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A review of early life history dynamics of Barents Sea cod

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Summary
We review the literature on early life dynamics of Barents Sea (BS, also known as Northeast Arctic or Arcto-Norwegian) cod (Figure 1). Focus is on the biotic and abiotic drivers that accumulated determine the strength of the new year class, including recruitment, i.e., the abundance of a cohort surviving to enter the fishery. Also Russian work is included, parts of which until now has not been available to non-Russian readers. Physical drivers examined include sea temperature, advection and dispersal, wind-induced turbulence and light. Biotic mechanisms studied range from maternal effects and skipped spawning of the adult stock through egg quantity and quality, to prey availability for the larvae and effects of cannibalism on the juveniles. Statistical analyses of time series on recruitment itself, not one specific early life stage, and various explanatory variables are also reviewed. Finally, we by stage summarize the properties and mechanisms we believe to impose significant interannual variability in survival of BS cod, ultimately affecting recruitment.

Introduction
Since Hjort's seminal work was published a 100 years ago (Hjort, 1914) the pursuit towards understanding what regulates variability in recruitment of commercially exploited fish populations has been a key issue in quantitative fisheries science. Fish undergo different phases during early life and different mechanisms may dominate at any single stage. Typically, most of the variability in pre-juvenile survival is accounted for by density-independent environmental factors (Houde, 2008). Paleo-record studies on fish abundance variability prior to the onset of extensive fishing indicate the importance of environmental factors for population regulation (Emeis et al., 2010). On the other hand, density-dependent survival in the (late) juvenile phase is also generally believed to be of key importance in regulating the size of fish populations (Rothschild, 1986).

The Barents Sea stock of Atlantic cod (*Gadus morhua*) is currently the world's largest. It is also among the most well-studied. Not least has a lot of attention been directed towards the biotic and abiotic drivers influencing early life history dynamics. Accumulated they determine the strength of the new year class, including recruitment, i.e., the abundance of a cohort surviving to enter the fishery. Still, no comprehensive evaluation and review of the sizeable literature on this topic has yet been performed for Barents Sea cod. Here we undertake such a review of the literature on early life dynamics of BS cod.

Materials and Methods
A stage-by-stage approach is employed. We summarize and assess the significance of the different processes described in the literature to be at play during each specific life stage, from spawning stock, through eggs, larvae and pelagic juvenile, to demersal juvenile and recruitment at age 3.

Results and Discussion

The "Critical Period" hypothesis of Hjort (1914) was among the ideas evaluated. For BS there have been several studies looking at relative abundance indices and implicitly mortality at different early life stages. We can draw the conclusion that mortality at other stages of development than first-feeding larva also is important for the formation of year class strength. Interannual variability is high at all stages and in some years a cohort estimated at an early stage as rich might have their abundance estimate modified strongly afterwards (pointing towards density-dependence). However, beyond this the results diverge. Helle et al. (2000) showed that an index of early juvenile abundance was a better predictor of recruitment than estimates of SSB, TEP or age-0 abundance. On the other hand, Mukhina et al. (2003) found that a survey-based egg index provided better predictions of age-3 recruitment for BS cod than SSB or abundance indices of later life stages. We summarize our review by a conceptual Paulik diagram for the Barents Sea cod. Here the factors we suggest to be the most important in determining survival from one stage to the next are shown, from spawning stock through the egg stage, larvae, and 0-group to recruitment at age 3 and, closing the life cycle to spawning stock again (Figure 2).

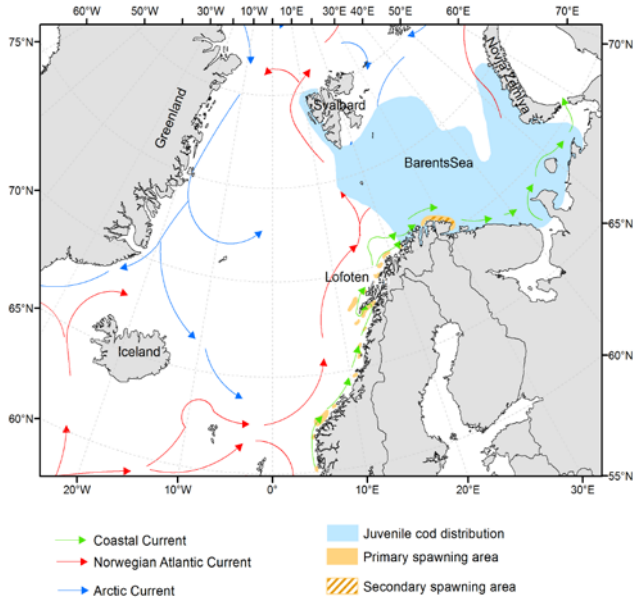

Figure 1. The Barents and Nordic Seas with Barents Sea cod spawning grounds and extent of juvenile distribution. The arrows indicate the dominating surface currents. Eggs, larvae and later juveniles are transported north- and eastwards in the upper water layers by wind and currents untill they are spread in the upper 100 m all over the southern Barents Sea and off Svalbard, 600–1200 km from their spawning grounds as so-called 0-group.

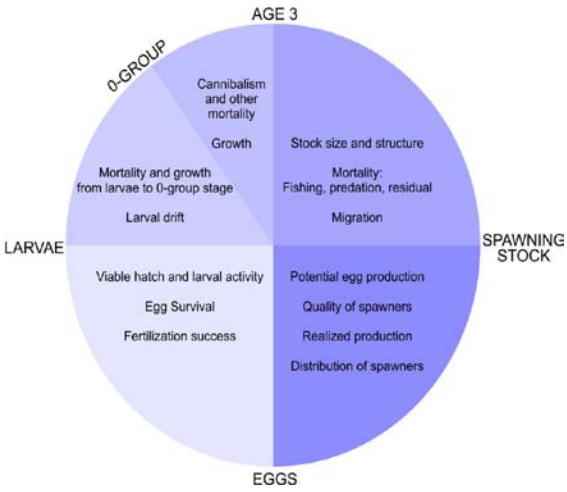

Figure 2. Conceptual Paulik diagram (Paulik, 1973) for Barents Sea cod. Factors determining survival from one stage to the next are shown in the sector between them. The diagram should be read clockwise, starting from the Spawning stock, thus following the development life cycle.

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