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ICES

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the Exploration of the Sea

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Executive Summary

What is Entrainment? Fish can learn and memorise. Entrainment is a behavioural mechanism based on fish learning from other fish to ensure that migration routes and habitat uses are maintained over generations. It can explain conservatism as well as changes in life-cycle patterns. ICES SGRESP 2006 stated the entrainment hypothesis in a way that could be tested. The objective of the workshop was to screen a variety of case study populations to support or contradict the entrainment hypothesis.

Evidence from case studies. None of the case studies were in conflict with the entrainment hypothesis. All showed overlap in size across ages as well as in space and time, which were necessary conditions for entrainment to happen. Entrainment relies on the behavioural interactions between groups of fish at certain critical periods during their life cycle. It could occur at any time in the life of a fish and for any type of migration. Major changes in life-cycle spatial patterns were related to major changes in abundance and in the proportion of naive to experienced fish. Highly abundant recruiting yearclasses could numerically dominate the standing stock, creating the opportunity for rapid changes of life-cycle patterns as a large fraction of the young fish would not be entrained to the classical migration pattern. Entrainment was demonstrated in herring by showing that spring- and autumn-spawning contingents were able to share progeny.

Patterns and mechanisms for life cycle diversity. All stocks showed internal structure with subunits and within-population life-cycle diversity. Entrainment by itself could explain the maintenance of such diversity. Other mechanisms for such diversity were reviewed, which related to physiological determinism and fitness. Terminology was revised in which contingents (groups of fish with different capabilities and life-cycle patterns) were the elementary groups of individual fish within populations. Contingency and entrainment as concepts were sufficient for the construction and maintenance of those of populations and Meta-populations. Entrainment could be an active factor in the crossover of individuals from one contingent to another. When within-population life-cycle diversity was known to relate to deterministic causes (physiological condition), entrainment was considered to behaviourally overlay these causes. Entrainment was not in conflict with other theories (e.g., partial migration, density-dependent habitat selection). Further, it had the ability to reinforce life-cycle diversity. Life-cycle diversity within populations could be maintained by entrainment without the need for genetic differentiation. Entrainment offered the possibility for a behavioural adaptation to rapidly and efficiently adapt to a changing environment.

Consequences (biological) and implications (management). A population-level consequence of entrainment was a population-level spatial memory in the occupancy of habitats. Essential habitats could change depending on the interaction between the oceanic regime and the population's spatial memory. Entrainment could act as a low pass filter in the response of populations to climate variation. Because entrainment develops a conservatism in habitat use, the occupancy of particular habitats could continue over the life time of several fish generations, even though the suitability of these habitats had become sub-optimal. Entrainment could generate non-linear effects in the response of populations to fishing. For example, the interaction between entrainment and local overexploitation could create the conditions of a vacuum effect for particular contingents. The preservation of a diversity of contingents and life cycles within populations was thought necessary to ensure population resilience and therefore should be objectives for fisheries management. This could imply spatial management measures as well as the protection of old fish. Stock collapse was associated with spatial memory collapse and contingent diversity collapse. Recovery of populations to historical abundances and habitat occupation may take much longer than forecasted by models that ignore sub-population structure and behavioural processes.

Recommendations. A theme session was recommended to review advances in the understanding of life-cycle diversity, entrainment-induced population spatial memory and their consequences. A large scale experiment was suggested to demonstrate unambiguously the entrainment and therefore establishing the importance of fish behaviour in dynamically structuring populations.

1 Introduction

In 2006, the Study Group on Regional Scale Ecology of Small Pelagic Fish (SGRESP), in examining the role played by experienced adults in maintaining diversity in life-cycle patterns within populations, had developed the « Entrainment hypothesis », to provide a theoretical framework in which to consider the effects of climate forcing and spatial structuring of fish populations on fisheries management. Also in 2006, Theme Session B at ICES Annual Science Conference on “Large-scale changes in the migration of small pelagic fish and the factors modulating such changes” (co-sponsored by PICES) offered a forum in which a variety of case study populations were presented to consider the importance of spatial management. During these meetings, the importance of testing the entrainment hypothesis on diagnostic case study populations was recognised as well as the need to challenge the hypothesis against other concepts that have been proposed in the literature to explain life-cycle diversity.

Terms of references for the Workshop (ICES resolution 2006/2/LRC11) were the following:

A Workshop on Testing the Entrainment Hypothesis [WKTEST] (Co-chairs: P. Petitgas, France, and I. McQuinn, Canada) will meet in Nantes, France from 4-7 June 2007 to:

- a) Document diagnostic case studies in pelagic, demersal and benthic fish that evidence / falsify the entrainment hypothesis
- b) Based on the above further define the understanding of the mechanisms by which life-cycle patterns are maintained or changed
- c) Report on the consequences of the understanding for spatial fisheries management and recovery plans

Ten participants met during the workshop (see Annex 1), each presenting a case study from a variety of diagnostic populations from around the world and each sharing different viewpoints on the importance of behaviour in shaping life-cycle spatial patterns.

Testing of the Entrainment Hypothesis was based on the observations presented in the population case studies. A table was made available to the participants which listed a set of sample observations that would provide consistent, supportive or demonstrative evidence. Each case study was presented, discussed and summarised. Based on the presented material, criteria were defined for evaluating the likelihood for entrainment existing in a given fish population.

The Entrainment Hypothesis was also compared to other concepts explaining life cycle-diversity which included genetic polymorphism, partial migration, natal homing, state-dependent migration and density-dependent habitat selection. These concepts were put together as non-conflicting and terminology was reviewed and revised. Consequences for spatial management and recovery plans were discussed.

2 Progress on the Terms of Reference

To explain both conservatism and change in life cycle patterns in herring populations, I. McQuinn (1997) and A. Corten (2002) suggested a behavioural mechanism resulting in spatial learning in which the young take from the old the knowledge of migration routes in the context of Meta-populations and hydroclimatic variability. The ICES CM paper 2006/B:07 (Petitgas *et al.*, 2006) formulated a similar idea as a generic hypothesis in a way that allowed for its falsification:

- 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.

2.1 ToR a): Document diagnostic case studies in pelagic, demersal and benthic fish that evidence / falsify the entrainment hypothesis

2.1.1 Approach used

The testing of the entrainment hypothesis was undertaken by assembling a series of case studies, built on data available to each investigator or from the literature. A variety of case study stocks were made available to the workshop (Table 1).

Table 1: Case studies available to the workshop

SPECIES	MARINE / DIADROM	LOCATION / FISH STOCK COMPLEX
Herring (<i>Clupea harengus</i>)	Marine	North West Atlantic herring
Herring (<i>Clupea harengus</i>)	Marine	North Sea herring
Herring (<i>Clupea harengus</i>)	Marine	Norwegian Spring Spawning herring
Sardine (<i>Sardinops Sagax</i>)	Marine	Pacific off west coast of american continent
Sardine (<i>Sardinops Sagax</i>)	Marine	South Africa
Whiting (<i>Merlangius merlangus</i>)	Marine	North East Atlantic
Anchovy (<i>Engraulis encrasicolus</i>)	Marine	Bay of Biscay
Plaice (<i>Pleuronectes platessa</i>)	Marine	North Sea
Bluefin Tuna (<i>Thunnus thynnus</i>)	Marine	Atlantic ocean and Mediterranean sea
White Perch (<i>Morone americana</i>)	Anadrom	Chesapeake bay and Patuxent river estuaries
Striped Bass (<i>Morone saxatilis</i>)	Anadrom	Chesapeake bay and Patuxent river estuaries

Since the entrainment hypothesis relies on the behavioural interactions between components of local populations or contingents at certain critical periods during their life-cycle, the case studies included a description of the life-history characteristics of each population / species to better understand the spatial dynamics of these interactions and to place the case study in the context of hypothesis testing.

To reconstruct the population life histories, investigators we requested to document:

- historic time series of biomass, demography, spatial occupation of the population, from before the collapse (if a collapse had occurred), through the collapse and the recovery of the biomass,
- life-history parameters (reproductive strategy, longevity, etc) to identify which species/populations exhibit favourable characteristics for the use of social transmission to ensure life-cycle closure,
- changes in the life cycle pattern,
- concomitant variations in the environment,
- loss and recolonisation (or not) of past habitats (feeding, wintering, spawning) with particular reference to spawning grounds.

Next, investigators were required to structure their presentations of the available data into evidence either for or against the entrainment hypothesis according to a template of data types. These data types were organized into three categories - demonstrative, supportive or consistent evidence. Evidence was considered demonstrative if the predictions of the entrainment hypothesis provided the only mechanistic explanation for the observation. Supportive evidence was defined as observations that could not be explained by any other hypothesis but for which the mechanism was not explicate. Finally, consistent evidence was not conflicting with the entrainment hypothesis, but which may also be explained by other theories. In addition, investigators were supplied with examples of data types that could be used for the testing process (Tables 2a-c) and, where applicable, with explanatory model types that could provide simulations in support or not for the predictive statements or consequences of the hypothesis (ICES SGRES P Report 2006). The workshop members then interpreted each population's historical variations (data / observations) and model results to identify evidence for or against each prediction. Finally, evidence sheets were produced for each case study where the results of each test prediction were summarized and referenced. The individual case study reports and the evidence sheets are annexed.

Table 2a: Consistent evidence. Working data and models required as consistent evidence to test various predictions of the entrainment hypothesis.

WHAT TO TEST	DATA FOR TESTING	EXPLANATORY MODEL
Overlap between adults and juveniles at a particular times and locations in the life cycle prior to first spawning.	Distribution patterns including maps of fish by age and length, and of ichthyoplankton, constructed using survey or commercial data	
Colonization of abandoned spawning grounds is predominantly by recruits.	Individual markers of colonizers : age, length, condition factor, otolith or genetic or other marker identifying population unit	
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).	Time series of seasonal surveys of habitat use	

Table 2b: Demonstrative evidence. Working data and models required as demonstrative evidence to test various predictions of the entrainment hypothesis.

WHAT TO TEST	DATA FOR TESTING	EXPLANATORY MODEL
Juveniles of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2	Individual markers (otolith, genetic, telemetry, etc.) identifying the population unit of colonizers and veteran spawners combined with life-history parameters (age, length, maturity stage, condition factor)	
Some juveniles from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism	Time series of demographics from recolonized spawning sites showing stability in yearclass-specific life-history parameters (proportions at age)	

Table 2c: Supportive evidence. Working data and models required as supportive evidence to test various predictions of the entrainment hypothesis.

WHAT TO TEST	DATA FOR TESTING	EXPLANATORY MODEL
Change in behaviour when recruits come in contact with “entrainers” : social facilitation	Acoustic schooling characteristics by age ; data on forcing parameters on behaviour including presence of predators	Conceptual behavioural IBM involving leaders and followers and meeting points
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners	Demographics of spawning-ground spatial occupation as a function of fish arrival time, maturity, length-age	
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);	Time series of distributional data documenting change or no change on spawning grounds ; environmental data documenting the hydrographic connectivity between units	Statistical, mechanistic or conceptual behavioural models involving leaders and followers or meeting points
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.	Environmental data suggesting a forcing change in the environment; abundance and length distribution of year classes; abundance, demography and spatial occupation by the veteran fish	Statistical, mechanistic or conceptual behavioural models involving leaders and followers, dispersion, meeting points or environmental guidance
Lack of age-specific genetic differences between population units	Genetic studies that examine the temporal stability of age-specific differences between units within a Meta-population	

2.1.2 Results from case studies

Each case study was analysed in detail and individual reports are annexed with their corresponding evidence sheet. In this section, the main points raised from the case studies are summarised and from them, the principle conclusions are drawn.

North West Atlantic herring

This case study provided a wide range of convincing evidence for the entrainment hypothesis. The north west Atlantic herring distributed between Cape Hatteras and Labrador is structured into several identifiable populations and each population shows internal structure. Within each population, there are various spawning contingents of which one or two dominate per population. Evidence for entrainment was demonstrated by showing that spring- and autumn-spawning contingents were able to share progeny. Significant numbers of recruits from one seasonal-spawning contingent were observed to spawn with members from the other contingent and the adopted spawning season was maintained. Consistent with the entrainment hypothesis, detailed information was gathered on how and when juveniles were ready to leave their nursery area and join the adult portion of the stock for their first annual migration cycle. Three supportive evidences were documented. Re-colonisation of Georges Bank spawning habitat was accomplished by a single strong year class, which was a large cohort throughout the Bay of Fundy and Gulf of Maine. In the subsequent years after re-colonisation, the colonisers returned to spawn accompanied by younger age classes. Overexploitation of the southern Gulf of St. Lawrence herring population led to the collapse of its dominant spawning

contingent and the autumn migration to the southwest Newfoundland coast ceased. This traditional migration pattern was not re-established, despite the rebuilding of the population to historical abundances. Entrainment could explain the maintenance of distinct sympatric herring populations when no temporally-stable genetic differences have been observed between them.

North Sea herring

This North Sea herring case study provided three strong supportive evidences of entrainment by detailing how changes occurred in spawning, wintering and feeding grounds. It described the change in a migration pattern in three steps: i) establishment of a habit (habitat colonisation) by naive individuals mainly driven by oceanographic regimes, ii) maintenance of that habit in subsequent years (habitat fidelity) together with iii) entrainment of younger individuals in the migration to the colonised grounds. The return of spawning herring to Aberdeen Bank after an absence of 16 years demonstrated the ability of a recruiting herring year-class to choose a new spawning ground, develop an attachment to it, and pass the habit on to following generations. Additional evidence came from the North Sea herring who temporarily adopted the Skagerrak as its wintering ground in 1962 - 1965. It was a recruiting year-class (1960) that took the initiative to spend the winter in this area and when it repeated the migration in subsequent years, it was followed by younger generations. The feeding period of herring in the eastern North Sea was extended in a particular year, apparently as the result of a prolonged *Calanus* season. Herring adopted the habit of staying in the eastern North Sea until June instead of May. They continued this habit for some years after the *Calanus* season had shortened again.

Norwegian spring spawning herring

The impressive changes in the choice of wintering grounds of Norwegian spring-spawning herring provided supportive evidence for the entrainment hypothesis. The case study also showed a combination of physiological determinism and entrainment in the colonisation and maintenance of far-away spawning grounds. The stock distribution pattern was characterised by the separation between the immature fish located in the Barents Sea and the spawning part of the stock located off the coast of Norway. The recruit spawners entered the life cycle of the mature fish when they overlapped on the feeding grounds after spawning and prior to overwintering. The stock experienced collapse and full recovery in abundance. Major changes were observed in the wintering areas and spawning areas. Changes in wintering areas were always associated with very high recruit year classes. New wintering grounds were established by recruit spawners that were numerically dominant and could not all be entrained by the less abundant elderly fish. Simulations from a behavioural individual based model were supportive in explaining the breakdown of entrainment by elderly fish because of the numerical dominance of the recruits. When the stock rebuilt and was made up of more elderly fish, spawning migrations were observed to vary depending on the length and condition factor of the fish, with larger fish in good condition undertaking the longest migrations. Far-away lost spawning grounds were re-established by particular contingents. However, these fish may have been raised in these far-way nursery areas which afforded superior growth conditions, and were simply returning to the associated spawning areas with the adults that had entrained them. Once re-established, fidelity was established to these grounds. Entrainment may overlay deterministic causes for the spawning migration.

Pacific american sardine

This Pacific sardine case study showed consistent evidence for the entrainment hypothesis. Overlap in lengths across ages and aggregation of fish by size rather than age were detailed. Recovery of migration routes and habitat use with the rebuilding of the stock was consistent

with entrainment but could also be explained with density-dependent selection. At the historical high abundance level, the stock was distributed from Baja California (Mexico) to British Columbia (Canada). In the northern part, only large fish occurred seasonally as the result of a feeding migration. The small fish were closer to the coast while the large fish that undertook large north-south migrations were off-shore. The stock experienced collapse and remained at low abundance levels for 20 years. It remained off California and rebuilt from that area, which has been understood to be a core area. Rebuilding was due to high recruitment of particular year classes. As they aged, these fish began to undertake the large north-south migration again and were again observed in British Columbia. In subsequent years, they entrained younger fish into that migration. The stock seemed to rebuild in a spatial configuration similar to that of prior to the collapse. However, density-dependent habitat selection could explain contraction and expansion with abundance. Entrainment had explanatory power in the way migration patterns rebuilt.

South African sardine

The entrainment hypothesis provided a coherent interpretation of the historical variations observed in the spatial organisation of South African sardine. This case study also illustrated the possibility of negative and non-linear effects of entrainment. The stock was composed of two sub-units in the west and south east of the Cape of Good Hope. The west supported larger recruitment than the south east because of its oceanographic regime. This population experienced collapse due to fishing. The fleets were based in the west and fishing pressure was high in the west. Total stock abundance rebuilt to the high levels seen prior to the collapse but the spatial configuration of the stock changed. Prior to the collapse, the western component was the largest while after the collapse the south-eastern component was more developed. A shift of the adult stock to the south east was observed. Rebuilding occurred due to high recruitment in the western part, but the adult part in the west stayed depleted. The entrainment hypothesis explained a capturing effect of the western recruits by the south east adults, thus building up the south east component and leaving the western component depleted. Overlap in lengths across ages and as well as in space provided conditions consistent for entrainment to occur. The maintenance of high fishing pressure in the west reinforced the capturing effect. According to this scenario, spatial management restricting fishing in the west to a point where adults can again entrain recruits would be a means to rebuild the western component of the stock.

Atlantic bluefin tuna

In this case study the disappearance of particular fishing grounds of Atlantic bluefin tuna was revisited using evidence consistent with the concepts of contingent structure and entrainment. Despite a pan-oceanic distribution, spawning habitats of Atlantic bluefin tuna are hypothesized to be restricted to the Gulf of Mexico and the eastern Mediterranean Sea. The high maintenance demands of tuna engender a higher dependency on exploratory behaviours to attain sufficient energy, suggesting the existence of a variety of contingents within the population. Important historical fisheries persisted off Brazil and Norway in the 1960s, but abruptly disappear in the 1970s. These fisheries at the southern and northern border of the fish distribution may have exploited particular contingents that were lost. Once lost, conservatism of migration pathways within other contingents could have precluded reinvasion of these historical feeding areas. Thus, the lack of recovery of these contingents is consistent with the idea of conservatism of entrained migratory pathways.

Anadromous sea bases

This case study of anadromous sea bases showed how the partial migration theory can be combined with the entrainment hypothesis. Entrainment is a consequence of behaviour that

overlays the physiological and genetic capabilities of fish. For striped bass and white perch, freshwater estuarine dependency during the larval stage is obligate. However, during sub-adult and adult stages, the two species exhibit patterns of estuarine and/or coastal habitat use which leads to the identification of 'contingents' (groups of fish) within populations. Contingents mix for reproduction. The divergence in behaviours by either migratory or sedentary contingents occurs early in ontogeny, which suggests an early switchpoint, consistent with a conditional strategy or partial migration. But observed mid-life changes in migration behaviours are less easily explained by a conditional strategy and are consistent with the entrainment hypothesis. Here resident individuals overlap in distribution with migratory individuals during the spawning season when contingents mix. Certain individuals could adopt the alternate contingent's behaviour. White perch or striped bass could be cases on which the entrainment hypothesis could be experimentally test.

North East Atlantic whiting

By comparing North Sea whiting and Western whiting stocks, this case study showed how populations may be phenotypically differentiated without any genetic structure. The life history characteristics of whiting (extended spawning season, high fecundity and long pelagic life of larvae) potentially ensure high connectivity between population units over large distances. Also, fast growth and inter-individual variability in growth induces a large overlap in size between year classes. In the North Sea, a differentiation between northern and southern units was identified using phenotypic and genetic markers as well as parasites, indicating little genetic transfer. Also, an oceanographic retention system prevented straying from one unit to the other at the larval stage. In contrast, to the west of the British Isles, phenotypic differentiation was evidenced using parasites but no genetic structure was found. Fidelity to the spawning sites associated with straying at the larval drift stage was concluded. Juveniles arriving to one unit would thus adopt the habit of that unit. The Entrainment hypothesis has explanatory power on the paradoxical subpopulation structures of whiting.

Bay of Biscay anchovy

This case study analysed how the schooling behaviour of Bay of Biscay sardine may differ when juveniles are independent from adults or mixed with adults and discussed the implications of these observations for survival and the recolonisation of habitats. Since the 1960s, the population has experienced major changes. Catches have decreased, fishing grounds have changed and habitats have been lost. Larvae which drift from major spawning grounds are believed to seed the lost habitats but re-colonisation is not occurring. Juvenile anchovy independent from the adult part of the stock formed schools that were different from those in which they were mixed with adults. A mechanism is proposed where the adult fish entrain the young into a particular schooling behaviour that is adapted to habitat use with sufficient survival. Overlap in length across ages and mixing at night between the young and the old at the surface in coastal waters was observed which is consistent with the possibility of entrainment.

Conclusions

None of the case studies were in conflict with the entrainment hypothesis. All showed overlap in size across ages as well as in space and time, which were necessary conditions for entrainment to happen. Entrainment relies on the behavioural interactions between components of contingents at certain critical periods during their life-cycle. It could occur at any time in a fish's life and for any type of migration. Long-lived species which form multiple age-structured populations and have a strong tendency for schooling afford good opportunity for entrainment.

Major changes in life-cycle spatial patterns were related to major changes in abundance and in the proportion of naïve to experienced fish. Highly abundant recruiting yearclasses could numerically dominate the standing stock, creating the opportunity for rapid changes of life-cycle patterns. Entrainment ensures knowledge transfer of suitable habitats across generations and creates traditions. The counter part is that potentially suitable habitats may stay unused. Many examples of unused habitats exist in nature. Entrainment creates inertia in the response to change. But the lack of entrainment, e.g. in the face of numerical domination by naïve recruits, can produce novelty (the establishment of a new tradition) when young fish are disconnected from older fish. Disconnection can also be forced by important changes in the environment or in the demography within the population (strong year class, population collapse).

A population level consequence of entrainment is the development of a spatial memory for migration routes and habitats uses. The existence of a population spatial memory influences the population's relationship with its environment. Entrainment could act as a low pass filter in the response of populations to climate variation. Because entrainment develops a tradition, the occupancy of particular habitats could continue over the life time of several fish generations even though suitability on these habitats has become sub-optimal. To predict the spatial distribution of populations, density-dependent models of habitat occupation could be further developed to combine habitat suitability functions with population spatial memory functions.

All stocks showed internal structure with subunits and life-cycle diversity. Entrainment by itself could explain the maintenance of such diversity. When this diversity was known to be based on deterministic causes (physiological condition), entrainment was considered to be overlaid on these causes. Entrainment was not in conflict with other theories explaining life-cycle diversity by deterministic causes (e.g., partial migration, density-dependent habitat selection). It had the ability to reinforce life-cycle diversity. Life cycle diversity within populations could be maintained by entrainment without genetic differentiation.

2.2 ToR b): Based on the above further define the understanding of the mechanisms by which life-cycle patterns are maintained or change

Though patterns for life-cycle diversity within populations have been documented, mechanisms explaining their establishment and maintenance are scarce. Entrainment suggests such a mechanism and through the workshop, was compared to other population structure theories. In doing so, terminology was revised and population concepts revisited.

2.2.1 Possible mechanisms for life-cycle diversity: entrainment versus partial migration

In contrast to the fish literature, avian studies emphasize alternate life cycles, largely due to wide-scale adoption of partial migration theory. Partial migration is a central theory in describing the evolution, control, and adaptability of bird migration behaviour (Berthold 2001). In partial migration, one portion of a population is migratory and the other portion is sedentary (Berthold 2001). Partial migration is further sub-divided into two types: 1) facultative, under environmental control; and 2) obligate, under both genetic and environmental control (Terrill and Able 1988, Berthold 1996). Obligate partial migration is believed to be the most prevalent control of bird migration and is thought to be maintained through a conditional strategy (Berthold 2001). Thus, the coexistence of migratory and sedentary life history tactics in a single genetic population is a function of an individual's fitness relative to the tradeoffs associated with each behaviour (Lundberg 1988).

Partial migration theory has been adopted to describe the diversity of migration patterns observed in Salmonidae, but has not been widely applied outside this family. Similar to birds,

the choice of alternative habitat use (resident vs. migrant) within many Salmonid populations is hypothesized to be under the control of a genetically-defined developmental switchpoint, or conditional strategy. Individual growth rate relative to a growth threshold serves as a cue to initiate migration if the current habitat is not meeting the individual's needs (Thorpe 1989, Thorpe *et al.* 1998, Mangel 1994). Similarly, migratoriness is conferred during the juvenile phase of birds (Berthold 2001). Thus partial migration is regulated by early developmental switchpoints related to growth rate, condition, or behaviour (e.g., feeding hierarchies) that have life-time consequences in terms of spatial behaviours.

Atlantic herring populations show a diverse pattern of intra-population spawning habitat use, which has stimulated debate on population structure, life-cycle closure, and alternate migration behaviours in this species (Iles and Sinclair 1982; Sinclair 1988; McQuinn 1997). There is recent interest and strong circumstantial evidence for the role of learned behaviours in conserving multiple migration circuits within herring populations. The so-called "adopted-migrant" or "entrainment" hypotheses postulate that behaviours associated with a particular life-cycle circuit are adopted by juveniles (sub-adults), learned from adults during periods of spatial overlap (McQuinn 1997; Corten 2002; Petitgas *et al.* 2006). Orientation behaviours are learned and reinforced through the association of multiple-age classes. Thus, a certain number of juveniles are entrained into an already established life cycle. Without association with older age classes, juveniles can establish novel migration circuits through exploration, although the adoption of novel life circuits is expected to be much less efficient than the adoption of already established circuits.

As populations decline, behavioural entrainment into minority groups becomes less efficient and entire circuits and associated patterns of habitat use can be lost to the population. As a population expands, density-dependent habitat selection can promote exploration of new habitats and establishment of novel migration circuits by juveniles. The entrainment hypothesis has been used to explain diverse patterns of winter, forage, and spawning habitat use in Norwegian, North Sea, and east-coast North American populations of Atlantic herring and could have more general application for other coastal species (Petitgas *et al.* 2006).

Partial migration and behavioural entrainment are complementary ideas in that they account for life-cycle diversity through a polyphenic response rather than a genetic polymorphism. For instance, following an initial threshold condition, a juvenile undertakes a migratory rather than a sedentary behaviour. Thereafter, later in life the individual behaviourally entrains into one of several migration circuits through its interaction with already entrained age-classes in a common wintering or feeding habitat. Genetic polymorphism – the idea that different life cycles represent discrete sub-populations - must be maintained through isolating mechanisms such as preferential mating. Sub-population structure has been associated with sedentary and migratory components of populations of Atlantic salmon and Atlantic cod, but results have been inconsistent for the same study populations or for other populations of the same species (Ruzzante *et al.* 1997; 2000; Verspoor and Cole 1989; Jonsson and Jonsson 1993; Beacham *et al.* 2002; Klemetsen *et al.* 2003).

Terms describing life-cycle diversity are numerous but centre on a dichotomy of migratory and sedentary descriptors. Partial migration theory fits well with the observed sedentary and migratory life cycles in diadromous and other types of fishes. In contrast, the entrainment hypothesis is more general in its application and indicates that modalities are not necessarily centred on sedentary and migratory behaviours and that more than two life cycle modalities can exist within populations.

Table 3a. Comparison of two theories related to life-cycle diversity in marine fishes: Background and conception of population life-cycle organisation

ENTRAINMENT HYPOTHESIS	PARTIAL MIGRATION HYPOTHESIS
Background	
Atlantic herring and pelagic schooling fish	Salmon and other anadromous fishes
Increased evidence of life-cycle diversity with historical records of landings, surveys and science on herring.	Increased evidence of life-cycle diversity with improved longitudinal approaches for tracking fishes.
Theory related to schooling and learned behaviour in animals. Life-cycle and Meta-population evolutionary constructs.	Theory related to mating systems in birds (Berthold's partial migration theory) and salmon (Thorpe's developmental programme). Life-cycle and Meta-population evolutionary constructs.
Emphasis on linking diversity in spawning units to conservatism of life cycles.	Emphasis on linking diversity in life-cycles to conservatism in spawning unit.
Conception of Population Life Cycle Organization	
Different spawning units share nursery, feeding, wintering habitats	Same spawning unit uses different nursery, feeding, and wintering habitats
Overlap of juvenile and adult habitat permits opportunity for adopted migration behaviour	Sedentary/dispersive behaviours during first year of life result in divergent life-cycles
Juveniles that do not adopt an adult behaviour are vagrants and can establish novel habitats	Dispersive contingent more likely to colonize new habitats or stray into adjacent populations
Life-cycle closure achieved through entrainment	Life-cycle closure achieved through natal homing

Table 3b. Comparison of two theories related to life-cycle diversity in marine fishes: Statement of hypothesis.

ENTRAINMENT HYPOTHESIS	PARTIAL MIGRATION HYPOTHESIS
Statement of Hypothesis	
Conveyance and conservatism of migration behaviour: repeat spawners to recruit spawners	Adoption of migratory behaviour during first year of life, with subsequent conservatism of life -cycle throughout sub-adult and adult period.
Adult/juvenile encounter takes place in habitat of life stage mixing	Conditional responses to environmental conditions (thresholds and developmental switches result in conservatism of life-cycle behaviours). Some studies also indicate migratory modes represent polymorphism.
The dominant spawning unit will influence the dominant life cycle pattern.	Environmental factors during the first year of life will influence the frequency of life cycle pattern in a year-class. Overlapping generations will determine how climate and other conditions affect frequency of life cycle patterns in the population.
Entrained migration is critical to philopatry and population persistence and therefore is a selected behaviour.	Sedentary and dispersive behaviours represent key components of population resiliency and growth; polyphenism is selected due to environmental variation.
Vagrancy occurs.	Straying occurs.

Table 3c. Comparison of two theories related to life-cycle diversity in marine fishes: Explanatory power.

ENTRAINMENT HYPOTHESIS	PARTIAL MIGRATION HYPOTHESIS
Explanatory Power	
Conservatism and persistence of alternate life-cycles	Persistence of alternate life-cycles
Juveniles are colonizers – leading to Meta-population consequences	Dispersive contingent members are colonizers – leading to Meta-population consequences
Inertia due to conservatism (memory loss) can lead to collapsed (empty) spawning, feeding, winter habitats despite population recoveries.	Shifting environments (climate) can lead to collapse of one or the other contingent.
High densities affect adoption of alternate life-cycles and can lead to increased vagrancy.	High densities affect adoption of alternate life-cycles and can lead to increased vagrancy.
Low densities of adults will reduce entrainment and cause increased vagrancy.	Low densities of adults will cause increased prevalence of the sedentary contingent.

Table 3d. Comparison of two theories related to life cycle diversity in marine fishes: Evidence

ENTRAINMENT HYPOTHESIS	PARTIAL MIGRATION HYPOTHESIS
Consistent Evidence	
Overlap of juveniles and adults	Early deliberate migratory behaviour of component(s) of a year-class during first year of life.
Non-recovery of spawning units	Oscillations of contingent prevalence related to environmental conditions
Juveniles more likely to colonize	Dispersive contingent more likely to colonize
Supportive evidence	
Change in behaviour in juveniles when alternative life cycles mix at critical stages	Persistent contingent behaviours across ontogeny.
Demonstrative evidence	
Longitudinal approaches for tracking migrations of first spawners and repeat spawners from differing spawning units.	Longitudinal approaches for tracking migrations ontogenetic migrations among juveniles that showed differences in condition, growth, spawn-dates.

Table 3e. Comparison of two theories related to life cycle-diversity in marine fishes: Consequences and conciliation

ENTRAINMENT HYPOTHESIS	PARTIAL MIGRATION HYPOTHESIS
Consequences	
Biomass reference point inadequate. Stock dynamics depends on age structure (storage effect) and spatial population sub-structure. Age structure effect due to variable behaviours of juveniles relative to adults (critical encounters).	Biomass reference point inadequate. Stock dynamics depends upon age structure (storage effect). Age structure effect due to inter-annual variations in contingent structure (cohort-splitting).
Modelling Frameworks	
Ideal Free Distribution, Basin Model, Viscosity (memory)	Delay Difference Model (Deriso 1980, Hilborn and Mangel 1997; Fogarty 1988; Porch 2003).
Response to Environmental Change	
Both conservatism and innovation in life cycles selected for.	Both conservatism and innovation in life cycles selected for.
Conciliation between the two Hypotheses	
Both developmental thresholds and entrained behaviour can occur in an ordered way and could be modelled through a dynamic programming approach (Mangel and Clark 1988). For instance, entrainment could occur after a developmental threshold determined a migratory behaviour. Otolith chemistry and electronic tagging does indicate that mid-life changes in migratory behaviour can “go against” early migratory patterns.	

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2.2.2 Glossary

Entrainment is a behavioural mechanism which is overlaid on top of innate and conditional-response mechanisms for the determination of life-cycle patterns. As such, the entrainment hypothesis offers a different perspective to explain the development of relationships between individuals in a population. In this light, concepts describing populations and their sub-structure were revisited and are redefined here.

Contingents: A contingent is a group of fish that have similar phenotypic capabilities and which form a behavioural entity. The diversity of contingents may result from genetic polymorphism, long spawning season, and an individual fish’s early-life history. Each year class may separate into one or more contingents. Individual fish may switch from one contingent to another during their life time depending on spatio-temporal overlap between groups of fish and individual capabilities. Contingents are elemental behavioural units that spatially embark on elemental life cycles. Examples of contingents at the workshop were: sedentary and migratory contingents in diadrom populations, spawning units in herring stocks, coastal resident and off-shore migratory groups in sardine stocks, and groups with fidelity to spawning and feeding grounds (plaice).

Entrainment: Entrainment is a behavioural property resulting from the spatial learning ability of fish to acquire information about their environment from other fish. Entrainment is a capturing mechanism of fish by a group of other fish. The entrained fish will undertake the

life-cycle pattern of its entrainers. An individual fish may be entrained at different moments of its life. Fish will normally be entrained into the life-cycle pattern of already existing contingents of elderly, experienced fish. The biological consequences of entrainment are the generation of traditions and re-enforcement of current life-cycle patterns. Non-entrainment (e.g., vagrancy) of large numbers of individuals will generate novelty in life-cycle patterns.

Population: A population is composed of a number (one or more) of contingents, whose genes are nonetheless mixed to various degrees at each reproduction to form a new cohort. The degree of mixing between contingents depends on their connectivity. Mixing can result either from larval dispersal and subsequent mixing of juveniles on nursery grounds as well as homing of different contingents to a common spawning ground or sufficient exchanges of individual fish between contingents (contingent switching). A population is then not a predefined unit but a resultant unit.

Meta-population: A Meta-population is a set of populations that are connected. Connectivity may happen at different moments of the life cycle: larval dispersal or contingent switching. Gene mixing between populations of a Meta-population may not occur at each reproduction. Fish stock complexes (e.g., such as herring may form) are populations comprising well defined contingents with different life-cycle patterns. Depending on abundance levels due to recruitment variability, Meta-populations can be grouped as one population for certain periods of time. Conversely in the case of population collapse, strong recruitment or environmental forcing, contingents may disappear, reappear or separate into unit populations.

Contingency (life-cycle diversity) and connectivity between contingents (e.g., via entrainment) as concepts are sufficient for the construction and maintenance of populations and Meta-populations. Genetic differentiation (generally poor in marine stocks) is not required to maintain structured populations with defined contingents.

When different contingents mix spatially during their respective life cycles, each individual may be entrained into another contingent and join its life-cycle depending on its capabilities at that time. The within population diversity of contingents will result in making available to each individual at various stages in its life a portfolio of life-cycle options. Oceanic regimes, contingent diversity, and entrainment are factors that modulate population structuring. Therefore population internal structure (life-cycle diversity) should be understood as a resultant property. Population internal structure is then dynamically updated depending on population demographic history and environmental variability.

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2.3 ToR c): Report on the consequences of the understanding for spatial fisheries management and recovery plans

Implications of entrainment on recovery plans and spatial management strategies were only briefly discussed at the workshop and this section summarises the discussion notes.

2.3.1 Management of the within population diversity

Previous sections of the workshop report have shown that entrainment can explain how population structure is dynamically updated without the need for genetic differentiation, each time there is a major change in the environment or in population demography.

Contingent diversity within populations and connectivity between them via entrainment are key elements in the hypothesis for ensuring population resilience. Therefore within population contingent diversity and its network of connectivity should be preserved and formulated as management objectives.

Currently, population abundance levels are managed using TAC. In some cases, special measures are applied for the preservation of young fish but the preservation of old fish is not generally seen to be important. Not only do old fish represent a higher reproductive potential, but their accumulated knowledge is essential to conserve the population's diversity of suitable life cycles. Therefore, a balanced population structure is believed to be a sound management objective, which could be obtained in various ways, including area closures.

Protection of a variety of habitats may protect the diversity of contingents. A network of habitats should be preserved rather than one habitat defined as essential. Essential habitats are defined for a particular stock configuration (contingent diversity and connectivity) and can change depending on population structure and climate change. The management unit should thus be the contingent rather than the population (see section 2.2 where populations are described as networks of connected contingents) and management measures should aim to conserve contingent diversity (e.g. spatial quota limits and habitat protection).

Another suggested management objective was analogous to the spawning potential per recruit (SPR). In the context of within population contingent diversity, the comparable quantity would be NRSPR (number of repeat spawners per recruit). Similar to SPR, management may want to avoid having NRSPR fall below some percentage of the virgin stock level, in order to ensure sufficient intergenerational knowledge transfer.

2.3.2 Entrainment-based scenarios for population recovery

After a population has collapsed due to overfishing, some contingents may disappear or the numerical dominance between contingents may be significantly modified. Rebuilding of the population will rely on the abundance and behaviour of recruiting year classes and the resulting life-cycle patterns will develop in a way that is a function of the connectivity and dominance between contingents. The recruits may get entrained into the life cycle of the most dominant post-collapse contingents, thus reinforcing the new spatial organisation of the population (e.g., South African sardine). In this case, entrainment may result in a vacuum effect of particular contingents that cannot recover to their historical abundance level. It will take a very abundant recruiting year class to generate the required disconnection between the young fish and the established contingents to enable the re-colonisation of lost habitats or the colonisation of novel ones (e.g. Norwegian spring-spawning herring, North west Atlantic herring). Re-colonisation of habitats is conceived as a difficult process with potentially high mortality as no experienced fish can play the role of facilitators (ex: Biscay anchovy). A population may rebuild to its historical abundance but with a different spatial organisation

than its historical one (e.g. all case studies, except Pacific American sardine. In this latter case, full recovery of the spatial configuration was observed after more than 30 years).

Accurate recovery predictions of collapsed populations were expected to require spatial population models that combined environmentally-induced habitat suitability with population history-induced spatial memory. Recovery of populations to their historical status (abundance and habitat occupation) could take much longer than forecasted by models that ignore within-population contingent diversity and behavioural processes ensuring connectivity between contingents (entrainment). The time horizon for recovery was thought to vary between populations, depending on contingent diversity, connectivity in the collapsed state and frequency of high recruitment events. For example, north west Atlantic cod was hypothesised to recover with a longer time horizon than north west Atlantic herring, as very high recruitment events are infrequent in cod and contingents have little overlap, reducing the possibility of numerical dominance by recruits and ensuring strong conservatism to life-cycle patterns within collapsed contingents.

3 Recommendations

The group felt that SIMWG should review the present work and consider the planning of large-scale experiments tracing individuals from different contingents to demonstrate the entrainment hypothesis.

WGLESP should also review the present work and consider continuing the study of the mechanisms for persistence and change of infra-population diversity, its population level consequences and its modelling.

The group thought it worthwhile to propose an article in the ICES newsletter to further communicate its ideas, as behavioural capabilities of fish may have strong impacts on internal structure of populations, on recovery plans and on spatial management that were not fully explored here. The co-chairs will be in contact with the secretariat to discuss how to proceed.

The group also thought it worthwhile to publish the workshop findings as a Cooperative Research Report. The co-chairs will be in contact with the secretariat and the Living Resources Committee to discuss how to proceed.

WKTEST liaised with SIMWG and suggested a Theme Session for ICES ASC in 2009. Title: “What do fish learn in schools? Life cycle diversity within populations, mechanisms and consequences”. Co-chairs: Dave Secor (USA), Pierre Petitgas (France), Ian McQuinn (Canada), Steve Cadrin (USA). Synopsis: Depleted fish stocks, degraded habitats, and uncertainty in forecasts of future ecosystem states emphasize the need to include the notions of resilience and associated life-cycle diversity as objectives for fisheries management. Life-cycle diversity within populations and knowledge transfer between generations are increasingly recognized as factors that can influence population resilience and thus fishery and habitat recovery actions. Concepts explaining life-cycle diversity within populations and its persistence include genetic polymorphism, partial migration, and social transmission of learned migration behaviour. Although life-cycle diversity is increasingly recognized as a pattern common across diverse fish taxa, mechanistic studies and concepts explaining this diversity are nascent. Further, relatively little attention has focused on the consequences of this diversity in particular for population resilience, spatial management strategies and recovery plans. Across marine and diadromous fishes, papers are welcome on the following topics: life cycle diversity within populations, its persistence and change; conditional strategies leading to partial migration; social transmission of habitat use; population genetic structure and polymorphism; population-level effects of infra-population diversity; mechanisms for population resilience; recovery plans accounting for spatial effects; spatial management strategies accounting for essential habitats.

Table of recommendations

RECOMMENDATION	ACTION
1. Publish in an ICES Cooperative Research Report the material compiled by WKTEST that support the entrainment hypothesis	ICES
2. WKTEST 2007 report should be reviewed by SIMWG and WGLESP in 2008 to further progress on the mechanisms and consequences of life cycle diversity within populations	SIMWG and WGLESP
3. Convene a Theme Session at ICES 2009 ASC on “What do fish learn in schools? Life cycle diversity within populations, mechanisms and consequences ”	LRC

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Annex 2: North West Atlantic herring (by Ian McQuinn)

Introduction:

The entrainment hypothesis has evolved in large part from the adopted-migrant hypothesis (McQuinn, 1997b) which was developed upon evidence drawn from populations of northwest Atlantic herring and is documented for the most part in the literature. However, to be consistent with the approach of WKTEST to structure the evidence for the entrainment hypothesis around a series of case studies and to add relevant information from the intervening 10 years, the available documentation has been summarized here.

Background:

Six populations of northwest Atlantic herring have been described (Hay *et al.*, 2001) between Cape Hatteras and Labrador (Figure 1). These population delineations are based more on a consensus of accumulated information than on proof of clear inter-population independence. However, for the purposes of this case study, we will use the divisions described in Hay *et al.* (2001) to identify populations.

Within each of these populations, there are various spawning contingents (see Glossary) of which one or two dominate per population. For example, along western Newfoundland, there are groups of herring spawning at one time or another from April to October, although the main spawning activity occurs in May and in August-September, defining the two main contingents, i.e. spring and autumn spawners. Within most of the six populations there are spring and autumn contingents, although in general, the spring contingents dominant in the north and the autumn contingents dominate in the southern populations. With few exceptions, these contingents are assessed and managed separately, although they are often found and fished in mixed aggregations, making application of independent management measures difficult.

Within each population, both main contingents have shown large fluctuations over the past several decades of commercial fishing (Figure 2). Fluctuations in population biomass can be by orders of magnitude, principally due to large fluctuations in recruitment (Figure 3). These north-western Atlantic herring populations are characterised by intermittent recruitment pulses which are more infrequent in time but more variable in abundance towards the northern extent of their range. For example, in western Newfoundland, a strong recruiting yearclass rebuilds this population about every 10 to 12 years (McQuinn *et al.*, 1999), while in the south-western Nova Scotia, the variability of the recruitment pulses is lower and the frequency is in the order of 4 to 6 years (see Power *et al.*, 2006). This leads to a paradoxical situation where, at least in the northern populations, the surplus production (net gain or loss in population growth before fishing) can be negative for several years between recruitment pulses, resulting in a natural decline in the population biomass in the absence of fishing (Figure 4).

These herring can be considered as shelf and coastal herring (Parrish and Saville, 1965), given that their annual migrations cover distances in the order of a few hundred nautical miles and they remain within approximately a hundred nautical miles of the coastline on the continental shelf or in some cases within more restricted geographic areas (e.g. Bras d'Or Lake herring). For example, western Newfoundland herring appear to spend their entire lives within approximately 10,000 sq. nautical miles (Figure 5) moving up and down the coast from spring to autumn, and then offshore into deeper waters to overwinter.

Demonstrative evidence:

Juveniles of unit 1 adopt the spawning behaviour of the adults of unit 2.

McQuinn (1997a) showed evidence that spring- and autumn-spawning contingents were able to share progeny and therefore formed a single Meta-population. By comparing the hatching season from their otoliths characteristics with the spawning season determined from maturity stages of spring- and autumn-hatched individuals, he showed that significant numbers of recruits from one seasonal-spawning contingent spawned with members from the other contingent (Table 1). Therefore the season within which a herring was spawned and hatched was not necessarily the season in which it ended up spawning. He also showed evidence by following the growth trajectories of mature spring and autumn spawners that the adopted season was maintained after the initial spawning since a significant length difference between the two spawning contingents with the same seasonal origin persisted until at least age 6 (Figure 6). Therefore, if a herring could change its reproductive season, these spring and autumn contingents were not discrete populations.

McQuinn (1997b) developed this hypothesis further within a Meta-population concept, suggesting that exchange between local herring populations, whether seasonal spawning contingents or sympatric populations with different spawning locations constituted local populations within a Meta-population.

Supportive evidence:

Temporal and spatial segregation patterns between repeat and first spawners on spawning sites

Herring spawn in waves over a protracted spawning season: the older herring usually spawn first, with the younger herring and recruits spawning in subsequent weeks and months (see Lambert, 1987 and references therein). Besides inferring an intra-seasonal iteroparity to their reproductive strategy, it affords an opportunity for young and naïve spawners to learn spawning and feeding migration patterns and spawning areas, if not actual spawning sites.

In the southern Gulf of St. Lawrence herring, the length (and age) of ripe mature herring arriving at the spawning grounds decreased over the spawning season as older herring matured earlier and arrived earlier on the spawning grounds (Lambert and Messieh, 1989). There was nonetheless an overlap in length distributions of the various yearclasses which is necessary for entrainment to occur.

Lack of age-specific genetic differences between population units

There is a long history of genetic studies on herring populations, using a variety of techniques. To date, no clear patterns of population delineation have been suggested, except perhaps over large geographic distances (NE versus NW Atlantic) or between extremes in morphs (e.g. Baltic (proper) herring versus Atlantic (proper) herring) or geographically isolated populations (e.g. Bras d'Or Lakes, Nova Scotia). No temporally-stable genetic differences have been observed between sympatric herring populations. However, with the development of more powerful techniques, statistically significant differences have occasionally been found within and among contingents (e.g. McPherson *et al.*, 2004), even between spawning waves (McPherson *et al.*, 2003), i.e. different cohorts spawning on the same site, within a one-week interval. However, the differences are rarely if ever found to stand up over repeated samplings (one year to the next), i.e. the inter-annual variability is as high as the inter-population variability, and suggests a genetic population substructure that is nonetheless transient on the scale of generations. For example, this instability in the measurement of within-population genetic differentiation may be due to non-random mixing of individuals within the population (e.g. Hay and McKinnell, 2002), resulting in non-random sampling. As noted above, herring arrive and school in spawning areas according to size, and possibly by "conspecific association" (Hay and McKinnell, 2002). Therefore a sample of a single school will not

necessarily be a random sample of the population. Statistically significant genetic differences between samples on the same spawning site 6 days apart suggest that non-random mixing does occur and that there is low-level and possibly ephemeral genetic structure within Meta-populations.

Consistent evidence:

Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.

In western Newfoundland, the spring contingent concentrates spawning activities in May in the southern bays close to shore, where the surface waters warm first in spring, while the autumn contingent spawns in deeper water more towards the north in August and September. Nursery areas are not well inventoried, but in general, juveniles are known to remain inshore in the large bays close to where they were hatched (Figure 7) and thus juveniles of the two contingents are separated geographically.

McQuinn (1997b) showed that the overlap between the entraining adults and the adopted juveniles occurs “after each spawning event, the spent adults entrain from the nursery areas those juveniles who are ready to undertake their first annual migration”. Each year, there is an influx of immature recruits into the commercial catch in the fall after spawning, most notably observed when a strong yearclass recruits to the population (McQuinn and Lambert, 1991). Consistent with the entrainment hypothesis, the most efficient period for entrainment to occur is when the recruiting juveniles are ready to leave their nursery area to begin their first annual feeding and over-wintering migration.

Colonization of abandoned spawning grounds is predominantly by recruits.

Georges Bank supported the largest herring fishery in eastern North America (Hay *et al.*, 2001) until it was fished to commercial extinction in the late 1970's. Although the fishery reopened in 1994, signs of population rebuilding began in 1986. Survey data support the theory that herring recolonised the Georges Bank region in stages during the late 1980s from adjacent components, most likely herring spawned in the Gulf of Maine (Smith and Morse, 1993; Overholtz and Friedland, 2002). Bottom trawl samples showed that the recruits to the bank were almost entirely from the 1983 yearclass (Stephenson *et al.*, 1990), which was a large cohort throughout the Bay of Fundy and Gulf of Maine. In 1987, survey catches showed spawning activity (larval herring) and an expansion of the age structure of the spawning population by subsequent cohorts who were entrained onto the bank by the 1983 yearclass.

Modification of migration route, feeding and/or wintering area usage patterns follows a population perturbation (boom, collapse, environmental shift).

In the 1960s and 1970s, the southern Gulf of St. Lawrence herring population was subjected to a 100,000+ t annual fishery. At that time, this large population underwent a regular autumnal migration to the southwest coast of Newfoundland (Figure 8), where it was again heavily exploited during the winter for meal oil (Winters and Hodder, 1973). Various morphometric, meristic and tagging studies confirmed the southern Gulf origins of these fish (Winters and Beckett, 1978). Overexploitation led to a greatly-reduced biomass of the autumn-spawning stock (the dominant contingent) in the mid-1970s (Leblanc *et al.*, 2006), dropping to below 10% of its historical abundance by 1980 (see Ahrens, 1985) to a point where only 10% of the catch at age was from herring older than age 6 (see Cleary, 1983). During this time, their autumn migration to south-western Newfoundland ceased and catches dropped to zero in this area by 1974 (Winters, 1978). This traditional migration pattern has not been re-established, despite the rebuilding of the population in the late 1980s and 1990s to historical abundances.

Discussion and Syntheses:

This evidence has been summarised in the annexed Evidence sheets. Taken together, there is quite convincing support for the entrainment hypothesis to explain the patterns of population structure seen in northwest Atlantic herring. From this evidence, several general demographic properties can be associated with these populations that are either favourable for entrainment to occur, or are consequences of entrainment:

- Annual surplus production is often negative, therefore populations depend upon the intermittent occurrence of strong yearclasses to rebuild their biomass between periods of population decline. This boom and bust recruitment pattern characteristic of herring, creates a situation where a recruiting yearclass may numerically dominate the standing stock and affords the opportunity for rapid changes of life-cycle patterns - both for the recolonisation of abandoned feeding, overwintering and spawning sites and for the modification of migration patterns, i.e. the creation of new routes or the abandonment of old ones.
- Herring are a long-lived species which form multiple age-structured populations and have a strong tendency for schooling which affords the opportunity for entrainment, through the social transmission of traditions from older to younger individuals and explains the observed conservatism in life-cycle patterns (Corten, 2002).
- Annual migration patterns within north-western Atlantic populations are limited to shelf and coastal areas, each within relatively clearly-defined geographic ranges resulting in limited connectivity between adjacent populations. Therefore the 6 populations as defined in Figure 1 may be considered as Meta-populations, given the relatively low exchange and interaction between them.
- Seasonal spawning and nursery grounds within the Meta-populations are often separated in space which leads to the development of local populations. Local populations intermix to various extents at times other than spawning throughout the range of the Meta-population and may be ephemeral on the scale of generations. The connectivity between these local populations is controlled by physiological and behavioural factors which infer a dynamic of exchange among local populations which is not entirely a function of physical proximity. Exchange between sympatric local populations depends upon the opportunity for social transmission occurring at various developmental stages throughout the life trajectory, which may or may not be related to the distance between their respective spawning grounds, as has been suggested (McPherson *et al.*, 2004).
- The local population can be considered as the basic biological unit to be protected from overexploitation to optimise spawning potential, but the Meta-population defines the management unit.

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Table 1. Percent autumn- and spring-hatched herring which became mature autumn and spring spawners within the 1979, 1981 and 1986 autumn-spawning and 1980, 1982 and 1987 spring-spawning year-classes off western Newfoundland (age is expressed as the number of otolith rings)(from McQuinn (1997a).

Year	No. of rings	1979 Autumn-spawning year-class			1980 Spring-spawning year-class		
		Autumn-hatched	Spring-hatched	n	Spring-hatched	Autumn-hatched	n
1983	3	34.5	65.5	712	90.6	9.4	402
1984	4	55.6	44.4	1923	92.3	7.7	1438
1985	5	60.4	39.6	1760	92.4	7.6	2590
Year	No. of rings	1981 Autumn-spawning year-class			1982 Spring-spawning year-class		
		Autumn-hatched	Spring-hatched	n	Spring-hatched	Autumn-hatched	n
1985	3	54.4	45.6	68	92.2	7.8	192
1986	4	30.7	69.3	140	95.2	4.8	481
1987	5	22.6	77.4	186	97.2	2.8	966
Year	No. of rings	1986 Autumn-spawning year-class			1987 Spring-spawning year-class		
		Autumn-hatched	Spring-hatched	n	Spring-hatched	Autumn-hatched	n
1990	3	86.0	14.0	57	68.8	31.2	32

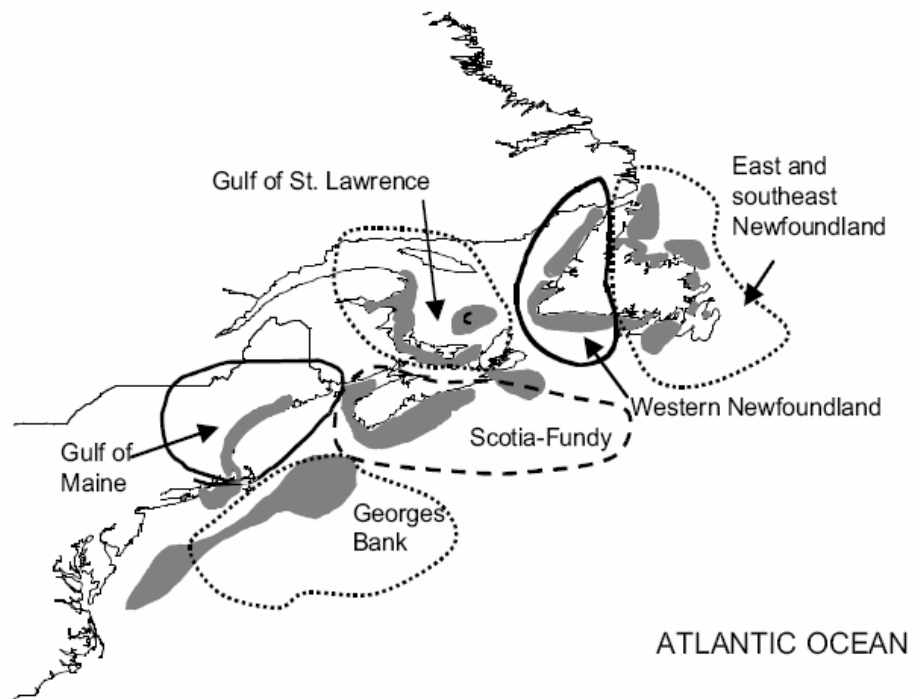


Figure 1. The western North Atlantic showing areas occupied by the major herring stocks separated by solid, dashed, or dotted lines. For most stocks, dark areas indicate the appropriate locations of spawning grounds. (from Hay *et al.*, 2001)

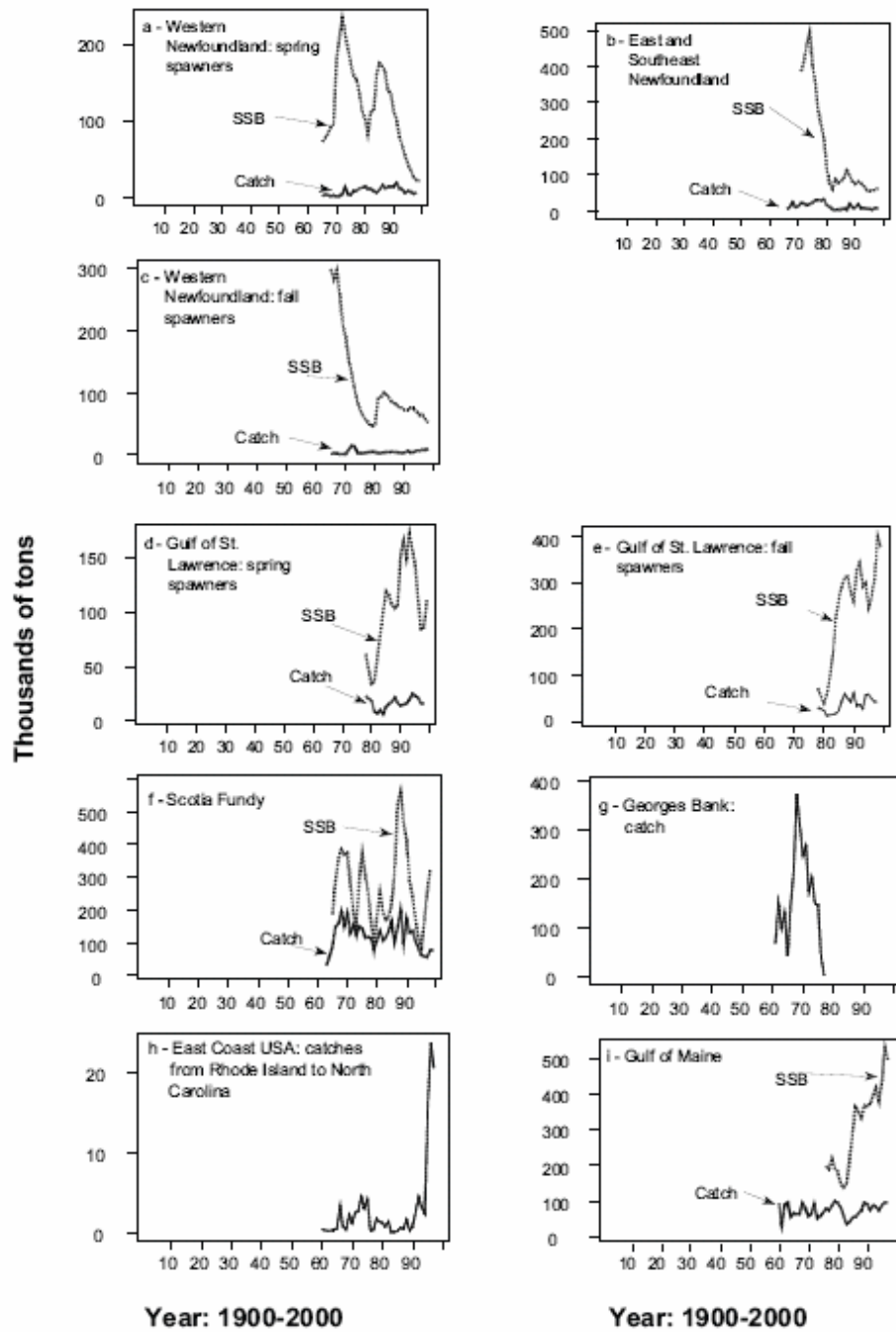


Figure 2. Catch (solid dark line) and spawning stock biomass (SSB, dashed line) for western North Atlantic herring stocks. (from Hay *et al.*, 2001)

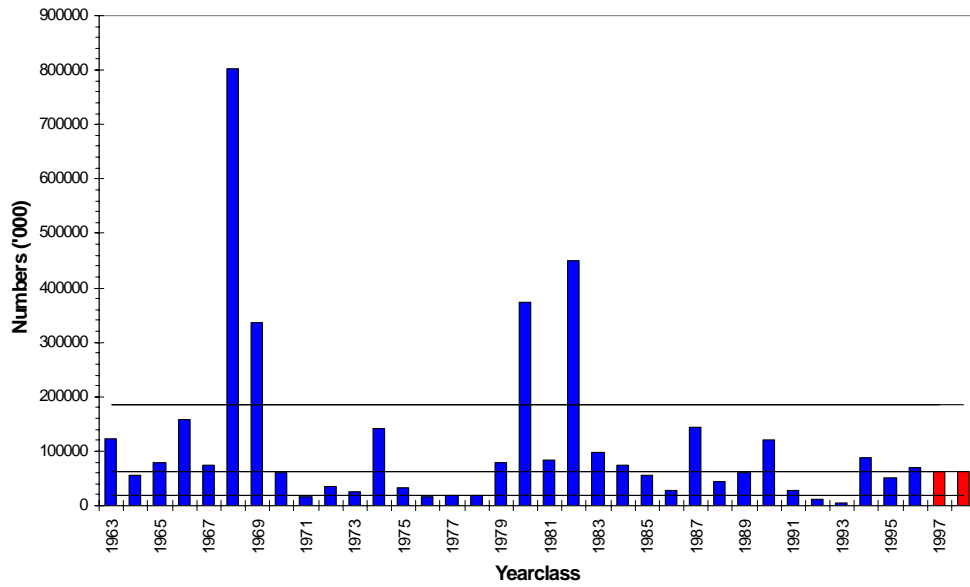


Figure 3. SPA estimates of recruitment at age 2 for autumn-spawning herring for year-classes 1975 to 1994 (year-classes 1995 to 1996 are fixed at medium recruitment)(from McQuinn *et al.*, 1999).

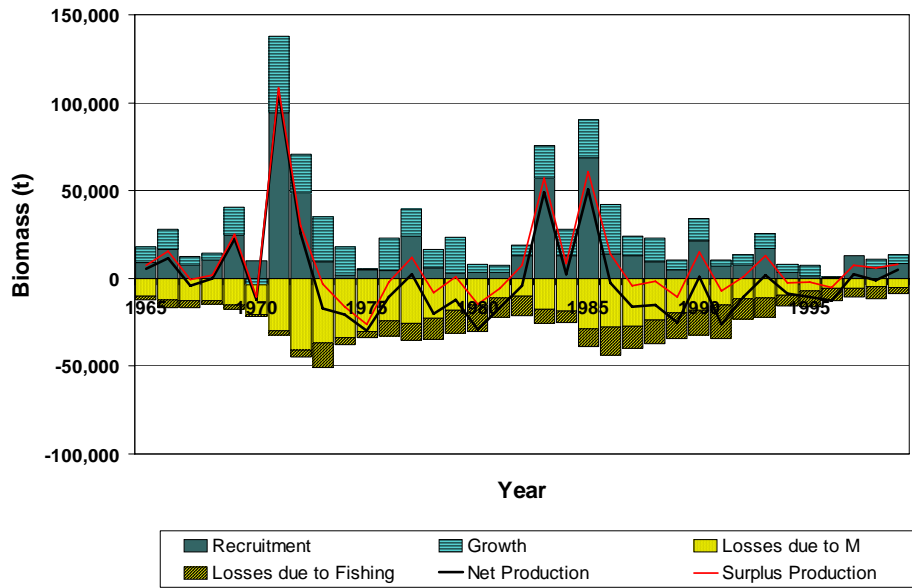


Figure 4. SPA estimates of biological production of west coast of Newfoundland autumn-spawning herring from 1973 to 1997 showing gains through recruitment and growth and losses through natural mortality (M) and fishing. Surplus production (what is available to fishing) is expressed as gains minus losses due to M, and net production is expressed as surplus production minus losses due to fishing (from McQuinn *et al.*, 1999)

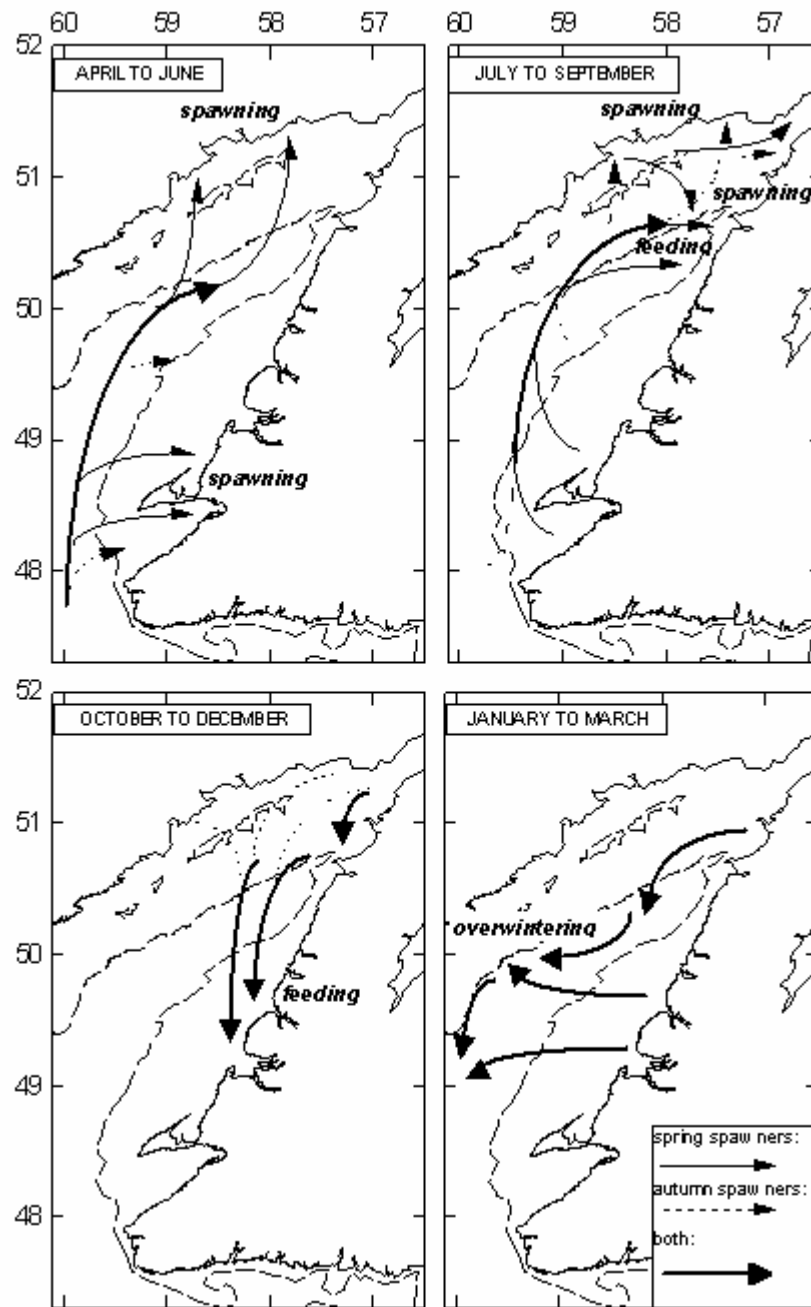


Figure 5. Annual migration pattern of spring- and autumn-spawning contingents of Atlantic herring along western Newfoundland (from McQuinn *et al.*, 1999)

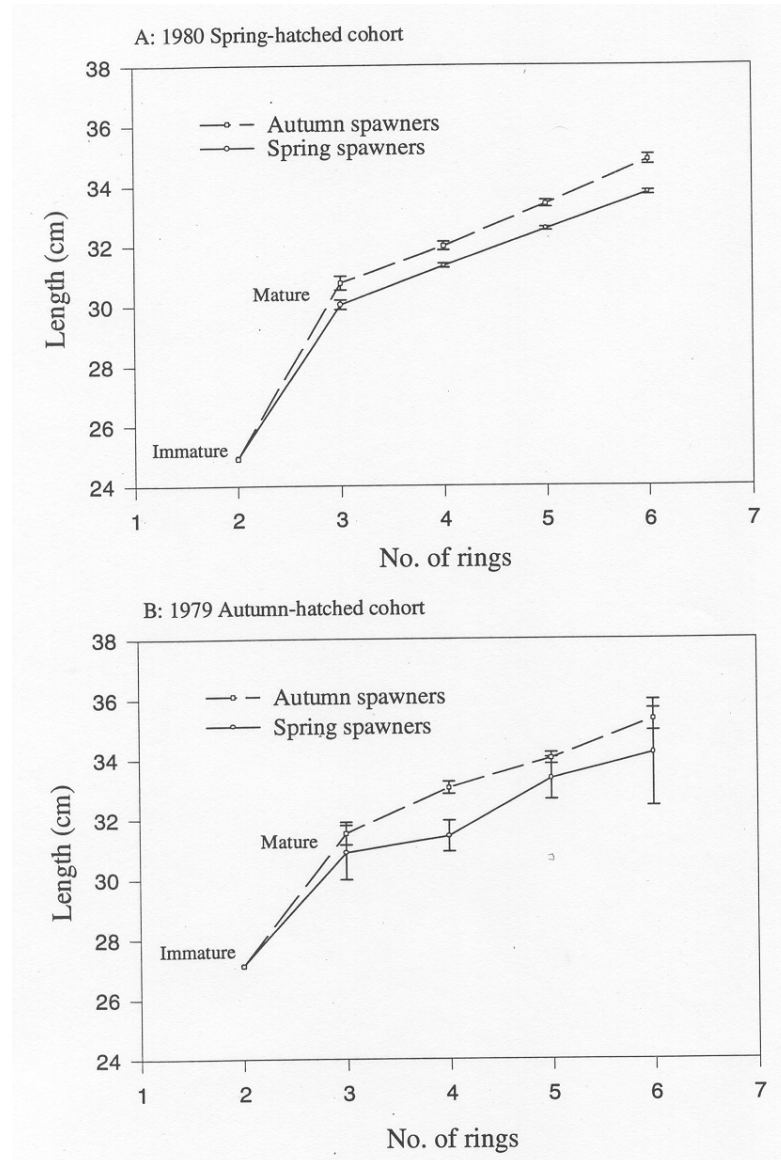


Figure 6. Length at age and 95% C.I. of the (A) 1980 spring-hatched and (B) 1979 autumn-hatched cohorts in the late fall (October-December) once the spawning season had been established as determined by their maturity stages. (age is expressed as the number of otolith rings)(from McQuinn, 1997a).

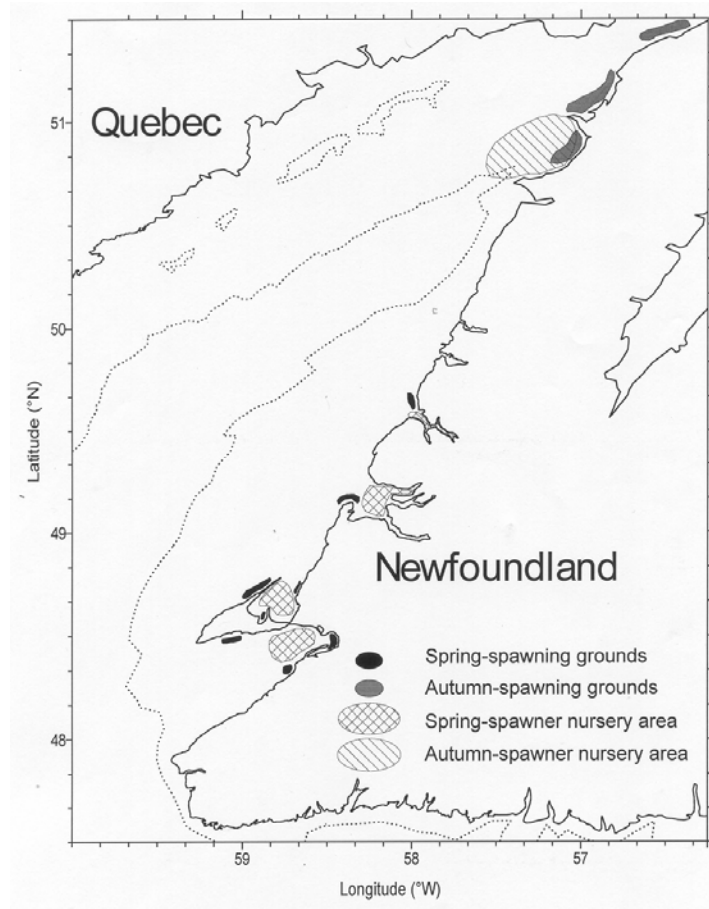


Figure 7. Spawning and nursery areas for spring- and autumn-spawning contingents of Atlantic herring along western Newfoundland (dotted line represents the 200-m depth contour)(from McQuinn 1997b).

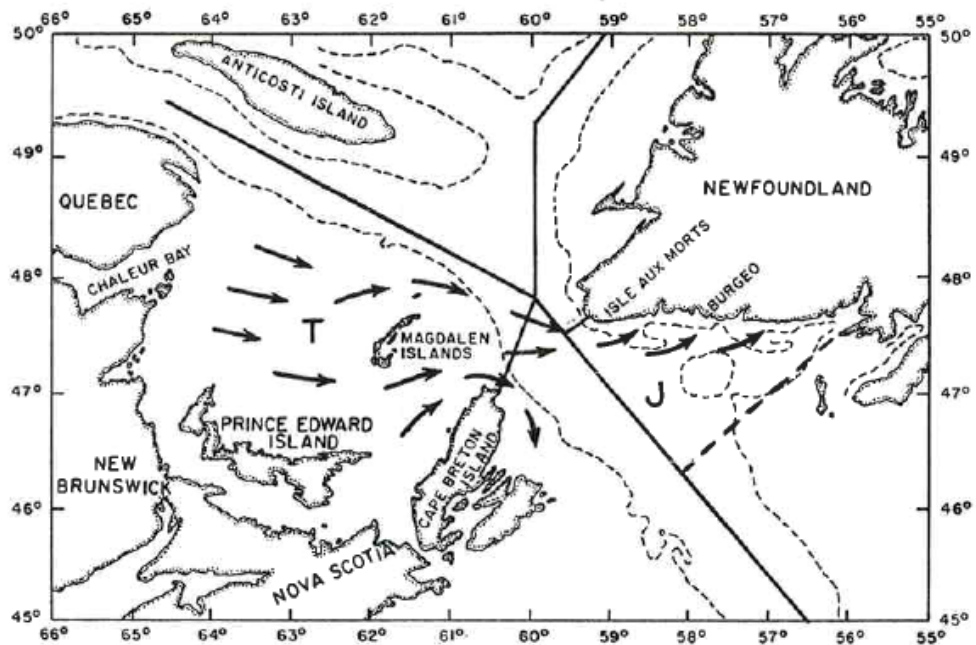


Figure 8. Autumn migration of southern Gulf of St. Lawrence Atlantic herring up to the mid-1970s (from Winters and Hodder, 1973)

Annex 3: North Sea herring (by Ad Corten)

Case study North Sea herring #1

Re-colonisation Aberdeen Bank spawning ground

The return of spawning herring to Aberdeen after an absence of 16 years demonstrates the ability of a recruiting herring year-class to choose a new spawning ground, develop an attachment to it, and pass the habit on to following generations.

Prior to 1965, two main spawning grounds for herring existed in the north-western North Sea; the Aberdeen Bank and the Shetland/Orkney area (Fig. 1). Spawning intensity on these grounds showed long-term, opposite cycles with the Shetland/Orkney area being dominant prior to 1950 and the Aberdeen Bank from 1950-1965. These long-term variations were ascribed by British authors to variations in the inflow of Atlantic water into the north-western North Sea (see for references Corten 1999a).

In 1967 spawning at Aberdeen Bank stopped completely, probably as the combined result of intensive fishing and poor recruitment. After the end of the fishery, scientists continued to monitor larval abundance on the former spawning grounds as part of the ICES coordinated herring larval surveys in the North Sea. Between 1967 and 1981, no larvae were detected in these grounds, which may be taken as evidence for the complete extinction of the earlier spawning population.

In 1983 (to a small extent already in 1982), herring started to spawn again at Aberdeen Bank. Scientists detected large concentrations of larvae, indicating the presence of a substantial spawning population (Fig. 2). In the following years, the herring returned for spawning at this position. It was only in 1986 that the herring fleet started to exploit the spawning herring on Aberdeen Bank. From age compositions taken from the catches, it appeared that the fish belonged to year-classes 1980 and later ones. The spawning in 1983 was most likely started by year-class 1980 which was recruiting in that year.

The spawners of year-class 1980 cannot have originated themselves from Aberdeen bank, but they must have been born at the more northern spawning grounds at Shetland/Orkney. For some reason this year-class in 1983 decided to choose Aberdeen bank as its spawning ground instead of the more northern grounds.

Corten (1999a) put forward the hypothesis that year-class 1980 had been feeding more to the south than usual, due to a strong inflow of Atlantic water into the north-western North Sea and a displacement of the maximum food concentration to the south. The southern distribution of the recruit spawners may have caused a disconnection between this year-class and the older fish in the population. By the time the recruiting year-class had to spawn, the older fish had already returned to the traditional spawning grounds at Shetland/Orkney. Lacking the guidance of the older herring, the recruiting year-class choose the nearest place with a suitable bottom substrate for spawning, which happened to be the Aberdeen Bank. As a result of site attachment, year-class 1980 returned to Aberdeen Bank the following years. This time it was leading the way to younger year-classes that also adopted the habit of spawning at Aberdeen bank.

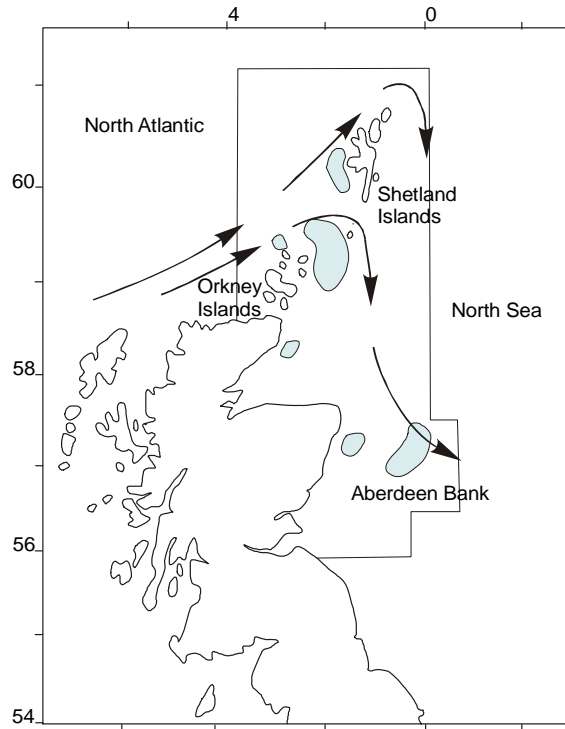


Fig. 1: Traditional spawning areas for herring in north-western North Sea

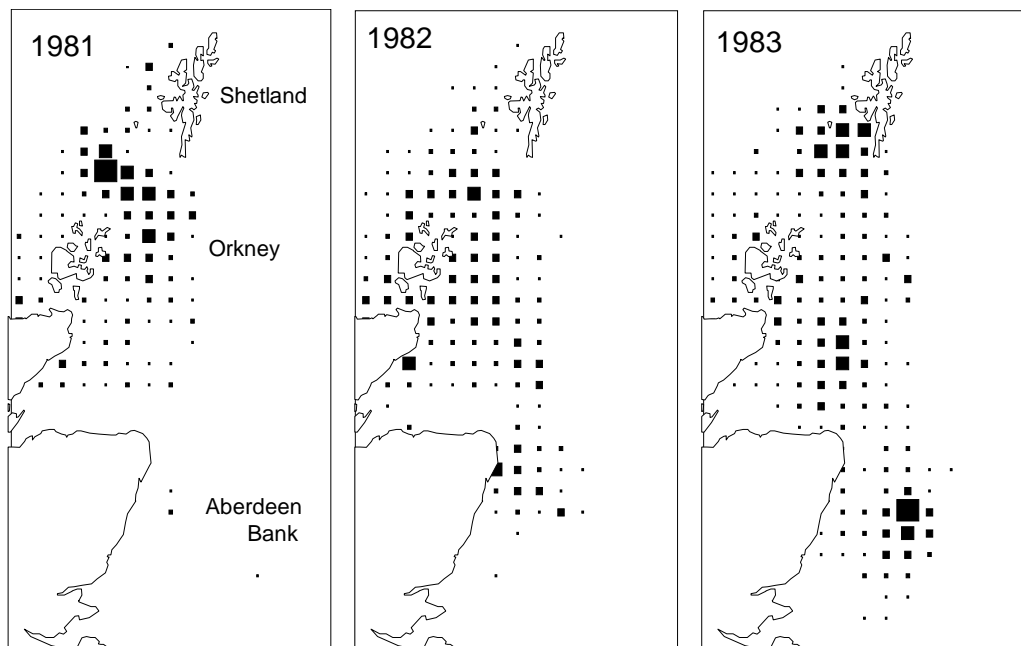


Fig. 2: The re-appearance of spawning at Aberdeen Bank as illustrated by the abundance of herring larvae < 10mm. Data from ICES coordinated herring larvae surveys.

Case study North Sea herring #2

Wintering of North Sea herring in Skagerrak

North Sea herring temporarily adopted the Skagerrak as its wintering ground in 1962 - 1965. It was a recruiting year-class (1960) that took the initiative to spend the winter in this area and when it repeated the migration in subsequent years, it was followed by younger generations.

In normal years, most North Sea herring spend the winter along the northern slope of the continental shelf and along the western side of the Norwegian Trench. This is actually the continuation of the shelf slope (Fig. 3). Few adult herring are found wintering in Skagerrak. In the winters of 1962-65, however, massive amounts of North Sea herring entered the Skagerrak during the autumn and stayed there during the winter (Fig. 4). In the autumn of 1965 the herring no longer entered this area although they did assemble near the entrance of the Skagerrak. According to Swedish scientists, the fish were deterred by the large international fleet that had exploited the wintering concentrations in Skagerrak in the previous winters.

The fish that started the wintering migration in the autumn of 1962 and 1963 were recruiting fish of year-class 1960. The recruiting year-class in autumn is normally distributed in the eastern North Sea in the vicinity of the Skagerrak. Corten (1999b) postulated that year-class 1960 was caught by an unusually strong sub-surface Norwegian Trench Current, and thereby transported passively into the Skagerrak. The fish returned to the same area the following winter, this time followed by younger herring of year-class 1961.

The observations illustrate that a recruiting year-class may choose a new wintering ground which is different from the existing one. As a result of site attachment, the fish will return to the same place the following winters. Younger herring will follow the first year-class to the new wintering ground, and thereby copy the new migration.

The Skagerrak invasions in the early 1960s ended probably as a result of intensive fishing on the wintering concentrations. In earlier centuries, North Sea herring also occasionally invaded Skagerrak during winter. These invasions would be repeated annually during several decades, and these episodes were named "Bohuslån herring periods". It is assumed that these periods were started in the same way as the 1960s invasions, i.e. by the chance displacement of a recruiting year-class into Skagerrak, due to a strong Norwegian Trench Current.

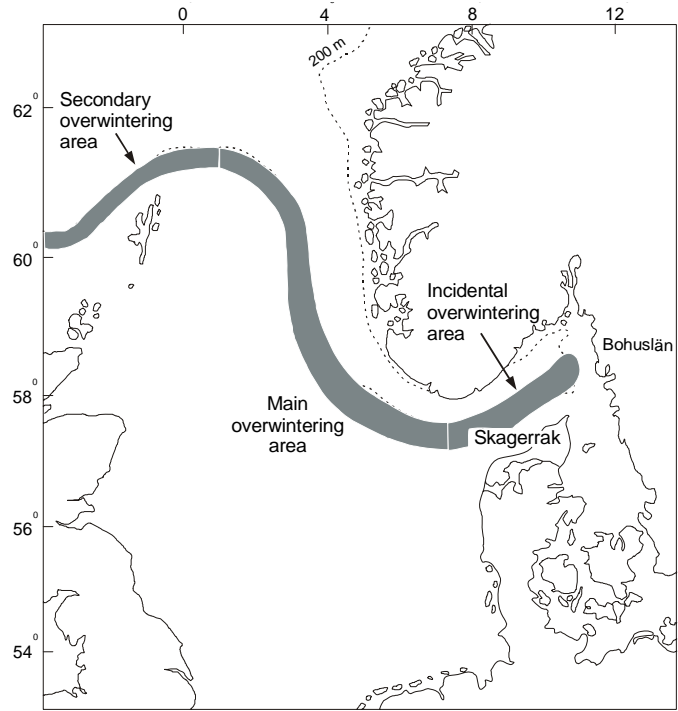


Fig. 3: Wintering areas of North Sea herring

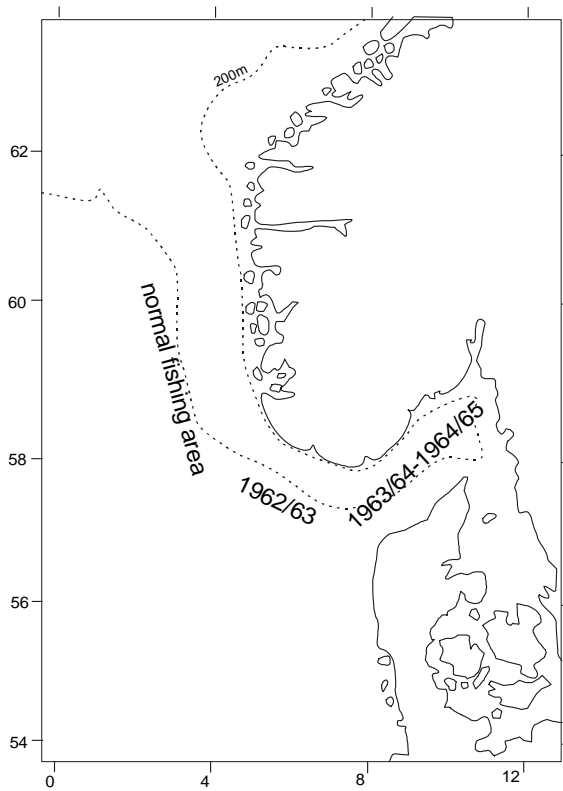


Fig. 4: Fishing areas in the winters of 1962/63 - 1964/65 compared to the normal fishing area during winter.

Case study North Sea herring #3

Prolonged feeding of herring in eastern North Sea

The feeding period of herring in the eastern North Sea was extended in 19xx, apparently as the results of a prolonged Calanus season. Herring adopted the habit of staying in the eastern North Sea until June instead of till May. They continued this habit for some years after the Calanus season had shortened again.

After wintering in the eastern North Sea, herring start feeding in this area in March/April. They exploit the spring bloom of *Calanus finmarchicus*, which starts early in this area due to the influx of a seed population by the Norwegian Trench Current. By the end of May, the *Calanus* bloom in the eastern North Sea ends, and the herring then migrate towards the western North Sea to take advantage of the increased food production in that area (Fig. 5).

In the early 1980s, herring appeared to delay their migration from the eastern to the western North Sea. This seemed to be related to a prolonged *Calanus* season in the eastern North Sea (Corten 2000). The herring apparently felt no need to migrate westwards as long as food was plentiful in the eastern North Sea.

Starting from 1985, the *Calanus* season in the eastern North Sea shortened again. The herring showed a delayed response to this shortening of the feeding season. For two more years, the herring lingered on in the eastern North Sea during the month of June, despite the fact that *Calanus* had become scarce (Fig. 6). It seemed that the herring was reluctant to change its migration again, after it had become accustomed to a longer spawning season in the eastern North Sea.

The prolonged stay of herring in the eastern North Sea is an example of a new feeding habit that the herring has adapted a result of a changed environment. When the environment changes back to normal, the fish is slow in giving up the newly established habit. This (learned) behaviour seems to allow the fish to adjust its feeding migrations to long-term environmental trends. In order to avoid over-reaction to short-term environmental fluctuations, the fish are "conservative" in their behaviour, and change their migration only if the new situation persists for some time (Corten 2002).

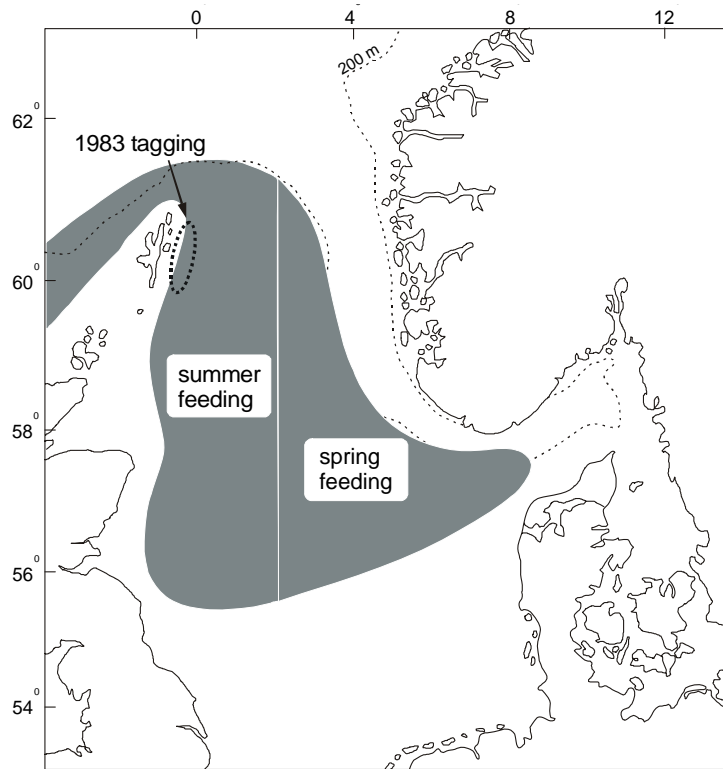


Fig. 5: Herring feeding areas in central and northern North Sea

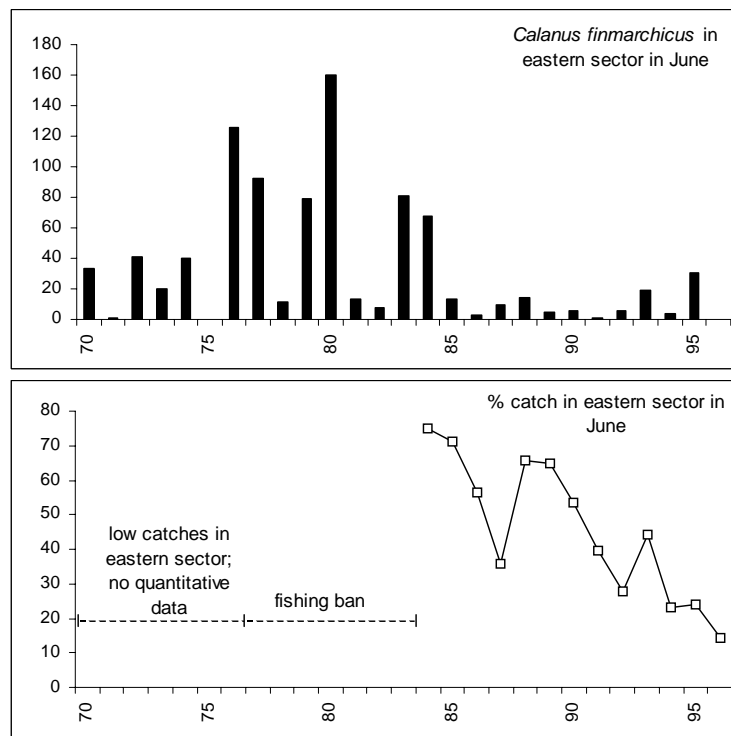


Fig. 6: Percentage total North Sea catch in eastern sector in June, compared to *Calanus* abundance in the same month.

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Annex 4: Norwegian Spring Spawning herring (by Georg Skaret)

Background

Norwegian spring spawning (NSS) herring (*Clupea harengus*) has a history during the past 60 years of initially high abundance in the early 50ies (SSB >10 million tonnes), gradual decrease towards depletion in the late 60ies due to overexploitation and rebuilding up to present almost to the high levels from the 50ies starting with the strong 1983 year-class. The population is long-lived (up to 25 years old) with a distinct seasonal migration pattern: Feeding in the Norwegian Sea during May-August followed by a non-feeding overwintering period where normally the whole population is concentrated within a limited geographical area. After overwintering the population migrates to the spawning areas along the Norwegian coast followed by a new migration to the feeding area. The main nursery area is in the Barents Sea but a proportion of the juveniles grow up in fjords along the coast. The coastal proportion is usually small, but may be high in years of low population abundance (Holst & Slotte 1998). Juveniles in the Barents Sea tend to be aggregated according to age with the youngest fish furthest to the east. As recruit spawners they enter the Norwegian Sea during the summer feeding, normally as 4-year-olds. With regards to conservatism in migration pattern, where fish are hypothesised to be entrained into a persisting migration route, NSS-herring is a particularly well-studied and interesting population (Corten 2001, Slotte 2001, Huse *et al.* 2002). In the following we summarise findings of migrations to the wintering areas and the spawning grounds.

Wintering areas

The period when the recruit spawners enter the Norwegian Sea has been demonstrated to be decisive of future migration pattern of the NSS herring. In normal years the recruits join the main population during feeding in the Norwegian Sea and adopt their migration to the wintering areas. However, when a recruiting year-class is abundant relative to the existing unit, the migration pattern may change (Dragesund *et al.* 1997, Corten 2001, Huse *et al.* 2002). When the strong 1959-year-class entered the Norwegian Sea they established a new feeding area east of the Bear Island and wintering area between the Bear Island and the Norwegian coast while the main population remained in the traditional feeding and wintering areas. This yearclass also established a new spawning area off Lofoten (Dragesund *et al.* 1997). After two years the recruits had adopted the wintering and spawning areas of the main population, whereas the main population had adopted the feeding areas established by the recruits. The first strong yearclass after the depletion, the 1983 year-class established a new wintering area in Tysfjord and Ofotfjord, whereas the 1991-year-class when they recruited established a wintering area further out in the same fjord system, in the Vestfjord. In both cases recruits in subsequent years adopted the new established wintering areas. With the strong 1998-1999 year-classes yet a new wintering area was established further north off the coast, whereas the existing unit maintained the traditional wintering area in Vestfjord. Not in any of the cases when a shift in wintering area has been documented has the ratio between recruits and existing unit been below 1.3 (Huse *et al.* in prep.). On average the ratio is 12.9 for the six documented years with shifts in wintering areas compared to 0.4 for other years. (Huse *et al.* 2002) demonstrated through an individual based model how this could be an effect of what they termed 'numerical domination' when the relative number of experienced individuals is too low to guide naïve individuals in a population with a mix of experienced and naïve. They found that 7 % or more experienced guided naïve towards a predefined target, whereas below 4 % the naïve remained unaffected. A similar ratio was shown by (Couzin *et al.* 2005) in a more generic model. The model results provide support to what was indicated

by in situ observations that the population structure is crucially decisive when a traditional migration route is disrupted.

Spawning areas

NSS-herring spawn off the Norwegian coast on grounds of rock and gravel ranging in depth from 30-250 m (Runnström 1941). The relation between homing, state-dependency and environmental conditions in choice of spawning grounds is not clear for NSS-herring. Natal homing is probably of little importance to this population (Runnström 1941, Slotte 2001). Even though NSS herring to a certain degree return loyally to spawning grounds, there is large variation over time. (Runnström 1941) found that the main spawning in the years 1931-37 took place south of Bergen. He described 14 spawning locations that were used in this area during the 7 years, but the use of the grounds varied from year to year, in some years herring being entirely absent from historical important grounds. He related this to the hydrographical conditions, as herring were found to spawn on grounds covered by coastal bank water (Salinity 34-35 and Temp. 4.5-5.5 °C) and seemed to avoid cold, less saline water for spawning. The figure of herring catches given in (Devold 1963) (Fig. 2) indicates how spawning grounds gradually shifted northwards during 1946-1961. However, there seems to be a certain fidelity in the choice of a few areas. (Slotte 1999) showed that the spawning migration varied depending on the length and condition factor of the fish, with long fish with high condition undertaking the longest migrations. In a paper evaluating different conceptual hypotheses regarding spawning migrations (Slotte 2001) showed that the spawning migration even for a single particular year-class depended on the condition factor that particular year supporting that migration is state-dependent (Fig. 3). In a modeling simulation (Slotte & Fiksen 2000) demonstrated that long migrations despite the high energetic investments can be advantageous for an individual due to higher larval survival in more southerly areas. There are hence strong indications that state-dependency and environmental cues play a role in the choice of spawning grounds adding to the observed homing to particular grounds in subsequent years.

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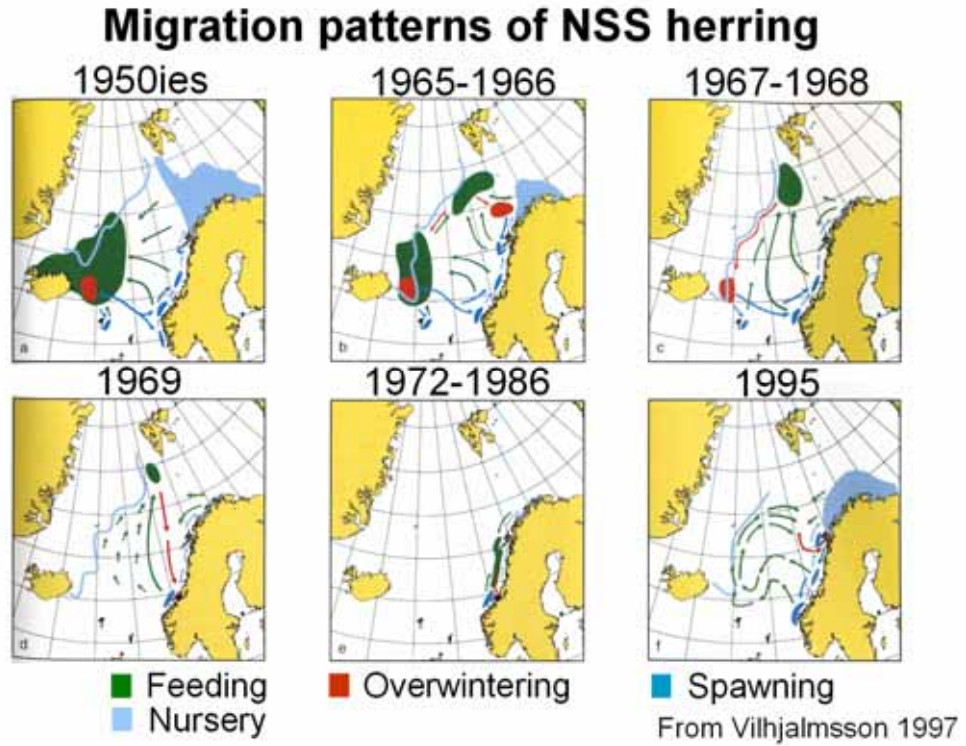


Fig. 1: Migration pattern of NSS-herring from the 1950ies to mid-1990ies

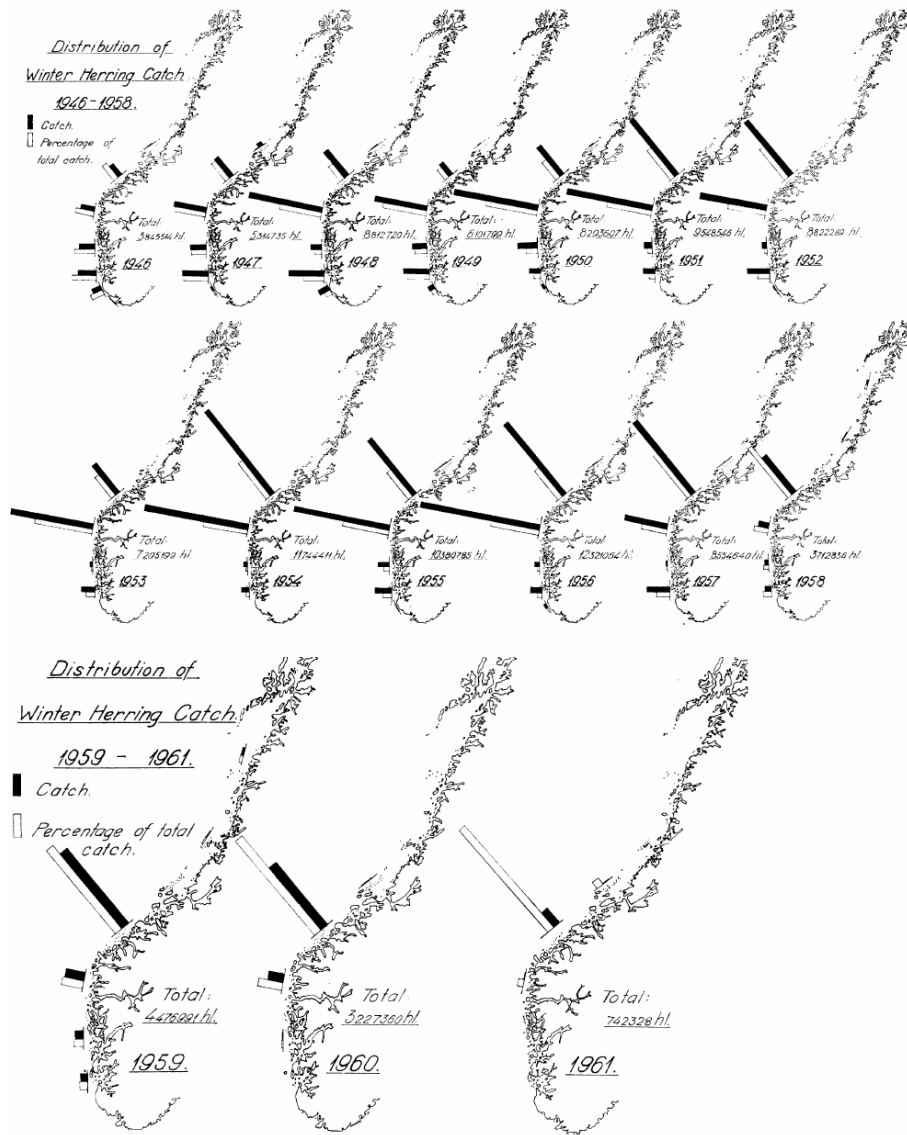


Fig. 2. Catches of NSS-herring during pre-spawning and spawning 1946-1961.

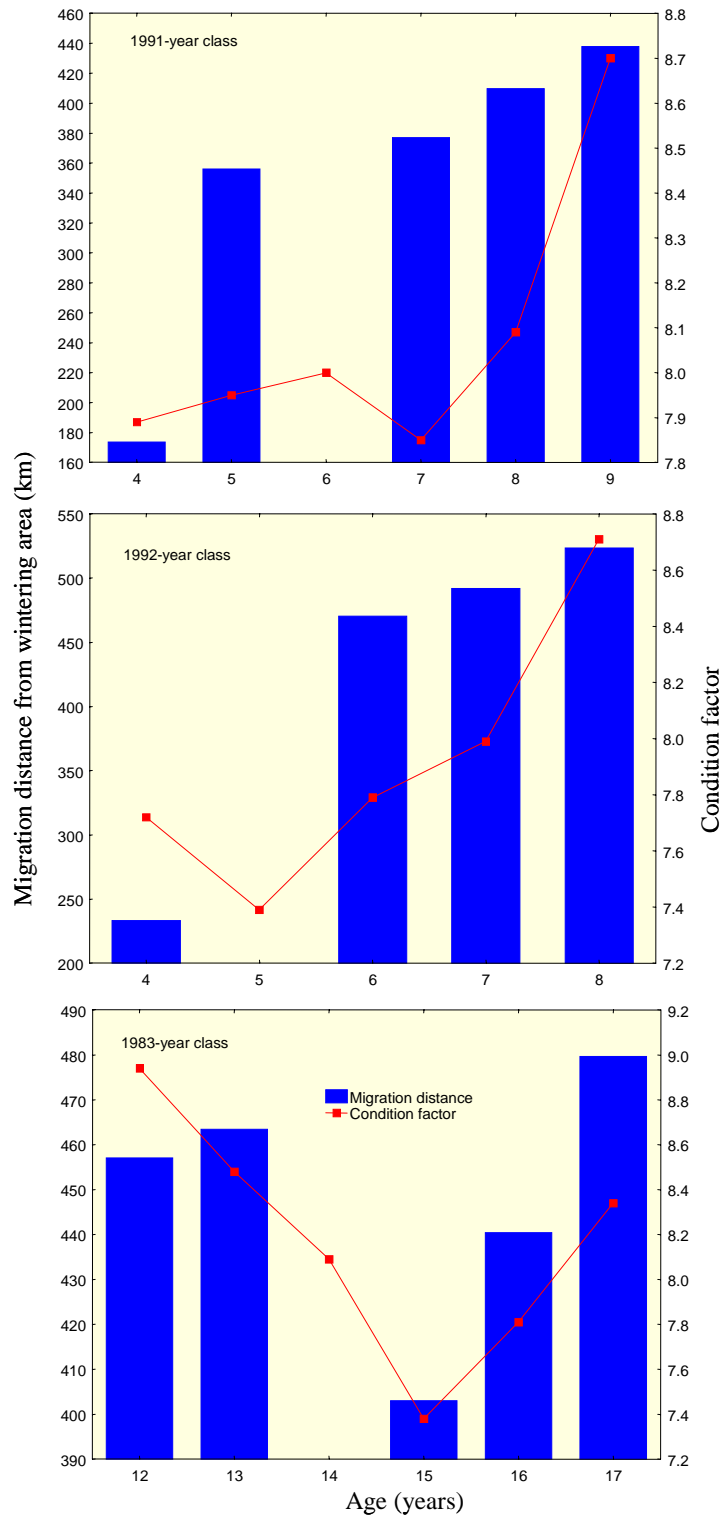


Fig. 3. Migration distance (weighted by acoustic abundance) of NSS herring southwards from wintering grounds in Vestfjorden to spawning grounds along the coast in relation to age and condition of the fish. Examples from year classes recruiting to the stock (1991 and 1992-year classes and old herring (1983-year class). Adapted from Slotte (2001).

Annex 5: Pacific sardine (*Sardinops Sagax*) off west coast of American continent (by Nancy Lo)

Background

The population of Pacific sardine (*Sardinops Sagax*) was high in the mid-1930's and distributed from Baja California, Mexico to British Columbia, Canada (Murphy 1966, Marr, 1960; MacCall, 1976; McFarlane *et al.* 2002)) (Figure 1 and 2). The population collapsed in 1947 and continued to decline through mid-1960. Sardine eggs and larvae were absent in samples of California Cooperative Oceanographic Fisheries Investigations (CalCOFI) ichthyoplankton surveys off the coast north of Baja California. Sardine reappeared in the mid-1980's in the wet fisheries off California (Wolf 1992) and sardine eggs and larvae were present in the samples of CalCOFI surveys from the mid-1980's, with eggs concentrated off Southern California, California, U.S.A. (32°N-34°N) (Scannell, 1996) and gradually covered the coast of California. During a triennial hake survey from northwest to San Francisco in July, 1989, no single sardine was caught (MacFarlane *et al.* 2005), but in 1992, sardine population started to expand to the northwest area, and sardine were once again captured off the southwest coast of Vancouver Island, Canada.

Data

To obtain possible evidence of entrainment (Corten, 2002; McQuinn, 1997, and Petitgas *et al.*, 2006) of Pacific sardine, data of adult sardines off the northwest (NW: British Columbia, Canada, Washington and Oregon, US) and California based on both commercial catches and trawl surveys from early 1930's – present were examined for the length-age distributions in time and space. Any overlap of lengths among fish of different age groups may indicate the possibility of young and old fish schooling together, consistent with the entrainment hypothesis. Sardine egg data from ichthyoplankton surveys were examined for any possible changes of the location of spawning area or the homing of the spawning area. Data includes

- 1930s :samples from surveys (Smith 1990), commercial catches (Mosher and Eckler 1954)
- 1940s: samples from commercial catches (Felin and Phillips 1948), and tagging data (Clark and Janssen 1945)
- 1982-present: commercial catches off California, Oregon and Washington (K. Hill, pers. Comm.)
- 1950-present: CalCOFI ichthyoplankton surveys
- After 1992: Trawl surveys off BC, Canada (MacFarlane *et al.* 2005) and Washington and Oregon, US (Emmett *et al.* 2005)
- NW surveys in 2003-2005 and Daily Egg production Method (DEPM) survey in March-May, 2005 off California conducted by Southwest Fisheries Science Center.

Evidence of possible entrainment

Three 'consistent' lines of evidence (Petigas *et al.* 2006) were observed: 1. Overlap of new spawners with old spawners in schooling: Length-age distribution before the sardine collapse and after the recovery off NW and California; 2. Homing: Spatial distributions of eggs before the collapse and after the recovery off California; and 3. Migration between feeding grounds and spawning area off California and off NW and California : possible indication of entrainment and Meta-populations off California, Washington, Oregon and British Columbia, Canada.

- 1) Overlap of new spawners with old spawners

Yearly overall age and length distributions based on samples collected from commercial catches at various ports were examined a) off BC and Monterey and San Pedro, California based on commercial catch data in the 1930's when the population was high (Figure 1b). b) in the 1940's, when the population started to decline, from BC, Washington, San Francisco, Monterey and San Pedro, California (figure 3-5); and c) from 2002-2005 when the population was recovering, off Southern California (Figure 6).

The lack of overlapping of lengths between fish of 2 year olds and fish of older age groups increased northward from San Francisco to British Columbia (BC), in particular off BC in 1947 when no young fish were observed (Figure 4 and 5). If entrainment is an import factor of population dynamics, the non-overlapping of length between young and older adults would mean the young adults were not led by the old adults which could be detrimental to the population growth. Adult samples from each trawl based on trawl survey data from 1990's off BC, Canada; Washington and Oregon, US were also examined. The overlap of length between age groups within a trawl at different locations was strong and is consistent with an interpretation of the entrainment, with young adult sardine following older sardine (Figure 7).

2) Possible homing

The spatial distributions (presence and absence) of sardine eggs off California during the high peak period (1930's) (Figure 8; Smith 1990), after collapse (1951-1969) and after recovery (1991-2005) (Figure 9: McClatchie, pers. comm.) were similar off California: The similarity of spatial distributions of eggs in these three periods may indicate possible homing, i.e. fish return to the same spawning ground prior to, and after the recovery of the population. Further statistical tests are needed for the patches and gaps. The expansion of presence of eggs after the recovery toward offshore may be a phenomena claimed by the Basin model (MacCall 1990).

3) Spawning migration between feeding area and spawning area off California in 2005

Sardines spawn primarily off shore , perhaps to avoid predation in the inshore area, and eggs are distributed primarily offshore (Lo *et al.* 2005; Lo and Macewicz 2006). Larvae disperse offshore and inshore. Juveniles move inshore in the summer to feed as the seasonal upwelling ends. Length distributions of Pacific sardine in the spawning area (offshore) and feeding area (inshore) off California from the 2005 DEPM March-May survey (Figure 10, Lo and Beverly 2006) were examined to see if there was any evidence of entrainment, e.g. young spawners following older spawners to the spawning area from the feeding area.

Length frequency distributions of Pacific sardine in the offshore and inshore area are different with mean length 158mm inshore ranging from 121-195 mm (age 0-5 year old) and 179mm offshore ranging from 161-265mm (1-8 year old) (Figure 11, Butler 1996.). It is possible that some fish older than 2 year old come to the feeding area (inshore area) and entrain some 2 year old to the spawning area (offshore area). The overlap of length between 150-200mm mostly likely for several age groups (although those fish were not aged) may indicate movement of fish, young and old adult sardine, between inshore and offshore areas , thus both creating potential conditions for entrainment.

The migration of Pacific sardine between California and the NW was well known from the tagging experiments conducted in the 1930-40's (Clark and Janssen, 1946). The conceptual migration schedule is that the sardine migrate from California to the NW in May-June, stay off the NW for feeding in July-October, and start to migrate south in November-December for spawning off California in March-April. This pattern still remains as the length distributions from four NW ichthyoplankton and trawl surveys from Oregon to BC, Canada, conducted

between July 2003 and March 2005 by the Southwest Fisheries Science Center, indicated that large fish occurred in July survey while small fish in March surveys (Figure 12). The biomass estimates of sardine were higher in July surveys than those in March surveys (325,000 mt for July 2003, 33,000mt for March 2004, 83,000mt for July 2004 and 43,000 mt for March 2005). Thus, the current migration route remains the same as that before the collapse. The consistent migration pattern between NW and California may be partially due to entrainment and the movement may also be an indication that populations off California and NW are a Meta-population (McQuinne 1997) instead of genetically distinguished populations.

Management implication for entrainment population

A possible management reference point: analogous to spawning potential per recruit (SPR), which is widely used, but which overlooks the possible importance of repeat spawners. The comparable quantity is NRSPR (number of repeat migrational spawners per recruit). Similarly to SPR, management may want to avoid having NRSPR fall below some percentage of the unfished level, in order to ensure sufficient intergenerational knowledge transfer. The WKTEST working group may be able to consider this. The NRSPR may be much more sensitive than SPR to fishing (MacCall in prep).

Discussions

We see possible evidences for entrainment. However, the phenomena may be caused by other factors. Entrainment is a sufficient condition, e.g. if entrainment is true, then overlap of age and length would be true. However it is difficult to provide examples of a necessary condition for entrainment, e.g. overlap of age and length implies entrainment. Perhaps, we can use a Bayesian approach to compute the probability (entrainment | evidence). A probability greater than 50% would be interpreted as indicating a convincing evidence. The example of diurnal migration of anchovy in the Bay of Biscay based on acoustic survey (the presentation by Petitgas at the workshop) is such an example. Data need to be collected to increase the sample size on the number of schools that made such movement for both pure young adult schools and mixed schools, respectively. If most of those schools that make the movement are mixed schools, this can be a strong ‘demonstrative’ evidence of entrainment.

More literature searching on both the concept of entrainment and on the topics related to entrainment; and experiments on behaviour of fish like Helfman and Schutz (1984) to verify the entrainment hypothesis are needed. Efforts need to be made to include testing this hypothesis in future surveys, in particular, trawl-acoustic surveys

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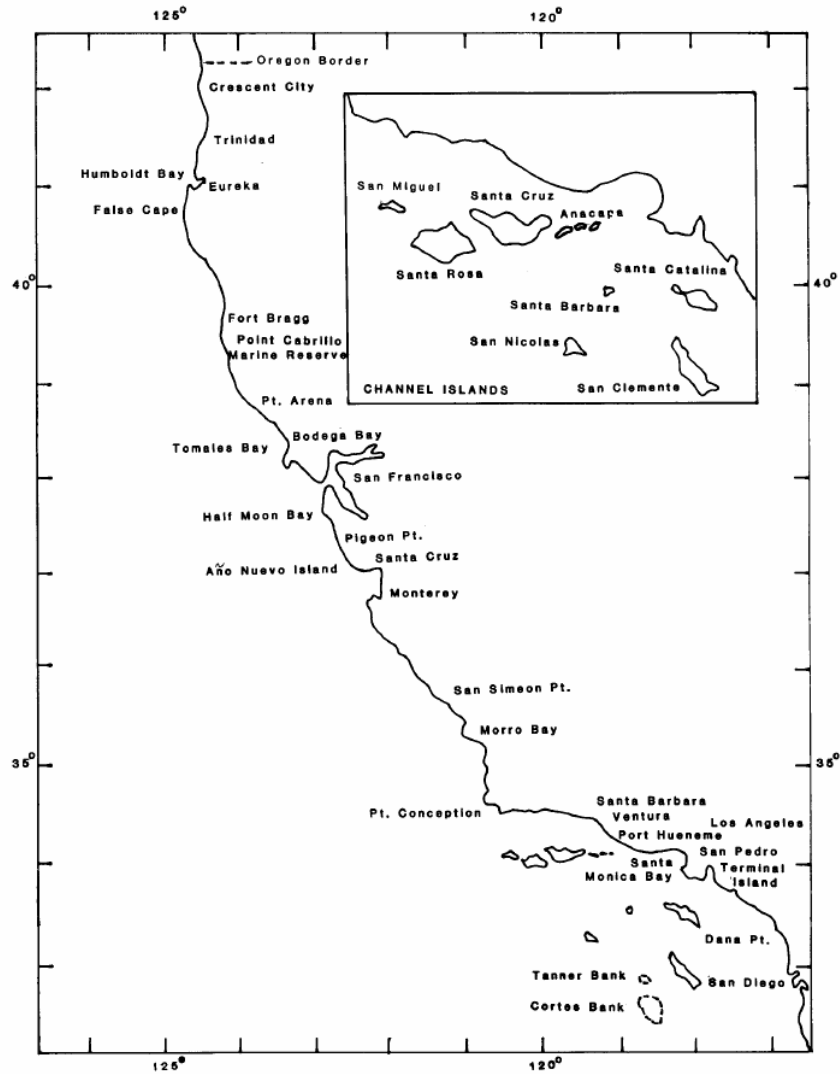


Fig. 1a: The coastal extent of the major Pacific sardine (*Sardinops Sagax*) fisheries, spawning habitat, and migratory range. A) An unpublished diagram of the fisheries (horizontal lines) and spawning areas (vertical lines) showing unmeasured regions (?) for spawning based on knowledge in 1935a. and B) A diagrammatic summary of sardine spawning centers and seasons based on the 1952–1956 CalCOFI surveys (Marr 1960)(from Smith 2005)

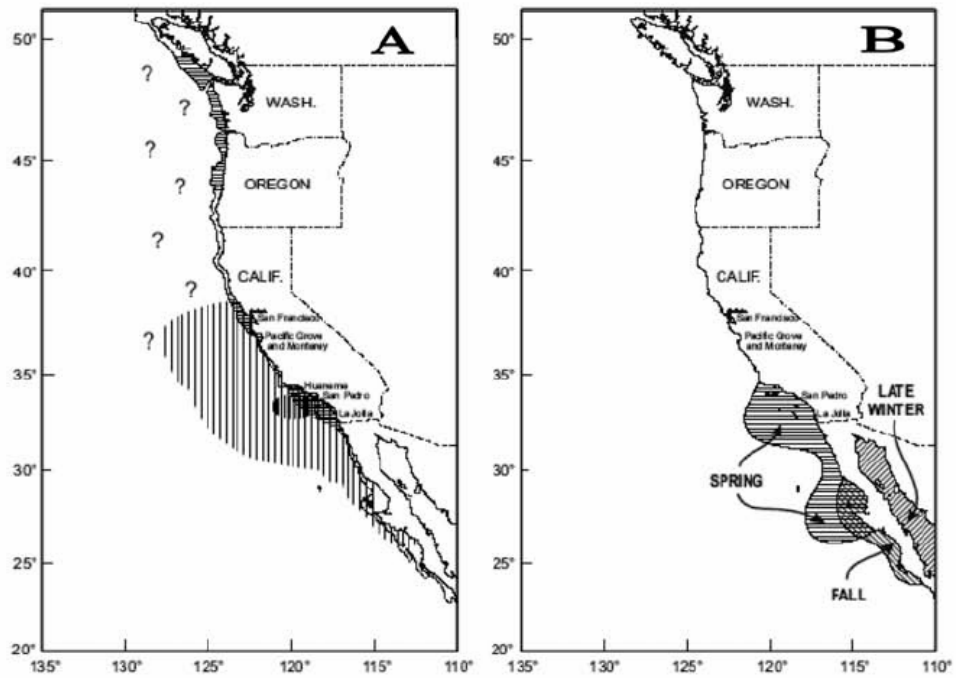


Figure 1b. California ports and fishing area (California Department of Fish and Game, 1992)

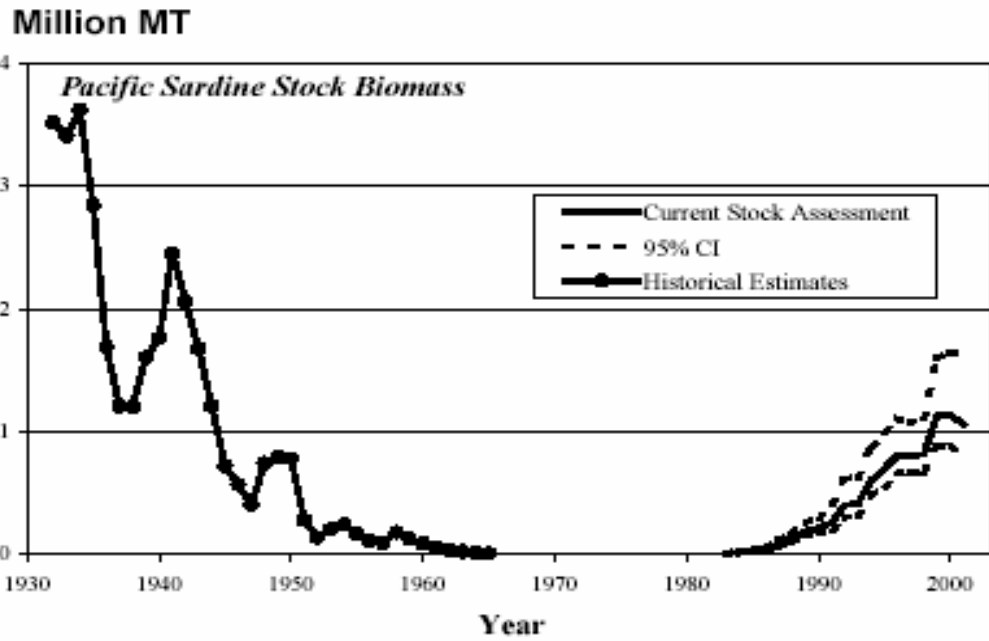


Fig. 2: The biomass estimates of Pacific sardine off California from 1930-2001 (Conser, pers. comm.)

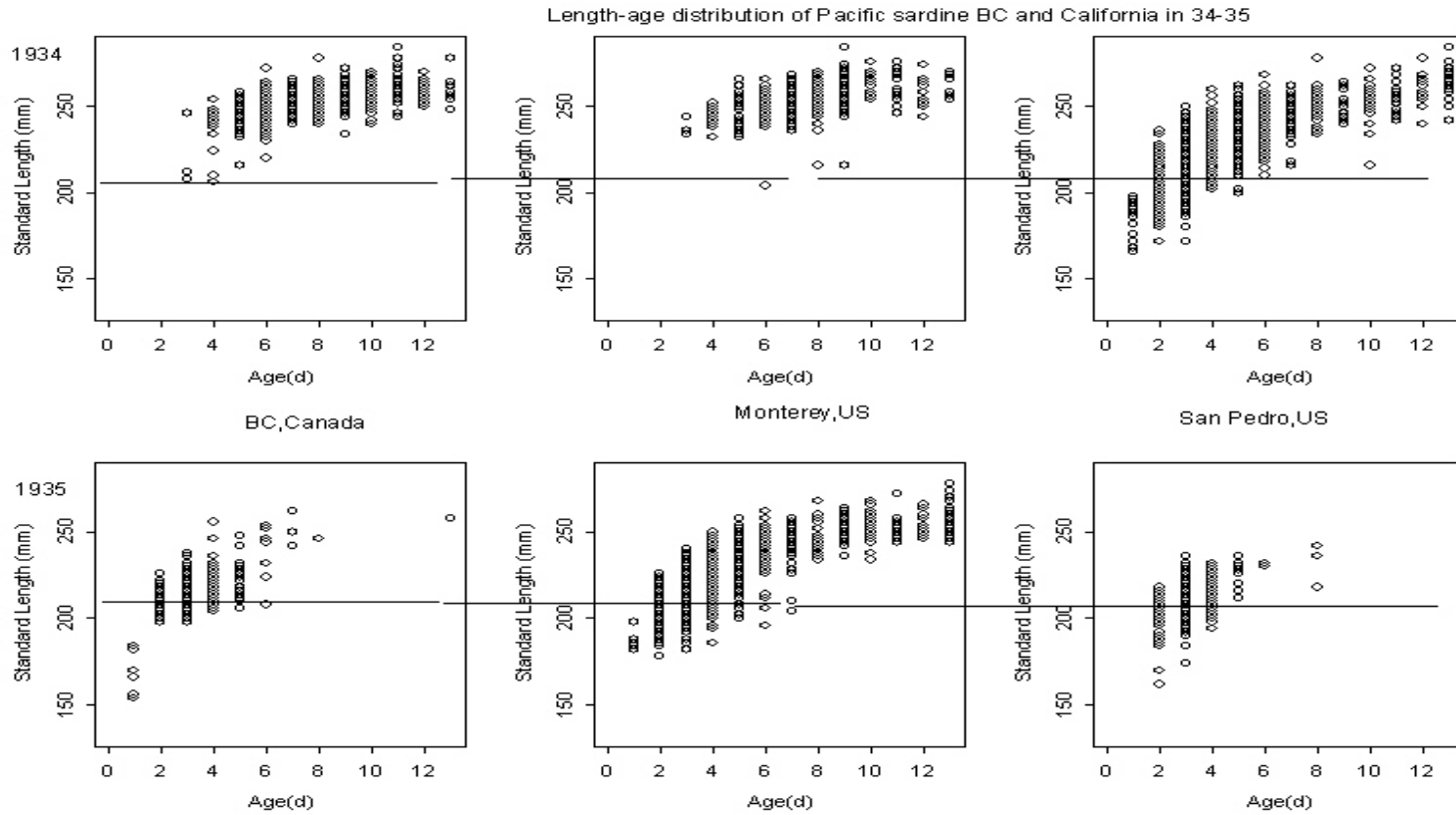


Figure 3. Length-age of Pacific sardine off NW and California in 1934 and 1935 when data of all three areas were available. Horizontal line is 220 mm length

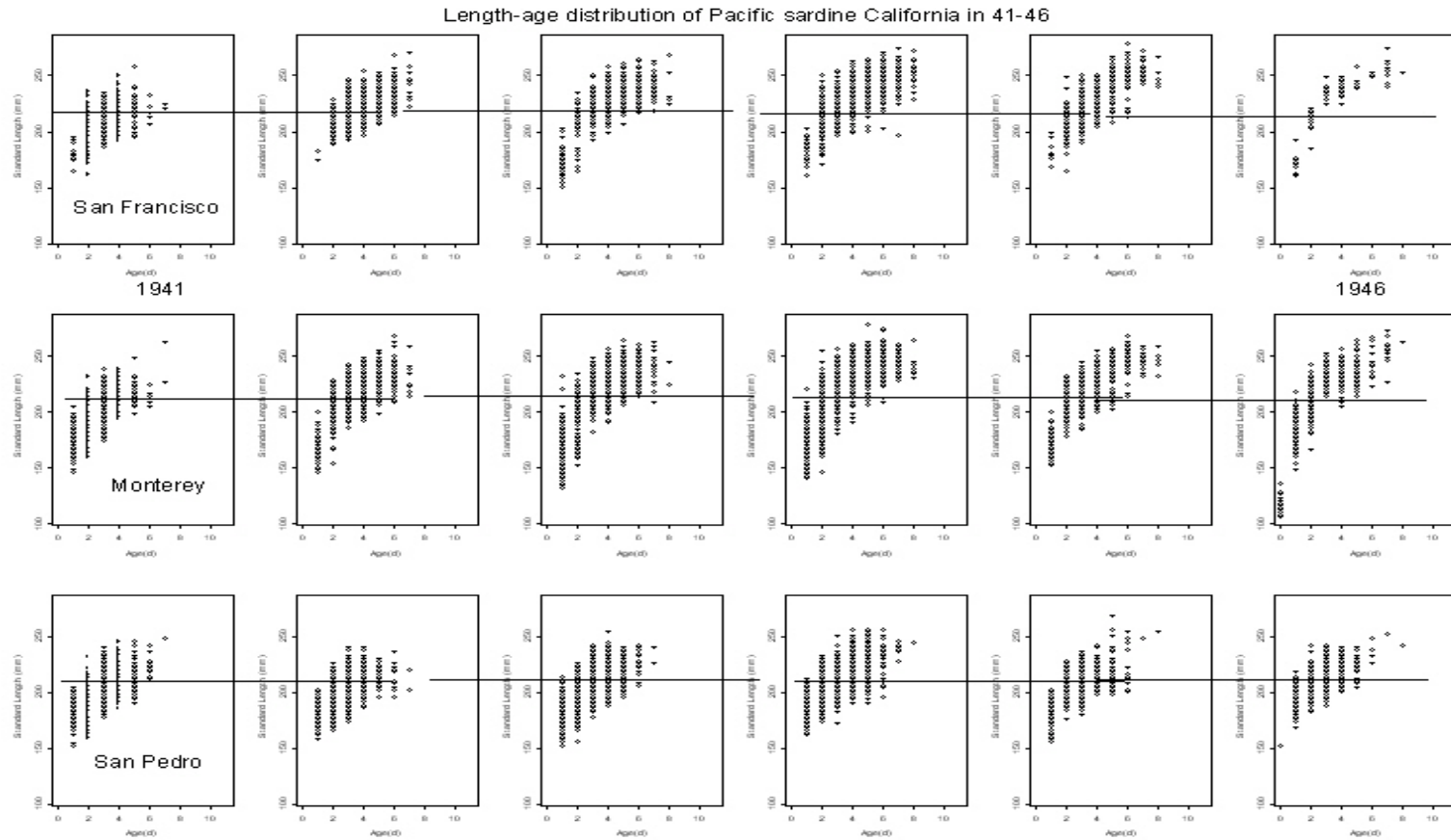


Figure 4. Length age of Pacific sardine from commercial catches in 1941-42 to 1946-47 seasons off California: horizontal line is length 22cm (2-3yr). Note there was non-overlap of length-between two years old and older fish in 46-47 seasons off San Francisco. Y axis is standard length (mm) and X axis is age in days (0 2 4 6 8 10).

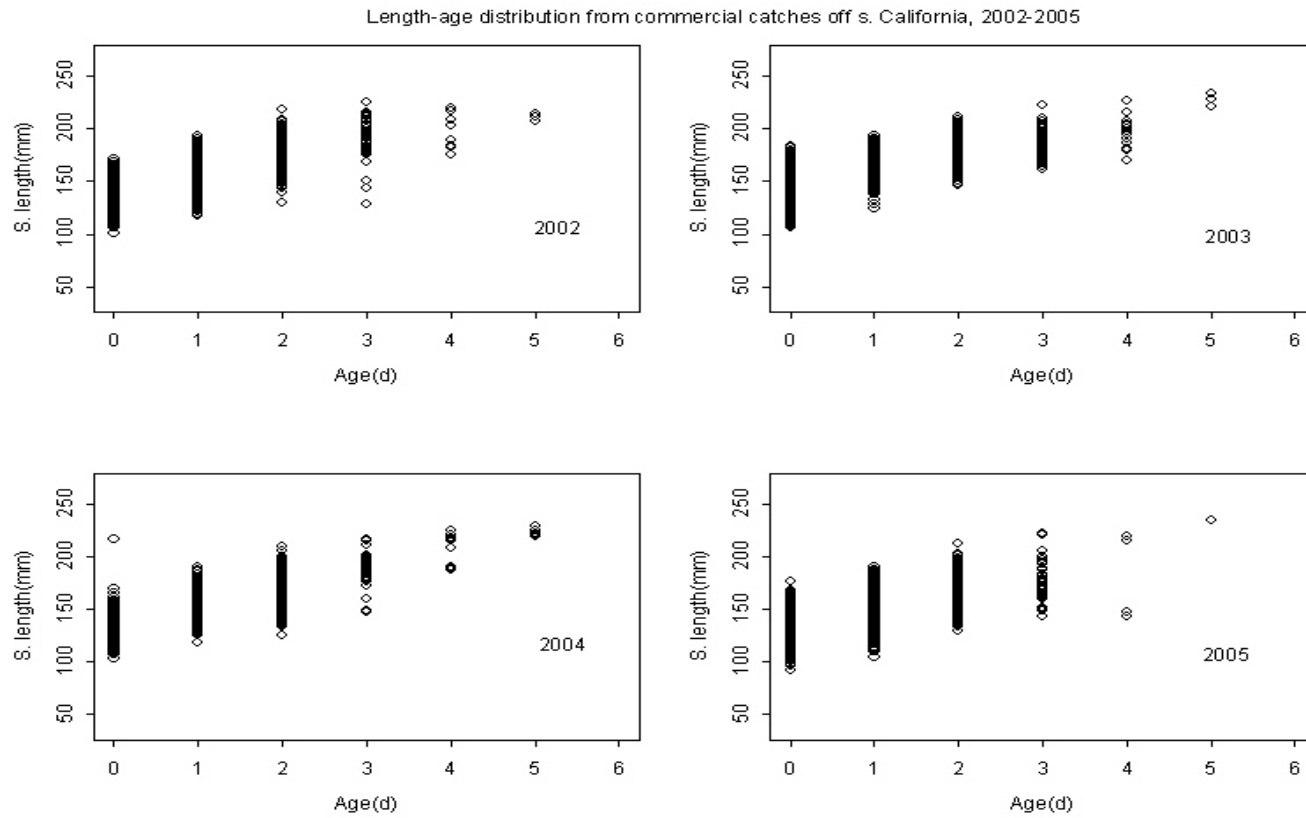


Figure 6. Length-age distribution of Pacific sardine off coastal area of Southern California in 2002-2005.

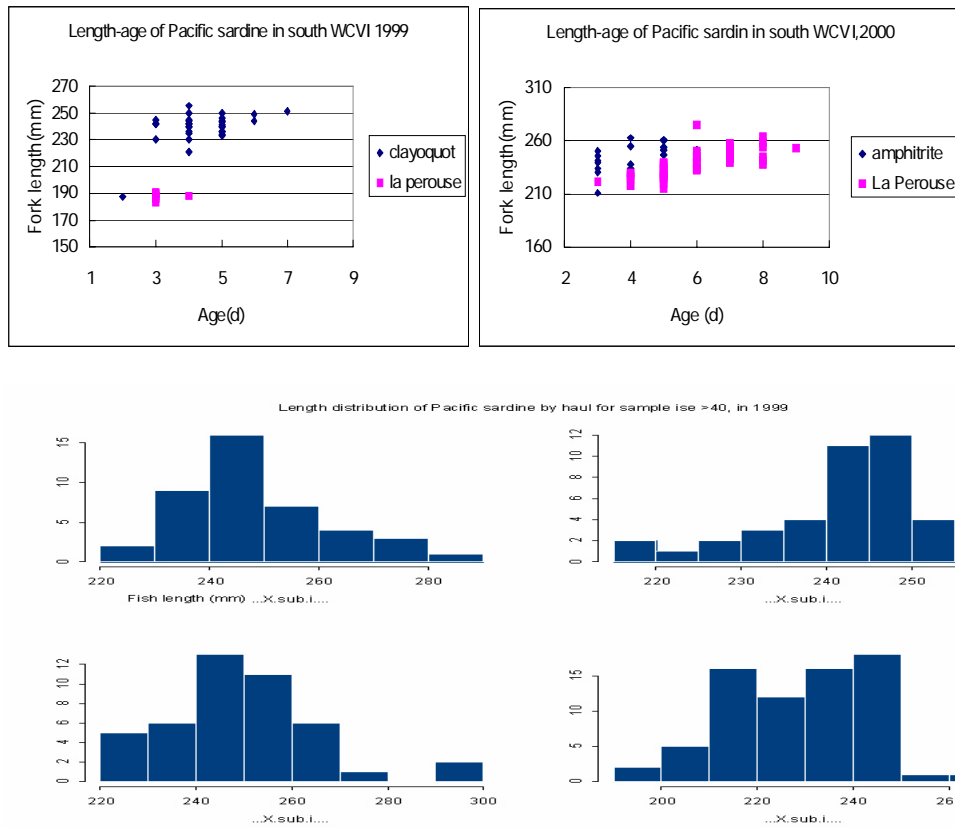


Figure 7 Length age distribution of Pacific sardine off British Columbia by trawl in different localities in the north and south of Vancouver Island in 1999 and 2000 from trawl surveys (above). Length distribution of Pacific sardine by haul for sample size >40 off Oregon all in 1999 (below).

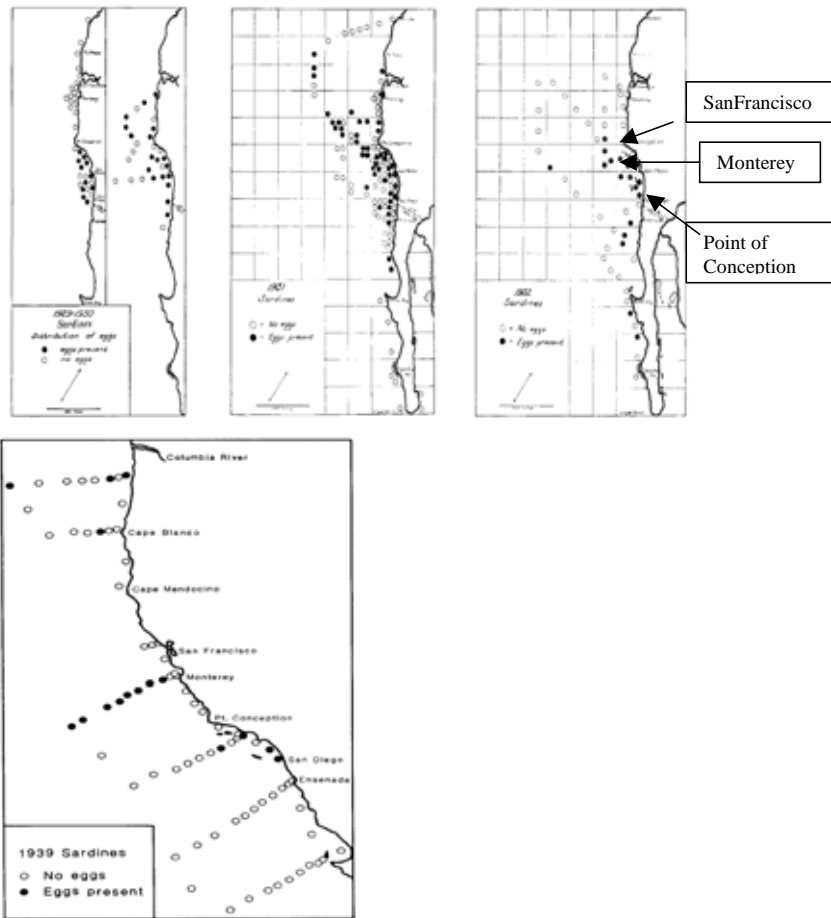


Figure 8 Above: Presence and absence of sardine eggs from surveys in 1929-32 off California. Below: May-June 1939 egg survey from Baja California, Mexico to Oregon, US. (from Smith, 1990)

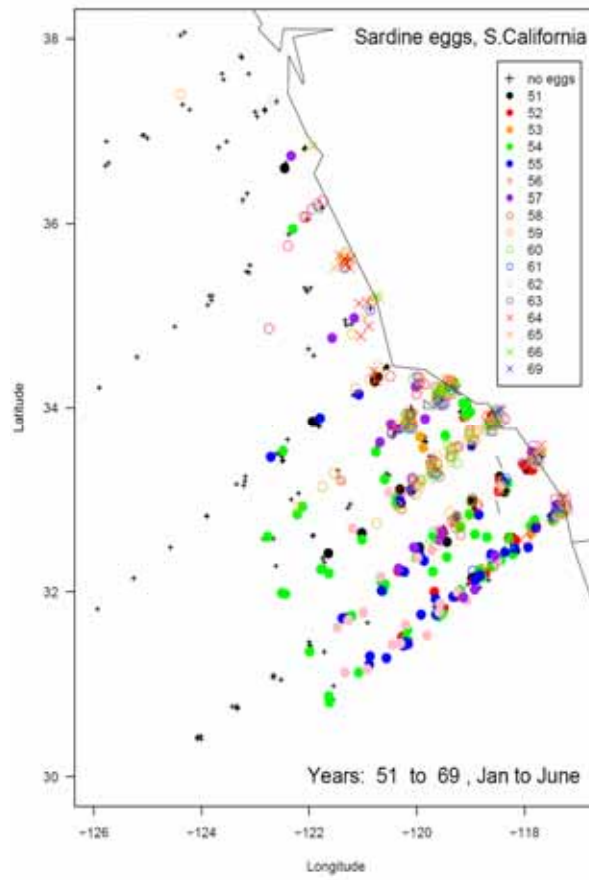


Fig. 9: Positive Bongo tows of sardine eggs in 1951-69 (left) and 1991-2005 (right)

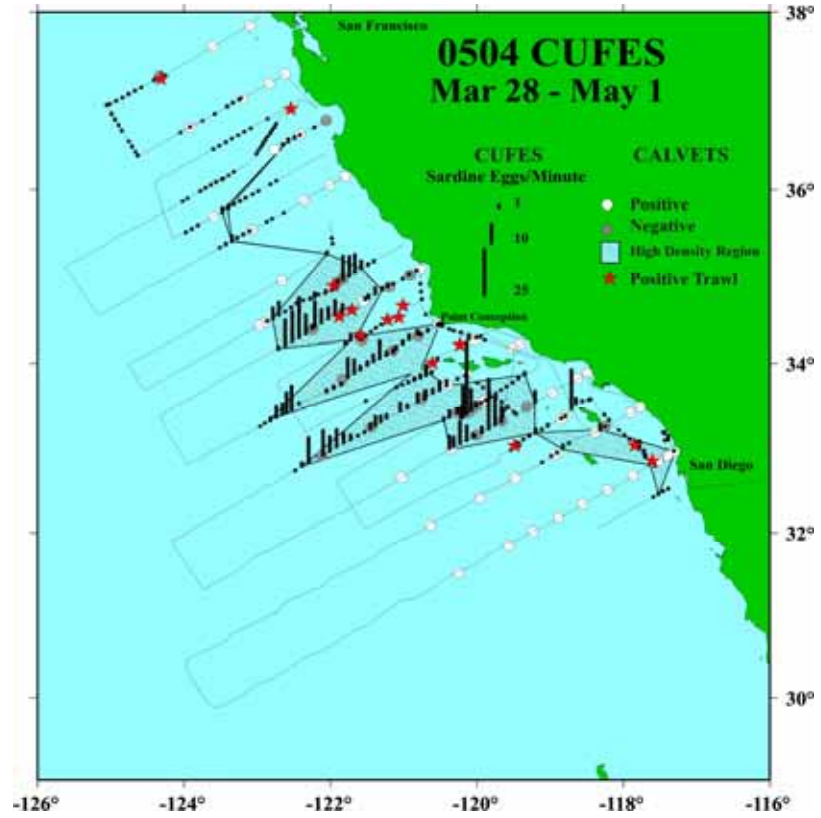


Fig. 10. The 0504 Daily egg production method (DEPM) Ichthyoplankton and trawl survey for Pacific sardine off California in March-May, 2005

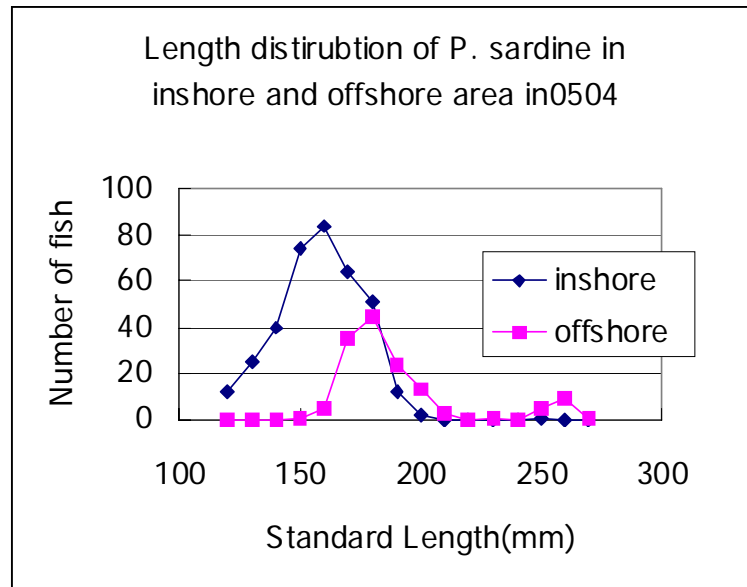


Fig. 11. Length distribution of Pacific sardine in inshore area (feeding area) and offshore area (spawning area) off California from 0504 DEPM survey in 2005.

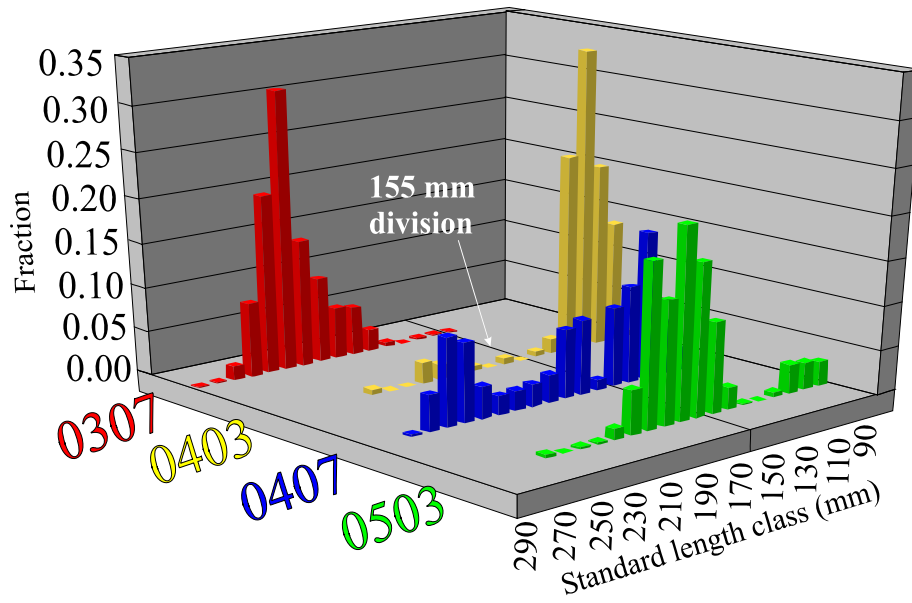


Fig. 12. Length distribution of Pacific sardine off NW during four surveys from July 2003-March 2005 (from Macewicz and Griffith, 2006).

Annex 6: The South African Sardine Population – evidence of entrainment? (by Janet Coetzee)

Background

The productive southern Benguela ecosystem off the South West coast of Africa supports large albeit fluctuating populations of small pelagic fish (Schwartzlose *et al.* 1999). Anchovy *Engraulis encrasicolus* and sardine *Sardinops Sagax* have been the dominant schooling fish of the pelagic system at different stages (Crawford *et al.* 1980, Crawford 1981, Crawford *et al.* 1987, Roel *et al.* 1994, Agenbag *et al.* 2003, van der Lingen *et al.* 2006). These fish are an important component of the ecosystem where their occupation of the mid-trophic level niche makes them important prey items for various top predators such as birds and marine mammals while at the same time exerting substantial predation pressure on zooplankton (Cury *et al.* 2000). In terms of commercial value, both anchovy and sardine form the basis of a large scale commercial purse seine fishery.

The fishery for Sardine off the west coast of South Africa started in the late 1940's (Crawford *et al.* 1980). Adult sardine were generally targeted for canning, although some juveniles were and are still caught as by-catch in the anchovy recruitment fishery on the west coast (Fig.1). Initially, unregulated fishing practices led to rapidly increasing, unsustainable catches of sardine off the west coast of South Africa during the 1950's. Catches of sardine eventually peaked at around 400 000 tons by 1962 (Fig. 2). Estimates of biomass during this period, from virtual population analyses, were estimated to fluctuate between one and two million tons. During the remainder of the 1960s and early 1970s, in an attempt to sustain catches of sardine which were rapidly declining, there was an expansion of the fishing ground for sardine southwards and eastwards as far as Cape Agulhas on the South west coast of South Africa (Crawford 1981, Roel *et al.* 1994). The continued high exploitation level, however led to an inevitable collapse of the sardine population. The sardine biomass remained at a very low level of less than 250 000 tons throughout the following two decades.

A fishery independent acoustic survey programme, which comprises two surveys annually, was initiated in the early 1980's (Hampton 1992, Barange *et al.* 1999) and a stock rebuilding strategy was implemented. This led to a slow, but persistent recovery of the sardine population throughout the 1990's (Cochrane *et al.* 1998, De Oliveira *et al.* 1998, Barange *et al.* 1999) and a total recovery by the turn of the century with the biomass reaching a peak of around 4 million tons by 2002 (Fig. 2) and recent catches have been in the order of 200 to 400 thousand tonnes annually (Fairweather *et al.* 2006).

Although the life history strategy of sardine is not well understood, it is assumed to be similar to that of anchovy which has been well documented (Crawford 1980, 1981, Shelton and Hutchings 1982, Armstrong *et al.* 1985, Shelton 1986, Hampton 1987, Hutchings *et al.* 1998). The South African sardine population has a distributional range that extends from the northern border of South Africa to the east coast of South Africa off Richard's Bay (Beckley and van der Lingen 1999). Most of the adult biomass is, however, located on the south west and south coast of the continent (Fig. 3) during their major spawning season from spring to late summer (Crawford 1980; Crawford *et al.* 1980; Armstrong *et al.* 1985, 1987, 1991; Hampton 1987, 1992; Shelton 1986; van der Lingen and Huggett 2003; Miller *et al.* 2006). Spawning products are transported west and northward, both by perennial wind induced surface currents as well as a jet current off the Cape coast (Shelton and Hutchings 1982; Nelson and Hutchings 1987; Fowler and Boyd 1998; Miller *et al.* 2006), to a nursery area that stretches along the nutrient rich inshore areas of the west coast. A return migration of juveniles southwards along the west coast is initiated during late summer/early autumn, with recruitment to the adult population on the Agulhas Bank occurring during autumn and winter (Hutchings 1992; Hutchings *et al.* 1998; Barange *et al.* 1999; Hutchings *et al.* 2002). While some sardine recruits are at times

also observed on the south coast during winter acoustic surveys, the bulk of sardine recruitment is from the west coast (Fig. 4).

Major changes in the distribution of sardine have been observed over the past 50 years in which the fishery has been operational with a gradual increase in catches further away from the west coast. While the fishery was initially concentrated on the west coast, North of Cape Town, resulting in intensive development of infrastructure related to fish processing centered around the harbour at St. Helena Bay, most of the sardine are currently caught off the south coast (Fig. 5) in the area east of Cape Agulhas and almost no sardine is caught off the west coast (Coetzee *et al.* 2006, Fairweather *et al.* 1996, van der Lingen *et al.* 2005, 2006). The distribution of sardine eggs collected during the summer acoustic spawner biomass surveys has also shown that spawning areas have changed several times (van der Lingen *et al.* 2005). Switches between west coast and east coast spawning have occurred frequently indicating unspecific selection of spawning habitat by sardine (van der Lingen *et al.* 2001, Twatwa *et al.* 2005, Miller *et al.* 2006). While a mechanism exists whereby eggs and larvae from south and east coast spawning may be retained on the south coast (Lett *et al.* 2006; Miller *et al.* 2006), transport models show reduced transport success from the south coast to the west coast nursery grounds compared to transport success of spawning products released further to the west (Miller *et al.* 2006). This may indicate that the success of spawning on the south coast may be compromised and result in fewer larvae and juveniles arriving at the west coast nursery area which is still the major source of recruitment.

Hypothesis for explaining changes in observed distribution patterns of the South African sardine population

Several hypotheses may help to explain the major shift eastward that has been observed in the distribution of South African sardine (van der Lingen *et al.* 2005, Coetzee *et al.* 2006):

- Fishery induced west coast depletion of fish stocks.
- Environmentally driven changes in spawning habitat selection
- Increased south coast spawning has resulted in natal homing of recruits to the south coast
- Basin model whereby recruits from the west spill over into secondary habitats to the south and east
- Entrainment of very strong 2001 to 2003 year classes by adults on the south coast

The entrainment hypothesis

The 'Entrainment hypothesis' states that maintenance of the life cycle depends on the establishment and sustainability of spawning migrations by repeat spawners who pass on the knowledge of migration patterns to the young (Corten 2002, McQuinn 1997, Petitgas *et al.* 2006).

Evidence for entrainment

While no demonstrative evidence is available to confirm that entrainment is indeed the mechanism which ensures or contributes towards persistence of the sardine life cycle spatial organization, some consistent and supportive evidence exists which suggests that entrainment could be important:

- The distribution of adult and juvenile sardine overlaps for a large part of the year, particularly in inshore areas on the south west coast which would allow for young fish to follow older fish to spawning areas.
- The non recovery of a successful spawning unit on the west coast after the initial collapse of the sardine population in the 1960s. Data from the fishery suggests

that the west coast was the preferred habitat of adult sardine from the start of the fishery in the 1940's up until the time of the collapse in the mid 1960's. Following the recovery of the sardine population, very little adult sardine have been found on the west coast, possibly leading to the inability of juveniles to be entrained on the west coast.

- While stocks at high abundance level are dominated by conservatism in the life cycle pattern, low abundance correspond to lower entrainment and thus to periods of higher vagrancy. This could have led to a larger number of recruits not being entrained on the south west coast in years of high recruitment, such as 2001 when the abundance of adults in this area was much lower than that on the south coast. Juveniles would in this case be more likely to colonize new habitats, or to be entrained by adults on the south coast.

Expansion of the south coast subpopulation—does the data suggest entrainment?

Analysis of distribution patterns, biomass estimates and length frequency distributions for the area west of Cape Agulhas (the south west coast) and the area east of Cape Agulhas (the south coast) may lend support to entrainment being the mechanism for the large shift observed in the sardine distribution. Data from both the summer (October/November) spawner biomass surveys and winter (May/June) recruit surveys need to be analysed in order to detect spatial trends in the data of both recruits and adults. Preliminary investigations of the data tend to support the following general statements:

- There is supportive evidence to suggest that the South African sardine population consists of two separate spawning subpopulations, one to the west of Cape Agulhas and the other to the east of Cape Agulhas, occupying the mid-shelf and offshore areas. These subpopulations are not genetically distinct and overlap may occur at times of high biomass when the distributions of both subpopulations expand. A third subpopulation may have existed on the west coast, north of Cape Point in earlier years (prior to the start of the acoustic time-series) based on location of the catches made by the fishing industry. Alternatively, this west coast spawning unit was merely an expansion of the south west coast subpopulation at times of high biomass during the period 1940 to 1960.
- Recruitment to both spawning units emanates predominantly from the west coast nursery area which may be seeded from both subpopulations. Successful transport of spawning products from the south coast subpopulation to the west coast nursery area may, however, be reduced (low recruitment since 2004 even though the overall adult biomass was high). The south coast subpopulation may also benefit (to a lesser degree) from local south coast recruitment resulting from retention of eggs and larvae inshore on the south coast.
- The earliest acoustic survey data (1984) available suggests that a small south coast adult subpopulation was already in existence and that the size of this subpopulation increased during the 1980's, although in terms of absolute numbers the sardine population was dominated by the west and south west coast subpopulation.
- For years in which the abundance of the south west coast subpopulation is low, a relatively larger number of juvenile fish are not retained on the south west coast, but continue to migrate eastward past Cape Agulhas and may therefore be more likely to get entrained by adults of the south coast subpopulation.

Possible consequences of entrainment for the South African sardine population.

If entrainment was indeed the mechanism whereby a large part of the strong year classes (between 2001 and 2003) colonized the south coast, the recovery of the adult population on the south west coast may not be straightforward. This is because conservatism of the life cycle pattern relies on having sufficient adults in a subpopulation to sustain life cycle patterns. Alternatively, a large number of recruits would need to play the role of colonizers on the south west coast and remain there to spawn. The protection of old adults, who hold the memory of

life cycle patterns, would be a more feasible and less risky option for maintaining subpopulation diversity.

Entrainment by adults of the south coast subpopulation may, in the case of the South African sardine, have negative consequences contrary to the positive life cycle closure benefits suggested in other regions where entrainment ensures the maintenance of successful spawning migration patterns through passing on learned information from the adults to the young. If successful recruitment in the South African sardine population is compromised by a decrease in transport efficiency of spawning products from the south coast adult subpopulation to the dominant nursery grounds on the west coast, continued entrainment of recruits to the south coast subpopulation would be counterproductive to the overall growth of the sardine population. Evidence of this has been witnessed since 2003 where the bulk of sardine spawning has occurred on the south and east coast and very low recruitment has been measured in subsequent years.

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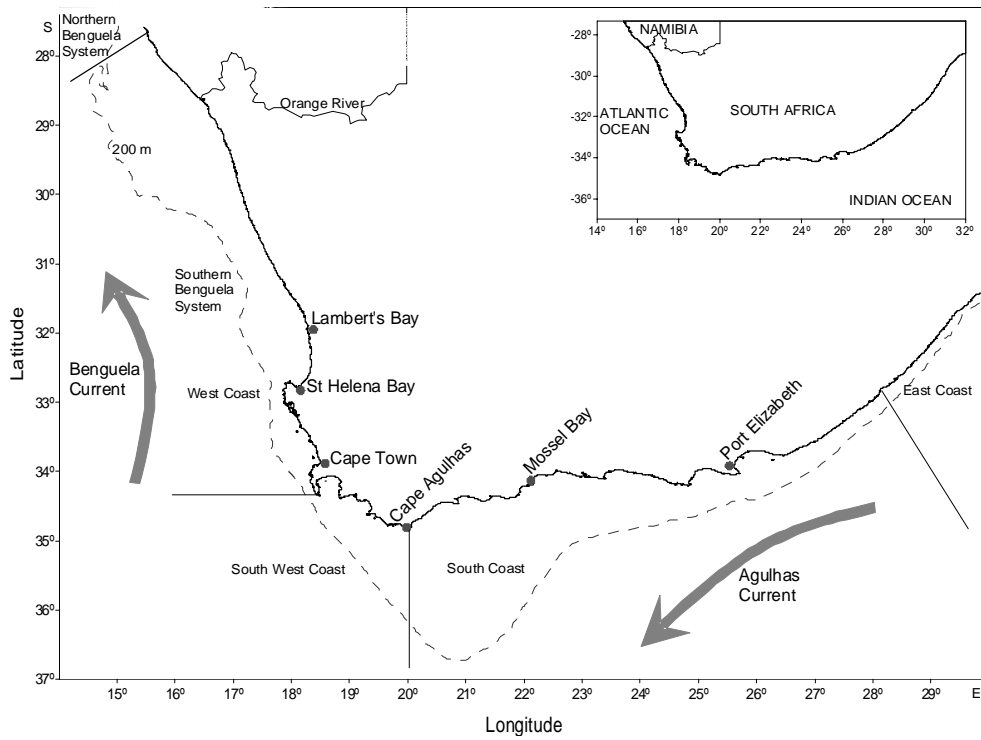


Fig. 1. Map of the coast of South Africa indicating place names and geographic location of areas mentioned in the text.

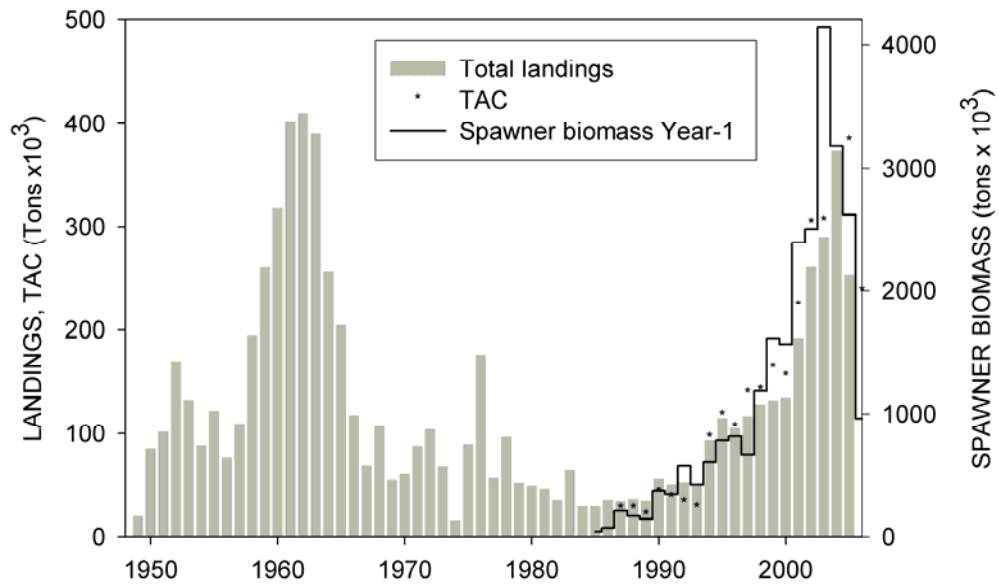


Fig. 2. Catches of sardine made by the purse seine fleet since 1949 and estimates of biomass from acoustic surveys since 1984.

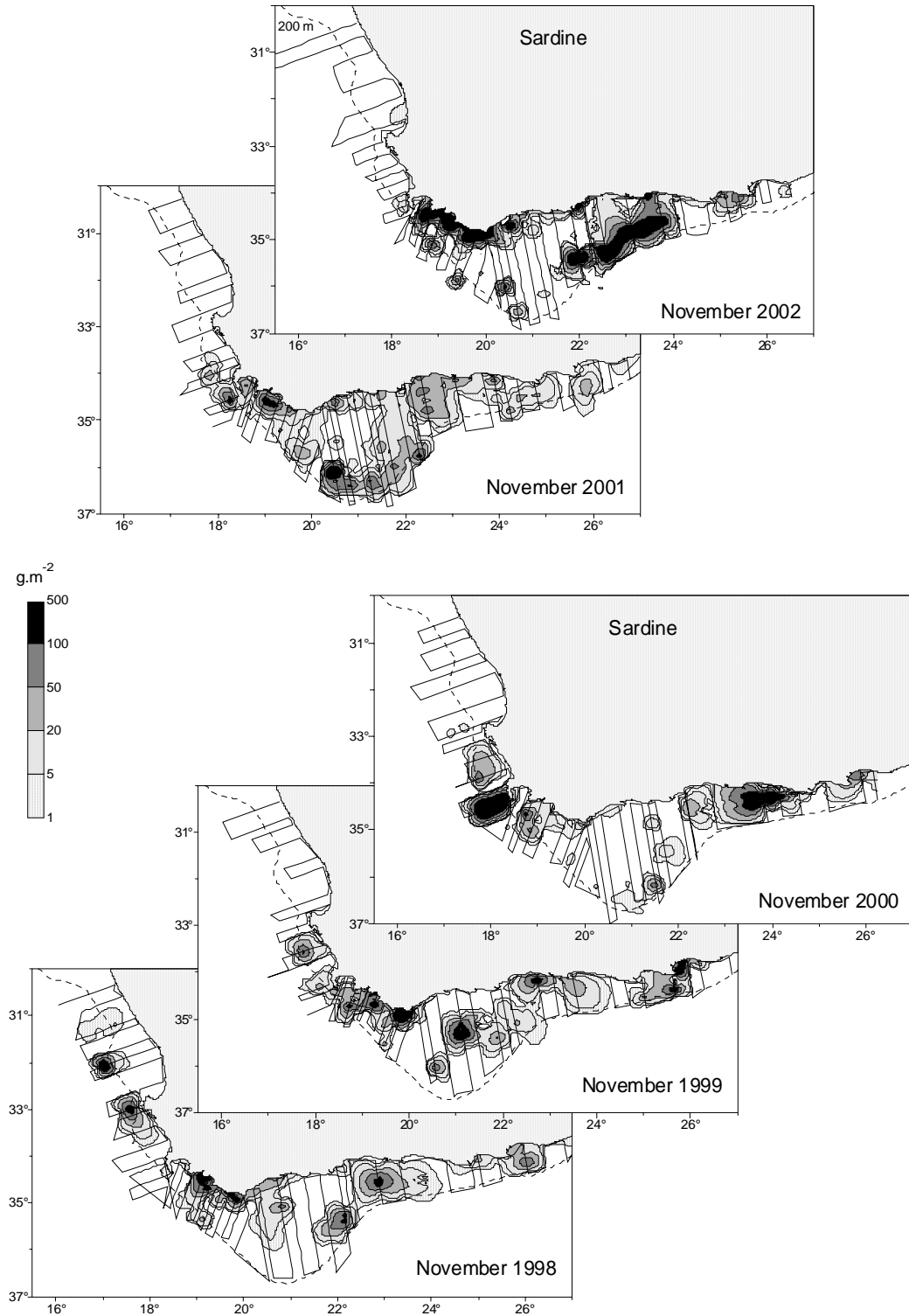


Fig. 3. Distribution and relative abundance of sardine as measured during summer spawner biomass surveys between 1998 and 2002.

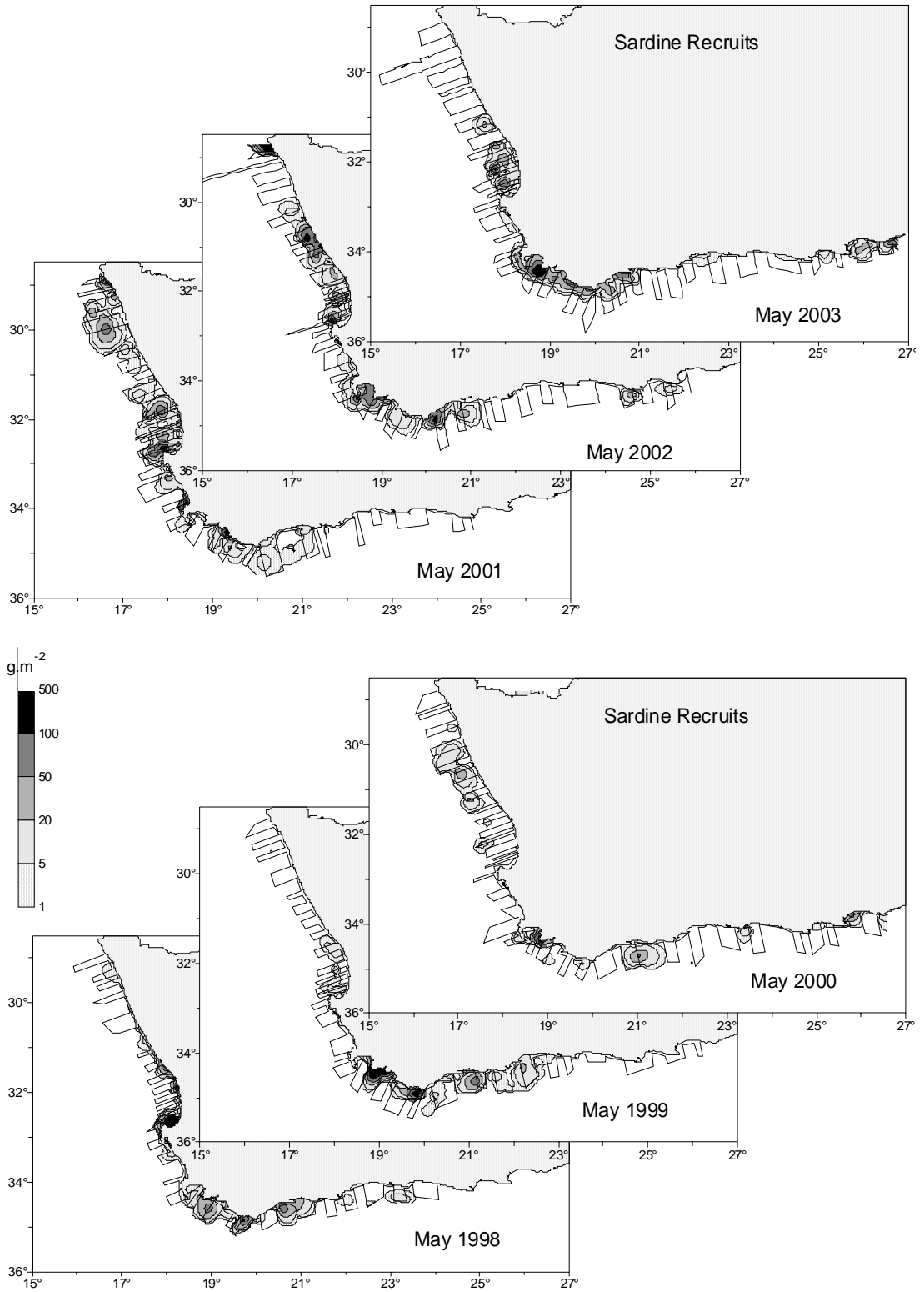


Fig. 4. Distribution and relative abundance of sardine recruits as measured during winter recruitment surveys between 1998 and 2003.

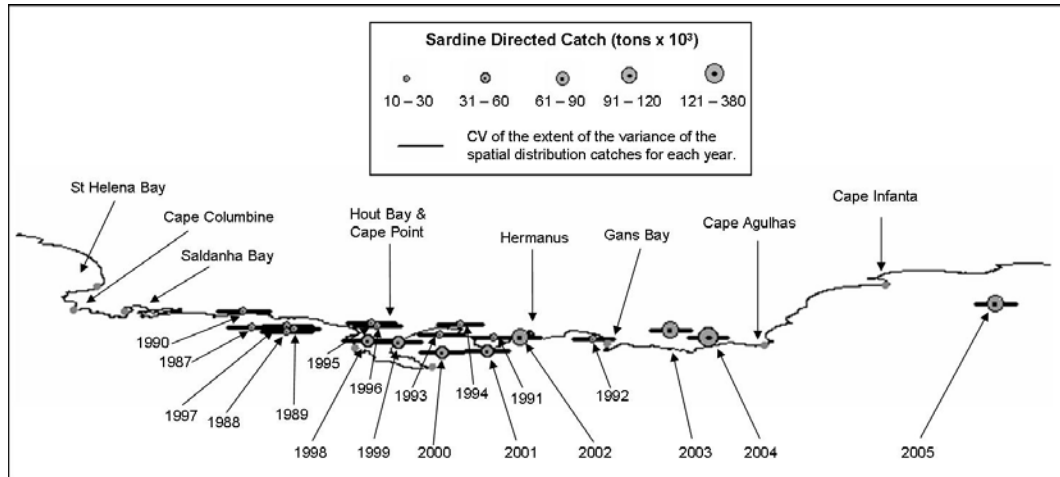


Fig. 5. Annual catch centroids for sardine depicted on a linearised South African coastline. Each point represents an annual centroid and point size is proportional to total catch for that year (From Fairweather *et al.* 2006).

Annex 7: Atlantic Bluefin Tuna (*Thunnus thynnus*) (by David Secor)

Ecology and Population Structure

The Atlantic Bluefin Tuna, *Thunnus thynnus*, occurring in the Atlantic Ocean epitomizes form, size, and energetics adaptive to highly migratory behaviour. The largest member of the tuna family (Scombridae), high demand over the past several decades particularly for the fatty flesh of giant Bluefin Tuna (>130 kg) has contributed to declining abundances of Atlantic bluefin tuna caught in coastal waters adjacent to North America (Magnuson *et al.* 1994; Fromentin and Powers 2005). The species matures late in life (females at ages 3 and 10 years for Mediterranean and Western Atlantic populations, respectively) and can reach longevity in excess of 30 years. Migratory behaviours of Atlantic Bluefin Tuna cause them to be harvested in jurisdictional waters of many countries, as well as in interjurisdictional regions. The high worldwide demand for giant Atlantic bluefin tuna and the fish's migratory behaviours dictate careful international management of this species. Yet failure by EU nations to effectively monitor and regulate harvests has now placed the species in particular jeopardy (ICCAT 2006).

Atlantic Bluefin Tuna occur throughout northern latitude Atlantic waters and historically ranged from Brazilian to Norwegian waters. Despite pan-oceanic distribution, spawning habitats are hypothesized to be restricted to the Gulf of Mexico and the eastern Mediterranean Sea. Conventional tagging studies have revealed low rates (<5% on average) of transoceanic migrations by both juveniles and adults (Magnuson *et al.* 2004; Rooker *et al.* In Press). Disparate spawning regions and past evidence for low rates of transoceanic migrations; together with recent electronic tagging, genetic, and otolith microconstituent studies support the concept of two separate spawning populations for Atlantic Bluefin Tuna (Nemerson *et al.* 2000; Fromentin and Powers 2005; Rooker *et al.* In press).

"Anomalous" Occurrences and Possible Entrainment

Tunas often show anomalous occurrences, where migrations are highly variable and apparently related to the effects of climate change, ocean circulation and related changes in prey distribution (Povlina 1990; Kimura *et al.* 1997). The high maintenance demands by tunas engender a higher dependence on exploratory behaviours to attain sufficient energy. Atlantic Bluefin Tuna are peculiar among tunas in having a temperate distribution and in the Atlantic Ocean historically bluefin tuna ranged between Brazil and Norway. Indeed important historical fisheries persisted off Brazil in Norway in the 1960s, but abruptly disappear in the 1970s (Figure 1). Fonteneau and Soubrier (1996) speculated that these previous "frontier" fisheries for adult Bluefin Tuna occurred on unique segments of the population. These frontier contingents may have been lost initially because they were more vulnerable to the effects of exploitation. Once lost, conservatism of migration pathways within other contingents, could have precluded reinvasion of these historical feeding areas. Thus, the lack of recovery of these contingents is consistent with the idea of conservatism of entrained migratory pathways.

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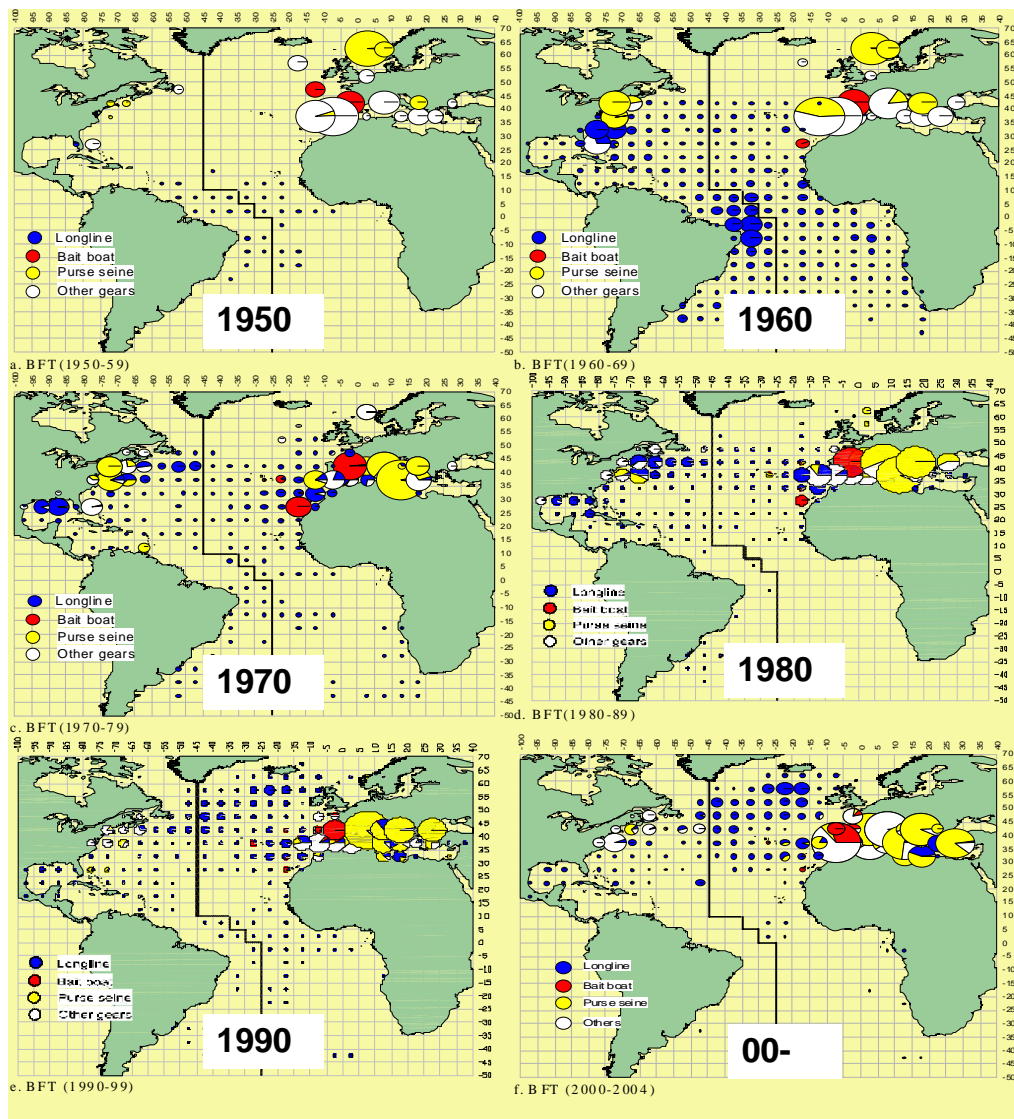


Fig. 1. Evolution of fisheries for Atlantic Bluefin Tuna from ICCAT database (modified from ICCAT 2006). Note large landings of purse seines off Norway and longline gear off Brazil for the 1960s.

Annex 8: Anadromous temperate sea basses, White Perch (*Morone americana*) and Striped Bass (*Morone saxatilis*) (by David Secor)

Zoogeography and Phylogeny

White Perch and Striped Bass are members of the temperate sea bass group, Moronidae. Based upon adult characters and early life history attributes, Johnson (1984) placed the temperate sea basses *Morone*, *Dicentrarchus*, *Lateolabrax* and *Sinoperca* into the single family Moronidae. Prior to this revision, Gosline (1966) had placed these genera into the polyphyletic Percichthyidae. Waldman (1986) provided a more comprehensive morphometric analysis of *Morone* sp. and concluded that Moronidae should not include *Lateolabrax* and *Sinoperca*, but that *Morone*, *Lateolabrax* and *Perca* (Percidae) showed very strong taxonomic affinities despite disparate family membership. While genetic affinity among these taxa has not been reported, strong taxonomic affinities suggest a common phylogeny among temperate sea basses.

In North America, there exist two estuarine associated anadromous moronids, White Perch and Striped Bass and two exclusively freshwater species: White Bass (*Morone chrysops*) and Yellow Bass (*Morone mississippiensis*). Secor (2002) suggested that this guild of estuarine and freshwater moronids was likely derived from a marine ancestor, which had a similar life history to *Dicentrarchus* and *Lateolabrax* species. Life cycle diversity is quite apparent in White Perch and Striped Bass and may have contributed to exploitation of new habitat types (Tsukamoto and Aoyama 1998; Secor 2002).

Life History and Ecology

White Perch and Striped Bass are anadromous, spawning in freshwater tidal reaches of major estuaries along the broad coastal plane of eastern North America. White Perch complete their life cycles in estuaries (Mansueti 1961), whereas some fraction of Striped Bass will emigrate into coastal waters and undertake seasonal migrations, which can range over 1000 km (Secor and Piccoli 2007). White Perch tend not to occur at salinities greater than 15 (Kraus and Secor 2005). Striped Bass migrate widely along the North American Continent. For instance, Chesapeake Bay population striped bass are known to migrate seasonally from North Carolina to New England waters.

The two species vary considerably in age at female maturation, and maximum size and age. In the Chesapeake age at maturation is c. 3 and 6 years, maximum size 35 and 140 cm, and longevity 15 and 35 years for White Perch and Striped Bass, respectively (Secor *et al.* 1995; Secor 2000; Kraus and Secor 2004). Both species exhibit strongly varying year-class strength, in part due to ephemeral spring conditions that can cause high mortalities of eggs and larvae (Secor and Houde 1995). As a possible consequence of highly variable recruitment, both species fairly long lived (Secor 2000; 2007).

The two species are ecologically and economically important in estuarine and coastal waters. Striped Bass are major piscivores, which can exert top down control (Hartman and Brandt 1995). White perch in many years are the dominant demersal fish in the Chesapeake and other major estuaries (Jung and Houde 2003). Both species support important commercial and recreational fishes. Indeed this group ranks second in importance among US marine recreational fishes. In 2005 commercial landings of Striped Bass were valued at 15.8 million dollars, US; recreational value of both species would be considerably higher.

Estuarine Dependency, Contingent Structure and Entrainment

For Striped Bass and White Perch, estuarine dependency during the larval and juvenile stage is obligate. However, during sub-adult and adult stages, the two species exhibit variable

patterns of estuarine and/or coastal habitat use. Based upon otolith microchemistry of Hudson Striped Bass, Secor (1999) concluded that groups of fish - "contingents" - could be classified based upon their life-time occurrence in estuarine v. coastal habitats (Figure 1). Further, otolith elemental fingerprints were distinct for individuals that spent the majority of their sub-adult and adult life in freshwater, estuarine, or marine habitats (Secor *et al.* 2001). For White Perch, some individuals complete their life cycles in freshwater, whereas others utilize brackish portions of the estuary (Figure 3) (Kraus and Secor 2004; Kerr and Secor, unpublished).

The divergence in behaviours by either migratory or sedentary contingents within populations of anadromous temperate basses occurs early in ontogeny, approximately during the larval-juvenile transition (Figure 1) (Kraus *et al.* 2004). Early divergence in migratory behaviour suggests an early switchpoint, consistent with a conditional strategy or partial migration. The data supports that early divergence in migration behaviours has lifetime consequences in later patterns of habitat use. On the other hand, mid-life behavioural reversals have been observed where formerly resident contingents become migratory and vice versa (Figure 2) (Zlokovitz *et al.* 2003; Secor and Piccoli 2007; Kerr and Secor, unpublished).

Mid-life changes in migration behaviours could be consistent with the entrainment hypothesis. Here resident individuals overlap in distribution with migratory individuals during the spawning season when contingents mix. Certain individuals adopt the alternate contingent's behaviour. Note that this type of entrainment contrasts with that proposed to explain diversity in spawning units in Atlantic Herring (McQuinn 1997). For White Perch and Striped Bass, only a single spawning unit occurs, yet multiple life cycles exist within each spawning unit (aka population).

Testing the entrainment hypothesis for White Perch or Striped Bass could be feasible through acoustic tagging experiments. Resident and migratory components of a population could be tagged during summer or fall and then tracked through the subsequent period of overlap. Remote arrays of acoustic receivers could make this study more efficient (Figure 4). In general diadromous species could be more tractable in studies of entrainment and partial migration given the curtailed distribution of habitats that sedentary contingents utilize.

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Contingent behavior

Each contingent
 “maintains its integrity
 by engaging in a
 distinct pattern of
 seasonal migrations
 not shared by fish of
 other contingents”
 Clark 1968

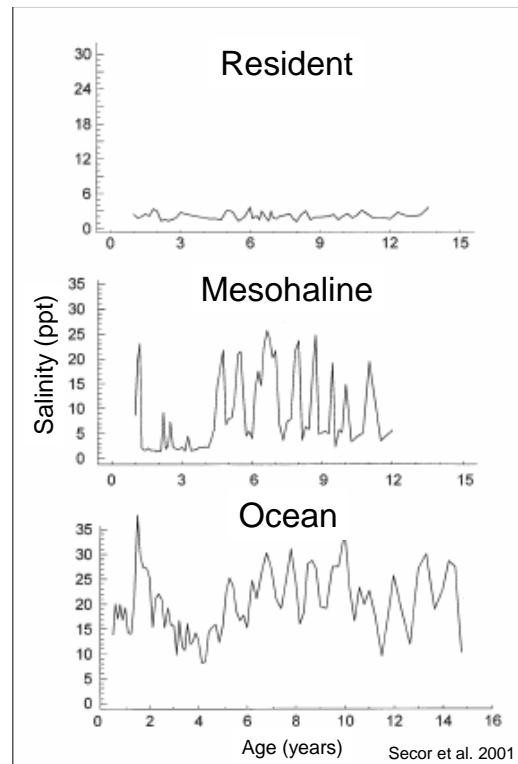
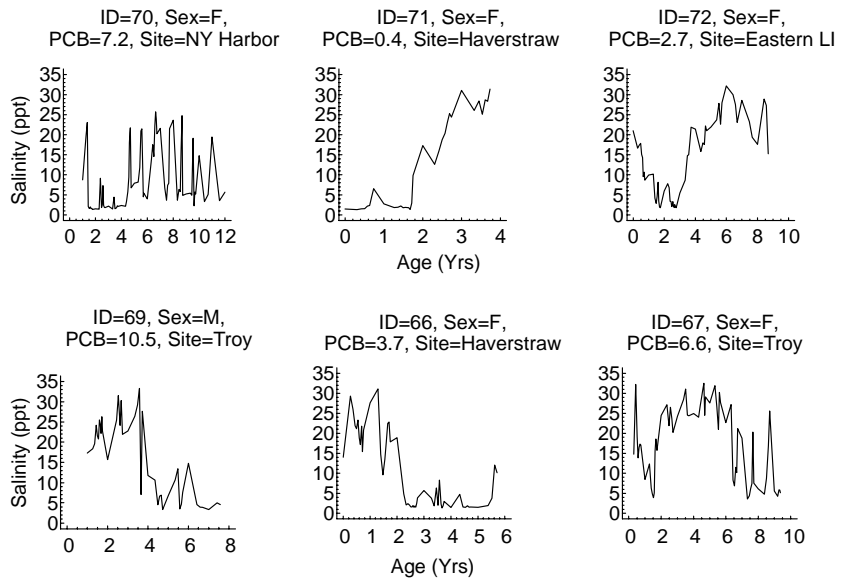


Fig. 1. Life history profiles of Hudson River striped bass based upon analysis of otolith Sr:Ca. Each plot represents an individual fish’s longitudinal exposure to differing salinity levels (inferred by tracer Sr). Each individual represents a contingent, a group that initiates early divergence in migratory behaviour that persists throughout the fish’s life. From Secor *et al.* 2001.

Habitat Shifts - Fall



Habitat Shifts - Spring

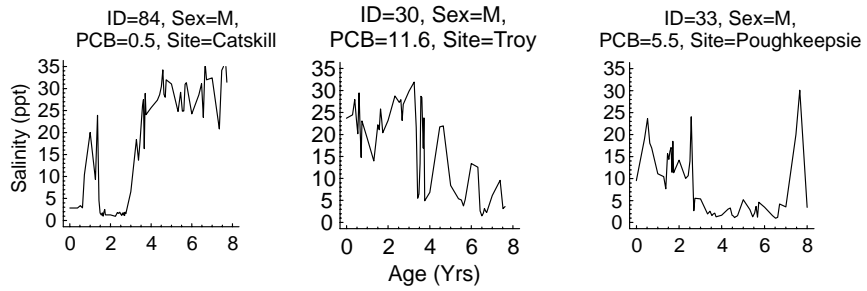


Fig. 2. Life history profiles of Hudson River striped bass showing evidence of mid-life migration changes, possibly consistent with the entrainment hypothesis. From Zlokovitz *et al.* 2003).

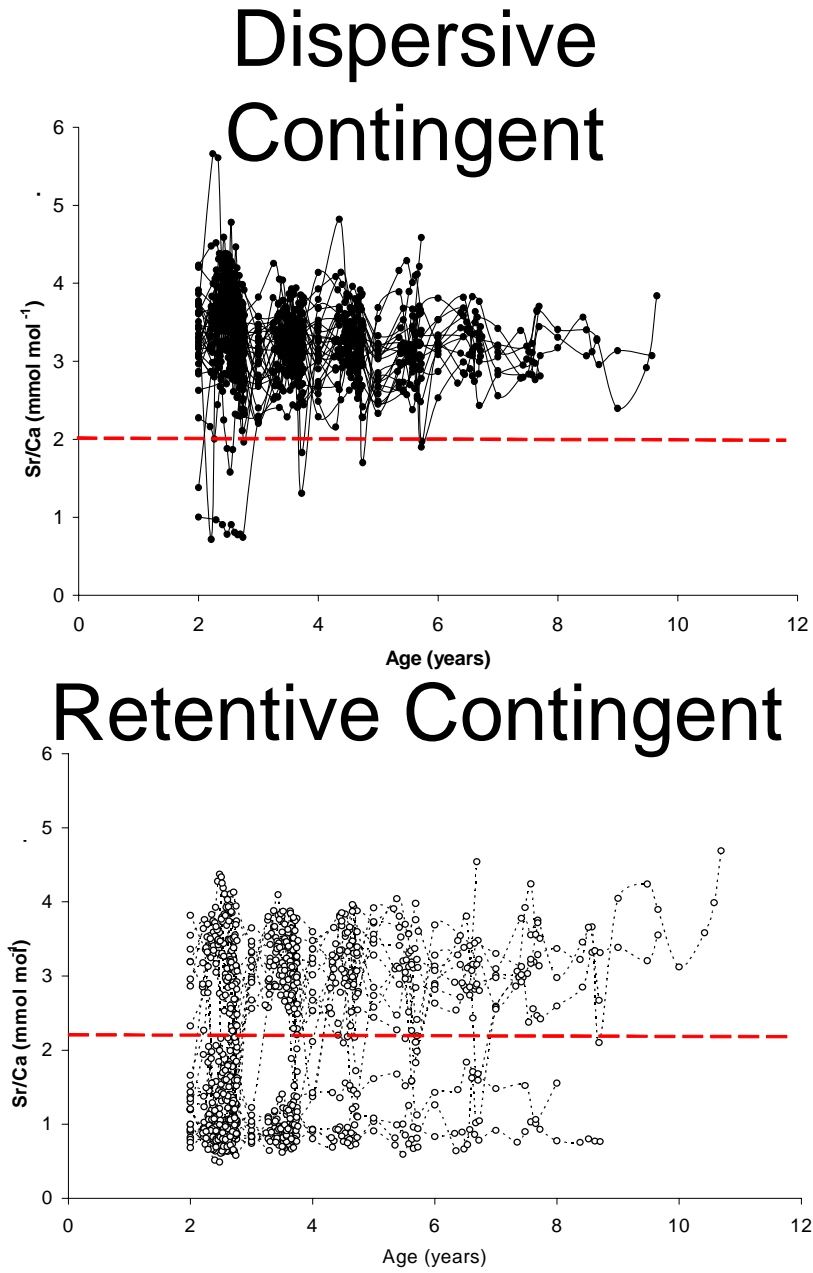
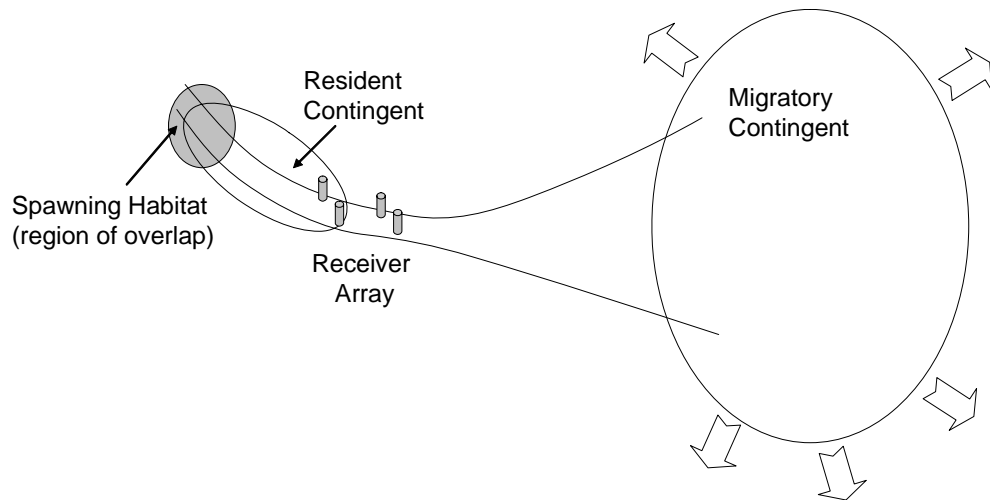


Fig. 3. Life history profiles of Chesapeake Bay white perch (Patuxent River) for a migratory and resident contingent. The dashed line demarcates behaviours associated with residency in freshwater (below line) or brackish water (above line). Note that for the resident contingent, many individuals become migratory at various adult ages, possibly the result of entrainment (Kerr and Secor, unpublished).



Experimental Protocol to Test Component of Entrainment Hyp. for an Anadromous Species

1. Electronically tag each contingent during period of habitat separation
2. Monitor through mobile and fixed array receivers during period of habitat overlap (migratory contingent returns to spawning area and overlaps with resident contingent).
3. Evaluate whether changed migration behaviors occur after habitat overlap.

Fig. 4. Possible configuration for a test of a component of the Entrainment Hypothesis for an anadromous species.

Annex 9: Population structure of whiting (*Merlangius merlangus*) in the North-East Atlantic and adjacent waters (by Gregory Charrier)

Species description

Whiting (*Merlangius merlangus*) is encountered on soft bottoms between 10 and 200m, from Portugal to Iceland and northern Norway (two sub-species have also been described in the Mediterranean, Adriatic, Black and Aegean seas). *M. merlangius* is widely distributed within the North Sea, and despite some substantial variations in the spatial distribution reported for the species in this area, no clear patterns of collapse/recovery of spawning units have been detected (fig. 1). During the spawning period, fish aggregations are still identified over years in three main areas: (1) the north-western area, from Flamborough Head to the Shetland Islands, (2) Southern Bight and (3) the Skagerrak/Kattegat area. There is a wide spatial overlap between immature fish (< 2 years old), new recruits (2 years old) and more experienced individuals, thus providing a favorable situation for entrainment mechanisms between younger and older whittings.

M. merlangus grows very fast during the first year and then the growth speed decreases. Moreover, the inter-individual variability in growth is very important, thus inducing a large overlap in size between year-classes. Most of the fish are mature at two years old and the spawning period occurs from January to July in function of the latitude. In addition, the spawning period of females extends over 14 weeks (Hislop *et al.* 1991), thus providing a high potential for gene flow between spawning units with possible migrations of mature females between distinct spawning grounds during their long period of sexual maturity. The fecundity of whiting is relatively high in comparison to other gadids (Russell 1976). The pelagic life is longer than in other gadoids: after a larval pelagic phase common to all Gadidae, young individuals >12 mm long live in commensalism with jellyfishes (*Cyanea sp.* or *Chrysaora sp.*) and finally move to the seabed when they reach a length of 5 to 10 cm to assume a demersal life (Quéro & Vayne 1997). As a consequence, the young life-stages of *M. merlangus* are characterized by a wide potential for dispersal from spawning areas. The long pelagic stage, associated to the extended spawning period of females and their large fecundity may potentially ensure a high connectivity of population units over large areas.

Review of population structure investigations

Despite the high potential for dispersal of *M. merlangus*, considerable evidence of substantial population structure has been reported around the British Isles, on the basis of several approaches, including meristic counts (Gamble 1959), parasitic infestation studies (Kabata 1967, Hislop & MacKenzie 1976, Pilcher *et al.* 1989), tag-recapture data (Williams & Prime 1966, Hislop & MacKenzie 1976) and genetics (Charrier *et al.* 2007). In particular, parasitic infestation studies and tag-recapture data have suggested limited mixing during adult demersal life between whiting populations from southern and northern North Sea and along the western margin of the British Isles (fig. 2). Concerning the North Sea, these results are supported by genetics that have underlined a significant genetic structure within this area based on microsatellite markers (Charrier *et al.* 2007), with a significant genetic heterogeneity between (1) Southern Bight, (2) Flamborough Head and (3) northern samples (e.g. Dogger Bank and southern Norwegian coast) (fig. 4; see fig. 3 for sampling locations). Furthermore, genetic data provided evidence of a more complex population structure within the North Sea than suggested by other studies, with the identification of a significant differentiation of a population located in the area of Flamborough Head. The Dogger Bank has been hypothesized to act as a physical barrier reducing mixing between northern and southern North Sea. Moreover, the segregation of population units could be associated with the Flamborough front

separating mixed water of the southern North Sea from seasonally stratified waters of the central and northern North Sea. Passive dispersal in the central and northern North Sea may be limited also by cyclonic patterns of water circulation in this area (Brown *et al.* 1999), thus preventing mixing between the populations at the larval and juvenile pelagic stages. This isolation during early developmental stages, between the southern and northern North Sea, is well supported by the differences observed in the number of vertebrae in whiting from north and south of the Dogger Bank (Gamble 1959). Indeed, given the fact that meristic traits are fixed during early-life development and are largely influenced by environmental factors (Lindsey 1975), such differences in vertebrae counts may thus indicate the existence of discrete larval retention systems associated with particular hydrographic features. However, oceanographic retention systems of pelagic stages may not be sufficient by themselves to maintain genetic differentiation in limited areas of the North Sea. For this, it appears essential that adults repeatedly return to spawn with relatively high fidelity to their natal spawning area.

Along the western margin of the British Isles, genetic data have shown a lack of genetic differentiation (fig. 4) that may result, at least in part, from the widespread dispersal of the young pelagic stages through passive drift with the current systems (Charrier *et al.* 2007). Passive dispersal may be ensured from Porcupine Bank to northern Scotland by the general north-northeasterly drift of the North Atlantic Current and possible advection by the Shelf Edge Current (Pingree & Le Cann 1989), as demonstrated for blue whiting *Micromesistius poutassou* and mackerel *Scomber scombrus* (Bartsch & Coombs 1997, 2004). The genetic homogeneity observed off the west of UK mainland contrasts with the phenotypic differentiation detected in the same area by Kabata *et al.* (1967) on the basis of gall-bladder parasites (fig. 2), that have indicated a low degree of mixing of adults between population units along the western coasts of the British Isles (as within the North Sea). This suggests that gene flow may be ensured essentially during the larval pelagic phase and that adults may acquire a substantial degree of fidelity to the spawning unit they have adopted. Thus, natal homing appears unrealistic in whiting and the entrainment hypothesis seems more probable to explain the fidelity of individuals to spawning areas. When hydrographic factors prevent larval dispersal to neighboring populations, like in the North Sea, young fish would most likely recruit to their natal population and adopt the behaviour patterns of that population. In this case populations may exhibit both genetic and phenotypic differentiation. In more dispersive environments, such as that to the west of the British Isles, the passive dispersion of young stages may be substantial, and thus a significant number of juveniles would likely recruit to neighboring populations. This hypothesis is well supported by tag-recapture data of Garrod & Gambell (1965) which showed that a large part of the Irish Sea and Clyde whiting recruits may come from a common spawning ground located on their boundaries. Therefore, populations may be phenotypically differentiated without any genetic structure.

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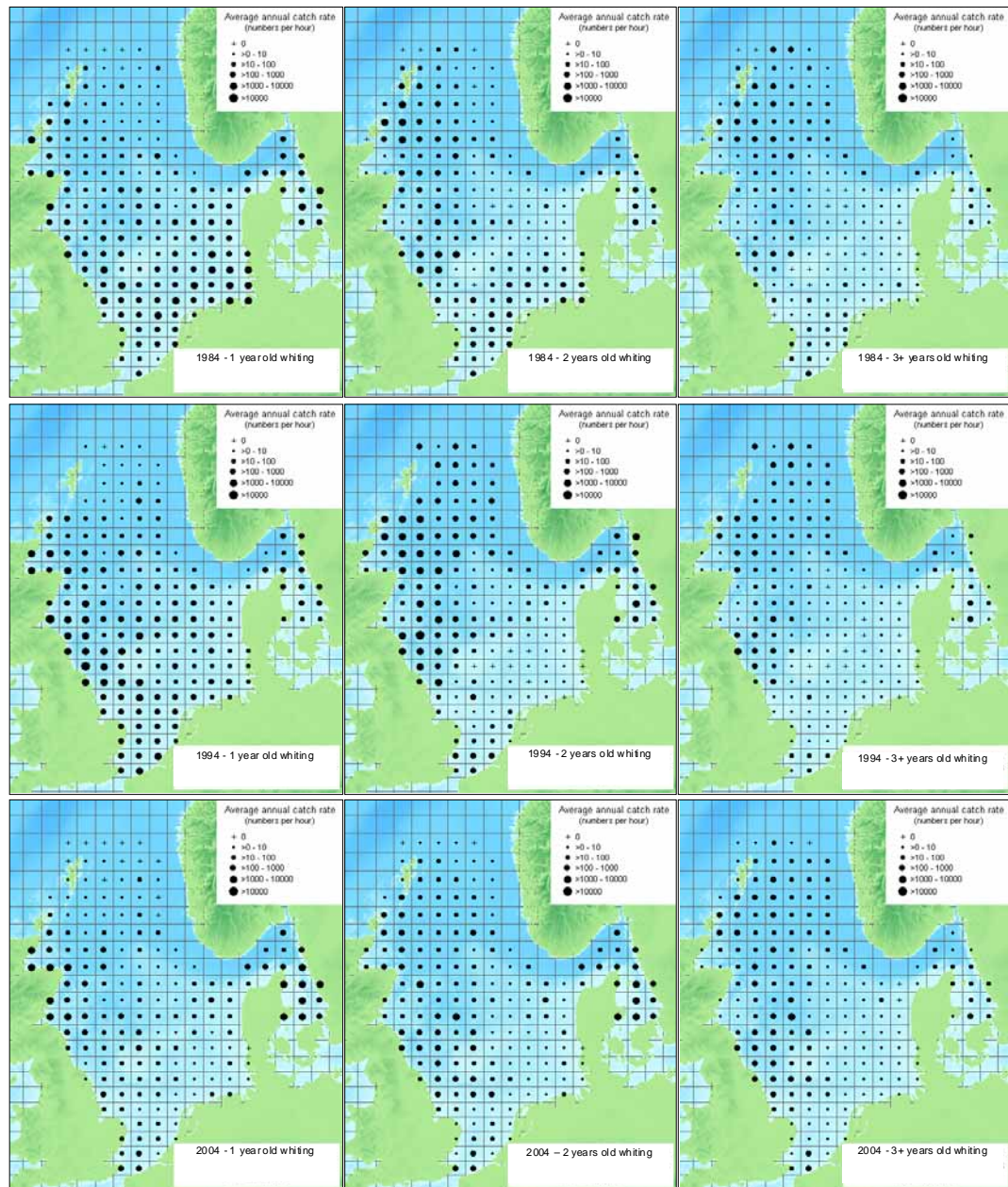


Fig. 1: Distribution of the whiting catch rate for the IBTS surveys conducted during the first quarter of the year in 1984, 1994 and 2004: juveniles (1 year old), new recruits (2 years old) and experienced adults (3+ years old). Distribution maps acquired from the ICES Fishmap (<http://www.ices.dk/marineworld/ices-fishmap.asp>).



Fig. 2: Population units identified on the basis of gall-bladder parasites by Kabata (1967) and supported by other parasite infestation studies and tag-recapture data (Williams & Prime 1966, Hislop & MacKenzie 1976, Pilcher *et al.* 1989)

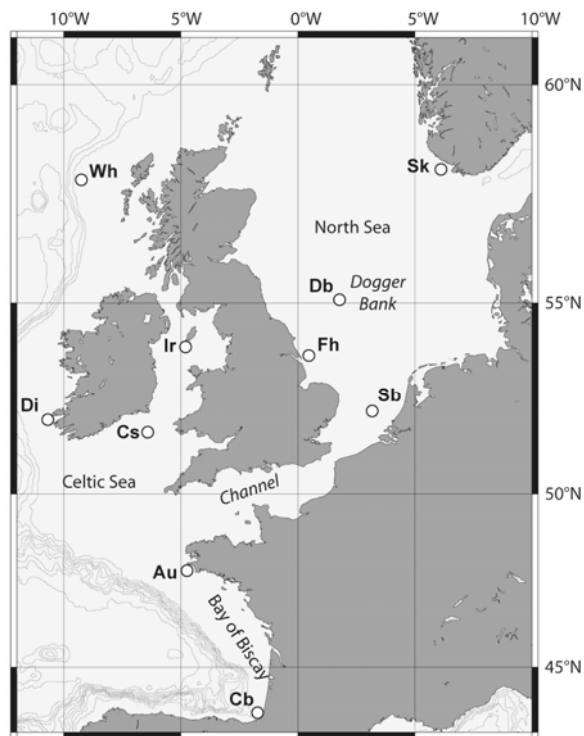


Fig. 3 (right) Sampling locations for the population genetics study of Charrier *et al.* (2007): Cap Breton (Cb), Bay of Audierne (Au), Celtic Sea (Cs), Dingle (Di), Irish Sea (Ir), Western Hebrides (Wh), Southern Bight (Sb), Flamborough Head (Fh), Dogger Bank (Db) and Skarvöyni (Sk).

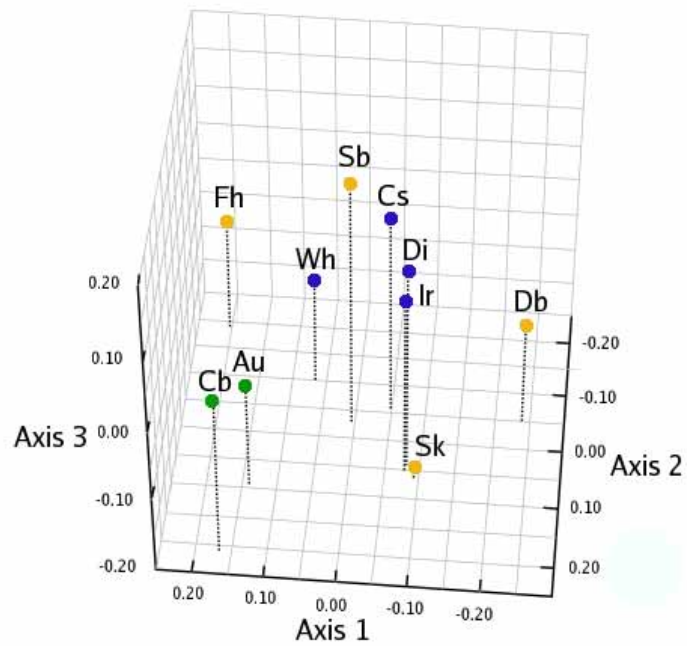


Fig. 4: Arrangement of the samples on the three first axes of the principal components analysis performed on allele frequencies of microsatellite markers (Charrier *et al.* 2007): (1) North Sea samples in orange, (2) areas along the western margin of the British Isles in blue and (3) Bay of Biscay locations in green (see fig. 3 for the sample codes).

Annex 10: Bay of Biscay anchovy: do adults facilitate the adoption by recruits of schooling behaviour and habitat occupation? (by Pierre Petitgas)

This note compiles biological information gained in acoustic surveys in spring on spawning adults and in autumn on juveniles. A hypothesis is build explaining the acquisition of adult-like schooling behaviour of juveniles. The importance of adults as facilitators is hypothesised to explain the non recolonisation of lost habitats off the Spanish coast.

Historical changes in the fishery

The anchovy fishery has experienced important changes since the 1960s (Fig.1; see also ICES, 2004; Junquera, 1984). In the 1960s and 70s, the fishery for anchovy in the Bay of Biscay was mainly Spanish and vessels operated off the Spanish coast. Highest catches are observed in that period. At the end of the 70s the catches dropped. In the mid-80s, a french fishery developed and the spatial distribution of the catches changed as an autumn fishery on the french platform developed replacing so to speak that off the spanish coast in earlier years. Nowadays, anchovy is sporadically fished off the spanish coast.

Recruitment of juveniles to the adult population : observations

Larval drift, as simulated by the Ifremer hydrodynamic model for the Bay of Biscay (Allain *et al.*, 2003), seed the off shore areas of the Bay of Biscay and the Spanish coast with larvae born on the major spawning ground off the Gironde estuary along the French coast. Though this seeding does not seem to contribute to the colonisation of the Spanish coast as the majority of the juvenile and adult anchovies are seen on the French shelf (Fig. 2). Juveniles surveys have allowed to observe in autumn the young of the year (age-0 or juveniles) in two configurations (Petitgas *et al.*, 2004): off-shore or over of the mid-shelf independent from the adult population forming typical juvenile aggregations staying in sub-surface day and night (Fig.3); and in coastal waters mixed with the adult population forming typical adult-like schools that undertake day/night aggregation/de-aggregation cycles (Fig.4). On Figs.3 and 4, age-0 fish of similar length shows different schooling behaviour when independent from adults off-shore and when mixed with adults in coastal waters.

Entrainment into a particular schooling behaviour : interpretation

Couzin *et al.* (2005) and Huse *et al.* (2002) have shown by individual based behavioural modelling that 5% of experienced fish may entrain a school of naïve fish into reproducing the experienced behaviour. Fig. 5 suggests a mechanism of spatial overlap facilitating the entrainment of age-0 fish into an adult-like schooling behaviour. The juveniles form aggregations in the surface layers by day and night and move towards the coast. When in the coastal waters juveniles and adults are mixed at night in the surface layers. At dawn, when experienced adults form schools again, they may entrain juvenile fish in this behaviour which is then learned by the young fish. The length distribution of ages classes overlap very much (Fig. 6) making the previous mechanism plausible.

It is hypothesised that the acquisition of the adult-like schooling behaviour has the selective advantage of decreasing predation mortality and therefore facilitates the colonisation of the coastal habitats by the young of the year. Only a few percentage of adults in the schools would be necessary. It is not understood why juveniles do not colonise the coastal waters along the spanish coast: are there then not enough adults ?, is natural and fishing mortality too high ?

Remaining questions

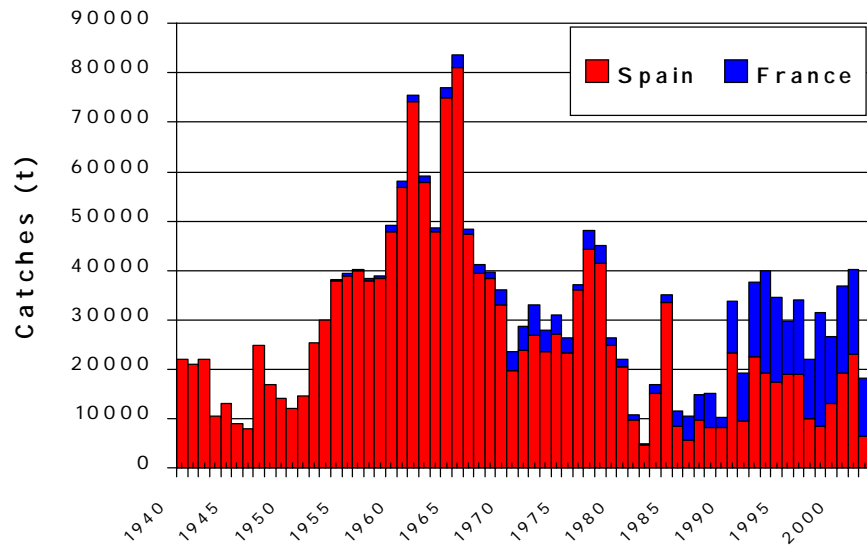
What are the cues for the supposed innate juvenile migration towards coastal waters ?

Does the adult-like schooling behaviour prevent predation mortality (even fishing mortality) in comparison to the juvenile aggregations that are less active ?

In Biscay, juvenile anchovies independent from adults have not been observed in coastal waters and therefore it is not known whether the adult-like schooling behaviour is innate or not. But there are observations in other areas (e.g., Mauritania: Ad Corten; South Africa: Janet Coetzee, comm.pers.) that would tend to say that adult-like schooling is innate. Though there might be facilitation and more rapid acquisition of the behaviour when adults are present.

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Spatial evolution of the fishery:

- a : Spring fishery first half of XXth century (up to 1960), mostly spanish.
- b : Spring fishery (1966-1975), mostly spanish.
- c : Spring Spanish fishery since mid-eighties
- d : Summer-Autum French fishery since mid-eighties

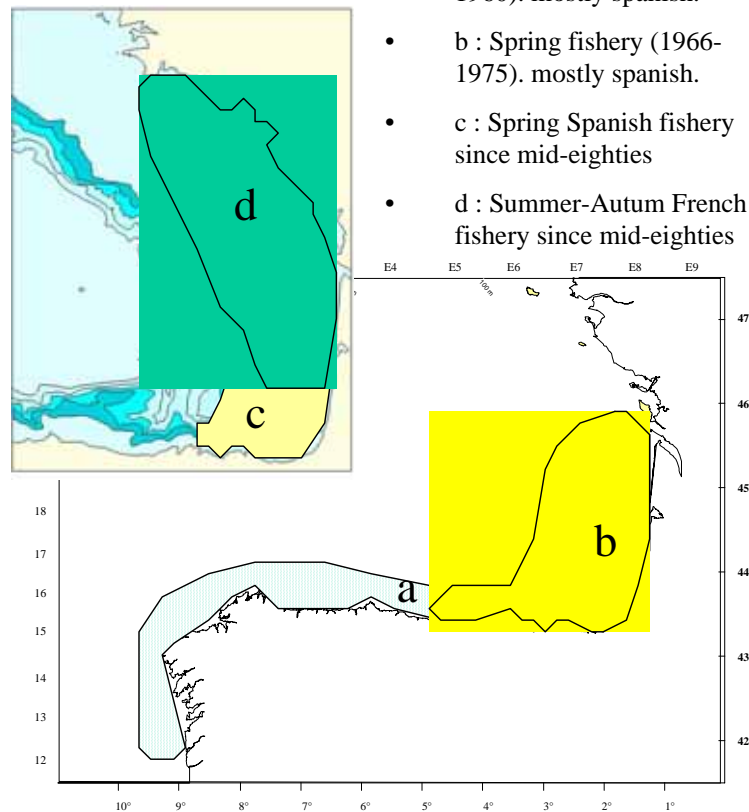


Figure 1: Historical changes in the characteristics of the fishery for anchovy in the Bay of Biscay in the catches (above) and in the spatial distribution of the fishing grounds (below). (after ICES, 2004).

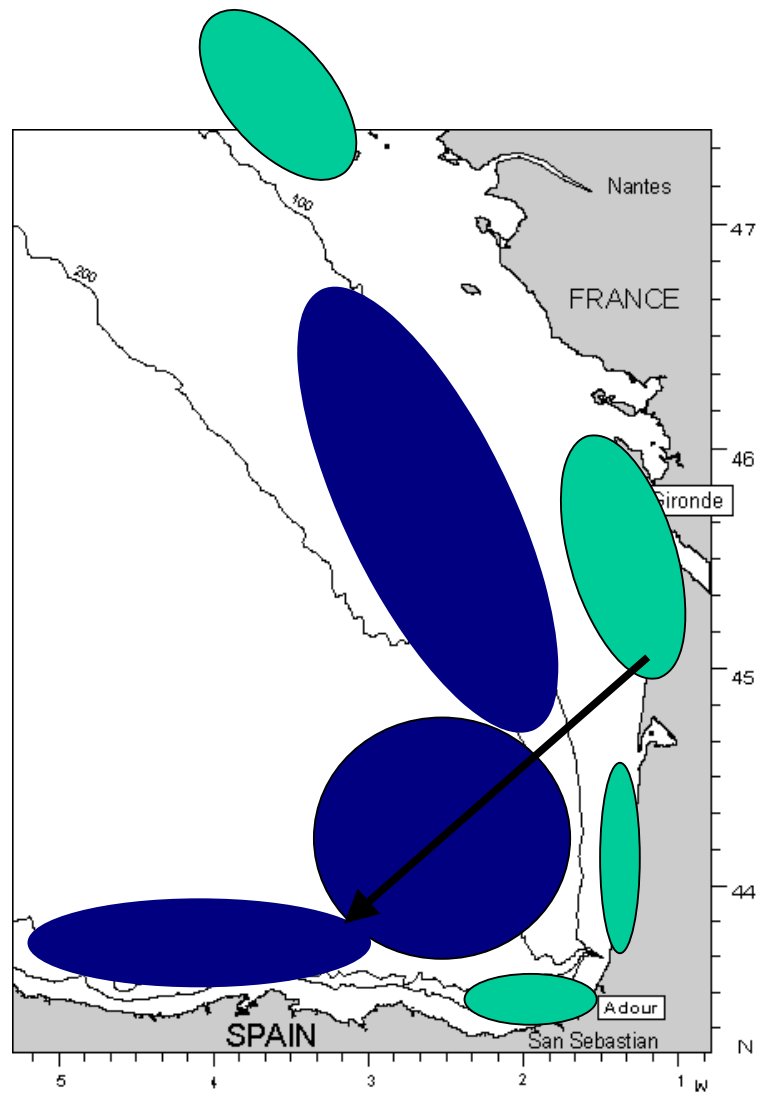


Fig. 2: Schematic diagram showing the spatial distribution of young of the year (YoY) anchovy in autumn. Blue : areas where the YoY are found independent of the adult population ; green : areas where they are found mixed with the adult population (age1+). The diagram based on the acoustic surveys Juvaga 2003 and 2005 of Ifremer (Petitgas *et al.*, 2004 and 2005). The black line shows the direction of larval drift from the major spawning ground to the SW based on larval drift simulations (Allain *et al.*, 2003).

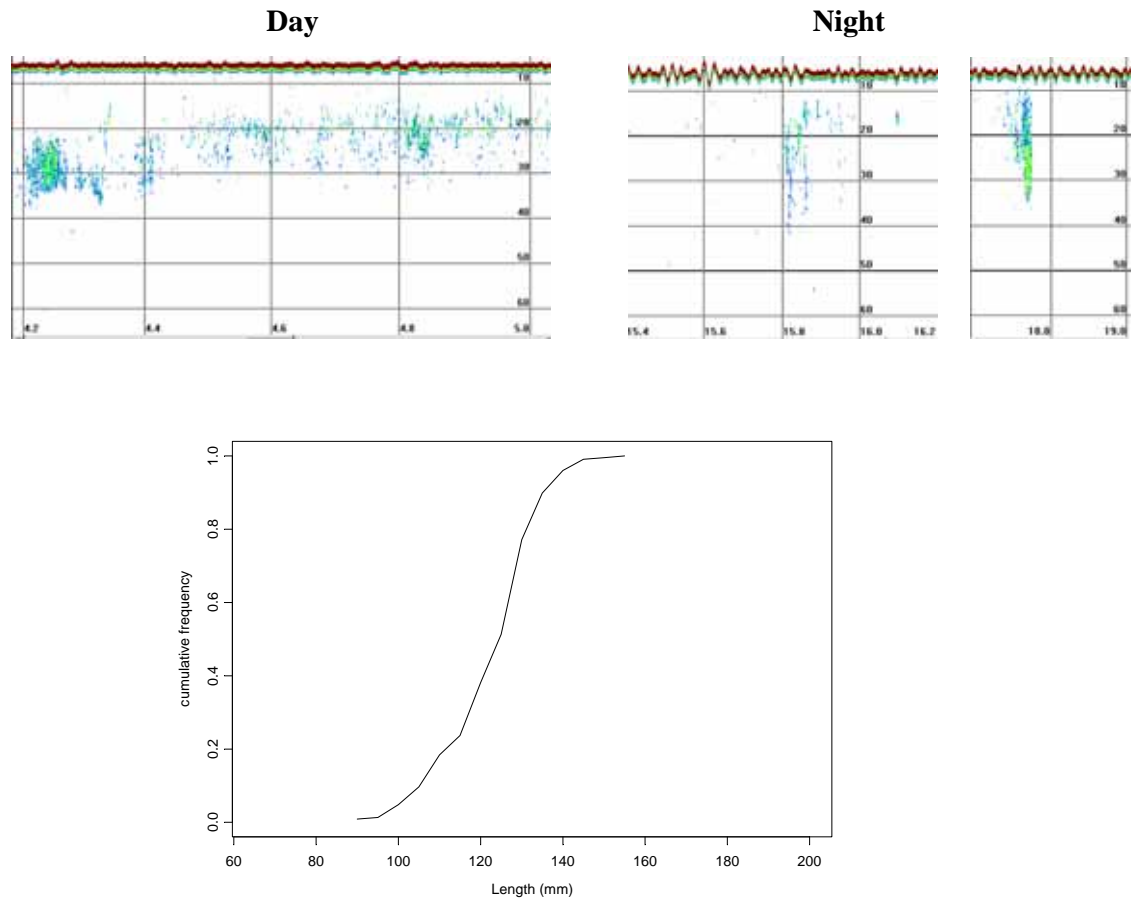


Fig.3. Above: Echogram recorded at 10 knots showing typical sub-surface (0-30m) aggregation of age-0 anchovy independent from adults by day (left) and night (right). Acoustic survey Juvaga03 of Ifremer, October 2003, Trawl station 15 on mid-shelf. Below : Cumulative length distribution of age-0 anchovy sampled at Station 15.

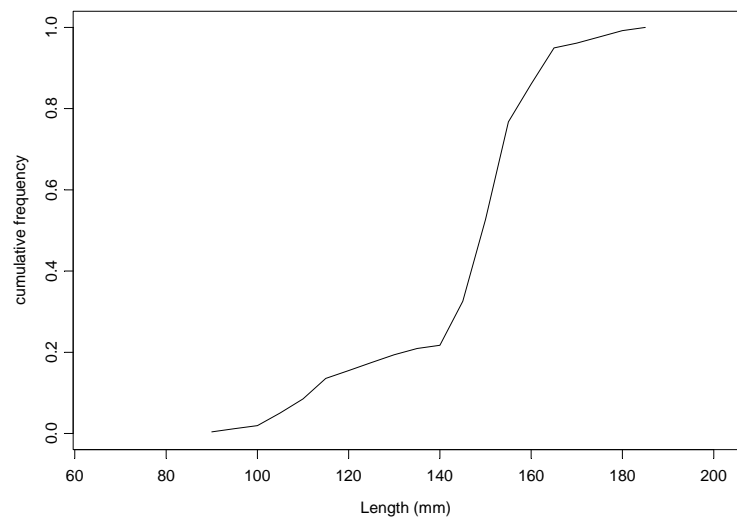
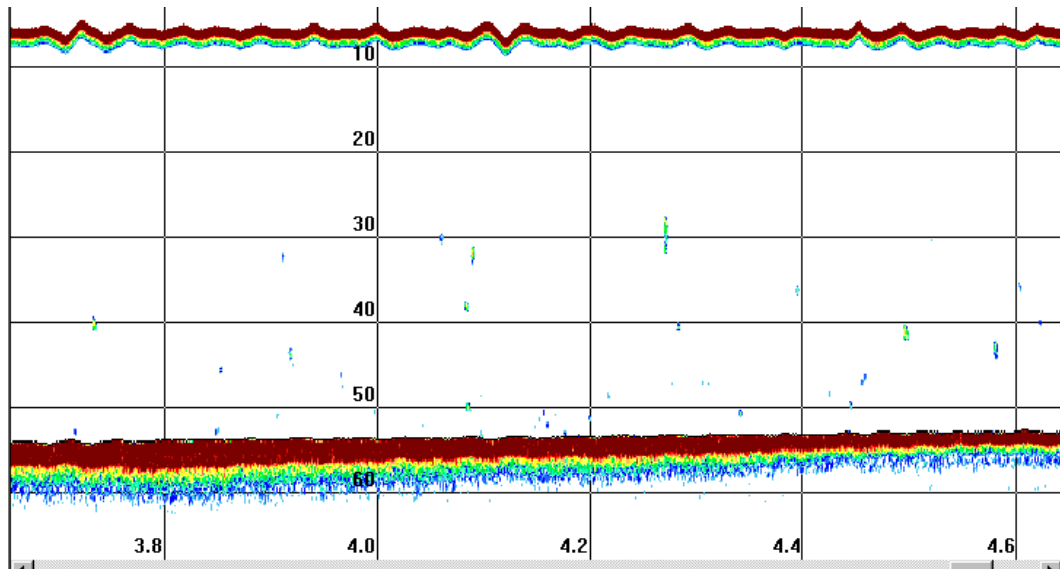


Fig. 4. Above: Echogram recorded at 10 knots showing typical adult-like schools of anchovy by day. Acoustic survey Juvaga03 of Ifremer, October 2003, Trawl station 11 in coastal area off Gironde. Below : Cumulative length distribution of anchovy sampled at Station 11 containing a mixture of juvenile age-0 and adult age-1+ anchovies.

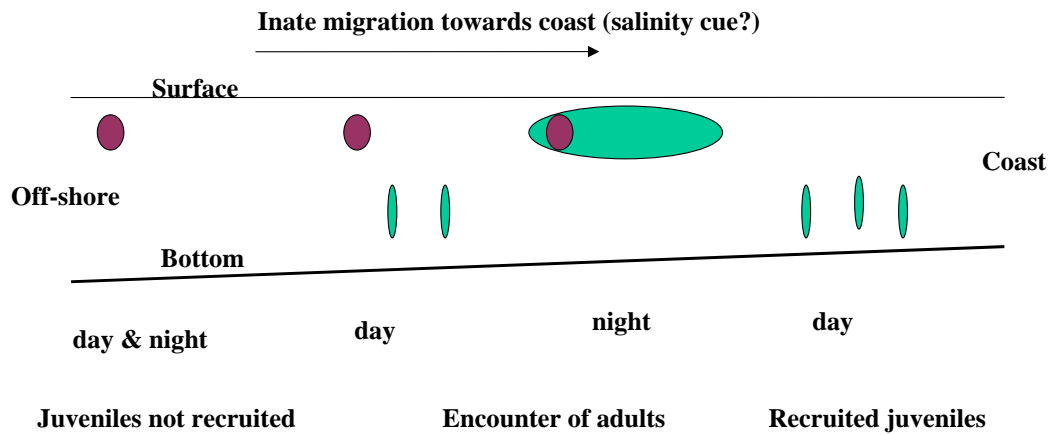


Fig. 5: Schematic diagram showing how juveniles may encounter adults in the coastal areas by spatial overlap at nights at the surface and switch from juvenile-like schooling behaviour to adult-like schooling behaviour. Purple : juvenile schools by day and night ; green near bottom : adult-like schools during day ; green at surface : adult-like desegregated schools at night

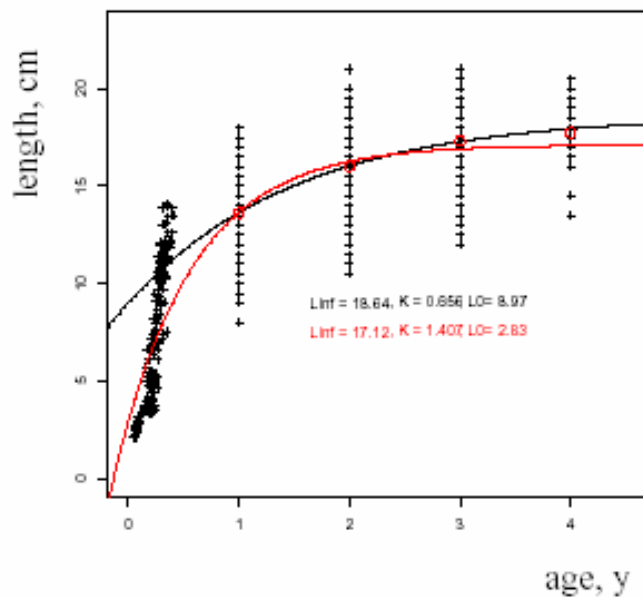


Fig. 6: Anchovy growth curve based on otolith age readings of individual anchovies sampled during the acoustic surveys of Ifremer in spring (Pelgas 2000-2005) and in autumn (Juvaga 2003, 2005). Note the overlap in length between large age-0 and small age1+ fish. The van Bertalanffy growth parameters fitted when including age-0 (red) are: $L_{inf}=17.12$, $k=1.40$, $L_0=2.83$ and excluding age-0 (black) : $L_{inf}=18.64$, $k=0.65$, $L_0=8.97$.

Annex 11: Evidence sheets of case studies

North west Atlantic Herring				
What to test	Evidence For	Population	Reference	
Demonstrative evidence				
Recruit spawners of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2	According to the comparison between hatching season (otolith characteristics) and spawning season (maturity stages), significant numbers of recruits from one seasonal spawning populations spawn with members from the other.	West coast Newfoundland herring	McQuinn (1997b)	
Some recruit spawners from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism				
Supportive evidence				
Change in behaviour when recruits come in contact with "entrainers" : social facilitation				
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners	Herring spawn in waves over a protracted spawning season, the older herring usually spawning first, with the younger herring and recruits spawning in subsequent weeks, but with an overlapping size and age distribution	southern Gulf of St Lawrence herring	Jean (1956); Lambert and Ware (1984); Lambert (1987); Lambert and Messieh (1989)	
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);				
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.				
Lack of age-specific genetic differences between population units	No temporally stable genetic differences have been observed between sympatric herring populations.		Grant (1984); Rymann et al. (1984); King et al. (1987); Dahle and Eriksen (1990); Safford and Bookey (1992); Kornfield et al. (1982); Kornfield and Bogdanowicz (1987)	
Consistent evidence				
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	After each spawning event, the spent adults entrain from the nursery areas those juveniles which are ready to undertake their first annual migration	West coast Newfoundland herring	McQuinn and Lambert (1991)	
Colonization of abandoned spawning grounds is predominantly by recruits.	Georges Bank was recolonised primarily by the 1983 year-class which was large throughout the Gulf of Maine. Survey data support the theory that herring recolonized the Georges Bank region in stages from adjacent components during the late 1980s, most likely from herring spawning in the Gulf of Maine.	Georges Bank herring	Stephenson et al. (1990); Smith and Morse (1993); Overholtz and Friedland (2002)	
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).	Overexploitation in the early 1980s virtually eliminated the older individuals in the population. At that same time, their winter migration to south-western Newfoundland ceased. This traditional migration pattern has not been re-established, despite the rebuilding of the population in the 1990s.	southern Gulf of St Lawrence herring	Winters (1978); Winters and Beckett (1978); Cleary (1983)	

North Sea Herring						
What to test	Evidence For	Population	Reference	Evidence Against	Population	Reference
Demonstrative evidence						
Juveniles of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2						
Some juveniles from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism						
Supportive evidence						
Adults of unit 1 are found spawning with adults of unit 2	Herring with different otolith characteristics are found on the same spawning ground	Aberdeen Bank				
Change in behaviour when recruits come in contact with "entrainers" : social facilitation						
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners						
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);	Spawning grounds where the population is removed by overfishing remain unused, even when neighbouring populations do recover	Southern and central North Sea	Corten 2002			
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.	Central North Sea unit has not recovered; more clearly separated units (Northern and Southern) have recovered.					
Lack of age-specific genetic differences between population units	lack of genetic differences		Mariani et al. 2005			
Consistent evidence						
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	Mixtures of juvenile and adult herring are found in the central North Sea prior to spawning time	all North Sea populations	ICES survey reports IBTSWG			
Colonization of abandoned spawning grounds is predominantly by recruits.	New spawning populations are established by recruit spawners; in subsequent years these are followed by younger year-classes	Aberdeen Bank	Corten 1999a			
Colonization of abandoned spawning grounds is predominantly by recruits.	Georges Bank was recolonised primarily by the 1983 year-class which was large throughout the Gulf of Maine. Survey data support the theory that herring recolonized the Georges Bank region in stages from adjacent components during the late 1980s, most likely from herring spawning in the Gulf of Maine.	Georges Bank herring	Stephenson et al. (1990); Smith and Morse (1993); Overholtz and Friedland (2002)			
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).	Overexploitation in the early 1980s virtually eliminated the older individuals in the population. At that same time, their winter migration to south-western Newfoundland ceased. This traditional migration pattern has not been re-established, despite the rebuilding of the population in the 1990s.	southern Gulf of St Lawrence herring	Winters (1978); Winters and Beckett (1978); Cleary (1983)			

Norwegian Spring-Spawning Herring						
What to test	Evidence For	Population	Reference	Evidence Against	Population	Reference
Demonstrative evidence						
Recruit spawners of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2	After feeding, existing unit entrain recruit spawners to adopt existing migration to wintering areas	Norwegian Spring spawning herring	Huse et al. (2002); Huse et al. (submitted)			
Some recruit spawners from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism	Six changes in wintering area during last 50 years strongly correlated with high ratio of recruit spawners to existing population. Also examples of establishment of new spawning and feeding areas in years with numerous recruit spawners in relation to existing population. Though circumstantial, repetition of pattern gains evidence strength.		Huse et al. (2002); Huse et al. (submitted)			
Supportive evidence						
Change in behaviour when recruits come in contact with "entrainers" : social facilitation	period 1965-66 : old and young components of the population were disconnected: different feeding and winter areas. Degree of determination of leaders: young entrained old to feeding ground in 1967		Jakobsen 1969			
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners	Herring spawn in waves over a protracted spawning season, the older herring usually spawning first, with the younger herring and recruits spawning in subsequent weeks		Devold et al. (1963). Huse et al. (2002); Couzin et al. (2005);	Spawning migration demonstrated to be dependent on fish length and condition. Use of spawning habitat density dependent. Note: this is however not inconsistent with entrainment	Norwegian Spring spawning herring	Slotte (1999); Slotte Fiksen (2000); Dragesund et al. (1
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);						
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.	period 1965-66					
Lack of a ge-specific genetic differences between population units	No temporally stable genetic differences have been observed between several sympatric herring populations (exception Balsfjord herring).	Norwegian Spring spawning herring; Balsfjord herring	Dahle and Eriksen (1990);Kjørsvik et al. (1991)			
Consistent evidence						
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	Otolith characteristics show that recruits are mixed with adult population during overwintering	Norwegian Spring spawning herring	Vilhjalmsson 1997; Slotte (1999); Huse et al. (submitted)			
Colonization of abandoned spawning grounds is predominantly by recruits.						
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).	1) Six changes in wintering area during last 50 years strongly correlated with high ratio of recruit spawners to main population		Corten (2002); Huse et al. (2002); Huse et al. (submitted)			
	2) When ratio recruit spawners/existing population is low recruit spawners adapt existing migration pattern of existing population. Also example of existing unit adopting to migration of recruit spawners (when 1959-yearclass established new wintering area)		Corten (2002); Huse et al. (submitted)			

American Pacific West Coast Sardine						
What to test	Evidence For	Population	Reference	Evidence Against	Population	Refer
Demonstrative evidence						
Recruit spawners of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2						
Some recruit spawners from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism						
Supportive evidence						
Change in behaviour when recruits come in contact with "entrainers" : social facilitation			Grimm et al. 2005			
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners						
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);	the collapse of sardine in 1960's and 1970's in all habitats. Recovery off California mid 1980's and off BC early 1990's.	off California				
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.						
Lack of age-specific genetic differences between population units	Possible metapopulations: old adult migration making the link	off Canada and US	Smith (2005), Felix-Uraga et al. (2005), Hedgecock et al. 1989, Clark and Janssen 1945			
Consistent evidence						
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	There are differences in length distribution in the feeding ground (inshore) and spawning area (offshore) from 2005 survey. Off California, age ranged from 0-5 yr inshore and 1-8 yr offshore. Overlap in Length distribution (around 20cm) for several ages inshore. Movement between inshore and offshore, both creating potential condition for entrainment. trawl catches off British Columbia, Canada; Washington, Oregon, US from 1990's -present and overall Length-age distribution from commercial catches in 1930's and 40's and from 1980's-now off California: fish caught together are of similar size but spread across different ages.	North West coast of American continent	MacFarlane, Emmitt, Hill (per.comm); Mosher and Eckle 1954; Felin and Phillips 1948; Lo and Macewicz 2006			
Colonization of abandoned spawning grounds is predominantly by recruits.	age 0-5 yr in the mid-90's : recovery by small fish	off California	Butler 1996			
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).	No change in migration routes after recovery. Expanding the spawning area while also remaining in the original spawning area based on egg distribution from surveys in early 1930's and CalCOFI survey from 1951-present (evidence of homing) after the recovery of sardine population off California to the offshore area	off California	Smith, 1990; McChlatchie (per comm)			

South African Sardine						
What to test	Evidence For	Population	Reference	Evidence Against	Population	Refer
Demonstrative evidence						
Recruit spawners of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2						
Some recruit spawners from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism						
Supportive evidence						
Change in behaviour when recruits come in contact with "entrainers" : social facilitation	None found yet					
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners						
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);	decline of western spawning unit probably due to local fishing depletion and capturing effect of the western recruits by the eastern component, eg. large 2001 year class has not occupied the west.					
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.	increased abundance in the East after high 2001 recruitment. Western component not able to entrain all the recruits					
Lack of age-specific genetic differences between population units	non conclusive studies. Unlikely					
Consistent evidence						
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	Overlap of adults and recruits throughout the year					
Colonization of abandoned spawning grounds is predominantly by recruits.	West coast used to be dominant spawning ground - evidence from fishery in early 50/60's. Currently no adult sardine found there...no mechanism for entraining/learning of recruits to colonize this area					
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).	Not enough data on pre-sardine collapse of mid 60's. Is possible that sardine distribution patterns were different than current. Sardine recruits (strong 2001 year class) which resulted mainly from western spawning unit are entrained by adults from eastern spawning unit.	South Coast Sardine spawning unit				

Northeast Atlantic Whiting						
What to test	Evidence For	Population	Reference	Evidence Against	Population	Refer
Demonstrative evidence						
Recruit spawners of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2	Indirect evidence: Discrepancies between genetic structure and parasite infestation data. A large part of recruits in Clyde and Irish Sea population units may come from a common spawning grounds located on their boundaries.	western margin of British Isles; Irish Sea and Clyde	Charrier et al. (2007), Kabata (1967), Pilcher et al. (1989), Garrod & Gambell (1965)			
Some recruit spawners from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism						
Supportive evidence						
Change in behaviour when recruits come in contact with "entrainers" : social facilitation						
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners						
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);						
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.						
Lack of age-specific genetic differences between population units						
Consistent evidence						
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	Overlap of adults and juveniles commonly observed.	North Sea, eastern English Channel	Carpentier (1998), IBTS, CGFS			
Colonization of abandoned spawning grounds is predominantly by recruits.	Observed in cod	Flamborough Head – Southern Bight	Hutchinson et al. (2003)			
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).						

Bay of Biscay Anchovy						
What to test	Evidence For	Population	Reference	Evidence Against	Population	Refer
Demonstrative evidence						
Recruit spawners of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2						
Some recruit spawners from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism						
Supportive evidence						
Change in behaviour when recruits come in contact with "entrainers" : social facilitation	Acoustically observed schools of YoY different when offshore independent from adults and inshore with adults. Possible confounding of coastal area and adult presence.	Biscay Anchovy (ICES areas VIIIa,b,c)	Petitgas et al. (2003)			
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners	protracted and longer spawning season of larger and older fish	Biscay Anchovy (ICES areas VIIIa,b,c)	Motos (1996) ; Millan (2002)			
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);	Disappearance of habitat occupation of Northern coast of Spain. Possibility of relict populations suffering high F and low Recruitment	Biscay Anchovy (ICES areas VIIIa,b,c)	Junquera (198?)			
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.	Some years, age-1 fish in spring found in Northern Biscay	Biscay Anchovy (ICES areas VIIIa,b,c)	survey data reports in ICES MHSR reports			
Lack of age-specific genetic differences between population units	No temporally stable genetic (allozyme) differences have been observed	Biscay Anchovy (ICES areas VIIIa,b,c)	unpubl. Ifremer internal report			
Consistent evidence						
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	Overlap in length across ages. N-S length spatial segregation of YoY coherent with that of adults	Biscay Anchovy (ICES areas VIIIa,b,c)	Unpubl. survey reports of Ifremer. ICES SGRESP reports			
Colonization of abandoned spawning grounds is predominantly by recruits.						
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).	possibility of that happening. Age-1 found in spring outside the 'conventional' distribution area (North Biscay)	Biscay Anchovy (ICES areas VIIIa,b,c)	survey data reports in ICES MHSR reports			

North Sea Plaice						
What to test	Evidence For	Population	Reference	Evidence Against	Population	Refer
Demonstrative evidence						
Recruit spawners of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2	In the German Bight spawning ground, there is a mix of the northern with the eastern population and these are close to the nursery grounds so it can have a mix of juveniles and adults of the different sub-population	North Sea Plaice	Hunter et al., 2004; Wegner et al., 2003			
Some recruit spawners from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism						
Supportive evidence						
Change in behaviour when recruits come in contact with "entrainers" : social facilitation						
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners	First time spawners meet the adults on spawning grounds and older fishes spawn earlier than younger fishes	North Sea Plaice	Rijnsdorp, 1989; Cushing, 1990			
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);	Change in position of spawning areas during the century. Change in spawning activity of spawning grounds	North Sea Plaice	Rijnsdorp, 1989; Harding et al., 1978; Bannister et al., 1973			
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.						
Lack of age-specific genetic differences between population units	No temporally stable genetic differences have been observed between sub-unit populations.	North Sea Plaice	Hoarau et al., 2002			
Consistent evidence						
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	Adults overlap with first time spawners on spawning grounds, so they can entrain them and learn them the way. It's possible that adults visit sometimes nursery grounds	North Sea Plaice southern bight and German Bight	Cushing, 1990			
Colonization of abandoned spawning grounds is predominantly by recruits.						
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).						

Atlantic Ocean and Mediterranean Sea Bluefin Tuna						
What to test	Evidence For Entrainment Hyp	Population	Reference	Evidence Against	Population	Reference
Demonstrative evidence						
Recruit spawners of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2						
Some recruit spawners from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism						
Supportive evidence						
Change in behaviour when recruits come in contact with "entrainers" : social facilitation						
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners						
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);						
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.	Emergent fisheries in Brazil, Norway, Central Atlantic; US-North Carolina; unique migration pathway for NC contingent of bluefin	Gulf of Mexico and Mediterranean Populations	Fromentin and Powers 2005; Block et al. 2005			
Lack of age-specific genetic differences between population units				Genetic data supports two principal populations for species		Graves et al.
Consistent evidence						
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	Overlap of sub-adults and adults in North Atlantic	Gulf of Mexico and Mediterranean Populations	Rooker et al. in press			
Colonization of abandoned spawning grounds is predominantly by recruits.						
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).	Evidence for individuals with W. Atlantic reproductive schedule spawning in Mediterranean		Block et al. 2005; Rooker et al. in press			

Chesapeake Bay and Patuxent River Estuary White Perch						
What to test	Evidence For	Population	Reference	Evidence Against	Population	Refel
Demonstrative evidence						
Recruit spawners of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2						
Some recruit spawners from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism						
Supportive evidence						
Change in behaviour when recruits come in contact with "entrainers" : social facilitation	Mid-life transitions indicating that some retentive contingents will shift suddenly to dispersive one.	Chesapeake Bay	Kraus and Secor 2004, 2005a,b. Kerr, unpubl.	Initial migration of juveniles to more dispersed habitat occurs substantially later than older juvenile and adult spring emigration	Chesapeake Bay	Kraus and S 2005a,b. Ke
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners						
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);				Degree of recruitment of sedentary and migratory types dependent upon climate over decadal period. Storage effect (overlapping generations) insures that neither unit is extirpated.	Chesapeake Bay	Kraus and S 2005a,b.
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.						
Lack of age-specific genetic differences between population units	Genetic homogeneity within each white perch population across age-classes and presumed contingents.		Mulligan and Chapman 1989			
Consistent evidence						
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	Overwintering habitats contain both juveniles and adult white perch	Chesapeake Bay, Hudson River	Setler-Hamilton 1991			
Colonization of abandoned spawning grounds is predominantly by recruits.						
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).				Degree of recruitment of sedentary and migratory types dependent upon climate over decadal period. Storage effect (overlapping generations) insures that neither unit is extirpated.	Chesapeake Bay	Kraus and S 2005a,b.

Chesapeake Bay and Patuxent River Estuary Striped bass						
What to test	Evidence For	Population	Reference	Evidence Against	Population	Refer
Demonstrative evidence						
Recruit spawners of unit 1 are found with adults of unit 2 and subsequently adopt the spawning behaviour of the adults of unit 2						
Some recruit spawners from large year-classes are not entrained with existing units resulting in a change in the life cycle pattern that is later fixed in conservatism						
Supportive evidence						
Change in behaviour when recruits come in contact with "entrainers" : social facilitation	Mid-life transitions indicating that some retentive contingents will shift suddenly to dispersive one.	Hudson River, Chesapeake	Secor and Piccoli 1996, 2007; Zlokovitz et al. 2003, Wingate and Secor 2007	Despite overlap in distributions during spring spawning, life history transects indicate divergent migration pattern established during YOY stage.	Hudson River, Chesapeake	Secor and P 2007; Zlokov 2003, Wingate and Secor 2007
Temporal and spatial segregation pattern on spawning sites between repeat and first spawners	Larger adults tend to spawn early in the season	Chesapeake	Secor 2000	Small (first spawners) occur throughout most of spawning season.	Chesapeake	Secor 2000
Non-recovery of particular population units; vacuum effect on the smaller units by the larger (entrainment of the offspring of one unit by the numerically dominant unit);						
Non-entrainment of particular year-classes (novelty in life cycle pattern through exploration); appearance of new population units where none existed before or since several generations following the recruitment of a large year class.						
Lack of age-specific genetic differences between population units	Genetic homogeneity within striped bass populations across age-classes and presumed contingents.	Chesapeake, Hudson	Wirgin et al. 1993			
Consistent evidence						
Overlap between adults of the entraining population and juveniles at particular times and locations in the life cycle prior to first spawning.	Overwintering habitats contain both juveniles and adult striped bass	Chesapeake Bay, Hudson River	Settler-Hamilton and Hall 1991, Dovel 1992			
Colonization of abandoned spawning grounds is predominantly by recruits.						
Modification of migration route, feeding and/or wintering area usage patterns following a population perturbation (boom, collapse, environmental shift).						