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Juvenile fish habitat across the inner Danish waters: Habitat association models and habitat growth models for European plaice, flounder and common sole informed by a targeted survey

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6 **Abstract**

7 The management of coastal fisheries and coastal marine areas both require information on the use and
8 importance of coastal marine habitats for marine species. This information is certainly pertinent for
9 exploited species dependent on these coastal habitats for specific life-history stages. This study uses two
10 different measures of habitat suitability to build Habitat Association Models (HAMs) and Habitat Growth
11 Models (HGMs) for juveniles of three commercially and recreationally important fish species (*Pleuronectes*
12 *platessa*, *Platichthys flesus*, and *Solea solea*) of the Inner Danish Waters (IDW). A large scale, one-off
13 juvenile survey was used to collect juvenile fish and directly observed environmental data. The survey
14 informed Generalised Linear (Mixed) Models (GLMs and GLMMs), which were fit and run through repeated
15 random sub-sampling cross-validation before being utilised to build interpolative maps of both prediction
16 and model uncertainty. The limitations of this approach are discussed in reference to the future works
17 required to complement and improve such static habitat suitability maps. These results can be used to
18 inform marine spatial planning and future work into the role of juvenile habitats in supporting fishery
19 species.

20 **Keywords**

21 juvenile habitat, inner Danish waters, Baltic Sea, transitional waters, habitat suitability, growth modelling,
22 habitat association modelling

23 **1. Introduction**

24 Coastal marine habitats play an essential role in one or more life-history stages of many marine fishes
25 (Litvin et al., 2018). This is especially true in the case of species that are exploited both commercially
26 (Kritzer et al., 2016; Seitz et al., 2014) and recreationally (Lellis-Dibble et al., 2008; Støttrup et al., 2018;
27 Sundblad and Bergström, 2014). These high rates of exploitation of coastal species are a function of their
28 proximity to human development, which also leads to high levels of multiple, indirect, human impacts on
29 coastal fish populations (Airoldi and Beck, 2007). Before quantifying and addressing anthropogenic
30 impacts on coastal fish, we must first determine the natural drivers of habitat suitability for the species that
31 inhabit them (Brown et al., 2018). Knowledge of these natural drivers of fish distribution and habitat
32 suitability are also of interest in the management of fisheries. Ecosystem based fisheries management (Link
33 and Browman, 2017 and other titles in the themed section) has been implemented in the form of multi-
34 species management plans (Rindorf et al., 2017), considerations of population and life-history connectivity
35 (Kimoto et al., 2007; Lipcius et al., 2008; Ulrich et al., 2017), and the concept of essential fish habitat
36 (Kraufvelin et al., 2018) being considered in policy advice (HELCOM et al., 2018). Coastal dependence in
37 important fisheries species occurs during juvenile life-history stages (Seitz et al., 2014). Species which
38 concentrate in specific habitats during these juvenile life-history stages experience strong regulation on
39 cohort size (Iles and Beverton, 2000; Juanes, 2007). Therefore, understanding the drivers of juvenile fish
40 abundance and growth is important for both the management of the fish stock and the coastal
41 environment. This study therefore focusses on juvenile habitat suitability for three such commercially and

42 recreationally important flatfish species of the Inner Danish Waters (IDW), namely the European plaice
43 (*Pleuronectes platessa*), European flounder (*Platichthys flesus*), and common sole (*Solea solea*).

44 The three species in focus exhibit typical coastal flatfish life-history patterns and have been the subjects of
45 many previous works (Gibson, 2005). Eggs and larvae develop pelagically, during which a combination of
46 passive and selective transport brings them in contact with coastal habitats (Rijnsdorp et al., 1985) where
47 they metamorphose and settle into concentrated, near-shore juvenile habitats (Gibson, 1999) .

48 Interannual variability in settler supply is dampened during the first summer grow-out period spent in the
49 juvenile habitats (Gibson, 1994), with evidence indicating early post-settlement, density dependent
50 mortality as a key mechanism regulating recruitment to the adult stock (van der Veer et al., 2015). As they
51 grow they extend their ranges deeper, where mature plaice and flounder spawn off-shore in deeper more
52 saline conditions (Kijewska et al., 2009), and sole appear to spawn more coastally, closer to juvenile
53 habitats (Rijnsdorp et al., 1992; Wegner et al., 2008). While there are strong similarities between plaice
54 and flounder life-history patterns, plaice inhabit marine areas throughout their life cycle (Petitgas et al.,
55 2013) whereas flounder are more amphidromous, with juveniles and adults (outside of the spawning
56 season) found high up in estuaries (Kerstan, 1991; Summers, 1979).

57 Different approaches can be taken when trying to describe the environmental drivers of juvenile fish
58 habitat suitability and one of the first choices to be made is the measure used to represent “suitability”.
59 Measures of presence have been used to describe species’ ranges (Elith et al., 2011), while absences have
60 been used to infer physiological and hence environmental limits (Li et al., 2017). With standardised gears
61 and methodologies presence/absence measures extend to abundance or density measures, providing more
62 information on realised distributions (Guisan and Zimmermann, 2000; Sundermeyer et al., 2005). However,
63 there are many reasons why a species may not extend across the whole of its potential habitat which aren’t
64 accounted for with observations of abundance (Stoner, 2003). Presence/absence and abundance can
65 provide information on habitat selection, however they should be combined with other measures of

66 habitat suitability such as the demographic rates mortality and growth (Johnson et al., 2013; Vasconcelos et
67 al., 2014). While these demographic rates can be easily determined through counts and repeated
68 measures in experimental laboratory set ups, field observational studies pose more of a challenge. For
69 example: Changes in cohort size can be biased through immigration of new settlers and emigration of
70 larger individuals (Jager et al., 1995), tagging studies to estimate growth and mortality require very large
71 sample sizes to overcome poor recapture rates (Barbour et al., 2012), and interventions such as tethering
72 have unknown influences on rates of predation (Manderson et al., 2004). However, determining growth
73 rates from once-caught wild fish is possible, by analysing bio-archived information in bony structures (such
74 as otolith incremental growth) (Geffen et al., 2011; Stevenson and Campana, 1992). The current study
75 employs both density and growth rate, determined by otolith increment analysis, as proxies for juvenile
76 flatfish habitat suitability.

77 The selection of covariates, or explanatory variables, is also important because circumstantial inclusion of
78 different explanatory variables can lead to spurious correlations and misinterpretation of real driver effects
79 (Lecours et al., 2016). Covariates should be selected based on biological knowledge of the system being
80 modelled, so that there are plausible mechanisms by which the covariates can influence the response
81 (Guisan and Zimmermann, 2000). For juvenile fish in coastal habitats, hydrographic properties such as
82 temperature, salinity, and oxygen have direct impacts on metabolism and habitat utilisation (Augley et al.,
83 2008; Fonds et al., 1992; Karakiri and von Westerhagen, 1989; Maxwell et al., 2009; Schram et al., 2013).
84 Shallow depths are thought to provide refuge from larger predators (Manderson et al., 2004). Substrate
85 type plays an indirect role in the prey species available (Nicolas et al., 2007) and a direct role for flatfishes'
86 ability to bury and avoid predation (Gibson and Robb, 2000), while wave exposure influences foraging
87 ability (Eriksson et al., 2005). In addition to the direct effects of environmental conditions on individual
88 growth and survival, a habitat's proximity/connectivity to sources of settling larvae can influence the
89 density of juveniles (Petereit et al., 2014), and the degree to which juveniles are adapted to local
90 conditions. Furthermore, the presence of con-specifics may depress growth rates and survival through

91 competition and predator attraction (Ciotti et al., 2014; Wennhage and Pihl, 2001). This study employs
92 these environmental parameters as system-sensible explanatory variables in describing habitat suitability
93 for juvenile flatfish of the IDW.

94 The next question to be addressed is one of scale; both spatial and temporal scales depend on the aims of
95 the study (Gong et al., 2014; Graf et al., 2005). Studies aiming to describe the production of juvenile
96 habitats for the function of population and fishery replenishment are often carried out at regional scales,
97 over multiple years (Le Pape et al., 2003b; Vasconcelos et al., 2010). Other studies aiming to describe more
98 fundamental eco-physiological responses are carried out at local scales and pay more attention to within
99 year, sub-cohort temporal dynamics (Nicolas et al., 2007; Vinagre et al., 2009), where the aforementioned
100 sub-cohort settlement and emigration can influence observations of both densities (Jager et al., 1995) and
101 growth rates (Ciotti et al., 2013). The current study considers the former situation, namely investigating
102 juvenile habitats at a scale across fisheries stock boundaries but at a temporal snapshot of a single year.
103 The snapshot was planned to coincide with the mid to late portion of the juvenile growth period (Nielsen
104 and Bagge, 1985) to allow for the majority of settlement and early mortality to have occurred (van der Veer
105 et al., 2000), with low rates of larger individual emigration.

106 One further consideration to be taken is the choice of statistical framework with which to model the effects
107 of environmental features on habitat suitability. This topic has been well reviewed for species distribution
108 modelling generally (Guisan and Zimmermann, 2000) and considered for benthic organism habitat
109 distribution specifically (Bučas et al., 2013). The use of generalised linear models, and their extension
110 generalised linear mixed models, provide a good balance between being interpreted as physiologically
111 driven and accurately descriptive of the real world (Guisan et al., 2002) while providing flexibility in the
112 underlying distributions suited to counts and abundance data (Brooks et al., 2017). Furthermore, these
113 tools have a strong history in being applied to fish (and specifically juvenile fish) habitat modelling (De
114 Raedemaecker et al., 2012; Le Pape et al., 2003b; Vasconcelos et al., 2013).

115 The primary aim of this study was to create maps of juvenile habitat suitability for European plaice,
116 flounder and common sole of the inner Danish waters. To achieve this it aims to build Habitat Association
117 Models (HAMs) describing juvenile density in relation to physical habitat characteristics and to build Habitat
118 Growth Models (HGMs) to describe the growth rates of juveniles under the different physical conditions
119 that they inhabit.

120 **2. Methods**

121 *2.1. Study area*

122 The IDW are bounded in the west by the Jutland Peninsula and the east by the Swedish maritime border
123 and ultimately the Scandinavian Peninsula (Figure 1). In the north, there is a steep transition to the
124 Skagerrak/North Sea from intracontinental to continental shelf (Schwarzer et al., 2008) The demarcation
125 between the deep Skagerrak and the body of water known as the Kattegat is a line from the top of the
126 Jutland peninsula due east to Sweden. Between this northern limit and the top of the Danish archipelago is
127 the Kattegat where relatively deep channels run north to south. These channels carry deep marine waters
128 which mix with the outflow of surface brackish water from the Baltic Sea (She et al., 2007). The degree of
129 mixing in the southern Kattegat is dependent on meteorological drivers of Baltic water outflow across the
130 sills throughout the Danish archipelago (Lehmann and Hinrichsen, 2000). The bodies of water over these
131 sills are collectively known as the “Belt Seas” and specifically as: The “Little Belt”, the western most
132 channel between the Jutland peninsula and the island of Funen. The “Great Belt” is the middle channel
133 between Funen and the island of Zealand. Finally in the east is “The Sound” which joins the Kattegat and
134 the Southwest Baltic Sea between Zealand and Sweden. South of the Belt Seas’ sills, the IDW are primarily
135 brackish and are bounded by maritime borders with Germany and Sweden. The peninsula and archipelago
136 provide a large area of coastline which is interspersed with fjords and smaller archipelagos. Due to the
137 large amount of water exchange through the IDW, there is potential for dispersal of larvae from adult
138 stocks of neighbouring water bodies, such as the North Sea/Skagerrak in the North and the southwest

139 Baltic in the south. There exist general north to south gradients associated with this transition area, with
140 average seafloor temperatures at the coast decreasing $\sim 3^{\circ}\text{C}$ and salinities at the coast increasing from ~ 12
141 to ~ 28 , from south to north. Contrary to this overall trend are large deviations in hydrological conditions at
142 the coast associated with terrestrial freshwater inflows and large shallow bays.

143 2.2. Field collections

144 From July 18th to August 22nd 2016 a survey (Fig. 1a) was undertaken of the near-shore marine coastal
145 habitat of the IDW. The survey consisted of 146 juvenile beam trawl sites (2 m beam, 5 mm stretched
146 mesh, single tickler chain, towed at ~ 1 knot, over ~ 100 m). Sites were stratified by four depth ranges (0-1, 1-
147 2, 2-3, and 3-4 m) and four soft-bottom types (muddy-sand, sand, sandy-gravel, sand & boulders) informed
148 by draft sediment data later supplied to EMODnet-Geology (2016). Shallow (0-1 m) sites were trawled by
149 hand (two people wading ahead and wide of the trawl), while deeper sites were trawled by boat. Not all
150 planned sites conformed to their prior stratification. Attempts were made to match depth and bottom type
151 categories in the vicinity of planned sites, however if not possible the planned site was used. In addition to
152 the trawl position, depth and time, the environmental parameters of temperature ($^{\circ}\text{C}$), salinity (practical
153 salinity scale), oxygen concentration ($\text{mg}\cdot\text{L}^{-1}$) and oxygen saturation were recorded at the sea-bottom using
154 a Multi 3620 IDS hand held meter with FDO[®] 925 and TetraCon[®] 925 probes (WTW). Furthermore, a
155 sediment sample was taken at each site using a hand held Haps corer ($150\text{cm}^2 \times 30\text{cm}$) for later grain-size
156 analysis.

157 Flatfish under 15 cm standard length were killed using an overdose of benzocaine dissolved in aerated
158 seawater ($250\text{mg}\cdot\text{L}^{-1}$) before being individually labelled, bagged and snap frozen on dry-ice. At the end of a
159 day of sampling, fish and sediment samples were transferred to -18°C freezers until laboratory processing.

160 Grain size analysis was carried out on the defrosted sediment samples according to the Danish Standard (*DS*
161 *405-4 Testing of sand, gravel and stone materials*, 1998), and substrate classes were assigned to sites

162 according to the Folk (1954) five-class sediment texture classification system adopted by EMODnet Geology
163 (2016).

164 2.3. Species identification and otolith extraction

165 Individual fish were defrosted, their standard length and wet mass measured, and identification to the
166 family level was made. To identify to the species level, dorsal, anal and caudal fin rays were counted using
167 magnifying glasses, binocular microscopes and clicker-counters. A fin ray count was recorded only after
168 three corresponding counts were made and species was determined according to the counts summarised
169 in Haynes (2011) and corroborated by Munk and Nielsen (2005). Right and left sagittal otoliths were
170 extracted, cleaned of soft tissue, air-dried and stored in labelled plastic zip lock bags.

171 2.4. Otolith microstructure analyses

172 Right sagittal otoliths were retained for microstructure analyses. Up to three individuals of each species
173 from each site were selected (randomly for sites with greater than three individuals) for microstructure
174 analyses. Whole otoliths were mounted sulcus side up on glass microscope slides using a thin layer of
175 crystalbond 509™ so that the core of the otolith remained above the mounting material. Otoliths were
176 ground and polished by hand with Buehler MicroCut PSA, P4000 silicon carbide paper until daily rings were
177 distinguishable in the anterior of the otolith from the first, secondary growth centres to the edge. Larger
178 samples were flipped, ground and polished from the outer surface, but observations of increments were
179 always made from the inside face of the otolith. Polished otoliths were photographed under oil immersion
180 with 2.5x and 20x objective lenses (whole otoliths and increments, respectively) using a *Leica DMLB 100T*
181 compound microscope and an *Imaging Source* digital camera (1.63x lens). Counts and measures of daily
182 increments were made using the *ObjectJ* (v1.04e) plugin for the image analysis software *ImageJ* (v1.51k;
183 Schneider et al., 2012). Whole otolith lengths were measured along the longest axis, core to edge
184 measurements were made from the core to the anterior tip of the otolith. Counts were made from the first
185 uninterrupted ring around the secondary growth centres and recorded as age post-settlement (Al-Hossaini

186 and Pitcher, 1988; Geffen et al., 2011; Modin et al., 1996). Increment widths were measured from the first
187 uninterrupted ring to the anterior edge close to the sulcus. Daily calibrations were made at both
188 magnifications and unit conversions were made in *ObjectJ*.

189 2.5. Data analyses and visualisation

190 The observed environmental data was supplemented with modelled wave exposure data (Wijkmark and
191 Isæus, 2010) downloaded from EMODNet (European Marine Observation and Data Network, 2018). Sites
192 where depth and weather prevented sediment sampling (24/146), were assigned substrate classes based
193 on substrate maps from EMODnet Geology (2016).

194 All data analyses were carried out in R statistical software(R Core Team, 2018). Fish length frequency
195 distributions were investigated using the package *mixtools* (Benaglia et al., 2009). Models were fit using
196 the package *glmmTMB* (Brooks et al., 2017) and tests of dispersion, zero inflation and residual patterns
197 were carried out using *DHARMa* (Hartig, 2018). Model validation utilised components of the package *caret*
198 (Kuhn et al., 2018) and model averaging was carried out using the package *MuMIn* (Barton, 2018). All
199 figures were produced using *ggplot2* (Wickham, 2016) and *gridExtra* (Auguie, 2017) with spatial data
200 transformed and integrated using *raster* (Hijmans, 2017), *rgdal* (Bivand et al., 2018), *rgeos* (Bivand and
201 Rundel, 2018) and *sp* (Bivand et al., 2013).

202 2.6. Habitat association models (HAMs)

203 Species abundances were modelled as functions of depth, substrate, sea-bottom temperature, and sea-
204 bottom salinity, as well as the natural log of the modelled wave exposure metric. Latitude was included as
205 an explanatory variable to describe variation in densities across the transition from North Sea to Baltic that
206 was not explained by salinity and primarily considered a proxy for proximity to alternate sources of settling
207 larvae. Oxygen, although measured in the field, was not used in modelling as all observed values were
208 above 90% saturation and hence were unlikely to impose limitations on fish presence or density. The
209 response variable was individual species abundance, including zero observations, and an offset of trawled

210 area was used to account for variation in effort across sites. An offset term is included in the linear
211 predictor to account for differences in observed counts due to changes in sampling effort. The coefficient
212 of the offset (trawled area) is set to 1, not estimated during model fitting. Because the linear predictor is
213 log-linked to the response, trawled area is log transformed to maintain the expected linear relationship.
214 The frequency distribution of densities and early data exploration (see supplementary materials) indicated
215 that abundances would be best modelled by either a zero-inflated Poisson or negative binomial
216 distributions. For each species, the full model (including all explanatory variables) was fit using four
217 different distributions, namely: Poisson, Poisson with a single zero inflation parameter (Rhodes, 2015),
218 negative binomial with variance increasing linearly with the mean (nbinom1), and negative binomial with
219 variance increasing quadratically with the mean (nbinom2) (Hardin and Hilbe, 2007); all of which utilised a
220 log-link between the response and linear predictor. Model residuals were standardised by comparing
221 observed values with the cumulative density function calculated from simulating each data point (1000
222 times) based on the fitted model and tests were made for uniformity, over/under-dispersion, and zero
223 inflation (see Hartig, 2018, and an example in the supplementary material of the current paper). The best
224 distribution to approximate the response was selected from those full models that satisfied residual tests
225 and by Akaike's Information Criterion (AIC). Using AIC to compare between distributions was valid because
226 all models used discrete probability distributions from exponential families. Drop-1 model selection was
227 carried out using AIC, where ΔAIC of six was used as a selection limit (Richards, 2008). If the final set of
228 models from drop-1 contained nested models, the significance of the extra explanatory variable was tested
229 with a likelihood ratio test.

230 *2.7. Habitat growth models (HGMs)*

231 The absolute growth of individual fish was determined from otolith growth in the ten days immediately
232 prior to capture. Growth in terms of somatic length was assumed to be linearly correlated with otolith
233 growth so that increment widths represent daily somatic growth. The width of the ten increments at the
234 otolith edge, as a proportion of the total otolith length, was considered equal to the change in somatic

length as a proportion of total length over the preceding ten day period prior to capture. This assumption of correlation between otolith length and somatic length was tested via linear regression of individual fish morphometry. The ten day growth rate was calculated as % increase in length per day over ten days (Lugert et al., 2016):

eq. 1
$$DLSGR = \left(\frac{\Delta FL}{FL - \Delta FL} \right) \times \frac{100}{\Delta T}$$

Where *DLSGR* is the daily length specific growth rate (percentage change per day), *FL* is fish length at capture, ΔFL is the change in fish length calculated from otolith growth, and ΔT is the change in time in days or the number of daily increments used to determine recent growth which was always ten.

These DLSGRs were used as the response variable in habitat growth models where they were modelled as a Gaussian response with a log link to the explanatory variables. The explanatory variables were the same as for the HAMs (section 2.6) but excluded the trawled area offset, included con-specific density (as catch per unit effort), the intrinsic effect of age, and included a random effect of site to account for the multiple fish caught per site. Residual tests, and model selection was carried out in the same manner as for the HAMs (section 2.6).

2.8. Model validation

All HAMs and HGMs retained from model selection were validated using repeated random subsampling, whereby 90% of the data were randomly allocated for re-estimating the parameters of the selected model before using the new fit to predict the 10% of data retained as a testing set. Because of the low sample size for the sole HGM, training and testing datasets were 85% and 15% respectively, so that test datasets were large enough to calculate validation metrics. This process was repeated 500 times and the bias, mean absolute error (MAE), root mean squared error (RMSE) and the coefficient of determination between predicted and observed values (*Rsq*) were recorded for the predictions made with each iteration.

257 *2.9. Predicted maps of habitat suitability*

258 The selected and validated models were used to predict density and site specific growth on a grid (0.025
259 decimal degrees latitude and longitude) across the study area. The grid was limited to the geographical
260 extent, the maximum depth (4m), and the substrate types (not rocks or boulders) that were sampled to
261 inform the model building. The grid contained exposure and substrate data from the sources used in
262 model building (see section 2.5), as well as temperature and salinity at 0.5m from the sea floor derived
263 from the coupled IBMlib framework (Christensen et al., 2018) and HBM model output (Berg and Poulsen,
264 2012; She et al., 2006). Temperatures and salinities used in predictions were monthly midday means for
265 the month of August, 2013. August was selected as the month in which most of the sampling to inform the
266 models took place and 2013 was the latest year for which these data were available. Where multiple
267 models were retained from model selection, weighted model averaging based on *MuMIn*'s AICc was used
268 prior to making predictions and plotting. When predicting with HAMs, the offset of the trawl area was set
269 to 200m² (the target size for the survey). When predicting with HGMs, the age was set to the species-
270 specific, median age of the dataset used to inform the models. Both expected values and standard errors of
271 predictions were plotted.

272 **3. Results**

273 *3.1. Summary of catches*

274 In total 476 plaice, 147 flounder and 88 sole were caught (Figure 1b, c & d). Plaice and flounder lengths
275 were both unimodal in distribution with means of 63 and 66 mm, respectively, and were all categorised as
276 young of the year (y0). Sole lengths were bimodal in distribution and mixture models indicated mean
277 lengths of 44 and 130 mm, these were categorised as y0 and age 1+ (y1) respectively. Ages were confirmed
278 in the subsample of fish used in otolith microstructure analyses. Young of the year plaice were caught at 67
279 sites, y0 flounder at 37 and combined y0+y1 sole were captured at 35 sites, so that the proportion of sites
280 with zero catches was 0.54, 0.75 and 0.76 respectively.

3.2. Otolith microstructure and growth

The sub-sample of individuals selected for otolith microstructure analyses (maximum of three per site) were all from the y0 cohort, confirming the earlier categorisation based on length. In total 161 plaice, 72 flounder, and 27 sole contributed to HGMs. Ages, in days post-settlement, ranged from 27 to 138 days for plaice, from 14 to 102 days for flounder, and 5 to 68 days for sole. Sole younger than 10 days post-settlement were excluded from HGM modelling due to the inability to calculate the ten-day DLSGR. Before otolith growth was used as a proxy for somatic growth the correlation between otolith size and fish size was confirmed via a linear regression of otolith total length and fish standard length. The linear relationship was strong for all species (Figure 2).

3.3. Habitat association models (HAMs)

Juvenile plaice density was best approximated by a negative binomial distribution where variation increased quadratically with the mean and changes in density were best estimated by a model with salinity, wave exposure and latitude as explanatory variables (Table 1). Flounder was best approximated by a negative binomial distribution, but with variation increasing linearly with the mean. Depth and salinity were the explanatory variables in the most parsimonious model of flounder density. There were too few of each age-class of juvenile sole to fit HAMs, and no models would converge for the individual datasets. Combined y0 and y1 abundances were high enough to fit models to and were best approximated by the negative binomial distribution with variance increasing quadratically with the mean. While combining y0 and y1 abundances provided enough data, there are significant limitations to this approach, which are outlined in the discussion, and the results of this exercise must be considered in this context. The effect of the explanatory variables at the scale of the response was determined by exponentiating (inverse of the log link) the regression coefficient of the linear predictor because the effects were not conditional on any random effects. Model validation showed that none of the models exhibit an overall bias. However, in some iterations of validation, biases were relatively strong, especially for plaice (Figure 3). Similarly, for the

305 measures of error (MAE and RMSE) the model for plaice density exhibited larger predictive errors than the
306 models for flounder and sole. The median of all R-squared values from correlations between predicted and
307 observed values was below 0.1 for all models. All iterations where the predicted vs. observed correlation
308 yielded an R-squared value higher than 0.5 were considered outliers in box and whisker plots (i.e. more
309 than 1.5 times the inter-quartile range of the median). These validation metrics indicate that the predictive
310 ability of the models was generally poor across all species.

311 *3.4. Habitat growth models (HGMs)*

312 Juvenile plaice growth rates per site increased with salinity but decreased with higher latitudes (Table 2).
313 YO flounder growth was positively influenced by increasing temperature and salinity per site. Site specific
314 YO sole growth was positively affected by increasing exposure. All three species exhibited a decreasing
315 length specific growth rate with increasing age post-settlement. Conspecific density was not retained for
316 any of the three species, and nor was there any apparent effect observed during data exploration.
317 Validation of the models selected to describe YO growth were all unbiased, had relatively low metrics for
318 error and high correlations between predicted and observed DLSGRs when predicting on test data (Figure
319 4). The ranges of the metrics derived from each iteration of cross-validation were especially large for sole,
320 where the 85%: 15% split of training and test data leaves the parameter estimation procedure with only 21
321 data points.

322 *3.5. Mapping potential juvenile habitat*

323 Interpolative maps of predicted density (Figure 5a, c, e) were produced for all three species and paired with
324 uncertainty maps of the predictions' standard errors (Figure 5b, d, f). Predictions (and standard errors) for
325 sole density were made with averaged models from the two HAMs retained at selection. Plaice densities
326 (Figure 5a) were predicted to be highest at positions inside and at the mouth of large fjord systems. Plaice
327 densities were also predicted to be high along the open coasts of the northern Kattegat. Flounder (Figure
328 5c) and sole (Figure 5e) were predicted to occur at much lower densities than plaice overall but both were

329 still predicted to have large scale gradients in density, increasing from north to south for flounder and,
330 conversely, south to north for sole. Standard errors for all three species were high and especially so for
331 plaice.

332 The HGMs were also employed in producing inferential maps to indicate habitat suitability based on growth
333 rates (Figure 6). Based on salinity and latitude, YO plaice growth was predicted to be high through the Belt
334 seas with the highest predicted values coming from the central Great Belt and the southern Little Belt
335 (Figure 6a). YO flounder growth rates were generally predicted to be higher than plaice across the study
336 area (Figure 6**Error! Reference source not found.**c). Predicted growth rates were near the extremes of the
337 range of predictions with close proximity in the north of the Jutland peninsula. YO sole growth predictions,
338 being driven by exposure, were highest in the north of the study area with isolated areas of high predicted
339 growth in the south-east (Figure 6**Error! Reference source not found.**e). Standard errors tended to
340 increase with the magnitude of the predicted value and provide a direct visualisation of the uncertainty in
341 the predictions (Figure 6**Error! Reference source not found.**b, d, and f).

342 **4. Discussion**

343 This study describes species specific models of fish density and growth for juvenile European plaice,
344 flounder and common sole. Furthermore, maps of potential habitat suitability are presented as
345 interpolative predictions of both density and growth throughout the inner Danish waters. Habitat
346 Association Models (HAMs), informed by directly observed environmental conditions, were able to describe
347 patterns of juvenile abundance observed in a targeted survey of a single growing season but exhibited poor
348 predictive ability during model validation. In contrast Habitat Growth Models (HGMs) exhibited relatively
349 strong predictive ability; however, this was likely driven by the inclusion of the intrinsic variable “age”,
350 rather than the environmental predictors. Both sets of models are used to describe juvenile habitat
351 suitability and although their validation metrics appear poor in isolation, they perform comparatively to

352 similar applications of generalised linear and mixed models (De Raedemaeker et al., 2012; Le Pape et al.,
353 2003b; Vasconcelos et al., 2013). Although model predictions performed similarly to other studies, their
354 limitations are evident in paired maps of predictions and the standard errors of the predictions, which
355 provide a direct visual representation of the underlying models' uncertainty.

356 While the empirical modelling approach employed in this study cannot indicate causative relationships
357 between the environmental predictors and fish responses, the biological mechanisms can be inferred by
358 comparison with findings from experimental studies. Furthermore, the correlative relationships can be
359 compared and contrasted with other empirical studies from other areas of the species' ranges. The
360 following two sections consider this study's findings in the context of the wider literature.

361 *4.1. Biological interpretation and support of models*

362 With the exclusion of the con-specific density variable from the HGMs during model selection, there was no
363 evidence for density dependent effects on growth in the data set. For plaice this finding concurs with more
364 temporally resolved growth studies from the British Isles (Ciotti et al., 2013; Nash et al., 2007) and a range
365 of field observations of predator/prey dynamics in the Wadden Sea (Karakiri et al., 1991; Van der Veer and
366 Witte, 1993). However, for all species, it is not possible to determine the reasons for this apparent absence
367 of a density dependent effect on growth. It may be due to the juvenile habitats not being saturated by
368 settlers (Nash et al., 2007; Nielsen et al., 1998), or that density dependence acts via higher mortality, earlier
369 in the season, when juveniles were both smaller and more numerous (Pihl and van der Veer, 1992; van der
370 Veer, 1986). Alternatively, density dependent growth limitation may not be apparent in the late-season
371 juveniles sampled, as those individuals that experienced depressed growth were more heavily predated
372 throughout the season due to their smaller size (Le Pape and Bonhommeau, 2015). Because there was no
373 observed effect of density dependence, and it is not possible to determine whether this is due to a real
374 absence of the effect or not, it is not considered in the remaining interpretation of the models.

375 The HAM for juvenile flounder describes a negative response of density to increasing salinity; for plaice the
376 retained salinity term was not significant, while sole densities were positively correlated with salinity.
377 Increases in the probability of occurrence and densities of y0 flounder in juvenile habitats have been
378 correlated to decreases in salinity along estuarine gradients throughout the majority of their range
379 (Amorim et al., 2018; Bos, 1999; Kerstan, 1991; Vinagre et al., 2008), which matches the current study's
380 findings. A key exception to this is in the Baltic proper, where the flounder exists at the lower limits of its
381 salinity tolerance (Florin et al., 2009; Martinsson and Nissling, 2011) and exhibits local adaptation
382 (Hemmer-Hansen et al., 2007a, 2007b) to the extent of speciation (Momigliano et al., 2018, 2017). The
383 relationship between flounder and salinity in the current study suggests that flounder of the inner Danish
384 waters follow patterns of distribution observed for western populations of flounder, where the transition
385 between estuarine and marine habitats are more abrupt. However, in the south of the study area, the
386 brackish nature of the coastal waters means they are suitable for life-stages where flounder would
387 ordinarily be found in riverine estuaries (Dando, 2011). Differences in flounder presence and density may
388 be driven by selection for low salinity at settlement (Jager, 1998) or juvenile dispersal post-settlement
389 (Andersen et al., 2005; Bos and Thiel, 2006). Juvenile plaice density has previously been demonstrated to
390 respond to salinity, but with conflicting reports of the direction in which it acts. On the Irish west coast
391 juvenile plaice density increased with salinity (De Raedemaeker et al., 2012), while in juvenile habitats in
392 the Bay of Biscay they reportedly decreased (Trimoreau et al., 2013). In Portuguese estuaries, juvenile sole
393 presence and density was negatively correlated with salinity (Vasconcelos et al., 2013) while Eastwood et al
394 (2003) employed salinity as a predictor variable in a similar manner but it was not retained as significant in
395 their models for juvenile sole of the Dover Straits. Le Pape et al (2003b) described a negative effect of
396 increased salinity, but this differentiation was made with a dichotomous "low" and "high" salinity being
397 below and above 31, where it was more of an indicator of increased productivity on juvenile habitats due
398 to nutrient input from the local river plume (Le Pape et al., 2003a). Older reports state salinity ranges of
399 between 10 and 35 as required for sole presence (Marchand, 1991; Riley et al., 1981), which extend beyond

400 the ranges of those observed in this study. The HGMs illustrate increased growth rates with increased site
401 salinity for both flounder and plaice. This response from flounder is in contrast to the aforementioned
402 observations of density and habitat selection, but aligns with the physiological response of laboratory
403 experiments on metamorphosing and newly-settled flounder (O'Neill et al., 2011). A field study on flounder
404 from the IDW has shown that juvenile flounder maintain high growth rates in both relatively high and low
405 salinity conditions, but to have significantly reduced growth rates under unstable, variable salinities
406 (Andersen et al., 2005). Neither the current study, nor the literature, provide evidence or even a
407 suggestion as to why this contradiction in behaviour and growth response might exist. However, given the
408 opportunity to speculate, one might envisage a trade-off between increased growth in saline coastal waters
409 and reduced competition/predation in the physically dynamic estuarine waters, or some other benefit of
410 estuarine habitats. Augley (2007) confirmed field observations of increased plaice growth rates in lower
411 salinities using controlled growth experiments (Augley et al., 2008) and attributed this response to reduced
412 osmoregulatory costs (Schreiber, 2001) under reduced (but still typically marine) salinities. The growth
413 model for juvenile plaice described in the current study contradicts this hypothesis by describing a positive
414 correlation between site salinity and growth rate.

415 Wave exposure had a negative influence on plaice density, and a positive effect on sole growth rate. Wave
416 exposure can influence juvenile density on soft-bottom habitats in multiple indirect ways, by means of
417 probability of larval supply, the sediment structure/organic matter content, and the density of predators
418 (Pihl et al., 2002; Pihl and van der Veer, 1992). In the bays of Sweden's western archipelago, Pihl et al
419 (2000) were unable to find correlations between juvenile plaice density and a fetch-based exposure metric,
420 they did however, show greater densities in bays of the outer archipelago, closer to the pelagic marine
421 habitat that supplies settling larvae. In the Bay of Biscay, average wave height was inversely correlated
422 with both plaice and sole density (Trimoreau et al., 2013) which the current study corroborates for plaice.
423 Trimoreau *et al* (2013) suggest that the mechanism that leads to increased juvenile sole abundance in less
424 exposed habitat may be the selection of habitat with appropriate sediment types at settlement. However,

425 the positive effect of exposure on site specific growth and not density, in the current study, suggests a
426 possible alternate mechanism; namely habitat selection by post-settled juveniles. These two forms of
427 habitat selection are certainly not mutually exclusive.

428 Juvenile plaice and flounder are often found sympatrically, however plaice have been shown to extend
429 their distribution to slightly deeper water while flounder remain restricted to the extreme shallows (Modin
430 and Pihl, 1996). This tendency between the two species has been illustrated again in this study where
431 flounder density is negatively correlated with depth while the depth ranges sampled are within the range of
432 depths that juvenile plaice likely inhabit, and hence no effect is detected. The absence of an effect of depth
433 on juvenile sole is likely due to the combination of y0 and y1 ages as the response. Young of the year sole
434 are known to inhabit much shallower water than older larger con-specifics, and so by combining their
435 abundances, the HAMs are unable to detect the effect of depth on either of these ages.

436 Temperature is of crucial importance to metabolic activity and hence growth in ectothermic fishes
437 (Magnuson et al., 1979) so it was surprising to find that the effect of temperature was only retained in the
438 HGM for flounder. Being mobile, these post-settled fish may simply move away from areas with a less
439 desirable temperature (Coutant, 1987), reducing the chance that temperature becomes a limiting factor for
440 growth. Indeed, we did see a negative effect of increasing temperatures on sole density, although
441 laboratory studies were unable to elicit avoidance behaviours at high temperatures (Schram et al., 2013).
442 Alternatively, flatfishes may be able to use burying to regulate their internal temperatures (Ziegler and
443 Frisk, 2019) against fluctuations in the shallow near-shore water columns, thus making measurements of
444 water temperature less related to the temperatures experienced. The signal of temperature effects in field
445 observational studies may be further confounded by food limitation (Sogard and Olla, 2001), hypoxia
446 (Pörtner and Knust, 2007), growth rates (Killen, 2014) or other physiological pressures that interact with
447 temperature.

448 Substrate type was not retained in any of the HAM or HGM models, which is surprising given flatfishes'
449 tight association with the seafloor and their experimentally determined preferences for different burying
450 sediments (Amezcuca and Nash, 2001; Gibson and Robb, 2000). Furthermore, Trimoreau *et al.* (2013) found
451 sediment type to have a significant influence on density of both common sole and plaice when applying a
452 similar approach as this study to model abiotic drivers of juvenile fish density. Other studies included
453 substrate types that were highly unlikely to be utilised, such as hard rock and boulders (Florin *et al.*, 2009;
454 Le Pape *et al.*, 2003b) and were able to determine significant effects of substrate from these disparate
455 types. However, other examples from the literature found substrate type did not contribute to significantly
456 improve models of juvenile flatfish density. For example: The exclusion of substrate type was attributed to
457 either the correlation with biotic predictor variables (De Raedemaecker *et al.*, 2012; Vinagre *et al.*, 2009),
458 the effect being partitioned out in the binomial part of a hurdle/Delta model (Vasconcelos *et al.*, 2013), or
459 offer no theory as to why sediment type was not retained (Vinagre *et al.*, 2005). In the current study,
460 restricting sampling to only soft-bottom habitats prevented the strong signal of absences on rocky bottoms.
461 Additionally, fish may have been utilising smaller patches of different substrate types found along the
462 200m² trawled area, which was represented by a single substrate sample. Smaller-scale, higher resolution
463 sampling would be required to investigate this further.

464 Overall the responses of juvenile fish density and growth described by the HAM and HGM models fit within
465 findings reported for these species in other areas of their range. Furthermore, the current study's results
466 match intrinsic and extrinsic mechanisms of juvenile fish distribution proposed by previous studies.

467 *4.2. Inclusion of the indirect predictors latitude and age*

468 Both HAMs and HGMs in this study included predictors that were not representative of a direct effect of
469 the physical environment at the study sites; for HAMs, this variable was latitude and for HGMs it was both
470 latitude and the age of the individual fish.

471 The transitional nature of the study area means that there is potential for different rates of colonisation in
472 juvenile habitats by populations from the brackish Baltic in the south (Petereit et al., 2014) and marine
473 populations in the north (Ulrich et al., 2013). Whilst salinity, another covariate, exhibits a large gradient
474 with latitude, close to the coast local and regional inflows of terrestrial water cause large perturbations to
475 this overall trend. The inclusion of latitude and salinity in the full models allowed model selection to
476 determine which predictor best explained the observed densities, the physiological driver of salinity or the
477 indirect effects of latitude – likely a proxy for proximity to additional sources of settlers. For plaice, both
478 variables were retained in model selection, where latitude had a strong positive effect on density, while the
479 effect of salinity was not significant but negative. This supports the theory of increased settlement from
480 North Sea/Skagerrak populations into the less saline Kattegat coast as proposed by Ulrich et al (2017). No
481 equivalent trend was seen for flounder nor sole, which is to be expected given previous descriptions of
482 Kattegat sole population(s) as relatively disconnected from North Sea populations (Cuveliers et al., 2012).

483 Age is a strong determinant of growth rate in teleost fish (Deniel, 1990) and it remained the strongest
484 determinant in the HGMs. The inclusion of age post settlement in the HGMs partitioned off a large
485 proportion of the variation in the observed growth rates (observed as changes in AIC), allowing effects of
486 environmental drivers to be more readily discerned from the remaining variation (Matta et al., 2018). The
487 retention of latitude in the plaice HGM indicates that juvenile growth rates were lower in the north. This
488 decrease in growth rate with latitude was in contrast to increasing growth rates with increased salinity,
489 which are generally higher in the north of the study area. Given the evidence that juveniles in the north of
490 the Kattegat may be supplemented with settlers from North Sea/Skagerrak spawning populations (Ulrich et
491 al., 2017; this study's HAM), the plaice HGM suggests there may exist an inherent difference in juvenile
492 growth trajectories between the two stocks. Such a difference may indicate local adaptation, as the local
493 northern (immigrant) juveniles have depressed growth rates. Whether such a difference between juveniles
494 of these stocks exists, and whether it is brought about via physiological or behavioural adaptations,
495 requires controlled growth trials to compare juveniles of known origin.

4.3. Current limitations and future development

The contradictory response of density and growth to certain environmental drivers illustrates the need to consider multiple measures of habitat suitability; for example, salinity's effect on both plaice and flounder. Future attempts at modelling juvenile habitat should utilise multiple proxies to represent the suitability of habitat, ideally including growth and mortality.

The habitat suitability metrics described in the current study cannot be used in isolation to determine overall juvenile habitat quality. The relative amount / temporal stability of the supply of settling larvae, the environmental conditions that contribute to juvenile production, and the connectivity of juvenile habitats to sub-adult/adult habitats must all be considered together before assessments of relative quality across all potential habitats can be made (Litvin et al., 2018).

To better understand the supply of settlers to juvenile habitats early in the season, the contribution of different spawning populations (Guinand et al., 2008) and mechanisms of larval transport to juvenile habitats (Mackenzie et al., 1994; Petereit et al., 2014; Ulrich et al., 2017) need to be considered together. Indeed the combination of data and expertise covering these species (Hemmer-Hansen et al., 2007a, 2007b) and the current study's area (Christensen et al., 2018) make such studies increasingly possible.

While the supply of settlers to juvenile habitats influences density, the combination of end of season density and growth in these habitats is what the current study deals with by employing an end-of-season snapshot sampling regime. Improvements to descriptions of habitat suitability can be made by improving the temporal scale to include both the variation in hydrography and juvenile habitat selection throughout the juvenile growing season as well as the inter-annual variability in hydrography that is especially pertinent in the transitional waters of the IDW (She et al., 2006).

Furthermore, the current study focussed primarily on open-coast habitats, so increasing sampling further into fjord systems would provide a greater breadth of possible conditions. This could potentially improve

519 the uncertainty of predictions in these areas, while also allowing comparisons between the productivity of
520 open coast and fjord system habitats. Increasing the breadth of temporal sampling and including more
521 sites within fjord systems would in turn increase the sample sizes available for HGMs, which were relatively
522 low for flounder and especially sole. The low sample sizes for sole forced the combination of the y0 and y1
523 age classes. Because of the ontological shift in habitat selection of common sole (Koutsikopoulos et al.,
524 1989), the combining of y0 and y1 abundances may have masked potential effects from different
525 environmental drivers. However, combining y0 and y1 individuals has been used previously (Vasconcelos
526 et al., 2013, 2010) and these two age groups are often assumed to live in the same or similar habitats
527 (Archambault et al., 2018) albeit with y1 able to extend their habitat to deeper waters (Rogers, 1993).
528 Interestingly, in spite of this confounding effect, temperature and salinity were still found to influence the
529 combined juvenile sole abundances, indicating similar responses to these environmental drivers across the
530 two age-groups. In the absence of any other information on juvenile sole habitat use from the IDW, the
531 results from the combined y0 and y1 abundances are presented here. However, the HAM models and
532 resultant predicted density maps for common sole in this study should be considered with caution and in
533 the context of this limitation. Future studies should aim to sample the different age groups of this valuable
534 fisheries species in higher numbers to better inform their different responses to environmental drivers.

535 The spatial scale of surveys and studies often reflect managerial jurisdictions, arbitrarily limiting sampling
536 areas to a subset of those that are relevant to natural processes such as dispersal and migration (Crowder
537 and Norse, 2008) and the current study is another example of this. Efforts should be made in future work
538 to include adjacent habitat areas from the Swedish west coast and the German Baltic coast to better
539 understand the full range of near-shore juvenile habitats servicing the transitional waters from Baltic to
540 North Sea.

541 The spatial scale of projects also influences the environmental variables that are considered. Measurement
542 of biological components of the environment, such as prey and predator densities, is resource intensive to

543 the point of being prohibitory in studies with large numbers of sites. Future work should pair with smaller
544 scaled, higher resolution investigations of habitat use in relation to prey, predators and habitat mosaics
545 (Nagelkerken et al., 2015; Sheaves et al., 2015), to better elucidate finer scale habitat selection and
546 alternative drivers of distribution.

547 In order for a well-supplied and highly suitable juvenile habitat to be considered productive for both the
548 population and the fishery, juveniles must migrate and recruit into adult populations (Beck et al., 2001;
549 Dahlgren et al., 2006). To quantify juvenile habitat quality at this scale, studies incorporating in-habitat
550 productivity (e.g. the current study) should be paired with connectivity studies tracking juvenile migrations
551 into fishery and spawning areas (Brown et al., 2019; Gillanders and Kingsford, 2003; Reis-Santos et al.,
552 2018; Vasconcelos et al., 2011). Combinations of habitat productivity and dispersal at different life history
553 stages can ultimately be used to build complex descriptions of population connectivity and production (e.g.
554 Archambault et al., 2018).

555 **5. Conclusions**

556 This study identified physical environmental variables that describe juvenile habitat suitability for European
557 plaice, flounder and common sole. Different aspects of the physical environment influenced habitat
558 suitability dependent on whether fish density or growth was employed as the proxy, highlighting the need
559 for multiple proxies to be considered before assigning “suitability” to different habitat areas. While this
560 study is the first to provide maps of juvenile fish habitat suitability throughout the inner Danish waters,
561 there is substantial scope for both improving the models predicting these suitability metrics and to further
562 develop understanding of settler supply and juvenile recruitment in these dynamic, transitional waters.

563

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950 *Figure 1. Top panel: Location of study area within northern Europe.. A: all sampling locations undertaken by*
951 *boat (○) and by hand (▽) as well as depth, with a limit of 120m placed on the scale to show the variation*
952 *through the majority of the study area . B, C, & D: Catch Per Unit Effort (number per square metre) of*
953 *European plaice, flounder and common sole (respectively) where symbol sizes are all on the same scale.*

954 Table 1. Habitat association models (HAMs) for European plaice, flounder and common sole of the inner Danish waters. Parameter Estimates are
955 reported on the scale of the link function and are inverse-link transformed under the column “Effect on Abundance”, and the associated probabilities
956 are derived from Wald-z statistics against a chi-squared distribution. For every one unit increase in the explanatory variable, the response will be
957 multiplied by the effect on abundance. *’s represent significance at $p < 0.05$ level.

Model	Explanatory Variable	Parameter Estimate	Parameter Probability	Effect on Abundance	N. Binom. Disp. Factor
$Abundance_{Plaice_{Y_0}} \sim \mu; \mu * (1 + \frac{\mu}{\varphi})$ $+ Latitude + offset(\ln(TrawledArea))$	Intercept	-47.944	0.006 *	~0	0.27
	Salinity	-0.028	0.486	0.972	
	Exposure	-0.606	0.008 *	0.546	
	Latitude	0.912	0.006 *	2.489	
$Abundance_{Flounder_{Y_0}} \sim \mu; \mu * (1 + \varphi)$ $+ offset(\ln(TrawledArea))$	Intercept	-4	<0.001 *	0.018	5
	Depth	-0.402	0.020 *	0.669	
	Salinity	-0.051	0.028 *	0.950	
$Abundance_{Sole_{Y_0+Y_1}} \sim \mu; \mu * (1 + \frac{\mu}{\varphi})$ $+ offset(\ln(TrawledArea))$	Intercept	-7.663	<0.001 *	~0	0.275
	Salinity	-0.070	0.013 *	1.073	
$Abundance_{Sole_{Y_0+Y_1}} \sim \mu; \mu * (1 + \frac{\mu}{\varphi})$ $+ offset(\ln(TrawledArea))$	Intercept	-1.203	0.565	0.300	0.265
	Temperature	-0.279	0.018 *	0.757

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959 *Figure 2 Linear relationships between otolith maximum diameter and fish standard length where points are*
 960 *individual fish, lines are linear regressions for young of the year (y0) European Plaice ($R^2 = 0.91$, $F_{1,157} =$*
 961 *1500, $p < 0.001$), flounder ($R^2 = 0.83$, $F_{1,69} = 337$, $p < 0.001$), and common sole ($R^2 = 0.84$, $F_{1,24} = 126$, $p <$*
 962 *0.001) in A, B, & C respectively. Shaded ribbons are standard errors around the regressions.*

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 964 individual fish, lines are linear regressions for young of the year (y0) European Plaice ($R^2 = 0.91$, $F_{1, 157} =$
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 966 0.001) in A, B, & C respectively. Shaded ribbons are standard errors around the regressions.

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969 Figure 3. Model validation metrics for the selected Habitat Association Models for European plaice, flounder
 970 and common sole. Box and whiskers are the metrics derived from 500 iterations of random repeated sub-
 971 sampling, training on 90% of the data and testing on the remaining 10%. Asterisks (*) indicate the metric
 972 calculated for the model trained on and subsequently predicting over the whole data set. The two models
 973 labelled for sole are those with either salinity (S) or temperature (T) as explanatory variables.

974 Table 2. Habitat Growth Models (HGMs) for young of the year European plaice, flounder and common sole. Parameter estimates are reported on the
975 scale of the linear predictor and the associated probabilities are derived from Wald-z statistics against a chi-squared distribution. The column “Effect
976 on DLSGR per site” contains the inverse link transformed parameter estimates and represent the effect of the explanatory variable but conditioned on
977 the random effect of site. *’s represent significance at $p < 0.05$ level.

Model	Explanatory Variable	Parameter Estimate	Parameter Probability	Effect on DLSGR per site	Variance in Random Effect
$DLSGR_{Plaice_{y0}} \sim \text{LogN}(\mu, \sigma^2)$ $+ RE(site)$ <i>Salinity + Age + Latitude</i>	Intercept	12.09	<0.001 *	-	0.024
	Salinity	0.018	0.011 *	1.018	
	Age	-0.028	<0.001 *	0.977	
	Latitude	-0.193	<0.001 *	0.824	
$DLSGR_{Flounder_{y0}} \sim \text{LogN}(\mu, \sigma^2)$ $+ Age + RE(site)$ <i>Temperature + Salinity</i>	Intercept	0.562	0.181	-	0.014
	Temperature	0.041	0.025 *	1.042	
	Salinity	0.016	0.003 *	1.016	
	Age	-0.022	<0.001 *	0.978	
$DLSGR_{Sole_{y0}} \sim \text{LogN}(\mu, \sigma^2)$ $+ RE(site)$ <i>ln(Exposure) + Age</i>	Intercept	-0.393	0.617	-	0.03
	Exposure	0.155	0.018 *	1.167	
	Age	-0.019	<0.001 *	0.981

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Figure 4. Model validation metrics for the selected Habitat Growth Models (HGMs) for European flounder and common sole. Box and whiskers are the metrics derived from 500 iterations of random repeated subsampling, training on 90% of the data and testing on the remaining 10%. Asterisks () indicate the metric calculated for the model trained on and subsequently predicting over the whole data set*

985 *Figure 5 Predicted (A, C, & E) Densities and associated standard errors of the predictions (B, D, & E) for*
986 *European plaice (A & B), flounder (C&D), and common sole (E & F). Predictions are based on Habitat*
987 *Association Models (see section 3.3 and 3.5), where the environmental variables are averages from midday*
988 *across the month of August in 2013. Colour scales are limited to 1.5 times the interquartile range above the*
989 *median abundance (corresponding to the end of the whisker on a box and whisker plot) to better illustrate*
990 *the variation through the middle of the range of predicted abundances.*

992 *Figure 6. Predicted (A, C, & E) Daily Length Specific Growth Rates and the associated standard errors of the*
993 *predictions(B, D, & F) for European plaice (A & B), flounder (C & D), and common sole (E & F). Predictions*
994 *are based on Habitat Growth Models (HGMs) (see section 3.4 and 3.5), where the environmental variables*
995 *are averages from midday across the month of August in 2013 and age is set to 58, 61 and 40 days (plaice,*
996 *flounder and sole, respectively) post-settlement based on the median of individuals used to inform the*
997 *models.*