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Modeling marine shad distribution using data from French bycatch fishery surveys

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Abstract :

In the last few decades, there has been a marked decline in the number of shad (Alosa alosa and A. fallax) landed in France, which prompted the French committee of the International Union for Conservation of Nature to list shad as a 'Vulnerable' species in 2010. The freshwater phases of shad life cycles have been extensively studied, but the marine phases remain poorly understood. The present study aimed to provide new insights into shad ecology by describing the marine distributions of twaite and allis shad using a presence/absence model based on bycatch data from commercial fishery surveys. Depth and salinity were identified as the main factors influencing shad distribution. Both species were primarily located in shallow areas, at depths of between 0 and 100 m. As expected for anadromous species, low-salinity areas were preferred. Substrate and latitude played minor roles in the observed distribution of shad. Our results suggest that latitudinal migration between winter and summer habitats does not occur in twaite and allis shad populations. Furthermore, substrate does not appear to be a key factor contributing to shad distribution. A better understanding of the distribution of shad species throughout their life cycles, particularly in the open sea where they are vulnerable to bycatch, would help in the selection of key protected areas for the sustainability of shad populations.

Keywords : Alosa alosa, Alosa fallax, Distribution, Migration, Binomial model

Introduction

Shads are a group of anadromous fish species that mature in the sea and spawn in the midstream to upstream sections of rivers, although there are also some landlocked populations. Shads have been extensively studied, particularly in North America. There are two sympatric shad species inhabiting the coastal Atlantic waters of Western Europe (i.e., the Atlantic Ocean), namely, the allis shad (*Alosa alosa*) and the twaite shad (*Alosa fallax*). Since the end of the 20th century, a marked decline in the size and number of shad populations has been observed throughout European coastal waters (Limburg & Waldman 2009). Several causes have been identified, including dam construction, overfishing, water quality, degradation of spawning grounds (Bagliniere & Elie 2000, De Groot 2002, Limburg & Waldman 2009), and the Allee effect (i.e., a positive correlation between population density and growth rate) (Rougier et al. 2012). In the Gironde basin, which is known to host the largest populations for both species, stakeholders responded to this reduction by imposing a total moratorium on the shad fishery in 2008. Other conservation measures are also already in place.

One example is the framework of the marine application of the EC Habitat Directive (92/43/EEC), which compels European Member States to build a network of sites (i.e., the Natura 2000 network) that guarantees the conservation or restoration of populations of species listed in Annex II (which includes shads) and their associated marine and estuarine habitats. To date, France has listed approximately 207 marine sites under the Habitats and Birds Directives, covering more than 41,000 km² of its territory. For shads, Natura 2000 sites were designated using the “best expert judgment”; exact judgments could not be made because the distribution of shads at sea remains largely unknown. Principal Natura 2000 sites designated for shads (and other diadromous fish species) correspond to estuaries and river plumes of large catchments in the Bay of Biscay, such as the Loire and Gironde rivers, which are known to host important shad populations. Additional data on the actual distribution of shad at sea would clarify the accuracy of the Natura 2000 network sites.

However, information pertaining to shads in marine areas remains largely unknown. To the best of our knowledge, only Taverny & Elie (2001) and Sabatié (1993) have studied the spatiotemporal distribution and feeding habitats of European shads at sea. On the basis of an analysis of 20 scientific trawl survey campaigns (1016 stations) conducted between 1986 and 1989, Taverny & Elie (2001) demonstrated that twaite shads were distributed primarily at water depths <50 m. Allis shads were observed in waters deeper than 100 m. The distributions of allis and twaite shad showed that they aggregated and were located in the river mouths of the most important watersheds (the Gironde and Loire). However, shad distributions at sea could have changed since the late 1980s as a result of marine trophic and thermal changes; thus, it is important to update and expand upon this information using a more recent dataset. Shads are not targeted at sea but are caught as bycatch. Bycatch is a critical source of mortality for marine species, and so-called “trash fish” species (the importance of which in marine food webs is now being recognized). Finally, data on shad ecology and distributions at sea are required in order to implement efficient conservation policies.

To increase knowledge on the distribution of shads at sea, we used a large and recent (2003–2010) dataset comprising observations taken onboard fishery fleets (i.e., the ObsMer program). The present study aimed to use these data to develop a habitat suitability model and predict distribution maps for allis and twaite shads. Combined with an analysis of seasonal variations, knowledge of their spatial marine distribution and ecology could permit more effective management, such as a relevant delimitation of the Natura 2000 network at sea.

MATERIALS AND METHODS

Fisheries data: the ObsMer program

In France, ObsMer program manages all the marine observations required by fisheries regulations. It aims to gather information to minimize bycatch and assess the incidental catches of endangered species, mainly cetaceans and turtles but also migratory fish, such as shads. Onboard, scientific observers randomly sampled bycatch from 9049 commercial catches between 2003 and 2010. In the Obsmer database used in the present study, the mesh sizes of trawls ranged from 6 mm (glass eels boats) to 320 mm (tuna boats). 43 different gears were used, to catch 68 different marine species, from the coast to the continental slopes. Preliminary analysis showed that, with the great number of different fishing gears and different target species, the number of fishing operations likely to capture shads remained steady in time and space.

Allis and twaite shads were systematically reported, when present, thus assuring no false absence in the sample/trawl. Observations included the dates, locations of the trips (i.e., latitude and longitude), fishing gear, and the number of twaite and allis shads (when present). The data used in this study were collected from the mid of Bay of Biscay to the English Channel, ranging from 51.08 to 45.22°N and -6.09 to 1.45°E (Fig. 1). Fish total length, for the few samples reported, ranged from 50 to 690 mm for allis shads and from 100 to 640 mm for twaite shads. This length range indicated that juveniles (i.e., <100 mm) and mature adults (i.e., >430 mm) were included in the database. However, as biometry was rarely reported, possible juveniles were not separated from adults in the analyses. About 84 % of shads observed in this database were collected with only 5 different fishing gears, that were the gears the most commonly used by professional fishermen (60 % of total effort was made by them). Previous analysis showed that there is no spatial bias in gear type, no seasonal bias in the location of trawls and nets associated with shad bycatch. We thus assumed that the present bycatch data are representative of shad distribution at-sea.

The limited number of observations with biometry did not allow us to account for differences in measurements among the various types of fishing gear utilized. Therefore, only presence/absence data were used. These data, sometimes considered “basic”, can lead to inferences regarding the ecology and distribution of a species (MacKenzie 2005, Vojta 2005).

Grid system principle

Shads are not frequently present in the catches of the database. Thus, data were unbalanced in favor of the absence of shad, which did not allow either a correct fit for the habitat suitability model or robust distribution mapping. Indeed, Liu et al. (2005) recommended a good balance between the presence and absence data so that the threshold value separating the modeled probabilities of presence into presence or absence is ~0.5.

As the occurrence of shads was rare in the collected samples, we assumed that a single observation of a shad in a specific site was an indication that the site contained suitable shad habitat, even if absence was recorded more frequently. Following this assumption, we divided the study area into a regular grid of 20 × 20 km. For each grid cell, the central point was assigned a value of one if at least one individual was observed within the grid cell, and a value of zero was assigned for the total absence of shad; no value was assigned if no observation was made. This grid cell dataset was used for the modeling. A sensitivity analysis completed the approach by testing for the effect of 10 × 10-km and 40 × 40-km grid cells. This methodology has been presented by Keil et al. (2013).

Environmental descriptors

Habitat suitability modeling allows the presence/absence data to be linked to environmental descriptors. Environmental variables that might influence shad distribution at sea were selected for testing in the models and included the following: (i) depth, which has been cited as a strong structuring factor (Taverny & Elie (2001)); (ii) salinity and temperature, which are known to have direct physiological effects on anadromous fish (Zydlewski et al. 2003, Boisneau et al. 2008); (iii) latitude, which is considered a proxy for large-scale temperature regimes and ecosystem functioning; and (iv) the substrate, which can be considered a proxy for food availability. The average value of the environmental variables was allocated to the grid cell centers. Variables were obtained from the following sources:

- Bathymetry was produced by the SHOM and Ifremer at 200-m resolution (Loubrieu et al. 2001). This was transformed to a class factor for statistical analyses as follows: 0–50 m, 50–100 m, and 100–150 m. No shad were found deeper than 150 m.
- A sediment map was provided by IFREMER (modified from Chassé & Glémarec (1976); Larsonneur et al. (1979); Lesueur & Klingebiel (1986)). Three classes of sediment were used according to grain size: mud (≤2 mm), sand (>2 mm and ≤4 mm), and gravels or coarse grains (>4 mm); the sediment size allocated to a grid cell was the size that was most represented in the cell.
- Salinity (‰) and temperature (°C) in surface were provided by the MARS3D hydrodynamical model at a 4-km resolution (Lazure & Dumas 2008), coupled to ECOMARS3D for the physical parameters (PREVIMER project). Both variables were extracted as monthly means. Three salinity classes (i.e., 31–33, 33–35, and >35 PSU) and six temperature classes (i.e., 8–10, 10–12, 12–14, 14–16, 16–18, and 18–20°C) were utilized.

Temporal descriptors

Spatial distributions of organisms such as fish may vary depending on the time of year, as a result of temporal changes in trophic or reproductive behaviors.

Three temporal scales were examined in the models, including seasonal (four modalities: spring, summer, autumn, and winter), bimonthly (i.e., every 2 months with six modalities starting in January/February and ending with November/December), and monthly (12 modalities) scales.

Selectivity of fishing gear

The grid system approach did not account for the fishing gear. However, it is well known that different types of fishing gear have different selectivities. The ObsMer data revealed the presence of shad primarily in trawl and net fishing. In order to evaluate this potential bias, we performed a preliminary test that did not reveal a geographic trend in the use of fishing gear, indicating that the use of each type of fishing gear occurred in similar proportions throughout each square of the grid system. No temporal effect of each fishing gears was observed in preliminary tests.

Modeling process

A generalized linear model (GLM) was applied to the presence/absence survey data (binomial model with a logit link function) in order to describe the distribution of the two shad species with respect to the temporal parameters (i.e., month of capture, bimonthly period, or season) and environmental factors as follows:

Logit(p0/1) ~ Temporal parameters + Environmental factors × Temporal scale (Eq. 1)

All possible combinations using one to five physical parameters, including interactions when relevant, were tested. The model that best fit the observed data and allowed predictions was chosen according to two indicators: (i) the accuracy of the prediction was estimated using a bootstrap cross-validation, and null and residual deviances for each validation were averaged to obtain a mean deviance explained by the cross-validation; and

(ii) the parsimony of the model was evaluated based on the Akaike Information Criterion (AIC) (Akaike 1974).

For cross-validation, a random subset of 80% of the dataset was used for parameter estimation. The probability of presence and the explained deviance for each of the remaining 20% of the observations (validation dataset) were calculated. This procedure was replicated 1000 times, and the mean explained deviance was calculated for each model tested. Models with all possible combinations of variables were tested using the same 1000 estimation–validation random subsets. Models yielding the smallest AIC with the best mean explained deviance were retained for the analysis and utilized for predicting the habitat suitability distribution of shads. To evaluate the efficiency of the selected model, the Area Under the Curve (AUC) method (Hanley & McNeil 1982) was performed, giving the percentage of good predictions in the previous cross-validation loops.

Figures representing the effects of the physical parameters in the following results section are shown with the uncertainty of prediction for the average effects of variables. The average effect of a variable was obtained from the following method: for each combination of the other factors, a prediction of the probability of presence was obtained from Eq. 1. The predictions for each combination of factors were then averaged to obtain the mean variable effect. Uncertainty was estimated by Monte Carlo sampling (5000 trials) in the estimation distribution of each parameter needed to compute the prediction in Eq. 1.

All descriptive statistics, models and prediction maps were made with the R CRAN free software environment (http://cran.r-project.org/). Probability values were considered statistically significant for $p < 0.05$.

RESULTS

Grid and seasonal approach selection

The change in the spatial grid resolution (10 × 10 km, 20 × 20 km, or 40 × 40 km) revealed no influence on the selected combination of physical parameters and yielded only marginal visible changes in the predicted distributions. Hence, only the 20 × 20-km grid resolution is discussed hereafter. For the temporal scale, only the 6 × 2-month scale is presented in the results section. The monthly scale was too small to allow a robust estimation of the parameters; the amount of presence data was too limited and the number of degrees of freedom was too high when using interactions between temporal and physical parameters. Conversely, the seasonal scale was too coarse to capture the temporal variability in shad distributions.

Models selected and evaluation

According to the two selection methods (smallest AIC with the best mean explained deviance *via* cross-validation), the distributions of both shad species were best explained by the following factors (Eq. 2):

$$
\begin{aligned}
\mathbf{logit(Shad_{0/1})} \sim\ & \text{Salinity:factor (2-month period)} \\
& + \text{factor (Depth):factor (2-month period)} \\
& + \text{factor (Sediment):factor (2-month period)} \\
& + \text{Latitude:factor (2-month period)}
\end{aligned}
$$

where $\mathbf{Shad_{0/1}}$ is the shad probability of presence.

These AUC indexes were 0.8151 for allis shads, and 0.7697 for twaite shads.

Analysis of allis shad model factors

The effect of depth dominated the explained deviance of the allis shad data (Table 1). Although significant, the effect of sediment was low. Allis shad showed a clear global preference for low salinity areas (31–33 PSU), shallow areas (<100 m), low latitude areas, and muddy substrates (Fig. 2).

Taking into account the temporal variation, we present the following general overview for allis shad (Fig. 3):

Depth: The combination of depth with the 2-month temporal scale showed slight variations in depth preference in the fifth temporal class (September–October) and presence in deeper areas during March–April (Fig. 3).

Salinity: Shad appeared to be present in areas of low salinity (31–33 PSU) during most of the year, but this preference was inverted in the fifth class (September–October) (Fig. 3).

Latitude: The preference for low latitude areas (Fig. 2) was clear for 10/12 months of the year, including March–December. The difference was less notable from January to February, when the probability of presence was low (Fig. 3).

Substrate: The differences in the substrate effects changed throughout the year (Fig. 2). Although gravel appears to be an unsuitable substrate for shads, the differences between sand and mud may have arisen from a sampling effect.

Analysis of twaite shad model factors

Depth was the main factor influencing the presence of twaite shad (Table 2). The effect of sediment had a probability of $P = 0.055$, but the cross-validation approach showed a gain in explained deviance, thus reflecting its importance in predictions. The analysis indicated a strong global preference for areas of low salinity, depth, and latitude, and areas that contain gravels.

Depth: According to the model, *s*hallow depths were clearly preferred throughout the year, except from January to February, when the probability of twaite shad presence was low (Fig. 5).

Salinity: The preference for lower salinity was primarily correlated with the period from January to April; the repartition of twaite shads was homogeneous throughout the remaining months of the year (Fig. 5).

Latitude: The effect of latitude was small but was retained in the selection method because it appeared to be changing throughout the year, thus showing a higher probability of presence in the north from January to April and in the south throughout the remainder of the year (Fig. 5).

Substrate: The positive effect of a hard substrate was more pronounced from January to March but was almost insignificant throughout the remainder of the year (Fig. 5).

Distribution prediction for Allis and twaite shads

Prediction maps were generated using the models selected and merged with the physical variables maps. For allis shads, the maps predicted distributional patterns for the following three time periods (Fig. 6):

(i) during the first 2 months (January and February), allis shads would be minimally present in the sea and primarily localized near estuaries or in coastal areas, mainly in Natura

2000 areas; (ii) from March to August their presence was predicted in coastal areas; and (iii) from September to December, the models predicted the presence of shad in oceanic waters.

Although the three temporal distributions observed in the twaite shad prediction maps were similar to those for allis shad, some differences were noted (Fig. 7):

(i) From January to February, twaite shad were predicted to occur primarily in the English Channel; (ii) from March to August, a high concentration of twaite shads was predicted in coastal waters, including areas protected by the Natura 2000 network; they were also predicted to occur in coastal waters more often than the allis shads; and (iii) from September to December, they were predicted to move to oceanic waters.

DISCUSSION

There is a considerable lack of knowledge with regard to the distribution of European shad species in the sea, which limits the development of efficient population management policies. The absence of shad fisheries at sea may explain the lack of interest; commercial fisheries prevail only in estuaries. Additionally, very few scientific studies have focused on the ecology of shad during the marine stages of their life cycles. The present study aimed to compensate for this gap in knowledge by using marine fisheries bycatch data, which provided new information on shad species ecology and distribution.

Limitations of the methodology

Our model and the sensitivity analysis were built using bycatch data. To date, studies using bycatch data are not widespread (see for instance Dell et al. (2011). We assumed that bycatch data could be used to model habitat preferences for two main reasons:

(i): shads are not a target species because their population is limited and not commercially interesting for a professional exploitation.

(ii): even if shads are by-caught, it is « classical » clupeidae-like species, with morphology, size and biology similar at numerous commercial species, like Atlantic herring or Atlantic mackerel, suggesting the presence of shads in commercial surveys targeting these species.

(iii): commercial fisheries data are often considered biased with respect to mapping species distributions because fishers choose to target species at the center of their distribution to maximize catches and minimize search costs (Dell et al. 2011). In the present study, we have used a consequent database (>9000 trawls) using a numerous of different fishing gears (43) and with a large range of mesh size used (6-320 mm), that were not focused on shads and therefore are not biased. The use of such database could reduce the potential bias linked to bycatch. Preliminary analysis was also done to support this conclusion.

Then, we think it is reasonable to assume that bycatch data are adequate to model species presence.

These commercial fisheries focused on large fish (with the exception of specific fisheries such as those for glass-eels or shrimps). In this context, it is relevant to address the question of the representativeness of the size distribution in the catches. Records of fish length were not sufficiently accurate to be integrated into the models. A simple descriptive analysis showed that the smallest total length of an individual fish in the database was 50 mm, suggesting that young-of-the-year [i.e., <100 mm (Lochet 2006)] samples could be integrated into the ObsMer database. Future studies should integrate information on fish size in the analyses because habitat use patterns might be size/age dependent; however, it is reasonable to assume that the models were sufficiently representative of the entire shad population in the field. Another limit may be the absence of data for areas closer to the English coasts; this may create bias with regard to the effect of high latitude. Thus, the northernmost effects, particularly for twaite shad, should be interpreted with caution.

Model efficiency

The first indications of the efficiency of the model developed in the present study were the good AUC index observed in the cross-validation procedure, showing that more of 76 % of predictions from both models (allis and twaite shads) were goods.

Moreover, the depth effect observed in the current model is in accordance with the literature. Allis and twaite shad were not observed at depths >150 m, which was used as a limit for the model. The factor analysis from our models showed that allis and twaite shads primarily selected depths of 0–50 m. Into the wild, allis shad around Morocco are found at depths of 30-150 m, near areas of summer upwelling (Sabatié 1993). Allis and twaite shad were also found to inhabit shallow waters, 15 to 115 m, along the northwest coast of France (Taverny & Elie 2001). In our model, fish were caught from depths of 15 to 115 m. In total 100 % and 78 % of twaite and allis shad, respectively, were caught at depths <100 m. Twaite shad tended to occur at shallower depths than the allis shad ((Baglinière & Elie 2000), like in our model (Figures 2 & 4).

Moreover, the oceanic distribution of another shad species, the American shad *A. sapidissima*, along the Pacific coast of North America is primarily confined to the continental shelf (Pearcy & Fisher 2011). No evidence for large-scale seasonal migrations has been found for this area (Pearcy & Fisher 2011), although such migration has been reported for the Atlantic coast (Neves & Depres 1979), corroborating the results from our model. In this study, shad were caught in shallow waters (depths <150 m). Along the Atlantic coast, the majority of shad have been captured at depths <100 m (Neves & Depres 1979). Nevertheless, some shad were caught at greater depths, 150 to >200 m (Neves & Depres 1979) and an increased frequency of shad presence was found at depths >60 m (Bethoney et al. 2013). This association to deeper areas corresponded to shad winter habitats (Neves & Depres 1979, Bethoney et al. 2013).

The salinity was also preliminary described like a migration factor for American shads (Dodson et al. 1972). The authors showed that the high increase in salinity was a physiological dam for the inland migration of shads, requiring meandering between salt and freshwater.

All these studies lead to confirm the results from our model. However, for American shad again, Legget & Whitney (1972) that the water temperature was the main cue for inland migrations. The authors showed that 90% of the runs take place when river temperatures are between 16 and 19.5°C. But in our model, the water temperature was tested but not selected by AIC and cross-validation selections. We can assume that the water temperature was correlated with the interaction between depth and month, leading to its reject by the selection procedure.

Latitudinal effect: Do fish remain in the same geographic area throughout the year?

Latitudinal factors appear to have marginal effects on the distribution of twaite and allis shad: the probability to capture shads is nearly the same along the latitudinal gradient. On the basis of a global analysis, the distribution of allis shad was slightly more southerly than that of the twaite shad. This result is in accordance with Baglinière & Elie (2000) who highlighted that the most important allis shad population was found in the mouth of the Loire River (France, 47.2654°N), the southernmost region of the present study area. Our analysis showed a twaite shad preference for more northern latitudes, which is in accordance with the literature. From an extensive bibliography review, Lassalle et al. (2008) identified the presence of allis shad from the Sebou estuary (Morocco) to the Solway Firth (United Kingdom), with small populations in Sebou. Baglinière & Elie (2000) observed an important twaite shad population in the Coastal waters of United Kingdom and North Sea.

According to our bimonthly analysis, no change in latitude effect was observed for allis shad, which may suggest the absence of massive latitudinal migration between winter and summer habitats. This indicates that, globally, allis shad populations remain in the same geographic area throughout the year, undertaking only longitudinal (i.e., river to ocean) migrations. Nevertheless, individual surveys are required to confirm this migration pattern because the picture provided by the bycatch data may conceal individual variation in space-use behavior. Conversely, a slight difference was observed for twaite shad, which may be due to variation in the timing of their upstream migration from south to north.

Substrate preference: An opportunist trophic cline?

The sensitivity analysis from our model showed that there was a greater presence of allis shad in areas with muddy substrates than in areas with other types of habitats. From the output of the model, twaite shad showed a weak preference for gravels. It is generally accepted that fish diet and home-range substrate are profoundly linked. Allis shad feed on a wide range of planktonic crustaceans; larger adults feed on small schooling fish (Whitehead 1985, Rochard & Elie 1994). Twaite shad are more ichthyophagous, feeding on small fish and crustaceans (Whitehead 1985, Rochard & Elie 1994). This difference in shad diets could explain the difference in substrate preferences. The preference for soft bottoms and hard substrates for allis shad and twaite shad, respectively, was more pronounced during periods yielding higher probabilities for the presence of shad overall or for each species.

Allis shad pattern of oceanic movements

Our results from the model for allis shad movement patterns at sea over the course of a year are in accordance with the classical view of the life cycles of anadromous species derived from freshwater or estuarine observations; they also could provide additional information on movement patterns within marine habitats (e.g., distribution and timing).

Of note, the model used in the current study was able to analyze temporal variations in the distribution of shads. In winter (January and February), allis shad were preferentially present in the 0–50 m depth class and low salinity areas of the coastal and estuarine regions. However, the model predicted low occurrence probabilities, which indicated that a large portion of the shad populations had not been sampled at sea. It appears that the shads inhabited the inner estuaries or rivers during this period. From March to August, model showed that allis shad were primarily shown to live in coastal areas, with a preference for shallow depth and low salinity environments. Taking into consideration the migration phenology and information available from reproductive studies in riverine environments, this shift in distribution may be related to the spawning migration. During the last part of the year, allis shad were observed to move from coastal to oceanic areas. This movement was also confirmed by the factor analysis, which indicated minimal differences in depth and salinity preferences. Because allis shad are primarily semelparous (Baglinière & Elie 2000), we cannot conclude that this movement corresponds to the downstream migration of post-reproductive adults. Nevertheless, the young-of-the-year may have reached a length of 100 mm by this time of the year (Lochet 2006), suggesting that they could be integrated into the ObsMer database, and therefore our model. Hence, this migration could comprise some iteroparous adults and young-of-the-year individuals.

Twaite shad pattern of migration

From the outputs of the model, twaite shad exhibited similar patterns of movement to allis shad; the prediction maps and factor analysis also suggested an annual three-step marine distribution. Some slight differences were noted, however. From January to February, twaite shad were mainly located in English waters, with an almost uniform distribution (with no preference for shallow depth areas). In the second step, with regard to allis shad, movement toward coastal areas was observed between March and August, with a strong preference for areas of shallow depth and low salinity. We can assume that this represents iteroparous adults and young-of-the-year fish. This assumption is in accordance with Baglinière & Elie (2000). In the last part of the year, the results suggest a strong movement toward oceanic areas. Because twaite shad are iteroparous (Baglinière & Elie 2000), this movement could represent a second annual migration, from coastal to oceanic areas. The distribution of recorded fish lengths also suggests that young-of-the-year individuals were present in the migrating population (Baglinière & Elie (2000)).

On the basis of the model global analysis, allis shad distribution was slightly more southerly than that of the twaite shad. This is in agreement with Baglinière & Elie (2000), who showed that the most important allis shad population was found in the mouth of the Loire River (France, 47.2654°N). Lassalle et al. (2008) found allis shad to be present from the Sebou Estuary (Morocco) to the Solway Firth (United Kingdom), with small populations in Sebou. Indeed, Baglinière & Elie (2000) noted an important twaite shad population in the United Kingdom and North Sea.

Moreover, according to our bimonthly analyses, no change was observed for allis shad distribution. We can suppose that there is no important latitudinal migration between the winter and summer habitats, suggesting that, globally, allis shad populations remain in the same geographic area throughout the year, performing only longitudinal (i.e., river to ocean) migrations. The fact that allis shad only perform longitudinal migrations may have to do with the populations being greatly reduced in size, but it is impossible to clearly conclude with our data, without precise abundance information.

Pertinence of the Natura 2000 network at sea

The results of the current study indicate that the Natura 2000 areas are not entirely pertinent for shad protection management. Allis and twaite shads inhabit a high proportion of the Natura 2000 areas only from January to April and March to June, respectively. Indeed, although shads live in relatively shallow waters, their life cycle is not limited to coastal regions, and thus managing this species *via* Natura 2000 management is necessary but not sufficient. Moreover, although the two most important French basins (Loire and Gironde) are included in the Natura 2000 network, there are additional basins that could be considered equally as important for shad distribution according to our models. For instance, to date, the Vilaine and Scorff rivers in Brittany (middle of the area) have been excluded from the Natura 2000 network; however, they are high probability areas for shad presence. The present modeling approach, therefore, could be used as a tool for the selection of additional protected sites.

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TABLES AND FIGURES

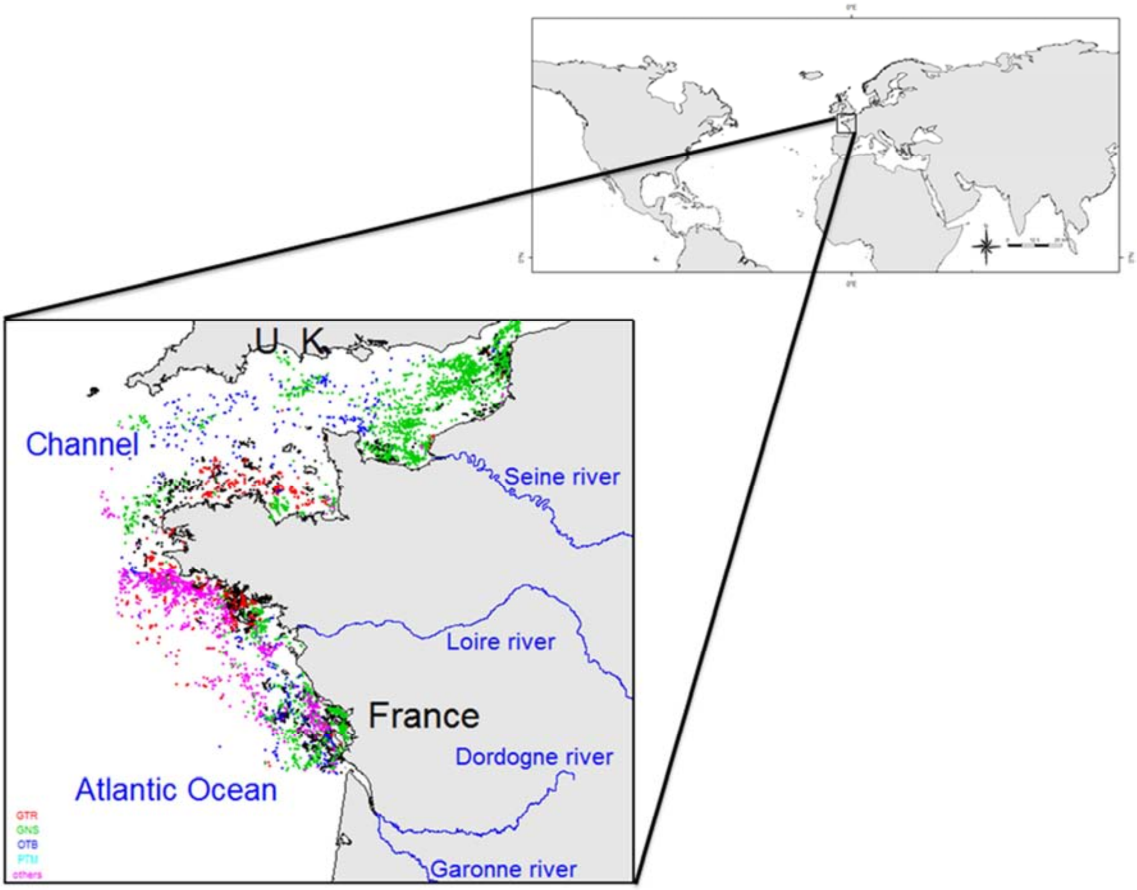

Figure 1: Global position of study site. Locations of all commercial surveys from dataset. Trammel-nets (GTR) have caught 19.97 % of shads. Fixed gill nets (GNS): 18.69 %. Benthic bottom otter trawls (OTB): 16.31 %. Midwater trawl (PTM): 15.55 %. Others: 29.48%.

Table 1. Analysis of deviances for the *Alosa alosa* binomial generalized linear model

	Degrees of freedom	**Explained deviance (%)**	***P*-value**
Salinity:factor (2-month period)	6	6.19	4.40e-13
Latitude:factor (2-month period)	6	5.98	1.33e-12
Factor (Depth):factor (2-month period)	18	7.82	2.91e-11
Factor (Sediment):factor (2-month period)	9	2.32	1.87e-3
Total (%)		22.31	

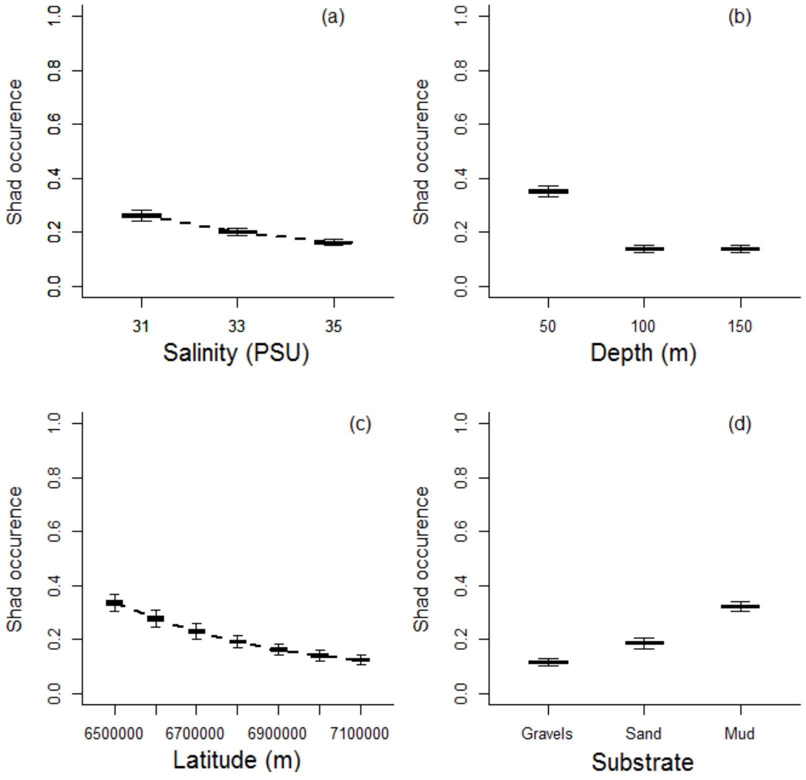

Figure 2: Global effects of the four main parameters on the allis shad occurence: (a) salinity (PSU); (b) depth (m); (c) latitude (m); and (d) substrate.

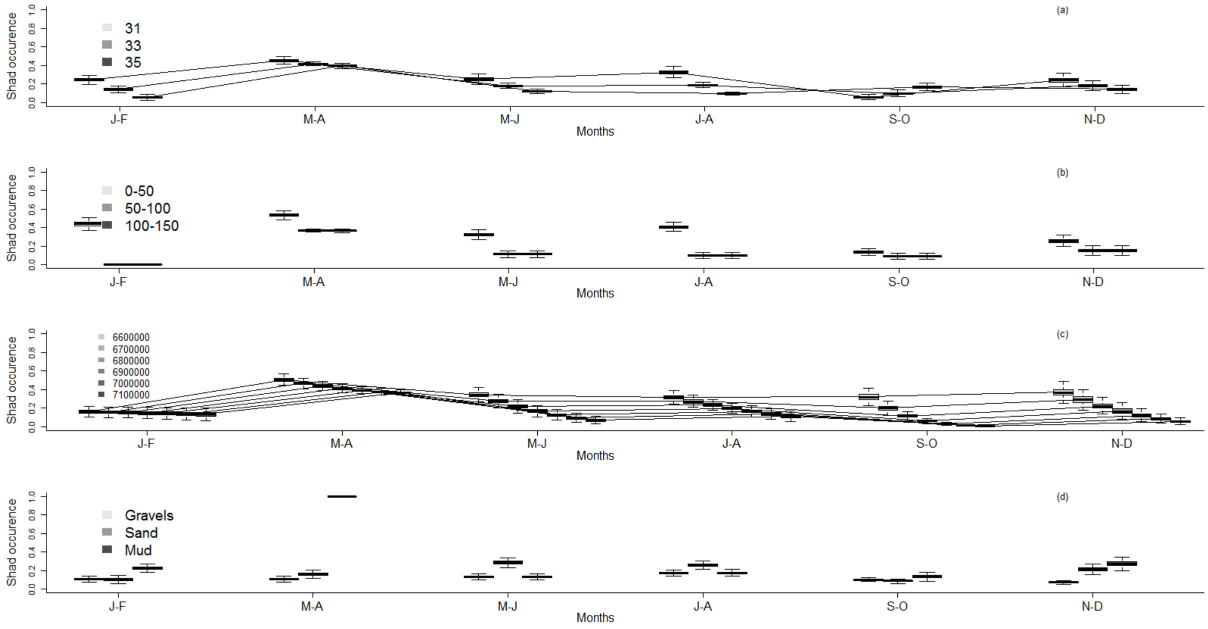

Figure 3 : Two-month period approach for allis shad: temporal change for the four main parameters: (a) salinity (PSU); (b) depth (m); (c) latitude (m); and (d) substrate. X-axis: from J-F (January-February) to N-D (November-December)

Table 2: Analysis of deviances for the *Alosa fallax* binomial generalized linear model

	Degrees of freedom	**Explained deviance (%)**	***P*-value**
Salinity:factor (2-month period)	6	3.95	2.18e-06
Latitude:factor (2-month period)	6	5.77	9.96e-10
Factor (Depth):factor (2-month period)	18	9.74	1.38e-11
Factor (Sediment):factor (2-month period)	10	0.95	5.49e-1
Total (%)		20.41	

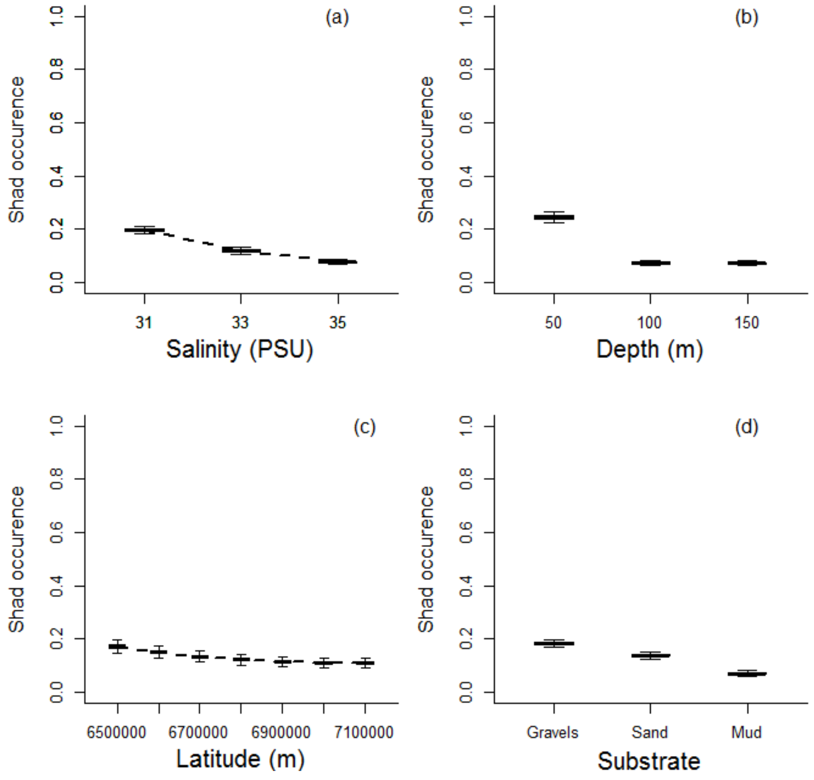

Figure 4: Global effects of the four main parameters on the twaite shad occurence: (a) salinity (PSU); (b) depth (m); (c) latitude (m); and (d) substrate.

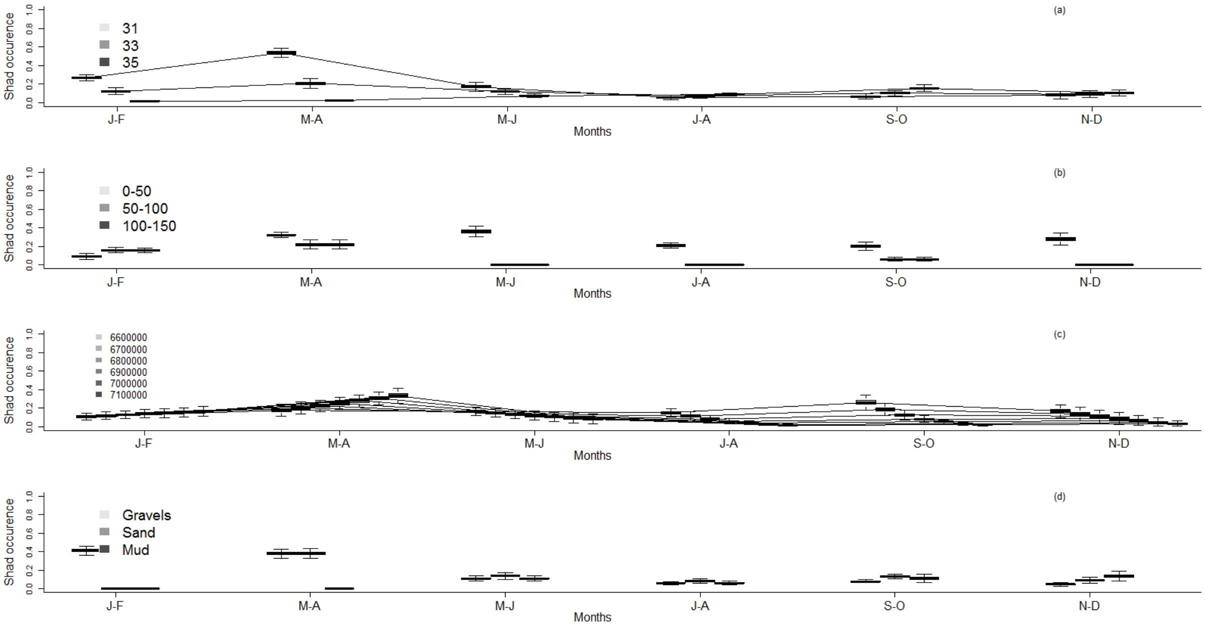

Figure 5: Two-month period approach for twaite shads: temporal change for the four main parameters: (a) salinity (PSU); (b) depth (m); (c) latitude (m); and (d) substrate. X-axis: from J-F (January-February) to N-D (November-December)

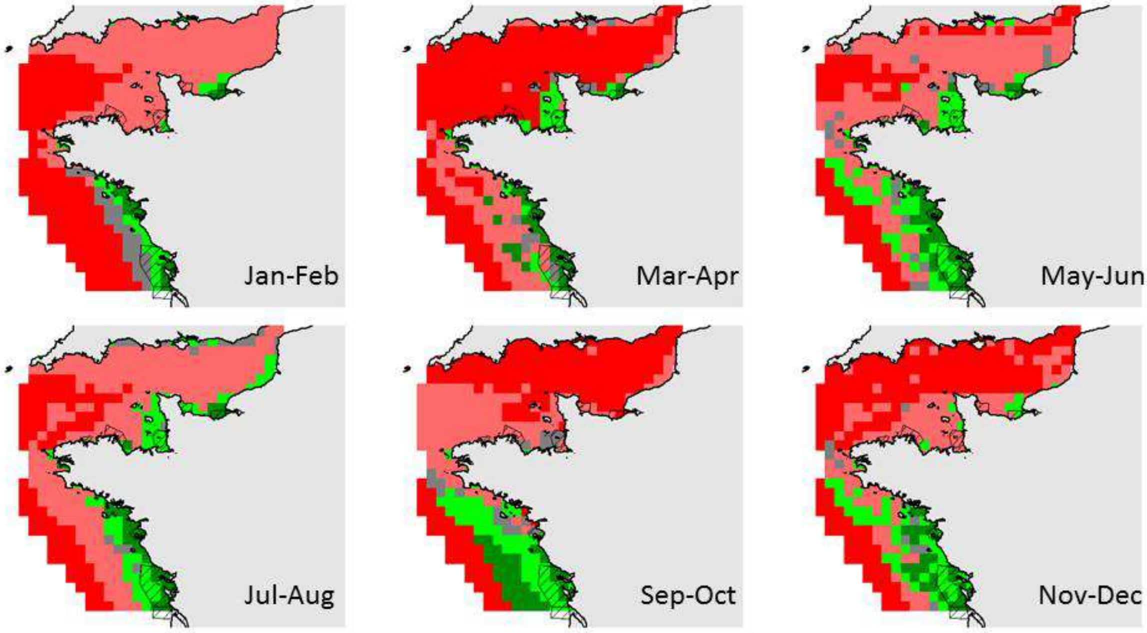

Figure 6: Prediction maps for allis shad (20 × 20-km cells) in the 2-month period approach. Dark green: probabilities ranging from 1 to 0.8. Light green: probabilities ranging from 0.8 to 0.6. Gray: probabilities ranging from 0.6 to 0.4. Pink: probabilities ranging from 0.4 to 0.2. Red: probabilities ranging from 0.2 to 0. Probabilities <0.4 may indicate the absence of shad. Striped areas indicate Natura 2000 shad-designated sites.

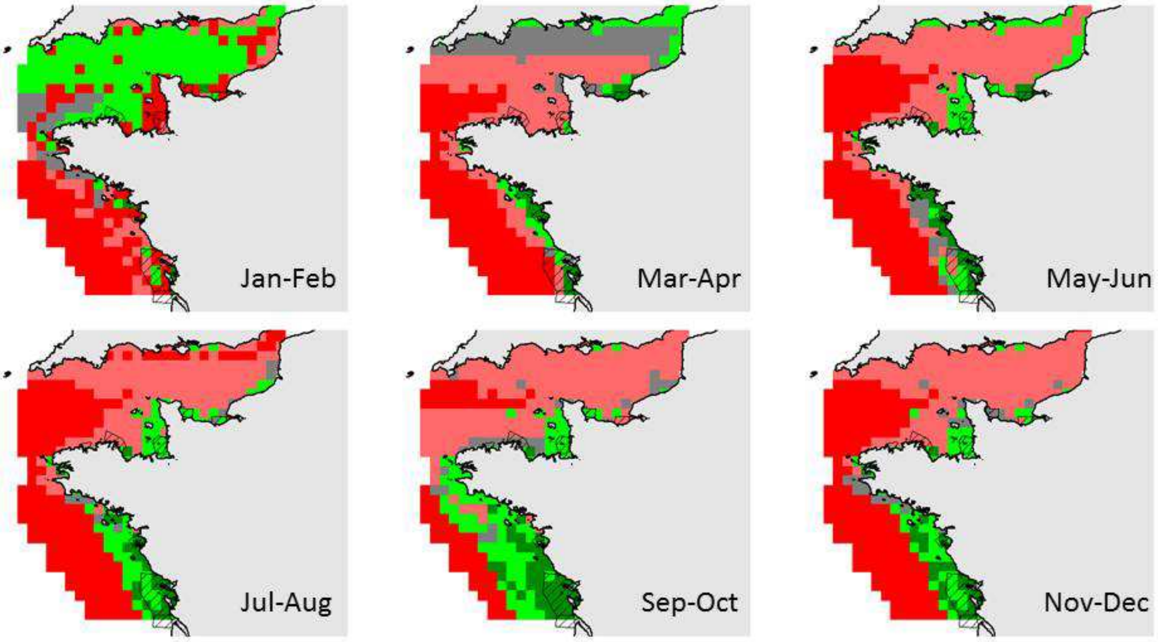

Figure 7: Prediction maps for twaite shad (20 × 20-km cells) in the 2-month period approach. Dark green: probabilities ranging from 1 to 0.8. Light green: probabilities ranging from 0.8 to 0.6. Gray: probabilities ranging from 0.6 to 0.4. Pink: probabilities ranging from 0.4 to 0.2. Red: probabilities ranging from 0.2 to 0. Probabilities <0.4 may indicate the absence of shad. Striped areas indicate Natura 2000 shad-designated sites.