

The population dynamics of little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*: predicting exploitation limits using matrix analyses

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Over the past thirty years catches of skates have increased in the western Atlantic as a result of targeted fisheries and as by-catch. Presently, sustainable harvest levels for skates in the western Atlantic are unknown. Available life history information was used to model three western Atlantic skate species, little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*, to determine their population growth rate and susceptibility to population decline under exploitation. Population characteristics were estimated using age-based matrix analyses for little and winter skate and a stage-based matrix approach for barndoor skate. The intrinsic rate of population increase (r) for little, winter and barndoor skates were 0.21, 0.13 and 0.20, respectively. Fishing mortality resulting in equilibrium conditions, where the intrinsic rate of increase is zero, were 0.35 for little skate, 0.17 for winter skate and 0.20 for barndoor skate. Elasticity analyses indicated that juvenile survival contributed most to population growth in little skate and winter skate, and adult survival contributed the most in barndoor skate. Thus, conservation measures should focus on juvenile and adult stages of these species. In the absence of fishing mortality, elasticity of fecundity was low for all species, however; at high exploitation levels the contribution of fecundity to population growth rate increased. Stochastic analyses were performed by varying first year mortality (egg stage to the completion of one year of life), and model parameters for each species to generate estimates of the distributions of biological reference points. Our study supports the finding that long-lived, slower growing, late maturing species are highly vulnerable to exploitation.

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Keywords: elasticity, stochastic, little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, barndoor skate *Dipturus laevis*, population dynamics, exploitation, fishing limits, matrix models, rajidae, elasmobranchs.

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Introduction

In Europe and Asia skates are prized and have been fished for centuries. In these areas, skates have experienced commercial harvest pressure and populations have declined under low to moderate levels of exploitation. Brander (1981) warned of the susceptibility of skates to fishing, using the example of local extirpation of the once abundant common skate *Dipturus batiss* in the Irish Sea. Recently, skate populations in the western

Atlantic have declined due to commercial, recreational and by-catch harvests (NEFSC, 1999). Casey and Myers (1998) described the potential extinction of the barndoor skate *Dipturus laevis* in the western Atlantic. However, while some species, such as the barndoor skate, have decreased, others, such as the little skate *Leucoraja erinacea* and winter skate *Leucoraja ocellata*, have exhibited periods of increase in the western Atlantic (NEFSC, 1999). Thus, resilience to fishing pressure seems to vary among the skate species. Are there

biological differences in these skates that affect their ability to sustain fishing pressure and thus the need for conservation measures?

Skates have not traditionally supported directed fisheries in the United States, but skates were exploited heavily by distant water fleets operating off the New England coast during 1961–1975, prior to the implementation of US extended jurisdiction (Fogarty and Murawski, 1998). Exploitation of skates has continued largely through by-catch in multi-species fisheries. More recently, skates have been targeted and kept for the market as other historically valuable species have declined. Landings have increased from less than 2 000 metric tonnes (Mt) in the early 1980s to over 16 000 Mt in the late 1990s (NEFSC, 1999). In spite of indications that some skate species are declining, measures to conserve skates have not yet been taken. A lack of understanding of the life history and compensatory responses of species of the family Rajidae to exploitation has left management agencies with little information on which to develop conservation policies.

The life history and population dynamics of skates differ from teleost species in several key respects (Frisk *et al.*, 2001). In bony fish, the effects of biotic and abiotic factors on survival and/or growth during the early life stages produce wide fluctuations in recruitment. Chance variation in recruitment provides a mechanism for teleost species to rebound from harvest reduction, often over short time periods (but see Hutchings, 2000). In contrast, skates produce fewer eggs than teleosts but invest more energy per egg, presumably reducing the variability in survival rates during early life history. Skates are oviparous, and the eggs undergo long developmental periods of several months in protective cases. The young hatch as fully formed juveniles. However, their low fecundity and delayed maturity mean that skates are probably susceptible to overfishing. In addition, if skate populations are reduced dramatically by overharvesting they may take a longer time to recover than teleost species.

Management options for elasmobranch species have been derived from life history information in matrix models (Fogarty *et al.*, 1987; Walker and Hislop, 1998; Cortes, 1999; Heppell *et al.*, 1999; Brewster-Geisz and Miller, 2000). Matrix models provide a convenient way of projecting population levels under different patterns of exploitation. Exploring the population response in such models to a range of exploitation provides an approach to determining long-term sustainability and critical fishing levels. Elasticity analyses of matrix models can be used to indicate which parameters and ages contribute most to population growth rate (de Kroon *et al.*, 2000). However, elasticity analysis alone does not necessarily provide the best management alternative (Caswell, 2000; de Kroon *et al.*, 2000). The ability of management scenarios to alter the value of

specific parameters also has to be considered when setting policy (Caswell, 2000; de Kroon *et al.*, 2000). With these caveats, elasticity can be used to gauge where management strategies should concentrate in order to determine efficient harvest policies.

Matrix models provide an indicator of the nature and the response of animal populations to exploitation. However, their utility as a management tool is only as reliable as the model inputs. In many cases, parameters are estimated from a limited number of studies. The resulting uncertainty in the model inputs and resulting outputs may lead to incorrect management advice. One approach to address this uncertainty is to include variability in parameter values and present the model outputs and resulting biological reference points as probability distributions.

In this paper we determine the population growth rate (r), stable age distribution (C_x), reproductive value (V_x), elasticity of input parameters and provide a sensitivity analysis based on the sample distributions of input parameters of three western Atlantic skate species. The optimal management strategy is investigated by varying the age of entry to the fishery and fishing mortality. Sustainable limits to exploitation of little skate, winter skate and barndoor skate are provided. The implications of our models are compared to those found for skates in the eastern Atlantic.

Methods

The models

Both age-based and stage-based models were developed. Age-based approaches were used for little and winter skates. However a lack of vital rate estimates for the barndoor skate mandated the use of a stage-based model for this species. A conceptual representation of a skate's life history, from egg to juvenile to mature adult is provided in Figure 1. It is important to note that both the juvenile and adult stages may last many years. In order for a population to be stable, on average, a single female must live long enough to produce one successfully reproducing female offspring. In age-structured models individuals can experience two fates: individuals either die or survive and enter the next age class. In contrast in stage-based models, individuals can experience three fates. Individuals may die, they may survive and remain in the same stage or they may survive and grow into the next stage. However, despite these fundamental differences, the analytical framework for both models is identical. Our models are female only.

Both age and size-structured models use a matrix to project a vector of the age or stage-specific abundance forward in time. The projection model is:

$$N_t = A^t \cdot N_0 \quad (1)$$

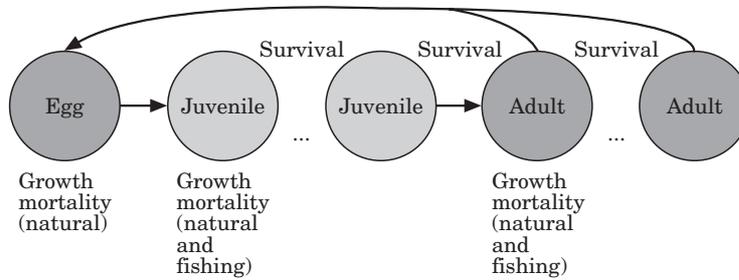


Figure 1. A conceptual representation of a skates' life history from egg to juvenile to mature adult.

For age-based models (A) was given by a Leslie matrix expressed in the following form:

$$A = \begin{bmatrix} f_1 & f_2 & \dots & f_{(l-1)} & f(l) \\ P_1 & 0 & \dots & 0 & 0 \\ 0 & P_2 & \dots & 0 & 0 \\ 0 & 0 & \dots & P_{(l-1)} & 0 \end{bmatrix} \quad (2)$$

where P_i represents age-specific survival ($P_i = \exp[-(M_i + F_i)]$ (where age-specific instantaneous natural mortality is M_i and F_i is fishing mortality) and f represents age-specific annual fertility. We used a birth-pulse formulation (Caswell, 2001) with a post-breeding census for all models where fertility was determined with the following equation:

$$f_i = P_i \cdot m_i \quad (3)$$

where f_i is fertility at age/stage i and m_i is the age/stage specific fecundity.

Based on von Bertalanffy growth models, little and winter skate will reach 20 cm or more at the completion of two years of life (Johnson, 1979; Simon and Frank, 1996). Current mesh size limits on Georges Bank are 15.2 cm for bottom trawls (Fogarty and Murawski, 1998). Accordingly, age three is assumed fully recruited to the fishery. Because our models are based on a post-breeding census, fishing mortality is assessed for age two and older for winter and little skates.

For barndoor skate we recognized three life stages: (1) egg to the end of the first year, (2) juvenile to, but not including, maturation and; (3) adult. For the stage-based projection matrix, G represents the probability of surviving and growing through each stage (Eq. 4). P represents the probability of surviving and remaining in the same stage. The resulting projection matrix for the stage based model takes the form:

$$A = \begin{bmatrix} P_1 & 0 & f_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{bmatrix} \quad (4)$$

G and P values were calculated using estimates of the probability that an individual survives (σ) and the probability that an individual grows to the next stage (γ_i) as:

$$G_i = \sigma_i \cdot \gamma_i \quad (5)$$

$$P_i = \sigma_i(1 - \gamma_i) \quad (6)$$

We used Caswell's (2001) approach to estimating γ in the stage-based model. Caswell's approach assumes that individuals within a stage have equal survival regardless of age:

$$\gamma_i = \frac{\left(\frac{\sigma_i}{\lambda_{init}}\right)^{T_i} - \left(\frac{\sigma_i}{\lambda_{init}}\right)^{T_i-1}}{\left(\frac{\sigma_i}{\lambda_{init}}\right)^{T_i} - 1} \quad (7)$$

The model assumed an initial value of $\lambda_{init}=1$. We iterated the values until the initial λ value equalled the value of the population growth rate from the eigen-analysis of the projection matrix equation. The σ_i for which this equality held was then used in the model. Fishing mortality was not imposed for the first stage but was imposed on the juvenile and adult stages.

For both age- and stage-structured models the population growth rate (λ) was determined from the dominant eigenvalue of the matrix A . The natural log of the rate of population increase (λ) is the intrinsic growth rate of the population (r). When growing at a rate, r , the population converges eventually to one in which the proportion at age or stage is constant. This is termed the stable age distribution. It is also possible to calculate the reproductive value for each age or stage class, which is an indication of that class's contribution of young to future year classes. Following Caswell (2001) and Ebert (1999), an eigen-analysis was performed to calculate the reproductive value and stable age distribution using the left (v) and right (w) eigenvectors of the projection matrix respectively.

Table 1. Data for egg mortality.

Species	No. of eggs	% closed hatching slits	% hatching success	Location	Source
<i>Leucoraja erinacea</i>	34	41	—	Wonderland Beach, M.E.	Cox & Koob (1993)
<i>Leucoraja erinacea</i>	19	37	—	Bidleford Pool beach, M.E.	Cox & Koob (1993)
<i>Leucoraja erinacea</i>	18	17	—	Cape Henlopen, Delaware	Cox & Koob (1993)
<i>Raja eglanteria</i>	20	15	—	Cape Henlopen, Delaware	Cox & Koob (1993)
<i>Amblyraja radiata</i>	138	48	—	Danish coast	Cox <i>et al.</i> (1999)
<i>Cephaloscyllium ventriosum</i>	*	—	20–27.5	—	Grover (1972)
Rajidae	*	—	57	South Africa	Smith & Griffiths (1997)
Haplobelparus	*	—	60	South Africa	Smith & Griffiths (1997)
Poroderma	*	—	47	South Africa	Smith & Griffiths (1997)

Note: *Indicates that samples were collected from two sites on the South African coastline, with 574 collected along False Bay and 583 from Port Alfredand. With species breakdowns as follows: at both sites 70% of sample were Haplobelpharus species, Rajidae made up 5 and 19% per site respectively, and the genus Poroderma making up 1 and 7% respectively.

Elasticity measures the proportional change in population growth rate to changes in individual elements of the projection matrix. Elasticity values for individual parameters can be combined to judge the contribution of ages or stages to the growth rate of the population. The following formula was used to calculate elasticity (Caswell, 2001):

$$e_{i,j} = \left(\frac{a_{i,j}}{\lambda} \right) \left(\frac{\partial \lambda}{\partial a_{i,j}} \right) \quad (8)$$

Parameter estimation

Egg and juvenile mortality

One of the most challenging problems in demographic analysis of skates is assessing survival during the egg and early juvenile stages. Little is known about mortality associated with predation on skate egg capsules. Based on the number of bore-holes found on specimens, egg capsules show varying levels of predation. However, the presence of bore-holes does not mean the intrusion was fatal. The only definitive gauge of predation is the presence of closed hatching slits. Cox *et al.* (1999) data indicated that closed hatching slits occurred in 48% of thorny skate *Amblyraja radiata* egg capsules collected off the Danish coast. Cox and Koob (1993) reported that closed hatching slits in little skate and clearnose skate *R. eglanteria* eggs ranged from 15–37% based on museum collections from the northeast Atlantic and southwestern Pacific. Cox and Koob (1993) estimated predation on little skate and clearnose skate *R. eglanteria* eggs from 15–37% based on museum collections from the northeast Atlantic and southwestern Pacific. Smith and Griffiths (1997) found a hatching success rate for several oviparous species to range from 47–60%. Grover (1972) found a hatching success rate of 20–27.5% of the swell shark *Cephaloscyllium ventriosum*.

Merely knowing the predation rate does not lead to an estimate of survival, since mortality rates incurred from other causes are unknown for skate eggs. Predation from other fish, marine mammals or cannibalism may play important roles in the survival of egg cases. We assessed different survivals for the first year of life (M_1), defined as the egg stage and early juvenile period up to the end of the first year of life. It should be noted that egg stage duration varies among the different skate species. In order to incorporate all possibilities, survival was varied between 10–80%. Point estimates were based on a first year survival of 30%, which was deemed the most realistic value when considering egg predation and adult natural mortality rates of these species (Table 1). A first year survival of 30% was also used for calculation of reproductive values and stable age distribution.

Age of maturation, fecundity and adult survival

Adult natural mortality was obtained from the literature or from longevity estimates using Hoenig's method (Hoenig, 1983). Life history parameters for little skate were adopted from Johnson's (1979) data for Block Island Sound, Rhode Island, USA, and Waring's (1984) data for Georges Bank and Delaware Bay: longevity $T_{max}=8$, age of 50% maturity $T_m=4$, annual fecundity per year $f=30$ (fecundity values were halved for the models assuming a 1:1 sex ratio, $f/2$) and natural mortality $M=0.45$. We assumed that fecundity remains constant once maturity is reached.

Life history parameters of longevity and natural mortality for winter skate were adopted from Simon and Frank (1996) based on samples collected in Canadian waters: $T_{max}=20.8$ years (we used a value of 20 years, $M=0.21$). Age at maturity for winter skate was estimated using an empirical life history approach developed in Frisk *et al.* (2001) to predict age of maturity based on elasmobranch species life span or maximum

size. Estimates of age of maturity for winter skate were 8.9 and 9.6 using a life span of 20 years and total length as reported by McEachran (2002) of 150 cm. It should be noted that the US National Marine Fisheries Service's (NMFS) annual surveys have never collected a winter skate greater than 113 cm (which would produce a $T_m=8.2$). An age at maturity of $T_m=9$ was used for the model. Winter skate fecundity was estimated between 21–35 based on 106 ovaries collected from the mid-Atlantic region (M. G. Frisk, unpublished data). A value of 35 was used in our model for all ages as there was no evidence that fecundity increases with age (M. G. Frisk, unpublished data).

Barndoor skate estimates were obtained by utilizing characteristics of the common skate (*D. batis*) for fecundity and longevity and previously published estimates of vital rates, a strategy used by Casey and Myers (1998). Longevity was estimated at T_{max} of approximately 50 years [determined from common skate longevity of 51 years estimated from von Bertalanffy growth parameters (Abdel-Aziz, 1992)]. Maximum size was estimated at $L_{max} \sim 150$ cm, although reports of individual barndoors as large as 180 cm have been claimed (Bigelow and Schroeder, 1953). Empirical relationships from Frisk *et al.* (2001) produced a $T_m=15.6$ and $T_m=9$ using T_{max} and L_{max} , respectively. For our models we used an intermediate level of $T_m=12$. Natural mortality calculated with Hoenig's method was $M=0.09$, and fecundity was $f=47$ eggs annually (Casey and Myers, 1998).

Base simulation

We ran base simulations using Equation (1), assuming first year survival of 30% and other parameters as noted above. Sustainable limits to exploitation, population growth rate, and elasticity were all calculated. In addition, base runs were performed with values of first year survival of 10% and 80%. These extreme first year survivals were used only for calculation of population growth rates and varying exploitation levels.

Stochastic analysis

In a separate analysis to further test the sensitivity of our little skate model to parameter estimation, fecundity and both first year survival (M_1) and adult survival (M) were varied. Values of M , M_1 and fecundity were drawn from normal distributions. For first year survival we used a sampling distribution with a mean of 1.21 and standard deviation of 0.4 to reflect variation in natural populations and estimation error. For little skate we used an average adult survival $M=0.45$ with a s.d. of 0.05 (Waring, 1984). Little skate fecundity is estimated to range from 28–33 eggs per year (Johnson, 1979). The values used for annual fecundity in little skate was

15 (assuming 50:50 sex ratio) with a s.d. of 2.5. For winter skate we varied first year survival and fecundity as for little skate. Adult mortality was not varied for lack of adequate information to determine a range of values. Annual fecundity for winter skate was 17.5 (assuming 50:50 sex ratio) and a $SD=5$ was used in projections (M. G. Frisk, unpublished data). Because of inadequate data, barndoor skate was not included in the stochastic analysis. Our approach will produce "prospective" results with the assumption that s.d. in parameter estimation reflects likely variation occurring in natural populations in the future and parameter estimation (Caswell, 2000).

Results

Base simulations

Estimated intrinsic rates of population increase declined as F increased in all species (Figure 2). The fishing mortality that results in population equilibrium ($r=0$) was 0.35 for little skate, 0.17 for the winter skate and 0.20 for barndoor skate (Figure 2). Model results were very sensitive to estimates of the mortality of skate juveniles.

Intrinsic rates of population increase increased non-linearly with increasing fecundity for all species (Figure 3). Calculated values of r are very sensitive to the estimated fecundity when fecundities are low (high slopes). However, the calculated value of r is insensitive to changes in fecundity (low slopes) when fecundities are high.

The stable age distributions for little skate, winter skate and barndoor skate are provided in Table 2. The schedule of stable ages (C_x) for little and winter skate were similar; an initial steep drop in abundance was followed by a gradual drop over the juvenile and adult periods. The stage-based model for barndoor skate showed a small decline in stable age distribution as the species moved from egg, to juvenile and a large decline in the adult stage (Table 2). Reproductive values also were similar for little and winter skate, with a gradual increase and peak at age of maturation, followed by a gradual decline as the fish aged (Table 2). The longer-lived winter skate maintained a peak in reproductive values for several years, as compared to the immediate drop off for the short-lived little skate. Barndoor skate reproductive values gradually increased during the juvenile stage and rapidly increased after maturation in the adult stage (Table 2).

Elasticity for little and winter skate to survival were higher than elasticities for reproduction (Table 2). For little and winter skate survival, elasticity was constant for pre-reproductive stages. After this plateau, elasticities of survival declined for both species. Elasticity was

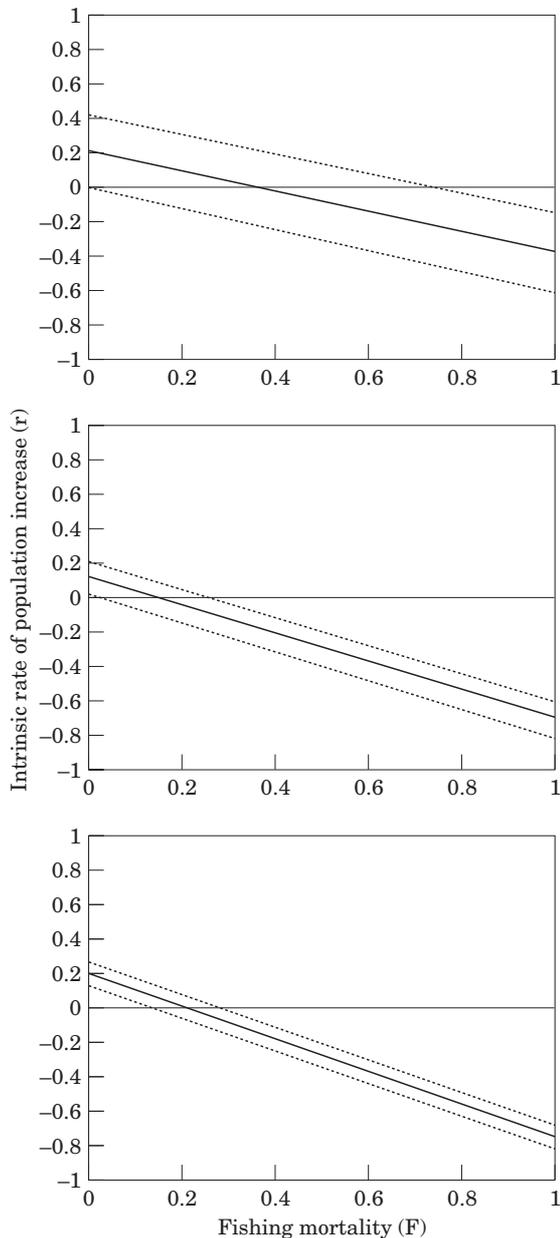


Figure 2. The resulting intrinsic rate of increase (r) for varying levels of fishing mortality (F) for little skate (top), winter skate (middle) and barndoor skate (bottom). The maximum and minimum line represent two extremes of first year survival of 10% and 80% corresponding to $M_1=0.22$ and $M_1=2.3$. The middle line is the 30% ($M_1=1.2$) survival chosen for our analysis.

highest for little and winter skate during the period of survival before maturation. For the barndoor skate adult survival was highest followed by juvenile and the transition element. Fecundity in barndoor skate had a low elasticity.

Stochastic simulations

Little skate and winter skate population growth rates responded differently to variation in survival and fecundity estimates (Figure 4). Distributions of r values had a s.d. of 0.1 or less for both species, with more extreme values ranging ± 0.25 of the central value of a $M_1=1.21$, equivalent to a survival of 30% and $M=0.45$ for little skate. The distributions represent possible variation based on estimates of parameters used in our analyses, which reflect both natural variation in populations and uncertainty in parameter estimates.

Analysis of delaying entry to the fishery

Values of the intrinsic rate of population increase (r) for winter skate and little skate varied with the age of entry to the fishery and fishing mortality rate (Figure 5). Effects of exploitation during the first year of life were not assessed for any of the species. Both winter and little skates show an increasing level of sustainable exploitation as age of entry to the fishery is increased. The barndoor skates model only had two stages with which to vary the stage of entry to the fishery (Figure 5). Delaying fishing on barndoor skate until maturation produced sustainable harvest levels for the range of fishing mortality used in our analysis.

Discussion

Holden (1973) warned that there was an upper limit to exploitation for elasmobranchs and at high enough exploitation levels their populations would decline. Recently, with the decline of many skate species, especially large species, Dulvy *et al.* (2000) have suggested that skates are one of the marine taxa most vulnerable to overexploitation. Our results indicate that the large, later maturing, and long-lived winter and barndoor skate are indeed vulnerable to overfishing.

Winter and little are the skate species most frequently taken commercially and make up a large portion of the total skate catch in the western North Atlantic (NOAA Technical Memorandum NMFS-NE-108, 1994). Barndoor skate occurs at much lower abundances, and although it is exploited commercially, makes up very little of the overall skate catch. Sustainable fishing levels (F), defined here as levels resulting in a positive population growth rate (r), for all three species are very low to moderate. Little skate can support a total mortality of $Z \leq 0.81$ (equivalent to fishing mortality of $F \leq 0.35$). Winter skate will retain a positive population growth rate with a total mortality of $Z \leq 0.38$ ($F \leq 0.17$). Barndoor skate will retain positive population growth with a total mortality of $Z \leq 0.29$ ($F \leq 0.2$). Walker and Hislop (1998) used a matrix approach to estimate the equilibrium mortality of five skate species in the North Sea.

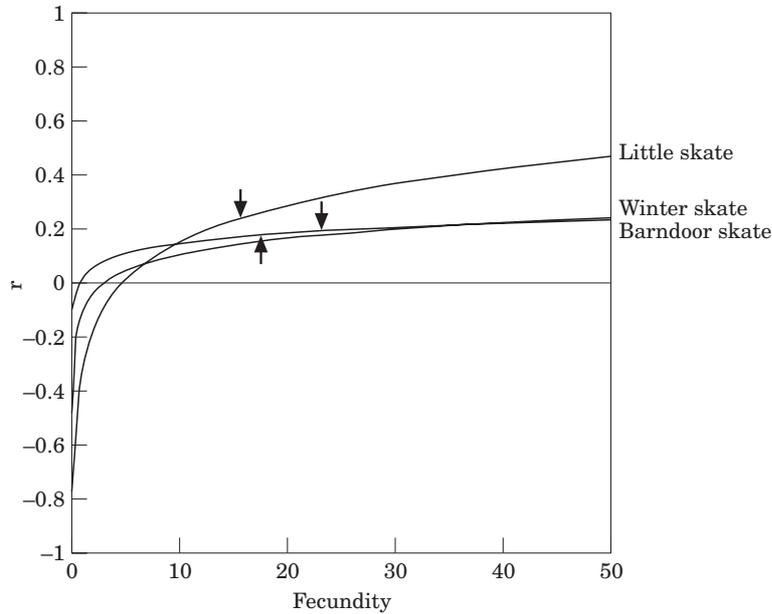


Figure 3. The resulting intrinsic rate of increase (r) with increasing fecundity for little, winter and barndoor skate. The arrows indicate the estimated annual fecundity for each species.

Table 2. The stable age distribution (C_x), reproductive value (V_x), elasticity (e) of survival (p) and fecundity (f) for each stage or age class for little skate, winter skate and barndoor skate. In addition the elasticity of the transition probability (t) is shown for barndoor skate for each stage.

Age or stage	Little skate				Winter skate				Barndoor skate				
	C_x	V_x	$e(p)$	$e(f)$	C_x	V_x	$e(p)$	$e(f)$	C_x	V_x	$e(p)$	$e(f)$	$e(t)$
0	00.67	01.00	00.20	00.00	00.52	01.00	00.09	00.00	00.50	01.00	00.00	00.00	00.11
1	00.16	04.10	00.20	00.00	00.14	03.78	00.09	00.00	00.47	04.08	00.32	00.00	00.11
2	00.08	07.90	00.20	00.00	00.10	05.33	00.09	00.00	00.03	71.01	00.34	00.11	00.00
3	00.04	15.41	00.10	00.10	00.07	07.51	00.09	00.00	*	*	*	*	*
4	00.02	14.86	00.05	00.05	00.05	10.58	00.09	00.00	*	*	*	*	*
5	00.01	13.79	00.02	00.03	00.04	14.91	00.09	00.00	*	*	*	*	*
6	00.00	11.73	00.00	00.01	00.02	21.02	00.09	00.00	*	*	*	*	*
7	00.00	07.74	00.00	00.01	00.02	29.62	00.09	00.00	*	*	*	*	*
8	*	*	*	*	00.01	41.76	00.06	00.03	*	*	*	*	*
9	*	*	*	*	00.01	41.35	00.04	00.02	*	*	*	*	*
10	*	*	*	*	00.01	40.79	00.03	00.01	*	*	*	*	*
11	*	*	*	*	00.00	39.99	00.02	00.01	*	*	*	*	*
12	*	*	*	*	00.00	38.87	00.01	00.01	*	*	*	*	*
13	*	*	*	*	00.00	37.29	00.01	00.00	*	*	*	*	*
14	*	*	*	*	00.00	35.05	00.01	00.00	*	*	*	*	*
15	*	*	*	*	00.00	31.91	00.00	00.00	*	*	*	*	*
16	*	*	*	*	00.00	27.47	00.00	00.00	*	*	*	*	*
17	*	*	*	*	00.00	21.22	00.00	00.00	*	*	*	*	*
18	*	*	*	*	00.00	12.42	00.00	00.00	*	*	*	*	*
19	*	*	*	*	00.00	00.00	00.00	00.00	*	*	*	*	*

Their values were 0.38 for common skate *D. batis*, 0.52 for thornback ray *R. clavata*, 0.54 for spotted ray *R. montagui*, 0.58 for cuckoo ray *L. naevis* and 0.73 for starry ray *A. radiata*. A comparison of the total allowable mortality (Z) or the equilibrium mortality of little,

winter and barndoor skate was made to the five species Walker and Hilsop (1998) studied from the eastern Atlantic (Figure 6). There is a significant negative, nonlinear association between species total allowable mortality, and species maximum size (L_{max}).

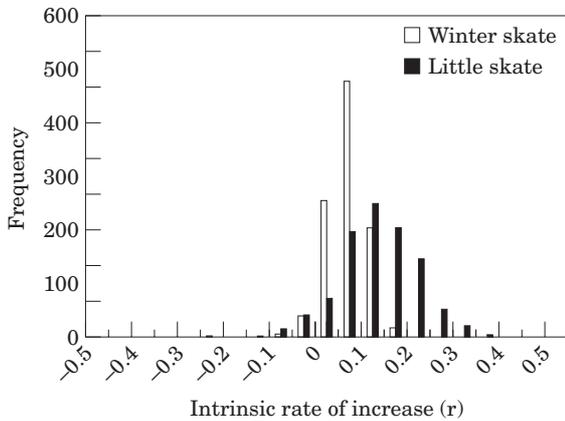


Figure 4. The range of values for (r) calculated through a lognormal distribution of first year mortality and adult mortality and through a normal distribution of fecundity for little skate and the previous two for winter skate. The model was run for 1000 random trials.

Similar to most long-lived species, survival is the dominant trait in the life strategy of the three skate species especially in juveniles stages (Heppell *et al.*, 1999). Stable age distributions and reproductive values for all three skate species indicate the importance of survival to maturation. Elasticity analyses of little and winter skate also indicate that survival during the period before maturation contributes the most to variation in population growth rate. After maturation, the contribution of stage specific survival to overall population growth rate decreases. Adult survival in the long-lived barndoor skate is the dominant trait in its life strategy.

Elasticity of fecundity was low for all three species. This seems to be counter-intuitive for a group of species that have low fecundity. However, our analyses indicate that at very low fecundity an increase in annual egg production would have a substantial impact on population growth rate. Once fecundity is increased to a reasonable estimate, the rise in population growth is minimal, possibly reflecting a biological trade off between egg production and individual growth. The fecundity estimates for all three species suggest that population growth rates should be relatively insensitive to changes in fecundity.

This result may not differ from that expected for other groups of fish. However, skate species, characterized with large eggs with high-energy investment, together with body cavity size and energetic constraints may experience limited variation in annual egg production. In light of our elasticity values, unless fecundity appears to be unusually low for a particular species of interest, it may be more fruitful to focus current research on egg and adult survival before refining estimates of fecundity. It should be noted that when the models are run at high fishing levels, elasticity of fecundity increases in relative

proportion to that of survival, indicating the increased importance of fecundity for population stability under heavy exploitation.

Intrinsic rates of increase can be used to gauge and compare the population productivity of fish species (Stevens, 1999). Levels of productivity and potential population growth rates appear correlated. Stevens (1999) studying school *Galeorhinus galeus* and gummy *Mustelus antarcticus* sharks found that, of the two species harvested together in an Australian fishery, the school shark with a lower productivity (=lower r) declined, while the more productive gummy shark appeared more resilient to exploitation. Our findings suggest a similar trend with the larger less productive species, winter and barndoor skate, sustaining lower exploitation levels, while the smaller, more productive little skate supporting moderate exploitation levels.

Recently, several authors have suggested that the size of elasmobranch species has a profound influence on the level of sustainable exploitation. These papers correlate species maximum size to the reduction of species populations, (Walker and Hislop, 1998; Dulvy *et al.*, 2000; Stevens *et al.*, 2000), and species size and life histories to potential population decline (Frisk *et al.*, 2001). Using the potential rate of population increase (r'), Jennings *et al.* (1999) linked life history strategy to the resilience of populations to fishing pressure in the North Sea. They provided evidence that later-maturing, slower-growing, larger species are more susceptible to declines when exploited. These trends were particularly apparent when comparing nearest phylogenetic relatives. Frisk *et al.* (2001) calculated potential rates of increase (r') for elasmobranchs as a group and found an association of increased body size with lower r' . In these cases, comparative analyses of life histories have yielded valuable insights for fishery management.

This study supports the hypothesis that late maturing species are more vulnerable to exploitation. However, it may be the relation between maximum body size and age/length of maturity that is important rather than size per se. Larger elasmobranchs are associated with delayed/larger maturity (Frisk *et al.*, 2001). The ratio of age of maturity to maximum age is 0.5, 0.45, and 0.24 for little, winter and barndoor skate, respectively (Frisk *et al.*, 2001). The relation between age of maturity and life span is logarithmic in elasmobranchs (Frisk *et al.*, 2001), suggesting that longer lived skate species partition more of their life span as mature adults. This leads to the hypothesis that multiple reproductive years, or adult survival, is of greater importance for barndoor skate compared to little skate. Heppell *et al.* (1999) suggests that for many long-lived species, population growth is more sensitive to late/large juvenile and adult stages than early stage survival and fecundity. Given the nature of the skate fishery in New England, the delayed

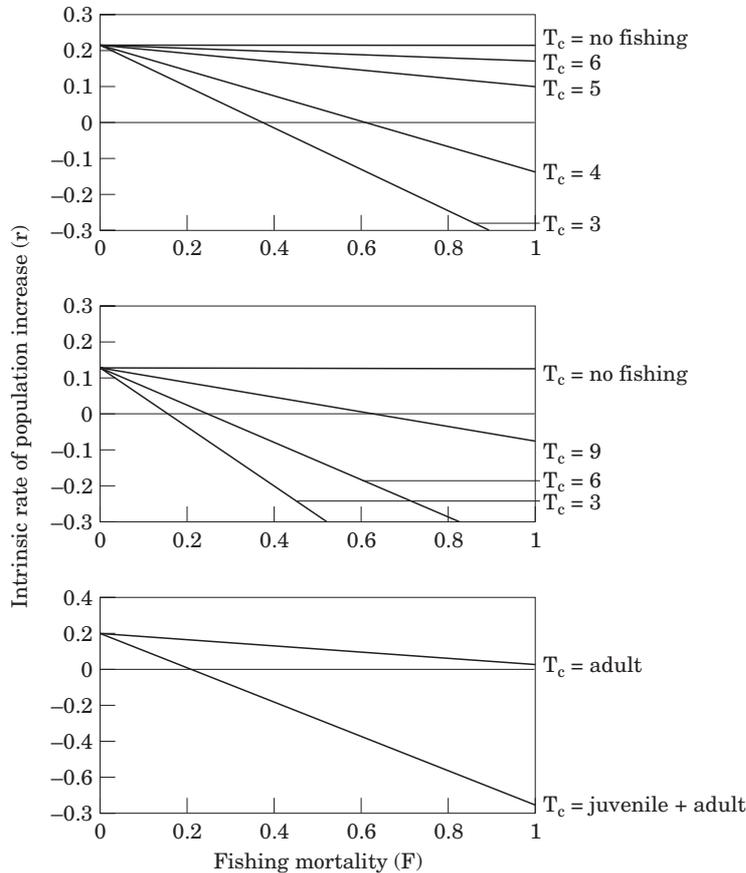


Figure 5. An analysis of age of entry to the fishery, fishing mortality, and the intrinsic rate of population increase (r) for little skate (top), winter skate (middle) and barndoor skate (bottom). T_c = age of entry to the fishery. For barndoor skate, fishing mortality was assessed on the adult stage alone and the juvenile and adult stage combined.

maturity of barndoor skate and winter skate should raise a warning flag.

Elasticity can be used to gauge important aspects of the biology of animals, both in an evolutionary sense and as a way to guide effective management (de Kroon *et al.*, 2000). Elasticity analysis of winter and little skate indicates that reducing first year and juvenile mortality (M_1) would yield the greatest result in terms of increasing growth rate. However, since regulating fishing mortality on the egg stage is impossible, and population growth rate is also heavily influenced by juvenile survival, a more effective approach would be to reduce juvenile mortality. Size limits and mesh size regulations are convenient methods for attempting to increase juvenile survival. However, skates are vulnerable to fishing shortly after hatching and are relatively large at maturation. These characteristics interacting with the action of non-selective multi-species fisheries and species with large differences in sustainable harvest levels make managing skate species difficult or impossible without overall reductions in exploitation. Two apparent solutions to

deal with the problem of reducing exploitation in a multi-species fishery are the use of closed areas and efforts to reduce by-catch.

Evidence is growing that marine reserves are effective management tools for protecting targeted and non-targeted flora and fauna in marine ecosystems (National Research Council, 2001). Using closed areas to protect a portion of the biomass of skate species may increase the resilience of the little, winter and barndoor skate populations. However, several skate species appear to make seasonal migrations on and off shore in the western Atlantic (NEFSC, 1999). If future research can link movements to spawning, closed areas could target spawning grounds. However, presently this detailed information of skate biology is lacking. Another difficulty is determining how large an area would be needed to reduce exploitation enough to adequately protect their populations. Further understanding of little, winter and barndoor skates seasonal migratory behaviour is needed to understand what proportion, and what duration of the year their populations are protected under

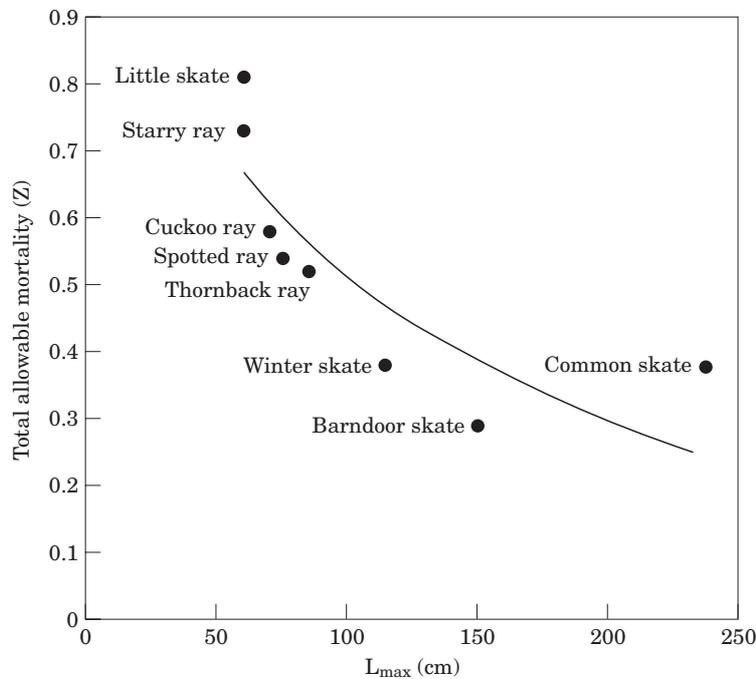


Figure 6. The relationship between total allowable mortality and species maximum size (L_{\max}). The least-squares regression model is: $Z = -0.14 \cdot (L_{\max}) + 3.35$, $n=8$, $r^2=0.82$, $p=0.013$.

existing closures. The Secretary of Commerce took emergency action in 1994 to reduce fishing pressure on groundfish by imposing closed areas on Georges Bank, the Gulf of Maine and Southern New England (Fogarty and Murawski, 1998). All three closed areas are located within the historic ranges of little, winter and barndoor skates. Studies of the dynamics and distributions of skates within these marine reserves can serve as a test of the suitability of closed areas to protect skates.

In July of 2001, the American Elasmobranch Society accepted a resolution that asked the New England Fishery Management Council and the NMFS to develop and implement fishery management plans for skates in the western Atlantic and that the plans include prohibitions on the possession of barndoor and thorny skate. Prohibition of the possession of skate species may be an effective method for reducing overall exploitation. However, little is known of the discard survival of Rajidae. The hardy nature of the family Rajidae may make decreasing by-catch mortality a reasonable management option. Kaiser and Spencer (1995), in a study on the survival of discard from a beam trawl in the North Sea, found that 100% of cuckoo ray *L. naevus* and 97% of lesser-spotted dogfish *Scyliorhinus canicula* another elasmobranch, initially were still alive when released on the ship's deck. After a sorting process and period of 120 hours in a holding tank, 59% of the cuckoo ray and 79% of the lesser-spotted dogfish were alive. Although these data are limited, elasmobranchs appear to experience

low to moderate discard mortality rates. However, without estimates of trawl survival for little, winter and barndoor skates, the effectiveness of this management action will be unknown.

Evidence indicating that some skate species are highly susceptible to overfishing is growing (Frisk *et al.* 2001; Dulvy *et al.*, 2000; Casey and Myers, 1998; Walker and Hislop, 1998; Brander, 1981). This raises the question: can large skate species be sustainably exploited in multi-species bottom fisheries? Management policies are needed for skate species in the western Atlantic. Our analysis varying input parameter estimates used for the skate species modelled herein, emphasized the need to set conservative fishing targets that incorporate the probability of achieving management targets. Until further data is collected, area closures and reducing by-catch, in the absence of overall reductions in exploitation, remain among the most viable policies for effective management.

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