DEVELOPING A STOCK ASSESSMENT FOR THE BARNDOOR SKATE (*Dipturus laevis*) IN THE NORTHEAST UNITED STATES

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APPROVAL SHEET

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The barndoor skate *Dipturus laevis* is one of seven species in the United States Northwest Atlantic skate complex. The species received little attention until a recent article published in *Science* reported that the barndoor skate might be on the brink of extinction. In this study, we address not only the virtual lack of information on the life history of the species, but also develop methodologies to assist in the assessment of the barndoor skate population.

To investigate the life history of the species, data were collected from 2,310 specimens caught during commercial sea scallop dredging in the southern section of Georges Bank Closed Area II. Vertebral analysis was used to generate an age-growth relationship, and a visual inspection of reproductive tracts provided the timing of maturity. Our results suggest faster growth and younger female maturation than previously believed. Stomach samples were also collected from specimens to study food habits. Ontogenetic shifts in the utilization of prey items were observed, and above the size at maturity, food habits were significantly different between the sexes.

In the second part of this work, we develop three methodologies for use in stock assessments. The first method is an extension of the Beverton-Holt mean length mortality estimator. This methodology is commonly used but has the restrictive assumption of equilibrium conditions. We derive an equation to describe the transitional behavior of the mean length statistic for use in non-equilibrium conditions and apply it to data from Goosefish (*Lophius americanus*) in the northwest Atlantic. For the second method, we begin by discussing some common problems in the application of demographic models (i.e. Leslie matrices and life tables) to elasmobranchs. We illustrate these problems, and describe methods for estimating the maximum population growth rate, and present applications to two species of elasmobranch: barndoor skate *Dipturus laevis* and lemon shark *Negaprion brevirostris*. The third method we develop is an extension of the Heincke method. This method requires only recruits and non-recruits to be identifiable and uses catch rate data from two consecutive years to estimate a mortality rate. We generalize the approach to include more than two years of data and compare results to those obtained from the Goosefish mean length analysis.

In the last section we use information from the NMFS annual groundfish surveys, our newly-derived life history parameters and our methodological developments to conduct a stock assessment of the barndoor skate. Mortality rates, estimated from both our mean length and catch rate methods, appear to have been very high in the 1960's and are currently at very low levels. There is no evidence of a high current fishing mortality rates or any threat to the population. In the final manuscript we develop both a stock-recruit and Leslie matrix model to gain insights on the population dynamics of the species. The results of both approaches were comparable suggesting that species may be more resilient to fishing pressure than previously believed and capable oft growing at an annual rate in excess of 40%.

Chapter 1

GENERAL INTRODUCTION

The barndoor skate *Dipturus laevis* (Mitchill 1817), is one of many skate and ray species caught as bycatch in finfish trawl and scallop dredges in the Northwest Atlantic. Until recently, this species has received little attention, due primarily to its low market value (Musick et al., 1999; Dulvy et al., 2000; Kulka et. al., MS 2002), until a recent study suggested its potential extinction (Casey and Myers, 1998). Casey and Myers (1998) reported that the barndoor skate, once a common bycatch species off southern Newfoundland, had become locally extirpated in parts of its northern range due to overfishing. They also contended that "long-term research surveys on the continental shelf between the Grand Banks of Newfoundland and southern New England reveal that….the barndoor skate….is close to extinction (Casey and Myers, 1998)."

Environmental groups quickly responded to the results presented in the Casey and Myers (1998) article. Greenworld Organization and the Center for Marine Conservation filed petitions with the National Marine Fisheries service to 1) list the barndoor skate as an endangered species 2) immediately designate Georges Bank as critical habitat and implement large area closures and 3) list other similarly appearing species of skates as a precautionary measure (NOAA 1999). The IUCN (Union for the Conservation of Nature and Natural Resources) followed suit and after initially listing the species as vulnerable, they upgraded the threat status to endangered. Thus, the barndoor skate became the focus of many conservation and extinction risk debates (Diaz-Soltera, 1999; Musick et. al., 1999; NEFSC, 2000).

As the controversy brewed, I began my research in this arena while conducting field work for my Masters thesis on commercial scallop vessels on Georges Bank. Based on the data presented in the Casey and Myers (1998) article I had expected to encounter a

lone skate or two, and was only prepared to work up a few dozen animals.   I was pleasantly surprised to document over 100 barndoor skates in the first two days of fishing. My dissertation was born. It began as a straightforward investigation of the life history of the species and has evolved to include the development and application of stock assessment methodologies to assess the status of the barndoor skate. Including this general introduction and a conclusion chapter, the dissertation consists of seven manuscripts, written in journal format, that fall under three general topics: 1) Life history 2) Stock assessment methods 3) Barndoor skate stock assessment.

Life History

Age-growth and Maturity

Understanding the life history traits and quantifying the age and growth parameters for individual species has been recognized as crucial in the risk assessment and management of marine fishes (Parent and Schrimi, 1995; Musick, 1999a; Musick, 1999b). A recent stock assessment of the United States Northwest Atlantic skate complex (NEFSC, 2000) listed the three largest species; barndoor, winter (*Leucoraja ocellata*), and thorny skates (*Amblyraja radiata*), as overfished and identified a need for further studies of the age, growth, and reproduction. Our work has focused on defining these critical life history parameters for the barndoor skate. The manuscript in Chapter 2, entitled "Observations on the Life History of the Barndoor Skate, *Dipturus laevis*, on Georges Bank (Western North Atlantic)" was published in 2005 in the Journal of Northwest Atlantic Fishery Science (35:67-78).

Food Habits

Understanding the feeding habits of the barndoor skate can bring valuable insight into predator-prey relationships and can contribute to future studies of trophic interactions (Caddy and Sharp 1986). Unfortunately, very little is known about their food habits and how they fit into the overall ecosystem. Limited information from descriptive studies of the Northwest Atlantic fish complex report that juvenile barndoor skates apparently subsist mainly on benthic invertebrates, while larger individuals eat larger and more active prey (Bigelow and Schroeder, 1953; Mceachran and Musick, 1975; NOAA, 2003). Primary prey is believed to consist of polychaetes, copepods, amphipods, isopods, the sand shrimp *Crangon septemspinosa*, and fish such as spiny dogfish, alewife, Atlantic herring, menhaden, hakes, sculpins, cunner, tautog, sand lance, butterfish and various flounders. There is simply not enough data available to assess habitats which are critical for the feeding, growth or reproduction of the species.

The current study provides vital information to the current closed area management strategy on Georges Bank and assists in the designation of essential fish habitat defined as "those waters and substrate necessary to fish spawning, breeding, feeding, or growth to maturity *(16 U.S.C. 1802(1*0))". Chapter 3, entitled "Ontogenetic and Sex-specific Shifts in the Feeding Habits of the Barndoor Skate (*Dipturus laevis*) on Georges Bank", addresses a research need identified in both the 2001 SAFE report (NEFMC, 2001) and the recent essential fish habitat source documents (NOAA, 2003) to "investigate trophic interactions between skate species in the complex, and between skates and other groundfish."

Stock Assessment Methods

Estimating mortality from mean length data

Baranov (1918, cited in Ricker 1975) was apparently the first to deduce that equilibrium mean length in a fish population is inversely related to the mortality rate experienced by the population. Beverton and Holt (1956, 1957) observed the same thing for a more realistic situation where length is an asymptotic, rather than linear, function of time. They also derived an expression for estimating the total instantaneous mortality rate, Z, from the mean length of those animals above the length L_c, $\overline{L}$;

$$Z = \frac{K(L_\infty - \overline{L})}{\overline{L} - L_c}$$

where K and L_∞, are the von Bertalanffy growth parameters, L_c is the so-called length of first capture (smallest size at which animals are fully vulnerable to the fishery and to the sampling gear), and $\overline{L}$ is the mean length of the animals above the length L_c.

The Beverton-Holt mortality estimator has received widespread use, especially in data-limited situations; however, it is based on a restrictive assumption of equilibrium conditions. In this chapter, we derive the transitional behavior of the mean length statistic for use in non-equilibrium conditions. We investigate conditions affecting the reliability of the Beverton-Holt results and then develop a new procedure that allows mortality rates to be estimated from non-equilibrium mean length data following a permanent change in mortality, based on the relationship:

$$\overline{L} = L_\infty - \frac{Z_1 Z_2 (L_\infty - L_c)\{Z_1 + K + (Z_2 - Z_1)\exp(-(Z_2 + K)d)\}}{(Z_1 + K)(Z_2 + K)(Z_1 + (Z_2 - Z_1)\exp(-Z_2 d))}$$

where Z_1 is the first level of mortality, Z_2 is the second level of mortality, and d is the years since the change in mortality occurred.   The equation has also been generalized to

account for multiple changes in mortality and incorporated into a likelihood function to fit actual time-series survey data.

We then apply this new methodology to the goosefish (*Lophius americanus*) assessment, which was criticized for its use of the Beverton-Holt estimator under non-equilibrium conditions. Using data from the 1963-2002 National Marine Fisheries Service annual fall groundfish surveys off the Northeast United States, we estimated using the method of maximum-likelihood that total mortality of goosefish in two distinct management regions. The new, non-equilibrium estimator allows a change in mortality to be characterized reliably several years faster than if the Beverton-Holt estimator is used and results compare extremely well with information from landings data and the conclusions of the goosefish stock assessment.

The manuscript in Chapter 4, entitled "Estimating mortality from mean length data in non-equilibrium situations, with application to the assessment of goosefish (*Lophius americanus*)" was published in 2006 in the Transactions of the American Fisheries Society (135:476-487). Having found the new procedure to have worked well in a simple case with small sample sizes, we proceeded to modify the model to the more complicated case of the barndoor skate where recruitment may be linked to mortality rates (Chapter 8).

Estimating mortality from catch rates

Survival rates can be estimated from annual surveys by tracking the abundance of one or more cohorts, as measured by catch per unit of sampling effort, from one year to the next. It can be difficult to attain reasonable precision unless sampling effort is

extensive. Indeed, estimates of survival exceeding 100% are not infrequently obtained. Heincke (1913) was apparently the first to suggest pooling data over ages although he formulated the estimation procedure in terms of a cross-sectional catch curve (age composition observed in one year) rather than as a longitudinal catch curve (changes in abundance of specified cohorts monitored over time).

A generalization of this which includes more than two years of data has not been given previously and is developed in our study. We show that data from several years can be analyzed simultaneously to obtain a single estimate of survival under the assumption that survival is constant over the period analyzed. The method requires that only a single age group need be identifiable and thus has minimal data requirements. Estimates of goosefish (*Lophius americanus*) survival obtained by this method compare favorably with estimates obtained by analyzing changes in mean length over time. The manuscript in Chapter 5, entitled "Simple Methods for Estimating Survival Rate from Catch Rates from Multiple Years", is currently under review in the Transactions of the American Fisheries Society.

Demographic models for elasmobranchs: pitfalls, advances and applications

Leslie matrices and life tables are demographic models commonly used to evaluate the ability of specific elasmobranch life history strategies to sustain given levels and patterns of fishing pressure. These models are generally density-independent and provide an instantaneous rate of population growth for a specified set of life history traits which correspond to a specific population size. Many investigators are using these models to compute rates of population growth that they claim are estimates of maximum

population growth rate ($r_{intrinsic}$); they then use these estimates to compute purported estimates of maximum sustainable fishing mortality (Cortes 2004). However, neither a Leslie matrix nor a life table can be used to estimate $r_{intrinsic}$ without additional information except in the special case where a severely depleted population is modeled. Only in a severely depleted population will competition for resources be at a minimum and both density-dependent compensation and the rate of growth be at a maximum (i.e., at $r_{intrinsic}$). The fundamental problem is to determine the life history parameters that would occur if the population were extremely depleted because extensive observations on extremely depleted populations are rare. In the absence of such data, $r_{intrinsic}$ can only be estimated from these types of density-independent models by extrapolating observed population growth rates towards zero population size.

In this chapter, we illustrate the problems in, and describe methods for, estimating $r_{intrinsic}$, and making further inferences when additional information can be utilized. We derive methods for estimating $r_{intrinsic}$ and apply them to two species of elasmobranch: barndoor skate *Dipturus laevis* and lemon shark *Negaprion brevirostris*. The manuscript in Chapter 6, entitled "Using demographic models to determine intrinsic rate of increase and sustainable fishing for elasmobranchs: pitfalls, advances and applications", is currently under review with The North American Journal of Fisheries Management.

Barndoor Skate Stock Assessment

Estimating Total Mortality

Following the Casey and Myers (1998) article, managers were faced with the task of assessing a population with limited life history information and survey data that

contained only a few animals a year. One of the key pieces of information to assess the threat to the species is the current mortality rate. Unfortunately, estimating this parameter through classical approaches proved difficult. In this study we use variants of commonly used methodologies to estimate total mortality. We present two methods: a length based estimator based on the logic presented in Chapter 4, and the application of the catch rate estimator developed in Chapter 5. The length based estimator has been restructured to include actual recruitment into the model, thus avoiding the assumption of constant recruitment which is likely to be violated considering the reproductive strategy of the barndoor skate. With this approach we are able to evaluate the historical and current mortality rates on the barndoor skate population and gain insights as to the population dynamics of the species. The manuscript in Chapter 7 is entitled "Total Mortality Rates of the Barndoor Skate, *Dipturus laevis,* in the Northeast United States, 1963-2005."

Stock-recruit dynamics and the maximum population growth rate

   Although we present some information on mortality rates, the overall population dynamics of the barndoor skate remains largely unexplored. In this chapter we use information from the NMFS annual groundfish surveys on Georges Bank and the Gulf of Maine to develop both a stock-recruit and Leslie matrix models to gain insights on the population dynamics of the species.   We follow the methodology laid out by Myer's et al. (1997, 1999) for the analysis of the stock-recruit relationship and that of Chapter 6 for the demographic analysis to investigate two critical (and related) components of the barndoor skate population dynamics: the relationship of recruitment to spawner

abundance and the maximum population growth rate. A compelling stock-recruitment was found in the fall survey data suggesting that recruitment is closely tied to spawner abundance. Data were fit with both the Ricker and Beverton-Holt stock-recruit models and estimates of the slope at the origin generated. As in Myers et al. (1997) these parameters provided an estimate of the maximum annual reproductive rate and were then converted to estimate an instantaneous maximum population growth rate.

A second analysis was also conducted using a Leslie matrix, data from the NMFS survey, and the methods outlined in chapter 6. Observed rates of population change were used to estimate first year survival and incorporate density dependant logic into the density dependant framework of a Leslie matrix demographic model. The results of both approaches were comparable suggesting that species may be more resilient to fishing pressure than previously believed and capable of growing at an annual rate in excess of 40%. The manuscript in Chapter 8 is entitled "Total Mortality Rates of the Barndoor Skate, *Dipturus laevis,* in the Northeast United States, 1963-2005."

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Chapter 2

Observations on the Life History of the Barndoor Skate, *Dipturus laevis*, on Georges

Bank (Western North Atlantic)

Abstract

The barndoor skate (*Dipturus laevis*) has been reported to be close to extinction in parts of its northern range and is believed to be particularly vulnerable to fishing mortality due to its relatively large size. A lack of basic life history information, however, has hampered an accurate assessment and management of north Atlantic populations. In an attempt to fill this void, information was collected from 2,310 specimens caught during commercial sea scallop dredging in the southern section of Georges Bank Closed Area II. Eighty-seven fish were determined to be mature from a visual inspection of reproductive tracts and the allometric growth of claspers, oviducal glands, and developing ova. Sexual dimorphism was apparent in length at 50% maturity with females maturing at 116.3 cm and males at 107.9 cm. A preliminary analysis of 118 vertebrae indicates faster growth ($k = 0.14$ to 0.18 yr^{-1}) and younger female maturation (6.5 to 7.2 yrs.) than previously believed. Thus, resilience of the barndoor skate to overfishing may be higher than recently assumed.

Introduction

The barndoor skate *Dipturus laevis* (Mitchill 1817), is one of many skate and ray species caught as bycatch in finfish trawl and scallop dredges in the Northwest Atlantic. Until recently, this species has received little attention, due primarily to its low market value (Musick et al., 1999; Dulvy et al., 2000; Kulka et. al., MS 2002), until a recent study suggested its potential extinction (Casey and Myers, 1998). Casey and Myers (1998) reported that the barndoor skate, once a common bycatch species off southern Newfoundland, had become locally extirpated in parts of its northern range due to overfishing. They also contended that "long-term research surveys on the continental shelf between the Grand Banks of Newfoundland and southern New England reveal that….the barndoor skate….is close to extinction (Casey and Myers, 1998)." Subsequent petitions to place the species on the U.S. National Marine Fisheries Service Endangered Species List and listing of the barndoor skate as vulnerable by the IUCN (Union for the Conservation of Nature and Natural Resources) placed the barndoor skate in the middle of conservation and extinction risk debates (Diaz-Soltera, 1999; Musick et. al., 1999; NEFSC, 2000).

The barndoor skate is the largest member of the family Rajidae found in the northwestern Atlantic, reaching a maximum length of 152 cm and a weight of 20 kg (Bigelow and Schroeder, 1953a). The species is found from Cape Hatteras to the Grand Banks of Newfoundland, Gulf of St. Lawrence and Nova Scotia (Leim and Scott, 1966; McEachran and Musick, 1975). It ranges from shallow coastal waters to depths greater than 400 meters and tolerates water temperatures of 1.2-20^0 C (Bigelow and Schroeder, 1953b; McEachran and Musick, 1975). Recent analysis of Canadian survey and

commercial fisheries data suggests that the overall distribution of the species is far more

extensive than originally thought both in terms of depth and northern range (Kulka et al.,

MS 2002; Simon et al., MS 2002). Barndoor skates were found as far north as the

Labrador Shelf to 62^0 N and into depths of about 1600 meters with significantly higher

catch rates at depths below 450 meters (Kulka et al., 2002; Simon et al., MS 2002). These

studies strongly indicate that Casey and Myers (1998) used a data set that poorly sampled

barndoor skate overall distribution and as such substantially underestimated the actual

barndoor skate population.

Due primarily to their large size and therefore presumed late maturation, barndoor

skates are believed to be particularly vulnerable to the effects of high levels of fishing

mortality; however, very little information is available on the biology and ecology of the

barndoor skate to make an accurate assessment. Elasmobranchs in general have

relatively low reproductive rates and low intrinsic rates of population increase due to

their late maturity and low fecundity (Hoenig and Gruber, 1990; Camhi et al, 1998;

Walker and Hislop, 1998).

This life history strategy relies on a relatively high survival of a few well-

developed offspring and results in a direct and limiting relationship between the number

of adults in the population and number of young-of-year. The pattern of more productive

species, like that exhibited in most teleost fishes involves the highly variable survival of

many fragile offspring and greater fluctuations in the relative number of surviving young-

of-year. In both strategies, changes in environmental conditions or fishing pressure can

result in the increased survival of offspring but the potential for a large recruitment event

or a quick recovery from overfished or depressed populations is much lower in the less

productive species. Compounding the effects of excessive fishing on recovery potential is the interrelationship of life history traits and the trend towards later maturity among the larger, less fecund species. This results in longer generation times, a greater chance of juvenescence, and a significant delay between a reduction of fishing mortality and an increase in the number of spawning adults. Holden (1973) and Brander (1981) have shown that differences in life history parameters of elasmobranchs, particularly size at maturity and overall body size, result in species-specific responses to fishing mortality. The European common skate (*Dipturus batis*) and at least four other North Sea skates have all undergone severe regional population declines due in part to their relatively large size, late maturation, low fecundity and resulting sensitivity to fishing mortality (Brander, 1981; Walker and Heessen, 1996; Dulvy et al., 2000), an affect less apparent in smaller species

Understanding these life history traits and quantifying the age and growth parameters for individual species have been recognized as crucial in the risk assessment and management of marine fishes (Parent and Schrimi, 1995; Musick, 1999a; Musick, 1999b). A recent stock assessment of the United States Northwest Atlantic skate complex (NEFSC, 2000) listed the three largest species; barndoor, winter (*Leucoraja ocellata*), and thorny skates (*Amblyraja radiata*), as overfished and identified a need for further studies of the age, growth, and reproduction of these species. Our recent work has focused on defining these critical life history parameters for the barndoor skate. This paper presents the first significant information on the life history of the barndoor skate collected from 2,310 specimens in the western North Atlantic.

Methods

All of the specimens used in this study were collected onboard commercial scallop vessels fishing in the southern portion (south of 41^0 30" N) of Georges Bank Closed Area II. (Figure1). This area was closed to the use of mobile fishing gear in December of 1994 in an effort to rebuild groundfish stocks. Following five years of no fishing effort in this area, the southern portion of Closed Area II was opened to limited commercial scallop fishing in June of 1999. Data was collected on twelve trips between June and November of 1999, 2000, and 2001. Vessels fished with two 15-foot New Bedford style sea scallop dredges (Posgay, 1957) constructed with a 10 inch mesh twine top and either 3.5 or 4 inch ring bags. Gear was towed in 55-73 meters of water at an average speed of 9.2 km/hr. A total of 1,311 tows were made from seven different commercial vessels during 90 days at sea.

Although the barndoor skates were not a significant percentage of fish bycatch, we observed enough individuals to initiate a comprehensive study of the barndoor skate in Georges Bank Closed Area II. Positive identification of the barndoor, which has been a concern in some published material (McEachran and Musick, 1975), was assured by the senior author or trained staff from The Virginia Institute of Marine Science. The barndoor was easily recognized by its long rostrum, acute angle of the anterior margin of the disk, grey ventral surface, and mucous pores (Bigelow and Schroeder, 1953a).

Disk width (DW), disk length (DL) and total length (TL) measurements were taken from all individuals. Clasper length (CL) was also taken for all males and measured as described for clasper inner length in the FAO species catalogue (Compagno, 1984). TL was measured from the tip of the snout to the tip of the tail and was recorded

for all but 230 individuals. For these, TL was calculated from the TL/DW relationship (TL = 1.4115 • DW - 0.7741; n = 2,080; R^2 = 0.99) generated from the remaining specimens. Total length has been used throughout this report for ease in comparison to previously published literature on other skate species and elasmobranchs (Walker and Hislop, 1998; Frisk et al., 2001).

Specimens were measured as soon as possible following capture. After measurements were taken, specimens were dissected and sampled or marked and released to avoid duplicate records of the same individuals. Biological samples including vertebrae, gastrointestinal and reproductive tracts, and tissue samples were taken from a representative sub-sample of sizes and sexes. Reproductive tracts were preserved in 10% formalin and examined in a laboratory at the Virginia Institute of Marine Science in Gloucester Point, VA. This paper will focus primarily on information from morphometrics and the reproductive tracts in addition to preliminary results of an age and growth analysis. A more comprehensive analysis of age and growth, population genetics, and food habits will be addressed in later papers.

Maturity

The allometric growth and expression of secondary sexual characteristics were utilized to determine the reproductive status of each individual and the size at maturity for each sex. Male barndoor skates were considered to be mature based on the following criteria: 1) an abrupt change in clasper length relative to total length (Babel, 1967; Struhsaker, 1969; Pratt, 1979); 2) the presence and degree of coiling in the vas deferentia (Pratt, 1979; Martin and Cailliet, 1988); 3) the internal morphology and the

size, shape and appearance of the testes. Immature individuals had small flaccid testes that were homogenous in appearance while mature individuals had enlarged testes with visible differentiated follicles on the dorsal-lateral margins. Criterion 3 was only utilized in cases where coiling in vas deferentia was marginal.

The stage of sexual maturity in females was determined by: 1) the presence of developing or ripe eggs in the ovary (Holden, 1975; Pratt, 1979; Martin and Cailliet, 1988) and 2) the allometric growth of the oviducal gland (Pratt, 1979; Smale and Goosen, 1999). Individuals containing five large yolked eggs with a mean size >10mm were considered to be mature while individuals that contained white or clear eggs <10mm were judged to be immature. Oviducal gland measurements were taken across the widest part of the gland, generally perpendicular to the oviduct. Maturity was indicated by the accelerated growth of this organ as compared to total length.

Once individuals were classified as either mature or immature based on the criteria described above, the point of 50% maturity was calculated using a logistic probit analysis in Minitab (version 4.10.1998, Release 12). The phrase "length at maturity" will refer to the point of 50% maturity throughout this paper.

Age and Growth

Vertebral samples were taken from a sub-sample of all sizes captured and frozen for later analysis. In the laboratory, samples were thawed, separated into individual centra, cleaned and then placed in 70% ETOH for a minimum of 24 hours. Following this treatment, vertebral banding was apparent even with the naked eye suggesting that relatively simple techniques such as graphite microtopography (Neer and Cailliet, 2001)

and/or oil immersion might be viable. Whole centrum ring counts were recorded on a number of specimens and then centra were sectioned through the focus along the central longitudinal axis using an Isomet rotary diamond saw (Buehler, 41 Lake Bluff, IL). If the remaining centrum half was large enough it was cut again or simply sanded to leave a bow-tie slice through the focus. Centra sections were then dried between two pieces of Plexiglas to prevent warping and mounted to microscope slides using Permount. Mounted sections were then sanded and polished with wet sandpaper (320, 400, then 600 grit) to approximately 0.5 - 1.0 mm. Slides were then examined under a compound video microscope with the Optimus image analysis system (Media Cybernetics, 1999).

Banding patterns in the sectioned centra were apparent and similar to that described in Daiber (1960) for the clearnose skate, *Raja eglanteria* and by Waring (1984) for the little skate, *Raja erinacea*. Alternating wide and narrow bands were observed and hypothesized to be indicative of an annual cycle (Figure 2). The narrow bands, henceforth called "growth rings" were counted to determine a putative age for each specimen. The first of these rings was generally faint, occurred at approximately 0.6 - 0.8 mm from the focus, and at the same location as an angle change and thickening of the corpus calcareum. This was considered to represent a birthmark and was consistent with observations from our smallest young-of-year specimens.

Growth rings were counted by at least two readers several times until a consensus was reached. Of the vertebrae samples collected from 1999 to 2001, 118 have been processed, read by at least two readers and included in this paper. Although growth ring counts on whole centra appear consistent, only the results from the sectioned centra are presented in this paper. The effect of sample placement along the vertebral column,

reader precision, or validation of the annual nature of the growth rings is in progress.

Until such time as validation is complete, ages in this paper shall remain putative.

Age at maturity was calculated from specimens in which both vertebral banding and reproductive tracts were analyzed. A logistic probit analysis in Minitab (version 4.10.1998, Release 12) was utilized on the age/maturity data (mature individuals were assigned a 1 and immature a 0) to estimate the point of 50% maturity. The von Bertalanffy growth function was then fit to all of the age-at length data with the PROC NLIN function in SAS (SAS, 1999). The von Bertalanffy growth function is:

$$L_t = L_\infty \cdot [1 - \exp(-k \cdot (t - t_0))]$$

Where L_t = length at age 't', L_∞ = asymptotic or maximum length, k = growth coefficient, and t_0 = theoretical age when length equals zero. All of the smaller size classes were well represented so back calculation of larger specimens was not necessary. Growth parameters were estimated for the sexes combined due to small sample sizes.

Results

The sex ratio of all captured individuals was relatively even: 1,181 females (51.1%) and 1,129 males (48.9%). Total lengths ranged from 20.0 - 133.5 cm with an overall mean of 56.6 cm (Figure 3). Catch rates increased each year over the course of the study but further spatial and length-specific analysis are necessary before any conclusions can be drawn. A total length-weight relationship was also generated (Weight in grams = 0.001125 • (TL in cm)$^{3.339}$; n = 28, and R^2 = 0.97) but should be used

with caution because only 4 individuals greater than 80 cm were included in the weight samples.

Maturity

A logistic probit analysis on all individuals sampled estimated length at 50% maturity at 112.4 cm (95% CI's = 110.2 – 114.6 cm; n = 290), however, barndoor skates like many elasmobranchs exhibit sexual dimorphism in their development (Struhsaker, 1969; Holden, 1972; Gelsleichter, 1998). For the males, clasper lengths (n = 1,126) and the examination of reproductive tracts from 148 specimens indicate the onset of adolescence at approximately 85-90 cm. At this point, the ratio of clasper length to total length begins to noticeably change and then begins to dramatically increase at around 100 cm (Figure 4). All specimens less than 103 cm were considered to be immature showing only minimal signs of development. Eighteen individuals between 82 and 113 cm had slightly enlarged testes and/or minimal coiling of the vas deferentia and were considered to be developing yet still immature. All individuals over 113 cm were mature, having highly coiled vas deferentia, large claspers, and enlarged testes with visible follicles. A total of 48 mature males were captured with a calculated length at maturity of 107.9 cm with 95% confidence intervals of 105.2 – 110.6 cm (Table 1).

For the females, oviducal gland measurements and the examination of 142 reproductive tracts indicate that adolescence in female barndoor skates begins at approximately 90-95 cm (Figure 5). The smallest individual with developing or ripe eggs indicating first maturity was observed at 114 cm, with 100% maturity occurring at sizes greater than 124 cm. Two females were captured with fully developed encapsulated eggs

in each oviduct on November 10th 1999 (124 cm) and on July 13th, 2000 (121 cm). A total of thirty-nine mature individuals were captured with the calculated length at maturity for the female barndoor skate of 116.3 cm with 95% confidence intervals of 114.2 – 118.5 cm (Table 1).

Age and Growth

Vertebrae samples were taken from fish that ranged from a 22 cm young-of-year male to a 133.5 cm female, the largest specimens captured. The relationship between TL and vertebral radius (VR) was significant supporting the use of vertebral sectioning for estimation of growth rates (Figure 6).   The oldest observed individuals were 11 years old. A size-at-age plot of all processed vertebral samples (sexes combined) was described well by the von Bertalanffy growth model (Figure 7) with parameter estimates of: L_∞ = 166.3 cm , k = 0.1414 yr^{-1}, and t_0 = -1.2912 yr.

The results of a probit analysis on those specimens where both age and maturity were assessed (n=86) estimated the age at 50% maturity for males and females to be 5.8 and 6.5 years, respectively. Although samples sizes were relatively low (male = 51, female = 35), the 95% confidence intervals were reasonably tight at 5.3 - 6.3 years for males and 6.1 – 6.9 years for females (Table 1). Substituting our length at maturity estimates for L_t in the von Bertalanffy growth model and solving for age (t) then generated an alternate estimate of age at maturity. Estimates from this technique were slightly higher but very similar to those from the direct age/maturity probit analysis: 6.1 and 7.2 years for males and females respectively.

Discussion

 Inspection of reproductive tracts and the allometric growth of secondary sexual structures provided an easy means for quickly assessing maturity in sampled individuals. In male elasmobranchs, the development of claspers coincides with the differentiation of the testes (Wourms, 1977) and depending on the species, relative clasper length will increase either gradually or abruptly as an individual reaches sexual maturity (Pratt, 1979). As in several other batoid species, the growth of the claspers in the barndoor skate exhibited this type of easily identifiable abrupt change (Babel, 1967; Struhsaker, 1969). Accelerated clasper growth was observed between 100 and 120 cm providing obvious upper and lower bounds for our maturity estimate.

 In female elasmobranchs, nearly every structure of the reproductive tract has been used as an indication of various stages of sexual development: the size shape and appearance of the ovary (Joung and Chen, 1995); the development of the oviduct (Springer, 1960), and the oviducal gland (Pratt, 1979; Smale and Goosen, 1999). In the barndoor skate, the allometric growth of the oviducal gland, which is a heart shaped organ where sperm may be stored, fertilization occurs and egg cases are produced, was a visually apparent and quantifiable indicator of the onset of adolescence. Significant maturation begins around 90 cm and was obviously nearing completion around 115 cm when large yolky eggs began appearing in a number of individuals.

 Previously published values for length at maturity of the barndoor skate have been equivocal, making a comparison of our data to earlier findings difficult. Richards et al. (1963) reported a length at sexual maturity for the barndoor skate of 92 cm, however the source, study site, and supporting information for this conclusion were not presented.

Casey and Myers (1998) suggested that the barndoor may be similar to the European common skate (*D. batis*) and utilized the life history parameters of this species (age at maturity (A_{mat}) = 11 yrs, and fecundity (F) = 47 eggs) in reaching their conclusions. A recent stock assessment of the seven skate species found in the north Atlantic United States waters (NEFSC, 2000) used a maximum observed length of 136 cm and predictive equations to generate estimates of length at maturity (L_{mat}) of 102 cm and A_{mat} of 8 years (Frisk et al., 2001). The results of the present study however show that female barndoor skates on the eastern end of Georges Bank reach sexual maturity at a larger size (L_{mat}=116.3) and suggest sexual dimorphism in length at maturity.

The findings of this study also suggest that the barndoor skate matures at a similar point in their development as other female elasmobranchs. Holden (1974) suggested that the mean length of maturity for female elasmobranchs occurs at 60-90% of their asymptotic length. This ratio (L_{mat}/L_{max}) can then be used to compare reproductive life history strategies among species. If L_{max} is taken to be 152 cm, which is the largest individual ever recorded, the female barndoor skates in our study matured at a L_{mat}/L_{max} ratio of 0.76.   This is comparable to values reported in other studies that have shown this ratio to be 0.74 for *Raja eglanteria*, 0.73-0.81 for *Leucoraja erinacea*, and 0.80 for *Raja clavata* (Fitz and Daiber, 1963; Holden, 1974; Waring, 1984). For the seven species common to the northwest Atlantic, observed and predicted L_{mat} and L_{max} values used in the 30th SAW (NEFSC, 2000; Frisk et al., 2001) result in L_{mat}/L_{max} ratios of 0.52-0.81.

Although there appears to be some variability in the exact timing of ring and growth band formation, vertebral growth patterns have been successfully used in a number of different elasmobranch age and growth studies (Holden and Vince, 1973; Pratt

and Casey, 1983; Ryland and Ajayi, 1984). For the barndoor skate, the validation of annual ring formation has not been accomplished, however the validity of this technique has been demonstrated for at least five other similar skate species. Studies on *Raja erinacea* (Natanson, 1993), *Raja microocellata* (Ryland and Ajayi, 1984), *Raja eglanteria* (Gelseichter, 1998), *Raja montagui* (Ryland and Ajayi, 1984) and *Raja clavata* (Holden and Vince, 1973; Ryland and Ajayi, 1984) have utilized biological markers, such as the antibiotic tetracycline, to successfully validate the formation of annual rings. Although a few studies on shark species have proposed that bands may form twice a year (Pratt and Casey, 1983) or may be related to somatic growth (Natanson and Cailliet, 1990), there is no evidence from skate species closely related to the barndoor skate to suggest any pattern other than an annual cycle.

The application of the von Bertalanffy growth model to our age-at-size data provides a theoretical maximum total length (L_∞) of 166.3 cm and a growth coefficient (k) of 0.14 yr^{-1}. Although these values are comparable to those found in other skate species (Table 2) and our samples covered the known size range, L_∞ may be slightly overestimated due to low sample numbers in the oldest age classes. If we consider the largest barndoor skate ever reported (152 cm) (Bigelow and Schroeder 1953a) and the largest individual recorded on Georges Bank since 1963 (136 cm) our estimate of L_∞ appears slightly high. When the von Bertalanffy growth model is fit to our data with an assumed L_∞ of 150 cm the growth coefficient (k) increases to 0.18 yr^{-1}.

These empirically derived growth rates and the corresponding age at maturity estimates suggest that the barndoor skate may not be as susceptible to fishing pressure as recently assumed. Lacking direct information, Casey and Myers (1998) chose to use the

life history parameters of the common skate, *D. batis*, in their discussion. The common skate reaches a maximum length of nearly 90 cm greater than the barndoor skate suggesting k values of near 0.05 and an age at maturity estimate of 11 years. Skate species such as *Raja clavata, R. microocellata, R. brachyura,* or *Leucoraja ocellata*, which reach maximum sizes within 25 - 60 cm of the barndoor skate, would have served as important additional comparative species. Growth coefficients have been estimated between 0.07 and 0.22 for these species with estimates of age at maturity of around 5 or 6 years. As expected by maximum size alone, the barndoor skate matures at the high end of the age range for these smaller skates and well below that of *D. batis*.

Although these types of comparisons can provide guidance in situations where no direct information is available, differences in the life history strategies of even closely related species can lead to significant variability in parameter estimates. Stock assessments and subsequent management decisions should reflect the potential uncertainty inherent in these generalizations. Further research on the barndoor skate including histology of reproductive organs and annual ring validation are in progress to yield a more comprehensive life history analysis; however, we are confident that both our maturity and age-growth estimates will withstand further scrutiny.

The prudent application of our results to stock assessments and management decisions should consider the limitations of our study. Samples were taken from a very small area located in both the southern and shallow ends of the species distribution. At higher latitudes or at greater depths where water temperatures would be lower, growth may be slowed and age at maturity delayed. Under these circumstances, our age at maturity and growth rate estimates are likely to be negatively biased and might

overestimate the potential productivity of a regional population. Another factor that might suggest a conservative application of our results is the unknown catchability of our sampling gear. Commercial scallop dredges, like many other fishing gears, are likely to be biased against catching large individuals. Although our data do not show a large size range within older cohorts, this scenario might result in the underestimation of age at maturity. It is also probable that this same selective fishing pressure over long periods of time would result in a reduction of both maximum age and age at maturity in comparison to a virgin population. This theory is supported by the absence of individuals as large as those reported by Bigelow and Schroeder (1953a) some 50 years ago.

Finally, samples were collected during a six-month period of June through November. Although there is no evidence to support that any of our parameter estimates are biased as a result, the bimodal nature of our length frequency data suggest either size-specific migrations out of the sampled area or a potential mixing of two different stocks. Although one would not expect the effect to be large it is impossible to determine the presence, magnitude, or direction of any bias in parameter estimates without further work to determine if seasonal migrations are occurring and to what degree.

The lack of species-specific information and failure to review historical data has allowed the decline of species such as the barndoor skate (Casey and Myers, 1998), common skate (*Dipturus batis*) (Brander, 1981), longnose skate (*Dipturus oxyrhinchus*) (Dulvy et al., 2000) and the white skate (*Rostroraja alba*) (Dulvy et al., 2000) to occur virtually unnoticed for long periods of time. Our results coupled with the relatively large numbers of observed animals and the recent increase in research survey biomass estimates (NEFSC, 2000) suggest that the barndoor skate may be more resilient to

overfishing than previously believed and that the extinction of the species on the eastern Georges Bank is not imminent. Regardless, the life history strategy of this elasmobranch still renders it much more vulnerable to overharvest than the vast majority of bony fishes.

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Table 1. Results of logarithmic probit analysis estimating length and age at 50% maturity.

Parameter being Estimated	N	N (mature)	50% Maturity Estimate	95% Confidence Intervals
Total Length:			(cm)	(cm)
Male	148	48	107.9	105.2 – 110.6
Female	142	39	116.3	114.2 – 118.5
Combined	290	87	112.4	110.2 – 114.6
Age:			(years)	(years)
Male	51	19	5.8	5.3 - 6.3
Female	35	15	6.5	6.1 - 6.9
Combined	86	34	6.0	5.7 - 6.3

Table 2. Summary of von Bertalanffy growth coefficients (k) and maximum size (L_∞) estimated for select skate species. Sexes were combined to generate estimates unless otherwise indicated.

Species	L_∞ (cm)	k (yr^{-1})	Reference
Dipturus batis	253.7	0.06	Du Buit, 1977
Dipturus laevis	166.3	0.14	This Study
Raja clavata	139.2	0.09	Ryland and Ajayi, 1984
	105	0.21	Brander and Palmer, 1985
	107.0 ♀	0.13 ♀	Holden, 1972
	85.6 ♂	0.21♂	
Raja microcellata	137.0	0.07	Ryland and Ajayi, 1984
Raja brachyura	118.4 ♀	0.19 ♀	Holden, 1972
	115.0 ♂	0.19 ♂	
Leucoraja ocellata	114.1	0.14	Simon and Frank, 1996
Raja eglantera	104.2 ♀	0.17 ♀	Gelsleichter, 1998
	95.5 ♂	0.19 ♂	
Leucoraja erinacea	52.7	0.35	Waring, 1984
Raja montagui	97.8	0.15	Ryland and Ajayi, 1984
	72.8 ♀	0.19 ♀	Holden, 1972
	68.7 ♂	0.18 ♂	

FIGURE HEADINGS

Figure 1. Location of study site (CA-2 is Closed Area II, CA-1 is Closed Area I, NLCA is Nantucket Lightship Closed Area).

Figure 2. Sectioned vertebral centrum from a 7-year-old barndoor skate. Arrows indicate growth rings. The slide was painted black to enhance image for publication.

Figure 3. Length-frequency histogram for all barndoor skates observed on Georges Bank from 1999 - 2001. Samples have been plotted in 5 cm bins (n = 2,310).

Figure 4. Allometric relationship of clasper length to total length (n = 1,126).

Figure 5. Allometric relationship of mean ova diameter and oviducal gland width to total length for the female barndoor skate (n = 142).

Figure 6. Relationship of vertebral radius to total length (n = 118).

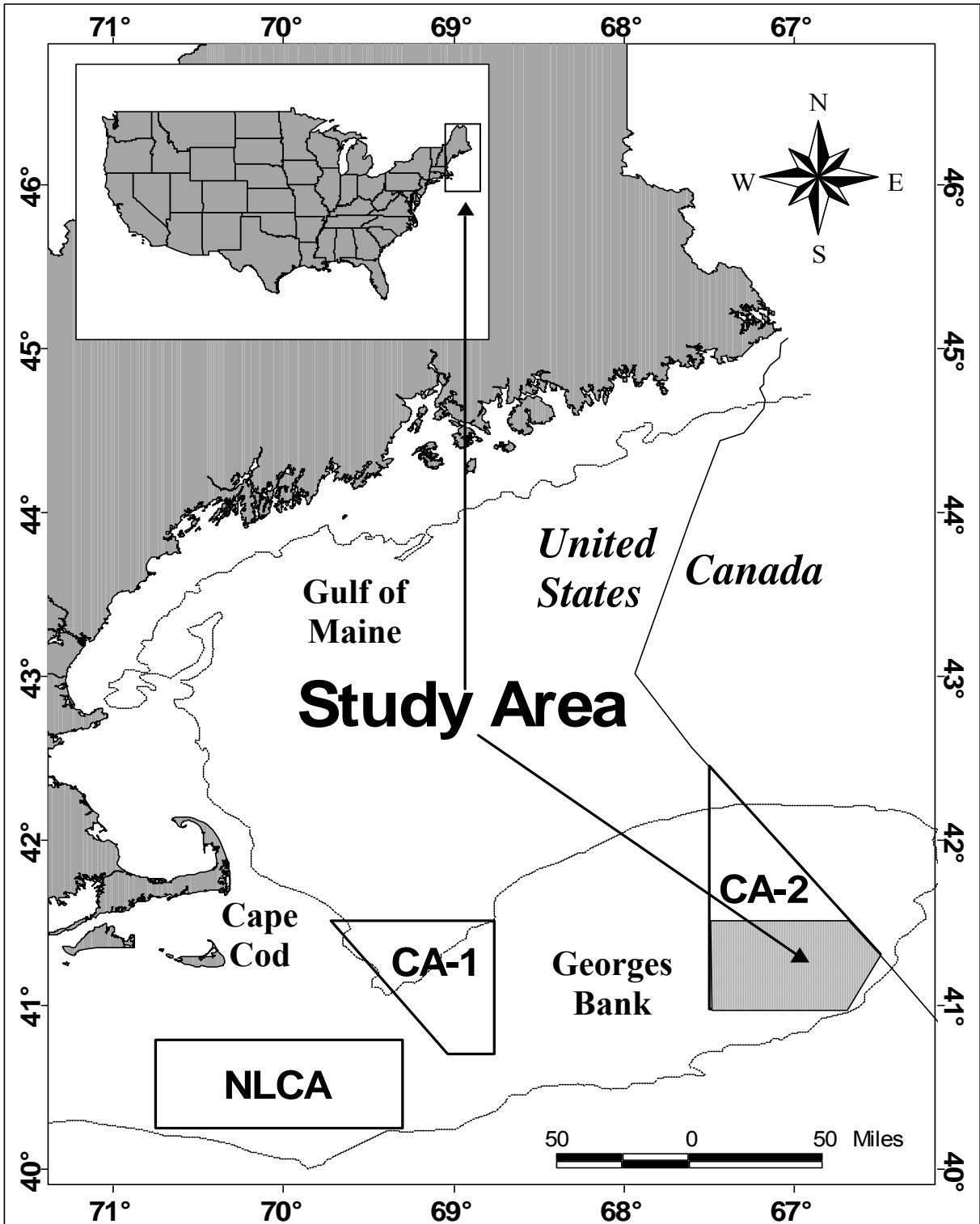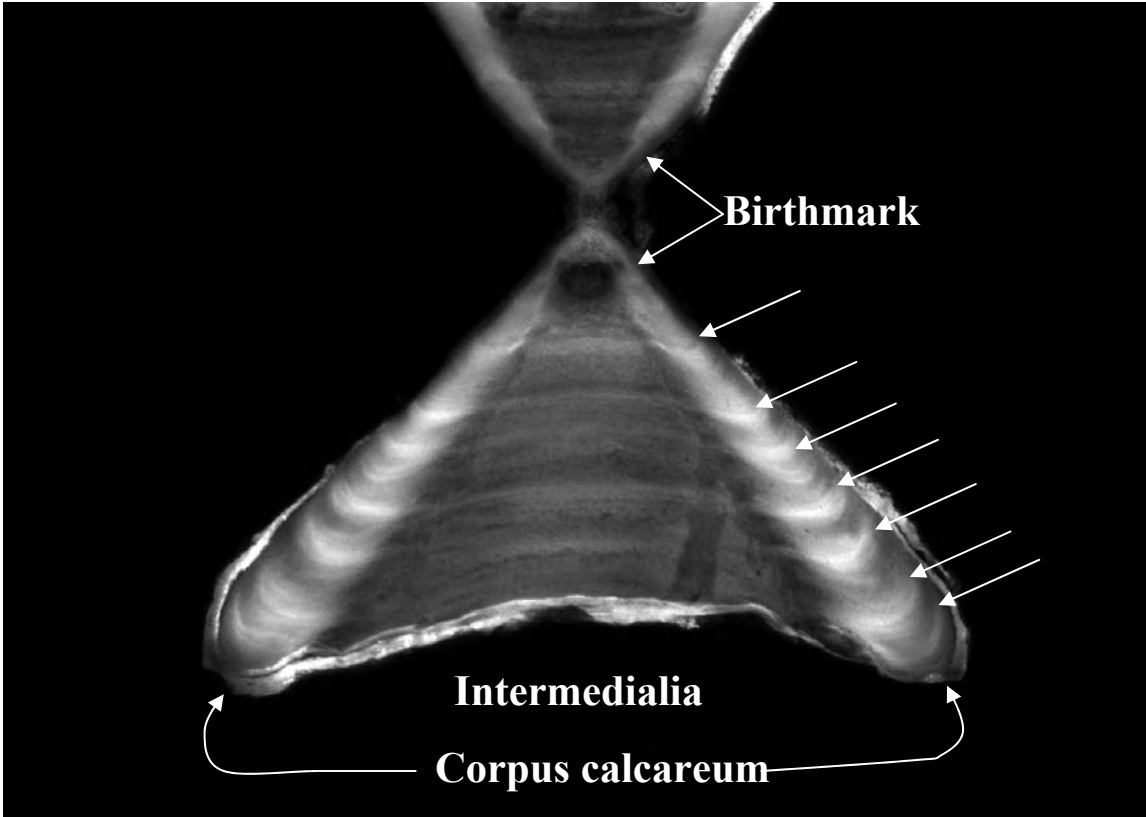Figure 7. Total length at age plot fitted with the von Bertalanffy growth curve (n = 118).
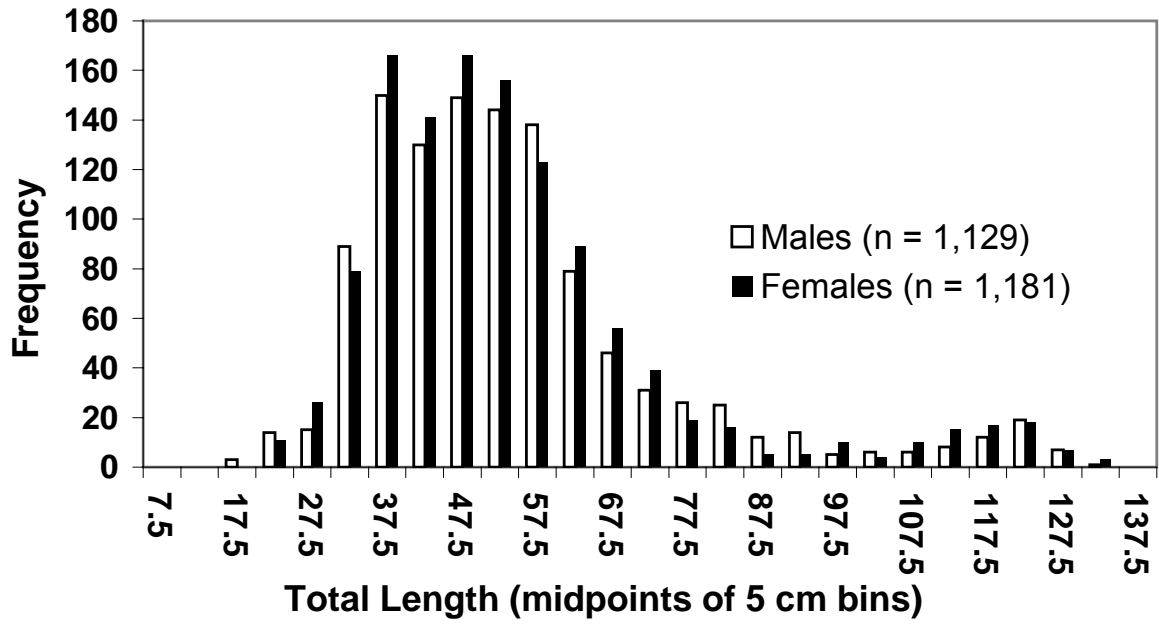
Figure 1

Birthmark

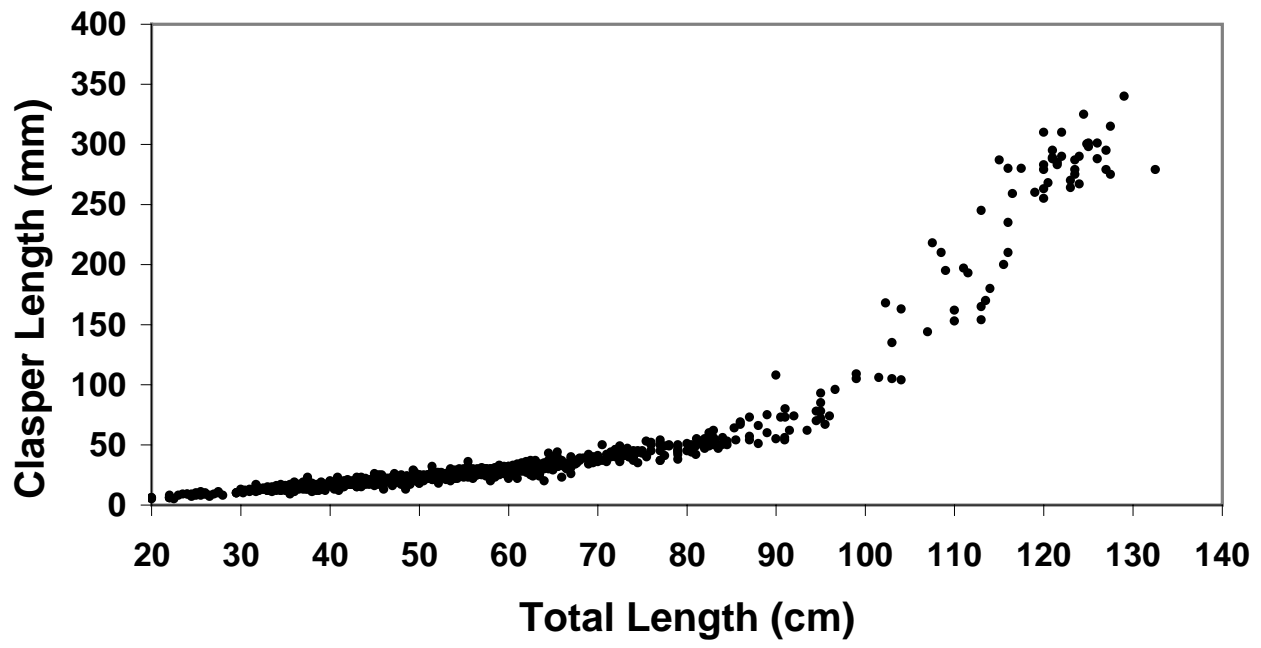**Intermedialia**

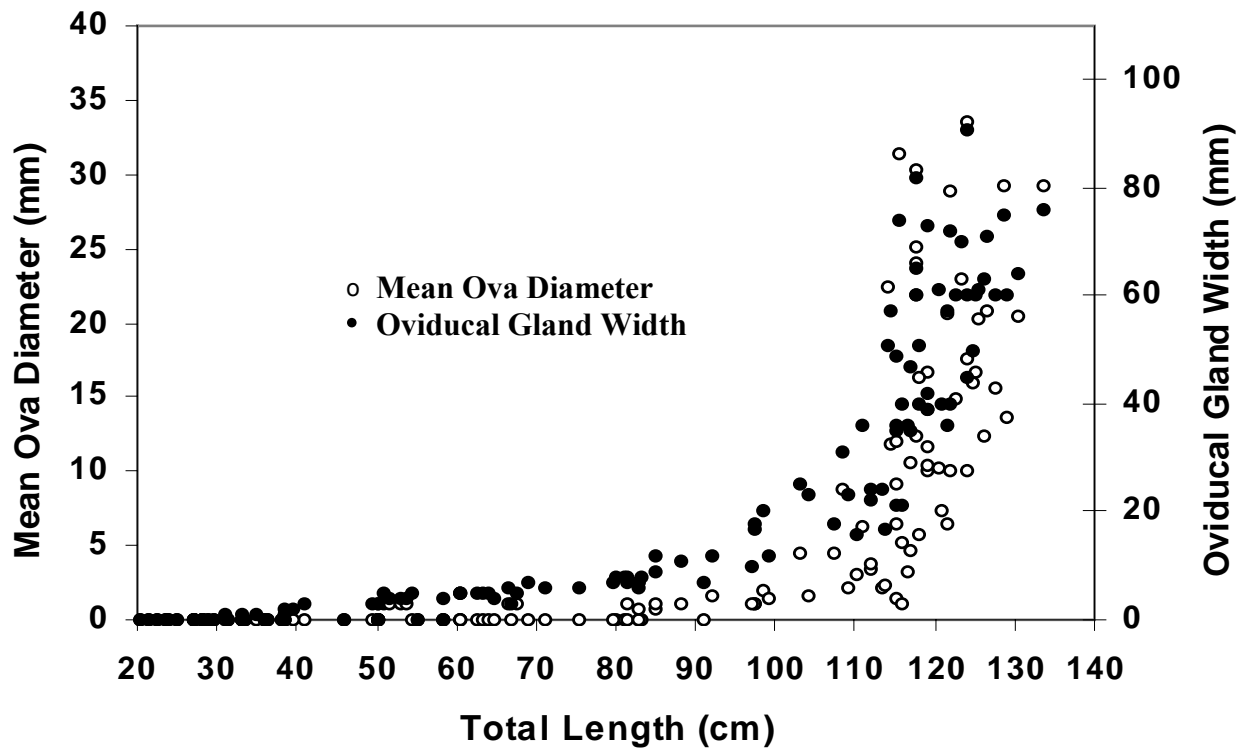**Corpus calcareum**

Figure 2

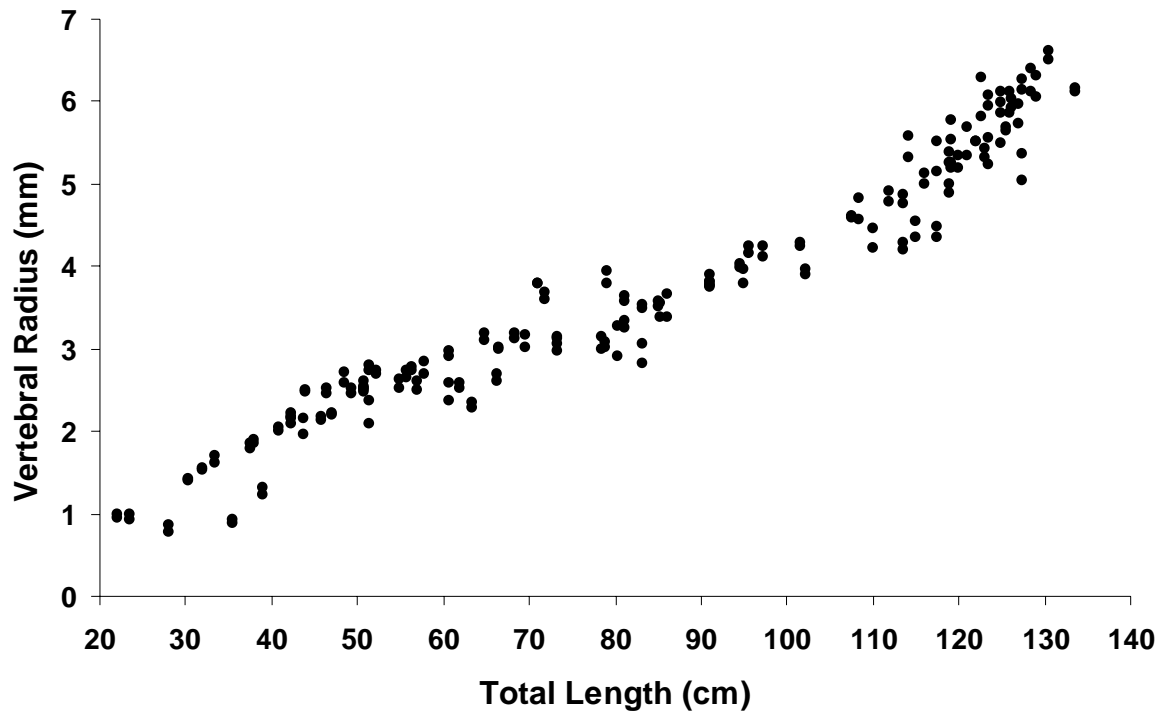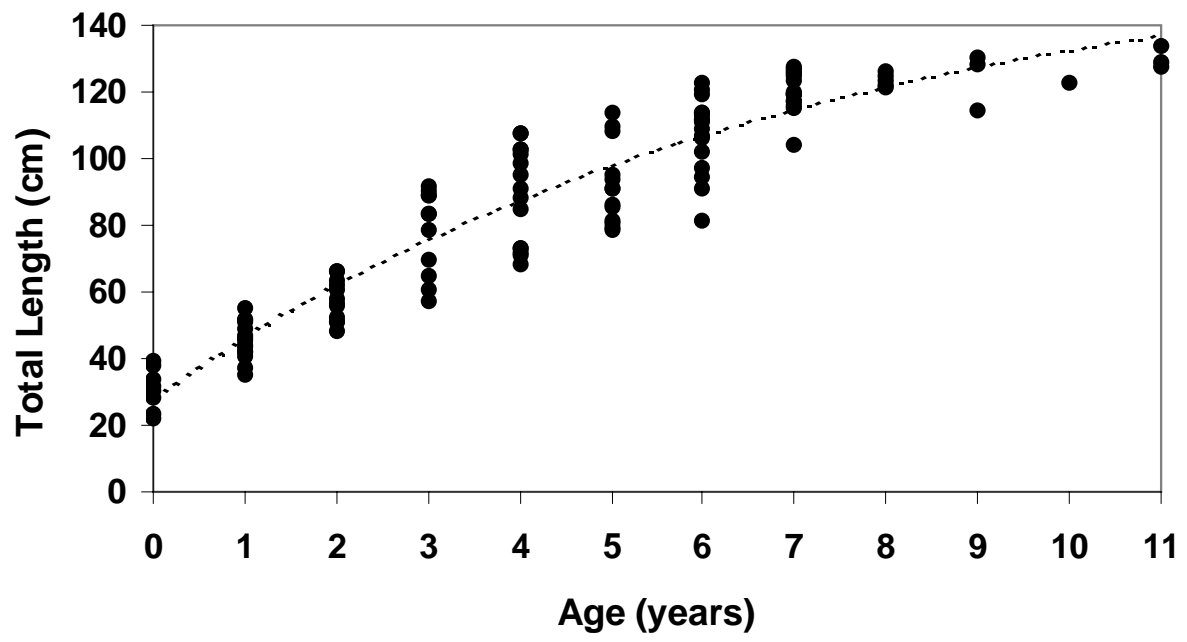Figure 3

43

Figure 4

Figure 5

Figure 6

Figure 7

Chapter 3

Ontogenetic and Sex-specific Shifts in the Feeding Habits of the Barndoor Skate

(*Dipturus laevis*) on Georges Bank

Abstract

An examination of the stomach contents of the barndoor skate (D*ipturus laevis*) was conducted on 273 individuals caught as bycatch in the commercial scallop fishery on Georges Bank. Samples were collected in 1999, 2000, and 2003 in both Georges Bank Closed Area II and the Nantucket Lightship Closed area. To study ontogenetic shifts in prey selection, a length specific analysis was conducted by calculating the mean percent weight in each stomach and then averaging these values over 10 cm length bins. A total of 31 prey items were identified with the diet dominated by sand shrimp (*Crangon septemspinosa*), the rock crab (*Cancer irroratus*), the acadian hermit crab (*Pagurus acadianus*) and teleost fish. The length specific analysis revealed that small juveniles (<35 cm total length) were specialized feeders foraging solely on Carid shrimp. With increased size (>35 cm) the diet introduced the rock crab, and at slightly greater lengths (>45 cm) the diet began to include the acadian hermit crab. At above 70 cm, no Carid shrimp were found and the prevalence of crustaceans began to decrease with size as the prevalence of teleost fish began to increase. Sex specific differences in food habits were observed in mature animals (>105cm) with males feeding primarily on teleost fish (~80%) while females maintained a diet of approximately equal amounts of fish and crustaceans. It is hypothesized that sexually dimorphic dentition results in the observed sex specific feeding patterns and differential food niche utilization.

The barndoor skate is the largest member of the family Rajidae found in the northwestern Atlantic, reaching a maximum length of 152 cm and a weight of 20 kg (Bigelow and Schroeder, 1953a). The species has been reported to range from Cape Hatteras to the Grand Banks of Newfoundland, Gulf of St. Lawrence and Nova Scotia (Leim and Scott, 1966; McEachran and Musick, 1975). It ranges from shallow coastal waters to depths greater than 450 meters and tolerates water temperatures of $1.2\text{-}20^0$ C (Bigelow and Schroeder, 1953b; McEachran and Musick, 1975; Kulka et. al., 2002)

Over the last forty years the marine ecosystems which encompasses much of the barndoor skate's primary historical range (Georges Bank and the Gulf of Maine) has experienced major changes (Fogarty and Murowski, 1998). The decline of many stocks and commercially valuable species (i.e. cod and many flatfish) has been attributed to fishing pressure. In the case of the barndoor skate (*Dipturus laevis*), overfishing was reported to be threatening the survival of the species as a whole (Casey and Myers, 1998).

As an elasmobranch, the barndoor skate was believed to be particularly vulnerable to fishing pressure due to its large size and presumed late maturation. Over the last ten years, however, a dramatic recovery in the population has been observed (Gedamke 2006). Although a reduction in fishing pressure is clearly a critical component in the recovery of the species it may only be a single factor in a more complex picture. To accurately evaluate the population dynamics of the barndoor skate, more information about its life history and trophic interactions (i.e. predator-prey relationships) must be incorporated into our analysis.

The overall life history of the barndoor skate has only recently been investigated (Gedamke et al. 2005), yet very little is known about their food habits and how they fit into the overall ecosystem. Understanding the feeding habits of the barndoor skate can bring valuable insight into predator-prey relationships and can contribute to future studies of trophic interactions (Caddy and Sharp 1986).   Limited information from descriptive studies of the Northwest Atlantic fish complex report that the barndoor skate apparently subsist mainly on benthic invertebrates as juveniles, while larger individuals eat larger and more active prey (Bigelow and Schroeder, 1953b; Mceachran and Musick, 1975; NOAA, 2003). Primary prey is believed to consist of polychaetes, copepods, amphipods, isopods, the sand shrimp *Crangon septemspinosa*, and fish such as spiny dogfish, alewife, Atlantic herring, menhaden, hakes, sculpins, cunner, tautog, sand lance, butterfish and various flounders. There is simply not enough data available to assess habitats which are critical for the feeding, growth or reproduction of the species.

The current study will provide vital information to the current closed area management strategy on Georges Bank and assist in the designation of essential fish habitat defined as "those waters and substrate necessary to fish spawning, breeding, feeding, or growth to maturity *(16 U.S.C. 1802(1*0))". Our work addresses a research need identified in both the 2001 SAFE report (NEFMC, 2001) and the recent essential fish habitat source documents (NOAA, 2003) to "investigate trophic interactions between skate species in the complex, and between skates and other groundfish."

In 1999, the commercial scallop fleet began a limited access program to the Georges Bank closed areas resulting in a unique research opportunity to investigate the food habits of the barndoor skate. This region is a historical area of high abundance and

these commercial fishing events provided a platform to sample the large number of individuals captured as bycatch.

The present study represents the first comprehensive analysis of the food habits of the barndoor skate on Georges Bank. The goals of this study are threefold: 1) to establish a basic description of the food habits 2) to evaluate the possible ontogenetic shifts in prey items and 3) to explore the possibility that sexual dimorphic mature dentition influences prey selection.

Materials and Methods

All specimens included in this study were collected onboard commercial scallop vessels on Georges Bank. A majority of the specimens were collected in the southern portion (south of 41^0 30" N) of Closed Area II while a limited number were collected from the Nantucket Lightship Closed Area (Figure 1). Both of these areas were closed to the use of mobile fishing gear in December of 1994 in an effort to rebuild groundfish stocks. In June of 1999, access to the closed areas began on a limited basis as the development of a rotational management strategy was being explored in the commercial scallop fishery. Data was collected on eight trips between June and November in 1999, 2000 and 2003. Vessels fished with two 15-foot New Bedford style sea scallop dredges (Posgay, 1957) constructed with a 10 inch mesh twine top and either 3.5 or 4 inch ring bags. Gear was towed in 55-73 meters of water at an average speed of 9.2 km/hr.

Total length, sex, and maturity stage were recorded for all specimens. Since tooth morphology in the males develops from malariform (i.e. plate-like) to cuspidate dentition (i.e. pointed teeth) at maturity, the presence or development of this secondary sexual

characteristic was noted. Entire stomachs were preserved in a solution of 10% phosphate-buffered formalin and then transferred to 70% ETOH prior to sorting. Stomachs were rinsed to remove all contents and then each prey item was identified to the lowest taxonomic level possible. To assist in the identification of teleost fishes, the museum collection at the Virginia Institute of Marine Science was utilized for comparative morphology and verification of initial identification. In addition, many of the invertebrates and fish species caught as bycatch were preserved to act as a reference library for stomach content identification. The number of individual prey items was also recorded. In cases where prey were unrecognizable by gross morphology, remaining body parts (i.e. eyes, vertebrae, shell fragments) were used to make individual prey counts.

Following sorting, samples were weighed to obtain wet weights, placed in a drying oven for at least 24 hours, and then reweighed to obtain dry weights. Plots and regressions of wet weights versus dry weights were evaluated to determine any differential patterns in the use of one metric versus the other. For an initial evaluation of feeding habits the following commonly used measures were used: 1) percent frequency (%F) was calculated as the fraction of stomachs which contained a particular prey item to the total number of stomachs sampled 2) percent abundance (%N) was calculated as the fraction of the total number of a particular prey item found in all samples to the total number of all prey items in the study, and 3) percent weight (%W) was calculated as the total weight of a prey item divided by the weight of all prey items in the study. These measures are pooled across all the samples in the study and are difficult to interpret and must be used cautiously (Chipps and Garvey, 2006; Graham et al. 2006).

Since our study contained samples from all size classes, these common measures were only used to identify which prey items were likely to be important and then a more detailed length based analysis was performed. Samples were pooled over 10 cm bins and the mean percent abundance (%MN) and mean percent weight (%MW) were calculated and used as the primary tool to evaluate feeding habits (Graham et al. 2006).   These were calculated as follows: 1) for each individual the weight (or number) of each prey item was divided by the total weight (or number) of all contents in that particular stomach to obtain percent weight (%w) or percent abundance (%n) of each prey item in each individual sample 2) the mean of these values was then calculated for each 10 cm bin to obtain the mean percent weight (%MW) or mean percent abundance (%MN).

The %MW and %MN were then plotted against the midpoint of each length bin to determine trends in food habits, while plots of %w and %n against the total length of that individual provided a visual representation of the variability in our samples.   Ontogenetic shifts in food habits were immediately obvious and prey items were grouped into larger sub-categories (shrimp, crustacean, and fish) and the analysis repeated.

Results

Stomach samples were taken from a total of 273 individuals, of which 267 (97.8%) contained prey items.   A majority (N=256) of the specimens were collected in the southern portion (south of 41^0 30" N) of Closed Area II while a limited number (N=17) were collected from the Nantucket Lightship Closed Area. Samples were taken from 137 females and 136 males ranging from 20 cm to 133.5 cm (Figure 2).

For all prey items, linear regressions of wet versus dry weights showed no pattern to the residuals and only wet weights will be referred to throughout the rest of this manuscript. A total of 31 prey items were recorded (Table 1) with two major prey groups dominating the diet: crustaceans and teleost fish. Three major individual prey items were also identified: the sand shrimp *Crangon septemspinosa,* the acadian hermit crab *Pagurus acadianus*, and the rock crab *Cancer irroratus*.

The length specific analysis showed clear ontogentic shifts in diet. Diets of the smallest individuals (20-35 cm) were dominated by a single species indicating specialization at this life stage. As size increased to 70 cm, the number of prey items increased to a mean of near 3 (ranging from 1.8 to 2.8) and remained relatively constant for the remainder of the size classes (Figure 3).

Until a size of approximately 35 cm, individual stomach samples contained only one species of Carid shrimp. Samples taken from Georges Bank Closed Area II contained only *Crangon septemspinosa* while those samples from the Nantucket Lightship Closed Area contained only *Dichelopandalus leptocerus*.   A plot of the %w of the three major prey items shows a clear shift from the utilization of these small shrimp to include the rock crab *Cancer irroratus* at approximately 35 cm (Figure 4). At around 45 cm, prey begins to include the acadian hermit crab, *Pagurus acadianus* (Figure 4). At approximately 70 cm, no Carid shrimp are found and the prevalence of the rock crab begins to decline in both males and females. At above 105 cm the diet of females continues to contain a significant amount of the acadian hermit crab while males appear to be utilizing a different food source.

Based on these initial results we sub-grouped all prey items into three categories: shrimp (containing all three species of Carid shrimp), crustaceans (except Carid shrimp), and fish (all teleosts). The patterns exhibited by the three main prey items persist and a difference in food preferences is apparent between the larger males and females. Both sexes utilize shrimp as the primary food source at the smallest sizes and begin to include crustaceans in their diet. Above 80 cm, male stomachs begin to contain slightly more teleost fish than do those of the females (Figure 5). At above 105 cm, the differences in diet between the sexes becomes more apparent (Figure 6).

For comparisons to other studies, and to show the importance of individual prey items, we recalculated %N, %W, and %F considering our new understanding of the ontogenetic shifts in food habits. Data was pooled over four size classes (0-35 cm, 35-70, 70-105, and > 105 cm) and the results are consistent with our conclusions from the graphical analysis just presented (Tables 2-5).

Discussion

The diet of *Dipturus laevis* was dominated by a limited number of prey items with clear ontogenetic shifts in food habits. Smaller animals relied entirely on benthic invertebrates while larger animals began including more fish in their diet. Previous studies on skates have elucidated similar patterns but the behavior does not appear to be consistent, even for species studied in similar geographic regions. In a study of six skate species off the South African coast, Small and Cowley (1992) described three species as crustacean feeders (*Raja miraletus*, *Raja clavata* and *Cruriraja parcomaculata*), one as a specialist piscivore throughout its size range (*Raja alba*) and two having ontogenetic

changes in feeding habits. These two species, *Raja wallacei* and *Raja pullopunctata,* exhibited a pattern consistent with our results and fed primarily on crustaceans when small and then became mainly piscivorous when large. Ontogenetic changes in diet have also been described for a number of other batoids (McEachran et al. 1976; Ajayi 1982; Orlov, 1998; Platell et al. 1998) and have been attributed to morphological constraints (e.g. gape limited, tooth morphology) or better mobility, strength and overall foraging ability of larger animals.

Our results for smaller individuals would appear to support the hypothesis of morphological constraints as distinct shifts in diet were observed. The smallest individuals were specialized feeders foraging entirely on Carid shrimp although other small prey such as crabs (*Cancer* sp.) would have been available. Only when individuals were greater than 35 cm did they include these crabs in their diet. A similar shift to include hermit crabs (*Pagurus acadianus*) was observed at approximately 45 cm. Considering that all three of these prey are relatively slow moving, relatively common (in our study area), and shouldn't require great predatory swimming speeds to capture, there must be other factors limiting the barndoor skate from utilizing these food sources. Although the size of the mouth may play a role initially, many of the smaller *Cancer* sp. crabs and *Pagurus acadianus* crabs should be available as prey items. The simplest, but not the only, explanation may be found in the relationship between growth and increased strength. The sequential addition of these prey items may be a result of the strength required to crush thicker shelled prey. It is important to note here that only a couple shell fragments were observed in our samples indicating that the shells of *Pagurus acadianus* were crushed prior to ingestion of the prey.

The most interesting aspect of the ontogenetic changes in feeding habits we observed is the sex specific habits of the largest animals. Above 105 cm males appeared to preferentially utilize teleost fish (80% by weight) rather than benthic invertebrates. The diet of large females, on the other hand, was comprised of approximately equal weights of both benthic invertebrates and fish. This sex specific change in feeding habits was evident at approximately the same size as maturity. Although there are a number of potential causes, the correlation between the size at maturity (males at 108 cm, females at 116 cm; Gedamke et al. 2005) and divergent sex-specific feeding habits is striking. One factor which is likely to play a role is a sexual dimorphism in tooth structure. At maturity, females retain their malariform (i.e. plate like) teeth while males develop cuspidate dentition (i.e. pointed teeth). The dimorphism in tooth structure in the barndoor skate was apparent by even a cursory examination of sampled jaws. We noted that the development of cuspidate dentition in the males coincided with the development of other secondary sexual characteristics (i.e. allometric growth of claspers and development of alar thorns).

In the elasmobranchs, the role of sexual dimorphic dentition is generally attributed to the reproductive behavior of the group and ability of males to grasp and hold females during mating. Males will bite prospective mates in courtship behavior and during mating to facilitate insertion of the clasper and to maintain intromission (Springer, 1960; Tricas and LeFeuvre, 1985; Carrier et al., 1994). This behavior has been documented in a number of the batoids including: the atlantic stingray *Dasyatis sabina* (Kajiura et al., 2000), the eagle ray *Aetobatis narinari* (Tricas, 1980), the roughtail stingray *Dasyatis centroura* (Reed and Gilmore, 1981), and the round stingray *Urolophus*

halleri (Nordell, 1994). Evolutionarily, the development of sexually dimorphic tooth morphology was likely to have evolved from not only the selective pressures of maximizing reproductive success but also from the selective pressures on both sexes for feeding efficiency.

It has been suggested that the strongly dimorphic tooth morphology in the Rajids represents differential niche utilization between the sexes (Feduccia and Slaughter, 1974). This phenomenon has been demonstrated in bird, anole and freshwater fish populations and results in reduced intraspecific competition for food, benefiting the population as a whole (Feduccia and Slaughter, 1974). A number of authors studying the food habits of skates have suggested or shown that dentition plays a role in feeding habits (McEachran et al. 1976; Ebert et al. 1991; Small and Cowley, 1992) but as far as the authors of this paper are aware, this has not been confirmed for any elasmobranch.

Although the correlation between divergent sex specific feeding habits and maturity in the barndoor is evident, we have not proven the cause. Although sexually dimorphic tooth structure is the simplest and likely explanation, this difference could be due to other factors. For example, mature females may simply have different dietary needs than males or the benthic feeding strategy of females conserves energy better utilized for reproduction.

In interpreting and generalizing the results of our study it is important to note three aspects of our methodology: 1) all samples were collected from a small geographic area 2) all samples were collected between June and November and 3) samples were collected on commercial vessels actively fishing in the region. The small geographic area makes the interpretation of our results easier due to a limited number of prey species.

Greater variability would have been observed if samples were taken from a larger geographic area. For example, our samples from the Nantucket Light Ship closed area contained a different species of Carid shrimp than those from Georges Bank Closed Area II. Both of the prey species, *Crangon septemspinosa* and *Dichelopandalus leptocerus*, are morphologically similar and only reach maximum carapace lengths of 12 and 20 mm, respectively (Squires 1990). In each area, the smallest barndoor skates were feeding on only one species exhibiting clear specialization. If samples had been taken from a larger number of areas, a larger number of prey species would have been recorded for each size class and interpreting the results would have been more difficult. As such, food habit studies should carefully consider the spatial aspects of sampling and resulting differences in prey availability.

Similarly, samples were only collected between June and November. Feeding patterns may be different at other times of the year. In fact, even our hypothesis about tooth morphology may have been more difficult to address if samples had been pooled over the entire year. In the Atlantic stingray, *Dasyatis Sabina*, it has been shown that the malariform morphology of the teeth in females is stable while male dentition shows a periodic shift from a female-like malariform to a recurved cuspidate form during the reproductive season (Kajiura and Tricas 1996).

Finally, while the opportunity to sample onboard commercial vessels allowed us to obtain a large number of samples, a significant amount of bycatch was also introduced into the environment. Although this may have facilitated the capture of teleost prey utilized by our sampled barndoor skate population, the differential utilization by males

and females would have persisted. Males and females were captured simultaneously in very similar abundances, and prey availability would have been constant for both sexes.

The analytical methods applied in this study were carefully chosen to not only address the problems with pooling data over large spatial scales, but also to deal with the significant limitations of pooling data over a wide range of size classes.   No one method can provide an accurate picture of the feeding habits of a species (Hyslop, 1980).   Our application of the common metrics (%N, %W, and %F) to the entire sample set allowed us to identify common prey items but the details of size-specific prey selection were obscured.   Only after a careful analysis of length-specific feeding patterns and re-analysis over distinct size classes did the ontogenetic shifts in feeding habits become apparent. The combined use of a length-specific graphic analysis and pooled metrics not only allowed for the primary population-wide food sources to be identified but also extracted a compelling picture of the specificity of food preferences at the different life stages of the barndoor skate.

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Table 1. Dietary composition of all barndoor skates *Dipturus laevis* sampled (n=273) on Georges Bank, displayed as percent by number (%N), weight (% W), and frequency of occurrence (% F).

Prey items	%N	%W	%FO
Teleost fishes			
Scomber scombrus	0.02	0.33	0.37
Clupea harengus	0.59	10.90	6.59
Myoxocephalus sp.	0.43	5.15	5.13
Urophycis sp.	0.21	6.40	3.30
Urophycis chuss	0.12	5.91	1.10
Macrozoarces americanus	0.14	14.82	2.20
Limanda ferruginea	0.15	2.51	0.73
Paralichthys dentatus	0.02	0.98	0.37
Peprilus triacanthus	0.02	0.34	0.37
Hemitripterus americanus	0.05	1.38	0.73
Paralichthys oblongus	0.07	1.72	0.73
Unidentified fish	0.05	3.32	7.33
Unidentified flatfish	0.17	2.94	2.20
Crustacea			
Carid shrimps			
Crangon septemspinosa	34.61	1.64	38.83
Pandalus propinquus	0.66	0.01	2.20
Dichelopandalus leptocerus	2.44	0.12	4.76
Pagurid crabs			
Pagurus acadianus	20.79	14.43	38.46
Pagurus pubescens	0.05	0.01	0.73
Cancer crabs			
Cancer irroratus	29.60	17.83	54.95
Cancer borealis	2.13	4.14	6.59
Cancer sp.	0.12	0.06	0.37
Other			
Unidentified crab	0.43	0.31	4.40
Unidentified decapod	0.28	0.19	4.40
Unidentified amphipod	1.11	0.08	1.83
Unidentified isopod	0.66	0.04	1.83
Unidentified barnacle	0.02	0.00	0.37
Mollusca			
Unidentified snail	1.07	0.08	8.06
Unidentified bivalve	0.05	0.00	0.73
Nematoda			
Unidentified nematode	2.47	0.02	13.19
Trematoda			
Unidentified trematode	0.07	0.00	0.37
Unidentified Organic Matter	0.92	3.62	14.29

Table 2. Dietary composition of barndoor skates *Dipturus laevis* (0 – 35 cm total length) sampled (n=25) on Georges Bank, displayed as percent by number (%N), weight (%W), and frequency of occurrence (% F).

Prey items	%N		%W		%FO	
	M	F	M	F	M	F
Crustacea						
Carid shrimps						
Crangon septemspinosa	65.35	80.53	89.70	50.94	53.33	70.00
Dichelopandalus leptocerus	33.66	16.81	8.37	48.21	26.67	30.00
Cancer crabs						
Cancer irroratus	-	0.88	1.84	-	-	10.00
Other						
Unidentified crab	0.99	-	-	0.85	6.67	-
Nematoda						
Unidentified nematode	-	1.77	0.09	-	-	10.00

Table 3. Dietary composition of barndoor skates *Dipturus laevis* (35 – 70 cm total length) sampled (n=126) on Georges Bank, displayed as percent by number (%N), weight (%W), and frequency of occurrence (% F).

Prey items	%N		%W		%FO	
	M	F	M	F	M	F
Teleost fishes						
Unidentified fish	0.08	0.07	0.00	0.05	1.72	1.45
Unidentified flatfish	-	0.14	-	0.03	-	1.45
Crustacea						
Carid shrimps						
Crangon septemspinosa	53.97	42.94	18.68	9.86	74.14	60.87
Pandalus propinquus	0.08	1.63	0.09	0.09	24.14	4.35
Dichelopandalus leptocerus	1.57	1.63	0.89	0.23	1.72	4.35
Pagurid crabs						
Pagurus acadianus	5.54	13.50	8.78	23.28	24.14	40.58
Pagurus pubescens	-	0.07	-	0.04	-	1.45
Cancer crabs						
Cancer irroratus	35.29	33.72	62.51	60.27	77.59	69.57
Cancer borealis	1.32	2.17	2.01	4.56	3.45	4.35
Cancer sp.	0.41	-	1.29	-	1.72	-
Other						
Unidentified crab	0.08	0.20	0.15	0.01	1.72	1.45
Unidentified isopod	-	0.34	-	0.05	-	2.90
Mollusca						
Unidentified snail	0.17	0.81	0.03	0.07	1.72	8.70
Unidentified bivalve	0.08	-	0.03	-	1.72	-
Nematoda						
Unidentified nematode	0.91	2.37	0.08	0.05	10.34	17.39
Unidentified Organic Matter	0.50	0.41	5.46	1.40	10.34	8.70

Table 4. Dietary composition of barndoor skates *Dipturus laevis* (70 – 105 cm total length) sampled (n=52) on Georges Bank, displayed as percent by number (%N), weight (%W), and frequency of occurrence (% F).

Prey items	%N M	%N F	%W M	%W F	%FO M	%FO F
Teleost fishes						
Clupea harengus	0.78	1.00	10.56	8.38	5.03	11.11
Myoxocephalus sp.	0.39	-	4.67	-	6.06	-
Urophycis sp.	0.39	1.00	3.96	12.60	6.06	11.11
Urophycis chuss	0.58	-	11.08	-	3.03	-
Macrozoarces americanus	0.19	-	26.31	-	3.03	-
Peprilus triacanthus	0.19	-	1.58	-	3.03	-
Hemitripterus americanus	-	0.50	-	14.66	-	5.56
Unidentified fish	0.97	-	1.94	-	12.12	-
Crustacea						
Carid shrimps						
Crangon septemspinosa	1.17	2.00	0.03	0.02	9.09	5.56
Pandalus propinquus	-	0.50	-	0.01	-	5.56
Dichelopandalus leptocerus	-	1.50	-	0.17	-	5.56
Pagurid crabs						
Pagurus acadianus	49.12	32.00	15.83	10.46	57.58	66.67
Cancer crabs						
Cancer irroratus	34.50	41.50	18.55	28.38	63.64	77.78
Cancer borealis	1.36	10.00	1.11	14.68	9.09	22.22
Other						
Unidentified crab	0.19	1.00	0.28	0.28	3.03	11.11
Unidentified decapod	0.39	1.00	0.01	0.01	6.06	11.11
Mollusca						
Unidentified snail	2.53	2.00	0.05	0.19	15.15	11.11
Unidentified bivalve	0.19	-	0.00	-	3.03	-
Nematoda						
Unidentified nematode	5.26	1.00	0.01	0.01	24.24	11.11
Unidentified Organic Matter	1.75	5.00	4.01	10.13	27.27	55.56

Table 5. Dietary composition of barndoor skates *Dipturus laevis* (> 105 cm total length) sampled (n=70) on Georges Bank, displayed as percent by number (%N), weight (%W), and frequency of occurrence (% F).

Prey items	%N M	%N F	%W M	%W F	%FO M	%FO F
Teleost fishes						
Scomber scombrus	0.50	-	1.48	-	3.33	-
Clupea harengus	3.94	2.7	13.32	13.92	23.33	20.00
Myoxocephalus sp.	6.97	0.49	13.36	3.25	33.33	5.00
Urophycis sp.	1.49	0.49	10.34	5.88	10.00	5.00
Urophycis chuss	1.00	-	15.68	-	6.67	-
Macrozoarces americanus	1.00	0.74	15.42	16.33	6.67	7.5
Limanda ferruginea	0.50	0.25	4.29	4.42	3.33	2.5
Paralichthys dentatus	-	0.25	-	2.79	-	2.5
Hemitripterus americanus	0.50	-	0.13	-	3.33	-
Paralichthys oblongus	1.49	-	7.65	-	6.67	-
Unidentified fish	5.47	1.97	8.06	5.15	36.66	20.00
Unidentified flatfish	1.49	0.49	4.89	5.26	10.00	5.00
Crustacea						
Carid shrimps						
Crangon septemspinosa	2.99	0.25	0.00	0.00	3.33	2.50
Pandalus propinquus	1.00	-	0.01	-	3.33	-
Dichelopandalus leptocerus	1.99	-	0.03	-	3.33	-
Pagurid crabs						
Pagurus acadianus	8.96	68.06	1.02	22.11	20.00	65.00
Cancer crabs						
Cancer irroratus	8.96	11.30	2.87	9.81	20.00	37.50
Cancer borealis	0.50	3.44	0.23	5.92	3.33	12.50
Other						
Unidentified crab	3.48	0.74	0.47	0.33	13.33	5.00
Unidentified decapod	1.00	1.47	0.01	0.52	6.67	15.00
Unidentified amphipod	23.38	-	0.35	-	16.67	-
Unidentified isopod	9.95	0.74	0.14	0.01	6.67	2.50
Unidentified barnacle	-	0.25	-	0.01	-	2.50
Mollusca						
Unidentified snail	-	3.44	-	0.13	-	20.00
Nematoda						
Unidentified nematode	10.95	1.23	0.00	0.03	13.33	7.50
Trematoda						
Unidentified trematode	1.49	-	0.00	-	3.33	-
Unidentified Organic Matter	1.00	1.47	0.25	4.11	6.67	15.00
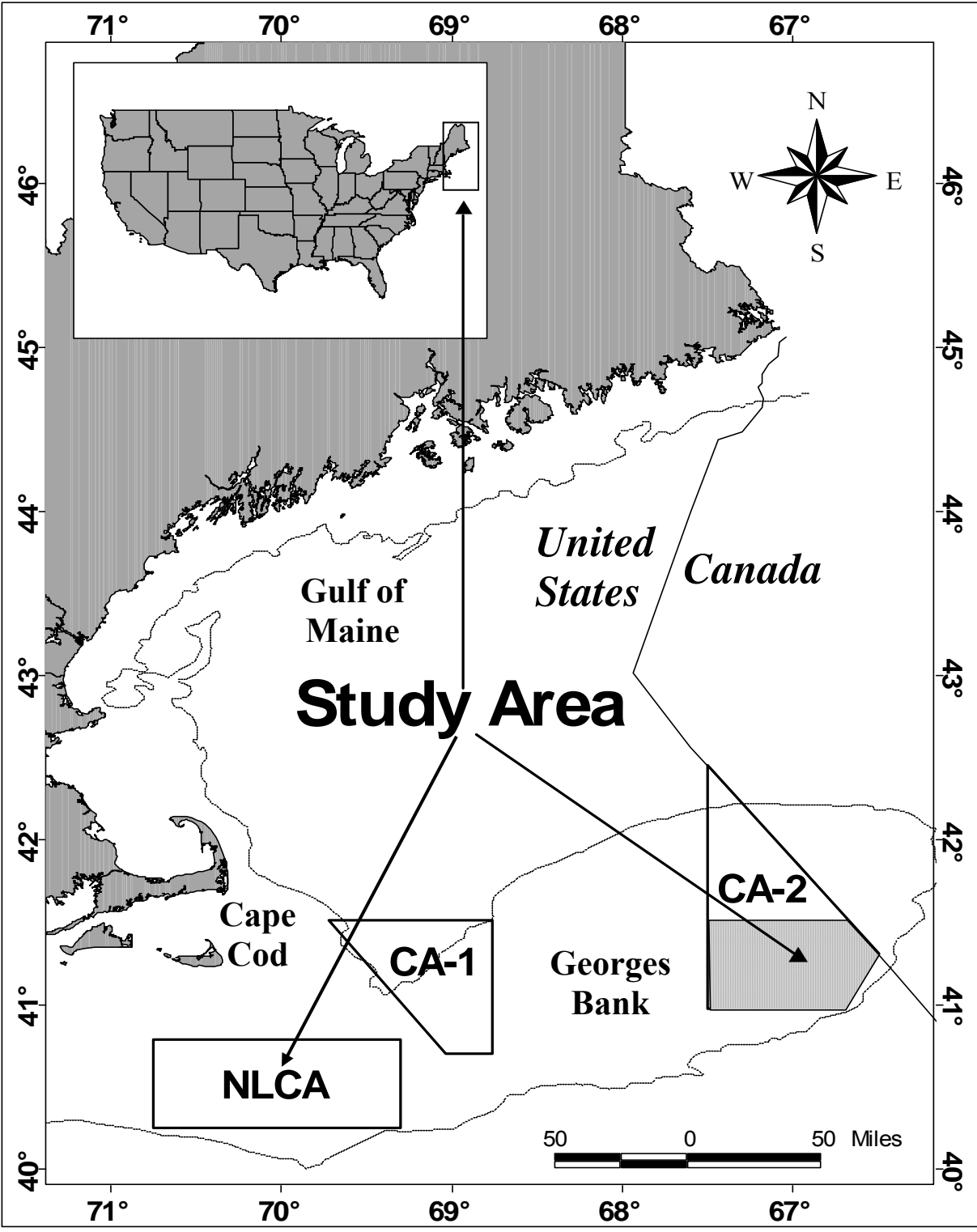
Figure 1. Sample Locations. CA-2 is Georges Bank closed Area II, CA-1 is Georges Bank Closed Area I, and NLCA is Nantucket Lightship Closed Area
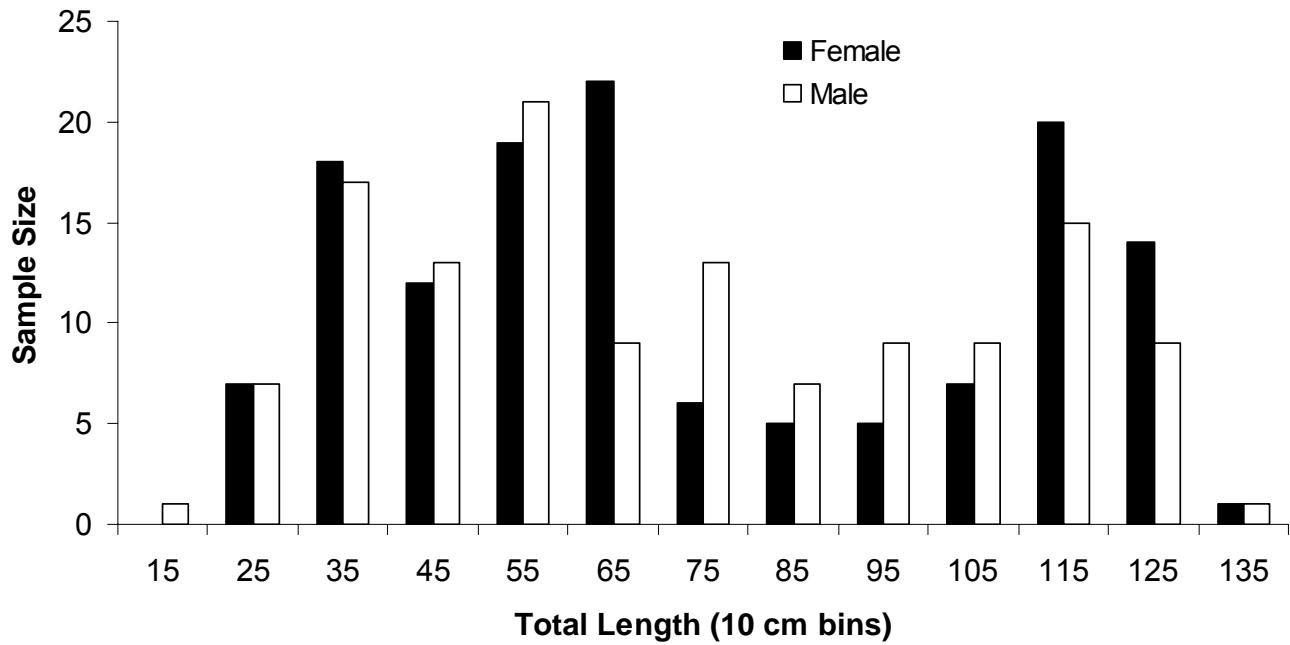
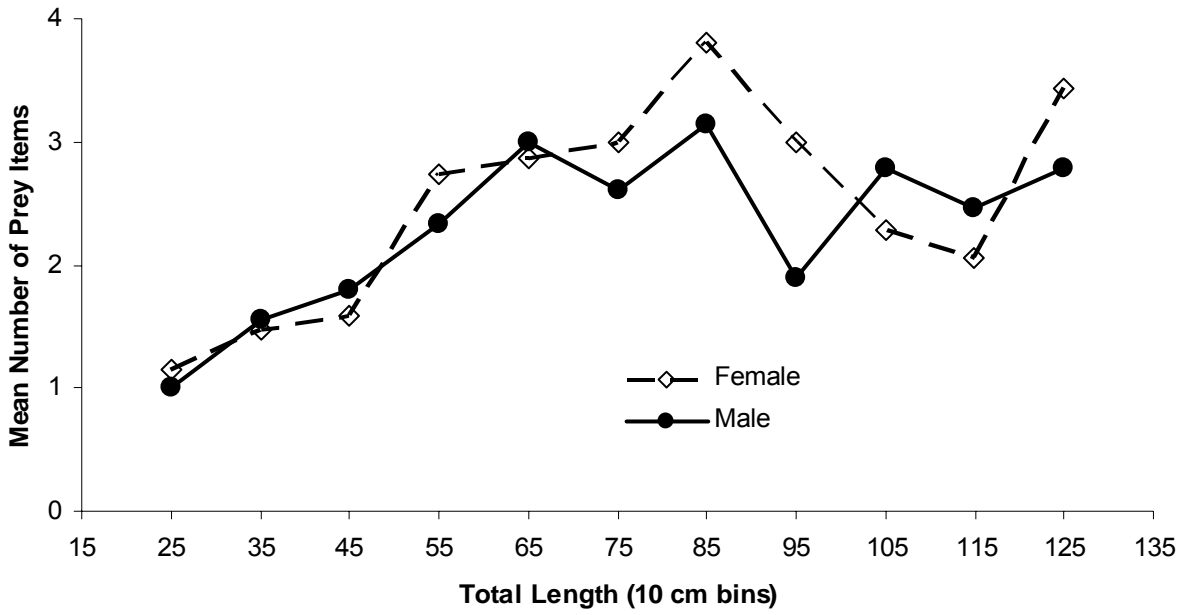Figure 2. Number of samples by sex for each 10 cm length bin.

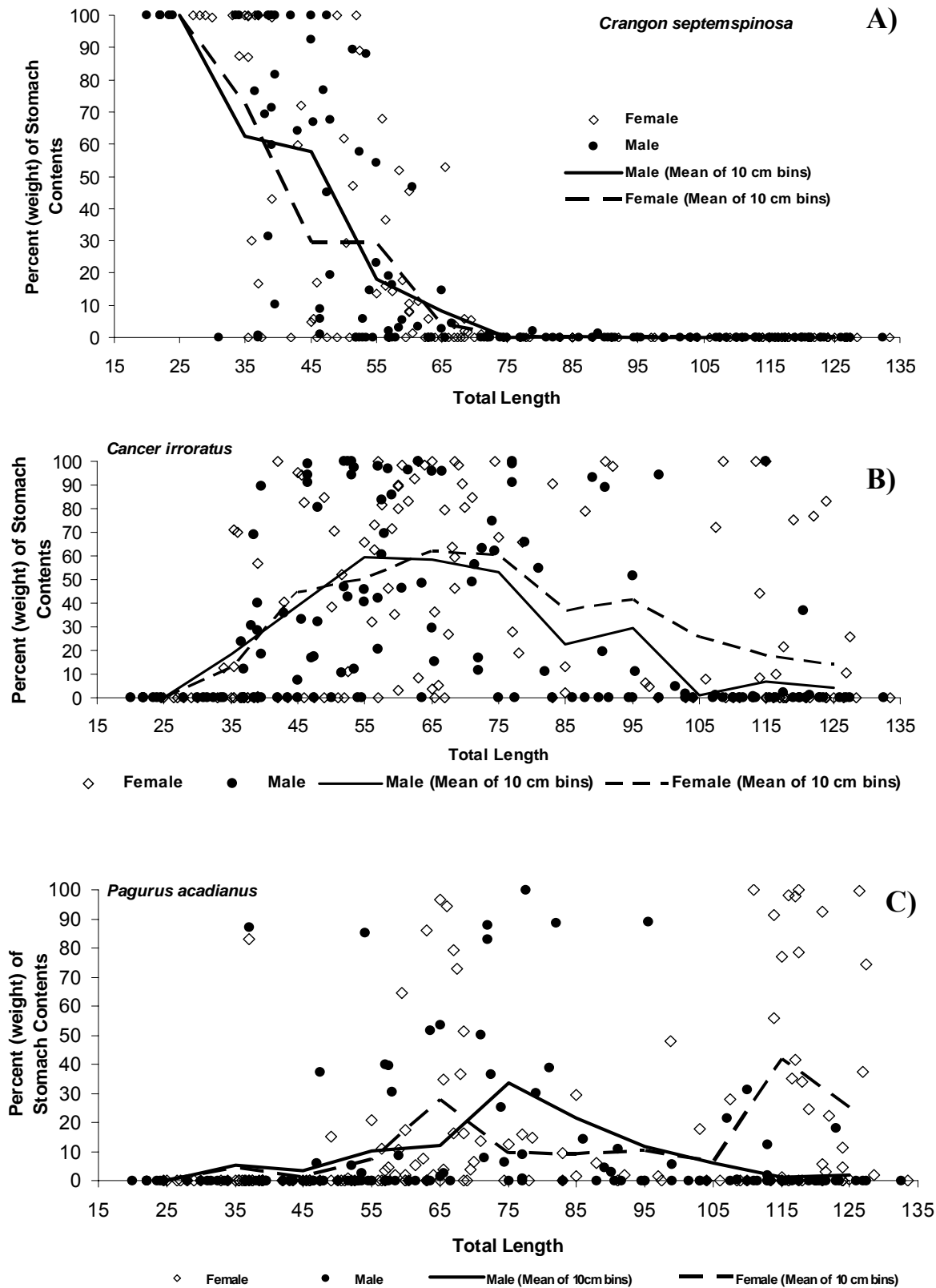Figure 3. Mean number of prey items per stomach in each 10 cm length bins.

Figure 4. Percent by weight of three major prey items. A) *Crangon septemspinosa* B) *Cancer irroratus* C) *Pagurus acadianus*. Solid circles (males) and diamonds (females) represent percent weight in individual stomachs. Solid line (male) and dashed line (female) represent mean percent weight of each length bin.
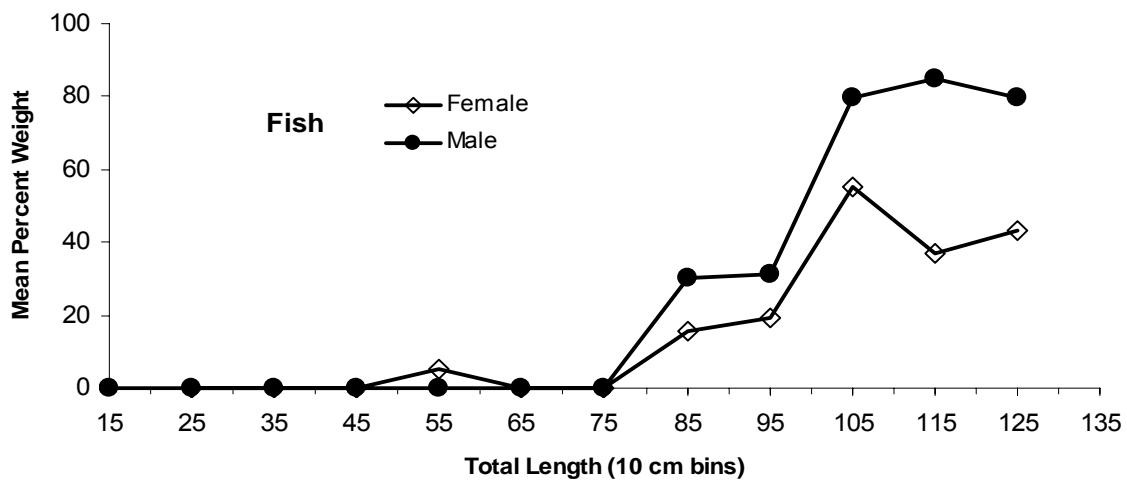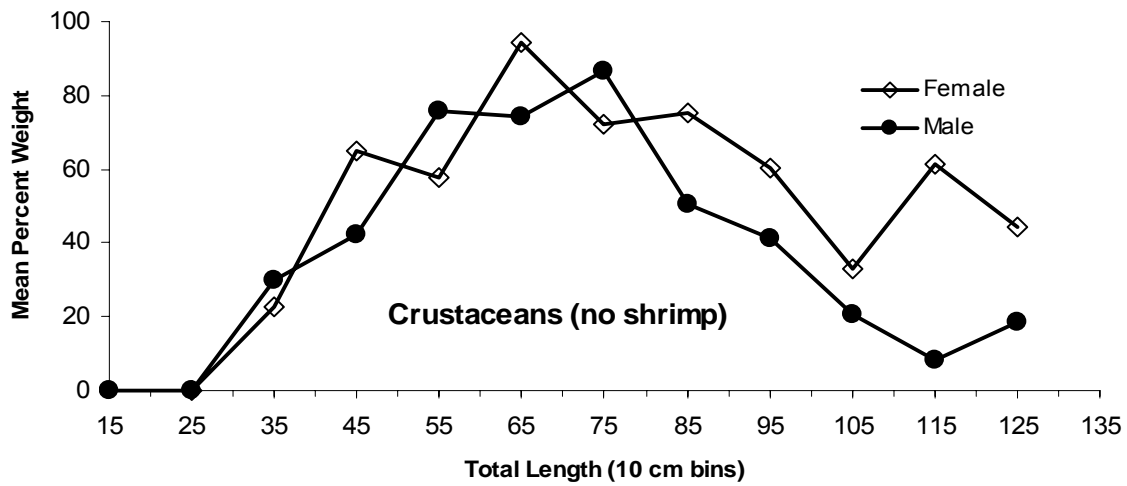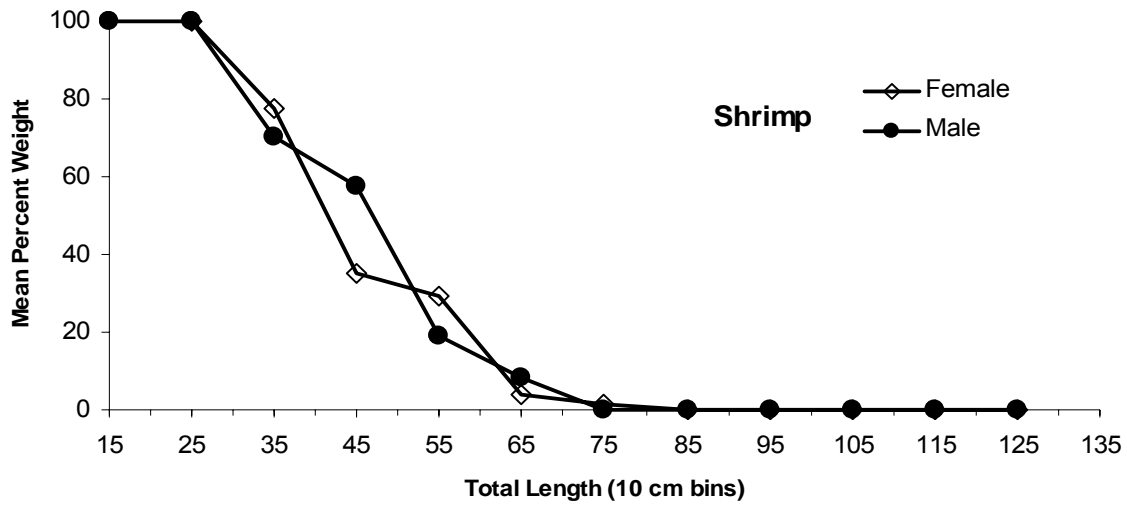
Figure 5. Mean percent weight of each prey sub-category for each 10 cm length bin
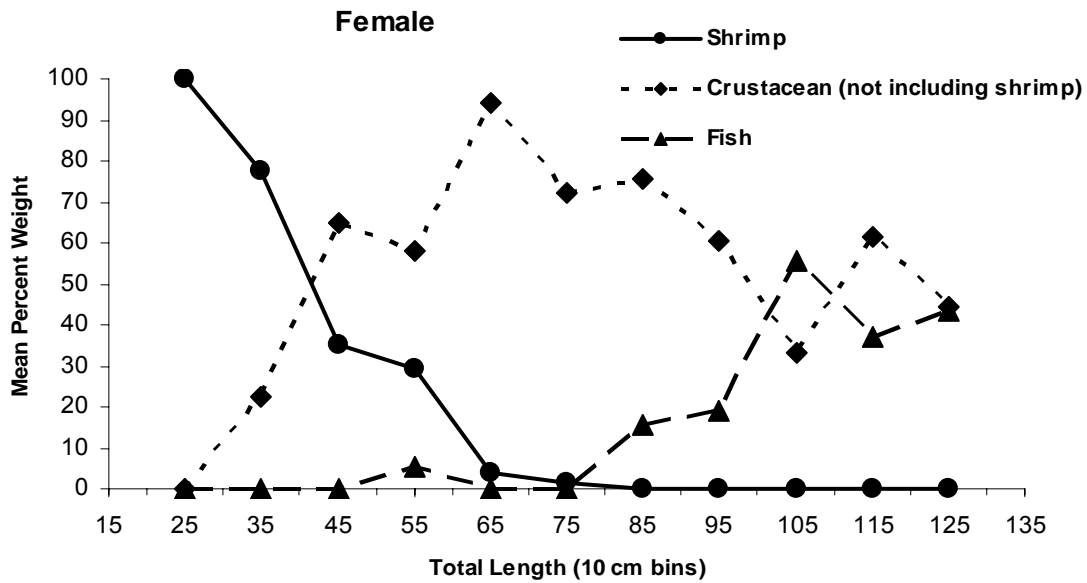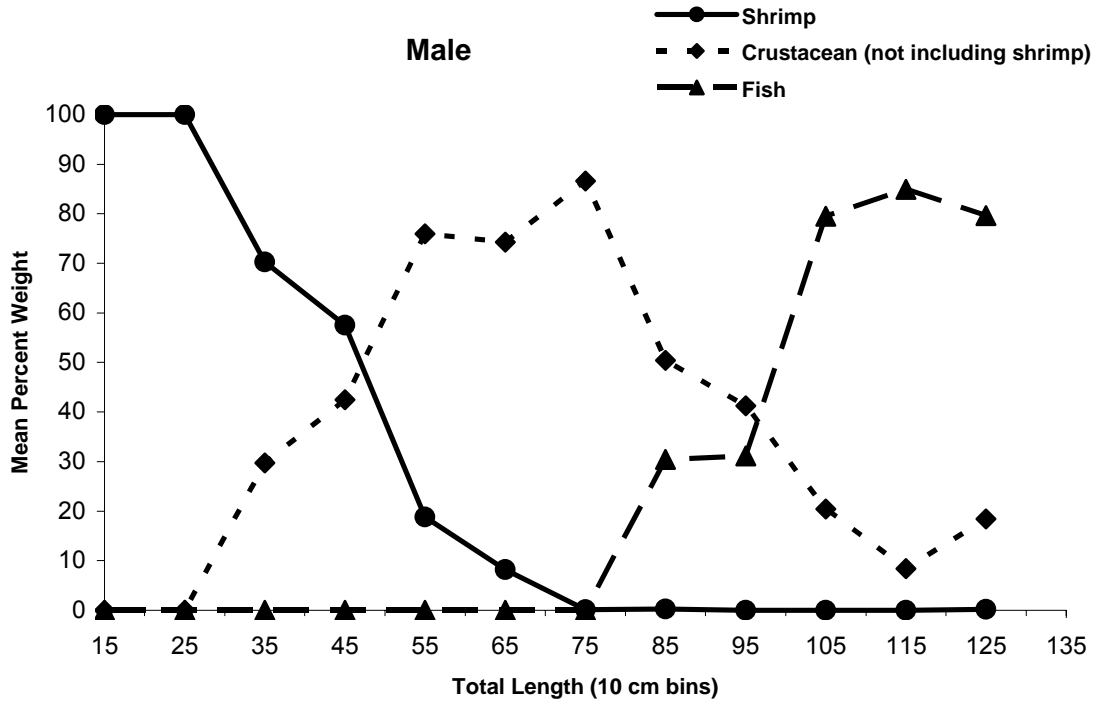
Figure 6. Mean percent weight of each prey sub-category, by sex, for each 10 cm length bin

Chapter 4

Estimating Mortality from Mean Length Data in Non-equilibrium Situations, with Application to the Assessment of Goosefish (*Lophius americanus*)

Abstract

The Beverton-Holt length-based mortality estimator has received widespread use primarily due to its applicability in data-limited situations. The mean length of animals fully vulnerable to the sampling gear can be used to estimate total mortality using only basic growth parameters and a known length at first capture. This method requires equilibrium conditions because the mean length of a population will change only gradually following a change in mortality. In this study, we derive the transitional behavior of the mean length statistic for use in non-equilibrium conditions. We investigate conditions affecting the reliability of the Beverton-Holt results and then develop a new procedure that allows a series of mortality rates to be estimated from mean length data representing non-equilibrium conditions in multiple years. We then examine the goosefish (*Lophius americanus*) assessment which was criticized for its use of the Beverton-Holt estimator under non-equilibrium conditions. Using data from the 1963-2002 National Marine Fisheries Service annual fall groundfish surveys off the Northeast United States, and assuming a single change in total mortality, we estimated using the method of maximum-likelihood that total mortality of goosefish in the southern assessment region increased from 0.31 to 0.60 yr^{-1} in 1977. Estimates of the new mortality rate made 3 or more years after the change were relatively stable and ranged only from 0.55 to 0.71 yr^{-1} while estimates from the standard Beverton-Holt approach ranged from 0.37 to 1.1 yr^{-1}. The results for goosefish in the northern assessment region showed changes in total mortality from 0.14 to 0.29 yr^{-1} in 1978 and then to 0.55 yr^{-1} in 1987.   The new, non-equilibrium estimator allows a change in mortality to be characterized reliably several years faster than if the Beverton-Holt estimator is used.

Baranov (1918, cited in Ricker (1975)) was apparently the first to deduce that equilibrium mean length in a fish population is inversely related to the mortality rate experienced by the population. Beverton and Holt (1956, 1957) observed the same thing for a more realistic situation where length is an asymptotic, rather than linear, function of time. They also derived an expression for estimating the total instantaneous mortality rate, Z, from the mean length, $\overline{L}$.

The Beverton-Holt mortality estimator has received widespread use, especially in data-limited situations, because the only required information is the von Bertalanffy growth parameters K and L_∞, the so-called length of first capture (smallest size at which animals are fully vulnerable to the fishery and to the sampling gear), L_c, and the mean length of the animals above the length L_c.

The Beverton-Holt mortality estimator is based on the assumption of equilibrium conditions. Hilborn and Walters (1992, p. 426) presented a graph showing the transitional behavior of a similar estimator when the population experiences a change in total mortality to a higher level. Essentially, if the mortality estimator is applied continually to mean length data over time, the resulting estimates will show a gradual increase over time and will approach the true (new) value as the new equilibrium condition is approached. Hilborn and Walters used this example merely to illustrate the pitfalls of applying analytical techniques based on assumptions of equilibrium to situations where the assumption is not met. They did not present any expression to describe the transitional behavior of the estimator and obtained their results by simulation.

In this study, we derive the transitional behavior of the mean length statistic for use in non-equilibrium conditions. We investigate conditions affecting the reliability of

the Beverton-Holt results and then develop a new procedure that allows a series of

mortality rates to be estimated from mean length data representing non-equilibrium

conditions from multiple years. We then examine the northeast United States goosefish

(*Lophius americanus*) assessment which was criticized for its use of the Beverton-Holt

estimator under non-equilibrium conditions. Data from the 1963-2002 National Marine

Fisheries Service (NMFS) annual fall groundfish surveys off the Northeast United States

were analyzed using the method of maximum-likelihood to estimate the years in which

changes in mortality occurred, and to reconstruct the mortality history.

The Beverton-Holt Estimator

Assume deterministic asymptotic growth as described by the von Bertalanffy

equation

$$L_t = L_\infty(1 - \exp(-K(t - t_o))) \tag{1}$$

where L_t is the length at age t, and L_∞, K and t_o are the parameters. Also assume that the

instantaneous total mortality rate is constant over time and over age for all ages $t > t_c$,

where t_c is the age at which animals are fully vulnerable to the fishery and to the

sampling gear. Denote this mortality rate by Z yr^{-1}. Further, assume that recruitment is

continuous over time at constant rate R. The mean length of those animals above the

length L_c corresponding to the age t_c is

$$\overline{L} = \frac{\int_{t_c}^{\infty} N_t L_t dt}{\int_{t_c}^{\infty} N_t dt}$$

$$\tag{2}$$

where L_t is given by (1) and $N_t = R \exp(-Z(t-t_c))$. Performing the integrations in (2) and simplifying yields

$$\overline{L} = L_\infty(1 - \frac{Z}{Z+K}\exp(-K(t_c - t_o))) \quad.$$

(3)

Equation (3) is easily solved for the mortality rate. Thus,

$$Z = \frac{K(L_\infty - \overline{L})}{\overline{L} - L_c} \quad.$$

(4)

Note that the parameter t_o has been eliminated from the solution through algebraic manipulation using equation (1).

There are six assumptions behind this method.

1) Asymptotic growth with known parameters K and L_∞ which are constant over time.

2) No individual variability in growth.

3) Constant and continuous recruitment over time.

4) Mortality rate is constant with age for all ages $t > t_c$.

5) Mortality rate is constant over time.

6) Population is in equilibrium (i.e., enough time has passed following any change in mortality that mean length now reflects the new mortality level).

Some of these assumptions will be considered further in the discussion section.

Transitional Behavior

We now deal with the situation when assumption 6 is violated. Suppose the mean length in a population is determined d years after a permanent change in total mortality from Z_1 to Z_2 yr^{-1}. Let $g = t_c + d$. The mean length in the population d years after the change in mortality is

$$\bar{L} = \frac{\int_{t_c}^{g} R\exp(-Z_2(t-t_c))L_t dt + \int_{g}^{\infty} R\exp(-Z_2 d)\exp(-Z_1(t-g))L_t dt}{\int_{t_c}^{g} R\exp(-Z_2(t-t_c))dt + \int_{g}^{\infty} R\exp(-Z_2 d)\exp(-Z_1(t-g))dt} \ . \quad (5)$$

In the numerator and the denominator, the integrals on the left represent fish recruited after the change in mortality – these animals have experienced just the mortality rate Z_2. The integrals on the right represent fish that were recruited before the change in mortality – these fish have experienced both the old and the new mortality rates.

After integration and simplification (see Appendix A) we obtain

$$\bar{L} = L_{\infty} - \frac{Z_1 Z_2 (L_{\infty} - L_c)\{Z_1 + K + (Z_2 - Z_1)\exp(-(Z_2 + K)d)\}}{(Z_1 + K)(Z_2 + K)(Z_1 + (Z_2 - Z_1)\exp(-Z_2 d))} \ . \quad (6)$$

Note that when $d = 0$ equation (6) provides the equilibrium mean length for the case where $Z = Z_1$, as expected. As d approaches infinity, equation (6) provides results approaching the equilibrium mean length when $Z = Z_2$, as expected. And when $Z_1 = Z_2$, equation (6) gives the same result as equation (3). In appendix B, we generalize equations (5) and (6) to allow for multiple changes in mortality rate over time.

Thus, for any amount of elapsed time after a known change in mortality, we can determine the mean length in the population and, by inserting this value into equation (4), we can determine how the Beverton-Holt estimator responds. We examined the effect of

the von Bertalanffy parameter K on the estimates for the case where Z increased suddenly from 0.4 to 1.0 yr^{-1} (Figure 1). The estimates approach the new equilibrium value faster when K is higher. Thus, after three years, the estimate reflects 76% of the increase in Z when K = 0.1, 83% of the increase when K = 0.5, and 87% when K = 1.0 yr^{-1}. Changing the value of L_∞, while holding K and L_c constant, has no effect on the rate at which the estimator approaches equilibrium.

The time to reach equilibrium is also dependant on the magnitude and direction of the change in mortality (Table 1). The time to reach equilibrium is greatest when fishing pressure has been significantly reduced to near virgin levels. In this scenario, only growth over time can restore the original population structure and affect the mean length. On the other hand, the response to increases in fishing pressure occurs more rapidly as the removal of the larger older animals has an immediate affect on the mean length of the population.

Estimation in non-equilibrium situations

Estimation of mortality rates in non-equilibrium situations can be accomplished by selecting the year of change and the value of Z_1 and Z_2 that cause predicted mean lengths from equation (6) to best match a time series of estimated mean lengths. We use the method of maximum likelihood estimation. The probability density function of a normally distributed sample mean $\bar{x}$, when the sample size is m, is

$$f\left(x\,;\mu\,,\sigma^{2}\right) = \frac{\sqrt{m}}{\sqrt{2\pi\sigma^{2}}} \cdot e^{-\frac{m}{2\sigma^{2}}\cdot(\bar{x}-\mu)^{2}}. \qquad (7)$$

The product likelihood function (Λ) for n years of observed mean lengths results by

substitution with (6): $\mu = E(\bar{L})$, $\sigma^2 = \text{Var(L)} = $ variance of lengths that are greater than

L_c. Thus,

$$\Lambda = \prod_{y=1}^{n} \frac{m_y}{\sqrt{2\pi\sigma^2}} \cdot e^{-\frac{m_y}{2\sigma^2}\cdot[\bar{L}_y - L_{pred,y}]^2} \tag{8}$$

where m_y is the number of fish greater than size L_c measured in year y, $\bar{L}_y$ is the

observed mean length in year y, and $L_{pred,y}$ is the mean length computed using equation

(6) or, more generally, from Appendix equation (B1). The log-likelihood is proportional

to

$$\ln(\Lambda) \propto -n \cdot (\ln\sigma) - \frac{1}{2\sigma^2} \cdot \sum_{y=1}^{n} m_y \cdot [\bar{L}_y - L_{pred,y}]^2 \quad . \tag{9}$$

Equation (9) was maximized, and confidence intervals generated for each variable, using

the PROC NLP procedure in SAS version 8 (SAS, 1999). The year in which the

mortality change occurred was specified and Z_1, Z_2, and the variance (σ^2) were

estimated. If the year in which a change in mortality occurs is unknown the model can be

fitted separately for each year where the change is possible. The year of change which

maximizes the likelihood provides the maximum likelihood estimates. Alternatively, the

year of change can be estimated along with the other parameters.

Application to the Assessment of Goosefish

Length-frequency data from the NMFS annual fall groundfish trawl surveys were obtained for two defined management zones. Although this survey was not designed specifically for the purpose of sampling goosefish, and sample sizes are relatively low, changes in the mean length of goosefish have been observed over the 40 year time series. The survey is described in detail in NEFSC (2002). In the NMFS assessment of goosefish in the northeast United States, estimates of mortality from the Beverton-Holt length-based method, using the NMFS survey data, have been used to describe the historical pattern in fishing mortality rates (NEFSC 2002). As in the NMFS assessment, we analyze data from the Mid-Atlantic Bight (southern management region) and from the Gulf of Maine, Southern New England, and Georges Bank (northern management region) separately.

Analysis of Southern Management Region Data

Consider the mean length data recorded in the NMFS annual fall groundfish survey in the southern management region from 1963-2002 (Figure 2). Records of landings of goosefish began to increase in the southern management region fishery in the late 1970's and the first step in our analysis is to determine if the data reflect a change in Z. The model was fitted repeatedly, each time specifying a different year of the time series as the year in which the change in mortality occurred and the objective function values were evaluated (Figure 3). The objective function was maximized by specifying the year of change to be 1977, which is consistent with the landings data presented in the 34$^{\text{th}}$ Stock Assessment Workshop (SAW) (NEFSC, 2002). Mortality was estimated to

have changed from 0.31 to 0.60 yr^{-1} in 1977.   We also estimated the year of change

directly in the maximization procedure. The parameter estimates were very similar to

those obtained by fixing the year of change (Table 2). The slight discrepancy is

explained by the year of change being a continuous variable in the simultaneous

estimation scheme and a discrete variable in the grid search (the estimates being 1977.2

yr and 1977, respectively, for the year of change). It is seen that Z_1, is estimated quite

precisely while Z_2 is less so. Estimated correlations of the parameter estimates were

highest between the two estimated mortality rates and the year of change (0.23 and 0.38

for Z_1 and Z_2 respectively) with all other values being less than 0.04.

The predictive power of the transitional form of the length based estimator was

then evaluated by making estimates from data as if an assessment were done in each year.

In other words, an estimate of Z_1 and Z_2 was made for each year using data only up to

that year, assuming the year of change was known to be 1977 (Figure 4). The estimates

from the transitional form using only data through 1980 (three years after the change in

mortality) were near 0.7 yr^{-1} and became very stable at near 0.6 yr^{-1} by 1984. Estimates

from the classic annual Beverton-Holt estimator were highly variable and ranged from

0.2 to 1.14 yr^{-1} (for 1977 and 1999, respectively).

The results from the transitional model are also consistent with the mean values of

the annual Beverton-Holt estimator summarized over different periods of the entire time

series ($Z = 0.32$, 0.75, and 0.65 yr^{-1} for 1970-1979, 1991-1995, and 1996-2000

respectively). Estimates from the transitional model, however, were stable in each year

they were made without the need to average over a number of years or wait for future

years to smooth the variability in the data. Note that the stability in estimates was

achieved even though the annual groundfish survey was not specifically designed for goosefish and sample sizes were very low (number of fish measured in a year's survey ranged from 14 to 196) leading to a high degree of variability in mean length estimates. Furthermore, sample sizes prior to 1977 were generally larger than after 1977 which partially explains the smaller standard error for Z_1 than for Z_2.

Analysis of Northern Management Region Data

Data from the northern management area were also analyzed and required a slightly more complex analysis. The model initially assumed a single change in mortality and the best fit indicated the change occurred in 1982 (Figure 5, top). However, an examination of the results showed residuals were positive from 1986 to 1993 and mostly negative from 1994 to 2002. This pattern in the residuals indicated that our data did not fit the model well and that additional changes in mortality were likely. Thus, the model was modified to incorporate a second change in mortality. All possible combinations of first change and second years of change were tried and a two-dimensional grid search of the change years showed changes most likely occurred in 1978 and 1987 (Figure 6). The data appeared to fit the model well with no discernable pattern in the residuals (Figure 5, bottom). The model was refitted with the two years of change estimated simultaneously with the mortality rates and variance (Table 3). Parameter estimates were again extremely close to those obtained from the grid search. Estimated correlations of the parameter estimates were in all cases less than 0.6 and for 11 of the 15 parameter pairs were less than 0.2.

Model Sensitivity

To test the model's sensitivity to input parameters, a simulated data set was created with a known change in mortality from 0.3 to 0.6 yr^{-1} in 1977 using growth parameters from goosefish in the southern management region (K = 0.1198 yr^{-1}, L_∞ = 129.2 cm) and a known L_c of 30 cm. The model was then fit assuming that estimates of K and L_∞ were mis-specified by 10-20%. Since estimates of K and L_∞ are generally inversely correlated, we also tested scenarios where K and L_∞ are mis-specified in opposite directions. Estimates of the change in mortality were most sensitive to the mis-specification of L_∞ and approximately half as sensitive to the mis-specification of K (Table 4). Model results were relatively stable when estimates of K and L_∞ were varied inversely with estimates of Z_1 ranging from 0.23 – 0.33 yr^{-1} and estimates of Z_2 ranging from 0.51 – 0.63 yr^{-1}.

Discussion

Fishery managers are continually faced with the challenge of matching methods and data sets such that all the critical assumptions can be met. The method presented in this paper is attractive because it requires minimal data that are commonly available and it does not require the assumption that catch rate is proportional to abundance. It advances a frequently used technique by removing an equilibrium assumption that is typically difficult to meet in real world situations. This allows for the broader application of a mean length analysis approach and allows the use of an entire time series of data resulting in increased information. The approach may in some cases represent the best opportunity to reconstruct the mortality history of a stock. In addition, the transitional

form of the model allows mortality estimates to be made within a few years of a change rather than having to wait for the mean lengths to stabilize at their new equilibrium level. In other words, as soon as a decline in mean lengths is detected, our model can be applied and the trajectory of decline can be used to estimate the new Z and how mean lengths will change over time. Estimates of multiple mortality rates and the years of change appear to have the desirable property of having only a low to moderate correlation.

In our goosefish example, it appears that the population was in equilibrium at the start of our time series. This is not a requirement of the model. A population that is undergoing a change in mean length at the start of a time series can also be successfully analyzed because an initial change in mortality that occurs prior to the start of the time series can be estimated in the model. However, this requires the shape of the trajectory of mean length over time to be well defined. If this is not the case, then it may be possible to set Z_1 equal to the natural mortality rate in cases where observations began to be collected shortly after the fishery began.

The method presented here is not fully efficient because, in theory, there is information contained in the variability of length measurements within a year (i.e., the sample variance) that is not used in the estimation of mortality rates and change points. That is, under high mortality there are few large fish and thus the variance in length decreases with increasing mortality rate. An expression for the variance of length measurements as a function of the mortality and growth parameters and the years of change could be derived and incorporated in the likelihood function. This would be appropriate if the sampling design consisted of simple random sampling of lengths. However, such a sampling scheme is uncommon and sampling almost always involves

some form of cluster sampling (e.g., a boat catches clusters of animals from trawl hauls, pot hauls, etc.). Thus, the sample variance of lengths will not be a simple function of the population variance of lengths.

Choice of cutoff, L_c

This method is predicated on the assumption of knife-edge selection in the fishery at a size L_c. Thus, all fish below the size L_c experience just natural mortality and all fish above the size L_c experience a total mortality rate of Z. One can thus sample the commercial catch to estimate the mean length of those animals above the size L_c. If the fishery does not have knife-edge selection then there is a problem. One can define L_c to be the size of full vulnerability to the commercial gear and compute the mean length above L_c. However, this means that fish below L_c will experience some fishing mortality and thus changes in fishing effort may affect the number of fish reaching the size L_c. As a practical matter, this will be important if selectivity increases gradually with length. But, for steep selection curves this may not be a problem.

Often, length composition data will be available from research surveys. If the size of full vulnerability to the survey gear is less than or equal to the size of full vulnerability L_c in the fishery, one can simply compute the mean of those fish in the survey above the size L_c. In practice, length frequency data are often collected in bins (i.e., as a histogram). The lower limit to one bin is defined to be the cut-off L_c. Then, the mean length in the sample (above the cutoff L_c) is computed by treating all fish in a bin as being the size at the midpoint of the size range defining the bin.

We also note that with historical data sets, sometimes only the mean length of the catch is available and one cannot construct size frequency histograms. The size at first capture L_c may only be known approximately and there may be some animals below the size L_c that are included in the mean length statistic. If it can be assumed that the selection pattern has remained stable over time, then the method presented in this paper may still be used to study the history of mortality; however, the results will reflect trends in mortality over time but estimates of absolute mortality rate will be biased.

Assumption of constant recruitment

The method in this paper is based on the assumption of constant recruitment. In reality, recruitment is likely to vary from year to year. This will not cause a bias but it may lead to autocorrelated errors in a time series of estimates. To study this, we created an extreme case in which there was a complete failure of recruitment in one year and observed the effect over time (Figure 7). The failure of recruitment in an incoming year class at first raises the population mean length, thus resulting in an underestimate of total mortality. Later, as that missing year class reaches an age where there should be large animals, the mean size of the population declines resulting in an overestimate of mortality rate. In practice, complete year class failure is rare and, to the extent that recruitment variability is random (rather than showing a trend over time), one can expect some cancellation of errors arising from variable recruitment. Thus, recruitment variability should not negate the use of this method although the reader would be well advised to consider the possibility of a trend in mean length arising from a particularly large or small year class.

Generalizing the approach

It may occur that observations are available on mean weight but not on mean length. This can be accommodated by deriving an expression for mean weight by replacing L_t in the derivations with the age-specific weight W_t where

$$W_t = aL_t^b \tag{10}$$

where *a* and *b* are constants defining the shape of the power function. When the exponent *b* is exactly 3, an analytical solution can be obtained for the mean weight. Otherwise, the mean weights can be calculated by numerical methods.

In some circumstances, it may be preferable to model reproduction as occurring in an annual pulse rather than continuously over the course of the year. This can be accomplished by replacing the integrals in the derivations with sums over the discrete age classes.

A more difficult assumption to deal with is that recruitment is constant over the time series being analyzed. If recruitment varies with the stock size, the model in its current form will underestimate the magnitude of any change in mortality.

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Table 1. Lag time in years for the mean length of fully vulnerable individuals to approach equilibrium and provide an estimate of mortality within 10% of the new level following a change in mortality from Z_1 to Z_2. In this example, growth parameters for goosefish in the southern management region of the Northeast United States were used in the calculations (k = 0.1198 yr^{-1}, L_∞ = 129.2 cm, L_c = 30 cm). Note that the natural mortality of goosefish is believed to be around 0.2 yr^{-1} so the first row and first column do not appear possible for goosefish. The shaded cell (Z_1 = 0.4, Z_2 = 1.0) is indicated as the example used in Figure 1.

		Z_2									
		0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1
	0.1	-	16	14	12	11	10	9	8	7	7
	0.2	23	-	9	9	8	8	7	7	6	6
	0.3	26	11	-	6	6	6	6	6	6	5
Z_1	0.4	27	13	7	-	4	5	5	5	5	5
	0.5	28	14	8	4	-	3	4	4	4	4
	0.6	28	15	9	6	3	-	2	3	4	4
	0.7	29	15	10	7	5	2	-	2	3	3
	0.8	29	15	10	7	5	4	2	-	2	2
	0.9	29	16	10	8	6	4	3	2	-	2
	1	29	16	10	8	6	5	4	3	2	-

Table 2. Results for goosefish from the southern management region.

Parameter	Estimate	Standard Error	t value	95% Profile Likelihood Confidence Intervals
Variance	37.44	4.29	8.72***	30.37 – 47.74
Z_1	0.33	0.02	17.94***	0.29 - 0.37
Z_2	0.58	0.06	9.62***	0.48 - 0.72
Year of Change	1977.23	1.00	1973.55***	1975.26 - 1979.19

*** Significant at $p < 0.0001$

Table 3. Results for goosefish from the northern management region.

Parameter	Estimate	Standard Error	t value	95% Profile Likelihood Confidence Intervals
Variance	22.93	2.63	8.72***	18.61 – 29.25
Z_1	0.14	< 0.01	28.46***	0.13 - 0.15
Z_2	0.30	0.03	8.83***	0.24 - 0.38
Z_3	0.56	0.05	10.78***	0.47 - 0.69
Year of first change	1978.21	0.91	2167.74***	1975.96 - 1980.26
Years until next change*	9.58 (1987.79)	1.33	7.19***	6.37 (1984.58) - 12.85 (1991.06)

*Corresponding year indicated in parentheses
*** Significant at $p < 0.0001$

Table 4. Sensitivity of Z estimates to over or underestimation of actual K and L_∞. A simulated data set was used with a known change in Z from 0.3 to 0.6 with growth parameters from the goosefish southern management region (K = 0.1198 yr^{-1}, L_∞ = 129.2 cm).

K Estimate	L_∞ Estimate	Z_1	Z_2
Actual	Actual	0.30	0.60
Actual	10% Low	0.25	0.52
Actual	10% High	0.35	0.68
10% High	Actual	0.33	0.65
10% Low	Actual	0.27	0.55
10% High	10% Low	0.27	0.56
10% Low	10% High	0.32	0.62
Actual	20% High	0.41	0.77
Actual	20% Low	0.19	0.43
20% High	Actual	0.36	0.71
20% Low	Actual	0.24	0.49
20% Low	20% High	0.33	0.63
20% High	20% Low	0.23	0.51

List of Figures

Figure 6. Contour plot of objective function values to determine the two years in which Z

changed in the northern management region. The objective function was maximized

(indicated by the dotted line) by an initial change in 1978 and a second change in

1987.

Figure 7. Response of the Beverton-Holt estimator to a violation of the assumption of

constant recruitment. A complete reproductive failure under two different levels of

fishing mortality is simulated in year three. Life history parameters for goosefish in

the southern management region were used for this example.
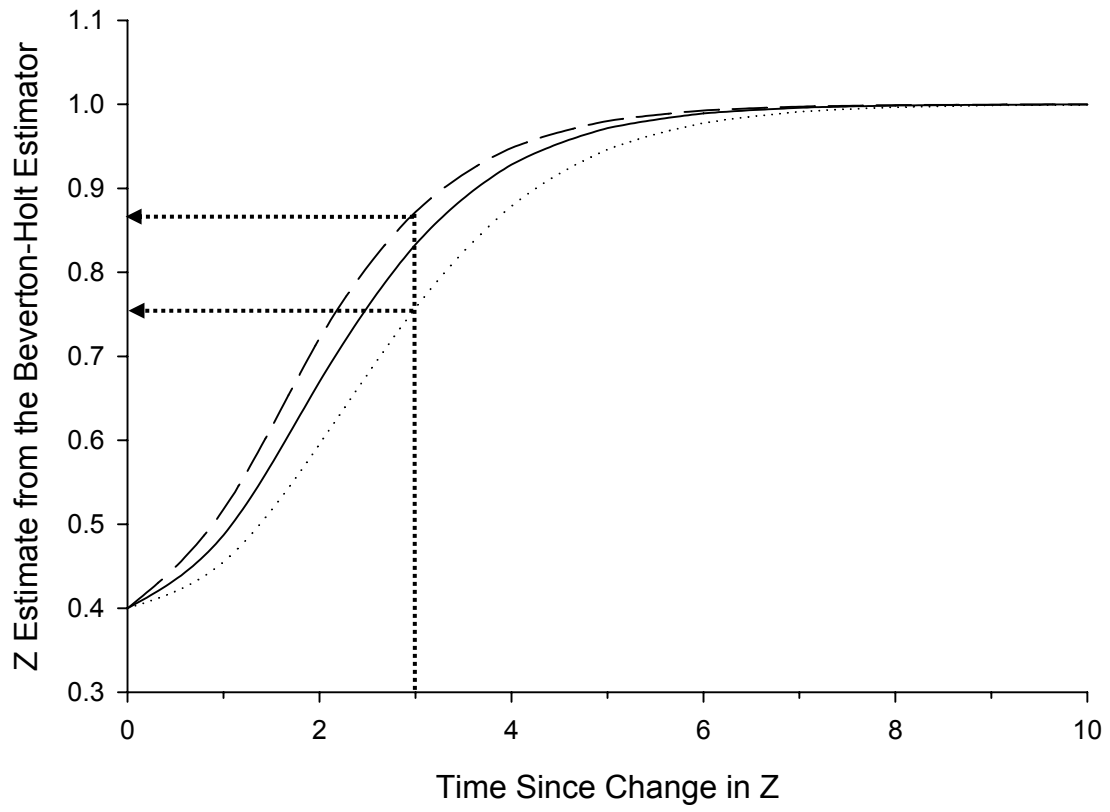
Figure 1
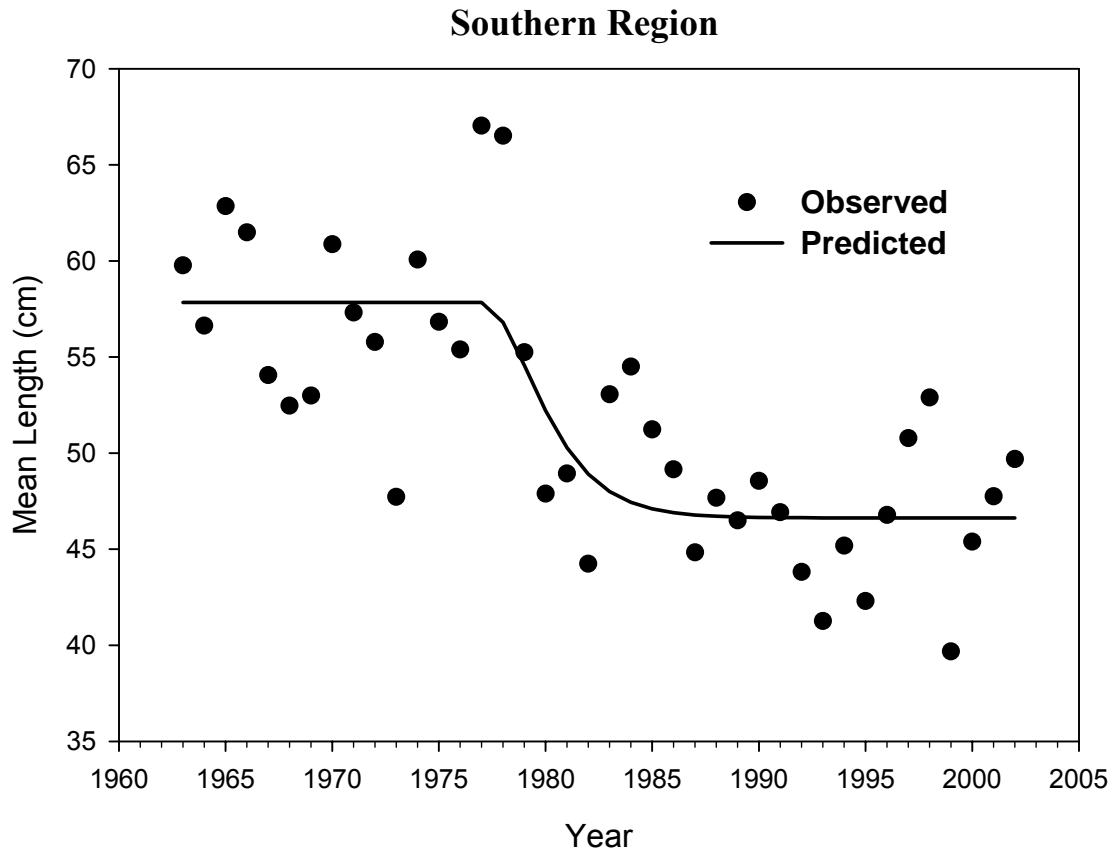
Southern Region

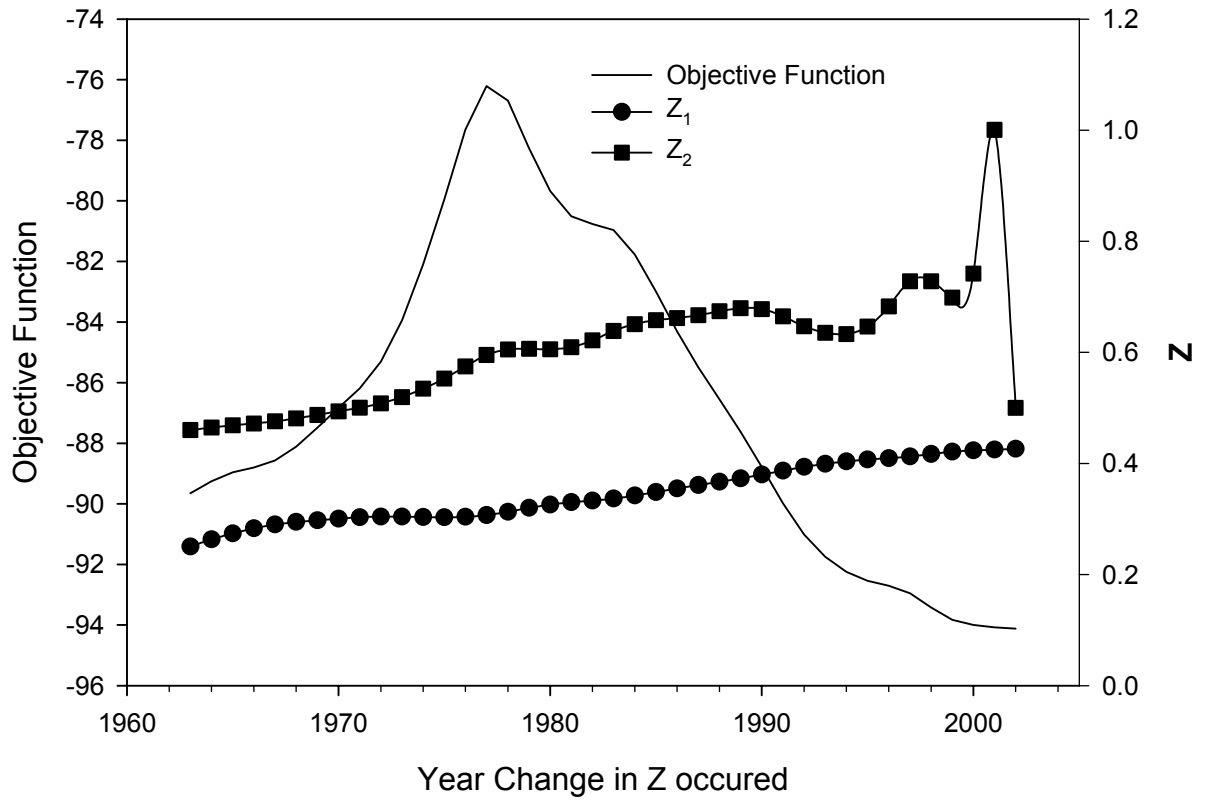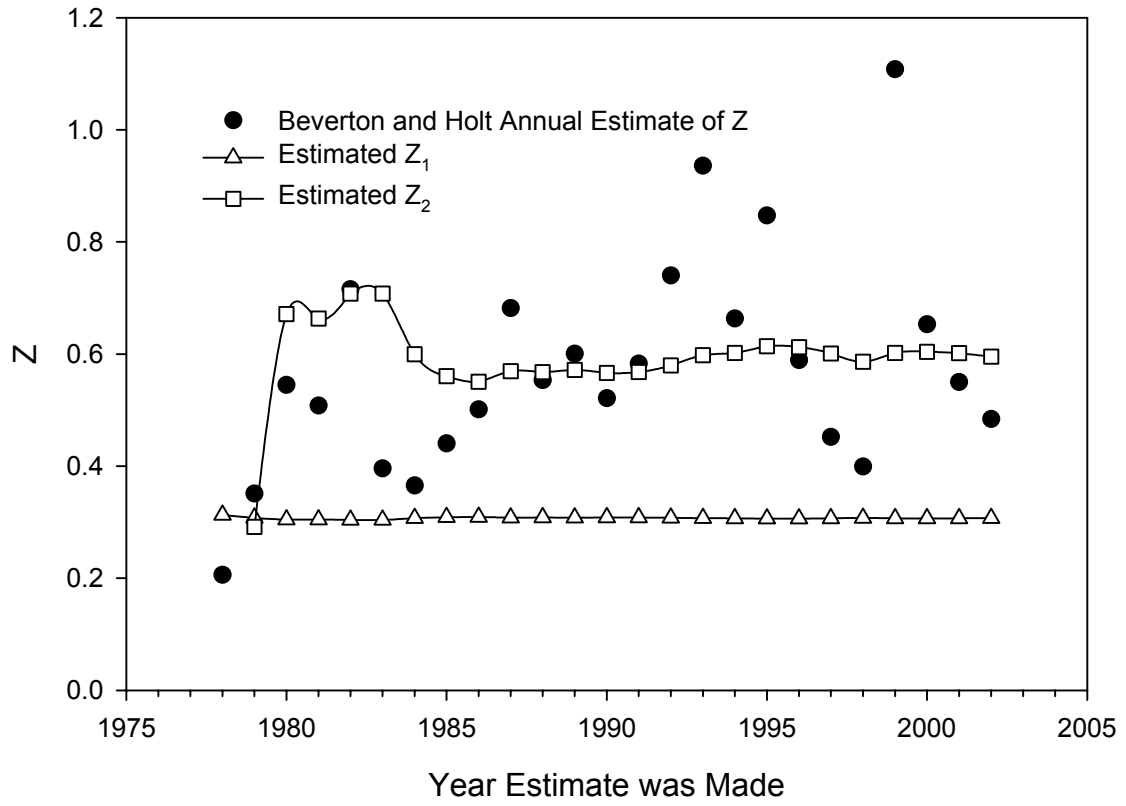Figure 2

Southern Region

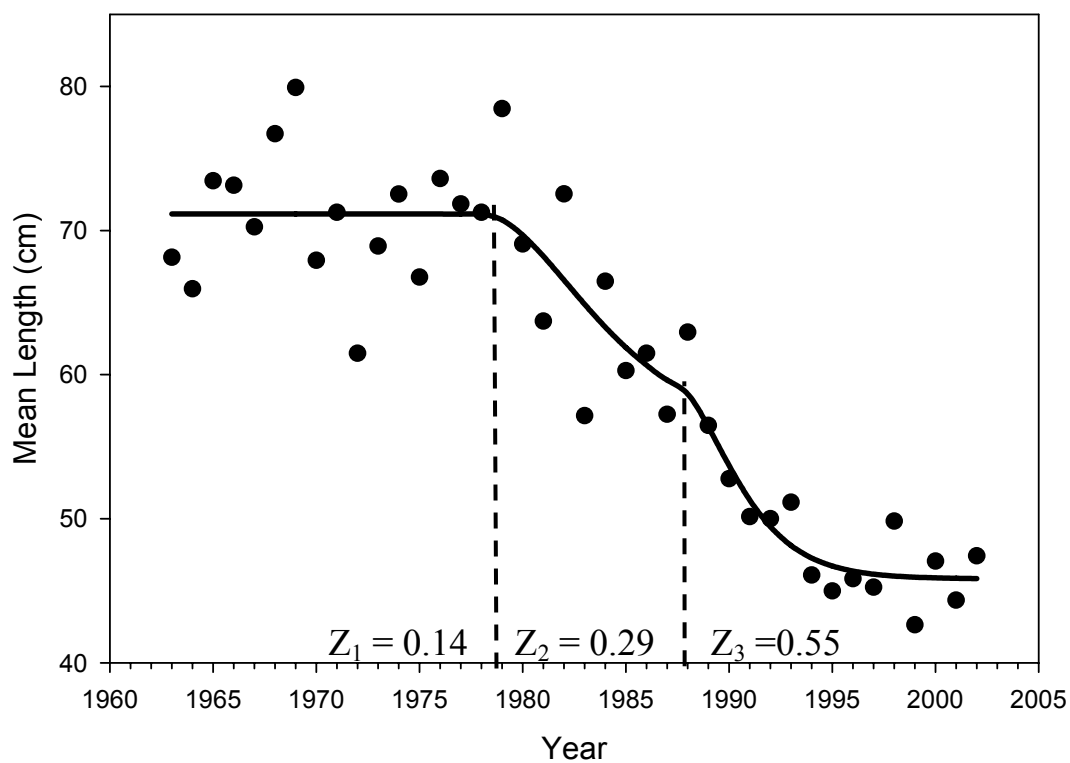Figure 3

Southern Region

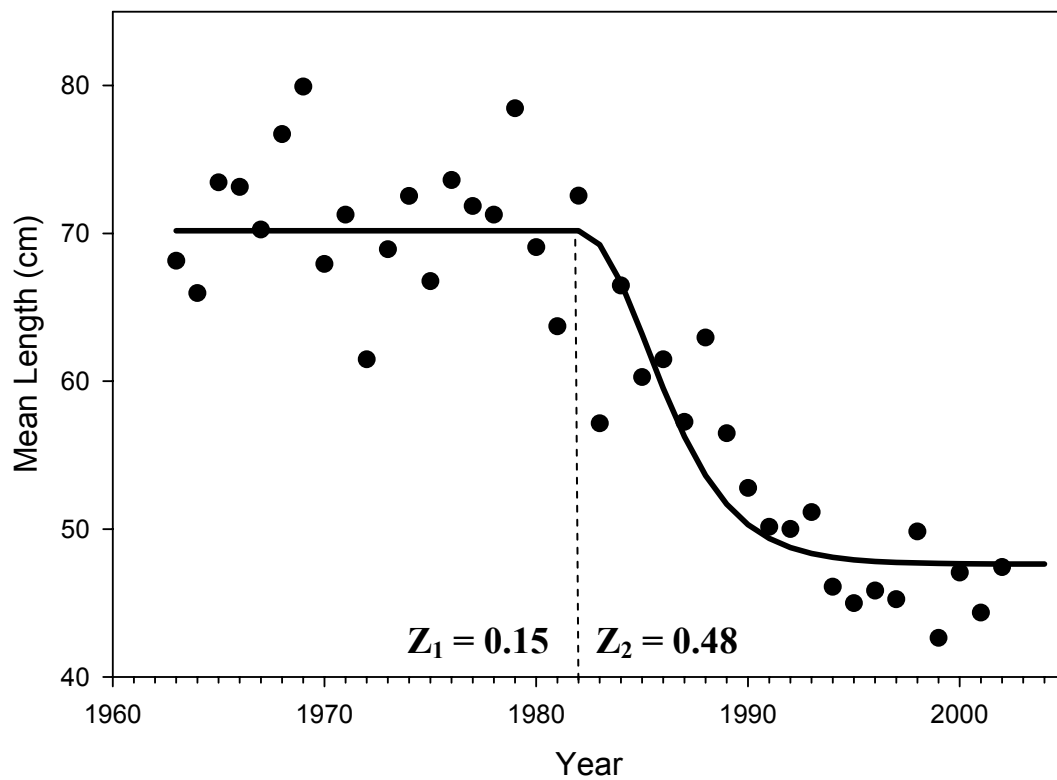Figure 4

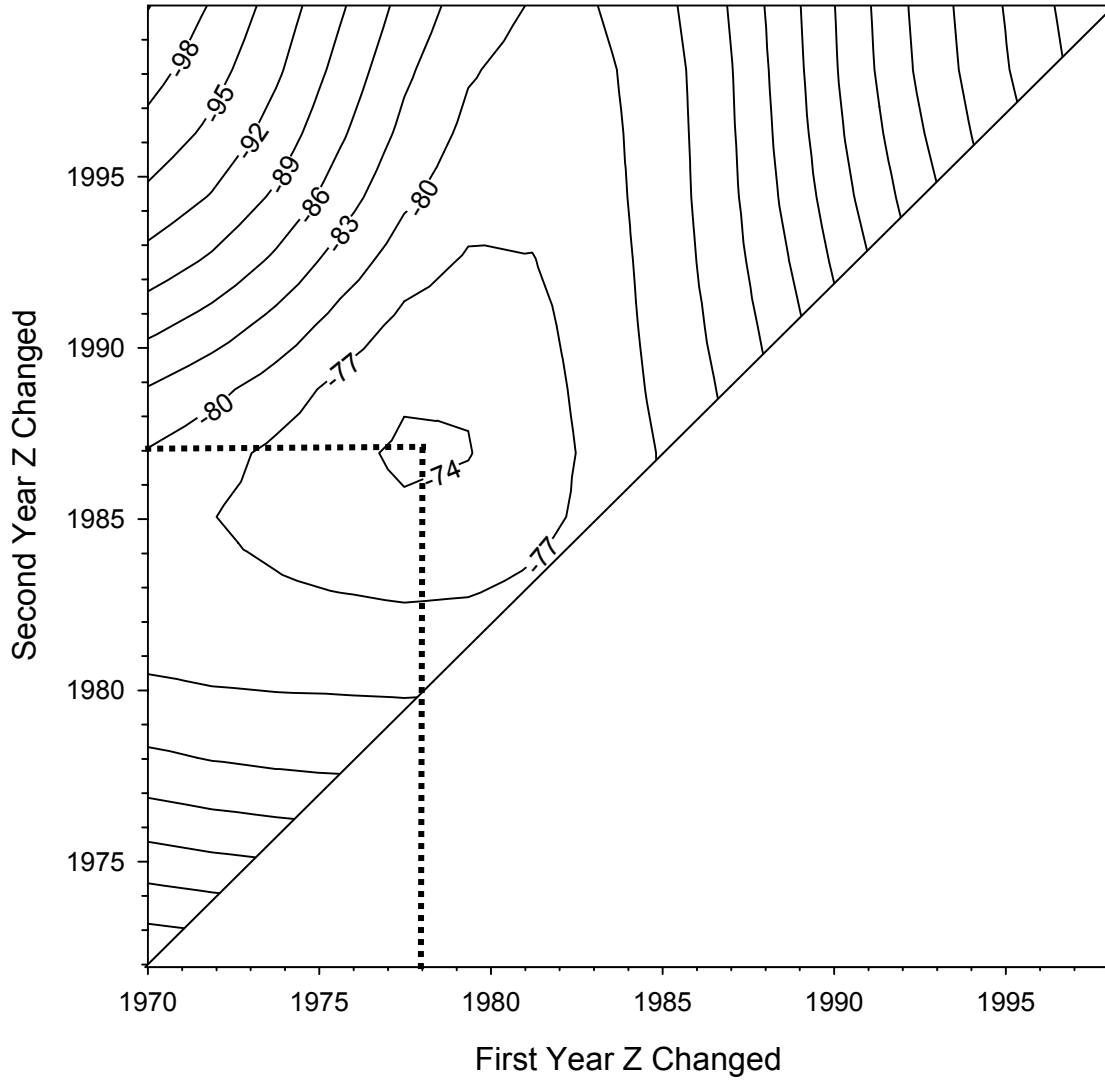# Northern Region

Figure 5

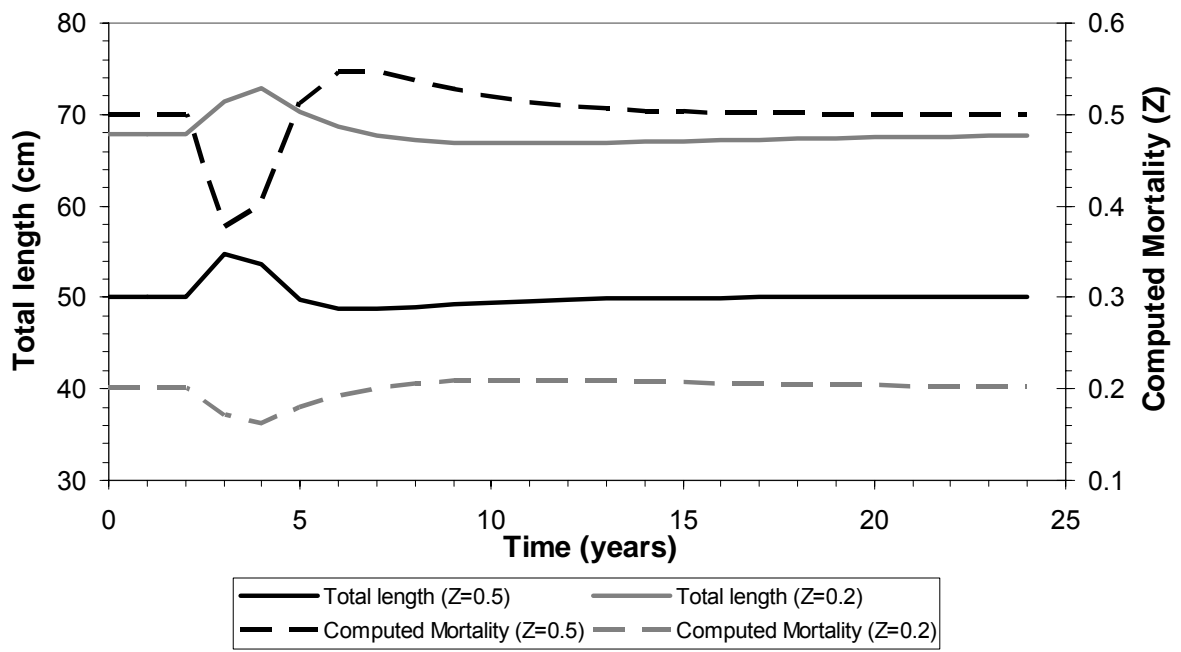**Northern Region**

Figure 6

Figure 7

Appendix A. Derivation of the Mean Length d Years After a Change in Mortality Rate

As indicated in the main text, the mean length in the population d years after a change in mortality is

$$\overline{L} = \frac{\int_{t_c}^{g} R\exp(-Z_2(t-t_c))L_t dt + \int_{g}^{\infty} R\exp(-Z_2 d)\exp(-Z_1(t-g))L_t dt}{\int_{t_c}^{g} R\exp(-Z_2(t-t_c))dt + \int_{g}^{\infty} R\exp(-Z_2 d)\exp(-Z_1(t-g))dt}$$

where the notation is as defined in the main text. The denominator, *DEN*, is

$$DEN = \frac{1-\exp(-Z_2 d)}{Z_2} + \frac{\exp(-Z_2 d)}{Z_1} = \frac{Z_1 + (Z_2 - Z_1)\exp(-Z_2 d)}{Z_1 Z_2}.$$

The numerator, *NUM*, is

$$NUM = L_\infty \{ \frac{1-\exp(-Z_2 d)}{Z_2} - \frac{\exp(-K(t_c - t_o)) - \exp(-Z_2 d - K(g - t_o))}{Z_2 + K}$$

$$+ \frac{\exp(-Z_2 d)}{Z_1} - \frac{\exp(-Z_2 d - K(g - t_o))}{Z_1 + K} \}.$$

We would like to get rid of t_o in the numerator. Solving the von Bertalanffy growth equation for t_o we obtain

$$t_o = t_c + \frac{\ln(1 - L_c / L_\infty)}{K}.$$

Substituting this into the numerator NUM and simplifying gives

$$NUM = \frac{L_\infty(1-\exp(-Z_2 d))}{Z_2} - \frac{L_\infty - L_c}{Z_2 + K} + \frac{(L_\infty - L_g)\exp(-Z_2 d)}{Z_2 + K} +$$

$$\frac{L_\infty \exp(-Z_2 d)}{Z_1} - \frac{(L_\infty - L_g)\exp(-Z_2 d)}{Z_1 + K}$$

where L_g is defined to be the length at age g $(= t_c + d)$. Now, the only problem is that we have the parameter L_g which we would prefer to express as a function of L_c. The difference between L_g and L_c is

$$L_g - L_c = L_\infty b \exp(-Kt_c) - L_\infty b \exp(-Kg)$$

where $b = \exp(Kt_o)$. Solving for L_g and simplifying, we obtain

$$L_g = L_\infty - (L_\infty - L_c)\exp(-Kd).$$

Substituting this into the numerator gives

$$\frac{Z_1 L\infty + (Z_2 - Z_1)L_\infty \exp(-Z_2 d)}{Z_1 Z_2} - \frac{(L_\infty - L_c)(1-\exp(-(Z_2 + K)d)}{Z_2 + K} - \frac{(L_\infty - L_c)(1-\exp(-(Z_2 + K)d)}{Z_1 + K}$$

Finally, dividing the numerator by the denominator gives equation (6) in the main text.

Appendix B. Derivation of the Mean Length after Multiple Changes in Mortality Rate.

Here, we present a general expression for the mean length when there have been k changes in mortality rate over time. We define the variables d_i to be the time elapsed between the ith and $i+1$th change in mortality, for $i = 1, \ldots, k\text{-}1$, and d_k to be the time from the last change in mortality to the point where the mean length was observed. In other words, d_i measures the duration of the period when Z_{i+1} was affecting the population. The mean length is

$$\bar{L} = \frac{\displaystyle\sum_{i=1}^{k+1} a_i \int_{\lambda_i}^{\gamma_i} \exp(-Z_{k+2-i}(t-\lambda_i))L_t\, dt}{\displaystyle\sum_{i=1}^{k+1} a_i \int_{\lambda_i}^{\gamma_i} \exp(-Z_{k+2-i}(t-\lambda_i))\, dt} \tag{B1}$$

where

$$\lambda_1 = t_c$$

$$\lambda_i = t_c + \sum_{j=k-i+2}^{k} d_j \quad , \text{for } i = 2, \ldots, k+1$$

$$\gamma_i = t_c + \sum_{j=k-i+1}^{k} d_j \quad , \text{for } i \leq k$$

$$\gamma_{k+1} = \infty$$

$$a_1 = 1$$

$$a_i = \exp(-\sum_{j=1}^{i-1} Z_{k+2-j} d_{k+1-j}) \quad , \text{for } i = 2, \ldots, k+1$$

$$L_t = L_\infty (1 - e^{-K(t-t_o)})$$

The denominator, *DEN*, is

$$DEN = \sum_{i=1}^{k+1} \frac{a_i(1-e^{-Z_{k+2-i}d_{k+1-i}})}{Z_{k+2-i}}.$$

The numerator, *NUM*, is

$$NUM = L_\infty \left(DEN - \sum_{i=1}^{k+1} \frac{\left(1 - \dfrac{L_c}{L_\infty}\right) r_i s_i}{Z_{k+2-i} + K} \right)$$

where

$$r_1 = 1$$

$$r_i = \exp\left(\sum_{j=1}^{i-1} -(Z_{k+2-j} + K) d_{k+1-j} \right) \quad , \quad i = 2, ..., k+1$$

$$s_i = 1 - e^{-(Z_{k+2-i} + K) d_{k+1-i}} \quad , i = 1, ..., k$$

$$s_{k+1} = 1$$

Chapter 5

Simple Methods for Estimating Survival Rate

from Catch Rates from Multiple Years

Abstract

Survival rates can be estimated from annual surveys by tracking the abundance of one or more cohorts, as measured by catch per unit of sampling effort, from one year to the next. It can be difficult to attain reasonable precision unless sampling effort is extensive. Indeed, estimates of survival exceeding 100% are not infrequently obtained. We show that data from several years can be analyzed simultaneously to obtain a single estimate of survival under the assumption that survival is constant over the period analyzed. The method requires that only a single age group need be identifiable and thus has minimal data requirements. Estimates of goosefish (*Lophius americanus*) survival obtained by this method compare favorably with estimates obtained by analyzing changes in mean length over time.

Annual survival rate, S, can be estimated from annual surveys using a longitudinal catch curve to follow a cohort over time. This is based on the relationships that

$$N_{a+1,t+1} = S \, N_{a,t}$$

and

$$I_{at} = q N_{at}$$

where $N_{a,t}$ is the number of animals of age a alive at the time of the survey in year t, I_{at} is an index of abundance of the animals of age a in year t, and q is the catchability coefficient. The survival rate can thus be estimated by linear regression of the index on the previous year's value for the same cohort. The assumptions are that survival and catchability are both constant over time and age, and that the ages of the animals observed in the survey can be determined.

Sometimes, it is difficult to determine ages for older animals. If one age group can be identified and separated from the others, and two years of data are considered, then the survival rate can be estimated by

$$S_t = \frac{N_{\geq a+1 \; t+1}}{N_{\geq a \; t}} = \frac{I_{\geq a+1 \; t+1}}{I_{\geq a \; t}} \tag{1}$$

where the ^ indicates an estimate and the notation $\geq a$ means all ages greater than or equal to a. That is, age groups are pooled and the abundance of a group of cohorts is followed from one year (when they are age a and above) to the next (when they are age $a+1$ and above). Heincke (1913, cited in Ricker 1975) was apparently the first to suggest pooling data over ages although he formulated the estimation procedure in terms of a cross-sectional catch curve (age composition observed in one year) rather than as a longitudinal catch curve (changes in abundance of specified cohorts monitored over time). A generalization of this to include more than two years of data has not been given previously and is developed below.

Development of multi-year estimators

We consider just two age groups in the population – recruits and previously recruited animals. Recruits are defined to be those animals that will join the previously recruited animals the next year (if they survive the year). The relationship between the number of previously recruited animals in year $t+1$, N_{t+1}, and the number of recruits R_t and previously recruited animals N_t in year t is:

$$N_{t+1} = S\,N_t + \phi^* R_t \,, \qquad t = 1, \dots, T\text{-}1$$

where ϕ^* and S are the survival rates of the recruits and previously recruited animals, respectively, and T is the number of years of survey data. In terms of indices of abundance, we have

$$I_{t+1} = S\,I_t + \phi\,r_t \ , \qquad t = 1, \ldots, T\text{-}1 \qquad (2)$$

where r_t is the index of recruits in year t and ϕ subsumes the survival of recruits and the selectivity of the survey gear for recruits. If the indices I_t are independent then equation (2) is in the form of a multiple linear regression with no intercept. Parameter estimates can be found easily by minimizing the sum of squared deviations between observed indices and predictions obtained from the previous year's index:

$$\sum_{t=1}^{T-1} (I_{t+1} - S\,I_t - \phi\,r_t)^2 \ .$$

Estimates of S and ϕ may be highly negatively correlated and unstable unless appreciable contrast is observed in the recruitment over time. When recruitment is not highly variable, an alternative is to ignore the recruitment altogether and replace equation (2) with

$$I_{t+1} = S\,I_t + \beta \ , \qquad t = 1, \ldots, T\text{-}1 \qquad (3)$$

where β is the intercept in a linear regression.

Another alternative is based on the idea that the parameter ϕ likely is close to the value of S. Recruits may have a higher natural mortality than previously recruited animals but likely have a lower fishing mortality and a lower catchability so that, on balance, it may be reasonable to set ϕ equal to S to obtain an estimate of survival. Thus, equation (2) would be replaced by

$$I_{t+1} = S \left(I_t + r_t \right), \qquad t = 1, \ldots, T\text{-}1. \tag{4}$$

Example: Goosefish

Goosefish (*Lophius americanus*) are captured in the annual groundfish trawl survey conducted by the National Marine Fisheries Service Woods Hole Laboratory in the fall of each year. However, the survey was not designed to sample this species and the catches are always low, ranging from 14 to 196 animals per survey. Despite this, the mean length data from the survey have proved useful for estimating mortality rates even though the mean lengths vary greatly from year to year (see Gedamke and Hoenig 2006). Estimates were made for two regions: the northern management area, comprising the Gulf of Maine, southern New England and Georges Bank, and the southern management area, comprising waters from Rhode Island to North Carolina. It is of interest to see how well those values are reproduced when mortality is estimated from catch rates (Table 1) instead of mean lengths.

Goosefish are believed to be fully vulnerable to the survey trawl when they reach

30 cm in total length (NEFSC 2002). We determined the first fully vulnerable age class

using the von Bertalanffy growth models developed by the National Marine Fisheries

Service. Growth parameters for the northern region are: L_∞ = 126.0 cm, K = 0.1080 yr^{-1};

for the southern region the values are L_∞ = 129.2 cm, K = 0.1198 yr^{-1} (NEFSC 2002). No

values were given for the parameter t_o so a value of 0.0 yr was assumed for both regions.

It is seen that fish from age 2.5 to 3.5 have predicted lengths of 29.8 to 39.7 cm in the

northern region. Consequently, fish in the size range 30 to 40 cm are taken to be the

recruits, and all fish above the size 40 cm are considered the previously recruited animals.

For the southern region, the recruits are 33 to 44 cm.

We apply equation (1) to the catch rate data in Table 1 and Figure 1 to obtain

annual estimates of survival rate and then convert these to estimates of instantaneous

rates of total mortality, Z, according to the formula $Z = -\ln(S)$ (Figures 2 and 3). Data

from the 1963 and 1964 surveys give rise to an estimate of survival between the surveys,

i.e., between fall 1963 and fall 1964. We refer to this as the survival in 1964 because

most of the time interval is in 1964. Not unexpectedly, the results are highly variable and

often infeasible (i.e., estimates of mortality rate are negative). We computed the

arithmetic mean of the results from (1) over the periods of years of stable mortality

identified by Gedamke and Hoenig (2006) from their analysis of mean sizes (Table 2,

Figures 2 and 3). Averaging the annual estimates gives results roughly similar to those

obtained by Gedamke and Hoenig but the agreement is strong only in one comparison.

We apply the estimators in (2), (3) and (4) to those same ranges of years. Results from

equations (2) and (3) were poor and are not shown here.

The results of applying equation (4) are extremely close to the results of Gedamke and Hoenig (2006) for four of the five comparisons. Only for the period 1963 to 1976 for the southern region was there a large discrepancy ($Z = 0.33$ yr^{-1} based on mean lengths and $= 0.55$ yr^{-1} based on (4)).

Sensitivity Analysis

Assumption that $\phi = S$

A key assumption in applying equation (4) is that the parameter ϕ is equal to S. We specify departures from this assumption by specifying $\gamma S = \phi$. Then (2) can be written

$$I_{t+1} = S I_t + \gamma S r_t \ , \qquad t = 1, \ldots, T\text{-}1.$$

The effect of assuming $\gamma = 1$, when it is really some other value, can be determined by multiplying all the recruitment index values by the other value and then re-estimating the survival rate. We did this for the northern management region data from 1963 to 1977 and converted the results to instantaneous rates of total mortality, Z. The computed Z is an increasing function of the value of γ used and is described by: computed $Z = 0.0554 \, \gamma + 0.123$ such that when $\gamma = 1$ the computed Z is 0.1784, as reported in Table 2. If ϕ is really 90% of S (i.e., $\gamma = 0.9$), the estimate of Z should be 0.17286 and the percent difference in results is

$$\% \text{ difference} = 100(.1784 - .17286)/.17286 = 3\% .$$

Thus, a 10% error in the specification of γ results in a 3% error in the estimate of Z. In this case, at least, the estimator is insensitive to model misspecification.

Effects of systematic errors in age composition

      There are two effects of systematic errors in the specification of age composition. First, if only a portion of the animals in age group 1 (the recruits) is included in the analysis the result will be a positive bias in the survival estimator. This is easily seen from equation (1) where the denominator is made smaller by the exclusion of some recruits. Similarly, including some animals in the new recruits category that will not reach the size of the second age group in one year results in a negative bias.

      The second consequence of systematic misspecification of age composition is that the estimator is no longer unaffected by recruitment variability. Suppose the fraction α of age group 1 included in the analysis is constant. Then, as recruitment approaches zero, the estimator approaches the survival rate, *S*. As recruitment increases without bound, the estimator tends to *S/(1 - α)*. If recruitment is overestimated (some animals are included in age group 1 that will not grow into age category 2 in one year) but recruitment approaches zero then the estimator tends to the true survival rate *S*. If recruitment is overestimated and recruitment approaches infinity, the estimator is too low and tends to *S/(1 + α)*. These conclusions are justified in the Appendix.

Discussion

We have presented a new approach to estimating survival rate from multiple years of survey data. The big advantages of this approach are that one does not need to know the magnitude of the landings and one does not have to be able to age the catch beyond identifying the recruits.

For the goosefish example, it appears that the survey catch rates are more variable than the mean lengths and, consequently, that the precision of the estimates from the new approach may be less than those based on the Gedamke and Hoenig (2006) approach based on mean lengths. However, it should be noted that both methods can be applied to the same data. For goosefish, it is reassuring that the two approaches gave very similar results for five of the six time-area comparisons. Estimates obtained by averaging two-year estimates obtained by equation (1) appeared reasonable in most cases. However, averaging a set of numbers that contain nonsensical values (survivals greater than 1.0) may be troubling and hard to justify.

We relied on the model described by equation (4) because the survey catches of goosefish were low and the catch rates highly variable. In cases where a species is better sampled, it may be worthwhile to use the models in (2) and (3).

Our example involved survey catch rate data. It is also possible to apply the method to commercial catch rate data provided these represent relatively short periods of time. For example, catch rate in the first two months of year $t+1$ can be compared to catch rates in the same period in year t. The restricted period of time within a year is necessary for two reasons. First, catch rate in a time interval is proportional to average

abundance in that interval. Thus, over an extended period of time the effort may be large and the commercial catch rate reflects both the initial abundance and the depletion of the population. The second reason for using a restricted period of time is that catchability, recruitment and other factors may change seasonally so that catch rate is harder to interpret.

In the appendix we investigate the impact of errors in determining the fraction of the survey catch that will recruit in the next year and place bounds on these errors. In cases where errors in determining the catch composition may be appreciable, the survival estimators are more properly thought of as providing an index of survival rather than absolute survival. That is, the estimators can be used to monitor trends in survival rate over time rather than to quantify the level of survival.

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Appendix: effects of systematic errors in age composition on survival estimates

Referring to figure A.1, we note the survival estimator in equation (1) can be viewed geometrically as a ratio of areas

$$\hat{S} = \frac{b_2}{a_1 + b_1} \tag{A.1}$$

where a_1 represents the abundance of recruits in year 1 and b_1 and b_2 are the abundances of previously recruited animals in years 1 and 2, respectively. If a portion of the animals that will recruit in year 2, say, $\alpha\, a_1$, is excluded from the recruitment, then the estimate of survival will be biased high. Similarly, if some animals are included in the recruitment that will not, in fact, recruit in year 2 (a_1 is specified to be too large), the estimate will be biased low.

We now consider how the magnitude of the recruitment affects this result. We note that

$$b_2 = S(\, a_1 + b_1). \tag{A.2}$$

If a portion of the recruitment, say, $\alpha\, a_1$, is excluded from the calculation of survival, then (A.1) becomes an erroneous estimate of survival, $\hat{S}_{err}$, given by

$$\hat{S}_{err} = \frac{b_2}{a_1 + b_1 - \alpha a_1} = \frac{S(a_1 + b_1)}{a_1 + b_1 - \alpha a_1}.$$

Suppose the recruitment a_1 approaches zero. This implies that the amount of recruitment

not included in the calculation, αa_1, also approaches zero. Then, $\hat{S}_{err}$ approaches

$S(b_1/b_1) = S$. On the other hand, suppose $a_1 \rightarrow \infty$ while α remains constant. Then,

$$\hat{S}_{err} \rightarrow S\left(\frac{a_1}{a_1 - a_1\alpha}\right) = \frac{S}{1 - \alpha}.$$

Similarly, it can be shown that if recruitment is overstated by an amount α, but

recruitment approaches zero, then the erroneous estimator approaches the true survival

rate, S. And, under the same circumstances, if recruitment approaches infinity, the

survival estimate approaches $S/(1+\alpha)$.

Table 1. Survey stratified mean number per tow for goosefish off northeastern United States. The surveys were conducted in the fall of each year.

	northern region catch per tow of size		southern region catch per tow of size	
survey year	> 40 cm	> 30 cm	> 44 cm	> 33 cm
1963	1.035	1.218	0.266	0.330
1964	0.777	0.938	0.311	0.333
1965	1.137	1.384	0.489	0.492
1966	0.172	0.234	0.189	0.189
1967	0.225	0.272	0.259	0.259
1968	0.228	0.307	0.411	0.411
1969	0.266	0.282	0.375	0.389
1970	0.120	0.168	0.439	0.451
1971	0.764	1.081	0.246	0.282
1972	0.289	0.558	0.455	0.476
1973	0.128	0.167	0.250	0.270
1974	0.349	0.442	0.260	0.276
1975	0.196	0.263	0.370	0.409
1976	0.231	0.253	0.577	0.616
1977	0.188	0.192	0.495	0.539
1978	0.258	0.357	0.408	0.432
1979	0.234	0.451	0.440	0.481
1980	0.344	0.577	0.338	0.346
1981	0.115	0.254	0.130	0.130

1982	0.430	0.577	0.341	0.418
1983	0.201	0.222	0.379	0.445
1984	0.234	0.336	0.234	0.305
1985	0.107	0.168	0.411	0.475
1986	0.048	0.099	0.189	0.232
1987	0.086	0.120	0.245	0.274
1988	0.168	0.274	0.217	0.260
1989	0.084	0.120	0.180	0.232
1990	0.148	0.254	0.219	0.349
1991	0.077	0.147	0.294	0.406
1992	0.042	0.139	0.234	0.315
1993	0.109	0.168	0.219	0.356
1994	0.079	0.204	0.344	0.709
1995	0.115	0.168	0.308	0.502
1996	0.182	0.224	0.208	0.342
1997	0.116	0.172	0.217	0.323
1998	0.053	0.157	0.157	0.376
1999	0.105	0.227	0.528	0.954
2000	0.159	0.251	0.588	0.924
2001	0.377	0.523	0.501	0.776
2002	0.238	0.325	0.575	0.660

Table 2. Estimates, Z, of total mortality rate for goosefish in two management areas.

The Z from lengths were taken from Gedamke and Hoenig (2006).

Northern management area.

Period	Z from lengths	Z from (4)	average of Z from (1)
1963-1977	0.14	0.18	0.07
1978-1988	0.29	0.28	0.19
1989-2002	0.55	0.48	0.39

Southern management area

Period	Z from lengths	Z from (4)	average of Z from (1)
1963-1976	0.33	0.55	0.37
1977-2002	0.58	0.56	0.47

List of Figures

Appendix Figure 1. Hypothetical length frequency distributions showing two modes representing one identifiable age class (a_i) and one "composite" or "plus" group consisting of multiple age classes (b_i), for years $i = 1, 2$. The text discusses the effect on the estimated survival rate of not including the area marked $\alpha\, a_1$ as part of the recruitment in year 1. Length frequencies are shown as triangular distributions merely for convenience.
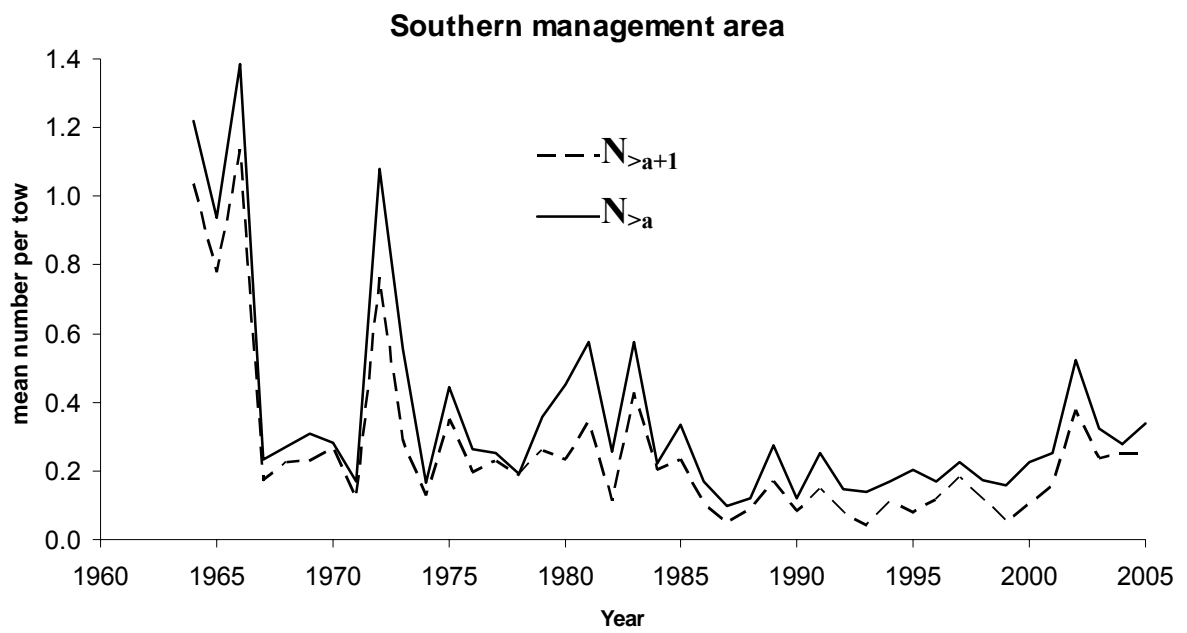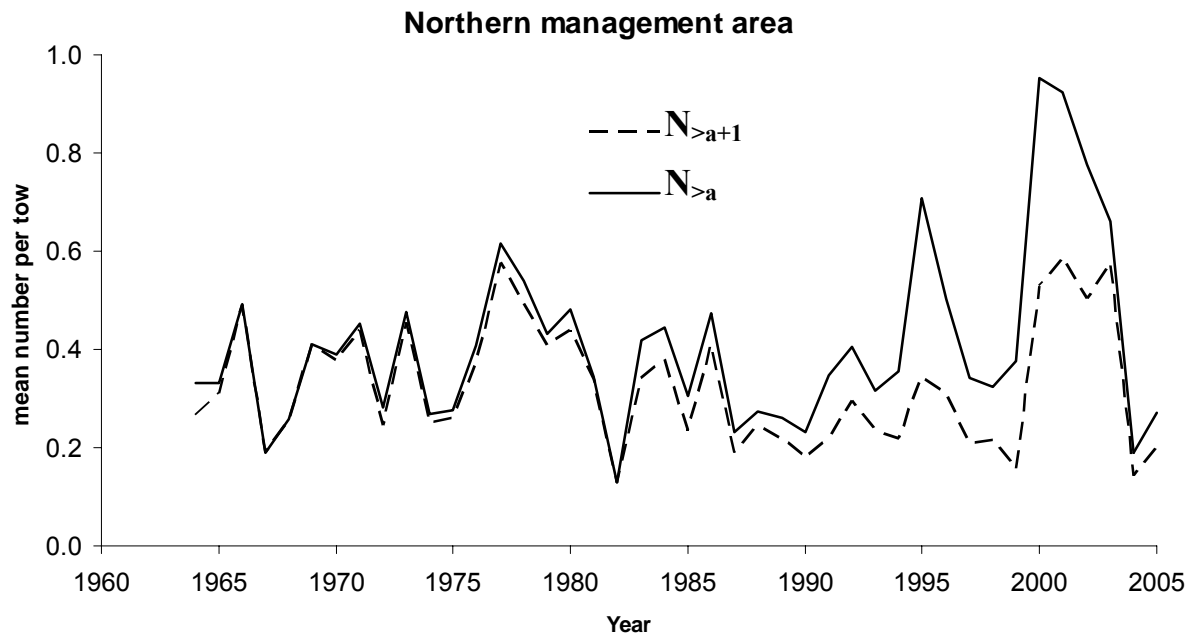
Northern management area
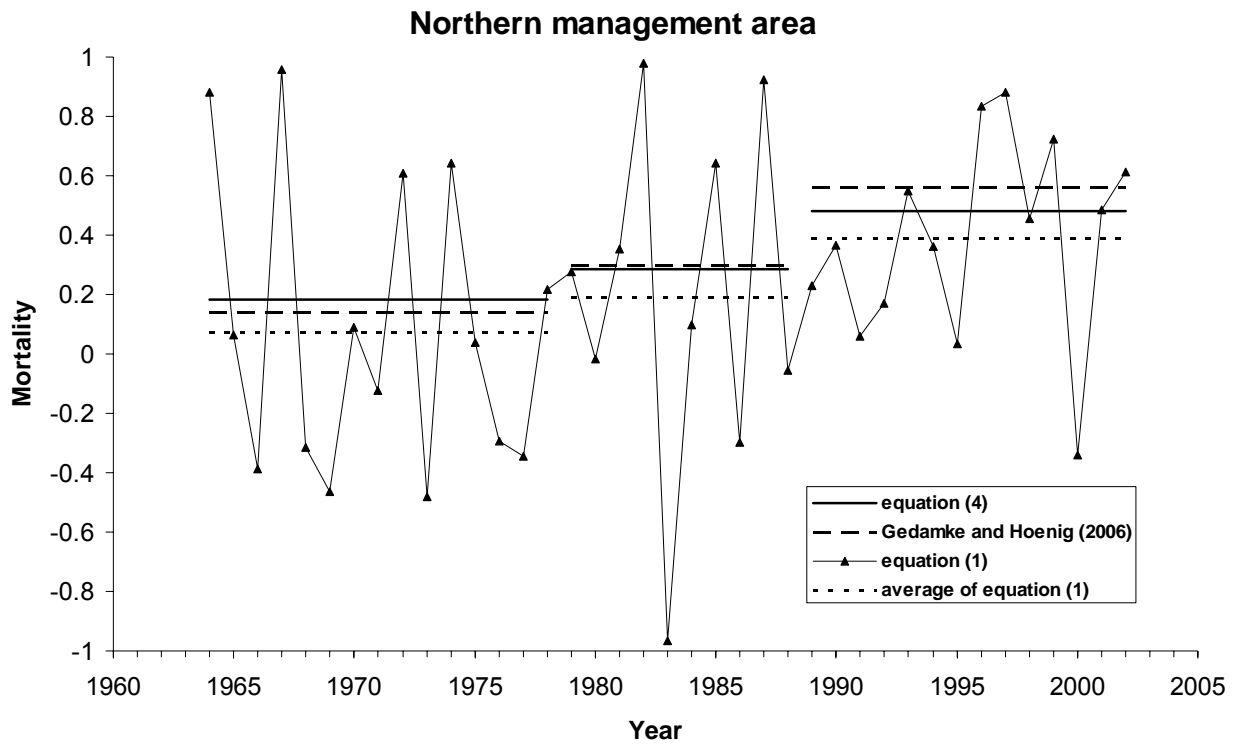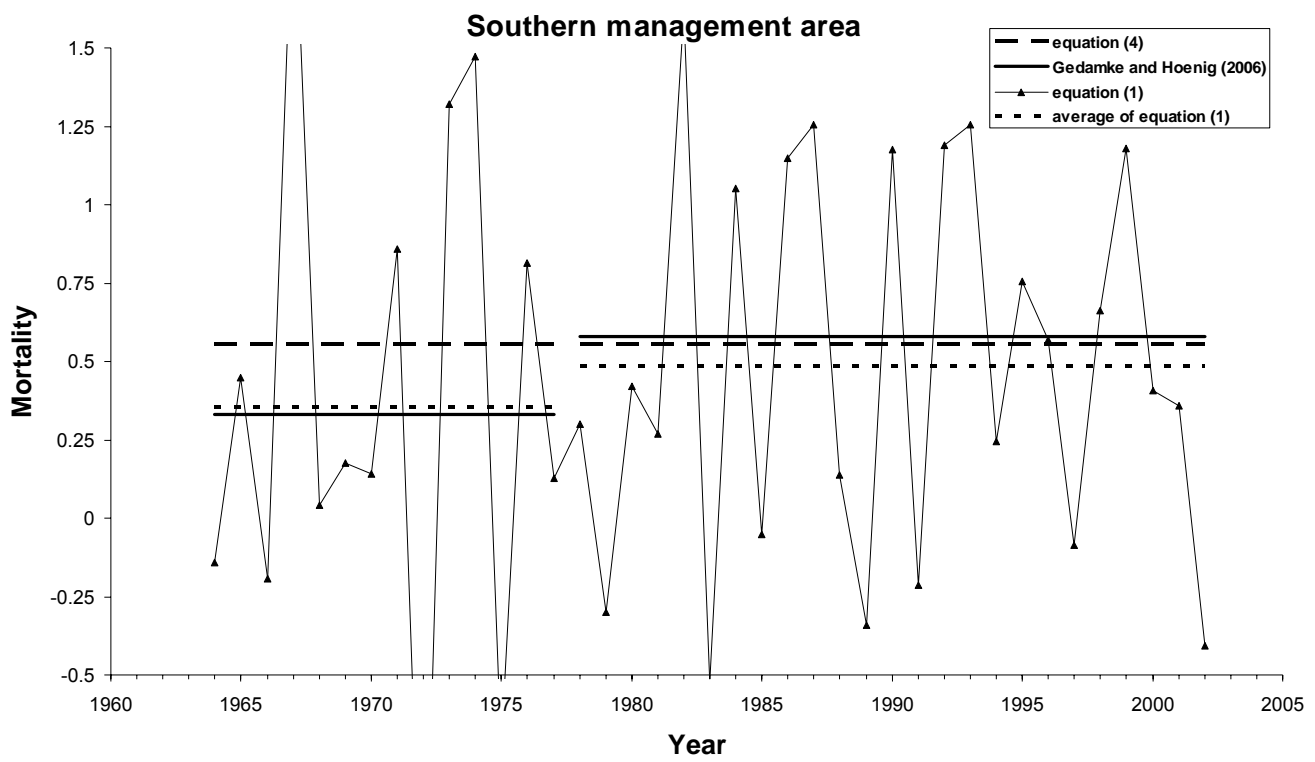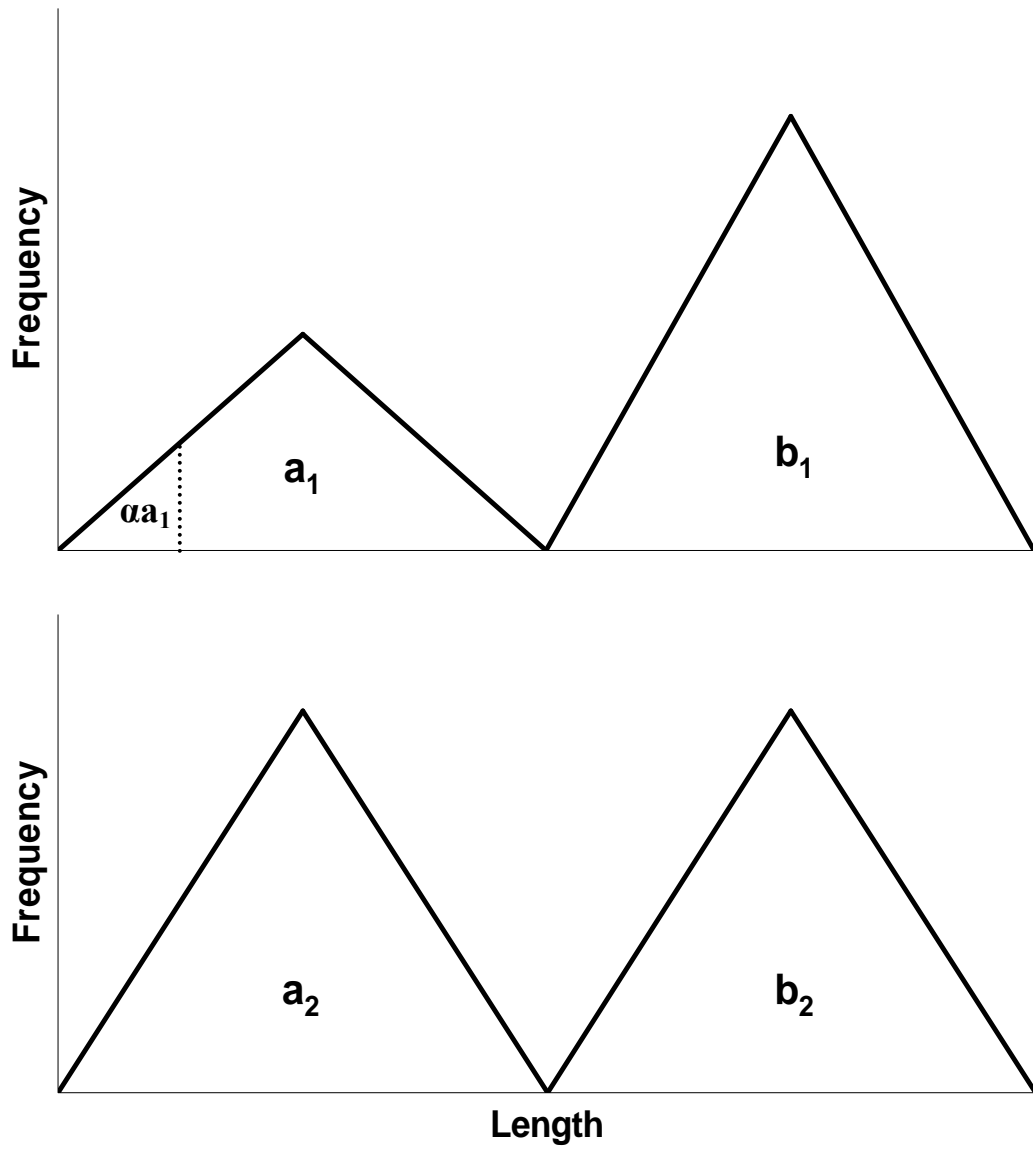
Southern management area

Figure 1

Figure 2

Figure 3

Appendix Figure 1.

Chapter 6

Using demographic models to determine intrinsic rate of increase and sustainable

fishing for elasmobranchs: pitfalls, advances and applications

Abstract

Leslie matrices and life tables are demographic models commonly used to evaluate the ability of specific elasmobranch life history strategies to sustain given levels and patterns of fishing pressure. These models are generally density-independent and provide an instantaneous rate of population growth for a specified set of life history traits which correspond to a specific population size. Many investigators are using these models to compute rates of population growth that they claim are estimates of maximum population growth rate ($r_{intrinsic}$); they then use these estimates to compute purported estimates of maximum sustainable fishing mortality. However, neither a Leslie matrix nor a life table can be used to estimate $r_{intrinsic}$ without additional information except in the special case where a severely depleted population is modeled. Only in a severely depleted population will competition for resources be at a minimum and both density-dependent compensation and the rate of growth be at a maximum (i.e., at $r_{intrinsic}$). The fundamental problem is to determine the life history parameters that would occur if the population were extremely depleted because extensive observations on extremely depleted populations are rare. In the absence of such data, $r_{intrinsic}$ can only be estimated from these types of density-independent models by extrapolating observed population growth rates towards zero population size. We illustrate the problems in, and describe methods for, estimating $r_{intrinsic}$, and present information on two species of elasmobranch: barndoor skate *Dipturus laevis* and lemon shark *Negaprion brevirostris*.

Classic demographic analysis, based on a life table or Leslie matrix, provides an estimate of the exponential (or, more properly, geometric) 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 current (short-term) rate of population change under current conditions. For the elasmobranchs, where many stocks have been severely depleted, the question is to what extent these populations can withstand fishing pressure. Recently, this question has been approached by attempting to use demographic models to determine the intrinsic or maximum rate of population increase, $r_{intrinsic}$, and therefore the maximum sustainable fishing pressure. However, fundamental errors in the interpretation of the models are common.

Problems in the use of a basic demographic analysis for estimating $r_{intrinsic}$ arise from the density-independent nature of their structure and the use of static life history parameter inputs. In reality, at least some life history traits must be pliable and able to respond to changes in population size. This forms the basic logic behind density-dependent compensation which explains why populations rarely go extinct and cannot grow beyond the bounds fixed by limiting factors (such as food sources or space) for extended periods (i.e., there is a carrying capacity of the environment).

Throughout most of this paper, we will assume for simplification of exposition that all compensatory response occurs in the survival in the first year of life (S_0) rather than in maturity, fecundity, or survival after the first year. This may be particularly justifiable in the case of elasmobranchs as it is unlikely that litter size or mating frequency could change appreciably and S_0 appears to be related to population size in at least the lemon shark (Gruber et al. 2001). When evidence exists that compensation can

occur in other parameters, this is easily incorporated into the models. In our analysis of the lemon shark (see Applications section), for example, we had evidence to support extending the compensatory response into the survival of age one animals.

Direct evidence to define density-dependent relationships is rarely available. In fact, even estimating the survival of the youngest animals, regardless of population size, is extremely difficult. Therefore, these models can be used in reverse, allowing first year survival (S_0) to be calculated assuming a schedule of reproductive output and survival (excluding S_0) and a known rate of population growth, e.g., a 10% rate of increase might be observed when a stock is released from fishing pressure, or zero growth might be observed or hypothesized when the population is at equilibrium (Vaughan and Saila 1976). Hoenig and Gruber (1990) expanded on this approach by estimating S_0 for a virgin population of lemon sharks *Negaprion brevirostris* assumed to be at equilibrium. They assume that changes in S_0 are the principal mechanism for density-dependent compensation and for a series of increasing values of fishing mortality, they calculated the S_0 that would result in equilibrium. Since it is unlikely that first year survival can rise to that of unfished adults, the value of fishing mortality that would require the first year survival to rise above that of an adult in an unfished population was interpreted as an upper limit to sustainable fishing mortality. Similarly, an upper limit to the intrinsic rate of population growth ($r_{intrinsic}$) is estimated by removing fishing pressure from this model. However, there is no guarantee that these upper limit estimates can be achieved.

A number of studies have followed this upper limit approach (Sminkey and Musick 1996; Casey and Myers 1998; Mollet and Cailliet 2002). However, Cortés' (2004) summary of studies using demographic analysis for elasmobranchs reveals that

many investigators purported to 1) calculate an actual value for $r_{intrinsic}$ (or, equivalently, for maximum sustainable fishing pressure) rather than an upper bound, or 2) tried to rank species by the amount of fishing mortality they can withstand.   The logic behind these attempts is generally unclear and is either flawed or based on unstated assumptions.

In this paper we first review the logic of simple demographic analysis using the Leslie matrix (but the same logic holds for life tables), show basic relationships, and discuss what can and cannot be inferred. We then discuss how additional information can be utilized to make additional inferences. We derive methods for estimating $r_{intrinsic}$ and apply them to two species of elasmobranch: barndoor skate *Dipturus laevis* and lemon shark *Negaprion brevirostris*.

Basics of Population Dynamics and Demographic Analysis

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 (Gotelli 1998; Caswell 2001). Models can be constructed assuming continuous or annual reproduction and, if the latter, assuming abundances pertain to just before breeding or just after breeding occurs.

Suppose we have the following information which would be required for an age-based demographic analysis: age at maturity (a_{mat}) = 3 years, longevity (a_{max}) = 6 years, survivorship at each age ($S_0, S_1, S_2,…,S_5$), and the production of females per female (f_1, $f_2, f_3,…,f_6$) which is a function of the percentage reproducing in each age class, frequency of births, sex ratio, and litter size. We assume numbers are tallied before reproduction takes place (pre-breeding census). We can then calculate from the number of females at

each age ($n_{1,t}$, $n_{2,t}$,...,$n_{6,t}$) the numbers of females there will be in the following year

($n_{1,t+1}$, $n_{2,t+1}$,...,$n_{6,t+1}$) where n_{ij} is the number of animals of age i at the start of year j. The

number of age-0 females produced will be:

$$n_{1,t+1} = S_0 \sum_{i=1}^{6} n_{i,t} f_i .$$
(1)

The number of females at all other ages is given by:

$$n_{i+1,t+1} = n_{i,t} S_i .$$
(2)

These basic relationships are fundamental to any demographic analysis including

life tables, matrix analysis, and Euler-Lotka approaches. In a Leslie matrix analysis the

life history information for our example is organized in a projection matrix **A** as:

$$A = \begin{bmatrix} 0 & 0 & S_0 f_3 & S_0 f_4 & S_0 f_5 & S_0 f_6 \\ S_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_5 & 0 \end{bmatrix} .$$

The number of females at each age at time t is denoted by:

$$N_t = \begin{bmatrix} n_{1,t} , n_{2,t} , n_{3,t} , n_{4,t} , n_{5,t} , n_{6,t} \end{bmatrix}^T .$$

The female population at time t + 1 is then given by

$$N_{t+1} = A N_t$$
(3)

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 (λ) of the matrix $\mathbf{A}$ as $r_{predicted} = \log_e(\lambda)$ (Vaughan and Saila 1976).   In a follow up study, Vaughan (1977) derived a computational method to calculate $r_{predicted}$ which is often used in practice.

In this type of demographic model, $r_{predicted}$ represents a snapshot of the population growth rate based on a fixed set of life history parameters and a given schedule of fishing mortality. In reality, populations are not governed by a fixed set of life history parameters, but by the dynamic relationship of these parameters to stock size. The basic logistic model of population growth has been used extensively in both fisheries and ecological research and is the simplest to include the logic of density-dependent compensation through a linear relationship of population growth rate to population size. Throughout this paper, the logistic model will simply serve to illustrate the importance of including stock size in the design and interpretation of a demographic model.   In reality the relationship may be curvilinear (see, e.g., Sibley et al. (2005)), but use of a nonlinear model requires more data which often will not be available.

The logistic model (and, in general, density-dependent models) states that under virgin conditions, a population will reach an equilibrium state around a carrying capacity (K) (Figure 1a). The number of births will equal the number of deaths and the population growth rate will equal zero until some force, such as fishing pressure, reduces the population size. At lower numbers, more resources are available to each individual and survival, particularly of first-year individuals (S_0), increases. If released from the fishing pressure, as in our example, a recovery begins in the population at a rate which is conditional on the population size relative to the virgin stock size. The logistic model

states that the instantaneous rate of growth will be greatest in an uncrowded condition.

As the population begins to recover and resources become increasingly limiting,

population growth slows and eventually approaches zero (i.e. births equals deaths). In

reality, virgin populations and populations that have not been fished for a very long time

may not have a zero growth rate at any particular point in time. However, we stress that

the expected or long-term average growth rate must be zero.

We will need the following definitions of instantaneous population growth rate

for this paper:

$r_{intrinsic}$ = maximum 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

$r_{conditional}$ = rate of population growth when there is no fishing mortality, given a

schedule of survival and reproduction (conditional on population size and

resulting density-dependent compensation) and given a stable age distribution

$r_{predicted}$ = predicted rate of population growth 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

$r_{observed}$ = observed rate of population growth (assuming no measurement error; no

assumption of stable age distribution is made)

It is important to note that the rate of population growth observed from actual field data,

$r_{observed,}$ should be expected to equal $r_{predicted}$ when a stable age distribution is present in the

population (Figure 2).

The concept of the population growth rate being linked to population abundance is critical to the design and interpretation of any elasmobranch demographic analysis (Vaughan 1977; Hoenig and Gruber 1990). Consider a hypothetical elasmobranch population under three different levels of exploitation: virgin, moderately fished, and depleted (Figure 1b). Assume that the fishing history has been stable for long enough that by time "a" any density-dependent compensation that could occur, has occurred, and the populations are at equilibrium. The three populations have realized different levels of density-dependent compensation to remain at equilibrium at different population sizes (N) and different levels of fishing mortality (F). Note that this implies that the predicted rate of population change is equal to 0 in all cases. Removing the fishing mortality (time "b") in each scenario reveals the rate of population increase, $r_{conditional}$, that can result at the given population size. The virgin population can realize no change in fishing mortality and continues at its carrying capacity in an equilibrium state ($r_{conditional} = r_{predicted} = 0$). The moderately fished population has been released from some level of fishing mortality and the calculated $r_{conditional}$ represents the short term growth potential of a population of that size when released from exploitation. In the depleted population, density-dependent compensation is at its maximum (S_0 is at its maximum in our example) and once released from fishing pressure the population will recover at its maximal rate ($r_{conditional} = r_{intrinsic}$). Thus, 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 being used in our example, population growth rate is related to the intrinsic rate of increase in the absence of fishing by the linear relationship (Figure 3):

$$r_{conditional} = r_{intrinsic} \left(1 - N/K\right).$$ (4)

When fishing occurs on all ages at an instantaneous rate F (per year),

$$r_{predicted} = r_{conditional} - F = r_{intrinsic} \left(1 - N/K\right) - F.$$ (5)

Using the calculated $r_{conditional}$ in each population to project the population growth forward in time after the cessation of fishing (Figure 1b) further illustrates the density-independent nature of the Leslie matrix/life table model. Exponential growth is predicted. This is realistic over the short term but becomes increasingly unrealistic as the stock grows larger. The value of $r_{conditional}$ is dependent on the life history parameters (S_0 in our example) which, in turn, are dependent on stock size. The value of $r_{conditional}$ and predicted exponential growth approximates the more realistic logistic growth model only for a specific stock size and thus only for a short period of time. It is therefore only possible to compute $r_{intrinsic}$ from a demographic analysis if the model parameters represent conditions in a severely depleted population or if additional information is available. In all other cases, all that is known about the calculated rate of population increase ($r_{conditional}$) is that it falls somewhere between 0 and $r_{intrinsic}$ (Figure 3).

Uses of the Leslie Matrix

The above is not meant to imply that a Leslie matrix has no value by itself. A demographic analysis can be used to check the validity of parameter estimates. For example, Grusha (2005) found that parameter values from the literature for cownose ray *Rhinoptera bonasus* in Chesapeake Bay seemed reasonable but led to a life table prediction that the population would crash under no fishing pressure unless S_0 exceeded

100%. In this case, or when S_0 is required to be greater than adult survival, life history parameters are suspect and need to be re-evaluated.

Unfortunately, for most elasmobranchs, the information necessary to determine $r_{intrinsic}$ through classic demographic modeling is unavailable. Even in the most well studied species where age-at-maturity, fecundity, natural mortality and even stock size are known, estimates of S_0, fishing mortality (F), and observed rate of increase ($r_{observed}$) are rare. These three parameters are closely linked. In situations where two of the three parameters are known, the Leslie model can be used to solve for the remaining one (assuming that all other model parameters are known). For example, in situations where F can be assumed to be zero, and survey data provides a known rate of population increase ($r_{observed}$), the model can be solved for S_0 (as in Vaughan and Saila 1976; Hoenig and Gruber 1990). Alternatively, if F is assumed to be zero and S_0 is known, the model can be solved for the current rate of population increase (in this case $r_{predicted}$ should equal $r_{conditional}$) (we return to this case when we consider the lemon shark data in the example section).   If F and S_0 are not known, as in most cases, there are an infinite number of solutions to the model that will result in equilibrium (or in a specified rate of population growth).

In situations where even less information is available, matrix models can be used to examine the effects of individual parameters while holding all the other parameters constant and accounting for initial conditions (age-composition). This can provide insights into the dynamics of the population, e.g., how various age-specific harvesting strategies affect the dynamics (Cortés 1994; Heppell et al. 1999; Beerkircher et al. 2002),

but does not allow quantitative predictions if some parameters are unknown and fixed at arbitrary values.

Pitfalls of Interpreting Demographic Analyses

For most elasmobranch stocks, empirical estimates of the necessary model inputs for determining $r_{intrinsic}$ and maximum sustainable fishing mortality are simply unavailable. Typically, parameter estimates are available for maturity-at-age, fecundity, longevity, and survival in the absence of fishing mortality for all but the youngest age class(es). In a few cases, estimates of observed population growth are available.

Lacking direct information, many studies have used empirical relationships to obtain survival rates. These relationships are of two types: those that provide a single value (e.g., Pauly 1980; Hoenig 1983; Jensen 1996) and those that provide age-specific values (Peterson and Wroblewski 1984; Chen and Watanabe 1989; Table 1). The assumptions behind the use of the two types of estimates are different and should result in a different interpretation of model results.

Most studies use empirical relationships that provide a single survival rate which presumably pertains to most of the lifespan in the absence of fishing. When this single value is used in a demographic analysis, it is assumed that first year survival (S_0) in a severely depleted population equals that of unfished adults and represents the maximum possible value, $S_{0,max}$. The calculated rate of population increase is then often interpreted as $r_{intrinsic}$. Although this can be a useful upper limit biological reference point there is no guarantee that a stock can exhibit this degree of compensation and growth, and thus no evidence that this represents $r_{intrinsic}$. The maximum achievable S_0 is likely to be species-

specific, lower than that of an adult, and a function of size at birth. Assuming that S_0 can reach adult levels will clearly tend to overestimate $r_{intrinsic}$ but to what degree is unknown. Thus, the rate of increase calculated by setting S_0 equal to survival of unfished adults gives us an upper bound proxy for $r_{intrinsic}$, i.e., a quantity related to $r_{intrinsic}$ that may have some use for fisheries management.

In some studies, purported estimates of $r_{intrinsic}$ have been calculated by specifying age-specific survival rates, including the first year, based on empirical relationships described by Chen and Watanabe (1983) or Peterson and Wroblewski (1984). However, these empirical relationships were not based on modeling severely depleted populations but, rather, are describing "normal" or virginal survival. Therefore, analysis of a Leslie matrix based on these parameter values should result in a value of $r_{conditional}$ of zero (i.e., the value corresponding to the average growth of a virgin population). Any departure from zero represents measurement error, not intrinsic rate of population increase. The expectation in much of the literature is that estimates of population growth calculated from a demographic analysis with no fishing mortality should be positive and that the amount of fishing mortality that results in an equilibrium state ($r_{predicted} = 0$) represents the maximum sustainable fishing pressure that can occur before a species is at risk of extinction. This is false.

If we consider the hypothetical populations presented in Figure 1b the error in this logic is clear. In the depleted population at time "a", $r_{conditional}$ is equal to $r_{intrinsic}$ while in the virgin population $r_{conditional}$ is equal to zero. In our depleted scenario, the F that results in equilibrium is the maximum sustainable fishing pressure. In contrast, the removal of a single fish per year (i.e., any F > 0) in our virgin population will result in negative

population growth under the Leslie (exponential) model (which does not allow for compensation). According to the widespread logic, this means that a virgin population is more susceptible to fishing pressure than a depleted population of the same species. This conclusion is obviously false and highlights the strong relationship between the results of a simple demographic model and the population size for which model parameters have been specified.

Ranking Species

A number of studies have suggested demographic analyses can be used for comparative purposes among species, i.e., to rank species according to their ability to withstand exploitation based on calculated values of rate of population increase (Smith et al. 1998; Walker and Hislop 1998; Frisk et al. 2002). Therefore, it is worth examining if a Leslie matrix or life table can be used to rank species if we can't get unbiased estimates of the intrinsic rate of increase. We consider four proxies for $r_{intrinsic}$, where rate of increase is computed with S_0

1) set equal to a constant for all species (Frisk et al. 2002);

2) set equal to survival of unexploited adults;

3) set equal to virgin survival, as computed from the formulae of Chen and Watanabe (1989) or Peterson and Wroblewski (1984);

4) solved for after setting adult survival equal to the square of the unexploited survival rate, i.e., equal to exp(-2M) (Smith et al. 1998).

 Species vary in their size at birth and thus presumably in their first year survival. However, under approach #1, it is assumed that all populations being considered have the

same maximum first year survival (Figure 4). That is, although we know the species

vary in life history traits, this approach assumes they don't vary at all in the parameter -

maximum S_0 - that is likely to play a major role in determining a species' scope for

compensation and therefore its intrinsic rate of increase. Thus, differences among

species in intrinsic rate of increase are due to differences in fertility and adult survival

only, according to this model. We would argue it is just as plausible, or more plausible,

that the first year survival of all species can rise to half way between virgin S_o and virgin

adult survival. In fact, the constant S_0 approach has important implied assumptions

regarding scope of density-dependent compensation which are illustrated in Figure 4.

Population A and the barndoor skate are assumed to have almost no scope for

compensation while first year survival in population D and the little skate is fully

compensated reaching close to adult values. Species B resembles species D in having

very low survival in virgin populations but the first year survival of D can rise to that of

adults whereas the first year survival of B can only rise half way to adult survival. It is

not clear that this is a reasonable assumption. Therefore, this ranking of species'

resiliency is conditional on the model of compensation being correct, which hasn't been

demonstrated.

Many studies compute an upper bound proxy for $r_{intrinsic}$ by setting first year

survival equal to virgin adult survival. This has the advantage of inducing a positive bias

so that upper bounds to both intrinsic rate, and thus sustainable fishing mortality, can be

obtained. That is, with this procedure we can conclude certain levels of fishing mortality

are not sustainable. However, this proxy may or may not be appropriate for ranking

species' growth potential. Consider the sand tiger shark *Carcharias taurus* versus the

tiger shark *Galeocerdo cuvieri*. Both species have large maximum sizes and high

longevities but the former has two large pups while the latter has dozens of small pups.

The sand tiger pups probably have high survival under virgin conditions and it is not

unreasonable to suppose their survival could rise the small distance to equal adult

survival. The tiger shark pups are much smaller and presumably have much lower

survival under virgin conditions than the sand tiger. It is less likely that the survival of

small tiger pups can approach the survival of adults. In other words, the potential scope

of compensation may be markedly different even for these two apparently similar

species. Thus, investigators can disagree over whether the use of this proxy for ranking

species' population growth potential is reasonable.

Next, consider the estimates that result when first year survival is set equal to the

Chen and Watanabe (1989) or the Peterson and Wroblewski (1984) estimates. All the

estimates of population growth rate should be close to zero so all we're getting from this

procedure is measurement error which clearly is not a basis for ranking species.

Finally, consider the procedure of Smith et al. (1998). These investigators

recognized the problems that result from the density-independent nature of demographic

models and began the process of developing a methodology and a biological bench mark

which is comparable across species. The main assumption in their model is that a

population being fished to produce maximum sustainable yield (MSY) will be at half of

the virgin stock size and will have adult mortality equal to $Z = F + M = 2M$. They then

assume that any density-dependent compensation occurs in S_{juv} (survival of juveniles)

rather than simply in S_0. With these clearly stated assumptions, they then follow the

methodology of Vaughan (1977) and solve the model for the S_{juv} that results in

equilibrium under the MSY fishing conditions. They then remove the fishing mortality

from the model and solve for the resulting instantaneous rate of population growth which

they term "rebound potential" or r_{2M}. In this way they have attempted to standardize the

level of density-dependent compensation in different species by deriving an estimate of

S_{juv} that is directly related to the life history parameters of the species. Their r_{2M} may be

a valid proxy for $r_{intrinsic}$, and has the potential to be used in the comparative demography

among species.

Although the Smith et al. (1998) approach has avoided some of the main pitfalls

of demographic analysis by accounting for density-dependent compensation through

clear logical assumptions, their assumptions have not been validated and their procedure

provides no indication of how far these "rebound potentials" may be from $r_{intrinsic}$. Thus,

managers are still faced with uncertainty about the maximum sustainable fishing

pressure. To determine this, an actual estimate of $r_{intrinsic}$ is required.

Advances in Methodology

The absence of detailed information about a depleted population necessitates the

use of alternative methods to estimate $r_{intrinsic}$. There are two aspects to the problem: 1)

determining (parameter) values of $r_{conditional}$ that are tied to a corresponding stock size and

2) determining $r_{intrinsic}$ from two or more values of $r_{conditional}$. The tools to obtain an actual

estimate of $r_{intrinsic}$ have long been in use in both fisheries and ecological research. Ricker

(1975) summarized the early use of the logistic model for fishery assessment (and

estimating $r_{intrinsic}$) when only limited data were available. Although he dealt with

biomass models, the mathematics are the same if one substitutes numbers for biomass. We build our results on those presented by Ricker.

We assume that the schedule of age-specific natural mortality for all ages above the first, and age-specific fecundity, are known for a particular population. Thus, everything is known except three parameters: first year survival, fishing mortality, and rate of population increase, $r_{observed}$. As previously described (in Uses of the Leslie Matrix section), these three parameters are closely linked and if two of the three are known, the Leslie model (or a life table) can be used to solve for the third. For example, suppose the instantaneous natural mortality rate is estimated to be 0.2 year^{-1} and the instantaneous fishing mortality rate is determined from a tagging study to be 0.3 year^{-1}. Then all survivals except S_0 are exp(-.2 - .3) = 0.6. If we know the population is currently declining by, say, 5% per year ($r_{observed} = \ln(0.95) = -0.051$ year^{-1}), then the model can be solved for S_0 using Vaughan's (1977) method. Then, we can analyze a Leslie matrix with the same fecundities and same S_0 but with the other survivals adjusted to eliminate the fishing, i.e., survival for all ages except the first = exp(-.2) = 0.8. This provides an estimate of $r_{conditional}$. If the population being modeled is at low abundance, the calculated value of $r_{conditional}$ should be close to $r_{intrinsic}$.

For the example above, where fishing mortality applies to all ages, there is a simpler solution:

$$r_{predicted} = r_{conditional} - F \ . \hspace{4cm} (6)$$

Hence, $r_{conditional}$ for our example = -0.051 + 0.30 = 0.249 year^{-1}.

The second step is to use the estimates of $r_{conditional}$ to estimate $r_{intrinsic}$. We make use of the linear relationship between $r_{conditional}$ and population size (eq. (4)), and utilize

observations on population behavior at two or more stock sizes. There are two cases to consider. First, suppose that an estimate of the conditional rate of population growth ($r_{conditional}$) is available along with an estimate of the corresponding population size (N) as a fraction of the virgin population size (K), i.e., an estimate of N/K is available. Then by virtue of the fact that the conditional rate is a linear function of population size (Figure 3; Equation 4), and the value of $r_{conditional}$ is zero when N = K, we can solve for the intercept as:

$$ r_{intrinsic} = \frac{r_{conditional}}{1 - \dfrac{N}{K}} = \frac{K \, r_{conditional}}{K-N} \, . \tag{7} $$

This methodology differs from all the current approaches to demographic analysis of elasmobranchs in that the results do not simply provide a snapshot of population growth under a given set of circumstances but rather defines the overall relationship between population size and rate of population growth according to the theory of logistic growth.

The second case is where we have information collected when the population is observed at two or more stock sizes, but we do not know how those stock sizes relate to the virgin population level. Instead, we know the relative size of the population at the various times. Let us assume we have survey data that gives relative population size (qN, where q is the catchability coefficient, a constant relating the index to the population size N) at two points in time and the corresponding information necessary to calculate $r_{conditional}$ (Figure 3). Since we're assuming the relationship between $r_{conditional}$ and N is linear and now know the ratio of qN's we can derive the following equations:

$$ r_{conditional \, 1} = \frac{r_{intrinsic} \, (q \, K - q \, N_1)}{q \, K} \tag{8} $$

$$r_{conditional\ 2} = \frac{r_{intrinsic}\ (q\,K - c\,q\,N_1)}{q\,K}, \tag{9}$$

with c as a known constant ($N_2 = c\,N_1$). Although these two equations have three

unknowns (K, $r_{intrinsic}$, and N_1), a unique solution for $r_{intrinsic}$ results as:

$$r_{intrinsic} = \frac{(r_{conditional\ 2} - c\,r_{conditional\ 1})}{1-c}. \tag{10}$$

Therefore, to obtain an estimate of $r_{intrinsic}$ we can calculate $r_{conditional}$ at two points in time

for which the relative population sizes are known.

Application to Elasmobranchs

      To illustrate the points in this manuscript we consider two species of

elasmobranch: lemon shark and barndoor skate. For both species sufficient data are

available to illustrate the methods presented in this paper and generate at least

preliminary estimates of $r_{intrinsic}$. Our intent is to demonstrate the methodology while a

more detailed analysis is in preparation for both species.

      Lemon shark-- The lemon shark is one of only a few elasmobranch species for

which empirical estimates of S_0 are available. Estimates of S_0 were obtained for differing

stock sizes between 1995 and 1999 through a tagging and depletion study in Bimini,

Bahamas (Gruber et al. 2001; Gruber unpublished). Results from this study suggest that

density dependence is occurring in the lemon shark nursery area with an apparent inverse

relationship between first year survival and size of age-0 population (Figure 5). Since

there is no directed fishery for the lemon shark juveniles at Bimini, we assume that F for

juveniles is equal to zero. A pre-breeding, birth-pulse, female only Leslie matrix model

was constructed with age at maturity of 12 years, and a longevity of 25 years. Lemon

sharks are believed to have biennial parturition with an average of 12 pups resulting in a fecundity term for the matrix of 3 females per year (Feldhiem et al. 2002). Since lemon sharks have been shown to stay in the nursery lagoon at Bimini for the few years of life (Morrissey and Gruber 1993), second year survival was set at the mean of first year and adult survival.

The model was then solved for the population growth ($r_{conditional}$) that would occur given each estimate of first year survival (note that this implies we set survival after the second year equal to that which would occur in the absence of fishing; in this case we used S = 0.85 based on the Hoenig (1983) maximum age formulation). The relationship between each years' estimated population size and $r_{conditional}$ allows us to extrapolate to a population growth rate as the population size approaches zero (i.e., $r_{intrinsic}$) of 0.08 year^{-1} (Figure 5). As a check on the feasibility of this estimate, the model was solved for the S_0 that would be required for the population to grow at a rate of 0.08 year^{-1} assuming F = 0. Given the life history parameters used in our model, S_0 would be required to be 110% for the population to grow at our estimated $r_{intrinsic}$. Clearly this is infeasible and not surprising given an extrapolation from five data points. However, if we use the lower confidence limit from our relationship between $r_{conditional}$ and population size, the estimate of $r_{intrinsic}$ is 0.03 year^{-1} which would require a first year survival of 64% (Figure 5). Assuming that S_0 cannot be greater than adult survival (S = 85%) we now have an upper bound for $r_{intrinsic}$ of 0.06 year^{-1} and therefore an overall potential range of $r_{intrinsic}$ for the lemon shark of 0.03 – 0.06 year^{-1}.

Barndoor Skate--The barndoor skate was reported to be on the brink of extinction in 1998 (Casey and Myers 1998). As international fishing fleets were heavily fishing the

northwest Atlantic, National Marine Fisheries Service (NMFS) survey indices for the

barndoor skate in the Gulf of Maine and Southern New England went from highs of near

0.8 fish/tow in the early 1960s to lows of near zero for the 1970s and 1980s. In 1994,

three large areas on Georges Bank (off Massachusetts) were closed to all mobile fishing

gear. Since then, survey indices for the barndoor skate have been increasing at an annual

rate of approximately 38% providing an estimate of $r_{observed}$ of $\log_e(1.38) = 0.32$ year^{-1}.

An estimate of $F = 0.1$ year^{-1} was generated by using a new non-equilibrium form of the

Beverton-Holt mean length mortality estimator (Gedamke and Hoenig 2006) to estimate

a total instantaneous mortality rate (Z) of 0.25 to 0.31 year^{-1}, and then subtracting the

Pauly (1980) estimate for instantaneous natural mortality (M) of 0.17 year^{-1}. We assume

this fishing mortality pertains to all ages because the skates are born at a large size of

nearly 20 cm total length. Given an F of 0.1 year^{-1} we solved the Leslie matrix model for

an S_0 of 56% which would be necessary for the population to be growing at an $r_{predicted}$ of

0.32 year^{-1}. Fishing pressure was then removed from the model to generate an estimate

of $r_{conditional}$ of 0.41 year^{-1} (Equation 6).

  Although the barndoor skate population is clearly depleted and our estimated

$r_{conditional}$ should approximate $r_{intrinsic}$, we can take our analysis one step further by

considering relative stock sizes from the NMFS survey data. In 1994 the index was at

approximately 10% of the high recorded at the start of the time series in 1963. If we plot

the 0.8 fish/tow maximum observed in 1963 as representing the virgin condition (i.e., r =

0) with our estimate of $r_{conditional}$ at the corresponding survey index (0.07 fish/tow), we get

two points which uniquely define a straight line. Extrapolating to a stock size of zero

gives an estimate of $r_{intrinsic}$ of 0.45 year^{-1} (Figure 6). If the index in 1963 represents the

situation with some fishing, then the rightmost point in Figure 6 should be farther to the

right, thus lowering the y-intercept. Because the barndoor skate population was so low in

1994, the uncertainty in the virgin stock size affects the estimated $r_{intrinsic}$ only slightly.

The increase in the barndoor skate population size observed in the NMFS surveys

provides compelling evidence that the skate population can grow rapidly, in excess of

30% per year. The corrections for fishing mortality and population size may be less

compelling at this point but clearly demonstrate that such calculations are feasible.

Discussion

We have shown that estimation of the intrinsic rate of increase can be simple if

observations can be made on a severely depleted population released from fishing

pressure. This was approximately the case for the barndoor skate. But, in general,

estimation of intrinsic rate of increase is an involved process that requires some

information on relative stock size. Thus, most reports of intrinsic rate of population

increase are wrong *sensu strictu* although they may have value as an index of, or proxy

for, the intrinsic rate. Indeed, one may ask if the confusion in the literature between

proxies and actual estimates of $r_{intrinsic}$ may be little more than a matter of semantics. We

do not feel this is the case. Rather, we think that the basic requirement for estimating

$r_{intrinsic}$ from a Leslie matrix (i.e. modeling a depleted population) is largely being

overlooked and there are three different aspects to the problem.

First, the confusion is understandable because the standard texts do not emphasize

the relationships between $r_{intrinsic}$, $r_{conditional}$ and $r_{predicted}$. For example, one textbook

(Gotelli 1998) defines the symbol *r* to be the intrinsic rate of increase and then estimates *r*

157

for a virgin population and after 50% of the population is removed. We see these

problems translated to the elasmobranch literature with such conclusions as positive

values for "virginal intrinsic rate of increase" (Xiao and Walker 2000) (i.e., estimating

that an unexploited population will increase exponentially forever).

Second, the perception that intrinsic rate of increase can easily be obtained from a

Leslie matrix or life table negates the importance of advancing the field through

development of new techniques. The importance of collecting additional information is

thus missed.

Third, results from demographic analyses are being used as the basis for

management recommendations in ways that are probably not reasonable in the sense of

not accomplishing what is intended. We now amplify this last point by looking at studies

that touched on the population growth potential of lemon sharks.

Cortés (2002) recognized that knowledge about some population parameters is

uncertain and developed a demographic analysis that translates uncertainty in input

parameters to uncertainty in output parameters through a Monte Carlo simulation

procedure.   Although this method clearly addresses an important problem in the

demographic modeling of species with limited data, the uncertainty defined for model

inputs provides only subjective opinions about the uncertainty in the outputs (Restrepo et

al. 1992). How first year survival (or survival in the first few years) of the lemon shark

was handled is critical because most of the scope for compensation probably occurs in

these juvenile stages, particularly the first year or two. A probability density function was

created for first year survival as a triangular distribution with the lower limit coming from

the weight-specific methods for unexploited populations and the upper limit coming from

the methods that assume equal survival for all ages (in the absence of fishing). The peak

of the triangular distribution was at the extreme left rather than the right. This, in effect,

is saying that the most likely amount of compensation is zero and the greater the

compensation postulated the less likely it is. One cannot be surprised, then, if the

estimates of rate of population growth averaged over the subjective probability

distribution of first year survival turn out low. In effect the model is based *a priori* on an

assumption of low compensation.

Although Cortés (2002) clearly stated that his estimates of population growth

should be treated as indices, the underlying assumption of the study design must be

recognized in the interpretation of results. Our concern is that the confusion about

appropriate modeling may have important management implications. For example, if

parameters representing virgin populations are erroneously used to compute intrinsic rate,

the resulting low estimates may lead to the conclusion that only extremely low catches

can be tolerated by some species and modest levels of bycatch may lead to stock collapse

and possibly extinction. In contrast, a more realistic analysis that recognizes the

importance of compensation in early life survival may suggest modest fishing pressure is

sustainable and thus allow for bycatch. The credibility of scientists may be at stake if

predictions of collapse prove wrong.

Conclusions

The use of a basic Leslie matrix or life table demographic analysis on

elasmobranch populations is generally challenging due to limited information on

population trends, fishing mortality and life history parameters. Study designs must

carefully consider the information available and take one of three approaches. The first is to determine the life history parameters that would occur if the population were extremely depleted. In this case, the instantaneous rate of increase calculated from the model can be assumed to approximate $r_{intrinsic}$ and therefore one can estimate maximum sustainable fishing mortality. For most species, however, not enough information is available and a second more complex approach must be taken. One must recognize that a basic demographic analysis only provides an instantaneous rate of population growth for a specific set of life history parameters associated with a specific population size and not $r_{intrinsic}$. With additional data, as we present in this paper, it is possible to estimate $r_{intrinsic}$ from the results of basic demographic analyses by extrapolating observed population growth rates towards zero population size. The third approach, when data are insufficient for estimating $r_{intrinsic}$, is to be content with calculating a proxy for $r_{intrinsic}$ such as an upper bound, and presenting it as such.

Researchers must recognize the close link between the methods of parameter estimation, population size and the results of a density-independent demographic model. When using age specific estimates of survivorship (e.g., based on Chen and Watanabe (1989) or Peterson and Wroblewski (1984)), and without incorporating stock size in the analysis, estimates of $r_{intrinsic}$ and maximum sustainable fishing pressure will be underestimated. From a management perspective, this is clearly a conservative approach. However, the credibility of scientists and the practice of demographic modeling will be thrown into question if predictions of collapse or extinctions are proven wrong. On the other hand, when adult survival is used for all age classes only proxies for $r_{intrinsic}$ are generated and there is no guarantee that the population can exhibit this degree of

compensation. These estimates must be considered only as upper bounds and used cautiously in management decisions.

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Table 1. Methods commonly used to determine survival rates in demographic analysis with required

parameters. Estimates were made with parameters for the barndoor skate from Gedamke et

al. 2004 (age at maturity (A_{mat}) of 6.5 years, and von Bertalanffy growth parameters (k, L_{inf},

and t_0) of 0.14 yr^{-1}, 166.3 cm, and -1.29 yr, respectively), an assumed maximum age (A_{max})

of 25 years, and a water temperature of 8.5 ^{0}C (Myers et al. 1997). Methods used: Hoenig

(1983); Pauly (1980), Chen and Watanabe (1989), Jensen (1996), Petersen and Wroblewski

Age	Hoenig (A_{max})	Pauly (L_{inf}, k, Water temperature)	Jensen (A_{mat})	Jensen (k)	Chen and Watanabe (Age, k, t_0)	Peterson and Wroblewski (Weight at age)
0	0.846	0.843	0.776	0.811	0.429	0.517
1	0.846	0.843	0.776	0.811	0.600	0.649
2	0.846	0.843	0.776	0.811	0.684	0.714
3	0.846	0.843	0.776	0.811	0.733	0.752
4	0.846	0.843	0.776	0.811	0.765	0.777
5	0.846	0.843	0.776	0.811	0.787	0.795
6	0.846	0.843	0.776	0.811	0.803	0.808
7	0.846	0.843	0.776	0.811	0.844	0.818
8	0.846	0.843	0.776	0.811	0.844	0.826
9	0.846	0.843	0.776	0.811	0.844	0.832
10	0.846	0.843	0.776	0.811	0.844	0.837
11	0.846	0.843	0.776	0.811	0.844	0.841
12	0.846	0.843	0.776	0.811	0.844	0.844
13	0.846	0.843	0.776	0.811	0.844	0.847
14	0.846	0.843	0.776	0.811	0.844	0.850
15	0.846	0.843	0.776	0.811	0.844	0.852

Figure Headings

Figure 1. a. Population dynamics and density-dependent response in $r_{predicted}$ to the

addition and removal of two levels of constant fishing pressure F,

according to the logistic model of population growth.

b. Steady state (point a) and logistic growth of populations recovering from

three levels of exploitation (point b) and relationship to model predictions

of exponential growth. The shaded regions show where logistic and

exponential models give similar results

Figure 2. Population size assuming initial population size and schedules of reproduction

and survival are known; as predicted under fishing pressure ($r_{predicted}$), under

conditions of no fishing pressure ($r_{conditional}$) and at the maximum rate ($r_{intrinsic}$)

assuming a stable age distribution, and as observed from catch data ($r_{observed}$) if a

stable age distribution is not present as an initial condition.

Figure 3. The instantaneous rate of population growth, $r_{conditional}$, for a stock as a function

of stock size under logistic growth when fishing mortality is zero. When fishing

mortality = F on all ages, $r_{predicted}$ = $r_{conditional}$ – F = $r_{intrinsic}$ (1-N/K) – F.

Relationships used to derive equations (8)-(10) for $r_{intrinsic}$ based on survey indices

are indicated. q is a constant relating the index to actual population size.

Figure 4. Model for compensation in which all species attain the same maximum value

of S_0 (indicated by the dashed line) regardless of first year survival in a virgin

population (bottom of bars) and regardless of adult survival in the absence of

fishing (top of bars). Species A, B, C and D represent hypothetical populations.

For the little, winter and barndoor skates adult survival is as used in Frisk et al.

(2002) and first year survival was calculated using the method of Peterson and Wroblewski (1984). Note the differing levels of compensation that are assumed when a constant S_0 is used.

Figure 5. Upper solid line: relationship between first year survival S_0 of lemon sharks and population size of juveniles at Bimini Bahamas as determined from a tagging depletion study. Note one additional data point has been calculated beyond that presented by Gruber et al. (2001).

Lower solid line: relationship between $r_{conditional}$ and corresponding population size (first year survival used to calculate each $r_{conditional}$ is also indicated). The y-intercept represents the estimated $r_{intrinsic}$ and the dotted lines represent the 95% confidence intervals for the regression. Also shown on the y-axis are the first year survival rates corresponding to three values of $r_{conditional}$. The shaded area shows the range of possible values for $r_{intrinsic}$ consistent with the data and consistent with the maximum value of S_0 not exceeding adult survival.

Figure 6. Relationship between population growth rate and NMFS survey index of population size for the barndoor skate. Point 'a' is $r_{observed}$ based on change in the survey index over time, point 'b' is calculated $r_{conditional}$ at abundance $= 0.07$ fish/tow, and point 'c' indicates estimated $r_{intrinsic}$. The dashed line indicates the slight reduction in $r_{intrinsic}$ that would occur if the virgin population size (0.8 fish/tow) is an underestimate.

Figure 1.
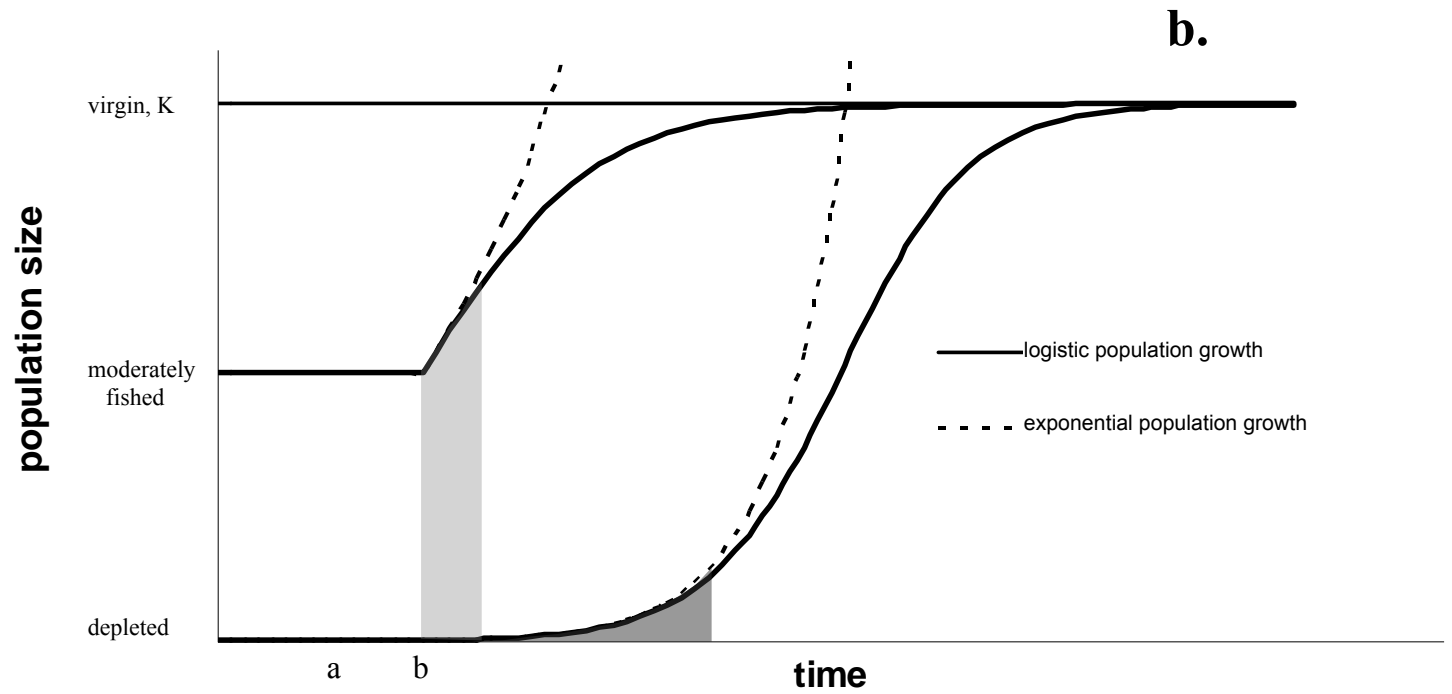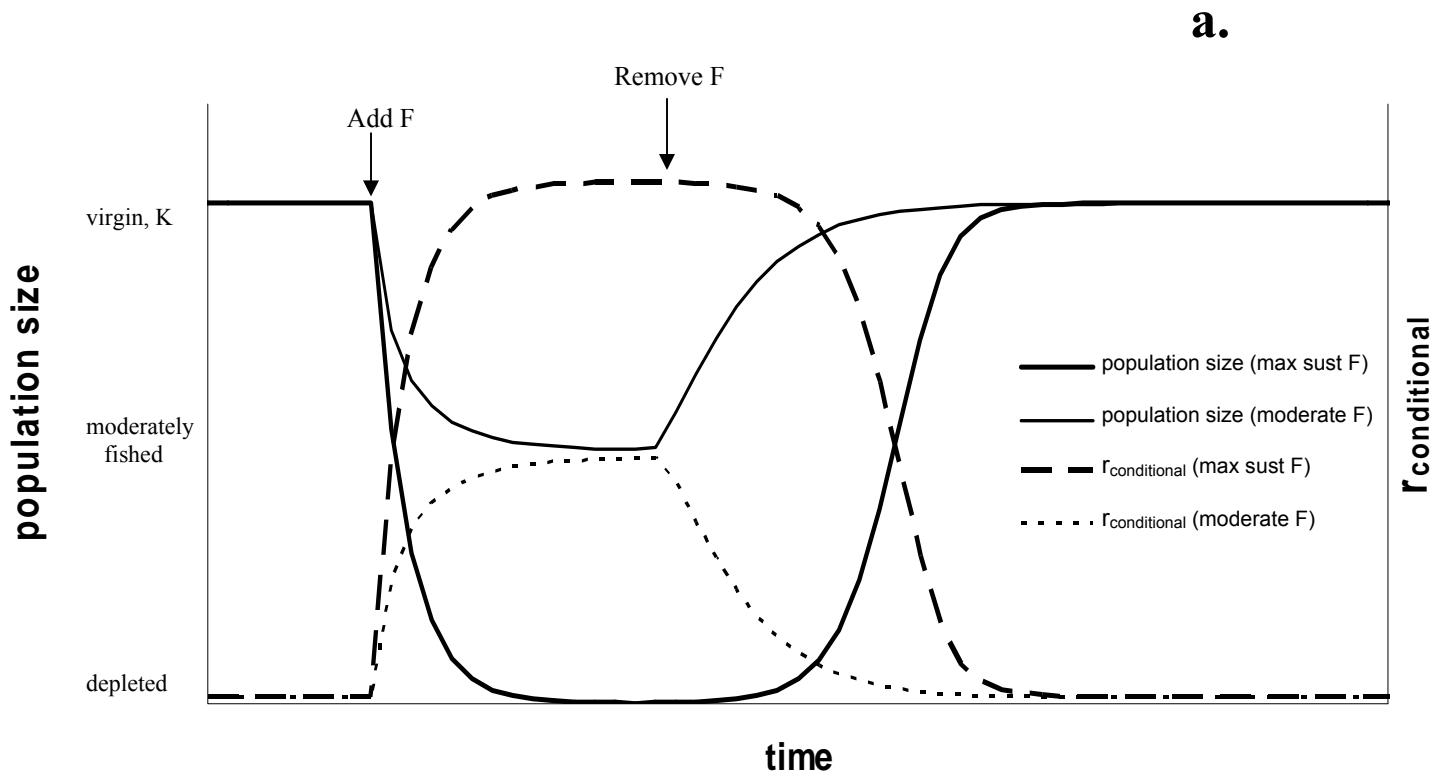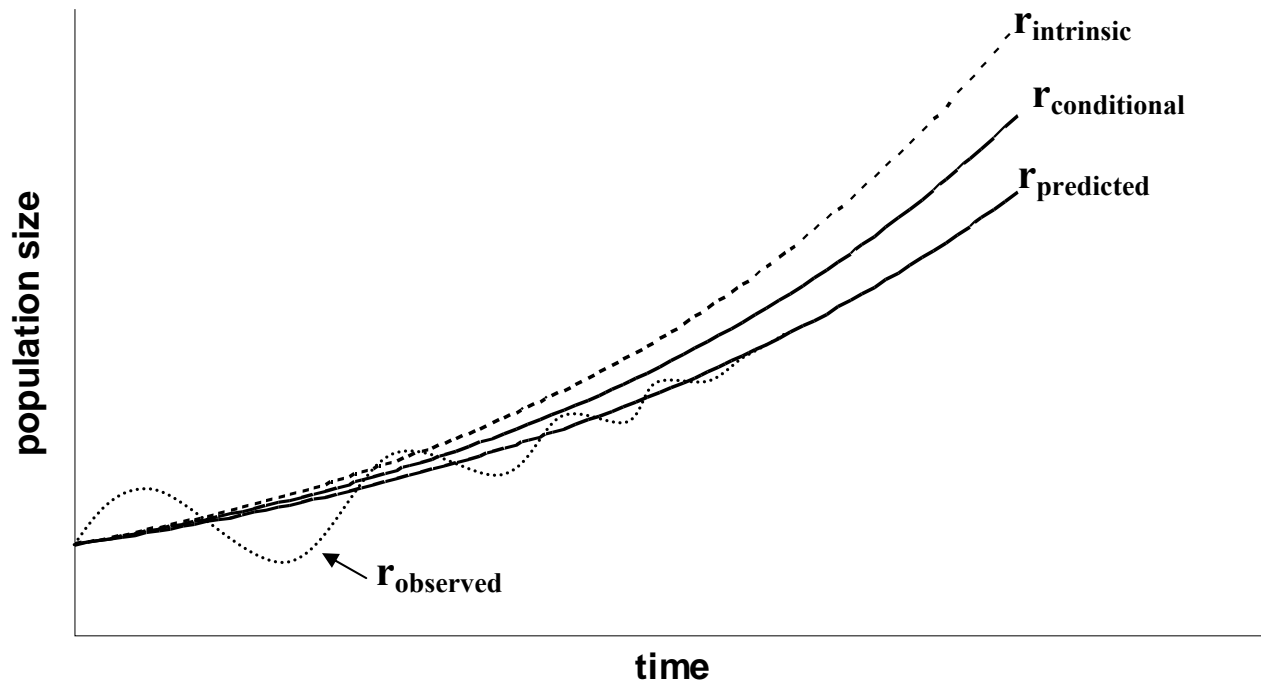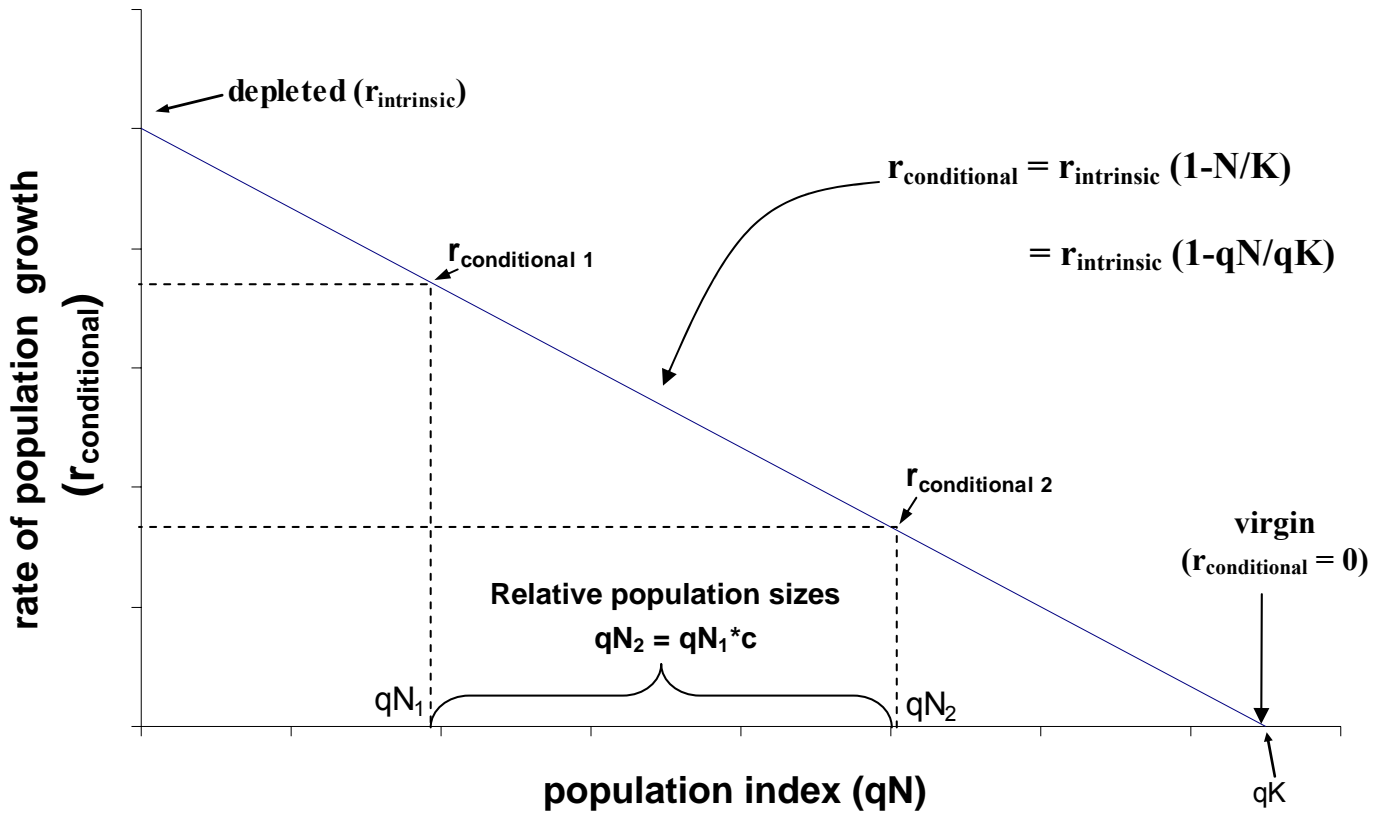
Figure 2.

rate of population growth ($r_{conditional}$)

depleted ($r_{intrinsic}$)

$r_{conditional} = r_{intrinsic} (1-N/K)$

$= r_{intrinsic} (1-qN/qK)$

$r_{conditional\ 1}$

$r_{conditional\ 2}$

virgin ($r_{conditional} = 0$)

Relative population sizes
$qN_2 = qN_1*c$

qN_1

qN_2

qK
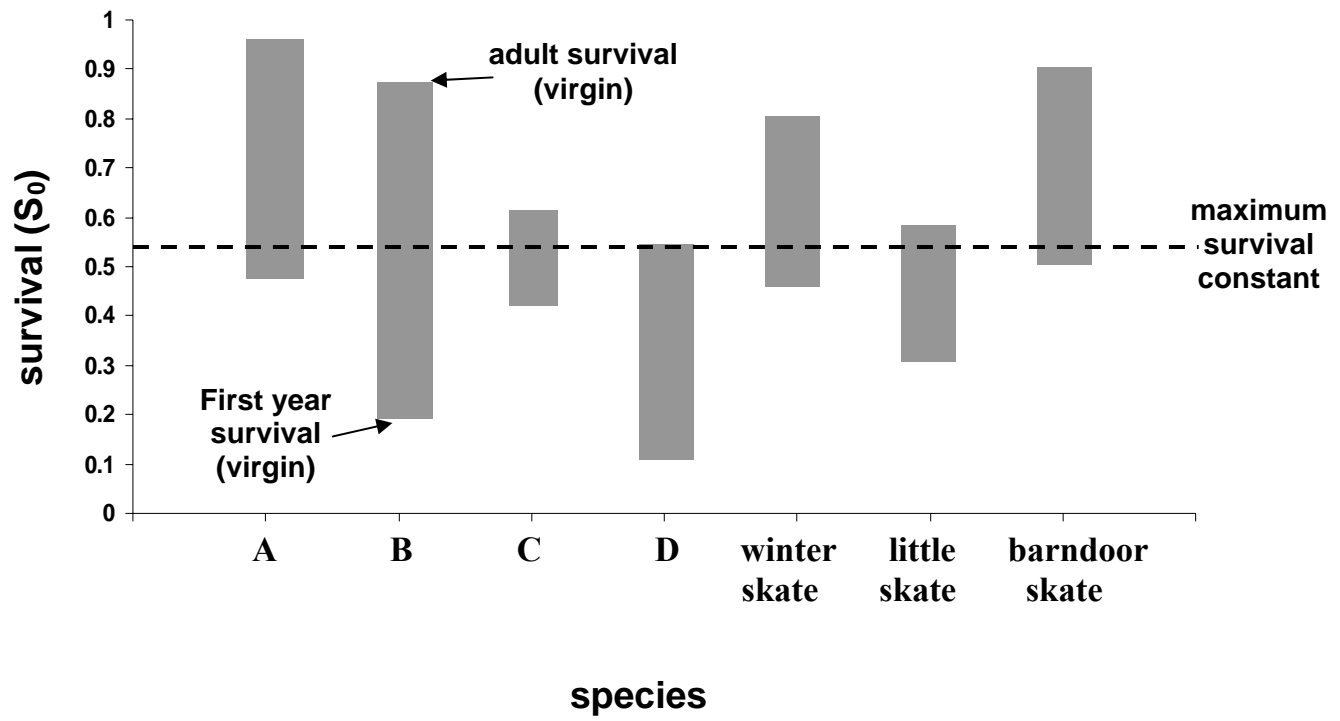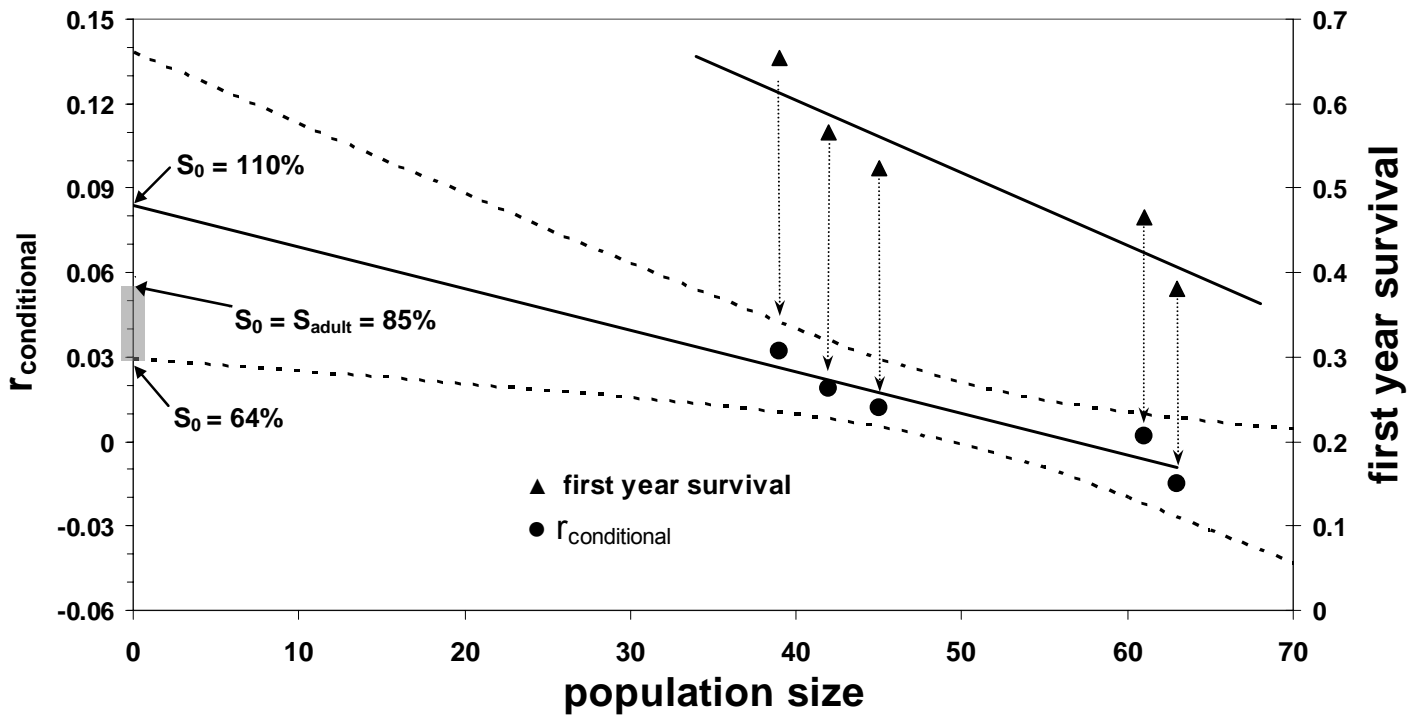
population index (qN)
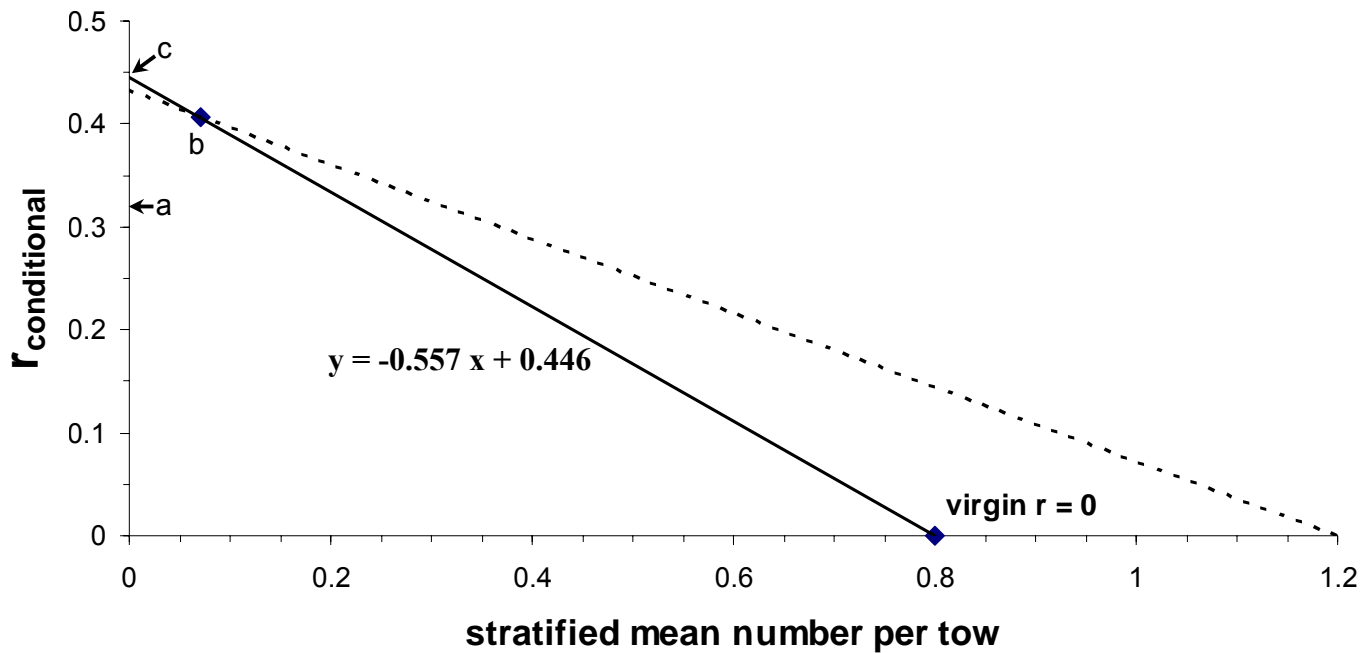
Figure 3.

Figure 4.

Figure 5.

Figure 6.

Chapter 7

Total Mortality Rates of the Barndoor Skate, *Dipturus laevis,* **in the Northeast**

United States, 1963-2005

Abstract

The barndoor skate population in the offshore waters of the Northeast United States was reported to be possibly on the brink of extinction in 1998. Managers were faced with the task of assessing a population with limited life history information and survey data that contained only a few animals a year. One of the key pieces of information to assess the threat to the species is the current mortality rate. Unfortunately, estimating this parameter through classical approaches proved difficult. In this study we develop variants of commonly used methodologies to estimate total mortality. We present two methods: a length based estimator and one based on the catch rates of recruits and adults. Both approaches provided similar results suggesting that mortality rates were very high (0.89 – 1.0) in the late 1960's. Recently, and at approximately the same time as the large area closures on Georges Bank, the total mortality rate appears to have been reduced to very low levels.

Introduction

The barndoor skate *Dipturus laevis* is one of seven species in the United States Northwest Atlantic skate complex. Although in the past there have been a limited number of vessels targeting the species, it is now only caught as bycatch in the groundfish trawl and scallop dredge fisheries. The species received little attention until a recent article published in *Science* reported that the barndoor skate might be on the brink of extinction (Casey and Myers 1998). Casey and Myers (1998) reported that the barndoor skate, once a common bycatch species off southern Newfoundland, had become locally extirpated in parts of its northern range due to overfishing and the pattern of decline was similar throughout its range.

The National Marine Fisheries Service (NMFS) began the difficult task of evaluating the threat to the species with virtually no information available on the life history of the species and only limited information available from a 40 year time series of trawl survey data. One of the key parameters necessary to accurately assess stocks, in this process, is the level of total mortality that is occurring in the population. Total mortality results from both natural mortality (M) and fishing mortality (F) and when compared to trends in abundance can provide valuable insights into the population dynamics of the species.

Unfortunately, estimating this parameter through classical approaches proved difficult. Data from the Northeast Fisheries Science Center (NEFSC) groundfish surveys on Georges Bank and the Gulf of Maine was extremely limited as survey catches had declined to near zero soon after the start of the survey's in 1963.. In fact, the NEFSC fall groundfish survey, which is the longest standardized time series of data available, caught

only 116 individuals in the 30 years between 1970 and 2000. In seven of those years, no barndoor skates were observed in the survey. An obvious recovery in the population has only been evident since the late 1990's as more individuals have been caught and survey indices have been steadily increasing.

In this study we evaluate the historical and current mortality on the barndoor skate population by developing two variants of commonly used methodologies.   We use two types of data from the NEFSC fall survey: mean lengths and catch rates.   Mean length data are commonly used to estimate mortality through the Beverton-Holt mean length mortality estimator because this method has limited data requirements. Gedamke and Hoenig (2005) developed an extension of this method for utilization in non-equilibrium situations but the application of this approach to an elasmobranch required the incorporation of trends in recruitment and further developments. Our second data source, catch rates, is also commonly used to estimate mortality through the Heincke method. However, this approach is formulated to include only information from two consecutive survey years (Heincke 1913, cited in Ricker 1975). Due to the variability of the survey indices available for the barndoor skate, we use the recent generalization of this approach which includes information from multiple years when survival is assumed to have been constant (Gedamke, 2006).

Materials and Methods

Available Trawl Survey Data

The National Marine Fisheries Service has conducted research surveys in both the US and Canadian waters of the Northwest Atlantic for over three decades. Surveys have

been conducted in the fall and spring beginning in 1963 and 1968, respectively (NEFSC 1999). A stratified random sampling design is used with stations stratified based on depth, latitude, and historical fishing pattern. The offshore surveys were designed to sample groundfish and have used a Yankee bottom trawl. Surveys were generally conducted in 27 to 366 meters of water, with an occasional deeper tow in the canyons of the continental shelf.

The spring and fall surveys are the primary indices used by the skate plan development team (PDT) and the New England Fisheries Management Council for the assessment of the NW Atlantic skate complex. In this study we focus on the fall survey as catch rates are generally higher than those in the spring and it provides the longest time series of standardized data. Barndoor skates are rarely caught in the mid-Atlantic survey so we also limit ourselves to an analysis of the New England offshore survey which covers Georges Bank and the Gulf of Maine. Between 1963 and 2005, between 167 and 374 survey tows were conducted in these regions. At each station the number and aggregate weight of each species is recorded in addition to the total length of each individual.

Model Development

Estimating Mortality from Mean Lengths

The basic process behind our methodology is the decrease in mean lengths that occurs when a population is exploited. Baranov (1919; cited in Ricker, 1975) was apparently the first to deduce this concept and note that the equilibrium mean length in a fish population is inversely related to the mortality rate experienced by the population.

Beverton and Holt (1956, 1957) derived an expression for estimating the total instantaneous mortality rate, Z, from the mean length, $\overline{L}$. The Beverton-Holt mortality estimator has received widespread use, especially in data-limited situations, because the only required information are the von Bertalanffy growth parameters K and L_∞, the so-called length of first capture (smallest size at which animals are fully vulnerable to the fishery and to the sampling gear), L_c, and the mean length of the animals above the length L_c.

There are six assumptions behind this method.

7) Asymptotic growth with known parameters K and L_∞ which are constant over time.

8) No individual variability in growth.

9) Constant and continuous recruitment over time.

10) Mortality rate is constant with age for all ages $t > t_c$.

11) Mortality rate is constant over time.

12) Population is in equilibrium (i.e., enough time has passed following any change in mortality that mean length now reflects the new mortality level).

The final assumption of equilibrium conditions tends to be the hardest to meet in real world situations. Gedamke and Hoenig (2005) have recently relaxed the need to meet this assumption by developing a transitional form of the mean length statistic for use in non-equilibrium conditions. This makes the approach applicable in a broader range of situations. In the case of the barndoor skate, however, we have to consider the reproductive strategy of the species and address the fact that assumption #3 (constant recruitment) is clearly violated. As an elasmobranch, the barndoor skate has a rate of

recruitment which is strongly tied to the adult population size (Gedamke 2006).   Simply applying the Gedamke and Hoenig (2006) approach, without taking trends in recruitment into consideration, will result in mortality estimates that are biased high when recruitment is increasing (during a population recovery) and low when recruitment is declining (during a population decline; see Appendix A).

To address variable recruitment, the continuous model of Gedamke and Hoenig (2006) must be recast in a discrete form. We start this approach with an analysis of the length frequency data from the fall NEFSC groundfish survey. This is the longest standardized time-series of data available and provides an index of recruitment from 1963-2005. A cumulative plot of all individuals captured during the entire time series demonstrates that barndoor skates become fully vulnerable to the gear at approximately 55 cm. Using life history parameters from Gedamke et al. (2005; $k = 0.1414$ yr $^{-1}$, $L_{inf} =$ 166.3 cm total length, and $t_0 = -1.29$ yr) a length age conversion was applied and an age at full recruitment to the gear was estimated at 2 years old, corresponding to a size of 54 to 69 cm. The number of two year olds caught per year was calculated and this vector of recruitment was then projected forward in time. Given a total mortality rate for each year, the numbers at age in each year are predicted. Prior to 1963, no data was available and we assumed constant recruitment at a value that was the mean of the first three data points in the time series (1963-1965).

To simplify our explanation of the methodology, only one change in mortality is presented. In practice, and in our application that follows, additional changes are included in the model depending on the nature of the data being analyzed. The overall approach is illustrated in Figure 1 (projection Matrix) where a single change in mortality

is indicated as having occurred in 2001, and we have assumed that total mortality (both

fishing and natural mortality) is constant across all age classes. Thus, the only

information required to predict the numbers at each age, in each year, is the total

mortality rate in each period (Z_1 and Z_2), the year in which mortality changed (T_1), and

the given vector of recruitment. The age to length conversion is then used in conjunction

with the numbers at age to calculate a predicted mean length in each year.

The estimation of the unknown parameters (Z_1, Z_2, and T_1) can then be

accomplished by selecting parameters which minimize the difference between the

observed and predicted mean lengths. We use the method of maximum likelihood

estimation. The probability density function of a normally distributed sample mean $\overline{x}$,

when the sample size is m, is

$$f\left(x; \mu, \sigma^2\right) = \frac{\sqrt{m}}{\sqrt{2\pi\sigma^2}} \cdot e^{-\frac{m}{2\sigma^2}\cdot(\overline{x}-\mu)^2} \ . \tag{1}$$

The product likelihood function (Λ) for n years of observed mean lengths results

by substitution: $\mu = E(\overline{L})$, $\sigma^2 = \text{Var}(L) = $ variance of lengths that are greater than L_c.

Thus,

$$\Lambda = \prod_{y=1}^{n} \frac{m_y}{\sqrt{2\pi\sigma^2}} \cdot e^{-\frac{m_y}{2\sigma^2}\cdot[\overline{L}_y - L_{pred,y}]^2} \tag{2}$$

where m_y is the number of fish greater than size L_c measured in year y, $\overline{L}_y$ is the

observed mean length in year y, and $L_{pred,y}$ is the mean length computed for year y using

our population projection just described. The log-likelihood is proportional to

$$\ln(\Lambda) \propto -n \cdot (\ln \sigma) \; - \frac{1}{2\sigma^2} \cdot \sum_{y=1}^{n} m_y \cdot [\bar{L}_y - L_{pred,y}]^2 \quad . \qquad\qquad (3)$$

Equation (3) was maximized, and parameters estimated using the PROC NLP

procedure in SAS version 9 (SAS, 2004). Initially the year in which the mortality change

occurred (T_1) was specified and Z_1, Z_2, and the variance (σ^2) were estimated. The

likelihood surface was then evaluated to detect local maxima and any potential problems

with fitting the model with an increased numbers of parameters. This approach also

provided reasonable initial estimates for starting our broader fit to the data. If the year in

which a change in mortality occurs is unknown the model can be fitted separately for

each year where the change is possible. The year of change which maximizes the

likelihood provides the maximum likelihood estimates. Alternatively, the year of change

can be estimated along with the other parameters.

Estimating Survival from Catch Rates

To obtain additional estimates of total mortality the application of another

approach using catch rates from the fall NEFSC survey data is presented here. A detailed

description of the derivation of the model is presented in Gedamke (2006) and will only

be described briefly. The basic premise is that the annual survival rate, S, can be

estimated from annual surveys using a longitudinal catch curve to follow a cohort over

time. This is based on the relationships that

$$N_{a+1,t+1} = S\,N_{a,t} \qquad\qquad\qquad (4)$$

and

$$I_{at} = qN_{at} \qquad\qquad\qquad (5)$$

where $N_{a,t}$ is the number of animals of age a alive at the time of the survey in year t, I_{at} is an index of abundance of the animals of age a in year t, and q is the catchability coefficient. The survival rate can thus be estimated by linear regression of the index on the previous year's value for the same cohort. The assumptions are that survival and catchability are both constant over time and age, and that the ages of the animals observed in the survey can be determined.

Heincke (1913, cited in Ricker 1975) recognized that it can be difficult to get accurate ages for the older animals in a population and suggested pooling the older age classes. In other words, if a cohort of recruits can be separated from the rest of the age classes an annual survival rate can be estimated by comparing the total number of animals in one year with the number of animals above recruit age (or size) in the following year. Heincke formulated the estimation procedure in terms of a cross-sectional catch curve (age composition observed in one year) rather than as a longitudinal catch curve (changes in abundance of specified cohorts are monitored over time). Cross-sectional catch analysis is commonly used in stock assessments but has the limiting assumptions of constant survival and catchability over time and over all age classes. The Heincke method, also commonly used in stock assessment, does not have the assumption

of constant survival over time but was formulated to use information from two consecutive survey years. For application to the limited data available for the barndoor skate we utilize the generalization of this method developed by Gedamke (2006).

We consider just two age groups in the population – recruits and previously recruited animals. Recruits are defined to be those animals that will join the previously recruited animals the next year (if they survive the year). The relationship between the number of previously recruited animals in year $t+1$, N_{t+1}, and the number of recruits R_t and previously recruited animals N_t in year t is:

$$N_{t+1} = S\,N_t + \phi\,R_t \,, \qquad t = 1, \ldots, T\text{-}1 \qquad (6)$$

where ϕ and S are the survival rates of the recruits and previously recruited animals, respectively, and T is the number of years of survey data.

Due to the limited information and relatively low survey indices for the barndoor skate, we make the assumption that non-recruit and recruit survival is the same. This is not an unrealistic assumption as barndoor skates are fully recruited to the gear at age 2 and at a size of approximately 60 cm total length. This results in the following equation:

$$I_{t+1} = S\,(I_t + r_t)\,, \qquad t = 1, \ldots, T\text{-}1. \qquad (7)$$

This model can then be fitted to the data and S estimated, using the method of least squares. Thus, we minimize

$$\sum_{t=1}^{T-1}\left(I_{t+1} - I_{pred,\,t+1}\right)^2 \qquad (8)$$

where the predicted index is given by (7).

Results

Estimating Mortality from Mean Lengths

The mean lengths recorded from the fall NEFSC survey were highly variable and likely to be the result of small sample sizes (Figure 2). Nonetheless, a clear downward trend was observed in the 1960's and an upward trend was observed in the 1990's. The time series of catch rates of 2 yr olds caught in the survey also showed a downward trend in the 1960's and an upward trend in the 1990's. The time series also showed an apparent cyclical pattern to the recruitment with a strong year class arising every 3 to 5 years (Figure 3).

We first assumed that there were two changes in mortality, hereinafter referred to as the two-break model. This is the simplest model that would explain the decline in survey indices at the start of the time series and then also provide a mechanism for the observed recovery. This also provides a starting point for our analysis with the least number of parameters to fit: first year of change (T_1), the second year of change (T_2), the three different mortality levels (Z_1, Z_2, and Z_3), and the variance (σ^2). Our initial grid search over all possible combinations of years of change and inspection of the likelihood surface resulted in a clear maximization of the function with the first change in mortality occurring near the start of the time series and the second change occurring in the mid 1990's (Figure 4).

The model was then refitted to the data with all 6 parameters being estimated and initial guesses for T_1 of 1960 and T_2 of 1995. The first year of change was estimated to

be 1962.8, and the second year of change to have occurred in 1992.5. The corresponding estimates of total mortality were 0.30, 0.88, and -0.01 for Z_1, Z_2, and Z_3, respectively (Figure 5). No apparent pattern to the residuals was observed. The cyclical pattern in recruitment perpetuated itself through our projection and predicted mean lengths had similar peaks and dips to that which was observed. Between 1976 and 1984 an unrealistic spike in our predicted mean length resulted from a total lack of recruits being captured. In this time period, the predicted mean lengths result from the growth of the 1976 cohort, and only when new recruits were observed in 1984 do our predicted mean lengths once again fall in line with the observed values.

Although there was no pattern to the residuals in the two-break model, it is unlikely that the barndoor skate population began a recovery under the high (0.89) levels of total mortality that were predicted. Thus, we added another change in mortality (three-break model) and repeated the same procedure as for the two-break model. The results of our initial grid search evaluation and the corresponding likelihood surfaces are too complex to adequately present here. However we conducted an extensive analysis to evaluate the behavior of the fitting procedure. The results of these grid searches did find some uncertainty and local maxima surrounding the estimation of the second year of change and the initial estimate for this parameter into the fitting procedure proved important. However, the estimates for all other parameters were relatively consistent with the years of change never varying more than a year from the final results presented and the estimates of mortality never varying more than 0.05.

The three break model estimated the years of change to be 1962.9, 1977.8 and 1994.4. Mortality in the four time periods was estimated to be 0.31, 0.90, 0.41, and 0.04 for Z_1, Z_2, Z_3, and Z_4 respectively (Figure 6).

Estimating Survival from Catch Rates

An evaluation of survey indices from 1963 – 2005 showed significant declines at the start of the time series and then an obvious recovery beginning in the late 1990's (Figure 3). A log transformation of this data allows us to view the rate of change of the population and it appears that the decline occurred at a relatively consistent rate through 1975 (Figure 7). The recovery, on the other hand, appears to have occurred in at least two distinct phases. A linear fit to the data from 1984-2005 shows a clear pattern to the residuals and indicates at least one significant change in mortality occurred. There appears to be a break in the trend around 1996 which is soon after three large areas on Georges Bank were closed to fishing.

Using our observations from the survey indices and the results of the mean length analysis just presented, we estimated the total mortality occurring on the population in three different time periods. The first predicted data point available for this analysis is 1964 because the number of recruits and non-recruits from the previous year are used to make the prediction. Using data from 1964-1980, total mortality was estimated to be 1.04. The estimation is driven heavily by the decline in the first few years and is insensitive to the inclusion or exclusion of data from 1970-1980. On the other hand if 1965 is used as the first data point, total mortality is estimated to be 0.89.

Estimates of total mortality for the recovery were done in two phases with the break points estimated by the mean length estimator. The total mortality estimate from 1984-1992 is 1.34, while the estimate of total mortality from 1984-1994 is 1.06. For the most recent years total mortality is estimated to be 0.23 from fitting both 1993-2005 and 1995-2005. The results were relatively sensitive to the inclusion or exclusion of data from 1992 when the survey caught no individuals above the recruit size. Regardless of the years selected for the analysis, results ranged from 0.67 to 1.33 prior to 1991-1994 and from -0.1 to 0.37 during the last 10 years. This suggests a clear drop in mortality occurred by 1994. To further illustrate this, estimates were made in five year bins which smoothed the results but clearly show the declining trend in mortality that occurred during the mid 1990's (Figure 8).

Discussion

The results of our study show that, although information was limited, the use of mean length data and pooled catch rate data provided insights as to the relative exploitation pattern in the barndoor skate. Both approaches presented in this study suggest that fishing pressure was at very high levels at the start of the time series and was reduced to very low levels in the mid 1990's (Figure 9).

Although the current estimates of total mortality from the mean length approach are clearly too low, the overall pattern of exploitation is compelling. The difficulty in obtaining accurate absolute estimates of total mortality arises from the lack of information in the entire middle part of the time series. Estimates from the two-break model suggest a total mortality of 0.89 was occurring until the early 1990's when an

instantaneous drop to near zero mortality occurred. It is unlikely that this relatively high

constant mortality rate was present in the population for over 30 years and that the

population began to recover under these conditions. Therefore the mortality rate prior to

the predicted drop in 1992 would be too high and an extremely low value is necessary for

the mean lengths to recover the values observed during the last 10 years.

Results from the three break model suggest a two-step reduction in mortality

beginning in 1978. Not only does this shift the current estimate of mortality in a more

realistic direction, the predicted change in mortality occurs at approximately the same

time as the cessation of the distant water fleets fishing activity on Georges Bank. With

more information in the middle part of the time series more accurate absolute estimates of

mortality could be generated.

An alternative explanation for the low estimates of current mortality can be drawn

from Figure 5. The pattern of cyclical recruitment can be seen occurring every 3-5 years

except during the middle part of the time series when no individuals were captured. The

only place where this pattern breaks down is the seven year period between 1995 and

2002. Although there is a weak signal of increased recruitment in 1999, the magnitude of

difference is not nearly as clear as other places in the time series. If, for one reason or

another, the survey missed a pulse of recruits during this year, the model would need an

extremely low value of mortality to compensate and produce a tight fit to the larger

sample sizes at the end of the time series.

It is important to note that although the absolute estimates of mortality may be

variable due to measurement error, the relative changes in mortality and the estimates of

when changes in mortality occurred are consistent throughout our mean length analysis.

Confidence in the mean length model can also be gained from an inspection of the predicted values, observed values and the residuals of the fit. There is no apparent pattern providing no indication that the model is mis-specified or that our assumptions are unrealistic. The mean length data initially appeared to be highly variable, and potentially unusable. However we have shown that this pattern results from variable recruitment and the cyclical addition of a large number of small animals to the population.

An additional benefit of the mean length analysis is the ability to estimate the mortality level that was occurring prior to the time series and available data. This estimate (0.3) is clearly driven by our assumption of constant recruitment prior to 1963 but is also extremely reasonable considering our understanding of both natural mortality and the fishing pressure that was occurring prior to the time series.

In our mean length model formulation, due to a lack of information, we were forced to assume that fishing mortality is knife-edge and applied to all ages equally. In cases where more information is available (i.e. a selectivity curve from a tagging study), one could easily apply age specific estimates of total mortality. There would be no resulting increase in the number of parameters that have to be estimated as a given vector of partial selectivity will simply scale the differing levels of mortality ($Z_1, Z_2, Z_3,…Z_n$) already in the model we presented.

The results and conclusions from our catch rate method are in agreement with those from the mean length analysis. During the decline of the barndoor skate population, our catch rate analysis suggests a total mortality 0.9- 1.0 depending on which years of data are included in the analysis. The stability of our results can be attributed to

the significant amount of information contained in the relatively large survey catches in the first four years of the time series (1963 – 1966). Estimates from the early part of the recovery in the early 1990's were made with data that contained no more than three individuals caught per year. As a result, estimates could have ranged from 0.7 to 1.3 depending on which years were included in the analysis and the inclusion or exclusion of a zero catch year in 1992. Estimates using data after 1992 and 1994 (years mortality changed as predicted in the mean length analysis) were stable and consistently estimated at 0.23. Early in our analysis, prior to receiving data for 2005, estimates of 0.14 were obtained. A sensitivity of results to the addition of the most recent years of data showed results could range from -0.1 to 0.37 depending on which years were included.

Although there is some variability and uncertainty in the absolute estimates presented in our study, the pattern of exploitation is clear. There is no evidence to suggest that the barndoor skate population is experiencing high levels of mortality and is in any current threat in the area studied. In fact, the data strongly support the idea that a significant reduction in mortality occurred sometime around the closure of the areas on Georges Bank and that the current mortality level is very low.

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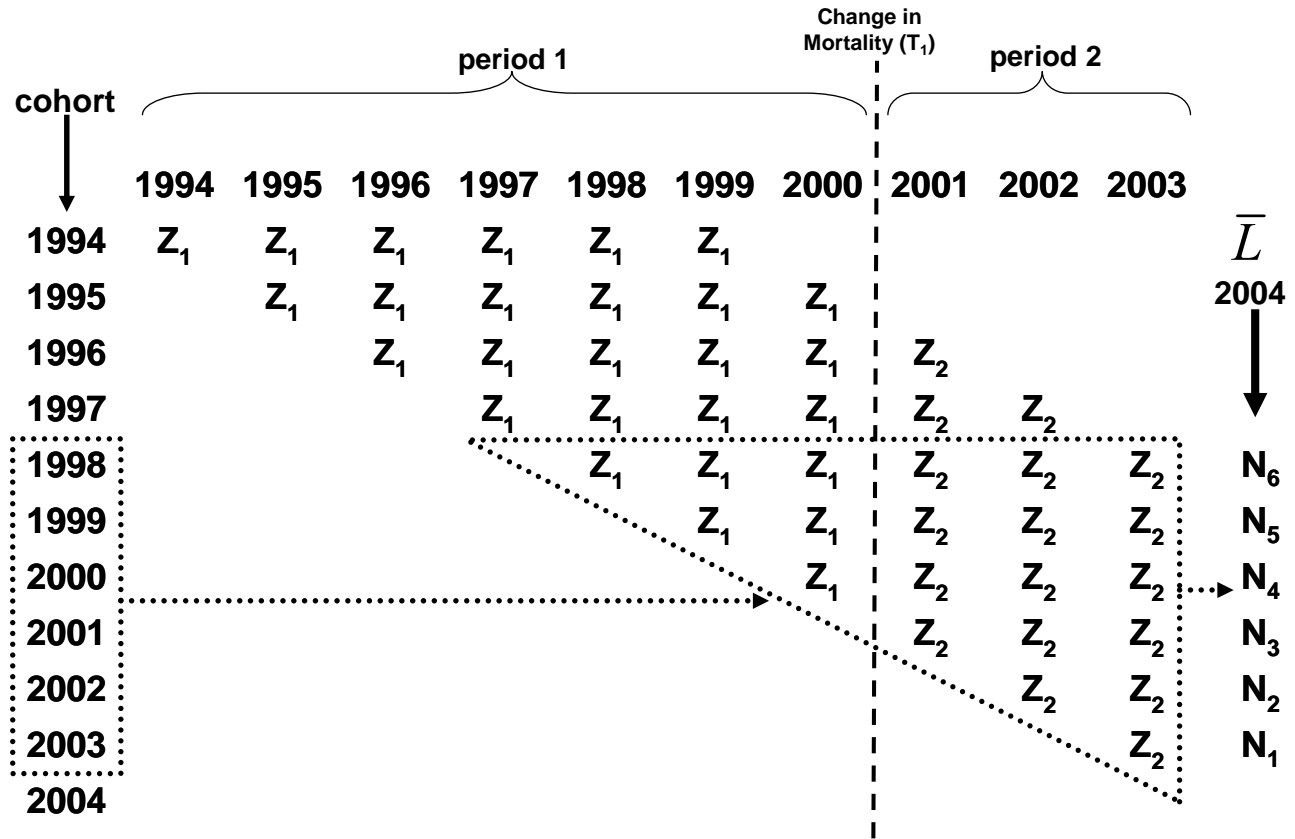
   Inc., 2004.

cohort	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	
1994	Z_1	Z_1	Z_1	Z_1	Z_1	Z_1					$\overline{L}$
1995		Z_1	Z_1	Z_1	Z_1	Z_1	Z_1				2004
1996			Z_1	Z_1	Z_1	Z_1	Z_1	Z_2			
1997				Z_1	Z_1	Z_1	Z_1	Z_2	Z_2		
1998					Z_1	Z_1	Z_1	Z_2	Z_2	Z_2	N_6
1999						Z_1	Z_1	Z_2	Z_2	Z_2	N_5
2000							Z_1	Z_2	Z_2	Z_2	N_4
2001								Z_2	Z_2	Z_2	N_3
2002									Z_2	Z_2	N_2
2003										Z_2	N_1
2004											

period 1 (1994–2000) — Change in Mortality (T_1) — period 2 (2001–2003)

Figure 1. Conceptul framework of projection used to predict the number of animals at each age from a vector of recruitment and a total mortality rate in each year. A single change in mortality is indicated in 2001 and a hypothetical maximum age of 6 is represented. The number of recruits (dashed box) is projected forward given the mortality rates in each year (dashed triangle) to obtain a number of animals at each age in 2004. These predicted numbers in 2004 are then converted to a mean length through an age to length conversion assuming an average size for the animals in each age class.
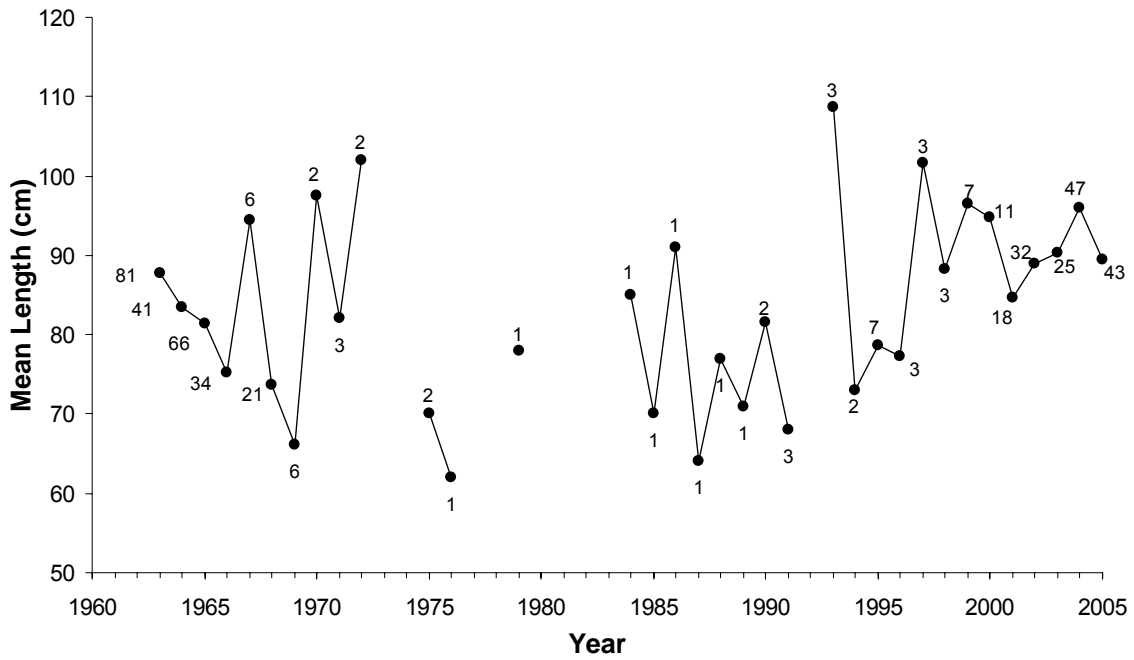
Figure 2. Observed mean lengths and sample sizes of all animals greater than 60 cm (L_c) captured in

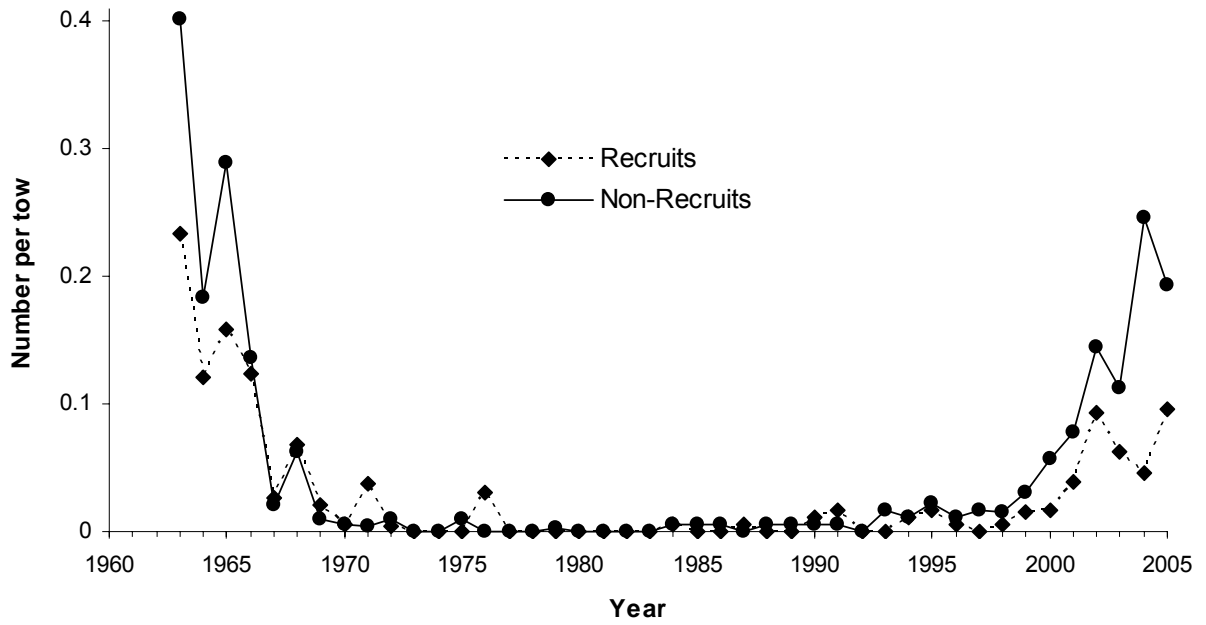the NEFSC fall groundfish survey.

Figure 3. Survey indices for number of recruits (2 year olds) and non-recruits (3 years and older) from the NEFSC groundfish survey.
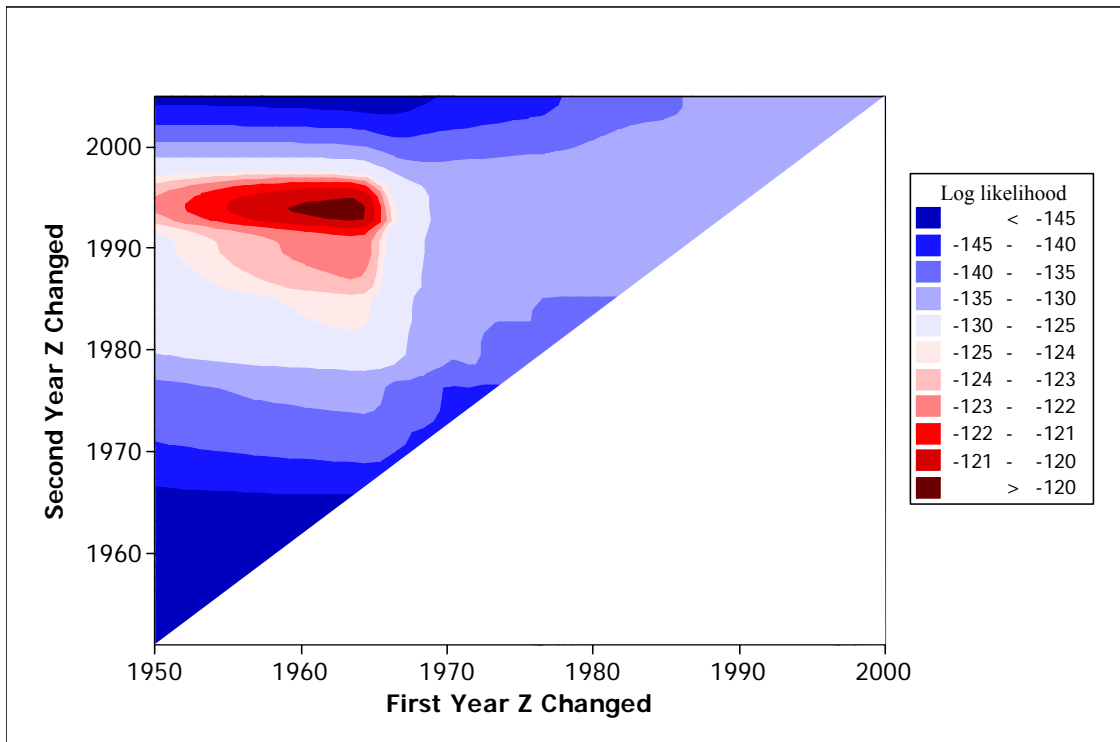
Figure 4. Likelihood surface for all possible combinations of years in which two changes in

   mortality occurred. The time of the second change is clearly indicated between 1990 and

   1996 while the time of the first change is indicated less precisely to have occurred around

   1960.
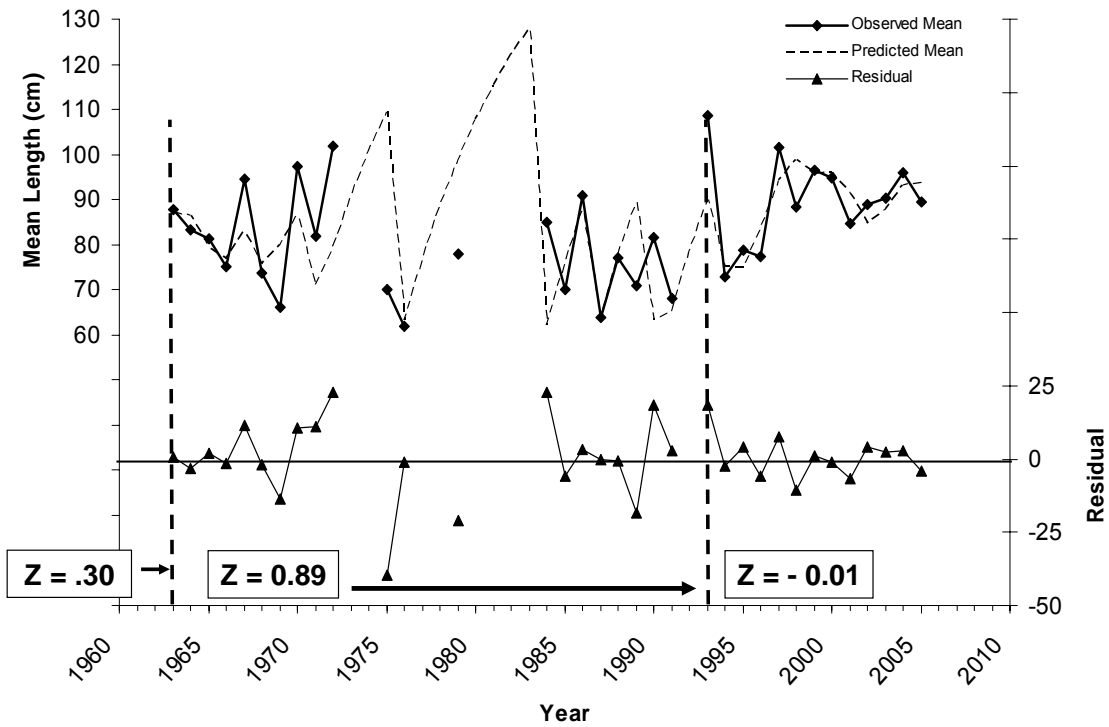
Figure 5. Results of the two-break model indicating an increase in mortality in 1962.8 and a

decrease in 1992.5. The residuals of the predicted versus observed values are presented.
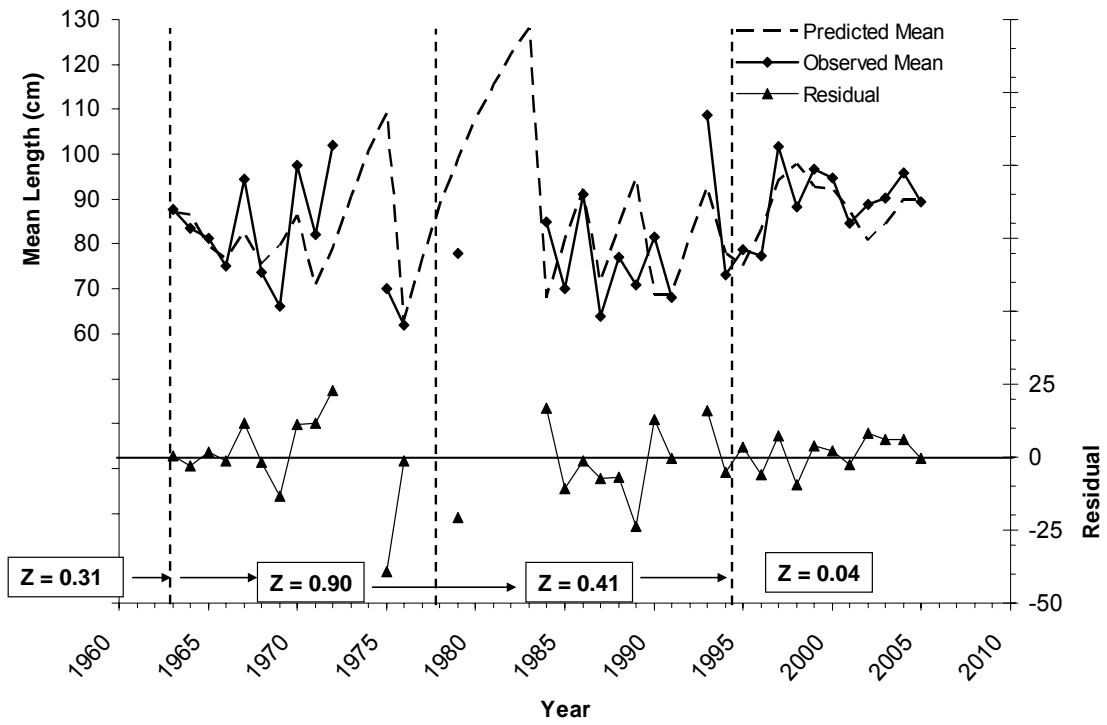
Figure 6. Results of the three-break model indicating an increase in mortality in 1962.9, a decrease

in 1977.8, and a further reduction in 1994.4. The residuals of the predicted versus observed
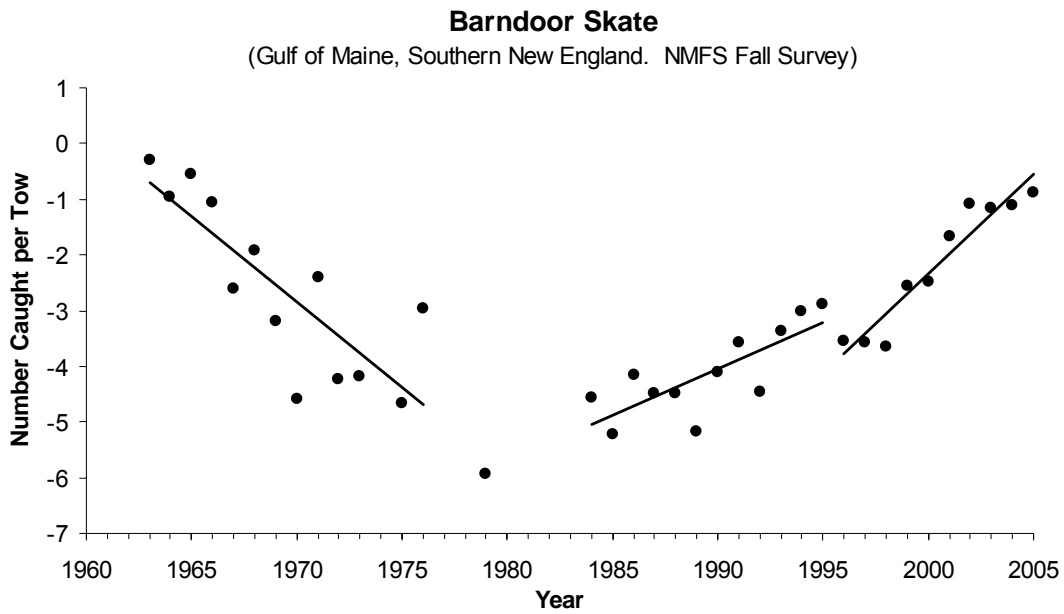
values are presented.

Barndoor Skate

(Gulf of Maine, Southern New England. NMFS Fall Survey)

Figure 7. Log transformed survey indices from NEFSC fall groundfish survey. A single linear fit

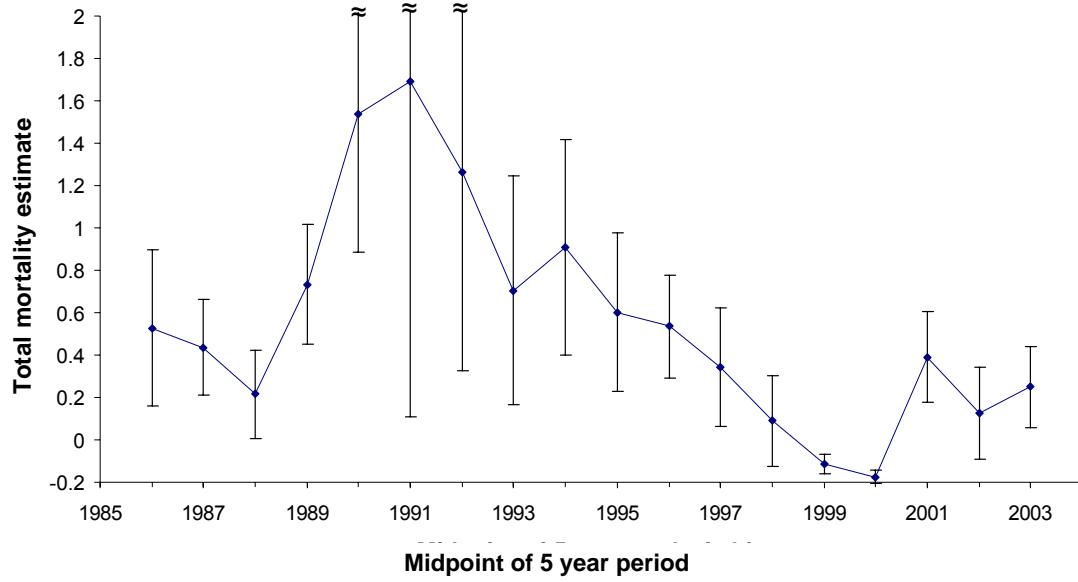is presented for the decline and two segments are fit to the recovery.

Figure 8. Results of estimating mortality over 5 year periods. Estimates are plotted against the midpoint of

each bin and the standard error of each estimate is indicated. Note that estimates for years that are

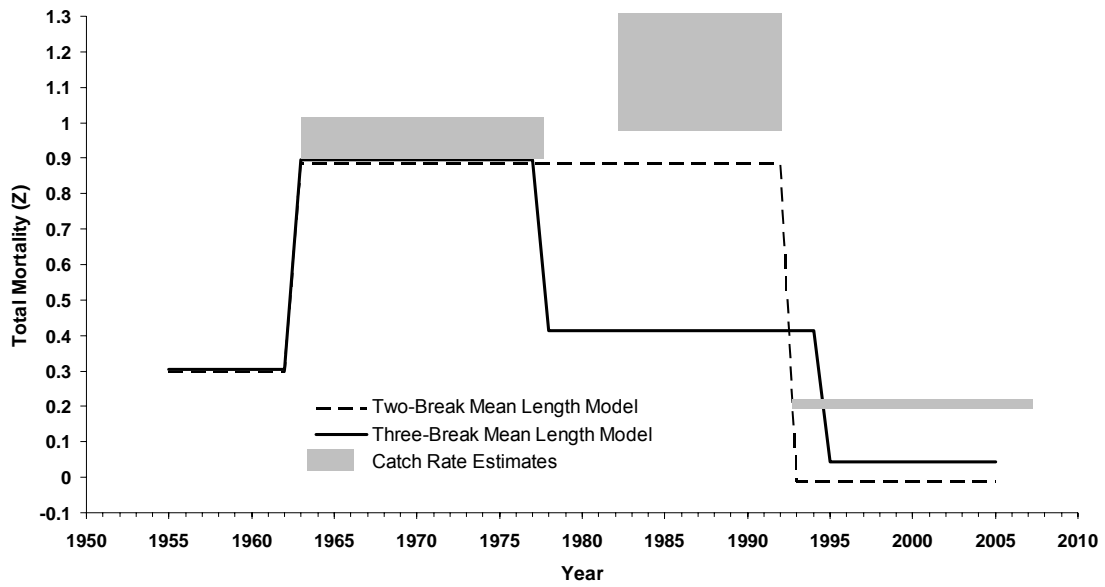within three years of each other use overlapping information.

Figure 9. Comparison of results from both the mean length and catch rate approaches. The range

of estimates for the catch rate method is indicated by the shaded grey region.

Appendix Figure 1. Results of the two-break model assuming constant recruitment. Residuals

and sample sizes are presented. Results are presented below figure
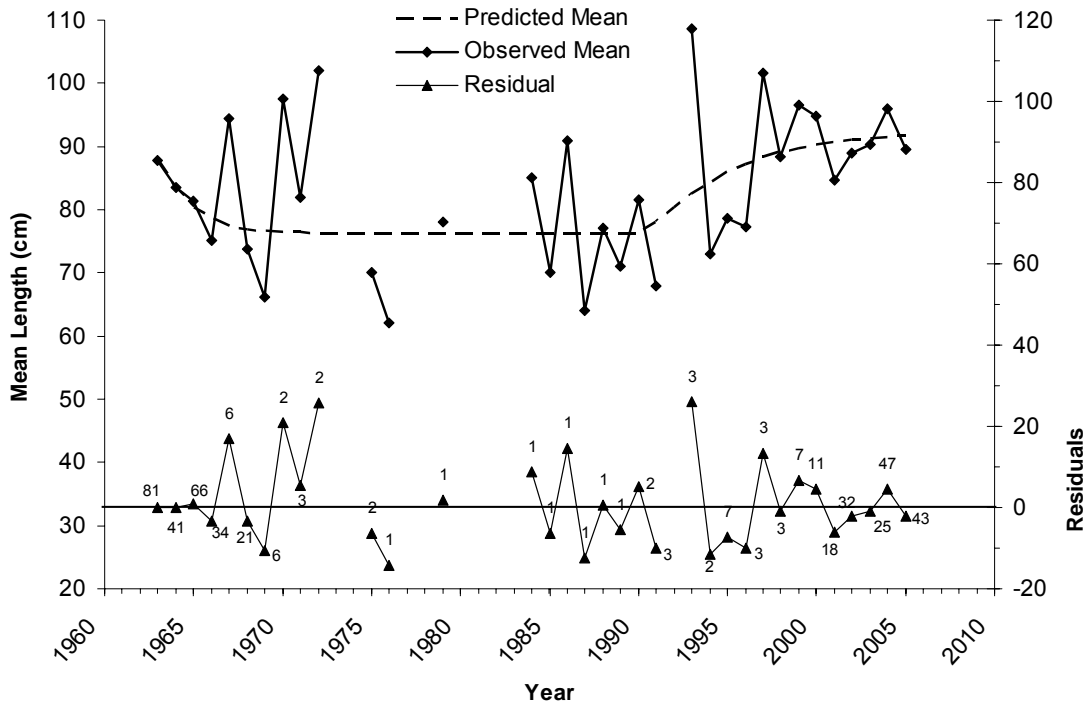
Two-Break Model. Mean Length Estimator

Results:

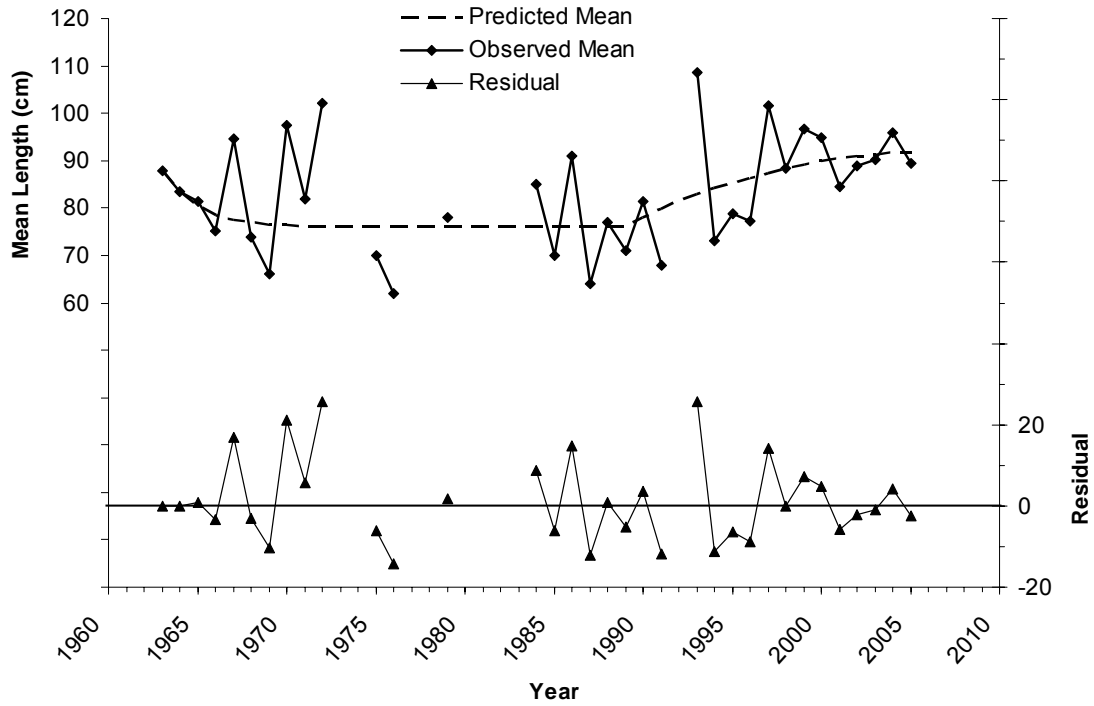$Z_1 = 0.11$ $T_1 = 1958.9$

$Z_2 = 0.60$ $T_2 = 1990.1$

$Z_3 = 0.28$

Appendix A; Figure 2. Results of the three-break model assuming constant recruitment. Residuals and also are presented. Results are presented below the Figure

Three-Break Model. Mean Length Estimator
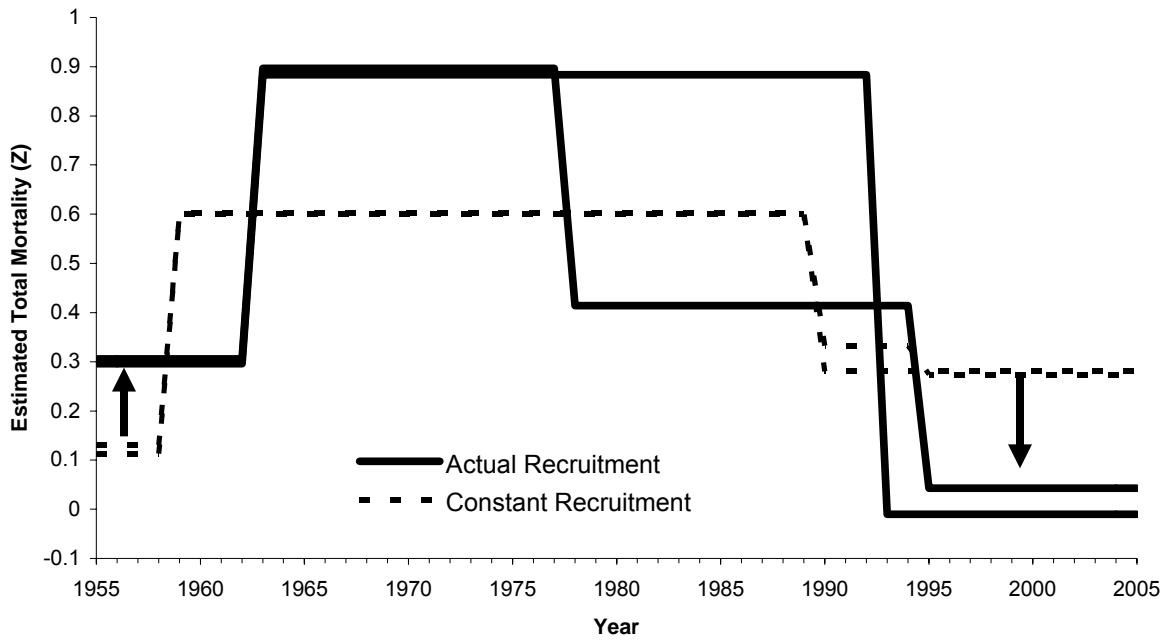
Results:

$Z_1 = 0.13$ $T_1 = 1959.2$

$Z_2 = 0.60$ $T_2 = 1989.0$

$Z_3 = 0.33$ $T_3 = 1995.0$

$Z_4 = 0.27$

Appendix A; Figure 3. Results of two and three-break models including actual recruitment or

assuming constant recruitment. The expected bias of the constant recruitment estimate is

indicated by the bold arrows.

Chapter 8

Stock-Recruitment dynamics and the Maximum Population Growth Rate of the

Barndoor Skate *Dipturus laevis* in the Northeast United States

Abstract

In 1998, the barndoor skate, *Dipturus laevis,* was reported to have been locally extirpated in parts of its northern range and potentially be on the brink of extinction. Managers were faced with assessing the species with virtually no information other than a limited number of individuals that had been 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 unexplored. In this study we use information from the National Marine Fisheries Service (NMFS) annual groundfish surveys to investigate two critical components of the barndoor skate population dynamics: the relationship of recruitment to spawner abundance and the maximum population growth rate. A compelling 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 an estimate of the slope at the origin was generated. These parameters provided an estimate of the maximum annual reproductive rate and were then converted to estimate an instantaneous maximum population growth rate of 0.35 yr^{-1}. 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 first year survival and incorporate density dependant logic into the density dependant 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 to 0.45 yr^{-1}. Our results suggest that the species may be more resilient to fishing pressure than previously believed and capable of growing at an annual rate in excess of 40%.

As an elasmobranch, the barndoor skate (*Dipturus laevis*) 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 have hampered the further assessment and management of north Atlantic populations. Although recent studies have provided estimates of basic life history parameters (Gedamke 2006), fundamental aspects of the species population dynamics remain unexplored. Because the observed decline and the potential for extinction of the species were attributed to overfishing, estimates of the maximum population growth rate are necessary to understand the population dynamics and manage the species.

Recently, this question has been approached by the use of both stock-recruit and demographic models to determine the intrinsic, or maximum, rate of population increase ($r_{intrinsic}$) and therefore the maximum sustainable fishing pressure (Myers et al. 1997; Myers et al. 1999; McAllister et al. 2001; Gedamke 2006). An important aspect of this process, and commonly overlooked in elasmobranch demographic models, is the recognition that a population will only grow at a maximal rate at the lowest stock sizes. Only in this condition will competition for resources be at a minimum and the subsequent increased survival result in $r_{intrinsic}$.

Stock-recruitment models address this issue as they incorporate stock size explicitly in the analysis and are formulated to estimate $r_{intrinsic}$ at low population sizes. The underlying relationship in these models, 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. In its simplest form these models describe an inverse

relationship between stock size and recruitment to the population. 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 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 (i.e., 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 current (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 equal $r_{intrinsic}$. Unfortunately, parameter estimates from depleted populations are rarely available and therefore estimating $r_{intrinsic}$ remains difficult. In a recent study, Gedamke et al. (2006) addressed this dilemma and provided suggestions as to how to incorporate stock size and the logic of density dependant compensation into the density-independent framework of a Leslie matrix demographic model.

In this study, we use information from the National Marine Fisheries Service (NMFS) annual groundfish surveys on Georges Bank and the Gulf of Maine to develop both a stock-recruit and Leslie matrix models to gain insights on the population dynamics of the barndoor skate. We follow the methodology of Myers et al. (1997, 1999) for the analysis of the stock-recruit relationship and that of Gedamke (2006) for the demographic analysis.

Materials and Methods

Available Trawl Survey Data

The National Marine Fisheries Service has conducted research surveys in the both the US and Canadian waters of the Northwest Atlantic for over four decades. Surveys have been conducted in the fall and spring beginning in 1963 and 1968 respectively (NEFSC 1999). 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 offshore surveys were designed to sample groundfish and have used a Yankee bottom trawl. Surveys were generally conducted in 27 – 366 meters of water, with an occasional deeper tow 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 and has been towed at 6.5 km/h (3.7 kts) for 30 minutes at each station. Comparison trawls and conversion factors have been generated and the data provided to us for this study was previously standardized. The spring and fall surveys are the primary indices used by the Northeast Fisheries Management Council (NFMC) and NMFS for the assessment of the Northwest Atlantic skate complex. Between 1963 and 2005, between 167 and 374 survey tows were conducted annually in this region (Figure 1). At each station the number and weight of each species is recorded in addition to the total length of each individual (Figure 2).

Data from the winter survey, which overlaps the southern regions of the fall and spring surveys, is also used in monitoring the population of the NW Atlantic skate complex including the barndoor skate. This survey began in 1992 and provides a shorter

time series than the fall and spring. In addition, the gear for the winter survey has been

rigged specifically to target small flatfish, with rollers (used in the spring and fall

surveys) replaced with a chain sweep covered by rubber disks and the addition of 30

fathom ground cables.

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 from this study were: a maximum length (L_∞) of 166.3 cm, a growth

coefficient (k) of 0.1414 yr^{-1}, and an intercept (t_0) of -0.129 yr. The oldest animal

observed in the Gedamke et al. (2005) study was 11 years old. However, for this study, a

maximum age of 20 years was used as recent vertebral analysis has found individuals as

old as 15 years (Gedamke unpublished observations.).

An estimate of fecundity was calculated using Holden's (1973) relationship of

birth weight to maximum fecundity of:

$$f_{max} \; = \; 10.9^{\,*} \,(\text{weight in kg})^{\,-0.45} \quad\quad\quad\quad (1)$$

The smallest individual captured by Gedamke et al. (2005) was 20 cm in length and

weighed 28.5 g resulting in a maximum fecundity estimate of 54 young per year.

Estimates of natural mortality (M) were calculated using six different methods:

Hoenig (1983), Pauly (1980), Jensen (1996) age at maturity and k method, Peterson and

Wrobleski (1984), and Chen and Watanabe (1989). Estimates ranged from 0.16 from the

Chen and Watanabe (1989) estimator to highs of 0.21 and 0.25 from the two Jensen

methods (1996). Based on the low estimates of total mortality reported by Gedamke

(2006) and the similar estimates for adult mortality of three of the estimators (Pauly

1980; Peterson and Wrobleski 1984; Chen and Watanabe 1989) we use an estimate of

0.18 for natural mortality. 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) was used to calculate the number of

recruits and the number of spawners caught per tow for each year and for each survey. A

cumulative plot of all individuals captured during the entire time series demonstrates that

barndoor skates become fully vulnerable to the gear at approximately 55 cm. A length

age conversion was applied and an age at full recruitment to the gear was estimated at 2

years old, corresponding to a size of 54 to 69 cm. Thus, animals captured in this size

range were counted as recruits and standardized for each survey by the number caught

per tow. A female size at maturity of 116 cm was used as a minimum size cutoff to

estimate the spawner abundance index, also standardized as number per tow (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 one of the two following models:

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

$$R = \frac{\alpha \cdot S}{\left(1 + \left(S/K\right)\right)} \qquad \text{Beverton and Holt} \qquad\qquad (3)$$

where R is recruitment and S is spawner abundance (Ricker, 1954; Beverton and Holt, 1957). The parameter α 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 β are density-dependent terms which incorporate density-dependant compensation at low population sizes in the form of increased survival. The product of $\beta *S$ can be interpreted as the density dependent mortality while the K parameter of the Beverton-Holt model can be thought of as a threshold which, 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 does not simply asymptote but begins to decline at very high spawner abundances. Overcompensation can result at these high spawner abundances as the availability of resources in the environment (i.e. food and/or space) is exceeded. This conceptually provides a mechanism for a population to hover at or near a carrying capacity (K).

The relationship between spawners and recruits must take into account the lag period between the spawner abundance recorded in one year and the time it takes for the resulting recruits to appear in the survey. In the case of the barndoor skate, egg cases are believed to have an incubation period of close to one year. 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 three year

lag period and fit to both the Ricker and Beverton-Holt models. The slope at the origin was estimated for each model.

To understand and work with the slope at origin parameter (α) it must be standardized to units common to population dynamics and can be expressed as the maximum reproductive rate. The maximum annual reproductive rate is a critical parameter in population dynamics and can be used to estimate the maximum population growth rate ($r_{intrinsic}$) and to estimate the limits of overfishing (Mace 1994; Myers et al. 1997; Myers and Mertz 1998). The explanation and calculations closely follow that of Myers et al. (1997, 1999). The first step in standardizing the slope at origin begins with including the mortality of a recruit in reaching maturity as:

$$\hat{\alpha} = \alpha \cdot \text{SPR}_{F=0}$$
(4)

where $\text{SPR}_{F=0}$ is the number of spawners resulting from each recruit. The result, $\hat{\alpha}$, represents the number of recruits per recruit (or alternatively, spawners per spawner) at very low population sizes (or at very low spawner abundances). This quantity can also be thought of as the maximum lifetime production of spawners per spawner. Note that this standardization (inclusion of $\text{SPR}_{F=0}$) of the slope at the origin includes a lag period for recruits to reach the age at maturity (A_{mat}). For our application to the barndoor skate, A_{mat} is 6.5 yrs, but the resulting lag period (A_{lag}) is 4.5 yrs because our recruit index is animals 2 yrs of age.

To take this approach one step farther, we then calculate the number of spawners produced by each spawner per year. If adult survival is p_s then the maximum annual reproductive rate ($\tilde{\alpha}$) results from:

$$\tilde{\alpha} = \hat{\alpha} \cdot (1 - p_s)$$. $\qquad$ (5)

The maximum annual reproductive rate can then be used to approximate the maximum population growth rate ($r_{intrinsic}$) as:

$$\exp^{r_{intrinsic} \cdot A_{lag}} - \exp^{r_{intrinsic} \cdot (A_{lag} - 1) - M} - \tilde{\alpha} = 0 \qquad (6)$$

This equation can be solved iteratively for $r_{intrinsic}$ given an estimate of M, $\tilde{\alpha}$, and A_{lag}.

Although this methodology is commonly applied to biomass estimates (e.g. SSB), McAllister et al. (2001) showed that identical results are produced using either biomass or numbers.

Demographic Model - Leslie Matrix Analysis

An alternate 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 at time t + 1 is given by

$$N_{t+1} = A \ N_t \qquad (7)$$

where **A** is a female-only population projection matrix (i.e. Leslie matrix) containing a schedule of reproduction and mortality (i.e. fecundity, survival, fishing mortality, age at

217

maturity)

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 (λ) of the matrix **A** as $r_{predicted} = \log_e(\lambda)$ (Vaughan and Saila 1976; Caswell 2001). Vaughan (1977) derived a computational method to calculate $r_{predicted}$ which is often used in practice.

The $r_{predicted}$, or instantaneous growth rate, calculated from these models is density independent and, as such, 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 (Gedamke 2006). Only in the case of a depleted population will competition for resources (i.e. food, space) be at a minimum and the effects of density dependant 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. (2006) reviewed the basic logic behind the construction of a demographic model and provided suggestions as to how to incorporate the logic of density dependant compensation into the density-independent framework of a Leslie matrix demographic model. Our explanation of our methodology closely follows that of Gedamke et al. (2006) and uses the following definitions of instantaneous population growth rate described in that paper:

$r_{intrinsic}$ = maximum 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

$r_{conditional}$ = rate of population growth when there is no fishing mortality, given a

schedule of survival and reproduction (conditional on population size and

resulting density-dependent compensation) and given a stable age distribution

$r_{predicted}$ = predicted rate of population growth 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

$r_{observed}$ = observed rate of population growth (assuming no measurement error; no

assumption of stable age distribution is made)

Our analysis consists of four primary steps: 1) estimating $r_{observed}$ from survey

data 2) constructing a Leslie matrix and solving for the first year survival (S_0) that results

in $r_{observed} = r_{predicted}$ 3) removing F from the model to estimate potential rate of

population growth at specified population size ($r_{conditional}$) 4) extrapolating $r_{conditional}$ to

zero population size to estimate $r_{intrinsic}$.

We start our analysis by obtaining an estimate of $r_{observed}$ from the NEFMC fall

survey data. A basic 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.

We then constructed a Leslie matrix that solves for the first year survival so that the

model predicts a rate of population growth that matches what we estimated from the

survey data ($r_{observed} = r_{predicted}$). There are a couple of important points to note about this

step of the analysis. First, the predicted rate of population growth, $r_{predicted}$ will only equal

the observed rate of population growth, $r_{observed}$, when a stable age distribution is present in the population and all other parameters are known.

Unfortunately estimates of juvenile or first year survival are rare and unavailable for the barndoor skate. Thus, we use estimates of total mortality from Gedamke (2006), our observed rate of population growth, and Vaughan's (1977) method to solve for S_0. This is a critical step as many life history parameters in elasmobranchs are believed to be relatively fixed (i.e. fecundity and adult survival, age-at-maturity), but the survival of the smallest animals is likely to be strongly tied to the population size and a key mechanism in the process of density dependent compensation. Throughout the rest of this manuscript, as in Gedamke (2006), we will assume that the effects of density dependent compensation are realized in the pliability of first year survival (S_0) alone. If other information is available, this can be easily incorporated into the model.

This approach provides an estimate of S_0 that is specific to the conditions being modeled and dependant on the estimated fishing mortality and the observed rate of population growth. Now, by removing fishing pressure from the model, we obtain an estimate of how fast the population could grow, given the same life history parameters, under the condition of no fishing pressure (i.e. $r_{conditional}$). For our application to the barndoor skate no selectivity curve is available but, 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 apply 50% of F to age one 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 3):

$$r_{conditional} = r_{intrinsic}\ (1 - N/K) \qquad\qquad (8)$$

When fishing occurs on all ages at an instantaneous rate F (per year),

$$r_{predicted} = r_{conditional} - F = r_{intrinsic}\ (1 - N/K) - F. \qquad (9)$$

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 implicitly states that the instantaneous rate of growth will be equal to zero when $N = K$ and $F = 0$. Rearranging the equation and presenting it in terms of survey indices we can solve for the intercept ($r_{intrinsic}$) as:

$$r_{intrinsic} = \frac{r_{conditional}}{1 - \dfrac{I}{I_K}} = \frac{I_K\ r_{conditional}}{I_K - I} \qquad\qquad (10)$$

with I representing the survey index at the time we measured $r_{observed}$, and I_K representing the index value of a virgin population. We use the highest value of the survey index to represent I_K.

Results

Stock Recruit Analysis

A compelling stock recruit relationship was clearly present in the fall survey data and less so in both the winter and spring surveys (Figures 3-5). Catch rates for both adults and recruits in the spring survey were considerably lower than for both the winter and fall. The adult catch rates for both the fall and winter were comparable, however the winter catch rates of recruits were approximately double that of the fall.

Estimates of the slope at the origin were the most precise from the fall survey data and were 3.97 RS^{-1} from the Ricker model and 4.40 RS^{-1} from the Beverton-Holt model (Table 1). Results from the winter and spring had a much wider range (3.95 to 27.56 RS^{-1}) and much greater standard errors. In the spring survey was there also a discernable pattern to the residuals for both the Ricker and Beverton-Holt models, due primarily to a number of years in which no spawners were recorded.

The resulting estimates of the maximum annual reproductive rate ($\tilde{\alpha}$) were from 1.76 and 1.96 from the fall data and from 1.76 to 12.26 from the winter and spring data. Estimates of $r_{intrinsic}$, transformed from the fall $\tilde{\alpha}$, were 0.33 from the Ricker model and 0.35 from the Beverton-Holt model. Estimates of $r_{intrinsic}$ from the spring and winter surveys ranged from 0.33 to 0.68.

Demographic Model - Leslie Matrix Analysis

The barndoor skate population was observed ($r_{observed}$) to be declining at an instantaneous rate of -0.32 between 1963 and 1979 and recovering at a rate of 0.36 between 1996 and 2005 (Figure 7). Total mortality for the same time periods was

estimated from mean lengths and catch rates by Gedamke (2006) to be 0.89 and 1.04 for the decline (63-79) and 0.04 to 0.23 for recovery (96-05). Using a natural mortality of 0.18, F was thus, estimated to be 0.71 and 0.86 for the decline and 0.05 for the recovery. An F of 0.1 was also included as a sensitivity test in our analysis for the recovery. A Leslie matrix was constructed with these parameters and solved for the S_0 that would result in the $r_{observed}$ from the survey data given the two different estimates of F for each time period. Our base model, which assumes 50% selectivity at age 1 and 100% by age 2, resulted in a S_0 that were 0.19 and 0.45 for the decline and 0.56 and 0.76 for the recovery. With fishing pressure removed from these models, and keeping S_0 constant, $r_{conditional}$ was estimated to be 0.26 and 0.37 from the decline and 0.40 and 0.44 from the recovery. As a check on the realism of these estimates we set S_0 at a theoretical maximum (equal to adult survival; 0.84) and estimated an upper bound for the instantaneous rate of growth of 0.45.

Estimates of $r_{conditional}$ were sensitive to the age-at-entry to the fishery only when modeling the decline. In this case the calculated $r_{conditional}$'s declined significantly as age-at-entry increased, while estimates from the recovery were robust to this aspect of our model (Figure 8).

For the majority of both the decline and recovery time segments we analyzed, the barndoor skate population was clearly depleted and our estimated $r_{conditional}$ should approximate $r_{intrinsic.}$ Using equation 10, or alternatively plotting our estimates of $r_{conditional}$ versus the corresponding survey index provides an estimate of $r_{intrinsic}$. For both the recovery and the decline, the time segments being analyzed covered similar stock sizes (i.e. survey indices) with the decline containing the highest values. In 2000,

halfway through the modeled recovery, survey indices were 0.08 fish per tow, approximately 10% of the high of 0.8 fish/tow recorded in 1963. For the decline the range of indices were similar to that of the recovery but showed very little absolute changes in value after 5 years (1968). Thus, we made a conservative approximation with a survey index of 0.1 from the 1967-1969 data. Solving for the intercept, we obtain estimates of 0.29 and 0.42 from the decline and 0.44 and 0.49 from the recovery (Figure 9).

There are two points to note: First, the estimate of 0.49 that resulted from the recovery model with an F of 0.1 would require first year survival to be greater than that of an adult and is therefore an infeasible estimate. Secondly, if the index in 1963 represents the situation with some fishing, then the rightmost point in Figure 9 should be farther to the right, thus lowering the y-intercept. Because our extrapolation is over such a short range of survey indices, the uncertainty in the virgin stock size affects the estimated $r_{intrinsic}$ only slightly.

Discussion

The results of our study suggest that the barndoor skate population in the US waters of the North Atlantic is able to grow at a rate that is higher than previously believed and higher than for most other studied elasmobranchs (Casey and Myers 1998; Frisk et al. 2002; Cortes 2004). The population, over the past 10 years, has been observed growing at a rate of approximately 0.36. The results of our demographic model, which are dependent on this growth rate, suggest there is still some scope for

compensation and rates of up to 0.45 are possible. Our analysis of the stock-recruit

model shows a compelling relationship and that the rate of recruitment is closely tied to

the spawner abundance. Estimates of $r_{intrinsic}$ from this approach suggest that the barndoor

skate population has recently been growing at or near an estimated maximum growth rate

of 0.35.

Previously published values for any life history or population dynamic parameters

of the barndoor skate have been equivocal, making a comparison of our results to earlier

findings difficult. Prior to our work, only two studies have attempted to estimate the

maximum population growth rate of the species. Having no direct information available,

researchers were forced to make numerous assumptions about the basic life history

information of the species. Casey and Myers (1998) suggested that the barndoor may be

similar to the European common skate (*D. batis*) and utilized the life history parameters

of this species [age at maturity (A_{mat})=11 yrs, and fecundity (F)=47 eggs] to make some

broad conclusions based on a life table analysis.   Casey and Myers (1998) suggested that

an instantaneous mortality (Z) of 0.4 would drive the species to extinction on Georges

Bank and that the colder waters and resulting later maturation in parts of the species

northern range would make the species vulnerable to extinction at half that level (Z =

0.2). Although few details are given regarding the specifics of their analysis, they

conclude that if the mortality of juveniles is twice that of an adult, the theoretical

maximum total mortality the species could withstand is 0.45.

Frisk et al. (2002) reported that a fishing mortality of 0.20 would result in a

negative population growth and is therefore unsustainable. In their study, they developed

a stage based model for the barndoor skate and compared their results to age-based

models for the little skate *Leucoraja erinacea* and the winter skate *Leucoraja ocellata*.

As in the Casey and Myers (1998) study, they were faced with a paucity of data and used

parameters from the common skate (*D. batis*) for fecundity (47) and a maximum age of

50 years which they translated to a natural mortality estimate of 0.09 by the Hoenig

(1983) method. Empirical relationships from Frisk et al. (2001) provided estimates for

the age-at-maturity 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 to our study.

   The results of our work compare most favorably with the approximate upper

limits of total mortality presented in the Casey and Myers (1998) study. They report that

a total mortality of 0.45 will drive the species to extinction when juvenile mortality is

twice that of adults, however, they also report an upper limit of 0.4 when adult and

juvenile survival is equal. This is clearly infeasible but with no further information on

the details of their model the cause remains unknown. Regardless of this slight

discrepancy, the results of our demographic model also suggest that 0.45 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 growth rates and therefore a much greater

sensitivity to fishing pressure.

   It is difficult to directly compare the results of these three demographic studies,

however. 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 and decisions for

parameters that needed to be estimated (i.e. natural mortality, fecundity). Also, unlike the

other two studies, our approach also incorporates the logic of density dependent

compensation into the analysis and uses observed growth rates to estimate the survival of

the youngest animals. As such, our results are directly tied to the observed growth rates

estimated from the NEFSC survey data. Although the contrast present in the survey data

is generally a very desirable property, our estimates of $r_{observed}$ 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 if smaller time segments were used. The trade-

off in this decision is was a potential bias that could result from smoothing over larger

time periods and also determining the appropriate stock size that corresponds to our

estimated rate of growth.

Despite these concerns the assumptions, logic and details of our approach are

clear and, like any demographic analysis, the interpretation of the absolute results must

take these factors into consideration. For example, the results of our analysis from the

recovery phase should be considered more reliable than those from the decline due to the

assumptions we were forced to make about age-at-entry to the fishery. 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 decline analysis, high estimates of fishing

mortality resulted in variable results depending on our assumption of when animals were

recruited to the gear. The affect of this assumption on the results was insignificant when

we include the low levels of fishing mortality in the recovery.

In our study we also have the luxury of comparing the results of our demographic

analysis to 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 is generally unavailable. Recently, a number of elasmobranch stock assessments have attempted to estimate the related Beverton-Holt steepness parameter from age structured models (Apostolaki et al. 2002; Brooks et al. 2002). 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* (Rago, pers. comm.). Our results, compared to the analysis of over 700 spawner-recruit relationships conducted by Myers et al. (1999), suggest the barndoor skate has a relatively low maximum annual reproductive rate. For a majority of the species in their study the maximum annual reproductive rate ranged from 1 to 7. Our results put the barndoor skate at the low end of this spectrum with an estimated maximum annual reproductive rate of 1.76 to 2.21. This is reassuring considering the reproductive strategy of the species.

It is interesting to note that the strong stock-recruit relationship we observed in the fall survey was due, in part, to the two estimates at the highest spawner abundances. These represent both the first and last pairing of data available from the fall survey when abundance has been highest. Over the next few years it will be enlightening to watch both the overall trends in survey abundance but also the pattern of recruitment that results from the highest abundances on record. In addition, as more years of data from the winter survey become available, the variability in parameter estimates should also be reduced providing another stock recruit relationship to compare to that which was generated from the fall.

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Survey (n)	Stock-Recruit Model	α	Standard Error	α LCLM	α UCLM	K / β	$\hat{\alpha}$	$\tilde{\alpha}$	Ln ($\tilde{\alpha}$)	$r_{intrinsic}$
Fall (26)	Beverton-Holt	4.40	1.05	2.27	6.54	0.05	11.89	1.96	0.67	**0.35**
Fall (26)	Ricker	3.97	0.77	2.42	5.52	11.49	10.71	1.76	0.57	**0.33**
Spring (18)	Beverton-Holt	4.97	7.06	-9.40	19.34	0.01	13.42	2.21	0.79	**0.37**
Spring (18)	Ricker	3.95	2.46	-1.06	8.97	45.43	10.68	1.76	0.56	**0.33**
Winter (11)	Beverton-Holt	_27.56_	_25.16_	-29.37	84.48	0.01	74.42	12.26	2.51	0.68
Winter (11)	Ricker	_12.63_	_5.77_	-0.41	25.68	18.73	34.12	5.62	1.73	0.53

Table 1. Results of the stock-recruit analysis for the barndoor skate on Georges Bank and the Gulf of Maine. The survey and model are indicated with n representing the number of years in which at least one skate was caught. α is the slope at the origin parameter with associated standard errors and 95% confidence intervals (UCLM, LCLM). K is the carrying capacity parameter from the Beverton-Holt model and β is the density dependant parameter from the Ricker model. $\hat{\alpha}$ is the lifetime production of spawners per spawner and $\tilde{\alpha}$ is the maximum annual reproductive rate (i.e. number of spawners produced by each spawner per year. The maximum population growth rate is $r_{intrinsic}$. Note that results from the winter survey are the least credible because of low sample sizes and high standard error (indicated by underlined italic typeface). The most credible estimates for the maximum population growth rate are from the fall and spring, indicated by underlined bold typeface.
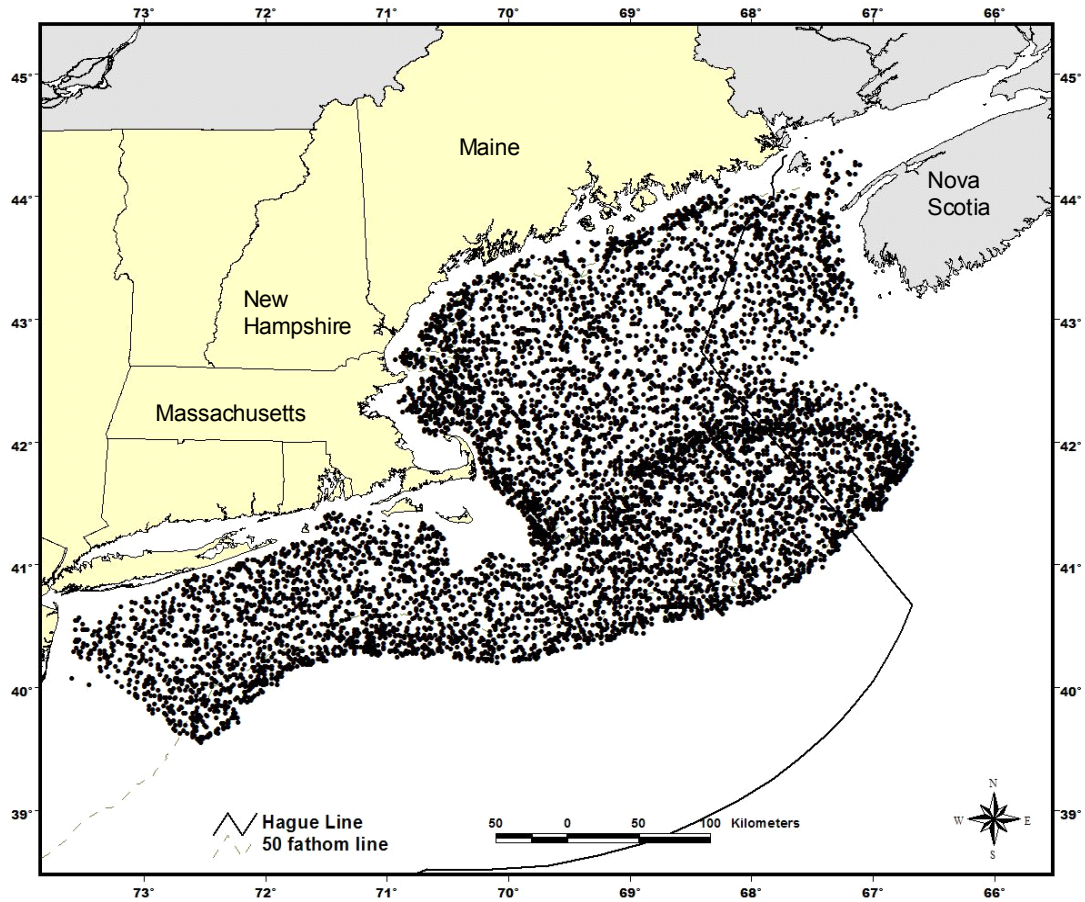
Figure 1. All survey stations sampled (n = 8,424) by the National NMFS annual fall
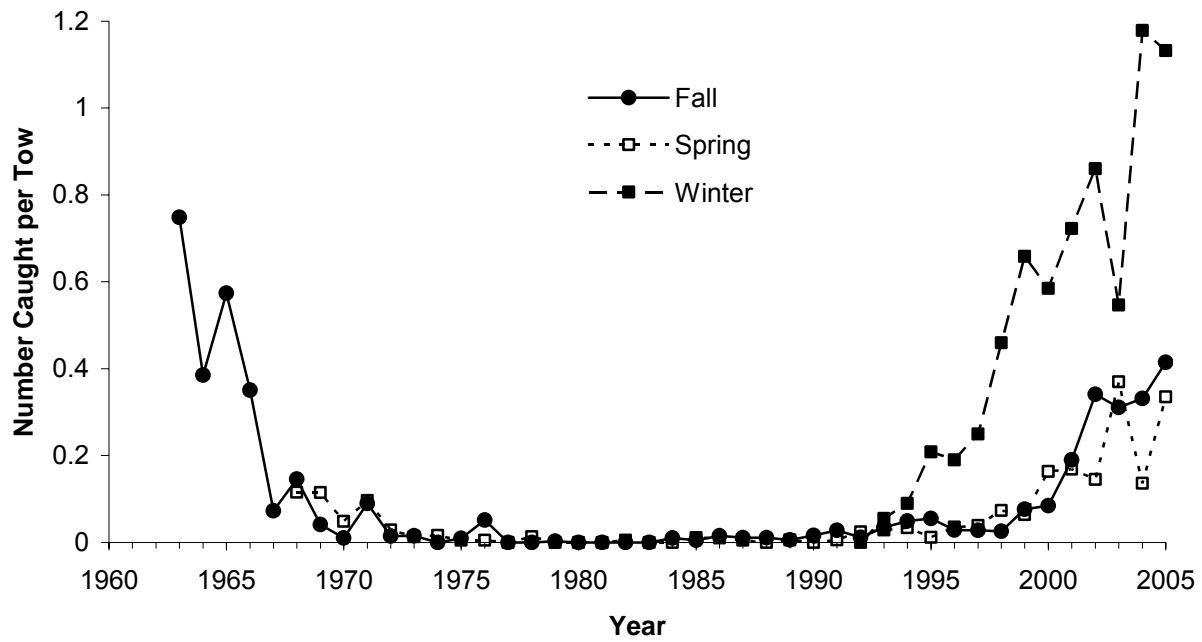groundfish survey from 1963-2005.

Figure 2. Number of barndoor skates caught per tow for each of the seasonal NMFS groundfish surveys.
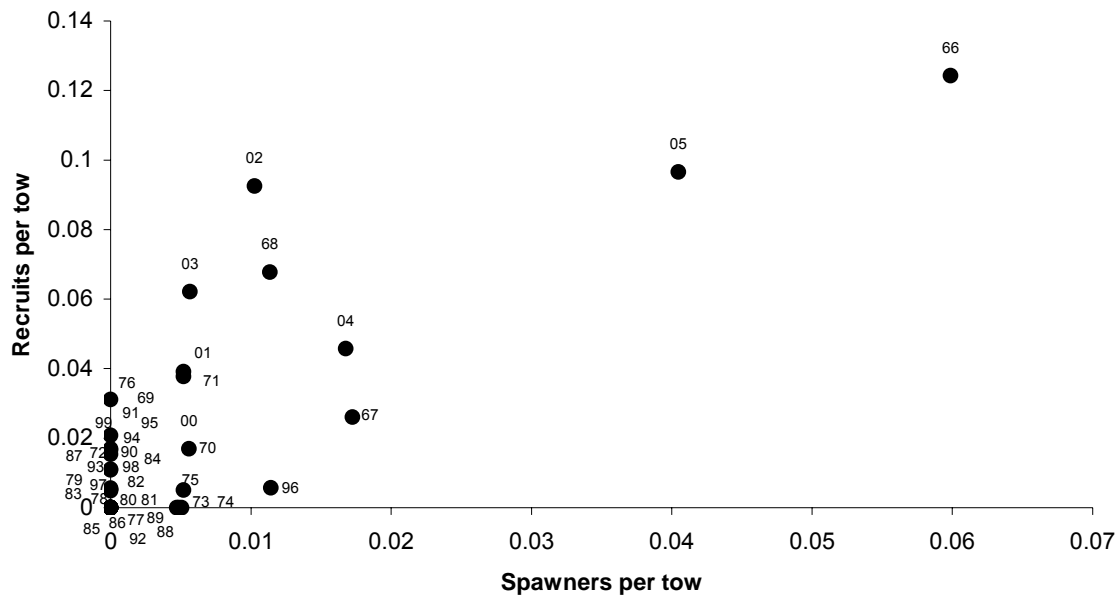
Figure 3. Stock-recruit relationship from the fall NMFS groundfish survey from 1963 to 2005 (n = 26; years in which at least one skate was caught). The year in which recruits were measured is indicated.
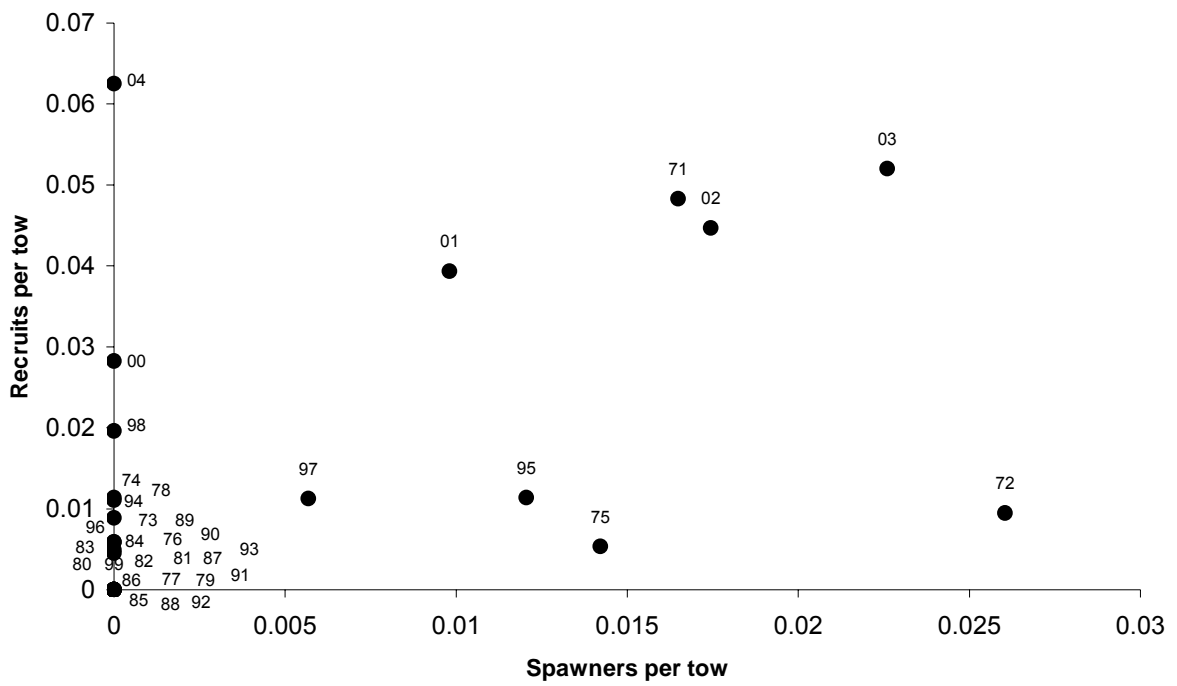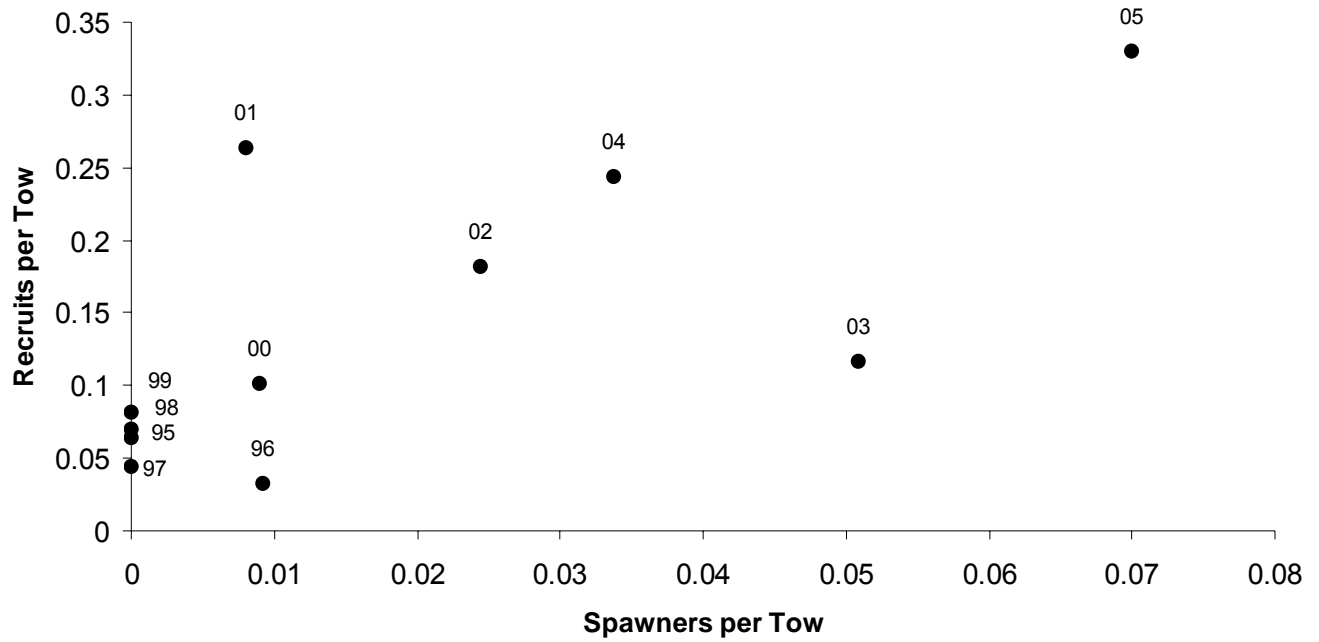
Figure 4. Stock-recruit relationship from the spring NMFS groundfish survey from 1968 to 2005 (n = 18; years in which at least one skate was caught). The year in which recruits were measured is indicated.
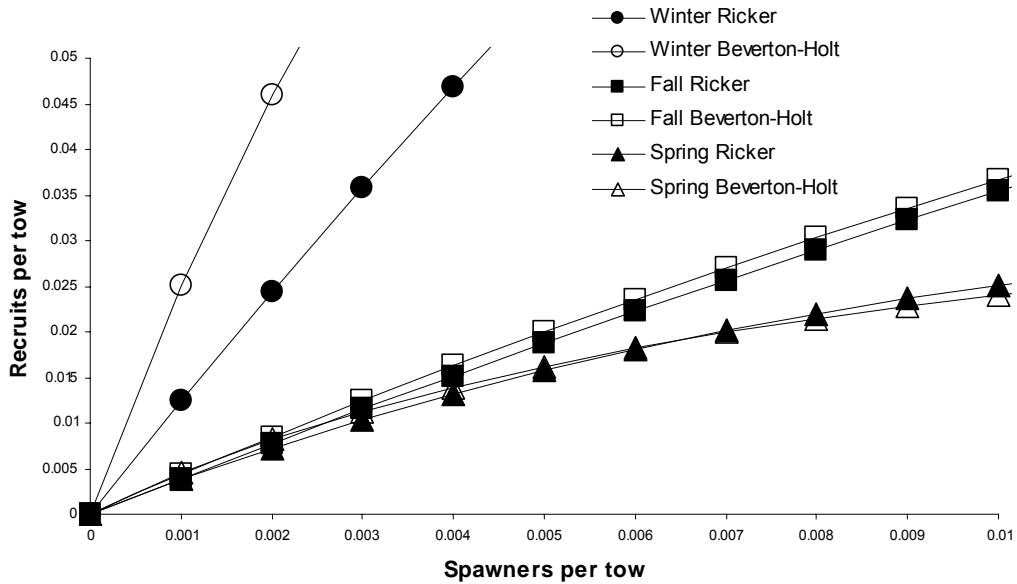
Figure 5. Stock-recruit relationship from the winter NMFS groundfish survey from 1992
to 2005 (n = 11; years in which at least one skate was caught). The year in
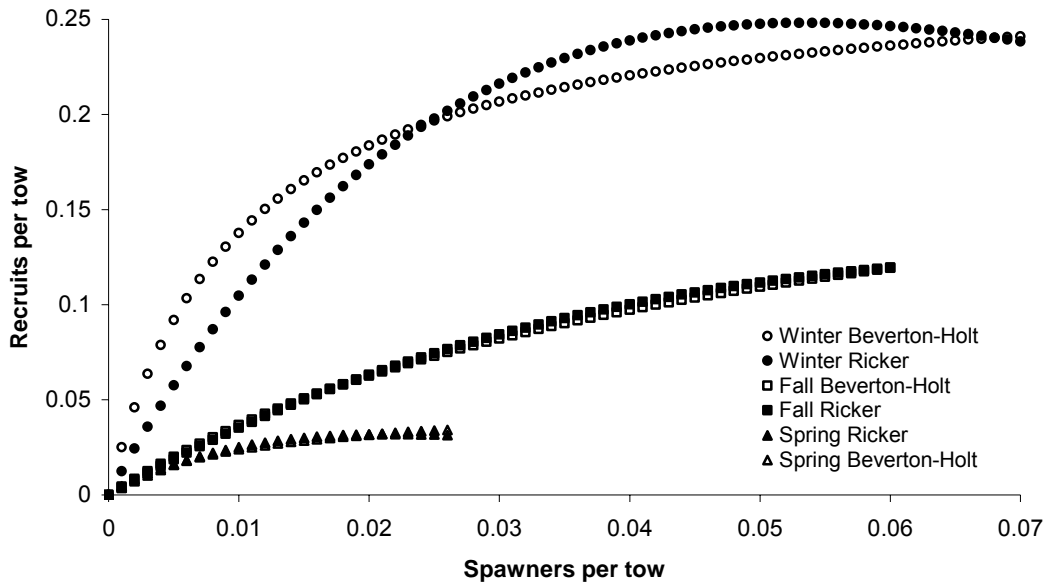which recruits were measured is indicated.

Figure 6. Stock-recruit relationship, as described by the Beverton-Holt and Ricker

models, from all three seasonal NMFS groundfish surveys. The top figure is

over the entire range of observed spawner abundances and the bottom figure is

focused on the lowest abundances to provide detail for the slope at the origin.
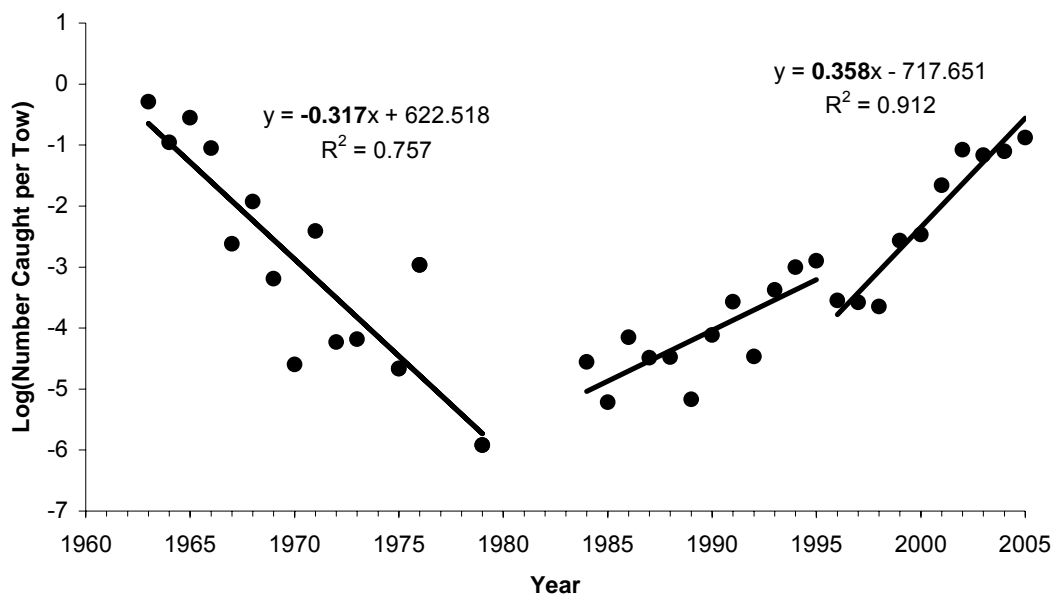
Figure 7. Survey indices from the fall NMFS groundfish survey on Georges Bank and

the Gulf of Maine. Data has been log transformed to estimate the rate of

population change. Resulting estimates for the observed rate of population

change from 1963-1979 (decline) and for 1996-2005 (recovery) is indicated by

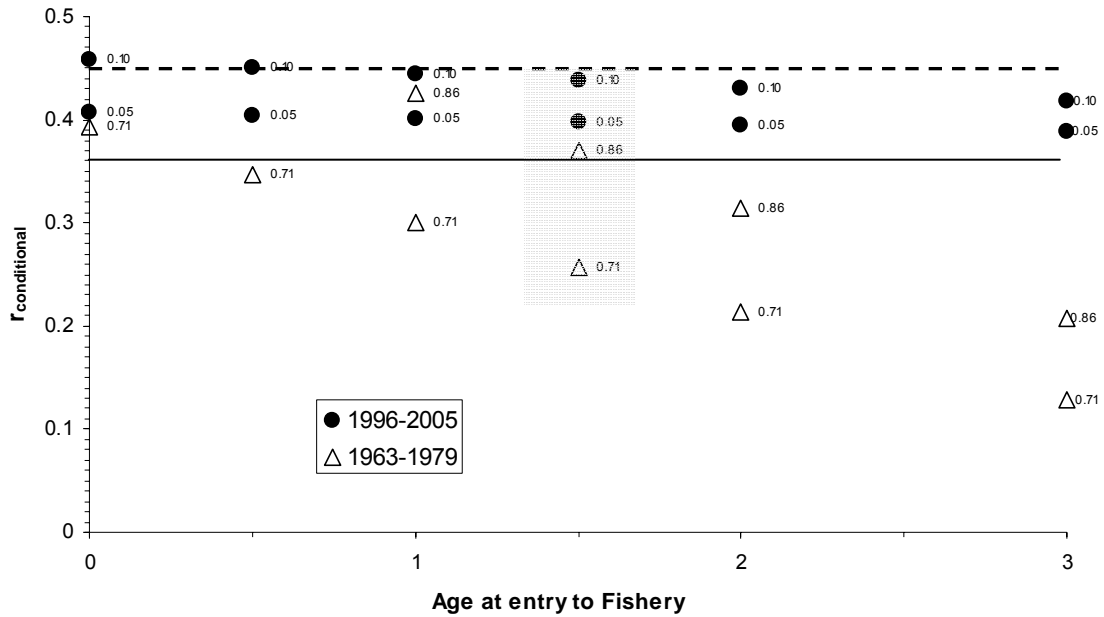the slope parameter (bold face type) in the linear equations.

Figure 8. Estimates of $r_{conditional}$ from a of Leslie matrix demographic analysis for the barndoor skate. Estimates from the decline and recovery are indicated as is the sensitivity of $r_{conditional}$ estimates to assumptions of age at entry and assumed fishing pressure for each scenario (indicated by the number next to each data point). The most believable scenario is indicated by the shaded region. The solid line represents the observed rate of population growth between 1996 and 2005 and the dashed line represents $r_{conditional}$ when first year survival is equal to adult. Note that two data points for the high F (0.86) decline analysis (age at entry of 0 and 0.5) are not plotted as they would have required a first year survival greater than adult.
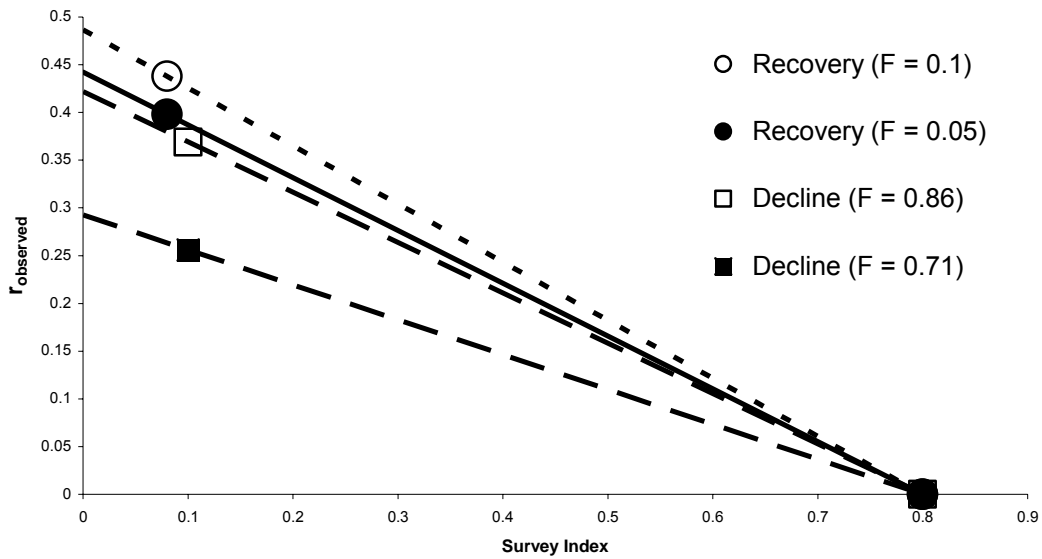
Figure 9. Extrapolation of calculated $r_{conditional}$'s to a zero population size to estimate $r_{intrinsic}$. Estimates from the most believable age at entry scenario (shaded region in Figure 8) were used and $r_{intrinsic}$ was estimated as the y-intercept from each relationship. The rightmost point represents the highest value recorded in the fall survey and assumed to represent virgin conditions where a long term growth rate of 0 would be realized. Note that if this assumption was incorrect, and the actual survey index should be higher (the 0.8 point shifted to the right), the extrapolation is over such short distances that estimates of $r_{intrinsic}$ would not be drastically altered.

Chapter 9

Conclusions and Future Work

Although our work has shed light on a number of different aspects of both the United States barndoor skate population and the methodologies used to assess marine species, there are two broad conclusions that can be drawn from this work. First, we have shown that although data were extremely limited, a lot of information can be gleaned from a careful analysis of the available data. Our field work provided many of the necessary life history parameters while our methodological developments provided the tools to extract information from the small sample sizes in the NMFS surveys. Secondly, the barndoor skate population not only appears to be in a solid recovery phase and in no current threat, but it also appears to be much more resilient to fishing pressure than previously believed.

The results and methods presented in this dissertation should, by no means, be thought of as a final step in the process. There is still work to be done. Our life history studies have provided the necessary basic parameters but there are a couple of aspects which still need to be considered. First, our vertebral analysis assumed that rings were formed annually and a formal verification process (i.e. marginal increment analysis) has not been completed. Annual ring formation has been shown in a number of other similar skate species and there is no reason to believe that the barndoor skate should be any different. To be thorough, however, we have obtained samples from NMFS from the winter months and this verification is forthcoming.

The other aspect of the life history for which no empirical data exists is fecundity. The Holden (1973) relationship was used out of necessity and like any other relationship that spans such a wide range of species, there is considerable uncertainty in these estimates. The reproductive tracts from our study have been preserved and a further

analysis, such as ovarian egg counts, may shed some light on this aspect of the barndoor skate reproduction. Another potential source of information may come from the Montreal Aquarium where they began successfully reproducing barndoor skates a couple years ago. We have been in contact with the curator and hope to gain further insights from the species reproductive behavior in captivity.

In our food habits study, we showed a clear pattern in differential niche utilization between mature male and mature female barndoor skates. Although the correlation between the sex-specific dentition is strong the cause of this shift in food habits remains unknown. Since the different food will surely contain different nutritional values, the possibility of exploring the energetics of mature barndoor skates may shed some light on the driving force of the observed sex-specific feeding habits. Further work should also be done on the specifics of the tooth morphology included the possibility of season changes in dentition and the exact timing of the expression of this secondary sexual characteristic in males.

Although the methods we developed were designed to avoid assumption violations in commonly used approaches, every method, including ours, have assumptions which must continue to be taken into consideration.   For example, the transitional form of the mean length statistic developed in chapter 4 worked well with Goosefish but the application to the barndoor skate required a different approach which took into account the reproductive strategy of the species and a strong stock-recruit relationship.   The application of any of these models must take into account the biological realism of the required assumptions. Another example is in our demographic analysis. Our estimates of observed population growth were done over a large range of

stock sizes and we assumed that growth was constant over those time periods due to no discernable pattern in the residuals. One of the premises of this work, however is that density dependant compensation plays a role in the differential survival of juveniles. Therefore, although it wasn't obvious in our data, one would expect changes in survival to be occurring within these ranges even if fishing pressure has remained relatively constant. Future work to address this issue and to further advance the methodology is planned. A time series fitting approach (i.e. Pella and Tomlinson, 1969) would allow the incorporation of data from each year and should result in more stable results.

On a final note, our work is not the only research which has suggested that the barndoor skate population may not have been in as much danger as proposed by Casey and Myers (1998). As mentioned in the life history section, analysis of Canadian survey and commercial fisheries data suggests that the overall distribution of the species is far more extensive than originally thought both in terms of depth and northern range (Kulka et al., MS 2002; Simon et al., MS 2002). Barndoor skates were found as far north as the Labrador Shelf to 62^0 N and into depths of about 1600 meters with significantly higher catch rates at depths below 450 meters (Kulka et al., 2002; Simon et al., MS 2002). These studies strongly indicate that Casey and Myers (1998) used a data set that poorly sampled barndoor skate overall distribution and as such substantially underestimated the actual barndoor skate population. It is important to note, however that although the US population now appear to be healthy and there are deep water populations in Canada, only a careful spatial analysis of historical data will allow conclusions to be drawn on range reductions and/or localized extirpations that may have occurred.

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