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TITLE OF THE Ph.D. THESIS

**BIO-ECOLOGICAL AND ANATOMICAL ASPECTS OF THE EUROPEAN EEL
ANGUILLA ANGUILLA (L. 1758)**

Scientific Disciplinary Sector(s)

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Index

Acknowledgment

Abstract	<i>i</i>
1. Chapter 1	<i>iv</i>
1.1 Thesis Outline.....	<i>iv</i>
1.2 Aims.....	<i>vii</i>
1.3 Main life history traits of the European eel (<i>A. anguilla</i> , L.)	<i>ix</i>
2. Chapter 2 Hard times for catadromous fish: The case of the European eel <i>Anguilla anguilla</i> (L. 1758)	1
<i>Abstract</i>	1
2.1 Introduction.....	1
2.2 Life cycle, habitat occupancy, and migration patterns of <i>A. anguilla</i>	3
2.2.1. <i>The life cycle of the genus Anguilla: common features</i>	3
2.2.2. <i>Habitat occupancy</i>	4
2.2.3. <i>Juveniles' migration and orientation</i>	5
2.2.4. <i>Adult migration behavior</i>	7
2.3. Eels' recruitment dynamics.....	8
2.4. Threats to <i>A. anguilla</i>	9
2.5. Success and limits of eels' restocking practices.....	14
2.6. The way forward.....	16
3. Chapter 3 Changes in dendritic spine morphology and density of granule cells in the olfactory bulb of <i>Anguilla anguilla</i> (L., 1758): a possible way to understand orientation and migratory behavior	18
<i>Abstract</i>	18
3.1. Introduction.....	19
3.2. Material and Methods.....	22
3.2.1. <i>Eel samples</i>	22
3.2.2. <i>Golgi-Cox Processing</i>	23
3.2.3. <i>Laser Scanning Confocal Microscopy</i>	24
3.2.4. <i>Rendering</i>	24
3.2.5. <i>Statistical Analysis</i>	25
3.3. Results.....	26
3.4. Discussion.....	30
4. Chapter 4 Recruitment dynamics of <i>Anguilla anguilla</i> (L., 1758) the western Mediterranean basin: single and in multiple sites study, and implementation of alternative sampling methods	34
4.1. Introduction.....	34

4.1.1. Environmental influences on the recruitment dynamics of juvenile European eels, <i>Anguilla anguilla</i>, in a small estuary of the Tyrrhenian Sea, Sardinia, Italy	35
Abstract	35
4.1.1.1. Introduction	35
4.1.1.2. Material and Methods	38
4.1.1.2.1. Study area.....	38
4.1.1.2.2. Data collection.....	39
4.1.1.2.3. Model analysis.....	40
4.1.1.3. Results	41
4.1.1.3.1. Population structure and seasonal migration.....	41
4.1.1.3.2. Factors affecting juvenile eel abundance.....	45
4.1.1.4. Discussions	47
4.1.1.5. Supplementary Materials	52
4.1.2. Inter-annual and month-to-month variations of glass eels' recruitment within and among estuaries in the western Mediterranean	58
4.1.2.1. Material and Methods	58
4.1.2.1.1. Study sites, data collection, and statistics.....	58
4.1.2.2. Results	61
4.1.2.2.1. Catch data.....	61
4.1.2.2.2. Biometric data.....	62
4.1.2.2.3. TL comparisons within estuaries.....	65
4.1.2.2.4. TL comparisons among estuaries.....	67
4.1.2.2.5. Pigmentation comparisons.....	68
4.1.2.3. Discussions	70
4.1.3. Assessment of glass eels' settlement in three Sardinian estuaries (Central-Weastern Mediterranean) through a new sampling method	73
4.1.3.1. Material and Methods	73
4.1.3.1.1. Study area.....	73
4.1.3.1.2. Environmental characterization of the three estuaries.....	75
4.1.3.1.3. Floating trap and sampling method.....	76
4.1.3.1.4. Glass eels' catch data.....	76
4.1.3.1.5. Glass eels' biometrics, Fulton's condition factor and pigmentation.....	77
4.1.3.1.6. Statistical comparisons.....	77
4.1.3.2. Results	78
4.1.3.2.1. Environmental characterization of the three estuaries.....	78
4.1.3.2.2. Glass eels' catch data.....	78
4.1.3.2.3. Glass eels' biometrics.....	81
4.1.3.2.4. Biometrics comparisons among estuaries and between floating traps and fyke nets.....	83

4.1.3.2.5. <i>Fulton's condition factor and glass eels' pigmentation</i>	84
4.1.3.3. Discussions	85
5. Chapter 5 Growth performances of the European eel in Sardinia	87
5.1. Restocking with wild-caught farmed European eels: an alternative approach to understanding eels' early growth in captivity and the yellow eel phase adaptation to the wild	88
5.1.1. Introduction.....	88
5.1.2. Material and Methods.....	90
5.1.2.1. <i>Study area</i>	90
5.1.2.2. <i>Experiment I: survival and growth in rearing conditions</i>	92
5.1.2.3. <i>Experiment II: marking, restocking, and recapturing</i>	93
5.1.2.4. <i>Data analysis</i>	95
5.1.3. Results.....	96
5.1.4. Discussions.....	100
5.2. Otolith shape analysis on European eel populations (<i>Anguilla anguilla</i>, L.) from several rivers and lagoons of Sardinia, and eel's age and growth from a Sardinian stream as a study case	105
5.2.1. Introduction.....	105
5.2.2. Material and Methods.....	107
5.2.2.1. <i>Study locations</i>	107
5.2.2.2. <i>Eel's samples</i>	109
5.2.2.3. <i>Otoliths extraction and shape analysis</i>	110
5.2.2.4. <i>The Von Bertalanffy growth model</i>	111
5.2.3. Results.....	113
5.2.3.1. <i>The otolith shape analysis</i>	113
5.2.3.2. <i>The Von Bertalanffy growth model</i>	122
5.2.4. Discussions.....	123
5.2.4.1. <i>The otolith shape analysis</i>	123
5.2.4.2. <i>The Von Bertalanffy growth model</i>	124
5.2.5. Conclusions.....	125
6. Chapter 6 Threats that are contributing to imperiling the European eel in freshwaters: the impact of larger dams in riverine systems	127
6.1. When the Eel meets dams: Larger dams' long-term impacts on <i>Anguilla anguilla</i> (L., 1758)	127
<i>Abstract</i>	127
6.1.1. Introduction.....	128
6.1.2. Material and Methods.....	130
6.1.2.1. <i>Study area</i>	130
6.1.2.2. <i>Eels' data</i>	131

6.1.2.3. <i>Data analysis</i>	131
6.1.3. Results	134
6.1.3.1. <i>Dams in the Sardinian hydrographic district</i>	134
6.1.3.2. <i>Eel's occurrence in Sardinian Rivers</i>	135
6.1.3.3. <i>Effect of Larger Dams on Eel's Occurrence</i>	136
6.1.4. Discussions	138
6.1.4.1. <i>Impacts of large dams on eel's occurrence</i>	138
6.1.4.2. <i>Giving future to the European eel</i>	140
6.1.5. Supplementary Materials	142
7. Chapter 7 Summary and perspectives	147
7.1. Summary of the most relevant results	147
7.2. Future perspectives	149
8. References	152
9. Appendix: Bibliography of the Ph.D. student	210
9.1. Publications on topics pertinent to the Ph.D. thesis	210
9.2. Other publications on topics not pertinent to the Ph.D. thesis	214
9.3. Congress participation	214
9.4 Awards	216

Abstract

Catadromous fish can be considered important species for their ecological, economical, and cultural value. Because of their complex life cycle, they are subjected to the cumulative effects of multiple anthropogenic threats that resulted in worldwide decline since the beginning of the 20th century. Among the most iconic catadromous species, the European eel *Anguilla anguilla* (L.) has aroused considerable interest since ancient times, though, to date, many aspects of its life cycle remain relatively unknown. Moreover, the most recent interest increase in eel biology is primarily linked to conservation issues. This is because *A. anguilla* showed a progressively declining since the 1970s and, starting from 2007, accordingly has been protected by the European Council Regulation n. 1100/2007, and successively classified as Critically Endangered (CR). Therefore, although conspicuous efforts by the research have been conducted, to implement knowledge and identify possible solutions to preserve the future survivorship of *A. anguilla*, there is an urgent need to gain further insights into its life history. A review of the bibliography and the state of the art allowed me to focus on an updated state of knowledge about the European eel life cycle, biology, ecology, and the main threats that affect it. Starting from this knowledge, I identified several knowledge lacks and some critical issues on the eel, which led me to the formulation of some questions that structured my thesis project. Questions have been developed in the topics of the doctoral research with the general aim of providing a contribution to the implementation of the knowledge of the bio-ecology and anatomy of this species in relation to the various environmental and anthropic factors through different ecological and anatomical approaches.

- i) Is olfaction involved in the migratory behavior of the European eel? How does the olfactory system develop in the different continental eel's life stages?
- ii) Environmental and hydrological factors influence the eel's recruitment dynamics? How do the spatio-temporal eel's recruitment patterns vary in the central-western Mediterranean?
- iii) What are the eels' growth performances in breeding and in the natural environment after restocking in the central-western Mediterranean?
- iv) How eel growth differs between rivers and lagoons of Sardinia?
- v) Can be the continental distribution of *A. anguilla* a function of the effects exerted by the presence of anthropogenic river interruptions (dams)?

From these questions, through a multidisciplinary approach that involved numerous sampling activities accompanied by complex data collection, laboratory experiments, and statistical analyses, new insights have emerged.

First, I demonstrated the presence of synaptic development in the olfactory bulb, in terms of morphology and density of dendritic spines, that is shaped according to a pattern linked to the migratory life stages of the European eel (glass eels and silver eels).

Second, I described the glass eels' migration temporal peak for the first time in the central-western Mediterranean in relation to the effects of main environmental factors. I also identified a spatio-temporal variability between four sites in the western Mediterranean in terms of the peak of recruitment and the biometric and pigmentation patterns of glass eels. Moreover, I tested new floating traps as an alternative sampling method in three Sardinian estuaries to further deepen and understand glass eels' recruitment dynamics in Sardinia.

Third, I analysed eels' survival and growth performances during a rearing experiment using wild glass eels from Sardinia. I estimated recapture and growth rates on marked and unmarked farmed eels after restocking after a four-year study. Results suggest a good readjustment to the wild environment and demonstrated that this technique represents a valid alternative restocking approach. Furthermore, I found that eels' growth, in terms of otoliths' shape differences, clustered separately for rivers and lagoons, revealing more rounded shapes in otoliths of eels from rivers than lagoons, but with annual body growth quicker in lagoons than in rivers, showing that eel's growth can differ according to habitat types. I fitted Von Bertalanffy's growth curves for female and male eels from a Sardinian stream, that exhibited the already-known sexual dimorphism in growth parameters with higher values in females.

Finally, I pinpointed an overall decrease in eels' occurrence in the Sardinian river network because of dams' building features and the time from their construction.

The achieved results might have several implications beyond the regional interest and add new points from which to start further investigations that, over specific actions, may guide the implementation of new studies and appropriate monitoring programs, highlighting also an urgent need for collaboration between the various stakeholders, researchers, decision-makers, authorities, professionals, and common people as an essential step to creating a sense of awareness on the criticalities that impact this species and the need to mitigate them.

Keywords

Anguilla anguilla, catadromous, migratory species, olfaction, recruitment dynamics, growth, farming, restocking, otoliths, freshwater threats, dams' impact.

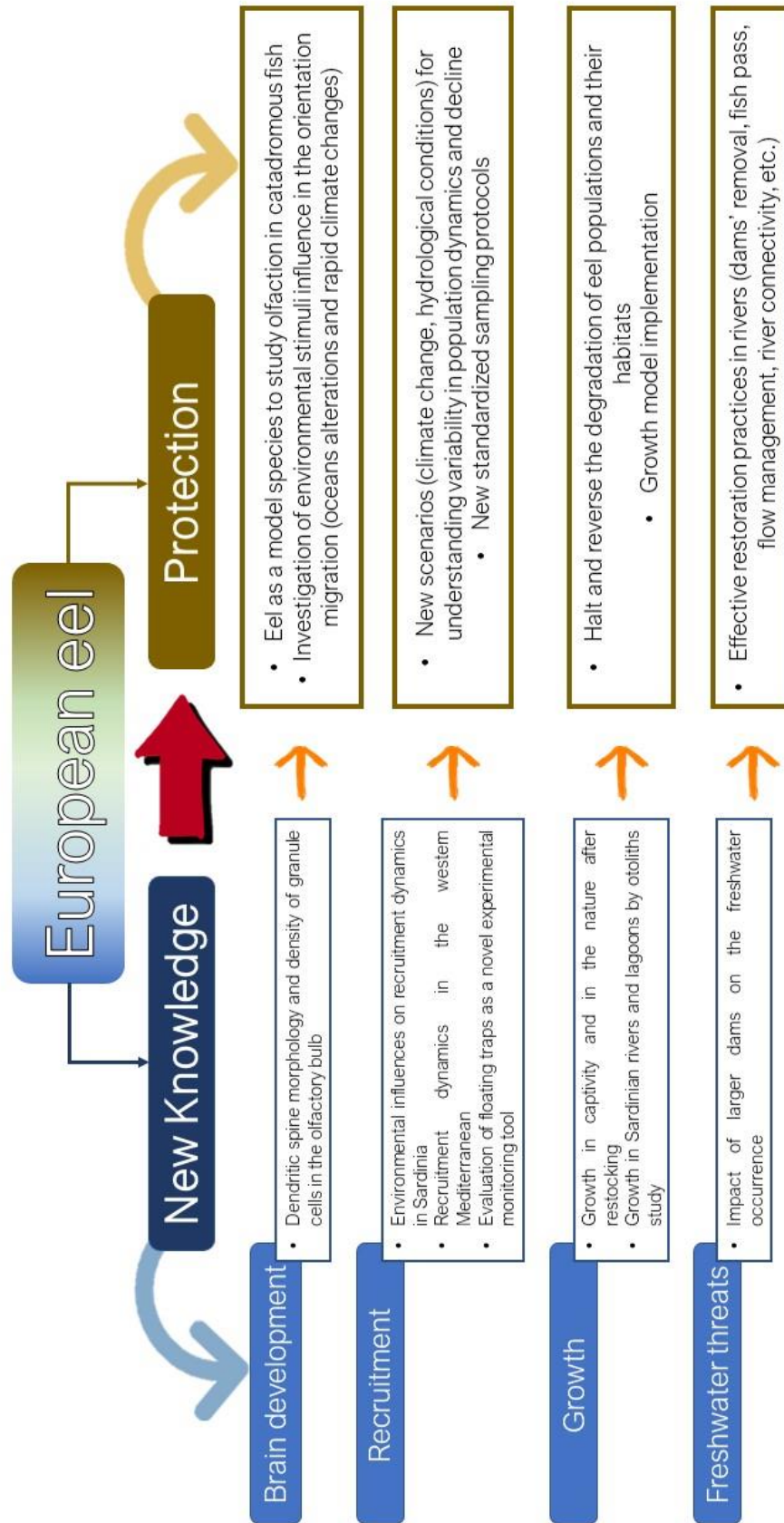


Figure i - Schematic abstract of the Ph.D. thesis

1. Chapter 1

1.1. Thesis outline

My doctoral thesis work is organized into six main Chapters. Besides this introductory **Chapter 1**, the first part introduces the general topic of the thesis (Review). I developed the following four Chapters according to the scientific article style (Introduction, Materials and Methods, Results, and Discussions). Some contain specific Subchapters. Finally, I reported general conclusions of the work and future perspectives.

Two Chapters and two Subchapters have been fully published in international journals while the remaining Chapters or Subchapters are being defined for submission. Each published section also reports the abstract of the paper. At the end of the thesis, I reported all bibliographic references. Finally, the Appendix contains the list of publications in which I am the author or coauthor, the list of my congress participations, and the awards that I obtained for the products of my Ph.D.

During my doctoral path, I tried to follow the logical thread of the life cycle of the European eel in relation to some potential criticalities that the species could encounter in its life. The European eel is a catadromous teleost species with a peculiar and complex cycle characterized by two extraordinary transoceanic migrations, a wide range of distribution, particular longevity, and a series of metamorphoses necessary for adaptation to different aquatic environments. Human, since ancient times, has tried to understand this mysterious species, its origin, its migratory routes, and the mechanisms that regulate them; however, some of these questions have not yet found a complete answer. Added to this is the considerable commercial interest of the species, but overfishing is only one of the numerous natural, but above all, anthropogenic threats which have caused, over time, a drastic decline since the 1970s, for all the continental stages. To address this decline, several international organizations and regulations have been implemented to conserve this species, however, the decline continues to persist. The improvement of knowledge, therefore, represents a fundamental tool for protecting the European eel, especially in those areas of its distribution range where knowledge is still scarce or fragmentary, as in the case of the Mediterranean and, in particular Sardinia.

Right from the identification of knowledge gaps, my research started. Through a narrative review, in **Chapter 2**, I tried to report on the state of knowledge about the European eel biology and ecology in relation to environmental factors and major threats that contributed to its decline.

This allowed me to identify the main topics, that made up the body of the thesis, which have been treated starting from the complexity of the life cycle and various aspects of the bio-ecology and anatomy of the species, developed through a multidisciplinary approach.



Figure ii - Keywords of the thesis

Starting from the complexity of the whole life cycle of the species, I tried to clarify if olfaction plays a role in the orientation of the European eel, therefore, if olfaction could represent a cofactor involved in the migratory behavior and in the life of this species. To understand this, in **Chapter 3**, I studied olfaction, at the level of the anatomy of the brain, by the morphological classification and the density estimation of dendritic spines, in granule cells of the olfactory bulb, in the different continental stages.

Proceeding, in **Chapter 4**, I tried to deepen some aspects related to recruitment dynamics of early juvenile stages of European eel in relation to the main involved environmental drivers in the western Mediterranean, at several spatial scales (single estuary and multiple sites). Recruitment represents one of the two migratory phases of the eel, in which, arriving from the sea, the species colonizes continental waters (estuaries, lagoons, rivers) as small unpigmented eels (glass eels). Because, to date, artificial reproduction of this species is not yet completed, this life stage represents the only source of supply of wild and in captivity eel stocks. Considering this, understanding recruitment phenomena is crucial to address its decline and it is precisely starting from the deepening of these dynamics and related issues that, consequently, it could be possible to address issues that the species could encounter during subsequent stages, but that are directly dependent by the recruitment decline. This is even more urgent in the Mediterranean area where data are still limited and fragmentary.

Chapter 4 contains a general introduction followed by three Subchapters, each composed of materials and methods, results, and discussions.

After recruitment, the eel colonizes the continental waters in which it will spend a big part of its life to growing. Similarly, juvenile eels are caught to be reared in captivity (farming) or repopulated. In **Chapter 5**, I investigated the growth of the eel using two approaches: during a farming and restocking experiment and using otolith shape as a growth descriptor. I also considered the otolith age determination to fit the von Bertalanffy growth models of eels from a Sardinian stream as a case study. Each Subchapter contains an introduction followed by materials and methods, results, and discussions.

During the long continental phase, eels are subject to numerous impacts, among these, in **Chapter 6** I described eels' threats in freshwater habitats by focusing on the negative impact of larger dams (height > 15 m) on the eel occurrence in Sardinian rivers. It is known that dams can directly affect the successful survival of the European eel by causing migration delay, migration stop, mortality, and loss of orientation. But indirectly, dams can also create unfavorable conditions due to the interruption of river connectivity, the interruption or reduction of the river flow, the closure of estuaries, and therefore, the continuum between river and sea. This can prevent the migration, both upstream of juveniles and downstream for spawners, seriously affecting the overall survival of the species.

This Chapter contains an introduction followed by materials and methods, results, and discussions.

Finally, in **Chapter 7** I report overall final considerations and conclusions, future perspectives, and some new ideas deriving from the cognitive contribution obtained from the Ph.D. research to support the enhancement of knowledge to favor survivorship and protection of the European eel.

1.2. Aims

The general purpose of my Ph.D. thesis aspires to bring new knowledge about several aspects of eel bio-ecology and anatomy through a multidisciplinary approach, and to deepen some aspects related to eel the farming, restocking practices, and eel growth under experimental conditions.

Starting from a review of the state of the art of bio-ecology and the critical issues of the European eel (**Chapter 2**) I summarized the specific objectives of my Ph.D. thesis as follows:

Chapter 3: Because of its complexity, the European eel developed one of the most sensitive olfactory systems among fish, which plays a central role in its life. However, the morphological development of brain areas involved in olfaction remains unknown. To fill this gap, I investigated the morphological characterization and the density of dendritic spines in granule cells of the olfactory bulb between the different eels' continental life stages.

Chapter 4: The glass eel recruitment represents the first stage that undergoes the impact of human activities and could be considered an indicator for assessing the status of the eel's population. To increase knowledge about recruitment dynamics, I developed Chapter 4 into the following three sub-chapters:

Subchapter 4.1: I analysed the recruitment dynamics and the influence of environmental factors on eel recruitment in a small estuary in the central-western Mediterranean (Sardinia).

Subchapter 4.2: I investigated inter-annual and short-term variations of the recruitment and of biometrics within and between multiple sites of the western Mediterranean (Sardinia, France, Spain).

Subchapter 4.3: I tested floating traps as an alternative tool to study glass eels' recruitment dynamics in three Sardinian estuaries. I analysed catches and biometrics data and compared them with respect to conventional fyke nets.

Chapter 5: I investigated the growth of the eel in captivity and in nature in Sardinian continental waters in a farming and restocking experiment, and by using otoliths as growth descriptors. I divided Chapter 5 into two parts as follows:

Subchapter 5.1: I studied eels' growth during a nine-month rearing experiment and in nature after restocking in a small stream of Sardinia, with a focus on the

feasibility of restocking practices using farmed wild-caught glass eels through a 4-years study.

Subchapter 5.2: I analysed otolith shape differences among eel populations from five rivers and three lagoons of Sardinia. I used otolith age determination to fit the von Bertalanffy growth models of female and male eels from a Sardinian stream as a case study.

Chapter 6: In the Anthropocene, human disturbances are having detrimental impacts on freshwater ecosystems threatening of extinction their ichthyofauna, particularly diadromous migratory fish species. Despite their evolutionary robustness and habitat plasticity, the cumulative effects of anthropogenic activities are leading the European eel to the edge of collapse. In Chapter 6, I focused on a specific threat that is contributing to imperil eels in freshwaters, the impact of dams. I investigated the impacts of large dams on the long-term occurrence of the eel in the Sardinian hydrographic district, with a focus on the negative effects of a set of temporal, spatial, and dams' related descriptors.

1.3. Main life history traits of the European eel (*A. anguilla*, L.)

The European eel (*A. anguilla* L.) is a semelparous catadromous migratory fish (Tesch, 2003; van Ginneken and Maes, 2005), which undertakes one of the longest and most complex oceanic migration among anguillid species (more than 5000 km), develops in freshwaters and returns to the sea to spawn (Aoyama, 2009; Tsukamoto et al., 2002; Wright et al., 2022). Only recently, Wright et al. (2022) traced the migration route of the species up to the breeding site in the Sargasso Sea, however, the exact site of reproduction remains still an unsolved mystery.

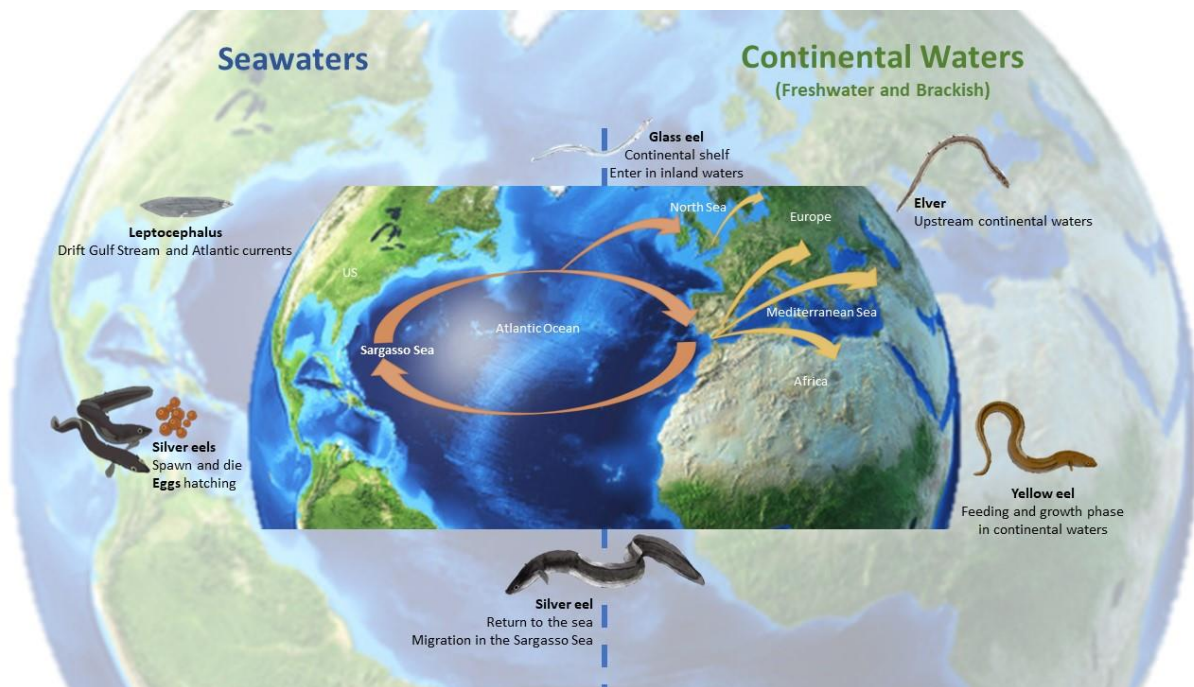


Figure iii - Scheme of the life cycle of the European eel

After spawning in the Sargasso Sea, adults die and leptocephalus larvae are transported by the Gulf Stream and oceanic currents toward the continental shelf for about two years on average (Davey and Jellyman, 2005; Zenimoto et al., 2011). When leptocephali reach the continental shelf metamorphose into unpigmented glass eels. Once settled continental waters (estuaries rivers and lagoons), eels undergo a transitioning phase between saltwater and freshwater, called elvers, pigmented juvenile yellow eels, sexually undifferentiated, to adapt to freshwater. The yellow phase represents the resident growing phase whose duration can vary from 5 to 25 years (Tesch, 2003; Schneebauer et al., 2017; Cresci, 2020). After this period, yellow eels start the metamorphosis into silver eels. During the silvering phase, gonad differentiation and development, and regression of the digestive tract occur (Durif et al., 2009a, b), together with the increasing of pectoral fin length and the ocular diameter. During migration, silver eels stop feeding, the digestive tract atrophies, and sexual maturation reaches completion.

The distribution area of the European eel covers all the European coasts and the northern coasts of Africa (ICES, 2018a). Despite this extensive geographic range, the genetic data indicate that the entire species represents a single panmictic population (Palm et al., 2009; Jacobsen et al., 2014; Enbody et al., 2021).

Freshwater eels, genus *Anguilla* (Schrank, 1978), are among the most unique groups of freshwater eels, currently recognized as 19 species (Arai, 2022). According to their biogeography, are splitted into 13 species/subspecies of tropical eels and 6 temperate eels species/subspecies (Arai 2022).

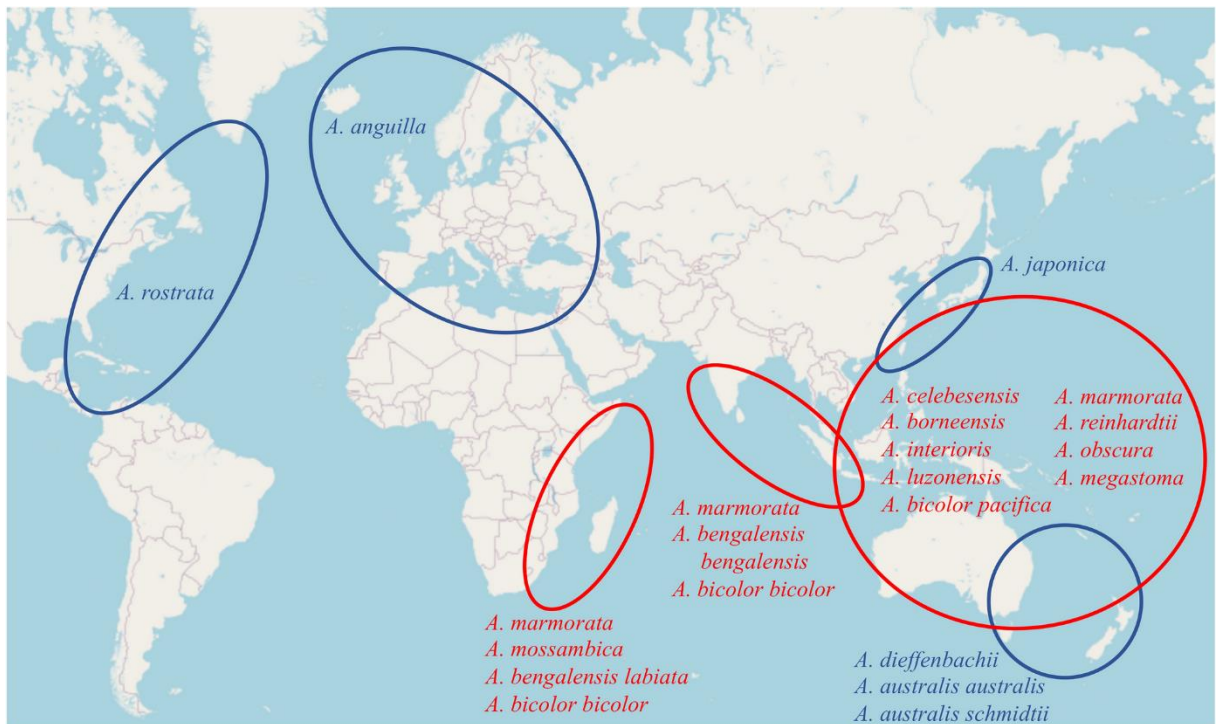


Figure iv - Biogeography of freshwater eels of the genus *Anguilla*. Blue: temperate eels, red: tropical eels. (From Arai, 2022: Migration ecology in the freshwater eels of the genus *Anguilla* Schrank, 1798).

Table i - Systematic of the European eel *A. anguilla*

Kingdom	Animalia
Phylum	Chordata
Subphylum	Vertebrata
Infraphylum	Gnathostomata
Superclass	Actinopterygii
Class	Teleostei
Superorder	Elopomorpha
Order	Anguilliformes
Family	Anguillidae
Genus	<i>Anguilla</i> (Shrank, 1798)
Species	<i>Anguilla anguilla</i> (Linnaeus, 1758)
Common name	European eel

1 **2. Chapter 2**

2 **Hard times for catadromous fish: The case of the European eel** 3 ***Anguilla anguilla* (L. 1758)**

4 Published as: **Podda C.**, Palmas F., Pusceddu A., Sabatini A. (2021). Hard times for catadromous fish: The
5 case of the European eel *Anguilla anguilla* (L. 1758). *Adv. Oceanogr. Limnol.*, 12: 9997. doi:
6 10.4081/aiol.2021.9997.

7 ***Abstract***

8 *Catadromous fish species can be defined important organisms for their ecological,*
9 *economical, and cultural value. Because of a complex life cycle, catadromous fish species*
10 *are exhibited to the cumulative effect of multiple anthropogenic threats that resulted in*
11 *worldwide decline since the beginning of the 20th century. Among the most iconic*
12 *catadromous species, the European eel *Anguilla anguilla* has aroused considerable*
13 *interest, and to date, many aspects of its life cycle remain relatively unknown. Although*
14 *conspicuous efforts by the research to ensure the perpetuation of the species were*
15 *conducted, the identification of the best tools to reduce the threats that affect eels remains*
16 *challenging. In this narrative review, I reported the state of the knowledge and main*
17 *threats about the life cycle, the habitat occupancy, the recruitment, and migration*
18 *patterns of the European eel.*

19 **2.1. Introduction**

20 The term diadromy describes migrations between freshwater and marine environments
21 (Myers, 1949; Mc Dowall, 1988; McDowall, 1992). Diadromous species include less than
22 3% of the world's fish fauna (Eschmeyer and Fong, 2016), among which several ones are
23 economically and culturally important, such as freshwater anguillid eels and salmon
24 (Chapman et al., 2012).

25 Catadromous fish are characterized by a complex life cycle where fish breed in
26 the ocean and growth in continental coastal and/or inland waters (McCleave, 2001a), as
27 seen in anguillids (Tesch, 2003; Elliot et al., 2007). The main ecological services provided
28 by catadromous fish consist for example in the provision of food, and in the regulation of
29 ecosystem functions by transporting nutrients and linking different biomes (Drouineau et
30 al., 2018a). Globally, these animals have been appreciated for human consumption
31 showing a relevant economic interest (Costa-Dias et al., 2009; Feunteun and Laffaille,
32 2011). Catadromous fish can be also used as indicators of environmental quality and

33 functionality (Smith et al., 2016). For instance, they are also commonly used as a metric
34 in the assessment of water bodies' ecological status in the European Water Framework
35 Directive (Delpech et al., 2010), or as bio-indicators of water quality (Amara et al., 2009),
36 reflecting both habitat longitudinal connectivity and habitat quality. In this context, an
37 exiguous number of catadromous fish species are identified as 'umbrella species' to
38 ensure the protection of these species and their habitats (Rochard et al., 2009). They are
39 also magnified by many cultures, foster a belonging sense, and support million-dollar
40 fishing (Garman, 1992; Close et al., 2002; Montgomery, 2003; Chasco et al. 2017;
41 NOAA, 2017). Because of this general interest, catadromous fish are the object of studies
42 in all their dimensions (Drouineau et al., 2018b) and are strongly linked to research
43 questions associated with animal migration (Secor, 2015; Morais and Daverat, 2016).

44 Catadromous fish use, along their migration pathways, a variety of habitats and
45 face many diverse environmental threats (McIntyre et al., 2016). In Europe, as observed
46 for most migratory animals (Sanderson et al., 2006; Wilcove and Wikelski, 2008), a
47 worldwide decline of migratory fish has been recorded at least since the beginning of the
48 20th century (Béguet et al., 2007; Wolter, 2015; Lambert et al., 2019). The causes are
49 numerous and likely cumulative (e.g., obstacles to migration, deterioration in essential
50 habitat and water quality, unsustainable fisheries, and parasite introductions), although
51 quantitative evidence has been rarely demonstrated (Dekker and Casselman, 2014). As a
52 result, many catadromous species are now classified as rare, endangered, or extinct, in
53 the IUCN Red List (IUCN, 2019). There is, therefore, an urgent need to develop
54 approaches that provide reliable quantification of the specific impacts of the different
55 anthropogenic pressures acting on catadromous species. This would help support the
56 implementation of effective mitigation measures and provide adequate tools for national
57 and international regulation around the world.

58 Among the most iconic catadromous species, the European eel *Anguilla anguilla*
59 (Linnaeus, 1758) has been the focus of many studies (e.g., Dekker, 2003a; Bonhommeau
60 et al., 2008; Kettle et al., 2011; Baltazar-Soares et al., 2014; Schiavina et al., 2015; Aalto
61 et al., 2016; Righton et al., 2016; Bornarel et al., 2018; Bevacqua et al., 2019; Dekker,
62 2019; Wright et al., 2022). The life cycle of the European eel has stimulated great
63 curiosity and interest since at least the 4th century BC, where already some important
64 Greek philosophers like Aristotle hypothesized the origin of this species, which remained
65 enshrouded in mystery for millennia. The recent interest increase in eel biology is
66 primarily linked to conservation issues. Therefore, to implement knowledge about the

67 main natural and anthropogenic threats to its survivorship and identify possible solutions
68 to preserve it, there is an urgent need to gain further insights into *A. anguilla* life-history.

69 In this narrative review, I present the state of the knowledge about the life cycle,
70 habitat occupancy, recruitment, and migration patterns of the European eel and about the
71 major threats most likely have contributed to its decline.

72 **2.2. Life cycle, habitat occupancy, and migration patterns of *A.*** 73 ***anguilla***

74 ***2.2.1. The life cycle of the genus Anguilla: common features***

75 Eels of the genus *Anguilla* (Schrank, 1798) are the only genus of Anguilliformes with a
76 catadromous life cycle (McDowall, 1988). The life cycle of anguillid eels involves five
77 developmental stages: leptocephalus (larvae), glass eel (transparent juvenile stage), elver
78 (pigmented juvenile stage), yellow eel (immature adult) and silver eel (partially mature
79 adult) (Bertin, 1956; Tesch, 1977; Cresci, 2020).

80 The larval stage duration varies in different regions worldwide and can last from
81 several months to some years, according to the species and biogeographic region
82 (Tsukamoto, 1990; Lecomte-Finiger, 1992; Cheng and Tzeng, 1996; Arai et al., 1999,
83 2001, 2003; Wang and Tzeng, 2000; Marui et al., 2001; Robinet et al., 2003; Robinet et
84 al., 2008; Reveillac et al., 2008; 2009; Bonhommeau et al., 2010; Han et al., 2016; 2019;
85 Hewavitharane et al., 2020). The larval phase suffers high mortality thereby influencing
86 recruitment success (Cushing, 1990; Durant et al., 2007). After metamorphosis into glass
87 eels, juveniles leave oceanic waters, starting the upstream migration crossing coastal
88 waters (Tesch, 2003; Cresci, 2020).

89 Glass eels represent the recruitment phase to continental waters (ICES, 2011), and
90 constitute the natural source of supply of the species because its artificial reproduction is
91 not yet possible (Pedersen and Ramussen, 2016). Glass eels develop into elvers and settle
92 as yellow eels for many years (about 5-25 years) in coastal and inland water habitats (e.g.,
93 estuaries, rivers, streams, ponds, and lakes) (Tesch, 2003; Cresci, 2020).

94 After this trophic phase, eels start the downstream migration during the silver eel
95 stage (Tesch, 2003) which is initiated by endogenous and exogenous signals that coincide
96 with optimal conditions for successful migration (Sandlund et al., 2017). The migration
97 peaks in rivers properly occur during rainfall events associated with flow pulses, affecting
98 water velocity, turbidity, and conductivity (Cullen and McCarthy, 2003; Durif et al.,

99 2008; Drouineau et al., 2017). Once gonad maturation starts, eels run downstream mainly
100 at night, during rising river flow phases (Behrmann-Godel and Eckmann, 2003), which
101 also provide protection against predation and reduce the swimming energy cost to return
102 to the offshore spawning area (Tesch, 2003; Sandlund et al., 2017; Cresci, 2020).

103 **2.2.2. Habitat occupancy**

104 The European eel is a panmictic species (Palm et al., 2009; Enbody et al., 2021)
105 distributed across most of the coastal countries in Europe and North Africa and spanning
106 the entire Mediterranean basin (ICES, 2018a). Because of the complex life cycle, the
107 cryptic behavior, and the body shape features of eels, results hard to find appropriate and
108 standardized sampling techniques for the monitoring of the European eel in several
109 aquatic environments (Naismith and Knight, 1990; Lasne and Laffaille, 2009).
110 Furthermore, many aspects of the resident stage of eels in freshwaters during their growth
111 phase are still insufficiently understood such as ecology in terms of space and time use
112 (Feunteun et al., 2003; Imbert et al., 2010).

113 The habitats occupancy can be investigated through the otolith microchemistry
114 used to determine the type of habitat of individuals throughout their life, primarily using
115 the strontium (Sr) to calcium (Ca) ratio to distinguish freshwater phases from brackish
116 and seawater phases (Tsukamoto and Aoyama, 1998; Arai et al., 2006; Shiao et al., 2006;
117 Lin et al., 2011 Arai et al., 2019). More recently, other elements, such as barium (Ba) and
118 manganese (Mn), have been used to assess finer-scale movement patterns (Benchetrit et
119 al., 2017). This technique constitutes a reliable tool for the assessment of habitat use and
120 growth throughout the entire life span between freshwater and saline waters (Clément et
121 al., 2014).

122 Experimental electrofishing has been recognized as an efficient sampling method
123 to catch eel in freshwaters despite some limits (e.g., deep waters) (Laffaille and Rigaud,
124 2008), while fishery-based time-series are usually utilized to assess eels' temporal trends
125 (ICES, 2020a). Glass eel fisheries are carried out in the estuaries, or under dams, to study
126 the natural abundance of glass eels in time and space (Dekker et al., 2003). Several dipnet
127 types are applied, on foot or using boats (Aubrun, 1986), trawls (Aubrun, 1987), stow
128 nets (Weber, 1986), and fyke nets (Ciccotti et al., 2000). Fisheries for yellow and silver
129 eels foresee a wide range of gears that include nets, spears, pots, and hooks, in coastal
130 areas, lagoons, rivers, lakes, and streams (Dekker et al., 2003).

131 Several studies used telemetry to investigate individual movement patterns, site
132 fidelity, habitat use, and home range exploitation in relation to seasonal and
133 environmental factors (e.g., Ovidio et al., 2013; Barry et al., 2015; Piper et al., 2017;
134 Trancart et al., 2018; Dorow et al., 2019; Piper et al., 2019; Teichert et al., 2020).

135 Furthermore, diel, seasonal phenology, and the effect of environmental drivers on
136 non-migrant eel movements were investigated using the acoustic camera to evaluate the
137 presence of eels swimming toward the inland waters (Lagarde et al., 2021). Studies on
138 the presence of the eels' population were conducted also with visual observations in
139 inland waters (e.g., lakes and reservoirs) (Rossier, 1997; Schulze et al., 2004).

140 Another tool that could support understanding the eels' habitat occupancy is
141 represented by the environmental DNA (eDNA) analysis (Knudsen et al., 2019). eDNA
142 assays for target species and eDNA metabarcoding are both promising techniques for
143 establishing species presence from environmental samples (Taberlet et al., 2012; Evans
144 et al., 2016; Deiner et al., 2017). These indirect methods are cheap to implement at a large
145 scale and can be used to quickly establish the spatial distribution of a target species
146 (Atkinson et al., 2018; Bracken et al., 2019). Instead, when it is difficult to assess the
147 presence of a species because the species could not simply be present, direct methods
148 (fish tagging) or physical survey assessments may be more appropriate (Kemp and
149 O'Hanley, 2010).

150 ***2.2.3. Juveniles' migration and orientation***

151 Migration mechanisms, including orientation, behavior and route architecture throughout
152 the entire life of anguillid eels have been revealed by means of the recent advanced
153 technologies like agent-based model, ABM, particle tracking model of upstream
154 migrating juvenile eels (Padgett et al., 2020; Benson et al., 2021), motion analysis of glass
155 eels (Eldrogi et al., 2018), tiny acoustic transmitters (Fischer et al., 2019; Mueller et al.,
156 2019; Liss et al., 2021), satellite tracking for migrant adults (e.g., Aarestrup et al., 2009;
157 Westerberg et al., 2014; Wysujack et al., 2015; Amilhat et al., 2016; Righton et al., 2016;
158 Wright et al., 2022 for the European eel; Manabe et al., 2011; Higuchi et al., 2018 for the
159 Japanese eel *Anguilla japonica*; Schabetsberger et al., 2013; 2015; 2019 for Pacific eels
160 *Anguilla marmorata* and *Anguilla megastoma*; Beguer-Pon et al., 2015 for the American
161 eel *Anguilla rostrata*).

162 To reduce migration energy costs (Forward and Tankersley, 2001; Bureau du
163 Colombier et al., 2007; Edeline, 2007), juvenile catadromous species are transported in

164 continental waters by entering the water column during floodtides and descending to the
165 bottom during ebbtides using flood tide transport (FTT) to migrate through estuaries and
166 thus colonize catchments (Forward and Tankersley, 2001). But in absence of this
167 condition, an alternative migratory tactic to undertake upstream migration reckon on
168 active swimming running after the salinity gradient (Cresci, 2020), and using earthy and
169 green odors as attractants (Sola and Tongiorgi, 1996). For instance, several authors
170 showed that chemical cues (e.g., green odors, amino acids, and bile salts) such as
171 freshwater plumes and salinity gradients transporting inland odors into estuaries can
172 guide estuarine juveniles' migration (Tosi et al., 1988; Tosi et al., 1989; Crnjar et al.,
173 1992; Tosi and Sola, 1993; Sola, 1995; Atta et al., 2013). Indeed, eels possess one of the
174 most sensitive olfactory systems among fish, and olfaction plays a central role in their life
175 (Huertas et al., 2008). Glass eels, for example, are attracted by inland odors, derived from
176 the decomposition of detritus associated with the flora and microfauna in freshwater
177 (Sorensen, 1986). Among inland odors, geosmin (trans-1,10-dimethyltrans- 9-decalol)
178 plays a role in attracting glass eels (Tosi and Sola, 1993; Sola, 1995). In addition, it would
179 seem that geosmin operates as an attractant in freshwater and as a repellent in seawater
180 (Tosi and Sola, 1993). Moreover, glass eels' migratory behavior may be also affected by
181 physiological changes, alterations of locomotor activity, and decreasing of body condition
182 (Edeline et al., 2007). Social interactions represent a selective element for the migration
183 and timing of glass eels' settlement linked to specific habitat survival and growth (Edeline
184 et al., 2009).

185 Some studies provided evidence that thyroid hormones are involved in glass eel
186 migration (Edeline et al., 2004, 2005). Decreasing levels of thyroid hormones in juvenile
187 eels might explain the decreasing rate of development and the decreasing propensity to
188 migrate during the transition from the leptocephalus larval to the elver stage (Jegstrup and
189 Rosenkilde, 2003). This hypothesis is corroborated in subadults of the American eel *A.*
190 *rostrata*, in which elevated T4 plasma levels are correlated with increased locomotion
191 activity (Castonguay et al., 1990). Furthermore, European glass eels' river colonizers
192 exhibit increased thyroid hormone concentrations when compared to estuarine migrants
193 (Castonguay et al. 1990; Edeline et al., 2004) suggesting a switch from a high migrating
194 to settling behavior strongly linked to thyroid hormones production.

195 The migration of catadromous fish can also be explained with the 'pheromone
196 hypothesis', according to which fish can release particular odors into the water
197 (pheromones, likely amino acids; Crnjar et al., 1992) functioning as attractants for

198 conspecifics (Schmucker et al., 2016). The attractive power of these cues is stage-
199 dependent in the eels, it is more accentuated on glass eels and gradually disappears in
200 pigmented glass eels and elvers likely due to physiological and behavioral changes,
201 alternative cues possibly become the main attractants (Schmucker et al., 2016; Galbraith
202 et al., 2017).

203 Mechanisms regulating glass eels' orientation are most likely innate and involve
204 geomagnetic-based compass mechanisms based on the inclination and intensity of the
205 magnetic field (Cresci et al., 2017, 2019; Naisbett-Jones et al., 2017). However, the
206 leptocephalus stage presents in the Sargasso Sea may not possess the same magnetic
207 sensing ability as the glass eels because of substantial body rearrangements and related
208 physiological changes (Tesch, 2003; Baltazar-Soares and Eizaguirre, 2017; Durif et al.,
209 2017).

210 More recent studies confirmed that glass eels can orient their migration using the
211 Earth's magnetic field (Cresci et al., 2017, Cresci et al., 2019a) and lunar cues (Cresci et
212 al., 2019b), as a reference to imprint a memory of tidal currents in estuaries and to
213 facilitate position holding and upstream migration (Cresci et al., 2019b). However,
214 although many individual pieces of the complex puzzle of glass eels' orientation and
215 migratory behavior have been elucidated, a holistic mechanism to discriminate how they
216 migrate from the continental slope to estuaries and whether this path is memorized until
217 returning to the sea in the adult stages is still far from being identified.

218 ***2.2.4. Adult migration behavior***

219 The spawning migration patterns of the European eel in the Atlantic Ocean have been
220 studied due to their long distances (about 2000–8000 km) (Schmidt, 1922; Miller et al.,
221 2019; Wright et al., 2022). The long migration paths are notable because of the amplitude
222 of their scale and the excellent ability to trace the birth location using an unrevealed
223 combination of sensory cues (McCleave and Kleckner, 1985).

224 Mark–recapture studies have been used to evaluate eels' home range, habitat preferences,
225 diel and seasonal movements (Jellyman et al. 1996; Oliveira, 1997; Laffaille et al., 2003).

226 Direct observations of the migratory behavior of yellow and silver eels were made using
227 electronic tags (e.g., Amilhat et al., 2016; Righton et al., 2016; Béguer-Pon et al., 2018;
228 Dorow et al., 2019; Teichert et al., 2020; Trancart et al., 2020; Wright et al., 2022).
229 Telemetry represents a reliable method to study the spatial ecology of eels, providing the
230 opportunity to track fish in real-time or from archived data to remote receivers, enabling

231 data to be retrieved without recapturing the tag (Torstad et al., 2013). The development
232 and miniaturization of pop-up satellite archival tags have allowed the tracking of silver
233 eels at sea, unraveling part of the mystery surrounding the oceanic migration of anguillid
234 eels (Jellyman and Tsukamoto 2002; Aarestrup et al. 2009; Béguer-Pon et al. 2015,
235 Amilhat et al., 2016; Wright et al., 2022). Fundamental telemetry studies on silver eels
236 investigated their migration from freshwaters to oceanic spawning areas, including
237 survival, progression rate, and behavioral and external physical factors associated with
238 migration. To date, no telemetry studies on eels have been used with other available
239 physiologically oriented sensors, such as electrocardiography or electromyography
240 (Cooke et al. 2013), or any other environmental sensors, such as conductivity or oxygen,
241 while tracking eels in the wild.

242 Recently, some studies have shed light on the possible effects of global change on
243 eels' migration patterns: climate change and warming-related thermal and hydrological
244 modifications of aquatic ecosystems could delay or bring forward silver eels (Verreault
245 et al., 2012) and alter patterns of glass eels' migration (Moore and Jarvis, 2008).
246 Migratory phenology and habitat change as affected by current climate change should
247 therefore be a priority of future studies.

248 **2.3. Eels' recruitment dynamics**

249 The success and extent of eels' recruitment depend both on global (Knights, 2003; Kettle
250 and Haines, 2006; Bonhommeau et al., 2008; Pacariz et al., 2014; Gutierrez-Estrada and
251 Pulido-Calvo, 2015; Bornarel et al., 2018) and local factors, whose interaction modulates
252 spatial and temporal dynamics of recruits entering brackish environments and freshwaters
253 (Gascuel et al., 1995; Arribas et al., 2012; Harrison et al., 2014; Trancart et al., 2014;
254 Aranburu et al., 2016). Recruitment dynamics at the local scale can vary daily, seasonally,
255 and annually (Bru et al., 2009; Laffaille et al., 2007; Zompola et al., 2008; Arribas et al.,
256 2012, Podda et al., 2020a), are well known for Atlantic estuaries and rivers of Europe
257 (Beaulaton and Castelnaud, 2005; Harrison et al., 2014), and relatively less known for the
258 estuaries located in the southernmost distribution area (Arribas et al., 2012).

259 Although only one cohort recruits each year (Desaunay and Guerault, 1997), glass
260 eels arrive in different waves from different routes (Boëtius and Harding, 1985; Briand et
261 al., 2018). The preference of glass eels for freshwater or brackish water varies with the
262 body condition and the timing of arrival to the continental shelf (Edeline et al., 2005).
263 Reconstructions of the exact hatching site and migration routes of the larvae and glass

264 eel, based on mere analyses of recruitment and sampling data (Dekker, 1998; Lecomte-
265 Finger, 1992), have been carried out since the early twentieth century (Boëtius and
266 Harding, 1985; Van Ginneken and Maes, 2005; Westerberg et al., 2018).

267 Most of the available multi-year temporal series on glass eels' recruitment to
268 European estuaries are based on fishery and/or scientific surveys, however, pluriannual
269 fishery-independent studies are very scarce. Fishery data based on glass eels' recruitment
270 estimates generally suffer from sampling (methods and protocols) and temporal biases
271 (fishing season). For example, in Europe, most surveys to estimate recruitment rates have
272 been conducted in rivers or estuaries, where the eels' dispersion is influenced by the
273 riverbed or river mouth width, allowing easier glass eel samplings (Adam et al., 2008;
274 Zompola et al., 2008; Bru et al., 2009).

275 Models like the glass eel recruitment estimation model (GEREM) (Drouineau et
276 al., 2016) estimated the annual glass eel recruitment at different spatial scales, providing
277 a recruitment index to robustly compare spatial variation trends, with large biases for
278 specific regions where data are scarce or not existent (e.g., North Africa, Eastern
279 Mediterranean, and the Baltic Sea).

280 Moreover, it must be noticed that an accurate knowledge of the physico-chemical
281 characteristics of the surveyed environments is also needed to properly assess the
282 movement and distribution of eels in both the biomes hosting their life cycle (Adam et
283 al., 2008). This need creates a significant challenge: precise information on eels' numbers
284 entering inland waters and moving through the biomes would be collected to understand
285 recruitment dynamics, but, yet it is hard to be obtained because of the complex, often
286 unpredictable, environmental variability of shallow water ecosystems that can mask
287 natural patterns at the relevant spatial scales. Implementing standardized data collection
288 programs of glass eels' abundance should be therefore a major investment of future
289 research and stock assessment protocols.

290 **2.4. Threats to *A. anguilla***

291 The global status of the eel is primarily a consequence of a prolonged decline in its
292 recruitment across the entire distribution area (Moriarty and Dekker, 1997; ICES, 2020a
293 and author therein). Many factors have been identified as recruitment short- or medium-
294 term drivers but, so far, it has been difficult to reach clear conclusions about what are the
295 primary drivers of its decline. Multiple environmental factors (e.g., river flow, changes in
296 the North Atlantic Oscillation, warming of sea surface temperature, currents) probably

297 affected the documented decline (e.g., Gandolfi et al., 1984; Domingos, 1992; Elie and
298 Rochard, 1994; de Casamajor et al., 1999; Prouzet, 2002; Jellyman and Lambert, 2003;
299 Knights, 2003; Polyakov et al., 2005; Bouvet et al., 2006; Bureau Du Colombier et al.,
300 2007; Friedland et al., 2007; Laffaille et al., 2007; Adam et al., 2008; Bonhommeau et
301 al., 2008; Crivelli et al., 2008; Kettle et al., 2008; Zompola et al., 2008; Miller et al., 2009;
302 Durif et al., 2011; Kettle et al., 2011; Arribas et al., 2012; Baltazar-Soares et al., 2014;
303 Hanel et al., 2014; Milardi et al., 2018; Podda et al., 2020a).

304 While eels are still a common species throughout Europe, their stocks have been
305 declining rapidly during the last 40-50 years (Dekker, 2016). The global decline,
306 encountered from 1980s, affects indeed its entire geographical range, with less than 6%
307 for recruitment data and less than 19% for yellow eels data compared to 1960-1979 levels
308 (ICES, 2022). This decline also concerning the southern part of its distribution area, as
309 documented by a concurrent decline in glass eels' recruitment, as well as by contracting
310 local stocks in the Mediterranean Region (Ciccotti, 2005; Aalto et al., 2016; Amilhat et
311 al., 2016). Silver eels' abundance decreased by as much as 90% between 1975 and 2010
312 (Bevacqua et al., 2015) with human-mediated activities being a contributing factor to this
313 decline (Feunteun, 2002; Calles et al., 2010; Piper et al., 2013). It is known that a
314 combination of natural causes and anthropogenic pressures has been impacting both the
315 eel stock and its habitats (Jacoby et al., 2015; Miller et al., 2016; Drouineau et al., 2018b).
316 The European eel is subjected to fishing activities at all continental life stages (from
317 juveniles to adults) and high fishing mortality estimated over the entire life cycle suggests
318 that overfishing represents one of the main threats to the survival of the entire eel
319 population (FAO, 2007). Glass eels' landings showed a sharp decline since 1980
320 decreasing from 2,000 tonnes to around 40-60 tonnes, nowadays, as well as landings of
321 yellow and silver eels decreased from about 18000-20000 tonnes in the 1950s to about
322 2000-3500 tonnes (ICES, 2022). Furthermore, all commercial production of *A. anguilla*
323 (intensive and extensive farming, commercial and recreational fishing) depends on the
324 exploitation of wild stocks (juveniles to supply farms, adults for fishing) (OSPAR, 2010).

325 To deal with this problem, there are various regional management measures
326 currently undertaken to regulate European eel fisheries. Principal conservation measures
327 in place for glass, yellow and silver eels include a ban on commercial fishing of glass
328 eels, gear regulations, quotas, closed seasons, licenses for fishing, size limits, free gaps
329 in weirs, and requirements for elver passes (Ringuet et al., 2002; ICES, 2022). Other
330 pressures play an important role in the decline of the European eel, and also include

331 habitat loss, water pollution, parasitism, and migration obstacles (dams, weirs, pumping
332 stations) (e.g., Baltazar-Soares et al., 2014; Culurgioni et al., 2014; 2015; Bevacqua et al.,
333 2015; Aalto et al., 2016; Dekker and Beaulaton, 2016). These factors affect European eels
334 most in the continental phase of their life cycle, while environmental factors, such as
335 climate change, mostly influence their oceanic phase (Drouineau et al., 2018b). However,
336 as eels can spend most of their life in freshwater (Tesch, 2003), the environmental
337 stressors affecting their life in this biome need to be studied thoroughly.

338 In 2007, the European Commission developed specific legislation (Council
339 Regulation EC No. 1100/2007) to protect eels (European Commission, 2007). The
340 European eel has been listed also in Appendix II of the Convention on International Trade
341 in Endangered Species (CITES, 2020a) and in Appendix II of the Convention for the
342 Conservation of Migratory Species (CMS) (CITES, 2020b). Most recently, the
343 International Union for Conservation of Nature (IUCN) has recently classified the
344 European eel as Critically Endangered (IUCN, 2014; Pike et al., 2020).

345 The stock of the European eel is currently at its historical minimum. For more
346 than half a century, stock abundance and fishing yield have declined by about 5% per
347 year, to less than 10% of their historical level (Dekker, 2003a, 2004; ICES, 2022). From
348 1980 to 2010, recruitment of young eels (glass eels) from the ocean towards the continent
349 dropped consistently by approximately 15% per year, to 1-10% of its former levels
350 (Dekker, 2000; ICES, 2020a). The causes of these downward trends are not clear, and,
351 consequently, efficient remedies and mitigation measures are hard to design (Dekker,
352 2016). Hence, the dynamics of the population are only marginally known (Dekker, 2004)
353 in the current relatively well-documented years, and even more so for the decades during
354 which the stock declined (Dekker, 2016). To fill these gaps of knowledge, monitoring
355 programs have been established, and models of stock dynamics have also been developed
356 (De Leo et al., 2009; Walker et al., 2013; Briand et al., 2018, 2019).

357 Many discoveries were made in the 20th century about the behavior and
358 movement ecology of this species. Extensive sampling programs were conducted in the
359 Atlantic Ocean to understand the horizontal and vertical movement of eel leptocephali
360 (Hanel et al., 2014; Miller et al., 2015), and direct observations of the migratory behavior
361 of yellow and silver eels were made using telemetry (Amilhat et al., 2016; Righton et al.,
362 2016; Béguer-Pon et al., 2018; Wright et al., 2022). However, less is known about the

363 migratory behavior of glass eels during their complex journey from the continental slope
364 to estuaries.

365 General threats to the survivorship of *A. anguilla* span across their entire home
366 range including either freshwater, marine coastal, or oceanic habitats. Threats to
367 reproducing stocks in freshwater are, obviously, conceivably more of a concern.

368 Freshwater ecosystems are threatened habitats by multiple human disturbances
369 (Vörösmarty et al., 2010), which are expected to affect future species ranges (Comte et
370 al., 2016; Radinger et al., 2016). From a legislative perspective, the presence of obstacles
371 to river flow is important for determining the hydro-morphological status of a river in
372 terms of hydrological regime, continuity, morphological condition, and ecological flows
373 (EU Water Framework Directive (WFD) 2000/60/EC; Moccia et al., 2020).

374 Indeed, in recent years, there has been a growing interest in the ecological
375 consequences of river fragmentation by physical obstacles (Garcia de Leániz, 2008;
376 Januchowski-Hartley et al., 2013; Kroon and Phillips, 2016; Birnie-Gauvin et al., 2017;
377 Jones et al., 2019). Recent estimates of fragmentation suggest that 63% of rivers
378 worldwide are no longer free-flowing and that half of all rivers reached have diminished
379 connectivity (Grill et al., 2019). Rivers' flows have been regulated for the purposes of
380 flood protection, navigation, and agricultural development, as well as for electricity
381 production and other human uses. However, these regulations have overall degraded river
382 geomorphological and hydrological conditions (e.g., by the fragmentation of river
383 networks and generating a deficit of sediment transport) (Alexander et al., 2012; Grill et
384 al., 2019).

385 In river ecosystems, fragmentation due to dam building and changes to river flows
386 due to drought may affect river continuity and can be considered a key driver of the
387 Anthropocene biodiversity crisis (Meybeck, 2003; Dudgeon et al., 2006; Zarfl et al.,
388 2015). River connectivity interruption threatens ecosystems' structure and functioning by
389 hindering the movements of migratory species, the exchange of individuals and of genetic
390 information between populations (Wofford et al., 2005; Raeymaekers et al., 2008;),
391 altering aquatic habitats, flow, and sediment transport regimes (Bunn and Arthington,
392 2002).

393 Disruption of natural movements can affect the extent, viability, and persistence
394 of native aquatic species, and has caused a decline in the distribution and abundance of

395 many fish populations, including eels (Feunteun, 2002; Burkhead, 2012; Katz et al.,
396 2013). In this regard, we stress here that catadromous fish are declining worldwide, also
397 because of direct and indirect effects generated by dams building (Shields et al., 2005;
398 Clavero and Hermoso, 2010; Collas et al., 2018).

399 In particular, dam-mediated river fragmentation limits fish dispersal and likely
400 increases their extinction risk (Carvajal-Quintero et al., 2017; Dias et al., 2017). For
401 example, hydroelectric dams can cause injury, direct mortality, delays in migration times,
402 and inhibit downstream migration in *A. anguilla* (Behrmann-Godel and Eckmann, 2003;
403 Durif et al., 2003; Winter et al., 2006; Bruijs and Durif, 2009). Downstream passage at
404 non-powered dams (i.e., dams not equipped with turbines) can have minor impacts, as the
405 passage of fish through them is usually safe (Besson et al., 2016), but anyway can delay
406 migration (Larinier, 2000; Larinier and Travade, 2002; Besson et al., 2016) and result in
407 lower (20%) annual migration rates when compared to equivalent non-obstructed rivers
408 (Feunteun et al., 2000; Acou, 2006).

409 A high level of connectivity between habitats in a river system and between a river
410 and the sea is vital for sustaining healthy stream fish populations and assemblages that
411 migrate among several habitats, for suitable feeding, spawning, and refuge conditions
412 (Lucas and Baras, 2001; Maitland, 2003; Carlsson et al., 2004; Perkin and Gido, 2012;
413 van Puijenbroek et al., 2019): this holds conceivably true, particularly for the survivorship
414 of catadromous fish that migrate across different aquatic biomes.

415 Eels can climb along waterfalls and the weirs of hydropowers (Byrne and Beckett,
416 2012). Nevertheless, most counteracting methods applied to mitigate the negative effects
417 of dams on fish migration, do not grant success for all migratory fish upstream, and even
418 if they do, successful catadromous fish species can encounter unfavorable habitat
419 conditions in reached reservoirs (Larinier, 2001a; van Puijenbroek et al., 2019).

420 Upstream migration in presence of dams may be also delayed given the required
421 time to obtain further fish passages (Larinier, 2001a; Lucas and Baras, 2001; Brink et al.,
422 2018). Moreover, because the general upstream effects of dams increase with the size of
423 the dam and reservoir (Birnie-Gauvin et al., 2017; Brink et al., 2018), large dams, usually,
424 tend to be more harmful than smaller barriers. Downstream migration in presence of dams
425 can enhance mortality due to predation in reservoirs and passage in hydropower turbines
426 or spillways (Larinier, 2001a; Wilkes et al., 2018).

427 Hence, independently of the movement direction and of the presence of fish
428 transposition devices, dams can severely impair catadromous fish movement and, thus,
429 are partly responsible for the decline of catadromous species and, in particular, of eels
430 (Calles et al., 2010; Feunteun, 2002; Piper et al., 2013). Widespread eel ladders could aid
431 upstream migration, although, to date, few efficiency assessments of their efficiency exist
432 (Jellyman and Arai, 2016).

433 Alternative approaches to the capture and the transfer of adult eels downstream of
434 a barrier are also used worldwide (ICES, 2016a; Jellyman and Unwin, 2017; Béguer-Pon
435 et al., 2018). Management of the water regimes alterations of the dams during the fish
436 migratory peaks could be also an effective measure (Boubee et al., 2001; Trancart et al.,
437 2013), but they can be complicated if they are not predicted to limit the economic loss
438 (Teichert et al., 2020).

439 **2.5. Success and limits of eels' restocking practices**

440 Restocking practices are used for conservation, protection, or recovery purposes of
441 endangered species and to increase the productivity of fish stocks (FAO, 2003). Among
442 the actions undertaken to recover the European eel population, restocking practices in
443 continental systems where natural recruitment is low or absent are still underdeveloped
444 (Moriarty and McCarthy, 1982; Andersson et al., 1991; Wickström et al., 1996; Pedersen,
445 1998; Simon and Dörner, 2014; Ovidio et al., 2015; Hanel et al., 2019). Eels' restocking
446 was initiated in Europe before the 20th century and has been done for decades across the
447 entire continent (Wickström et al., 1996; Moriarty and Dekker, 1997; Psuty and Draganik,
448 2008; Dekker and Beaulaton, 2016).

449 The release of glass eels in closed catchments can efficiently support local eels'
450 production and as well as promote local employment (Wickström et al., 1996; Pedersen,
451 2000; Rosell et al., 2005; Psuty and Draganik, 2008). Moreover, among the conservation
452 measures conceived for inland waters that are distant from the sea, restocking is the only
453 solution that enhances the local stocks (Simon et al., 2013; Ovidio et al., 2015; Nzau
454 Matondo et al., 2019). Considering that a proportion of stocked eels needs to escape as
455 silver eels, contrasting for example hydropower-induced mortality during the downstream
456 migration (Winter et al., 2006), restocking is probably the best long-term plan to meet the
457 silver eels' escapement target in the Eel Recovery Plan of the European Union.

458 Because, to date, the success of eels' artificial reproduction in captivity has not
459 yet been totally obtained, this measure cannot be considered a realistic option for directed

460 stock recovery effort (Hanel et al., 2019). In this sense, the species represents a true
461 challenge for breeding and production (e.g., egg quality, fertilization rate, and larval
462 survival are the main challenges). Therefore, domestication and aquaculture might
463 represent an effective tool to satisfy purchaser requests and to preserve natural stocks
464 (Guarniero et al., 2020). However, eel's restocking remains controversial (ICES 2018b),
465 implications and potential benefits and losses caused by stocking are not scientifically
466 monitored or evaluated and a European strategy for the use of stocking as a measure for
467 stock recovery is already lacking (Hanel et al., 2019).

468 Wild-caught glass eels and elvers represent the only supply of restocking, that can
469 be translocated from estuaries to rivers with low or without natural immigration (Pedersen
470 et al., 2000; Nzau Matondo et al., 2019). In their new freshwater environments, restocked
471 young eels can survive, grow, and mature into silver eels that, ultimately, display a
472 seaward migration behavior that is similar to the one exhibited by naturally recruited wild
473 eels (e.g., Shiao et al., 2006; Ovidio et al., 2015; Kullmann and Thiel, 2018; Nzau
474 Matondo et al., 2019; Felix et al., 2020). Nevertheless, it is yet to be demonstrated whether
475 restocking is an efficient measure to restore the eels' stocks and also to produce new
476 mature individuals that could successfully contribute to the successive spawning stocks
477 (Westin, 1998, 2003; Prigge et al., 2013; Westerberg et al., 2014). Moreover, further
478 studies are also needed to assess the impact of restocking practices on the future sexual
479 differentiation of restocked individuals (Geffroy and Bardonnet, 2015; Ovidio et al.,
480 2015). Restocked eels' long-term survival is also still debated (Westin, 1998, 2003;
481 Prigge et al., 2013; Westerberg et al., 2014).

482 The size and stage of restocking material (glass eel vs. yellow eel), their origin
483 (cultured vs. wild eels), their health status (e.g., parasites, infections, diseases), and the
484 trophic status of the water body may altogether influence the restocking yield (Prigge et
485 al., 2013; Pedersen et al., 2016; Ovidio et al., 2015). The annual growth in length and the
486 survival rates of restocked eels vary strongly among different recipient environments and
487 depend upon the characteristics of rearing location, the wild origin of reared eels, and the
488 stage used (juvenile vs. adult eels) (Bisgaard and Pedersen, 1991; Pedersen, 1998; Lin et
489 al., 2007; Simon et al., 2013; Simon and Dörner, 2014).

490 Recent studies reported that the natural mortality of restocked populations
491 decreases with increasing individual body mass and, thus, restocking carried out with
492 larger eels resulted in a better survival rate and, consequently, in a higher yield (Pedersen

493 et al., 2016). More recent experiments showed that restocked eels have an initial delay in
494 their downstream migration, and those recaptured eels have lower body length and
495 weight, likely attributable to their allochthonous origin (Prigge et al., 2013). Interestingly,
496 however, both restocked and farmed eels show similar migratory behaviors and routes
497 during spawning migrations in the open ocean (Westerberg et al., 2014; Chen et al., 2018).

498 Information about the effects of restocked eels' density on the restocking yield is
499 much less, and densities used for restocking are, typically, site-specific and established
500 based on the natural recruitment and yield per recruit estimates (Moriarty and Dekker,
501 1997). Moreover, few studies have contextually investigated the survival, growth,
502 dispersal, and movement of restocked eels (Shiao et al., 2006; Pedersen et al., 2009;
503 Desprez et al., 2013; Wickström et al., 2014; Ovidio et al., 2015; Sjöberg et al., 2017),
504 little is known about the best procedure for implementing restocking with maximum
505 survival rates in riverine ecosystems and, even, about how to accurately assess the level
506 of restocking success (Pedersen 2000; Pedersen, 2009; Deprez et al., 2013; Nzau
507 Matondo et al., 2019).

508 Based on the above cues and considering the still large gaps of knowledge about
509 the best protocol to restock efficiently depauperated eels' populations (Wickström and
510 Sjöberg, 2014; Stacey et al., 2015), I claim the already known need for new and science-
511 based assessments of restocking protocols in different scenarios (ICES, 2016b), possibly
512 coping with the expected habitat quality modifications caused by climate change and
513 unintentionally to the anthropogenic emergence and spread of pathogens (e.g.,
514 *Anguillicola crassus* Kirk, 2003; Wickström et al., 2014, and Anguillid Herpesvirus 1,
515 AngHV-1, Kullmann et al., 2017; Delrez et al., 2021).

516 **2.6. The way forward**

517 Despite the research effort to date, identification of the best technologies to reduce the
518 threats that impair *A. anguilla* remains challenging. Data about the distribution range of
519 the European eel are still spatially and temporally fragmented, and the available ones are
520 still affected by a large heterogeneity in the sampling methods and in analysis protocols.

521 These gaps of knowledge represent altogether major biases for any possible
522 generalization about the life cycle of eels. Thus, the put in place of standardized
523 monitoring programs represents a priority to increase information of the eels' life cycle
524 and their migration patterns. Only when these gaps of knowledge will be filled, restoration
525 of environmental connectivity, particularly when rivers' flow is interrupted by artificial

526 obstacles like dams, will contribute to enhancing eels' stocks and their ability to fuel
527 future generations.

528 In this regard, I anticipate that the removal or mitigation of migration barriers, by
529 promoting fish passage and habitat restoration, could represent a key step to enhance the
530 yield of any eventual restocking practice without prejudice to the risk that restoring
531 connectivity could facilitate the dispersion of alien fish species in a catchment (Clavero
532 and Hermoso, 2010).

533 A better understanding of habitat-eel relationships is probably one of the most
534 promising ways that may contribute to habitat restoration for restoring inland eel stocks
535 (Laffaille et al., 2004).

536 Using eels to study water contamination based on an integrated approach
537 (ecotoxicological, parasitological, pathogens and virus, pollution topics) is crucial for the
538 evaluation of environmental health, and chemical status of water bodies, and will directly
539 be beneficial for the restoration of eels' stocks and consequently for ensuring water
540 quality and habitat conservation as well as affecting the quality of spawners (Maes et al.,
541 2005; Belpaire and Goemans, 2007; Bourillon et al., 2020; Capoccioni et al., 2020).

542 With this in mind, I contend that identifying river basins and the minimum
543 proportion of river stretches that could serve as "eel reserves" is also needed, along with
544 a collaborative research approach between researchers and stakeholders, with the final
545 aim of establishing protocols of eels' exploitation that respond to the principles of
546 sustainable use of resources and development.

547 **3. Chapter 3**

548 **Changes in dendritic spine morphology and density of granule**
549 **cells in the olfactory bulb of *Anguilla anguilla* (L., 1758): a**
550 **possible way to understand orientation and migratory**
551 **behavior**

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554 *anguilla* (L., 1758): a possible way to understand orientation and migratory behavior. *Biology*, 11: 1244.
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556 * These authors contributed equally to this work

557 ***Abstract***

558 *Olfaction could represent a pivotal process involved in fish orientation and migration.*
559 *The olfactory bulb can manage olfactive signals at the granular cell (GC) and dendritic*
560 *spine levels*
561 *for their synaptic plasticity properties and changing their morphology and structural*
562 *stability after environmental odour cues. I analysed the GCs' dendritic spine density and*
563 *morphology across the life stages of the catadromous *Anguilla anguilla*. According to the*
564 *head and neck morphology, I classified spines as mushroom (M), long thin (LT), stubby*
565 *(S), and filopodia (F). Total spines density decreased from juvenile migrants to no-*
566 *migrant stages, to increase again in the adult migrant stage. Mean spines' density was*
567 *comparable between glass and silver eels as an adaptation to migration. At non-*
568 *migrating phases, spines' density decreased for M and LT, while M, LT, and S density*
569 *increased in silver eels. A great dendritic spine development was found in the two*
570 *migratory phases, regressing in trophic phases, but that could be recreated in adults,*
571 *tracing the migratory memory of the routes travelled in juvenile phases. For its*
572 *phylogenetic Elopomorph attribution and its complex life cycle, *A. anguilla* could be*
573 *recommended as a model species to study the development of dendritic spines in GCs of*
574 *the olfactory bulb as an index of synaptic plasticity involved in the modulation of olfactory*
575 *stimuli. If olfaction is involved in the orientation and migration of *A. anguilla* and if eels*
576 *possess a memory, these processes could be influenced by the modification of*
577 *environmental stimuli (ocean alterations and rapid climate change) contributing to*
578 *threatening this critically endangered species.*

579 **3.1. Introduction**

580 Olfaction is a pivotal process involved in many behaviors of fish (orientation, migration,
581 feeding, defense, spawning, and schooling) whose life is entirely restricted to the aqueous
582 environment (Kleerekoper, 1967; Hara, 1975; Calvo-Ochoa and Byrd-Jacobs, 2019). The
583 behavioral significance of the signals arriving at the brain through different channels
584 varies greatly from one species to another. The importance of olfaction in the behavior
585 pattern known as homing is displayed by many fish species (e.g., eel, rainbow trout,
586 Pacific, and Atlantic salmon) (Gunning, 1959; Creutzberg, 1961; Miles, 1968a, 1968b;
587 Thunberg, 1971; Atema et al., 1973; Ramenofsky and Wingfield, 2007).

588 Olfaction cues, reached first by olfactory neurons, are managed by the olfactory
589 bulb (OB), whose projections lead to higher telencephalic areas (Oka, 1980; Fujita et al.,
590 1984) and reciprocally receive projections from the telencephalon itself (Murakami et al.,
591 1983; Rink and Wullimann, 2004). Different neurobiological studies have been
592 performed on fish olfactory circuits, searching for a possible area involved in olfactory
593 memory formation. For instance, in *Cyprinus carpio* (L., 1758), the OB shows general
594 properties for neural plasticity in vivo and in vitro as examples of input-specific, activity-
595 dependent synaptic plasticity (Anzai and Satou, 1996; Satou et al., 2005, 2006). These
596 synaptic activities can take place at the dendro-dendritic synapses between glutamatergic
597 mitral cells (MCs) and granular cells (GCs, interneurons Gamma Amino Butirric Acid
598 GABA releasing) at the peripheral dendrites. Their activity is also regulated by synapses
599 with noradrenergic afferent projections by the telencephalon, which are mainly located at
600 the deep dendrites (Satou et al., 2005, 2006).

601 Furthermore, OB shows that both intrinsic and environmental factors can
602 rearrange the dendritic spines of GCs (Rehn et al., 1986; Matsutani and Yamamoto,
603 2004a, 2004b; Mizrahi, 2007; Huang et al., 2015; McDole et al., 2015; Mandairon et al.,
604 2018). A single dendritic spine of a GC can change its morphology and structural stability
605 after environmental odor enrichment or removal (Zhang et al., 2016). Dendritic spines
606 are the most common postsynaptic structures of most excitatory synapses, connecting
607 presynaptic and postsynaptic neurons (Alvarez and Sabatini, 2007). They consist of a
608 small bulbous head connected to its dendrite through a neck, which provides biochemical
609 and electrochemical compartmentalization of the synapse. The dimension of the head is
610 directly proportional to the quantity of structural synaptic proteins and postsynaptic

611 functional receptors (Matsuzaki et al., 2001). Moreover, synaptic activity is associated
612 with physical growth or shrinkage of the spine (Matsuzaki et al., 2004).

613 Dendritic spines can mutate in various shapes and sizes, depending on brain areas,
614 cell types, and animal species (Ghani et al., 2017). Their structure is classified into four
615 conventional classes according to the morphological features of the head and neck:
616 mushroom, long thin, stubby, and filopodia (Spiga et al., 2014; Zhang et al., 2016;
617 Pchitskya and Bezprozvanny, 2020). Mushroom spines are characterised by a large head
618 and a small neck, able to establish strong synaptic connections, showing the longest
619 lifetime, and constituting the sites of long-term memory storage (Hayashi and Majewska,
620 2005; Bourne and Harris, 2007). Long thin spines are structurally similar to mushroom
621 spines but have a smaller head. They are more changeable and, for this reason, can be
622 considered the learning spines, able to learn new memories during synaptic plasticity,
623 followed by head growth (Hayashi and Majewska, 2005; Bourne and Harris, 2007).
624 Stubby spines usually do not have a neck and are the predominant spine type during early
625 postnatal development stages, but a small amount is present also in adulthood due to the
626 disappearance of mushroom spines (Hering and Sheng, 2001). Filopodia are long
627 dendritic protrusions without a well-defined head, typically observed in young
628 developing neurons (Yoshihara et al., 2009). These structures are mobile and flexible but
629 with a short lifetime (Berry and Nedivi, 2017).

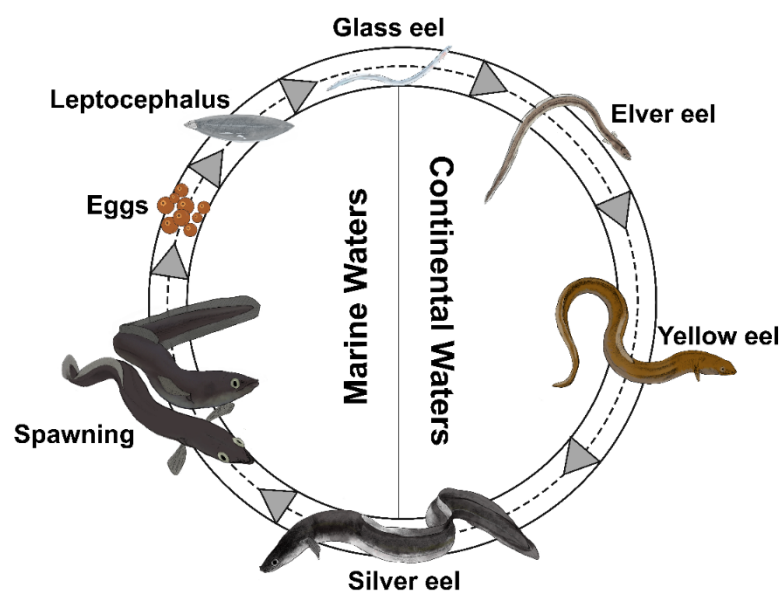
630 The shape, structural organization, synaptic function, and morphological
631 rearrangements of dendritic spines are potentially related to development or experience
632 (Matsutani and Yamamoto, 2004a, 2004b; Mizrahi, 2007; Lendvai et al., 2000; Kasai et
633 al., 2010; Muller and Nikonenko, 2013; Huang et al., 2015).

634 Furthermore, the stability of spines determines the maturity of neural circuits, and
635 their maturation is related to learning, memory formation and storage, and memory
636 consolidation (Zhou et al., 2004; Bourne and Harris, 2007; Yang et al., 2009; Kasai et al.,
637 2010; Fu and Zuo, 2011; Bailey et al., 2015; Zhang et al., 2015).

638 The catadromous European eel *Anguilla anguilla* (L., 1758) during its life
639 undertakes one of the most extraordinary migrations in the animal kingdom (Tesch,
640 2003). Indeed, the European eel crosses the entire Atlantic Ocean twice, first as larvae
641 and finally as an adult. The species spawns in the Sargasso Sea, then leptocephali larvae
642 migrate towards the European and North African coasts for more than 5000 km (Schmidt,
643 1923; Miller et al., 2019; Wright et al., 2022), transported by the Gulf Stream (Tesch,

644 1977; Bonhommeau et al., 2010; Hanel et al., 2014; Miller et al., 2015). Larvae
 645 metamorphose into unpigmented glass eels (Tesch, 1980) able to reach continental areas
 646 (Deelder, 1952; Tesch, 1977) where, under stimulation by chemical attractants
 647 (pheromones, green odors, amino acids, and bile salts), magnetic and lunar orientation
 648 mechanisms, and/or salinity gradients (Tosi et al., 1988; Crnjar et al., 1992; Sola and
 649 Tosi, 1993; Sola, 1995; Schmucker et al., 2016; Cresci et al., 2017, 2019a, 2019b) recruit
 650 estuarine environments, starting their upstream migration (Tzeng et al., 2000). Reaching
 651 continental waters, glass eels pigment into juvenile yellow eels (elvers), developing all
 652 morphological and physiological features necessary for life in inland waters (Wood et al.,
 653 1992; Ciccotti et L., 1993). Eels spend most of their life in these habitats (5–25 years or
 654 more) at the adult yellow eel stage, then metamorphose into silver eels towards sexual
 655 maturity during seaward migration (Tesch, 1977; Durif et al., 2009a, b; Amilhat et al.,
 656 2016; Righton et al., 2016; Béguer-Pon et al., 2018). At this stage, eels swim across the
 657 Atlantic Ocean to the spawning area in the Sargasso Sea to die after spawning (Schmidt,
 658 1923; Righton et al., 2016; Béguer-Pon et al., 2018).

659 Because of the complex life cycle (Figure 3.1), characterized by metamorphosis,
 660 migratory behavior, and the capacity to live in different habitats (marine, brackish, and
 661 freshwater) (Tesch, 2003), the European eel developed one of the most sensitive olfactory
 662 systems among fish and olfaction plays a central role in its life (Westin, 1990, 1998;
 663 Tesch, 2003; Huertas et al., 2008). However, the morphological development of brain
 664 areas involved in olfaction remains unknown.



665
 666

Figure 3.1. The life cycle of the European eel (*Anguilla anguilla*)

667 To fill these gaps, in general, with this study I investigated the development of
668 dendritic spines in the secondary dendritic trunk of OB GCs of the European eel, which
669 resulted as the peripheral ones, known for the presence of synapses between MCs and
670 GCs, characterised by general properties for neural plasticity (Anzai and Satou, 1996;
671 Satou et al., 2005, 2006). In particular, this study aimed: (1) to investigate the
672 morphological characterisation of dendritic spines along the entire eel's life cycle and (2)
673 using a cytomorphological Golgi staining approach, the differences in the density of these
674 structures for each eel's continental life stage.

675 **3.2. Material and Methods**

676 **3.2.1. Eel samples**

677 Eels were collected between November 2019 and January 2021 from the Pramaera river
678 (Central-Eastern Sardinia, Italy). The Pramaera river is a typical Mediterranean small
679 watercourse characterised by bi-seasonal climatic features, with hot arid summers, rainy
680 autumn/winter seasons along with extreme precipitation events, determined irregular
681 flow, and strong seasonal hydrological fluctuations (De Waele et al., 2010; Sabatini et al.,
682 2018; Palmas et al., 2020; Podda et al., 2022). The river showed well-oxygenated waters
683 (dissolved oxygen = 9.40 ± 12.35 mg L⁻¹), good conductivity (1324.16 ± 1564.71 μ S cm⁻¹),
684 and typically Mediterranean average water temperatures (16.01 ± 5.32 °C). Erosion
685 was not very evident indicating a high level of naturalness and integrity and good fish
686 suitability (VV. AA., 2022). Euryhaline fish species (e.g., mullets and seabass), and
687 mostly European eels populate this river (Podda et al., 2020a). The extension of the
688 watercourse is 10 km, with a catchment area of 180.7 km², currently devoid of fluvial
689 interruptions of anthropogenic origin (i.e., dams or other anthropogenic barriers).

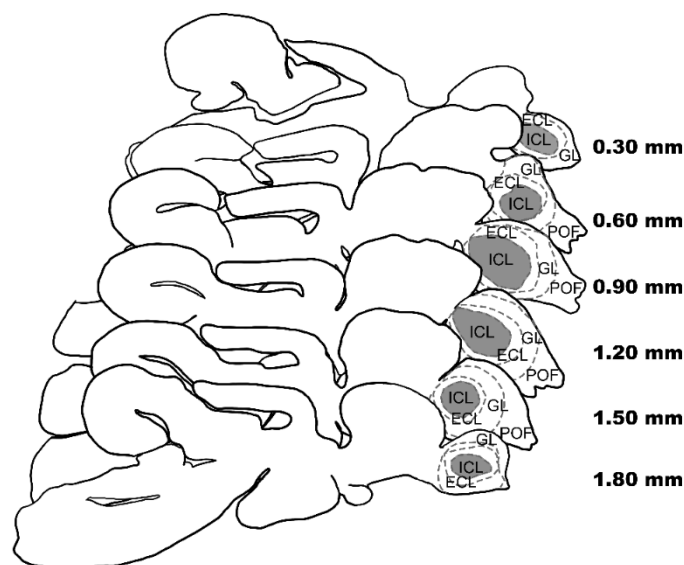
690 Nineteen animals were used for the experiment. According to the peak migration
691 periods of this species in Sardinia (Podda et al., 2020a), five glass eels and five elvers
692 were caught using experimental fyke nets. Five yellow and four male silver eels were
693 captured using low-frequency, pulsed DC electrofishing. All individuals were
694 immediately stored in cool and aerated water and anaesthetised by immersion in a bath
695 of MS 222 until the termination of opercular movements (Gilderhus and Marking, 1987)
696 and measured for total length (TL, cm) and total weight (TW, g). Then, animals were
697 sacrificed in situ using decapitation, conforming with the guidelines and protocols
698 approved by the European Community and Italian legislation for the protection of animals
699 used for scientific purposes (Directive 2010/63/UE L 276 20/10/2010, implemented by

700 Italian Legislative Decree 26/2014). Finally, eel heads were immediately fixed in 4.0%
701 paraformaldehyde in phosphate buffer solution (PBS, pH 7.40) and stored on ice for
702 transfer to the laboratory for subsequent analysis.

703 3.2.2. *Golgi-Cox Processing*

704 In the laboratory, the whole brain (including rostral and caudal portions) was removed
705 from the skull and kept in paraformaldehyde solution at 4 °C overnight. All brains were
706 washed in PBS, weighed (brain weight, BW), and placed in 20 mL Golgi-Cox solution
707 (known for randomly providing the most complete morphology about 5% of the total
708 neuron population) (Cox, 1891; Glaser and Van der Loos, 1981) 2 weeks at room
709 temperature in the dark. Brains were quickly washed in distilled water and transferred in
710 a 30% sucrose plus 0.2% Sodium Azyde solution in PBS for cryoprotection for a
711 minimum of 3 days at 4 °C to accurately remove the Golgi-Cox solution in excess (Zaqout
712 and Kaindl, 2016).

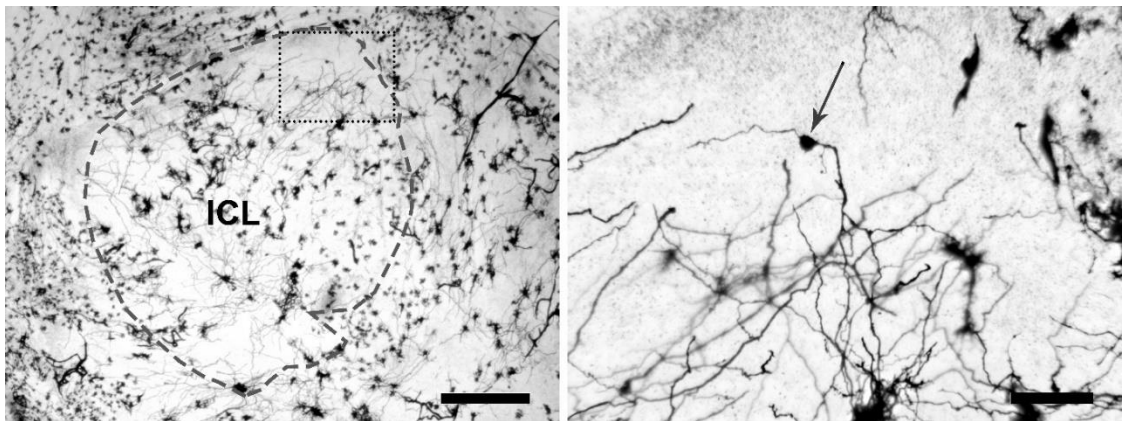
713 Afterward, brains were included in 35% gelatine/25% sucrose in PBS and cut at
714 80 to 100 µm thick sagittal slices using a vibratome (Leica VT1000S). Slices were
715 collected in a cryoprotectant in series, selecting those involved in OB, using a
716 stereomicroscope to identify the target brain area according to the zebrafish brain atlas
717 ‘Neuroanatomy of the Zebrafish Brain’ (Wullimann et al., 1996) as a reference (Figure
718 3.2). Slices were developed using the procedure described by Kolb and McClimans
719 (1986), dehydrated, cleared, and mounted with Canada balsam.



720
721 **Figure 3.2.** Sagittal slices of the eel's brain. Representation of the sagittal slices of a male Silver eel's brain.
722 The intern cellular layer (ICL) (grey area) of the left OB is included

723 **3.2.3. Laser Scanning Confocal Microscopy**

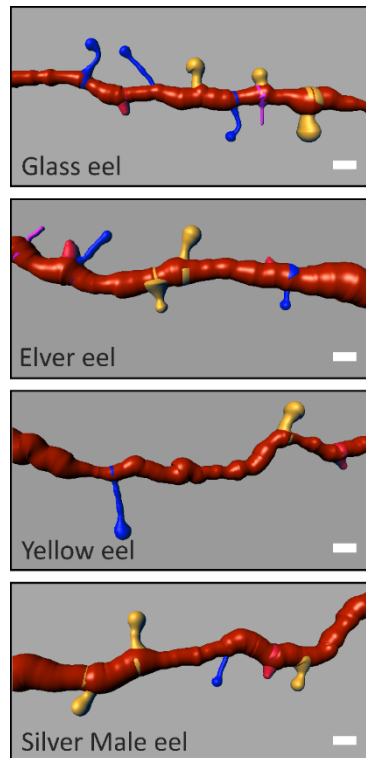
724 Quantitative analysis was performed using a Leica 4D confocal laser scanning
725 microscope (CLSM) with an argon-krypton laser (Leica, Heidelberg, Germany).
726 Confocal images were generated using 100x oil (n.a. = 1.3) in reflection mode (488
727 excitation wavelength). Each frame (512 lines and 512 columns) was acquired eight times
728 and averaged to obtain noise-free images. Confocal images were obtained from the
729 maximum number of scans allowed by the dendrite thickness. Optical sections, usually at
730 consecutive intervals of 0.5 μm , were imaged through the depth of the labeled neurons
731 and saved as image stacks. All confocal images were white labeled on a black background
732 in grayscale ranging from 0 (black) to 255 (white) and processed in grayscale values with
733 Scanware 4.2a Leica. Criteria for morphological analyses were: (i) internal cell layer,
734 where GABAergic GCs were more concentrated, with somata diameter of 7 to 10 μm
735 (Medina et al., 1994) were considered; (ii) only clearly and completely countable GCs
736 were classified; (iii) type IIIb sub-cells (Alonso et al., 1986) were included (Figure 3.3).



737
738 **Figure 3.3.** Golgi-Cox Staining in Light Microscopy. The left image shows the ICL of a male Silver eel's
739 OB (grey dotted line) (scale bar = 250 μm). The right image shows a magnification of the rectangular field
740 in the left image (black dotted line), where a subtype IIIb GC (somata indicated by the grey arrow) is located
741 (scale bar = 50 μm)

742 **3.2.4. Rendering**

743 Image analysis was performed using the software Bitplane Imaris 7.4.2.
744 (<http://www.bitplane.com/imaris/imaris>) by two independent observers blind to the eel
745 life stage using the libraries Filament Tracer and Classifying Spine. Spine density was
746 calculated by tracing at least a 10 μm long spline curve along the secondary dendritic
747 trunk of GCs (Figure 3.4).



748 **Figure 3.4.** Representative GC's secondary dendritic branches (orange). Spine class densities and
 749 differences among the Glass, the Elver, the Yellow, and male Silver eels. (Scale Bar = 1 μ m). Mushroom
 750 spine (yellow); long thin spine (blue); stubby spine (red); filopodia (magenta)
 751

752 Primary dendritic trunks, known for being primarily innervated by inputs of
 753 telencephalic origin (Satou et al., 2005, 2006) were not considered. For each eel
 754 continental life stage, for spine density evaluation, about 75 dendritic segments were
 755 generated. According to the head and neck morphological/metric criteria reported by
 756 Spiga et al. (2014), spines were classified into four classes: stubby spines (S) (no
 757 distinguishable head and total length less than 1 μ m), mushroom spines (M) (head
 758 diameter greater than the maximum diameter of the neck, well-formed head, and neck
 759 diameter greater than its length), long thin spines (LT) (head diameter greater than the
 760 maximum diameter of the neck, well-formed head, and neck length greater than its
 761 diameter), and filopodia (F) (no distinguishable head and total length greater than 10 μ m).

762 **3.2.5. Statistical Analysis**

763 The relationships between TL, TW, BW, and spine density in the OB GC secondary
 764 dendritic trunk were evaluated for each specimen using linear correlation analysis
 765 (correlation coefficient R^2). Before linear regression, the extreme difference between the
 766 values of body characteristics was down-weighted by applying a log transformation.
 767 Spine density was checked for normality (Shapiro-Wilk's test, S-W, $p < 0.05$).
 768 Therefore, differences in spine density among life stages and spine classes were analysed
 769 by the nonparametric Kruskal-Wallis's test (K-W test) to verify the equality of the

770 medians between different groups. When significant differences were obtained, pairwise
 771 comparisons were conducted using Dunn's post hoc test (Z test). All values were
 772 expressed as the mean and standard error (\pm SE) unless otherwise indicated. Significance
 773 was set at $p < 0.05$. All data were analysed by R (R core Team, 2021).

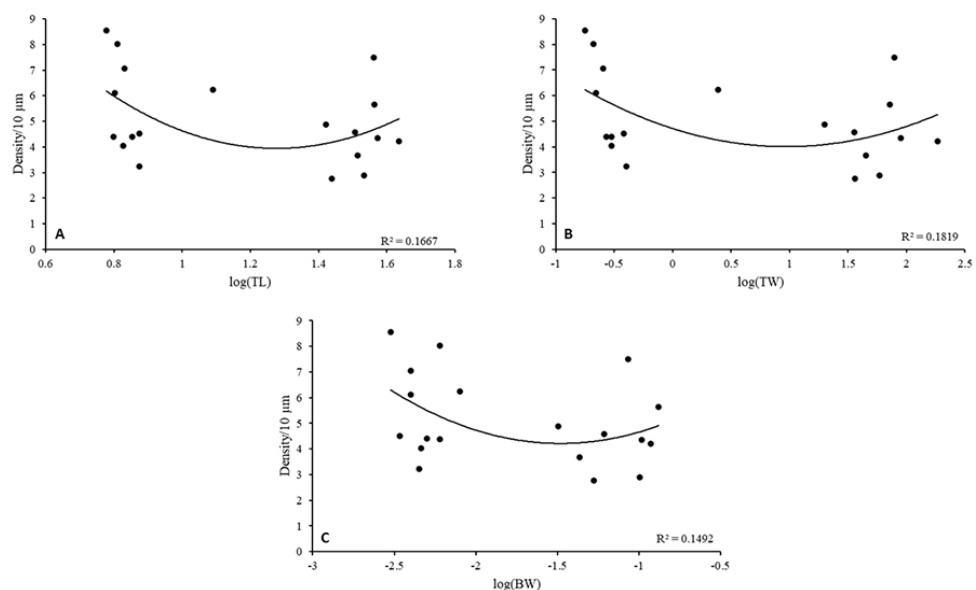
774 3.3. Results

775 Basic statistics relative to TL, TW, and BW of different eel life stages are reported in
 776 Table 3.1.

777 **Table 3.1.** Biometrics of sampled eels. Mean total length (TL), mean total weight (TW), and brain weight
 778 (BW) of sampled eels (\pm standard deviation) for different life stages

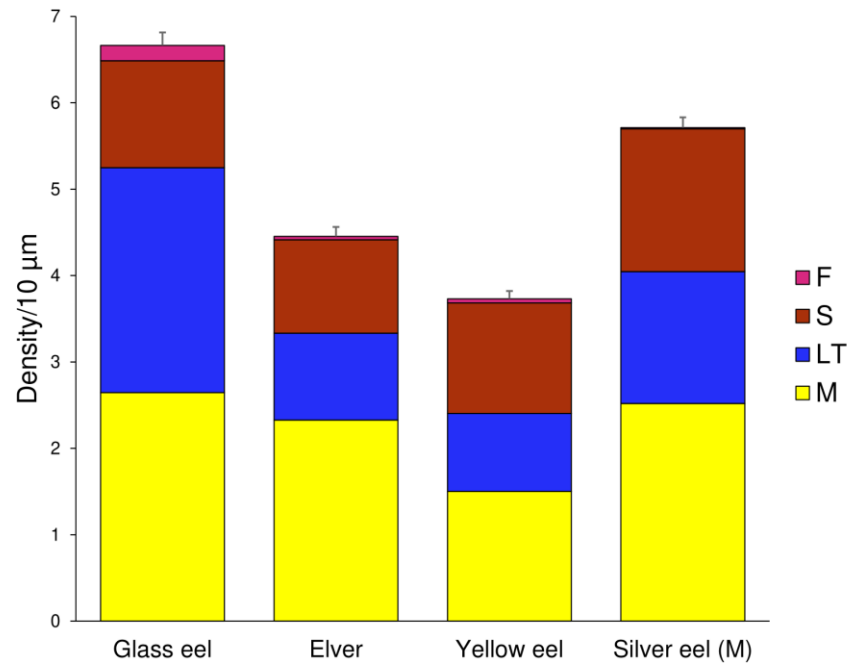
Life Stage	TL (cm)	TW (g)	BW (g)
Glass eel	6.53 \pm 0.43	0.23 \pm 0.04	0.004 \pm 0.001
Elver	8.06 \pm 2.43	0.77 \pm 0.94	0.005 \pm 0.002
Yellow eel	30.56 \pm 3.41	39.04 \pm 14.04	0.058 \pm 0.026
Silver eel	38.40 \pm 3.23	105.75 \pm 52.22	0.11 \pm 0.049

779 From the image analysis, 308 segments (about 10 μ m long) from secondary dendritic
 780 trunks in eel OB GCs were collected and dendritic spine classes were characterized
 781 (Figure 3.4). Linear regression between body characteristics (TL, TW, and BW) and spine
 782 density for each eel life stage showed no significant correlations (R^2 coefficient < 0.7 , p
 783 < 0.05). However, the highest total spine density was observed in relation to eels' body
 784 characteristics for the glass eel stage. In elvers and yellow eels, the density decreases and
 785 increases again at the silver eel stage (Figure 3.5).



786 **Figure 3.5.** Relationships between eels' body characteristics and spine total density from secondary
 787 dendritic trunks in the GCs of the OB. (A) log-transformed total length (TL), (B) log-transformed total
 788 weight (TW), (C) log-transformed brain weight (BW)

790 Total spine density was abundant in the glass eel stage (6.67 ± 0.15 spines/ $10 \mu\text{m}$),
 791 reducing progressively in the elver (4.45 ± 0.11 spines/ $10 \mu\text{m}$) and yellow eel ($3.73 \pm$
 792 0.09 spines/ $10 \mu\text{m}$) stages, to increase again in the silver eel stage (5.71 ± 0.12 spines/ 10
 793 μm) (Figure 3.6).



794 **Figure 3.6.** Dendritic spine density per $10 \mu\text{m}$ of dendritic trunk length \pm standard error (SE), grouped for
 795 eels' life stage and for spine class. Bars are repartitioned according to the life stage of eels and the dendritic
 796 spine class, respectively (M: mushroom in yellow, LT: long thin in blue, S: stubby in red, F: filopodia in
 797 pink)
 798

799 Significant differences were highlighted in the median values of total spine
 800 density among life stages (K-W: 42.77, $p < 0.0001$). Post hoc Dunn's test showed no
 801 statistical differences, only between elvers and yellow eels ($Z: -1.42$, $p > 0.05$).

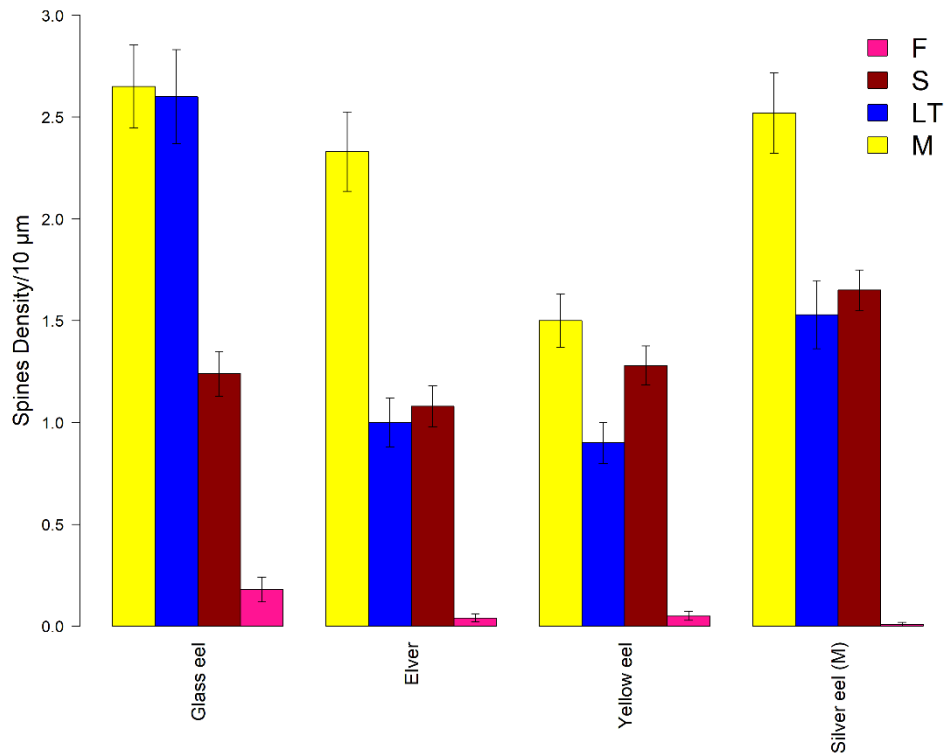
802 Densities within dendritic spine classes (M, LT, S, F) revealed significant
 803 differences for each eel life stage (Table 3.2).

804 **Table 3.2.** Summary of K-W test among eels' life stages. Paired post hoc Dunn's test between dendritic
 805 spine classes. *p* values < 0.05 are significant. Asterisks indicate the significance code: *p* < 0.0001 = ****;
 806 *p* < 0.001 = ***; *p* < 0.01 = **; *p* < 0.05 = *; *p* > 0.05 = ns (non-significant)

	Glass eel		Elver		Yellow eel		Silver eel (M)	
	K-W = 130.19		K-W= 134.86		K-W= 122.46		K-W= 154.93	
	<i>p</i> < 0.001		<i>p</i> < 0.001		<i>p</i> < 0.001		<i>p</i> < 0.001	
Paired groups	<i>p</i> value	significance	<i>p</i> value	significance	<i>p</i> value	significance	<i>p</i> value	significance
M-S	<0.0001	****	<0.0001	****	0.4912	ns	0.0014	**
M-LT	0.6921	ns	<0.0001	****	<0.0001	****	<0.0001	****
M-F	<0.0001	****	<0.0001	****	<0.0001	****	<0.0001	****
LT-S	<0.0001	****	0.3539	ns	0.0028	****	0.051	ns
LT-F	<0.0001	****	<0.0001	****	<0.0001	****	<0.0001	****
S-F	<0.0001	****	<0.0001	****	<0.0001	****	<0.0001	****

807 M = Mushroom; S = Stubby; LT = Long thin; F = Filopodia

808 For glass eels (K-W: 130.19, *p* < 0.05), greater mean densities were found for M and LT
 809 spine classes (2.65 ± 0.20 spines/10 μm , and 2.60 ± 0.23 spines/10 μm , respectively) that,
 810 indeed, were detected as statistically similar (*Z*: 0.48, *p* > 0.05) (Figure 3.7). For elvers
 811 (K-W: 134.86, *p* < 0.05), M spines were the most abundant class (2.33 ± 0.20 spines/10
 812 μm). In addition, no differences were observed between S and LT spine (Figure 3.7). In
 813 the yellow eel stage (K-W: 122.46, *p* < 0.05), both M and S classes showed higher density
 814 values (1.50 ± 0.13 spines/10 μm , and 1.28 ± 0.10 spines/10 μm , respectively) with no
 815 statistical differences (*Z*: -0.51, *p* > 0.05) (Figure 3.7). Lastly, greater density spines (K-
 816 W: 154.93, *p* < 0.05) were obtained for the M spine class (2.52 ± 0.20 spines/10 μm) for
 817 silver eels. Furthermore, no differences were detected between S and LT classes (*Z*: 1.53,
 818 *p* > 0.05) (Figure 3.7).



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Figure 3.7. Mean density of dendritic spines. Mean spine density per 10 μm in the European eel per life stage and per spine class (M: mushroom in yellow, LT: long thin in blue, S: stubby in red, F: filopodia in pink). Error bars represent the standard error of the mean

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Based on the analysis of the density of different dendritic spine classes, the total spine density was greater in M spines (2.25 ± 0.19 spines/ $10 \mu\text{m}$), lower in F (0.07 ± 0.03 spines/ $10 \mu\text{m}$), and intermediate in LT (1.51 ± 0.18 spines/ $10 \mu\text{m}$) and S (1.31 ± 0.10 spines/ $10 \mu\text{m}$) spines. Moreover, median spine density was significantly different among all spine classes (K-W: 571.23, $p < 0.001$). Post hoc Dunn's test explained no statistical differences only between LT and S spine classes ($Z: 0.52, p > 0.05$).

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Considering all dendritic spine classes separately (Figure 3.7), M and LT spines showed a reduction in spine density in the elver and yellow eels' stages to increase again in the silver eel stage. Regarding the S spine class, a slight decrease in spine density was found between glass eel and elver stages to increase again in yellow and silver eels. Finally, the density of the F class decreased progressively until it almost disappeared in silver eels. Within each spine class, significant differences were identified (Table 3.3).

835 **Table 3.3.** Summary of K-W test among dendritic spine classes. Paired post hoc Dunn's test between eels'
 836 life stages. p values < 0.05 are significant. Asterisks indicate the significance code: $p < 0.0001 = ****$; $p <$
 837 $0.001 = ***$; $p < 0.01 = **$; $p < 0.05 = *$; $p > 0.05 = ns$ (non-significant)

	Mushroom (M)		Stubby (S)		Long Thin (LT)		Filopodia (F)	
	K-W = 23.52		K-W = 130.19		K-W = 47.23		K-W = 7.90	
	$p < 0.001$		$p < 0.001$		$p < 0.001$		$p = 0.048$	
Paired groups	p value	significance	p value	significance	p value	significance	p value	significance
Glass eel-Elver	0.2479	ns	0.3944	ns	<0.0001	****	0.0793	ns
Glass eel-Yellow eel	<0.0001	****	0.5585	ns	<0.0001	****	0.1318	ns
Glass eel-Silver eel (M)	0.6584	ns	0.0042	**	<0.0001	****	0.0128	*
Elver-Yellow eel	0.0013	**	0.0953	ns	0.7401	ns	0.7591	ns
Elver-Silver eel (M)	0.3719	ns	<0.0001	****	0.0145	*	0.3738	ns
Yellow eel-Silver eel (M)	<0.0001	****	0.0097	**	0.0040	**	0.2338	ns

838 The density in M spines was quite similar between glass eels and elvers ($Z: 1.17, p >$
 839 0.05), glass eels and silver eels ($Z: -0.37, p > 0.05$), and elvers and silver eels ($Z: 0.81, p$
 840 > 0.05), respectively, showing greater values (glass eel 2.65 ± 0.20 spines/10 μm ; silver
 841 eel 2.52 ± 0.20 spines/10 μm ; elver 2.33 ± 0.20 spines/10 μm). Regarding LT spine
 842 density, a greater value was detected in the glass eel stage (2.60 ± 0.23 spines/10 μm) and
 843 no differences were observed between the elver and yellow eel stages ($Z: -0.37, p > 0.05$).
 844 For S spines, the most abundant were in the silver eel stage (1.65 ± 0.10 spines/10 μm).
 845 The pairwise Dunn's test confirmed that this stage was statistically different from the
 846 others (silver eels vs glass eels: $Z: 3.01, p < 0.05$, silver eels vs. elvers: $Z: 3.98, p < 0.05$,
 847 silver eels vs. yellow eels: $Z: -2.45, p < 0.05$). F class showed greater density in the glass
 848 eel life stage (0.18 ± 0.06 spines/10 μm), with the only significant difference between the
 849 glass eel and silver eel stages ($Z: -2.70, p < 0.05$).

850 **3.4. Discussion**

851 Although the role of olfactory stimuli in the modulation of different functions in fish is
 852 known (e.g., social relationships, prey or predator recognition, and the search for food)
 853 (Døving, 1986), some studies have suggested a key role of olfaction in migration in the
 854 genus *Anguilla* (Westin, 1990; Huertas et al., 2008).

855 In this study, I tried to understand if the olfactory system could play a specific role
 856 in the migratory behavior and orientation of *A. anguilla*, focusing on the development of
 857 dendritic spines in OB GCs as an index of synaptic plasticity involved in the possible
 858 modulation of olfactory stimuli that drive these behaviors.

859 Considering the specific evolution of dendritic spines, starting from the pattern
860 described in the vertebrate central nervous system, it is well known that the total spine
861 density decreases from younger to older individuals, mostly connected with ageing
862 (Okabe et al., 1999; Dickstein et al., 2013; Zhang et al., 2016). In the OB, mushroom and
863 long thin spines are the most abundant spine classes, with mushroom spines representing
864 a more stable synapse than long thin spines (Zhang et al., 2016). Mushroom spines are
865 characterised by a large amount of structural synaptic proteins and postsynaptic receptors
866 (Peters and Kaisermann-Abramof, 1970; Harris et al., 1992; Huang et al., 2015) and by
867 long-term potentiation (Stewart et al., 2005). Furthermore, long thin morphology shows
868 a smaller head and a lower number of synaptic proteins and postsynaptic receptors than
869 the mushroom shape (Peters and Kaisermann-Abramof, 1970; Huang et al., 2015). Stubby
870 spines can represent immature spines (Peters and Kaisermann-Abramof, 1970; Harris et
871 al., 1992, 1999; Fiala et al., 2002) that may disappear or evolve into long thin spines
872 (Kasai et al., 2010). During the second postnatal week of young mammals, dendritic
873 filopodia can emerge and interact with other neurons to form nascent synapses (Harris et
874 al., 1992; Brocco et al., 2010), which can later develop into stubby spines (Ziv and Smith,
875 1996; Fiala et al., 1998; Sorra and Harris, 2000).

876 In general, results showed that the total dendritic spine density decreases
877 progressively from glass eels to non-migrant stages (elvers and yellow eels) to increase
878 again in the adult migrant silver stage. The amount of dendritic spines is comparable
879 between glass eels and silver eels, demonstrating a quantitative and qualitative adaptation
880 of these structures during the two migratory phases of the species. It was hypothesised
881 that this overall trend is initially dictated by the decrease in the density of mushroom and
882 long thin spines during the non-migrating trophic phase. Subsequently, the total spine
883 density increases again in the silver eel stage due to the increment of mushroom, long
884 thin, and stubby spines. Therefore, this model is in contrast to what is known in other
885 vertebrates, revealing a relationship between the trend of the total spine density and the
886 catadromous life cycle and the consequent two migratory phases of this species rather
887 than with the aging of the animal.

888 By analysing the single spine classes, mature mushroom and long thin spines were
889 very similar in the migratory glass eel stage. Instead, in adult silver eels, there was a
890 similar increase between long thin and stubby spines. These results suggested that there
891 would be an increase in synaptogenesis in juvenile and adult stages, correlated by the
892 increment in the number of mushroom, long thin, and stubby spines, with respect to elver

893 and yellow eel stages. Furthermore, in the silver eel stage, the increase in these three spine
894 classes suggested that this migratory phase could stimulate the processing of a large
895 amount of new olfactory cues, which may correspond to only reproductive functions,
896 including pheromone detection (Churcher et al., 2015). Stubby spines would constitute
897 the source of the future mature mushroom and long thin spines, necessary in the migration
898 phase to reach the spawning area. Higher-density values of filopodia were found at the
899 juvenile glass eel stage and this value gradually decreased in the subsequent development
900 stages, which were statistically homogeneous with each other. Although it was the lowest
901 abundant class, their greatest production in the glass eel stage could be attributable to the
902 possible role of these spines in the neural network formation in the OB during the still-
903 stabilising juvenile stage. However, these results were in line with those reported in the
904 developmental model of filopodia in other vertebrates, where a greater filopodia
905 production was observed in the first weeks of life (Harris et al., 1992; Brocco et al., 2010;
906 Zhang et al., 2016).

907 Studies on the olfactory system development in fish species using the plasticity of
908 dendritic spines of GCs of OBs as an index for possible dendritic spine rearrangements
909 are scarce or absent. To date, few descriptive studies exist on the OB's GCs morphology
910 and prolongations in the common carp *C. carpio* and in the Mediterranean barbel *Barbus*
911 *meridionalis* (Risso, 1826), where the presence of dendritic spines is reported only in
912 these neurons (Alonso et al., 1986). Other studies demonstrated the plasticity of these
913 structures in the pyramidal neurons of the optic tectum of the jewel fish *Hemichromis*
914 *bimaculatus* (Gill, 1862) (Coss and Globus, 1978, 1979; Coss, 1979; Burgess and Coss,
915 1980; Berard et al., 1981; Coss and Burgess, 1981) and in zebrafish *Danio rerio*
916 (Hamilton, 1882) (Plata and Robles, 2022), as well as the spiny-medium-like neurons in
917 the telencephalon of the zebrafish (Song et al., 2018).

918 Therefore, This work can represents a pilot study for verifying, first, the presence
919 of the GCs in European eel's OB, the presence of dendritic spines in this brain area, then
920 the quality evaluation of Golgi-Cox Staining, the morphological characterization of
921 dendritic spines, and their density estimation.

922 Findings showed great synaptic development activity in the migratory phases of
923 eels, which regresses in the trophic phase but must necessarily be recreated by tracing the
924 migratory memory of the routes previously traveled in the juvenile phases. If olfaction
925 plays a role in the orientation and migratory behavior throughout the complex and long

926 life cycle of *A. anguilla*, and if eels possess a memory, all these processes could be
927 influenced by changes in the olfactory stimuli under several internal and external
928 conditions (e.g., adaptation to different aquatic environments; sexual development
929 phases, growing or fasting phases, climate changes, ocean alterations) (Durif et al., 2011;
930 Bevacqua et al., 2015; Podda et al., 2021), making it difficult or impossible to cover wide
931 reproductive migratory routes and constituting a cofactor that contributes to threaten this
932 critically endangered species (CR) (Pike et al., 2020).

933 For these reasons and due to its ancient phylogenetic attribution to the
934 Elopomorph teleost group, the European eel *A. anguilla* could be recommended as a
935 model species to study and understand the development of olfaction in catadromous fish
936 species (Lauder et al., 1983).

937 **4. Chapter 4**

938 **Recruitment dynamics of *Anguilla anguilla* (L., 1758) the**
939 **western Mediterranean basin: single and in multiple sites**
940 **study, and implementation of alternative sampling methods**

941 **4.1. Introduction**

942 The glass eel phase represents the recruitment of the European eel, and constitutes the
943 first life stage that undergoes the impact of human activities both on a local (Åström and
944 Dekker, 2007; Beaulaton and Briand, 2007; Drouineau et al., 2018) and on a global scale
945 (Knights, 2003; Kettle and Haines, 2006; Bonhommeau et al., 2008; Pacariz et al., 2014;
946 Gutierrez-Estrada and Pulido-Calvo, 2015; Bornarel et al., 2018). The success rate of the
947 recruitment is a consequence of multiple environmental and anthropogenic factors, whose
948 interactions can modulate the dynamics of recruits entering continental waters (Gascuel
949 et al., 1995; Arribas et al., 2012; Harrison et al., 2014; Trancart et al., 2014; Aranburu et
950 al., 2016). Moreover, these dynamics are subjected to spatio-temporal fluctuations (Bru
951 et al., 2009; Laffaille et al., 2007; Zompola et al., 2008; Arribas et al., 2012, Podda et al.,
952 2020a), which are reflected in the state of global stocks and the perpetuation of the
953 species. For these reasons, recruitment phase could be considered a useful indicator for
954 assessing the impacts of local anthropogenic pressures, and a good indicator of the large-
955 scale status of the eel's population to be accompanied by the escapement estimates of eels,
956 in order to evaluate the survival of local stocks.

957 For a better understanding of recruitment phenomena, it would be necessary to
958 need precise information on glass eels' abundance entering continental waters. However,
959 this is still challenging to achieve due to the complex, often unpredictable, environmental
960 variability and impacts of multiple stressors affecting the species, as well as the lack of
961 standardized programs to study the glass eels' dynamics as in the Mediterranean, and, in
962 particular in Sardinia.

963 In this Chapter I tried to improve the knowledge on several aspects of eels'
964 recruitment both on a local scale (Sardinia) and on a sub-basin scale in some distribution
965 areas of the Mediterranean, where information is still scarce or spatially and temporally
966 fragmented.

967 **4.1.1. Environmental influences on the recruitment dynamics of**
968 **juvenile European eels, *Anguilla anguilla*, in a small**
969 **estuary of the Tyrrhenian Sea, Sardinia, Italy**

970 Published as: **Podda C.**, Palmas F., Frau G., Chessa G., Culurgioni J., Diciotti R., Fois N., Sabatini A.
971 (2020). Environmental influences on the recruitment dynamics of juvenile European eels, *Anguilla*
972 *anguilla*, in a small estuary of the Tyrrhenian Sea, Sardinia, Italy. *Aquat. Conserv. Mar. Freshw. Ecosyst.*,
973 30: 1638-1648. doi: 10.1002/aqc.3362.

974 **Abstract**

975 *The European eel, *Anguilla anguilla*, is a catadromous and migratory species of*
976 *commercial importance. Its complex life cycle results in its exposure to many risk factors,*
977 *which have resulted in stock declines across all life stages since the 1970s. I investigated*
978 *temporal recruitment dynamics of juvenile eels (glass eels and elvers) in a small*
979 *Mediterranean estuary (Sardinia, Italy). The composition of the population and the*
980 *monthly and seasonal variations in the abundance of juvenile eels was assessed over 78*
981 *sampling events (from February 2017 to February 2018). Furthermore, I investigated the*
982 *effects of abiotic variables on the abundance of glass eels and elvers using generalized*
983 *additive models (GAMs). Glass eels had the greatest abundance during the winter*
984 *months, whereas elvers had the greatest abundance during spring. Modeling revealed*
985 *that the abundance of glass eels was mostly explained by the combined effects of water*
986 *temperature (12.3-14.5 °C), tidal coefficient (40-110 cm), moon phase, season, and river*
987 *mouth condition, whereas the abundance of elvers was associated with water temperature*
988 *(14–21 °C), dissolved oxygen content (> 7 mg L⁻¹), and season. These results suggest that*
989 *the annual recruitment of juvenile eels occurs throughout the year, with clear seasonal*
990 *migration dynamics. The use of multiple statistical approaches allowed me to identify the*
991 *importance of several environmental variables in regulating the recruitment dynamics,*
992 *providing useful information for conserving eel stocks through the restoration of the*
993 *natural flow regime and the connectivity between freshwater habitats and the sea.*

994 **4.1.1.1. Introduction**

995 The European eel, *Anguilla anguilla* (L.), is a catadromous, highly migratory, and
996 euryhaline species of commercial importance (Tesch, 2003). The species' continental
997 distribution extends over Europe and northern Africa, from Morocco to Norway, and
998 throughout the Mediterranean and the Baltic Seas (Dekker, 2003a; Tesch, 2003). The

999 European eel has a complex life cycle, during which a growth phase occurs in continental
1000 waters and panmictic reproduction occurs in the Sargasso Sea (Andrello et al., 2009; Als
1001 et al., 2011; Amilhat et al., 2016). After spawning events, leptocephali are transported
1002 along the Gulf Stream and North Atlantic Drift on a long journey that lasts 7-12 months
1003 (Boëtius and Harding, 1985; Lecomte-Finiger, 1992; Arai et al., 2000). On reaching the
1004 continental shelf, leptocephalus larvae undergo a first metamorphosis into glass eels and
1005 colonize estuarine, coastal, and river habitats (Kleckner and McCleave, 1982; McCleave
1006 and Kleckner, 1982). After entering continental waters, eels undergo an acclimation
1007 period to adjust to freshwater (Ciccotti et al., 1993; Birrel et al., 2000) before completing
1008 their migration into continental feeding habitats as elvers and yellow eels (Van Ginneken
1009 and Maes, 2005). After a long feeding and growing period (of more than 20 years)
1010 (Naismith and Knights, 1993; Tesch, 2003), eels undergo a second metamorphosis into
1011 adult silver eels and finally migrate and spawn in the Sargasso Sea (Amilhat et al., 2016;
1012 Righton et al., 2016; Wright et al., 2022).

1013 This complex life cycle exposes European eels to many risk factors contributing
1014 to the decline of the species, although the exact causes have not yet been clearly
1015 established because of difficulties in assessing spawning stock abundance (Moriarty and
1016 Dekker, 1997; Dekker, 2001; Knights, 2003; Friedland et al., 2007; Harrison et al., 2014).
1017 Several factors have been proposed as being responsible for this crisis (Dekker, 2003a;
1018 Miller et al., 2016), including potential threats related to the cumulative effects of human
1019 impacts, such as overfishing (ICES, 2002; Dekker, 2004;), habitat loss (McCleave,
1020 2001b; Knights, 2003), the presence of pathogens (Lefebvre et al., 2007; Palstra et al.,
1021 2007; Culurgioni et al., 2014, 2015), pollution (Van Ginneken et al., 2009; Capaldo et al.,
1022 2012), and ocean climate changes (Castonguay et al., 1994; Miller et al., 2009, 2016;
1023 Jacoby et al., 2015). With all life stages of the European eel has been in decline since the
1024 early 1970s, the stock reached its lowest level in the last few decades, with variable
1025 impacts on fisheries (Aalto et al., 2015; ICES, 2015; Bornarel et al., 2018). In Sardinia,
1026 based on commercial fishery data recorded in coastal lagoons, this decline was already
1027 evident in the 1950s (Moriarty and Dekker, 1997). Consequently, in 2007 a European
1028 Council Regulation established that all EU members must define and implement
1029 protection and conservation measures for the recovery of the European eel stock
1030 (European Council, EC, 2007). In Italy, the national plan indicates Sardinia as a single
1031 eel management unit (EMU). In Sardinia, the fishing of glass eels is forbidden, and it is
1032 expected that any individual with a total length of < 28 cm is immediately released

1033 (regional decree no. 2617/DECA/53; September 27, 2018). The European eel was also
1034 added to CITES Annex II to control its international trade, and in 2008 it was listed as
1035 Critically Endangered in the International Union for Conservation of Nature (IUCN) Red
1036 List of Threatened Species (IUCN, 2014).

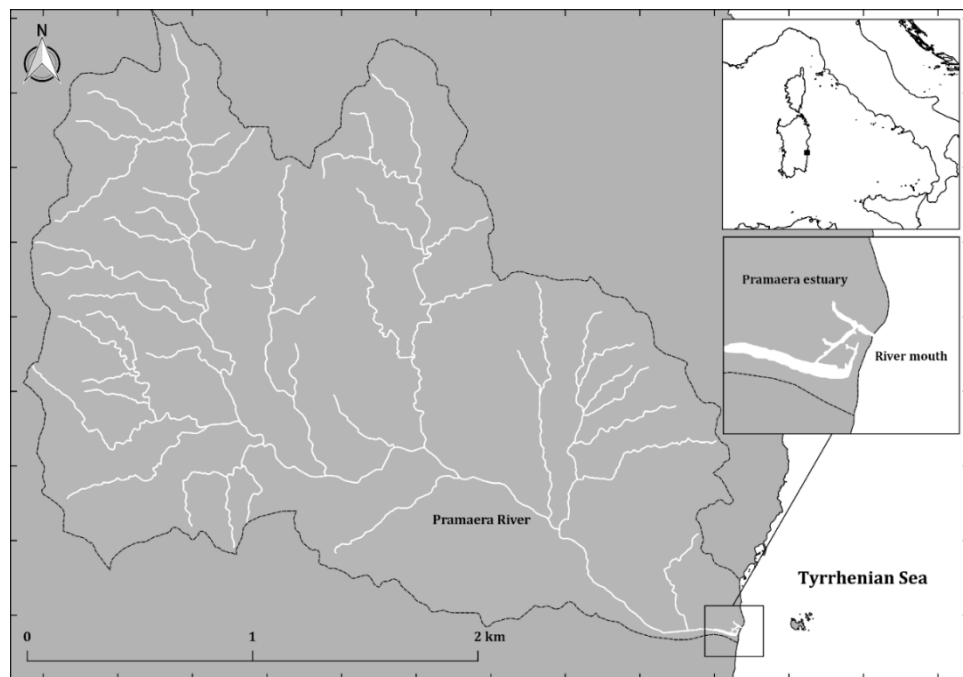
1037 Juvenile eels (glass eels and elvers) represent the recruitment phase to continental
1038 waters (ICES, 2011) and exhibit variable abundances, depending on latitudinal,
1039 morphological, climatic, hydrodynamic, and site-specific abiotic factors (Harrison et al.,
1040 2014; Trancart et al., 2014). The timing of recruitment and the spatial dynamics at a local
1041 scale have already been characterized for many estuaries and rivers located on the Atlantic
1042 coast of Europe (Beaulaton and Castelnaud, 2005; Bru et al., 2009; Arribas et al., 2012;
1043 Harrison et al., 2014; Walmsley et al., 2018). Only sporadic information is available along
1044 the Mediterranean coastline, however, and most of these data are restricted to the northern
1045 part of the western basin (Gandolfi et al., 1984; Ciccotti et al., 1995; Crivelli et al., 2008;
1046 Zompola et al., 2008; Leone et al., 2016; Westerberg et al., 2018). Juveniles may settle in
1047 coastal waters throughout the year, with recruitment peaks occurring at different times
1048 depending on latitudinal gradients (Zompola et al., 2008 and references therein). Along
1049 the north-western coast of the Mediterranean Sea, the recruitment peaks are usually
1050 observed from autumn to spring (Crivelli et al., 1995, 2008), whereas, in the Tyrrhenian
1051 Sea, the peak also occurs during winter (Gandolfi et al., 1984; Ciccotti et al., 1995).

1052 The recruitment has been studied along the Mediterranean and Atlantic European
1053 coasts and appears to be controlled by an interaction between physiological and abiotic
1054 factors (water temperature, river discharge, salinity, lunar phases, tidal cycle, turbidity,
1055 rainfall, and water odours) (Edeline et al., 2006; Zompola et al., 2008; Jellyman et al.,
1056 2009). However, most of the data currently available almost exclusively concern large
1057 estuary systems. The influence of environmental factors on eel recruitment in small-scale
1058 systems remains poorly studied. Although the behavioral and environmental processes
1059 that modulate recruitment patterns are reasonably well understood, site-specific factors
1060 may play a significant role in determining fine-scale distribution patterns at an individual
1061 small coastal system level. Therefore, the aims of this study were: (i) to analyse the
1062 temporal recruitment pattern of juvenile eels in a small Mediterranean estuary; and (ii) to
1063 model the effects of abiotic factors on recruitment dynamics.

1064 **4.1.1.2. Material and Methods**

1065 *4.1.1.2.1. Study area*

1066 The study was conducted in the Pramaera river, Sardinia, Italy, a typical Mediterranean
1067 small watercourse characterised by a transient torrential regime and summer dryness. The
1068 watercourse has a catchment area of 17 km², and is entirely located in central-eastern
1069 Sardinia (Figure 4.1.1.).



1070
1071

Figure 4.1.1. Map of the Pramaera River, located in the central-eastern coast of Sardinia

1072 The Pramaera river does not currently experience fluvial interruptions of anthropogenic
1073 origin (i.e., dams or other artificial barriers). The study focused on the stretch of the river
1074 located near the river mouth (39°58.312'N, 9°41.175'E). This area is characterized by
1075 brackish water, with a mean river width of 15 m. In the Pramaera estuary, artisanal fishing
1076 is carried out in the freshwater habitat and in the river mouth using fyke nets and gillnets
1077 to target euryhaline fish species (mulletts and seabass), and particularly eels. The Pramaera
1078 river mouth has an estuarine typology, assuming a funnel shape when the watercourse
1079 flows into the sea, and it is characterized by a substrate that is largely dominated by sand.
1080 Such substrate, together with hydrological forces, river flow rate, precipitation, and tidal
1081 flow, mainly affects changes in river mouth hydromorphology. Sudden extreme events
1082 (such as floods or sea storms) can modify the river mouth morphology very quickly. The
1083 shores of the river mouth near the sea are characterized by a lack of vegetation, whereas
1084 the area further back from the sea is characterized by the presence of reeds and rushes,
1085 which is typical of the Mediterranean retro-dune environment.

1086 4.1.1.2.2. *Data collection*

1087 Sampling campaigns were carried out monthly from February 2017 to February 2018
1088 during the weeks of the new moon (Elie and Rochard, 1994; De Casamajor et al., 1999),
1089 with the goal of catching juvenile eels at different times during their upstream migration
1090 and different phases of the settlement process. To evaluate the abundance of juvenile eels
1091 entering the watercourse from the sea, three experimental fyke nets (3.2 m long, two
1092 chambers, 31 and 28 cm wide, with 2-mm mesh size and two wings of 2.5 m) were
1093 installed near the river mouth, approximately 50 m from the sea (with one along each
1094 bank and one in the middle), with their mouths facing to the sea in order to capture
1095 individuals arriving from the sea. The sampling started at sunset and ended in the early
1096 hours of dawn. The fyke nets were inspected, when possible, every morning over seven
1097 consecutive days. Although this sampling allowed all eel stages to be captured, it was
1098 designed to be stage selective (with a mesh size of 2 mm). Only glass eels (< 7.4 cm,
1099 unpigmented eels) and elvers (< 15 cm, pigmented eels) were considered separately in
1100 the present analysis.

1101 All captured individuals were immediately placed in containers (20 L) filled with
1102 river water and anesthetized by immersion in a bath of clove oil (eugenol dissolved in
1103 ethyl alcohol) (Walsh and Pease, 2002). The glass eels and elvers captured on each
1104 sampling day were counted and weighed separately. Catch per unit effort (CPUE,
1105 hereafter referred to as ‘abundance’) corresponded to the total number of individuals
1106 caught per day divided by the number of fyke nets used on that same day (n individuals/n
1107 fyke nets). When total catches were high, a subsample of 50 individuals was randomly
1108 selected for further measurements. The total length (TL, to the nearest mm) and total
1109 weight (TW, to the nearest 0.01 g) of each individual were measured directly in the field.
1110 Once the measurements had been taken, the eels were transferred to another container (20
1111 L) with a continuous supply of river water for recovery and were monitored for 1 hour
1112 before their release upstream of the fyke nets.

1113 These biotic data were used to analyse the relationship between TL and TW for
1114 both the glass eel and the elver stages using regression analysis (Ricker, 1973, 1975).
1115 Monthly and seasonal size differences were compared separately for each stage using the
1116 Kruskal-Wallis non-parametric test (K-W, $p < 0.05$). Seasonal variation in abundance was
1117 assessed by plotting the mean monthly capture trend (standard error, \pm SE) for each stage.

1118 Environmental parameters were also measured on each sampling day using a
1119 multiparameter probe (smarTROLL Multiparameter Handheld, InSitu Europe, North
1120 Moons Moat, Redditch, Worcs. B98 9ND, United Kingdom), including the water and air
1121 temperatures ($^{\circ}\text{C}$), salinity, pH, dissolved oxygen content (mg L^{-1}), and oxygen saturation
1122 levels (%). In addition, rainfall (mm), moon phase, tidal coefficient (cm), and river mouth
1123 condition were recorded. Rainfall data were provided by the regional meteorological
1124 department (Sardinia Environmental Protection Agency, ARPAS) from three
1125 meteorological stations situated in the area of the Pramaera river basin and were estimated
1126 as the average rainfall recorded during the week before each sampling date. Moon phase
1127 data were collected using an online application (<https://www.calendario-365.it/luna/calendario-lunare.html>). Because sampling was performed during the week of
1128 the new moon for each sampling campaign, this covered a period of the waning moon
1129 (i.e., the days before the new moon), the new moon, and the waxing moon (i.e., the days
1130 after the new moon). The tidal coefficient was also recorded for each day of sampling,
1131 which was calculated as the difference in height between consecutive high and low tides.
1132 Finally, river mouth condition was considered as a local factor (open or nearly open river
1133 mouth). A summary of the environmental features of each season is given in Table S4.1.1.
1134

1135 4.1.1.2.3. *Model analysis*

1136 Before undertaking the modeling, the abundance data were tested for normality (Shapiro-
1137 Wilk test, S-W, $p < 0.01$) and homogeneity of variance (Levene's test, $p < 0.01$), which
1138 showed that they had a nonnormal distribution. Therefore, to address this and to handle
1139 zero inflation, which seriously affects juvenile eel samples, a Tweedie distribution family
1140 was fitted to the abundance data (Shono, 2008; Augustin et al., 2013).

1141 For the abiotic parameters, the Zuur et al., (2010) protocol was followed, whereby
1142 collinearity was examined by computing pairwise scatter plots that compared continuous
1143 covariates and those combinations that had relevant Spearman's rho coefficients ($\rho > 0.7$)
1144 were discarded prior to modeling. The variance inflation factor (VIF) was also used to
1145 check collinearities among the predictive variables, and variables with $\text{VIF} > 3$ were
1146 discarded. Data exploration revealed nonlinear patterns among the response variables, so
1147 juvenile abundance (dependent variable) and its relationships with environmental,
1148 temporal, and site-specific variables were described using generalized additive models
1149 (GAMs) by a log link function (Hastie and Tibshirani, 1990; Maunder and Punt, 2004).
1150 Seasons and moon phases (waning, new, or waxing moon) were included as temporal

1151 factors, whereas river mouth conditions (open or nearly open) were included as site-
1152 specific factors. Only days on which the river mouth was open or nearly open were
1153 included in the analysis because a closed river mouth represents a physical barrier to the
1154 ascent of juvenile eels.

1155 A GAM can be considered a generalized linear model in which part of the linear
1156 predictor is specified as a sum of the smooth functions (smooth function, s) of the
1157 predictor variables and where the challenge is to find suitable parametric representations
1158 for the smooth functions and to control the degree of smoothness appropriately (Wood
1159 and Augustin, 2002). A stepwise backward selection procedure was implemented to
1160 identify the best-fitting model, based on the minimization of Akaike's information
1161 criterion (AIC) (Akaike, 1973). At each step in the selection procedure, the variables with
1162 the highest P values ($p > 0.05$) were dropped to produce a model with a lower AIC, and
1163 backward selection continued until the lowest AIC was reached.

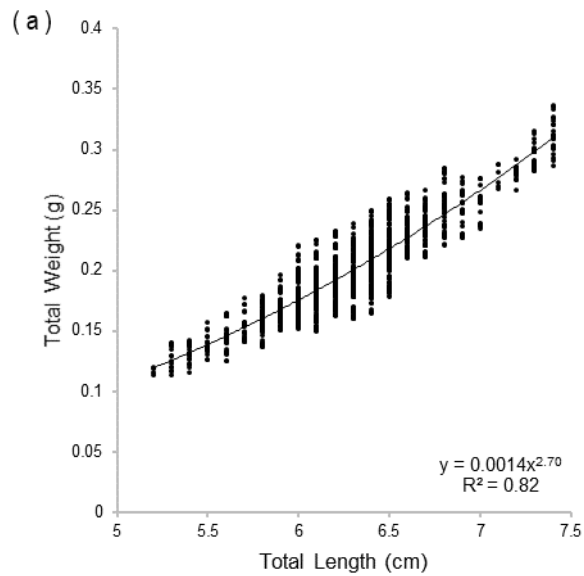
1164 The total explained deviance and the relative contribution of each factor were
1165 evaluated for each model and the performance of the models was evaluated with cross-
1166 validation using Pearson's correlation coefficients between the observed and predicted
1167 abundances. All statistical analyses were performed using R software (R Core Team,
1168 2018), with a significance level of $p < 0.05$, and the GAM approach, as proposed by Wood
1169 (2006), was performed using the library *mgcv* 1.8-12 ([https://CRAN.R-](https://CRAN.R-project.org/package=mgcv)
1170 [project.org/package=mgcv](https://CRAN.R-project.org/package=mgcv)).

1171 **4.1.1.3. Results**

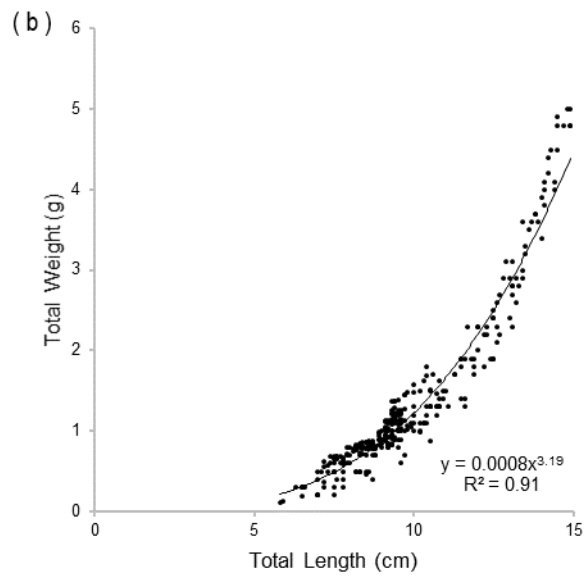
1172 *4.1.1.3.1. Population structure and seasonal migration*

1173 Twelve sampling campaigns were carried out from February 2017 to February 2018
1174 during the weeks of the new moon. The river mouth was closed during the campaign of
1175 November 2017, so these data were not available for the analysis. The total catches over
1176 the entire study period were 28,999 glass eels, weighing 7,212.68 g, and 620 elvers,
1177 weighing 640.28 g. A total of 2,064 glass eels and 313 elver specimens were measured
1178 during the 78 sampling events. There was a negative allometric relationship between size
1179 and weight for the glass eels that favored body length development ($b = 2.70$, $R^2 = 0.82$,
1180 $y = 0.0014x^{2.70}$) (Figure 4.1.2.a). The mean values for TL and TW (mean \pm SD) for glass
1181 eels were 6.3 ± 0.33 cm and 0.25 ± 0.04 g, respectively. The largest individual was
1182 captured in winter (7.4 cm and 0.33 g), whereas the smallest was captured in spring (5.2

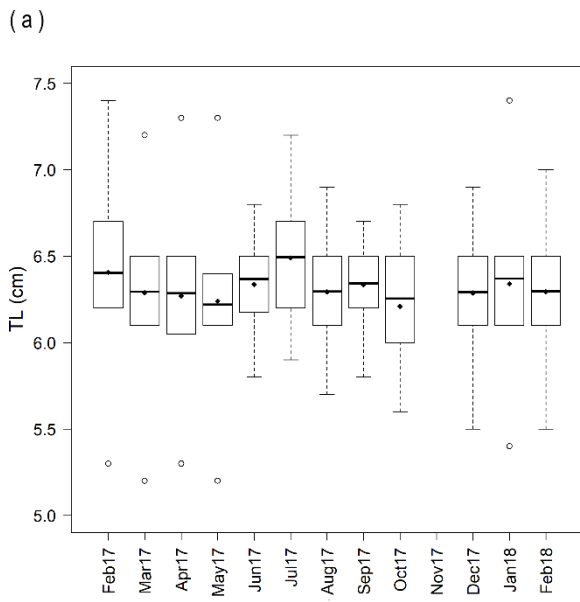
1183 cm and 0.12 g); however, there was no significant difference in the median TL of glass
1184 eels among the months and seasons (K-W, $p > 0.05$) (Figure 4.1.3.a).



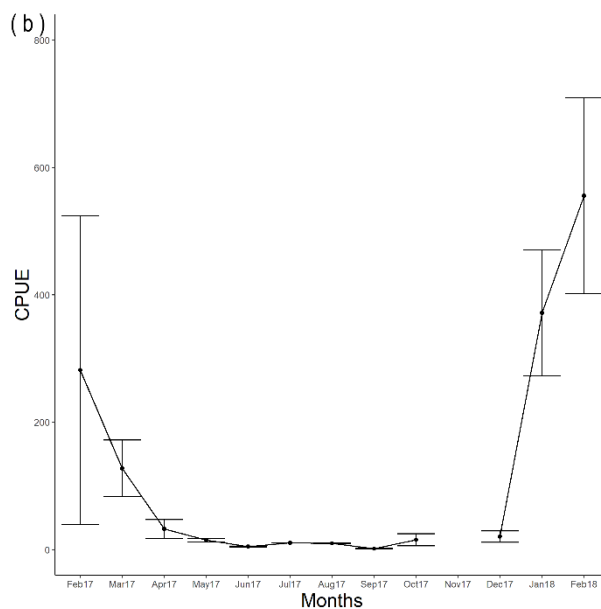
1185



1186
1187 **Figure 4.1.2.** Size–weight relationship for (a) glass eels (n = 2064) and (b) elvers (n = 313) from the
1188 Pramaera River



1189



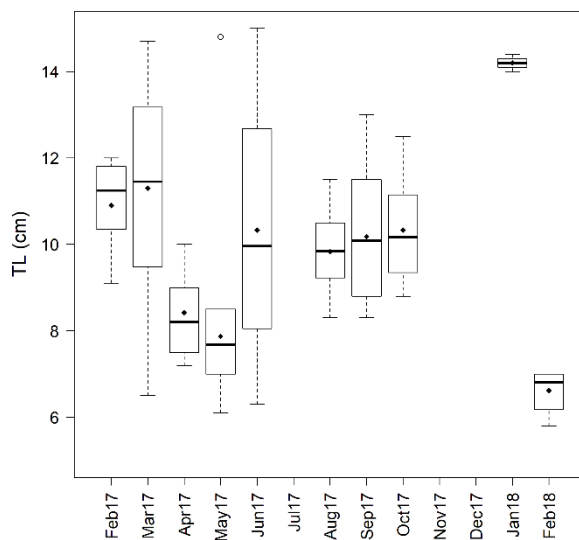
1190

1191 **Figure 4.1.3. (a)** Relationship between total length and month of the year for glass eels. **(b)** Relationship
 1192 between catch per unit effort (CPUE, i.e., number per trap per day) and month of the year for glass eels.
 1193 Box lengths represent interquartile ranges, bar lengths represent ranges, horizontal lines represent median
 1194 values, and black dots represent mean values. Error lines represent the standard errors for each month. The
 1195 black line denotes the trend of the CPUE data

1196 On average, higher glass eel abundances (mean \pm SE) occurred during the winter months
 1197 (February 2017, 281.8 ± 242.24 individuals per day; January 2018, 371.68 ± 98.63
 1198 individuals per day; and February 2018, 555.54 ± 153.66 individuals per day), whereas
 1199 the lowest recruitment was observed from late spring to early autumn (with a minimum
 1200 mean value in September of 1.5 ± 0.27 individuals per day) (Figure 4.1.3.b). Overall,
 1201 80.45% of the glass eel catches were recorded in February 2017 and 2018, and in January
 1202 2018.

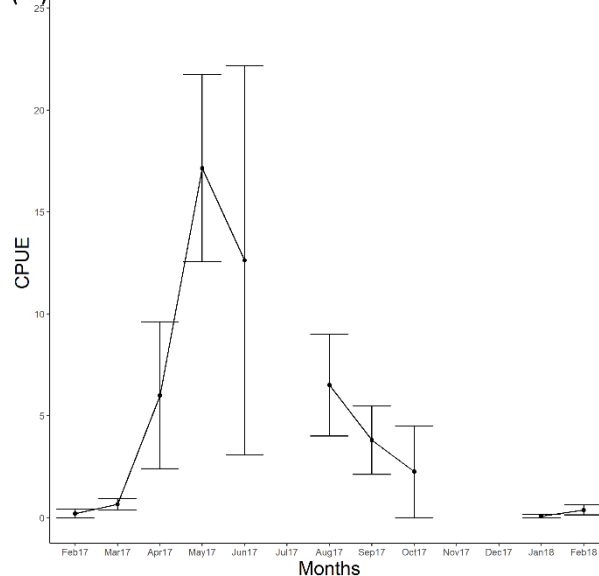
1203 The size–weight relationships for elvers had allometric coefficients of > 3 ($b =$
 1204 3.19 , $R^2 = 0.91$, $y = 0.0008x^{3.19}$, Figure 4.1.2.b). The mean values for TL and TW (mean
 1205 \pm SD) for elvers were 9.4 ± 2.4 cm and 1.03 ± 7.35 g, respectively, and size differences
 1206 were detected among months, with the smallest elvers being captured in spring, after
 1207 which time there was a progressive increase in TL during the summer and autumn months
 1208 so that the largest individuals were captured during the winter months (K-W, $p < 0.001$)
 1209 (Figure 4.1.4.a). The elver abundance (mean \pm SE) was highest during spring, with two
 1210 peaks in May and June (17.15 ± 4.59 and 12.62 ± 9.54 individuals per day, respectively,
 1211 Figure 4.1.4.b), representing 71.60% of the total catches. No elvers were captured in July
 1212 and December.

(a)



1213

(b)



1214

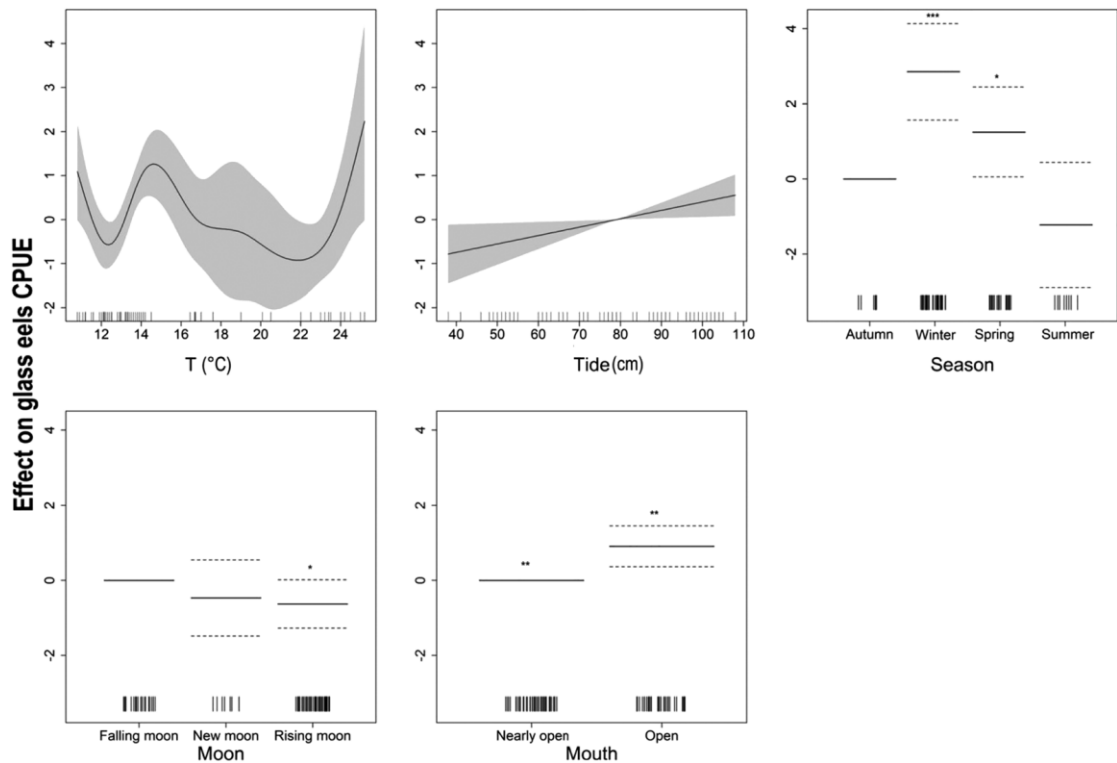
1215 **Figure 4.1.4. (a)** Relationship between total length and month of the year for elvers. **(b)** Relationship
 1216 between catch per unit effort (CPUE, i.e., number per trap per day) and month of the year for elvers. Box
 1217 lengths represent interquartile ranges, bar lengths represent ranges, horizontal lines represent median

1218 values, and black dots represent mean values. Error lines represent the standard errors for each month. The
1219 black line denotes the trend of the CPUE data

1220 *4.1.1.3.2. Factors affecting juvenile eel abundance*

1221 Air temperature (°C), oxygen saturation (%), pH, and salinity were eliminated from the
1222 analysis based on the VIF criteria used. Therefore, in the modeling, water temperature
1223 (T), dissolved oxygen (DO), rainfall (Rain), and tidal coefficient (Tide) were considered
1224 as continuous variables, and season (Season), moon phase (Moon), and river mouth
1225 condition (Mouth) were considered as categorical factors.

1226 Three models were tested for glass eels (Table S4.1.2.). The best model included
1227 five exploratory variables (AIC = 842.3): water temperature (T), tidal coefficient (Tide),
1228 seasons (Season), moon phase (Moon), and river mouth condition (Mouth) (Table
1229 S4.1.3.). The final model had statistically significant goodness of fit and explained 66.1%
1230 of the total deviance. Examination of the relative contribution of each variable to the total
1231 explained deviance revealed that water temperature was the most important factor
1232 (48.7%), followed by the tidal coefficient (10.4%). In addition, season, moon phase, and
1233 river mouth condition showed some importance, explaining 7% of the total deviance. The
1234 response plots for each variable included in the best-fitting GAM are shown in Figure
1235 4.1.5. Glass eel abundance decreased at temperatures of 10–12 °C, to reach a local
1236 minimum of about 12 °C, and then increased to reach a maximum of approximately 14–
1237 15 °C. Temperatures above this resulted in relatively high variation. The probability of
1238 glass eel abundance was also significantly affected by season, reaching a maximum value
1239 in winter and a minimum value in summer. The likelihood of a large increase in
1240 abundance was clearly associated with an open river mouth condition. The abundance of
1241 glass eels increased steadily and positively with tidal coefficient, ranging from 40 to 110
1242 cm. Finally, the model revealed that the waxing moon phase appeared to have a slight,
1243 but statically significant, effect on glass eel abundance. Cross-validation indicated a
1244 moderate correlation between the observed and fitted abundance values (CPUE, $R^2 =$
1245 0.52, Figure S4.1.1.a).

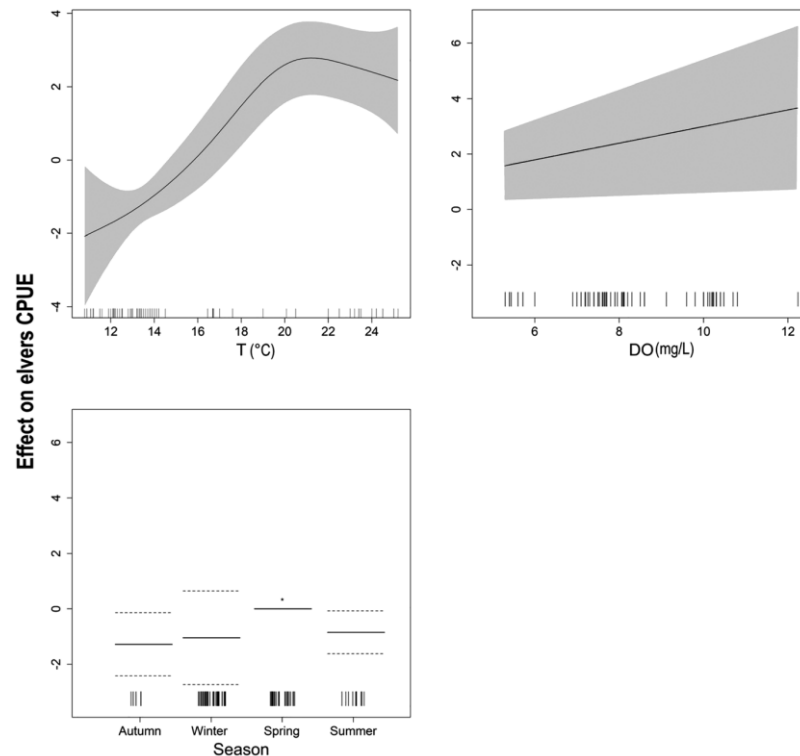


1246

1247 **Figure 4.1.5.** Generalized additive model (GAM)-derived effect of covariate modeling
 1248 for the abundance (catch per unit effort, CPUE) of glass eels. Shaded areas and dashed
 1249 lines indicate 95% confidence bands; tick marks on the x-axes of the depth plots indicate
 1250 sampling intensity. The y-axis represents the partial effect of each variable

1251

1252 Five GAM models were tested for elvers, the best fitting (AIC = 268.9, Table
 1253 S4.1.4.) of which retained three of the nine covariates: water temperature (T), dissolved
 1254 oxygen (DO), and season (Season) (Table S4.1.5.). The final model explained 74.1% of
 1255 the total deviance and all the terms were significant. Examination of the relative
 1256 contribution of the individual covariates indicated that water temperature (67.7%) and
 1257 dissolved oxygen (5.09%) explained the largest level of the observed variation in elver
 1258 abundance, whereas season had a relatively lower contribution to the model (1.31%).
 1259 Response plots showed that elver abundance was positively related to water temperature,
 1260 with the highest abundance occurring at 21 °C (Figure 4.1.6.). In addition, the abundance
 1261 of elvers was significantly affected by season, with a greater abundance being observed
 1262 in spring, and was slightly positively related to the dissolved oxygen content (DO) for
 1263 values > 7 mg L⁻¹. The model validation that was developed showed good predictive
 power ($R^2 = 0.68$, Figure S4.1.1.b).



1264

1265 **Figure 4.1.6.** Generalized additive model (GAM)-derived effect of covariate modeling for the abundance
 1266 (catch per unit effort, CPUE) of elvers. Shaded areas and dashed lines indicate 95% confidence bands; tick
 1267 marks on the x-axes of the depth plots indicate sampling intensity. The y-axis represents the
 1268 partial effect of each variable

1269 **4.1.1.4. Discussions**

1270 The recruitment of juvenile eels in a small estuary on the coast of the Tyrrhenian Sea in
 1271 Sardinia occurred throughout the year, with evident seasonal migration dynamics. The
 1272 period of maximum recruitment for glass eels was between winter and early spring, with
 1273 peaks from January to March, matching the findings of previous studies conducted in
 1274 estuaries along the Atlantic coast of south-western Europe and in the Mediterranean Sea
 1275 (Gandolfi et al., 1984; Ciccotti et al., 1995; Zompola et al., 2008; Arribas et al., 2012;
 1276 Aranburu et al., 2016; Aschonitis et al., 2017). My findings also confirmed the results of
 1277 previous studies conducted in Sardinia, which reported maximum concentrations of glass
 1278 eels during the first few months of the year (Cau et al., 1982).

1279 The TL of glass eels recorded in the Pramaera estuary ranged from 5.2 to 7.4 cm,
 1280 which is lower than previous data reported for the eastern coast of Sardinia (Flumendosa
 1281 River) (Cau et al., 1982). At a wider geographical scale, data from the Atlantic coast
 1282 confirmed a decrease in TL in association with a decrease in recruitment (Desaunay and
 1283 Guerault, 1997). At a seasonal scale, the differences in mean TL were quite moderate,
 1284 with the lowest values recorded in spring. Similarly, Cau et al. (1982) found that glass

1285 eels that were captured in spring were smaller than those caught in the other seasons.
1286 Previous studies conducted in the European Atlantic and Mediterranean Tyrrhenian coast
1287 reported that glass eels entering the estuary in spring were shorter and lighter than those
1288 arriving in autumn and summer (Gandolfi et al., 1984; Bardonnnet and Riera, 2005).

1289 Recruitment of the elver stage in the Pramaera estuary began in late winter, peaked
1290 sharply in May, and persisted through October, supporting the findings of other studies
1291 conducted in both Mediterranean (Ezzat and El-Serafy, 1977; Gandolfi et al., 1984;
1292 Boëtius and Boëtius, 1989; Leone et al., 2016) and Atlantic estuaries (Naismith and
1293 Knights, 1988). The seasonal occurrence of elvers near the river mouth suggests a
1294 temporary period of residency during their upstream migration, and results in an increase
1295 in abundance and therefore an increase in their catchability. This pattern, which has also
1296 been observed in many previous studies (Naismith and Knights, 1988; Gascuel et al.,
1297 1995; Bardonnnet and Riera, 2005; Laffaille et al., 2007), was confirmed by the fact that
1298 the mean size of elvers in the Pramaera estuary increased from May to October. I
1299 hypothesized a horizontal active movement of the elvers from the river to the estuary
1300 because they are prone to use the sandy area near the river mouth as a foraging ground.

1301 The use of multiple statistical approaches allowed me to identify the importance
1302 of some environmental variables in the recruitment of juvenile eels. Models, which were
1303 based on correlational observations in the field, revealed that water temperature is the
1304 most important factor controlling the abundance of glass eels. Similarly, water
1305 temperature has previously been reported as being one of the most significant predictors
1306 of the periodicity and magnitude of upstream eel migration among the numerous potential
1307 environmental factors (Crivelli et al., 2008; Arribas et al., 2012). Results support the
1308 findings of previous studies that glass eels become inactive and less susceptible to capture
1309 when the water temperature drops below a threshold of 10–12 °C (Gascuel, 1986; Edeline
1310 et al., 2006); however, the active migration of glass eels was associated with temperatures
1311 of 12.3–14.5 °C, which were often recorded during the winter season (12 ± 0.15 °C), and
1312 this was statistically confirmed by the model.

1313 The conspicuous abundance of glass eels was predicted to be associated with the
1314 open river mouth condition. Sardinian rivers tend to represent intermittently estuarine
1315 systems as a result of the large water-level fluctuations that are caused by summer drought
1316 conditions (Sabatini et al., 2011, 2018). Such estuaries are closed off from the sea for

1317 varying periods by a sandbar that develops at the mouth when there is little to no water
1318 discharge (Suari et al., 2019). These systems are also subject to rapid changes over short
1319 periods of time during mouth opening and river flooding events, however, which are
1320 generally associated with heavy rainfall. In these types of estuaries, prolonged mouth
1321 closure leads to a cumulative discharge of fresh water, which acts as a lure that guides
1322 glass eel migration (Crivelli et al., 2008). Supporting this, laboratory experiments have
1323 shown that chemical stimuli, such as geosmine, play an important role as inland water
1324 markers that are involved in the orientation of glass eels towards freshwater (Tosi et al.,
1325 1989; Tosi and Sola, 1993). The recruitment of glass eels was also associated with an
1326 increase in the tidal coefficient. Even if the tidal range is extremely reduced in the
1327 Mediterranean Sea in comparison with the Atlantic Ocean, the tides would continue to
1328 move water in and out of the estuary, potentially exerting a strong influence on glass eels,
1329 which might be carried by the tidal currents. This result confirms previous experimental
1330 evidence, indicating that the tidal cycle plays a pivotal role as a migration vector to fresh
1331 water for glass eels (Gandolfi et al., 1984; Ciccotti et al., 1995; Aranburu et al., 2016).
1332 The moon phase also influenced the upstream migration of glass eels in the estuary, with
1333 higher catches being obtained around the time of the waxing moon. An association
1334 between glass eel migration and lunar phases has been widely reported in the literature
1335 (Sorensen and Bianchini, 1986; Leone et al., 2016; Milardi et al., 2018), but this link has
1336 been mainly attributed to the coupled relationship between the moon and the tide (Tesch,
1337 2003). Finally, the results revealed that oxygen concentration, salinity, and rainfall were
1338 not significantly correlated with glass eel abundance in the study area. Other
1339 environmental factors, not investigated in this study, could explain the observed patterns
1340 in glass eel abundance. In this regard, coastal storms from the sea, and wind speed and
1341 direction have been suggested to affect glass eel migration toward the river mouth
1342 (Lecomte-Finiger and Razouls, 1981; Arribas et al., 2012; Leone et al., 2016).

1343 The temperature was also found to be the most important predictor of the
1344 abundance of elvers in the Pramaera estuary, with higher abundances being observed at
1345 temperatures of 14-21 °C, which occur during spring. Seasonal water temperatures are
1346 often considered to influence the movements of elvers in lagoons (Leone et al., 2016),
1347 with most studies arguing that seasonal increases in water temperature are positively
1348 correlated with active swimming, upstream migration, growth, metabolism, and
1349 pigmentation along both the Atlantic and Mediterranean coasts (Ezzat and El-Serafy,
1350 1977; Boëtius and Boëtius, 1989; Edeline et al., 2006). Dissolved oxygen showed

1351 remarkable temporal variability as a result of the combined effects of climatic factors,
1352 anthropogenic activities, and the specific features of the system. Seasonally, the
1353 maximum of dissolved oxygen recorded in spring could be related to the autotrophic
1354 production of oxygen by phytoplankton. Therefore, I hypothesized that the association
1355 with dissolved oxygen for values above 7 mg/L could be interpreted as an indirect effect
1356 related to the greater abundance of elvers during spring rather than an active preference.
1357 On the other hand, the European eel is able to tolerate relatively high levels of hypoxia
1358 (Trischitta et al., 2014), thanks to its ability to use both branchial and cutaneous modes
1359 of respiratory gas exchange (Tesch, 2003).

1360 The present study has provided, for the first time, information on environmental
1361 factors that control juvenile eel recruitment in a small Mediterranean estuary. In this
1362 context, site-specific data represent valuable and robust tools to assess stock status,
1363 especially in data-poor situations, as asserted by ICES (2016a). Analyses suggests that
1364 the seasonal recruitment of European eels at the study site is similar to the patterns seen
1365 along the Atlantic coast of southwestern Europe and the Mediterranean coast.
1366 Furthermore, the model demonstrated that the migration dynamics of juvenile eels are
1367 related to environmental, temporal, and site-specific factors, such as the water
1368 temperature, tidal coefficient, oxygen concentration, moon phase, and river mouth
1369 condition. One key management measure to preserve juvenile eel recruitment in small
1370 Mediterranean watersheds could be to restore the thermal regime through river flow
1371 control. Many of the small estuaries in Sardinia are intermittently and partly closed as a
1372 result of the reduction of natural freshwater flow as a consequence of the presence of
1373 dams and weirs. In this context, many authors have stressed the critical importance of
1374 maintaining natural flow conditions and connectivity between freshwater habitats and the
1375 sea (Moriarty and Dekker, 1997; Lafaille et al., 2005a; ICES, 2011; Ciccotti et al., 2014;
1376 Besson et al., 2016). Therefore, further studies should be carried out to investigate the
1377 role of marine currents on the differences in the fluctuation dynamics of juvenile eels that
1378 are observed between the western and eastern sides of Sardinia (Cau et al., 1982). The
1379 use of Lagrangian models, which are already used to assess other species with pelagic
1380 larval forms in the Sea of Sardinia (Palmas et al., 2017), could represent an important tool
1381 for investigating the dispersion and recruitment of larvae in the Mediterranean Sea. Such
1382 studies will be important not only to understand the recruitment dynamics of European
1383 eels in the Mediterranean Sea but also to predict the time of arrival of glass eels in the
1384 proximity of the estuaries and the development of local management strategies.

1385 **4.1.1.5. Supplementary Materials**

1386 **Table S4.1.1.** Environmental parameters in the Pramaera estuary in different seasons

Season	Water T (°C)	Air T (°C)	Salinity	pH	Dissolved	O ₂ Saturation (%)	Tide Coeff (cm)	Rainfall (mm)
					O ₂ (mg L ⁻¹)			
Winter	12.7 ± 0.15	15.7 ± 0.8	10.6 ± 1.9	7.9 ± 0.14	8.6 ± 0.37	81.4 ± 2.01	76 ± 2.4	2.1 ± 1.3
Spring	18.6 ± 0.84	21.4 ± 0.78	6.1 ± 1.17	7.2 ± 0.04	8.01 ± 0.24	81.1 ± 2.52	79.8 ± 4.58	0.24 ± 0.16
Summer	23.6 ± 0.35	29.8 ± 1.05	6.2 ± 1.14	7.2 ± 0.04	7.8 ± 0.16	75 ± 1.08	85.9 ± 7.39	0.22 ± 0.22
Autumn	17.8 ± 2.02	22.9 ± 2.27	5.6 ± 2.75	7.4 ± 0.15	7.3 ± 0.06	67.8 ± 1.43	83.7 ± 4.4	1.6 ± 1.56

1387

1388 **Table S4.1.2.** AIC and explained deviance for all glass eels model combinations. $s(T)$ is the smooth effect
 1389 associated with water temperature, $s(DO)$ is a smooth effect associated with dissolved oxygen, Tide is the
 1390 tidal coefficient, $s(Rainfall)$ is the smooth effect associated with rainfall, Season represents the four seasons
 1391 of the year, Moon is the moon phase and Mouth denotes the river mouth condition. AIC: Akaike
 1392 Information Criterion; % Deviance: total deviance explained. The best model is highlighted in bold

Component Model	AIC	% Deviance
Glass eels CPUE ~ $s(T)$ + $s(DO)$ + Tide + $s(Rainfall)$ + Season + Moon + Mouth	844.8	64.5
Glass eels CPUE ~ $s(T)$ + Tide + $s(Rainfall)$ + Season + Moon + Mouth	843.6	65.2
Glass eels CPUE ~ $s(T)$ + Tide + Season + Moon + Mouth	842.3	66.1

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1394 **Table S4.1.3.** Summary of each single explanatory variable for the glass eels' best model

Variables	p-value
T	***
Tide	*
Season	***
Moon	*
Mouth	**

1395

1396 **Table S4.1.4.** AIC and explained deviance for all elver model combinations. $s(T)$ is the smooth effect
 1397 associated with water temperature, DO is the dissolved oxygen, Tide is the tidal coefficient, $s(\text{Rainfall})$ is
 1398 the smooth effect associated with rainfall, Season represents the four seasons, Moon is the moon phase and
 1399 Mouth denotes the river mouth condition. AIC: Akaike Information Criterion; % Deviance: total deviance
 1400 explained. The best model is highlighted in bold

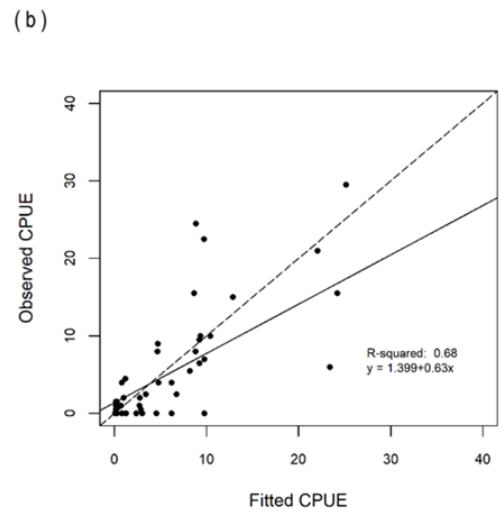
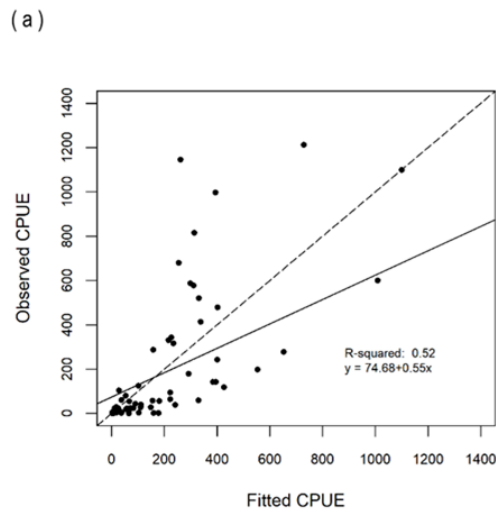
Component Model	AIC	% Deviance
Elvers CPUE ~ $s(T)$ + DO + Tide + $s(\text{Rainfall})$ + Season + Moon + Mouth	278.5	70.9
Elvers CPUE ~ $s(T)$ + DO + Tide + $s(\text{Rainfall})$ + Season + Mouth	274.5	72.3
Elvers CPUE ~ $s(T)$ + DO + $s(\text{Rainfall})$ + Season + Mouth	272.8	73.5
Elvers CPUE ~ $s(T)$ + DO + Season + Mouth	271.5	73.9
Elvers CPUE ~ $s(T)$ + DO + Season	268.9	74.1

1401

1402 **Table S4.1.5.** Summary of each single explanatory variable for the elver best model

Variables	p-value
T	***
DO	*
Season	*

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Figure S4.1.1. Graphical summary of linear regression analyses between observed and predicted abundance of juvenile eel with the generalized additive models (GAMs). **(a)** glass eel and **(b)** elver. The black line represents the linear regressions. The dashed line represents the 1:1 unbiased relationship between observed and predicted values

1409 ***4.1.2. Inter-annual and month-to-month variations of glass eels’***
1410 ***recruitment within and among estuaries in the central-***
1411 ***western Mediterranean***

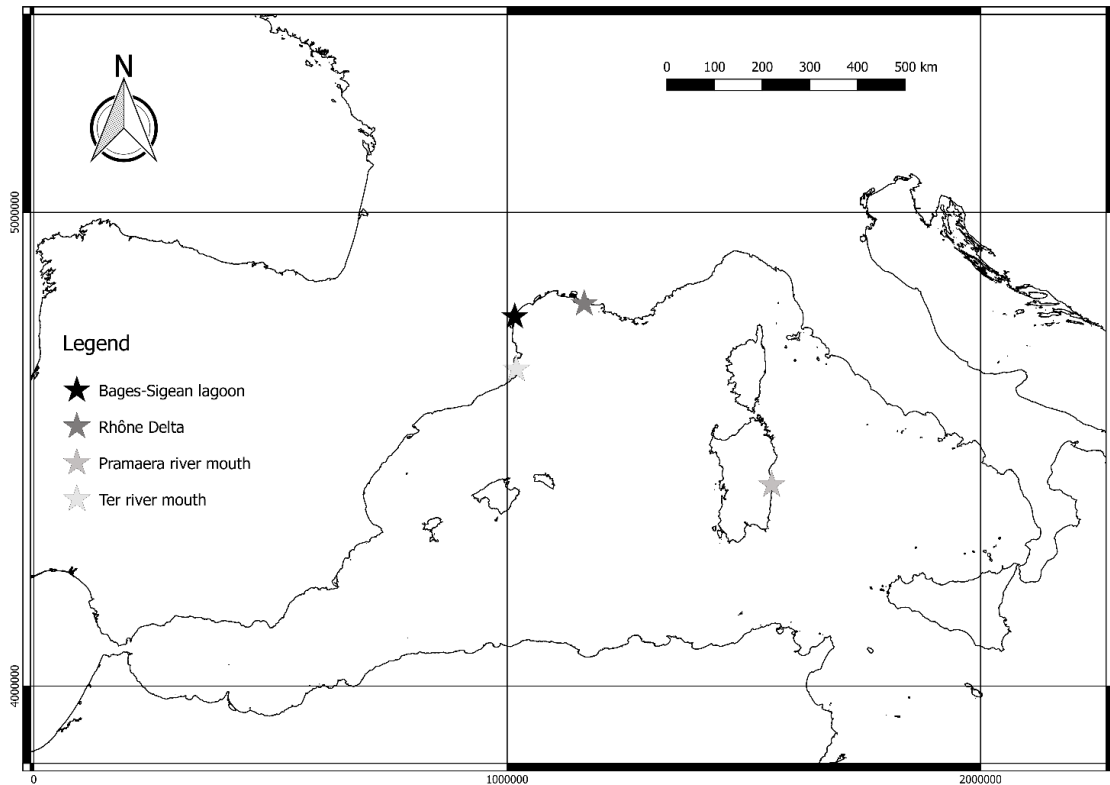
1412 Glass eels’ migration timing varies among estuaries, with peaks occurring at different
1413 times (Gascuel et al., 1995; Briand et al., 2003, 2019; Laffaille et al., 2007; Arribas et al.,
1414 2012; Harrison et al., 2014), even though glass eels’ recruitment happens all the year.
1415 Previous studies provided that, eels’ migration peaks have different timings across
1416 different Mediterranean estuaries, making it difficult to identify recurrent temporal and
1417 geographical patterns of distribution and abundance (ICES, 2020b), and it is known that
1418 these differences are related to latitudinal gradients and local environmental conditions
1419 (Lecomte-Finiger, 1981; Bolliet et al., 2007; Harrison et al., 2014; Cresci, 2020; Podda
1420 et al., 2020a).

1421 In this study, I investigated glass eels’ recruitment in four estuaries located in the
1422 central-western Mediterranean. More specifically, I described the recruitment peak
1423 temporal window, and compared biometric variations within and among investigated
1424 areas.

1425 **4.1.2.1. Material and Methods**

1426 ***4.1.2.1.1. Study sites, data collection, and statistics***

1427 Glass eels’ recruitment and biometric data have been collected from four estuarine areas
1428 in the central-western Mediterranean (Figure 4.2.1.): the Bages-Sigean lagoon (Lagarde
1429 et al., 2022) and the Rhône delta (Camargue) (Bouchard et al., 2022) in southern France,
1430 the Pramaera river mouth in the central-east of Sardinia (Italy) (Podda et al., 2020a;
1431 Porceddu et al., 2022), and the Ter river mouth in the south-east of Spain (Zamora and
1432 Costarrosa, 2019).



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Figure 4.2.1. The four studied areas of glass eels' recruitment in the western Mediterranean (grey-scale stars)

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Recruitment data from the Bages-Sigean lagoon were collected from December 2018 to March 2021 through an experimental survey using floating traps. The dataset from the Rhône delta was obtained through experimental samplings from November 2016 to May 2021 using experimental fyke nets (mesh size 1.5 mm). Glass eels' data from the Pramaera river mouth were collected during an experimental fishing campaign from February 2017 to May 2021. Samplings were made using experimental fyke nets (mesh size 2 mm). No data were collected in November 2017, 2019, and 2020. For the Ter river mouth, glass eels' catches were collected from December 2016 to January 2020 by professional fishermen using fyke nets (mesh size 1.5 mm). No catch data were collected between February 2017 to March 2019 and from February 2020 to March 2021. In addition, biometric data were also collected during experimental surveys from November 2018 to February 2020.

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The migration of glass eels takes place all year round, but in the Mediterranean, the maximum recruitment season begins in October to end in May of the following year, with the maximum peak occurring between November and March (Crivelli et al., 2008; Zompola et al., 2008; ICES, 2020b; Podda et al., 2020a; Lagarde et al., 2021, 2022;

1452 Bouchard et al., 2022). In this study, the analysed data refer to the peak period of
1453 recruitment (from November to March).

1454 For each site, recruitment data correspond to the daily catches in terms of the total
1455 number or total weight of caught glass eels. Average monthly trends of catch data were
1456 qualitatively described for each studied area. Since different tools and sampling protocols
1457 were used, and different units of measurement were applied (some as the total number
1458 and others as the total weight of captured individuals), catch data were not statistically
1459 compared.

1460 For the biometrics study, the total length (TL, mm), the total weight (TW, g), and
1461 the pigmentation stage (Briand, 2009) of glass eels were considered, respectively.
1462 Furthermore, relationships between TL and TW measurements were analysed using
1463 regression analysis (Ricker, 1973, 1975).

1464 For both catches as well as biometrics, the Shapiro test was applied for the
1465 normality assumption. Because the test revealed a non-normality of data (Shapiro test, p
1466 < 0.05), inferential comparisons were performed using the non-parametric Kruskal-
1467 Wallis (K-W) test followed by a multiple comparison post hoc Dunn's (Z) test.
1468 Significance was set at p value < 0.05 . For catches, comparisons were made within each
1469 studied area separately, to investigate statistical interannual differences (the same month
1470 among different years). Biometrics were compared to discriminate differences among the
1471 studied areas (month-to-month of the same year and among the same month of different
1472 years).

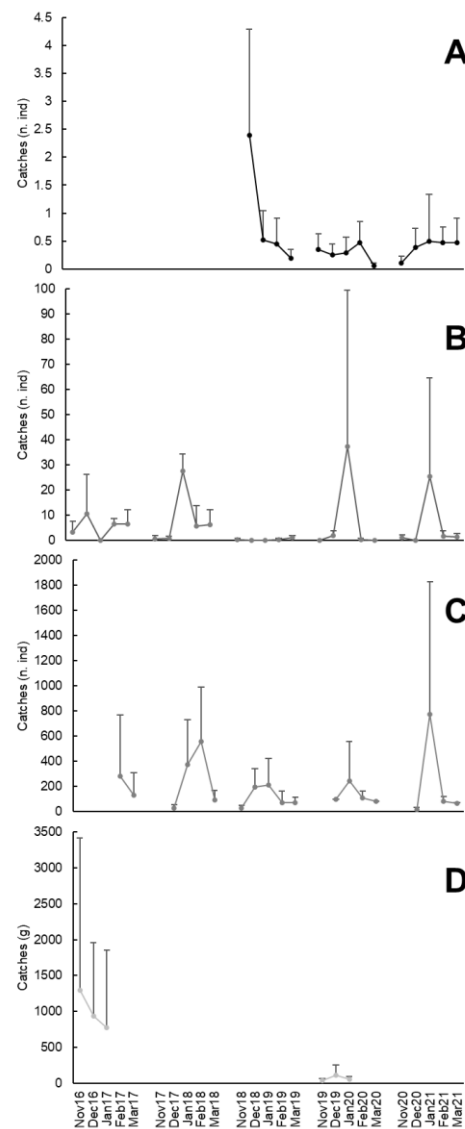
1473 Pigmentation stages were classified according to Briand (2009) and grouped into
1474 three categories (VA, VB, and VIA0 as category I; VIA1, and VIA2 as category II; VIA3,
1475 VIA4, and VIB as category III). Groups were evaluated preliminarily to assess the
1476 contribution of the less pigmented stages (VA, VB, VIA0, VIA1, and VIA2) in proportion
1477 to the most advanced ones (VIA3, VIA4, and VIB). In all study sites, pigmentation stages
1478 between VA to VIA2 represented about the 90% of the proportion of all the stages, and
1479 for this reason also glass eels with the more advanced pigmentation stages, representing
1480 a minority fraction, were included in the analyses. The three pigmentation groups were
1481 compared using the χ^2 test ($p < 0.05$).

1482 Due to the restrictions related to the COVID-19 pandemic, no glass eels' biometrics were available in March 2020 for the Bages-Sigean lagoon, the Pramaera river mouth, and the Ter river mouth, while only four glass eels were sampled in Rhône Delta.

1485 4.1.2.2. Results

1486 4.1.2.2.1. Catch data

1487 For all investigated areas, the maximum mean catches occurred in mid-winter with a peak between December and February, and exhibited site-specific and interannual variability, both between different sites and within the same site (Figure 4.2.2.).



1490

1491 **Figure 4.2.2.** CPUE temporal trend for Bages-Sigean Lagoon (A), Rhône Delta (B), Pramaera river mouth
1492 (C), and Ter river mouth (D)

1493 In Bages-Sigean lagoon significant differences were found among months of
1494 several years of study (K-W = 107.12, $p < 0.0001$). Month-to-month differences (Table
1495 4.2.1.) were identified for December 2018 versus December 2019 and versus December

1496 2020 ($Z = -5.31, p < 0.0001$ and $Z = -4.28, p = 0.0017$) with a higher number of catches
 1497 in 2018, between March 2020 and March 2021 ($Z = 4.55, p < 0.001$), with greater values
 1498 in 2021, and between November 2019 versus November 2020 ($Z = -3.98, p = 0.0062$),
 1499 with higher values in 2019.

1500 In Rhône Delta, catches statistically differed ($K-W = 49.37, p = 0.0017$) only
 1501 between January 2017 and January 2018, whereas in 2017 no catches occurred.

1502 In Pramaera estuary, no differences occurred between the same month of several
 1503 investigated years ($K-W = 47.03, p > 0.05$).

1504 In Ter estuary, statistical differences ($K-W = 27.38, p < 0.0001$) were found
 1505 between December 2016 and December 2019 ($Z = -3.50, p = 0.0070$), with higher catch
 1506 values in 2016 than in 2019.

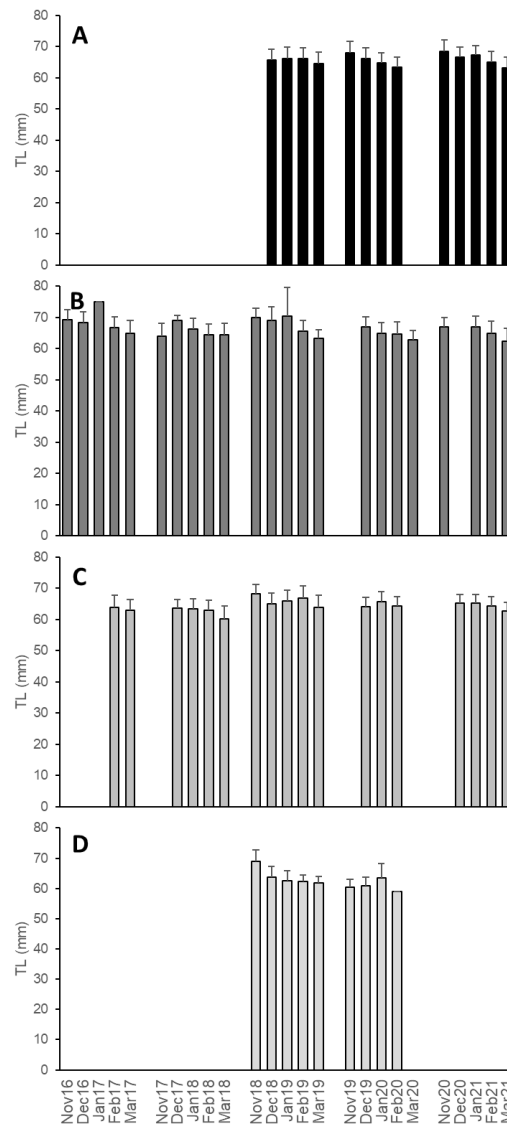
1507 **Table 4.2.1.** Dunn's paired test on catch values within areas between the same month of several studied
 1508 years. Only significant differences are reported

	Months of comparison	p-value	Significance
Bages-Sigean			
$K-W = 107.12, p < 0.0001$	December 2018-December 2019	< 0.0001	****
	December 2018-December 2020	0.0017	**
	March 2020-March 2021	< 0.001	***
	November 2019-November 2020	0.0062	**
Rhône Delta			
$K-W = 49.37, p = 0.0017$	January 2017- January 2018	0.00021	***
Ter			
$K-W = 27.38, p < 0.001$	December 2016-December 2019	0.0070	**

1509 Asterisks indicate the significance code: $p < 0.0001 = ****$; $p < 0.001 = ***$; $p < 0.01 = **$; $p < 0.05 = *$

1510 4.1.2.2.2. *Biometric data*

1511 Biometrics were collected on a total of 7,563 glass eels across the four study sites, of
 1512 which 936 in the Bages-Sigean lagoon, 1,898 in Rhône Delta, 3,421 in the Pramaera river
 1513 mouth, and 1,308 in the Ter river mouth (Figure 4.2.3.).



1514

1515 **Figure 4.2.3.** Total length (TL, mm) monthly median values for all four sampling areas (A: Bages-Sigean
 1516 lagoon; B: Rhône Delta; C: Pramaera river mouth; D: Ter river mouth). Error bars indicate the standard
 1517 deviation for each month

1518 For the Bages-Sigean lagoon, glass eels' TL ranged from 51 to 76 mm (65.3 ± 4.6
 1519 mm), and TW from 0.10 to 44 g (0.23 ± 0.05 g). Maximum TL and TW were observed
 1520 in the first winter months (November-January), while the minimum values occurred in
 1521 March 2019 and 2021.

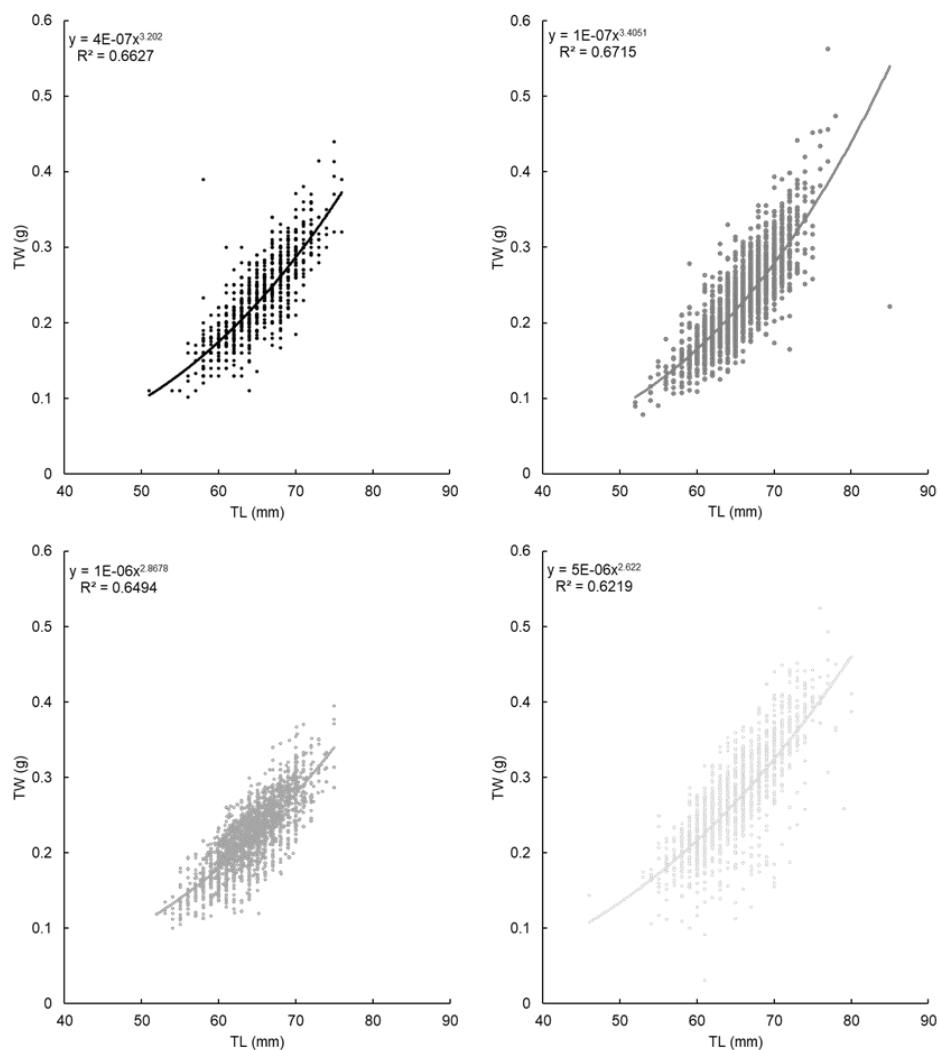
1522 In Rhône Delta, glass eels' TL ranged from 52 to 85 mm (65.7 ± 3.9 mm), while
 1523 TW ranged from 0.07 to 0.56 g (0.23 ± 0.06 g). In this area, the greatest TL and TW were
 1524 observed in the central winter months (January and February), while the smallest ones
 1525 were observed in March 2021.

1526 In the Pramaera river mouth, the TL of glass eels varied from 52 to 75 mm (mean
 1527 \pm standard deviation = 64.2 ± 3.6 mm), and their TW varied from 0.10 to 0.39 g ($0.22 \pm$

1528 0.04 g). The greatest TL and TW were observed in January 2019, while the smallest ones
1529 were in March 2018.

1530 In the Ter river mouth, the TL of glass eels varied from 46 to 80 mm (mean \pm
1531 standard deviation = 65.0 ± 4.8 mm), and their TW varied from 0.03 to 0.52 g ($0.27 \pm$
1532 0.07 g). The greatest TL and TW were observed in November 2018, while the smallest
1533 ones were collected in the months of December.

1534 Because TL and TW were significantly related at each investigated area level
1535 (Figure 4.2.4.) ($R^2 > 0.6$, $p < 0.05$), subsequent analyses of biometrics were performed
1536 considering only the TL as a proxy of glass eels' body size. Furthermore, there was a
1537 positive allometric relationship between TL and TW ($b > 3$) in Bages-Sigean lagoon and
1538 in the Rhône Delta, while negative allometry ($b < 3$) was found in the Pramaera and Ter
1539 river mouths.



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1541 **Figure 4.2.4.** Exponential relationships between total length (TL, mm) and total weight (TW, g) for each
1542 investigated area (top-left: Bages-Sigean lagoon; top-right: Rhône Delta; bottom-left: Pramaera river

1543 mouth; bottom-right: Ter river mouth). In the top-left of each graphic the equation and the R^2 of the
 1544 regression, respectively

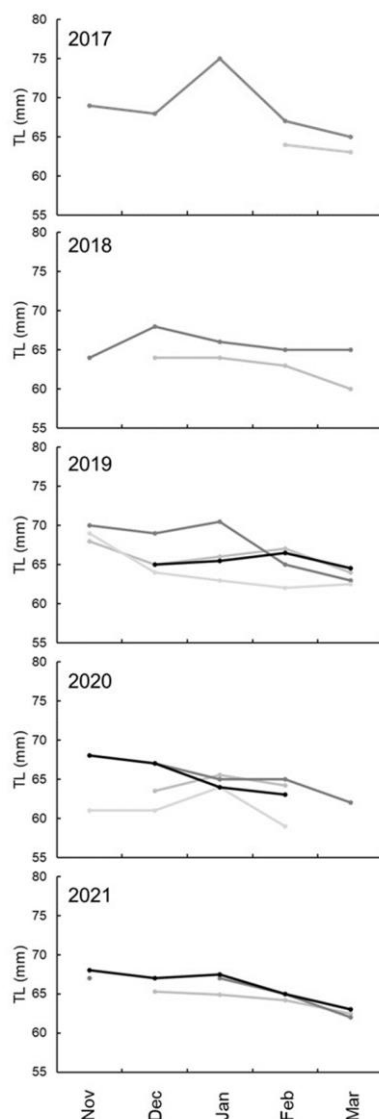
1545 **4.1.2.2.3. TL comparisons within estuaries**

1546 Intra-annual (in the same area) and interannual (among areas) differences in TL were
 1547 observed (Table 4.2.2. and Figure 4.2.5.).

1548 **Table 4.2.2.** Dunn’s paired test on TL values within areas between the same month of several studied years.
 1549 Only significant differences are reported

	Years of comparison	p-value	Significance
November			
Ter	2018-2019	< 0.0001	****
K-W = 54.61 $p < 0.0001$			
December			
Rhône Delta	2018-2019	0.04	*
K-W = 11.39 $p = 0.0098$			
Pramaera	2017-2018	< 0.0001	****
K-W = 62.20 $p < 0.0001$	2017-2020	< 0.0001	****
	Ter	2018-2019	< 0.0001
K-W = 54.61 $p < 0.0001$			
January			
Bages-Sigean	2020-2021	< 0.0001	****
K-W = 19.74 $p < 0.0001$			
Rhône Delta	2018-2020	0.0014	**
	2020-2021	< 0.0001	****
K-W = 31.27 $p < 0.0001$			
Pramaera	2018-2019	< 0.0001	****
	2018-2020	< 0.0001	****
	2018-2021	< 0.0001	****
K-W = 104.57 $p < 0.0001$			
February			
Bages-Sigean	2019-2020	0.0026	**
	2020-2021	0.0021	**
K-W = 17.03 $p < 0.0001$			
Rhône Delta	2017-2018	< 0.0001	****
	2017-2020	< 0.0001	****
	2017-2021	< 0.0001	****
K-W = 44.85 $p < 0.0001$			
Pramaera	2017-2018	0.0088	**
	2017-2019	<0.0001	****
	2018-2019	<0.0001	****
	2018-2020	0.0061	**
	2018-2021	0.0047	**
	2019-2020	<0.0001	****
	2019-2021	<0.0001	****
K-W = 83.52 $p < 0.0001$			
March			
Rhône Delta	2017-2019	0.021	*
	2017-2021	0.005	**
	2018-2021	0.0231	*
K-W = 19.54 $p < 0.0001$			
Pramaera	2017-2018	<0.0001	****
	2017-2019	0.039	*
	2018-2019	<0.0001	****
	2018-2021	0.0012	**
	2019-2021	0.01	*
K-W = 33.21 $p < 0.0001$			

1550 Asterisks indicate the significance code: $p < 0.0001 = ****$; $p < 0.001 = ***$; $p < 0.01 = **$; $p < 0.05 = *$



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Figure 4.2.5. Median TL trends for each investigated year. Dark lines represent Bages-Sigean lagoon, dark gray Rhône Delta, gray Pramaera river mouth, and light gray Ter river mouth

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In November, intra-annual differences were obtained only in the Ter river mouth (K-W = 54.61, $p < 0.05$) with higher median values in 2018 than in 2019.

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In December, significant differences were obtained in Rhône Delta (K-W = 11.39, $p < 0.05$) with higher median TL in 2018 than in 2019 ($Z = -2.71$, $p = 0.04$). In the Pramaera river mouth (K-W = 62.20, $p < 0.05$) significantly smaller TL median values were found in 2017 than in 2018 and 2020 ($Z = 4.55$ and 4.80 , $p < 0.0001$). In the Ter river mouth, significantly higher TL mean values were found in 2018 than in 2019 (K-W = 64.93, $p < 0.05$; $Z = -8.06$, $p < 0.0001$).

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In January, for Bages-Sigean lagoon, differences (K-W = 19.74, $p < 0.05$) were found only between January 2020 and 2021 ($Z = 4.44$, $p < 0.0001$), with lower median TL in 2020. In Rhône Delta, median TL was statistically different (K-W = 31.27, $p <$

1565 0.05) in 2020 compared to 2018 ($Z = -3.80$, $p = 0.0014$) and 2021 ($Z = 5.08$, $p < 0.0001$),
1566 showing smaller values in 2020. In the Pramaera river mouth median TL was significantly
1567 lower in 2018 compared to the other years (K-W = 104.57, $p < 0.05$; $Z = 8.52$ for 2018-
1568 2019 comparison, 7.96 for 2018-2020, 5.97 for 2018-2021, $p < 0.0001$).

1569 In Bages-Sigean lagoon, February 2020 was the month with the lowest median
1570 TL values (K-W = 17.03, $p < 0.05$; $Z = -3.33$ for 2019-2020 comparison, 3.39 for 2020-
1571 2021, $p < 0.01$), while, in Rhône Delta, February 2017 turned out to be the month with
1572 the lowest median TL values (K-W = 44.85, $p < 0.05$; $Z = -4.31$ for 2017-2018
1573 comparison, -5.45 for 2017-2020, -4.73 for 2017-2021, $p < 0.0001$). Median TL was
1574 particularly heterogeneous in February in the Pramaera river mouth (K-W = 83.52, $p <$
1575 0.05), with the lowest values in 2018 ($Z = -3.33$ for 2017-2018 comparison, 9.11 for 2018-
1576 2019, 3.43 for 2018-2020, 3.50 for 2018-2021, $p < 0.01$), and the greatest median values
1577 in 2019 ($Z = 6.12$ for 2017-2019 comparison, 9.11 for 2018-2019, -5.40 for 2019-2020, -
1578 4.74 for 2019-2021, $p < 0.0001$).

1579 Finally, in Rhône Delta, the median TL was lower in March 2021 than in 2017
1580 and 2018 (K-W = 19.54, $p < 0.001$; $Z = -3.48$ for 2017-2021 comparison, -3.05 for 2018-
1581 2021, $p < 0.05$), and March 2017 was slightly higher than 2019 and 2021 ($Z = -3.08$ for
1582 2017-2019 comparison, -3.08 for 2017-2021, $p < 0.05$). March median TL was highly
1583 variable among years in the Pramaera river mouth (K-W = 33.21, $p < 0.05$). March 2019
1584 was the month with the highest TL median values ($Z = 2.72$ for the 2017-2019
1585 comparison, 5.65 for 2018-2019, -3.14 for 2019-2021, $p < 0.05$), and March 2018 was
1586 the lowest one ($Z = -4.64$ for 2017-2018 comparison, 5.65 for 2018-2019, 3.72 for 2018-
1587 2021, $p < 0.05$).

1588 4.1.2.2.4. *TL comparisons among estuaries*

1589 Monthly median TL showed significant differences in all 2017 and 2018 months
1590 investigated between Rhône Delta and the Pramaera river mouth (February and March,
1591 respectively) (K-W: $p < 0.0001$), with significantly larger glass eels in Rhône Delta
1592 (Table 4.2.3). In 2019, 2020, and 2021, great variability was found in December and
1593 January, respectively (K-W: $p < 0.0001$), with the highest median TL in the Rhône Delta
1594 and the lowest one in the Ter river mouth. TL in Bages-Sigean lagoon showed instead
1595 values higher than Pramaera river mouth.

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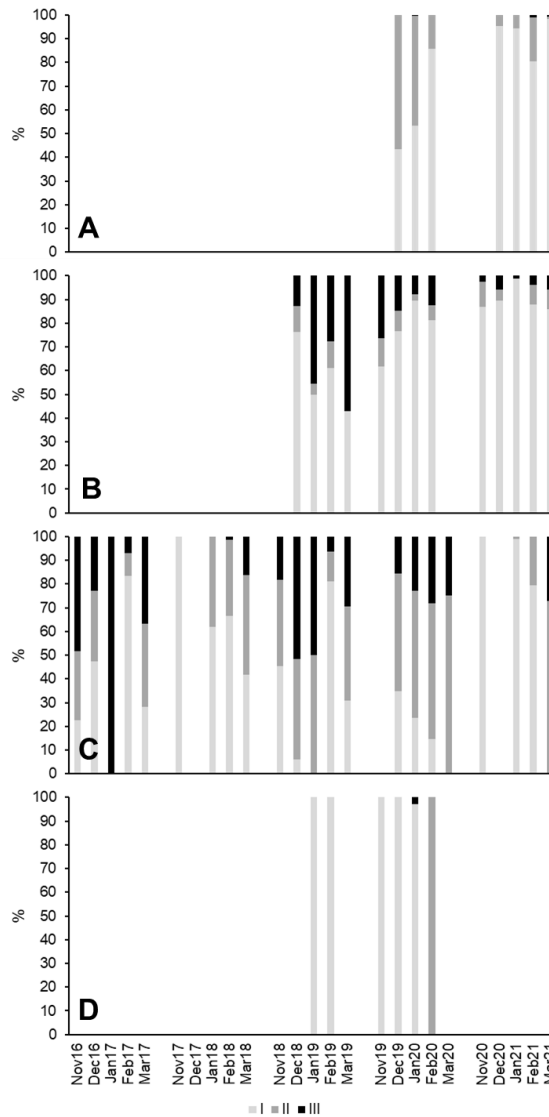
Table 4.2.3. Dunn's paired test on TL values between areas during the same months and years of investigations. Only significant differences are reported

	Sites of comparison	p-value	Significance
2017			
February K-W = 62.2 $p < 0.0001$	Rhône Delta/Pramaera	< 0.0001	****
March K-W = 25.54 $p < 0.0001$	Rhône Delta/Pramaera	< 0.0001	****
2018			
December K-W = 7.44 $p = 0.0064$	Rhône Delta/Pramaera	0.0064	**
January K-W = 93.53 $p < 0.0001$	Rhône Delta/Pramaera	< 0.0001	****
February K-W = 12.62 $p < 0.0001$	Rhône Delta/Pramaera	0.00038	***
March K-W = 32.65 $p < 0.0001$	Rhône Delta/Pramaera	< 0.0001	****
2019			
December K-W = 58.51 $p < 0.0001$	Bages-Sigean/ Rhône Delta	0.0084	**
	Bages-Sigean/Ter	0.0041	*
	Rhône Delta/Pramaera	< 0.0001	****
	Rhône Delta/Ter	< 0.0001	****
January K-W = 98.04 $p < 0.0001$	Pramaera/Ter	< 0.0001	****
	Bages-Sigean/Ter	0.0032	**
2020			
December K-W = 176.43 $p < 0.0001$	Bages-Sigean/Ter	< 0.0001	****
	Rhône Delta/Pramaera	0.0049	**
	Rhône Delta/Ter	< 0.0001	****
	Pramaera/Ter	0.0075	**
January K-W = 24.87 $p < 0.0001$	Pramaera/Ter	< 0.0001	****
February K-W = 12.43 $p = 0.006$	Bages-Sigean/ Rhône Delta	0.01	*
2021			
December K-W = 12.95 $p = 0.00032$	Bages-Sigean/Pramaera	< 0.001	***
January K-W = 24.87 $p < 0.0001$	Bages-Sigean/Pramaera	< 0.0001	****
	Rhône Delta/Pramaera	< 0.0001	****

1598 Asterisks indicate the significance code: $p < 0.0001 = ****$; $p < 0.001 = ***$; $p < 0.01 = **$; $p < 0.05 = *$

1599 **4.1.2.2.5. Pigmentation comparisons**

1600 The pigmentation stages were determined on the same glass eels used for the biometrics
1601 analysis (Figure 4.2.6.). For all investigated areas, the relative percentage of pigmentation
1602 stages (%) was significantly different between years in the same site (χ^2 test, $p < 0.001$),
1603 with the exception of the Ter river mouth (χ^2 test, $p = 0.28$). In all cases, the group I
1604 (stages VA, VB, and VIA0) showed the highest percentages (> 56%), except for the
1605 Rhône Delta where, in 2019 and 2020, the highest percentage was recorded for group II
1606 (37% and 53%, respectively).



1607
 1608 **Figure 4.2.6.** Monthly relative pigmentation percentage (%), according to groupings I, II, and III in the
 1609 Bages-Sigean lagoon (A), in Rhône Delta (B), in the Pramaera river mouth (C), and in the Ter river mouth
 1610 (D)

1611 Comparing the pigmentation stage groupings among different areas in the same
 1612 year of sampling, for 2017 and 2018 data were available only from Rhône Delta, therefore
 1613 no comparisons were made. In 2019, differences between Bages-Sigean, Rhône Delta,
 1614 and Ter (χ^2 test, $p < 0.001$) were found with group I which was predominant in all areas,
 1615 but with the highest percentage in Ter (97%), followed by Bages-Sigean (64%). In 2020,
 1616 pigmentation stages were significantly different among all four areas (χ^2 test, $p < 0.001$),
 1617 with the prevalence of group I and the highest percentage in Ter river mouth (98%),
 1618 followed by Bages-Sigean (77%), and Pramaera river mouth (65%). Last, in 2021,
 1619 differences between Pramaera, Bages-Sigean, and Rhône Delta (χ^2 test, $p < 0.001$) were
 1620 found with group I which was always predominant, but with the highest percentage in the

1621 Pramaera river mouth (93%), followed by Bages-Sigean lagoon (89%), and Rhône Delta
1622 (74%).

1623 **4.1.2.3. Discussions**

1624 To improve the knowledge of the inter and intra-annual variations of the recruitment of
1625 *A. anguilla*, in this study I analysed for the first time, to my best knowledge, the trend of
1626 glass eels' catches and body differences in four different areas in the central-western
1627 Mediterranean (Bages-Sigean lagoon, southwestern France; Rhône delta, southeastern
1628 France; Pramaera river mouth – Sardinia, Italy; Ter river mouth, southeastern Spain) in a
1629 five-years data series (2016-2021). These habitats are located from a minimum of about
1630 110 to a maximum of ca. 650 km distance to each other.

1631 Although it is known that recruitment takes place all year round, I observed the
1632 maximum peak of catches from December to February consistently in all estuaries. This
1633 result confirms previous studies conducted in the Mediterranean (Ciccotti et al., 1995;
1634 Lefebvre et al., 2003; Crivelli et al., 2008; Zompola et al., 2008; Leone et al., 2016; Podda
1635 et al., 2020a; Lanzoni et al., 2021; Bouchard et al., 2022; Lagarde et al., 2022). Despite
1636 the temporal window of the peak was almost contemporary at all investigated areas,
1637 statistical differences were found within each estuary, suggesting that environmental site-
1638 specific features may influence the recruitment dynamics at a local level. However, the
1639 detectable local environmental parameters in the single study areas could merely be a
1640 fictitious representation of the conditions that drive the recruitment. In fact, recruitment
1641 fluctuations could be also the result of several other drivers that act out of the recruitment
1642 area, from the Sargasso Sea to the Mediterranean, for instance in the whole migration area
1643 (e.g., oceanic currents, climate changes, North Atlantic Oscillation index, thermic
1644 gradient, and food availability) (Martin, 1995; Jellymann and Chisnall, 1999; Arribas et
1645 al., 2012; Drouineau et al. 2018; Lagarde et al., 2022; O'Leary et al., 2022). These factors
1646 probably affect the migration of larvae and juvenile eels in the marine phase up to the
1647 proximity of the coasts, consequently also impacting the abundance and body conditions
1648 of the recruits that colonize continental waters. By studying recruitment short-term
1649 variations, it is possible to identify the maximum migration peak, a crucial period for
1650 recruiting. The comparisons of its occurrence intervals among different areas could help
1651 to highlight the used migration paths (Bouchard et al., 2022).

1652 In the Sargasso Sea, leptocephalus larvae (TL about 5 mm) can be observed all
1653 year round, suggesting that the reproduction period of the species is very extensive
1654 (Boëtius and Harding, 1985; Miller et al., 2009, 2015, 2019). However, it is also known
1655 that the maximum reproductive period occurs in spring (Lecomte-Finiger et al., 1993;
1656 McCleave, 1993). The duration of the transoceanic migration lasting about 9-10 months
1657 (Lecomte-Finiger, 1992; Bonhommeau et al., 2008), would be enough to explain the
1658 abundance peaks observed, in this study, in winter. However, since other studies have
1659 argued that the transoceanic migration of glass eels would occur in consecutive waves
1660 (Cantrelle, 1984; Boëtius and Boëtius, 1989; Ciccotti et al., 1995;), further investigations
1661 are needed to make light on eels' migratory paths.

1662 For biometric data, the absolute smallest glass eels were collected in the Ter river
1663 mouth, showing values that were not observed in the other areas, while maximum values
1664 were found in the Rhône delta. Instead, the average size (TL) was similar between the
1665 sites of Spain and France (about 65 mm), while on the coast of Sardinia glass eels' average
1666 sizes were lower (about 64 mm) deepening the existence of spatial and temporal
1667 variability in glass eels' biometrics. Moreover, at a temporal level, the TL always tended
1668 to decrease toward the end of the study period (March), as has already been observed
1669 previously in European coasts (Lefevbre et al., 2003; Jellyman and Lambert, 2003;
1670 Iglesias et al., 2010; Lagarde et al., 2022).

1671 Despite previous studies pointing out that a decrease in less pigmented glass eels
1672 (stages VA, VB, and VIA0) occurs in spring, I showed that glass eels' pigmentation did
1673 not follow consistent patterns, showing ample variability both among areas and in each
1674 area across the years (Lefevbre et al., 2003; Iglesias et al., 2010; Lagarde et al., 2022).
1675 This variability could be linked to the hypothesis that not just one, but several waves of
1676 glass eels colonize European estuaries throughout the year. This indeed would explain
1677 the seasonal evolution of pigmentation in relation to the existence of longer post-
1678 metamorphic marine life for later arrivals during the recruitment season. Furthermore,
1679 this difference in pigmentation stages may be related also to changing pigmentation speed
1680 depending on environmental factors during the month of arrival (Lagarde et al., 2022).
1681 For example, glass eels pigment faster when water temperature increases and salinity
1682 decreases (Briand et al., 2004).

1683 Although no generalized spatial and temporal patterns were found for catches,
1684 biometrics, and pigmentation, this study highlighted the existence of monthly glass eels'
1685 cohorts differently distributed across the western Mediterranean depending on the period
1686 of the year, and among years. This spatio-temporal heterogeneity could be explained by
1687 the geographical position and the local environmental variability of estuaries, as well as
1688 by the marine hydrological conditions that can influence the divergent arrival routes
1689 between the coasts, at the local scale.

1690 Despite the uncontrollable biases associated with the heterogeneity of sampling
1691 areas, the different sampling methodologies, and protocols, I provided here a qualitative
1692 description of the glass eel recruitment patterns in the western Mediterranean. I was
1693 instead able to investigate the temporal variability within each area, revealing the greatest
1694 variability in the Bages-Sigean lagoon, and few or no changes within each of the other
1695 areas.

1696 This study, therefore, highlights the already known fragmentary nature of
1697 knowledge about eels' recruitment in the Mediterranean (Podda et al., 2020) and the need
1698 to standardize protocols and survey methodologies. Besides this, I pointed out the
1699 importance of investigating further other drivers of the temporal (inter- and intra-annual)
1700 fluctuations within and among several Mediterranean areas (e.g., oceanic hydrological
1701 conditions, silver eel escapement) (Rossi et al., 2014; ICES, 2020b).

1702 **4.1.3. Assessment of glass eels' settlement in three Sardinian**
1703 **estuaries (Central-Western Mediterranean) through a new**
1704 **sampling method**

1705 Several monitoring programs for glass eels' recruitment using different methods have
1706 been deployed across Europe since the 1970s (ICES, 2020b). Hand nets, fyke nets, or
1707 trapping ladders are among the most common and effective conventional traps used for
1708 these studies (ICES, 2018a). Projects have also been launched in Sardinia for several
1709 years (starting from 2017) for the monitoring of the eels' recruitment through protocols
1710 based on the use of experimental fyke nets (Podda et al., 2020a).

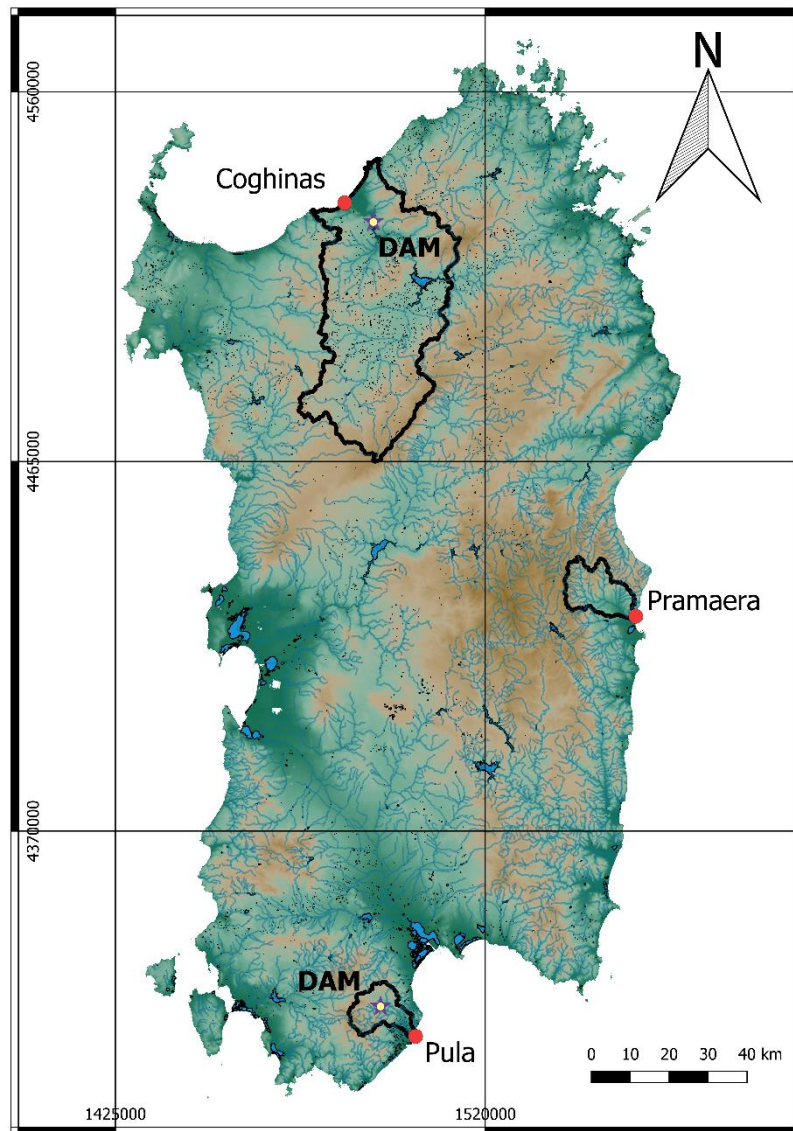
1711 In this context, to further deepen and understand glass eels' recruitment dynamics
1712 in Sardinian estuaries, new floating traps have been tested as an alternative sampling
1713 method to fyke nets. This study was carried out in three Sardinian estuaries with different
1714 local characteristics. The efficiency of floating traps was evaluated compared to fyke net
1715 data, commonly used to study recruitment in Sardinia, as part of the Eel Regional
1716 Management Plan.

1717 **4.1.3.1. Material and Methods**

1718 **4.1.3.1.1. Study area**

1719 Glass eels entering continental waters were sampled using experimental floating traps in
1720 three Sardinian estuaries (Pramaera, Pula, and Coghinas river mouths) (Figure 4.3.1),
1721 located respectively in the central-eastern, southern, and northern areas of the island.
1722 These sites have been chosen, in addition to their geographical position, to be
1723 representative of different hydrological characteristics. Furthermore, two of these
1724 (Pramaera and Coghinas river mouths) are also monitored with experimental fyke nets,
1725 whose glass eels sampling data were used for comparisons between the two tools in the
1726 survey period.

1727 In general, Sardinian rivers are characterized by an intermittent regime with
1728 periods of hot and arid summers alternating with rainy autumn/winter seasons with
1729 extreme rains, irregular flow, and strong seasonal hydrological fluctuations (De Waele et
1730 al., 2010; Sabatini et al., 2018; Palmas et al., 2020; V.V. A.A., 2022).



1731
1732 **Figure 4.3.1.** Study site investigated using floating traps

1733 The Pramaera stream is located in the central-eastern of Sardinia, with an
1734 extension of the drained basin area of about 17 km² and characterized by no fluvial
1735 anthropogenic interruptions. The river mouth is characterized by transitional waters
1736 (mean river width 15 m), and a funnel shape with the substrate largely dominated by sand,
1737 and free from vegetation. Artisanal fishing is carried out to target euryhaline fish species
1738 and particularly eels (Podda et al., 2020a; Porceddu et al., 2022), and glass eels are fished
1739 experimentally with fyke nets since 2017 (Podda et al., 2020a). The Pula stream is located
1740 in southern Sardinia and extends for a basin area of about 12 km². Its river mouth, with a
1741 substrate formed by sand and pebbles, partially retracts in summer due to seasonal
1742 drought. Along its watercourse, there is a dam still under construction (ca. 10 km from
1743 the river mouth) and several concrete fords that interrupt the natural fluvial continuity,
1744 especially in drought periods. There are no professional fishing activities in this area. The

1745 Coghinas river is the third longest Sardinian watercourse, located in the northern part of
1746 the island, it extends for an area of about 170 km². This river is regulated by two dams
1747 and flows into the sea through the river mouth in Valledoria. The dam further downstream
1748 (ca. 16 km distant from the river mouth) has an eel ladder that guarantees river
1749 connectivity. Its river mouth is the largest brackish area of northern Sardinia. The estuarial
1750 portion covers a three-kilometer coastal stretch that runs parallel to the coastline to form
1751 a delta swamp rich in birdlife. The river mouth consists of sand bars and a lack of
1752 vegetation and can extend up to 500 m width. Artisanal and recreational fishing and,
1753 thanks to its naturalistic value, a series of tourist activities are also carried out (V.V. A.A.,
1754 2014). All three estuaries are characterized by the presence of reeds and rushes, which
1755 are typical of the Mediterranean retro-dune environment. Despite some common
1756 characteristics, each estuary shows some peculiarities. In the Pramaera river mouth, the
1757 opening of the mouth is influenced by the natural seasonal hydrological and rainfall
1758 regimes, as well as by storm surges. In the case of the Pula stream and the Coghinas river,
1759 the opening of the river mouth to the sea is influenced not only by the variability of the
1760 hydrological and pluviometric regimes but also by the impulses of freshwater coming
1761 from the dams.

1762 4.1.3.1.2. *Environmental characterization of the three estuaries*

1763 For each sampling site and for each sampling event, environmental data including water
1764 temperature (°C), salinity, conductivity ($\mu\text{S cm}^{-1}$), and dissolved oxygen (mg L^{-1}) were
1765 measured using a multiparameter probe (smarTROLL Multiparameter Handheld, InSitu
1766 Europe, North Moons Moat, Redditch, Worcs. B989ND, United Kingdom). Furthermore,
1767 the tidal coefficient (cm) was calculated as the difference in height between consecutive
1768 high and low tides (Podda et al., 2020a). Turbidity (NTU) was measured by using a
1769 turbidimeter as an implementation of the set of environmental variables collected in the
1770 glass eels sampling protocol, as a result of my previously published work (Podda et al.,
1771 2020a). These environmental parameters were chosen as they are known to be the main
1772 factors influencing the establishment of glass eels in continental habitats (Gandolfi et al.,
1773 1984; Ciccotti et al., 1995; Edeline et al., 2006; Arribas et al., 2012; Aranburu et al., 2016;
1774 Leone et al., 2016; Podda et al., 2020a; Lanzoni et al., 2021; Lagarde et al., 2022). The
1775 monthly average values of these environmental parameters have been reported for each
1776 sampled estuary.

1777 *4.1.3.1.3. Floating trap and sampling method*

1778 Tools I used to sample glass eels in this study were floating traps consisting of ten square
1779 geotextile layers (50 × 50 cm) (MACMAT/Geomat, MACCAFERRI) (Figure 4.3.2),
1780 which can act as floating shelter for ascending juvenile eels (Lagarde et al., 2022). Two
1781 floating traps were installed in each studied estuary and fixed near the riverbanks using a
1782 line of ca. 2.5 m long. To protect the traps from flow turbulence and to detect glass eels
1783 passing, in Pramaera and Pula river mouths, traps were positioned at about 50 meters and
1784 30 meters from the mouth to the sea, respectively. In the Coghinas river mouth, traps were
1785 positioned about 500 meters from the mouth. After placement, but before starting the
1786 experiments, each trap was allowed to acclimate to the environment for about one month
1787 (November 2020).



1788
1789

Figure 4.3.2. Floating traps

1790 Samplings were carried out from December 2020 through May 2021 (6 months).
1791 In each site, traps were inspected once a month (6 times per site), during the new moon
1792 week (known to be the maximum monthly recruitment peak period) (Podda et al., 2020a),
1793 except for the Coghinas river mouth where, for reasons related to the conditions of the
1794 mouth (excessive flow), it was not possible to detect the data in January and March 2021.
1795 Contemporarily, samples were also collected using fyke nets in the Pramaera, and in the
1796 Coghinas rivers (in the Coghinas, samples in January and May 2021 were not collected).

1797 *4.1.3.1.4. Glass eels' catch data*

1798 Captured glass eels were counted, measured (TL, mm), and weighted (TW, g) after
1799 anesthesia by immersion in a bath of clove oil (eugenol dissolved in ethyl alcohol) (Walsh

1800 and Pease, 2002). The pigmentation stages were determined on each specimen according
1801 to Briand (2009) to understand at which pigmentation stage glass eels are preferentially
1802 captured with floating traps, as well as when the floating traps are attractive for the glass
1803 eels after colonizing the estuaries. Subsequently, all glass eels were released at alive in
1804 the same sampling site. Captures of glass eels were expressed as catches per unit effort
1805 (number and total weight of glass eels per trap).

1806 Monthly trends of total catches, obtained with floating traps (monthly trends of
1807 the median number of individuals per unit effort \pm standard deviation, and total weight
1808 per unit effort \pm standard deviation), have been described for each studied estuary and no
1809 statistical comparisons were made because only one sampling day per month was
1810 collected.

1811 *4.1.3.1.5. Glass eels' biometrics, Fulton's condition factor and* 1812 *pigmentation*

1813 Glass eels' biometrics (TL and TW) monthly median values were reported for all estuaries
1814 both for data obtained with floating traps as well as with fyke nets. Furthermore, Fulton's
1815 condition factor was derived ($Fulton = TW TL^{-3} 100$) (Ricker, 1975) to provide insight
1816 into the body condition, nutritional status, and feeding activity of eels (Cone, 1989).

1817 To schematize the results relating to the pigmentation stages, these were grouped
1818 into three categories. Group I from unpigmented or lightly pigmented includes stages VA,
1819 VB, and VIA0, typical of the newly entered glass eels. Group II shows the intermediate
1820 pigmentation and includes the stages VIA1 and VIA2, typical of glass eels that are living
1821 in inland waters since recent times (days or few weeks). Group III includes advanced or
1822 almost fully pigmented stages VIA3, VIA4, and VIB, typical of glass eels that have
1823 colonized inland waters for the longest time (on the order of weeks to a few months). The
1824 percentage frequencies of pigmentation groups (I, II, III) were described monthly for each
1825 investigated site during the study period.

1826 *4.1.3.1.6. Statistical comparisons*

1827 Overall, catch data were statistically compared between sites and for floating traps versus
1828 fyke nets, as well as monthly median biometrics (TL and TW) differences were analysed
1829 between months within each site, among sites in the same month, and with the two
1830 different sampling tools by means of the non-parametric Kruskal-Wallis (K-W) test,

1831 followed by the pairwise post hoc Dunn's (Z) test, after testing the normality of the data
 1832 (Shapiro test, $p < 0.05$). Significance was set at $p < 0.05$.

1833 **4.1.3.2. Results**

1834 *4.1.3.2.1. Environmental characterization of the three estuaries*

1835 Considering environmental parameters (Table 4.3.1), water temperature mean values
 1836 were highest in Pramaera (14.98 ± 3.02 °C), and lowest in the Coghinas river (12.9 ± 3.32
 1837 °C). Salinity and conductivity showed similar mean values in all sites, which correspond
 1838 to freshwater (ca. 0.5). The Pula site showed higher mean turbidity values (2.50 ± 1.79
 1839 NTU). Oxygen showed high values for all three sites (> 8 mg L⁻¹), while the tidal
 1840 coefficients were similar in all three sites (ca. 82-84 cm).

1841 **Table 4.3.1.** Environmental characterization of the three sampling sites obtained by the mean \pm standard
 1842 deviation of each parameter during the investigated period

Environmental Parameter	Pramaera River	Pula River	Coghinas River
Water Temp (°C)	14.98±3.02	15.88±3.03	12.9±3.32
Salinity	0.54±0.34	0.45±0.31	0.47±0.54
Conductivity (µS cm ⁻¹)	831.14±506.23	856.33±608.83	768.53±918.52
Turbidity (NTU)	1.07±0.73	2.5±1.79	-
Dissolved Oxygen (mg L ⁻¹)	8.49±1.16	9.22±2.38	9.7±1.34
Tidal Coefficient (cm)	82.17±4.62	84.17±3.31	84.33±6.15

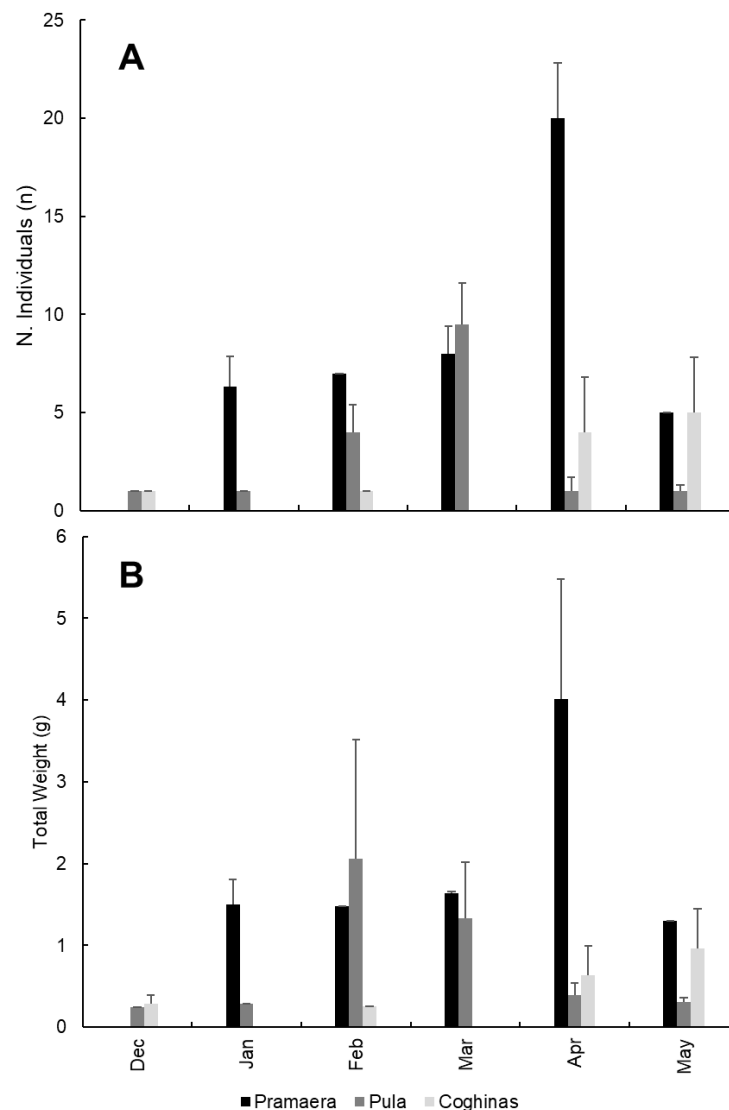
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1844 *4.1.3.2.2. Glass eels' catch data*

1845 A total of 133 glass eels were sampled using floating traps in the three investigated
 1846 Sardinian estuaries during the six months of study (43, 21, and 69 glass eels in Pramaera,
 1847 Pula, and Coghinas river mouths, respectively), with the highest number of total catches
 1848 in the Coghinas river mouth. Overall catch data obtained by using fyke net amounted by
 1849 814 glass eels in the Pramaera river mouth and 71 glass eels in the Coghinas river mouth,
 1850 respectively.

1851 Mean monthly captures with floating traps were higher in April in the Pramaera
 1852 river mouth (20 ± 2.83 individuals, 4.01 ± 1.47 g), in March in the Pula river mouth (9.50
 1853 ± 2.12 individuals, 1.33 ± 0.69 g), and in May in the Coghinas estuary (5 ± 2.83
 1854 individuals, 0.96 ± 0.49 g) (Figure 4.3.3), with variability in mean daily values from 0 to
 1855 20 glass eels per floating trap. A time-shift between sites was also observed, with the peak

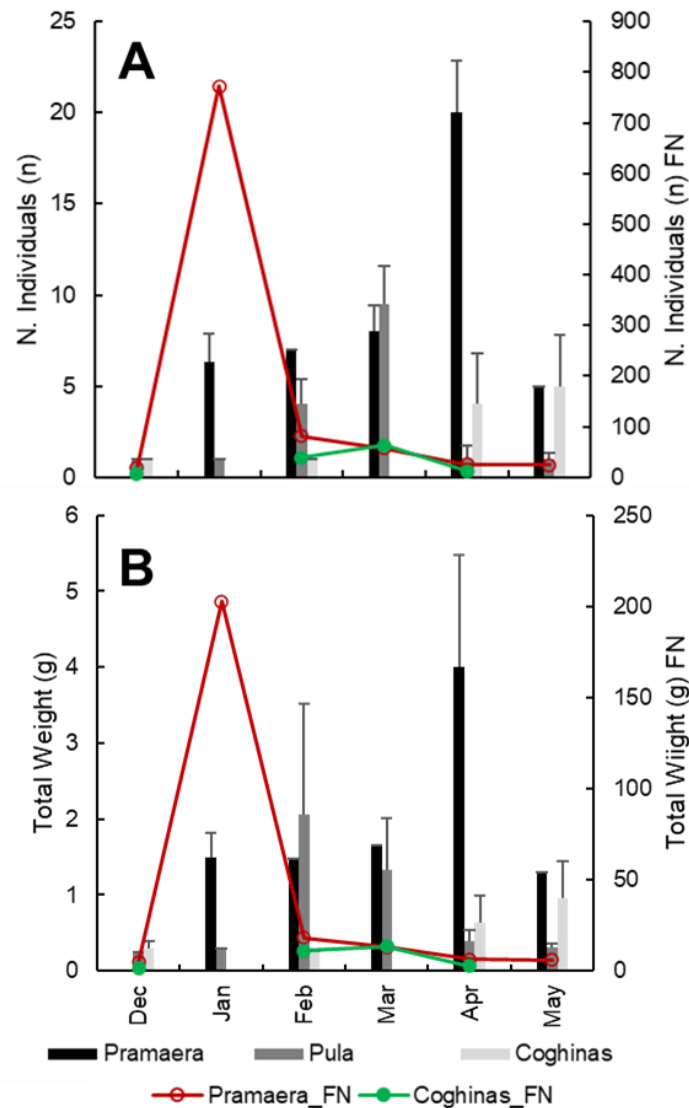
1856 occurring first in Pula, then in Pramaera, and finally in Coghinas according to an apparent
 1857 south-east-north gradient.



1858
 1859 **Figure 4.3.3.** Bars represent the median monthly number of individuals (A) and total weight (B) obtained
 1860 in the three sampling sites using floating traps (dark: Pramaera river mouth; grey: Pula river mouth; light
 1861 grey: Coghinas river mouth). Error bars indicate the standard deviation for each month.

1862 Significant differences in overall catches were also observed among the three river
 1863 mouths and between floating traps and fyke nets, both in terms of total number and total
 1864 weight of sampled glass eels (number of individuals: K-W = 17.36, $p = 0.0016$; total
 1865 weight: K-W = 17.76, $p = 0.0014$). Pairwise comparisons revealed statistical differences
 1866 for catch data obtained between floating traps versus fyke nets within the same site, but
 1867 no differences were observed between data obtained with floating traps among the three
 1868 river mouths (Tables 4.3.2 and 4.3.3). In fact, in Pramaera and Coghinas estuaries, a
 1869 temporal shift was observed between mean monthly catches obtained with floating traps
 1870 and fyke nets, respectively. Using fyke nets the peak occurs two months before the peak

1871 obtained with floating traps for both sites (January in Pramaera, and March in Coghinas
 1872 sites) (Figure 4.3.4).



1873
 1874 **Figure 4.3.4.** Bars represent the median monthly number of individuals (A) and total weight (B) obtained
 1875 in the three sampling sites using floating traps (dark: Pramaera river mouth; grey: Pula river mouth; light
 1876 grey: Coghinas river mouth). Error bars indicate the standard deviation for each month. Red and green lines
 1877 define the median monthly trend of the number of individuals (A) and the total weight (B) obtained with
 1878 fyke nets in the Pramaera and in the Coghinas river mouths

1879 **Table 4.3.2.** Dunn's paired test on catches (number of individuals) values between the three sampling sites
 1880 investigated with floating traps (Pramaera, Pula, and Coghinas) and by using fyke nets (Pramaera and
 1881 Coghinas)

Pairwise sites	<i>p</i> value	Significance
Pramaera-Pula	0.27	Ns
Pramaera-Coghinas	0.32	Ns
Pula-Coghinas	0.99	Ns
Pramaera(Fyke net)-Pramaera	0.019	*
Coghinas(Fyke net)-Coghinas	0.026	*

1882 Asterisks indicate the significance code: $p < 0.0001 = ****$; $p < 0.001 = ***$; $p < 0.01 = **$; $p < 0.05 = *$;
 1883 $p > 0.05 = ns$

1884 **Table 4.3.3.** Dunn’s paired test on catches (total weight) values between the three sampling sites investigated
 1885 with floating traps (Pramaera, Pula, and Coghinas) and by using fyke nets (Pramaera and Coghinas)

Pairwise sites	<i>p</i> value	Significance
Pramaera-Pula	0.39	ns
Pramaera-Coghinas	0.29	ns
Pula-Coghinas	0.77	ns
Pramaera(Fyke net)-Pramaera	0.014	*
Coghinas(Fyke net)-Coghinas	0.016	*

1886 Asterisks indicate the significance code: $p < 0.0001 = ****$; $p < 0.001 = ***$; $p < 0.01 = **$; $p < 0.05 = *$;
 1887 $p > 0.05 = ns$

1888 **4.1.3.2.3. Glass eel’s biometrics**

1889 Glass eels’ biometrics in the Pramaera river mouth ranged in TL from 55.4 to 71 mm,
 1890 while the TW ranged from 0.12 to 0.34 g, with the greatest median TL in February, and
 1891 the greatest median TW in May, the smallest median TL, and TW in March (Tables 4.3.4
 1892 and 4.3.5). No statistical differences among TL were observed (K-W = 3.85, $p = 0.43$)
 1893 (Figure 4.3.5A), instead, statistical differences were observed in TW (K-W = 10.53, $p =$
 1894 0.032) for January versus March, and March and April versus May (Z test, $p < 0.05$)
 1895 (Figure 4.3.5B).

1896 **Table 4.3.4.** Median monthly total length (TL, mm) obtained in the three sampling sites with floating traps
 1897 and by using fyke nets in Pramaera and Coghinas river mouths

Site	December	January	February	March	April	May
Pramaera	0	64.47 ± 2.60	65.99 ± 3.43	62.99 ± 4.08	64.35 ± 2.99	63.65 ± 4.39
Pula	66.0 ± 0	65.90 ± 0	62.63 ± 1.60	62.34 ± 2.72	63.23 ± 4.65	66.40 ± 0
Coghinas	66.0 ± 2.83	NA	63 ± 0	NA	59.25 ± 3.20	62.50 ± 3.57
Pramaera-Fyke net	65.31 ± 2.79	65.32 ± 2.62	64.39 ± 3.05	63.56 ± 2.80	64.61 ± 3.58	64.60 ± 3.67
Coghinas-Fyke net	63.18 ± 4.16	NA	61.55 ± 1.51	61.83 ± 3.03	61.30 ± 3.25	NA

1898 NA = data not available

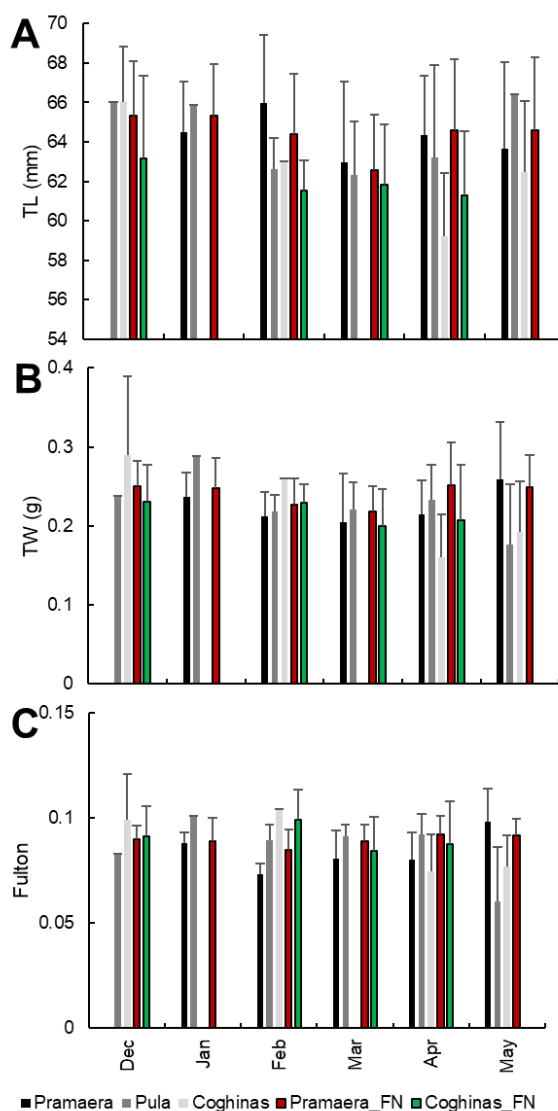
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Table 4.3.5. Median monthly total weight (TW, g) obtained in the three sampling sites with floating traps and by using fyke nets in Pramaera and Coghinas river mouths

Site	December	January	February	March	April	May
Pramaera	0	0.24 ± 0.03	0.21 ± 0.03	0.20 ± 0.06	0.21 ± 0.04	0.26 ± 0.07
Pula	0.24 ± 0	0.29 ± 0	0.22 ± 0.02	0.22 ± 0.03	0.23 ± 0.04	0.18 ± 0.08
Coghinas	0.29 ± 0.10	NA	0.26 ± 0	NA	0.16 ± 0.05	0.19 ± 0.06
Pramaera-Fyke net	0.25 ± 0.03	0.24 ± 0.04	0.23 ± 0.03	0.22 ± 0.03	0.25 ± 0.05	0.25 ± 0.04
Coghinas-Fyke net	0.23 ± 0.04	NA	0.23 ± 0.02	0.20 ± 0.05	0.21 ± 0.07	NA

1901

NA = data not available



1902
1903
1904
1905
1906
1907

Figure 4.3.5. Bars represent the median monthly TL (A), TW (B) and Fulton condition factor (C) obtained in the three sampling sites using floating traps (dark: Pramaera river mouth; grey: Pula river mouth; light grey: Coghinas river mouth) and with fyke nets in the Pramaera and in the Coghinas river mouths (red: Pramaera river mouth; green: Coghinas river mouth). Error bars indicate the standard deviation for each month.

1908
1909

In the Pula river mouth, TL ranged between 55.3 and 68.6 mm, while the minimum TW was 0.12 g, the maximum one was 0.29 g. The highest median TL was in

1910 May, and the median TW in January, with the smallest median values of TL in March,
1911 and TW in May. Comparisons between monthly TL in Pula river mouth showed
1912 differences (K-W = 11.17, $p = 0.048$) for May versus February, March, and April,
1913 respectively (Z test, $p < 0.05$), while no differences were observed for TW comparisons
1914 among sampling data (K-W = 6.75, $p = 0.24$).

1915 The TL of glass eels caught in the Coghinas estuary varied from 55 to 70 mm, and
1916 their TW varied from 0.08 to 0.36 g. The greatest median TL and TW were recorded in
1917 December and the smallest in April. In Coghinas river mouth, no monthly significant
1918 differences were revealed neither in TL (K-W = 6.83, $p = 0.077$) nor in TW (K-W = 5.95,
1919 $p = 0.072$).

1920 Observing biometrics measured using fyke nets, in the Pramaera river mouth the
1921 median values of TL and TW were statistically different (K-W = 101.7, and K-W = 112.
1922 69, $p < 0.0001$) for March versus all the other sampling months (Z test, $p < 0.05$), where
1923 March displayed the lowest values for both TL and TW. TW was statistically different
1924 also in February versus December, January, and May (Z test, $p < 0.05$) that resulted
1925 inferior to the other months. However, the maximum values were recorded in December,
1926 January, April, and May, while the smaller values in March. Finally, data obtained in
1927 Coghinas estuary with fyke nets were not different neither for TL (K-W = 2.06, $p = 0.56$)
1928 nor to TW (K-W = 5.56, $p = 0.135$), with the highest values in December, while the
1929 smallest in February, and April.

1930 4.1.3.2.4. *Biometrics comparisons among estuaries and between floating* 1931 *traps and fyke nets*

1932 Significant differences in TL were observed among estuaries in December (K-W = 8.34,
1933 $p = 0.0395$) between Pramaera and Coghinas for data obtained with fyke nets (Z test, $p =$
1934 0.028) with greater TL values in Pramaera (Figure 4.3.5A), but no differences were
1935 observed for TW data (K-W = 4.70, $p = 0.195$).

1936 In January, no significant differences in TL and TW were observed among
1937 estuaries (K-W = 2.11, $p = 0.348$ and K-W = 3.64, $p = 0.162$, respectively).

1938 In February, TL values obtained with fyke nets statistically differed (K-W = 15.8,
1939 $p = 0.0034$) between Pramaera and Coghinas river mouths (Z test, $p = 0.012$), with higher

1940 values in the Pramaera estuary, while TW values were not different among estuaries (K-
1941 W = 3.00, $p = 0.557$).

1942 In March, no significant differences were found in TL among estuaries (K-W =
1943 1.81, $p = 0.614$), instead significant comparisons were observed for TW (K-W = 12.3, p
1944 = 0.0064) between Pramaera and Coghinas sampling data obtained by using fyke nets (Z
1945 test, $p = 0.017$), and between Pramaera sampling data collected with fyke nets and Pula
1946 river mouth (Z test, $p = 0.014$).

1947 In April, statistical differences were found both for TL and TW data (K-W = 21.1,
1948 $p = 0.0030$ and K-W = 15.3, $p = 0.0042$). Pairwise TL differences were found for
1949 Pramaera (data of fyke nets) versus Coghinas (with floating traps), Pramaera versus
1950 Coghinas, Pramaera (with floating traps) versus Coghinas (with fyke nets) (Z test, $p <$
1951 0.05). Instead, for TW, comparisons resulted significant between Pramaera (with fyke
1952 nets) and Coghinas (with floating traps) (Z test, $p = 0.0043$).

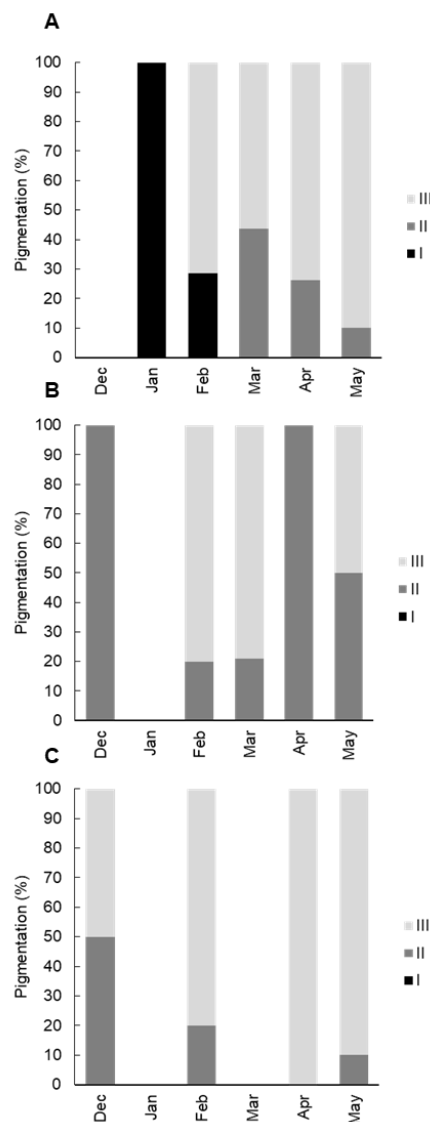
1953 In May, statistical comparisons showed differences only for TW data (K-W =
1954 10.5, $p = 0.015$) between Coghinas (with floating traps) and Pramaera (fyke nets) (Z test,
1955 $p = 0.017$), and between Coghinas and Pramaera for data collected with floating traps (Z
1956 test, $p = 0.031$).

1957 4.1.3.2.5. *Fulton's condition factor and glass eels' pigmentation*

1958 Fulton's condition factor was derived and described for each sampling site (Figure
1959 4.3.5C). The greatest median values were obtained in May in the Pramaera site ($0.098 \pm$
1960 0.015), in January in the Pula site (0.10 ± 0), although on only one glass eel, in February
1961 and in December in the Coghinas river mouth (0.099 ± 0.021 and 0.104 ± 0 , respectively).

1962 Regarding the relative proportions (%) of pigmentation groups, in the Pramaera
1963 estuary the presence of less pigmented glass eels (group I) occurred in December (100%)
1964 and in January (30%) (Figure 4.3.6). Intermediate group II showed higher percentages in
1965 March (45%) to gradually decrease until May (10%), while group III occurred in all
1966 months except in January, with the highest percentages in May (90%). In Pula river
1967 mouth, intermediate group II occurred in all months with 100% in December and April.
1968 Group III showed greater values in February and March, while group I was not detected.
1969 In the Coghinas estuary, greater proportions of group III, representing the more advanced
1970 pigmentation, were observed in all investigated months, with the greatest values in April

1971 (100%) and May (90%). Intermediate group II occurred in December (50%), February
 1972 (20%), and May (less than 10%), while group I, as in Pula river mouth, was not observed.



1973
 1974 **Figure 4.3.6.** Monthly relative pigmentation percentage (%), according to groupings I, II, and III in the
 1975 Pramaera (A), in the Pula (B), and in the Coghinas (C) river mouths

1976 **4.1.3.3. Discussions**

1977 In this study, I evaluated differences in spatial and temporal recruitment of glass eels
 1978 entering three Sardinian estuaries, by using floating traps as an alternative monitoring
 1979 tool. Samplings were conducted for six months during the peak of the recruitment
 1980 migration period (December 2020-May 2021). Spatio-temporal trends of glass eel
 1981 captures were qualitatively different among estuaries, showing site-specific patterns of
 1982 colonization. The peak of captures occurred in March in the Pula river mouth, followed
 1983 by the Pramaera and Coghinas ones, showing an apparent spreading counterclockwise
 1984 gradient south-east-north. Furthermore, Coghinas river mouth revealed the maximum

1985 total number of sampled glass eels than the other two estuaries. This result was different
1986 than those obtained with fyke nets, although placed at the same site and inspected at the
1987 same sampling event which, instead, captured the greatest number of glass eels in the
1988 Pramaera river mouth. In addition, captures obtained with floating traps were
1989 quantitatively reduced and temporally shifted compared to fyke nets, with a peak obtained
1990 with the floating traps occurring two months later the peak obtained with the fyke nets.
1991 This variability between sampling tools could reflect their capture capacity differences,
1992 probably related to the different typologies of the investigated environments which allow
1993 for more efficient capture performance with one tool over the other.

1994 Fyke nets were more efficient and precise in the Pramaera river mouth, a relatively
1995 small and intermittent river, with low flows, reduced depths, and without interruptions
1996 that artificially modify its flow, where I was able to rely on the logistical support and
1997 surveillance of a professional fisherman, concessionaire of the study area. On the other
1998 hand, floating traps showed a more efficient capture power in the Coghinas river mouth,
1999 the third largest watercourse in Sardinia, characterized by particularly high flow rates and
2000 control of the water regime due to the presence of a dam, located few kilometers upstream.
2001 The study area, with little surveillance by fishermen, is also subjected, during periods of
2002 heavy rainfall, to intense releases of fresh water from the dam which make monitoring
2003 with fyke nets impracticable for logistical and safety reasons to the advantage of the
2004 methodology of floating traps. Furthermore, sites with greater flow rates and consequent
2005 greater abundances of eels it is possible that could be detectables only by using floating
2006 traps (Watz et al., 2017).

2007 Biometrics analysis explained differences among sites especially in April and
2008 May, and between Pramaera and Coghinas estuaries, regardless from the sampling
2009 method, but not revealing a clear spatial gradient as the catches. Higher TL and TW were
2010 observed in the Pramaera river mouth, and lower values in the Coghinas river mouth,
2011 respectively, suggesting that larger catches could be likely reflected in smaller sizes and
2012 vice versa. This heterogeneity could be also linked with differences found by analyzing
2013 the stages of pigmentation among estuaries, where the least pigmented glass eels were
2014 found in the Pramaera river mouth, followed by the Pula and the Coghinas river mouths.
2015 However, glass eels captured with floating traps showed more advanced pigmentation
2016 than those captured with fyke nets (personal observations), regardless of the distance from
2017 the river mouth, highlighting the different capture capacity of the two sampling tools.

2018 Environmental characterization of the three estuaries pointed out differences in
2019 the lower average temperature values in the Coghinas river compared to the other two
2020 sites. This data, if associated with the greater capture data observed for this site, could
2021 suggest a potential relationship between the temperature and the abundance of the glass
2022 eels as demonstrated in a recent study (Podda et al., 2020a). It is likely that variations in
2023 environmental conditions around Sardinia such as temperature gradient, wind direction,
2024 and freshwater plume may influence spatially and temporally the glass eels' migration
2025 (Podda et al., 2020a; Lagarde et al., 2022).

2026 Few studies used floating traps as artificial refuge habitats to study glass eels
2027 entering continental waters (Lagarde et al., 2022; Cellule Migrateurs Charente et Seudre,
2028 2014), but only in single sites and through comparisons with electric fishing, not with
2029 parallel fyke nets investigations (in the same site at the same sampling event), as in this
2030 study.

2031 Although floating traps do not allow an estimate of the abundance of glass eels
2032 entering continental waters, they nevertheless provide a clear signal about the dynamics
2033 of eel colonization in these systems. Furthermore, although it has not been demonstrated,
2034 I have been able to observe that, as the floating trap is a passive tool, compared to the
2035 fyke net, this could have a lower impact on the survival of the caught eels which have
2036 always resulted in good visual condition and none never found dead, unlike the fyke net
2037 (personal observations). On this aspect it would be interesting to conduct any future
2038 studies comparing the mortality of the two gears.

2039 Considering this, floating traps can be considered a useful alternative tool
2040 especially in those sites where it is not possible to use the more common and conventional
2041 ones. Moreover, these instruments, easily realizable and at low cost and management, due
2042 to their constructive characteristics, return data that can be easily standardized regardless
2043 of the sampling sites' heterogeneity.

2044 To improve the knowledge on the recruitment of the threatened European eel,
2045 better methods and sampling protocols need to be developed that more efficiently collect
2046 juvenile eels entering continental waters. These first results obtained using floating traps
2047 in parallel with conventional tools will make it possible to develop a protocol proposal
2048 for the monitoring of glass eels in Sardinia as part of the eel regional management plan.

2049 **5. Chapter 5**

2050 **Growth performances of the European eel in Sardinia**

2051 Knowledge on the growth of eels is still limited in Mediterranean continental habitats,
2052 despite their important contribution for the European eel. Studies of individual and
2053 population growth are important for understanding life-history strategies (Brown et al.,
2054 2004), and to support population dynamic studies, stock assessment and management
2055 across the range of habitats used by the species. To my best knowledge, the variation of
2056 European eel growth in Sardinian habitats have never been examined. For these reasons
2057 in Chapter 5 I tried to provide new information on the growth and development of the
2058 European eel in Sardinia through two different approaches developed in the two
2059 Subchapter 5.1 and 5.2, respectively. The first deals the eel growth during an experiment
2060 of restocking by using wild-caught farmed eels for understanding early growth of eels in
2061 captivity and the yellow eel phase adaptation to the wild after restocking. In Subchapter
2062 5.2, I tried to study the eel growth by using the otolith shape analysis of European eel
2063 populations from several rivers and lagoons of Sardinia, and by a case study to estimate
2064 eel's age and growth in a Sardinian stream.

2065 **5.1. Restocking with wild-caught farmed European eels: an**
2066 **alternative approach to understanding eels' early growth in**
2067 **captivity and the yellow eel phase adaptation to the wild**

2068 **5.1.1. Introduction**

2069 Since the 70s of the last century, the European eel, *Anguilla anguilla* (L.), has drastically
2070 declined throughout its distribution range, as a result of multiple natural and
2071 anthropogenic stressors (barriers, habitat loss, pollution, diseases, overfishing, and
2072 changes in oceanic currents) (Dekker, 2003a; Friedland et al., 2007; Belpaire et al., 2009;
2073 Baltazar-Soares et al., 2014; Bevacqua et al., 2015; Aalto et al., 2016; Dekker and
2074 Beaulaton, 2016a; Drouineau et al., 2018a; Podda et al., 2021, 2022; Bourillon et al.,
2075 2022).

2076 According to the International Council for the Exploitation of the Sea (ICES),
2077 because of these threats, the species results outside of its safe biological limits (ICES,
2078 2021, 2022), and it has been classified as Critically Endangered by the International
2079 Union for Conservation of Nature (IUCN) (Pike et al., 2020). Consequently, in 2007, the
2080 Council of the European Union (EU) adopted Regulation n. 1100/2007 (EC, 2007), that
2081 establishes measures for the recovery of European eel stocks with the aim to ensure that
2082 40% of the pristine silver eel biomass (the migratory phase with an advanced maturation
2083 status) can migrate to the sea from each aquatic continental system. In defiance of many
2084 uncertainties, a potential conservation measure of high relevance, to support the recovery
2085 of the eel population, is to restock continental systems, where natural recruitment is scarce
2086 or absent (Moriarty and McCarthy, 1982; Andersson et al., 1991; Wickström et al., 1996;
2087 Pedersen, 1998; Simon and Dörner, 2014; Ovidio et al., 2015). These measures are even
2088 more important given that artificial eel production is still not possible, and therefore to
2089 date, farming and restocking are totally dependent on wild-caught glass eels from waters
2090 with relatively high natural recruitment rates (e.g., Spain, France, Portugal) (Pedersen and
2091 Rasmussen, 2016; Righton et al., 2021).

2092 Starting from 1900, there is a long tradition of eel restocking in Europe (Walter,
2093 1910; Le Clerc, 1935; Wickström, 1984; Moriarty and Dekker, 1997; Feunteun, 2002;
2094 Psuty and Draganik, 2008). Commonly, restocking consists of the capture of natural
2095 recruits (glass eels or juvenile yellow eels) in estuaries, or by using farmed eels for their
2096 redistribution in waters potentially more suitable for both growth and survival (Pedersen,

2097 2000; Feunteun, 2002; Josset et al., 2015; Ovidio et al., 2015; Nzau Matondo et al., 2019).
2098 On-grown eels from aquaculture (farmed eels) are commonly used for restocking
2099 throughout Europe. For instance, Sweden and Finland release glass eels in open waters at
2100 a size of 1.2 g (Wickström and Sjöberg, 2014). In Denmark, eels have been restocked in
2101 rivers, lakes, and estuaries using on-grown glass eels from commercial eel farms to a mass
2102 of 2-6 g (Pedersen et al., 2017), as well as in Germany 5-8 g farmed eels are used (Simon
2103 et al., 2013).

2104 Although restocking can be considered an important conservation measure for the
2105 enhancement of local eel stocks, according to the European Eel Recovery Plan's goals, it
2106 has been rarely scientifically monitored. In fact, it is yet to be shown whether restocking
2107 is an efficient measure to restore the eel stock, allowing to obtain mature individuals able
2108 to successfully contribute to the spawning stock over and above that which would have
2109 been produced without human intervention (Westin, 1998, 2003; Prigge et al., 2013;
2110 Westerberg et al., 2014). Moreover, this practice might offer hope and constitute a
2111 suitable tool for countries with growing eel riverine ecosystems that are distant from the
2112 sea, so that they can contribute to eel sustainability by boosting the number and biomass
2113 of potential spawners, which escape to the sea at the silver eel stage (Brämick et al., 2016;
2114 Nzau Matondo et al., 2020).

2115 Only in recent decades, an increasing number of studies have focused on the
2116 survival, growth, dispersal, and movement of the restocked eels in rivers, marshes,
2117 lagoons, and lakes (Pedersen, 2000; Shiao et al., 2006; Pedersen, 2009; Desprez et al.,
2118 2013; Simon et al., 2013; Simon and Dörner, 2014; Wickström and Sjöberg, 2014; Josset
2119 et al., 2015; Ovidio et al., 2015; Sjöberg et al., 2017; Nzau Matondo et al., 2019). The
2120 variety of restocking environments may contribute to a better understanding the adaptive
2121 capacity of this life stage in different habitats, considering the difficulties in the
2122 implementation of efficient monitoring actions due to the low recapture efficiency.

2123 Several studies on restocking practice have been performed within the same
2124 catchment area at sites located along a longitudinal gradient, and during short time periods
2125 (Desprez et al., 2013; Josset et al., 2015; Kullmann and Thiel, 2018; Félix et al., 2020a,
2126 2020b). In their new environment, the restocked young eels are surviving, dispersing,
2127 growing, and maturing into silver eels that are displaying similar seaward migration
2128 behavior to the naturally recruited wild eels (Pedersen et al., 2017). Such encouraging
2129 outcomes are signs of significant progress in restocking practice knowledge; thus, there

2130 is great hope for inland waters, where the eel stocks are declining (Bisgaard and Pedersen,
2131 1991). Nevertheless, little is known about which procedure is the best for implementing
2132 restocking with maximum survival in inland riverine ecosystems, and how to accurately
2133 assess the level of restocking success in absence of multiple marks and recapture sessions
2134 (Pedersen, 2000; Pedersen, 2009; Desprez et al., 2013; Nzau Matondo et al., 2019). Given
2135 the plasticity of the species to colonize and adapt to a wide range of aquatic ecosystems,
2136 with encouraging outcomes from restocking in inland freshwaters recently reported
2137 (Ovidio et al., 2015; Nzau Matondo et al., 2019, 2020; Félix et al., 2020a, 2020b; Delrez
2138 et al., 2021), this practice sounds interesting to investigate.

2139 To date, no restocking methodology has never been used in small Mediterranean
2140 rivers, including Sardinian ones, for the European eel, least of all by using reared eels,
2141 because glass eels commercial fishing in Sardinia is forbidden.

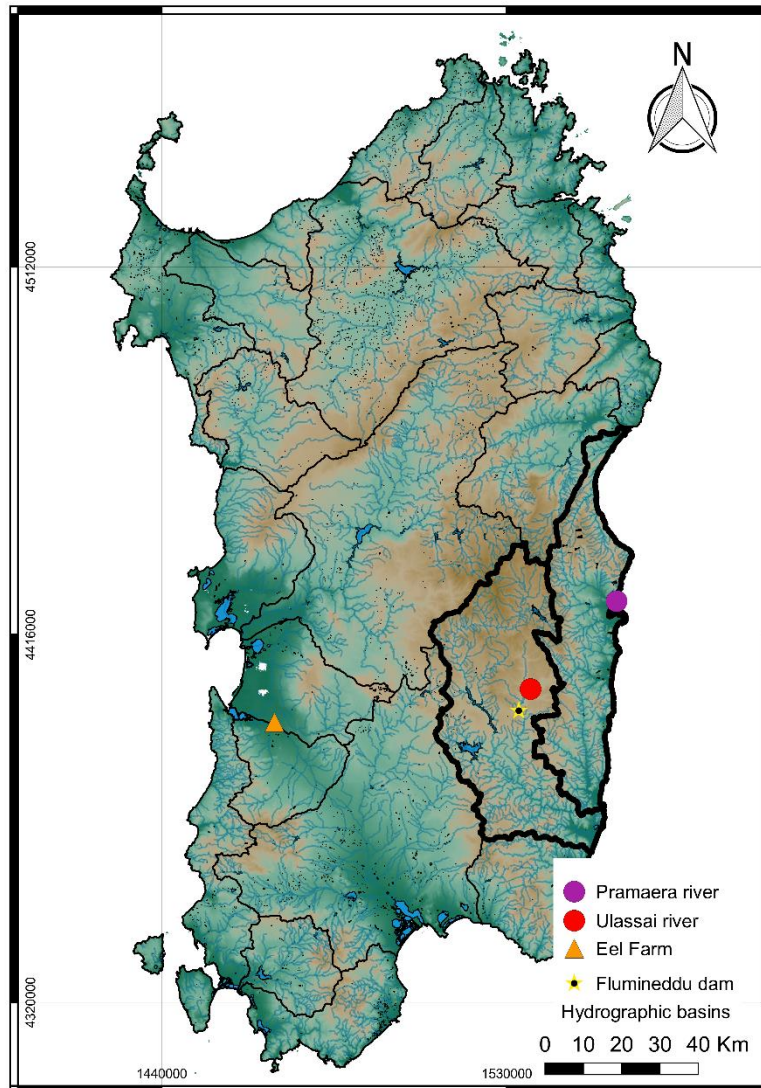
2142 In this study, I investigated the outcomes of a repopulation experiment as an
2143 alternative approach by using glass eels raised for nine months in captivity. I analysed
2144 growth performances during the rearing experiment in an eel farm (Experiment I). Then,
2145 I evaluated the feasibility of restocking practices in a small Mediterranean stream (Ulassai
2146 river) using alternatively yellow eels obtained from farmed wild-caught glass eels
2147 (Experiment II). I also studied demographic data on released marked and unmarked eels,
2148 to examine eels' responses in terms of growth trend in captivity during the rearing phase,
2149 and then in nature after releasing in a 4-years study (2018-2022).

2150 **5.1.2. Material and Methods**

2151 **5.1.2.1. Study area**

2152 Glass eels' catches were carried out in the Pramaera river mouth (central-western
2153 Sardinia), a pilot site where samplings have been underway since 2017, for the study of
2154 the glass eels' recruitment in Sardinia as part of the Regional Eel Plan (Podda et al.,
2155 2020a; Porceddu et al., 2022) (Figure 5.1.1). The Pramaera river is a typical
2156 Mediterranean small watercourse showing a torrential regime and summer dryness
2157 (central-eastern Sardinia). This river does not currently experience fluvial anthropogenic
2158 interruptions (e.g., dams or weirs). The glass eels' capture and releasing area is located
2159 on the stretch of the river near the river mouth, an area characterized by brackish water,
2160 and a mean river width of 15 m. The river mouth has an estuarine typology, with a funnel
2161 shape at the meeting point between freshwaters and marine waters, and it is characterized
2162 by a substrate dominated by sand. Near the river mouth, riverbanks are characterized by

2163 a lack of vegetation, while the area further back is characterized by the presence of reeds
2164 and rushes, typical of the Mediterranean retro-dune environments. Furthermore, the area
2165 is subject to extreme events (floods or sea storms), capable of rapidly altering the
2166 morphology of the estuary. Artisanal fishing is carried out in the freshwater habitat and
2167 in the river mouth using fyke nets and gillnets to target euryhaline fish species (mulletts
2168 and seabass), and mostly eels.



2169
2170 **Figure 5.1.1. - Study area**

2171 Eels were then transferred and reared in an eel farm located in the central western of
2172 Sardinia (Figure 5.1.1).

2173 Reared eels were restocked in the Ulassai river, an eco-Mediterranean
2174 watercourse, belonging to the Flumendosa hydrographic basin, in the central-eastern of
2175 Sardinia (Italy) (Figure 5.1.1). The selected study area extends for about 1.2 km, in a
2176 stretch of an integral fishing reserve, under the concession to a recreational sport fishing

2177 association which contributed to the surveillance of the experimental area. The European
2178 eel, present in the Ulassai river until the 1980s, results locally extinct after the
2179 construction of the Flumineddu dam (1976) (Podda et al., 2022), but, for the
2180 environmental conditions of the watercourse above the dam, it was appropriate to
2181 investigate the restocking of the eel, in a historically and potentially suitable environment.
2182 The river shows a torrential regime, with flowing, well-oxygenated, and good waters
2183 brought all year round (V.V. A.A., 2022). It exhibits bi-seasonal behavior with consistent
2184 drought in summer, and periods of greater flow in winter (V.V. A.A., 2022). From the
2185 geomorphological point of view, the studied stretch results homogeneous and composed
2186 of a rocky calcareous substrate with variable granulometry, with wide and engraved
2187 valleys subjected to occasional alluvial phenomena. It is also characterized by fluvial
2188 vegetation in which predominate oleanders and alders. These waters were once populated
2189 exclusively by salmonids and eels (V.V. A.A., 2022). The current fauna consists of
2190 salmonids (*Salmo trutta* complex), and sporadically, other allochthonous fish species due
2191 to the probable ascent from Flumendosa lake through the tunnel that connects the river
2192 with such a lake. The concerned river stretch is also heavily exploited by poaching, and
2193 in the area close to the watercourse pastoralism is practiced.

2194 **5.1.2.2. *Experiment I: survival and growth in rearing conditions***

2195 In February 2018, during the maximum recruitment peak period (Podda et al., 2020a), a
2196 total of ca. 1450 g of eels (ca. 7400 eels) were caught using experimental fyke nets (2 mm
2197 mesh size) in the Pramaera river mouth. Eels were transferred, through proper life support
2198 systems assuring constant aeration, to an intensive eel farm and reared for 9 months.

2199 Eels were raised in quadrangular concrete tanks (ten thousand liters), with
2200 controlled water parameters (water temperature about 21-25°C, pH between 7 and 8,
2201 salinity less than 0.5, dissolved oxygen greater than 5 mg L⁻¹. Eels were fed with a diet
2202 based on mullet eggs and fish feed according to age. Three nutrition plans were followed:
2203 mullet eggs for the first four months; a mix of mullet eggs and fish feed specific for eel
2204 growing for the subsequent three months; fish feed specific for fish fattening for the last
2205 two months.

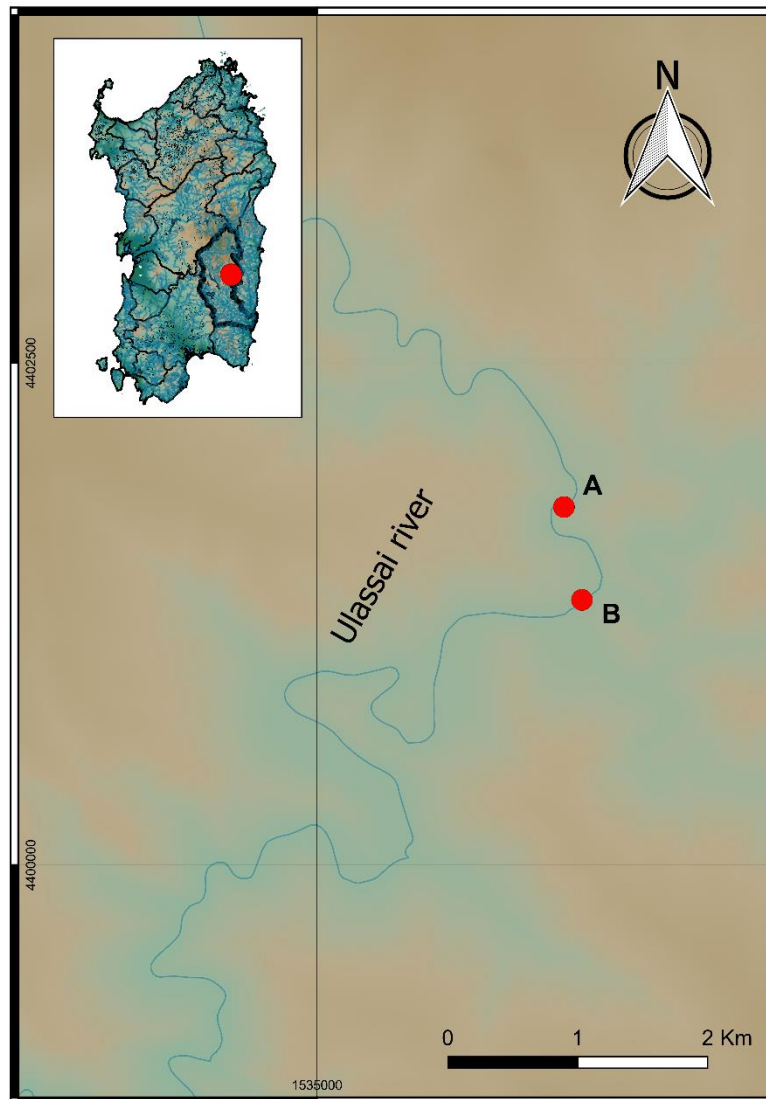
2206 The rearing was conducted from February 2018 to November 2018, where a sub-
2207 sample of 50 specimens was analysed about every two weeks (19 sampling events) to
2208 study the growth performance using the individual total length (TL, cm, to the nearest 0.1
2209 cm), and total weight (TW, g, to the nearest 0.1 g) measurements. Moreover, visual health

2210 status was also evaluated (e.g., parasites, wounds). To avoid stress, before the biometric
2211 measurements, eels were anesthetized with eugenol and then released into the breeding
2212 tank.

2213 In November 2018, after the rearing period a total of 22.25 kg of eels was
2214 obtained. Farmed eels have been subdivided according to their size. Of these, a group of
2215 136 individuals (TL > 20 cm) was selected for the marking which, together with an
2216 unmarked group of 4.5 kg (ca. 850 eels), were released in the river stretch identified in
2217 the Ulassai River. The remaining 10.8 kg (ca. 1050 eels) were released in the Pramaera
2218 river, to return part of the recruitment that had been taken for the rearing phases, with the
2219 sole purpose of increasing the population present in the river.

2220 **5.1.2.3. *Experiment II: marking, restocking, and recapturing in the***
2221 ***Ulassai river***

2222 Each eel with a size greater than 20 cm, selected for marking, was measured (TL),
2223 weighed (TW), and at last tagged with an individually coded PIT tag (Mini HTP10 Pre-
2224 Load Tray). After tagging, eels were acclimatized to the water conditions of the
2225 restocking site before release. Unmarked eels were only measured in terms of TL and
2226 TW. Subsequently, marked and unmarked eels were released in two sites (Site A,
2227 upstream and Site B, downstream) at one km from each other (50% per site) (Figure
2228 5.1.2).



2229
 2230 **Figure 5.1.2.** - Ulassai river stretch with releasing points (Site A and Site B, respectively) where reared
 2231 eels were restocked

2232 Eels' samplings were conducted from 2019 to 2022 (one per year) during the
 2233 summer dry season (June-July), to facilitate the recapture of eels in the km involved in
 2234 the Ulassai river restocking actions. Recaptures were carried out using low-frequency,
 2235 pulsed DC electrofishing. Then, eels were measured (TL), weighed (TW), and scanned
 2236 to identify the presence and to read the code of PIT tags. In addition, morpho-anatomical
 2237 external measurements were made to calculate the silvering index according to Durif et
 2238 al., (2009b) on eels with TL greater than 30 cm, known lower silvering size limit for eels.
 2239 Length of the pectoral fin (FL, mm) was measured from the insertion to the tip of the fin,
 2240 both vertical (Dv, mm) and horizontal (Dh, mm) eye diameters were measured on the left
 2241 eye.

2242 Once measured and eventually identified, eels were released in the same capture
 2243 location. Before biometric measurements and for tagging operations, eels were

2244 anesthetized by immersion in eugenol. Before subsequent procedures, eels were then
2245 placed in containers with well-oxygenated water taken from the restocking site, and after
2246 complete recovery, defined as correct orientation and response to stimuli, were released
2247 in the same sampling site.

2248 **5.1.2.4. Data analysis**

2249 A descriptive analysis was carried out to estimate the average growth trend, in terms of
2250 TL and TW, by using the sub-sample of measured eels during the rearing period
2251 (Experiment I), and on the eels released in Ulassai river (Experiment II) separately for
2252 the two experiments, and distinguishing marked eels from the unmarked ones.

2253 In addition, Fulton's condition factor ($K = TW \cdot TL^{-3} \cdot 100$) (Ricker, 1975) was
2254 calculated for each measured specimen to provide insight into the condition, nutritional
2255 status, and feeding activity of fish (Cone, 1989; Schäperclaus, 1990).

2256 Relationships between TL and TW were identified using regression analysis
2257 (Ricker, 1975), to define the growing typology (isometric or allometric). TL, TW, and
2258 Fulton's condition factor were checked for normality (Shapiro-Wilk's test, S-W, $p <$
2259 0.05). Growing differences (in TL, TW, and Fulton's condition factor) were analyzed
2260 between each measurement (ca. every two weeks) using the nonparametric Kruskal-
2261 Wallis's test (K-W test) to verify the equality of the medians between different
2262 measurements.

2263 The survival rate was estimated at the end of Experiment I, while the average
2264 growth rate and the overall increase in TL and TW were calculated for both experiments
2265 (%). Eels' recapture percentage was estimated at the end of Experiment II for both marked
2266 and unmarked eels, respectively.

2267 All values were expressed as the mean and standard deviation (\pm St. Dev.) unless
2268 otherwise indicated. Significance was set at $p < 0.05$.

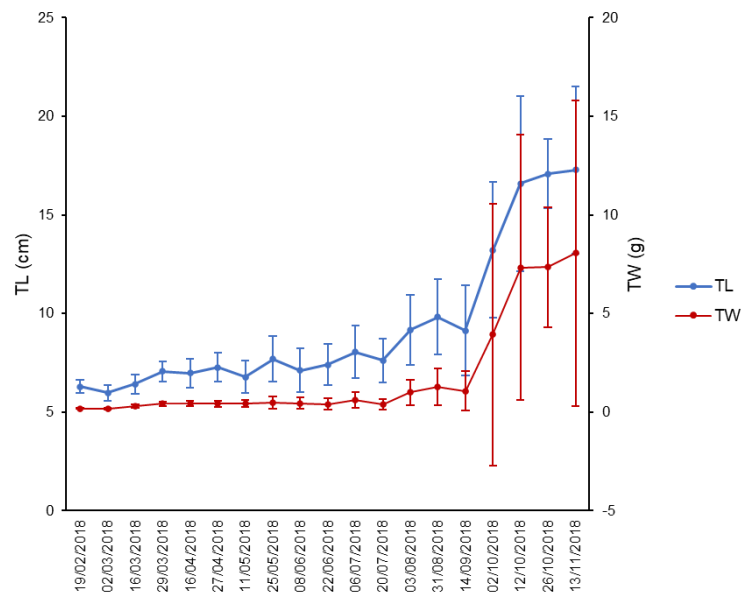
2269 For calculate silvering index on recaptured eels the classification by Durif et al.,
2270 (2009b) was used. It consists of six stages, which represent a growth phase (stages I and
2271 FII), a premigrant stage (FIII), and migrating stages (FIV, FV, MII) for male and female
2272 eels, respectively. Calculation of silvering index was carried out according to the "stacomi
2273 project", an open access bundle (Postgres database, JAVA, R), to treat migration
2274 monitoring information that allows to calculate Durif's stages. Analysis was conducted
2275 by using *stacomiR* package (Legrand and Briand, 2022).

2276 All data were analysed by R (R Core Team, 2021).

2277 5.1.3. Results

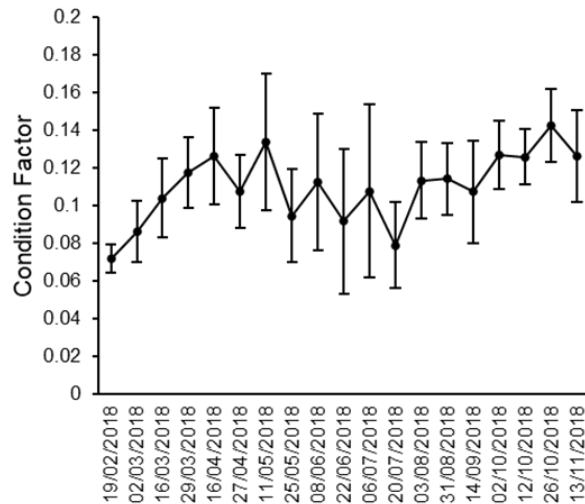
2278 For Experiment I, approximately 7400 glass eels used for breeding showed an average
2279 initial TL of 6.34 ± 0.66 cm, while TW was 0.20 ± 0.24 g, respectively (February 2018).
2280 After nine months of rearing (November 2018), the mean TL was 17.29 ± 4.24 cm, and
2281 the mean TW was 8.06 ± 7.75 g.

2282 In November 2018, at the end of Experiment I, the survival rate amounted to about
2283 28% (ca. 2000 survived eels). Eels' average growth rate amounted to 9.70% for TL, and
2284 244.11% for TW, respectively. The overall increase in TL was about 190%, and TW was
2285 ca. 4380%. The increases in terms of TL, TW, and Fulton's condition factor were
2286 statistically different from initial values versus final values for all three variables (K-W
2287 tests, $p < 0.001$), and with significant increases especially in the last period of rearing
2288 (Figures 5.1.3 and 5.1.4).



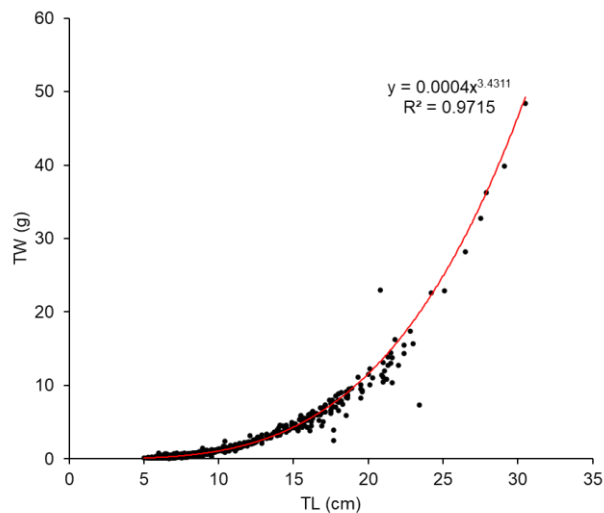
2289
2290

Figure 5.1.3. - Mean TL and TW (\pm standard deviation) trend during the eel-rearing period



2291
2292 **Figure 5.1.4.** - Mean Condition factor (\pm standard deviation) trend during the eel-rearing period

2293 The regression analysis between TL and TW (Figure 5.1.5) showed positive
2294 allometric growth, with a robust correlation between length and weight ($R^2 = 0.9715$).

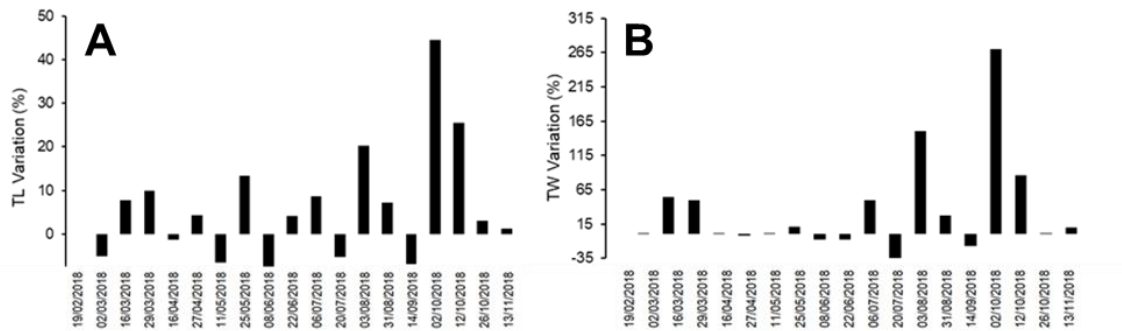


2295
2296 **Figure 5.1.5.** - Regression between TL and TW of farmed eels obtained after the rearing period

2297 After the rearing months, eels were transferred from the farm to the release sites.
2298 A total of 136 eels, size-selected ($TL > 20$ cm) (ca. 6.95 kg) (mean $TL = 31.01 \pm 3.96$ cm,
2299 mean $TW = 51.10 \pm 24.10$ g, mean Fulton's condition factor = 0.16 ± 0.02), were marked
2300 using PIT tag before releasing in the Ulassai river. In the same river, 4.5 kg of unmarked
2301 eels (ca. 850 eels) ($TL < 20$ cm) (mean $TL = 13.7 \pm 5.89$ cm, mean $TW = 5.24 \pm 7.12$ g,
2302 mean Fulton's condition factor = 0.16 ± 0.02) were released.

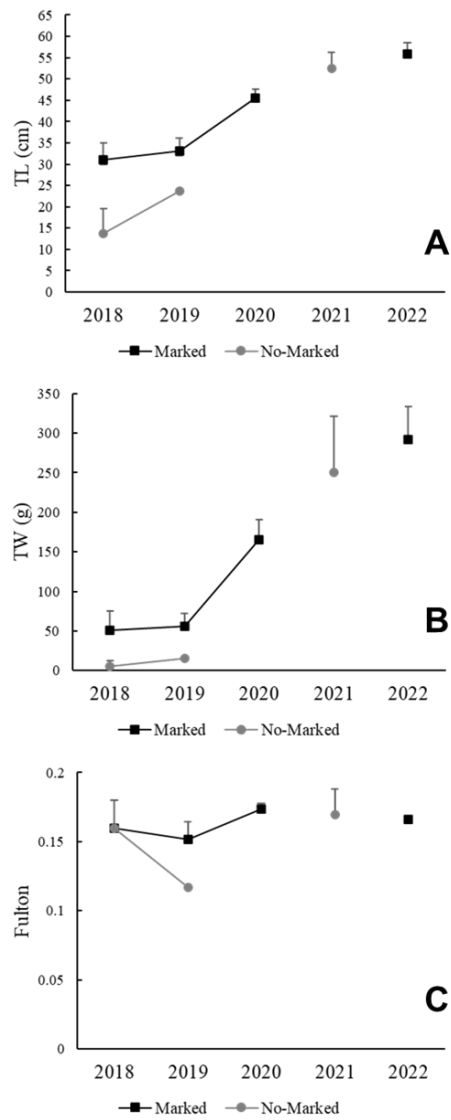
2303 During 4-years of experiments in the Ulassai river, eels were recaptured only in
2304 the Site A, the upper site of the investigated river stretch, while no recaptures were
2305 obtained at the Site B, the more downstream site (Figure 5.1.2).

2306 At the end of Experiment II, the overall recapture rate for marked eels was about
 2307 22% (15 recaptured eels), and for unmarked eels was about 1.65% (7 eels). The overall
 2308 increase for marked eels was 80.4% for TL and ca. 471.4% for TW. The total increase of
 2309 unmarked eel amounted to 282.5% for TL, and 4680% for TW, respectively. Eels’
 2310 average annual growth rate amounted to 20.1% for TL and 117.9% for TW of marked
 2311 eels. While for unmarked eels was 70.6% for TL and 1170% for TW (Figure 5.1.6).



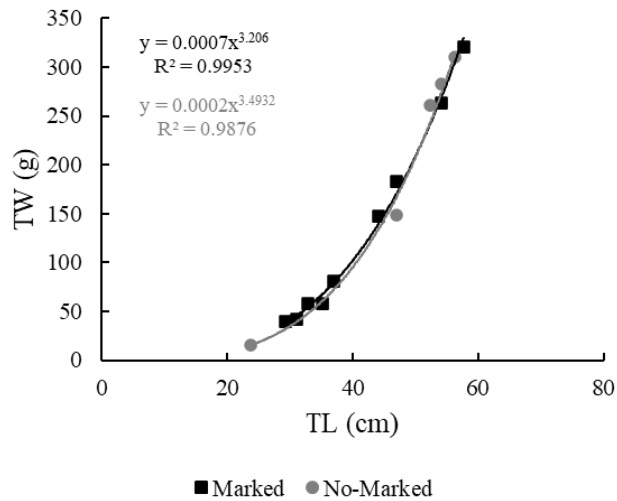
2312 **Figure 5.1.6.** - Eels’ growth rate (%) for TL (A), and for TW (B)
 2313

2314 Marked eels showed mean TL by 55.95 ± 2.48 cm, mean TW equal to 292 ± 41.15
 2315 g, and the mean Fulton’s condition factor equal to 0.166 ± 0.001 . For unmarked eels mean
 2316 TL was 52.40 ± 3.94 cm, mean TW was 250.46 ± 71.13 g, and mean Fulton coefficient
 2317 was 0.169 ± 0.018 , respectively (Figures 5.1.7A, 5.1.7B, and 5.1.7C). In particular, the
 2318 Fulton condition factor looked similar between the 4-years of study, and between marked
 2319 vs unmarked eels, indicating a state of the body that remained constant over the years of
 2320 investigation.



2321 **Figure 5.1.7.** - Average eels' TL (A), TW (B), and Fulton (C) trends between years for marked (black)
 2322 and unmarked (grey) recaptured eels
 2323

2324 Relationships between TL and TW using the regression analysis (Figure 5.1.8)
 2325 showed positive allometric growth, with a robust correlation between length and weight
 2326 for both recaptured eels' groups ($R^2 = 0.9953$ marked eels; $R^2 = 0.09876$ unmarked eels).

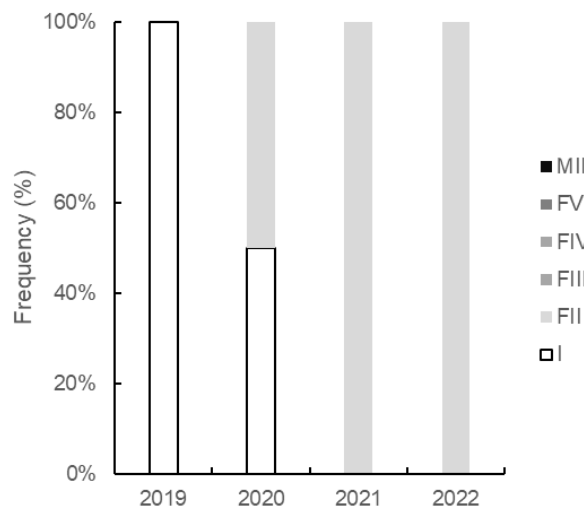


2327
2328
2329

Figure 5.1.8. - Relationships between TL and TW using the regression analysis of marked (black) and unmarked (grey) recaptured eels' groups

2330
2331
2332
2333
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2335

Variations of silvering stages during the restocking experiment were analysed by calculating the silvering index during the different studied years and yearly proportions were calculated showing that eels were classified in two stages I and FII (Figure 5.1.9). Only eels at Stage I occurred in the first year after restocking (2019), in 2020 Stage I and FII occur in 50% of eels recaptured, respectively. In 2021 and 2022 eels were only at Stage FII (100%). Migratory eels (FIV, FV, and MII) were not identified.



2336
2337
2338

Figure 5.1.9 - Proportions of the various stages associated with silvering (I, FII, FIII, FIV, FV, and MII) by years

2339 **5.1.4. Discussions**

2340 This study provides new scientific knowledge for implementing restocking practices by
2341 using reared wild glass eels (Experiment I). After a nine-month experiment, the
2342 demographic trend after their release in a small Mediterranean stream (Rio Ulassai) using

2343 PIT-tagged and unmarked restocked eels was evaluated after four years (2018-2022,
2344 Experiment II).

2345 The total survival rate (approx. 28%) of wild glass eels during the rearing phase
2346 confirmed the known survival rates for Italian eel's stocks (approx. 30%) (Capoccioni et
2347 al., 2017). During this on-growing phase, eels were weaned and fed with specially
2348 formulated food by tripling their length on average and increasing up to forty times in
2349 weight, confirming the rapid growth rates during rearing obtained in previous studies
2350 (e.g., up to 10 times after about 6 months of breeding and up to 70 times after one year)
2351 (Dainys et al., 2017). Farmed eels showed positive allometric growth with significant
2352 increases in Fulton's condition factor (from 0.07 to 0.14), as previously observed
2353 (Pedersen et al., 2017).

2354 After four years of restocking experiment (Experiment II), the length of the eels
2355 has increased between 2 and 12.5 cm per year, with a mean of ca. 6 cm, confirming growth
2356 rates of restocked eels reported in other studies carried out using farmed eels in other
2357 European countries (Bisgaard and Pedersen, 1991; Pedersen et al., 2000; Lin et al., 2007;
2358 Mazel et al., 2013; Simon et al., 2013; Ovidio et al., 2015; Silm et al., 2017; Nzau
2359 Matondo et al., 2019). The variability found in eel growth rates between these studies
2360 may be the result of differences in age and size of the individuals analyzed and growth
2361 assessment methods (otolith increases or capture and recapture experiments), as well as
2362 in the ability to habitat load. Furthermore, most of these studies were conducted in the
2363 short term, addressing the efficiency of repopulations only in terms of growth and survival
2364 performance (Andersson et al., 1991; Bisgaard and Pedersen, 1991; Lin et al., 2007;
2365 Pedersen, 2009; Simon and Dörner, 2014).

2366 There are several issues that have not yet been clarified regarding the duration of
2367 the growth benefits of farmed and restocked eels (White and Knights, 1994). It has been
2368 also speculated that the growth in aquaculture facilities negatively affects the ability to
2369 wean the eel using natural food after the release period (ICES, 2013; Smirnov et al.,
2370 1994). Besides this, the time necessary for restocked eels to recover from stress associated
2371 with transport and introduction to a new water body as well as the time they take to start
2372 feeding are still unknown (Bernotas et al., 2020).

2373 Regardless of the marking, restocked eels showed quite higher Fulton's condition
2374 factor after release than during the farmed phases which remained constant in all four
2375 subsequent years (between 0.15 and 0.16). This result could indicate that conditions for

2376 growth were probably favored by suitable environmental conditions such as water
2377 temperatures and food availability and not negatively affected by PIT tags, especially in
2378 the absence of competition with other already present conspecifics. In addition, Fulton's
2379 values estimated in the present study were also consistent with values obtained previously
2380 (Bisgaard and Pedersen, 1991; Methling et al. 2011; Simon et al., 2013; Bernotas et al.,
2381 2020).

2382 Among restocked eels, the allometric index was higher in marked recaptured eels
2383 than in unmarked ones ($b = 3.4932$ vs $b = 3.206$, respectively), probably due to the
2384 different initial sizes of the two groups. In contrast, the final size, four years after release,
2385 showed similar growth between marked and unmarked individuals. The increase in
2386 length, mass, and the high body condition found after restocking suggest a good
2387 readjustment to the wild environment after captivity, regardless of the starting sizes.
2388 Furthermore, I tried to detect new information on the silvering stages of recaptured eels.
2389 In particular, the released eels showed that, in a Mediterranean riverine habitat, such as
2390 the site of release, they remain undifferentiated (yellow eel stage) in the first two years
2391 after restocking, and that it necessarily takes more than four years, as in this study, to
2392 reach more advanced migratory stages. The recaptured eels were therefore still in a
2393 growth and development phase which will require further investigations in the following
2394 years and the continuation of the study to better understand the dynamics of the silvering
2395 process (time and duration of the metamorphosis).

2396 Although in a new release habitat, these first achievements reflect the absence of
2397 any major influence on the origin and characteristics of reared glass eels and the
2398 experimental period since the European eel comprises a single panmictic population (van
2399 Ginneken and Maes, 2005; Palm et al., 2009; Als et al., 2011; Nzau Matondo et al., 2020).
2400 For this reason, there is no genetic argument against the translocation of eels within their
2401 distribution area or between river basins for restocking purposes (Nzau Matondo et al.,
2402 2020).

2403 Of the recaptured eels, 15 eels owned the PIT tag, while the remaining 7 did not.
2404 The overall recapture rate found in this study for marked eels (ca. 22%) exceeds what is
2405 known in the literature for river ecosystems (18% Feunteun, 2002; 12% Nzau Matondo
2406 et al., 2020). However, unexpected results were found regarding the recapture rates of the
2407 unmarked group (less than 2%). To this discrepancy, I associated the lower mean sizes in
2408 unmarked eels than marked ones and the fact that they were released at significantly

2409 higher densities, conditions which I hypothesized may have affected the survival rates of
2410 this group.

2411 In all cases, all recaptured eels have been found within the river stretch sampled
2412 over the years of study, thus indicating a resident behavior of these animals. It is known
2413 that freshwater habitats increase eel survival because they are generally less risky in terms
2414 of predation (Jonsson and Jonsson, 1993) and competition compared to marine and
2415 brackish ecosystems (Van den Thillart et al., 2004; van Ginneken and Maes, 2005;
2416 Carpentier et al., 2009; Palm et al., 2009; Imbert et al., 2010; Nzau Matondo et al., 2020).
2417 These findings support current evidence that *Anguilla* sp. establishes a resident home
2418 range during the continental life stages (Parker, 1995; Morrison and Secor, 2003). In fact,
2419 it is known that in freshwater environments, restocked eels remain in the vicinity of the
2420 repopulation site (Nzau Matondo et al., 2019). These ecosystems show a good availability
2421 of shelters that provide better burial for increased protection of the eels (Nzau Matondo
2422 et al., 2019; Pedersen, 2000). The choice of two close release points was adopted to
2423 increase precision on the dispersion pattern, as the quantities of restocked eels were quite
2424 limited. The low mobility may also be influenced by the low eel density; however,
2425 obtained recapture outcomes do not include the eels that emigrated outside the monitored
2426 area and were no longer redetected.

2427 Little is known about the behavioral traits of the first movements, the dispersion,
2428 and the choice of the habitat of reared and then repopulated eels. These aspects could be
2429 useful to better understand the adaptation capacity of eels to identify the preferences of
2430 microhabitats in small streams with the final aim to provide useful information to
2431 optimize restocking practices. Determining eel space use in small-stream systems could
2432 therefore be important for understanding eel ecology and ultimately conservation
2433 management in such systems. Information on how they use these habitats is essential to
2434 aid direct conservation strategies.

2435 Through the improved growth performance (the strong link between eel length
2436 and weight, larger eels, positive allometric growth) and the good recapture data of the
2437 eels repopulated in the Ulassai river, I observed that the growing conditions of the eel
2438 were suitable in this river, suggesting the need to identify the most appropriate habitats
2439 (Nzau Matondo et al., 2021) to be implemented for effective eel repopulation operations.
2440 Although the use of farmed eels for restocking requires great resources and effort it could
2441 be profitable for eels' survivorship in new habitats.

2442 This finding also highlighted the importance of the timing of tagging because this
2443 species shows high behavioral plasticity, with strategies such as ‘founder’ and ‘pioneer’
2444 prevailing in the youngest stages (glass eels and elvers) during their first period in rivers
2445 (Feunteun et al., 2003; Laffaille et al., 2005b). Such restocking practices should also be
2446 accompanied by measures such as barrier removal and the use of specific fish passages
2447 to allow the safe downstream migration of silver eels, as well as to improve juvenile
2448 upstream dispersal (Podda et al., 2021, 2022). Eels' dispersion outside present limited
2449 study site probably occurred by swimming with and against the current or through passive
2450 migration caused by flooding rather than for natural mortality (Beaulaton and Castelnaud,
2451 2005; Bureau du Colombier et al., 2009).

2452 Results of this experiment produced encouraging results, although it has requested
2453 considerable effort and resources. However, the efficiency of restocking to counter eel
2454 decline, also in rivers, remains difficult to evaluate, and the implications and potential
2455 benefits caused by restocking are still debated (ICES, 2018b).

2456 **5.2. Otolith shape analysis on European eel populations**
2457 **(*Anguilla anguilla*, L.) from several rivers and lagoons of**
2458 **Sardinia, and eel's age and growth from a Sardinian stream as**
2459 **a study case**

2460 **5.2.1. Introduction**

2461 The European eel (*Anguilla anguilla* L. 1758) is a catadromous, semelparous, and
2462 panmictic bone fish (Tesch, 2003). It shows a unique life cycle that includes two
2463 migrations of ca. 5000 km that the species undertakes from the spawning grounds in the
2464 Sargasso Sea to the European and Northern African coasts (Schmidt, 1923; Dekker,
2465 2003b; Miller et al., 2015; Chang et al., 2020). Leptocephali (larvae) drift across the
2466 Atlantic Ocean and metamorphose into glass eels before entering the continental shelf.
2467 At the glass eel stage, the species colonize continental waters (e.g., rivers, lakes, lagoons),
2468 where it grows and lives from 2 to 20 years as the yellow eel stage. After this period, eels
2469 start to metamorphose into silver eels (mature adults) and return to their spawning
2470 grounds (Tesch, 2003; Van Den Thillart et al., 2004; Trancart et al., 2015; Righton et al.,
2471 2016; Wright et al., 2022).

2472 Despite their remarkable ability to adapt to several aquatic environments, the
2473 species has undergone the synergistic effect of numerous natural and anthropogenic
2474 factors to the point that the European eel strongly declined since 1980 (ICES, 2022). As
2475 consequence, this fishery species (Starkie, 2003) became threatened in European
2476 continental waters, and for this reason, is classified as critically endangered by the
2477 International Union for the Conservation of Nature and Natural Resources (Pike et al.
2478 2020) and protected by the European regulation n. 1100/2007 (EC, 2007).

2479 Because of its complex life cycle and its widespread geographical distribution,
2480 life-history traits result very variably (Vøllestad 1992). Describing population dynamics
2481 is fundamental in stock assessment (Morais and Bellwood, 2018), however, some aspects
2482 remain still not fully documented, and they do not provide a comprehensive overview of
2483 the eel life history parameters at a local scale. Among the possible parameters, age and
2484 growth are important for providing basic information required for population analysis
2485 (Brown et al. 2004). Nevertheless, the eel's body growth can vary highly within the same
2486 sub-population because of interindividual variation, and geographically among different
2487 habitats (Vøllestad 1992; Panfili et al., 1994; Melià et al. 2006; Daverat et al. 2012). In

2488 addition, the species shows a marked sexual dimorphism, with larger females than males
2489 of similar age in terms of body size (Vøllestad 1992; De Leo and Gatto 1995; Daverat et
2490 al. 2012). It is also known that eel growth rates can vary along latitudinal gradients of
2491 some environmental factors (e.g., temperature, photoperiod, hydrology, and productivity)
2492 (Helfman et al., 1987; Vøllestad et al., 1992; Daverat et al., 2006, 2012; Tesch, 2003). To
2493 better investigate fish populations' development variations and age estimation, otoliths
2494 and their morphology as phenotypic markers are widely used (Begg et al., 2005;
2495 Campana, 2005; ICES 2009; Capoccioni et al., 2011).

2496 Otoliths are biomineralized crystalline-organic complexes composed mainly of
2497 calcium carbonate (Aydın, 2006). With a metabolically inert structure, otoliths are less
2498 vulnerable to structural modification and grow under the influence of the environmental
2499 seasonality to which the fish is subjected throughout its life (Campana and Thorrold,
2500 2001; Thorrold et al., 1997; Elsdon et al., 2002; Lecomte-Finiger, 1992). For these
2501 reasons, otoliths can be defined as one of the most useful anatomical structures to study
2502 growth fish (ICES, 2015; Tsukamoto and Nakai, 1998; Limburg et al., 2003) in the
2503 ichthyology field, in ecological studies (Dekker, 2003b; Antunes and Tesch, 1997), in the
2504 fishery biology (Edeline et al., 2005, 2006; Vøllestad, 1992; Bertin, 1956; Van Den
2505 Thillart et al., 2004; Helfman et al., 1987), in the population age structure studies (Tesch,
2506 2003; Daverat et al., 2012), in the fisheries management (Jessop et al., 2004; Krueger and
2507 Oliveira, 1999), and to study adaptations of fish to different environmental conditions.

2508 Although otoliths have a species-specific morphological structure, they may also
2509 exhibit intraspecific changes in shape and size in relation to physiological and
2510 environmental factors (Mille et al., 2015). Otolith morphology can vary between
2511 populations (Morat et al., 2012; Ozpicak et al., 2018) or stocks of the same species (Paul
2512 et al., 2013; Zhao et al., 2018), and within a species depending on sex (Yılmaz et al.,
2513 2014; Başusta and Khan, 2021), diet (Gagliano and McCormick, 2004; Mille et al., 2016),
2514 and ontogeny (Campana, 2004).

2515 Despite its ecological and commercial importance, there are still several aspects
2516 to be studied on the ecology of *A. anguilla* in the Sardinian island and no studies examined
2517 the eels' growth in terms of otolith shape and growth models. To date only one studied
2518 the population dynamics and the eels' growth by using otoliths (Rossi and Cannas, 1984).

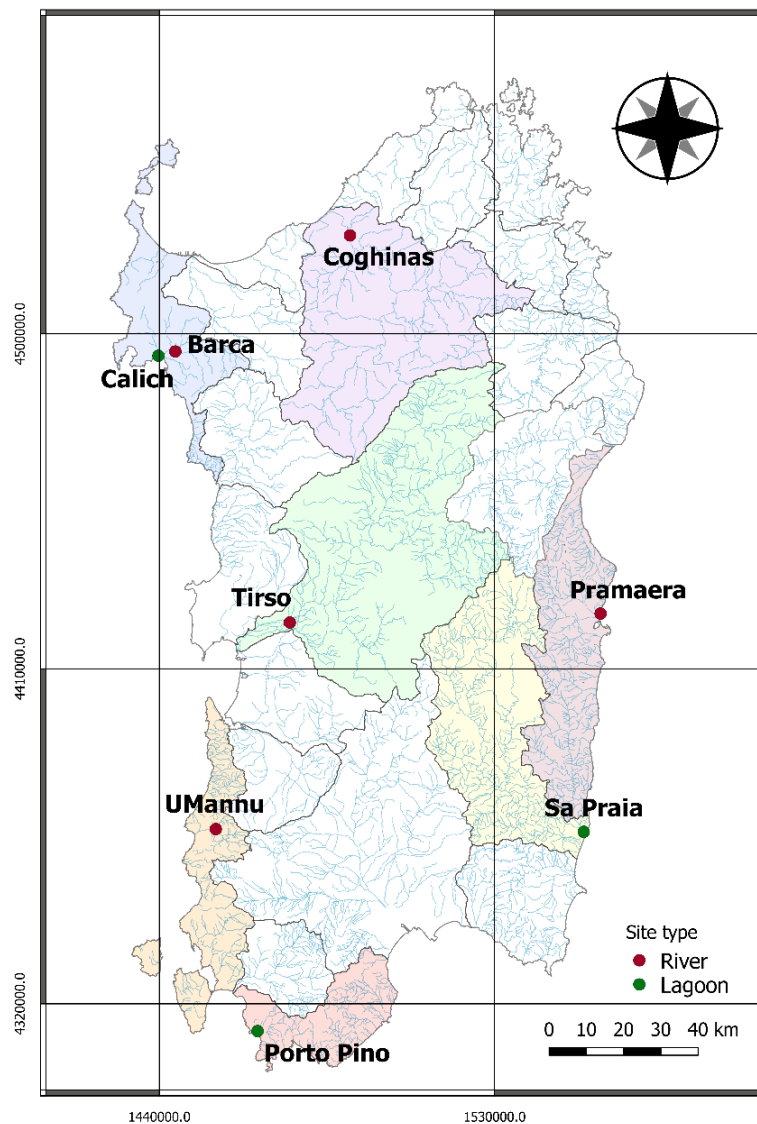
2519 In this study I provided a description of the eel's *sagittae* otoliths with
2520 morphometrical measurements and comparisons through a shape analysis, between

2521 several populations of Sardinian rivers and lagoons. Last, I modeled the growth of eels in
2522 the Pramaera river system, as a case study, trying to investigate intraspecific otolith
2523 variability and modeling its growth at the local scale.

2524 5.2.2. Material and Methods

2525 5.2.2.1. Study locations

2526 Samplings were conducted in five rivers and three lagoons of Sardinia, selected to
2527 representatively cover several geographic areas of the island (Figure 5.2.1).



2528 **Figure 5.2.1.** - Location of the height areas studied within the Sardinian continental waters, (rivers with red
2529 dots, lagoons with green dots)
2530

2531 As for rivers, the regional hydrographic network is characterized by a reduced presence
2532 of perennial streams. Most of the watercourses are torrential streams with a hydrographic
2533 network characterized by high slopes and short downstream sections. In fact, Sardinian
2534 streams often have an ephemeral or intermittent character with periods of hot arid

2535 summers, alternating with rainy autumn/winter seasons, characterized by extreme
2536 precipitation events which can cause strong seasonal hydrological flow fluctuations
2537 (flooding) (De Waele et al., 2010; Sabatini et al., 2018; Palmas et al., 2020; V.V. A.A.,
2538 2022).

2539 The Pramaera river is a typical Mediterranean small watercourse located in the
2540 central-eastern of Sardinia. Its extension area is about 17 km², and no fluvial interruptions
2541 of anthropogenic origin occur (i.e., dams or other anthropogenic barriers) (Podda et al.,
2542 2020a; Porceddu et al., 2022). The Tirso river represents the main watercourse of the
2543 island, with a basin extension of about 189 km² (V.V. A.A., 2022), it rises in the center
2544 of Sardinia and develops from northeast to southwest. Its course differs considerably as
2545 it proceeds from the source to the mouth of the river, differentiating in the upstream part
2546 with a winding path and considerable slopes, to take on a regular appearance in the central
2547 part, up to presenting minimal slopes and large meanders in the downstream section. An
2548 important element is the presence of numerous artificial reservoirs that are relevant from
2549 the point of view of the quantity of invasable water. While, the coastal area has a series
2550 of coastal lagoons, some of which dry up completely in the summer. The Coghinas river
2551 is the third mainstream in Sardinia, it is located in the northern part of the island and
2552 extends for about 170 km². Along its course, the Coghinas river is regulated by two dams
2553 and then flows into the sea in the Asinara Gulf. The Barca river is found in north-western
2554 Sardinia and is a first-order watercourse with an extension area of ca. 33 km², its
2555 downstream trait flows in the Calich lagoon. In the Barca river basin, there are several
2556 reservoirs and the natural lake of Baratz. The Mannu di Fluminimaggiore river (hereafter
2557 UMannu) is located in the southwestern part of Sardinia and is a first-order watercourse
2558 belonging to the Riu Mannu basin. The river, with its winding path, extends for about 12
2559 km².

2560 Sardinian lagoons extend for a total of about 120 km², representing about 10% of
2561 the entire national heritage, and are particularly interesting for their naturalistic value and
2562 their productivity (V.V. A.A., 2010). The Calich lagoon is located on the north-western
2563 coast of Sardinia and has a surface of ca. 0.90 km². It communicates with the sea through
2564 a channel located in the northwestern area of the lagoon. The main tributaries are the
2565 Barca and the Calvia rivers, and the Oruni canal. The continuous tidal flow and the
2566 freshwater inputs result in a very variable brackish condition which results in fishing
2567 yields that do not exceed 50 kg ha⁻¹. The salinity can vary from 5 in the winter season to

2568 38 in summer (V.V. A.A., 2010). The Porto Pino lagoon is located on the southern coast
2569 of Sardinia, with an extension of about 0.25 km², consists of a series of small basins (Porto
2570 Pino, Maestrале, Is Brebeis, Foxi, and Corvo) in communication with each other and used
2571 as tanks pre-evaporating from the saline. The salinity can vary from the marine values
2572 (ca. 37) and can increase up to 50 (Rossi and Cannas, 1984). In this lagoon, a good
2573 integration has been achieved between salt production and fishing activities through the
2574 management of the bulkheads with which the water flow is regulated. The fishing activity
2575 is carried out using artisanal gill nets, pots, and fyke nets. The Sa Praia lagoon is located
2576 on the southeastern coast of Sardinia and extends for about 0.86 km². It is provisioned by
2577 the Gironi river and is connected to the sea by a canal on which a traditional downstream
2578 trap called “lavoriero” is positioned. The salinity ranges from 22.3 to 39.3 (Fish Products
2579 Service of Agricultural Research Agency of Sardinia, Agris).

2580 **5.2.2.2. *Eel's samples***

2581 Eels were collected between June 2015 and February 2020. In the Pramaera and Coghinas
2582 rivers, eels were collected through experimental fyke nets (2 mm mesh size), while in
2583 Tirso, Barca, and UMannu rivers fish were captured using low-frequency, pulsed DC
2584 electrofishing. Lastly, in Calich, Porto Pino, and Sa Praia lagoons, eels were caught with
2585 fyke nets (10 mm mesh size).

2586 All caught individuals were immediately stored in cool and aerated water and
2587 anesthetized by immersion in a bath of clove oil (eugenol dissolved in ethyl alcohol)
2588 (Walsh and Pease, 2002) until the termination of opercular movements, and measured for
2589 total length (TL, cm) and total weight (TW, g). Eels were then sacrificed *in situ* by
2590 decapitation, according to the European Community regulation and Italian legislation for
2591 the protection of animals used for scientific purposes (Directive 2010/63/UE L 276
2592 20/10/2010, implemented by Italian Legislative Decree 26/2014). Individuals were put
2593 on ice and were kept frozen until head dissection for otoliths' extraction.

2594 Moreover, in the laboratory macroscopic sex determination was also assessed,
2595 when possible, by the criteria of Sinha and Jones (1975), and Tesch (2003), discriminating
2596 eels into females, males, and undifferentiated, respectively. In Pramaera river's eels, it
2597 was also possible to conduct histological analysis to ascertain sex (Colombo et al., 1984).

2598 **5.2.2.3. *Otoliths extraction and shape analysis***

2599 The right and left otoliths of eels were extracted for the analysis, cleaned with distilled
2600 water to remove remaining adhering tissues, and placed dry in tubes. Each dried otolith
2601 was weighted (W_OTO, g), and observed in the dorsal position under a stereomicroscope
2602 fitted with a digital camera (Leica S9i Stereozoom LSR w/TL3000 ergo). Digital images
2603 were acquired using the software Leica LAS 4.12 to obtain the most highly contrasted
2604 image. The extraction and preparation of the otoliths' method were developed according
2605 to the methodology defined in the "Manual for the Ageing of Atlantic Eel" (ICES, 2009).

2606 According to the methodology of otolith shape analysis previously described in
2607 Morat et al. (2012) and in Mérigot et al. (2007), the elliptic Fourier analysis (Stransky
2608 and MacLellan 2005; Mérigot et al., 2007; Morat et al., 2012; 2018), and the shape indices
2609 (Tuset et al., 2003) were applied on otoliths.

2610 The elliptic Fourier analysis describes the otoliths' outline starting from several
2611 components named harmonics, each one characterized by 4 coefficients, derived from the
2612 projection of each point along the x- and y-axes. The higher the number of harmonics,
2613 the greater the accuracy of the outline description (Kuhl and Giardina, 1982). Fourier
2614 coefficients for each numerical image were calculated using the software Shape 1.3
2615 (Iwata, 2006) to make them invariants to the otolith size, its orientation, and regarding
2616 the beginning of the outline, which is arbitrarily defined. The Fourier power spectrum
2617 was calculated for each otolith to determine the best number of harmonics for the optimal
2618 reconstruction of the otolith outline (Crampton, 1995) considering both the right and left
2619 otolith of the same individual separately, as well as combined. Finally, a total of 11
2620 harmonics of the right otoliths were set up to obtain a threshold of 99.99% of the outline.
2621 Because the first harmonic was not considered (representing a simple ellipse), a total of
2622 40 Fourier coefficients were used to describe each otolith.

2623 Otolith shape differences between each river and lagoon were determined using
2624 the canonical discriminant analysis (CDA) performed with the 40 Fourier coefficients.
2625 This classification method investigates the groups' integrity (each river and lagoon) by
2626 finding a linear combination of the descriptors that maximizes Wilk's lambda (λ)
2627 obtaining values ranging from 0 (low discrimination) to 1 (high discrimination) (Ramsay
2628 & Silveman, 2005). The Cohen kappa statistic was used to estimate the global
2629 reclassification rate of all groups (Titus et al., 1984). The dissimilarity between groups
2630 was evaluated by the Euclidian distance (d) between the barycenter of each group.

2631 Different measurements were performed on each otolith sample to characterize
2632 the otoliths and calculate the shape indices defined by Tuset et al. (2003) using the
2633 software ImageJ. In detail, five indices were derived from the area (A), the perimeter (P),
2634 the Feret length (L) and the Feret width (w) of otoliths: the form factor ($4\pi A/P^2$), the
2635 circularity (P^2/A), the roundness ($4A/\pi L^2$), the ellipticity $(L-w)/(L+w)$, and the
2636 rectangularity (A/Lw). All indexes range from 0 to 1.

2637 Pairwise collinearity in the five shape indexes was examined by scatter plots to
2638 exclude redundancy between paired variables using Spearman's $\rho > 0.7$. Shape indexes
2639 were discarded from the pairwise combination based on the Variance Inflation Factor
2640 (VIF) discarding observation with $VIF > 3$ (Zuur et al., 2010).

2641 Differences in shape indices were then analysed to describe and compare the
2642 otoliths in the different study sites (each river and lagoon). Furthermore, comparisons
2643 were made also between the measured distances of the first three rings and the core in the
2644 different sites to assess the otolith development in several environments. Finally, the
2645 annual growth (cm year^{-1}) was analyzed to identify differences between the rivers and
2646 lagoons. The assumption of linearity (normality and homoscedasticity) was rejected and
2647 therefore nonparametric Kruskal-Wallis (K-W) test followed by a pairwise comparison
2648 post hoc Dunn's (Z) test was performed to test for differences of the median between
2649 different rivers and lagoons. Significance was set at $p < 0.05$.

2650 **5.2.2.4. The Von Bertalanffy growth model**

2651 For the age reading (ICES, 2009), otoliths were prepared by grinding and polishing along
2652 the sagittal plane, followed by staining. Eels' otoliths under 5 years were analysed without
2653 any preparation (in toto), except for their immersion in lavender essential oil to improve
2654 the visualization of growth marks.

2655 Fish growth can be estimated by relating fish length with the age. One of the most
2656 common methods for aging fish is the analysis of growth rings found on otoliths
2657 (Campana and Thorrold, 2001; Simon et al., 2013). Eel growth was described by using
2658 Von Bertalanffy growth equation

$$2659 \quad L_t = L_\infty (1 - e^{-k(t - t_0)})$$

2660 where L_t (in mm) is the average length at the time t , L_∞ (in mm) is the asymptotic average
2661 length, k is the growth rate coefficient, and t_0 is the (hypothetical) age at which the fish
2662 length would have been zero if it had always grown.

2663 Because of sexual dimorphism in body growth by the European eel (male silver
 2664 eels can reach a size of only 29-54 cm, whereas female silver eels can grow up to a size
 2665 of 133 cm), I developed two growth models separated by sex. Having a complete
 2666 subdivision by sexes only in the Pramaera river, it was possible to obtain growth models
 2667 only on this studied site.

2668 To fit the eel growth model, a standardized transect across each right otolith
 2669 previously analyzed for shape analysis allowed to obtain individual growth trajectories
 2670 by measuring the distances between growth rings from the nucleus to the edge and
 2671 transforming these to fish lengths by a process called back-calculation (Morat et al., 2020;
 2672 Vigliola et al., 2000; Vigliola and Meekan, 2009) to quantify the uncertainty around the
 2673 obtained length estimates according to the relationship between the length at capture (L_{cpt})
 2674 and the radius of the otolith at capture (R_{cpt}). Individuals with estimated age at the capture
 2675 of one year were not included in the back-calculation.

2676 Along this transect, the age of eels was estimated, and distances between each
 2677 annual growth increment were measured using the software ImageJ. The age estimation
 2678 was performed twice by two independent operators to prevent biases induced by a single
 2679 observer. When the coefficient of variation between the two observers was greater than
 2680 5%, a common reading was assessed for each section (Panfili et al., 2002).

2681 The dataset to fit the models should contain a set of variables that allow the
 2682 estimation of multiple growth parameters (Table 5.2.1).

2683 **Table 5.2.1.** - Parameters included in the dataset to fit Von Bertalanffy growth models

Parameter	Definition	Unit
Rad_i	Measurements of otolith growth rings	mm
Age_i	Age i	years
R_i	Radius of otolith at age i	mm
Age_{cpt}	Age at capture	years
Len_{cpt}	Length at capture	mm
Rad_{cpt}	Radius of otolith at capture	mm
L_0^*	Length of fish at hatching	mm
R_0^{**}	Radius of otolith at hatching	mm

2684 *From Sorensen et al., 2016

2685 **From Ayala et al., 2018

2686 In the models, informative priors for growth parameters were extracted from
 2687 FishBase (<https://www.fishbase.se/search.php>) and Ayala et al., (2018). Growth models

2688 were done with the software R (R Core Team, 2021) and the packages *fishgrowbot*
 2689 (Schiettekatte, 2021), *dplyr*, *rstan*, and *bayesplot*.

2690 **5.2.3. Results**

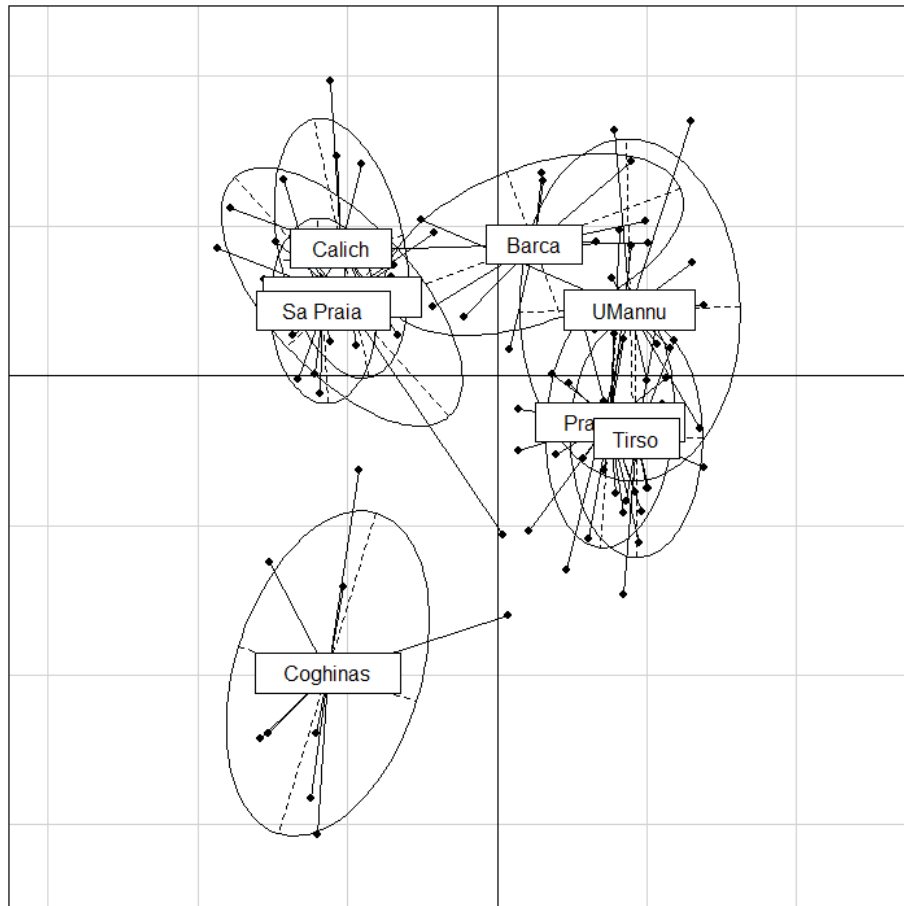
2691 **5.2.3.1. The otolith shape analysis**

2692 A total of 100 eels were caught for the otolith analysis (Table 5.2.2). An exploratory
 2693 analysis was carried out first on otoliths of the Pramaera river in which it was possible to
 2694 find the largest number of samples and on which the sex of eels was determined on a
 2695 macro and microscopic basis. In this analysis, the shape indices between male and female
 2696 otoliths were compared and no significant differences were found between sexes (K-W
 2697 test, $p > 0.05$).

2698 **Table 5.2.2.** - Biometrics of sampled eels. Type of environment (river or lagoon), mean total length (TL),
 2699 mean total weight (TW), and mean otoliths' weight (W_OTO) (\pm standard deviation, st. dev.) for different
 2700 study sites

Site	Environment type	n	TL \pm st. dev. (cm)	TW \pm st. dev. (g)	W_OTO \pm st. dev. (g)
Pramaera	River	26	33.29 \pm 17.68	117.4 \pm 143.64	0.0033 \pm 0.0032
Tirso	River	13	23.03 \pm 39.09	25.35 \pm 20.15	0.0015 \pm 0.00066
UMannu	River	11	30.47 \pm 2.49	40.9 \pm 11.07	0.0024 \pm 0.00037
Barca	River	10	38.09 \pm 14.46	159.255 \pm 278.39	0.0050 \pm 0.0068
Coghinas	River	10	15.02 \pm 2.86	4.41 \pm 2.85	0.00077 \pm 0.00026
Calich	Lagoon	10	40.77 \pm 9.82	163.59 \pm 133.55	0.0031 \pm 0.0017
Porto Pino	Lagoon	10	43.97 \pm 15.64	181.43 \pm 195.02	0.0048 \pm 0.0047
Sa Praia	Lagoon	10	40.56 \pm 8.74	129.69 \pm 110.50	0.0041 \pm 0.0027

2701 Starting from this result, according to which the development of the otolith form
 2702 is not sex-dependent, the Fourier coefficients of right otoliths were used in the CDA to
 2703 show the relative classification of the eight study sites (Figure 5.2.2). The CDA showed
 2704 Wilks λ equal to 0.06 and 0.17 for the x and y axes respectively, indicating low
 2705 discrimination between groups. While the percentage of reclassification assessed with
 2706 Cohen's kappa test was 75.7%.



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Figure 5.2.2. - Canonical Discriminant Analysis (CDA) output between the five rivers and three lagoons investigated in the present study

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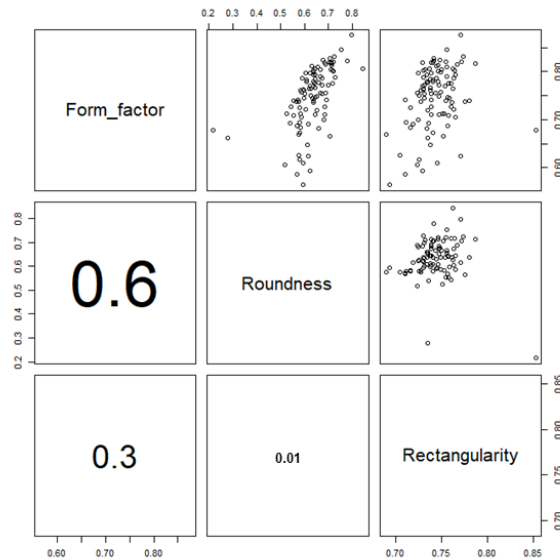
Euclidian distances between the barycenter of each group (rivers and lagoons), resulting from the CDA, showed a clustering between the Pramaera, Tirso, and UMannu rivers with values of $d < 0.9$, and a net grouping between the three lagoons ($d < 0.4$). Barca river showed intermediate characteristics between the rivers and lagoons groups, while the Coghinas river did not grouped with any other site showing $d > 2.4$ compared to all other sites (Table 5.2.3).

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Table 5.2.3. - Euclidian distances between barycenter of study sites resulting from the CDA performed with right otoliths (Euclidian distance < 1 in bold, representing the strong clustering between sites)

Site	Pramaera	Tirso	UMannu	Barca	Coghinas	Calich	Porto Pino	Sa Praia
Pramaera	0							
Tirso	0.21	0						
UMannu	0.76	0.86	0					
Barca	1.29	1.47	0.78	0				
Coghinas	2.52	2.59	3.16	3.18	0			
Calich	2.14	2.34	1.97	1.28	2.84	0		
Porto Pino	1.98	2.18	1.93	1.33	2.52	0.32	0	
Sa Praia	2.06	2.26	2.05	1.47	2.42	0.43	0.16	0

2718 After analyzing shape indices through Spearman correlation ($\rho < 0.7$) (Figure
 2719 5.2.3) and using VIF score < 3 as a threshold (Table 5.2.4), only the form factor,
 2720 roundness, and rectangularity were included for the subsequent shape analysis. The
 2721 remaining shape indices (area, perimeter, Feret length, Feret width, and circularity)
 2722 showed a correlation higher than 0.7 and VIF greater than 3, therefore they were discarded
 2723 from subsequent analyses.

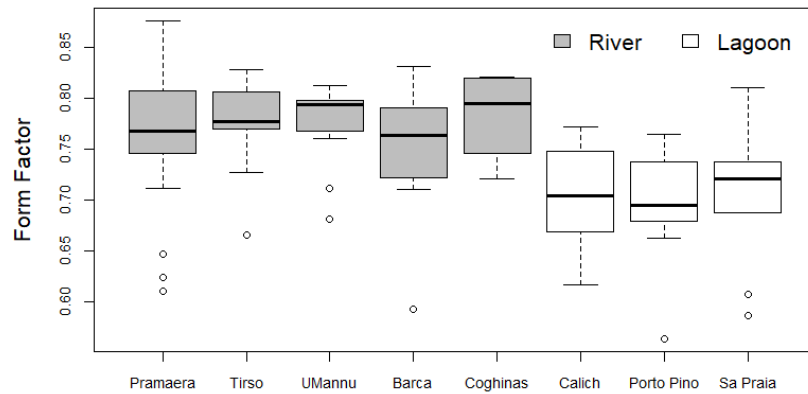


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 2725 **Figure 5.2.3.** - Spearman rank correlation for shape otoliths' indexes

2726 **Table 5.2.4.** - Variance Inflation Factors for shape indexes

Shape index	VIF
Form Factor	1.70
Roundness	1.57
Rectangularity	1.18

2727 Between study sites, the form factor showed significant differences between rivers
 2728 and lagoons ($K-W = 29.34$, $p = 0.00012$) (Figure 5.2.4). Form factor values were higher
 2729 in rivers than in lagoons (Table 5.2.5). This result was also confirmed by the post hoc
 2730 Dunn's test revealing significant differences, especially between Calich and Porto Pino
 2731 lagoons against Coghinas, Pramaera, and Tirso rivers (Z tests, $p < 0.05$).



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Figure 5.2.4. - Boxplot for the form factor index for rivers (grey) and for lagoons (white). The horizontal line within the box = median; ends of the box = 25th and 75th percentiles; ends of whiskers = 10th and 90th percentiles; circles = outliers.

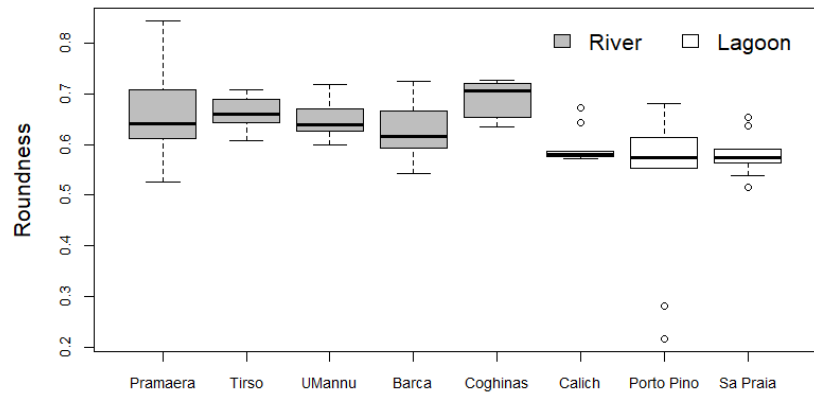
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Table 5.2.5. - In grey cell, median values \pm standard deviation (st. dev.) of form factor shape index are described. In the lower box, the p values are reported, in bold the significant values ($p < 0.05$) and in the upper box, asterisks indicate the significance code: $p < 0.0001 = ****$; $p < 0.001 = ***$; $p < 0.01 = **$; $p < 0.05 = *$; $p > 0.05 = ns$ (non-significant).

	Pramaera	Tirso	UMannu	Barca	Coghinas	Calich	Porto Pino	Sa Praia
Pramaera	0.767 \pm 0.063	ns	ns	ns	ns	ns	*	ns
Tirso	1	0.777 \pm 0.044	ns	ns	ns	ns	*	ns
UMannu	1	1	0.794 \pm 0.041	ns	ns	ns	ns	ns
Barca	1	1	1	0.763 \pm 0.067	ns	ns	ns	ns
Coghinas	1	1	1	1	0.794 \pm 0.038	*	*	ns
Calich	0.14	0.08	0.19	1	0.04	0.704 \pm 0.055	ns	ns
Porto Pino	0.03	0.02	0.06	0.90	0.01	1	0.695 \pm 0.055	ns
Sa Praia	0.44	0.24	0.49	1	0.14	1	1	0.720 \pm 0.071

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A similar outline was obtained for the roundness index (Figure 5.2.5), highlighting statistical differences between sites (K-W = 42.11, $p < 0.0001$), with greater values of roundness in rivers than in lagoons, especially the Coghinas river (Table 5.2.6). These differences concerned all three lagoons compared to Pramaera, Tirso, and Coghinas rivers (Z tests, $p < 0.05$).



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Figure 5.2.5. - Boxplot for the roundness index of otoliths for rivers (grey) and for lagoons) (white). The horizontal line within the box = median; ends of the box = 25th and 75th percentiles; ends of whiskers = 10th and 90th percentiles; circles = outliers.

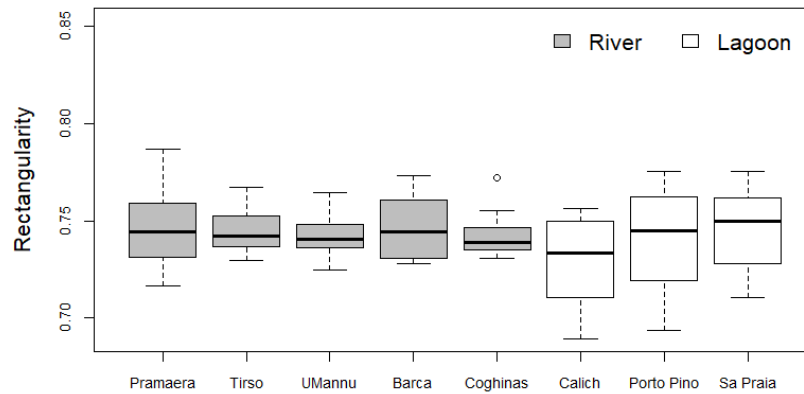
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Table 5.2.6. - In grey cell, median values \pm standard deviation (st. dev.) of roundness shape index are described. In the lower box, the p values are reported, in bold the significant values ($p < 0.05$) and in the upper box, asterisks indicate the significance code: $p < 0.0001 = ****$; $p < 0.001 = ***$; $p < 0.01 = **$; $p < 0.05 = *$; $p > 0.05 = ns$ (non-significant).

	Pramaera	Tirso	UMannu	Barca	Coghinas	Calich	Porto Pino	Sa Praia
Pramaera	0.642 \pm 0.073	ns	ns	ns	ns	ns	*	*
Tirso	1	0.660 \pm 0.032	ns	ns	ns	*	*	**
UMannu	1	1	0.639 \pm 0.040	ns	ns	ns	ns	ns
Barca	1	1	1	0.616 \pm 0.051	ns	ns	ns	ns
Coghinas	1	1	1	0.30	0.705 \pm 0.035	**	***	***
Calich	0.07	0.03	0.39	1	0.002	0.580 \pm 0.034	ns	ns
Porto Pino	0.03	0.01	0.19	1	< 0.001	1	0.573 \pm 0.015	ns
Sa Praia	0.01	0.007	0.12	1	< 0.001	1	1	0.574 \pm 0.041

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Last, the rectangularity index (Figure 5.2.6) instead did not show significant differences in medians between the sites (Table 5.2.7) (K-W = 3.88, $p = 0.79$).



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Figure 5.2.6. - Boxplot for the rectangularity index of otoliths for rivers (grey) and for lagoons (white). The horizontal line within the box = median; ends of the box = 25th and 75th percentiles; ends of whiskers = 10th and 90th percentiles; circles = outliers.

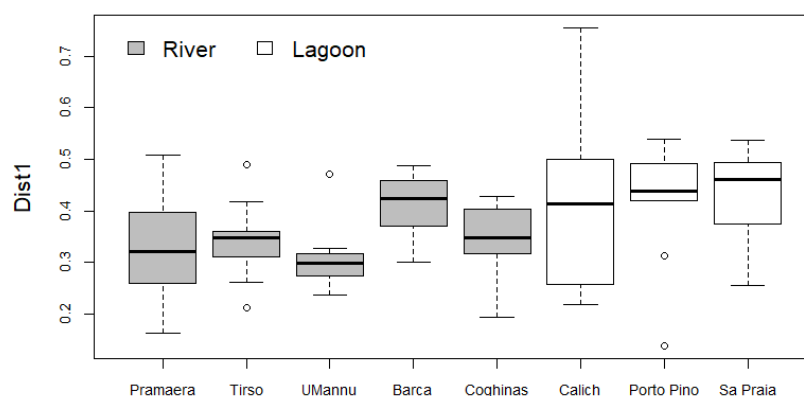
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Table 5.2.7. - In grey cell, median values \pm standard deviation (st. dev.) of rectangularity shape index are described. In the lower box, the p values are reported, in bold the significant values ($p < 0.05$) and in the upper box, asterisks indicate the significance code: $p < 0.0001 = ****$; $p < 0.001 = ***$; $p < 0.01 = **$; $p < 0.05 = *$; $p > 0.05 = ns$ (non-significant).

	Pramaera	Tirso	UMannu	Barca	Coghinas	Calich	Porto Pino	Sa Praia
Pramaera	0.744 \pm 0.018	ns	ns	ns	ns	ns	ns	ns
Tirso	1	0.742 \pm 0.012	ns	ns	ns	ns	ns	ns
UMannu	1	1	0.741 \pm 0.012	ns	ns	ns	ns	ns
Barca	1	1	1	0.745 \pm 0.016	ns	ns	ns	ns
Coghinas	1	1	1	1	0.739 \pm 0.013	ns	ns	ns
Calich	1	1	1	1	1	0.733 \pm 0.024	ns	ns
Porto Pino	1	1	1	1	1	1	0.745 \pm 0.044	ns
Sa Praia	1	1	1	1	1	1	1	0.750 \pm 0.021

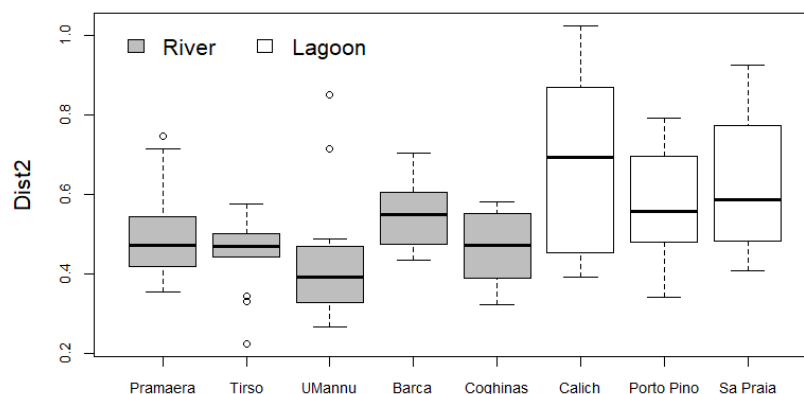
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Ring distances of the first three years were analysed to determine differences in otolith dimension between rivers and lagoons. For the first and the second ring distances (Figures 5.2.7 and 5.2.8), no evident significant differences were found although median values result higher in lagoons than in rivers (Tables 5.2.8 and 5.2.9) (K-W = 22.57, $p = 0.0019$; K-W = 19.30, $p = 0.0073$), with pairwise significant differences only between Calich and Sa Praia lagoons against UMannu river (Z tests, $p < 0.05$).



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Figure 5.2.7. - Boxplot for the first ring distance from the otolith core for rivers (grey) and for lagoons (white). The horizontal line within the box = median; ends of the box = 25th and 75th percentiles; ends of whiskers = 10th and 90th percentiles; circles = outliers



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Figure 5.2.8. - Boxplot for the second ring distance from the otolith core for rivers (grey) and for lagoons (white). The horizontal line within the box = median; ends of the box = 25th and 75th percentiles; ends of whiskers = 10th and 90th percentiles; circles = outliers

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Table 5.2.8. - In grey cell, median values \pm standard deviation (st. dev.) of the first ring distance from the otolith core are described. In the lower box, the p values are reported, in bold the significant values ($p < 0.05$) and in the upper box, asterisks indicate the significance code: $p < 0.0001 = ****$; $p < 0.001 = ***$; $p < 0.01 = **$; $p < 0.05 = *$; $p > 0.05 = ns$ (non-significant).

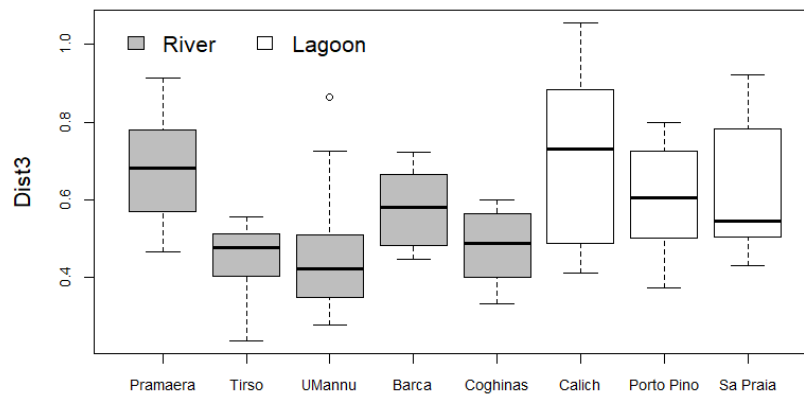
	Pramaera	Tirso	UMannu	Barca	Coghinas	Calich	Porto Pino	Sa Praia
Pramaera	0.326 \pm 0.088	ns	ns	ns	ns	ns	ns	*
Tirso	1	0.347 \pm 0.069	ns	ns	ns	ns	ns	ns
UMannu	1	1	0.298 \pm 0.061	ns	ns	ns	ns	ns
Barca	0.45	1	0.15	0.424 \pm 0.060	ns	ns	ns	ns
Coghinas	1	1	1	1	0.347 \pm 0.68	ns	ns	ns
Calich	1	1	0.73	1	1	0.414 \pm 0.166	ns	ns
Porto Pino	0.39	1	0.07	1	1	1	0.439 \pm 0.116	ns

Sa Praia	0.07	0.61	0.03	1	1	1	1	0.460 ± 0.086
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2781 **Table 5.2.9** - In grey cell, median values ± standard deviation (st. dev.) of the second ring distance from
 2782 the otolith core are described. In the lower box, the *p* values are reported, in bold the significant values (*p*
 2783 < 0.05) and in the upper box, asterisks indicate the significance code: *p* < 0.0001 = ****; *p* < 0.001 = ***;
 2784 *p* < 0.01 = **; *p* < 0.05 = *; *p* > 0.05 = ns (non-significant).

	Pramaera	Tirso	UMannu	Barca	Coghinas	Calich	Porto Pino	Sa Praia
Pramaera	0.496 ± 0.126	ns	ns	ns	ns	ns	ns	ns
Tirso	1	0.469 ± 0.099	ns	ns	ns	ns	ns	ns
UMannu	1	1	0.390 ± 0.184	ns	ns	*	ns	ns
Barca	1	1	0.49	0.549 ± 0.088	ns	ns	ns	ns
Coghinas	1	1	1	1	0.471 ± 0.088	ns	ns	ns
Calich	1	0.36	0.04	1	0.89	0.694 ± 0.223	ns	ns
Porto Pino	1	1	0.31	1	1	1	0.556 ± 0.145	ns
Sa Praia	1	0.51	0.07	1	1	1	1	0.587 ± 0.188

2785 In the third ring (K-W = 26.33, *p* < 0.001), the differences in the distances seem
 2786 site-specific manner regardless of the distinction between rivers or lagoons (Figure 5.2.9
 2787 and Table 5.2.10). The only significant differences are between the Pramaera versus
 2788 Tirso, and Pramaera versus UMannu rivers, respectively (Z tests, *p* < 0.05).

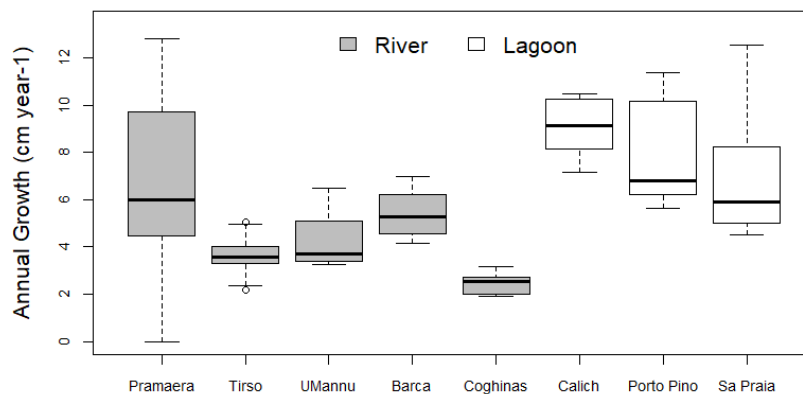


2789 **Figure 5.2.9** - Boxplot for the third ring distance from the otolith core for rivers (grey) and for lagoons
 2790 (white). The horizontal line within the box = median; ends of the box = 25th and 75th percentiles; ends of
 2791 whiskers = 10th and 90th percentiles; circles = outliers
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2793 **Table 5.2.10.** - In grey cell, median values \pm standard deviation (st. dev.) of the third ring distance from the
 2794 otolith core are described. In the lower box, the p values are reported, in bold the significant values ($p <$
 2795 0.05) and in the upper box, asterisks indicate the significance code: $p < 0.0001 = ****$; $p < 0.001 = ***$; p
 2796 $< 0.01 = **$; $p < 0.05 = *$; $p > 0.05 = ns$ (non-significant).

	Pramaera	Tirso	UMannu	Barca	Coghinas	Calich	Porto Pino	Sa Praia
Pramaera	0.693 \pm 0.154	**	*	ns	ns	ns	ns	ns
Tirso	0.007	0.476 \pm 0.095	ns	ns	ns	ns	ns	ns
UMannu	0.01	1	0.421 \pm 0.180	ns	ns	ns	ns	ns
Barca	1	1	1	0.581 \pm 0.100	ns	ns	ns	ns
Coghinas	0.10	1	1	1	0.488 \pm 0.094	ns	ns	ns
Calich	1	0.08	0.13	1	0.46	0.729 \pm 0.234	ns	ns
Porto Pino	1	0.45	0.66	1	1	1	0.605 \pm 0.140	ns
Sa Praia	1	0.52	0.75	1	1	1	1	0.546 \pm 0.168

2797 The annual growth differed between rivers and lagoons (Figure 5.2.10) (K-W =
 2798 58.27, $p < 0.0001$), showing greater median values in lagoons except for the Pramaera
 2799 which shows values close to the lagoons, and the Coghinas river who presents median
 2800 values which are the smallest ones (Table 5.2.11) (Z tests, $p < 0.05$).



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2802 **Figure 5.2.10.** - Boxplot for the annual growth (cm year-1) for rivers (grey) and for lagoons) (white). The
 2803 horizontal line within the box = median; ends of the box = 25th and 75th percentiles; ends of whiskers =
 2804 10th and 90th percentiles; circles = outliers

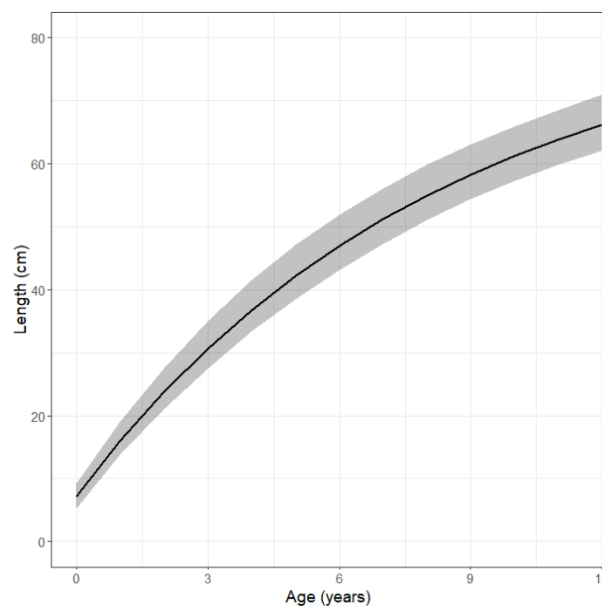
2805 **Table 5.2.11.** - In grey cell, median values \pm standard deviation (st. dev.) of the annual growth (cm year⁻¹)
 2806 are described. In the lower box, the *p* values are reported, in bold the significant values (*p* < 0.05) and in
 2807 the upper box, asterisks indicate the significance code: *p* < 0.0001 = ****; *p* < 0.001 = ***; *p* < 0.01 = **;
 2808 *p* < 0.05 = *; *p* > 0.05 = ns (non-significant).

	Pramaera	Tirso	UMannu	Barca	Coghinas	Calich	Porto Pino	Sa Praia
Pramaera	6.00 \pm 3.50	*	ns	ns	****	ns	ns	ns
Tirso	0.01	3.58 \pm 0.84	ns	ns	ns	****	**	ns
UMannu	0.33	1	3.70 \pm 1.33	ns	ns	**	ns	ns
Barca	1	0.87	1	5.29 \pm 1.03	*	ns	ns	ns
Coghinas	< 0.0001	1	1	0.03	7.60 \pm 2.86	****	****	***
Calich	0.72	< 0.0001	0.002	0.31	< 0.0001	9.15 \pm 1.77	ns	ns
Porto Pino	1	0.002	0.57	1	< 0.0001	1	6.81 \pm 2.16	ns
Sa Praia	1	0.57	0.65	1	< 0.001	1	1	5.90 \pm 2.64

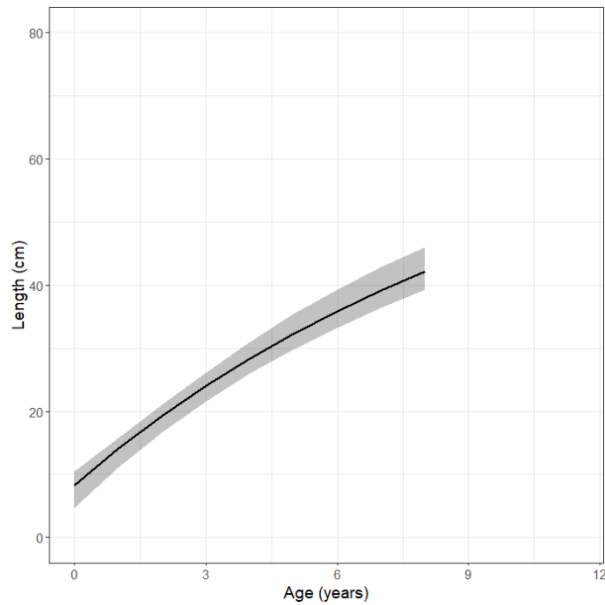
2809 The numerous differences found in the Coghinas could be connected to the small
 2810 size of the individuals that it was possible to collect from this river (TL \leq 20.5 cm).

2811 5.2.3.2. *The Von Bertalanffy growth model*

2812 For the Von Bertalanffy growth models, since I do not have a differentiation of the sexes
 2813 that allows an analysis of growth models for all sites, models (separately for females and
 2814 males) were developed only for the Pramaera river as a case study (Figures 5.2.11 and
 2815 5.2.12). In the Pramaera river, female eels (5 eels, mean TL = 57.28 \pm 6.10 cm) TL ranged
 2816 from 49.5 to 65.0 cm, male eels (11 eels, mean TL = 36.40 \pm 3.44 cm) TL ranged from
 2817 31.1 to 41.9 cm, while undifferentiated eels (10 eels, mean TL = 15.92 \pm 9.17 cm) had a
 2818 TL ranging from 6.80 cm to 31.6 cm.



2819 **Figure 5.2.11.** - Back-calculated Von Bertalanffy growth curves of female eels from the Pramaera river
 2820



2821
2822 **Figure 5.2.12.** - Back-calculated Von Bertalanffy growth curves of male eels from the Pramaera river

2823 The Von Bertalanffy growth parameters (L_{∞} , k , and t_0) for female and male eels
2824 from the Pramaera river were modeled separately (Figures 5.2.11 and 5.2.12). The
2825 growth model of female eels in the Pramaera river is described as the following equation
2826 $L_t = 847(1 - e^{-0.12(t + 0.73)})$. In males, the Von Bertalanffy growth model was fitted as
2827 follows $L_t = 736(1 - e^{-0.09(t + 1.32)})$.

2828 **5.2.4. Discussions**

2829 **5.2.4.1. *The otoliths shape analysis***

2830 In this study, for the first time, I described populations of *A. anguilla* in Sardinian
2831 continental waters through otolith shape analysis, to assess the possible role of different
2832 aquatic environments on otolith shape. I applied the canonical discriminant analysis to
2833 the right otoliths obtaining a high value of reclassification (75.7%) at the regional spatial
2834 scale of the studied area. The classification analysis and shape indexes comparisons can
2835 represent useful tools in discriminating eels' populations that grow in different habitats
2836 (rivers and lagoons) at the local level as already observed in other regional studies on
2837 some eel Mediterranean stocks (Capoccioni et al., 2011; Milošević et al., 2021).

2838 In the present study, I found that otoliths of riverine eels were rounder and less
2839 irregular, with a higher form factor than in lagoons, confirming what was obtained in
2840 other shape otoliths studies (Capoccioni et al., 2011; Moura et al., 2022). This result
2841 highlights also different growth patterns between the lagoon and river habitats, where, in
2842 the latter, the initial circular shape of juvenile eels remains for their entire life. The only
2843 exception is represented by otoliths of eels from the Coghinas river, which showed a

2844 shape differentiation resulting in a more circular shape than all otoliths of the other rivers.
2845 This result can be considered as a bias in the collected sample, consisting only of small
2846 specimens (TL \leq 20.5 cm) but that, despite the reduced TL values, showed an age ranging
2847 from two to five years.

2848 Besides this, several environmental abiotic characteristics (e.g., temperature,
2849 salinity, depth, food availability, and ecological niche) could determine variability in fish
2850 development, that can be reflected in the otoliths' shape (Moura et al., 2022; Campana
2851 and Thorrold, 2001; Wilson, 1985; Campana and Neilson, 1985; Morales-Nin, 2000;
2852 Aguirre and Lombarte 1999; Mériqot et al. 2007; Gonzales-Salas and Lenfant 2007;
2853 Gagliano and McCormick 2004). Furthermore, different eels' development strategies, in
2854 a variety of aquatic habitats located in different geographic areas, can reflect the
2855 complexity of these environments, helping in the understanding of habitat suitability, the
2856 success of recruitment, and the eel productivity (Schiavina et al., 2015; Bevacqua et al.,
2857 2019). These results, however, allowed me to discriminate local eels' populations,
2858 corroborating the hypothesis that ecological and morphological differences in otolith
2859 shape depend on the used environments (Morat et al., 2012). Eels with rounder otoliths
2860 were found in freshwater rivers. These areas tend to be less susceptible to variations in
2861 salinity or temperature and depth than brackish estuaries or lagoons (Whigham et al.,
2862 2019). However, it remains unknown how environmental abiotic variables could be
2863 acting together, influencing, or limiting the development of the species (Daverat et al.,
2864 2012).

2865 **5.2.4.2. *The Von Bertalanffy growth model***

2866 The European eel shows sex-specific life-history strategies. Females take long
2867 maturation periods to produce eggs, requiring higher energetic demands than males. This
2868 leads to a sexual dimorphism based on differences in body length at maturity to reach a
2869 higher fecundity (females about 130 cm, males about 60 cm, respectively) (Costa, 1991;
2870 Vøllestad, 1992; Tesch, 2003; Durif et al., 2009a, b). This sex differentiation strategy, is
2871 also reflected in the otoliths' growth and formation, depends by the growing habitat, and
2872 by the indirect effects of environmental conditions (Poole and Reynolds, 1996; Poole and
2873 Reynolds, 1998; Oliveira, 1999; Melià et al., 2006; Geffroy and Bardonnnet, 2016; Simon,
2874 2015). Thus, I modeled the eel's growth, differentiated by sex considering the sexual
2875 dimorphism in growth, in the Pramaera river as a case study. Indeed, the analysis of Von
2876 Bertalanffy's growth curves showed sex-specific changes in growth, with females'

2877 growth curve towards an L_{∞} of 847 mm and k of 0.12, and the curve for males tending
2878 toward an L_{∞} of 736 mm and k of 0.09. These results provided a first preliminary vision
2879 of the eel's growth in Sardinia, through models defined with the certainty of the sex at
2880 the histological level, with the purpose of further deepen the investigation with a greater
2881 number of specimens and on other sites.

2882 Moreover, it is known that parameters from the von Bertalanffy growth model are
2883 highly variable throughout the eel distribution range (Correia et al., 2021). This is
2884 consistent with the results obtained by other authors in other Mediterranean and European
2885 areas. In Sardinia, only another dated study was carried out in Porto Pino lagoon (Rossi
2886 and Cannas, 1984), showing asymptotic lengths of growth shorter than in my present
2887 study, consistent with the fastest known eel body developments, for lagoon systems
2888 (Melià et al. 2006; Daverat et al. 2012; Simon et al., 2013; Correia et al., 2021). These
2889 site-specific differences, in local variations in eel populations' growth, comparing other
2890 Mediterranean riverine systems and lagoons, might be due to environmental factors and
2891 latitudinal variations (Melià et al., 2006; De Leo and Gatto, 1995). For instance, it is
2892 known that habitats with higher temperatures show faster growth, in southern Europe,
2893 compared to the populations in the north (Morais and Bellwood 2018).

2894 **5.2.5. Conclusions**

2895 Although the European eel is protected according to regional, national, and
2896 international regulations, and despite its commercial importance, little has been published
2897 on the ecology of this species in Sardinia (Rossi and Cannas, 1984; Podda et al., 2020a,
2898 2021, 2022; Porceddu et al., 2022). No studies have analysed the shape of eels' otoliths
2899 for Sardinian continental waters (rivers and lagoons), and only one paper examined the
2900 relationship between otoliths development and the growth of the European eel in the Porto
2901 Pino lagoon (Rossi and Cannas, 1984). Considering this, the mean growth of the stock
2902 should be estimated by sorting eels by size classes at capture to obtain an unbiased
2903 reflection of the age structure and growth of eels' stocks in Sardinia.

2904 All differences that I found in otolith shape among studied sites could lead to
2905 changes between different local stocks and they could be related to environmental
2906 peculiarities. It is difficult to find a direct correlation between environmental factors and
2907 variations in otolith morphology, and further studies would be necessary to relate the type
2908 of habitat and environmental variability with the eel growth and body characteristics.
2909 Therefore, because otolith shape has been studied for the European eel in some European

2910 areas successfully discriminating eels that grow in different habitat types (Capoccioni et
2911 al., 2011; Moura et al., 2022), I also support that this method can be considered a valuable
2912 tool to study the species' phenology. Furthermore, most of the studies conducted on eel
2913 growth were developed in freshwater habitats and at higher latitudes (Moriarty 1983;
2914 Vøllestad 1985; Aprahamian et al. 2007), while have been poorly investigated in
2915 southwest Europe, where rivers, estuaries, and coastal lagoons are the most important
2916 habitats for the species (Domingos 2003; Costa et al. 2008). Therefore, finding the links
2917 between phenotypic attributes, and habitat features would be crucial to estimate the eel's
2918 growth for a more precise stock assessment.

2919 **6. Chapter 6**

2920 **Threats that are contributing to imperiling the European eel in**
2921 **freshwaters: the impact of larger dams in riverine systems**

2922 **6.1. When the Eel meets dams: Larger dams' long-term impacts**
2923 **on *Anguilla anguilla* (L., 1758)**

2924 Published as: **Podda C.**, Palmas F., Pusceddu A., Sabatini A. (2022). When the eel meets dams: larger
2925 dams' long-term impacts on *Anguilla anguilla* (L., 1758). *Front. Environ. Sci.*, 10: 876369. doi:
2926 10.3389/fenvs.2022.876369.

2927 ***Abstract***

2928 *Diadromous fish, like the European eel *Anguilla anguilla* (L., 1758), are highly*
2929 *threatened by dams that disrupt river connectivity, consequently impeding fish*
2930 *movements to reach feeding and spawning habitats. In this study, I assessed variations in*
2931 *eel occurrence between a historical period (1940–1970) and recent data (2016–2020)*
2932 *throughout the Sardinian rivers' network (more than 450 sites). Using Boosted*
2933 *Regression Trees (BRT), I investigated relationships between eel's occurrence and a set*
2934 *of spatial and temporal environmental variables, including a set of dams' construction*
2935 *features for each period. I noticed an overall decrease by 65% of eel's occurrence during*
2936 *the ca. 80-years period under scrutiny. Considering a subset (105 and 88 sites for the*
2937 *historical and the recent period, respectively) characterized by the presence of larger*
2938 *dams (height >15 m), eel's occurrence dropped by 85%. Conversely, eel's occurrence*
2939 *dropped only by ca. 44% in dam-free sites. During the historical period, eel's occurrence*
2940 *was mostly affected by time since the initial habitat fragmentation, flow, distance to dams,*
2941 *connectivity, and dams' height. In the most recent period, eel's occurrence is mostly*
2942 *affected by dams' building year, dam-to-sea distance, and, again, dams' height. Results*
2943 *pinpoint that dams' construction features and the time from their construction have*
2944 *significant negative effects on eel's occurrence. Addition of future effective eel restoration*
2945 *practices, apart any other adverse environmental stressor, must consider dams' removal,*
2946 *wherever socially sustainable or alternatively, the modification of construction features*
2947 *of dams (like excessive height) and the addition of fish ladders.*

2948 **6.1.1. Introduction**

2949 Freshwaters are biodiversity hotspots with 13,000 fish species inhabiting rivers and lakes
2950 (Lévêque et al., 2008). Free-flowing rivers provide migration routes for aquatic and
2951 riparian species, allow the transportation of sediments and nutrients, enable groundwater
2952 recharge, and mitigate flooding (Poff et al., 1997; Tickner et al., 2020). At the same time,
2953 rivers are essential elements for biodiversity and humans' wellbeing (Addams et al., 2009;
2954 Russi et al., 2013). Rivers are among the most threatened ecosystems by anthropogenic
2955 disturbances (Vörösmarty et al., 2010) including a large variety of obstacles (e.g., dams
2956 and weirs, road crossings, hydroelectric power plants, water abstraction for irrigation,
2957 flood control systems for municipal water security) (Welcomme, 1995; Jungwirth et al.,
2958 2000; Nilsson et al., 2005). Dams' construction has seen an acceleration worldwide
2959 during 1950/1960s (Dynesius and Nilsson, 1994; Postel and Richter, 2003; MacGregor
2960 et al., 2009), and more than two thirds of larger rivers have been fragmented (Grill et al.,
2961 2015). At present, ca. 2.8 million dams are operating and roughly 3,700 major dams are
2962 being constructed or planned (Zarfl et al., 2015; Grill et al., 2019).

2963 Environmental alterations caused by anthropogenic obstacles affect the natural
2964 hydrology and connectivity of stream networks, and their ability to transport sediments
2965 (Bednarek 2001; Fullerton et al., 2010; Grill et al., 2015; Rincón et al., 2017). Modifying
2966 the river flow (Grill et al., 2015), dams pose increasing threats to freshwater ecosystems
2967 and mobile biota, particularly fish (Arthington et al., 2016). These barriers play a role in
2968 the degradation of water quality (Chowdhury and Kipgen, 2013; Galipeau et al., 2013;
2969 Opperman et al., 2019; Barbarossa et al., 2020), cause variations in temperature and water
2970 flows (Poff et al., 1997; Richter et al., 2010; Opperman et al., 2017), impair biodiversity,
2971 and in particular impede migration, threaten the spawning habitats and alter the natural gene
2972 flows (Silva et al., 2018; Wilkes et al., 2018; Birnie-Gauvin and Aarestrup, 2019),
2973 ultimately increasing the risk of extinction of fish (Lucas and Baras, 2001; Ding et al.,
2974 2018). In addition, to adequate habitat for spawning and development, fish require
2975 connectivity to migrate freely between different areas of the river and to lakes, and to the
2976 sea. High connectivity between freshwater and marine habitats facilitates the exchange
2977 of matter, energy, and nutrients, with species contributing to the longitudinal transfer and
2978 supporting important ecosystem services (Holmlund and Hammer, 1999). For instance,
2979 anthropogenic intervention in river discharge result in reduced flushing up to unnaturally
2980 extended periods of estuary mouth closure and reduce the connectivity between

2981 freshwater habitats and the sea (Potter et al., 2010; Lloyd et al., 2012; Podda et al., 2020).
2982 In many estuarine systems, especially those with a Mediterranean climate, sand bars are
2983 deposited during low flow periods at the river mouth, resulting in truncation of the
2984 connection between freshwater and marine habitats (Potter et al., 2010; Suari et al., 2019;
2985 Podda et al., 2020). These interruptions and the river flow alteration can have severe
2986 implications, especially for diadromous species (Gillanders et al., 2003), like the
2987 European eel *Anguilla anguilla* (L., 1758). This diadromous species demonstrates high
2988 plasticity in habitat use (Daverat et al., 2006), and is currently exposed to numerous
2989 threats along the migratory routes in both marine and freshwater realms (Culurgioni et
2990 al., 2014, 2015; Bevacqua et al., 2015; Aalto et al., 2016; Baltazar-Soares et al., 2014;
2991 Dekker and Beaulaton, 2016a; Drouineau et al., 2018b; Podda et al., 2021). Because of
2992 these hazards, *A. anguilla* is progressively declining since the 1970s (ICES, 2021), and is
2993 currently classified as Critically Endangered (CR) (IUCN, 2014; Pike et al., 2020) and
2994 protected according to the European Council regulation 1100/2007 (EC, 2007).

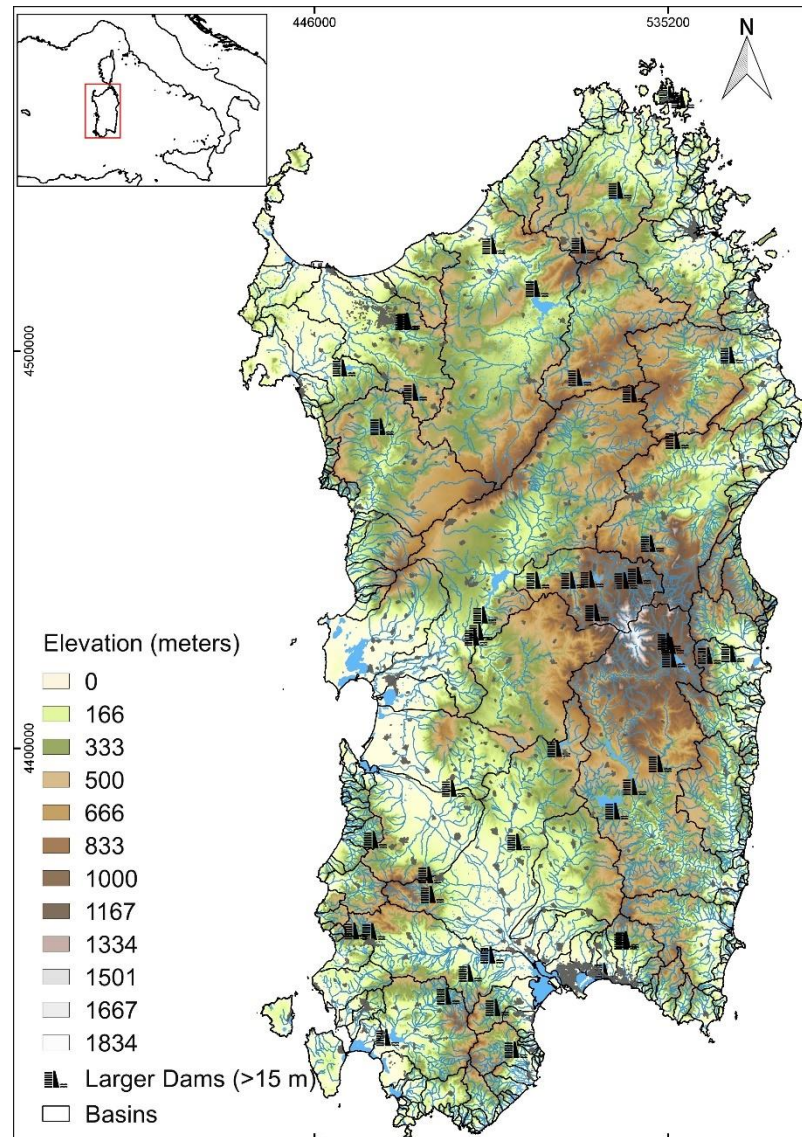
2995 One of the major threats to the European eel is the presence of large instream
2996 barriers restricting access to juveniles leaving the sea after recruitment (Dekker, 2003b;
2997 Piper et al., 2013; Tamario et al., 2019). The more so as the natural recruitment is the only
2998 source of supply of the species (Pedersen and Rasmussen, 2016). Despite their
2999 extraordinary climbing ability, only a minor proportion of eels can successfully overcome
3000 large dams (White and Knights, 1997). Furthermore, direct mortality and sublethal
3001 injuries can occur during obstacle passages because of impingements on hard structures,
3002 even in the absence of turbines (Brujjs and Durif, 2009). Moreover, increased costs of
3003 metabolic energy caused by obstacle passage may have a delayed impact on eel's
3004 migration success and fecundity (Van Ginneken and van den Thillart, 2000). Delays
3005 induced by dams can impair escapement, especially when the migration suitability
3006 window is limited (Verbiest et al., 2012; Drouineau et al., 2017).

3007 In this study, I investigated the impacts of large dams on the occurrence of the
3008 European eel *A. anguilla* in the Sardinian hydrographic district (Central-Western
3009 Mediterranean), considering how the pre and post dams building can affect the long-term
3010 presence of eels. I studied relationships among current and historical occurrences of the
3011 European eel, hypothesizing potential negative effects of a set of temporal, spatial, and
3012 dams' related descriptors using a multivariate approach.

3013 **6.1.2. Material and Methods**

3014 **6.1.2.1. Study area**

3015 Sardinia (Italy) is the second largest island in the Mediterranean (area = 24,106 km²). Its
3016 hydrographic district coincides with the entire regional territory (Figure 6.1.1).



3017 **Figure 6.1.1.** - Study area, location of rivers and larger dams (height > 15 m) in the Sardinian hydrographic
3018 district
3019

3020 The Sardinian hydrographic network is characterized by a reduced number of
3021 perennial rivers and the prevalence of intermittent streams (Palmas et al., 2022).
3022 Mediterranean climate is typically bi-seasonal with severe drought summer and rainy
3023 autumn/winter that determine irregular flow and strong seasonal hydrological fluctuations
3024 (Sabatini et al., 2011, 2018; Palmas et al., 2020; Podda et al., 2020). Average annual
3025 precipitations range from 500 to 900 mm (De Waele et al., 2010; Moccia et al., 2020).
3026 Artificial interruptions of longitudinal river continuity, like dams, strongly influence the
3027 annual hydrological cycle of these streams (Naselli-Flores and Lugliè, 2014). Increasing

3028 construction of artificial barriers has been observed since the end of the 19th century to
3029 provide water for human use (Marchetto et al., 2009; Montaldo and Sarigu, 2017).

3030 **6.1.2.2. Eels' data**

3031 Two datasets were collected in the frame of the monitoring program for the official Fish
3032 Inventory of the Sardinian region (V.V. A.A., 2022).

3033 The point-to-point historical occurrence data available from 1940 (1940-1970,
3034 hereafter historical period), derive from scientific and informative publications of
3035 regional origin for a total of 238 sites (Supplementary Table S6.1.1) and were
3036 georeferenced in a Geographical Information System (GIS) through the Open-Source
3037 Software Quantum Gis 2.18.3 (QGIS) (<http://www.qgis.org/>).

3038 Recent occurrence data (2016-2020; hereafter current period) were collected for
3039 214 sites. Surveys were conducted mainly during the dry season using electrofishing (0-
3040 4 Ampere, 0- 600 Volt) in habitats ranging from sea level to 1,262 m a.s.l. For
3041 comparisons, current data were then integrated into the GIS layer including historical
3042 data. Sites have been selected in proportion to the amplitude of the hydrographic basin
3043 and in order to have a historical continuity with the data deriving from the previous
3044 historical period allowing an appropriate spatial coverage in relation to the extension of
3045 the whole hydrographic network of Sardinia (V.V. A.A., 2022).

3046 Datasets were analyzed separately, and sites influenced by at least one
3047 downstream dam were identified. In each dataset, sites located on free-flow rivers or
3048 under dams have been analyzed separately from those located above dams.

3049 **6.1.2.3. Data analysis**

3050 Twelve variables, ten continuous and two dummies, have been investigated as potential
3051 factors explaining the eel's occurrence related to dams' effects. The variables were
3052 subdivided into four categories: temporal, spatial, dams' features, and site-specific,
3053 respectively (Table 6.1.1). Geospatial information on dams were acquired from the
3054 Regional Land Information System of Sardinia (RAS, 2021).

3055

Table 6.1.1. - Description of the investigated variables

Variable Name (ABBREVIATION)	Description	Type	Unit
Year of fragmentation (FRAGMENTATION)	Number of years since dam construction compared to sampling year or the year of construction of the oldest dam in cases with multiple dams	Temporal	
Year of dam building (YEAR)	Year of construction of the nearest dam downstream the site	Temporal	
Height (HEIGHT)	Dam height	Dam feature	m
Volume (VOL)	Dam volume	Dam feature	m ³
Flow (FLOW)	Dam flow	Dam feature	m ³ s ⁻¹
Elevation (ELEV)	Elevation above sea level	Dam feature	m
Distance of the dam from the site (D_STA)	The distance of the dam from the site	Spatial	km
Distance of the dam from the sea (D_SEA)	The distance of the dam from the sea	Spatial	km
Dendritic Connectivity Index (DCI) (Cote et al., 2009)	Proxy of the fragmentation of the longitudinal river connectivity caused by dams in relation to the presence of eels. DCI = 100 l L-1 where l is the current length of the river from the sea to the first barrier without fish passage, and L is the maximum historical eel migration distance for each site	Spatial	%
Number of dams (DAM)	Number of downstream dams in each site	Site-specific	1 or 2 in the historical dataset From 1 to 6 in the current dataset
River mouth condition (MOUTH)		Site-specific	0 = closed, for rivers which don't flow into a lagoon. 1 = open, rivers which flow into a lagoon.
Fishing pressure (FISH)	Presence of fishing pressure along the river to its river mouth, (http://www.sardegnaagricoltura.it)	Site-specific	0 = absence of fishing activities. 1 = presence of fishing activities.

3056

3057

3058

3059

Differences between the percentage of eel occurrence during the historical and recent periods were evaluated using the X² test (p -value < 0.05). Pairwise collinearity in explanatory variables was examined by scatter plots to exclude redundancy between paired variables disregarding combinations with Spearman's $\rho > 0.7$. Variables were

3060 discarded from the pairwise combination based on the Variance Inflation Factor (VIF)
3061 discarding observation with $VIF > 3$ (Zuur et al., 2010).

3062 The set of dams' descriptors for the two datasets was fitted using Boosted
3063 Regression Tree models (BRT) (Friedman 2001; Elith et al., 2008). BRT is a machine-
3064 learning method for data exploration and analysis recently introduced into the fields of
3065 ecology and conservation biology (Déath, 2007; Elith et al., 2008). BRTs are suited to
3066 select the most relevant predictors from a large set of candidate variables, do not depend
3067 on the normality and homoscedasticity of the data, integrate nonlinear responses, and
3068 reduce the problem of 'overfitting' (Elith et al., 2008). BRTs allow to calculate multiple
3069 regression models (regression trees) and include an adaptive method to combine many
3070 simple models to give improve predictive performance (boosting). Within the BRT
3071 model, terms that are used to optimize predictive performance are represented by the
3072 learning rate, tree complexity, and bagging factor (Friedman, 2001; Elith et al., 2008).
3073 BRTs were adjusted with a learning rate to return an optimal number of regression trees
3074 (1,000–1,500), which has been associated with data overfitting. Trees' complexity of two
3075 refers to the number of nodes in a tree that has been selected (Elith et al., 2008). We use
3076 tree complexity to control the number of nodes, to set the maximum number of
3077 interactions between predictor variables that are possible, and we used a bagging factor
3078 of 0.5 (Friedman, 2001). Variable selection is not necessary for constructing BRTs
3079 because they generally ignore non-informative predictors (Elith et al., 2008). The BRT
3080 analysis was conducted using the Bernoulli family of occurrence. For visualizing the
3081 results, we calculated the partial dependencies that depict the relationships between the
3082 response and each predictor variable while controlling for the average effects of the
3083 remaining predictors (Friedman, 2001; Friedman and Meulman, 2003).

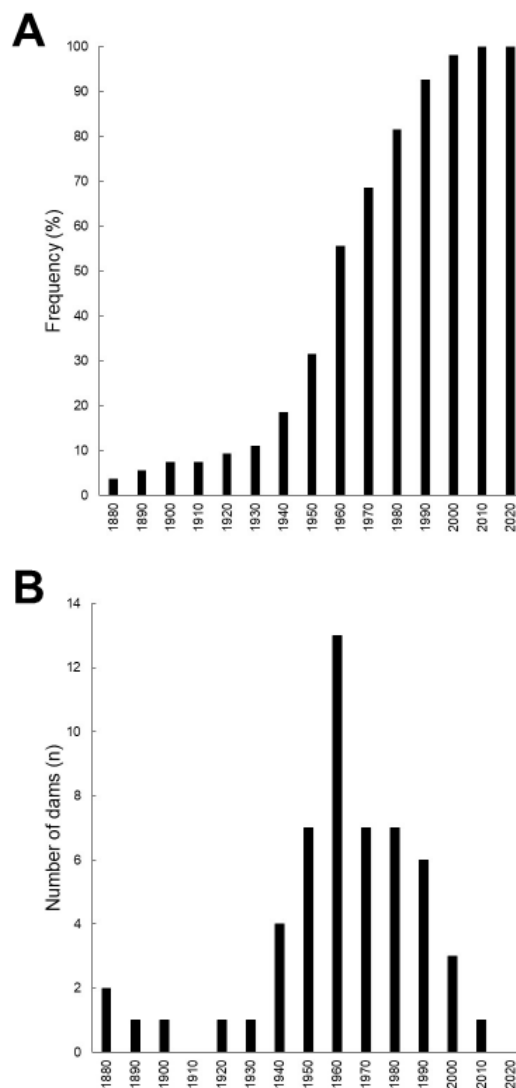
3084 This approach did not allow to assess confidence intervals for BRTs, used when a
3085 large number of BRT sub-models are fitted. The partial dependence plots for parameters
3086 with a contribution $>10\%$ were used to visualize the effect of each variable on the eel's
3087 occurrence. As this method does not deliver p -values but uses internal validation
3088 processes, BTRs performances were evaluated using the amount of total deviance
3089 explained (%) and cross-validated correlation between model prediction and observed
3090 data (CV correlation) (Derville et al., 2016; Nieto and Mélin, 2017; Ju et al., 2021; Saha
3091 et al., 2021). Statistical analyses were conducted using open-source R software (R Core

3092 Team, 2021). Specifically, *gbm* (Greenwell et al., 2020), and *dismo* (Hijmans et al., 2011)
 3093 packages for BRT analyses, and partial dependence plots for each variable.

3094 **6.1.3. Results**

3095 **6.1.3.1. Dams in the Sardinian hydrographic district**

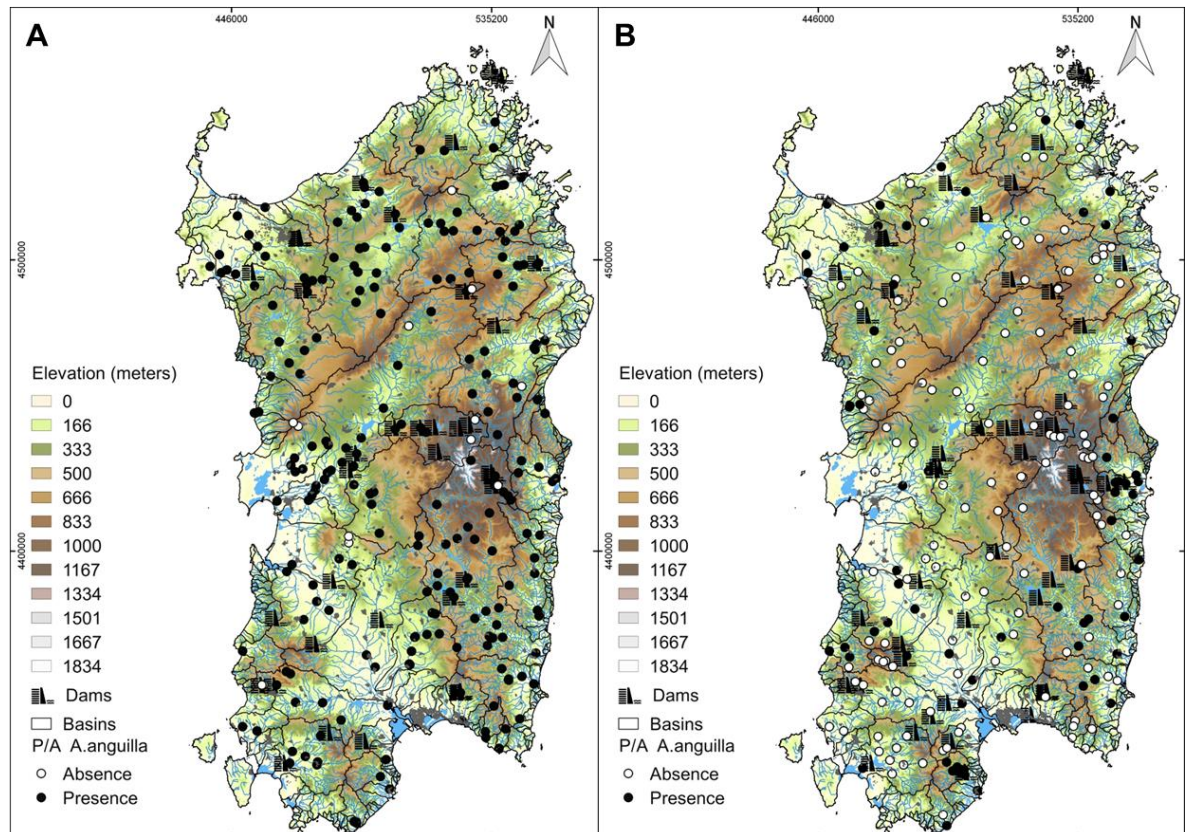
3096 Although the first dam in Sardinia date back to the end of the 19th century, a rapid
 3097 increase in dam's construction has been observed from the late 1960s to the late 1990s
 3098 (Figure 6.1.2A). More than 50% of the 54 larger dams (>15 m height, mean height \pm
 3099 Standard Deviation-SD, 42.5 ± 22.3 m) were built between 1940 and 1960 (Figure
 3100 6.1.2B), with two of the most recent dams not completely built yet. Furthermore, Sardinia
 3101 is currently lacking river flow regulations, and fishways or fish ladders are mainly absent
 3102 or not working with one single exception (i.e., Casteldoria dam, height = 26.6 m,
 3103 $40^{\circ}53.3843$ N– $08^{\circ}53.7534$ E, recently built, 2015).



3104 **Figure 6.1.2.** - (A) Cumulative frequency in dam building in Sardinia (%). (B) Number of dams in Sardinia.
 3105

3106 **6.1.3.2. *Eel's occurrence in Sardinian Rivers***

3107 Comparing sites' correspondence (one observation per site for each dataset) between the
3108 historical and the current datasets, a total of 54 sites matched (23% and 25% of sites,
3109 respectively). The analysis of the historical period (1940-1970) revealed that eel
3110 occurrence amounted to ca. 95% (Figure 6.1.3A). In the current period (2016-2020), I
3111 observed a strong contraction (ca. 65%, $X^2, p < 0.001$) of eel occurrence, which decreased
3112 to only 30% (Figure 6.1.3B).



3113 **Figure 6.1.3.** - (A) Historical European eel's occurrence (1940-1970). (B) Current European eel occurrence
3114 (2016-2020)
3115

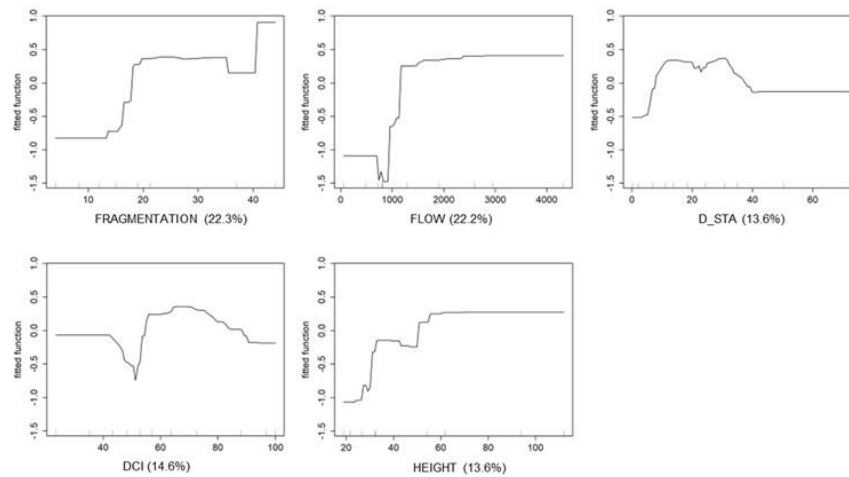
3116 Considering only sites with downstream dams (88 and 105 sites for the historical
3117 and current period, respectively), eel occurrence dropped from 92% to 7% respectively,
3118 with a total (statistically significant) decrease of ca. 85% ($X^2, p < 0.001$). In this subset,
3119 the proportion of sites influenced by downstream dams was ca. 37% and 49% for the two
3120 periods, respectively.

3121 During the historical period, 96% of free-flow sites (i.e., sites without dams or
3122 sites without downstream dams) had eels, whereas in the current period this value dropped
3123 to 52%, with a decreasing rate between the two periods of ca. 44% ($X^2, p < 0.001$).

3124 **6.1.3.3. *Effect of Larger Dams on Eel's Occurrence***

3125 After analyzing dams' descriptors through Spearman correlation (Supplementary Figures
3126 S6.1.1 and S6.1.2) and using VIF score > 3 as a threshold (Supplementary Tables S6.1.2
3127 and S6.1.3), only eight descriptors were included for the modeling of the data from the
3128 historical period, and seven for the current one. Five descriptors were common between
3129 the datasets: dendritic connectivity index (DCI), height (HEIGHT) and flow (FLOW) of
3130 dams, river mouth condition (MOUTH), and fishing pressure (FISH). The predictors in
3131 the modeling of the historical period also included the temporal fragmentation
3132 (FRAGMENTATION), the distance of dams from each site (D_STA), and the dams'
3133 elevation (ELEV), while the year of dams' building (YEAR) and the distance of dams
3134 from the sea (D_SEA) were included in the modeling of the current period.

3135 The historical BRT model shows that five descriptors cumulatively explain 88.4%
3136 of the model: FRAGMENTATION (relative contribution = 22.3%), FLOW (22.2%),
3137 D_STA (14.7%), DCI (14.6%), HEIGHT (14.6%). Explained deviance (51%) and CV
3138 correlation (0.40) suggest that the relationships between dams' characteristics and the
3139 eel's occurrence are quite robust. The partial dependence plots obtained after BRT models
3140 (Figure 6.1.4) show that the contribution of FRAGMENTATION to eel's occurrence is
3141 greatest 20 years after the dams' building. The difference across that threshold is very
3142 narrow, with a value of 91% and 94% occurrence, below and above downstream dams,
3143 respectively. The contribution of FLOW to the eel's occurrence is maximum over a
3144 threshold of ca. $1,300 \text{ m}^3 \text{ s}^{-1}$, with a value of 87% below and 100% above the threshold.
3145 The highest effect of D_STA is observed more than 5 km far from dams, where mean eel
3146 occurrence is 75%, whereas at closer sites this value is 96%. The HEIGHT effect was
3147 highest above ca. 60 m, where eel's occurrence (100%) was higher than that (90%) in
3148 sites with downstream dams < 60 m height. The index of river connectivity (DCI) has the
3149 highest effect on the eel's occurrence within the interval of 60%–80% DCI with mean
3150 eel's occurrence of 86% below 60% of DCI, and 100% above this threshold.

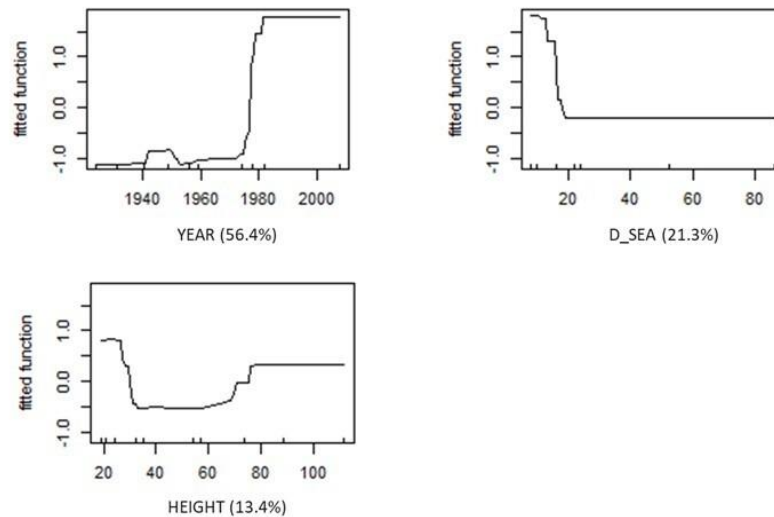


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Figure 6.1.4. - Partial dependence plots of the five variables (FRAGMENTATION, FLOW, D_STA, DCI, and HEIGHT) affecting eels 'occurrence in Sardinian rivers during the historical period (1940-70). The relative contribution of each variable is reported within parentheses. Black lines refer to the raw model output

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The BRT model for the most recent period reveals that three descriptors, YEAR (54.6% of relative contribution), D_SEA (21.3%), and HEIGHT (13.4%), explain cumulatively 91% of the model. There is well goodness of fit of the BRT with an explained deviance of 62% and a CV correlation of 0.67. The partial dependence plots obtained after BRT models (Figure 6.1.5) show that the effect of dams' age is highest (25%) after 1980 (i.e., dams with less than ca. 40 years) and drops to 2% in more recent years. The contribution of D_SEA to eel's occurrence is highest below 20 km, with the highest mean occurrence (13%) in sites close to the sea and the lowest (2%) in the farthest ones. The highest contribution of HEIGHT is observed for dams between 30 and 80 m, which have a mean eel occurrence of 5%. In sites with dams <30 m occurrence is 10%, whereas in sites with dams >80 m (some of which are still not completed) the mean eel's occurrence is 7%.



3168
 3169 **Figure 6.1.5.** - Partial dependence plots of the three variables (YEAR, D_SEA, and HEIGHT) affecting
 3170 eels 'occurrence in Sardinian rivers during the recent period (2016-20). The relative contribution of each
 3171 variable is reported within parentheses. Black lines refer to the raw model output

3172 **6.1.4. Discussions**

3173 **6.1.4.1. Impacts of large dams on eel's occurrence**

3174 *A. anguilla* is worldwide ranked as a critically endangered species due to an ample array
 3175 of often synergistic, anthropogenic threats (Jacoby et al., 2015; Miller et al., 2016;
 3176 Drouineau et al., 2018b). Moreover, the presence of dams, causing a physical interruption
 3177 of river connectivity, river flow reduction or modification, and loss and deterioration of
 3178 habitats, may also critically affect eel's survival during their freshwater life stage
 3179 (Feunteun, 2002; Tamario et al., 2019; Watz et al., 2019).

3180 The dramatic decline of the European eel's recruitment reported worldwide
 3181 (Dekker, 2003b, 2004; ICES, 2021) also affects the Sardinian rivers' network, where I
 3182 observed a huge decrease in eel occurrence. Indeed, considering only free-flow sites (i.e.,
 3183 sites in dam-free rivers or sites without downstream dams), the European eel occupied
 3184 most of the main Sardinian rivers until the 1970s (ca. 95%). The overall 44% reduction
 3185 in species' occurrence between the two periods in these sites suggests that a relevant
 3186 proportion of such a decline is independent by dams. Nevertheless, the decline of eel
 3187 occurrence in Sardinian rivers is also severely affected by damming with eel occurrence
 3188 in sites above dams dropping by 85% between the two periods. Results, ultimately,
 3189 confirm that dams have a severe impact on eels due to the fragmentation of migration
 3190 habitats and the alteration of river flow (Poff and Schmidt, 2016; Dias et al., 2017).

3191 I hypothesized that dams' height (Larinier, 2001b; Merg et al., 2020), dams age
3192 (Atkinson et al., 2020) and the decreased river flow due to the oldest dams (Legault et al.,
3193 2003) could negatively affect eel's migration. In both periods under scrutiny, as expected,
3194 the height of dams could have had a negative effect on eel occurrence and such an impact
3195 was lower during the old period but severely exacerbated in recent years. In the most
3196 recent period, the eel's occurrence above dams >80 m high is, counterintuitively, higher
3197 than that in lower dams. This apparent discrepancy can be ascribed to the fact that
3198 especially some of the very tall dams (> 80 m) were built only very recently, thus the
3199 presence of eels above the dam stems from times before the dam was finalized or filled.
3200 For catadromous fish, including eels, climbing out of the water to surpass a barrier is
3201 challenging and linked to high metabolic costs (Edeline et al., 2004; Briand et al., 2005;
3202 Bult and Dekker 2007).

3203 The age of the dams (estimated using either year of construction in the most recent
3204 period, or temporal fragmentation in the old one) negatively influences eel's occurrence.
3205 I contend that the oldest dams installed in Sardinia, possibly due to technical and financial
3206 limitations, have been built in rivers of lower order or in the upper part of the rivers, thus
3207 having a minor negative effect on the overall river connectivity (Segurado et al., 2013).
3208 In the most recent period, the strongest impact of fragmentation by dams could be
3209 attributable to the technological progress and modernization that allowed building dams
3210 with more effective water retention and, thus, the stronger capacity of interrupting the
3211 river flow in more downstream river sections (Haidvogel, 2018; Merg et al., 2020).
3212 Nevertheless, the effect of river flow is a major factor influencing eel's occurrence only
3213 in the old period. The minimum or nihil effect of river flow and the DCI index on eel's
3214 occurrence in the most recent period could be attributable to the very low river flow in
3215 the last 30 years, caused by prolonged drought, which, most probably impaired eels'
3216 ability to migrate upstream. The negative effect of dams appears more evident during the
3217 old period when either river flow or the DCI index explains significant proportions of eel
3218 occurrence variations. The major role of river flow and the DCI index, in the old period
3219 only, and their ininfluence in the most recent one, is corroborated by the intensity of water
3220 flow involved in the route choice (Legault et al., 2003), causing the silencing of
3221 environmental stimuli when it is too low (Trancart et al., 2018, 2020) and, in the most
3222 extreme cases, interrupting downstream (Durif, 2003) and upstream migration (Podda et
3223 al., 2020a).

3224 In both periods, the distance from the sea explains significant proportions of eel
3225 occurrence. The more distant from the sea the more probable is the presence of natural
3226 (and artificial) obstacles to be crossed by fish (Merg et al., 2020), which, indeed, becomes
3227 a severe impediment to migration, especially when river connectivity is limited due to
3228 low river flow.

3229 **6.1.4.2. Giving future to the European eel**

3230 This study reveals that different dams' attributes can explain the current decline of *A.*
3231 *anguilla*. Along with damming, other factors, associated with excessive human pressure
3232 but also with climate change, are severely impairing eel occurrence. To foster the
3233 conservation of the European eel, many authors have pushed to mitigate its commercial
3234 exploitation (Nielsen and Prouzet, 2008; Henderson et al., 2011; Aalto et al., 2016; ICES,
3235 2021). In addition, I contend that a strong effort should be paid to eliminate highly
3236 impacting artificial barriers or, at least, to mitigate their impacts with more sustainable
3237 actions, tools, and devices. While creating unobstructed migration routes between the
3238 spawning area in the sea and freshwater growth habitats could be preferable (Feunteun,
3239 2002; Drouineau et al., 2018b; Rodeles et al., 2021), the removal of artificial barriers
3240 could be, locally, socially, and economically impracticable. Some attempts have been
3241 made and succeeded with other catadromous endangered species (Graf, 2003; Stanley
3242 and Doyle, 2003; Harris et al., 2016), including the American eel *Anguilla rostrata*
3243 (Lesueur, 1817) (Hitt et al., 2012; Turner et al., 2018). The removal of artificial barriers
3244 could be not exempt from collateral negative effects, including, for instance, the
3245 facilitation of biological invasions (Rahel, 2013; Milt et al., 2018), the spill of toxic
3246 sediments, and sudden changes in hydromorphology (Stanley and Doyle, 2003; Gangloff,
3247 2013).

3248 Except for these general suggestions, in this context, it could be crucial to control
3249 and reduce the uptake of water for human use above dams and, at the same time, ensure
3250 a Minimum Vital Flow (MVF; Moccia et al., 2020) that guarantees the morphological,
3251 hydrological, physical-chemical, and biological integrity downstream will enable the
3252 protection of eel's habitats in the short and long term (Dudgeon et al., 2006). A potentially
3253 compensative solution for partial restoration of the dammed river connectivity, without
3254 eliminating dams, could also profit from the construction of artificial fishways to allow
3255 eels' passage beyond dams (Seliger and Zeiringer, 2018), management measures both
3256 still lacking in Sardinia. Moreover, it would be advisable that any management, operation,

3257 and maintenance of large dams in Sardinia would be implemented within a regional
3258 control system aimed at harmonizing and standardizing information to support the correct
3259 use and management of these structures. Although this study was conducted on a purely
3260 regional scale, results highlighted the major impact of dams on the European eel's
3261 occurrence in Sardinian rivers and its apparent worsening in the last 10 years. I conclude
3262 that, based on the general current crisis of this species, urgent actions are needed
3263 worldwide to restore their habitats by reducing human pressure, ensuring a minimum vital
3264 flow, abating, wherever possible, artificial barriers to river connectivity, or, at least,
3265 implementing natural migration routes with artificial fishways.

3266 **6.1.5. Supplementary Materials**

3267 **Table S6.1.1.** - Bibliographic sources for the historical data collection

Bibliographic source	Title	Sites (n)	Sampling method
Pomini, 1940	Ricerche sul <i>Salmo macrostigma</i>	9	Fishing Nets
Manca, 1965	Contributo alla conoscenza di <i>Salmo macrostigma</i>	1	Fishing Nets
Cottiglia, 1968	La distribuzione dell'ittiofauna dulciacquicola in Sardegna	228	Fishing Nets

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3269 **Table S6.1.2.** - Variance inflation factors for historical dataset

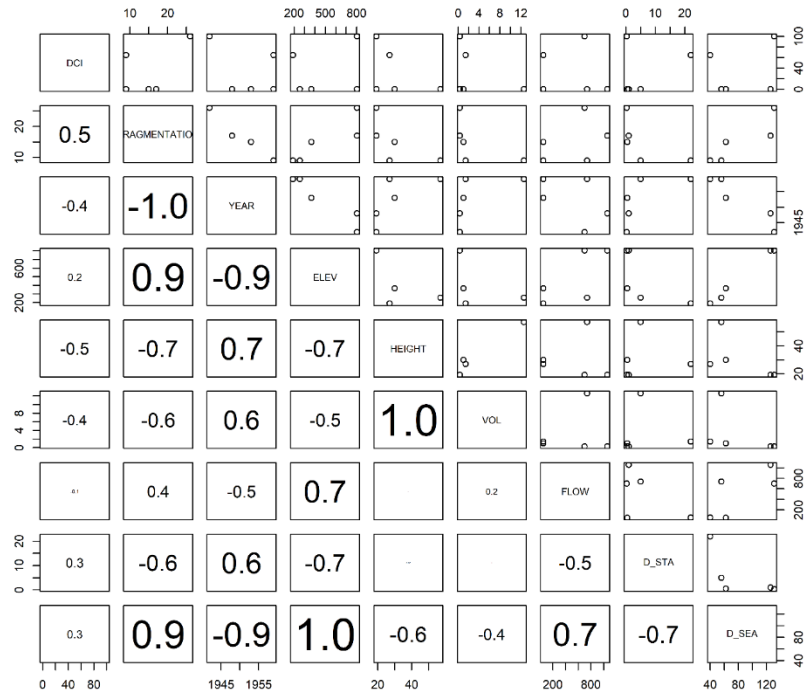
Variable	VIF score
DCI	1.456380
FRAGMENTATION	1.682986
HEIGHT	1.444884
FLOW	1.752856
D_STA	1.824285
ELEVATION	1.109053

3270

3271 **Table S6.1.3.** - Variance inflation factors for current dataset

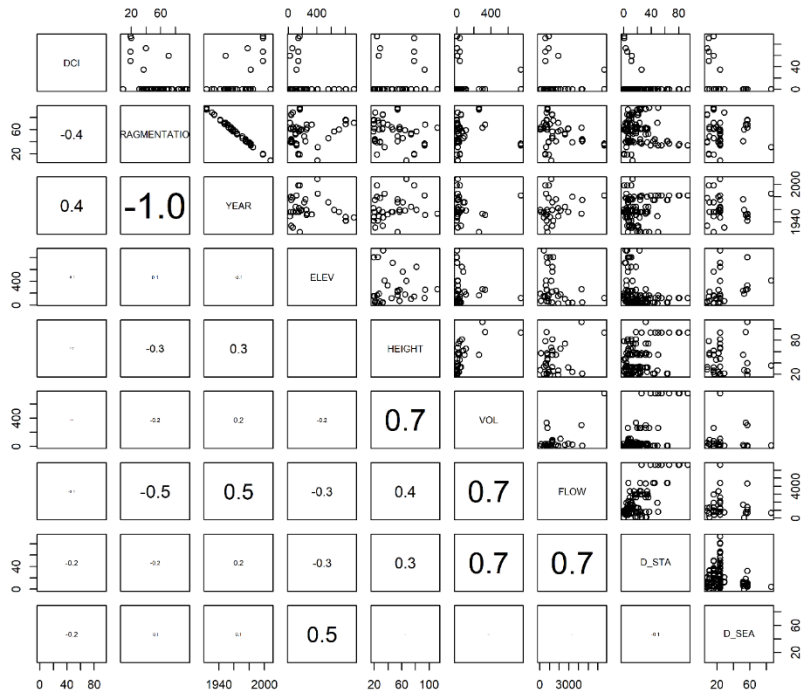
Variable	VIF score
DCI	1.463288
YEAR	1.867565
HEIGHT	1.165867
FLOW	1.656202
D_SEA	1.114161

3272



3273

3274 **Figure S6.1.1.** - Spearman rank correlation for historical dataset



3275

3276 **Figure S6.1.2.** - Spearman rank correlation for current dataset

3277 **7. Chapter 7**

3278 **Summary and perspectives**

3279 **7.1. Summary of the most relevant results**

3280 My Ph.D. research allowed me to obtain new results and knowledge on the bio-ecology
3281 and anatomy of the European eel *A. anguilla*, in relation to the complexity of the species
3282 and its response to various environmental factors and anthropogenic threats. Obtained
3283 results, if on the one hand have led to the implementation of knowledge, on the other they
3284 have highlighted and/or corroborated important critical issues that affect the species.

3285 Starting from a narrative review (**Chapter 2**) on the state of the knowledge and main
3286 threats affecting the European eel, I identified gaps of knowledge from which I developed
3287 the objectives of my Ph.D. thesis.

3288 Starting from the complexity of the whole life cycle of the species, I investigated the role
3289 of olfaction in the orientation and migratory behavior of the European eel in the different
3290 continental stages (**Chapter 3**). I classified, for the first time, the morphology of dendritic
3291 spines of granule cells in the olfactory bulb and examined their density. Results showed
3292 the presence of synaptic development according to a pattern linked to the migratory
3293 behavior of the species. I described that immature spines are mainly present in the juvenile
3294 glass eels' stages and that instead the greatest density of spines is produced mainly in the
3295 two migratory phases of the eel life cycle (glass eels and silver eels). These findings
3296 suggest that olfaction plays a critical role in the migratory behavior and orientation of the
3297 eel and raise concerns that climatic and hydrological environmental changes could affect
3298 the ability to recognize migratory routes, making it difficult or impossible to cover wide
3299 reproductive migratory routes and constituting a cofactor that threaten this species.

3300 I presented new insight into the recruitment dynamics of migratory juvenile eels in the
3301 western Mediterranean (**Chapter 4**). Specifically, I described the glass eels' migration
3302 peak for the first time in a Sardinian estuary and developed a model to assess the main
3303 environmental factors affecting glass eels' recruitment. I identified a strong intra- and
3304 inter-annual and spatial variability at a large scale (four sites in the western
3305 Mediterranean), both for the peak of recruitment and the biometric and pigmentation
3306 patterns of glass eels. I also tested new floating traps as an alternative sampling method
3307 to study glass eels' recruitment in three Sardinian estuaries. These results highlighted the
3308 need to further investigations on the role of hydrological and climatic factors that

3309 determine this temporal and spatial heterogeneity, as well as the need to standardize
3310 sampling protocols.

3311 After the recruitment and colonization phase, eels grow spending many years in
3312 continental waters or, otherwise, are caught farming or restocking. Considering this, I
3313 investigated eels' growth performances in captivity and in nature using farmed wild-
3314 caught glass eels in Sardinia (**Chapter 5**). I described the total survival and the growth
3315 performances in terms of total length and total weight during the rearing experiment in
3316 an intensive eel farm. The recapture and the growth rates were estimated on marked and
3317 unmarked farmed eels after restocking in a Sardinian stream in a four-year study. Findings
3318 suggested a good readjustment to the wild environment of restocked eels. Considering
3319 this, restocking with farmed eels obtained in captivity from wild glass eels may represent
3320 a valid alternative restocking approach to the common direct release of glass eels.
3321 Furthermore, I also analysed the eels' growth in terms of otoliths' shape differences
3322 between several rivers and lagoons of Sardinia. Otolith shape clustered rivers and lagoons
3323 separately, revealing more rounded shapes in otoliths of eels from rivers than lagoons.
3324 On the contrary, annual body growth resulted quicker in lagoons than in rivers. Here I
3325 demonstrated that eel's growth can differ according to habitat types, and I contend that
3326 the use of otoliths can be considered a valuable method to study this species' ontogeny. I
3327 also fitted Von Bertalanffy's growth curves for female and male eels from a Sardinian
3328 stream as a case study that exhibited the already known sexual dimorphism in growth
3329 parameters of the model, with higher values in females.

3330 Last, considering the long period of life that eels spend in freshwater habitats, I analysed
3331 the negative impact of dams on the variations in eel occurrence between a historical
3332 period and recent data throughout the Sardinian rivers' network (**Chapter 6**). Using
3333 multivariate models, I investigated relationships between eels' occurrence and spatio-
3334 temporal environmental variables including a set of dams' construction features pointing
3335 out an overall decrease in eels' occurrence during the 80-years period under scrutiny.
3336 Results pinpointed that dams' construction features and the time from their construction
3337 negatively affect eels' occurrence. Future eel restoration practices must consider dams'
3338 removal, wherever socially sustainable, or, alternatively, their mitigations through the
3339 modification of dams' construction features (e.g., excessive height) or the addition of fish
3340 ladders.

3341 Although Chapters have been developed separately for a structural organization, all the
3342 topics analysed and discussed can be considered strictly connected to each other by the
3343 general decline that the European eel has been experiencing throughout its life cycle. This
3344 is the cumulative result of several natural and anthropogenic impacts despite management
3345 plans and protective measures for its recovery have been in place for over fifteen years.
3346 Although studied since very ancient times, and although there is an increasing amount of
3347 data that allows a better evaluation of the status of this species, there is still much to study
3348 and understand to reverse the decline of the European eel.

3349 **7.2. Future perspectives**

3350 To protect the European eel and to counter at its decline, more knowledge about its bio-
3351 ecology and anatomy are still to be accumulated. This is even more necessary especially
3352 in some areas of its little-studied distribution range, such as Sardinia, the central position
3353 of which in the Mediterranean makes it an area of strategic investigation but lacks
3354 punctual and extended long-term data.

3355 Specifically, my Ph.D. thesis made it possible to clarify some issues relating to the bio-
3356 ecology and the anatomical development of the European eel. Some of my results have
3357 already been published, while others are being submitted for publication or are only
3358 preliminary studies that require more data to conduct further analyses and insights. My
3359 results have also raised new questions and new research perspectives for future studies.

3360 Starting from gaps of knowledge identified in the review on the state of the art of the
3361 European eel (Chapter 2), I set the objectives of my thesis with particular attention to the
3362 bio-ecological and anatomical aspects in relation to various environmental factors and
3363 anthropogenic stressors that affect the species.

3364 From the study of the development of the olfactory system in the different continental life
3365 stages of the eel to identify the role of the olfaction in the migratory behavior of the
3366 species (Chapter 3) it would be interesting identifying the neural network involved in
3367 olfaction and olfactory memory up to the upper nervous centers in the telencephalon. This
3368 could be achieved by continuing the neuroanatomical studies by means of neuroimaging
3369 and the use of neuronal tracers.

3370 The discovery of spatio-temporal heterogeneity in the recruitment dynamics at several
3371 scales in the western Mediterranean basin (Chapter 4) highlighted the need to deepen the
3372 results obtained through a correlation with hydrological models (ocean currents, marine

3373 thermal gradients, river plume) for a complete and in-depth understanding of the
3374 variability in recruitment phenomena. In my study, I used floating traps as an alternative
3375 monitoring tool. I tried to identify some of the potential conditions that a site should have
3376 to be monitored with fyke nets or floating traps, in relation with advantages and
3377 limitations by the environmental point of view (e.g., flow, deep), the surveillance, and the
3378 security for operators and tools. Further studies involving the use of floating traps as an
3379 alternative tool for investigating the phenomenon of settlement of continental waters (e.g.,
3380 estuaries, rivers, lagoons) along the longitudinal gradient (from the sea towards the
3381 inland) and for the study of the dynamics of glass eels' metamorphosis to juvenile yellow
3382 eel would be opportune. Future appropriate research programs need to be conducted to
3383 increase the longer time series, together with the standardization of sampling protocols
3384 and data analysis methods of glass eels.

3385 To study the eel's growth to implement demographic information for the assessment of
3386 stocks in Sardinia (Chapter 5), it would be useful to create growth models in other
3387 representative rivers and lagoons of Sardinia. This will help to understand how the growth
3388 differs over time and in several habitats on a fine scale. Since the effectiveness of
3389 repopulation has not yet been cleared, especially in those sites where the species is locally
3390 extinct, and considering the encouraging results obtained, it would be interesting to test a
3391 new restocking experiment, in the same release site, using reared eels (marked and
3392 unmarked), with particular attention not only to growth performance and recapture rates,
3393 but also to the characterization of the habitats selected by the released eels.

3394 Regarding the anthropogenic impacts that affected the eel in freshwater (Chapter 6),
3395 considering the damming issue in Sardinia, the need to implement bypass systems that
3396 allow the eels to overcome these barriers, and the need for water regulation measures have
3397 emerged. Sampling programs above and below the dams would also be needed using
3398 different possible methodologies (marking, environmental DNA) to evaluate the
3399 migration success of the species, upstream and downstream of dams.

3400 In this context, the achieved results in my thesis have several implications beyond the
3401 regional interest and add new points from which to start further investigations that, over
3402 specific actions, may guide the implementation of new studies and appropriate monitoring
3403 programs.

3404 Since the European eel is a critically endangered species, the implementation of
3405 knowledge is not the only element to take into consideration. To this, I would like to add

3406 a reflection on the need to use increasingly less lethal and invasive approaches for the
3407 study of endangered species such as eels, such as indirect methods (environmental DNA),
3408 less invasive trapping tools (such as floating traps), by minimizing the number of animals
3409 in case of sacrifice of the same, and implementing protocols that use external
3410 morphometric information without resorting to low-cost procedures (e.g. silvering index),
3411 but capable of providing useful and valid information for the study of the species, without
3412 prejudice it being understood that in some areas of study, it is still necessary the sacrifice
3413 of the animal (e.g., sex determination, age estimation, gonadosomatic and hepatosomatic
3414 indices, etc.).

3415 In conclusion, what I presented in this thesis highlights the urgency of close collaboration
3416 and dialogue between the various stakeholders, researchers, decision-makers, authorities,
3417 professionals, and common people as an essential step to create a sense of awareness on
3418 the critical issues that impact this species and the need to mitigate and remedy them.

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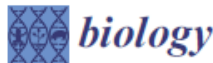
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9. Appendix: Bibliography of the Ph.D. student

9.1. Publications on topics pertinent to the Ph.D. thesis

Porceddu R.†, Podda C.†, Mulas G., Palmas F., Picci L., Scano C., Spiga S., Sabatini A. (2022). Changes in Dendritic Spine Morphology and Density of Granule Cells in the Olfactory Bulb of *Anguilla anguilla* (L., 1758): A Possible Way to Understand Orientation and Migratory Behavior. *Biology*, 8: 1244. doi: 10.3390/biology11081244.



Article

Changes in Dendritic Spine Morphology and Density of Granule Cells in the Olfactory Bulb of *Anguilla anguilla* (L., 1758): A Possible Way to Understand Orientation and Migratory Behavior

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Simple Summary: The olfactory bulb can process odour cues through granular cells (GCs) and dendritic spines, changing their synaptic plasticity properties and their morphology. The GCs' dendritic spines density and morphology were analysed in *Anguilla anguilla*, considering the olfaction as a driver involved in fish orientation and migration. For the head and neck morphology, spines were classified as mushroom, long thin, stubby, and filopodia. Spines' density decreased from juvenile migrants to no-migrant stages and increased in the adult migrants. Spines' density was comparable between glass and silver eels as an adaptation to migration, while at non-migrating phases, spines' density decreased. For its phylogenetic Elopomorph attribution and its complex life cycle, *A. anguilla* could be recommended as a model species to study the development of dendritic spines in GCs of the olfactory bulb. Considering the role of olfaction in the orientation and migration of *A. anguilla*, the modification of environmental stimuli (ocean alterations and climate change) could represent contributing factors that threaten this critically endangered species.

Abstract: Olfaction could represent a pivotal process involved in fish orientation and migration. The olfactory bulb can manage olfactory signals at the granular cell (GC) and dendritic spine levels for their synaptic plasticity properties and changing their morphology and structural stability after environmental odour cues. The GCs' dendritic spine density and morphology were analysed across the life stages of the catadromous *Anguilla anguilla*. According to the head and neck morphology, spines were classified as mushroom (M), long thin (LT), stubby (S), and filopodia (F). Total spines' density decreased from juvenile migrants to no-migrant stages, to increase again in the adult migrant stage. Mean spines' density was comparable between glass and silver eels as an adaptation to migration. At non-migrating phases, spines' density decreased for M and LT, while M, LT, and S density increased in silver eels. A great dendritic spine development was found in the two migratory phases, regressing in trophic phases, but that could be recreated in adults, tracing the migratory memory of the routes travelled in juvenile phases. For its phylogenetic Elopomorph attribution and its complex life cycle, *A. anguilla* could be recommended as a model species to study the development of dendritic spines in GCs of the olfactory bulb as an index of synaptic plasticity involved in the modulation of olfactory stimuli. If olfaction is involved in the orientation and migration of *A. anguilla* and if eels possess a memory, these processes could be influenced by the modification of environmental stimuli (ocean alterations and rapid climate change) contributing to threatening this critically endangered species.

Keywords: catadromous fish olfaction; olfactory bulb; olfactory granule cell; dendritic spine development; European eel; orientation; migratory behaviour



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Podda C., Palmas F., Pusceddu A., Sabatini, A. (2022). When the eel meets dams: Larger dams' long-term impacts on *Anguilla anguilla* (L., 1758). *Front. Environ. Sci.*, 10, 876369. doi: 10.3389/fenvs.2022.876369.



When the Eel Meets Dams: Larger Dams' Long-Term Impacts on *Anguilla anguilla* (L., 1758)

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Diadromous fish, like the European eel *Anguilla anguilla* (L., 1758), are highly threatened by dams that disrupt river connectivity, consequently impeding fish movements to reach feeding and spawning habitats. In this study, variation in eel occurrence between a historical period (1940–1970) and recent data (2016–2020) was assessed throughout the Sardinian rivers' network (more than 450 sites). Using Boosted Regression Trees (BRT) we investigated relationships between eel's occurrence and a set of spatial and temporal environmental variables including a set of dams' construction features for each period. An overall decrease by 65% of eel's occurrence was noticed during the ca. 80-years period under scrutiny. Considering a subset (105 and 88 sites for the historical and the recent period, respectively) characterized by the presence of larger dams (height >15 m), eel's occurrence dropped by 85%. Conversely, eel's occurrence dropped only by ca. 44% in dam-free sites. During the historical period, eel's occurrence was mostly affected by time since the initial habitat fragmentation, flow, distance to dams, connectivity, and dams' height. In the most recent period, eel's occurrence is mostly affected by dams' building year, dam-to-sea distance, and, again, dams' height. Results pinpoint that dams' construction features and the time from their construction have significant negative effects on eel's occurrence. Addition of future effective eel restoration practices, apart any other adverse environmental stressor, must consider dams' removal, wherever socially sustainable or alternatively, the modification of construction features of dams (like excessive height) and the addition of fish ladders.

Keywords: Diadromous species, European eel, freshwater ecosystems, damming, river fragmentation

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INTRODUCTION

Freshwaters are biodiversity hotspots with 13,000 fish species inhabiting rivers and lakes (Lévêque et al., 2008). Free-flowing rivers provide migration routes for aquatic and riparian species, allow the transportation of sediments and nutrients, enable groundwater recharge, and mitigate flooding (Poff et al., 1997; Tickner et al., 2020). At the same time, rivers are essential elements for biodiversity and humans' wellbeing (Addams et al., 2009; Russi et al., 2013). Rivers are among the most threatened ecosystems by anthropogenic disturbances (Vörösmarty et al., 2010) including a large variety of obstacles (e.g., dams and weirs, road crossings, hydroelectric power plants, water abstraction for irrigation, flood control systems for municipal water security) (Welcomme, 1995; Jungwirth et al., 2000; Nilsson et al., 2005). Dams' construction has seen an acceleration worldwide during 1950/1960s (Dynesius and Nilsson, 1994; Postel and Richter, 2003; MacGregor et al., 2009), and more than two thirds of larger rivers have been fragmented (Grill et al., 2015). At present, ca. 2.8 million dams

Podda C., Palmas, F., Pusceddu, A., Sabatini, A. (2021). Hard times for catadromous fish: The case of the European eel *Anguilla anguilla* (L. 1758). *Adv. Oc. Limn.*, 12(2), 9997. doi: 10.4081/aiol.2021.9997.

REVIEW

Hard times for catadromous fish: the case of the European eel *Anguilla anguilla* (L. 1758)

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ABSTRACT

Catadromous fish species can be defined important organisms for their ecological, economical, and cultural value. Because of a complex life cycle, catadromous fish species are exhibited to the cumulative effect of multiple anthropogenic threats that resulted in worldwide decline since the beginning of the 20th century. Among the most iconic catadromous species, the European eel *Anguilla anguilla* has aroused considerable interest, and to date, many aspects of its life cycle remain relatively unknown. Although conspicuous efforts by the research to ensure the perpetuation of the species were conducted, the identification of the best tools to reduce the threats that affect eels remains challenging. In this narrative review, the state of the knowledge and main threats about the life cycle, the habitat occupancy, the recruitment, and migration patterns of the European eel have been reported.

INTRODUCTION

The term diadromy describes migrations between freshwater and marine environments (Myers, 1949; McDowall, 1988; McDowall, 1992). Diadromous species include less than 3% of the world fish fauna (Eschmeyer and Fong, 2016), among which several ones are economically and culturally important, such as freshwater anguillid eels and salmon (Chapman *et al.*, 2012).

Catadromous fish are characterized by a complex life cycle where fish breed in the ocean and grow in continental coastal and/or inland waters (McCleave, 2001), as seen in anguillids (Tesch, 2003; Elliot *et al.*, 2007). Main ecological services provided by catadromous fish consist for example in the provision of food, and in the regulation of ecosystem functions by transporting nutrients and linking different biomes (Druineau *et al.*, 2018a). Globally, these animals have been appreciated for human consumption showing a relevant economic interest (Costa-Dias *et al.*, 2009; Feunteun and Laffaille, 2011). Catadromous fish can be also used as indicators of environmental quality and functionality (Smith *et al.*, 2016). For instance, they are also commonly used as a metric in the assessment of water bodies ecological status in the European Water Framework Directive (Delpech *et al.*, 2010) or as bio-indicators of water quality (Amara *et al.*, 2009), reflecting both habitat longitudinal connectivity and habitat quality. In this context, an exiguous number of catadromous fish species are identified as 'umbrella species' in order to ensure the protection of these species and their habitats (Rochard *et al.*, 2009). They are also magnified by many cultures, foster a belonging sense, and support million-dollar fishing (Garman, 1992; Close *et al.*, 2002; Montgomery, 2003; Chasco *et al.*, 2017; NOAA, 2017). Because of this general interest, catadromous fish are object of studies in all their dimensions (Drouineau *et al.*, 2018b) and strongly linked to research questions associated with animal migration (Secor, 2015; Morais and Daverat, 2016).

Catadromous fish use along their migration pathways a variety of habitats and face many diverse environmental threats (McIntyre *et al.*, 2016). In Europe, as observed for most migratory animals (Sanderson *et al.*, 2006; Wilcove and Wikelski, 2008), a worldwide decline of migratory fish has been recorded at least since the beginning of the 20th century (Béguier *et al.*, 2007; Wolter, 2015; Lambert *et al.*, 2019). The causes are numerous and likely cumulative (*e.g.*, obstacles to migration, deterioration in essential habitat and water quality, unsustainable fisheries, parasite introductions), although quantitative evidence has been rarely demonstrated (Dekker and Casselman, 2014). As a result, many catadromous species are now classified as rare, endangered, or extinct, in the IUCN Red List (IUCN, 2019). There is, therefore, an urgent need to develop approaches that provide reliable quantification of the specific impacts of the different anthropogenic pressures acting on catadromous species. This would help support the implementation of effective mitigation measures and provide adequate tools for national and international regulation around the world. Among the most iconic catadromous species, the European eel *Anguilla anguilla* (Linnaeus, 1758) has been the focus of many studies (*e.g.*, Dekker, 2003a; Bonhommeau *et al.*, 2008; Kettle *et al.*, 2011; Baltazar-Soares *et al.*, 2014; Schiavina *et al.*, 2015; Aalto *et al.*, 2016; Righton *et al.*, 2016; Bomarel *et al.*, 2018; Bevacqua *et al.*, 2019; Dekker, 2019). The life cycle of the European eel *A. anguilla* has stimulated great curiosity and interest since at least the 4th century BC, where already some important Greek philosophers like Aristotle hypothesized on the origin of this species, which remained enshrouded in mystery for millennia. The recent interest increase in eel biology is primarily linked to conservation issues. Therefore, to implement our knowledge about the main natural and anthropogenic threats to its survivorship and identify possible solutions to preserve it, there is an urgent need to gain further insights into *A. anguilla* life-history.



Podda C., Palmas F., Frau G., Chessa G., Culurgioni J., Diciotti R., Fois N., Sabatini A. (2020). Environmental influences on the recruitment dynamics of juvenile European eels, *Anguilla anguilla* (L.), in a small estuary of the Tyrrhenian Sea (Sardinia, Italy). *Aquat. Conserv.: Mar. Freshw. Ecosyst.*, 30(8): 1638-1648. doi: 10.1002/aqc.3362.

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RESEARCH ARTICLE

WILEY

Environmental influences on the recruitment dynamics of juvenile European eels, *Anguilla anguilla*, in a small estuary of the Tyrrhenian Sea, Sardinia, Italy

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Abstract

1. The European eel, *Anguilla anguilla*, is a catadromous and migratory species of commercial importance. Its complex life cycle results in its exposure to many risk factors, which have resulted in stock declines across all life stages since the 1970s.
2. The temporal recruitment dynamics of juvenile eels (glass eels and elvers) were investigated in a small Mediterranean estuary (Sardinia, Italy). The composition of the population and the monthly and seasonal variations in the abundances of juvenile eels was assessed over 78 sampling events (from February 2017 to February 2018). Furthermore, the effects of abiotic variables on the abundances of glass eels and elvers were investigated using generalized additive models (GAMs).
3. Glass eels had the greatest abundance during the winter months, whereas elvers had the greatest abundance during spring. Modelling revealed that the abundance of glass eels was mostly explained by the combined effects of water temperature (12.3–14.5 °C), tidal coefficient (40–110 cm), moon phase, season, and river mouth condition, whereas the abundance of elvers was associated with water temperature (14–21 °C), dissolved oxygen content (>7 mg/L), and season. These results suggest that the annual recruitment of juvenile eels occurs throughout the year, with clear seasonal migration dynamics.
4. The use of multiple statistical approaches allowed us to identify the importance of several environmental variables in regulating the recruitment dynamics, providing useful information for conserving eel stocks through the restoration of the natural flow regime and the connectivity between freshwater habitats and the sea.

KEYWORDS

Anguilla anguilla, environmental factors, GAM, juvenile recruitment, Mediterranean Sea, small estuary

Cinzia Podda and Francesco Palmas contributed equally to this work.

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9.2. Other publications on topics not pertinent to the Ph.D. thesis

- Palmas, F., Cau, A., **Podda, C.**, Musu, A., Serra, M., Pusceddu, A., et al. (2022). Rivers of waste: Anthropogenic litter in intermittent Sardinian rivers, Italy (Central Mediterranean), *Env. Poll.* 302, 119073. doi: 10.1016/j.envpol.2022.119073.
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9.3. Congress participation

- Podda C.** Mechanisms driving juvenile eels' recruitment in a small estuary of the Tyrrhenian Sea. 13-15 April 2021: Incontro dei dottorandi e dei giovani ricercatori in Ecologia e Scienze dei Sistemi Acquatici - online.
- Dessì C., **Podda C.**, Pittura L., Cau A. Preliminary data on European eel skin mucus as trapper of microplastics in riverine ecosystems. 13-15 April 2021: Incontro dei dottorandi e dei giovani ricercatori in Ecologia e Scienze dei Sistemi Acquatici - online.

- Podda C.**, Musu A., Palmas F., Serra M., Pusceddu A., Sabatini A. Impact of larger dams on freshwater distribution of *Anguilla anguilla* (L., 1758). 30 June - 2 July 2021: XXV Congresso AIOL - online.
- Podda C.**, Culurgioni J., Chessa G., Diciotti R., Maxia M., Alessio M., Palmas F., Serra G., Serra M., Fois N., Sabatini A. Glass eels (*Anguilla anguilla*, L. 1758) recruitment evaluation through a new sampling method. 30 June - 2 July 2021: XXV Congresso AIOL - online.
- Diciotti R., Chessa G., Culurgioni J., Manca S., **Podda C.**, Palmas F., Fois N., Sabatini A. Farming wild-caught glass eels for habitat restocking in Sardinia. 21-24 September 2021: XXIV Congresso ASPA – Padova.
- Chessa F., Mara L., Casula P., Gallus M., Palmas F., **Podda C.**, Sabatini A., Dattena M. Freezing semen of wild trout with the use of commercial medium. Preliminary study. 21-24 September 2021: XXIV Congresso ASPA – Padova.
- Podda C.**, Musu A., Palmas F., Serra M., Pusceddu A., Sabatini A. Effects of larger dams on the occurrence of the catadromous European eel (*Anguilla anguilla*, L. 1758). 25-27 October 2021: XXX Congresso SITE - online.
- Podda C.**, Pusceddu A., Sabatini A. Effects of larger dams on the occurrence of the catadromous European eel *Anguilla anguilla* (L. 1758). 19 November 2021: X PhD Congress, UPVDOC, University of Perpignan (France).
- Podda C.** Restocking with wild-caught farmed European eels. 25-26 May 2022: Incontro Giovani Ricercatori in Ecologia e Scienze dei Sistemi Acquatici - online.
- Podda C.**, Palmas F., Chessa G., Culurgioni J., Diciotti R., Fois N., Sabatini A. Restocking with wild caught farmed European eels: an alternative approach. 27 June - 1 July 2022: XXVI Congresso AIOL.
- Podda C.**, Porceddu R., Mulas G., Palmas F., Picci L., Scano C., Spiga S., Sabatini A. Dendritic spine morphology and density of granule cells in the olfactory bulb of *Anguilla anguilla* (L. 1758). 20 – 23 September 2022: 81° Congresso UZI, Trieste.
- Palmas F., Casula P., **Podda C.**, Curreli F., Sabatini A. Detention of endangered mediterranean trout *Salmo trutta* L.,1758 complex (osteichthyes: salmonidae) using non-harmful visual methods. 20 – 23 September 2022: 81° Congresso UZI, Trieste.

Podda C., Palmas F., Cau A., Pittura L., Pusceddu A., Sabatini A. Ingestione di microplastiche nell'anguilla Europea *Anguilla anguilla* (L. 1758) in un corso d'acqua della Sardegna (Mediterraneo centro-occidentale): studio preliminare. 29 September - 2 October 2022: XVIII Congresso AIIAD, Sulmona.

Sabatini A., Cappai L., Careddu M. B., Frau G., Musu A., **Podda C.**, Serra M., Palmas F. La carta ittica della Sardegna (Italia): risultati e indicazioni gestionali. 29 September - 2 October 2022: XVIII Congresso AIIAD, Sulmona.

9.4. Awards

1. "AIOL – Giuseppe Morabito" Award for the best oral presentation at the XXV AIOL (Italian Association of Oceanography and Limnology) Congress (online) with the contribution **Impact of larger dams on freshwater distribution of *Anguilla anguilla* (L., 1758)**. 30 June - 2 July 2021.
2. "Riccardo Cattaneo Vietti" Award for the best oral presentation at the XXX SIte (Italian Society of Ecology) Congress (online) with the contribution **Effects of larger dams on the occurrence of the catadromous European eel (*Anguilla anguilla*, L. 1758)**. 25-27 October 2021.
3. "Subsidy application" Award for the scientific relevance of the contribution presented concerning topics related to Zoology at the 81° UZI (Italian Zoologic Union) Congress with the contribution **Dendritic spine morphology and density of granule cells in the olfactory bulb of *Anguilla anguilla* (L. 1758)**. 20-23 September 2022.