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Journal of Sea Research



journal homepage: www.elsevier.com/locate/seares

(Flat)fish stocks in an ecosystem and evolutionary perspective

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ARTICLE INFO

Article history: Received 23 December 2011 Received in revised form 18 June 2012 Accepted 24 June 2012 Available online 17 July 2012

Keywords: Adaptation Evolution Fisheries Gene Flow Population Dynamics Stock

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, harbor 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 of 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.

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1. Introduction

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, due to 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). 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 Box 1: 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 (Hutchings and Myers, 1994) and food certification of Patagonian toothfish, commercialized 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.

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 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 organized, 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 focuses 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 demographic model, where migration is a key concept, and the evolutionary model, where gene flow (see Box 1: 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

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^{1385-1101/\$ –} see front matter 0 2012 Elsevier B.V. All rights reserved. doi:10.1016/j.seares.2012.06.011

been studied independently from each other. However, there is mounting evidence that ecological and evolutionary dynamics may occur at 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 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 among 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) that co-occur in a community (see Box 1: 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 et al., 2003) or "ecosystem based fisheries management" (EBFM – see Box 1: 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 favoring 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 the cost efficient high-throughput sequencing methods as the most noticeable (Metzker, 2010), and also the access to increased calculation power and adapted bioinformatic and biostatistical tools.

This 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 (Cerda 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 behavioral 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 meiobenthic predators and adults are 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 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 1980s in the North Sea (Rijnsdorp and Millner, 1996). Flatfish aquaculture (Cerda et al., 2010; Imsland et al., 2003) is increasing steadily and has reached 148,800 metric tonnes in 2008 (FAO, 2010). At the moment olive flounder *Platichtys 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 interchangeably, with stock being linked to fishery 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 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.

The most striking observation of marine fish populations is the low level 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 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 freshwater (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 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 as to whether these differences between populations at low differentiation

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