Stock collapses and their recovery: mechanisms that establish and maintain life-cycle closure in space and time

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Experience has established that the recovery of many collapsed stocks takes much longer than predicted by traditional fishery population models. We put forward the hypothesis that stock collapse is associated with disruption of the biological mechanisms that sustain life-cycle closure of intrapopulation contingents. Based on a review of case studies of nine marine fish stocks, we argue that stock collapses not only involve biomass loss, but also the loss of structural elements related to life-cycle diversity (contingents), as well as the breakdown of socially transmitted traditions (through a curtailed age range). Behavioural mechanisms associated with these structural elements could facilitate recovery of depleted populations. Migratory behaviour is argued to relate to phenotypic plasticity and the persistence of migration routes to social interactions. The case studies represent collapsed or depleted populations that recovered after a relatively short period (striped bass, capelin), after more than a decade (herring and sardine), or not at all (anchovy, cod). Contrasting the population dynamics from these stocks leads us to make a distinction between a depleted and a collapsed population, where, in addition to biomass depletion, the latter includes damage to contingent structure or space-use pattern. We also propose a mechanism to explain how lost habitats are recolonized.

Keywords: behaviour, collapse, life-cycle diversity, recovery.

Received 6 November 2009; accepted 2 May 2010; advance access publication 23 June 2010.

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Introduction

Great historical fisheries, whether pelagic or demersal, have experienced severe and long-lasting stock collapses (Beverton, 1990; Myers *et al.*, 1996). Typically, collapses are characterized by a reduction in catch to less than 10% of the maximum and by a long recovery time after reaching a biomass minimum (Mullon *et al.*, 2005; Worm *et al.*, 2009). Previous studies on stock collapses and recoveries focused on the phenomenology of the abundance time-series (Shepherd and Cushing, 1990; Hutchings, 2000; Mullon *et al.*, 2005), whereas less attention has been paid to the roles of population structure and behaviour in persistence and rebuilding (but see Hutchings, 1996; Fogarty, 1998). The positive relationship between time to recovery and severity of depletion (Hutchings, 2000) is often parametrized as a declining population growth rate below some low level of abundance, a process termed demographic depensation (Courchamp *et al.*, 1999; Liermann and Hilborn, 2001). The mechanisms explaining depensation include a negative, density-dependent fitness of individual fish (component Allee effect; Stephens *et al.*, 1999). Because social interactions enhance the ability to learn efficient feeding, anti-predator, and migratory behaviours (Krause and Ruxton, 2002), they could be expected to be key in population persistence; the disruption of the latter could result in depensation.

We hypothesize that the collapse of a stock's biomass is accompanied by the loss of key structural and behavioural elements that affect the life-cycle patterns existing within the stock, resulting in a long recovery time. We furthermore hypothesize that the existence of complex life-cycle patterns in marine fish populations is related to phenotypic diversity and that the persistence or reappearance of these patterns is based on learned behaviour. These hypotheses on how phenotypic diversity and behaviour contribute to the persistence and recovery pathways of fish stocks are based on the understanding of partial migration and social learning in fish. The persistence of a spatially defined entity, such as a population, could only be accomplished if life stages occur in a certain sequence of habitats leading eventually to life-cycle closure. Therefore, patterns of larval dispersal and migration of juveniles and adults, as well as habitat selection, are viewed here as structural attributes that are critical for persistence.

After reviewing the determinants of complex life cycles, we examine in nine case studies the concurrent change in these attributes with collapse and recovery in trying to explain loss and resurgence of habitat-use patterns and differences in recovery time-scales. The populations represent a diversity of systems and species: northern cod (*Gadus morhua*), North Sea herring (*Clupea harengus*), Gulf of Maine herring, Gulf of St Lawrence herring, Norwegian spring-spawning (NSS) herring, California sardine (*Sardinops sagax*), Bay of Biscay anchovy (*Engraulis encrasicolus*), striped bass (*Morone saxatilis*) in Chesapeake Bay, and capelin (*Mallotus villosus*) in the Barents Sea.

Our evaluation framework comprises the abundance time-series, as well as structural and behavioural changes documented in the literature. Proof of the effects of learning and social behaviour on migration routes and life-cycle patterns in marine fish requires experimental manipulation of groups of animals, which has been so far limited to studies on gobies and reef fish (reviews by Dodson, 1988; Krause and Ruxton, 2002). Here we look more for supportive evidence.

Determinants of complex life-cycle patterns
Phenotypic plasticity and contingent structure
A life-cycle pattern could be defined by recurring and persistent migration and dispersion processes that link the sequential habitats used by the different life stages. A population could be characterized by a single pattern (Sinclair, 1988), but it might also display within-population diversity of patterns (contingent structure: Secor, 1999). Large marine fish stocks are now recognized to represent metapopulations (McQuinn, 1997a; Smedbol and Wroblewski, 2002; Kritzer and Sale, 2004), where components displaying different patterns (contingents) could be linked by straying of individuals through dispersal in the larval, juvenile, and/or adult phase. These contingents do not necessarily represent discrete genetic entities (Hjort, 1914; Secor, 1999). Their life cycles are usually contained within persistent oceanographic structures that ensure larval retention and/or control migration of adults (Harden-Jones, 1968; Sinclair, 1988). Life-cycle patterns are not necessarily genetically inherited and their persistence could be explained by phenotypic plasticity and social behaviour.

Developmental thresholds could result in migratory or sedentary life cycles within populations (partial migration; Jonsson and Jonsson, 1993), enhancing phenotypic plasticity. Migration evolves in concert with non-behavioural traits, because of an unavoidable trade-off between the energy required for migration and the energy invested in reproduction (Roff, 1988). Therefore, migratory individuals are expected to exhibit a higher initial growth rate and larger size-at-maturity than resident individuals do. For Atlantic salmon, the early-growth trajectory influences the adoption of early-migration, late-migration, or completely resident behaviours (Thorpe, 1989), whereas the offspring of residents and migrants in crossbreeding experiments across populations could adopt either behaviour (Nordeng, 1983; Thrower *et al.*, 2004). Hence, the determinants of partial migration are partly developmental, depending on environmental conditions influencing early growth, and partly genetic, being inherited as a quantitative trait (development threshold; Jonsson and Jonsson, 1993). Partial migration is a well-known feature among anadromous species. Individuals migrating to marine feeding habitats grow larger, but suffer greater mortality than their congeners staying in estuarine or freshwater habitats. In addition, midlife changes in migratory behaviour could happen, with individuals joining different contingents sometimes several times during their lifetime (Jonsson and Jonsson, 1993; Secor, 1999). The expression of alternative life-history tactics [migrants vs. residents (Gross, 1985); homing vs. straying (Quinn, 1984)] permits a dynamic balance between individual fitness in varying environments.

Learning and social interaction
Diversity of life-cycle patterns associated with seasonal, annual, and generational time-scales has its origin in individual motivations and capabilities. Once a fish has adopted an initial

migration trajectory, persistence in using that pathway could be reinforced by social interaction. It has long been recognized that fish have the sensory capabilities for communication and maintenance of group cohesion (Wynne-Edwards, 1962). Sharing of information within groups of social animals increases individual fitness, for instance, by enhancing learning and transmission of adaptive behaviours in a given habitat that are efficient for feeding and avoiding predators (Giraldeau, 1997). Learning from experienced congeners involves copying of behaviour and could result in long-lasting traditions (Giraldeau, 1997). Fish can learn and memorize efficient behaviours and migration routes (Dodson, 1988; Brown and Laland, 2003), and the probability of transmission is increased by conditions that favour fish aggregation, such as shoaling (Dodson, 1988).

Some facts support prioritizing behaviour among factors shaping life-cycle patterns in marine fish. For herring, McQuinn (1997a) observed straying between spring- and autumn-spawning contingents and hypothesized that migration routes were learned and adopted by recruit spawners as they joined repeat spawners, whereas Corten (2002) demonstrated that learning applied also to feeding and wintering migrations. These findings support the view that learning develops traditions in the use of habitats over multiple generations. Rose (1993) described how aggregations of migrating cod were organized by size and age classes and how this type of organization could facilitate learning migration routes, as well as adequate feeding behaviour. In a review of case studies, ICES (2007) provided circumstantial evidence that learning could have a role in maintaining contingent structure across a range of diverse species (clupeoids, tuna, striped bass, whiting). This evidence implies that entrainment into the migration patterns of numerically dominant contingents could act as a capturing mechanism that jeopardizes the recovery of depleted contingents (vacuum effect: Petitgas *et al.*, 2006; Secor *et al.*, 2009). As opposed to entrainment, Huse *et al.* (2002) demonstrated that the ratio between naïve and experienced herring explained major changes in migration patterns to wintering habitats. Numerical dominance of naïve fish resulted in innovation in habitat use and colonization of new habitats, which, if favourable, might initiate novel life-cycle patterns. Learning from congeners, vs. by oneself by trial and error, could be viewed as alternative tactics of individuals, resulting in entrainment in and non-compliance with traditional behaviour (innovation), respectively. In a varying environment and depending on population abundance, either tactic could be selected for (Krause and Ruxton, 2002).

Case studies
Northern cod: non-recovery of offshore contingents
The northern cod stock complex off Newfoundland and Labrador consisted historically of various contingents, which were interconnected through straying at the larval or adult stages (Smedbol and Wroblewski, 2002). Three major types were distinguished: resident, coastal, and offshore. The resident contingents completed their entire life cycle within individual bays. The coastal contingents spawned in bays exhibiting a high degree of philopatry (Rochibaud and Rose, 2001), whereas their feeding and nursery grounds were coastal, in and out of the bays. The offshore contingents spawned at the shelf break, with the larvae drifting in a west–southwest direction across the shelf towards the coast. Their nursery and feeding grounds were coastal and largely the same as those of the coastal contingents. The mature adults undertook

cross-shelf migrations between spawning and feeding areas (Rose, 1993). This type of organization is common in this species, its characteristics being shared with cod along the Norwegian coast where coastal contingents coexist with migratory contingents (Sundby and Nakken, 2008). It is noteworthy that the residents in both Canadian coastal bays (Hu and Wroblewski, 2009) and Norwegian fjords (Sundby and Nakken, 2008) typically grow to a smaller size than the migrants and that the migratory contingents dominate numerically. This situation resembles the partial migration observed in anadromous fish populations (Jonsson and Jonsson, 1993).

Hu and Wroblewski (2009) reviewed the history of the northern cod stock collapse. In the late 1960s, the Labrador components (areas 2GH) collapsed, followed in the early 1990s by the components in areas 2J3KL, which resulted in a moratorium on fishing on the entire complex in 1992. In 1998, a fishery was reopened in the coastal waters northeast of Newfoundland where coastal cod were more abundant, but this fishery was closed again in 2003. The once dominant offshore, migratory contingents have not recovered since 1992. Rose (1993) hypothesized that the knowledge of migration routes and offshore spawning habitats might have been lost. Future rebuilding is thought to depend on individuals straying from the coastal and bay contingents and re-establishing those offshore contingents (Hu and Wroblewski, 2009). In other words, the scenario for the recolonization of offshore habitats is based on partial migration, where a migratory tactic reappears in the progeny of resident contingents.

North Sea and Georges Bank herring: loss and recovery of spawning grounds

A striking example of the difficulties met by a collapsed stock in restoring the full distributional extent of its former spawning grounds involves North Sea herring. Even today, the Dogger Bank, once an important spawning ground, is not being used, more than 40 years after the collapse in 1967, although the stock has rebuilt in the mid-1980s to levels comparable with the level prior to the collapse (Schmidt *et al.*, 2009). In contrast, another spawning ground, the Aberdeen Bank, stayed vacated for 17 years, but the stock eventually recovered fully on this spawning ground. Corten (2002) documented the long-term absence of spawning and subsequent recolonization of the Aberdeen Bank using information from larvae surveys, whereas trawl samples revealed that spawning was reinitiated by recruit spawners belonging to the large 1980 year class. The segregation of these fish from their original contingent was attributed to a change in hydrographic conditions favouring a southern displacement of recruiting herring towards the bank. Subsequently, fish from the 1980 year class continued to return to spawn on the bank, while entraining younger year classes.

Similarly, the spawning grounds on the northeastern side of the Georges Bank were left unused for 10 years after the collapse of the Gulf of Maine–Georges Bank herring stock in 1976. The recolonization of the bank has been described based on larval (Smith and Morse, 1993) and trawl (Stephenson and Kornfield, 1990; Overholtz and Friedland, 2002) surveys. The larval surveys revealed a 3-year transition period of recolonization beginning with increased spawning in the western Gulf of Maine, including Massachusetts Bay and the Nantucket Shoals, and extending progressively eastwards towards the Georges Bank in subsequent years. Similar to the Aberdeen Bank case, colonizing individuals were recruit spawners from the large 1983 year class, which

returned to spawn in subsequent years, accompanied by younger fish from later year classes. Stephenson and Kornfield (1990) viewed the first colonizers as remnants from a relict Georges Bank spawning contingent that went undetected for 10 years. However, the data used in support of their arguments did not include the spawning in the western Gulf of Maine and the Nantucket Shoals, which clearly indicate that the colonizers originated from these areas. They also argued that if the bank were recolonized from adjacent populations, the colonizers should have been made up of a proportional mix of all year classes, rather than mostly recruit spawners, as had been observed. However, the hypothesis of straying of members of a strong year class and entrainment of younger fish fits the data well and counteracts this argument.

These two examples indicate that abandoned spawning grounds might be rediscovered by individuals with no former spawning experience. Entrainment presumably happens in mixed aggregations, where younger fish follow repeat spawners and learn and memorize their migration route through repetition. Thus, knowledge is passed on over generations. For a recolonization event to be persistent, recruit spawners would have to overlap with repeat spawners regarding size and condition, to facilitate the formation of mixed schools (allowing entrainment), and these would also have to memorize the migration route.

Gulf of St Lawrence herring: choice of spawning season

The herring stock in the northern Gulf of St Lawrence consists of spring- and autumn-spawning contingents characterized by distinct spawning and nursery grounds. Based on otolith and maturity analyses, McQuinn (1997b) demonstrated substantial straying among contingents by recruit spawners, the choice of joining one of the two contingents being influenced by juvenile growth rates. When autumn spawners start their annual maturation cycle, they are joined by spring-spawned recruits large enough to mature, whereas autumn-spawned fish not large enough at that time join the spring-spawning contingent the following year. After joining one contingent or the other, the choice is maintained throughout adult life. This example illustrates that herring might adopt life-history characteristics and migratory behaviours that differ from those of their parents, suggesting that the differences observed are largely phenotypic, rather than being genetically determined. In adopting a specific contingent, individuals comply with the associated energy-budget constraints. Bradford (1993) demonstrated that the energy allocation to reproduction and metabolism depends on the reproductive strategy (rapid maturation during summer for autumn spawners or prolonged maturation during overwintering for spring spawners). The original choice of spawning season is favoured by overlapping size distributions between recruit and repeat spawners, as well as by overlapping spatial distributions of juveniles and adults in the feeding areas (McQuinn, 1997b). Processes that could explain the adoption of a particular spawning contingent are essentially behavioural: schooling, learning, and memorizing.

NSS herring: tradition, novelty, and ontogenetic change

During the past 60 years, NSS herring have displayed major changes in spawning, wintering, and feeding grounds, concurrent with the collapse of the stock in the 1960s and its recovery in the 1980s. The spawning grounds are located along the Norwegian coast between 60°N and 70°N. Larvae from offshore and northern spawning areas drift into the Barents Sea, whereas larvae from

coastal spawning areas farther south tend to be retained within the fjords. Nursery habitats are hence found in coastal areas and in the Barents Sea, with growth and survival rates differing accordingly. The different growth trajectories of juveniles raised in these two habitats define two contingents (Holst and Slotte, 1998). Although growth rate is faster in the coastal areas, the carrying capacity of the Barents Sea is much larger and consequently large year classes originate in the latter region. Normally, recruit spawners join the spawning contingents from which they originated during feeding along the coast, or in the Norwegian Sea, and adopt their respective migration patterns.

When the stock collapsed in the 1960s, its distributional range shrank considerably (Dragesund et al., 1997). The entire life cycle was completed near the coast within a much-reduced area, the spawning grounds being restricted to the area of 62–68°N. Year classes originated almost exclusively from local coastal regions, and the contribution of the Barents Sea contingent was marginal. Feeding grounds were on-shelf and did not extend offshore into the Norwegian Sea. Wintering grounds were coastal and located at the two extremities of the population's spatial distribution: near 70°N (Lofoten area) and near 60°N (Møre area).

Two strong year classes (1983 and 1988) allowed the stock to rebuild in the late 1980s and 1990s (Dragesund et al., 1997; Corten, 2002). Huse et al. (2002) related temporal changes observed in the wintering areas and migration routes to the numerical dominance of strong year classes, each one establishing new wintering grounds, which were revisited annually until the year class completely recruited to the main population. Such changes in wintering grounds had also happened before the stock collapsed. Part of the strong 1959 year class, after leaving the Barents Sea and recruiting to the stock, established novel wintering grounds that were revisited for a few years before the entire year class joined the traditional migration pattern (Dragesund et al., 1997).

Recruit spawners of the Barents Sea contingent tend to spawn northwards, but with age, its members progressively distribute themselves southwards to occupy in the end all spawning areas (Holst and Slotte, 1998). During the period of low abundance (1959–1986), spawning grounds south of 60°N were left unused for more than 25 years. During the recovery of the spawning stock in the 1980s, the southernmost grounds were recolonized and the distance travelled from the wintering grounds in the Lofoten area to the spawning grounds correlated positively with fish length and condition factor (Slotte and Fiksen, 2000). The southern colonizers, therefore, apparently represent the faster growers and/or older members of a mixed reproductive stock.

We conclude that the ratio of naïve to experienced fish could also determine whether juveniles are entrained into the established migration pattern of a stock or whether they might establish a novel migration pattern. In addition, midlife changes in migratory behaviour could happen, depending on conditions for growth and reproduction.

Californian sardine: social disruption and cessation of migration

ICES (2007, Annex 5) reviewed major changes in the migration pattern of Californian sardine concurrent with the stock's history of collapse and rebuilding. The stock was large in the mid-1930s and distributed from 25°N (Baja California, Mexico) to 50°N (British Columbia, Canada). Spawning took place in spring between 30°N and 35°N (South California). Nearshore individuals attained a smaller length than offshore individuals.

The offshore contingent made an extensive northwest migration to its northern summer–autumn feeding areas, which extended all along the western coast of the USA and into British Columbia. During the 1930s, most fish found farther north were large and encompassed a wide range of ages (2–12 years old; length >22 cm). Severe population depletion started in the late 1940s. From the 1950s to the mid-1960s, the biomass progressively declined to less than 1% of its peak in the 1930s. During that period, the fish migrating to British Columbia were initially 4–8 years old, whereas younger age groups were lacking, until the migration ceased completely in the late 1950s. The period of complete collapse was from the mid-1960s to the mid-1980s, when sardine eggs and larvae were absent from the ichthyoplankton surveys that covered the major Californian spawning area. The period from the mid-1980s to the early 1990s was one of progressive rebuilding of the stock, and the distribution of eggs and larvae became similar to the situation before the collapse. In the early 1990s, large migrants (>20 cm) were observed again in British Columbia after an absence of 35 years (1957–1992), with both young and old (2–9 years) fish mixed in the catches. The long hiatus in the feeding migration might have resulted from the lack of young fish in the late 1940s, which hampered knowledge of the migration route to be transmitted. In addition, the available information provides further support for the notion of condition-dependent large-scale migration, as observed above in NSS herring. Fish appear able to adopt new behaviours at different times during their lives, depending on their condition, environmental cues, and interaction with experienced congeners.

Bay of Biscay anchovy: collapse or depletion?

The Bay of Biscay anchovy completes its life cycle within ICES Subarea VIII. Catches increased in the 1960s, peaked in 1970, then progressively declined in the mid-1980s to below 10% of the peak (ICES, 2010, Chapter 8), concurrent with a progressive contraction of the spatial distribution along the Spanish north coast from west to east (Junquera, 1984). In the 1990s, the catches increased again to 40% of the peak, with fluctuations caused by recruitment variability. Since the 1970s, the western areas have remained abandoned and the stock has been restricted to the area east of 3°W in the southeast corner of the bay. This suggests that a western contingent might have been lost. The reasons why no recolonization has taken place are unclear, because the larval drift from the spawning grounds east of 3°W would tend to seed the western areas. Since 2002, the remaining eastern contingents have suffered low recruitment repeatedly, and catches have declined again to below 10% of the historical peak, but no major further loss in habitat has been detected. Although the fishery has been closed since 2005 to protect the remaining spawning biomass, recruitment has remained low, possibly because of a hypothesized "predator pit" (Bakun, 2006) situation. The decline in the 1970s resembles other collapses discussed, because the population appears to have lost contingents and effective connectivity between them. In contrast, the recent decline in the remaining eastern contingent has not been accompanied by drastic changes in life-cycle patterns.

Chesapeake Bay striped bass: rapid rebuilding after depletion

Atlantic striped bass is a long-lived anadromous species. The stock along the east coast of North America is principally fed by recruitment from Chesapeake Bay (Merriman, 1941). Most mature

females are migratory, whereas relatively few males emigrate from the bay (Secor and Piccoli, 2007). During spring, adults undertake spawning runs into the local estuaries. During other seasons, migratory striped bass range from the St Lawrence (Quebec) to Cape Hatteras (North Carolina). In the late 1970s to early 1980s, targeting of small individuals (30–46 cm) by fisheries resulted in recruitment overfishing and stock collapse (Richards and Rago, 1999). Stringent regulations were enforced, which allowed the relatively strong 1982 year class to recruit fully to the spawning population. Several subsequent strong year classes (1989, 1993, and 1996) resulted in exponential population growth, with a doubling time of ∼5 years. This remarkable recovery is regarded as a success story of timely regulatory action (Field, 1997). Available evidence from recreational records by state (Maine to North Carolina; NOAA 2009, http:// www.st.nmfs.noaa.gov/st1/recreational/queries/index.html) indicates that the coastal distribution did not change markedly among the periods before, during, and after stock depletion, suggesting a stable distribution during the entire record. In this case, the rate of recovery could have been enhanced by the partial conservation of the age structure during the depleted state. Secor (2000) demonstrated that the enforced regulation effectively protected striped bass >90 cm (∼7 kg) and that their egg production played a large role in stimulating the recovery. In addition, these older fish (10–30 years) might have contributed to sustained migration patterns in coastal waters during the period of depletion and recovery. This contrasts with previous examples, where migration patterns were disrupted during the period of biomass depletion and age truncation.

Capelin: no tradition in habitat use

The Barents Sea capelin stock has gone through tremendous variations in abundance during the period 1984–1990, from 3 to 0.1 million tonnes and back to 5.8 million tonnes (Gjøsæter, 1998). The stock displayed vulnerability to recruitment failure, as well as the capacity to rebuild biomass rapidly. An analysis of anecdotal evidence ranging back 300 years suggests that the collapse–recovery pattern of this stock observed during 1984–1990 is common or even cyclical (Øiestad, 1992). Because of its short lifespan and semelparous reproduction, capelin cannot rely on social learning in choosing a particular migration pattern. Instead, the annual migration pattern appears modified in response to environmental conditions (Ozhigin and Luka, 1985; Huse and Ellingsen, 2008). All populations of this short-lived, semelparous species in the Atlantic have displayed large changes in spatial distribution and abundance, which seem to be mutually disconnected and solely environmentally driven (Rose, 2005), revealing no sign of socially transmitted tradition in habitat-use patterns.

Conclusions

The long-lived marine fish stocks examined display complex life-cycle patterns, which appear to rely on behavioural processes (partial migration and learning) for their persistence. Severe reductions in their abundance have often been associated with structural and social disruption. The rebuilding of their biomass has not always been accompanied by a full recovery of their original spatial distributions and associated life-cycle patterns. When population structure had remained largely intact (striped bass), rebuilding could be achieved within a relatively short time-span, because this depended on vital rates only. In contrast, when age and contingent structure had been damaged substantially

(herring, sardine, cod), full recovery also depended on re-establishing behavioural patterns, and recovery time exceeded a decade, if recovery has been observed at all. The evidence of whether behaviour is important in determining life-cycle patterns in short-lived species was inconsistent. Anchovy displayed population structure and long recovery time, but capelin did not. The reproductive strategy (iteroparity for anchovy vs. semelparity for capelin) and type of schooling behaviour (many small schools for anchovy vs. few large aggregations for capelin) might affect the existence and persistence of complex life-cycle patterns in populations of these species.

Based on the case studies examined, a distinction can be made between collapse and depletion in relation to stock dynamics. A stock would be termed depleted when only its biomass is severely reduced, while its contingent structure and associated habitat-use patterns remain intact. In contrast, a stock would be termed collapsed when the severe reduction is accompanied by a disruption of its contingent structure and habitat-use patterns. We also examined how behavioural processes determine persistence in habitat-use patterns. We distinguished between two types of behaviour, those based on individual physiology and metabolism (migrant vs. resident behaviour) and those based on sensory capability and social interaction (learning and memorizing). The former is a phenotypic response, critical to the establishment of complex life-cycle patterns, whereas the latter is a social response, critical to the persistence of these patterns.

Some of the stocks examined were characterized by migratory (offshore) and resident (inshore) contingents. As such, they resembled anadromous fish populations that display partial migration. The offshore contingents were the largest and the first to collapse. Their recovery depended on the reappearance of a phenotypic migratory contingent to re-establish the use of the offshore habitats, possibly induced by density-dependence inshore. Common population properties are apparently that resident contingents confer stability, whereas migratory contingents confer productivity, and connectivity between the two tends to increase stock size. This type of population often rebuilds from strong year classes produced by resident contingents.

To re-establish a large migratory contingent, we hypothesize that: (i) substantial recruitment outbursts must occur, resulting in increased diversity in early-growth trajectories (therefore in the expression of the reaction norm for a migratory phenotype), as well as in a greater probability for groups of individuals not to become entrained in the habits of the existing population; (ii) sufficient numbers of the migratory phenotype must be produced to overcome the high mortality incurred by naïve colonizers when exploring new habitats; and (iii) once established, the new migration patterns and habitat use must be socially transmitted to later generations by "teaching" successful behaviours. The time to recovery will depend on the frequency in recruitment outbursts of the population's less-depleted contingents, as well as the spatial setting of habitats and their accessibility to the migrants. Such a recolonization scheme (Figure 1) agrees with the "propagule" colonization scheme in metapopulation theory (Hellberg, 2006). In MacCall's (1990) basin model, where the spatial extension of a population is density-dependent, all individuals have a similar phenotype. Here, we argue that the colonization of distant habitats is conditioned by phenotypic diversity, which could explain the long recovery time of collapsed migratory contingents.
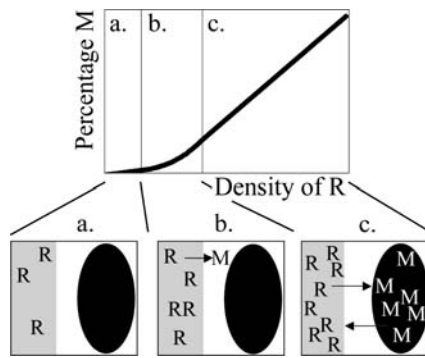
Figure 1. Proposed mechanism, combining partial migration, behavioural entrainment, and density-dependence (top panel showing three phases a, b, and c), for the resurgence of a contingent of migrant phenotypes (M; oval habitat), from a contingent of resident phenotypes (R; rectangular habitat): (a) collapsed situation where only R has survived at low abundance; (b) as R increases, a number of M is expressed, but these naïve individuals suffer high mortality in the novel habitat jeopardizing their colonization; and (c): recruitment outbursts allow enough M to survive in the novel habitat. Contingents are maintained through entrainment and learning, with sustained connectivity (arrows), thus establishing a different contingent with a tradition in habitat-use patterns.

Although we are concerned by the importance of behaviour in driving distributional changes, large environmental changes might ultimately override all other biological and behavioural forcing. Hydroclimatic effects on stocks are naturally important drivers of change. Collapses are often the result of an interaction between heavy fishing and low stock production, the latter caused by adverse environmental conditions (northern cod; Rose et al., 2000). Rebuilding often depends on strong recruitment events that are ultimately under environmental control. Environmental cues that contribute to re-establishing lost migration routes have not been included in our review, but do also come into play (Corten, 2002).

Collapses and recoveries have been a common natural feature in many marine fish stocks over geological times (Baumgartner et al., 1992). The combination of phenotypic diversity and social behaviour constructs a framework of mechanisms that allow resurgence of long-lived species after collapses at the metapopulation level. In this context, the dynamic equilibrium between tradition and innovation in habitat-use patterns appears an important factor. It could also confer a scope for adaptation at evolutionary time-scales. In varying environments, selection could dynamically modulate the frequency of alternative tactics for learning efficient behaviours (copying vs. trial and error), as well as for partial migration (migration vs. residency).

An important implication of recognizing contingent structure within populations is that protecting the overall level of spawning biomass might not be sufficient for rebuilding a collapsed stock. Concentrating only on biomass recovery through management action could easily overshadow the more basic need for structural recovery of the full-contingent diversity that confers to a population the capability to exploit the full range of suitable habitats. Therefore, recovery plans should include spatial measures to rebuild contingent structure when a stock has collapsed. For example, continued fishing at low levels jeopardizes the expansion of a remaining resident contingent, consequently retarding or preventing the emergence of others, as well as the reuse of abandoned habitats, if new colonizers are instantly fished out. From a precautionary point of view, spatial measures could proactively protect contingent diversity and prevent their disruption in the first place. Consequently, the monitoring of fish stock status should also include identifying and monitoring spatial distributions and associated contingents. Monitoring within-stock structure and intercontingent connectivity might involve a more consistent application of other methods than currently used in stock assessment, which, depending on the situation, could be larval-drift models, tagging experiments, otolith microstructure, genetic tracers, or characterization of schooling aggregations.

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