MODEL STUDIES OF
FISH EGG AND LARVAL TRANSPORT IN
THE KATTEGAT AND THE NORTH ATLANTIC

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Abstract

For the early life stages of fish, the dispersal and retention are important factors regarding present and future survivorship, growth and reproduction. The main objective of this thesis is to analyse fish egg and larval transport in two different marine systems, the Kattegat and the North Atlantic. The focus is on two different species, namely Atlantic cod (*Gadus morhua*) eggs in the Kattegat-Öresund-Belt area and European eel (*Anguilla anguilla*) leptocephalus larvae in the North Atlantic.

The stock of cod in the Kattegat has been severely depleted due to fishery and is presently classified as exhibiting reduced reproductive capacity. It is, therefore, of interest to update information on cod spawning activity and get an understanding of the dispersal of eggs. As to evaluate spawning, data were analysed from dedicated egg surveys in the Kattegat between 2004 and 2006. Genetically identified cod eggs confirmed that cod were spawning in the studied area during the sampling period. The estimated daily egg production was high in the south-eastern part of the surveyed area ($\sim$20 eggs m^{-2} d^{-1}) while it was low (0–5 eggs m^{-2} d^{-1}) in the central and northern part. This emphasises the importance of the southernmost spawning area in the Kattegat, close to the Öresund. A process oriented model was used to investigate transport of cod eggs and early larvae in relation to egg density as well as how the interannual variation of retention and dispersal is related to the meteorological forcing. The model results clearly indicated that transport is highly dependent on the egg density; lighter eggs are transported northwards, whereas heavier eggs are retained to a larger extent or are transported southwards. An optimum of retention is defined in the density range 1023-1026 kg m^{-3}. Combining the model results of the amount of retention, distribution and sedimentation with observations of vertical distribution of cod-like eggs in the range 1017-1022 kg m^{-3}, suggests that gadoid eggs are mainly retained in the southern Kattegat, but also simultaneously dispersed northwards. Further investigation showed that interannual variation of retention, transport and sedimentation are highly correlated to the changes of local wind forcing. Strong westerly winds induce southward transport and high sedimentation while weak variable winds tend to retain eggs in the spawning area. The results of this study provide a starting point for future studies of spawning and life history characteristics of the Kattegat cod, and also in studies designed to entangle the stock complex in the Kattegat-Öresund-Belt area.

Climatic variation affecting the ocean conditions for passive drift of eel larvae is one of the factors suspected to be related to the decline of eel recruitment. A simple Lagrangian model was used to simulate the passive drift of the European eel (*Anguilla anguilla*) leptocephalus larvae from the spawning area in the Sargasso Sea to the European shelf (20°W). The simulation utilised the velocity data from a reanalysis of ocean climate, the Simple Ocean Data Assimilation (SODA 2.1.6), for the period from 1958 to 2008. The period which was modelled covers the time of a regime shift in eel recruitment in the 1980s. The average drift time and latitudinal distribution of the arrival of larvae (particles in the model) was explored for a range of constant depth levels and instantaneous mortalities. The model showed that the proportion of eel larvae carried by the North-east Atlantic current to northern latitudes of arrival was greater before 1970 whereas there was an increase in amount of eel larvae being entrained into the southbound current branches in later part of simulation. The overall success of drift from the spawning area to the eastern Atlantic clearly contradicts that this could explain the dramatic recruitment decline.

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List of publications

I. Börjesson P., Jonsson P., Pacariz, S., Björk, G., Taylor, M. I. and Svedäng, H. (2013) **Spawning of Kattegat cod (*Gadus morhua*) – mapping spatial distribution by egg surveys.** *Under revision - Fisheries Research*

Pacariz had a minor role in writing, contributed with field work, analysis of the hydrographical data, comments on the text.

II. Pacariz, S., Björk, G., Jonsson, P., Börjesson, P., and Svedäng, H. (2013). **A model study of the large scale transport of fish eggs in the Kattegat in relation to egg density.** *Under revision - ICES Journal of Marine Science*

Pacariz had a leading role in writing, contributed with modelling and analysis of the results and prepared all figures.

III. Pacariz, S., Björk, G., Svedäng, H. **Interannual variability of transport of fish eggs in the Kattegat and Öresund *- relation to recruitment.*** *Submitted to ICES Journal of Marine Science, February* 2013

Pacariz had a leading role in writing, contributed with modelling and analysis of the results and prepared the most of the figures.

IV. Pacariz, S., Westerberg, H. and Björk, G. (2013) **Climate change and passive transport of European eel leptocephalus larvae.** *Accepted for publication in Ecology of Freshwater fishes.*

Pacariz had a leading role in writing, contributed with the modelling and analysis of the modelling results and prepared half of the figures.

CONTENTS

I.   Summary

1. INTRODUCTION

1.1. Oceanography and Fisheries

In the 19th century, scientists started to connect characteristics and variations of physical and chemical factors of the marine environment to fishery. An example is the Swedish scientist Otto Pettersson (1848-1941), a specialist in marine chemistry with a strong interest in biological and physical oceanography who together with the colleague Gustaf Ekman studied the influence of abiotic factors on herring periods (i.e. variation over time in herring abundance) at the coast of Bohuslän, Sweden (Svansson, 2004). Their work initiated the idea of a synoptic exploration of the sea. In 1890, an expedition was organised to the northern Kattegat, engaging five Swedish vessels at the same time. Pettersson early understood the importance of these kinds of observations and the need for international cooperation, in order to carry out such surveys. At the International Geographical Congress in 1895, he suggested an international engagement to establish a continuation of the surveys he had initiated. As a result, an international organisation for monitoring and exploration of the seas, the International Council of Exploration of Seas (ICES), was formed in 1902 in Copenhagen (Svansson, 2004). Today, ICES is an increasingly important organisation that promotes and encourages research and exploration of the oceans but also provides the guidelines for regulations of fishery with sustainability as the overall aim.

The interest in sustainable use of resources is older than what might be generally acknowledged. In Sweden as early as in 1749, during the Age of Enlightenment, decreases in fish resources were recognised and the need for regulation of fishing was consequently suggested (Westerberg and Ask, 2011). The development of fishing technologies has had a serious impact on fish resources, in particular over the last 50 years. Unfortunately, the fisheries research and management have not always followed the same pace of development. Today, we are trying to achieve sustainability in fishery by letting depleted stocks recover as well as preventing others from being overfished. New studies are continuously adding knowledge and understanding of interactions between the marine ecosystems and physical oceanographic processes although many links are still missing.

Physical processes in the oceans create conditions for processes that are important for the life cycle of the marine organisms. Change of temperature in the ocean regions, like the Northern Atlantic, can induce a shift in population of planktonic organisms which can make impact high up in the food chain in the region (Beaugrand et al., 2002). The water movement acts on different time and length scales and includes large scale processes, such as thermohaline circulation, as well as small scale as turbulence. The thermohaline circulation covers a global or ocean basin scale and completes its cycle in hundreds of years, while turbulence operates on length and time scale down to millimetres and seconds respectively. In that way, the effect of the water movement on the marine organisms comprises a wide range of processes such as the transport of nutrients and detritus, retention and dispersal of planktonic organisms, migration or control of food availability. Upwelling waters enriched by nutrients generate production of small planktonic organisms and attract predators making these regions, at the shelf break fronts or in the coastal regions, high productivity zones (Mann and Lazier, 2006).

Early life stages of fish, such as pelagic eggs and early larvae, have no (or very restricted) swimming abilities and drift passively through the waters with ocean currents. Many marine species have developed life strategies using the currents in the spawning region for dispersal of eggs or for retention of eggs in the spawning area. An example is the spawning of the anchovy in the South African waters where, after fertilisation, anchovy eggs are transported by the current system northwards along the west coast of southern Africa to the nursery grounds (Parada et al., 2003). Conversely, anchovy in the Humboldt Current, of the Peruvian coast, spawn eggs that are positioned vertically in the water column in order to be retained in the spawning area (Brochier et al., 2008). An additional example is the north-eastern Arctic cod and the Norwegian coastal cod spawning in the same area. The eggs of north-eastern Arctic cod are light, floating in the surface layer, and are dispersed by the surface currents while coastal cod spawn heavier eggs, floating in the more stagnate deep waters, where they are retained (Stenevik et al., 2008).

Studying the dynamics of the early life stages provide valuable information for fish stock management. Corell et al. (2012) used estimations of dispersal and level of connectivity of fish larvae to evaluate the efficiency of marine protected areas in the Baltic Sea. Transport of eggs and larvae may strongly influence later stages of the fish life cycle as retention and dispersal are important factors determining survival rate, stock separation and choice of nursery areas. The present thesis addresses some of these issues by investigating retention and dispersal of early life stages of two fish species in two fairly different marine systems, namely Atlantic cod (*Gadus morhua*) eggs in the Kattegat-Öresund-Belt area and European eel (*Anguilla anguilla*) leptocephalus larvae in the North Atlantic.

The first part of the study was cooperatively initiated by the Institute of Marine Research at the Swedish Board of Fisheries and the Department of Earth Sciences at the University of Gothenburg which, noteworthy, both were part of the Swedish Hydrologic-Biologic Commission (SHBK) funded in 1901. The objective was to verify and evaluate previously recognised spawning areas in the Kattegat by more direct methods, namely dedicated egg surveys conducted during the cod spawning season in the Kattegat together with hydrographical observations (Paper I). This developed further into objectives of: quantifying the long term average of retention, dispersal and sedimentation of eggs in relation to egg density, in the Kattegat-Öresund-Belt area, (Paper II) and examining the relationship between the interannual variability of egg abundance and meteorological forcing (Paper III).

As a separate part, a study has been carried out in cooperation with Håkan Westerberg at the Swedish University of Agricultural Sciences as part of the EELIAD project (European Eels in the Atlantic: Assessment of Their Decline). The objective here was to examine possible climatic variation of ocean circulation and consequently the passive drift of European eel leptocephalus larvae across the North Atlantic. The temporal and spatial passive drift patterns of larvae were simulated, and variation of the passive drift was examined over decadal and multidecadal scales (Paper IV).
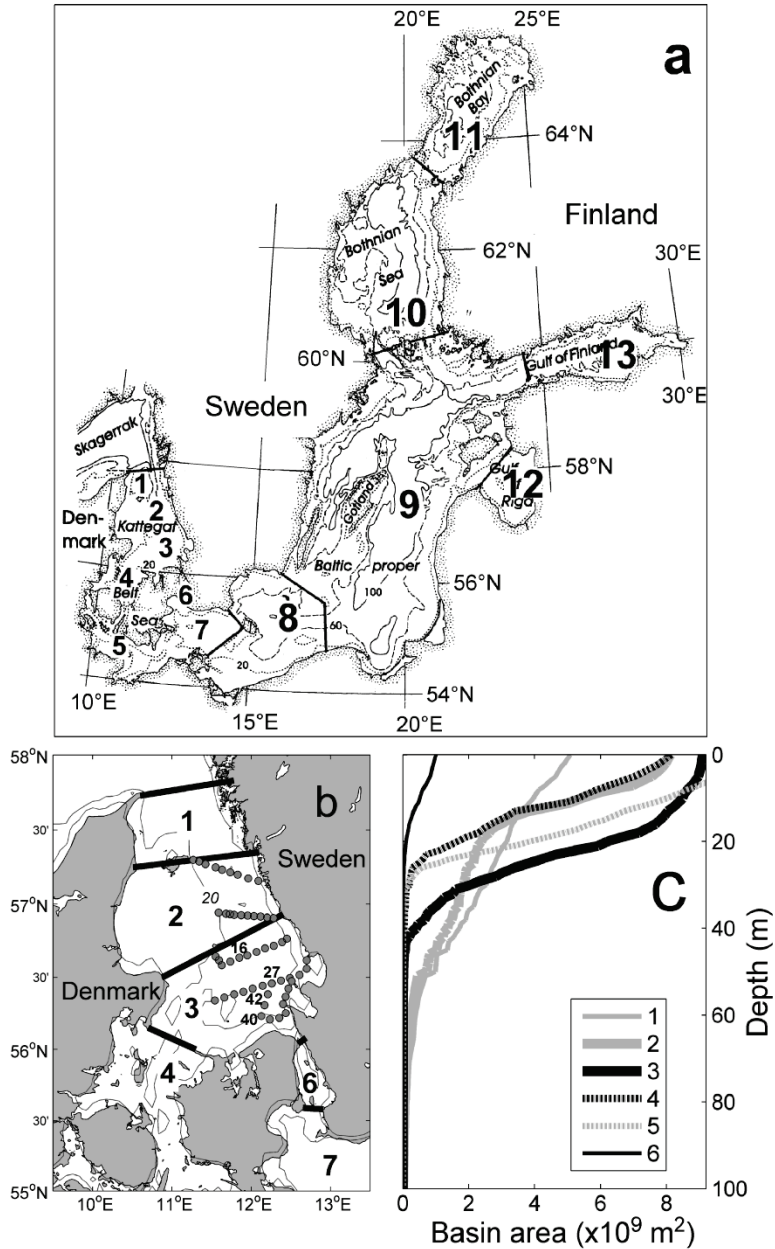
Figure 1. *(a) Map of the Baltic and the Kattegat including borders between the model sub-basins. Adapted from (Gustafsson, 2003) (b) Enlargement of the Kattegat area showing model sub-basins (1 –northern Kattegat, 2 – central Kattegat, 3 –southern Kattegat, 4 –Great Belt, 5 –Little Belt, 6 –Öresund and 7 –Arkona) and sampled stations during surveys in 2005 and 2006 (dots). Numbers next to dots indicate stations at which multiple hauls from different depths were made, see also Fig. 3. (c) Hypsographic curves for sub-basins 1 – 6. (Figure 1 in Paper II)*

2. EGG TRANSPORT IN THE KATTEGAT AND THE ÖRESUND

2.1. The Atlantic Cod (Gadus morhua) - life cycle and spawning

Cod is one of the commercially most important fish species in the Atlantic region with a strong influence on both the economy and the politics of fishing nations. Habitats occupied by cod stretch from the shallow coastal waters to the continental shelf at the Atlantic coasts of America, Greenland and Europe as well as into the Barents Sea (ICES, 2012). The north-eastern Atlantic cod is composed of the north-eastern Arctic stock and the North Sea stock, with a number of local stocks. Like many other stocks since about the 1980s, the North Sea cod have declined to critically low levels due to intense fishing (ICES, 2010). A rebuilding plan for cod was agreed upon by the European Commission in 2004. Cod found in Swedish coastal waters are separated into several stock units: North Sea/Skagerrak cod, Kattegat cod, western Baltic (the Belt Sea, Öresund and Arkona), and eastern Baltic cod stocks (Hüssy, 2011; Svedäng and Bardon, 2003). Still, it has been suggested that this is a somewhat simplified definition of stocks, since the stock dynamics appear to be more complex as indicated by spatial heterogeneity (Hüssy, 2011; Svedäng, 2003; Svedäng et al., 2010b). The decline of the cod stock due to overfishing has strongly influenced the age structure, as today's stock is dominated by young age groups, mainly 1-year and 2-year groups (ICES, 2012). Generally, cod reach maturity at the age of 2-6 years. Mature females carry, on average, 500 ripe eggs per gram body mass. The size of eggs ranges from 1.2 to 1.6 mm in diameter while the egg density differs among the spawning areas. For example, in the Baltic it is about 1012 kg m^{-3} (Nissling et al., 1994) and in the North Sea 1027 kg m^{-3} (Kjesbu et al., 1992; Stenevik et al., 2008), corresponding to salinity 15 ‰ and 35 ‰ respectively. The eggs are pelagic and they float either at the very surface or deeper in the water column depending on environment. The development of eggs progresses in five stages and is dependent on the ambient temperature (Thompson and Riley, 1981). For instance, in the Kattegat it takes about 20-30 days between fertilisation and hatching. After hatching, the larvae are relatively passive and only gradually develop their swimming ability. Finally, larvae metamorphose into juveniles and after approximately 6 months juveniles begin living close to the sea floor (ICES, 2012).

In the 1980s, the Kattegat cod occupied spawning areas from the northern to the southern Kattegat including the Laholmsbukten and the Skälderviken (Svedäng and Bardon, 2003). Today, the spawning is restricted to the south-eastern part of the Kattegat (Vitale et al., 2008). In their study, Vitale et al. (2008) identified the spawning sites by indirect methods (e.g. log book information, maturity indices from International Bottom Trawl Survey (IBTS)) which tend to give information about abundance of sexually mature fish. Detailed direct studies, such as eggs surveys, which can assess the areas not accessible to fishing gears, are desirable to confirm the previous findings.

Using data from egg sampling (Figure 1b and 2), from the Kattegat in 2004 – 2006, the results in *Paper I* confirmed spawning of cod, based on both visually identified cod eggs and cod eggs identified by molecular methods. Genetically analysed egg samples from 2004 showed that 78-90 % of sampled eggs were cod. The spatial distribution of the daily egg production was similar within and between years, providing strong support for the existence of stable spawning areas in the south-

eastern part of the study area (Figure 2; cruise 1 and 2, 2004). North of latitude 56°45´N, the daily production of cod-like eggs was low. The results confirmed that the spawning sites in the central Kattegat, close to Fladen, were not as pronounced as in earlier studies.

Figure 2. *Distribution of stage I cod eggs (2004) or cod-like eggs (2005 and 2006) from replicated egg surveys in the Kattegat during February and March 2004 to 2006. The area of the circles is proportional to daily egg production (egg m² day⁻¹) at each station. Crosses represent sampled stations where no stage I cod-like eggs were found. (Figure 6 in Paper I)*

In the Kattegat, the spawning period is previously known to occur between January and the end of April, peaking in February to March (Vitale et al., 2005). The early spawning in the Kattegat was verified by the findings in *Paper I*, showing that the proportion of stage I eggs was highest during the first cruise each year. Further into the Baltic Sea, the spawning begins later in the year, and eastern Baltic cod spawn between May and August.

2.2. Vertical and horizontal distribution of eggs

Fish eggs can be seen as small buoyant particles, having density specific for the region of spawning. After fertilisation, the eggs move towards the level of neutral buoyancy in the water column (where eggs and water have the same density). The vertical distribution of eggs is determined by a combination of egg density, density stratification of the water column, and vertical mixing. Floating freely in the water column, eggs follow the currents which often vary with depth. Thus, the horizontal transport of eggs is determined by the vertical position of the eggs (Sundby, 1983; Sundby, 1991). Characteristic patterns of ocean density and vertical variation of currents are utilised and developed into lifecycle strategies of fish, specific for a species and a region. One such example is the spawning in the fjords of the northern Norway. The north-eastern Arctic cod spawn light eggs in the surface layer and coastal cod spawn heavier eggs, neutrally buoyant in the deep water of the fjords, as a strategy to optimise egg dispersal and egg retention, respectively. The typical estuarine circulation with offshore directed flow in the low salinity surface layer will disperse lighter eggs towards the open ocean while the tendency to onshore flow in the saline water at the greater depths will retain the eggs (Myksvoll et al., 2011; Stenevik et al., 2008). It is noteworthy that the typical density range for cod eggs in the Kattegat is not well known since direct density measurements are unavailable. The reported estimates of cod egg density in the neighbouring area were made on eggs from breeding experiments of cod from the Gullmar fjord and Öresund, showing an egg density range from 1015 to 1018 kg m^{-3} (Nissling and Westin, 1997).

The Kattegat is a shallow transition area located between the North Sea and the Baltic Sea which has typical estuarine-like circulation induced by the large supply of brackish water from the Baltic (Bergstrom and Carlsson, 1994; Stigebrandt and Gustafsson, 2003). The large outflow of the Baltic brackish water forms a low salinity surface layer in the Kattegat (from 15 ‰ in the south to 20 ‰ in the north), which generally flows in a northerly direction (Gustafsson, 2000a; 2000b; Svansson, 1975). The bottom water, originating from the Skagerrak, has a salinity of about 33-34 ‰ and generally flows southwards (Gustafsson, 2000a; Nielsen, 2005; Winsor et al., 2001; 2003). The halocline, present throughout the year, is typically located at a depth of 15 m and is very thin, sometimes only one-two meters, spanning a salinity gradient of up to 10 ‰ (Svansson, 1975). Given the generally large variation of the density structure and opposite circulation pattern of the surface and the bottom water, it is likely that the egg density is crucial for dispersal and retention of fish eggs in the Kattegat.

The results from the model (BALTSEM, Gustafsson , 2003) in *Paper II* highlighted the importance of egg density for the horizontal transport of fish eggs in the Kattegat and the Öresund. Eggs of low density are easily mixed into the brackish surface layer where they are transported by the relatively swift northward flow and usually flow into the Skagerrak (Figure 3). By contrast, eggs with higher density tend to follow the

slower deep water flow southwards. Generally, heavier eggs are retained in the southern Kattegat, but also suffer a considerable loss through sedimentation.

For the southern Kattegat, the model results (*Paper II*) showed that the optimal egg densities, which maximise the amount of eggs in the water column close to the spawning area, would be in the range corresponding to the lower part of the pycnocline, 1023-1026 kg m^{-3} (Figure 3). The analysis of vertically separated hauls from the south-eastern part of the Kattegat suggested that gadoid eggs were aggregated in the upper part of the pycnocline, within the density range defined at 1017-1022 kg m^{-3}. Relating the observed egg density range to dispersal, retention and sedimentation from the model results (Figure 3), this study indicates that cod eggs from the southern Kattegat are affected by mechanisms leading both to retention and dispersal. A large number of eggs in the observed density range (1017-1022 kg m^{-3}) remain in the spawning area concurrently as eggs are transported northwards (Figure 3). Similarly, the analysis of the centre of gravity (of horizontal egg distribution) in *Paper I* indicated short term transports towards north-northwest, but the average advection distance was small, and typically eggs were retained in approximately the same area from the early to the late development stage. The measured density range of cod eggs in the Öresund (1015 -1018 kg m^{-3}) also corresponds to densities in the upper part of the halocline (*Paper II*).
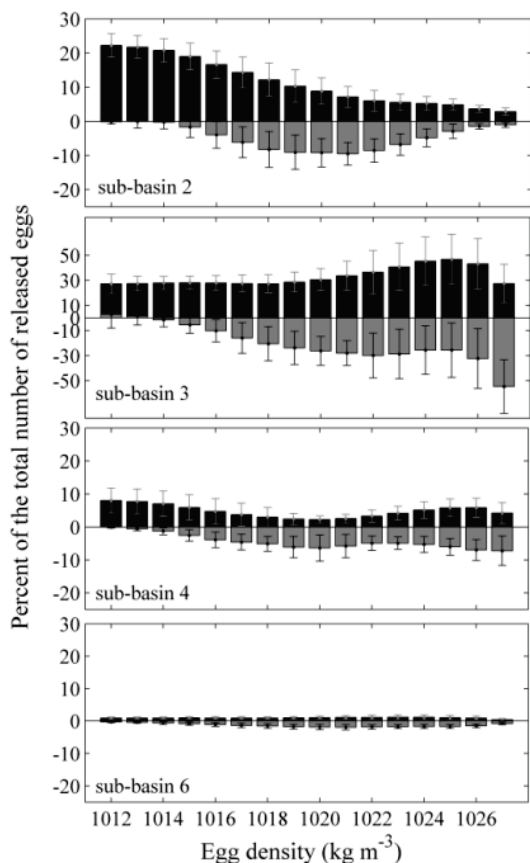

Figure 3. The effect of the egg density on the transport and sedimentation of eggs released in sub-basin 3 (the southern Kattegat) is shown for sub-basin 2-4, and 6 (basin boundaries shown in fig 2). The percentage of eggs m^{-3} remaining in each sub-basin 28 days after release is a mean of four batches and over 36 years. The amount of eggs remaining in the water column is represented by positive bars (dark grey) sedimentation is represented by negative bars (light grey). Note that the vertical axis for sub-basin 3 is different. (Figure 7 in Paper II)

In *Paper II*, the modelling results showed that sedimentation is an important mechanism for egg mortality in regions with strong stratification, and in particular it can be high in shallow areas above the mean pycnocline depth. In general, the egg density in combination with mixing and hypsography controls the amount of sedimentation. For instance, eggs in the density range 1020-1023 kg m^{-3} (Figure 3), equivalent to the middle part of pycnocline, are repeatedly mixed into the surface layer. Since the Kattegat has large shallow areas with depths equal to or shallower than the surface layer depth (Figure 1c), the eggs sediment before they reach the depth of neutral buoyancy. The mortality of eggs that settle in the sediment is excessive as the predation at the bottom is high, and it is not likely that eggs are re-suspended in the water column even if the hydrographical conditions would be favourable (Westerberg, 1994; Westerberg et al., 1996).

The results from the BALTSEM simulation can be compared with integrated results from a study using particle tracking in the western Baltic and Kattegat, based on velocity fields from a three dimensional model (Hinrichsen et al., 2012). The average retention over all densities in the southern Kattegat, as shown in *Paper II*, adds up to 33.5 %, which corresponds well to the 26 % (±16 %) estimated from the three dimensional model. The average sedimentation over all densities estimated in our study, in the southern Kattegat, is 19.6 %. The Hinrichsen et al. (2012) study estimated an egg mortality of 17 % (±11%) in the Kattegat due to contact with the bottom. Possibly, the difference in results could be due to the fact that the three dimensional model does not allow vertical transport of eggs, which might be an important process for dispersal and retention of eggs in this area, giving somewhat lower sedimentation. On the other hand, it might be that the dispersion is somewhat exaggerated in the BALTSEM model where the eggs are treated as a concentration, which by definition results in instantaneous horizontal mixing over the individual layers in the model sub-basins.

Generally, the surface salinity in the Kattegat is relatively low and it can vary considerably both in time and space as it is controlled by the highly variable water exchange with the Baltic Sea (Svansson, 1975; Winsor et al., 2001). For retention and dispersal of eggs, this implies a high interannual variation as shown by the standard deviation in Figure 3. Also in the Lagrangian simulation of the plaice eggs and larvae (*Pleuronectes platessa*) in the Kattegat, Blüthgen (2011) showed large variations of larval supply caused by hydrodynamic forcing. The water exchange between the Kattegat and the Baltic is constricted by the shallow and narrow straits in the Belt Sea and Öresund areas (Mattsson, 1995; Mattsson, 1996). The freshwater supply of about 15 000 m^3 s^{-1} generates a mean flow in the straits, but superimposed on this there are much larger fluctuations of the flow (up to 100 000 m^3 s^{-1}) driven by sea level differences between the Baltic and the Kattegat (Bergstrom and Carlsson, 1994; Gustafsson, 1997; Omstedt et al., 2004). In the Kattegat, the sea level has a strong and nearly direct response to the large scale winds over the North Sea and the Skagerrak while in the Baltic, the response to the Kattegat sea level variations occurs on longer time scales (Andersson, 2002; Gustafsson and Andersson, 2001; Mattsson, 1996).

In *Paper III,* the interannual variation of retention and dispersal of eggs has been related to the meteorological forcing factors. Extreme years with low retention of eggs (such as 1990 and 2002, dark colour shades in Figure 4) are generally connected to strong winds with a dominant westerly component while extreme years with high retention of eggs (such as 1982 and 2006, dark grey bars in Figure 4) are a
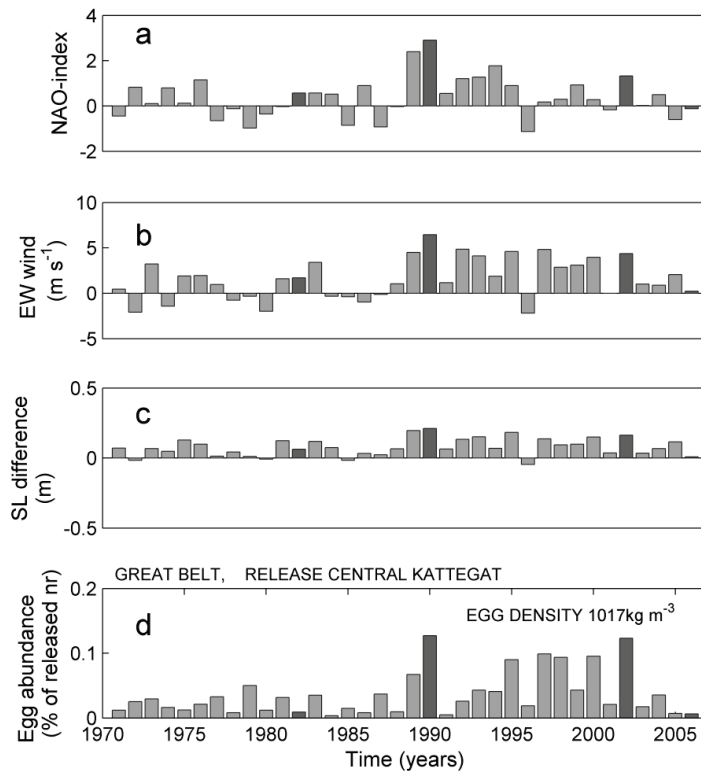
Figure 4. *Interannual variation of a) NAO index (January-April), b) EW component of the local wind (January-April), c) sea level difference between the Baltic Proper (modelled) and southern Kattegat (measured) (January-April), d) egg abundance in Great Belt transported from the release sub-basin 2, the central Kattegat. Dark grey bars mark years 1982, 1990, 2002 and 2006 that exemplify low and high retention years. (Figure 3 in Paper III)*

result of weak variable winds (Figure 4b and d). Further analysis shows a relatively strong direct correlation between local winds and egg transport to the other basins, but also between local winds and sedimentation. The Bornholm Basin study, of the relationship between wind forcing and retention and transport of eggs, showed intensified larval transport due to westerly winds from the basin to coastal areas, and higher retention during weak variable winds (Hinrichsen et al., 2001). Our results showed that the dramatic change in egg abundance and dispersal patterns after 1989 is reflected in the local winds that were dominantly of westerly direction over the same period of time (Figure 4b and d). Similarly, there was a change in the large scale wind pattern over the North Atlantic with intensified westerly winds during the spawning period, indicated by high and positive NAO index in the period from 1989 to 1995 (Figure 4a).

The analysis of interannual variation of retention, dispersal and sedimentation and their correlation to local winds, implies that there might be a fairly fixed amount of eggs in the water column in the spawning basin from year to year while the mortality

due to sedimentation or dispersal of eggs to other areas is highly affected by changes in the physical environment. In the analysis of mortality due to unfavourable temperature condition and sedimentation, Hinrichsen et al. (2012) also pointed out that the transport has a significant effect on the extent of mortality. Unfavourable environmental conditions can have a great impact on the recruitment and should be an important objective in sustainable fishery management, together with other factors like the impact of fishing (Hinrichsen et al., 2012; Larkin, 1996).

As the results in *Paper II* showed, the transport and sedimentation are highly dependent on egg density, which means that in certain years this factor determines the spawning success. An example is the year 1990, when lighter eggs were kept in the water column and heavy eggs were exposed to an extreme sedimentation and thus mortality (*Paper III*). Considering the amount of dispersal, retention and sedimentation in concert with risk of low survival success for high density eggs during the extremely unfavourable conditions, argues for cod eggs to be in the upper part of halocline in this area. This vertical location of eggs was also indicated in *Paper II* with observed egg density range at 1017-1022 kg m^{-3}.

3. LARVAL TRANSPORT IN THE NORTH ATLANTIC

3.1. European eel (Anguilla anguilla) – life cycle and spawning

The European eel is a catadromous species, migrating from the fresh and brackish waters of Iceland and Scandinavia in the north, and the Mediterranean and North Africa in the south, back to the spawning area in the Sargasso Sea (Figure 6) (Schmidt, 1923; Tesch, 2003) Not until the late 19th century, when the specimens of *Leptocephalus brevirostris* were observed metamorphosing into common eels, the freshwater mature eels were linked to marine larvae (Grassi, 1896). Earlier, the marine larvae (*Leptocephalus brevirostris,* now called leptocephalus larvae) were supposed to be a separate species. Eels have often been referred as mysterious species since their life cycle for a long time remained elusive. There are many aspects of their life cycle that are still not very well understood.
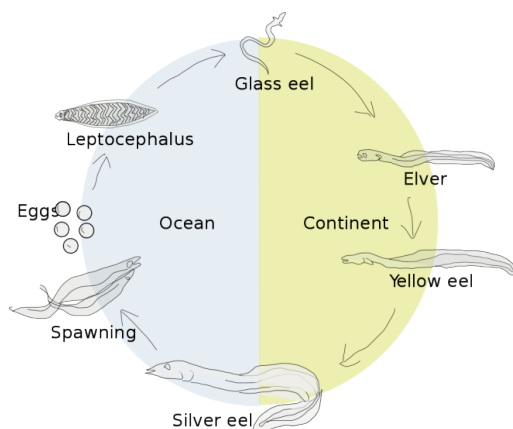

Figure 5. *Life cycle of the European eel showing the oceanic stages of development on the left and fresh water stages on the right. Original drawing by Salvor Gissurardottir (2006).*

During the fresh water stage, eels are referred to as yellow eels (Figure 5), based on the colouring on the sides of the body. Being nocturnal species, the European eels spend their lives hiding burrowed in mud or under stones during daylight and predating at dusk. After 6-12 years in freshwater they reach maturity, and metamorphose into silver eels and start migrating back to the Sargasso Sea for spawning (Han, 2001; Tesch, 2003). This is a widely accepted knowledge, but the question of how eels find their way back to the spawning area and what routes they take remain unanswered. Up until now, just a few silver eels have been caught in the open ocean and none in the Sargasso Sea.
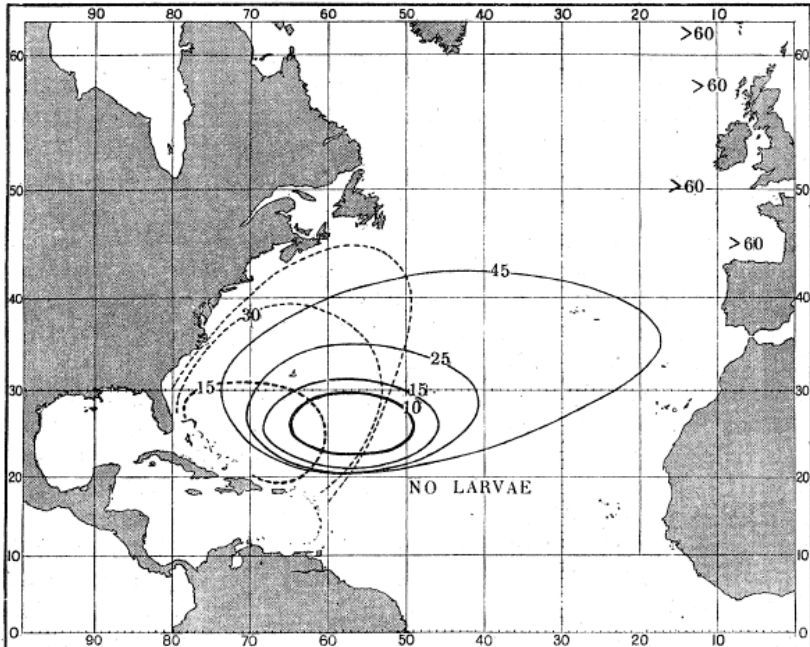

Figure 6: Distribution of Atlantic Anguilla larvae. A. anguilla (solid lines) and A. rostrata (dashed lines). The curves show the limits of occurrence of larvae of the indicated mm lengths. (From Schmidt (1923)).

In the early 20th century, the Danish scientist Johannes Schmidt started the quest for learning more about the oceanic phase of the life of eels. Starting from the Mediterranean through the central North Atlantic to Florida, the decrease in size of leptocephalus larvae guided Schmidt towards the spawning site (Figure 6). Based on the finding of the smallest larvae, the breeding place of the European (*A. anguilla*) and the North American (*A. rostrata*) eel species was defined and located in the Sargasso Sea (Schmidt, 1923). After hatching, leptocephali drift with the ocean currents from the spawning area across the North Atlantic and arrive off the North African, European and Scandinavian coasts where they metamorphose into glass eels. Finally, after entering the freshwaters they become young eels, elvers (Figure 5) that eventually grow into adult yellow eels.

Recruitment of the European eel is currently at a historically low level. All glass eel recruitment series show clear and marked reductions since the early 1980s (Dekker, 2003b). Over the last 5 years, glass eel recruitment has averaged between 1% (in the continental North Sea area) and 7% (in the continental Atlantic area) of the 1960-1979 levels (ICES, 2010). The abundance of other life stages (yellow and silver eel) has also declined, but reliable data are too sparse for a reliable quantitative assessment. As the eel is a species with a single common spawning stock for the whole distribution range (Als et al., 2011), the lack of a meta-population structure means that there is a real threat of extinction of the species (Hanski, 1998). The cause of the decline in eel recruitment is unclear. Fishery, habitat deterioration (including migration barriers), parasites or diseases and climate change may all contribute to the decline (Bonhommeau et al., 2008; Castonguay et al., 1994; Dekker, 2003a; Feunteun, 2002; Friedland et al., 2007; Knights, 2003). A parallel decline in recruitment of the North American eel (with an overlapping spawning area) has led to the hypothesis that there is a common factor in the ocean environment causing the decline.

3.2. Passive drift of the leptocephalus larvae

During the leptocephalus stage, eel larvae are carried with currents across the North Atlantic to the European coasts where they metamorphose into glass eels. The duration of the passive drift of leptocephali is directly related to the mortality, since many factors during migration may influence the survival and thereby recruitment. Schmidt (1923) identified three year classes of leptocephali larvae and from the growth curve calculation estimated the marine phase to be two to three years long. There are several ways of calculating the migration time. Different estimations of age from calculating presumed daily rings in the otoliths generally resulted in a shorter migration time in comparison with Schmidt's calculations, although results from different studies varied greatly, from 6 to 16 months (Arai et al., 2000; Lecomte-Finiger, 1992; Wang and Tzeng, 2000). Yet another way of estimating the migration time is by calculation of duration of the passive drift across the North Atlantic. Several simulations of the larval drift have been made. The first attempt was an advection-diffusion model using monthly mean ship drift data for the velocity field and a length scale dependent diffusivity coefficient (Power and McCleave, 1983). The simulation of 270 days of passive drift showed accumulation of larvae in the northwest of the Sargasso Sea. Based on Lagrangian drift, in data assimilation model of ocean circulation for the period 1993-1996, Kettle and Haines (2006) showed paths of particle drift and latitudinal distribution of arrival. They concluded that European eel larvae should be able to cross the North Atlantic in 2 years based on the passive drift. More recently, Bonhommeau et al. (2009) used Lagrangian simulation to explore the transit time and latitude distribution of particles emanating from the presumed breeding area, applying different assumptions about mortality, diurnal vertical distribution and spawning time. According to this study, the transit time is 21 months at a mortality rate of 3.8 year^{-1}.

In the Lagrangian simulation presented in this thesis in *Paper IV,* the median time of the drift was estimated to be 24.4 months (for mortality of 2 year^{-1} and drift depth level 129.5 m), but the range of drift time is large, depending on which trajectory or path the particles followed. Generally the particles follows the large scale current systems with the majority being involved in the Gulf Stream meandering pattern and transported into the North Atlantic Drift (NAD) (Figure 7a). Reaching the European
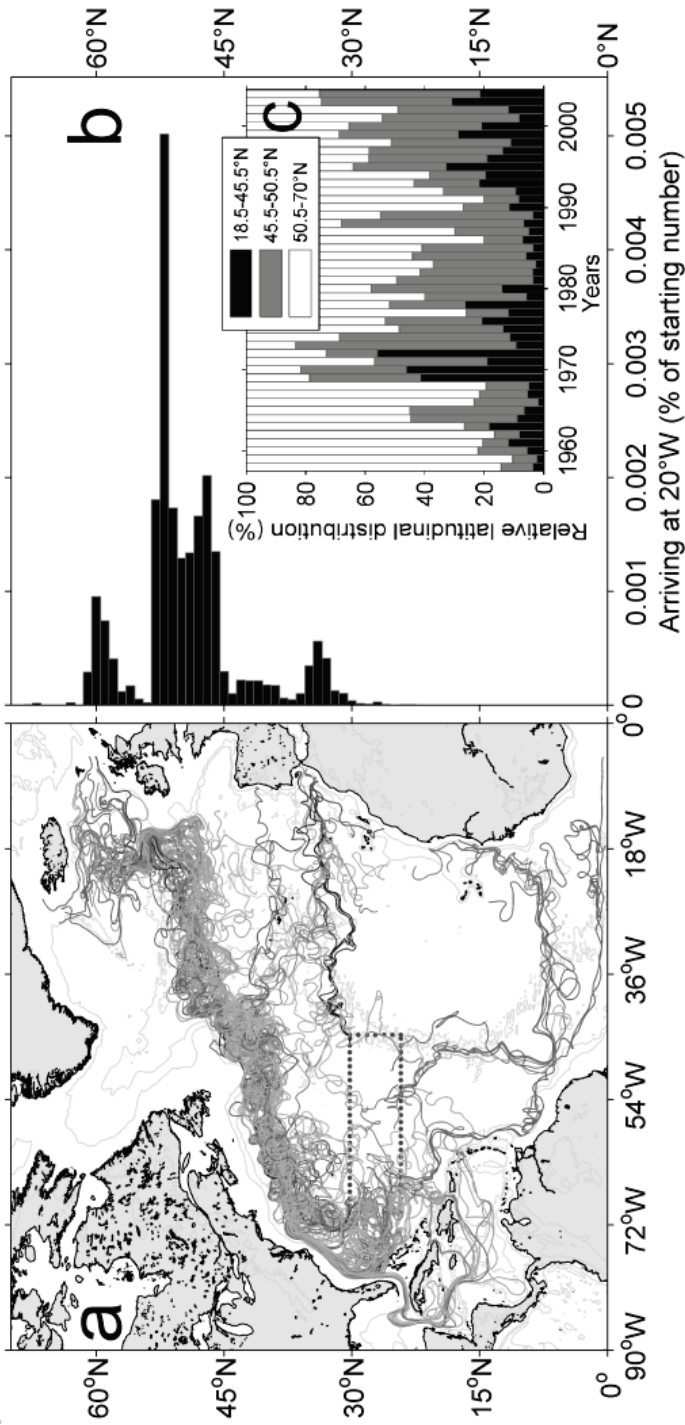
Figure 7. *a) Trajectories illustrate the simulated passive drift for year 1972. Only particles passing the longitude 20°W for latitudes 0-70° N are shown, dark grey indicating shorter drift time and light grey longer drift time. The starting area is marked with grey dots. b) The average latitudinal distribution at the longitude 20°W for latitudes 19-70°N during the period 1958 to 2004. c) The relative proportion of particles crossing 20°W, as a function of release year. In all graphs, the applied mortality is M= 2 year⁻¹.(Figure 5 in Paper IV)*

continental shelf, the NAD bifurcates into the North-east Atlantic current transporting particles to the northern Europe and into the Canary current, bringing particles southwards to the region of the Bay of Biscay. Some of the fastest particles followed this path through the Gulf Stream and to the European shelf. At about 40°N and 40°W a branch from the Gulf Stream breaks off that supplies larvae, through the Azores current, to the Iberian Peninsula and North Africa. Some of the particles, starting in the north-eastern part of the spawning area, headed straight eastwards, joined the Azores Current and arrived in record time at 20°W, in about 6 months (dark trajectories in Figure 7a).

3.3. Climatic change in the passive drift

The effect of climatic changes on the passive drift of leptocephali was examined in Paper IV. The arrival success and survival of larvae based on passive drift give no support for the hypothesis that a climate shift in the circulation of the subtropical gyre is the reason for the decline in recruitment of glass eel in the Europe (Figure 8). On the contrary, given a constant output from the spawning area, the recruitment should have been at an all-time high from 1997 to 2004, which is the last part of the simulation period. This applied to all drift depths and levels of larval mortality being tested in the simulations. Nevertheless, the indirect effects of climatic variations, such as changes in food availability or predation pressure may be important (Bonhommeau et al., 2008).
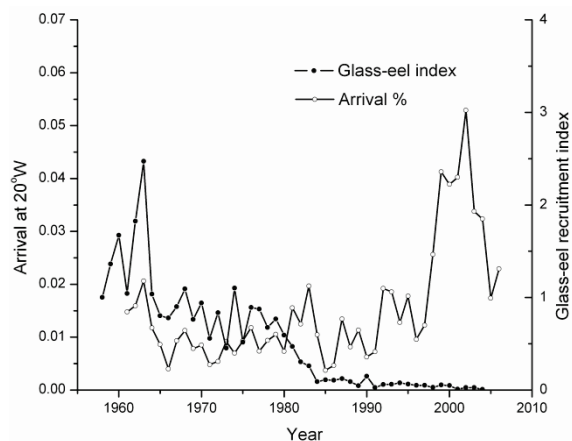

Figure 8. *Comparison between the success rate of particles (drift depth 129.5 m and M=2 year^{-1}) and arriving at 20°W as a function of release year and the general linear model prediction for glass eel recruitment indices in the North Sea area (ICES, 2010). (Figure 8 in Paper IV)*

A relation between variations in the recruitment of *A. anguilla* and the North Atlantic Oscillation (NAO) was suggested by Knights (2003) and Friedland et al. (2007). A significant statistical relation between NAO and the European recruitment time series of eel has been shown by Kettle et al. (2008), who suggested a feedback mechanism via the adult population. A recent hypothesis is that the causal connection to climate is indirect, via a change to a dryer climate combined with dam development in the Iberian and Northwest African part of the range (Kettle et al., 2011).

At a shorter time scale there was a certain co-variation between the calculated drift success and the observed recruitment level (Figure 8). This pattern ceased to exist around 1980. The particles arrived off the European coast at the latitudes of historically high glass eel catches with the highest concentrations at 45-55°N (Figure 7b). The model shows that the proportion of eel larvae carried by the North-east Atlantic current to northern latitudes was greater before 1970, whereas there was an increase in the amount of particles being entrained into the southbound current branches after the 1970s (Figure 7c). The decline in recruitment at the northern latitudes was observed prior the decline in the southern Europe (Svärdson, 1976).

In this study, we also examined the importance of the starting position and time for the larval success. The longitudinal variation in the starting position had a strong influence on the larval success rate. The highest proportion of larvae that reached 20°W started from the westernmost part of the spawning area, which may be explained with its proximity to the Gulf Stream. On the other hand, the time of release showed no significant difference in the success rate.

4. CONCLUSIONS AND FUTURE PERSPECTIVES

Restoration and management of many fish stocks will in the future require much improved knowledge about these resources. Modelling studies as presented in this thesis can give valuable knowledge about stock connectivity, location of the nursery areas and success of survival during the passive life stage. The information provided can give a background for decision making about the need for more specific stock management, location and size of marine protected areas.

In conclusion, this study has shown that density of pelagic eggs (or buoyant particles) in the regions like the Kattegat and the Belt Sea is of great importance for the retention, transport and sedimentation. We have also defined the density range that provides highest retention of eggs in the studied area. A large portion of eggs in the observed density range, both in the Kattegat and Öresund, remain in the spawning area concurrently as eggs are transported northwards because they are typically located in the upper part of halocline. Additionally we have pointed out the high correlation among the local wind and transport and sedimentation of eggs. To end with, the overall success of leptocephali drift from the spawning area to the eastern Atlantic clearly contradicts that this could explain the dramatic recruitment decline of eel.

The results in this thesis confirm the existence of stable spawning areas in the south-eastern part of the Kattegat and the density of the eggs in the Kattegat and the Belt Sea being of great importance for retention, transport and sedimentation. As shown in Paper II, there is an obvious need of determining egg densities more accurately for future studies. Thus, an accurate estimate of the egg density may lead to more realistic model simulations and a better understanding of the process behind retention and sedimentation.

Sedimentation turned out to represent an important mortality factor (e.g. due to high predation at the bottom) both in the BALTSEM model used in this study and in the three dimensional model used by Hinrichsen et al. (2012). We showed how the hypsography and vertical mixing can be decisive for the amount of sedimentation. Accordingly, it would be valuable to evaluate how the distance of spawning locations

to shallow areas influence the rate of sedimentation. Similarly, evaluation of the effect of particularly strong coastal currents and more detailed circulation patterns would improve the quantification of sedimentation for the investigated region. A more detailed study of sedimentation processes in the Kattegat and the western Baltic region, using a model with higher horizontal resolution, would be an interesting continuation of the findings presented here.

The search for answers concerning the drift duration of eel larvae continues. Backwards modelling, from the location of high recruit catches to the spawning area, could be the next method for estimating migration duration of eel larvae. In particular, it would be interesting to examine migration and origin of the Icelandic eels, as very little is known about this stock. Examination of the yearly distribution of several age classes found in recruit catches, compared to the yearly distribution of the migration length would add information on how well the simulations of passive drift duration represent the actual age of glass eel. Earlier studies suggested that the spawning ground was determined by the temperature front (that varies spatially and temporally) in the subtropical convergence zone. It would be interesting to model displacement of the spawning place following the location of the temperature front and investigate the effect of it on the duration and path of the passive drift of leptocephali.

In Lagrangian simulations in this as well as in other studies, a portion of particles drifted through the Caribbean Sea. In earlier studies this route was first suggested to be taken mainly by the American eel. Looking at the starting position and duration of passive drift of particles taking the route through the Caribbean Sea could increase the understanding of stock separation mechanisms of European and American eels. This type of investigation can also give an indication of the origin of the mixed stocks in the Iceland.

The location of the spawning ground of eel has been determined by catches of the smallest leptocephali. No eel eggs have ever been sampled and no mature eels have been caught in the Sargasso Sea. A more correct definition of the spawning place (through a survey of distribution of eel eggs and early larvae) would surely be a difficult task, but most certainly it is of great importance for further studies.

"Considering these points, I perceived that if the problem were to be solved in anything like a satisfactory manner it would be necessary to ascertain, not only where the youngest larvae were to be found, but also where they were not."

(Johannes Schmidt, 1922)

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REFERENCES

Als, T. D., Hansen, M. M., Maes, G. E., Castonguay, M., Riemann, L., Aarestrup, K., Munk, P., et al. 2011. All roads lead to home: panmixia of European eel in the Sargasso Sea. Molecular Ecology, 20: 1333-1346.

Andersson, H. C. 2002. Influence of long-term regional and large-scale atmospheric circulation on the Baltic sea level. Tellus A, 54: 76-88.

Arai, T., Otake, T., and Tsukamoto, K. 2000. Timing of metamorphosis and larval segregation of the Atlantic eels Anguilla rostrata and A. anguilla, as revealed by otolith microstructure and microchemistry. Marine Biology, 137: 39-45.

Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic Marine Copepod Biodiversity and Climate. Science, 296: 1692-1694.

Bergstrom, S., and Carlsson, B. 1994. River runoff to the Baltic sea - 1950-1990. Ambio, 23: 280-287.

Blüthgen, J. 2011. Transport of Plaice Pleuronectes platessa eggs and larvae in the Skagerrak and Kattegat in a coupled hydrodynamic - individual-based model p. 130. University of Bergen, Bergen, Norway.

Bonhommeau, S., Chassot, E., Planque, B., Rivot, E., Knap, A. H., and Le Pape, O. 2008. Impact of climate on eel populations of the Northern Hemisphere. Marine Ecology-Progress Series, 373: 71-80.

Bonhommeau, S., Le Pape, O., Gascuel, D., Blanke, B., Treguier, A. M., Grima, N., Vermard, Y., et al. 2009. Estimates of the mortality and the duration of the trans-Atlantic migration of European eel *Anguilla anguilla* leptocephali using a particle tracking model. Journal of Fish Biology, 74: 1891-1914.

Brochier, T., Lett, C., Tam, J., Freon, P., Colas, F., and Ayon, P. 2008. An individual-based model study of anchovy early life history in the northern Humboldt Current system. Progress in Oceanography, 79: 313-325.

Castonguay, M., Hodson, P. V., Moriarty, C., Drinkwater, K. F., and Jessop, B. M. 1994. Is there a role of ocean environment in American and European eel decline? Fisheries Oceanography, 3: 197-203.

Corell, H., Moksnes, P.-O., Engqvist, A., Doos, K., and Jonsson, P. R. 2012. Depth distribution of larvae critically affects their dispersal and the efficiency of marine protected areas. Marine Ecology Progress Series, 467: 29-+.

Dekker, W. 2003a. Did lack of spawners cause the collapse of the European eel, Anguilla anguilla? Fisheries Management and Ecology, 10: 365-376.

Dekker, W. 2003b. Status of the European eel stock and fisheries.

Feunteun, E. 2002. Management and restoration of European eel population (Anguilla anguilla): An impossible bargain. Ecological Engineering, 18: 575-591.

Friedland, K. D., Miller, M. J., and Knights, B. 2007. Oceanic changes in the Sargasso Sea and declines in recruitment of the European eel. Ices Journal of Marine Science, 64: 519-530.

Grassi, G. B. 1896. The Reproduction and Metamorphosis of the Common Eel (Anguilla vulgaris). Proceedings of the Royal Society of London, 60: 260-271.

Gustafsson, B. 1997. Interaction between Baltic Sea and North Sea. Deutsche Hydrografische Zeitschrift, 49: 165-183.

Gustafsson, B. 2003. A time-dependent coupled-basin model of the Baltic Sea. C47.

Gustafsson, B. G. 2000a. Time-dependent modeling of the Baltic entrance area. 1. Quantification of circulation and residence times in the Kattegat and the straits of the Baltic sill. Estuaries, 23: 231-252.

Gustafsson, B. G. 2000b. Time-dependent modeling of the Baltic entrance area. 2. Water and salt exchange of the Baltic Sea. Estuaries, 23: 253-266.

Gustafsson, B. G., and Andersson, H. C. 2001. Modeling the exchange of the Baltic Sea from the meridional atmospheric pressure difference across the North Sea. Journal of Geophysical Research: Oceans, 106: 19731-19744.

Han, Y.-S. T., W.-N. Huang, Y.-S. I Liao, I C. 2001. Silvering in the eel: changes in morphology, body fat content, and gonadal development Journal of Taiwan Fisheries Research, 9: 119-127.

Hanski, I. 1998. Metapopulation dynamics. Nature, 396: 41-49.

Hinrichsen, H.-H., Hüssy, K., and Huwer, B. 2012. Spatio-temporal variability in western Baltic cod early life stage survival mediated by egg buoyancy, hydrography and hydrodynamics. ICES Journal of Marine Science: Journal du Conseil.

Hinrichsen, H. H., John, M. S., Aro, E., Gronkjaer, P., and Voss, R. 2001. Testing the larval drift hypothesis in the Baltic Sea: retention versus dispersion caused by wind-driven circulation. Ices Journal of Marine Science, 58: 973-984.

Hüssy, K. 2011. Review of western Baltic cod (Gadus morhua) recruitment dynamics. Ices Journal of Marine Science, 68: 1459-1471.

ICES 2010. ICES Advice 2010, Book 9.

ICES 2012. The Cod. *In* FishMap. http://www.ices.dk/marineworld/fishmap/ices/pdf/cod.pdf.

Kettle, A. J., and Haines, K. 2006. How does the European eel (*Anguilla anguilla*) retain its population structure during its larval migration across the North Atlantic Ocean? Canadian Journal of Fisheries and Aquatic Sciences, 63: 90-106.

Kettle, A. J., Bakker, D. C. E., and Haines, K. 2008. Impact of the North Atlantic Oscillation on the trans-Atlantic migrations of the European eel (*Anguilla anguilla*). Journal of Geophysical Research-Biogeosciences, 113.

Kettle, A. J., Vollestad, L. A., and Wibig, J. 2011. Where once the eel and the elephant were together: decline of the European eel because of changing hydrology in southwest Europe and northwest Africa? Fish and Fisheries, 12: 380-411.

Kjesbu, O. S., Kryvi, H., Sundby, S., and Solemdal, P. 1992. Buoyancy variations in eggs of Atlantic cod (*Gadus-morhua* L) in relation to chorion thickness and egg size - theory and observations. Journal of Fish Biology, 41: 581-599.

Knights, B. 2003. A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of *anguillid* eels of the Northern Hemisphere. Science of the Total Environment, 310: 237-244.

Larkin, P. A. 1996. Concepts and issues in marine ecosystem management. Reviews in Fish Biology and Fisheries, 6: 139-164.

Lecomte-Finiger, R. 1992. Growth history and age at recruitment of European glass eels (Anguilla anguilla) as revealed by otolith microstructure. Marine Biology, 114: 205-210.

Mann, K. H., and Lazier, J. R. N. 2006. Dynamics of marine ecosystems: biological-physical interactions in the oceans*,* Blackwell Publishing, Oxford, UK.

Mattsson, J. 1995. Observed Linear Flow Resistance in the Oresund due to Rotation. Journal of Geophysical Research-Oceans, 100: 20779-20791.

Mattsson, J. 1996. Analysis of the exchange of salt between the Baltic and the Kattegat through the Oresund using a three-layer model. Journal of Geophysical Research-Oceans, 101: 16571-16584.

Myksvoll, M. S., Sundby, S., Adlandsvik, B., and Vikebo, F. B. 2011. Retention of Coastal Cod Eggs in a Fjord Caused by Interactions between Egg Buoyancy and Circulation Pattern. Marine and Coastal Fisheries, 3: 279-294.

Nielsen, M. H. 2005. The baroclinic surface currents in the Kattegat. Journal of Marine Systems, 55: 97-121.

Nissling, A., Kryvi, H., and Vallin, L. 1994. Variation in Egg Buoyancy of Baltic Cod (*Gadus-Morhua*) and its Implications for Egg Survival in Prevailing Conditions in the Baltic Sea. Marine Ecology-Progress Series, 110: 67-74.

Nissling, A., and Westin, L. 1997. Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. Marine Ecology-Progress Series, 152: 261-271.

Omstedt, A., Elken, J., Lehmann, A., and Piechura, J. 2004. Knowledge of the Baltic Sea physics gained during the BALTEX and related programmes. Progress in Oceanography, 63: 1-28.

Parada, C., van der Lingen, C. D., Mullon, C., and Penven, P. 2003. Modelling the effect of buoyancy on the transport of anchovy (*Engraulis capensis*) eggs from spawning to nursery grounds in the southern Benguela: an IBM approach. Fisheries Oceanography, 12: 170-184.

Power, J. H., and McCleave, J. D. 1983. Simulation of the North-Atlantic Ocean drift of *Anguilla leptocephali*. Fishery Bulletin, 81: 483-500.

Schmidt, J. 1923. The Breeding Places of the Eel. Philosophical Transactions of the Royal Society of London. Series B, Containing Papers of a Biological Character, 211: 179-208.

Stenevik, E. K., Sundby, S., and Agnalt, A. L. 2008. Buoyancy and vertical distribution of Norwegian coastal cod (*Gadus morhua*) eggs from different areas along the coast. Ices Journal of Marine Science, 65: 1198-1202.

Stigebrandt, A., and Gustafsson, B. G. 2003. Response of the Baltic Sea to climate change - theory and observations. Journal of Sea Research, 49: 243-256.

Sundby, S. 1983. A one-dimentional model for verical-distribution of pelagic fish eggs in the mixed layer. Deep-Sea Research Part a-Oceanographic Research Papers, 30: 645-661.

Sundby, S. 1991. Factors affecting the vertical-distribution of eggs. Ecology and Management Aspects of Extensive Mariculture, 192: 33-38.

Svansson, A. 1975. Physical and chemical oceanography of the Skagerrak and the Kattegat, 1. Open sea conditions. Report 1. 1-88 pp.

Svansson, A. 2004. Otto Pettersson the oceanographer (1848-1941). Extracts from a biography in preparation.- In Ocean Sciences Bridging the Millenia, A spectrum of historical accounts, Proceedings of ICHO VI, Qingdao, China, 1998. ed. Morcos, S et al., UNESCO (Paris) and China Ocean Press, Beijing: 17-28.

Svedäng, H. 2003. The inshore demersal fish community on the Swedish Skagerrak coast: regulation by recruitment from offshore sources. ICES Journal of Marine Science: Journal du Conseil, 60: 23-31.

Svedäng, H., and Bardon, G. 2003. Spatial and temporal aspects of the decline in cod (*Gadus morhua* L.) abundance in the Kattegat and eastern Skagerrak. Ices Journal of Marine Science, 60: 32-37.

Svedäng, H., André, C., Jonsson, P., Elfman, M., and Limburg, K. 2010b. Migratory behaviour and otolith chemistry suggest fine-scale sub-population structure within a genetically homogenous Atlantic Cod population. Environmental Biology on Fishes.

Svärdson, G. 1976. The decline of the Baltic eel population. Report Institute of Freshwater Research, Drottningholm, 55: 136-143.

Tesch, F.-W. 2003. The eel Blackwell Science, cop, Oxford, UK

Thompson, B. M., and Riley, J. D. 1981. Egg and larval development studies in the North Sea cod *Gadus-morhua*. Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer, 178: 553-559.

Wang, C. H., and Tzeng, W. N. 2000. The timing of metamorphosis and growth rates of American and European eel leptocephali:: A mechanism of larval segregative migration. Fisheries Research, 46: 191-205.

Westerberg, H. 1994. The transport of cod eggs and larvae through Oresund.

Westerberg, H., Rönnbäck, P., and H., F. 1996. Effects of suspended sediment on cod egg and larvae and the behaviour of adult herring and cod.

Westerberg, H., and Ask, L. 2011. Staten och Fisket - nedslag i fiskeriförvaltningens historia.

Winsor, P., Rodhe, J., and Omstedt, A. 2001. Baltic Sea ocean climate: an analysis of 100 yr of hydrographic data with focus on the freshwater budget. Climate Research, 18: 5-15.

Winsor, P., Rodhe, J., and Omstedt, A. 2003. Baltic Sea ocean climate: an analysis of 100 yr of hydrographical data with focus on the freshwater budget (vol 18, pg 8, 2001). Climate Research, 25: 183-183.

Vitale, F., Cardinale, M., and Svedäng, H. 2005. Evaluation of the temporal development of the ovaries in *Gadus morhua* from the Sound and Kattegat, North Sea. Journal of Fish Biology, 67: 669-683.

Vitale, F., Borjesson, P., Svedäng, H., and Casini, A. 2008. The spatial distribution of cod (*Gadus morhua* L.) spawning grounds in the Kattegat, eastern North Sea. Fisheries Research, 90: 36-44.

II. Papers I–IV