Research Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
DOI: http://dx.doi.org/10.12681/mms.18857

Juvenile fish in *Cystoseira* forests: influence of habitat complexity and depth on fish behaviour and assemblage composition

Amalia CUADROS[1,2] , Joan MORANTA[3], Luis CARDONA[4], Pierre THIRIET[5], Patrice FRANCOUR[5], Eva VIDAL[1], Jaime SINTES[1] and Adrien CHEMINEE[2]

[1] Instituto Español de Oceanografía (IEO), Estació d'Investigació Jaume Ferrer, PO Box 502, 07701 Maó, Spain
[2] Univ. Perpignan Via Domitia, Centre de Formation et de Recherche sur les Environnements Méditerranéens, UMR 5110, 66860 Perpignan, France
[3] Instituto Español de Oceanografía (IEO), Centre Oceanogràfic de Balears (COB), Grup of Ecosystem Oceanography (GRECO), Moll de Ponent s/n, 07015 Palma de Mallorca, Spain
[4] IRBio and Department of Evolutionary Biology, Ecology and Environmental Science, Av. Diagonal 643, 08028 Barcelona, Spain
[5] Université Côte d'Azur, CNRS, UMR 7035 ECOSEAS, Parc Valrose, 06108 Nice, France

Corresponding author: amalia.cuadros1@gmail.com

Handling Editor: Paolo GUIDETTI

Received: 10 October 2018; Accepted: 11 March 2019; Published on line: 4 July 2019

Abstract

The sublittoral forests formed by the fucoid algae *Cystoseira* spp. are important juvenile habitats for many Mediterranean fish species. However, the spatial variability of juvenile fish assemblages within the forests and the potential environmental drivers, such as depth and habitat complexity, remain poorly understood. We estimated the density, size and behaviour of juvenile fish assemblages in subtidal (0-15 meters depth) *Cystoseira brachycarpa* var. *balearica* forests in north Minorca Island (North-western Mediterranean Sea) over two consecutive autumns (2012 and 2013). Depth and forest complexity, here measured as canopy volume, had both a significant and independent effect on the juvenile fish assemblages in terms of species abundance composition and body size. Assemblages found in the shallowest depth range (3-4m) were characterized by greater density of the ornate wrasse *Thalassoma pavo,* while those deeper down (10-12m) had higher density of the rainbow wrasse *Coris julis*, independently of its size composition. Juveniles of both species were more abundant in less complex forests; conversely, juveniles of wrasse of the genus *Symphodus* were more abundant in more complex forests. The smallest sizes of *T. pavo* occurred in the most complex forests. On the other hand, our results demonstrated that juvenile fish behaviour was unrelated to the complexity of the *Cystoseira* forests, but mainly related to the body length. The effects of body length on behaviour were however species-dependent. Cryptic and transitory behaviour was mostly observed in the smallest and largest juveniles of *T. pavo* and *C. julis*, respectively, while the behaviour of *Symphodus* spp. was unrelated to their body length. Our study highlights the importance of preserving healthy *Cystoseira* forests and their intrinsically patchy nature, as this habitat, with its mosaic of different degrees of complexity and bathymetric variability, enable the presence of different fish species at various life stages.

Highlights

1. Depth influenced juvenile fish species density distributions (*C. julis*, *T. pavo*) in the depth range studied (3-12m).
2. For certain species, juveniles of different sizes (*T. pavo*, *Symphodus* spp.) had similar depth distributions.
3. *Genus Symphodus* was more abundant in more complex forests, *T. pavo* and *C. julis* in less complex forests.
4. The smallest sizes of *T. pavo* occurred in the most complex forests.
5. Juvenile fish behaviour was influenced by their size rather than the forest complexity.
6. Intrinsic structural variability of *Cystoseira* forests influences patterns of fish species composition and life stages.
7. Appropriate spatial management strategies should act at seascape scale and protect *Cystoseira* habitats with their own bathymetric and structural variability.

Keywords: Juvenile fish; behaviour; depth; habitat complexity; *Cystoseira* forests; Mediterranean Sea.

Introduction

The Mediterranean basin is considered as a hotspot of diversity for *Cystoseira* species (Gianni *et al.*, 2013). They are extremely productive and important algal foundation species in the Mediterranean euphotic zone, exhibiting high phytal and invertebrate biodiversity (Ballesteros, 1988, 1990a, 1990b; Pitacco *et al.*, 2014). *Cystoseira* dominated habitats are also preferential habitats for different life cycle stages of many coastal fish (Lejeune, 1985a; Rodrigues, 2010; Cheminée *et al.*, 2013; Thiriet, 2014). Despite the ecosystem services provided, these habitats are threatened, with conspicuous historical cases of the decline of subtidal *Cystoseira* forests reported in many regions (Thibaut *et al.*, 2005; Airoldi & Beck, 2007; Gianni *et al.*, 2013; Thibaut *et al.*, 2015) - but see Thibaut *et al.*, (2016). These are caused by anthropogenic stressors such as coastline urbanization, pollution, increased water turbidity and predator-overfishing which may cause overgrazing by native herbivores including sea urchins and *Sarpa salpa* (Rodríguez Prieto & Polo Albertí, 1996; Sala *et al.*, 1998; Cormaci & Furnari, 1999; Soltan, 2001; Hereu, 2004). Furthermore, in recent decades, *Cystoseira* forests have been subject to additional threats, including invasive herbivores (e.g. the rabbitfish of genus *Siganus* in the Eastern Mediterranean (Sala *et al.*, 2011; Vergés *et al.*, 2014)) and invasive algae (Cebrian *et al.*, 2018).

It has been suggested that *Cystoseira* forests exhibit a high nursery value (i.e. production of juveniles per unit of surface, *sensu* Beck *et al.* (2001)) for some Labridae (i.e. *Symphodus* spp., *Coris julis*) and Serranidae (i.e. *Serranus* spp.) fish species (Cheminée *et al.*, 2013, 2017). This is because *Cystoseira* forests present higher densities of juveniles of such species than less structured habitats such as shrubby assemblages dominated by Dictyotales and Sphacelariales across large spatial scales of hundreds or thousands of kilometres (Thiriet, 2014). These findings are important since such species have significant ecological roles in Mediterranean ecosystems, for example, they are included among the important prey of many marine top-predator fishes (Reñones *et al.*, 2002) and seabirds (Velando & Freire, 1999), cleaning fish (Zander & Sötje, 2002) and controllers of sea urchin spread (Sala *et al.*, 1998).

Habitat structure is defined as the amount, composition and three-dimensional arrangement of physical matter (both abiotic and biotic) at a location, and is determined by complexity (absolute abundance of individual structural components) and heterogeneity (relative abundance of different structural components) under a specific spatio-temporal scale (Bell *et al.*, 1991; Beck, 2000; Byrne, 2007). In previous studies, habitat structure has been proven to exert a major influence on juvenile fish assemblages (Levin & Hay, 1996; Jenkins & Wheatley, 1998; Guidetti, 2000; Laegdsgaard & Johnson, 2001; Nagelkerken & Van der Velde, 2002). Accordingly, the most highly structured habitats (more complex and/or heterogeneous habitats) harbour richer and more abundant juvenile fish assemblages (but see e.g. Grenouillet *et al.* (2002) and Guidetti & Bussotti (2002)), mainly due to the greater availability of both prey and shelter for juveniles, reducing starvation and/or predation-induced mortality compared with other less structured habitats (Thiriet *et al.*, 2014).

In the case of Macrophyte habitats, including forests, their three-dimensional structure can be defined by verticality (or height) and density, both as a measure of complexity, and percent cover and patchiness, both as a measure of heterogeneity (August, 1983; Guidetti & Bussotti, 2002; García-Charton *et al.*, 2004; Wilson *et al.*, 2007). A general descriptor, volume (i.e. height x cover), has also been used as a measure of this three-dimensional structure (Cheminée *et al.*, 2017), and can be considered as a proxy of forest complexity. A more complex and/or heterogeneous arrangement of a given macrophyte habitat increases fish density and size (Levin & Hay, 1996; Cheminée, 2012; Cheminée *et al.*, 2013; Parsons *et al.*, 2014), and influences the behaviour of fish (i.e. the type of relationship with the habitat). Thus, Lejeune (1985b) and Cheminée (2012) found that in a more complex and/or heterogeneous arrangement of a given macrophyte habitat, fish displayed more resident behaviour, especially small fish. Consequently, habitat structure contributes to explaining the variability of juvenile density distribution within a *Cystoseira* forest (Cheminée, 2012).

To assess the effect of habitat structure on the spatial variability of fish density requires taking into account the influence of other factors, such as depth (Friedlander & Parrish, 1998; Anderson & Millar, 2004). Juvenile depth distributions are taxon-specific (García-Rubies & Macpherson, 1995; Harmelin-Vivien *et al.*, 1995; Francour, 1997; Vigliola & Harmelin-Vivien, 2001). Although knowledge of fish juveniles` depth-related trends remains sparse in the Mediterranean, it is known that juvenile labrids tend to be concentrated) in the shallowest 10 meters (García-Rubies & Macpherson, 1995; Letourneur *et al.*, 2003). Furthermore, for some species depth distributions of juveniles are size-dependent and the smallest juveniles present a narrower depth range distribution pattern than larger ones (Vigliola, 1998).

Despite the evidence demonstrating that within-habitat variability of juvenile fish density depends strongly upon habitat structure and depth, little is known about how the interaction of the two affects juvenile fish distribution patterns within subtidal Mediterranean rocky reefs, and more particularly within *Cystoseira* forests. The purpose of this paper is to study the effects of *Cystoseira brachycarpa* var. *balearica* forest complexity (i.e. canopy volume) and depth gradient (considering three depth strata between 0 and 12 meters) on juvenile fish at assemblage (in terms of total density, richness and assemblage composition, i.e. relative density of each taxon), and species (density, size and behaviour) level. This knowledge of habitat features and juvenile fish associations is of paramount importance in order to design future management actions which would ensure supply of juveniles and therefore the replenishment of adult fish populations.

Material and Methods

Study area

The study was conducted off the northern coast of Minorca island (Balearic Archipelago) (Fig.1.), where rocky bottoms and seagrass meadows prevail on shallow subtidal bottoms, with a few scattered areas of bare sand. Over subtidal rocky bottoms, extensive areas of the long-lived fucoid algae *Cystoseira brachycarpa* J. Agardh, 1986 forests (Fucales), hereafter named simply *Cystoseira* forests, thrive at depths between 1 and 15 meters (Sales & Ballesteros, 2009). A Marine Protected Area (MPA), 'Reserva Marina del Norte de Menorca', was established in 1999 along the northern coast of Minorca (Fig.1). The MPA covers 5.20 km^2 and encompasses two no-take areas, covering 838 ha of rocky bottoms in the west and 217 ha of soft bottoms in the innermost part of Fornells bay (Coll *et al.*, 2012). Study sites were selected following an extensive exploration of the northern coast, both outside and within the MPA. The study sites were a minimum of ~500 meters apart and were established over rocky bottoms covered by wide and dense *Cystoseira* forests of >50% cover. In order to avoid possible bias resulting from confusion between our study variables and other environmental variables, sites of similar rugosity (flat rock), slope (≤45º) and exposure to swell were chosen, and *Cystoseira* forests were only mixed with shrubby-turf algae (i.e. ≤2.5 cm height). The effect of environmental protection (i.e. inside *vs.* outside the MPA) on juvenile fishes was not taken into account, since: 1) our previous studies revealed no differences between juvenile assemblages inside and outside MPAs, nor between juveniles' diurnal predator or competitive conspecific-adult densities - i.e. small labrids (Cardona *et al.*, 2007, 2013; Cuadros, 2015), 2) the depth range sampled (0-15 m) is virtually free of fishing: both professional and recreational fisheries typically exploit deeper ecosystems as boats avoid areas shallower than 10 m because they are too close to the rocky seashore (Cardona *et al.*, 2007), 3) juvenile fish of any species or adults (except adults of *C. julis*, which are exploited by recreational angling fishing) of the species studied are not targeted by fisheries in the Balearic Islands (Planes *et al.*, 1999; Morales-Nin *et al.*, 2005).

Sampling design and data collection

Juvenile fish assemblages associated with *Cystoseira* forests were surveyed in two consecutive years (2012 and 2013), between 20th of September and 15th of October, by underwater visual census (UVC). This sampling time coincides with the occurrence of juveniles of many Mediterranean littoral fish species, especially in the case of Labrid species such as *Symphodus ocellatus* and *Coris julis* (Lejeune, 1985a,b; García-Rubies & Macpherson, 1995; Raventos & Macpherson, 2001; Froese & Pauly, 2016). Six out of eight sampling sites were randomly sampled each year as follows: sites 2-7 in 2012 and sites 1-4, 7 and 8 in 2013 (Fig. 1). At each site, censuses were conducted at three depth strata (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m). In each depth stratum, 8 random replicates of a 1 m² point-count along a 50 m transect were carried out. Cheminée (2012) demonstrated that seven 1 m² replicates are enough to provide an accurate estimate of the juvenile fish density of Labridae (*Symphodus* spp.) at 20 sites in NW Mediteranean (Corsica), within the *Cystoseira* forest

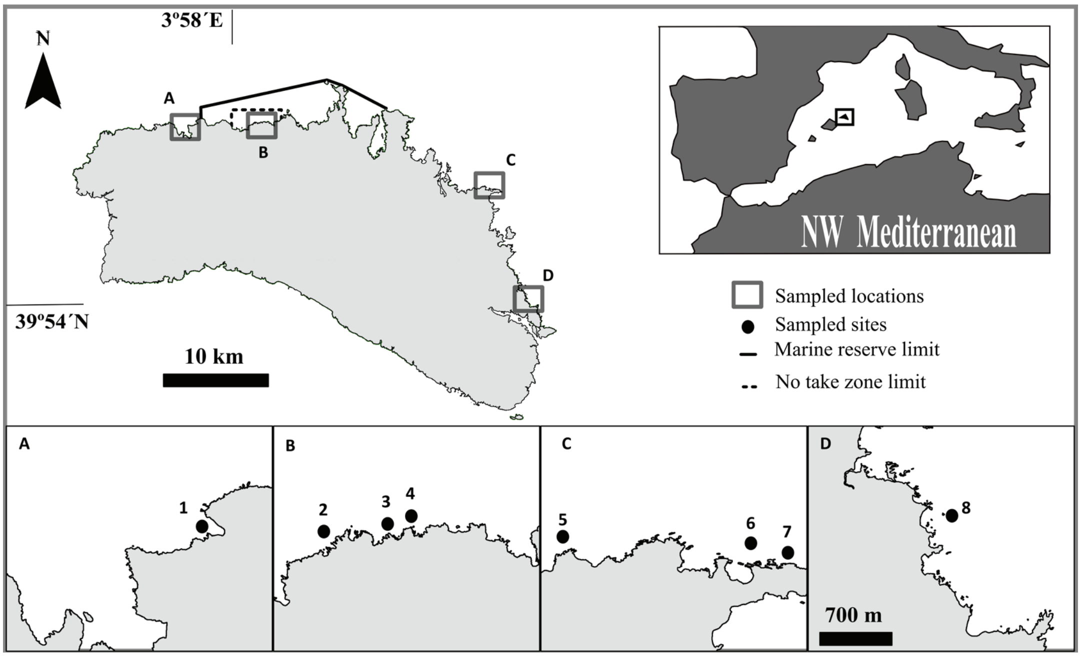


Fig. 1: Location of Minorca Island and the sites sampled in 2012 and 2013. Thick line represents MPA limits. Thick dotted line represents no-take zone limit. Empty squares (locations) are zoomed to show the details of study sites. Sites (black dots) were: 1 (40.05823° N, 3.99093° E), 2 (40.05988° N, 4.00165° E), 3 (40.05923° N, 3.99927° E), 4 (39.99927° N, 4.26247° E), 5 (39.99952° N, 4.25922° E), 6 (40.00118° N, 4.2375° E), 7 (40.05780° N, 3.92828° E), and 8 (39.92613° N, 4.28973° E).

habitat. All censuses were conducted during daylight (between 9 am and 4 pm) (Francour & Le Direac'h, 1994; García-Rubies & Macpherson, 1995; Cheminée *et al.*, 2013; Thiriet *et al.*, 2016, Cheminée *et al.*, 2017). Sampling days with moderate to rough sea conditions, as well as poor visibility, were avoided. Inter-calibration between observers was carried out to reduce sampling bias.

Replicates were haphazardly selected by the diver during a preliminary exploration at each study site and marked by a steel picket. At each point-count, the diver inspected a 1 m² plot where abundance, total length (TL) and behaviour of juvenile fish were recorded during 5 minutes, thus allowing for observation of fish juvenile interactions with the habitat and provision of an effective standardised sample unit (Cheminée *et al.*, 2013, 2017). The TL of individuals was estimated with the help of a plastic slate containing fish silhouettes of different sizes (5 mm TL size-classes) (Macpherson, 1998). For each species, all individuals smaller than one third of adult mean total length were considered as juveniles, as suggested by monthly juvenile size studies performed by Cheminée (2012). Identification of juvenile fishes was based on the identification guide of Louisy (2015).

Fish behaviour was recorded using 3 behavioural categories: cryptic, wandering or transitory. 'Cryptic' individuals were those strictly associated with the canopy and which remained hidden between thalli for a minimum of 30 consecutive seconds (Fig. S1a); 'wandering' individuals were hidden in the canopy for less than 30 seconds, but remained inside the sample plot (Fig. S1b); 'transitory' individuals spent less than 30 seconds in the sample plot (Fig. S1c) (Cheminée, 2012). The size of the squares was such that the diver could handle the different data to record: number, species, fish length and behaviour.

In order to explore the correlation between fish assemblage or taxon-specific descriptors and forest structure, i.e., volume, percent coverage and height (to the nearest cm) of *Cystoseira* canopy within the 1m² plots was visually estimated and recorded (Cheminée, 2012; Cheminée *et al.*, 2017). A value of coverage (%) was assigned according to reference subdivisions of plots. This method is widely used in phytosociological studies (Montes & Ramirez Diaz, 1978). Height was obtained by averaging the height of six random algae.

In order to include in the analyses all the observed individuals and avoid problems of potential misidentification among similar species, some species were pooled together and analysed at the level of the genus (*Symphodus* spp. for *S. roissali*, *S. tinca* and *S. ocellatus*; *Serranus* spp. for *S. cabrilla* and *S. scriba*) or family (Blenniidae, Gobiidae and Tripterygiidae) (hereafter referred to as 'taxa'). Taxa or species accounting for more than 15% of the total assemblage density were considered as 'dominant', while all the remainder were 'minority', since most of the recorded species were below this threshold (Table 1).

Statistical analyses

Data were analysed by means of permutational univariate and multivarate analyses of variance, since assumptions of normality could not be met. Furthermore, these routines enabled the use of stratified random design to test the effect of covariates (forest volume, fish TL) and could explain random (year, site) or fixed (depth) factors on our response variables. The stratified sampling design was used to increase the power of the analyses, by removing some portions of variances from the residual variance, putatively explained by the random factors year and site, which are proxies for a large array of environmental variables (at present, impossible to disentangle) (Anderson *et al.*, 2008).

Three different models were used. The base-model included three factors: i) year, random and with two levels (2012 and 2013); ii) site, random and with six levels (the six randomly selected sites sampled each year); iii) depth, fixed and with three levels (d1, d2 and d3). Firstly, we analysed forest complexity to assess the spatial and temporal variability among levels of the studied factors (year, site and depth). To do so, we calculated the canopy volume (proxy of forest complexity). For each sample (i.e. each 1m² replicate), we obtained canopy volume (in cm^3) from *Cystoseira* cover and height. For this permutational ANOVA analysis, we used the base-model. Sums of squares (SS) were performed as a fully partial analysis (type III).

Secondly, we analysed fish assemblage variability (in terms of univariate total density and richness, and multivariate assemblage composition, i.e, relative density of each taxon) under the influence of both forest complexity (i.e volume in the model) and depth. In this case, the permutational ANCOVA and MANCOVA models included the base-model plus the factor volume included as covariate.

Thirdly, we studied taxa-specific univariate descriptors (density and TL) and multivariate descriptors (behavioural categories), but only for dominant species (see above) with a necto-benthic spatial distribution. Other dominant species, if planktivores, were not considered (Harmelin, 1987). These analyses were carried out using permutational ANCOVA and MANCOVA routines with the aforementioned base-model, and with volume as covariate. In addition, TL was included as a covariate - set at first place in the terms order - for analysing behaviour multivariate contingency tables, since previous works support the influence of fish size on behaviour (Cheminée, 2012).

Sums of squares (SS) for the permutational analyses of covariance were performed sequentially, i.e., type I. Covariates were introduced in the first place into the models (without including the interaction terms between covariates and factors). This allowed assessment of the variations in the response variable(s) that are due to variations in the covariates, prior to testing the putative effects of depth levels (Anderson *et al.*, 2008). Due to co-linearity between depth and *Cystoseira* volume (see Results section), when in permutational ANCOVA or MANCOVA routines volume and depth both had a significant effect on univariate response variables, graphical representations of residuals were used. The residuals were calculated by means of linear models, as implemented in the

Table 1. Juvenile fish observed in *Cystoseira* forests in 2012 and 2013: total number (n), dominance categories (Dom, m = minority, d = dominant), mean number (Mean ± se), minimum (Min) and maximum (Max) total length (TL, mm). Total sampled area per year = 288 m².

Species	n	Dom	Mean	Min TL	Max TL
Chromis chromis	220	m	0.76±0.28	30	55
Coris julis	429	d	1.49±0.12	7	65
Diplodus sargus	105	m	0.36±0.05	25	90
Diplodus vulgaris	75	m	0.26±0.06	10	90
Oblada melanura	275	m	0.95±0.19	30	90
Sarpa salpa	38	m	0.13±0.05	70	100
Serranus spp.	32	m	0.11±0.02	50	90
Symphodus spp.	300	d	1.04±0.19	20	60
Thalassoma pavo	711	d	2.47±0.14	10	60
Blenniidae-Gobiidae-Tripterygiidae	50	m	0.17±0.03	25	45

permutational analyses of variance routines. Therefore, residuals displayed on the graph allow a true visual representation of the effect of each covariate tested by analyses. For visualising the effect of forest volume on response variables (e.g. fish density or TL) once the effect of depth was removed, XY biplot was used, where X was volume and Y displayed residuals of the linear regression fitting the response variable as a function of depth. The effect of depth on response variables was visualized in the same way, once the effect of volume was removed, XY biplot represented in X depth, and in Y the residuals of the linear regression fitting the response variable as a function of volume. These visual representations were accomplished by using boxplots in the case of the categorical variable (depth ranges, d1, d2, d3), and by using smoothed conditional mean in the case of the continuous variable (volume).

In these analyses, P-values were obtained by 9999 permutations of residuals under a reduced model. Monte Carlo P-values were considered when there were not enough possible permutations (<200). Terms were pooled as suggested by Anderson et. al (2008). Tests were considered significant for p-values <0.05.

In addition, differences in juvenile assemblage composition among sample plots were explored through two complementary multivariate exploratory approaches: first, we used a Canonical Analysis of Principal coordinates (CAP) biplot of samples based on Bray-Curtis dissimilarity (Anderson & Willis, 2003): for each taxon (specific abundance), correlations of taxon-specific density with the 2-D ordination plot of samples were plotted by displaying correlation vectors conditioned in scores. Secondly, SIMPER test was used as analysis of species contributions to significant differences between sets of samples (Clarke & Warwick, 2001). For multivariate inferential analyses of density, we used Binomial deviance dissimilarities, which is an improvement of the Bray-Curtis measure proposed by Anderson & Millar (2004). Multivariate behaviour composition (proportions) was analysed through Sogard resemblance matrix, which is an alternative to the Chi-squared measure of distance (Clarke & Warwick, 2001). Univariate data (density or TL) were analysed with Euclidian distances.

Exploratory analyses and inferential tests were performed using the PRIMER 6 and PERMANOVA + B20 package (Clarke & Gorley, 2006; Anderson *et al.*, 2008). Graphical visualizations and CAP ordinations were performed in R Environment (R Core Team, 2013) using the packages ggplot2 (Wickham, 2009) and vegan (Oksanen *et al.*, 2010).

Results

Forest structure

The mean (±se) height, percent cover and volume of *Cystoseira* canopy per sample plot were 8.71 cm (±3.11), 75.10% (±10.89) and 66.79 dm^3 (±29.35), respectively. Moderate correlation was observed between canopy height and cover (Spearman rank correlation, rho: 0.378). For the remaining analyses, volume was used as an overall descriptor of the forest complexity. Forest volume increased with depth from d1 (3-5m) to d2 (6-8 m) or d3 (10-15 m), but patterns of variation from d2 to d3 differed among sites (Permutational ANOVA and pair-wise results in Fig. S2 and Table S1).

Juvenile fish assemblage composition

A total of 10 juvenile fish taxa were observed (Table 1). Overall, the total density and the taxonomical richness of the juvenile fish assemblage were not affected by *Cystoseira* volume or depth. A significant interaction observed for total density from factors year and depth was due to differences in density patterns across depth ranges among years (Table 2).

Juvenile assemblage composition was significantly affected by *Cystoseira* volume and depth (Fig. 2, permutational MANCOVA, Table 2). Both years' d1 (3-5 m) was predominantly significantly different from d3 (10-

Table 2. Permutational ANCOVAs and MANCOVAs table of results. Influence of *Cystoseira* forest structure (volume), year, site and depth on the univariate (total density, richness) and multivariate (juvenile fish assemblage composition) descriptors of juvenile fish assemblages. Significance: ·$P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. *P*-values were obtained by 9999 permutations of residuals under a reduced model.

Considered response variable	Source of variation	Df	MS	Pseudo-F	P(perm)
Total density	volume	1	27.64	0.33	0.570
	Year (ye)	1	3281.6	26.75	0.002**
	Site (si)	7	110.37	0.90	0.646
	Depth (de)	2	329.9	1.22	0.376
	yexsi	3	125.02	2.76	0.041*
	Yexde	2	315.79	4.24	0.042*
	sixde	14	61.05	0.79	0.666
	yexsixde	6	77.67	1.72	0.122
	Residuals	251	45.28		
	Total	287			
Richness	volume	1	1.74	0.77	0.377
	Year (ye)	1	86.32	24.28	0.003**
	Site (si)	7	3.20	0.1	0.579
	Depth (de)	2	4.04	1.1	0.384
	yexsi	3	3.62	3.91	0.010**
	Yexde	2	2.78	1.75	0.223
	sixde	14	2.14	1.56	0.294
	yexsixde	6	1.38	1.49	0.187
	Residuals	251	0.93		
	Total	287			
Assemblage composition	volume	1	10.87	4.27	0.009***
	Year (ye)	1	30.10	4.49	0.025*
	Site (si)	7	6.65	1.00	0.528
	Depth (de)	2	62.10	3.48	0.028*
	yexsi	3	6.61	4.88	0.000***
	Yexde	2	14.15	5.70	0.000***
	sixde	14	4.00	2.00	0.097·
	yexsixde	6	2.01	1.48	0.13
	Residuals	251	1.35		
	Total	287			

15m) (permutational MANCOVA, pairwise tests, $p < 0.05$). The taxon-specific analyses demonstrated that (see 3.3) multivariate differences in juvenile fish relative density between depth strata were primarily driven by *Thalassoma pavo* and *Coris julis* (SIMPER test, Table S2), where *T. pavo* density decreased with depth, while *C. julis* density increased with depth (see also Fig. 3).

Juvenile taxon-specific trends

Density of the dominant taxa

C. julis, *Symphodus* spp. and *T. pavo* were the most abundant taxa sampled (excluding planktivore species) (Table 1). Density of *C. julis* significantly differed between depth strata in both years. An increase in density of *C. julis* from shallower to deeper depth strata was usually observed in 2012, although this pattern varied significantly among sites. The same pattern was observed in 2013, even if marginally significant (Table S3, Fig. 3A). Independently of depth, *C. julis* density also significantly decreased with increasing forest volume values, at least for values less than 50-70 dm^3 (Fig. 3A, permutational ANCOVAs in Table S3). Density of *T. pavo* significantly decreased with increasing depth (d1 *vs.* d3, with similarities of d2 to d3 or d1 depending of years) or volume (Fig.3B, permutational ANCOVAs in Table S3). Finally, density of *Symphodus* spp. juveniles significantly increased with increasing *Cystoseira* forest volume, and

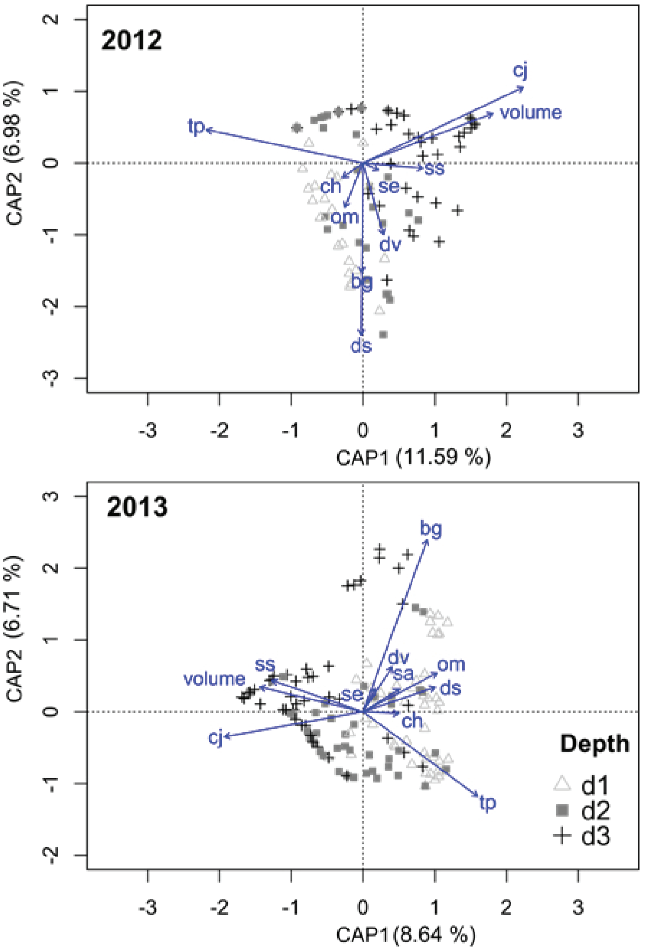


Fig. 2: CAP ordination plots of juvenile fish assemblages within *Cystoseira* forests for the two sampling years (2012, 2013) according to depth strata (from the shallowest d1 to the deepest d3; d1: 3-5 m, d2: 6-8 m, d3: 10-12 m). Correlation vectors of forest structure (volume) and taxa specific densities are plotted. Taxa: ch = *Chromis chromis;* bg = Blenniidae-Gobiidae-Tripterygiidae; dv = *Diplodus vulgaris;* ds = *Diplodus sargus;* cj = *Coris julis;* om = *Oblada melanura;* sa = *Sarpa salpa;* se = *Serranus* spp.; ss = *Symphodus* spp.; tp =*Thalassoma pavo.*

their density patterns across depth strata were inconsistent between years (Fig. 3C, permutational ANCOVAs in Table S3).

Total length (TL) distributions of the dominant taxa

TL of *T. pavo* juveniles significantly varied with *Cystoseira* forest volume. The smallest sizes of *T. pavo* were mostly observed in the most complex forests. *C. julis* TL was unrelated with forest complexity (Fig. 4, permutational ANCOVAs, Table S4). *T. pavo* displayed slightly higher TL in d3 *vs*. d1; however, *T. pavo* TL in d2 was similar to d1 and d3. Although analyses displayed a significant year-site-depth interaction for *C. julis*, no patterns could be observed since pair-wise results were incomplete, due to the insufficient number of individuals for each level of factors. Consequently, no graphical representation was possible. In the case of *Symphodus* spp., neither depth nor forest volume had a significant effect on juvenile TL.

Behavioural traits of the dominant taxa

The behaviour of *C. julis or T. pavo* juveniles was not affected by depth or forest volume. However, both *C. julis* and *T. pavo* juveniles' behaviour was affected by their size. They displayed significantly more cryptic or wandering behaviour for the smallest sizes, while more transitory behaviour was observed in larger individuals (Fig. 5). The behaviour of *Symphodus* spp. was unrelated with forest volume. They exhibited significance of the interaction between Year, Site and Depth terms. However, pair-wise analysis gave incomplete results, due to the insufficient number of individuals for each level of factors. Finally, behaviour of *Symphodus* juveniles was not affected by the size (permutational MANCOVAs, see Table S5). *Symphodus* juveniles' sampled behaviour was 46.97 % cryptic, 28.19 % wandering and 24.83 % transitory.

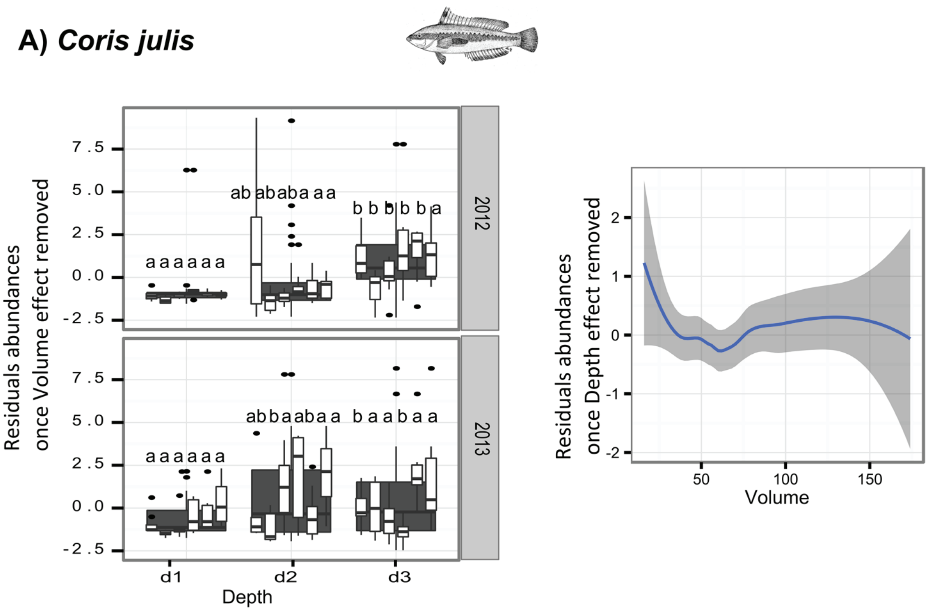
Discussion

This work highlights the significant and independent influence of both *Cystoseira* forest complexity and depth on the juvenile fish assemblage. Juvenile fish behaviour was however found to be taxon-specific and independent of the *Cystoseira* forest complexity (for *C. julis*, *T. pavo* and *Symphodus* spp.) and depth (at least for *C. julis* and *T. pavo*).

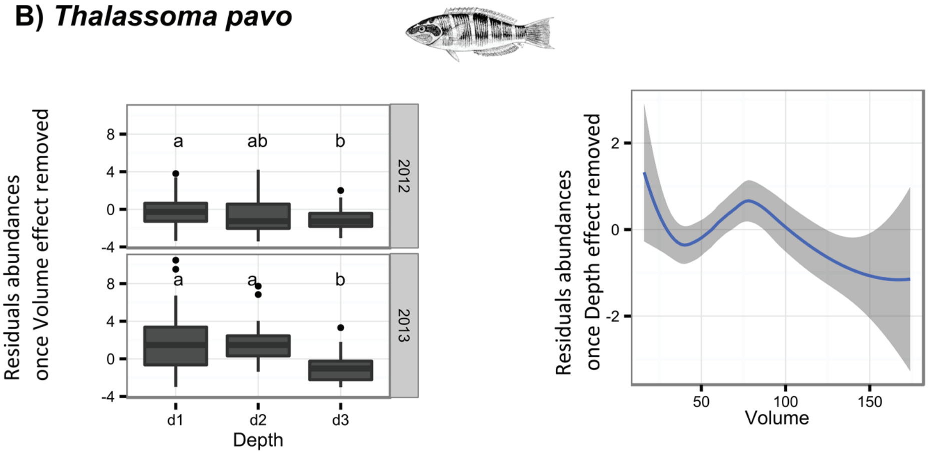
Firstly, the composition of the juvenile fish assemblage was significantly influenced by forest complexity. The density of *C. julis* and *T. pavo* juveniles decreased sharply in the most complex forests (at least down to a threshold for *C. julis* of 50-70 dm^3), whereas the opposite trend was observed for juveniles of *Symphodus* spp. These observations are in agreement with previous works which also reported the association of juvenile *C. julis* with sparse forests and juvenile *Symphodus* spp. with denser forests (Cheminée, 2012; Cheminée *et al.*, 2017).

According to the habitat quality trade-off hypothesis, the highest quality habitat minimises mortality rate by offering a trade-off between foraging and safety (Dahlgren and Eggleston, 2000). These two resources (food and shelter) are essential for juvenile survival. The species observed here prey upon small invertebrates (Kabasakal, 2001; Guidetti, 2004; Thiriet *et al.*, 2014) which may have been more abundant and available in sparse than in more complex *Cystoseira* forests. This is especially likely to have been true for gastropod and sea urchin juveniles (Kelaher, 2003; Bonaviri *et al.*, 2012), due to intense predation by hermit crabs, shrimps and other micro-predators in dense forests (Bonaviri *et al.*, 2012). Unfortunately, prey availability for juvenile fishes in *Cystoseira* forests of different complexities remains unknown and should be further investigated. Other macrophyte habitat studies suggest that, in general, complex habitats offer both more shelter and food, in comparison with simpler ones (Connell & Jones, 1991; Laegdsgaard & Johnson,

A) *Coris julis*



B) *Thalassoma pavo*



C) *Symphodus* spp.

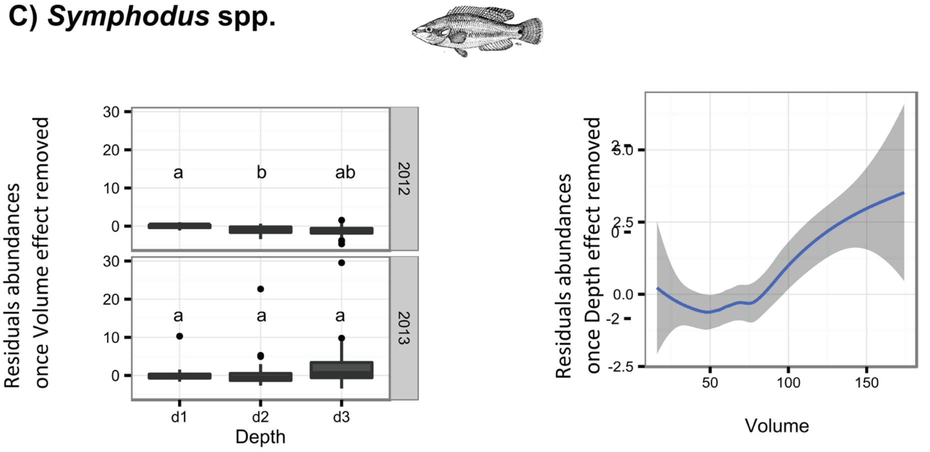


Fig. 3: Boxplots and smoothed curves of residuals of mean abundance of the dominant taxa (*Coris julis, Thalassoma pavo* and *Symphodus* spp.) in *Cystoseira* forests once habitat structure (volume, in dm3) or depth effects were removed (see M & M section). Graphs show significant terms from tests (Table S4). Box plots indicate the median (bold line near the center), the first and third quartile (the box), the extreme values with a distance from the box of at most 1.5 times the inter quartile range (whiskers), and remaining outliers (black dots). Shaded areas of curves represent s.e. Pair-wise tests between treatments are given for boxplots of A) yearxsitexdepth interaction, B) yearxdepth interaction and C) yearxdepth interaction. Different lower case characters indicate significant differences between treatments in boxplots. Depth categories are: d1: 3-5 m, d2: 6-8 m, d3: 10-12 m.

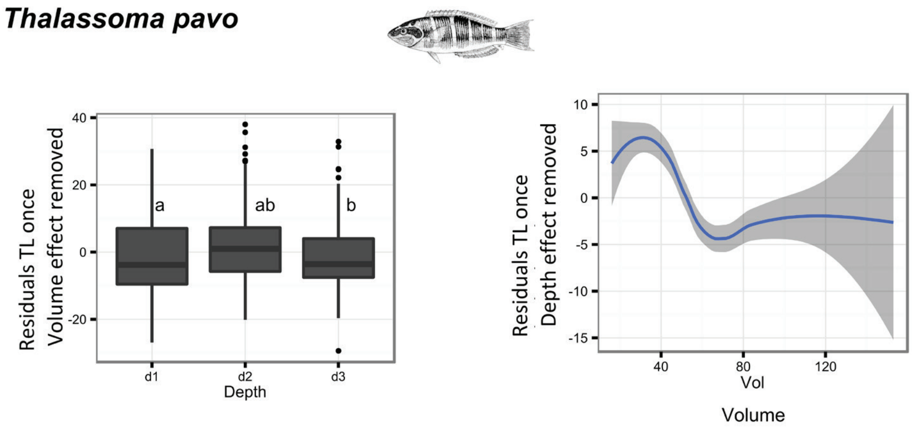


Fig. 4: Boxplot and smoothed curve of residuals of mean TL (mm) of the dominant taxa *Thalassoma pavo* in *Cystoseira* forests once habitat structure (volume, in dm3) or depth effects were removed (see M & M section). Graphs show significant terms from tests. Pair-wise test between depth are given (Table S4). Different lower case characters indicate significant differences between treatments. *C. julis* yearxsitexdepth significant interaction term could not be represented since pair-wise results were incomplete. Depth categories are: d1: 3-5 m, d2: 6-8 m, d3: 10-12 m.

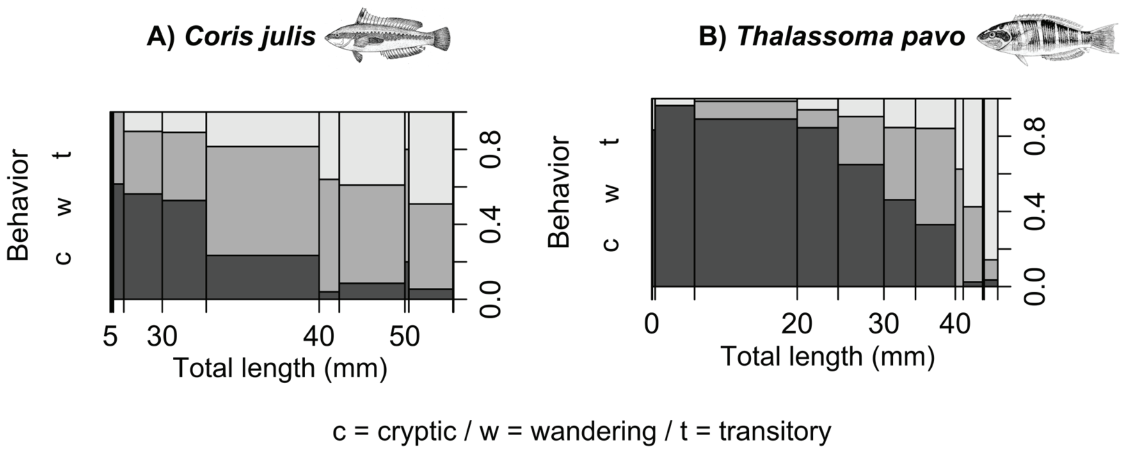


Fig. 5: Proportion of behavioural categories (c, cryptic; w, wandering; t, transitory) in relation to juvenile total length in the dominant species (*Coris julis* and *Thalassoma pavo*) in *Cystoseira* forests. Graphs show significant terms from tests. Bars have different dimensions due to the abundance of the length group.

2001), or that food availability is at a maximum for intermediate values of vegetation complexity (Grenouillet *et al.*, 2002). More studies are needed to clarify food availability according to macrophyte degrees of complexity and to relate this with the diet of every fish species.

The differences in the distribution pattern observed between juvenile *C. julis*, *T. pavo* and *Symphodus* spp. according to forest complexity may also be explained by the differences in their morphology. Morphological variation between species can be responsible for enhanced predator avoidance and feeding success, within the selected complexity. These morphological differences are in terms of colour patterns and locomotor efficiency due to differences in body shape (Hertel, 1966; Motta *et al.*, 1995; Schmid & Senn, 2002). Juveniles of *Symphodus* spp. are pale brown, which provides them with more effective camouflage in the canopy of similar colour. In contrast, juvenile *C. julis* and *T. pavo* are characterised by more colourful patterns and hence may be less cryptic. Fish with a compressed, sub-gibbose body, with long and pointed pectoral fins and a subterminal mouth, are often mobile and manoeuvrable epibenthic foragers inhabiting complex habitats, whereas streamlined fish are better adapted for fast swimming in open water (Keast & Webb, 1966; Hoar & Randall, 1979; Motta *et al.*, 1995; Recasens *et al.*, 2006). *Symphodus* spp. have a much deeper body compared to *C. julis* and *T. pavo*, which may favour their movements within the canopy and explain why they are often observed in association with structurally complex habitats (Bussotti & Guidetti, 2010). This manoeuvrability in a complex habitat favours their foraging efficiency in structurally complex environments, but may be a disadvantage for their speed, resulting in slower movement and thus increased reliance on shelter in the canopy for protection from predation. More streamlined bodies such as those of *C. julis* and *T. pavo* are less manoeuvrable in a complex habitat but enable these species to escape from predators or quickly reach the safety of a refuge, thus especially benefitting from less complex habitats. In accordance with this notion, juvenile *Symphodus* spp. in our study, independently of body length, usually displayed cryptic and wandering behaviour and were abundant in the most complex forests. However, the behaviour of *C. julis* and *T. pavo* was size dependent. Cryptic behaviour was mainly observed in the smallest juveniles, and wandering and transitory behaviour in the larger individuals. Furthermore, the smallest juveniles of *T. pavo* occurred in the most complex forests. The increase in swimming speed experienced with age most likely reduces predation risk in the open areas and allows larger juveniles of these species to venture further from their refuge to forage.

Consequently, juvenile pattern distributions in *Cystoseira* forests according to the structural variability may vary among species. It could be interpreted that *Symphodus* spp. have potentially a stronger preference for complex forests, whereas *C. julis* and *T. pavo* have potentially a stronger preference for forests with less complexity.

Depth also influenced the juvenile fish assemblage and taxon-specific density in our study, findings which are in accordance with those previously published (García-Rubies & Macpherson, 1995; Harmelin-Vivien *et al.*, 1995; Francour, 1997; Vigliola & Harmelin-Vivien, 2001). In our study, however, only assemblage composition, but not species richness or total density, changed with depth, mainly due to the opposed trends of *C. julis* and *T. pavo*. Shallow assemblages were characterized by higher density of *T. pavo* while deeper assemblages had higher density of *C. julis.* These taxon-specific trends are also found in other studies (García-Rubies & Macpherson, 1995; Guidetti & D´Ambrosio, 2004) - but see Milazzo *et al.*, (2011). In addition, no clear relationship patterns between TL and depth were found for *T. pavo or Symphodus* spp., which may suggest the absence of ontogenetic shifts in bathymetry at least in the investigated depth range.

Juveniles of *T. pavo*, *C. julis* and *Symphodus* spp. can be found simultaneously in *Cystoseira* forests; however, inter-specific competition could be reduced by differentiated microhabitat use: *Symphodus* spp. in more complex and *T. pavo* and *C. julis* in less complex forests; and *T. pavo* in shallower and *C. julis* in deeper forests (Guidetti & D´Ambrosio, 2004). Juvenile fish partitioning across space, time and depth has also been observed in other habitats (Harmelin-Vivien *et al.*, 1995).

Whether the preferences are due to active choice of the most suitable microhabitat (Dahlgren & Eggleston, 2000) or due to different juvenile fish mortality rates remains unclear (Thiriet *et al.*, 2014) and should be investigated in future works.

Conclusions

In conclusion, depth gradient and *Cystoseira* complexity both affected the juvenile fish assemblages studied. Variation in depth determined a taxon-specific pattern of distribution of the juveniles, while habitat complexity affected the assemblage composition and body size, which in turn notably induced behavioural differences. We argue that the optimum net production of juveniles of different species is acquired through the intrinsically patchy nature of the forests, displaying a mosaic of various microhabitat characteristics, in terms of depth and habitat complexity. Future protection and management measures, as well as restoration projects, should take these findings into account in order to optimise management efforts. Thus, appropriate spatial management strategies should act at seascape scale and protect a mosaic of habitat types, encompassing each of them with their own bathymetric and three-dimensional variability.

Acknowledgements

This study was carried out from a Balearic Island Government owned research station, Jaume Ferrer (Estació d´Investigació Jaume Ferrer, Govern de les Illes Balears), managed by the Oceanographic Institute for the Balearic Islands (Centre Oceanografic de les Balears). The study forms part of ACU's PhD thesis, funded by these institutions. Study permits for field work within the MPA 'Reserva Marina del Nord de Menorca' were approved by the Balearic Island Government. Authors would like to thank M. Sales and D. Carreras (OBSAM, IME) for their advice on the cartography of the island and members of ECOSEAS, MIO and CEFREM labs who provided helpful criticism of the manuscript at various stages of completion. The authors would also like to express their gratitude to the Septentrion Environnement team and Carlos Domínguez who helped with field work. English language revision was conducted by Adam Gouraguine and Michel Paul. Finally, we would also like to thank the anonymous reviewers for their constructive comments.

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