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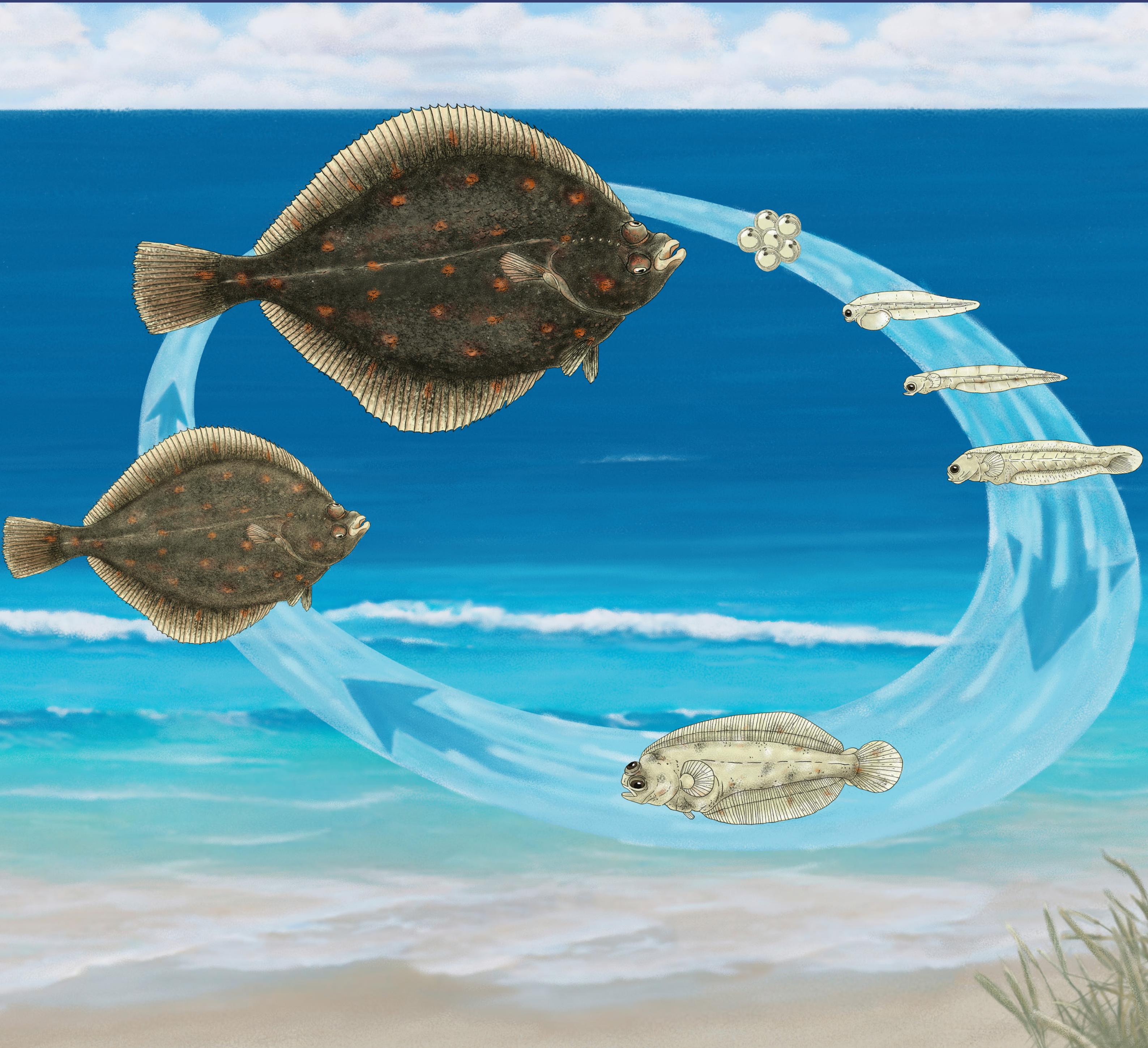

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Dansk resumé

Formålet med dette projekt er at kortlægge fiske habitater for 10 af de vigtigste fiskearter, der indgår i det kommercielle fiskeri i de indre danske farvande. Der indsamles nye data til supplement af eksisterende data for en bedre beskrivelse af årstidsvariationen i udbredelse. Den spatiale sammenhæng mellem de forskellige livsstadie habitater for de enkelte arter vurderes i forhold til den nuværende forvaltning og graden af overlap mellem fiske habitater og eksisterende beskyttede og lukkede områder (eks. Natura2000) vurderes med henblik på at identificere hvor fiskenes habitater allerede er beskyttet. De opnåede fiskehabitatskort vil indgå i den maritime spatial forvaltning, der sikrer at fiskene kan gennemføre deres livscyklus og dermed bevare, forbedre eller genoprette vigtige habitater af betydning for bestandenes udvikling. Derefter er formålet at sammensætte disse resultater samt relevante informationer fra andre både nationale og internationale projekter og integrere disse i bestandsanalyser for de enkelte arter.

Fokus arterne på projektet var: torsk *Gadus morhua*, rødspætte *Pleuronectes platessa*, tunge *Solea solea*, pighvar *Scophthalmus maximus*/*Psetta maxima*, skrubbe *Platichthys flesus*, sild *Clupea harengus*, brisling *Sprattus sprattus*, ål *Anguilla anguilla*, stenbider *Cyclopterus lumpus* og jomfruhummer *Nephrops norvegicus*.

Udover at anvende eksisterende tidsserie data fra nationale og internationale forsøgsfiskeri, blev der indsamlet nye data. Et ekstra Kattegat togt (KASU) blev gennemført i sommer 2016 (Q3) på samme stationer og samme metode som KASU togterne gennemføres i vinter (Q1) og efteråret (Q4). Sommer fourageringsområder blev identificeret med disse nye data. Disse sommer fourageringsområder var for nogle arter forskellige fra overvinteringsområder (Q1 og Q4) eller gydeområder (Q1). Dette var især tydeligt for torsk, rødspætter, skrubbe og brisling. Kortene viser også hvor meget/lidt overlap der var mellem voksne og juvenile fisk for de arter hvor det var muligt at skelne mellem adulte og juvenile fisk (torsk, rødspætte, tunge, skrubbe og sild). Gydeområder blev identificeret for torsk, rødspætter og skrubber, der gyder i vintersæsonen (Q1) men ikke for tunge og pighvar, der gyder i maj/juni (Q2) på grund af manglende overlap mellem gydetidspunkt og togt tidspunktet. Endvidere dækker disse togter ikke de kystnære områder, og derfor er det ikke muligt at kortlægge fiske habitater i kystområder. Dette gælder for eksempel for sild, der gyder langs kysterne.

Nye data blev også indhentet gennem et juvenil fisk togt, hvor der blev samplet 146 stationer i de indre danske farvande. Habitat kvalitetskort blev udviklet på fisketæthed data og vækstdata (ud fra øresten) for tre fladfiskearter: rødspætte, skrubbe og tunge. Dette arbejde er afrapporteret i en særskilt videnskabelig publikation som indsendes til et internationalt tidsskrift (Brown m.fl. 2019). Togtet dækkede kystområderne i de indre danske farvande men ekskluderede fjord systemer, som kan være vigtige gyde eller opvækstområder.

Fra interviews med fiskere blev der dannet kort over fiskeforekomster. Oplysninger om gydeområder og juvenile områder for de enkelte arter var for sparsomt til at blive oparbejdet særskilt og derfor viser disse kort de områder hvor flest fiskere identificerede dem som forekomst områder for hver af de 10 arter.

Der blev udviklet fiske habitat kort for fokus arterne ud fra eksisterende og de nye indhentede fangstdata fra togterne i dette projekt. Disse data blev anvendt til at udvikle statistiske modeller på forhold mellem fiskeforekomster og miljødata som temperatur, saltholdighed, dybde og sediment type. Den model der bedst passede til data blev derefter anvendt til at udpege potentielle fiske habitater på hele studieområdet. De årlige togt data blev anvendt til at vise den general fordeling af fisk over årene fordelt på sæson og livsstadie (adulte, juvenile, gydning). Der blev udviklet kort for juvenile og voksne torsk, rødspætter, tunger, skrubber og sild. Endvidere blev der udviklet kort for brisling og pighvar. For alle disse kort blev der samtidig dannet kort, der viser hvor stor "usikkerhed" der var omkring estimaterne. For de andre arter var der ikke tilstrækkelig data til at producere kort. For enkelte arter var det kun muligt ud fra fiskernes information eller baseret på fiskeri data at identificere de områder hvor de fiskes.

Fordi kortene er opdelt på sæson, er det muligt at identificere gydeområder, fourageringsområder eller overvintringsområder for nogle arter. Gydeområder kan kun identificeres når gyde tidspunktet falder sammen med tidspunktet for dataindsamlingen. Feltstudier fra det international anerkendt litteratur blev anvendt til at validere tolkningen af disse kort. Kort udarbejdet på baggrund af fisker interviews (Støttrup m. fl. 2019) blev også anvendt til at validere tolkningen af kortene. En workshop om torsk hvor kortene blev vist og drøftet blev afholdt og flere mindre møder afholdt med kollegaer med ekspertise inden for nogle af arterne.

De individuelle artsfordelinger blev sammenlagt i et kort. Disse aggregerede kort fremhævede nogle kerne områder af betydning (hot-spots) for flere kommercielt vigtige arter. Som forventet var der ikke en god sammenhæng mellem de aggregerede kort og kort over fordeling af Natura2000 områder, primært fordi Natura2000 områder vælges ud fra andre formål end beskyttelse af fisk. Fiskeriforvaltningsområdet nord for sundet "Kilen", overlapper med gydeområdet for torsk og samtidig beskytter andre arter, men dækker ikke de vigtige fiske habitater som blev vist i dette studie.

English summary

The aim of this project is to map Essential Fish Habitats (EFH) for ten of the commercially most important species in the inner Danish waters. New data were collected to supplement existing data to better describe seasonal differences in distribution. The spatial overlap between habitats of the different life stages is evaluated as well as the degree of overlap between EFH and existing management areas such as Natura 2000 areas and fishery management areas. The EFH maps will be incorporated into Maritime Spatial Planning to ensure that fish species can complete their life-cycle and thus preserve, improve or restore important habitats, essential for the development of a species. The species studied are: Atlantic cod *Gadus morhua*, European plaice *Pleuronectes platessa*, common sole *Solea solea*, turbot *Scophthalmus maximus*/*Psetta maxima*, European flounder *Platichthys flesus*, Atlantic herring *Clupea harengus*, European sprat *Sprattus sprattus*, European eel *Anguilla anguilla*, lumpfish *Cyclopterus lumpus* and Norway lobster *Nephrops norvegicus.*

Apart from using existing time-series data from national and international fishing surveys, new data were collected. An additional Kattegat Survey (KASU) survey was conducted during summer 2016 (Q3) using the same methods and visiting the same stations that KASU surveys conduct in Q1 and Q4 every year. Summer feeding grounds were identified with the new data. These summer feeding grounds were significantly different to overwintering (Q1 and Q4) areas or spawning areas (Q1). This was true for cod, plaice, flounder and sprat. The EFH maps showed the degree of overlap between juvenile and adult habitats for those species where distinction could be made between adult and juvenile fish (cod, plaice, sole, flounder and herring). Spawning grounds were identified for cod, plaice and flounder that spawn in the winter season (Q1) but could not be identified for sole and turbot that spawn in May/June (Q2) due to lack of seasonal overlap between spawning season and timing of survey. The surveys do not cover coastal areas and thus coastal habitats could not be mapped. This was the case for example for herring that spawns in shallow coastal areas.

New data was also collated through a juvenile fish survey that sampled 146 stations in the inner Danish waters. Habitat quality maps were developed using fish abundance data and growth data obtained from otoliths for Young-of-the-Year (YOY) of three flatfish species, plaice, flounder and sole. This work is reported in a separate paper intended for peer-review (Brown et al. 2019). This survey covered the coastal areas in the inner Danish waters and excluded fjord systems, which can be essential growth or spawning areas for several species.

Interviews with fishermen provided information on presence for the 10 species. Since particular information on spawning or juvenile areas for individual species was too sparse to produce separate maps, composite maps were produced on fish presence per species as provided by the fishermen.

EFH maps were produced for the focus species from existing data and the newly obtained data from the surveys in this project. The data was used to develop statistical

models on the relationship between fish abundance and environmental variables such as temperature, salinity, depth and sediment type. The best fitting model was then used to predict potential fish habitats within the whole study area. The yearly survey data were used to map the general fish distributions over the years during different seasons and different life-stages (adult, spawning, juvenile). Maps for juvenile and adult cod, plaice, sole, flounder and herring were developed. Also maps for turbot and sprat are shown. Error maps were developed to provide information on the “uncertainty” of the estimations. For the remaining species data was insufficient to produce maps. For some species presence maps only were available from the fishermen interview data.

As seasonal maps were produced, it was possible to identify spawning areas, feeding grounds or overwintering grounds for the different species. Spawning areas can only be identified when spawning time and survey timing coincide. Peer-reviewed literature field studies were used to validate the interpretation of the predictive maps. Maps produced from the fishermen interviews (Støttrup et al. 2019) were also used to validate interpretation. A workshop dedicated to cod allowed for the discussion of the cod maps and exchange of relevant information. several subsequent short meetings were held with colleagues who had specific expertise on some of the species.

The aggregated maps of the individual species distributions highlighted hot-spot areas for multiple commercially important fish species. Not surprisingly, a poor overlap was found between the aggregated maps and a map of the Danish marine Natura2000 sites, since the latter are generally designated for other purposes than fish protection. The overlap with the fisheries management area just north of the Sound, “kilen”, coincides with the spawning area for cod and provides some protection for other species, but does not capture the important multiple fish habitats captured in this study.

1. Introduction

The ability to spatially locate resources in the marine environment with confidence and at high resolution is important to marine planning. Many exploited species use different habitats (nursery, feeding, spawning) throughout different life stages and are dependent on the availability of these habitats to sustain them even at the population level (Seitz et al., 2014; Brown et al., 2018). Fish switch between habitats at different times of the year or during their lifetime. Most flatfish, such as plaice *Pleuronectes platessa*, flounder *Platichthys flesus* and sole *Solea solea*, spend most of their time on soft-bottom habitats, the switch between life-stages being mostly determined by water depth, where they depend on coastal soft-bottom sediments during the juvenile stages and move to offshore areas as adults or to spawn (Fig.1.1). Other species may depend upon a particular type of sea bottom. For example herring *Clupea harengus* depend on a solid substrate such as gravel/ boulders (Geffen, 2009) or macroalgae or mussel beds (Casini, 2010). Juvenile cod *Gadus morhua* depend on the presence of hard-bottom, complex topography or biogenic habitats for their growth and survival (Tupper & Boutilier, 1995a; Pihl et al., 2006a). Specific habitat requirements may be critical for the status of a species and its response to climate change and/or anthropogenic pressures.

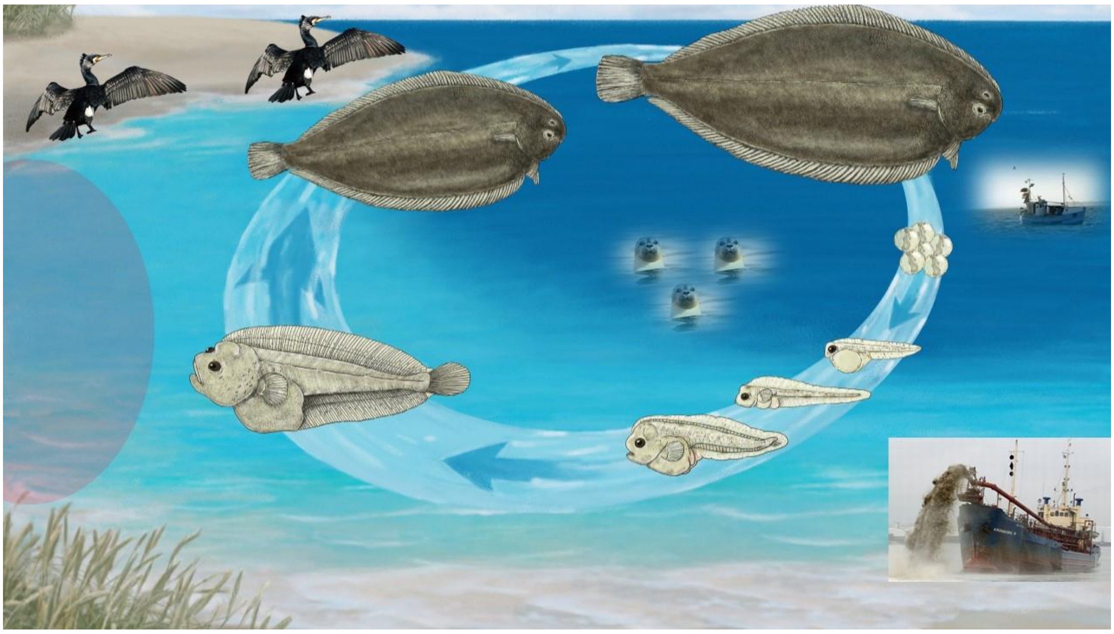

Fig. 1.1. A schematic life-cycle for sole *Solea solea*, where the adults spawn off-shore and the pelagic eggs and newly-hatched larvae drift towards the coastal nursery areas, where they grow during their juvenile stage. Juveniles move progressively off-shore and recruit to the adult population and contribute to the spawning biomass or enter the fisheries. Pressures that may negatively impact the development of the species during one or more of its life-stages include fishery, coastal defense, predators such as seals and cormorants, climate change causing coastal warming or eutrophication.

Essential fish habitats (EFH) are defined as those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity (1996 US Magnuson-Stevens Act). EFH was indirectly introduced in the common fisheries policy through the EnviEFH (Environmental Approach to Essential Fish Habitat Designation) specific support action (Valavanis, 2008). This was the initial effort to introduce a spatial component to fishery management. Fisheries protection zones e.g. areas identified as EFH, could be declared through the Marine Strategy Directive. However, defining "essential" as it applies to essential fish habitats has been a challenge. One approach was to classify fish habitats into different categories as suggested by Planque et al. (2007): (a) *potential* habitats where water masses or substrates can uphold a particular function for a fish species during a particular life-stage or period of time; (b) *realised* habitats which are the areas actually inhabited by fish during a particular life-stage or period of time and; (c) *effective* habitats which correspond to those areas which support the highest densities, growth or survival, which could hypothetically be the most important for the completion of a particular life-stage or which have the highest relative contribution to a population. This approach is slightly different to the legal concept of "essential fish habitat, which is an area "critical to the long-term survival and health of fish populations" (Valavanis, 2008), which is more similar to the *effective* habitats definition.

Habitats are not essential simply because fish utilise the area for a short (season) period. They become essential if their presence and magnitude is important for a fish species to complete its life-cycle or to maintain a certain level of recruitment for a population. Changes in the environment can essentially alter the *realised* habitat and it may be possible to identify the environmental variable that constrains the use of a potential habitat by a particular species. The effective habitat may be a result of the interaction of ecosystem productivity, population dynamics and connectivity. These interact to not only influence the distribution of fish but the outcome of that life-stage during their occupation of a particular area/habitat. Maps that spatially identify essential fish habitats may represent an important tool in marine planning.

The transition to ecosystem-based approach to fishery management reflects the perception that declines in fish populations may, in addition to overfishing, be due to habitat changes or losses. Mapping EFH supports the ecosystem approach to fisheries management by safeguarding critical habitats or critical stages of harvested species, thus contributing to the health of fish stocks. The identification of nursery areas, where juvenile aggregate, contributes to reduce discards or to reduce unwanted catches of fish individuals too small for use in human consumption. EFH mapping also contributes towards MSY objectives in providing information towards the conservation of that proportion of a fish stock responsible for its future state.

The value of coastal habitats is not well documented but there is emerging evidence of their importance for sustaining commercially important species (Seitz et al., 2014; Brown et al., 2018). The high early life-stage mortality implies that for many fish species there is no correlation between spawning biomass and juvenile recruitment. Consequently, the functionality of nursery areas (also termed juvenile growth areas) play a vital role in supplying recruits to fish populations. Juvenile flatfish utilise sandy shallow coastal areas during their first summer(s), but gradually disperse to deeper areas, as they grow older. The loss of shallow areas, or their function as growth areas, may negatively affect recruitment. This loss could be due to a variety of biotic or abiotic factors, such as invasive species or inflated predator growth (eg. cormorants, seals), climate change, fishery, sediment extraction, coastal defence or decline in habitat quality due to eutrophication (see Fig. 1.2). Thus, declines or losses of habitats may be observed as a decline of realised habitat vs potential habitat. However, declines or losses of effective habitat may significantly affect a population. Furthermore, effective habitats may be crucial for more than one species and thus should be high on the list for protective management, which can only be carried out once they are identified.

Field data on fish habitats are scarce. Collecting such data requires ample resources, and thus few studies have been conducted aimed at mapping important fish habitats such as spawning areas for cod (Svedäng & Bardon, 2003; Bartolino et al., 2012), plaice (Nielsen et al., 2004) and nursery areas for sole (Le Pape et al., 2003). In the absence or paucity of field data, numerical models can help us map suitable habitats that combine relevant environmental parameters with the spatial distribution of fish. These parameters are typically temperature, salinity, depth, sediment type and oxygen, although other parameters may be valid for certain species. The maps produced with species distribution modelling can be validated with field data, where these are available. The maps produced are predictive maps since the statistical model produced then identifies other areas with similar environmental properties which are then potential fish habitats. It may be sufficient here to compare potential habitats with realised habitats to explore impacts of human activity on fish habitats and predict potential affects. In dealing with conflicts of spatial uses, effective habitats may be more useful to help protect those areas most valuable to fish or fisheries, in cases of multiple uses on particular areas. Thus fish habitat mapping may be useful for ecosytem-based mangement in that it encompasse both fisheries and the enviroment.

Aim of the study

The aim of this study was to produce EFH maps for adult and juvenile populations of ten commercially important species in the inner Danish waters. Seasonal habitat maps were produced for one year covering 3 year-quarters. We attempted to assess habitat function by equating the spawning season, which is well known for many species, to the relevant quarter map. The summer season, unless coinciding with spawning, was equated to the summer feeding grounds. The species studied are: Atlantic cod *Gadus morhua*, European plaice *Pleuronectes platessa*, common sole *Solea solea*, turbot *Scophthalmus maximus*/*Psetta maxima*, European flounder *Platichthys flesus*, Atlantic herring *Clupea harengus*, European sprat *Sprattus sprattus*, European eel *Anguilla anguilla*, lumpfish *Cyclopterus lumpus* and Norway lobster *Nephrops norvegicus.*

The fish habitat maps that were produced for the individual species are necessary to identify important areas for each of the species. The next logical step is to identify the areas that are important for more than one species simultaneously. This information can be directly used in maritime spatial management, where consideration can be taken for important commercial species, not as single species but in a multi-species context. The aim of this task was to combine the essential habitats information of all the single species that we focused on, into one aggregated map that can be used to improve maritime spatial planning. To evaluate the effectiveness of existing protected areas, we overlaid the aggregated maps with maps on current protected areas, i.e. Natura2000 areas and cod management areas.

2. Methods

2.1 Study area

Habitat mapping in this study was limited to the Kattegat, Belt Seas, the Sound and the western Baltic Sea area (from 9.5 to 14 °E and from 54 to 58 °N).

2.2. Fish data

The offshore part of the study area is regularly monitored by scientific surveys. The data sources used in this study are summarised in Table 2.1. An extra KASU survey was conducted in July 2016 sampling the same stations in the regular KASU surveys. Figure 2 shows the sampling stations for all the surveys in 2016.

Acronym	Name	Years used	Timing
NS-IBTS	North Sea International Bottom Trawl Survey	2005 - 2016	Q1, Q3
BITS	Baltic International Trawl Survey	2005 - 2016	Q1, Q4
KASU*	Kattegat Survey	2016	Q3

Table 2.1. Trawl surveys used for habitat modelling in this report.

* KASU is the Danish part of the BITS.

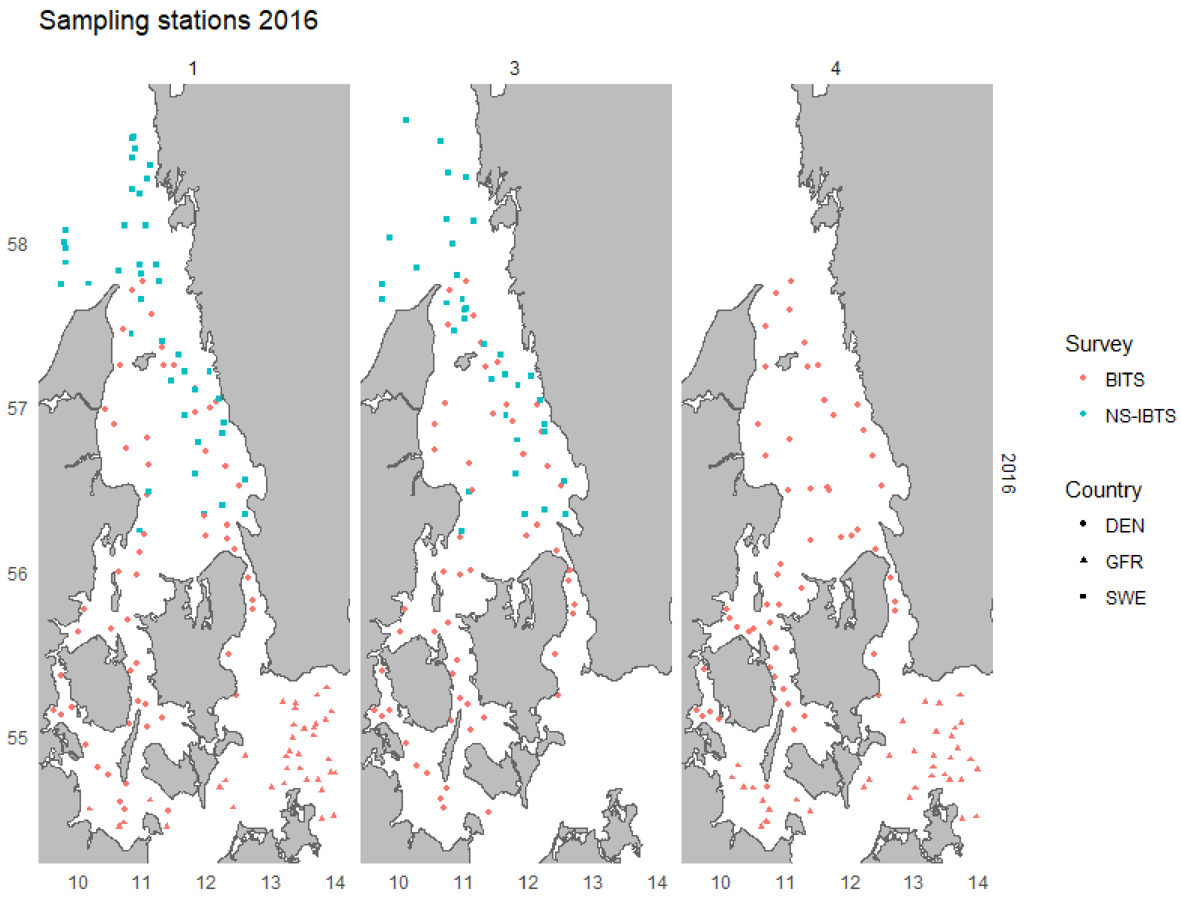

Fig. 2.1. Left map (a) are the sampled stations for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). The BITS stations in quarter 3 are from the extra KASU that is described in Section 2.2.

For each haul, information was recorded that falls under three categories: haul information (e.g. position, date and time of the start and end of the haul), species information (e.g. species, numbers per length) , and biological information of some of the species based on sub-samples (e.g. sex, maturity stage, weight, age).

The surveys have a duration of several weeks. For the analysis, we aggregate the observations in quarter of the year, i.e. split the year into four levels: Q1(January - March), Q2 (April - June), Q3 (July - September), and Q4 (October - December).

By modelling the proportion mature at being proportional to the individual length with a binomial distribution, we could calculate the maturity ogives. The maturity ogives were estimated for each year. For species with lacking maturity information in specific years, or with a low number of samples, maturity ogives were estimated for the entire time series (2005-2016). The maturity ogive of the total time series was used for the years with insufficient data.

2.3 Juvenile fish data

Data for mapping juvenile habitats for age-0 plaice, flounder and sole are derived from a survey conducted in 2016. The survey consisted of 146 stations; each with four depth intervals; 0-1,1-2, 2-3 and 3-4 m. A juvenile beam trawl was used for the stations deeper than 1m, while the 0-1 m stations were trawled manually. For more details on this part of the study see Brown et al. 2019.

2.4 Environmental data

The environmental data (temperature (°C), salinity (PSU), oxygen (ml/l) and current speed (m/s)) were extracted from a high-resolution hydrodynamic model (Lehmann 2000). Monthly mean values of the environmental variables were available. In each station, the conditions were assumed to correspond to the monthly average on that location. In order to make prediction maps, a grid of 0.05 x 0.05 degrees was used where the average monthly environmental conditions of 2016 were extracted from the hydrodynamic model.

Data on sediment type originate from a seabed substrate map at 1: 250 000 scale from the EMODNET geology website (https://www.emodnet-seabedhabitats.eu).

2.5. Models

2.5.1. Model selection

To model the abundance patterns of the different species of interest based on habitat characteristics GAMs were developed. GAMs are used extensively to model species distributions and fisheries catch rates based on hydrographic and ecosystem variables (Drexler and Ainsworth, 2013; Grüss, Chagaris, *et al.*, 2018; Grüss, Drexler, *et al.*, 2018).

The models were built in R using the ‘mgcv’ package (Wood, 2006), with abundance data as response variable and hydrographical conditions and sediment type at the sampling locations as explanatory variables. The tweedie distribution is used as it is more flexible compared to the negative binomial and the quasi-Poisson distributions, especially with regard to zero inflation (Miller *et al.*, 2013). The logarithm of trawling duration was used as offset to allow for variations in effort, and a log link function was used to assure the predictions were non-negative. For all habitat variables thin-plate regression splines were used. The final models were selected manually in a stepwise selection process based on the minimization of the corrected Akaike Information Criterion (AICc), the AIC corrected for small sample sizes (Akaike, 1974; Burnham et al., 2011). Ideally, the AICc converges to the AIC with increasing sample size. Before model selection, collinearity between environmental factors was investigated using the Spearman correlation coefficient (ρ). If the Spearman coefficient between two factors was larger than 0.6, the effect of the variables was investigated with GAMs containing only one explanatory variable. The variable that led to a better higher deviance explained was included in the full model used for backward selection (Guisan and Thuiller, 2005).

Profiles of the seasonal and spatial distributions in the inner Danish waters where the depth > 5m were developed for adult and juvenile cod, adult and juvenile plaice, adult and juvenile flounder, adult and juvenile sole, adult and juvenile herring, sprat and turbot. The grids for the distribution profiles of 0.05° latitude by 0.05° longitude were generated in R. Abundance indices for all species were predicted at each geographical coordinate based on the fitted GAMs to create seasonal distribution profiles.

Habitat Association Models (HAM) and Habitat Growth Models (HGM) were developed for the juvenile fish data. The methods are described in detail in Brown et al. (2019, in prep.). The maps are not presented here due to copyright issues.

2.5.2. Model validation

The models were validated by randomly splitting the data into training and testing sets: 90% of the data was used for training and 10% of the data was used for model validation. Model performance was validated by predicting the number of individuals of the data points in the test data. These predictions were compared to the observed numbers at each point, based on the root mean squared error (RMSE). This procedure was carried out 100 times.

2.6. Aggregated Maps

2.6.1. Habitat overlap between species

The species distribution maps were aggregated. For each species, we included the area corresponding to the 75th percentile of the distribution and above.

2.6.2. Habitat overlap with other management measures

The aggregated maps were then overlaid with the Natura2000 maps. GIS data of the Natura2000 areas in the study area were obtained from the European Environmental Agency (https://www.eea.europa.eu/data-and-maps/data/natura-9).

3. Results

3.1. Atlantic cod *Gadus morhua*

3.1.1. General background

Stock structure

Despite low genetic differentiation between North Sea and Kattegat cod stocks, it is believed these have discrete spawning populations that exhibit natal homing (André et al., 2016). The eastern North Sea cod stock consists of resident and migratory stocks. The Kattegat cod are apparently primarily resident stocks, which are unlikely to be replenished from elsewhere at least for the time being. The Kattegat cod in the northern part exhibit more migratory tendencies towards Skagerrak. The Skagerrak stock exhibits a westerly movement, the directional movement interpreted as natal homing behavior (Svedäng et al., 2007). The return migrations from Kattegat/Skagerrak to the eastern North Sea also included immature fish, although the mechanisms for this migration in non-mature adults is not understood (Svedäng et al., 2007). There is some speculation that there may be a demographically separate cod subpopulation in the Sound.

The North Sea stock is genetically differentiated from the Baltic Sea stocks, which are two separate stocks; eastern Baltic stock (Bornholm and east of this island) and the western Baltic stock distributed in the Arcona Basin, Belt Sea and Sound (ICES, 2005).

Fisheries

In the Kattegat, cod are primarily caught in trawls, but also in gillnets and Danish seines. Cod targeted fisheries takes place mainly in quarter 1, but cod are also caught in the *Nephrops* and flatfish fisheries (ICES, 2017a). In 2009, a protected zone consisting of three areas was introduced in the southeastern part of the Kattegat. In this protected zone, the fisheries are either banned or limited to certain gear during all the year or temporally.

Trawling in the Sound (ICES area 23) has been banned since 1932 due to heavy shipping activity, but is allowed in the area called “Kilen” at the entrance to the Sound and adjacent to Kattegat (ICES area 21) (ICES, 2017b). In SD23 cod are taken by gillnetters, primarily in vessels smaller than 12 m that do not have VMS on board (Sørensen et al., 2016). However in “Kilen”, trawl catches dominate. There is also a substantial sports fishery in the Sound targeting mainly cod. A commercial cod fishing ban has existed since 2009 in the northern part of the Sound in February and March. In “Kilen”, only selective gears are allowed during February and March. Since 2015, a discard ban was put in place.

In the western Baltic (ICES SD 22) cod are mainly caught by trawlers, gillnetters and to a smaller degree Danish Seiners. Most of the Danish fleet operating here consists of smaller vessels < 15 m and most of the cod fished during the spawning season (quarter 1).

Life-history stages

A schematic diagram of the habitats associated with the different life-history stages of cod is shown in Fig. 3.1.1. Adult cod have distinct spawning sites where they aggregate. The pelagic eggs and newly-hatched larvae drift towards coastal areas, where they become demersal and settle in rocky areas or areas with vegetation (Hüssy et al., 1997).

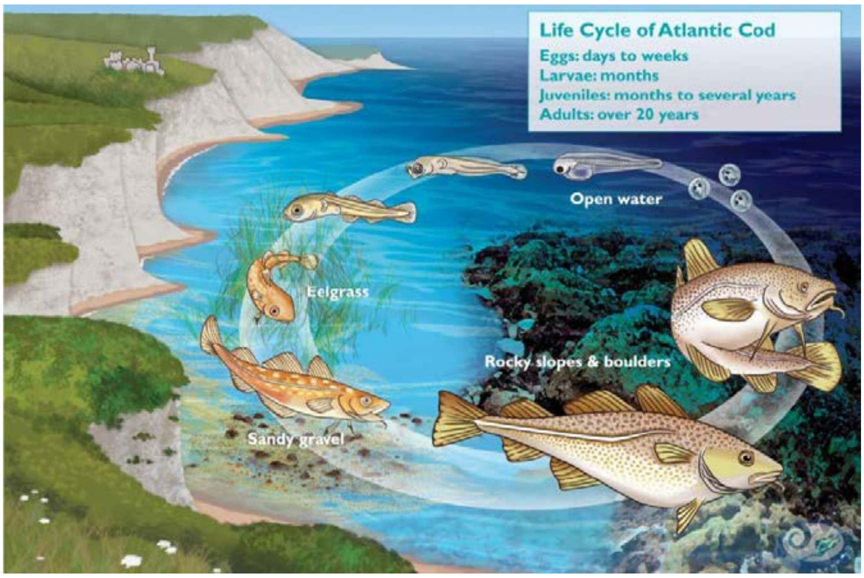

Fig. 3.1.1. Cod life cycle. Source: Partnership for Interdisciplinary Studies of Coastal Oceans, 2011.

Spawning season and area. Spawning in Kattegat takes place from beginning of January to end of April peaking in January/February in the Kattegat and the Sound (Vitale et al., 2005) but subject to a spatial gradient with later spawning in the southern areas. Spawning aggregations have been observed north of Læsø in the central Kattegat (Bartolino et al., 2012), southern Kattegat including Skälderviken and Laholmsbugten (Hagstrom & Wickström, 1990; Svedäng & Bardon, 2003), in the Sound and Great Belt (Bagge et al., 1994). However, with the declining stock, many of the earlier spawning sites are no longer observed, and active spawning sites are reported off the coast of Falkenberg, Sweden or more predominantly, in the SE part of the Kattegat, very close to the entrance to the Sound (Vitale et al., 2008; Börjesson et al., 2013). The predicted fish habitat maps for quarter 1, 2 and 3 are shown in Fig. 3.1.3. Salinity and depth were the environmental parameters that were used to describe the cod habitat. There is good correspondence between earlier observations of spawning sites for the Kattegat cod and the results from this study (Fig 3.1.3a). Spawning aggregations north of Læsø and in the Belt Seas are no longer evident as suggested from the available literature. The spawning site off Falkenberg and to the south along the Swedish coast in the south-eastern part of the Kattegat, the area around the entrance to the Sound and the Sound identified by Vitale *et al*. (2008) and Börjesson *et al* (2013) are still active and important spawning grounds.

The western Baltic stock spawns from January to May, with the main spawning period being from March to April (Bleil et al., 2009). The spawning areas are regions of > 20 m depth in the Kiel Bight, the Fehmarn Belt and the Mecklenburg Bight. Only the Kiel Bight area is included in this study.

Adults. The distinction between adult and juvenile cod was made from maturity data for cod (Fig. 3.1.2). Salinity and depth were the environmental parameters that were used to describe the adult cod habitat. There are differences in cod distribution between quarters. The summer feeding grounds of the Kattegat cod are located along the Swedish west coast and the northern part of the Sound (Fig 3.1.3b). Some cod aggregate in the north around Skagen, but data from Skagerrak need to be included in the model to better localize a summer feeding ground here. In the autumn, the Kattegat cod adults congregate along the whole of the Swedish west coast from the Skagerrak to the Sound, and throughout the Sound.

During summer, the western Baltic cod is located in the Kiel Bight, in the area South of Fyn, east of Als and west of Ærø (Fig.3.1.3b). The Kiel Bight seems to be less important for the western Baltic cod during quarter 4.

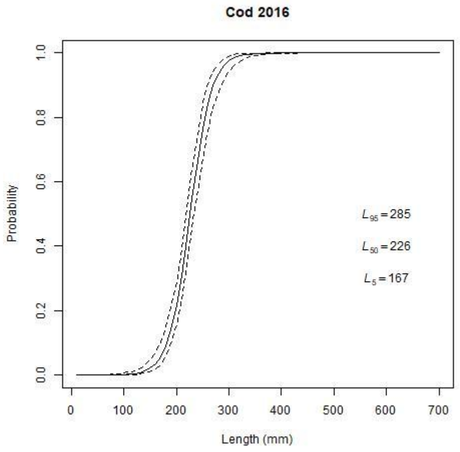

Fig. 3.1.2. Maturity ogive and 95% CI for cod in 2016.

Early life-stages and juveniles. Eggs are pelagic and drift passively with the currents. Environmental threshold values for egg development and survival in different spawning areas are provided in Table 3.1.1.

A high dispersal of the propagules of the eastern North Sea and Skagerrak cod (Munk et al., 1999) is suggested to enhance the opportunity to utilize a larger nursery area, resulting in return migrations during spawning period (Svedäng et al., 2007).

YOY cod. The young of the year (YOY/ age-0) juveniles are strongly associated to particular habitats that provide refuge (greater structural complexity than sand/mud) such as seagrass (Borg et al., 1997; Laurel et al., 2004; Pihl et al., 2006b), cobble (Tupper & Boutilier, 1995a), and granule/pebble (Lough, 2010). Age-0 cod density was reduced by 96% at sites where eelgrass Zostera marina had disappeared in the Swedish Skagerrak (Pihl et al., 2006b). The growth of 0-group Atlantic cod was significantly higher in *Zostera marina* habitat relative to barren, open water, cobble and rocky reef environments (Tupper & Boutilier, 1995b; Renkawitz et al., 2011). Depth ranges are less than 36 m water depth and temperatures generally above 9°C (Gregory & Anderson, 1997; Cote et al., 2004; Knickle & Rose, 2014). GAMs were developed for cod <15 cm in the North Sea, Skagerrak and Kattegat (Kempf et al., 2013). Surface salinity (between 25 and 34) was found to significantly explain spatial distribution, then depth (40-120 m). Surface temperature was found to be significant in some years (below 16°C).

Table 3.1.1. Environmental threshold values for egg development and survival in the different spawning areas of the Baltic Sea. Taken from Hüssy et al., (2012).

Parameter	**Stock**	**Optimal value**	**Threshold value**	**Reference**
Salinity	Kattegat	>21.2+1.2 psu	18 psu	Nissling and Westin (1997)
	Western Baltic	>20–22 psu	18–33 psu	von Westernhagen (1970), Westerberg (1994), Nissling and Westin (1997)
Temperature	Western Baltic	4–8.5°C	2°C	von Westernhagen (1970), Bleil (1995)

The Skagerrak was identified as the most important nursery area for cod <15 cm (Kempf et al., 2013). On average, 67% of the total 3rd quarter IBTS 0-group cod catches stem from this relatively small area. Juvenile cod in this area could also originate from the North Sea. The high occurrence of cod juveniles in the Skagerrak was attributed to Skagerrak being a large-scale prey refuge from grey gurnard, since the latter does not appear to expand its high density areas to the Skagerrak. Information on cod nursery areas in the Kattegat was not available. Age-0 cod are caught in the fall in the key-fisher data in certain areas such as Ålborg Bay, Vejle Fjord, Århus Bay.

Older cod juveniles. Cod during the first year (age-0) can reach around 10 cm (Støttrup et al., 1994). Age-1+ cod are generally found in deeper depths often associated with rocky, kelp habitats (Cote et al., 2004). A number of studies indicated that older juvenile cod prefer coarser substrates, as boulders become an important feature of preferred habitats for older juveniles (Gregory & Anderson, 1997; Cote et al., 2004; Knickle & Rose, 2014). Older (age-2–age-3) juvenile cod have been found to use high relief (i.e., ledge, boulder and cobble) habitat in this region significantly more than expected given availability, but not seagrass habitat (Gregory & Anderson, 1997; Cote et al., 2004). Interestingly, older juvenile cod were more prevalent in granule/pebble habitat at warmer than at colder temperatures, suggesting that temperature also influences the distribution of these age classes in coastal Maine, USA.

Salinity, temperature, oxygen and depth were the environmental parameters that were used to describe the juvenile cod habitat.The substrate maps in inner Danish waters are not sufficiently detailed to be useful to map fish habitats. It is noteworthy that failure to include consideration of cod use of more complex habitats that are incapable of being sampled by trawl surveys could result in largely skewed and unrepresentative estimates of the abundance of juvenile cod populations. This needs to be kept in mind when addressing the juvenile habitat maps for Atlantic cod produced in this study.

The overlap between the adult and juvenile cod is very little in the Little Belt area and the western Baltic throughout the year. In the Sound they overlap in winter (Q1) but the juveniles move away in Q3 and Q4. In the northern Kattegat there is a higher likelihood for overlap.

3.1.2. Essential Fish Habitat for Atlantic cod

- ***Spawning.*** The main spawning areas identified for the Kattegat cod are off Falkenberg, Sweden and to the south along the Swedish coast in the south-eastern part of the Kattegat, the area around the entrance to the Sound and the Sound (Fig. 3.1.3a).

  The Kiel Bight, formerly identified as a major spawning area for the western Baltic cod is still an important spawning area (Fig 3.1.3a).

- ***Adult.*** The summer feeding grounds are significantly different to the winter (Q1 and Q4) grounds. They are located along the Swedish west coast of Kattegat (Fig 3.1.3b). The northern part of the Sound is important year round. In the summer and fall, the areas in the northern Kattegat, bordering to Skagerrak, along the Danish and Swedish coasts are important, but it is unclear if the cod in these areas would be Kattegat cod, Skagerrak cod or a mixture.

  The Arkona Basin is important for the western Baltic cod especially in Q1 and Q4 (Fig 3.1.3a,c).

  Highest prediction error occurs in the third quarter in the Western Baltic, due to insufficient sampling (Fig 3.1.5b).

- ***Juveniles.*** Insufficient data on juvenile cod habitats in the study area. Coastal areas are not covered in the surveys and only soft bottom is sampled.

  Age-0 cod. Based on the literature, coastal areas with eelgrass beds, cobble or pebbles are important. The Swedish coast in south-east Kattegat and the Sound area may likely be highly important given that the spawning takes place in these areas and prevailing westerly winds.

  Older juveniles. The south-eastern part of the Kattegat, northern part of the Sound and northern Kattegat bordering Skagerrak and the western Baltic area in Q3 (Fig 3.1.4). Similarly to adult cod, highest prediction error occurs in the third quarter in the Western Baltic due to insufficient sampling (Fig 3.1.6b).

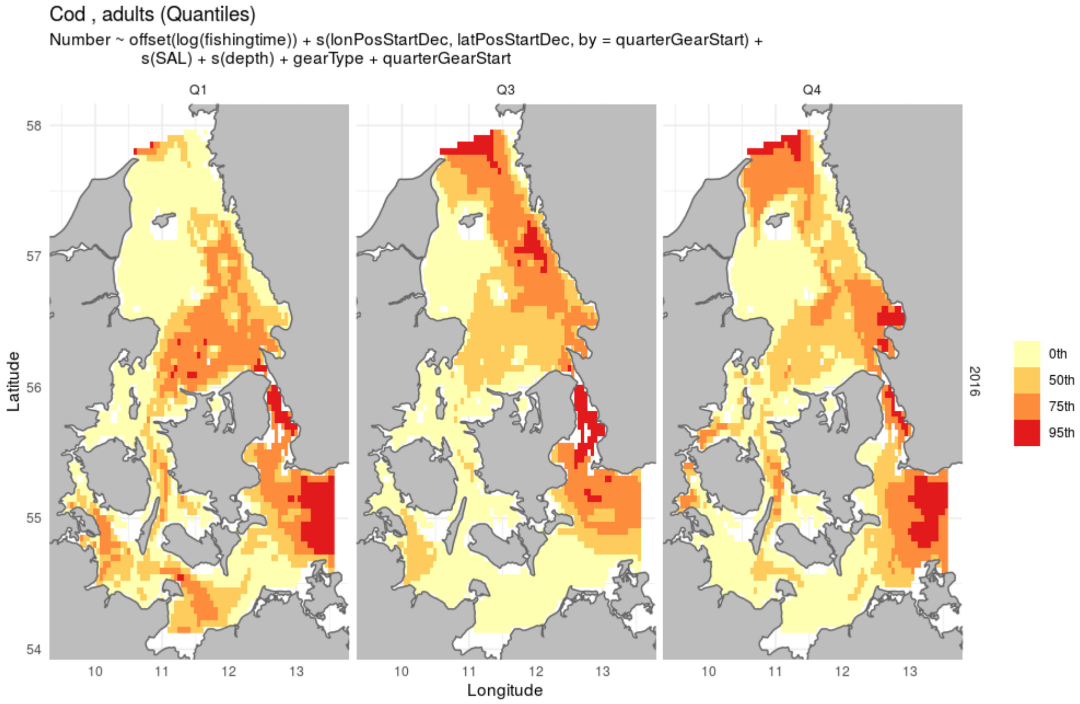

Fig. 3.1.3. Left map (a) are predicted adult cod habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). Salinity: p < 0.001, depth: p < 0.001. Q1-Q3 p < 0.005, Q1-Q4 p < 0.05.

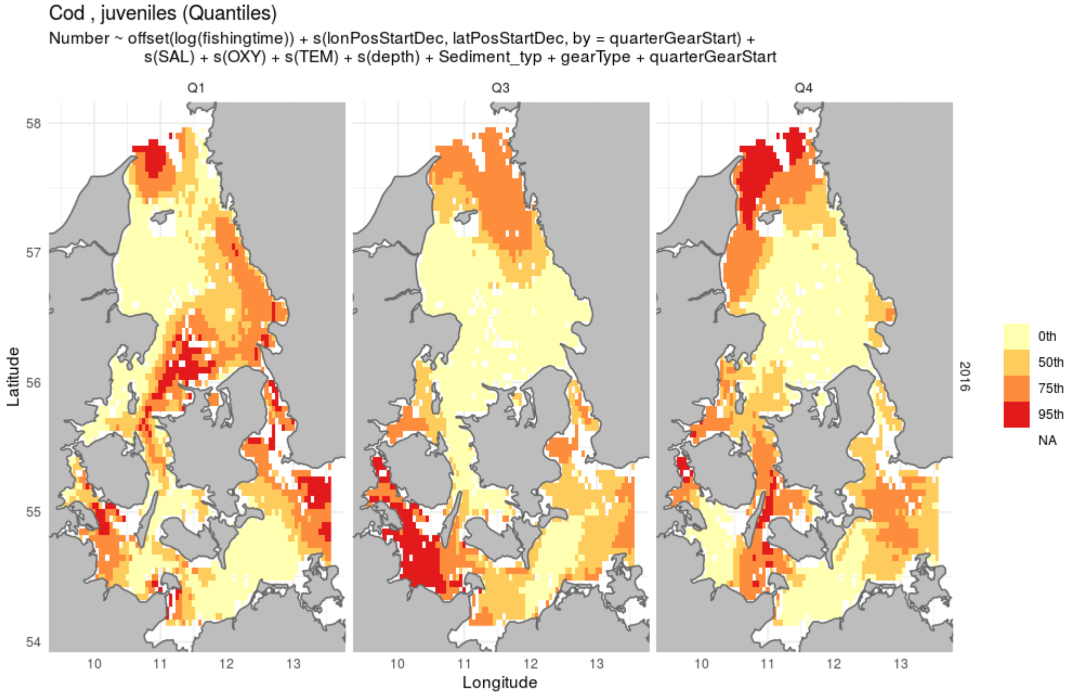

Fig. 3.1.4. Left map (a) are predicted juvenile cod habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). Salinity: p< 0.001, temperature: p < 0.001, oxygen: p < 0.001, depth: p < 0.001. Q1-Q3: NS. Q1-Q4 p < 0.001.

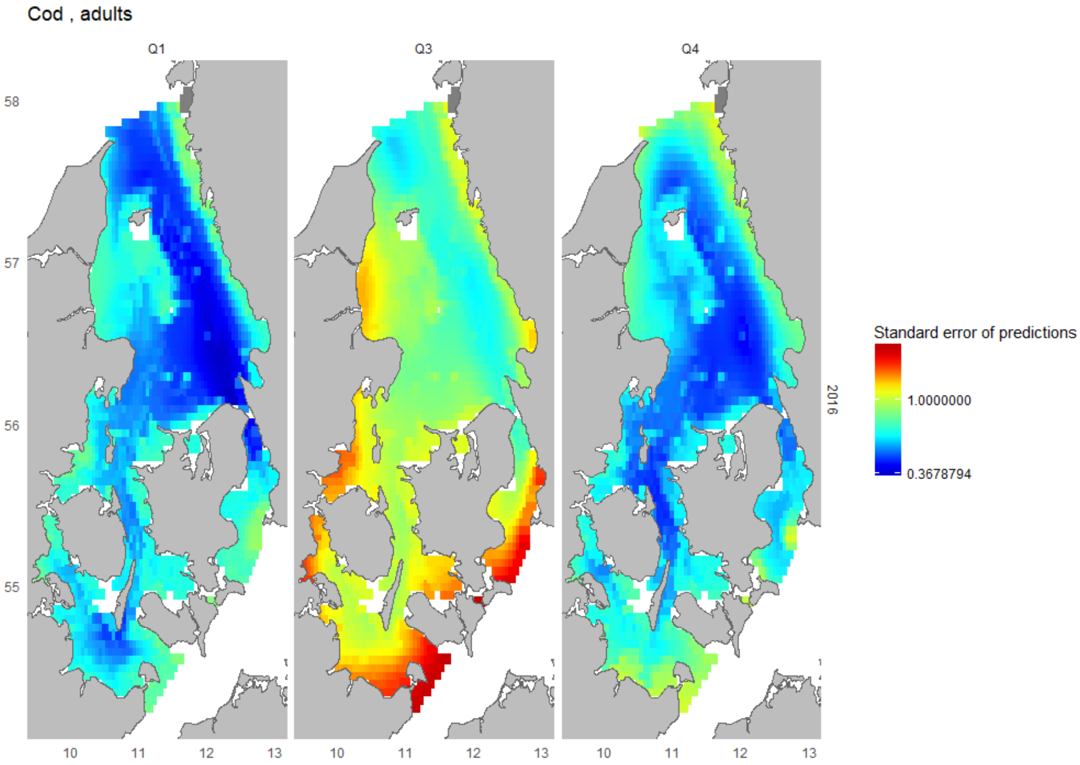

Fig. 3.1.5. Left map (a) are the standardized errors of the predictions (standard error/predicted value) of adult cod habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

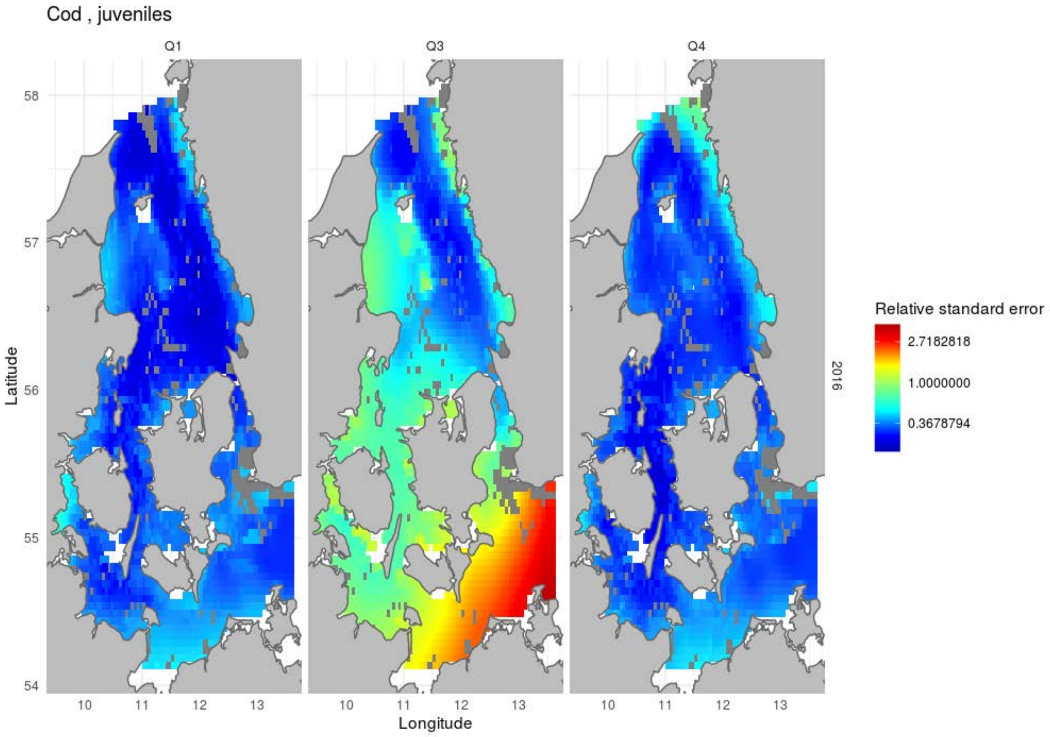

Fig. 3.1.6. Left map (a) are the standardized errors of the predictions (standard error/predicted value) of adult cod habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

3.2. European plaice *Pleuronectes platessa*

3.2.1. General background

Stock structure

Plaice in the Skagerrak is considered to have two components: an Eastern and Western. The western component occurs in a mix with plaice migrating in from the North Sea (Ulrich et al., 2013) and the predominance of catches occurs on summer feeding aggregations in the Western Skagerrak. In a benchmark (WKPLE 2015), it was decided that plaice in the Skagerrak would be assessed together with the North Sea stock (ICES, 2015b).

The Kattegat, Belt Sea and Western Baltic plaice (ICES subdivisions 21, 22 and 23) are considered as one stock, clearly delineated from the Skagerrak (no exchange observed) (ICES 2015a), but less clear delineation with the plaice in ICES subdivision 24 in the western Baltic. The latter needs further research.

The Baltic Sea plaice stock covers ICES subdivisions 24 to 32 and is thus distributed in the Eastern Baltic Sea including the Bornholm Basin and the area of Arkona.

Fisheries

The fishery in these areas seldom targets the plaice stock in the Kattegat, Belt Sea and Western Baltic and catches are mostly as by-catch (ICES, 2015b). In the Kattegat (SD 21), plaice are caught mainly be Danish fishermen as bycatch in the *Nephrops* and sole fishery. In the Belt Seas (SD23), plaice are caught by gillnetters and in the western Baltic (SD22) they are caught by trawlers and gillnetters, often as bycatch in the cod fishery. The latter area is where most plaice catches come from in the present day. Since January 2017 plaice is included in the discard ban in the Baltic Sea (SD 22-32).

Life-history stages

A schematic life-cycle for plaice *Pleuronectes platessa* is shown in Fig. 3.2.1. Adults spawn off-shore and the pelagic eggs and newly-hatched larvae drift towards the coastal nursery areas, where they grow during their juvenile stage. Juveniles move progressively off-shore and recruit to the adult population and contribute to the spawning biomass or enter the fisheries.

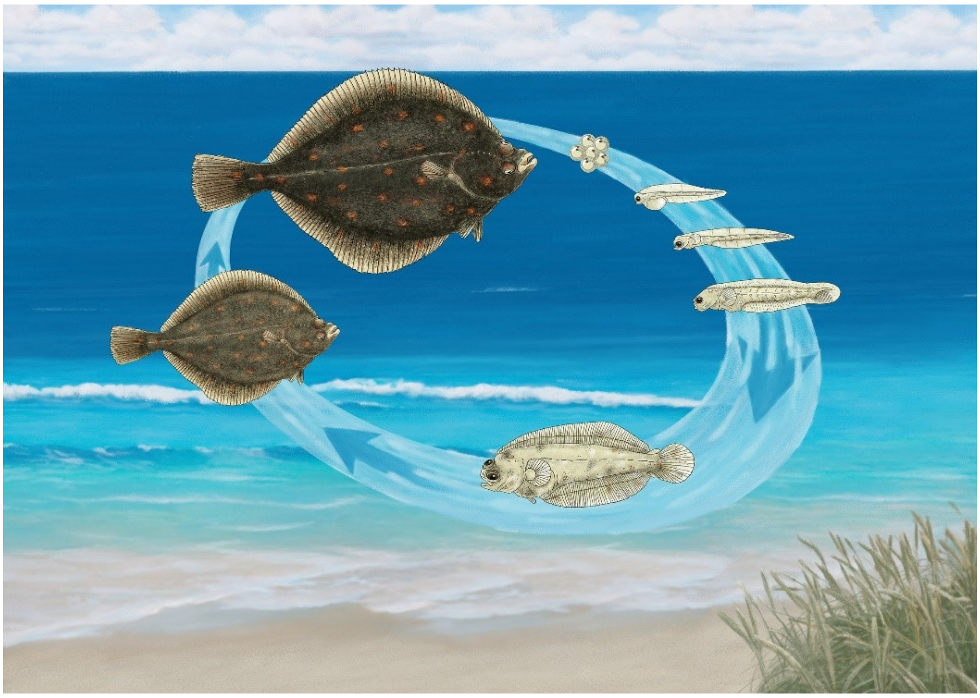

Fig. 3.2.1. Plaice life-cycle.

Spawning season and area. The spawning occurs between late February and late March in Kattegat waters mainly at depth between 30 and 40 meters (Nielsen et al., 2004). Nielsen et al. (2004) observed the existence of two spawning areas in Kattegat, one in the north eastern part and another one, of greater importance in terms of production, in the south western part. Historically, four discrete spawning aggregations were observed as shown in Fig. 3.2.2 (Cardinale et al., 2011). The results from this study show remnants of the historic spawning areas in the northern part of the Swedish Kattegat coast and northwest Kattegat (Fig. 3.2.4a). The Swedish southern Kattegat coast seems to be no longer an active plaice spawning area. The southwestern Kattegat remains the main spawning area that extends to the Great Belt. Spawning was suggested to take place in the Belt Sea and in the Sound but has not been confirmed with published field studies (Svedang et al., 2004 in Ulrick 2013). In this study, aggregations were observed in the Great Belt and the northern part of the Little Belt, supporting the suggestion of Svedang et al. (2004, in Ulrick, 2013). Small aggregations are observed in the northern part of the Sound, and the Swedish Bays north of the Sound and may likely be remnants of historic observations (Cardinale et al. 2011) also suggested by Svedang et al. (2004, in Ulrick 2013).

Adults. The distinction between adult and juvenile plaice was made from maturity data for plaice (Fig. 3.2.3). The distribution of plaice in summer (Q3) is not different to the winter distribution (Q1) (Fig. 3.2.4). The results from this study show depth and salinity to be of high importance for habitat choice in adult plaice.

Sediment type has been assumed to be less important for the burial of adult flatfish because they are physically capable of burying themselves in a wider range of sediment types (Gibson & Robb, 1992). Moreover, cryptic predator avoidance may become less crucial as the number of potential predators decreases with increasing body size (Gibson & Robb, 1992, 2000; Stoner & Abookire, 2002). Adult plaice (>26 cm) inhabit primarily sandy sediments and seem to avoid sediments with either a high gravel or mud content (Hinz et al., 2006).

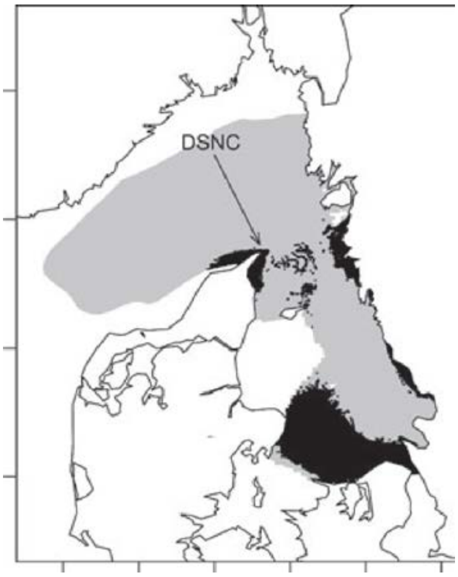

Fig. 3.2.2. Localization of the four major areas of aggregation of adult plaice biomass as identified during 1901–10. Danish Skagerrak northern coasts (DSNC), southwestern Kattegat (SWK), Swedish Skagerrak Coasts (SSC) and Swedish eastern Kattegat (SEK). From: Cardinale et al. (2011) with permission from John Wiley and Sons, licence number 4621900194991.

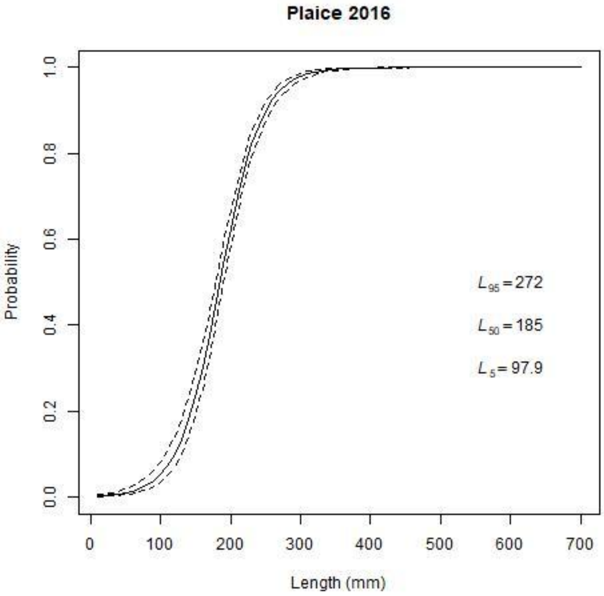

Fig. 3.2.3. Maturity ogive and 95% CI for plaice in 2016.

In the English Channel, depth range for highest abundances of adult plaice (>26 cm) was 20-30 m with hardly any or zero catches at 40-50 m depth (Hinz et al., 2006). Surface temperatures in august were 18.4-18.7 °C in the sites where plaice were most abundant. Plaice are visual predators and good visibility is therefore important for successful prey capture. Adult plaice feed primarily on epibenthic crustaceans, small fish, and echinoderms (Piet et al., 1998). In the field plaice biomass (mainly age-II to age-IV) at 25- 40 m depth in the SE Kattegat was negatively correlated with hypoxia (< 3 mg l-1) (Petersen & Pihl, 1995).

The results from this study indicated important plaice summer feeding areas to be located in deeper waters in the southwestern part of Kattegat, the Belt Seas and the western Baltic (Fig. 3.2.4b). Adult plaice are present in the northwestern part of the Kattegat year-round (Fig. 3.2.4a-c).

Early life stages and juveniles. YOY fish. Juvenile flatfish bury in sediment to escape predation (Gibson & Robb, 2000; Stoner & Abookire, 2002). In laboratory experiments juvenile plaice (1-11 cm in length preferred the finest sediment type presented (<0.5 mm grain size). Similar results were obtained from field experiments using tray with different grain sizes in artificial tide pools (Gibson & Robb, 2000). YOY in the east coast of Scotland were most abundant in areas with sediment grain size ranging 200-400 µm, although other environmental factors are also important habitat parameters. Unfortunately, maps with detailed sediment grain size are not available from Danish waters. Presence of food and predators may also affect habitat choice. For visual predators such as plaice, benthic habitats with emergent epifauna are preferred as these habitats provide higher habitat complexity and prey diversity (i.e. predation avoidance and prey abundance). Plaice nursery grounds are restricted to shallow soft bottom areas. The Swedish west coast was estimated to produce 77% of the juveniles from the Skagerrak/Kattegat nursery grounds (Wennhage et al., 2007). The results from the targeted juvenile survey were used to generate habitat association models (HAMs) and habitat growth models (HGMs) for plaice (Brown et al. 2019). The maps are not shown here due to copyright issues. Plaice occurrence decreased with increasing site salinity whereas growth rates increased. These results supported the theory of increased settlement form the North Sea/Skagerrak populations (Ulrich et al., 2017). Maps for plaice YOY indicated areas at the mouth of large fjord systems such as Roskilde Fjord, Odense Fjord and Limfjord on the Kattegat side to be important nursery areas (Brown et al., 2019). Also the coast along the northern Kattegat is an important plaice nursery.

Older juveniles. Reduced growth was observed in juvenile plaice (10-15 cm) in laboratory experiments during 20 days at 15°C, 30-34 psu and oxygen saturation of 50% and 30% (Petersen & Pihl, 1995). Frequency of fish eating was reduced at 30% oxygen saturation.

With increasing size, plaice undergo an ontogenetic change in diet from feeding mainly on infaunal polychaetes and bivalves, to adult plaice taking a large proportion of epibenthic crustaceans, small fish, and echinoderms (Piet et al., 1998).

The results from this study show depth, salinity and oxygen to be of high importance for habitat choice in juvenile plaice. Southwestern Kattegat and the Great Belt are important juvenile overwintering areas for plaice (Fig. 3.2.5a, c). During summer juvenile plaice still occupy the southwestern Kattegat and Great Belt areas, and also Little Belt, but possibly due to the high aggregations in the Arkona Basin, this is less evident in the Q3 model (Fig. 3.2.5b).

There is a high likelihood for overlap between adult and juvenile habitats especially in Q1 and Q4.

3.2.2. Essential Fish Habitat for plaice

- ***Spawning.*** The main spawning area identified for the Kattegat plaice is the south-western part of Kattegat extending to the Great Belt. Northwest Kattegat. The northern part of the Sound, central part of Little Belt, and the outer part of Flensborg Fjord are also potential spawning areas (Fig. 3.2.4a).
- ***Adult.*** The summer feeding grounds are similar to the spawning areas (Fig. 3.2.4b).

  The adults are aggregated *year-round* in the northwestern part of Kattegat, the Great Belt, and the central part of Little Belt (Fig. 3.2.4a-c).

  In the south the distribution extends from the Great Belt south to the area around Femern (Fig. 3.2.4c).

  In general, the data fit adequately well to the model (Fig. 3.2.6). Highest prediction error occurs in the western Baltic and in Q3 (Fig 3.2.6).
- ***Juveniles.*** Age-0 plaice. The maps produced in Brown et al. (2019, in prep.) indicate the mouths of larger fjords (Roskilde, Odense and Limfjord) to be important plaice nurseries, as well as the northern Kattegat on the west coast. Maps are not reproduced here due to copyright issues.

  Older juveniles. The soft bottom areas of the Great Belt, central part of Little Belt and the southwestern part of Kattegat are juvenile areas, especially for overwintering (Fig. 3.2.5).

  Similar to the adult maps, the juvenile data provide a good fit to the model. Highest prediction error occurs in Q3 in the western Baltic (Fig. 3.2.7).

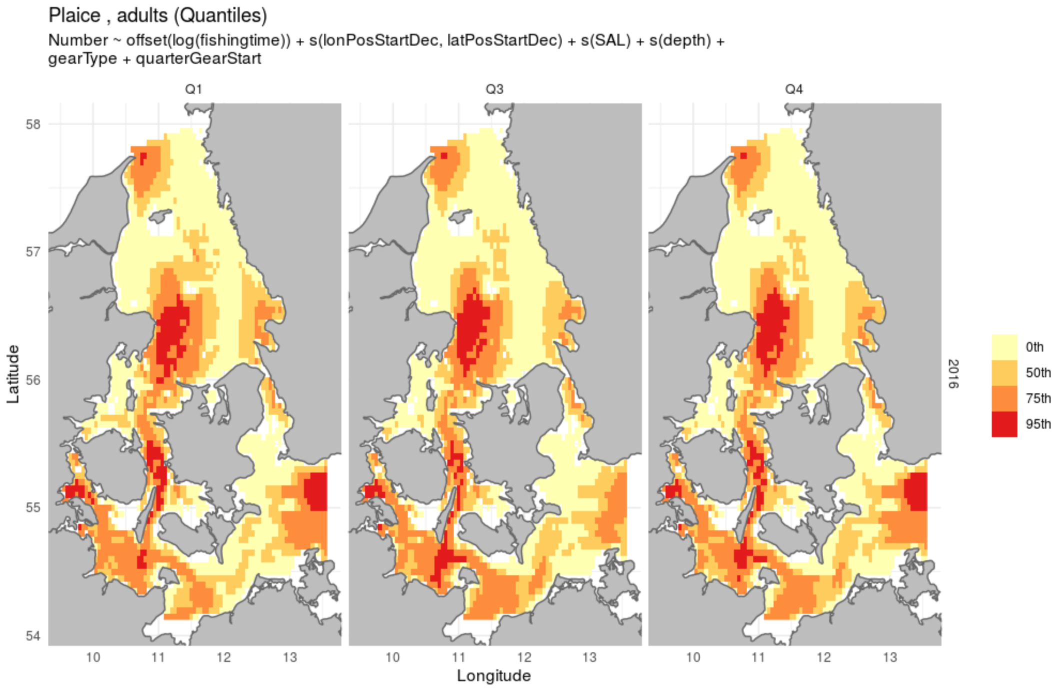

Fig. 3.2.4. Left map (a) are predicted adult plaice habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). Salinity: $p < 0.001$, depth: $p < 0.001$. Q1-Q3: NS, Q1-Q4: $p < 0.001$.

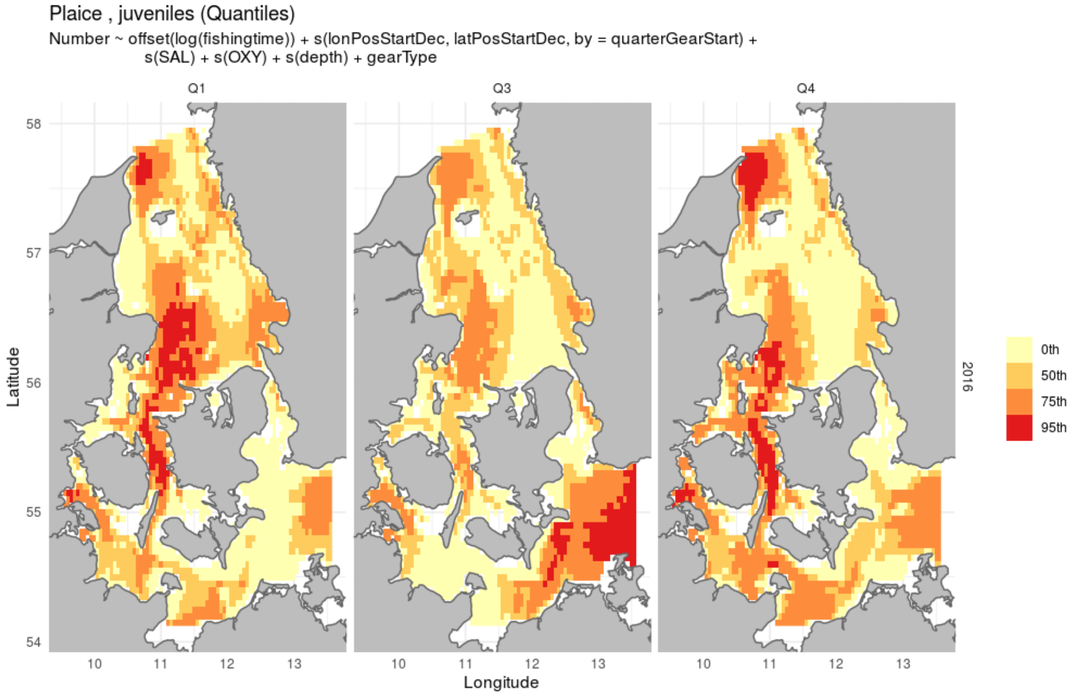

Fig. 3.2.5. Left map (a) are predicted juvenile plaice habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). Salinity: $p< 0.001$, oxygen: $p < 0.001$, depth: $p < 0.001$.

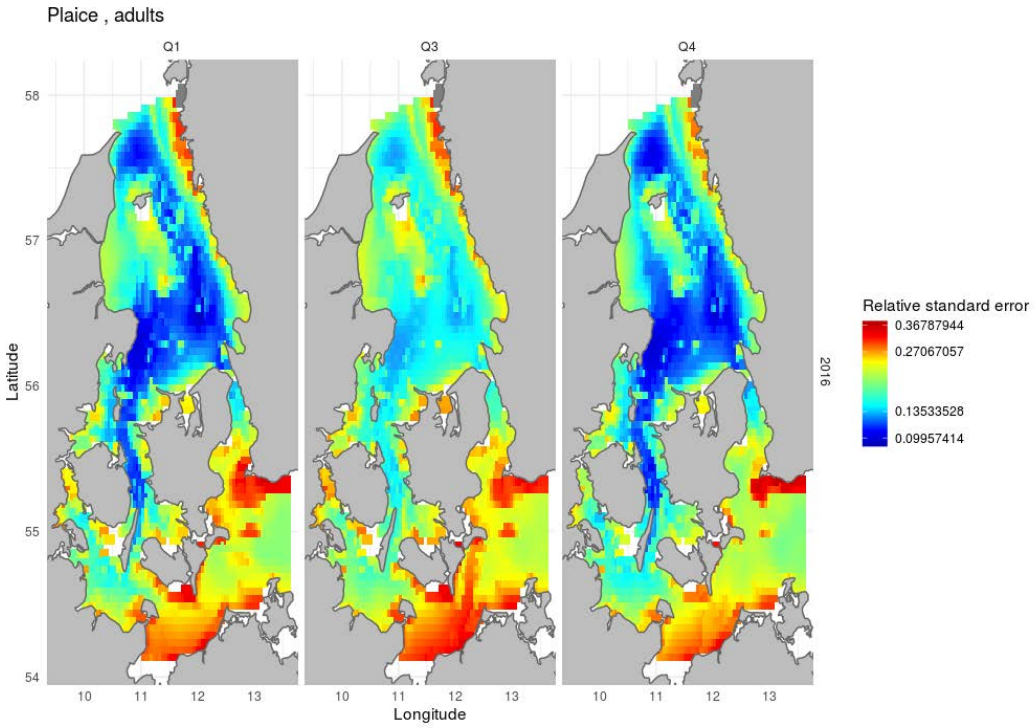

Fig. 3.2.6. Left map (a) are the standardized errors of the predictions (standard error/predicted value) of adult plaice habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

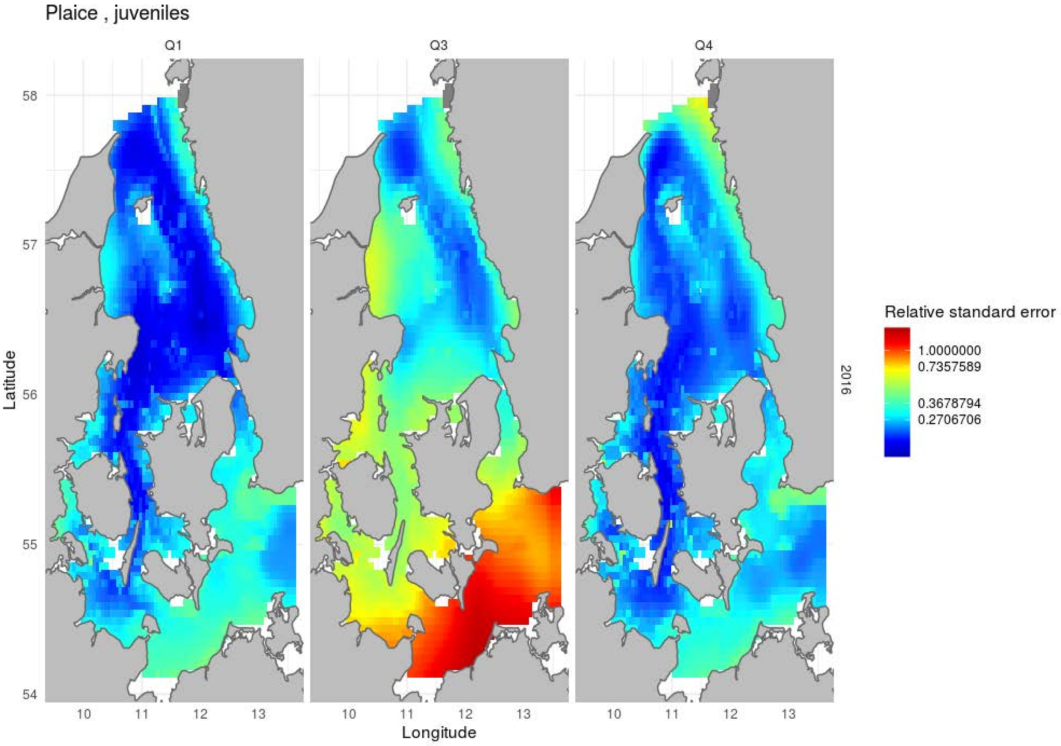

Fig. 3.2.7. Left map (a) are the standardized errors of the predictions (standard error/predicted value) of juvenile plaice habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

3.3. Sole *Solea solea*

3.3.1. General background

Stock structure

The sole in Skagerrak (ICES subdivision 20) and Kattegat (21) are considered as one stock, possibly intermingling with the North Sea stock, but distribution to the south limited by the declining salinity (ICES 2015c). The extent or magnitude of the interchange between Skagerrak/Kattegat and the North Sea is largely unstudied. In a recent study (Anon., 2018), it was concluded that it was unlikely there exists an inflow of recruits from the North Sea due to a poor relationship in recruitment strength between these two areas. However, it is highly likely there is some interchange between Skagerrak and Kattegat. According to Bagge (1993), sole spillover into the Belt Sea (SD 22) and the Sound (SD 23) when the sole population in the Kattegat is large. Similar recruitment trends for sole from ICES areas 20-24 indicated that the sole from these areas could be considered as one stock (Anon., 2018). This was not supported by a concurrent genetic study that showed clear genetic differences between sole collected in the Kattegat and the Skagerrak (Anon., 2018).

Temperature and salinity is believed to influence sole distribution. Sole are limited by low salinity and are confined to warm, saline waters.

Fisheries

Kattegat is the most important fishery area for sole in the inner Danish waters (ICES 2015c). Since 2004 increased sole landing have derived from the Belts coinciding with increases in sole abundances in these areas. Sole is caught in trawl and gillnets. Low season for trawl is May to September and during this time sole is primarily caught as by-catch in the *Nephrops* fishery. Gillnet season is primarily April to September. Discard are believed to be negligible partly due to the high price of sole and partly due to the fact that since 2005, TACs no longer limited the fishery.

Life-history stages

A schematic life-cycle for sole is shown in Fig. 3.3.1. Adults spawn off-shore and the pelagic eggs and newly-hatched larvae drift towards the coastal nursery areas, where they grow during their juvenile stage. Juveniles move progressively off-shore and recruit to the adult population and contribute to the spawning biomass or enter the fisheries.

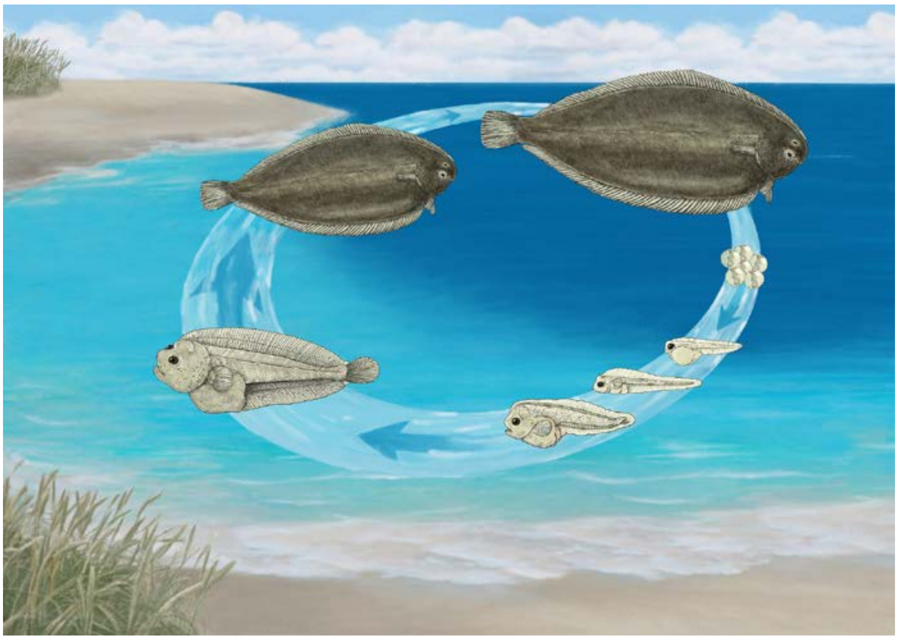

Fig. 3.3.1. Sole life-cycle.

Spawning season and area. Sole spawn in the Kattegat and Skagerrak but spawning locations are imprecise. They spawn in late May /early June (ICES 2015c); thus, the spawning areas cannot be captured by the data available.

Adults. The distinction between adult and juvenile sole was made from maturity data for sole (Fig. 3.3.2). The southward distribution of sole is limited by the salinity, which decreases southwards and eastwards. In the English Channel, sole (<23 cm) were observed in sediment types ranging from muddy to sandy substrata, but seemed to avoid sediments with high gravel content (Hinz et al., 2006). Highest abundances of adult sole (>23 cm) were primarily observed in depths of 20-30 m, temperatures of 18-19 °C and salinity of 33.8-34.6 (Hinz et al., 2006). No sole were caught at depths of 40-50 m. These were results from data spanning 1990-1998, from the autumn ground fish survey cruises.

Our results show that sole aggregate in the southern Kattegat, then central part south of Læsø and the Great Belt during the winter period (mostly Q1 and also Q4). During summer they are distributed more towards the Danish coast in the areas southern Kattegat and off the Danish east coast, from Læsø to around Frederikshavn. Also the northern part of the Sound is important for sole in summer. Sole habitat is defined by the environmental parameters salinity and current speed.

Sole have small eyes (Piet et al., 1998) and rely on tactile and chemosensory cues to detect prey (Rogers, 1994). They are nocturnal predators and prey on infaunal invertebrates such as polychaetes and molluscs during their juvenile and adult stages (Piet et al., 1998). Sole mature around age 3-5 (ICES 2015c).

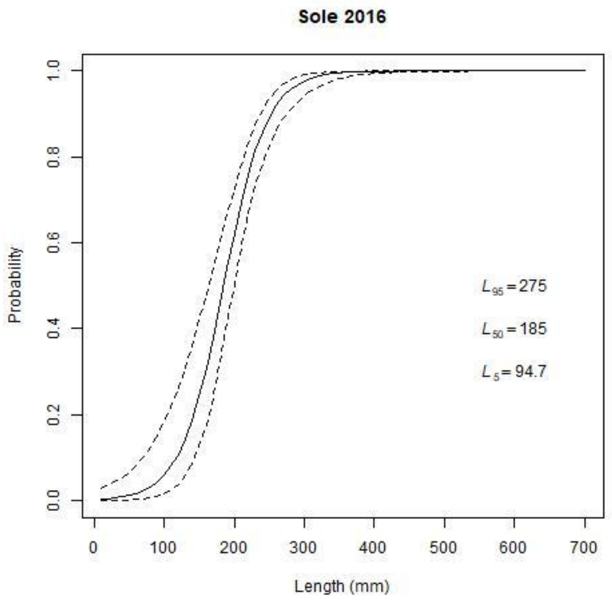

Fig. 3.3.2. Maturity ogive and 95% CI for sole in 2016.

Early life stages and juveniles. YOY sole utilize shallow, muddy estuarine areas as nursery grounds in the Bay of Biscay and the Irish Sea (Rogers, 1992; Le Pape et al., 2003). They exhibit limited movements between nursery grounds (Riou et al., 2001). These habitats are restricted to water depth < 5m and depths >20 are considered totally unsuitable (Le Pape et al., 2003). The spatial distribution of sole is thus known to be influenced by sediment structure, bathymetry and estuarine influence. Only larvae completing metamorphosis within coastal nursery areas are likely to develop (Amara et al., 2000). Muddy sediment is highly important and increasing granule size render the habitat less important for sole. YOY (41 -91mm length) preferred very fine (63-180 um) and fine (150-250 um) sediment irrespective of temperature (11 and 20°C) in experimental laboratory studies (Post et al., 2017).

In normoxia, sole (ca 10 g in weight) settled preferentially on sand whereas under hypoxic conditions, sole settled preferentially on the muddy substratum. In order to explain these apparently counterintuitive observations, Couturier et al. (2008) proposed that, via cutaneous respiration, young sole are able to take advantage of the large quantities of oxygen produced by microphytobenthic organisms present in the upper few millimetres of muddy substratum. Estuarine influence (river plume) is also considered important habitat characteristic for YOY sole, probably due to a high productivity of invertebrate prey.

Maps with detailed sediment grain size are not available for the inner Danish waters. Also, the juvenile survey only sampled the open coast areas in the inner Danish waters (Brown et al. 2019). Thus sole nursery habitats may be underrepresented in this study. In our study sole densities were positively correlated with salinity and negatively correlated with temperature. Thus salinity and temperature best explained the distribution of YOY sole (Brown et al. 2019). Sole abundance was highest in the northern part of the study area, decreasing towards the western Baltic.

Le Pape et al., (2003) showed a good relationship between the nursery habitat index for YOY sole to Age 2 sole. Habitat suitability models for sole YOY were improved by Le Pape et al., (2007) and Nicolas et al., (2007), by including macro- and megafauna collected during beam trawl surveys. The abundance of YOY sole was correlated with an index of the benthic invertebrate biomass and, more specifically, with the biomass of suspension feeders. This result was reinforced by a one-dimensional spatial statistical analysis, which pointed out the similar distribution of invertebrate macrobenthos and juvenile sole along the upstream/downstream gradient of the estuary. Moreover, the inter-annual variations of abundance and distribution of juveniles were synchronous with those of the macrobenthos. A further study by Vinagre (2006) also on habitat suitability modelling showed that amphipod abundance together with abiotic variables were good in predicting sole abundance. For this work the author used abundance of amphipod, polychaetes and bivalves together with abiotic variables such as sal, temp, substrate, depth and intertidal (Fig. 3.3.3). The areas identified were located in the upper estuary, which is dominated by large extensions of intertidal mudflats (Bay of Biscay).

Gilliers et al., (2006a, 2006b) found that growth and density were preferable to condition indices as indicators of habitat quality for juvenile sole, and was able to demonstrate that areas with low combination of density and growth also were high in contaminants, illustrating anthropogenic negative impact at population level.

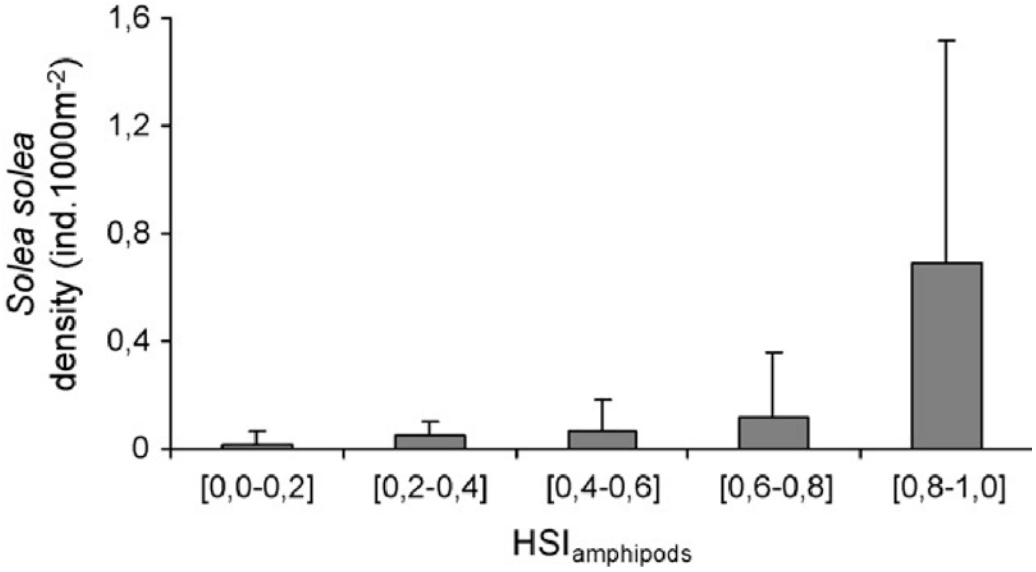

Fig. 3.3.3. *S. Solea* 0-group juveniles density prediction of the HIS amphipods model (SI salinity SI temperature SI substrate SI depth SI intertidal SI amphipods) 1/6 for the month of May 2001. Mean density and standard deviation. From Vinagre et al. (2006) with permission from Elsevier, licence number 4625901439204.

Sediment size may become less important for the older fish, as cryptic predator avoidance may become less crucial as the number of potential predators decreases with increasing body size in flatfish such as plaice (Gibson & Robb, 1992, 2000) and Pacific halibut (Stoner & Abookire, 2002).

Our results showed a juvenile distribution very similar to that of adult sole with a high degree of overlap. The environmental variables predicting sole juvenile habitat were salinity and oxygen. The Great Belt is an important overwintering ground for juvenile sole, extending in southern Kattegat to north of Anholt. In the summer they are more northerly distributed. The Jutland coast from Læsø to around Frederikshavn and the northern part of the Sound are important in the summer.

3.3.2. Essential Fish Habitat for the common sole

- ***Spawning.*** Insufficient data. The timing of spawning and survey data do not coincide.
- ***Adult.*** The central area in mid Kattegat, southern Kattegat and the Great Belt in Q1 and Q4, and in the summer the northern part of the Sound and east Jutland coast from Læsø to Frederikshavn (Fig. 3.3.4).

  Highest prediction error occurs in Q3, especially in the southern part in the western Baltic (Fig. 3.3.6)
- ***Juveniles.*** YOY sole habitats showed a gradient increasing in importance from south to north in the inner Danish waters (Brown et al. 2019). Maps are not shown here due to copyright issues.

  Older juveniles. The juvenile habitats are very similar to the adult habitats (fig. 3.3.5). The identified offshore habitats for older juveniles seem to be mainly located in the area of Southern Kattegat just north of Anholt and extending to the Great Belt. In the summer, the aggregations are on the Danish east coast of the Kattegat off Djursland and north of Læsø. The Great Belt is an important area during winter (Q1 and Q4) and the northern part of the Sound in summer.

  The main year-round juvenile sole habitat is focused in the southern Kattegat area from just north of Anholt extending through the Great Belt to Langeland.

  Highest prediction error occurs in Q3 in the southern part in the western Baltic and in Q1 in the area south of the Sound (Fig. 3.3.7).

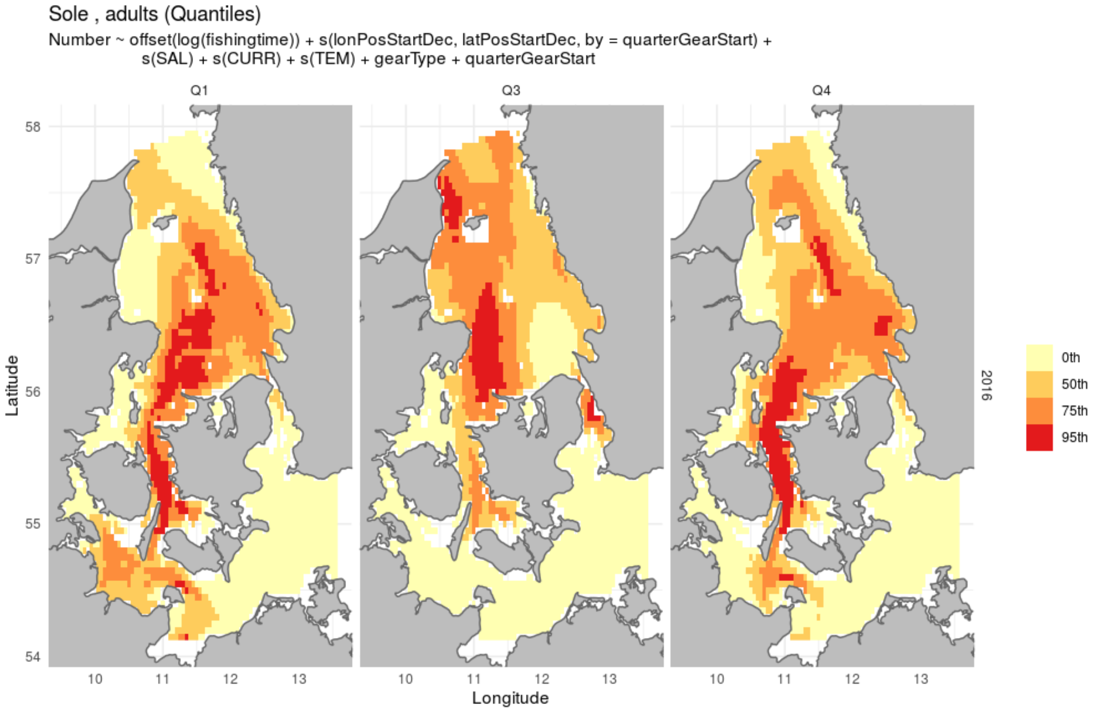

Fig. 3.3.4. Left map (3.3.) are predicted adult sole habitats for first quarter (Jan-Mar), middle (3.1.1b) for quarter 3 (Jul-Sept) and right map (3.1.1c) for quarter 4 (Oct-Dec). Salinity: p < 0.001, current speed: p < 0.01. Q1-Q3 NS, Q1-Q4 p < 0.001.

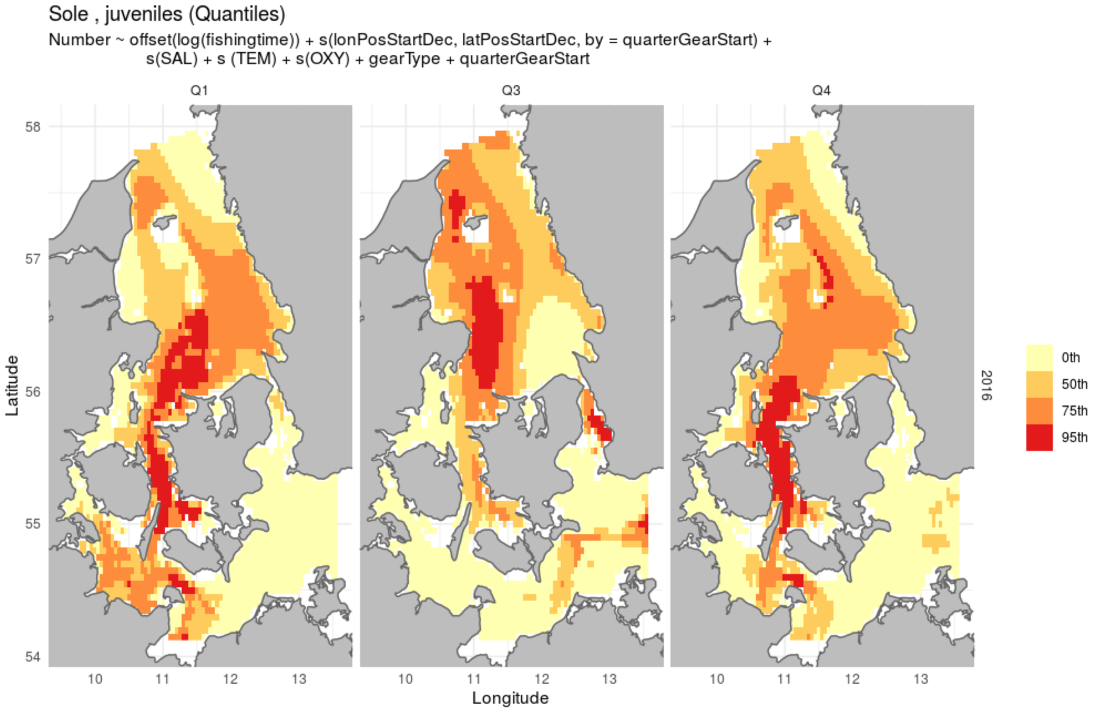

Fig. 3.3.5. Left map (3.) are predicted juvenile sole habitats for first quarter (Jan-Mar), middle (3.1.2b) for quarter 3 (Jul-Sept) and right map (3.1.2c) for quarter 4 (Oct-Dec). Salinity: p< 0.001, oxygen: p < 0.1. Q1-Q3: NS, Q1-Q4 p < 0.001.

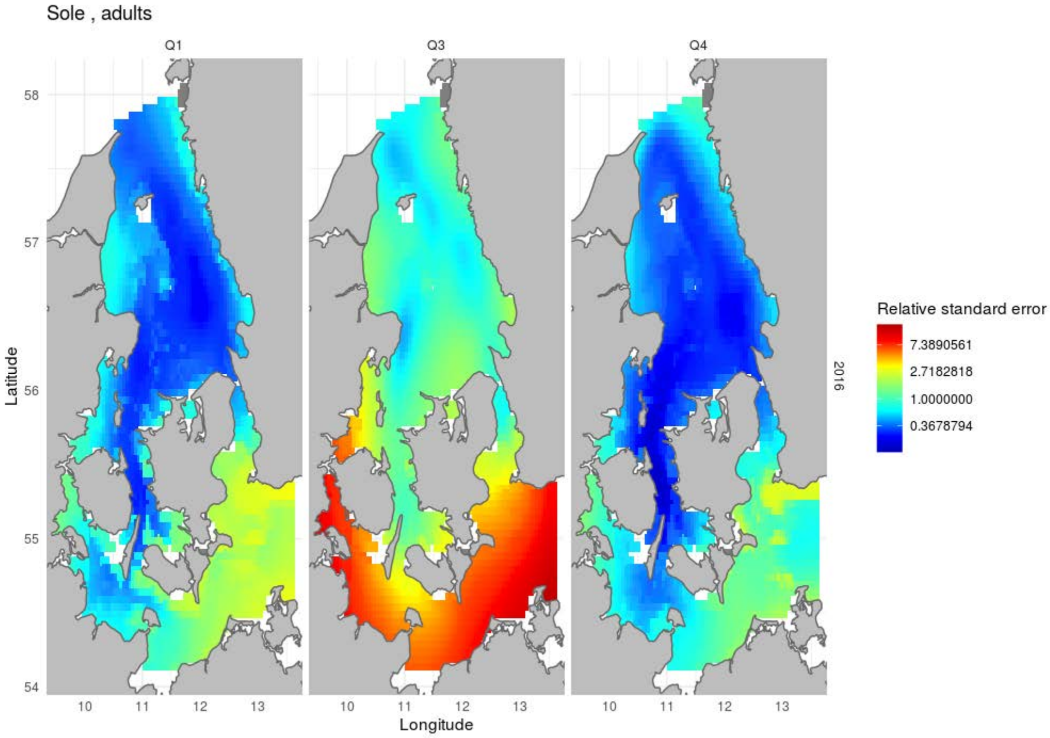

Fig. 3.3.6. Left map (a) are the standardized errors of the predictions (standard error/predicted value) of adult sole habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

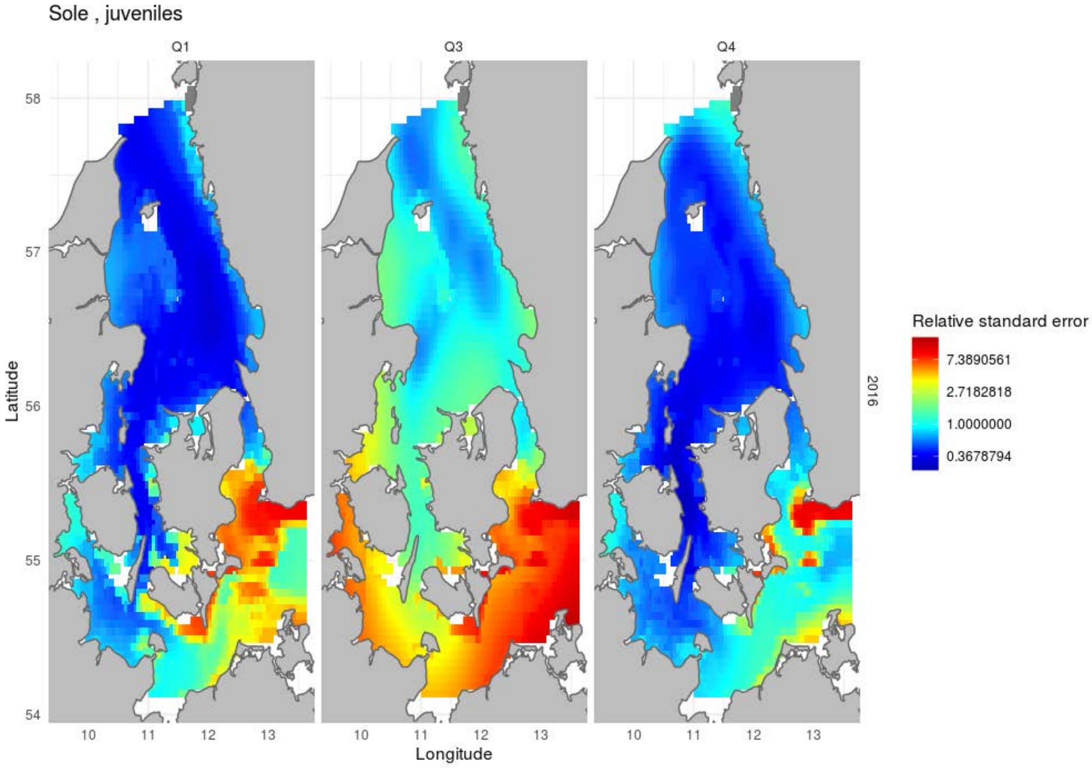

Fig. 3.3.7. Left map (a) are the standardized errors of the predictions (standard error/predicted value) of juvenile sole habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

3.4. Turbot *Scophthalmus maximus/Psetta maxima*

3.4.1. General background

Stock structure

The Skagerrak and Kattegat turbot populations are believed to be inherently different from the populations of the North Sea and the Baltic Sea (Nielsen et al., 2004b).

Turbot are highly adaptive with regards to survival and reproduction at different salinities (Vandamme et al., 2014). Eggs from North Sea turbot populations have an optimal development between 20 and 35 psu and do not survive at lower salinities. However, in the Baltic Sea, turbot eggs survive at salinities as low as 7 psu (Nissling et al., 2006, 2013). This, together with the relatively sedentary nature of adult turbot and high spawning site fidelity provide the basis for separate stock units.

The Baltic Sea stock is considered to be uniform, despite the suggestion of local stocks from tagging experiments (Nissling et al., 2013).

Fisheries

Turbot in Skagerrak-Kattegat are today only caught as by-catch in the trawl, trammelnet and gillnet fisheries. Historically, around 300 tons per year were caught (1950-1989) in the Kattegat (Ices IIIa), but decreased to less than 100 tons per year in 2011 (ICES, 2012).

Life-history stages

A schematic life-cycle for turbot is shown in Fig. 3.4.1. Turbot are batch spawners with pelagic eggs. Adults spawn off-shore and the pelagic eggs and newly-hatched larvae drift towards the coastal nursery areas, where they grow during their juvenile stage. Juveniles move progressively off-shore and recruit to the adult population and contribute to the spawning biomass or enter the fisheries.

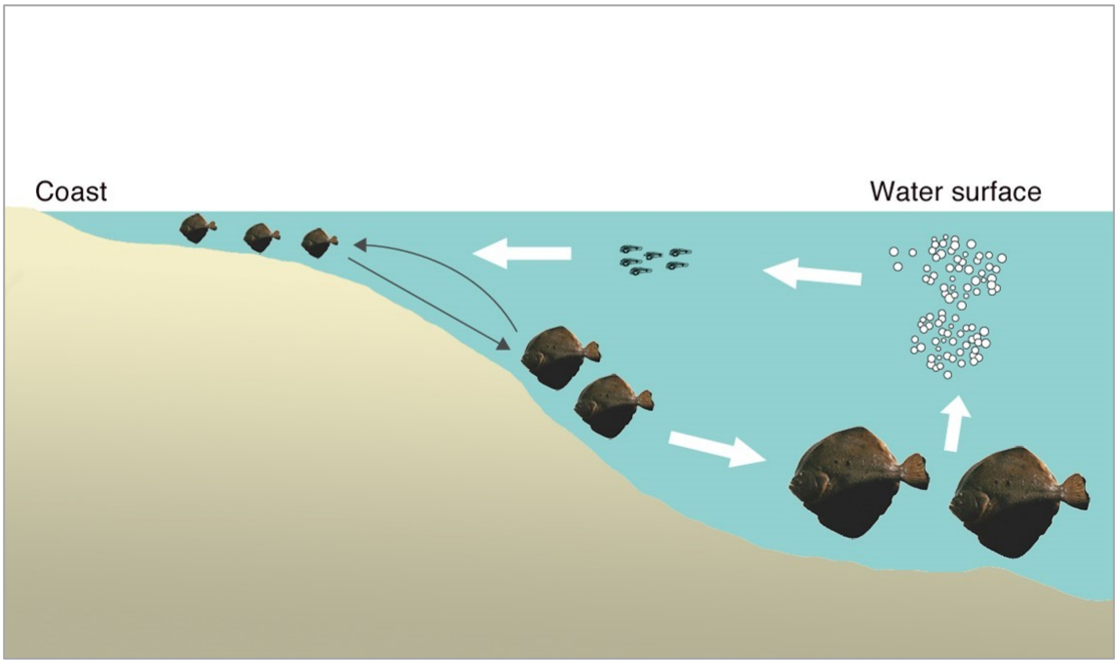

Fig. 3.4.1. Turbot life-cycle.

Spawning season and area. The Skagerrak and Kattegat populations were historically composed of two major spawning components, one in the Eastern Skagerrak and one in the southern part of the Kattegat (Fig. 3.4.2; Cardinale et al., 2009). Our results confirm the winter aggregation of turbot in the south western part of Kattegat off the Danish coast (Fig. 3.4.3a). Furthermore, the reduction of the northern component observed in the data by Cardinale et al. (2009) is also observed in our studies (Fig. 3.4.3a) indicating that this component is not yet recovered.

Spawning in the Kattegat has not been examined and only anecdotal information is available. It is believed to spawn at depths of 10-40 m (Støttrup et al., 2002), around May-June in this area. Tagging studies have revealed that adult turbot are sedentary (Aneer & Westin, 1990; Støttrup et al., 2002), display a strong spawning site fidelity and have restricted movement during the spawning season (Florin & Franzén, 2010). Since the maps from Cardinale et al. (2002) are from the winter quarter (Fig. 3.4.2), and turbot spawn in latter part of Q2, the spawning sites cannot be assumed from this data. Our Q3 survey does not capture the spawning season either, as it occurs after the end of the spawning season and the turbot may have moved to feeding grounds. In the Baltic Sea, spawning takes place from late May to July along the coast and on off-shore banks at 3-40 m depth, with demersal eggs (Nissling et al., 2006).

Spawning takes place at temperatures around 12-15 °C and salinities around 6-8 psu. Florin & Frandsén (2010) found a median depth of 12 m during spawning, and a distribution in deeper waters during feeding with a median depth of around 20 m. From historic data, the largest fishes were caught at depths > 35 m. In recent times, the maximum size has decreased by about 20 cm due to fishing pressure (Cardinale et al., 2009).

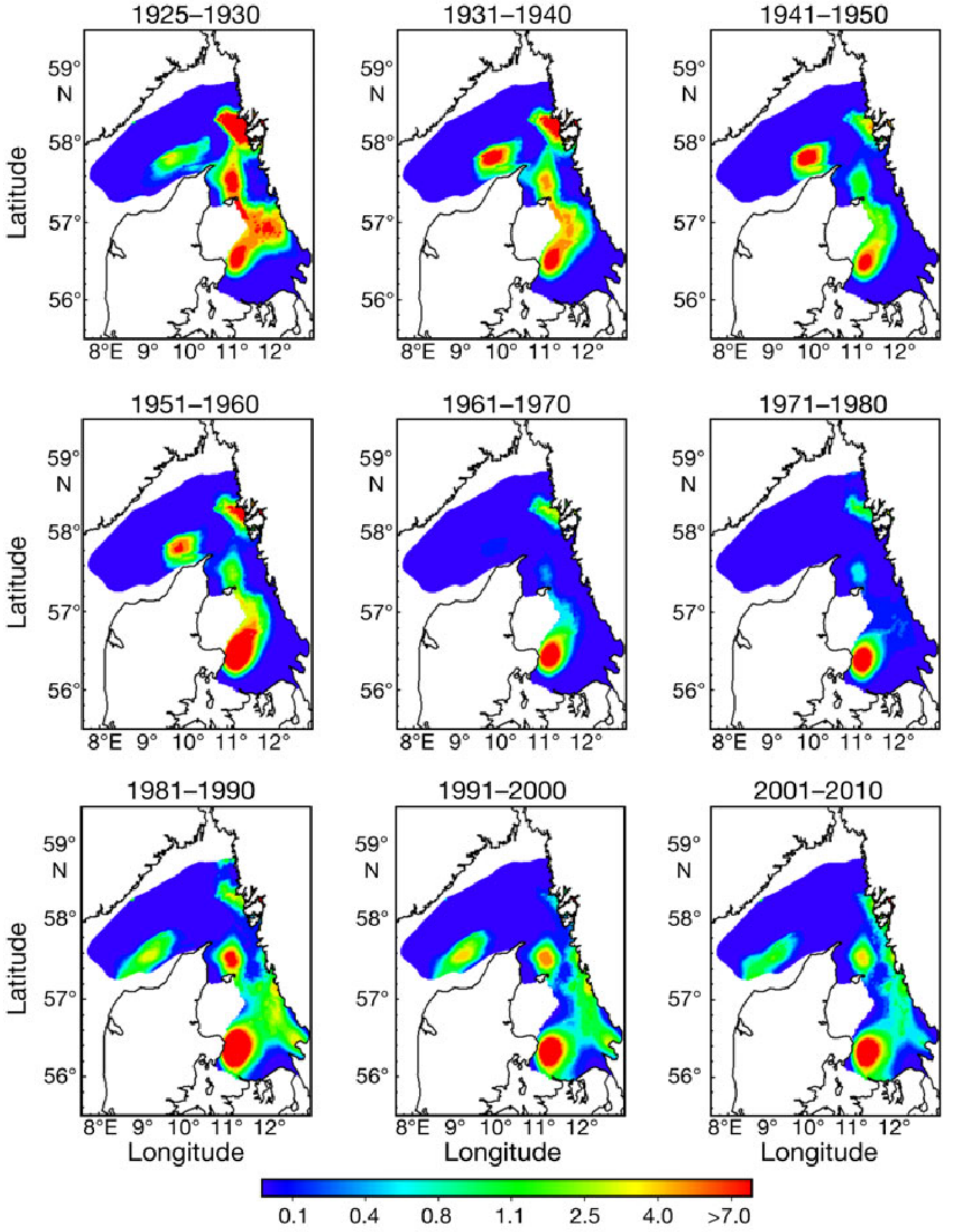

Fig. 3.4.2. Historical trends in spatial distribution of CPUE (kg h–1) and aggregation pattern of turbot in the Kattegat-Skagerrak (decadal average) estimated between January and March. Taken from Cardinale et al. (2009) with permission from MEPS ©Inter-Research 2009.

Adult. Adult turbot prefer sandy, rocky or mixed bottoms (Kerby et al., 2013). Optimal temperature for growth is 16-18 °C (van der Hammen et al. 2013). It is distributed in a wide salinity range down to a salinity of 5. Using historical data, Cardinale et al. (2009) mapped decadal changes in the geographical distribution of adult (<25 cm) turbot during the first quarter. Adult turbot was distributed throughout

Skagerrak and Kattegat until the 1950'ies, it is now concentrated in the southern part of Kattegat. Cardinale et al. (2009) estimated that between 1925 and 2007, turbot biomass in Skagerrak-Kattegat declined by around 86%, maximum body size decreased by about 20 cm and the northern component of the population had virtually vanished (Fig. 3.4.2). The results of Cardinale et al. (2009) only cover the Kattegat area and are not reflected in our our results, which show very high aggregations in the western Baltic, and may thus mask any aggregations that do occur in the Kattegat area, possibly due to the decline of the population in the Kattegat area.

Our results show small aggregations along the Swedish west coast and in the area around Sejerø Bay (Fig. 3.4.3a-c). Smaller aggregations around Læsø are evident in Q3 but highest aggregations occur in the western Baltic south of Lolland to the German coast in the winter (Q1 and Q4) and in the southern Sound to the German coast in the summer (Q3). The Belt Seas are important areas for turbot in the winter period (Q1 and Q4).

Early life-stages and juveniles. In the Baltic Sea YOY turbot were found in waters above 5.3 psu, indicating a lower salinity threshold for this turbot population (Florin et al., 2009) and preferred depths of less than 1 m (Nissling et al., 2007). In the Kattegat, YOY and age-I turbot were distributed to depths of around 4 m, whereas older turbot occupied deeper depths (Støttrup et al., 2002). The juvenile distribution in the Kattegat seems to cover a broader depth range than that reported for other areas. Juvenile turbot has experimentally been shown to prefer sand over sand/vegetation (Sparrevohn & Støttrup, 2003). Turbot exhibit fast growth rates and juvenile turbot reach approximately 30 cm by age three (Kerby et al., 2013). In southern Kattegat, wild turbot reached on average 20 cm by age two, although some individuals did reach 30 cm towards the end of the second year (Støttrup et al., 2002). Turbot grow up to 10-11 cm per year in the first years in favorable habitats (Sparrevohn & Støttrup, 2008). Turbot juveniles were observed to occur in high densities along the north coast of Zealand (Støttrup et al., 2002) indicating a high natural recruitment of newly settled juveniles to this area. However, the broader depth distribution of juveniles in this area also indicated that the area might be a suboptimal nursery area (Sparrevohn & Støttrup, 2008) and other areas may be better suited as juvenile growth areas. As it was not possible to split the data into adult and juvenile, the areas described under adults may also apply to age-1+ juveniles. In the Baltic Sea, the best habitat descriptors in order of contribution were occurrence of filamentous algae, substrate and turbidity. Turbot showed a preference for areas with a low cover of filamentous algae, high turbidity and sandy substrate (Florin et al., 2009).

3.4.2. Essential Fish Habitat for turbot

- ***Spawning.*** Insufficient data.
- ***Adult.*** The seasonal maps combine adults and age-1+ juveniles. The south western part of Kattegat and coast off North Zealand, Belt Seas. The western Baltic south of Lolland and southern part of the Sound to the German coast.

Estimation error are generally low. Highest prediction error occurs in Q3 in the western Baltic (Fig. 3.4.4) due to insufficient data.

- ***Juveniles.*** Insufficient information on YOY-turbot.

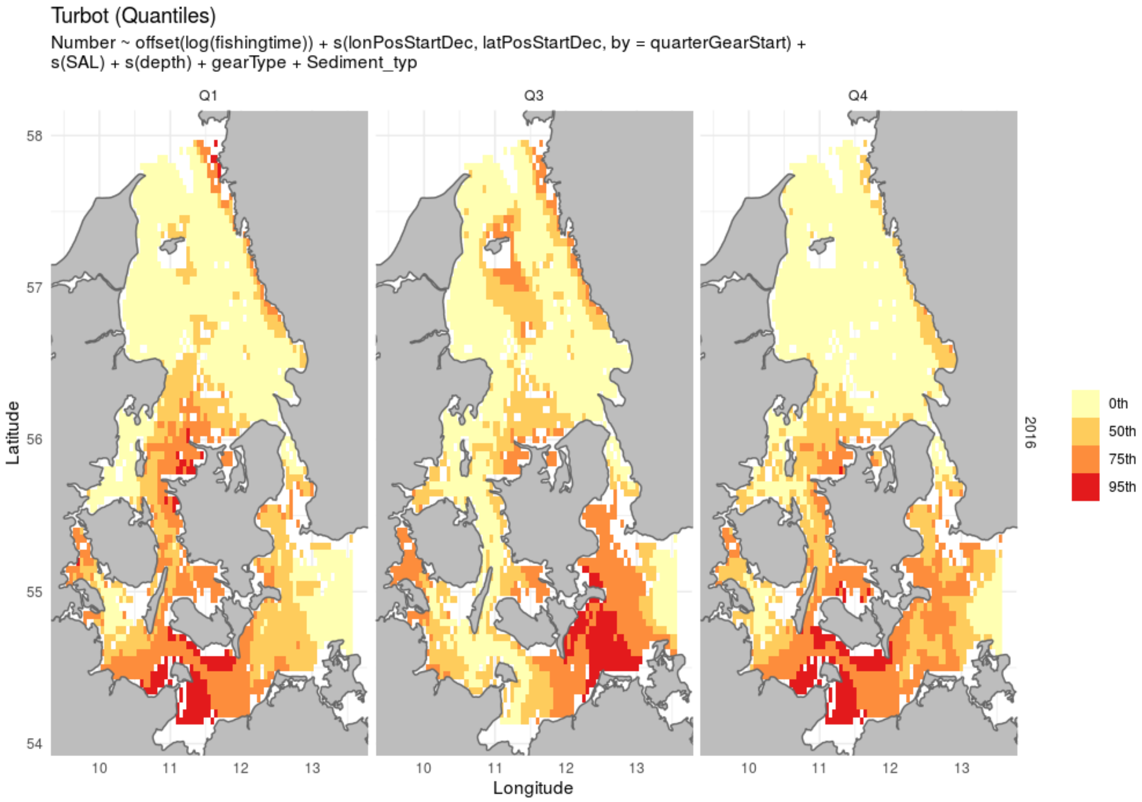

Fig. 3.4.3. Left map (a) are predicted turbot habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). Depth: p< 0.001.

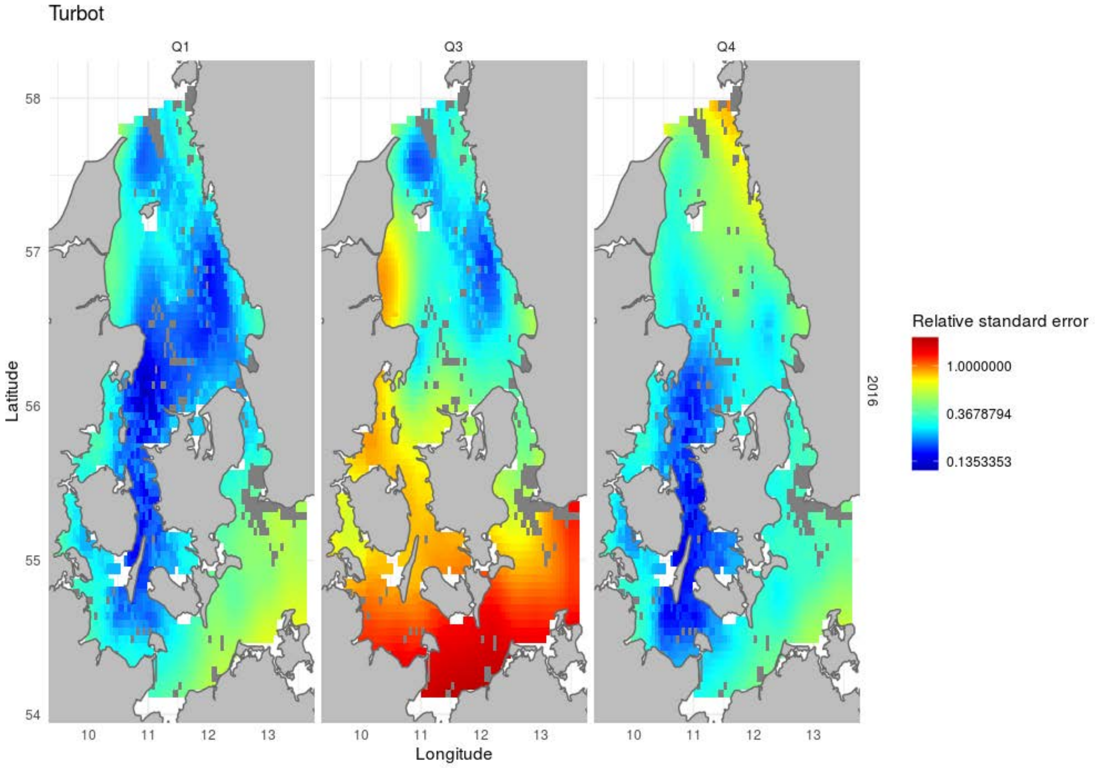

Fig. 3.4.4. Left map (a) are relative standard errors of the predictions (standard error/predicted value) of turbot habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

3.5. European flounder *Platichthys flesus*

3.5.1. General background

Stock structure

In the Baltic Sea, there are two sympatric flounder populations with different spawning habitats. Demersal spawners produce small and heavy eggs on shallow banks and coastal areas in the northern part of the Baltic Sea whereas in the southern Baltic Sea, pelagic spawners spawn eggs that are neutrally buoyant at 10-12 psu at 70-130 m depth (Nissling et al., 2017). The pelagic spawners are further separated into three stocks. ICES SD 22-23 constitutes one population (Belt Seas, Sound and southern Fyn area), that is different to that in the ICES SD 24-25 (west and east of Bornholm) by egg buoyancy, length at maturity and to some extent genetics (Nissling et al., 2017). The salinity of neutral buoyancy for SD23 plaice is around 26 psu, whereas it is around 15 in SD24. The third population is in the northern Baltic Sea (SD 26 and 28). Some overlap between these two populations is ignored for practical reasons in assessments.

Bearing in mind that salinity and temperature are known candidate drivers of evolution, it is not surprising to observe that despite little neutral genetic divergence between populations, flounder seem to be adapted to local salinity conditions (Larsen et al., 2007).

Fisheries

Flounder are mostly caught as bycatch in cod fisheries (mainly trawlers) and mixed flatfish fisheries (mainly gillnetters) (ICES 2014). In SD 22 flounder are mostly caught by trawlers, whereas in SD 23 mostly by gillnetters.

Life history stages

The life-cycle of flounder is very similar to that of turbot or plaice (Fig. 3.2.1 or Fig. 3.4.1). Adults spawn off-shore in deeper waters. Eggs and larvae drift inshore and settle once metamorphosed in the shallow coastal areas, where they feed and grow. They move offshore in the winter and return to the coastal feeding grounds in the spring. As they grow older they are distributed more offshore.

Spawning season and area. Flounder population west of England showed that timing of spawning migration was not fixed but associated to temperature regime, with up to 1-2 months difference in peak abundance when temperatures were lower by up to 2°C (Sims et al., 2016). Also, in colder periods more arrived at spawning grounds over a short time period (2-6 days) than in warmer years (12-15 days).

Flounder pelagic spawners are believed to spawn in the Sound and Arkona basin (Nissling et al., 2002). Favourable conditions for successful reproduction include salinity greater than ca 11-12 psu and ≥ 2 ml O_2/l). In areas SD 22, 23 and 24 flounder spawn around March - April (Nissling et al., 2017).

For the pelagic spawning Baltic Sea flounder, the model (GAM using a negative binomial distribution) showed a negative relation with temperature and bottom current and a positive relation with salinity (Orio et al., 2017). Spatial predictions of potential spawning areas of flounder showed a decrease in habitat availability for the pelagic spawning flounder over the last 20 years in the central part of the Baltic Sea, which may explain part of the observed changes in populations' biomass. The predicted high probability spawning areas for European flounder in the western Baltic are west and east of Bornholm (HELCOM, 2019). These were predicted from environmental threshold values.

The results from this study show important spawning areas in the southeastern Kattegat, northern part of Zealand and the Great Belt (Fig. 3.5.3a). Arkona basin, is also an important area and confirms an earlier reported spawning site (Nissling et al., 2002). The flounder spawning habitat is defined by salinity, temperature and depth.

Adults. The distinction between adult and juvenile flounder was made from maturity data for flounder (Fig. 3.5.1). The distribution in Q1 is different to that in Q3 and Q4. In the summer the flounder are more distributed to the south around and in Arkona Basin (Fig. 3.5.3), but this predicted habitat is highly uncertain (Fig. 3.5.5). Adult flounder habitat preference is guided by salinity, temperature and depth.

The survey data does not cover the fjord areas. However, it is evident from the key-fisher data that flounder adults are caught in the coastal areas all around Denmark, especially in the fjord systems (Støttrup et al. 2018).

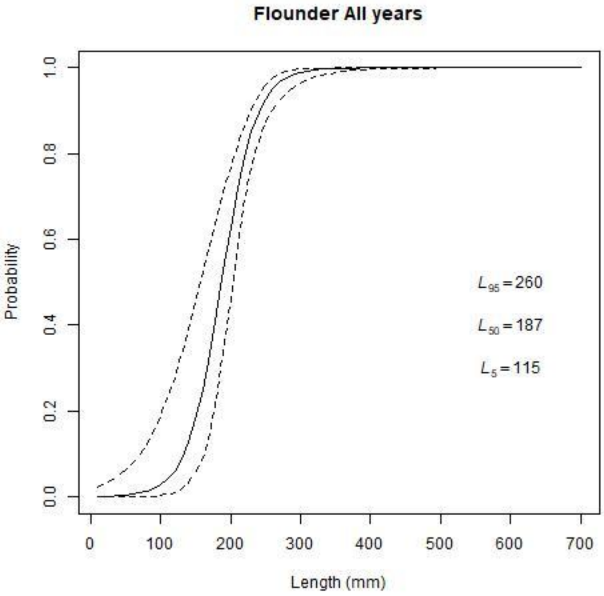

Fig. 3.5.1. Maturity ogive and 95% CI for flounder, based on data for all years.

Early life stages and juveniles. YOY flounder. Juvenile flounder distribution seems to be highly influenced by salinity Kerstan (1991). The 0-group flounder were in the Wadden Sea area congregated in the oligohaline and limnitic tributaries of the Elbe system (salinities 0,3 – 5,5) and low temperatures ranging 3-10°C, but can also be found at temperatures up to around 20°C. In inner Danish waters, they are restricted to depths of 0 - 1,5 m (Muus, 1967; Andersen et al., 2005a).

In the Baltic Sea, no YOY flounder were found below 5.8 psu (Florin et al., 2009). Age-0 flounder feed chiefly on *Corophium* spp. (Martinho et al., 2008), an amphipod abundant in bare sand habitat in Danish inner waters and dominant prey of flounder (Andersen et al., 2005b). In the absence of *Corophium* spp., flounder juveniles feed on polychaetes that are relatively active on the sediment surface (Andersen et al., 2005b) From field enclosure studies and using growth rates, bare sand habitat was found to be more suitable for juvenile flounder than eelgrass meadows (Tarpgaard et al., 2005). This is further supported by field studies that have shown that flounder is associated with bare sand habitat compared to vegetated areas (Wennhage & Pihl, 2007).

In this study, age-0 flounder are rarely caught with the gear used in the international fishery surveys. Furthermore, the data used in this study does not include coastal areas or estuaries and thus the value of estuaries or low tidal flats for age-0 flounder can only be obtained from localized studies. For example, on the mud-flats around Egense on the Kattegat west coast, fishing was carried out over a 3-year period 1996-1998 at intervals from May to October at depths of 20-40 cm (Nicolajsen, 2005). CPUE for age-0 flounder was highest in August in 1996 (66), July in 1997 (102) and June in 1998 (270), although in the latter year high catches were also observed in July (85). The CPUE was catch per hand-trawled beam trawl (200 steps = 95-125 m = 185-215 m^2 area covered). Unpublished drop-trap data show densities in June 2000, 2002 and 2004 varying from 0.1 to 1.6 individuals/m^2. The high densities found here indicate a valuable nursery area for flounder.

It is evident from the key-fisher data that flounder juveniles are caught in the coastal areas all around Denmark (Støttrup et al. 2018). The juvenile survey conducted in 2016 supports this evidence. Depth and salinity were the explanatory variables in the simplest model of flounder density which were highest in the southern areas of the inner Danish waters (Brown et al., 2019). Flounder seem to select low saline areas for settlement. Growth in juvenile flounder was positively related to high salinities and temperatures and thus there were contrasting results between HAM and HGM for this species (Brown et al., 2019).

Older juveniles. Length obtained during age-0 in the wild in Mariager Fjord or Egense was around 8-9 cm, whereas released juveniles (age-0 flounder) reached 12 cm by October in Løkkedyb, Limfjorden (Nicolajsen, 2005).

Age-I flounder inhabited more saline waters, although in the south-west coast of France, Le Pichon et al. (2014), showed that age-2 and age 3 European flounder also use rivers as optimum feeding habitats during summer. Tidal river estuaries are therefore important nursery areas for flounder (Kerstan, 1991). Highest densities were observed at temperatures below 20°C and salinity below 10 psu. Although tidal estuaries are not common in inner Danish waters the mud flats exposed at low tide eg. Egense may be important for flounder, where they have been observed to occur in high densities (Nicolajsen, 2005).

In the Baltic proper, the main predictors in the flounder model were in order of model contribution, substrate, structure, salinity, wave exposure and to lesser degree filamentous algae (Florin et al., 2009). Gravel and sand were preferred over stone and soft substrates and presence of structural complexity such as large stones, boulders and vegetation had a positive effect. Along the Swedish west coast flounder was associated with bare sand habitat compared to vegetated areas (Wennhage & Pihl, 2007).

The distribution of juvenile flounder varied little between seasons (Fig. 3.5.3a-c) and overlapped the adult distribution in several areas such as the southern Kattegat, Great Belt and the Arkona Basin (Fig. 3.5.2). In winter, high aggregations of flounder occur in the southern Kattegat area and Great Belt Sea (Fig. 3.5.3a). This shifts to the South of the Sound and Arkona Basin during summer (Fig. 3.5.3b) and autumn (Q4) with an extension to south of Sealand during autumn (Fig. 3.5.3c). The environmental variables predicting juvenile flounder habitat were temperature, oxygen and depth.

3.5.2. Essential Fish Habitat for flounder

- ***Spawning.*** The main spawning areas identified for the Kattegat flounder are the southeastern Kattegat, northern coast of Zealand and the Great Belt (Fig. 3.5.2a)
- ***Adult.*** The summer feeding grounds are located towards coastal areas in the Belt Seas and the southeast coast of Sealand, towards Arkona basin (Fig 3.5.3b).

Estimation errors in Q1 and Q4 are low throughout the study area. Highest prediction error occurs in Q3 in the Arcona Basin area (Fig. 3.5.4).

- ***Juveniles.*** YOY, most soft bottom shallow coastal areas in inner Danish waters. Older juveniles aggregate in the Great Belt and North of the sound in Q1 and in western Baltic later in the summer and autumn (Fig. 3.5.3).

  Highest prediction error occurs in Q3 in the Arcona Basin area (Fig. 3.5.5).

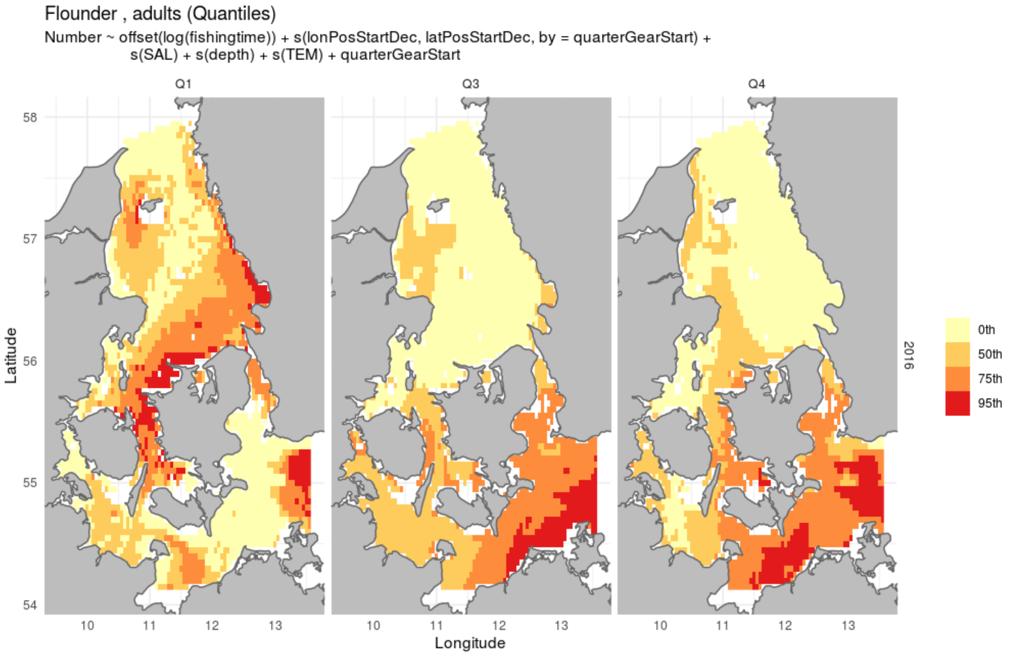

Fig. 3.5.2. Left map (a) are predicted adult flounder habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). Temperature: $p < 0.001$, depth: $p < 0.001$, salinity: $p<0.001$. Q1-Q3: $p <0.1$. Q1-Q4: $p <0.001$.

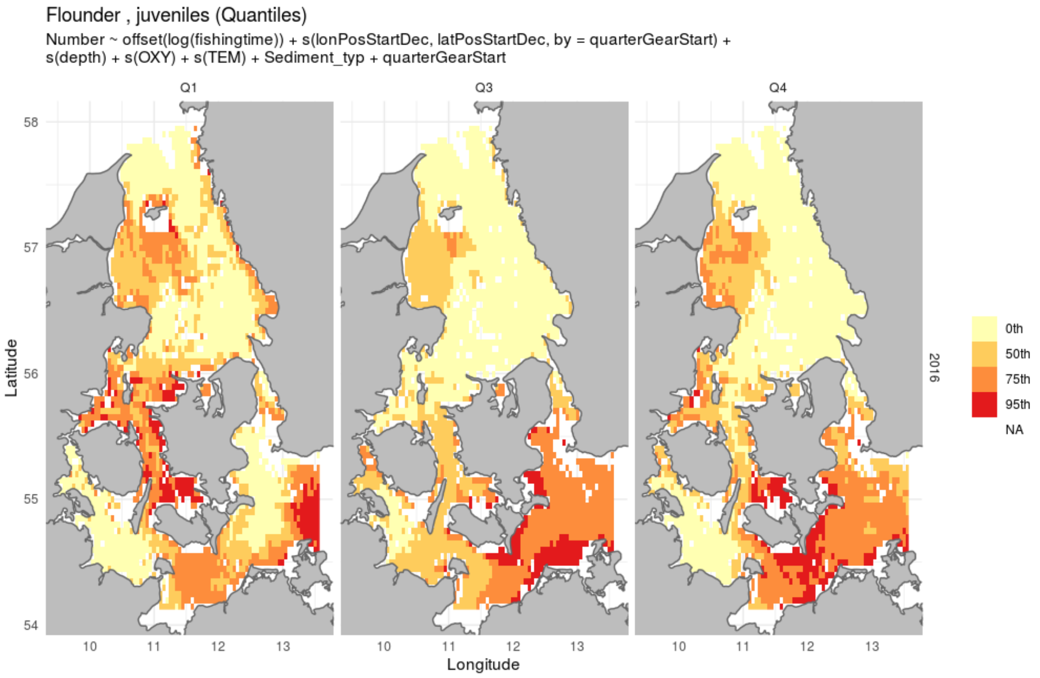

Fig. 3.5.3. Left map (a) are predicted juvenile flounder habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). Temperature: p < 0.001, oxygen: p<0.001, depth: p < 0.1. Q1-Q3: p<0.01, Q1-Q4: p<0.001.

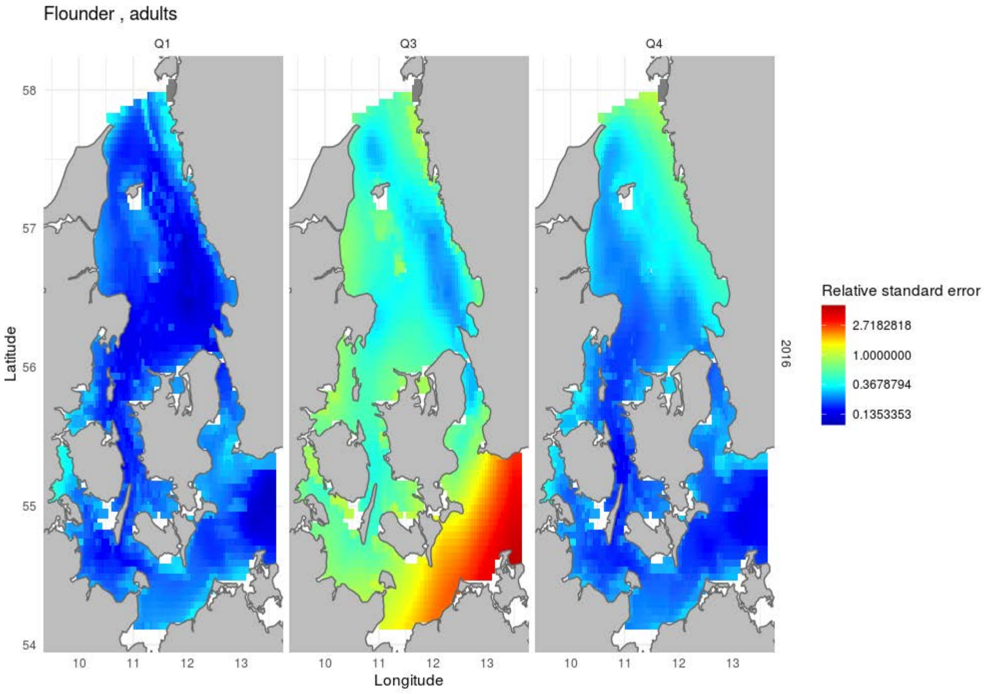

Fig. 3.5.4. Left map (a) are relative standard errors of the predictions (standard error/predicted value) of adult flounder habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

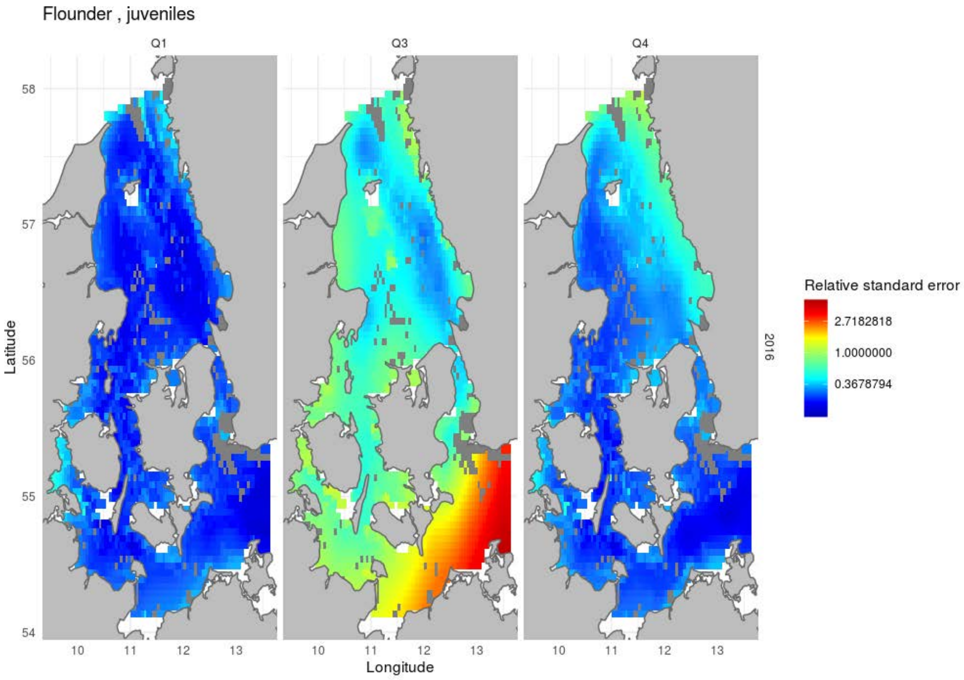

Fig. 3.5.5. Left map (a) are relative standard errors of the predictions (standard error/predicted value) of juvenile flounder habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

3.6. Atlantic herring *Clupea harengus*

3.6.1. General background

Stock structure

The North Sea Autumn Spawning (NSAS) herring stock comprises four spawning components (Shetland/Orkney, Buchan, Banks and Downs) (ICES, 2018a). Although they do not spawn in the inner Danish waters, they mix outside the spawning season with the Western Baltic Spring Spawning (WBSS) herring in the Skagerrak and Kattegat. The WBSS stock is distributed in the Skagerrak, Kattegat, around the Belts and the western Baltic Sea (ICES, 2018b). The WBSS stock also comprises several spawning components that mix outside the spawning season. The spring-spawning Rügen herring is the largest component. Other smaller spawning components that spawn in either the autumn or spring exist in the Kattegat, inner Danish waters and western Baltic. These may be small highly localized populations. Despite the extensive mixing of adults and juveniles, the spawning components remain distinct, possibly due to natal homing and larval retention (Bekkevold et al., 2005).

Fisheries

The WBSS and NASA herring are exploited as a mixed fishery in the Western Baltic, Kattegat and Skagerrak (ICES, 2018b). Since 1996, the fishery takes place mostly in the first and third quarter. In the Kattegat and Skagerrak, herring are caught for human consumption by trawlers with min. mesh size of 32 mm, or by purse seiners. The Swedish fishery uses smaller mesh sizes. By-catch of herring in the Skagerrak and Kattegat occurs in the sprat fishery or fishery for Norway pout and blue whiting. There is a directed fishery for herring the Belt Seas and western Baltic, or it is caught as by-catch in the sprat fishery.

Life history stages

Herring spawn demersal eggs on hard bottom or vegetative substrate in shallow areas. The eggs hatch into pelagic larvae that drift with local currents. Adults may perform migrations over large geographical areas.

Spawning season and area. The Rügen herring is the largest component of the WBSS stock, spawning during March-May (ICES, 2018b). The spawning areas of the Rügen Island on the German coast are important spawning grounds for this spring-spawner (Fig. 3.6.1).

Around Fehmarn there is a local autumn spawning herring population. The spawning areas in the Kattegat and inner Danish waters are not specifically known. There may also be other smaller western Baltic herring spawning stocks. These may be small highly localized populations in Kiel, Møn, Flensburg, Fåborg and possibly also an autumn spawning Rügen herring. Some of these smaller stocks may also spawn during winter.

Herring have demersal eggs, which attach to substrate. They depend upon hard-bottom substrate in the photic zone (< 10 m). In the Baltic Sea, herring prefer aquatic vegetation as a substrate for spawning (Aneer, 1989). Herring visit the same spawning grounds one generation after another and some spawning areas are used successively during the spawning season (Rajasilta et al., 1993).

Adults. The distinction between adult and juvenile herring was made from maturity data for herring (Fig. 3.6.1).

Most herring populations are migratory and congregate on common feeding and overwintering grounds. It is believed that spring spawning Rügen herring perform a feeding migration towards the Skagerrak and North Sea every summer, returning to the southern Kattegat and the Sound for overwintering and to the spawning areas of the Rügen Island on the German coast in the spring (Fig. 3.6.2) (ICES, 2018b).

In our study, the overwintering grounds seem to be located in the northern Kattegat area off the Danish and Swedish coasts (Fig. 3.6.4a, c). These were different to the summer distributions which were located more centrally and south east of Læsø, and in the northern part of the Sound (Fig. 3.6.4b). The environmental variables predicting adult herring habitat were salinity, temperature, oxygen and depth.

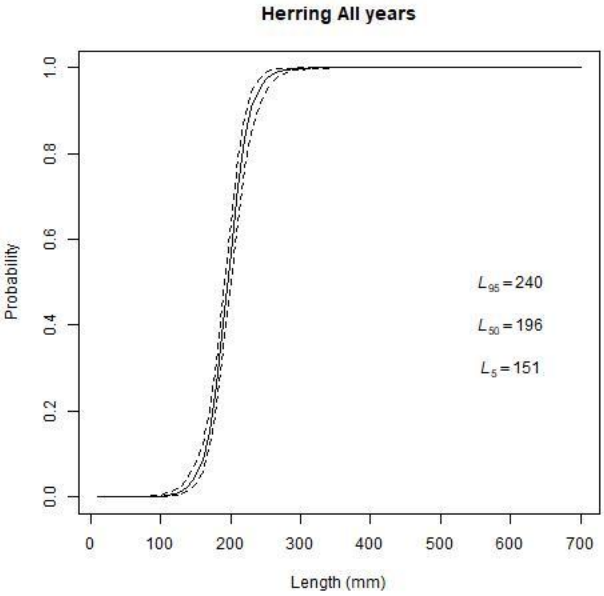

Fig. 3.6.1. Maturity ogive and 95% CI for herring, based on data from all years.

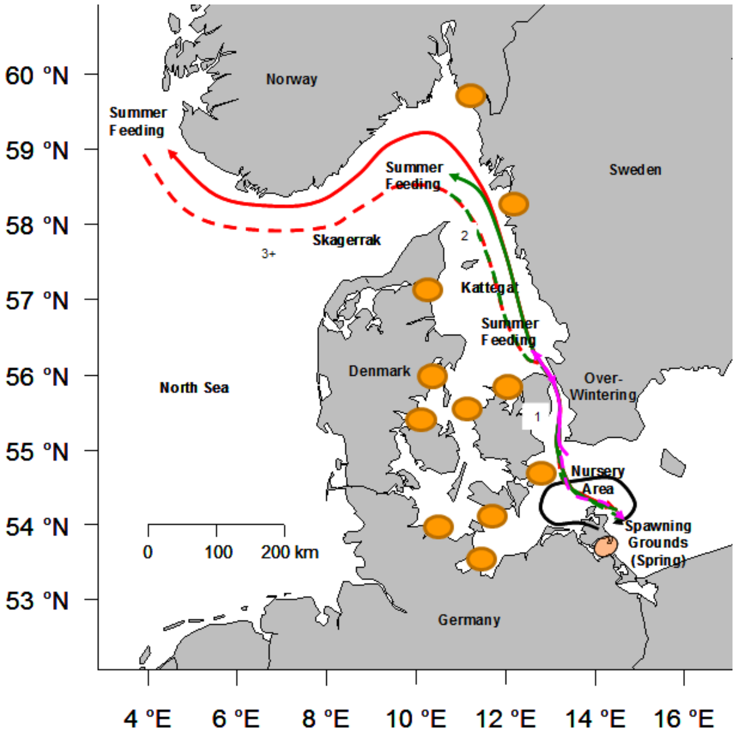

Fig. 3.6.2. General migration patterns of the WBSS. The yellow circles indicate local spawning populations. The numbers adjacent to the arrow-lines indicate the direction and extent of the age-dependent migration patterns. Taken from ICES 2018b.

Early life stages and juveniles. The spatial and temporal distribution of larvae is highly dependent on the spawning time and magnitude coupled with hydrological conditions that influence direction and speed of drift and extent of dispersion. From icthyoplankton surveys conducted during late January – mid February 1992-2010, the general distribution of larvae and juveniles was along the northern part of the Swedish west coast extending south to around Læsø (Fig. 3.6.3; Munk et al., 2014). The NSAS juveniles use the Skagerrak and Kattegat as nursery areas (Iles and Sinclair 1982 – in Ulrich et al., 2012). This corresponds well with our predicted juvenile herring habitat in the winter (Fig. 3.6.5a) and to a degree also in autumn (Fig. 3.6.5c). This distribution was however different to the summer distribution which was along the Swedish west coast (Fig. 3.6.5b). The environmental variables predicting juvenile herring habitat were oxygen, salinity and depth.

The regular and predictable schooling of juvenile herring in the Skagerrak and Kattegat renders this species more vulnerable to predation by avian piscivores than other species (Skov et al., 2000). Avian piscivores wintering in the eastern Kattegat especially around the area of Little Middelground, NE of the island of Anholt, in the Swedish zone seem to be dependent on the schooling of herring for their survival.

The distribution of adult and juvenile herring seems very similar in the three quarters (Fig. 3.6.4 and 3.6.5).

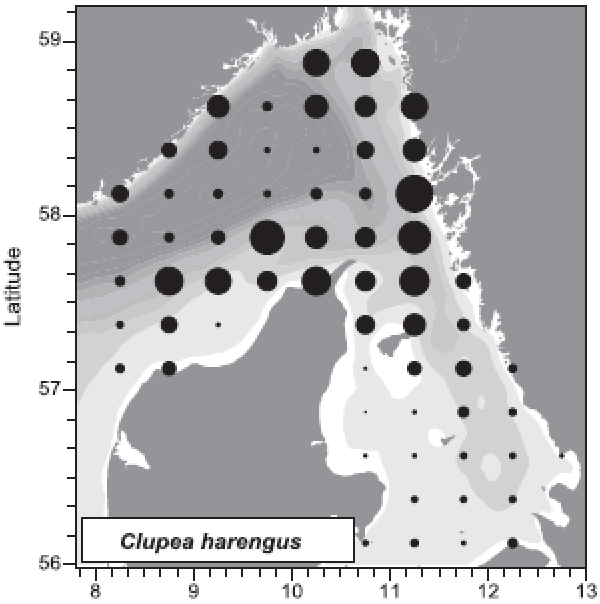

Fig. 3.6.3. Distribution of herring in ichthyoplankton samples during IBTS in February between 1992-2010. Abundance estimates averaged in rectangles of 0.25° latitude and 0.5° longitude for all years 1992-2010. Areas of circles illustrate relative abundance. From Munk et al., (2014) with permission from Elsevier, license number 4625910194596.

3.6.2. Essential fish habitat for herring

- ***Spawning.*** Insufficient data on spawning. The potential spawning grounds are characterized by hard bottom and submerged vegetation in shallow (<10 m) areas. Directed surveys to study herring spawning grounds are not available.

HELCOM has produced maps based on threshold values for spawning habitat for herring in the Baltic Sea. these cover most of the coastal areas with either hard substrate or vegetation (HELCOM, 2019).

- ***Adult.*** The northern part of Kattegat on the Danish coast in the winter half-year. The area south east of Læsø and northern part of the Sound in summer (Fig. 3.6.4).

  Highest prediction error occurs in Q3 in the Arcona Basin area (Fig. 3.6.6).
- ***Juveniles.*** The northern part of the Kattegat and the Swedish west coast (Fig. 3.6.5).

  Highest prediction error occurs in Q3 in the Arcona Basin area (Fig. 3.6.7).

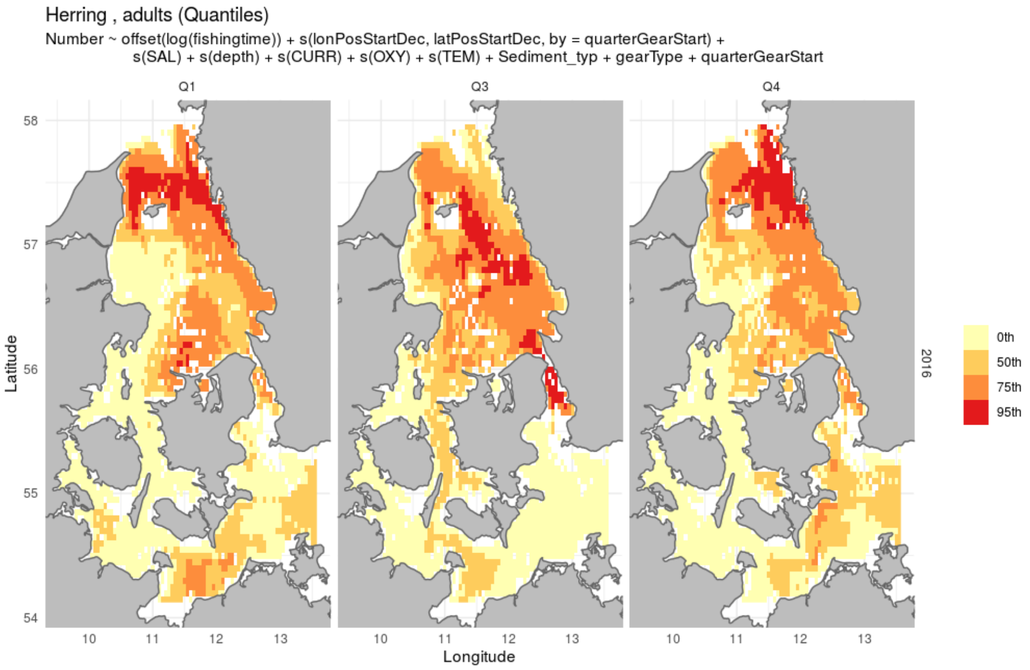

Fig. 3.6.4. Left map (a) are predicted adult herring habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). Temperature: $p < 0.001$, oxygen: $p < 0.1$, salinity: $p < 0.05$, depth: $p<0.001$. Q1-Q3: NS. Q1-Q4: $p <0.001$.

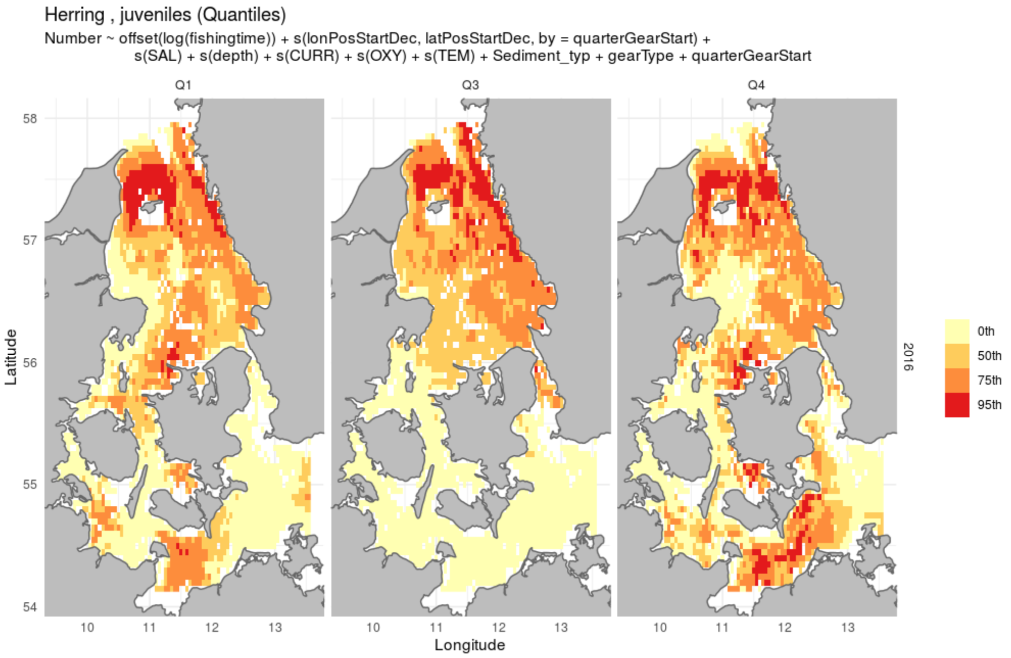

Fig. 3.6.5. Left map (a) are predicted juvenile herring habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). Oxygen: p < 0.001, salinity: p < 0.01, depth: p< 0.001. Q1-Q3: p <0.1. Q1-Q4: p<0.001.

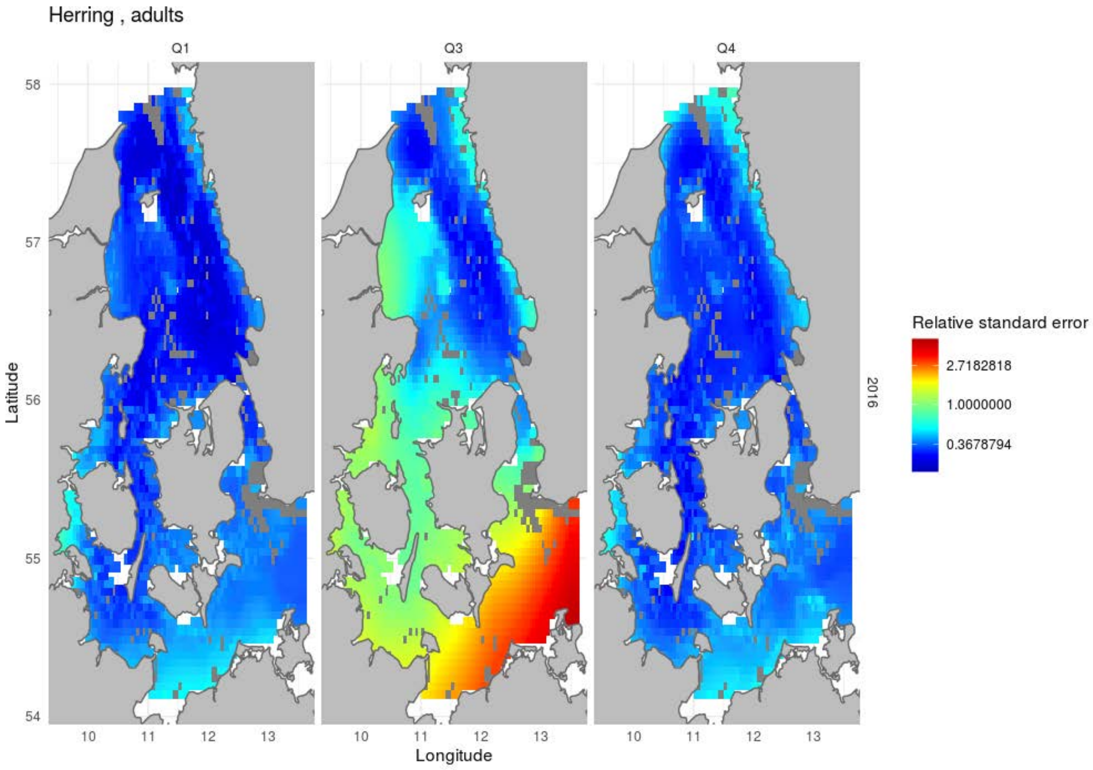

Fig. 3.6.6. Left map (a) are relative standard errors of the predictions (standard error/predicted value) of juvenile flounder habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

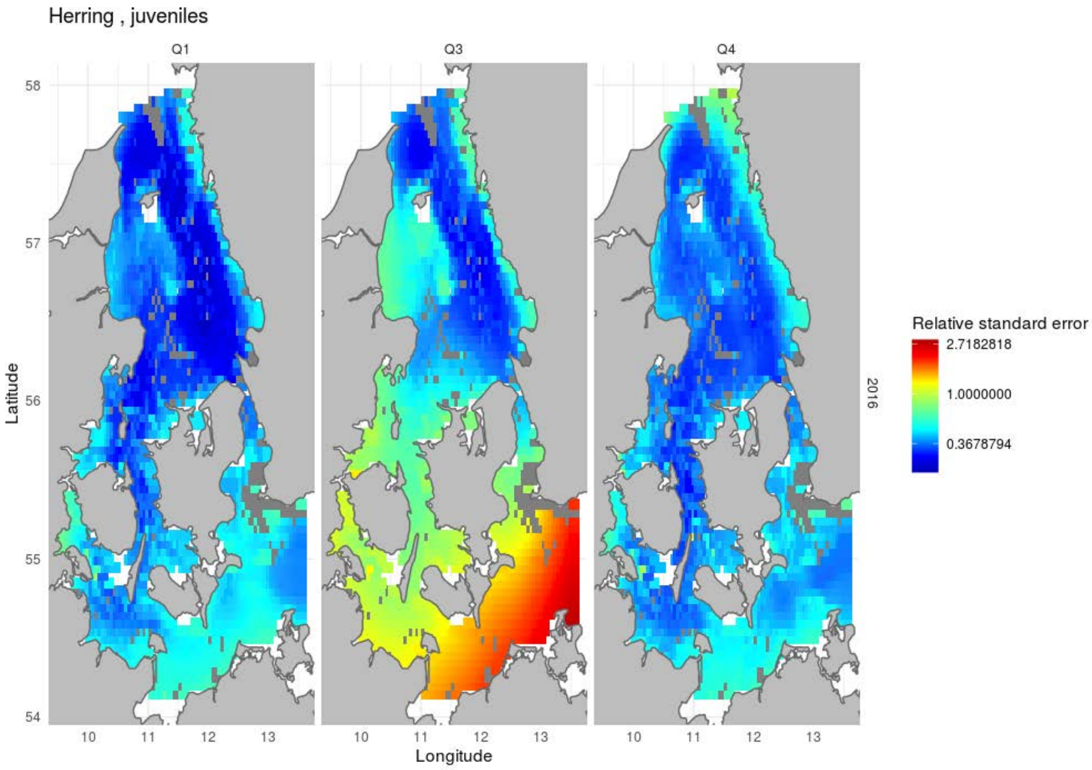

Fig. 3.6.7. Left map (a) are relative standard errors of the predictions (standard error/predicted value) of juvenile flounder habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

3.7. European sprat *Sprattus sprattus*

3.7.1. General background

Stock structure

Sprat distributed in ICES area IIIa (Skagerrak and Kattegat) is managed as one stock unit (ICES, 2013). The population structure is however still uncertain. There are indications of genetic differences between sprat from the Kattegat and the North Sea or the Baltic Sea (Limborg et al., 2012), but the work is based on neutral markers which are relatively insensitive. Whether or not sprat derived from the North Sea migrate to ICES area IIIa is not known.

Fisheries

The majority of the landings of sprat are taken by the Danish fleet (ICES, 2013). Sprat in ICES area IIIa are caught in the industrial fishery by Danish trawlers using < 16 mm mesh size. Some of the landings are by-catch from the herring fishery using 16 mm mesh-size codends. Sprat in this area is also caught for human consumption. Other countries fishing sprat in the area are Sweden and Norway.

Life history stages

Sprat spawn pelagic eggs in deep waters. The eggs and larvae drift with currents and are thus caught in ichthyoplankton surveys. Nursery grounds are located in coastal areas where it feeds on zooplankton and eggs. Larger juveniles and adults form schools.

Spawning season and area. In the Kattegat sprat spawn around March to July, whereas they seem to start spawning earlier (February) in the Skagerrak (Vitale et al., 2015). Males mature around 90 mm (L50) and females around 102 mm in both Skagerrak and Kattegat. Spawning locations have not been identified but potential areas for spawning are delineated by selecting those areas that are deeper than 30 m and have a higher salinity than 6 (HELCOM, 2019). Whether or not this is appropriate for the Kattegat area is not known. Sprat eggs are buoyant and the larvae and juveniles of this species have been regularly found in the ichthyoplankton samples in the IBTS surveys (Fig. 3.7.1), and indicate that spawning does take place in the Kattegat especially in the northern part and in Skagerrak.

Adults. Little information is available on the biology and ecology of this species; eg. size and weight at age and juvenile and adult habitats. Some populations are apparently highly sedentary (Vitale et al., 2015). Our study showed aggregations of sprat (adult and juvenile) in the northern part of the Kattegat along the Danish coast in winter (Q1 and Q4) and extending to the Swedish coast in summer (Fig. 3.7.2). The aggregations of sprat differed between winter and summer (Fig. 3.7.2.a, b), with an aggregation south of Falster in winter not observed in the summer. These distributions varied significantly from the summer distributions where the southern Kattegat was favoured with aggregations in the Swedish west coast and the Danish east coast of southern Kattegat (Fig. 3.7.2b).

Early life stages and juveniles. The juveniles are not as widespread as herring but from ichthyoplankton surveys conducted during late January – mid February 1992-2010, the highest abundances were in the northern part of Kattegat, north of Læsø. Considering the timing, this could be the Skagerrak sprat that spawn earlier in February (Vitale et al., 2015).

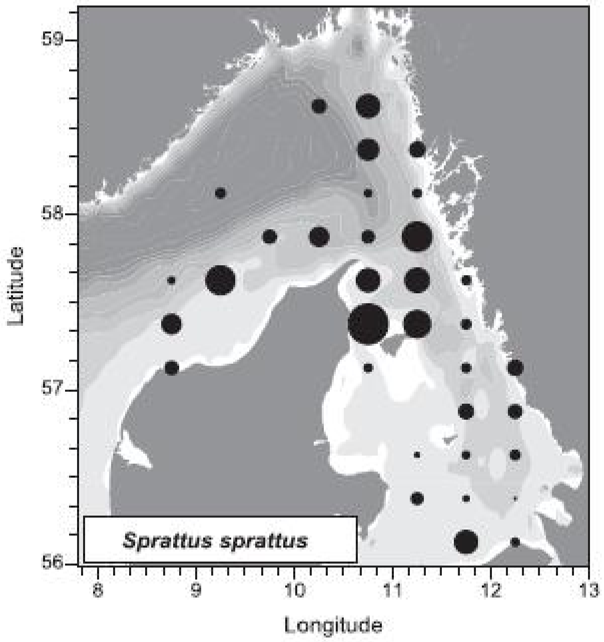

Fig. 3.7.1. Distribution of sprat in ichthyoplankton samples during IBTS in February between 1992-2010. Abundance estimates averaged in rectangles of 0.25° latitude and 0.5° longitude for all years 1992-2010. Areas of circles illustrate relative abundance. From Munk et al. (2014) with permission from Elsevier, license number 4625910194596.

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3.7.2. Essential fish habitat for sprat

- ***Spawning.*** Insufficient data.

  HELCOM has produced maps based on threshold values for spawning habitat for sprat in the Baltic Sea. The potential spawning areas for sprat at deeper than 30 m and salinity higher than 6.

  Ichthyoplankton surveys indicate northern part of Kattegat may be an important spawning area for the Skagerrak sprat (Fig.3.7.1).
- ***Adult.*** Adult and juvenile distributions were mapped together. Area in the north part of Kattegat and north of Fyn and the Great Belt throughout the year and also in the western Baltic in the autumn (Fig. 3.7.1).

  Due to insufficient data, the prediction errors are high in all quarters and all areas. Highest prediction error occurs in Q3.
- ***Juveniles.*** No specific data on juvenile sprat.

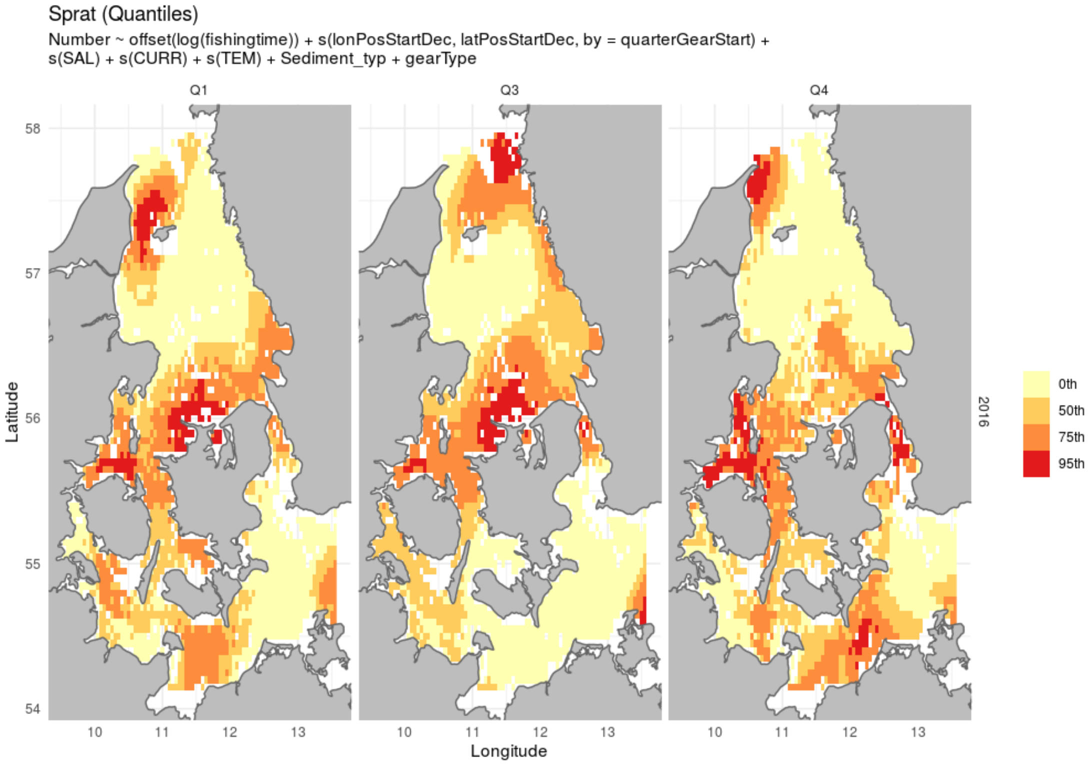

Fig. 3.7.2. Left map (a) are predicted sprat habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec). Temperature: p < 0.01. Q1-Q3: p <0.001. Q1-Q4: p<0.01.

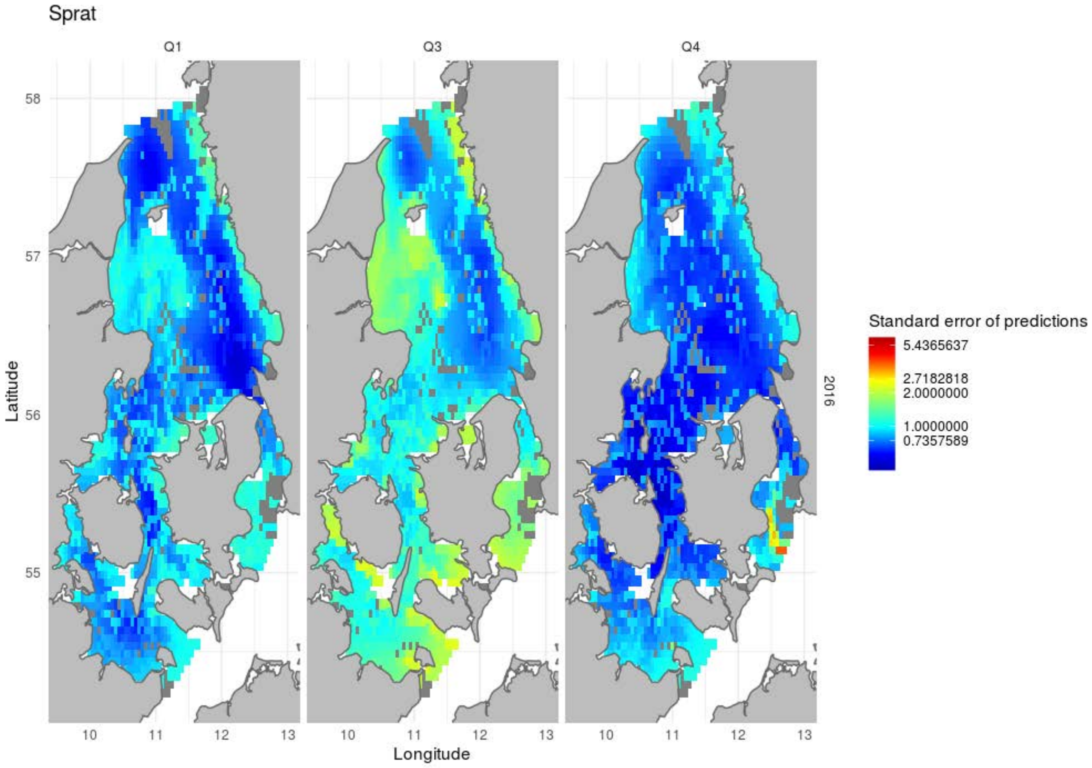

Fig. 3.7.3. Left map (a) are relative standard errors of the predictions (standard error/predicted value) of sprat habitats for first quarter (Jan-Mar), middle (b) for quarter 3 (Jul-Sept) and right map (c) for quarter 4 (Oct-Dec).

3.8. European Eel *Anguilla anguilla*

3.8.1. General background

Stock structure

The European eel is believed to consist of a single panmictic stock (Palm et al. 2009) distributed across the majority of coastal countries in Europe and North Africa with its southern limit in Mauritania (30°N) and its northern limit in the Barents Sea (72°N) and spanning the entire Mediterranean basin.

Fisheries

Eel is fished during all of its continental life stages; as glass eels, elvers, yellow eel and silver eel (ICES, 2018a). Due to its status as a severely depleted stock (listed in Appendix II of the Convention on International Trade in Endangered Species (CITES) since 2007), several fisheries restrictions have been put into action since 2007, mostly in the EU countries. In general, landings are at historic low levels. Not all countries that fish eel report their commercial landings of eel. Landings data thus represent minimum catches and changes in the landings cannot be interpreted correctly without information on the fishing effort or the fleet capacity.

Glass eel fisheries within EU take place in France, UK, Spain, Portugal and Italy. Yellow and silver eel are fishes take place in most EU countries and Tunisia).

Recreational fisheries are restricted within the EU countries but generally not monitored. Data on recreational catches of eel is estimated through interview surveys. Recreational fisheries for glass-eels in France and Spain have though been prohibited since 2010.

Eels are also fished for aquaculture purposes for ongrowing or for restocking purposes (release in the freshwater or estuarine environment).

Life history stages

The life history of the European eel is complex (Fig. 3.8.1). The pelagic eggs hatch into yolk-sac larvae with protruding teeth. Towards the end of the yolk-sac stage the leptocephalus larvae develop normal teeth (Butts et al., 2016). They drift with ocean currents to the continental shelf of Europe and North Africa where they metamorphose into glass eels and enter continental waters. Elvers and the larger yellow eel may occupy marine, brackish or freshwater systems and this growth phase may last several years or decades before metamorphosing to the silver eel stage and maturation. Despite the biological importance of the marine phase, most research to date has focused on the fresh water phase of the life history.

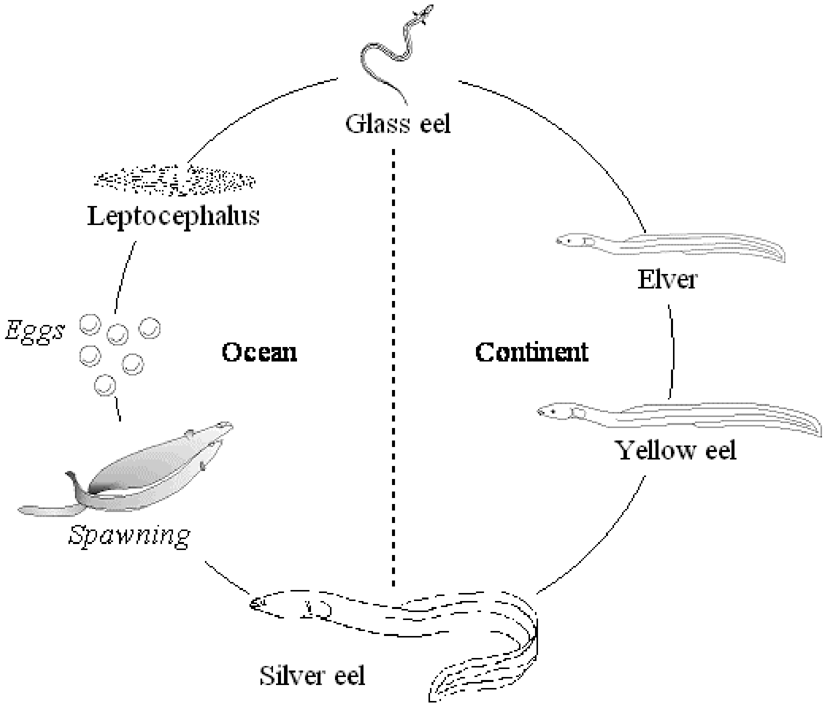

Fig. 3.8.1. Eel life-cycle. From (ICES, 2018a).

Spawning season and area. Spawning is believed to take place in the Sargasso Sea but so far no spawning adults have been caught.

Adults. Yellow eel recruitment was estimated at 29% of the baseline level (1960-1979) (ICES 2018). Many do not distinguish between yellow eel and silver eel. They occupy both the freshwater and marine environment. In coastal areas, yellow eel burrow and remain relatively inactive in colder (5-8 C) waters and migrate to rocky areas in warmer (>9 C) waters (Nyman 1972). Sheltering individuals seemed to prefer rocky rather than sandy areas in coastal systems.

No data is available to provide information on eel presence/absence or abundance. From the fishermen interviews there is some information on presence, but without absence information this map is incomplete (Fig. 3.8.2). Coastal areas in the sound and the central part of the Sound are areas identified by the fishermen to be areas with eel presence.

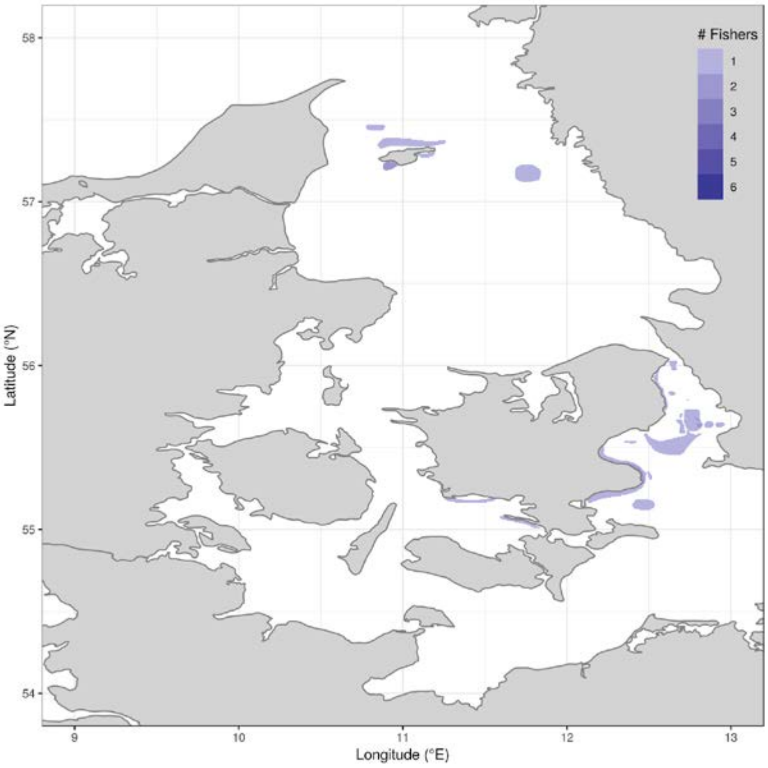

Fig. 3.8.2. Composite map concerning information on eel based on interviews with 7 fishermen. From: Støttrup et al. (2019).

Early life stages and juveniles. Glass eel recruitment is low across its geographical range (Fig. 3.8.3: ICES, 2018a). Compared to the recruitment during 1960-1979, this was estimated at 2% in the North Sea and 10% in the rest of Europe, where it was monitored (ICES, 2018a).

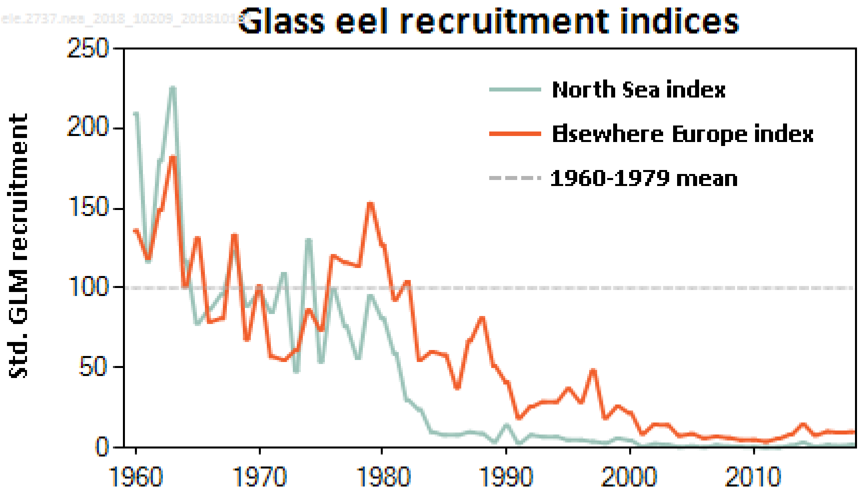

Fig. 3.8.3. Glass eel recruitment in the North Sea and elsewhere in Europe. From ICES (2018a).

Most research conducted on the elver stage is in fresh water systems, despite evidence that a large proportion of glass eels that enter the coastal areas of northern Europe never enter freshwater systems (Tsukamoto et al., 1998). One Danish study showed that elvers in a marine environment prefer coarse gravel substrate to finer gravel or sand substrates (Christoffersen et al., 2018). This raises concern to the aggregate extraction of coarse sediment (grus) where already 52.2% of the area of coarse sediment is estimated as lost in the inner Danish waters (Miljø og Fødevareministeriet, 2018).

3.8.2. Essential fish habitat for eel

- ***Spawning.*** The main spawning area/s is located in the Sargasso Sea.
- ***Adult.*** Insufficient knowledge of habitats for yellow and silver eel. Believed to be coastal muddy, sandy and coarse sediment areas.
- ***Juveniles.*** Insufficient knowledge of juvenile habitat in the coastal marine environment. Emerging indication of the importance of coarse gravel substrate (grus) being an important habitat substrate for juveniles.

3.9. Lumpfish *Cyclopterus lumpus*

3.9.1. General background

Stock structure

Very few studies have targeted this species. The Baltic Sea population is genetically distinct from the population in the Northeast Atlantic (Pampoulie et al., 2014). It is not known if there are further distinctions within the Northeast Atlantic population. On the one hand, a lack of differentiation between Icelandic and Norway samples indicates a broad distribution of the species. On the other hand, biological and tagging information indicate a sedentary species with spawning site fidelity suggesting the development of divergent species (Goulet et al., 1986; Whittaker et al., 2018). The possibility of small lumpfish populations with low genetic diversity suggests high vulnerability to over-exploitation (Whittaker et al., 2018).

Fisheries

Lumpfish are fished for human consumption in Danish waters. It is primarily ripe females that are targeted for their roe, which is sold as a substitute for caviar. Thus, the fisheries on this species is highly seasonal. In the last decade, this species has also been targeted for aquaculture, used as a cleaner fish for the salmon farming industry (Powell et al., 2018).

Life history stages

Adults perform extensive migrations but return during spring to the spawning sites to breed in the same area (Warner et al., 2012). They spawn in shallow waters along rocky coasts. After spawning the females move offshore while the males stay with the eggs until they hatch. After hatching larvae and juveniles live in coastal areas, among vegetation. After one year they move offshore and live semi-pelagically.

Spawning season and area. Ripe females appear in Danish waters around February-March where they seek shallow (1-5 m) hard-bottom (stones) waters (Powell et al., 2018). Hard-bottom with vegetation is an important habitat type for spawning (Mochek, 1973). The exact spawning locations are not documented but interviews with local fishermen have indicated stone areas to be breeding ground for lumpfish. The locations identified by fishermen for lumpfish most likely coincide with their breeding grounds as this fishery targets ripe females. However, without absence information this map is incomplete (Fig. 3.9.1), The presence locations indicated by the fishermen are off the north coast of Zealand, the east Jutland coast, north of Hals and the mid part of the Sound (Fig. 3.9.1) on the Danish side from around Humlebæk to around Saltholm (Fig. 3.9.2: Sørensen et al., 2016b). There are indications from tagging studies of homing behavior associated with breeding (Kennedy et al., 2014).

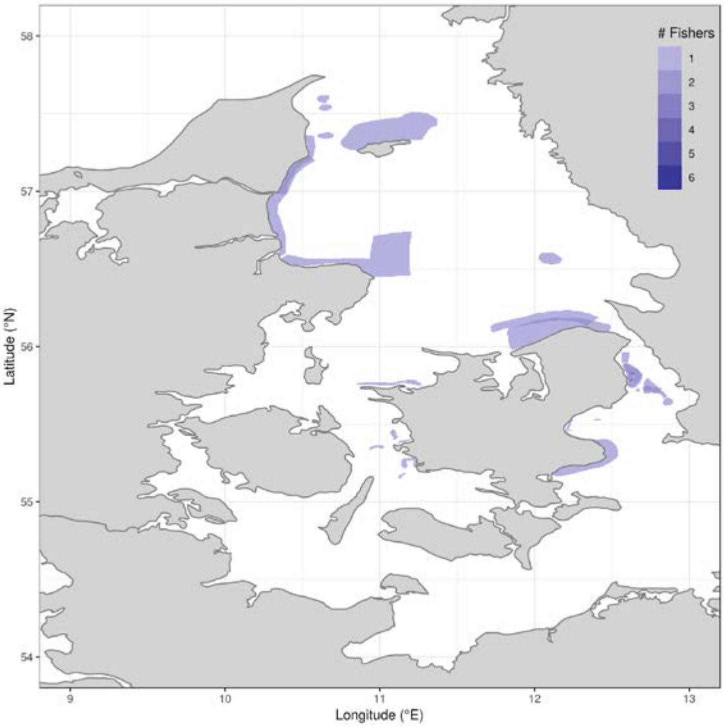

Fig. 3.9.1. Fishermen information on lumpfish occurrence derived from fishermen interviews. From: Støttrup et al. (2019).

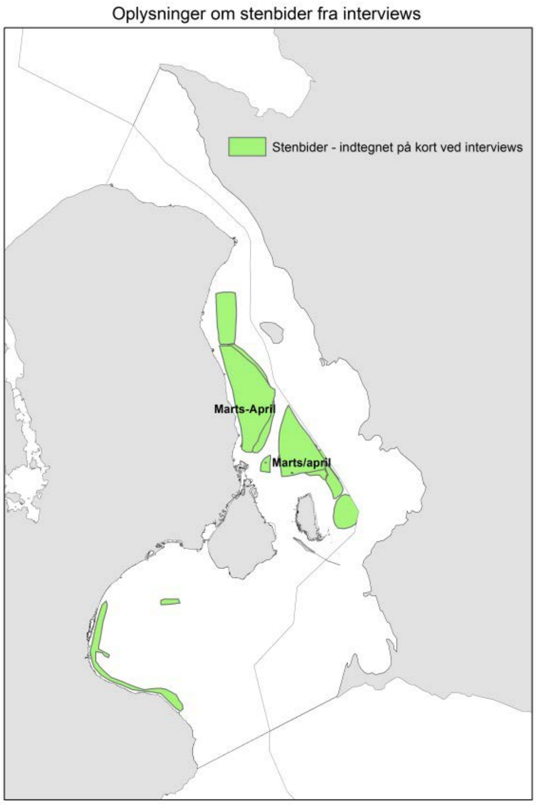

Fig. 3.9.2. Fishermen information on lumpfish occurrence derived from fishermen interviews. From: Sørensen et al. (2016).

Adults. In Skagerrak and Kattegat, lumpfish occur at higher densities around Skagen and in the northern and southeastern Kattegat (Warnar et al., 2012). Tagging studies indicate extensive movements with homing behavior to breed in the same area (Kennedy et al., 2014). From late-summer to early spring adult lumpfish live offshore semi-pelagically or benthically feeding on euphasiids, pelagic amphipods, jellyfish and small fish (Goulet et al., 1986).

Early life stages and juveniles. Eggs are protected by the male lumpfish until they hatch. The newly-hatched larvae remain in shallow coastal waters. Lumpfish larvae leave surface waters and adopt a bentho-pelagic existence once they reach about 5 cm in length (Daborn & Gregory 1983), at which time they may be found associated with floating or attached seaweed. They remain in the coastal environment until they are around one year old, after which they leave the coastal areas at around 6-8 cm in length. Little is known about lumpfish nursery habitats. A study in the Great Bay estuary, New Hampshire, USA showed lumpfish to utilize coastal habitats with threshold values of 9-22 °C and 22-34 salinity and were only caught in the outer parts of the Bay (Rackovan & Howell, 2017).

3.9.2. Essential fish habitat for lumpfish

- ***Spawning.*** Insufficient data. Fisheries locations indicate spawning grounds as ripe females are targeted for fishing. These are stony areas off the north coast of Zealand, the east Jutland coast north of the Hals and the mid part on the Danish side of the Sound.
- ***Adult.*** Insufficient data
- ***Juveniles.*** Insufficient data

3.10 Norway lobster *Nephrops norvegicus*

3.10.1. General background

Stock structure

There is little genetic variation between *Nephrops* populations in different areas (Johnson *et al.*, 2013).Benthic population size structure is linked to recruitment and size-selective mortality, as well as growth of individuals. Larval dispersal depends on hydrographic features and thus metapopulation dynamics of source area (surplus production of surviving offspring to own and other populations) and sink areas (no input of surviving recruits to the metapopulation) play an important role in recruitment.

Whereas *Nephrops* forage on the seafloor, the resting time is spent in its burrow. The burrowing nature of the species is a challenge in estimation population sizes and structures. Population analyses today are based on standardised Under Water Video Transect (UWTV) assessments of burrow-complexes visible on the sediment surface (ICES, 2009). Moreover, stock assessments are primarily conducted in fished areas, which are probably the most productive areas with medium to high density of individuals. Thus, population structures in non-fished areas are little known, as are the habitat preferences throughout its wider distribution (reviewed by Johnson *et al.*, 2013), including in the Kattegat and Skagerrak.

Fisheries

The *Nephrops* fishery in the Kattegat and Skagerrak is considered as biologically and economically sustainable for the stock (Frandsen, 2015). The fishery was MSC certified in 2014, however, assessment of the environmental sustainability of this demersal fishery regarding co-occurring sensitive species of sponges, sea pens, molluscs and tube-building crustaceans are currently undertaken.

In the Kattegat and Skagerrak area, a recent study based on at-sea-sampling data in fished areas showed that time of day, season, depth, temperature, year, trawl type and location all significantly affected the catch rates of *Nephrops* (Feekings et al., 2015).

In the Danish Economic Exclusive zone in the Kattegat and Skagerrak, *Nephrops* are primarily caught by bottom trawls as the target species of the most important Danish fishery in the area, with annual landings in 2016-2018 ranging between 3.5-

5.2 tones (in fresh weight) with values of between 228-265 mill DKK (~€29-35 mill). In the Swedish EEZ of the Kattegat and Skagerrak, *Nephrops* fisheries by Swedish fishers are conducted by stationary gears, such as creels (Frandsen, 2015).

The spatial distribution of the Danish *Nephrops* trawl fishery is fairly stable between years with the highest landings (and trawling intensities) occurring in the northern Kattegat (in the Vinga Trench) and on the Danish shelf and slope in the Skagerrak (see the example for 2016 in Figure 3.10.1).

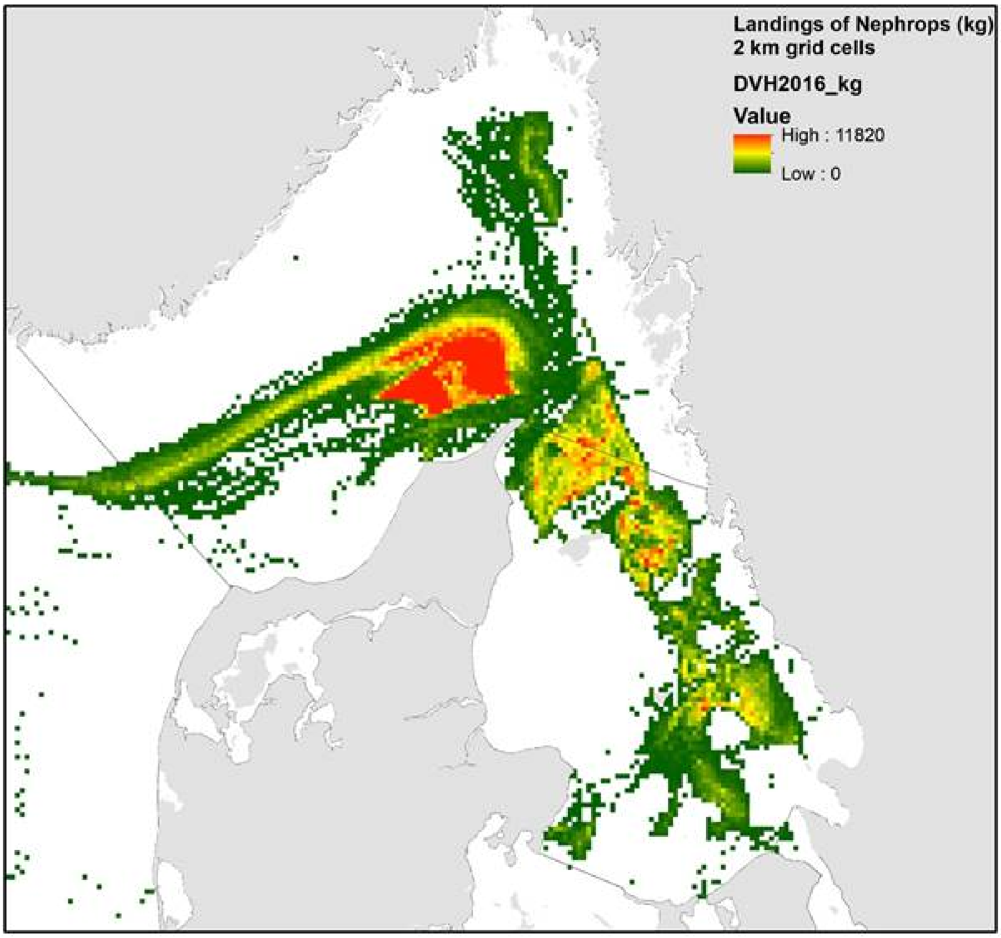

Figure 3.10.1. Distribution and density in landings (kg) of the Danish *Nephrops* fishery in the Danish Economic Exclusive Zone (EEZ) in the Kattegat and Skagerrak. The landings are based on data from the Vessel Monitoring System (VMS) and logbook information from vessels of and exceeding 12 meters of length.

Life history stages

Female reproduces annually (or biennially in the northern part of the geographic distribution) and carry out partial brood protection. After spawning of the fertilised eggs, the female carries the developing embryos attached to their abdominal segments and held by the pleopods. Embryo development last for 6-10 months sustained by yolk reserves, after which it hatches as a Zoea larvae. These larvae stay pelagic for up to 50 days, whereupon they settle on the seafloor.

Spawning season and area. The first reviewed of the reproductive biology of Norway lobster by Farmer (1974) has been updated more recently by Powell and Eiriksson (2013). *Nephrops* is dioecious and following maturity female growth rates decreases in comparisons with the same sized males, of the same age, which results in proportionally fewer females in the size groups larger than that of onset of fecundity of ~2.5 cm carapace length (Powell and Eiriksson, 2013). The reproductive cycle has been correlated with depth and geographic distribution accounting for climate and weather related parameters such as temperature and photoperiod (Powell and Eiriksson, 2013).

Adults. Norway lobster lives in the seafloor where it excavates complex burrows in soft sediments. Individual burrows may reach a depth of 2-5 meters into the sediment and have multiple openings at the sediment surface. More than 50 individuals may inhabit a single burrow complex. This species is one of the most important bioturbator within it’s geographic range on the continental shelf and slopes of the northeast Atlantic and adjacent waters.

Nephrops individuals may reach a length of 24 cm, although the maximum length appears to be density dependant. Maximum size differed between localities (in the north-eastern Atlantic), which indicates differences in carrying capacity among areas (Johnson et al., 2013). If such were the case, it would be guided mainly by competition for food (and/or space), and lower individual maximum sizes would be expected in areas with high numbers of recruits (sink areas) (Johnson et al., 2013). Norway lobster feeds on a variety of benthic fauna, including foraminifera, molluscs, polychaetes, crustaceans and echinoderms, as well as fish, and may also scavenge on carry-on or suspension-feed on plankton (Johnson et al., 2013).

The main predator of Norway lobster throughout most of its distribution is thought to be cod (Johnson et al., 2013). In deeper, muddy areas with high abundances of hagfish, *Myxine glutinosa*, these ghostly scavengers may be another important predator on Nephrops. The population structure and ecological importance of hagfish are however little known.

Habitat suitability for *Nephrops* within its geographical range has been modelled using MAXENT based on presence-only data from the OBIS database and environmental data from the Hexacoral database (see details in Johnson et al., 2013). Density of *Nephrops* was explained foremost by the combined silt and clay content of the sediment. In West of Ireland, density of Nephrops burrows were the highest in sediments composed of 40-80% silt and clay, although the actual density varied between sites of similar silt and clay composition (~0.4-1.25 burrows m^{-1}) (Campbell et al., 2009b). More sandy sediments are less cohesive and appeared unsuitable for burrow building. Thus, the distribution of the EUNIS level 3 habitats, A5.3. Sublittoral mud and A6.4. Deep-sea mud, in the Kattegat and Skagerrak may provide an indication of the distribution of potential Nephrops habitats in the area (Fig. 3.10.2).

However, as pointed out for the potential habitat model by Johnson et al. (2013), additional environmental parameters and biological processes are essential the habitat suitability for Nephrops. These included high salinity levels (salinity minimum ~31.8) and oxygen concentrations (minimum ~5.9 mg O_2 L^{-1}) (Johnson et al., 2013). Moreover, mean annual bottom temperature and mean depth and mean annual surface chlorophyll may delineate essential habitat boundaries in the northeast Atlantic (Johnson et al., 2013). The importance of these environmental parameters in determining the distribution of Nephrops habitats are even more pronounced in coastal areas of high topographic and hydrographic complexity, such as the Kattegat and Skagerrak.

Early life-stages and juveniles. The *Nephrops* larvae stages (Zoea I-III and Mysis I) may stay pelagic for up to 50 days, thus larvae may experience horizontal advection of up to ~50 km day^{-1} in the Skagerrak-Kattegat area before settlement on the seafloor as (postlarval Mysis II or PL1) (Powell and Eiriksson, 2013).

Recruitment patterns of *Nephrops* in the Kattegat are less well known, however, larvae are restricted to the mainly inflowing bottom layer of high saline (and lower temperature) water below the permanent pycnocline (typically at between ~15-25 meters depth). This may account for *Nephrops* typically occurring in deeper waters exceeding 25 meters in the Kattegat, with a few exceptions where high saline waters enters shallower, muddy trench systems, such as the Læsø Trench (where *Nephrops* occurs from as shallow as 16 meters and downwards). Thus, in the Kattegat, the stock likely recruits mainly by drifted larvae produced by populations in the northern North Sea and Norwegian trench-Skagerrak area (up to ~1000 km away), although part of the population may be of local origin. In areas, where the deeper water masses are retained locally, such as in the Skagerrak (and the Irish Sea, see Johnson *et al.*, 2013), *Nephrops* stock recruitment relies more heavily on locally reared offspring.

After settlement of Nephrops, individual growth may be reduced in areas of high population density, which indicates competition for space and food resources (Johnson et al., 2013). There appear to be an inverse relationship between growth (Bertalanfy L_∞ of carapace length) and density of males in several areas, thus supporting the hypothesis of density dependant suppression of growth at larger geographic scale (Campbell et al., 2009a, ICES, 2009).

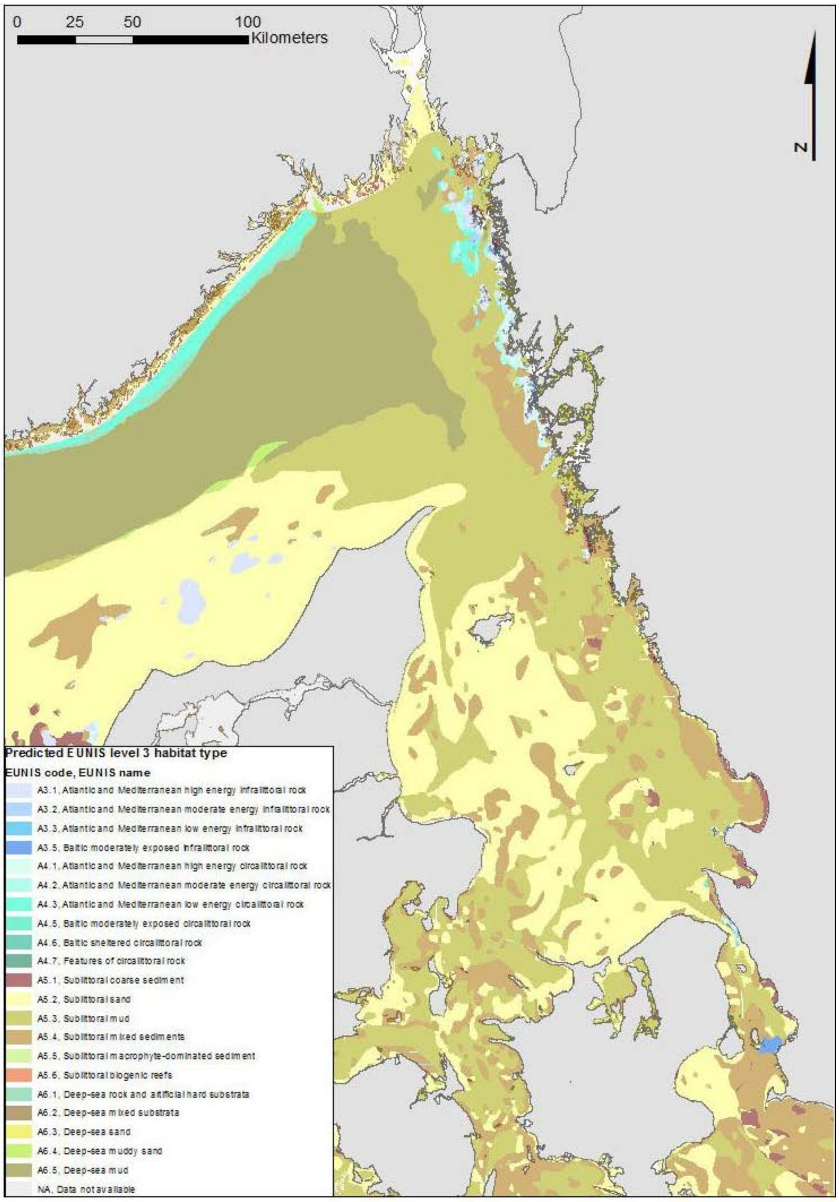

Fig. 3.10.2. Predicted distribution of the EUNIS level 3 habitats in the Kattegat and Skagerrak (data from EMODnet, https://www.emodnet-seabedhabitats.eu/access-data/).

3.10.2. Essential fish habitat for Norway lobster

- ***Spawning.*** Insufficient data. EUNIS level 3 habitats describe well the type of sediment preferred by Norway lobster. Furthermore, high salinity (>31) and oxygen levels > 5.9 mg O_2 L^{-1} were also requirements for suitable *Nephrops* habitat
- ***Adult.*** Same as for Spawning.
- ***Juveniles.*** Same as for Spawning.

4. Spatial Context of Habitat Maps

4.1. Assessment of habitat overlap between species

A map was produced including the adult stage distribution of cod, sole, plaice, herring and flounder and total population distribution of turbot and sprat and one that includes the juvenile population distribution of the former five species.

The aggregated maps with the adult population distributions are shown in Fig. 4.1. This includes the total population of turbot and sprat. The aggregated maps highlighted some hot-spot areas as being highly important for adult fish of several commercially important species (cod, sole, plaice, herring, flounder, turbot and sprat) during more than one season. The areas that are important are the southern Kattegat area, the northern Kattegat on the Danish east coast from around Læsø to Skagen, the Great belt Sea and the northern part of the Sound. These areas are marked in circles in Fig. 4.1a.

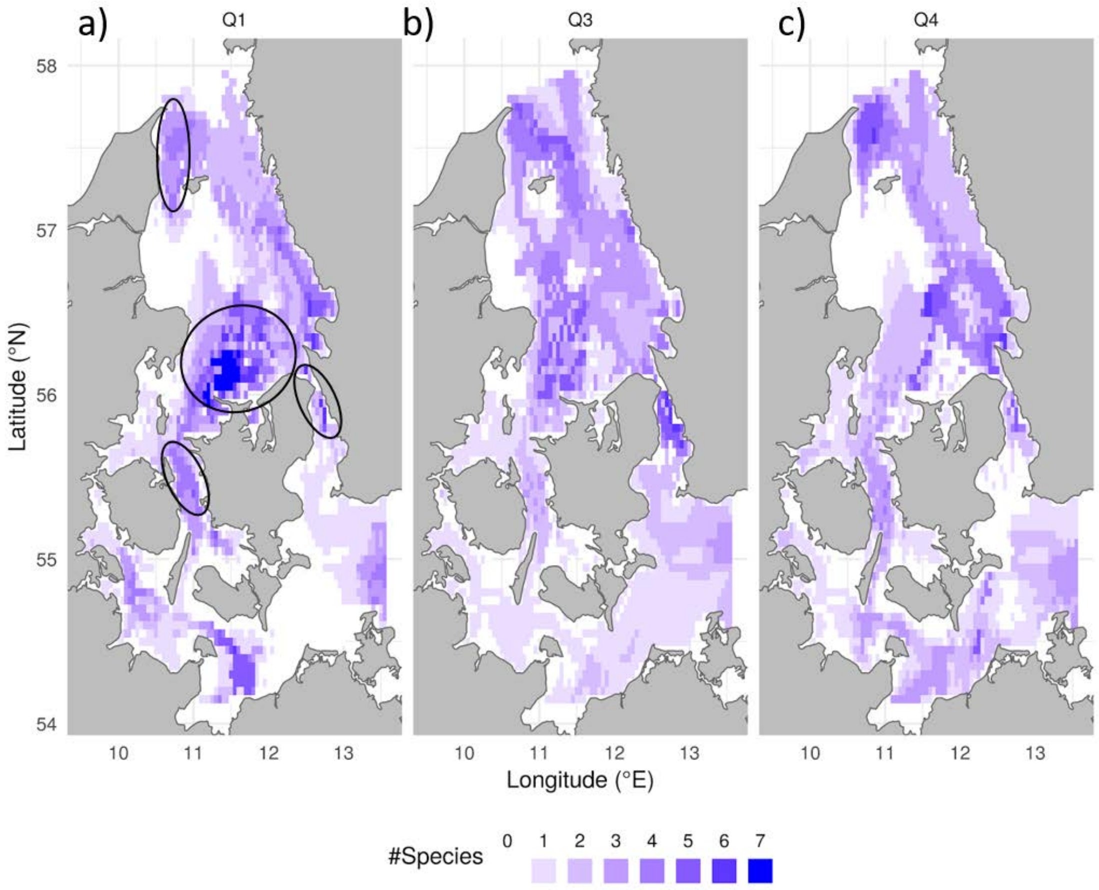

Fig 4.1. Overlap between the adult population distribution of cod, sole, plaice, herring and flounder and total population distribution of turbot and sprat in the first quarter (a: Q1: Jan-Mar), third quarter (b: Q3: Jul-Sept), and fourth quarter (c: Q4: Okt-Dec). Black circles in a denote the areas where fish habitats from several species and more than one season coincide.

The aggregated map with the juvenile population of cod, sole, plaice, herring and flounder is shown in Fig. 4.2. Some areas stand out as being utilised by juvenile fish of more than one species and in more than one season.

The multiple layers of juvenile distribution show the important areas as marked in Fig 4.2a: southern Kattegat including Sejerø Bay, the Great Belt and the northern part of the Kattegat off the Danish coast to be habitat areas for primarily age 1+ juveniles.

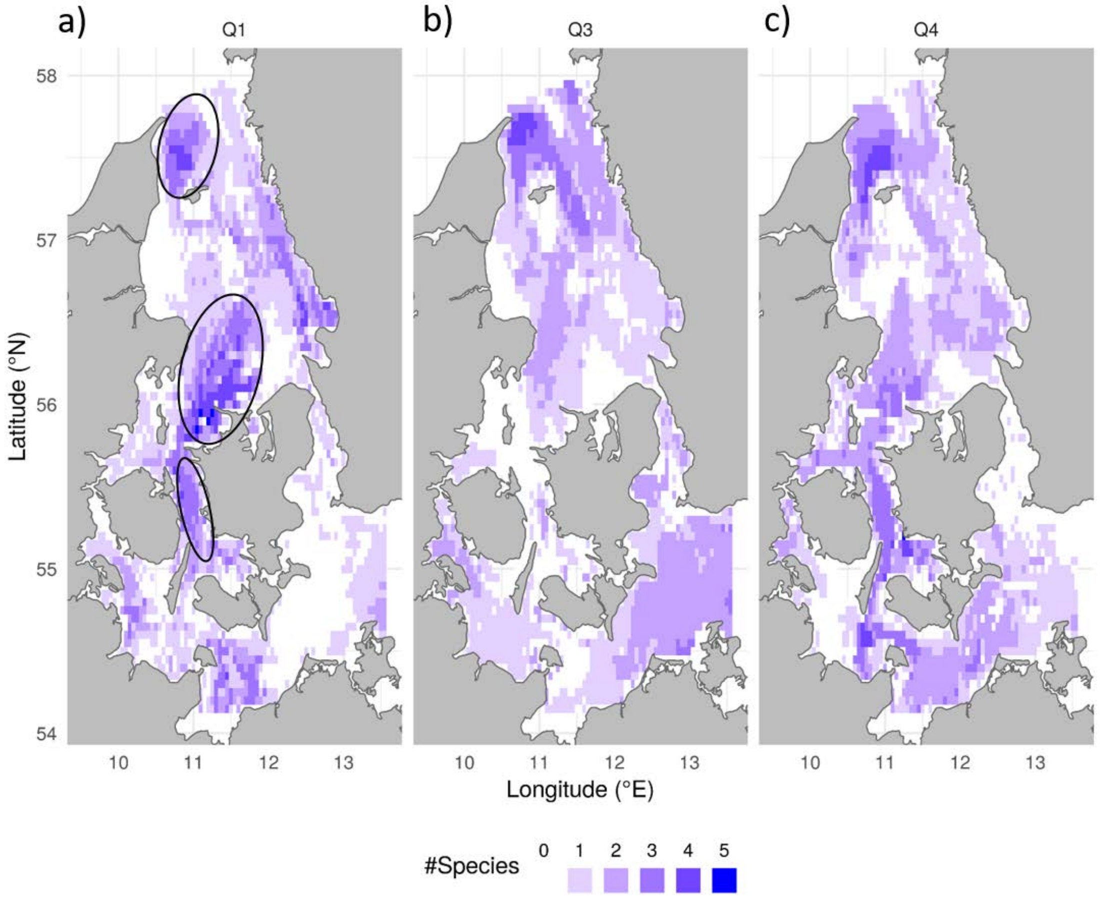

Fig 4.2. Overlap between the juvenile population distribution of cod, sole, plaice, herring and flounder in the first quarter (a: Q1: Jan-Mar), third quarter (b: Q3: Jul-Sept), and fourth quarter (c: Q4: Okt-Dec). Black circles in Fig. 4.2a denote the areas where fish habitats from several species and more than one season coincide.

The YOY juvenile maps for plaice, flounder and sole are not depicted in this report due to copyright issues but are shown in Brown et al. (2019). The survey area for that study was limited to coastal areas 0-4 m depth, so YOY habitats in fjords and estuaries or deeper than 4 m in coastal areas remain uncharted. The juvenile areas for plaice, flounder and sole in the depth interval 0-4 m appear all along the Danish inner coasts. Sole and plaice predominantly in the Kattegat area, flounder predominantly in the Belt Seas, and western Baltic. For plaice, the habitat maps indicated the mouth of large fjord systems such as Odense Fjord, Limfjord to be important nursery areas. As these areas are impacted by compound human activities and also affected by the consequences of climate change, measures are needed to protect these areas. It should be noted that YOY fish habitats in fjords and estuaries or deeper than 4 m in coastal areas remain uncharted.

4.2. Multiple Essential Fish Habitats

- ***Adults***. Important fish habitat areas for adults of multiple species: southern Kattegat area, the northern Kattegat on the Danish east coast from around Læsø to Skagen, the Great belt Sea and the northern part of the Sound (Fig. 4.1a)
- ***Age 1+ juveniles.*** Important habitat areas for juveniles of multiple species: southern Kattegat including Sejerø Bay, the Great Belt and the northern part of the Kattegat off the Danish coast (Fig. 4.2a)
- ***YOY Juveniles***. The maps are not depicted here due to copyright issues but are given in Brown et al. (2019). The juvenile areas for plaice, flounder and sole in depths 0-4 m are along the whole Danish inner coasts. Sole and plaice predominantly in the Kattegat area, flounder predominantly in the Belt Seas, and western Baltic. Mouth of larger fjord systems are important plaice nurseries.

4.3. Assessment of degrees of habitat overlap with other management measures

Superimposing the aggregated maps (Figs. 4.1 and 4.2), with Natura2000 sites (Fig. 4.3 and 4.4) showed not surprisingly a poor overlap since the Natura2000 sites are mostly designated for other conservation purposes than fish. The overlap with the fisheries management area just north of the Sound, “Kilen” coincides with the spawning area for cod and provides some protection also for other species, but does not capture the important multiple fish habitats uncovered in this study.

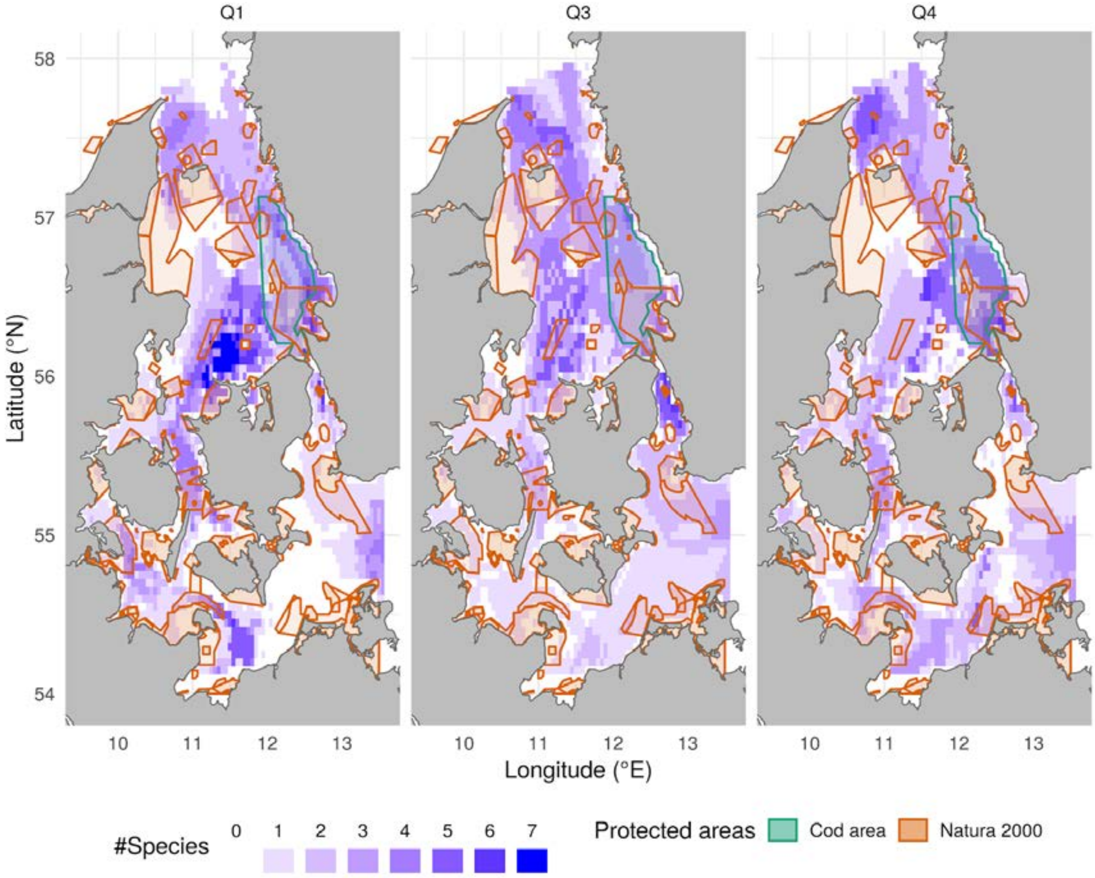

Fig 4.3. Marine protected areas (Natura 2000 and cod management area) overlayed to the aggregated adult species distribution map from Fig. 4.1. Q1: first quarter, Jan-Mar, Q3: third quarter, Jul-Sept, Q4: fourth quarter, Okt-Dec.

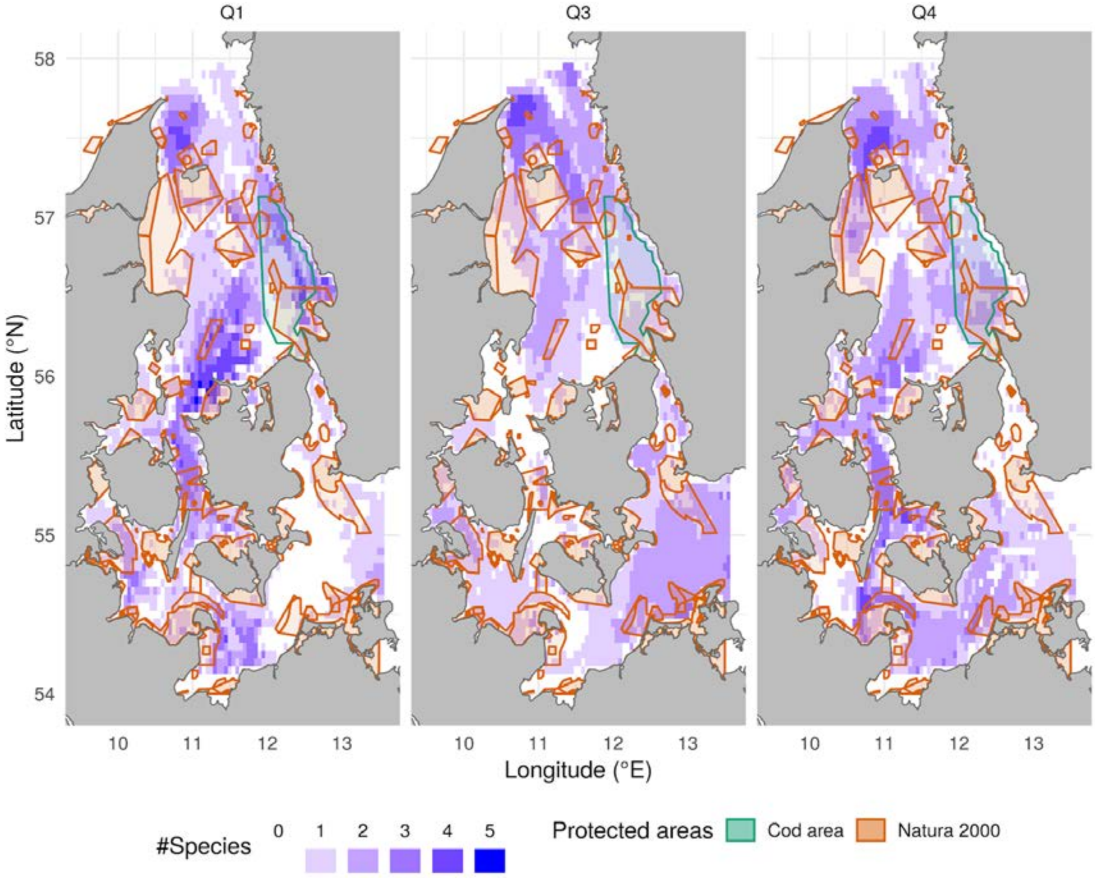

Fig 4.4. Marine protected areas (Natura 2000 and cod management area) overlayed to the aggregated juvenile species distribution map from Fig. 4.2. Q1: first quarter, Jan-Mar, Q3: third quarter, Jul-Sept, Q4: fourth quarter, Okt-Dec.

5. Conclusions

Significant developments were made in mapping essential fish habitat maps for different life-stages of commercially important species in the inner Danish waters. The additional data obtained through the two surveys conducted provided new data and information and it was possible to identify “hot-spot” areas important to several species.

Maps for juvenile and adult cod, plaice, sole, flounder and herring were developed. Also maps for turbot and sprat are shown. Error maps were developed to provide information on the “uncertainty” of the estimations.

New, additional data obtained through the unique summer KASU survey revealed differences in habitat use during summer for cod, plaice, flounder and sprat and helped to identify summer feeding grounds for these species. Spawning grounds were identified for cod, plaice and flounder that spawn in the winter season (Q1) but could not be identified for sole and turbot that spawn in May/June (Q2) due to lack of seasonal overlap between spawning season and timing of survey. The maps also showed the likelihood of overlap between adults and juvenile habitats in the different seasons, information important for fisheries management.

The juvenile coastal survey provided an array of data to support predictive modelling of habitats. Habitat quality maps were developed using fish abundance data and growth data obtained from otoliths for Young-of-the-Year (YOY) of three flatfish species, plaice, flounder and sole. Although it is well known that other species such as cod utilise coastal areas during the juvenile phase, little is known of their whereabouts as was confirmed by one of the conclusions of the Cod Workshop.

Peer-reviewed literature field studies were used to validate the interpretation of the predictive maps. Maps produced from the fishermen interviews were also used to validate interpretation. A workshop dedicated to cod allowed for the discussion of the cod maps and exchange of relevant information. several subsequent short meetings were held with colleagues who had specific expertise on some of the species.

The available data was also insufficient to map spawning grounds for herring and sprat. It was also not possible to map fish habitats for eel and lumpfish. Only fisheries data was available for mapping Norway lobster, which only indicates where the fishing pressure is for this species and can be likened to a “presence” map.

The aggregated maps with the juvenile and adult population distributions of cod, sole, plaice, herring and flounder and whole populations of turbot and sprat highlighted some hot-spot areas. These were the southern Kattegat area, the northern

Kattegat on the Danish east coast from around Læsø to Skagen and the Great belt Sea for both adults and juveniles of the species and in addition the northern part of the Sound for the adults. The YOY juveniles of plaice, flounder and sole are distributed in the shallow coastal areas all along the Danish coasts. Sole and plaice predominantly in the Kattegat area, flounder predominantly in the Belt Seas, and western Baltic. For plaice, the habitat maps indicated the mouth of large fjord systems such as Odense Fjord, Limfjord to be important nursery areas. As these areas are impacted by compound human activities and also affected by the consequences of climate change, measures are needed to protect these areas. It should be noted that YOY fish habitats in fjords and estuaries or deeper than 4 m in coastal areas remain uncharted.

Superimposing the aggregated maps with Natura2000 sites showed not surprisingly a poor overlap since the Natura2000 sites are mostly designated for other conservation purposes than fish. The overlap with the fisheries management area just north of the Sound, “Kilen” coincides with the spawning area for cod and provides some protection also for other species, but does not capture the important multiple fish habitats uncovered in this study.

Depth was one of the environmental parameters used in most models to describe a fish habitat, thus any human activity (e.g. aggregate extraction, dumping, coastal protection), or consequences of climate change that affect depth, may affect the habitat quality for the species.

Temperature and oxygen were also important environmental parameters for defining fish habitats for many of the examined species. Changes that affect these parameters (eutrophication, climate change) will also impact habitat quality.

Substrate maps in the inner Danish waters were not sufficiently detailed to be useful to map fish habitats, although the available data was included in the models and did define preferred habitats for turbot and juvenile flounder. More detailed sediment data, combined with improved sampling (e.g that cover hard bottom, vegetated areas) may help improve the habitat models and also inform on the relationships between fish habitats and sediment types.

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Technical
University of
Denmark

DTU Aqua
Kemitorvet
2800 Kgs. Lyngby

www.aqua.dtu.dk