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Stage-specific distribution models can predict eel (*Anguilla anguilla*) occurrence during settlement in coastal lagoons

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ABSTRACT

Eel (*Anguilla anguilla*) is a catadromous fish species typical of Mediterranean coastal lagoons, that currently suffers from several anthropogenic and natural impacts. These are thought to be the cause of a stock-wide decline that this panmictic species is facing, in inland and coastal waters of Europe and North Africa. The decline affects both adult phases and recruitment, i.e. glass eel arrival to coastal waters and their ascent to inland waters. Quantitative features of eel recruitment reflect a transoceanic global scale, but also depend on local environmental conditions, the latter also affecting settlement dynamics in transitional waters. There is only little information on the dynamics of these two processes in coastal lagoons, notwithstanding the paramount importance of both in sustaining local stocks abundance and their demographic structure for this typical but also economically important inhabitant of Mediterranean lagoons, habitats that constitute an important share of the eel distribution area. The present study aims, therefore, to clarify space and time dynamics of local scale recruitment and of settlement in a coastal lagoon in the Mediterranean area, also by setting up a specific methodological approach. For this purpose, data from field surveys in combination with Species Distribution Models (SDMs) have been used in order to relate distribution of eel juvenile stages to the environmental conditions within the lagoon. Specifically, models were calibrated to quantify the relationship between presence of juvenile eel and the main environmental drivers, with the aim of identifying potential habitats for eel settlement within the lagoon. Results gained by modelling suggest certain spatial and temporal colonization patterns for the juvenile eel in the Fogliano lagoon, a typical Mediterranean coastal lake. The modelling approach has therefore proved to be a useful tool for predicting habitats for eel recruitment at the local scale and settlement, because adequate to catch the spatio-temporal dimensions of the processes under study, in coastal lagoon habitats.

1. Introduction

Coastal lagoons and estuaries are among the aquatic habitats with the highest biological productivity (Day, 1989; Pérez-Ruzafa and Marcos, 2012) and provide suitable habitats for many fish species that dwell in these transitional water bodies to feed and grow (Pihl et al., 2002; Franco et al., 2008). Among lagoon fishes, several are marine migrant species that use these habitats as nursery grounds (Minello et al., 2003; Burke et al., 2009; Franco

et al., 2010). One of these is the eel, *Anguilla anguilla*, a typical inhabitant of Mediterranean lagoons, which is also one of the most economically important (Pérez-Ruzafa and Marcos, 2012; Capoccioni et al., 2014; Cataudella et al., 2014; Aalto et al., 2015). The eel uses Mediterranean lagoons as migratory pathways and/or feeding grounds to complete its life cycle, and these habitats constitute a significant fraction (amounting to over 400 lagoons for a total surface area of approx. 580,000 ha) of the overall continental habitat of the European eel (Aalto et al., 2015), This teleostean is a catadromous panmictic species that migrates as an adult from European and Northern African inland and coastal waters to the ocean, to finally spawn in the Sargasso Sea, and back to coastal

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waters and then continental growing habitats at the larval (lepto-cephalus) and juvenile (glass eel) stages (van Ginneken et al., 2005; Als et al., 2011; Miller et al., 2014).

The eel currently suffers from a number of problems related to many impacts of anthropogenic nature: overfishing, habitat loss, pollution and climate change (Harrison et al., 2014) are all thought to cause the stock-wide decline that this species is facing throughout its entire distribution area. The general concern for the global stock of eel is primarily due to a prolonged decline of its recruitment throughout the continent (Moriarty and Dekker, 1997; ICES, 1999 and ICES, 2001; ICES, 2002; ICES, 2004; ICES, 2006; ICES, 2009; ICES, 2011; ICES, 2012). Eel recruitment, which depends primarily, at the global scale, on the magnitude of the transoceanic larval migration, is a crucial process because it sustains the many local stocks. These are distributed across the entire distribution area in several water systems of varying typology, i.e. river catchments, channels, lakes, wetlands, coastal lagoons and near shore marine environments. The features of this decline have been summarized by Harrison et al., 2014, who also review behavioural and environmental processes, modulating juvenile eel recruitment patterns to the catchment level. The success and entity of such a process depends in fact not only on global scale processes (Knights, 2003; Kettle and Haines, 2006; Bonhommeau et al., 2008; Pacariz et al., 2014; Gutiérrez-Estrada and Pulido-Calvo, 2015), but also on local environment conditions related to the hydrological, morphological and meteorological features of a specific site, which modulate space and time dynamics of the ascent (Gascuel et al.,1995; Arribas et al., 2012; Harrison et al., 2014; Trancart et al., 2014; Aranburu et al., 2015).

The importance of recruitment within the species life cycle explains the attention paid by researchers to the larval (Miller et al., 2014 for a review) and glass eel (Harrison et al., 2014 for a review) stages. Recruitment time and space dynamics at the local scale are well known for estuaries and rivers (Beaulaton and Castelnaud, 2005; Harrison et al., 2014), in particular for many systems located on the Atlantic side of Europe. Less information is available for the southernmost estuaries of the eel European distribution area (Arribas et al., 2012) and even less for recruitment and settlement of juvenile eel in coastal lagoons ecosystems, notwithstanding the importance that these habitats play for the eel in the southern part of its distribution area. To our knowledge only Crivelli et al. (2008), Lecomte-Finiger and Razouls (1981) and Finiger (1976) have tried to determine which factors are involved in the glass eel migration to Mediterranean coastal lagoons.

Whatever the general mechanisms and the specific role of environmental cues, recruitment and effective settlement are crucial when estimating eel production and hence breeder escapement and their contribution to the global spawning stock biomass (Aalto et al., 2015). Although overall recruitment may be very low today (Dekker, 2003a), settlement in lagoons has always been partially dependent on factors such as lagoon morphology and hydrology and related to the effects of meteorological patterns on glass eel movement (Finiger, 1976; Crivelli et al., 2008). Taken together, these result in an extremely variable recruitment level to lagoons which in turn makes it very difficult to evaluate if recruitment level is the main limiting factor for eel production in these habitats or simply one of several.

Against this background, this study aims to understand the space and time dynamics of recruitment and settlement in a typical Mediterranean coastal lagoon, by setting up a specific methodological approach allowing to seize the processes and to try to elucidate the correlations regulating them. For this purpose, data from field surveys in combination with Species Distribution Models (SDMs) have been used in order to link space and time dynamics to the environmental conditions within the lagoon. SDMs use quantitative methods to infer environmental requirements of species from conditions at known occurrences (Guisan and Zimmermann, 2000; Elith and Graham, 2009). SDMs are largely used for ecological applications in land ecosystems, but they also have increasingly been used in aquatic environments (Robinson et al., 2011) to evaluate the nursery role of coastal areas (Stoner et al., 2001, 2007; Eastwood et al., 2003; Le Pape et al., 2003; Vaz et al., 2008) and of transitional waters (e.g. Zucchetta et al., 2010).

In this study, stage-specific SDMs have been developed on the basis of *ad hoc* fieldwork, considering glass eel, elver and young 0 + yellow eel. The models were applied using a set of predictor variables, which were chosen from the many known environmental drivers of glass eel migration and young eel movements and behaviour in order to highlight their role for juvenile eel colonization of coastal lagoons. The results, besides providing further insight into a scarcely known aspect of eel ecology, could be of use for setting up and improving management strategies in coastal lagoons, also bearing in mind their potential role towards eel stock recovery.

2. Materials and methods

2.1. Study area

The study site (Fig. 1) is the Fogliano lagoon (41° 24′ 12° 54′), since 1975 included within the Parco Nazionale del Circeo. The surface of the lagoon is 404 ha, mean depth is 0.89 m (2.00 m maximum depth). It is oriented parallel to the coastal line and - due to reclamation interventions carried out between 1926 and 1935 - the lagoon has a rectangular shape with straight shorelines. On the western side, a tidal channel (length 270 m, width 16 m) connects the lagoon to the sea, while a second channel (length 495 m, width 38 m) on the southern side used to connect the lagoon to the mouth of a nearby river, Rio Martino. In the late 1980s, this connection was interrupted by a sluice to prevent water exchanges with the river, due to its poor water quality. Similarly, other surface tributaries, mostly located in the north-western part of the lagoon, were diverted in a channel (the Cicerchia channel, Fig. 1) to avoid excessive organic enrichment to the lagoon and subsequent eutrophication. As a consequence, freshwater inputs are currently drastically reduced, apart random runoffs from the continental side of the lagoon where occasional overflows can occur from a perimeter channel along the inner shore of the lagoon (Fig. 1) or occasional river overflows of the Martino river mouth at incoming tides (Fig. 1). Several authors have observed a general increase of salinity values over time (e.g.: Mariani, 2001: annual average salinity 36 (range: 30–47); Signorini et al., 2008: 37 (range: 30–45); Manzo, 2010: 39 (range 29–49)).

Maximum range of spring tide amounts to about 23 cm, with 17 cm of range during the semidiurnal tide. In normal sea conditions, at each tide the lagoon receives 42.300 m^3 from the sea, while during the ebb tide it returns 37.700 m^3; on the other hand during coastal storms there is a continuous flow into the lagoon. Essentially, water volumes in and out the lagoon show a marked variability of outflows with differences in volumes in relation to the changing hydrological conditions that are established between the lagoon and the sea (Progetto Laghi costieri, 1985).

As for management, in this lagoon, a small-scale artisanal fishery was present, targeting euryhaline fish species and eel as well. The fishery was stopped in 2007, which resulted in the protection of recruiting and growing stages, and the implementation of silver eel escapement (Ciccotti, pers. obs), due to ceased fishing pressure and related mortality.
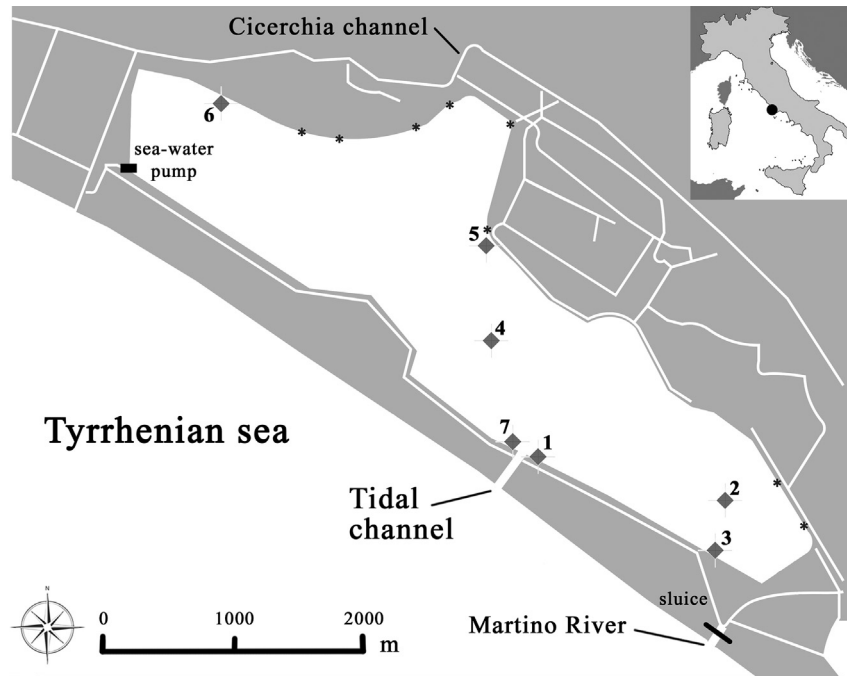
Fig. 1. Study area and sampling stations. Asterisks indicate the outlet of freshwater inputs from channels, now closed in order to avoid excessive nutrient inputs to the lagoon (see text). At present, occasional freshwater inputs to the lagoon can occur only from occasional overflows from the perimeter channels running along the inner shore of the lagoon (one behind station 5, one behind station 2), or at incoming tides near the mouth of river Martino.

2.2. Sampling

Three 7-day long sampling campaigns were carried out in December 2012, February and April 2013, in coincidence with new moon, aiming at catching juvenile eels at different moments of the ascending seasons, and eventually in different phases of the settlement process. Samplings were carried out at seven stations (Fig. 1, numbered anticlockwise) chosen in order to cover most of the environmental variability of the lagoon: two stations are near the main tidal channel (1,7), one close to the channel leading to Martino river (3), two stations in the central area of the lagoon (2, 4), one the continental side of the lagoon (5) and one in the northern part of the lagoon (6).

Samplings were aimed at catching all possible stages of juvenile eel: unpigmented glass eel (GLE), pigmented elver (ELV) and small $0+$ juvenile eel up to 15 cm, conventionally called 'bootlace' (BTL). Zompola et al. (2008) highlight the importance of taking into account the ontogenetic stage of juvenile eel when studying recruitment dynamics. This study targeted all the juvenile stages, and individuals caught by samplings were then assigned to those three stages, GLE being the unpigmented or pigmenting stage up to stage VIA_{II} according to Strubberg (1913) and adapted by Bertin (1956), ELV being the stage completely pigmented, with activated swim bladder (Hickman, 1981) and functional digestive tract and BTL being the small growing yellow eel up to 15 cm.

Silberschneider et al. (2001) proposed and validated the use of artificial habitat collection devices for studying resettlement patterns in anguillid glass eels. Therefore, specific traps (T) are designed and built for this study using PVC tubes (30.0 cm diameter and 50.0 cm long) closed at one end by 1.0 mm mesh. Traps were filled with bundles of olive leaves, to encourage colonization, as Silberschneider et al. (2001) suggest. In each station glass eel fyke nets (GEfy, 1.6 m long, 4 chambers, 40 cm wide, with a 1.5 mm mesh size and wings of 1.3 m) and eel fyke nets (Efy, 2.7 m long, 6 chambers, mouth diameter of 40 cm, wings of 2.5 m and a mesh

size 4.0 mm) were also installed, simultaneously at each sampling campaign. In order to reduce artificial appearance and odour, all sampling devices were kept under water in the lagoon for three weeks prior to the beginning of sampling, as also suggested by Silberschneider et al. (2001).

Sampling gears in each station were inspected daily for the whole duration of each campaign, for a total of twenty-one fishing gears a day (three gears x seven stations) over the whole lagoon. All captured individuals were anaesthetized with clove oil (Walsh and Pease, 2002) and then counted, weighed and their length measured. Assessment of pigmentation (according to the scale of Strubberg, 1913), swim bladder activation (Hickman, 1981) and gut content, examined *in vivo* by means of a stereo-microscope to verify the onset of swimming behaviour and food intake, allowed assignment to one of the three considered stages. All eels were released alive in a nearby channel.

Environmental parameters (temperature (T), salinity (Sal), dissolved oxygen (DO) and Chlorophyll-*a*) were recorded daily at each sampling station with a multiparameter sonde (OxyGuard Handy Gamma). In March 2013, no in-field monitoring of the presence of eel was performed, but an extra campaign was carried out to gather additional environmental data (15 sampling stations all around the lagoon) and thereby expanding the predictor variable dataset to apply SDMs. Distances between each sampling station and the tidal channel (Δ inlet) or any possible fresh water supply (Δ FW) were measured by Geographic Information System (GIS), in order to assess sea and fresh water influence. Even if semidiurnal tidal range was extremely reduced, the tide phase was taken into account, considering it as predictor for the variable describing the lag (expressed as days) from the maximum of the new moon spring tide.

Given the importance of considering biotic variables in ecological studies on fish in coastal lagoons ecosystems, attention was given to the possible role of juvenile eel feeding behaviour in influencing settlement. Bardonnet and Riera (2005) have shown

that glass eels keep a marine isotopic signature during migration but pigmented eels present an isotopic signature typical of inland sources, possibly originated from benthic macro-invertebrates or small fishes. Therefore, among the possible biotic variables the choice has fallen on the zoo-benthic community and in particular on the abundance of some macro-benthic invertebrate taxa, in order to portray prey abundance.

Two replicate sediment samples were collected at each station by a Van Veen grab (250 cm^3). Each sample was sieved in water with a 0.5 mm sieve and immediately frozen and stored at - 20 °C for successive sorting. After defrosting, organisms were extracted from the sediment, identified to the lower taxonomic level (genus or species), counted and measured. For the identification, the following literature was used: Fauvel (1923, 1927), Ruffo (1982-1888), Gravina and Somaschini (1990), Sconfietti (2004) and Doneddu and Trainito (2005). Among all benthic species, only those that could be considered prey/food for the juvenile eel were retained, based on literature information (Tesch, 2003), size range (<0.10 cm), abundance and *expert judgement*.

2.3. Development of Species Distribution Models (SDMs)

Relationships between the presence of GLE, ELV and BTL and the predictor variables were studied by means of *Generalized Additive Models* (GAM) (Hastie and Tibshirani, 1990). Specifically, data of presence and of abundance were coupled per eel stage and sampling station. A matrix of presence/absence was used for setting up the models, while abundance data were used to observe changes in time and space of eel distribution. Only predictors supported by strong biological reasoning, based on *a priori* investigation of the scientific literature, as suggested by Burnham and Anderson (2002), were used to generate set models by means of combinations of predictors, representing different hypotheses on how environmental conditions affect eel distribution (Table 3). To reduce the risk of collinearity in the model only variables with a Pearson correlation lower than 0.7 (a common inclusion threshold) have been considered (Table A.1). Overall, the predictor variables retained for further analysis were: temperature (T), salinity (Sal), dissolved oxygen (DO), days after new moon (Moon), distance from the tidal channel (Δ inlet), distance from the freshwater input (Δ FW) and abundances (n) of six benthic invertebrate species representing potential preys: Chironomidae larvae (Chi), *Monocorophium insidiosum* (Min), *Microdeutopus gryllotalpa* (Mgr), *Gammarus aequicauda* (Gae), *Platynereis dumerilii* (Pdu) and *Nereiphylla rubiginosa* (Nru).

The most suitable model was chosen based on the framework of an information-theoretical approach (Burnham and Anderson, 2002) and corresponded to the most reasonable hypothesis (i.e. better supported by the data). The approach to GAM as proposed by Wood (2006) was followed for fitting the models, using the 'mgcv' library (Family: binomial; Link function: logit) for the R software packages (R Development Core Team, 2014). For each response variable (presence/absence of each eel stage), model selection is based on the Akaike Information Criterion, corrected for small sample sizes (AICc), considering the model with the lowest AICc as the best model of the set. When it was not possible to identify a clear best model (differences of AICc between the two best model smaller than 4), models were combined following a *model averaging approach*, based on AICc-derived weights (Freckleton, 2011). Finally, the averaged model was delineated using the 95% confidence of models (95% of the summed weight, Burnham and Anderson, 2002). The dataset was split by random sampling, in order to use two independent sets for model calibration and evaluation. About 70% of the data (103 observations) were used for model building, while the remaining 30% (44 observations) were used to test the models for each of the three stages. Considering the importance of using different performance estimations for the habitat model (Zurell et al., 2009), we used several statistics to infer the model's predictive capability: sensitivity (conditional probability that a presence is correctly classified); specificity (conditional probability that an absence is correctly classified); percent of correctly classified observations (PCC); Cohen's kappa, and the area under the receiver operator curve (AUC) (Fielding and Bell, 1997). Thresholds for the first four statistics were defined following the minimized difference threshold criterion (difference between sensitivity and specificity) (Jimenez-Valverde and Lobo, 2007). To obtain the spatial predictions for the whole lagoon basin, the fitted models (or the ensembles of fitted models) were applied in a predictive way using raster layers as predictors. All predictive variables were interpolated by using *ordinary kriging* (library automap; Hiemstra et al., 2008) to generate daily maps, and models predictions were carried out in order to predict temporal and spatial presence of the early life stages of *Anguilla anguilla* during the recruitment and settlement phases. Monthly maps for December, February and April for the three stages were obtained averaging the daily prediction maps.

Table 1
Results of the three sampling campaigns.

		GLE	ELV	BTL
December	Days of presence	7	2	1
	Total number (mean)	28 (0.6)	3 (0.1)	1
	Range of length	46—70 mm	58—71 mm	15 cm
	Stations	1,2,3,7	3,4	5
	Gears	T	T, GEfy	GEfy, Efy
February	Days of presence	7	4	3
	Total number (mean)	311 (6.3)	16 (0.3)	3 (0.1)
	Range of length	50—65 mm	57—68 mm	13—15 cm
	Stations	1,3,7	2,3,4,5	4,5,6
	Gears	T, GEfy	GEfy	GEfy, Efy
April	Days of presence	1	2	6
	Total number (mean)	1	2 (0.0)	22 (0.4)
	Range of length	56 mm	58—65 mm	12—15 cm
	Stations	7	4,7	1,2,3,5,6,7
	Gears	T, GEfy	T	T, GEfy, Efy

Days of presence during the sampling campaign, abundance ranges (total number and mean value of individuals) and range of length are shown for each sampling campaign (December, February and April) and for each stage (GLE = glass eel; ELV = elver; BTL = bootlace), specifying where (station number) and how (gears, T = traps; GEfy = glass eel fyke nets; Efy = eel fyke nets) samples were taken.

Table 2
Environmental variables.

	Station	Temperature (°C)	Salinity (PSU)	Dissolved Oxygen (mg l^{-1})	Chlorophyll-a (µg l^{-1})
December	1	7.7 (3.8–10.9)	27.9 (24.6–29.8)	8.6 (7.8–9.6)	0.4 (0.0–0.9)
	2	8.2 (6.1–10.0)	26.2 (22.6–28.0)	8.5 (8.0–9.4)	0.9 (0.0–1.7)
	3	7.2 (4.7–10.1)	26.1 (19.5–29.2)	8.8 (8.1–10.2)	0.9 (0.0–1.6)
	4	7.0 (4.6–10.1)	27.5 (23.9–29.1)	8.8 (8.2–10.1)	1.0 (0.4–1.9)
	5	6.9 (5.5–9.2)	28.1 (26.1–29.0)	8.9 (8.5–9.9)	0.8 (0.5–1.1)
	6	7.1 (5.3–9.4)	27.7 (24.6–29.1)	9.1 (8.5–10.3)	0.5 (0.0–1.1)
	7	7.8 (4.5–10.9)	27.5 (21.2–30.0)	8.9 (7.9–10.6)	0.7 (0.1–1.5)
February	1	8.7 (8.2–9.4)	22.9 (20.6–23.9)	9.1 (8.1–11.2)	0.2 (0.0–0.4)
	2	9.2 (8.6–9.7)	21.2 (14.5–23.7)	9.6 (8.2–13.7)	0.8 (0.0–1.8)
	3	9.1 (8.3–9.7)	22.6 (20.5–23.7)	9.6 (7.9–12.9)	0.8 (0.0–3.1)
	4	9.0 (8.7–9.3)	22.0 (19.8–24.2)	9.3 (7.8–10.5)	0.3 (0.0–0.6)
	5	9.3 (8.3–10.0)	21.8 (20.1–23.5)	9.5 (7.8–11.1)	1.0 (0.1–2.2)
	6	9.4 (9.1–9.9)	21.4 (20.3–21.8)	11.8 (9.7–13.2)	1.5 (0.6–2.6)
	7	8.7 (8.2–9.3)	23.2 (21.3–24.1)	9.7 (7.9–12.8)	0.4 (0.0–1.0)
April	1	18.4 (16.8–20.1)	25.0 (22.5–28.3)	7.5 (7.0–8.1)	0.1 (0.0–0.6)
	2	18.9 (17.5–20.6)	24.6 (24.1–25.2)	6.8 (5.9–7.2)	0.2 (0.0–1.2)
	3	18.9 (17.4–20.3)	23.7 (20.7–25.0)	7.4 (6.8–7.8)	0.1 (0.0–0.2)
	4	18.6 (17.3–20.6)	24.1 (22.8–24.8)	7.2 (6.7–7.6)	0.1 (0.0–0.8)
	5	19.2 (17.9–20.8)	23.4 (22.3–24.2)	7.2 (6.6–7.6)	0.1 (0.0–0.4)
	6	19.0 (17.8–20.9)	24.2 (23.5–24.6)	6.5 (5.7–8.3)	1.5 (1.0–3.0)
	7	18.2 (16.6–19.2)	25.2 (24.6–25.6)	7.8 (7.5–8.2)	0.2 (0.0–0.4)

Mean values and range of variation of environmental variables for each month of sampling and each station.

Table 3
AICc for all model combinations.

Component Model	Glass eel (GLE)		Elver (ELV)		Bootlace (BTL)	
	AICc	Weight	AICc	Weight	AICc	Weight
T			66.28	0.02	73.45	0.02
T + Moon					73.45	0.02
T + DO					73.45	0.02
T + Moon + DO					73.45	0.02
Sal			66.23	0.02		
Δ FW+Δ inlet			61.51	0.19		
PSU + DO+Δ FW+Δ inlet			58.78	0.73		
T + Moon + Sal+Δ inlet	89.15	0.01			70.93	0.08
T + Moon + Sal +Δ FW					69.9	0.14
T + Moon + Sal +Δ inlet + DO	87.81	0.03			70.93	0.08
T + Moon + Sal +Δ FW + DO					69.9	0.14
T + Moon + Chi + Min + Mgr + Gae + Pdu + Nru + DO	85.32	0.1			71.46	0.06
T + Moon + Chi					73.45	0.02
T + Moon + Min + Mgr + Gae					71.46	0.06
T + Moon + Pdu + Nru					73.45	0.02
PSU + DO+Δ FW + Chi + Min + Mgr + Gae + Pdu + Nru	90.16	0.01				
T + Moon + Sal + DO+Δ inlet + Chi + Min + Mgr + Gae + Pdu + Nru	81.79	0.58			70.22	0.12
T + Moon + Sal + DO+Δ FW + Chi + Min + Mgr + Gae + Pdu + Nru	83.51	0.25			69.87	0.14

AICc for the combination of the best set of models for each stage is given by the combination of models reported, for which the sum of the AICc weights is equal to 95%. AICc: Akaike Information Criterion corrected; T: Temperature; Moon: tidal phase; Δ inlet: distance from the tidal channel; Δ FW: distance from the fresh water supply; DO: Oxygen; Sal: Salinity; Chi: Chironomidae larvae; Min: *Monocorophium insidiosum*; Gae: *Gammarus aequicauda*; Mgr: *Microdeutopus gryllotalpa*; Nru: *Nereiphylla rubiginosa*; Pdu: *Platynereis dumerilii*.

3. Results

3.1. Presence and abundance

Juvenile eel abundances recorded in the three sampling campaigns (December, February and April) are summarized in Table 1 and shown in Fig. 2. Information on temperature, salinity, oxygen and chlorophyll are also reported in order to illustrate the spatial and temporal environmental variation in lagoon, in support of the distribution of eel life stage presence (Table 2). GLE (glass eel) was the most frequent and the most abundant stage present in December. Its peak of abundance occurred in February, while only one presence was recorded in April. In both campaigns, GLE was present at the two stations closest to the tidal channel (St. 1, 7) and at the connection with the adjoining river (St. 3). ELV (elver), on the other hand, were caught on the inner side of the lagoon (St. 2, 3, 4,

5) where they were present in all campaigns, predominantly in February. BTL (bootlace), were most abundant in April when they were the dominant stage and were distributed evenly throughout the entire lagoon (all stations).

3.2. SDM development

It was not possible to identify a single best model for any stage, and the best set of models used in the averaging approach differed for the three stages, delineating different relationships with environmental conditions (Table 3). Models included for GLE are complex because of the high number of variables and they include many biotic (prey abundance) as well as abiotic variables. Models for ELV describe its distribution in relation to salinity, and distance to sea-inlet and freshwater inputs. A higher uncertainty is associated with the selection of models for BTL, as testified by the larger
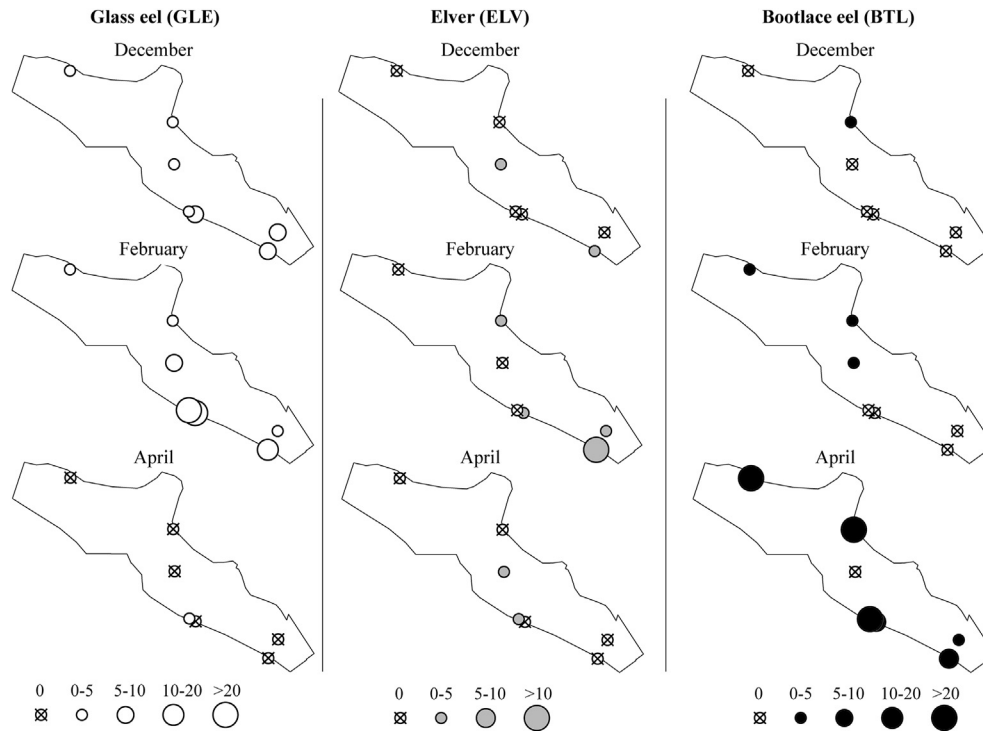
Fig. 2. Abundances (n) of the three juvenile eel stages during the three sampling campaigns at all sampling stations (see Fig. 1 for details).

number of models included in the 95% confidence set and by the fact that among the models none seems to have a stronger weight than the others.

The statistics evaluated on the validation dataset, suggest that fitted models proved to have a good to very good prediction capability comparing predicted probability of presence with observations (AUC - GLE: 0.80; ELV: 0.70; BTL: 0.75). Models predictions could also be transformed into presence/absence predictions yielding a high percentage of records correctly classified (PCC - GLE: 0.70; ELV: 0.73; BTL:0.73) and maintaining a good balance between omission and commission errors for glass eel and bootlace but not for elvers, for which the model seems to underestimate presence (sensitivity - GLE: 0.73; ELV: 0.40; BTL: 0.80; specificity - GLE: 0.70; ELV: 0.78; BTL: 0.72; Kappa - GLE: 0.35; ELV: 0.11; BTL: 0.28).

3.3. SDM application

The application of the models allowed to predict the probability of presence of the three juvenile eel stages in the Fogliano lagoon as a function of environmental variables used as predictors (Fig. 3). GLE-probability of presence is higher in association with lower salinity conditions and with temperature values between 5 and 10 °C. The probability of ELV-presence can also be predicted by salinity, but not by temperature, whereas the probability of BTL-presence is associated with higher temperatures.

A decrease of the probability of presence of GLE and ELV is associated with the distance from the tidal channel. Distance from the freshwater inlets, on the other hand, does not seem to influence the probability of presence of GLE, though it affects slightly the older stages in the opposite way: ELV are more likely to be present closer to the freshwater inputs, whereas BTL are more likely to be present far from freshwater channels. A negative relationship with oxygen content is recorded for GLE, while this variable does not seem to affect ELV and BTL distributions. Probably this is related to

the fact that the oxygen concentration never reached critical values (minimum concentration: 5.7 mgl^{-1}) and ELV is only indirectly associated to this variable, i.e. GLE prefer conditions found in areas with a relatively low oxygen content. The moon phase seems to be hardly relevant in affecting probability of presence of GLE and it is not-relevant for older stages.

Concerning to the role played by potential prey in influencing juvenile eel stages distribution in the lagoon and against time, no role is shown by any of the benthic species considered for ELV nor for BTL, contrary to what expected. On the other hand, selected sets of models (Table 3) show an association of probability of presence of GLE with some benthic species such as the Amphipods *M. insidiosum* (Min), *M. gryllotalpa* (Mgr) and *G. aequicauda* (Gae) and the Polychaetes *N. rubiginosa* (Nru), *P. dumerilii* (Pdu) and Chironomids larvae (Chi) (Fig. 3).

SDMs application allowed to predict and display the probability of presence of GLE, ELV and BTL in the whole lagoon basin. The monthly maps (Fig. 4) generalise the patterns described by the daily maps (Figures A.1, A.2 and A.3). Predictions for March were obtained on the basis of environmental data collected during the extra campaign across the lagoon (see Section 2.2).

In detail, monthly maps show how GLE peak (in terms of probability of presence) is likely to occur in December and February (Fig. 4), with a space pattern that see GLE propagating from the tidal channel to the rest of the lagoon. In the case of ELV, the probability of presence is higher in February and March and with a concentration in the southern area of the lagoon. For BTL, for which a very complex set of models has been retained (Table 3), only temperature seems to play a dominant role in the period of presence (April). BTL presence is homogeneous in terms of distribution across the lagoon, but with a higher probability of presence in the northern area, the most confined sector of the lagoon.
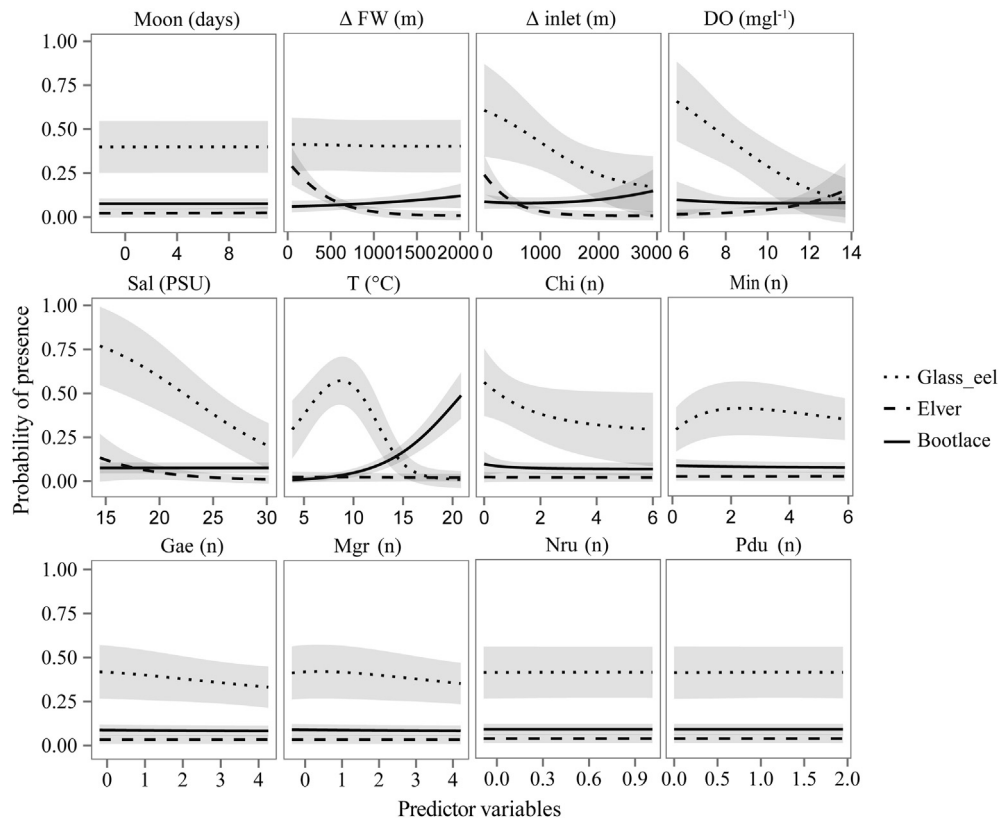
Fig. 3. Relationships between predictor variables and probability of presence for glass eel (dotted line), elver (dashed line) and bootlace (continuous line). Grey bands are 95% point wise confidence intervals.

4. Discussion

4.1. Methodological aspects

This study has several notable different aspects. One is methodological and concerns the sampling scheme that proved to be adequate to catch the space-temporal dimensions of the processes, i.e.coastal lagoon juvenile eel recruitment and settlement. The combined use of three different sampling gears, aimed at capturing different eel juvenile stages in an adequate number of sampling stations and at opportune time intervals i.e. time windows significantly different one from another in terms of environmental conditions and representing different phases of the settlement process, allowed to observe the evolution of juvenile eel requirements in space and in time. The proof of this assumption was an important prerequisite for our work and of particular importance for the purpose of this study, as the conditions observed in a survey define the accuracy, precision and generality (i.e. transferability in time and space) of a species distribution model (Austin, 2002). Highly variable environments, such as estuaries and lagoons, are characterized by marked temporal dynamics in species–habitat associations (Gibson, 1997; Able et al., 2005), which is also true, though, for the association between specific habitats and definite juvenile eel stages. The complex sampling scheme was therefore necessary to adequately cover the environmental variability of the recruitment period in a typical Mediterranean lagoon and to catch some characteristics crucial for fitting SDMs. First, the description of the spatio-temporal dynamic of colonisation allowed splitting the problem of model development into a multi-stage approach, which is the optimal solution for species experiencing sharp ontogenetic shifts (Robinson et al., 2011). Second, even if the distribution

models were developed using presence/absence data, the adequateness/robustness of the collected information, related to the frequency of presence (and synthesised by the number of collected specimens for each stage), seems to influence model accuracy and reliability (higher for GLE and BTL). Indeed, the strong imbalance between presence and absence (stronger for ELV than for the other stages) may influence the capability of an empirical model to link the distribution to environmental conditions. This could be the possible explanation for why models underestimated the presence of elvers and not the other stages.

4.2. Ecological aspects

SDMs development and application allowed predicting juvenile eel presence inside the lagoon on the basis of a set of predictor variables, chosen from existing knowledge about environmental drivers of glass eel migration and young eel movements and behaviour. If we assume that the predictors that have yielded good results are the variables that influence recruitment dynamics, then these parameters are those that affect juvenile eel colonization in the Fogliano coastal lake, and more generally in coastal lagoons. The results of this study show that it is possible to describe the role of different groups of variables influencing recruitment, and further the settlement of the various stages.

The physical variable that plays the most influential role is *temperature*. For glass eels, the optimal temperature range was between 5 and 10 °C, which influenced glass eel movements on an intra-seasonal basis. The lower value is in accordance with what reported by most authors, i.e. that temperature values lower then 5–4 °C render glass eel inactive, while it has been reported that when the difference in temperature between sea and lagoon
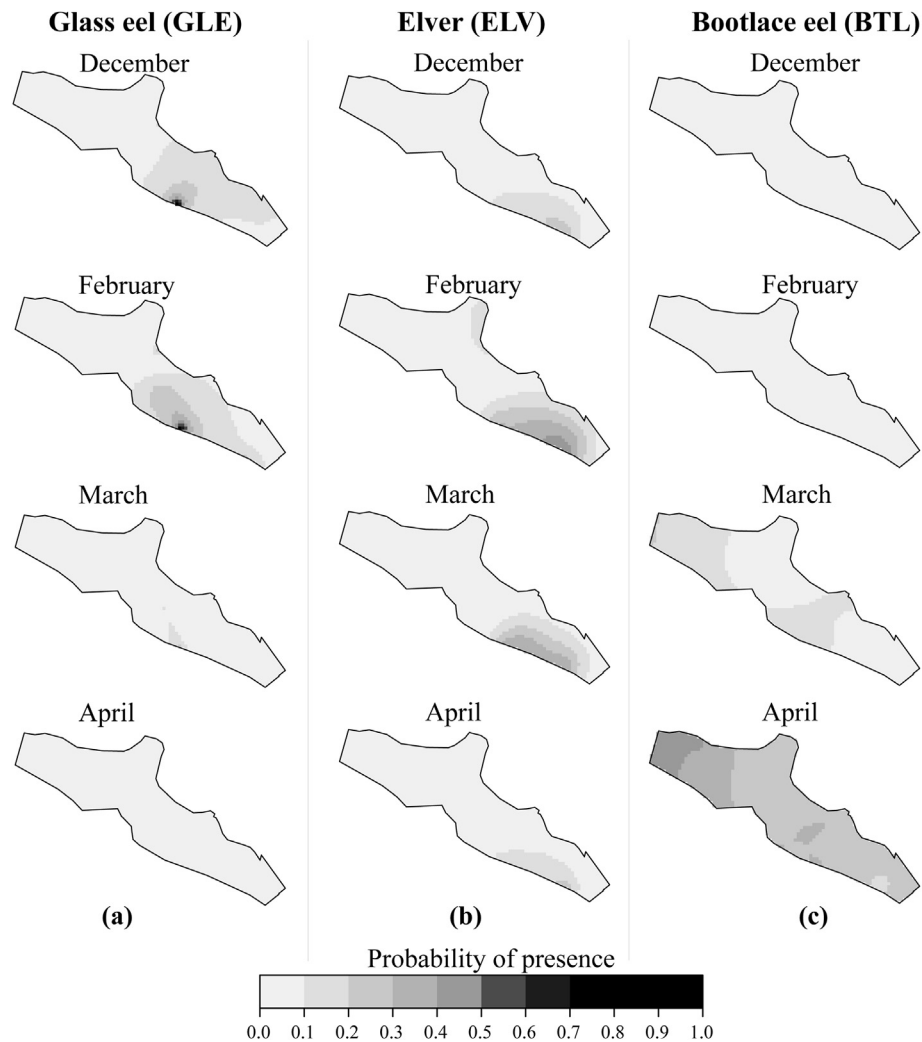
Fig. 4. Model's prediction of the probability of presence of GLE (a), ELV (b) and BTL (c) in the whole basin. The maps show the monthly evolution of the eel estimated probability of presence during the sampling campaigns carried out in December, February, March and April.

exceeds 5 or 6 °C, glass eel entrance into colder waters may be prevented (Gandolfi et al., 1984; Jessop, 2003; Edeline et al., 2006). On the other hand, seasonal water temperatures influence movements of the younger eel stages (elver and bootlace stages) within the lagoon. Most studies explain that warmer water temperature is positively correlated with active swimming, growth, metabolism and pigmentation in both Atlantic and Pacific eel (Haro and Krueger, 1988; White and Knights, 1997; August and Hicks, 2008; Edeline et al., 2006; Luers et al., 2011).

The overall *environmental gradients* in the lagoon are also important, although to different degrees for the three stages, as outlined by the role of chemical (salinity and to a lesser extent oxygen) and morphological (distance from the tidal channel, distance from freshwater inputs) parameters. Within a lagoon, environmental variables generally generate specific gradients that depend upon two main parameters: the saltwater/freshwater balance and the degree of confinement (Miller et al., 1990; Guelorget and Perthuisot, 1992). Our results on glass eel and elver distribution and spreading around the lagoon arise from this structuring of environmental gradients across the lagoon. Once entered, glass eels remain in the area under marine influence in the initial phase of recruitment, consistent with the results obtained by other authors (e.g. White and Knights, 1997; Feunteun et al., 2003; Edeline, 2007;

Trancart et al., 2014). During this phase, glass eels are still unpigmented, and they undergo a period of adaptation that involves onset of pigmentation, swim bladder activation and beginning of active swimming, or the so called counter-current swimming (Trancart et al., 2014). The definitive settlement, when elvers move across nearby areas under freshwater influence, confirms the high importance of the *freshwater appeal* for driving movements of juvenile eels. According to Tosi et al. (1990), Tosi and Sola (1993) and Sola and Tongiorgi (1996), this is due to specific olfactory cues attracting elvers, which has also been pointed out by Jellyman and Lambert (2003) and Crivelli et al. (2008). Freshwater appeal causes young eel to move differently in lagoons with respect to what is observed in estuarine and river systems. This causes a redistribution and settlement of eel along the specific environmental gradients inside the lagoon.

An important parameter to be considered is *tide*, which is coupled to the moon phase, a relevant factor in controlling glass eel upstream migration in estuaries (Gascuel, 1986; Elie and Rochard, 1994; Tesch, 2003). The influence of tidal cycles and *moonlight* on glass eel movement has been well documented (Sorensen and Bianchini, 1986; Ciccotti et al., 1995; Jellyman and Lambert, 2003; Crivelli et al., 2008; Zompola et al., 2008; Sullivan et al., 2009). In our study, even though, glass eels have been observed in respect

with new moon and first quarter moon, model predictions did not reveal a correlation. This factor might therefore not play a role in driving glass eel movement when already inside the lagoon, contrary to what happens for glass eels recruiting in an estuarine area or in a channel where they still move by Selective Tidal Transport (STT) (Wippelhauser and McCleave, 1987; for review see Harrison et al., 2014). Therefore, tide will probably influence glass eel recruitment most likely at the interface sea-lagoon, specifically at the entrance of the channels connecting the lagoon to the sea. Whereas tidal amplitude along Mediterranean coasts is reduced, it still induces tidal currents through the sea channels, which allow the exchange of water, dissolved elements and suspended matter, as well as organisms between the lagoon systems and the open sea. To tidal currents, water movements driven by winds and by coastal drift will also add, enhancing or reducing the exchange. Compared to Atlantic estuaries and lagoons, however, Mediterranean coastal lagoons are overall less affected by the tide (Elliott and Hemingway, 2002). This can explain why we failed to observe a clear relationship between glass eel presence and coupled moon and tide. The modest flows in the channels and the limited tidal range of most lagoons - especially in the Mediterranean Sea, where tidal currents are too weak to orientate massively glass eels towards the inlets to lagoons systems - may quantitatively limit glass eel and other marine fish recruitment. Hence, in coastal lagoons, recruitment of marine fish such as eel is more affected by the efficiency of the sea connections due to their morphology and management regime and to its resulting hydro-dynamism (Crivelli et al., 2008).

A factor possibly influencing juvenile eel settlement in lagoons is *food availability*. Several authors have suggested that eels do not feed throughout metamorphosis up until their arrival and definitive settlement in brackish and freshwaters (Tesch, 1977; Lee and Lee, 1989; Lecomte-Finiger, 1992; Kawakami et al., 1999). The results of this study suggest weak interactions between presence of both zoo-benthic prey and glass eel; among the potential preys, Chironomids and *M. insidiosum* was shown to be associated with a high probability of presence of glass eels. These are the only taxa tolerant to low salinities, and their distribution in the lagoon might be driven by the same environmental gradients that drive glass eels, which could be the possible explanation of these finding.

Contrary to what was expected, the presence of potential preys does not seem to play any role in driving neither elver distribution, nor bootlace eel throughout the lagoon. This may be explained by taking into account the feeding habits of eel at these stages. Young eels are opportunist feeders consuming benthos. Temperature and food supply have been widely individuated as environmental factors related to the growth of eel, because of the temperature role in influencing eel metabolism, mobility and therefore search for food (Yalçin et al., 2006). On the basis of these observations, our findings on ELV and BTL feeding activity could be explained because of the inhibition due to the low temperature of waters, and for a failure of synchrony, in terms of seasons and stations, among presence/density of eels and presence/density of potential preys (Dörner et al., 2009).

On the whole, the present study has provided information on the behavioural and environmental processes modulating eel recruitment and settlement to coastal lagoons. These habitats are particularly important for this species, characterized by an overall plasticity of habitat use, which begins at the juvenile stage, as confirmed by our findings. This plasticity is particularly evident in lagoon environments, where growth rates and habitat use show typical patterns that are different from those observed in rivers and coastal habitats at more northern latitudes (Capoccioni et al., 2014), which also concerns recruitment and settlement dynamics. The prevailing habitat use behaviour in Mediterranean transitional waters is residency, whereas nomadic behaviour is less frequent

(Capoccioni et al., 2014). Moreover, with respect to Northern European environments, high productive coastal lagoons provide a more favourable condition for growth, and therefore show higher growth rates (Melia et al., 2006; Bevacqua et al., 2012) as phenotypic growth is positively correlated with latitude and temperature (Vollestad, 1992). Again, the knowledge of how fish use their habitat in space and time throughout their life span appears to be fundamental for understanding their ecology and population dynamics, and to determine habitat properties important for the development of effective conservation measures (Gillanders, 2003).

For eel, a management framework aimed at the recovery of the global stock is currently ongoing under a specific European Regulation (EC Council of the European Union, Regulation 1100/2007). It has been suggested that Mediterranean coastal lagoons might play an important role (Dekker, 2003b; ICES, 2007; Aalto et al., 2015), because they constitute an important share of the overall continental habitat of the eel. The general decrease in recruitment has been one of the causes of the decline in eel production in Mediterranean coastal lagoons (Aalto et al., 2015). Other causes are the progressively declining water quality, overfishing and the reduced management efficiency that also have affected overall fish production and hence eel (Pérez-Ruzafa and Marcos, 2012, Katselis et al., 2013) in these sensitive habitats. If on the one hand the overall level of recruitment determines the general order of magnitude of recruitment, it should on the other hand also apply that site-specific factors play a significant role in determining fine scale distribution patterns of recruitment at an individual catchment level. Our results point to the fact that an optimal management of coastal lagoons, in particular maintaining the efficiency of tidal channels and preserving freshwater inputs, might prove to be a measure to sustain juvenile eel recruitment at the local level, thus sustaining local stocks which has also been pointed out by Crivelli et al., 2008. This, coupled to measures aiming at sustaining and protecting the escapement of breeders from coastal lagoons in the Mediterranean could contribute to restoring the stock of this unique species.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2016.01.005.

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