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Original Article

Fisheries measures protect European seabass groups with distinct habitat use differently

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We investigated the movements of European seabass, *Dicentrarchus labrax*, to understand habitat use and connectivity to evaluate how individual seabass are protected by the spatiotemporal fisheries restrictions in place. We tagged seabass with acoustic transmitters in a study area in the Port of Zeebrugge (Belgium) in the southern North Sea. The 370,200 detections of 57 seabass in the study area revealed high residency in the period from late March–May to September–November, as well as high site fidelity (70.7%). Whereas the majority of seabass left the area in winter, 13 seabass stayed in the harbour experiencing temperatures as low as 2.8°C. Two groups of seabass were identified having different core movement areas in the inner and outer harbours, although movement between the two areas was possible. The distinct differences in habitat use between these groups resulted in a significantly different level of exposure to fisheries under the same policy framework. By quantifying the level of protection of seabass, based on the spatiotemporal fisheries management in place, our study underlines the importance of taking into account movement behaviour when evaluating conservation measures.

Keywords: fisheries management, *Dicentrarchus labrax*, acoustic telemetry, movement ecology, residency, site fidelity, network analysis.

Introduction

The vulnerability of a fish to being captured by a certain fishery is at the intersection of the spatiotemporal dynamics of both the fish and the fisheries (Abesamis et al., 2014). The failure to recognize these spatiotemporal dynamics, and their scale, can lead to flawed fisheries management (Kerr et al., 2017; Cadrin, 2020). An example is the case of the European seabass, *Dicentrarchus labrax*. After more than a decade of excessive exploitation (ICES, 2022a), the European Parliament and Commission committed in 2015 to the preservation of seabass (EU, 2015). Fisheries measures include catch restrictions, gear limitations, and a spatial and seasonal closure for commercial fisheries, as well as a bag limit and a catch-and-release season for recreational fisheries (EU, 2022a; EU, 2022b). Underlining the limited understanding of both seabass fisheries and ecology (Steadman et al., 2014), the countless alterations of seabass fisheries measures, often amended within the year, illustrate the ad-hoc, changeful nature of the management.

For assessment purposes, ICES divides seabass in the Northeast Atlantic in four stocks: southern Bay of Biscay and Atlantic Iberian waters (ICES divisions 8c,9b), northern and central Bay of Biscay (8ab), West of Scotland, West of Ireland and eastern part of southwest of Ireland (6a,7b,j), and the “Northern stock”, which includes the central and southern North Sea, Irish Sea, English Channel, Bristol Cannel, and Celtic Sea (4b,c, 7a,d–h) (ICES, 2020). Our study area is located in the North Sea, where seabass fisheries are managed under the EU multiannual plan (MAP) for Western Waters since 2019 (EU, 2019). The yearly ICES advice for the Northern stock provides the estimates of fishing mortality (F) based on this MAP (ICES, 2022a). F is estimated to have been below the reference point for maximum sustainable yield (MSY) from 2016 onwards, since the emergency measures have been in place. At the time of writing, the biomass has not fully recovered (ICES, 2022a). Understanding the effect of the fisheries measures on the protection of seabass could aid the conservation management.

European seabass is a highly mobile fish. The species tolerates a wide range of temperatures (2–32°C) and salinities (0–40 ppt) and predates on various prey species of crustaceans, polychaetes, bivalves, gastropods, cephalopods, and fish (Vázquez and Muñoz-Cueto, 2014; López et al., 2015). These fast-moving predators generally feed along the coast, in estuaries and lagoons, but head to offshore deeper and warmer waters for winter spawning (López et al., 2015). Despite low genetic differentiation across the Northeast Atlantic population (Souche et al., 2015; Robinet et al., 2020), individual movement patterns illustrate a complex population structure. Mark-recapture (Pawson et al., 2007) and electronic tagging studies (Doyle et al., 2017; O’Neill et al., 2018; de Pontual et al., 2019; Stamp et al., 2021; de Pontual et al., 2023) have revealed interannual site fidelity to both feeding and spawning areas. Individual seabass

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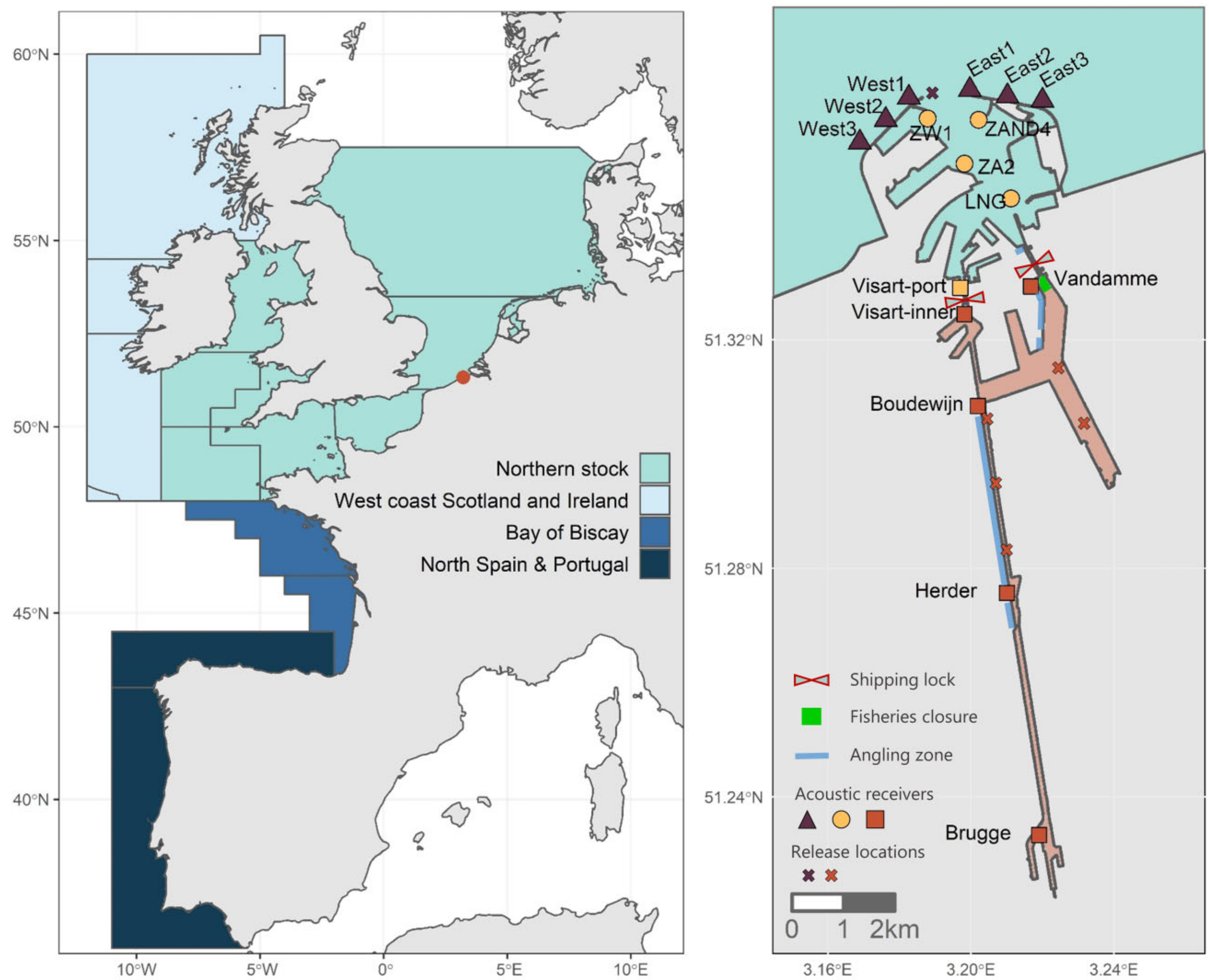

Figure 1. Left: ICES stock division of European seabass (*D. labrax*) in the Northeast Atlantic with the location of the study area (orange dot). Right: Map of the study area in the port of Zeebrugge with two shipping locks, Vandamme, and Visart. Angling is only allowed in specific zones (light blue), as imposed by the port authorities, and one location is specifically closed for seabass fishing (green), as legislated by the Flemish government. Locations of fish release (cross) and of receivers, deployed on tripod frames (triangle), navigation buoys (circle) and harbour infrastructure (square), were coloured by harbour zone (port walls: purple; outer harbour: yellow; inner harbour: orange). Shape files originated from ICES (https://gis.ices.dk), Marine Regions (https://www.marineregions.org/) and GRBgis (https://www.geopunt.be).

Table 1. Overview of deployment period and attachment type for each acoustic receiver station.

Harbour zone	Station name	Receiver attachment	Start date	End date
Port walls	West1	Tripod mooring	11/4/2019	10/2/2021
	West2	Tripod mooring	11/4/2019	3/3/2020
	West3	Tripod mooring	11/4/2019	3/3/2020
	East1	Tripod mooring	11/4/2019	12/5/2021
	East2	Tripod mooring	11/4/2019	3/3/2020
	East3	Tripod mooring	11/4/2019	3/3/2020
Outer harbour	ZOKN	Navigation buoy	27/6/2018	19/3/2019
	ZW1	Navigation buoy	19/3/2019	11/8/2022
	ZAND4	Navigation buoy	27/6/2018	11/8/2022
	LNG	Navigation buoy	25/11/2020	11/8/2022
	ZA2	Navigation buoy	25/11/2020	13/4/2022
	Visart-port	Harbour infrastructure	25/11/2020	13/4/2022
Inner harbour	Visart-inner	Harbour infrastructure	11/1/2021	8/11/2022
	Boudewijn	Harbour infrastructure	12/6/2018	8/11/2022
	Vandamme	Harbour infrastructure	12/6/2018	8/11/2022
	Herder	Harbour infrastructure	11/1/2021	8/11/2022
	Brugge	Harbour infrastructure	25/11/2020	8/11/2022

Table 2. Overview of analysis metrics and methods, listing the applied temporal resolution (hour or day) and range (month or TAL) and spatial resolution (receivers station, harbour zone, entire study area, or LL.

Metric / Method	Time scale		Space scale	Purpose / Definition
	Resolution	Range	Resolution	
Site fidelity	–	TALTAL	Zone Study area	Percentage of detected animals that returned or stayed in the area six months after tagging
Residence index (RI)	Hour Day	Month Month	Zone Zone	Percentage of time an animal spent at a receiver out of its TAL
	Day	TAL	Station	Input of the correspondence analysis (CA)
Correspondence Analysis (CA, calculated with RI)	Day	TAL	Station	Multivariate analysis (station and fish ID) to visualize association of fish with stations
Empirical derived Markov Chain (EDMC)	Hour	TAL	Station	Calculate transition probability of one station to another
Eigenvector centrality (EVC)	Hour	TAL	Station	Quantify the use of a receiver station
GLMM Spatial closure	Hour	TAL	Station	Model to compare presence and activity at Vandamme
GLMM Fisheries protection	Hour	Month	Study area + LL	Model protection from fisheries measures for individual seabass

exhibited long-term residency, staying in limited areas for long periods of time. The behaviours of long-term residency and interannual fidelity put seabass at risk of local depletion (Doyle et al., 2017), a mechanism that can contribute to the slow recovery of fish populations (Petitgas et al., 2006).

Seabass movement ecology has only been limitedly studied in the North Sea (Quayle et al., 2009; de Pontual et al., 2023). Our study area, the port of Zeebrugge (Belgium), is considered a hotspot for recreational angling due to its high seabass abundance (Deputter pers. comm.). In marine waters, seabass fisheries measures are legislated in a yearly Council Regulation (EU, 2022a). The national (i.c. the Department of Environment of the Flemish government)) jurisdiction stipulates seabass fisheries measures for inland waters (Flemish Government, 2017). Additionally, the port authorities regulate the access to the port of Zeebrugge by means of maritime security measures. Depending on their space use over time, seabass will therefore be differently exposed to fisheries regulated on different policy levels. This semi-confined study area is therefore a clear example of the interplay of spatiotemporal dynamics of both the fish and fisheries. In this study we investigated local seabass movements to (1) thoroughly understand habitat use and connectivity in the port area, and to (2) evaluate the prevailing spatiotemporal fisheries restrictions by quantifying how seabass are protected by these measures.

Material and methods

Study site

Seabass were tracked in the Port of Zeebrugge (Belgium, Figure 1), which consists of an outer, marine harbour, and an inner harbour, which are connected through two shipping lock complexes. The main shipping lock, Vandamme, operates multiple times a day for regular and large ship traffic, whereas the smaller lock, Visart, is rarely operational. The outer harbour shores consist of sandy beaches, straight quay walls and large, concrete stones, that surround the two seaside port walls on either side. The shipping canal Boudewijn connects the port with the city of Bruges. The canal is not used to discharge excess of freshwater, but seawater is regularly fed into the Boudewijn canal via an opening on the west side of the Vandamme shipping lock to maintain a specific water level. Both the inner harbour and the canal are lined with straight quay walls, as well as sandy beaches and oyster reefs.

Seabass fishing in the study area is regulated under different spatiotemporal fisheries measures on different policy levels (full overview of legislation in Supplementary Material). Maritime security measures spatially limited fishing in the port to specific zones because of safety regulations (blue lines in Figure 1). An additional spatial closure consisted of the zone 200 m inland of the Vandamme shipping lock where seabass fishing was specifically prohibited to halt seabass poaching that was prevalent in this area (Flemish Government, 2017). Temporal closures covered January–June in riverine waters and February–March (2018–2019) or February (2020–2022) in marine waters. Recreational angling inside the port was considered to mainly take place during day (Goossens pers. obs.).

Fish tagging and acoustic monitoring array

During the summers of 2018–2020, 63 European seabass were caught in the inner (22) and outer (41) harbour (Figure 1) with rod and line by recreational anglers using plastic lures and wobblers. Fish were tagged with transmitters of the type ADST-V9TP (45), V13AP (9), and V9P (9) (Innovasea Ltd., USA; details in Supplementary Material). Through a small surgery at the ventral side of the fish, the transmitters were placed in the abdominal cavity, as approved under the ethical certificate EC2017-080 (for more details about the tagging procedure, we refer to (Goossens et al., 2023).

Acoustic receivers (VR2W, VR2AR and VR2Tx; Innovasea Ltd., USA) were placed strategically to study fish movements along the port walls, the outer and inner harbour, and the Boudewijn Canal (Figure 1). Due to practical and budgetary reasons, the receiver array changed considerably in lay-out between the earliest deployment in June 2018 and last recovery in November 2022 (Table 1). Receivers were attached to existing harbour infrastructure and navigation buoys with steel cable, metal chain and stone (Reubens et al., 2019), as well as tripod moorings deployed on the seabed (Goossens et al., 2020). Previous range testing in the Belgian part of the North Sea (BPNS) resulted in estimated detection ranges (defined here as the transmitter-receiver distance with 50% detection probability of observing a tagged animal's presence under median environmental conditions) of 502 m (hourly time bin) and 566 m (daily time bin) for observing European seabass (Goossens et al., 2022). The hard surfaces of the harbour infrastructure (e.g. concrete walls) might have caused acoustic signal reflection (Vergeynst et al., 2020). Data and metadata were managed using the online database of the European Tracking Network (ETN; https://lifewatch.be/etn), enabling us to directly access transmitter detections on other arrays, such as the permanent Belgian acoustic receiver network (PBARN) (Reubens et al., 2019).

Data analysis

All analyses were performed in R software (R Core Team, 2022), using the packages lme4 (Bates et al., 2015) and afex (Singmann et al., 2022). R scripts are made available on the GitHub repository https://github.com/JolienGoossens/SeabassTelPort.

Data processing

For each seabass, the time at large (TAL) was defined as the period from the tagging event to the last detection or recapture of the fish. Detection data were organized in hourly and daily time bins throughout the TAL. If a fish was detected at least once in an hour or day, we considered that time bin as detection positive hour (DPH) or detection positive day (DPD). DPD were categorized as day or night using the R package suncalc for extracting the times of sunrise and sunset (Thieurmel and Elmarhraoui, 2022). For the time steps when an animal wasn't detected, information on its probable whereabouts could be deducted from its previous and/or next location of detection, building on the concept of epistemic uncertainty (Bruneel et al., 2020). Seabass had to pass through one of the shipping locks (detection stations Vandamme, Visart, and Visart-inner) to leave the inner harbour. Therefore, we considered a seabass to likely be present in the inner harbour if the previous and following detection were located in the inner harbour. If the last detection of a transmitter was registered in the inner harbour, the fish was considered to likely have been in the inner harbour for the remaining TAL. In all other cases, the seabass was considered to likely be in the outer harbour or at open sea. These likely locations (LL) were used for visualization and in the fisheries vulnerability model (see below). An overview of analysis metrics and methods and their spatiotemporal resolutions is provided in table 2.

Habitat use and network analysis

First, we investigated spatiotemporal patterns in seabass use of the study area. A seabass was considered to exhibit site fidelity if it was detected in the study area at least 6 months after the tagging event. Site fidelity thus reflected if a fish returned to or stayed in the study area for the subsequent feeding period. The RI was used to evaluate what percentage of time an individual fish spent at a particular location. For visual comparison of RI between harbour zones, daily, and hourly RI per month were calculated as the number of DPD and DPH out of the total number of days or hours within that month (within the TAL, e.g. if a fish was tagged within that month, only the time bins after the tagging event were considered). Daily RI was also calculated per receiver station as the detected daily time bins out of the tagged fish' TAL to be used in the correspondence analysis (CA).

We used network analysis to discern spatial patterns in seabass use of the study area. CA was applied to infer grouping of stations and animals, based on the amount of time individual seabass spent at each station. Given a contingency table of daily RI for every animal ID at every receiver station, Chi-square distances quantified the similarity of how individual seabass frequented different stations. As a multivariate statistical method, CA enabled to visualize multidimensional complex data in fewer dimensions, where the distances between data points reflect the similarity between them (van Dam et al., 2021). The interconnectedness between the different stations in the harbours was investigated using Empirical derived Markov Chain (EDMC) analysis (Stehfest et al., 2015), following the approach of (Garcia et al., 2015). We calculated transition probabilities from one station to the other, as well as EVC, which quantified the use (the centrality) of that station in relation to the use of the stations it is connected to. In contrast to (Garcia et al., 2015), we didn't regard a lack of detection as a true absence, as we considered the scarcity of our receiver array would wrongly inform the Markov process on absence. CA was performed with the R package FactoMiner (Lê et al., 2008) and EMDC was applied with the code of (Stehfest et al., 2015). For the visual exploration of the spatial network, the counts of directed movements between receiver stations were plotted on a map of the study site (Jacoby et al., 2012).

Spatial closure

Seabass fishing was prohibited around Vandamme station (see above). As recreational seabass angling in the port was assumed to mainly take place during daylight hours (Goossens pers. comm.), we compared circadian patterns in presence and activity within the protected area (station Vandamme) and outside of it. Presence was modelled as the number of DPH in a generalized linear mixed model (GLMM) with a Poisson distribution. A GLMM following a Gamma distribution with a log link function was used for activity, enumerated as hourly mean vertical distance (in m) between detections for tags with a pressure sensor and as the hourly mean acceleration (3D, in m/s^2) for accelerometer tags. For the dependent variables, the selected distributions were evaluated and validated by visual exploration of the raw data and Pearson residuals. Explanatory variables were day/night, station and their interaction, with fish ID as a random effect. Model selection was performed with single-term deletion using Chi-square tests and the Akaike Information Criterion (AIC) (Zuur et al., 2009).

Fisheries vulnerability

From a fish' perspective, how much time would a fish spend in an area where and at a time when no fishing was allowed? A seabass was considered to be protected from fishing (both commercial and recreational) if the legislation prohibited fishing at that location and time (full overview of legislation in Supplementary Material) under different management scenarios (Table 3). We assigned a seabass to be 'exposed' (0) or 'protected' (1) per hourly time bin, using DPH as well as LL. For the assumed locations, seabass was considered to be subject to riverine management (national, i.e. Flemish, jurisdiction) in the inner harbour zone and to the fisheries measures from Council Regulations outside of the inner harbour zone. For every seabass, we calculated the number of "protected" hours out of the total hours in a month. The probability of protection π was predicted with a GLMM with a binomial distribution. Explanatory variables were tagging location (outer

Table 3. Management scenarios used to predict the probability of protection of individual European seabass (*D. labrax*). An individual seabass was considered 'protected' (1) in an hourly time bin if it met the condition of the mentioned LL or a DPH at a specific station. If it didn't meet any of the conditions, the individual was considered as 'exposed' (0) for that hour bin. The measures taken into account for the different scenarios are marked with X. For names of detection stations, see table 1 and figure 1).

Scenario	Spatial closure Maritime access	Spatial closure Vandamme	Temporal closure EU	Temporal closure riverine	No fishing at night
Condition for protection	DPH any station excl. Boudewijn, Herder, Vandamme	DPH Vandamme	LL marine waters (during closed period)	DPH or LL inner harbour (during closed period)	DPH or LL inner harbour at night
Maritime access measures	X				
Current regulation	X	X	X	X	
Current regulation without seasonal closure EU	X	X		X	
Current regulation without seasonal closure riverine	X	X	X		
Current regulation without spatial closure Vandamme	X		X	X	
Current regulation without spatial closure Vandamme, without fishing at night	X		X	X	X
Current regulation without fishing at night	X	X	X	X	X

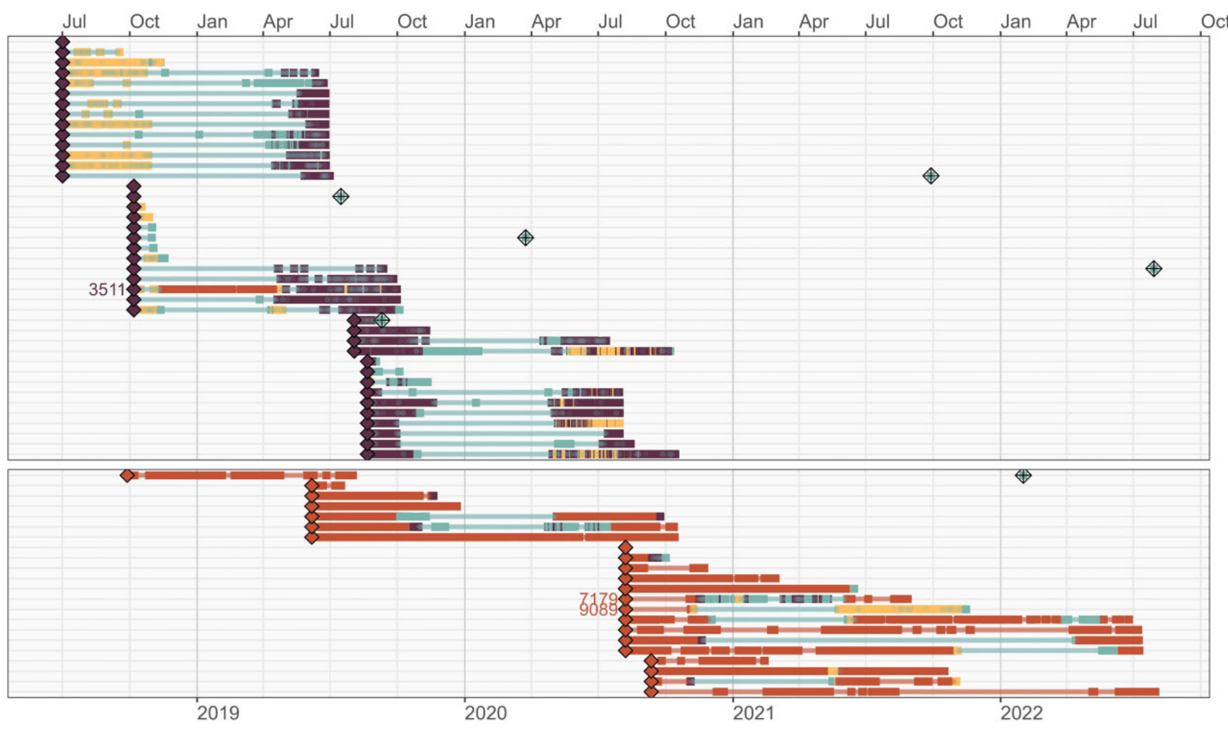

Figure 2. Abacus plot depicting a time line (x-axis) for individual (y-axis) European seabass (*D. labrax*), tagged along the port walls (top) and inner harbour (bottom) with detections (bold) and LL (translucent), as well as the events of release (diamond) and tag recovery (crossed diamond) and colored by location zones (port walls: purple; outer harbour: yellow; inner harbour: orange; marine waters: light blue). The ID numbers of three seabass (3511, 7179, and 9089) were highlighted: these individuals were found to deviate in habitat use patterns through the CA (Figure 4).

Table 4. Results of site fidelity for European seabass (*D. labrax*) (individuals exhibiting site fidelity out of the total number of detected animals with a TAL longer than 6 months) to the entire study area and to the tagging zone (inner or outer harbour) and daily and hourly residence index (RI, median [range]).

Tagging location	Length (cm)	Site fidelity Study area	Tagging zone	Daily RI	Hourly RI
Inner harbour ($n = 22$)	46.5 [39.0–63.0]	16/21 (76.2%)	15/21 (71.4%)	0.29 [0.03–0.92]	0.12 [0.01–0.52]
Outer harbour ($n = 41$)	47.0 [38.0–74.0]	25/37 (67.6%)	25/37 (67.6%)	0.16 [0.00–0.56]	0.02 [0.00–0.20]

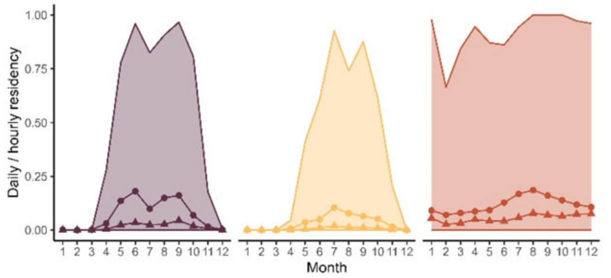

Figure 3. Mean daily (circle) and hourly (triangle) value for RI, calculated for each month as the percentage of time an individual European seabass (*D. labrax*) spent in the different harbour zones (port walls: purple; outer harbour: yellow; inner harbour: orange), with the 95% quantile of daily RI (shaded area).

or inner harbour, fixed) and the random effects of month and fish ID nested in tagging location. Model validation was performed through visual inspection of residuals and through Chi-square tests comparing the full model with single term deletions. Using the model, we investigated how this predicted protection π varied under different hypothetical management scenarios (Table 3).

Results

Habitat use

Out of the 63 tagged seabass, 57 were observed in the port counting a total of 370,200 detections (Figure 2). Seabass were detected at all stations in the study area, except for Visart-port. An additional 26,785 detections were registered on marine stations of the PBARN, including detections of two fish that weren't detected in the port array (for a total of 59 detected seabass). One seabass was caught after 38 days off the coast of Dunkerque (France), 50 km southwest of the tagging location, and was not included in the calculation of site fidelity. Site fidelity to the study area was seen for 41 out of 58 detected seabass with a TAL exceeding 6 months (70.7%, Table 4). High daily RI (median 0.19, range 0.00–0.92) showed high seabass presence, with lower hourly RI (median 0.04, range 0.00–0.52) indicating they would not spend the entire day around the receiver stations.

The majority of seabass were detected in the study area until September–November ($n = 48$, 77.4%) and a lot returned the next year from late March to May after seemingly leaving the area ($n = 31$, 50.0%). Remarkably, thirteen seabass (39.0–57.0 cm total length at release) were detected in the harbour in winter (January–March): twelve in the inner harbour and one at the outer port and along the port walls. During winter the transmitted sensor measurements showed a minimum water temperature of 2.8°C in the port (median 6.9°C in winter). The differential temporal use of harbour zones was also reflected in the monthly variability of RI (Figure 3). While mean daily RI per month in the inner port was 0.07–0.18 throughout the year, seabass were largely absent from the port walls and outer port from December to March. Out of five transmitters with TAL of nearly 2 years, three revealed interannual variability in habitat use. One fish stayed in the port during winter 2021, but left in 2022. Another seabass was tagged in summer 2020, left the port late autumn and didn't return until the summer of 2022.

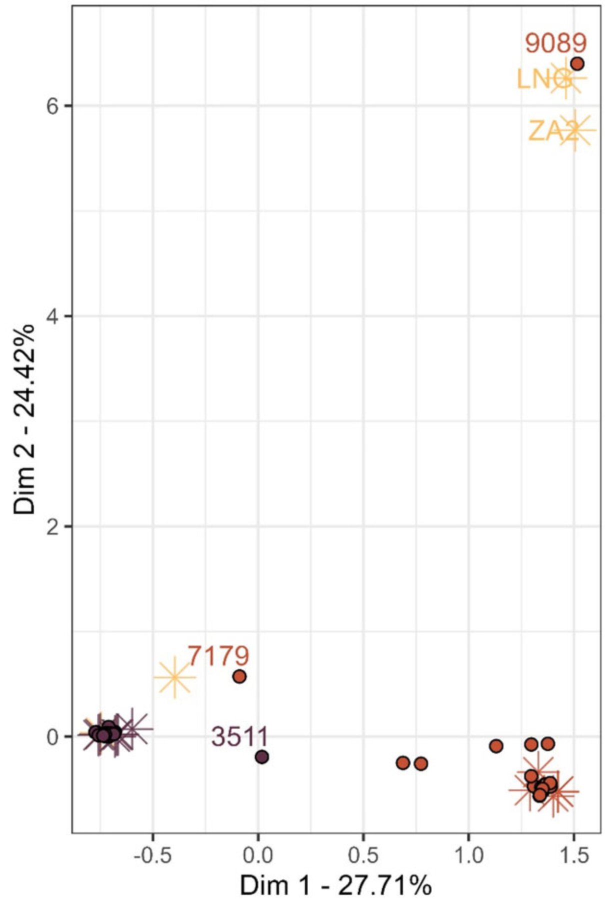

Figure 4. Chi-square distances along two dimensions between individual European seabass (*D. labrax*) (circles) and receiver stations (stars), as calculated by CA on daily residence indices. Colours reflect the harbour zones of the receiver position or animal release location (port walls: purple; outer harbour: yellow; inner harbour: orange).

Network analysis

The CA revealed a clear grouping of fish habitat use, based on tagging location (Figure 4). The first two dimensions of the CA accounted for 27.71 and 24.42% of the total variation. Fish tagged in a specific zone would mainly be associated to the stations in that zone and have a similar RI at stations as the ones tagged in the same zone. Three exceptions were noted (these ID numbers were also stated in Figure 2). Tagged along the port walls, ID 3511 didn't undertake a winter migration, but instead spent the winter in the inner port. ID 7179 performed the opposite movement, using stations along the port walls and in the outer port, performing a habitat use dissimilar to the majority tagged in the inner port. The seabass with ID 9089 was the only individual observed to frequent stations LNG and ZA2. However, these stations were not deployed throughout the entire study period.

The highest values for EVC (Figure 5) were found for the stations West1 (0.23), Vandamme (0.28), and Boudewijn (0.30), indicating these stations were highly frequented and served as transition points. Station Vandamme was the key transition location between inner and outer port. At least 13 fish travelled through the shipping lock, making 16 movements from inner to outer port and 10 from outer to inner port. One fish was not detected at Vandamme during this travel, which was likely due to a missed detection rather

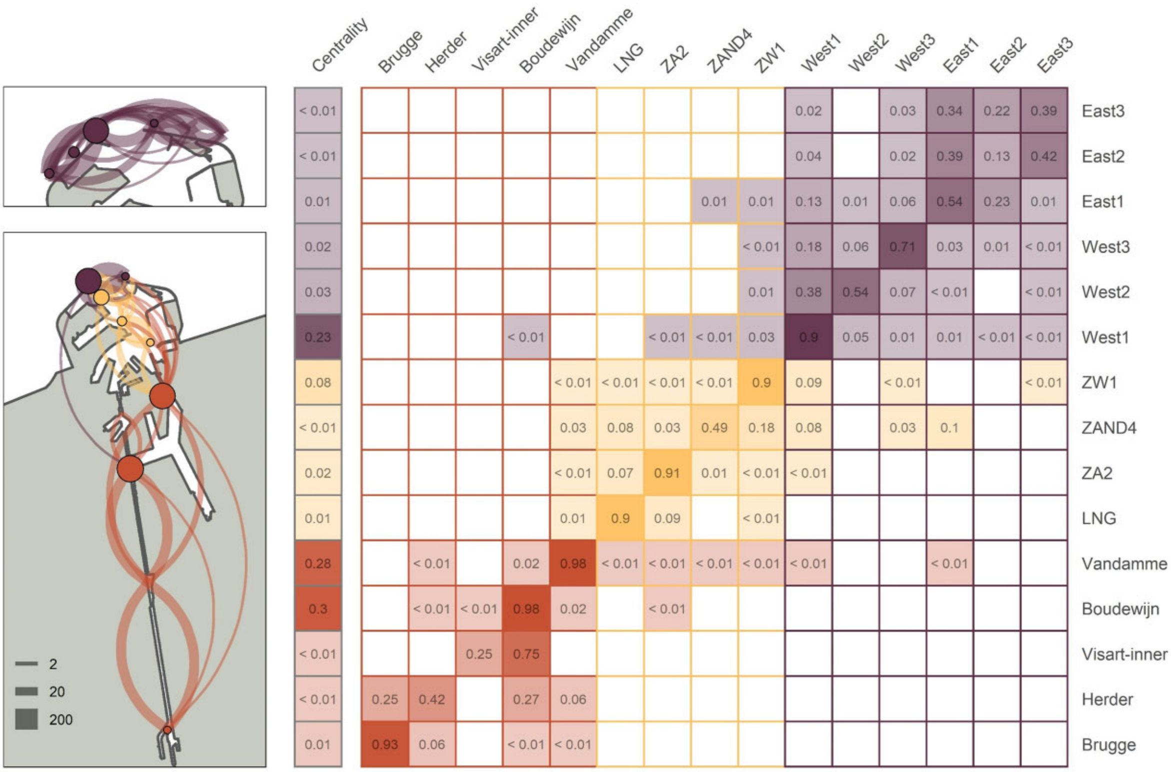

Figure 5. Spatial network maps of the port wall zone in detail (top left) and the entire harbour (bottom left) with nodes representing receiver location, sized by EVC (right), and edges representing frequencies of movement between receivers (right-hand curved from origin to destination receiver station, coloured by zone of origin receiver). The transition probability matrix (D) with cells coloured by origin station (y-axis) and grid lines coloured by destination station (x-axis). Colours correspond to location zones (port walls: purple; outer harbour: yellow; inner harbour: orange).

than another route. The transition probability matrix showed that movements were strongest within harbour zones. Station West1 (located near the fish capture site) served as the main transit point between the port walls and the outer port. Transition probabilities were generally highest for the same station, indicating high residency. This was less true for the port walls, where there were a lot of transits between the stations, likely due (in part) to the closer proximity between the stations here. In the inner port, the stations Herder and Visart-inner were strongly connected to Boudewijn.

Spatial closure

In total, 21 tagged seabass were detected at Vandamme station (9,832 DPH), where fishing was prohibited. Since Boudewijn station was the only station with comparable detection numbers ($n = 18$, 11,665 DPH), we limited the comparison in circadian habitat use to these two stations (Figure 6), considering only the fish that were detected at both stations. Model output and validation of the GLMMs were detailed in Supplementary Material. The GLMM of presence resulted in a significant interaction between the factors station and day/night, indicating seabass spent more hours at Vandamme during the day and at Boudewijn during the night. In terms of both vertical distance travelled and acceleration, seabass were significantly more active during the day and at Vandamme with no significant interaction effect (Table 5).

Fisheries vulnerability

When linking spatiotemporal patterns of seabass' habitat use to the protection in space and time, full models were the most appropriate for all scenarios, except for the scenario excluding the riverine seasonal closure (details on model validation in Supplementary Material). Under the prevailing measures in place during the study (Figure 7), the protection probability of the fish tagged in the outer harbour (median π_{outer} 0.17, 95% CI 0.04–0.34) was predicted to be significantly lower than those of the inner harbour group (median π_{inner} 0.35, 95% CI 0.03-0.70). The high inter-individual variability in protection of the inner harbour group, particularly from January to June (excluding February), was attributed to the differences in habitat use of fish staying in the inner harbour and those who left during the winter.

Comparing the different scenarios showed that seabass fisheries measures increased π markedly in comparison with the scenario considering only the maritime security measures (Table 6). Seasonal closures increased π for both groups, but the EU seasonal closure of marine seabass fisheries mostly impacted seabass tagged at the port walls (median estimate π_{inner} increase of 0.15), while the riverine fisheries measures increased π_{inner} by 0.25. The closure of the small area around the shipping lock Vandamme hardly impacted π_{outer}, but caused a reduction of π_{inner} by 0.11. When we regarded fishing in the inner harbour during the night as non-existent, the median predicted π_{inner} was as high as 0.63.

Discussion

Habitat use in the study area

Our results show that seabass exhibited residency and site fidelity to such an extent that we considered two different

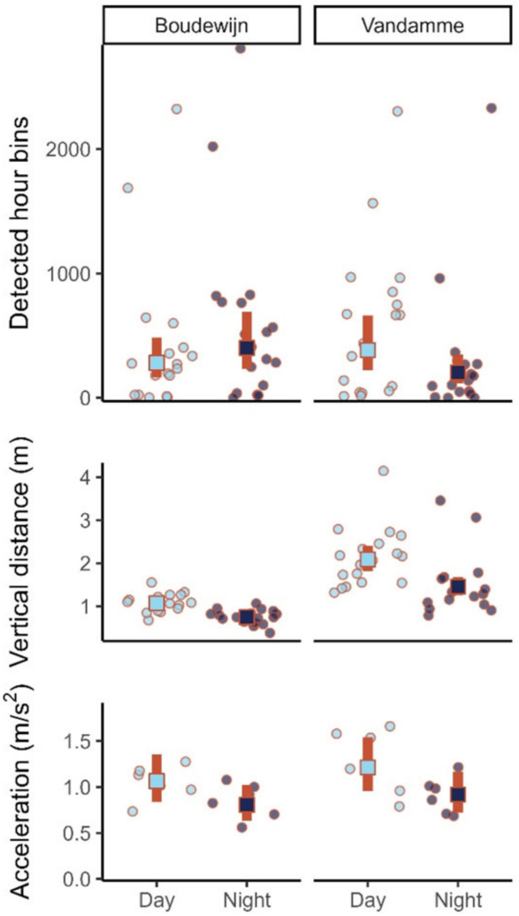

Figure 6. Diel differences in presence and activity of European seabass (*D. labrax*) at receiver stations Boudewijn and Vandamme, as evaluated with GLMMs. Plots display observed values (circles) and GLMM fitted value and 95% confidence interval (squares and lines) for detected hourly time bins per fish (top, $n = 18$), hourly mean vertical distance (m) travelled between detections (middle, $n = 18$) and hourly mean acceleration (m/s^2) (bottom, $n = 6$) during day (light blue) and night (dark blue). GLMMs showed significant differences ($p < 0.05$) between day and night and between stations for all metrics, and a significant interaction effect for the presence model (Table 5).

groups in the relatively small study area of the port of Zeebrugge. Largely sticking to their areas within the port, these two seabass groups used the space in the study area differently. Seabass tagged in the inner or outer harbour were mainly detected at stations in these respective zones. Both groups generally exhibited high summer residency until October–November, which resumed from April–June onwards. The inner harbour seabass that left the port area during winter, spent limited time in the outer port when transiting seawards. Corroborating previous findings of high summer residency and site fidelity to small inshore areas (Doyle et al., 2017; Stamp et al., 2021), our results of two groups or population subunits at merely 3–15 km apart implied a complex population structure.

The majority of seabass were not detected in the port during winter, when they were presumably undertaking migrations. However, at least thirteen seabass were in the study area in winter, enduring temperatures considered too low for gonad maturation (minimum 9°C for females, (López et al., 2015). Potentially, some seabass don't migrate every year and skip spawning (Le Luherne et al., 2022), as illustrated by two of the seabass with tag battery times exceeding one year. Another possibility could be that some seabass never perform spawning migrations. Total 12 of the overwintering bass stayed in the inner harbour, where it was possible that these seabass were not able to pass through the shipping lock. However, at least 13 tagged bass moved from inner to outer harbour and vice versa in a seemingly targeted way.

The area specifically closed for seabass fishing at Vandamme station proved to be highly frequented by the seabass tagged in the inner harbour. The Vandamme shipping lock was the transition point between the inner and outer parts of the harbour. As seabass also frequented the Vandamme station without passing through the lock, it was impossible to conclude from our data to what extent the shipping lock could have obstructed fish movement. Local anglers stated that seabass would predate on prey fish that were gushed when the sluice opened (Deputter pers. comm.), which our findings seemed to corroborate. The diel patterns in presence and activity showed seabass were present at Vandamme mostly during the day, exhibiting high activity. At night seabass were less active and showed higher presence at station Boudewijn, a key point of passage in the inner harbour. These findings add a horizontal dimension to previously described diel vertical movement pattern (Quayle et al., 2009; Heerah et al., 2017; de Pontual et al., 2019). Interestingly, fishing was allowed at Boudewijn, but angling would mainly take place during the day. Thus, during the day seabass were mainly at Vandamme, where seabass fishing was prohibited, and headed to Boudewijn at night, when fishing was assumed to be rare. Seabass' spatiotemporal movement patterns therefore increased the protection that the spatial closure provided.

Quantifying fisheries exposure

By modelling the fisheries protection an individual seabass would benefit from, considering its habitat use, we found that seabass from the inner harbour group had a higher probability of being protected from capture. For both inner and outer harbour groups, the current seabass fisheries regulation framework increased the predicted protection substantially compared to the maritime access regulations. As expected from the diel habitat use patterns, the spatial closure at Vandamme especially contributed to seabass protection when inner harbour fishing at night was considered to be non-existent. In the model, seasonal closures were found to have a high impact on the predicted protection. Based on the spatiotemporal patterns in fish movement and fisheries closures, protection of seabass varied throughout the year, but was consistently higher for the inner harbour group. Although aquatic tagging data has been used in numerous ways to contribute to conservation policy (Brooks et al., 2018; Hays et al., 2019; Lowerre-Barbieri et al., 2019; Brownscombe et al., 2022), we know of no other studies that quantified a fish' protection based on the spatiotemporal fisheries management in place. The approach demonstrated a direct application of how detailed knowledge on habitat use can inform and improve fisheries management for a better conservation policy of species and habitats.

In our approach, linking habitat use to management measures, some concerns should be taken into account when interpreting the results. First of all, we used fisheries legislation, but didn't quantify fishing pressure as data on the relevant spatiotemporal scale were non-existent. Qualitative knowledge

Table 5. Output of (generalized) linear mixed models of presence and activity, listing the distribution and number of European seabass (*D. labrax*) (N) used for the model, as well as the fixed effect estimates and SE and the *SD* of random effects. Significant effects had *p*-values of <0.001 (∗) and <0.05 (^).

Model	**Presence**	**Activity**	**Activity**
Response variable	Number of DPH	Hourly mean vertical distance (m)	Hourly mean acceleration (3D, m/s^2)
Distribution	Poisson	Gamma	Gamma
N	18	18	6
Fixed effect Estimate (SE)			
Intercept Night	5.64 (0.27)∗ 0.35 (0.01)∗	0.07 (0.07) −0.36 (0.06)∗	0.06 (0.11) −0.28 (0.05)∗
Vandamme	0.31 (0.01)∗	0.67 (0.07)∗	0.13 (0.05)^
Night:Vandamme	−0.10 (0.02)∗	–	–
Random effect SD			
Fish ID	1.16	0.13	0.13

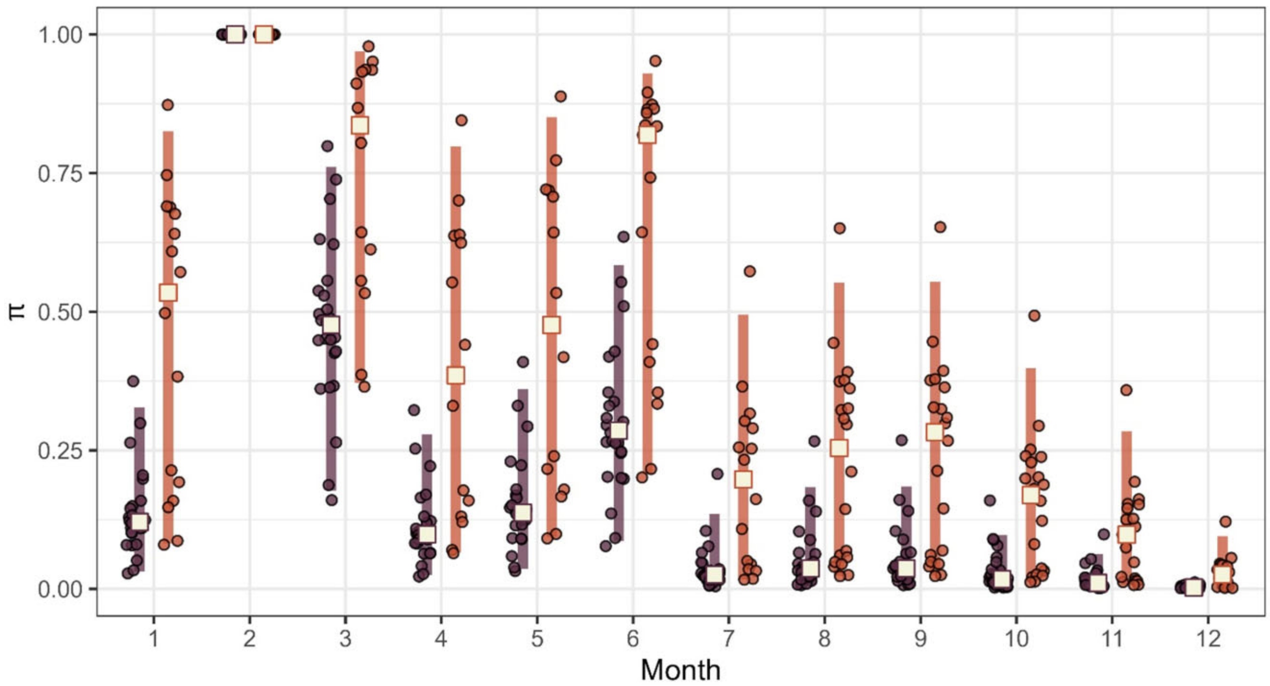

Figure 7. Predicted probability of protection π for individual European seabass (*D. labrax*) (square: median; lines: 95% prediction intervals; circles: predictions for individuals) tagged in the outer (π_{outer}, purple) and inner harbour (π_{inner}, orange), under the regulations in place during the study (scenario current regulation).

Table 6. Summary of GLMM output for the different scenarios with fixed effect estimates and SE, as well as the *SD* of the random effects ID and month. Median [range] values of the predicted probability of protection π were shown for European seabass (*D. labrax*) tagged in the outer (π_{outer}) and inner (π_{inner}) harbour. Significant effects had *p*-values of <0.001 (∗) and <0.05 (^).

Scenario	π_{outer}	π_{inner}	Fixed (SE)	ID SD	Month SD
Maritime security measures	0.02 [0.00–0.21]	0.00 [0.00–0.05]	– 4.35 (0.60)∗	2.05	2.84
Current regulation	0.17 [0.04–0.34]	0.35 [0.03–0.70]	1.86 (0.31)∗	1.13	4.19
Current regulation without seasonal closure EU	0.02 [0.00–0.34]	0.33 [0.03–0.70]	2.89 (0.43)∗	1.60	1.46
Current regulation without seasonal closure rivers	0.16 [0.00–0.29]	0.10 [0.00–0.46]	– 0.67 (0.44)	1.63	1.74
Current regulation without spatial closure Vandamme	0.17 [0.00–0.34]	0.24 [0.00–0.55]	1.11 (0.37)^	1.36	4.87
Current regulation without spatial closure Vandamme, without fishing at night	0.18 [0.00–0.43]	0.53 [0.25–0.81]	2.90 (0.30)∗	1.13	3.71
Current regulation without fishing at night	0.18 [0.00–0.43]	0.63 [0.25–0.83]	3.13 (0.31)∗	1.16	3.70

on fisheries practices could be incorporated (Marshall et al., 2023) in a similar way as the assumption that seabass angling at night in the inner harbour was rare. In light of ecosystem-based management, fish movement could also be linked to natural predation or anthropogenic stressors, such as the thermal stress and oxygen limitation in the inner harbour during heat waves or the ongoing expansion of port infrastructure. Moreover, a high probability of protection at a certain point in time would be meaningless if the exposure to fisheries was extremely high at another point in time (e.g. when leaving a protected area, a fish has to transit a passage that is blocked with nets). Quintessential to movement ecology research, spatiotemporal scale and resolution should be carefully considered. We used hourly time bins, whereby one detection could suffice to classify a fish as protected within an hour, although seabass could have roamed outside of a protected zone within 60 minutes (Pita and Freire, 2011). For hourly time steps without detections, we inferred a fish' LL, which unequivocally came with error (Bruneel et al., 2020). Moreover, the LL presented great unevenness in spatial scale, when comparing the confinement of the inner harbour with the vastness of the potential marine range of seabass.

Our approach illustrates that different population subunits can be differentially affected or protected by the same policy framework. Quantifying the level of protection a management measure provides for an individual fish reveals the fisheries policy consequences of the common behaviour of residency and site fidelity. The behaviours of residency and site fidelity illustrate that habitat selection is highly driven by conservatism, rather than by a continuous search for the optimal habitat (Petitgas et al., 2006). As telemetry scientists call to design studies specifically to assess habitat suitability (Rudolfsen et al., 2021; Brownscombe et al., 2022), we must be wary of ignoring (learned) individual behaviour. According to the 'Entrainment hypothesis' (Petitgas et al., 2006), fish generally stick to the places and migration routes they know. Conservatism of (successful) life-cycle patterns can then be dependent on old adults transferring this knowledge and behaviour to younger individuals. Local depletion, i.e. the loss of population subunits, potentially entails the loss of learned life cycle patterns, hampering the resilience and recovery of populations that experienced overfishing (Petitgas et al., 2006; Steadman et al., 2014; Doyle et al., 2017). Behavioural conservatism of seabass and the consequential population structuring (Doyle et al., 2017; O'Neill et al., 2018; de Pontual et al., 2019; Le Luherne et al., 2022; de Pontual et al., 2023) can thus aid to clarify why the Northern seabass stock biomass has not recovered and has repeatedly been overestimated (ICES, 2022b). As the value of including behavioural ecology in fisheries assessment and management is increasingly highlighted (Walker et al., 2020; Malone and Polivka, 2022), our results highlight the importance of considering conservatism and entrainment in fisheries assessment and management.

By setting out from individual fish vulnerability rather than from a fisheries need, this study compels to recognize the complexity of ecological reality. When investigating fish as a commodity by default, this economic viewpoint may bias biologists and fisheries managers to ignore the complex reality of fish' learning behaviours, personalities and variability in movement ecology (Bolnick et al., 2011; Knott et al., 2021; Vigliano Relva and Jung, 2021). Moreover, the plea for straightforward, simplified advice to environmental managers (Kraak et al., 2010) is in stark contrast to the distrust when sharing detailed information with stakeholders, who would very much know how to apply this knowledge (Glenn et al., 2012; Crossin et al., 2017). Rather than averaging out the individual variability in habitat use, ecological research and environmental policy should take into account the plurality of behaviours (Spiegel et al., 2017). Although the range of biological complexities and scientific uncertainties may seem overwhelming to include in policy, they directly relate to the precautionary approach, the supposed guiding principle of environmental and fisheries management (United Nations, 1995; EU, 2013). For species exhibiting the abovementioned conservatism, frequented habitats and locations will likely be important to a population subunit. Rather than validating the importance of specific habitats in separate case studies, we could assume that these fish are resident to these areas, until proven otherwise. This reversed 'burden of proof' would specifically counter the risk of local depletion, which can be of utmost urgency in light of habitat loss (Stamp et al., 2022) and cumulative impacts of anthropogenic stressors (Hodgson and Halpern, 2019). A true application of the precautionary approach would thus depart from the vulnerability of a fish based on its behaviour to then set out what type and extent of fisheries would be sustainable.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Conflict of interest

The authors have no conflicts of interest to declare.

Data availability

Data are available in the DOI repository https://doi.org/10.14284/609. All scripts are available on the GitHub repository https://github.com/JolienGoossens/SeabassTelPort.

Author contributions

J.G. led the analysis and writing. G.D.P., J.R., T.M., E.T., P.V., and J.G. designed the study. G.D.P., J.R., P.V., and J.G. carried out the field work. DV, ET and JG investigated policy measures. All authors read and reviewed the drafts and approved the final manuscript.

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