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BRIEF COMMUNICATION

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Not so much a sea bass: Divergent European sea bass (*Dicentrarchus labrax* L.) freshwater incursions

R. Almeida[1] | S. E. Tanner[1,2] | C. S. Mateus[3] | F. Ribeiro[1] | B. R. Quintella[1,2]

[1]MARE—Marine and Environmental Sciences Centre/ARNET—Aquatic Research Network, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal

[2]Departmento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal

[3]MARE—Marine and Environmental Sciences Centre/ARNET—Aquatic Research Network, Institute for Research and Advanced Training (IIFA), Universidade de Évora, Évora, Portugal

Correspondence
R. Almeida, Faculdade de Ciências, Universidade de Lisboa, Edifício MARE, Campo Grande, 1749-016 Lisbon, Portugal.
Email: arpalmeida@ciencias.ulisboa.pt

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Abstract

European sea bass (*Dicentrarchus labrax* [Linnaeus, 1758]) is a euryhaline marine migrant fish highly valuable for fisheries and aquaculture. Although juveniles are known to use estuaries and occasionally move to freshwater environments, these freshwater incursions had not been reported for adults. Recently, this behavior was observed in the Tagus River (Portugal) for adults occurring up to 150 km from the river mouth, about 80 km upstream from the tidal influence, suggesting the existence of a freshwater contingent. Fisheries management of sea bass should consider the putative existence of a freshwater contingent.

KEYWORDS
freshwater contingent, Moronidae, movement behavior, partial migration, Tagus River

Migratory strategies in fish are generally linked to feeding, reproduction, and avoidance of predators or unfavorable seasonal changes in abiotic conditions (Chapman et al., 2013). Recent technological and analytical advances in different methods (e.g., biotelemetry, biologging, genetics) used to study fish movement improve our understanding of the widespread coexistence of distinct migratory and resident phenotypes within populations, a phenomenon referred to as partial migration (Chapman, Hulthén, et al., 2012). The migration of only a fraction of a population entails a trade-off between multiple factors and can evolve and be maintained either when different life-history strategies produce the same lifetime fitness or as a result of conditional strategies dependent on individual phenotypes (Chapman, Hulthén, et al., 2012).

A good example of multiple migratory strategies lays within the family of the temperate basses (Moronidae), where white perch (*Morone americana* [Gmelin, 1789]) and striped bass (*Morone saxatilis* [Walbaum, 1792]) populations exhibit contingents or subpopulations, that is, intrapopulation groups that have different movement behaviors along the marine-freshwater gradient (reviewed by Chapman, Skov, et al., 2012, Secor, 1999). Yet, these are the only examples described within this family, despite the occurrence of, for instance, European sea bass *Dicentrarchus labrax* (Linnaeus, 1758) juveniles, often described as vagrant individuals, in freshwater environments (e.g., Dufour et al., 2009).

The European sea bass is a highly valuable species targeted by both commercial and recreational fisheries. The species is considered euryhaline and is a marine migrant that spawns at sea and uses transitional habitats like coastal lagoons and estuaries as nursery and feeding grounds (e.g., Elliott et al., 2007; L'Honoré et al., 2019; Pawson et al., 2007). The coexistence of sea bass residents and seasonal migrants has been described using tagging methodologies in different areas throughout the species distribution (Pontual et al., 2019; Stamp et al., 2021). In fact, juveniles, sub-adults, and sexually mature sea bass display short-range movements within the area of initial capture and long-range movements to offshore areas in the winter in the English Channel (25–312 km; Stamp et al., 2021) and in the Iroise Sea

(8–600 km; Pontual et al., 2019). However, the partial migration is not confirmed for the species, with uncertainties remaining regarding the presence of distinct migratory behavior in areas such as the Bay of Biscay and the Iberian coast (Pontual et al., 2019).

Here we report the occurrence of European sea bass adults detected along the Tagus River, describing a putative partial migration fraction of the Atlantic European sea bass population, and a preliminary characterization of this contingent that moves to freshwater habitats.

We obtained individuals captured by anglers (spin fishing) immediately downstream the Abrantes weir, the first obstacle to fish migrations in the Tagus mainstem. This site is located ~150 km upstream from the Tagus River mouth and 80 km upstream from the tidal influence (Figure 1). A total of 66 sea bass were sampled between June and November of two consecutive years (2021 and 2022).

Biometric data were collected from each individual, with total length recorded in millimeters (Tl) and total weight in grams (Tw). The sex of each individual was determined macroscopically, and gonads were weighed (Gw) to calculate the gonado-somatic index using the following equation: $GSI = \frac{Gw}{Tw} \times 100$. To estimate the age, 10 scales of each individual were collected, and annuli were counted following ICES (2021) guidelines.

To identify current and past patterns and temporal freshwater use by sea bass in the Tagus River, surveys targeting commercial and recreational fishers were conducted. A total of 38 fishers (22 professional and 16 recreational fishers) were interviewed between January and October 2022, along the Tagus freshwater area between Salvaterra de Magos (65 km from the river mouth) and the Abrantes weir (150 km from the river mouth; Figure 1).

The surveys contained nine questions that varied between multiple choice, dichotomous, and open-ended answer and were divided in four parts: (1) fishing area and gear identification, (2) characterization of sea bass capture in freshwater (i.e., frequency and abundance, capture period, and weight classes), (3) temporal perception of sea bass capture in the area (i.e., historical captures of sea bass, differences observed in relative abundance, time of the year, and weight classes), and lastly (4) potential reasons for the species' use of freshwater habitats.

All statistical analyses were conducted in R statistical software version 4.2.2 (R Core Team, 2022) using "ggplot2" package (version 3.4.1; Wickham, 2016) for the figures.

Results demonstrated the use of freshwater environments up to 150 km upstream from the Tagus River mouth, suggesting the existence of a freshwater contingent of the species. The 66 European sea

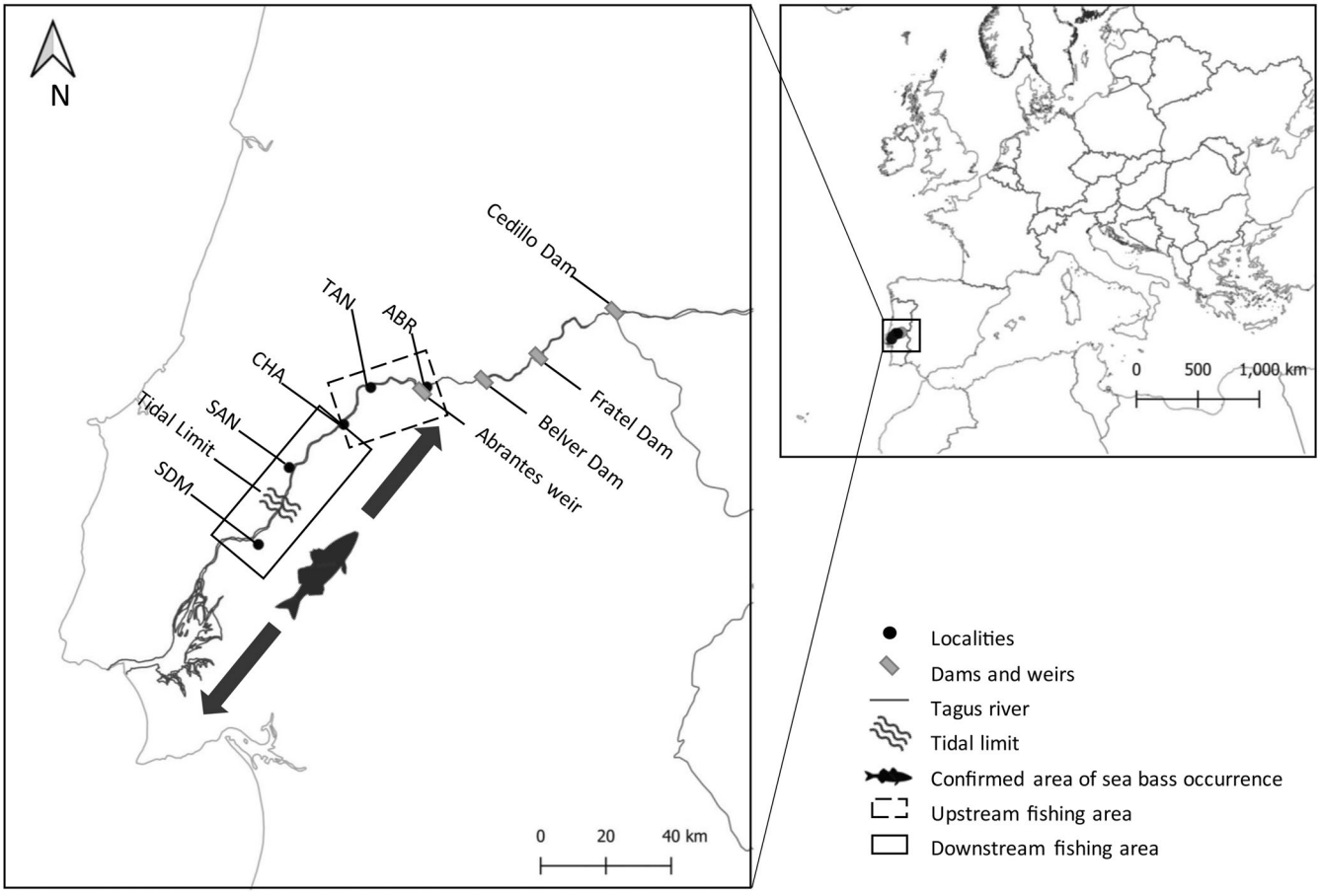

FIGURE 1 Map of the study area with the identification of the Tagus River stretch with the confirmed occurrence of the European sea bass, identification of obstacles to fish migration, the tidal limit, and areas where the surveyed fishers operate. The principal localities along the Tagus River are identified as: ABR, Abrantes; CHA, Chamusca; SAN, Santaréml; SDM, Salvaterra de Magos; TAN, Tancos.

bass captured in the Tagus River freshwater section, immediately downstream the Abrantes weir, consisted of 24 males (36.36%), 41 females (62.12%), and 1 undetermined (1.51%). The total length of the individuals ranged between 285 and 597 mm (mean Tl = 396 mm), and the majority of the sampled sea bass ($N = 39$) corresponded to the 300–400 mm length class (Figure S1). The mean total weight of sampled sea bass was 703.76 g, ranging from 222.57 to 1836.72 g. Although no significant differences were observed between sexes (Wilcoxon test = 580.50; p-value = 0.23), the higher mean total length and weight obtained for the females (females: mean Tl of 404 mm and mean Tw of 746.09 g; males: mean Tl of 387 mm and mean Tw of 649.00 g; Figure S2) and the predominance of females in the sample are in line with previous reports of European sea bass sexual dimorphism (Saillant et al., 2001) and sex ratio (Vandeputte et al., 2012). Additionally, the length-weight change rate of 3.07 (Figure S1) suggests an isometric growth in the sampled individuals. Along the study area, fishers reported more frequent captures of individuals weighing less than 1 kg, followed by individuals weighing between 1 and 2 kg and only rare captures of individuals weighing more than 2 kg.

According to the annuli identified in the scales, the sampled sea bass ranged between 1 and 6 years old (Figure 2).

Although the fishing gear used is not efficient in capturing small fish, a clear predominance of juveniles in the freshwater contingent was seen as most sampled individuals (68%) were 2–3 years old. However, the results suggest the occurrence not only of juveniles but also of sub-adults and adults in freshwater habitats. Previous studies focused on sea bass sexual maturity concluded that the species exhibits an extended adolescent phase, taking between 2 and 6 years to reach maturity (Pawson et al., 2000). However, in some areas such as the Mediterranean Sea, sea bass seem to attain sexual maturity at a smaller size and younger age (males: Tl 200–250 mm, 2 years old; females: 290–345 mm, 3–4 years old; reviewed by López et al., 2015) than in the English and Welsh waters (males: Tl 320–360 mm, 4–5 years old; females: superior to 420 mm, 5–7 years old; Pawson & Pickett, 1996).

The gonado-somatic index values obtained for fish captured in the vicinity of the Abrantes weir both male and female (0.02–0.12 and 0.29–1.04, respectively) were relatively low for the species (Rodríguez et al., 2001; Saillant et al., 2001). However, not many conclusions can be drawn from this result, because all individuals were captured between June and November, before the species' breeding season, coinciding with the same period for which Pawson and Pickett (1996) observed a decrease in the gonadosomatic index percentage in the English and Welsh waters.

Although sea bass are occasionally captured throughout the year, by anglers and/or trammel nets, fishers reported increased occurrences during spring and summer months (Figure 3). The months during which captures were less frequent coincide with sea bass spawning season (December–April; Dambrine et al., 2021). Additionally, this period is characterized by lower water temperature, potentially reducing feeding activity, and by higher river flow that can affect capture efficiency. Nonetheless, it is also noteworthy that the fishing effort varies over the year, and this could potentially influence fishers' perception of sea bass occurrence and abundance. In fact, because a key part of the local fisheries activity corresponds to the capture of anadromous species (i.e., lampreys and shads), fishing effort is typically higher from January to May for commercial fishing and from April to September for recreational fishing. Furthermore, whereas in downstream areas of the Tagus River, near the tidal influence limit (Salvaterra de Magos—Chamusca; 65–110 km from the river mouth), fishers reported to capture sea bass more frequently during spring and the beginning of summer, in the upstream areas of the river (Chamusca—Abrantes, more than 110 km from the river mouth) captures were reported to be more frequent during summer and beginning of autumn. These reported temporal differences suggest the occurrence of seasonal freshwater migrations along the river, yet unknown in terms of movement patterns.

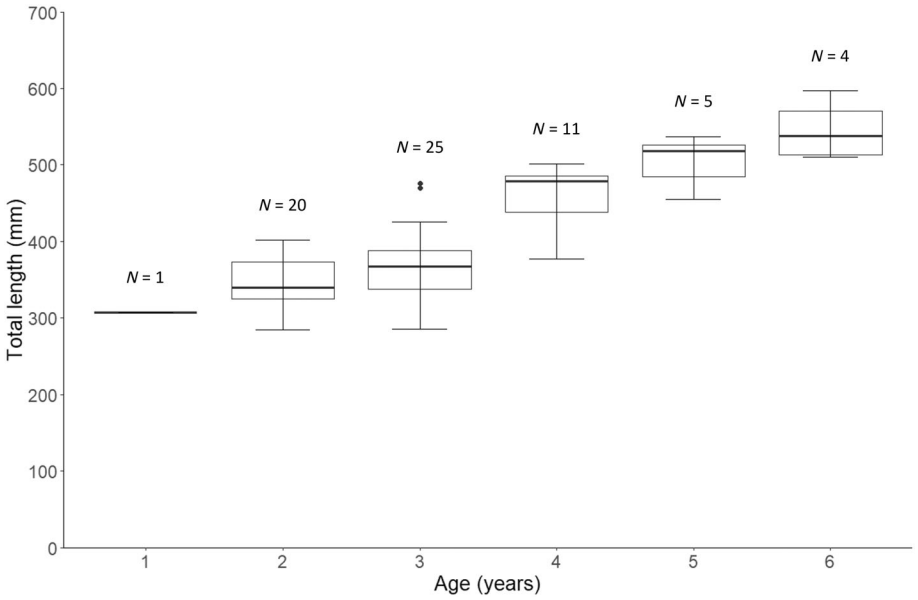

FIGURE 2 Total length distribution per age class (scale reading) of the European sea bass sampled in the freshwater stretch of the Tagus River. The line in the central box represents the median, the whiskers show the distribution outside the first and third quartiles, and the circles are outliers.

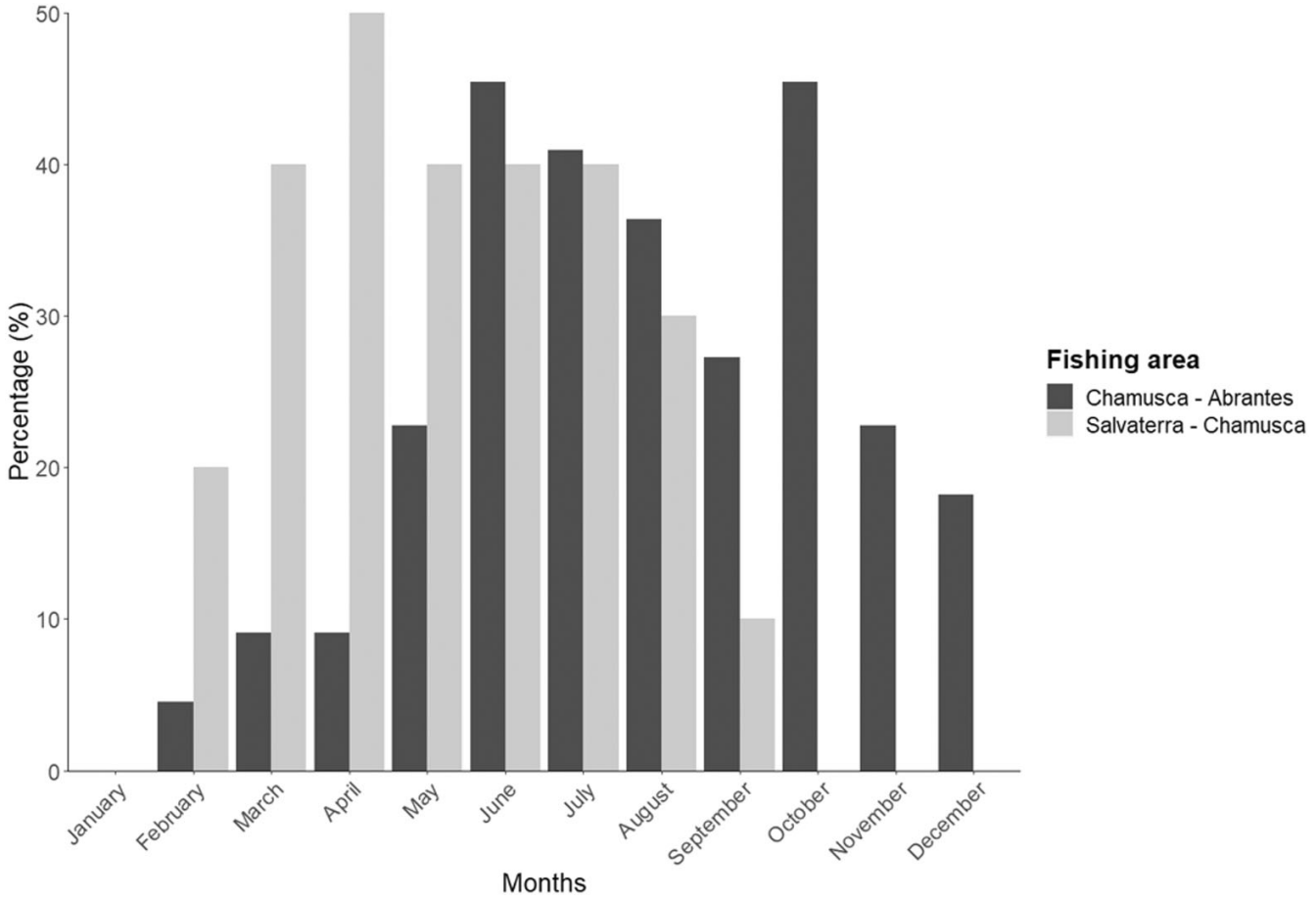

FIGURE 3 Months of increased captures of European sea bass in the freshwater stretch of the Tagus River, as reported by local fishers. The gray bars correspond to the percentage of the 10 fishers from the downstream freshwater section of the Tagus River (Salvaterra de Magos—Chamusca, 65–110 km from the river mouth), and the black bars correspond to the percentage of the 22 fishers from the stretch immediately downstream Abrantes weir (Chamusca—Abrantes, more than 110 km from the river mouth).

Survey results suggest that sea bass occurrence in the freshwater stretch of the Tagus River is not recent. Although most of the fishers (55%, $N = 21$) recall the occurrence of the species in freshwater 3–8 years ago, 24% of the fishers ($N = 9$) remember the species occurrence 10–20 years ago and 16% ($N = 6$) more than 20 years ago. Moreover, the majority (55%) of the fishers reported that the abundance of the species in freshwater has increased over the years, whereas 33% reported that the abundance has been similar and the remaining 4% report that the abundance highly fluctuates from year to year. The fact that sea bass catches are occasional in freshwater habitats makes it difficult to analyse the status and dynamics of this population contingent. Therefore, no clear pattern of variation was noticed by fishers over the years, in terms of months of higher captures and individuals' length and weight.

Furthermore, although no sea bass captures upstream of the Abrantes weir were reported for the period after its construction, six fishers from the Abrantes area claimed to have caught the species upstream of the weir before its construction in 2004 (near Belver dam, 175 km upstream the river mouth).

The main reason suggested by the fishers to justify the occurrence of sea bass in freshwater was food availability, with several fishers mentioning the presence of the invasive bleak (*Alburnus alburnus* [Linnaeus, 1758]) in the captured sea bass stomach contents. Additionally, fishers from downstream areas of the Tagus River stretch mentioned increasing salinity 50 km from the river mouth, due to the reduction in river flow, as a possible factor for the upstream movement of the species. However, and despite the irregular flow regimes due to power production and climate change, there is no scientific information supporting increased salinity incursion up the Tagus River.

For most species, migrations between marine and freshwater environments require physiological changes in osmotic and ionic regulation. However, euryhaline species such as the European sea bass are adapted to move across a wide salinity gradient. Because most of the individuals captured in the Tagus River are juveniles, the migratory movements could be explained by individuals seeking more favorable feeding sites (López et al., 2015). In fact, although estuaries provide favorable conditions to the species growth and survival (e.g., Vasconcelos et al., 2010 and Vinagre et al., 2009), several factors, such as competition and predation, could act as triggers to partial migrations (Chapman, Hulthén, et al., 2012). However, the coincidence of the migration toward the upstream areas with the species

pre-breeding period and the occasional occurrence of mature adults in freshwater could indicate that this migration is a favorable cost–benefit strategy for the species. This seems to be corroborated by the fact that different contingents have already been identified in other species of the Moronidae family (Secor, 1999). Contrary to the European sea bass, the white perch populations inhabit freshwater environments, presenting partial migrations to estuarine areas (Kerr and Secor 2012). In this species, the predominance of migratory or resident behaviors differs among rivers (Kerr and Secor 2012). Another example is the striped bass that is reported to group into three different contingents: an oceanic, a lower estuary, and an upper estuary contingent (Gahagan et al., 2015).

The coexistence of different migratory strategies within a species may increase the species' resilience against multiple pressures, such as climate change and overexploitation. Unraveling the species migratory patterns is crucial to ensure efficient fisheries management and to protect intraspecific variations within species. For the European sea bass, the occurrence of adults in freshwater has not been yet described, and there is still a lack of information about this phenomenon. Therefore, future studies should focus on sea bass movements, within and between freshwater-estuarine-marine environments, and the drivers of the partial migration. Multidisciplinary studies involving methodologies such as biotelemetry, otolith chemistry, genetics, and metabolomics could significantly contribute to identify the proximate and ultimate causes for this divergent habitat shift toward freshwater and allow for a better understanding of the species different life strategies.

AUTHOR CONTRIBUTIONS

Conceptualization: S. E. Tanner, C. S. Mateus, F. Ribeiro, and B. R. Quintella. Methodology: R. Almeida, S. E. Tanner, C. S. Mateus, and B. R. Quintella. Sampling: R. Almeida. Data analysis: R. Almeida. Resources: C. S. Mateus and B. R. Quintella. Writing—original draft preparation: R. Almeida. Writing—review and editing: R. Almeida, S. E. Tanner, C. S. Mateus, F. Ribeiro, and B. R. Quintella. Supervision: S. E. Tanner, C. S. Mateus, and B. R. Quintella. Project administration: B. R. Quintella. Funding acquisition: S. E. Tanner, C. S. Mateus, F. Ribeiro, and B. R. Quintella.

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ORCID

R. Almeida https://orcid.org/0000-0001-9188-8831

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