

**Discrepancies between population genetic structure and adult migration patterns in cod (*Gadus morhua*) and whiting (*Merlangius merlangus*): evidences for entrainment ?**

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Whiting and cod are two closely related gadoids, sharing the same grounds in the northern European waters as well as most of their life-cycle features. Many studies have investigated the level of mixing of adults in both species for more than one century, using a wide spectrum of methods such as tagging experiments, parasitic tags, otolith analysis, meristics and morphometrics. This large amount of data is particularly valuable to evaluate the migration patterns of adults and to detect homing behaviour, but do not allow to draw any conclusion about the natal origin of the fish and thus to discriminate natal homing from entrainment. Since the last decade, several studies have depicted the population genetic structure of cod and whiting in the NE Atlantic, providing useful informations about the extent of gene flow between populations through the passive drift of eggs and larvae or the active migration of adults. Population genetic structure and adult migration patterns displayed substantial discrepancies, and the purpose of this talk is to review all these discrepancies reported in the literature for cod and whiting. The comparison of gene flow and adult migration patterns in both species offers a very interesting opportunity to disentangle natal homing from entrainment.

Key words: cod, whiting, *Gadus morhua*, *Merlangius merlangus*, genetic structure, migration, gene flow, natal homing, entrainment

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## Introduction

*Cod (Gadus morhua) and whiting (Merlangius merlangus) are among the most important commercial fish species in the northern European waters, especially in the North Sea. Both species are submitted to a strong fishing pressure and significant signs of over-fishing have been widely reported. Therefore it is now urgent to increase our efforts to manage properly these species in order to ensure sustainable fisheries in the future.*

*One of the crucial steps to set up appropriate and efficient management plans for marine fisheries consists in the accurate identification of fish stocks. It is particularly important to understand the level of connectivity between the spawning units in order to be able to predict as precisely as possible the origin and the strength of the recruitment in each stock. To this aim, depicting the processes underlying the migratory behaviour and the spawning-site fidelity patterns of individuals appears as a major issue.*

*Spawning-site fidelity of marine fish has been a very controversial topic for a long time. This behaviour has been widely demonstrated in cod and is largely suspected in whiting. However, the mechanisms shaping these migratory patterns are still poorly understood and different hypotheses have been suggested. On the one hand, natal homing, as observed in salmonids, has been hypothesized: in this case, spawning-site fidelity would be a genetically inherited feature with the fish migrating back to their natal spawning ground when they become mature. In the other hand, the entrainment hypothesis (ICES 2007, Petitgas et al. 2006) suggests another scenario: the spawning-site fidelity would be a socially learned behaviour transmitted from experienced fish to the new recruits, and thus the young adults might not necessarily come back to their natal spawning ground but may adopt another spawning unit. These two alternative hypotheses suggest very different processes with highly divergent consequences on the dynamic of the recruitment.*

*The purpose of this contribution is to investigate the discrepancies observed between migratory behaviour of adults and population genetic structure patterns in cod and whiting, by reviewing the data published in the literature. By focusing on the processes underlying these discrepancies, this study aims to explore the mechanisms by which individuals are recruited into spawning units, and thus to test the likelihood of the entrainment hypothesis in both species.*

## 1- Migration patterns of adults and level of mixing between spawning units

### 1.1- Migration patterns in cod

Movements of cod have been widely investigated for the last century, essentially with tagging experiments. Hence, Robichaud & Rose (2004) have reported several hundreds of thousands of individuals tagged and tens of thousands of recaptures. Through the analysis of this large amount of data, these authors have classified the observed migration patterns into four behavioural categories, depending on the levels of site fidelity and homing (*according to Robichaud & Rose (2004): site fidelity = residency within a relatively small geographical area; homing = migration back to the tagging/releasing area after having moved away*):

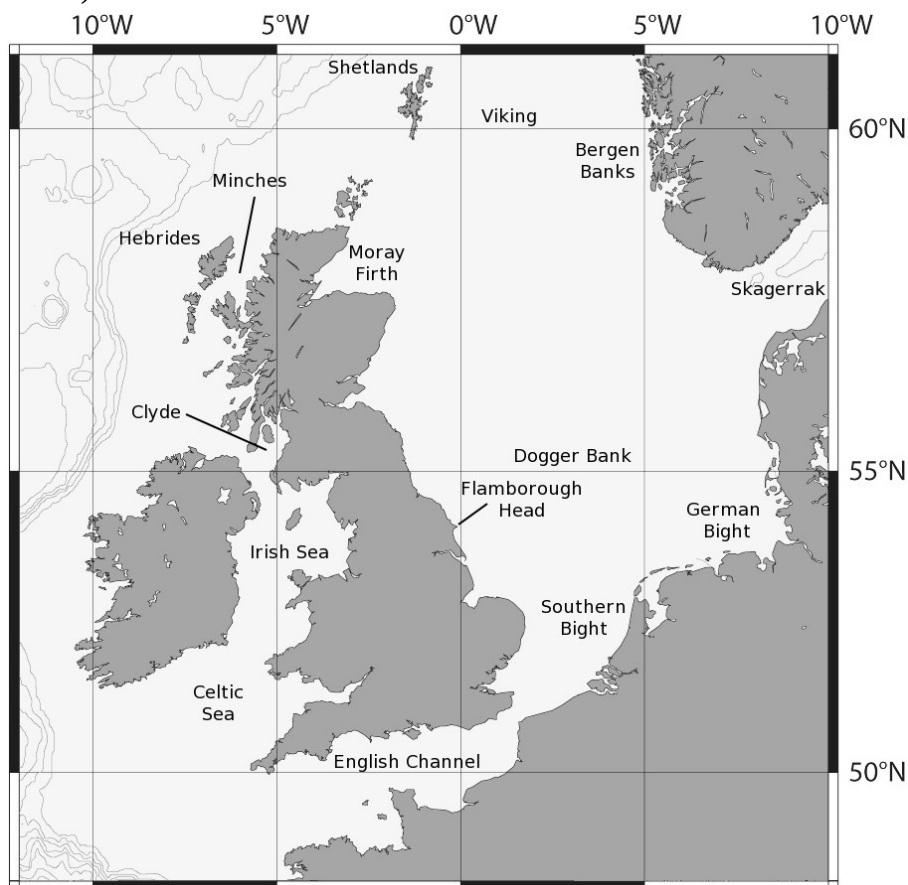
- 1) Sedentary: strong site fidelity and relatively small geographic range;
- 2) Accurate homing: seasonal migrations and homing to a relatively small area;
- 3) Inaccurate homing: seasonal migrations and homing to a relatively wide area;
- 4) Dispersing: dispersion over broad areas.



Tagging experiments have underlined limited mixing between inshore spawning units located into Scandinavian fjords (Danielssen & Gjøsæter 1994, Espeland et al. 2007, 2008), as well as between the main coastal spawning aggregations occurring in the northern North Sea and west of Scotland (Neat et al. 2006, Wright et al. 2006a, 2006b), in the southern North Sea and English Channel (Righton et al. 2007), or within the Irish Sea (Brander 1975, Connolly & Officer 2001). Overall, it seems that the northern European waters are mainly occupied by the two first behavioural categories identified by Robichaud & Rose (2004): sedentary and accurate homing.

#### *a- Small sedentary populations in coastal fjords*

Several small local cod populations are known to spawn into the Norwegian and Swedish coastal fjords. Mark-recapture data (Danielssen & Gjøsæter 1994, Espeland et al. 2008, Svedäng et al. 2007), as well as acoustic telemetry (Espeland et al. 2007) have demonstrated that these coastal populations are composed of sedentary resident individuals, that remain fairly stationary all the year-round with a high degree of spawning-site fidelity. Hence, these populations are characterized by a small home range, commonly smaller than 160 km<sup>2</sup>, and in some cases smaller than 10 km<sup>2</sup> (Espeland et al. 2008).



**Figure 1** Map of the northern European waters

#### *b- Sedentary spawning units in open coastal areas*

Other sedentary groups have been shown in several spawning grounds in the northern North Sea (Moray Firth, Shetlands) as well as to the west of Scotland (the Clyde and the Minch) (Neat et al. 2006, Wright et al. 2006a, 2006b). Conventional tag-recapture experiments have demonstrated that adults belonging to these sedentary residential spawning groups display a high degree of site-fidelity all the year-round and limited movements, with home range distances of up to 80 km (Brander 1975, Connolly & Officer 2001, Wright et al. 2006a). The existence of sedentary



spawning groups has also been hypothesized in the eastern English Channel (Righton et al. 2007).

Spawning units off the northern Scottish coast seem to be more dispersive with a relatively lower degree of spawning-site fidelity and larger displacement distances (Easey 1987, Wright et al. 2006a). However, according to Wright et al. (2006a), it remains unclear whether this dispersive pattern might be due to a larger geographical extent of the spawning area or to inaccurate homing.

#### *c- Seasonal migrations and accurate homing*

In the southern North Sea, tagging experiments have highlighted a limited mixing between cod spawning in the Southern Bight (ICES area IVc) and those spawning in the eastern English Channel (ICES area VIId) (Righton et al. 2007).

Cod spawning in the Southern Bight migrate up to 250 km between this spawning ground and some feeding grounds located in the Central North Sea (Turner et al. 2002). Moreover, these migrations between spawning and feeding grounds follow a clear seasonal cycle, with fish spreading essentially toward the central North Sea during the feeding period and coming back to their Southern Bight for the spawning period, with a high level of spawning-site fidelity (Righton et al. 2007).

### **1.2- Migration patterns in whiting**

A significantly smaller amount of data has been collected during the last decades concerning the movements of whiting. Nevertheless, conventional tagging experiments or parasite infestation studies have demonstrated a substantial population structure within the North Sea and to the West of the British Isles.

The main evidence for this limited mixing between adult stocks has been provided by the use of parasites as biological tags (Hislop & MacKenzie 1976, Kabata 1967, Pilcher et al. 1989). These parasite infestation studies have shown a significant geographical structuring between the southern and the northern North Sea, with a boundary located at the Dogger Bank. Along the western margins of the British Isles, a significant structure has also been identified with three differentiated areas: (i) Irish Sea, (ii) north and west of Ireland, and (iii) north of Scotland (Orkney to Shetland) (Kabata 1967). No structure has been reported by Kabata (1967) between the north of Scotland and the northern North Sea.

Tag-recapture data have confirmed the geographical structuring between the southern and northern North Sea, with limited mixing observed between areas located north and south of the Dogger Bank (Hislop & MacKenzie 1976, Williams & Prime 1966). Interestingly, homing behaviour might be hypothesized from the seasonal migrations shown by Williams & Prime (1966) in the southern North Sea, with released fish spreading northward during the summer and then migrating back to the southern North Sea in September-December, before the spawning season.

## **2- Genetic structure of cod and whiting populations**

### **2.1- Population genetic structure in cod**

The first microsatellite investigation performed in the northern European waters have highlighted a weak but significant genetic differentiation among cod populations (Hutchinson et al. 2001). This study has depicted a significant population structure within the North Sea, while no clear structuring pattern has been shown along the western margins of the British Isles, from the Celtic Sea to the waters north-west off Scotland. In summary, Hutchinson et al. (2001) have identified four



genetically differentiated spawning units within the North Sea: (1) Moray Firth, (2) Bergen Banks, (3) Flamborough Head, and (4) Southern Bight.

However, the last study conducted on the genetic structure of cod populations in the NE Atlantic has not shown any evidence of genetic structuring in the northern North Sea and West of Scotland, with a substantial temporal variability in the patterns of genetic differentiation between the spawning grounds (Nielsen et al. 2009).

Overall, the genetic data collected on cod during the last decade have suggested the existence of some structuring patterns around the British Isles with probably three differentiated units:

- (1) Scottish coastal waters
- (2) Flamborough Head
- (3) Southern Bight and eastern English Channel.

Several studies have also been conducted at a small geographical scale along the Norwegian coasts, in order to depict the genetic structure of the cod populations inhabiting the coastal fjords (Jorde et al. 2007, Knutsen et al. 2003). A significant genetic differentiation has been observed between sedentary resident populations from neighbouring fjords, even at a very small geographical scale, with significant differentiation even between fjords separated by less than 30 km (Jorde et al. 2007).

## ***2.2- Population genetic structure in whiting***

As for the adult migration patterns, the number of published studies focusing on the genetic structuring of whiting populations is considerably smaller compared to those available on cod. Based on microsatellite markers, Charrier et al. (2007) have depicted a weak genetic differentiation of whiting populations. In particular these authors have underlined a lack of genetic structuring in the waters off the western coasts of the British Isles (from the Celtic Sea to the Hebrides). Nevertheless, Charrier et al. (2007) have demonstrated a significant genetic structure within the North Sea with the identification of three differentiated population units:

- (1) Southern Bight
- (2) Flamborough Head
- (3) A third unit grouping the Dogger Bank and the southern Norwegian coast.

## **3- Discrepancies between adult migrations and population genetic structure patterns**

Overall, similar patterns of adult movements have been described in both species, with a generally low level of mixing between the spawning units and high degree of spawning-site fidelity of adults. The majority of the whiting and cod populations in the northern European waters seem to be either sedentary residents or accurate homers (Robichaud & Rose 2004).

Concerning the population genetic structure, similar results have also been found in cod and whiting, with some genetically differentiated populations in the southern North Sea (Southern Bight, Flamborough Head) and a lack of genetic structure in the northern North Sea and west off the British Isles (from the Celtic Sea to north of Scotland).

Hence, adult migrations and population genetic structure patterns are congruent in the southern North Sea and in the Scandinavian fjords, with significant genetic differentiation between the spawning units, associated with a low level of mixing of adults between the spawning grounds. However, in the northern North Sea and along the western margins of the British Isles, the data are



not in agreement, with adult movements showing limited mixing between the spawning units, whereas genetic data suggest substantial gene flow between the different spawning groups.

Two main hypotheses might be proposed to explain these discrepancies observed in the coastal Scottish waters:

- (1) First of all, we can suspect a limited power of the genetic markers to detect the population structure of cod and whiting to the west of the British Isles and in the northern North Sea. The marine environment is highly dispersive with generally high levels of gene flow between populations. In addition marine population are relatively recent at the evolutionary time scale and display generally large effective sizes. For all these reasons, investigating the genetic structure of marine fish is always a challenging task. However, this explanation appears unrealistic given the significant levels of genetic differentiation demonstrated for both cod and whiting within the North Sea. A possible limited power of the genetic tools might explain the generally weak genetic differentiation observed in both species, but does not provide any satisfying explanation to justify the contrasted genetic structure patterns observed between (i) the southern North Sea and (ii) the northern North Sea and along the western British coasts.
- (2) An alternative explanation to the discrepancies observed between adult movements and population genetic structure patterns might be linked to the processes underlying the recruitment of first spawners into the spawning units. The large degree of spawning-site fidelity displayed by the adults does not mean that the spawning units are self-recruiting. Pelagic eggs and larvae can either disperse passively over wide areas with the oceanic currents, or be retained in the neighbourhood of their natal population by physical barrier such as oceanic fronts, gyres or fjord sills. According to the entrainment hypothesis (ICES 2007, Petitgas et al. 2006), the first spawners may not necessarily be recruited in their natal population (as suggested in the natal homing hypothesis), but might be adopted by the population in which they have settled down after dispersal during the early-life stages. Thus, these new recruits would then be susceptible to learn the local migratory behaviour with a significant site-fidelity to the local spawning ground. Following this scenario, in the absence of barriers to egg and larval dispersal, significant gene flow would be ensured even with a high degree of spawning-site fidelity of the adults.

This last hypothesis seems more likely. Hence, the next section of this literature review will focus on (1) the dispersal of pelagic eggs and larvae and (2) the movements of juveniles in order to depict the processes by which first spawners are recruited into spawning units.

#### **4- Gene flow opportunities associated with the dispersal of early-life stages**

##### ***4.1-Passive dispersal of pelagic eggs and larvae***

###### ***a- Passive dispersal along the western margins of the British Isles***

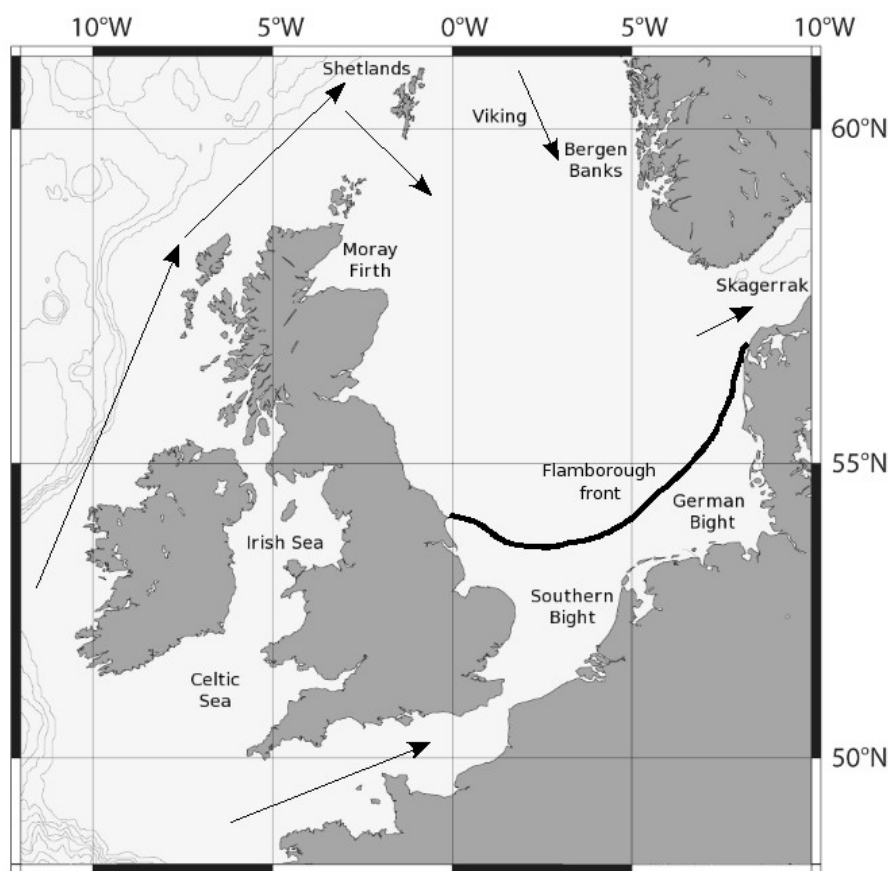
Simulations performed by Heath et al. (2008) on cod have underlined very different patterns of passive dispersal of the early-life stages between the southern North Sea and the coastal Scottish waters. Whilst southern spawning grounds display a high degree of retention of eggs and larvae, these pelagic stages can spread over large distances in the northern North Sea and west of Scotland. As an example, Heath et al. (2008) have shown that larvae produced along the western and northern coasts of Scotland (i.e. from the Clyde to the Minches) can drift to the northern North Sea and settle down with high survival rates on nursery grounds located in Moray Firth or in the Shetlands.

Therefore, it appears that the lack of genetic differentiation observed in both cod and whiting to the



west of the British Isles and in the northern North Sea (Charrier et al. 2007, Hutchinson et al. 2001, Nielsen et al. 2009) may result, at least in part, from the widespread dispersal of pelagic eggs and larvae through passive drift with the current systems. Passive dispersal may be ensured from Porcupine Bank to northern Scotland by the general north-north-easterly drift of the North Atlantic Current and possible advection by the Shelf Edge Current (**figure 2**; Pingree & Le Cann 1989), as demonstrated for blue whiting *Micromesistius poutassou* and mackerel *Scomber scombrus* (**figure 2**; Bartsch & Coombs 1997, 2004). Furthermore, the branching of the North Atlantic Current into the North Sea (**figure 2**; Turell 1992) may allow the transport of early-life pelagic stages from the grounds located to west of Scotland to the northern North Sea, as suggested by the model developed by Heath et al. (2008).

Moreover, substantial gene flow might be ensured between the southwestern British Isles and the southern North Sea through passive drift with the residual current flowing eastwards from the Atlantic to the Southern Bight through the English Channel (**figure 2**; Prandle et al. 1996). This would explain the lack of clear genetic structure patterns observed from the Celtic Sea to the southern North Sea in both cod and whiting (Charrier et al. 2007, Hutchinson et al. 2001).



**Figure 2** Summary of the main hydrographical features in the northern European waters (black arrows represent advective currents; the bold line represents the seasonal Flamborough front)

#### *b- Barriers to dispersal within the North Sea*

The North Sea is characterized by significant hydrographical features that may limit the passive dispersal of pelagic eggs and larvae. For example, during the summer, the seasonal Flamborough front separates the mixed waters of the southern North Sea from seasonally stratified waters of the central and northern North Sea (**figure 2**; Pingree & Griffiths 1978). Thus, this front acts as a physical barriers preventing dispersal between southern grounds (i.e. Southern Bight, German Bight) and northern areas. Such frontal areas may significantly influence the dispersal of the pelagic



early-life stages, as demonstrated by Munk et al. (1995, 1999, 2002).

Overall, all these potential barriers to larval and egg dispersal are consistent with the results from Heath et al. (2008), showing a high degree of retention of pelagic eggs and larvae followed by a settlement in local nursery grounds in the southern North Sea (i.e. Flamborough Head, Southern Bight).

Concerning whiting, the Dogger Bank has been suggested to act as a physical barrier that prevents mixing between southern and northern populations (Pilcher et al. 1989). This limited dispersal of pelagic early-life 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, meristic characters are influenced by environmental factors and are fixed during early-life development (Lindsey 1975). Consequently, differences in these phenotypical traits indicate that individuals experienced distinct environments during their early life stages, thus suggesting the existence of discrete larval retention systems associated with particular hydrographical features.

These barriers preventing the dispersal of pelagic eggs and larvae are consistent with the significant genetic structure patterns observed among cod and whiting populations in the southern North Sea (i.e. significant genetic differentiation of Flamborough Head and Southern Bight populations in both cod and whiting; Charrier et al. 2007, Hutchinson et al. 2001).

#### *c- Retention systems in the Scandinavian fjords*

Coastal cod populations located into Scandinavian fjords display a significant genetic differentiation, even at a very small geographical scale (Jorde et al. 2007, Knutsen et al. 2003). Knutsen et al. (2003) have suggested that this significant genetic structure observed between coastal fjord populations is mainly driven by patterns of larval transport rather than by adult movements. Egg distribution surveys have clearly demonstrated a retention of pelagic early-life stages inside the fjords (Espeland et al 2007, Knutsen et al. 2007). Such retention systems prevent (or at least limit drastically) the mixing between inshore and offshore eggs and larvae, as demonstrated by the significant genetic differentiation detected between larval groups collected inside and outside the Gullmar Fjord (Øresland & André 2008).

#### **4.2- Movements of juveniles**

Investigating the movements of juvenile fish by the mean of tagging-recapture experiments is particularly challenging for two major reasons. Firstly, the small size of the juveniles is a considerable constrain for the tag size. Secondly, the high rates of mortality observed during the juvenile stage would imply low recapture rates and thus, it might be necessary to conduct a massive tagging effort in order to get some chances to recover a satisfying number of individuals.

Alternatively, other approaches such as otolith microchemistry have been used to investigate the movement patterns of juveniles. The concentration of trace elements in the otoliths is under the influence of the concentration of these elements in the environment (Campana 1999). Hence, elemental signatures in otoliths can be used to characterize fish groups inhabiting different grounds, and to evaluate the extent of fish movements between these grounds (Thresher 1999).

Otolith microchemistry has provided a strong evidence of a high degree of residency of juvenile cod in nurseries located in the northern North Sea and to the west of Scotland (Gibb et al. 2007, Wright et al. 2006b). Moreover, Wright et al.(2006b) compared the elemental composition of equivalent parts of the otolith between juveniles and adults from the same year class, collected in 2001 on nurseries and in 2003 on spawning grounds, respectively. This study has clearly demonstrated that



most of the adults recruited on the spawning grounds originate from the local nurseries.

Therefore, it appears that cod juveniles do not move over large distances but remain relatively stationary, and most of them are recruited in the local spawning unit. So, the only source of gene flow that might explain the lack of genetic structure along the western margins of the British Isles and in the northern North Sea might be mainly linked to the passive dispersal of pelagic eggs and larvae with advective currents (**figure 2**).

## **5- Likelihood of the entrainment hypothesis in cod and whiting**

This literature review has provided interesting elements to investigate the mechanisms underlying the discrepancies observed between migration patterns of adults and population genetic structure in cod and whiting.

The population genetic structure in both species seems strongly linked to the passive dispersal of eggs and larvae (**table 1**), as suggested by Knutsen et al. (2003). Gene flow between population units is probably mainly driven by the transport of pelagic early-life stages between the different grounds. After settlement, juveniles appear relatively sedentary and are mainly recruited in the local spawning unit (Wright et al. 2006b). Therefore, juveniles do not necessarily recruit to their natal spawning unit, but may be adopted by the population in which they have settled down, thus adopting a spawning-site fidelity behaviour to the local spawning ground. So, this implies that the spawning-site fidelity displayed by repeat spawners would not be a genetically inherited feature but a learned behaviour, as suggested in the entrainment hypothesis (ICES 2007, Petitgas et al. 2006).

According to the entrainment theory, when hydrographic factors prevent larval dispersal, as observed in the southern North Sea, young fish would most likely recruit to their natal population and adopt the behaviour patterns of that population, thus inducing spawning-site fidelity associated with significant population genetic structure. In more dispersive environments, such as that to the west of the British Isles and in the northern North Sea, a significant number of juveniles would likely recruit to neighbouring populations and adopt a non-natal migratory behaviour, such preventing population genetic differentiation despite the spawning-site fidelity of adults.

A learned migratory behaviour implies a social transmission of migration routes from older, experienced fish to young recruits. This behaviour is central to the metapopulation concept (i.e. “adopted migrant” hypothesis) described by McQuinn (1997). The likelihood of the “adopted migrant” hypothesis has already been largely discussed by Charrier et al. (2007) to explain the patterns of genetic structure observed among whiting populations. Then, this hypothesis has been reformulated in a more comprehensive manner as the “entrainment hypothesis” (ICES 2007, Petitgas et al. 2006). Considering this theory, the extent of temporal stability of the physical or behavioural isolating systems limiting the transport of early-life stages to surrounding populations determines the degree of genetic exchange among them. Inter-annual variability in the strength of these isolating mechanisms would result in variable inter-annual mixing between local populations.

Alternatively, natal homing has often been suggested to explain the migratory behaviour depicted in marine fish such as cod (i.e. Svedäng et al. 2007). This behaviour is assumed to involve endogenous processes, such as an internal sense of direction, sensitivity to pheromonal molecules, or imprinting processes (see references in McQuinn 1997). Such behaviour is central to the discrete population concept (i.e. “member/vagrant” hypothesis) that considers larval retention mechanisms and natal homing as key factors to ensure life-cycle closure and temporal persistence of discrete populations (Iles & Sinclair 1982). Based on the present literature review, natal homing seems rather unrealistic to explain the discrepancies observed between adult movements and population genetic structure



observed in the northern North Sea and to the west of the British Isles.

The entrainment hypothesis (ICES 2007, Petitgas 2006) seems more likely to be at the origin of the discrepancies observed between migration patterns and population genetic structure. Such a process has already been demonstrated in herring *Clupea harengus* by McQuinn (1997), who argued that a social transmission mechanism for passing on habitat information between generations is more advantageous than natal homing in variable marine environments. Indeed, in such an unstable and unpredictable environment, learned homing allows rapid colonisation of new habitats or recolonisation after collapse, thus increasing species resilience.

Area	Adult migratory behaviour	Juvenile movements	Egg & larvae dispersal	Genetic structure
<b>Cod</b>				
Southern Bight	accurate homing	?	Retention	YES
coastal Scottish waters	sedentary	sedentary	Dispersal	NO
Scandinavian fjords	sedentary	?	Retention	YES
<b>Whiting</b>				
southern North Sea	homing	?	Retention	YES
West of British Isles	homing ?	?	Dispersal	NO

**Table 1** Summary of the results reviewed in cod and whiting

In the NW Atlantic, Windle & Rose (2005) have demonstrated a clear evidence of spatial learning of the migration routes in cod, thus suggesting that the spatial familiarity is a key factor in cod homing. These authors finally hypothesized that this spatial learning might be learned by the new recruits. This study provides an additional evidence supporting the entrainment hypothesis as a key factor in shaping the migratory behaviour in cod (and probably also in whiting).

## 6- Implications for fisheries management, and perspectives for further investigations

The entrainment hypothesis has major implications for fisheries management. Indeed, a socially learned homing (entrainment) might induce more complex patterns depending on the dispersal of the early-life stages with the oceanographic currents, from self-recruiting populations in the case of low dispersal of the young stages, to spawning units recruiting essentially individuals from other areas.

An accurate identification of recruitment patterns is particularly important to allow managers to set up appropriate and efficient management plans for the commercial fisheries: while self-recruiting populations should be managed as independent stocks, spawning units significantly connected by important import/export fluxes of new recruits should be managed together. Moreover, understanding the mechanisms shaping the spawning-site fidelity of individuals is particularly important to estimate the potential for recovery of depleted stocks after over-exploitation or collapse.

Therefore, further investigations concerning the spawning-site fidelity of adults should be a major task in the next future. To this aim, the Skagerrak/Kattegat waters might provide a valuable opportunity to test further the entrainment hypothesis. Indeed, while significant population genetic structure and limited adult movements have been depicted in inshore populations located in coastal



fjords (Espeland et al. 2007, 2008, Jorde et al. 2007, Knutsen et al. 2003), a large inflow of larvae stemming from North Sea spawning grounds and drifting into the Skagerrak has been shown, with a temporal variability in the strength of this inflow (Knutsen et al. 2004). Genetic and dynamic consequences of this input of larvae from the North Sea into the Skagerrak have been demonstrated by Stenseth et al. (2006). In addition, natal homing has been hypothesized by Svedäng et al. (2007) to explain the migrations toward the North Sea observed during the spawning season for cod tagged in the eastern Skagerrak. However, the natal origin of these fish migrating back to the north Sea remains questionable (Bradbury & Laurel 2007), making the natal homing hypothesis not so evident in that case. Therefore, elucidating the processes shaping these migration patterns described by Svedäng et al. (2007) in an area characterized by the occurrence of numerous coastal sedentary populations and by a temporally variable inflow of larvae from the North Sea might be an ideal opportunity to compare the likelihood of the natal homing and entrainment theories.

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