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Recruitment Variability and Range of Three Fish Species

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Recruitment variability is a central problem in fisheries, and yet there are few systematic tests of biological hypotheses concerning recruitment variability (Heath and Richardson, 1989; Pepin and Myers, 1991). Here the temporal variability in recruitment throughout the species range is examined. If populations at the edge of ranges are more susceptible to density-independent factors than those at the centre, as has been suggested (Haldane, 1956), then the relative variability in population density should be greater at the edge of a species range than at the centre (Gaston, 1990). Density-independent factors are usually more important than density-dependent factors in determining recruitment (Myers and Drinkwater, 1989); thus, marine fish should be an excellent group to test if population variability is greater at the edges of a species range.

Here recruitment variability is examined in 53 populations of three marine fish species, cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus* L.) and herring (*Clupea harengus* L.). The analyses are carried out separately for each species on each side of the Atlantic, because the oceanographic conditions result in different distributions with latitude on each side. For example, the most southerly population of haddock in eastern Atlantic spawns around 59° N, while the most northerly population in western Atlantic spawns around 45° N.

The data used here are available in Myers *et al*. (1990) with the exception of herring data from Georges Bank (NAFO Subdiv. 5Ze) the Gulf of Maine (NAFO Div. 5Y), which were obtained from Mike Fogarty (National Marine Fisheries Service, Woods Hole, Mass., USA, pers. comm.), and the Thames estuary and the Celtic Sea obtained from Heath and Richardson (1989). The population boundaries generally follow those defined by the statistical areas of ICNAF and NAFO or the International Council for Exploration of the Sea (ICES).

It is assumed that each of the 53 populations are independent and that the variability in abundance represents the variability of an entire population and not changes in distribution within a population. The separation of the populations has been extensively investigated by a variety of methods, e.g. tagging and genetic analysis; these studies indicate that many of the populations are largely reproductively isolated (Sinclair, 1988). Another potential problem is that some of the populations may actually consist of several subpopulations whose population ranges overlap because of feeding migrations. In this case, the variability in abundance would be underestimated because it would be an average of several subpopulations whose population dynamics may be largely independent. However, the strong correlation in abundance among years in nearby populations (Koslow, 1984) should minimize the bias in population variability. If population definitions are incorrect (as is likely to be at the edge of the range where they are of less commercial importance) their movements between areas may show up as extra variability. The reliability of the population definitions must be considered a weak point in this study.

The standard deviation of the log (base 10) transformed recruitment denoted by s, is used here to measure temporal variability. The hypothesis of greater variability at the edge of the range was tested by determining the significance of the quadratic term in a quadratic regression of the standard deviation of the log abundance of juvenile fish *versus* the latitude of the spawning location for each population, i.e. $s = \beta_o + \beta_1 L + \beta_2 L^2$ where L is the latitude of the spawning location. The *a priori* hypothesis is that $\beta_2 > 0$. As a test of the robustness of the conclusions, a nonparametric rank test was used. The absolute difference in latitude for each population from the median latitude for that species and side of the Atlantic was calculated. Then a Kendall's rank correlation, r, between this absolute difference and the s was calculated.

Estimates of the variability of marine populations are usually greater if longer records are used because the spectrum of population size contains significant low frequency variation (Myers *et al*., 1990). A test was performed to make sure the observed pattern was not an artifact of the association of estimates of a population's variability with the number of years, n, used to estimate the variability. The regression equation was : $s = \beta_o + \beta_1 n + \beta_2 L + \beta_3 L^2$. The *a priori* hypothesis was that $\beta_3 > 0$. As a further check on the robustness of the hypotheses tests, the above analyses were repeated using an alternative measure of temporal variability. The temporal variability of recruitment was calculated as the standard deviation of the detrended log (base 10) transformed data. That is, a linear regression of the log transformed abundance data against year was calculated; the standard deviation of the residuals was used as the estimate of variability.

The regressions were estimated separately for each species on each side of the Atlantic (Table 1). Although the significance levels for each regression and rank correlation analysis are given individually, the more important concern is with the general hypothesis and thus have combined probabilities from each test of significance (Fisher, 1954).

Recruitment appears to be more variable at the edges of the range. When the significance tests are combined (Fig. 1) the overall results provide strong evidence for the hypothesis that the populations on the northern and southern ends of their range are more variable ($P<.001$). The above analysis was repeated using (Table 1) an alternative measure of population variability, the standard deviation of the detrended log abundance. Again, when the significance tests were combined there was strong

TABLE 1. Tests of the hypothesis. The parametric tests are the quadratic term in a regression of s, the standard deviation of the logarithmically (base 10) transformed recruitment, *versus* latitude. The analysis was repeated using the standard deivation of the detrended. The parameter β_3 includes the number of years used to estimate s as a covariate in the regression, while β_2 does not. The nonparametric test is described in the text. The number of populations used in each analysis is n.

			Nonparametric tests	Parametric tests	
Species	Area	n	P (H_0; $\tau \leq 0$)	P (H_0; $\beta_2 \leq 0$)	P (H_0; $\beta_3 \leq 0$)
			Results using log abundance		
Cod	Eastern Atlantic	10	.015	.007	.015
Cod	Western Atlantic	11	.036	.08	.082
Haddock	Eastern Atlantic	5	.025	0.48	.13
Haddock	Western Atlantic	6	.155	.024	.06
Herring	Eastern Atlantic	9	.046	.061	.078
Herring	Western Atlantic	12	.72	.36	.036
Combined probabilities		—	<0.001	<0.001	<0.001
			Results using detrended log abundance		
Cod	Eastern Atlantic	10	.029	.076	.016
Cod	Western Atlantic	11	.068	.086	.095
Haddock	Eastern Atlantic	5	.025	.037	.11
Haddock	Western Atlantic	6	.086	.031	.071
Herring	Eastern Atlantic	9	.046	.018	.03
Herring	Western Atlantic	12	.93	.718	.77
Combined probabilities		—	0.003	<0.001	0.003

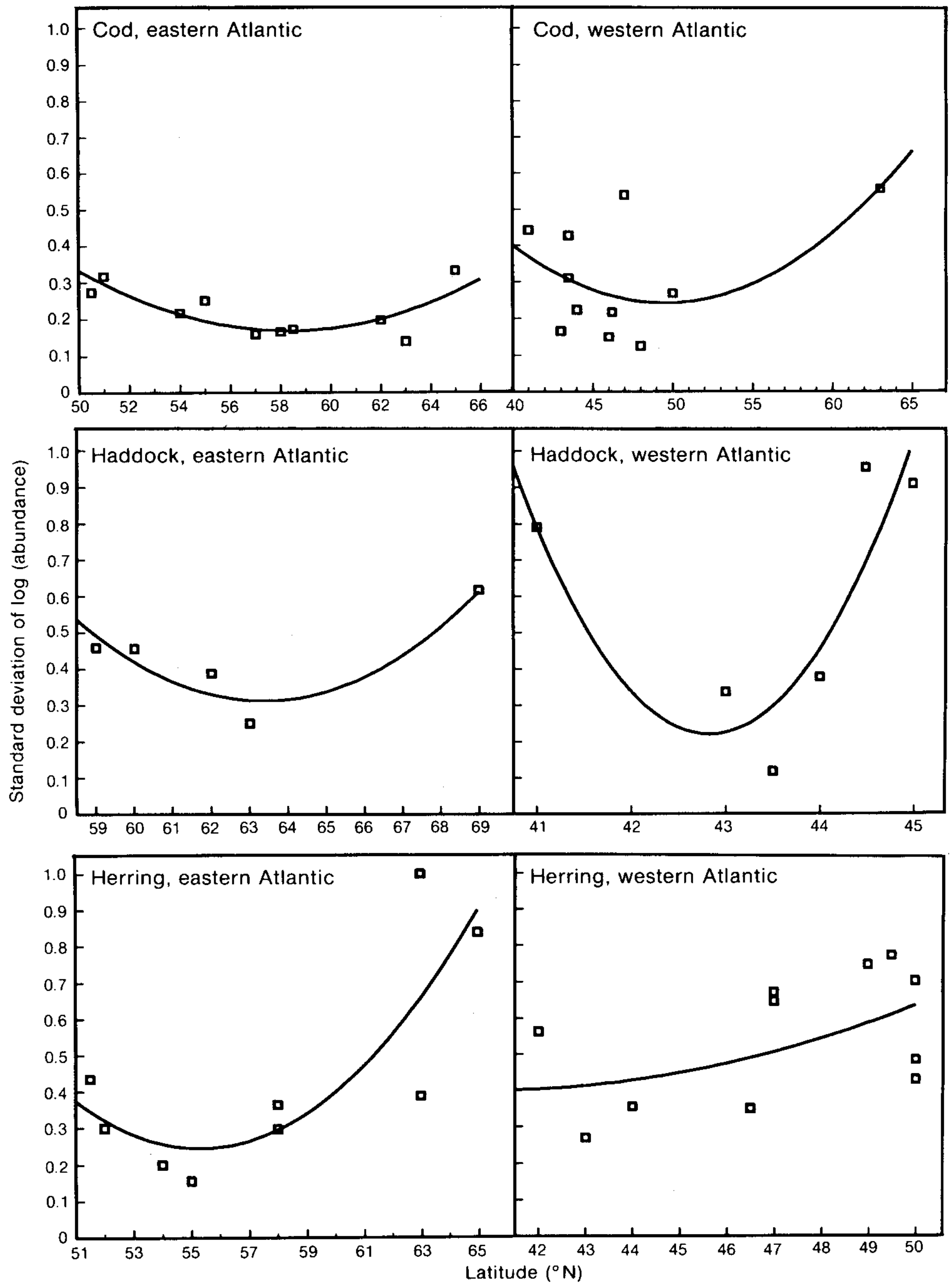

Fig. 1. The standard deviation of the logarithmically (base 10) transformed recruitment (s) *versus* the latitude of the spawning location. Also shown are the quadratic regression lines; significance levels are given in Table 1.

evidence for the hypothesis ($P<.001$), although the sign of the quadratic term for latitude was not positive for herring in the western Atlantic. Research surveys were only used for some of the stocks for cod and haddock in the western Atlantic. The combined hypothesis tests were still significant when these two categories were removed from the analysis ($P<0.005$).

The question of whether the variability of recruitment is greater at the northern and southern limits of their range can be tentatively answered for three species. The analyses here suggest strongly that variability is generally greater at the northern and southern limits of their range. Details of the results can be found in Myers (in press).

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