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Habitat Suitability for Juvenile Flatfish of the Inner Danish Waters

Section for Ecosystem Based Marine Management

Elliot John Brown

PhD Thesis

Supervisor: Josianne G. Støttrup

Advisor: Ulf Bergström
Preface

This thesis was submitted in partial fulfilment of the requirements for the degree Doctor of Philosophy (PhD) at the Technical University of Denmark. The research presented in this thesis was carried out under the supervision of Senior Researcher Josianne Støttrup within the Section for Ecosystem Based Management of the National Institute of Aquatic Resources (DTU Aqua). Researcher Ulf Bergström of the Department of Aquatic Resources at the Swedish University of Agricultural Sciences acted as an informal advisor. An external research stay was undertaken at the University of Adelaide’s Southern Seas Ecology Laboratories in collaboration with Professor Bronwyn Gillanders and Dr. Patrick Reis-Santos.

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Liza, you have been a constant source of love and support. You have both grounded me and provided me new perspectives; you’ve encouraged and made possible a life of both new experiences and real meaning. Your ethic and determination has inspired me throughout our shared PhD experience; not least, during the business end of this thesis. I thoroughly look forward to whatever it is that next comes our way.

Finally, I dedicate this collection of work to my daughter, Nora. I can only hope to provide you with the opportunities and support that I have been lucky enough to receive.
English Summary

Coastal fish play important roles in ecosystem functioning in addition to their disproportionately large contribution to fisheries. By inhabiting coastal areas, fish are exposed to a wide range of human activities over and above their direct exploitation. This thesis illustrates the extent of these indirect anthropogenic impacts by reviewing evidence of human activities effects on exploited, coastal fish species from the northeast Atlantic, where ~92% of those species were impacted in at least one life-history stage. Furthermore, there is evidence of anthropogenic impacts acting on 78% of the juvenile life-history stages as they utilise coastal habitats.

With a clear need to understand the role that coastal habitats play in provisioning juveniles for replenishing exploited fish populations, this thesis continues by quantifying habitat suitability for juvenile flatfish of the inner Danish waters and establishing a method to trace their contributions to fished adult populations.

Two approaches are used to quantify habitat suitability, one obtains fish data and environmental data from a targeted survey of near-shore habitats, the other utilises existing surveys of juvenile fish and pairs it with modelled environmental data. Juvenile habitat suitability models are presented describing juvenile density and growth responses to changes in the physical environment. The results of both approaches are critically assessed and used to make interpolative maps of predicted habitat suitability across the inner Danish waters. The species-specific trends described in these models and predictions are discussed with reference to previous empirical findings from across their ranges. These two studies propose potential mechanisms creating the observed patterns of density and growth and discuss them in the context of current theories of density dependence and population connectivity.

The fourth work included in this thesis, documents the efficacy of otolith chemistry to differentiate between contiguous coastal juvenile habitats of the inner Danish waters, to enable future work on the connectivity between juvenile and adult habitats in this area as well as the neighbouring North and Baltic Seas.

Together, the four key studies that comprise the majority of this thesis provide both information for preliminary advice on the importance of juvenile habitats of the inner Danish waters, and a foundation for future work to further develop juvenile habitat models and describe the life-history connectivity of important fisheries species.
Dansk Resumé

Fisk i det kystnære marine miljø spiller en vigtig rolle i økosystemets funktionalitet i tillegg til deres ude af proportioner store bidrag til fiskeriet. Ved at leve kystnært, er fiskene eksponeret for en bred vifte af menneskelig aktivitet udover den direkte udnyttelse i fiskeriet. Denne afhandling beskriver først, med et review af litteraturen fra det nordøstlige Atlanterhav med fokus på de arter der rådgives om af ICES (International Council for the Exploration of the Sea), hvordan der er evidens for at 92% af kystnære fiskearter påvirkes af menneskelig aktivitet i mindst et af deres livsstadier. Yderligere er der evidens for at menneskeskabte påvirkninger har en effekt på 78% af de juvenile livsstadier hos fisk tilstede i kystnære habitater.

Med et klart behov for at forstå den rolle kystnære habitater spiller i tilførslen af juvenile fisk til opretholdelse af udnyttede fiskepopulationer, fortsætter denne afhandling med at kvantificere udbredelsen af habitater egnet til juvenile fladfisk i de indre danske farvande, og etablerer en metode til at spore deres bidrag til adulte fiskepopulationer der udnyttes i fiskeriet.


I et fjerde studie, dokumenteres anvendeligheden af otolit kemi til differentiering af sammenhængende kystnære habitater, egnet til juvenile fisk, i de indre danske farvande. Med denne metode muliggøres fremtidige undersøgelser af konnektiviteten mellem habitater egnet til juvenile og adulte fisk i det nordøstlige Atlanterhav samt Nordsøen og Østersøen. Samlet set tilfører de fire centrale undersøgelser, inkluderet i denne afhandling, information til indledende rådgivning om betydningen af habitater egnet til juvenile fisk i de indre danske farvande. Yderligere skabes der et fundament for fremtidig udvikling af modeller over sådanne habitater samt beskrivelsen af konnektiviteten i livsstadiene af vigtige fiskearter.
General Introduction

“Coastal fishes are better than pelagic ones for their feeding is more abundant and better... there exists a good blend of the hot and the cold in the coastal regions of the sea...”

- Aristotle, History of Animals, 598a2 (cited in Gancias et al., 2017)

Coastal fish
Coastal fishes are those which utilise coastal habitats during one or more developmental stage throughout their life-history (Kroodsma et al., 2018; Seitz et al., 2014). Fish habitats are deemed coastal where they occur below the high-water mark in semi-enclosed bays, estuaries, and fjords, but also along open exposed areas of the coast. In these open coast settings, where natural geographic enclosures aren’t so apparent, limits are often imposed based on bathymetry (Federal Geographic Data Committee, 2013), the distance from shore, the influence of terrestrial waters (Council Directive 2000/60/EC), or combinations of shared environmental attributes (Aquatic Ecosystems Task Group, 2012). Regardless of how their habitats are defined, coastal fish play important roles in ecosystem functioning and are valuable resources for humans. To help document and categorise the diversity and importance of these roles, they can be considered in terms of ecosystem services (Holmlund and Hammer, 1999).

Ecosystem Services of Coastal Fish
The classifications of ecosystem services are diverse and somewhat subjective (Hattam et al., 2015). Here I briefly describe some of the key services that coastal fish provide, in general terms, across two broad subcategories; namely ecosystem functions and ecosystem services (Costanza et al., 1997). I consider ecosystem functions as services provided within the community which contribute to the maintenance and continued productivity of the system. Alternatively, I consider ecosystem services as those which humans derive from coastal fish.

Ecosystem function
Coastal fish can play a direct role in ecosystem functioning as meso-predators of herbivorous, grazing organisms and as piscivores predating on those meso-predators. In these roles, the removal of fish can release pressure at either of these trophic levels thus initiating cascading
effects that drastically impact the ecosystem forming algal community (Leleu et al., 2012; Östman et al., 2016). Being relatively large and mobile, demersal fish can play a role in nutrient flux at the surface of the seafloor through sediment disturbance, or bioturbation (Yahel et al., 2008). These energy and nutrient fluxes can be extended to larger scales as mobile coastal fish make daily foraging migrations between productive shallow areas and more stable, deeper, coastal waters (Lefeuvre et al., 1999). These scales increase even further when considering energy and nutrient transport occurring as a result of migrations between different life-history stages; be they seaward (Deegan, 1993) or shoreward (Varpe et al., 2005). Simply by foraging at the coast, fish play a role in linking marine and terrestrial systems by accumulating energy and nutrients before being predated by terrestrial animals (Hentati-Sundberg et al., 2018). Diversity in coastal fish assemblages is accompanied by diversity in the ecosystem functions they perform but also the higher-level function of ecosystem resilience (Elmqvist et al., 2003; Worm et al., 2006). The loss of fishes and the functional services they provide, can lead to regime shifts which perpetuate lower abundances by making the habitat less favourable for those fish initially excluded (Rocha et al., 2014; Troell et al., 2005).

**Ecosystem services**

The collection of ecosystem functions that coastal fish provide are in and of themselves an ecosystem service, in that they maintain a system from which humans derive other services (Barbier et al., 2011). Coastal fish also provide more direct forms of ecosystem services to humans, some examples being the recreational value of observing them whilst diving or snorkelling (Gill et al., 2015), by providing information on ecosystem status and changes (HELCOM et al., 2018), and their position as culturally iconic species (Poe et al., 2014; Rönnbäck et al., 2007). The most commonly cited services provided by coastal fish are those linked to their direct exploitation; namely recreational fishing (Toivonen et al., 2004) and food provisioning through commercial and subsistence fisheries (Garcia and Rosenberg, 2010).

While the terminology used to identify and categorise them may change, the valuable roles that coastal fish play, both in their environments and in supporting human populations, are well documented.
Anthropogenic impacts on coastal fish

While many fish stocks are heavily exploited for the provisioning of food, coastal fish are, by nature of the areas they inhabit, closer to dense human populations which results in their disproportionate exploitation (Champbers, 1991 cited in Fodrie and Mendoza, 2006; Seitz et al., 2014). This proximity to human development also means that they are exposed to a wide variety of human activities (Airoldi and Beck, 2007). The effect of exposure to these activities are termed anthropogenic impacts and they often operate indirectly, via fish habitat rather than directly on fish, such as fishing gear reducing habitat complexity (Kamenos et al., 2004), excess nutrient run-off causing eutrophication and excess algal growth (Isaksson et al., 1994), or habitat loss to coastal development (Sundblad and Bergström, 2014). Such environmentally diffuse impacts are not mutually exclusive and interact with one another to increase the total impact (i.e. additive effects), to amplify each individual impact’s effect (i.e. synergistic effects) or to decrease the total impact (i.e. antagonistic effects) (Crain et al., 2008).

Management of coastal fish and their habitats

In recent history the mitigation of these direct and indirect anthropogenic impacts have been considered separately, with the direct exploitation by fisheries being managed independently of other environmental considerations (Guerry, 2005). Over the past two decades, calls for an “Ecosystem Approach to Management” (EAM) have emerged (Larkin, 1996), where the general underlying principle is of a more holistic context to the management of human activities within naturally variable systems. Proponents of EAM have come from both conservation and resource management backgrounds, which exemplifies some of the pluralist views that the approach seeks to integrate and ameliorate (Browman et al., 2004 and contributions therein).

At a policy level, the management of coastal marine resources often remains siloed but with some shared visions; exemplified by the European Union’s combination of the Marine Strategy Framework Directive, Water Framework Directive, and Common Fisheries Policy (Llope, 2016), as well as the United States’ combination of Magnuson-Stevens Act, and the Outer Continental Shelf Land Act (Harvey et al., 2017).

At an advisory level, a variety of methods to integrate the function of marine ecosystems and the fisheries they support have been proposed, and in some cases implemented, but with a large degree of variability in their complexity and co-ordination. Some examples of these approaches
are the inclusion of expert opinion and qualitative indicators of ecosystem function paired with quantitative fisheries advice for fisheries managers (Zador et al., 2017). With more data available some cases have been able to quantify and integrate environmental and anthropogenic drivers to predict potential future outcomes and present alternate future scenarios for consideration by managers of single species (Möllmann et al., 2014). In other circumstances, the overall theme of holistic assessment that is embodied in EAM has been readily adopted by researchers but took time to amass the relevant data and knowledge needed to inform EAM policies, especially with a lack of political direction (Llope, 2016; Österblom et al., 2016).

Whatever the political context, providing advice for EAM policy makers is a scientifically demanding task, requiring both a broad and a deep understanding of the natural and human elements of the system in question (G. S. Cook et al., 2014; Oates and Dodds, 2017; Samhouri et al., 2014). In order to establish the impact of human activities we must first understand the natural drivers of species distributions (Crowder and Norse, 2008). The complexity of these dynamic systems dictates that scientific understanding, and the advice it provides, can only be attained iteratively (Langton and Steneck, 1996; Steneck et al., 1997) and must openly recognise what it remains ignorant of, while continuing to support policy makers and managers (Auster et al., 1997; Litvin et al., 2018).

**Quantifying habitat suitability for fish**

To contribute to a broad and deep understanding of coastal ecosystems and the roles that fish play within them, we must be able to describe their habitat use and the environmental drivers of their distributions throughout their life-history. In this section I provide an overview of methods used to describe the relationships between fish and their environment, in terms of habitat suitability.

**Habitat suitability models**

The distribution of different species in space has long been of interest to humans, indeed even in prehistory Aristotle sought to explain why different fish species would enter estuaries while others would not (Ganias et al., 2017). Over time, defining the geographic limits to ranges have informed some of the most fundamental concepts in biology, such as the Wallace line dividing the
Indonesian archipelago and inspiring theories of natural selection (Wallace, 1863). Through the 19th and 20th centuries descriptions of different plants’ ranges were linked to environmental factors such as topography and soil type, and extended to map areas of “terminal community”, or potential habitat (European Environment Agency, 2014). This linking of individual environmental components to organism ranges is the beginning of what we today recognise as habitat modelling or Species Distribution Modelling (SDM). With the increase in computational power through the 20th and into the 21st century these methods were developed and applied to different domains, including the three dimensional habitats of pelagic ecosystems (Hobday et al., 2016; Hüsey et al., 2012; Planque et al., 2007). The application of SDMs in coastal settings is more traditional, in that it is often considered in two dimensions and linked to geographic features, rather than the dynamic movements of pelagic systems (Pittman et al., 2011). This location specificity is often discussed as a key limitation of the SDM approach, that it is a static description of habit use based on previous observations (Guisan and Zimmermann, 2000). Nevertheless, if the importance of a geographic location to a certain species is what is of interest, then the results of this approach quantify species specific habit suitability (Boyce et al., 2002), albeit with the caveat that this will vary in time with other elements of the environment (Litvin et al., 2018; Vasconcelos et al., 2014).

The rest of this thesis refers to the use of SDMs for quantifying habitat suitability as Habitat Suitability Models (HSMs). Before undertaking a project to create HSMs certain decisions need to be made, such as the modelling approach to be applied, which measure will represent habitat quality, what set of environmental features are relevant, which data sources are going to inform the model, and what statistical tools will be used to describe the relationships.

Modelling approaches

Before we consider the statistical tools to use in an HSM project, we must consider a more fundamental question of what we are trying to represent in a model. The trade-offs between describing reality, creating generally applicable models, and maintaining accurate descriptions of that reality have been well reviewed in Guisan and Zimmerman (2000).

The use of analytical models forgoes considerations of the variability observed in nature to provide precise descriptions of generally applicable phenomena, some examples being models of density-dependent populations sizes (MacCall, 1990) and variation of this phenomenon at different life-history stages (Andersen et al., 2017). Analytical models are useful for developing understanding
of the range of possible drivers that may be acting in a system; however their simplicity limits their ability to provide relevant descriptions of real world cases. It is this limitation that can lead to case-specific challenges to the theories derived from them (e.g. Jutfelt et al., 2018; Pörtner et al., 2017).

In order to move closer to reality, we could consider the use of mechanistic models; those that utilise cause and effect relationships between individual aspects of the environment and a species’ ability to grow and survive (D. G. Cook et al., 2014; Schram et al., 2013). These relationships are usually modelled from highly controlled experimental set-ups in order to establish the cause and effect relationship, independent of other confounding environmental conditions (Teal et al., 2018). These same conditions make possible the observation of responses to environmental conditions outside of ranges experienced in nature, and thus a fuller range of possible responses can be observed (Chabot and Claireaux, 2008). Different environmental conditions (Christensen et al., 2018; Lavergne et al., 2015) and different fish states (Brown et al., 2011; Bucking et al., 2012; Killen, 2014) can be varied together to provide descriptions of their interactions, but such interactive effects are hard to scale experimentally. For species with extensively studied physiological responses to a range of environmental variables, the combination of all of these responses can be combined to describe the overall effect on a fish’s metabolic capacity for growth and reproduction (Marras et al., 2015). For cases where these eco-physiological relationships are poorly known, or the species aren’t suited to laboratory experimentation (Araújo and Peterson, 2012), general features of a species from observation can be substituted in to generic frameworks that have been established across a range of species (such as the DEB model; van der Meer, 2006).

The result of either of these approaches can be coupled with environmental data to predict habitat suitability in the form of maximised biomass, or individual growth and survival from individual based models (Martin et al., 2012; Teal et al., 2012; Van De Wolfshaar et al., 2015).

To build models that most closely approximate reality, but may not be generally applicable, we employ empirical models; sometimes called statistical models. These models are informed by observations of species, and the environmental conditions, in their natural habitats (Le Pape et al., 2014). In these circumstances observations of the environment vary of their own accord and so empirical models use probabilistic methods to identifying the strongest co-variation between environmental variables and the selected response (Lecours, 2017). This is in contrast to the
attempts of analytical or mechanistic models to establish general rules or causal relationships (Guisan and Zimmermann, 2000). Because of empirical models’ reliance on natural environmental variation, sampling design is important to ensure the complete range of environmental conditions likely to be experienced by the species in question are covered (Austin, 2002). Because empirical models are by design, specific and not general, their use in prediction should be limited to the extent of the observations used to inform them, such that predictions of species distributions should only ever be interpolative (Guisan and Thuiller, 2005). While the resulting models do not provide evidence of causative effects, the relationships they describe can be compared to mechanistic effects determined by other studies to aid in the biological interpretation of the outcomes.

The three model types described above, namely analytical, mechanistic and empirical, provide useful terminology for the comparison of different approaches; however, these are discrete classifications of what is, in reality, a spectrum of approaches. Categorising and describing general methodological angles in this way helps us to consider our own approaches with reference to what we are trying to achieve or represent with our own models. The rest of this thesis deals primarily with empirical type models.

Proxies for suitability

The most fundamental decision in creating HSMs is, perhaps, the selection of which measure will represent a species’ response to changes in the environment, and hence represent habitat suitability. The simplest measure is that of presence; a reflection of the environmental conditions that are found across the entire species’ range (Elith et al., 2011). Depending on the methods of observation that are employed, presence is usually paired with observations of absences which provides information on exclusionary conditions of the environment (Guisan and Zimmermann, 2000; Li et al., 2017). If observation effort is standardised, then simple binary responses can be extended to the more information rich abundance, or count data (Blanchard et al., 2007; Sundermeyer et al., 2005). However, using the presence and abundances of individuals assumes that the population being surveyed is large enough to utilise all areas of high-quality habitat, and will only move to low quality habitats in low numbers to avoid some form of density dependence (MacCall, 1990). This assumption is based on the MacCall basin hypothesis and it is unlikely to hold for heavily exploited species with depleted populations (Morfin et al., 2012). Furthermore,
there are many other reasons why organisms may or may not inhabit some component of potential habitat, such as barriers to dispersal (Stoner, 2003; Stoner et al., 2001). So while fish are likely to move and disperse into habitats with favourable conditions, the use of presence/absence and abundance is an imperfect representation of habitat quality.

Alternative measures have been adopted that are truer representations of habitat quality because they are linked to the survival and fitness of the individuals inhabiting them (Vasconcelos et al., 2014). The ability of individuals to survive and reproduce is fundamental to their fitness and so is an ideal representation of habitat suitability, however, in field observations, survival rates can be difficult to determine as migration confounds abundances observed during repeated sampling for cohort size (Jager et al., 1995) or in tagging studies (Barbour et al., 2012; Sparrevohn et al., 2002). Intensive sampling of isolated populations may overcome such limitations (Fodrie et al., 2009), especially when paired with density by age data from otolith microstructure analyses (Geffen et al., 2011). Tethering experiments have inherently unknown impacts on predator avoidance (Manderson et al., 2004) and so mortality rates are linked to predation and can be unreliable.

Growth is another determinant of fitness, especially in juvenile fish, as larger sizes reduce predation and thus increase survival (van der Veer and Bergman, 1987; van der Veer, 1986). Furthermore, fish that grow fast reach maturity sooner (Kjesbu and Witthames, 2007), and allocate more energy into reproduction sooner (Barneche et al., 2018). The use of cohort length frequencies can provide information on growth rates, but similar to mortality, migration can have confounding effects. Alternative measures of growth are possible from the field, such as RNA:DNA ratios as proxies for cellular capacity for work and hence growth (Ciotti et al., 2010; Gilliers et al., 2004; Vinagre et al., 2008), and the incremental widths of otolith growth (Al-Hossaini and Pitcher, 1988; Stevenson and Campana, 1992).

In fish, reproductive success of individuals is difficult to determine given the often broadcast nature of spawning, however the survival rate of fertilised eggs can be used to reflect the suitability of spawning habitats, whether they be pelagic (Hüssy et al., 2012; Petereit et al., 2014; Planque et al., 2007) or demersal (von Nordheim et al., 2018).

While abundances can provide information on the degree of habitat utilisation, without evidence that the local population is saturating its available habitats (e.g. in Fodrie and Levin, 2008; Sundblad et al., 2014), as a single measure it can inaccurately represent habitat suitability. Where
logistically possible, other measures that are linked to demographic rates such as survival, growth and reproduction, should also be used as response variables to attain a fuller representation of habitat suitability (Vasconcelos et al., 2014).

**Explanatory variable selection**

In addition to the selection of an appropriate response, the environmental variables that are selected for inclusion in the initial full models are important, not least because the inclusion of arbitrary predictors can introduce spurious correlations (Le Pape et al., 2014). When this occurs, the effect of the spurious correlation persists, undetected, through model selection and can have substantial effects on predictions of habitat suitability (Lecours et al., 2016).

Quantified descriptions of the physical, or biological, environment can be classified as having direct effects on fish physiology (e.g. temperature) or acting indirectly (e.g. nutrient load driving productivity and prey availability) (Austin, 2002). Where possible, predictors with a known mechanistic effect on fish growth and survival should be included in the full model, so that more inference can be drawn from the final model (Austin, 2007). Conversely, indirect predictors can often greatly improve model fits and hence improve the precision of their predictions. Here, even within the realm of the empirical approach (discussed above), including predictors with proven mechanistic effects can increase the generality of the models while the trade-off of including indirect drivers is an increase in the model’s precision but limiting its predictions to within the extent of the input data (Guisan and Zimmermann, 2000).

The more mechanistic an empirical habitat suitability model becomes, the more its predictions represent the potential habitat (or fundamental niche) of that species. Alternatively with little understanding of the mechanisms by which predictors act, predictions of habitat suitability models will describe only the realised habitat (or ecological niche) (Guisan and Thuiller, 2005). Interpreting the extent to which predictions represent potential or realised habitats depends on the set of explanatory variables that are retained in the final model and the degree to which the mechanism of each variable’s effect on the response is, or is not, known.

**Data sources**

Often the explanatory variables that are included in model fitting are determined by their availability, or by the resources required to collect them in the field. While being grounded in realistic constraints placed on researchers, there are different limitations of different data sets,
that when used, should be acknowledged. Where environmental data was not collected concurrently with the species of interest, the use of modelled hydrographic data, similar to the bioclimatic maps of the terrestrial realm, is common practice. The modelled nature of the data extracted from these data sets means that predictors have inherent spatial uncertainties such as interpolation errors or poor/uneven sampling resolution (Guisan and Zimmermann, 2000) in addition to thematic uncertainty of their own (Lecours et al., 2016; Moudrý and Šímová, 2012). Methods to combine these different levels of uncertainty and to properly represent their effects as they are propagated through modelling and prediction are poorly developed (Lecours et al., 2015). However, an interim solution that has been proposed is to use publicly available, or published and well described data, so as to be as transparent as possible about the potential sources of error (Lecours, 2017).

Relevant scales
The effect of scale has long been studied in both ecology in spatial sciences (Guisan and Thuiller, 2005; Levin, 1992). When trying to model potential habitat for a species using an empirical approach, spatial scales should include the full range of potential levels for each explanatory variable (Le Pape et al., 2014). These full ranges may only exist across different seasons and possibly only on the scale of decadal meteorological phenomena (Lecours et al., 2015). In reality, the appropriate scales are defined by the species and the system being modelled (Graf et al., 2005). Researchers should therefore consider that the effects of environmental drivers vary across multiple scales (Buhl-Mortensen et al., 2015) and while selecting an appropriate scale for the research question at hand is important (Johnson et al., 2013), investigating these phenomena at multiple scales provides a deeper understanding of habitat use (Litvin et al., 2018) and can improve models’ predictive power (Pearson et al., 2004; Thuiller et al., 2004).

Statistical approaches
The range of statistical tools available for modelling habitat suitability was recently well reviewed by Lecours (2017), where he also demonstrated that the choice of tool can have significant impacts on the outcome of predicted habitat suitability. However, there are no universal decision rules for selecting which tools to employ (Dixon Hamil et al., 2016), probably due to ambiguity from studies that report no discernible way to pre-select the most accurate modelling approach (e.g. Bučas et al., 2013; Elith and Graham, 2009). The current situation requires that researchers
review the available tools and determine which tool best matches their understanding of the system being modelled and the desired outcomes (Austin, 2002).

Sometimes this decision is restricted by the data, an example being where presence only data is used as a response (Elith et al., 2011). Additionally, in modelling count data, a statistical framework that can accommodate non-gaussian response distributions is essential, because count data regularly follow a Poisson-like distribution. Here, I use “poisson-like”, because some species are rare, some are more likely to cluster, and sampling techniques are often imperfect in their detection of all individuals, all of which are factors leading to systematic deviations of count data away from a Poisson estimating distribution (Guisan et al., 2002). To accommodate this, statistical methods for modelling habitat suitability from count data need to be flexible and able to accommodate parameters explaining data traits such as over-dispersion and zero-inflation (Brooks et al., 2017). Where studies are sampling over seasons and years, it is important to include methods that can represent the cyclical nature of phenological patterns of distributions (Teal et al., 2018) and if sites are repeatedly sampled, then statistical tools that can represent these repeated measures need to be selected (Bolker et al., 2009). An alternative to selecting a single approach is to undertake multiple analyses use an ensemble approach to incorporate predictions, but this approach fits far to the empirical end of a mechanistic-empirical continuum (Bučas et al., 2013; Loots et al., 2010; Robert et al., 2016).

Whichever statistical framework is applied, there is broad consensus that model validation be used to describe a model’s predictive ability (Le Pape et al., 2014). Approaches can range from including the collection of test data in the sampling design, fitting and selecting models to a subset of a dataset and testing against the remaining data, or fitting and selecting models based on an entire dataset and subsequently refitting the selected models to subsets of training data before predicting test data (Radosavljevic and Anderson, 2014). Because ecological data are often resource-intensive to collect (Jaeger, 2006), the latter of these examples is most commonly employed in the validation of habitat suitability models. Because these datasets are often large, it can be computationally expensive to undertake exhaustive cross validation, whereby the entire dataset is used as test data, that the model predicts naively, either individually or as part of a group (Valavi et al., 2019). Alternative methods use re-sampling from the data to extract representative samples for testing, without having to test all data points, reducing computational
time. Divisions of training and test data are derived, multiple metrics of the resulting predictive precision and accuracy should be reported (e.g. bias, measures of error, and measures of correlation between predictions and observations), as using only a single metric only provides a narrow insight into how the model performs (Pearce and Ferrier, 2000).

While there are many approaches and methods to be considered in planning to establish and use habitat suitability models, there is a large focus on developing guidelines and accessible tools for ecologists, from the spatial sciences. Updates to these methods and their proper use should be followed closely, and warnings heeded, in the preparation of new modelling and mapping projects.

Coastal habitat as juvenile fish habitat

Paradigms in juvenile fish habitat

It has long been known that juvenile fish can be found aggregating in shallow coastal areas, but real research interest in the biology of these early life-history stages only developed in the 20th century, as the role of juveniles in supplying fisheries became of concern (Browman, 2014). The focus of much of this work has been on heavily exploited species with life-history strategies that see juveniles concentrate in specific habitat types separate from adults (Beverton, 1995; Iles and Beverton, 2000). This can be typified by the European plaice (*Pleuronectes platessa*) (Gibson, 1999), whose life-history strategy is similar to many other flatfish and coastal fish, albeit with different timing and habitat requirements (Rijnsdorp et al., 2009). Adult plaice are found in deeper coastal shelf waters where, in winter, they spawn pelagic eggs. These eggs move passively with ocean currents and vertically with density gradients. This passive behaviour continues post-hatch with early larvae, but shifts into the active use of vertical migrations to utilise different tidal flows to move toward shallow, near-shore habitats with soft sediments. At this stage a period of metamorphosis coincides with the juvenile fish settling out, that is it becomes more closely associated with the seafloor, which occurs in spring or summer. During the remainder of the summer period, juvenile fish feed and grow in these shallow habitats before moving offshore the following winter. This pattern of spending spring and summer in shallow, near-shore habitats and
winters in deeper waters continues for another one or two years before the juvenile fish recruit into the adult population, remaining mostly in deeper waters (Gibson, 2005).

Early work focussed on explaining the reasons for variability in the number of new recruits joining the adult stock and quickly differentiated between the processes acting on pelagic eggs and larvae and those acting on settled juveniles in benthic near-shore habitats (Leggett and Deblois, 1994; van der Veer, 1986; van der Veer et al., 2015). It has been established that, for most species with the above life-history, the growth and survival of pelagic stages varies greatly from year to year due to large scale fluctuations in hydrography and meteorological forcing (Duffy-Anderson et al., 2014; Horwood et al., 2000). The comparatively stable supply of recruits, in contrast to the large inter-annual variation in the number of settlers arriving into juvenile habitats, is attributed to regulating processes occurring in juvenile habitats (Iles and Beverton, 2000; van der Veer et al., 2000).

Because of the regulating role that juvenile habitats play in governing the number of fish recruiting into a fishery, their importance was recognised by researchers and policy makers alike. Identification of nursery areas as essential fish habitat led to many areas of coastline being labelled essential, due to the mere presence of juvenile fish (Minello, 1999). This broad classification has been refined over time, starting with developing a functioning definition of what a nursery area might be. Beck et al. (2001) provided a sensible definition, stating that “nurseries” are those areas of juvenile habitat that contribute a greater number per unit area of recruits into an adult stock. While intuitive, this definition overlooks the importance of scale. Dahlgren et al. (2006) expanded on this theory to describe “effective juvenile habitats” as those that contribute a greater proportion of the total recruits to a population, independent of the juvenile density. This definition recognises that habitats with low densities of juveniles, but are abundant, may contribute the majority of recruits to support and maintain adult populations.

Both of these definitions provide a nice, intuitive framework for identifying habitats and areas of importance but they are also limited, in that they define importance solely by the contribution of habitats to local fisheries, ignoring both the regulating mechanisms acting within these habitats and the other ecosystem functions and services which they provide. This criticism, led by the work of Sheaves et al. (2015) and Nagelkerken et al. (2015) once again brings the integration of resource
management and conservation to the fore, by illustrating the different approaches researchers have taken to inform ecosystem approaches to management (Litvin et al., 2018).

**Conditions and processes in juvenile flatfish habitats**

While the definitions being developed may have glossed over the regulating mechanisms acting within juvenile habitats, fisheries researchers and ecologists have not. A large body of work has been accumulated looking at the different conditions and processes that act within juvenile habitats many of which focus on flatfish species. The conditions influencing juvenile growth and survival, and hence recruitment, can be categorised into the physical and biological elements of the environment, while the key processes occurring can be classified as density dependence and connectivity.

**Physical conditions**

The physical conditions in juvenile habitat have typically been used to define them; “shallow” and “near-shore”, describe both the bathymetry and the degree of terrestrial influence that were identified early-on as characteristic of habitat for juveniles of many species (Riley et al., 1981; Zijlstra, 1972 - cited in Zijlstra et al., 1982). The relationship between size and depth for many flatfish species has been well documented (Pihl, 1989; Riley et al., 1981), however depth’s influence on growth and survival is indirect, with the extreme shallows being described as both a refuge from predation (Manderson et al., 2004) and highly productive prey-rich areas (Chesney et al., 2000; Le Pape et al., 2007). Being ectothermic, the environmental temperature dictates, to a large extent, the metabolic condition of juvenile fish. While extremes of temperature can lead to death or exclusion from an area, within their tolerances, temperature impacts juvenile fishes’ ability to both consume and digest food, but also their cellular capacity for growth (Petitgas et al., 2013; Schram et al., 2013; Vinagre et al., 2013). There is some evidence that flatfish can behaviourally regulate their body temperature, avoiding the extremes of large fluctuations experienced in the shallows, by burying in the more stable sediment (Ziegler and Frisk, 2019). This ability to bury also aids in flatfishes’ predator avoidance (Kristensen et al., 2014), thus a habitat’s sediment type also plays a role in their survival (Gibson, 2000). Being found close to the coast and to terrestrial sources of water, the salinities that juvenile flatfish experience are also variable, relative to deeper waters. Fishes’ dependence on gas exchange with waters of varying salinities requires a degree of physiological tolerance or behavioural avoidance (Bos and Thiel, 2006),
however when avoidance is not possible, juvenile fish must incur an energetic cost to maintain an osmotic balance which can reduce their scope for growth (A. K. Andersen et al., 2005; Augley et al., 2008). Furthermore, coastal waters are not always well oxygenated, and where hypoxia occurs, it may limit juvenile flatfishes’ scope for growth both directly (Chabot and Claireaux, 2008), and indirectly by limiting movement and their ability to forage (Tallqvist et al., 1999).

**Biological conditions**

The community that juvenile flatfish are part of also determines their ability to survive and grow. The presence of organisms that create a lot of structure can exclude juvenile flatfish from shallow nearshore habitats where they restrict their ability to forage and bury (B. S. Andersen et al., 2005; Wennhage and Pihl, 1994). As newly settled juveniles, flatfish diets are primarily comprised of small crustaceans, worms and bivalve siphons (Aarnio et al., 1996 and references therein; Beyst et al., 1999), however these prey exist in different densities and as different species in different habitats. While individuals can select for their preferred prey (Haynes et al., 2011), the make-up of the local in- and epifauna determines prey-availability (B. S. Andersen et al., 2005; Wyche and Shackley, 1986). These differences in available prey influence the foraging efficiency and digestibility of juvenile fish diets, ultimately impacting on the energy they have available for growth (Ciotti et al., 2013). Whilst being predators themselves, the presence and abundance of juvenile flatfishes’ own predators has a direct impact on their survival (Bailey, 1994), but also their ability to forage and hence their growth (Maia et al., 2009).

**Density-dependent processes**

Species such as flatfish experience a large reduction in their potential habitat as they transition from pelagic larvae to settled, benthic juveniles. They move from a three-dimensional pelagic habitat, unbounded by bathymetry, to a two-dimensional benthic habitat which is further restricted to shallow coastal areas. This period in their life-history is described as a period of concentration (Beverton, 1995), during which density-dependent process act to reduce fluctuations in the size of the cohort from earlier life-history stages. For juvenile life-history stages experiencing concentration, density-dependent processes can act directly via mortality or indirectly through decreased growth rates to reduce the population size. It has been shown for plaice that, early in the juvenile growth season when settled juveniles are smallest and most susceptible to predation (Ellis and Gibson, 1997), higher densities lead to higher mortality, most
likely due to increased predation (van der Veer, 1986; Wennhage, 2002). This positive relationship between density and mortality indicates that in years of large settler supply, cohorts of juvenile flatfish will likely suffer higher mortality in juvenile habitats. The fact that this is most likely to occur early in the juvenile growth season reduces the competition for food later in the juvenile growth season (Le Pape and Bonhommeau, 2015). This does not, however, exclude food-limitation as a density-dependent process; early in the settlement period, the effect of food limitation reduces growth rate, resulting in a prolonged period of higher predation. Furthermore, if predation is reduced over any particular period, then the early occurring density-dependent mortality won’t occur and may give way to sporadic episodes of density-dependent growth limitation, which is observable throughout the summer growth period (Nash et al., 2007).

Connectivity processes
Before density-dependent regulation is to act on settled fish in juvenile habitats, settling larvae need to be able to reach them. That is, there needs to be connectivity between the habitat of the larval life-history stage and the juvenile habitat. Because of the predominantly passive nature of the egg and early larval dispersal (Bergman et al., 1989), the degree of connectivity between spawning and juvenile habitats is dependent upon their proximity, the local hydrography and egg and larval development characteristics (Hinrichsen et al., 2001). This degree of connectivity can determine the rates of settler supply to juvenile habitats (Wennhage et al., 2007) but also the relative supply from different spawning populations. This has been shown to create differing degrees of dependence on local or more distant spawning aggregations (Hufnagl et al., 2013; Petereit et al., 2014; Rochette et al., 2012). This period of interconnectivity is also an important dispersal period between populations (Duffy-Anderson et al., 2014) acting to increase or limit gene flow and hence influence rates of local adaptation (Diopere et al., 2018). These same rates of genetic differentiation have been used to show that even in relatively open coastal systems, certain areas of juvenile habitats can be interdependent with local spawning stocks, increasing their relative importance when compared with the total potential juvenile habitat across the species range (Cuveliers et al., 2012). Independent of the source, rate of settler supply is an important aspect of juvenile habitat suitability, as it dictates the habitat’s production of recruits (Nash et al., 2007). Following settlement the habitat conditions and density-dependent processes described above will act to produce a number of potential recruits, the migration of these large
juveniles out to adult habitats determines the actual recruitment contribution from any one juvenile habitat or habitat type (Beck et al., 2001; Dahlgren et al., 2006). This connectivity of the juvenile habitat to adult populations is mediated by the species’ intrinsic dispersal capability relative to any bathymetric and hydrographic barriers (Gillanders et al., 2003). Natural tags, such as otolith chemistry, can be used to characterise juvenile habitat areas and subsequently link adults back to these areas (Gillanders and Kingsford, 1996; Reis-Santos et al., 2018). The results of such studies have shown that juvenile habitats contribute to adult populations in different proportions over time (Reis-Santos et al., 2013), however, this method is yet to be applied to cases where juveniles from the same habitat area recruit to different adult populations.

Proximately, environmental conditions, density-dependent effects and connectivity mediate the demographic rates of settler immigration, survival, growth and successful recruit emigration, which ultimately determine a habitat’s suitability. Descriptions of the relationships between these proximate drivers and ultimate rates can be used to identify productive “source”, type habitats and their relative importance among other habitats servicing the same population (Vasconcelos et al., 2014). Attaining an understanding of all of these relationships for any one population is a substantial task, however by taking an iterative approach we can build up to well described systems where complex life cycle models can be used to disentangle natural variation and anthropogenic impacts (Archambault et al., 2018; Meynecke and Richards, 2014). As long as we present the iterative results appropriately and in context, then both they, and the subsequent more complex maps and models of fish habitat use, can be useful tools for informing marine resource management (Le Pape et al., 2014; Lecours, 2017).
**Thesis aims**

With this thesis I address three main aims: The first is to illustrate the value of studying nearshore juvenile habitats, the second is to describe juvenile habitat suitability for important fisheries species from the inner Danish waters (IDW), and the third aim is to demonstrate the efficacy of otolith chemistry for differentiating between juvenile habitat areas of the IDW.

To illustrate the need to study juvenile fish habitats, I present a literature review of indirect anthropogenic impacts acting on important coastal fish species at different life-history stages (Synopsis 1).

I then use two empirical approaches to model juvenile habitat suitability for important fisheries species of the IDW and I present maps of predicted habitat suitability (Synopses 2 & 3).

For the third aim, I use two important fisheries species as case studies to demonstrate the use of otolith chemistry to discriminate between individuals from different habitat areas of the IDW (Synopsis 4).
Synopses of Appended Articles

Synopsis 1 – Conflicts in the coastal zone: human impacts on commercially important fish species utilizing coastal habitat


Coastal habitats are widely regarded as important juvenile growth areas, foraging areas and migration corridors for exploited marine species (Elliott and Hemingway, 2002; Seitz et al., 2014) that provide important food and economic resources (Costanza et al., 1997; de Groot et al., 2012). The concentration of human settlement and development at the coast means these habitats encounter many different anthropogenic pressures (Airoldi and Beck, 2007; Lotze, 2006) which can have additive or even synergistic impacts on reproduction, survival and growth (Halpern et al., 2009, 2007; Vasconcelos et al., 2017).

This study critically assesses the impacts of different categories of human activities on coastal fish populations of the northwest Atlantic. Building on the seminal work by Seitz et al (2014), a review of literature was undertaken specifically looking for evidence of human activities impacting on fish species for which formal scientific advice is given for fisheries management (termed ICES species). The review collected information on the species, the specific life-history stage, and the type of human activity having an impact.

Ninety-two percent of the fish species reviewed (22/24) were impacted by at least one type of human activity in at least one life-history stage in coastal habitats. These impacts were broken down across four different life history stages (Figure 1) and five different categories of human activities (Figure 2).
The percentage of fish species utilising coastal habitats that were impacted by human activities was high overall and for all life-history stages, despite this review’s limitation to only those human impacts which have been documented in primary literature. The juvenile life-history stage had the most evidence of anthropogenic impacts in coastal habitats, while “toxicants and pollutants” were the most commonly reported types of impact. Multiple types of human activities were found to impact upon single species, both within single life-history stages but also across multiple life history stages, a good example being European plaice (*Pleuronectes platessa*) where evidence of all five categories of anthropogenic impact were found in the juvenile life-history stage.
Quantification of population level effects of human activities remain infrequently reported in the literature. Determining the impacts of human activities requires a well-studied model system where natural drivers of demographic rates, such as growth, survival and reproduction, are quantified across the different life-history stages (Archambault et al., 2018; Meynecke and Richards, 2014). In these systems anthropogenic impacts can be disentangled from natural variation (van de Wolfshaar et al., 2011).

Once population level effects of human activities are known, spatially resolved representations of cumulative impacts (Andersen et al., 2015; Foden et al., 2011) can be considered by planners and managers (Goodsir et al., 2015; Knights et al., 2015).
Synopsis 2 – Juvenile fish habitat across the IDW: Habitat association models and habitat growth models for European plaice, flounder and common sole informed by a targeted survey

Appended work 2:

There is a demand for models of fish habitat use and to understand the environmental drivers of their distributions in order to inform managers and policy makers aiming to implement ecosystem based fisheries management (Link and Browman, 2017). In the cases where exploited species concentrate in coastal habitats for specific life history stages (Juanes, 2007), there is further demand to understand habitat use in order to inform spatial management of coastal development (Brown et al., 2018).

The European plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and common sole (*Solea solea*) are all flatfish of the family Pleuronectidae that are exploited in Danish fisheries, both recreational (Støttrup et al., 2018) and commercial (Ulrich et al., 2017). These three species also concentrate in near-shore, coastal habitats as juveniles, after metamorphosing and settling out of their planktonic larval stages (Gibson, 1999; Rijnsdorp et al., 1985). This study aimed to create Habitat Association Models (HAMs) and Habitat Growth Models (HGMs) for the 0-group of each species, informed by a targeted survey of coastal habitats across the IDW. Furthermore, it aimed to utilise these models to predict and create maps of relative habitat suitability using both density and growth as proxies for suitability.

A targeted survey using a juvenile beam trawl, sampled 146 sites from a range of near-shore coastal habitats around the IDW, in July and August of 2016 (Figure 3). Juveniles of the target species were collected together with measurements of the physical environment.
Figure 3. Juvenile survey of the IDW from 2016. Panel A shows sampling locations where the juvenile trawls were made by hand (▽) or small boat (○) and the inset places Denmark within northwest Europe. The CPUE as young of the year fish m$^{-2}$, is broken down for each target species, namely European plaice (Pleuronectes platessa; B), flounder (Platichthys flesus; C), and common sole (Solea solea; D). The depth scale across all panels is limited to 120m to better illustrate changes through the study area. Figure is taken directly from Brown et al (n.d.).
In the laboratory, Daily Length Specific Growth Rates (DLSGR) for the ten days prior to capture were determined, from a sub-sample of fish per site, using otolith microstructure analysis. Both the density of individuals and the growth rates were modelled as functions of the environment using generalised linear models and their mixed model equivalents (GLMs and GLMMs, respectively). Full models went through selection to find the most parsimonious set per species, and these were put through repeated sub-sampling cross validation. These models were then utilised to predict juvenile fish densities and growth rates, as proxies for habitat suitability, across the IDW. These predictions were based on modelled environmental data from various sources that were sampled across a grid covering the near-shore, soft-bottom habitats of the IDW. Predicted maps were paired with maps of standard errors to indicate the underlying uncertainty inherent in the models (Figure 4 & Figure 5).
Figure 4. Maps of predicted density based on Habitat Association Models (HAMs) for European plaice (Pleuronectes Platessa; A & B), flounder (Platichthys flesus; C & D), and common sole (Solea solea; E & F). Predictions are mean values (A, C, & E) and are paired with standard errors of the predictions (B, D, & F) to illustrate uncertainty. Figure is taken directly from Brown et al (n.d.).

Figure 5. Maps of predicted Daily Specific Growth Rates (DLSGR) based on Habitat Growth Models (HGMs) for European plaice (Pleuronectes Platessa; A & B), flounder (Platichthys flesus; C & D), and common sole (Solea solea; E & F). Predictions are mean values (A, C, & E) and are paired with standard errors of the predictions (B, D, & F). Figure is taken directly from Brown et al (n.d.).
The correlations described in the HAMs and HGMs were discussed with particular reference to the findings of other observational studies throughout the species’ ranges and the potential biological mechanisms for these relationships. Furthermore the methods and approaches were critically assessed with the intention of informing future work.

The main conclusions of this study were that drivers of 0-group density and growth were identified. The relationships between suitability and environmental drivers were sometimes contradictory between the metrics of density and growth, which illustrates the need to consider multiple metrics of habitat suitability. It was also concluded that while this study is the first to provide indications of habitat suitability for juvenile fish of the IDW, there remains substantial scope for improving both the static habitat suitability models and our understanding of the fluxes of settler supply and juvenile recruitment, into and out of these juvenile habitats.
Synopsis 3 – Juvenile fish habitat across the inner-Danish waters: Suitability modelling of coastal marine habitats for commercially important species from historic surveys

Appended work 3:

Demand for spatially explicit descriptions of fish habitat use and importance is increasing as resource managers implement and move toward policies based on marine spatial planning and ecosystem based fisheries management (Leslie, 2005). Providing maps of habitat use and importance is an effective way for researchers to communicate their findings but the methods and data used to inform and create habitat maps can be opaque and lead to improper interpretations (Lecours, 2017). In marine coastal habitats there is a large overlap between natural productivity and human activities (Airoldi and Beck, 2007) which can be exemplified by the multiple anthropogenic impacts acting on juveniles of important fisheries species in near-shore juvenile habitats (Brown et al., 2018). Before disentangling the multiple cumulative impacts on these systems, the natural components of juvenile fish habitat need to be described on a scale relevant to the fishery they support. Large observational studies of this kind are resource intensive so it is pertinent to utilise existing data, where it is available, to investigate habitat suitability. This study used well documented, historic juvenile surveys coupled with modelled environmental data to create habitat suitability models for 0-group juveniles of four important fisheries species from the IDW. The most parsimonious models are selected and validated using repeated, sub-sampling cross validation. Interpolative predictions of juvenile fish densities were mapped across the study area and were paired with maps of lower and upper 95% confidence limits to illustrate the uncertainty in the underlying models (for example: Figure 6). The underlying habitat association models were discussed with reference to other works on the biology of the species and the possible mechanisms driving the correlations before the limitations of the data, methods and created maps were contextualised. The created maps were deemed good indicators to aid in the development of future research.
Figure 6. 0-group European plaice (Pleuronectes platessa) densities predicted for July (A-C) and August (D-F) of 1998. Predictions (A&D) are the mode of the response and are based on habitat association models from the years 1991-2007. Uncertainty is illustrated in the lower (B&E) and upper (C&F) 95% confidence limits of the predictions.
Many marine fish species have different habitat requirements across different life history stages, and so knowledge of the connectivity between these different life-history stages and the areas they inhabit is important for managers of both fisheries and marine habitats (Vasconcelos et al., 2014). For many marine species, dispersal is most significant in the pelagic egg and larval phase, where individuals from different spawning populations mix before settling in juvenile habitats (Duffy-Anderson et al., 2014). In these juvenile habitats mortality and growth rates regulate the level of recruitment back into the adult stock (Gibson, 1994). The contributions of different spawning stocks to settlers in juvenile habitats can be traced using genetic tools (Ulrich et al., 2017), however because of the mixed nature of populations in juvenile habitats these tools are unable to trace the contributions of juvenile habitats back to the adult stocks. To trace adults back to previously inhabited areas requires tags and one such naturally occurring tag is the relative concentrations of trace elements that are incorporated into a fish’ otolith throughout its life (Reis-Santos et al., 2018). These trace elements are incorporated at different rates depending on the environmental exposure to different elements, the inherent physiology of the species and the mediating effect of the environment on that physiology (Izzo et al., 2018). This study used otolith chemistry to determine if the physiologically compatible, hybridising con-familials of European plaice (Pleuronectes platessa) and flounder (Platichthys flesus) can be distinguished from one another where they have been caught in the same habitat. Furthermore, it investigated whether this natural tag can be used to differentiate between contiguous, coastal juvenile habitats using the important fisheries species of plaice and common sole (Solea solea) from the IDW as case studies.
A survey of juvenile habitats across the IDW provided samples from sites where both 0-group plaice and flounder were caught together, as well as samples of 0-group plaice and combined 0- and 1-group sole from four habitat areas (Figure 7). Trace element analysis was carried out on spots at the edge of the otolith to represent the signal laid down in the habitat in which they were caught. A Canonical Analysis of Principle-coordinates (CAP) was carried out on a suite of 8-9 trace element concentrations to group and test reassignment of individuals back to their species or habitat area (Anderson and Willis, 2003). All differences utilised in the CAP were confirmed via PERMANOVA analyses (Anderson, 2006, 2001).
Figure 7. Sampling locations (A) indicating gear type used where juvenile trawls were made with a boat (⊙) or by hand (△), or where fyke nets were set (□). The locations where European plaice (Pleuronectes platessa) and flounder (Platichthys flesus) were captured together are plotted as the number of pairs (B). The locations of sites contributing plaice (C) and common sole (Solea solea) (D) are illustrated with the size of symbols representing the number of individuals and the habitat area they were caught in represented by shape (Skagerrak (★), Northern Kattegat (⊙), Southern Kattegat (□), and Belt Seas (△)). Figure taken directly from: Brown, E.J., Reis-Santos, P., Gillanders, B.M., Støttrup, J.G., 2019. Juvenile fish habitat across the inner Danish waters: Using otolith chemistry to discriminate between hybridising con-familials and contiguous, coastal habitat. Estuar. Coast. Shelf Sci. 220, 111–119. doi:10.1016/j.ecss.2019.02.025
These natural tags were able to correctly assign sympatric 0-group plaice and flounder to the right species ~72% of the time. Furthermore, more than two thirds of plaice and ~80% of sole were correctly assigned to their juvenile habitat areas (Figure 8).

**Figure 8.** Proportions of individuals assigned (“Assigned”) to the different habitat areas of origin (“Original”) using canonical analyses of principal coordinates for European plaice (Pleuronectes platessa; A) and sole (Solea solea; B). Cells on the diagonal represent correct allocations while those on off the diagonal represent incorrect allocations and shading indicates the proportion of fish assigned per origin where lighter = closer to zero and darker = closer to 1. Figure taken directly from: Brown, E.J., Reis-Santos, P., Gillanders, B.M., Støttrup, J.G., 2019. Juvenile fish habitat across the inner Danish waters: Using otolith chemistry to discriminate between hybridising con-familials and contiguous, coastal habitat. Estuar. Coast. Shelf Sci. 220, 111–119. doi:10.1016/j.ecss.2019.02.025
This study suggested that further work on the degree of plaice-flounder hybridisation in this area is warranted and that the small scale ecology of each species should be investigated where they and their hybrids are found in the same juvenile habitats. This species complex may be an interesting model for investigating the roles of intrinsic and environmental mechanisms to the incorporation of trace elements in otoliths. Furthermore, the successful differentiation between contiguous juvenile habitats indicates that otolith chemistry is an appropriate tool for use in tracing juvenile habitat contributions to adult stocks, even in systems with large areas of juvenile habitat occur outside of discrete estuaries and fjords.
Synopsis 5 – Ancillary projects

Appended works 5:
A collection of short communication format reports on other projects undertaken during the PhD program.

An important determinant of fish densities in juvenile habitats is the supply of settling larvae ready to colonise them. The rates of supply are determined both by growth and survival of the pelagic eggs and larvae (Horwood et al., 2000), and also the connectivity of the juvenile habitats to the spawning habitats (Lacroix et al., 2013; Petereit et al., 2014). The effects of settler supply are especially observable early in the juvenile growth season, prior to the action of regulating effects that occur in juvenile habitats over the first summer (van der Veer et al., 2015). These regulating effects can be examined through different rates of sub-cohort survival and growth throughout the juvenile growth season (Ciotti et al., 2014; van der Veer, 1986). Additionally, the presence and density of other organisms influence habitat suitability in their roles as prey, predators (Modin and Pihl, 1996) and habitat structuring organisms (Pihl et al., 2005; Wennhage and Pihl, 1994). Quantifying biotic drivers of habitat suitability for juvenile fish is more resource intensive than measuring physical characteristics (Le Pape et al., 2007, 2003) and can become prohibitive at larger spatial and temporal scales (De Raedemaeker et al., 2012, vs. 2011).

This collection of reports describes two studies aimed at quantifying the supply of settling juveniles and following their growth and survival throughout a growing season, and one study investigating the role of biotic drivers of habitat suitability. In all three cases, catches of target species were insufficient to address these aims; however, they are included here as ancillary projects for two reasons. The first is to demonstrate that settler supply, sub-cohort dynamics and biotic drivers of fish distribution were all recognised as important extensions of describing juvenile habitat suitability and significant attempts were made to quantify and describe them. The second reason is to document the methods applied so that future attempts to address these questions can be informed by the experience of these three studies.
Synthesis and Conclusions

Synthesis of presented research
In this thesis I have demonstrated that the vast majority of exploited fish species utilise coastal habitats during at least one life-history stage (~75% of species) and provided evidence that while inhabiting coastal areas they (92% of coastal, exploited species) are subject to a variety of anthropogenic impacts in addition to their direct exploitation. I have identified the juvenile life-history stage as being the most frequently impacted in coastal habitats and described how they are often subject to impacts from multiple human activities. The high rates and diversity of impacts that juvenile fish in coastal habitats face warrants further attention but in order to identify and quantify these impacts the role of natural environmental drivers needs to be more fully understood.

I have used two different empirical approaches to address the role of natural drivers in determining juvenile habitat suitability in the IDW, namely one of direct survey and observation, and one utilising pre-existing data.

The first consisted of undertaking a large-scale survey of near-shore habitats throughout the transitional waters of Denmark and using direct observation of environmental conditions to model habitat suitability for the 0-group of three key fisheries species. In this approach, both densities and growth rates (derived from otolith micro-structure analyses) were used as proxies for habitat suitability, which was described in terms of the physical environment, using generalised linear (mixed) models. These habitat suitability models showed that individual components of the physical environment may act in a complementary or contrasting manner with regard to their effects on density or growth; further justifying the use of multiple proxies for describing habitat suitability.

In the second approach, I utilised records of abundances from historic juvenile trawl surveys coupled with modelled environmental data to determine the role of different environmental drivers in describing 0-group habitat suitability for four key fisheries species. The use of historic surveys provided data across a much larger temporal scale than otherwise possible, but required a critical approach to data appraisal.
Using these two approaches I have presented juvenile habitat suitability models, and indicative maps of habitat suitability, at a scale relevant for resource management across the IDW. These studies build upon local scale, more targeted descriptions of species’ responses to their environment, reported from within the IDW. They also add to the literature on regional descriptions of habitat suitability for these species outside of the IDW. The majority of the relationships described in these two approaches corroborate the findings of other regional scale studies and are supported by the results of field and laboratory studies that describe the mechanisms underlying the species’ distributions. I applied these habitat suitability models to produce maps of predicted densities and growth throughout the extent of the study area. These maps, when paired with maps of their uncertainty, are an effective tool for visualising and communicating the complex models. I have openly presented the results of model validation, discussed the limitations of my selected methods, and contextualised these maps as static representations in a dynamic system, all in an attempt to ensure they are properly interpreted.

A common trend described in these two works is the latitudinal gradient of 0-group fish densities across the IDW, many of which were not attributed to other environmental co-variates. For species such as plaice, which consistently exhibited increased densities at higher latitudes, increased supply of settlers from populations outside of the study area is the likely mechanism driving this correlation. This raises an important question; do juvenile fish that were spawned from outside populations, but settle in juvenile habitats of the IDW, recruit to local adult populations or do they migrate back to their natal spawning populations?

The answer to this question has implications for evaluating the productivity of juvenile habitats in sustaining local fish stocks, for understanding the degree and mechanisms of population mixing, and for understanding the source-sink dynamics of different life-history stages in different habitat areas. The fourth study I have presented in this thesis provides a foundation for addressing this question by demonstrating the efficacy of otolith chemistry as a tool for discriminating between individuals that utilised different juvenile habitat areas. Using plaice and sole, I show that otolith chemistry can differentiate between trace element signals incorporated in open coastal habitats which, unlike estuaries and fjords, are not dominated by a single watershed’s chemical loading. In this study I also compare the otolith chemistry of plaice and flounder juveniles caught together in
an area where they are reported to hybridise, which encourages further work on this under-studied hybridising complex.

In addition to these four completed works, I have appended a collection of short reports which describe attempts to quantify settler supply to juvenile habitats and incorporate biological drivers of juvenile fish habitat suitability. These short communication styled reports are intended to be used in the development and planning of future work that might look to address these questions.

**Future perspectives**

While the results presented in this thesis provide a foundation for quantifying juvenile habitat suitability throughout the IDW, there are multiple areas where this work should be expanded and further developed. There are currently no regular surveys that adequately sample the near-shore juvenile habitats of the IDW, such as those undertaken in the past. Having multi-annual survey data, with concurrently observed environmental conditions, would help to investigate how juvenile habitats change under different hydrological conditions and with different rates of settler supply. Regularly quantifying juvenile abundance at the end of the juvenile growth period may also facilitate the development of juvenile-stock relationships to inform fisheries management. Furthermore, multi-annual libraries of juvenile otolith chemistry are required to be able to link adult fish from the fishery or spawning habitats back to their juvenile habitat areas, thus describing an aspect of life-history connectivity that is not possible with genetic tools.

Increasing within-year sampling resolution could help to quantify sub-cohort population dynamics. Knowledge of rates of settlement, growth and survival across the juvenile growth season would allow investigations of ontogenetic habitat shifts, habitat specific density dependence, and how juveniles of different spawning populations interact where they mix in juvenile habitats.

Combining high spatial resolution sampling at a small scale within a programme of larger scale surveys could help to identify the mechanisms that drive patterns of habitat use observed at the larger scale by investigating how different patches are utilised within habitats.
Conclusion

With the collection of works presented in this thesis I have illustrated the motivations for studying juvenile fish habitat and based on these needs, I have focussed on juveniles of exploited flatfish from the IDW to model aspects of the physical environment that determine habitat suitability. From this modelling I have produced the first maps of juvenile habitat suitability for the IDW. Furthermore, I have demonstrated the use of otolith chemistry for discriminating between contiguous juvenile habitat areas. These results provide a foundation for larger programmes of work to continue to improve maps of fish habitat suitability and the extent of connectivity between life-history stages.
Supplementary Contributions


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Appendices 1 – 4:

Due to copyright restrictions these four appendices have been removed from this publicly available version. Below are links to the published articles which will be updated as articles are published.

**Appendix 1**


**Appendix 2**


**Appendix 3**


**Appendix 4**

Appendix 5.
Juvenile fish habitat across the inner Danish waters: Citizen Scientists report on the arrival and abundance of juvenile flatfish settling in near-shore juvenile habitats

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Abstract
Understanding the dynamics of larval settlement, the subsequent juvenile growth and mortality that occur throughout a growing season, and how these vary across different juvenile habitats is an important component of understanding juvenile habitat suitability. A citizen science observational study was undertaken to provide the spatial scale and temporal resolution required to sample multiple juvenile habitat areas across a whole settlement and growth season, with the aim to describe differences in timing and abundance of settlers across the inner Danish waters. While samples were too few to address the scientific aims, close to 1500 hours of sampling were undertaken by 22 citizen scientists and this short communication describes the engagement and sampling effort before discussing the experience and lessons for future citizen science projects to consider.

Introduction
Surveying the abundances of adult fish stocks and their contributions to recruitment can be carried out through the analyses of fisheries landings but is often supplemented with fisheries independent surveys. However, many fish populations are regulated by processes occurring in early life stages, both pelagically and in juvenile habitats (van der Veer et al., 2015, 2000). These juvenile habitats are often geographically removed from adult habitats (Gibson, 2005), and thus the fisheries targeting them and the surveys targeting adult fish. Quantifying the contribution of different juvenile habitats back to adult populations is then outside the scope of typical fisheries monitoring but is important for fisheries managers in moving toward ecosystem approaches to fisheries management (Litvin et al., 2018) and to properly inform the planning of coastal marine development (Sundblad et al., 2014).

Undertaking targeted juvenile surveys is resource demanding (Le Pape et al., 2007) and carrying them out repeatedly throughout a juvenile growth season becomes logistically challenging to the point of being prohibitive at larger spatial scales (De Raedemaeker et al., 2012, vs. 2011). Because different regulating processes, such as changes to mortality (van der Veer, 1986) and growth rates (Ciotti et al., 2014), operate across the first summer growth period in juvenile habitats, there is a strong motivation to try and sample with higher temporal resolution.
Across Denmark there are many amateur fishers operating in near-shore areas who have abundant experience and knowledge of their local systems (Sparrevohn and Storr-Paulsen, 2015; Støttrup et al., 2018). These fishers are well organised into local, regional and national associations, and are motivated to understand more about the biology of the species they target. They are already engaged with the national fisheries research institute and have provided standardised catch registrations for coastal fish monitoring over the past 15 years (Støttrup et al., 2018). This study aimed to utilise this network of trained and highly motivated citizen scientists to undertake coastal sampling for juvenile fish with the specific research aims: 1. To identify the timing at which settlement occurs in different regions. 2. To determine the relative abundances of settlers across different regions of the inner Danish waters. 3. To provide samples for laboratory analyses of changes in growth across the first summer of select flatfish species’ life.

**Methods**

**Engagement**

In Autumn of 2015, a plan for the recruitment and engagement of member fishers was made with the guidance of the liaison from the Danish Amateur Fishers Association. Information articles on the project and its goals were published in local amateur fishing magazines and advertisements calling for volunteers were placed in multiple issues. Volunteer registrations were mapped and selections made to enable a broad geographic coverage. Early registering participants were informally surveyed for their advice on catching young of the year flatfish before a final design was mutually agreed upon with the liaison from the association. An induction and instruction meeting was held in February of 2016 with 24 participants and extra volunteers who were interested in being substitutes in areas where there were too many volunteers. Details regarding sampling methodology, fish identification and other questions were addressed and gear was distributed (Figure 1). Unfortunately, in 2016, the custom made nets were delayed in manufacturing and the project had to be postponed until 2017. In late 2016, the above engagement process started again.
Figure 1. Distribution of standardised gear and recording sheets to citizen scientists as part of project "Småfisk" in 2016. Top panel shows authors in reverse order from left to right. Images courtesy of Viola and Henning Nielsen from “Danske Fritidsfiskere”.

**Sampling**

Citizen scientists used standard gear, which were three sets of double-ended, free-standing fyke nets with 11mm mesh wings leading to 10mm and 8mm mesh in the front and back of the fyke respectively. The traps had 55, 50, 45, and 40 cm concentric rings with square funnel openings. The three sets of fykes were set together along the 1-1.5m depth contour for ~12hours overnight. Sampling was planned for every two weeks from the beginning of April 2017 to the end of August 2017 and each citizen scientist used the same location every time, in accordance with the Danish Nature Agency’s Dispensation (16-7521-000006). Citizen scientists were provided with three levels of data-collection forms pertaining to a one-off
description of their sampling position, a sampling day record of catches and conditions, and a per-fish label for identification information (Figure 2). Citizen scientists were responsible for identification, counting and length measurements to the nearest cm. Once a month (every second sampling), citizen scientists collected subsamples of target species, identified and individually froze them for confirmation of their identifications and further laboratory analyses. Data collection forms and frozen samples were collected once every two months throughout the study. In the middle of July, after low collections the study was cancelled.

**Results**

Twenty citizen scientists including recreational fishers and Nature-school leaders, were able to regularly perform coastal sampling at 22 stations using the standard gear (Figure 3). In total ~1500 hours of fishing time were undertaken across the four and half month period (Figure 4). Reported catches during this time were dominated by cod and flounder (Figure 5), many of which were not 0-group settlers (uncollated length data).
Figure 3. Positions of sampling locations. Twenty citizen scientists undertook sampling across 22 fixed locations with standard gear every two weeks from April to September of 2017. The depth scale is limited to 120m to allow for variation throughout the study area to be visualised.

Figure 4. Cumulative fishing hours undertaken by citizen scientists targeting settling juvenile fish from April to July of 2017.
Figure 5. Catches of fisheries species from juvenile fyke nets deployed in shallow, near-shore habitats by citizen scientists.

Discussion

Unfortunately, due to the low catch rates of the target organisms, namely 0-group settling flatfish, participant morale fell, and the return on effort for both the volunteers and the researchers was deemed too low to continue the study through to the planned end-date and was concluded 1.5 months early. There were many noteworthy experiences from this project that should be considered in any future attempts at citizen science projects; be they with this group, or matching the aims of this study but with other citizen scientists from with different demographic profiles. The following discussion will elaborate on these in a chronological order.

The selection of sampling equipment was made in collaboration with representatives of the participant group. There was a consensus among fishers, who used both shrimp fykes and eel fykes close to the coast, that juvenile flatfish were caught plentifully and often in these types of gear, and subsequently released. The idea to combine the two designs to form a specific juvenile fish fyke seemed logical and helped to ensure a standard gear was used across the whole study. However, due to the timeframes involved, no pilot study was carried out using this new gear type and large numbers of crabs were found to enter the traps and predate both juvenile and adult fish which further reduced already low catch rates. A pilot study in a tank setting may have provided insight to the efficiency of the traps and perhaps juvenile fish behaviour in relation to the “wings”, and the traps themselves. A recommendation for future projects would be to pilot study the selected gear types, both in the lab and in the field if possible.
The pool of volunteers that the citizen scientists for this study were drawn from, were previously engaged and highly-motivated. Working with pre-formed organisations and networks made communication and recruitment much easier and taking time to identify and approach such organisations is recommended. In the current study, many of the pool of potential volunteers had previous training in the collection and recording of fisheries data, not to mention their wealth of experience operating in these conditions. The fact that many citizen scientists are volunteer, means that through self-selection, the group will already be engaged and motivated. However it is the authors’ opinion that the additional data collection training that this volunteer pool had received, is a requirement for any project.

Prior to sampling beginning all citizen scientists were called to a planning meeting. This practice is to be highly encouraged, as it allowed for all gear to be properly distributed, the same set of instructions to be delivered to all participants, and the whole group could hear answers to questions they may not have otherwise asked. Furthermore, forming a common group on some form of social media allows for these types of discussions to continue in an open forum once everyone has dispersed.

While the direct sampling effort is distributed among the citizen scientists, there remains a large amount of time and work for the researcher in a support and coordination capacity. Replacement gear, sample collection, technical support and feedback are constantly required and demand a large amount of time. Additionally, volunteers like to see the result of their contributions; in the current study updates on progress were given verbally, in telephone conversations and during sample collection trips. It is highly recommended that future studies operating over extended periods of time, pre-arrange a data visualisation portal to allow citizen scientists to keep up with the data collection progress as data is collated.

As with all projects, closure is important. Although the current study did not achieve its scientific aims, a summary of the work undertaken and the project’s reception by the wider scientific community (Brown et al., 2017) was presented to the participants, and the wider pool of recreational fishers which they were drawn from.
Conclusions

The current study did not achieve its scientific aims of describing juvenile fish settlement rates across the inner Danish waters. However, this failure cannot be attributed to the citizen science approach, conversely, the group of highly engaged and motivated volunteers involved in this study undertook a sampling effort across temporal and spatial scales that were well in excess of any attempts a single researcher could make. Key aspects that a researcher engaging in a citizen science project should consider are: 1) Methods and equipment should be developed together with participants, but should be critically evaluated by the researcher prior to the broader project commencing. 2) Appropriate audiences should be targeted for recruitment to the project, and where possible it is beneficial to utilise existing organisation and their networks. 3) Communication is key; where possible bring citizen scientists together for meetings to share important information and maintain open forum style communication for the duration of the project. Results should be presented to the citizen scientists, if this is done real time it can provide additional motivation. 4) Researchers need to ensure they are well resourced to accommodate the increased scale that citizen science projects can bring to observational studies.

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Timing and abundance of settling 0-group flatfish in juvenile habitats of the South Funen Archipelago
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Abstract
Attempts to describe juvenile fish habitat suitability should consider the effects of settler supply when investigating juvenile density. A regular survey was undertaken throughout the settlement period for 0-group plaice, flounder, turbot and brill in juvenile habitats of the South Funen Archipelago, Denmark. Too few individuals were caught to describe settlement rates across different degrees of site exposure or throughout the settlement period. The low catch rates are discussed in regard to methodology, site selection and environmental drivers of larval distribution.

Introduction
Many marine fish species utilise different habitats across different life-history stages. For many flatfish species of the northwest Atlantic, juveniles concentrate in shallow, near-shore habitats following a period of dispersal as pelagic eggs and larvae (Gibson, 2005). In these juvenile habitats, mortality (Modin and Pihl, 1996; van der Veer, 1986) and differential growth rates (Ciotti et al., 2014; Nash et al., 2007) can act to regulate the size of a cohort before they recruit into adult stocks. Understanding the drivers of survival and growth in these habitats is important for predicting habitat suitability (Brown et al., n.d.), however their connectivity to adult stocks determines whether larvae will encounter suitable areas of habitat (Petereit et al., 2014) and whether juveniles that have survived and grown out of such habitats will recruit back to replenish the population (Beck et al., 2001; Gillanders and Kingsford, 2000; Vasconcelos et al., 2008).

European plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*), turbot (*Scophthalmus maximus*), and brill (*Scophthalmus rhombus*) are four flatfish species of commercial and recreational importance in Denmark (Sparrevohn et al., 2013; Støttrup et al., 2018) and which utilise shallow, near-shore areas as juvenile habitat (Pihl, 1989). Denmark, consisting of a peninsula and an archipelago, has a relatively large coastline with many large areas of shallow, near-shore habitat (Schwarzer et al., 2008). One such area is the South Funen Archipelago which boarders the southern side of two out of three straights connecting the Baltic Sea with the North Sea. The hydrography in this region is predominantly brackish but with large fluctuations in salinity, and temperature depending on regional meteorological conditions (Nielsen, 2005; Stedmon et al., 2010) and local wind forcing (She et al., 2007).

Ahead of a survey of the biophysical conditions in juvenile habitats of the South Funen Archipelago, this study aimed to describe differential rates of settler supply at three different levels of exposure and to chart
length frequency distribution changes throughout the settlement and growing season to determine the
timing of sub-cohort settlement peaks and estimate growth rate changes throughout the season.

Methods
Once every two calendar weeks, from the end of April to the end of July in 2015, nine sites across the South
Funen Archipelago were surveyed (Figure 1). Sampling consisted of a juvenile beam trawl (2 m beam, 5
mm stretched mesh, and a single tickler chain) being towed by hand at approximately one knot, over
~100m, at depths of approximately one metre. Sites were categorised into three localities, each with three
relative levels of exposure, and were sampled with three hauls per site per sampling day. To reduce
disturbance of the haul area prior to sampling, the trawl was set and an oversize tow with 10m markings
was walked in a large loop around the intended haul area. At 100m from the static trawl a buoy was
anchored to the sea floor and the trawl was hauled until it reached the marker. Juvenile flatfish that were
catched were identified, had length measured and were returned.
Figure 1. Sampling locations used to determine rates and timing of juvenile flatfish settlement in the South Funen Archipelago, in 2015. For context Denmark is shown within NW Europe (A) and the South Funen Archipelago is located within Denmark (B). The sampling locations are spread across three areas, namely: Helnæs (▲), Aerø (●), and Langeland (■). Each location contained three sites with different categories of exposure, namely: Inside Sheltered (IS; orange), Inside Exposed (IE; green), and Outside Exposed (OS; purple). The depth scale is limited to a maximum of 50m to better visualise the ranges through the majority of the study area.
Results
Too few individuals of any one species were caught (Figure 2) for meaningful statistical analyses to be conducted, so only descriptive results are presented here. Juvenile plaice from the previous year (1-group) were initially caught but numbers quickly reduced to zero. A peak in 0-group turbot at the end of the study period was limited to exposed locations and predominantly came from the Langeland, Internal Exposed site. No brill were caught at any location at any time.
Figure 2. Catches of juvenile flatfish (Pleuronectes platessa, Platichthys flesus, Scophthalmus maximus, and Scophthalmus rhombus) from April to August of 2015. The top four plots are of 0-group catches while the bottom four are of 1-group. Catches are pooled across localities and coloured by relative site exposure.
**Discussion**

The South Funen Archipelago was selected as a study area because of the relatively large area of shallow coastal habitats and the variation in exposures. Additionally, the area is close to the basins of the south western Baltic, commonly reported as spawning areas, and between two of the straights where there is large water exchange between the Baltic and Kattegat potentially carrying settling larvae. The assumptions that this area would provide substantial catches of 0-group juveniles did not hold up, possible reasons being flawed sampling methodology, poor overall habitat that settlers selected against, or poor settler supply.

To address the first of these issues, the sampling methodology was tested in a pilot study in Nivå bay (Danish Øresund) prior to this settlement study and was subsequently successfully used in a juvenile fish survey across the extent of the inner Danish waters in 2016 (Brown et al., n.d.). In both circumstances, high catch rates were attained so it is not expected that gear efficacy, nor other aspects of methodology, were the cause of low catch rates.

This survey mentioned above also predicted that the juvenile habitats within the South Funen Archipelago could supply median levels of 0-group plaice abundance and medium to high levels of 0-group plaice abundance relative to other Danish coastal habitats. This suggests that larvae would be unlikely actively select against this area for settlement.

Particle tracking models of the pelagic early life stages of plaice and flounder, seeded from spawning grounds in the southwest Baltic, predicted high rates of settlement ready larvae to the South Funen Archipelago under different hydrographic and spawning time scenarios (Petereit et al., 2014). Only one scenario out of six predicted low rates of settler supply to this area; a major inflow of marine water through the Danish straits coupled with early season spawning. In December of 2014 the third largest major Baltic inflow event on record occurred (Mohrholz et al., 2015), meaning that if spawning for plaice and flounder occurred relatively early in the spawning season, chances that settling plaice and flounder larvae would have encountered the juvenile habitats of the South Funen Archipelago were at their lowest.

**Conclusion**

A fortnightly survey of juvenile fish habitats in the South Funen Archipelago of Denmark, undertaken across the settlement period for juvenile flatfish, caught too few juvenile fish to explore the effects of exposure on settlement or the temporal variation in settlement and growth within a season. This was likely due to a significant hydrological anomaly reducing settling larval supply to the area.
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Local scale biophysical modelling of habitat suitability for juvenile flatfish of the South Funen Archipelago
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Abstract
Understanding the biological determinants of fish distribution can improve descriptions of habitat suitability but require resource intensive sampling and laboratory analyses. A local scale survey of juvenile fish habitats from around the South Funen Archipelago was carried out at the end of the juvenile growth period in 2015. Stomach contents analysis was carried out to determine key prey items to inform further biological sampling for juvenile habitat suitability modelling and results are compared to diets described from other areas of the species’ ranges. Unexpectedly low catches of juvenile flatfish were attained and this is discussed with reference to the combination of the local scale and the year’s hydrographic conditions.

Introduction
Descriptions of fish habitat suitability are often carried out at scales relevant to fisheries management and use physical qualities of the environment to explain variation in fish abundances and growth. While the inclusion of biological drivers can improve models of juvenile fish habitat suitability (Le Pape et al., 2007, 2003), the sampling and processing of relevant biota is resource intensive and can be unrealistic when studies consider large spatial or temporal scales (De Raedemaeker et al., 2012, vs. 2011). However to understand smaller scale juvenile fish distributions and the mechanisms driving them, then higher resolution sampling, including relevant biological predictors, is crucial (Litvin et al., 2018; Nagelkerken et al., 2015).

The inner Danish waters support coastal fisheries for a range of flatfish species including the near-shore, juvenile habitats that replenish them. Juveniles share these habitats with a variety of other organisms that can influence their movements and distribution through a variety of mechanisms, such as foraging for prey (Vinagre et al., 2009), hiding from predators (Modin and Pihl, 1996), or avoiding structural complexity created by algae that hinder their feeding and/or burying ability (Pihl et al., 2006; Wennhage and Pihl, 1994).
This study aimed to describe the diets of juvenile fish from the South Funen Archipelago to determine which elements of the biota should be considered as potential biological predictors of juvenile habitat suitability. The subsequent aim was to evaluate the relative contribution of biotic variables to models of juvenile fish habitat suitability.

**Methods**

**Field collections**

From the 10th to the 19th of August in 2015, 44 sites from the South Funen Archipelago were sampled (Figure 1). Using ArcGIS 10.1 and data sources internal to the institute, ninety sites were randomly selected from areas that were reported to be soft bottom (not boulder reefs or sedimentary rock) and shallower than three metres depth. Where substrate and depth did not match the randomly selected position, the closest matching location was used, or if no such location was found close by, the site was abandoned. Sampling consisted of a 100m trawl of a two metre wide juvenile beam trawl at approximately one knot. The trawl was fitted with a five millimetre stretched-mesh net and one tickler chain. The physical environment was recorded as depth, temperature and salinity at the sea-bottom, and a sediment core was taken using a hand-held haps-corer for later grain-size analyses. A second core sample was taken for infaunal sample analyses and epibenthic organisms caught in the trawl were also collected.
Sample preparation
Juvenile fish of the target species were killed using an overdose of benzocaine (250mg.L⁻¹) in aerated seawater before being frozen in individual ziplock bags. Volumes of sea-grass, categorised as dead or alive, and different types of algae were measured in volumetric jugs after having excess water removed. Infaunal sediment samples were sorted on successively finer (4mm, 1mm, 0.5mm) sieves with each fraction being picked through independently. The epibenthos from the trawl were sorted in a similar fashion, by size.
Infauna and epibenthic fauna from each fraction were stored in their own sample container with 4% formaldehyde solution in borax buffered, seawater. Seawater was sieved at 0.1mm before use as a formaldehyde solvent.

**Fish Processing**
In the lab, individual fish were defrosted and dorsal, anal and caudal fin rays were counted. Counts were made under binocular dissecting microscopes, using a clicker-counter and were only finalised after three consecutive counts were in agreement. Fish were subsequently pat dry before being weighed and having their standard lengths measured. Entire alimentary canals were removed and weighed, while the remaining organs were removed from the body cavity and the fish re-weighed to attain a “cleaned weight”. Sagittal otoliths were removed, cleaned, dried and stored as pairs in individual ziplock bags. The entire alimentary canal was dissected open so as not to crush the partially digested organisms, prey items were then identified to the lowest possible taxonomic group before being counted (if discrete bodies or body parts could be distinguished) and added to pre-weighed crucibles for the determination of Ash-Free Dry Weight (AFDW). Unidentifiable contents were recorded as “digesta” and treated as another taxa, while items that were only identifiable to higher taxonomic levels were pooled into “other_*”, groups at the lowest level identifiable.

**Infauna and epibenthic fauna processing**
Infauna and epibenthic fauna was cleaned of formalin and stored in 80% ethanol. Samples were sorted and identified to at least family level, but to lower taxonomic levels where possible and higher levels if the specimens were damaged. Individuals were counted and placed in pre-weighed crucibles for the determination of AFDW. Larger bivalves that remained closed had their shell broken or levered open before drying.

**Determining Ash-Free Dry Weight**
Aluminium crucibles were prepared by burning at 500° C for two hours before being weighed. The samples were dried in the pre-weighed crucibles at 65° C for 12-16 hours. Dried samples were weighed before being burnt in a muffle oven at 500° C for 6 hours, after which the remaining ash was weighed in the crucibles and the change in weight from the dried samples to the ash was recorded as the AFDW.

**Data analyses and visualisation**
All data analyses subsequent to site selection was carried out using *R statistical software* (R Core Team, 2018) and figures were made using *ggplot2* (Wickham, 2016). Gut contents were converted to per-taxon dietary importance metrics based on their proportion of ASFDW in individual stomach contents and normalised across all individuals within species by weight according to the least biased gravimetric method described in Ahlbeck et al. (2012; method “MM3”):
\[ eq. 2 \quad \text{Importance}_i = \frac{\sum_{j=1}^{N_{Fish}} \frac{w_{ij} m_j}{N_{Fish}}}{\sum_{j=1}^{N_{Fish}} \frac{w_j}{m_j}} \times 100 \]

Where the \( \text{Importance}_i \) represents the relative contribution of taxon \( i \) as prey to a particular species of predator, \( N_{Fish} \) is the number of stomachs from the predator species of interest, \( w_{ij} \) is the ASFDW of taxon \( i \) in fish stomach \( j \), \( m_j \) is the cleaned/gutted wet mass of fish \( j \), and \( w_j \) is the total ASFDW of stomach contents for fish \( j \).

Results

Juveniles of target species were caught at just over half of sites surveyed (Table 1). Juvenile flounder were the most abundant of the target species, both in absolute number and the number of sites they were present in.

**Table 1. Catches of juvenile flatfish from a beam trawl survey of juvenile habitats around the South Funen Archipelago in August 2015.** Totals are of the number of fish and the collated number of sites where at least one target species was caught, the latter of which is by chance equal to the sum of the sites for each species.

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Fish</th>
<th>Sites Present</th>
<th>Length Ranges (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flounder</td>
<td>35</td>
<td>13</td>
<td>48-134</td>
</tr>
<tr>
<td>Plaice</td>
<td>9</td>
<td>2</td>
<td>72-104</td>
</tr>
<tr>
<td>Dab</td>
<td>9</td>
<td>3</td>
<td>75-125</td>
</tr>
<tr>
<td>Turbot</td>
<td>13</td>
<td>4</td>
<td>39-85</td>
</tr>
<tr>
<td>Brill</td>
<td>1</td>
<td>1</td>
<td>82</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>67</strong></td>
<td><strong>23 / 44</strong></td>
<td></td>
</tr>
</tbody>
</table>

Flounder, being the most abundant species, had the most diverse stomach contents at the family level (Figure 2). Amphipoda dominated their diet, especially the family Bathyporeiidae. Bivalves, especially the families Cardiidae and Mytilidae, were the second most important group for flounder, followed by the phylum Annelida whose members were not identifiable beyond the Phylum. Plaice diets were almost entirely dominated by Arthropoda, especially two families of Amphipoda. Bivalves contributed little to plaice diets and Annelids were much less important than for flounder. Bathyporeiidae was also very important for the dab. Turbot was the most different, with two families of larger shrimps and small fishes.
being the most important prey groups. The gut contents of the single brill specimen are not presented.

Figure 2. Relative importance of different Families as prey for juveniles of four flatfish species: The European flounder (Platichthys flesus), plaice (Pleuronectes platessa), dab (Limanda limanda), and turbot (Scophthalmus maximus). Relative importance measures are proportions of stomach contents by mass, and are mass corrected across individual fish.
**Discussion**

Few specimens of target species were caught and were often caught together at only few sites, providing little data for diet analyses and habitat association modelling. However, the taxa observed in the stomachs and their relative importance as prey for juvenile flatfish matches what has been reported for juveniles of these species in studies with much larger sample sizes (Augley, 2007; Beyst et al., 1999; Nissling et al., 2007; Ustups et al., 2007; Wyche and Shackley, 1986). The size ranges of fish in the current study are also above the lengths at which major ontological shifts in diet have been reported for these species (Aarnio et al., 1996; Nissling et al., 2007; Ustups et al., 2007; Wyche and Shackley, 1986), meaning it is not necessary to break the samples down further fish size.

The high importance of Bathyporeiidae in juvenile flounder diets observed here has also been reported up to the northern reaches of the Baltic (Aarnio et al., 1996). This same study also reported juvenile turbot diets that were dominated by Mysidae and small fishes, which matches the turbot in the present study (Aarnio et al., 1996). Outside of the Baltic, diets of flounder in a Danish fjord, a Scottish Estuary (Summers, 1980) and a Portuguese estuary (Vinagre et al., 2008) were largely comprised of the infaunal amphipod *Corophium volutator* with a similar habit to Bathyporeia species (Hayward and Ryland, 2017). The substitution of different amphipods was also reported across different studies of plaice diet (Beyst et al., 1999; De Raedemaeker et al., 2011; Gibson et al., 1998). While juvenile turbot from the Irish west coast are reported to have very different diets to those of the current study and the Baltic proper (Haynes et al., 2011), those in juvenile, sandy coastal habitats of the Belgian coast are more similar to the current findings, dominated by *Crangon crangon*, Mysidae and small fishes (Beyst et al., 1999).

Gravimetric analyses of stomach contents indicate some prey overlap between juvenile Pleuronectids, especially with regard to the prey family Bathyporeiidae and the other Amphipoda. The dominance of small mobile Arthropods in the diets of plaice suggests more specialised predation compared to flounder and dab. However, De Raedemaeker et al. (2011) report that the contribution of different taxa in plaice diets can fluctuate from extremes of dominance by one prey type to another in both space and time. The higher diversity in the diet of the flounder is probably due to their opportunistic feeding strategy (Andersen et al., 2005) combined with samples coming from a larger number of sites. The dab’s prey importance were spread across more taxa than was observed for the plaice, although they were derived from the same number of individuals perhaps indicating a more generalist foraging approach.

The low abundances of target fish species observed in this study may be attributable to poor larval supply. This situation was indirectly predicted by Petereit et al (2014) who demonstrated that under significant Baltic inflow conditions early in the spawning season, the area around the south Funen archipelago would be poorly supplied with ready to settle plaice and flounder larvae. These conditions were realised in the
spawning and distribution period prior to this study (Mohrholz et al., 2015). Irrespective of the cause, with a lack of fish data for model building, the analysis of infauna and epibenthos has been carried out opportunistically among other project work and remains underway at the time of writing. The construction of habitat models will not be attempted but further comparisons of gut contents and available fauna are warranted.

**Conclusion**

The limited findings of this study do indicate that certain taxa are more relevant for inclusion as explanatory variables in models of juvenile fish habitat suitability. Furthermore it appears that juvenile diets in habitats of the South Funen Archipelago are more similar to those from the Baltic proper than those of the British Isles and Ireland.

**References**


