Maturation of Little Skate and Winter Skate in the Western Atlantic from Cape Hatteras to Georges Bank

MICHAEL G. FRISK*

School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, New York 11794, USA

THOMAS J. MILLER

*Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science,
Post Office Box 38, Solomons, Maryland 20688, USA*

Abstract.—We estimated the length and age of maturation in little skate *Leucoraja erinacea* and winter skate *L. ocellata* based on samples of 1,884 little skate and 1,153 winter skate ovaries collected from Cape Hatteras, North Carolina, to Georges Bank. Two levels of maturity were recognized: onset maturity, which marks the onset of the allocation of energy from somatic growth to reproduction; and "functional" maturity, which marks the point when mature oocytes are released. Size at maturation increased with latitude in little skate, 50% onset maturity occurring at 42.5, 43.0, and 46.5 cm (total length) and 50% functional maturity at 43, 44, and 46 cm for the mid-Atlantic, southern New England–Georges Bank, and Gulf of Maine regions, respectively. Based on age estimates from previously published work, the age at which little skate achieve functional maturation ranged between 7.0 and 7.5 years for the U.S. northeast coast. In winter skate, no statistically significant regional differences in maturation rates were found. Size at 50% onset maturity was estimated to be 66 cm and at 50% functional maturity 76 cm for the U.S. northeast coast. In winter skate, onset maturity occurred at 9.5 years and functional maturity at 12.5 years. Thus, functional maturity in this species occurred 3 years after the onset of maturation, indicating that the species has a long adolescence before contributing offspring to the population.

Population growth rates are key parameters for both developing management strategies (Myers et al. 1999) and understanding the evolution of life histories (Roff 2002). In both management and evolutionary contexts, population growth rates (e.g., the net reproductive rate, the intrinsic rate of population increase) are very sensitive to the age at which a species matures (Stearns 1992). Thus, many life history traits are correlated with age at maturity, including the pattern of allocation of energy between somatic and reproductive processes. Generally, species that mature late are characterized by long generation times and low productivity and are termed "slow" species (Musick 1999), whereas those that mature early and are characterized by rapid growth are termed "fast" species (Fenchel 1974; Cortes 2002; Denney et al. 2002).

Elasmobranchs are often considered the quintessential example of species with slow life histories. However, this broad generalization should not be taken to imply that reproductive strategies within this order are uniform. Within elasmobranchs, faster and slower

species can be identified (Cortes 2002; Frisk et al. 2005). Little skate *Leucoraja erinacea* and winter skate *L. ocellata* are conspecific species with a similar phylogeny, body plan, habitat, and life history (McEachran and Musick 1973; Gabriel 1992; Alvarado Bremer et al. 2005; Frisk and Miller 2006). Yet, these two species have different positions on the fast–slow continuum of elasmobranch life histories (Frisk et al. 2005). Little skate is a small (total length [TL] = 57 cm), moderately fast growing species (von Bertalanffy growth rate = 0.19 cm/year) and moderately long lived (12 years), whereas winter skate is larger (111 cm), slow growing (0.07 cm/year), and long lived (20+ years; Frisk and Miller 2006). In the western Atlantic, little skate and winter skate are the most frequently captured skates in commercial fisheries (NEFSC 1999; Frisk et al. 2008). Winter skate is taken for the consumption of their wings (pectoral fins), little skate mostly for use as fish meal and bait (Waring 1984). Yet scientific surveys have indicated that little skate has maintained a relatively stable population, whereas winter skate has gone through fairly substantial population fluctuations (NEFSC 1999; Frisk et al. 2008).

Little skate and winter skate occur along the western Atlantic coast from Newfoundland to North Carolina (McEachran 2002). Little skate has a more southern distribution and is less common than winter skate north
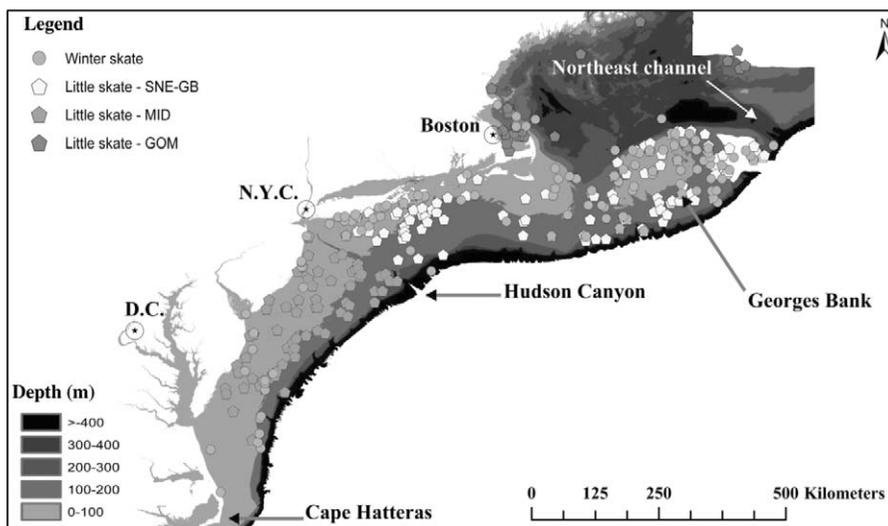
FIGURE 1.—Areas from which little skate and winter skate ovaries were collected. The data for little skate were disaggregated by region, namely, the mid-Atlantic (from north of Cape Hatteras to the Hudson River canyon), southern New England–Georges Bank (from north of the Hudson River canyon to the outer edges of Georges Bank), and the Gulf of Maine (from north of the northeast channel southwest to Cape Cod). Samples taken in close proximity to Ocean City, Maryland, were not included on the map as their exact location was unknown.

of LaHave Bank off Nova Scotia (McEachran 2002). Both species occur on sandy to gravelly bottoms and are common in depths up to 110 m (McEachran 2002). Like all members of the family Rajidae, both species have internal fertilization, are oviparous, and produce large oocytes which are protected by a rectangular egg case with long tendrils extending from each corner. Offspring develop in the egg case for several months, eventually hatching as a fully formed juvenile skate.

It is not uncommon for marine species in northern sections of their range to exhibit slower growth, later age at maturation, and increased longevity (Taylor 1958; Beverton and Holt 1959; Jennings and Beverton 1991; Beverton 1992; Frisk and Miller 2006). Frisk and Miller (2006) recently highlighted the geographic variation in the life history parameters of little skate, showing that individuals grow more slowly in the northern part of the species' range. Local variation can have important implications for the population growth rate and ultimately the sustainable level of exploitation that a species can support (Frisk 2004; Frisk and Miller 2006). For species that occur over a large geographic range, it is not appropriate to assume a continuous stock within which vital rates such as the growth rate and age of maturity are invariant (Ebert et al. 2008). While spatial patterns can be complex (and even "countergradient"; Conover and Present 1990), there is commonly a continuous latitudinal pattern in vital rates (Beverton and Holt 1959; Conover and Present 1990;

Jennings and Beverton 1991; Beverton 1992). These trends indicate that over a species' range there are trade-offs that are expressed in the plasticity of vital rates of mortality, growth, and longevity.

Several factors have been used to estimate female maturation in elasmobranch species, including ovary weight (OW; Walmsley-Hart et al. 1999; Mollet et al. 2000), cloacal length (Sosebee 2005), oocyte stage or size (Fitz and Daiber 1963; Richards et al. 1963; Johnson 1979; Mollet et al. 2000; Francis et al. 2001; Conrath and Musick 2002), histological staging, and steroid levels (Sulikowski et al. 2005). Here we examine the reproductive patterns in little skate and winter skate as defined by OW and oocyte stage, using specimens collected during the spring and fall of 1999 and during all seasons of 2001–2002 in the western Atlantic from Cape Hatteras, North Carolina, to Canadian waters. Specifically, we (1) estimate the size and age of onset and functional maturity for little skate and winter skate and (2) compare regional estimates of the reproductive traits of little skate in the mid-Atlantic, southern New England–Georges Bank, and Gulf of Maine regions.

Methods

Sampling

Samples of little skate and winter skate were collected in offshore waters from North Carolina to Georges bank (Figure 1). Most sampling was conduct-

ed as part of the National Marine Fisheries Service's (NMFS) annual fall (September and October 1999, 2001), winter (February 2002), spring (March and April 1999, 2002) and summer (June, July, and August: 2001) surveys conducted from the National Oceanic Atmospheric Administration RV *Albatross IV*. During the winter, spring, and fall surveys, samples were collected by means of a bottom trawl with a 1.27-cm-mesh liner that was towed for 30 min at 1.95 m/s (Sosebee and Cadrin 2006). Summer samples were collected with a standard New Bedford scallop dredge with a 5.08-cm ring chain bag and 3.81-cm mesh lining. A total of 103 winter skate were collected in 1999 during the NMFS fall and spring surveys. During the 2001–2002 NMFS surveys, 1,844 female little skate and 1,050 winter skate specimens were collected. Even with this number of specimens, not all geographic areas were well covered by the NMFS surveys. To ensure broad geographic coverage, an additional sample of 40 little skate were collected from the mid-Atlantic Bight over three dates in the winter (December 12, 2000), spring (March 29, 2001) and summer (May 25, 2001) of 2000 and 2001 from the catch of the FV *Tony & Jane*, a 17.4-m scalloper registered in Ocean City, Maryland, and captained by J. Eustler. The lengths and weights of all individual skate were recorded aboard the ship. Ovaries were removed, frozen, and transferred to the Chesapeake Biological Laboratory.

Subsampling Procedures and Regional Analysis

At the Chesapeake Biological Laboratory, the specimens were processed to ensure adequate coverage of geographical regions and maturing and mature length-classes. Our goal was to process 100 specimens of each species from each geographic region. Thus, only a subset of the total number collected during sampling were processed for the analyses reported herein. Geographic regions were identified based on likely biogeographic ecotones defined by the geographic features of the environments, such as the Great South Channel separating Georges Bank and southern New England (Jordaan et al. 2007). If local populations exist, vital rates could be expected to be more similar within than between regions. The three locations used in the analyses were (1) the mid-Atlantic, defined here as the area from Cape Hatteras north to the Hudson River canyon; (2) southern New England–Georges Bank, defined here as the area from the Hudson River canyon to the northern edges of Georges Bank; and (3) the Gulf of Maine, defined here as the area north and west of the northern edge of Georges Bank and bounded by the Bay of Fundy to the north. For nonspatial analyses, we refer to the entire area sampled as the northeast coast.

Laboratory Procedures

Individual ovaries were thawed in the fixative Bouin's solution. The fixed weight of each ovary was recorded. We measured eggs greater than 5 mm in diameter because these eggs mark the beginning of estrogen production (I. P. Callard, Boston University, personal communication) and are deemed maturing eggs (Fitz 1956; Johnson 1979). The eggs were enumerated and their individual diameters estimated as the average of three measurements (nearest 0.1 mm) using vernier calipers. In a few cases ($<1\%$), the eggs were broken and the diameters had to be estimated.

Maturation Scoring

In general, the maturation of animals can be assessed by the point when energy is reallocated from somatic growth to reproduction, the point when offspring are produced, or both (Kooijman 2000). The former is vital in understanding energetic trade-offs and evolutionary fitness by marking the stage when energy is first invested in reproduction, and the latter is important for population dynamics by specifically marking the stage at which mature individuals contribute offspring to the population.

In Richards et al.'s (1963) work on female little skate, they recognized that the maturation process could be divided into three stages and used the following scoring system: "immaturity" when the uterus is undeveloped, shell glands are invisible, and there are no follicles in the ovaries; "adolescence" when the uterus is developing, shell glands are visible, and there are follicles but no eggs present in the ovaries; and "maturity" when the uterus, oviducts, and shell glands are well developed and there are large follicles or definite eggs present in the ovaries. Accordingly, and following Ebert et al. (2008) and Simon and Frank (1998), we recognized three distinct stages of maturation.

Oocyte stage and maturity scoring.—We defined immaturity as did Richards et al. (1963) but recognized two stages of maturity within their maturity stage. Onset maturity was defined as the stage when oocytes begin to develop and adolescence begins; importantly, this is when energy begins to be allocated to reproduction. In little skate, the ovaries contain a hierarchy of yolked oocytes during oocyte production periods, an increase in plasma estrogen marking the follicular phase (Callard et al. 1995). It has been observed that oocytes 5 mm or larger produce estrogen (I. P. Callard, personal communication). Thus, a female skate is recognized as having onset maturity if her ovaries contain oocytes 5 mm or larger. The second type of maturity, functional maturity, is characterized

by the presence of ripe oocytes that will probably be spawned in the ensuing spawning season.

OW and maturity scoring.—The maturation process in skates is also indicated by increases in ovary and shell gland weight (Richards et al. 1963; Johnson 1979; Sulikowski et al. 2005). A pilot study showed that shell gland weight was highly correlated with OW in little skate ($r = 0.83$; $n = 70$; length, 42–52 cm) and winter skate ($r = 0.94$; $n = 36$; length, 61–88 cm). Based on these results, we decided to score maturation according to oocyte stage and OW criteria alone, as the inclusion of shell gland weight would add very little in terms of statistical power to the maturation estimates.

Maturation analysis.—Individual skate were scored as immature, onset mature, or functionally mature based on the characteristics of their eggs and their OW. For the current analyses, female little skate and winter skate were scored as onset mature if they were carrying eggs 5 mm in diameter or larger and their OW was 3 g or more (little skate) or 18 g or more (winter skate). These OW thresholds correspond to the maturity stage at which ovaries rapidly increase in size in preparation for mature egg production. This size threshold is in agreement with previously conducted research on winter skate (Sulikowski et al. 2005). Functional maturity was characterized by the presence of mature oocytes. Maturing oocytes develop toward the end of adolescence and can be visually identified by a darkening pigmentation and quantified by an increase in size (Richards et al. 1963). Mature oocytes were defined as oocytes that were darkening and as large as or larger than those found in the developing egg cases or located in the shell gland or oviducts immediately before release. The diameter of such mature oocytes was estimated from samples of oocytes in the shell glands or within egg cases found in the oviducts of the female. To ensure that there was not a significant increase in oocyte size during the final stage of ovulation, the largest 5% of the eggs within the ovaries of little skate were compared with the average oocyte size within the egg cases.

Statistical Analysis

To estimate maturation, the abrupt changes in the weight of ovaries, shell glands, and oocytes were plotted against age- or length-classes. Logistic regression was then used to characterize these relationships (Mollet et al. 2000; Conrath and Musick 2002). The maturity status of a sufficient number of little skate was determined to permit analyses to be conducted at the regional level. More than 100 specimens were each evaluated for the mid-Atlantic and southern New England–Georges Bank regions. Only a limited number of specimens were available for the Gulf of
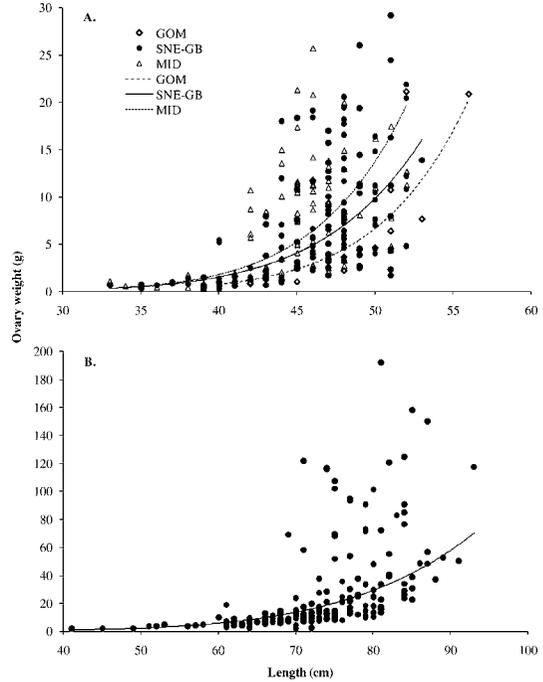

FIGURE 2.—Panel **(A)** shows ovary weight regressed on individual female total length for little skate. Power functions were fit to data from three geographical regions: the mid-Atlantic (MID), southern New England–Georges Bank (SNE–GB), and the Gulf of Maine (GOM). Most little skate ovaries are mature and increase in weight rapidly after attaining a weight of approximately 3 g. Panel **(B)** shows ovary weight regressed on individual female total length for winter skate. A power function was fit to data for the entire northeast coast. Most winter skate ovaries are mature and increase in weight rapidly after attaining a weight of approximately 18 g.

Maine. We tested for regional differences in size at maturity among little skate using pairwise, preplanned orthogonal contrasts following logistic regression. The limited number of female winter skate collected meant that we did not have sufficient statistical power to test for regional patterns in the size dependence of maturity, and thus only coastwide values are reported. To estimate age at maturity, size-dependent probability-of-maturity functions derived from the logistic regression and expected age-at-size curves developed from analysis of vertebral centra were overlaid and compared. The vertebral analysis and age-at-size estimates were based on growth estimates for the northwestern Atlantic (Frisk and Miller 2006).

Results

Maturation

Ovary weight was significantly related to TL in both little and winter skate (Figure 2; Tables 1, 2). Ovary

TABLE 1.—Regression summary and parameter estimates for ovary weight versus length relationships in little skate and winter skate. Abbreviations are as follows: n = the sample size, L_{max} = the maximum length observed, W_{max} = the maximum ovary weight observed, a = the intercept, b = the shape parameter, MID = mid-Atlantic, SNE-GB = southern New England–Georges Bank, GOM = Gulf of Maine. The regressions were fit to log transformed data.

Population	n	L_{max} (cm)	W_{max} (g)	a	b	SE (b)	P
Little skate							
MID	112	52	26.7	−19.2	9.0	0.8	<0.001
SNE–GB	155	53	29.1	−13.3	8.4	0.6	<0.001
GOM	23	56	21.1	−15.2	9.4	1.2	<0.001
Winter skate							
Northeast coast	207	93	192	−9.7	5.8	0.4	<0.001

weights of approximately 3 g in little skate and 18 g in winter skate appear to characterize the stage when mature egg formation proceeds (Figure 2A, B).

The capture of specimens with egg cases in the process of being released was relatively rare, especially for winter skate. In little skate, the average mature oocyte diameter in egg cases was 17.8 mm (SD = 2.5, range = 13–23, n = 20), which is consistent with previous research (Richards et al. 1963; Johnson 1979). The mature eggs of winter skate were larger than those of little skate, with an average diameter of 25.2 mm (SD = 2.9, range = 21.7–29.9, n = 6). The average size of the largest 5% of oocytes within little skate ovaries was larger than the average size of the oocytes within egg cases (ovary average = 22.9 mm, SD = 2.21, n = 198; egg average = 17.8 mm, SD = 2.5, n = 20). These results indicate that oocytes do not significantly increase in size during the final stages of ovulation just before release. Eggs with diameters of at least 10 mm were assumed to be rapidly maturing or mature for little skate; the corresponding value for winter skate was 15 mm. Skate with eggs of those sizes were considered mature. Mature eggs can be expected to be released in the ensuing spawning season. Thus, for female little skate functional maturity was defined as carrying eggs 10 mm or larger or having an OW of 3 g or more. Similarly, for female winter skate functional maturity was defined as the presence of eggs 15 mm or larger or having an OW of 18 g or more.

The smallest little skate found to contain eggs exceeding 5 mm in diameter was 38 cm long. Most females began egg production at a length of 40–43 cm

TABLE 2.—Results from orthogonal contrasts of regional ovary weight versus length models for little skate. No significant contrasts were found. See Table 1 for region abbreviations.

Comparison	F	P
GOM versus MID	0.45	0.50
GOM versus SNE–GB	0.28	0.59
MID versus SNE–GB	0.11	0.74

or more (Figure 3A). The winter skate with eggs exceeding 5 mm were larger than the little skate with eggs of that size (Figure 3B). The smallest winter skate with eggs exceeding 5 mm was 60 cm long, most individuals beginning egg production at lengths exceeding 65 cm (Figure 3B). Onset maturity was significantly related to female length in little skate, the trends indicating that the size of maturity increases with latitude (Figure 4A; Table 3). The size of 50% onset maturity in little skate was 42.5, 43.0, and 46.5 cm in the mid-Atlantic, southern New England–Georges Bank, and the Gulf of Maine regions, respectively (Figure 4A). The overall test of regional differences was significant (χ^2 = 16.74, P = 0.0002). All regional pairwise comparisons were significant (Table 3), indicating that the results were not affected by the low sample size in the Gulf of Maine. In winter skate, the onset of maturity was significantly related to length, 50% onset maturity occurring at 66 cm for the northeast coast (n = 212, χ^2 = 122.72, P = 0.0001; Figure 4C).

Logistic regression indicated that in little skate 50% functional maturity occurred at longer lengths at higher latitudes (Figure 4B); the size at 50% functional maturity was 43 cm for the mid-Atlantic region, 44 cm for the southern New England–Georges Bank region, and 46 cm for the Gulf of Maine regions (Figure 4B; Table 3). However, these differences were not significantly different (χ^2 = 2.93, P = 0.23). Using growth data from the von Bertalanffy equation estimated by Frisk and Miller (2006), we found that the approximate age of functional maturity was 7.0–7.5 years for the northeast coast. In little skate, there did not appear to be any significant delay between onset and functional maturity.

In winter skate, the estimated size at 50% functional maturity was 76 cm (n = 212, χ^2 = 113.53, P = 0.0001; Figure 4C). Using previous age estimates, we found that onset maturity occurs at approximately 9.5 years and functional maturity at 12–12.5 years (Figure 4C). In winter skate, there appears to be a 3-year delay between onset maturity and functional maturity.
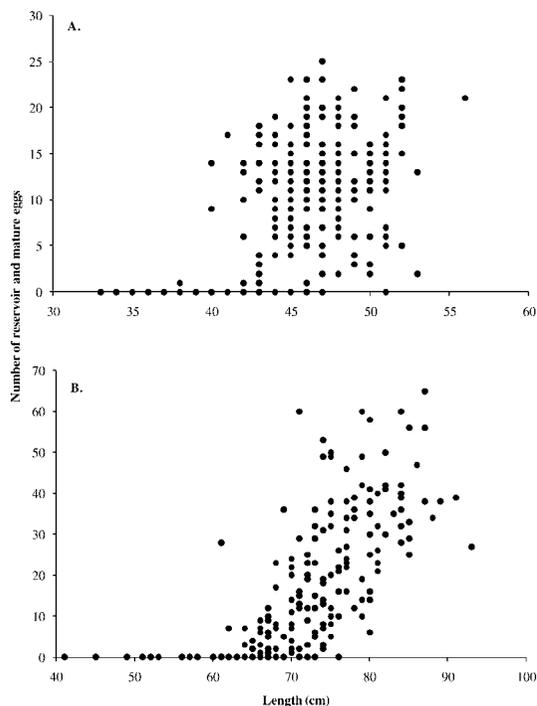
FIGURE 3.—Number of reservoir and mature eggs (eggs > 5 mm in diameter) versus length (cm) for **(A)** little skate and **(B)** winter skate. In both species, there is a steep increase in egg production with length.

The production of mature oocytes appears to increase as a knife-edged function of size for little skate and, to a lesser extent, for winter skate (Figure 5A, B). The numbers of mature females carrying mature eggs were calculated for length intervals of 2 cm as follows: 41–42 ($n = 21$), 43–44 ($n = 34$), 45–46 ($n = 57$), 47–48 ($n = 72$), 48–49 ($n = 47$), 50–51 ($n = 29$), and 52+ cm ($n = 11$), for a total sample size of 260. The corresponding values for winter skate were as follows: 69–70 ($n = 15$), 71–72 ($n = 19$), 73–74 ($n = 20$), 75–76 ($n = 22$), 77–78 ($n = 14$), 79–80 ($n = 17$), 81–82 ($n = 12$), 83–84 ($n = 9$), and 85+ cm ($n = 12$), for a total sample size of 140. On average, the proportion of mature female little skate carrying mature eggs was 0.73 (95% confidence interval, ±0.11), and that of winter skate was 0.55 (±0.04).

Discussion

The reproductive ecologies of little and winter skate differ substantially, the two species representing different positions along the fast–slow continuum of life histories in elasmobranchs. We previously documented differences in growth rates (Frisk and Miller 2006). Here, we documented differences in vital rates

related to maturation and reproduction between these two sibling species and found a latitudinal gradient in the size at maturation in little skate. What features of the life history variation in these two species account for the observed differences? Life history theory predicts that delayed maturity is associated with additional growth leading to a larger size, increased fecundity, and greater quality or size of offspring (Stearns 1992). Neither winter skate nor little skate show substantial size-dependent increases in fecundity (Frisk 2004). Winter skate delay maturation, thereby gaining a longer time to grow and reach a larger size with higher fecundity (Frisk 2004). However, the cost of delayed maturity is lower growth rates, longer generation times, and thus (probably) lower compensatory ability and less resilience to exploitation (Frisk et al. 2002, 2005).

Evidence was found for latitudinal gradients in the reproductive ecology of little skate. Size at maturation slightly increased with latitude in little skate. All regional estimates of onset and functional maturity were significant, while only onset maturity was significantly different by region. These results are consistent with previous observations that size at maturation increases with latitude in little skate (McEachran and Martin 1977). Our estimates of the age at maturity were 7 years in the mid-Atlantic region and 7.5 years in the southern New England–Georges Bank region and the Gulf of Maine. Frisk and Miller (2006) found some evidence that the life span was higher and the growth rate lower for little skate north of the mid-Atlantic region. Commonly, a larger size at maturation is associated with a later age at maturation (Stearns 1992). Our finding of different sizes at maturity but not ages at maturity may reflect imprecision in the aging of skates.

Evidence is growing that Rajidae species display geographic variation in vital rates. Ebert et al. (2008) presented evidence of local differences in TL in yellow spotted skate *Leucoraja wallacei* and biscuit skate *Raja straeleni*. Ebert et al. (2008) reported a difference in the TL of male skates for both species on the west and south coasts of South Africa. Similarly, thorny skate, *Amblyraja radiata* (Templeman 1987), and little skate in the western Atlantic both show regional differences in vital rates (Richards et al. 1963; Frisk and Miller 2006). To better understand the mechanisms behind such regional differences, we need more knowledge of local stock structure and genetic mixing between stocks. Without knowledge of stock structure, it is difficult to differentiate local adaptation from environmentally driven variation in growth and other vital rates (Frisk 2004).

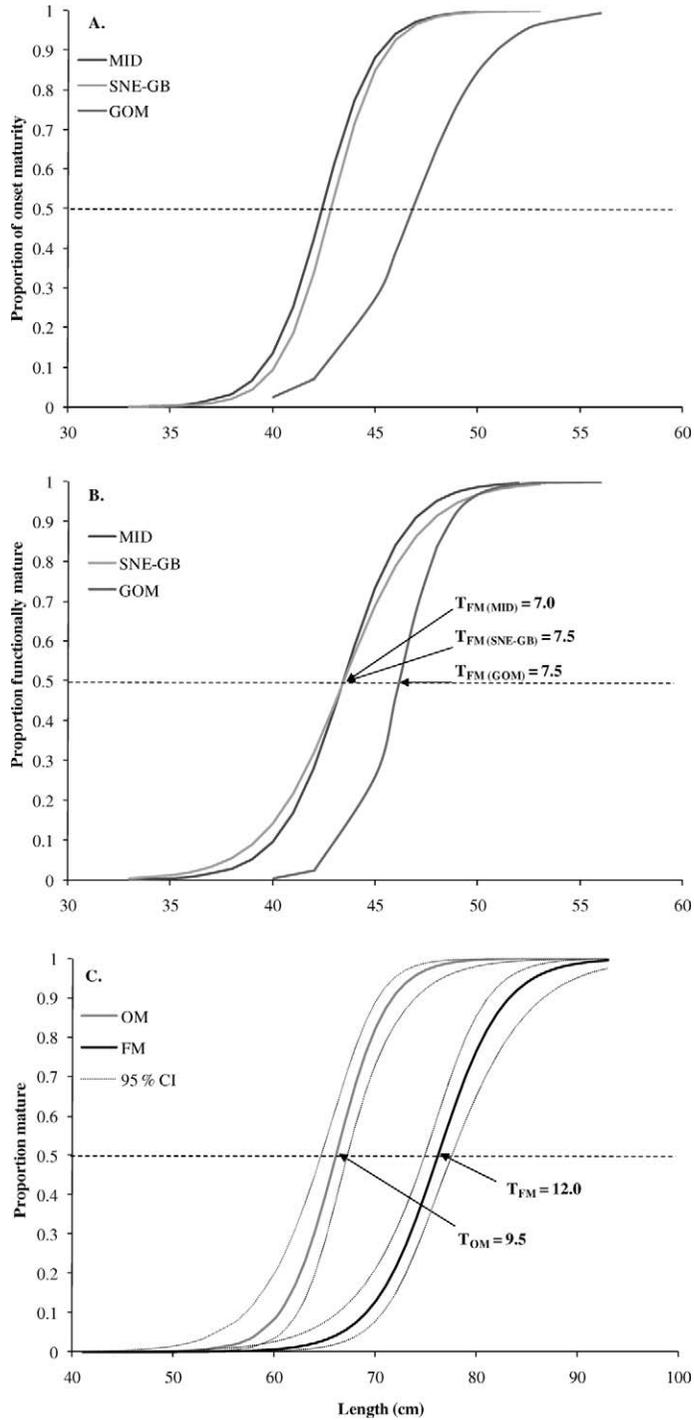Frisk et al. (2008) argue that winter skate population

FIGURE 4.—Maturation regressions estimated with presence–absence data and a logistic model. In panels **(A)** and **(B)**, onset and functional maturity are regressed on length for little skate from the mid-Atlantic (MID), southern New England–Georges Bank (SNE–GB), and Gulf of Maine (GOM) regions. Also shown are the ages of functional maturity (T_{FM}) based on data from Frisk and Miller (2006). Panel **(C)** shows onset (T_{OM}) and functional maturity (T_{FM}) in winter skate. The ages at 50% onset maturity and functional maturity are indicated by arrows and a horizontal dashed line.

TABLE 3.—Summary of logistic regression analyses of regional maturity in little skate. See Table 1 for abbreviations. All pairwise regional contrasts were significant for onset maturity; there were no significant pairwise regional differences in functional maturity.

Region	n	χ^2	P
Onset maturity			
MID	120	52.96	0.00
SNE–GB	144	96.54	0.00
GOM	16	9.99	0.00
Functional maturity			
MID	92	43.60	0.00
SNE–GB	144	71.35	0.00
GOM	16	13.86	0.00
Contrasts for onset maturity			
SNE–GB versus GOM		4.83	0.03
GOM versus MID		14.34	0.00
MID versus SNE–GB		11.14	0.00

dynamics on Georges Bank, specifically the emergence of large skates in the early 1980s, cannot be explained without assuming an open population. The Scotian Shelf was hypothesized as a source of the large adults that were observed on Georges Bank in the 1980s. Of the two sibling species studied here, winter skate is known to make long north–south seasonal migrations, while the evidence for little skate only supports onshore–offshore movement (NEFSC 1999; Frisk et al. 2008). Therefore, it is consistent with the migration hypothesis that Simon and Frank (1998) and McPhie (2007) working on the Scotian Shelf found sizes of functional maturity for winter skate (75 and 77 cm, respectively) similar to our estimate of 76 cm. In little skate, the size at maturation appears to increase with latitude, the Gulf of Maine and Scotian Shelf showing the largest size of maturity (46 cm; McPhie 2007). Regional differences in little skate vital rates suggest less population exchange, less migration, or both. The openness of the winter skate population is probably not universal across the species' range, as McEachran and Martin (1977) found that winter skate in the Gulf of Saint Lawrence attained a smaller size and reached maturity at a smaller length. Clearly, the migratory behavior and population connectivity of winter skate need further investigation.

We estimated the sizes at onset and functional maturity in winter skate for the western Atlantic. Onset maturity occurred at 66 cm and functional maturity at 76 cm throughout the northeast coast, which is equivalent to ages of 9.5 and 12–12.5 years. A significant finding is that in winter skate functional maturity appears to be delayed 3 years relative to onset maturity. This suggests that in some skate species estimating onset maturation only may drastically underestimate the age and size at which individuals
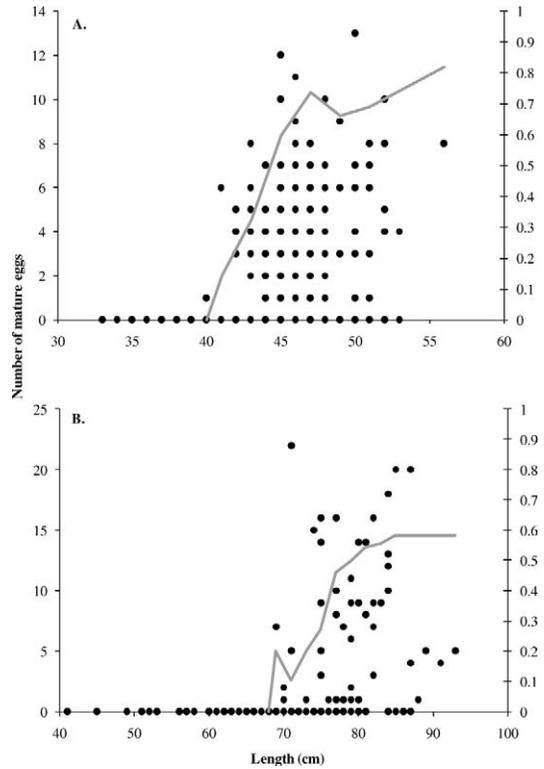

FIGURE 5.—Mature eggs (dots; left axes) and proportion of females with mature eggs (lines; right axes), with respect to total length, for (A) female little skate and (B) female winter skate. Mature eggs were defined as eggs exceeding 10 mm in diameter for little skate and 15 mm in diameter for winter skate.

actually contribute to the reproductive effort of the population. Importantly, it appears that energy allocation to reproduction occurs 3 years before fully mature oocytes are formed and egg cases released. This finding supports the notion of three-stage maturity scoring in skate species, as some species display an extended adolescent period (Richards et al. 1963; Simon and Frank 1998; Ebert et al. 2008).

The difference between onset maturity and functional maturity was small in little skate (approximately 1 cm). Our data suggest only a limited delay between the allocation of energy to reproduction and the production of mature oocytes and release of egg cases. We suggest that little skate have a short adolescence and that their maturation process is completed during a single season.

Although our knowledge of the population dynamics of skates is increasing (Walker and Hislop 1998; Dulvy et al. 2000; Stevens et al. 2000; Frisk et al. 2002; McPhie 2007; Gedamke et al. 2008), much work is still needed to understand the varying resiliency to

exploitation of Rajidae species (Walker and Hislop 1998; Frisk et al. 2002). A recent analysis by McPhie (2007) documented the reproductive collapse of several skate species on the Scotian Shelf and warned that winter skate are declining at 10% per year and are at risk of collapse. Much remains to be learned about life history and evolutionary trends among elasmobranchs, many of which display biological demographics at the extreme end of the life history strategies of fishes (Frisk 2004). We analyzed the contrasting life histories of two closely related species occupying different places along the fast–slow life history continuum. Further understanding these differences will help elucidate the underlying biological trade-offs that result in different degrees of resiliency to exploitation among species.

Acknowledgments

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