear model with subarea, month, fishing vessel, and year as factors. All factors were significant in the model predicting the catch rate of mature porbeagles. Several interaction terms with the year factor were also significant, but their inclusion did

TABLE 4.—Observed bycatch associated with directed porbeagle fisheries between 1981 and 1999.

		Bycatch (%)									
Country	Porbeagle fisheries (metric tons)	Blue shark *Prionace glauca*	Mako	Other sharks	Swordfish	Bluefin tuna *Thunnus thynnus*	Albacore *Thunnus alalunga*	Bigeye tuna *Thunnus obesus*	Yellowfin tuna *Thunnus albacares*	Groundfish	Other
Canada	995	6.99	0.20	0.03	0.03	0.04	0.00	0.00	0.00	0.03	1.61
Faroe Islands	3,378	5.91	0.13	0.41	0.01	0.06	0.00	0.00	0.00	0.02	0.15
Total	4,373	6.15	0.14	0.32	0.01	0.05	0.00	0.00	0.00	0.03	0.48

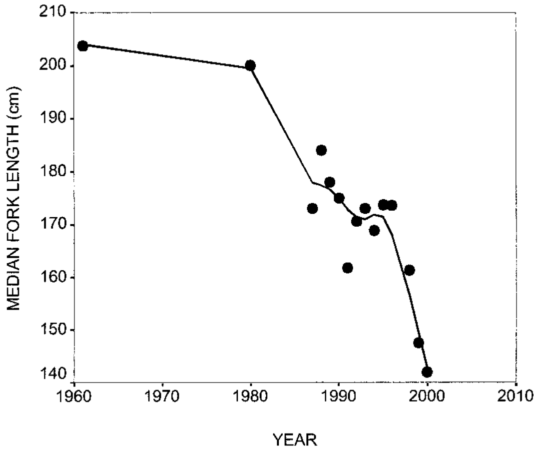

FIGURE 4.—Long term changes in the median fork length of porbeagles in the commercial catch by the offshore fleet during September–October on the southern Newfoundland (NF–Gulf) mating grounds. A LOESS curve has been fit to the data.

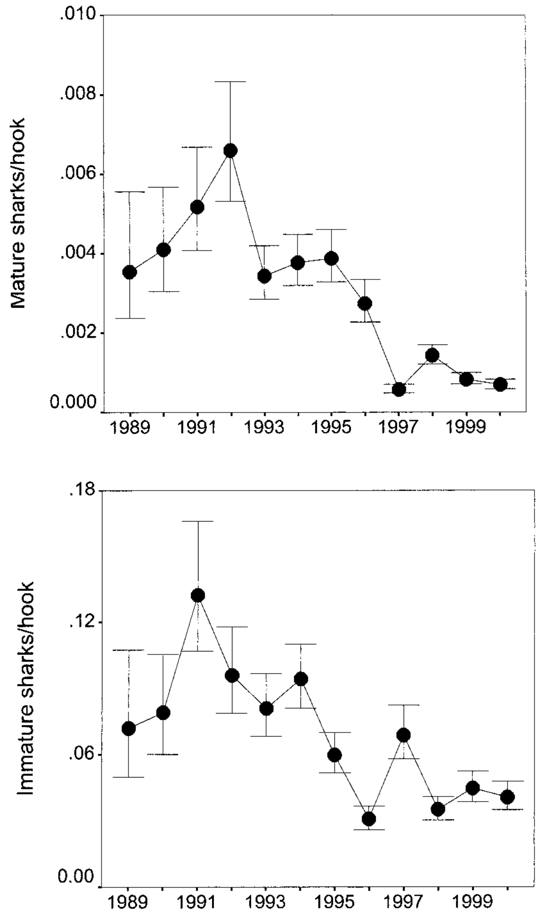

FIGURE 5.—Standardized catch rate (number/hook) of sexually mature (>200 cm fork length, FL) and immature (<200 cm FL) porbeagles. Factors in the analysis included year, month, area, and vessel. Error bars are 95% confidence intervals.

not change the overall trend in catch rate, which is shown in Figure 5. The standardized catch rate of mature porbeagles increased significantly between 1989 and 1992 but declined sharply afterwards as effort increased and the abundance of the large sharks declined. The 2000 point is the second lowest in the time series and is 10% of the 1992 value. The standardized catch rate model for immature porbeagles was also highly significant and also showed a significant decline since the early 1990s (Figure 5). The 2000 point is about 30% of the 1991 point. However, the catch rate has remained roughly stable since 1996 (ignoring the 1997 value, which is also anomalous in the mature catch rate series), which is consistent with the fleet-specific catch rates (Campana et al. 2001). Overall, these catch rates suggest a monotonic and disturbing decline in the abundance of mature sharks, with a low but stable rate for immature sharks.

Recent Mortality Rates Based on Paloheimo Zs

Total instantaneous mortality rate in the most recent years was estimated through use of Paloheimo *Z*s (Table 6). All five of the mortality estimates ranged between 0.27 and 0.37, with a mean of 0.32. The *Z*-estimate for mature porbeagles on the NF mating grounds was not significantly different from that for immature porbeagles on the Shelf.

With a mean $Z = 0.32$ for ages 3–9 on the Shelf (Table 6), and given an immature $M = 0.10$ (Campana et al. 2001), recent fishing mortality on immature Shelf porbeagles would be 0.22. This estimate would be slightly inflated if older but immature females were less available on the Shelf in the spring. In the NF–Gulf area in fall, mean *Z* for ages 9–13 was estimated as 0.33. Assuming an $M = 0.15$ intermediate to that of immature and mature sharks, fishing mortality would be estimated at 0.18.

Petersen Calculations of Recent Exploitation Rate

The exploitation rate of the fished population in the 1990s was estimated through Petersen analysis of tag recaptures (Table 7). The unadjusted exploitation rate based on the Petersen calculations ranged between 4% and 12%, with a mean of 8%.

TABLE 5.—Catch at age (number) by year, aggregated across subareas and sexes.

	Year										
Age	1961	1980	1981	1987	1988	1989	1990	1991	1992	1993	1994
1	633	790	179	1,770	1,108	1,180	1,166	2,488	3,400	3,739	5,589
2	806	826	183	1,594	1,244	620	1,303	2,651	3,035	3,454	4,737
3	1,120	878	227	1,537	1,256	609	1,325	3,259	3,293	3,113	4,190
4	1,463	769	271	1,359	1,149	704	1,225	3,720	3,613	2,793	3,671
5	1,746	624	315	1,143	989	754	1,105	3,772	3,799	2,550	3,206
6	1,973	572	380	979	805	735	1,021	3,498	3,813	2,362	2,843
7	2,101	590	449	852	639	696	957	3,099	3,669	2,176	2,551
8	2,083	589	498	740	509	666	876	2,673	3,396	1,968	2,279
9	1,969	534	513	629	406	629	762	2,240	3,030	1,728	1,987
10	1,835	447	493	518	321	566	625	1,813	2,608	1,460	1,661
11	1,707	361	442	413	249	478	487	1,416	2,169	1,181	1,318
12	1,574	294	371	321	190	380	366	1,072	1,747	920	996
13	1,425	244	295	246	143	291	269	793	1,369	695	723
14	1,260	203	223	187	106	219	196	577	1,049	515	510
15	1,088	166	163	142	78	167	141	415	791	377	353
16	917	131	116	108	57	131	102	296	589	276	242
17	756	99	82	82	42	106	73	211	434	202	166
18	612	73	56	62	31	89	53	151	319	148	113
19	487	52	39	47	23	76	39	108	234	109	78
20	383	36	27	36	18	65	29	77	171	81	54
21	298	25	18	27	14	56	21	56	126	61	38
22	230	17	12	20	11	48	16	41	93	46	26
23	177	11	9	15	9	41	12	30	69	35	19
24	136	8	6	12	7	35	10	22	52	26	14
25	105	5	4	9	6	29	8	16	39	20	10
26	81	4	3	7	5	25	6	12	30	16	7
27	63	2	2	5	5	21	5	9	23	12	6
28	49	2	2	4	4	17	4	7	18	10	4
29	38	1	1	3	4	14	3	6	14	8	3
30	30	1	1	3	3	12	3	4	11	6	2
Sum	27,146	8,353	5,381	12,871	9,431	9,458	12,208	34,533	43,000	30,088	37,397

No trend was apparent across recent years, and the independent tagging studies of the USA and Canada provided similar estimates of exploitation rate since 1994. When adjusted for age-specific selectivity (Table 8), the exploitation rate was estimated to lie between 5% and 20%, with a mean of about 11% (Figure 6).

Life Table Analysis

As part of a life table analysis for porbeagles, fishing mortality (F) was added to natural mortality (M) to investigate various fishing strategies, subject to area-specific selectivities (Table 8). A fishery in which all ages were fully selected was also investigated. The results indicated that the intrinsic rate of population growth (r) in an unfished population varied between 0.05 and 0.07, depending on the natural mortality assumptions that were made (Table 9). Such values are very low compared with that of most fishes (Myers et al. 1999) and indicate that the porbeagle population is intrinsically unproductive and slow to recover from stock depletion. Fishing at $F_{0.1}$ = 0.18 was unsustainable and resulted in population decline under all scenarios. A fishing scenario with F = 0.08 resulted in population decline when the selectivity of the mature fish was high (e.g., in NF–Gulf) and produced only marginal growth when mature selectivity was low (e.g., on the Shelf). A fishing mortality of 0.08 corresponded to zero population growth using the area-combined selectivity vector, and thus serves as the biological reference point for $F_{\text{replacement}}$. Fishing mortality at maximum sustainable yield (F_{msy}) was calculated as 0.04.

Discussion

Porbeagles produce few offspring and mature at a late age compared with the age of first capture. This combination of life history characteristics makes porbeagles more susceptible to overexploitation than most teleosts. Average catches of about 4,500 mt per year in the early 1960s resulted in a fishery that collapsed after only 6 years and that did not recover for another 25 years. The fishery appeared sustainable during the 1970s and

TABLE 5.—Extended.

	Year					
Age	1995	1996	1997	1998	1999	2000
1	2,932	2,006	5,757	1,799	3,654	3,823
2	3,336	2,098	5,483	2,291	3,980	3,844
3	3,674	2,242	5,008	2,406	3,549	3,260
4	3,620	2,207	4,363	2,267	2,857	2,589
5	3,208	2,033	3,538	2,054	2,211	1,987
6	2,693	1,826	2,664	1,836	1,726	1,492
7	2,230	1,622	1,869	1,602	1,365	1,120
8	1,864	1,430	1,246	1,376	1,101	881
9	1,577	1,249	812	1,171	912	743
10	1,337	1,076	526	981	766	645
11	1,124	911	339	802	642	552
12	934	757	215	642	531	459
13	767	618	134	505	434	371
14	622	498	83	392	349	293
15	500	395	51	301	276	227
16	397	311	31	229	216	172
17	312	244	19	172	167	129
18	244	190	12	129	128	95
19	189	149	7	97	98	69
20	146	117	5	73	76	50
21	113	92	3	55	58	37
22	88	73	2	42	45	26
23	68	59	1	33	35	19
24	54	47	1	26	28	14
25	42	39	1	21	22	10
26	34	32	0	17	18	8
27	28	26	0	14	14	6
28	23	22	0	12	12	4
29	19	19	0	10	10	3
30	16	16	0	9	8	3
Sum	32,190	22,404	32,171	21,361	25,289	22,932

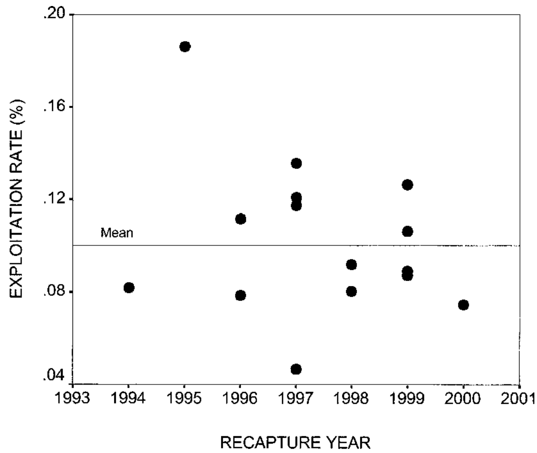

FIGURE 6.—Exploitation rate of the porbeagle in recent years based on Petersen analysis of tag recaptures from Canadian and U.S. tagging studies. The analysis was restricted to years with three or more recaptures and to sharks tagged at fork lengths less than 125 cm; thus the exploitation rates are most applicable to the spring fishery on the Scotian Shelf. Exploitation rates have been divided by age-specific selectivity (Table 8) to calculate the fully recruited exploitation rate.

1980s, when landings averaged 350 mt annually. However, annual catches of 1,000–2,000 mt throughout the 1990s appear to have once again impacted the population, producing lower catch rates, reduced numbers of large sharks, and markedly lower numbers of mature females. Such short-term population declines and long-term rebuilding times have seldom been observed in teleosts (Shepherd and Cushing 1990), highlighting the very different life history characteristics of sharks and teleosts.

The catch quota of 850 mt introduced in 1999, based on preliminary scientific information and with excellent cooperation from the porbeagle fishing industry, resulted in preliminary estimates of $F_{0.1}$ yield, mortality, and stock abundance. Nevertheless, it was acknowledged at the time that the $F_{0.1}$ yield was probably not sustainable. The current analysis confirms the unsustainability of fishing at $F_{0.1} = 0.18$ for porbeagle, and indicates that a fishing mortality above 0.08 will cause the population to decline. A fishing mortality of 0.04 corresponds to the maximum sustainable yield (MSY) and is required if the population is to be allowed to recover. Several independent estimates of recent fishing mortality all suggest that recent catches averaging 1,000 mt per year have resulted in an F of about 0.20 (Figure 7). An annual catch of 200–250 mt would correspond to fishing at MSY and would allow population recovery. Annual catches of 400 mt would not allow any population growth or room for error in the estimates. Current population size appears to be at 10–20% of virgin levels (Campana et al. 2001). The completion of an age- and sex-structured population model should allow the time series of population biomass and exploitation rates to be reconstructed (S. Harley, Dalhousie University, unpublished).

Fishing quotas based on ‘‘conservative’’ strategies such as $F_{0.1}$ are commonly used to minimize the probability of either recruitment or growth overfishing in teleost fishes (Mace 1994). However, many shark species are unproductive compared with teleosts (Musick 1999), and with the production of only four pups per year, the porbeagle is among the least fecund of the shark species (Aasen 1963; Francis and Stevens 2000). Reporting results that would be viewed with skepticism in a teleost fishery, Rago et al. (1998) calculated that F_{max} exceeded the fishing mortality at which population replacement of spiny dogfish

TABLE 6.—Catch at age (number), standardized by effort (number of hooks), for the Scotian Shelf (Shelf) and Newfoundland and the Gulf of St. Lawrence (NFGulf). Also shown are estimates of recent mortality rates (Paloheimo *Z*s) for different age-groups and years.

Age and no. of hooks	Shelf			NFGulf		
	1998	1999	2000	1998	1999	2000
1	1,358	3,293	3,422	441	361	401
2	1,771	3,511	3,298	520	469	546
3	1,857	3,048	2,670	549	501	591
4	1,706	2,380	2,047	561	477	542
5	1,497	1,775	1,536	557	436	451
6	1,300	1,333	1,129	535	392	363
7	1,114	1,019	827	488	345	293
8	951	803	632	425	298	249
9	815	658	516	357	253	227
10	688	552	433	293	214	211
11	564	462	359	237	180	193
12	449	380	287	193	151	171
13	348	306	223	157	128	148
14	265	241	168	128	108	125
15	198	185	123	103	91	103
16	145	140	89	83	76	83
17	106	104	63	66	64	65
18	76	76	45	53	53	50
19	55	55	31	42	43	38
20	39	40	22	33	36	29
Hooks	446,118	466,955	400,666	172,850	155,836	191,381

Paloheimo *Z*

$Z_{3\text{–}5,\ 1999\ \text{to}\ 4\text{–}6,\ 2000} = 0.27$

$Z_{6\text{–}8,\ 1998\ \text{to}\ 7\text{–}9,\ 1999} = 0.35$

$Z_{6\text{–}8,\ 1999\ \text{to}\ 7\text{–}9,\ 2000} = 0.32$

$Z_{9\text{–}12,\ 1998\ \text{to}\ 10\text{–}13,\ 1999} = 0.37$

$Z_{9\text{–}12,\ 1999\ \text{to}\ 10\text{–}13,\ 2000} = 0.30$

Squalus acanthias could occur. The implications of our calculations extend beyond those of Rago et al. (1998), demonstrating that even the more conservative $F_{0.1}$ fishing target is anything but conservative for porbeagles and will eventually lead to stock collapse. Similar conclusions have been reached qualitatively for a wide range of low-productivity shark species, many of which

TABLE 7.—Exploitation rate of porbeagles in recent years based on Petersen analysis of tag recaptures from Canadian (Can) and U.S. tagging studies. Exploitation rates have been divided by age-specific selectivity (Table 8) to calculate the fully recruited exploitation rate.

Study	Year tagged	Interval	Number tagged	Year recaptured	Number recaptured	Previously recaptured	Probability of Tag loss	Probability of Reporting	Probability of Tagging mortality	Exploitation rate
US	1993	1	106	1994	3	0	.10	.90	.20	.08
US	1993	4	106	1997	5	6	.10	.90	.20	.12
US	1993	6	106	1999	3	13	.10	.90	.20	.09
Can–US	1994	1	171	1995	11	0	.10	.90	.20	.19
US	1994	2	131	1996	6	10	.10	.90	.20	.11
Can–US	1994	3	171	1997	9	17	.10	.90	.20	.14
US	1994	4	131	1998	4	22	.10	.90	.20	.09
US	1994	5	131	1999	5	26	.10	.90	.20	.13
Can–US	1995	1	295	1996	8	0	.10	.90	.20	.08
Can–US	1995	2	295	1997	6	9	.10	.90	.20	.05
Can	1995	3	179	1998	6	8	.10	.90	.20	.08
Can–US	1995	4	295	1999	10	21	.10	.75	.20	.11
Can–US	1996	1	74	1997	3	0	.10	.90	.20	.12
US	1997	2	99	1999	4	0	.10	.90	.20	.09
Can–US	1997	3	122	2000	3	4	.10	.70	.20	.07

TABLE 8.—Natural mortality (M), number of female pups produced per year, and area-specific selectivities for porbeagles by age. Shelf = the Scotian Shelf, NF–Gulf = Newfoundland and the Gulf of St. Lawrence. Values for porbeagles older than age 20 are not shown.

			Selectivity		
Age	M	Female pups	Shelf	NF–Gulf	Combined areas
0	0.2	0	0.05	0.05	0.05
1	0.1	0	0.40	0.15	0.32
2	0.1	0	0.70	0.20	0.53
3	0.1	0	1.00	0.30	0.77
4	0.1	0	1.00	0.50	0.83
5	0.1	0	1.00	0.60	0.87
6	0.1	0	1.00	0.75	0.92
7	0.1	0	1.00	0.90	0.97
8	0.1	0	0.80	0.95	0.85
9	0.1	0	0.60	1.00	0.73
10	0.1	0	0.40	1.00	0.60
11	0.1	0.18	0.20	1.00	0.47
12	0.1	0.45	0.10	1.00	0.40
13	0.2	0.98	0.10	1.00	0.40
14	0.2	1.50	0.10	1.00	0.40
15	0.2	1.64	0.10	1.00	0.40
16	0.2	1.87	0.10	1.00	0.40
17	0.2	1.93	0.10	1.00	0.40
18	0.2	1.95	0.10	1.00	0.40
19	0.2	1.95	0.10	1.00	0.40
20	0.2	1.95	0.10	1.00	0.40

TABLE 9.—Life table analysis results for porbeagles in the northwest Atlantic Ocean. The first section shows the rate of population growth (r) without fishing at two different rates of natural mortality (M) for the mature population. The other two sections show the rate of population growth at two different fishing mortality rates (F) and various selectivities (given in Table 8) with $M = 0.2$. The analysis reveals that $F = 0.08$ leads to zero population growth and $F = 0.04$ to the maximum sustainable yield. Harvesting at $F_{0.1} = 0.18$ leads to population decline.

M_{mature}	Selectivity	r
	$F = 0$	
0.1	0	0.071
0.2	0	0.051
	$F = 0.08$	
0.2	1	−0.028
	Shelf	0.012
	NF–Gulf	−0.005
	Both areas	0
	$F = 0.04$	
0.2	1	0.013
	Shelf	0.031
	NF–Gulf	0.024
	Both areas	0.029

appear incapable of supporting more than a nominal fishing mortality (Cortés 1998, 1999; Walker 1998; Musick 1999; Simpfendorfer 1999; Stevens 1999). The inherent vulnerability of sharks and other elasmobranchs to overfishing and stock collapse was recently highlighted in an American Fisheries Society policy statement, which noted that most elasmobranch populations decline more rapidly and recover less quickly than do other fish populations (Musick et al. 2000).

Despite obvious indicators of overexploitation, there are some key differences between the current porbeagle fishery and the fishery that was present before the 1967 collapse, which suggest that sustainability may yet be possible. More than 80% of the recent annual catch has been taken on the Scotian Shelf in the spring, a time when availability is largely limited to immature sharks. A fishery that preferentially targets immature sharks is very different from the fishery in the 1960s before the fishery collapse, when the fishery focused on aggregations of mature (and possibly mating) sharks in the fall off of southern Newfoundland. Fishing mortality is now low and strictly regulated, with minimal bycatch in other fisheries. In addition, the fishing industry provides accurate catch and effort data and measures each shark individually, thus

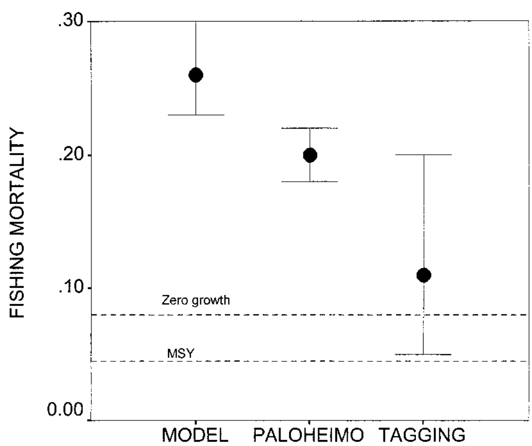

FIGURE 7.—Summary of recent fishing mortality (F) estimates derived from independent analyses. Estimates are drawn from analysis of the years 1994–2000 (tagging), 1998–2000 (Paloheimo Zs), and 2000 (population model; Campana et al. 2001). Error bars indicate the approximate range of uncertainty based on multiple estimates. All estimates of recent F are above a level which would allow population recovery (MSY) or maintain current population size (zero growth).

facilitating population monitoring. Management measures to restrict or eliminate fishing of mature females through closed areas are recent innovations. Finally, the current porbeagle fishing industry in the northwest Atlantic is highly motivated to conserve the population and has assisted in its scientific study. While it remains to be seen if the porbeagle population can be fished sustainably, the necessary elements for a sustainable fishery appear to be in place.

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