

Recruitment of cod and haddock in the North Atlantic: a comparative analysis

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We examined recruitment patterns of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) from eight regions in the North Atlantic (Georges Bank, Browns Bank, the Eastern Scotian Shelf, the Faroe Plateau, Iceland, the Barents Sea, the North Sea, and West of Scotland). The selection was based on the availability of contemporaneous estimates of stock and recruitment for both species within each location. We considered the following metrics for both species by region: recruitment variability (measured as absolute numbers at age 1 and as deviations from a fitted stock-recruitment curve), the rate of recruitment at low spawning stock sizes (the maximum reproductive rate, a measure of resilience of the stock to exploitation) and autocorrelation in recruitment adjusted for spawning stock size. We also examined the correlation of cod and haddock recruitment within regions. Differences in recruitment variability and resilience between cod and haddock in paired comparison tests were highly significant. Haddock consistently exhibited higher recruitment variability and lower resilience than cod. Autocorrelation in recruitment of the two species within region was related, possibly indicating serial correlation in forcing mechanisms affecting both species. Cod and haddock exhibited moderate synchrony in recruitment patterns within regions. In six out of the eight regions, the correlation between recruitment (adjusted for spawning stock size) was ~ 0.5 , suggesting that common environmental conditions experienced by both species did affect recruitment. Research-vessel survey information available for three of the regions (North Sea, Barents Sea, and Georges Bank) and one additional location (Gulf of Maine) were analyzed for evidence of density dependence and for levels of post-larval abundance variability. Cod exhibited stronger density-dependent mortality in three out of four regions. Post-larval abundance variability was not different between the two species.

Keywords: recruitment variability, resilience to exploitation.

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Introduction

Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) populations have long supported important fisheries throughout the North Atlantic. Cod in particular has played a dominant role that can be traced over five centuries (Hutchings and Myers, 1994), serving both as an early catalyst for exploration and an essential commodity in the trade of nations (Kurlansky, 1997). Both species have experienced sharp declines in abundance during the last several decades under intensive exploitation (Hutchings and Myers 1994; Cook *et al.*, 1997; Fogarty and Murawski, 1998). The collapse of the northern cod fishery off Newfoundland and Labrador serves as a particularly

dramatic example of the ecological, social, and economic consequences of overexploitation (Hutchings and Myers, 1994). Despite an ongoing moratorium on fishing, this stock has not recovered in over a decade. Similarly, the haddock population on Georges Bank shifted to a much lower productivity state under heavy fishing more than three decades ago and is only now showing signs of recovery (Fogarty and Murawski, 1998; Murawski *et al.*, 2000).

Cod and haddock are closely related gadoid species that co-occur in many regions in the North Atlantic. Haddock have been reported to exhibit higher recruitment variability than cod in the North Sea, Georges Bank, and Barents Sea regions (Hennemuth *et al.*, 1980; Hislop, 1984). Evidence for synchrony in cod and

haddock recruitment within and among regions has been examined in several studies (Templeman, 1972; Garrod and Colebrook, 1978; Koslow *et al.*, 1987; Thompson and Page, 1989; Cohen *et al.*, 1991; Myers *et al.*, 1995a), following an early consideration of co-variation in recruitment of these species by Hjort (1914). Differences in the resilience to exploitation of these and a suite of other species has also been explored (Mace and Sissenwine, 1994; Myers *et al.*, 1997a,b). Understanding fundamental life history characteristics that affect the response of species to exploitation and factors that affect overall levels of variability in recruitment is essential in devising effective management strategies.

Ultimately, the interplay of life history traits and environmental variability determines fluctuations in recruitment. Recruitment variability in marine fishes has been examined in the context egg and larval size (Rothschild and DiNardo, 1987; Miller *et al.*, 1988; Pepin and Myers, 1991), fecundity (Koslow, 1992; Mertz and Myers, 1996; Rickman *et al.*, 2000), mortality rates during the early life stages (Houde, 1987; Bradford, 1992; Bradford and Cabana, 1995), and the timing of larval production relative to seasonal prey availability (Cushing, 1969, 1990; Pepin, 1990; Mertz and Myers, 1994). The role of environmental forcing in recruitment variability has been explored in an extensive catalogue of empirical studies (for a recent review and evaluation: Myers, 1998), and through the development of stochastic recruitment models (Fogarty *et al.*, 1991; Fogarty, 1993a,b).

Our objective is to characterize patterns in recruitment variability and potential resilience to exploitation of sympatric cod and haddock populations throughout the North Atlantic in a comparative analysis. We relate observed differences in these attributes to fundamental biological and ecological characteristics of these species and to environmental regimes. An explicitly comparative approach has been adopted in the evaluation of recruitment variability (Myers *et al.*, 1995a,b) and resilience (Myers *et al.*, 1997a,b) of cod in the North Atlantic. Our cross-species comparisons provide additional insights into factors controlling recruitment of these two closely related gadoid species.

Methods

We examined stock and recruitment estimates for cod and haddock populations in eight regions where these species co-occur and for which contemporaneous population estimates were available. The regions considered were: North Sea, Iceland, Barents Sea, West of Scotland, Faroe Islands, Eastern Scotian Shelf, Browns Bank, and Georges Bank. The estimates were obtained from the extensive compilation of stock and recruitment data assembled by Myers *et al.* (1995b) and updates thereof.

The analysis of recruitment variability and population resilience was restricted to estimates derived from sequential population analysis to ensure that any differences in recruitment characteristics were not attributable to differences in estimation method.

For each region and species, we determined the rate of recruitment at low spawning stock sizes, the variance in the recruitment series, the variance in the residuals from the Ricker stock-recruitment model, the correlation between these residuals for sympatric cod and haddock populations, and the first-order autocorrelation in the residuals of the stock-recruitment curve.

We used a process-error formulation of the Ricker model:

$$R = \alpha S \exp(-\beta S + \epsilon_t)$$

where R is recruitment (number of one-year-old fish), S is the adult biomass, α is the rate of recruitment at low adult population size, βS is the rate of compensatory mortality, and ϵ_t is a random perturbation. Maximum likelihood estimates of the parameters were made under the assumption of lognormally distributed errors. Previous application of the Ricker model to cod and haddock populations (Myers *et al.*, 1995b) indicated the general suitability of this approach for our purpose. The parameter α is a measure of the resilience of the population to stress, including harvesting: higher values will result in higher resilience. We scale α as the number of spawners produced per spawner at low abundance in the absence of fishing, i.e. the maximum annual reproductive rate (Myers *et al.*, 1999).

If juvenile abundance is measured through research-vessel surveys at several stages, density-dependent mortality during the pre-recruit phase can be estimated (Myers and Cadigan, 1993a,b).

Following their approach, the model used to test for density-dependent mortality in the juvenile stage was:

$$N_{t,a} = N_{t,o} \exp[-m_a - (1 - \lambda_a) \ln N_{t,o} + \epsilon_t]$$

where $N_{t,a}$ is the number of individuals at age a alive at time t , m_a is the density-independent mortality during the period from the earliest age (denoted o) and age a , and $(1 - \lambda_a) \ln N_{t,o}$ is the density-dependent mortality rate. Transformation to natural logarithms gives the linear model:

$$\ln N_{t,a} = -m_a + \lambda_a \ln N_{t,o} + \epsilon_t$$

which can be readily fit to a time-series of abundance estimates at different ages to test for density dependence. Survey data for such analyses were available only for the North Sea, the Barents Sea, and Georges Bank stocks of cod and haddock, and in addition for the Gulf of Maine stocks.

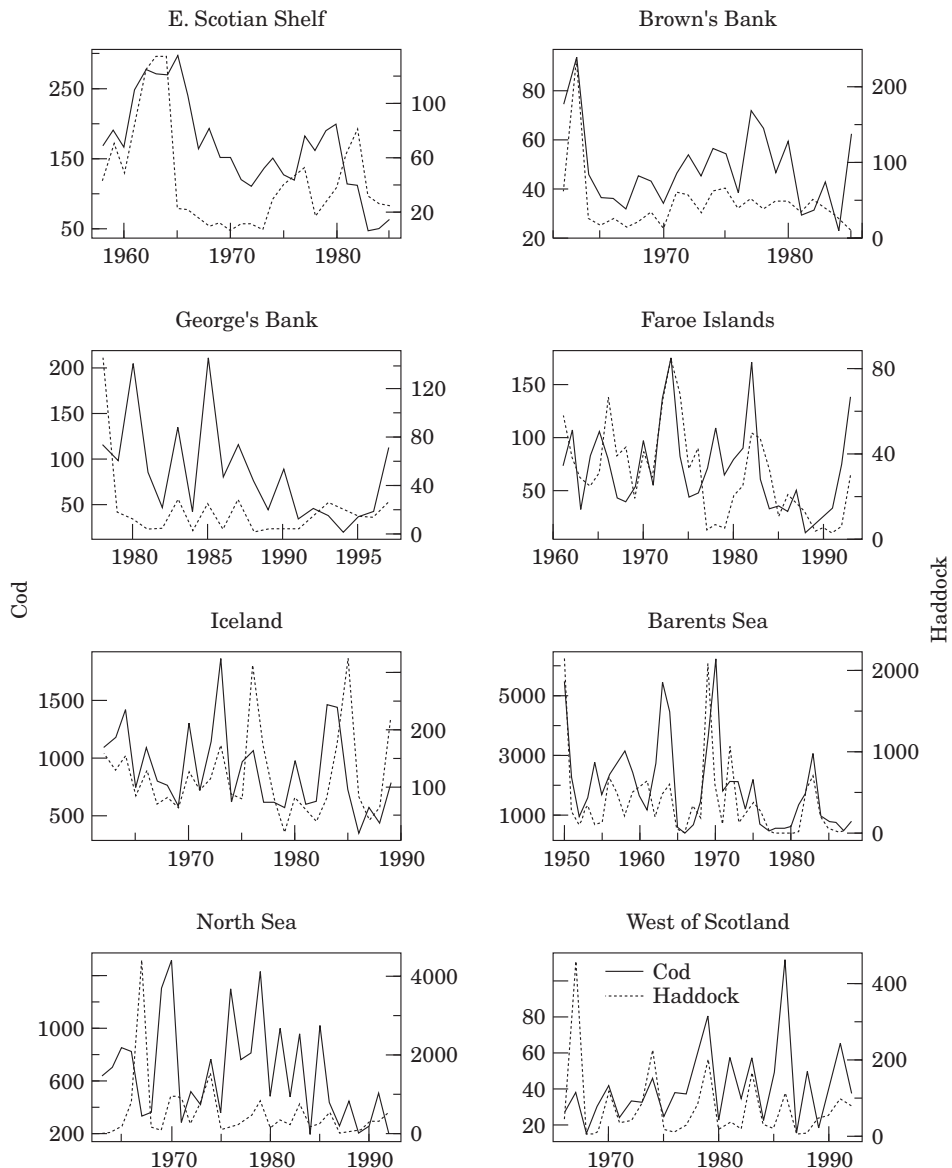


Figure 1. Recruitment ($\times 10^{-6}$ one-year-old fish) time-series of cod (solid line; left-hand scale) and haddock (broken line; right-hand scale) for each of the eight regions.

Results

Multi-decadal recruitment time-series for cod and haddock show relatively high levels of variability, characteristic of many marine fish populations (Figure 1). Variability in recruitment for both species is dominated by the effects of strong year classes. Their occurrence is consistent with the assumed underlying lognormal error structure for recruitment, representing observations in the tails of the distributions. The adult populations of both species have been strongly affected by exploitation. To account for possible differential

impacts on the adult populations and their influence on recruitment, estimates were corrected for spawning stock size (measured as the residuals from the fitted stock-recruitment curve; Figure 2) in subsequent analyses.

Recruitment variability, measured as the standard deviation of the residuals from the Ricker recruitment curve, was higher for haddock in all regions (Table 1; Figure 3). Paired comparison tests indicate that the difference is highly significant (Wilcoxon signed rank test; $p < 0.01$). Recruitment variability was highest for haddock in the Barents Sea, west of Scotland, and on

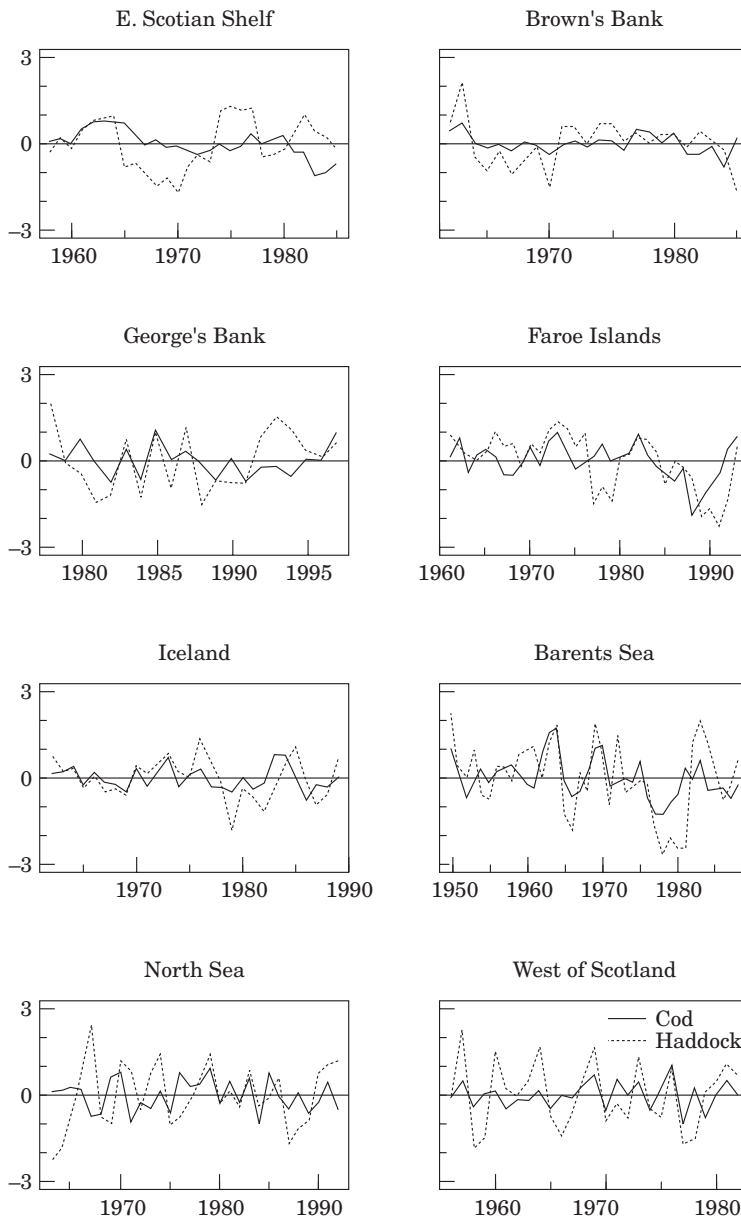


Figure 2. Time-series of residuals from Ricker stock-recruitment curve for cod (solid line) and haddock (broken line) for each of the eight regions (same scale).

Georges Bank and for cod in the Barents Sea and on the Faroe Plateau.

Autocorrelation in the residuals of the stock recruitment curve did not differ between species (Wilcoxon Signed Rank tests; $p > 0.05$). However, clear differences in serial dependence of estimated recruitment was evident among regions with high autocorrelation (Eastern Scotian Shelf and Browns Bank). Only West of Scotland exhibited negative autocorrelation for both cod and haddock (Table 1).

Moderate levels of synchrony in recruitment, measured as the correlation between the residuals of the cod and haddock recruitment series were noted in six of the eight regions (Figure 4). The Pearson product moment correlation coefficients for these six areas were approximately 0.5. Two regions (Eastern Scotian Shelf and the North Sea) exhibited low correlations.

Maximum annual reproductive rate was higher for cod than haddock in all regions with the exception of the Scotian Shelf (Table 1; Figure 5). The differences in the

Table 1. Regions (No. used for identification in Figures) examined for recruitment variability for cod (C) and haddock (H) populations, number of years available for analysis (n), estimate of the slope of recruitment curve at the origin ($\ln \alpha$), the standard deviation (s.d.) of the residuals of the fitted Ricker curve, and the first-order autocorrelation coefficient of the residuals.

No.	Region	Species	n	$\ln \alpha$	s.d.	Autocorrelation
1	North Sea	C	30	1.87	0.54	-0.21
		H	30	0.90	1.10	0.22
2	West of Scotland	C	27	1.63	0.46	-0.40
		H	27	0.79	1.18	-0.05
3	Faroe Plateau	C	33	1.38	0.62	0.53
		H	33	0.38	0.96	0.62
4	Barents Sea	C	39	2.04	0.68	0.51
		H	39	0.40	1.27	0.41
5	Iceland	C	28	1.48	0.39	0.17
		H	28	0.76	0.71	0.36
6	Eastern Scotian Shelf	C	28	2.20	0.47	0.77
		H	28	0.88	0.85	0.67
7	Browns Bank	C	24	1.14	0.33	0.20
		H	24	1.28	0.79	0.18
8	Georges Bank	C	20	0.66	0.52	-0.16
		H	20	-0.49	1.07	0.01

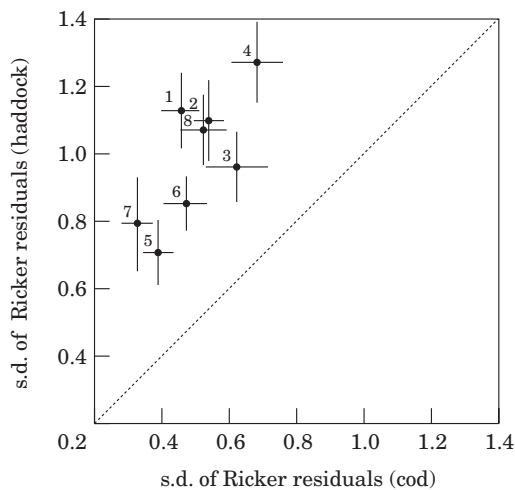


Figure 3. Standard deviation of log residuals from stock-recruitment curve (and 95% confidence intervals) for haddock stocks plotted against cod stocks in the same region (see Table 1 for numerical codes).

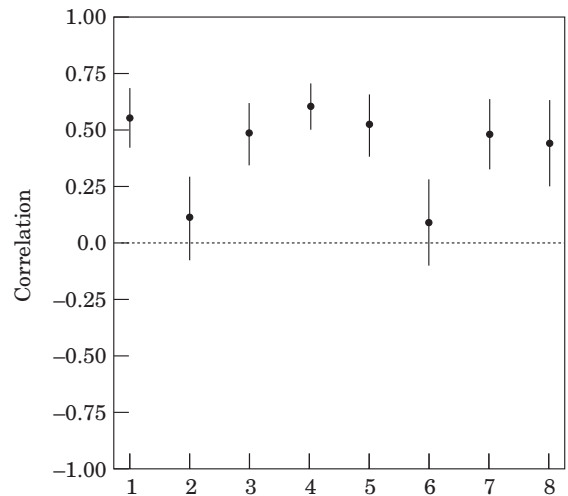


Figure 4. Correlation of log recruitment estimates and 95% confidence intervals between cod and haddock for each region (see Table 1 for numerical codes).

slope of the recruitment curves at the origin were statistically significant (Wilcoxon Signed Rank test; $p < 0.05$). The slopes were substantially lower for both species on Georges Bank relative to the other seven regions (Figure 5).

Based on research-vessel survey data, no systematic difference in the variance of post-larval abundance of cod and haddock is evident [Figure 6(a)]. Because of the limited number of geographical regions available for this analysis, we did not attempt formal statistical comparisons. Stronger density dependence for cod in the

juvenile phase was evident in three of the four regions [Figure 6(b)].

Discussion

Recruitment variability for haddock was consistently higher than for cod in eight major production regions in the North Atlantic. These results are in accord with previous observations for sympatric cod and haddock populations in several of these areas (Hennemuth *et al.*, 1980; Hislop, 1984; Sherman *et al.*, 1984). Our results

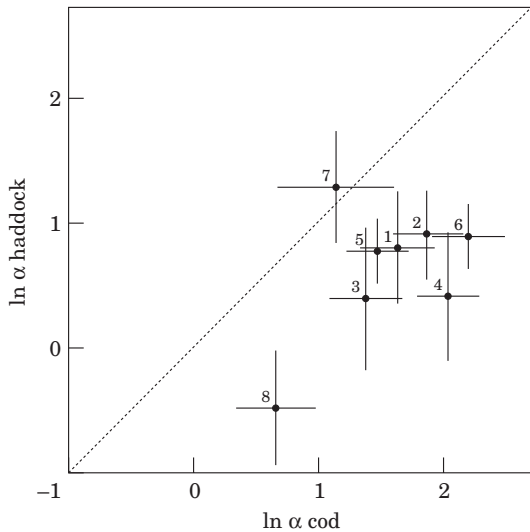


Figure 5. Estimated slope at the origin ($\ln \alpha$, i.e. maximum annual reproductive rate) of the recruitment curve (and 95% confidence intervals) for haddock stocks plotted against those of cod stocks in the same region (see Table 1 for numerical codes).

confirm the generality of this pattern for all cases where direct comparisons are possible. Recruitment variability depends on life history traits of the species and on the magnitude and timing of environmental variation affecting growth and survival during the early life stages. Seasonal spawning periods of cod and haddock overlap in areas where both species occur, and they therefore experience similar oceanographic regimes during the early life stages. However, the spawning period of cod is more protracted than that of haddock (Colton *et al.*, 1979; Scott, 1983; Brander and Hurley, 1992; Hislop, 1984). For example, the standard deviation of the mean spawning date (as measured by the estimated abundance of stage I eggs during 1978–1988) for cod on Georges Bank is 46% higher than for haddock (based on data supplied by P. Berrien). Interannual variation in the period of peak spawning has been reported for haddock (Hurley and Campana, 1987), possibly contributing to higher variation in survival rates during haddock early life stages because of mismatches with the timing of prey production.

An extended spawning season may represent a risk-spreading strategy in which the overall risk of factors such as episodic predation events and advective loss is reduced. Species characterized by a shorter spawning window are subject to the vagaries of environmental conditions, food supply, and predation risk during a restricted time interval. Mertz and Myers (1994) demonstrate in a model of the match-mismatch hypothesis that species characterized by a lower seasonal spread in spawning activity can be expected to experience higher

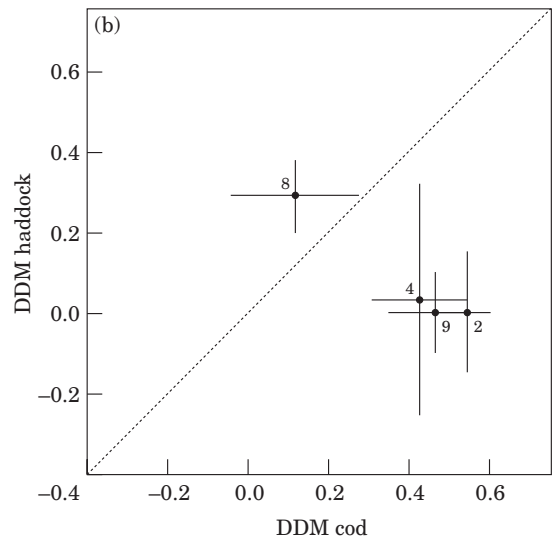
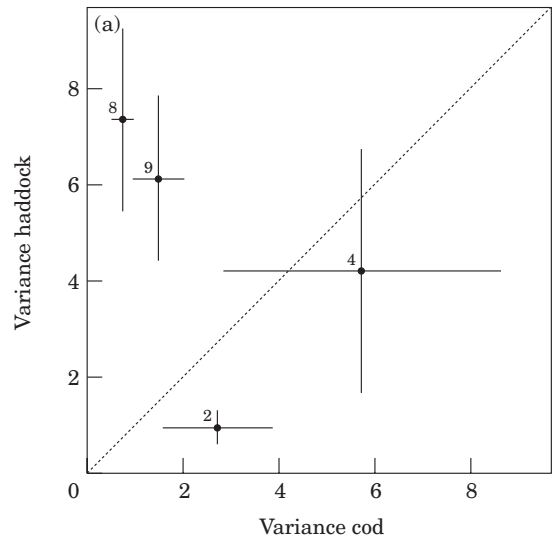


Figure 6. (a) Variance of post-larval log recruitment and (b) density-dependent juvenile mortality (and 95% confidence intervals) of haddock stocks plotted against those of cod stocks in the same region (see Table 1 for numerical codes; 9: Gulf of Maine), based on research-vessel survey data.

recruitment variability. Empirical support for this prediction has been obtained for cod stocks in different regions with varying spawning duration (Mertz and Myers, 1994). Our results are consistent with the hypothesis of an inverse relationship between spawning duration and variability in recruitment in direct comparisons of cod and haddock.

Regional differences in variability in adjusted recruitment exist for the two species. Variability was higher for stocks on Georges Bank and in the Barents Sea. These regions are at the extremes of the ranges of cod and

haddock, possibly contributing to higher variability. Myers (1991) reported higher variation in recruitment for cod, haddock, and herring populations at the extremes of their latitudinal range. Myers and Pepin (1994) examined cod recruitment variability on a number of offshore bank and continental shelf systems and concluded that higher levels occur in bank-associated stocks because of interannual variation in retention features. In our analysis, while Georges Bank stocks did exhibit high variation, populations on adjacent Browns Bank were characterized by low recruitment variability, and differences in bank vs. shelf systems could not be fully resolved.

In laboratory experiments, cod larvae exhibit higher tolerance to variation in temperature and salinity than haddock (Laurence and Rogers, 1976; Laurence, 1977), with growth and survival being higher over a broader range of conditions. If cod is both eurythermal and euryhaline relative to haddock, random variation in hydrographic conditions during early life can be expected to exert lower impact on cod, resulting in lower variation in survival and recruitment. Variation in environmental forcing conditions is unquestionably a dominant source of variation in growth and survival of fishes during the pre-recruit phase with direct consequences for recruitment and its predictability (Mertz and Myers, 1995).

Egg and larval size reflects energetic investment in the progeny and potential vulnerability to starvation and predation. It has been postulated that larger size confers selective advantage (Miller *et al.*, 1988; Anderson, 1988). Differences in cod and haddock egg sizes have been reported (e.g. Garrod, 1982; Hislop, 1984; Houde and Zastrowe, 1993) although the differences are relatively small and are not consistent among sources. Empirical evidence suggests a weak relationship between egg and larval size and recruitment variability in temperate-water marine fishes (Pepin, 1991; Pepin and Myers, 1991; Rothschild and DiNardo, 1994). Accordingly, it is unlikely that observed differences in recruitment variability of cod and haddock can be attributed to size-related characteristics at the egg or larval stages.

Density-dependent processes during the pre-recruit phase are stronger for cod than for haddock. Among the potential regulatory mechanisms operating in cod populations is cannibalism. The importance of intraspecific predation in juvenile and adult cod is well established although substantial spatial and temporal variability in incidence of cannibalism is observed (Daan, 1973). The potential for cannibalism for cod in the larval stages has received far less attention. Laurence *et al.* (1981) noted that results of larval cod rearing experiments in pure culture are consistent with cannibalism while those for haddock are not. However, cannibalism among cod larvae was not observed directly in these experiments. Density dependence can exert a strong dampening effect

on recruitment variability relative to the density-independent case (Fogarty *et al.*, 1991; Fogarty, 1993a,b). The lower recruitment variability in cod is consistent with the effects of recruitment modulation through density-dependent mechanisms.

Haddock exhibit more restricted overall distributions than cod within at least some regions where these species co-occur (Hislop 1984; Sherman *et al.*, 1984). It has been hypothesized that differences in overall distribution and spatial occurrence between these species may also affect their relative vulnerability to variation in the physical and biological environment. Higher concentration in more restricted regions may place haddock at greater risk to localized events affecting growth and survival rates.

We found no statistically significant differences in autocorrelation in the residuals of the Ricker stock-recruitment model between cod and haddock within regions. However, we did observe differences among regions. Autocorrelation was positive and relatively high for the Eastern Scotian Shelf, Faroe Plateau, and Barents Sea stocks. In contrast, autocorrelation was negative for the West of Scotland stocks and for cod in the North Sea and on Georges Bank. Positive autocorrelation may be related to persistent environmental conditions affecting recruitment. It may also be due, however, to errors in age determination in which misclassification of fish by age results in a smoothing of adjacent year classes, leading to the appearance of autocorrelated recruitment patterns. With existing information one cannot distinguish between these possible explanations for positive autocorrelation. However, it is not immediately obvious why ageing errors would predominate in some stocks but not in others if identical age-determination methods are employed (particularly for adjacent stocks such as Browns Bank vs. Eastern Scotian Shelf). Negative autocorrelation could reflect interactions among adjacent year classes through cannibalism or other mechanisms. Negative autocorrelation for cod in some regions might reflect inter-cohort cannibalism. The occurrence of autocorrelated residuals also involves an entirely different set of considerations in assessing statistical significance of the models because the effective degrees of freedom are reduced relative to nominal levels.

Cod and haddock recruitment adjusted for changes in spawning stock size was positively correlated in six of the eight production regions. We have not adjusted the significance tests to account for autocorrelation and therefore the coefficients should be interpreted as general guides to the direction and magnitude of the correlation. Because of the substantial spatial and temporal overlap in spawning times and locations of these species in most regions and their ecological similarity, some coherence in recruitment within areas is to be expected: the similar hydrographic conditions experienced, food availability,

and predation risk should result in some commonality in survival during the early life stages. Differences can be expected to arise because the spawning periods are not wholly coincident in space and time, and therefore some segments of the cod and haddock cohorts are subject to different environmental conditions with different consequences for growth and survival. As noted above, we postulate that these factors underlie the clear difference in recruitment variability. It is possible that the lack of correlation in the North Sea and the Eastern Scotian Shelf regions is attributable to greater spatial differences in distribution at different life stages. In the North Sea at least, haddock are restricted to deeper water than cod (Hislop, 1984).

Recruitment rates at low spawning stock size were higher for cod relative to haddock. Higher recruitment rates should result in a higher overall resilience to sustained perturbations such as harvesting. Our results are consistent with previous studies for these species (Mace and Sissenwine, 1993; Myers *et al.*, 1999) using non-paired comparisons. The slope of the recruitment curve at the origin is dependent on the fecundity per unit female biomass of the species and density-independent mortality rates during the pre-recruit phase. The fecundity per unit female biomass is similar for the two species, although slightly higher for haddock than for cod (Hislop, 1984). However, important differences in survival rates when fish are reared in mixed culture have been observed: cod larvae exhibited higher growth and survival rates than haddock (Laurence, 1974). The difference in the rate of recruitment at low stock sizes appears to be related to lower density-independent mortality for cod. The slopes were substantially lower for both stocks on Georges Bank relative to the other regions. For haddock, the slope for the time period encompassed in this analysis is substantially lower than for the period prior to the early 1960s (Fogarty *et al.*, 1992). The sharp decline in the haddock population following intensive exploitation by distant-water fleets has been accompanied by an apparent shift to a lower productivity state. Estimates of population size for cod based on sequential population analysis for the earlier period are not available, and it is not possible to determine if a similar shift in cod production has occurred.

Conclusions

The lower variability in cod recruitment is consistent with the hypothesis of a risk-spreading reproductive strategy with a protracted spawning season and broader spatial structure relative to haddock. Cod larvae are more tolerant of variation in temperature and salinity and are therefore presumably less sensitive to random fluctuations in environmental conditions. Stronger density-dependent mechanisms in cod may also serve to

dampen recruitment variability. Intraspecific predation is potentially an important regulatory mechanism in cod. We suggest that the combination of a broader spawning window in space and time, higher tolerance to variation in key environmental factors, and stronger internal population regulation collectively result in lower variability in cod recruitment. Other life history traits such as egg and larval size and fecundity seem less important.

Cod exhibit a steeper slope of the recruitment curve at the origin relative to haddock. This can contribute to higher resilience to exploitation in cod. Currently available evidence suggests that the higher recruitment rate of cod is attributable to lower density-independent mortality rates. In mixed laboratory cultures, cod outcompete haddock and exhibit higher growth and survival rates. Differences in relative fecundity cannot explain the higher rate of recruitment in cod at low population levels.

These results hold important implications for management. Haddock is more vulnerable to recruitment overfishing than cod. Both species have been overexploited, have experienced population declines in the North Atlantic, and must be managed more conservatively. For depleted populations, an incoming strong year class can serve as a nucleus for stock recovery if the cohort is protected from high exploitation. The higher recruitment variability in haddock may enhance this possibility, and chance recruitment events may play a more important role in the rate of recovery of depleted haddock stocks relative to cod.

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