Population integrity and connectivity in Northwest Atlantic herring: a review of assumptions and evidence

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The issue of herring population structure has been debated for more than a century. Population integrity and connectivity have become an increasingly important problem for both resource evaluation (e.g. concern for the use of appropriate modelling approaches) and management (e.g. increasing attention to the preservation of within-species diversity and the complexity of mixed-stock fisheries). In recent decades, there has been considerable advancement in the scientific information related to herring population structure, but papers continue to demonstrate a spectrum of conclusions related to population integrity and connectivity at various scales. We review herring stock structure in the western Atlantic, specifically addressing the assumptions currently being used in management and the validity of scientific evidence on which these assumptions are based. Herring of the western Atlantic exhibit considerable population discreteness and limited connectivity on the temporal and spatial scales that are of relevance to management. Maintaining the resulting population complexity is a challenge, particularly because preservation of within-species diversity is an important element of an ecosystem approach to management.

Keywords: Clupea harengus, marine population connectivity, population structure, within-species diversity.

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Introduction

The issue of population integrity and connectivity (as a descriptor of stock structure and discreteness) has been an important topic in herring science and management for more than a century (Sinclair and Solemdal, 1988; Stephenson, 2001; Stephenson and Clark, 2002). Although there has been considerable attention to aspects of herring population structure and discreteness in the literature of the past 25 years (Iles and Sinclair, 1982; Sinclair, 1988; McQuinn, 1997; Smedbol and Stephenson, 2001; Corten, 2002) and at symposia (Wespestad et al., 1991; Funk et al., 2001), the question of population structure (and connectivity) in relation to migration, which was basic to the formation of ICES a century ago (Sinclair and Smith, 2002; Stephenson, 2002; Sinclair, 2009), remains a major theme.

Population integrity is an issue for both resource evaluation and management because uncertainty about population structure continues to confound the appropriate choice of modelling approaches. In addition, increasing attention is being paid by management to the preservation of within-species diversity and the complexity of mixed-stock fisheries (Smedbol and Stephenson, 2001). With the growing interest in biodiversity and spatial management, connectivity has become an important theme in the literature (Roberts, 1997; Cowen et al., 2000, 2006, 2007).

We discuss the concept of population integrity and connectivity as it applies to herring; review the biological basis for, and current treatment of, population integrity in the management of herring stocks in the western Atlantic; and comment on the implications for future research and management.

Definitions

Population complexity (or biocomplexity, Ruzzante et al., 2006; or richness, Sinclair, 1988) is a measure of the diversity of subpopulations within a unit stock. Connectivity is used in this paper, in the sense of Cowen et al. (2007), to refer to the degree of exchange of individuals among subpopulations. Population integrity refers to the independence or discreteness (Iles and Sinclair, 1982) of subpopulations. Therefore, population complexity is the result of the trade-off between connectivity and integrity. Herring have been reported previously (Sinclair, 1988) as having a relatively high degree of population complexity (more like salmon than like species such as mackerel or eels), such that managed stocks are commonly referred to as “stock complexes” made up of a number of subpopulations.

A conceptual figure of the structure of herring populations (stocks) that has emerged in recent years (Stephenson et al., 2001) is illustrated in Figure 1. According to this concept, a population may be made up of several “subpopulations” that utilize distinct spawning areas and have overlapping larval retention areas (and even a completely overlapping nursery area), but maintain a high degree of integrity, and therefore remain discrete. Although there is general agreement about the overall concept, the discussion about the degree of connectivity among spawning grounds (i.e. the integrity of subpopulations) at various spatial...
scales has been considerable (McPherson et al., 2001, 2003, 2004), and there is debate regarding how the observations of structure and integrity fit within a metapopulation concept (Collie, 1991; McQuinn, 1997). Discussion of the relative importance of the complexity and the treatment of subpopulations in management is continuing (Smedbol and Stephenson, 2001; Ruzzante et al., 2006).

Review of the biological basis

The biological basis for the conceptual view presented above, and for the current management of most herring stocks, is based, explicitly or implicitly, on the following observations and/or assumptions related to the integrity of population structure (the “herring credo”):

(i) Herring spawn in multiple, discrete locations within a stock distribution area, and these are predictable in space and time. This seems to be a well-established fact, both in the western Atlantic (Figure 2) and for Atlantic herring generally, with ample evidence from the pattern of fisheries and from research (Hay et al., 2001). The fishery in the Bay of Fundy/Gulf of Maine has documented discrete locations at which tightly aggregated schools of herring spawn every year (Power et al., 2007). Each area has a predictable spawning time, but the timing differs among areas. Dive surveys on Fisherman’s Bank in the Gulf of St Lawrence (Cairns et al., 1993) demonstrated the precise locations of spawning over several years. The observed persistence and stability of discrete spawning grounds is major evidence to support the conclusion that herring stocks are composed of subpopulations with a high degree of integrity.

(ii) Herring spawn once a year in schooling events (“waves”), but spawning grounds may see multiple waves during a spawning season. It is a general characteristic of herring that they spawn only once a year and that all the eggs are released within a single spawning event (Hay et al., 2001). Spawning events involve whole schools. Once spawning is complete, the spent fish disperse rapidly, making way for a new wave to occupy the spawning grounds. There are typically several waves of spawning within a season (Lambert, 1987). Participation in single annual spawning events at fixed locations is considered to contribute to subpopulation integrity.

(iii) Herring larvae remain aggregated in predictable patterns related to oceanographic conditions (“larval retention” areas; Iles and Sinclair, 1982). The literature on larval herring distribution is considerable and has led to debate in the past regarding the degree to which larvae remain aggregated (retention) vs. move with currents (drift). Based on the long-term (1975–1996) distribution and abundance of larvae originating from spawning grounds off Southwest Nova Scotia and in the Bay of Fundy (Sinclair and Iles, 1985; Sinclair, 1988; Chenoweth et al., 1989; Bradford and Iles, 1993), the inevitable conclusions are that dense aggregations of larvae occur in the proximity of known spawning grounds, the distributions of larvae of different age overlap, the annual centre of mass is relatively stable (persistent) over time (indicating “retention”), and the distribution pattern is similar each year (Figure 3). Larval retention in the Bay of Fundy involves an active behavioural component in the form of vertical migration (Stephenson and Power, 1988, 1989) and has been proposed as an important mechanism in the maintenance of population structure in the face of dispersal by diffusion, and thereby a major factor contributing to population integrity (Iles and Sinclair, 1982; Sinclair, 1988).
Juvenile and adult herring undertake extensive annual migrations among spawning, overwintering, and summer feeding areas. Hay et al. (2001), summarizing information from the world’s major stocks of both Atlantic and Pacific herring, concluded: “Most herring tend to migrate between summer feeding areas on shelf waters, to overwintering areas, which may be in nearshore protected waters, and then to spawning locations”. Tagging of fish on spawning grounds, in overwintering areas, and in nurseries has demonstrated that herring in the western Atlantic migrate extensively, often moving great distances within fairly short periods (Creaser et al., 1984; Stobo, 1987). The distribution of the fishery reflects the seasonal availability and confirms the separate distributions of juveniles and adults and their seasonal patterns of movement (Creaser et al., 1984; Stobo, 1987; Stephenson et al., 1993; Power et al., 2007). The interannual predictability of the distribution at various life-history stages exhibits a gradient: spawning areas are fixed, overwintering areas vary to a small extent, and summer feeding areas may change considerably with the availability of food (Sinclair and Iles, 1985). Widespread movement and mixing of juveniles and adults offer an opportunity for connectivity among subpopulations.

Herring return (annually) to spawning grounds they have used previously and have fidelity to the spawning area from which they originated (“homing”). Herring tagged on spawning grounds in the 1970s have been recovered from the same spawning ground in successive years (Stobo, 1987; Wheeler and Winters, 1984a). This has been reconfirmed by recent tagging experiments of fish in ripe and running condition on a Bay of Fundy spawning ground (Figure 4). Although these fish clearly migrate over substantial distances and were taken in mixed aggregations outside the spawning season, not a single fish among several thousand tag returns has been returned from any other spawning area in subsequent years. This can only indicate a strong fidelity to the spawning ground after herring have once spawned there. The “homing” hypothesis proposes that herring return, with a high degree of fidelity, to the spawning area where they were hatched. Although this has not yet been proven—and will be difficult to prove—the body of evidence, including differential trends in abundance and differences in growth, supports homing over the alternate hypothesis: that there is a high degree of connectivity among herring spawning at different grounds through mixing during the juvenile stages.

Subpopulations exhibit differential trends in abundance and differences in growth. Marked differences have been observed in abundance trends at neighbouring spawning areas over time, including losses (or slow recoveries) of
subpopulations, despite the presence of flourishing sub-populations close by. In the western Atlantic, collapses at both large (Georges Bank) and small (Trinity Ledge) spawning grounds, during a period when neighbouring spawning grounds remained occupied, have been well-documented, and the apparent lack of rapid recolonization of these spawning areas has been considered as evidence for homing, as well as for discreteness of the subpopulations that utilize them (Stephenson and Kornfield, 1990; Stephenson, 1997). Several subpopulations have collapsed in response to exploitation, but recovery has usually been slow, even when protective measures were taken (Stephenson, 1997). More than a decade elapsed before the Georges Bank subpopulation started to recover following collapse (Stephenson and Kornfield, 1990; Melvin and Stephenson, 2007), and the Trinity Ledge subpopulation has not recovered substantially more than a decade after collapse (Power et al., 2007). Clark et al. (1999) and Crawford (1979) documented several spawning locations along the coast of Nova Scotia that have been occupied historically, but are not being used at present (Figure 5). Overall, the spatial and temporal extent of spawning on the Scotian Shelf and in the Gulf of Maine appears to have reduced over time. Sampling data over the past three decades show variation in size-at-age on different spawning grounds, as well as consistent differences in timing of spawning (Power et al., 2007). Spawning time on each ground is well-defined, and acoustic surveys show consistent differences among grounds, although the interpretation is complicated by strong evidence of temporal differences in size-at-age on a spawning ground as the season progresses (in essence, larger fish arrive earlier than smaller fish; Messieh, 1989, Power et al., 2007). Persistent differences in population dynamics and growth indicate an integrity, at least on the temporal scale, that is relevant to fishery management.

(vii) Although herring from different spawning areas mix during the juvenile stages and as adults outside the spawning season, mixing within an area is not uniform; fish of different origin remain aggregated or clumped in schools. Tagging experiments provide strong evidence for mixing away from the spawning grounds. Individual herring from groups tagged as juveniles (e.g. in the New Brunswick weir fishery; Stobo et al., 1975) have been recovered from different spawning grounds, indicating that the juveniles from several populations have a similar spatial distribution and that some mechanism must exist that guides them to a particular spawning ground (Creaser et al., 1984; Waters and Clark, 2005). Stobo (1987), based on tagging in the 1970s, provided many examples of herring that were tagged in the same feeding or overwintering area subsequently showing up in different spawning areas. However, on a finer scale, there is evidence that mixing is not necessarily uniform. Hay et al. (2001) concluded that, in general, herring schools consist of individuals of similar size and/or age. Both tagging and morphometric analyses indicate persistence of clumping/schooling, including observations of herring that were tagged together being recovered together at a later date (Hay and McKinnell, 2002). While mixing provides an opportunity for connectivity, persistent schooling allows maintenance of integrity.

(viii) Herring subpopulations may exhibit genetic differentiation. McPherson et al. (2001, 2003, 2004) have provided evidence for genetic differentiation among spawning groups at different spatial and temporal scales in the western Atlantic using nine tetranucleotide microsatellites. Although significant differences existed among many samples of the Bay of Fundy and Gulf of Maine stocks, these could not be explained by geographic distance in absolute terms (e.g. there was no evidence of “isolation by distance”). Differences between two “waves” of spawning herring at one location (Devastation Shoal, Southwest Nova Scotia) were among the greatest observed. Bras d’Or Lakes herring appeared to be quite distinct. McPherson et al. (2004) concluded that “populations of Atlantic herring in the NW Atlantic may be temporally as well as spatially structured”. Recent genetic studies of eastern Atlantic herring have arrived at a similar conclusion (Bekkevold et al., 2005; Ruzzante et al., 2006).

Clearly, several features of herring life history allow for some degree of connectivity among subpopulations. These include mixing of herring from a variety of spawning areas at juvenile and non-spawning adult stages, and change in the general patterns of movement among spawning, overwintering, and summer feeding areas. However, there are more features that are indicative of integrity or discreteness at small temporal (interannual) and spatial scales. Apart from the major discontinuities in herring distribution at spawning, both in space and time, there is sufficient evidence for repeated use of spawning grounds and indications of homing, at least during the adult stage, to suggest that spawning components have a high degree of integrity. There are also discontinuities in the distribution of the larvae (larval retention), which may help to maintain stock structure. Stephenson et al. (2001) have proposed that the connectivity would be expected to be highest among neighbouring spawning components within a management unit.

Management for population integrity

Herring in the western Atlantic are currently managed as a number of stock complexes (Figure 2). The management units, developed

![Figure 5. Herring spawning locations on the Scotian Shelf and Gulf of Maine that have been used recently (filled circles, autumn; filled squares, spring) or only historically (open circles, autumn; open squares, spring).](https://academic.oup.com/icesjms/article-abstract/66/8/1733/677110/Downloaded-from-https://academic.oup.com/icesjms/article-abstract/66/8/1733/677110)
more than three decades ago, were based partly on known spawning areas and fish movements, but also on considerations of fleet operations and national jurisdictions. A major tagging programme in the 1970s, together with other biological studies and fishery information, resulted in minor modifications of the original stock structure (ICNAF, 1976).

All the management units are recognized as containing complex populations, each with several subpopulations, mostly designated based on predictable spawning locations or spawning times (Melvin et al., 2009). A considerable level of discreteness of these subpopulations is also recognized, and there is little if any disagreement on their biological characteristics. The real issue, however, is the degree of integrity/connectivity among subpopulations within a management unit and how this is treated in management.

The treatment of population integrity and connectivity in the management of Northwest Atlantic herring is not uniform. In the Gulf of Maine (NAFO Divisions 5YZ), there is a cumulative (global) assessment, with subsequent suballocation of quotas into inshore and offshore fisheries (Overholtz et al., 2004). Although fishing on spawning grounds during the spawning season is prohibited, no further consideration is given to the relative performance of individual subpopulations. In eastern Newfoundland (3KL), different bays within the management unit are evaluated and managed separately, but some of these bays contain several spawning grounds that are not recognized explicitly in management (Wheeler and Winters, 1984b; Wheeler et al., 2006). In the Southern Gulf of St Lawrence (4T), spring- and autumn-spawning components are evaluated and managed separately, and quotas are allocated among spawning grounds within each component because of the spatial distribution of the coastal fishery (LeBlanc et al., 2007). Southwest Nova Scotia/Bay of Fundy (4WX) have received the most attention in regard to discrete subpopulation structure (Power et al., 2007). The spawning grounds of autumn spawners are recognized in management and are surveyed separately. Awareness of the possibility of erosion of individual subpopulations led this region to adopt specific measures for apportioning total allowable catch based on their relative abundance (Stephenson et al., 1999). In the most extreme case, within-season management measures are taken to ensure that the biomass of each component is documented as being sufficient before fishing can start (Stephenson et al., 1999; Melvin et al., 2001). Therefore, although there is little difference in the population structure within management units (each unit contains subpopulations), the attention paid to subpopulation integrity varies.

These differences in treatment have potentially major consequences. The concern when exploiting an aggregation of subpopulations is the potential for a disproportionately high effort being directed onto one of the subpopulations, which could lead to its erosion, even within a catch limit that might be appropriate for the aggregated stock complex (Smedbol and Stephenson, 2001). This is thought to have been the case for the Trinity Ledge component in Southwest Nova Scotia (Stephenson et al., 2001).

Discussion

Although the existence of subpopulations within all management units is recognized, the degree of integrity as perceived by the responsible management authorities apparently varies widely, especially at small spatial scales. This does not necessarily reflect a real difference in population integrity, but rather a difference in the attention given to the issue. The different strategies currently applied to the adjacent Southwest Nova Scotia and Gulf of Maine herring stocks provide an illuminating example (Stephenson et al., 2001; Overholtz, 2002).

Clearly, herring stocks do not represent single homogeneous populations; instead they have a complex population structure (sensu Sinclair, 1988) comprising a number of discrete subpopulations that may mix at various times during their life history, but separate to spawn at subpopulation-specific locations. McQuinn’s (1997) adopted-vagrant hypothesis has been used to suggest rather more connectivity than is evident in the western Atlantic. On the temporal scale of relevance (years), the subpopulations exhibit a high degree of integrity that should be respected in managing the stocks because the consequences of making an erroneous assumption here are quite different. The assumption of connectivity for a discrete subpopulation could lead to its overexploitation, and thereby to a reduction in within-species diversity, whereas the reverse situation (wrongly assuming discreteness when there is connectivity) would have no consequences other than influencing where and when the fishery is allowed to operate.

The ecosystem approach to management requires attention to a broader suite of conservation objectives that includes biodiversity issues, of which the conservation of within-species diversity is an important element. Therefore, addressing population integrity contributes to the evolution of herring-fishery management towards an ecosystem approach. When little or no exchange occurs among subpopulations, to assume that there is exchange increases the risk of overexploitation of any one of them, potentially leading to a loss of within-species diversity. To assume that there is integrity rather than connectivity appears to be the more prudent approach. We suggest that specific recognition of the complex stock structure of herring in the western Atlantic, with different components using specific spawning grounds within a unit-stock area, and management action to prevent reduction of the spatial and temporal within-species diversity is required.

References


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