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The entrainment hypothesis: an explanation for the persistence and innovation in spawning migrations and life cycle spatial patterns

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Fish stock dynamics is commonly modelled using vital traits only. But here, it is argued that the life cycle spatial pattern is a determinant of population dynamics. Stock recoveries have taken longer than predicted and important changes in the geographical organisation of life cycles have been observed. The paper proposes a conceptual framework in which to envisage population functioning under climate change and change in population demography and substructure. The 'Entrainment hypothesis' is formulated to address conservatism and variation in life cycle geographic patterns. The 'Entrainment hypothesis' states that life cycle closure results from spawning migrations and that spawning migrations are sustained by repeat spawners. Repeat spawners would have the knowledge of migration routes and would be those that are responsible for the persistence of the life cycle spatial organisation. They would lead first spawners to maintain the life cycle pattern. The adult / young fish encounter would take place in definable geographic / temporal areas (e.g., feeding grounds), which would allow for the entrainment of the young into the adult spawning migration. The paper further suggests a plan for the falsification of the hypothesis. Required information is listed that would provide consistency, support or demonstration of the hypothesis. Spatial behaviour and learning between generations are seen as central for sustaining migration routes and selecting spawning habitats. As a consequence it is suggested to consider in the spatial modelling of habitat selection a stock memory function based on population status. Finally implications of the hypothesis for spatial management are reviewed.

Keywords: life cycle, behaviour, migration, meta-population

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Introduction – The need for a synthesis on population functioning

Population dynamics is concerned by modelling the fluctuation of population numbers under the control of the fish vital traits with added fishing mortality and environmental variability. It assumes that the population life cycle gets closed. Therefore, it cannot predict the evolution of collapsed or depleted populations which have shown disruption in their life cycle closure. A more general theory, that of population functioning, is required in fisheries science for dealing with conservation problems, in particular for predicting the future of depleted sotcks that have lost essential habitats. Population functioning is here defined as the way by which populations close their life cycle, occupy habitats, support external variation in the environment as well as internal variation in the population demography and substock structure. Population functioning includes population dynamics in a broader context. This broader context is first that of stock geographical occupancy for life cycle maintenance with environmental and substock effects. Second, it is that of selective behavioural ecology. We here attempt to make links between spatial occupation, behaviour, genetics and population dynamics.

Collapse and recovery in demersal and pelagic stocks have shown that habitats are lossed after collapse and need be recolonised for complete recovery. Thus the life cycle spatial pattern would be a key determinant of population functioning. There are stricking similarities in changes in the life cycle spatial patterns in collapsed cod and herring stocks. Since its collapse in the early 90s, NW Atlantic cod lost its shelf-break spawning grounds (Rose et al., 2000 ; Smedbol et al., 2002; ICES, 2005). After its collpase in the 70s, Arcto-Norwegian herring changed completly its life cycle pattern (Dragesund et al., 1997; ICES, 2004). Bakun (2001) also reports spectacular changes in the spatial occupation in pacific sardines. When the North Sea herring stock collapsed in the 70s, the 3 components (Buchan, Banks and Downs: ICES, 1965) did not collpase in a similar manner and did not all recover although total North Sea herring recovered biomass levels comparable to that prior to the collapse (e.g., the Banks component stayed depleted: ICES, 2005b). Re-colonisation of lost spawning grounds in herring has been described to occur more than 10 years after the collapse (Corten, 2000, in the North Sea ; Smith and Morse, 1990, on Georges bank). In all cases, colonisors were first spawners. For NW Atlantic cod, recovery of lost spawning grounds has still not occurred. In cod, behaviour was shown to play an important role in the maintenance by learning of migration routes and feeding habits (Rose, 1993). On pelagic fish, Huse et al. (2002) showed by simulation of behavioural rules that a few individuals are sufficient to lead a school on a migration route.

Adult fish spatial behaviour is thus identified as key to ensure the persistence of the life cycle spatial organisation. Life cycle closure would be ensured by adult selection of spawning habitats (larvae drift would be less critical to live cycle closure than adult selection of useful spawning grounds). The paper proposes a conceptual framework, the entrainment hypothesis, in which to envisage population functioning under climate change and change in population demography and substructure.

1. The entrainment hypothesis

1.1. A prior conception of population life cycle organisation

Stocks are made of one or several different spawning units (local populations). Different spawning units separate for spawning but may share similar adult feeding grounds and nursery grounds. Adult and juvenile habitats spatially overlap at a particular time, allowing adult / juvenile encounter and juvenile entrainment into the different spawning units. A juvenile fish that does not encounter or join an adult spawning group will keep a juvenile schooling behaviour and as a result will keep aside from already established life cycles. Larvae and juvenile stages use innate mechanisms and are only responsive to the environment. In contrast, the adult spawning part of the population uses adopted (learned) behavioural mechanisms to ensure closure of the life cycle and its persistence. The spawning migration is understood to be the biological phase of the life cycle that ensures its closure. Persistence in the closure of the life cycle is made possible by adult entrainment when juveniles recruit to the adult spawning part of the population.

1.2. Statement of the entrainment hypothesis

- Old adults (i.e., repeat spawners) have the knowledge of migration routes and are those that are responsible for the persistence of the life cycle spatial organisation. They can lead (entrain) younger fish to close and maintain the life cycle pattern.
- The adult / juvenile encounter takes place in a definable geographic / temporal area, which allows for the entrainment of the young into the adult spawning migration.
- The entrainment is a capturing mechanism of the young by groups of adults. Offspring from a particular spawning unit can be entrained (captured) to undertake the life cycle pattern of the dominant spawning unit.

- There is a selective advantage for the young to encounter or join adults. Juvenile fish on their own have limited colonisation capability of new or lost spawning grounds: they depend on adults for accomplishing that part of the life cycle.
- A fraction of the population does not get entrained. Vagrancy may occur at juvenile or adult stage.

The entrainment hypothesis is schematically pictured on Figure 1.

1.3. Explanatory power of the entrainment hypothesis

- Adult entrainment results in the conservation and persistence of life cycle spatial patterns.
- Vagrancy out of the entrainment effect for example by failing to meet with the adults, provides the potential for a different life cycle spatial pattern. Juveniles are more likely to colonise new habitats than adults.
- In the case of stocks that collapsed and that had different spawning units, some spawning units are observed to stay at a collapsed level though total abundance may have recovered. This can be explained by the entrainment effect of the dominant spawning unit which captures the majority of the offspring from all units. Some migration routes and spawning habitats may not be recovered if corresponding units stay depressed at low levels.
- The novel encounter of lost habitats and migration routes (their recovery) will depend on a high and sufficient level of vagrancy, resulting in the entrainment in a novel life cycle pattern at subsequent spawning. Density-dependent diffusion at high abundance level could be a mechanism.
- Nursery grounds and adult feeding grounds are similar concepts: juveniles and adults migrate actively to these grounds, independently.
- Stocks at high abundance level are dominated by conservatism in the life cycle pattern while low abundance levels correspond to lower adult entrainment thus to periods of higher vagrancy and therefore innovation / adaptation to environmental conditions.

1.4. How to test the entrainment hypothesis

Consistent evidence (not conflicting)

- Overlap between juvenile and adult distributions.

Review life cycle descriptions and report on the possibility of overlap in space and time between juvenile and adult distributions. Report on whether juveniles migrate by their own to spawning grounds or whether spatial overlap is observed (e.g., adult feeding grounds and nurseries) between adults and juveniles.

- Non recovery of particular spawning units.

Report on the confinement to a limited number of life cycle patterns after stock collapse. Describe whether the collapse affects all spawning units similarly, whether they all recover at abundance levels similar to prior to the collapse or whether some units only recover and other stay at collapsed level.

- Which are the colonisers, the repeat spawners or the first spawners ?

A consequence of the fact that the adults hold the memory of a life cycle pattern is that they are trapped in conserving this pattern. Hence, colonisers would then be juvenile vagrants (non-entrained juveniles) that become first spawners on novel grounds. But major external (environment) forcing can drive change in the adult migration. Thus environment forcing and juveniles are two candidates for colonisation and evidence should be searched for the two. Report on the length distribution of the individuals that are first observed in a previously unused habitat. Report on environmental change of importance for adult migration.

Supportive evidence (not explained by other theory)

- Change in the behaviour of juveniles when in contact with adults.

Report on behaviour difference between juveniles when independent from the adults and juveniles when in contact with adults: schooling behaviour; geographic distribution when adults have not been encountered; difference in geographic distribution between adult-entrained and non-entrained juveniles

Demonstrative evidence (demonstrative of the mechanism)

- The capturing effects

The demonstration would require the use of tracers of subpopulation units (e.g., tagging, meristic characters, otolith microstructure and chemistry, micro-satellite DNA). A high percentage presence of one unit in the other unit (the entraining unit) would need to be tested using the tracers. Mixed stock analysis would need be undertaken at times / locations when different units should be separate (e.g., on spawning grounds). Tracing first spawners would demonstrate entrainment, while tracing adult repeat spawners would demonstrate conservatism. For the entrainment hypothesis to be correct, phenotypic plasticity must be important.

2. Consequences of the entrainment hypothesis

2.2. recovery plans and spatial fisheries management

- Use of biomass in assessment

The Assessment of stock status requires assessment of its different subunits. Stock dynamics depends on its internal structure. Thus, total population abundance on its own is not sufficient.

- Role of recruited juveniles and role of adults

Protecting juveniles is a short-term measure that allows higher seeding in the population. Because conservatism of life cycle patterns relies on the adults, protecting old adults is a long-term measure that protects the diversity of subpopulation units and life cycle patterns. Loss of subpopulation units cannot be recovered simply. Their recovery requires that juveniles in sufficient numbers do not integrate a life cycle pattern and play the role of colonizors : a process that is regarded as risky and little probable.

2.2. Spatial population modelling

Because the occupation of habitats depends on the stock memory and because spawning behaviour is not only forced by the immediate environment, current habitat suitability is expected to be insufficient to predict spatial spawning distributions. We here suggest to combine habitat suitability and stock spatial memory in an advection-diffusion dynamic spatial model.

The Ideal Free Distribution concept (IFD: Fretwell & Lucas, 1972) was developed to model spatial distributions for terrestrial nesting birds. The « ideal individual » goes to the habitat that has greatest suitability. Habitat suitability varies with the density of individuals: suitability decreases with increasing density. The ideal free distribution is that of ideal individuals that would distribute freely resulting in each habitat having the same per capita suitability. The IFD concept predicts an asymptotic distribution with the assumption that equal suitability in all areas is attained by adjusting animal density. The distribution predicted takes into account the combined effects of environment and density-dependence. In applying the IFD, the difficulty is the definition of the suitability function that guides the spatial distribution of the fish. In fisheries applications of the IFD, different suitability indices have been used: population growth rate (California anchovy : McCall, 1990); temperature forcing individual body growth rate (North Sea cod : Blanchard et al., 2005).

The entrainment by adults acts as a spatial memory in the population. Therefore, habitat suitability may not be enough to predict fish density: a combination of a suitability map with that of a stock memory map would be required (Fig. 2). This could result in the occupation of only parts of the potential habitats, which is not uncommonly observed in pelagic fish populations (ICES, 2006) or in populations that have collapsed and lost habitats.

In an advection-diffusion model (e.g., Okubo and Levin, 2001), the variation of N (animal concentration) along time in each cell of the gridded distribution area is given by :

$$\frac{dN}{dt} = \frac{\partial}{\partial x}(D\frac{\partial N}{\partial x}) - \frac{\partial}{\partial x}(uN)$$

where x is the index of space, u the advection coefficient and D the dispersion coefficient.

Considering that advective movements of fish are guided by gradients in the environment (e.g., suitability index, I), the equation can be further developed as follows :

$$u = \frac{\partial}{\partial x}kI \;\; ; \;\; \frac{dN}{dt} = \frac{\partial}{\partial x}(D\frac{\partial N}{\partial x}) - \frac{\partial}{\partial x}(kN\frac{\partial I}{\partial x})$$

The advection term becomes a diffusion term along a gradient of an indicator of the environment’s suitability, I.

The index I defines the population’s basin (sensu McCall, 1990) and will guide the fish movements. How to define the index I is the enormous question. Various approaches can be thought of: the use of environmental variables (e.g., temperature), that of biological production models (e.g., a food index), or a combination of indices (e.g., potential spawning index derived from a statistical regression). Incorporation of a spatial memory could be made as follows. The guiding index I could have different components (Fig. 2): the immediate environment (suitability, s: e.g., food requirements) being one component; the stock memory, m, being another one: $I = \alpha\, s + (1-\alpha)\, m$. The prediction of the spatial distribution would then require one updated map for s and one for m at each time step.

2.3. Reponse to environmental change

Even though shifts in environmental conditions are identified as potentially important for the spawning fish, the particular selection of habitats in a given year will depend on the capacity of the adult stock to respond to these changes. Subpopulation structure is then key in driving the population response. A consequence of that is the necessity to develop population habitat selection models that combine a stock memory index with a habitat quality index. A distinction is to be made between two types of environmental changes: overwhelming changes that affect adult migrations, resulting in the stock being driven by the environment; non-overwhelming changes understood as inter-annual variability, that result in the stock being driven by its own behavioural capacity. To face differences in scales of environmental changes on an evolutionary basis, fish populations are expected to show mechanisms for conservatism and innovation in their life cycle patterns. Necessary tools to predict population response to environment change are then models that link processes in the fish to environmental requirements, e.g., population habitat selection models (including spatial stock memory), individual fish energy budget models, potential spawning habitat models, individual larvae drift and survival models.

3. Discussion

3.1. Synthetic perspective

The entrainment hypothesis formulates a generic fish spatial behaviour with selective advantage that is responsible for subpopulation structure. It provides a renewed perspective for population functioning that relates population dynamics, spatial population organisation, subpopulation genetic structure, as well as linkeage with the environment. It explains observed conservatism and innovation in the spatial life cycle patterns. It represents another way to envisage fluxes of individuals between substock components. In the entrainment hypothesis, the substock structure and its entrainment capacity (stock memory, conservatism) become key in controlling the response to environmental change (occupation of potential spawning grounds, recruitment).

3.2. Links with existing population thinking

Sinclair (1988) reviewed the founding contributions of fisheries science in the first part of the 20th century to population thinking. He pictured population functioning in its spatial context and conceived a population as a spatially organised life cycle that matched physical oceanographic features. He developed the hypothesis that population mean size (abundance and area coverage) was controlled by the size (area) of the larval retention system, which was physically defined. He further formulated the member / vagrant hypothesis stating that membership to the population was spatially controlled by ocean physical processes, as the life cycle was spatially organised to match physical structures, resulting in vagrants to the life cycle being lost to the population. The spatially organised life cycle conception of Sinclair (1988) allowed him to address the question of variation in population size across populations of the same species. He did not address the question of changes in the life cycle spatial organisation of a particular population, which is what we intend to address. Since Sinclair's synthesis on population functioning, major collapses in fish stocks have occurred in which the life cycle was disrupted.

Collapses of stocks have demonstrated that population and life cycle are not exactly synonymous. Some populations have rebuilt with a different life cycle spatial organisation than prior to the collapse. Our hypothesis is a behavioural hypothesis related to evolutionary biology that explains observed change / maintenance in life cycle spatial organisation. It is a prolongation of Sinclair's spatially organised life cycle concept that suggests a behavioural underlying mechanism for closing the life cycle and maintaining its persistence. In Sinclair's (1988) conception of the life cycle, the processes in the population that maintain its closure (stock memory) are implicit, whereas the adult entrainment hypothesis explicitly addresses the processes in the stock that result in a stock memory that sustains the life cycle spatial organisation and its closure. The entrainment hypothesis formulates that such processes are of a behavioural nature, occurring when first time spawners mix with repeat adult spawners at the time of their first spawning migration. The entrainment hypothesis further formulates the consequences of stock memory for life cycle persistence and recovery.

Harden Jones (1968) conceived adult spawning migrations as being contranatant to the eggs and larvae drift, resulting in making the spawning adults actively responsible of the life cycle closure. He further suggested a selective advantage for returning to the same spawning grounds which ensured successful reproduction. The entrainment hypothesis agrees with the concept of 'contranatant' spawning migration and explains this migration with a behavioural mechanism. The entrainment hypothesis results in a repeated use of similar spawning grounds (conservatism) without involving natal homing to parental grounds at first-spawning.

The entrainment hypothesis shares similarities with the school trap concept (Bakun and Cury, 1999; Bakun, 2001). In the entrainment hypothesis, the juveniles adopt the life cycle behaviour of the adults that they encounter or join when these entraining adults are not necessarily their (genotypic) parents. The entrainment leads to a trapping of juveniles into the life cycle pattern of the adults and results in conserving a memorised (learned) life cycle pattern. The school trap concept is a mechanism while the entrainment hypothesis addresses the result of being trapped with no reference to a specific mechanism at individual fish level. The school trap concept does not consider knowledge transfer between individuals, nor selective advantage of being trapped. In contrast, in the entrainment hypothesis, some kind of knowledge transfer takes place. An entrained fish becomes a full member of its new group and has a selective advantage in adopting the group's behaviour.

The entrainment hypothesis is similar to the adopt-migrant hypothesis (McQuinn, 1997) developed in the case of Atlantic herring to explain that seasonal-spawning (local) populations do not necessarily recruit to their parental spawning unit. In the adopt-migrant hypothesis, first-spawners adopt the life cycle pattern of a repeat spawner unit in accordance with their pre-spawning maturation conditions. Adoption is hypothesised to take place via learning a spatial behaviour from the adults. The adopt-migrant hypothesis is designed to explain local population integrity in the context of known straying between local populations. Corten (2000) extended the adopt-migrant hypothesis not only for spawning migrations but also for wintering and feeding migrations and recognised two behavioural stages: the adoption of the migration (colonisation) in which the environment may play an important role and the habit formation (conservatism) in which learning is determinant. The adopt-migrant hypothesis was formulated in the case of herring stocks. Our work aims at generalising for all fish stocks a spatial behaviour with selective advantage that is responsible for subpopulation structure.

The entrainment hypothesis fits in the conceptual framework of metatpopulations (Hanski, 1999). This framework is designed to predict local population dynamics in the context of exchanges between local populations. The type of exchange between local populations need not be specified precisely as the rate of exchanges between local populations is sufficient for the prediction. The entrainment hypothesis defines one way by which links/exchanges occur. But the entrainment hypothesis is designed to predict life cycle closure, spatial pattern maintenance and variation, whether subpopulation structure is complex or simple. In that sense, the entrainment hypothesis relates to thinking about populations not metapopulations and will consider a metapopulation as being a stock with complex substructure.

The entrainment hypothesis is not in contradiction with subpopulation genetic structure and may offer a framework to think about gene fluxes between subpopulation components and the stability/variation in subpopulation genetic structure over time. Population genetic substructure (Ruzzante et al., 1999, for cod ; Mariani et al., 2005, for herring) is often unclear, best seen with the most separated substock components and is perhaps not stable depending on gene fluxes between components. Spawning units in a population with high entrainment capability will contain alleles from many population units, while spawning units with low entrainment capability may show a lower allelic diversity. Genetic subpopulation structure will vary in time depending on the factors affecting the way the entrainment occurs in the population. This may have consequences on the sampling strategy of genetic studies, in particular their design over time across generations.

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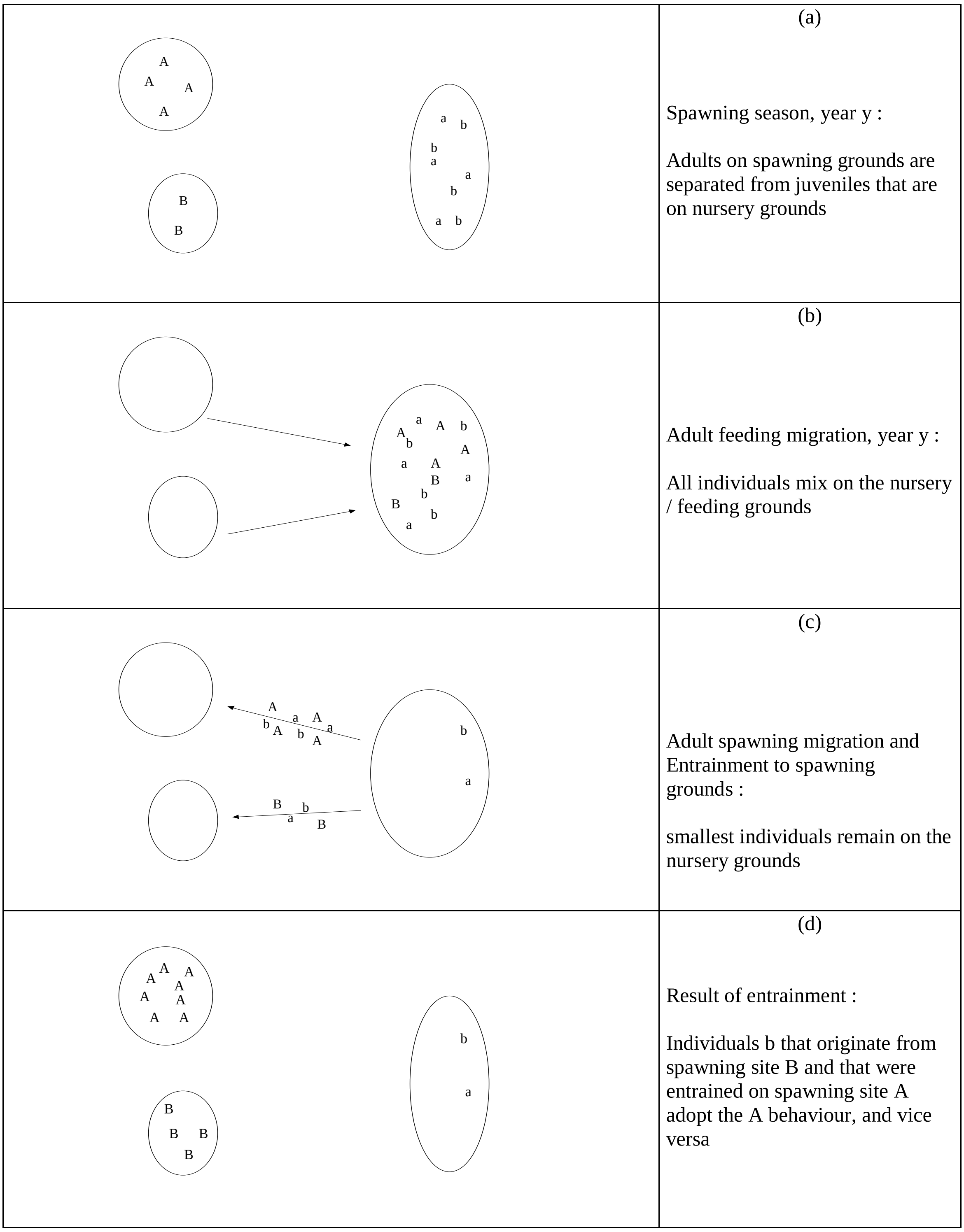

(a)

Spawning season, year y :

Adults on spawning grounds are separated from juveniles that are on nursery grounds

(b)

Adult feeding migration, year y :

All individuals mix on the nursery / feeding grounds

(c)

Adult spawning migration and Entrainment to spawning grounds :

smallest individuals remain on the nursery grounds

(d)

Result of entrainment :

Individuals b that originate from spawning site B and that were entrained on spawning site A adopt the A behaviour, and vice versa

Fig. 1: The entrainment hypothesis. The contact between juvenile and adults takes place at a definite space-time location (e.g., summer feeding on nursery / feeding grounds). When adults return to their specific spawning grounds they behaviourally entrain juveniles that have similar swimming capability. The entrained juveniles adopt the behavioural pattern of the group that entrained them and become full members of the different spawning groups. A and B : spawning units ; a and b : offspring from units A and B. Spawning units are different groups, each with the specific memory of its learned life cycle.

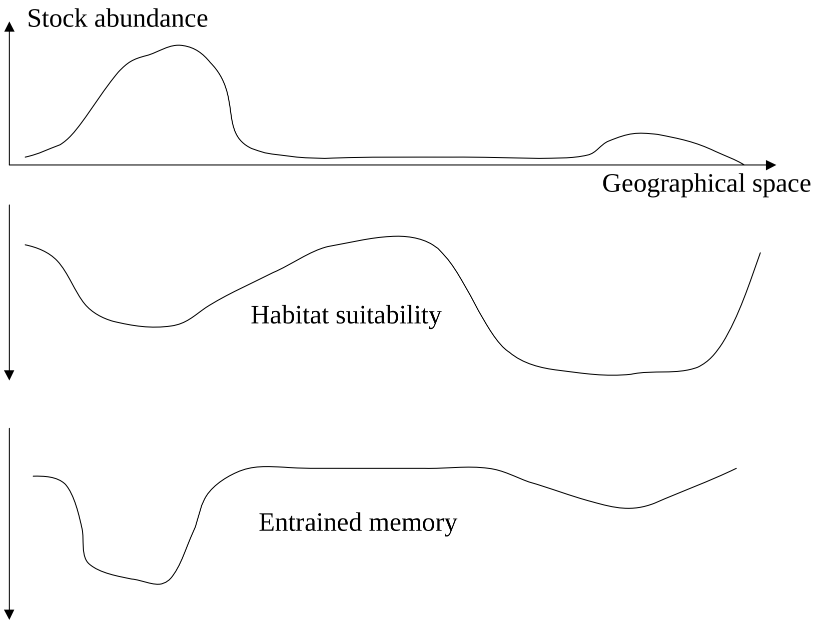

Fig. 2 : Schematic representation of the spatial distribution of a fish population as the result of a combination of habitat suitability and entrained stock memory. In such a scheme, suitable habitats may be left poorly occupied.