

NEW HYPOTHESIS HELPS EXPLAIN ELASMOBRANCH “OUTBURST” ON GEORGES BANK IN THE 1980s

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Abstract. Regime shifts are a feature of many ecosystems. During the last 40 years, intensive commercial exploitation and environmental changes have driven substantial shifts in ecosystem structure and function in the northwest Atlantic. In the Georges Bank–southern New England region, commercially important species have declined, and the ecosystem shifted to one dominated by economically undesirable species such as skates and dogfish. Aggregated abundance indices indicate a large increase of small and medium-sized elasmobranchs in the early 1980s following the decline of many commercial species. It has been hypothesized that ecological interactions such as competition and predation within the Georges Bank region were responsible for and are maintaining the “elasmobranch outburst” at the heart of the observed ecosystem shift. We offer an alternative hypothesis invoking population connectivity among winter skate populations such that the observed abundance increase is a result of migratory dynamics, perhaps with the Scotian Shelf (i.e., it is an open population). Here we critically evaluate the survey data for winter skate, the species principally responsible for the increase in total skate abundance during the 1980s on Georges Bank, to assess support for both hypotheses. We show that time series from different surveys within the Georges Bank region exhibit low coherence, indicating that a widespread population increase was not consistently shown by all surveys. Further, we argue that observed length-frequency data for Georges Bank indicate biologically unrealistic population fluctuations if the population is closed. Neither finding supports the elasmobranch outburst hypothesis. In contrast, survey time series for Georges Bank and the Scotian Shelf are negatively correlated, in support of the population connectivity hypothesis. Further, we argue that understanding the mechanisms of ecosystem state changes and population connectivity are needed to make inferences about both the causes and appropriate management responses to large-scale system change.

Key words: *elasmobranchs; Georges Bank; Leucoraja ocellata; regime shift; Scotian Shelf; winter skate.*

INTRODUCTION

Many ecosystems are apparently stable for long periods of time. However, it is becoming widely appreciated that ecosystems may also experience periods of rapid change between apparently stable configurations of structure, process, and function (Scheffer et al. 2001, Mangel and Levin 2005). Research into such regime shifts has revealed differences in the frequency of occurrence of shifts and multiple patterns of causation (Lees et al. 2006). For example, external climatic forcing often causes regime shifts in terrestrial and aquatic ecosystems as evidenced by studies of the impact of the climatic oscillations in the Atlantic (Ottersen et al. 2001) and the Pacific (Gargett 1997, Beamish et al. 2004, Pederson et al. 2006) basins. However, not all regime

shifts are driven by climate. Changes in nutrient loading or top-down predation pressure have been shown to cause wholesale shifts in ecosystem structure in lakes (Carpenter et al. 2001, McGowan et al. 2005) and on coral reefs (Nystrom et al. 2000). Top-down control also helps to structure savanna ecosystems (van Langevelde et al. 2003). Regardless of cause, regime shifts hinder our ability to manage ecosystems because the profound changes they engender are often unpredictable and rapid (Folke et al. 2004). Accordingly documenting, explaining, and ultimately predicting regime shifts is an important challenge for ecosystem-based management.

In addition to the examples of regime shifts driven by these natural causes, human-induced regime shifts have also been identified. Mechanisms responsible for these changes include fire suppression (Fuller et al. 1998), grazing (Cingolani et al. 2005), and interruption of top-down control by predation as a result of fishing (Myers and Worm 2005) or other mechanisms (Ripple and Beschta 2006). With respect to the impacts of fishing,

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one of the most widely cited examples is that of Georges Bank on the northeast continental shelf of the United States. Since the 1960s, exploitation in the northwest Atlantic has been associated with large changes in abundance of individual species and in ecosystem structure generally (Fogarty and Murawski 1998, Link et al. 2002, Choi et al. 2004, Link and Ford 2006). While not every area within the northwest Atlantic ecosystem experienced identical dynamics, the well-studied Georges Bank and southern New England region can serve as examples for the U.S. northwest Atlantic region generally. In this region, many species were declared overfished during the 1970s and early 1980s, including haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*), and herring (*Clupea harengus*), in addition to the well-documented decline of Atlantic cod (*Gadus morhua*) (Hutchings and Myers 1994, Fogarty and Murawski 1998). Subsequently, during the mid-1980s large increases in abundance of small and medium-sized elasmobranchs in the northwest Atlantic raised concerns that commercially important groundfishes (e.g., cod, haddock, and flounders) were being replaced by economically undesirable elasmobranchs (Murawski 1991, Mayo et al. 1992, Murawski and Idoine 1992, Safina 1995, Fogarty and Murawski 1998).

Analyses of survey data indicated that small elasmobranchs (skates and dogfish) had increased in abundance in the 1980s (Fogarty and Murawski 1998). However, the apparent regime shift favoring elasmobranchs, termed the elasmobranch outbreak, was not consistently observed for all elasmobranch species (Fig. 1A, B). For example, the majority of skate species did not increase in abundance. Thorny skates (*Amblyraja radiata*) and barndoor skates (*Dipturus laevis*) remained below their management biomass thresholds for most of the 1970s and 1980s (Northeast Fisheries Science Center 1999). In fact, the barndoor skate was very rarely caught by National Marine Fisheries Service (NMFS) surveys throughout the 1980s (Northeast Fisheries Science Center 1999) and was considered at risk of local extirpation (Casey and Myers 1998). The smooth skate, *Malacoraja senta*, appears to have declined in abundance from highs in the 1970s (Northeast Fisheries Science Center 1999). In fact, of the seven common skate species in the northwest Atlantic region, only winter skate, *Leucoraja ocellata*, increased sufficiently to account for the patterns evident in total elasmobranch abundance in the 1980s (Fig. 1B). Spiny dogfish, *Squalus acanthias*, also exhibited substantial increases during this period (Fogarty and Murawski 1998). Thus the increases of winter skate and spiny dogfish are at the heart of the proposed regime change in the northwest Atlantic and of our understanding of the ecology and the approach to management of this ecosystem.

Although the patterns of increase in winter skate and spiny dogfish are clear, the causes and consequences of the change remain more controversial. It has been hypothesized that the increase in elasmobranch abun-

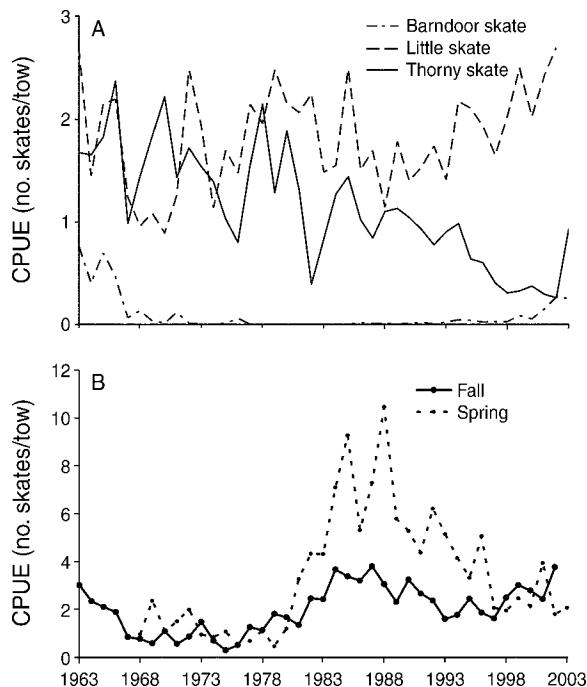


FIG. 1. (A) Abundance indices, as catch per unit effort (CPUE), for three western Atlantic skates for the Georges Bank-southern New England region from 1963 to 2003. (B) Aggregated winter skate abundance trends for the National Marine Fisheries Service (NMFS) bottom-trawl surveys for the Georges Bank-southern New England region for fall and spring.

dance was caused by and is now in turn limiting the recovery of groundfish as a result of competition and/or predation (Murawski 1991, Mayo et al. 1992, Fogarty and Murawski 1998). These hypotheses implicate a population dynamic response of each elasmobranch population. However, Link et al. (2002) found little evidence that direct predation by elasmobranchs was causing the decline or repressing recovery of groundfish. Importantly, Link et al. (2002) noted that conclusions regarding the regime shift were sensitive to the survey-based estimates of abundance of elasmobranch species. Thus inferences regarding the importance of elasmobranchs in changes in the northwest Atlantic ecosystem are tied to the degree to which NMFS annual trawl surveys accurately reflect elasmobranch population dynamics within the region.

Here we focus on the dynamics of winter skate in the northwest Atlantic as being central to the hypothesized regime shift. Although spiny dogfish also experienced increases during the same period, survey data indicate that skates were often more abundant (Fogarty and Murawski 1998) and occupied the same habitat as many groundfish species (Gabriel 1992). Additionally, dietary overlaps between skates and groundfish and between dogfish and groundfish are similar (Garrison and Link 2000). Finally, and perhaps most important for the analyses we undertake, detailed information regarding

the life history and population dynamics of winter skate in this region was available (Frisk et al. 2002, Frisk 2004; M. G. Frisk and T. J. Miller, *unpublished manuscript*).

The traditional hypothesis suggests that skate populations increased as a result of internal dynamics of growth and reproduction. Here we propose a new, alternative hypothesis to explain the patterns observed in winter skate abundance in the northwest Atlantic. We propose that the increases in abundance observed in U.S. waters resulted from an exchange with other skate populations, most likely involving populations in Canadian waters. After presenting each hypothesis, we assess the degree of support provided by the data. We conclude that the alternative hypothesis we present is a viable explanation of the patterns observed in the data.

THE HYPOTHESES

The elasmobranch "outburst" hypothesis

This hypothesis suggests that the winter skate population on Georges Bank–southern New England increased as a result of internal dynamics of growth and reproduction. If this hypothesis is true, two predictions regarding the population of winter skate can be made: (1) Abundance patterns from the available fishery-independent surveys should be coherent. Specifically, all surveys should demonstrate an increase over the same time period. (2) Times series of population structure should reflect an elaboration of size (age) classes appropriate to what is known about winter skate growth rates.

We review the first prediction by examining NMFS groundfish surveys conducted in the northwestern Atlantic and surveys by the Massachusetts Division of Marine Fisheries (MDMF). Survey data are available for spring and fall seasons. We review the second prediction by examining length frequency patterns in the NMFS spring and fall surveys.

The population connectivity hypothesis

The Scotian Shelf is one of many coastal banks of glacial origin that stretch from the Grand Banks in the north to Georges Bank in the south. On the Scotian Shelf winter skate is common on Browns, Sable Island, Western, and Banquereau Banks (Canadian Department of Fisheries and Oceans 2000). Browns Bank, on the southern limit of the Scotian Shelf, is separated from Georges Bank by approximately 50 km. Could movement from the Scotian Shelf south to Georges Bank account for patterns observed in surveys over the last three decades? In short, this hypothesis suggests that the Georges Bank–southern New England population is not closed, but rather is connected to other populations so that neighboring populations exchange individuals.

If this hypothesis is true, we can make the following predictions: (1) the abundance patterns inferred from surveys of the Scotian Shelf and Georges Bank should be complementary; and (2) skates, like many elasmobranchs,

show limited compensatory dynamics (Frisk et al. 2005). Thus estimates of survival to recruitment in a closed population should exhibit relatively low levels of variation over the survey time series. In contrast, if the population is open, estimates of the survival probability of eggs to recruitment on Georges Bank should show an increase coincident with periods of migration from the Scotian Shelf.

We review these predictions by comparing NMFS and Canadian Department of Fisheries and Oceans (DFO) survey time series, and by estimating probabilities of "survival to recruitment" required to produce the recruitment observed in the NMFS survey data.

METHODS

To test the predictions from the two hypotheses, we analyzed fishery-independent survey data to assess patterns of both coherence among surveys and elaboration of population structure over time. Additionally, we used times series of spawning stock biomass and recruits, appropriately lagged in time (Frisk and Miller 2006), to develop a time series of survival probabilities. These probabilities are estimates of the level of survival that would be required to explain the recruit abundance given the observed spawning stock biomass.

Survey abundance time series

We analyzed data from three fishery-independent surveys: the NMFS groundfish survey (spring and fall), the MDMF inshore bottom trawl survey (spring and fall), and the DFO summer trawl survey. For each survey, winter skate <30 cm total length (TL) were not included in any correlation analysis or plot. Winter skate and little skate are difficult to distinguish below 30 cm TL based on morphometrics (Bremer et al. 2005). Hence inclusion of skate <30 cm TL would risk confounding the potentially different dynamics of two separate species.

We summarize survey coverage, design, station allocation, and gear for each survey. The NMFS fall survey began sampling offshore waters of southern New England, Georges Bank, and the Gulf of Maine in 1963 and was expanded to inshore waters in 1972 (Azarovitz 1981). The NMFS spring bottom trawl survey has been conducted since 1968 in offshore waters of southern New England, Georges Bank, and the Gulf of Maine. It was expanded to sample inshore waters in 1973. The surveys were conducted primarily by the research vessels Albatross IV and Delaware II. The surveys use a Yankee 36 bottom trawl with 1.27-cm mesh liner, towed for 30 min at 1.95 m/s (Sosebee and Cadrin 2006). Each season 300–400 stations were sampled, allocated in a stratified random design with strata defined by latitude and depth. Our analyses of survey time series included all survey strata, as trends were similar whether analyses were limited to Georges Bank data only or whether data from all regions were included.

The MDMF inshore bottom trawl survey has been conducted since 1978 in the spring and fall (Howe 1989). The survey uses a 3/4 North Atlantic type two-seam ("whiting") otter trawl towed for 20 min at 1.28 m/s. The trawl is equipped with 8.9-cm mesh wings, 6.3-cm mesh belly, and a codend with a 0.63-cm mesh liner. During the spring and fall, approximately 95 stations are occupied along the coast of Massachusetts.

DFO has conducted a summer bottom trawl survey on the Scotian Shelf since 1970. The survey is depth stratified, occupying more than 200 stations/yr, and employs a Western IIA bottom trawl with a small mesh codend, towed at 1.8 m/s for 30 min. Survey data have been calibrated to adjust for any changes in catchability with gear changes.

To assess patterns in the survey time series, we applied simple parametric (Pearson) and nonparametric (Spearman rank) correlation methods. To permit easier visual comparisons, all data are plotted as standardized normal deviates, i.e.,

$$Z_t = \frac{(C_t - \bar{C})}{\sigma_C} \quad (1)$$

where Z is a standardized normal deviate and C is the survey catch per unit effort (CPUE) in year t . We note that results of correlation analysis are not affected by this transformation.

To assess trends in size structure in skate populations, we binned survey catches into 1 cm TL-sized bins. The catch per unit effort of size-structured abundances was plotted for each survey year. Frisk and Miller (2006) published results of an analysis of size-at-age of winter skate from waters from the Gulf of Maine to the mid-Atlantic bight caught in conjunction with the NMFS trawl surveys. They estimated von Bertalanffy parameters as $t_0 = -2.06$ yr; growth coefficient, $k = 0.07$ /yr; and asymptotic length, $L_\infty = 122.1$ cm. Their analysis indicated winter skate is a slow-growing species, with individuals attaining 30–40 cm by age two to three years of age and 95% of L_∞ by 35 years of age. We analyzed patterns in the length frequencies from both NMFS and MDMF surveys for the northwest Atlantic for compatibility with estimated growth rates of winter skate (Sulikowski et al. 2003, Frisk and Miller 2006).

Probability of survival estimates

Data from the NMFS survey were used to estimate probabilities of survival for annual recruitments. Spawning biomass (S_t) in year t was estimated as the CPUE of mature winter skate (>79 cm) for each year using the NMFS spring and fall survey individually. Annual egg production (σ) was estimated as

$$\sigma_t = fS_t \quad (2)$$

where f is fecundity adjusted for a 50:50 sex ratio. We assumed a female produced 60 eggs/yr (Frisk 2004). We assumed that adults experienced no mortality.

Because skates <30 cm cannot be reliably identified to species, we estimated the observed recruit level using a three-year running average of recruits 30–40 cm TL, which corresponds to two to three years of age (Frisk and Miller 2006). Separate analyses were performed on the spring and fall surveys. The annual recruitment survival in year t was estimated as follows:

$$\begin{aligned} N_{a+1} &= \sigma_a \exp^{-M} \\ N_{a+2} &= N_{a+1} \exp^{-M} \\ N_{a+3} &= N_{a+2} \exp^{-M} \end{aligned} \quad (3)$$

where M is mortality, and N_a is numbers at age. Then we calculated the natural mortality necessary to explain the observed recruitment ($R_{t+2} + R_{t+3}$) by estimating M that satisfies the following equation:

$$R_{a+2} + R_{a+3} = N_{a+2} + N_{a+3}. \quad (4)$$

RESULTS

The two alternative hypotheses lead to differing predictions regarding the coherence of survey time series, patterns in the elaboration of population structure, and estimated survival. Here we review analyses pertinent to each prediction.

Coherence of aggregated survey time series

Catches per tow (CPUE) in the NMFS surveys provide an index of abundance for winter skate. Data from the NMFS spring and fall surveys indicate a distinct increase in winter skate abundance in the early 1980s, followed by a clear decline in abundance through the 1990s (Fig. 1B). However, a more abrupt increase in the 1980s is evident in the spring survey than in the fall survey data. Fall survey data indicate that the winter skate population was characterized by an average CPUE of 0.96 fish per tow (all CPUE data will be in these units) from 1967 to 1980 and then suddenly a more than doubled average CPUE of 2.88 from 1981 to 1990. During the period of lowest estimated abundance in the 1970s, spring survey CPUE was 1.01 (average of 1970 to 1980); 10 yr later during the peak of winter skate abundance estimates, the CPUE was 6.50 (average of 1981 to 1989).

The two NMFS surveys show a strong positive correlation (Table 1, Fig. 2). Thus at the aggregate level, within the NMFS surveys, there is support for the coherency prediction. However, when the analysis is broadened to include the MDMF surveys, the support for the prediction of coherence is much weaker (Table 1, Fig. 2). Of the six possible pairwise comparisons of the surveys conducted in the Georges Bank–southern New England region, only three of the correlations were significant. Two of these significant correlations were between seasons within the same survey; only one was for a comparison between surveys.

Development of size and age structure

If the elasmobranch outbreak was the result of a population dynamic-driven increase in abundance, then

TABLE 1. Pearson correlation coefficients resulting from analyses of catches of winter skate in different fishery-independent surveys.

Survey	NMFS spring	NMFS fall	MDMF spring	MDMF fall	DFO spring
NMFS spring					
NMFS fall	0.806***				
MDMF spring	0.394*	-0.113			
MDMF fall	0.147	0.095	0.488*		
DFO summer	-0.008	-0.168	0.291	0.220	

Notes: Key to abbreviations: NMFS, National Marine Fisheries Service; MDMF, Massachusetts Division of Marine Fisheries; DFO, Canadian Department of Fisheries and Oceans.

* $P < 0.05$; *** $P < 0.001$.

we predicted that the size or age structure in the population should have expanded in a manner compatible with known patterns of winter skate growth.

For brevity, we present only the NMFS data, although patterns in size structure were similar in the MDMF surveys. The NMFS fall trawl survey provides the longest-running fishery-independent survey in the region, with surveys dating back to 1963. The dynamics of the size structure of winter skate in the northwest Atlantic as inferred from this survey show four general

phases (Fig. 3A). From 1963 to 1968, winter skate in the survey were dominated by a high abundance of three- to five-year-old skates (TL, 30–50 cm; Fig. 3A). Surprisingly, the data indicate the relative absence of adults during the 1960s. Recruits observed during 1963–1968 were likely a result of either a spawning biomass that was removed in the years prior to survey operation or the movement of spawners or recruits into the region. During the 1970s a second phase can be identified with very few winter skate of any length observed in the survey. A third phase between 1982 and 1992 can be recognized in the survey time series. This phase is characterized by the abrupt appearance and continued presence of higher abundances of a wide size range of skates, suggesting near-instantaneous emergence of a fully age-structured population (recruits to 20+ years old). The distribution of sizes and their associated abundances are hard to reconcile with the population structure in the first phase and estimates of growth in winter skate. In the final phase of the time series, the abundance of adult-sized skate is greatly reduced, but recruitment of recruits and small juveniles, presumably resulting from the adults evident in the second phase, is maintained. A similar triphasic pattern can be recognized in data from the NMFS spring survey, which began five years after the fall survey (Fig. 3B).

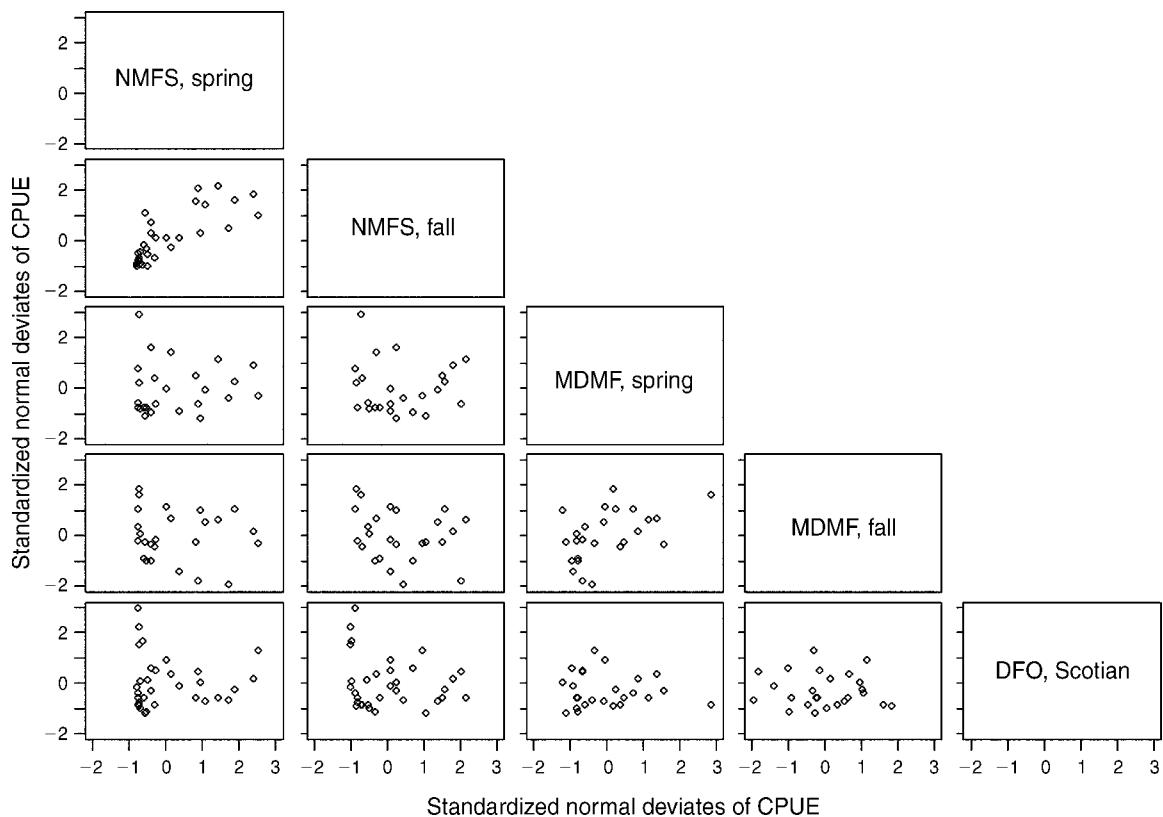


FIG. 2. Relationships among CPUE for all winter skate among five different fishery-independent surveys. Survey data are plotted as standardized normal deviates to aid in visualization. Key to abbreviations: NMFS, National Marine Fisheries Service; MDMF, Massachusetts Division of Marine Fisheries; DFO, Canadian Department of Fisheries and Oceans.

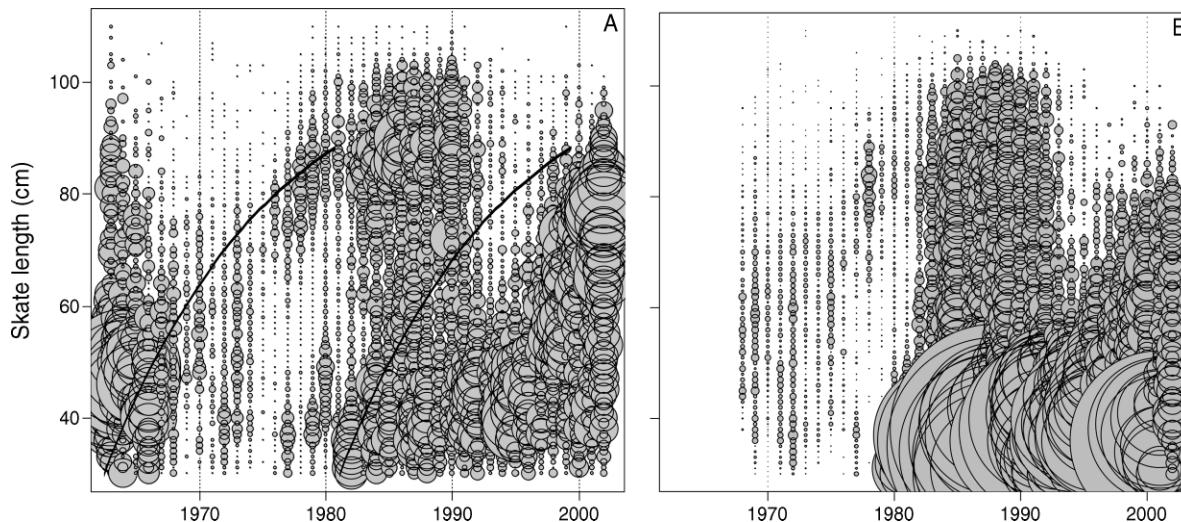


FIG. 3. Age-structured dynamics of winter skate for the Georges Bank region for National Marine Fisheries Service (A) fall and (B) spring surveys. Size classes <30 cm are not shown because small individuals of little skate and winter skate are not easily distinguished. The solid black lines represent the size at age for winter skate based on theoretical cohorts born in 1963 and 1983, using growth curves from Frisk and Miller (2006). Sizes of circles indicate numbers of skates.

Coherence between NMFS and DFO surveys

The first prediction made by our alternative open-population hypothesis is that the abundance time series on the Scotian Shelf and Georges Bank should be complementary. There are two aspects of complementarity. During the early 1990s, surveys conducted in the two areas do indeed appear to show opposite adult abundance trends, such that when abundance on the Scotian Shelf increases, that on Georges Bank decreases (Fig. 4A). The size structure data for the three populations indicates that during periods when adults were largely absent from the Georges Bank system, they were present on the Scotian Shelf. These adults may provide the source for the recruits evident in the Georges Bank population during the early 1980s that could not be explained solely by the size structure on Georges Bank.

To examine this relationship in more detail, we correlated the survey CPUE for adults only from the NMFS and DFO surveys. There was a negative, nonlinear, and almost identical relationship between both the NMFS fall and the NMFS spring survey with the DFO survey. We show the pattern for the NMFS fall data only for brevity (Fig. 4B). We conducted one-tailed tests of the hypothesis that the correlations between the NMFS and DFO surveys were negative. For the comparison of the NMFS fall survey and the DFO Scotian Shelf survey, both correlation measures were negative but marginally nonsignificant (Pearson $r = -0.168$, $P = 0.16$; Spearman $\rho = -0.243$, $P = 0.08$). However, results were mixed for the NMFS spring survey vs. DFO Scotian Shelf surveys (Pearson $r = -0.008$, $P = 0.48$; Spearman $\rho = 0.097$, $P = 0.75$).

Probability of survival

The second prediction derived from the open-population hypothesis is that a subsidy of adults to Georges Bank from the Scotian Shelf would cause an increase in the apparent probability of survival of young skates. Specifically, we hypothesized that if the two areas are linked, periods of emigration or immigration of adults to the Georges Bank–southern New England region from the Scotian Shelf should be reflected in estimates of juvenile survival.

The survival patterns, calculated from either spring or fall data, indicate two periods where apparent survival to recruitment reached peak levels (Fig. 5). These periods correspond to the sudden increase of winter skate in the early 1980s and then again in the 1990s during a reduction in the large adult population in Georges Bank–southern New England. To interpret these results, let us first assume the winter skate population in the Georges Bank–southern New England region is closed. For example, based on the spring survey, our analyses suggest that cohort survival from the egg stage to 3-year-old recruits increased from 1–2% in the mid-1970s to 6–11% by the early 1980s. Given that elasmobranchs are generally assumed to show little compensatory ability, a three- to fivefold increase in survival over a short time period would seem biologically unrealistic. If a closed population is not assumed, the increase in survival can be interpreted as a subsidy of spawning adults and/or recruits from outside Georges Bank.

DISCUSSION

Understanding the mechanisms responsible for the observed changes in the abundance and size distribution

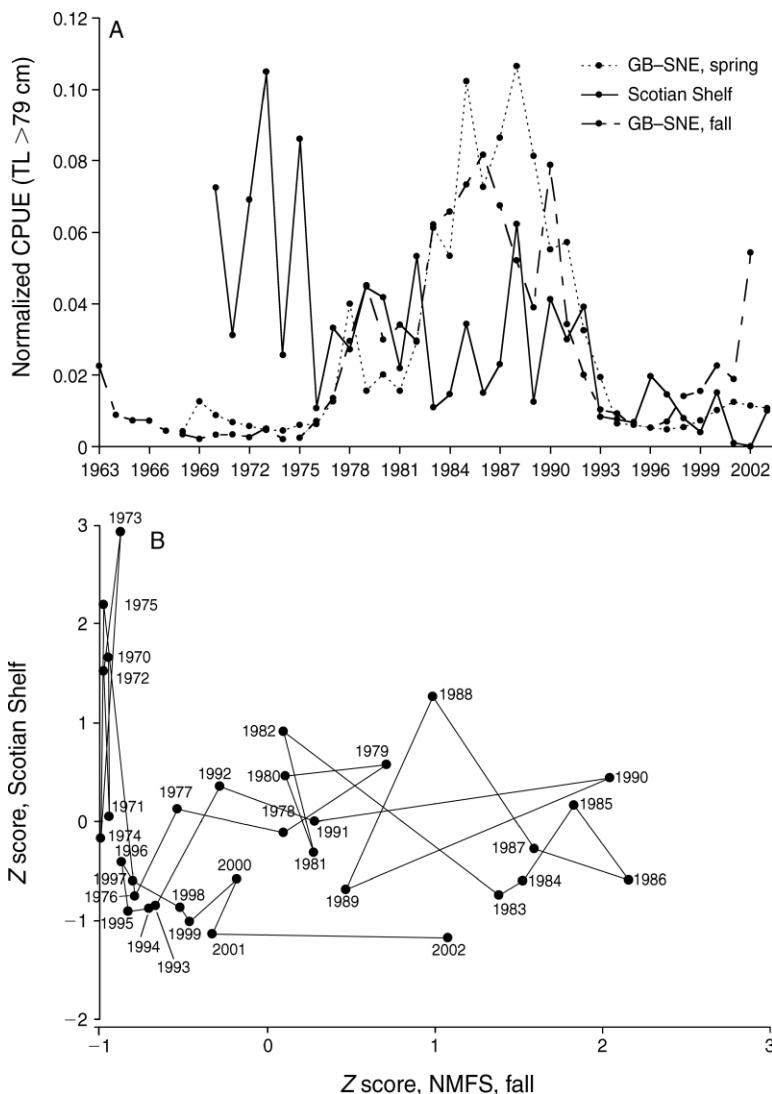


FIG. 4. Relationships between survey data for the Georges Bank and Scotian Shelf regions. (A) Survey catch per unit effort (CPUE) over time for the Georges Bank-southern New England (GB-SNE) region and the Scotian Shelf for 1963–2003 for skates >79 cm total length (TL). (B) Plot of standardized National Marine Fisheries Service (NMFS) fall survey catches against standardized Scotian Shelf survey catches. Both surveys are plotted as Z score values. Lines link successive years, indicated near each data point.

of winter skate on Georges Bank is central to assessing the nature of the proposed regime shift in the northwest Atlantic. The current paradigm is that a competitive or predation pressure release caused by the removal of groundfish by commercial fisheries led to the elasmobranch outburst. Support for this hypothesis largely depends on, and remains tied to survey trends. Here we have provided a detailed review of the same survey data and identified trends that appear at odds with the outburst hypothesis as originally proposed. We have shown that abundance and size data from fishery-independent surveys indicate a population rate of increase in the winter skate in the 1980s that was biologically unrealistic, assuming a closed population. Moreover, the elaboration of size (age) classes shown in

NMFS surveys does not conform to our current understanding of growth dynamics in winter skate (Sulikowski et al. 2003, Frisk and Miller 2006). Accordingly, we believe that the increase in winter skate most likely was not driven by internal population dynamics. Thus we conclude that competitive release or other proposed mechanisms are not solely responsible, and perhaps are unrelated to the observed increase in population size of winter skate during the early 1980s.

We presented an alternative explanation of winter skate population dynamics. Specifically, we proposed the hypothesis that connectivity among skate populations leading to movements among adjacent populations resulted in the trends observed in survey estimates. We demonstrated a complementary pattern in the NMFS

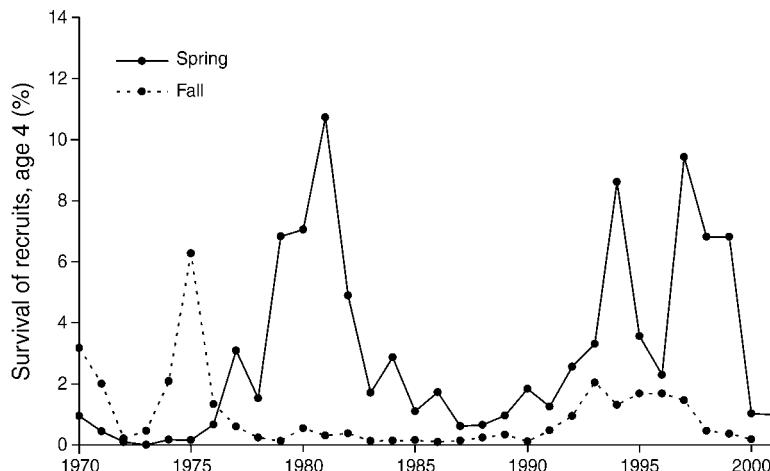


FIG. 5. Estimated percentage survival of winter skate recruits for the spring and fall National Marine Fisheries Service surveys.

and DFO survey time series that is compatible with the alternative hypothesis we have proposed. Moreover, the magnitude of the sudden increase in survival rate of recruits in the early 1980s and 1990s is not compatible with what is known of compensatory dynamics in skate populations (Frisk et al. 2001), but is compatible with a subsidy from another population involving an exchange between the adult and/or juvenile stages of the populations.

What might cause the movement of winter skate from one ecosystem to another? During the last 30 years, the Scotian shelf ecosystem has gone through dramatic changes in species composition, trophic structure, and physical properties (Choi et al. 2005). Distinct changes occurred in the ocean climate of the Scotian Shelf over this 30-year period. A warm period occurred during the late 1970s and early 1980s. This period was associated with the first recordings on the Scotian Shelf of several temperate/subtropical species. In contrast, a cool period during the mid-1980s and 1990s was associated with several subarctic species. The physiological condition of species on the Scotian Shelf varied with these ecosystem changes (Canadian Department of Fisheries and Oceans 2003, Choi et al. 2005). Several benthic fish species including winter skate, yellowtail flounder (*Limanda ferruginea*), longhorn sculpin (*Myoxocephalus octodecemspinosus*), striped wolfish (*Anarhichas lupus*), silver hake, haddock, and cod exhibited high physiological condition during the 1970s (Canadian Department of Fisheries and Oceans 2003). During the warm late 1970s and early 1980s, declines in physiological condition indices for many species, including cod and winter skate, were recorded. For example, beginning in 1979, winter skates' physiological condition decreased to average levels and then declined to poor levels throughout the 1980s (Canadian Department of Fisheries and Oceans 2003). Ecosystem changes on the Scotian Shelf, possibly driven by the interaction of temperature and changing trophic dynamics during the 1980s (Choi et al. 2005),

provide a reason why winter skate might migrate south to Georges Bank. However, we were unable to estimate the physiological condition of winter skate on Georges Bank during the 1980s, and it remains difficult to determine underpinning mechanisms leading to winter skate movement off the Scotian Shelf and onto Georges Bank.

We believe that we have shown that population connectivity in the northwestern Atlantic is a parsimonious and plausible explanation of the patterns in the survey abundance and size structure data. But we recognize that we are unable to conclude that such movements definitively lead to the observed population patterns. Several types of data could help to test our ideas further. Most directly, direct tracking of winter skate would help to fully evaluate the migration hypothesis. Less directly, we have inferred a mismatch between known growth patterns and observed size structure. Such inferences would be far stronger if they were supported by a fully age- and size-structured population model. A fully age-structured model of winter skate that includes a random walk in adult mortality and stochastic recruitment process error to mimic a migration would be useful. Such a model could clearly indicate whether there is truly a mismatch between the temporal pattern in size structure in the surveys and known rates of skate growth as we claim. The finding of periods of positive recruitment anomalies in one area that matches a period of negative recruitment anomalies in another area would be strong evidence of a population subsidy from one area to another.

Equally, there are several arguments against our hypothesis. One argument against our hypothesis might be that skates display minimal movement and short migrations. For example, a recent analysis of seasonal migration of thornback rays, *Raja clavata*, in the North Sea has indicated the existence of local populations that have little exchange (Hunter et al. 2005). These data

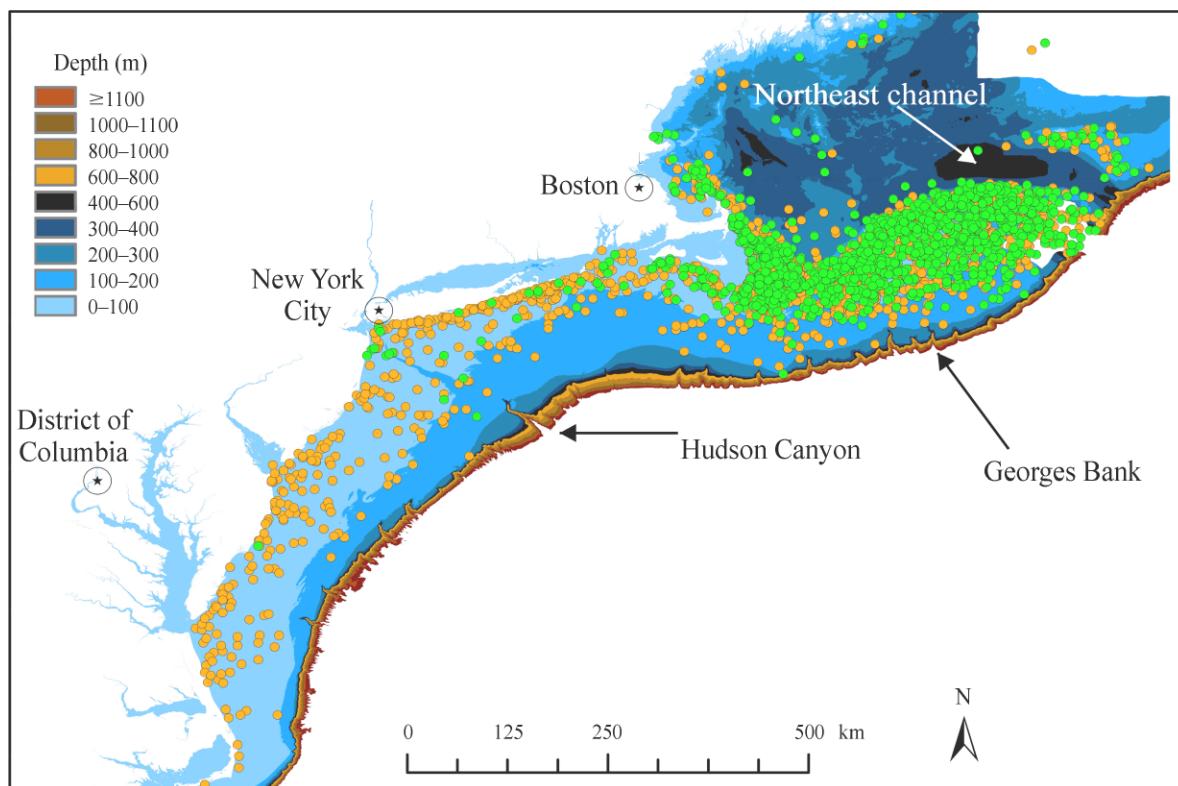


FIG. 6. Fall and spring distribution of winter skate >79 cm total length based on National Marine Fisheries Service surveys. Green circles represent the fall, and orange circles represent the spring.

indicate that during the summer and spring the rays migrate to shallow waters to reproduce and then return to deep water in the autumn. Further, the migratory route of individual fish indicated that the species may show site and migratory route fidelity. However, the NMFS survey data indicate winter skate exhibit large seasonal distributional changes, suggesting seasonal migrations with the adult population spread over the northwest Atlantic south to Cape Hatteras during the spring and clustered on Georges Bank and the western southern New England regions during the fall (Fig. 6).

It might also be suggested that there are barriers to movement between the two regions. In order for winter skate to migrate from the Scotian Shelf, skates would have to travel through the Northeast Channel. The NMFS spring and fall surveys have conducted stations within the channel as part of the groundfish survey. While sampling effort is not high in the channel, winter skate of various sizes have been caught in this region (Fig. 7). Depth does not appear to limit distributions greatly in this region. For example, in a single tow during the 2007 spring NMFS survey, 277 barndoor skate, of the survey total of 325, were caught along with 146 winter skate between the sizes of 70 cm to 100 cm (K. Sosebee, *personal observation*). Especially surprising is that the station was located at a depth of 296 m on the southeastern flank of Georges Bank, suggesting the

possibility that portions of the populations of both species may move to deep water outside the survey range. However, this was only one tow, and until tracking is conducted, an off-shelf migration is speculative.

The patterns in abundance and size distribution we demonstrate in the surveys may be potentially confounded with gear changes that were made within the NMFS survey that could affect the selectivity and availability of winter skate to survey gear. The spring survey employed a Yankee 36 bottom trawl, except for survey years 1973–1981 in which a Yankee 41 bottom trawl was used. A gear conversion factor for abundance of 0.25 was applied to data for little skate, but no gear conversions were deemed necessary for winter skate. Data for 1973–1981, when the Yankee 41 trawl was used, correspond to the lowest abundance estimates for winter skate for the spring survey. Thus the impacts of the gear change appear to warrant further attention. However, there are two reasons to doubt gear changes as a major source of survey bias: (1) gear changes did not fall on the years of drastic abundance fluctuations, and (2) the Massachusetts survey length frequency data are in agreement with the NMFS surveys for winter skate.

If the winter skate population on Georges Bank is assumed closed, changes in selectivity and availability of skate to survey gear could account for the observed

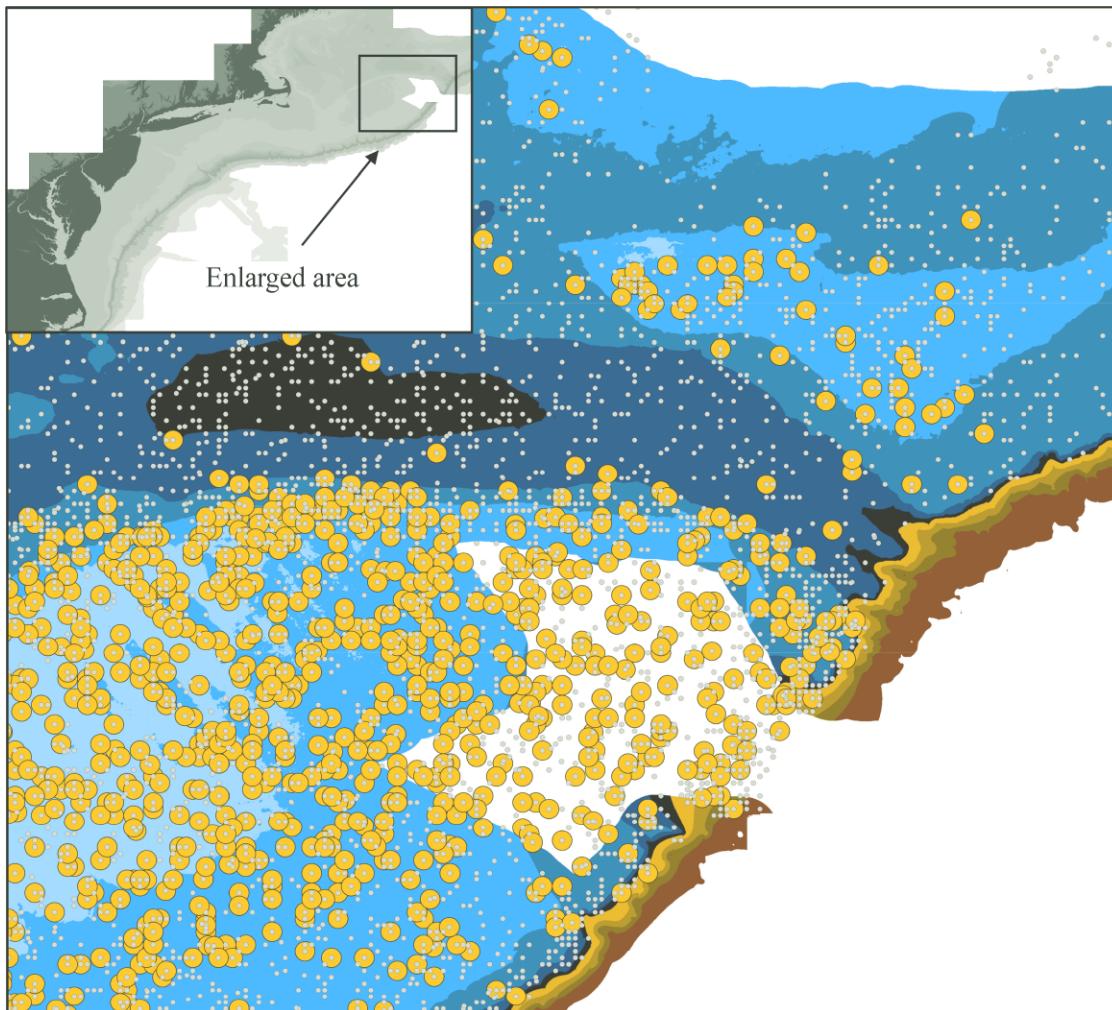


FIG. 7. Georges Bank, Northeast Channel, and Scotian Shelf survey data for National Marine Fisheries Service stations from 1963 to 2002 (fall and spring combined). Small gray dots indicate survey stations, and orange circles represent stations where winter skate were caught. Depth is indicated according to the color key in Fig. 6.

patterns, but only under these restrictive assumptions: (1) changes in selectivity would have to have occurred in the late 1970s and result in an increase in selectivity for the remaining years of the data set, and (2) selectivity would have to be increasing with size for small individuals (30–40 cm TL) (as is normal), but then increase again for large individuals, creating the unusual bimodal distribution of lengths observed in the fall survey during the 1980s. While both gear selectivity and availability are plausible explanations for the length frequency data, we have no reason to accept them as likely.

In our survey analysis we have shown that there is a lack of coherency in aggregated abundance estimates among the surveys conducted in the Georges Bank–southern New England region. This observation could be used to argue that surveys are too variable to discern a widespread increase in winter skate abundance during the 1980s. These differences may in part be due to

different areas covered by each survey, and it should be pointed out that the two NMFS surveys that cover the same area show coherency. However, length frequency data (not shown here for brevity) between the NMFS and MDMF survey show very similar trends, suggesting that broad-scale changes in length/age structure are likely more coherent between surveys than abundance estimates.

In our examination of the elasmobranch outburst hypothesis, we have assumed that growth estimates have remained invariant over the time period. It is generally accepted that vital rates in elasmobranchs do not show high levels of compensatory changes under exploitation (Holden 1974, Sminkey and Musick 1995, Frisk et al. 2005, Sosebee 2005). However, for a species to persist it must have at least a minimal capacity to compensate for changes in mortality to recover from population declines. Frisk (2004) developed a length-based statistical catch-at-age model fit to the survey data presented

herein. Model runs were only able to capture the increases in observed length frequencies and aggregated abundance trends in the late 1970s by allowing for substantial process error in the stock recruitment function and steepness values that are too great for elasmobranch species (Frisk 2004). While it remains likely that compensatory changes in vital rates in winter skate occurred during the last 40 years in response to population density and exploitation patterns, the level of change in vital rates needed to produce the outburst of a fully size-structured population in the late 1970s is outside of the biological capacity of winter skate given current understanding of elasmobranch life history.

Identifying mechanisms underlying broad-scale ecosystem change in the northwest Atlantic continues to challenge researchers. Conclusive statements regarding the 1980s and mechanisms underlying the increase in winter skate abundance should be met with caution until further research is conducted or survey biases are identified. Yet it is important that alternative hypotheses are assessed, because the management implications of alternative hypotheses may differ substantially. For example, some regime shifts appear to be irreversible (Folke et al. 2004), while others appear reversible (Gargett 1997). Moreover, for reversible systems, recent theoretical work has suggested that the threshold that characterized the shift from one regime to another may not be same in both directions (Scheffer and Carpenter 2003). Indeed this same body of theory strongly suggests that most regime shifts are brought about by multiple sources of causation. This suggests that evaluating hypotheses as strict alternatives is perhaps not a fruitful avenue for exploration; rather, researchers should seek to address the relative contribution of different potential mechanisms.

Regardless of causation, managers have to respond to the observed shift in regime, whether such be recognized by the demonstration of the formal existence of multiple stable states or by empirically determined interdecadal anomalies (Overland et al. 2006). In the case of the northwest Atlantic ecosystem, the alternative hypotheses suggested to date have profoundly different implications for management. If the regime shift on Georges Bank was driven purely by population dynamics internal to the system, then local management action has the potential to drive the system back to its former state. The mortality rates necessary to achieve this goal may be different from those that are thought to have brought about the change, but no external consideration is required. If on the other hand, skate populations in the northwest Atlantic exhibit connectivity, as suggested in our alternative hypothesis, then management of skates must be integrated across the whole northwest Atlantic. In turn, this management requirement has consequences for the integration of fishery-independent sampling, as well as catch and effort monitoring. In short, the restoration of the northwest Atlantic ecosystem will remain difficult until mechanisms underlying changes in

ecosystem states and population connectivity are clearly understood and accounted for in management actions.

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