Vol. 309: 307–309, 2006 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published March 15

AS WE SEE IT

Marine fish recruitment variability and climate indices

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The physical environment is an essential factor in regulating marine fish populations (Cushing 1982, Steele 1985). Recently, this has received a great deal of attention due to the discussion of climate change and, in particular, of global warming. Hence, temperature is often the principal variable investigated in biological studies, since it regulates rates in many physiological processes (Brett 1979), in particular recruitment of marine fishes (e.g. Planque & Fredou 1999). The link between the number of recruits and temperature is crucial for the management of marine resources and predicting the long-term consequences of a variable environment on fisheries (Myers 1998). The importance of this topic within fishery science is demonstrated by the increasing amount of literature dedicated to explore the impact of the physical environment on recruitment variability for several fish species in the North Atlantic (see *ICES Journal of Marine Science*, Vol. 62, 2005, and references therein). These studies usually focused on temperature and/or the North Atlantic Oscillation (NAO) as physical variables, using the number of individuals or recruitment success as recruitment proxy in comparisons of different stocks; most of these studies ignored spawning stock biomass (SSB) effects (e.g. Planque & Frédou 1999, Brander 2000, 2005, Toresen 2001, Brander & Mahon 2004, Brodziak & O'Brian 2005, Cook & Heath 2005, Drinkwater 2005, Megrey et al. 2005).

There are 2 general statistical approaches commonly used to establish a link between some proxy for recruitment and the physical environment (hereafter: climate), as seen from an ecological perspective:

(1) The 'recruitment approach' used in several papers analyses the relation between the observed number of recruits (R; *y* variable) with various climate variables (*x* variable), such as temperature or NAO. However, R is in many cases related to adult biomass (SSB). This is obviously true in the trivial scenario when SSB is zero, since in this situation no recruitment can take place, but SSB can be important also in a more general sense. Hence, the relation of the number of recruits to a climate variable may contain both R variability due to the adult biomass, and variability caused by climate, i.e. it is impossible to disentangle the effect of physical environment from that of SSB.

(2) The 'recruitment success approach' recently seen in the literature accounts for the effect of SSB on recruitment by using recruitment success (i.e. number of recruits produced per biomass of adult individuals; R_s) or some other variable (*y* variable) where the SSB effect has been considered, against various climate variables (*x* variable). This approach assumes that part of the variability in recruitment depends on adult biomass in a first stage, and on climate in a second stage. The rationale behind this assumption is mathematically formalized in the classical Ricker (1954) or Beverton & Holt (1995) recruitment functions, and these functions are in turn based on sound ecological mechanisms (e.g. cannibalism and predation). The point here is that the number of recruits in a fish species is generally related to egg number or SSB, a proxy of egg production (Myers & Barrowman 1996). The recruitment success approach obviously removes or reduces the effect of SSB on recruitment in contrast to the recruitment approach presented above.

Neither approach account for other biological factors such as age structure of the stock (Marshall et al. 1998, Marteinsdotter & Begg 2002), fecundity and condition of the spawners (Olsen et al. 2005, Scott et al. 2006), predation (e.g. Köster & Schnack 1994), Allee effects (Frank & Brickman 2000), changes in species distribution (Rose 2005) etc., which may play a crucial role in explaining part of the observed recruitment variability. The use of R_s is justified only if there is a significant

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relationship between R_s and SSB. Failing to account for the SSB effect in climate–recruitment studies could mask the influence of climate variability on recruitment dynamics (Myers 1998). During the last decade, several publications (and, to our knowledge, all papers comparing several stocks), including most of the recent papers in the *ICES Journal of Marine Science* 58(5) and 62(7), have used some climate proxy to explain observed recruitment variability or R_s without exploring and disentangling the actual effect of adult biomass. This lack of mechanistic understanding makes it difficult to judge their conclusions regarding the effect of climate on fish recruitment.

We suggest that in future climate–recruitment studies a more formalised approach should be considered. The first step is to test for and disentangle the SSB effect on R. In one of his last lectures at Woods Hole, Beverton (2002) suggested an approach for exploring this relationship. Because of the biological mechanisms behind the classical SSB–R relationships, recruitment success (R_s) should improve as SSB decreases (Fig. 1). However, if recruitment is mediated by physical environmental events, this negative relationship may not be as obvious. For example, when the stock is declining, a negative effect of the climate on R will result in a decrease in R_s; this is reversed in the case of a positive effect of climate on R (Fig. 1). Therefore, the variability in the relationship between R_s and SSB can be considered as a proxy for recruitment anomalies (R_a) and is assumed to be partially determined by the stochasticity in the physical environment (Beverton 2002). Nevertheless, this approach is only

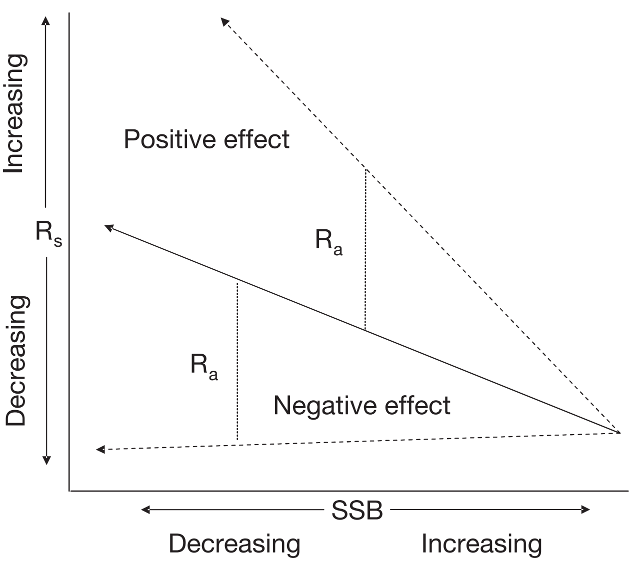

Fig. 1. Relationship between spawning stock biomass (SSB) and recruitment success (R_s) (R/SSB, where R is number of recruits), when the physical environment has positive or negative effects (dashed lines) on R_s. R_a: recruitment anomaly

valid when a significant effect of SSB on R_s can be demonstrated. Only in such cases can R_s — and therefore R_a — be used in climate–recruitment analysis. On the other hand, and as a second step, when SSB has no significant effect on R_s, climate variables can be directly correlated to recruitment itself. Importantly, if SSB has no effect on R, using R_s instead of R can actually mask any recruitment–climate relationship. We argue that future analyses of climate–recruitment data should incorporate the more formalised, and in our view more correct approach suggested here.

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Editorial responsibility: Howard I. Browman (Associate Editor-in-Chief), Storebø, Norway

Submitted: January 25, 2006; Accepted: February 6, 2006
Proofs received from author(s): February 16, 2006