



Fisheries stocks from an ecological perspective: Disentangling ecological connectivity from genetic interchange

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ABSTRACT

The concept of a stock of fish as a management unit has been around for well over a hundred years, and this has formed the basis for fisheries science. Methods for delimiting stocks have advanced considerably over recent years, including genetic, telemetric, tagging, geochemical and phenotypic information. In parallel with these developments, concepts in population ecology such as meta-population dynamics and connectivity have advanced. The pragmatic view of stocks has always accepted some mixing during spawning, feeding and/or larval drift. Here we consider the mismatch between ecological connectivity of a matrix of populations typically focussed on demographic measurements, and genetic connectivity of populations that focus on genetic exchange detected using modern molecular approaches. We suggest that from an ecological-connectivity perspective populations can be delimited as management units if there is limited exchange during recruitment or via migration in most years. From a genetic-connectivity perspective such limited exchange can maintain panmixia. We use case-studies of species endangered by overexploitation and/or habitat degradation to show how current methods of stock delimitation can help in managing populations and in conservation.

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1. Introduction

The concept of a 'stock' as a population unit that forms the basis of assessment and management is deeply rooted in fisheries science and practice. Russell (1931) was a pioneer in formalizing how a stock of fish would change over time due to recruitment, growth, fishing and natural mortality:

$$S_2 = S_1 + (R + G) - (F + M)$$

where S_2 is stock in year 2, S_1 is stock in year 1, R = recruitment to the fished stock, G is growth of individuals in the fished stock, F is fishing mortality and M is natural mortality.

This straightforward expression helped to form the basis of contemporary quantitative fisheries science. It informed the Beverton–Holt yield per recruit equation, formulated to manage growth overfishing typical of long-lived demersal fish species, such as flatfish and gadoids (Beverton and Holt, 1957). Russell's equation first defined the terms used to understand the relationship between recruitment and stock (Shepherd, 1982), but it had no terms for emigration or immigration and assumed these to be negligible or balanced in exchange with other populations. Advances in theory and empirical observations have shown that this assumption is rarely true, so an understanding of the degree of interchange between populations is crucial to managing exploited species.

A key assumption of fisheries management is that a stock or management unit can be rigorously defined. The formal definition of "stock" has, however, remained a challenge for over 100 years of fisheries science (Begg et al., 1999; Booke, 1999). In this review we discuss how this traditional concept in fisheries biology has been

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informed by recent advances in molecular genetics and population ecology, especially the emerging theory of metapopulation dynamics. We first return to basics and consider fish life histories, and consider where mixing occurs between stocks. We then introduce tools that can be used to quantify the segregation of stocks at different stages of their life history. We then provide a brief introduction to metapopulation dynamics and consider examples of where it has been applied to exploited finfish and shellfish species. Next, we use a series of case studies to illustrate how telemetric, ecological and molecular genetic approaches provide insights into stock definition. A recurring theme in this review are the differences between genetic interchange of populations, and the extent of interchange of individuals among ecologically-connected populations.

2. Basic life history concepts and traditional tools

A useful starting point for consideration of the stock concept in fully marine systems is to consider life history patterns. In finfish that can undergo extensive circuits of migration. The classic Harden-Jones triangular model (Harden-Jones, 1968) is a helpful simplification of a typical life history (Fig. 1a). Under this model regional scale (100–1000 km) current patterns provide the environmental context for life histories of teleost fish with pelagic larval stages. These fish aggregate to spawn, and engage in broadcast spawning and external fertilisation. Aggregation usually occurs by swimming against currents. Metcalfe et al. (2002), however, provide an example of tidal stream transport to spawning grounds. Post-spawning eggs and larvae drift with the currents until they end up on juvenile nursery grounds, while spent adults drift back to adult feeding grounds. After a period of time in nursery grounds which are often shallow, highly productive and provide some refuge from predators, juveniles migrate against currents to adult feeding grounds. From there, the cycle resumes by counter-current migration to spawning grounds. For a particular species of fish there may be several distinct stocks, sometimes overlapping temporally and geographically during cycles of migration. Some of the earliest work in contemporary fisheries sciences focussed on defining such stocks, for example Atlantic herring (*Clupea harengus*) on the European shelf in the late 19th and early 20th century (Cushing, 1967).

The Harden-Jones Model can be easily extended to migratory fish that spawn in freshwater (salmonids, alosines, lampreys) or the sea (anguillid eels). It is not applicable to sessile or highly sedentary shellfish, and here source-sink metapopulation models are more applicable. Many shellfish do, however, have distinct settlement sites or nursery areas (e.g. scallops, mussels, limpets) but the distance moved from the adult site is often very small (1–10 m). In these cases nurseries for sedentary species are mosaics of suitable habitat scattered among adults, for example rock pools in the case of intertidal limpets (Lewis and Bowman, 1975) or algal turfs in the case of primary settlement of intertidal mussels. Sometimes adult shells provide the nursery for juveniles, as is the case for some limpets (Branch, 1975).

There is extensive “traditional” evidence for discrete subpopulations (or stocks) of many marine fishes, based on morphological characters, spawning phenology and tagging data. Examples include Atlantic herring (Smith and Jamieson, 1986), European plaice (*Pleuronectes platessa*) (Hunter et al., 2004) and Atlantic cod (*Gadus morhua*) (Smedbol and Wroblewski, 2002). There is, however, little evidence of strong population genetic structure over regional spatial scales in any of these species. This could, in some cases, result from drift in the plankton and shared inshore nursery grounds, before populations segregate on the basis of non-genetic cues. Alternatively, adult movement could lead to extensive mixing of stocks that occurs during the adult phase on spawning grounds

(Hunter et al., 2004), where exchange of genetic material presumably occurs and prevents evolution of genetic differentiation. Such adult migrations could be over long distances (> 1000 km), such as the migration that leads to broad-scale genetic similarity among stocks of European hake (*Merluccius merluccius*) (Pita et al., 2011).

The approaches used to define stocks are varied (Fig. 1b). These range from conventional tags with individual identifiers (e.g. Kleiber et al., 1987; Begg and Waldman, 1999; Kohler and Turner, 2001), to meristic counts of fin rays or vertebrae (e.g. Meng and Stocker, 1984). Parasites have long been recognized as potential biological tags (Lester, 1990), while more recently telemetry based on electronic tags has been used to define movements of larger fish such as basking sharks (Sims, 2010). Advances in technology are driving the miniaturisation of devices, enhancing memory capacity and the spatial scale of studies through satellite linkages (Priede, 1984; Sims et al., 2009; Sims, 2010). Now, a wide range of fish species have been tagged, including Atlantic cod, European hake and anglerfish (*Lophius piscatorius*) (de Pontual et al., 2013; Righton et al., 2006; Turner et al., 2002; Wearmouth et al., 2014). These fish are mainly large-bodied and/or in the adult phase, however, although tagging of wild juvenile fish for telemetry is technically feasible (McMichael et al., 2010). Additionally methods such as passive integrated transponder (PIT) tagging with unique individual ‘bar codes’ allows juveniles to be tagged because the tags are small and no bulky batteries are required (Gibbons and Andrews, 2004; Skalski et al., 1998). Long-term, long-range telemetric tracking for most species is limited by the challenge of fish size on the nursery grounds. Thus using traditional or telemetric methods, typically only the adult, subadult and late juvenile phases of migration are tractable to study (Sims, 2010). As an alternative to traditional methods of stock delimitation, in the 1970s, genetic-based methods were tested and have since increased in prevalence. Early work used allozymes (Grant et al., 1980; Mork et al., 1985), whereas subsequently, assays of mitochondrial and nuclear DNA sequence variation have been more commonly used. In parallel there have been significant developments in the application of geochemical analytical methods to quantify sclerochronological records in otoliths, scales and shells (Fig. 1c).

3. The metapopulation concept and connectivity

The metapopulation concept provides a valuable theoretical framework for discussing the spatial and temporal dynamics of fish stocks. Going back to the early ideas of island biogeography proposed by MacArthur and Wilson (1967) and first formulated by Levins (1969), a metapopulation is today defined as any ‘assemblage of discrete local populations with migration between them’ (Hanski and Gilpin, 1997). Extinctions of local populations may occur. Their subsequent recolonization through the dispersal by a few individuals will, however, result in the long-term persistence of this ‘population of (sub-) populations’. The level of connectivity between the local populations as well as differences in features of the local habitats lead to a range of possible metapopulation systems (Harrison and Taylor, 1997; Fullerton et al., 2011; Fig. 2). The classical metapopulation consists of similar, discrete populations (Fronhofer et al., 2012). These are connected by relatively rare dispersal events that only just prevent complete isolation of the individual populations (Fig. 2b). If, however, connectivity is very low, this may lead to a non-equilibrium metapopulation consisting of completely isolated local populations (Fig. 2c). Here, persistence of the individual populations is unlikely as recolonization from neighbouring populations following local extinction events is unlikely. On the other end of the ‘dispersal scale’, complete mixing of these populations would likely result in a single large panmictic population (Fig. 2a). In the case of non-equilibrium, classical

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