

Effects of Fishing on Inter and Intra Stock Diversity of Marine Resources

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Maintenance of phenotypic, and in particular genetic, diversity between and within stocks is one of the most critical goals of fisheries management and conservation. Fishing has been held responsible for the extinction and depletion of a number of stocks, and the majority of those remaining are threatened by over-exploitation. Fishing mortality often exceeds that which is natural and in addition fishing activities tend to be highly selective. Accumulating evidence suggests that selection pressures exerted through harvesting that is selective for size, age, sex, maturity and/or certain behavioural/genetic components have influenced the structure, plasticity, production, sustainability and recovery potential of a growing number of exploited stocks. In this paper we review the known effects that fishing has had on inter- and intra-stock diversity, and the potential consequences for fish stocks in terms of alteration of genetic and phenotypic properties.

KEYWORDS phenotypic, genetic diversity; fishery management; conservation; population richness

1. Introduction

Commercial fishing has had extensive effects on exploited fish stocks. For many stocks, fishing is the main source of mortality and may exceed natural mortality by more than 400% (Mertz and Myers 1998). In all stocks,

declines have been very rapid with catch rates often falling dramatically during the first 10 years of exploitation (Myers and Worm 2003). Greatest changes have been among predator species, and it has been estimated that more than 90% of large predatory fishes have been lost from the global oceans (Myers and Worm 2003). Through

their removal, not only global catches but also the mean trophic level of catches have consistently declined (Pauly *et al.* 1998; Myers and Worm 2003).

Due to their highly selective nature, most fishing practices not only affect fish communities at the inter-stock level, but also composition and diversity at the intra-stock level. Changes in age and size structure due to excessive removal of large and old individuals have been reported for many exploited fish stocks (Trippel *et al.* 1997; Marteinsdóttir and Thorarinsson 1998; Marteinsdóttir *et al.* 2005; Ottersen *et al.* 2006). In recent years, evidence that fishing not only affects populations demographically but also changes their genetic composition has accumulated (Heino and Godø 2002). Evolutionary pressures are exerted through fishing that is most frequently selective with respect to size, maturity status, morphology or behaviour (Jørgensen *et al.* 2007). Changes in life-history traits, particularly age and size at maturation, have been reported in an increasing number of commercially exploited fish stocks (see reviews by Trippel 1995; Dieckmann and Heino 2007; Jørgensen *et al.* 2007). In the majority of cases, such trends are unlikely to be explained by environmental influences alone, and fisheries-induced evolution has repeatedly been found to offer the most parsimonious explanation (Jørgensen *et al.* 2007).

These changes in the characteristics of the stocks range from being easily observable and measurable (size and age structures), to those that are not as easily determined due to interacting and confounding effects of density dependence and the environment. Still to be discovered are potential changes in genetic diversity that are undoubtedly ongoing, but are largely concealed due to our lack of knowledge of population structures.

Traditionally in fisheries science, the term 'stock' has described an arbitrary group of individuals belonging to a fish species,

numerous enough to be self-reproducing, relatively homogenous in life-history and demography, and occupying a sub-area of the geographic range of the species (Hilborn and Walters 1992; see Begg and Waldman 1999 for a review). The terms 'stock' and 'population' are frequently used interchangeably, although, at times confusingly, a population may be a unit recognised by taxonomists whereas a stock is not (Cushing 1968; Begg and Waldman 1999). However, regardless of the criteria used to define a particular stock (Waples and Gaggiotti 2006), the 'stock concept' is essentially based on the interaction between an exploited species and the management of that exploitation (Begg and Waldman 1999), and is therefore fundamental to fisheries science and management. These management units (stocks) are commonly geographically based, assuming the existence of a single stock within management regions. This spatial definition is thus infrequently based on concise information on stock structures. Today however, many commercially important fish stocks, for example Atlantic cod, halibut, turbot, and herring have been found to consist of smaller sub-units which vary in fitness-related traits, behaviour, and in some cases are genetically distinct (Ruzzante *et al.* 1999, 2000, 2006; Imsland *et al.* 2000; Jonassen *et al.* 2000; Hutchinson *et al.* 2001; Purchase and Brown 2001; 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).

Maintaining diversity between and within stocks is one of the critical aspects of conservation. All major international agreements on conduct for fisheries adopted during the last two decades emphasise the need for adoption of an ecosystem approach to fisheries (EAF). Explicit sub-goals of ecosystem based management are to assure sustainability and conserve genetic, species and ecosystem diversity (FAO 2003). While management advice regarding many of our most important fish stocks is often either

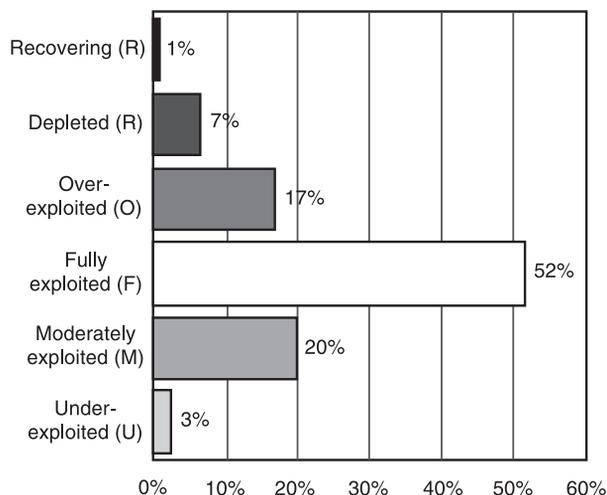


Fig. 1. State of world fish stocks in 2004 (from Garcia *et al.* 2005).

ignored or only partially implemented, recent developments in fisheries research have revealed immediate dangers due to potential erosion of stock properties.

In this overview, we focus on changes that have occurred at both the inter- and intra-stock levels due to fishing. Our objective is to provide up to date information on the potential consequences and importance that these changes have for the general fitness, productivity and sustainability of the stocks. Where applicable, examples are provided involving commercially exploited fish stocks.

2. Inter-Stock Diversity

2.1. Effect of fishing on inter-stock diversity

To date, a single fish species has been documented extinct on a global scale as a result of fishing, and two more due to habitat loss or other causes (Dulvy *et al.* 2003). Furthermore, fishing has been held responsible for the extinction of a number of marine and anadromous stocks, including several stocks of Pacific salmon, the beluga sturgeon in the Adriatic Sea (see overview and references

in Kenchington 2001) and the Icelandic spring spawning herring (Jakobsson 1980a). Additionally, a high number of marine stocks are considered severely overfished and depleted (Musick *et al.* 2000; Dankel *et al.* 2007). According to global statistics compiled by the United Nations' Food and Agriculture Organization (FAO) in Rome, 52% of the world's fish stocks were fully exploited, 17% overexploited and 7% depleted in 2004 (Fig. 1; Garcia *et al.* 2005). At a regional scale, more than 80% of the exploited fish stocks in the North Atlantic are overfished (ICES 2004). Of these, 34% are considered to be in danger of collapse and under ICES advice should be closed to all fishing activities (ICES 2004).

Exploited stocks commonly originate from more than one spawning component, with these spawning aggregations contributing unevenly to the harvestable stock (Begg *et al.* 1999). If these spawning aggregations consist mainly of philopatric individuals, genetic differentiation between the spawning components may be expected (Wootton 1998). Tagging studies have provided evidence of the presence of natal homing and spawning site fidelity within a

number of marine fish stocks (Godø 1984; Thorsteinsson and Marteinsdóttir 1993; Jónsson 1996; Thorsteinsson *et al.* 1998; Robichaud and Rose 2001, 2004).

Features of the environment which influence the biological and demographic characteristics of a fish stock are rarely distributed uniformly across the geographic range of that stock. Fish which reside in, or return to, particular habitats for significant parts of the year tend to develop phenotypic characteristics reflecting local adaptation. This picture of patchy distribution becomes more complex when there is ontogenetic (e.g. between spawning, nursery and adult areas) and/or seasonal (e.g. between feeding and spawning areas) changes in habitat occupancy. As a result, many exploited fish stocks do not represent single spawning stocks, but complex aggregations of sub-units that have variable or limited interaction. The degree of mixing between individuals within different habitats will determine whether a stock is truly a single panmictic population or a combination of sub-components that have limited interaction across their geographic range (Metcalf 2006).

Depletion of inter-stock diversity is likely to be manifested as an overall reduction in genetic diversity, less optimal use of habitat space and reduction in species' ability to contend with stochastic environmental conditions. What's more, the magnitude of stock erosion that has been observed may be only a fraction of the actual depletion that has taken place. Over the last decades, new and improved discrimination techniques have enabled us to identify stock structure that is often considerably more complex than was previously assumed (see examples below).

2.2. Examples of inter-stock diversity

Of all marine species, few have been studied more than Atlantic cod. During the last decade, an increasing number of studies have provided evidence of complex stock struc-

ture at relatively small scales. In the NW Atlantic, genetic differences have been reported between most of the major population complexes (NE Newfoundland Shelf, Grand Banks, Flemish Cap, Scotian Shelf, Georges Bank). At even smaller scales, genetic differences have been detected between inshore and offshore components of the Northern cod stock (Ruzzante *et al.* 1996, 1997) and between migratory cod that spawn in the Gulf of St. Lawrence and cod that reside and spawn outside of this area (Ruzzante *et al.* 2000). In the NE Atlantic, genetic differences have been established between North East Arctic cod and coastal cod (Fevolden and Pogson 1997; Sarvas and Fevolden 2005; Westgaard and Fevoldin 2007), as well as among coastal populations inhabiting different fjords along the Norwegian coast (Knutsen *et al.* 2003; Westgaard and Fevoldin 2007 and references therein). Evidence for gradual transition between putative populations and an existence of a hybrid zone was established for the North Sea and Baltic cod (Nielsen *et al.* 2003). West of Scotland and in the northern North Sea, the existence of resident spawning groups were suggested based on limited home range and exchange between spawning areas up to 200 km apart. In Icelandic waters, spatial analysis of molecular variance revealed three potential populations; two in the southwest separated by depth and one in the northeast region (Pampoulie *et al.* 2006). These findings were supported by tagging data and discrimination based on otolith shape and elemental fingerprints (Jónsdóttir *et al.* 2006a, b; Pampoulie *et al.* 2006).

Similarly, a number of genetically distinct population complexes have been described in herring. Ruzzante *et al.* (2006) demonstrated genetic differences ($F_{ST} = 0.027$) among herring from three regions: a) North Sea autumn spawners, English Channel winter spawners and Norwegian spring spawners b) Skagerrak spring spawners and c) the Western Baltic. This

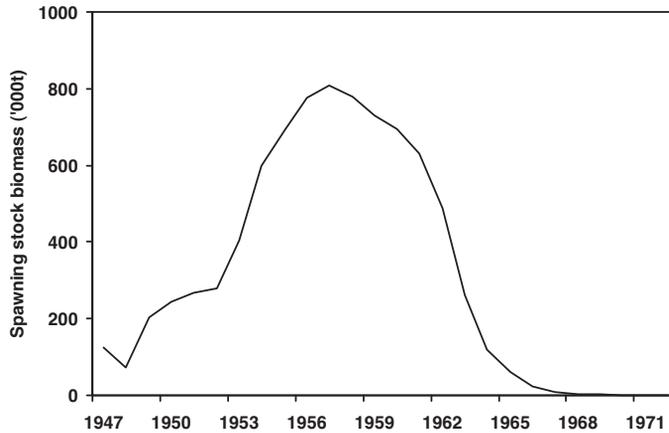


Fig. 2. Estimated spawning stock biomass of Icelandic spring-spawning herring in 1947–1972 (Jakobsson 1980a).

variation was supported by differences in life history strategies including migratory behaviour and spawning time and location, despite mixing of offspring during early life history stages (Ruzzante *et al.* 2006).

2.3. Examples of loss of inter-stock diversity

Of the three stocks of herring that have been identified in Icelandic waters; Icelandic summer-, Norwegian spring-, and Icelandic spring-spawners, only two are still present today. The Icelandic spring-spawning stock, which provided catches of 50–270 thousand tonnes in the 1940–1960's, collapsed in the late 1960's (Jakobsson 1980a) (Fig. 2). The collapse of this stock was not solely due to over-exploitation. Environmental conditions were difficult in Icelandic waters at this time due to low salinity and cold temperatures associated with the "Great Salinity Anomaly" of the late 1960's (Dickson *et al.* 1988). Resulting declines in primary and secondary production (Thórdardóttir 1976; Jakobsson 1980b) were held responsible for the sharp reduction in recruitment in 1965 (Jakobsson 1980a). Despite harsh environmental conditions, Jakobsson (1980a) demonstrated that

the stock could potentially have been saved if fishing effort had been kept at very low levels during the 1960's. Unfortunately, reduced recruitment levels and the decreasing stock size were not detected early enough due to the high efficiency of the purse-seine fleet (Jakobsson 1980a).

The northern cod was once one of the largest groundfish resources in the Northwest Atlantic. The stock responded to increasing fishing pressure in the 1960's–1970's with a rapid decline in abundance; the stock declined from a maximum of 3 million to less than 500,000 tonnes (Lilly and Carscadden 2002; Lilly *et al.* 2004; Lilly 2005). Following the extension of the fisheries jurisdiction to 200 miles in 1977, there was some improvement with the fishable stock exceeding 1 million tonnes in the 1980's. However, stock levels decreased rapidly in the early 1990's and a moratorium on fishing was declared in 1992. Although the causes are under ongoing debate, most scientists agree that overfishing was one of the most important factors leading to the decline and later collapse of this commercially and biologically important fish stock.

In the North Sea, genetic evidence suggests that one of four cod populations, the

Flamborough Head population, has disappeared since the 1950's (Hutchinson *et al.* 2003). This population became depleted twice in the period between 1954 and 1970. Microsatellite data indicated a significant reduction in genetic diversity during this time, followed by a recovery between 1970 and 1998; although this was characterized by a significant change in allele frequencies. The results were consistent with a period of prolonged genetic drift, accompanied by replacement of the Flamborough Head population with others nearby, most likely from the Aberdeen ground and German Bight.

In the 1970s, the Barents Sea capelin stock was one of Europe's largest single species fisheries (Hjermann *et al.* 2004a). Since then it has undergone two collapses during which biomass fell by >95%. The role of harvesting as the main cause of these collapses has been a matter of debate (Gjøsaeter 1998; Ushakov and Prozorkevich 2002). Several studies have demonstrated the importance of larval predation, particularly by herring, for subsequent capelin stock dynamics (Gjøsaeter 1998; Hamre 1994; Hjermann *et al.* 2004b). Hjermann *et al.* (2004a, b) described the additive nature of several mortality factors (harvesting, herring predation, cod predation and climate) and emphasised that one factor is unlikely to be counteracted by a decrease in another. Instead, overharvesting will tend to render a population more susceptible and sensitive to predation, leading to potentially large and abrupt changes in biomass.

Lastly, many Atlantic salmon stocks have declined dramatically, particularly within the southern range of the species (Parrish *et al.* 1998). As with capelin, the causes of these declines are of diverse origin. Impacts of climate, overfishing, aquaculture and oceanic conditions are likely to have had additive effects (Friedland *et al.* 2003; Dempson *et al.* 2004; Jonsson and Jonsson 2004, 2006).

3. Intra-Stock Diversity

3.1. Effects of fishing on intra-stock diversity

The first and most obvious response of a fish stock to exploitation is a decline in abundance. Severely reduced stock sizes will lead to fragmentation and shrinkage in overall distribution as well as spawning areas (Frank and Brickmann 2000; Hutchings 2000; Kenchington 2001; Smedbol and Stephenson 2001 and references therein). Associated with this are declines in intra-stock diversity, with respect to both phenotypic and genotypic variation.

Changes in phenotypic variation may result from size selective harvesting, along with unequal exploitation pressure on a particular sex or distinct life history units, leading to excessive removal of certain stock components (see further below). Such selection will naturally lead to changes in genetic diversity of the stocks, and may in some cases remove certain genetic components responsible for variation or plasticity in essential life history traits.

Evidence for size selective harvesting is plentiful (Trippel 1995; Fenberg and Roy 2008). Typically, fishing gear removes the largest (and fastest growing) individuals of a cohort at the time they enter the harvested part of the stock. Commonly, large individuals are also specifically targeted to maximize yield per unit effort. Even if size selective harvesting is not intentional, intensive exploitation will always lead to truncation of age and size structures simply because members of a cohort are not allowed to survive and attain a relatively old age. Indeed, one of the first indications of overharvesting is truncation in the age structure of a stock, leading to a decline in age diversity (Marteinsdóttir and Thorarinnsson 1998).

Most, if not all, temporally persistent changes in phenotypic diversity are likely to

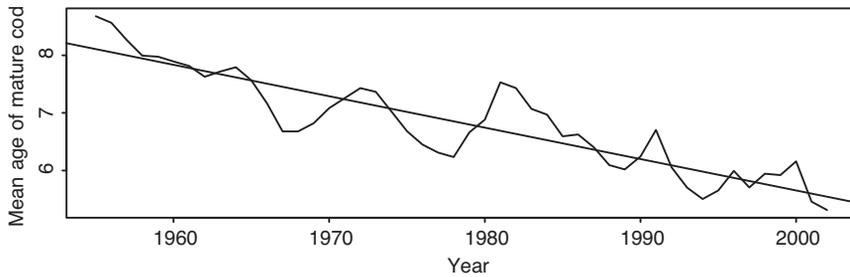


Fig. 3. Mean age of mature cod in Icelandic waters during 1955–2002 based on VPA results (Anon 2006).

be accompanied by changes in genetic diversity. Our knowledge of heritabilities associated with life history traits is somewhat limited. However, breeding studies have demonstrated that the heritability of characteristics such as growth and age at maturity are high enough to facilitate a rapid response to directional selection (Gjedrem 1983, 2000; Weigensberg and Roff 1996; Roff 2002; Henryon *et al.* 2002; Kause *et al.* 2003; Thrower *et al.* 2004; Reznick and Ghalambor 2005; Wang *et al.* 2006), and laboratory experiments have shown that size selective harvesting can cause evolution of growth rates and multiple other traits including fecundity, offspring size and food consumption rates (Conover and Munch 2002; Walsh *et al.* 2006).

3.2. Examples demonstrating importance of maintaining intra-stock diversity

3.2.1. Age and size structures

Declines in average age and size of spawners have been reported for many commercially exploited fish stocks. In the Arcto-Norwegian cod stock, average age and length of spawners decreased by more than 3 years (from 10–11 years to 7–8 years) and 10 cm (from 90–80 cm) between 1949 and 1990 (Ottersen *et al.* 2006). In the Icelandic cod stock, average age of spawners has also de-

creased by around 3 years (from approximately 8 to nearly 5 years) during the last 50 years (Fig. 3). In these stocks, as well as most other cod stocks in the North Atlantic, the number of age classes contributing to the spawning stock has decreased in a similar manner (Marteinsdóttir and Thorarinsson 1998; Marteinsdóttir *et al.* 2005; Ottersen *et al.* 2006). The importance of maintaining intra-stock diversity has been demonstrated for both these stocks because of the link between high age diversity, successful recruitment and greater resilience to environmental fluctuations (Marteinsdóttir and Thorarinsson 1998; Ottersen *et al.* 2006).

Long-term temporal changes in body size have also been reported for salmon (Ricker 1981), bluegill, black crappie and yellow perch (Beard and Kampa 1999), a variety of species on the Scotian Shelf (Zwanenburg 2000), several rockfishes in the Northeast Pacific (Harvey *et al.* 2006) and herring (Power and Iles 2001).

3.2.2. Reproductive potential

Changes in age and size structures will inevitably have large effects on the reproductive potential of stocks.

Many studies, addressing a variety of species, have provided ample evidence for the relationship between size and spawning experience of spawners and the number, quality, duration and time of offspring

Table 1. Relative fecundity (number of eggs/g) of small, medium and large: cod (50, 80, 110 cm), Icelandic herring (25, 30, 35 cm) and Irish Sea plaice (200, 600 1000 g).

Species	Spawner size			Citation
	Small	Medium	Large	
Icelandic cod (<i>Gadus morhua</i> L.)	525	628	781	Marteinsdóttir and Begg (2002)
Herring, Icelandic summer spawners (<i>Clupea harengus</i> L.)	200	480	565	Óskarsson and Taggart (2006)
Irish Sea plaice (<i>Pleuronectes platessa</i> L.)	186	264	310	Kennedy <i>et al.</i> (2007)

production (Solemdal 1997; Trippel *et al.* 1997; Trippel 1998; Kjesbu *et al.* 1996, 1998; Marteinsdóttir and Björnsson 1999; Marteinsdóttir and Begg 2002; Berkley *et al.* 2004). The impact of these relationships cannot be easily evaluated in nature (see below however) but results from laboratory and modelling studies indicate that only small changes in age or size distributions can have large effects on the immediate productivity of the stocks (Marshall *et al.* 2000; Trippel *et al.* 1997; O'Brien *et al.* 2003). Indeed just by looking at a simple measure like fecundity, it has been demonstrated that by decreasing or eliminating the number of large spawners in a population, potential egg production will be lowered by as much as 50% (Table 1). The amplitude of these changes, in terms of stock productivity, is likely to be much larger when other factors such as atresia, egg and larval size and quality, spawning time and duration are also considered.

In addition to the above studies on Icelandic and Arcto-Norwegian cod, that by O'Brien *et al.* (2003) on Georges Bank cod is one of the few empirical studies to actually provide evidence for the effects of maternal size on offspring abundance or survival in nature; it was found that egg survival was positively related to wider egg distribution and age diversity of spawners (Fig. 4).

Declines in population size due to exploitation are expected to be compensated for by increased fecundity at maturity. This has been found to be true among many Gadiformes and Pleuronectiformes including North Sea sole and plaice (Rochet *et al.* 2000 and references therein). However this does not apply to some other taxa, including Clupeiformes and Salmoniformes. Clupeiformes do not compensate for high adult mortality by increasing their current reproduction. Increased fecundity associated with decreased density does not occur in the smaller size-classes, but by steeper increases in size-dependent fecundity (Armstrong *et al.* 1989; Rochet *et al.* 2000). Similarly, in Salmonids and Osmeridae, fecundity has been found to be only weakly related to changes in density (Rochet *et al.* 2000 and references therein).

Reproductive potential can also be impaired due to disproportionate selection of the sexes and consequential changes in the operational sex ratio (Rowe and Hutchings 2003). In crab and lobster fisheries, size selective harvesting tends to remove large males in greater numbers than smaller females (see review in Fenberg and Roy 2008). In gadoids, skewed sex ratios in catches of spawning cod have been suggested to result from earlier arrival and greater activity of male compared to female spawners (Morgan and Trippel 1996). Robichaud and Rose

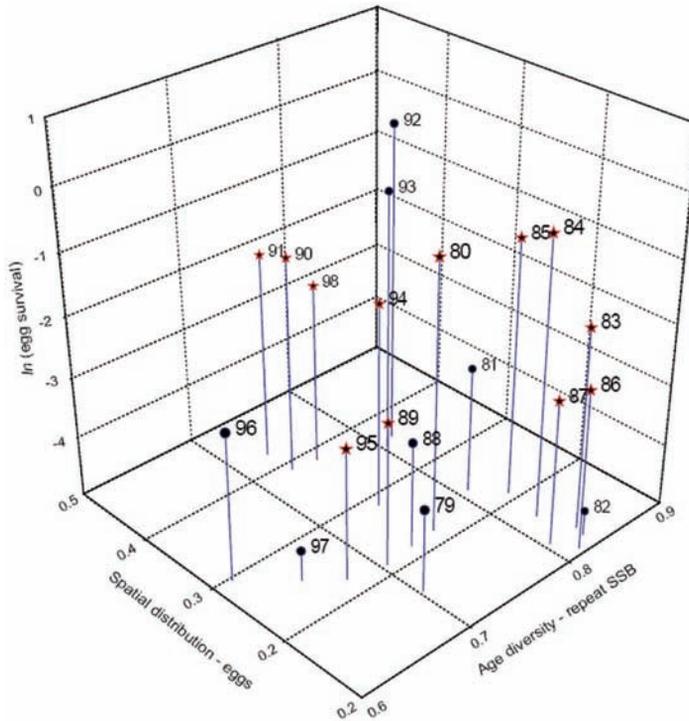


Fig. 4. Georges Bank cod: Age diversity of repeat spawner biomass, spatial distribution of eggs, egg survival rate and bottom temperature anomaly (circle = cold years, stars = warm years) during 1979–1998 (O'Brien *et al.* 2003).

(2003) lacked information on arrival of spawning cod, but showed that male spawners departed earlier than female spawners. Therefore, depending on when harvesting takes place with respect to spawning, and the magnitude of differentiation in characteristics which affect vulnerability to exploitation such as growth and behaviour (Rowe and Hutchings 2003), fishing activities targeting spawners are likely to remove the different sexes in an unequal manner.

The effect of size selective harvesting and its impact on behavioural ecology of fish species is unclear, and available information is painfully scarce. In cod, courtship rituals and vocalization are likely to be size related (Brawn 1961; Hutchings *et al.* 1999). Larger males were found to possess larger drumming bladder muscles, and the size of these

muscles was positively related to condition and fertilization potential (Rowe and Hutchings 2004). Size has also been shown to play a role in migration of spawning cod (Rose 1993) where large spawning migrations consisting of age structured aggregations were lead by large “scouts”. Similar phenomenon has also been reported for groupers for which it was observed that the young joined spawning migrations lead by more experienced adults (Birkeland and Dayton 2005).

The potential implications of harvest mortality, particularly that which is size selective, for age and size at maturation of exploited fish are both better understood and documented. According to life-history theory, increased mortality favours maturation at younger ages and smaller sizes. If in addition this mortality is size selective, those

evolutionary pressures will be stronger. Such changes in age and size at maturation have been observed in a number of commercially exploited fish stocks (see reviews by Trippel 1995; Dieckmann and Heino 2007; Jørgensen *et al.* 2007). Fisheries-induced evolution in these life-history traits has repeatedly been found to offer the most parsimonious explanation for these trends (Jørgensen *et al.* 2007). However, establishing that these changes are definitely of a genetic basis before such methods and data become available is highly problematic because of the confounding effects of phenotypic plasticity. Density-dependent changes in growth and condition as stocks are reduced in size, along with direct effects of other stochastic environmental factors such as temperature on maturation schedules, offer alternative hypotheses for these observed trends (Marshall and McAdam 2007; Wright 2007).

3.2.3. Population structure

Studies on small-scale population differentiation have suffered from the widely held perception that marine fish represent large, high gene flow populations, which are limited only by geographical boundaries of relatively large scales, i.e. continental shelf or ocean basins (De Woody and Avise 2000; Hutchings and Baum 2005). Not only have recent discoveries shown that many of our commercial fish stocks are composed of a multitude of genetically distinct populations (Hutchinson *et al.* 2001; Knutsen *et al.* 2003; Pampoulie *et al.* 2006; Ruzzante *et al.* 2006), but also that structure in terms of genetic properties linked with behavioural ecology is, in some cases, much more complicated than previously believed. For example, in Icelandic cod a number of different behavioural types have been recognized (Pálsson and Thorsteinsson 2003). Two of these, a shallow water type foraging in coastal waters and a deep water type migrating and foraging in temperature fronts, have been shown to differ in terms of gene frequencies at the

Pan I loci (Pampoulie *et al.* 2008). Regardless of whether the cod spawned at a southerly or northerly located spawning ground, those that undertook the deep water migrations were dominantly of the *Pan* I^{BB} genotype, while those that remained in shelf waters after spawning were more likely to carry the *Pan* I^{AA} genotype. Cod of the *Pan* I^{AB} genotype displayed either of the two behaviours.

One of the implications of these divergent behavioural patterns is that fishing pressure may vary between the different types. Those cod that migrate into the frontal areas undergo intense vertical migration throughout the year (Pálsson and Thorsteinsson 2003; Pampoulie *et al.* 2008) and do not appear to spend much time at the sea floor or in the vicinity of bottom trawls (Thorsteinsson unpublished data). Conversely, those cod that stay in shelf waters (shallow migrating cod) are likely to spend more time at the bottom and thus be exposed to traditional gear types. Therefore, harvesting may differentially remove the different behavioural types and thus influence the overall genetic diversity of the stock.

Selection can be linked with behaviour in various ways and is likely to be happening at a much larger scale than is presently recognized. For example, in a study on rainbow trout, genotypes with high intrinsic growth rate and bold behavioural traits were more vulnerable to simulated commercial fishing than slow-growing and shy genotypes (Biro and Post 2008). This was true even in the absence of directional size selective harvesting.

Genetic differences have also been detected over small spatial scales in herring. McPherson *et al.* (2003) detected genetic divergence between different spawning waves of herring at Devastation Shoal on the Scotian shelf ($F_{ST} = 0.005$), while at three other locations in the vicinity of Nova Scotia, no significant differences were detected among spawning waves. Similar results were

obtained for herring spawning at Rügen in the West Baltic, while at Gdansk Bay, differences between spawning waves were not significant (Jørgensen *et al.* 2005). In this respect, it should be noted that estimation of genetic divergence may result in a positive bias, especially among large gene flow species such as many marine fish. Kitada *et al.* (2007) have demonstrated a way to overcome this problem by using a Bayes procedure to estimate locus-specific pairwise F_{ST} 's.

For North Sea cod found in waters off west Scotland; despite the fact that genetic tools have not been useful in discriminating among populations, tag-recapture studies have provided evidence for resident adult populations in this region (Wright *et al.* 2006; Neat *et al.* 2006). Evidence for re-colonisation at one North Sea spawning area has also been found from a recent study of long-term genetic variation (Hutchinson *et al.* 2003). Furthermore, differences in population dynamics within spawning groups in this region, as well as limited exchange between these sites during the early life history period have been verified (Wright *et al.* 2006; Gibb *et al.* 2007). These studies illustrate that even if we are unable to discriminate among local populations using the genetic tools presently available, population structure may still exist.

Consequently, failure to account for such population richness in fisheries management may lead to the depletion of stock components and intra-stock diversity.

4. Future Goals of Fisheries Management

It is undisputable that harvesting of marine resources is selective by nature (Law 2001; Fenberg and Roy 2008). Selection occurs through unbalanced removal of fish in terms of size, age, growth, maturity, sex and behaviour. As discussed earlier, such strong, directional selection for heritable traits can induce evolutionary responses that may even

occur on decadal time scales. Theoretically, the concept of fisheries-induced evolution appears sound, and indeed the increasing number of studies reporting changes in life history traits in commercially exploited fish stocks are providing supporting evidence for the presence of contemporary evolution (Olsen *et al.* 2004; Walsh *et al.* 2006; Jørgensen *et al.* 2007; Biro and Post 2008 and references therein).

Of additional concern for management is the message provided by those studies that demonstrate potential anthropogenic selection of different behavioural types (Pampoulie *et al.* 2008; Biro and Post 2008). There is urgent need for more information on behavioural and evolutionary ecology of targeted species, and as pointed out by Myers and Worm (2003); managers may not always be aware of the true magnitude of change in the marine ecosystem as the majority of stock declines happened during the first years of exploitation, or prior to present day assessments. Furthermore, due to lack of knowledge on behavioural ecology of fish, harvesting is without doubt causing a number of changes to our stocks that present-day management and stock assessment methods are incapable of detecting.

Many authors have expressed the need for an evolutionary perspective to fisheries management (e.g. Conover 2000; Law 2000; Olsen *et al.* 2004; Williams and Shertzer 2005; Jørgensen *et al.* 2007; Kuparinen and Merilä 2007), but fewer have suggested or provided solutions for how to avoid fisheries-induced evolution. Management suggestions have included establishment of Marine Protected Areas (MPAs) (Baskett *et al.* 2005), use of minimum or maximum size restrictions (Conover and Munch 2002; Ernande *et al.* 2004), alternation of size at first capture between years (Kenchington 2001), avoidance of "derby" style harvests (Williams and Shertzer 2005) and maintenance of wide age distributions; particularly through the preservation of old and large

individuals in the stock (Martensdóttir and Thorarinnsson 1998; Birkeland and Dayton 2005; Ottersen *et al.* 2006; Law 2007; Hutchings and Fraser 2008).

The design and implementation of any management strategy that is intended to prevent the loss of phenotypic or genetic diversity requires knowledge of the life history, ecological and behavioural traits of the exploited species. Even for the most intensely studied species such as cod, such detailed information is often lacking. The recent emergence of evidence of stock complexity and behavioural vulnerability indicates that we are still far from comprehending the total variation that is built into these stocks. What is urgently needed, for any commercially exploited species, is a complete inventory of phenotypic plasticity and

as many genetically linked traits as possible. Fisheries data should be collected with high spatial resolution in order to enable identification of potential sub-division that may later be found to be important for management. Due to the potentially rapid rate of erosion of genetic diversity from these stocks, and because such changes are likely to be hard to reverse (Law 2000), this needs to be achieved at a much faster pace than has been previously realised. Until then, stocks should be managed at the smallest possible scale (spawning and/or behavioural units) in order that the loss of important, and perhaps unknown, components may be prevented; a strategy that is in compliance with the precautionary approach to fisheries management.

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