

The influence of stock structure on fisheries-induced evolution in Icelandic cod

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Goal

To model component structure in a fish stock such as Icelandic cod and investigate its influence on fisheries-induced evolution.

Background and motivation

In recent years, evidence that fishing not only affects populations demographically but also changes their genetic composition has accumulated (Heino and Godø 2002). Fishing mortality is most often non-random: typically, gear is designed to select individuals that are larger, older or fastest-growing. Such selective fishing could lead to significant changes in life-history traits, which, if they are heritable, will lead to fishing-induced evolution (Law 2000; Heino and Godø 2002; Olsen et al. 2004). Changes in life-history traits, particularly in age and size at maturation, have been reported in a number of commercially exploited fish stocks (see reviews by Trippel 1995; Dieckmann and Heino 2007). Many studies have found fisheries-induced evolution to be a plausible explanation for observed trends towards earlier and smaller maturation in a number of stocks (Northeast Arctic cod: Heino et al. 2002b; Baltic cod: Vainikka et al. in prep; Atlantic cod: Barot et al. 2004; Olsen et al. 2004; Olsen et al. 2005; American plaice: Barot et al. 2005; North Sea plaice: Rijnsdorp 1993; Grift et al. 2003, 2007; North Sea sole: Mollet et al. 2006). Alternatively, changes in these life-history traits could be the result of phenotypic plasticity alone, for example, as a response to alterations in density-dependent growth rates with declining population abundance (Reznick 1990; Law 2000). Disentanglement of phenotypically plastic life-history responses to fishing from genetic responses has been made possible by application of the probabilistic reaction norm method developed by Heino et al. (2002a). Probabilistic maturation reaction norms are an extension of the original deterministic notion of maturation reaction norms (Stearns and Koella 1986) and describe the probability that immature individuals of a given age and size will mature during a given time interval (Heino et al. 2002a; Olsen et al. 2005). Fisheries-induced evolution is of concern to the sustainable management of fish stocks as it can result in lower sustainable yields (Law 2000; Conover and Munch 2002) and reduced stock stability (Olsen et al. 2004) as manifestations of the impact of life-history trait changes at the individual level, such as the influence of age and size at maturation on growth rate, fecundity and survival probability (Heino et al. 2002b). Furthermore, reversal of genetic change is likely to be slow (Law 2000).

Evidence of adaptive variation in northern temperate marine fish at spatial scales that are smaller than was previously thought has been documented in recent geographical comparisons of fitness-related traits (McIntyre and Hutchings 2003). For example, genetic differences in growth rate and feeding efficiency have been reported for populations of Northwest Atlantic cod (Purchase and Brown 2001), Atlantic halibut, and turbot (Imsland et al. 2000; Jonassen et al. 2000). A number of studies exploring small-scale structure of cod populations have provided evidence for the exis-

tence of adaptive variation and local populations (Ruzzante et al. 1999, 2000; Knutsen et al. 2003; McIntyre and Hutchings 2003; Salvanes et al. 2004; Neat et al. 2006; Jónsdóttir et al. 2006a,b; Pampoulie et al. 2006). The majority of fisheries assessments are based on modelling the dynamics of closed populations and assume homogeneous life-history characteristics. However, misleading results can be obtained if several closed populations, or a portion of a population, are the components actually modelled (NRC 1994). Failure to recognise or account for stock diversity can lead to erosion of spawning components, with known ecological consequences, but modelling structure in stock assessments is far from straightforward due to an inherent level of uncertainty concerning the actual configuration of the stock (Stephenson 1999; Begg and Marteinsdóttir 2002b).

Atlantic cod remains the most economically important fish stock in Iceland. Over the past 30 years, annual landings have varied from 180,000 to 470,000 tonnes, with an average catch of approximately 290,000 tonnes (MRI Iceland 2006). Preliminary investigations suggest that the age at maturation of the Icelandic cod stock has declined over the last few decades. Fishing mortality of the Icelandic cod stock is unevenly distributed on the Icelandic shelf. High levels of exploitation occur off the northwest and southwest coasts, corresponding to the main feeding and spawning grounds, respectively; these are also the areas where mature/spawning cod are most abundant. Conversely, cod on regional spawning grounds are exposed to relatively low exploitation, particularly in the north where the main nursery grounds are situated (Begg and Marteinsdóttir 2003). This provides relatively protected habitats for juvenile cod and thus ensures a supply of recruits for the main spawning component and stock as a whole (Begg and Marteinsdóttir 2003).

Recent studies have confirmed that in addition to the main spawning component off the southwest coast, smaller regional spawning components are significant sources of productivity and recruitment for the Icelandic cod stock (Begg and Marteinsdóttir 2000, 2002a,b; Marteinsdóttir et al. 2000a,b). Furthermore, life-history characteristics (e.g. somatic growth rates, age and size at maturity, and reproductive potential), condition and abundance of mature Icelandic cod have been found to exhibit spatial disparity (Marteinsdóttir and Begg 2002; Begg and Marteinsdóttir 2002a, 2003; Pétursdóttir et al. 2006; Pardoe et al. in prep). More recently, studies of otolith shape and chemistry and of genetic markers have provided evidence that the Icelandic cod stock is structured, with differentiation detected between cod from the north-eastern and south-western regions and also with depth (Jónsdóttir et al. 2006a,b; Pampoulie et al. 2006). Oceanic currents and environmental conditions are thought to have contributed to the spatial distribution and genetic composition of Icelandic cod (Begg and Marteinsdóttir 2002a; Pampoulie et al. 2006). Marteinsdóttir et al. (2000a) suggested that this population richness may be responsible for the relatively low recruitment fluctuation in this stock compared to most other cod stocks in the North Atlantic. The Icelandic cod stock is currently managed as a single homogenous unit but as evidence of stock structure accumulates, it seems it may be necessary to revise this management strategy (Begg and Marteinsdóttir 2002b; Jónsdóttir et al. 2006a,b; Pampoulie et al. 2006).

An investigation of the effect of stock structure on the rate, detection, and management of fisheries-induced evolution in commercially exploited fish stocks at risk of genetic change in life-history traits is an area that requires attention. In this project, my aim is to investigate the development and subsequent dynamics of structure in a stock such as Icelandic cod and its influence on fisheries-induced evolution, with additional consideration of the role of variable fishing pressure on individual stock com-

ponents. The development of an individual-based eco-genetic model (Dunlop et al. 2005a, 2007) will help tackle these research questions where empirical analysis would fail due to the limitations imposed by data availability.

Research questions

The questions that will be the focus of this research project are as follows:

- Are the observed life-history differences between cod in northern and southern Icelandic waters likely the result of genetic adaptation or are they a purely plastic response?
- What conditions are necessary to cause genetic divergence, as opposed to purely phenotypic differences, between stocks inhabiting different environments?
- How does stock structure influence the magnitude and rate of, and recovery from, fisheries-induced evolution in a stock exposed to selective harvesting?
- What effect does differential fishing pressure on the subunits of a structured stock have on fisheries-induced evolution?
- What does stock structure mean for the detection and management of fisheries-induced evolution?

Methods and work plan

To study stock structure and its influence on fisheries-induced evolution of probabilistic maturation reaction norms (PMRNs) (Heino et al. 2002a), I will develop a model that builds upon the existing individual-based eco-genetic model of Dunlop et al. (2005a, 2007 and in prep). Where possible, the model will be parameterized for the Icelandic cod stock. The model will be based on a ‘southern’ and ‘northern’ environment, which will differ in temperature and fishing mortality. Such differences will likely emerge as component specific biological processes, such as faster growth rates and earlier maturation in the southern environment. Individuals can be born in either environment and, accordingly, are referred to as belonging to the southern or northern population or stock component. Three types of migration will likely be included in the model to reflect the general life cycle of Icelandic cod:

- Juvenile migration - after birth juveniles in the southern population will mostly migrate to the northern environment.
- Spawning migration/Natal homing - once mature, individuals will migrate to one of the two environments to spawn. This will occur on an annual basis. The probability of migration will depend on the degree of natal homing, which will be modified between simulations.
- Adult migration - post-spawning, adults will stay in their current environment or migrate to the other. This will occur on an annual basis. The probability of migration will depend on the degree of adult migration, which will be modified between simulations.

Evolution of the following traits will be examined: reproductive investment, growth capacity, and the width, slope, and intercept of linear PMRNs. Model simulations will run on discrete, one-year time steps. The model will include a trade-off between growth and reproduction, implemented using the bi-phasic growth model of Lester et al. (2004), so that prior to maturation growth will be assumed to be linear, but after maturation will follow the Von Bertalanffy growth model. The reduction of adult growth rates relative to juvenile growth rates represents reproductive investment (Roff

1983). Growth will be density-dependent with a decreasing, non-linear function relating growth rate to population biomass. There will also be a linear trade-off between growth capacity and survival. Growth rate will be influenced by temperature and based on relationships for Icelandic cod reported by Björnsson et al. (2001). Natural mortality will be stage-specific. Reproduction will occur randomly between pairs of mature individuals. Inheritance will be based on a constant-segregation kernel and fecundity will be a function of maternal body size. Offspring mortality will be density-dependent and modelled using the Ricker stock-recruitment relationship.

Harvesting will reflect the exploitation history of Icelandic cod, and the consequences of realistic management scenarios for fisheries-induced evolution will be investigated (time allowing). Increased complexity (i.e. increased parameterisation for the Icelandic cod stock, non-linear maturation reaction norms, variable food availability and influence of energy allocation/nutritional status on maturation) will be added to the model as time permits.

Relevance and link to EEP's research plan

This project aims to assess the influence of population structure and spatially variable exploitation pressure on the response of a commercially important stock such as Icelandic cod to fisheries-induced evolution. It is therefore directly linked to the evolutionary fisheries management project of the EEP. In addition, studying fisheries-induced evolution in genetically and spatially structured populations is a novel contribution to existing applications of eco-genetic models.

Expected output and publications

This work will be included in my PhD thesis and is intended for publication as a co-authored research article.

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