



## Short communication

# Hidden persistence of salinity and productivity gradients shaping pelagic diversity in highly dynamic marine ecosystems



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## ABSTRACT

While large-scale patterns of pelagic marine diversity are generally well described, they remain elusive at regional-scale given the high temporal and spatial dynamics of biological and local oceanographic processes. We here evaluated whether the main drivers of pelagic diversity can be more pervasive than expected at regional scale, using a meroplankton community of a frontal system in the Western Mediterranean. We evidence that regional biodiversity in a highly dynamic ecosystem can be summarized attending to both static (bathymetric) and ephemeral (biological and hydrographical) environmental axes of seascape. This pattern can be observed irrespectively of the regional hydroclimatic scenario with distance to coast, salinity gradient and chlorophyll *a* concentration being the main and recurrent drivers. By contrast, their effect is overridden in common analyses given that different non-linear effects are buffered between years of contrasting scenarios, emerging the influence of secondary effects on diversity. We conclude that community studies may reveal hidden persistent processes when they take into account different functional effects related to hydroclimatic variability. A better understanding of regional dynamics of the pelagic realm will improve our capability to forecast future responses of plankton communities as well as impacts of climate change on marine biodiversity.

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## 1. Introduction

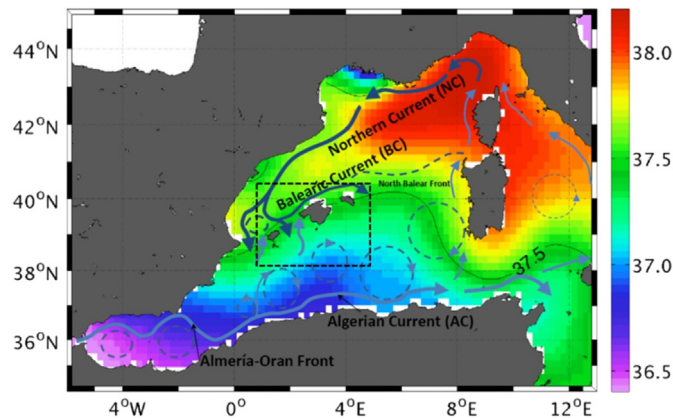
Macroecological studies show that biodiversity patterns of pelagic marine ecosystems are pervasive features mainly ascribed to latitudinal and hydrographical gradients such as temperature, or to the seasonal heterogeneity of environment (e.g. Barton et al., 2010; Beaugrand et al., 2013). Recent studies show that the global pattern of marine fish larvae follows large scale gradients (Reglero et al., 2014). At small spatial scale, however, the mesoscale oceanographic processes are not overridden, and the physical–biological coupling between adult spawning strategies, larval behaviour and the different components of the pelagic seascape results on a variety of species-specific connectivity scenarios, ranging from local retention to broad dispersion (Shanks and Eckert, 2005; Cowen and Sponaugle, 2009). This heterogeneity of connectivity scenarios

ultimately shapes the spatial diversity of meroplankton (i.e. organisms that spend egg and larval stage as plankton) community. Although the spatial distribution patterns of meroplankton taxa (fish, decapod crustaceans, cephalopods, echinoderms, molluscs or polychaetes) are generally well described by mesoscale oceanographic processes (Cowen and Sponaugle, 2009; Asch and Checkley, 2013), the dynamic contribution of these patterns to the community diversity changes between years and the understanding of this dynamics is often hindered (but see e.g. Duffy-Anderson et al., 2006; Siddon et al., 2011). This is particularly relevant in coastal areas with highly stochastic hydrographical processes (Siegel et al., 2008), or in the frontal systems due to the confluence of oceanographic and biological processes of contrasting origin.

Oceanic frontal systems provide a challenging but unique opportunity to understand small scale drivers of plankton diversity and the ecology of species co-existence due to the complex mixture of pelagic habitats in these systems. Besides the species-specific

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**Fig. 1.** Average July salinity for the Western Mediterranean (adapted from Reglero et al., 2012) with the Balearic Islands identified with a black dashed square. The isohaline 37.5 approximately separates the fresh Atlantic waters to the south from the resident Atlantic waters to the north. Arrows indicate major currents.

influence of mesoscale structures, the biological and hydrographical gradients of frontal systems are expected to be the baseline of the pelagic seascape that shapes the structure of planktonic communities (Olson and Backus, 1985). However, these gradients show high interannual variability depending on the shape of the front, seasonal hydrography or large-scale climate forcing (Balbín et al., 2014). Current spatio-temporal analyses do not often account for the inter-annual oceanographic specificities of highly dynamic ecosystems of the pelagic realm. Particularly, varying functional forms of the effect of key drivers (e.g. non-linear shape) can be buffered at temporal scale due to the overlapping of different or contrasting effects between years of different environmental or climatic scenarios. We here hypothesises that key seascape drivers shaping the regional diversity in frontal ecosystems in years with contrasting environmental scenarios may differ from those observed in common integrated analyses. To test this hypothesis, we reduce the test to a single between-years comparison of the recurrent summer front at the Balearic Sea (Fig. 1). We use a complete meroplankton data set that combines ichthyoplankton, crustacean larvae and cephalopods paralarvae (Hidalgo et al., 2014), to investigate small scale diversity patterns in the pelagic realm.

## 2. Material and methods

The study system is the Balearic Sea (Western Mediterranean), characterized by a summer haline front resulting from the confluence of recent and fresh Atlantic waters that flow to the north and the resident Atlantic waters (Fig. 1). The inter-annual variation of the front structure results from the different patterns of circulation within the archipelago channels during spring and is determined by the previous winter forcing that ultimately shape salinity seascape (Balbín et al., 2014).

Data were obtained around the Balearic Islands during early summer in two consecutive years with contrasting hydroclimatic conditions: 2004 and 2005 (Balbín et al., 2014; Hidalgo et al., 2014). A total of 194 and 221 hydrographic-planktonic stations were sampled in 2004 and 2005 respectively, over a regular grid covering the archipelago, following a systematic survey design (see Hidalgo et al., 2014 for details). At each station, a hydrographic profile and a zooplankton oblique tow were performed with a CTD probe SBE911 and a Bongo net, respectively. Salinity and temperature at 25 m depth were used a reference following recent studies (Hidalgo et al., 2014). The module of the geostrophic velocity ( $\text{cm s}^{-1}$ ) and the Brunt–Väisälä frequency squared ( $\text{s}^{-1}$ ) were estimated and used as a measure of current strength and water stability respectively in addition to mixed layer depth (m). Fluorescence was used as a proxy of Chlorophyll *a* concentration ( $\text{mg Chl } a \text{ m}^{-3}$ ) at 25 m depth, the depth of deep chlorophyll maximum (m, DCM) and integrated between 10 and 100 m ( $\text{mg Chl } a \text{ m}^{-3}$ ).

Zooplankton was sampled by means of Bongo nets of 60 cm mouth opening towed obliquely from 70 m depth. Meroplankton information obtained includes larvae of fish and decapod crustaceans, and paralarvae of cephalopods present in the 333  $\mu\text{m}$  mesh sample. Larvae and paralarvae identification was conducted to the lowest possible taxonomic level in the laboratory. Mesozooplankton dry weight ( $\text{mg m}^{-3}$ ) was obtained from samples collected with the 200  $\mu\text{m}$  mesh (see Hidalgo et al., 2014 for details).

The number of stations analysed for combined information of fish and crustacean larvae, and cephalopods paralarvae was 73 and 80 in 2004 and 2005 respectively (Hidalgo et al., 2014). Rare taxa were removed and only those that appeared in more than 5% of the stations across the two years (i.e. 8 stations) were analysed (for the complete list of taxa included see Hidalgo et al., 2014). The diversity of the meroplankton community was calculated at each station

**Table 1**  
Best general additive models obtained for Shannon diversity index (H) of two years combined and year-independent analyses. Best model was chosen based on the minimization of the General Crossed Validation (GCV) score. *a*: intercept, *s*: 1- dimensional smoothing functions, *D*: depth; *T*: temperature at 25 m depth; *S*: salinity at 25 m depth; *Mesozoo*: mesozooplankton biomass; *Fluor*: Mean integrated fluorescence between 10 and 100 m depth; *MLD*: mixed layer depth; *dens*: density of meroplankton at each station; *t*: year;  $\epsilon$  error term. DE (%): percentage of deviance explained. Best models are indicated in bold.

Model structure	DE (%)	GCV
<b>Two-years combined</b>		
<b><math>H_t = a + s_1(\log[D_t]) + s_2(MLD_t) + s_3(\log[Mesozoo_t]) + s_4(\log[dens_t]) + \epsilon_t</math></b>	<b>48.2</b>	<b>0.0231</b>
$H_t = a + s_1(\log[D_t]) + s_2(T_t) + s_3(\log[Mesozoo_t]) + s_4(\log[dens_t]) + \epsilon_t$	45.6	0.0242
$H_t = a + s_1(\log[D_t]) + s_2(\log[Mesozoo_t]) + s_3(\log[dens_t]) + \epsilon_t$	43.3	0.0249
<b>Year-dependent analyses</b>		
<b>2004</b>		
<b><math>H = a + s_1(\log[D]) + s_2(S) + s_3(\text{Fluor}) + \epsilon</math></b>	<b>57.9</b>	<b>0.0214</b>
$H = a + s_1(\log[D]) + s_2(S) + s_3(\log[Mesozoo]) + \epsilon$	42.4	0.0246
$H = a + s_1(\log[D]) + s_2(\text{Fluor}) + \epsilon$	46	0.0247
<b>2005</b>		
<b><math>H = a + s_1(\log[D]) + s_2(S) + s_3(\text{Fluor}) + \epsilon</math></b>	<b>49.9</b>	<b>0.0216</b>
$H = a + s_1(\log[D]) + s_2(S) + \epsilon_t$	40.2	0.0239
$H = a + s_1(\log[D]) + s_2(S) + s_3(\log[Mesozoo]) + \epsilon$	38.9	0.0270

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