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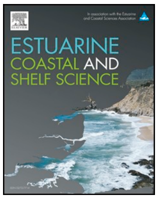

Tides and moon drive fish movements in a brackish lagoon

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ABSTRACT

Brackish lagoons, on the edge between marine and freshwater ecosystems, are vulnerable aquatic environments that act as nursery grounds for several of the most commercially exploited fish families. We used long-term passive gear data, to investigate whether the moon and tides affected fish movement between inner and outer habitats in a Northern Mediterranean coastal lagoon. In particular, we used multivariate, threshold and non-linear correlation analyses to explore the relationship between fish catches and moon and tide variables in transitional habitats, accounting for the presence of potential prey and other major temporal and environmental variables. Fish movements between habitats were influenced by moon and tide factors, which had effects comparable to annual and seasonal variations, respectively. Overall, the magnitude of effects related to the moon parameters were smaller than most environmental parameters examined, but still larger than e.g. the presence of invertebrate prey (lagoon shrimp) or some of the tide factors. European flounder catches were positively correlated with disk illumination, while sand and black goby were influenced by the moon phase. Other benthic and pelagic species showed no significant correlation. Tide direction affected negatively the movement of boxlip mullet and tide amplitude prior to sampling had far more effect than tide amplitude during sampling. Water temperature, salinity and the presence of invertebrate prey (grey shrimp) had significant but contrasting effects on some, but not all, of the species examined. Ultimately, this information could improve the understanding of the drivers in these ecosystem as well as potentially provide useful insights for improved fisheries management.

1. Introduction

Brackish lagoons are some of the most important and vulnerable aquatic environments worldwide, sitting on the edge between marine and freshwater ecosystems (Newton et al., 2014). Their biotopes thrive on a delicate balance between multiple factors where salinity plays a key role (Blaber and Blaber, 1980; Gelin et al., 2001; Young et al., 1997). Some species have adapted specifically to this balance and complete their whole life cycle in coastal lagoons (e.g. the sand goby *Potamoschistus minutus*, Leitão et al., 2006). However, both marine and freshwater fish species can temporarily inhabit lagoons, when the environmental conditions allow their presence (Franco et al., 2008). Furthermore, brackish lagoons constitute nursery grounds for several of the most commercially exploited families of marine fish such as Pleuronectidae, Sparidae or Clupeidae (Tournois et al., 2017). Juvenile fishes might reside in coastal lagoons for a variable amount of time, since some of the lagoon habitats can provide abundant prey and refuge from predators (Beck et al., 2001). Yet, despite their reduced movement capabilities, juveniles can and will move from one habitat to the other within the lagoon to capitalize on the available resources (Verdiell-Cubedo et al., 2013), often transitioning to coastal waters. However, while much effort has been devoted to investigate the role of these habitats in juvenile fish growth (e.g. Tournois et al., 2017), much less is known about the factors that affect fish movement between inner and outer lagoon habitats.

Fish movement has been traditionally investigated in the field using tracking systems, which can identify the position of single individuals equipped with passive or active transmitters to a certain degree of precision (Abecasis and Erzini, 2008; Gonzalez and Gerlotto, 1998; Hussey et al., 2015). Alternatively, some insights could also be derived through the capture of individuals with passive fishing gear, provided that the gear is operated in a suitable position (i.e. on movement routes, e.g. channels between different habitats). This is very well known to fishermen, who traditionally set their gears in these positions in an attempt to maximize their catches. Some insights could be derived from catches and traditional knowledge but fishermen's knowledge has not yet been fully recognized as relevant for the management of marine fish resources (Johannes and Hviding, 2000). Among this traditional knowledge, there is a wealth of contrasting theories about the effects of the moon and tides, which are yet to be thoroughly investigated. Perhaps the most famous is the “Solunar” theory, which is at the origin of tables claiming to predict periods of increased fish activity based on

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lunar, tidal and solar information (Knight, 1942). Moon cycles are supposed to affect catches through an influence on the behavior and movements of fishes (Banks, 1969; Stoner, 2004), but neither their effect nor mechanisms seem to be fully understood.

There are multiple ways in which the moon can affect fish movement, but these could be simplified in two categories: primary (i.e. gravitational) and secondary (i.e. illumination and tide influence) effects (Kuparinen, O'hara, & Merilä, 2009). Primary effects would assumedly be regulated by the presence/absence of the moon in the sky, while secondary effects would also be modulated by the moon phase (waxing or waning) and the disk illumination (Battaglia et al., 2017; Griffiths, 1999; Kuparinen et al., 2010). The moon cycle and its position in the sky can also affect tides: tides move water in and out of the lagoon, therefore potentially exerting a strong influence on juvenile fishes, which are poor swimmers and might be dragged by tidal currents but could also be adapted to exploit these currents to move between different foraging grounds (Bennett et al., 2015; Childs et al., 2008; Næsje et al., 2012). Some of these effects have been recognized as relevant factors in fisheries catches (Pulver, 2017), and it has been suggested that they could potentially affect our estimates of population size (Stoner, 2004).

The Mediterranean Sea could be a prime ground to test whether fishermen knowledge on moon and tides reflects actual patterns in juvenile fish movement between marine and brackish habitats. In this area, coastal lagoons are prime nursery areas for juvenile fish and have also been the focus of extensive ecological research and environmental monitoring (e.g. Aschonitis et al., 2017; Franco et al., 2006; Zucchetta et al., 2010), creating ideal conditions for further research. The Fattibello Lagoon, in the Northern Adriatic Sea, hosts a long-standing fishing tradition with lift nets along channels, which could act as fish pathways both within the lagoon and between the freshwater and marine environments. We thus used traditional passive fishing gear operated in channels to gauge fish presence in transitional habitats of a coastal lagoon in northern Italy. Based on local fishermen knowledge, we hypothesized that both moon and tides would have a significant effect on the movement of fish between marine and brackish habitats, with new moon and rising tide constituting the best conditions for movement. Specifically, we hypothesized that new moon phases would favor the movement of fish during the day and that marine fishes would enter the lagoon on flooding tides. We used multivariate, threshold and nonlinear correlation analyses to explore the relationship between fish catches and moon and tide variables, taking also into account the presence of potential prey and other major temporal and environmental variables. Ultimately, this information would not only test whether there is a basis for traditional knowledge, but also improve the understanding of the drivers in these ecosystem as well as potentially provide useful insights for improved fisheries management.

2. Materials and methods

2.1. Study area

This study focused on the Fattibello Lagoon, a small (ca. 700 ha) brackish (salinity ca. 13–31) lagoon in the north-western shore of the Adriatic Sea (Fig. 1). It constitutes the northernmost part of the Comacchio Lagoons, an area renown worldwide for its long-standing tradition in extensive aquaculture of European eel (*Anguilla anguilla* L.). The Fattibello Lagoon is connected to the sea through the Navigabile and Logonovo channels, two large waterways which are nowadays used mostly for recreational boat transit. The Navigabile Channel also extends inland and, together with the Fosse Foce Channel, can occasionally input freshwaters into the lagoon. Both channels are transitional habitats, used by marine and brackish fishes to move between sea and lagoon environments, constituting the only passage between the two.

Depth varies from a minimum of a few centimeters on the shallowest sandbars to a maximum of 3 m in the deepest channels (average depth 1 m). The lagoon substrate is also very variable, including muds and silts as well as sands and harder substrates (mussel beds, shell hash). Water currents reshape the softer sediments, sometimes creating temporally shifting patterns of sandbars. The average tidal event in this area has a magnitude of approximately 40 cm, but tidal range is rather variable (5–90 cm tidal amplitude).

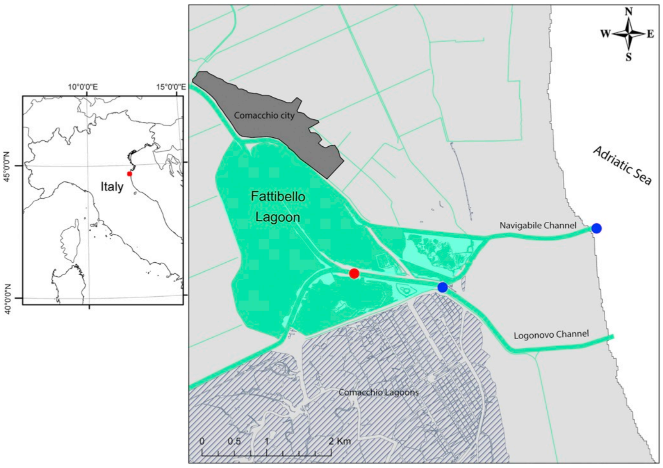

Fig. 1. Map showing the location of the Fattibello Lagoon and its area, as well as the sampling point (red dot) and location of the water chemistry and tide probes (blue dots). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The high habitat complexity and variability, as well as the connection to the sea, make this lagoon an ideal nursery for several fish species of commercial interest, including European eel, European flounder, European seabass and gilthead seabream.

2.2. Fish sampling

A total of 32 fish sampling events were carried out over the span of 6 years, between 2009 and 2014 (Table 1). Sampling events were not equally distributed in all years but, in each year, covered at least the relevant seasons when juveniles of marine species are present in the lagoon. In 2011, at least one sampling event was carried out in each month, to ensure that the full year spectrum was taken into account.

Fish sampling was performed using stationary lift nets, a traditional fishing method in the area adapted to capture also juvenile individuals. Lift nets are 15 × 15 m square nets with an outer mesh of 12 mm, a second of 8 mm, and an inner one of 6 mm. Nets are operated from a sheltered housing through a series of beams and pulleys, which keep the net stretched and lower it into the water until the bottom; the net is subsequently lifted through the same system, capturing the fish in the water column and collecting them in the inner mesh. Sampling was undertaken at a fixed location on the banks of the Logonovo Channel, at the entrance of the Fattibello Lagoon and about 700 m inland from the sea (Fig. 1). Given this setup, the amount and composition of the catch in each sampling event depended on the number of net lifts. Each net lift captured a number of individuals of different species of fishes (each with their own catchability) moving through the channel and over the net area when it was being lifted. All catch data was converted in catch per unit of effort (CPUE, based on number of net lifts) to account for different sampling efforts.

All captured fish specimens were identified to the species level, measured (total length, TL, to the nearest mm) and weighted with a resolution of 0.1 g. When samples contained a large amount of individuals of the same species, a subsample of 100 specimens was randomly selected to be measured in detail. Freshwater species were occasionally sampled but were not retained in this analysis.

Table 1
Sampling event schedule detailing for each event its effort as well as its duration and timing.

Fishing event	Date	Start Time	End Time	Total duration (hours)	N of net lifts
1	3/25/2009	19:25	20:22	0:57	12
2	4/14/2009	20:35	21:42	1:07	19
3	4/24/2009	19:45	21:25	1:40	18
4	5/7/2009	17:50	20:25	2:35	12
5	3/4/2010	13:52	18:50	4:58	29
6	3/25/2010	16:18	20:57	4:39	30
7	5/11/2010	18:20	22:30	4:10	32
8	9/23/2010	17:30	21:38	4:08	30
9	1/20/2011	10:20	19:20	9:00	32
10	2/9/2011	13:20	22:00	8:40	27
11	4/18/2011	18:10	23:30	5:20	15
12	5/10/2011	17:40	23:00	5:20	15
13	6/7/2011	16:20	21:40	5:20	17
14	6/28/2011	17:00	22:40	5:40	17
15	7/14/2011	16:30	22:30	6:00	18
16	8/8/2011	13:00	19:10	6:10	19
17	9/9/2011	16:20	21:40	5:20	15
18	10/20/2011	15:45	21:45	6:00	18
19	11/22/2011	12:50	19:15	6:25	19
20	12/2/2011	13:00	18:00	5:00	17
21	3/28/2012	17:30	23:00	5:30	15
22	5/16/2012	17:10	22:40	5:30	15
23	6/13/2012	16:40	22:20	5:40	17
24	9/15/2012	16:20	18:00	1:40	14
25	10/20/2012	15:50	19:30	3:40	14
26	5/22/2013	16:20	21:40	5:20	17
27	7/14/2013	15:00	16:10	1:10	12
28	2/24/2014	15:50	21:00	5:10	15
29	3/12/2014	16:20	19:35	3:15	14
30	3/20/2014	14:30	19:30	5:00	16
31	4/14/2014	15:30	20:10	4:40	16
32	4/22/2014	14:10	20:20	6:10	17

2.3. *Environmental parameters*

To account for seasonal and annual factors, both the month (*Month*) and the year (*Year*) of sampling were used as environmental parameters in our analysis.

Moon data were derived through an online application of the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneDay.php) using the location and date of fishing as input parameters. Both the moon phase itself (waxing or waning, *MoonPhas*) and the percentage of illuminated moon disk (*%Disk*) were used in the analysis, as these two parameters are able to describe accurately the aspect of the moon as seen from earth. Additionally, we used moon rise and set times to estimate the share of fishing time that was carried out while the moon was in the sky (*MoonPres*), under the assumption that moon presence in the sky could have an additional effect on fishes.

Tide data were recorded by an automated tide station (OTT LOGOSENS), equipped with both radar and floater measuring systems. The station is positioned at the outlet of the Navigabile Channel, roughly 700 m seaward from the sampling location, and operated by the Emilia-Romagna Region Environmental Protection Agency (*ARPA Emilia Romagna*). A time delay of 30 min was applied to the data, to account for the different timing of tides between the tide station and the Fattibello Lagoon (derived from spot measures comparing tidal times at the tide station and at the fish sampling location). Both prevalent tide direction (i.e. the most represented tide direction during sampling, *TideDir*) and tide amplitude (i.e. the maximum recorded amplitude during sampling, *TideFish*) were used in the analysis, as well as the direction (TideDirPrev) and total amplitude (*TideMax*) of the strongest tide event prior to sampling. The latter was used in order to account for factors that could potentially influence fish presence before sampling began.

Dissolved oxygen (*DO*), salinity (*Salinity*) and temperature (*Temp*) of the water were also measured by the Emilia-Romagna Region Environmental Protection Agency (*ARPA Emilia Romagna*) with a multiparametric probe (OTT DUOSENS) in the Logonovo Channel, in close proximity of the sampling site. The probe logs data with an hourly resolution, but an average daily value for each of the three parameters was considered as representative for each sampling event. These parameters had no significant spatial variations between the probe location and the fish sampling location, as verified by spot measures performed during sampling.

As crustaceans prey has been suggested as a relevant factor for the distribution of some species by previous studies (Maree et al., 2016), small-sized crustaceans captured while sampling fishes were also tested as environmental descriptors (*LagoonShrimp*). Crustacean catches comprised two relevant species: the grey shrimp (*Crangon crangon* L.) and the lagoon shrimp (*Palaemon* spp.), but these were caught only occasionally (13 out of 32 events), and their total biomass in the catch never exceeded a total of 1.2 kg per sampling event. These species constitute a relevant food resource for several fish species in the Fattibello Lagoon (e.g. for European eel, Lanzoni et al., 2018; and for other species, Lanzoni, unpublished data) and in other Mediterranean lagoons (Rogdakis et al., 2010; Sá et al., 2006).

2.4. *Statistical analysis*

In order to explore the relationship between fish catches and environmental factors (seasonal, annual, moon, tidal, dissolved oxygen levels, salinity, temperature and the presence of crustacean prey) multivariate statistics were employed. A Detrended Correspondence Analysis (DCA) was initially performed to select the most appropriate response model for gradient analysis (Lepš; Šmilauer, 2003). The dominant gradient length in DCA was always lower than 3 so the Redundancy Analysis (RDA) was finally chosen (Lepš; Šmilauer, 2003). RDA is a linear gradient analysis that allows to quantify the variation of a multivariate data set explained by independent variables (Ter Braak and Smilauer, 2002). The month and year of sampling (to account for seasonal and annual factors), as well as the moon, tides, environmental and crustacean prey variables were considered as independent parameters, whereas the CPUEs of each fish species were considered as dependent. All environmental and fish CPUE data were $\log_{10}(X+1)$ transformed, except moon disk illumination which was arcsin transformed. Rare species sampled in less than 3 sampling events were excluded from the analysis to avoid distortions. Variables were investigated through Variance Inflaction Factor to exclude collinearity problems, however no variable was found to be collinear. These analyses were performed using the CANOCO 4.5 *for Windows* software (Lepš; Šmilauer, 2003).

We used the Spearman rank test to investigate the presence of correlations between single fish species and moon and tide factors. We also used the Threshold Indicator Taxa ANalysis (TITAN, Baker and King, 2010) on all environmental parameters to identify the environmental threshold (the optimum value of a continuous variable) that partitions sampling units and distinguishes negative (= losses: z−) and positive (= gains: z+) taxon responses. Thus, TITAN helps to identify taxon-specific change points along an environmental gradient at which the decline/increase in a given taxon's frequency and abundance is most prominent. Bootstrapping (500 repetitions) was used to estimate two important diagnostic indices (reliability and purity) as well as uncertainty around the location of individual taxa and community change points (Baker and King, 2010). Both Spearman correlations and TITAN analysis were performed using R software (R Core Team, 2017).

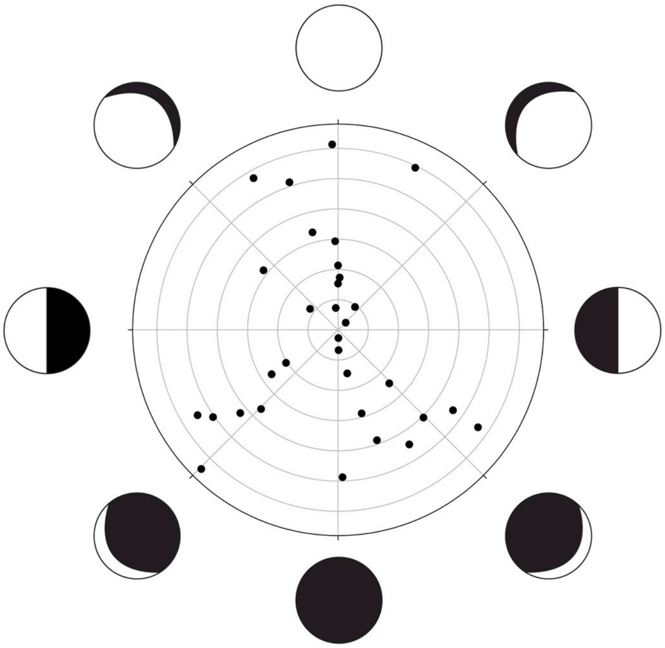

Fig. 2. Moon disk illumination and its phase. Each point represents a fishing event, with the angular position indicating the exact moon phase (waxing or waning and degree of illumination). The distance of each point from the center represents the progressive number of sampling events.

3. Results

Sampling collected a very variable amount of fish: from 0.49 to 38.2 kg captured in a single event. CPUE also varied widely, from a minimum of 56.2 g to a maximum of 1378.7 g of fish per net lift. A total of 36,336 individuals of 32 different fish species were captured, belonging to 19 families (Table 2).

Sampling events were rather equally distributed between waning (17 events) and waxing (15 events) moon phases, with two events occurring when the moon was full (Fig. 2). However, a smaller amount of

Table 2
List of fish species captured in the Logonovo Channel between 2009 and 2014, detailing the number of individuals per each species, their average size (in cm) and its standard deviation.

Family	Scientific name	Common name	Number of individuals	Average size (cm)	Standard Deviation
Anguillidae	*Anguilla anguilla*	European eel	78	24.3	12.0
Atherinidae	*Atherina boyeri*	Big scale sand smelt	5050	6.7	2.0
Belonidae	*Belone belone*	Garfish	3	38.0	3.8
Blenniidae	*Salaria pavo*	Peacock blenny	2	8.9	1.2
Clupeidae	*Alosa fallax*	Twaite shad	26	12.4	5.4
	Sprattus sprattus	European sprat	8484	5.8	1.2
Cyprinodontidae	*Aphanius fasciatus*	Mediterranean banded killifish	9	3.7	0.2
Engraulidae	*Engraulis encrasicolous*	European anchovy	12398	7.4	2.4
Gobiidae	*Zosterisessor ophiocephalus*	Grass goby	15	11.2	3.0
	Pomatoschistus canestrinii	Canestrini's goby	191	4.8	1.2
	Knipowitschia panizzae	Adriatic dwarf goby	50	3.5	1.0
	Pomatoschistus minutus	Sand goby	55	4.2	0.8
	Gobius niger	Black goby	27	8.0	1.3
	Gobius paganellus	Rock goby	133	8.0	2.1
Moronidae	*Dicentrarchus labrax*	European seabass	17	10.9	3.5
Mugilidae	*Liza ramada*	Thinlip mullet	1463	11.5	6.9
	Liza aurata	Golden grey mullet	320	13.4	6.7
	Liza saliens	Leaping mullet	368	10.2	5.1
	Mugil cephalus	Flathead grey mullet	24	10.5	9.1
	Chelon labrosus	Thicklip grey mullet	18	11.9	7.0
Mullidae	*Mullus barbatus*	Red mullet	225	8.0	1.7
Pleuronectidae	*Plathychtys flesus*	European flounder	986	7.2	3.3
Sciaenidae	*Pagellus bogaraevo*	Blackspot seabream	1	7.8	–
	Umbrina cirrosa	Shi drum	2	14.2	5.4
Scombridae	*Scomber scombrus*	Atlantic mackerel	11	7.5	4.2
Scophthalmidae	*Scophthalmus maximus*	Turbot	2	7.3	1.1
Soleidae	*Solea solea*	Common sole	267	5.6	3.0
Sparidae	*Sparus aurata*	Gilt-head bream	84	7.2	3.4
	Diplodus vulgaris	Common two-banded seabream	1	7.5	–
Syngnathidae	*Sygnatus acus*	Greater pipefish	76	12.3	3.6
	Sygnathus abaster	Black striped pipefish	15	9.4	3.3
Triglidae	*Chelidonichthys lucerna*	Tub gurnard	14	7.3	3.8

fishing events occurred between the first quarter and the full moon (Fig. 2). The vast majority of fishing events occurred while the moon was either always in the sky (15) or not in the sky at all (11), with only few events (a total of 6) between these two extremes.

Tide direction during fish sampling was unevenly distributed: most fishing events (19) occurred with flooding tide, a smaller part (8) occurred with ebbing tide and only few (5) with dead tide (Fig. 3). Tide magnitude during sampling events showed greater variations, with a minimum of 0.003 m and a maximum of 0.807 m level variation. Tide direction in the period before sampling events was relatively evenly distributed, with only one period of dead tide and the other periods distributed among flooding (13 events) and ebbing (18 events). Tide magnitude in the period before sampling varied from 0.066 to 0.889 m water level variation.

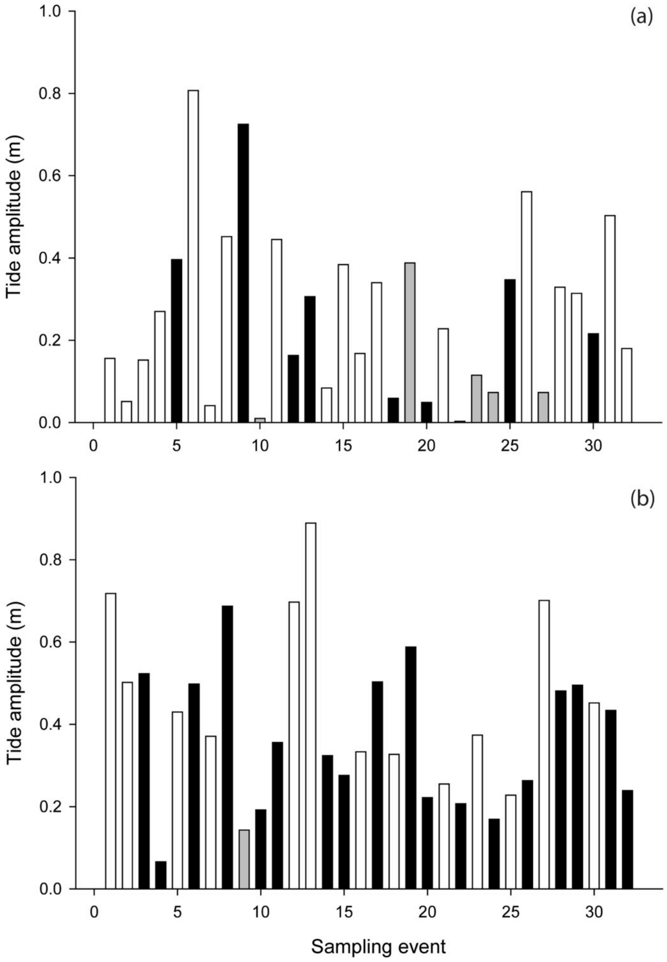

Fig. 3. Tide amplitude during (a) and right before (b) each sampling event. Bar colors indicate whther sampling occurred during prevalent flowing tides (white), dead tides (grey) and ebbing tides (black).

RDA analysis confirmed the relevance of moon and tide factors, which had effects comparable to annual and seasonal variations, respectively (Fig. 4). Overall, the RDA had a fair explanatory potential (the horizontal axis explained 35.2% of the fish data variance, the vertical axis 20.2%). Moon phase (waxing or waning) and duration of moon presence in the sky during sampling had greater effects than the actual illumination of the moon disk. Overall the magnitude of effects related to the moon parameters were smaller than most environmental parameters examined, but still larger than e.g. the presence of lagoon shrimp and some of the tide factors. Tide direction (ebb or flood) during sampling had a greater effect than tide direction prior to sampling. Conversely, tide amplitude prior to sampling had far more effect than tide amplitude during sampling.

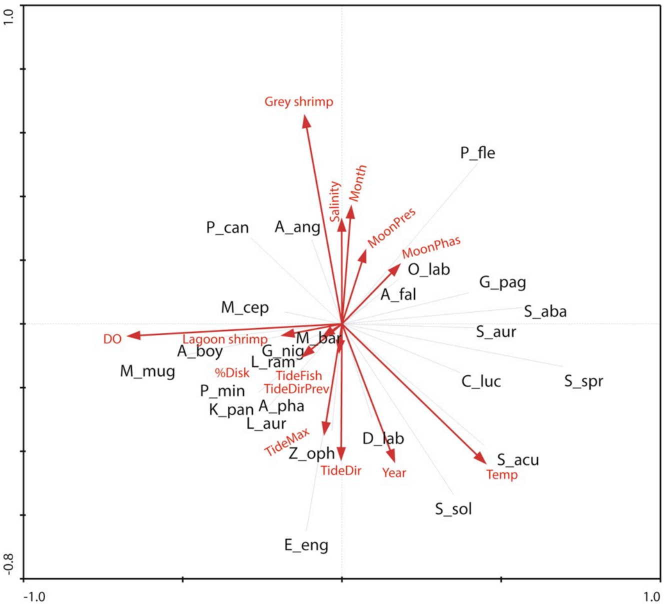

Fig. 4. Redundancy analysis (RDA) triplot showing the relationships between fish species (black labels) and environmental parameters (red arrows and labels). Fish species labels consist of abbreviations where the first letter is the initial of the genus and the three following are the first letters of the species name. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Disk illumination had an overall weak effect on fish (Fig. 4). Some of the highest CPUE of European flounder were sampled during periods of high moon illumination (Spearman rank $P = 0.05$, correlation coefficient 0.34, Fig. 4), but there was no significant correlation with other moon parameters. Other benthic species (i.e. gobies) showed different degrees of correlation with moon variables: the Spearman Rank P was > 0.12 for most goby species and all moon parameters considered, with the exception of sand goby (Spearman Rank $P = 0.06$, correlation coefficient -0.33) and black goby (Spearman Rank $P < 0.05$, correlation coefficient -0.4) which negatively correlated with moon phase. However, moon variables were also poorly correlated with pelagic species (European anchovy and sprat, Spearman Rank $P > 0.09$ for all moon parameters and both species). Tide direction negatively affected boxlip mullet and garfish (Spearman Rank $P < 0.05$, correlation coefficients of -0.47 and -0.38, respectively) but the latter was only caught once. On the other hand, maximum tide amplitude positively affected European anchovy (Spearman Rank $P = 0.05$, correlation coefficient 0.35). However, the other fish species seem not to be affected by tides (Spearman Rank $P > 0.09$ for all species and tide parameters).

Water temperature was a significant factor for several species movement (Fig. 5a). Common sole and red mullet had significant but opposite threshold for salinity (Fig. 5b). European flounder presence in the catch was correlated with the catch of grey shrimp (Fig. 5c).

4. Discussion

Our results confirmed that juvenile fish movements in the Fattibello Lagoon were indeed influenced by moon and tide factors, which had effects comparable to annual and seasonal variations, respectively. Overall, the magnitude of effects related to the moon parameters were smaller than most environmental parameters examined, but still larger than e.g. the presence of invertebrate prey (lagoon shrimp) or some of the tide factors. Contrarily to the fishermen knowledge and our initial hypothesis, European flounder movement was positively correlated with disk illumination, while sand and black goby were influenced by

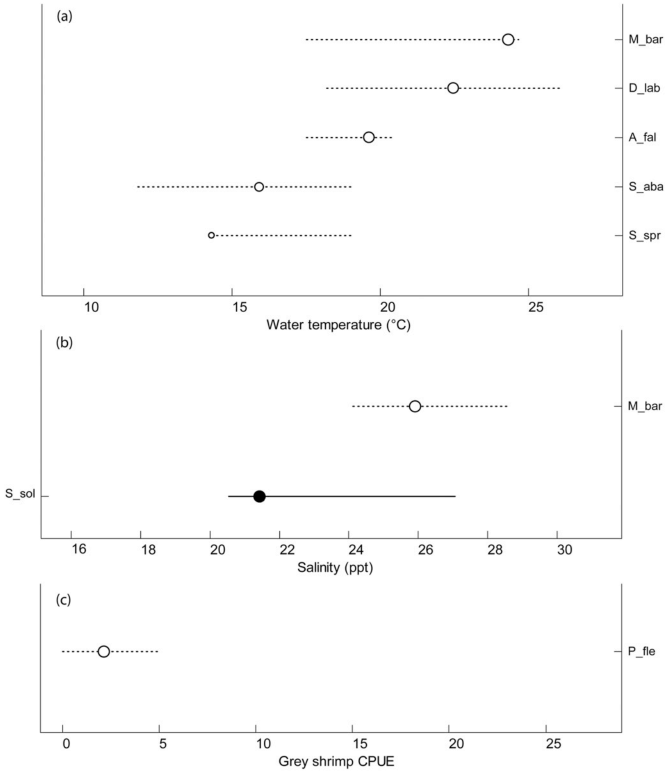

Fig. 5. Significant thresholds for different taxa along temperature (a), salinity (b) and presence of grey shrimp in the catch (c), according to the TITAN analysis. Lines represent the 95% Confidence Interval of the bootstrapped distribution across the gradient, with circles identifying the species change points across the gradient. Solid lines and circles represent species that decline along the gradient (listed on the left axis), while dashed lines and empty circles represent species which distribution increases along the gradient (listed on the right axis). Species not shown in these figures have a distribution not predictable according to the environmental gradients examined.

the moon phase. Other benthic and pelagic species showed no significant correlation. On the other hand, tide direction affected negatively the movement of boxlip mullet and tide amplitude prior to sampling had far more effect than tide amplitude during sampling, positively affecting European anchovy presence and somewhat conforming to traditional knowledge. Among other factors, water temperature, salinity and the presence of invertebrate prey (grey shrimp) had significant but contrasting effects on some, but not all, of the species examined. Ultimately, our study represents a significant albeit preliminary look at the effect of these variables, but could not completely disentangle or quantify the direct and indirect effects of moon and tide variations.

It is not yet clear if and how the direct gravitational effect of the moon could be sensed by fish or other animals, given that the sensitivity of the known body structures devoted to sense gravity (i.e. the otoliths in fish, or similar structures in other animals) do not seem to be sufficient to detect such small changes. While traditional fisheries knowledge often refers to direct effects of the moon on the catches of fish it is not easy to disentangle such effects from secondary effects. Exceptionally, Kuparinen et al. (2009) were able to investigate the moon direct influence on Atlantic salmon (*Salmo salar* L.) spawning runs in a place where secondary effects were negligible, but did not find a significant effect. In our case, moon direct effects could not be fully disentangled, as the moon creates tides even in the northern Adriatic Sea. However, strongest tides should be created during full and new moon phases because during these phases the gravitational effects of the moon and the sun are combined, creating so-called spring tides. This suggests that we should be able to detect an additional direct effect, should this effect be added to indirect effects (Stoner, 2004). Conversely, in our dataset, full and new moon phases did not correspond to higher catches of all species, suggesting that there is probably a relatively weak direct effect on the juvenile fishes of the Fattibello Lagoon.

On the other hand, among indirect effects, the illumination provided by the moon is commonly believed to provide increased light during the night, allowing fishes to effectively move and forage during this period and, as a consequence, less during daytime. An artificial supply of light has been previously investigated as a factor for fish aggregation (Becker et al., 2013), and the moon illumination could act in a similar way. If present, this effect should be all the more evident in shallow lagoons, especially where water transparency allows for a tighter coupling between moon illumination and light penetration in the water. However, this effect could be masked by other factors; the presence of a thick cloud cover or high turbidity should negate the effects of a strong moonlight. Cloud cover and water turbidity could act as regulators of the moonlight penetration in the water column, thus influencing which species could be most affected. In our results, European flounder, a benthic invertebrate predator, was mostly caught when the moon illumination was high, perhaps as a result of the increased movement during the night. However, we did not fully resolve whether there was a direct link between fishing effort distribution between day/night times and European flounder catches. That a benthic species was affected would suggest that moonlight can penetrate all the way to the bottom and therefore other fish, living in higher layers of the water column, should be even more influenced by moonlight. Yet, this was not seen in our data, since pelagic species (e.g. European anchovy) movement was not significantly correlated with moon illumination. This could partly depend on sampling timing, which often included both daylight and moonlight conditions in the same sampling event and thus mix contrasting effects. Moreover, turbidity is highly variable in the lagoon and was not recorded in our data, adding a potentially confounding factor to the interpretation of our results on moon.

Among its indirect effects, the moon influences heavily the amplitude and timing of tides, so that moon and tides cannot be analyzed separately. In our data, tide amplitude, particularly of the event before sampling rather than during the sampling, had an effect on at least some species. European anchovy and boxlip mullet, two marine species, were found to enter the lagoon with flooding tides, conforming to traditional knowledge. In this area, tides can be further enhanced by winds if the wind strength and direction push water towards the shore, which could in turn affect the presence, abundance and movement of marine fish in the lagoon (Bruno and Acha, 2015). However, this effect was not evident in a parallel study conducted on the same Fattibello Lagoon dataset (Milardi et al., 2018; under review). Flooding tides can also contribute to increase salinity in the lagoon, by bringing in saltier water from the open sea. However, in the Fattibello Lagoon, only common sole and red mullet had significant (but opposite) thresholds for salinity. Both common sole and red mullet do not spawn in brackish waters and come into the lagoon only to feed, moving in and out with the tides and following salinity gradients. It is not easy to relate our results to previously published research (Bennett et al., 2015; Næsje et al., 2012), as species-specific and local factors might come into play in these interactions. Ultimately, the lack of stronger effects of tides on all species could perhaps be attributed to the complexity of some of the habitats within the lagoon (which can shelter fish from currents) and to the wide range of species, from benthic to pelagic ones.

Some of these species (e.g. European anchovy) have a rather relevant seasonality in the commercial catches of the Fattibello Lagoon (Lanzoni, unpublished data), suggesting that temporal factors might also play a role in regulating the presence of these species in the lagoon, more than just their movements. Annual fluctuations in the population of engraulids are very well known (see e.g. Kawasaki, 1983) and this was reflected also in our data. Seasonal and annual factors were indeed some of the strongest in our multivariate analysis, but their magnitude was still comparable to moon and tide factors. However, seasonal factors could have also been at the root of the temperature thresholds found for several species, which seemed to prefer warmer waters during summer and fall rather than cold winter and spring waters. Similarly, the presence of grey shrimp in the lagoon is known to increase during the winter and spring (Lanzoni, unpublished data, but see also e.g. Spaargaren (2000)), when also European flounder enters the lagoon to spawn (Franzoi et al., 2010; Zucchetta et al., 2010). This could partly explain the linkage underlined by our analyses, but it must be noted that the catch was comprised mostly of juveniles, whereas spawners were relatively rare. Perhaps specifically-aimed studies could help to resolve prey-predator linkages in the lagoon, similarly to what was undertaken in other areas by Maree et al. (2016).

Ultimately, our data did not have the necessary resolution to fully disentangle and quantify the primary and secondary effects of moon and tidal factors. However, it was sufficiently detailed to assess that their magnitudes were at least comparable. Furthermore, our results underlined that overall moon and tides factors are potentially strong drivers for fish movement, confirming at least in part the local fishermen traditional knowledge. The Fattibello Lagoon is a good example of brackish lagoon in the Mediterranean with long standing fisheries traditions, which had not been previously investigated from the fish ecology perspective. Our results underline that this area is a spawning and feeding ground for a variety of species, as well as a vital nursery area used by juvenile individuals of several species of commercial interest. As such, it would be vital to preserve its ecological balance and its ability to provide a primary ecosystem service (i.e. healthy fish stocks). While our results might not directly translate into clear recommendations for fisheries management, they shed some further light on previously unknown ecology and movement of fishes in the lagoon and should at least be taken into account when trying to regulate fishing with passive gear.

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Appendix A. Supplementary data

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