Population Dynamics of Exploited Fish Stocks at Low Population Levels

R. A. Myers, N. J. Barrowman, J. A. Hutchings, A. A. Rosenberg

Models of population dynamics in which per capita reproductive success declines at low population levels (variously known as depensation, the Allee effect, and inverse density-dependence) predict that populations can have multiple equilibria and may suddenly shift from one equilibrium to another. If such depensatory dynamics exist, reduced mortality may be insufficient to allow recovery of a population after abundance has been severely reduced by harvesting. Estimates of spawner abundance and number of surviving progeny for 128 fish stocks indicated only 3 stocks with significant depensation. Estimates of the statistical power of the tests strengthen the conclusion that depensatory dynamics are not apparent for fish populations at the levels studied.

Many of the world's fisheries are heavily exploited, and a number of stocks have experienced severe declines in abundance, many of them very suddenly (*1*). The causes of the sudden declines and the potential for recovery for a stock when fishing is reduced have remained undetermined. The existence of depensatory dynamics would affect this potential for recovery.

Ecosystems that exhibit multiple stable states typically include a highly nonlinear functional feeding response in which predators are saturated at high levels of prey (*2*). Similar dynamics will result if reproductive success is reduced at low population densities because of the difficulty in finding mates; this is sometimes known as the Allee effect. Both predator saturation and the Allee effect can result in a low per capita production of new recruits to a population if the number of reproducing animals is reduced to a low level, an effect known as depensation (*3*). Although these arguments are appealing, no rigorous empirical studies have examined the hypothesis that natural populations exhibit depensatory dynamics.

We analyzed models with and without depensation, using maximum likelihood estimation assuming log-normally distributed variation about the mean, and compared their goodness of fit to the observed data (Table 1) (*4*). This is equivalent to estimation using log-transformed data and assuming additive normal errors. The models used the Beverton-Holt spawner and recruitment function, modified to include depensatory recruitment (*5*), given by

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

where R is recruitment of new fish to the population; S is a metric of spawner abundance; and α, K, and δ are all positive parameters. The parameter δ controls the depensation in the recruitment curve. If δ equals 1, there is no depensation. Depensatory dynamics are characterized by $\delta > 1$ and a sigmoidally shaped recruitment curve, with an unstable equilibrium point at low spawner abundance (Fig. 1). Our test used the likelihood ratio between the maximum likelihood fit of the model with δ as a free parameter and the model with δ fixed at 1.

Data on 128 fish stocks were extracted from the database prepared by Myers *et al.* (*4*). Spawner and recruitment time series for each stock were obtained from assessments prepared to advise management on the harvest of marine and anadromous fishes. We selected from the database those stocks for which the time series encompassed at least 15 years.

For 9 of the 128 stocks, the model with δ as a free parameter gave a significantly better fit at the 0.05 level (Fig. 2 and Table

Table 1. Results of the likelihood ratio tests for depensation and results from the power analyses using the modified Beverton-Holt function for the 26 stocks for which the estimated power (when the true $\delta = 2$) was found to be >0.95. The table lists the number of pairs of data points *n*, the estimated depensation parameter δ, the *P* value from the likelihood ratio test, and the estimated power (when the true $\delta = 2$).

Population	*n*	δ	*P* value	Power
Clupeiformes				
Clupeidae				
Herring (*Clupea harengus*)				
Central Baltic	16	1.12	0.89	1.00
Downs stock	65	0.56	<0.01	1.00
Iceland (spring spawners)	23	1.78	<0.01	1.00
Iceland (summer spawners)	43	0.58	0.02	0.99
North Sea	41	1.42	0.29	0.97
Pacific sardine (*Sardinops caerulea*)				
California	31	1.21	0.18	1.00
Engraulidae				
Peruvian anchoveta (*Engraulis ringens*)				
Northern-Central Stock Peru	19	1.86	0.12	1.00
Gadiformes				
Gadidae				
Cod (*Gadus morhua*)				
Labrador	28	0.60	0.04	0.98
Southeast Baltic	22	0.82	0.59	1.00
Celtic Sea	20	1.14	0.82	1.00
Kattegat	19	1.06	0.95	1.00
Haddock (*Melanogrammus aeglefinus*)				
Georges Bank	58	1.19	0.43	1.00
Northeast Arctic	39	0.95	0.88	0.98
Merlucciidae				
Silver hake (*Merluccius bilinearis*)				
Georges Bank	33	0.86	0.25	1.00
Mid-Atlantic Bight	33	1.00	1.00	1.00
Salmoniformes				
Salmonidae				
Pink salmon (*Oncorhynchus gorbuscha*)				
Sashin Creek, Little Port Walter, Alaska	25	1.35	0.03	1.00
Prince William Sound, Alaska	15	1.47	0.04	1.00
Central Alaska	25	0.67	0.04	1.00
Sockeye salmon (*Oncorhynchus nerka*)				
Adams Complex, British Columbia, Canada	38	0.99	0.92	1.00
Chilko River, Canada	38	1.07	0.82	1.00
Egegik, Alaska	32	0.80	0.62	1.00
Horsefly River, Canada	38	1.00	0.96	1.00
Kvichak River, Alaska	25	0.91	0.53	1.00
Skeena River, Canada	39	1.24	0.69	0.96
Stellako River, Canada	38	0.76	0.60	1.00
Early Stuart Complex, Canada	38	0.73	0.02	1.00

R. A. Myers and N. J. Barrowman, Northwest Atlantic Fisheries Centre, Science Branch, Post Office Box 5667, St. John's, Newfoundland A1C 5X1, Canada.
J. A. Hutchings, Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H 4J1 Canada.
A. A. Rosenberg, National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543, USA.

1). In three cases, the estimate of δ was greater than 1 (Fig. 3). Spring-spawning Icelandic herring constitute the only population we examined in which the fishery collapsed and remained commercially extinct. Strong environmental changes have been identified that likely affected this stock and may have been responsible for its demise (6). The only other stocks with significant depensation are Pacific salmon stocks, which have been driven to extremely low levels by fishing and habitat loss (7).

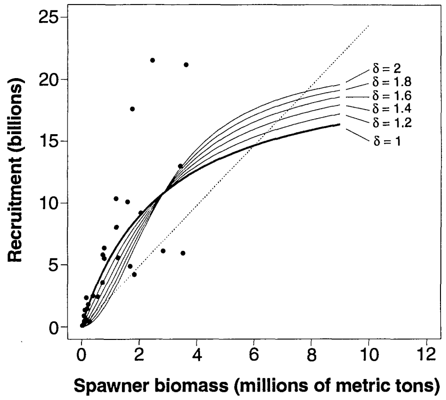

Fig. 1. Spawner recruitment data for the California sardine (dots) compared with theoretical modified Beverton-Holt spawner recruitment curves illustrating depensatory dynamics as determined by δ. The heavy solid line is the estimated Beverton-Holt curve (δ = 1) for these data, whereas the light solid lines show the estimated curve modified to demonstrate depensation at levels δ = 1.2, 1.4, 1.6, 1.8, and 2.0. To keep the modified curves close to the estimated one, they were constrained to have the same asymptotic recruitment as the estimated curve and to pass through the same point of 50% asymptotic recruitment. The dashed line indicates the number of spawners produced by a given number of recruits if no fishing is assumed. Stable populations occur at the intersections of the solid and dashed lines.

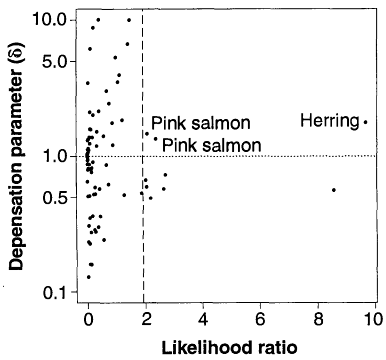

Fig. 2. Results of likelihood ratio tests for depensatory recruitment for 128 fish populations. The null hypothesis was that the depensation parameter δ was equal to 1. When the likelihood ratio (abscissa) is greater than $\frac{1}{2}\chi^2_{1,0.05}$ (the vertical dashed line), the null hypothesis is 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 spawner and recruitment relations with high slopes at the origin, indicating no apparent decline of recruitment at low spawner abundance. The populations with statistically significant depensation ($\delta > 1$) are spring-spawning Icelandic herring and pink salmon.

Although not statistically significant at the 0.05 level, two other stocks show some evidence of depensatory dynamics. Pacific sardines and Georges Bank herring were both driven to very low abundance by overexploitation (8). In both cases, no recovery was observed for decades, but now both stocks are appearing to increase. Depensation in the population dynamics of these two important stocks cannot be entirely ruled out, given this historical pattern. Depensatory dynamics may arise by multispecies interactions, but if present, they will appear in single-species data provided that many data sets are examined.

Depensatory recruitment, appearing as an inflection in the spawner-to-recruitment relation at low spawner abundance, will 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 (9) to assess the probability of detecting depensation if it was actually present. For each data set, we estimated the parameters α and K of the Beverton-Holt model, with the additional constraint that the asymptotic recruitment could be no greater than the maximum observed recruitment. Next, we set δ equal to 2 and constructed a sigmoid Beverton-Holt model that matched the fitted model at the 50% asymptotic recruitment point and at the asymptote at infinite spawner abundance. We then generated pseudo-random recruitment from a log-normal distribution, with the shape parameter estimated from the fitted model and the mean given by

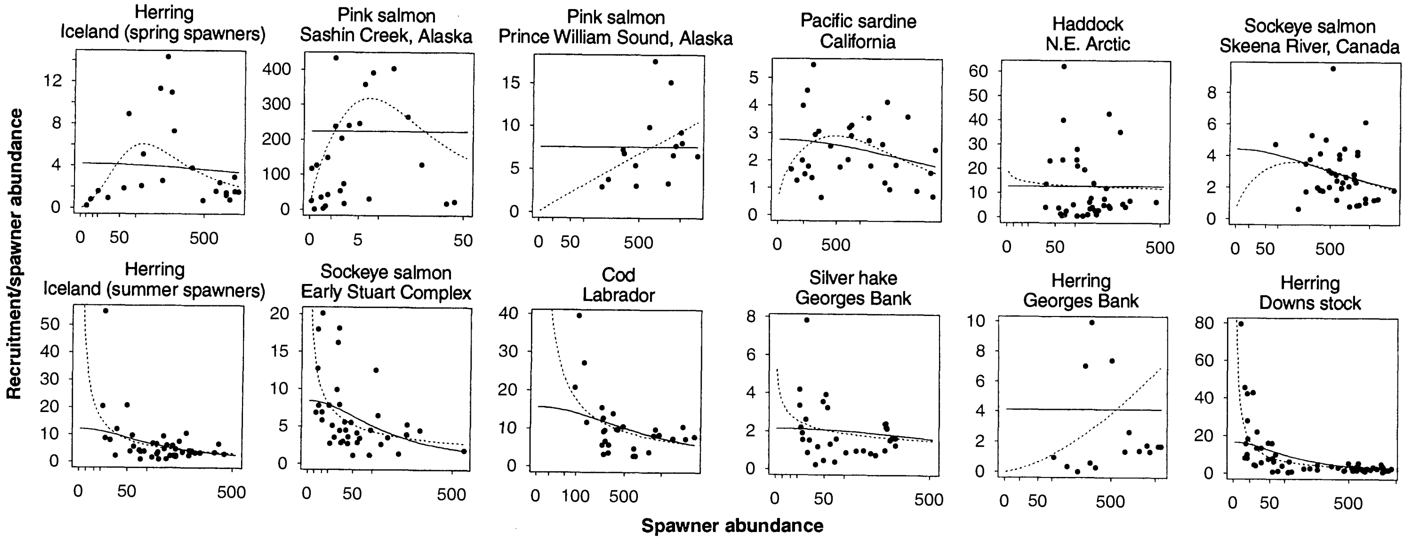

Fig. 3. Survival (recruits per spawner) versus spawner abundance (on a square root scale) for populations with significant depensation or high power to detect depensation. Evidence for depensation is decreased survival at low population levels (first three panels in the top row). Generally, survival was higher at low population levels. We computed survival by transforming recruitment and spawner abundance to the same units and then taking their ratio; thus, it is scaled in terms of replacement levels. When survival is less than 1, the population cannot replace itself (pink salmon from Sashin Creek were an exception; recruitment in that case was in terms of fry). Spawner units are in thousands of metric tons of spawners for marine fish and thousands of individuals for the salmon species. The solid curve is the fitted spawner and recruitment relation with δ fixed at 1. The dotted curve is the fitted relation with δ estimated as a free parameter. The curves were fit to the original recruitment and spawner data.

the constructed curve at each of the observed spawner abundances. Finally, we performed the likelihood ratio test for depensation described above and repeated the procedure 100 times to estimate the statistical power.

Statistical power was greater than 0.95 for 26 stocks for $\delta = 2$ (Fig. 3). In each of these, large declines in abundance have occurred, providing data at reduced spawner abundances. If depensatory recruitment is a general phenomenon in fish populations through this observed range of decrease, we would have expected more than 3 of the 128 stocks examined to show significant depensation in the observed data. These results are robust to gamma- instead of log-normally distributed residuals, reasonable estimation error of spawners, and serial correlation in recruitment (*10*). It is possible that more complex behavior might be masked by shortcomings in our approach.

Theoretical analyses and previous nonstatistical descriptions of depensatory recruitment for fish stocks (*11*) are not substantiated by our comparative analysis of the available data. None of the extant stocks of cod, plaice, hakes, or other commercially valuable species, many of which have been very heavily exploited, displayed depensatory dynamics in reproduction. The great majority of the populations show evidence of increased survival at lower population levels (*12*). This analysis indicates that models with strongly reduced per capita reproductive success at the spawner abundance typical of currently surviving fish stocks are not generally applicable to fish population dynamics. The fish population collapses so far observed cannot be attributed to depensatory dynamics. The implication is that reductions in fishing mortality rates implemented by resource managers should enable currently remaining stocks to rebuild, unless environmental or ecosystem-level changes occur that alter the underlying dynamics of the stock. We conclude that the effects of overfishing are, at this point, still generally reversible.

REFERENCES AND NOTES

1. C. W. Clark, *The Optimal Management of Renewable Resources* (Wiley, New York, ed. 2, 1990), pp. 16–18; B. Dennis, *Nat. Resour. Model.* **3**, 481 (1989); C. W. Clark, *J. Cons. Int. Explor. Mer.* **36**, 7 (1974); J. A. Gulland, *ibid.* **37**, 199 (1977); R. M. Peterman, *J. Fish. Res. Board Can.* **34**, 1130 (1977).
2. J. R. Beddington, in *Variability and Management of Large Marine Ecosystems*, K. Sherman and L. M. Alexander, Eds. (Selected Symposium 99, American Association for the Advancement of Science, Washington, DC, 1986); C. W. Clark, *Mathematical Bioeconomics* (Wiley-Interscience, New York, ed. 2, 1990); U.S. Department of Commerce, *Our Living Oceans* (NOAA Technical Memo NMFS-F/SPO-2, Washington, DC, 1992).
3. W. C. Allee, *The Social Life of Animals* (Norton, New York, 1938), p. 239; P. A. Larkin, R. F. Raleigh, N. J. Wilimovsky, *J. Fish. Res. Board Can.* **21**, 477 (1964); G. C. Varley, G. R. Gradwell, M. P. Hassell, *Insect Population Ecology: An Analytical Approach* (Blackwell, Oxford, 1973).
4. R. A. Myers, J. Bridson, N. J. Barrowman, *Can. Tech. Rep. Fish. Aquat. Sci.* **2024** (1995).
5. R. J. H. Beverton and S. J. Holt, *On the Dynamics of Exploited Fish Populations* (U.K. Ministry of Agriculture, Fisheries and Food Fishery Investment Series 2, no. 19, 1957); G. G. Thompson, *Can. Spec. Publ. Fish. Aquat. Sci.* **120**, 303 (1993).
6. J. Jakobssen, *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.* **177**, 23 (1980).
7. For the salmonids, there were two statistically significant estimates of the depensation parameter that were greater than 1 and two that were less than 1. The most convincing case of depensation is that of pink salmon in Sashin Creek, AK, at a population abundance of less than 100 females; it is perhaps at this level that depensation is expected to occur for salmonids.
8. G. I. Murphy, *Proc. Calif. Acad. Sci.* **34**, 1 (1966); V. C. Anthony and G. Waring, *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.* **177**, 72 (1980).
9. R. M. Peterman, *Can. J. Fish. Aquat. Sci.* **46**, 2 (1990).
10. We repeated the analyses assuming gamma- instead of log-normally distributed residuals; the results were almost identical. Robustness to estimation error in spawners and serial correlation in recruitment were investigated by introduction of these effects into the procedure used to estimate power. Log-normal errors in the estimation of spawners ($\sigma = 0.2$) and first-order autocorrelation of 0.4 in recruitment did not increase type 1 errors if δ was held at 1. As expected, the power was reduced if depensation was present ($\delta = 2$); for the 26 high-power stocks, with errors in the estimation of spawners, the power was reduced by approximately 3% on average, whereas with autocorrelation, the power was reduced by approximately 1% on average. In addition, we tested the adequacy of the chi-square approximation to the distribution of the likelihood ratio statistic by calculating the type 1 error rate when $\delta = 1$ (approximately 3% on average for the 26 high-power stocks).
11. F. Neave, *J. Fish. Res. Board Can.* **9**, 450 (1953); J. G. Hunter, *ibid.* **16**, 835 (1959); O. Ulltang, *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.* **177**, 489 (1980).
12. R. A. Myers and N. G. Cadigan, *Can. J. Fish. Aquat. Sci.* **50**, 8 (1993).
13. We thank the many fish population biologists who generously provided their data and the Canadian Department of Fisheries and Oceans Northern Cod Science Program for financial assistance.

3 February 1995; accepted 3 July 1995

Impaired Energy Homeostasis in C/EBPα Knockout Mice

Nai-dy Wang, Milton J. Finegold, Allan Bradley, Ching N. Ou, Sandy V. Abdelsayed, Margaret D. Wilde, L. Ranee Taylor, Deborah R. Wilson, Gretchen J. Darlington*

Mice homozygous for the targeted deletion of the *c/ebpα* gene, which expresses the CCAAT/enhancer-binding protein α (C/EBPα), did not store hepatic glycogen and died from hypoglycemia within 8 hours after birth. In these mutant mice, the amounts of glycogen synthase messenger RNA were 50 to 70 percent of normal and the transcriptional induction of the genes for two gluconeogenic enzymes, phosphoenolpyruvate carboxykinase and glucose-6-phosphatase, was delayed. The hepatocytes and adipocytes of the mutant mice failed to accumulate lipid and the expression of the gene for uncoupling protein, the defining marker of brown adipose tissue, was reduced. This study demonstrates that C/EBPα is critical for the establishment and maintenance of energy homeostasis in neonates.

C/EBPα, a basic leucine zipper (bZIP) transcription factor (*1*) detectable in the brain, lung, and gut, is most abundant in liver and adipose tissue (*2*). C/EBPα transactivates the promoters of energy-related genes such as lipid-binding protein (422/aP2) (*3*), insulin-responsive glucose transporter (GLUT4) (*4*), and phosphoenolpyruvate carboxykinase (PEPCK) (*5*) and has been proposed to be a regulator of genes involved in energy metabolism (*6*). C/EBPα is expressed late in gestation (*2*) coincidentally with increased glycogen synthase (GS) activity and the accumulation of hepatic glycogen (*7*). Mobilization of this glycogen provides glucose to the neonate during the first hours after birth, before suckling. Because prenatal gluconeogenesis is negligible (*8*), the fetus depends on maternal blood glucose as the source for energy and glycogen storage. At birth, expression of the genes for the gluconeogenic enzymes PEPCK and glucose-6-phosphatase (G6Pase) must occur for the newborn to establish energy homeostasis (*8*). Here, we report the development of a mouse strain with a deletion of the *c/ebpα* gene. Analysis of the homozygous *c/ebpα*-deleted mice demonstrates that the C/EBPα protein is critical to the production and maintenance

---

N. D. Wang, M. J. Finegold, C. N. Ou, S. V. Abdelsayed, M. D. Wilde, D. R. Wilson, Department of Pathology, Baylor College of Medicine, Houston, TX 77030, USA.
A. Bradley, Department of Molecular and Human Genetics and Howard Hughes Medical Institute, Baylor College of Medicine, Houston, TX 77030, USA.
L. R. Taylor, Department of Molecular and Human Genetics, Baylor College of Medicine, Houston, TX 77030, USA.
G. J. Darlington, Departments of Pathology and Molecular and Human Genetics, Baylor College of Medicine, Houston, TX 77030, USA.

*To whom correspondence should be addressed.