Is fish recruitment related to spawner abundance?

Abstract.–We analyzed 364 spawner-recruitment time series 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 rather than below the median? We found 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. Recruitment overfishing appears to be a common problem.

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Perhaps the most fundamental issue for the study and management of fish populations is the relation between spawner abundance and subsequent recruitment. There is surprisingly little consensus on this issue; many researchers believe that there is no relevant relationship between species abundance and recruitment (reviewed by Wooster and Bailey, 1989; Koslow et al., 1987) whereas others believe it to be fundamental (e.g. Ricker, 1954; Beverton and Holt, 1957; Cushing, 1971; Myers et al., 1995a). 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 a sustainable abundance or biomass of 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 approach the problem using 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 examine systematically 364 data sets from the most recent version of the database compiled by Myers et al. (1995b) as part of an ongoing study of recruitment variability. By analyzing many populations with identical methods, it is possible to arrive at conclusions with greater reliability.

The nonparametric methods we used 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 examined the rank of spawner abundance associated with the largest recruitment. Second: Does the smallest recruitment occur when spawner abundance is low? This time we examined the rank of spawner abundance associated with the smallest recruitment. Third: Is the mean recruitment higher if spawner abundance is above rather than below the median? To answer this question, we examined the ratio of mean recruitment when spawner abundance is above the median to mean recruitment when spawner abundance is below the median.

Data

By "spawner abundance" we mean any of the following metrics of the size of the spawning stock: spawning stock biomass, the number of spawners, the number of eggs, or some index of spawner abundance (derived from catch per unit of effort or research vessels).

We tried to assemble all time series of reliable data on spawner abundance and recruitment. We started with the 477 time series from the most recent version of the database by Myers et al. (1995b). Of these, 77 series were eliminated because they had less than 5 years of spawner-recruitment data, 5 series were eliminated because they were for invertebrates, 17 pink and chum salmon series were eliminated because they were described as less reliable, and 14 series were eliminated because they were different versions of other series or because they overlapped other series. We were left with 364 series. Sometimes the same population was included more than once because of incompatible time periods or because different life stages were examined.

For each population, Table 1 lists the method used to estimate spawner abundance and recruitment. For most marine populations, spawning biomass and recruitment had been estimated by sequential population analysis (SPA) of commercial catch-at-age data. SPA techniques include virtual population analysis (VPA; Gulland[1]), cohort analysis (Pope, 1972), and related methods that 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 were not available; therefore research vessel (RV) surveys estimates were used. For a few populations, other types of data were used, e.g. spawning stock biomass was estimated from SPA and recruitment was estimated from research vessel surveys. We did not include populations for which there was only commercial catch-per-unit-of-effort estimates of abundance.

For populations in the family Salmonidae, series were sometimes available for several different life-stage transitions. The life stages are denoted in Table 1 as follows: a = adults (or eggs); f = fry; s = smolts (sea-bound migrating juveniles); and p = parr (juveniles within the river).

For most of the Pacific salmonid populations, the numbers of spawners and recruits were reconstructed from commercial catch-at-age data and independent estimates of fishing mortality or from an independent estimate of escapement from surveys of spawning, or both. In these cases, the method is termed "stock reconstruction," and is denoted as SR in Table 1. Some of the estimates were derived from experiments in which the number of spawners and recruits, 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.

Methods and results

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 used 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.

Hypothesis 1: Does the largest recruitment occur when spawner abundance is high?

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

To help summarize the data and to test hypotheses, cumulative weighted means were calculated. The weighted mean of k relative ranks $r_{max,i}$ is

$$\frac{\sum_{i=1}^{k} n_i r_{\text{max},i}}{\sum_{i=1}^{k} n_i}, \tag{1}$$

where n_i is the number of observations in the ith spawner-recruitment series. The cumulative weighted mean was calculated by starting with the relative rank associated with the largest value of S_{max}/S_{min} and by continuing through the relative rank associated with the smallest value of S_{max}/S_{min}.

If, for a given population, spawner abundance and highest recruitment were independent, each possible relative rank would be equally likely, i.e. the expected value of $r_{max,i}$ would be 0.5. If this were true for each population, then the expected value of the weighted mean relative rank would also be 0.5. Therefore we

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[1] Gulland, J. A. 1965. Estimation of mortality rates. Annex to Rep., Arctic Fish. Working Group ICES Council Meeting 1965(3), 9 p.

Table 1

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; $\overline{R}_{above}/\overline{R}_{below}$ 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, MR=mark recapture). For populations within the family Salmonidae, series were sometimes available for several different life-stage transitions. The life stages are denoted as follows: a = adults (or eggs), f = fry, s = smolt, and p = parr. They are shown in the table with an arrow notation so that "a ⇒ f" means spawners were "adults" and recruits were "fry."

Population	n	$\dfrac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\dfrac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Aulopiformes						
Synodontidae						
Greater lizardfish (*Saurida tumbil*)						
East China Sea	10	6.8	0.67	0.22	1.7	CPUE
Clupeiformes						
Clupeidae						
Blueback herring (*Alosa aestivalis*)						
Saint John River	14	65.2	0.77	0.08	2.9	Count
Alewife (*Alosa pseudoharengus*)						
Damariscotta Lake, Maine	8	5.6	0.21	0.43	1.0	Count
Lake Ontario	7	7.4	0.50	0.00	0.3	RV
Saint John River	16	54.8	1.00	0.33	2.2	Count
Anadromous American shad (*Alosa sapidissima*)						
Connecticut River	16	4.5	0.67	0.20	1.2	MR and count
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, Bothnian Sea	15	1.6	0.93	0.79	0.9	SPA
S.W. Baltic	19	2.8	0.39	0.94	0.8	SPA
S. Baltic	15	1.2	0.57	0.07	1.0	SPA
Central Baltic	16	1.4	0.67	0.53	1.4	SPA
Baltic, 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
Craig, Alaska	16	13.4	0.53	0.73	2.6	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
West of Scotland	18	10.4	0.76	0.53	1.2	SPA
West of Ireland	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)	46	39.6	0.91	0.04	2.9	SPA
N. Gulf of St. Lawrence (fall spawners)	13	4.7	0.33	0.67	0.2	SPA
N. Gulf of St. Lawrence (spring spawners)	13	6.0	0.33	0.75	0.3	SPA
S. Gulf of St. Lawrence (fall spawners)	9	9.1	0.62	0.38	1.2	SPA
S. Nova Scotia	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)	41	8,986.4	1.00	0.03	5.5	SPA

Table 1 (continued)

Population	n	$\dfrac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\dfrac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
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
Revilla Channel (Kah Shakes), Alaska	16	3.1	0.33	0.47	0.6	SPA
S.E. Alaska	30	6.0	0.03	0.52	1.2	SPA
Seymour Canal, Alaska	16	8.4	0.73	0.33	1.0	SPA
Sitka, Alaska	21	14.8	0.95	0.15	3.2	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
Yellow Sea or Huanghai Sea	15	51.2	0.93	0.79	1.9	SPA
Spanish sardine (*Sardina pilchardus*)						
Iberian Atlantic Coast	14	5.7	0.96	0.46	0.9	SPA
Brazilian sardine (*Sardinella brasiliensis*)						
South Eastern Brazil	15	3.4	0.57	0.00	1.6	Length-based SPA
Sardine (*Sardinops sagax*)						
California	31	134.4	0.87	0.00	6.4	SPA
Chile-Northern zone	13	4.1	1.00	0.25	1.0	SPA
Gulf of California	13	15.1	0.75	0.17	2.2	SPA
Eastern Japan	14	6.4	0.15	0.77	0.6	SPA
Sea of Japan	13	26.2	0.58	0.92	1.7	SPA
South Africa	31	19.0	0.53	0.83	1.7	SPA
South Africa	8	69.2	0.00	1.00	0.8	SPA
Sprat (*Sprattus sprattus*)						
Central Baltic	15	5.6	0.93	0.43	0.7	SPA
S.E. Baltic	19	19.7	0.11	0.50	1.7	SPA
Engraulidae						
S.A. anchovy (*Engraulis capensis*)						
South Africa	18	3.5	0.00	0.53	1.3	SPA
South Africa	10	3.7	0.67	0.06	2.5	Acoustics
Northern anchovy (*Engraulis mordax*)						
California	25	4.7	0.79	0.33	0.9	SPA
Peruvian anchoveta (*Engraulis ringens*)						
Northern and central stock, Peru	19	18.4	0.61	0.00	2.2	SPA
Cypriniformes						
Cyprinidae						
Bream (*Abramis brama*)						
Lake Tjeukemeer, the Netherlands	11	4.5	0.50	0.30	0.5	RV
Golden shiner (*Notemigonus crysoleucas*)						
Lake St. George, Ontario	8	6.7	0.43	0.29	0.2	MR and beach seine
Roach (*Rutilus rutilus*)						
Klicava Reservoir	11	1.9	0.00	0.40	0.8	MR
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*)						
S.E. Baltic	22	5.3	0.43	0.10	1.4	SPA
Central Baltic	22	5.4	0.52	0.24	1.7	SPA
Celtic Sea	20	4.4	0.89	0.53	1.6	SPA
Faroe Plateau	31	6.7	0.58	0.20	0.9	SPA
Eastern English Channel	12	4.3	0.73	0.18	1.4	SPA
West of Scotland	27	3.7	0.10	1.00	0.8	SPA

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Table 1 (continued)

Population	n	$\dfrac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\dfrac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Iceland	38	7.3	0.49	0.08	1.2	SPA
Irish Sea	25	3.6	0.17	1.00	0.8	SPA
Kattegat	21	12.7	1.00	0.10	1.8	SPA
W. Coast of Greenland	31	55.7	0.83	0.30	2.3	SPA
Labrador and N.E. Newfoundland	28	17.2	0.93	0.28	2.7	SPA
Flemish Cap	10	18.7	0.56	0.78	2.6	RV
S. Grand Banks	31	9.0	0.67	0.53	1.9	SPA
N. Gulf of St. Lawrence	17	4.7	0.31	0.06	1.0	SPA
St. Pierre Bank	31	4.2	0.83	0.00	1.2	SPA
S. Gulf of St. Lawrence	41	5.9	0.66	0.19	1.1	SPA
E. Scotian Shelf	33	4.7	0.75	0.25	1.1	SPA
S.W. Scotian Shelf	45	2.0	0.64	0.66	1.0	SPA
Gulf of Maine	7	1.8	0.17	0.50	0.6	SPA
Georges Bank	14	1.7	0.00	0.15	1.2	SPA
North East Arctic	43	15.8	0.81	0.02	1.6	SPA
North Sea	28	4.4	1.00	0.22	1.2	SPA
Skagerrak	13	2.3	0.50	0.42	1.1	SPA
Haddock (*Melanogrammus aeglefinus*)						
Faroe Plateau	30	4.1	0.72	0.00	1.1	SPA
West of Scotland	28	10.9	0.41	0.33	0.7	SPA
Iceland	28	8.6	0.48	0.52	0.8	SPA
E. Scotian Shelf	38	23.2	0.84	0.32	2.9	SPA
S.W. Scotian Shelf	24	3.7	0.91	0.00	1.2	SPA
Georges Bank	58	17.2	0.93	0.02	2.7	SPA
North East Arctic	41	12.0	0.93	0.12	2.0	SPA
North Sea	31	23.4	0.52	0.17	0.8	SPA
Rockall Bank	6	4.1	0.20	0.80	0.5	SPA
Whiting (*Merlangius merlangus*)						
Celtic Sea	9	2.9	0.75	0.88	1.1	SPA
Eastern English Channel	14	3.9	0.46	0.38	1.2	SPA
West of Scotland	27	4.1	0.56	0.23	1.2	SPA
Irish Sea	13	3.2	0.58	1.00	1.0	SPA
North Sea	27	2.7	0.38	0.62	0.9	SPA
Silver hake (*Merluccius bilinearis*)						
Mid Atlantic Bight	33	27.1	0.88	0.31	2.9	SPA
Scotian Shelf	13	2.0	0.67	0.75	1.2	SPA
Georges Bank	33	25.3	0.78	0.28	5.1	SPA
S.A. hake (*Merluccius capensis*)						
South Africa	20	5.6	0.74	0.58	1.1	SPA
South Africa South Coast	12	1.5	0.64	1.00	1.0	SPA
Peruvian hake (*Merluccius gayi*)						
Chile-South Central zone	14	1.7	0.15	1.00	0.8	SPA
Chile-Northern zone	14	2.4	0.85	0.54	1.3	SPA
Peru	8	3.0	0.43	1.00	0.6	SPA
Hake (*Merluccius merluccius*)						
West of France and British Isles	14	1.8	1.00	0.31	1.0	SPA
Iberian Atlantic Coast	9	3.2	0.88	0.00	2.0	SPA
Jabuka Pit, Adriatic Sea	26	8.5	1.00	0.20	1.1	CPUE
Pacific hake (*Merluccius productus*)						
W. U.S. + Canada	33	2.2	0.06	1.00	1.0	SPA
Blue whiting (*Micromesistius poutassou*)						
N.E. Atlantic (North)	20	3.5	0.21	0.79	0.6	SPA
N.E. Atlantic (South)	10	1.2	1.00	0.72	1.1	SPA
Pollock or saithe (*Pollachius virens*)						
Faroe	30	2.4	0.03	0.93	0.8	SPA

Table 1 (continued)

Population	n	$\dfrac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\dfrac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
West of Scotland	20	3.2	0.39	0.79	0.8	SPA
Iceland	26	4.1	0.56	0.26	1.0	SPA
Scotian Shelf and Georges Bank	10	1.7	0.78	0.33	1.5	SPA
North East Arctic	32	8.9	0.19	0.06	1.3	SPA
North Sea	22	7.0	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
Gulf of Alaska, Alaska	25	4.3	0.38	0.50	0.5	SPA
Japan-Pacific Coast of Hokkaido	15	3.8	0.29	0.43	0.9	SPA
West Bering Sea	8	2.8	1.00	0.00	2.1	SPA
Norway pout (*Trisopterus esmarkii*)						
North Sea	12	4.3	0.45	0.27	1.2	SPA
Red hake (*Urophycis chuss*)						
Gulf of Maine and N. Georges Bank	13	8.6	0.50	0.17	1.4	SPA
S. New England	15	5.7	0.64	0.07	2.6	SPA
White hake (*Urophycis tenuis*)						
S. Gulf of St. Lawrence	14	2.7	0.08	0.38	0.7	SPA
Lophiformes						
Lophiidae						
Monkfish (*Lophius piscatorius*)						
Celtic Sea and West of France	6	1.6	1.00	0.40	2.7	SPA
Perciformes						
Ammodytidae						
Sandeel (*Ammodytes marinus*)						
West of Scotland	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
Branchiostegidae						
Branquillo (*Branchiostegus japonicus*)						
Wakasa Bay	7	2.4	0.50	0.92	0.4	Leslie
Carangidae						
Cape horse mackerel (*Trachurus capensis*)						
Namibian Coast	17	3.9	0.31	0.94	0.5	SPA
Horse mackerel (*Trachurus symetricus murphyi*)						
South Pacific Ocean	15	5.5	0.50	0.79	1.1	SPA
Horse mackerel (*Trachurus trachurus*)						
Iberian Atlantic Coast	8	1.7	0.14	0.43	0.6	SPA
N.E. Atlantic	8	4.3	0.14	0.00	0.2	SPA
Lactariidae						
False trevally (*Lactarius lactarius*)						
Gulf of Thailand	8	521.8	0.43	0.00	0.9	CPUE
Lutjanidae						
Silk snapper (*Lutjanus synagris*)						
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
Pentacerotidae						
Pelagic armourhead (*Pseudopentaceros wheeleri*)						
Southeast Hancock Seamount, Hawaii	11	19.1	1.00	0.70	7.1	Leslie
Percidae						
Yellow perch (*Perca flavescens*)						

Table 1 (continued)

Population	n	$\dfrac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\dfrac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
Oneida Lake, New York	7	1.6	0.00	0.67	0.3	Seine
South Bay, Lake Huron	27	582.9	0.62	0.58	1.6	Research nets
Eurasian perch (*Perca fluviatilis*)						
Lake Ijssel, the Netherlands	16	6.2	0.50	0.77	0.8	SPA, RV
Pikeperch (*Stizostedion lucioperca*)						
Lake Ijssel, the Netherlands	17	43.0	0.50	1.00	0.5	SPA, RV
Walleye (*Stizostedion vitreum*)						
Escanaba Lake, Wisconsin	16	3.9	0.07	0.60	0.4	MR
Lake Erie	14	23.7	0.23	0.77	0.6	SPA
Lake Erie, Michigan	22	452.7	0.81	0.14	3.6	CPUE
Mille Lacs Lake, Minnesota	12	3.3	0.91	0.45	5.2	SPA
Rainy Lake, Minnesota	15	2.1	0.93	0.00	1.6	CPUE
Scianidae						
White croaker (*Argyrosomus argentatus*)						
East China Sea	15	1.9	0.79	0.64	1.1	SPA
Black croaker (*Argyrosomus nibe*)						
East China Sea	13	61.0	0.58	0.17	2.3	CPUE
Yellow croaker (*Pseudociaena polyactis*)						
East China Sea	10	15.0	0.78	0.22	2.7	Catch curve
Scombridae						
Chub mackerel (*Scomber japonicus*)						
Pacific Coast of Japan	16	33.5	0.27	0.53	0.4	Egg survey
Pacific Coast of Japan	12	33.5	1.00	0.09	2.6	Egg survey
Southern California	36	64.1	0.89	0.23	2.5	SPA
Mackerel (*Scomber scombrus*)						
N.W. Atlantic	28	10.7	0.30	0.44	1.1	SPA
N.E. Atlantic	19	1.9	0.56	0.50	1.0	SPA
Yellowfin tuna (*Thunnus albacares*)						
Eastern Pacific Ocean	25	3.4	0.88	0.58	1.4	SPA
Indian Ocean	25	9.1	0.83	0.04	2.2	SPA
Southern bluefin tuna (*Thunnus maccoyii*)						
Southern Pacific	26	4.2	0.64	0.04	1.2	SPA
Atlantic bluefin tuna (*Thunnus thynnus*)						
West Atlantic	23	8.2	0.91	0.00	2.2	SPA
Sparidae						
Sea bream (*Chrysophrys major*)						
Yellow Sea	17	440.3	0.81	0.00	2.2	CPUE
Red porgy (*Pagrus pagrus*)						
Atlantic Ocean off North Carolina	14	3.0	0.23	0.00	1.2	SPA
Yellow sea bream (*Taius tumifrons*)						
Central East China Sea	20	4.3	0.26	0.00	1.7	Catch curve
East China Sea	8	3.2	0.00	0.57	0.7	CPUE
Japan Coast	20	6.2	0.89	0.05	2.1	Catch curve
South East China Sea	18	9.9	1.00	0.00	3.8	Catch curve
Pleuronectiformes						
Bothidae						
Summer flounder (*Paralichthys dentatus*)						
Middle Atlantic Bight	9	3.1	1.00	0.12	1.8	SPA
Pleuronectidae						
American plaice (*Hippoglossoides platessoides*)						
Grand Banks	19	4.0	0.72	0.28	1.3	SPA
Georges Bank	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
Rock sole (*Lepidopsetta bilineata*)						

Table 1 (continued)

Population	n	$\dfrac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\dfrac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Hecate Strait, B.C.	24	4.6	0.39	0.70	1.0	CPUE
Yellowfin sole (*Limanda aspera*)						
E. Bering Sea	12	1.9	0.91	0.45	1.3	SPA
Yellowtail flounder (*Limanda ferruginae*)						
Grand Banks	15	3.1	0.50	0.00	1.0	SPA
Georges Bank	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	14	3.4	0.85	0.31	1.2	SPA
Skagerrak and Kattegat	12	2.2	0.45	0.73	0.5	SPA
Eastern English Channel	11	2.2	0.60	0.10	1.3	SPA
Western English Channel	15	2.9	0.71	0.00	1.4	SPA
Irish Sea	28	3.7	0.00	0.56	0.9	SPA
Kattegat	22	10.7	0.67	0.14	2.4	SPA
North Sea	35	1.9	0.35	0.63	0.8	SPA
Skagerrak	10	2.2	0.56	0.44	0.9	SPA
Greenland halibut (*Reinhardtius hippoglossoides*)						
W. Greenland and Iceland	14	2.5	0.31	0.92	0.9	SPA
North East Arctic	21	4.3	0.40	0.10	1.3	SPA
Northwest Atlantic	15	2.6	0.14	0.86	0.8	SPA
Scophthalmidae						
Megrim (*Lepidorhombus whiffiagonis*)						
West of France and British Isles	7	1.5	0.83	0.50	1.1	SPA
Iberian Atlantic Coast	6	1.6	0.20	1.00	0.2	SPA
Soleidae						
Sole (*Solea vulgaris*)						
Bay of Biscay (VIII)	13	2.0	0.17	0.75	0.9	SPA
Celtic Sea	18	2.4	0.00	0.88	0.4	SPA
Skagerrak and Kattegat	5	2.2	1.00	0.50	1.4	SPA
Eastern English Channel	20	5.4	0.42	1.00	1.1	SPA
Western English Channel	22	2.7	0.90	0.48	1.3	SPA
Irish Sea	21	2.0	0.00	0.65	0.5	SPA
North Sea	36	5.7	0.96	0.19	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*)						
Barents Sea	20	138.0	0.79	0.84	2.2	RV
Iceland	12	5.2	0.27	0.36	0.9	SPA
Plecoglossidae						
Ayu (*Plecoglossus altivelis*)						
Lake Biwa, Japan	12	19.3	0.82	0.00	1.0	SPA
Salmonidae						
Lake Whitefish (*Coregonus clupeaformis*)						
Lake Huron (a ⇒ a)	28	77.3	0.78	0.89	1.4	Research nets
Bloater (*Coregonus hoyi*)						
Lake Michigan (a ⇒ a)	11	49.5	0.90	0.10	37.1	RV
Whitefish (*Coregonus lavaretus*)						
Lake Constance, Europe (a ⇒ a)	21	7.9	0.65	0.00	3.2	SPA
Pink salmon (*Oncorhynchus gorbuscha*)						
Auke Creek, Alaska (f ⇒ a)	14	10.4	0.92	0.00	1.6	Count
Auke Creek, Alaska (a ⇒ f)	16	15.5	0.73	0.00	1.6	Count

Table 1 (continued)

Population	n	$\dfrac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\dfrac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
Bakhura River, Sakhalin Is. (a ⇒ f)	26	54.0	0.24	0.04	0.7	Count
Bakhura River, Sakhalin Is. (f ⇒ a)	24	35.1	0.65	0.22	1.4	Count
Bakhura River, Sakhalin Is. (a ⇒ a)	24	54.0	0.91	0.13	1.4	Count
Bentinck, B.C. (a ⇒ a)	11	76.4	0.70	0.10	2.4	SR
Brown's Peak Creek, Cook Inlet, Alaska (a ⇒ a)	22	280.0	0.48	0.12	1.1	SR
Bruin Bay, Cook Inlet, Alaska (a ⇒ a)	17	252.4	0.88	0.06	15.1	SR
Central Alaska (a ⇒ a)	25	310.0	0.75	0.17	2.9	SR
Central B.C. (Areas 6–8) (a ⇒ a)	14	4.1	0.77	0.69	1.1	SR
Central Coast Area 7, B.C. (a ⇒ a)	11	4.2	0.80	0.20	1.4	SR
Central Coast Area 9, B.C. (a ⇒ a)	11	51.5	0.70	0.20	4.5	SR
Dagi River, Sakhalin Is. (a ⇒ f)	11	81.0	0.90	0.00	2.3	Count
Desire Lake, Cook Inlet, Alaska (a ⇒ a)	8	12.5	0.14	0.86	0.5	SR
Douglas, B.C. (a ⇒ a)	11	5.2	0.80	0.50	3.4	SR
Fraser River, B.C. (a ⇒ a)	16	6.0	0.93	0.00	1.8	SR
Gardner, B.C. (a ⇒ a)	11	54.0	0.50	0.20	1.5	SR
Hooknose Creek, B.C., Canada (a ⇒ f)	14	35.8	0.85	0.69	4.1	Count
Humpy Creek, Cook Inlet, Alaska (a ⇒ a)	27	37.0	0.85	0.27	1.3	SR
Island Creek, Cook Inlet, Alaska (a ⇒ a)	25	350.0	0.83	0.92	3.9	SR
James Lagoon, Cook Inlet, Alaska (a ⇒ a)	8	12.7	0.43	0.71	0.3	SR
Kitimat, B.C. (a ⇒ a)	11	69.8	0.90	0.10	5.9	SR
Kodiak Archipelago, Alaska (a ⇒ a)	42	37.2	0.76	0.15	2.0	SR
Kodiak Archipelago, Alaska (a ⇒ f)	19	9.6	0.78	0.22	1.5	SR
Lakelse River, B.C. (a ⇒ f)	8	10.8	0.71	0.00	1.9	MR and count
Lakelse River, B.C. (f ⇒ a)	8	4.4	1.00	0.43	2.0	MR and count
Lakelse River, B.C. (a ⇒ a)	9	10.8	0.75	0.88	1.2	MR and count
Lesnaya River, Sakhalin Is. (a ⇒ f)	9	36.1	0.75	0.00	1.4	Count
Lower Skeena, B.C. (a ⇒ a)	11	7.6	0.70	0.30	1.8	SR
Lutoga River, Sakhalin Is. (a ⇒ f)	20	29.7	0.95	0.11	2.4	Count
Lutoga River, Sakhalin Is. (f ⇒ a)	19	17.6	0.94	0.06	2.1	Count
Lutoga River, Sakhalin Is. (a ⇒ a)	19	29.7	1.00	0.33	2.8	Count
North Coast Area 4, B.C. (a ⇒ a)	11	8.9	0.50	0.90	1.1	SR
Northern Panhandle, Alaska (a ⇒ a)	34	6.0	0.92	0.11	2.0	SR
Pokosnaya River, Sakhalin Is. (a ⇒ f)	25	384.6	0.88	0.06	8.1	Count
Pokosnaya River, Sakhalin Is. (f ⇒ a)	24	244.2	0.57	0.04	4.9	Count
Pokosnaya River, Sakhalin Is. (a ⇒ a)	23	384.6	0.82	0.00	6.5	Count
Poronal River, Sakhalin Is. (a ⇒ a)	21	84.1	0.95	0.10	3.1	Count
Port Chatham, Cook Inlet, Alaska (a ⇒ a)	15	69.3	0.86	0.07	4.4	SR
Port Dick, Cook Inlet, Alaska (a ⇒ a)	27	77.3	0.96	0.04	2.3	SR
Port Graham, Cook Inlet, Alaska (a ⇒ a)	27	33.3	0.69	0.58	1.7	SR
Prince William Sound, Alaska (a ⇒ a)	25	17.0	0.58	0.00	2.4	SR
Rocky River, Cook Inlet, Alaska (a ⇒ a)	20	85.0	0.32	0.03	1.4	SR
Sashin Creek, Alaska (a ⇒ f)	25	11,084.8	0.83	0.08	17.1	Count
Seldovia, Cook Inlet, Alaska (a ⇒ a)	27	14.8	0.15	0.23	1.1	SR
Southern Panhandle, Alaska (a ⇒ a)	34	8.3	0.94	0.15	2.3	SR
Sunday Creek, Cook Inlet, Alaska (a ⇒ a)	18	1,090.0	0.71	0.26	2.9	SR
Upper Skeena, B.C. (a ⇒ a)	11	19.6	1.00	0.20	1.5	SR
Utka River, Kamchatka (a ⇒ f)	12	182.0	0.45	0.00	2.0	Count
Utka River, Kamchatka (f ⇒ a)	10	7.7	0.78	0.06	10.4	Count
Utka River, Kamchatka (a ⇒ a)	10	124.7	0.67	1.00	2.9	Count
Windy Left, Cook Inlet, Alaska (a ⇒ a)	27	748.0	0.96	0.08	7.0	SR
Windy Right, Cook Inlet, Alaska (a ⇒ a)	27	187.0	0.88	0.19	3.6	SR
Chum salmon (*Oncorhynchus keta*)						
Central Coast, B.C. (a ⇒ a)	30	4.8	1.00	0.24	1.5	SR
Fraser River, B.C. (a ⇒ a)	14	5.0	1.00	0.00	2.0	SR
Hooknose Creek, B.C. (a ⇒ f)	14	15.4	0.92	0.00	2.5	Count
Johnstone Strait (a ⇒ a)	28	4.7	0.89	0.63	2.0	SR

Table 1 (continued)

Population	n	$\dfrac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\dfrac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Minter Creek, Washington (a ⇒ f)	14	352.5	1.00	0.08	4.2	Count
North Coast, B.C. (a ⇒ a)	30	4.6	0.48	0.24	1.0	SR
Queen Charlotte Islands, B.C. (a ⇒ a)	25	11.0	0.21	0.04	1.0	SR
West Coast Vancouver Island, B.C. (a ⇒ a)	25	6.0	0.83	0.21	1.6	SR
Coho salmon (*Oncorhynchus kisutch*)						
Minter Creek, Washington (a ⇒ s)	10	14.2	0.39	0.00	1.1	Count
Steelhead trout (*Oncorhynchus mykiss*)						
Keogh River, B.C. (s ⇒ a)	7	5.7	1.00	0.00	3.3	Count
Keogh River, B.C. (a ⇒ f)	7	5.6	1.00	0.00	3.4	MR and removal
Keogh River, B.C. (a ⇒ s)	7	5.6	1.00	0.33	1.2	MR and count
Sockeye salmon (*Oncorhynchus nerka*)						
Adams Complex, B.C. (a ⇒ a)	39	7,498.8	0.95	0.00	160.8	SR
Ayakulik, Kodiak Island, Alaska (a ⇒ a)	22	25.6	0.95	0.00	2.9	SR
Babine Lake, B.C. (s ⇒ a)	23	14.6	0.86	0.36	1.8	MR and count
Babine Lake, B.C. (f ⇒ s)	23	10.0	0.86	0.23	3.0	MR and count
Babine Lake, B.C. (a ⇒ s)	10	14.7	1.00	0.22	3.6	MR and count
Birkenhead River, B.C. (a ⇒ a)	39	33.0	0.95	0.05	1.4	SR
Black Lake, Alaska (a ⇒ a)	38	22.3	0.69	0.22	2.3	SR
Branch River, Alaska (a ⇒ a)	33	35.5	0.94	0.31	1.5	SR
Bristol Bay, Alaska (a ⇒ a)	45	13.1	0.98	0.00	2.5	SR
Chignik Lake, Alaska (a ⇒ a)	38	7.2	0.31	0.08	0.9	SR
Chilko Lake, B.C. (a ⇒ s)	44	88.2	1.00	0.00	3.5	Count
Chilko River, B.C. (a ⇒ a)	39	72.5	0.68	0.11	2.9	SR
Chilko River, B.C. (s ⇒ a)	41	29.6	0.65	0.03	3.5	Count
Chilko South End, B.C. (s ⇒ a)	14	485.1	1.00	0.15	8.3	Count
Columbia River (a ⇒ a)	19	126.3	0.50	0.00	1.2	SR
Early Stuart Complex, B.C. (a ⇒ a)	39	305.8	0.97	0.00	4.7	SR
Egegik River, Alaska (a ⇒ a)	32	8.3	0.95	0.13	2.0	SR
Egegik River, Alaska (a ⇒ a)	39	8.9	0.84	0.08	2.6	SR
Egegik River, Alaska (a ⇒ s)	12	4.0	0.64	0.36	1.4	SR
Frazer Lake, Alaska (a ⇒ a)	24	54.0	0.63	0.00	3.2	SR
Fulton River, B.C. (a ⇒ f)	28	25.3	0.70	0.22	1.3	Count
Fulton River, Channel 1, B.C. (a ⇒ f)	21	48.1	0.80	0.00	1.8	Count
Fulton River, Channel 2, B.C. (a ⇒ f)	17	6.3	0.94	0.62	1.1	Count
Gates Creek, B.C. (f ⇒ a)	16	741.2	0.80	0.00	6.9	Count
Horsefly River, B.C. (a ⇒ a)	39	27,562.1	1.00	0.05	714.8	SR
Igushik River, Alaska (a ⇒ a)	39	124.2	0.55	0.24	1.6	SR
Karluk River, Alaska (a ⇒ a)	62	8.7	0.66	0.56	1.3	SR
Karymaisky Spring, Kamchatka (a ⇒ f)	8	34.0	1.00	0.00	5.0	Count
Kasilof River, Alaska (a ⇒ a)	21	13.0	0.90	0.10	2.3	SR
Kenai River, Alaska (a ⇒ a)	21	27.1	1.00	0.20	2.5	SR
Kvichak River, Alaska (a ⇒ s)	23	77.3	0.82	0.05	3.9	Count
Kvichak River, Alaska (a ⇒ a)	38	107.2	0.95	0.14	7.6	SR
Lake Dalnee, Kamchatka (a ⇒ s)	12	7.6	0.55	0.27	1.3	Count
Lakelse Lake, B.C. (a ⇒ s)	8	14.8	0.86	0.14	1.8	Count
Late Nadina River, B.C. (f ⇒ a)	11	15.6	0.60	0.00	5.9	Count
Late Stuart Complex, B.C. (a ⇒ a)	38	18,441.8	0.92	0.16	27.9	SR
Little Kitoi Lake, Afognak Is., Alaska (a ⇒ s)	7	9.2	0.50	0.00	1.4	Count
Naknek, Alaska (a ⇒ a)	38	26.4	0.92	0.07	1.9	SR
Naknek-Kvichak Rivers, Alaska (a ⇒ a)	32	16.2	0.95	0.00	1.9	SR
Nushagak River, Alaska (a ⇒ a)	32	33.7	0.58	0.00	1.3	SR
Nuyakuk River, Alaska (a ⇒ a)	20	30.9	0.84	0.47	3.4	SR
Pinkut Channel, B.C. (a ⇒ f)	17	3.2	0.94	0.69	1.5	Count
Pinkut Creek, B.C. (a ⇒ f)	26	27.4	0.44	0.08	1.5	Count
Port John Lake, B.C. (a ⇒ s)	9	30.9	0.50	0.62	0.5	Count
Quesnel Lake, Fraser River, B.C. (a ⇒ f)	10	7,211.9	0.67	0.00	2.7	Acoustics

Table 1 (continued)

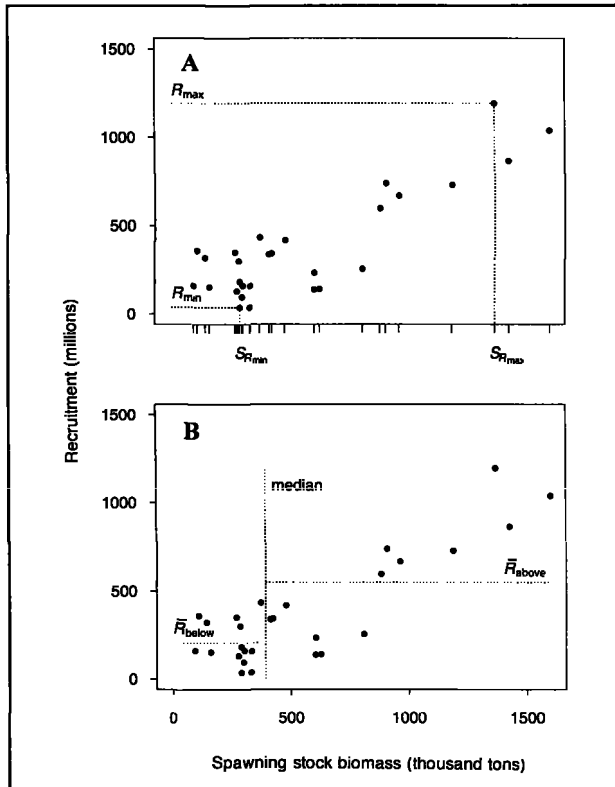| Population	n	$\dfrac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\dfrac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
Red River, Alaska (a ⇒ a)	23	22.8	0.95	0.00	3.1	SR
Rivers Inlet, B.C. (a ⇒ a)	42	9.8	0.98	0.77	1.0	SR
Shuswap Lake, Fraser River, B.C. (a ⇒ f)	14	256.0	0.62	0.23	2.7	Acoustics
Skeena River, B.C. (a ⇒ a)	39	16.0	0.87	0.03	1.4	SR
Smith Inlet, B.C. (a ⇒ a)	10	2.8	0.72	1.00	1.3	SR
Stellako River, B.C. (a ⇒ a)	39	17.1	0.97	0.11	2.6	SR
Tahltan Lake, B.C. (a ⇒ f)	9	26.5	0.12	0.75	0.6	Count
Tahltan Lake, B.C. (a ⇒ s)	9	26.5	0.12	0.88	0.5	Count
Tahltan Lake, B.C. (a ⇒ a)	12	8.3	0.18	0.36	0.8	SR
Tally Creek, B.C. (a ⇒ f)	11	6.7	0.70	0.20	2.4	Count
Togiak River, Alaska (a ⇒ a)	14	9.0	0.85	0.62	1.3	SR
Togiak River, Alaska (a ⇒ a)	33	21.1	0.78	0.34	1.8	SR
Ugashik River, Alaska (a ⇒ a)	30	9.2	0.90	0.72	2.0	SR
Ugashik River, Alaska (a ⇒ a)	38	85.5	1.00	0.05	2.8	SR
Ugashik River, Alaska (a ⇒ s)	9	3.8	0.50	0.38	0.9	SR
Upper Pinkut Creek, B.C. (a ⇒ f)	9	3.4	1.00	0.75	1.2	Count
Weaver Creek, B.C. (a ⇒ a)	39	190.1	1.00	0.11	3.1	SR
Weaver Creek, B.C. (f ⇒ a)	26	16.4	1.00	0.44	1.9	Count
Wood River, Alaska (a ⇒ a)	40	12.9	0.38	0.03	1.5	SR
Chinook salmon (*Oncorhynchus tshawytscha*)						
Wild Canadian Coastwide (a ⇒ a)	26	2.1	0.28	0.88	0.9	SR
Atlantic salmon (*Salmo salar*)						
Bec-Scie, Canada (a ⇒ s)	5	2.5	1.00	0.50	1.5	Count
Ellidaar River, Iceland (a ⇒ a)	37	7.7	0.25	0.69	1.0	Count
Girnock Burn, Scotland (a ⇒ p)	9	5.2	0.25	0.00	1.3	Count
Little Codroy River, Canada (a ⇒ s)	7	16.6	1.00	0.00	1.5	Count
Margaree River, N.S., Canada (a ⇒ a)	37	13.3	0.94	0.22	1.4	Count
Miramichi River, N.B., Canada (a ⇒ p)	13	5.7	0.92	0.00	1.8	Count
Pollett River, Canada (a ⇒ s)	8	28.7	1.00	0.71	2.4	Count
Restigouche River, Canada (a ⇒ p)	11	6.8	0.50	0.20	1.6	Count
River Bush, Northern Ireland (a ⇒ f)	12	4.5	0.27	0.00	0.8	Count and electrofishing
River Bush, Northern Ireland (a ⇒ s)	17	4.5	0.56	0.00	1.1	Count
Shelligan Burn, Section D, Scotland (f ⇒ a)	6	12.0	0.20	0.00	0.9	Count
Tobique River, Canada (a ⇒ a)	9	57.8	0.75	0.00	1.7	Count
Trinite, Canada (a ⇒ s)	8	2.9	1.00	0.57	0.9	Count
Western Arm Brook, Canada (a ⇒ a)	16	13.2	0.47	1.00	0.7	Count
Western Arm Brook, Canada (a ⇒ s)	15	13.2	1.00	0.14	1.4	Count
Brook trout (*Salvelinus fontinalis*)						
Hunt Creek, Michigan (a ⇒ f)	9	2.0	0.88	0.62	1.0	Count
Scorpaeniformes						
Scorpaenidae						
Pacific ocean perch (*Sebastes alutus*)						
Aleutian Is.	30	6.8	0.97	0.79	0.8	SPA
Gulf of Alaska	31	17.1	0.97	0.57	1.9	SPA
U.S. West Coast	29	7.6	0.86	0.07	2.9	SPA
Widow rockfish (*Sebastes entomelas*)						
W. U.S. + Canada	12	5.3	0.73	0.82	1.0	SPA
Redfish (*Sebastes marinus*)						
W. Greenland and Iceland	10	2.9	0.22	0.67	0.2	RV and SPA
Iceland	7	1.4	1.00	0.50	1.2	SPA
Redfish (*Sebastes mentella*)						
North East Arctic	23	19.6	0.91	0.05	3.9	SPA and RV
Squaliformes						
Squalidae						
Spiny dogfish (*Squalus acanthias*)						
Northwest Atlantic	21	11.2	0.85	0.05	1.3	RV

Figure 1

Illustration of the three nonparametric methods applied to spawner-recruitment data for Labrador–Newfoundland cod (Cod NAFO 2J3KL, Table 1). Here spawner abundance is measured as spawning stock biomass. (**A**) The maximum recruitment is R_{max} and the corresponding spawner abundance is S_{Rmax}, which ranks 26th out of 28. Hence $r_{max} = (26-1)/(28-1) \approx 0.93$. Similarly, the minimum recruitment is R_{min} and the corresponding spawner abundance is S_{Rmin} which ranks 8.5 out of 28 (since there is a tie). Hence $r_{max} = (8.5-1)/(28-1) \approx 0.28$. (**B**) The mean recruitment below the median spawner abundance is $\bar{R}_{below}$ whereas the mean recruitment above the median spawner abundance is $\bar{R}_{above}$.

Figure 2

Scatter plots of the relative rank of spawner abundance for the highest recruitment versus the ratio S_{max}/S_{min} for all stocks and for three major families. Data points from series with fewer than 10 pairs of observations are shown as open circles. The horizontal axis has a logarithmic scale. If spawner abundance and recruitment were independent, the distributions would be expected to have a median of 0.5. To help summarize the data, we superimposed curves representing cumulative (from the right) weighted means on the plots in each figure.

tested the null hypothesis that the weighted mean relative rank is less than or equal to 0.5 versus the alternative hypothesis that it is greater than 0.5. A sampled randomization test (Manly, 1991) of the null hypothesis of independence was easily performed. For the ith series, a random rank between 1 and n_i was selected, and the corresponding relative rank computed. This was performed for each series, and the weighted mean of the relative ranks was then computed. Repetition of this procedure (10,000 times sampling with replacement) gives an empirical null distribution of weighted mean relative ranks. If m of these 10,000 weighted means were greater than or equal to the observed weighted mean, we then assigned a one-sided P-value of $\frac{m+1}{10,001}$. The smallest one-sided P-value is thus $\frac{1}{10,001}$.

As with the cumulative weighted means, we took into account the varying reliability of the data based on the range of spawner abundance. Therefore, we performed significance tests beginning with the data having large values of S_{max}/S_{min} and progressively including data with smaller values of S_{max}/S_{min}.

For each family, the highest recruitment tends to occur when spawner abundance is high (Fig. 2). The cumulative weighted means never fell below 0.5 for any family. The cumulative weighted mean began on the right-hand side and accumulated to the left-hand side because we had greater confidence in the relative ranks obtained from time series having wide ranges of spawner abundance. Consequently, the value of the cumulative weighted mean on the extreme left-hand side encompassed all the data shown in the plot. Using the sample size as a weighting factor, we incorporated a greater confidence in the relative ranks obtained from long time series. The randomized test showed that the null hypothesis that

the weighted mean relative rank is less than or equal to 0.5 can be rejected for all stocks combined and for most of the taxonomic groups considered (Table 2A). In moving from left to right in the figure, the sample size used in the test decreased, whereas the reliability of the data (as gauged by S_{max}/S_{min}) increased. The tests were performed for all stocks, and separately for 3 major families. The overall trend of increase from left to right was due to the loss of power as the sample size used in the test decreased.

Hypothesis 2: Does the smallest recruitment occur when spawner abundance is low?

Next, we examined r_{min}, the relative rank of spawner abundance for the lowest recruitment (Fig. 1A). This time, $r_{min} = 0$ implies that the lowest recruitment occurs for the lowest spawner abundance, whereas $r_{min} = 1$ implies that the lowest recruitment occurs for the highest spawner abundance. As before, cumulative weighted means were calculated and a randomization test was performed.

The lowest recruitment tended to occur when spawner abundance was low (Fig. 3). Again, the pattern held for all stocks combined and for most of the taxonomic groups considered. The effect for the lowest recruitment appeared to be less than the effect for highest 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).

Hypothesis 3: Is recruitment greater if spawner abundance is above rather than below the median?

Finally, for each spawner-recruitment series we asked 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 computed the mean recruitment for each section, which we denote as $\bar{R}_{above}$ and $\bar{R}_{below}$ respectively. When the mean recruitment is identical on both sides of the median spawner abundance, the ratio $\bar{R}_{above}/\bar{R}_{below}$ equals 1, or equivalently log($\bar{R}_{above}/\bar{R}_{below}$) = 0. A distribution-free test of this null hypothesis is the one-sample Wilcoxon signed rank test (Conover, 1980; Lehmann, 1975). We computed the ranks of the absolute values of the log ratios. The test statistic was given by the sum of the ranks of the positive log ratios. The logarithm was used because ratios of (for example) 1:2 and 2:1 would result in ties.
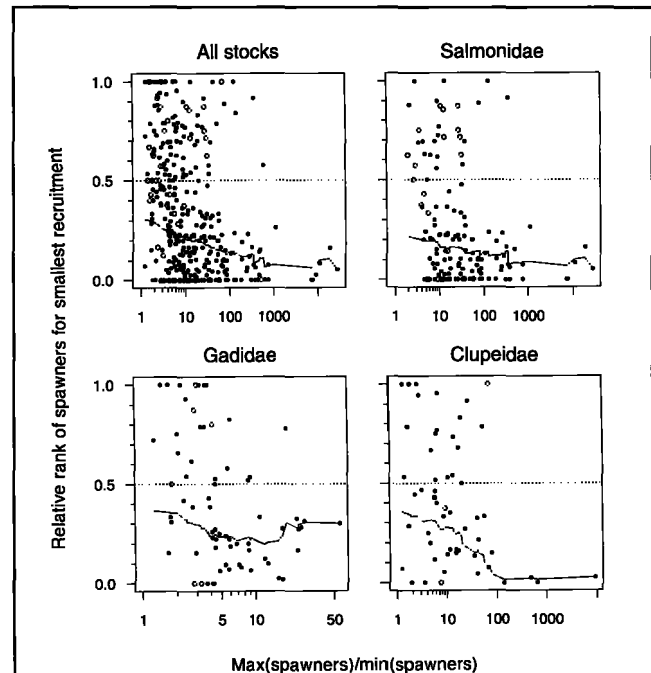

Figure 3

Scatter plots of the relative rank of the spawner abundance for the lowest recruitment versus the ratio S_{max}/S_{min} for all stocks and for three major families. See Figure 2 for explanation of data points, axis labels, and lines.

Our alternative hypothesis was that the median of the distribution of log ratios was greater than 0. For this one-sided test, in order to reject the null hypothesis (at the 5% significance level), we required at least 5 observations. When there were 25 or fewer log ratios, an exact probability for the test was computed; otherwise a normal approximation was used. Note that there were no ties in the absolute values of the log ratios.

This test is conservative because errors in the estimates of the range will bias the estimate of the slope downward (Judge et al., 1984). The ratio of the mean recruitment above the median level of spawners to that below, $\bar{R}_{above}/\bar{R}_{below}$, is greater than 1 for all families if the range of observed spawners is large (Fig. 4). For narrow ranges of spawner data, the ratio is closely clustered. When the data are grouped taxonomically, the pattern holds. The Wilcoxon signed rank test shows that the null hypothesis that the median of the distribution of $\bar{R}_{above}/\bar{R}_{below}$ is 1 can be rejected for all stocks combined and for most of the taxonomic groups considered.

Taxonomic variation

The Clupeidae show strong evidence of greater recruitment at large spawner-abundance levels. This

Table 2

Observed levels of significance for tests based on the data shown in Figure 2 (A) in Figure 3 (B), and in Figure 4 (C). The tests were conducted by 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. Empty cells indicate that there were no observations with the specified values of S_{max}/S_{min}. For populations within the family Salmonidae, series were sometimes available for several different life-stage transitions. The life stages are denoted as follows: a = adults (or eggs); f = fry; s = smolt; and p = parr. They are shown in the table with an arrow notation so that "a ⇒ f" means spawners were adults and recruits were fry or smolts.

A *P*-values corresponding to Figure 2 from one-sided randomization tests with 10,000 samples (with associated numbers of data sets in parentheses). The null hypothesis is that the weighted mean relative rank is less than or equal to 0.5. The alternative hypothesis is that the weighted mean relative rank is greater than 0.5.

Group	S_{max}/S_{min} ≥1		≥2		≥5		≥10		≥50		≥100	
All stocks	< 0.0001	(364)	< 0.0001	(338)	< 0.0001	(243)	< 0.0001	(162)	< 0.0001	(61)	< 0.0001	(35)
Clupeidae	< 0.0001	(55)	0.0002	(48)	0.0001	(40)	< 0.0001	(26)	0.0044	(9)	0.014	(4)
Herring	0.0007	(37)	0.0018	(30)	0.0006	(25)	< 0.0001	(16)	0.017	(5)	0.04	(3)
Sardine	0.18	(7)	0.18	(7)	0.31	(6)	0.2	(5)	0.28	(2)	0.16	(1)
Gadidae	0.004	(68)	0.0025	(61)	0.0003	(28)	< 0.0001	(13)	0.19	(1)		
Cod	0.023	(23)	0.014	(21)	0.024	(11)	0.0042	(5)	0.19	(1)		
Haddock	0.012	(9)	0.012	(9)	0.028	(6)	0.021	(5)				
Merluccius	0.043	(12)	0.047	(9)	0.0082	(4)	0.074	(2)				
Pollock or saithe	0.74	(6)	0.78	(5)	0.49	(2)						
Percidae	0.34	(9)	0.25	(8)	0.33	(5)	0.32	(4)	0.19	(2)	0.19	(2)
Scombridae	0.024	(9)	0.025	(8)	0.06	(6)	0.26	(4)	0.14	(1)		
Sparidae	0.23	(6)	0.23	(6)	0.008	(3)	0.24	(1)	0.24	(1)	0.25	(1)
Pleuronectidae	0.63	(19)	0.63	(17)	0.21	(4)	0.079	(3)				
Plaice	0.63	(8)	0.53	(7)	0.36	(1)	0.36	(1)				
Soleidae	0.45	(7)	0.45	(7)	0.13	(2)						
Salmonidae	< 0.0001	(150)	< 0.0001	(149)	< 0.0001	(133)	< 0.0001	(101)	< 0.0001	(44)	< 0.0001	(26)
Pink salmon	< 0.0001	(53)	< 0.0001	(53)	< 0.0001	(50)	< 0.0001	(42)	< 0.0001	(24)	0.0007	(13)
(a ⇒ a)	< 0.0001	(36)	< 0.0001	(36)	< 0.0001	(34)	< 0.0001	(28)	0.0001	(18)	0.0018	(9)
(a ⇒ f)	0.0098	(11)	0.0094	(11)	0.0091	(11)	0.017	(10)	0.15	(5)	0.067	(3)
(f ⇒ a)	0.023	(6)	0.022	(6)	0.041	(5)	0.059	(4)	0.46	(1)	0.45	(1)
Chum salmon	0.0092	(8)	0.0082	(8)	0.049	(5)	0.29	(3)	0.074	(1)	0.074	(1)
Sockeye salmon	< 0.0001	(65)	< 0.0001	(65)	< 0.0001	(60)	< 0.0001	(46)	< 0.0001	(17)	< 0.0001	(12)
(a ⇒ a)	< 0.0001	(37)	< 0.0001	(37)	< 0.0001	(36)	< 0.0001	(27)	< 0.0001	(11)	< 0.0001	(8)
(a ⇒ f,s)	0.0009	(21)	0.0014	(21)	0.0042	(17)	0.01	(13)	0.012	(4)	0.28	(2)
(f,s ⇒ a)	0.007	(6)	0.0079	(6)	0.008	(6)	0.0081	(6)	0.032	(2)	0.03	(2)
Atlantic salmon	0.065	(15)	0.068	(15)	0.091	(11)	0.0055	(7)	0.33	(1)		
Scorpaenidae	0.0007	(7)	0.0017	(6)	0.0005	(5)	0.012	(2)				

relationship clearly holds for herring, whereas the evidence for sardines is not as strong.

The Gadidae, and particularly cod, show strong evidence for all three hypotheses. Haddock show strong evidence for the first two hypotheses, and weak nonsignificance for the third. The hakes of the genus *Merluccius*, show strong evidence for the hypothesis that strong year classes result from relatively high spawner abundance, fair evidence that the mean recruitment is greater for larger spawner abundances, and no evidence for the second hypothesis, except if there is a wide range of spawner abundances.

There is a relatively small range in observed spawner abundances for pollock, known as "saithe" in the eastern Atlantic. Given the narrow range of observed spawner abundances, there is evidence against the first hypothesis, some evidence for the second hypothesis, and no evidence for the third. An examination of the spawner recruitment curves for this species shows stronger evidence for overcompensation, i.e. reduced recruitment at high spawner abundances, than for any other group (see plots in Myers et al., 1995b). This species appears to be more cannibalistic than other Gadidae. Whiting, which is also highly cannibalistic, shows a similar narrow

Table 2 (continued)

B P-values corresponding to Figure 3 from one-sided randomization tests with 10,000 samples (with associated numbers of data sets in parentheses). The null hypothesis is that the weighted mean relative rank is greater than or equal to 0.5. The alternative hypothesis is that the weighted mean relative rank is less than 0.5.

Group	S_{max}/S_{min} ≥1	≥2	≥5	≥10	≥50	≥100
All stocks	< 0.0001 (364)	< 0.0001 (338)	< 0.0001 (243)	< 0.0001 (162)	< 0.0001(61)	< 0.0001 (35)
Clupeidae	0.0004 (55)	0.0003 (48)	0.0002 (40)	0.0004 (26)	0.0003 (9)	(4)
Herring	0.0021 (37)	0.0014 (30)	0.0002 (25)	0.0002 (16)	0.0011 (5)	(3)
Sardine	0.5 (7)	0.52 (7)	0.59 (6)	0.49 (5)	0.15 (2)	0.032 (1)
Gadidae	0.0007 (68)	0.0001 (61)	< 0.0001 (28)	0.0001 (13)	0.32 (1)	
Cod	0.0037 (23)	0.0042 (21)	0.0003 (11)	0.018 (5)	0.33 (1)	
Haddock	0.001 (9)	0.0006 (9)	0.0093 (6)	0.0053 (5)		
Merluccius	0.68 (12)	0.5 (9)	0.13 (4)	0.19 (2)		
Pollock or saithe	0.26 (6)	0.28 (5)	0.018 (2)			
Percidae	0.63 (9)	0.6 (8)	0.78 (5)	0.7 (4)	0.3 (2)	0.29 (2)
Scombridae	0.011 (9)	0.009 (8)	0.013 (6)	0.16 (4)	0.26 (1)	
Sparidae	< 0.0001 (6)	0.0001 (6)	0.0002 (3)	0.059 (1)	0.065 (1)	0.057 (1)
Pleuronectidae	0.11 (19)	0.068 (17)	0.03 (4)	0.01 (3)		
Plaice	0.21 (8)	0.089 (7)	0.18 (1)	0.19 (1)		
Soleidae	0.75 (7)	0.75 (7)	0.45 (2)			
Salmonidae	< 0.0001 (150)	< 0.0001 (149)	< 0.0001 (133)	< 0.0001 (101)	< 0.0001(44)	< 0.0001 (26)
Pink salmon	< 0.0001 (53)	< 0.0001 (53)	< 0.0001 (50)	< 0.0001 (42)	< 0.0001(24)	0.0002 (13)
(a ⇒ a)	< 0.0001 (36)	< 0.0001 (36)	< 0.0001 (34)	< 0.0001 (28)	< 0.0001(18)	0.013 (9)
(a ⇒ f)	< 0.0001 (11)	< 0.0001 (11)	< 0.0001 (11)	< 0.0001 (10)	0.0001 (5)	0.0023 (3)
(f ⇒ a)	0.0005 (6)	0.0004 (6)	0.0001 (5)	0.0015 (4)	0.081 (1)	0.081 (1)
Chum salmon	0.0034 (8)	0.0042 (8)	0.0004 (5)	0.0025 (3)	0.15 (1)	0.14 (1)
Sockeye salmon	< 0.0001 (65)	< 0.0001 (65)	< 0.0001 (60)	< 0.0001 (46)	< 0.0001(17)	< 0.0001 (12)
(a ⇒ a)	< 0.0001 (37)	< 0.0001 (37)	< 0.0001 (36)	< 0.0001 (27)	< 0.0001(11)	< 0.0001 (8)
(a ⇒ f,s)	0.0005 (21)	0.0004 (21)	0.0001 (17)	0.0002 (13)	0.0002 (4)	0.049 (2)
(f,s ⇒ aa)	0.0055 (6)	0.0049 (6)	0.0042 (6)	0.0047 (6)	0.024 (2)	0.026 (2)
Atlantic salmon	0.026 (15)	0.026 (15)	0.099 (11)	0.11 (7)	0.11 (1)	
Scorpaenidae	0.36 (7)	0.36 (6)	0.33 (5)	0.24 (2)		

range in observed spawner abundance and provides no evidence for our hypotheses.

Within the Perciformes, the freshwater Percidae, represented by perch of the genus *Perca*, and walleye and pikeperch of the genus *Stizostedion*, provide moderate evidence for the three hypotheses only when there is a very wide range of observed spawner abundance. However, for most of the marine species of the order Perciformes (e.g. the Scombridae, the mackerel and tunas, and the Sparidae, the sea breams) there was very strong evidence for all three hypotheses. One explanation for this pattern is that freshwater species for which we had data may have been less subject to overexploitation, but the question certainly deserves further study.

The order that showed the weakest amount of the relationship between the abundance of spawners and subsequent recruitment was the flatfish, i.e. the Pleuronectiformes. There was evidence for this rela-

tionship with both Pleuronectidae and Soleidae in all the tests for wider ranges in spawner abundance, i.e. the P-values in Table 2 were less than 0.5; however, these relationships were not statistically significant. The relatively weak relationship for flatfish may be caused by the strong density-dependent mortality for these populations (Myers and Cadigan, 1993; Iles, 1994). Furthermore, many of these populations have juvenile nursery grounds in regions where exploitation cannot take place. For these reasons, the range of spawner abundance has been relatively narrow, which reduces our ability to detect any relationship.

For the salmonids included in this analysis, large year classes almost always are associated with high spawner levels. This conclusion is true for the pink, chum, sockeye, and Atlantic salmon for each life-stage transition considered (Table 2). Our conclusion differs from that of Larkin (1977), who stated that for the Pa-

Table 2 (continued)

C P-values corresponding to Figure 4 from one-sample Wilcoxon signed-rank tests (with associated numbers of data sets in parentheses). The null hypothesis is that the median of $\log(R_{above}/R_{below})$, is less than or equal to 0. The alternative hypothesis is that the median is greater than 0. For this test, at least 5 observations were required to obtain a P-value less than 0.05.

Group	S_{max}/S_{min} ≥1		≥2		≥5		≥10		≥50		≥100	
All stocks	< 0.0001	(364)	< 0.0001	(338)	< 0.0001	(243)	< 0.0001	(162)	< 0.0001	(61)	< 0.0001	(35)
Clupeidae	0.0041	(55)	0.0068	(48)	0.0018	(40)	< 0.0001	(26)	0.0039	(9)	0.062	(4)
Herring	0.025	(37)	0.04	(30)	0.0031	(25)	0.0013	(16)	0.031	(5)	0.12	(3)
Sardine	0.15	(7)	0.15	(7)	0.16	(6)	0.062	(5)	0.5	(2)	0.5	(1)
Gadidae	0.0016	(68)	0.0011	(61)	0.00028	(28)	0.00061	(13)	0.5	(1)		
Cod	0.0017	(23)	0.00069	(21)	0.00098	(11)	0.031	(5)	0.5	(1)		
Haddock	0.33	(9)	0.33	(9)	0.22	(6)	0.16	(5)				
Merluccius	0.076	(12)	0.027	(9)	0.062	(4)	0.25	(2)				
Pollock or saithe	0.28	(6)	0.5	(5)	0.25	(2)						
Percidae	0.54	(9)	0.42	(8)	0.59	(5)	0.56	(4)	0.25	(2)	0.25	(2)
Scombridae	0.064	(9)	0.098	(8)	0.22	(6)	0.44	(4)	0.5	(1)		
Sparidae	0.047	(6)	0.047	(6)	0.12	(3)	0.5	(1)	0.5	(1)	0.5	(1)
Pleuronectidae	0.24	(19)	0.24	(17)	0.19	(4)	0.12	(3)				
Plaice	0.32	(8)	0.23	(7)	0.5	(1)	0.5	(1)				
Soleidae	0.53	(7)	0.53	(7)	0.25	(2)						
Salmonidae	< 0.0001	(150)	< 0.0001	(149)	< 0.0001	(133)	< 0.0001	(101)	< 0.0001	(44)	< 0.0001	(26)
Pink salmon	< 0.0001	(53)	< 0.0001	(53)	< 0.0001	(50)	< 0.0001	(42)	< 0.0001	(24)	0.00012	(13)
(a ⇒ a)	< 0.0001	(36)	< 0.0001	(36)	< 0.0001	(34)	< 0.0001	(28)	< 0.0001	(18)	0.002	(9)
(a ⇒ f)	0.00098	(11)	0.00098	(11)	0.00098	(11)	0.002	(10)	0.062	(5)	0.12	(3)
(f ⇒ a)	0.016	(6)	0.016	(6)	0.031	(5)	0.062	(4)	0.5	(1)	0.5	(1)
Chum salmon	0.012	(8)	0.012	(8)	0.031	(5)	0.12	(3)	0.5	(1)	0.5	(1)
Sockeye salmon	< 0.0001	(65)	< 0.0001	(65)	< 0.0001	(60)	< 0.0001	(46)	< 0.0001	(17)	0.00024	(12)
(a ⇒ a)	< 0.0001	(37)	< 0.0001	(37)	< 0.0001	(36)	< 0.0001	(27)	0.00049	(11)	0.0039	(8)
(a ⇒ f,s)	0.0031	(21)	0.0031	(21)	0.0064	(17)	0.02	(13)	0.062	(4)	0.25	(2)
(f,s ⇒ a)	0.016	(6)	0.016	(6)	0.016	(6)	0.016	(6)	0.25	(2)	0.25	(2)
Atlantic salmon	0.021	(15)	0.021	(15)	0.021	(11)	0.11	(7)	0.5	(1)		
Scorpaenidae	0.29	(7)	0.34	(6)	0.094	(5)	0.25	(2)				

Discussion

cific salmon species of the genus *Oncorhynchus*, "recruitment is maximum at some intermediate stock size." The three hypotheses hold for the four salmon species in Table 2 and for all life-stage transitions.

Could our results be an artifact of the necessary relationship between recruitment and subsequent spawner abundance? It has been argued that the observed relationships between spawners and recruitment is a by-product of the high autocorrelations present in some spawner and recruitment series. Consider a simple example in which recruitment is unrelated to the spawner abundance but is completely determined by the environment. Let recruitment be a first-order autoregressive process with autocorrelation parameter ρ, i.e. the correlation of recruitment with lag t is ρ^t. For a semelparous spe-

cies, or a heavily-exploited species with relatively little survival after reproduction, the amount of variance in recruitment that would be "explained" by this process is ρ^{2a}, where a is the age at maturity. For example, if the age at maturity is $a = 4$ and the autocorrelation in recruitment is $\rho = 0.4$, then only 0.066% of the variance would be explained by spawner abundance. Thus, this mechanism will be important only when there is high environmental autocorrelation in recruitment and low age at maturity. However, when we restricted our analysis to data series with estimated autocorrelation less than 0.4, the observed patterns remained (Fig. 5). Alternative cutoff values for the degree of autocorrelation produced similar results. We conclude that our results are not caused by autocorrelation in recruitment and the necessary relationship between recruitment and subsequent spawner abundance.

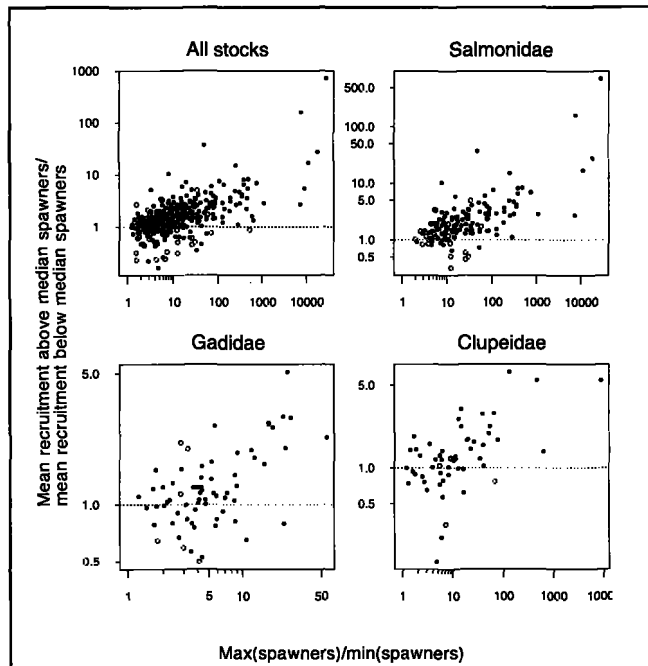In each of our three tests, the hypothesis that there is no practical relationship between spawners and

Figure 4

Scatter plots of the ratio $\overline{R}_{above}/\overline{R}_{below}$ versus the ratio S_{max}/S_{min} for all stocks, and for three major families. Data points from series with fewer than 10 pairs of observations are shown as open circles. Both axes have logarithmic scales. If spawner abundance and recruitment were independent, the distribution would be expected to have a median of 1.

Figure 5

Test of the hypothesis that our results are caused by autocorrelation of recruitment. This scatterplot repeats the analysis shown in Figure 2 (the relative rank of spawner abundance for the highest recruitment versus the ratio S_{max}/S_{min}), except that populations with an autocorrelation in recruitment of 0.4 or greater are eliminated. Data points from series with fewer than 10 pairs of observations are shown as open circles. If spawner abundance and recruitment were independent, the distributions would be expected to have a median of 0.5. To help summarize the data, curves representing cumulative (from the right) weighted means are superimposed on the plots in each figure.

subsequent recruitment can be rejected. These conclusions hold for almost every species and family analyzed. These results also help to explain the widely-held belief that spawner abundance and recruitment are not related. When there is little variation in spawner abundance, no practical relation between spawners and subsequent recruitment may seem to be the case; however, wider ranges of spawner data reveal that the relationship holds. 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 a rejection of spawner-recruitment relationships.

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
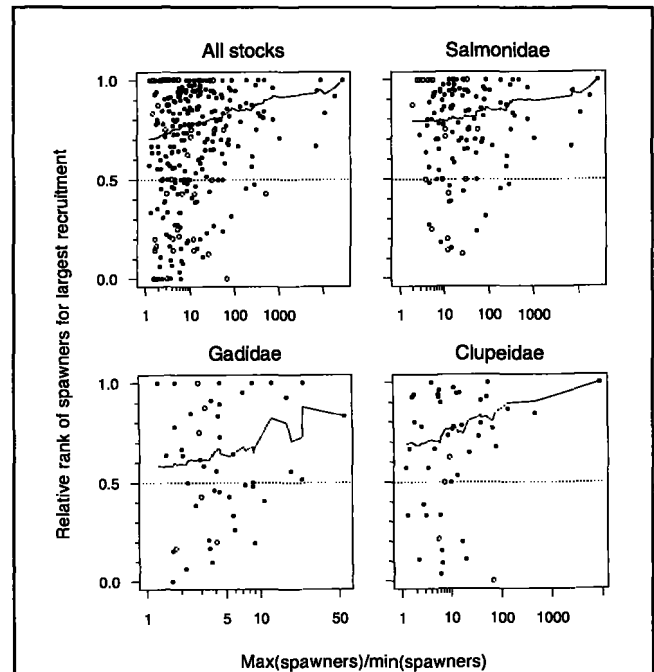
$\overline{R}_{above}/\overline{R}_{below}$. A second potential source of bias arises in the statistical analysis of spawner-recruitment relationships because the "independent" variable, spawners, is not independent of the interannual variation in the spawner-recruitment relationship. For a given spawning population, above-average recruitment tends to result in higher spawning populations, whereas 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; Myers and Barrowman, 1995). 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.

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, analyses. If a population is "managed" such that spawner abundance is reduced to low levels, the manager should not be surprised to observe the smallest recruitment ever recorded.

Are our results of practical importance for the management of fish populations? We believe the answer is clearly "yes." The simple observation that recruitment is generally lower at lower spawner abundances implies that recruitment overfishing is a pervasive problem among heavily exploited fish populations. The collapse of many of the fish stocks in the world, e.g. cod in eastern Canada (Myers et al., in press), can be at least partially blamed on reduced recruitment associated with reduction in spawner abundance.

We conclude that fish populations should be managed so as to maintain sufficient spawner abundance to yield high recruitment. Recruitment overfishing appears to be a common problem.

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