

Recruitment of marine fish: the relative roles of density-dependent and density-independent mortality in the egg, larval, and juvenile stages

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In their excellent review of recruitment in marine fish, Leggett & DeBlois (1994) attempt to synthesize the vast amount of literature that has been produced over the last 80 yr. The enormity of this task lies in the fact that there are many studies that have yielded inconsistent results, because many processes are operating and the power of many tests is very low. The crux of the recruitment problem is to determine the magnitude and cause of density-dependent and density-independent components of mortality during the egg, larval, and juvenile stages. Some progress has been made. Leggett & DeBlois conclude that the primary source of variability in recruitment is the enormous interannual variability in density-independent mortality during the egg and larval stages. However, they were unable to identify the source of the interannual variability in density-independent mortality. I suggest that the following points are crucial for further progress.

(1) There is a need for meta-analysis. When studies are being reviewed it is often examined how often an effect is statistically significant. This can be a very misleading approach, even though it is intuitively appealing. For example, if the reviewer simply examines how often an outcome is statistically significant, then there will be a strong bias towards the conclusion that the process or treatment has no effect (Hedges & Olkin 1985). Furthermore, this bias is not reduced as the number of studies increases. If a large number of studies or populations are examined, the proportion of studies that yield statistically significant results is approximately the average power of the test used (Hedges & Olkin 1985). That is, a reviewer of research studies may assume that he is examining the importance of an ecological process, but may only be examining the power of the tests used to examine it. Research synthesis without considering the statistical problems can lead to serious mistakes. I believe that

Leggett & DeBlois were mistaken in expecting 'definitive studies'.

(2) Work should focus on obtaining quantitative estimates of the components of density-independent mortality that can be attributed to different causes, e.g. starvation, predation, and advection, and quantitative estimates of density-dependent mortality at different stages.

(3) Error in estimating abundance imposes fundamental limitations on the kinds of questions that can be addressed. For demersal fish, it is possible to estimate the density-dependent and density-independent component of mortality between the egg and demersal stages, or within the demersal stage. However, reliable estimates of the sources of variability within the egg and larval stages are almost impossible except for a very few species and using enormous sampling effort, e.g. the California Cooperative Oceanic Fisheries Investigation (CalCOFI).

(4) Results should be presented in such a way that they can be compared among populations and species. The components of the interannual variability in mortality can be compared among populations and species (Myers 1995). Similarly, if mortality is proportional to log density, then the coefficient of density dependence can be compared across populations, which is assumed in key factor analysis in the analysis of insect populations (Myers & Cadigan 1993).

(5) Very few studies reviewed by Leggett & DeBlois are taken beyond the interpretive stage, in the sense that they claim only that observations are consistent with a hypothesis, without ever fully testing the hypothesis. That is, the statistical power of an analysis is not addressed before the study is undertaken.

(6) Advection may be more important than biological processes, e.g. despite the extensive plankton records in the North Sea from the Continuous Plankton Recorder, Brander (1992) was unable to find any link with cod recruitment.

(7) There is a need for quantitative theories. Most of the theories discussed by Leggett & DeBlois are conceptual rather than quantitative. There is a clear need for quantitative theories of recruitment that make falsifiable predictions. For example, Mertz & Myers (1994) recently developed a model of D. H. Cushing's match/mismatch theory that predicted that recruitment variability should increase as spawning duration decreases, a prediction that was supported by an analysis of Atlantic cod, *Gadus morhua*, data.

In conclusion, the next major review of recruitment studies should use formal meta-analysis. The difficulties of estimating egg and larval mortality should be recognized, because these impose fundamental limitations on the type of questions that can be addressed in recruitment studies.

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