

Reproductive characteristics and population decline of four species of skate (Rajidae) off the eastern coast of Canada

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Four of the most common species of skate (Rajidae) were studied off eastern Canada to determine if their reproductive characteristics were linked to their population trajectories. The fecundity of the winter skate *Leucoraja ocellata*, the little skate *Leucoraja erinacea*, the thorny skate *Amblyraja radiata* and the smooth skate *Malacoraja senta* averaged between 41 and 56 egg cases per year for each species. For all species but *L. ocellata*, males matured at larger sizes and at later ages than females. Theoretical rates of population increase for non-equilibrium populations of *L. ocellata* (c. 0.07), *M. senta* (c. 0.14) and *L. erinacea* and *A. radiata* (c. 0.20) were low compared to most fishes, indicating that north-west Atlantic skates are intrinsically unproductive, yet are theoretically capable of supporting low-level fisheries. Nevertheless, the results of 36 years of research surveys indicate that the abundance of mature *L. ocellata*, *A. radiata* and *M. senta* all decreased by >90% since 1970, indicating that past fishing mortality (both directed and undirected) has outstripped the net productivity of the skate populations on the eastern Scotian Shelf. The relationship between maximum age (t_{\max}) and age of maturity (t_{mat}) was a better predictor of population growth rate than was body size, with the species exhibiting the highest ratios of $t_{\text{mat}}:t_{\max}$ (*L. ocellata* = 0.68, *M. senta* = 0.66) having the lowest predicted population growth rates. *L. ocellata* appears to have the lowest productivity and has experienced the greatest population decline, thus raising concerns over its future status.

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INTRODUCTION

In recent years, the vulnerability of elasmobranchs to collapse due to overexploitation has been well documented (Bonfil, 1994; Musick, 1999). Many species have low intrinsic rates of population increase due to their 'equilibrium strategist' life history characteristics such as slow growth rates, late sexual maturation, low fecundities and relatively long lives (Holden, 1974; Frisk *et al.*, 2001) and are thus unable to withstand even moderate levels of fishing mortality (Hoenig & Gruber, 1990). Although accounting for <1% of world fish catch, directed fisheries for elasmobranchs are increasing in response to declines in traditional finfish stocks

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(Bonfil, 1994). Multispecies fisheries and by-catch in demersal and longline fisheries targeting other species pose additional, and in some cases substantial threats to populations of elasmobranchs (Bonfil, 1994; Musick, 1999; Stobutzki *et al.*, 2002).

Batoids are among the most fecund of the elasmobranchs due to their oviparous reproductive strategy (Dulvy *et al.*, 2000) and are therefore thought to be more resilient to overexploitation than other shark-like fishes (Stevens *et al.*, 2000). Many batoid species, however, have experienced marked population declines in recent years. The disappearance of the common skate *Dipturus batis* (L.) from the Irish Sea (Brander, 1981), the reported absence of the long nose skate *Dipturus oxyrinchus* (L.) and the white skate *Rostroraja alba* (Lacépède) from extensive areas of their ranges (Dulvy & Reynolds, 2002), and the reported decline of the barndoor skate *Dipturus laevis* (Mitchill) in the north-western Atlantic [Casey & Myers (1998); although Gedamke *et al.* (2009) present strong evidence that the 'near extinction' of *D. laevis* reported by Casey & Myers (1998) is incorrect and the population has been increasing for more than a decade] suggest that as a group, batoids may be at risk.

In the north-west Atlantic, little is known about four of the most commonly occurring species of skate (Rajidae): the winter skate *Leucoraja ocellata* (Mitchill), the little skate *Leucoraja erinacea* (Mitchill), the thorny skate *Amblyraja radiata* (Donovan) and the smooth skate *Malacoraja senta* (Garman). All four species have been commercially landed in some portions of their ranges since the 1950s, and recent population declines have been noted in most areas for all but *L. erinacea* (Sosebee & Terceiro, 2000; NEFMC, 2005; Swain *et al.*, 2006). In the Gulf of Maine, precipitous declines in abundance and concurrent changes in population size structure have been documented for *A. radiata* and *M. senta*, prompting their protection from commercial landing (NEFMC, 2005). On the eastern Scotian Shelf (ESS) off the coast of Nova Scotia, Canada, *L. ocellata* abundance has declined markedly, resulting in a consideration of this species for listing as threatened under Canada's Species at Risk Act (Swain *et al.*, 2006).

Knowledge of the reproductive characteristics of a species is key to both assessing vulnerability and proper management. Although some aspects of reproduction have been reported for all four species of north-west Atlantic skate, previous studies have focused largely on the Gulf of Maine (Sulikowski *et al.*, 2004, 2005a, b, 2006, 2007a) and the U.S. north-eastern coast (Waring, 1984; Templeman, 1987; Sosebee, 2005). Nothing is known about size and age at maturity for each species on the more northerly ESS, where the characteristics are likely to vary from those reported for other areas given the relatively cold annual bottom water temperatures. Demographic analyses on elasmobranchs have found that under increasing levels of exploitation those species with the lowest length and age at maturity have the greatest population growth rates and the highest chances of survival (Walker & Hislop, 1998; Jennings *et al.*, 1999; Frisk *et al.*, 2001). At present, the identification of the appropriate conservation status of each species of skate in Canadian waters is hampered by a lack of species and region-specific reproductive information.

In view of the concern over skate stocks in the North Atlantic and the need for biological information on skates on the ESS for the development of conservation strategies, the objectives of this study were to (1) describe the reproductive characteristics of all four skate species on the ESS, (2) use research vessel survey data to document the population trajectories of all four species on the ESS since the 1970s;

and (3) use demographic analyses to quantify relationships between life-history traits and susceptibility to decline in north-west Atlantic skates. This paper concludes by commenting on the sustainability of the existing skate populations on the ESS given current mortality rates.

MATERIALS AND METHODS

COLLECTION AND ANALYSIS OF SAMPLES

Skates were collected seasonally between May of 2004 and March of 2006 from the Department of Fisheries and Oceans (DFO) research vessel (RV) survey cruises (69 *L. ocellata*, 86 *L. erinacea*, 168 *A. radiata* and 91 *M. senta*), cooperative industry–science and sentinel cruises (59 *L. ocellata*, 6 *L. erinacea*, 100 *A. radiata* and 22 *M. senta*) and commercial longline vessels (14 *A. radiata*) along the ESS (NAFO division 4VsW; Fig. 1). Bottom trawl surveys were carried out at depths ranging from 69 to 366 m; specimens caught on longline were captured at depths ≤ 658 m. Sex and total length (L_T)-stratified skate samples of each species were frozen on board and returned to the laboratory for detailed reproductive analyses.

Once specimens were thawed, measurements of total wet mass (W , kg) and total length (L_T , mm) and disc width (W_D , mm) to the nearest 5 mm were taken following the conventions of Bigelow & Schroeder (1948). It is extremely difficult to differentiate between *L. erinacea* and *L. ocellata* below 300 mm L_T using conventional methods such as dorsal spine and tooth counts (McEachran & Musick, 1973). Accordingly, species were identified morphologically except in the case of skate ≤ 300 –350 mm L_T , which were identified genetically using a rapid polymerase chain reaction restriction fragment length polymorphism (PCR-RFLP) assay (Alvarado Bremer *et al.*, 2005). The relationship between L_T and W_D was determined for each species using non-linear least-squares regression analyses (SPSS 11.5; www.spss.com). ANCOVA on ln-transformed data were used to test for sex-specific differences.

Maturity status was assigned to each skate based on a number of macroscopic measurements and observations of reproductive organ condition, with specific stages modified from Snelson *et al.* (1988) and Mabragana & Cousseau (2004). In males, clasper length (L_C , mm) was measured on the inside edge from the point of insertion to the distal end, and clasper rigidity (or the degree of calcification) was assessed as either (1) ‘uncalcified’ when the organ was soft and easily bent; (2) ‘plastic’ when the organ was flexible but showing some structure and development of the tips (glans); or (3) ‘calcified’ when the organ was completely stiff and resisted deformation, and the glans structure opened readily upon flexion. Other corroborative indices of maturity, which were recorded were: testes mass (g) (including mass of the epigonal organ due to its close association with the gonads); the development (or bulging) of testicular lobes; the diameter (mm) and shape of the both the epididymis and the vas deferens at their widest points; and the presence of sperm in the lower part of the ductus deferens, all of which are indicative of active sperm production. The presence, total number and state (soft, semi-soft or hard) of thorns in the alar thorn patch were also noted for each specimen.

In females, uterus diameter (mm), shell gland diameter (D_{SG} ; mm), ovary mass (W_O ; g) and shell gland mass (W_{SG} ; g) were recorded for each specimen. The total number of ovarian follicles (to a maximum of 30) was also determined, along with the length and width (to a maximum of 30) of a random selection of all fixed ovoid follicles averaged to give egg diameter to the nearest 0.1 mm. The average diameter of the five largest ovarian follicles was calculated, and the presence or absence of vitellogenic follicles was noted. Only those females either in the process of encapsulation or with shell glands and follicles approximately equal to or larger in diameter than the shell glands and largest yolked follicles of spawning-stage skates were considered reproductively capable. When egg capsules were found, the state of formation of each capsule was recorded, as was egg capsule mass (W_{ec} ; g) and dissected yolk mass (W_{yolk} ; g). Linear regression analysis was used to test for the effects of maternal body size (W , kg) on W_{ec} (g) and W_{yolk} (g) in *A. radiata*.

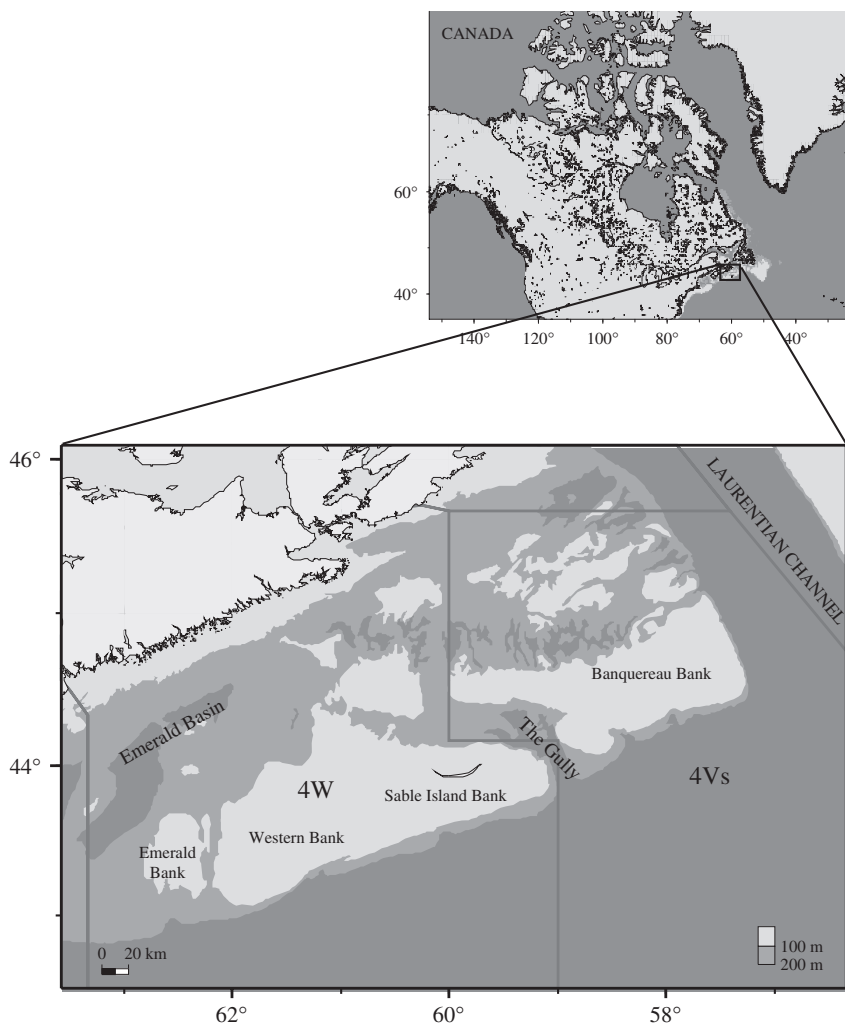


FIG. 1. Map of the study area. *Leucoraja ocellata*, *Leucoraja erinacea*, *Amblyraja radiata* and *Malacoraja senta* specimens were collected from research vessel (RV) surveys, industry surveys and fishing vessels throughout the eastern Scotian Shelf (NAFO Divisions 4VsW).

In previous studies on elasmobranchs, size at maturity has been associated with a distinct inflection or a marked increase in reproductive organ size (Templeman, 1987; Jensen *et al.*, 2002). In this study, size-at-maturity estimates from individual reproductive organs were obtained by fitting a logistic growth model formulated following Piner *et al.* (2005) to relationships between each reproductive variable and L_T for each species using non-linear least squares: $\hat{y} = y_{\min} + k\{1 + e^{[b(a-x)]}\}^{-1}$, where \hat{y} = reproductive organ size (*i.e.* clasper length L_C), y_{\min} = minimum observed value of reproductive organ size, $x = L_T$, and the estimated parameters are k = absolute range of increase, a = inflection point and b = shape parameter. The value of a of the resulting sigmoid curve was used to estimate maturity in each case. Preliminary analyses indicated that there were no significant differences between the morphometric characteristics of the left and right reproductive organs of each species (paired sample *t*-tests, $P > 0.05$). There were also no significant differences between the numbers and diameter of follicles in the left and right ovaries of females ($P > 0.05$), and

egg capsules were observed in both uteri of spawning females, indicating functional left and right reproductive tracts. As such, it was assumed that observations of only one reproductive organ would be representative of maturation in each species, and measurements of the left reproductive organ were used in all subsequent analyses.

SIZE AND AGE AT MATURITY

L_T at 50% maturity (L_{T50}) and age at 50%-maturity (A_{50}) were estimated for males and females of each species using maturity ogives. Logit curves were fitted to sex-specific plots of per cent maturity and L_T (mm) and band pair count (age in years) for each species using R-Project 2.3.1 (<http://cran.r-project.org/bin/windows/base/old/2.3.1/>). Per cent maturity was determined for each L_T interval (200 mm) and band count interval (1 year) using a binomial maturity classification (mature *v.* immature). Ages for males and females of each species were estimated from vertebral band counts; ageing accuracy was validated only for *A. radiata*, but identical methods were used to age the other species (McPhie & Campana, 2009).

POPULATION TRAJECTORIES

July DFO RV survey data from 1970 to 2006 were used to plot population trajectories for each species on the ESS. Stratified mean catch (number per tow) over time was plotted for groups corresponding roughly to immature and mature individuals of each species based on sex-averaged L_{T50} (*L. ocellata* = 760 mm, *L. erinacea* = 470 mm, *A. radiata* = 580 mm and *M. senta* = 480 mm).

Rate of change was determined for mature individuals of each species by fitting an exponential model to each time series using non-linear least squares: $N_t = N_0 e^{\delta t}$, where N_0 is abundance in the first year of the time series (1970), t is the time since the first year and δ is the instantaneous rate of decline (or increase). Zero catches were replaced by half the minimum non-zero value for each species. The slope (δ), or the estimated rate of decline, was also used to estimate the per cent decline over the entire time series (t years) using the equation: $\Delta = 100(1 - e^{-\delta t})$. Capture locations and total number of mature females of each species, from July RV survey data (1971–1988 and 1989–2006) were mapped using statistical analysis software (ACON; <http://www.mar.dfo-mpo.gc.ca/science/acon/index.html>). Lengths at maturity were based on L_{T50} calculations for females of each species from maturity ogives.

DEMOGRAPHIC ANALYSES

Life tables (Leslie matrices) were constructed for each species based on best estimates of longevity, age at maturity, fecundity and mortality on the ESS. Age interpretations for all four species were described in the study by McPhie & Campana (2009). Estimates of net reproductive rate per generation (R_0), mean generation time (G , year) and the predicted rate of population increase (r_{pred} , year⁻¹) were calculated using standard demographic techniques (Cortés, 1998; Simpfendorfer, 1999), where r_{pred} was defined as the instantaneous rate of growth of the population given the parameters used in the life table matrix and assuming a stable age distribution. As noted by Gedamke *et al.* (in press), r_{pred} as calculated from life-history tables is not equivalent to $r_{\text{intrinsic}}$, although it is often reported as such, since it represents a snapshot of population growth based on a fixed set of life-history parameters and a given mortality schedule and excludes density-dependent effects. Given that the skate populations described in this study were at relatively low levels, but that the existence of density dependence could not be excluded, it is likely that the estimates of r_{pred} are somewhat lower than the true maximum population growth rate, $r_{\text{intrinsic}}$.

Age at 50% maturity (A_{50}) was used to approximate the timing of first reproductive activity for female skate of each species (t_{mat}). Two estimates of longevity were used for each species, the first being the oldest skate aged using band pair counts (t_{max}) and the second being a theoretical longevity ($T_{\text{max(th)}}$) (because observed values from fished populations are likely to underestimate true maximum ages). Theoretical longevity was determined using Taylor's (1958) definition of the life span of teleosts as the time required to reach 95% of the mean

theoretical maximum length (L_∞): $T_{\max(\text{th})} = t_0 - [\ln(1 - 0.95)K^{-1}]$, where t_0 and K are coefficients of the von Bertalanffy growth curve.

To estimate the natality function (m_x), it was assumed that skates on the ESS are capable of reproduction year round; that all females older than A_{50} are indeed mature, and all mature females breed over the course of every year. Rough approximations of the number of eggs laid per year per female of each species were obtained using two methods. First, potential fecundity was determined by plotting ova diameter (mm) frequency distributions for randomly selected immature ($N = 10$ per species) skates and using the 95th percentiles to approximate the size of immature ova. For all females deemed mature, the number of mature ova in each ovary with diameters exceeding the species-specific immature ova diameter (*i.e.* 95th percentile) was then determined. Relationships between maternal size (L_T) and the sum of mature ova in the left and right ovaries (O_{sum}) were either very weak (*L. erinacea*: $O_{\text{sum}} = e^{[9.317 + (-281.4L_T^{-1})]}$, $R^2 = 0.30$, $P < 0.05$, $n = 16$; *A. radiata*: $O_{\text{sum}} = 42.47 + (0.2186L_T)$, $R^2 = 0.12$, $P < 0.05$, $n = 52$) or not significant (*L. ocellata* and *M. senta*, $P > 0.05$). As such, age-specific natality (or potential fecundity) was fixed for each species and was calculated by averaging the sum of left and right mature ova counts for all mature females. Approximate fecundities for each species were also obtained from the literature or by applying calculated fecundities for skate species of similar maximum size. The fecundity of *L. ocellata* (48 eggs year⁻¹) and *A. radiata* (41 eggs year⁻¹) in an aquarium setting was reported by Parent *et al.* (2008), and the fecundity of *Raja montagui* Fowler (750 mm L_T , 60 eggs year⁻¹) (Holden *et al.*, 1971) was used to approximate that of *M. senta*. For *L. erinacea*, the average fecundity of *Raja eglanteria* Bosc (60 eggs year⁻¹) (Luer & Gilbert, 1985) was used, since it was postulated to lay the same number of eggs per year as *R. erinacea* by Holden (1975) due to similar maximum observed rates of egg laying. A sex ratio at birth of 1:1 was assumed for all species; fecundity estimates were subsequently divided by two because m_x represents the number of female offspring per female.

Four methods were used to estimate natural instantaneous mortality (M) for each species: (1) Pauly's (1980) equation which relates M to von Bertalanffy growth factor (VBGF) parameters and to an estimate of mean annual water temperature in the area in which the study population occurs; (2) one of Jensen's (1996) two equations which estimates M using A_{50} ($M = 1.65A_{50}^{-1}$); (3) the second of Jensen's (1996) equations using the von Bertalanffy growth coefficient ($M = 1.5K$); (4) Petersen & Wroblewski's (1984) size-dependent equation which assumes that mortality is primarily a function of predation and was derived using pre-existing theory on the distribution of biomass in the pelagic marine environment. Mass-at-age values for the last equation were calculated using species-specific allometric L_T and W relationships and VBGF. W (g) was used for all species due to unrealistically high levels of M calculated with dry mass (using a dry mass to wet mass conversion ratio of 0.2) (Cortés, 2002; Beerkircher *et al.*, 2003).

Length-converted catch curve (LCCC) analyses using stratified L_T frequencies from spring (March) and summer (July) DFO RV survey data from 2001–2006 were used to estimate total instantaneous mortality (Z). Data from 2004 were excluded due to a vessel change and a lack of an appropriate conversion factor. For each season, L_T (in 30 mm intervals for *L. ocellata* and *A. radiata*, and 10 mm intervals for *L. erinacea* and *M. senta*) were converted to integer ages using species-specific, sex-combined VBGF (McPhie & Campana, 2009), and plotted against the natural logarithm of stratified catch at age for the entire five year period. The slope of the descending right limb of each curve (Z) was estimated through least-squares linear regression, with the first point included in each linear regression being that immediately to the right of the highest point (Ricker, 1975). Points to the right of the last point used to calculate each linear regression were deemed negligible based on the small numbers of individuals in the associated age classes (*i.e.* one individual), and the high probability that some individuals were either misidentified or misrecorded based on a comparison of species-specific L_∞ values with recorded L_T .

Survivorship (S_i) was calculated using natural mortality estimates, where $S = e^{-M}$. To simulate the decreased survivorship expected of young-of-the-year skates and to better account for the unknown mortality of the extruded egg cases, M values were doubled for the first age class. Survivorship for age 1+ year skates was assumed to be constant.

Net population change was estimated as the difference between Z (from catch curves) and the sum of r_{pred} and M . This calculation is only an approximation, since Z integrates total mortality over many years, while r_{pred} represents a static image from recent years only.

RESULTS

A total of 128 *L. ocellata* (73 males and 55 females), 92 *L. erinacea* (43 males and 49 females), 282 *A. radiata* (139 males and 143 females) and 113 *M. senta* (62 males and 51 females) were examined. The sampled L_T length ranges for each species reflected expected ranges based on previously published values, except in the case of *L. ocellata* where young fish and mature females were under-sampled. Based on PCR-RFLP analyses, *L. erinacea* dominated catches of *L. ocellata* and *L. erinacea* < 300 mm L_T (18 out of 26 = 69%). The smallest *L. ocellata* caught was 210 mm L_T .

W varied significantly with L_T for all species, with power curves best describing the L_T and W data in all cases (*L. ocellata*: $W = 0.0018L_T^{3.321}$, $R^2 = 0.97$, $n = 128$; *L. erinacea*: $W = 0.0028L_T^{3.193}$, $R^2 = 0.97$, $n = 92$; *A. radiata*: $W = 0.0073L_T^{3.048}$, $R^2 = 0.98$, $n = 282$; *M. senta*: $W = 0.0027L_T^{3.147}$, $R^2 = 0.98$, $n = 112$). There were no significant differences in allometric W and L_T relationships between males and females of each species (ln-transformed data, ANCOVA, $P > 0.05$).

Skates of all maturity stages and both sexes were collected for each species. For males, significant logistic relationships ($P < 0.05$) between L_C and L_T were present in each species (*L. ocellata* $R^2 = 0.87$, $n = 73$; *L. erinacea* $R^2 = 0.95$, $n = 43$; *A. radiata* $R^2 = 0.75$, $n = 139$; *M. senta* $R^2 = 0.91$, $n = 62$; Fig. 2). Estimated mean \pm s.d. values of a representing c . L_{T50} for males of each species were 698 ± 70 mm for *L. ocellata*, 422 ± 15 mm for *L. erinacea*, 514 ± 37 mm for *A. radiata* and 450 ± 16 mm for *M. senta*.

For females, significant ($P < 0.05$) logistic relationships between W_O and L_T were generally weak (*L. ocellata*: $R^2 = 0.77$, $n = 55$; *A. radiata*: $R^2 = 0.71$, $n = 143$; *M. senta*: $R^2 = 0.53$, $n = 51$) resulting in mean \pm s.d. values a of 904 ± 377 mm for *L. ocellata*, 1160 ± 1123 mm for *A. radiata* and 418 ± 44 mm for *M. senta* (Fig. 3). Significant logistic relationships between D_{SG} and L_T were slightly stronger (*L. ocellata*: $R^2 = 0.79$, $n = 55$; *L. erinacea*: $R^2 = 0.85$, $n = 49$; *A. radiata*: $R^2 = 0.71$, $n = 143$; *M. senta*: $R^2 = 0.96$, $n = 51$; Fig. 3). Resulting mean \pm s.d. values of a (*L. ocellata*: 897 ± 521 mm; *L. erinacea*: 440 ± 24 mm; *A. radiata*: 435 ± 21 mm; *M. senta*: 394 ± 16 mm) were markedly different from those estimated using W_O and much closer to those estimated using maturity ogives, with the exception of *M. senta* (Fig. 3).

The values of W_{ec} and W_{yolk} varied linearly with W in female *A. radiata* (W_{ec} : $R^2 = 0.71$, $P < 0.05$, $n = 8$; W_{yolk} : $R^2 = 0.87$, $P < 0.05$, $n = 8$; Fig. 4).

SIZE AND AGE AT MATURITY

When all reproductive organ characteristics were taken into account, all four species varied considerably in the sizes at which maturity was reached (Table I). *A. radiata*, in particular, showed great variation in L_{T50} within each sex, with some

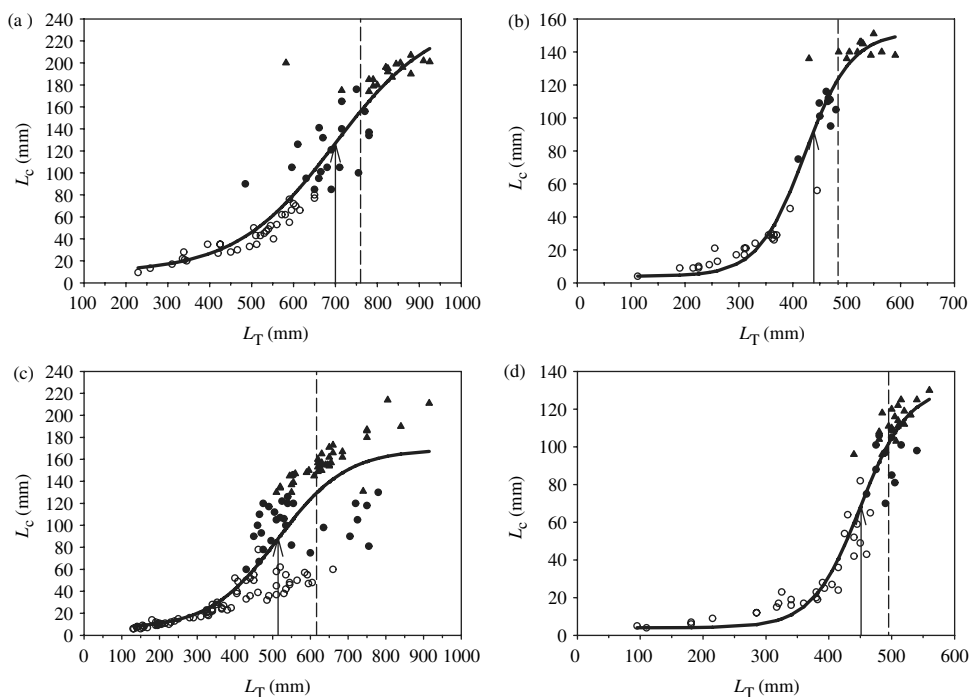


FIG. 2. Relationship between left clasper length (L_C), clasper calcification (\blacktriangle , calcified; \circ , not calcified; \bullet , plastic), and total length (L_T) for (a) *Leucoraja ocellata*, (b) *Leucoraja erinacea*, (c) *Amblyraja radiata* and (d) *Malacoraja senta*, and associated estimates of the inflection point (\dagger) of fitted logistic growth curves (—). L_T at 50% maturity estimates (\dagger) from maturity ogives are shown for each species.

individuals maturing at sizes as low as 390 mm L_T (female) and 510 mm L_T (male) and others not reaching maturity until 745 mm L_T (female) and 780 mm L_T (male) (Table I). The large disparity in L_{T50} among *A. radiata* of the same sex suggested two separate groups, a bimodal pattern which was also apparent in the relationships between L_C and L_T (and to a lesser extent between D_{SG} and L_T) for this species [Figs 2(c) and 3(c)]. When L_T was plotted against age for each suspected group (sexes separate and sexes combined), no substantial differences in growth were apparent between groups, although low sample sizes precluded a statistical comparison of growth curves.

L. ocellata males and females reached 50% maturity at approximately the same size (L_{T50}) and age (A_{50}) (Table I). For *L. erinacea*, L_{T50} was comparable between the sexes whereas males matured at a significantly later age. For *A. radiata* and *M. senta*, both L_{T50} and A_{50} were significantly larger for males than for females, with *A. radiata* showing the greatest variation of all four species in size and age at maturity between the sexes (Table I).

POPULATION TRAJECTORIES

Population abundance (stratified mean number per tow) of *L. ocellata*, *A. radiata* and *M. senta* on the ESS declined significantly after 1970, most notably in sizes

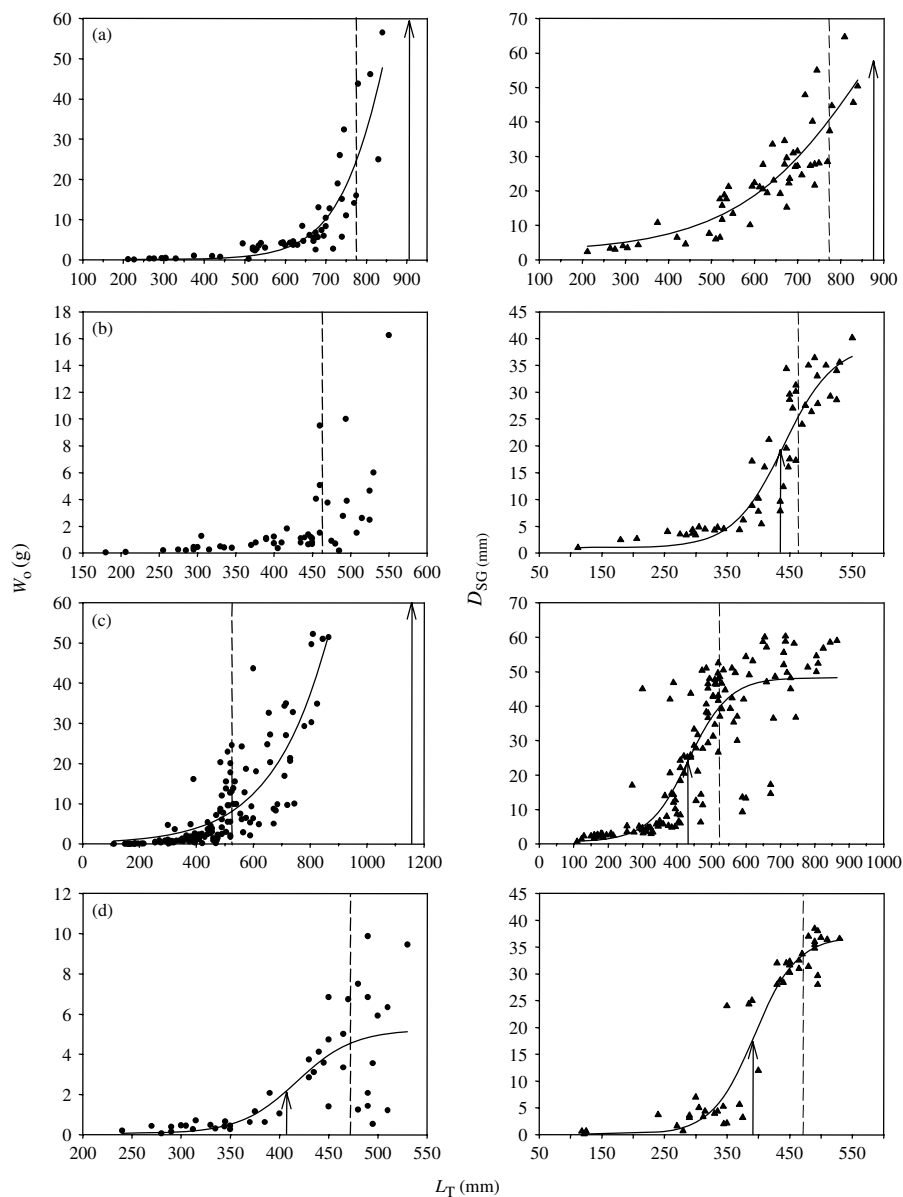


FIG. 3. Relationship between ovary mass (W_o) (●) and shell gland diameter (D_{SG}) (▲) and total length (L_T) for (a) *Leucoraja ocellata* (b) *Leucoraja erinacea* (c) *Amblyraja radiata* and (d) *Malacoraja senta*, and associated estimates of the inflection point (↑) of fitted logistic growth curves (—). L_T at 50% maturity estimates (†) from maturity ogives are shown for each species.

corresponding to mature individuals (Fig. 5). When the total number of mature females was mapped in 18 year time intervals, substantially fewer adult females of these three species remained on the ESS from 1989 to 2006 compared to 1971–1988 (Fig. 6). Over the entire 36 year time period (1970–2006), *A. radiata*

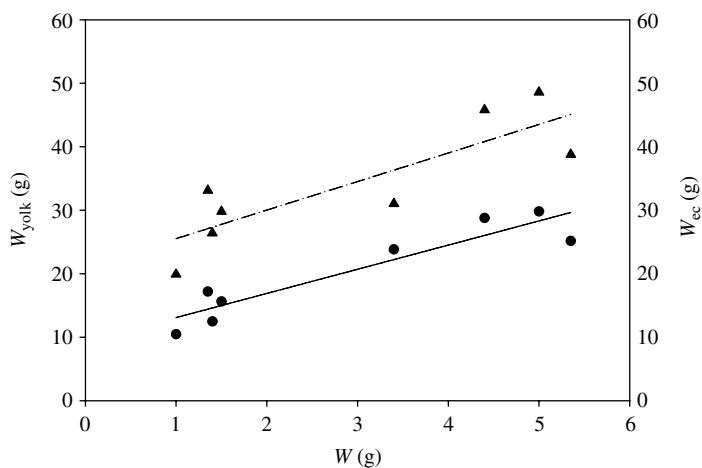


FIG. 4. Linear relationships between yolk mass (W_{yolk}) and total maternal mass (W) for mature female *Amblyraja radiata* (●; —; $y = 3.81x + 9.28$) and egg capsule mass (W_{ec}) and W for mature female *A. radiata* (▲; ---; $y = 4.50x + 21.02$).

TABLE I. Maximum immature and minimum mature total lengths (L_T) for male and female north-west Atlantic skates. L_T at 50% maturity (L_{T50}) and age at 50% maturity (A_{50}) with S.E. are given for *Leucoraja ocellata*, *Leucoraja erinacea*, *Amblyraja radiata* and *Malacoraja senta* from maturity ogives. Significant differences between sexes are noted ($P < 0.05^*$)

	Largest immature L_T (mm)	Smallest mature L_T (mm)	L_{T50} (mm)	A_{50} (years)
<i>L. ocellata</i>				
Males	780	580	759 ± 17	11.3 ± 0.9
Females	775	720	770 ± 17	13.4 ± 2.2
<i>L. erinacea</i>				
Males	480	485	$484 \pm 8^*$	7.1 ± 0.6
Females	515	450	$464 \pm 8^*$	6.9 ± 0.4
<i>A. radiata</i>				
Males	780	510	$626 \pm 20^*$	$14.7 \pm 1.4^*$
Females	745	390	$534 \pm 18^*$	$10.7^* \pm 0.7$
<i>M. senta</i>				
Males	540	440	$498 \pm 8^*$	$11.7 \pm 0.8^*$
Females	495	440	$472 \pm 12^*$	$10.1 \pm 0.8^*$

adults experienced the greatest decline in abundance (95.8%) followed by *M. senta* (95.6%) and *L. ocellata* adults (92.5%) (Fig. 5). In contrast, mature *L. erinacea* increased by 80.2% over the entire 36 year period (Figs 5 and 6).

DEMOGRAPHY

Theoretical longevity ($T_{\text{max(th)}}$) obtained using Taylor's (1958) equation varied from 15 years (*L. erinacea*) to 39 years (*A. radiata*). *L. ocellata* and *M. senta* $T_{\text{max(th)}}$ values were 19 and 23 years, respectively.

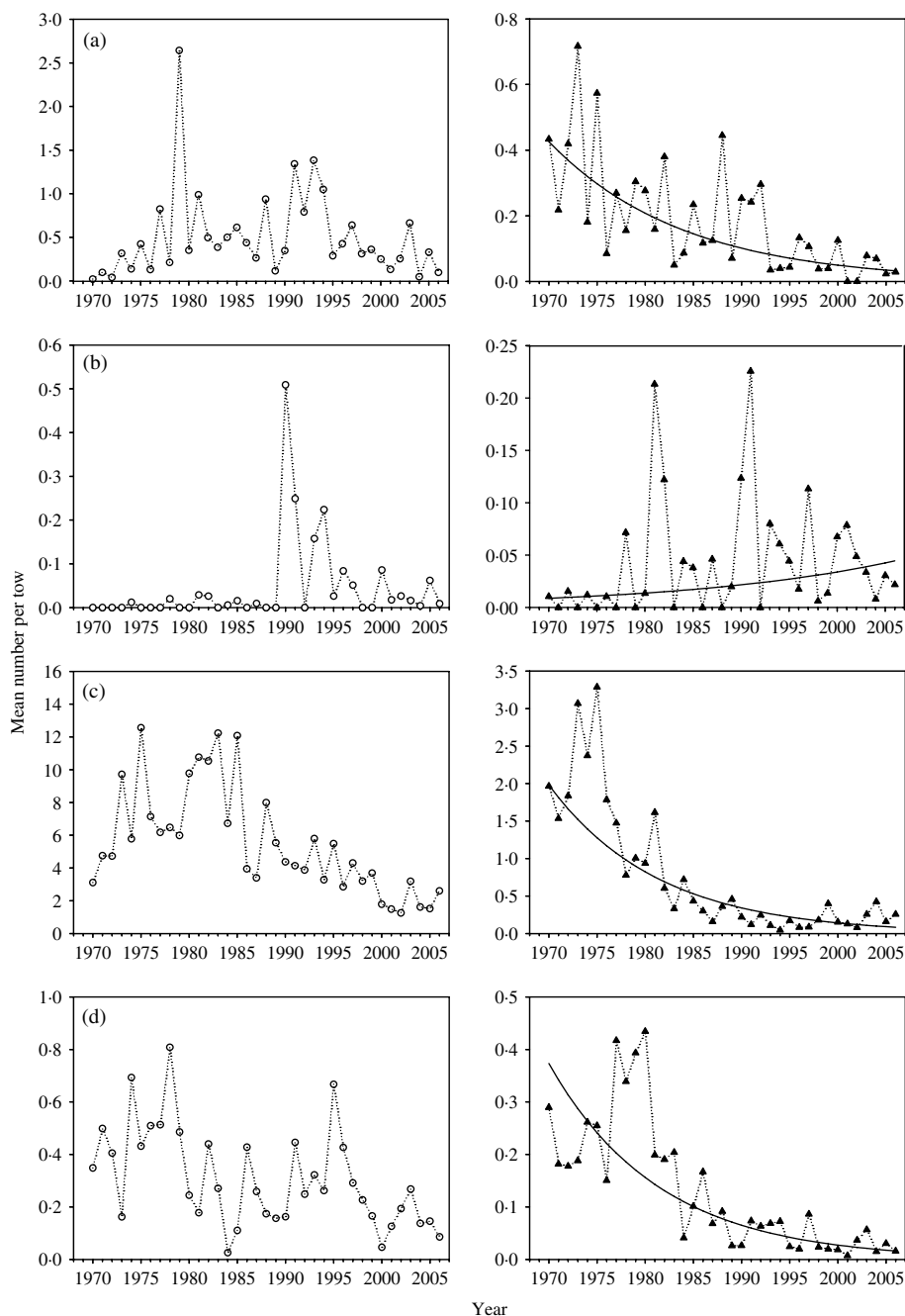


FIG. 5. Stratified mean number per tow of (a) *Leucoraja ocellata*, (b) *Leucoraja erinacea*, (c) *Amblyraja radiata* and (d) *Malacoraja senta* from the July research vessel survey on the eastern Scotian Shelf. Total length classes corresponding to immature (\circ) *L. ocellata* (≤ 750 mm), *L. erinacea* (≤ 460 mm), *A. radiata* (≤ 570 mm) and *M. senta* (≤ 470 mm) and mature (\blacktriangle) *L. ocellata* (760+ mm), *L. erinacea* (470+ mm), *A. radiata* (580+ mm) and *M. senta* (480+ mm) are shown separately. Exponential rates of change of adult skate of each species are shown (—).

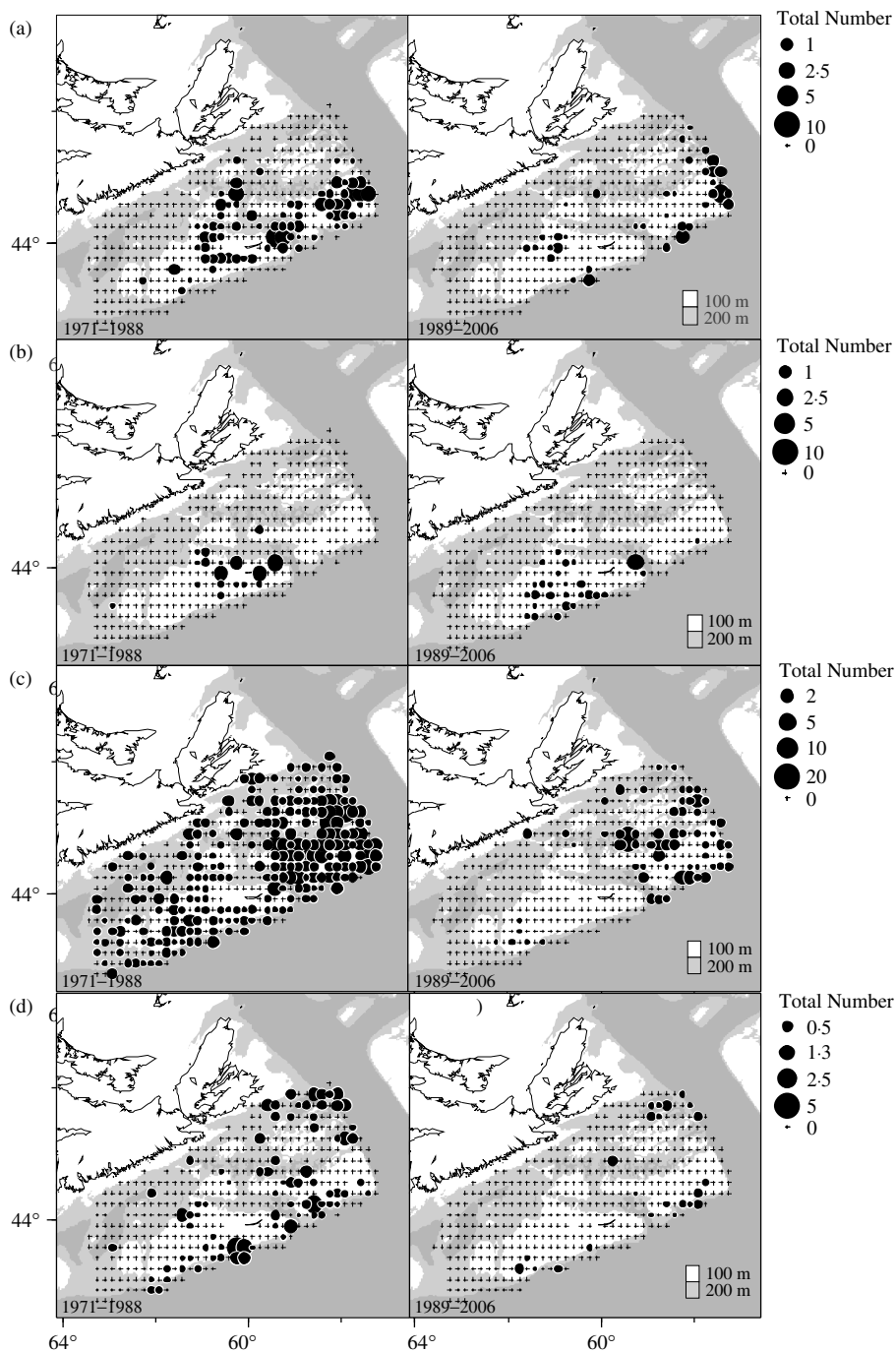


FIG. 6. Capture locations and stratified total number of mature female (a) *Leucoraja ocellata* (770+ mm total length), (b) *Leucoraja erinacea* (460+ mm), (c) *Amblyraja radiata* (530+ mm) and (d) *Malacoraja senta* (470+ mm) from July research vessel survey data since 1971. Maps show changes in abundance for each species between 1971 and 1988 and 1989 and 2006 (*i.e.* 18 year time series).

TABLE II. Biological input parameters and demographic output parameters for skates on the eastern Scotian Shelf under a number of natality and mortality situations (1 to 10)

Species	Situations	Input parameters			Mortality equation	Output parameters						
		t_{\max}	t_{mat}	m_x		No exploitation						
						S_n	R_0	G	r_{pred}	Exploited Z	Net change	
<i>Leucoraja ocellata</i>	1	19	13	25-85	Average	0.26	0.77	2.34	15.00	0.06	0.42	-0.10
	2	19	13	45-00	Jensen (T_{50})	0.26	0.77	4.07	15.00	0.09	0.42	-0.06
	3	19	13	25-85		0.13	0.87	19.29	15.47	0.20	0.42	-0.09
	4	19	13	45-00		0.13	0.87	33.59	15.47	0.23	0.42	-0.05
	5	19	13	25-85	Jensen (K)	0.22	0.80	4.75	15.16	0.10	0.42	-0.10
	6	19	13	45-00	Pauly	0.22	0.80	8.27	15.16	0.14	0.42	-0.06
	7	19	13	25-85		0.44	0.65	0.15	14.48	-0.13	0.42	-0.11
	8	19	13	45-00		0.44	0.65	0.26	14.48	-0.09	0.42	-0.07
	9	19	13	25-85	Petersen Wroblewski	size-dependent		0.84	15.11	-0.01	0.42	
	10	19	13	45-00	Average	size-dependent		1.46	15.11	0.03	0.42	
1	12	7	20-65	0.34		0.71	4.24	8.58	0.17	0.55	-0.04	
<i>Leucoraja erinacea</i>	2	12	7	30-00	Jensen (T_{50})	0.34	0.71	6.16	8.58	0.22	0.55	0.00
	3	12	7	20-65		0.24	0.79	11.33	8.84	0.29	0.55	-0.03
	4	12	7	30-00		0.24	0.79	16.46	8.84	0.33	0.55	0.02
	5	12	7	20-65	Jensen (K)	0.28	0.76	7.34	8.72	0.24	0.55	-0.03
	6	12	7	30-00	Pauly	0.28	0.76	10.66	8.72	0.28	0.55	0.01
	7	12	7	20-65		0.49	0.61	0.96	8.24	-0.01	0.55	-0.06
	8	12	7	30-00		0.49	0.61	1.39	8.24	0.04	0.55	-0.01
	9	12	7	20-65	Petersen Wroblewski	size-dependent		0.72	8.51	-0.04	0.55	
	10	12	7	30-00	Average	size-dependent		1.05	8.51	0.01	0.55	

TABLE II. Continued

Species	Situations	Input parameters			Mortality equation	M	Output parameters				Net change	
		t_{\max}	t_{mat}	m_x			No exploitation			r_{pred}		Exploited Z
							S_n	R_0	G			
<i>Amblyraja radiata</i>	1	19	11	27.80	Average	0.21	0.81	10.36	13.69	0.18	0.30	0.03
	2	19	11	45.00	Jensen (T_{50})	0.21	0.81	16.76	13.69	0.21	0.30	0.12
	3	19	11	27.80		0.13	0.88	33.19	14.15	0.26	0.30	0.09
	4	19	11	45.00		0.13	0.88	53.73	14.15	0.30	0.30	0.13
	5	19	11	27.80	Jensen (K)	0.11	0.90	45.03	14.28	0.28	0.30	0.09
	6	19	11	45.00	Pauly	0.11	0.90	72.89	14.28	0.32	0.30	0.13
	7	19	11	27.80		0.38	0.68	0.84	12.84	−0.01	0.30	0.07
	8	19	11	45.00	Petersen Wroblewski size-dependent	0.38	0.68	1.36	12.84	0.02	0.30	0.11
	9	19	11	27.80		0.56	0.56	13.29	−0.04	0.30		
	10	19	11	45.00	0.90	0.90	13.29	−0.01	0.30			
<i>Malacoraja senta</i>	1	15	10	25.40	Average	0.26	0.77	4.78	11.76	0.13	0.18	0.04
	2	15	10	30.00	Jensen (T_{50})	0.26	0.77	5.64	11.76	0.15	0.18	0.23
	3	15	10	25.40		0.15	0.86	20.41	12.07	0.26	0.18	0.23
	4	15	10	30.00		0.15	0.86	24.11	12.07	0.27	0.18	0.24
	5	15	10	25.40	Jensen (K)	0.18	0.84	14.39	11.99	0.23	0.18	0.23
	6	15	10	30.00	Pauly	0.18	0.84	17.00	11.99	0.24	0.18	0.24
	7	15	10	25.40		0.46	0.63	0.40	11.30	−0.08	0.18	0.20
	8	15	10	30.00	Petersen Wroblewski size-dependent	0.46	0.63	0.47	11.30	−0.07	0.18	0.22
	9	15	10	25.40		0.12	0.12	11.44	−0.18	0.18		
	10	15	10	30.00	0.14	0.14	11.44	−0.17	0.18			

t_{\max} , maximum observed age; t_{mat} , female age at maturity; m_x , fecundity (number of female offspring per year); M , natural instantaneous mortality; S_n , survivorship; R_0 , net reproductive rate per generation; G , generation time; r_{pred} , predicted rate of population increase; Z , total instantaneous mortality estimates obtained from catch curves apply to all situations.

Annual fecundity estimates (*L. ocellata*: 52, $n = 7$; *L. erinacea*: 41, $n = 16$; *A. radiata*: 56, $n = 52$; *M. senta*: 51, $n = 12$) obtained using average counts of species-specific mature-sized ova yielded estimates very similar to those obtained from the literature (Table II). Similarly, M estimates for age 1+ year skates varied considerably among species depending on the method used. Within each species, Pauly's (1980) and Petersen & Wroblewski's (1984) equations tended to yield higher mortality estimates than those derived from life-history parameters (Jensen, 1996). Average natural mortality estimates (\overline{M}) derived from Pauly's and Jensen's equations yielded values ranging from 0.21 (*A. radiata*) to 0.34 (*L. erinacea*).

Estimates of Z from catch curves were significant ($P < 0.05$) in all instances except for *L. erinacea* caught in the spring (Table III and Fig. 7), ranging between 0.18 and 0.55. Given that catch curves provide an index of mortality over an extended time period (at least 10 years), and assuming that skate recruitment declined through time as adult biomass declined, it is likely that the Z estimates underestimate actual Z values.

Life tables constructed for each species resulted in positive values of r_{pred} under all longevity and natality schedules when \overline{M} values were used (Table II, situations 1 and 2), as would be expected for healthy, increasing populations. Values of r_{pred} obtained using t_{max} values and potential fecundity estimates calculated in this study ranged from 0.06 (*L. ocellata*, 5.9% year⁻¹) to 0.18 (*A. radiata*, 19.3% year⁻¹) (Table II, situation 1). When $T_{\text{max (th)}}$ values were used, r_{pred} , R_0 , and G all increased marginally. *M. senta* exhibited the greatest increases in output parameters with an increase in longevity (from 15 to 23 years), with r_{pred} , R_0 and G values being 6, 23 and 10% greater, respectively. Therefore, t_{max} values were used in all subsequent life tables, whereby changes in fecundity and individual estimates of natural mortality were assessed for their effect on demographic output parameters.

Estimated M values greatly affected demographic output parameters for all species. Under zero levels of exploitation, 'best case' situations (*i.e.* highest r_{pred} values) for *L. ocellata*, *L. erinacea* and *M. senta* were obtained using Jensen's (1996) relationship relating M to A_{50} (Table II, situations 3 and 4). For *A. radiata*, the highest r_{pred} value was obtained using Jensen's (1996) K -dependent natural mortality equation (Table II, situations 5 and 6). Worst-case situations (*i.e.* lowest r_{pred} values) were obtained using either Pauly's (1980) equation (Table II, situations 7 and 8) or Petersen & Wroblewski's (1984) size-dependent equation (Table II, situations 9 and 10), with input parameters often yielding negative, non-viable r_{pred} values. For each species, increases in m_x resulted in increases in r_{pred} values, in some instances by as much as 66% (*i.e.* with a change in m_x of 25.85 to 45, Table II, *L. ocellata* -1 to *L. ocellata* -2). The highest r_{pred} value obtained under best-case, species-specific mortality and fecundity schedules was for *L. erinacea* (0.33 or 39.3% year⁻¹) (Table II, *L. erinacea* -4), and the lowest was for *L. ocellata* (0.23 or 26.3% year⁻¹) (Table II, *L. ocellata* -4). When \overline{M} values were used, *A. radiata* and *L. erinacea* had the highest r_{pred} values (depending on which values of m_x was used), followed by *M. senta* and then *L. ocellata* (Table II, situations 1 and 2). Overall, *L. ocellata* exhibited the lowest positive (viable) r_{pred} values under all mortality and fecundity situations.

Given the different time scales represented by the estimates of Z (from the catch curves) and r_{pred} , it was not possible to provide a rigorous estimate of the rate of net population growth in the fished population. The estimates of net population growth

TABLE III. Total length-converted catch-curve (LCCC) regression results for north-west Atlantic skate species caught during July and March research vessel surveys of eastern Scotian Shelf (2001–2006, excluding 2004). The negative of the slope of the descending right limb of each curve = total instantaneous mortality (Z)

	Season	LCCC linear regression coefficients			
		R^2	P	slope ($-Z$)	S.E.
<i>Leucoraja ocellata</i>	Summer	0.84	<0.001	−0.33	0.05
	Spring	0.91	<0.001	−0.51	0.05
	Mean			−0.42	
<i>Leucoraja erinacea</i>	Summer	0.89	0.01	−0.55	0.10
	Spring	0.48	NS	−0.25	0.12
	Mean			−0.55	
<i>Amblyraja radiata</i>	Summer	0.87	<0.001	−0.24	0.02
	Spring	0.89	<0.001	−0.36	0.03
	Mean			−0.30	
<i>Malacoraja senta</i>	Summer	0.46	0.01	−0.12	0.04
	Spring	0.77	<0.001	−0.24	0.03
	Mean			−0.18	

NS, not significant and not included in calculation of Z .

from Table II, however, suggest that the *L. ocellata* population will continue to decline unless fishing mortality is reduced, that *L. erinacea* is close to zero population growth, and that the *A. radiata* and *M. senta* populations are increasing.

DISCUSSION

In two pivotal papers, Holden (1973, 1974) concluded that ‘elasmobranch stocks offer very limited opportunities for long-term exploitation’ due to their K -selected life-history traits which make them highly susceptible to recruitment over-fishing. Over the years, Holden’s conclusion has been both supported (Musick *et al.*, 1993) and contested (Stevens *et al.*, 1997; Simpfendorfer, 1999) through studies of shark populations under exploitation. Rising evidence that shark species could in fact be harvested sustainably led Walker (1998) to revisit Holden’s (1973, 1974) initial question: are sustainable fisheries for elasmobranchs possible? He emphasized the importance of relative productivity to sustainability, reiterating that long-lived species with low natural mortality and low reproductive rates have low productivity, and can only sustain very low levels of exploitation. In the present study, theoretical rates of population increase for non-equilibrium populations of *L. ocellata* (c. 0.07), *M. senta* (c. 0.14) and *L. erinacea* and *A. radiata* (c. 0.20) were low compared to most fishes (Frisk *et al.* 2001), indicating that north-west Atlantic skates are intrinsically unproductive, yet are theoretically capable of supporting low-level fisheries. Nevertheless, the results of 36 years of research surveys indicate that the abundance of mature *L. ocellata*, *A. radiata* and *M. senta* all decreased by >90% since 1970, indicating that fishing mortality (both directed and undirected) outstripped the net productivity of the skate populations on the eastern Scotian Shelf. Abundance

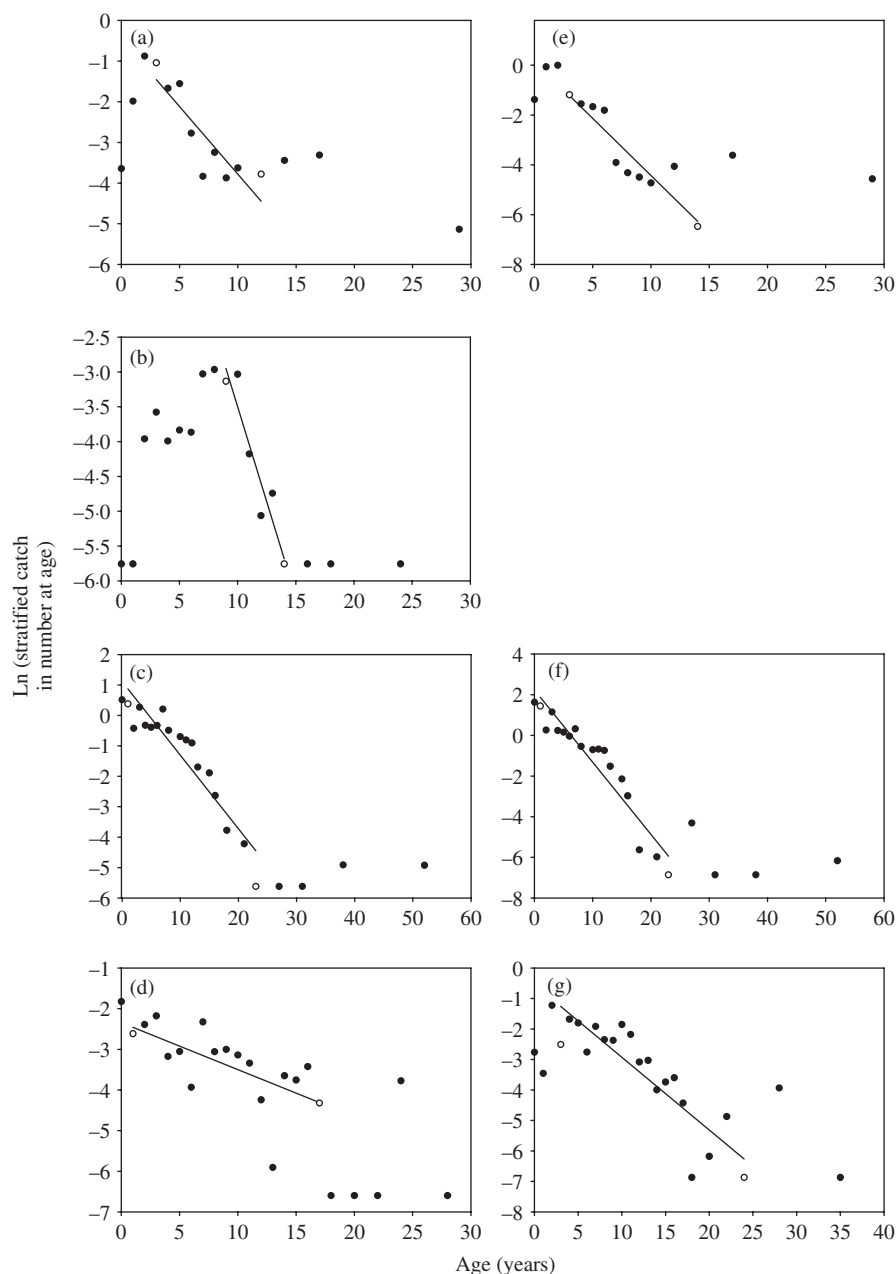


FIG. 7. Catch curves for (a, e) *Leucoraja ocellata* (b) *Leucoraja erinacea*, (c, f) *Amblyraja radiata* and (d, g) *Malacoraja senta* derived from July (a, b, c, d) and March (e, f, g) research vessel survey (2001–2006, excluding 2004) total length (L_T)-frequency distributions and L_T -age relationships and used to estimate total instantaneous mortality (Z). The ordinates are the natural logarithm of the stratified number of skates within each age interval; the abscissas are age class (whole integer) in years. ○, the first and last points used to calculate linear regressions.

trends in immature skates were less marked, but they too have declined significantly since at least 1990.

In the case of *L. erinacea*, the apparent abundance increase since 1970 could be artifactual due to misidentification issues, a hypothesis supported by both (1) the marked increase in mean number of *L. erinacea* per tow in the late 1970s (mature) and late 1980s (immature) coincident with improved identification techniques (McEachran & Musick, 1973) and (2) the great variability in *L. erinacea* adult abundance from year to year. Although identification issues are usually most applicable to immature skates <300 mm L_T (McEachran & Musick, 1973; Alvarado Bremer *et al.*, 2005), there are also many morphometric similarities between *L. ocellata* and *L. erinacea* of larger sizes (McEachran & Martin, 1978), making classification of the smaller *L. erinacea* potentially difficult for inexperienced observers. Alternately, an increase in *L. erinacea* abundance on the ESS could be partly due to competitive release, a theory used previously to explain increases in smaller skate species such as *R. radiata* Donovan in the North Sea (Walker & Heesen, 1996) following the removal of larger skates (Dulvy *et al.*, 2000). Nevertheless, the high variability in *L. erinacea* abundance from year to year suggests that misidentification is the primary cause for the apparent increase in *L. erinacea* abundance on the ESS over the last 36 years.

Although life-history tables are often useful tools in studies of elasmobranch population sensitivity (Cortés 1998), they appear to be most valuable when coupled with empirical estimates of population abundance (from RV surveys) and Z (from catch curves). The estimates of r_{pred} reported here were most likely underestimates of the intrinsic population growth rate, since they were based on static life-history parameters with unknown density dependence (Gedamke *et al.*, in press). The r_{pred} estimates were also strongly influenced by the assumed rate of M and other parameters that made them imprecise. Nevertheless, the low r_{pred} value estimated for *L. ocellata* was consistent with the fact that its observed population decline and mortality rate was greatest of all of the species studied. Unfortunately, the estimate of total instantaneous mortality from the catch curves provides a view of mortality integrated across many years, and thus cannot be compared directly with the sustainable mortality inferred from the demographic analysis. Nevertheless, it is clear that total mortality rates exceeding *c.* 0.4 are not sustainable in these populations. It can also be inferred that the low productivity of these four skate species is due at least in part to their reproductive characteristics.

The results of the current study indicate that maturity status in both males and females is best assessed through examination of a number of reproductive organ measurements rather than through assessment of a single characteristic. In male north-west Atlantic skates (with the exception of *L. ocellata*) there was an abrupt increase in L_C length and calcification relative to L_T at sizes significantly smaller than the calculated sizes at maturity based on all reproductive characteristics, including the presence of sperm. Similarly, in female north-west Atlantic skates, estimated L_{T50} from maturity ogives tended to be greater than those estimated from W_0 and W_{SG} inflection points, suggesting there might be a delay between the maturation of certain organs and the actual presence of vitellogenic eggs that will be spawned in the ensuing spawning season. These observations suggest that any estimates of size at maturity based on a single reproductive organ characteristic would be underestimates of the true timing of co-ordinated 'functional' maturity.

Functional maturity in skates on the ESS tended to occur at relatively large sizes and late ages. In *L. ocellata*, where size and age at maturity did not differ significantly between the sexes, functional maturity only occurred once *c.* 83% of the observed maximum L_T and 65% of the maximum age had been reached, suggesting that growth in both sexes slowed considerably after the onset of maturity. Similar maturity and growth patterns were exhibited by *L. erinacea* and *M. senta* in this study and have been demonstrated in a number of other species of elasmobranch, with maturity occurring at 80–90% of the maximum L_T and at 60–70% of the maximum age (Holden, 1974; Francis *et al.*, 2001; Sulikowski *et al.*, 2007b;). In contrast, functional maturity in *A. radiata* males and females was reached at 68 and 58% of the observed maximum L_T , and 77 and 56% of the maximum observed age.

Among skates, it is common for both sexes to mature at approximately the same size (Walmsley-Hart *et al.*, 1999; Ebert, 2005), or for females to mature at larger sizes and to attain larger maximum sizes than males (Jardas, 1973; Nottage & Perkins, 1983). In this study, however, males matured at larger sizes and later ages than females for all species except *L. ocellata* (Table I). Templeman (1987) also observed greater L_T at maturity and maximum L_T for male *A. radiata* in the north-west Atlantic than for females, and Sosebee (2005) noticed that female *A. radiata* and *M. senta* along the north-east coast of the U.S.A. began maturing at smaller sizes than males. This mosaic pattern among skate species, with some species being sexually dimorphic in size and age at maturity and maximum size and others exhibiting opposite trends or no sexual dimorphism at all, indicates that selection pressure for large female size in oviparous elasmobranchs may be less than for viviparous elasmobranchs (Ebert, 2005). Life history theory holds that the advantages of delayed maturity, such as higher fecundity or larger, more fit offspring, will outweigh the advantages of early maturation only when the productivity gained through increased fecundity or juvenile survivorship is greater than the fitness lost through longer generation time and lower survival to maturity (Roff, 1992; Smith *et al.*, 1998). In oviparous species, delayed maturity does not necessarily impart increased fecundity, given that only two eggs can be deposited at a time. Although significant increases in *A. radiata* egg characteristics with maternal L_T and W were found in this study (Fig. 4) and in a prior study by Templeman (1982), the benefits of greater egg capsule mass and yolk mass and volume to offspring survival remain unclear. Moreover, skates (as with all other elasmobranchs) have internal fertilization; as such, sexual selection in skates may favour large males that are better able to control and impregnate females than smaller males, a strategy commonly observed in mammals and birds.

Size and age-at-maturity estimates for *L. ocellata* and *A. radiata* differed in magnitude from those previously reported from other areas. In *L. ocellata*, size and age-at-maturity estimates were greater on the ESS than along the entire U.S. north-eastern coast (Frisk 2004) or in the western Gulf of Maine (Sulikowski *et al.*, 2005a). In contrast, *A. radiata* on the ESS reached maturity at significantly smaller sizes than those from the western Gulf of Maine, which were found to reach maturity at 865 mm (males) and 875 mm (females) (Sulikowski *et al.*, 2006). This pattern of greater L_{T50} in *A. radiata* at lower latitudes was also observed by Templeman (1987), who theorized that there was a cline of increasing size at sexual maturity from north to south. In *L. erinacea*, females along the north-east coast of the U.S.A. attained

maturity at approximately the same size and age as those from the ESS (Frisk 2004). There are no other published studies reporting maturity estimates for *M. senta*.

In the case of *A. radiata*, the disparity in maturity estimates from different areas is probably due to the great variability in *A. radiata* maturation within each area. Similar to the present study, Templeman (1987) reported a bimodal maturity pattern in both male and female *A. radiata* on the ESS, with some individuals maturing at substantially smaller sizes than others. This has also been noted for *A. radiata* in other, more southerly geographic areas (Sosebee, 2005; J. A. Sulikowski, pers. comm.). These observations suggest that there may be more than one stock in each of these regions, each with different sizes at maturity. Alternately, given the great depth range occupied by *A. radiata* (18 to 966 m, McEachran & Musick, 1975), differences in L_{T50} and A_{50} both within and among regions might be reflecting different habitat use patterns within the species, although a preliminary examination of growth differences in *A. radiata* on the ESS by depth of capture indicated that depth was not a significant factor. Nor was there evidence of differences in size-selective predation or differential fishing pressure among areas which might be affecting the timing of maturation. Further studies are required to determine if the observed within and among population variability in skate sexual maturation is a result of adaptive or phenotypic responses.

In keeping with ecological and evolutionary theory, the results of this study show that the largest species on the ESS (*L. ocellata*) is the least productive and therefore able to sustain only very low exploitation levels while the smallest species on the ESS (*L. erinacea*) is the most productive and therefore able to support more moderate exploitation levels. Similar trends have been reported by several authors who correlated body size and sustainable exploitation levels in elasmobranchs, stating that larger species are generally more susceptible to decline (Jennings *et al.*, 1998; Walker & Hislop, 1998; Dulvy *et al.*, 2000; Stevens *et al.*, 2000; Frisk *et al.*, 2001). In this study, however, body size alone was not necessarily a good predictor of susceptibility. For example, *A. radiata*, which grow to sizes ≥ 900 mm L_T exhibited r_{pred} values close to (and in some cases greater than) *L. erinacea* which grows to a much smaller maximum L_T of c. 540 mm (Bigelow & Schroeder, 2002). *M. senta*, which grows to a maximum L_T of c. 580 mm (Bigelow & Schroeder, 2002), exhibited the second lowest r_{pred} values, above only that of *L. ocellata*. Instead of body size predicting population growth rate, the relationship between maximum age and age of maturity appeared to be a better predictor of vulnerability, with the species exhibiting the highest ratios of $t_{\text{mat}}:t_{\text{max}}$ (*L. ocellata* = 0.68, *M. senta* = 0.66) having the lowest predicted population growth rates. These values represent the proportion of time and growth, which occurs before the onset of maturation, with species allocating proportionately less time to reproduction exhibiting lower rates of population increase. Although Frisk *et al.* (2002) obtained estimates of r_{pred} for *L. erinacea* (0.21) and *L. ocellata* (0.13) similar to those reported here, they found that *L. erinacea*, the species with the highest r_{pred} value and thus the least susceptible to decline, was the species with the highest ratio of age at maturity to maximum age ($t_{\text{mat}}:t_{\text{max}}$ = 0.50). The difference between the two studies is almost certainly due to their use of an empirical life history approach to estimate age at maturity, rather than the direct estimates which were used in this study.

Empirical work on marine fishes has shown that low productivity and a slow recovery rate are correlated (Dulvy & Reynolds, 2002; Hutchings & Reynolds,

2004); as such, the recovery of north-west Atlantic skate populations from depletion, in particular that of *L. ocellata*, will probably be slow relative to teleosts and other relatively small elasmobranchs (Simpfendorfer, 1999) even if fishing effort is reduced. The low productivity of the *L. ocellata* population, the near absence of mature female *L. ocellata* with egg capsules, and the scarcity of young of the year and deposited egg capsules all raise concerns regarding the reproductive status of the *L. ocellata* population and the ability of this population to recover from depletion.

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