



Identification of critical essential habitat for demersal fish in the Gulf of Guinea

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Abstract – Habitats of three marine fish species of major interest (*Epinephelus aeneus*, *Pseudotolithus senegalensis*, and *Pagellus bellottii*) at both juvenile and adult life stages were identified and mapped in the western part of the Gulf of Guinea. Habitat suitability models (HSMs) were designed to quantify species- and stage-specific fish densities from scientific survey data collected for the last 40 years according to two environmental descriptors (bathymetry, distance to river mouth) and accounting for temporal contrasts. Delta general linear models were selected to fit with the 0-inflated distribution of the fish density data. Despite their high residual deviance, both the prediction accuracy and robustness of these HSMs were satisfactory. HSMs showed a strong influence of bathymetry on stage-specific fish distribution and a lower and non systematic influence of proximity to river mouths. The spatial distribution of juveniles of *E. aeneus* and *P. senegalensis* evidenced their concentration in shallow coastal nurseries. The adults of *P. senegalensis* were also located in nearshore habitats under estuarine influence, whereas adults of *E. aeneus* were spread towards deeper waters. *P. bellottii* did not rely on coastal fringes at juvenile or adult stages. Finally, model outputs showed a decrease in abundance in recent decades for all species at both life stages. These HSMs and maps reveal the importance of the coastal fringe as a critical essential habitat for two of the three studied species and the usefulness of space-based management measures to maintain populations and ensure sustainable fishing exploitation.

Keywords: Fish habitat model / demersal fish / Gulf of Guinea / *Epinephelus aeneus* / *Pseudotolithus senegalensis* / *Pagellus bellottii*

1 Introduction

Estuarine and coastal ecosystems (ECEs) shelter a wide biological diversity and provide many ecosystem services (Barbier et al., 2011). Many marine species of fisheries interest carry out at least a part of their life cycle in ECEs (Seitz et al., 2014); in particular, the juvenile stage is frequently concentrated in these areas because they provide optimal growth conditions and protection from predators (Beck et al., 2001). This tendency was verified under temperate but also tropical latitudes for

various ECEs, namely, mangroves (Manson et al., 2005), seagrasses (McDevitt-Irwin et al., 2016), and saltmarshes (Jänes et al., 2020), and the effects of these ECEs were found to be even stronger due to the combination of these complementary habitats and their connectivity (Barbier et al., 2011; Nagelkerken et al., 2015; Whitfield, 2017). For species relying on ECEs at the juvenile stage, both the size and the suitability of nursery habitats contribute to population renewal and productivity, and to sustain fisheries on adult stage in open ocean, at dramatically wider scale. However, ECEs usually faces a large panel of anthropogenic pressures (Halpern et al., 2012), especially in tropical zones (Friess, 2016). The cumulative effects of surface reduction and alteration of the quality of ECEs impact the suitability of juvenile habitats for many dependent exploited

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species (Brown et al., 2018; Worm et al., 2006). The management of exploited fisheries resources requires an ecological approach that considers not only fishing mortality but also recognizes the main role played by critical essential habitats (CEHs) and the related potential bottlenecks throughout the life cycle (Beck et al., 2001; Dahlke et al., 2020). The identification of nursery areas is a seminal crucial phase for the management of fisheries resources; it is essential for moving forward with the protection of these CEHs (Curnick et al., 2019).

The Gulf of Guinea is a biogeographical province with productive ecosystems, enhanced by large freshwater inflows and seasonal upwellings. These ecosystems sustain a large diversity of exploited marine species and related fisheries of main interest for local food supply (Hicks et al., 2019). The coastline of the Gulf of Guinea hosts a mosaic of ECEs (e.g., mud and sand flats, mangroves, saltmarshes) in river mouths, lagoons, deltas, bays or along the open coast (Okyere and Blay, 2020). Many exploited species in the Gulf of Guinea rely on these ECEs for their life cycle (John and Lawson, 1990). In particular, juveniles of many exploited marine species have been observed in and close to coastal lagoons and estuaries (Aheto et al., 2014; Bakari et al., 2016; Eugenia et al., 2019; Nunoo et al., 2006; Okyere et al., 2011; Okyere and Blay, 2020). Thus, the ECEs of the Gulf of Guinea contain nursery habitats (Cosme De Esteban et al., 2023), on which adverse effects of anthropogenic pressures (i.e., drop in area size due to land reclamation, degradation of habitat and water quality linked to eutrophication and pollution; cf. 2.1.) have been evidenced. However, the spatial extent of both juvenile and adult fish distributions, which is needed to identify CEHs, was still not delineated for exploited species in the Gulf of Guinea.

The present study focused on CEHs of three exploited species (*E. aeneus*, *P. senegalensis*, *P. bellottii*), selected regarding their high commercial value and landing volumes. The white grouper (*Epinephelus aeneus*, Saint-Hilaire, 1817) is the most important grouper (the common name “grouper” is usually given to fish in one of two large genera: *Epinephelus* and *Mycteroperca*) species in terms of catches. It has a very high local commercial and cultural value (this led to the inclusion of its drawing on a currency used banknote in West Africa). The white grouper landings, however, remain low: 127 tons in 2019; i.e. 0.1% of the demersal catches contributing to 0.4% of the commercial value in the study area (ZEE of Ivory Coast and Ghana, Sea Around Us data, Derrick 2020; Polido et al., 2020), and there is no information on its exploitation level. The cassava croaker (*Pseudotolithus senegalensis*, Valenciennes, 1833) is an economically important species (Sossoukpe et al., 2013b) with 7,432 tons of landings (calculated from *Pseudotolithus* spp. landings based on the proportion of *P. senegalensis*/*Pseudotolithus* spp. abundance in scientific survey data described in 2.2.); it represented 3.4% of the demersal catches in 2019 and 3.8% of the commercial values (Derrick, 2020; Polido et al., 2020). The cassava croaker is considered overexploited in the study area (FAO, 2022; Okyere and Blay, 2020). Red pandora (*Pagellus bellottii*, Steindachner, 1882) is the most widespread species in the Sparidae family; it represented 2.5% of the demersal catches (5,438 tons) and reached 4.6% of commercial value in 2019 (Derrick, 2020; Polido et al., 2020); it is considered at the full exploitation level in the study area (FAO, 2022; Kouame et al., 2020; Sylla et al., 2017).

White grouper and Cassava croaker are both fish species found in open lagoons and bays on the continental shelf of Gulf of Guinea (Bakari et al., 2016; Eugenia et al., 2019; Nunoo et al., 2006; Okyere and Blay 2020; Sossoukpe et al., 2013b). Red pandora are found in open waters (Kouame et al., 2020; Sylla et al., 2017).

The aim of this study was to map the spatial distribution of these three exploited species at the juvenile and adult life stages on the continental shelf of the western Gulf of Guinea. This involved (i) collating and standardizing scientific demersal trawl survey data from the last 4 decades in the study area, (ii) selecting habitat suitability models (HSMs) adapted to 0-inflated data distribution of species-specific fish abundance, and (iii) mapping these distributions with relation to environmental descriptors to identify CEHs for these three species.

2 Material and methods

2.1 Study site, selected species, fisheries and management

The coastal shelf of Côte d’Ivoire and Ghana spans along the western shore of the Gulf of Guinea (Fig. 1). From the shore to the 150 m depth (beginning of the continental slope), the continental shelf extent reaches 34,000 km². This continental shelf is enriched by coastal upwellings during the cold marine season from June to October and January to February and by terrigenous inputs from rivers during the continental rain seasons, from June to July and then September to November. On this shelf, the fish community is highly diverse, with species of major interest for fisheries and food supply (Le Loeuff, 2001). The land–sea interface hosts a mosaic of habitats: open and closed lagoons (Bakari et al., 2016; Laleye et al., 2007), deltas and estuaries (Okyere et al., 2011), and mangroves (Aheto et al., 2014; Osemwegie et al., 2016). These ECEs face cumulative anthropogenic pressures: mangrove surface loss (Abé and Affian, 1993; Osemwegie et al., 2016), eutrophication (Adingra and Kouassi, 2011), siltation and deoxygenation (Okyere and Nortey, 2018), and xenobiotic loadings (Koffi et al., 2014).

The studied species, i.e., White grouper, Cassava croaker and Red pandora are demersal fishes (Serranidae, Sciaenidae and Sparidae, respectively). Their distribution spans along the West African coasts to Angola, with some presences in the Mediterranean Sea for white grouper and red pandora (Kouame et al., 2020).

The cassava croaker is a gonochoric species; i.e., it maintains only one sex throughout its life cycle (male or female). White grouper and red pandora are hermaphroditic protogynous; i.e., they are born female and later become male. Sizes at first maturity (i.e., female maturity for protogynous species) vary among the three species (Tab. 1, see Supp. Tab. 1 for the related bibliographic review).

The management measures for the fishery resources in the study area are not mono specific. They focus on biological rest periods and consist of a temporary ban lasting 1 (July) to 2 (July–August) months for artisanal and industrial fishing fleets, respectively. The existence of a marine protected area for turtles also contributes to partial spatial conservation of marine fish populations.

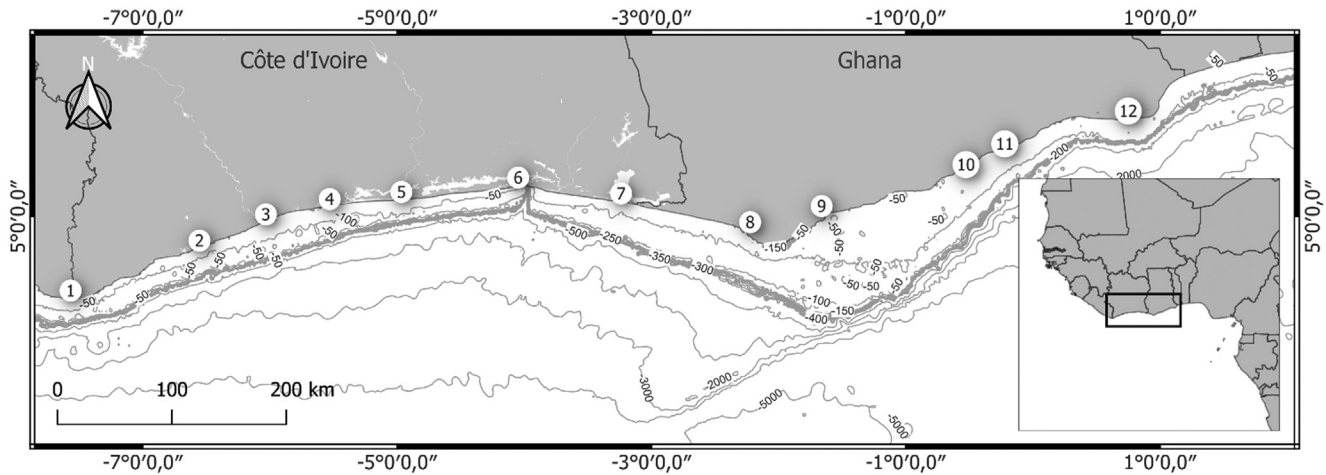


Fig. 1. Map of the study area in the Gulf of Guinea with river and lagoon mouths. 1: Cavally River; 2: San Pedro River; 3: Sassandra River; 4: Fresco Lagoon; 5: Grand-Lahou Lagoon; 6: Ebrié Lagoon; 7: Aby Lagoon; 8: Ankobra River; 9: Pra River; 10: Ayensu River; 11: Densu Delta; 12: Volta River. In the lower right corner: general location.

Table 1. Maturity information for the three studied species used to split juveniles and adults in the catches.

Species	Size at maturity used in this study* (cm)	Mean weight at 1st maturity** (kg)
<i>Epinephelus aeneus</i>	50	1.9
<i>Pseudotolithus senegalensis</i>	32	0.4
<i>Pagellus bellottii</i>	13	0.1

* Arbitrary selected from the bibliographic review supporting these estimates (see Supp Tab. 1), and provided for the first maturity (female) for the two hermaphrodite protogynous species.

** Calculated from the length/weight in catch data from scientific surveys in our dataset (Tab. 2) based on the size at maturity*.

2.2 Trawl survey data

Both national and international scientific demersal trawl surveys carried out from 1978 to 2019 on the continental shelf of the study area were collected (temporal distribution, sampling effort, and technical characteristics of the fishing gear are given in Tab. 2). These surveys spanned from the coastal area (10 m depth) to the continental slope (Supp Fig. 1). Trawling speed and hauls duration were between [3–3.2] knots and [20–60] mins, respectively.

For each trawl haul (sample unit), the following information was collated: date, geographical position, area swept, and bathymetry. For the three studied species, catches were systematically identified, counted and weighted, but length structure was measured on a fraction of the trawl hauls only (on almost half of the trawl hauls where the species is caught for cassava croaker and red pandora and on less than 20% for white grouper; Tab. 3).

2.3 Descriptors of spatiotemporal patterns in fish density used in HSMs

2.3.1 Environmental descriptors of fish habitat

Environmental data concern the descriptors used to model the spatial distribution for the three studied species at juvenile and adult stages; in this study, the data used are bathymetry and

the proximity to habitats under riverine influence (Olds et al., 2012). See the Discussion for potential inclusion or other environmental descriptors.

2.3.1.1 Bathymetry

The bathymetry map (in m) is a raster with a spatial resolution of 15 arc seconds (NOAA, 2022; Supp. Fig. 2). Preliminary analysis showed that bathymetric distribution of the three species at juvenile or adult life stage was not monotonous (for an illustration, see the Results (Sect. 3.2.1) and the dome-shaped bathymetric distribution of white grouper and red pandora; Fig. 5). Regarding the amount of available trawl data (Tab. 2), this prevents the use of bathymetry as a covariate in habitat suitability models (HSMs) without overparametrization (Le Pape et al., 2014). Indeed, a choice was made to transform bathymetry into a class factor in HSMs. Bathymetry was split into ten categories (in m): [10–20], [20–30], [30–40], [40–50], [50–60], [60–70], [70–80], [80–90], [90, to 100] and >100, with a sufficient number of trawl hauls (Fig. 2) per class.

2.3.1.2 Proximity of river mouth or lagoon entrance

Twelve sites were selected as major estuarine entries in the study zone (Fig. 1). To describe the proximity with these connections to freshwater loadings, we used the shortest

Table 2. Demersal trawl survey data.

Survey	Vessels	Fishing gear		Years	Number of hauls/year	Total number of hauls	Source
		Mean distance between wings* during towing	Mesh size (codend**)				
CHALCI	O/V André Nizery	PICARD bottom trawl: 13 m	39–48 mm	1978	83	826	Centre de Recherches Océanologiques (CRO), Côte d'Ivoire
				1979	110		
				1980	108		
				1983	157		
				1984	129		
	1985			120			
	1986			119	434		
	1993			145			
	1994			145			
	1995			144			
1999	78						
NANSEN	R/V Dr Fridtjof Nansen	Gisund super bottom trawl: 21 m	10–20 mm	2000	103	736	CRO; Fisheries Commission, Ghana
				2002	53		
				2004	110		
				2005	118		
				2006	92		
				2007	41		
				2019	141		
UEMOA-SOUTH	O/V Général Lansana Conté	Bottom trawl 15.85 m	25 mm	2015	81	81	UEMOA; CRO; Fisheries Commission of Ghana

* trawl width during fishing.

** at the bottom of the trawl.

Table 3. Proportion of fish caught, measured vs unmeasured.

Species	Total number of trawl hauls where the species were caught*	Trawl hauls where fish were measured (in %)	Trawl hauls where fish were unmeasured (in %)	
			Catch = 1 fish	> 1 fish
<i>Epinephelus aeneus</i>	691	17.08	27.78	55.14
<i>Pseudotolithus senegalensis</i>	452	46.46	4.87	48.67
<i>Pagellus bellottii</i>	1,383	52.42	2.46	45.12

*according to the total of trawl hauls: 2,077.

distance between the trawling stations and the river mouths. A threshold of distance was retained in two class factors: close to the river mouth (<50 km) and far from the river mouth (Fig. 2; Supp. Fig. 3). 50 km is a compromise between the number of hauls in each category and the effect detected on fish density in preliminary analyses. Preliminary analysis showed that in a range of distances from 30 to 60 km, fish density at the life stage was not significantly sensitive to this threshold. Note that regarding the narrowness of the continental shelf, the distance to the river mouth is not correlated with bathymetry (Supp. Fig. 4).

2.3.2 Temporal stratification

Survey data spread over 41 discontinuous years. To incorporate the evolution of resources over time, the dataset was divided into two periods: one before 2000 and the other

from 2000, i.e., 11 years of distinct trawl surveys (65.4% of the trawl hauls) and 8 years of distinct trawl surveys (35.6% of the trawl hauls), respectively (Fig. 2). The 2000 year was chosen as a good balance in terms of years and trawl hauls in the two categories.

2.4 Estimating the respective proportions of juveniles and adults in catches

For each species, catches needed to be split into juveniles and adults before modelling stage-specific distribution. When fish were measured, the proportion of juveniles regarding size at 1st maturity (Tab. 1) was directly derived from the length structure in catches. However, this was limited to a fraction of the samples (Tab. 3); for a large proportion of trawl hauls, only the total number of individuals caught and the total weight

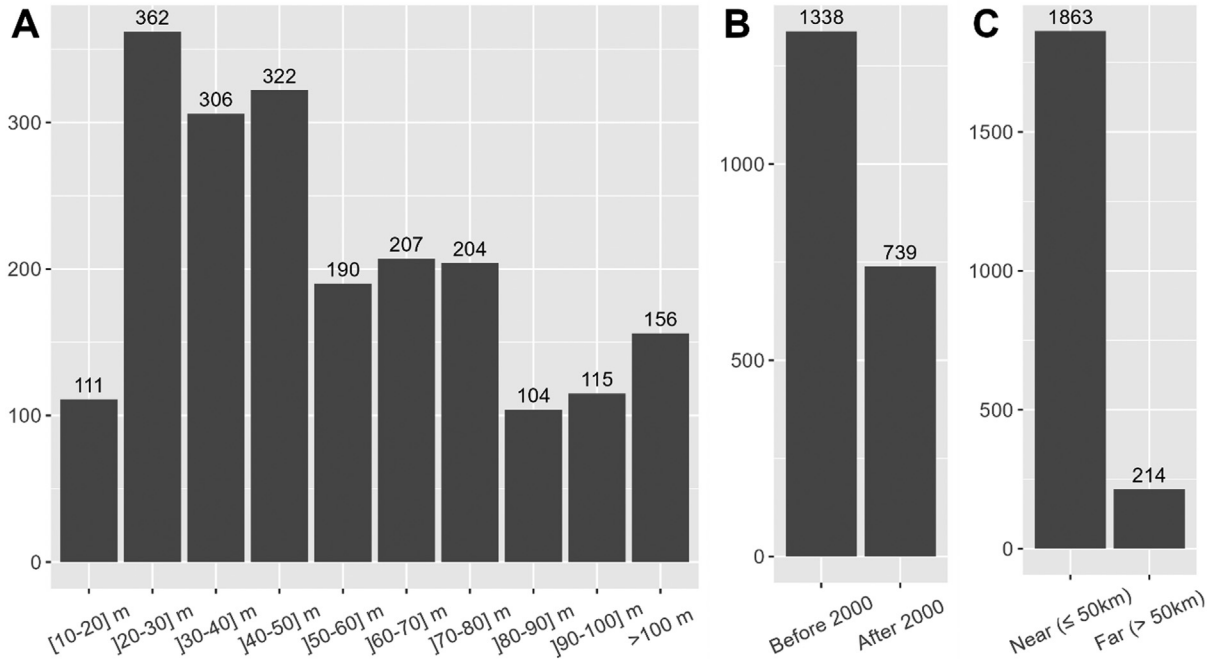


Fig. 2. Number of samples (trawl hauls) per modality of descriptor. A: Bathymetry descriptor; B: Period descriptor; C: Proximity to river mouth descriptor.

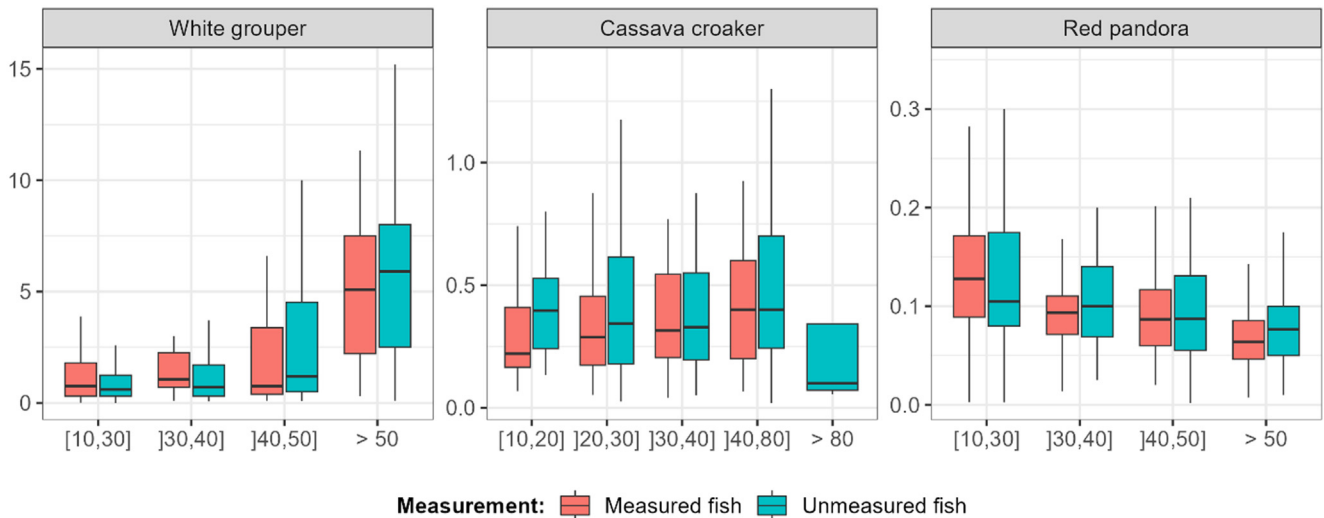


Fig. 3. Mean weight by bathymetry class (in m) for measured vs unmeasured fish.

were available by species. The following method was used to categorize catches as juveniles or adults when length data were missing:

- When a single individual was caught in a trawl haul for a studied species, its weight and the weight at 1st maturity were used to categorize it as juvenile or adult. The weight at 1st maturity (Tab. 1) was calculated regarding the size at maturity and the length and weight data available in the trawl survey dataset (Tab. 2).
- When more than one individual was caught, a statistical approach was used. A preliminary analysis tested for potential biases in mean weight between measured/unmeasured fish

data for the studied species. Then, for each species, generalized linear models (GLMs, McCullagh and Nelder, 1989) with Bernoulli distributions were used to estimate the species-specific proportion of juveniles in trawl hauls for which length structures are available (Eq. (1)):

$$J \approx \text{covariate}(X) + \epsilon, \text{ weights} = C, \quad (1)$$

where J is the response variable, the proportion of juveniles in the sampling unit (trawl haul), X is the mean weight, ϵ is the residuals, and C is the number of fish measured.

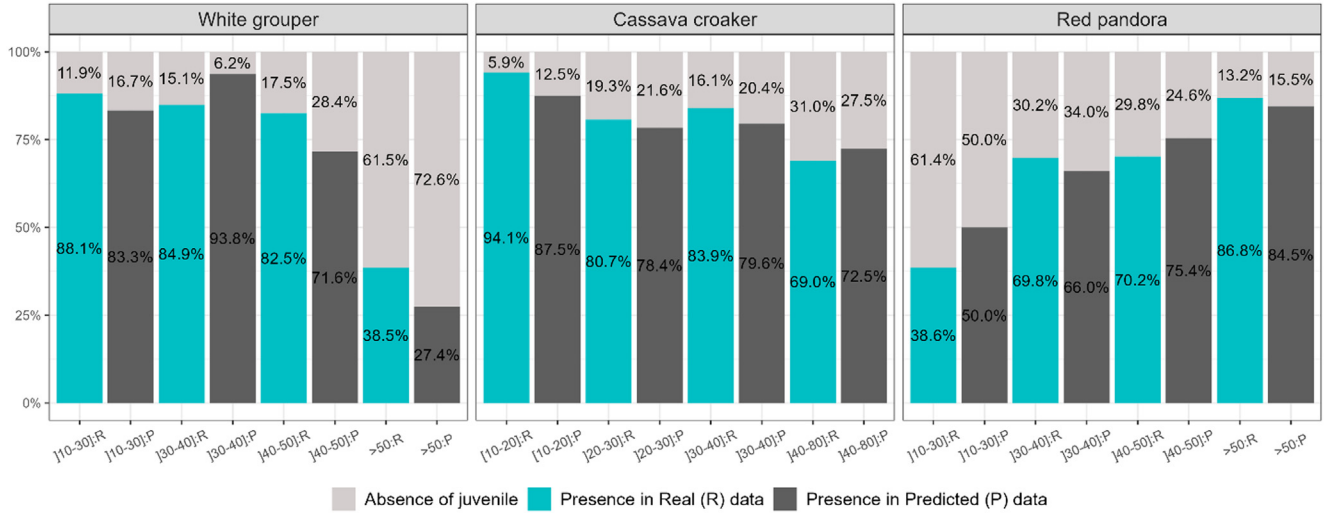


Fig. 4. Proportion of presence for real vs predicted values by bathymetry levels (in m). Illustration for juvenile.

The outputs of the 3 species-specific models were used to predict the proportion of juveniles in trawl hauls for which only mean weights are available (and catches are >1 fish) and infer the respective number of juveniles and adults in catches (Eq. (2)).

$$N = \hat{J} \times C, \quad (2)$$

where N is the number of juvenile fish in catches in the trawl haul, \hat{J} is the predicted proportion of juveniles, and C is the number of fish caught in the trawl haul. A threshold is used when $N < 1$, N is replaced by 0 (absence). Number of adults = $C - N$.

In the whole dataset, catches by species were allocated in juveniles or adults; a complete dataset was available (2,077 trawl hauls), with:

- The respective catch per unit of effort (relative density of fish in number per trawled surface) of juveniles and adults per species.
- The environmental (i.e., bathymetry and proximity to freshwater mouth, derived from crossing the respective spatial maps Supp. Figs. 2 and 3 with the average geographic position of each trawl haul), and temporal (period) descriptors.

2.5 HSMs

Quantitative analysis consists of modelling nursery habitat suitability based on GLM methods (Le Pape et al., 2014; McCullagh and Nelder, 1989). The proportions of occurrence (Tab. 3) of white grouper, cassava croaker, and red pandora at all trawled stations are 33.26%, 21.76%, and 66.58%, respectively, and even less when the data are split by life stage. With regard to this 0-inflated distribution of catch data by species and life stage (Supp. Tab. 2), a delta model was

used. A delta model is a combination of two submodels: one based on presence–absence and the other on abundance for non null densities (Le Pape et al., 2014; Trimoreau et al., 2013). Building this model needed three steps:

2.5.1 Submodel 1: probability of presence $Y_{0/1}$

The presence–absence model aims to explain the probability of the presence of the fish for a given life stage, with a binomial distribution (Eq. (3)) based on presence/absence data (Boolean values: 0 when the relative density of fish in number per trawled surface is null, 1 otherwise).

$$Y_{0/1} \approx \beta_{Period} + \beta_{Bathymetry} + \beta_{Prox.to\ river\ mouth} + \epsilon_{0/1}, \quad (3)$$

with $Y_{0/1}$, the response variable, the probability of presence, β_{period} , cofactor 1, period (2 categories; cf. 2.3.2.), $\beta_{Bathymetry}$, cofactor 2, bathymetry (in 10 categories; cf. 2.3.1.), $\beta_{prox. to river mouth}$, cofactor 3, proximity to river mouth (2 categories; cf. 2.3.1.), $\epsilon_{0/1}$, residuals.

2.5.2 Submodel 2: positive densities Y^+

The second submodel (Eq. (4)) uses a Gaussian GLM on log-transformed positive densities to normalize the skewed distribution of the proxies of positive densities (CPUE). Preliminary analyses showed that this option was the best to describe the distribution of positive values in the dataset, as usually found for positive fish densities from survey data (Trimoreau et al., 2013).

$$\log(Y^+) \approx \beta_{Period} + \beta_{Bathymetry} + \beta_{Prox.to\ river\ mouth} + \epsilon_+, \quad (4)$$

with $\log(Y^+)$, log-transformed positive density in number per km^2 , β , explaining cofactors (cf. Eq. (3)), ϵ_+ , residuals.

Table 4. Results of extrapolation models to estimate the proportion of juveniles.

Species	Descriptors	DoF	Deviance	P-values	AIC	ED (%)
i) <i>Epinephelus aeneus</i>	NULL	70	236	–	296	–
	Mean weight	69	63	1.9E-39	125	73.29
ii) <i>Pseudotolithus senegalensis</i>	NULL	198	3189	–	3795	–
	Mean weight	197	754	0	1363	76.34
iii) <i>Pagellus bellottii</i>	NULL	712	18532	–	20606	–
	Mean weight	711	7001	0	9077	62.22

DoF: degree of freedom and deviance are shown as residuals.

ED: explained deviance in %.

2.5.3 Selection of explanatory variables

For the 2 submodels, for each species and life stage, the selection of explanatory factors was based on the Akaike information criterion (AIC), with a difference of 3 considered significant (Bozdogan, 1987). The submodels are compared one by one by adding an additional factor.

2.5.4 Coupling of both submodels: The delta model

Once the best submodels were selected for each species and life stage, they were coupled (Eq. (5)) by applying a correction to obtain an unbiased estimate from a linear model based on log-transformation (Trimoreau et al., 2013).

$$YS = YS_{0/1} \times e^{(\log(YS_{+}))} \times e^{\left(\frac{\hat{\sigma}^2(\log(YS_{+}))}{2}\right)}, \quad (5)$$

with YS estimation of the density from the delta model, $YS_{0/1}$, estimation of the probability of presence (Submodel 1, Eq. (3)), YS_{+} , estimation of the positive log-density (Submodel 2, Eq. (4)), $\hat{\sigma}^2(\log(YS_{+}))$, standard error of estimation of the log-transformed density (from Submodel 2).

2.5.5 Validation

To assess the goodness of fit (GOF) of the presence-absence models based on Boolean values (Submodel 1), the area under the curve (AUC) of the receiver operating characteristic (ROC) was used. The AUC is a threshold-independent measure aiming to assess the model performances at discriminating between presences and absences using a range of threshold values (Hanley and McNeil, 1982). The coefficient of determination (r^2) was used to assess the GOF of Submodel 2 on positive densities.

As models with poor and/or biased prediction power could lead to spurious conclusions, their validation requires attention. To validate the models, their GOF was evaluated by comparing observed versus predicted values with a calibration/validation procedure. Each dataset (12, 2 submodels \times 2 life stages \times 3 species) was randomly split into two parts: calibration, 75% of the data, and validation, 25% of the remaining data. This random split was performed with respect to the relative amount of data

within the different classes of factors (i.e., bathymetric classes, proximity to river mouth and period). For each species and life stage, binomial and positive models were fitted using the calibration dataset, and the GOF was tested both on the calibration and the validation datasets by comparing the model predictions with the data (predictions are the model-fitted values for the calibration dataset and the model estimates for the validation dataset; Trimoreau et al., 2013). This procedure was replicated 100 times, and the average calibration versus validation estimates were compared. Note that to overcome potential spatial correlation, this procedure was also tested after splitting the dataset into 2 geographical units (separated by economic exclusive zones, i.e. Côte d'Ivoire/Ghana). Similar results led us to consider the “simple” version without this spatial structure in the presented results.

2.6 Prediction with confidence intervals and mapping

In a delta model, the combined effects of the descriptors on the binomial distribution and on the positive log-data cannot be directly interpreted together (Le Pape et al., 2014). Combined mean effects have been computed to obtain relative effects of each modality of factor, with their associated uncertainty. Using a Monte-Carlo method (Jia, 2018), we proceeded in 3 steps: (i) generate 5000 random predictions from the presence-absence submodel $N(Y_{0/1}, \sigma_{0/1})$ and the positive density submodel $N(Y_{+}, \sigma_{+})$ for each combination of modalities of the descriptors, (ii) couple the values obtained from the two submodels to obtain predicted densities (Eq. (6)), (iii) calculate the 5%, 50% and 95% quantiles of the distribution, i.e., the median and the associated 90% confidence interval, and show outputs by modality of the descriptor.

$$YS = YS_{0/1} \times e^{(\log(YS_{+}))}. \quad (6)$$

Note that the estimation of the average positive density in equation (5) requires a correction used when logtransformation is applied ($e^{(\log(YS_{+}))} \times e^{\left(\frac{\hat{\sigma}^2(\log(YS_{+}))}{2}\right)}$, Trimoreau et al., 2013). In equation (6), random predictions of positive densities are estimated by $e^{(\log(YS_{+}))}$, without correction. Finally, quantile 50

Table 5. Habitat suitability models fit.

Species and life stage	Descriptors	Model of presence-absence (A)					Model of positive density (B)				
		DoF	Deviance	Pr(>Chi)	AIC	ED(%)	DoF	Deviance	Pr(>Chi)	AIC	ED(%)
i) <i>Epinephelus aeneus</i>											
Juvenile	NULL	2076	2102	–	2104	–	423	376	–	1156	–
Juvenile	Period						422	362	5.4E-05	1142	3.72
Juvenile	+Bathymetry ^a	2067	1885	7.2E-42	1905	10.34					
Juvenile	+River mouth	<i>Not significant</i>									
Adult	NULL	2076	1934	–	2104	–	365	359	–	1035	–
Adult	Period	2075	1834	1.7E-23	1838	5.16	364	342	1.9E-05	1020	4.73
Adult	+Bathymetry ^a	2066	1686	1.9E-27	1708	12.83					
Adult	+River mouth	2065	1682	4.8E-02	1706	13.03	363	337	2.7E-02	1017	6.00
ii) <i>Pseudotolithus senegalensis</i>											
Juvenile	NULL	2076	1912	–	1914	–	358	2172	–	1669	–
Juvenile	Period	2075	1892	5.4E-06	1435	1.08	357	2134	5.7E-03	1665	1.76
Juvenile	+Bathymetry ^{b,c}	2069	1399	3.7E-103	1415	26.83	355	1779	4.0E-16	1603	18.12
Juvenile	+River mouth	2068	1383	5.3E-05	1401	27.68					
Adult	NULL	2076	2058	–	1914	–	407	2003	–	1811	–
Adult	Period	2075	2039	1.3E-05	2043	0.93	406	1926	2.7E-05	1797	3.80
Adult	+Bathymetry ^{b,c}	2069	1501	5.4E-113	1517	27.07	404	1745	7.9E-10	1761	12.84
Adult	+River mouth	2068	1492	2.6E-03	1510	27.51					
iii) <i>Pagellus bellottii</i>											
Juvenile	NULL	2076	2879	–	2881	–	1020	5907	–	4694	–
Juvenile	Period	2075	2864	1.0E-04	2868	0.52					
Juvenile	+Bathymetry ^{a,b}	2066	2439	8.6E-86	2461	15.26	1014	5335	3.9E-21	4602	9.68
Juvenile	+River mouth	<i>Not significant</i>									
Adult	NULL	2076	2678	–	2881	–	1358	8681	–	6381	–
Adult	Period	2075	2657	3.3E-06	2661	0.81	1357	8657	4.0E-02	6379	0.28
Adult	+Bathymetry ^{a,b}	2066	2327	1.2E-65	2349	13.12	1351	7811	4.8E-29	6251	10.02
Adult	+River mouth	<i>Not significant</i>									

DoF: degree of freedom and deviance are shown as residuals.

ED: explained deviance in %.

^{a, b, c}: bathymetry as factor with respectively 10 classes, 7 classes, 3 classes.

of *YS* obtained here with equation (6) on 5000 random predictions is equivalent to *YS* estimated from equation (5).

Habitat mapping consisted of combining the predicted densities (Eq. (5)) for each species and life stage with the geographic data (on each point of the spatial map, and for the two periods, the prediction of the density is done regarding the value of the spatial descriptors, bathymetry and proximity to the river mouths).

3 Results

3.1 Allocation of catches in life stage when length structure is lacking

The explained deviance of the extrapolation models of the proportion of juveniles in survey data reached 73%, 76%, and 62% for white grouper, cassava croaker, and red pandora, respectively (Tab. 4). Without different patterns in mean weight between measured and unmeasured data (Fig. 3), the models provide unbiased predictions of the proportion of juvenile fish in survey catches (Fig. 4). These models were used to predict the proportion of juveniles and complement the data with the number of juveniles and

adults in catches when the length structure was not available.

3.2 Model selection, predictions and uncertainty

3.2.1 Selection of descriptors and model validation

The 3 descriptors, i.e., bathymetry, distance to river mouth, and period, were retained at least partly in the delta models for the three species (Tab. 5). For the three species and the two life stages, the two submodels very partly explained the deviance of the presence [10–28] % (min/max on the three species) and of the positive densities [3–18] %, respectively, with a better explanatory power for cassava croaker and worse for white grouper (Tab. 5).

The results of the juvenile and adult AUC data range from 0.701 ± 0.020 to 0.844 ± 0.015 except for the adult presence-absence submodel of white grouper (Tab. 6). The calibration and validation values are very close. The presence-absence submodels are therefore considered robust, except for white grouper adults. For the positive density submodels, the r^2 coefficient is analytically equivalent to the percentage of explained deviance; thus, the

Table 6. Calibration and validation results of habitat suitability sub-models (\pm standard deviation).

Parameters	Species	Juvenile		Adult	
		Calibration	Validation	Calibration	Validation
AUC	<i>Epinephelus aeneus</i>	0.709 \pm 0.006	0.701 \pm 0.020	0.442 \pm 0.009	0.432 \pm 0.027
	<i>Pseudotolithus senegalensis</i>	0.845 \pm 0.004	0.844 \pm 0.013	0.841 \pm 0.005	0.844 \pm 0.015
	<i>Pagellus bellottii</i>	0.752 \pm 0.005	0.748 \pm 0.016	0.737 \pm 0.007	0.735 \pm 0.016
r^2	<i>Epinephelus aeneus</i>	0.037 \pm 0.013	0.049 \pm 0.038	0.065 \pm 0.013	0.049 \pm 0.037
	<i>Pseudotolithus senegalensis</i>	0.178 \pm 0.023	0.192 \pm 0.068	0.132 \pm 0.017	0.119 \pm 0.048
	<i>Pagellus bellottii</i>	0.097 \pm 0.010	0.091 \pm 0.028	0.099 \pm 0.010	0.097 \pm 0.028

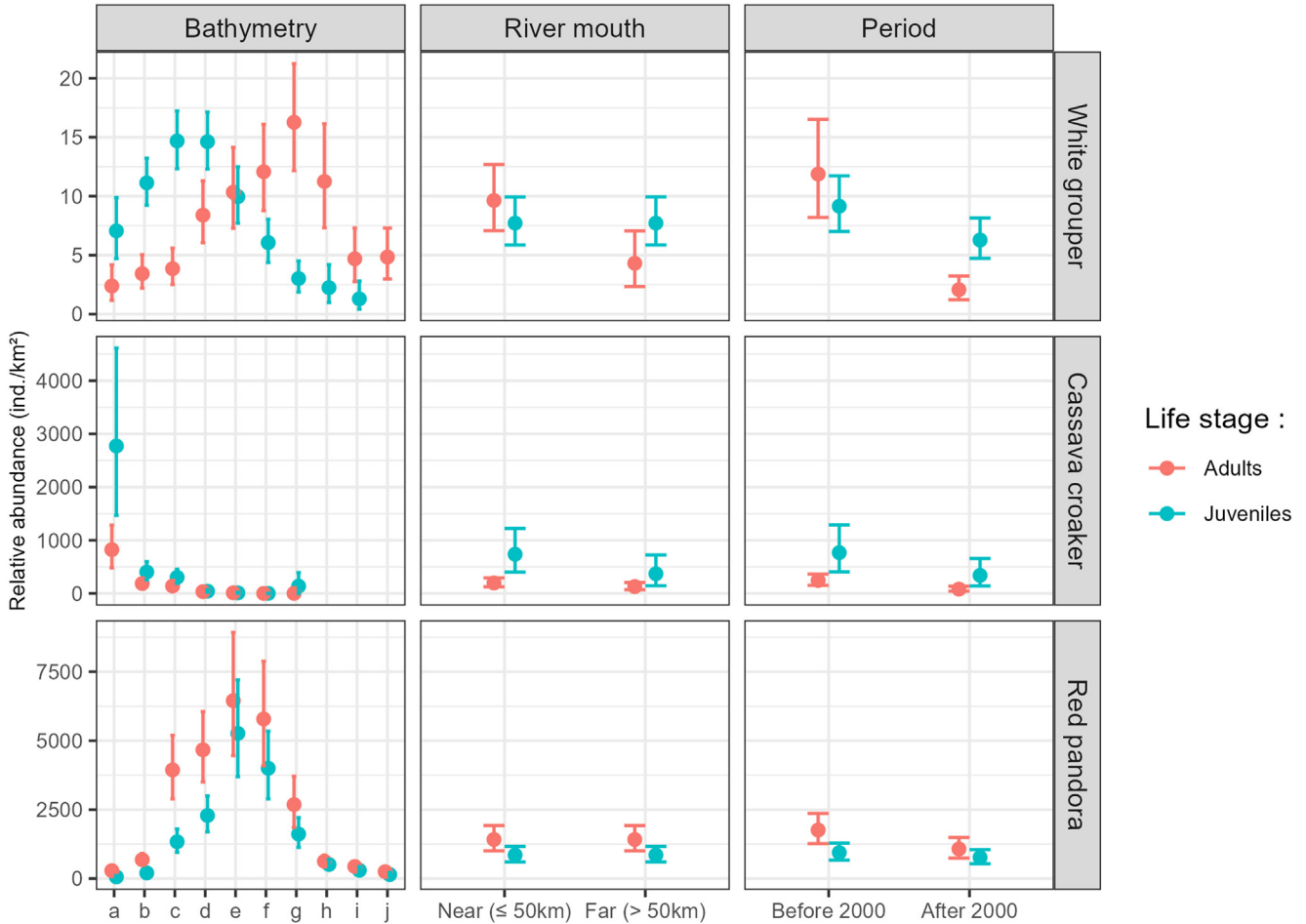


Fig. 5. Prediction and mean effects of habitat descriptors. a:[10,20] m, b: [20,30] m, c: [30,40] m, d: [40,50] m, e: [50,60] m, f: [60,70] m, g: [70,80] m, h: [80,90] m, i: [90,100] m, j: >100m (except for cassava croaker for which f: [60,80] m and g: > 80m).

performance of the models is similar for the calibration dataset (Tab. 6) than in the overall model fit (Tab. 5). Except for the adult white grouper, the degradation of r^2 from calibration to validation data was below 20% for the three species and was considered reliable.

3.2.2 Model prediction and mapping

Overall, bathymetry had an important influence on habitat suitability (Tab. 5). The density of white grouper peaks in shallow areas for juveniles, is abundant between 10 and 50 m, whereas it is deeper for adults (Figs. 5 and 6). The cassava

croaker is concentrated in the shallowest areas, below 20 m (Figs. 5 and 7). The red pandora has a wider distribution towards the open ocean, with a maximum abundance from 40 to 70 m and low density in the shallow coastal fringe (Figs. 5 and 8). For both cassava croaker and red pandora, the bathymetric distributions of juveniles and adults overlap (Fig. 5).

Distance to river mouth had an additional partial and moderate life-stage- and species-specific influence. Adults of white grouper are more abundant, and both life stages of cassava croaker more frequently occur close to the river mouths (Tab. 5; Fig. 5).

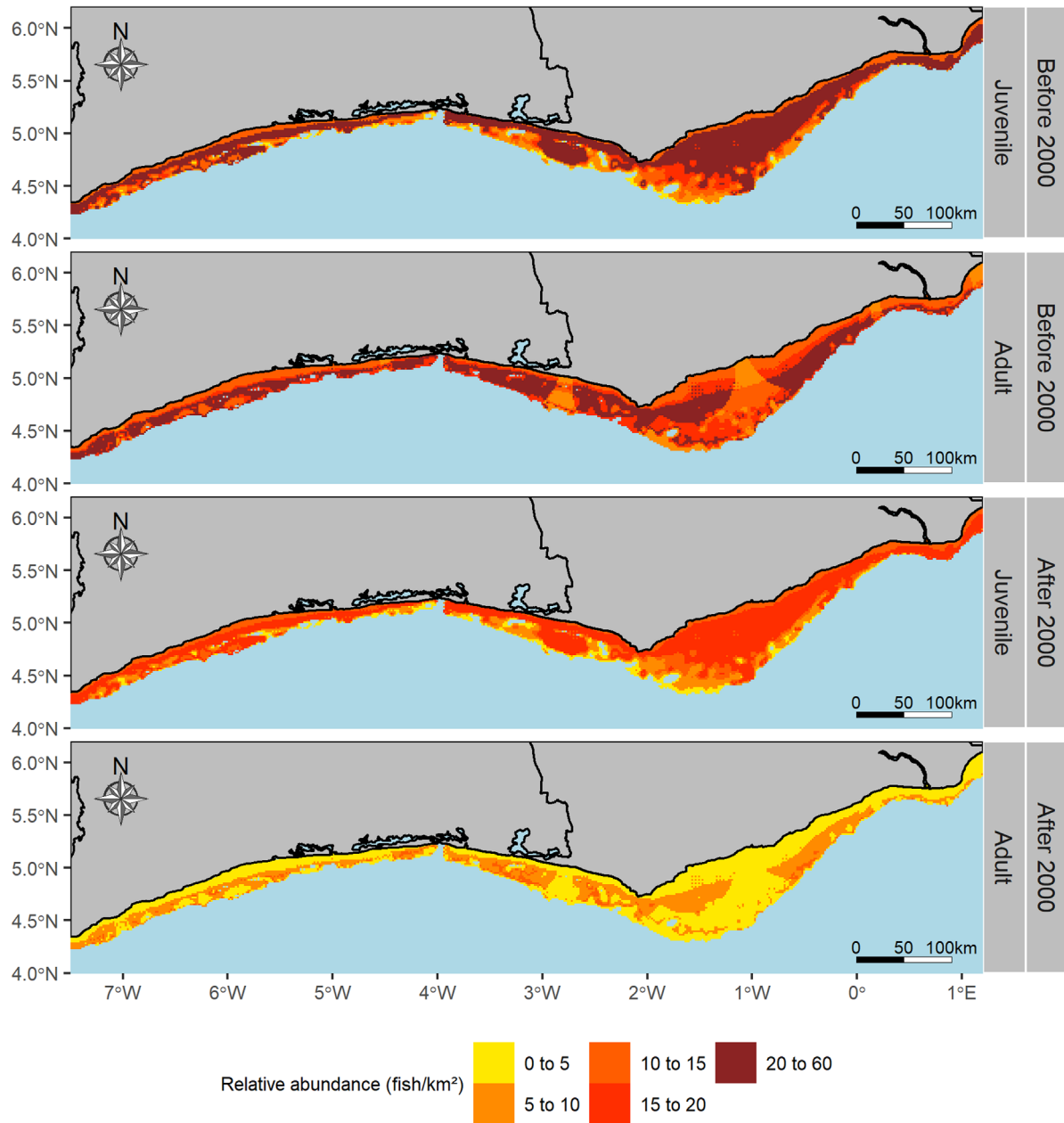


Fig. 6. Habitat maps of white grouper (*E. aeneus*), relative abundance (number of fish caught/km²). Regarding the low model accuracy for the adult stage, the adults map has to be considered as indicative.

The period was significant, except for the presence of juveniles of white grouper and positive density for red pandora, indicating a general decrease in the abundance of both juvenile and adult fish for the three species (Tab. 5; Fig. 5).

4 Discussion

The present study aimed to model and map the spatial distribution of both juvenile and adult distributions of three fish species of main fishing interest in the western Gulf of Guinea. Data from trawl surveys carried out in the study area since the late 1970s were collated and pretreated to estimate the

respective species-specific CPUE of juveniles and adults. The HSMs were developed to describe these CPUE with relation to environmental factors. Survey data (species- and life-stage-specific CPUE) were 0-inflated and prevented the use of conventional linear models. Delta GLMs combining two submodels for the probability of presence and positive densities, respectively, were applied to fit these 0-inflated data (Le Pape et al., 2014). These HSMs based on abiotic descriptors of the environment (bathymetry) and seascape (proximity to river mouths) and accounting for 2 time periods partly explained the spatial distribution of juveniles and adults and the temporal patterns in densities for the three species, with a large remaining part of the variability in distribution not explained by the descriptors.

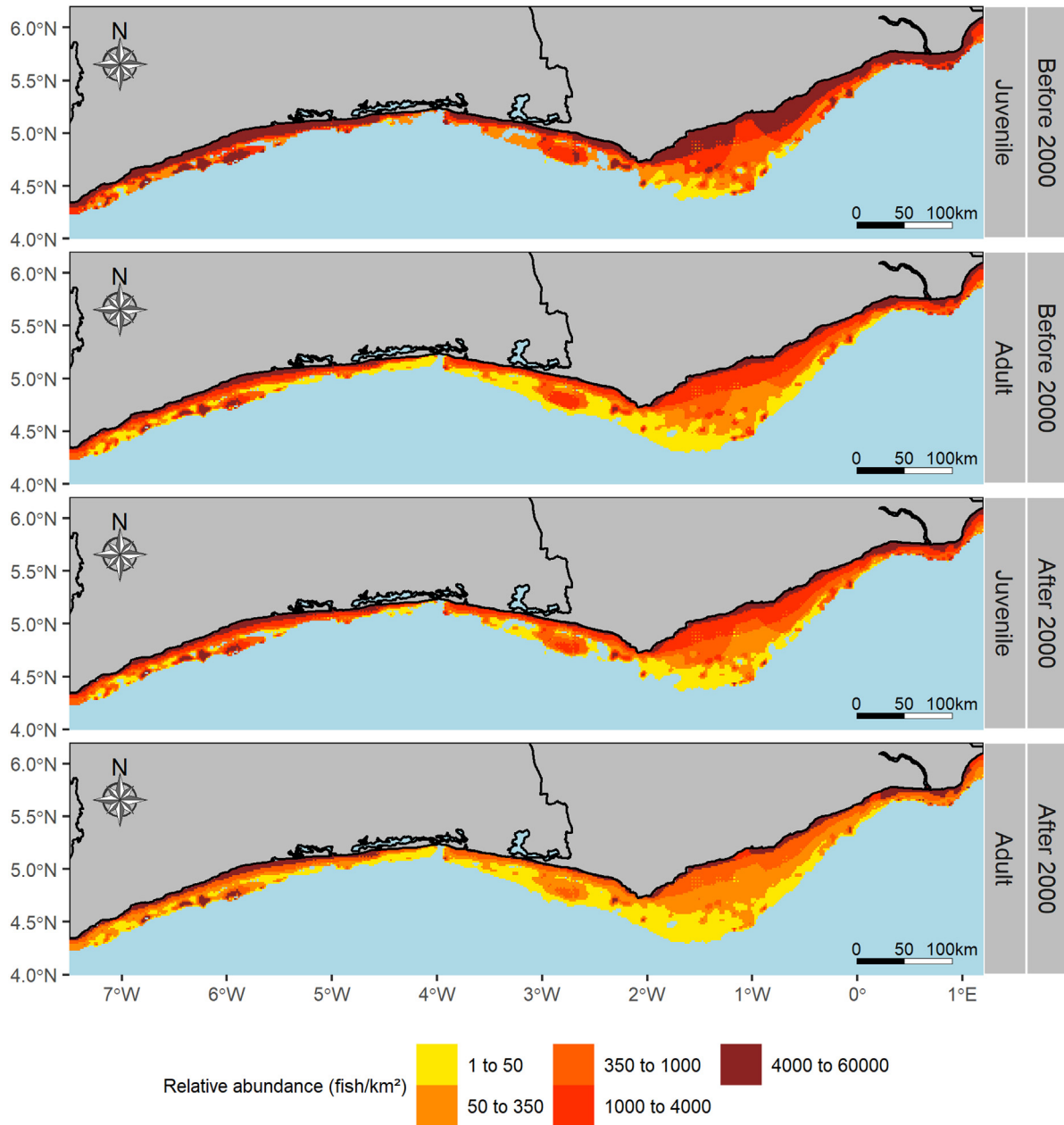


Fig. 7. Habitat map of cassava croaker (*P. senegalensis*), relative abundance (number of fish caught/km²).

4.1 Model limits and potential improvements

A poor level of explanatory power is common in marine fish HSMs, and residual variability is important (Le Pape et al., 2014). This was verified from the present case study: Uncertainties arise from observation processes (data paucity, small spatial scale and short-term temporal variability) but also from the lack of structuring environmental descriptors accounted for in model formulation.

The observation process is especially critical when the dataset merges various scientific surveys operated with various trawls and spanning 4 decades. Contrasts in trawl catchability and selectivity (Tab. 2) could have reduced the accuracy of

CPUE estimates, especially for young juveniles. However, no reliable intercalibration information was available from these surveys carried out in various areas at different periods. In addition, the use of a single 1st size at maturity during the whole period (Tab. 1) could be a weakness. Accordingly, considering all individuals that were past their first maturity as adults led to considering protogynous fish as mature before male maturity and provided only a proxy of life-stage structure.

Accounting for a restricted number of environmental descriptors is another limit to the level of explanation of marine fish HSMs:

- *Sediment structure*. Maps of sediment structures were not available with sufficient precision for the Ghanaian

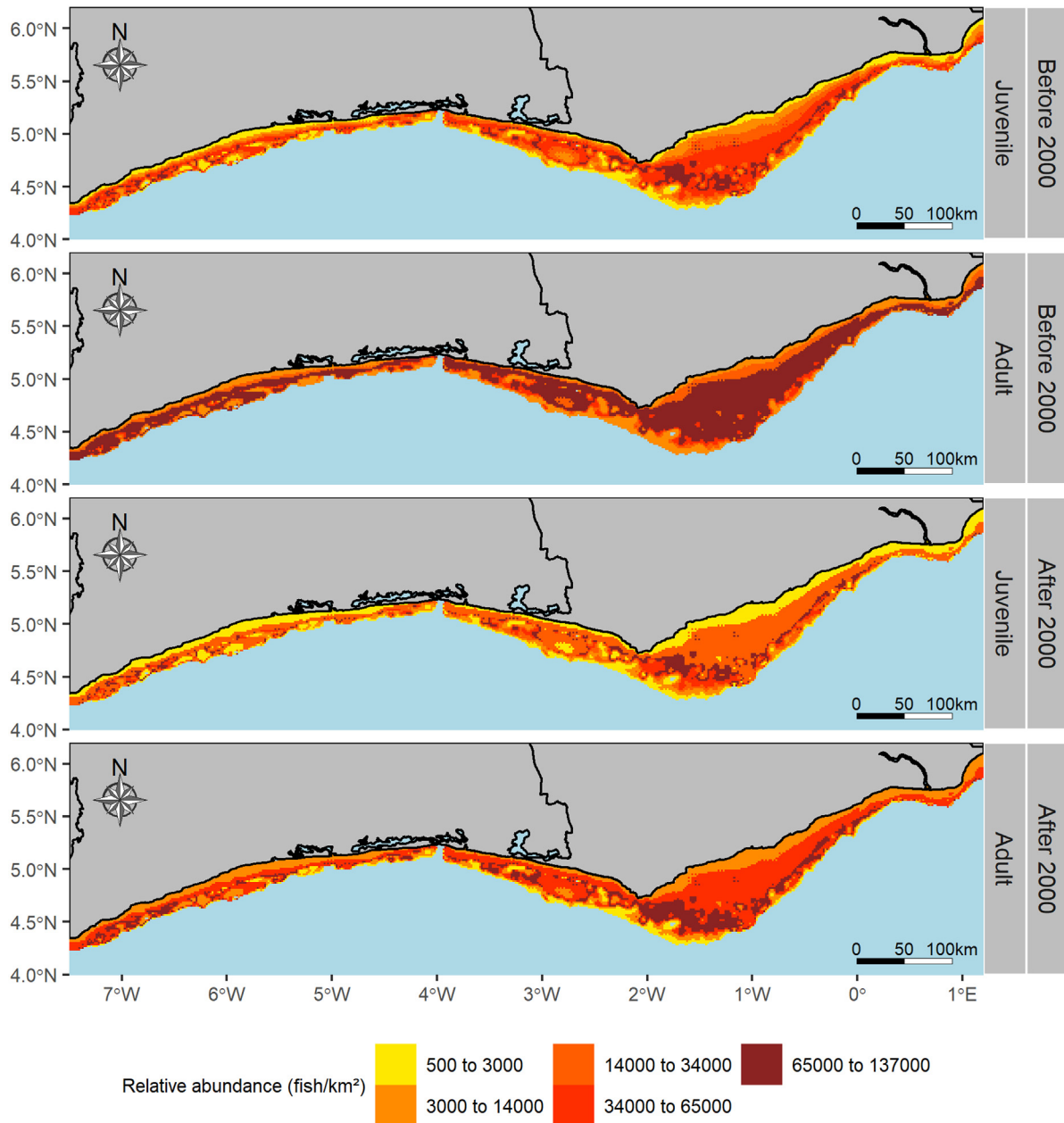


Fig. 8. Habitat map of red pandora (*P. bellottii*), relative abundance (number of fish caught/km²).

waters, and this parameter was not used as a habitat descriptor. However, HSMs based on a restricted dataset on Ivorian waters (Supp. Fig. 5) did not evidence a significant influence of this descriptor.

- *Additional longitudinal patterns.* In response to differences in fisheries management between Ghana and Côte d'Ivoire, or to other underlying processes, species- and life stage-specific distributions of fish could present longitudinal patterns in the study area. However, tests using a “country” effect did not show any significant effect.
- *Temporal variability and hydrologic parameters.* Salinity and/or nutrient concentration are potential complementary

habitat descriptors, with, for instance, a better accuracy than seascape distance to the river mouth to describe the influence of estuarine enrichment (Trimoreau et al., 2013). In the context of climate change, a more accurate description of temporal patterns, integrating a descriptor of temperature, could also have improved model accuracy. However, these descriptors were not accounted for in the present analysis. The paucity of data mainly prevented this use. Hydrologic maps of surface temperature and salinity are not available for the first years of the time series of trawl surveys, and no information is available for the bottom waters, where these three demersal species are living.

– Moreover, adding hydrology would imply to consider some temporal models, i.e., to account for interannual variability (Trimoreau et al., 2013) and to integrate the seasonal response of fish distribution to temperature, which is far from constant all year long. The paucity of trawl survey data (Tab. 1) did not allow for the development of such complex models. However, tests using a “season” effect in the model did not show any significant effect. Accounting for hydrologic variability is of course a major research avenue that would need further consideration in the future.

This modelling approach could thus be considered raw, providing only a proxy of fish density and partly explaining the average spatial distribution and temporal patterns in the long term, without integrating fine-scale distributions linked to biotic factors (food resources, Jänes et al., 2020; Le Pape et al., 2013) or multiscale temporal variability. However, an “out of the bag” cross-validation procedure (Le Pape et al., 2014) allowed us to validate HSMs robustness, except for adults of white grouper, for which model accuracy was lower. Even if more accurate datasets and environmental descriptors would certainly have refined the description and mapping, the present HSMs described some drivers of life-stage specific distribution for the three species and allowed us to map their distribution.

4.2 Species- and life stage-specific habitats and temporal patterns

The identification of habitats was carried out with two environmental descriptors: bathymetry and proximity to river mouths. Bathymetry is well known to structure the demersal fish distribution (Trimoreau et al., 2013) at both the juvenile and adult stages. The bathymetric factor was the most important driver of spatial distribution at both life stages for the three studied species. The influence of estuarine inputs is a complementary factor partly explaining the spatial distribution of marine species (Olds et al., 2012; Trimoreau et al., 2013), especially at juvenile stages (Beck et al., 2001). The enrichment of the coastal part of the continental shelf by river inputs from estuaries (Le Pape et al., 2013) makes the areas in their vicinity particularly suitable for the growth and survival of juveniles (Trimoreau et al., 2013). However, the contribution of this seascape component (Drakou et al., 2017; Nagelkerken et al., 2015) to the HSMs remained dramatically lower than that of bathymetry and logically concerned only the two coastal species.

Of the three studied species, white grouper was the one for which HSM performance was the lowest; it was robust for juveniles but less robust for adults. However, the similarity with conclusions drawn elsewhere for this species led us to validate HSM outputs and related maps. White grouper lives in ECEs such as open lagoons, bays, and estuaries (Bakari et al., 2016; Eugenia et al., 2019; Nunoo et al., 2006; Okyere and Blay 2020; Okyere and Nortey 2018; Sossoukpe et al., 2013b) at the juvenile stage. Out of the estuarine environment, juveniles are dramatically more abundant below 50 m of depth, confirming their high concentration on the coastal fringe of the continental shelf (Vally et al., 2023). At the adult stage, white grouper prefer deeper areas and have dramatically wider

distributions; however, there is a preference for the proximity of estuaries (Vally et al., 2023).

Cassava croaker is frequently observed in ECEs (Nunoo et al., 2006; Okyere and Blay 2020; Okyere and Nortey 2018; Sossoukpe et al., 2013b). On the continental shelf, its spatial distribution is unimodal with a preference for shallow waters (<20 m) at both juvenile and adult stages and with a preference for the vicinity of estuaries (FAO, 1991). This species uses nearshore areas under riverine influence as nurseries, adult feeding and spawning areas (Sossoukpe et al., 2013a).

Red pandora live in the open sea (Kouame et al., 2020; Sylla et al., 2017). Juveniles and adults share the same living area, mainly from 30 to 80 m, with no dependency on coastal habitats.

For the three species, abundance decreased after 2000 at both the juvenile and adult stages. This decrease could be linked to a large panel of factors, including environmental changes and habitat degradation (Brown et al., 2018), evidenced in coastal habitats of the study area: land reclamation and habitat loss (Abé and Affian, 1993; Osemwegie et al., 2016), eutrophication (Adingra and Kouassi, 2011), siltation and deoxygenation (Okyere and Nortey, 2018), and xenobiotic loadings (Koffi et al., 2014). However, in the study area, global fishery landings have increased in recent decades, with overexploitation for *Pseudotolithus* spp. (Derrick, 2020; FAO, 2022; Polido et al., 2020) and, more precisely, for cassava croaker (Okyere and Blay, 2020; Tia et al., 2017), and full exploitation for *red pandora* (FAO 2022; Kouame et al., 2020; Sylla et al., 2017). In addition to the unestimated impact of climate change and habitat degradation, the impact of fisheries is partly responsive to the observed temporal changes in abundance for the three studied species.

4.3 Management recommendations

The quantitative identification and mapping of CEHs is a crucial preliminary step for an ecosystemic approach to preserve marine exploited resources (Le Pape et al., 2014). The protection of CEHs is important for the renewal of fish stock (Beck et al., 2001) and is needed in combination with fisheries management to sustain resources and fisheries (Worm et al., 2006).

The juveniles of white grouper and cassava croaker during their whole life cycle are concentrated at 0–50 m and 0–20 m, respectively. Thus, there is an urgent need to preserve/restore this coastal fringe of the continental shelf to enhance population renewal for these two species. The impacts of local anthropogenic disturbance on nearshore-dependent species are well documented (Brown et al., 2018). These disturbances, evidenced in the study area (cf. 4.2), could have detrimental impacts at the population level for production and exploitation. Local habitat degradation could impact populations of species residing in coastal habitats throughout their life cycle, such as cassava croaker, but could also have detrimental consequences at a dramatically larger scale for species concentrated in ECEs at the juvenile stage (Archambault et al., 2018; Drakou et al., 2017), such as white grouper. However, the consequences of habitat degradation for exploited fish population renewal remain poorly understood (Brown et al., 2018).

At the same time, there is a need to regulate fishing in the coastal part of the continental shelf. Pushing the fishing effort beyond CEHs using protected areas could be an effective option to protect nursery grounds for white grouper, with a positive impact on fish stocks without pushing fishermen out of fishing grounds for adults (Mesnildrey et al., 2013). However, this would imply restricting access to both juvenile and adult stages for cassava croaker. This would dramatically reduce its overexploitation level (FAO, 2022; Okyere and Blay, 2020) but will prevent sustaining fisheries landings. Regulation of the mesh sizes of the fishing gear targeting these species in the coastal fringe could be a complementary option to avoid catching juveniles, (i) concentrated there for white grouper, and (ii) as juveniles represent a high proportion of the fish landings for *Pseudotolithus spp.* (Sossoukpe et al., 2013b; Wehye et al., 2017).

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Data availability statement

The authors do not have permission to share data.

Supplementary material

Supp Fig. 1. Geographic position of the trawl hauls in scientific surveys used in this study.

Supp Fig. 2. Bathymetry map of the continental shelf in the study area.

Supp Fig. 3. Buffer of 50 km from the entrance of river mouths to the continental shelf covering in the study area.

Supp Fig. 4. Number of trawl hauls per class of bathymetry x descriptor of proximity to the river mouths.

Supp Fig. 5. Sediment map of the continental shelf on the study zone.

Supp Table 1. Bibliographic review of the size at maturity of the three studied species.

Supp Table 2. Proportion of trawl hauls with the presence of the specie based on the total trawl hauls, including catches in life stages where the length structure was estimated.

The Supplementary Material is available at <https://www.alr-journal.org/10.1051/alr/2024005/olm>.

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