REPLY COMMENT

Defining 'natal homing' in marine fish populations; need for inference in fishery science: reply to Bradbury & Laurel (2007)

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ABSTRACT: On the basis of prior information on Atlantic cod *Gadus morhua* in the eastern North Sea region, including larval drift, location of spawning sites, and genetic characterisations, natal homing was thought to be the most parsimonious explanation of the juvenile and adult distributions. We tested this hypothesis in an archival tagging experiment that gave clear evidence of non-random migration runs toward remotely situated spawning grounds during the reproductive season, inferring strong support for natal homing (Svedäng et al. 2007; Mar Ecol Prog Ser 345:1–12). Bradbury & Laurel (2007, this volume) found this inference ambiguous, as the whole life cycle was not embraced in a single study, i.e. due to obvious logistical problems, single individuals had not been tracked from fertilization to spawning. We consider that none of the major hypotheses on population structuring mechanisms should a *priori* be given precedence, and the likelihood for environmental forcing versus natal homing should be inferred on the basis of the accumulating facts at hand. Admittedly, our understanding could be strengthened through testing whether the behavioural entities comply with their postulated population origin, using natural natal tags. Promisingly, efforts are being made that will eventually shed further light on this important issue.

KEY WORDS: Atlantic cod \cdot Environmental forcing \cdot Inference \cdot Natal homing \cdot Marine fish \cdot Population structuring mechanism

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Bradbury & Laurel (2007; this volume) questioned the evidence of natal homing in Atlantic cod *Gadus morhua* presented by Svedäng et al. (2007). They argued that adult tagging alone was insufficient for establishing the existence of natal homing since the ichthyoplanktonic phase had been omitted in the study. However, the study was conducted and planned in regard to known facts about the ichthyoplanktonic phase in the area and the distribution of the active spawning sites, from which the tagged fish likely originated.

It was recognised that the almost complete disappearance of local spawning aggregations along the eastern Skagerrak coast represented an excellent opportunity for testing homing behaviour and recolonisation processes. Pursuing this track, it has been substantiated that most juvenile cod in the eastern

Skagerrak are recruited from offshore spawning areas, mainly in the North Sea (Svedäng 2003, Cardinale & Svedäng 2004), from which they are passively transported (Munk et al. 1999). This theory was further supported by the fact that a relatively strong year class of cod in 2001 in the Skagerrak was genetically assigned to eastern North Sea cod populations, in contrast to the results in the year before when genetic analysis suggested local origin (Knutsen et al. 2003, 2004). Consequently, the continuous and unexpected low abundance of adult cod following strong recruitment episodes was suggested to be due to return migration of juvenile/maturing fish at a certain size or age (Pihl & Ulmestrand 1993, Svedäng 2003, Svedäng & Svenson 2006).

According to theories emphasizing the importance of juvenile dispersal and retention (Secor 2005), juvenile

fish should remain fairly close to the areas where they eventually settled, where some fish will be 'lost at sea' once transported outside the population defining retention area. The alternative hypothesis is that juvenile fish do not remain where they originally settled, unless they are in close vicinity to their parental spawning grounds. These 2 hypotheses are challenged by data from an archival tagging experiment which showed clear evidence of non-random migration towards remotely situated spawning grounds during the reproductive season, thus giving (further) support for natal homing as the most succinct explanation (Svedäng et al. 2007).

It is, however, likely that environmental forcing will also influence population structures in marine fishes, as Bradbury & Laurel (2007) point out, i.e. retention and dispersal during the ichthyoplanktonic phase will always to some extent determine the connectivity between population units. However, the crucial point is whether spawning aggregations/subpopulations are behavioural units and whether those units are formed by opportunistic and non-philopatric recruitment of juveniles to adult aggregations (McQuinn 1997, Wright et al. 2006) or by natal homing. Our data suggest natal homing, as most tagged cod moved uni-directionally from the eastern Skagerrak towards the North Sea during the spawning season. In addition, even in the presence of spawning activity, such as in the Kattegat (Vitale et al. 2007) and the Gullmarsfjord, some fish swam towards the North Sea during the spawning season. All the identified behavioural entities in our study represented well-fitted study objects for the assignment of individuals to potential source locations using geochemical or genetic natal tags, and thereby for further testing of the theory of population structuring.

There is a long history of debate surrounding the mechanisms that structure marine fish populations (Secor 2005). Our conclusions about natal homing in cod are based on observations from archival tagging and are strongly supported by other lines of biological evidence. That our results further stimulate the debate about the way in which marine fish populations are structured is healthy and, we hope, will lead to additional work to test the natal homing hypothesis.

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