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Contribution to the Themed Section: 'The Value of Coastal Habitats for Exploited Species'

Nursery habitat availability limits adult stock sizes of predatory coastal fish

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Habitat protection is a strategy often proposed in fisheries management to help maintain viable populations of exploited species. Yet, quantifying the importance of habitat availability for population sizes is difficult, as the precise distribution of essential habitats is poorly known. To quantify the contribution from coastal nursery habitats to exploited fish population sizes, we related adult density to the amount of nursery habitat available for 12 populations of the two dominant predatory fish species in a 40 000-km^2 archipelago area of the Baltic Sea. Habitat distribution was mapped using three conceptually different techniques, Maxent, generalized additive models, and random forest, using spawning and 0-group point samples. Adult densities were estimated from gillnet surveys. Regressions demonstrated no evident effect from fishing, whereas habitat availability had a positive effect, explaining almost half of the variation in population sizes of both species. This result shows that a substantial proportion of the potential production of adult fish can be estimated by mapping essential nursery habitats distribution. Responses were non-linear, indicating that habitat protection has largest effects where there is little available habitat. By demonstrating the importance of habitat limitation of two exploited fish species, we provide quantitative support to the benefits of habitat protection for fisheries.

Keywords: coastal management, conservation, essential fish habitat, fisheries management, generalized additive models, maximum entropy, niche models, random forest, species distribution modelling.

Introduction

The use of protected areas in ecosystem-based management of freshwater, coastal, and offshore habitats has been proposed as a primary means to restore and conserve declining fish stocks worldwide (Abell *et al.*, 2007; Thrush and Dayton, 2010). To this end, two main mechanisms are at work, the actual protection of fish by reducing fishing (Worm *et al.*, 2009) and the protection of essential habitats (Thrush and Dayton, 2010). Although the former mechanism is well-established, the influence of the amount of essential habitats on fish population dynamics are poorly described and rarely incorporated into scientific advice for fisheries management (Mangel *et al.*, 2006; Armstrong and Falk-Petersen, 2008; Thrush and Dayton, 2010). This can largely be attributed to the difficulties of establishing an empirical link between habitat availability and fish population sizes (but see Rijnsdorp *et al.*, 1992; Mumby *et al.*, 2004; Fodrie and Levin, 2008). Progress within this area has been hampered, mainly by a lack of knowledge of the actual distribution of habitats (Mangel *et al.*, 2006; Armstrong and Falk-Petersen, 2008). Although mapping of habitat distributions may be considered less of a problem in ecosystems where water visibility is high, e.g. coral reefs (Mumby *et al.*, 1997), direct mapping of habitats is difficult in turbid waters and when habitats are characterized by a combination of several continuous environmental gradients. However, with the development of species distribution modelling techniques, whereby species occurrence or abundance is related to map-based predictor variables, fine-scale mapping of species and habitat distributions across spatially heterogeneous ecosystems is becoming a manageable task (Elith and Leathwick, 2009; Pittman and Brown, 2011). A wide range of modelling techniques is available but method-specific differences can yield varying predictive performance (Elith and Graham, 2009). To reduce the bias and uncertainty related to the choice of modelling method, ensemble approaches have been suggested to obtain more robust predictions (Araújo and New, 2007). The concept applied in this study includes using the mean of multiple model techniques, so that the error associated with any given model and technique is reduced and higher predictive accuracy is achieved (Grenouillet *et al.*, 2011).

By using three different techniques for modelling species distributions, we quantitatively assessed the relationship between adult fish density and the availability of nursery habitats, the areas utilized by the earliest life stages, for 12 populations of the two dominating predatory fish species, pikeperch (*Sander lucioperca*) and Eurasian perch (*Perca fluviatilis*), in the coastal areas of the Baltic Sea (Ådjers *et al.*, 2006). Perch in particular but also pikeperch closely resemble their North American relatives, yellow perch (*Perca flavescens*) and walleye (*Sander vitreus*; Craig, 2000). We expected that limited availability of suitable habitats for a specific life stage would influence the population size in species that shift habitat and diet with ontogeny, as the amount of a critical habitat may act as a bottleneck limiting the abundance of later life stages (Halpern, 2004). Perch is highly selective in its choice of spawning habitat, preferring shallow and sheltered areas with suitable vegetation and temperature development during spring (Snickars *et al.*, 2010). The larvae remain in the close vicinity of the spawning grounds and initially feed on zooplankton (Karås, 1996b). Pikeperch typically spawn in waters with low visibility primarily in the inner parts of the archipelago (Veneranta *et al.*, 2011), where the juveniles also stay during their first year of life (Sandström and Karås, 2002). Both species are fished commercially and are highly sought after by recreational fishers (FGFRI, 2009; Thörnqvist, 2009; ICES catch statistics).

Methods

Study area and field sampling

The highly complex topography of the 40 000-km^2 archipelago study area, situated between the mainland of Sweden and Finland in the central Baltic Sea, is characterized by a patchy habitat distribution (Figure 1). In this coastal environment, broad-scale habitat mapping by comprehensive field surveys is not feasible due to the cost of detailed surveys in such a large and heterogeneous area with poor water visibility and strong environmental gradients. Instead, distribution modelling of habitats and associated fish communities, based on a combination of field surveys, statistical modelling, and spatial prediction, provides a more cost-efficient way of obtaining full-coverage maps. Our approach aimed to detect a habitat–stock relationship rather than a stock-recruitment relationship (i.e. a bottom-up effect based on the availability of nursery habitats). Therefore, it was important to separate the recruitment estimates, i.e. predicted nursery habitat availability, from the abundance of spawning individuals. Hence, we largely separated the sampling of adult and earlier life stages in space and, importantly, based the habitat distribution modelling of nursery habitats on the presence–absence of recruits, rather than abundance. Actual spawning observations, i.e. the presence of egg strands, were used to model the distribution of perch nursery habitats, since larval drift is very restricted for this species and most larvae are found in proximity (∼100–2000 m) to the spawning habitat (Karås, 1996b). The distribution of perch egg strands was surveyed at regular intervals while manually snorkelling along transects at 22 sites (i.e. bays) during spring 2003 (described in Snickars *et al.*, 2010), and in spring 2007 by observation from boats, slowly manoeuvred along the shoreline. The 2007 survey was conducted at 15 sites at 1–3 occasions between April 24 and June 6, covering the full spawning season (Snickars *et al.*, 2010). Environmental conditions and the occurrence of egg strands were recorded at every 10 m section along the surveyed transects, resulting in 302 individual egg strand presences out of a total of 4039 transect sections. To model the distribution of pikeperch nursery habitats, 0-group fish was sampled in late summer 2005–2007 and 2009 using small (10 g explosive) underwater detonations (Sundblad *et al.*, 2011). This active sampling method, which is non-destructive with respect to other biota than fish, is used by Scandinavian fish researchers to obtain point abundance samples in heterogeneous environments where other methods such as beach-seines, small trawls, and drop-samplers are difficult to use (Snickars *et al.*, 2007). The method captures all species with gas-filled cavities within approximately a 5-m radius of the detonation and yields representative length distributions of fish between 3 and 20 cm total length (unpublished data). In total, 570 detonations (with 33 presences) of pikeperch were used in the subsequent distribution models. Importantly, both field surveys were designed to cover the gradients of the environmental variables used as predictors in the models by sampling from the lowest to the highest values of all environmental descriptors and ensuring that all combinations had been surveyed. Although this resulted in relatively few presences of pikeperch, it also minimized the risk that the model predictions were skewed as a consequence of a non-representative sampling design.

Adult population estimates in 12 areas were derived from standardized Nordic multimesh gillnet monitoring of coastal fish communities carried out annually in August, i.e. outside the spawning season, at fixed stations randomly stratified by depth (Ådjers *et al.*, 2006; Figure 1). Adult population abundance (catch per unit effort, cpue) was measured as catch in numbers per station (0–10-m water depth) and fishing night of perch of >20 cm total length and pikeperch of >30 cm total length, i.e. the length corresponding to maturity (Sandström *et al.*, 1995; Heikinheimo *et al.*, 2006). Age at maturity for both species is for males normally 2–4 and for females 3–5 years. In general, all monitoring areas have been chosen to reflect the natural fish community composition by minimizing local anthropogenic influence such as pollutants and physical habitat disturbance. The study area was limited in latitude (58.8°–60.5°N) to minimize differences in latitudinal gradients such as day length and temperature, which might otherwise influence our estimates of adult population size by adding variability in, for example, growth rates. Simultaneously, we wanted to reduce temporal variation and maximize spatial replication within the study area to capture the spatial variability in fish community composition (Ådjers *et al.*, 2006). Consequently, we used the mean cpue from

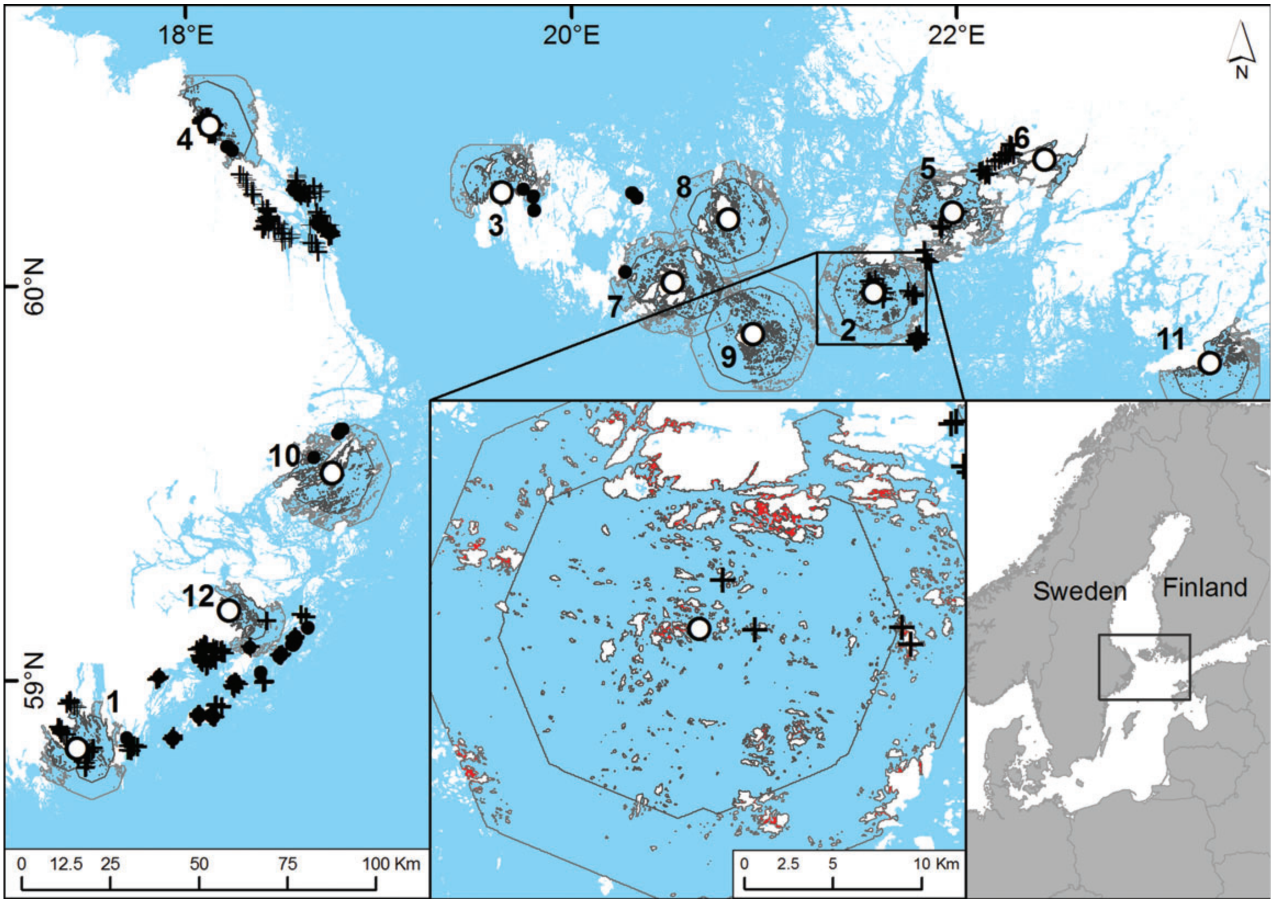

Figure 1. Distribution of adult fish population estimates and sampling localities in the Baltic Sea archipelago between Sweden and Finland. The studied fish populations were defined as being within 10 and 15 km water distance (black and grey polygons) from the centre of each gillnet monitoring area (white points). Small solid circles denote sampling stations for perch and crosses denote stations sampled for pikeperch. The inset exemplifies the predicted habitats for perch (red) and numbers correspond to Table 1.

2005 and 2006 ($n = 773$ net nights, Table 1) as these years had the highest number of populations sampled. cpue from these years did not deviate from the mean of the time-series in the seven areas where 4–7 years of monitoring data were available, ensuring that our results were not related to specific or extreme year-classes.

Habitat distribution models

To predict the availability of nursery habitats, high-resolution maps of water depth, wave exposure, and water transparency (Secchi depth) were chosen as ecologically relevant environmental descriptors as they are known to influence habitat conditions and thus recruitment (Snickars *et al.*, 2009, 2010; Sundblad *et al.*, 2011). For fitting the distribution models, we used water depth measured during sampling of fish in the field, and the projection to geographical space was based on interpolated depth models from digital sea charts and terrain databases. Log_{10} transformed wave exposure estimates were derived from a specific software, WaveImpact (Isæus, 2004), which has been extensively used for predicting distribution patterns in Baltic Sea coastal areas (e.g. Sundblad *et al.*, 2011). Water transparency was measured as the mean summer Secchi depth derived from a spatial model based on monitoring data between 2000 and 2008. The model explained 85% of the variation and evaluation against with-held data resulted in an r^2 of 0.79 and a root mean square error of 0.69 m (Bergström *et al.*, in press).

To obtain more robust predictions (Araújo and New, 2007; Grenouillet *et al.*, 2011), three unrelated and conceptually different modelling techniques, generalized additive models (GAMs), Maxent, and random forest (rF), were employed for relating the earliest life stages of perch and pikeperch distributions to the environmental descriptors and for producing map predictions of nursery habitat availability. These methods were chosen as they together provide a multifaceted analysis of the descriptors regulating the habitat distribution. In our opinion, GAMs display how the individual main effects influence the response, in a flexible data-driven approach (see below). Maxent similarly provides the individual effects but with a presence-only technique, which is interesting to contrast as absences are inherently more uncertain than presences. Finally, rF complements the other two methods in the sense that it is a highly flexible discrimination method capable of fitting a multitude of both main and interactive effects. Thus, this ensemble modelling approach is likely to provide predictions with a higher confidence than relying on any of the techniques individually (Araújo and New, 2007; Grenouillet *et al.*, 2011).

GAMs are semi-parametric extensions of generalized linear models, useful for fitting non-linear relationships without prior

Table 1. Adult population abundance measured as catch in numbers per station and fishing night (cpue) of perch of >20 cm and pikeperch of >30 cm for the populations monitored by gillnets.

Number	Name	Effort (net nights)	Perch (cpue)	Pikeperch (cpue)	Years sampled
1	Askö	72	3.24	0.38	2005/2006
2	Brunskär	72	16.08	0.13	2005/2006
3	Finbo	80	5.44	0.19	2005/2006
4	Forsmark	89	5.47	0.22	2005/2006
5	Skärgårdshavet	30	7.97	0.27	2005
6	Åbo	73	1.18	0.37	2005/2006
7	Åland East	40	15.68	0.00	2006
8	Kumlinge	80	9.86	0.05	2005/2006
9	Kökar	43	13.21	0.05	2005
10	Lagnö	80	5.95	0.00	2005/2006
11	Tvärminne	60	4.10	0.50	2005/2006
12	Tyresö	54	3.17	0.13	2005/2006

Numbers correspond to the map in Figure 1.

assumptions on the shape of the response (Wood, 2006). GAMs with binomial error distributions were run on presence–absence data using the "mgcv" package for R (Wood, 2006). Model selection was based on penalized regression splines with default gamma values and a maximum of 2 degrees of freedom for continuous predictor variables to maintain ecologically interpretable models (Wood and Augustin, 2002).

Maximum entropy modelling as implemented in the software Maxent is a machine-learning technique based on a probability density estimation method (Elith *et al.*, 2011). Maxent utilizes the information in presence-only data together with background layers of the environment and has been shown to perform well compared with other commonly used methods for modelling species distributions (Elith *et al.*, 2006). The models were run under version 3.3.3a. As recommended (Phillips *et al.*, 2009), we restricted all background environmental layers to the maximum sampling depth, i.e. 6 m, to ensure that the background environmental data used in model fitting was not randomly sampled outside the extent of this study. The regularization parameter was set to 2 for both species to make the responses smooth and ecologically interpretable.

rF is an ensemble method where a large number of decision trees are built and responses are predicted based on majority rules from all trees (Breiman, 2001; Cutler *et al.*, 2007). Compared with traditional classification trees, the main advantages are that rF produces more accurate predictions, is easier to use as it requires no pruning, and provides a measure of predictor variable importance. For modelling and predicting presence–absence, we used the package "randomForest" for R (Breiman, 2001). We developed models with 1000 classification trees each, but exploratory graphs indicated that error rates became stable well before this number of trees was developed. To ease interpretation of the partial response curves, we applied a smooth spline function with 5 degrees of freedom on the predicted values.

To assess GAM and Maxent model performance, we used tenfold cross-validation and the area under the curve (AUC) value of receiver operating characteristic plots (Fielding and Bell, 1997). For each fold, a subset of the data is withheld during model building and used as a test set, which has the advantage of utilizing all available data for both model building and validation. AUC values range between 0.5 and 1 and is a threshold-independent measure of the discriminatory ability of the model. A model that performs no better than a random model has an AUC value of 0.5, whereas a model that perfectly discriminates between occupied and unoccupied sites has a value of 1. Values above 0.8 can be considered excellent (Hosmer and Lemeshow, 2000). For rF, models were validated using the bootstrapped out-of-bag (OOB) error estimate, which is given as percentage error rates. OOB is estimated internally in the model runs and is conceptually similar to cross-validation as the sample is split into a training and a validation part in the construction of each tree. Based on each model and using maps of the three environmental descriptors, the predictions of probability of presence were made. The predicted distributions of nursery habitats were evaluated using AUC values by comparing the predicted probabilities with observed distribution patterns. This measure, $\mathrm{AUC}_{\mathrm{map}}$, compared with the internally estimated discriminatory ability, thus reflects the quality of the environmental predictor layers and how each method has performed when projected into geographical space. Lastly, each prediction was dichotomized into suitable and unsuitable nursery habitats by applying a cut-off value at the probability that maximized sensitivity and specificity, the ability to correctly predict both presences and absences (Jiménez-Valverde and Lobo, 2007).

Habitat availability

Genetic studies have shown that perch exhibits a population structure that varies on fine spatial scales (Olsson *et al.*, 2011), and the longest typical adult migration distance is ~10 km (Saulamo and Neuman, 2002). Comparably, typical adult migration distance for pikeperch in this area is ~15 km (Saulamo and Neuman, 2002). Thus, habitat availability per population was measured within 10 and 15 km water distance (i.e. moving around land and islands), respectively, from the centre of each monitoring area to match the population scale. Habitat availability was expressed as the per cent of the monitoring area predicted as suitable habitat by each modelling method. Agreement in the amount of predicted nursery habitats among modelling methods were evaluated by Pearson's correlation coefficient. Lastly, the mean per cent suitable habitat predicted by the three modelling techniques was used as an independent variable in a linear regression with cpue of adult fish as dependent response. Independent variables were ln-transformed to meet normality assumptions. Since two populations of pikeperch were predicted to have zero per cent available habitats, we needed to add a constant to be able to apply the transformation. This constant was set to one quarter the size of the smallest positive value (i.e. 0.02% available nursery habitat).

Fishing pressure

Fishing pressure was mapped for the whole study area by combining spatial information on commercial and recreational fishing. Commercial fishery catch statistics for the years 2005/2006 were available per ICES statistical rectangle, which are ~55 by 55 km. For each rectangle and species, we calculated the mean catch per year and square kilometre water area. Recreational catch statistics for Finland and Sweden were obtained from national enquiries (FGFRI, 2009; Thörnqvist, 2009). Similar to Nadon *et al.* (2012), we used census data to allocate recreational catches spatially within the study area in two ways. First, the distribution of recreational fishers was estimated using a moving window function on a human population density map (Sweitzer *et al.*, 1996). The window size was set to 30 km, based on enquiry data on the average travel distance of fishing trips (Thörnqvist, 2009). Second, total catches within the study area were allocated according to the distribution of fishers and were calculated as catch per year and square kilometre water area. The sum of the layers of commercial and recreational catches provided a map estimate of total fishing pressure per species and population. Fishing pressure was ln-transformed to meet normality assumptions.

Results

All modelling methods had an excellent predictive performance regarding nursery habitat availability (Table 2). As expected, there was a slight decrease in performance when the models were projected into geographical space, most likely primarily due to the low accuracy of the interpolated depth models on which the distribution models were projected, compared with the field measured depth that were used in model fitting. Nevertheless, all methods still performed satisfactorily by bordering to or exceeding excellent discriminatory ability ($\text{AUC}_{\text{map}} \geq 0.8$), except for rF predictions of perch nursery habitats (Table 2). Corroborating earlier studies, nursery habitats for both species were characterized as shallow and sheltered areas, which are most often found in the inner to middle archipelago regions, while the opposite patterns were apparent regarding preference for water transparency (Figure 2). Pikeperch showed a strong affinity for turbid waters (Secchi disc depth <2–3 m), while perch partial response to Secchi depth indicated a general preference for clearer waters. In general, the three modelling techniques showed a good agreement regarding the shape of the relationships between the probability of presence and the environmental predictor variables for both species, with a few deviations. The relationship between perch and Secchi depth indicated a more positive response around 2 m and a small dip around 3 m Secchi depth for the rF model, followed by a general increase in preference for clearer water. However, the curviness of the relationship was generally close to the upper and lower bounds indicated by the other two techniques. Similarly, for pikeperch response to wave exposure, rF deviated from the other two techniques at values below 3.4, corresponding to the very sheltered range where no pikeperch was present. This illustrates the uncertainty of the species–environment relationships related to any specific technique, which was accounted for by utilizing the mean predicted availability of nursery habitats of the three modelling techniques. As a result of the differences regarding the fit to the environmental descriptors, the three techniques differed somewhat in the exact distribution of nursery habitats at a cell-by-cell basis (metre scale). Nevertheless, the availability of nursery habitats predicted by the three modelling techniques significantly correlated at the population scale (Table 3), i.e. all three techniques showed strong agreement within 10 and 15 km from the centre of the monitoring stations at which scale adult population sizes were estimated.

Table 2. Predictive performance of the distribution models.

	Perch (*P. fluviatilis*)	Pikeperch (*S. lucioperca*)
Maxent cvAUC	0.98 (0.02)	0.96 (0.03)
GAM cvAUC	0.85 (0.03)	0.94 (0.04)
rF OOB	2.8	6.1
Maxent AUC_{map}	0.79	0.86
GAM AUC_{map}	0.80	0.87
rF AUC_{map}	0.65	0.95

For Maxent and the GAM, model performance, i.e. discriminatory ability, is measured as cross-validated AUC values (cvAUC ± s.d.) and for rF as OOB error rate (OOB %). AUC_{map} is the performance when applied in the geographical space and is therefore dependent on the quality of the environmental predictor layers.

The mean availability of nursery habitats explained almost half of the variation in adult population size for both species (Figure 3). For perch, the model $y = a \times \ln(x) + b$ had $a = 2.03 \pm 0.69$ (s.e.) and $b = 9.39 \pm 1.27$ (s.e., $n = 12$) and explained 46% of the variation in adult population density ($p = 0.0148$, $F_{1,10} = 8.643$). For pikeperch, the model $y = a \times \ln(x + 0.02) + b$ had $a = 0.05 \pm 0.02$ (s.e.) and $b = 0.21 \pm 0.04$ (s.e., $n = 12$) and explained 48% of the variation in adult population density ($p = 0.013$, $F_{1,10} = 9.098$).

Fishing pressure was subsequently tested to ascertain that areas with low cpue did not have a high fishing pressure, as this could obscure observed habitat effects. However, for pikeperch, there was a non-significant positive correlation between fishing pressure and adult population size ($r = 0.54$, $p = 0.071$, $t = 2.02$, d.f. $= 10$), and no trend was found for perch ($r = 0.08$, $p = 0.795$, $t = 0.267$, d.f. $= 10$). Fishing pressure in the 12 areas was generally low with mean and maximum catch estimates being 27 and 133 kg km^{-2} year^{-1} for perch and 16 and 93 kg km^{-2} year^{-1} for pikeperch.

Discussion

By mapping the availability of essential nursery areas, we demonstrate that habitat bottlenecks at early life stages may limit the abundance of later adult stages of predatory fish. These results provide support for the importance of essential habitat protection as a tool to restore and sustain exploited fish stocks of coastal species. The strong relationship between fish population size and nursery habitat availability suggests that nursery habitat abundance, in combination with low to moderate adult fish mobility, constrains the population size in a given local area, thus highlighting the importance of the landscape habitat distribution for intra-population dynamics. To mechanistically understand what regulates fish population sizes at the scale of the current study is a challenging task (e.g. Houde, 2008). Previous work on perch and pikeperch year-class strength has pointed out water temperature during early summer as the main driver behind their recruitment dynamics (Kjellman *et al.*, 2003), i.e. temporal variation. However, from a spatial perspective, we suggest that the availability of suitable habitats for specific life stages may limit the production of fish. In other words, it appears that for a given population, the variation between years is primarily influenced by temperature, whereas, as suggested by the patterns observed in this study, the mean differences in recruitment between populations are to a substantial part dependent on the availability of nursery habitats. These sheltered nursery habitats become warmer early in spring and have extended macrophyte vegetation that provide refuge from predation and substantially higher densities of zooplankton prey than surrounding waters, thus providing suitable conditions for larval survival and growth (Karås, 1996a; Ljunggren, 2002; Kallasvuo *et al.*, 2009; Ljunggren *et al.*, 2010; Snickars *et al.*, 2010). An important pattern in our results is the non-linear relationship between habitat and population size (i.e. the ln-transformed *x*-axis in Figure 3). This suggests that high access to nursery habitats is only important up to a certain threshold, thereafter the relationship appears to level out, indicating that other regulating mechanisms override the

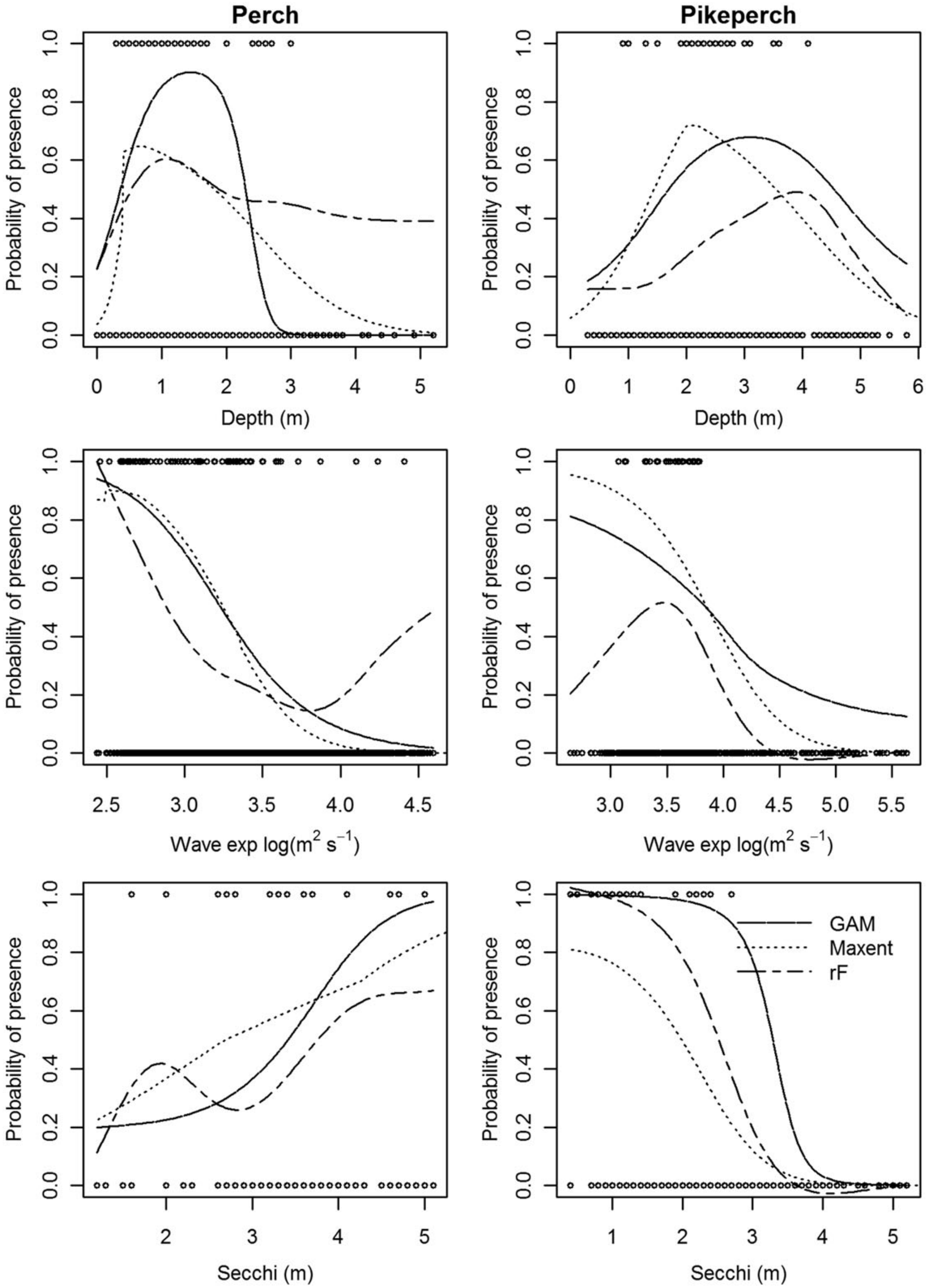

Figure 2. Partial response curves along the three environmental predictors from three separate modelling methods. Circles within panels indicate observed presence (top) and absence (bottom) along each environmental predictor. Modified after Bergström *et al*. (in press).

Table 3. Correlation coefficients, *r*, for the availability of nursery habitats per population predicted by the three modelling techniques.

	Maxent	GAM	rF
Maxent		0.72	0.59
GAM	0.98		0.96
rF	0.99	0.95	

The upper triangle shows Pearson's coefficients for perch and the lower triangle for pikeperch. All correlations were significant at $p < 0.05$.

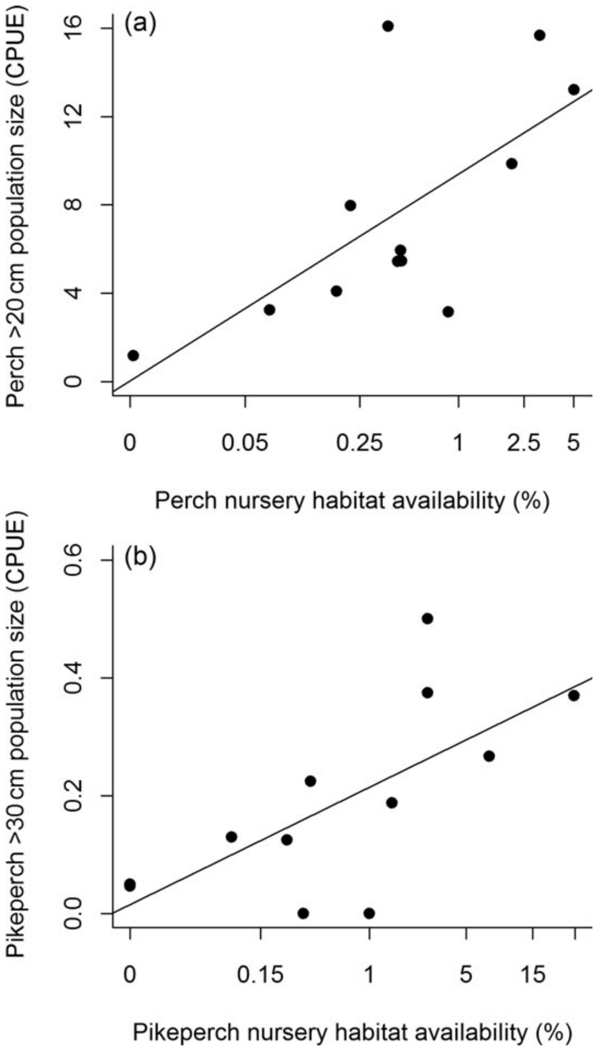

Figure 3. Adult fish population size as a function of nursery habitat availability for 12 populations of (a) perch ($r^2 = 0.46$) and (b) pikeperch ($r^2 = 0.48$) in the Baltic Sea. cpue and habitat availability were measured within the average migration distance of the 12 populations. The *x*-axes are presented on a ln scale.

importance of habitat availability. Also, the decreasing slope of the function with increased habitat availability indicates that measures directed at habitat protection, or restoration, would have larger effects in areas where there is currently little available habitat. Similar relationships, where access to high-quality juvenile habitats may regulate the stock size, have previously been emphasized in the management of riverine fish, where such considerations have been used to determine the production potential for species like trout and salmon (ICES, 2012). Our observation that similar patterns also occur in complex, open marine systems underscores the importance of understanding the spatial component of the environment when assessing differences in fish production. This study further shows that by recognizing a critical habitat limiting population size, fisheries may actually gain from habitat protection directed at earlier life stages in spatially separate areas (Roberts *et al.*, 2001; Meynecke *et al.*, 2008). An increased survival of juvenile fish dependent on specific habitats has been exemplified in habitat types that are distinct and easy to identify, such as coral reef and mangrove systems (Doherty and Fowler, 1994). However, for most fish species, habitats are characterized by a combination of several continuous environmental gradients and are, hence, difficult to map. We show how these indistinct habitats can be delineated using spatial modelling. By quantitatively relating the distribution of stage-specific habitats to population size, the approach we present thus allow researchers and managers to get an approximate estimate of the expected production of adult fish based on the predicted availability of essential habitats. This yields an estimate that could be considered a baseline for expected stock size under natural conditions. Such a habitat-based measure of potential productivity would be highly useful in fisheries and marine ecosystem management, e.g. by predicting impacts from habitat loss or changes in habitat productivity following alterations in environmental conditions.

The distribution of nursery habitats is, however, not static over time, and temporal dynamics may reduce the long-term generality of the habitat predictions. We have tried to take into account this temporal uncertainty and the use of both optimal and suboptimal nursery habitats by using field data from multiple years to predict the temporal average distribution of nursery habitats. Additionally, we have only included general environmental descriptors such as depth, 10-year averaged wave exposure, and summer Secchi depth, which may also serve to increase the generality of the predictions. To account for the uncertainty in the modelling process, three different statistical techniques were employed. The species–environment relationships, as indicated by the partial response curves, and the spatial predictions were in general similar between techniques, indicating that the predictions were reliable. One exception was the rF prediction for perch, which became quite poor when projected to geographical space ($\text{AUC}_{\text{map}} = 0.65$). Nevertheless, the predicted habitat availability for perch based on the three techniques were correlated at the population scale, i.e. the methods showed strong agreement in availability per population, and removing rF would not affect the relationship between nursery habitat and population size.

For fish species that critically depend on specific habitats during larval and early juvenile stages, habitat degradation and loss may seriously affect population viability. However, responses are difficult to predict, since habitat degradation may not have linear effects on population size. For example, the removal of large predatory fish can impact the lowest parts of the foodweb through trophic cascades increasing the amount of bloom-forming macroalgae (Eriksson *et al.*, 2009). Also, there is a risk of feedback loops, where a limited removal of essential habitats may have vast negative effects through a weakened top-down control leading to excessive epiphytic algal growth, destroying the habitats needed for fish recruitment (Nyström *et al.*, 2012). That is, our results suggest that if the availability of critical nursery habitats decreases, so does the abundance of large predators and the subsequent reduction in top-down control may, in a negative spiral, further reduce the functioning of the nursery habitats by increasing epiphytic algal growth (Eriksson *et al.*, 2009). However, species-specific responses to water transparency (Figure 2) strongly suggest that while nursery habitat availability for perch would decrease under a scenario with increased eutrophication (decreased Secchi depth), pikeperch habitat availability would increase (Bergström *et al.*, in press). This scenario is further supported by the observation of similar reductions in walleye stocks following increases in water transparency (Chu *et al.*, 2004). As responses are species-specific, estimates of the net benefits on overall fish production stemming from changes in habitat status should also be based on a nested species-specific approach. With increasing exploitation rates of coastal areas (Lotze *et al.*, 2006; Airoldi and Beck, 2007) and associated habitat loss and degradation, our results underscore the need for a better understanding of habitat effects on fish population sizes in a landscape context, i.e. essential habitat–stock relationships. We propose that the use of species distribution models as presented here can aid these analyses on multiple scales. Understanding bottom-up habitat effects on fish population dynamics provides a major future challenge that needs to be addressed if nature conservation and fisheries management are to be successfully integrated in an ecosystem-based approach to marine management (Thrush and Dayton, 2010).

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