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Quantitative mapping of effective habitats for the White grouper *Epinephelus aeneus* (Geoffroy Saint-Hilaire, 1817) in North West Africa

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ABSTRACT

Within the Mauritania–Senegal maritime zone, we have identified and mapped habitats of the white grouper (*Epinephelus aeneus*). To this end, data collected since the 1980s through scientific sampling surveys along the coastline and on the continental shelf in the study zone have been analysed. On the basis of data collected in shallow coastal and estuarine environments, it has been shown that only the juvenile fraction of the *E. aeneus* population lives in the diverse habitats (mangroves, sea grass beds, salt marshes, etc.) of both the Banc d'Arguin and the estuaries. On the continental slope, habitat suitability of both juvenile and adult was modelled, using descriptors relating to environment (bathymetry, sediment) and landscape (proximity of estuaries and the Banc d'Arguin). Bathymetry is a major factor driving these distribution patterns, while other environmental descriptors also have significant influence, though to a lesser degree: juveniles of *E. Aeneus* live in nearshore zones and their density is higher near the Banc d'Arguin and the estuaries, unlike the adult populations found further offshore. The density of both populations has varied over time, falling significantly in 1990, and partly recovering since 2010. These habitat maps tell us the importance of the coastal fringe as essential habitat for juvenile *E. aeneus* and the usefulness of space-based management measures to enhance the population and allow for sustainable fishing exploitation.

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1. Introduction

Coastal habitats (estuaries, mangroves, sea grass beds, salt marshes, etc.) play a multitude of environmental roles (Baran, 2000; Beck et al., 2001) and are of great interest for ecosystem services (Costanza et al., 2014). They are characterised by their high level of primary and secondary productivity and sustain high abundance and diversity of fish and invertebrates (Skilleter et al., 2005). These coastal sectors are often considered as nurseries because of their high concentration in juvenile for many species of fishing interest (Beck et al., 2001; Seitz et al., 2014; Cheminée et al., 2021; Kimirei et al., 2013; Rochette et al., 2010). The renewal of exploited resources depends on the spawning biomass but also on the quality of the habitats in which the successive phases of their life cycle take place (Le Pape and Bonhommeau, 2015). In particular, the juvenile stages are heavily reliant on

specific nursery habitats, often located in coastal zones (Kimirei et al., 2013; Riou et al., 2001; Skilleter et al., 2005). The ecosystem approach to fisheries stipulates that the management of fisheries resources does not only involve controlling fishing effort and catches (Howell et al., 2021), but also taking into account the entire life cycle of resources and their habitats, including coastal nursery areas, which play an essential role in population renewal (Beck et al., 2001; Le Pape and Bonhommeau, 2015).

The Mauritania–Senegal continental shelf is marked by strong productivity (Aristegui et al., 2009). Its coastal section hosts a patchwork of productive ecosystems that shelter multiple fish and invertebrate species of fisheries interest, especially at the juvenile stage (Colléter et al., 2012; Jager, 1993; Schaffmeister et al., 2006; Simier et al., 2004). The life cycle of these species is characterised by geographically distinct phases: (i) the adults colonise the continental shelf; (ii) growing juveniles are dependent upon the coastal habitats of the estuaries and lagoons (Okyerere and Blay, 2020; Seeley and Walther, 2018; Sheaves and Johnston, 2008); mudflats (Bloomfield and Gillanders, 2005; Marley et al.,

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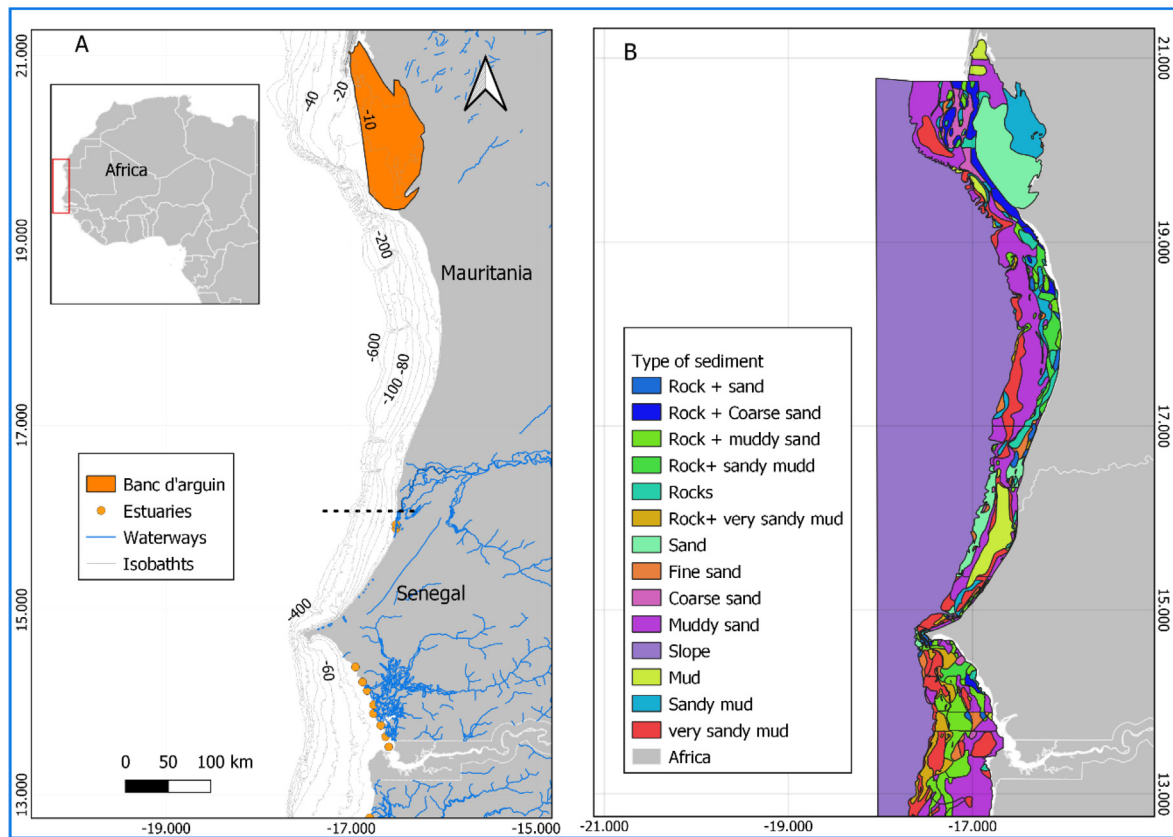


Fig. 1. Map of the study area. (A) bathymetry, location of the Banc d'Arguin and of the estuarine mouths, and limit between the latitudinal zones (bold horizontal bracket line); (B) sedimentary structure. Top left-hand corner: the zone's location in West Africa.

2020), mangroves (Ellis and Bell, 2004; Laegdsgaard and Johnson, 2001; Manson et al., 2005; Sandoval et al., 2022), sea grass (Heck Hay et al., 2003; Hewitt et al., 2020; McDevitt-Irwin et al., 2016; Wasserman et al., 2020), and upon a combination of these habitats (Hammerschlag-Peyer and Layman, 2010; Lefcheck et al., 2017; Marley et al., 2020; Whitfield, 2017).

However, there is insufficient knowledge on the Mauritania–Senegal coastline to allow for determining which habitats are effective (sensu (Dahlgren et al., 2006), i.e., habitats that make a greater than average overall contribution to the population) for the renewal of fish resources. This study focused on an emblematic demersal species of this zone, the white grouper (*Epinephelus aeneus*, Saint-Hilaire, 1817), whose life cycle relies on coastal and estuarine nurseries (Domain, 1980; Özbek et al., 2013). The white grouper, is a tropical Serranidae (González-Lorenzo et al., 2021) present from the southern coasts of the Mediterranean Sea to the north-western coasts of Africa and frequently observed on the shelf and along the shores of Mauritania and Senegal (Bruslé, 1985; Cury and Worms, 1982). The reported maximum total length of this species is 120 cm (Heemstra and Randall, 1993). It is a protogynous species (Özbek et al., 2013; Bouain and Siau, 1983). Its size at first sexual maturity is between 49 and 55 cm (Ndiaye et al., 2013). *E. aeneus* is known by the vernacular name “Thiof” in Senegal and Mauritania where it has a legendary status, occupies a main place in the local market, supplied mainly by small-scale fishing. *E. aeneus* is considered as overfished in most Atlantic zones and features on the endangered species Red List kept by the International Union for Conservation of Nature (Ba et al., 2018; Meissa et al., 2013; Pollard et al., 2018). We aimed to use all the available data collated over the last four decades during scientific fishing surveys to: (i) determine the spatial and temporal distribution of both juvenile and adult of *E. aeneus* in the

Mauritania–Senegal zone, (ii) model this distribution according to environmental and landscape descriptors, and finally (iii) use the output from these models to map distribution patterns and identify effective fish habitats (Dahlgren et al., 2006; Le Pape et al., 2014).

2. Materials and methods

2.1. Area description

The study zone covers the coast and the continental shelf of Mauritania and Senegal (Fig. 1A). This Senegal–Mauritania zone constitutes a single ecoregion (Spalding et al., 2007). It extends over 1400 km of latitude and covers approximately 58,200 km². Under the influence of the Canary and Guinea Currents, this zone is strongly marked by an upwelling regime (Aristegui et al., 2009; Benazzouz et al., 2014) and terrigenous input. Its productivity and species richness (2,403 and 1,737 marine taxons from around thirty different phyla in the Mauritania and Senegalese zones, respectively; Inejih et al., 2014) is remarkable, not only regarding biodiversity but also because it includes species of large fisheries interest, important for the food supply (Hicks et al., 2019), the economy, as well as for the local history and culture. The coastal part of the study zone is highly productive, with varied habitats within estuaries and bays: abundant mangrove forests (Iguu et al., 2014; Sidi Cheikh et al., 2022; Simier et al., 2004), salt-marshes and seagrass beds (Schaffmeister et al., 2006; Trégarot et al., 2020).

2.2. Scientific surveys data

Data obtained during scientific surveys on fish conducted in the study zone since 1980 were collated.

Table 1
Fishing surveys and stations in the coastal section (bay and estuaries).

Zone	Coverage	Nb. Surveys	Nb. Stations	Start date	End date
South	Sine Saloum	63	1.416	20/04/1990	26/10/2007
	Bolon Bamboung	30	432	11/03/2003	16/10/2012
	Petite-Côte	7	15	27/04/2012	15/05/2012
	Joal and Saint-Louis	10	92	10/04/2015	06/10/2016
North	Banc d'Arguin	9	370	08/02/2000	18/04/2004
	Banc d'Arguin and Diawling	4	52	07/01/2019	24/10/2019
	Banc d'Arguin	15	335	14/10/2000	23/06/2020
Total		138	2.712		

Table 2
Demersal trawl surveys on the continental shelf.

Zone	Boat	Nb. Surveys	Nb. Stations	Years
North	NDIAGO	71	3.207	1982–1996
	AL-AWAM	150	5.972	1997–2019
	ALMORAVIDE	10	146	1982–1986
	LUBLINO	1	126	1990
South	LAURENT AMARO	16	345	1968–1985
	LOUIS SAUGER	16	1.761	1986–1999
	ITAF_DEME	21	1.681	Since 2000
	GLC (Général Lansana Conté)	2	48	2012 and 2015
Overall total		287	13.007	

2.2.1. Coastal data

Data came from 138 surveys (2712 fishing stations; Table 1). These surveys focussed on estuaries and coastal zones of ecological interest such as the Banc d'Arguin and the Diawling in Mauritania (Jager, 1993; Sidi Cheikh et al., 2022), and the Sine Saloum, Joal and the Saint-Louis estuaries in Senegal (Simier et al., 2019).

These coastal data were collected using a variety of fishing gear, including beach seine, purse seine, beam trawl, fish trap, etc. They record catches of *E. aeneus* and almost always include individual measurements. However, these data do not allow standardised densities of *E. aeneus* to be calculated. They were analysed qualitatively, in order to determine the presence of juvenile and adult *E. aeneus* in estuaries and nearshore zones.

2.2.2. Continental shelf data

Since 1980, 287 demersal trawl surveys have been carried out by research vessels from both countries or through international cooperation (Table 2).

Surveys to explore demersal resources on the Senegalese continental shelf were carried out by trawling on the basis of random stratified sampling. A total of 55 surveys are listed (3835 trawling stations). They were carried out using a 'Le Drezén' trawling net intended for groundfish. The technical characteristics of the fishing gear remained unchanged throughout the trawling period: 31.82 m in length, a 33.9 m footrope, a float line of 24.5 m, and an extended mesh size of 45 mm (Massal, 2009).

A total of 232 surveys were carried out (9451 trawling stations) on the Mauritanian shelf, based on stratified random sampling. Trawl hauls were carried out according to a standardised protocol using an Irish-type trawling net with a 45-m float line and an equal mesh size of 41 mm. The fishing gear was modified in 1989; this change was followed by intercalibration surveys which made it possible to calculate a standardised correction coefficient per group of species. All observations made prior to 1989 can therefore be corrected by multiplying the catches by this coefficient (1.96 for *E. aeneus*).

On the dataset (Table 2), catches of *E. aeneus* were systematically recorded, counted and weighed. These data made it possible to estimate a density per haul (catches/km²).

Table 3
Pooled substrate types.

Sediment type	Grouped type
Rock+Mud	Discontinuous rocks + mud
Rock+Coarse sand	Discontinuous rocks + Sand
Rock+Muddy-sand_	Discontinuous rocks + Sand
Rocks+very sandy mud	Discontinuous rocks + mud
Sand	Sand
Muddy sand	Sand
Fine sand	Sand
Coarse sand	Sand
Mud	mud
Sandy mud	mud
Very sandy mud	mud
Rocks	Rock bank

2.3. Environmental data and spatial and temporal stratification

Environmental data concern the descriptors driving the spatial distribution of life-cycle stages, essentially bathymetry, seabed type and components of the seascape: proximity to habitats such as estuaries, mangroves, salt marshes and sea grass.

2.3.1. Seabed type

A sedimentology map of the Senegal–Mauritania continental shelf (Domain, 1985, 1977) has been digitalised. Given that the boats used to carry out this mapping were unable to explore the nearshore shallowest zone, we called upon other data sources to complete this map: for the Banc d'Arguin we used data from the SSPAC database and the observations made by Maigret (1976) and Piessens (1979), and for the coastal zone of Senegal, IRD's PPEAO system (Simier et al., 2019) which describes the substrate at each trawl fishing stations.

To keep the sedimentology straightforward for the description of fish habitats, these maps (Fig. 1B) have been simplified and only four categories used (Table 3), with a consistent number of trawl hauls (continental shelf data, Table 2) per category (Fig. 2A).

2.3.2. Bathymetry

The GEBCO 2020 database (General Bathymetric Chart of the Oceans, www.gebco.net), was used (Fig. 1A). The GEBCO_2020 grid is a continuous global numeric model of the land and ocean

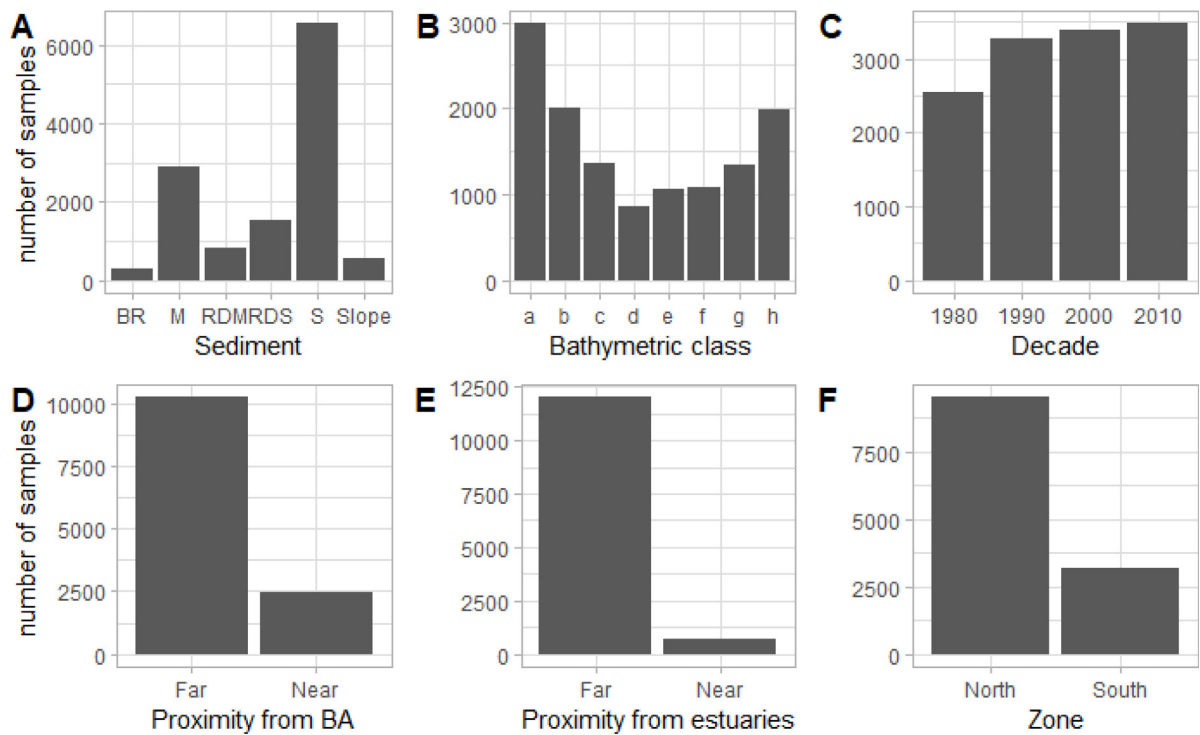


Fig. 2. Number of samples (trawl hauls) per modality of descriptor. (A) Sediment (BR = Rock bank, RDS = Discontinuous rocks + Sand, DRM = Discontinuous rocks + mud, S = Sand, M = Mud), (B) Bathymetry (a = <20, b = [20,30], c = [30,40], d = [40,50], e = [50,60], f = [60,80], g = [80,100], h = >100), (C) Decade, (D) & (E) Proximity to important coastal habitats (BA = Banc d'arguin), and (F) Latitudinal zone.

with a spatial resolution of 15 arc seconds (approximately 450 m in the study zone). The bathymetry was split into 8 categories (in metres): <20, [20,30], [30,40], [40,50], [50,60], [60,80], [80,100], >100 (Fig. 2B).

2.3.3. Proximity to estuaries and the Banc d'Arguin

At all latitudes, estuaries have a nursery role (Beck et al., 2001). We have noted 13 river mouths in the study zone (Fig. 1A). To take into account their impact on the distribution of juvenile populations, we used the shortest distance between the trawling stations and the river mouths as a seascape component (Olds et al., 2012). We judged as being close to an estuary only those stations located within 30 km. Similarly, in our consideration of the influence of the specific habitats (sea grass, mud flats, shallows banks and sheltered bays) of the Banc d'Arguin, we considered its entire area (Fig. 1A) and the same proximity criteria as for the river mouths. Each trawl haul is therefore characterised as being near (within 30 km) or distant from an estuary or from the Banc d'Arguin (Fig. 2DE).

2.3.4. Spatial and temporal stratification

Because management measures and fishing pressure differed between the two countries during the study period, two geographical entities were considered, North and South, separated by the country border on the coast (Fig. 1A and 2F).

The data extends over a 40-year period, from 1980 to 2020. To incorporate the evolution of resources over time, the dataset was divided into four ten-year periods (Fig. 2C).

2.4. Modelling of *E. Aeneus* distribution on the continental shelf

2.4.1. Splitting trawl catches in juvenile and adult specimens

E. aeneus were measured for only 15% of the trawl hauls where the species was present. A total of 2994 individuals of 10 to 99 cm in total length were measured. The aim of this project required

distinguishing between juveniles and adults. When individuals were measured, this distinction was made from measurements with regards to size at maturity (50 cm; (Ndiaye et al., 2013)). For trawl stations where the species was observed but not measured, we completed the measurement data using the following method:

- Wherever only one individual was captured, we based the distinction between juveniles and adults on its weight. For this, on the basis of both our measurement data and Bruslé (1985), we estimated the maximum weight of juveniles at 1.8 kg. This was applied to 39% of our data.
- When more than one specimen was caught, the following method was applied: we used the trawl data with *E. Aeneus* measurements to estimate the proportion of juveniles with a general linear model (GLM) using a Bernoulli distribution and a logit link function (Eq. (1)):

$$Y_{\%} \approx F_{\text{Bathymetry}} + F_{\text{Average_weight}} \cdot \text{weight} = \text{number} \quad (1)$$

with $Y_{\%}$, proportion of juveniles per trawl haul, response variable,

$F_{\text{Bathymetry}}$, covariate 1, bathymetry,

$F_{\text{Average_weight}}$, covariate 2, average weight of captured individuals,

number, number of measured individuals per trawl haul, used as a weighting factor.

Following this preliminary phase of allocating catch data between juveniles and adults when no measurements were available (*cf.* Results), the continental shelf fishing survey data were compiled into a table of *E. aeneus* juvenile and adult relative densities (number of individuals catches/km²). This table incorporated the stations where the species was not observed (absent), those where it was measured, and those where the juvenile/adult split was estimated. These density data were combined with environmental and spatio-temporal descriptors described in 2.3.

2.4.2. Structure, selection and validation of habitat suitability models

A habitat model was fitted to these data to determine which co-variables have a significant influence on the distribution of juveniles and/or adults of *E. aeneus*.

The low rate of presence of *E. aeneus* in the trawl hauls (22%) led us to use a Delta-type model to analyse these zero-inflated data (Le Pape et al., 2003; Stefánsson and Stefánsson, 1996; Vasconcelos et al., 2013). The delta model was obtained from the adjustment of two GLMs: the Bernoulli distribution for presence/absence data, combined with a model applied only to the abundance data when the species is present.

Sub-model 1: presence probability

This probability is modelled on the basis of a Boolean response variable with a Bernoulli distribution (Eq. (2)):

$$Y_{0/1} \approx F_{\text{Bathymetry}} + F_{\text{decades}} + F_{\text{Sediment}} + F_{\text{zone}} + F_{\text{Near_BA}} + F_{\text{Near_Estu}} \quad (2)$$

with $Y_{0/1}$, response variable, probability of presence estimated from Boolean data (presence 1/ absence 0),

$F_{\text{bathymetry}}$, cofactor 1, bathymetry (in 8 categories; cf. 2.3.2.),
 F_{decades} , cofactor 2, decades (4 categories),
 F_{Sediment} , cofactor 3, sediment type (in 5 categories, cf. 2.3.1.),
 F_{zone} , cofactor 4, zone (north or south),
 $F_{\text{Near_BA}}$, cofactor 5, proximity to Banc d'Arguin (close or distant),
 $F_{\text{Near_Estu}}$, cofactor 6, proximity to estuaries (close or distant).

Sub-model 2: positive densities

This sub-model estimates the density of juveniles or adults (number of fish caught per km²) taking into account only those trawl hauls where the species was present (non zero values) at the life stage. Following a preliminary analysis of the data distribution, the GLM has been applied to these data after log-transformation, using the normal distribution (Eq. (3)).

$$\text{Log}(Y_+) \approx F_{\text{Bathymetry}} + F_{\text{decades}} + F_{\text{Sediment}} + F_{\text{zone}} + F_{\text{Near_BA}} + F_{\text{Near_Estu}} \quad (3)$$

$\text{Log}(Y_+)$: positive density log response variable in number per km².

Selection of descriptors in each sub-model

The 6 potential descriptors have been tested in the two separate submodels (GLM, Bernoulli for probability of presence (Eq. (2)) and Gaussian for positive densities (Eq. (3)). The selection of descriptors in each sub-model was based on the Akaike information criterion (AIC). For each sub-model, this procedure results in a formula incorporating only the descriptors with a significant impact (AIC difference > 3).

Delta model

The Delta model is obtained by combining both sub-models (Eq. (4)):

$$\hat{Y}_{\text{delta}} = Y_{0/1} * e^{(\text{Log}(Y_+))} * e^{\left(\frac{\sigma^2(\text{Log}(Y_+))}{2}\right)} \quad (4)$$

with \hat{Y}_{delta} , estimation of the density,

$Y_{0/1}$, estimation of the probability of presence according to the Bernoulli sub-model (Eq. (2)),

Y_+ , estimation of the density logarithm according to the Gaussian sub-model (Eq. (3)). This estimation takes into account the correction (Laurent, 1963) required to obtain an unbiased estimation from a linear model based on the logarithmic transformation (for Y_+).

This overall approach was applied to both juvenile and adult, separately. Hence, 2 delta models were developed.

Validation of the models

We randomly selected 25% of the data using the “splitstack-shape” package under R (Mahto, 2022): 75% of the data were used to calibrate the models and to determine their level of adjustment (Piñeiro et al., 2008). These models were then applied to 25% of the remaining data for validation of their reliability (Planque et al., 2011).

The Area Under Curve (AUC) was used as an adjustment and validation criterion for the presence-absence sub-model, and the R^2 on $\text{Log}(Y_+)$ for the positive densities sub-model (Trimoreau et al., 2013; Vasconcelos et al., 2013).

2.4.3. Density predictions combined with uncertainties and mapping

Calculation of confidence intervals for density predictions

For each of the models (juvenile/adult), the predicted values were calculated with the delta model, for all of the combinations of descriptor retained in the sub-models. In order to estimate the uncertainty, 5000 datasets were randomly generated following the Monte Carlo method: 5000 probabilities of presence and positive density were randomly generated for each combination of descriptors, taking into account the estimation uncertainty for each sub-model. Both matrices collate all the combination of modalities in explaining factors in rows and the 5000 sub-model prediction values, in columns. They were combined to obtain density estimations (Eq. (5)).

$$YS = YS_0 \times e^{(\text{Log}(YS_+))} \quad (5)$$

Finally, the 5% and 95% distribution quantiles were calculated for each descriptor category.

Cartography of juvenile and adult *E. aeneus* distribution

In order to illustrate spatial distribution, we mapped juvenile and adult densities. The values predicted by the Delta models (Eq. (4)) were generated by the “expand.grid” function under R, for all combinations of descriptor categories on the maps. The cartography per decade is given whenever this time factor has a significant impact.

Calculation of the contribution of different habitats

The relative density of juveniles predicted by the model, and the area of each stratum of physical descriptors (e.g., each of the 8 classes of bathymetry) were combined to estimate the contribution (Dahlgren et al., 2006) of each type habitat to the stock (i.e., the percentage of juveniles hosted in each habitat stratum).

3. Results

3.1. Qualitative analysis of coastal data

Scientific fishing operations in coastal environments were carried out at depths of less than 20 m and, in 91% of cases, less than 10 m. The occurrence of *E. aeneus* in coastal data is low (9%). This occurrence varies dramatically according to the zone, from 9.4% in the Sine Saloum to 3% in the Banc d'Arguin. The size of the caught individuals *E. aeneus* was consistently below 50 cm, with a mode around 25 cm (Fig. 3). All individuals caught during these coastal surveys were juveniles.

3.2. Habitat suitability models on the continental shelf

3.2.1. Extrapolation of measurements

For the different categories of bathymetry, the average weight of measured and non-measured individuals follows the same trend (Fig. 4); average weight increases with depth but there is no bias in weight between measured and non-measured captures.

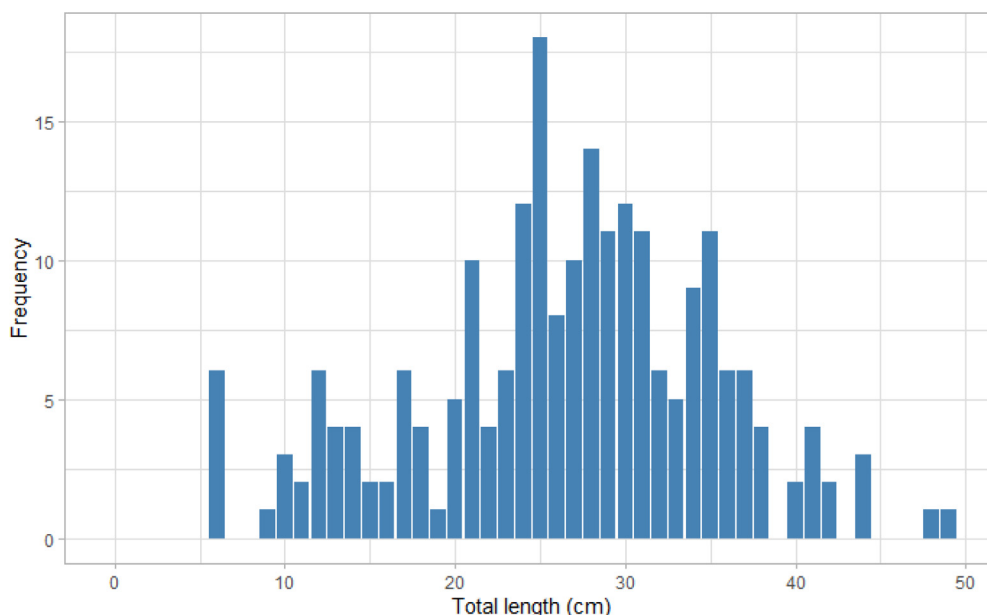


Fig. 3. *E. aeneus* size structure in coastal data (all individuals are juvenile; size <50cm).

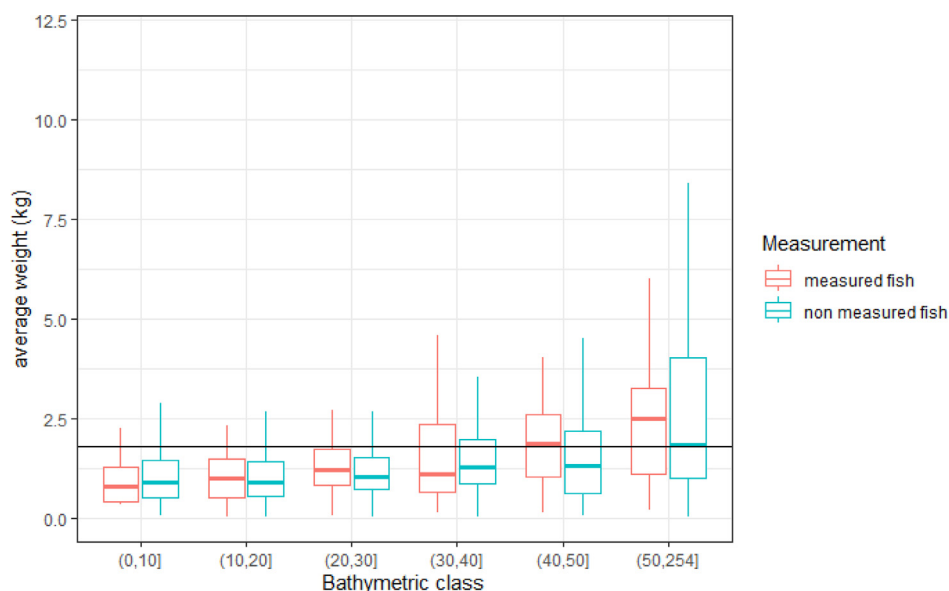


Fig. 4. Average weight of measured and non-measured individuals, the horizontal line indicates the weight at maturity.

The proportion of juveniles was estimated, according to the bathymetry and the average weight of individuals caught per haul (Eq. (1)); deviance explained by this model reaches 31% (Table 4). This model provides unbiased (Fig. 4) estimates of the respective densities of juveniles and adults for trawl hauls with more than one individual caught.

3.2.2. Selection and validation of sub-models

The juvenile presence sub-model explains 16.2% of total deviance (Table 5) with an almost identical AUC between the calibration and validation datasets (Table 6). The Gaussian sub-model applied to positive density explained 11.5% of the total deviance and its prediction performance is also similar for the validation data.

For the adults, the presence sub-model explains 7.9% of the total deviance for an AUC of 0.7, and the positive density sub-model 14.2% (Table 5). On the validation dataset the results are in the same range (Table 6).

Table 4

Binomial model for prediction of the proportion of juveniles and adult based on data from demersal cruises conducted on the continental shelf.

	DoF	Deviance	Dev_explained	Pr(>Chi)
NULL	314	1.231		NA
Bathymetry	313	1.119	9%	3.61E-26
+Average weight	312	843	31%	8.63E-62

3.2.3. Distribution of juvenile and adult *e. aeneus*

The influence of bathymetry was highly significant for the presence and positive density of juveniles and adults (Table 5). The delta model revealed the juveniles’ preference for the shallowest waters, while the adults reached their maximum density at depths of 60 to 80 m (Fig. 5).

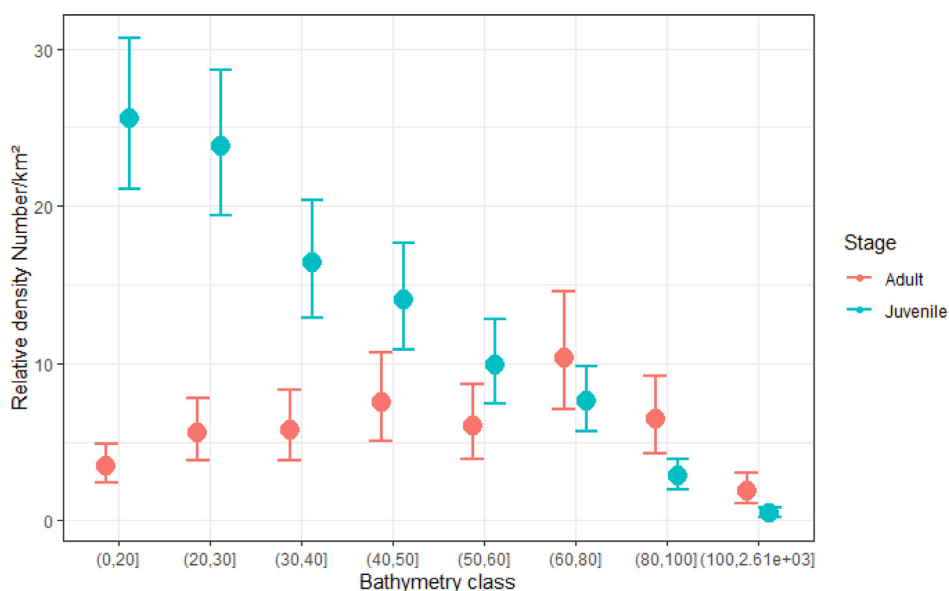


Fig. 5. Predicted density of juvenile and adult *E. aeneus* (in number caught per km²) per bathymetric category.

Table 5
Analysis of deviances of delta generalised linear model for juveniles and adults *E. aeneus*.

	Binomial					Gaussian on log(positive densitie)				
	DoF	Deviance	ED	Pr(>Chi)	AIC	DoF	Deviance	ED	Pr(>Chi)	AIC
(a) Juveniles										
NULL	12 680	12 313			12 315	2402	2440		-	6860
+Bathymetry	12 673	10 795	12.33	<2.2E-16	10 811	2397	2360	3.29	1.26E-17	6790
+Sediment	12 668	10 694	13.15	<2.2E-16	10 720	<i>Non significant</i>				
+Near BA	12 667	10 675	13.30	1.58E-05	10 703	2396	2344	3.94	2.82E-05	6776
+Near estuaries	12 666	10 668	13.36	5.96E-03	10 698	2395	2333	4.42	3.14E-04	6766
+Decade * Zone	12 659	10 318	16.20	1.38E-08	10 362	2388	2160	11.49	2.77E-04	6595
(b) Adultes										
NULL	12 680	5867			5869	471	285			1105
+Bathymetry	12 673	5664	3.46	<2.2E-16	5680	466	277	2.70	1.37E-02	1103
+Decade	12 670	5513	6.03	<2.2E-16	5535	459	258	6.29	1.58E-04	1091
+Sediment	12 665	5431	7.42	3.9E-16	5463	462	268	9.64	2.21E-03	1082
+Near BA	12 664	5405	7.87	2.6E-07	5439	<i>Non significant</i>				
+Zone	<i>Non significant</i>					458	254	11.00	7.31 E-03	1076
+Decade * Zone	<i>Non significant</i>					455	244	14.24	6.3E-04	1065

Degrees of Freedom (DoF) and deviance are presented as residuals.
ED (%) : explained deviance.
Pr(Chi) are values p of a test χ^2 - used for significance.

Table 6
Results of calibration and validation for the Delta models on juvenile and adults *E. aeneus*.

Model	AUC		r ²	
	Calib ^a .	Valid ^b .	Calib.	Valid.
Juveniles	0.77	0.76	0.11	0.10
Adults	0.71	0.70	0.15	0.11

^aCalibration data (75% of sub-model data).

^bValidation data (25% of sub-model data).

The other environmental descriptors have a more limited and less systematic effect, with small differences related to the sediment structure at both life stages, and moderately higher juvenile densities near the estuaries and the Banc d'Arguin (Table 5).

Maps illustrate these results with a concentration of juveniles in the nearshore zones (Fig. 6), and a positive effect of the proximity to the estuaries and the Banc d'Arguin on juveniles densities. The respective contributions of the different habitats evidence that 58% of the juveniles are concentrated on the less

than 20 m shallow area, which represent only 26% of the surface of the continental shelf. On the contrary, densities of adults are distributed further offshore (Fig. 6).

Densities also varied over time in the two zones (Table 5; Fig. 7). They have dropped significantly in the 1990s and have partly recovered since 2010. These evolutions concerned both juveniles and adults, and were more obvious in the North than in the South.

4. Discussion

This study is based on two types of data: A qualitative analysis of coastal data has shown an exclusively juvenile presence of *E. aeneus* in the estuaries and in the Banc d'Arguin. On the continental shelf, a habitat suitability model was fitted for juveniles and adults densities, based on scientific trawl surveys data. A delta-type model was selected, as suitable for data with a high absence ratio (Stefánsson and Stefánsson, 1996; Vasconcelos et al., 2013). Both the juvenile and adult models partly explain the variability of these densities. These models were tested by

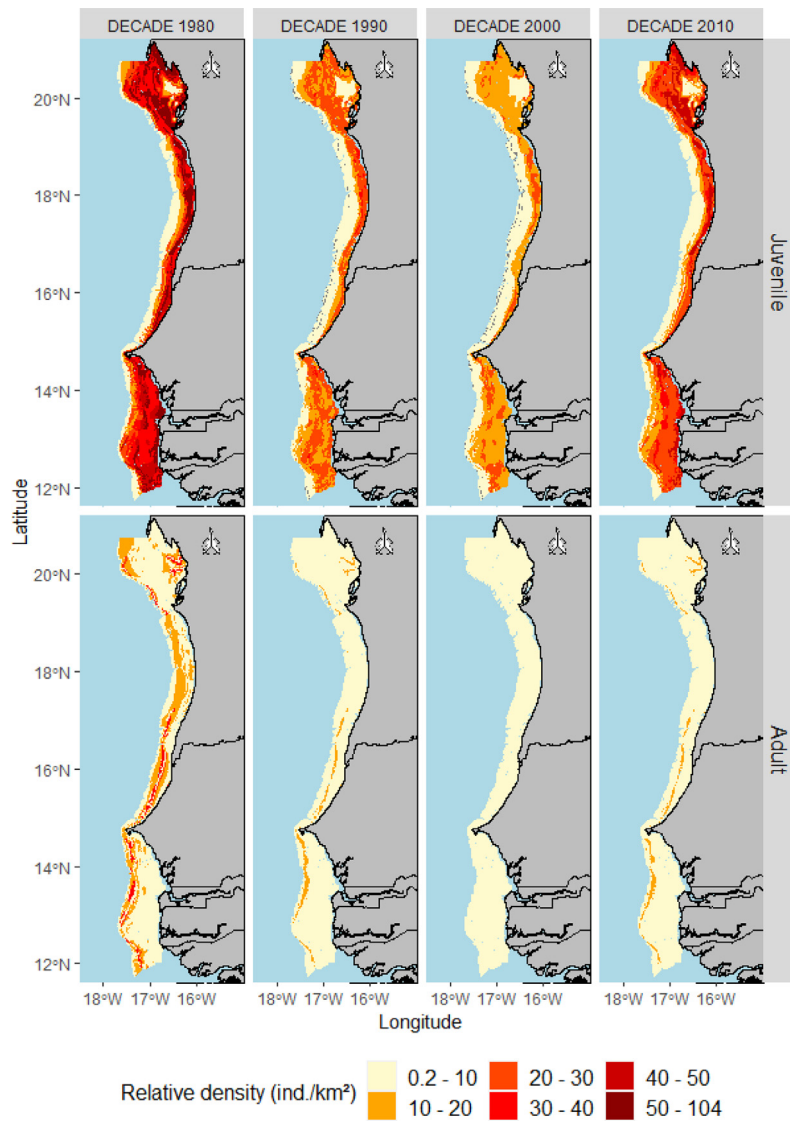


Fig. 6. Maps of juvenile and adult *E. aeneus* densities (catches/km²) per decade.

separating a calibration from a validation dataset, which validated their reliability (Planque et al., 2011; Vasconcelos et al., 2013). These models revealed opposing distributions between juveniles and adults. The adults are present offshore, while the juveniles are restricted to the coastal area and more concentrated near the estuaries and the Banc d'Arguin. In addition, similar temporal trends were evidenced for juvenile and adults, with a decline in the 1990s, followed by a recent restoration.

Distribution of juveniles and identification of *E. aeneus* nursery zones The coastal data confirmed the nursery role of the estuaries and coastal bays with an exclusive presence of juvenile, as previously demonstrated in the Sine Saloum by (Vidy, 2000). The diversity of habitats in these interface areas between land and sea, in particular the mangrove forests (Igulu et al., 2014; Sidi Cheikh et al., 2022), salt marshes and sea grass beds (Clavier et al., 2011; Hemminga and Nieuwenhuize, 1990; Honkoop et al., 2008; Schaffmeister et al., 2006) host an exclusively juvenile fraction of the *E. aeneus* population (Coll  ter et al., 2012; Gning et al., 2010; Jager, 1993; Simier et al., 2004).

Outside the bays and estuaries, the highest concentration of juveniles is observed in the bathymetric category of less than 20 m then juvenile densities declines with increasing depth, confirming their concentration on the coastal fringe on the West

African shelf (Domain, 1980), as in the Mediterranean Sea (  zbek et al., 2013). The concentration of juveniles on this shallow fraction of the shelf, where 58% of the juvenile are concentrated, allows for considering this coastal fringe as effective juvenile habitat (Dahlgren et al., 2006) for *E. aeneus*.

Moreover, juvenile distribution along this coastal fringe varies with other seascape components (Drakou et al., 2017; Drew et al., 2008; Nagelkerken et al., 2015; Olds et al., 2012) contributing to the habitat suitability model (Moore et al., 2011). High concentrations are observed near the Banc d'Arguin in the north, and near the estuaries in the south (especially the Sine Saloum delta): in other words, in the nearshore zones that have been evidenced by coastal data and previous studies to act as nurseries. These areas benefit from the high biological productivity observed in such land–sea interface zones (Sheaves and Johnston, 2008). The primary and secondary production is enhanced in various tropical coastal and estuarine habitats: mudflats (Marley et al., 2020), salt marshes (Sidi Cheikh et al., 2022), sea grass beds (Buelow et al., 2022; Heck Hay et al., 2003; Wasserman et al., 2020), and mangroves (Curnick et al., 2019; Duke et al., 2007; Friess et al., 2016; zu Ermgassen et al., 2020). The enrichment of the coastal part of the continental shelf, which is close to these productive zones, makes them particularly suitable for the growth and survival of

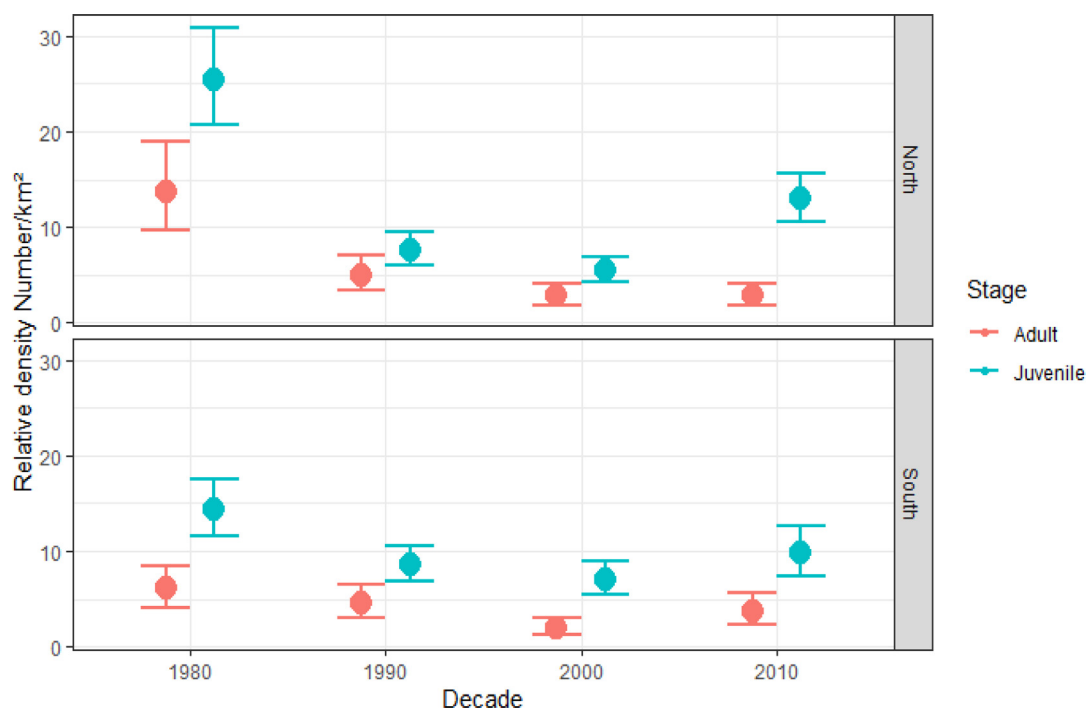


Fig. 7. Predicted density per decade and per zone.

juveniles (Berkström et al., 2020; Eggertsen et al., 2022; Kimball et al., 2021; Olson et al., 2019).

Adults distribution and temporal patterns

Adult distribution contrasted with that of juveniles. Adults were found much further offshore, mostly between 40 and 100 m, which confirmed previous studies (Cury and Worms, 1982). However, our model, based on data from surveys conducted throughout the year (i.e. not focused during the spawning season), did not allow us to identify high concentrations during the spawning period in Cape Verde, off the Sine Saloum, and in the south of Cape Timiris, in front of the Banc d'Arguin (Cury and Worms, 1982). While the adults distribution is large, these spawning grounds concentrated in front of the main nurseries optimise larval drift towards suitable juvenile habitats and recruitment success (Le Pape et al., 2003).

The variability between ten-year periods, similar for both juvenile and adults, fits largely to fishing pressure which has impacted this species. The biomass have declined by around 80% in comparison to its untouched state until the early 2010s (Ba et al., 2018; Meissa et al., 2013). However, the delta models outputs confirm that the densities of both juveniles and adults have recently been partly restored (FAO CECAF, 2022). In the northern zone, this improvement is explained by the application since 2006 of zoning prohibiting trawling below the 20 m. isobath and the introduction of a four-month fishing closure. In the southern zone, the improvement is probably due to the change in fishing strategy and the withdrawal of European fleets after the end of the EU-Senegal fishing agreement in 2006, suggesting that the number of foreign industrial vessels has decreased (Ba et al., 2018).

Identification of effective juvenile habitats and ecosystem management

The quantitative identification of restricted effective fish habitats is crucial to prioritise conservation areas and to enhance exploited resources (Archambault et al., 2018; Champagnat et al., 2021; Enchelmaier et al., 2020; Lotze et al., 2006) on the dramatically larger population scale (i.e. extra-ecosystem service,

Drakou et al., 2017). For some species, juveniles demonstrate great flexibility in their use of habitat, while others are heavily reliant on a limited number and restricted areas of nurseries (Igulu et al., 2014; Trimoreau et al., 2013). In the Mauritania-Senegal zone, *E. aeneus* juveniles show a strong preference for coastal areas. Catches on the shallow fraction of the continental shelf are largely dominated by juvenile specimens (Ndiaye et al., 2013). It seems appropriate to implement spatial restrictions in these fishing grounds, limiting fishing to areas beyond the 20-m isobaths, as partly implemented on the Northern zone. This would protect the effective juvenile habitats and have a positive impact on fish stocks (Mesnildrey et al., 2013). It would also be pertinent to change the legal minimum size (30 cm in Senegal, 40 cm in Mauritania) and to simultaneously increase the net meshes of fishing gears in order to limit juveniles bycatch.

CRedit authorship contribution statement

Yeslem El Vally: Data collection, Database management, Statistical analyse, Mapping, Wrting. **Crespin Luc Quenum:** Statistical analyse. **Modou Thiaw:** Data collection. **Jérôme Guitton:** Data collection, Database management, Mapping. **Beyah Meissa:** Data collection. **Olivier Le Pape:** Statical analyse, Wrintng.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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