Changes in baseline growth and maturation parameters of Northwest Atlantic porbeagle, *Lamna nasus*, following heavy exploitation

Rachel M. Cassoff, Steven E. Campana, and Sigmund Myklevoll

Abstract: We tested for density-dependent changes in growth and maturation of Northwest Atlantic porbeagle (*Lamna nasus*) after the population declined by 75%–80% from fishing. Vertebrae and reproductive data collected from the virgin (1961–1966) and exploited (1993–2004) populations were analysed to test for differences in growth rate and age and length at maturity between the time periods. We detected significant differences between reparameterized von Bertalanffy growth models for each period, using likelihood ratio tests. Beyond an age of 7 years, mean length at age was greater during 1993–2004 than during 1961–1966. Between 1961–1963 and 1999–2001, length at maturity decreased in males (from 179 to 174 cm curved fork length (CFL)) and was invariant in females (216 cm CFL), whereas age at maturity declined in both males (from 8 to 7 years) and females (from 19 to 14 years). An analysis of porbeagle temperature associations indicated that sharks occupied comparable temperature conditions during the mid-1960s and 1990s, ruling out the possibility of temperature-induced growth changes. The observed increase in growth rate and decrease in age at maturity following exploitation support the hypothesis of a compensatory density-dependent growth response.

Résumé : Après que la population de maraîches (*Lamna nasus*) du nord-ouest de l'Atlantique eût décliné de 75–80 % à cause de la pêche, nous avons recherché l'existence de changements reliés à la densité dans la croissance et la maturation. Nous avons analysé des données sur les vertèbres et la reproduction récoltées dans la population non exploitée (1961–1966) et la population exploitée (1993–2004) afin de vérifier les différences de taux de croissance et d'âges et longueurs à la maturité durant ces deux périodes. Des tests de rapports de vraisemblance indiquent des différences significatives entre les modèles de croissance de Bertalanffy reparamétrisés durant les deux périodes. Au-delà de l'âge de 7 ans, la longueur moyenne en fonction de l'âge est plus grande en 1993–2004 qu'en 1961–1966. Entre 1961–1963 et 1999–2001, la longueur à la maturité a diminué chez les mâles (de 179 à 174 cm de longueur courbée à la fourche, CFL), mais elle est demeurée la même chez les femelles (216 cm CFL); cependant, l'âge à la maturité a décliné, tant chez les mâles (de 8 à 7 ans) que chez les femelles (de 19 à 14 ans). Une analyse des associations des maraîches avec la température indique que ces requins ont vécu dans des conditions thermiques comparables durant le milieu des années 1960 et les années 1990, ce qui élimine la possibilité que les changements de croissance aient été causés par la température. L'accroissement du taux de croissance et le déclin de l'âge à la maturité observés après l'exploitation est compatible avec l'hypothèse d'une réaction de croissance dépendante de la densité.

[Traduit par la Rédaction]

Introduction

The porbeagle, *Lamna nasus*, is a large, cold-temperate, pelagic shark species found in the eastern and western North Atlantic and more broadly throughout the oceans of the southern hemisphere (Svetlov 1978; Compagno 2001). Porbeagles residing in the Northwest Atlantic are considered to be members of a single population (Campana et al. 1999) ranging from northern Newfoundland to at least New Jersey and perhaps to South Carolina (Templeman 1963; Campana et al. 1999). Porbeagles in this population are most abundant on and along the continental shelves in the area encompassing the Gulf of Maine (off New England) to the Grand Banks (off southern Newfoundland). However, distribution varies seasonally across this region as a result of size and sex-specific north–south migrations (Aasen 1963; Campana et al. 2001).

In the Northwest Atlantic, porbeagle abundance has declined by an estimated 75%–80% since the early 1960s (Department of Fisheries and Oceans (DFO) 2005), warranting

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R.M. Cassoff.[1,2] Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4J1, Canada.
S.E. Campana. Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.
S. Myklevoll. Institute of Marine Research, P.O. Box 1870, Nordnes, N-5817 Bergen, Norway.

[1] Corresponding author (e-mail: rcassoff@hotmail.com).
[2] Present address: 413 Maple Lane, Sewickley, PA 15143, USA.

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their recent designation as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004). Several independent lines of evidence strongly implicate exploitation in commercial target fisheries as the cause of this decline (Campana et al. 2003). Commercial harvesting of porbeagles started in 1961, when Norwegian longliners began exploratory fishing on the virgin (previously unexploited) population. Historically, exploitation was most intense during the first few years of the fishery. From 1961 to 1964, total reported annual landings in the Northwest Atlantic rose from 1900 to 9000 tonnes (t) (Campana et al. 2002*a*). These intense fishing efforts precipitated the collapse of the Norwegian fishery in the late 1960s and reduced the population to an estimated 50% of the virgin abundance (DFO 2005). A modest recovery of porbeagle numbers occurred throughout the 1970s and 1980s, as landings averaged less than 350 $t{\cdot}year^{-1}$ (Campana et al. 2002*a*). However, annual catches increased to 1000–2000 t during the 1990s, and the abundance of porbeagles once again fell sharply (Campana et al. 2003). Subsequent catch restrictions, implemented under a Canadian Shark Management Plan, reduced annual landings to less than 250 t by 2002 (Campana et al. 2003). A recent stock assessment indicated that these measures were effective in stabilizing the population at its current low level (DFO 2005).

Given the magnitude of the decline in porbeagle abundance since the early 1960s, a density-dependent compensatory response would be expected. One process that could potentially lead to compensation in depleted shark populations is a density-dependent increase in somatic growth rates owing to reduced prey limitation and a concomitant decrease in the age at sexual maturity (as maturation is largely size-dependent) (Holden 1973). Demographic analyses have demonstrated that a compensatory growth response may be one of the main mechanisms of population regulation in sharks (Smith et al. 1998; Cortés 2002; Frisk et al. 2005). Compensatory changes in growth have been observed in a large number of teleost populations (see Rose et al. (2001) and references therein). However, because reliable, long-term biological and fisheries data are lacking for the majority of elasmobranch species (Compagno 1990; Stevens et al. 2000), few rigorous empirical investigations have addressed compensatory processes in sharks.

Two recent studies have provided the only empirical evidence to date of density-dependent growth in sharks. Carlson and Baremore (2003) reported increased juvenile growth rates and earlier sexual maturation of Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) in the Gulf of Mexico after a period of intensified exploitation. Similarly, off the southeastern US, Sminkey and Musick (1995) observed faster growth in juvenile sandbar sharks (*Carcharhinus plumbeus*) following declines in population size. Although density-dependent effects were strongly implicated in these changes, neither study was able to evaluate the relative influence of other factors that affect rates of growth, such as changes in environmental conditions. Furthermore, sampling occurred well after the onset of exploitation in both studies. Therefore, the documented changes in life history likely do not represent the full scope for compensatory response in either shark species.

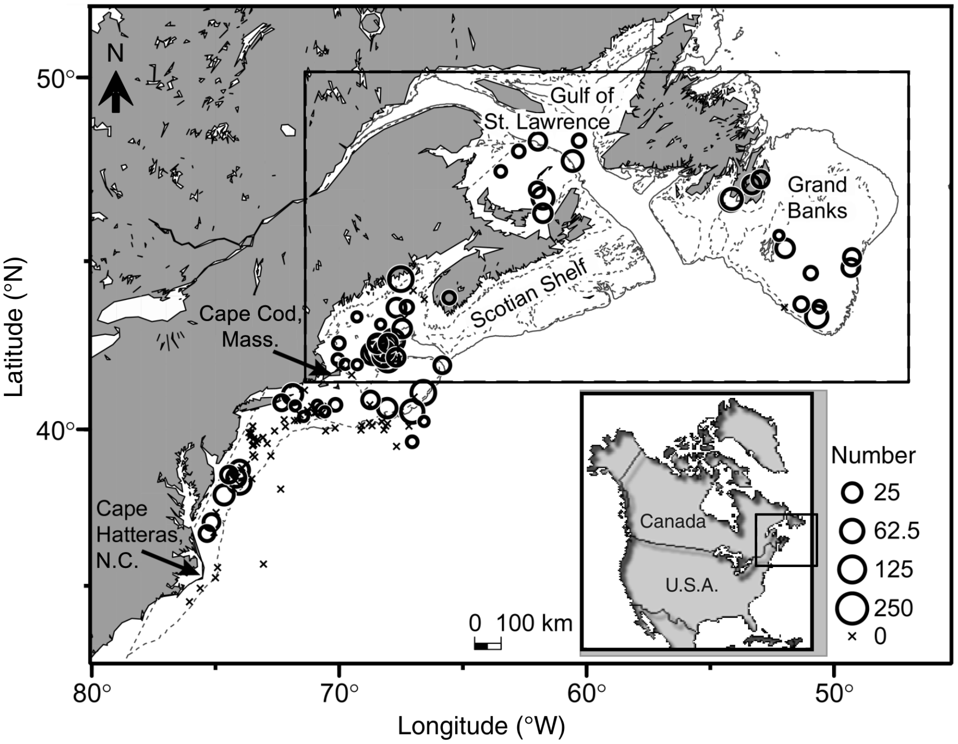
The biology of the porbeagle in the Northwest Atlantic has been the subject of research since the commencement of commercial harvesting in the early 1960s. As a result, vertebral samples and reproductive data were available from the periods 1961–1966 and 1993–2004, providing us with the opportunity to examine possible density-dependent changes in baseline growth and maturation parameters. As far as we are aware, this is the only shark population for which pre-exploitation life history data are available. The first objective of our study was to reconstruct porbeagle growth rate and estimate age and length at maturity in order to test for differences between the time periods. If porbeagle growth was responsive to changes in density, then we would expect an increase in growth rate, as well as a decline in the age at maturity between the sampling periods. In addition to evaluating density-dependent effects, we also considered the effects of variation in ambient water temperature on porbeagle growth as an alternative explanation of observed growth rate changes. Finally, we evaluate the implications of our findings to the understanding of life history theory in sharks.

Materials and methods

Two sets of porbeagle vertebrae were used for age and growth analysis: one taken after three to four decades of heavy exploitation in the Northwest Atlantic and one taken from the virgin (previously unfished) population. Collectively, 615 samples were available from the recent past: 558 prepared vertebrae available from 1993–1999, which were used for a previous age determination study (Natanson et al. 2002), and 57 additional vertebrae obtained in 2004. Sampling took place primarily in the spring and fall on commercial and research vessels operating with longline gear in an area encompassing the Gulf of Maine to the Grand Banks (off southern Newfoundland) and Gulf of St. Lawrence (Fig. 1). Captured individuals were considered to be members of a single population, an assumption strongly supported by long-term tagging studies by Canada, the US, and Norway (Campana et al. 1999). Vertebrae were taken from sharks between the head and the branchial chamber (numbers 10–15) and stored frozen or in 70% ethanol. Body lengths were reported to the nearest centimetre as curved fork length (CFL; over the body distance from the tip of the snout to the fork in the tail) (CFL = straight fork length, r^2 = 0.998; Campana et al. 1999). Reproductive information, including maturity status and length of reproductive organs, was available for the years 1999–2001 (Jensen et al. 2002).

Vertebral samples collected in 1961–1966 were analyzed to reconstruct the growth rate of the virgin porbeagle population. A total of 229 samples were acquired from the archives of the Institute of Marine Research (IMR) in Bergen, Norway. Most of the vertebrae (99%) were collected in the first 2 years of the fishery. Sampling was carried out between May and August by Olav Aasen (IMR) onboard the Norwegian longliners that first targeted porbeagles in the Northwest Atlantic. Vertebrae were taken on the same fishing grounds as the more recent samples (with the exception of one shark captured off North Carolina) and with comparable fishing gear (Joyce 1999). Four to six vertebrae were reportedly removed midway between the head and the caudal

Fig. 1. Map of the Northwest Atlantic showing the distribution of porbeagle (*Lamna nasus*) catch recorded in the 1965 and 1966 fishing logs of the Norwegian longliner *M.S. Volstad*. Fishing locations for the remainder of the sampling period (1961–1964) are not shown. Expanding circles are proportional in size to the number of sharks captured, and ×s represent zero catch. The principal porbeagle fishing grounds, where historical and recent vertebral samples were collected, are delineated by the rectangle. The 100 m (broken lines) and 200 m (solid lines) depth contours are shown.



fin of each shark (numbers 50–60) (S. Myklevoll, personal communication, 2005) and stored either dry or in formalin. Aasen (1963) recorded exterior clasper and uterus lengths to the nearest millimetre and either a nonstandard total length (TL) or dorsal length (DL; distance from the anterior edge of the first dorsal fin to the anterior precaudal pit) to the nearest centimetre. The following regression models were used to convert Aasen's body length measurements to CFL (Campana et al. 1999, 2001):

$$\mathrm{CFL} = 0.947\,\mathrm{TL} + 3.64 \quad (n = 361, r^2 = 0.99)$$

$$\mathrm{CFL} = 3.03\,\mathrm{DL}^{0.904} \quad (n = 356, r^2 = 0.99)$$

One vertebra from each shark was processed according to the methods of Natanson et al. (2002). This entailed removing excess tissue and measuring medial dorso-ventral centrum diameter (CD) with calipers to the nearest millimetre. A sagittal (bow tie) cross section of each centrum was made through the center with a diamond-bladed Isomet saw. Digital images of sections were taken using an image analysis system under reflected light (1280 × 1024 resolution). To increase the contrast between adjacent growth bands, images were digitally enhanced using Adobe Photoshop 7.0® (Adobe Systems Inc. 2002). Centrum radius (CR) was measured to the nearest millimetre on these images with Optimas 5.2® (Meyer Instruments Inc. 2000), unless both section halves were broken during processing. Measurements were taken on each half bow tie from the base, which is located just above the isthmus, to the distal edge along the intersection of the corpus calcareum with the intermediala.

Rigorous validation studies, using several techniques, have confirmed that deposition of a single pair of opaque and translucent bands (growth increment) occurs annually in porbeagles from birth to an age of at least 26 years (Campana et al. 2002*b*; Natanson et al. 2002). To ensure the accuracy of age determinations in the present study, interpretation of annuli was calibrated with a reference collection of more than 500 sectioned vertebrae of known or consensus-derived ages, used in the aforementioned studies. Samples from both time periods were then aged twice by the senior author, in a random order, following a double-blind procedure. Those deemed unreadable (recent sample, $n = 31$; historical sample, $n = 26$) were excluded from further analysis. The consistency of the new age interpretations with those published previously was evaluated using age-bias plots, and the coefficient of variation (CV) was used as a measure of precision (Campana et al. 1995).

Some of the sample tags attached to dried, historical vertebrae had deteriorated, making it impossible to link these samples to Aasen's recorded data. To estimate the lengths of these sharks, CFL was derived from a regression model fitted to the CFL–CR data or, in the absence of CR measurements, from the calculated relationship between CFL and CD. Both of these regressions were generated from a subsample of Aasen's vertebrae for which TL was recorded.

To compare growth characteristics between the virgin and exploited porbeagle populations, the von Bertalanffy growth function (VBGF), as well as a reparameterized version of this model, were fitted to each set of length at age data using nonlinear least squares in Systat 10.0® (Systat Software Inc. 2002). The conventional VBGF (von Bertalanffy 1938; Ricker 1979) is expressed as

$$L_t = L_\infty [1 - \mathrm{e}^{-K(t-t_0)}]$$

where L_t is the mean length at age t, L_∞ is the mean asymptotic length, K is the Brody growth coefficient, which determines how rapidly the horizontal asymptote is approached, and t_0 is the mean age at length zero. The alternative parameterization was formulated by Francis (1988) as

$$L = l_\phi + (l_\psi - l_\phi)(1 - r^{2(T-\phi)/(\psi-\phi)})/(1 - r^2)$$

where

$$r = (l_\psi - l_\chi)/(l_\chi - l_\phi)$$

The parameter L represents the mean length at age T, and l_ϕ, l_χ, and l_ψ represent the mean lengths at ages ϕ, $(\phi + \psi)/2$, and ψ, respectively, which were selected to fall within the range of both data sets. In addition, locally weighted least squares regression (lowess) curves were used to describe patterns of growth during each time period and were fitted to length at age data using the Lowess function in SPSS 11.5.0® (SPSS Inc. 2002).

Both the reparameterized and traditional von Bertalanffy growth models were used to test for statistical differences between the virgin and exploited length at age data sets. The reparameterized model was selected, because it overcomes two of the shortfalls of the conventional VBGF: the L_∞ and K parameters tend to be strongly correlated and the estimation of some parameter values involves extrapolation (Francis 1988). Likelihood ratio tests were employed to test for differences in growth curves between the time periods (Kimura 1980). Of the most commonly used statistical procedures for growth curve comparison, this approach is considered to be the most accurate on the basis of empirical analyses conducted by Cerrato (1990). This test assumes a normal, additive error structure and equal variances between data sets. The validity of the latter assumption was assessed using a Bartlett's test (Zar 1996).

Male length at maturity in porbeagles is associated with a distinct inflection in clasper growth (Jensen et al. 2002). Differences in male length at maturity between time periods were evaluated by fitting a logistic growth model to each set of clasper length (CL) – CFL data using nonlinear least squares and comparing their inflection points, which were used as a common reference point. The model was formulated following Piner et al. (2005):

$$\hat{y} = y_{\min} + k[1 + \exp(b(a - x))]^{-1}$$

with fixed parameters y = CL, $y_{\min}$ = the minimum observed CL, and x = CFL and estimated parameters k = maximum observed CL – minimum observed CL, a = inflection point, and b = shape parameter. Length at female maturity, which corresponds with a marked increase in uterus development (Jensen et al. 2002), was clearly visible from graphs of uterus length versus CFL. The length at maturity for the virgin population, estimated from a plot of uterus growth, was compared with the reproductive information from more recent years reported by Jensen et al. (2002).

An analysis of historical porbeagle temperature associations was carried out using catch (number of sharks), effort (number of hooks per set), and fishing locations obtained from the 1965 logs of the Norwegian longliner *M.S. Volstad*. Vessel positions were given as Loran-A readings (to the nearest 5 μs) and were converted to latitude and longitude with LoranGPS 6.0® (Andren Software Co. 2005). Analyses were limited to the principal porbeagle fishing grounds extending north of Cape Cod, Mass. (Fig. 1).

To estimate the temperature at the depth of the longline gear associated with each fishing location, we extracted temperature profiles from the year 1965 from the Atlantic Fisheries Adjustment Program database (Bedford Institute of Oceanography, Dartmouth, Nova Scotia). Temperatures were averaged over the depth range (10–30 m) at which the Norwegian fleet set the longline hooks (Aasen 1963). Contour maps displaying temperature at mean gear depth, overlaid with catch per unit effort, were then produced for each month and area (e.g., Grand Banks) in which porbeagles were caught. Temperatures at fishing locations were estimated from these maps only if fishing sites were bounded on all sides by temperature contours.

The same set of contour maps was used to determine the range of temperatures available to porbeagles in areas surrounding fishing sets (environmental temperature). Broad fishing areas, which included the Gulf of Maine, Grand Banks, and Gulf of St. Lawrence, were delineated on the maps by polygons enclosing all of the 1965 fishing locations. Temperature observations lying within these polygons were drawn from the maps along a 30′ latitude × 30′ longitude grid pattern.

To identify porbeagle temperature associations, we compared cumulative distribution functions (CDFs) of two variables: temperature at fishing locations, weighted by catch per unit effort, and environmental temperature (Perry and Smith 1994). Cumulative distribution functions were generated with temperatures pooled across months (May–August) and areas because of limited data availability. Disparities between CDFs imply that porbeagles prefer a particular temperature range, whereas similarities suggest a lack of association between porbeagle catch and specific temperature conditions within the range available in the environment. Results were compared with findings from a similar analysis of temperature profiles from 1994 to 2000 (Campana and Joyce 2004).

Results

Aged specimens from the exploited population consisted of 291 males, 290 females, and 3 of unknown sex ranging in size from 77 to 261 cm CFL (Table 1). Those collected from the virgin population included 34 males, 43 females, and 126 samples that could not be matched to Aasen's recorded data and, therefore, were of unknown sex and body length (Table 1). These sharks had a CFL range of 70 to 245 cm. The coefficient of variation for the replicated age readings was 7%.

The modeled CFL–CR and CFL–CD relationships were used to reconstruct body lengths of 107 and 19 historical

Table 1. Summary of vertebral samples used to reconstruct growth in the virgin (1961–1966) and exploited (1993–2004) porbeagle (*Lamna nasus*) populations.

			Sample size				CFL of males (cm)		CFL of females (cm)	
Area	Season	Year	Males	Females	Unknown sex	Total	Min	Max	Min	Max
Virgin										
Gulf of Maine	Summer	1961	13	10	0	23	112	176	103	164
		1962	17	20	0	37	132	220	125	216
Scotian Shelf	Summer	1961	3	11	0	14	96	226	90	245
Grand Banks	Summer	1961	0	0	126	126*	92	231	92	231
Southeastern US	Spring	1966	0	1	0	1	—	—	146	146
Unknown	Unknown	1965	1	1	0	2	70	70	72	72
Total	—	—	34	43	126	203	70	226	72	245
Exploited										
Gulf of Maine	Summer	1999	3	0	0	3	182	219	—	—
	Spring	1994	17	16	0	33	104	239	101	203
		1999	75	66	0	141	77	232	97	241
	Summer	1997	1	1	0	2	156	156	193	193
		1999	3	6	0	9	105	144	128	228
		2004	31	17	0	48	113	202	110	181
	Autumn	1993	19	19	0	38	89	216	90	192
		1999	13	15	0	28	92	226	101	240
	Winter	1999	0	2	0	2	—	—	95	167
Grand Banks	Spring	1999	7	4	0	11	135	208	167	220
	Autumn	1993	9	15	1	25	170	232	113	236
		1997	0	1	0	1	—	—	169	169
		1999	64	80	0	144	95	246	94	256
	Winter	1999	7	13	0	20	107	240	200	261
Gulf of St. Lawrence	Autumn	1993	1	0	0	1	148	148	—	—
		1999	28	26	0	54	99	230	100	242
Unknown	Spring	1997	10	3	0	13	162	201	184	221
		1999	1	0	0	1	97	97	—	—
	Summer	1993	0	1	0	1	—	—	183	183
		1997	1	1	0	2	159	159	202	202
		1999	0	0	1	1	236	236	236	236
	Autumn	1996	1	1	0	2	189	189	139	139
		1997	0	1	0	1	—	—	100	100
	Winter	1996	0	1	0	1	—	—	224	224
	Unknown	—	0	1	1	2	97	102	97	102
Total	—	—	291	290	3	584	77	246	90	261

Note: Sample size and curved fork length (CFL) range are given separately for each sex by sampling area, season, and year. Seasons: spring, March–May; summer, June–August; autumn, September–November; winter, December–February. Min, minimum; max, maximum.

*Fork lengths were reconstructed from vertebral size.

samples, respectively, for which only centrum measurements were available. CFL and CR displayed a moderately curvilinear relationship, which was linearized by applying a $\log_e$–$\log_e$ transformation (Fig. 2). The least squares equation calculated from the transformed data was

$$\log_e(\mathrm{CFL}) = 0.74\log_e(\mathrm{CR}) + 3.21 \quad (n = 76, r^2 = 0.95)$$

In the case of the CFL and CD data, the untransformed relationship provided a better fit:

$$\mathrm{CFL} = 5.08\,\mathrm{CD} + 24.05 \quad (n = 74, r^2 = 0.94)$$

Both linear regressions were highly significant ($P < 0.0001$), and neither differed significantly between the sexes (analysis of covariance, ANCOVA, $P > 0.7$).

Plots of length at age data for the sexes combined (Figs. 3 and 4) indicated that porbeagles from the virgin population grew more slowly throughout most of the observed age range. Age estimates ranged from 0 to 23 years in 1961–1966 and from 0 to 24 years in 1993–2004. In the virgin population, the youngest age classes (<3 years) displayed slightly higher growth rates. However, the growth curves for the two time periods overlapped between the ages of 4 and 7 years and then diverged as the relative growth in the virgin population slowed. Although differences in length at age were less pronounced beyond an age of about 20 years, few

Fig. 2. Least squares relationship between $\log_e$-transformed curved fork length and $\log_e$-transformed centrum radius for the virgin (1961–1966) porbeagle (*Lamna nasus*) population, which was used to reconstruct curved fork length of samples when body length data were missing. Observed values for males (◆, n = 34) and females (□, n = 42) are shown separately.

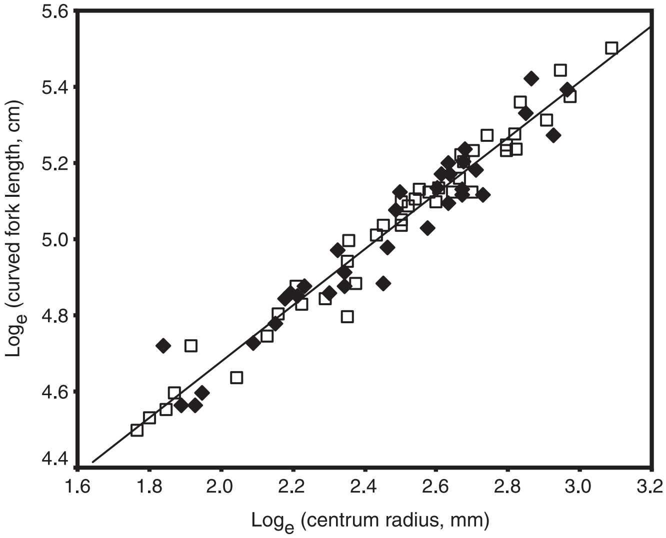


Fig. 3. Observations of porbeagle (*Lamna nasus*) length at age for the sexes combined based on vertebral ages from 1961–1966 (○) and 1993–2004 (△). Fitted lowess curves are shown (historical sample, broken line; recent sample, solid line). Historical data points have been jittered slightly to improve visibility.

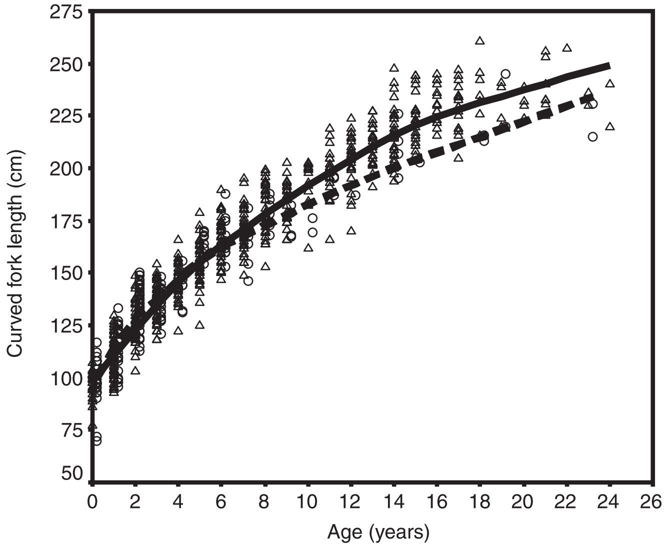
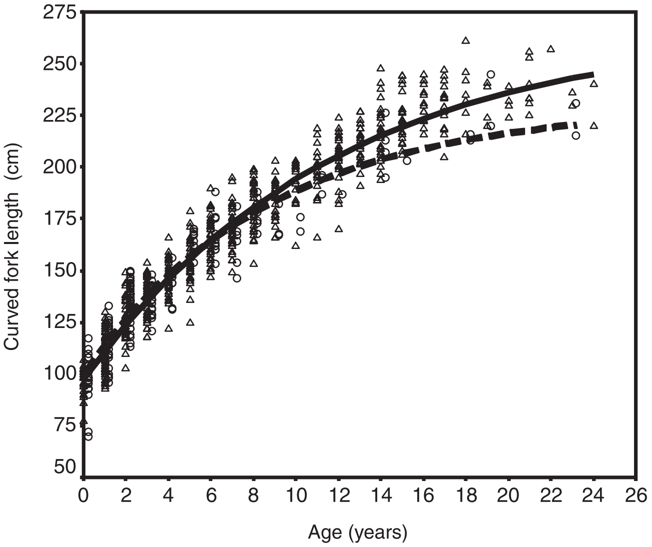


Fig. 4. Observations of porbeagle (*Lamna nasus*) length at age for the sexes combined based on vertebral ages from 1961–1966 (○) and 1993–2004 (△). Fitted von Bertalanffy growth models are shown (historical sample, broken line; recent sample, solid line). Historical data points have been jittered slightly to improve visibility.



observations lay within this portion of the data range, particularly in the historical sample. Low sample sizes of known-sex sharks from the 1960s precluded the examination of sex-specific growth differences between the sampling periods. However, disparities in growth patterns between the sexes were considered to be minor on the basis of findings from a previous study on Northwest Atlantic porbeagle growth (Natanson et al. 2002).

Comparisons of both the fitted von Bertalanffy and reparameterized growth models revealed that differences in age–length data between the virgin and exploited porbeagle populations were significant ($P < 0.01$) (Table 2). Because the largest size classes were poorly represented in the historical data set (Figs. 3 and 4), the length range over which both types of growth curves were fitted and compared was limited to CFLs less than the maximum observed size in the historical sample (245 cm). The reference ages selected for the reparameterized model (ϕ = 0, χ = 11.5, and ψ = 23) spanned 99.7% (exploited) and 100% (virgin) of the observations lying within the restricted data range. The reparameterized growth models yielded a significantly larger predicted mean CFL at age 0 for the 1961–1966 sample (l_0 = 102.8 cm) compared with the 1993–2004 sample (l_0 = 97.2 cm) (Tables 2 and 3). The remaining parameter values for the virgin population ($l_{11.5}$ = 196.0 cm, l_{23} = 220.5 cm) were significantly smaller than those for the exploited population ($l_{11.5}$ = 202.6 cm, l_{23} = 242.8 cm) (Tables 2 and 3). Pronounced differences, likewise, were observed between values of the VBGF parameter L_∞: virgin, 229.2 cm; exploited, 267.6 cm (Tables 2 and 3). The variance assumption of the likelihood ratio approach for comparing growth curves was met (χ^2 = 0.316, P = 0.574). Likelihood ratio tests detected significant differences in the overall reparameterized growth models and in all three of its parameters between the sampling periods ($P < 0.01$) (Table 3).

Comparisons of porbeagle reproductive data indicated a small shift in the male length at maturity but no change in the female length at maturity between the sampling periods 1961–1963 and 1999–2001. Clasper measurements were available for 285 and 365 males from the virgin and exploited populations, respectively. These data covered a similar range of fork lengths: virgin, 84–253 cm; exploited, 86–246 cm (Fig. 5). The estimated inflection points of the logistic growth models used to describe clasper development

Table 2. von Bertalanffy and reparameterized growth model parameter estimates for porbeagles (*Lamna nasus*) (sexes combined) collected in 1961–1966 and 1993–2004.

		von Bertalanffy parameters			Francis parameters			
Time period	n	L_∞ (cm)	K (year^{-1})	t_0 (years)	l_0 (cm)	$l_{11.5}$ (cm)	l_{23} (cm)	R^2
1961–1966	203	229.2±11.9	0.116±0.021	–5.12±0.75	102.8±3.0	196.0±3.1	220.5±7.4	0.90
1993–2004	577	267.6±9.3	0.084±0.009	–5.39±0.47	97.2±2.3	202.6±1.1	242.8±3.5	0.94

Note: 95% confidence intervals are given directly to the right of parameter values.

Table 3. Outcome of likelihood ratio tests comparing traditional and reparameterized von Bertalanffy growth curves between virgin (1961–1966) and exploited (1993–2004) porbeagle (*Lamna nasus*) populations.

Hypothesis	RSS	χ^2	df	P
H_1: No parameters are equal	77 973	—	—	—
H_{0a}: All parameters are equal	83 063	49.32	3	<0.001
von Bertalanffy growth parameters				
H_{0b}: L_∞s are equal	79 516	15.28	1	<0.001
H_{0c}: Ks are equal	78 720	7.44	1	<0.01
H_{0d}: t_0s are equal	78 004	0.31	1	0.578 ns
Reparameterized growth parameters				
H_{0b}: l_0s are equal	78 764	7.87	1	<0.01
H_{0c}: $l_{11.5}$s are equal	79 493	15.06	1	<0.001
H_{0d}: l_{23}s are equal	80 282	22.76	1	<0.001

Note: ns, not significant. Growth models containing parameter constraints (H_0s) were tested against a base model (H_1), in which all parameter values differed between data sets. The residual sum of squares (RSS) for each is given.

in the virgin (a = 148.3 ± 1.5 cm CFL) and exploited (a = 143.6 ± 1.1 cm CFL) populations indicated a significant decline in male length at maturity of about 5 cm between 1961–1963 and 1999–2001 (Fig. 5). Therefore, we assumed that the body lengths corresponding with the onset of male sexual maturity in the virgin and exploited populations were also offset by 5 cm. Jensen et al. (2002) estimated the median length at maturity in recently captured male porbeagles as 174 cm, based on clasper condition. Therefore, median length at maturity in males captured in 1961–1963 was estimated as 179 cm. In contrast, females from the virgin (n = 165) and exploited (n = 243) populations displayed very similar relationships between uterus length and body length (Fig. 6). A rapid increase in uterus growth, associated with sexual maturation, occurred in both samples at a CFL of approximately 216 cm. This value is comparable to the female length at 50% maturity (218 cm FL) reported by Jensen et al. (2002) for the more recent sampling period.

The temperature range occupied by porbeagles in 1965 was comparable to that reported by Campana and Joyce (2004) for the years 1994–2000. The 1965 catch-weighted (n = 34) and environmental (n = 82) temperature CDFs indicated that porbeagle catch rates were moderately enhanced at intermediate temperatures (Fig. 7). About 97% of captured sharks occupied a temperature range of 4–12 °C, which encompassed less than 80% of the environmental temperature observations. Published CDFs for more recent years showed that most porbeagles were caught in temperatures of 4–12 °C in the spring and 6–10 °C in the fall (Campana and Joyce 2004).

Discussion

We found an increase in growth rate and a decrease in the age at maturity of Northwest Atlantic porbeagles following large declines in abundance. Our results showed that recently collected sharks grew at a faster rate throughout most of their life span compared with sharks in the unfished population. Beyond an age of 7 years, the mean length of sharks captured in 1993–2004 was greater than that of sharks captured in 1961–1966. We also found that male length at maturity declined and female length at maturity remained unchanged following exploitation, and there was a reduction in the age at maturity in both sexes. Based on the reparameterized growth models for the sexes combined, age at maturity decreased from 8 to 7 years in males and from 19 to 14 years in females between 1961–1963 and 1999–2001. These observed changes in porbeagle growth and maturity are consistent with a compensatory growth response to reduced porbeagle abundance, whereby greater per capita food availability resulting from relaxed intraspecific competition promoted faster growth and thus enabled individuals to attain maturity earlier.

Juvenile porbeagles experienced declines in abundance of comparable magnitude to those of adults over the course of the commercial fishery (about 75% and 85%, respectively; DFO 2005). Surprisingly, though, our results indicate that the mean length of individuals in the first few age classes (0–3 years) decreased slightly between the sampling periods 1961–1966 and 1993–2004. This is reflected by the significantly higher mean length at age 0 predicted by the virgin

Fig. 5. Relationship between right outer clasper length and curved fork length for porbeagles (*Lamna nasus*) captured in (*a*) 1961–1963 and (*b*) 1999–2001 and associated estimates of the inflection point (broken lines) of fitted logistic growth curves (solid lines).

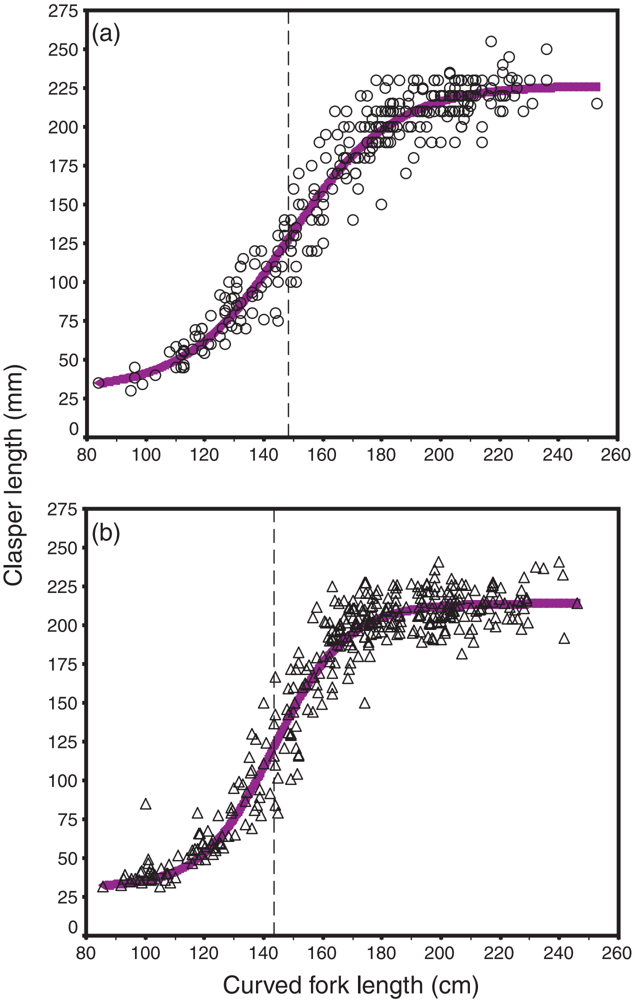
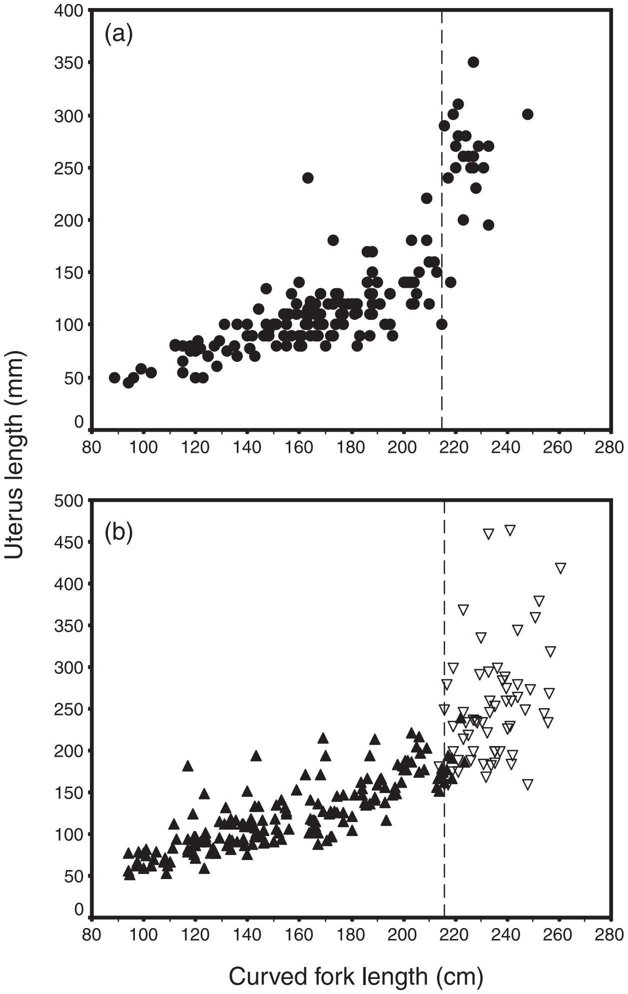


Fig. 6. Relationship between uterus length and curved fork length for porbeagles (*Lamna nasus*) captured in (*a*) 1961–1963 and (*b*) 1999–2001 and associated estimates of length at maturity (broken lines). The maturity status of individuals is indicated in the bottom plot: immature, ▲; mature, △.



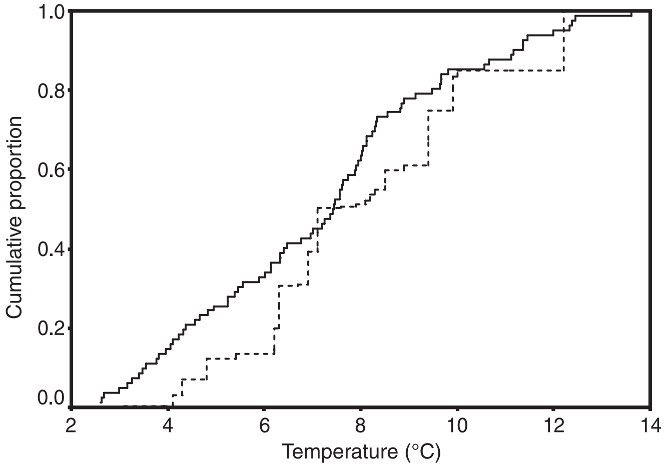
population's reparameterized VBGF than by the exploited population's reparameterized VBGF. We believe that this apparent decrease in relative growth following exploitation is attributable to sampling bias. The age at recruitment to the porbeagle fishery declined substantially after 1993, from 6–7 years to 2–3 years (Campana et al. 2002*a*). Smaller, slower-growing individuals in the youngest age classes would have been less vulnerable to capture by the longline gear during the earlier sampling period and, therefore, were most likely underrepresented in our historical sample.

Our results also showed that earlier maturation in recently collected male porbeagles was associated with a smaller length at maturity (1961–1963, 179 cm; 1999–2001, 174 cm), whereas in females, length at maturity was invariant (216 cm). This pattern is in contrast to that reported by Carlson and Baremore (2003) for the Atlantic sharpnose shark, in which faster growth and earlier maturation were accompanied by reduced length at maturity in both sexes. That female porbeagles did not experience a shift in length at maturity may reflect the importance of a large length at birth to fitness in this species. Survival of newborns in a pelagic environment is most likely highly dependent on their ability to capture prey and, in turn, on their body size (Smith et al. 1998). Therefore, the option for female porbeagles to begin breeding at a smaller length may be constrained by their ability to accommodate large embryos.

Several alternative hypotheses can be invoked to explain the observed increase in growth rates and decrease in age at maturity between the sampling periods 1961–1966 and 1993–2004. These include methodology or sampling, variation in ambient water temperature, genetic changes owing to size-selective fishing, and reductions in interspecific competition. We evaluate the plausibility of each in turn.

Variation in length at age data resulting from methodology or sample collection can give rise to differences in growth curves that are apparent rather than real. While evaluating previously reported differences in growth between two *Mustelus manazo* populations, Cailliet et al. (1990) identified several sources of variation that could bias growth curves: vertebral preparation techniques, reader accuracy and precision, sample size, and sample bias. These sources of

Fig. 7. Cumulative distribution functions of temperature at the mean depth of the longline gear based on data from 1965 for months and fishing areas combined. The broken line represents temperatures at porbeagle (*Lamna nasus*) fishing locations, weighted by catch per unit effort (number per hook), and the solid line represents temperatures in areas surrounding fishing sets.



variability most likely produced spurious growth parameter estimates for two populations of blue shark (*Prionace glauca*), resulting in apparent interpopulation differences (Tanaka et al. 1990). In the present study, we were able to minimize these sources of variability by using a standardized preparation technique and a single, experienced age reader for both historic and recent samples. Interpretation of growth increments was calibrated before aging and was based on criteria validated for all age classes included in our study. The level of precision between our replicated age readings was high relative to that reported in other aging studies utilizing shark vertebrae (reviewed by Campana 2001). Furthermore, potential problems related to sample size and bias were addressed by using a reparameterized VBGF and restricting the statistical comparison of growth curves to a body length range where sample sizes were adequate. Therefore, we are confident that the observed increase in porbeagle growth rate between the time periods 1961–1966 and 1993–2004 is not just an artifact of methodology or sampling.

Another possible explanation for the increase in growth rate between the sampling periods is variation in the ambient water temperature of porbeagles. Temperature is a major factor controlling physiological rates in fish, and its effects on growth rate have been documented for many teleosts (Brett 1979). Based on our analyses of porbeagle temperature associations and those of Campana and Joyce (2004), porbeagles occupied a very similar range of temperatures during the mid-1960s and 1990s. Although these analyses provide only a snapshot of temperature conditions, they do suggest that variation in ambient water temperature did not contribute substantially to the differences in growth rate observed between the sampling periods. Porbeagles, like other members of the family Lamnidae, possess an efficient countercurrent heat exchange system and, therefore, are able to maintain body temperatures more than 7 °C warmer than the surrounding water (Carey and Teal 1969; Carey et al. 1981). This thermoregulatory ability would most likely eliminate the effect of any changes in water temperature on growth.

Adaptive evolution in response to fishing is another possible explanation of the changes in growth rate and maturity observed in our study. Prolonged and heavy exploitation has the potential to cause genetic changes in growth rates and maturity, because of the size-selective nature of fishing gear (Hutchings and Reynolds 2004). Such changes have been reported for populations of grayling (*Thymallus thymallus*) (Haugen and Vøllestad 2001) and northern Atlantic cod (*Gadus morhua*) (Olsen et al. 2004). Although porbeagles were subjected to intensive fishing pressure, the evolution of life history traits is likely to be slow relative to the period of commercial exploitation, which spanned less than three generations (generation time = 18 years) (Campana et al. 2003). Furthermore, the tendency of longline gear to preferentially capture the faster-growing members of the youngest age groups (Ricker 1979) would favor a reduction in mean length at age, which is contrary to the trend we observed. Therefore, it seems very doubtful that the observed changes in porbeagle life history represent a genetic response to fishing.

Another possible explanation for the observed increase in growth rate and decrease in age at maturity between the sampling periods is a reduction in interspecific competition for prey owing to the depletion of other large, pelagic predators in the temperate Northwest Atlantic. Porbeagles are tertiary consumers (Cortés 1999), feeding on a wide array of pelagic and demersal teleosts, as well as small elasmobranchs (Joyce et al. 2002). Since the general expansion of pelagic longline fisheries in the 1960s, many other tertiary predators have experienced substantial declines in response to exploitation (Ward and Myers 2005). Large temperate pelagic sharks, including threshers (*Alopias vulpinus*), great whites (*Carcharodon carcharias*), and blues (*Prionace glauca*), in the Northwest Atlantic declined by 60%–80% between 1986 and 2000 (Baum et al. 2003). If these predators exert top-down effects, their removal could have led to an increased abundance of porbeagle prey. Ward and Myers (2005) analyzed survey and observer data for the tropical Pacific pelagic community and found relatively little increase in the biomass of small fish species following pronounced declines in large predatory fishes. Nevertheless, top-down effects are difficult to assess in marine communities (Jennings and Kaiser 1998) and have not been quantified for the temperate Northwest Atlantic. Therefore, the possibility that porbeagle growth rate increased in response to reduced interspecific competition cannot be ruled out.

Holden (1973) advanced two mechanisms, in addition to compensatory growth, that might regulate population size in elasmobranchs: increased fecundity at lower densities owing to increased food availability, and decreased natural mortality at lower densities owing to reduced predation, cannibalism, or competition for food. Density-dependent fecundity is believed to play a minor role in regulating most shark populations (Stevens et al. 2000); the capacity of sharks to augment litter size is likely to be greatly constrained by the amount of space within the maternal body cavity (Holden 1973) and perhaps by the size of the maternal liver (Bone and Roberts 1969; Roff 1992). This may be particularly true of porbeagles, given their large length at birth relative to maximum adult body length (about 25%). The available reproductive information from the Northwest Atlantic suggests that porbeagle fecundity has not increased since the onset of commercial exploitation. Jensen et al. (2002) reported a litter size of 3–6 pups with an average of 4, which is comparable to that observed prior to exploitation (range of 1–5 pups, but more commonly 2–4 pups; Bigelow and Schroeder 1948). Furthermore, the duration of the porbeagle reproductive cycle (1 year) has remained unchanged since the early 1960s (Aasen 1963; Jensen et al. 2002). In the case of natural mortality rates, only estimates for juvenile porbeagles were available for both the virgin and exploited populations. Estimates for the years 1961 (0.10) and 1998–2000 (0.12), based on catch curves and tag-recapture studies, respectively, were comparable (Campana et al. 2001). Further research is needed to more rigorously evaluate the relative importance of various density-dependent mechanisms in regulating population size. However, based on the available information, porbeagle fecundity and natural mortality appear to be relatively insensitive to changes in density, lending support to the hypothesis that population regulation in porbeagles occurs through compensatory changes in growth.

In conclusion, this is the first study to document changes in baseline growth and maturation parameters in an elasmobranch population following exploitation. In addition, our findings represent the only evidence of temporal changes in both growth rate and maturity in a large, long-lived shark species. Our results showed an increase in growth rates and a decrease in the age at maturity in porbeagles, associated with pronounced declines in abundance. Although we cannot dismiss the possibility that reduced interspecific competition contributed to these changes, results from our study provide strong support for the hypothesis of a compensatory growth response. Because estimates of growth and maturity parameters are used to model population growth, information from this investigation should reduce uncertainty surrounding the current recovery trajectory of the porbeagle population and, in turn, better inform management decisions in the future, as the population rebuilds.

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