Theme Session H on Evolutionary effects of exploitation on living marine resources

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It is incontestable that fishing can lead to significant changes in life-history traits, such as age and size at maturation. If the traits in question are heritable, a genetic response to selection will always be realised. Selection pressures caused by fishing are often strong and specific: most fisheries target the largest, oldest, or fastest-growing individuals (H:20), such that fish genetically predisposed to grow fast, or to mature at larger sizes and older ages, are more likely to be caught before they can reproduce (H:06, H:11). Corresponding selection responses have been documented independently in several exploited stocks.

Given the high probability that intensive and prolonged fishing pressures will almost certainly exact a selection response to exploitation, the key questions addressed by presentations in this theme session concerned (a) the magnitude of the response, (b) the reversibility of the response, and (c) the consequences of the response. The session comprised 18 talks and one poster. The first set of talks were setting the stage by providing an overview of historic developments, concepts and methods, and theoretical expectations. The second set focused on empirical case studies. The final set examined means for managing unwanted fisheries-induced evolution. The session was well attended, with between 50 and 100 people in the audience.

As highlighted in the theme session's introduction, fisheries-induced evolution is not a new topic. The earliest explicit reference known to us is by Cloudsley Rutter, who already in 1902 raised concern about salmon fisheries in California taking the largest, finest salmon before they could spawn. Rutter cogently pointed out that such a strategy of differential breeding was diametrically opposite to what a prudent cattle breeder would do. Within ICES, fisheries-induced evolution has figured on the agenda of several working groups since 1996, with the most thorough treatment provided by the Working Group on the Application of Genetics in Fisheries and Mariculture.

The best current understanding of fisheries-induced evolution concerns changes in maturation schedules. Theoretical expectations are clear-cut: harvesting that is not directly selective on maturity status favours earlier maturation, while the relaxation of such exploitation pressures is expected to result in reverse, albeit much weaker, selection for later maturation (H:11, H:18). By shifting a population's reproductive strategy towards earlier maturation at smaller body size, fisheries-induced evolution must be expected to affect a population's reproductive potential and its ability to recover from low abundance (H:18). Non-intuitive patterns may also emerge. In response to size-selective harvesting, a population may evolve towards either smaller or larger size at maturation, depending on its initial maturation size (H:08). Furthermore, population living in seasonal environments may be "trapped" at maturing at a certain age, unable to undergo the large evolutionary changes required for reaching other possible maturation ages (H:05).

The first section of the theme session presented insights provided by evolutionary models. Such models come in different flavours, each with specific strengths and weaknesses. A particularly promising modelling framework, which allows including stock-specific characteristics while also incorporating the quantitative genetics of inheritance, is provided by so-called eco-genetic models (H:11). Applications of eco-genetic models were presented in several contributions (H:18, H:10, H:16).

Several novel aspects of fisheries-induced evolution were also addressed in the first section. In sex-changing species, fishing may not only select for earlier maturation, but also for sex changes at smaller body size (H:12). Another study (H:17) highlighted that harvesting in food webs may trigger cascading effects, both ecologically (harvesting one species may cause extinction of another species) and evolutionarily (a species may evolve to utilize the niche left vacant by an extinct species).

The papers in the theme session's second section ranged considerably in terms of species studied and geographical locations examined. The section opened with reports on new results concerning two fish stocks that have been at the forefront of research on fisheries-induced genetic changes. Based on data for 34 female cohorts (1963-1996) of North Sea plaice (*Solea solea*), and using the reaction-norm approach to estimating maturation schedules (H:08, H:11, H:18), plaice were found to have shifted their maturation to younger ages and smaller sizes (H:14). A study on northern cod (*Gadus morhua*) off Newfoundland demonstrated that similar reductions in age and size at maturation could not be explained by changes body condition alone, and therefore presumably are of evolutionary rather than plastic nature (H:19). Another study on cod examined Swedish survey data, to determine whether the maturation reaction norms of cod in the Baltic Sea changed from the late 1980s to the early 2000s (H:09). Providing some tentative conclusions about the degree to which age and size at maturation have changed in these stocks, the interesting possibility was raised that evolutionary responses to exploitation might differ between males and females.

In further contributions, geographical variety was coupled with taxonomic diversity. A study (H:01) on the potential evolutionary consequences of fishing on two species of squid in the Southwest Atlantic (short-finned squid, *Illex argentinus*, and Patagonian squid, *Loligo gahi*) was unable to detect any consistent genetic changes to the maturation schedules of these species, highlighting challenges in detecting selection responses in semelparous, annually-reproducing species. A particularly detailed examination of body lengths and vertebral number of walleye pollock (*Theragra chalcogramma*) captured by different parts of bottom-trawling gear in the northern Sea of Okhotsk provided insight into the question of how fishing might select for individuals with differential swimming ability (H:07). In addition to the study on squid, the only other examination of invertebrates in the theme session was one of farmed Pacific oysters (*Crassostrea gigas*) along the Atlantic coast of France (H:03), which provided an empirical and theoretical template for studying evolutionary change in bivalves.

The third section of the theme session focused on prospects for managing fisheries-induced evolution. The section's five talks were representative of the different perspectives from which such discussions can be developed: from the vantage point of specific stocks (Northeast Arctic cod: H:13 and H:16; Baltic cod: H:04), of alternative life-history types (differing in their reproductive behaviour: H:15), and of particular management measures (such as marine reserves: H:10). The synergistic confluence of discussions based on these different angles is a prerequisite for establishing an integrated approach to managing fisheries-induced evolution.

A study on the influence of reproductive behaviour on the direction and rate of fishery-induced evolution (H:15) demonstrated that sexual selection for larger mates may provide a counterforce to fisheries-induced selection for earlier maturation at smaller size. Model-based analyses for Atlantic cod (*Gadus morhua*) suggested that reproductive behaviour may either increase or decrease the rate of fisheries-induced evolution, depending on whether, respectively, a population's coefficient of variation in body size decreases or increases with the intensity of exploitation.

Based on a size-structured model for the dynamics of Baltic cod (*Gadus morhua*), the optimal maturation size and the expected rate of fisheries-induced evolution were estimated (H:04). The underlying model was suggested to be readily generalized, as it uses parameters that are well known for many fish stocks (von Bertalanffy growth, maturity ogives, and fishing mortality). For Baltic cod, three management options were explored: lowering fishing mortality, restricting fishing to mature individuals, and reducing fishing on large individuals.

Different regimes were examined for managing fisheries-induced evolution in Northeast Arctic cod (*Gadus morhua*). A state-dependent energy-allocation model for the life history of cod solved by dynamic programming was combined with the breeder's equation of quantitative genetics to predict the stock's expected evolutionary response to fishing mortalities of different strengths and size-selectivities (H:13). The effects of three different management regimes (marine protected areas, maximum size limits, and minimum size limits) could thus be explored.

While marine reserves are receiving mounting attention as important means of contemporary fisheries management, their effects on fisheries-induced evolution remain to be better understood. Based on a general eco-genetic model, steps in this direction were taken (H:10) by examining the implications of density-dependent growth and mortality, of multiple evolving traits (maturation schedule, reproductive investment, and somatic growth), and of marine reserves alternatively established on the feeding grounds or spawning grounds of an exploited stock.

Fisheries-induced evolution may lead to considerable economic losses, especially when evolution towards smaller body size reduces the revenue per unit of biomass. A study on Northeast Arctic cod (*Gadus morhua*) addressed this problem by integrating ecological, evolutionary, and economic modelling (H:16). Enhancing an eco-genetic model with a bioeconomic component, the effects of an open-access regime were explored, the costs of fisheries-induced evolution were quantified, and management scenarios were suggested to maximize the long-term profitability of the fishery.

The theme session ended with a plenary discussion. Limitations of phenotypic data for proving fisheries-induced evolution were discussed. It was emphasized that conclusive evidence of genetic change can never be obtained based on phenotypic fisheries data alone. Individual case studies will therefore always remain open to alternative interpretations. However, when several independent stocks in different parts of the oceans show similar patterns, all consistent with theoretical expectations about fisheries-induced evolution, genetic change caused by exploitation emerges as the most parsimonious explanation. This conclusion is supported by modelling studies that predict fisheries-induced evolution under a wide variety of circumstances, and at time scales compatible with empirical observations. The fundamental limitations of inferences drawn from phenotypic data naturally raise questions about the possibility of using genetic data for demonstrating adaptive evolution in exploited fish stocks. While this research area currently is under development, several years of innovative research will presumably still be required before methods of this kind become routinely applicable in practice.

In summary, fisheries-induced evolution is a real phenomenon deserving the attention of fisheries scientists and managers, to overcome the uncertainties that still prevail. It is probable that the scientific community's current perception and awareness about fisheries-induced evolution is restricted to only the tip of the iceberg, as most empirical studies suffer from limited temporal scope and largely have focused on documenting changes in maturation, which is characterized by just one out of several groups of life-history traits expected to undergo fisheries-induced evolution. According to present understanding, the consequences of fisheries-induced evolution are predominantly negative, in the sense of undermining the reproductive potential of living marine resources and reducing the economic revenues that can be extracted from them. Research has just started on management schemes aimed at mitigating the repercussions of fisheries-induced evolution. These efforts urgently need to be developed, both in scope and in depth.

Open questions about fisheries-induced evolution will be addressed in ICES's new Study Group on Fisheries-induced Adaptive Change (SGFIAC), which will commence its work in 2007.