**Short communication**

Data-limited management reference points to avoid collapse of stocks dependent on learned migration behaviour

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Risk of stock collapse associated with the loss of a stock’s migrational knowledge may be underestimated by conventional reference points. In this paper, I describe three different approaches: a data-poor precautionary approach is to ensure that individuals spawn at least twice; a data-intermediate approach is to calculate a repeat spawning potential ratio ($r_{SPR}$), which is analogous to the conventional $SPR$; and for data-rich cases, age-structured population simulations are recommended.

**Keywords:** adopted migrant hypothesis, biological reference points, entrainment hypothesis, episodic fisheries, feeding migration, precautionary approach to management, spawning migrations, spawning potential ratio, socially transmitted behaviour.

**Introduction**

One of the most intriguing recent developments in fisheries science is the hypothesis that the migratory patterns of fish may be a socially transmitted or learned behaviour, similar to the learning process that is now well understood for migratory birds (Berthold, 1996; Able and Able, 1998). This mechanism is also gaining acceptance for migratory whales (Clapham et al., 2008; Valenzuela et al., 2009). Rose (1993) speculated that Atlantic cod ($Gadus morhua$) migration paths may be learned from older fish. McQuinn (1997) proposed this learned migration hypothesis for herring ($Clupea$ spp.) stocks, based on the observations that herring migrations tend to adhere strongly to the established patterns despite environmental fluctuations and also that under intense fishing, some migration paths disappear permanently or new patterns may develop suddenly. This idea was expanded by Corten (2002), who also observed that sudden changes in herring migrations were often associated with the recruitment of strong year classes, especially when the adult stock was in a depleted condition. Petitgas et al. (2006) formalized this issue in terms of life history, which resulted in a dedicated ICES Working Group to explore the hypothesis in a wide variety of fisheries (ICES, 2007a; Petitgas et al., 2010). Subsequently, Huse et al. (2010) confirmed that new migratory patterns in Norwegian spring-spawning (NSS) herring ($Clupea harengus$) coincided with peaks in the ratio of first-time to repeat spawners. In the context of fishery management, changes in migratory behaviour are risky, and loss of migratory behaviours could lead to fishery decline or collapse.

The migratory behaviour may involve feeding migrations, wintering migrations, and spawning migrations. If a stock’s migratory knowledge is lost (or altered), growth and natural mortality rates may change, and the relationship between recruitment and parental stock size may no longer be predictable by a stock–recruitment relationship derived from preceding observations. Not only is stock collapse a likely result, but subsequent attempts to rehabilitate the stock based on the historical expectations of recruitment may be futile: stock rebuilding becomes a matter of chance and, within a specific time frame, it may no longer even be possible with any certainty. Short of extinction, this form of collapse is arguably the worst overexploitation scenario that a fishery can experience. Because learned migratory paths are not necessarily optimal, there is also some possibility that an altered migratory pattern could improve stock productivity, but it would not be wise to expect such an outcome. Rather, it is logical to assume that the existing migratory pattern is critical to supporting current productivity. Migratory fish populations may adopt a single behaviour or may have multiple subgroups or “demes” each with their own migratory pattern (e.g. Robichaud and...
The danger posed by the loss of migratory knowledge may depend on the number of migratory demes in the population, but the progressive loss of demes can occur with little outward evidence.

In this study, management is assumed to favour a precautionary approach (FAO, 1996) of assuming that socially transmitted or learned behaviour is the mechanism that maintains feeding and reproductive migrations of a productive fish stock. Petitgas et al. (2010) review supporting evidence for migratory species ranging from sardine (Sardinops spp.) to northern cod (G. morhua) and especially for herring (Clupea spp.) stocks. The question then is how can management best address the risk of stock collapse due to fishery-induced loss of migratory knowledge? Most preceding discussions of the learned migration behaviour hypothesis have explored whether this behaviour exists. This paper addresses the issue of defining alternative biological reference points for management depending on the relative richness of underlying biological knowledge and fishery data. For simplicity, most of the following discussion assumes that the migration involves spawning, but migrations to feeding grounds can be equally important to maintaining stock productivity. The management policies needed to conserve migratory behaviours are the same whether the stock comprises a single migratory deme or contains multiple behavioural demes.

A data-poor heuristic policy

In the extreme case where data cannot support any meaningful demographic analysis, a simple heuristic rule of thumb is used to introduce the management issues. Before the quantification of stock-recruitment relationships in fishery science, conventional wisdom in fishery management asserted that “fish should be allowed to spawn once” before being taken by a fishery. This rule was elaborated by Myers and Mertz (1998) who, with some provisos, concluded that under a “spawn-at-least-once” policy (not as an expected value, but explicitly delaying fishing until after the age of first spawning), “the stock will not collapse at any fishing mortality, no matter how high”. Clearly, the case of learned migration behaviour is an exception to this rule because it explicitly requires an overlap of at least two spawning cohorts. Therefore, in the present case, the conventional wisdom can logically be extended so that “fish should be allowed to spawn at least twice” before being taken by a fishery. The first spawning would be as an inexperienced recruit to the pool of experienced migrators, and the second spawning would be as a potential teacher of incoming recruits. The “spawn-at-least-twice” criterion could be satisfied in a data-poor fishery by establishing a minimum size limit corresponding to the size of fish at least one year older than the age of first maturity.

Data-intermediate policies

The spawning potential ratio (SPR) is a widely used metric for fishery impact on the demographic structure of the spawning stock (Goodyear, 1993; Mace and Sissenwine, 1993). In a simple form, expected lifetime spawning output at a given fishing intensity \([S(F)]\) is calculated by

\[
S(F) = N_0 \sum_i m_i f_i \exp \left( \sum_{t=1}^i (-M_t - \phi F) \right),
\]

where \(i\) is the integer age, \(N_0\) the initial cohort abundance, \(m\) the fraction mature at age, \(f_i\) the fecundity at age, \(M_t\) the natural mortality rate at age, and \(\phi\) the fishery selectivity (the ratio of fishing mortality rate \(F\) at age \(s\) to the value of \(F\) at a defined reference age). The SPR, often expressed as a percentage, expresses spawning output relative to its unfished value:

\[
SPR(F) = \frac{S(F)}{S(0)}.
\]

By eliminating the fecundity parameter, an equation similar to Equation (1) is easily developed for the expected number of spawning migrations experienced over a fish’s lifetime. Note that we are assuming that only mature individuals migrate (another issue that merits investigation; the governing factor may be fish length); if immature individuals participate in the spawning migration, learning presumably occurs at that age, and parameter values can be adjusted accordingly. However, for the purposes of tracking fishery impact on learned migrations, a fish does not possess the knowledge of the migration path until after its first spawning migration. Therefore, an appropriate measure of the abundance of experienced fish begins with those undertaking their “second” migration, or equivalently, the fraction that matured and migrated for the first time in the previous year \((m_{t-1})\). For a given fishing mortality rate, the expected number of repeat spawning migrations \(S_t(F)\) is

\[
S_t(F) = N_0 \sum m_{t-1} \exp \left( \sum_{s=1}^t (-M_s - \phi F) \right),
\]

and a quantity analogous to SPR can be termed the repeat SPR (rSPR), which is given by

\[
rSPR(F) = \frac{S_t(F)}{S_t(0)}.
\]

For management purposes, we could adopt a policy based on \(S_t\), but the threshold value of \(S_t\) depends on the age of recruitment and is difficult to generalize. In the special case where recruitment is defined as numbers at the age of maturity and where there is little fishing impact on prerecruits, a threshold of \(S_t > 1\) is equivalent to the spawn-at-least-twice criterion. The rSPR may be easier to work with, and we may want to establish a threshold such as \(rSPR > 30\%\) to ensure that a sufficient fraction of experienced migrators is maintained in the population. As is true with SPR, there is no single threshold value of rSPR that is necessarily suitable for all fish stocks. A comparison of historical rSPR values for migratory fish stocks would be useful. It is important to note that because of the age-lagged subscript of \(m\) and the property that \(m_{t-1} \leq m_{t}\) under increasing fishing pressure, Equations (3) and (4) approach zero faster than do Equations (1) and (2). This implies that it is possible to lose migratory knowledge while otherwise maintaining some possibly acceptable level of spawning potential and underscores the need for precaution. Implementation of rSPR-based management would use the same tactical tools that conventional SPR-based management uses (effort limitation, minimum size limits, etc.) with the added possibility that particular times and locations may merit additional protection. As a possible example, the recent collapse of the South African sardine fishery may have been associated with intense harvesting on the primary spawning grounds west of...
Cape Agulhas, favouring an alternative but less productive spawning migration to Port Elizabeth, far to the east of Cape Agulhas (Coetzee, 2007).

Data-rich policies
Huse et al. (2010) examined existing population analyses of the NSS herring (ICES, 2007b) and found sudden shifts in migration patterns to be associated with a high ratio of age 4 fish (first-time spawners, i.e. recruits) to age 5+ fish (repeat spawners and presumably experienced migrants). They found that the probability of a migratory disruption is relatively low \( (p \approx 0.1) \) when repeat spawners comprise \( > 30\% \) of the spawning population of NSS but rises sharply to \( p \approx 1.0 \) when repeat spawners fall to \( < 10\% \) of the spawning population. A key parameter is the underlying variability of recruitment, often represented by the quantity \( \sigma_r \), which is the s.d. of log-recruitment anomalies. Also, if mixing of cohorts is length-dependent (Nøttestad et al., 1999; Petitgas et al., 2010), growth patterns and variability may be influential.

For data-rich cases, a recommended approach is to simulate the long-term population behaviour as a function of \( \sigma_r \), age-specific fishery selectivities \( (\phi_f) \), fishing intensity, and growth (if appropriate). Although the model can become complicated, the equations are conventional, closely related to Equation (3), and will not be described here. Such a model is well suited to spreadsheet implementation (e.g. Haddon, 2011). A histogram of modelled frequencies for which the ratio of repeat spawners to total spawners attains low values \( (\text{e.g. } 0.3, 0.2, \text{ and } 0.1) \) can be combined with the probabilities of disruption described by Huse et al. (2010) to evaluate the risk associated with alternative fishing intensities.

Discussion
Calibration of these management reference points remains a problem, given that we have only a single case of NSS herring for which we have a quantitative analysis by Huse et al. (2010). Exploratory “data-rich” simulations indicate that the need for precaution is closely tied to recruitment variability, especially if \( \sigma_r \) is \( > 1 \) (for comparison, \( \sigma_r \) is \( \approx 0.8–1 \) for NSS herring). It would also be worthwhile comparing the range of fishing intensities associated with optimal, or at least prudent yield-based exploitation with the threshold values of \( F \) needed to avoid migrational instability. Based on a limited set of simulations, the impression is that there tends to be a low risk of migrational instability at \( F_{MSY} \). However, if management attempts to maintain a high level of catch despite reduced abundance (thus raising \( F \)), perhaps in the anticipation of improved recruitment soon, the arrival of that improved recruitment itself could cause a migrational disruption with resulting stock collapse (e.g. Corten, 2002).

A special difficulty is posed by episodic stocks based on migratory behaviours that last for prolonged periods, but are inherently temporary and cannot be sustained indefinitely. Note that I am not referring to a genetic stock but simply to a coherent segment of a population that can support a fishery. The Bohuslän herring fishery has existed perhaps nine times in the past 1000 years, with each episode lasting several decades (Alheit and Hagen, 1997; Corten, 1999). There appear to have been five multidecadal productive periods for the Japanese sardine \( (Sardinops melanostictus) \) in the last 450 years (Hiramoto, 1991), and palaeoecological evidence suggests 18 episodes for the California sardine \( (S. sagax) \) in the last 1700 years, each lasted for \( 10–190 \) years (Baumgartner et al., 1992). The existence of favourable conditions is episodic on a decadal time-scale, and the geographic regions occupied during favourable periods are abandoned entirely (and do not appear to be “probed” as might be expected if the behaviour had a genetic basis) during unfavourable periods. There is growing evidence that the duration of productivity of these episodic stocks can be greatly shortened by intense fishing pressure (MacCall, 2009). The development and maintenance of migration patterns needed for populations to exploit these episodic opportunities may well be based on learned migratory behaviour (Corten, 1999; Petitgas et al., 2010). If this is true, then the remarkably high fishing pressure that can be supported by some of these stocks during productive periods poses a severe risk of migratory disruption and sudden recruitment failure that is not predictable from the preceding stock–recruitment relationship (e.g. Wada and Jacobson, 1998; Coetzee 2007). An appropriate approach to manage these episodic stocks would be to treat them as if they are sustainable but fragile and to managing avoidance of migrational disruptions. Although this approach may require a reduction in allowable catches, there should be an offset in the long-term total yield that is possible because viability of the fishery is less likely to be terminated prematurely.

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References


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