DISCUSSION

Significance of larval condition: comment on laboratory experiments[1]

Iain Suthers

The significance of condition in larval fish for evaluating many hypotheses and processes in fisheries oceanography is uncertain (Ferron and Leggett 1994; Leggett and DeBlois 1994). Larvae in better condition are presumably less likely to die of starvation or predation on average and thus contribute proportionally more to the numbers at recruitment. Larval condition (or health) may be determined by a variety of biochemical indices (e.g., RNA/DNA ratios, relative lipid content), histological indices, or otolith growth indices. Tests of the growth/condition–mortality hypothesis are typically at two extremes of temporal scales. At the largest scale, condition of wild caught larvae is compared with subsequent recruitment, but the comparison is made over only 2–5 years (e.g., Setzler-Hamilton et al. 1987; Bailey et al. 1995; Ralston and Howard 1995; Campana 1996). At the other extreme, there are laboratory experiments that place larvae of variable condition in the presence of a predator and monitor the condition of the survivors (e.g., McCormick and Kerrigan 1996). There are intermediate spatial scale studies of larval condition (e.g., Buckley and Lough 1987; Suthers 1996; Lochmann et al. 1997), but these do not explicitly test the growth/condition–mortality hypothesis.

A recent article by Elliott and Leggett (1998) experimentally evaluated the hypothesis that fish larvae in poor nutritional condition experienced higher mortality rates due to predation. The authors concluded that the RNA/DNA ratio was not a reliable predictor of survival probability and that the ratio and dry weight were probably of limited use in prorating larval abundance as a predictor of recruitment. This conclusion overstates what can be drawn from their data and illustrates a more general problem in extending the results of laboratory experiments of larval condition to the field. My intention is to illustrate some pitfalls in this area and to offer some solutions to the definition of "larval condition" and how to test its significance.

Received September 13, 1999. Accepted January 31, 2000.
J15351

I. Suthers. School of Biological Science, University of New South Wales, Sydney 2052, New South Wales, Australia.
e-mail: i.suthers@unsw.edu.au

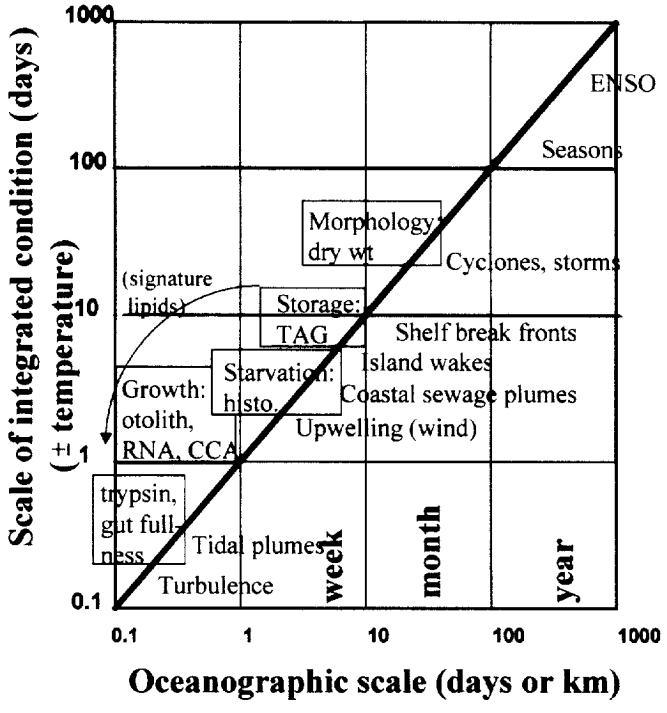
[1]Comment on paper by J.K. Elliott and W.C. Leggett. 1998. Larval condition and vulnerability to predation: an analysis based on mixed-prey experiments. Can. J. Fish. Aquat. Sci. **55**: 626–630.

The experimental arena of Elliott and Leggett (1998) consisted of a 38-L black plastic container containing 75 starved and 75 fed capelin (*Mallotus villosus*) larvae in the presence of a starved juvenile lumpfish (*Cyclopterus lumpus*) of around 30 mm standard length. Each trial lasted about 15 min when 75 larvae had been consumed, which is equivalent to one larva per 6 s. At this rate of removal, the predator is not exercising much discrimination. Additionally, in the field, there would exist planktonic refugia, in the form of floatsom, turbulence, turbidity, and simply extensive space not available in aquaria. Once the larvae left the confines of the beach, the densities of larvae would fall well below the laboratory density of $4 \cdot L^{-1}$, and light levels would be less than that provided by the two fluorescent tubes placed 1 m above the tank. Therefore, reduced light penetration in nature would lead to decreased detection of the larvae and mortality would be reduced as a result, and it may well be more selective.

Laboratory experiments are needed for hypothesis generation and in calibrating condition indices with the effects of capture, preservation, and starvation (e.g., McGurk 1985; Theilacker 1986). Designing ecologically relevant laboratory experiments to test the significance of larval condition is difficult. I suggest that the following be considered. Firstly, "larval condition" needs to be defined, as the term spans a range of time scales and ecological function for different species and stages of larvae (Suthers 1998). For most late-stage larvae, at the scale of weeks, there are morphometric indices (Fulton's K) and storage indices (lipid concentration), whereas at the scale of days, there are growth indices (RNA/DNA ratios, otolith growth, cell cycle analysis) or starvation indices (histological status, gut epithelium cell height), and at the scale of hours there are feeding indices (gut fullness, trypsin activity). The different indices are relevant at spatiotemporal scales appropriate to oceanographic phenomena (Fig. 1). Ontogenetic development has a considerable influence on an index, such that the morphometry of early-stage larvae may be sensitive on the order of days (Bisbal and Bengston 1995).

Secondly, as pointed out in Ferron and Leggett (1994), reared larvae (regardless of their condition) tend to be fatter, with less histological variation and bigger hearts, and condition is influenced by the container volume (see references in Suthers 1998). The survival of the reared larvae also needs to be reported, as differential survival (due to stress or dis-

Fig. 1. Summary of the temporal scales of condition indices (within boxes) related to some spatiotemporal oceanographic phenomena for typical late-stage larvae. Morphological indices may be temporally more sensitive in early-stage larval fish. Lipid indices are linked to short-term feeding indices by the use of characteristic phytoplankton-derived signature lipids.



ease) may leave a population of larvae of better condition. In Elliott and Leggett's (1998) study, the combined fed and starved negative growth rates in RNA/DNA ratio and dry weight of larvae (declines of over 30% in RNA/DNA and 15% in dry weight over 4 days; their fig. 2) show that the larvae were not particularly viable. Laboratory-reared, fed larvae may have full guts (as in their study) but for a variety of reasons may not be growing.

Thirdly, the effect of size needs to be removed from an index (and reported in the Materials and methods section), which may not be achieved simply by a ratio (Suthers et al. 1996). Finally, as the mortality rate of larvae in the ocean is effectively 1, it is expected that larvae in good condition will also suffer high mortality rates under certain conditions.

The larval survival process and the significance of larval condition involve other complexities as revealed by modelling (Sclafani et al. 1993) and an analysis of behaviour (Neilson et al. 1986; Chesney 1989) and in situ swimming speeds (Leis and Carson-Ewart 1997). The use of small predator arenas cannot produce ecologically useful conclusions about larval condition indices, and the general recommendation of Elliott and Leggett (1998) that RNA/DNA ratios have limited predictive use is not justified.

Laboratory rearing experiments do have their place for examining relative changes among species and relative ontogenetic changes within species. The growth/condition–mortality hypothesis may be tested under carefully designed and monitored laboratory experiments that match the temporal scale of the index with that of the hypothesis. Predator arenas should be as large as possible (5–10 m^3), with densities of larvae $<1 \cdot L^{-1}$, and should include refugia, with the experiment lasting for a period of days (not minutes). The relevant condition index needs to be justified on ecological grounds, and for many larvae, a growth index is probably the most useful. In fact, the ecological relevance of various condition indices still needs further investigation. At present, large-scale analyses of recruitment still provide the most convincing tests of significance of larval growth/condition–mortality (e.g., Campana 1996). Future studies should consider in situ small-scale spatial and temporal studies that link mortality and condition of cohorts, such as within an estuary. This would provide a rigorous test of the hypothesis and provide managers and scientists alike with a useful tool to investigate the cascade of events leading to annual fluctuations in recruitment.

References

Bailey, K.M., Canino, M.F., Napp, J.M., Spring, S.M., and Brown, A.L. 1995. Contrasting years of prey levels, feeding conditions and mortality of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska. Mar. Ecol. Prog. Ser. **119**: 11–23.

Bisbal, G.A. and Bengston, D.A. 1995. Description of the starving condition in summer flounder, *Paralichthys dentatus*, early life history stages. Fish. Bull. U.S. **93**: 217–230.

Buckey, L.J., and Lough, R.G. 1987. Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can. J. Fish. Aquat. Sci. **44**: 14–25.

Campana, S.E. 1996. Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. **135**: 21–26.

Chesney, E.J. 1989. Estimating the food requirements of striped bass larvae *Morone saxatilis*: effects of light, turbidity and turbulence. Mar. Ecol. Prog. Ser. **53**: 191–200.

Elliott, J.K. and Leggett, W.C. 1998. Larval condition and vulnerability to predation: an analysis based on mixed-prey experiments. Can. J. Fish. Aquat. Sci. **55**: 626–630.

Ferron, A., and Leggett, W.C. 1994. An appraisal of condition measures for marine fish larvae. Adv. Mar. Biol. **30**: 217–303.

Leggett, W.C., and DeBlois, E. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Neth. J. Sea Res. **32**: 119–134.

Leis, J.M., and Carson-Ewart, B.M. 1997. In situ swimming speeds of the late pelagic larvae of some Indo-Pacific coral-reef fishes. Mar. Ecol. Prog. Ser. **159**: 165–174.

Lochmann, S.E., Taggart, C.T., Griffin, D.A., Thompson, K.R., and Maillet, G.L. 1997. Abundance and condition of larval cod (*Gadus morhua*) at a convergent front on Western Bank, Scotian Shelf. Can. J. Fish. Aquat. Sci. **54**: 1461–1479.

McCormick, M.I., and Kerrigan, B.A. 1996. Predation and its influence on the condition of a newly settled tropical demersal fish. Mar. Freshwater Res. **47**: 557–562.

McGurk, M. D. 1985. Multivariate analysis of morphometry and dry weight of Pacific herring larvae. Mar. Biol. **86**: 1–11.

Neilson, J.D., Perry, R.I., Valerio, P., and Waiwood, K.G. 1986. Condition of Atlantic cod *Gadus morhua* larvae after the transition to exogenous feeding: morphometrics, buoyancy and predator avoidance. Mar. Ecol. Prog. Ser. **32**: 229–235.

Ralston, S., and Howard, D.F. 1995. On the development of year-class strength and cohort variability in two northern California rockfishes. Fish. Bull. U.S. **93**: 710–720.

Sclafani, M., Taggart, C.T., and Thompson, K.R. 1993. Condition, buoyancy and the distribution of larval fish: implications for vertical migration and retention. J. Plankton Res. **15**: 413–435.

Setzler-Hamilton, E.M., Wright, D.A., Martin, F.D., Millsaps, C.V., and Whitlow, S. I. 1987. Analysis of nutritional condition and its use in predicting striped bass recruitment: field studies. Am. Fish. Soc. Symp. **2**: 115–128.

Suthers, I.M. 1996. Spatial variability of recent otolith growth and RNA indices in pelagic juvenile *Diaphus kapalae* (Myctophidae): an effect of flow disturbance near an island? Mar. Freshwater Res. **47**: 273–282.

Suthers, I.M. 1998. Bigger? Fatter? Or is faster growth better? Considerations on condition in larval and juvenile coral-reef fish. Aust. J. Ecol. **23**: 265–273

Suthers, I.M., Cleary, J.J., Battaglene, S.C., and Evans, R. 1996. Relative RNA content as a measure of condition in larval and juvenile fish. Mar. Freshwater Res. **47**: 301–307.

Theilacker, G.H. 1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull. U.S. **84**: 1–17.