# Stock–Recruitment Dynamics and the Maximum Population Growth Rate of the Barndoor Skate on Georges Bank

TODD GEDAMKE,*[1] JOHN M. HOENIG, WILLIAM D. DUPAUL, AND JOHN A. MUSICK

*Virginia Institute of Marine Science, Post Office Box 1346, Gloucester Point, Virginia 23062, USA*

*Abstract.*—In 1998, the barndoor skate *Dipturus laevis* was reported to have been locally extirpated in parts of its northern range and to be potentially on the brink of extinction. Managers were faced with assessing the species with virtually no information other than a limited number of individuals observed in annual groundfish surveys. Since that time, a number of the primary life history parameters have been estimated, but the population dynamics of the species remain largely unexplored. In this study, we use information from the National Marine Fisheries Service (NMFS) annual groundfish surveys to investigate two critical components of barndoor skate population dynamics: the relationship of recruitment to spawner abundance and the maximum population growth rate. A strong stock–recruitment relationship was found in the fall survey data, suggesting that recruitment is closely tied to spawner abundance. The Ricker and Beverton–Holt stock–recruit models were fitted to the survey data, and estimates of the slope at the origin was generated. These parameters provided an estimate of the maximum annual reproductive rate, which was then converted to an estimate of the instantaneous maximum population growth rate of 0.37–0.38 per year. A second analysis was also conducted using a Leslie matrix and data from the NMFS survey. Observed rates of population change were used to estimate early life history parameters and incorporate density dependence into the density-independent framework of a Leslie matrix demographic model. From this method, the instantaneous maximum population growth for the barndoor skate was estimated to be 0.36–0.48 per year. Our results suggest that the species is more resilient to fishing pressure than previously believed and is capable of growing at an instantaneous rate in excess of 35% at low population sizes.

The barndoor skate *Dipturus laevis* is an elasmobranch that was believed to be particularly vulnerable to fishing mortality and reported to be close to extinction in parts of its northern range (Casey and Myers 1998). A lack of both basic life history information and an understanding of the overall population dynamics of the species has hampered the further assessment and management of North Atlantic populations. Although recent studies have provided estimates of basic life history parameters (Gedamke et al. 2005), a lack of historical catch records precluded the use of classic production models, and fundamental aspects of the population dynamics remain unexplored. Since the observed decline and the potential for extinction of the species were attributed to overfishing, an estimate of the maximum population growth rate is one option to gain a better understanding of the populations' susceptibility to fishing pressure and management options.

Recently, both stock–recruit and demographic models have been used to determine the intrinsic, or maximum, rate of population increase ($r_{intrinsic}$) and, therefore, the maximum sustainable fishing pressure (Myers et al. 1997, 1999; McAllister et al. 2001; Gedamke et al. 2007). An important aspect of this process that is commonly overlooked in elasmobranch demographic models is the recognition that a population will only grow at a maximal rate at the lowest stock sizes (McAllister et al. 2001; Gedamke et al. 2007). Only in this condition will competition for resources be at a minimum and the subsequent increased survival result in $r_{intrinsic}$. Mathematically, this is expressed as

$$r_{intrinsic} = \lim_{N \to 0} \frac{1}{N} \frac{dN}{dt}, \qquad (1)$$

where $N$ represents population abundance (Shertzer et al. 2008).

Stock–recruitment models address this issue because they incorporate stock size explicitly in the analysis and can be used to estimate the maximum growth rate ($r_{intrinsic}$) at low population sizes. In these models, the underlying relationship—between spawners (stock) and recruits—is a critical component to our understanding of the population dynamics of a species and is directly tied to population size. The slope at the origin (i.e., at the lowest stock sizes) can be converted to an estimate of the maximum annual reproductive rate. The maximum annual reproductive rate represents the

* Corresponding author: todd.gedamke@noaa.gov
[1] Present address: National Marine Fisheries Service, Miami Laboratory, 75 Virginia Beach Drive, Miami, Florida 33149, USA

number of spawners produced by each spawner per year and can be used to obtain an estimate of the maximum population growth rate (Myers et al. 1997).

Classic demographic analyses (e.g., life table or Leslie matrix), on the other hand, are independent of stock size and provide an estimate of the exponential rate of population growth (or decline) based on a fixed set of life history parameters. Alternatively, the model can be thought of as providing the short-term rate of population change under current conditions. Only when schedules of survival and reproduction from a depleted population are used in the construction of the model will the estimated rate of population growth approach $r_{intrinsic}$. Parameter estimates from depleted populations are rarely available, and therefore estimating $r_{intrinsic}$ remains difficult. In a recent study, Gedamke et al. (2007) addressed this dilemma and provided suggestions on how to incorporate stock size and density-dependent compensation into the density-independent framework of a Leslie matrix demographic model.

In this study, we used information from the National Marine Fisheries Service (NMFS) annual groundfish surveys on Georges Bank and the Gulf of Maine to develop stock–recruit and Leslie matrix models with the goal of gaining insights into the population dynamics of the barndoor skate. We followed the methodology of Myers et al. (1997, 1999) for the analysis of the stock–recruit relationship and the methodology of Gedamke et al. (2007) for the demographic analysis.

## Methods

*Available trawl survey data.*—Research surveys have been conducted by NMFS in U.S. and Canadian waters of the northwest Atlantic for over four decades; fall and spring surveys began in 1963 and 1968, respectively (Reid et al. 1999). Data from the winter survey, which overlaps the southern regions of the fall and spring surveys, is also used in monitoring the populations of the northwest Atlantic skate (family Rajidae) complex, including the barndoor skate. This survey began in 1992 and provides a shorter time series than the fall and spring surveys. In addition, the gear for the winter survey targets small flatfish: rollers (used in the spring and fall surveys) are replaced with a chain sweep covered by rubber disks and the addition of 54.9-m ground cables.

A stratified random sampling design is used to provide an unbiased estimate of fish availability to the sampling gears. Stations are stratified based on depth, latitude, and historical fishing pattern. The surveys were designed to sample groundfish and use a Yankee bottom trawl. Surveys were generally conducted in 27–

366 m of water, and a deeper tow was occasionally used in the canyons of the continental shelf. Although slightly different configurations have been used over the years, the gear has generally been rigged with 41-cm rollers and a 1.25-cm (stretched mesh) cod end; tows have been conducted at 6.5 km/h (3.7 knots) for 30 min at each station. Comparison trawl hauls have been made to standardize results across the various changes in the gear over the years. The data provided by NMFS for use in this study were already standardized. The spring and fall surveys are the primary indices used by the New England Fisheries Management Council and NMFS for the assessment of the northwest Atlantic skate complex and cover the distribution of the barndoor skate in United States waters. From 1963 to 2007, between 167 and 374 survey tows were conducted annually in this region (Figure 1). At each station, the number and weight of each species were recorded in addition to the total length of each individual (Figure 2).

*Life history parameters.*—Life history information from Gedamke et al. (2005) was used as a primary source to determine the parameters required for our analysis. The von Bertalanffy growth parameters reported in that study were a maximum length ($L_\infty$) of 166.3 cm, a growth coefficient ($k$) of 0.1414 per year, and an intercept ($t_0$) of −1.29 years. The maximum age observed in this study was 11 years; however, a recent exploratory investigation of the largest barndoor skate on record found a single, age-15 individual (T.G., unpublished observations). Since the age distribution is probably truncated due to extensive exploitation in the past, a maximum possible age of 25 was assumed.

Estimates of natural mortality ($M$) were calculated using six different methods: (1) Pauly (1980), (2) Hoenig (1983), (3) Peterson and Wroblewski (1984), (4) Chen and Watanabe (1989), (5) Jensen's (1996) age at maturity method, and (6) Jensen's (1996) $k$ method. Estimates for adults ranged from 0.16 per year from the Chen and Watanabe (1989) estimator to highs of 0.21 and 0.25 per year from the two methods by Jensen (1996). Very similar estimates for adult mortality resulted from four of the methods, and we use an estimate of 0.18 per year for $M$ (Table 1). Note that an estimate of water temperature is required for the Pauly (1980) estimator, and we used 8.5°C as reported by Myers et al. (1997).

Life history data from Gedamke et al. (2005) were used to calculate the number of recruits and the number of spawners caught per tow in each year and by each survey. A cumulative length frequency plot of all individuals captured in the surveys indicates that barndoor skate are fully vulnerable to the gear at
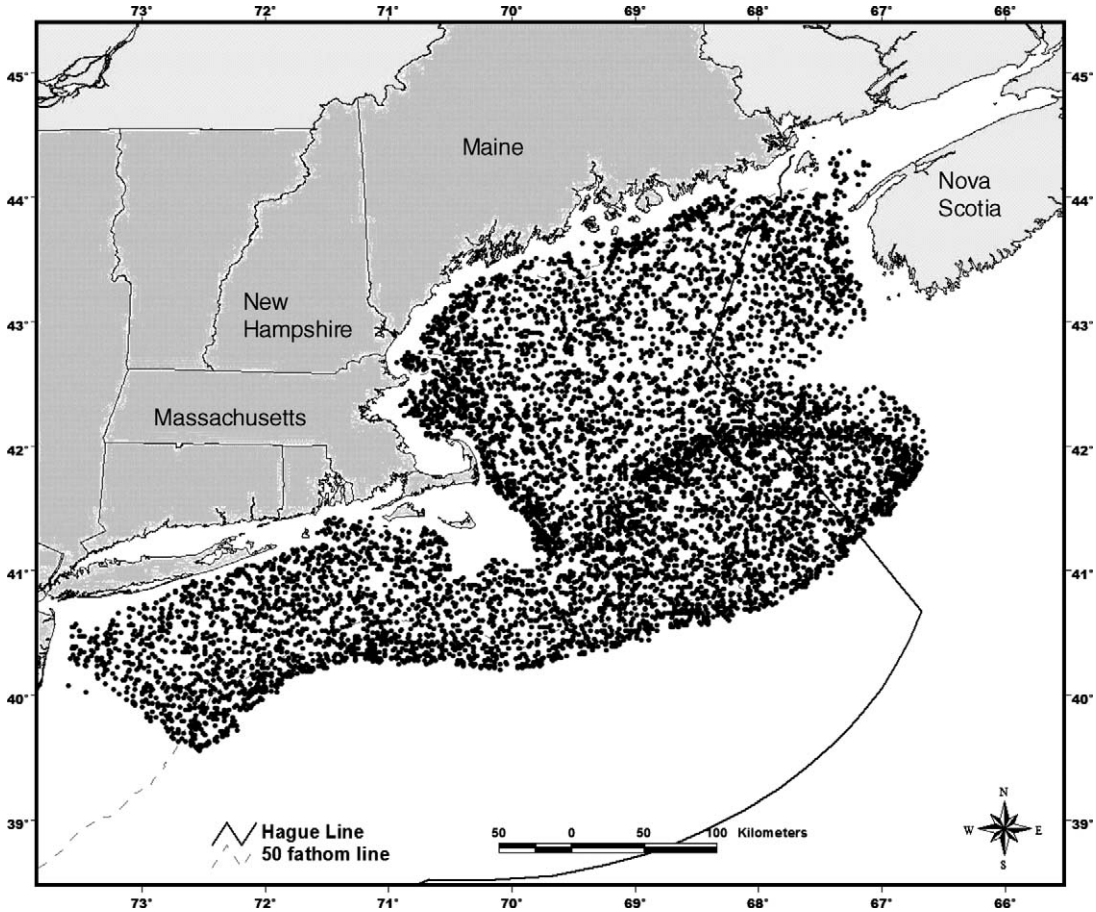
FIGURE 1.—Map of all stations sampled ($n = 8,817$) by the National Marine Fisheries Service annual fall groundfish survey from 1963 to 2007. Note that only the Gulf of Maine and southern New England offshore strata (1–30, 33–40) are included in this figure and in our analyses of the spring and fall surveys. The winter survey extends further south and includes strata 1–3, 5–7, 9–11, 61–63, 69–71, and 73–75.

approximately 55 cm in all three seasonal surveys (Figure 3). A length-to-age conversion was applied, and the age at full recruitment to the gear was estimated at 2 years, corresponding to a size of 54–69 cm. Thus, animals captured in this size range were counted as recruits. A female size-at-maturity value of 116 cm was used as a minimum size cutoff to estimate the spawner abundance index (Gedamke et al. 2005).

*Model development: stock–recruit analysis.*—The relationship between the number of recruits and the number of adults (i.e., stock–recruit relationship) is commonly described by either the Ricker (1954) model,

$$R = \alpha \cdot S \exp^{-\beta S}, \qquad (2)$$

or the Beverton and Holt (1957) model,

$$R = (\alpha \cdot S)/[1 + (S/K)], \qquad (3)$$

where $R$ is recruitment and $S$ is spawner abundance. The parameter $\alpha$ has units of recruitment per spawner and is an estimate of the slope of the function at the origin (when $S = 0$). The parameters $K$ and $\beta$ are density-dependent terms that incorporate compensation at low population sizes in the form of increased survival. The product of $\beta$ and $S$ can be interpreted as the density-dependent mortality, while the $K$ parameter of the Beverton–Holt model can be thought of as a threshold that, when exceeded, begins to reduce the rate of recruit survival to an asymptotic value. The Ricker model, on the other hand, allows for overcompensation in which recruit survival declines at very high spawner abundances. Overcompensation can result at these high spawner abundances from cannibalism or as the demand for resources (e.g., food, space, or both) in the environment exceeds the supply.
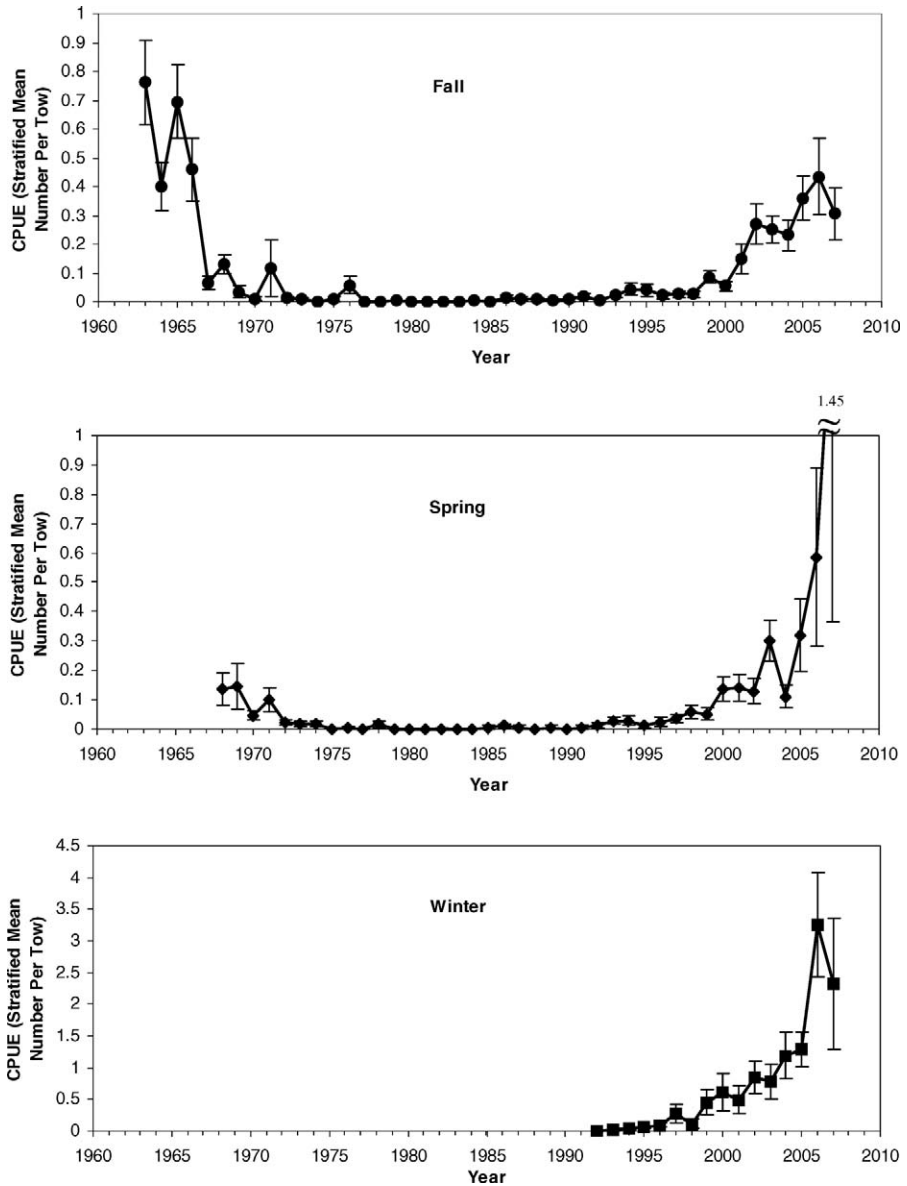
FIGURE 2.—Stratified mean (±SE calculated by collapsed strata method of Cochran 1977) barndoor skate catch per unit effort (CPUE; fish/tow) during each of the National Marine Fisheries Service seasonal groundfish surveys. Strata that contained only 1 tow/year for more than 1 year of the survey were paired with similar adjacent strata (4 and 8; 12 and 15; 17 and 18) to provide a conservative estimate of the survey variability.

The relationship between spawners and recruits must take into account the lag period between the year in which spawner abundance is recorded and the year in which the resulting recruits appear in the survey. In the case of the barndoor skate, egg cases have been observed hatching in captivity after 11 months, so we assumed an incubation period of 1 year (Parent et al. 2008). This, coupled with the 2 years it takes for recruits to become fully vulnerable to the gear, results in a 3-year lag period (e.g., spawners in 1995 give rise to recruits in 1998). Data were paired with this 3-year lag period, and both the Ricker and Beverton–Holt models were fitted to the data using a maximum likelihood analysis assuming a lognormal error structure. The probability density function of a lognormal random variable $x$ is

TABLE 1.—Estimates of barndoor skate natural mortality calculated by six different methods: Pauly (1980), Hoenig (1983), Peterson and Wroblewski (1984), Chen and Watanabe (1989), Jensen's (1996) age at maturity method, and Jensen's (1986) $k$ method ($L_\infty$, $k$, and $t_0$ are von Bertalanffy growth parameters defined in Methods).

| Age | Hoenig (maximum age) | Pauly ($L_\infty$, $k$, temperature) | Jensen (age at maturity) | Jensen ($k$) | Chen and Watanabe (age, $k$, $t_0$) | Peterson and Wroblewski (age, weight) |
|---|---|---|---|---|---|---|
| 0 | 0.167 | 0.177 | 0.254 | 0.212 | 0.848 | 0.654 |
| 1 | 0.167 | 0.177 | 0.254 | 0.212 | 0.511 | 0.429 |
| 2 | 0.167 | 0.177 | 0.254 | 0.212 | 0.380 | 0.335 |
| 3 | 0.167 | 0.177 | 0.254 | 0.212 | 0.311 | 0.283 |
| 4 | 0.167 | 0.177 | 0.254 | 0.212 | 0.268 | 0.251 |
| 5 | 0.167 | 0.177 | 0.254 | 0.212 | 0.240 | 0.228 |
| 6 | 0.167 | 0.177 | 0.254 | 0.212 | 0.220 | 0.212 |
| 7 | 0.167 | 0.177 | 0.254 | 0.212 | 0.178 | 0.200 |
| 8 | 0.167 | 0.177 | 0.254 | 0.212 | 0.178 | 0.190 |
| 9 | 0.167 | 0.177 | 0.254 | 0.212 | 0.178 | 0.183 |
| 10 | 0.167 | 0.177 | 0.254 | 0.212 | 0.178 | 0.177 |
| 11 | 0.167 | 0.177 | 0.254 | 0.212 | 0.178 | 0.172 |
| 12 | 0.167 | 0.177 | 0.254 | 0.212 | 0.178 | 0.168 |
| 13 | 0.167 | 0.177 | 0.254 | 0.212 | 0.178 | 0.165 |
| 14 | 0.167 | 0.177 | 0.254 | 0.212 | 0.178 | 0.162 |
| 15 | 0.167 | 0.177 | 0.254 | 0.212 | 0.178 | 0.160 |

$$f(x; \mu, \sigma^2) = \frac{1}{x\sigma\sqrt{2\pi}} \cdot \exp\left\{ -\frac{[\log_e x - \mu + (\sigma^2/2)]^2}{2\sigma^2} \right\}. \tag{4}$$

The product likelihood function ($\Lambda$) for $n$ years of observed recruits results by substitution (mean $\mu = E[\log_e R]$; variance $\sigma^2 = \text{var}[\log_e R]$). Thus,

$$\Lambda = \prod_{y=1}^{n} \frac{1}{\log_e R_y \sigma\sqrt{2\pi}}$$

$$\times \exp\left\{ -\frac{[\log_e R_y - \log_e R_{\text{pred},y} + (\sigma^2/2)]^2}{2\sigma^2} \right\}, \tag{5}$$

where $R_y$ is the observed catch rate of recruits in year $y$, $R_{\text{pred},y}$ is the catch rate of recruits predicted from equation (2) or (3), and $n$ is the number of spawner–recruit pairs in the data set. The log likelihood is proportional to

$$\log_e \Lambda \propto -n \log_e \sigma$$
$$- \frac{\sum_{y=1}^{n} \left( \log_e R_y - \log_e R_{\text{pred},y} + \frac{\sigma^2}{2} \right)^2}{2\sigma^2}. \tag{6}$$

Equation (6) was maximized and parameters were estimated using the NLP procedure in the Statistical Analysis System version 9 (SAS Institute 2004).

The estimated slope at origin can then be standardized to determine the maximum reproductive rate. The
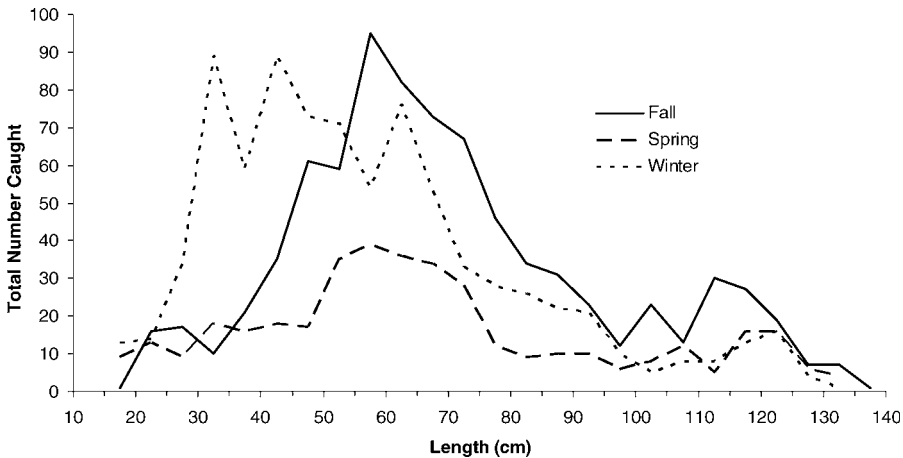


FIGURE 3.—Length frequency distribution (5-cm length bins) of all barndoor skates captured during each National Marine Fisheries Service seasonal groundfish survey.

maximum annual reproductive rate is a critical parameter in population dynamics and can be used to estimate $r_{intrinsic}$ and to estimate the limits of overfishing (Mace 1994; Myers et al. 1997; Myers and Mertz 1998). Our calculations closely follow those of Myers et al. (1997, 1999). The first step in standardizing the slope at the origin is to scale the slope by the spawners produced per recruit (SPR) under conditions of zero fishing mortality ($F$; $SPR_{F=0}$), which gives $\hat{\alpha}$:

$$\hat{\alpha} = \alpha \cdot SPR_{F=0}. \quad (7)$$

The value of $SPR_{F=0}$ is commonly calculated as

$$SPR_{F=0} = \sum_{a=1}^{A_{max}} w_a p_a \exp[-M(a-1)], \quad (8)$$

where $w_a$ is weight at age, $p_a$ is proportion mature at age, and $A_{max}$ is the oldest age (e.g., Goodyear 1993); the formulation in equation (8) presupposes that the stock–recruit relationship was estimated with spawners expressed as spawning biomass (i.e., weight was used as a surrogate for fecundity). That is not the case in our analysis, where we fit the stock–recruit relationship to the catch per unit effort (CPUE) in number of spawners and the CPUE in number of recruits. Therefore, we calculate $SPR_{F=0}$ as

$$SPR_{F=0} = [\exp(-M \cdot A_{lag})]/[1 - \exp(-M)], \quad (9)$$

which gives spawning abundance per recruit (equation 6.4.4 in Quinn and Deriso 1999). The $SPR_{F=0}$ is the number of spawners that would result from each recruit in the absence of fishing pressure given the lag time ($A_{lag}$) for a recruit to reach the age at maturity ($A_{mat}$). For our application to the barndoor skate, $A_{mat}$ is 6.5 years and the resulting $A_{lag}$ is 4.5 years because our recruit index is for age-2 animals. We note that our formulation explicitly assumes that all barndoor skate are fully mature at age 6.5 and older and that all mature individuals have the same relative fecundity.

The result of equation (7), $\hat{\alpha}$, represents the number of recruits per recruit or spawners per spawner (or alternatively, the maximum lifetime production of spawners per spawner) at very low spawner abundances. We then calculate the number of spawners produced by each spawner per year. If adult survival under only natural mortality is $p_s$, then the maximum annual reproductive rate ($\tilde{\alpha}$) results from

$$\tilde{\alpha} = \hat{\alpha}(1 - p_s). \quad (10)$$

The maximum annual reproductive rate can then be used to approximate $r_{intrinsic}$ as

$$\exp^{r_{intinsic} \cdot A_{lag}} - \exp^{r_{intinsic}(A_{lag}-1)-M} - \tilde{\alpha} = 0. \quad (11)$$

This equation can be solved iteratively for $r_{intrinsic}$ given an estimate of $M$, $\tilde{\alpha}$, and $A_{lag}$. See Myers et al. (1997, 1999) for further details and explanation.

*Demographic model: Leslie matrix analysis.*—An alternative approach to estimating the maximum population growth rate is the use of demographic models. Demographic analysis simply tracks the change over time in number of animals at different ages or stages given a schedule of age- (or stage-) specific reproductive output and mortality (Caswell 2001). The female population vector **N** at time $t+1$ is given by

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t, \quad (12)$$

where **A** is a female-only population projection matrix (i.e., Leslie matrix) containing a schedule of reproduction and mortality (i.e., fecundity, survival, $F$, and $A_{mat}$). The predicted rate of population increase ($r_{predicted}$) is defined here to be the instantaneous rate of growth of the population given the parameters used in the projection matrix and a stable age distribution. It is directly related to the largest eigenvalue ($\lambda$) of the matrix **A** (i.e., $r_{predicted} = \log_e \lambda$; Vaughan and Saila 1976; Caswell 2001).

The $r_{predicted}$, or instantaneous growth rate, calculated from these models is a constant and, as such, it only represents a snapshot of population growth based on a fixed set of life history parameters and a given schedule of fishing pressure. To estimate the maximum population growth rate, the model must be constructed using parameters from a depleted population and without the effects of fishing (Gedamke et al. 2007). Only in the case of a depleted population will competition for resources (e.g., food and space) be at a minimum and the effects of density-dependent compensation result in a maximal survival rate and, therefore, maximal population growth rate. The difficulty in this approach arises from the lack of the required estimates for life history parameters of species in depleted conditions.

In a recent study, Gedamke et al. (2007) reviewed the basic logic behind the construction of a demographic model and provided suggestions on how to incorporate the logic of density-dependent compensation into the density-independent framework of a Leslie matrix demographic model. Our explanation of the methodology closely follows that of Gedamke et al. (2007) and uses the four definitions of instantaneous population growth rates described in that paper.

$r_{intrinsic}$ = the maximum per capita population growth rate (can only occur in the absence of fishing, at the lowest population size, when density-dependent

compensation is at a maximum); a stable age distribution is assumed.

$r_{conditional}$ = the per capita rate of population growth in the absence of fishing mortality given a schedule of survival and reproduction (conditional on population size and resulting density-dependent compensation) and given a stable age distribution. In a logistic model, $r_{conditional}$ is equal to $r_{intrinsic}(1 - N/K)$, where $N$ is the population size and $K$ is the equilibrium population size at an $F$ of 0 (i.e., $K$ represents the carrying capacity).

$r_{predicted}$ = the predicted rate of population growth (per capita) when all other parameters are known (assuming a stable age distribution and a given population size); $r_{predicted}$ equals $r_{conditional}$ minus effects of any fishing mortality.

$r_{achieved}$ = the observed per capita rate of population growth; no assumption of a stable age distribution is made.

We now explain how $r_{intrinsic}$ can be estimated from a Leslie matrix. Our analysis consists of four primary steps: (1) estimating $r_{achieved}$ from survey data; (2) constructing a Leslie matrix and solving for the product of fecundity ($g$), egg survival ($S_{egg}$), and first-year survival ($S_0$) that results in an $r_{achieved}$ that is equal to $r_{predicted}$; (3) removing $F$ from the model to estimate potential rate of population growth at specified population size ($r_{conditional}$); and (4) extrapolating $r_{conditional}$ to zero population size to estimate $r_{intrinsic}$.

We start our analysis by obtaining an estimate of $r_{achieved}$ from the NMFS fall survey data. We only use the fall survey data in our demographic analysis because it provides the longest time series of data and is the only survey that was conducted during the population decline observed between 1963 and 1968. A log transformation of the survey indices (numbers caught per tow) provides an observed rate of population growth. Estimates were made from different segments of the time series where population growth (or decline) appeared to be constant and for time periods where estimates of total mortality were available from Gedamke et al. (2008).

We then constructed a Leslie matrix and solved for the product of $g$, $S_{egg}$, and $S_0$ so that the model predicted a rate of population growth that matched what we estimated from the survey data ($r_{achieved}$ = $r_{predicted}$). There are a couple of important points to note about this step of the analysis. First, the $r_{predicted}$ will only be exactly equal to the $r_{achieved}$ if a stable age distribution is present in the population and if all other parameters are known.

Second, as is the case for many oviparous elasmobranchs, accurate estimates of $g$, $S_{egg}$, and $S_0$ are

unavailable for the barndoor skate. Thus, we use estimates of total mortality from Gedamke et al. (2008) and solve the model for the product of these three parameters, which results in a growth rate equal to the observed rate of population growth (Vaughan and Saila 1976; Vaughan 1977; Gedamke et al. 2007). This approach takes into account the uncertainty in estimates of $g$, $S_{egg}$, and $S_0$, which is likely to be strongly tied to the population size and a key mechanism in the process of density-dependent compensation. Estimating the product of these three parameters incorporates density dependence into the analysis without the need to estimate each parameter individually (i.e., the cube root of $gS_{egg}S_0$ replaces each parameter in a standard Leslie matrix). That is, doubling one parameter (e.g., $S_0$) and halving another (e.g., $g$ or $S_{egg}$) results in the same rate of population growth. This has an important implication in determining the reasonableness of parameter values. An $S_0$ estimate of 200%, for example, does not imply a poor fit of the model to the data. Rather, it implies that the apportionment of recruitment ($gS_{egg}S_0$) to individual parameters is in error, and this is inconsequential for projecting short-term changes in the population. On the other hand, if one constrains the values of $S_{egg}$ and $S_0$ to be less than or equal to 1.0, one can determine the minimum value of $g$ that would be required for the population to grow at the observed rate.

This approach provides an estimate of recruitment ($gS_{egg}S_0$) that is specific to the conditions being modeled and dependent on the estimated $F$ and the observed rate of population growth. By removing fishing pressure from the model, we obtain an estimate of how fast the barndoor skate population could grow, given the same life history parameters, under the condition of no fishing pressure (i.e., $r_{conditional}$). No selectivity curve is available for our application to the barndoor skate; however, based on an analysis of the length frequencies of survey catches, we know that animals are fully recruited to the gear at age 2. We assume that some fishing pressure is occurring on younger animals, and we apply 50% of $F$ to age-1 animals. A sensitivity analysis with varying age of recruitment was also conducted to see how robust our results were to this assumption.

The next step is to use the estimates of $r_{conditional}$ to estimate $r_{intrinsic}$. To get an estimate of $r_{intrinsic}$, we must first recognize that the instantaneous potential population growth rate, $r_{conditional}$, depends on the size of the population. This is a property of all population models with density dependence. According to the logistic model, population growth rate is related to the intrinsic rate of increase in the absence of fishing by the linear relationship
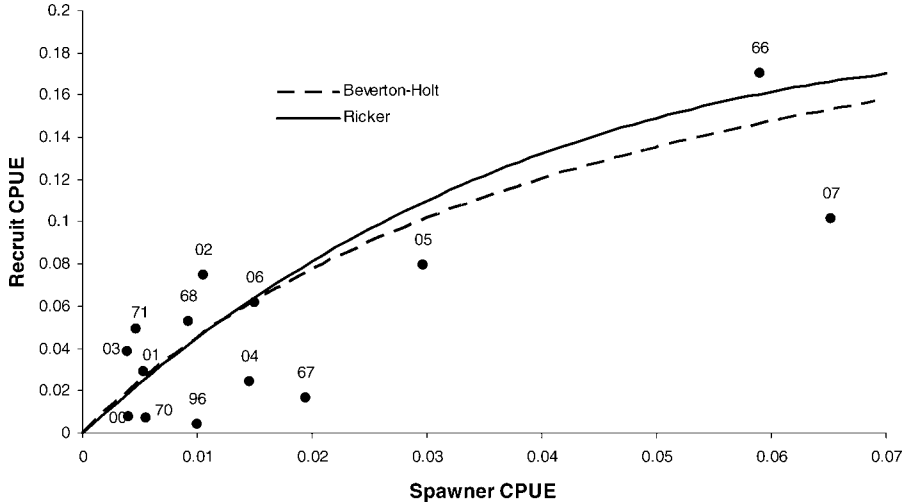
FIGURE 4.—Barndoor skate stock–recruit relationship (recruit catch per unit effort [CPUE] versus spawner CPUE) from the National Marine Fisheries Service fall groundfish survey from 1963 to 2007 ($n = 14$ year pairs in which at least one spawner and one recruit was caught). The year in which recruits were measured (2-digit number presented with each data point) and the resulting Ricker and Beverton–Holt stock–recruit relationships are indicated.

$$r_{conditional} = r_{intrinsic}(1 - N/K), \qquad (13)$$

with $N$ as the size of the population being modeled and $K$ as the virgin population size (i.e., carrying capacity). Note that this model implies that the instantaneous rate of growth ($r_{conditional}$) will be equal to zero when $N$ equals $K$ and that $r_{conditional}$ will approach $r_{intrinsic}$ as the population size approaches zero. When fishing occurs on all ages at an instantaneous rate $F$ (per year),

$$r_{predicted} = r_{conditional} - F = r_{intrinsic}(1 - N/K) - F. \qquad (14)$$

Rearranging the equation and presenting it in terms of survey indices, we can solve for the intercept ($r_{intrinsic}$) as

$$r_{intrinsic} = \frac{r_{conditional}}{1 - (I/I_K)} = \frac{I_K r_{conditional}}{I_K - I}, \qquad (15)$$

where $I$ represents the survey index at the time we measured $r_{achieved}$ and $I_K$ represents the index value of a virgin population. We use the highest value of the survey index over all years to represent $I_K$. This occurred at the start of the time series.

## Results

### Stock–Recruit Analysis

A strong stock–recruit relationship was present in the fall and spring survey data but was not obviously apparent in the winter data (Figures 4–7). Estimates of the slope at the origin were the most precise from the fall survey data; the fall survey estimates were 4.99 recruits/spawner (lower 95% confidence bound = 2.69) from the Ricker model and 5.46 recruits/spawner (lower 95% confidence bound = 2.71) from the Beverton–Holt model (Table 2). Results from the spring survey had larger SEs but were comparable with fall estimates; spring estimates were 6.62 and 10.11 recruits/spawner from the Ricker and Beverton–Holt models, respectively. Although the slope at the origin was not as well defined in the spring survey, the lower confidence bounds (1.87 and 1.91 for the Ricker and Beverton–Holt models, respectively) were comparable with fall confidence bounds. The Beverton–Holt model could not be fit to the winter survey data, and the Ricker model provided a highly uncertain estimate of 34.16 recruits/spawner. We limit the presentation and discussion of the results to the spring and fall survey data.

The resulting estimates of the maximum annual reproductive rate ($\tilde{\alpha}$) were 2.22–2.43 from the fall data and 2.95–4.50 from the spring data. Estimates of $r_{intrinsic}$, transformed from fall $\tilde{\alpha}$ through equation (11), were 0.37 per year from the Ricker model and 0.38 per year from the Beverton–Holt model. Estimates of $r_{intrinsic}$ from the spring survey were 0.42 and 0.49 per year from the Ricker and Beverton–Holt models, respectively.

If we carry the lower 95% confidence bound for the slope at the origin parameter through our calculations of $r_{intrinsic}$, estimates of 0.21 and 0.27 per year result from the spring and fall surveys, respectively (Table 2). This indicates that although the stock–recruit relationship is not precisely defined, the lower bounds are
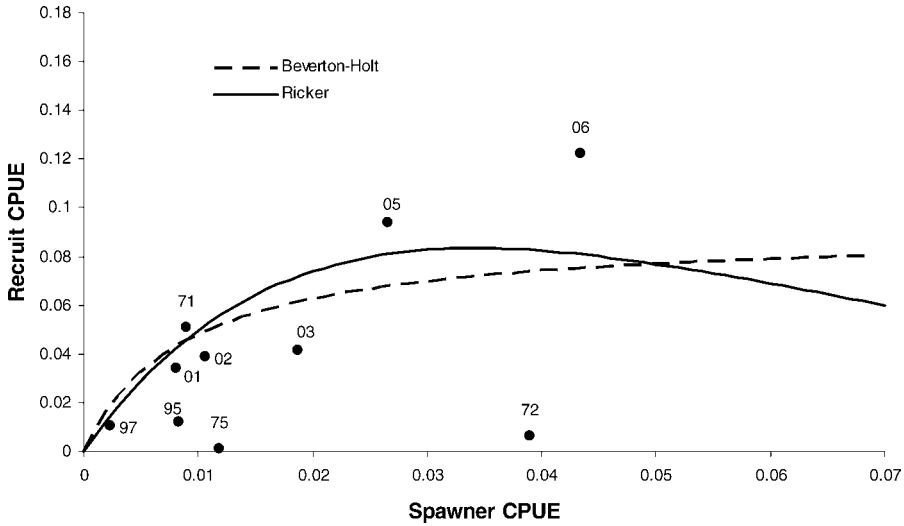
FIGURE 5.—Barndoor skate stock–recruit relationship (recruit catch per unit effort [CPUE] versus spawner CPUE) from the National Marine Fisheries Service spring groundfish survey from 1968 to 2007 ($n = 10$ year pairs in which at least one spawner and one recruit was caught). The year in which recruits were measured (2-digit number presented with each data point) and the resulting Ricker and Beverton–Holt stock–recruit relationships are indicated.

reasonably constrained. A further sensitivity analysis was also conducted to evaluate the models' response to our estimates of $M$ and $A_{lag}$. Within a range of reasonable values for these parameters, model results were sensitive only when both parameters were either underestimated or overestimated. When varying in opposite directions, model results were relatively insensitive. In the worst-case scenario with an $M$ of 0.24 per year and an $A_{lag}$ of 5.5 years, the lower bound of the fall Beverton–Holt model was reduced to 0.15 per year from the original estimate of 0.27 per year. Since we have no reason to assume that parameters would be in error in the same direction or that estimates would be out of the range explored, there is no evidence that our model is overly sensitive to these parameter inputs.
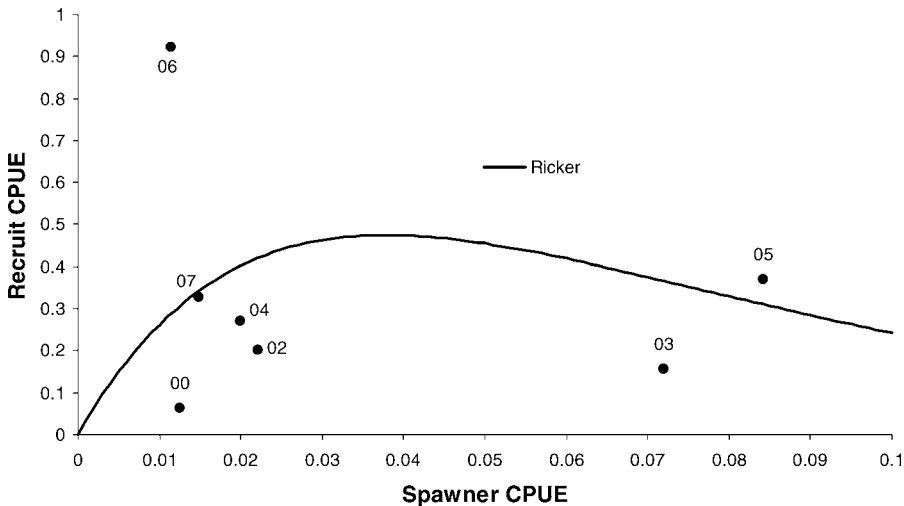


FIGURE 6.—Barndoor skate stock–recruit relationship (recruit catch per unit effort [CPUE] versus spawner CPUE) from the National Marine Fisheries Service winter groundfish survey from 1992 to 2007 ($n = 7$ year pairs in which at least one spawner and one recruit was caught). The year in which recruits were measured (2-digit number presented with each data point) and the resulting Ricker stock–recruit relationship are indicated. The Beverton–Holt model could not be fit to the winter survey data.
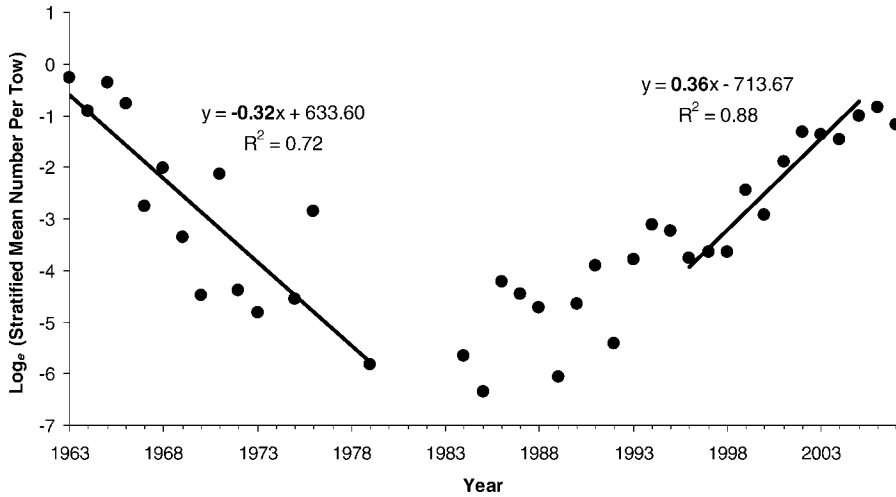
$y = -0.32x + 633.60$
$R^2 = 0.72$

$y = 0.36x - 713.67$
$R^2 = 0.88$

FIGURE 7.—Barndoor skate survey indices ($\log_e$[stratified mean number of fish/tow]) from the National Marine Fisheries Service fall groundfish survey on Georges Bank and the Gulf of Maine. Data were $\log_e$ transformed to estimate the rate of population change. Resulting estimates for the observed rate of population change during periods of decline (1963–1979) and recovery (1996–2005) are indicated by the slope parameter (in bold) in the linear equations.

## Demographic Model: Leslie Matrix Analysis

From the fall survey, the barndoor skate population was observed ($r_{achieved}$) to be declining at an instantaneous rate of $-0.32$ per year between 1963 and 1979 and recovering at an instantaneous rate of 0.36 per year between 1996 and 2005 (Figure 7). Total instantaneous mortality in the same time periods was estimated from mean lengths and catch rates by Gedamke et al. (2008) to be 0.89–1.04 per year during the decline (1963–1979) and 0.04–0.23 per year during the recovery (1996–2005). Using an $M$-value of 0.18 per year, $F$ was thus estimated to be 0.71 and 0.86 per year for the decline and 0.05 per year for the recovery (a total mortality rate of 0.04 is not consistent with an $M$ of 0.18 per year). An $F$ of 0.1 per year was also

included as a sensitivity test in our analysis of the recovery. A Leslie matrix was constructed with these parameters and solved for the $gS_{egg}S_0$ value that resulted in the $r_{achieved}$ observed in the surveys. Assuming that $S_0$ and $S_{egg}$ are less than or equal to 1.0 for all four scenarios, a minimum $g$-value of between 3.6 and 29.7 female eggs/year would be required for the population to grow at the observed rate. This is consistent with estimates of $g$ for similar oviparous species and is well below the observed annual egg production (>80 eggs/year) of captive barndoor skate at the Montreal aquarium (Musick and Ellis 2005; Parent et al. 2008).

With fishing pressure removed from our base model (50% selectivity at age 1 and 100% by age 2) and keeping all other parameters constant, $r_{conditional}$ was

TABLE 2.—Results of the stock–recruit analysis for the barndoor skate. The survey and model are indicated ($n$ = number of nonzero stock–recruit year pairings used in the analysis). The Beverton–Holt model could not be fit to the winter survey data. Parameters are the slope at the origin ($\alpha$; with associated SEs and 95% confidence intervals [CIs]; the three upper confidence bounds [CBs] in bold could not be determined by profile likelihood, and Wald CBs are presented); carrying capacity ($K$) from the Beverton–Holt model; density-dependent parameter ($\beta$) from the Ricker model; lifetime production of spawners per spawner ($\hat{\alpha}$); and maximum annual reproductive rate ($\tilde{\alpha}$; i.e., number of spawners produced by each spawner per year). The maximum population growth rate is $r_{intrinsic}$; values in parentheses are $r_{intrinsic}$ calculated from the lower CB of $\alpha$.

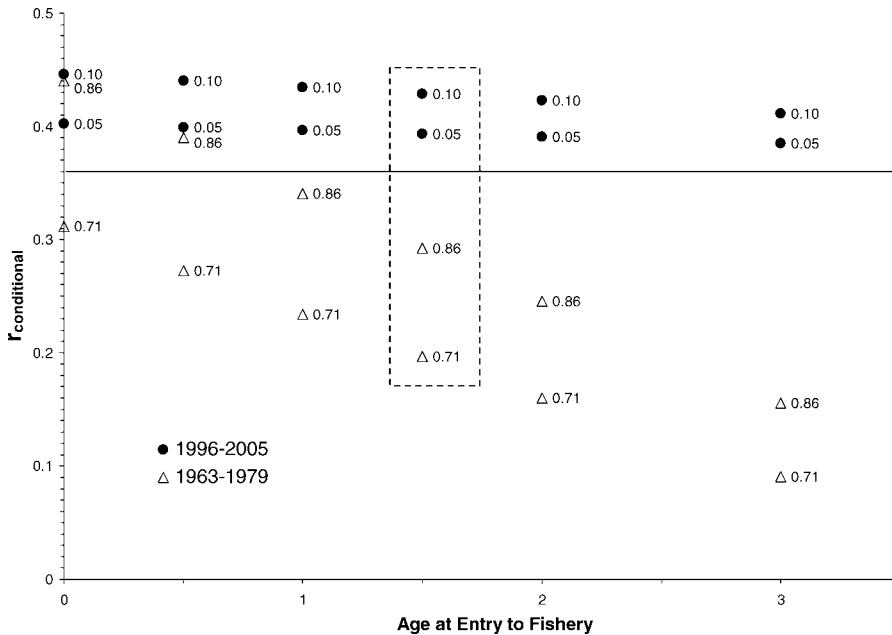| Survey ($n$) | Stock–recruit model | $\alpha$ Mean | $\alpha$ SE | $\alpha$ 95% CI | $K/\beta$ | $\hat{\alpha}$ | $\tilde{\alpha}$ | $\log_e \tilde{\alpha}$ | $r_{intrinsic}$ (lower 95% CB) |
|---|---|---|---|---|---|---|---|---|---|
| Fall (14) | Beverton–Holt | 5.46 | 2.57 | 2.71–**10.50** | 0.05 | 14.74 | 2.43 | 0.89 | 0.38 (0.27) |
| | Ricker | 4.99 | 1.80 | 2.69–12.43 | 10.28 | 13.48 | 2.22 | 0.80 | 0.37 (0.27) |
| Spring (10) | Beverton–Holt | 10.11 | 15.74 | 1.91–**40.97** | 0.01 | 27.30 | 4.50 | 1.50 | 0.49 (0.21) |
| | Ricker | 6.62 | 5.19 | 1.87–**16.8** | 29.21 | 17.88 | 2.95 | 1.08 | 0.42 (0.21) |
| Winter (7) | Beverton–Holt | | | | | | | | |
| | Ricker | 34.16 | 17.38 | 13.27–146.57 | 26.46 | 92.25 | 15.20 | 2.72 | 0.72 (0.54) |

FIGURE 8.—Estimates of $r_{conditional}$ (defined in Methods) from a Leslie matrix demographic analysis for the barndoor skate. Estimates from the decline (1963–1979) and recovery (1996–2005) periods are indicated, as is the sensitivity of $r_{conditional}$ estimates to assumptions of age at fishery entry and assumed fishing pressure for each scenario (indicated by the number next to each data point). The dashed line indicates the most likely scenario given that the cumulative length frequency distribution suggests full vulnerability to the fishery by age 2. The solid line represents the observed rate of population growth between 1996 and 2005, which is thus a lower bound for $r_{intrinsic}$.

estimated to be 0.20 and 0.29 per year from the decline and 0.39 and 0.43 per year from the recovery. Estimates of $r_{conditional}$ were sensitive to the age at entry into the fishery only when the decline was modeled. In this case, the calculated values of $r_{conditional}$ declined significantly as age at entry increased, while estimates from the recovery were robust to this aspect of our model (Figure 8).

During both the decline and recovery periods, the barndoor skate population was clearly depleted and our estimated $r_{conditional}$ should approximate $r_{intrinsic}$. Using equation (15) or by plotting our estimates of $r_{conditional}$ versus the corresponding survey index (Figure 9), an estimate of $r_{intrinsic}$ is obtained. For both the recovery and the decline, the analyzed time segments covered similar stock sizes (i.e., survey indices); the decline contained the highest values. Between 1998 and 2001, halfway through the modeled recovery, survey indices averaged 0.08 fish/tow, approximately 10% of the high of 0.80 fish/tow recorded in 1963. For the decline, the range of indices was similar to that of the recovery but showed very little absolute change in value after 5 years (1968). Thus, we approximated the population size using an average survey index of 0.22 fish/tow from the 1963–1973 data. Solving for the intercept, we

obtain $r_{intrinsic}$ estimates of 0.28 and 0.41 per year from the decline and 0.44 and 0.48 per year from the recovery, depending on the level of $F$ assumed (Figure 9).

## Discussion

The results of our study suggest that the barndoor skate population in the U.S. waters of the North Atlantic is able to grow at a rate that is higher than previously believed and higher than those reported for most other elasmobranchs studied (Casey and Myers 1998; Frisk et al. 2002; Cortés 2004). The population grew at an instantaneous rate of approximately 0.36 per year between 1996 and 2005. The results of our demographic model, which are dependent on this observed growth rate, suggest that at even lower population sizes there is still some scope for compensation and that rates of up to 0.48 per year are possible. Estimates of $r_{intrinsic}$ from the stock–recruit analysis suggest that the barndoor skate population has recently been growing at or near a maximum estimated rate of 0.38 per year.

Prior to this work, only two studies have attempted to estimate the maximum population growth rate of the barndoor skate. Having no direct information available,
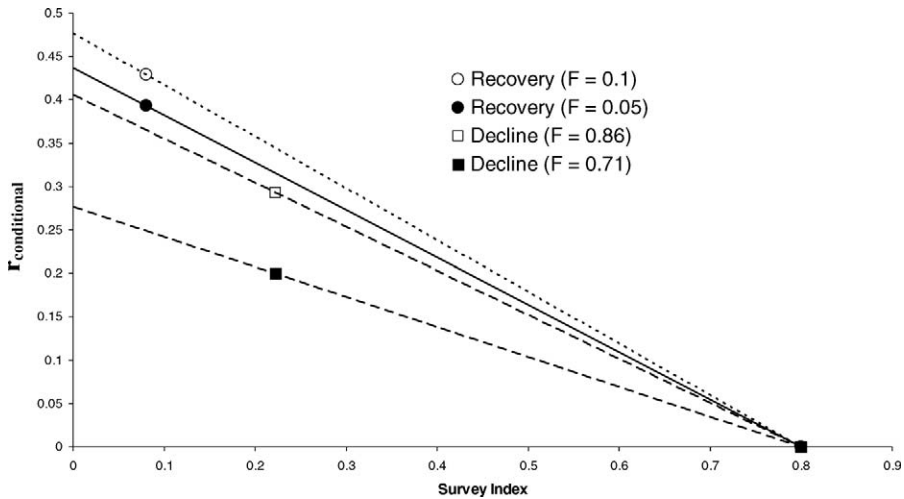
FIGURE 9.—Extrapolation of calculated $r_{conditional}$ values (defined in Methods) to a zero population size to estimate $r_{intrinsic}$ for the barndoor skate based on decline (1963–1979) and recovery (1996–2005) periods and two assumed levels of fishing mortality ($F$) for each period. The $r_{conditional}$ estimates assuming an age at fishery entry of 1.5 years (shaded region in Figure 8) were used, and $r_{intrinsic}$ was estimated as the $y$-intercept. The rightmost point represents the highest survey index value (fish/tow) recorded in the fall survey and is assumed to represent virgin conditions, where a long-term growth rate of zero would be realized. Note that if the virgin survey index was in error (i.e., underestimated due to fishing prior to 1963 or overestimated due to survey variability), the estimates of $r_{intrinsic}$ would not be drastically altered because the extrapolation is over such short ranges of survey indices. Alternatively, the gray arrow indicates that the same extrapolation can be done with two $r_{conditional}$ values measured at two different population sizes (see Gedamke et al. 2007 for details). An $r_{intrinsic}$ estimate of 0.55 per year would result from this approach but is dependent on the highly sensitive estimates from the decline analysis.

researchers were forced to make numerous assumptions about the basic life history information of the species. Casey and Myers (1998) suggested that the barndoor skate is similar to the European common skate *D. batis*, and they utilized the life history parameters of this species ($A_{mat} = 11$ years; $g = 47$ eggs) to make some broad conclusions based on a life table analysis. They suggested that an instantaneous mortality rate ($Z$) of 0.4 per year applied to all ages would drive the barndoor skate to extinction on Georges Bank and that the colder waters and resulting later maturation in parts of the species' northern range would make it vulnerable to extinction at half that level ($Z = 0.2$ per year). Note that all the estimates of population growth in this manuscript are also instantaneous rates, so they are directly comparable with estimates of $Z$. Since Casey and Myers' (1998) upper limit estimate to sustainable mortality was calculated by applying $F$ to all ages, it is equivalent to an estimate of $r_{intrinsic}$.

Frisk et al. (2002) reported an $r_{intrinsic}$ of 0.2 per year, and determined that an $F$ of 0.20 per year (applied to all ages after the first year) and an $M$ of 0.09 per year would result in negative population growth and is therefore unsustainable. In their study, they developed a stage-based model for the barndoor skate and

compared their results with those of age-based models for the little skate *Leucoraja erinacea* and the winter skate *L. ocellata*. As in the study by Casey and Myers (1998), Frisk et al. (2002) were faced with a paucity of data and used parameters from the European common skate for $g$ (47 eggs) and a maximum age of 50 years, which they translated to an $M$ estimate of 0.09 per year by the Hoenig (1983) method. Empirical relationships from Frisk et al. (2001) provided estimates for $A_{mat}$ ranging from 9 to 16 years, and they chose an intermediate value of 12 years. Although the Frisk et al. (2002) study used a stage-based model, Mollet and Cailliet (2002) found that the results of similar age-based models provide almost identical results and should therefore be comparable with our study.

The results of our work are comparable with the approximate upper limits of total mortality presented in the study by Casey and Myers (1998). They reported that a total mortality rate of 0.4 per year would drive the species to extinction when adult survival and juvenile survival are equal; however, they also reported an upper limit of 0.45 per year when juvenile mortality is twice that of adults. It is not possible for a higher juvenile survival rate to result in a greater resilience to fishing pressure (i.e., higher upper limit of mortality).

However, the specific details of their model were not presented, and the cause of this slight discrepancy remains unknown. Regardless, the results of our demographic model also suggest that 0.45 per year is a reasonable upper limit to the maximum population growth rate and, therefore, a reasonable approximation of the upper limit to the maximum sustainable total mortality. The results of the Frisk et al. (2002) model suggest lower population growth rates and, therefore, a much greater sensitivity to fishing pressure.

However, it is difficult to compare the results of these three demographic studies. Our work is the only one to have empirical estimates for many of the life history parameters, yet we were also forced to make assumptions about parameters that have not been estimated (e.g., $M$). Unlike the other two studies, our approach incorporates density-dependent compensation into the analysis and uses observed growth rates to estimate a parameter that includes the survival of the youngest animals, $g$, and $S_{egg}$. As such, our results are directly tied to the observed growth rates estimated from the NMFS survey data. Our estimates of $r_{achieved}$ were made over relatively long time periods and a wide range of stock sizes. This approach provided population growth rates that were less variable than those that would have been obtained using smaller time segments. The trade-off in this decision is the potential bias that could result from smoothing over longer time periods. Also, determining the appropriate stock size corresponding to our estimated rate of growth is difficult when the stock size is changing. Thus, there is some uncertainty in all of the stock sizes (i.e., those corresponding to the virgin population, recovery, and decline) used to estimate $r_{intrinsic}$ from equation (13) and in Figure 9. Since our estimates of $r_{conditional}$ were made at low abundances, the extrapolation is over short distances and the final results are not expected to be drastically altered by changing the estimates of relative stock size.

Despite these concerns, the assumptions, logic, and details of our approach are clear; like any demographic analysis, the interpretation of the absolute results must take these factors into consideration. For example, we consider the results of our analysis from the recovery phase to be more reliable than those from the decline due to (1) the shorter extrapolation from the recovery phase's initial stock size and (2) the weaker assumptions we were forced to make about age at entry into the fishery for the recovery phase. Matrix models are known to be particularly sensitive to the pattern of exploitation, and this was exhibited in our results (Figure 8; Caswell 2001). In our analysis of the population decline, high estimates of $F$ resulted in high sensitivity to our assumption of age at selection.

Sensitivity was quite low under the low values of $F$ seen during the recovery.

In our study, we also have the luxury of comparing the results of our demographic analysis with those of an independent approach: our stock–recruit analysis. For most stocks, the relationship between recruits and spawners is highly variable and not easily defined (Cushing 1995; Myers and Barrowman 1996). Although one would expect the reproductive strategy of an elasmobranch to result in a clear relationship, data to test this hypothesis are generally unavailable. However, as far as we are aware, the only other empirically derived stock–recruit relationship that has been demonstrated for an elasmobranch is for spiny dogfish *Squalus acanthias* (P. Rago, Northeast Fisheries Science Center, personal communication).

In our case, a stock–recruit relationship for the barndoor skate was apparent in both the spring and fall surveys. However, there is enough noise even in the fall data to limit the precision with which the slope at the origin could be estimated. Despite this uncertainty, the analysis shows that the lower confidence bounds on the slope are fairly well constrained and provide confidence that our estimates of $r_{intrinsic}$ are not likely to be significantly overestimated. This is an important point and of greatest interest to conservation and management discussions. A minimal estimate of $r_{intrinsic}$ allows conservative estimates for maximum sustainable fishing pressure to be generated; understanding the bias in the other direction and the potential maximum value of $r_{intrinsic}$ are of less importance. Our analysis also assumes that there is no fishing pressure prior to recruitment, which is unlikely and will also result in an underestimate of the slope at the origin and, therefore, underestimation of $r_{intrinsic}$ (Brooks and Powers 2007).

In comparison with the analysis of over 700 teleost spawner–recruit relationships compiled by Myers et al. (1999), our results suggest that the barndoor skate has a relatively low maximum annual reproductive rate. For a majority of the species in the study of Myers et al. (1999), the maximum annual reproductive rate ranged from 1 to 7 spawners/spawner. Our results put the barndoor skate at the lower end of this spectrum; estimated maximum annual reproductive rates were 2.22 and 2.43 spawners/spawner from the fall survey. This is consistent with the reproductive strategy of the species.

We have presented two independent methods that result in very similar estimates for the maximum population growth rate of the barndoor skate. The primary uncertainty in both methods is the upper limit rather than the lower bound. For the demographic analysis, for example, an observed growth rate of 0.36

per year serves as an obvious minimal estimate of $r_{\text{intrinsic}}$. Some uncertainty does arise from the extrapolations to lower stock sizes that suggest possible growth rates of around 0.5 per year. The analysis of the fall stock–recruit relationship, on the other hand, provides $r_{\text{intrinsic}}$ estimates of 0.37 and 0.38 per year (lower 95% confidence bound = 0.27 for both). Estimates from the spring data are less precise; $r_{\text{intrinsic}}$ is estimated at 0.42 and 0.49 per year (lower 95% confidence bound = 0.21 for both). Since some fishing mortality of prerecruits is likely to be occurring, these estimates should be biased low, as described by Brooks and Powers (2007). The interpretation from the results of both analyses suggests that $r_{\text{intrinsic}}$ is greater than 0.36 per year and possibly as high as 0.50 per year.

The results of this study are based on the assumption that immigration and emigration are not occurring. Although it is not possible with the available data to prove that this is the case, we explored two aspects of the survey data to see if this assumption was violated. First, there appears to be no evidence within the survey area that significant changes in distribution have occurred. Second, there has been no obvious "spontaneous generation," where larger animals appear without a previous increase in smaller animals. Thus, the two tests we could devise show no evidence of immigration. The data suggest that barndoor skate populations are capable of increasing fairly quickly under favorable circumstances.

Although our study suggests that barndoor skate populations are capable of growing at relatively fast rates and are less susceptible to fishing pressure than previously believed, the population declines that were observed during the 1960s remind us that the species is sensitive to exploitation. Estimates of $r_{\text{intrinsic}}$ provide a key piece of information to our understanding of the population dynamics because they represent an upper limit to sustainable exploitation. Thus, our results provide valuable information that can be used in the development of management benchmarks and in monitoring the populations. For example, by using lower and upper bound estimates of 0.35–0.50 per year from our study, one can employ simple surplus production theory to estimate an upper and lower bound for the $F$ at maximum sustainable yield as half of $r_{\text{intrinsic}}$ (e.g., 0.35/2 = 0.175 per year; 0.50/2 = 0.25 per year).

## Acknowledgments

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