

Hydrographic and biological components of the seascape structure the meroplankton community in a frontal system

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ABSTRACT: Studies investigating the environmental influence on the structure of meroplanktonic communities generally focus on fish larvae. To our knowledge, no study to date has combined information on other important groups of the meroplankton such as decapod crustaceans and cephalopods. Here, we investigate the spatiotemporal distribution of a summer meroplankton community in the upper water column of the Balearic Sea (Western Mediterranean). The study compares 2 contrasting years (2004 and 2005) in terms of hydrographic (i.e. thermal pattern, spatial structure of the oceanic front) and biological (i.e. origin and composition of phytoplankton) components of the pelagic seascape. Our results reveal that both year-specific drivers, such as salinity gradient, and common factors between years, such as chlorophyll concentration, influence the community structure. This resulted in a contrasting influence between years of hydrographic and biological components of the seascape, which implies an alternating effect of dispersal pathways and retention to coupling productive conditions. The study characterizes recurrent environmental scenarios associated with different co-occurring fish and decapod crustacean larvae (i.e. mixed assemblages), the most relevant being: (1) recent Atlantic waters of low salinity, (2) resident waters of higher salinity, and (3) high chlorophyll concentration at depth of chlorophyll maximum. This study sheds new light on the complex responses of plankton communities to exogenous drivers in highly variable environments such as frontal systems.

KEY WORDS: Pelagic seascape · Environmental gradients · Meroplankton community structure · Oceanic fronts · Ichthyoplankton · Decapod crustacean larvae · Western Mediterranean · Larvae coexistence

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INTRODUCTION

The structure and functioning of pelagic ecosystems are highly dynamic at both temporal and spatial scales. Inter-annual variability of global and regional climatic conditions affects the community organization of primary (Finkel et al. 2010, Marinov

et al. 2010) and secondary producers (Francis et al. 2012, Llope et al. 2012), as well as those of early life stages of fish (e.g. Hsieh et al. 2009, Auth et al. 2011). Current ichthyoplankton studies attempt to understand how the spatial pattern of community assemblages changes with time, in order to comprehend the influence of climate variability on larval commu-

nity structure (e.g. Duffy-Anderson et al. 2006, Sidon et al. 2011). In this sense, further studies are required to improve our understanding of the influence of the pelagic seascape on larval species distribution and coexistence. The pelagic seascape encompasses hydrographic (such as temperature, salinity or ocean currents) and biological (abundance and composition of primary and secondary producers) features of the sea. A foremost question for marine ecologists is to understand to which extent larval assemblages are shaped by biological and/or physical components of the seascape under different environmental scenarios in order to further comprehend the relative influence of dispersal pathways and the retention to couple productive conditions.

Meroplankton (i.e. organisms with planktonic egg and/or larval stages) community structure is often investigated for specific taxonomic groups of vertebrates (fish) and invertebrates (e.g. crustaceans, cephalopods, echinoderms, molluscs or polychaetes). Few studies combine information on fish larvae with that of decapod crustaceans (Olivar et al. 1998, Shanks & Eckert 2005, Roegner et al. 2013) or cephalopod paralarvae (Diekmann et al. 2006), while, to our knowledge, none have investigated meroplanktonic mixed assemblages. However, the combination of different taxonomic groups is of interest in order to identify mechanisms driving the adaptive convergence of species (i.e. independent evolution of similar life history in phylogenetically unrelated organisms; e.g. Cody & Mooney 1978) to recurrent components of the seascape. In addition, characterizing mixed assemblages of meroplankton species will contribute to the identification of potential ecological intra-group interactions (e.g. competition or predation; e.g. Roura et al. 2012) that can be directly affected by hydrographic variability. In contrast, the combination of different taxonomic groups represents a challenge due to the structural complexity of meroplankton communities, with groups displaying a broad spectrum of spawning phenology and life history strategies, in addition to differences in diet, behaviour and ontogenetic development of larvae (Bradbury & Snelgrove 2001, Shanks & Eckert 2005).

Advection of marine currents or mesoscale features (i.e. gyres, fronts, upwelling) can trigger contrasting effects on larvae of different taxa, from retention to dispersion, mainly because of the duration of planktonic stages and their capacity to control their vertical and horizontal distribution (Owen 1981, Bradbury & Snelgrove 2001). Frontal systems are habitats characterized by high productivity and accumulation of planktonic organisms associated with convergence

processes (e.g. Olson & Backus 1985, Le Fèvre 1986, Sabatés & Masó 1990). These characteristics make fronts optimal systems to investigate the temporal variation in spatial structure of meroplankton communities. Here, we investigate mixed assemblages of vertebrate larvae (fish), invertebrate larvae (decapod crustacean) and paralarvae (cephalopods) of the meroplankton community around a summer oceanic front of the Balearic Sea.

The Balearic Sea, located in the western Mediterranean basin, is a highly hydrodynamic system due to the variability of the Balearic current and the summer intrusion of surface water masses of Atlantic origin (Fig. 1a). As a consequence, an oceanic haline front and episodic mesoscale oceanographic structures (e.g. eddies and filaments) (Balbín et al. 2013) are recurrent features that serve as reproduction refuges for transoceanic migratory summer spawners, such as bluefin tuna (Alemany et al. 2010, Reglero et al. 2012), as well as reproductive habitat for other non-migratory fishes (Alemany et al. 2006, Torres et al. 2011).

In this study, we examine the meroplankton community structure in 2 contrasting oceanographic situations observed in early summer 2004 and 2005 (see Balbín et al. 2013 for details). The objective of the study is to identify the components of the pelagic seascape that structure the meroplankton community in mixed assemblages of vertebrate and invertebrate larvae, and to determine whether the influence of these components differed between the 2 years with contrasting oceanographic scenarios.

MATERIALS AND METHODS

Oceanographic and biological information

This study analysed information obtained around the Balearic Islands during early summer of 2004 (18 June to 10 July) and 2005 (27 June to 23 July), onboard the RV 'Cornide de Saavedra'. A total of 194 and 221 hydrographic-planktonic stations were sampled in 2004 and 2005, respectively, over a regular grid of 10 × 10 nautical miles (18.52 × 18.52 km) around the Balearic archipelago, following a systematic survey design from east to west of the archipelago (Fig. 1b; see Alemany et al. 2010 for details). At each station, a hydrographic profile and a mesozooplankton oblique tow were performed.

Hydrographic information (temperature, salinity and pressure) was obtained with a CTD probe SBE911 lowered down to 350 or 650 m depth, or 5 m

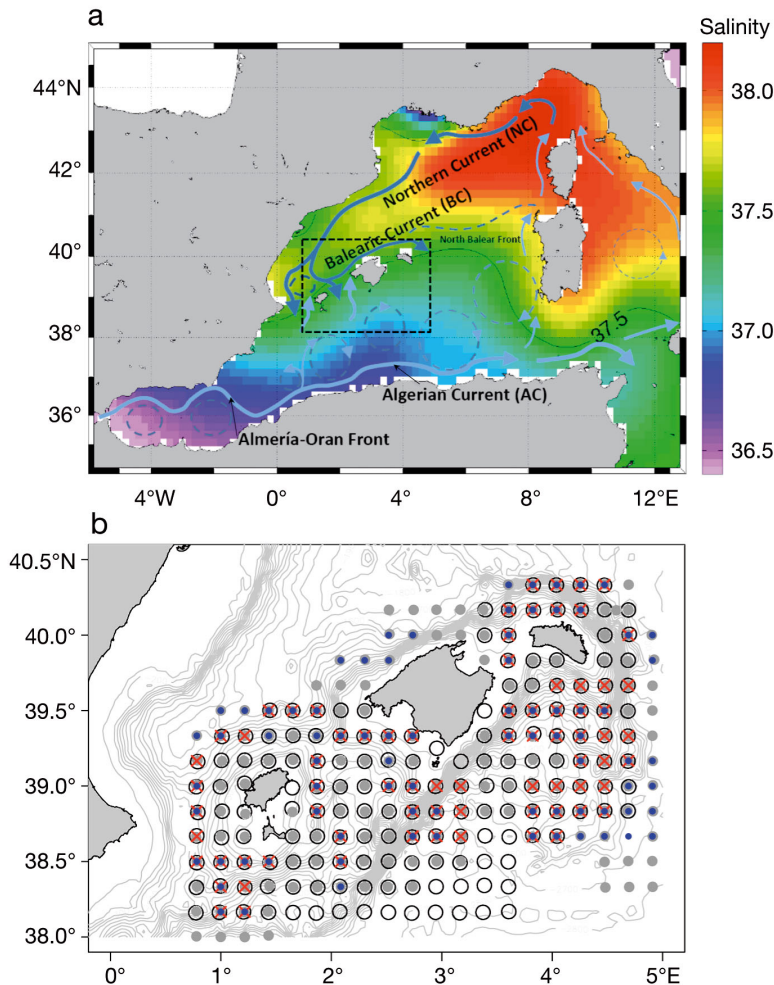


Fig. 1. (a) Average July salinity for the Western Mediterranean (data obtained from MEDAR Group; map adapted from Reglero et al. 2012) with the Balearic archipelago identified by a black dashed square. The isohaline 37.5 approximately separates the fresh Atlantic waters to the south from the resident Atlantic waters to the north. Major currents are shown by arrows: the Algerian current (light blue solid line), the Northern Current (wide dark blue solid line), the Balearic current (narrow dark blue solid line), the North Balear front (dark blue dashed line) and gyres (light blue dashed lines). (b) Study area and location of the hydrographic-plankton sampling stations in 2004 (black circles) and 2005 (grey filled circles). Red crosses and blue points indicate those stations with complete information of the meroplankton community in 2004 and 2005, respectively, included in the present study. Grey contours are the isobaths with an interval of 100 m

above the bottom in shallower stations (for more information on variables measured see Alemany et al. 2010). The module of the geostrophic velocity (cm s^{-1}) was estimated by differentiating the interpolated dynamic height calculated from CTD measurements as described in Torres et al. (2011). Brunt-Väisälä frequency squared (s^{-1}) was also calculated and used as a measure of water stability. In addition, chlorophyll *a* (chl *a*) concentration (mg m^{-3}) was pro-

vided by a fluorescence sensor, which captured information at 470/695 nm (Ex/Em). We used chlorophyll concentration at 25 m depth and at the depth of the deep chlorophyll maximum (DCM). Since the effect of a given covariate can change depending on the spatial scale at which the covariate is calculated (see for instance Ciannelli et al. 2008), we also assessed the influence of a regional pattern in addition to the small-scale information provided by CTDs. Thus, information of surface productivity (measured as surface phytoplankton pigment concentration; $\text{mg chl } a \text{ m}^{-3}$) and sea surface temperature was calculated from satellite data as the spatial mean in a 15 km^2 window from the MODIS-Aqua 8 d composite 4 km resolution Level-3 files (<http://oceancolor.gsfc.nasa.gov/>).

Mesozooplankton was sampled by Bongo nets of 60 cm mouth opening equipped with flowmeters and 2 different mesh sizes: 200 and 333 μm . Bongo nets were towed obliquely from 70 m depth to the surface in the open sea, or down to 5 m above the bottom in the shallower areas (see Alemany et al. 2010 for details). Samples from 333 μm meshes were fixed in seawater with 4% formalin buffered with borax. In the laboratory, fish and decapod larvae and cephalopod paralarvae were separated, identified to the lowest taxonomic level and counted. Larval counts were standardized to number of individuals per 100 m^3 to calculate the relative density of each taxon. The frequency of occurrence was also calculated. Mesozooplankton dry weight was obtained from 200 μm mesh samples frozen on board and analyzed following Lovegrove (1966). Weights were standardized to mg m^{-3} of seawater.

Meroplankton community

The number of stations analyzed for combined information of fish and crustacean larvae, and cephalopod paralarvae was 73 and 80 in 2004 and 2005, respectively. These stations representatively cover the Balearic Sea over the standardized regular grid (Fig. 1b). To simplify meroplankton community analyses, species of the same genus were grouped, with the exception of the fish species *Lampanyctus crocodilus* and *L. pusillus*, and *Thunnus thynnus* and

T. alalunga, which were abundant and with known and distinct environmental preferences in the study area (e.g. Olivar et al. 2012, Reglero et al. 2012). Only taxa that appeared in more than 5% of the stations (i.e. 8 stations) were analyzed.

Community analyses

We employed a combination of community analyses (nonmetric multidimensional scaling; NMDS) and non-linear regressions (general additive modelling; GAM) that have been shown to be a powerful combined tool to describe gradients in species composition relative to environmental drivers (see for instance Goring et al. 2009 and Muenchow et al. 2013 in terrestrial ecology, or Siddon et al. 2011 for marine larvae fish distribution). NMDS was used to summarize multispecies density data to the major modes (i.e. axis) by reducing the difference (i.e. stress) between the distance of the original matrices and its counterparts found in the ordination space (Field et al. 1982). GAM allowed interpreting the spatial structure of the community in relation to environmental information by analysing each of the NMDS axes. To find common patterns that structure the meroplankton community independently of the specific oceanographic situation at each year (e.g. geographical location of the haline front), we first performed this sequence of analyses with the data from 2004 and 2005 combined. Second, to identify distinct hydrographic and biological drivers that influenced the spatial pattern of the community structure each year, we conducted the sequence separately for 2004 and 2005.

Prior to analyses, 4th root transformation was used to reduce the weight of taxa with very high densities in the analyses. Transformed data were standardized to species maxima to provide equal weight to all taxa, notwithstanding their average numerical abundance (Field et al. 1982). Bray-Curtis similarity matrices were computed followed by an ordination using NMDS by station ('vegan' library in R). The procedure performed 100 random starts to find the final stable solution. We used the 3 ordination axes of the NMDS plot (dimensionless values or scores for each station) as variable response in the GAMs. Spearman rank correlations identified which species were most strongly related to each axis, correcting the significance following Bonferroni correction. An exact binomial test was then applied separately on the positive and negative correlation values for each axis to identify the origin of the taxa by evaluating 3 char-

acteristics of the adults: realm (benthic or pelagic), habitat (neritic or oceanic) and biological group (crustacean or fish; to simplify the analysis, cephalopod category was not included in this particular binomial test due to the comparatively lower presence in the list of correlated taxa). Note that complex life history strategies (i.e. epibenthic, nectobenthic, endobenthic or mesopelagic) were pooled to simplify the analyses.

The GAM model formulation for the 2 yr combined was:

$$\text{Axis}_{t,(\varphi,\lambda)}^i = a_t + \sum_j^{j=m} s_j(\mathbf{E}_{t,(\varphi,\lambda)}) + \varepsilon_{t,(\varphi,\lambda)} \quad (1)$$

where *Axis* represents the score of the NMDS axis *i* ($\forall i = 1, 2, 3$), *t* the year, φ and λ the latitude and longitude of the geographical location respectively, and a_t the year-specific intercept (a unique intercept *a* was applied when no differences between years were observed), \mathbf{E} a vector of *m* environmental and biological covariates at year *t* and geographical location (φ, λ), *s* the one-dimensional non-parametric smoothing functions (cubic splines with up to a maximum of 3 df; i.e. 4 knots), and ε a Gaussian error term.

Second, we applied the same model structure to each *Axisⁱ* for each year *t* (2004 and 2005) separately. In this case, we included a geographical effect accounted by g_1 , a 2-dimensional non-parametric smoothing function describing the geographical effect (thin plate regression spline with maximally 27 df; i.e. 28 knots):

$$\text{Axis}_{(\varphi,\lambda)}^{i,t} = a + g_1(\varphi, \lambda) + \sum_j^{j=m} s_j(\mathbf{E}_{(\varphi,\lambda)}) + \varepsilon_{(\varphi,\lambda)} \quad (2)$$

After preliminary analyses, 2-dimensional smoothing was explored for potentially interacting variables to evaluate the improvement in the performance of the GAM models.

To assess collinearity among environmental and biological covariates, we initially applied a variance inflation factor (VIF) and dropped collinear variables before starting GAM analyses. A cut-off VIF value of 5 was applied to get the final set of covariates (Zuur et al. 2009, p 387). Next, we adopted a step-wise procedure from a first initial GAM model, removing 1 non-significant covariate at a time. To obtain the final model, model selection was based on the minimization on the generalized cross validation (GCV). GCV is a proxy for the model's out-of-sample predictive performance analogous to Akaike's information criterion (AIC). Variance contribution of each covariate was explored for each final model to assess the most relevant covariate(s) to be plotted. All data are mean \pm SE.

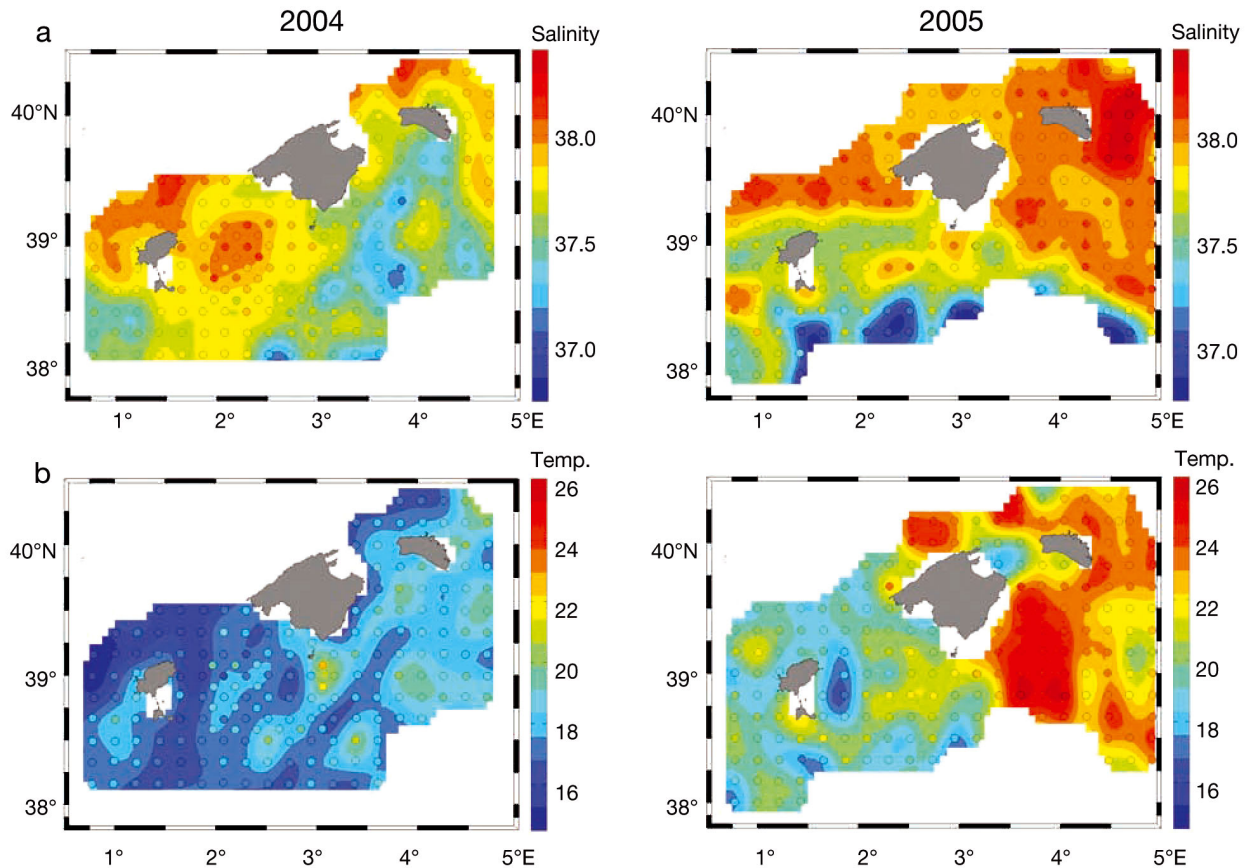


Fig. 2. (a) Salinity and (b) temperature at 25 m depth in 2004 and 2005. Note that the isohaline 37.5 approximately separates the fresh Atlantic waters to the south from the resident Atlantic waters to the north

RESULTS

Oceanographic and biological scenario

The spatial pattern of salinity characterized the location and shape of the summer haline front, which differed between years. In 2004, salinity at 25 m depth revealed the intrusion of fresh Atlantic surface waters (i.e. salinity < 37.5), displaying a heterogeneous forefront (Fig. 2a). In contrast, in 2005 Atlantic waters were located further south, displaying a regular and almost horizontal forefront. Temperature at 25 m showed an eastward warming of the upper water column as a result of the progressive rise in sea surface temperature in summer along the survey (Fig. 2b). Mean values of temperature at 25 m were higher in 2005 ($21.12 \pm 0.15^\circ\text{C}$) than in 2004 ($17.50 \pm 0.08^\circ\text{C}$).

The pattern of satellite chlorophyll concentration was similar in the 2 yr combined, with higher concentration north of Ibiza Island (Fig. 3a). Mean values were $0.115 \pm 0.002 \text{ mg m}^{-3}$ and $0.099 \pm 0.001 \text{ mg m}^{-3}$ in 2004 and 2005, respectively. While in 2004 the spatial pattern of chlorophyll at 25 m was similar to that

of satellite images, in 2005 they were different (Fig. 3b), with mean values of $0.110 \pm 0.004 \text{ mg m}^{-3}$ and $0.082 \pm 0.001 \text{ mg m}^{-3}$ in 2004 and 2005, respectively. In contrast, chlorophyll concentration at DCM showed a spatial pattern similar to that observed in 2005 at 25 m ($1.03 \pm 0.03 \text{ mg m}^{-3}$); this similarity was not observed in 2004 ($1.13 \pm 0.04 \text{ mg m}^{-3}$) (Fig. 3c). In 2005, the chlorophyll concentration at DCM was negatively correlated to DCM values (Fig. 4); this negative correlation was not observed in 2004. In contrast, DCM values in 2004 were closely related to chlorophyll concentration at 25 m, a pattern weakly observed in 2005. This evidences the different origin of phytoplankton production in the 2 yr combined, with 2004 production more dependent on the sub- and surface phytoplankton concentration, while that in 2005 more dependent on primary production at DCM.

The spatial pattern of mesozooplankton (>200 μm) biomass in 2004 was linked to the intrusion of fresh Atlantic surface waters (Fig. 3d; $6.17 \pm 0.26 \text{ mg m}^{-3}$) as depicted by the negative correlation with salinity at 25 m ($r = -0.4$, $p < 0.05$). In contrast, the spatial pattern of mesozooplankton

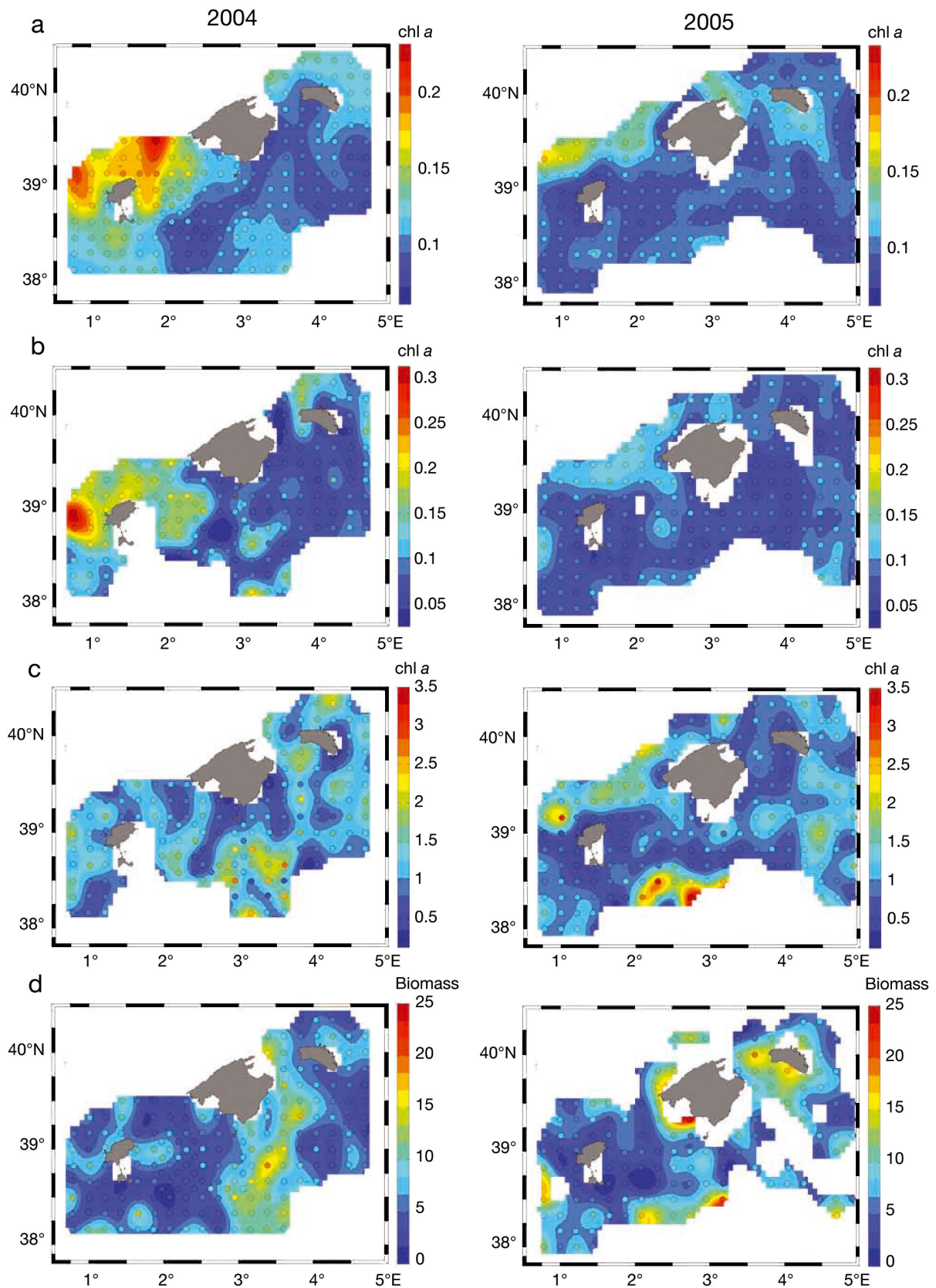


Fig. 3. Chl a concentration (mg m^{-3}) (a) from satellite data, (b) at 25 m depth, (c) at depth of chlorophyll maximum (DCM), (d) Mesozooplankton (>200 μm) biomass (mg m^{-3}) in 2004 and 2005

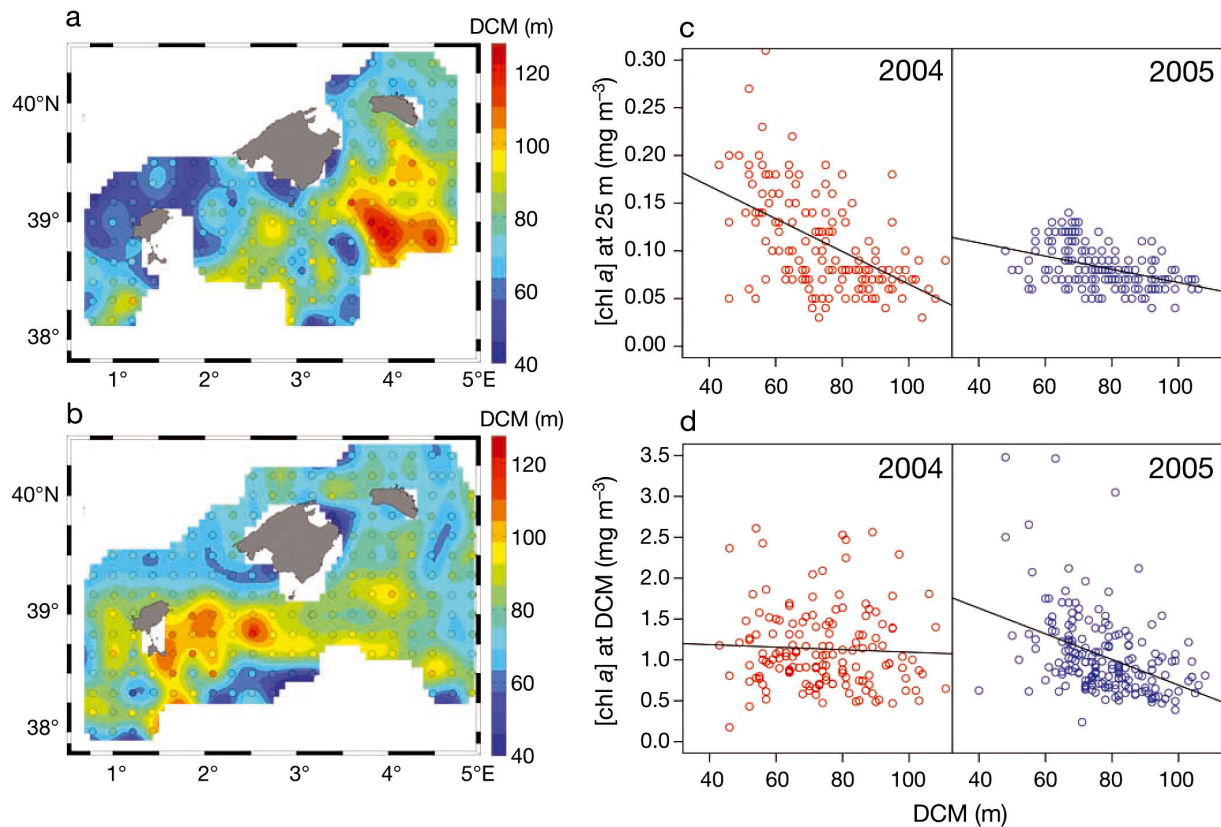


Fig. 4. Depth of chlorophyll maximum (DCM) in (a) 2004 and (b) 2005. Scatterplots of DCM plotted against (c) chl *a* concentration at 25 m depth and (d) chl *a* concentration at DCM for 2004 and 2005. All slopes from linear regressions were significant ($p < 0.05$) with the exception of the relationship between DCM and chl *a* concentration at DCM in 2005 ($p > 0.05$)

biomass in 2005 was bathymetry-dependent, with higher values close to Mallorca and Menorca islands (Fig. 3d; $7.12 \pm 0.37 \text{ mg m}^{-3}$).

Community structure

A total of 79 taxa (38 fishes, 38 decapod crustacean and 3 cephalopods) were included in the study. Table S1 (in the Supplement at www.int-res.com/articles/suppl/m505p065_supp.pdf) displays mean density and percentage of occurrence of all taxa included in the analyses, while Table 1 displays a subset of the more abundant fish and crustacean larvae (mean density of the 2 yr combined), in addition to the 3 cephalopod paralarvae taxa. Total mean density was 330.6 ± 1.9 and $238.8 \pm 1.1 \text{ larvae } 100 \text{ m}^{-3}$ in 2004 and 2005, respectively. The contribution of fish larvae to total density was 90% in 2004 and 82% in 2005, while the contribution of crustacean larvae was 9% in 2004 and 17% in 2005. The contribution of paralarvae was always less than 1%. From the 79 taxa analysed, 32 were benthic-neritic, 25 were pelagic-oceanic, 21 were benthic-oceanic, and 2 were pelagic-neritic (Table S1).

The most abundant taxa were the larvae of pelagic and oceanic fish, with 3 taxa accounting for two thirds of meroplankton density. *Cyclothone* spp. was the most abundant taxon in the 2 yr combined (one third of total density), followed by other lanternfishes, *Hygophum* spp. and *Ceratoscopelus madeirensis* (Table 1). In contrast, common crustaceans included taxa with different life strategies and habitats. Pelagic-oceanic *Sergestes* spp. were the most abundant in 2004, followed by benthic neritic *Xantho* spp. In 2005, pelagic-oceanic taxa such as *Parasergestes vigilax* and *Alpheus* spp. predominated, followed by benthic-neritic *Ealus* spp. (Table 1). Omastrephidae was the most abundant cephalopod taxa in the 2 yr combined data (Table 1).

Community analyses

Two year combined analyses

Once NMDS classified the individual stations of the 2 yr (Fig. S1a in the Supplement), the first axis was modelled with GAM. The axis was mainly influenced by depth, and thus described the gradient

Table 1. Mean (\pm SE) larval density (no. ind. 100 m⁻³), percentage of larval density (%D) and percentage of occurrence (%O) of most common taxa of fish and crustacean larvae for 2004, 2005 and the 2 yr combined (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m505p065_supp.pdf for a complete list of the species included in the study). The 3 taxa of cephalopod paralarvae investigated in the study are included. Note that species are sorted based on %D of 2004 and 2005 combined. Realm (pelagic or benthic) and habitat (oceanic or neritic) of the adults is also included (Torres et al. 2011, d'Udekem d'Acoz 1999, Moreno et al. 2009)

Taxon	Realm	Habitat	2004				2005				2004–2005			
			Mean	SE	%D	%O	Mean	SE	%D	%O	Mean	SE	%D	%O
Fish														
<i>Cyclothone</i> spp.	Pelagic	Oceanic	115.81	11.79	35.02	100	68.94	5.44	28.86	100	91.30	6.56	32.30	100
<i>Hygophum</i> spp.	Pelagic	Oceanic	64.01	9.40	19.36	98.63	43.41	5.03	18.17	97.50	53.24	5.25	18.84	98.04
<i>Ceratoscopelus maderensis</i>	Pelagic	Oceanic	68.46	5.95	20.70	100	33.69	2.68	14.10	98.75	50.28	3.45	17.79	99.35
<i>Lampanyctus crocodilus</i>	Pelagic	Oceanic	7.63	1.37	2.31	93.15	9.15	0.95	3.83	91.25	8.43	0.82	2.98	92.16
<i>Lampanyctus pusillus</i>	Pelagic	Oceanic	7.08	0.94	2.14	84.93	4.11	0.43	1.72	85	5.53	0.52	1.96	84.97
<i>Vinciguerria attenuata</i>	Pelagic	Oceanic	6.46	1.11	1.95	78.08	3.48	0.34	1.46	88.75	4.90	0.57	1.73	83.66
<i>Auxis rochei</i>	Pelagic	Oceanic	4.52	1.15	1.37	64.38	4.88	1.92	2.04	46.25	4.71	1.14	1.67	54.90
<i>Sardinella aurita</i>	Pelagic	Neritic	1.49	0.97	0.45	12.33	4.74	1.56	1.98	23.75	3.19	0.94	1.13	18.30
<i>Benthoosema glaciale</i>	Pelagic	Oceanic	1.16	0.35	0.35	34.25	3.28	0.84	1.37	58.75	2.27	0.48	0.80	47.06
Paralepididae	Pelagic	Oceanic	1.83	0.34	0.55	65.75	2.51	0.28	1.05	80	2.18	0.22	0.77	73.20
<i>Thunnus alalunga</i>	Pelagic	Oceanic	1.62	0.37	0.49	42.47	2.54	0.51	1.06	68.75	2.10	0.32	0.74	56.21
<i>Trachurus</i> spp.	Benthic	Neritic	1.73	0.61	0.52	38.36	1.63	0.58	0.68	31.25	1.68	0.42	0.59	34.64
<i>Engraulis encrasicolus</i>	Pelagic	Neritic	1.12	0.33	0.34	26.03	2.03	0.47	0.85	42.50	1.60	0.29	0.57	34.64
<i>Chromis chromis</i>	Benthic	Neritic	1.45	0.39	0.44	36.99	1.42	0.52	0.59	36.25	1.43	0.33	0.51	36.60
<i>Spicara smaris</i>	Benthic	Neritic	1.94	1.28	0.59	10.96	0.95	0.66	0.40	5.01	1.42	0.70	0.50	7.84
<i>Thunnus thynnus</i>	Pelagic	Oceanic	2.46	1.71	0.74	27.40	0.47	0.21	0.20	18.75	1.42	0.82	0.50	22.88
Crustaceans														
<i>Parasergestes vigilax</i>	Pelagic	Oceanic	3.23	0.48	0.98	84.93	7.67	5.54	3.21	75	5.55	2.90	1.96	79.74
<i>Sergestes</i> spp.	Pelagic	Oceanic	6.51	0.76	1.97	90.41	3.11	0.41	1.30	88.75	4.74	0.44	1.68	89.54
<i>Alpheus</i> spp.	Benthic	Oceanic	1.69	0.46	0.51	39.73	5.08	1.16	2.13	61.25	3.46	0.66	1.22	50.98
<i>Xantho</i> spp.	Benthic	Neritic	3.83	1.27	1.16	54.79	2.78	0.73	1.16	56.25	3.28	0.71	1.16	55.56
<i>Eusergestes arcticus</i>	Pelagic	Oceanic	3.73	0.89	1.13	69.86	1.96	0.39	0.82	50	2.80	0.47	0.99	59.48
<i>Eualus</i> spp.	Benthic	Neritic	0.21	0.14	0.06	9.59	4.35	3.06	1.82	15	2.38	1.60	0.84	12.42
<i>Processa</i> spp.	Benthic	Oceanic	1.30	0.54	0.39	32.88	2.99	1.38	1.25	38.75	2.18	0.77	0.77	35.95
<i>Ilia nucleus</i>	Benthic	Oceanic	2.07	1.12	0.63	24.66	0.63	0.18	0.26	31.25	1.32	0.54	0.47	28.10
<i>Galathea</i> spp.	Benthic	Neritic	1.21	0.72	0.36	19.18	1.37	1.05	0.57	10	1.29	0.64	0.46	14.38
<i>Anapagurus</i> spp.	Benthic	Neritic	0.58	0.31	0.17	10.96	1.73	1.01	0.72	5.01	1.18	0.55	0.42	7.84
<i>Calcinus tubularis</i>	Benthic	Neritic	0.40	0.32	0.12	12.33	1.55	0.40	0.65	53.75	1.00	0.26	0.35	33.99
<i>Liocarcinus</i> spp.	Benthic	Oceanic	1.12	0.44	0.34	24.66	0.67	0.32	0.28	17.50	0.89	0.27	0.31	20.92
<i>Parthenope</i> spp.	Benthic	Oceanic	1.19	0.45	0.36	36.99	0.59	0.12	0.25	35	0.88	0.22	0.31	35.95
<i>Gennadas elegans</i>	Pelagic	Oceanic	0.60	0.17	0.18	31.51	1.02	0.23	0.43	43.75	0.82	0.15	0.29	37.91
<i>Ebalia</i> spp.	Benthic	Oceanic	1.13	0.28	0.34	38.36	0.30	0.08	0.13	26.25	0.70	0.14	0.25	32.03
Cephalopods														
Ommastrephidae	Pelagic	Oceanic	0.04	0.02	0.01	5.48	0.39	0.07	0.17	42.50	0.23	0.04	0.08	24.84
Onychoteuthidae	Pelagic	Oceanic	0.03	0.02	0.01	4.11	0.20	0.05	0.08	22.50	0.12	0.03	0.04	13.73
Octopodidae	Benthic	Neritic	0.01	0.01	0.00	2.74	0.06	0.02	0.03	10	0.04	0.01	0.01	6.54

between oceanic assemblages (species positively correlated with Axis 1) and neritic assemblages (species negatively correlated with Axis 1) (Fig. 5a). In addition to depth (the most relevant covariate), mesozooplankton biomass and temperature at 25 m were included in the best model (Table 2). Species positively correlated with Axis 1 were significantly pelagic-oceanic fishes (all tests $p < 0.05$) (e.g. *Ceratoscopelus maderensis*, *Cyclothone* spp., *Hygophum* spp.), while those negatively correlated were significantly demersal or benthic ($p < 0.05$; e.g. *Trachurus* spp., *Serranus* spp., *Xantho* spp. or *Alpheus* spp.),

with no differences in habitat ($p = 0.12$) or taxonomic group ($p = 0.12$) (Table 3).

Axis 2 mainly described the inter-annual variability (year factor; Fig. 5b) in community assemblages (Table 2). Besides year and depth (which were also significant), 2 descriptors of the inter-annual variability of the oceanographic scenario—salinity at 25 m and geostrophic velocity—displayed a significant effect in the GAM model. Taxa positively correlated with Axis 2 had mean density comparatively higher in 2005 (e.g. Paralepididae, Ommastrephidae, *Engraulis encrasicolus*, *Calcinus tubularis* or *Thunnus ala-*

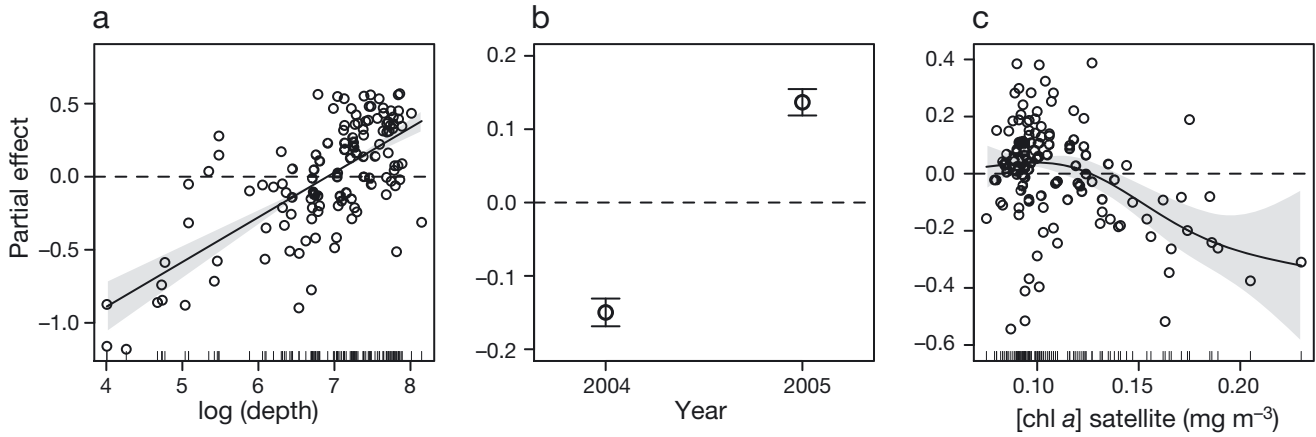


Fig. 5. Most relevant covariates of the 2 yr combined analyses performed on (a) Axis 1, (b) Axis 2 and (c) Axis 3 as response variables. Fitted lines (solid line), 95% confidence intervals (grey shaded areas) and partial residuals are shown in (a) and (c). Bars in (b) represent the standard error of the partial effect of year factor

lunga), while taxa negatively correlated with Axis 2 were more abundant in 2004 (e.g. Pandalidae, *Munida* spp. or *Diaphus holti*) (Table 3). No difference was observed in the habitat, biological group or realm of the correlated species (all $p > 0.05$).

Axis 3 was primary influenced by satellite chlorophyll concentration (Table 2, Fig. 5c), in addition to

mesozooplankton biomass and salinity at 25 m. Species positively correlated were related to areas of low sub-surface chlorophyll concentration, and were primarily oceanic fish ($p < 0.05$, e.g. *Lampanyctus pusillus*, *Thunnus alalunga*) (Table 3). Negatively correlated taxa were associated with areas of high sub-surface chlorophyll concentration, with no significant segregation of the life-history characteristics investigated (e.g. *Benthosema glaciale*, *Solenocera membranacea*) (Table 3).

Table 2. Best general additive models (GAMs) obtained for each nonmetric multidimensional scaling (NMDS) axis (dimensions) of 2 yr combined and year-dependent analyses. Deviance explained (%DE) is included. a = intercept, a_t = year-dependent intercept, s and g = 1- and 2-dimensional smoothing functions, respectively, D = depth; T = temperature at 25 m depth; S = salinity at 25 m depth; *Meso* = mesozooplankton biomass; *Gvel* = Geostrophic velocity; *C.sat* = chl *a* from satellite; *C.25* = chl *a* at 25 m depth; *C.dcm* = chl *a* at the DCM; *DCM* = depth of maximum chlorophyll; *SST* = sea surface temperature from satellite; *MLD* = mixed layer depth; t = year; φ , λ = longitude and latitude coordinates; ϵ = error term. Covariates in **bold** represent the most relevant covariates for each model plotted in Figs. 5 & 6

Formula	%DE
2 yr combined	
Axis 1 $Axis_{t(\varphi,\lambda)}^1 = a_t + \mathbf{s_1(\log[D]_{t(\varphi,\lambda)})} + s_2(T_{t(\varphi,\lambda)}) + s_3(Meso_{t(\varphi,\lambda)}) + \epsilon_{t(\varphi,\lambda)}$	53.9
Axis 2 $Axis_{t(\varphi,\lambda)}^2 = \mathbf{a_t} + s_1(\log[D]_{t(\varphi,\lambda)}) + s_2(S_{t(\varphi,\lambda)}) + s_3(Gvel_{t(\varphi,\lambda)}) + \epsilon_{t(\varphi,\lambda)}$	60.3
Axis 3 $Axis_{t(\varphi,\lambda)}^3 = s_1(S_{t(\varphi,\lambda)}) + \mathbf{s_2(C.sat)_{t(\varphi,\lambda)}} + s_3(Meso_{t(\varphi,\lambda)}) + \epsilon_{t(\varphi,\lambda)}$	34.7
Year-dependent analyses	
2004	
Axis 1 $Axis_{\varphi,\lambda}^1 = a + \mathbf{g_1(\varphi,\lambda)} + \mathbf{s_1(\log[D]_{\varphi,\lambda})} + s_2(T_{\varphi,\lambda}) + s_3(Meso_{\varphi,\lambda}) + \epsilon_{\varphi,\lambda}$	82
Axis 2 $Axis_{\varphi,\lambda}^2 = a + \mathbf{g_1(\varphi,\lambda)} + \mathbf{g_2(C.25_{\varphi,\lambda}, DCM_{\varphi,\lambda})} + \epsilon_{\varphi,\lambda}$	64.4
Axis 3 $Axis_{\varphi,\lambda}^3 = a + \mathbf{g_1(\varphi,\lambda)} + \mathbf{s_1(S_{\varphi,\lambda})} + s_2(SST_{\varphi,\lambda}) + \epsilon_{\varphi,\lambda}$	65.8
2005	
Axis 1 $Axis_{\varphi,\lambda}^1 = a + \mathbf{g_1(\varphi,\lambda)} + \mathbf{s_1(\log[D]_{\varphi,\lambda})} + s_2(Meso_{\varphi,\lambda}) + \epsilon_{\varphi,\lambda}$	75.3
Axis 2 $Axis_{\varphi,\lambda}^2 = a + \mathbf{s_1(\log[D]_{\varphi,\lambda})} + \mathbf{s_2(MLD_{\varphi,\lambda})} + \epsilon_{\varphi,\lambda}$	20.5
Axis 3 $Axis_{\varphi,\lambda}^3 = a + \mathbf{g_1(C.dmc_{\varphi,\lambda}, DMC_{\varphi,\lambda})} + \mathbf{s_1(MLD_{\varphi,\lambda})} + \epsilon_{\varphi,\lambda}$	37.9

Year-dependent analyses

Once NMDS classified the individual stations for 2004 (Fig. S1b in the Supplement) and 2005 (Fig. S1c), GAM modelling was applied on each axis for each year. The best models obtained for 2004 explained higher variance than those obtained for 2005 (Table 2). Analyses of the first axis of both 2004 and 2005 identified the bathymetric gradient as the main driver (Fig. 6a, Fig. S2a). Mesozooplankton biomass and a north–south geographic gradient were also common covariates in the 2 yr (Fig. 6a, Table 2). Taxa negatively correlated were always demersal or benthic (both years, $p < 0.05$), with a significant contribution of crustaceans in 2004 ($p < 0.05$) (Table 3). *Serranus* spp.,

Table 3. Spearman rank correlations of the 3 axes (dimensions) from the nonmetric multidimensional scaling (NMDS) performed for 2004, 2005 and 2 yr combined, correlated with taxa density. Only higher values (both positive and negative) of significant correlations following Bonferroni correction are shown for each group. Number (n) and mean of the significant correlations are also included for each group

Axis 1		Axis 2		Axis 3	
2004–2005					
n = 7; mean = 0.38		n = 9; mean = 0.41		n = 6; mean = 0.34	
<i>Ceratoscopelus maderensis</i>	0.50	Paralepididae	0.66	<i>Lampanyctus pusillus</i>	0.58
<i>Cyclothone</i> spp.	0.48	Ommastrephidae	0.55	<i>Thunnus alalunga</i>	0.35
<i>Hygophum</i> spp.	0.47	<i>Symbolophorus veranyi</i>	0.42	<i>Parasergestes vigilax</i>	0.30
<i>Lampanyctus crocodilus</i>	0.35	<i>Calcinus tubularis</i>	0.38	<i>Lestidiops</i> spp.	0.29
<i>Lestidiops</i> spp.	0.34	<i>Engraulis encrasicolus</i>	0.37	<i>Cyclothone</i> spp.	0.29
<i>Vinciguerria attenuata</i>	0.31	<i>Thunnus alalunga</i>	0.35	<i>Diaphus holti</i>	0.28
<i>Lampanyctus pusillus</i>	0.28	<i>Lysmata seticaudata</i>	0.35		
n = 43; mean = -0.53		n = 3; mean = -0.32		n = 5; mean = -0.39	
<i>Coris julis</i>	-0.68	<i>Diaphus holti</i>	-0.27	<i>Scyllarus</i> spp.	-0.28
<i>Chromis chromis</i>	-0.70	<i>Munida</i> spp.	-0.33	<i>Eusergestes arcticus</i>	-0.38
<i>Xantho</i> spp.	-0.72	Pandalidae	-0.38	<i>Myctophum punctatum</i>	-0.39
<i>Processa</i> spp.	-0.75			<i>Solenocera membranacea</i>	-0.40
<i>Alpheus</i> spp.	-0.79			<i>Benthoosema glaciale</i>	-0.51
<i>Serranus</i> spp.	-0.79				
<i>Trachurus</i> spp.	-0.79				
2004					
n = 9; mean = 0.36		n = 8; mean = 0.49		n = 6; mean = 0.52	
<i>Ceratoscopelus maderensis</i>	0.58	<i>Symbolophorus veranyi</i>	0.67	<i>Thunnus alalunga</i>	0.63
<i>Hygophum</i> spp.	0.40	<i>Myctophum punctatum</i>	0.54	<i>Lampanyctus pusillus</i>	0.59
<i>Cyclothone</i> spp.	0.37	<i>Engraulis encrasicolus</i>	0.48	<i>Auxis rochei</i>	0.59
Paralepididae	0.36	<i>Cyclothone</i> spp.	0.48	<i>Gennadas elegans</i>	0.50
<i>Lestidiops</i> spp.	0.35	<i>Vinciguerria attenuata</i>	0.47	<i>Parasergestes vigilax</i>	0.42
<i>Sergestes</i> spp.	0.32	<i>Lampanyctus crocodilus</i>	0.45	<i>Hygophum</i> spp.	0.41
<i>Eusergestes arcticus</i>	0.32	<i>Mullus</i> spp.	0.45		
n = 28; mean = -0.61		n = 2; mean = -0.26		n = 4; mean = -0.36	
<i>Ilia nucleus</i>	-0.75	<i>Lestidiops</i> spp.	-0.24	<i>Plesionika</i> spp.	-0.30
<i>Processa</i> spp.	-0.76	Pandalidae	-0.29	<i>Notoscopelus</i> spp.	-0.31
<i>Xantho</i> spp.	-0.77			Pandalidae	-0.33
Gobiidae	-0.77			<i>Benthoosema glaciale</i>	-0.53
<i>Liocarcinus</i> spp.	-0.79				
<i>Serranus</i> spp.	-0.80				
<i>Alpheus</i> spp.	-0.83				
2005					
n = 7; mean = 0.49		n = 3; mean = 0.32		n = 3; mean = 0.41	
<i>Cyclothone</i> spp.	0.64	<i>Lestidiops</i> spp.	0.35	<i>Lestidiops</i> spp.	0.45
<i>Hygophum</i> spp.	0.56	<i>Solenocera membranacea</i>	0.30	<i>Lobianchia dofleini</i>	0.45
<i>Lampanyctus crocodilus</i>	0.51	<i>Scyllarus</i> spp.	0.30	<i>Lysmata seticaudata</i>	0.35
<i>Ceratoscopelus maderensis</i>	0.51				
<i>Vinciguerria attenuata</i>	0.49				
<i>Symbolophorus veranyi</i>	0.37				
<i>Lampanyctus pusillus</i>	0.36				
n = 35; mean = -0.62		n = 5; mean = -0.45		n = 4; mean = -0.43	
<i>Coris julis</i>	-0.72	<i>Sergia robusta</i>	-0.38	<i>Monodaeus couchii</i>	-0.31
<i>Sardinella aurita</i>	-0.73	<i>Parasergestes vigilax</i>	-0.44	<i>Solenocera membranacea</i>	-0.37
<i>Engraulis encrasicolus</i>	-0.75	<i>Lampanyctus pusillus</i>	-0.46	<i>Myctophum punctatum</i>	-0.40
<i>Processa</i> spp.	-0.76	<i>Thunnus alalunga</i>	-0.49	<i>Eusergestes arcticus</i>	-0.63
<i>Alpheus</i> spp.	-0.79	<i>Sergestes</i> spp.	-0.49		
<i>Serranus</i> spp.	-0.79				
<i>Trachurus</i> spp.	-0.82				

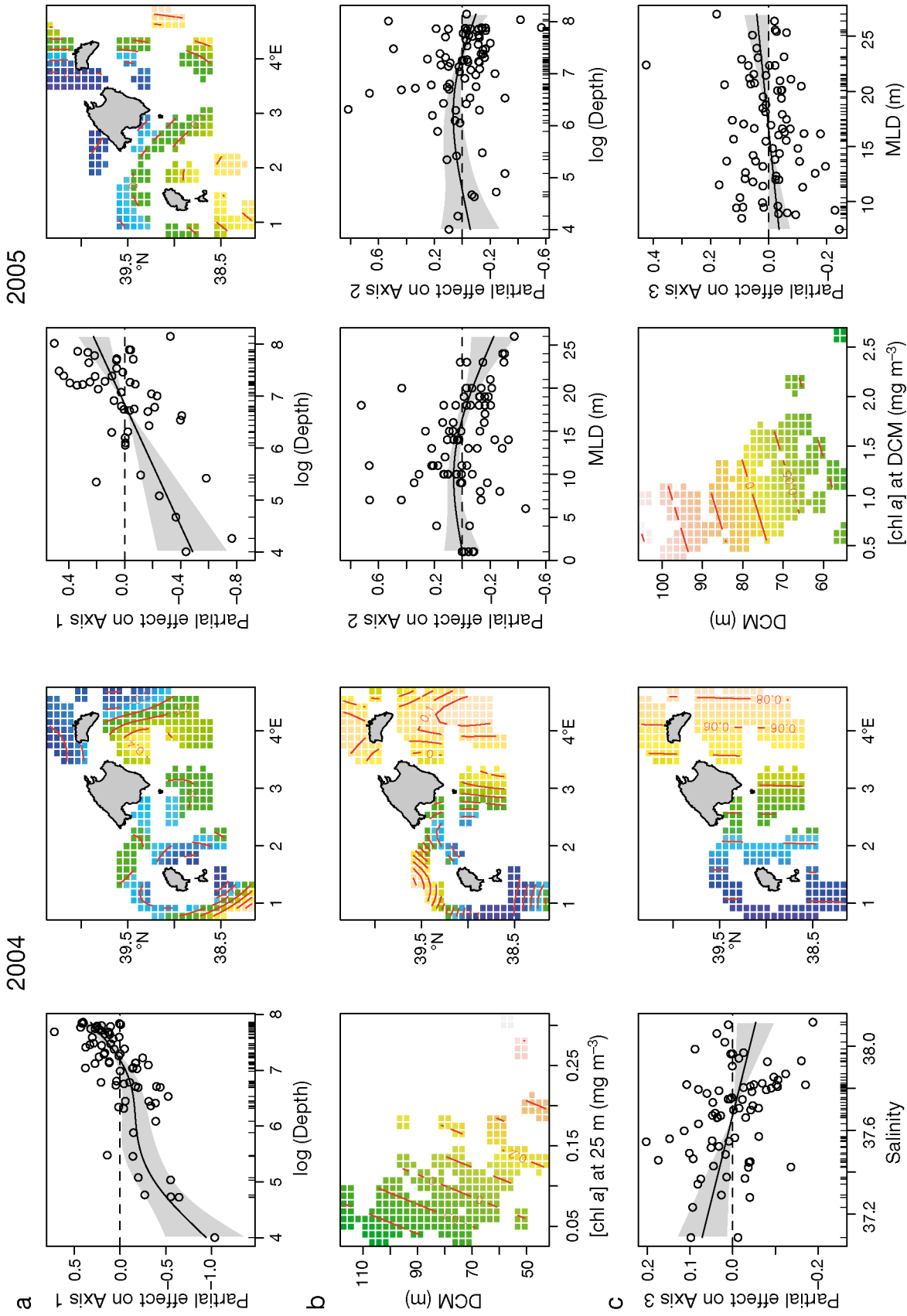


Fig. 6. Most relevant covariates of the year-dependent analyses performed on (a) Axis 1, (b) Axis 2 and (c) Axis 3 for 2004 and 2005. Fitted lines (solid line), 95% confidence intervals (grey shaded areas) and partial residuals are shown for univariate effects. Low values of the geographical effect are shown in purple–blue, while positive values appear in pink–yellow. Positive values of the bivariate effect of depth of deep chlorophyll maximum (DCM) and chl *a* concentration (at 25 m; and at DCM) are shown in pink while negative values appear in green

Alpheus spp. and *Processa* spp. were common taxa in both years. Taxa positively correlated were pelagic and oceanic, with no presence of crustaceans in 2005, with a similar contribution of the 2 groups in 2004 ($p > 0.05$) (Table 3).

Axis 2 displayed a different spatial pattern for each year (Fig. S2b in the Supplement), and was influenced by differing oceanographic processes in 2004 and 2005. In 2004, Axis 2 delineated the interaction between chlorophyll concentration at 25 m and the DCM, in addition to a longitudinal gradient depicted by the geographic effect (Fig. 6b, Table 2). High chlorophyll values at 25 m combined with shallow DCM explained positive Axis 2 values mainly observed in the north of the archipelago (Fig. S2b). This assemblage was mainly composed of fishes ($p < 0.05$); the most correlated species were pelagic-oceanic lanternfish (e.g. *Symbolophorus veranyi*, *Myctophum punctatum*, *Cyclothone* spp.) and anchovy *Engraulis encrasicolus* (Table 3). Conversely, in 2005, the best model explained a low percentage of variance (20.5%), with negative values of Axis 2 described by depth and the thickness of the mixed layer (MLD). This assemblage resulted of a combination of pelagic ($p < 0.05$) and oceanic ($p < 0.05$) taxa (e.g. crustaceans such as *Sergestes* spp. and *Parasergestes vigilax*, or fish such as *Thunnus alalunga* or *Lampanyctus pusillus*) (Table 3).

Axis 3 also displayed variation between years (Fig. S2c in the Supplement). In 2004, the third axis delineated species associated with water masses of different salinity (Fig. 6c, Table 2). Species positively correlated with Axis 3 were influenced by water masses of recent Atlantic origin (i.e. low salinity) and included oceanic ($p < 0.05$) and pelagic ($p < 0.05$) lanternfish *Lampanyctus pusillus*, tunids *Thunnus alalunga* and *Auxis rochei* and crustaceans *Gennadas elegans* and *Parasergestes vigilax* (Table 3). In contrast, in 2005, Axis 3 was delineated by chlorophyll concentration at DCM (Fig. 6c, Table 2). Spe-

cies negatively correlated with Axis 3 in 2005 were influenced by high concentrations of chlorophyll at DCM, when DCM was shallow. These species were oceanic ($p < 0.05$) and included crustaceans *Eusergestes arcticus* and *Solenocera membranacea*, and the lanternfish *Myctophum punctatum* (Table 3).

DISCUSSION

Three common patterns shape the structure of the summer meroplankton community around the Balearic archipelago: (1) the bathymetric gradient, (2) the inter-annual variability of the assemblages associated with both species-specific variation and the hydrographic seascape, and (3) the spatial distribution of phytoplankton. However, the relative contribution of hydrographic and biological components of the seascape changes between years, with the bathymetric gradient remaining as a fixed contribution to the community structure. From all assemblages described in the study, we highlight 4 mixed assemblages of fish and crustacean larvae that co-exist in the Balearic Sea associated with recurrent environmental scenarios (Table 4): (1) coastal environments, (2) productive waters flowing from the north, (3) intrusion of fresh and oligotrophic Atlantic waters flowing from the south, and (4) resident waters of higher salinity. These 4 scenarios synthesize how genetically unrelated taxa from the meroplankton assemblages studied have evolved to optimise their early life history, occupying the same pelagic environments.

The gradient between oceanic and neritic assemblages represents the main geographic pattern, which has also been observed in years of high stability (i.e. weak surface currents and absence of meso-scale features; Rodriguez et al. 2013). However, these results partially contrast with previous studies in the area, suggesting that factors other than depth influ-

Table 4. Mixed assemblages of fish and crustacean larvae observed co-occurring in the most relevant environmental scenarios

Environmental scenario	Co-occurring species	
	Fish	Crustacean
Coastal environments	<i>Serranus</i> spp. and <i>Trachurus</i> spp.	<i>Alpheus</i> spp., <i>Processa</i> spp. and <i>Xantho</i> spp.
High productivity coupled with DCM	<i>Myctophum punctatum</i>	<i>Eusergestes arcticus</i> and <i>Solenocera membranacea</i>
Atlantic water inflow	<i>Thunnus alalunga</i> , <i>Lampanyctus pusillus</i> and <i>Auxis rochei</i>	<i>Gennadas elegans</i> and <i>Parasergestes vigilax</i>
Resident Mediterranean waters	<i>Benthoosema glaciale</i> and <i>Notoscopelus</i> spp.	Pandalidae and <i>Plesionika</i> spp.

ence the spatial pattern of larval fish assemblages (Alemany et al. 2006, Torres et al. 2011). They suggested that it is likely due to the narrowness of the continental shelf around the archipelago and the relevance of the mesoscale hydrographic features in determining the nature of the assemblages. Here, we argue that the high diversity of taxa in neritic stations increases in a meroplankton compared with an ichthyoplankton context, resulting in a structural baseline of the community independent of the environmental scenario. Consistent with other studies, the shallower assemblage results from co-occurrence of common coastal species, such as *Serranus* spp. or *Xantho* spp., and other species with adult distributions at deeper habitats along the shelf-break and upper slope (e.g. fish such as *Trachurus* spp. or decapods *Processa* spp. and *Alpheus* spp.) (Alemany et al. 2006, Sabatés et al. 2007, Landeira et al. 2009, Álvarez et al. 2012) (Table 4). The combination of efficient retention mechanisms in coastal areas (Álvarez et al. 2012), a variety of planktonic larval durations to achieve larval dispersal at the scale where settlement maximizes offspring survival (Bradbury & Snelgrove 2001), and a possible shallower spawning of deeper species, may result in an adaptive coexistence of their early life stages in coastal areas.

Species-specific variation not linked to environmental variables may also explain the differences of assemblages between years (e.g. *Diaphus holti*, *Munida* spp. or Pandalidae in 2004; or Paralepididae and Ommastrephidae in 2005). Inter-annual variation in the abundance of spawners can be one of the main factors ascribed to species-specific variation, while changes in larval survival or timing of spawning may also influence inter-annual co-occurrence of species (Ciannelli et al. 2007, Stige et al. 2010). For instance, the contrasting thermal regime, which was significantly warmer in 2005 than in 2004, may have altered the timing of spawning of those species adapted to certain thermal cues (Sims et al. 2004). This could have advanced reproduction in 2005 in comparison to 2004, and was the main driver suggested for Ommastrephidae paralarvae (N. Zaragoza pers. comm.).

Salinity gradients resulting from mixing water masses are known drivers structuring the coexistence of meroplankton larvae in frontal systems (e.g. Olson & Backus 1985, Sabatés & Masó 1990). Our results for 2004 support previous studies describing contrasting larval fish assemblages in waters of Atlantic and Mediterranean origin (Alemany et al. 2006, Torres et al. 2011), while expanding these differences to the co-occurrence of crustaceans and fish

larvae. Larvae of some tuna species such as *Thunnus alalunga* or oceanic mesopelagic fish (e.g. *Lampasnyctus pusillus*) are often associated with low-salinity Atlantic waters or areas where mixture of water masses occurs (Torres et al. 2011, Reglero et al. 2012). Here, these species may spatially coexist with pelagic-oceanic species of crustaceans, likely advected by Atlantic water inflow (i.e. *Gennadas elegans* and *Parasergestes vigilax*) (Table 4). However, while *P. vigilax* and tuna species likely vertically co-occur because they mainly concentrate in the upper water column (i.e. above 20 to 30 m), *L. pusillus* and *G. elegans* often display a deeper distribution (Olivar & Sabatés 1997, Torres et al. 2013). In contrast, *Benthosema glaciale* is a non-ubiquitous mesopelagic fish in the Western Mediterranean, recurrent in the resident waters with comparatively higher salinity (Alemany 1997, Sabatés et al. 2007). This species was observed to co-occur with the nectobenthic crustacean Pandalidae (particularly *Plesionika* spp.), illustrating another example of convergent life histories (Table 4). Linked to the salinity-related assemblages identified in 2004, it is also relevant to notice that the model depicted an east–west geographic gradient. This gradient can result from the combination of 3 processes: the salinity seascape, the asynoptic pattern of the survey resulting in higher temperatures at the west of the archipelago, and quasi-stationary topographic eddy occurring every summer south Menorca that may act as retention area (Reglero et al. 2012).

Finally, the biological component of the seascape was also a general driver structuring the meroplankton community. However, the origin of primary producers encountered by meroplankton differed between years, triggering contrasting assemblages. In 2004, high values of chl *a* were more dependent on sub- and surface phytoplankton concentrations that were considerably higher than in 2005 due to massive arrival of productive water masses from the north (Balbín et al. 2013). In contrast, productivity dynamics at the DCM were more relevant in 2005. Higher and shallower concentration of phytoplankton in 2004 substantially increased the density of mesopelagic fish larvae, particularly the most abundant and ubiquitous species, suggesting a change in the vertical distribution of these species in order to cope with shallower productivity (Olivar & Sabatés 1997). Under this scenario, moderately abundant larvae of mesopelagic fish *Myctophum punctatum* and *Symbolophorus veranyi*, and anchovy *Engraulis encrasicolus* co-occurred. The presence of anchovy larvae is typically linked to productive mainland waters (Sabatés et al. 2007) and *M. punctatum* is relatively more abundant off the

Iberian coast (Sabatés & Masó 1990, Sabatés et al. 2007) than in the Balearic archipelago (Alemany et al. 2006, Torres et al. 2011). This supports a clear dependence of larvae of this assemblage upon the more productive water masses coming from the mainland, and the spatio-temporal coupling of high phytoplankton densities from the subsurface to DCM. It is noteworthy, however, that crustacean taxa were not observed related to this situation. In contrast, in 2005 the productive scenario at DCM was related to the co-existence of *M. punctatum* with the crustacean larvae of a different habitat, *Solenocera membranacea* and *Eusergestes arcticus* (Table 4). *S. membranacea* is a nectobenthic, shelf coastal species likely to co-occur with *M. punctatum* as a response to passive dispersal. Conversely, *E. arcticus* is a mesopelagic species found to couple with DCM off the Balearic Islands with high occurrence in the north of the archipelago (Torres et al. 2013). Therefore, the co-occurrence of these species in productive pelagic habitats may also indicate the convergence of contrasting early life histories.

Mesozooplankton biomass may contribute toward structuring the ichthyoplankton community due to high abundance of herbivorous zooplankton preying at the DCM (Olivar et al. 2010). However, we observed less influence at the meroplankton level, which we attribute to a lower trophic influence on the earlier-stage decapod crustacean larvae (primary phytoplankton filter-feeders). In addition, the effect of the spatial pattern of mesozooplankton on the meroplankton community in 2004 was partially accounted for by the influence of fresh Atlantic waters, while in 2005 the spatial pattern of mesozooplankton was bathymetry-dependent. The low contribution of copepods to the plankton community in low-salinity waters (Fernández de Puelles et al. 2004) suggests a potential influence on the prey-selective mesopelagic fish linked to low-salinity waters (e.g. *Lampanyctus pusillus*) that display size-selective prey foraging (Sabatés & Saiz 2000). In addition, fish larvae inhabiting fresh Atlantic waters have been demonstrated to display different trophic pathways compared to those inhabiting saltier waters, with consequently lower somatic condition and growth (e.g. *Auxis rochei*; Laiz-Carrión et al. 2013).

CONCLUSIONS

Oceanic boundaries such as frontal systems are unique scenarios in which to understand the drivers, mechanisms and ecological consequences of the adaptive convergence of life histories that result in

co-occurring species (Frank & Leggett 1983, Moser & Smith 1993). The combination of highly dynamic biological and hydrographic gradients in the Balearic front system provides a broad spectrum of environmental circumstances that Mediterranean species have evolved to optimize. Within this complexity, our study ascribes mixed assemblages of coexisting fish and crustacean larvae to the main geographic (i.e. bathymetry), hydrographic (i.e. salinity gradient) and biological (i.e. phytoplankton production) components of the seascape (Table 4). We also provide evidence of regional patterns that may be recurrently observed, independent of regional environmental variability, while shedding new light on how year-specific biological and hydrographic gradients structure the meroplankton community in oceanic fronts. Particularly, the varying contribution of hydrography and trophic resources in shaping the community depends on the salinity seascape and the vertical structure of the phytoplankton-rich water masses arriving from the north of the archipelago. This results in an alternating influence of dispersal pathways and coupling of larvae on productive conditions. The mixed assemblages identified in this study require further research to investigate the potential ecological consequence of overlapping taxa (e.g. Hunsicker et al. 2013) that can occur during the early life stages, as well as potential predation interactions observed for these groups (e.g. Roura et al. 2012). Our study may contribute to further understanding future responses of the pelagic ecosystem to climate variation, while it certainly calls for further research to improve our knowledge on the ecological complexity of the pelagic realm.

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LITERATURE CITED

- Alemany F (1997) Ictioplancton del Mar Balear. PhD dissertation, University of the Balearic Islands, Palma
 Alemany F, Deudero S, Morales-Nin B, López-Jurado JL, Jansá J, Palmer M, Palomera I (2006) Influence of physical environmental factors on the composition and hori-

- zonal distribution of summer larval fish assemblages off Mallorca island (Balearic archipelago, western Mediterranean). *J Plankton Res* 28:473–487
- Alemany F, Quintanilla L, Velez-Belchi P, Garcia A and others (2010) Characterization of the spawning habitat of Atlantic bluefin tuna and related species in the Balearic Sea (western Mediterranean). *Prog Oceanogr* 86:21–38
- Álvarez I, Catalán IA, Jordi A, Palmer M, Sabatés A, Basterretxea G (2012) Drivers of larval fish assemblage shift during the spring–summer transition in the coastal Mediterranean. *Estuar Coast Shelf Sci* 97:127–135
- Auth TD, Brodeur RD, Soulen HL, Ciannelli L, Peterson WT (2011) The response of fish larvae to decadal changes in environmental forcing factors off the Oregon coast. *Fish Oceanogr* 20:314–328
- Balbin R, López-Jurado JL, Flexas MM, Reglero P and others (2013) Interannual variability of the early summer circulation around the Balearic Islands: driving factors and potential effects on the marine ecosystem. *J Mar Syst*, doi:10.1016/j.jmarsys.2013.07.004
- Bradbury IR, Snelgrove PVR (2001) Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behaviour and advective processes in determining spatial pattern. *Can J Fish Aquat Sci* 58:811–823
- Ciannelli L, Bailey KM, Chan KS, Stenseth NC (2007) Phenological and geographical patterns of walleye pollock (*Theragra chalcogramma*) spawning in the western Gulf of Alaska. *Can J Fish Aquat Sci* 64:713–722
- Ciannelli L, Fauchald P, Chan KS, Agostini VN, Dingsør GE (2008) Spatial fisheries ecology: recent progress and future prospects. *J Mar Syst* 71:223–236
- Cody ML, Mooney HA (1978) Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annu Rev Ecol Syst* 9:265–321
- d'Udekem d'Acoz C (1999) Inventaire et distribution des crustacés décapodes de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales adjacentes au nord de 25 N. Collection Patrimoines Naturels, No. 40. Muséum National d'Histoire Naturelle, Paris
- Diekmann R, Nellen W, Piatkowski U (2006) A multivariate analysis of larval fish and paralarval cephalopod assemblages at Great Meteor Seamount. *Deep-Sea Res I* 53:1635–1657
- Duffy-Anderson JT, Busby MS, Mier KL, Deliyandis CM, Stabeno PJ (2006) Spatial and temporal patterns in summer ichthyoplankton assemblages on the eastern Bering Sea shelf 1996–2000. *Fish Oceanogr* 15:80–94
- Fernández de Puellas ML, Valencia J, Jansá J, Morillas A (2004) Hydrographical characteristics and zooplankton distribution in the Mallorca channel (Western Mediterranean): spring 2001. *ICES J Mar Sci* 61:654–666
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analyzing multispecies distribution patterns. *Mar Ecol Prog Ser* 8:37–52
- Finkel ZV, Beardall J, Flynn KJ, Quigg A, Rees TAV, Raven JA (2010) Phytoplankton in a changing world: cell size and elemental stoichiometry. *J Plankton Res* 32:119–137
- Francis TB, Scheuerell MD, Brodeur RD, Levin PS and others (2012) Climate shifts the interaction web of a marine plankton community. *Glob Change Biol* 18:2498–2508
- Frank KT, Leggett WC (1983) Multispecies larval fish associations: accident or adaptation? *Can J Fish Aquat Sci* 40:754–762
- Goring S, Pellatt MG, Lacourse T, Walker IR, Mathewes RW (2009) A new methodology for reconstructing climate and vegetation from modern pollen assemblages: an example from British Columbia. *J Biogeogr* 36:626–638
- Hsieh CH, Kim HJ, Watson W, Di Lorenzo E, Sugihara G (2009) Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region. *Glob Change Biol* 15:2137–2152
- Hunsicker ME, Ciannelli L, Bailey KM, Zador S, Stige LC (2013) Climate and demography dictate the strength of predator–prey overlap in a subarctic marine ecosystem. *PLoS ONE* 8(6):e66025
- Laiz-Carrión R, Quintanilla JM, Torres AP, Alemany F, García A (2013) Hydrographic patterns conditioning variable trophic pathways and early life dynamics of bullet tuna *Auxis rochei* larvae in the Balearic Sea. *Mar Ecol Prog Ser* 475:203–212
- Landeira JM, Lozano-Soldevilla F, Hernández-León S, Barton ED (2009) Horizontal distribution of invertebrate larvae around the oceanic island of Gran Canaria: the effect of mesoscale variability. *Sci Mar* 73:761–771
- Le Fèvre J (1986) Aspects of the biology of the frontal systems. *Adv Mar Biol* 23:164–299
- Llope M, Licandro P, Chan KS, Stenseth NC (2012) Spatial variability of the plankton trophic interaction in the North Sea: a new feature after the early 1970s. *Glob Change Biol* 18:106–117
- Lovegrove T (1966) The determination of the dry weight of plankton and the effect of various factors of the values obtained. In: Barnes H (ed) *Some contemporary studies in marine science*. Allen & Unwin, London, p 429–467
- Marinov I, Doney SC, Lima ID (2010) Response of ocean phytoplankton community structure to climate change over the 21st century: partitioning the effects of nutrients, temperature and light. *Biogeosciences* 7:3941–3959
- Moreno A, Santos A, Piatkowski U, Santos AMP, Cabral H (2009) Distribution of cephalopod paralarvae in relation to the regional oceanography of the western Iberia. *J Plankton Res* 31:73–91
- Moser HG, Smith PE (1993) Larval fish assemblages of the California Current region and their horizontal and vertical distributions across a front. *Bull Mar Sci* 53:645–691
- Muenchow J, Feilhauer H, Bräuning A, Rodríguez EF, Bayer F, Rodríguez RA, von Wehrden H (2013) Coupling ordination techniques and GAM to spatially predict vegetation assemblages along a climatic gradient in an ENSO-affected region of extremely high climate variability. *J Veg Sci* 24:1154–1166
- Olivar MP, Sabatés A (1997) Vertical distribution of fish larvae in the NW Mediterranean Sea in spring. *Mar Biol* 129:289–300
- Olivar MP, Sabatés A, Abelló P, Garcia M (1998) Transitory hydrographic structures and distribution of fish larvae and neustonic crustaceans in the north-western Mediterranean. *Oceanol Acta* 21:95–104
- Olivar MP, Emelianov M, Villate F, Uriarte I and others (2010) The role of oceanographic conditions and plankton availability in larval fish assemblages off the Catalan coast (NW Mediterranean). *Fish Oceanogr* 19:209–229
- Olivar MP, Bernal A, Molí B, Peña M and others (2012) Vertical distribution, diversity and assemblages of mesopelagic fishes in the western Mediterranean. *Deep-Sea Res I* 62:53–69
- Olson DB, Backus RH (1985) The concentrating of organisms at fronts: a cold-water fish and a warm core Gulf Stream ring. *J Mar Res* 43:113–137
- Owen RW (1981) Fronts and eddies in the sea: mechanisms,

- interaction and biological effects. In: Longhurst AR (ed) Analysis of marine ecosystems. Academic Press, London, p 197–233
- Reglero P, Ciannelli L, Alvarez-Berastegui D, Balbín R, López-Jurado JL, Alemany F (2012) Geographically and environmentally driven spawning distributions of tuna species in the western Mediterranean Sea. *Mar Ecol Prog Ser* 463:273–284
- Rodriguez JM, Alvarez I, Lopez-Jurado JL, Garcia A and others (2013) Environmental forcing and the larval fish community associated to the Atlantic bluefin tuna spawning habitat of the Balearic region (Western Mediterranean), in early summer 2005. *Deep-Sea Res I* 77: 11–22
- Roegner GC, Daly EA, Brodeur RD (2013) Surface distribution of brachyuran megalopae and ichthyoplankton in the Columbia River plume during transition from downwelling to upwelling conditions. *Cont Shelf Res* 60:70–86
- Roura A, González AF, Redd K, Guerra A (2012) Molecular prey identification in wild *Octopus vulgaris* paralarvae. *Mar Biol* 159:1335–1345
- Sabatés A, Masó M (1990) Effect of a shelf-slope front on the spatial distribution of mesopelagic fish larvae in the Western Mediterranean. *Deep-Sea Res* 37:1085–1098
- Sabatés A, Saiz E (2000) Intra- and interspecific variability in prey size and niche breadth of mesopelagic fish larvae. *Mar Ecol Prog Ser* 201:261–271
- Sabatés A, Olivar MP, Salat J, Palomera I, Alemany F (2007) Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Prog Oceanogr* 74:355–376
- Shanks AL, Eckert GL (2005) Life history traits and population persistence of California current fishes and benthic crustaceans: solution of a marine drift paradox. *Ecol Monogr* 75:505–524
- Siddon EC, Duffy-Anderson JT, Mueter FJ (2011) Community-level response of fish larvae to environmental variability in the southeastern Bering Sea. *Mar Ecol Prog Ser* 426:225–239
- Sims DW, Vearmouth VJ, Genner MJ, Southward AJ, Hawkins SJ (2004) Low-temperature-driven early spawning migration of a temperate marine fish. *J Anim Ecol* 73: 333–341
- Stige LC, Ottersen G, Dalpadado P, Chan KS and others (2010) Direct and indirect climate forcing in a multi-species marine system. *Proc Biol Sci* 277:3411–3420
- Torres AP, Reglero P, Balbín R, Urtizberea A, Alemany F (2011) Coexistence of larvae of tuna species and other fish in the surface mixed layer in the NW Mediterranean. *J Plankton Res* 33:1793–1812
- Torres AP, Dos Santos A, Balbín R, Alemany F, Massutí E, Reglero P (2013) Decapod crustacean larval communities in the Balearic Sea (western Mediterranean): seasonal composition, horizontal and vertical distribution patterns. *J Mar Syst*, doi:10.1016/j.jmarsys.2013.11.017
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith G (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY

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