

# *Population Trends and Status of Two Exploited Northwest Atlantic Grenadiers, *Coryphaenoides rupestris* and *Macrourus berglax**

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*Abstract.*—Roundnose grenadier *Coryphaenoides rupestris* and roughhead grenadier *Macrourus berglax* are well known slope species in the North Atlantic. Dramatic population declines in both species in Canadian waters of the Northwest Atlantic raised the question: was the decline a result of environmental changes or exploitation? Min–max autocorrelation factor analysis and dynamic factor analysis, two types of time series analysis, showed that a combination of factors acting on different temporal scales explained the trends in both species. Those in *Macrourus* were best explained by environmental factors operating on long time scales; those in *Coryphaenoides* were related to exploitation. Our results support the view that an unregulated deep-ocean fishery, as experienced by *Coryphaenoides*, has serious consequences for species that are slow-growing, long-lived and late-maturing.

## Introduction

Roundnose grenadier *Coryphaenoides rupestris* and roughhead grenadier *Macrourus berglax* are endemic species in temperate to Arctic continental shelf and slope waters around the North Atlantic rim (Scott and Scott 1988; Liem and Scott 1996). Both are long-lived, late-maturing, slow-growing, have low fecundity and, therefore, are potentially vulnerable to overfishing (Scott and Scott 1988; Cohen et al. 1990; Liem and Scott 1996; Kelly et al. 1997; Drazen 2008, this volume). Roundnose grenadier was the first ever mac-

rourid to be described (by Gunnerus in 1765), and the first to be commercially harvested. Once discovered by commercial interests, *Coryphaenoides* was immediately promoted as a superior product and the taste is still marketed as being equal to that of Atlantic cod *Gadus morhua* or orange roughy *Hoplostethus atlanticus* ([http://www.seafoodcanada.gc.ca/mini\\_grenadier-e.htm](http://www.seafoodcanada.gc.ca/mini_grenadier-e.htm)).

The story of the commercial fishery for roundnose grenadier in the Northwest Atlantic began in the late 1960s, when they were discovered by Russian exploratory deep-sea fishing expeditions (Atkinson 1995). Landings of roundnose grenadier peaked in the early 1970s at approximately 80 thousand

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metric tons and then declined abruptly (Koslow et al. 2000). As with many new fisheries, the initial quota was set quite high but was never achieved. As catches declined, subsequent quota revisions and reductions were not based on any particular biological or assessment information, primarily because that information was severely lacking (Atkinson 1995). The number of biological papers concerning the species were very few and most basic biological information was not gathered until 15–25 years after the fishery began (Haedrich et al. 2001). By the early 1990s, the fishery in the Northwest Atlantic was no longer commercially viable and came to a halt. One reason that the fishery lasted as

long as it did was that it serially exhausted populations beginning in the north and moving progressively across the entire western Atlantic range to finish up at the southern limit of the species off New England (Figure 1).

As the fishery in the Northwest Atlantic for roundnose grenadier drew to a close, attention turned to roughhead grenadier (Figure 2), another large macrourid with a very similar distribution and the only representative of its genus in the northern hemisphere. Peak catches were lower, only approximately 9000 metric tons in 2000 (NAFO statistical bulletins). *M. berglax* is taken as bycatch in the deep-water Greenland halibut *Reinhard-*

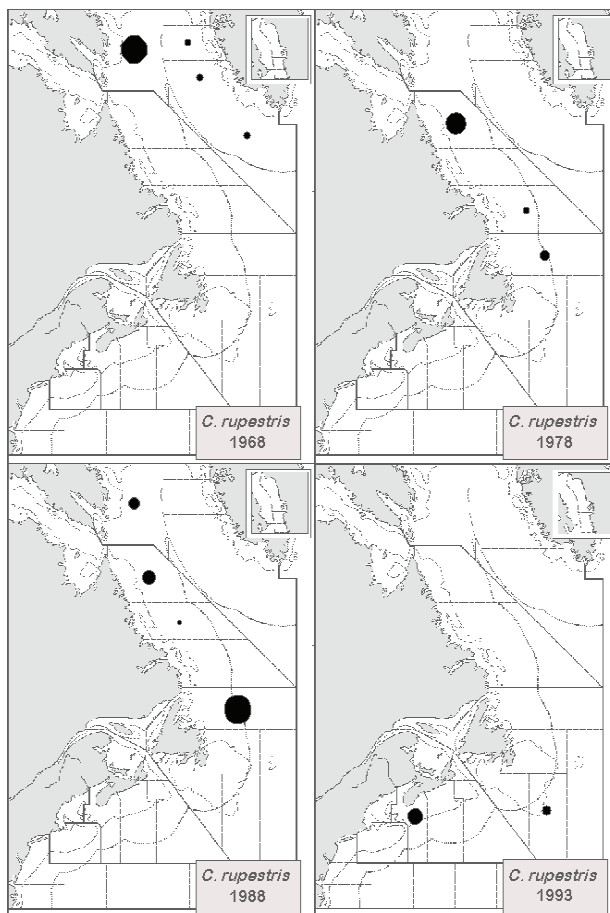


Figure 1. Landings of roundnose grenadier *Coryphaenoides rupestris* by NAFO Division, 1968–1993; size of the circle is proportional to the amount of fish taken from a given NAFO Division. Figure taken from Haedrich et al. (2001).

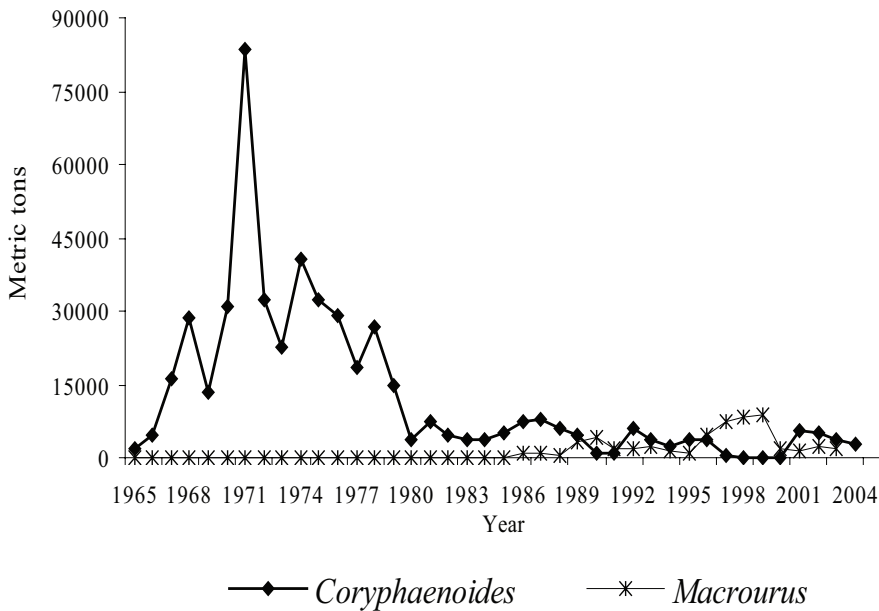


Figure 2. Landings of grenadiers, roundnose grenadier *Coryphaenoides rupestris* and roughhead grenadier *Macrourus berglax*, in the Northwest Atlantic, 1965–2004 (FAO statistics).

*tius hippoglossoides* fishery and there are currently no regulations for its harvest. Both roundnose and roughhead grenadier are recruited to the fishery before they fully mature (Atkinson 1995; Murua 2003).

Scientific studies of both species lagged behind the fishery, which meant that there existed no rational means to assess the true status of the populations and to set quotas. Generation time, the time taken for an individual to replace itself, was not even known until quite recently (Bergstad and Isaksen 1987; Murua 2000; Lorange et al. 2001). Generation time is needed to assign threat criteria to populations or stocks; threat criteria are typically based on the decline undergone over the greater of 10 years or 3 generations (Musick 1999; IUCN 2006). Once known, this information allowed, in connection with quantitative scientific assessment (e.g., generalized linear modeling of Canadian research survey data from consistently sampled areas), determination of population trends (Devine et al. 2006; Figure 3). The surprising result was that populations of both

species in Canadian waters had declined to such an extent that they meet the International World Conservation Union (IUCN) criteria for Critically Endangered Species (Devine et al. 2006; IUCN 2006).

This finding raised the question of what had contributed to such a dramatic decline: was it fishing, either in a target fishery or as bycatch in other fisheries, or was it the result of changes in the ocean environment? To address this question, we used two newer mathematical approaches that have only occasionally been applied to fisheries data (Solow 1994; Erzini 2005, Erzini et al. 2005; Machias et al. 2006; Devine et al. 2007). Our interest lay in determining what factor(s) best explained recent trends in abundance of both species.

Much debate exists over pinpointing the cause of changes in fish populations. There have been many well-documented dramatic shifts in abundance thought to be primarily caused by changing environmental conditions (e.g., Beamish et al. 1999; Klyashtorin

1998; Anderson and Piatt 1999; Bakun and Broad 2003; Hjermann et al. 2004). Overexploitation has also been blamed for causing fish populations to collapse (Hutchings and Myers 1994; Hutchings 1996; Myers et al. 1997; Bianchi et al. 2000; Myers and Worm 2003). Most likely, as recent studies have advocated, changes are due to a combination of factors that act in concert but at different spatial and temporal scales (Zwanenburg 2000; Shelton et al. 2006; Devine et al. 2007).

## Methods

### Time series analysis

Min/max autocorrelation factor analysis (MAFA) and dynamic factor analyses (DFA) are two methods of time series analysis only recently applied to fisheries data (e.g., Zuur et al. 2003a,b; Zuur and Pierce 2004; Erzini 2005, Erzini et al. 2005). MAFA and DFA require no preselection or de-trending of the data, and allow for an objective exploration of underlying trends in multiple datasets and the external fac-

tors that might explain observed trends. MAFA and DFA are multivariate methods designed specifically for shorter time series (at least 15–25 years) and are not burdened by many of the shortcomings of traditional time series analysis. They do not, for example, require long, stationary, and complete time series and are relatively efficient at handling common trends (Solow 1994; Zuur et al. 2003a).

MAFA, a type of principal component analysis (PCA), can be used to extract trends, estimate index functions, and for smoothing (Switzer and Green 1984; Shapiro and Switzer 1989; Solow 1994). Whereas PCA will estimate axes (or components) that have a decreasing variance, MAFA estimates axes that have decreasing autocorrelation with time lag 1. Since slowly declining autocorrelation functions indicate the presence of a trend, the first MAFA axis is the main trend underlying the entire time series and other axes represent less important trends. Randomization is used to obtain  $p$ -values to determine how many axes to use (Solow 1994). Factor loadings are used to determine the relationship of the response vari-

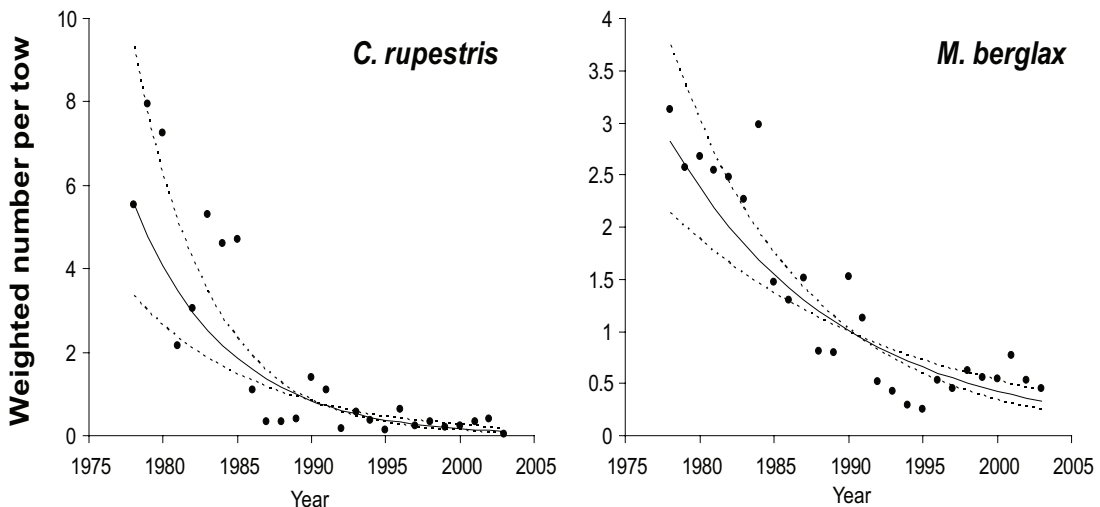


Figure 3. Weighted relative abundance (number per tow) over time in research survey data with estimated exponential declines (thick line) and 95% confidence projections of the estimate (dashed lines) for roundnose grenadier *Coryphaenoides rupestris* and roughhead grenadier *Macrourus berglax* in Canadian waters of the Northwest Atlantic, 1978–2003. Figure taken from Devine et al. (2006).

ables to a particular MAFA trend (Zuur et al. 2007). Canonical correlations, or cross-correlations between MAFA axes and response time series, can be estimated for the same purpose. Cross-correlations can be used to determine if significant relationships exist between MAFA trends and explanatory variables.

DFA is a dimension reduction technique that models short, multivariate time series in terms of common trends and explanatory variables (Zuur et al. 2003a, 2003b, Zuur and Pierce 2004). DFA can be used to assess common patterns in time series, evaluate interactions between response variables, and determine the effects of explanatory variables (Zuur et al. 2003a). DFA models  $N$  time series in terms of  $M$  common trends, where  $M$  is less than  $N$ . DFA is similar to other dimension reduction techniques in that the axes are restricted to smoothing functions over time, but differs in that it assumes trends correlate over time (Zuur et al. 2003a). With DFA, the effects of time lags in the explanatory variables can be explicitly evaluated.

The number of common trends modeled should ideally be less than the number of time series used and preferably as small as possible without sacrificing goodness of fit. The larger the number of common trends used, the better the model fit but the greater the number of parameters that must be estimated. Akaike's Information Criterion (AIC) was used initially to determine the optimal model in terms of goodness of fit and the number of parameters; the lowest AIC value indicates the better model and reflects the tradeoff between the fit of the model (log likelihood function) and the model's complexity (number of parameters) (Sakamoto et al. 1986). Factor loadings and canonical correlations were used to determine the importance of a trend to response variables.

### **Sources of data**

Indices of abundance for roundnose and roughhead grenadier came from the ECNA-

SAP (East Coast North American Strategic Assessment Project) dataset, 1978–1994; survey depths extended to approximately 1500 m (Doubleday and Rivard 1981; Brown et al. 1996). Research survey data 1995–2003 were obtained from the regional Department of Fisheries and Oceans branches for all Canadian waters. Additional data for adults-only from fall surveys, 1977–2004, were obtained for both grenadier species. Indices for the four datasets (two per species) are shown in Figure 4.

In Newfoundland-Labrador waters, survey gear was changed from an Engels 145 high lift otter trawl to a Campelen 1800 shrimp trawl mid-way through 1995. The Campelen trawl has a smaller mesh size, larger net, and is fished for a much shorter duration (15 min versus 30) at a slower speed than the Engels trawl (McCallum and Walsh 1996). Because of these factors, the Campelen trawl tends to catch juveniles of many species much more efficiently than adults (Warren 1996). A species-specific conversion factor, the ratio of mean catch 1993–1994 to mean catch 1996–1997 (the year of the gear change was excluded), was used to convert Campelen catches into equivalent Engels catches.

All data were collected in stratified random scientific surveys within Canada's Economic Exclusion Zone (Figure 5), where strata were determined by depth. Data for consistently sampled strata included only strata that were sampled for at least half of the time series and for at least two years during the first and last five years of the series. This was done to ensure the comparability of the index over the time period, an extremely important factor when assessing temporal trends. NAFO subareas retained in the analysis after filtering for consistently sampled strata include 2J3KLNOP4VX; data were excluded from the extreme northern part of the Labrador Shelf, the Gulf of St. Lawrence and part of the Scotian Shelf (Figure 5).

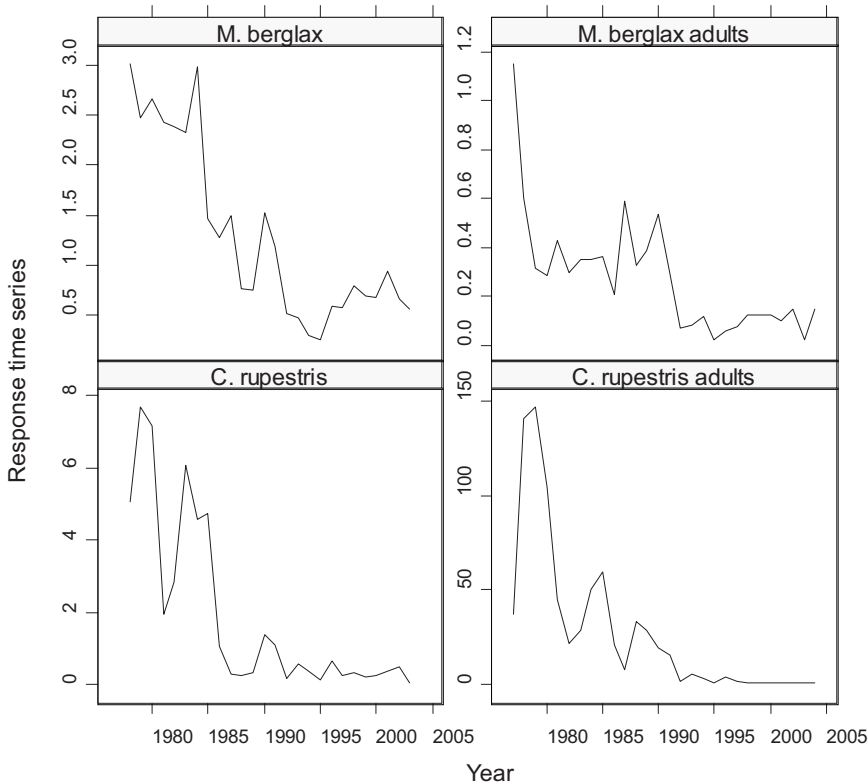


Figure 4. Relative abundance of *Coryphaenoides rupestris* and *Macrourus berglax* from Canadian waters of the Northwest Atlantic from consistently sampled strata (weighted number per tow, left), 1978–2003, and adults-only (number per tow, right), 1977–2004.

The increase in relative abundance in 1995 as seen in Figure 4 could indicate that both species increased in abundance; however, such rapid increases in abundance are unlikely due to the life history characteristics of these species (e.g., long-lived, slow-growing, late-maturing, low fecundity, and sporadic recruitment). The increase may indicate the species-specific conversion factor was not compensating completely for the gear change in 1995. Catchability of juveniles for many species is known to be higher with the Campelen trawl (Warren 1996). If juvenile grenadiers were captured in greater abundance by the Campelen trawl, this could partially explain the rapid increase after 1995. Therefore, trends in adults-only of both species were also investigated. For the adult-only dataset, all available data were

used because adults were not measured from every tow, thereby leaving insufficient data to filter for consistently sampled strata.

Six external factors were assessed: four related to environment and two to exploitation (Figure 6). Mean sea surface temperature (SST) were from NAFO Divisions 2GHJ3KL, 1960–2004, 0–100 m. Bottom temperature (BT), 1960–2004, were taken from NAFO Divisions 2GHJ3KL, 250–2000 m. Salinity (SAL), 1960–2004, was taken from NAFO Divisions 2GHJ3KL, 0–300 m depth. The North Atlantic Oscillation (NAO) Hurrell winter index ([www.cgd.ucar.edu/~jhurrell/nao.stat.ann.html](http://www.cgd.ucar.edu/~jhurrell/nao.stat.ann.html)) indicates the strength of large-scale atmospheric circulation across the ocean; a high positive index indicates stronger westerly winds across the North Atlantic and north-

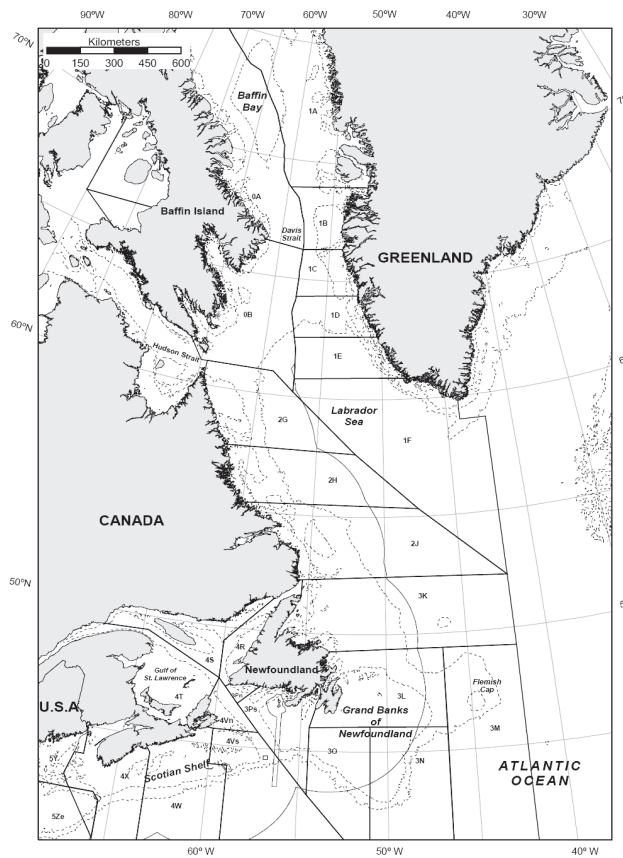


Figure 5. Canadian waters of the Northwest Atlantic, showing NAFO Divisions, location of the Canadian Economic Exclusion Zone (200-mile limit, thin line), and the 500 and 1000 m bathymetric contours (dashed lines).

westerly winds in the Labrador Sea (Hurrell et al. 2003). Exploitation (fishing pressure), 1960–2004, was quantified directly as combined landings of roundnose and roughhead grenadier (Catch) and indirectly as landings of Greenland halibut *Reinhardtius hippoglossoides* (GHcatch) from NAFO records. Both grenadiers are taken as bycatch in the Greenland halibut fishery (Gorchinsky and Savvatimsky 1994; Savvatimsky and Gorchinsky 2001; Costas and Murua 2005).

Before analysis, all response time series were  $\log_{10}$  transformed and both response and explanatory variables were standardized to a mean of zero and standard deviation of one. Time lags up to eighteen years

for all external factors were included in both MAFA and DFA. The number of lags was chosen based on the length of the environmental data and generation time for both grenadier species; generation time for *C. rupestris* and *M. berglax* is 17 and 19 years (Murua 2000; Lorange et al. 2001).

## Results

### *Consistently sampled strata*

The only MAFA trend underlying relative abundance of both species from consistently sampled strata showed a decline over time from 1978 to 1994, an abrupt increase and

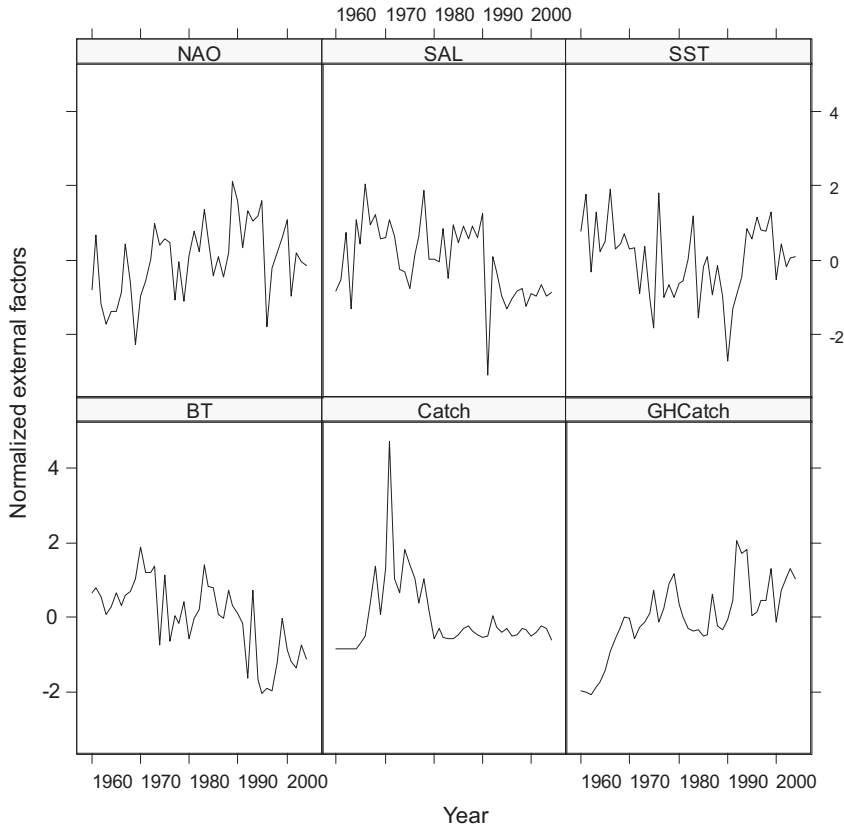


Figure 6. Explanatory variables included in MAFA and DFA, 1960–2004; variables are defined in the text (see Methods). NAO is the North Atlantic Oscillation winter index, SAL is salinity, SST is sea surface temperature, BT is bottom temperature, Catch is grenadier catch, GHcatch is Greenland halibut catch.

then a stabilization (autocorrelation = 0.855,  $p < 0.001$ , Figure 7A). Abundances of both roundnose and roughhead grenadier were significantly and positively correlated with the trend (correlation = 0.89 (*C. rupestris*), 0.99 (*M. berglax*); significance level for correlations = 0.39). All types (environment and exploitation) of external factors were significantly correlated with the main MAFA trend at several different scales, although there was no clear pattern; due to the size of the matrices, only the most significant results for each factor are presented in Table 1 (correlation matrices are available from the authors upon request). Correlations  $\geq 0.39$  between the MAFA trend and the explanatory factor were significant ( $p \leq 0.05$ ). Bottom temperature was significantly

correlated at low and mid-range lags, while the remaining environmental factors were significantly correlated at both long and short temporal scales. Grenadier catch was significantly correlated at all scales, whereas Greenland halibut catch was significantly correlated only at long and short temporal scales. Measures of exploitation had a higher number of significant correlations to the trend (55% significantly correlated) than did environmental measures (28% significantly correlated). Out of 114 combinations of explanatory variables and lags used in the consistently sampled strata analysis, 42 were significantly related to the trend. By chance alone, twelve correlations were expected to be significant. That so many variables were significantly related to

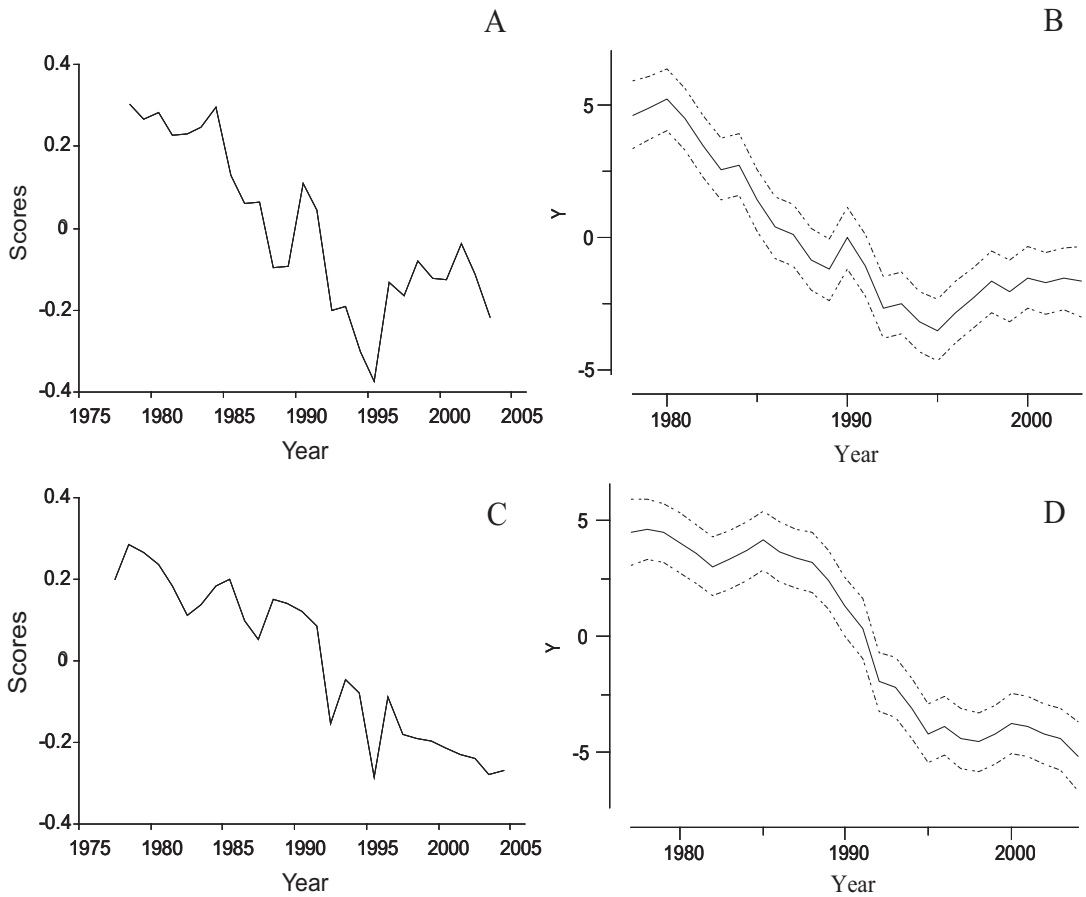


Figure 7. Trends in relative abundance of *Coryphaenoides rupestris* and *Macrourus berglax* in Canadian waters of the Northwest Atlantic, 1977–2004. (A) MAFA trend from consistently sampled strata, (B) DFA trend with confidence intervals from consistently sampled strata, (C) MAFA trend for adult-only data, and (D) DFA trend with confidence intervals from adult-only data.

the trend indicated that a strong relationship existed between the explanatory variables and the trend.

DFA also indicated one main trend existed in the abundance of both species. The best model was a one-trend, two explanatory diagonal covariance matrix model with Greenland halibut catch lagged 1 year and NAO winter index lagged 14 years (Table 2; Figure 7B). Inspection of the diagonal elements of the error covariance models indicated little residual information was left unexplained by the model (values  $\leq 0.13$ ). The trend was a decline over time with a very slight increase in 1995. Fac-

tor loadings and canonical correlations show that both species were highly and positively related to the trend (Table 3). Estimated  $t$ -values of regressions for individual species indicated that *Coryphaenoides* abundance was strongly related to Greenland halibut catch lagged 1 year and *Macrourus* abundance was strongly related to NAO winter index lagged 14 years, as indicated by high  $t$ -values (Table 4). Plots of observed and fitted abundance for the best DFA model for each species are given in Figure 8. The cross-correlation between Greenland halibut catch at lag 1 and the NAO index at lag 14 was not significant (correlation

Table 1. The most significant correlations between MAFA trends (MAF) and explanatory factors, including lags, for two indices of relative abundance for roughhead grenadier *Macrourus berglax* and roundnose grenadier *Coryphaenoides rupestris* in the North-west Atlantic, 1977–2004. Significance level ( $p \leq 0.05$ ) for correlations = 0.39 for consistently sampled strata and 0.38 for the adult index.

Consistently sampled strata		Adults-only	
Factor	MAF1	Factor	MAF1
Bottom temperature – no lag	0.64	Bottom temperature – no lag	0.72
Grenadier catch lagged 6 years	0.78	Grenadier catch lagged 7 years	0.61
Greenland halibut catch lagged 18 years	-0.79	Greenland halibut catch lagged 17 years	-0.67
NAO index lagged 14 years	-0.59	NAO index lagged 9 years	-0.64
Salinity lagged 1 year	0.56	Salinity lagged 1 year	0.74
Sea surface temperature lagged 14 years	0.54	Sea surface temperature – no lag	-0.50

= -0.09).

### Adults-only

The only MAFA trend in adults (auto-correlation = 0.896,  $p < 0.001$ ) was a fluctuating decline over time (Figure 7C). There was a small spike in 1996, the year following the gear change, however, the increase was in line with the main declining trend over the entire time period. Abundances of both roundnose and roughhead grenadier were significantly and positively correlated with the trend (correlation = 0.99 (*Coryphaenoides*), 0.82 (*Macrourus*); significance level for correlations = 0.38). All six external factors were significantly correlated with the MAFA trend for adult grenadiers. Only the most significant result for each of the explanatory factors are presented in Table 1 (matrices available from authors upon request). Bottom temperature and salinity were significantly correlated to the trend at short and mid-range temporal scales. The NAO index was significantly correlated at mid- and long range lags

and sea surface temperature was significantly correlated at short and long range lags. These results differed from results obtained from consistently sampled strata. Grenadier catch was significantly correlated at all scales, and Greenland halibut catch was significantly correlated to the trend at short and long scales. Sixty-one percent of the correlations between exploitation factors (and lags) and the trend were significant, while 46% of the environmental factors (and lags) were significant (significance level for correlations = 0.38,  $p \leq 0.05$ ). Out of 108 combinations of explanatory variables and lags used for adult data, 55 were significantly correlated with the MAFA trend. By chance alone, six correlations would be expected to be significant. That so many variables were significantly related to the trend indicated that a strong relationship existed between the explanatory variables and the trend.

The “best” DFA model when analyzing number of adults from autumn research surveys was a one-trend, two explanatory vari-

Table 2. Values of Akaike's Information Criterion (AIC) for DFA models with 1 trend and different sets of explanatory variables (exp), based on a diagonal covariance matrix. The number appended to the explanatory variable indicates the time lag in years. Bold type indicates the best model chosen for the analysis.

Model	Explanatory variable (exp)	AIC
Consistently sampled strata		
Relative abundance + noise	–	94.4
Relative abundance + exp + noise	Greenland halibut catch 1	86.4
	NAO index 14	80.6
Adults-only	Greenland halibut catch 1 + NAO index 14	<b>75.6</b>
Relative abundance + noise	–	97.4
Relative abundance + exp + noise	Greenland halibut catch 8	92.2
	Salinity 12	93.4
	Greenland halibut catch 8 + salinity 12	<b>85.9</b>

Table 3. Factor loadings and canonical correlations between roughhead grenadier *Macrourus berglax* and roundnose grenadier *Coryphaenoides rupestris* and the trends for the best DFA models for consistently sampled strata and adults-only abundance in the Northwest Atlantic, 1977–2004.

Consistently sampled strata		
	Factor loadings	Canonical correlations
<i>Macrourus</i>	0.27	0.93
<i>Coryphaenoides</i>	0.20	0.85
Adults-only		
	Factor loadings	Canonical correlations
<i>Macrourus</i>	0.20	0.82
<i>Coryphaenoides</i>	0.23	0.95

able diagonal covariance matrix model, with Greenland halibut catch lagged 8 years and salinity lagged 12 years (Table 2; Figure 7D). The diagonal elements from the error covariance matrix were low (values  $\leq 0.23$ ) indicating little residual information remained. Addition of a second trend showed a straight line and therefore no further trend existed in the data. The trend showed a decline until 1995, after which the trend remained fairly stable although at a low level. Abundances of both species were highly and positively correlated with this trend (Table 3). *Coryphaenoides* abundance was strongly related to Greenland halibut catch lagged 8 years and *Macrourus* abundance was strongly related to salinity lagged 12 years, as indicated by the regression parameters (Table 4). Cross-correlation between Greenland halibut catch at lag 8 and salinity at lag 12 was not significant (correlation =  $-0.03$ ). Plots of observed and fitted abundance for the best DFA model for each species are given in Figure 8.

## Discussion

MAFA and DFA found similar trends in relative abundance of roundnose and rough-

head grenadier. Overall, trends were a decline over time. Data from consistently sampled strata indicated an increase after 1995; this trend was not seen in the adults-only data. The data for both analyses used data sampled from the same strata; this may indicate that the increase was due to increased catchability of juveniles by the Campelen trawl and not an artifact of sampling different habitat. Application of a conversion ratio, while compensating partially for differences in catchability between the Engels and Campelen trawls, would not be able to compensate for an increased catch of small fish; a length-based index would have been more appropriate. Such an index would require data from comparative fishing trials, which were completed for only a few commercially important species and not for the grenadier species.

Immigration of fish from elsewhere might also explain the slight increase seen after 1995. However, if this was the cause, it should have been reflected as well in the adult data; it was not. Temperature fluctuations, often posited as the cause of distribution shifts for fish species in general (de Young and Rose 1993; Gomes et al. 1995; Drinkwater 2002), are so minimal in the deep-sea that they are unlike-

Table 4. Estimated regression parameters, standard errors and *t*-values for DFA models of relative abundance for roughhead grenadier *Macrourus berglax* and roundnose grenadier *Coryphaenoides rupestris* in Canadian waters of the Northwest Atlantic, 1977–2004; analyses with (1) consistently sampled strata only data and (2) adults-only data.

Parameter	<i>M. berglax</i>	<i>C. rupestris</i>
(1) Greenland halibut catch lagged 1 year		
Estimated value	−0.12	−0.48
Standard error	0.08	0.09
<i>t</i> -value	−1.48	−5.39
(1) NAO index lagged 14 years		
Estimated value	−0.33	−0.13
Standard error	0.09	0.09
<i>t</i> -value	−3.84	−1.43
(2) Greenland halibut catch lagged 8 years		
Estimated value	0.09	−0.23
Standard error	0.11	0.08
<i>t</i> -value	0.86	−2.96
(2) Salinity lagged 12 years		
Estimated value	0.32	0.13
Standard error	0.10	0.06
<i>t</i> -value	3.23	2.04

ly to have caused shifts (Atkinson 1994), a fact now acknowledged even by those who originally proposed this explanation for the changes displayed by *Coryphaenoides* (Savvatimsky 1991; Atkinson 1995).

MAFA has shown that many types of external factors were related to the trend in relative abundance of roughhead and roundnose grenadier. Although MAFA illustrated the importance of time lags in the system and was useful for exploring dynamics, it is mainly an exploratory tool and, as such,

did not clarify which factors were the most important for explaining the trend. DFA showed that environment was the most important factor explaining the trend in *Macrourus*, while exploitation was important for describing the trend in *Coryphaenoides*.

In the North Atlantic, combined grenadier catch over the entire period of the fishery, 1965–2004, was just over 1,000,000 metric tons (mt) (FAO data). The boom-and-bust story of the roundnose grenadier fishery is well known (Haedrich et al. 2001). As

the fishery collapsed in the northwest Atlantic, catches increased in the northeast. In the Northwest Atlantic, a moratorium has provided roundnose grenadier some protection since 1978 in Subareas 0 and 1 (Atkinson 1995) and since 1996 in Canadian waters of NAFO Subareas 2 and 3 (Power 1999), but roughhead grenadier is becoming an increasingly important commercial species. Currently, *Macrourus* catch is unregulated and the species is mainly taken, often in high numbers, as bycatch in the Greenland halibut fishery operating in NAFO Divisions 3LMNO (Costas and Murua 2005). In the

Russian trawl fishery for Greenland halibut, bycatch of *Macrourus* has been as much as 2–3 tons per haul (Savvatimsky and Gorchinsky 2001). In addition to the sometimes high bycatch rate, a high degree of misreporting of the bycatch exists for the Russian long-line fishery; *Macrourus* bycatch is reported as 5% of the catch, but levels may be as high as 9–13% at depths of 800–1200 m and 24–25% at depths 1200–1400 m (Savvatimsky and Gorchinsky 2001). Roughhead grenadier is also captured in small amounts in the Flemish Cap shrimp fishery (Bakanev 2002, 2003). *Coryphaenoides* was captured in high

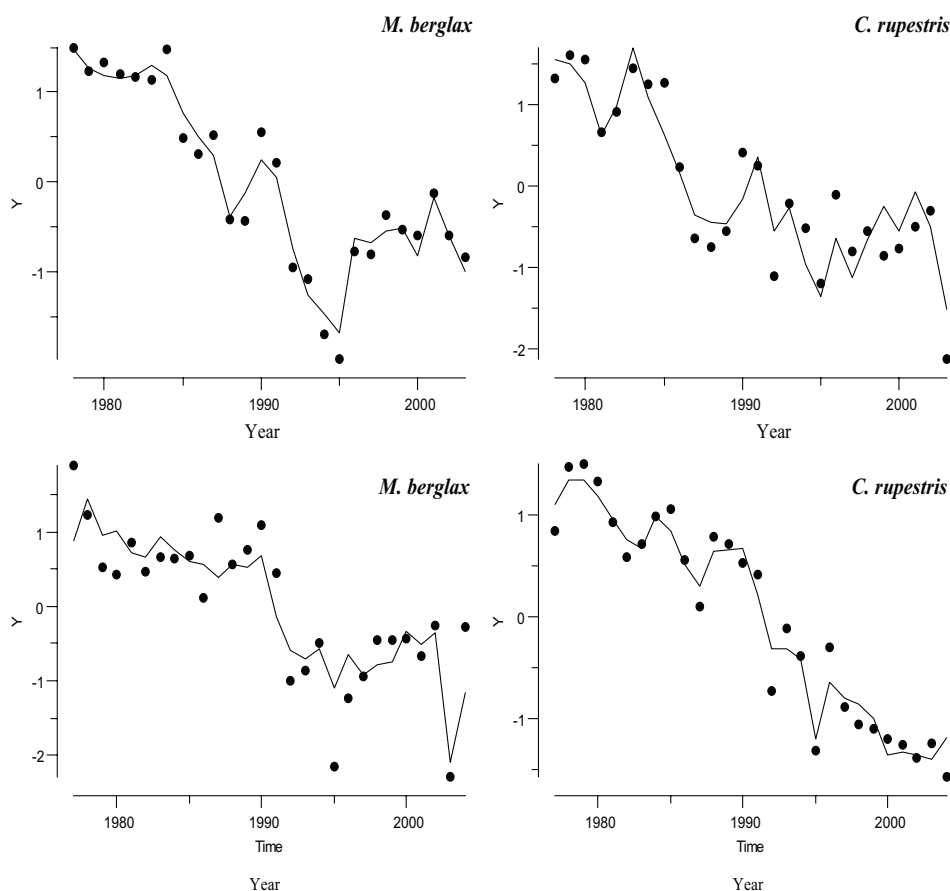


Figure 8. Observed (points) and fitted (line) abundance for the best DFA models for roughhead grenadier *Macrourus berglax* and roundnose grenadier *Coryphaenoides rupestris* from consistently sampled strata (top row; 1 trend, 2 explanatory variable model) and adult-only data (bottom row; 1 trend, 2 explanatory variable model) from Canadian waters of the Northwest Atlantic, 1977–2004.

amounts in the Greenland halibut fishery in the Flemish Pass when the fishery began in the 1990s, and catches were considered some of the highest bycatch rates for any species in that fishery (Gorchinsky and Savvatimsky 1994). Durán et al. (1997) found *Coryphaenoides* and *Macrourus* were two of the seven most commonly caught deepwater species in the Spanish deepwater Greenland halibut fishery in NAFO Divisions 3LMNO, 1991–1994. Given this, it is not surprising that measures of exploitation were found to be important for understanding trends in grenadier relative abundance.

Environmental factors were correlated with trends in relative abundance of both grenadier species. DFA found the NAO winter index and salinity at high lags were highly related to the trends. The NAO index, the atmospheric pressure differential between the Azores and Iceland, exerts a strong influence over the ocean and atmosphere of the North Atlantic Ocean. The NAO influences sea ice extent and rate of melt, water temperature, the distribution and fluxes of major water masses and currents, deep water formation in the Greenland Sea, and intermediate water formation in the Labrador Sea (Hurrell et al. 2003). The index has risen steadily since the mid-1960s with decadal peaks in the early 1970s, 1980s and 1990s (Drinkwater 2002); a positive NAO index is associated with negative salinity, sea ice, and temperature anomalies (Marsden et al. 1991; Colbourne et al. 1997, Belkin et al. 1998; Belkin 2004). Negative salinity anomalies not only result in lower temperatures and a freshening of the upper waters, but also an intensification of stratification and restricted heat and nutrient exchange with deep waters (Blindheim and Skjoldal 1993), thereby affecting primary production in surface waters and ultimately food availability. In addition, salinity anomalies have been linked to sea ice anomalies (Marsden et al. 1991), cooling and freshen-

ing the North Atlantic deep-water (Brewer et al. 1983; Aagaard and Carmack 1994), and changing ocean-scale current patterns (Belkin et al. 1998).

Roundnose and roughhead grenadier have declined in abundance in the northwest Atlantic. There is no one factor directly responsible for the declines; however, target and nontarget fisheries and a large-scale, basin-wide atmospheric condition, the NAO winter index, have been shown to be key factors related to the trends. These factors are operating on different spatial and temporal scales. Populations of deep-sea species decline dramatically under light exploitation and continued fishing, and species with extreme life history characteristics will continue to show the effects of overfishing for several generations (Koslow et al. 2000). The possibility exists that species with extreme life history characteristics may never recover from severe exploitation (Atkinson 1995; Roberts 2002; Drazen 2008). Baker et al. (in prep.) used life history characteristics of *Macrourus* and *Coryphaenoides* to estimate recovery rates under minimal fishing impacts (e.g., as bycatch); recovery rates were 22–174 years and 23–261 years, respectively.

There is disagreement over whether the Canadian survey truly captures the population trends of *Macrourus* and *Coryphaenoides* and it has been suggested to us informally that these surveys sample only the fringes of the populations. Other survey data are available in the Northwest Atlantic: the EU (Spain and Portugal) summer surveys in NAFO Division 3M conducted since 1988 at depths to 730 m (Saborido-Rey and Vázquez 2003; Costas and Murua 2005), the Spanish 3NO survey conducted since 1995 and extending to 1500 m (Gonzalez-Tronco et al. 2005; Costas and Murua 2005), and surveys in Subarea 1 extending to 1500 m and conducted 1987–1997 and 1995–2004 (Jørgensen 1998; Jørgensen 2004;

Figure 5). The surveys were over a shorter time period than the Canadian research survey data, but encompassed waters beyond Canada's Economic Exclusion Zone. These data show roughhead grenadier abundance increased slightly in the 3M, 3NO and Subarea 1 data. The increase in 3M abundance data is driven largely by high values in the last two years of data, but is not significant (linear regression, log transformed data,  $F_{(1,15)} = 1.96$ ,  $p = 0.18$ ). The increase from deeper surveys in 3NO was borderline significant (linear regression, log transformed data,  $F_{(1,6)} = 5.33$ ,  $p = 0.06$ ). Surveys completed off West Greenland (NAFO Subarea 1) show *Macrourus* abundance in Subarea 1 increased, although again the relationship was not significant (linear regression, log transformed data,  $F_{(1,5)} = 5.33$ ,  $p = 0.07$ ). Roundnose grenadier abundance in Subarea 1 declined by 76% 1987–1995 and 85% 1997–2004, but these relationships were not significant (linear regression, log transformed data:  $F_{(1,8)} = 1.28$ ,  $p = 0.29$ ;  $F_{(1,5)} = 3.89$ ,  $p = 0.11$ ). The data from surveys outside Canadian waters thus add information to the general picture regarding population trends, but the results are rather inconclusive. It is difficult to determine, with much confidence, the true trend because the statistics indicate any apparent increase or decrease is not significantly different from zero. The results of various indices could support the argument that the species abundance appears to be relatively stable in recent years. To add further confusion, conflicting trends are presented utilizing the same data analyzed here (Costas and Murua 2005); their VPA estimates of *Macrourus* spawner biomass reveal a significant 80% decline 1993–2004 (about two-thirds of a *Macrourus* generation) with 95% confidence intervals of 62–89% ( $F_{(1,10)} = 32.7$ ,  $p = 0.0002$ ). This situation underscores the need for a robust analysis of all data in the Northwest Atlantic for the two species.

The impact of exploitation on abundance is a result of the life history and ecological characteristics of grenadiers. As with many deep-sea species, they are slow-growing, late-maturing, long-lived, and have low fecundity (Merrett 1994; Moore and Mace 1999; Koslow et al. 2000; Clark 2001). Clarke et al. (2003) found roundnose grenadier displayed slow growth in the Northeast Atlantic;  $K$ , the Brody growth coefficient from the von Bertalanffy growth model, was 0.1 for females and 0.13 for males. *Macrourus* also displays slow growth; Murua (2003) estimated average rates ( $K \cdot \text{yr}^{-1}$ ) in NAFO Divisions 3LMN of approximately 0.13 for males and 0.04 for females. In comparison, Atlantic cod *Gadus morhua* in the Irish Sea and Atlantic herring *Clupea harengus* in the Celtic Sea display much higher growth; estimated average rates are 0.43 and 0.56 respectively (Clarke et al. 2003). Maximum age attained from survey samples in the Northeast Atlantic for roundnose grenadier is 60 years for females and 50 years for males (Clarke et al. 2003), maturation is at age 11 and a modest number, <57,000, of large eggs are produced (Alekseyev et al. 1992; Kelly et al. 1997), attributes characteristic of species in low-energy environments (Ekau 1991). In the Northwest Atlantic, maximum age of *Macrourus* from catch data is 20 years, maturation is at approximately age 15 (Murua 2003; Costas and Murua 2005), similar to *Macrourus* in the Northeast Atlantic (Eliassen and Falk-Petersen 1985), and the amount of eggs spawned ranges between 8500 and 62,000 (Savvatimsky 1994; Murua 2003; Savvatimsky and Gorchinsky 2001). Both sexes of roughhead grenadier are fully recruited to the fishery at age 8 (Savvatimsky and Gorchinsky 2001; Murua 2003), i.e., while still immature. Mortality rates ( $Z$ ) for the Flemish cap range between 0.29 and 0.47 for females and 0.59–0.69 for males based on both survey and commercial data (Murua 2003).

The Canadian survey data have been claimed (*in litt.*) to be nonrepresentative because they sample only the edge of the population, an unwarranted and troubling assumption. Conservation ecology has shown that trouble at the edge of a range presages trouble over the entire range (Channell and Lomolino 2000; Fraser 2000). Furthermore, deep populations of slope species are not separate from shallow ones because of ontogenetic migrations. *Coryphaenoides* move up and down the slope seasonally, migrating to shallower water at the end of summer and shifting deeper in winter (Dushchenko and Savvatimsky 1987; Paz and Iglesias 1994). *Macrourus* also migrate seasonally (Paz and Iglesias 1994) and follow the 'bigger-deeper' rule in the northwest Atlantic, with smaller juveniles generally occurring shallower than the larger adults (Savvatimsky and Gorchinsky 2001).

Savvatimsky and Gorchinsky (2001) hypothesized that roughhead grenadier in NAFO Divisions 0B2GHJ3KLMN (see Figure 5) are a single stock based on size-age composition, although the isolation of the Flemish Cap from the Grand Banks by the cold waters of the Labrador Current render this conclusion questionable. Using parasites as natural tags allows for identification of distinct populations of fishes, especially in the deep-sea where parasite diversity decreases with distance from the continental slope (Kabata 1963; Templeman and Fleming 1963; Campbell et al. 1980). Analysis of parasites has shown that fish species, including *Macrourus*, on the Flemish Cap host a different suite of parasites than species from the Newfoundland Shelf and Grand Banks (Zubchenko 1981; Campbell 1983).

Whether roundnose grenadier is a single stock has also been debated. The existence of one North Atlantic stock was suggested based on differences in sex ratios (Podrazhanskaya 1971), but this was dismissed

by those that argued *Coryphaenoides* was incapable of long migrations (e.g., Savvatimsky 1982; Dushchenko 1983). However, Vinnichenko and Khlivnoy (2008, this volume) have found that juvenile *Coryphaenoides* appear to be widely distributed as the result of passive migrations by ocean currents. Savvatimsky (1982) claimed that differences in growth between fishes from the northeast and northwest Atlantic, differences in parasites in fish from different areas, and the existence of sexually maturing fish in the northwest Atlantic also argued for separate stocks.

Stock structure and life history characteristics of the grenadier species must be considered when attempting to develop management objectives. Because of the longevity of deep-sea species, any disturbance to the community may take decades to be noticed (Koslow et al. 2000), unlike many pelagic or shelf species that are re-selected and can respond quickly to changing conditions (Bakun 1986; Jørgensen 2002). The time scale over which deep-sea species have been studied is short, and the research is often not even begun before a directed fishery has peaked and collapsed (Atkinson 1995; Haedrich et al. 2001; Roberts 2002). Compounding problems are the difficulties in attempting to determine whether changes are primarily a result of the environment or overfishing; it is often easy to claim overfishing as the main cause. Fishing pressure is a main factor explaining trends in roundnose grenadier and roughhead grenadier, however, large-scale atmospheric conditions that operate across the North Atlantic also play a role. These populations are not virgin stocks, but have experienced several decades of intense exploitation, especially *Coryphaenoides*. Stocks already changed and weakened by overfishing are often more susceptible to the effects of changing environment (Pauly and Maclean 2003).

## References

- Aagaard, K., and E. C. Carmack. 1994. The Arctic Ocean and climate: a perspective, Pages 5–20 *In* O. M. Johannessen, R. D. Muench, and J. E. Overand, editors. The Polar Oceans and their role in shaping the global environment: the Nansen centennial volume. American Geophysical Union, Washington, D.C.
- Alekseyev, F. Y., Y. I. Alekseyeva, and A. N. Zakharov. 1992. Vitellogenesis, nature of spawning, fecundity, and gonad maturity stages in the roundnose grenadier, *Coryphaenoides rupestris*, in the North Atlantic. *Journal of Ichthyology* 32:32–45.
- Anderson, P. J., and Piatt, J. F. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189:117–123.
- Atkinson, A. 1994. Some observations on the biomass and abundance of fish captured during stratified random bottom trawl surveys in NAFO Divisions 2J and 3KL, autumn 1981–1991. *NAFO Scientific Council Studies* 21:43–66.
- Atkinson, D. B. 1995. The biology and fishery of roundnose grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the Northwest Atlantic. Pages 51–112 *in* A. G. Hopper, editor. Deep-water fisheries of the North Atlantic oceanic slope. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Bakanev, S. V. 2003. The Russian shrimp fishery (*Pandalus borealis*) on the Flemish Cap, NAFO Division 3M, in 1993–2003. *NAFO SCR Document* 03/88.
- Bakanev, S. V. 2002. Russian fishery for northern shrimp (*Pandalus borealis*) on Flemish Cap Bank, NAFO Division 3M and Grand Bank, Division 3L, in 2001 and January–September 2002. *NAFO SCR Document* 02/159.
- Baker, K. D., J. A. Devine, and R. L. Haedrich. (In press) Deep-sea fish populations: declines and recovery times.
- Bakun, A. 1986. Definition of environmental variability affecting biological processes in large marine ecosystems, Pages 89–108 *in* K. Sherman, and L. M. Alexander, editors. Variability and management of large marine ecosystems. American Association for the Advancement of Science. Westview Press, Boulder, Colorado.
- Bakun, A., and K. Broad. 2003. Environmental ‘loop-holes’ and fish population dynamics: comparative pattern recognition with focus on El Niño effects in the Pacific. *Fisheries Oceanography* 12:458–473.
- Beamish, R. J., D. J. Noakes, G. A. McFarlane, L. B. Klyashtorin, V. V. Ivanov, and V. Kurashov. 1999. The regime concept and natural trends in the production of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 56:516–526.
- Belkin, I. M. 2004. Propagation of the “Great Salinity Anomaly” of the 1990s around the northern North Atlantic. *Geophysical Research Letters* 31.
- Belkin, I. M., S. Levitus, J. Antonov, and S.-A. Malmberg. 1998. “Great Salinity Anomalies” in the North Atlantic. *Progress in Oceanography* 41:1–68.
- Bergstad, O. A., and B. Isaksen. 1987. Deepwater resources of the Northeast Atlantic: distribution, abundance and exploitation. *NAFO SCR Document* 87/85.
- Bianchi, G., H. Gislason, K. Graham, L. Hill, X. Jin, K. Koranteng, S. Manickchand-Heileman, I. Payá, K. Sainsbury, F. Sanchez, and K. Zwanenburg. 2000. Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science* 57:558–571.
- Blindheim, J., and H. R. Skjoldal. 1993. Effects of climatic changes on the biomass yield of the Barents Sea, Norwegian Sea, and West Greenland large marine ecosystems, Pages 185–198 *in* K. Sherman, L. M. Alexander, and B. Gold, editors. Large marine ecosystems V: stress, mitigation and sustainability of large marine ecosystems. American Association for the Advancement of Science. Washington, D.C.
- Brewer, P. G., W. S. Broecker, W. J. Jenkins, P. B. Rhines, C. G. Rooth, J. H. Swift, T. Takahashi, and R. T. Williams. 1983. A climatic freshening of the deep Atlantic north of 50° N over the past 20 years. *Science* 222:1237–1239.
- Brown, S. K., R. Mahon, K. C. T. Zwanenburg, K. R. Buja, L. W. Clafin, R. N. O’Boyle, B. Atkinson, M. Sinclair, G. Howell, and M. E. Monaco. 1996. East Coast of North America groundfish: initial explorations of biogeography and species assemblages. National Oceanic and Atmospheric Administration and Dartmouth, NS, Department of Fisheries and Oceans. Silver Spring, Maryland.
- Campbell, R. A. 1983. Parasitism in the deep sea, Pages 473–552 *In* G. T. Rowe, editor. Deep-sea biology. Wiley, New York.
- Campbell, R. A., R. L. Haedrich, and T. A. Munroe, T. A. 1980. Parasitism and ecological relationships among deep-sea benthic fishes. *Marine Biology* 57:301–313.
- Channell, R., and M. V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. *Nature (London)* 403:84–86.

- Clark, M. 2001. Are deepwater fisheries sustainable?—the example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fisheries Research* 51:123–135.
- Clarke, M. W., C. J. Kelly, P. L. Connolly, and J. P. Molloy. 2003. A life history approach to the assessment and management of deepwater fisheries in the Northeast Atlantic. *Journal of the Northwest Atlantic Fisheries Science* 31:401–411.
- Cohen, D. M., T. Inada, T. Iwamoto, and N. Scialabba. 1990. FAO species catalogue. volume 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Fisheries Synopsis 10(125). FAO, Rome.
- Colbourne, E., B. deYoung, S. Narayanan, and J. Helbig. 1997. Comparison of hydrography and circulation on the Newfoundland Shelf during 1990–1993 with the long-term mean. *Canadian Journal of Fisheries and Aquatic Sciences* 54 (Supplement 1):68–80.
- Costas, F. G., and H. Murua. 2005. Assessment of roughhead grenadier, *Macrourus berglax*, in NAFO Subareas 2 and 3. NAFO SCR Document 05/04.
- de Cardenas, E., Casas, J. M., Slapoin, R., and Murua, H. 1996. Preliminary results of the European long-line survey in the NAFO regulatory area. NAFO SCR Document 96/34.
- de Young, B., and G. A. Rose. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2729–2741.
- Devine, J. A., K. D. Baker, and R. L. Haedrich. 2006. Fisheries: Deep-sea fishes qualify as endangered. *Nature (London)* 439:29–29.
- Devine, J. A., A. F. Zuur, E. N. Ieno, and G. M. Smith. 2007. Complex dynamics in demersal communities on the Newfoundland-Labrador Shelf, Pages 589–598 in A. F. Zuur, E. N. Ieno, and G. M. Smith, editors. *Analysing Ecological Data*. Springer, Berlin.
- Doubleday, W. G., and D. Rivard. 1981. Bottom trawl surveys. *Canadian Special Publication of Fisheries and Aquatic Sciences* 58.
- Drazen, J. C. 2008. Energetics of grenadier fishes. Pages xxx in A. M. Orlov and T. Iwamoto, editors. *Grenadiers of the world oceans: biology, stock assessment, and fisheries*. American Fisheries Society, Symposium 63, Bethesda, Maryland.
- Drinkwater, K. F. 2002. A review of the role of climate variability in the decline of northern cod. Pages 113–130 in N. A. McGinn, editor. *Fisheries in a changing climate*. American Fisheries Society, Symposium 32, Bethesda, Maryland.
- Durán, P., Paz, J., and Ramilo, L. 1997. By-catch in the Spanish Greenland halibut fishery (NAFO Division 3LMNO): 1991–94. NAFO Scientific Council Studies 30:1–20.
- Dushchenko, V. V., and P. I. Savvatimsky. 1987. Intra-specific structure of rock grenadier, *Coryphaenoides rupestris*, of the North Atlantic: variability of local groups and reasons for their formation. *Voprosy Ikhtologii* 27:784–793.
- Dushchenko, V.V. 1983. The relationship between genetic stability and variability in populations of rock grenadier in the North Atlantic. Pages 34–37 in *Genetics of commercial and cultivated species: proceedings of the Second All-Union Conference on Genetics, Selective Breeding, and Hybridization of Fish*. Canadian Journal of Fisheries and Aquatic Sciences.
- Ekau, W. 1991. Morphological adaptations and mode of life in high Antarctic fish, Pages 23–39 In G. di Prisco, B. Maresca, and B. Tota, editors. *Biology and Antarctic fish*. Springer-Verlag, Berlin.
- Eliassen, J. E., and I.-B. Falk-Petersen. 1985. Reproductive biology of the roughhead grenadier (*Macrourus berglax* Lacepède) (Pisces, Gadiformes) from the continental slope of northern Norway. *Sarsia* 70:59–67.
- Erzini, K. 2005. Trends in NE Atlantic landings (southern Portugal): identifying the relative importance of fisheries and environmental variables. *Fisheries Oceanography* 14:195–209.
- Erzini, K., C. A. O. Inejih, and K. A. Stobberup. 2005. An application of two techniques for the analysis of short, multivariate non-stationary time-series of Mauritanian trawl survey data. *ICES Journal of Marine Science* 62:353–359.
- Fraser, D. F. 2000. Species at the edge: the case for listing of “peripheral” species. In L. M. Darling, editor. *Proceedings of a conference on the biology and management of species and habitats at risk*. Kamloops, BC 15–19, 1999. BC Ministry of Environment, Lands and Parks, Victoria BC and University College of the Cariboo, Kamloops, British Columbia.
- Gomes, M. C., R. L. Haedrich, and M. G. Villagarica. 1995. Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador Shelf, north-west Atlantic, 1978–1991. *Fisheries Oceanography* 4:85–101.
- González-Tronsco, D., and J. M. Casas. 2005. Calculation of the calibration factors from the comparative experience between the R/V Cornide de

- Saavedra and the R/V Vizconde de Eza in Flemish Cap in 2003 and 2004. NAFO SCR Document 05/29.
- Gorchinsky, K. V., and P. I. Savvatimsky. 1994. Composition of bottom trawl catches at different depths off the Flemish Pass in 1989–1993. NAFO SCR Document 94/29.
- Gordon, J. D. M., N. R. Merrett, and R. L. Haedrich. 1995. Environmental and biological aspects of slope-dwelling fishes of the North Atlantic. Pages 1–26 in A. G. Hopper, editor. Deep-water fisheries of the North Atlantic oceanic slope. Kluwer Academic Publishers, Boston.
- Haedrich, R. L., N. R. Merrett, and N. R. O’Dea. 2001. Can ecological knowledge catch up with deep-water fishing? A North Atlantic perspective. *Fisheries Research* 51:113–122.
- Hjermann, D. Ø., N. C. Stenseth, and G. Ottersen. 2004. Indirect climatic forcing of the Barents Sea capelin: a cohort effect. *Marine Ecology Progress Series* 273:229–238.
- Hurrell, J. W., Y. Kushnir, G. Ottersen, and M. Visbeck. 2003. An overview of the North Atlantic Oscillation. Pages 1–36 in J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck, editors. The North Atlantic Oscillation: climatic significance and environmental impact. American Geophysical Union, Washington, D.C.
- Hutchings, J. A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock’s collapse. *Canadian Journal of Fisheries and Aquatic Sciences* 53:943–962.
- Hutchings, J. A., and R. A. Myers. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences* 51:2126–2146.
- IUCN. 2006. IUCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK.
- Jørgensen, O. A. 2004. Survey for Greenland halibut in NAFO Divisions 1C–1D, 2003. NAFO SCR Doc 04/19:26.
- Jørgensen, S. E. 2002. Integration of ecosystem theories: a pattern. Kluwer Academic Publishers, Boston.
- Jørgensen, O. A. 1998. Results of the joint Japan-Greenland trawl surveys at West Greenland 1987–95 on Greenland halibut (*Reinhardtius hippoglossoides*) and roundnose grenadier (*Coryphaenoides rupestris*). NAFO Scientific Council Studies 31.
- Kabata, Z. 1963. Parasites as biological tags. International. Commission of Northwest Atlantic Fisheries Special Publications 4:31–37.
- Kelly, C. J., P. L. Connolly, and J. J. Bracken. 1997. Maturity, oocyte dynamics and fecundity of the roundnose grenadier from the Rockall Trough. *Journal of Fish Biology* 49 (Supplemental A):5–17.
- Klyashtorin, L. B. 1998. Long-term climate change and main commercial fish production in the Atlantic and Pacific. *Fisheries Research* 37:115–125.
- Koslow, J. A., G. W. Boehlert, J. D. M. Gordon, R. L. Haedrich, P. Lorange, and N. Parin. 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science* 57:548–557.
- Liem, A. H., and W. B. Scott. 1996. Fishes of the Atlantic coast of Canada. *Fisheries Research Board of Canada Bulletin* 28:461–462.
- Lorange, P., H. Dupouy, and V. Allain. 2001. Assessment of the roundnose grenadier (*Coryphaenoides rupestris*) stock in the Rockall Trough and neighbouring areas (ICES sub-areas V–VII). *Fisheries Research* 51:151–163.
- McCallum, B. R., and S. J. Walsh. 1996. Groundfish survey trawls used at the Northwest Atlantic Fisheries Centre, 1971–present. NAFO SCR Document 96/50.
- Machias, A., Giannoulaki, M., Somarakis, S., Maravelias, C. D., Neofitou, C., Koutsoubas, D., Papadopoulou, K. N., Karakassis, I. 2006. Fish farming effects on local fisheries landings in oligotrophic seas. *Aquaculture* 261:809–816.
- Marsden, R. F., Mysak, L. A., and Myers, R. A. 1991. Evidence for stability enhancement of sea ice in the Greenland and Labrador Seas. *Journal of Geophysical Research* 96:4783–4789.
- Marshall, N. B., and Iwamoto, T. 1973. Genus *Coeilorhynchus*, Family Macrouridae, Pages 538–563 in N. B. Marshall, editor. Fishes of the western North Atlantic, Sears Foundation for Marine Research 1(6):496–665.
- Merrett, N. R. 1994. Reproduction in the North Atlantic oceanic ichthyofauna and the relationship between fecundity and species’ sizes. *Environmental Biology of Fishes* 41:207–245.
- Moore, J. A., and Mace, P. M. 1999. Challenges and prospects for deep-sea finfish fisheries. *Fisheries Management* 24:22–23.
- Murua, H. 2003. Population structure, growth and reproduction of roughhead grenadier on the Flemish Cap and Flemish Pass. *Journal of Fish Biology* 63:356–373.
- Murua, H. 2000. A review on roughhead grenadier (*Macrourus berglax*) biology and population

- structure on Flemish Cap (NAFO Division 3M), 1991–1999. NAFO SCR Document 00/30.
- Musick, J. A. 1999. Criteria to define extinction risk in marine fishes. *Fisheries* 24:6–14.
- Myers, R. A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* (London) 423:280–283.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1997. Why do fish stocks collapse? *Ecological Application* 7:91–106.
- Parsons, L. S. 1976. Distribution and relative abundance of roundnose, roughhead and common grenadiers in the Northwest Atlantic. ICNAF Scientific Council Studies 1:73–78.
- Pauly, D., and J. Maclean. 2003. In a perfect ocean: the state of fisheries and ecosystems in the North Atlantic Ocean. Island Press, Washington.
- Paz, J., and S. Iglesias. 1994. Grenadiers in the Spanish fishery of Greenland halibut, NAFO Divisions #LM and 3N, 1991–1993. NAFO SCR Document 94/23.
- Podrazhanskaya, S. G. 1971. Feeding and migrations of the roundnose grenadier, *Macrourus rupestris*, in the Northwest Atlantic and Icelandic waters. ICNAF Redbook 3:211–220.
- Power, D. 1999. Roundnose Grenadier (*Coryphaenoides rupestris*) in NAFO Subareas 2+3. NAFO SCR Document 99/51.
- Roberts, C. M. 2002. Deep impact: the rising toll of fishing in the deep sea. *Trends in Ecology and Evolution* 17:242–245.
- Saborido-Rey, F., and A. Vazquez. 2003. Results from the bottom trawl survey of Flemish Cap in July 2002. NAFO SCR Document 03/42.
- Sahrhage, D. 1986. Commercially important grenadiers of the North Atlantic. Reports from the Institute of Deepsea Fisheries, Hamburg, Federal Republic of Germany. *Canadian Transactions of Fisheries and Aquatic Sciences* 37.
- Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. Akaike Information Criterion statistics. D. Reidel Publishing Company, Boston.
- Savvatimsky, P. I. 1982. Reproduction and sex composition of the North Atlantic roundnose grenadier. Pages 32–53 in *Abundance and modes of life of the Northwest Atlantic commercial fishes*. Canadian Transactions of Fisheries and Aquatic Sciences 5389.
- Savvatimsky, P. I. 1969. Grenadier of the North Atlantic. PINRO, Murmansk, Russia.
- Savvatimsky, P. I. 1991. Causes of decrease in total catch of roundnose grenadier (*Coryphaenoides rupestris* Gun.) in the Northwest Atlantic in 1979–1990. NAFO SCR Document 91/8.
- Savvatimsky, P. I. 1994. Age structure of roughhead grenadier (*Macrourus berglax*) in the northwest Atlantic, 1985. NAFO Scientific Council Studies 20:53–64.
- Savvatimsky, P. I., and K. V. Gorchinsky. 2001. Bycatch of grenadiers in directed fishery for Greenland halibut in Divisions 3LMN and size, age and sex composition of roughhead grenadier in 2000. NAFO SCR Document 01/9.
- Scott, W. B., and W. B. Scott. 1988. Atlantic fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences No. 219.
- Shapiro, D. E., and P. Switzer. 1989. Extracting time trends from multiple monitoring sites. Study on Statistics and Environmental Factors in Health (SIMS). Technical Report No. 132.
- Shelton, P. A., A. F. Sinclair, G. A. Chouinard, R. Mohn, and D. E. Duplisea. 2006. Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 63:235–238.
- Solow, A. R. 1994. Detecting Change in the Composition of a Multispecies Community. *Biometrics* 50:556–565.
- Switzer, P., and A. A. Green. 1984. Min/max autocorrelation factors for multivariate spatial imagery. Stanford University, SIMS Technical Report No. 6.
- Templeman, W., and A. M. Fleming. 1963. Distribution of *Lernaeocera branchialis* in cod as an indicator of cod movements in the Newfoundland area. International Commission of Northwest Atlantic Fisheries Special Publications 4:318–322.
- Vinnichenko, V. and V. Khlivnoy. 2008. New data on distribution of young roundnose grenadier *Coryphaenoides rupestris* in the North Atlantic. Pages xxx in A. M. Orlov and T. Iwamoto editors. Grenadiers of the world oceans: biology, stock assessment, and fisheries. American Fisheries Society, Symposium 63, Bethesda, Maryland.
- Warren, W. G. 1996. Report on the comparative fishing trial between the *Gadus Atlantica* and Teleost. NAFO SCS 29:81–92.
- Wheeler, A. 1969. The fishes of the British Isles and Northwest Europe: Anacanthini. MacMillan Ltd, London.
- Zubchenko, A. V. 1981. Parasitic fauna of some Macrouridae in Northwest Atlantic. *Journal of the Northwest Atlantic Fisheries Science* 2:67–72.
- Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. *Analyzing Ecological Data*. Springer, Berlin.
- Zuur, A. F., R. J. Fryer, I. T. Jolliffe, R. Dekker, and J. J. Beukema. 2003a. Estimating common trends

- in multivariate time series using dynamic factor analysis. *Environmetrics* 14:665–685.
- Zuur, A. F., I. D. Tuck, and N. Bailey. 2003b. Dynamic factor analysis to estimate common trends in fisheries time series. *Canadian Journal of Fisheries and Aquatic Sciences* 60:542–552.
- Zuur, A. F., and G. J. Pierce. 2004. Common trends in northeast Atlantic squid time series. *Journal of Sea Research* 52:57–72.
- Zwanenburg, K. C. T. 2000. The effects of fishing on demersal fish communities of the Scotian Shelf. *ICES Journal of Marine Science* 57:503–509.