

Numerical domination and herring migrations

Geir Huse, Anders Fernö and Jens Christian Holst

Abstract

There is accumulating evidence in favour of the hypothesis that herring migrations are influenced by social learning. The “adopted-migrant hypothesis” postulates that recruit spawning herring learn migration patterns by schooling with older individuals. However, this learning can be interrupted if the stock is unstable or if there are lack of overlap between recruits and the adult stock. There have been five reported changes in the location of the wintering area of Norwegian spring spawning (NSS) herring during the last 50 years. These changes co-occur with the recruitment of relatively strong year classes to the spawning stock. Simulations of schools containing naïve and experienced fish have shown that when abundant enough, naïve individuals repel guidance from a minority of experienced individuals. This process is referred to as numerical domination. We argue that numerical domination obstruct social learning from adults to recruits and plays a key role in establishing new wintering areas in NSS herring.

Keywords: herring, migration, schooling, social learning, demography.

Contact author:

Geir Huse: Institute of Marine Research, Box 1870 Nordnes, N-5817 Bergen, Norway, [tel: +47 55236988, fax: +47 55238687, e-mail: geir.huse@imr.no].

Introduction

There have been substantial changes in the location of the wintering area of Norwegian Spring Spawning (NSS) herring during the last 50 years (Røttingen, 1990; Dragesund *et al.*, 1997; Holst *et al.*, 2002). These changes have taken place both during the unstable phase during the late 1960ies to the early 1980ies, as well as during the recent flourishing period (Toresen and Østvedt, 2000). Presently the stock remains in a healthy state and at a spawning biomass of 6 million tonnes it is one of the most abundant fish stocks in the world. The “adopted-migrant hypothesis”(McQuinn, 1997) postulates that recruit herring spawners learn the location of their spawning area by schooling with older individuals and home to this area for spawning in subsequent years. This hypothesis is supported by data on herring populations from either side of the Atlantic (McQuinn, 1997; Corten, 1999a; Corten, 1999b). The NSS herring shows strong fidelity to wintering areas (Dragesund *et al.*, 1997; Holst *et al.*, 2002). The dynamics of the wintering congregations can therefore be explained by the adopted-migrant theory in the same manner that spawning area is determined. According to the adopted-migrant hypothesis, changes in migration pattern occur when populations become unstable, either due to stock collapse, strong recruitment, or environmental change.

The objectives of this paper are to briefly review the changes in wintering area of NSS herring during the last 50 years, and to try to identify the causes behind the changes.

Changes in wintering locations of NSS herring

Below we provide a brief review of the different wintering areas utilised by NSS herring in the last 50 years. The bullet numbers refer to wintering positions shown in Figure 1.

- 1) During the 1950ies and possibly for a long time prior, the wintering area was to the east of Iceland (Dragesund *et al.*, 1997).
- 2) The 1959 year class established a separate stock component when they were recruit spawners in 1963. This pattern was maintained for three years before this year class joined the main part of the stock and eventually adopted their migration pattern (Dragesund *et al.*, 1997).
- 3) The 1969 year class recruited to a very small spawning stock in 1973 and started to winter in fjords of Lofoten (Holst *et al.*, 2002). A small component of the 1969 year class set up a separate stock unit further south at Møre and continued wintering there throughout its life span.
- 4) The 1983 year class started wintering in Tysfjorden and Ofotfjorden in 1987 (Røttingen, 1990).
- 5) The 1991-1992 year classes started to winter in Vestfjorden, west of Tysfjorden and Ofotfjorden. This was not a major geographical change in wintering location, but still distinct from the previous wintering grounds (Foote *et al.*, 1997).
- 6) In 2002 when the 1998 and 1999 year classes recruited to the adult migration pattern, a new wintering area was initiated north-west of Vesterålen. At present time this remains the main wintering area of the NSS herring.

Numerical domination

All the initiations of new wintering areas in NSS herring co-occurred with the recruitment of abundant year classes to the spawning stock. This is illustrated in Figure 2, which shows the abundance of 4 year olds, and 5 year and older herring in the population, as well as the ratio between the two groups. The arrows indicate years when changes in the wintering location of the herring took place. These changes co-occur with peaks in the ratio of young to old. This ratio is 24.6 in the years when changes occurred (arrows 2-6 in Figure 2) compared to an average of 0.35 in years when no changes were reported. In a previous paper (Huse *et al.*, 2002) we performed a simple computer experiment to investigate the behaviour of schools containing both experienced and naïve individuals without any preferences. The behaviour of naïve individuals thus only relied on the rules, which told them to follow the movement of individuals in their vicinity, whereas the experienced individuals also had a common migratory preference. This experiment showed that the influence that experienced individuals have on the school is dependent on their relative abundance in the school, and below a threshold proportion the experienced individuals have very little impact on the behaviour of the rest of the school. The process where relatively abundant naïve individuals “repel” guidance from a minority of experienced individuals was termed numerical domination. Even though the experiment is highly simplified, the results can be valuable when discussing the behaviour of NSS herring. Thus in cases where recruiting year classes are normally abundant, the ratio of recruits to adults is sufficiently low so that the recruits are able to pursue the adult stock. In cases when the ratio is high, however, the recruits are mostly surrounded by their own naïve classmates and thus unable to pursue the adult stock. In these cases numerical domination can obstruct social learning from adults to recruits.

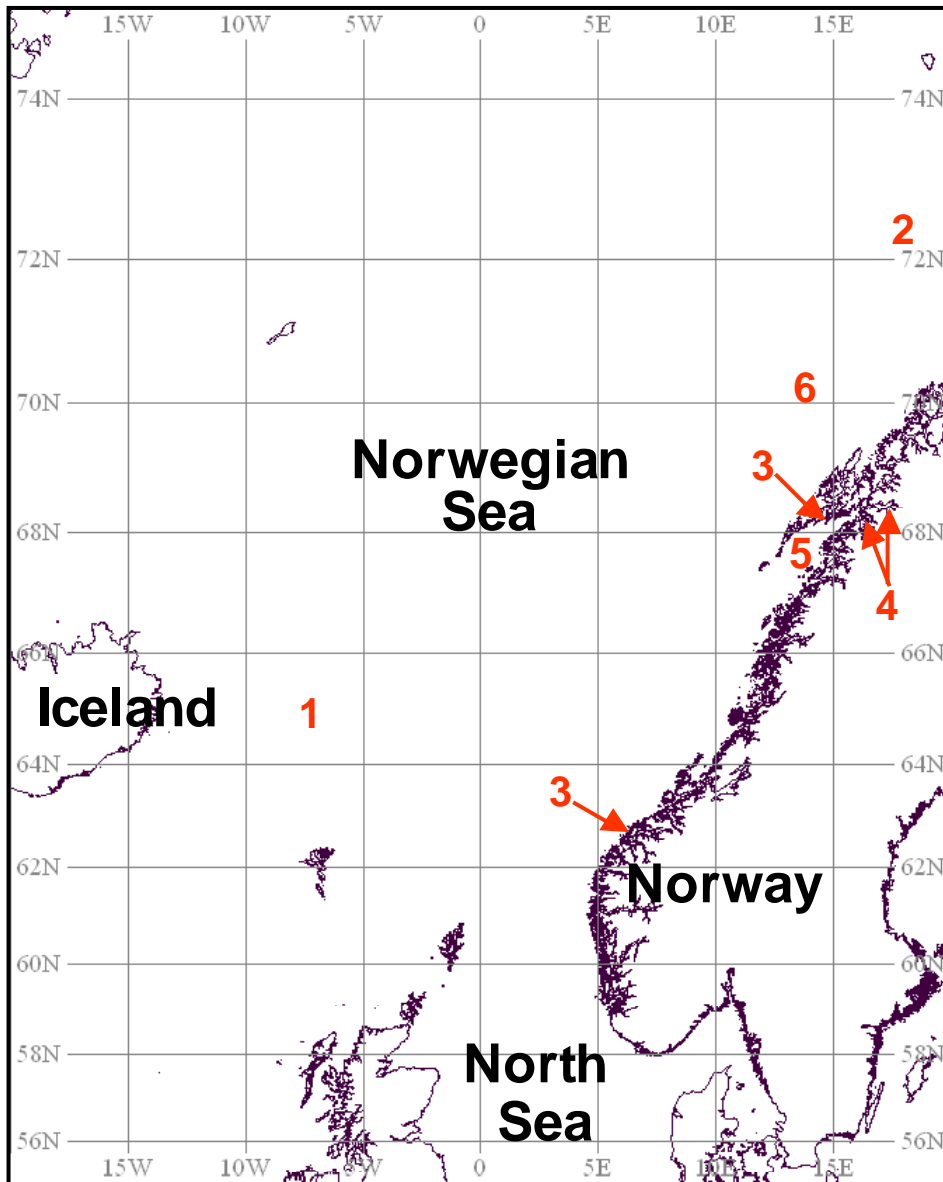


Figure 1. Reported wintering locations of NSS herring during the last 50 years. The numbers indicate chronological development of wintering location.

In addition to the internal school dynamics there is likely to be transfer of information between schools. Herring schools are dynamic, and events like splitting and joining in schools feeding in coastal areas have been observed to take place at short intervals (Pitcher et al., 1996). Since herring schools generally are tightly aggregated (Mackinson et al., 1999), the distribution and migration patterns of schools are not independent. A certain migration tendency in one school can then be transferred to nearby schools and eventually influence the whole population. The interaction among herring schools is at present little studied and needs a firmer observational basis before it can be addressed in model simulations.

Our previous computer experiment (Huse *et al.*, 2002) was an attempt to analyse how individual differences in behaviour can control school behaviour. In order to fully understand the relationship between individual decision-making and school behaviour, one should preferably perform similar experiments on real herring. To make the computer experiment more realistic for studying migration patterns in NSS herring, one should increase the number of individuals involved and address the interaction among different schools. However, since large-scale patterns result from individual decisions it is important to link the scales to provide an understanding of the underlying processes.

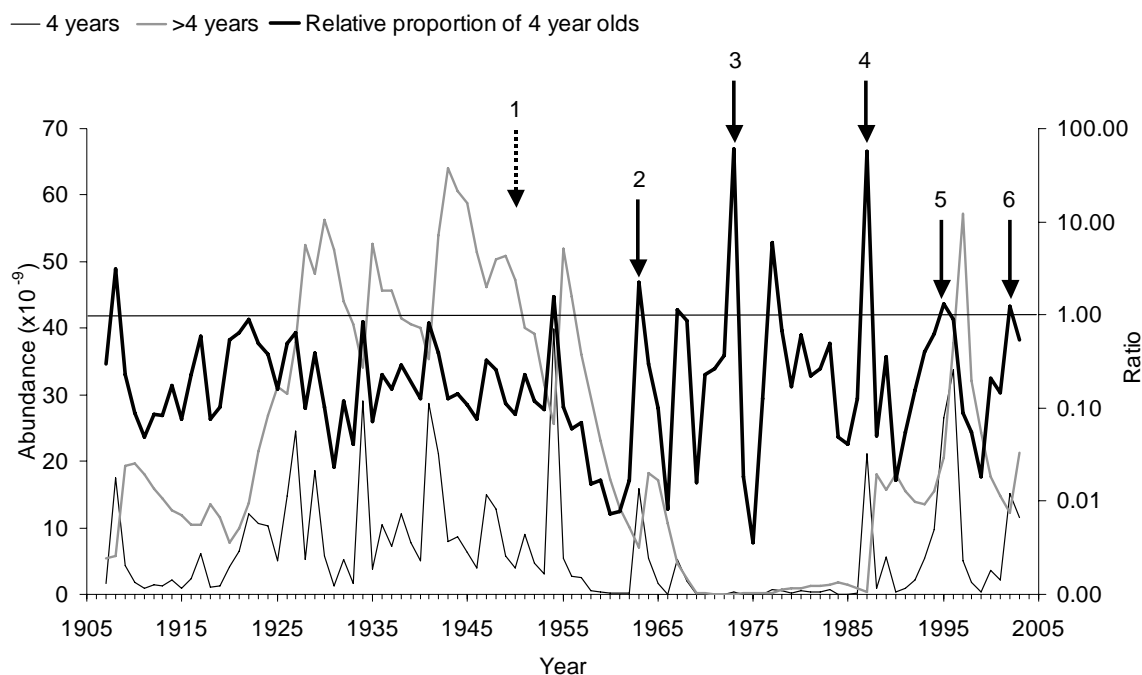


Figure 2. The abundance of NSS herring age 4 and older than 4, and their ratio respectively. The arrows indicate when changes in the wintering area have taken place, and the numbers refer to the positions of the wintering area in Figure 1.

Spatial overlap between recruits and adults

An alternative explanation for the changes in migration pattern of herring is lack of overlap between the recruits and the adult part of the stock (Corten, 2002). The adult herring initiates the migration towards the wintering areas during late summer. Since 1994 there has been an annual survey in July/August mapping the distribution of the herring in the Norwegian Sea (Anon., 2004; Holst *et al.*, 2004). The results from these surveys show that the herring is distributed close to the Norwegian coast in the area north-west of the Lofoten islands in July (near 3 and 6 in Figure 1). This is the area that the juvenile herring normally enter when leaving the Barents Sea. Consequently there appears to have been spatial overlap between recruits and older individuals in the period prior to wintering, at least in the last decade, and numerical domination therefore seems to be a key factor in bringing about changes in wintering area of NSS herring.

Acknowledgement

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