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Depensatory Recruitment and the Collapse of Fisheries

by

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Many of the world's fisheries resources are heavily exploited and a number of stocks have experienced severe declines in abundance[1-3]. An important question remains whether reducing fishing mortality will enable a stock to recover. Theoretical studies show that depensatory models of population dynamics, where per capita reproductive success in terms of recruitment declines at low population levels, can have multiple equilibria[2,4-10] that permit sudden changes in population abundance to occur (e.g., the collapse of a fishery). If depensation exists, possibly the result of predator saturation or increased difficulty in obtaining mates[4], reduced fishing may be insufficient to elicit stock recovery. We analyzed data for 106 fish populations to test statistically for depensation in the relationships between spawning stock abundance and recruitment; only two showed significant depensation. Power analyses strengthened our conclusions that most exploited populations do no exhibit depensatory stock-recruitment dynamics and that stocks collapse because of environmental change or over-exploitation. We predict that the effects of overfishing are, in general, reversible.

We fitted models with and without depensation, using maximum likelihood estimation, and compared their goodness of fit. The models used the Beverton-Holt stock and recruitment function[11], modified to include depensatory recruitment[10], given by

$$R = \frac{\alpha S^{\delta}}{1+(S^{\delta}/K)}$$

where R is recruitment of new fish to the population, S is spawning stock biomass and α, K and δ are parameters, all positive. The parameter δ controls the depensation in the recruitment curve. If δ equals 1, there is no depensation and the standard Beverton-Holt stock and recruitment relationship results. For δ greater than 1, the relationship becomes depensatory, with a sigmoid shape to the curve, resulting in a new, unstable equilibrium point at low spawning stock abundance. Our test used the likelihood ratio between the model with δ as a free parameter and the model with δ fixed at 1.

Data on 106 fish stocks were extracted from the database prepared by Myers et al.[12] Stock and recruitment time series for each stock were obtained from assessments prepared for management advice on the harvest of marine and anadromous fishes. We selected from the data base those stocks for which the time series encompassed at least 15 years.

For 6 of the 106 stocks, the model with δ as a free parameter gave a significantly better fit at the 0.05 level (Table 1; Fig. 1). In only 2 cases was the parameter greater than 1. One was Icelandic spring spawning herring (Fig. 2). This is the only population we examined in which the fishery collapsed and remained commercially extinct. Strong environmental changes have been identified which likely affected this stock and may have been responsible for its demise[13]. Decreased salinity and oxygen levels have been firmly established as the cause of the decline in the other population, Southern Baltic cod[14].

Depensatory recruitment, appearing as an inflection in the underlying stock and recruitment relationship at low stock sizes, will clearly be difficult to detect in many data sets because there may be few observations in this portion of the curve. Therefore we used a statistical power analysis[15] to assess the probability of detecting depensation if it was actually present in each data set. For each data set, we estimated the parameters α and K of the Beverton-Holt model. Next we set δ equal to 2 and constructed a sigmoid Beverton-Holt model that matched the fitted model at the 50% maximum recruitment point and at the asymptote at infinite stock size. We then generated pseudo-random recruitment from a lognormal distribution with the shape parameter estimated from the fitted model and the mean given by the constructed curve at each of the observed spawning stock biomasses. Finally, we performed the likelihood ratio test for depensation described above and repeated the procedure 100 times to estimate statistical power (Fig. 3).

Statistical power was greater than 0.5 for 27 stocks for $\delta = 2$ (Table 1). In each of these, large declines in abundance have occurred, providing some data at low stock size. If depensatory recruitment is a general phenomenon in fish populations, we would have expected more than 2 of the 106 stocks examined to show significant depensation in the observed data.

Theoretical analyses and previous, non-statistical descriptions of depensatory recruitment for fish stocks[9,10,16,17] are not substantiated by our comparative analysis of the available data. This suggests that models with strong nonlinear behaviour may not be applicable to fish population dynamics. In particular our analysis indicates that fish populations do not collapse because of depensation. The implication is that reductions in fishing mortality rates implemented by resource managers should enable stocks to rebuild, unless important environmental or ecosystem level changes occur which alter the underlying dynamics of the stock. We conclude that the effects of overfishing are, in general, reversible.

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Table 1. Results of the likelihood ratio tests for depensation and results from the power analyses using the modified Beverton-Holt function. The number of pairs of data points is shown as n. The estimated depensation parameter δ, the p-value from the likelihood ratio test (at a significance level $\alpha = 0.05$), and the estimated power (when the true $\delta = 2$) are given.

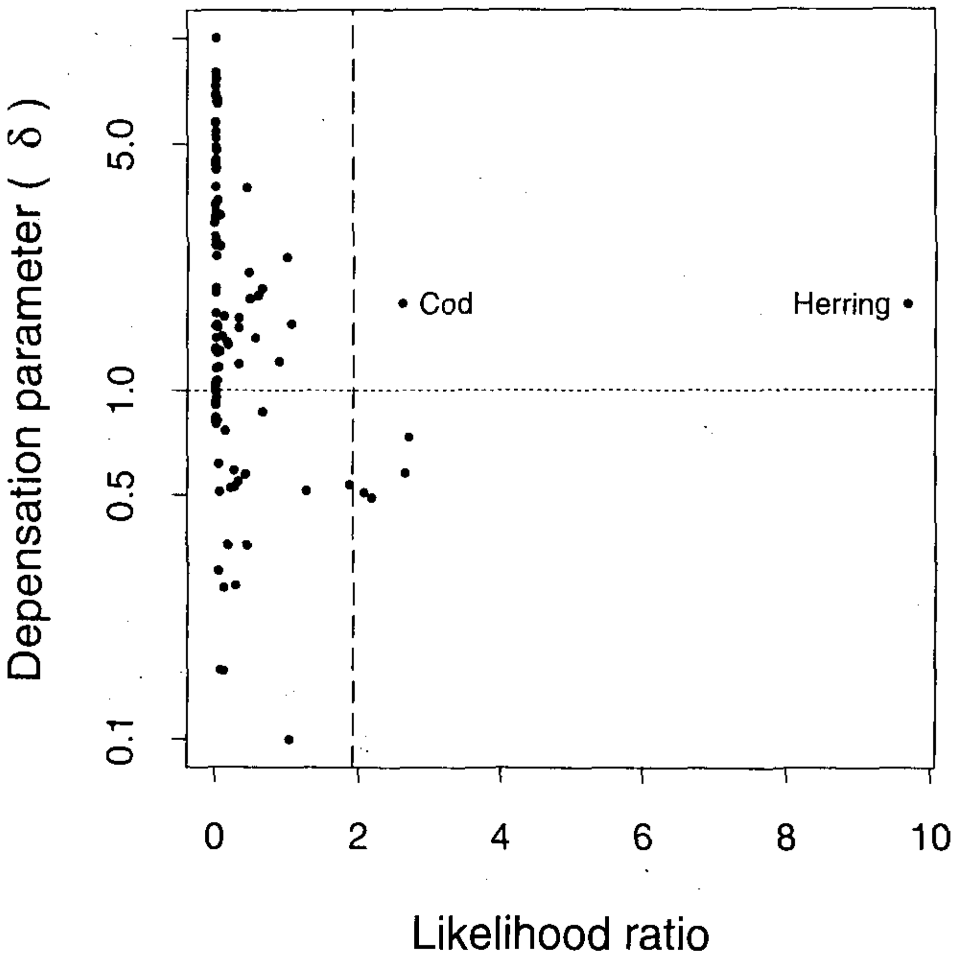
Stock	n	δ	p-value	power
Clupeiformes				
Clupeidae				
Atlantic Menhaden (*Brevoortia tyrannus*)				
U.S. Atlantic	35	0.93	0.96	0
Gulf Menhaden (*Brevoortia patronus*)				
Gulf of Mexico	19	0.36	0.35	0.31
Herring (*Clupea harengus*)				
Baltic, Bothnian Bay	15	1.16	0.96	0.01
Baltic, Bothnian Sea	15	4.24	0.94	0
S.W. Baltic	19	2.63	0.85	0.01
S. Baltic	15	1.91	0.94	0
Central Baltic	16	1.32	0.87	0.85
Gulf of Finland	18	1.96	0.91	0
Gulf of Riga	19	0.83	0.95	0.02
West of Scotland	18	1.31	0.91	0
West of Ireland	*19*	*2.59*	*0.9*	*0*
Iceland (Spring spawners)	23	1.78	< 0.01	1
Iceland (Summer spawners)	43	0.58	0.02	0.98
North Sea	41	1.42	0.29	0.94
Northern Irish Sea	18	0.55	0.43	0.01
Norway (Spring spawners)	39	0.52	0.11	0.82
Georges Bank	15	2.39	0.16	
Gulf of Maine	23	5.78	0.93	0
Central B.C., Canada	38	1.87	0.28	0
S. Strait of Georgia, Canada	38	1.62	0.42	0.05
N. Strait of Georgia, Canada	38	1.38	0.56	0.47
N. W. Vancourver Island, Canada	38	2.75	0.91	0.01
Prince Rupert District, Canada	38	1.03	0.99	0
Queen Charlotte Islands, Canada	38	1.95	0.26	0
S.W. Vancouver Island, Canada	38	2.99	0.97	0.01
S.E. Alaska	30	5.21	0.93	0
Eastern Bering Sea	26	4.91	0.94	0
Yellow Sea	15	0.36	0.56	0.06
Pacific sardine (*Sardinops caerulea*)				
California	31	1.21	0.18	1
Southern african pilchard (*Sardinops ocellatus*)				
South Africa	31	0.8	0.88	0.05
Sprat (*Sprattus sprattus*)				
Central Baltic	15	4.43	0.94	0
S.E. Baltic	19	0.16	0.62	0
Engraulidae				
Anchovy (*Engraulis capensis*)				
South Africa	18	0.28	0.46	0
Northern anchovy (*Engraulis mordax*)				
California	25	4.53	0.93	0
Peruvian anchoveta (*Engraulis ringens*)				
Northern/Central Stock Peru	19	1.56	0.15	0.96
Gadiformes				
Gadidae				
Blue whiting (*Micromesistius poutassou*)				
N.E. Atlantic	20	3.38	0.9	0
Cod (*Gadus morhua*)				
S.E. Baltic	20	1.78	0.02	0.53
Central Baltic	19	0.92	0.93	0
Celtic Sea	20	1.63	0.62	0.95
Faroe Plateau	28	1.53	0.93	0.01
West of Scotland	23	7.66	0.88	0
Iceland	34	0.81	0.95	0
Irish Sea	22	3.23	0.89	0
Kattegat	19	1.06	0.95	1
W. Coast of Greenland	31	0.49	0.04	0.53
Labrador - Newfoundland	27	0.51	0.04	0.77
S. Grand Banks	28	0.52	0.47	0.11
N. Gulf of St. Lawrence	15	2.42	0.91	0
St. Pierre Bank	26	1.36	0.54	0.01
S. Gulf of St. Lawrence	37	5.41	0.85	0
E. Scotian Shelf	31	1.67	0.94	0
Browns Bank	*41*	*6.57*	*0.82*	*0*
N.E. Arctic	38	1.3	0.71	0.85
North Sea	27	2.17	0.34	0

Table 1 (*continued*)

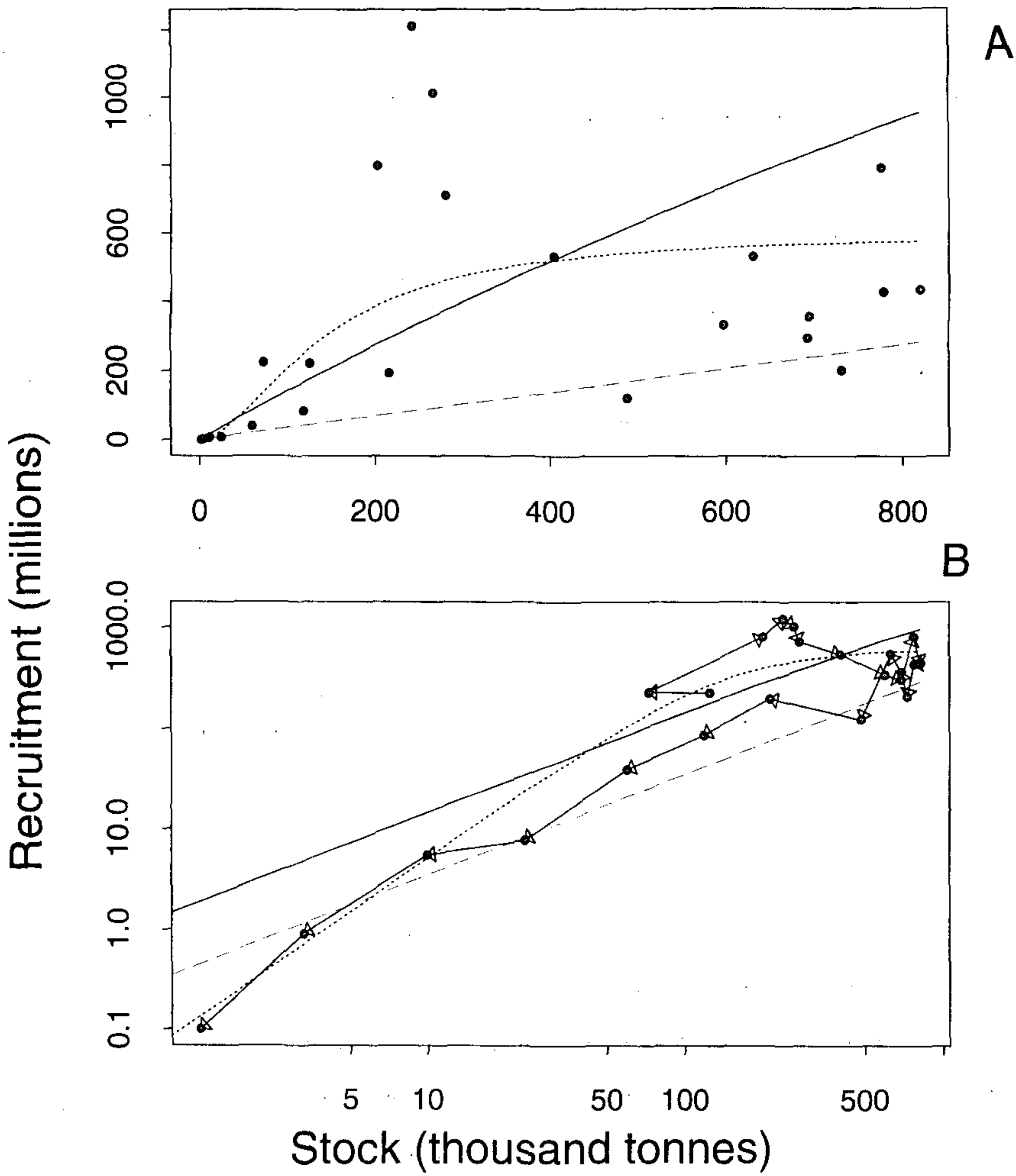
Stock	n	δ	p-value	power
Haddock (*Melanogrammus aeglefinus*)				
Faroe Plateau	27	2.68	0.92	0
Iceland	28	5.74	0.9	0
E. Scotian Shelf	38	0.54	0.05	0.81
Browns Bank	24	3.78	0.35	0
George's Bank	58	1.19	0.43	0.84
N.E. Arctic	39	0.95	0.88	0.88
North Sea	30	1.02	0.99	0
West of Scotland	24	6.96	0.94	0
Pollock or saithe (*Pollachius virens*)				
Faroe	28	2.59	0.85	0
West of Scotland	20	6.5	0.81	0
Iceland	26	2.63	0.86	0
N.E. Arctic	21	0.9	0.96	0
North Sea	21	0.61	0.78	0
Walleye pollock (*Theragra chalcogramma*)				
E. Bering Sea	24	6.73	0.81	0
Gulf of Alaska	21	1.01	0.93	0
Japan-Pacific coast of Hokkaido	15	0.27	0.64	0
Whiting (*Merlangius merlangus*)				
West of Scotland	25	3.15	0.7	0
North Sea	26	4.36	0.89	0
Merlucciidae				
Hake (*Merluccius capensis*)				
Southern African	20	4.81	0.87	0
Pacific hake (*Merluccius productus*)				
W. US. + Canada	30	0.3	0.81	0.01
Silver hake (*Merluccius bilinearis*)				
Mid Atlantic Bight	33	1	1	1
George's Bank	33	0.86	0.25	1
Phycidae				
Red hake (*Urophysics chuss*)				
NAFO S. New England	15	7.32	0.97	0
Perciformes				
Ammodytidae				
Sandeel (*Ammodytes marinus*)				
Shetland	16	1.52	0.79	0.01
Carangidae				
Cape horse mackerel (*Trachurus capensis*)				
Southern African	17	3.79	0.94	0
Lutjanidae				
Silk Snapper (*Lutjanus synagris*)				
Cuba	17	2.58	0.71	0
Scombridae				
Mackerel (*Scomber scombrus*)				
N.W. Atlantic	28	0.52	0.52	0.11
N.E. Atlantic	19	3.11	0.95	0
Pacific mackerel (*Scomber japonicus*)				
Southern California	36	7.99	0.95	0
Pleuronectiformes				
Pleuronectidae				
American plaice (*Hippoglossoides platessoides*)				
Grand Banks	19	1.17	0.77	0
Pacific halibut (*Hippoglossus stenolepis*)				
N. Pacific	47	1.42	0.88	0.01
Plaice (*Pleuronectes platessa*)				
English Channel	16	1.83	0.33	0.66
Irish Sea	26	3.45	0.8	0.01
Kattegat	22	0.59	0.47	0.6
North Sea	33	4.28	0.86	0
Yellowtail flounder (*Limanda ferruginae*)				
Grand Banks	15	1.43	0.67	0
George's Bank	16	0.51	0.74	0.25
S. New England	17	40.3	0.95	0
Soleidae				
Sole (*Solea vulgaris*)				
Celtic Sea	18	3.48	0.79	0
English Channel	19	1.55	0.82	0
English Channel	22	0.81	0.81	0.92
Irish Sea	20	3.37	0.91	0
North Sea	34	6.85	0.92	0

Table 1 (*continued*)

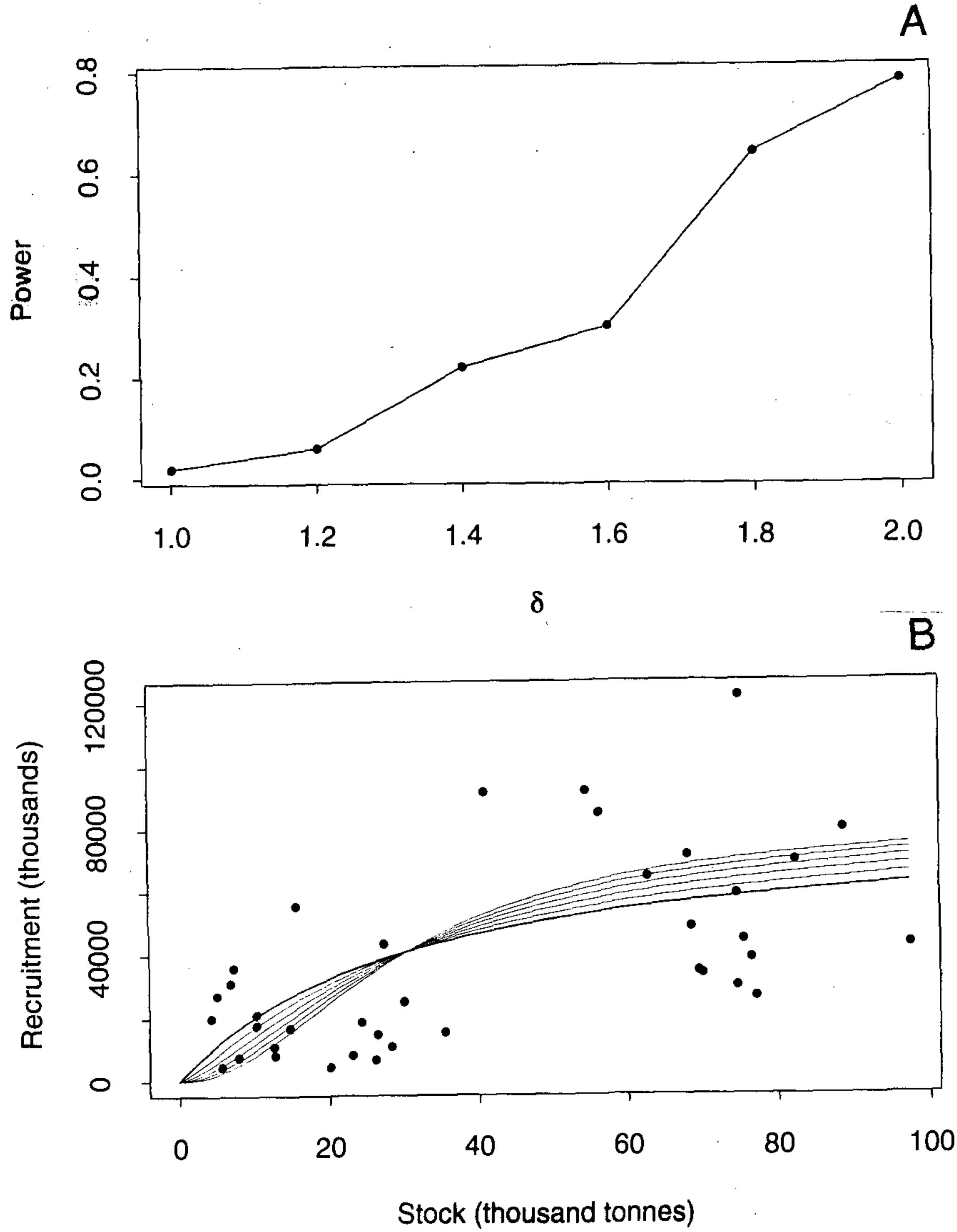
Stock	*n*	δ	p-value	power
Salmoniformes				
Salmonidae				
Pink salmon (*Oncorhynchus gorbuscha*)				
Fraser River, Canada	16	1.29	0.79	0.72
Sockeye salmon (*Oncorhynchus nerka*)				
Adams Complex, Canada	38	0.99	0.92	1
Birkenhead River, Canada	37	0.57	0.36	0.65
Chilko River, Canada	38	1.07	0.82	1
Early Stuart Complex, Canada	38	0.73	0.02	1
Horsefly River, Canada	38	1	0.96	0.32
Rivers Inlet, Canada	36	0.16	0.7	0.01
Skeena River, Canada	*45*	*1.52*	*0.42*	*1*
Stellako River, Canada	38	0.76	0.6	1



1. Results of likelihood ratio tests for depensatory recruitment for 106 fish populations. The null hypothesis was that the depensation parameter δ was equal to 1. When the likelihood ratio (abscissa) is greater than $\frac{1}{2}\chi^2_{1,0.05}$ (the vertical dashed line), the null hypothesis is rejected with a Type I error probability of 0.05. Depensation parameter estimates (ordinate) greater than 1 (the horizontal dashed line) indicate depensatory recruitment. Estimates less than 1 give stock and recruitment relationships with high slopes at the origin, indicating no apparent decline of recruitment at low spawning stock biomass. Two populations are found to have $\delta > 1$ and a significant likelihood ratio: Southern Baltic cod and spring spawning Icelandic herring.



2. Fitted stock and recruitment relationships for Icelandic spring spawning herring. A: Observed data are shown by solid circles. The solid line is the fitted Beverton-Holt relationship with depensation parameter, δ, fixed at 1. The dotted line is the same function with the depensation parameter fitted freely with a resulting estimate of 1.82 which is significant at the 0.05 Type I error level. The dashed line gives a replacement line of recruits to spawners when there is no fishing on the stock, i.e., the inverse of the slope of this line is the spawning biomass obtained per recruit in the absence of fishing. Points below this line indicate that the spawning biomass in those years would not have replaced itself even without additional mortality due to fishing. B: Same as in A, except on a logarithmic scale to highlight points near the origin. The time sequence of recruitments is shown by arrows.



3. Power analysis for the ability to detect depensatory recruitment for Gulf of St. Lawrence haddock. The power analysis is described in the text. A: The statistical power (the probability of concluding that the alternative hypothesis is true when in fact it is) is shown for underlying stock-recruitment curves with different levels of depensation. B: Stock and recruitment curves with different depensation parameters, δ, graduated from 1 to 2 in increments of 0.2.