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Is fish recruitment related to spawner abundance?

by

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ABSTRACT

We analyze data on almost 200 populations to determine whether recruitment is related to spawner abundance. We pose three questions: (1) does the highest recruitment occur when spawner abundance is high? (2) does the lowest recruitment occur when spawner abundance is low? and (3) is the mean recruitment higher if spawner abundance is above the median rather than below? We find that when there is a sufficient range in spawner abundance the answer to all three questions is almost always yes. Thus, spawner abundance cannot be ignored in the management of fish populations.

Introduction

Perhaps the most fundamental question for the study and management of fish populations is the relationship between spawner abundance and the subsequent recruitment. There is surprisingly little consensus; many researchers believe that there is no relevant relationship (reviewed by Wooser and Bailey 1989, Fogarty et al. 1991) while others believe that is fundamental (e.g. Ricker 1954, Beverton and Holt 1957, Cushing 1971). The assumed absence of a relationship between spawner abundance and recruitment has prompted some scientists to claim that recruitment overfishing is almost impossible (Laevastu 1993). This divergence of opinion has practical consequences for the management of fisheries, many fisheries are managed without consideration of maintaining spawners (Smith et al. 1993).

The purpose of this paper is to provide conclusive evidence that strong year classes are more likely when spawner abundance is large. We use the simplest possible nonparametric methods in order to avoid the many subtle, statistical difficulties in fitting spawner-recruitment functions (Walters 1985, 1990, Hilborn and Walters 1992). Our approach is to systematically examine almost 200 data sets. By analyzing many populations using identical methods it is possible to arrive at conclusions with greater reliability. As part of an ongoing study of recruitment variability, we have compiled, with coworkers, over 200 spawner-recruitment time series (Myers et al. 1994). This will form the basis of the analysis.

The nonparametric methods we use were devised in order to answer three deliberately simple questions. First, does the largest recruitment occur when the spawner abundance is high? To answer this question, we examine the rank of spawner abundance associated with the largest recruitment. Taking the opposite tack, our second question is: does the smallest recruitment occur when spawner abundance is low? This time we examine the rank of spawner abundance associated with the smallest recruitment. Finally, we ask: is the mean recruitment higher if spawner abundance is above the median rather than below? To answer this question, we examine the ratio of mean recruitment when spawner abundance is above the median to mean recruitment when spawner abundance is below.

Terminology and Data

By "spawner abundance" we mean any of the following: spawning stock biomass, the number of spawners, the number of eggs, or some index of spawner abundance (derived from CPUE or research vessels). We deliberately avoid using the word "stock" in this context (as in "stock-recruitment") because it is also used in fisheries to mean "distinct biological population" or "management units " (as in "the Georges Bank herring stock").

We have tried to assemble all time series of reliable data on spawner abundance and recruitment. The populations for which data were obtained are listed in Table 1. Several criteria were applied in selecting data sets to include in the analysis. First, we attempted to use estimates that covered the complete range of the population. Unfortunately, this is not always possible. Second, we used only data in which aging was reliable. In some species (e.g. tuna and swordfish), aging can only be undertaken via length-based methods. We have used such data in only a few cases.

For each population, Table 1 lists the method used to estimate spawner abundance and recruitment. For most marine populations, spawning biomass and recruitment have been estimated by sequential population analysis (SPA) of commercial catch at age data. SPA techniques include virtual population analysis (VPA; Gulland 1965), cohort analysis (Pope 1972), and related methods which reconstruct population size from catch at age data (Deriso et al. 1985, 1989, Megrey 1989, Gavaris 1988). For some marine populations, accurate commercial catch-at-age data are not available, and research vessel (RV) surveys estimates are used. For a few populations, both types of data are used, e.g. spawning stock biomass is estimated from SPA and recruitment is estimated from research vessel surveys. We have not included populations for which there is only commercial catch per unit effort estimates of abundance.

For most of the Pacific salmonids populations, the numbers of spawners and recruitment are reconstructed from commercial catch-at-age data and independent estimates of fishing mortality and/or an independent estimate of escapement from surveys of spawning. In these cases, the method is termed "stock reconstruction", and is denoted as SR in Table 1. Some of the estimates are from experiments in which the number of spawners and recruitment, e.g. number of parr produced, are direct counts.

We analyzed data by families and species separately if there were at least 6 populations per taxa.

The population boundaries in the North Atlantic generally follow those of the Northwest Atlantic Fisheries Organization (NAFO) or the International Council for the Exploration of the Sea (ICES) (Fig. 1). We sometimes refer to a region by an alternative name (e.g. the North Sea), if it commonly applies to the population in practice, or if the NAFO or ICES regions do not adequately describe current population boundaries. For populations outside the North Atlantic we have used the population boundaries accepted by the management and assessment organizations.

In the North Atlantic, data were taken from assessments from 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.

In several cases, e.g. Iceland capelin, alternative series have been included in the analysis. Similarly, there are different possible definitions of a population or management population. We have included a few cases where one "population" may be included as a subpopulation in another analysis. This only occurred for several herring (*Clupea harengus*) and sockeye salmon (*Oncorhynchus gorbuscha*) populations.

Does the largest recruitment occur when spawner abundance is high?

Methods

For each spawner-recruitment series we ask whether the largest recruitment, $R_{\max}$, occurred when spawner abundance was high. We computed the rank, rank($S_{R_{\max}}$), of the spawner abundance that gave rise to the largest recruitment, $S_{R_{\max}}$. In order to compare ranks across populations, we computed a "relative rank" $r_{\max} = (\text{rank}(S_{R_{\max}}) - 1)/(n-1)$, where n is the number of observations in the spawner-recruitment series (Fig. 2A). The relative rank therefore lies between 0 and 1, with $r_{\max} = 0$ implying that the largest recruitment occurs for the smallest spawner abundance, and conversely $r_{\max} = 1$ implying that the largest recruitment occurs for the largest spawner abundance.

In evaluating the relationship between spawners and recruitment, the range of the spawner data will clearly be important. For near constant spawner levels, changes in recruitment will reflect only variability in density-independent mortality. As an index of the range spanned by the spawner data, we use the ratio $S_{\max}/S_{\min}$, where $S_{\max}$ is the maximum observed spawner abundance and $S_{\min}$ is the minimum observed spawner abundance. When this ratio is near 1, the spawner level is nearly constant; the larger its value, the greater the range of spawner data. Values of $S_{\max}/S_{\min}$ for the data series examined in this paper are listed in Table 1.

To help summarize the data, curves representing cumulative weighted means are superimposed on the plots in each figure. The weighted mean of k relative ranks r_i, for $i = 1, \cdots, k$, is

$$\frac{\sum_{i=1}^{k} n_i r_i}{\sum_{i=1}^{k} n_i}, \tag{1}$$

where n_i is the number of observations in the i^{th} spawner-recruitment series. The cumulative weighted mean was calculated starting with the relative ranks associated with the the largest value of $S_{\max}/S_{\min}$ and continuing through the relative rank associated with the smallest value of $S_{\max}/S_{\min}$. Thus, in the figures, the cumulative weighted mean begins on the right-hand side and accumulates to the left-hand side. Consequently, the value of the cumulative weighted mean on the extreme left-hand side encompasses all the data shown in the plot. Using the sample size as a weighting factor incorporates our greater confidence in the relative ranks obtained from long time series. Similarly, we accumulate from the right-hand side because we have greater confidence in the relative ranks obtained from time series having wide ranges of spawner abundance.

If spawner abundance and largest recruitment are independent, then we would expect a distribution of relative ranks with a median of 0.5. A distribution-free test of this null hypothesis is the one-sample Wilcoxon signed rank test (Conover 1980). We first subtract 0.5 from each relative rank and then compute the ranks of the absolute values of the differences. The sign of each difference is assigned to the corresponding rank. The test statistic is given by the sum of the positive ranks. Our alternative hypothesis is that the median of the distribution of relative ranks is greater than 0.5. For this one-sided test, in order to reject the null hypothesis (at the 5% significance level), we require at least 5 relative ranks. Note that when there are ties in the absolute values of the differences, an exact probability for the test cannot be computed. In these cases, the normal approximation given by Lehmann (1975) is used. Also when the number of observations exceeds 25 or there are differences equal to zero, normal approximations are used. The above procedure gives a probability level for each observation. We will report the results for a selection of ranges of spawner abundance, S_{max}/S_{min}.

In the analysis, we have used data series with at least 10 pairs of observations; however, in the table we report the results for all populations with at least 5 pairs of observations.

Results

For each family, the largest recruitment tends to occur when spawner abundance is large (Fig. 3, Table 1). The cumulative weighted means never fall below 0.5 for any family. The Wilcoxon signed rank test (Table 2A) shows that the null hypothesis that the median of the distribution of the relative ranks is 0.5 can be rejected for all stocks combined and for the Salmonidae, the Clupeidae, and the Gadidae. Although, the results are generally not statistically significant for the Pleuronectidae and Merlucciidae, the tests show that the results are consistent with the hypothesis that the largest recruitment is produced from the larger quantities of spawners (Fig. 3).

At the species level, similar results are observed. In all species analyzed, i.e. those with at least 6 observations, the largest recruitment tends to occur if spawner abundance is large (Fig. 4, Table 1). For those species with relatively small variation in the range of spawners, i.e. plaice (*Hippoglossoides platessoides*), sole (*Solea vulgaris*), and pollock (*Pollachius virens*), the effect is less. Even in these cases, the cumulative weighted mean rank of the spawners that gave rise to the largest recruitment is greater than 0.5. The p-values for the signed rank are usually significant at the 0.05 level, and they are always less than 0.5, as is consistent with our hypothesis (Table 2A). Given the small number of populations it is not unexpected that the significance test is not always less than 0.05. The consistency of the results is very strong evidence for the hypothesis.

There is scatter in the relative ranks in Fig. 3 an 4, but this is to be expected. The important point is that the relative ranks are almost always above 0.5 if the range of the qunatity of spawners is large.

Does the smallest recruitment occur when spawner abundance is low?

Methods

Next, we examined r_{min}, the relative rank of spawner abundance for the *smallest* recruitment (Fig 2A). This time, $r_{min} = 0$ implies that the smallest recruitment occurs for the smallest spawner abundance, while $r_{min} = 1$ implies that the smallest recruitment occurs for the largest spawner abundance. We duplicated the methods described above.

Results

The lowest recruitment tends to occur when spawner abundance is low. Again, the pattern holds for all families, although it is clearly weaker for the Pleuronectidae and the Merlucciidae (Fig. 5). A similar pattern is repeated on a species level except for sole (Fig. 6).

The effect for the smallest recruitment appears to be less than the effect for largest recruitment. The statistical significance of the results is usually less than 0.05, but there is a tendency for the significance to be reduced if the range of spawners is small (Table 2B).

Is recruitment greater if spawner abundance is above the median than below?

Methods

For each spawner-recruitment series we ask whether the mean recruitment is the same when the spawner abundance is below or above the median. We split each spawner-recruitment series into two sections: the first section at or below the median spawner abundance, and the second section above the median spawner abundance. We then compute the mean recruitment for each section.

Let $\bar{R}_{\text{above}}$ be the mean recruitment above the median spawner abundance, and let $\bar{R}_{\text{below}}$ be the mean recruitment at or below the median abundance of spawners (Fig 2B). The ratio $\bar{R}_{\text{above}}/\bar{R}_{\text{below}}$ equals 1 when the mean recruitment is identical on both sides of the median spawner abundance. This test is conservative because errors in the estimates of the range will bias the estimate of the slope downward (Judge et al. 1984, chapter 15).

Results

The ratio of the mean recruitment above the median level of spawners to that below, $\bar{R}_{\text{above}}/\bar{R}_{\text{below}}$, is greater than 1 for all families if the range of observed spawners is large (Fig. 7). For narrow ranges of spawner data the ratio $\bar{R}_{\text{above}}/\bar{R}_{\text{below}}$ is clustered near 1, while for wider ranges, the ratio increases well above 1. When the data are grouped taxonomically, the pattern holds. The Wilcoxon signed rank test (Table 2C) shows that the null hypothesis that the median of the distribution of $\bar{R}_{\text{above}}/\bar{R}_{\text{below}}$ is 1 can be rejected for all stocks combined, and for the Salmonidae, the Clupeidae, and the Gadidae.

At the species level, similar results are observed (Fig. 8). There are very few populations, of any species, for which the mean recruitment above the median level of spawners is not greater than the mean below, if the range of observed spawners is large (Fig. 8). Again, the effect is weaker for sole and pollock. The results are generally statistical significance at the 0.05 level (Table 2C).

Discussion

The hypothesis that there is no practical relationship between spawners and subsequent recruitment can be rejected: (1) strong year-classes are derived from high spawner quantities (Fig. 3 and 4), (2) weak year-classes are derived from low spawner quantities (Fig. 5 and 6), and (3) recruitment is on average higher above the median spawner abundance than below (Fig. 7 and 8). These conclusions hold for almost every species and family analyzed, i.e. those with more than 6 populations per taxa. In addition, the results explain the widely-held belief that spawner abundance and recruitment are not related. If there is little variation in spawner abundance, this may seem to be the case. However, wider ranges of spawner data show that they are indeed related. Sadly, many of the populations for which wide ranges of spawner data are available are those that have been fished to low levels, perhaps due, in part, to the rejection of spawner-recruitment relationships. Fish populations should be managed to maintain sufficient spawners to increase the probability of obtaining large recruitment.

Our results are robust. We have considered three different approaches to our general question, and in each case the results are consistent with the hypothesis that recruitment is indeed linked to abundance of spawners. Errors in estimation of spawner abundance should have the effect of reducing the significance of our tests (Judge et al. 1984, chapter 5). For example, for our third question, errors in estimating spawner abundance would result in misclassifying observations and would reduce the magnitude of $\bar{R}_{\text{above}}/\bar{R}_{\text{below}}$. A second, potential source of bias arises in the statistical analysis of spawner-recruitment relationships because the "independent" variable, spawners, is not independent of the interannual variation in the spawner-recruitment relationship: for a given spawning population, above-average recruitment tends to result in higher spawning populations, while below-average recruitment tends to result in lower spawning populations. This is called "time series bias", and causes the density-dependent mortality to be overestimated (Walters 1985, 1990). If this source of bias is important in our problem it will cause our conclusions to be conservative because the importance of density-dependent mortality will be overestimated, and thus recruitment would appear to be less positively related to spawners.

For the salmonids included in this analysis, large year classes almost always are associated with high spawner levels. Our conclusion differs from that of Larkin (1977), who stated for the Pacific salmon species of the genus *Oncorhynchus* that "recruitment is maximum at some intermediate stock size".

There are two species, plaice (*Hippoglossoides platessoides*) and pollock (*Pollachius virens* called saithe in Europe), in which the maximum recruitment may be close to the median observed spawner levels (Fig. 4). Such a relationship is consistent with overcompensation in recruitment, i.e. recruitment is maximum at some intermediate spawner abundance (Ricker 1954). This analysis is not powerful enough to address this question, but we will test this hypothesis in another paper. There are considerable technical problems in testing this hypothesis because of the problem of time series bias discussed above.

Some, who are not familiar with the fisheries literature, may consider our analysis unnecessary because the results seem obvious. However, the results are not obvious and are not consistent with many claims that have been based on much less extensive, and less systematic analysis. If a population is "managed" such that spawner abundance is reduced to low levels, then the manager should not be surprised to observe the smallest recruitment ever recorded.

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TABLE 1. Simple statistics for each population. **Population** lists the order, family, species, and location, n lists the number of common years of spawner-recruitment data, S_{max}/S_{min} lists the ratio of maximum quantity of spawners to minimum quantity of spawners, r_{max} lists the relative rank of the quantity of spawners for the maximum recruitment, r_{min} lists the relative rank of the quantity of spawners for the minimum recruitment, $\bar{R}_{above}/\bar{R}_{below}$ lists the ratio of mean recruitment above the median quantity of spawners to mean recruitment below the median quantity of spawners, and **Method** lists the stock assessment method used (SPA = Sequential Population Analysis, Count = Direct Count, RV = Research Vessel, SR = Stock Reconstruction).

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
Clupeiformes						
Clupeidae						
Alewife (*Alosa pseudoharengus*)						
Lake Ontario	7	7.4	0.50	0.00	0.3	RV
Gulf Menhaden (*Brevoortia patronus*)						
Gulf of Mexico	19	11.2	0.78	0.17	1.2	SPA
Atlantic Menhaden (*Brevoortia tyrannus*)						
U.S. Atlantic	35	39.8	0.79	0.32	1.5	SPA
Herring (*Clupea harengus*)						
Archipelago and Bothnian Seas	13	1.3	0.33	1.00	0.7	SPA
Baltic area 30	15	1.6	0.93	0.79	0.9	SPA
Baltic areas 22 and 24	19	2.8	0.39	0.94	0.8	SPA
Baltic areas 25-29, 32 plus Gulf of Riga	15	1.2	0.57	0.07	1.0	SPA
Baltic areas 28 and 29S	16	1.4	0.67	0.53	1.4	SPA
Bothnian Bay	15	1.7	0.93	0.29	1.8	SPA
Central Coast B.C.	38	16.4	0.78	0.16	1.0	SPA
Downs stock	65	470.5	0.84	0.02	5.5	SPA
Eastern Bering Sea	26	16.7	0.20	0.68	0.6	SPA
Georges Bank	15	9.9	0.50	0.14	1.2	SPA
Gulf of Finland	18	1.8	0.94	1.00	0.9	SPA
Gulf of Maine	23	6.6	0.09	0.95	0.8	SPA
Gulf of Riga	19	2.2	0.11	0.44	1.3	SPA
ICES VIa (north)	18	10.4	0.76	0.53	1.2	SPA
ICES VIa (south) and VIIb,c	19	2.5	0.78	1.00	0.8	SPA
Iceland (Spring spawners)	23	630.0	0.45	0.00	1.4	SPA
Iceland (Summer spawners)	43	37.3	0.98	0.10	2.4	SPA
NAFO 4R (Fall spawners)	13	4.7	0.33	0.67	0.2	SPA
NAFO 4R (Spring spawners)	13	6.0	0.33	0.75	0.3	SPA
NAFO 4T (Fall spawners)	9	9.1	0.62	0.38	1.2	SPA
NAFO 4WX	11	6.2	0.90	0.40	1.4	SPA
North Sea	41	76.1	0.68	0.15	1.7	SPA
North Strait of Georgia	38	22.4	0.65	0.27	1.4	SPA
North West Coast Vancouver Island	38	13.0	0.95	0.54	1.0	SPA
Northern Irish Sea	18	5.5	0.94	0.12	1.3	SPA
Norway (Spring spawners)	39	1074.9	0.97	0.21	7.3	SPA
Prince Rupert District	38	11.3	0.97	0.35	1.2	SPA
Queen Charlotte Islands	38	34.2	0.73	0.14	1.2	SPA
S.E. Alaska	30	6.0	0.03	0.52	1.2	SPA
South West Coast Vancouver Island	38	42.0	0.86	0.22	1.0	SPA
Southern Central Baltic	11	1.9	0.80	0.00	1.4	SPA
Southern Strait of Georgia	38	8.4	0.49	0.05	0.9	SPA

TABLE 1 (*continued*)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
Yellow Sea or Huanghai Sea	15	51.2	0.93	0.79	1.9	SPA
Spanish sardine (*Sardina pilchardus*)						
ICES VIIIc-IXa	14	5.7	0.96	0.46	0.9	SPA
Pacific sardine (*Sardinops caerulea*)						
California	31	134.4	0.87	0.00	6.4	SPA
Japanese sardine (*Sardinops melanostictus*)						
Japan-E.	14	6.4	0.15	0.77	0.6	SPA
Southern african pilchard (*Sardinops ocellatus*)						
South Africa	31	19.0	0.53	0.83	1.7	SPA
South Africa	8	69.2	0.00	1.00	0.8	SPA
Spanish sardine (*Sardinops sagax*)						
Chile- North zone	13	4.1	1.00	0.25	1.0	SPA
Sprat (*Sprattus sprattus*)						
Baltic Areas 22-32	15	5.6	0.93	0.43	0.7	SPA
Baltic Areas 26 and 28	19	19.7	0.11	0.50	1.7	SPA
Engraulidae						
Anchovy (*Engraulis capensis*)						
South Africa	18	3.5	0.00	0.53	1.3	SPA
Northern anchovy (*Engraulis mordax*)						
California	25	4.7	0.79	0.33	0.9	SPA
Peruvian anchoveta (*Engraulis ringens*)						
Northern/Central Stock Peru	19	18.4	0.61	0.00	2.2	SPA
Gadiformes						
Gadidae						
Pacific cod (*Gadus macrocephalus*)						
Eastern Bering Sea	10	5.8	0.33	0.22	0.8	SPA
Hecate Strait	14	2.9	0.62	0.15	1.5	SPA
Cod (*Gadus morhua*)						
3M	10	18.7	0.56	0.78	2.6	RV
Baltic Areas 22 and 24	20	2.8	0.74	0.00	1.8	SPA
Baltic Areas 25-32	19	3.5	0.44	0.22	1.0	SPA
Celtic Sea	20	3.8	0.89	0.58	2.4	SPA
Faroe Plateau	28	5.8	0.30	0.26	0.9	SPA
ICES VIId	12	4.3	0.73	0.18	1.4	SPA
ICES VIa	23	2.7	0.00	1.00	0.7	SPA
Iceland	38	7.3	0.49	0.08	1.2	SPA
Irish Sea	22	1.8	0.05	1.00	0.7	SPA
Kattegat	19	5.1	1.00	0.00	1.7	SPA
NAFO 1	31	55.7	0.83	0.30	2.3	SPA
NAFO 2J3KL	28	17.2	0.93	0.28	2.4	SPA
NAFO 3NO	28	9.0	0.63	0.48	1.8	SPA
NAFO 3Pn4RS	15	2.9	0.21	1.00	0.6	SPA
NAFO 3Ps	26	4.2	0.80	0.00	1.1	SPA
NAFO 4TVn	39	6.2	0.61	0.50	1.1	SPA
NAFO 4VsW	31	4.7	0.73	0.43	1.0	SPA
NAFO 4X	41	2.0	0.62	0.65	1.0	SPA
NAFO 5Y	7	1.8	0.17	0.50	0.6	SPA
NAFO 5Z	13	1.7	0.08	0.42	1.2	SPA
North East Arctic	38	9.7	0.57	0.38	1.7	SPA

TABLE 1 (*continued*)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
North Sea	27	3.7	1.00	0.19	1.0	SPA
Skaggerak	12	2.3	0.45	0.27	1.0	SPA
Haddock (*Melanogrammus aeglefinus)*						
Faroe Plateau	27	2.7	0.58	1.00	0.6	SPA
Iceland	28	8.6	0.48	0.52	0.8	SPA
NAFO 4TVW	38	23.2	0.84	0.32	2.9	SPA
NAFO 4X	24	3.7	0.91	0.00	1.2	SPA
NAFO 5Z	58	17.2	0.93	0.02	2.7	SPA
North East Arctic	39	14.8	0.89	0.13	1.9	SPA
North Sea	30	16.9	0.52	0.14	2.0	SPA
VIa	24	7.6	0.39	0.26	0.6	SPA
Whiting (*Merlangius merlangus)*						
Celtic Sea	7	2.2	1.00	0.00	1.3	SPA
ICES VIId	14	3.9	0.46	0.38	1.2	SPA
ICES VIa	25	4.0	0.50	0.23	0.9	SPA
Irish Sea	11	2.4	0.30	1.00	0.7	SPA
North Sea	26	2.7	0.32	0.60	0.8	SPA
Blue whiting (*Micromesistius poutassou)*						
Northern ICES	20	3.5	0.21	0.79	0.6	SPA
Southern ICES	10	1.2	1.00	0.72	1.1	SPA
Pollock or saithe (*Pollachius virens)*						
Faroe	28	2.5	0.56	0.93	0.8	SPA
ICES VI	20	3.2	0.39	0.79	0.8	SPA
Iceland	26	4.1	0.56	0.26	1.0	SPA
NAFO 4VWX5	10	1.7	0.78	0.33	1.5	SPA
North East Arctic	21	5.9	0.75	0.35	1.4	SPA
North Sea	21	6.1	0.95	0.10	1.1	SPA
Walleye pollock (*Theragra chalcogramma)*						
E. Bering Sea	24	5.9	0.26	0.83	0.8	SPA
East Kamchatka	12	24.0	1.00	0.27	2.0	SPA
East Kamchatka	12	24.0	1.00	0.27	2.0	SPA
Gulf of Alaska	21	3.1	0.15	0.80	0.4	SPA
Japan-Pacific coast of Hokkaido	15	3.8	0.29	0.43	0.9	SPA
Norway pout (*Trisopterus esmarkii)*						
North Sea	12	4.3	0.45	0.27	1.2	SPA
Merlucciidae						
Silver hake (*Merluccius bilinearis)*						
Mid Atlantic Bight	33	27.1	0.88	0.31	2.9	SPA
NAFO 4VWX	13	2.0	0.67	0.75	1.2	SPA
NAFO 5Ze	33	25.3	0.78	0.28	5.1	SPA
S.A. Hake (*Merluccius capensis)*						
South Africa 1.6	20	5.6	0.74	0.58	1.1	SPA
South Africa South Coast	12	1.5	0.64	1.00	1.0	SPA
Common hake (*Merluccius gayi)*						
Chile - South Central zone	14	1.7	0.15	1.00	0.8	SPA
Chile- Females in Northern zone	14	2.4	0.85	0.54	1.3	SPA
Peruvian hake (*Merluccius gayi peruanus)*						
Peru	8	3.0	0.43	1.00	0.6	SPA
Hake (*Merluccius merluccius)*						
ICES IVa,VIa,VII,VIIIa and VIIIb	13	2.4	0.04	0.50	1.0	SPA

TABLE 1 (*continued*)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
ICES VIIIc and IXa	8	1.8	0.71	0.14	1.2	SPA
Pacific hake (*Merluccius productus*)						
W. US. + Canada	30	2.6	0.00	0.10	0.8	SPA
Phycidae						
Red hake (*Urophysics chuss*)						
NAFO Gulf of Maine, N. Georges Bank	13	8.6	0.50	0.17	1.4	SPA
NAFO S. New England	15	5.7	0.64	0.07	2.6	SPA
White hake (*Urophysics tenuis*)						
NAFO 4T	14	2.7	0.08	0.38	0.7	SPA
Perciformes						
Ammodytidae						
Sandeel (*Ammodytes marinus*)						
ICES VIa	10	8.5	0.44	0.78	0.8	SPA
Northern North Sea	14	7.1	0.08	0.23	0.7	SPA
Shetland	16	4.4	0.93	0.47	1.3	SPA
Southern North Sea	14	6.1	0.77	1.00	1.6	SPA
Carangidae						
Cape horse mackerel (*Trachurus capensis*)						
South Africa 1.3-1.5	17	3.9	0.31	0.94	0.5	SPA
Horse mackerel (*Trachurus trachurus*)						
Western ICES	8	4.3	0.14	0.00	0.2	SPA
Lutjanidae						
Silk Snapper (*Lutjanus synagris*)						
Zone B - Cuba	17	2.8	0.44	0.38	1.0	SPA
Mugilidae						
Grey mullet (*Mugil cephalus*)						
Taiwan	7	2.3	1.00	0.17	1.3	SPA
Scombridae						
Pacific mackerel (*Scomber japonicus*)						
Southern California	36	64.1	0.89	0.23	2.5	SPA
Mackerel (*Scomber scombrus*)						
NAFO 2 to 6	28	10.7	0.30	0.44	1.1	SPA
Western ICES	19	1.9	0.56	0.50	1.0	SPA
Southern bluefin tuna (*Thunnus maccoyii*)						
Pacific	26	4.2	0.64	0.04	1.2	SPA
Pleuronectiformes						
Paralichthydae						
Summer flounder (*Paralichthys dentatus*)						
Middle Atlantic Bight	9	3.1	1.00	0.12	1.8	SPA
Pleuronectidae						
American plaice (*Hippoglossoides platessoides*)						
NAFO 3LNO	19	4.0	0.72	0.28	1.3	SPA
NAFO 5YZ	11	6.3	0.00	0.70	0.6	SPA
Pacific halibut (*Hippoglossus stenolepis*)						
Pacific	47	2.8	0.39	0.46	0.9	SPA
Yellowfin sole (*Limanda aspera*)						
E. Bering Sea	12	1.9	0.91	0.45	1.3	SPA
Yellowtail flounder (*Limanda ferruginae*)						
NAFO 3LNO	15	3.1	0.50	0.00	1.0	SPA

TABLE 1 (*continued*)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
NAFO 5Z	20	11.8	0.95	0.21	2.7	SPA
Southern New England	20	16.7	0.63	0.00	1.1	SPA
Plaice (*Pleuronectes platessa*)						
Celtic Sea	10	2.4	1.00	0.33	1.4	SPA
ICES VIId	10	6.6	0.56	0.00	1.6	SPA
ICES VIIe	16	3.2	0.73	0.07	1.8	SPA
Irish Sea	26	3.3	0.00	0.20	0.9	SPA
Kattegat	22	10.7	0.67	0.14	2.4	SPA
North Sea	33	1.8	0.47	0.66	0.8	SPA
Skagerrak	10	2.2	0.56	0.44	0.9	SPA
Greenland halibut (*Reinhardtius hippoglossoides*)						
ICES V and XIV	10	1.8	0.44	0.56	0.8	SPA
North East Arctic	9	1.3	1.00	0.62	1.0	SPA
Soleidae						
Sole (*Solea vulgaris*)						
Celtic Sea	18	2.1	0.24	0.88	0.8	SPA
ICES IIIa	5	2.2	1.00	0.50	1.4	SPA
ICES VIII	10	1.7	0.89	0.44	1.1	SPA
ICES VIId	19	5.4	0.83	1.00	1.1	SPA
ICES VIIe	22	2.6	1.00	0.10	1.4	SPA
Irish Sea	20	2.8	0.00	0.63	0.5	SPA
North Sea	34	6.0	0.97	0.24	1.1	SPA
Salmoniformes						
Esociadae						
Pike (*Esox lucius*)						
North Basin, Windermere Lake	35	7.3	0.74	0.13	1.6	SPA
South Basin, Windermere Lake	35	5.8	0.57	0.07	1.5	SPA
Osmeridae						
Capelin (*Mallotus villosus*)						
Iceland	12	5.2	0.27	0.36	0.9	SPA
Iceland	14	5.2	0.00	0.08	0.8	RV
Salmonidae						
Pink salmon (*Oncorhynchus gorbuscha*)						
Central Alaska	25	310.0	0.75	0.17	2.9	SR
Central B.C., Canada	14	4.1	0.77	0.69	1.1	SR
Fraser River, B.C., Canada	16	6.0	0.93	0.00	1.8	SR
Hooknose Creek, B.C., Canada	14	35.8	0.85	0.69	4.1	Count
Prince William Sound, Alaska	15	6.3	0.64	0.00	2.2	SR
Sashin Creek, Little Port Walter, Alaska	25	11084.8	0.83	0.08	17.1	Count
Chum salmon (*Oncorhynchus keta*)						
Central Coast, B.C., Canada	30	4.8	1.00	0.24	1.5	SR
Fraser River, B.C., Canada	14	5.0	1.00	0.00	2.0	SR
Hooknose Creek, B.C., Canada	14	15.4	0.92	0.00	2.5	Count
Johnstone Strait	28	4.7	0.89	0.63	2.0	SR
Minter Creek, Washington	14	352.5	1.00	0.08	4.2	Count
North Coast, B.C., Canada	30	4.6	0.48	0.24	1.0	SR
Queen Charlotte Islands, B.C., Canada	25	11.0	0.21	0.04	1.0	SR
West Coast Vancouver Island, B.C., Canada	25	6.0	0.83	0.21	1.6	SR
Coho salmon (*Oncorhynchus kisutch*)						
Minter Creek, Washington	10	14.2	0.39	0.00	1.1	Count

TABLE 1 (*continued*)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
Sockeye salmon (*Oncorhynchus nerka)*						
Adams Complex,B.C., Canada	38	6995.1	0.95	0.00	153.5	SR
Birkenhead River, B.C., Canada	37	8.2	1.00	0.00	1.4	SR
Bristol Bay, Alaska	18	5.0	0.76	0.24	1.4	SR
Chilko River, B.C., Canada	38	57.7	0.86	0.11	3.3	SR
Columbia River, Washington	19	126.3	0.50	0.00	1.2	SR
Early Stuart Complex, B.C., Canada	38	383.0	0.78	0.00	4.6	SR
Egegik, Alaska	32	8.3	0.95	0.13	2.0	SR
Horsefly River, B.C., Canada	38	22263.4	1.00	0.04	875.8	SR
Karluk River, Alaska	62	8.7	0.66	0.56	1.3	SR
Kvichak River, Alaska	25	107.2	0.92	0.08	8.1	SR
Naknek-Kvichak, Alaska	32	16.2	0.95	0.00	1.9	SR
Nushagak, Alaska	32	33.7	0.58	0.00	1.3	SR
Pinkut Creek, B.C., Canada	22	30.8	0.95	0.05	2.7	Count
Rivers Inlet, B.C., Canada	36	9.8	0.97	0.76	1.4	SR
Skeena River, B.C., Canada	39	16.0	0.87	0.03	1.4	SR
Stellako River, B.C., Canada	38	18.4	0.97	0.11	2.8	SR
Ugashik, Alaska	32	9.2	0.90	0.74	1.9	SR
Chinook salmon (*Oncorhynchus tshawytscha)*						
Wild Canadian Coastwide	26	2.1	0.28	0.88	0.9	SR
Scorpaeniformes						
Scorpaenidae						
Widow rockfish (*Sebastes entomelas)*						
W. U.S. + Canada	12	5.3	0.73	0.82	1.0	SPA
Redfish (*Sebastes marinus)*						
ICES V and XIV	10	2.9	0.22	0.67	0.2	RV, SPA
Redfish (*Sebastes mentella)*						
North East Arctic	9	3.5	1.00	0.38	1.8	SPA, RV
Redfish (*Sebastes sp.)*						
Iceland	7	1.4	1.00	0.50	1.2	SPA

TABLE 2. Observed levels of significance for one-sample Wilcoxon signed-rank tests based on the data shown in Figures 2 and 3 (Table 2A), Figures 4 and 5 (Table 2B), and Figures 6 and 7 (Table 2C). The tests were conducted using the data with $S_{max}/S_{min} \geq 1$, 2, 5, 10, 50, and 100. As this lower limit increases, the reliability of the data improves, however the number of samples (shown in parentheses) decreases, thereby decreasing the power of the test.

A. P-values (with associated sample sizes in parentheses) corresponding to Figures 2 and 3. The null hypothesis is that the median relative rank of the quantity of spawners for the largest recruitment is 0.5. The alternative hypothesis is that the median is greater than 0.5.

	S_{max}/S_{min}					
Group	≥ 1	≥ 2	≥ 5	≥ 10	≥ 50	≥ 100
All stocks	< 0.0001 (177)	< 0.0001 (158)	< 0.0001 (102)	< 0.0001 (53)	0.00025 (17)	0.0023 (12)
Pleuronectidae	0.14 (15)	0.17 (12)	0.31 (5)	0.12 (3)	. (0)	. (0)
Plaice	0.15 (7)	0.17 (6)	0.25 (2)	0.5 (1)	. (0)	. (0)
Salmonidae	< 0.0001 (34)	< 0.0001 (34)	< 0.0001 (29)	5e-04 (18)	0.0053 (9)	0.0084 (8)
Chum salmon	0.021 (8)	0.021 (8)	0.052 (5)	0.25 (3)	0.5 (1)	0.5 (1)
Pink salmon	0.016 (6)	0.016 (6)	0.031 (5)	0.12 (3)	0.25 (2)	0.25 (2)
Sockeye salmon	0.00012 (18)	0.00012 (18)	0.00012 (18)	0.0022 (11)	0.023 (6)	0.038 (5)
Merlucciidae	0.52 (9)	0.47 (7)	0.12 (3)	0.25 (2)	. (0)	. (0)
Clupeidae	0.0014 (41)	0.0085 (34)	0.0075 (29)	0.002 (19)	0.031 (6)	0.12 (4)
Herring	0.0047 (32)	0.029 (25)	0.015 (21)	0.0015 (14)	0.062 (5)	0.25 (3)
Gadidae	0.037 (49)	0.029 (44)	0.0089 (20)	0.0039 (8)	0.5 (1)	. (0)
Haddock	0.055 (8)	0.055 (8)	0.16 (6)	0.062 (4)	. (0)	. (0)
Cod	0.094 (22)	0.022 (19)	0.037 (9)	0.12 (3)	0.5 (1)	. (0)
Pollock or saithe	0.078 (6)	0.16 (5)	0.25 (2)	. (0)	. (0)	. (0)
Soleidae (Sole)	0.23 (6)	0.34 (5)	0.25 (2)	. (0)	. (0)	. (0)

B. P-values (with associated sample sizes in parentheses) corresponding to Figures 4 and 5. The null hypothesis is that the median relative rank of the quantity of spawners for the smallest recruitment is 0.5. The alternative hypothesis is that the median is less than 0.5.

	S_{max}/S_{min}					
Group	≥ 1	≥ 2	≥ 5	≥ 10	≥ 50	≥ 100
All stocks	< 0.0001 (177)	< 0.0001 (158)	< 0.0001 (102)	< 0.0001 (53)	0.00026 (17)	0.0012 (12)
Pleuronectidae	0.0062 (15)	0.0034 (12)	0.052 (5)	0.12 (3)	. (0)	. (0)
Plaice	0.023 (7)	0.016 (6)	0.25 (2)	0.5 (1)	. (0)	. (0)
Salmonidae	< 0.0001 (34)	< 0.0001 (34)	< 0.0001 (29)	0.00011 (18)	0.0044 (9)	0.0068 (8)
Chum salmon	0.01 (8)	0.01 (8)	0.029 (5)	0.12 (3)	0.5 (1)	0.5 (1)
Pink salmon	0.07 (6)	0.07 (6)	0.052 (5)	0.25 (3)	0.25 (2)	0.25 (2)
Sockeye salmon	0.00027 (18)	0.00027 (18)	0.00027 (18)	0.0017 (11)	0.017 (6)	0.027 (5)
Merlucciidae	0.78 (9)	0.37 (7)	0.25 (3)	0.25 (2)	. (0)	. (0)
Clupeidae	0.077 (41)	0.037 (34)	0.0073 (29)	0.0059 (19)	0.029 (6)	0.049 (4)
Herring	0.15 (32)	0.079 (25)	0.0097 (21)	0.0067 (14)	0.062 (5)	0.12 (3)
Gadidae	0.058 (49)	0.034 (44)	0.0024 (20)	0.039 (8)	0.5 (1)	. (0)
Haddock	0.1 (8)	0.1 (8)	0.031 (6)	0.062 (4)	. (0)	. (0)
Cod	0.078 (22)	0.033 (19)	0.043 (9)	0.62 (3)	0.5 (1)	. (0)
Pollock or saithe	0.5 (6)	0.59 (5)	0.25 (2)	. (0)	. (0)	. (0)
Soleidae (Sole)	0.66 (6)	0.69 (5)	0.75 (2)	. (0)	. (0)	. (0)

C. P-values (with associated sample sizes in parentheses) corresponding to Figures 6 and 7. The null hypothesis is that the median $\bar{R}_{\text{above}}/\bar{R}_{\text{below}}$, is 1. The alternative hypothesis is that the median is greater than 1.

	$S_{\max}/S_{\min}$					
Group	≥ 1	≥ 2	≥ 5	≥ 10	≥ 50	≥ 100
All stocks	< 0.0001 (177)	< 0.0001 (158)	< 0.0001 (102)	< 0.0001 (53)	< 0.0001 (17)	0.00024 (12)
Pleuronectidae	0.068 (15)	0.046 (12)	0.094 (5)	0.12 (3)	. (0)	. (0)
Plaice	0.11 (7)	0.078 (6)	0.25 (2)	0.5 (1)	. (0)	. (0)
Salmonidae	< 0.0001 (34)	< 0.0001 (34)	< 0.0001 (29)	< 0.0001 (18)	0.002 (9)	0.0039 (8)
Chum salmon	0.012 (8)	0.012 (8)	0.031 (5)	0.12 (3)	0.5 (1)	0.5 (1)
Pink salmon	0.016 (6)	0.016 (6)	0.031 (5)	0.12 (3)	0.25 (2)	0.25 (2)
Sockeye salmon	< 0.0001 (18)	< 0.0001 (18)	< 0.0001 (18)	0.00049 (11)	0.016 (6)	0.031 (5)
Merlucciidae	0.082 (9)	0.039 (7)	0.12 (3)	0.25 (2)	. (0)	. (0)
Clupeidae	0.0083 (41)	0.014 (34)	0.0042 (29)	0.00017 (19)	0.016 (6)	0.062 (4)
Herring	0.019 (32)	0.033 (25)	0.0088 (21)	0.0043 (14)	0.031 (5)	0.12 (3)
Gadidae	0.012 (49)	0.015 (44)	0.0016 (20)	0.0039 (8)	0.5 (1)	. (0)
Haddock	0.098 (8)	0.098 (8)	0.078 (6)	0.062 (4)	. (0)	. (0)
Cod	0.0078 (22)	0.0041 (19)	0.0059 (9)	0.12 (3)	0.5 (1)	. (0)
Pollock or saithe	0.28 (6)	0.5 (5)	0.25 (2)	. (0)	. (0)	. (0)
Soleidae (Sole)	0.5 (6)	0.59 (5)	0.25 (2)	. (0)	. (0)	. (0)

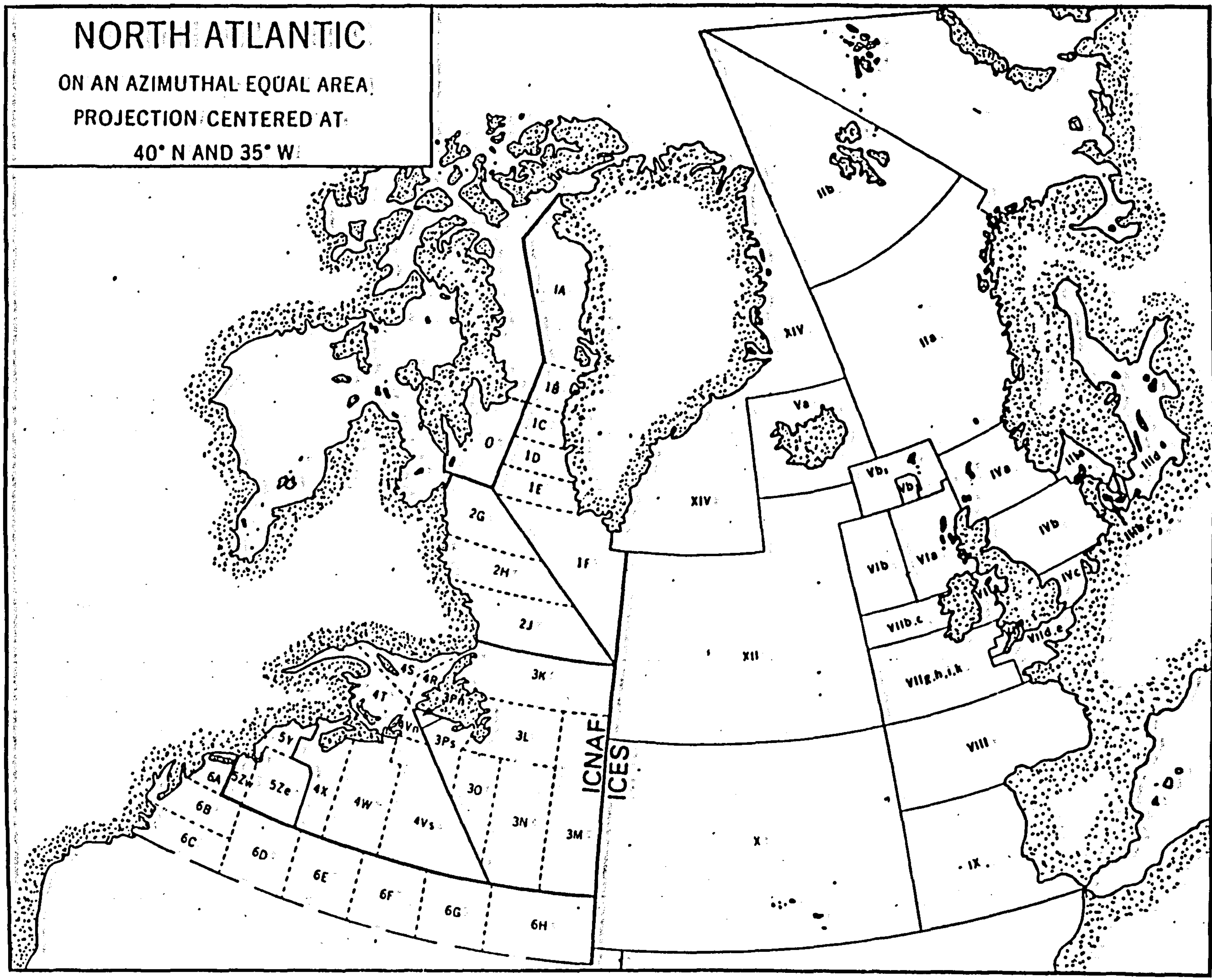

Figure 1. Stock boundaries in the North Atlantic.

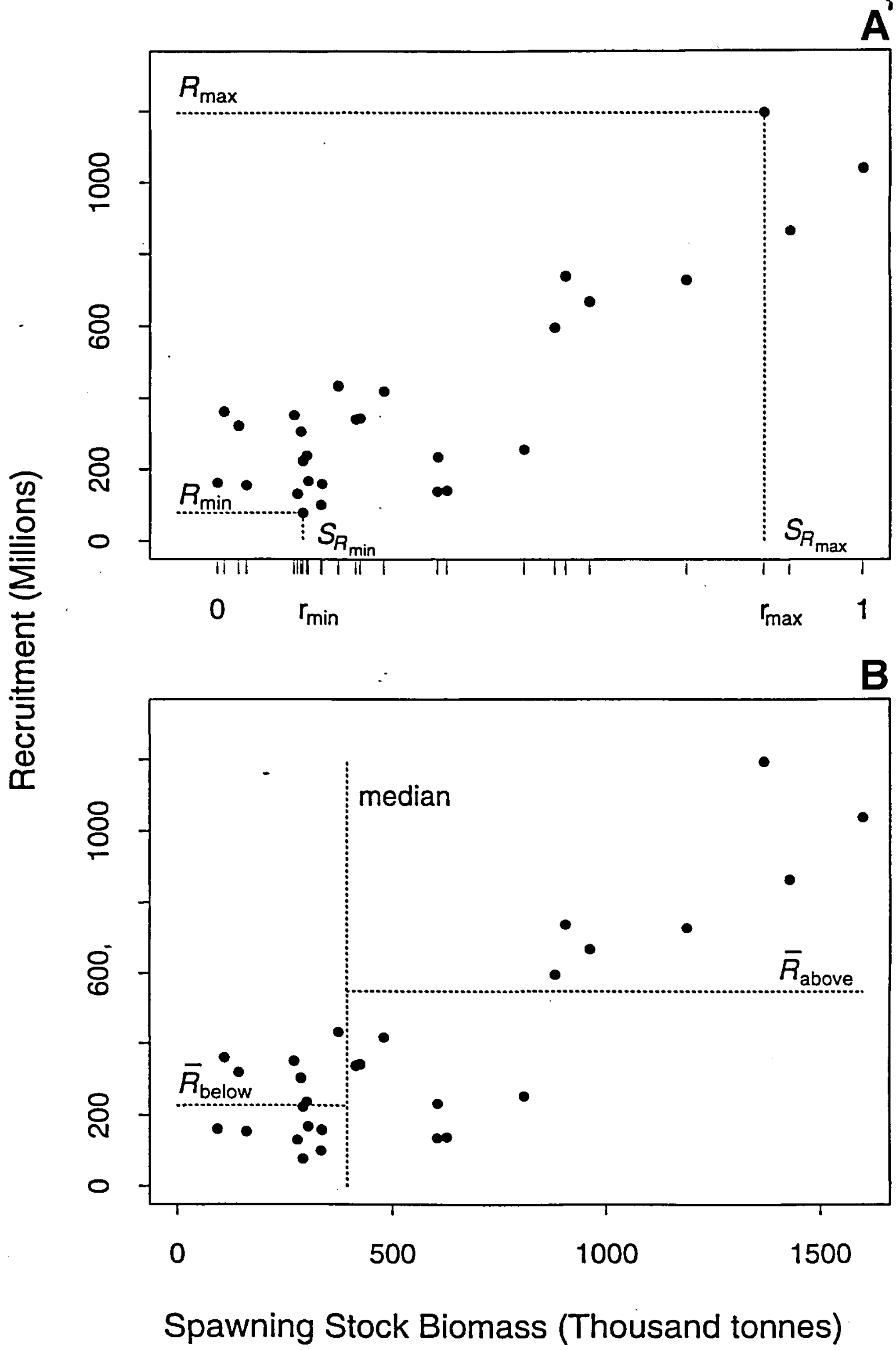

Figure 2. Illustration of the three nonparametric methods applied to spawner-recruitment data for cod in NAFO Div. 2J3KL. In this case spawner abundance is measured as spawning stock biomass. (A) The maximum recruitment is $R_{\max}$, the corresponding spawner abundance is $S_{R_{\max}}$, and the corresponding relative rank is $r_{\max}$. Similarly, the minimum recruitment is $R_{\min}$, the corresponding spawner abundance is $S_{R_{\min}}$, and the corresponding relative rank is $r_{\min}$. (B) The mean recruitment below the median spawner abundance is $\bar{R}_{\text{below}}$ while the mean recruitment above the median spawner abundance is $\bar{R}_{\text{above}}$.

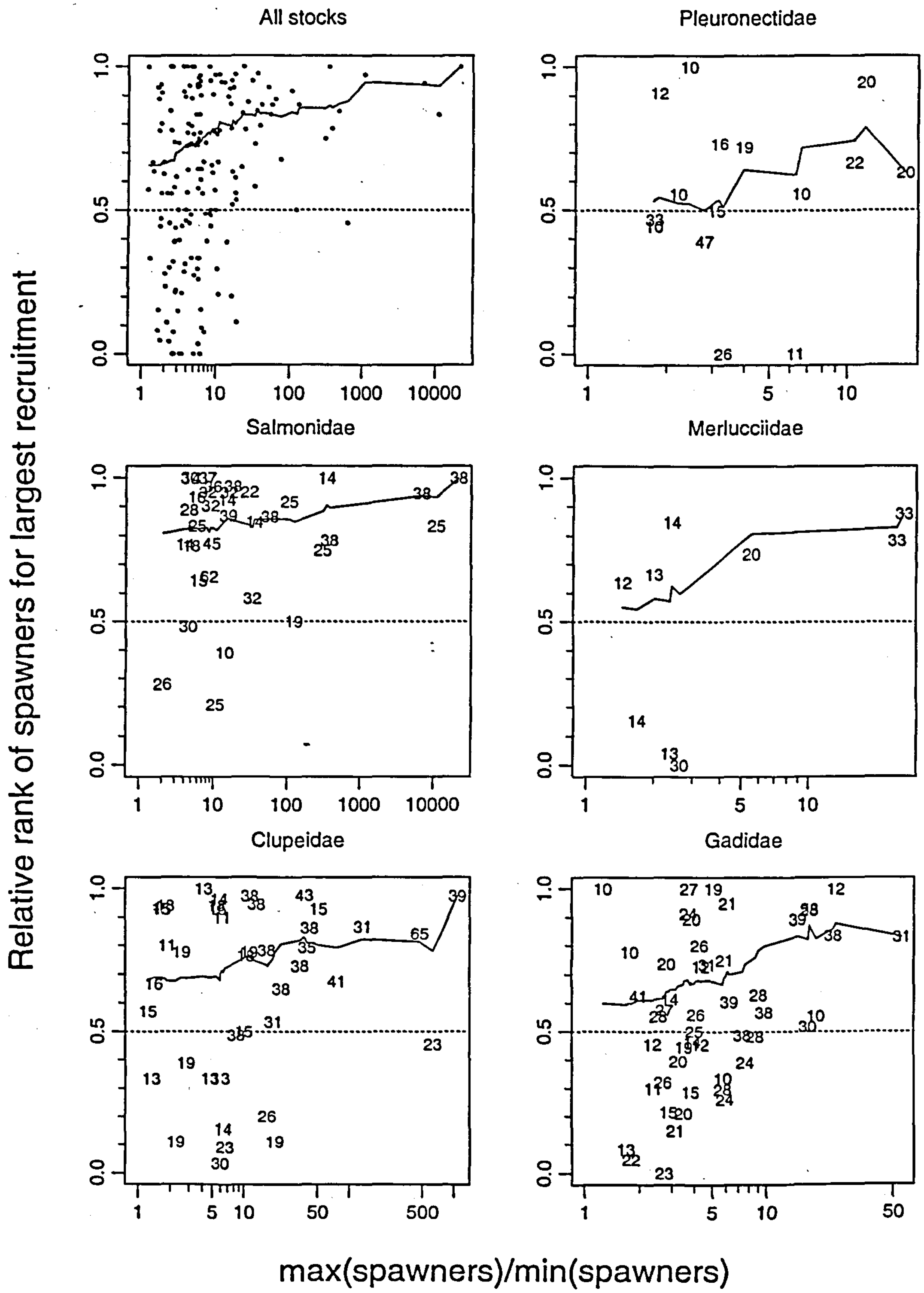

Figure 3. Scatter plots by family of the relative rank of spawner abundance for the largest recruitment versus the ratio $S_{\max}/S_{\min}$. The x-axis has a logarithmic scale. The numbers in the plots indicate the number of observations in the corresponding spawner-recruitment series. Smaller numbers should receive less weight. Also, these numbers can be used, along with Table 1, to identify the corresponding population. If spawner abundance and recruitment were independent, the distributions would be expected to have a median of 0.5. The superimposed curves represent cumulative weighted means (starting from the right-hand side; see description in text).

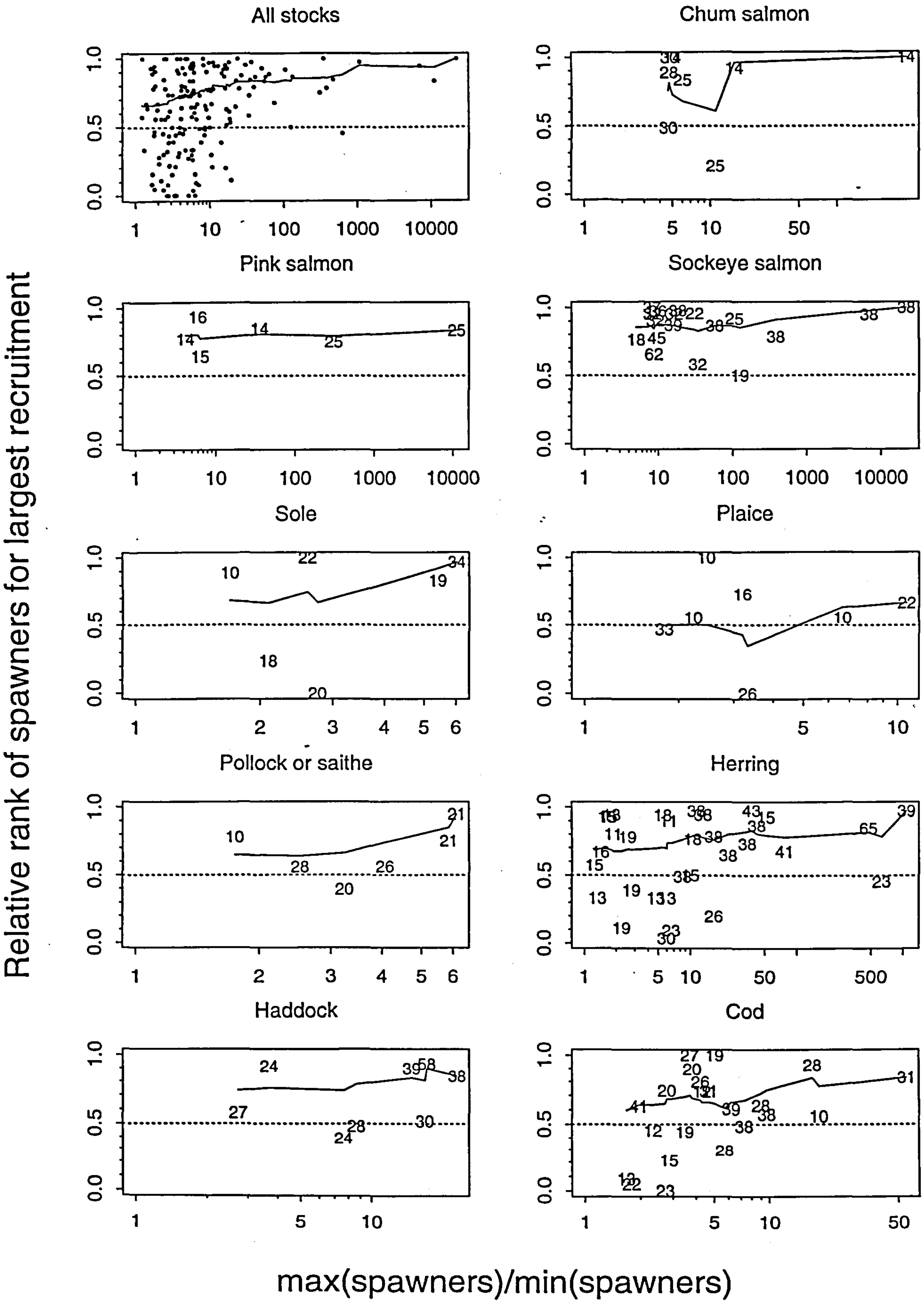

Figure 4. Scatter plots by species of the relative rank of the spawner abundance for the largest recruitment versus the ratio $S_{\max}/S_{\min}$. See Fig. 3 for explanation.

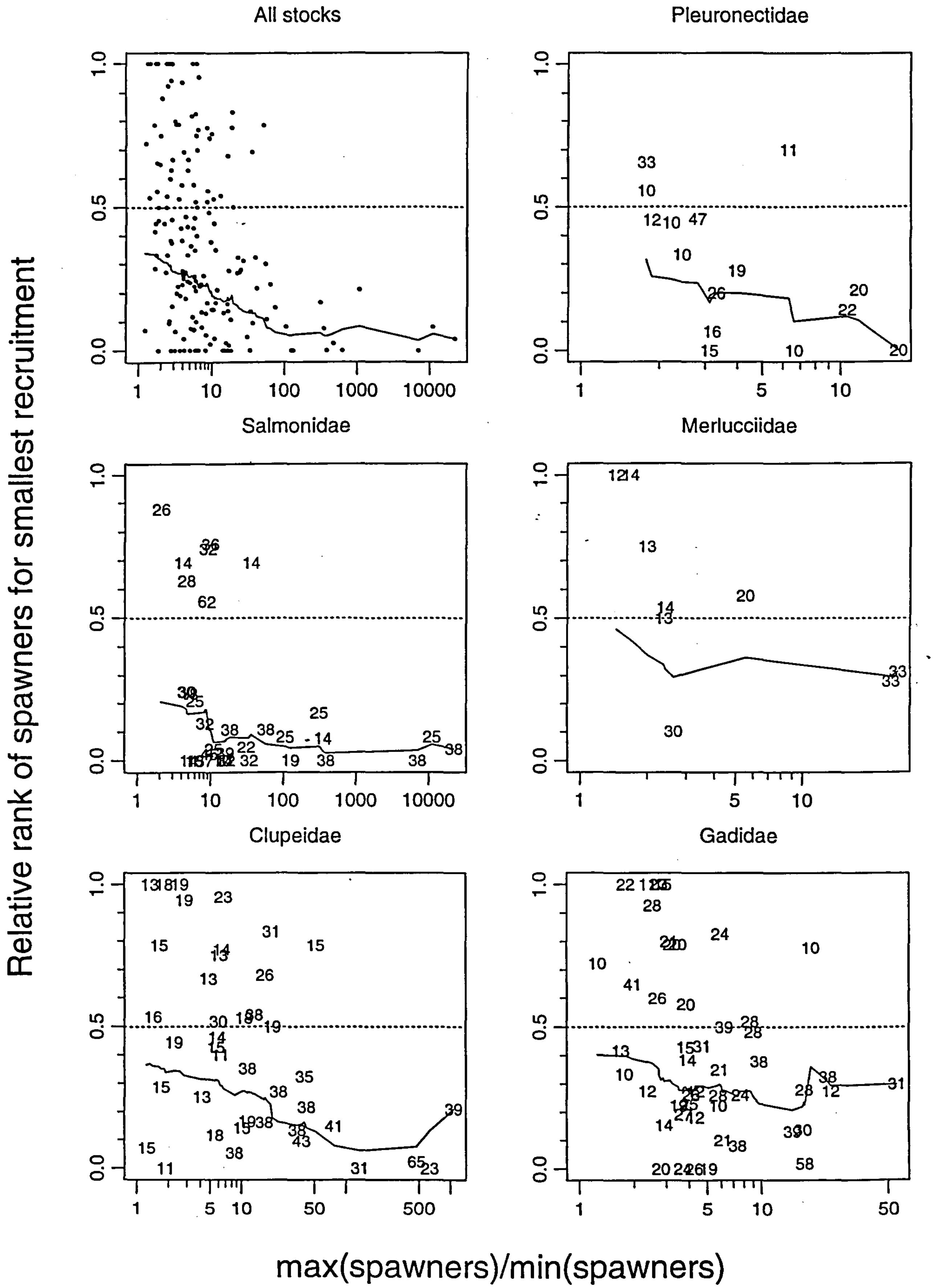

Figure 5. Scatter plots by family of the relative rank of the spawner abundance for the smallest recruitment versus the ratio $S_{\max}/S_{\min}$. See Fig. 3 for explanation.

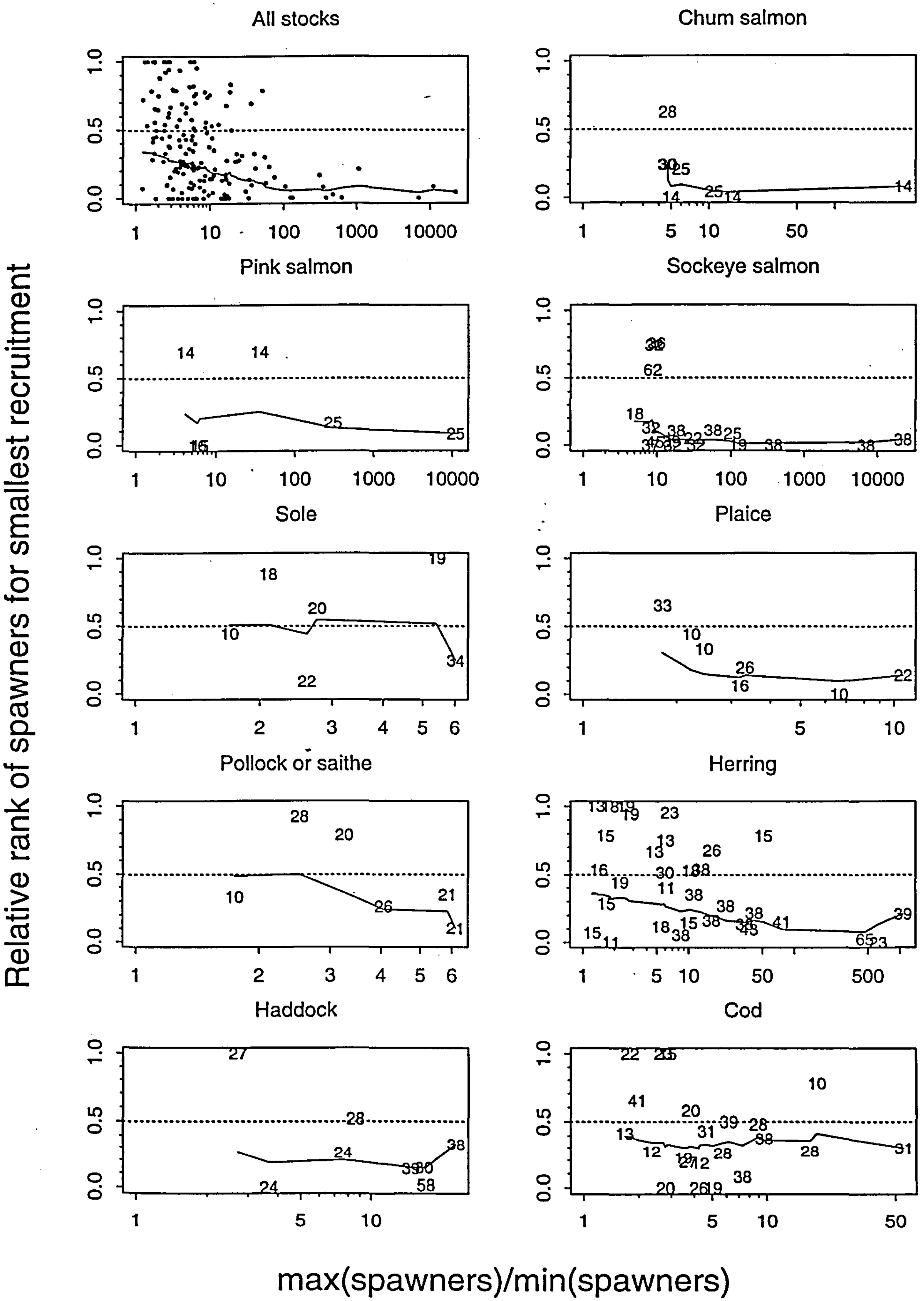

Figure 6. Scatter plots by species of the relative rank of the spawner abundance for the smallest recruitment versus the ratio S_{max}/S_{min}. See Fig. 3 for explanation.

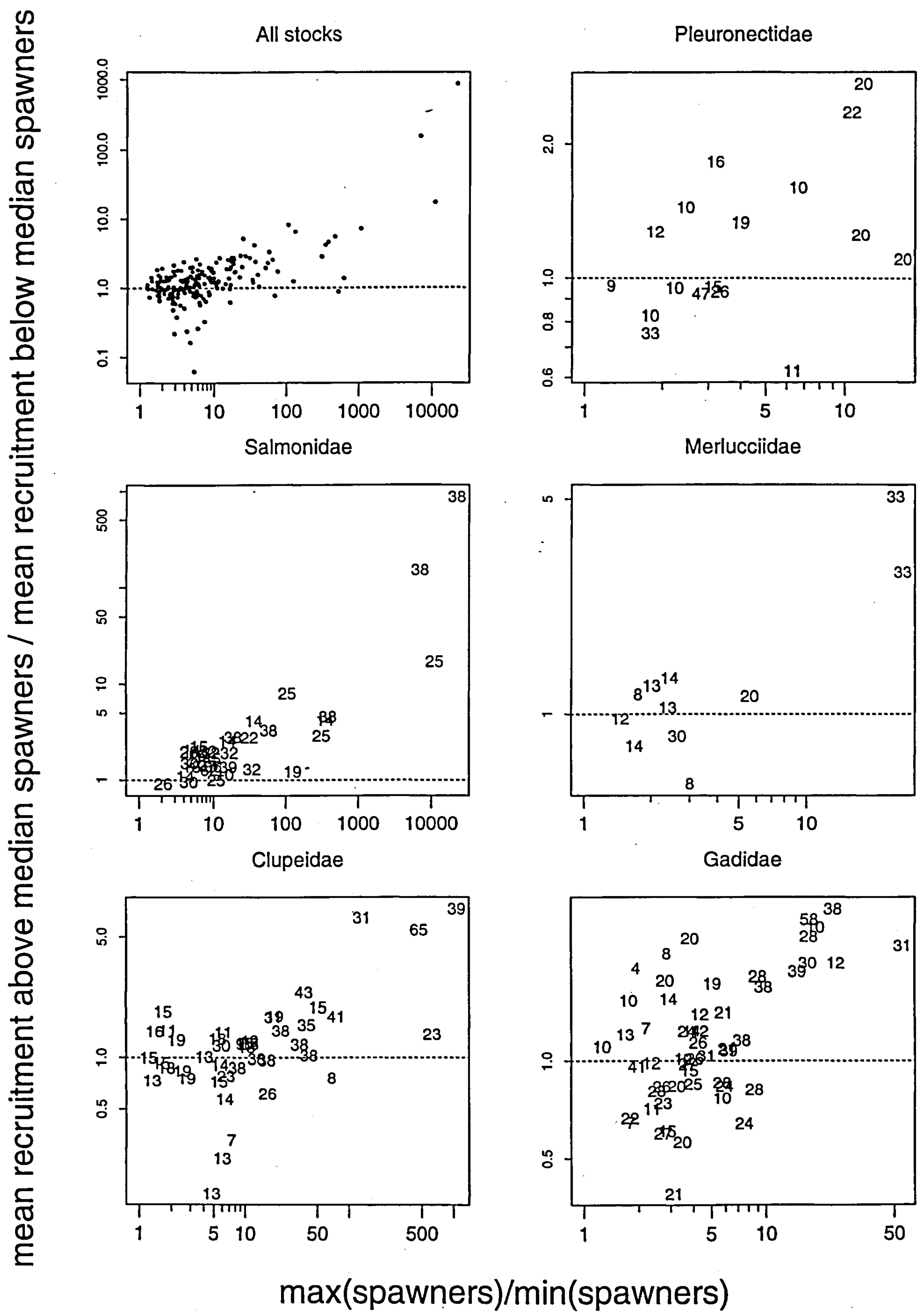

Figure 7. Scatter plots by family of the ratio $\bar{R}_{\text{above}}/\bar{R}_{\text{below}}$ versus the ratio $S_{\max}/S_{\min}$. Both axes have logarithmic scales. The numbers in the plots indicate the number of observations in the corresponding spawner-recruitment series. If spawner abundance and recruitment were independent, the distribution would be expected to have a median of 1.

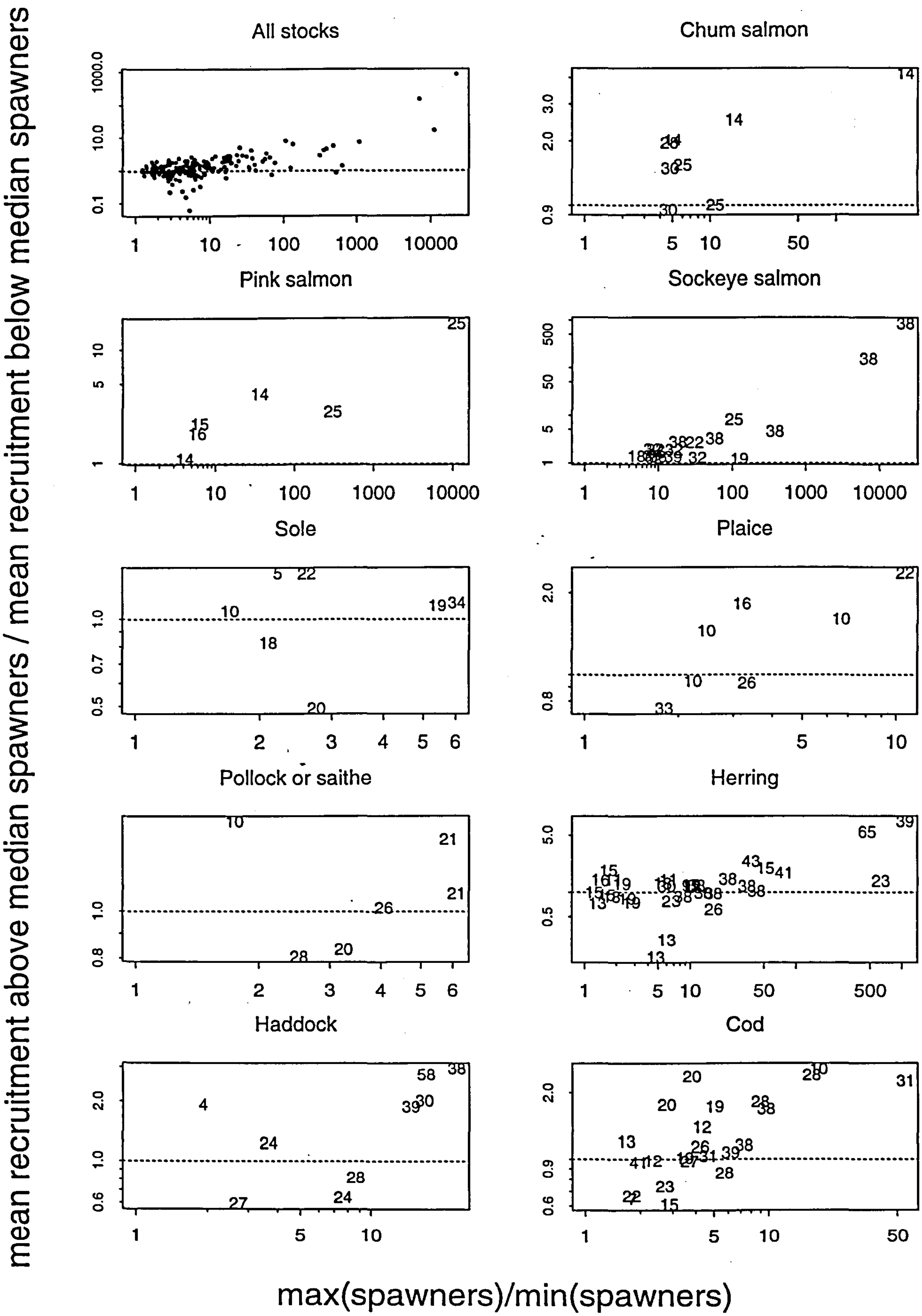

Figure 8. Scatter plots by species of the ratio $\bar{R}_{\text{above}}/\bar{R}_{\text{below}}$ versus the ratio $S_{\max}/S_{\min}$. See Fig. 7 for explanation.