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Contribution to the Theme Section 'Drivers of dynamics of small pelagic fish resources: biology, management and human factors'

Natural and anthropogenic effects on the early life stages of European anchovy in one of its essential fish habitats, the Guadalquivir estuary

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ABSTRACT: Essential fish habitats (EFHs) are all aquatic habitats and substrates fundamental for spawning, breeding, feeding and/or growing to maturity. Estuaries are a good example of this because they play an important role as nursery grounds for several marine species. Despite their importance for completing the life cycle of some fish stocks, little is known about how early stages of these species respond to changes within estuarine environments. Understanding the response of fish juveniles to combinations of multiple drivers in these highly dynamic ecosystems is not straightforward. By analysing an 18 yr time series of European anchovy *Engraulis encrasicolus* and 3 mysid species in the Guadalquivir estuary (SW Spain), we quantified the effects of both natural and anthropogenic factors on the early stages of this small pelagic fish and its prey. Of the factors assessed, freshwater discharges and turbidity — both influenced by human activities — showed a remarkable effect on the abundance of anchovy. Natural environmental variables such as temperature, salinity, winds and prey abundance were also important. The relationship between anchovy and mysids suggests that the Guadalquivir food web is predominantly resource-driven and that indirect environmental effects can cascade up through a web of interactions. This study provides empirical information on the response of anchovy to environmental changes within its main essential habitat in the Gulf of Cadiz. Since the human-influenced variables can be managed to some extent, we discuss their implications for maintaining a healthy EFH, which in turn would contribute to developing an ecosystem approach to fisheries management in the region.

KEY WORDS: *Engraulis encrasicolus* · Anchovy juveniles · Nursery area · Trophic control · Environmental effects · Reference points · *Mesopodopsis slabberi* · *Neomysis integer* · *Rhopalophthalmus tartessicus*

INTRODUCTION

Estuaries are among the most productive and biologically important ecosystems on Earth (Alongi 1998, Barbier et al. 2011). They supply vast numbers of goods and services such as nursery habitats, nutrient storage and cycling, climate regulation and carbon sequestration, as well as aesthetic and cultural

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benefits (Thrush et al. 2013). Estuarine ecosystems are particularly essential for fish owing to their ecological functions related to refugia for early life stages and high food availability (Beck et al. 2001, Elliott et al. 2007). These specific habitats, where fish can feed, grow, mature, breed and spawn to sustain their populations, are known as essential fish habitats (EFHs) as defined in the Magnuson-Stevens Act of 1996 (Rosenberg et al. 2000). The consideration of estuaries as EFHs is especially important if we are to develop an ecosystem approach to fisheries management (Schultz & Ludwig 2005, Link & Browman 2014, Long et al. 2015, Llope 2017).

The position of estuaries, interconnecting terrestrial and marine processes, and specific features, such as high salinity variations, high turbidity, muddy grounds and shallow depths, result in multiple combinations of conditions over space and time (Elliott et al. 2007, Cloern & Jassby 2012). On the other hand, estuaries are located at points that are highly prized by human activities and are therefore exposed to intense and increasing degradation, as coastal populations continue to expand (Kennish 2002).

In this context, the Guadalquivir estuary is not an exception (Fig. 1). Located in the northern half of the Gulf of Cadiz (GoC), Spain, with an area of influence that extends as far as the city of Seville, the estuary stands out as a key nursery area (Baldó & Drake 2002, Fernández-Delgado et al. 2007) embedded in a heavily degraded and continuously threatened setting (Vargas & Paneque 2015). The particularities of this socio-ecosystem require the consideration of multiple sectors and the corresponding conflicting interests. These include the shipping and tourism sectors, the agriculture, aquaculture, salt and mining industries, and the fisheries and conservation interests (Llope 2017). As a result of these pressures, the estuary has undergone various hydromorphological modifications over the last few decades that have

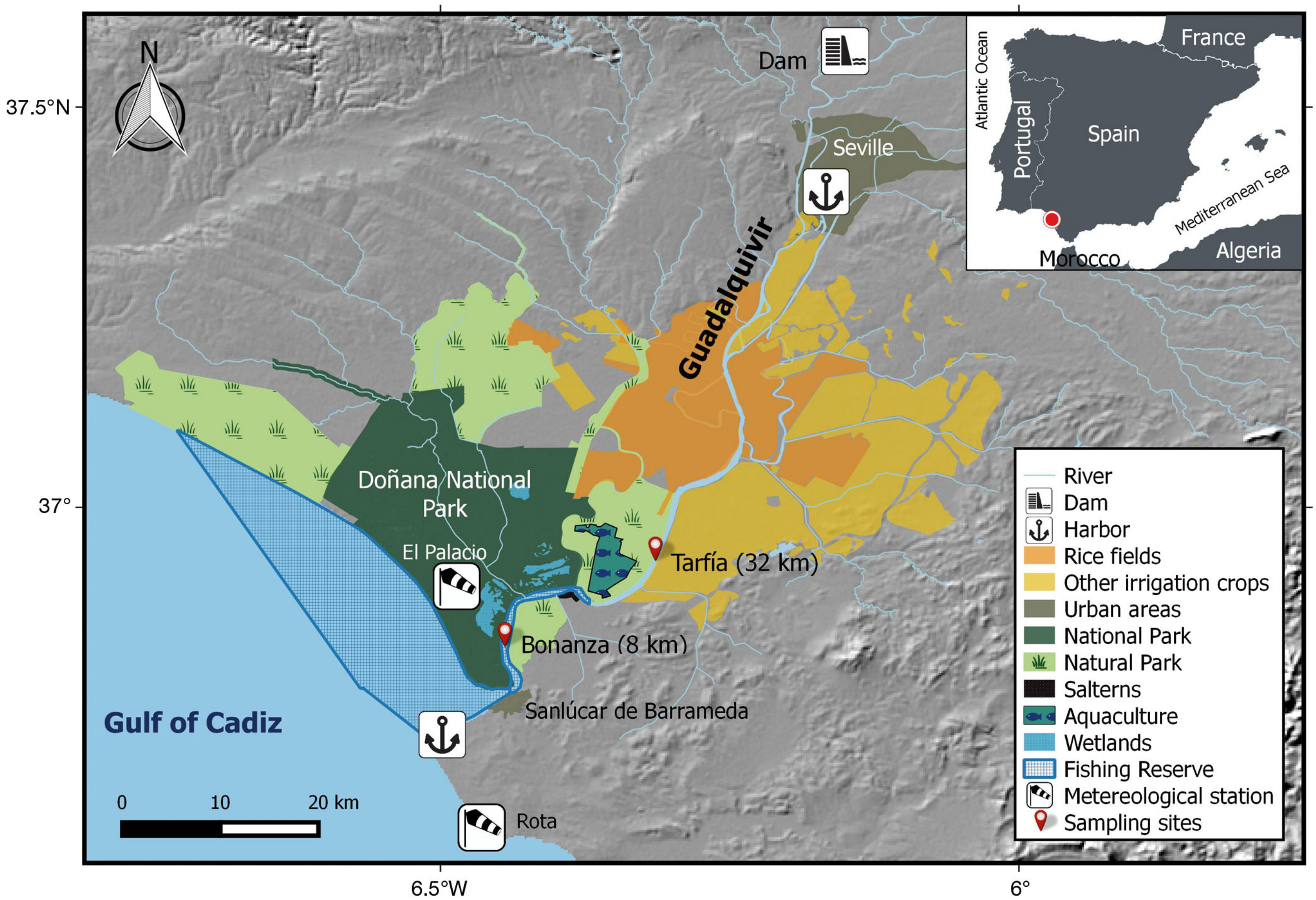

Fig. 1. Lower Guadalquivir area (SW Spain), showing the location of the 2 sampling sites — Bonanza (water masses I, II, sampled at ebb and flood tide, respectively) and Tarfía (water masses III, IV sampled at ebb and flood tide, respectively) — , Alcalá del Río dam and main land uses

resulted in alterations of its natural dynamics (del Moral 1991, Díez-Minguito et al. 2012). Today, the estuary covers an area of 1800 km^2 (Agencia Andaluza del Agua 2009) stretching over 90 km from its mouth to the Alcalá del Río dam (Fig. 1), which controls almost 80 % of the freshwater river flow (CSIC 2010).

As a short-lived species, European anchovy *Engraulis encrasicolus*, Linnaeus, 1758 is strongly dependent on recruitment and is affected by year-to-year fluctuations in environmental processes. Temperature, winds and freshwater discharges have been identified as key factors influencing its recruitment in the GoC (Ruiz et al. 2006, 2009, Prieto et al. 2009). Within the estuary, the combination of both natural (weather) and anthropogenic (discharges) effects results in a broad range of combinations that makes the ecological response of the ecosystem to freshwater inputs equivocal (González-Ortegón et al. 2010, 2012, 2015, González-Ortegón & Drake 2012, González-Ortegón & Giménez 2014). Some of these drivers (salinity, turbidity) are known to be relevant, but other factors may or may not be as important.

Previous studies have shown that 3 mysid species make up to over 80 % of total macrofauna biomass and are the major prey category of small fish (Baldó & Drake 2002). A synchrony between food availability (mysids) and the abundance of early life stages of several marine species, including anchovy, has also been reported (Baldó & Drake 2002, Drake et al. 2007), supporting the nursery role hypothesis. However, whether variations in mysid abundance have a statistical effect on anchovy has not been addressed.

Time series analyses have proven useful to reveal how populations respond to natural (climate) and anthropogenic (e.g. fishing) factors (Fernandes et al. 2010, Llope et al. 2011, Schmiing et al. 2013, Blenckner et al. 2015, Lynam et al. 2017). While the essential role of the Guadalquivir estuary as a nursery ground for the GoC anchovy stock has long been pointed out (IEO 2012), a comprehensive assessment of how the abundance of this species oscillates in response to varying environmental conditions and prey abundance is still missing.

To address this question, we developed nondeterministic statistical models (generalized additive models, GAMs) fitted to the empirical information provided by an 18 yr time series of monthly densities. GAMs are capable of modelling multiple effects and were used to estimate the combined effects that both natural (temperature, winds, precipitation) and anthropogenic (turbidity, freshwater discharges, salinity) factors have on the anchovy and mysid populations.

The goals of this study were to (1) assess how the population of this small pelagic species responds to environmental changes within its main essential habitat, (2) statistically test the effect of prey and (3) discuss the implications of these results in relation to maintaining a healthy EFH and hence contributing to a better managed stock according to ecosystem-based principles.

MATERIALS AND METHODS

Study area and dataset

The Guadalquivir estuary is a temperate well-mixed narrow estuary (Vannéy 1970) located on the Iberian margin of the GoC (Atlantic Ocean) (36° 47′ N, 04° 58′ W; 37° 25′ N, 07° 00′ W). Its tidal regime is semidiurnal, and the maximum tidal range at the river mouth is 3.86 m. The tidal influence reaches up to the Alcalá del Río dam (Fig. 1), which since 1938 controls the freshwater flow and salinity. This longitudinal gradient presents both short-term (tidal and dam-dependent) and long-term (seasonal and inter-annual) displacements along of the river course (Drake et al. 2002). Under normal or low river flow conditions (40 m^3 s^{-1}) the estuary is regulated by the dam (tidally energetic estuary). Sporadically, when freshwater discharges are greater than 400 m^3 s^{-1}, the estuary changes to a fluvial-dominated dynamic (Díez-Minguito et al. 2012) with consequences on turbidity and salinity (Díez-Minguito et al. 2013, 2014).

The dataset used in this work was compiled from several sources. Population densities and water environmental variables are the result of a long-term ecological research programme carried out between June 1997 and May 2015 in the Guadalquivir estuary (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m12562_supp.pdf). At each new moon, 2 samples were collected (each flood and ebb tide) at 2 sampling sites from a traditional river fishing boat at a standstill. Each sample consisted of a passive (tidal-powered) haul carried out during the first 2 h of each tide. Samples (both anchovy and mysids) were taken with 3 nets (10 m long, light mesh: 1 mm; net opening: 2.5 m wide and 3 m deep) working simultaneously. For more details see González-Ortegón et al. (2012, 2015). The 2 stations (Bonanza and Tarfía) are situated 8 and 32 km from the river mouth, respectively (Fig. 1). This scheme

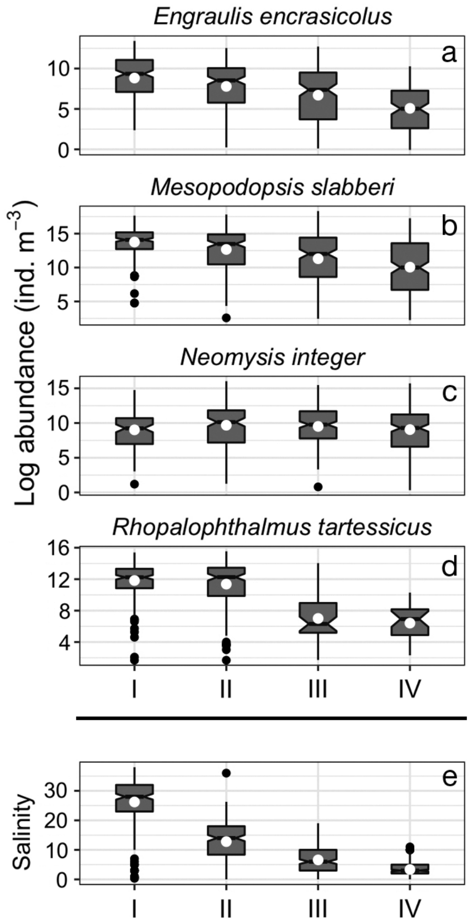

Fig. 2. Abundances of (a) anchovy and (b,c,d) the 3 mysid species, and (e) salinity in the 4 water masses (I, II, II, IV). Plots show the median, quartiles, minimum and maximum values, outliers (black dots) and means (white dots)

resulted in the sampling of 4 distinct water masses characterized by different salinities (I–IV, Fig. 2e), with a roughly monthly frequency, over a period of 18 yr. Water mass I had a mean salinity of 25.5 (sampled at Bonanza station at ebb tide), water mass II = 12.6 (Bonanza flood tide), water mass III = 6.6 (Tarfía ebb tide) and water mass IV = 3.4 (Tarfía flood tide). We considered water masses separately and did not average per station due to the considerable salinity differences observed between samples collected at ebb and flood at a given station (Fig. 2e).

Abundances of anchovy early stages (postlarvae and juveniles) and 3 mysid species, i.e. *Mesopodopsis slabberi* (Van Beneden, 1861), *Neomysis integer* (Leach, 1814) and *Rhopalophthalmus tartessicus* (Vilas-Fernandez, Drake & Sorbe, 2008), were estimated for the 4 water masses described above as ind. m^{-3} of filtered water. A digital flowmeter (Hydro-Bios®, 438 110) was used to calculate the volume of water. Most anchovy individuals were postlarvae (1 to 3 mo old). Their weight was quite homogeneous, ranging from 0.3 to 0.7 g along the estuary. Temperature (mercury thermometer ±0.1°C), salinity (refractometer ATAGO® S/Mill) and turbidity (NTU) were measured *in situ* at the start of each haul.

Wind data were obtained from the 'Rota' meteorological station (closest to the estuary) maintained by the Spanish Agencia Estatal de Metereología (www.aemet.es). Two indices were estimated: (1) average velocity of easterlies and westerlies in a range of days before the sampling date and (2) the number of days (7, 15, 30) with levanters greater than 25 or 30 km h^{-1} previous to the sampling day. Levanters are strong easterly winds (Dorman et al. 1995). See Table S1 for details.

Freshwater discharges from the Alcalá del Río dam were provide by the Regional River Authority Confederación Hidrográfica del Guadalquivir (www.chguadalquivir.es/saih/DatosHistoricos.aspx). Freshwater volumes were calculated by summing daily freshwater flow values (hm^3) recorded on a number of days (4, 7, 15, 30) prior to each sampling date (Table S1).

Precipitation in the area was acquired from 'El Palacio' meteorological station (http://icts.ebd.csic.es/datos-meteorologicos). Total rainfall (l m^{-2}) before the sampling date (4, 7, 15, 30 d) was estimated similarly to freshwater discharges (Table S1).

Statistical modelling

The statistical analysis followed a 4-step approach as follows:

Step 1. Covariates were examined for collinearity using Pearson's correlation coefficient ($r > 0.6$–0.7) (Figs. S3–S6 in the Supplement) and a variance inflation factor (VIF) of 3 using the R function corvif (Zuur et al. 2007, 2009) (Table S2). Abundances, turbidity and freshwater discharges were log-transformed.

Step 2. A generalized additive model (GAM, Wood 2000, 2006) was estimated for each species at each water mass. GAMs are powerful modelling techniques that consist of fitting smooth additive functions in order to capture the relationship between the response variable and the explanatory factors. To avoid model over-fitting, the maximum number of knots (degrees of freedom) of the smoother (k) was set to 4.

Individual model selection was based on a stepwise approach removing covariates with a $p > 0.05$

and attempting to minimize the generalized cross validation criterion (Wood 2000) (Table S3). Expert judgement was used when appropriate. Non-significant covariates were lagged to assess any possible retarded effect.

Model residuals were checked for normality, independence and homoscedasticity (Figs. S7–S10). Regression assumptions were met except for independence in some cases. Nevertheless, the presence of autocorrelation did not affect the overall model structure (see complementary analyses in Figs. S1 & S2).

Step 3. Deviance was partitioned across the explanatory variables in order to explore their relative contribution (Table S4).

Step 4. Finally, for validation purposes, the models were used to hindcast the observations. Predictions recreated the time-series close enough and satisfactorily reproduced the observed seasonal cycles (Figs. S11 & S12).

All analyses were performed in R (Version 3.3.1) (R Core Team 2016), using the mgcv (version 1.8-17; Wood 2017) and corrplot (version 0.77; Wei & Simko 2016) packages.

RESULTS

Species distributions along the salinity gradient

The relative abundances of anchovy and the 3 species of mysids across the 4 water masses reflect the species' salinity preferences and overlap between predator and main prey along the estuary (Fig. 2). While anchovy and *Mesopodopsis slabberi*, both marine species, showed higher and more stable densities in the outer water masses (I and II) (Fig. 2a,b), *Neomysis integer*, a genuine estuarine species, showed slightly higher densities in the inner water masses (III and IV) (Fig. 2c). *Rhopalophthalmus tartessicus* showed the most confined distribution, restricted to the high salinities found in the outer stretches of the estuary (Fig. 2d), reflecting its stenohaline character.

Anchovy

The best models for anchovy included a total of 7 explanatory variables: temperature, salinity, turbid-

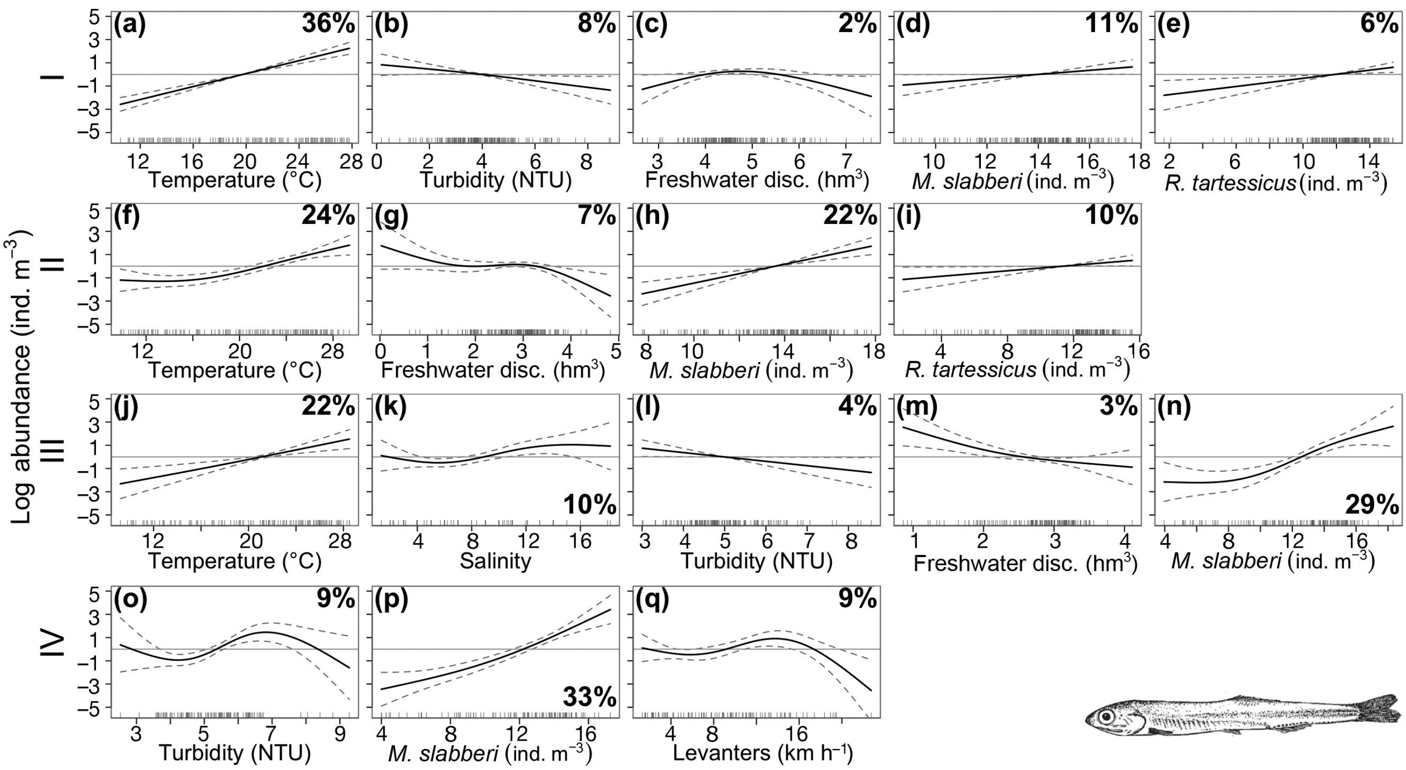

Fig. 3. Anchovy models for the 4 water masses (differentiated by salinity; see Fig. 2e): (a–e) I, (f–i) II, (j–n) III and (o–q) IV. Partial plots showing the effects (as fitted splines) of the various factors (*x*-axis) on the response variable (anchovy abundance). Dashed lines are 95% confidence intervals. Horizontal line at $y = 0$ is shown for reference. The percentage of deviance partition (by each covariate) is indicated. Estimated degrees of freedom and absolute deviance are presented in Tables S3 & S4 in the Supplement. Short vertical lines located on the *x*-axes of each plot indicate the values at which observations were made. 'disc.': discharge; hm^3: cubic hectometer

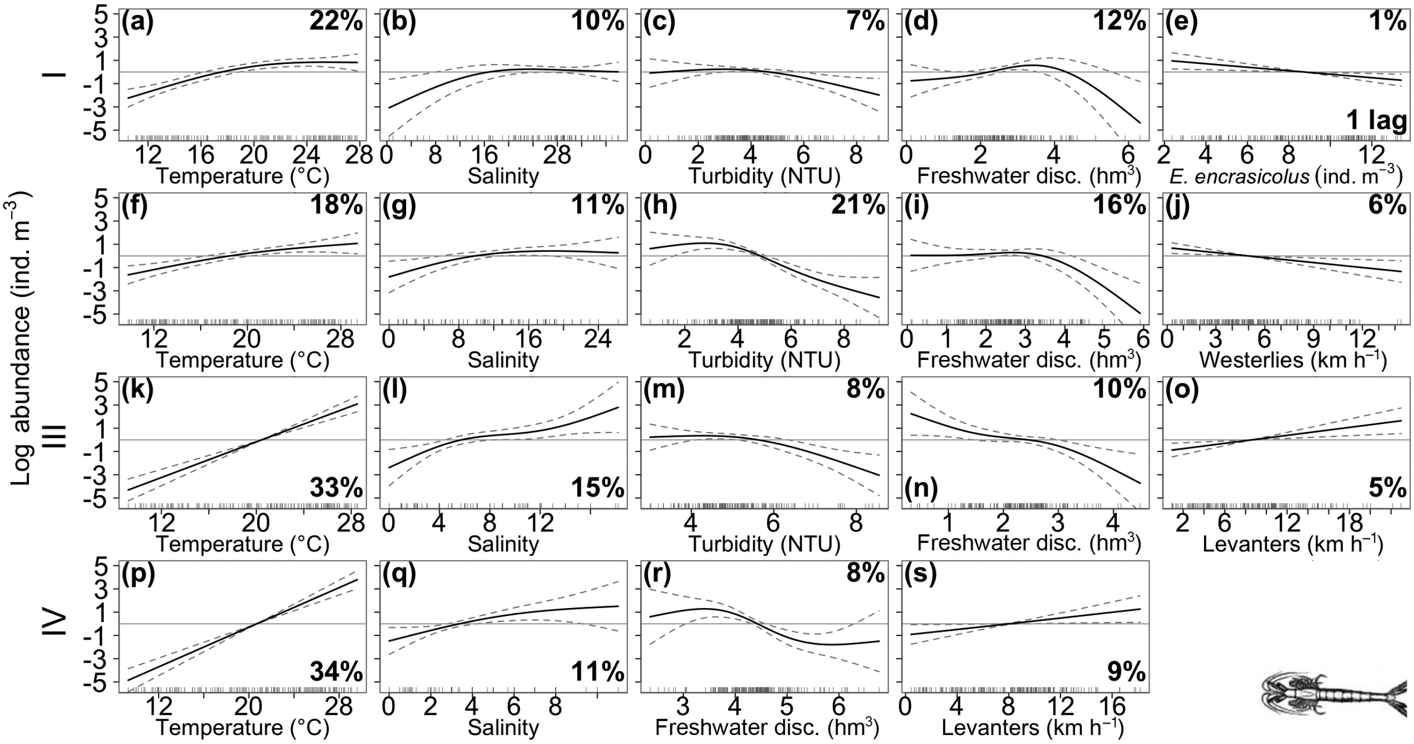

Fig. 4. As in Fig. 3, but for *Mesopodopsis slabberi* models (response variable is *M. slabberi* abundance) in water masses (a–e) I, (f–j) II, (k–o) III and (p–s) IV. Lags (when existing) are indicated

ity, freshwater discharges, levanters, *M. slabberi* and *R. tartessicus* (Fig. 3) and described between 50.3 and 68.3% of total deviance (Tables S3 & S4).

In the outer water masses (I and II), temperature was the most important term with positive effects on abundance (Fig. 3a,f). In the inner water masses (III and IV), this variable entered the model only for water mass III (Fig. 3j). The model for water mass III was the only one that detected a relationship with salinity, showing a relatively flat effect, turning slightly positive for salinities >9 (Fig. 3k).

Both turbidity and freshwater discharges showed negative effects. Turbidity indicated a decrease in abundance for values ≥100 NTU (~4.5 on a log scale) in water masses I and III (Fig. 3b,l). However, in water mass IV, a decrease in anchovy abundance tended to occur at higher concentrations of turbidity (7 on a log scale). The number of daily discharges with a significant impact on the abundance of anchovy can reflect both the buffer capacity of the different water masses and tolerance towards salinity. For example, in the outer water mass (I), the strongest signal was found for a cumulative effect of 30 d (Fig. 3c; Table S4), while in water masses II and III (under greater fluvial influence), this effect was noticeable with a cumulative sum of 7 d (Fig. 3m). In these water masses, anchovy are already at their salinity limit. Thus, any alteration, even if small, can lead to a large change in its density.

In the inner water mass (IV), the relationship with levanters was relatively flat for weak intensities, and negative for winds higher than ~16 km h^{-1} (Fig. 3q). Finally, the positive relationship with mysids (especially *M. slabberi*) across all water masses indicates a strong effect of this prey (Fig. 3d,e,h,i,n,p).

Mesopodopsis slabberi

The models for *M. slabberi* described between 52.8 and 71.4% of total deviance (Table S3), with 8 significant predictors (Fig. 4; Table S4).

Temperature was the most important positive factor in all water masses, except for water mass II, where it ranked second after turbidity (Fig. 4a,f,k,p). At this station, increases in temperature had a positive effect below 21°C, becoming slightly flat at higher temperatures. In the inner water masses, this factor presented a strong positive effect at both tides.

Salinity followed a similar pattern with a positive effect for increasing salinities until favourable conditions are established at around 8–12, depending on the water mass, and little effect after these 'turning' points (Fig. 4b,g,l,q).

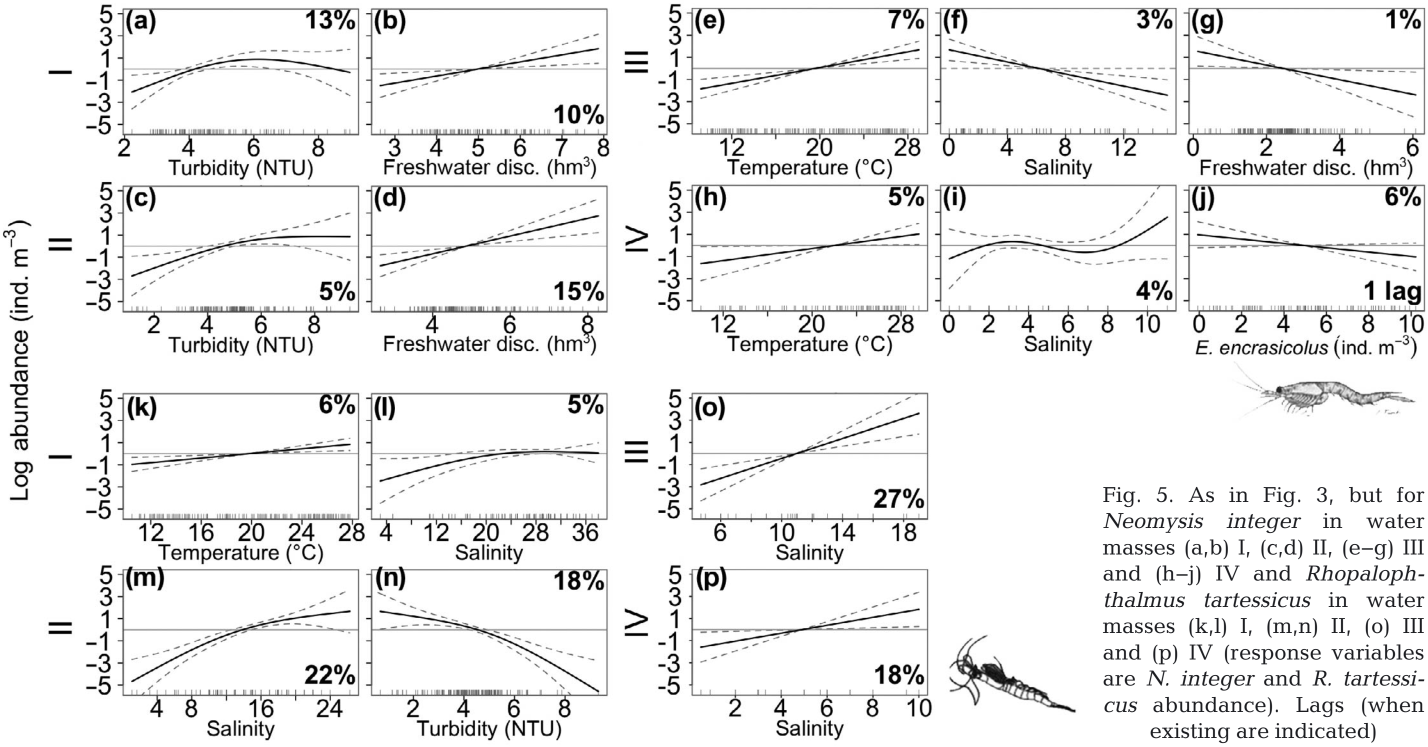

Fig. 5. As in Fig. 3, but for *Neomysis integer* in water masses (a,b) I, (c,d) II, (e–g) III and (h–j) IV and *Rhopalophthalmus tartessicus* in water masses (k,l) I, (m,n) II, (o) III and (p) IV (response variables are *N. integer* and *R. tartessicus* abundance). Lags (when existing are indicated)

The anthropogenically induced variables, i.e. turbidity and freshwater discharges, showed nonlinear negative relationships in almost all water masses. These variables exhibited little or no effect below a certain point (100 NTU and 40 hm^3, respectively) turning negative beyond it (Fig. 4).

Interestingly, although it explained just 1 % of variance, we found a negative effect of anchovy (lagged 1 mo) on *M. slabberi* abundance in the most saline water mass (I) (Fig. 4e).

M. slabberi decreased with increasing westerlies in water mass II (Fig. 4j), whereas for the upper estuary (III, IV), the abundance of this species increased linearly with strong levanters (Fig. 4o,s). Persistent levanters (30 d) are related to high turbidity in the outer estuary, whereas this is not necessarily the case in water masses III and IV.

Neomysis integer

N. integer models consisted of 5 covariates (Fig. 5a–j) and described between 10.8 and 22.9 % of total deviance (Table S3). At the outer station (most saline, water masses I and II), freshwater discharges had a positive effect on this estuarine mysid (Fig. 5b,d). Turbidity showed an overall positive effect mainly for intermediate values (Fig. 5a,c).

In the inner water masses (III, IV), positive relationships occurred with temperature (Fig. 5e,h). Salinity was not incorporated by water masses I and II models. The contrasting pattern in the inner water masses (Fig. 5f,i) suggests that *N. integer* prefers salinities up to approximately 10. Finally, increasing volumes of freshwater discharges and anchovy abundance resulted in decreased abundances.

Rhopalophthalmus tartessicus

R. tartessicus models included a total of 3 explanatory variables (Fig. 5k–p), and the deviance explained ranged from 11 to 32.4 % (Table S3).

Salinity was the most important and often sole driver across water masses, except I, where it ranked second after temperature (Fig. 5l,m,o,p). Turbidity showed a strong negative relationship in water mass II (Fig. 5n).

DISCUSSION

Almost 2 decades of continuous monitoring witnessed the evolution of the estuary under a wide range of environmental conditions and allowed us to empirically populate the interaction food web shown in Fig. 6. This conceptualisation reflects the complexity of inter-

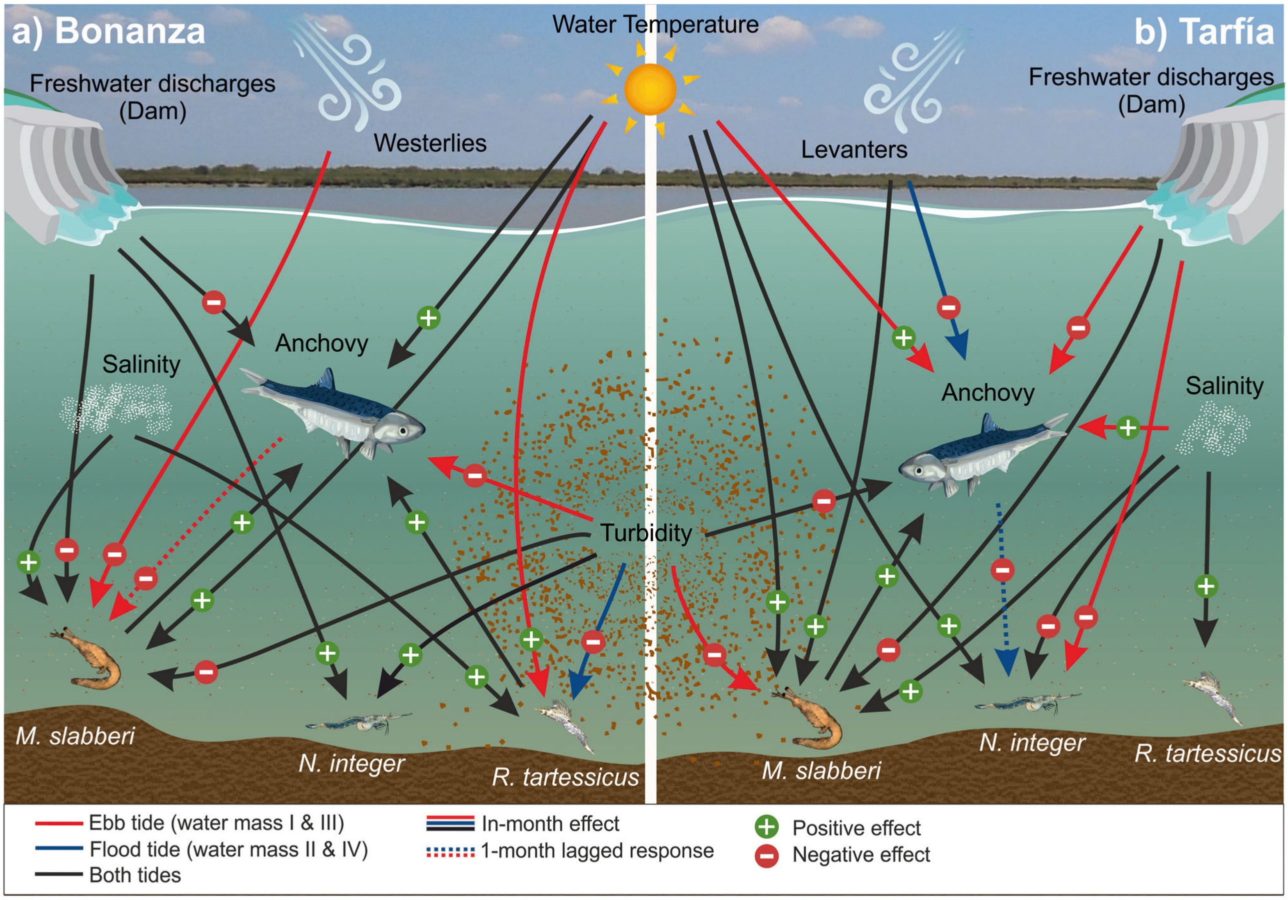

Fig. 6. Significant interactions modelled between anchovy, mysids and environmental drivers along the Guadalquivir estuary in (a) the outer (I and II) and (b) inner water masses (III and IV)

actions in an EFH for a small pelagic species, anchovy, which is the most important fishery in the GoC. Climate (temperature, winds) and human-induced effects (turbidity, freshwater discharges and to some extent salinity) show direct effects on the abundance of anchovy juveniles but also act indirectly through their effects on mysids. Particularly important are *Mesopodopsis slabberi* and the endemic *Rhopalophthalmus tartessicus*, whose strong positive effects reveal the prevailing bottom-up regulation in this EFH.

Climate change and warming

Globally, temperature is described as one of the main factors that control estuarine populations (Attrill & Power 2000, 2002, Pasquaud et al. 2012), as well as species richness (Vasconcelos et al. 2015) and trophic dynamics (Clasen et al. 2010). There is evidence that the Western Iberian Margin has warmed and a future increase of temperatures between 1.5 and 2.5°C is expected near the coast (Cordeiro Pires et al. 2016).

In our study, temperature stands out as the primary factor driving the abundance of anchovy and mysids. It most probably captures the well-defined seasonal pattern typical of temperate latitudes rather than an effect on survival through physiology or other processes. In any case, it seems that the temperature never becomes too hot, as there is no evidence of a negative effect at the highest temperatures.

Our results agree with studies carried out in other regions for this species. For example, in the Gironde estuary, water warming was related to increases in the abundance of anchovy juveniles (Pasquaud et al. 2012). In the Black Sea, using a bioenergetic model, Güraslan et al. (2014) demonstrated that warming could lead to an increase in the anchovy population. The forecasted warming of the Guadalquivir EFH could then, in principle, favour this marine species by enhancing its nursery function. However, note that this study does not consider temperature effects on anchovy spawning (intensity, phenology), which could have a major impact on the juvenile densities found within the estuary.

Other indirect consequences at community or ecosystem levels would also need be considered. Increases in temperature are known to affect mysids, through their physiology and life history traits (McKenney & Celestial 1995, Verslycke et al. 2004, Fockedey et al. 2005). There is some evidence that in the Guadalquivir estuary, the mean body size and fecundity of mysids could be reduced as a response to rising temperatures (C. Vilas pers. obs.). Therefore, the expected warming could also have indirect negative effects.

Salinity

Salinity plays a unique role in structuring spatial patterns and in the functioning of estuaries (Telesh & Khlebovich 2010). As occurs in most estuaries (Kennish 2002), salinity is influenced by multiple drivers such as tides, climate or infrastructures like dams (Contreras & Polo 2012, Navarro et al. 2012, Díez-Minguito et al. 2012).

The Guadalquivir salinity gradient is pronounced. At its inner stretch, water masses oscillate from oligohaline to mesohaline (0.5–5 and 5–16, respectively, Vilas et al. 2009). However, during the dry season, salinity is usually kept on average between 6 and 22 along the whole estuary, which contributes to expand the effective nursery habitat for anchovy (Drake et al. 2007, Fernández-Delgado et al. 2007). Salinity only entered the anchovy models at the inner Guadalquivir, reflecting that it is only a limiting factor here.

The response of mysids to salinity reflects their specific salinity tolerances. *Neomysis integer* is a genuine estuarine mysid and therefore the most euryhaline species. It thrives in the oligohaline zone where salinity can be lower than 5 (Mees 1993, Vilas et al. 2009). At its distributional limit, it benefits from salinity increases as it tends to avoid mesohaline water masses. On the other hand, *M. slabberi* and *R. tartessicus*, as marine species, are mainly found in the outer zone and show negative relationships with low salinities (Mees 1993, Baldó et al. 2001, Vilas et al. 2009).

Turbidity

Human regulation of freshwater inputs severely alters natural regimes (Poff et al. 2007). In the Guadalquivir, high turbidity seems to be linked to the discharge regime and has been found to lead to declines in various trophic levels (González-Ortegón et al. 2010, 2015).

Mean water turbidity is generally below 75 NTU in summer, below 150 NTU in spring–autumn and only occasionally exceeds 300 NTU in winter (González-Ortegón et al. 2010). On 2 occasions (November 1999 to May 2000 and December 2007 to February 2009) there were strong and sudden increases in freshwater discharges, coupled with high and persistent turbidity events (HPTEs, sensu González-Ortegón et al. 2010), with maximum values of 631 and 713 NTU, respectively.

Our models were able to capture these HPTE extreme events, which negatively impacted anchovy and mysid densities. Other effects of HPTEs have been reported, such as inhibition of phytoplankton growth (Navarro et al. 2012) or upstream population displacements, with impacts on prey–predator relationships and food web structure (González-Ortegón et al. 2010, 2012, 2015). Under these conditions, the nursery function is gravely impaired (González-Ortegón et al. 2015). Additionally, fish may leave or avoid areas of high turbidity since this would decrease their perceptive abilities (Liljendahl-Nurminen et al. 2008, Lunt & Smee 2014).

Indirect (trophic) effects

Estuarine production is regulated by abiotic (light, turbidity, nutrient and detritus supply) and biotic mechanisms (trophic interactions). Net production is the result of the interaction between top-down and bottom-up processes (Alpine & Cloern 1992, Cloern & Jassby 2012).

The abundance of anchovy was positively related to the abundance of mysids, especially *M. slabberi,* which is its main prey (Baldó & Drake 2002). *M. slabberi* accounted for a third (29 and 33%) of total anchovy variance in the inner water masses. The comparably high importance of trophic effects at these sites suggests that food availability would compensate for the physiological stress of a brackish environment, with salinities ranging from 0.5 to 16. These results support the hypothesis of high food availability (mysids) as one of the conditions (together with low predation) that grant the nursery function of the estuary (Baldó & Drake 2002, Drake et al. 2007, Fernández-Delgado et al. 2007).

Weak predation effects were also detected on *M. slabberi* and *N. integer*. Together, our results indicate that the Guadalquivir EFH is predominantly resource-driven and that mysids are key components in channelling production upwards.

Reference points

The setting of reference points has emerged in the last decade as a strategy to evaluate the status of aquatic ecosystems (Rice 2003, Samhouri et al. 2010, Foley et al. 2015) and comply with current legislation. Several EU policies use indicators for ecosystem assessments (Maes et al. 2016). The Marine Strategy Framework Directive (MSFD; European Commission 2008) and the Water Framework Directive (European Commission 2000) are relevant examples of this. Both directives seek to achieve good ecological status based on 'reference values' (European Commission 2017).

As additive models, GAMs can be helpful in identifying partial effects of drivers. This is clearly seen in the effect of freshwater discharges on anchovy or turbidity on *M. slabberi*. For the lower range of these 2 variables, there is little (or positive) effect. However, there exists a point (reference value) beyond which increasing values of the covariate result in decreasing abundances of the corresponding nekton species. Linear relationships can be interpreted in a similar fashion.

While identifying these points is not easy, especially in highly dynamic ecosystems, such as estuaries, ignoring them would be even more dangerous (Rice 2003). For that reason, we propose the use of these empirically estimated relationships to identify reference points of good (or bad) ecological status (sensu MSFD). The establishment of reference points for anthropogenically influenced factors is crucial because these are the ones that can be directly managed and therefore can be used to inform management decisions.

Based on turbidity and discharge reference points (Table S5), we illustrate the development of the estuary status over the last 18 yr by means of a colour scale (Fig. 7). We can see that on average, turbidity conditions have not improved in recent years and have oscillated between yellow and red (indicating a poor status) since 2008. The 2004–2006 (outer water masses) and 2001–2002 (inner water masses) periods stand out for their good status (green). The 2 HPTEs of 1999–2000 and 2007–2009 are marked as orange/red, indicating very bad ecological status. Freshwater discharges followed a comparable trend to that of turbidity.

From a seasonal perspective, the most important months are those from May to November, when anchovy (and mysid) densities are at their highest. There seems to be a positive relationship between discharge and turbidity, with the winter months being more turbid and more impacted by discharges (yellow to red) than the spring–summer period (green–yellow, Fig. 7). Although this (mean) seasonal pattern does not seem to be too detrimental to the

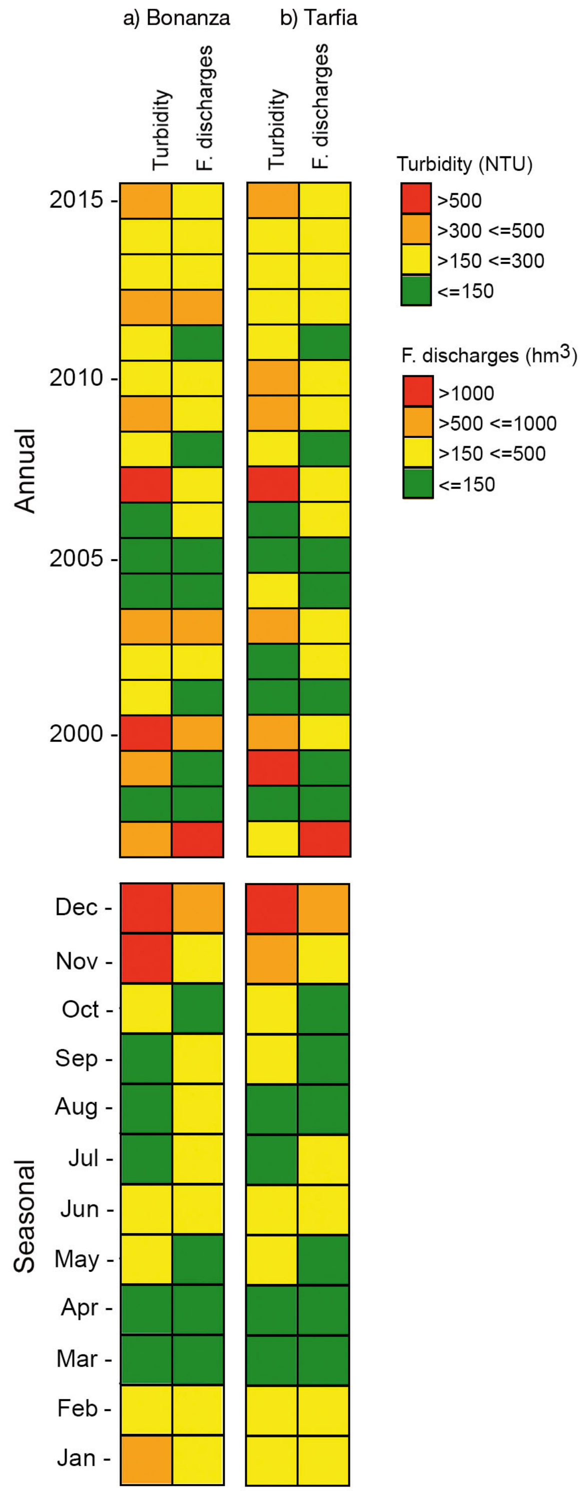

Fig. 7. Annual and seasonal classification of turbidity and freshwater (F.) discharges in (a) the outer (Bonanza station) and (b) inner (Tarfía station) water masses according to the reference points estimated by the models (see Figs. 3 & 4). The scale is composed of 4 categories: green if the effect is null or positive, yellow: slightly negative, orange: negative, red: extreme values (e.g. high and persistent turbidity events, HPTEs)

nursery function, there is room for improvement. The slightly negative (yellow) months could possibly improve (to green) if these considerations were taken into account when managing the dam.

Management implications

Temperature and mysids are overall the most important predictors for anchovy and hence the most important indicators to maintaining the nursery service that this particular habitat provides. On the other hand, turbidity, salinity and freshwater discharges have comparably less influence.

Despite the seemingly secondary role of the anthropogenic variables on anchovy, it is worth noting that these drivers also act through the other nekton components. For instance, salinity has a positive effect on *M. slabberi*, which in turn has a positive effect on anchovy (Fig. 6a). Increases in salinity can cascade up through this mysid species to positively impact anchovy. Unlike natural effects, the anthropogenic variables are not totally independent. The increase in salinity illustrated before could probably be the result of a decrease in freshwater discharges and be temporally associated with a decrease in turbidity. Again, discharges and turbidity have direct positive effects on anchovy and indirect effects via *M. slabberi*.

These anthropogenic variables have the particularity that they are to a certain extent influenced by the way humans perceive and manage the ecosystem. The most important infrastructure regarding the flow of freshwater into the estuary is the Alcalá del Río dam (Fig. 1), which contributes 80% of the total. As depicted in Fig. 6, discharges have direct effects on the Guadalquivir food web and indirectly affect salinity and turbidity, with knock-on effects on anchovy and mysids.

At present, river discharges essentially respond to the needs of the agriculture sector (rice irrigation) and do not take into account other side effects, such as those described above in relation to the nursery role of this EFH. This corresponds to the land use view (Llope 2017) and the historical inertia of the Guadalquivir socio-ecosystem (Vargas & Paneque 2015). An ecosystem approach to management of the anchovy fishery in the GoC should consider the trade-offs that the current management regime of the estuary has on its nursery function and hence on the recruitment of this species. The results presented in this study could be useful to inform management decisions, balance trade-offs, and by so doing, help the implementation of an ecosystem-based type of management.

CONCLUSIONS

Temperature, turbidity and freshwater discharges are key drivers in the Guadalquivir estuary. Turbidity and freshwater can be regarded as anthropogenic since these are, to a certain extent, manageable.

Bottom-up stands out as the prevailing type of trophic control and the mysids *M. slabberi* and *R. tartessicus* are identified as key in the upwards channelling of energy.

A number of issues, such as the effect of other prey items (zooplankton) on anchovy remain unknown and will need to be addressed in the future, as more information becomes available.

Using the Guadalquivir estuary as case study, our results show how indirect human activities (e.g. rice irrigation) can affect a fishery (e.g. anchovy, via recruitment) by impacting an EFH (nursery area).

Further studies will also need to quantify to which extent these sectoral activities (dam operation) propagate (via recruitment) all the way to the fishery.

Linking these apparently independent sectors — agriculture and fishing — will bring us a step forward in our understanding of this particular socio-ecosystem and its management.

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