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17. Growth and Reproduction of Spiny Dogfish off the Eastern Coast of Canada, Including Inferences on Stock Structure

Steven E. Campana*

Bedford Institute of Oceanography, Department of Fisheries and Oceans,
Post Office Box 1006, Dartmouth, Nova Scotia, B2Y 4A2, Canada

Warren Joyce

Bedford Institute of Oceanography, Department of Fisheries and Oceans,
Post Office Box 1006, Dartmouth, Nova Scotia, B2Y 4A2, Canada

David W. Kulka

Department of Fisheries and Oceans,
Post Office Box 5667, St. John's, Newfoundland, A1C 5X1, Canada

Abstract.—As part of an intensive study of spiny dogfish *Squalus acanthias* off the Atlantic coast of Canada, we studied the sexual maturation and growth of dogfish collected on research surveys and as part of the commercial fishery. Sexually mature and pregnant females were distributed throughout the waters of southwest Nova Scotia during the summer and fall but moved offshore to deeper waters in the winter. Juveniles were most abundant off Georges Bank and near the edge of the Scotian Shelf during the winter. The fork length at 50% maturity for males was 55.5 cm at age 10, while that for females was 72.5 cm at age 16. Free embryos were observed in 62% of all pregnant females (n = 1,491), the number of embryos increasing with the size of the female. Free embryos first became apparent in June at a fork length of 16 cm and would be expected to reach their birth size of 22–25 cm during the winter. Validated ages based on spine growth bands indicated a longevity of 31 years (n = 525). Males and females grew at similar rates until the size and age of male maturity, after which male growth rate slowed considerably. Two-parameter von Bertalanffy growth equations using a fixed size at birth gave L_∞ = 78.0 and K = 0.099 for the males and L_∞ = 119.5 and K = 0.042 for the females. Atlantic dogfish appear to grow more quickly and die at a younger age than do Northeast Pacific dogfish. Small amounts of offshore pupping in southern Nova Scotia waters probably represent the northern limits of an extended distribution centered in U.S. waters. Although they probably originate from the same population, dogfish living in the Gulf of St. Lawrence and off Newfoundland may be functionally isolated from dogfish found further south. Our results and published tagging studies suggest that both resident and migratory components of the Northwest Atlantic population occupy Canadian waters.

Introduction

Spiny dogfish *Squalus acanthias* are small squaloid sharks common in the surface mixed layer of coastal temperate oceans around the world. Studies to date suggest that they are both long-lived and slow-growing, reaching ages of more than 80 years (McFarlane and Beamish 1987; McFarlane and King 2009a, this volume). Reproductive productivity is also low, characterized by fewer than 10 pups born at two-year intervals to females that have reached sexual maturation at ages as great as 35 years (Saunders and McFarlane 1993). The combination of low reproductive potential and slow growth rate ranks

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* campanas@mar.dfo-mpo.gc.ca

the dogfish among the least productive of all shark species (Smith et al. 1998; Cortés 2000).

Spiny dogfish are ovoviviparous, the young feeding and growing off a yolk sac in utero before being born alive (Jensen 1966; Ketchen 1975; Nammack et al. 1985; Hanchet 1988; Jones and Ugland 2001; Henderson et al. 2002; Tribuzio et al. 2009, this volume). In maturing females, immature eggs turn yellow and grow to a diameter of 20–45 mm. The mature eggs pass through the shell gland, where they are fertilized and become enclosed in a protective capsule (candle) prior to passing through to the uterus. Candled embryos break free of the capsule after about a year, living as free embryos feeding off the yolk sac within the uterus for the remainder of the gestation period. The embryos continue to grow as the yolk sac shrinks, but embryos that have completely resorbed the yolk sac may remain in the uterus for some time before being born. This reproductive cycle takes 22–24 months, making it one of the longest gestation periods known for any vertebrate.

Although there is no question that spiny dogfish are relatively unproductive as a species, there is considerable variability in reported growth and fecundity among world populations, suggesting either that populations show a high degree of plasticity in their life history characteristics or that there have been methodological differences among the reported studies. Differences have been most marked in comparisons of Pacific and Atlantic populations: the population in the Northeast Pacific Ocean has been reported to grow much more slowly and reach a much greater longevity than does the population in the Northwest Atlantic (Ketchen 1975; Nammack et al. 1985; Saunders and McFarlane 1993). Age interpretations have been validated as accurate in the Pacific (McFarlane and Beamish 1987), but the recent age validation study of the Atlantic population (Campana et al. 2006) has not yet been applied to Atlantic growth data. Thus aging errors in previous Atlantic growth reports could be responsible for the high variability in reported longevities. On the other hand, it is possible that reported differences in fecundity and size at sexual maturity are correlated with real differences in growth rate among populations.

In this study, we report on sexual maturation and growth of more than 6,000 spiny dogfish collected off the Atlantic coast of Canada as part of an intensive study of dogfish population dynamics in the region. Dogfish off the Nova Scotia coast are at least partially mixed with those living in U.S. waters (Jensen 1969; Templeman 1984), suggesting that the results should be directly comparable with previous dogfish life history reports in the northwest Atlantic Ocean. We conclude by discussing the presence of both migratory and resident stock components in Canadian waters based on the distribution of pupping and nursery grounds.

Methods

Spiny dogfish for detailed reproductive and growth studies were obtained from both bottom trawl research surveys ($n = 515$) and sampling of commercial catches ($n = 6{,}709$). Bottom trawl surveys of the Scotian Shelf were carried out in July of 2003 to 2005, while commercial catches from handlines, longlines, and gill nets were sampled between March and October of 2002 to 2005. Approximately 30% of the commercial samples were collected at sea before any discarding, while the remainder were sampled from the landed catch.

All spiny dogfish were measured (straight line measurements of fork (FL) and total length (TL), with the upper lobe of the caudal fin depressed to the midline for the latter), then weighed and sexed. Fork length was used as the standard measurement, but fork length and total length were highly correlated ($P < 0.01$, $n = 6896$, $R^2 = 0.98$). Inter-conversion equations were as follows:

$$FL = -1.5 + 0.90 * TL$$
$$TL = 3.1 + 1.09 * FL$$

Males were considered to be sexually mature if sperm was present in the ampulla epididymis or if the claspers were calcified and could be freely rotated. Females were considered to be mature if the uterus was enlarged or flaccid or if embryos (candled or free) were present. If embryos were present, the number of free embryos was counted, and the fork length, sex, and yolk sac length of each embryo was recorded. The diameter of the five largest ova was also recorded. In a subsample of pregnant females, the total length of the candled embryos was measured as was the length of its yolk sac (see also Tribuzio et al. 2009).

The spatial distribution of pregnant females was available from detailed samples collected from the Scotian Shelf survey and commercial fishery since 2002. However sexual maturities were not recorded in other Department of Fisheries and Oceans surveys. To infer the distribution of mature females in surveys where maturity was not recorded, the length at 50%

maturity, or L_{50} (= 73 cm), calculated in this study was used to identify mature females in other surveys. The spatial distribution of juveniles (20–35 cm FL) and females of mature size (FL > 73 cm) was extracted from the July bottom trawl survey of the Scotian Shelf and Georges Bank (1979–2005), the March bottom trawl survey of the eastern Scotian Shelf (1986–2005), the February bottom trawl survey of Georges Bank (1986–2005), the September bottom trawl survey of the southern Gulf of St. Lawrence (1979–2005), and the August bottom trawl survey of the northern Gulf of St. Lawrence (1993–2005). Newfoundland surveys were conducted throughout the year between 1971 and 2004. Since dogfish sex and lengths were recorded in only some sets in the Newfoundland surveys, the relative abundance of females of mature size in any given 20-min square (an area at sea bounded by 20 mins of latitude on all sides) was estimated as the proportion of females of mature size (FL > 73 cm) relative to all measured dogfish in that 20-min square, times the mean number per tow across years for that same square.

Second dorsal spines for age determination were collected from a subsample of the dogfish from each sample. Spines were severed near the base, slightly below the epidermis. All spines were stored dry in paper envelopes after removal.

All ages were estimated based on replicated counts of annual growth increments (growth bands) that were visible on the external spine surface after light polishing. The validity of the growth bands as accurate age indicators has been confirmed through bomb radiocarbon dating (Campana et al. 2006). Age interpretation in the current study was carried out at 6X magnification under reflected light with a binocular microscope. Spine growth bands were also digitally photographed at a minimum resolution of 1280 × 1024 pixels per square inch, then enhanced. The strong white band near the spine base was assumed to represent a check rather than a growth band, and the first band distal to the white check was assumed to have formed in utero. Aging precision was quantified using the coefficient of variation (CV) (Campana 2001).

Since the enamel on the spine tips of many larger spiny dogfish had been lost due to erosion, an adjustment for lost growth bands was made. Ketchen (1975) derived an equation to estimate the number of growth bands lost due to spine erosion, but this equation is not applicable to populations with a different growth rate from that of the Pacific population. Therefore the equation was re-fit with spines from the northwest Atlantic population. Basal diameter was measured in 232 spines where minimal enamel erosion was present. An exponential regression was fit to these data, yielding the following relationship:

$$A = 0.594\, e^{0.696\, D} \qquad r^2 = 0.80$$

where A is the age in years and D is the spine base diameter in mm. In worn spines, the spine diameter was measured at the most distal point at which growth bands could be counted, and the above equation was used to estimate the number of missing growth bands distal to that point. A key assumption of all such procedures is that spine diameter at a given growth band does not increase as the dogfish grows larger. This assumption was tested using the relationship between dogfish age and the spine diameter at the 9th growth band from the tip of unworn spines, with the prediction that the diameter would increase with age if the spine continued to thicken at a given point after formation. There was no significant relationship ($P < 0.8$) and thus no reason to question the validity of the adjustment for lost growth bands.

Spiny dogfish growth was modeled using a two-parameter modification of the von Bertalanffy growth curve in which the size at birth is fixed (Fabens 1965; Neer et al. 2005):

$$L_t = L_\infty - (L_\infty - L_0)e^{-Kt}$$

where L_t = predicted fork length at age t,
L_∞ = theoretical maximum fork length,
K = a growth coefficient (year−1), and
L_0 = observed length at birth = 25 cm.

Results

The fork length of the 6,910 spiny dogfish that were sampled ranged from 21 to 100 cm, with a mean of 69 cm. The size range of the females (26–100 cm; mean = 71.6 cm) was broader than that of the males (21–85 cm; mean = 65.0 cm). Not surprisingly, the dogfish sampled from the commercial catch tended to be larger (42–100 cm; mean = 69.7 cm) than those from the research vessel survey (21–82 cm; mean = 63.6 cm). The length-weight relationship was described by:

$$W = 3 \times 10^{-6}\, L^{3.1554} \qquad r^2 = 0.89\ n = 6404$$

The L_{50} for males was calculated to be 55.5 cm based on binary logistic regression of 2,428 observations. The L_{50} for females was estimated to be 72.5 cm based on 3,204 observations. Virtually all females were mature at fork lengths exceeding 80 cm (Figure 1). Female maturity was assigned based on pregnancy; it is possible that a maturity assignment based on histological criteria would result in a slightly smaller length at maturity.

Eggs were clearly visible in the ovaries of virtually all female spiny dogfish greater than 50 cm in length. Egg diameter tended to be bimodal: undeveloped ova were usually 5–15 mm in diameter and were present in females of all sizes (Figure 2) while developing ova were 25–45 mm in diameter and present only in dogfish greater than about 62 cm. Undeveloped ova made up most of the eggs in immature females, while developing ova made up most of the eggs in mature females. Virtually all mature females contained both undeveloped and developing eggs as well as embryos, suggesting that eggs developed in preparation for fertilization while the female was still pregnant.

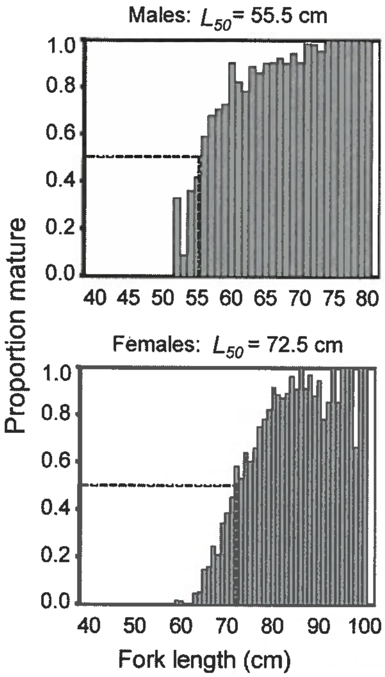

Figure 1. Maturity ogives for male (n = 1,723) and female (n = 3,101) spiny dogfish off southwest Nova Scotia. ---- = the length at 50% maturity (L_{50}) as defined by logistic regression.

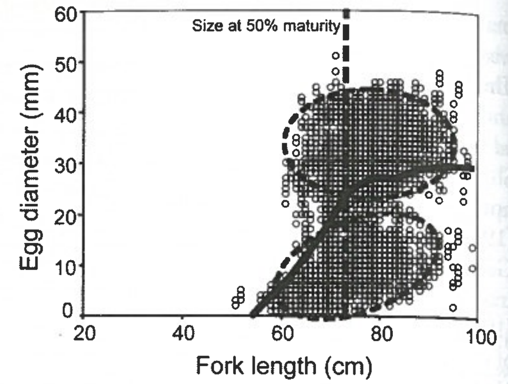

Figure 2. Diameter of the five largest unfertilized eggs in spiny dogfish females in relation to fork length (n = 1,420). A LOWESS regression (——) has been fit to the data. The vertical dashed line shows the length at which 50% of the females are pregnant.

Embryos were present in pregnant females both as "candles" (fertilized uterine eggs enclosed in a membranous envelope) and free embryos. Free embryos were observed in 62% of all pregnant females (n = 1,491). The number of free embryos in any given female ranged between 1 and 14 with a mode of 5 (mean = 4.7; SD = 2.2, n = 923) (Figure 3). Larger females tended to have significantly more free embryos; a 90-cm female, for example, had on average four times as many free embryos as a female 60 cm in length (Figure 4). The following cubic regression best explains the number of free embryos in pregnant females as a function of fork length:

$$\text{\# free embryos} = 9.8 - 0.0053 \cdot \mathrm{FL}^2 + 0.000056 \cdot \mathrm{FL}^2$$
$$r^2 = 0.51$$

Gestation time and month of pupping can be inferred from the rate of embryonic growth across collection months, assuming there is no differential immigration or emigration of pregnant females from the sampling area (Figure 5). Candled embryos and their yolk sacs grew significantly between July and October, reaching a total length of around 3 cm by October. Free embryos first became apparent in June with a fork length of about 16 cm, reaching almost 21 cm by October. As the length of the free embryos increased, the length of the associated yolk sacs shrank, losing 45% of their length in 4 months. Assuming continued development at the same rate, free embryos would be expected to reach their birth size of 22–25 cm during the winter. Yolk sac loss would be expected to be complete around the same time.

No well-delineated mating or pupping grounds

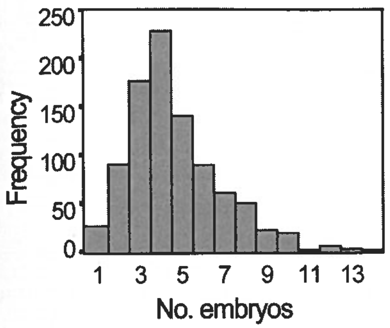

Figure 3. Frequency distribution of the number of free embryos contained within pregnant females (n = 907). The mean number was 4.7 (SD = 2.2).

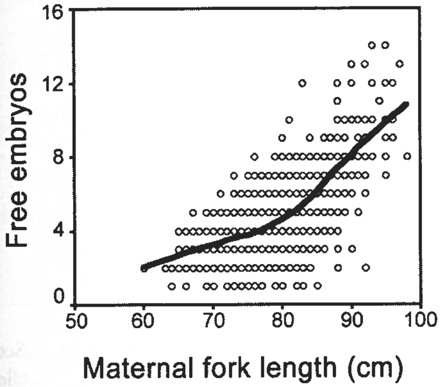

Figure 4. The relationship between the number of free embryos and maternal fork length (n = 907). A loess regression (——) has been fit to the data.

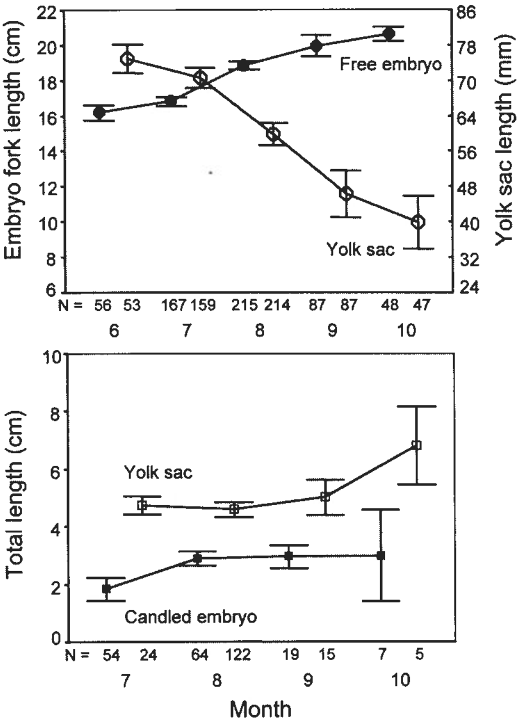

Figure 5. Embryonic development as shown by the relationship between embryo size and month of collection. Sample sizes are shown for each monthly measurement. Top—Increase in the fork length of free embryos (●) and decrease in the length of the associated yolk sac (o); bottom—Increase in the total length of candled embryos (■) and associated yolk sac (□).

were identified during this study. However, pregnant females were collected throughout the Bay of Fundy and the western half of the Scotian Shelf during the summer research vessel surveys of 2003–2005 (Figure 6). The spatial distribution of pregnant females sampled from the commercial catch between May and October of 2002–2005 was very similar to that of the research survey, being concentrated in the Bay of Fundy, the western Scotian Shelf, and inshore near the boundary of North Atlantic Fisheries Organization (NAFO) Divisions 4W and 4X. No pregnant females were collected in the southern Gulf of St. Lawrence between 2002 and 2005.

To broaden the search for mating or pupping grounds across areas and years where maturity was not recorded, the distribution of large, potentially mature females (>73 cm FL) was mapped (Figure 6). During the summer surveys of 1979–2005, large females of mature size were abundant in the same areas identified as containing pregnant females in the Scotian Shelf survey and spiny dogfish fishery of recent years. Large females were also observed in inshore regions of the southern Gulf of St. Lawrence, off the western coast of Newfoundland, and off the southern coast of Newfoundland near the shelf edge and along the western Grand Banks. Large females were very abundant along the edge of Georges Bank in February surveys of Georges Bank between 1986 and 2005. In March surveys of both the eastern Scotian Shelf (1986–2005) and the entire Scotian Shelf (1979–1984), large females were abundant along the edge of the Scotian Shelf as far north as the Laurentian Channel as well as in deep basins of the western Shelf and Gulf of Maine. Notably

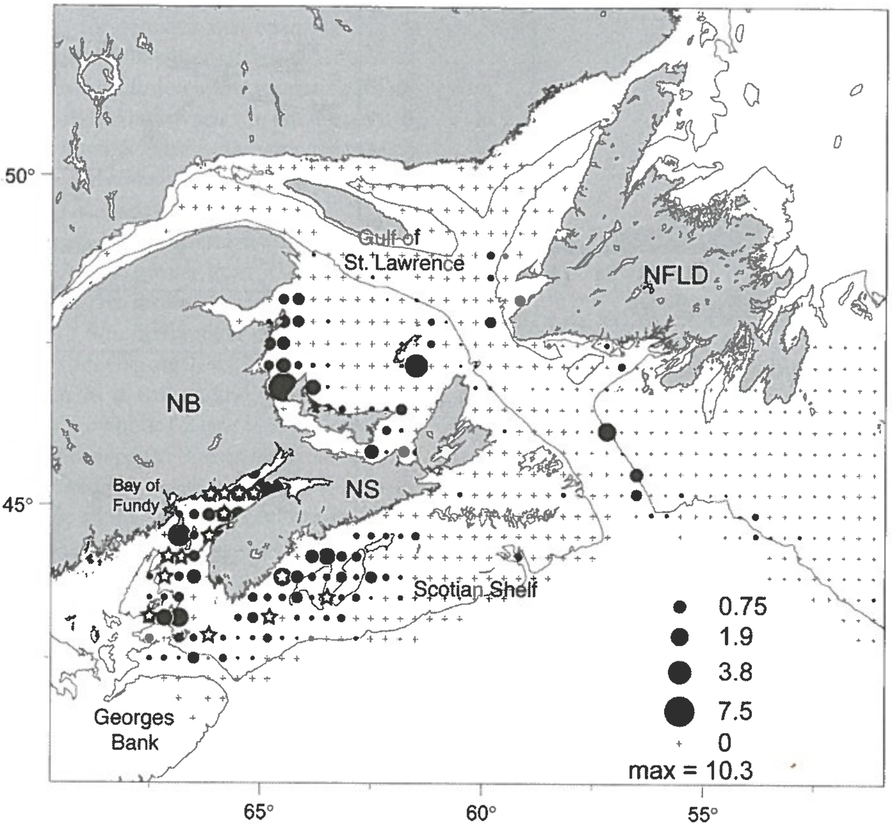

Figure 6. Distribution of female spiny dogfish of mature size (FL > 73 cm) in summer research surveys of the Scotian Shelf and Gulf of St. Lawrence. Symbols are proportional in size to the mean number of mature dogfish collected within each 20-min square between 1979 and 2005 inclusive. Survey coverage of the northern Gulf of St. Lawrence and around Newfoundland was 1993–2005 (August) and 1971–2004 (all months), respectively. Crosses represent survey sets where mature females were absent. Starred symbols show capture locations of pregnant females in 2003–2005 surveys of the Scotian Shelf; maturity examinations were not made in the Gulf or around Newfoundland. The 200-m depth contour is shown. NFLD = Newfoundland; NS = Nova Scotia; NB = New Brunswick.

however, they were absent from the Bay of Fundy in the whole-Shelf March survey. Fall surveys of the Shelf between 1978 and 1984 showed distributional patterns of large females similar to those of the summer surveys.

Juvenile dogfish (<35 cm FL) were most abundant on Georges Bank, in the Bay of Fundy, and on the outer Scotian Shelf during summer (Figure 7). During the winter, they tended to restrict their distribution to the outer shelf, particularly off Georges Bank. No juveniles have been observed in the southern Gulf of St. Lawrence since 1979, or off of Newfoundland.

A total of 525 spiny dogfish were aged with a mean precision (CV) of 12%. Ages ranged from 0 to 31 years, with a mean of just over 15 years. Males and females grew at similar rates to an age of about 12 years, after which male growth rate slowed considerably (Figure 8). The change in relative growth rate between the sexes roughly coincides with the size and age of male maturity. Although the maximum observed age of males and females was similar, large dogfish tended to be female. Male L_{50} was estimated to be about age 10, while female L_{50} was estimated to be about age 16.

Two-parameter von Bertalanffy growth equations fit to the length at age data suggested that males attain a smaller maximum size than females. Growth parameters and bootstrapped standard errors for the males were $L_{\infty} = 78.0$ (± 1.6) and $K = 0.099$ (± 0.007),

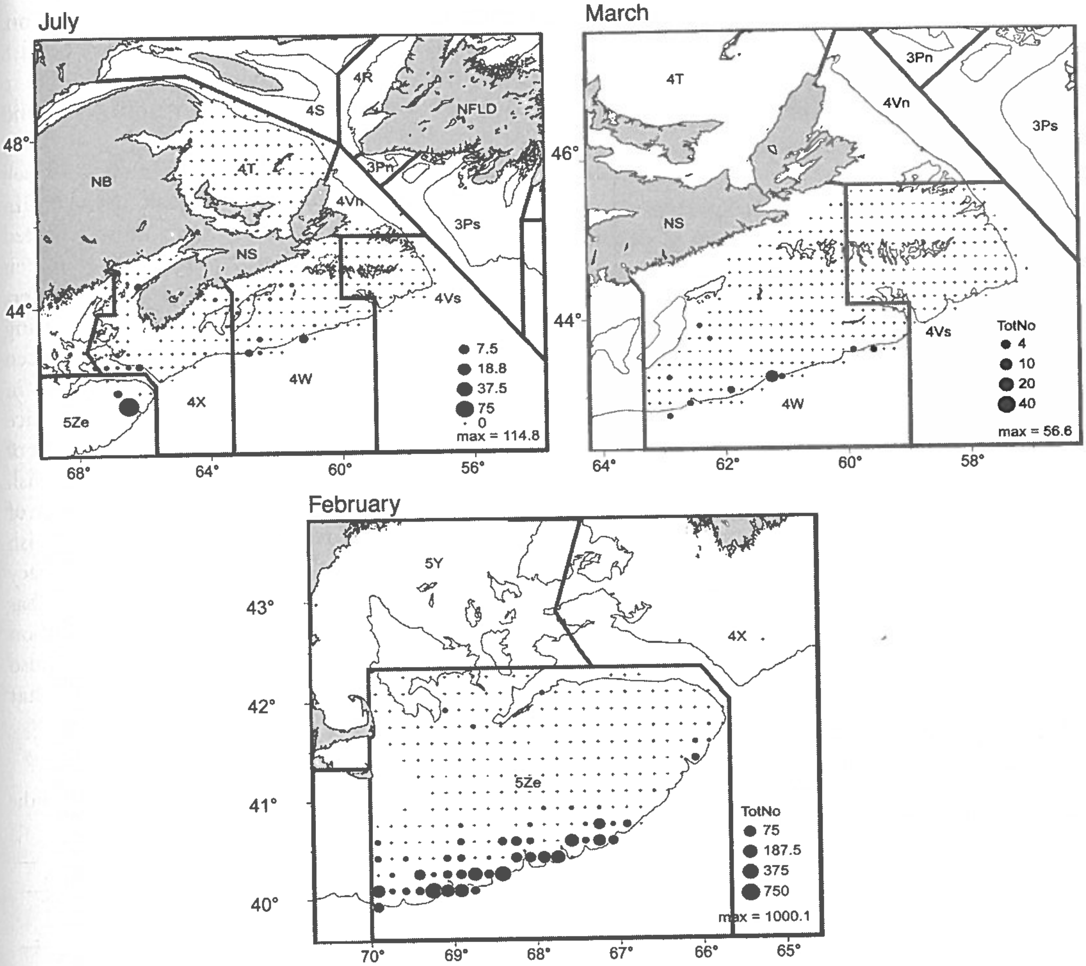

Figure 7. Distribution of juvenile spiny dogfish (20–35 cm FL) in standardized research surveys off eastern Canada. Top left: Juveniles in July research surveys of the Scotian Shelf and southern Gulf of St. Lawrence between 1979 and 2005; top right: March surveys of the eastern Scotian Shelf between 1986 and 2005; bottom: February surveys of Georges Bank between 1986 and 2005. The 200-m depth contour and NAFO subdivisions are shown. Symbols are proportional in size to the mean number of juveniles collected within each 20-min square.

while those for the females were L_∞ = 119.5 (± 8.7) and K = 0.042 (± 0.005). Selection of an alternate birth size (e.g., 22 rather than 25 cm) reduced L_∞ by about 6% and increased K by 15%.

Discussion

The growth and longevity of spiny dogfish in the northwest Atlantic was well characterized in this study, revealing a species with a low growth rate and a longevity of at least 31 years. Sexually dimorphic growth was apparent after the onset of sexual maturity, with males maturing first and thus reaching a smaller maximum size than females. Our results were similar to those in studies of other Atlantic populations (Figure 9 top), including those of the northeastern USA (Nammack et al. 1985), Norway (Jones and Ugland 2001), and Britain (Holden and Meadows 1962). Henderson et al. (2002) reported sex-specific differences in growth that seem too large to be biologically realistic, presumably due to inadequate sampling of fish smaller than 50 cm, but

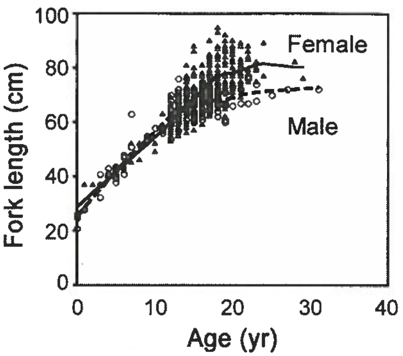

Figure 8. Length at age of male (O) and female (Δ) spiny dogfish off southwest Nova Scotia (n = 525). Loess regressions have been fit to the data for each sex.

with a mean growth rate similar to ours. In contrast, two reports of Black Sea spiny dogfish suggested that they grow to large size at a rate more than double, and a longevity less than half, of that seen elsewhere (Kirnosova 1989; Avsar 2001). These results seem unlikely, possibly due to errors in age determination, especially since a third study of Black Sea dogfish reported growth rates and a longevity similar to that of dogfish in the northwest Atlantic (Polat and Gumus 1995).

Our growth and longevity estimates, as well as those reported for spiny dogfish elsewhere in the Atlantic, differ markedly from those reported for the northeastern Pacific population (Ketchen 1975; Beamish and McFarlane 1985; Saunders and McFarlane 1993; see also McFarlane and King 2009a); see Table 1. To this point, it has not been possible to rule out methodological differences in comparing the growth of these populations (Rice et al. 2009, this volume). However, the accuracy of age interpretations for northeastern Pacific dogfish has been confirmed on the basis of recaptures of tetracycline-tagged releases (McFarlane and Beamish 1987; McFarlane and King 2009a) and the accuracy of Canadian Atlantic dogfish age interpretations has recently been confirmed using bomb radiocarbon dating (Campana et al. 2006). The latter study also compared spines between regions, noting that

Table 1. Comparison of published values for growth, longevity, fecundity and sexual maturation with values from the current study.

	Atlantic Ocean						Pacific Ocean	
	Atlantic Canada	NE USA[1]	Britain[2]	Ireland[3]	Norway[4]	Black Sea[5]	NE Pacific[6]	SW Pacific[7]
Male								
L_∞	78.0	72.7	70.2	69.6		113.7	85.0	
K	0.099	0.15	0.21	0.074		0.20	0.067	
L_{50} (cm FL)	55.5	52.0	56.1	50.3		72.3	63.3	50.2
Age_{50} (year)	10	6	7	15		5		
Female								
L_∞	119.5	89.0	89.8	99.3		129	114.7	
K	0.042	0.11	0.11	0.15		0.17	0.034	
L_{50} (cm FL)	72.5	70.4	75.0	68.9	71.4	77.8	82.6	64.0
Age_{50} (year)	16	12	15	15	17	5	35	
# free embryos at 90 cm	7.7	7.9			10.9	7.1	7.1	9.1†
Male and female								
Longevity (year)	31	40	22	30		14	81	
FL at birth (cm)	22–25††	23		21	> 19		22	20

[1] Nammack et al. (1985); [2] Holden and Meadows (1962); [3] Henderson et al. (2002); [4] Jones and Ugland (2001); [5] Avsar (2001); [6] Ketchen (1972, 1975), Saunders and McFarlane (1993); [7] Hanchet (1988); † Uterine eggs or embryos < 7 cm

growth bands in Pacific spines appeared markedly different than those from the northwest Atlantic. Given a reported longevity exceeding 80 years, and lengths at age significantly lower than observed in the Atlantic (Figure 9 bottom), it appears that Pacific dogfish do grow more slowly and live to greater ages than do northwest Atlantic dogfish (Vega et al. 2009, this volume). Thus productivity calculations based on Pacific dogfish represent the extreme lower end for the species (Smith et al. 1998; Cortés 2000) and are not particularly representative of Atlantic populations.

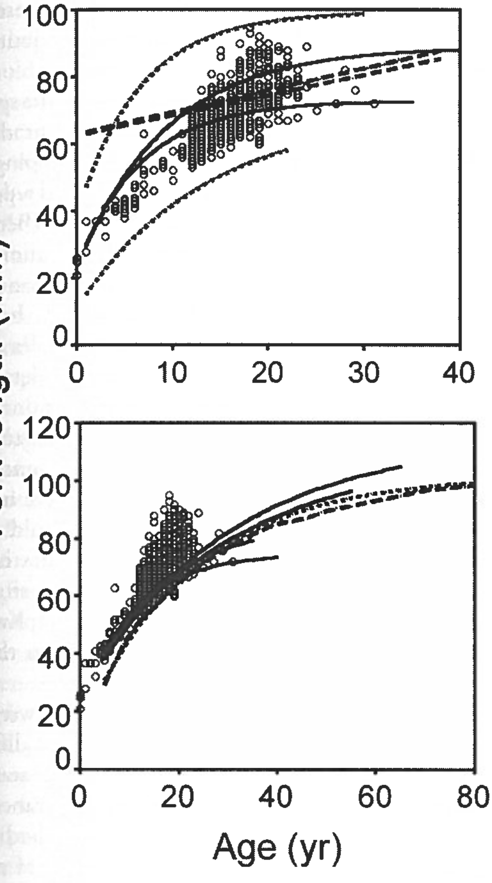

Figure 9. Length at age data for eastern Canadian spiny dogfish (o) in relation to published growth and longevity for spiny dogfish from the Atlantic Ocean (top panel) and Pacific Ocean (bottom panel). Top panel: Nammack et al. (1985) off the northeastern USA: upper —— = females; lower —— = males; Jones and Ugland (2001) off Norway: upper – – – = 1987 females; lower – – – line = 1997 females; Henderson et al. (2002) off Ireland: upper ···· line = females; lower ···· = males. Bottom panel: Ketchen (1975): solid —— = males and females from Hecate Strait and Strait of Georgia; Saunders and McFarlane (1993): ···· = Strait of Georgia females; McFarlane and Beamish (1987): – – – = combined sexes from Strait of Georgia.

Length–age at maturity and fecundity can contribute as much to population productivity as does growth rate. In this study, we found that fecundity increased substantially with maternal size, as has been reported for most other populations (Ketchen 1975; Nammack et al. 1985; Hanchet 1988; Jones and Ugland 2001; Henderson et al. 2002; Di Giacomo et al. 2009, this volume; Tribuzio et al. 2009). With such a strong relationship with maternal size, and with some reports not differentiating between uterine eggs and candled or free embryos, it can be misleading to compare fecundity among populations without first specifying what is being compared. We found that a 90-cm-FL female with free embryos carried an average of 7.7 free embryos. This fecundity is similar to the value reported for equivalently-sized females off the northeast coast of the USA, but slightly higher than that reported for the Northeast Pacific (Table 1) and slightly lower than that reported for the Southwest Atlantic (Di Giacomo et al. 2009). It is not yet clear if the fecundity of spiny dogfish from the Southwest Pacific is actually greater than all other populations, since Hanchet (1988) combined uterine eggs and small embryos in his estimate.

Female length at maturity differed only modestly among Atlantic populations; our estimate of FL_{50} = 72.5 cm at age 16 is approximately midway among the other reported values (Table 1) and slightly lower than that reported for the southwest Atlantic (Di Giacomo et al., 2009). It is possible that a maturity criterion based on ova development rather than pregnancy would have made these results even more similar. However, size and age at maturity appear to differ more substantially between Pacific and Atlantic ocean populations. Female maturity was reached at only 64 cm off New Zealand (Hanchet 1988), but at a fork length of 83 cm and an age of 35 years in the northeastern Pacific (Ketchen 1972; Saunders and McFarlane 1993). With such a large size and delayed age at maturity, the northeastern Pacific population appears to be the least productive reproductively as well as in terms of somatic growth.

Our observations on the rate of development of eggs and embryos are fully consistent with earlier suggestions of a 22–24-month gestation period

(Jensen 1966). Mature females in our study always contained eggs in both developmental stages: immature (<15 mm) and mature (>25 mm). Candled and free embryos were often present as well, but usually not at the same time. With a mean growth rate of 0.3–1.0 cm per month at the candled stage, a 3-cm candled embryo in June might well have been fertilized the previous winter. Subsequent growth to reach the 16-cm size of a free embryo in June of the following year would have to be about 1 cm per month, which is very similar to the growth rate that was observed. Similar embryonic growth rates have been reported elsewhere (Jones and Ugland 2001). Although we did not observe full-term pups, the projected date of birth based on embryonic growth rate would be in winter (January–March), similar to what has been reported for dogfish off the U.S. east coast (Jensen 1966; Nammack et al. 1985). Spiny dogfish in the northeast Pacific give birth in late fall (October–December) (Ketchen 1972).

No obvious mating or pupping grounds were identified in this study, perhaps because no maturity examinations were made north of the Scotian Shelf and perhaps because no samples were collected during the winter, the presumed season of pupping. Nevertheless, there were several indicators that pupping grounds might exist in Canadian waters. Pregnant females, many of which contained free embryos within 6 months of parturition, were collected throughout the Bay of Fundy and the central Scotian Shelf. In addition, juveniles less than 3 years old were present at all times of year off the edge of the Scotian Shelf and in the deep basins of the central Scotian Shelf. Off New Zealand, pregnant spiny dogfish spend the first year of their pregnancy inshore, but move out into deeper water (200–300 m) during the second year, where they subsequently give birth (Hanchet 1988). This pattern of offshore pupping and nursery grounds is consistent with what is known of dogfish off the northeastern USA (Jensen 1966; Nammack et al. 1985). Thus it appears likely that the pregnant dogfish observed around southern Nova Scotia move off the edge of the continental shelf and into the deep basins of the central shelf or off Georges Bank to give birth. An alternative possibility is that most or all of the pregnant females migrate to the south of Georges Bank in the fall and winter to give birth on the edge of the shelf in U.S. waters. Tagging studies have clearly shown that there is some degree of interchange between dogfish off southwest Nova Scotia and those in the USA (Jensen 1966, 1969; Shafer 1970). The very high densities of juveniles around and to the south of Georges Bank in February are consistent with this being the most important pupping ground, or at least point to much higher densities of pupping females in U.S. waters than in Canadian waters. The most probable reality is that the central distribution for pregnant females giving birth is in shelf-edge waters south of Georges Bank, with smaller amounts of shelf-edge pupping in southern Nova Scotia waters representing the northern limits of an extended distribution for pupping.

Although it appears that at least some of the spiny dogfish found off southern Nova Scotia reproduce there, it remains unclear if there is any pupping in more northerly waters. Survey and published reports indicate that both the Gulf of St. Lawrence (Benoit et al. 2003) and the waters around Newfoundland (Templeman 1963; Kulka 2006) often contain abundant populations of dogfish, which, based on the size composition, include many males and females of mature size. There has been little detailed sampling of dogfish in these waters, so it is unclear if large females in these northern waters are actually reproducing. However, mature males are common in these waters (Templeman 1984), so there is no obvious reason why the large females would not reproduce. Nevertheless, no small juveniles have been reported from the southern Gulf (this study) or around Newfoundland (Templeman 1984; Kulka 2006), suggesting that any reproduction in these areas must be of a relatively small scale.

Spiny dogfish living in the Gulf of St. Lawrence and off Newfoundland may represent very different groups of fish than those found further south. Benoit et al. (2003) noted the sudden appearance of substantial numbers of dogfish in the standardized groundfish survey in 1984, after 14 years of zero catches. In 1985, the length of the dogfish collected was unimodal across the range of 60–80 cm TL (mean = 75 cm), corresponding to an age of at least 10 years. Since that time, this same length frequency mode has been the only one observed each year in the research survey, gradually increasing to 70–100 cm (mean = 85 cm) in 2002. The increase in the size of the dogfish collected over this 18-year-period is entirely consistent with growth, and inconsistent with the addition of any new recruits. The absence of juveniles is also inconsistent with the possibility of a local pupping ground supplying recruits on an annual basis. However, the southern Gulf observations are readily explained by a mass incursion of immature dogfish from the main dogfish population to the south leading to an "inoculation" and subsequent residence of a large aggregation in the southern Gulf, perhaps due to favorable environmental conditions throughout the year (in coastal waters in the summer and deeper warm offshore waters in the winter). If a large group of dogfish did take up residence in the Gulf, their longevity and slow rate of growth would ensure that they would persist for at least 20 years. If this hypothesis is true, the dogfish in northerly waters should be genetically identical to those further south; they will, however, have spent most of their lives in isolation from their more southerly conspecifics and thus would be functionally separate. Geneticists refer to this as a "sink population."

Although the spiny dogfish aggregations in Newfoundland waters show some similarities to those in the southern Gulf, there are also differences. The appearance of large numbers of dogfish in Newfoundland waters each spring and their subsequent disappearance each fall is well documented (Templeman 1963; Jensen 1966). However, large numbers of dogfish do not migrate, but remain resident in Newfoundland offshore waters throughout the year. Through the course of his extensive dogfish tagging studies around Newfoundland, Templeman (1984) reported that more than 90% of the recaptures of dogfish tagged off Newfoundland were found off Newfoundland in the subsequent 20 years, across all months. Templeman (1963, 1984) also noted the absence of juveniles less than 55 cm TL (corresponding in age to about 8 years), as did Kulka (2006). If small juveniles are absent yet dogfish are continually present off the Grand Banks and Newfoundland for over 40 years, recruitment to the area must either occur periodically from sources further south or from an unknown local reservoir of juveniles. Assuming that recruitment occurs gradually (or periodically) through movement of southerly preadults northward along the continental shelf, the origin and nature of Newfoundland dogfish is similar to that of the southern Gulf dogfish: genetically identical to dogfish further south, but functionally isolated from southern components for most of their lifetime. What remains unclear is whether the dogfish in the Gulf of St. Lawrence and around Newfoundland begin to reproduce locally as they mature. And if they do, do they become self-sustaining? These questions can only be addressed through detailed sampling of dogfish north of Nova Scotia.

The presence of both migratory and resident spiny dogfish in Atlantic Canadian waters has significant implications for the interpretation of stock structure and thus the management of the dogfish stock in the northwest Atlantic. The tagging studies of Jensen (1966, 1969), Shafer (1970), and Templeman (1954, 1984) are widely cited as evidence that dogfish in the Northwest Atlantic form a single stock, migrating between Canadian and American waters on a seasonal basis.

However, these studies also reported that most dogfish were recaptured close to their tagging location for periods of up to 10 years. Some fish clearly migrated between Canadian and U.S. waters, particularly between U.S. waters and southwest Nova Scotia. However, in two separate tagging studies off southern Nova Scotia, no recaptures were reported north of Halifax (Moore 1998; S. Myklevoll, Havforskningsinstituttet, Bergen, Norway, unpublished data). Obvious explanations for the absence of recaptures north of Halifax include either the absence of fishing effort or the scarcity of dogfish in these more northern waters. Yet at about the same time that these early studies were under way, Templeman (1984) was tagging large numbers of dogfish around Newfoundland. Tagging studies on St. Pierre Bank in 1963–1965 found that 90% of the recaptures were made over a 20-year period around Newfoundland; the remaining 10% were recaptured in the Gulf of St. Lawrence, around Nova Scotia, the USA, and even Europe. In contrast, dogfish tagged in coastal Newfoundland waters were recaptured almost exclusively around Newfoundland.

A common theme in all of these studies is that some of the spiny dogfish appeared to be well mixed throughout the Canadian and American waters of the Gulf of Maine and Bay of Fundy. In addition, there was clearly some limited migration from the USA to the offshore waters of the Gulf of St. Lawrence and Newfoundland. However, inshore and more northerly dogfish were not nearly as well linked to U.S. waters, suggesting the presence of a significant Canadian resident component. The presence of large overwintering aggregations off the Scotian Shelf and Newfoundland, at a time when the annual migration had returned other dogfish to U.S. waters, is consistent with the view that a significant number of dogfish do not migrate between Canadian and U.S. waters. This situation is very similar to what has been reported for dogfish in the northeast Pacific. After tagging more than 70,000 dogfish in British

Columbia, McFarlane and King (2003) reported that about 85% of the coastal dogfish stayed in the Strait of Georgia, apparently forming a nonmigratory component, but that most of those tagged offshore or in northern waters migrated considerable distances (McFarlane and King, 2009b, this volume; Taylor et al. 2009, this volume).

In summary, tagging studies clearly indicate some exchange of spiny dogfish between the United States and Canadian waters around southwest Nova Scotia, limited, however, to specific areas and times; therefore, both resident and migratory components appear to be present in Canadian waters. Our own studies indicate that dogfish reproduce in Canadian waters but at lower levels than in U.S. waters, and that recruitment to more northerly waters in the Gulf of St. Lawrence and around Newfoundland is likely to be from southern sources. Therefore management of this trans-boundary resource must somehow take account of this complex stock structure.

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