



SCIENTIFIC COUNCIL MEETING - SEPTEMBER 1990

Population Variability and the Range of a Species

by

Ransom A. Myers

Science Branch, Dept. of Fisheries and Oceans  
P. O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1

Summary

(1) The temporal variability in the abundance of juvenile fish throughout the range of cod, haddock and herring was examined for 53 populations in the North Atlantic. The hypothesis that the temporal variability in the numbers of juveniles was greater in populations at the northern and southern limits of the species range than in the centre was tested.

(2) The results obtained by combining each of the independent analyses provides strong evidence that juvenile fish abundance was more variable at the northern and southern limits of a species range.

INTRODUCTION

The detection and understanding of patterns of variability in population abundance is a central problem in population ecology. If populations at the edge of ranges are more susceptible to density-independent factors than those at the centre, as has been suggested (Huffaker and Messenger 1984, Richards and Southwood 1968, Coulson and Whittaker 1978), then the relative variability in population density should be greater at the edge of a species range than at the centre (Gaston 1990). Several studies have failed to show any large differences between the importance of density-independent factors among populations (Grant & Antonovics 1978; Gilbert 1980; Hassell, Southwood & Reader, 1987). However, these studies cannot be considered definitive because they examined a relatively small number of populations, sometimes over a relatively short time scale, e.g. Gilbert (1980).

Here I examine population variability in 53 populations of three marine fish species, cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and herring (*Clupea harengus*), throughout their range to test if population variability is greater at the edges of the range than in the centre. The analysis is carried out separately for each species on each side of the Atlantic. The results of the six categories are combined to test the common hypothesis (Fisher 1953).

By examining a large number of populations the effect of the range should become clear. Furthermore, density-independent factors are usually more important than density-dependent factors in determining the abundance of juvenile marine fish (Myers and Drinkwater 1989); thus, marine fish should be an excellent group to test this hypothesis. The three species are commercially exploited throughout their range. Thus, variations in the size of the adult population cannot be used to test the hypothesis because variations in fishing mortality would mask natural variability. Population variability can be accurately assessed because there are long time records for these populations. The temporal variability of populations in terms of the abundance of young fish (age 1 to 3) is examined. The term "recruitment" is usually used in the fisheries literature to denote the number of juvenile of fish of the youngest age that can be assessed.

1. DATA

The population boundaries generally follow those of the Northwest Atlantic Fisheries Organization (NAFO), formerly ICNAF, or the International Council for the Exploration of the Sea (ICES). They are given in Figure 1. We sometimes refer to the region by an alternative name, e.g. the North Sea, if it commonly applies to the population in practice.

The data used here (Table 1) is available in Myers et al. (1990) with

the exception of herring data from Georges Bank (NAFO Div. 5Ze, Anthony and Waring 1980) the Gulf of (NAFO Div. 5Y, Mike Fogarty, pers. comm., National Marine Fisheries Service, Woods Hole, Mass. USA), the Thames estuary (Woods 1981), and the Celtic sea (Heath and Richardson 1989). Abundance of juvenile fish was estimated either from random stratified field sampling or by sequential population analysis (SPA). The latter includes such techniques as virtual population analysis (Gulland 1965), cohort analysis (Pope 1972), and related methods which reconstruct population size from fishery catch data which has been sampled to determine the age composition. Indices of abundance of juvenile fish from field sampling were calculated using more than one age. An index for a given population was constructed by averaging two or more ages of the same cohort after the data had been standardized by subtracting the mean and dividing by the standard deviation, calculated over some common time period. The common mean was then added to the standardized series. See Myers et al. (1990) for details.

Abundance data were compiled directly from analysis conducted by the National Marine Fisheries Service (USA) laboratory at Woods Hole, the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC), the Northwest Atlantic Fisheries Organization (NAFO), the International Council for the Exploration of the Seas (ICES), and the Marine Research Institute, Iceland. The documents used to obtain the data are given in Myers et al. (1990).

The 53 populations studied are thought to be separate populations that are largely reproductively isolated, or consist of several subpopulations whose population ranges mutually overlap because of feeding migrations. In particular, herring from the North Sea, the Gulf of St. Lawrence (NAFO Div. 4TVa), and cod from northern Newfoundland (NAFO Div. 2J3KL) are thought to have several discrete spawning sites within each of the "populations" area. The separation of the populations has been extensively investigated by a variety of methods, e.g. tagging and genetic analysis. The populations that are given here probably represent distinct populations with the exceptions noted above.

Problems with sampling at the proper spatial scale that have plagued previous work (McArdle et al. 1990) were eliminated here because the whole population was sampled using a random stratified design or the population history was reconstructed using commercial catch at age data.

The latitude of the spawning location for each population was assumed to determine the limits of the range of each species. The analysis was performed separately on each side of the Atlantic because of the very different oceanographic regimes on both sides of the Atlantic. Sources for the spawning locations for the western Atlantic populations are described in Myers and Drinkwater (1989). The spawning locations for the Eastern Atlantic populations were obtained from Anon (1981). Populations within the Baltic were not included in the analysis because of poor data and difficulties in interpreting whether the Baltic populations were at the edge of the species range.

## 2. METHODS

Estimates of the variability of marine populations is usually greater if longer records are used because the spectrum of population size is "red" (Steele 1985, Pimm and Redfern 1988, Myers et al. 1990). To minimize this problem we detrended the data. Most series are around 20 years in length.

The temporal variability in abundance of juvenile fish was calculated as the standard deviation of the detrended logarithmically (base 10) transformed data. That is, a linear regression of the logarithmically transformed abundance data against year was calculated; the standard deviation of the residuals were used as the estimate of variability. This standard deviation will be denoted by  $s$ . The standard deviation of the logarithmic transformed population abundance is a reliable measure of population variability, unless density is small, which is not the case for any of the populations studied here (McArdle et al. 1990). The use of a detrended time series removes much of variation in abundance of juvenile fish caused by the biomass of spawning adults.

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-detrended abundance of juvenile fish versus the latitude of the spawning location for each population. The hypothesis was tested using the quadratic regression  $s = \beta_0 + \beta_1 L + \beta_2 L^2$ . The hypothesis  $\beta_2 > 0$  was tested.

As a test of the robustness of our 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,  $\tau$ , with this absolute difference and the  $s$  was calculated. I tested the hypothesis that the sign of this correlation was positive, i.e.  $\tau > 0$ .

A further 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 (Pimm and Redfern 1988). The regression equation was  $s = \beta_0 + \beta_1 n + \beta_2 L + \beta_3 L^2$  and the hypothesis tested was  $\beta_3 > 0$ .

The analyses is applied separately for each species using data separately from each side of the Atlantic. Although the significance levels for each regression and rank correlation analysis are given, we are more concerned with the general hypothesis and thus have combined probabilities from each test of significance (Fisher, 1954, 21.1). Fisher's method is based upon the fact that the logarithm of the probability of a significance test is distributed as  $-\frac{1}{2}\chi^2_{[2]}$ , and the reproductive properties of the  $\chi^2$  distribution. This allows the results of one sided significance tests to be combined, and the results tested using a  $\chi^2$  distribution.

### 3. RESULTS

Abundance of juvenile fish appears to be more variable at the edges of the range for cod and haddock from both sides of the Atlantic, and for herring from the eastern Atlantic (Fig. 2). When the significance tests are combined (Table 2) the overall results provide strong evidence for the hypothesis that the populations on the Northern and Southern ends of their range are more variable.

The clearest support for the hypothesis comes for haddock for the North-western Atlantic. The high variability in abundance of juvenile fish for the northern population, 3Ps and 3NO, were confirmed by two independent field surveys (Myers et al. 1990). Similarly the population at the southern limit of the range, 5Z, shows a high degree of variability in sequential population analysis based upon commercial catch data and random stratified field sampling.

### DISCUSSION

The question of whether the variability of juvenile abundance is greater at the northern and southern limits of their range can be tentatively answered, at least for three species. The analysis here suggests strongly that they are; many other factors are probably important as well.

There are few terrestrial studies available for comparison because of the difficulty of monitoring population abundance throughout a species range over a large number of years. Baltensweiler (1968) found that outbreaks of Larch tortrix moth was more intense at the higher latitude limits of its range in the Alps. There are exceptions to the general trend. Cod from NAFO Div. 2J3KL had very low variability. The "population" actually consists of several subpopulations which are managed as one. Thus, the relatively low variability in abundance of juvenile fish for this population may be the result of averaging of several populations.

Herring from the western Atlantic did not appear more variable at the southern limit of their range. However, this may be an artifact. The Georges Bank (NAFO Div. 5Z) herring population, which is at the southern limit of the range became commercially extinct after the last data used in this analysis. The herring estimates are derived population reconstructions based upon commercial catch at age data. If the commercial fishery disappeared because of very poor survival of juvenile fish to the extent that the commercial fishery disappeared, then the estimate of variability of abundance of juvenile fish for this region may be negatively biased. Thus, it is possible that Georges Bank herring may in fact be much more variable than estimated here, and herring from the western Atlantic may conform to the general trend.

Are there alternative explanations for the observations? One possibility is that the error in estimating abundance of juvenile fish could be greater in populations at the margins of a species range; this would increase the apparent variability. This is not likely to be a general explanation. In some cases, e.g. haddock from the western Atlantic, the differences in variability is much greater than can be explained by simple measurement error. Moreover, the estimated  $s$  for two of these populations, 3Ps and 3NO haddock, was very similar during two different survey periods and methods (Myers et al. 1990). It may be that some of the small marginal populations, e.g. Thames estuary herring, may not be adequately assessed and may contain relatively high measurement error. It is perhaps more likely that the variability in marginal populations are underestimated because they are more likely to become commercially extinct, and thus the variability will be underestimated, e.g. Georges Bank (5Z) herring. Similarly, the herring population in the English channel, which is at the southern edge of the range, appears to present in commercial quantities in some years and not in others. If this pattern is general, then the variability at the margins of a species range may be underestimated here.

The results for any one of the above analyses are not strongly convincing. However, when the significance tests are combined (Table 2) the overall results provide strong evidence for the hypothesis. The result does not depend upon the inclusion of any one population, and appears to be robust and not dependent on the methods used in the analysis.

#### ACKNOWLEDGMENTS

This paper grew out of discussions with Keith Thompson and Ray Beverton. I thank M. Forgary, M. R. Heath, and the authors of assessment documents on which our analysis depends.

#### REFERENCES

- Anon. (1981). Atlas of the seas around the British Isles. Ministry of Agriculture, Fisheries and Food. U.K.
- Anthony, V.C. and G. Waring (1980). The assessment and management of the Georges Bank herring fishery. Rapp. P.-v. Réun. cons. int. Explor. Mer, 177:72-111.
- Baltensweiler, W. (1968). The cyclic population dynamics of the grey larch tortrix, *Zeiraphera priskeama* Hubner (= *Scemasia diniana* Guerne) (Lepidoptera: Tortricidae). Pages 88-97 in T. R. L. Southwood, ed. Insect abundance. Symp. R. Entomol. Soc. Lond. no. 4.
- Connell, J. F. and Sousa, W. P. (1983). On the evidence needed to judge ecological stability or persistence. American Naturalist 121, 789-824.
- Cook, R. M. and Armstrong, D. W. (1986). Stock-related effects in the recruitment of North Sea haddock and whiting. J. Cons. int. Explor. Mer 42, 272-280.
- Coulson, J.C. and J.B. Whittaker. (1978). Ecology of moorland animals. In *Ecological Studies 97. Production Ecology of British Moors and Montane Grasslands* (ed. O.W. Heal and D. F. Perkins), pp. 52-93. Springer-Verlag, Berlin.
- Fisher, R. A. (1954). Statistical Methods for Research Workers, 12th edition., Oliver and Boyd, Edingburgh. 356 pp.
- Garrod, D. J. (1983). On the variability of year-class strength. J. Cons. int. Explor. Mer, 41: 63-66.
- Gaston, K. J. (1988). Patterns in the local and regional dynamics of moth populations. Oikos, 53, 49-59.
- Gaston, K. J. (1990). Patterns in the geographical ranges of species. Biol. Rev. 65:105-129.
- Gaston, K. J. and Lawton, J. H. (1988). Patterns in the distribution and abundance of insect populations. Nature, London, 331, 709-712.
- Gaston, K. J. and Lawton, J. H. (1989). Patterns in body size, population dynamics and regional distribution of bracken herbivores. American Naturalist, in press.
- Gilbert, N. (1980). Comparative dynamics of a single-host aphid. I. The evidence. Journal of Animal Ecology. 49: 351-369.
- Grant, M.C. & Antonovics, J. (1978). Biology of ecologically marginal populations of *Anthoxanthum odoratum*. I. Phenetics and dynamics. Evolution 32: 822-838.
- Gulland, J.A. 1965. Estimation of mortality rates. Annex to Rep. Arctic Fish. Working Group, ICES C.M. 1965(3), 9 pp.
- Hassel, M. P., Southwood, T.R.E., & Reader, P. M. (1987). The dynamics of the viburnum whitefly (*Aleurotrachelus jelinekii*): a case study of population regulation. Journal of Animal Ecology 56: 283-300.
- Heath, M. and K. Richardson. (1989). Comparative study of early-life survival variability of herring, *Clupea harengus*, in the north-eastern Atlantic. J. Fish Biol. 35 (Supplement A), 49-57.
- Huffaker, B.B. and P. S. Messenger. (1964). The concept and significance of natural control. In Biological Control of Insects Pests and Weeds (ed. P. De Bach), pp. 74-117. Chapman and Hall, London.
- Myers, R. A., W. Blanchard, and K.R. Thompson. 1990. Summary of North Atlantic Fish Recruitment 1942-1987. Canadian Technical Report of Fisheries and Aquatic Sciences 1743: iii + 108p.
- Myers, R. A. and K. Drinkwater. 1989. The influence of Gulf Stream warm core rings on recruitment of fish in the Northwest Atlantic. J. Mar. Res., 47, 635-656.
- Myers, R. A. and K. Drinkwater. 1988. Ekman transport and larval fish survival. Biol. Oceanography 6:45-64.
- Ostfield, R. S. (1988). Fluctuations and constancy in populations of small rodents. American Naturalist, 131, 445-452.
- Pope, J. G. 1972. An investigation of the accuracy of virtual population analysis. ICNAF Res. Bull. 9, 65-74. Academic Press, Toronto.
- Pimm, S. L. and Redfern, A. (1988). The variability of population densities. Nature, London, 334, 613-614.

- Redfern, A. and Pimm, S. I. (1989). Population variability and polyphagy in herbivorous insect communities. *Ecological Monographs*, 58, 39-55.
- Rejmanek, M. and Spitzer, K. (1982). Bionomic strategies and long term fluctuations in abundance of Noctuidae (Lepidoptera). *Acta Entomologica Bohemoslovaca*, 79, 81-96.
- Richards, O.W. and T.R.E. Southwood. (1968). The abundance of insects: Introduction. In *Insect Abundance* (ed. T.R.E. Southwood), pp.1-7. Symposium of the Royal Entomological Society No. 4. Blackwell Scientific Publications, Oxford.
- Shepherd, J. G. (1982). A versatile new population and recruitment relationship for fishes and the construction of sustainable yield curves. *J. Cons. int. Explor. Mer* 40, 67-75.
- Spitzer, K. and Leps, J. (1988). Determinants of temporal variation in moth abundance. *Oikos*, 53, 31-36.
- Steele, J. H. (1985). A comparison of terrestrial and marine ecological systems. *Nature* 313:355-358.
- Thompson, A. B. and Hilden M. 1987. Relationship between March sea temperature and year-class strength for selected North Sea and west of Scotland fish populations, 1960-84. ICES C.M. 1987/G:49.
- Williamson, M. H. (1984). The measurement of population variability. *Ecological Entomology*, 9, 239-241.
- Williamson, M. H. (1987). Are communities ever stable? Colonisation, Succession and Stability (Ed. by A. J. Gray, M. J. Crawley, and P. J. Edwards), pp. 352-371.
- Winters, G. and J. P. Wheeler. (1987). Recruitment dynamics of spring-spawning herring in the northwest Atlantic. *Can. J. of Fish. Aquat. Sci.* 44:882-900.
- Wolda, H. (1978). Fluctuations in abundance of tropical insects. *American Naturalist*, 112, 1017-1045.
- Wolda, H. (1983a). "Long-term" stability of tropical insect populations. *Researches in Population Ecology*, Supplement No. 3, 112-126.
- Wood, R. J. (1981). The Thames estuary herring population. *Fish. Res. Tech. Rep. MAFF Direct. Fish. Res., Lowestoft* 64, 21 pp.

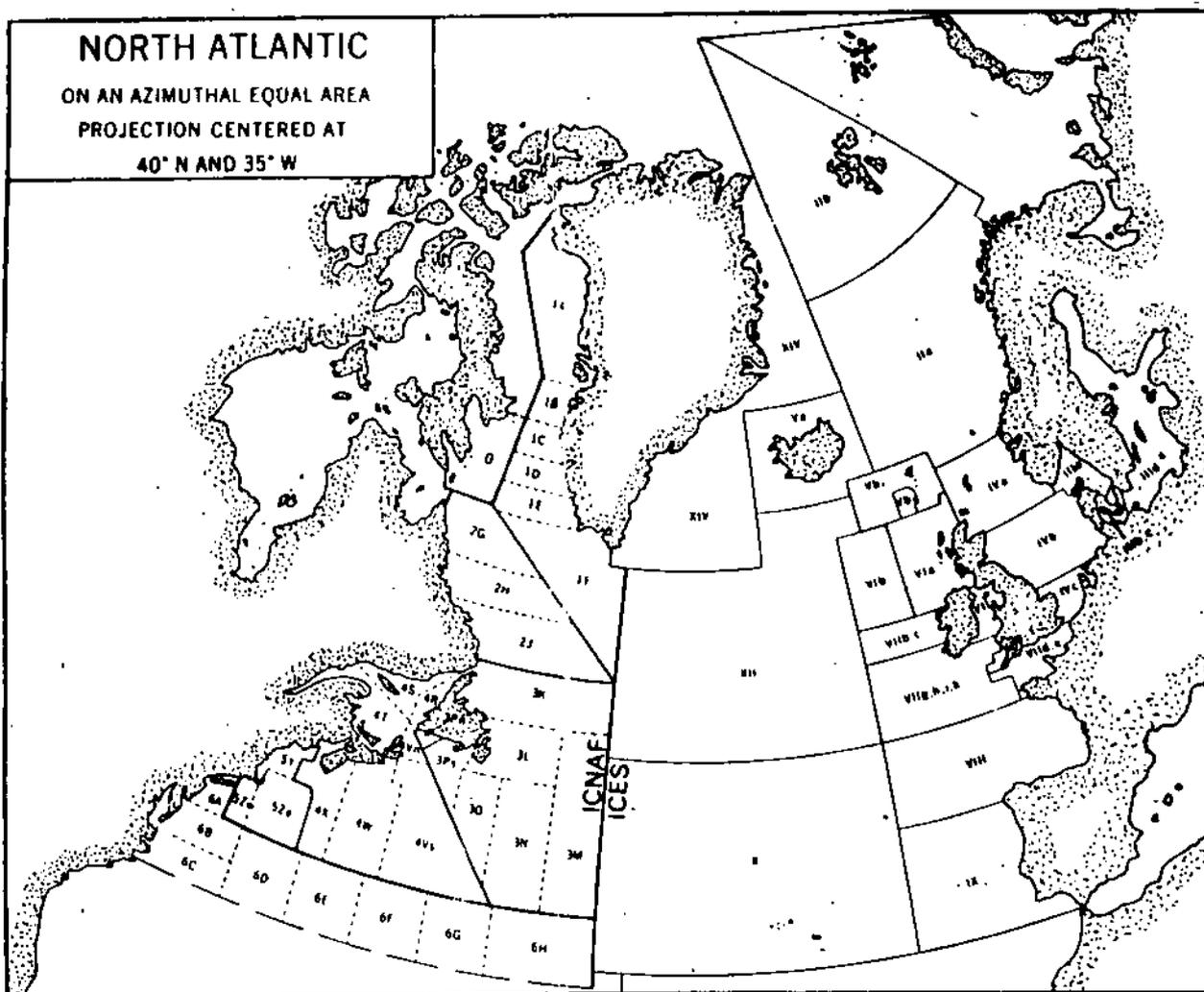
Table 1. Data on recruitment variability, as measured by the standard deviation of detrended log. transformed recruitment. Populations are designated NAFO boundaries, ICES boundaries or common names for the seas. Locations of the Newfoundland (Nfld) herring stocks can be found in Winters and Wheeler (1987). Herring populations that coexist within the same region are distinguished by the season they spawn.

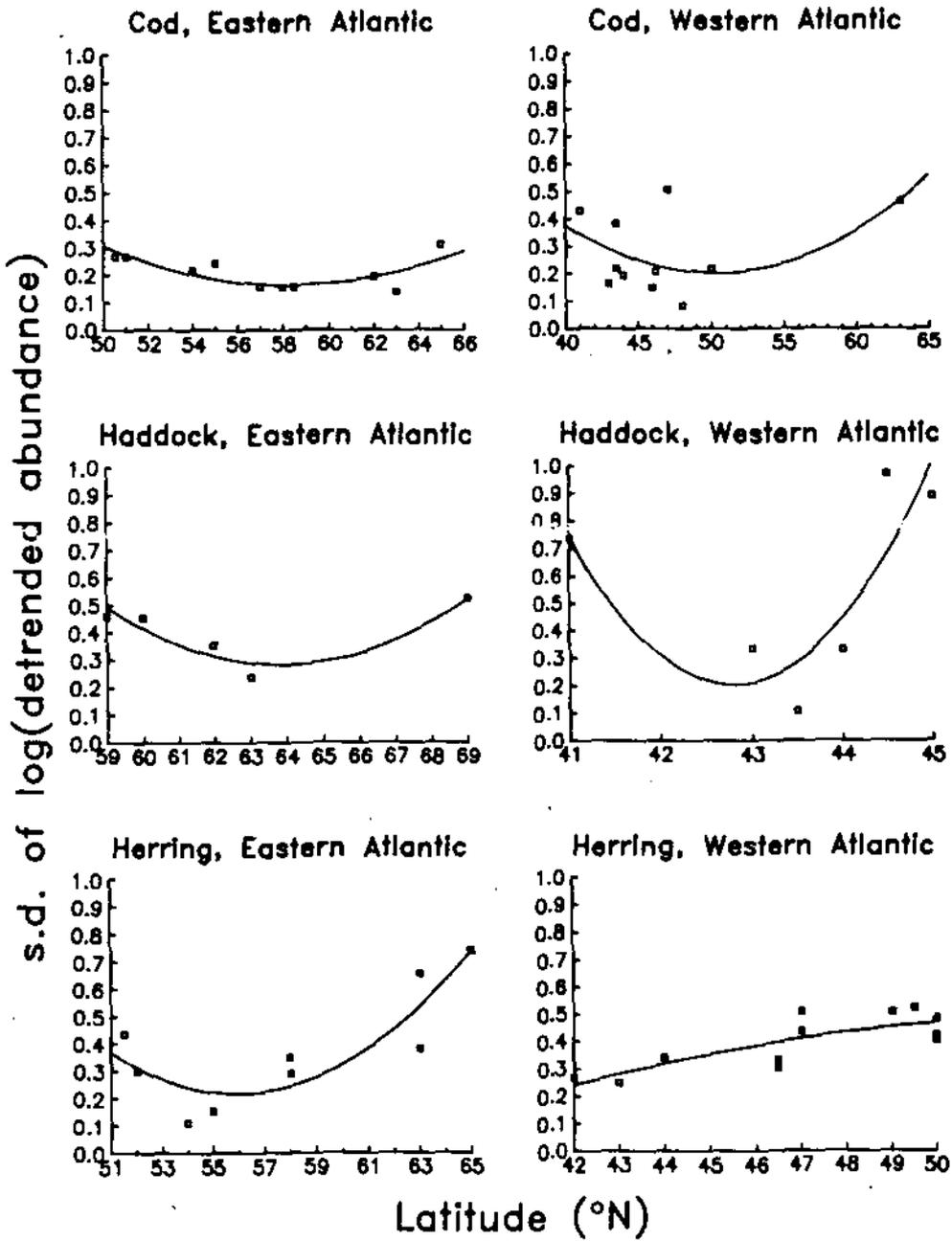
Population	S.D. of Recruitment	Latitude of spawning ( $^{\circ}N$ )	Number of Years
<b>Haddock, west Atlantic</b>			
5Z	.737	41	29
5Y	.108	43.5	25
4X	.336	43	25
4TVW	.332	44	39
3Ps	.89	45	23
3NO	.97	44.5	25
<b>Haddock, east Atlantic</b>			
North Sea	.456	60	27
Via	.459	59	19
Faroe	.352	62	23
Iceland	.239	63	25
North-east Arctic	.526	69	26
<b>Cod, west Atlantic</b>			
5Z	.433	41	24
5Y	.384	43.5	24
4X	.185	43	40
4VsW	.194	44	28
4TVn	.208	46.2	37
3Ps	.148	46	29
3NO	.22	43.5	29
3PaRS	.083	48	13
3M	.509	47	27
2J3KL	.219	50	27
1	.464	63	34
<b>Cod, east Atlantic</b>			
VIIId	.268	50.5	13
Celtic Sea	.269	51	15
Irish Sea	.218	54	16
North Sea	.245	55	26
Kattegat	.156	57	15
Skagerrak	.158	58	9
Via	.156	58.5	19
Faroes	.193	62	23
Iceland	.139	63	32
North-east Arctic	.312	65	27
<b>Herring, west Atlantic</b>			
5Z	.266	42	17
5Y	.250	43	22
4WX	.342	44	21
4T (spring)	.333	46.5	22
4T (fall)	.304	46.5	18
4R (spring)	.482	50	21
4R (fall)	.405	50	21
Nfld I	.436	47	14
Nfld GH	.509	47	14
Nfld EF	.506	49	14
Nfld CD	.523	49.5	14
Nfld AB	.425	50	14
<b>Herring, east Atlantic</b>			
Thames Estuary	.435	51.5	14
Celtic Sea	.299	52	16
sViaVII	.151	55	15
North Irish Sea	.110	54	19
North Sea	.35	58	41
nVia	.292	58	18
Iceland (spring)	.657	63	23
Iceland (summer)	.380	63	40
Norway	.741	65	37

Table 2

Tests of the hypothesis. The parametric tests are the quadratic term in a regression of  $s$ , the s.d. of the detrended logarithmically transformed juvenile abundance, versus latitude. The parameter  $\beta_3$  includes the number of years used to estimate  $s$  as a covariate in the regression, while  $\beta_2$  does not. The nonparametric test is described in the text.

	Number of Populations	Nonparametric Tests	Parametric Tests	
		$P(\tau \leq 0)$	$P(\beta_2 \leq 0)$	$P(\beta_3 \leq 0)$
Haddock, E. Atlantic	5	.025	.037	.11
Haddock, W. Atlantic	6	.086	.031	.071
Cod, E. Atlantic	10	.029	.076	.016
Cod, W. Atlantic	11	.068	.086	.095
Herring, E. Atlantic	9	.046	.018	.03
Herring, W. Atlantic	12	.93	.718	.77
Combined Probabilities	-	0.003	0.001	0.003





2. The standard deviation of the detrended logarithmically transformed juvenile abundance ( $s$ ) versus the latitude of the spawning location. Also shown are the quadratic regression lines; significance levels are given in Table 2.