(Flat)fish stocks in an ecosystem and evolutionary perspective

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Abstract

The delineation of natural populations has many faces. While a stock relates to a management unit of organisms, the biological concept of a population may relate to a demographic/ecological perspective on interacting organisms or an evolving group of organisms. In addition, it has become increasingly clear that the time and spatial scales of the ecological and evolutionary population have much in common. Evolutionary population models, which are the focus of this paper, harbour independent information on census population size, population dynamics, population history and population connectivity. Fish populations continuously adapt to the changing environmental conditions. However, the impact of and response to fishing, climate and pollution stress are disconnected in time and lead to measurable changes in the genomes. Several new insights have emerged lately, such as the limited but biologically meaningful subtle genetic differentiation, the contribution of population connectivity, the consequences of the very small effective population sizes and the interaction between environment and evolution. This leads to the importance for management of the genetic monitoring of populations, the inclusion of adaptation in management models and the contribution of marine protected areas to guarantee the long term integrity of marine ecosystems. Of immediate significance is the match between stocks and the biological population model.

Key words: adaptation; evolution; fisheries; flatfish; gene flow; population dynamics; stock

Running title: (Flat)fish stocks in an eco-evo perspective

1. Introduction

45 By tradition the resource unit or fish stock has been the fundamental biological organizational unit
for management measures in fisheries. However, the population is the natural unit of organization
within species. Unfortunately, for lack of resources it remains largely undetectable and
underestimated across all oceans. Consequently it is poorly studied in exploited species, except for
iconic species such as Atlantic cod *Gadus morhua* and herring *Clupea harengus* (Reiss et al., 2009).

50 There are good reasons for demanding information on fish stocks (Hauser and Carvalho, 2008): (i)
they are the natural units of evolutionary change, (ii) it is the level at which policy and management
measures are taken, and (iii) anthropogenic impact makes it essential to identify metapopulation
structure (see glossary). Failing to do so may have major consequences; mixed stock designation can
be catastrophic for management as was shown in the case of Atlantic cod off Eastern Canada

55 (Hutchings and Myers, 1994) and food certification of Patagonian toothfish, commercialised as
"Chilean sea bass", *Dissostichus eleginoides* (Marko et al., 2011). Most striking on the identification
of populations is that the lack of knowledge can't be compensated for by extrapolation from well
known taxa to others (Ward, 2000). There is a recurrent need for empirical assessment and
interpretation, albeit supported by an increasingly strong conceptual framework.

60 One question stands out in the extensive scientific literature and policy framework on stock
structure, factors and management implications: What is a fish stock? Various definitions exist (Cope
and Punt, 2009) and inherently it represents a fuzzy measure of nature (Dizon et al., 1992). Two
rather different concepts of a biological unit are in use: the demographic and the evolutionary
population. This may be attributed historically to the existence of two largely disjoint communities of

65 researchers interested in populations. The demographic population model has been used as the
reference unit at the ecological level. Various definitions have been proposed (see (Waples and
Gaggiotti, 2006), of which one may be formulated as a group of organisms of the same species
occupying a particular space at a particular time. It is largely lodged in the present and provides
largely quantitative information. It is also the level at which fisheries management is organised,

70 although not necessarily with a match between management units (stocks) and natural population
(Reiss et al., 2009). The evolutionary population model focuses on reproductive cohesion (Waples
and Gaggiotti, 2006) and provides information on changes in the composition of populations. As such
it focusses on qualitative change in the evolutionary patterns of the far and recent past (Hauser and
Carvalho, 2008). Different criteria have been proposed to differentiate populations in the

75 demographic model, where migration is a key concept, and the evolutionary model, where gene flow
(see glossary) which is equivalent to the number of migrants per generation is used. The scales of
ecological time cover seasons and years, while in evolutionary time up to tens to millions of years. As
a consequence, ecological and evolutionary processes have been studied independently from each
other. However, there is mounting evidence, that ecological and evolutionary dynamics may occur at

80 the same time scale and hence interact with each other (Pelletier et al., 2009)). Examples of eco-
evolutionary changes occurring over short time spans are common and involve anti-predator
behavior, such as pelvic spine loss in three-spined sticklebacks *Gasterosteus aculeatus* (Colosimo et
al., 2005) and in feeding ecology and life-history traits such as the pelagic and demersal morphs of
lake whitefish (Renaut et al., 2011). Eco-evolutionary feedbacks are obvious in the case of the

85 predator-prey interaction between daphnia and alewife *Alosa pseudoharengus*. Anadromous alewife
populations have a temporary impact on their daphnia prey, while the evolutionary impact of

landlocked populations is more persistent (Post and Palkovacs, 2009). Ignoring these interactions may amongst others distort our view on the human impact on natural ecosystems (Smith and Bernatchez, 2008), for instance in the context of fisheries (Jørgensen et al., 2007) and land use (Cheptou et al., 2008).

Stock and population concepts inherently focus on a single species, a necessary but insufficient approach. Populations and species are embedded in collections of species, communities and ecosystems. Ecosystems are defined as the biological environment of all organisms (Ridley and Jones, 2004) who co-occur in a community (see glossary). Since the eighties there has been a gradual move towards “ecosystem based management” (EBM) and in a more specific context an “ecosystem approach to fisheries” (EAF) (Garcia, 2003) or “ecosystem based fisheries management” (EBFM – see glossary) (Pikitch et al., 2004) as part of sustainable environmental management. ‘It is a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way’ (Fifth Conference of the Parties to the Convention on Biological Diversity, Decision V/6, Annex A, section 1). It promotes a multidisciplinary and comprehensive approach in response to the questioning of the viability and sustainability of exploitation systems (Fromentin et al., 2009).

Fish(eries) genetics and genomics, a partner discipline which aims to understand demographic and evolutionary populations, has come of age. Its progress is impressive as an important contributor of new knowledge and not mere “stamp collecting” (Ferguson and Danzmann, 1998). Conceptually population genetics has evolved from an adaptive framework (Darwinian evolution) in the sixties of last century over a neutral framework where mutations were largely deemed neutral (Kimura, 1968) to the current combined neutral-adaptive framework (Ridley and Jones, 2004). Full genomes are known to respond to population changes while selected regions reflect adaptation through the favouring of specific alleles. Such knowledge is partially based on improved sampling of the genome, starting from morphological traits, over protein and enzyme polymorphisms, dominant DNA fingerprints and microsatellite markers, and most recently a growing focus on single nucleotide polymorphisms (SNP) and copy number variation (CNV). Increasingly sophisticated genotyping tools allow now for the full or almost full sequencing of samples (Davey et al., 2011), with most noticeable the cost efficient high-throughput sequencing methods (Metzker, 2010), but also the access to increased calculation power and adapted bioinformatic and biostatistical tools.

The review has been prepared for an audience of marine and fisheries ecologists. Several stimulating reviews, which were prepared from an evolutionary perspective and relevant to the study of fish stocks, summarize original findings and crucial paradigm shifts (Hauser and Carvalho, 2008; Kochzius, 2009; Larsen et al., 2011; Oleksiak, 2010; Reiss et al., 2009; Ward, 2000). One review addresses specifically the genomic resources of flatfish (Cerdeira et al., 2010). There is consensus in the scientific community that fish species and communities make use of their habitat in a spatially constrained and time-dependent manner. Population-specific life-history and behavioural traits impose adaptive choices and specific decisions. This review focuses on flatfish stocks (Order of Pleuronectiformes) without being exclusive and aiming for completeness. Increasingly EBFM has shifted focus from species to communities, the natural units of management. This is very appropriate for continental shelves where flatfishes are a key component of demersal communities and may be considered an umbrella taxon (Rogers et al., 1999). They have evolved to a range of ecological and physiological

adaptations to benthic environments (Gibson, 2005). Their larvae are planktotrophic, postlarvae
 130 meiobenthic predators and adults first and second order carnivores occupying the middle to upper
 levels of the food web. They are biologically unique because of an asymmetric laterally flattened
 adult body plan. Survivorship curves have a negative binomial shape (type III), with a high fecundity
 and high juvenile mortality, a feature typical of many bony fishes. Adults may live older than 10
 135 years, even up to 55 years in the case of larger-sized taxa (e.g. Pacific halibut *Hippoglossus stenolepis*,
 (Munk, 2001). Flatfishes sustain an important fishery worldwide, mostly located on the continental
 shelves. Production reaches 926,268 metric tons in 2008 (FAO, 2010), considerably less than the
 1,392,000 tonnes at the end of last century. Pacific halibut as a species reaches the highest annual
 catches at 35,000 tonnes (Nielsen et al., 2010), although for example plaice reached 170,000 tonnes
 in the 1980ies in the North Sea (Rijnsdorp and Millner, 1996). Flatfish aquaculture (Cerdeira et al., 2010;
 140 Imsland et al., 2003) is increasing steadily and has reached 148,800 metric tonnes in 2008 (FAO,
 2010). At the moment olive flounder *Platichthys olivaceus* attains the highest production.

2. Fish stock patterns and processes – neutral evolution

The evolutionary population concept will be our reference; the words stock and population are used
 145 interchangeably, with stock linked to fisheries issues and population taking a conceptual angle.
 Genomes evolve in response to four processes of which mutation (a process which is not that
 common) and genetic drift (less likely to occur in large populations) are of lesser importance in this
 context. However, gene flow and selection play a major role. The former relates to the tendency of
 150 individuals to disperse in or between habitats and hence to belong to a metapopulation (Kritzer and
 Sale, 2006). Gene flow typically affects genetic variation across the full genome (neutral evolution).
 The latter relates to the Darwinian paradigm of the survival of the fittest, whose meaning should be
 understood as survival from mortality (viability) but also as survival of progeny (fecundity). Adaptive
 diversity is strongly linked to phenotype because selection acts on the phenotype; it has a local
 impact on the genome.

155 The most striking observation of marine fish populations are the low levels of differentiation
 compared to terrestrial and freshwater organisms. Values in the ocean are on average a factor ten
 lower than on land. This knowledge is generally accepted and is independent of the genetic marker
 used (DeWoody and Avise, 2000; Ward et al., 1994)). At larger spatial scales such as between the
 basins of the Atlantic Ocean and Mediterranean Sea (Patarnello et al., 2007), or long stretches of the
 160 continental shelf off eastern North America (Bernardi et al., 1993) differences between populations
 tend to be more striking. Such differences have most often been attributed to vicariance or isolation
 by distance (Avise, 2004). Also gradients of marine taxa in the transition from fully marine to fresh
 water (e.g. Baltic Sea, (Johannesson and André, 2006)) tend to be strong. For a long time the low
 level of differentiation was interpreted in terms of genetic homogeneity between organisms, which
 165 was attributed to above average levels of gene flow. Papers on pelagic and demersal fish alike,
 including the flatfishes Pacific halibut (Grant et al., 1984), European flounder *Platichthys flesus* (Borsa
 et al., 1997) and turbot *Scophthalmus maximus* (Blanquer et al., 1992), adhered to this
 interpretation. This is not unexpected given the highly dispersive and vagile life stages of marine
 organisms (Selkoe and Toonen, 2011; Shanks, 2009). However, gradually the question arose whether

these differences between populations at low differentiation levels are (1) statistically significant and above all (2) biologically meaningful? There are several arguments that may question statistical significance. For example sufficiently large sample sizes at very low levels of differentiation will tend to show significant differences anyway (Waples et al., 2008). Moreover technical issues such as sampling, genotyping and analytical artifacts tend to influence the signal to noise ratio (Waples, 1998). Regarding the biological meaningfulness, there is consensus that individuals (and hence populations) occupy a restricted space in response to habitat characteristics and imprinting. It has become clear that population size, demography, history, behaviour and connectivity play a major role in interpreting empirical evidence (Hauser and Carvalho, 2008).

Population size

Marine census population sizes (see glossary), especially of economically exploited populations, tend to be large and may count hundreds of millions of individuals at a biomass in the hundreds of thousands metric tonnes (Branch et al., 2012; Dickey-Collas et al., 2010). Species with large population sizes harbor a large genetic diversity; heterozygosities and allelic diversities of marine populations feature among the highest values recorded (DeWoody and Avise, 2000; McCusker and Bentzen, 2010; Ward et al., 1994). Consequently a separation between populations may go unnoticed for a long time because differences in allelic frequencies are slow to appear. The power of the differentiation signal is too low to be picked up at the level of neutral genomic variation (Hauser and Carvalho, 2008; Waples, 1998). The larger the population size the stronger interpopulation differences and the lower the gene flow have to be before they are significant. In the paragraph on adaptive evolution it is explained how subtle differences between large populations may be picked up.

Population biomass (and hence size) impacts ecosystem functioning and individual biological traits. A reduced biomass of predators will affect the composition of the community and may shift the ecosystem to a new equilibrium (Scheffer et al., 2005). This may lead to less profit (Worm et al., 2009). For example, during last century the hundredfold swings in herring *Clupea harengus* biomass in the North Sea have affected landings considerably and resulted in measurable effects on trophodynamic structure (Dickey-Collas et al., 2010). A well documented case is the collapse of ecotypes of three-spined stickleback (Taylor et al., 2006) and whitefish (Vonlanthen et al., 2012) due to eutrophication. But the changes in biomass must also have shifted the role of fish stocks in regards to predator-prey relationships, ecophysiology and behavior (Fitzsimmons and Warburton, 1992; Magnhagen et al., 2009; Post and Palkovacs, 2009). (Pre-)mating interactions of spawning populations are highly evolved and depend amongst others on population size and structure (Rowe et al., 2011). Reducing size below a threshold may limit the chances to find suitable mates, enhance inbreeding and hence increase the changes for the exposure of deleterious alleles (Frankham et al., 2002). Homing of fish to the breeding and feeding grounds includes acquired and inherited traits with chances for straying being inherently part of the process (Telles et al., 2011; Thorrold et al., 2001). Also to be considered is the highly skewed pattern of mating among potential subjects (Blonk et al., 2009; Jones and Hutchings, 2002) and skewed sex ratios due to selective fishing (female fish tend to be larger sized) (Rijnsdorp et al., 2010). Evidence in the marine environment for the impact of

population size on genetic diversity and phenotype (Allee effect) remains weak (Courchamp et al., 2009); but see (Hoarau et al., 2005). These are strong arguments to conserve biomass considerably above the MSY value (Branch et al., 2011).

215 **Population dynamics**

Understanding and predicting how population numbers change with time, is a key feature of fundamental and applied ecology. Individual genomic profiles and population genetic structure carry demographic signatures because life-history traits and demographic changes of populations affect genetic diversity measurably (coalescent; (Wakeley, 2005). In the case of population expansions, signatures of runaway alleles and increased allelic diversity may be observed (Aise, 2004). Latitudinal range shifts in species distribution lead to novel interspecific assemblages (Southward et al., 2005; ter Hofstede and Rijnsdorp, 2011) and intraspecific lineage sorting at the leading edge. New mutations, often constrained by the standing portfolio of allelic diversity, may surf on the wave of range extension (Klopfstein et al., 2006). Population reductions due to a natal deficit and bottlenecks due to population collapses or new colonization events lead to reduced allelic diversity and in more extreme cases the extirpation of populations (Hutchinson et al., 2003) see later). Bottlenecks may lead to genetic drift and the associated fixation of alleles. Reductions in population size may lead to inbreeding especially when effective population sizes (see glossary) have dropped below 500 individuals (see below). Above average chances towards homozygosity will increase exposure to deleterious or suboptimal fitness alleles (Frankham et al., 2002). Long term stable populations leave a genetic imprint of high genetic diversity with a mixture of ancestral and recent mutations.

High fishing pressure has not only affected biomass but also the age-frequency distribution. Elimination of large-sized (and older) fish, has truncated the age-frequency distribution of many stocks and reduced the generation time (Atlantic cod: (Hutchings, 2005) plaice: (Rijnsdorp, 1993); sole *Solea solea*: (Cuveliers et al., 2011)). This may affect short and long term cycles and trends in recruitment, competition, predation, exploitation and environmental change, and changes in catch ability (Bjørnstad et al., 1999; Garcia et al., 2012). Recruitment variability may increase with fishing pressure, leading to concerns for long-term survival (Essington et al., 2006; Rouyer et al., 2011) but see (Brunel et al., 2010). Modeling has learned that in an inherently variable environment such as the ocean, the addition of mortality from fishing will increase temporal variability (Shelton and Mangel, 2011). There is circumstantial evidence on the breakdown of population integrity from population dynamics (Atlantic cod from the Gulf of Saint Lawrence - (Swain and Chouinard, 2008); Atlantic herring from the former Zuiderzee - (DeJonge et al., 1993) and the Scotian Shelf - (Stephenson et al., 2009) and population genetics (Hauser et al., 2002; Hutchinson et al., 2003). Biological extinction seems of lesser concern (Branch et al., 2012; Dulvy et al., 2003) and has not yet been reported for flatfish.

Population history

Strong fluctuations in climate regime characterize the Pleistocene period. Ecosystems have changed, environmental ranges have shifted, and ecosystems with their populations have adapted by a combination of phenotypic plasticity and adaptation, and southward migration during cold periods and northward migration during warmer periods (Hewitt, 2004). Cold periods often lead to population reductions with small groups surviving in refuges. It leaves a genomic imprint of reduced and skewed diversity and generates distinct clades. The recurrent retraction to refuges and expansion from refuges in response to Glacial-Interglacial cycling has led to the evolution of distinct population groups. Also, continental shelves with their typical shallow water fauna expanded and shrunk with the repetitive melting and locking of water in ice masses. The genomes of populations bear testimony to the Pleistocene history and hence may help to understand stock structure. The discipline of phylogeography (see glossary) reveals these patterns embedded in the past. For example North-South range shifts in response to climate change are obvious along the North-South oriented ocean basins (Maggs et al., 2008), but take more complex patterns in enclosed seas such as the Mediterranean Sea (Patarnello et al., 2007). Unlike elsewhere, populations of the Southern Ocean have moved on and off the shelf in response to climate fluctuations (Thatje et al., 2005). Some regional patterns are strikingly differentiated due to historical fragmentation. For example, populations of many Mediterranean fish species, including *Pomatoschistus* gobies (Larmuseau et al., 2010), sole (Kotoulas et al., 1995) and European sea bass (Bahri-Sfar et al., 2005) are distinctly fragmented in groups of populations (named clades) inhabiting the basins of the Western Mediterranean, the Adriatic Sea and the Eastern Mediterranean. Another observation is that species may respond differently to climate change in accordance with their life-style and ecological function. Species with an inshore distribution tend to be more fragmented (common goby *Pomatoschistus microps* (Gysels et al., 2004); European flounder (Hemmer-Hansen et al., 2007b)a, while offshore species show more restricted genetic differentiation (mackerel *Scomber scombrus* (Zardoya et al., 2004); northern bluefin tuna *Thunnus thynnus* (Riccioni et al., 2010); Pacific halibut: (Nielsen et al., 2010). Coastal taxa often exhibit intermediate patterns (sole: Kotoulas et al., 1995; plaice: (Was et al., 2010); turbot: (Nielsen et al., 2004).

Population connectivity

Gene flow is a key process affecting populations; it has the tendency to homogenise interpopulation differences. The oceanic realm with its strong hydrodynamic continuity between habitats and obvious lack of barriers may lead to strong connectivity (see glossary). The various definitions attributed to connectivity seem to follow the demographic concept of a population: (i) a time-restricted perspective where dispersal is limited to movement from the spawning ground to nursery (Sinclair, 1988), (ii.) dispersal of individuals among subpopulations that survive to reproduce (reproductive connectivity) (Cowen and Sponaugle, 2009), and (iii) the exchange of individuals among geographically separated subpopulations that comprise a metapopulation (population connectivity) (Cowen and Sponaugle, 2009). Often realized dispersal has been overestimated because biological and physical factors counteract potential dispersal. A balance between dispersal and adaptation to the local environment is critical in shaping population characteristics. And even in an environment of high gene flow, divergence may still be possible provided that differentiating selection is strong (Pinho and Hey, 2010).

Patterns of genetic structure in a seemingly homogenous ocean are increasingly revealed provided that they are supported by well designed sampling protocols, genotyping with high-resolution genetic markers and advanced data analysis (including geospatial statistics). With time the initial reports of weak morphological differentiation and weak genetic structure (for a summary on flatfish see (Hoarau et al., 2002) have shifted to biologically meaningful subtle structures (European hake *Merluccius merluccius*: (Milano et al., 2011; Pita et al., 2011); northern bluefin tuna: Riccioni et al., 2010; Atlantic cod: Jakobsdóttir et al., 2011; herring: (Nielsen et al., 2012); sole: Cuveliers et al., 2011).

Contemporary genetic structure represents ongoing population connectivity and patterns due to historical phenomena. Several models of population structure have been proposed; all accommodate for subtle patterns, although they do not always explain fully the observations. The island model refers to the equal exchange of genes between islands and the stepping stone model assumes that the rate of migration between colonies is a function of the distance between them (Latter, 1972). Isolation-by-distance deals with populations uniformly distributed throughout a continuum; the further apart populations are removed, the higher the chances for genetically distinct allele frequencies. It has been widely cited in the flatfish literature (Kotoulas et al., 1995; Watts et al., 2010). If populations are composed of mixtures of individuals reproducing at different times, gene flow may be restricted between early and late reproducers (isolation-by-time; (Dickey-Collas et al., 2010; Hendry and Day, 2005; Maes et al., 2006). Finally chaotic genetic patchiness due to sweepstake reproductive success may structure populations (Hedgewick, 1994; Rolland et al., 2007). “A relatively small proportion of adults may account for the bulk of reproduction and recruitment, owing to chance matching of reproductive activity with temporally and spatially varying conditions conducive to fertilization, larval development, and settlement” (Hedgewick et al., 2007). As a consequence intergenerational and local genetic variation may be larger than on a wide geographical scale.

The weak genetic structure over large geographical areas raises the question whether biologically meaningful differences also exist on a small scale. As mentioned before, empirical evidence supports that the dispersal dynamics and connectivity of marine organisms affect their genetic structure (Kinlan and Gaines, 2003; Palumbi, 2003). Hence the assumption that planktonic larval dispersal homogenizes populations is not always met. For example, genotyped and capture-mark-recapture tagged Atlantic cod revealed over a period of 10 years a meaningful weak structure at the out- and in-fjord scale separated by a shallow sill (Knutsen et al., 2011). The metapopulation of plaice in the North Sea might not differentiate genetically (Hoarau et al., 2002; Was et al., 2010) but fish tracked with data storage tags from three release sites tend to inhabit distinct sites (Hunter et al., 2004). From population genetic differentiation and effective population size the population dispersal distance may be estimated (sole: from 150 km (Kotoulas et al., 1995) to 500 km (Cuveliers et al., 2012); Greenland halibut: 12,300 km (Table 1), although these values are indicative. They may be incorporated in proposals for the design of marine protected areas (Palumbi, 2003).

Some flatfish populations are interesting candidates to test genetic patterns because all have a combined planktonic and demersal life-style, play a key role in benthic food webs and make use of geographically distinct nurseries. In general, species lacking pelagic larval stages tend towards increased levels of population subdivision (Waples, 1987). Bio-hydrodynamic modeling shows that the key mechanisms for structuring populations impacts the planktonic life-stages (Bolle et al., 2009;

Galindo et al., 2006; Lacroix et al., In revision). Patterns are shaped by advection and diffusion, albeit with important behavioural and ecophysiological constraints. Interannual variation in spawning biomass, survival and advection are significant determinants of connectivity between spawning grounds (Lacroix et al., in revision). Adults tend to be more influenced by ecophysiological, behavioural and environmental constraints to their distribution and connectivity (Freitas et al., 2010). Some taxa prefer inshore habitats (European flounder and sole) while others offshore habitats (halibut and dab *Limanda limanda*). This opens perspectives on adaptive selection among populations across the range and between years, hence providing biological drivers for stock dynamics.

Population size and genome diversity

The impacts of fishing are obvious through increased mortality of target and non-target organisms. Selective harvesting of exploited species may shift size and age structure, sex ratio and hence reproductive output. The low biomass is never that low that there is an immediate threat for extinction due to low population counts (N_c) (Dulvy et al., 2005). Even after depletion, a stock will still consist of millions of individuals (Branch et al., 2012). But there are implications for population viability and resilience due to population fragmentation, inbreeding and loss of genetic diversity, a crucial component of biodiversity that affects reproductive performance, adaptation to environmental changes and resistance to disease (e.g. (Lage and Kornfield, 2006). Fortunately criteria for stock depletion and threat status do match and hence should be set and followed to reduce overexploitation (Dulvy et al., 2005).

Evolutionary and demographic approaches offer considerable opportunities to provide fisheries independent information (Fromentin et al., 2009). The genetic signals of demographic history such as immigration, expansion, extinction, bottlenecking, selective exploitation and hybridization are traced effectively through genetic profiling. The genome harbours signatures of allele loss (Garza and Williamson, 2001), changes in genetic diversity such as multi-locus heterozygosity and mean number of alleles (Hutchinson et al., 2003), fitness – heterozygosity correlations (Hansson and Westerberg, 2002), homozygote excess also known as inbreeding (Garoia et al., 2007; Hoarau et al., 2005), kinship as measured through relatedness (Watts et al., 2010) and changes in effective population size (Hare et al., 2011; Yi and Streelman, 2005).

The effective population size (N_e - see glossary) is an important parameter because it determines how large populations should be to maintain their evolutionary potential and avoid inbreeding depression (Frankham, 1995; Hare et al., 2011). It is widely accepted that at $N_e > 500$ populations won't suffer too much from changes in environment and ecosystem. At $N_e > 50$ there will be no negative impacts from exposure to homozygous deleterious alleles, but the long term viability of the population is not assured. Empirical evidence shows that the median N_e tends to be smaller in populations of conservation concern (Palstra and Ruzzante, 2008). In an ideal population N_e equals N , but in nature N_e is always smaller than N . There are multiple causes affecting the N_e value. Variable population sizes and variance in reproductive success have a strong impact on N_e (Hedrick, 2005). This is particularly relevant under high fishing pressure when temporal variability in

population size may be enhanced (Hsieh et al., 2006; Shelton and Mangel, 2011). Sex ratios may be unequal for various reasons such as habitat or size-segregation between sexes and differential fishing pressure. Social structure may be such that there is unequal contribution of gametes to the next generation. Generations may overlap such as in many long-lived species. An important consequence of these factors is that N_e values are lower than the census population sizes (N). If mammals have N_e to N ratios of 0.1, the size of an ideal population of marine bony fish (Hauser and Carvalho, 2008; Larsson et al., 2010; Portnoy et al., 2009) and flatfish (Watts et al., 2010; Cuveliers et al., 2011) is up to five orders of magnitude smaller than the census population size (Table 2). Initially, such values have been met with disbelief; a stock of one million fish would harbor just 10 to 100 parents effectively propagating their genes. However, unlike N N_e is measured at an evolutionary scale, which makes its interpretation more complex. In addition, their estimate under different long term and contemporary time frames influence interpretation (Hare et al., 2011). Overall, N_e is positively correlated with N (Hauser and Carvalho, 2008); hence fishing down N of commercial stocks may compromise the evolutionary potential. It is one of the arguments proposed why some overexploited stocks are so slow to recover after conservation measures have been implemented.

The question arises whether a measurably reduced N affects N_e and hence genetic integrity. This might be assessed by temporal changes in N_e , preferably covering a period starting with no fishing mortality. It has proven to be a challenging task; historical collections of biological material (most commonly otoliths) start at the earliest in the beginning of the twentieth century, a period with already heavy fishing pressure in the northern hemisphere. Against, expectation, temporal estimates of N_e have stayed almost unchanged for a number of fishes (Larsson et al., 2010; Pujolar et al., 2011; Therkildsen et al., 2010) and flatfishes (Was et al., 2010; Cuveliers et al., 2011) during the second part of the twentieth century. Dramatic declines in N of two orders of magnitude in species like European eel (Pujolar et al., 2011) and herring (Larsson et al., 2010) have yet to be detected in the genome. Cuveliers et al. (2011) observed no strong changes in effective population size in a time series of sole covering the period 1957-2007, despite evidence for tripling of fishing mortality. The increased N_e/N_c ratio was explained through several non-exclusive hypotheses: (i) genetic compensation acting against the negative genetic effects of low population numbers; (ii) the fishing-related removal of older fish with a highly reproductive success gives less reproductive females the opportunity to be winners; and (iii) N_e was estimated with a generation time which has almost halved compared with previous periods. Uncertainty over the N_e values, although estimated with increasing confidence, make that the values are indicative and not yet operational for the management of stocks. However, evidence for reduced genetic diversity, increased inbreeding and a lowered N_e over time has been documented in some cases; there is limited evidence on the impact from fishing mortality. The lower N_e of plaice in the North Sea (Hoarau et al., 2005), Atlantic cod in the North Sea (Hutchinson et al., 2003) and silver seabream *Pagrus auratus* off the coast of New Zealand (Hauser et al., 2002) coincided with increased fishing mortality after World War II. The data of Hoarau et al. (2005) has been reinterpreted by Was et al. (2010) based on the genotype scoring and Hutchinson et al. (2003) used a very small set of loci, questioning true genome coverage. Overall, effective population size has drawn attention to the need for a large population biomass to sustain a robust fishery resilient of environmental change.

3. Fish stock patterns and processes – adaptive evolution

Standing variation in genetic diversity is the principal source of organismal adaptation (Barrett and Schluter, 2008); new mutations have less to contribute since they are relatively rare and most often have a deleterious to (sub)lethal phenotype. The huge diversity so typical of large marine populations is a source of functional variants, which might be better adapted to the ruling environmental conditions at some time in the future. There are relatively few well documented cases as selection is hard to prove in nature and empirical evidence has to be validated experimentally and functionally (Endler, 1986). But it has become clear that populations acquire new traits from standing variation and gene-linked modifications (Jones et al., 2012; Renaut et al., 2011). For example, populations of three-spined stickleback colonizing freshwater lose their body armour of lateral plates, a phenotype which has been linked to a regulatory region of the *Eda* gene. However, what is actually happening is that a rare *Eda* allele present in marine populations is favoured in freshwater and outcompetes in parallel across freshwater systems phenotypes linked to other alleles (Colosimo et al., 2005).

Meaningful evolutionary units to study adaptive divergence are the spawning grounds, which are an eternal source of new genetic combinations through the sorting and recombination of gametes. Failure to identify the location of these natural units complicates the interpretation of genetic patterns throughout the life cycle, of connectivity and of the identification of stocks (e.g. Pacific halibut – (Nielsen et al., 2010). In addition to the sorting of chromosomes, egg and larval survival have a strong impact on cohort strength and hence the composite genetic profile of the population. Mortality, having a typical negative binomial distribution (type III survivorship), peaks at early life stages and exponentially decreases with increasing fish size. It is a consequence of the experienced mortality and growth rates, which are temperature-dependent and stage-specific (Houde, 1997; Pepin, 1991). Strong selection pressures may favour phenotypes associated with specific genotypes and families, and influence inbreeding.

The strong selection pressure at early life stages shapes the patterns of adaptive variation in the population. Although experimental genetic evidence for adaptation represents the ultimate explanatory argument, in most cases it has been limited to empirical evidence at the level of the gene and the genome. The list of candidate genes (see glossary) has been growing since the time that allozymes were screened. They include for example the protein haemoglobin (de Ligny, 1969; Koch et al., 1964), metabolic enzymes of the Krebs cycle (such as LDH-2 and PGHD) (Exadactylos et al., 1998) and the metal-binding protein metallothionein (Guinand et al., 2008). An alternative approach screens for evidence of selection at outlier loci, which are loci with above or below average genetic differentiation (Hemmer-Hansen et al., 2007a; Powers and Schulte, 1998)(Vilas et al., 2010). Such loci represent a minority in the genome but because of their functional importance or linkage to functionally important genes are highly relevant. Full genome characterization suggests that regulatory elements outside the genes play an important role in adaptive processes (Jones et al., 2012). Spatial patterns of adaptive divergence may have a smooth clinal, stepwise (staircase) or diminished phenotypic correlation with latitude (Conover et al., 2006). Clinal patterns are often linked to ecological gradients related to the mixing of water masses (e.g. transition between the Baltic Sea and North Sea at the Belt Sea – (Johannesson and André, 2006); transition between the Gulf Stream and the Labrador Current off Cape Hatteras - Powers and Schulte, 1998).

Local genetic adaptation may commonly act at relatively small spatial scales and hence at ecologically relevant scales. The smallest spatial scale of adaptive divergence in a flatfish was documented for turbot over a distance of just 60 km (Imsland et al., 2001). Growth rate tested under various temperature regimes in a common garden design measurably differed between sites. In another case the intrusion of salt water in the freshwater Baltic Sea some 8500 years BP has put strong selection pressure on the marine fauna (Johannesson and André, 2006). European flounder adapts well to local salinity gradients (phenotypic plasticity) and to large scale gradients, which were established some 2000 generations ago following the connection of the Baltic Sea to the North Sea. Transplanted populations retain their adaptive profile and hence support permanent genetic adaptation (Larsen et al., 2007). Also contaminants put a high selection pressure on coastal populations (see further). Post World War II environmental exposure to complex admixtures of toxicants (pesticides, nutrients, heavy metals and polycyclic aromatic hydrocarbons) has led to measurable genotypic adaptation in European flounder at spatial scales of 100 km (Marchand et al., 2003). Adaptation at short temporal scales, reflecting population dynamics at the cohort level plays a key role in each new cohort. Few cases have been documented in commercial species (Atlantic cod: (Ruzzante et al., 1996); European eel: (Pujolar et al., 2006); sole: (Guinand et al., 2008), but evidence across taxa (including fish) is convincing (Barrett et al., 2008; Conover and Munch, 2002).

As adaptive divergence may happen over a range of scales from fine (meters) to coarse-grained (thousands of kilometers), it is likely to be influenced by a balance between gene flow and selection (Pinho and Hey, 2010; Sanford and Kelly, 2011). For long gene flow was considered – often incorrectly so – to dominate the equation. Gene flow is in fact restricted because of important behavioral modulation with consequently small scale adaptive differentiation in fitness, life history traits and self replenishment of populations (Junge et al., 2011; Knutsen et al., 2011; Pinho and Hey, 2010). Also, in the case of strong divergent selection gene flow won't erase differentiation, although very low values of differentiation are measured (Conover et al., 2006). This is possible because ongoing selection eliminates inferior immigrant genotypes. Loci under high directional selection pressure differentiate stronger than neutral loci, and hence can be picked up in large-scale screens. For example, Atlantic cod and turbot populations, although experiencing high levels of gene flow, were characterised at a number of distinct outlier loci (Nielsen et al., 2009b)(Vilas et al., 2010). The recent adoption of SNPs (see box 2) has increasingly revealed biologically meaningful subtle population structure (Nielsen et al., 2010). Above average F_{ST} values at some loci point to a putative adaptive cause although final proof depends on independent environmental, molecular and experimental evidence (Endler, 1986; Hansen et al., 2012). Well documented cases include allelic variation at the *Pitx1* gene in three-spined stickleback under predation pressure (Chan et al., 2010) and at the rhodopsin gene of visual predators such as sand gobies *Pomatoschistus minutus*, which is under strong selection due to variation in the transparency of the water (Larmuseau et al., 2009). Adaptive SNP loci are now used to trace individuals to their source population provided that the SNP profile of all populations throughout the full range have been documented (Nielsen et al., 2012). It opens perspectives for the reliable routine monitoring of fish stocks (Hansen et al., 2012).

The ultimate goal of evolutionary biology is to explain and understand the molecular drivers of local adaptation. The phenotype is shaped by the genome and the interactions between genome and environment. Which are the major and minor effect genes, the regulatory elements and the chromosome architecture that affect evolutionary fitness in natural environments and populations

(Feder and Mitchell-Olds, 2003)? To what degree do epigenetic factors explain genetic - environment interactions? In the past decade, genome technology has increased considerably the means to study adaptive evolution such that the field of adaptation genomics has developed (Stapley et al., 2010). The genome of non-model organisms has become accessible and their quantitative traits can be linked to genomes in field populations.

While neutral evolution affects the dynamics of the complete genome, adaptation is highly local, to the extent that genomic “islands of divergence” are surrounded by “deserts of neutral evolution” (Turner et al., 2005). Adaptation acts on phenotypic variation, where large phenotypic changes may be driven by small genetic modifications. These may be polygenic and determined by major effect loci or a combination of minor effect loci. Also epigenetic effects linked to histone modification, DNA methylation and RNA interference influence the phenotype (Bossdorf et al., 2008). Full genome comparisons between individuals belonging to different populations have learned that relatively few regions are involved in the stable adaptation to abiotic factors (salinity tolerance - (Hohenlohe et al., 2010; Jones et al., 2012) or the divergence in ecotypes (Renaut et al., 2011). Linking genes associated with these islands of divergence to a function involves multiple approaches. Transcriptome profiling under standardized experimental conditions contributes to the understanding of adaptation through a catalogue of up-, down- and non-regulated genes (Cerdeira et al., 2010), while systems genetics allows the modeling of the metabolic response to allelic variation (Jeyasingh et al., 2011). A long standing knowledge gap between genotype and phenotype has impaired the quantification of adaptation (Naish and Hard, 2008). Phenotypic differentiation in structured pedigrees is larger than genetic differentiation ($P_{ST} \gg F_{ST}$); a well accepted approach to address phenotypic reaction norms uses common garden experiments (Conover et al., 2006; Larsen et al., 2007). Under natural conditions, where unstructured populations dominate, correlations between phenotype (Q_{ST}) and genotype (F_{ST}) are weak (Conover et al., 2006). However, genome wide association looks exactly for associations between major and minor effect loci (detected through SNP arrays) and phenotype in natural populations. It is a widely used tool in human disease-association studies and has found its way in non-model outbred populations such as three-spined stickleback (Davey et al., 2011). Cases in the high seas can be expected in the near future.

The intensity and persistence with which fishing has been performed on the high seas influences genetic structure and adaptive potential. Fishing induced mortality is a major factor exceeding too often natural mortality (Myers and Worm, 2005) and hence putting an additional selection pressure (Andersen and Brander, 2009). The rate of evolution may act fast (Darimont et al., 2009). It is highly selective for large-sized and late-maturing fish where the feeding grounds are targeted (*e.g.*, cod, herring and mackerel). There where it targets the spawning grounds (*e.g.*, Barents Sea cod (Jørgensen, 1990) and sole) fishing catches early maturing fish with their associated behavior, and hence selects for late maturing fish. Most often a mixed fishing strategy is applied with consequently a tendency towards earlier maturing slower growing fish with a higher reproductive investment. There is also an impact of fishing on natural mortality at the level of predation, food availability and reproductive investment (Jørgensen and Holt, 2012). The evolutionary impact of such permeating pressure may be assessed in the genome at the level of neutral and adaptive genetic variation.

Genetic variation is impacted through demographic processes, in this case massive population reductions with 58% of the fish populations declining 80% or more; for example flatfishes

(Pleuronectidae) showed median declines of 74% (Hutchings and Reynolds, 2004). Fishing also leads to population truncation as large-sized fish are highly desirable (Rouyer et al., 2011) reducing generation time (Rijnsdorp, 1993; Cuveliers et al., 2011) and leading to increased recruitment variability. Recruitment contribution has increasingly shifted to younger fish which are less able to buffer suboptimal circumstances. The phenotypic shifts in size (Conover and Munch, 2002) and life-history reactions norms (Grift et al., 2007; Mollet et al., 2007; Rijnsdorp, 1993) have now been confirmed with empirical genetic evidence (Jakobsdóttir et al., 2011; Nielsen et al., 2009b); Diopere, pers. comm.). By analogy with directional selection in plant and animal breeding, selective sweeps (see glossary) are expected.

Small populations tend to fragment in smaller breeding units, hence increasing the opportunities for inbreeding and the loss of genetic variation due to drift. Most important adaptability of the stock is increasingly compromised. While the loss of genetic variation due to fishing is slow to materialize (tens of years; Andersen and Brander, 2009), its rebuilding in overfished stocks takes hundreds of years (Dunlop et al., 2009). The rebuilding depends on a combination of factors such as generation time, age structure, recruitment variability, and behavior. Moreover, the reduced effective population size due to population bottlenecks leaves a lasting scar, even when populations have expanded back to their initial size. This effect is well known from the recurrent impact of the glaciations on population size during the Pleistocene (*e.g.*, (Coscia and Mariani, 2011)).

A complicating factor affecting long term adaptive integrity is the impact of pollution through physical change (*e.g.* shift in the mean and variability of temperature), eutrophication and contamination by a portfolio of chemicals (*e.g.*, heavy metals, polycyclic aromatic hydrocarbons (PAC) and polychlorinated organics). Especially coastal (estuaries and lagoons) and freshwater populations are affected transgenerationally. For example, multi-locus heterozygosity, growth rate and condition of European flounder and European eel were lower at polluted sites compared to the reference site (Maes et al., 2005; Marchand et al., 2003). The differential responses to pollution are registered in the expression profile of both species, providing a functional explanation (Marchand et al., 2006; Oleksiak, 2008). Evolutionary ecotoxicological evidence points to a quick multifactorial genetic and transcriptional response of populations exposed to pollutant stressors (Fisher and Oleksiak, 2007).

4. Emerging patterns

Insights on the link between neutral and adaptive evolution of populations at one side and demographic and life-history related patterns at the other side, are of global and general importance. Paradigm shifts formulated over the past decade (Hauser and Carvalho, 2008; Branch et al., 2012) have generated new knowledge and insights. I summarize in eight points a diverse group of emerging patterns which are of significance for the characterisation of fish stocks. They facilitate the synthesis of biological knowledge and promote an ecosystem approach to populations and species.

1. For a long time it was not clear why differentiation of marine populations was so low and whether the general occurrence of an almost panmictic pattern had a biological meaning. The scientific community realizes now that many populations are distinct, but that relatively high levels of gene

flow and large population sizes tend to weaken interpopulation differences and hence lead to subtle patterns in time and space. Hence subtle patterns of low genetic difference are biologically meaningful. Multiple evidence points to various topographical, hydrodynamical and behavioural drivers leading to population identity (Christie et al., 2011; Knutsen et al., 2011; Thorrold et al., 2001). The detection and, more important, the explanation of these patterns requires a multidisciplinary approach. Population differences might be small at a neutral genetic level as population dynamics might be concordant over large areas, but they become strong and biologically meaningful once they are interpreted in view of local adaptation (Cadrin, 2010; Nielsen et al., 2009a).

2. The tracing of demersal fish has learned that the spawning and nursery grounds are often spatially separated. Evidence from modeling (Erftemeijer et al., 2009; Lacroix et al., In revision; Savina et al., 2010), chemical trace analysis (Cuveliers et al., 2010; De Pontual et al., 2000; Vasconcelos et al., 2007), ecology (Beyst et al., 2001; van der Veer et al., 2011) and population dynamics suggests that a combination of environmental (hydrodynamics) and biological (behavior) factors carries the larvae to the nursery grounds for settlement. As development time is temperature dependent (Pepin, 1991; Houde, 1997), slower growth of northern populations leads to a higher potential to disperse (Bradbury et al., 2008). Hence models developed for (sub)tropical habitats do not fully match with the patterns observed in northern regions. The importance of connectivity between spawning and nursery grounds fits in a perspective of connectivity throughout the full life-cycle (Block et al., 2011). The metapopulation model with its connectivity landscape and differential source – sink dynamics (Crowder et al., 2000) highlights that the integrity of the spawning area is a link in the maintenance of population integrity.

3. The loss of exploited fish biodiversity and the vulnerability to extinction at the genetic level should be mitigated because of long lasting consequences at the population and ecosystem level. Few species have disappeared (Dulvy et al., 2003), many exploited stocks have reduced biomasses (Branch et al., 2010; Hutchings, 2005) and (small) populations are likely to vanish unnoticed (Hutchinson et al., 2003). It is most prevalent in anadromous species whose biannual migration through estuaries has become constrained due to habitat and hydrological modifications (Dulvy et al., 2003), but may also occur in species in which stocks comprise of several populations. Exploited populations characterized by a safe biomass level and enjoying modest fishing pressure are less prone to population collapse and hence biodiversity loss (Worm et al., 2009).

4. Intraspecific spatial differentiation occurs at various hierarchical levels. Patterns at a between-basin scale are often linked to historical events dating to the Pleistocene with its fluctuating climate conditions. There were multiple occasions for repetitive population isolation followed by merger (Patarnello et al., 2007; Maggs et al., 2008). Initially these historical patterns served as basis for stock delineation under the concept of evolutionary significant unit (Moritz, 1994). However historical and adaptive patterns do not necessarily cover the same scale. (Fraser and Bernatchez, 2001) proposed an adaptive approach, which implicitly included the ecological context. Local patterns reflect local adaptation and hence matter for a sustainable exploitation because they harbor the genetic variation so important to adapt to changing environmental conditions.

5. The effective population sizes (N_e) of marine populations are so small (Hauser and Carvalho, 2008) that a strong case can be made to maintain a high biomass. Although the population dynamics of

small pelagics such as herring are much more prone to strong cycling, also demersal and larger-sized fish show very low effective population sizes and especially very low ratios of effective to census population sizes. (Portnoy et al., 2009; Larsson et al., 2010). Consequently, fragmentation and reduction of density will affect population variance and hence resilience (Hoarau et al., 2005). Although the interpretation of the N_e value is controversial, the accuracy and precision of its value should benefit from genome-based estimates (Allendorf et al., 2010). The values are properly appreciated if the impact of behaviour on migration, kin recognition, spawning (sweepstake recruitment; Hedgecock, 1994), predator-prey and host-parasite interactions is included.

6. Evolution is a process acting over a range of time scales. On average it acts over thousands of generations. However, cases of fast adaptation, meaning adaptation over short (hundreds of generations) to very short (tens of generations) periods, do occur. When selection pressure is high and the ruling conditions are changing, phenotypes may shift to a new optimum in the adaptive landscape. Such selection pressures may originate from environmental and biotic factors. Most obvious is the adaptation of marine and fresh water organisms to a strong abiotic (*e.g.*, salinity) gradient (Johannesson and André, 2006; Colosimo et al., 2005). But the large swings in biomass must have left a genetic footprint, similar to what happened during the Pleistocene. Evidence is increasingly convincing in the case of Atlantic cod (Nielsen et al., 2009), where a shift in allele frequency at a single locus has been attributed to the loss of older fish (Jakobsdóttir et al., 2011). In small pelagic fish such as the Atlantic herring stock of the Northeast Atlantic Ocean, no genetic evidence has been found yet (Larsson et al., 2010), although statistical evidence points strongly in the direction of selective pressure (Engelhard and Heino, 2004). Flatfish may respond rapidly to changes (Grift et al., 2003; Mollet et al., 2007), although the degree to which this phenotypic plasticity includes a heritable component and is truly sourced in the local population from standing variation awaits further scrutiny (Naish and Hard, 2008).

7. In the process of changing population traits, so do the interactions of populations with the environment. Changes in population phenotype may influence community and ecosystem structure, and ecosystem dynamics through eco-evolutionary interactions. One outstanding process is the persistent removal of top predators, which has affected the trophic cascade (Scheffer et al., 2005) and changed the prey field in size, abundance and life history traits. This leads to adaptation of the focal species, initially through phenotypic plasticity but at a later stage through inheritable traits (Conover and Munch, 2002; Cousyn et al., 2001; Taylor et al., 2006). Once the phenotype and associated genotype has shifted, a new equilibrium may become established. This ecosystem perspective complements the population perspective which has dominated population genetics and fisheries management.

8. Greater detail on the genetics and evolution of fish stocks has emerged through improved access to affordable technologies which screen and monitor the genome and transcriptome. The methodological assets are impressive and include tools to genotype small and large population samples for just a few or hundreds of markers which may be judged neutral or adaptive (Milano et al., 2011), to sequence full genomes of tens (and soon thousands) of individuals (Jones et al., 2012), to identify large numbers of species (be it eggs, fillets, stomach contents or just water samples) through DNA barcoding (Kochzius et al., 2010), to analyse highly degraded ancient DNA from museum collections, burial and archaeological sites (Cuveliers et al., 2009; Nielsen and Hansen,

2008), to trace individual fish and fish products to their relatives and source population with medium density SNP arrays (Nielsen et al., 2012) and to profile expression patterns of populations with oligonucleotide micro-arrays (Larsen et al., 2007; Larsen et al., 2011). It is anticipated that automated *in situ* nucleic biosensors will be operational in the near future (see later). High-throughput phenotyping and function-to-phenotype assignment remains a bottleneck. These approaches make most sense when applied in a multidisciplinary context with oceanographers, environmental modelers (Galindo et al., 2006), biostatisticians, fish biologists and molecular biologists. It will make it possible to upgrade information density in space and time in the short and long-term (Fromentin et al., 2009).

5. Implications for fisheries management and conservation

Worldwide marine fish catches are unlikely to increase; most stocks are exploited at their maximum while unexplored (and collapsed) fisheries are unlikely to make a significant contribution (Branch et al., 2012). Therefore exploitation should aim for sustainability through maintaining integrity of the ecosystem, biomass and biodiversity. Critical is the implementation of fundamental knowledge on (fish) populations in conservation strategies at amongst others the level of harvest control (Froese et al., 2011) and ecosystem management, and its translation into policy. Success of this process hinges on translational knowledge, trade-offs and consensus at the environmental and socio-economic level (Jennings and Rice, 2011). There is considerable fundamental knowledge (although it will never prove sufficient), the principles of conservation biology and stock management convince, but implementation is notoriously slow (Jennings and Rice, 2011; Pitcher and Lam, 2010). At the same time there is a major disconnect in society between facts and perception, between short and long-term goals, between goals of the civil society and private sector. Here we summarise some of the issues of relevance to stock management from a genetic and evolutionary perspective.

The ecosystem approach is gradually being adopted to manage fisheries worldwide (Garcia, 2003; Jennings and Rice, 2011). The sizeable decrease in yield and the failure to manage stocks species-by-species, has stimulated a shift in strategy by adopting the ecosystem as reference unit. Societal support is increasing through its gradual implementation (*e.g.*, Australia (Smith et al., 2007); Marine Strategy Framework Directive of the European Union (EC, 2008). However EAF is not easy, as it will be tougher, more demanding on research resources and more complex to implement (Rice, 2011). Two aspects of EAF have major evolutionary consequences. First, the adaptation of MSY biomass as reference for exploitation (Froese et al., 2011) may provide for adaptive management in response to the extreme uncertainty in decision making in environment and natural resources (Walters, 2007). EAF should ease anthropogenic pressure on stocks by impinging less on genetic diversity (a consequence of stock reduction and fragmentation), by targeting less specific phenotypes (fast growers and late maturing fish) through harvest diversification, and by maintaining the adaptive potential in large population sizes, especially under the current conditions of fast global change. A collateral effect is that non-target species, some of which have low population sizes, are less likely to suffer from population reduction and even collapse. Second, the prioritisation and design of marine protected areas (MPAs) offers perspectives to incorporate evolutionary principles, particularly now that there is a multilateral agreement to protect 10% of the oceans by 2020 (UNEP/CBD/COP/10/27,

705 <http://www.cbd.int/cop10>). The evolution of (meta)populations is influenced by the size, size
 structure, spacing and coverage of MPAs (Gaines et al., 2010). Size refers to the relationship between
 habitat size and protected area, an important parameter for viable stocks. Size structure refers to the
 mosaic of MPAs to accommodate for a range of behaviours and life-history traits. Spacing is an
 710 important parameter for connectivity and coverage affects the total biomass. Realized dispersal,
 spawning and nursery habitats, feeding grounds, connectivity, population size and genetic diversity
 are crucial for the maintenance of exploited stocks. Genetic diversity harbours valuable insurance to
 cope with future change. For example, ecosystems of enclosed basins, such as the Baltic Sea, with a
 small species and genetic diversity, may fail to restore. Strong local adaptation, genetic isolation and
 local endemism affect the potential for evolutionary rescue (Johannesson et al., 2011).

715 The paradigm shift in the understanding of evolution and population dynamics by delineating stocks
 not only in a historical but also in an adaptive perspective fits well with the EAF management (Fraser
 and Bernatchez, 2001). The adaptive approach, also called Darwinian fisheries management (Dunlop
 et al., 2009), has allowed to put the large genetic diversity and weak genetic structure of marine
 populations in perspective in full agreement with population genetic theory. It has shown that local
 720 adaptation is widespread in marine populations, that it is common (albeit subtle in view of the high
 gene flow), that there is a disconnect between neutral and adaptive genetic variation, and that
 evolution can happen on contemporary scales (Conover et al., 2006; Jørgensen et al., 2007). This has
 led to the realisation that there may be serious mismatches between biological populations and
 fisheries management units (Reiss et al., 2009). In some cases such as the Northwestern Atlantic
 725 stocks of Atlantic cod this has led to painful failures (Hutchings and Myers, 1994). In case of the
 flatfishes of the Northeastern Atlantic Ocean, on average the natural populations seem to match the
 management units as they cover unique or several ICES management units (Reiss et al., 2009). This
 contrasts with the Mediterranean Sea where there is a persistent mismatch between natural
 population units and managed stocks because the highly fragmented nature of the basins (Patarnello
 et al., 2007) and the coarse management units defined by the Mediterranean Science Commission
 730 (CIESM). Consequences may be large. If several biological units are covered by a single management
 unit, flawed management may be an outcome; if one biological unit is covered by several
 management units, management may be optimised by combining the management units.

Climate change in the ocean will result in redistributions of marine species (Dulvy et al., 2008) and
 735 fish catch potential (Cheung et al., 2009; Cheung et al., 2010). This will affect ecosystem structure,
 reassemble communities (Parmesan, 2006) and lead to trophic mismatches (Scheffer et al., 2005). It
 will also lead to major changes at the genetic level which affect population size, distribution and
 diversity. Populations have the potential to either migrate or to adapt locally. The latter is based on
 standing genetic variation and/or inclusion of newly acquired genetic variation (Jones et al., 2012).
 740 Important is that the rate of adaptation depends on the match between the time and variability
 scales of stressor and system. While the principles of change are increasingly understood, case-by-
 case interpretations based on heuristic tools remain few. Hence, these are challenging and exciting
 times for conservation genetics and by extension conservation genomics (Allendorf et al., 2010).
 Genetic monitoring of populations provides a valuable information tool for “seeing the fish”, tracing
 745 adaptive genetic responses and hence assisting EAF management. Widespread environmental
 changes, with climate being the foremost important, but also exploitation playing a major role, affect
 selection regimes (Hansen et al., 2012). Repeated analysis of populations through time provides an

estimate of change. It requires methodological developments at three levels. (1) Genotyping with affordable and accessible tools facilitate implementation. At the moment lab-based genotyping has reached a high level of automation and throughput (see above). The first *in situ* nanoscale ecogenomic sensors have been mounted on environmental sample processors (Harvey et al., 2012; Preston et al., 2009) and should increasingly become operational in the next ten years (US (DOE, 2005). Traceability for the purpose of stock management becomes gradually implemented in real time. For example, the fishery on Norwegian coastal and Northeast Atlantic cod is monitored daily through mixed stock analysis and individual assignment with a set of microsatellite markers and the *Panl* gene (Wennevik et al., 2008). Stock admixture and fishery interceptions are monitored in the Canadian –USA transboundary fishery on several species of Pacific salmon (Waples et al., 2008). (2) The large data flow originating from routine genetic monitoring requires the maintenance of data banks for data repository and access. The global databanks on fish diversity (such as the World Registry on Marine Species - WORMS), fisheries data (FAO) and DNA sequence (GenBank) do not fully accommodate population genetic data yet. Data standardization across the fisheries community has been complicated by the diversity of genetic markers in use, but developments towards a focus on sequence are in progress. (3) Data integration requires smooth access, analysis and interpretation. The hierarchical access to high quality data, preferably through online data banks, will facilitate the integration of genetic data in Geographic Information Systems (e.g. Galindo et al., 2006; Nielsen et al., 2012) and is likely to speed up integration in management.

In conclusion, the evolutionary perspective on populations and ecosystems represents a welcome addition to the ecological perspective on fisheries management. But there is not really a need to differentiate flatfish among other fish taxa at a broad level when it comes to its implications for fisheries and conservation. Evolutionary changes impact diversity, demography, structure and adaptation in all marine organisms. However, at the specific and ecosystem level, generalities have to be translated into local and regional insights. Flatfish are common inhabitants of the sea bottom, they play a major role in shelf-based food webs and are a major target of the fishery. Their locally monitored genetic diversity and structure, and its interpretation provide important parameters for adaptive management.

BOX 1: Glossary

Candidate gene: a gene, located in a chromosome region suspected of being involved in the expression of a trait, whose protein product suggests that it could be the gene in question.

Census population (N): or absolute population size.

Community: a community represents the entire array of organisms inhabiting a particular ecosystem (Morin, 2011).

Connectivity: (i.) a time-restricted perspective where dispersal is limited to movement from the spawning ground to nursery (Sinclair, 1988), (ii.) dispersal of individuals among subpopulations that survive to reproduce (reproductive connectivity) (Cowen and Sponaugle, 2009), and (iii) the exchange

of individuals among geographically separated subpopulations that comprise a metapopulation (population connectivity) (Cowen and Sponaugle, 2009).

790 Demographic population: a group of organisms of the same species occupying a particular space at a particular time. It is largely lodged in the present and provides quantitative information (Waples and Gaggiotti, 2006).

Ecosystem-based fishery management (EBFM): a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way.

795 Effective population (N_e): the number of breeding individuals in an idealized population that would show the same amount of dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration (Wright, 1938).

Evolutionary population: a population model that focuses on reproductive cohesion and provides information on changes in the composition of populations (Waples and Gaggiotti, 2006).

Gene flow: the transfer of genes or alleles from one population to the other.

800 Genome: the complete hereditary information of an organism as embedded in the nuclear and mitochondrial DNA.

Metapopulation: an assemblage of discrete local populations with some measure of shared migration among them (Hanski and Gilpin, 1997).

Mixed stock: population with a mixed composition in regards to age, size, origin and/or geography.

805 Phylogeography: the study of the historical processes that may be the cause for the contemporary geographic distributions of individuals through gene genealogies (Avise, 2004).

Selective sweep: the reduction or elimination of variation among the nucleotides in neighboring DNA of a mutation as the result of recent and strong positive natural selection.

BOX 2: Genetic markers for fisheries management

810 There seems to be a bewildering array of markers available for fisheries applications to the uninitiated (Ferguson and Danzmann, 1998). Historically, biparentally inherited protein markers such as haemoglobin (Koch et al., 1964), Restriction Fragment Length Polymorphisms (RFLP) of maternally inherited mitochondrial DNA (mtDNA; e.g. (Graves et al., 1984) and nuclear allozyme markers (Utter, 1991) were deemed appropriate to discriminate between populations. However mtDNA markers
815 failed to account for the large pool of biparental nuclear variation and hence to quantify the full contemporary adaptive differentiation. Access to allozyme markers was limited and required adapted sampling protocols. Also a shift happened from identifying management units (MUs; (Moritz, 1994)) by rejecting panmixia to an approach based on the amount of genetic divergence at

which populations become geographically independent (Palsbøll et al., 2006). Hence, focus shifted to contemporary dispersal, connectivity, small scale patterns and adaptation to define stock structure. Markers required to detect such subtle structures abound in the nuclear genome but awaited accessible and cost-effective tools. Microsatellite DNA markers have been widely used to identify stocks (e.g. Cuveliers et al., 2011). Lately, high-throughput sequencing and array methods have improved resolution of stock identification considerably through a shift towards the highly standardised SNP markers (Nielsen et al., 2010), in some cases at the full genome level (Jones et al., 2012; Nielsen et al., 2012). Resolution has improved such that the tracing of individual fish and fish products (Nielsen et al., 2012) and the identification of ancient DNA products (Nielsen and Hansen, 2008) has become feasible.

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List of tables

1415 Table 1: Published estimates of genetically estimated dispersal distances of flatfish.

Species	Dispersal distance (km)	Genetic marker	Reference
Flounder <i>Platichthys flesus</i>	110* Confirms Borsa et al., 1997	23 allozymes 9 microsatellites	(Borsa et al., 1997) Hemmer-Hansen et al., 2007
Plaice <i>Pleuronectes platessa</i>	> 200** (continental population) 25** (Irish Sea and Scotland)	6 microsatellites 9 microsatellites	Hoarau et al., 2002 Watts et al., 2010
Sole <i>Solea solea</i>	134* 500**	12 allozymes 15 microsatellites	Kotoulas et al., 1995 Cuveliers et al., 2012
Greenland halibut <i>Reinhardtius hippoglossoides</i>	12,286**	6 microsatellites	(Knutsen et al., 2007)

* From (Kinlan and Gaines, 2003)

** original calculation based on Palumbi (2003)

1420 Table 2: Published short and long term estimates of census population size, scaled (Θ) or absolute (N_e) effective population size and the ratio of N_e to N_c of natural populations of flatfish.

Species	Census population size (N_c)	Effective population size (Θ or N_e)	N_e/N_c	Region - year	Genetic marker	Reference
Short term estimate						
Plaice <i>Pleuronectes platessa</i>	10^8	$N_e = 1733$ (Wang, 2001)	2×10^{-5}	Iceland - 2002	8 microsatellites	Hoarau et al., 2005
	10^9	$N_e = 19,535$ (Wang, 2001)	2×10^{-5}	North Sea - 2002		
	17×10^6	$N_e = 648.9$ (Waples, 2006)	3.76×10^{-5}	Irish Sea - 2001	9 microsatellites	Watts et al., 2010
	1.7×10^6	$N_e = 36.9$ (Waples, 2006)	2.19×10^{-5}	Scotland - 2001		
Sole <i>Solea solea</i>	341×10^6	$N_e = 669$ (Wang, 2001)	10^{-6}	North Sea - 1950-1960	11 microsatellites	Cuveliers et al., 2011
	200×10^6	$N_e = 669$	10^{-5}	North		

(Wang, 2001)

Sea -
1950-
2007

Long term estimate							
Flounder	<i>Platichthys flesus</i>	?	0.172< θ <0.417 (Beerli and Felsenstein, 2001)	?	NE Atlantic Ocean -	9 microsatellites	Hemmer-Hansen et al., 2007
Southern flounder	<i>Paralichthys lethostigma</i>	?	$\theta = 0.066$; $N_e = 82,500$ (Beerli and Felsenstein, 2001)	?	Gulf of Mexico - 2005-2009	tRNA ^{pro} and control region of mtDNA	Anderson et al., 2012
		?	$\theta = 0.042$; $N_e = 25,500$ (Beerli and Felsenstein, 2001)	?	Western Atlantic 2005-2009	tRNA ^{pro} and control region of mtDNA	Anderson et al., 2012