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Seasonal and depth-related biodiversity of leaf epiphytic Cheilostome Bryozoa in a Mediterranean *Posidonia oceanica* meadow

Gilles LEPOINT, Boris BALANCIER and Sylvie GOBERT
MARE, Laboratoire d'Océanologie, Bât. B6, Institut de Chimie, 3, Allée de la chimie, Université de Liège,
4000 Liège, Belgique. E-mail: G.Lepoint@ulg.ac.be

Abstract: Epiphytes living fixed on *Posidonia oceanica* L. (Delile) are important faunal and floral components of seagrass meadow ecosystems. They are involved as main actors in trophic web and major ecosystem processes of this endangered coastal habitat. This paper aims to assess the seasonality and the bathymetric variability of epiphytic Bryozoa which are the most important animal group in terms of both diversity and abundance living on *P. oceanica* leaves. *Posidonia* shoots were collected from the Revellata Bay (Corsica, France) in four seasons from 7 to 30 m depth. Colony densities reached more than 87000 colonies.m^{-2} at 10 m depth in spring. The bryozoan species distribution and abundance changed substantially according to seasons and depths, being maximum in spring and minimal in winter. Dominant colony morphotypes change according to depth, probably in relation with water motion gradient. This confirms that there are bathymetric and seasonal variability for different epiphytic organisms colonizing the *Posidonia* leaves. This enlightens the importance to protect *Posidonia* meadow on its full depth extension and in its connectivity with other habitats to conserve optimal epiphytic biodiversity and functions.

Résumé : *Biodiversité des Bryozoaires chilostomes épiphytes des feuilles de* Posidonia oceanica *d'un herbier méditerranéen en fonction de la saison et de la profondeur.* Les organismes épiphytes vivant attachés sur les feuilles de la posidonie *Posidonia oceanica* (L.) Delile sont d'importants composants de la faune et de la flore de ces écosystèmes. Ils sont parmi les acteurs principaux du réseau trophique associé et participent aux processus écologiques majeurs de cet écosystème méditerranéen côtier menacé. Notre étude tente d'établir quantitativement la variabilité saisonnière et bathymétrique des Bryozoaires chilostomes, un des groupes épiphyte animal dominant installé sur les feuilles de posidonies. Des faisceaux de posidonies ont été collectés en 4 occasions entre 7 et 30 mètres de profondeur dans la baie de la Revellata (Corse, France). La densité des colonies atteignait un maximum de 87.000 colonies.m^{-2} à 10 mètres de profondeur au printemps. L'abondance et la distribution des espèces changent substantiellement selon la saison et la profondeur, avec des abondances maximales au printemps et minimales en hiver. Les morphotypes dominant des colonies changent également en fonction de la profondeur, probablement en fonction des effets de l'hydrodynamisme. Ceci confirme qu'il s'agit d'une observation générale pour les différents types d'épiphytes colonisant les feuilles de posidonies. Ces observations démontrent également l'importance de protéger l'herbier de posidonies sur l'ensemble de son extension bathymétrique afin de conserver une biodiversité épiphytique optimale.

Keywords: Epiphytism ● Biofouling ● Seagrass ● Bryozoa ● Biodiversity ● Ecological traits ● Mediterranean Sea

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Introduction

The seagrass *Posidonia oceanica* (L.) Delile, characterized by long strap-shaped leaves and a relatively long life span, is fouled by organisms which constitute a complex epiphytic community, involving both micro- and macro-organisms (bacteria, diatoms, protist, macroalgae and sessile animals) (Van Der Ben, 1971; Novak, 1984; Mazzella et al., 1989). This epiphytic community was early recognized by French bionomists as "characteristic" of *P. oceanica* ecosystem (Peres & Picard, 1964) and fossil evidences date this association back to at least the Pliocene (*i.e.* from 5 to 1.8 My B.P.) (Moissette et al., 2007).

The depth range occupied by *P. oceanica* determines an environmental gradient that affects the colonization pattern, composition and biomass of the epiphytic community (Mazzella et al., 1989; Dalla Via et al., 1998). This depth-related variation is species-specific and determines a depth-related pattern consistent at different horizontal spatial scales (Nesti et al., 2009). For macroalgae, this zonation is relatively well known and is clearly driven by the algae demand and their tolerance in terms of light condition (Dalla Via et al., 1998). *P. oceanica* epiphytes display an important seasonality in relation to environmental parameters (Buia et al., 1992). It is determined by the seasonality of leaf growth pattern (e.g. spring leaf growth, autumnal leaf fall) and by the seasonality of environmental condition (e.g. light, nutrient concentration). For example, photophilous brown algae, such as *Giraudya sphacelarioides* Derbès & Solier, are restricted to the upper and the mid part of the *Posidonia* meadow (Mazzella et al., 1989) and appear in spring. On the contrary, erected red algae tend to be more diverse near the deepest limit of the seagrass bed (Van Der Ben, 1971) and are generally among the last colonizers of the plant. Some algae, such as the crustose corallines (i.e. calcareous red algae), are found everywhere in the meadow (Mazzella et al., 1989) and are already present in small amount in winter with early coloniser such as bryozoa (Lepoint et al., 1999).

The distribution of Hydrozoa or Bryozoa has been also documented along the depth range of the meadow (Boero et al., 1985; Balduzzi et al., 1983). For example, on *P. oceanica*, about twenty five species of hydrozoans are found as epiphytes of leaves (Boero et al., 1985). Characteristic hydrozoan species are mainly established in the shallow and intermediate meadow. Deepest zones of the meadow are colonized by less characteristic species, found also in other habitats. Only few species are found all along the bathymetric gradient (Boero et al., 1985). Reasons of such distribution are only poorly understood (Nesti et al., 2009).

Cheilostome Bryozoa are small colonial sessile organisms, occurring in almost all marine habitats. Bryozoa is often the dominant group of leaf epifauna in terms of species diversity and of biomass and some species such as the anascan cheilostome *Electra posidoniae* Gautier, 1957 have been described as exclusively epiphytic of this plant. Epiphytic Bryozoa have been well qualitatively described in various Mediterranean regions (NW Mediterranean, Tunisia, Tyrrhenian Sea, Cyprus, Aegean Sea) (Gautier, 1961; Harmelin, 1973; Hayward, 1975; Balduzzi et al., 1983; Castritsi-Catharios & Ganias, 1989; Chimenz et al., 1999; Kocak et al., 2002; Nesti et al., 2009; Mabrouk et al., 2013; Ben Ismail et al., 2012). Spatial variability of species composition at the scale of a shoot, of a meadow or a region has received considerable attention (Balata et al., 2007; Balduzzi et al., 1983; Nesti et al., 2009). However, numerical data, such as occurrence frequency, biomass and number of colonies are rarely provided. The seasonal variability of epiphytic Bryozoa assemblages has never been assessed quantitatively.

The aim of this study was therefore to assess quantitatively the depth-related and temporal variability of cheilostome Bryozoans settled on *P. oceanica* leaves. Bryozoan colony may adopt different growth forms in relation to their environmental conditions (particularly hydrodynamics), substrate characteristics (Chimenz et al., 1999) and feeding capacity or mechanism (McKinney, 1990). Because environmental and feeding condition may change according to depth, we will assess occurrence of different colony morphologies according to depth.

Material and Methods

All sampling and measurements were performed at Revellata Bay (Calvi, Corsica, France), near the marine research centre of STARESO (42°35'N-8°43'E) (University of Liège). Seagrass shoots were collected in triplicate in November 2002, March, June, September and November 2003 along the same permanent transects set at 7, 10, 15, 20, 25 and 30 m depth. Colonies counted (see above) were reported per meter square, accounting the average *P. oceanica* shoot density measured at each sampling depth. Shoot density, measured monthly using a quadrate with an area of 0.1 m^2 randomly set in the meadow. The shoot density did not show any significant variation during the duration of this study. Bathymetric variability of this parameter in Revellata Bay may be found in Gobert et al. (2003).

The shoots were immediately frozen. Previous work was performed to determine the number of shoots that accumulates at least the 75% of the leaf epiphyte bryozoan species.

Identifications under stereomicroscope (Stemi 2000, Zeiss) were done to the lowest systematic level using keys for Bryozoa (Prenant & Bobin, 1966; Zabala & Maluquer, 1988), and the works of Hayward & McKinney (2002), Gautier (1961) or Balduzzi et al. (1991). All the colonies found on the two sides of leaves were counted. Each sample is constituted of a single replicate gathering 3 shoots of *P. oceanica*. For *Electra posidoniae*, colonies fusion (or apparent fusion) is common. Therefore for this species, as a proxy of the colonies counted, the number of colonies founders (i.e. ancestrulae), which have a distinctive morphology, was counted.

The number of autozooids was counted for each colony, except *Electra posidoniae* and stolonate species such as *Aetea lepadiformis* Waters, 1906 and colonies were assigned to the following size categories: fewer than 10 autozooids, 11-20 autozooids, 21-50 autozooids, 51-100 autozooids and more than 101 autozooids.

The presence of reproductive structures, such as sacculi in *Aetea lepadiformis* (Balduzzi et al., 1991) and the average amount of ovicellate zooids were also recorded when possible.

For statistical analysis, the number of colonies per species for each sample (i.e. the sum of Bryozoa colonies found on 3 *P. oceanica* shoots) was calculated. Very rare species (*i.e.* defined by an occurrence < 3% and an abundance < 1% of the total colonies counted) were not taken into account. Data were square root transformed to reduce the influence of *E. posidoniae* that often accounted for more than 75% of colonies counted. A similarity matrix was built using the Bray-Curtis index. Results are presented as a non-metric multidimensional scaling ordination. Analyses were done using PRIMER 6 software package.

Results

Twenty-two taxa of cheilostome bryozoan were identified on the *P. oceanica* leaves, represented by 6476 colonies. The most abundant species in term of number of colonies was the anascan *Electra posidoniae*, representing almost 60% of the total (Table 1). *Haplopoma impressum* (Audouin, 1829), *Callopora lineata* (Linnaeus, 1767), *Chorizopora brongniartii* (Audouin, 1826), *Celleporina hassalli* (Johnston, 1847), *Microporella ciliata* (Pallas, 1766), *Collarina balzaci* (Audouin, 1826) represented each between 5 and 7% of the colonies counted. The total of the 15 remaining species or taxa represented less than 10 % of the total number of colonies. Some species, such as *Umbonula ovicellata* (Hastings, 1944), *Puellina gattyae (*Landsborough 1852) and *Puellina hincksi* (Friedl, 1917), were only found occasionally.

The most frequent species, *Haplopoma impressum* and *Electra posidoniae,* were found on 70 % of sampled shoots (Table 1), dominant species differing according to depth.

Colony abundance and the number of species were the lowest in November 2003 and the highest in June and showed a drastic decrease in September, particularly in the shallowest stations (Fig. 1).

Table 1. Contribution of the most abundant Cheilostomata Bryozoa species to the total number of colony settled on *P. oceanica* leaves.

Species	Contribution to total colony number (%)	Frequence of occurrence (%)
Electra posidoniae	56.6	70
Hapoploma impressum	6.7	71
Callopora lineata	6.1	25
Chorizopora brongnartii	5.8	57
Celleporina hassali	5.8	48
Microporella cilliata	5.3	53
Collarina balzaci	5.1	48
Other species (n = 15)	8.6	

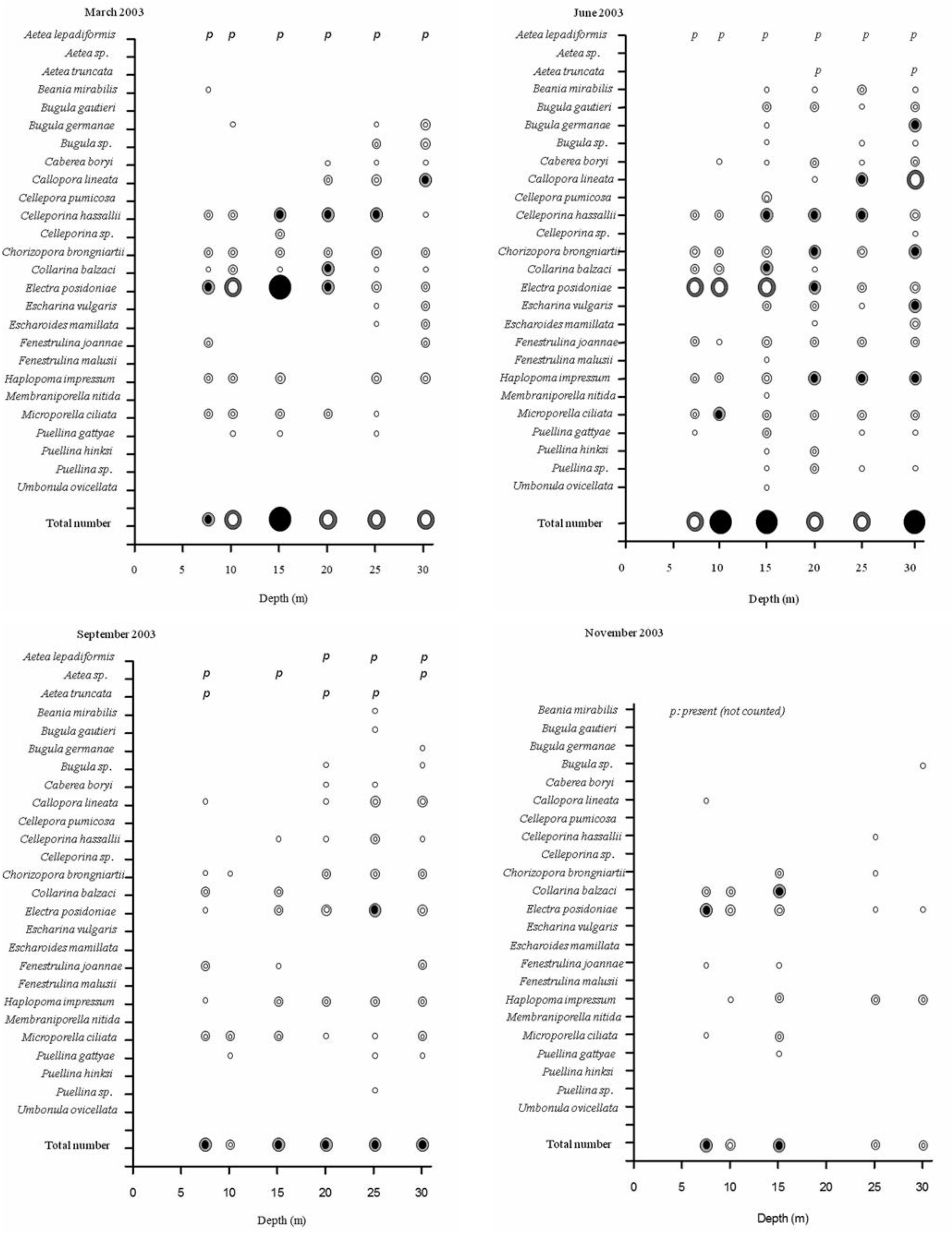
The seven most frequent species cited above and *Aetea lepadiformis*, another characteristic species of *P. oceanica* epiphytic assemblages, were observed all year round, but generally in very few numbers in September and November (Fig. 1).

Species number was lowest at 7 m depth and increased below 15 m depth. The increase in the number of species below 15 m depth was due to the occurrence of several species represented with limited number of colonies, except *Callopora lineata* that appeared below 15 m depth and became very abundant at 25 and 30 m depth (Fig. 1*)*.

Some species such as *Collarina balzaci*, *Fenestrulina joannae* (Calvet, 1902) and *Electra posidoniae* were mainly found between 7 and 15 m depth. *E. posidoniae* colonies were very small and less abundant at depth greater than 20 m. Conversely, many species were only found at the deepest sampling stations, especially *Callopora lineata*, and the majority of less frequent species (less than 3% occurrence). Finally, the relatively abundant *Celleporina hassalli* occurred mainly at 15-20 m depth while *Haplopoma impressum* and *Chorizopora brongniartii* were found at all depths.

On the nMDS based on a Bray-Curtis similarity matrix comparing the different samples, one sample, collected at 10 m depth in September, shared less than 25% similarity with the others (Fig. 2). This is likely caused by the very low number of colonies recorded in this sample. Five groups could be distinguished at a level of 50% of Bray-Curtis similarity. Group 1 contained three winter samples from 25 and 30 m depth; Group 2 one winter sample taken at 20 m depth and 8 autumn and winter samples from 7, 10, and 15 m depth sites; Group 3 autumn samples from 20, 25 and 30 m depth and one winter sample from 25 m depth; Group 4 all early and late spring samples.

Within Group 4, Group 5 (similarity > 75 %) included samples collected at 7 and 10 m depth in March and one sample taken in June at 10 m depth. Other June samples


March 2003
June 2003
September 2003
November 2003
Aetea lepadiformis
Aetea sp.
Aetea truncata
Beania mirabilis
Bugula gautieri
Bugula germanae
Bugula sp.
Caberea boryi
Callopora lineata
Cellepora pumicosa
Celleporina hassallii
Celleporina sp.
Chorizopora brongniartii
Collarina balzaci
Electra posidoniae
Escharina vulgaris
Escharoides mamillata
Fenestrulina joannae
Fenestrulina malusii
Haplopoma impressum
Membraniporella nitida
Microporella ciliata
Puellina gattyae
Puellina hinksi
Puellina sp.
Umbonula ovicellata
Total number
p
p: present (not counted)
0
5
10
15
20
25
30
Depth (m)

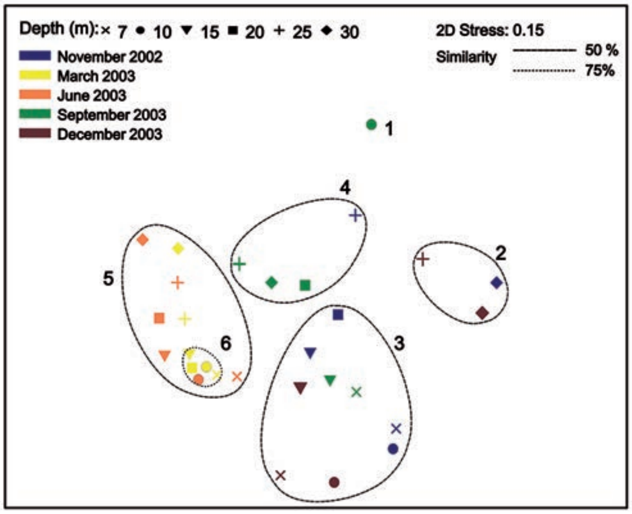


Figure 2. 2D ordination of samples obtained via non-metric multidimensional scaling, using Bray-Curtis similarities computed on square-root transformed numbers of colonies of the different bryozoan species.

taken at 7 and 15 m depth were close to this group (similarity > 60 %).

All species, small colonies with fewer than 10 zooids or in the 11-20 zooids colony size class were dominant, except *E. posidoniae*. For some species, it was possible to observe reproductive structures on these very small colonies (having 5 zooids in *H. impressum*, *Puellina* spp. and *Bugula* spp. for example). We present for each season the depth distribution of colonies classified in 5 size classes for four of the more abundant species found on the *P. oceanica* leaves: *Haplopoma impressum, Celleporina hassalli, Collarina balzaci and Callopora lineata* (Figs 3 to 6, respectively). *H. impressum* and *C. hassallii* were among the few species developing colonies with more than one hundred zooids. It was also the case that *E. posidoniae* sometimes covered the entire leaf. Nevertheless, for *H. impressum*, these "large" colonies generally did not dominate the population.

Haplopoma impressum, although occurring over the entire depth range, had the largest colonies at the deep sampling stations (Fig. 3). In this species, reproductive structures were found all year long whatever the depth. Nevertheless, the maximum of colonies counted with these structures was found in late spring at the deepest sampling station. Recruitment of ancestrulae seemed to begin before March sampling and was still occurring in late June.

Celleporina hassalli was almost restricted to March and June samples (Fig. 4). Recruitment of ancestrulae seemed to occur mainly before March but continued into June as confirmed by the presence of very small colonies and of reproductive structures in larger ones. Well developed colonies were mainly found between 15 and 25 m depth. The population was generally dominated by colonies containing more than ten zooids and large colonies of more than one hundred zooids were often observed.

Callopora lineata (Fig. 5) occupied only the deepest part of the *P. oceanica* meadow where it formed colonies of often more than 100 zooids. It was almost absent in November and recruitment seemed to begin before March. Ovicell on new colonies were observed until June. Well developed colonies represented a large part of the population, particularly in June.

Collarina balzaci (Fig. 6), a species almost restricted to the basal parts of the *Posidonia* leaves, rarely formed colonies of more than 50 zooids. In contrast to most other species, such colonies and their reproductive structures were found all year round from 7 to 20 m depth. Recruitment appeared to be independent of season. September corresponds to the leaf fall period and thus minimal colonization, nevertheless recruitment had already occurred in November.

Bryozoan colonies may be classified according to different morphotypes (Fig. 7). Multiserial runner morphotype dominated from 7 to 20 m depth sample. Small encrusting bryozoans dominated at 25 and 30 m depth. Celleporiform types (i.e. small and multilayered) appeared at 7 m depth, but their maximum occurrence was at 15-25 m depth range. Erect colonies appeared at 15 m depth but its contribution is maximum at 30 m depth.

Discussion

The number of cheilostome species found in our study is equivalent of species number found in Koçak et al. (2002) or Ben Ismail et al. (2012), *i.e.* about 20 cheilostome species. This is not the maximal number of species found in *P. oceanica* meadow as, generally, rhizomes display a more diverse community (Koçak et al., 2002; Cocito et al., 2012). Dominant species (*E. posidoniae, F. joanae, H. impressum, M. ciliata, C. balzaci, C. hassalli*) are also

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Figure 1. Colony number of bryozoan species settled on the leaves of *P. oceanica* (n = 3 shoots) collected between 7 and 30 m depth in the Revellata Bay (Corsica) between March 2003 and November 2003.

○ 1-2 ◎ 3-30 ◉ 31-150 ○ 151-450 ● >450 colonies

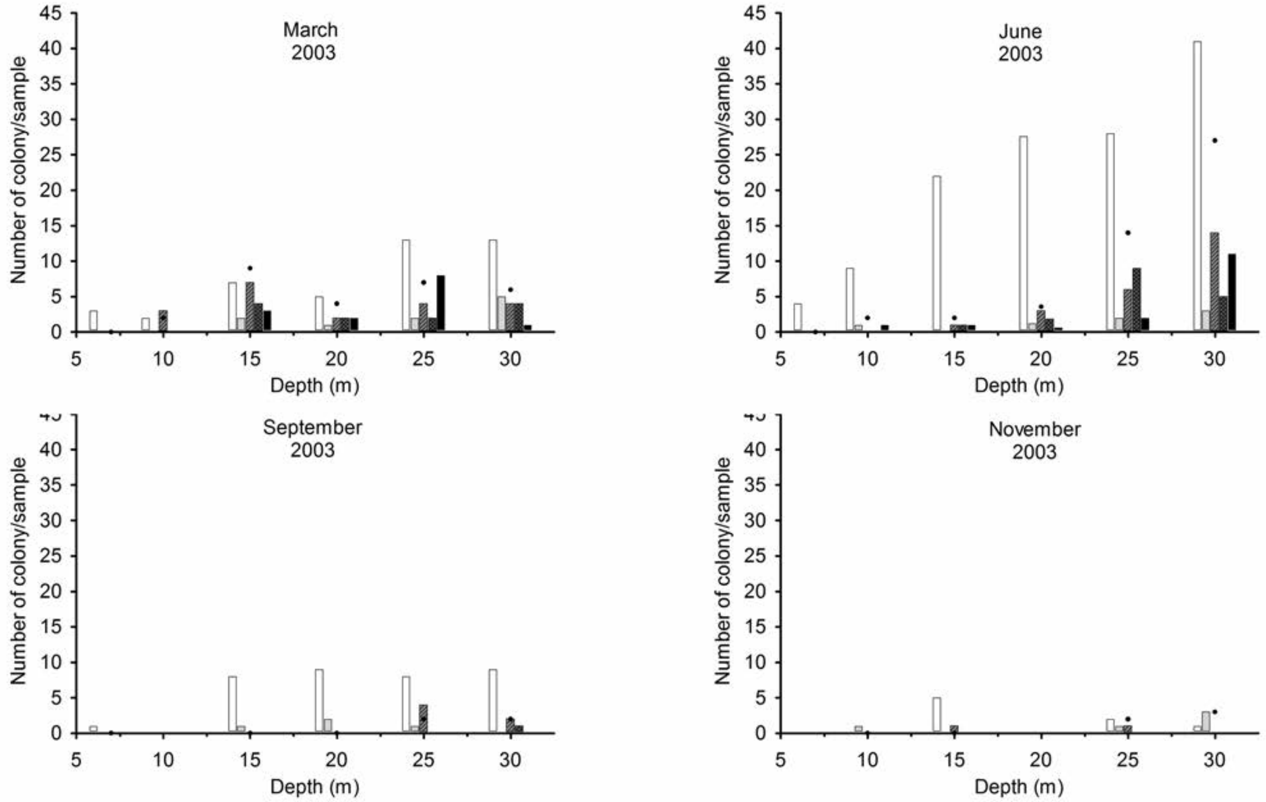

Figure 3. Population structure of *Haplopoma impressum* in relation to depth and season. Colony sizes were classified in 5 categories ranging from < 10 autozooids (open bar), 11-20 autozooids (light grey), 21-50 autozooids (middle grey), 51-100 autozooids (dark grey), > 100 autozooids (black). Black points represent the number of ovicellate colonies.

generally mentioned in the different studies, *E. posidoniae* being often considered as the dominant species, characteristic of the assemblage (Gautier, 1961; Harmelin, 1973; Hayward, 1975; Balduzzi et al., 1983; Casola et al., 1987; Castritsi-Catharios & Ganias, 1989; Chimenz et al., 1999; Kocak et al., 2002; Nesti et al., 2009; Ben Ismail et al., 2012; Mabrouk et al., 2013). Some of these species were also present in the fossil remains analysed by Moissette et al. (2007), demonstrating the long-term establishment of this particular epiphytic community.

Among *Bugula* spp., we have found specimen displaying the characteristic of *B. gautieri* Ryland, 1961, although this species was never described as epiphytes of *P. oceanica*. Another dominant *Bugula* species was probably *B. serrata* (Lamarck, 1816) (syn. *B. germanae* (Calvet, 1902)), but we are not confident about *Bugula* determination considering many colonies were very young or small and did not displayed reproductive structures.

Bryozoa assemblage and abundances showed to be highly seasonal. In contrast to early and late spring samples, winter and autumn samples showed very low diversity and colony abundance correlating with substratum availability and environmental conditions. Autumn and winter correspond also to low *P. oceanica* leaves biomass due to massive leaf fall in autumn and absence of significant leaf growth in winter (Gobert et al., 2003). End of winter to early spring correspond to the beginning of *P. oceanica* leaf growth in the Calvi Bay; but it also correspond to phytoplanktonic bloom (Lepoint et al., 2004). Considering the oligotrophic character of this area, planktonic biomass is very low all around the year, except few weeks in spring. Seasonality of phytoplankon dynamics is thought to affect dynamics of benthic suspension feeders, particularly in oligotrophic area (Coma et al., 2000). Massive bryozoan recruitment occurs during early spring and number and size of colony of most species increase in March compared to November and in June compared to March. This fits observation by Mariani et al. (2005) for epilithic species. Therefore, both dynamics of host growth and of phytoplankton influence the bryozoan seasonal dynamics. Moreover, epiphytic macroalgae, particularly the photophilous ones, develop generally later than sessile animals in relation to light availability seasonality (Jacquemart, 2009). Animal, and particularly bryozoans, tend to dominate the epiphytic assemblage from winter till March-April (Lepoint et al., 1999; Prado et al., 2008).

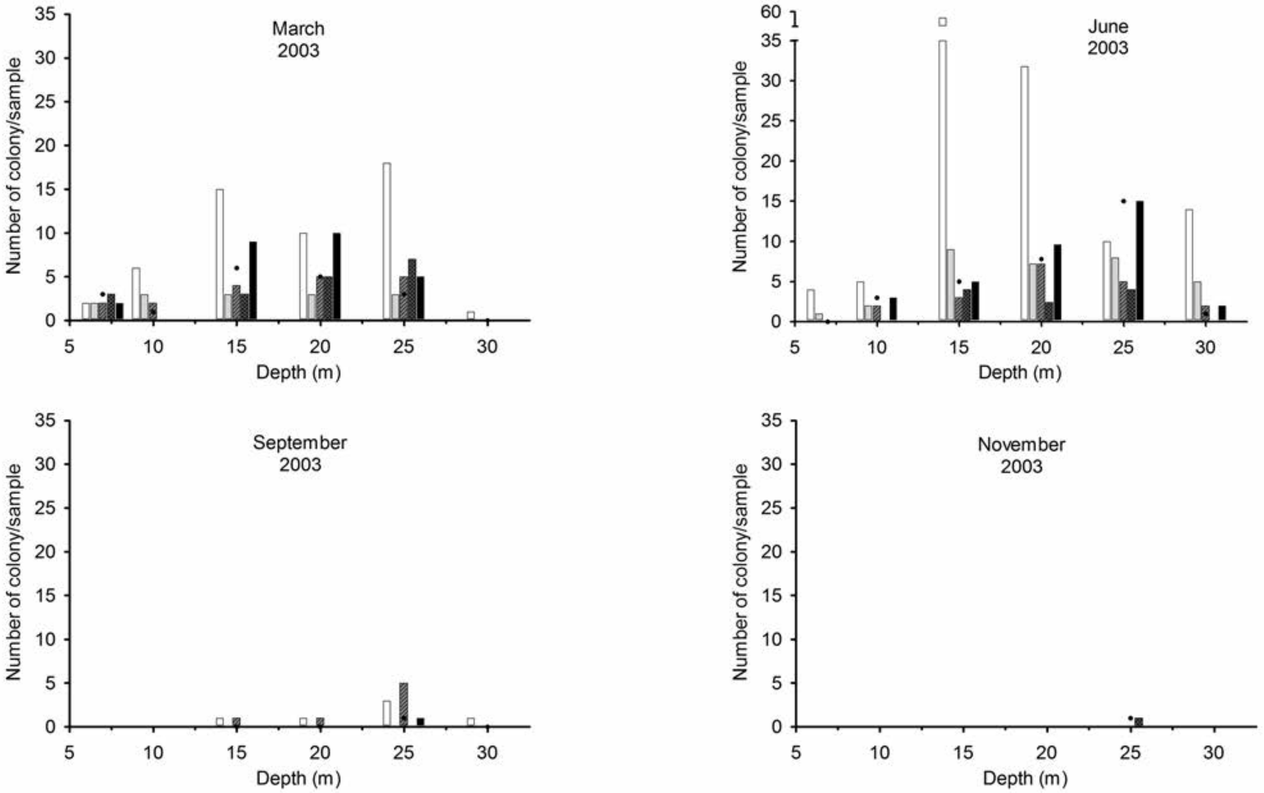

Figure 4. Population structure of *Celleporina hassalli* in relation to depth and season. Colony sizes were classified in 5 categories ranging from < 10 autozooids (open bar), 11-20 autozooids (light grey), 21-50 autozooids (middle grey), 51-100 autozooids (dark grey), > 100 autozooids (black). Black points represent the number of ovicellate colonies.

Reproductive periods and strategies are potentially affected by substratum seasonality and phytoplankton availability. For *C. balzaci*, the maximum number of colonies with ovicell was observed in different depth of the meadow depending on the season. Nevertheless, for all others, including *E. posidoniae* which is almost absent in winter, massive recruitment occurs in the end of winter and early spring during phytoplankton bloom and when *P. oceanica* leaves are growing (February-March). If we assume that recruitment occurs from leaf epiphyte population, it would mean that recruitment is mostly done from larvae produced in summer or late summer, before autumnal leaf abscission or by the small number of colonies remaining in winter. The first hypothesis corresponds to about a 4-5 month time lag, and this is untenable for most bryozoan species which have larvae that last for a matter of hours or a few days at most

For *E. posidoniae*, which is restricted to *Posidonia* leaves, recruitment is clearly only done from leaf epiphytic population and is partly possible because this species has a long-lived, planktonotrophic cyphonaute larvae. Nevertheless, cyphonaute life-span does not probably exceed few weeks (Gautier, 1961). Presently, there is no evidence for a longer life-span for *E. posidoniae* and, therefore, it is possible that the small overwintering population on leaves has a major role in the massive spring recruitment.

For species with short-lived larvae (hours-days), external recruitment from other habitats with overwintering colonies could be involved, considering the absence or the low number of colonies able to reproduce on leaves in winter. The first source of external recruits could be the bryozoan assemblage from the rhizome stratum of the *P. oceanica* meadow itself (Cocito et al., 2012) which shares some species with the leaf stratum (Balduzzi et al., 1983; Kocak et al., 2002) and which has a very low turnover rate that potentially allows the survival of overwintering colonies. Secondly, adjacent epilithic habitats may function as source of recruits, particularly for for non-obligate epiphytes. Thirdly, in Calvi Bay, the entrance of cold and deeper water in the bay along the sea floor is well established (Skliris et al., 2001) and could potentially be an alternative source of recruits, particularly for species colonizing the deep stands of the *Posidonia* meadow.

Bryozoan assemblages depended also on depth. The shallowest assemblages were characterized by the lowest

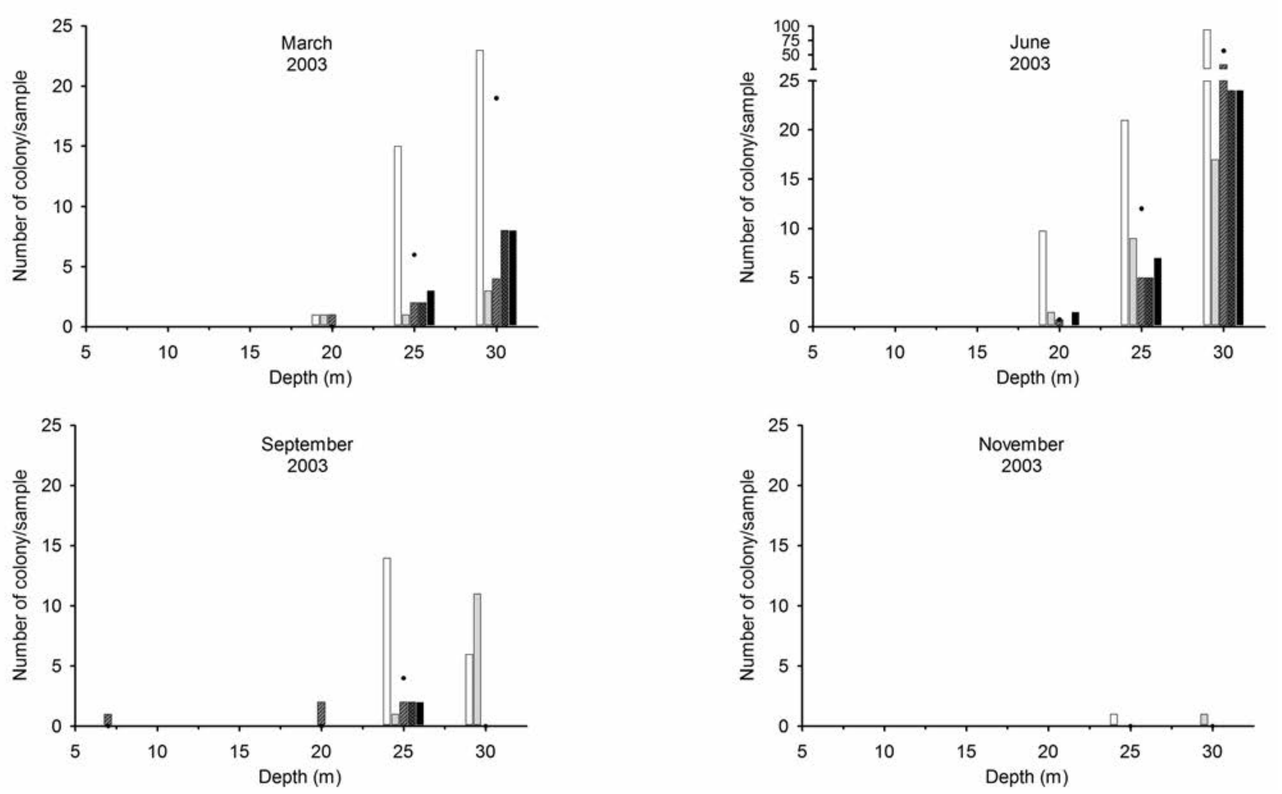

Figure 5. Population structure of Callopora lineata in relation to depth and season. Colony sizes were classified in 5 categories ranging from < 10 autozooids (open bar), 11-20 autozooids (light grey), 21-50 autozooids (middle grey), 51-100 autozooids (dark grey), > 100 autozooids (black). Black points represent the number of ovicellate colonies.

diversity and the lowest abundance of bryozoans, confirming earlier observations (Casola et al., 1987). This is linked to three interdependent factors. First, this meadow depth is the most affected by water motion (Casola et al., 1987). Second, the maximum of light available for both autotrophic epiphytes and *P. oceanica* it-self (Dalla Via et al., 1998), which show a higher growth and turnover rates at this depth and out compete bryozoans for leaf colonization. Thirdly, this is also the place of maximum herbivory which contributes to limit available substratum and strongly affects epiphyte dynamics (Prado et al., 2007).

Most of the species found between 7 and 20 m depth are recognized as characteristic of the *P. oceanica* epiphytic community (Peres & Picard, 1964). *Electra posidoniae* showed its maximum number of colonies, matching the results of Nesti et al. (2009). At this depth range, epiphytic photophilous macroalgae often dominate the epiphytic biomass and compete with Bryozoa for substratum colonization (Mazzella et al., 1989; Jacquemart, 2009; Lepoint et al., 1999).

Deeper stands, at 25 and 30 m depth, showed the highest species number of cheilostome Bryozoa, but many species (e.g. *Callopora lineata*, *Bugula* spp., *Beania mirabilis*, Jonhston 1839, *Umbulona ovicellata* Hastings, 1944, *Escharina vulgaris* (Moll, 1803), *Escharoides mamillata* (Wood, 1844)*)* were not particularly characteristic of epiphytic environments and could be also found as epilithic animals, sometimes associated with deeper zones of the coastal environment (Gautier, 1961). Assemblages were quite different from those occurring in shallower areas, notably by the addition of *Callopora lineata* as the dominant species and the presence of erect species as *Bugula* spp. or *Caberea boryi* (Audouin, 1826).

According to Chimenz et al. (1999), only few colony morphology types were recorded on the *P. oceanica* leaves. Generally, these colonies were lightly calcified and flexible, except celleporiform colony. Dominant colonial morphology varied according to depth, and, therefore, to the water motion gradient. Lightly calcified encrusting forms, both small encrusting colonies (*H. impressum, C. balzaci, F. joanae,…*) and multiserial colony of *E. posidoniae* were dominant colonizers between the surface and about 20 m depth. Celleporiform colonies, which are small but heavily calcified, appeared at 15 m depth, probably indicating a progressive decrease of water motion influence on epiphyte colonization. In deeper *Posidonia*

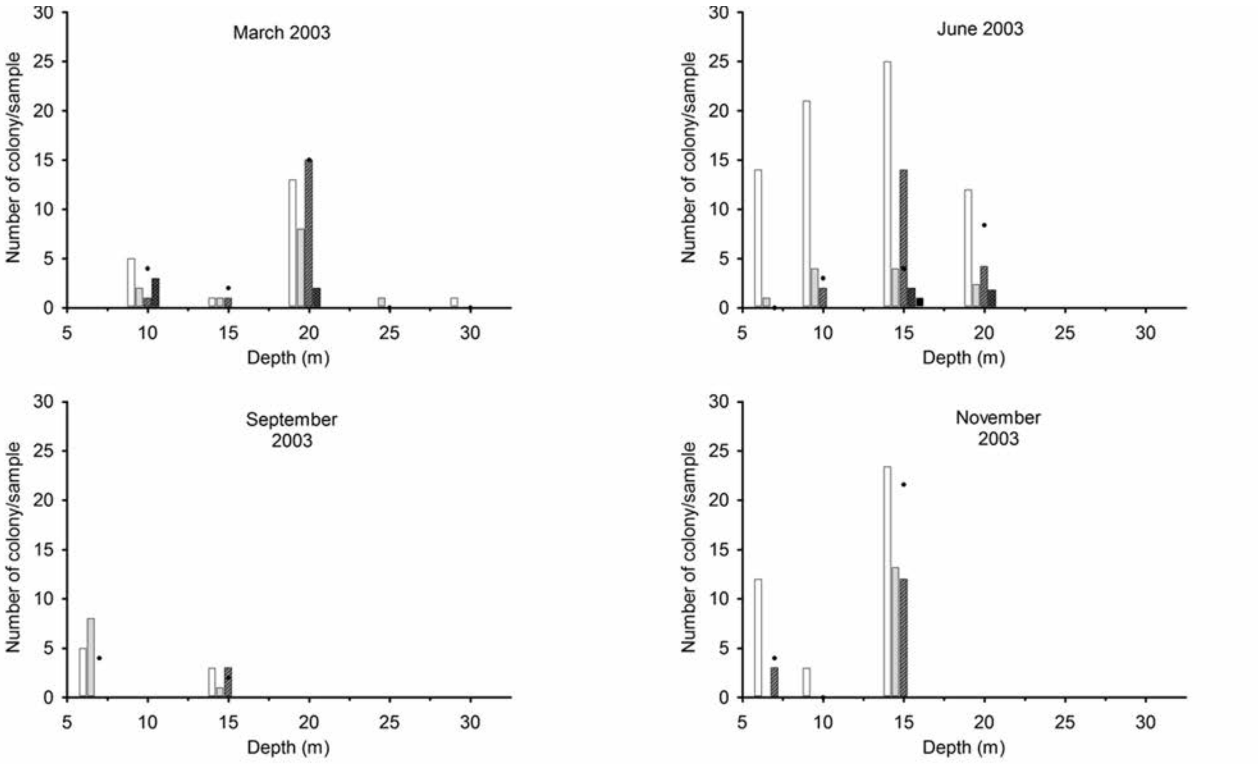

Figure 6. Population structure of *Collarina balzaci* in relation to depth and season. Colony sizes were classified in 5 categories ranging from < 10 autozooids (open bar), 11-20 autozooids (light grey), 21-50 autozooids (middle grey), 51-100 autozooids (dark grey), > 100 autozooids (black). Black points represent the number of ovicellate colonies.

stands, small encrusting and lightly calcified erect colonies were the most abundant colony morphotypes. This is probably a consequence of decreasing water motion according to depth.

In terms of colonies counted, bryozoan abundance was very variable, ranging from 400 colonies.m^{-2} at 30 m depth in December to 87,000 colonies.m^{-2} (of which 75% are *E. posidoniae*) at 10 m depth in June. Colony size distribution differed between *Collarina balzaci*, *Celleporina hassalli*, *Callopora lineata* and *Haplopoma impressum*, but, in all of these species, maximum colony size was < 200 zooids, which is far lower than the maximum size of colonies found on rocks. This is probably an effect of space limitation, of the limited life-span of plant substrate (Borowitzka & Lethbridge, 1989), and of competition with (and between) macroalgae and with *E. posidoniae* (Dalla Via et al., 1998; Lepoint et al., 1999). Another life trait that may be related to epiphytic life is the fact that colonies acquire reproductive structures very quickly. We have observed colonies of five zooids in *Haplopoma impressum* and *Collarina balzaci* that may produce ovicells. Therefore, small colony size, lightly-calcified colonies and ability to reproduce at very low colony size appear to be three characteristics shared by many leaf epiphyte Bryozoa, with the important exception of *E. posidoniae* which quantitatively dominates the assemblages (Chimenz et al., 1999). These are traits of so-called 'spot colonies' as defined by Bishop (1989).

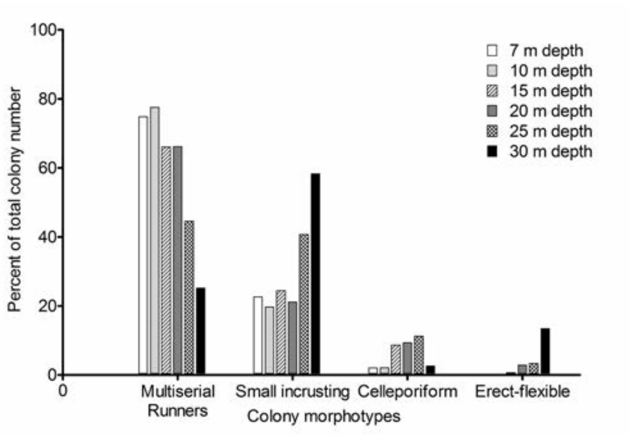

Figure 7. Occurrence percentage of main colony morphotypes in relation to depth.

Bryozoa colonization on *Posidonia* leaves, but also on other macrophytes, could be classified in three "life traits" categories. Category 1 gathers epiphytic specialists (or hyperspecialists) displaying different colonizing strategies. Category 2 gathers species "tolerant" to epiphytism and category 3 gathers species which are occasional and probably accidental epiphytes.

Category 1 is based on *E. posidoniae* life traits and groups species, which are epiphytic specialists, adapted to substratum flexibility and substratum renewal in a context of intensive competition for space. Adaptive strategies of category 1 involve development of large creeping zoids, forming large but flexible colony parallel to leaf veins, with high growth rate (i.e. runner colony morphotype). *E. posidoniae* zooids are far larger than those of other epiphytic Bryozoa and this may contribute to the generation of a feeding current more adapted to their habitat (i.e. lower water speed in the canopy), with a probable coordination of this feeding flow among the different parts of the colony (Chimenz et al., 1999). Reproduction is adapted to host life cycle (i.e. growing and falling period) and involves long lifespan planktonotrophic larvae.

The second group is exemplified by species like *Haplopoma impressum*, *Celleporina hassalli* , *Chorizopora brongniartii*, *Microporella ciliata* or *Callopora lineata*. These are very frequent and abundant on *Posidonia* leaves but are not restricted to this plant or to a vegetal substratum. These species are particularly plastic according to substratum nature. For example, most show miniaturized colony and/or zoids when colonizing a plant. Most are able to adapt their reproductive strategy or cycle to this ephemeral substratum. They occupy mostly the intermediate or the deep part of the meadow, contributing importantly to epiphytic diversity. Nevertheless, some are partly dependent to connectivity with other habitat (*Posidonia* rhizomes, rocks or deeper habitats) to supply their spring recruitment on *Posidonia* leaves.

At last, the fourth group is composed by species which occasionally or "accidentally" use seagrass leaves for their settlement. They are unable to reproduce and ensure their vital cycle. *Posidonia* leaves act as a reproductive cul-de-sac for this category. They often display the same morphological plasticity than group 3, except they do not have the capacity to adapt their reproduction to this particular substratum. These species are mainly found in the deepest *Posidonia* meadows part.

Conclusion

Our results demonstrate quantitatively the variability and the complexity of cheilostome assemblages on *P. oceanica* leaves in relation to season and depth gradient. This confirms that it is a general rule for epiphytic organisms to be affected by the depth where *Posidonia* occurs. Many epiphytic species depends on other habitats (or other meadow part) to ensure their complete life cycle. This enlightens the importance to protect *Posidonia* meadow on its full depth extension and in its connectivity with other habitats to conserve optimal epiphytic biodiversity and functions.

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