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High xenodiversity versus low native diversity in the south-eastern Mediterranean: bryozoans from the coastal zone of Lebanon

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Abstract

Because of its location in the warmest corner of the Mediterranean, its proximity to the northern entrance of the Suez Canal, i.e. the gateway for massive exotic biota introduction into the Mediterranean, the occurrence of intensive shipping activity and strong human pressure, the Lebanese coastal zone is an area that is exceptionally well-suited for investigating the effects of these extreme conditions on Mediterranean biodiversity.

Bryozoans, which are among the main components of sessile communities, dramatically reflect the impact of these particular conditions. Their assemblages, sampled by diving along the whole coast of Lebanon during a pluriannual programme, mainly between 1999 and 2003, consist of 93 species (12 Cyclostomata, 2 Ctenostomata, 79 Cheilostomata). The native part of this bryozoan fauna exhibits low diversity, with an unexpected absence of many taxa, from family to species level, which are very common in the rest of the Mediterranean. It is also characterized by a high proportion of endemic species, in contrast with the general eastward trend of decreasing endemicity observed in the Mediterranean, and by the strong presence of 'southern' thermophilic species.

With 27 non-indigenous species, the xenodiversity is exceptionally high, particularly in the cheilostome pool (26 species), but was probably undersampled. Moreover, one may assume that new non-indigenous bryozoans (NIB) are now established along the Levantine coasts. This trend is expected to increase in the near future with the intensification of surface water warming and the increase in shipping activity and propagule flux generated by the expansion of the Suez Canal.

Keywords: Biodiversity, biogeography, biological invasions, Bryozoa, climatic changes, endemism, Levantine basin, Suez Canal.

Introduction

The Mediterranean Sea is deemed to host a very high level of biodiversity for its size (Bianchi & Morri, 2000; Boudouresque, 2004; Coll *et al.*, 2010; Bianchi *et al*., 2012), but with contrasting local situations and a decreasing gradient from the western to the eastern Mediterranean (Fredj, 1974; Boudouresque, 2004; Bianchi, 2007; Coll *et al.*, 2010). Overall, Mediterranean species richness stems essentially from the combination of a complex paleogeographical history and a wide variety of subregional climatic conditions, resulting in the presence of numerous endemics and of biota of different biogeographical origins established during successive phases of the geological history of the Mediterranean (Pérès, 1967, 1985; Bianchi & Morri, 2000; Taviani, 2002). However, there is a wide disparity in knowledge of the biodiversity between Mediterranean subregions and taxonomic groups, with southern areas and some invertebrate groups, such as Bryozoa, remaining poorly investigated. Furthermore, the status of Mediterranean biodiversity needs constant re-assessment as its rate of change over time is increasing dramatically as a result of human stressors acting on coastal and offshore ecosystems, climate warming and introduction of non-indigenous species (Bianchi *et al*., 2012).

The Mediterranean Sea is an exceptionally rich recipient area of non-indigenous species, mainly fuelled by three anthropogenic pathways of introduction of alien species, i.e. aquaculture, shipping and the Suez Canal (e.g. Zibrowius, 1992, Streftaris *et al.*, 2005; Zenetos *et al*., 2012; Galil & Goren, 2014). The opening in 1869 of a connection between the Red Sea and the Mediterranean via the Suez Canal triggered an extensive colonization of the Mediterranean, particularly the eastern basin, by 'lessepsian' species belonging to most groups of flora and fauna (e.g. Por, 1990; Boudouresque, 1999a; Galil, 2007; Zenetos *et al.*, 2012). This trend is accelerating as a result of hydrological changes in the Canal and the general warming of the Mediterranean that favours thermophilic species (Boudouresque, 1999a; Occhipinti-Ambrogi, 2007; Lejeusne *et al.*, 2009; Bitar, 2008, 2010, Por, 2010).

The Levantine basin is the warmest corner of the Mediterranean (Abboud-Abi Saad *et al.* 2004; Taupier-

Letage, 2008), a condition exacerbated by global warming, which shapes the marine communities, entails the exclusion of shallow-water biota intolerant of warm temperatures, such as the sea-grass *Posidonia oceanica* (Celebi *et al*., 2006) and increases the invasibility of the coastal zone by thermophilic alien species (Occhipinti-Ambrogi, 2007; Lejeusne *et al*., 2009; Occhipinti-Ambrogi & Galil, 2010). The contiguity of the Levantine coasts with the northern entrance of the Suez Canal and the favourable circulation of surface waters (Hamad *et al.*, 2006) are other fundamental drivers of the intense colonization by lessepsian species observed along these coasts (e.g., Por, 1990; Galil, 2007). This process, in constant progression, may controversially be viewed as a rejuvenation of the Mediterranean with a return of the tropical Tethys conditions (Por, 2010). The present status of coastal marine communities at sites of interest for conservation in Lebanon was recently surveyed (RAC/SPA - UNEP/MAP, 2014) but, unfortunately, the baseline data on their past condition are very poor.

Rates and timing of colonization by alien species reported from different Mediterranean sub-regions in review papers are often biased by wide disparities in study effort and levels of expertise locally devoted to these issues (e.g. Nunes *et al.*, 2014). In addition, as stressed by Streftaris *et al*. (2005) and Por (2010), there is an imbalance in knowledge of the biological invasion of the Mediterranean Sea between taxonomic groups and some species are listed on the basis of unverified records (Zibrowius, 1992). The same remark also applies to the native elements of the same groups in the eastern Mediterranean, and particularly the Levantine basin.

Bryozoans are major components of benthic communities, displaying a wide variety of colony shapes, sizes and life history strategies. They also are among the main fouling organisms colonizing artificial substrata (Ryland, 1965; Gordon & Mawatari, 1992; Karlson & Osman, 2012). Because of particular traits of their morphology, life-history and ecology, many species are especially prone to dispersal outside their native geographical range by man-induced vectors (Gordon & Mawatari, 1992; Watts *et al*., 1998). Fouling on immerged surfaces of vessels is the most common mode of transport by shipping but larval transfer via ballast water is assumed to be effective for species producing long-lived cyphonautes larvae (Carlton, 1985). Translocation may also occur by means of rafting, i.e. settlement on drifting items, such as plastic debris (Winston *et al*., 1977; Barnes & Milner, 2005).

The actual magnitude of the non-indigenous bryozoan species in the Mediterranean as a whole is still imperfectly known and is underestimated (Zenetos *et al.*, 2012; Por, 2010). In addition, some old, poorly documented records need to be critically re-examined. According to a recent review (Zenetos *et al.* 2012), 31 alien bryozoan species have been recorded in the Mediterranean as a whole and 22 species in the eastern Mediterranean, the main pathways of their introduction being shipping and the Suez Canal.

Compared with the western Mediterranean, knowledge of the native bryozoan fauna of the eastern Mediterranean is deficient and more focused on the Aegean Sea (e.g. Harmelin, 1968-1969; Hayward, 1974, 1975; Ünsall, 1975; Ünsall & d'Hondt, 1978-1979; Morri *et al*., 1999; Koçak & Aydin Önen, 2014) than on the Levantine Basin (e.g. O'Donoghue & de Watteville, 1939; Gautier, 1956; d'Hondt, 1988; Koçak *et al.*, 2002; Abdelsalam & Ramadan, 2008; Abdelsalam, 2014; Sokolover, 2014). Non-indigenous bryozoans present in the Levantine basin were recorded from Egypt (Hastings, 1927), Israel (Powell, 1969; Eitan, 1972a; Goren, 1980; d'Hondt, 1988; Sokolover, 2014), Turkey (Ünsal, 1975; Ünsal & d'Hondt, 1978-1979; Koçak, 2007), North Cyprus (Koçak *et al*, 2002) and Lebanon (Bitar & Kouli-Bitar, 2001 and references below).

This study provides an inventory of the bryozoan assemblages from the whole coastal zone of Lebanon collected in the context of field surveys spread over several years. The studied collection has first given rise to several taxonomic revisions (Harmelin, 2014 a-b; Harmelin *et al.*, 2007, 2009, 2011, 2012). These previous works provided the basis for clarifying several taxonomic uncertainties, describing new taxa and highlighting the occurrence of many non-indigenous species never previously recorded in the Mediterranean. The present work provides new insights on the diversity and distribution of both native and exotic bryozoans in a region where knowledge on this group was very poor and which highlights the specificity of this corner of the Mediterranean, strongly impacted by the combined effects of non-indigenous species and the tropicalization of the Mediterranean.

Materials and Methods

The present bryozoan collection was provided by field surveys of the marine benthos carried out mainly between 1999 and 2003 within the framework of the French-Lebanese programme of scientific cooperation CEDRE. Sampling was performed by the authors by SCUBA diving between 2 m and 42 m depth from Tripoli (north) to Tyre (south), i.e. along ca. 80 % of the 225 km-long coast of Lebanon. Bryozoans were collected at 35 stations distributed in 18 localities (Table 1, Fig. 1). These localities are distributed to the north (loc. 1-9) and the south (loc. 10-18) of the 34° parallel, which delimits arbitrarily two regions in the present study. The northern region includes Tripoli, a major urban centre with a relatively active port and offshore uninhabited islands, and two towns, Batroun and Jbail (Byblos). The southern region comprises the city of Beirut, with satellite towns and a large port, and the towns of Saida and Tyre, with smaller harbours. For analysis of the species distribution, the northern and southern localities were grouped into two areas each: the Tripoli area (loc. 1-3), Batroun area

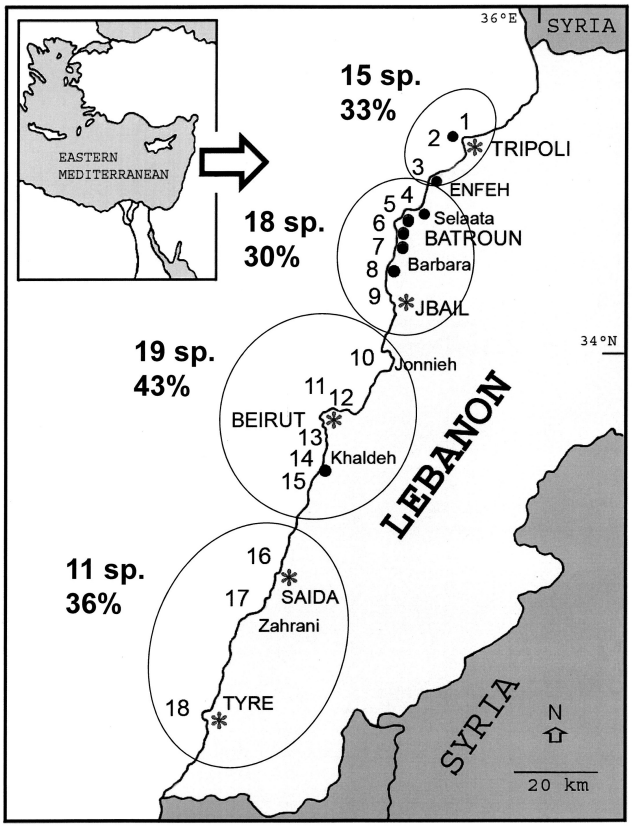

Fig. 1: Geographical distribution of the 18 localities sampled for bryozoans in four areas along the Lebanese coast. Number of non-indigenous bryozoan species recorded in these areas and their percentage in the local cheilostome pool.

(loc. 4-9), Beirut area (loc. 10-15) and Tyre area (loc. 16-18). Each species was coded according to four classes corresponding to the frequency of occurrence in the 18 sampled localities (class A: > 50 %; class B: 26-50 %; class C: 10-25 %; class D: < 10 %). Sampled stations were categorised *a posteriori* into four habitat types: (i) ports: piers, quays, jetty blocks; (ii) shaded habitats: cavities, overhangs on natural hard bottoms; (iii) exposed rock walls: upper and lateral surfaces of rocks; (iv) small substrata, biogenic concretions. This categorisation of habitat types reveals differences between the northern and southern batches of samples, with in particular a higher contribution of port habitats in the south (50.0 % vs. 10.5 % of stations). The depth range and mean depth (± standard deviation) of the sampled stations, on the other hand, were not significantly different between the two regions (north: 3-35 m, 14.9 ± 9.9 m; south: 3-42 m, 12.9 ± 11.5 m). The distribution of sampled stations in four depth ranges shows that sampling effort was roughly equal at < 5 m, 16-25 m and > 25 m, while it was greater in the 5-15 m depth range. An approximate indication of the abundance of species in each sample was given by using a semi-quantitative ranking limited to three classes (1: one or a few tiny or small colonies, 2: several small or medium-sized colonies, 3: numerous small and medium-sized colonies or several large colonies). These data were used only to identify the most and the least abundant species. Specimens were examined routinely with a stereomicroscope and, in some cases, with a Hitachi S 570 scanning electron microscope (SEM) after being cleaned in a 7.5 % solution of sodium hypochlorite, rinsed, air-dried and coated with gold. Taxa not identified at species level were not taken into account in the number of native species or when calculating proportions of non-indigenous species. The geographical distribution of the latter was categorized mainly according the classification in ecoregions by Spalding *et al.* (2007).

Results

General bryozoan diversity

Species richness for the whole collection amounts to 93 species (Tables 2, 3), including 12 cyclostomes, 2 ctenostomes and 79 cheilostomes. This assemblage includes 43 families, only eight of which comprise more than three species, while 25 (58 %) are monospecific. Seven taxa (5 cyclostomes, 2 cheilostomes) were not identified at species level (Tables 2, 3). Recorded diversity was higher in the northern region than in the southern region (82 vs. 66 species) and this N-S disparity in species richness was more pronounced for Cyclostomata (12 vs. 6 species) than for Cheilostomata (68 vs. 58 species). The Batroun area was the richest with 68 species, followed by the Tripoli area (57 species), while the two southern areas, Beirut and Tyre, accounted for 48 and 37 species, respectively. This bryozoan fauna included (i) a poorly diverse native component characterized by numerous 'southern' species, high endemicity, and unexpected absence of several taxa very common in the rest of the Mediterranean, and (ii) a high proportion of non-indigenous species.

Native bryozoan fauna: general features

With 59 taxa identified at species level, the native species richness was notably poor, especially in Cheilostomata (51 species), despite fairly intensive sampling in various habitats (Table 3). All native species were recorded in non-port habitats, except *Cryptosula palliasana*, recorded only once at Marina Villamar (loc. 15). In contrast, only 10 native species were recorded in ports. Among non-port habitats, the highest number of native species (56 species, including 7 cyclostomes and 1 ctenostome) were recorded on shaded rock walls (small semi-dark caves, overhangs), sampled between 6 and 42m depth. In this habitat, bryozoans often encrusted live and dead skeletons of three scleractinian species, *Madracis pharensis* (Heller, 1868), *Phyllangia mouchezi* (Lacaze-Duthiers, 1897) and *Polycyathus muellerae* (Abel, 1959), which were the most common corals on the sampled coastal bottoms.

The cheilostome assemblage comprises 24 species endemic to the Mediterranean (Table 2), i.e. 47 % of the native cheilostome pool. In contrast, only one species, *Copidozoum tenuirostre*, was identified in the category of

Table 1. List of 35 stations sampled at 18 localities along the coast of Lebanon.

Localities	Stations	Coordinates	Depth	Habitat	Date
1 -Tripoli city	1A: Port	34.45472 N 35.81754 E	2-5m	Jetty blocks	19/IX/2002
1 - *idem*	1B: Port	34.45472 N 35.81754 E	2-5m	Jetty blocks	08/VII/2003
2 - Tripoli islands	2A: Ramkine Island	34.49639 N 35.76056 E	14m	Overhang, cave	22/X/1999
2 - *idem*	2B: Lighthouse Island	34.49444 N 35.77806.E	12m	Pottery debris	22/X/1999
3 - Enfey	3A: Bay	34.35722 N 35.75972 E	14-24m	Biogenic concretions	26/X/1999
4 – Ras Al Chakaa	4A: Chak el Hatab	34.29722 N 35.66833 E	5-14m	Cave walls	18/IX/1999
4 - *idem*	4B: Hannouch	34.29417 N 35.66999 E	22m	Biogenic concretions	13/VII/2003
5 - Selaata	5A: Nearshore area	34.28611 N 35.66361 E	3-10m	Cave walls	18, 23/X/1999
5 - *idem*	5B: Nearshore area	34.28611 N 35.66361 E	10m	On *Spondylus spinosus* shell	02/V/2001
5 - *idem*	5C: Slope	34.28611 N 35.66361 E	22m	Cave walls	14/IX/2002
5 - *idem*	5D: Slope	34.28611 N 35.66361 E	35m	Rocky wall, on Corallinaceae	24/IX/2002
5 - *idem*	5E: Slope	34.28611 N 35.66361 E	35m	Rocky wall, on *Adeonella*	06/VII/2003
6 - Batroun	6A: Bay	34.28722 N 35.65555 E	6m	Rocks, on *Dictyopteris*	26/VI/1997
6 - *idem*	6B: 'Phoenician wall'	34.28722 N 35.65555 E	9m	Rocky wall	16/X/1999
6 - *idem*	6C: Nearshore area	34.28722 N 35.65555 E	2-6m	Biogenic concretions	26/IX/2002
7 - Kafar Abida	7A: Kafar Abida	34.22861 N 35.65333 E	10-12m	Rocky wall	06/VIII/1995
8 - Barbara	8A: Nearshore area	34.19556 N 35.62944 E	16m	Rocky wall	19/VIII/1993
8 - *idem*	8B: Nearshore area	34.19556 N 35.62944 E	28m	Biogenic concretions	08/VI/2000
8 - *idem*	8C: Small harbour	34.19250 N 35.63278 E	1-2m	Quay wall	19/VIII/1993 08/VI/2000
9 - Jbail (Byblos)	9A: Tablieh shoal	34.12417 N 35.63111 E	17m	Shells & *Cymodocea* leaves	17/X/1999
10 - Jounieh Bay	10A: Aquamarina	34.01417 N 35.63139 E	20-30m	Stones	10/VII/2003
11 Beirut offshore	11A: Harf el Kelb	33.91528 N 35.48780 E	34m	Rocks, shells	21/X/1999
12 Beirut port	12A: Commercial port	33.91222 N 35.52833 E	5m	Quay wall	02/VI/2000
12 - *idem*	12B: Commercial port	33.91222 N 35.52833 E	3-8m	On *Thais* shell	16/IX/2002
12 - *idem*	12C: Commercial port	33.91222 N 35.52833 E	5-8m	Pier, outside port	09/VII/2003
12 - *idem*	12D: Commercial port	33.90890 N 35.52280 E	14m	Pier, inside port	09/VII/2003
12 - *idem*	12E: Commercial port	33.90417 N 35.51917 E	5-7m	Pier, inside port	16/IX/2002
13 - Beirut sea-shore	13A: St Simon Islet	33.86250 N 35.48139 E	3-4m	Rocks	about 1968
13 - *idem*	13B: Raoucheh coast	33.88830 N 35.46694 E	5-8m	Shells & Corallinaceae	IX/1992, VI/2015
14 - Beirut S	14A: Airport	33.84306 N 35.47555 E	3-11m	Pier wall	16/VII/2003
15 - Khaldeh	15A: Marina Villamar	33.77888 N 35.46944 E	3m	Pier wall	07/VI/2000
16 - Saida	16A: Harf el Rijmeh	33.56666 N 35.36944 E	11m	On *Spondylus* shell	05/VI/2000
17 - Zahrani	17A: Harf el Jouani	33.50861 N 35.34028 E	14m	Overhang	06/VI/2000
18 - Tyre	18A: Nearshore area	33.26567 N 35.19000 E	10m	Rocks	25/X/1999
18 - Tyre	18B: El Kasmieh	33.26528 N 35.17917 E	36-42m	On *Phyllangia*, concretions	25/X/1999

temperate-boreal Atlantic species. Taxonomic uncertainties (possibility of cryptic species) concerning several so-called 'cosmopolitan' or 'circumtropical' species detract from the reliability of other biogeographical categories.

Mediterranean 'southern' species

The assemblage of native cheilostomes recorded in Lebanon comprised several species known for their particular abundance in warm areas of the Mediterranean, such as *Reptadeonella violacea* and *Schizoporella errata*, both in class A of occurrence frequency (Table 2). Among these thermophilic cheilostomes widely distributed in Lebanon, four species are remarkable for their limited geographical range in the Mediterranean (Figs. 2, 3). Three of them, *Cellepora posidoniae, Hippaliosina depressa* and *Monoporella bouchardi*, are endemic to the Mediterranean, while the actual taxonomic status of the fourth, *Exechonella* cf. *antillea,* needs to be clarified. In contrast, another endemic 'southern' species, *Adeonella pallasii,* is remarkable for its limited range observed in Lebanon.

Cellepora posidoniae was represented by numerous colonies collected at 12 localities from Tripoli islands to Zahrani (3-34m depth). This material was ascribed with some hesitation to *C. posidoniae*, a species originally described from Chios (Aegean Sea) by Hayward (1975) as *Rhamphostomellina posidoniae*, type species of a new genus, *Rhamphostomellina* Hayward, 1975. This species was subsequently placed in the genus *Cellepora* Linnaeus, 1767 by Hayward & McKinney (2002) and redescribed with SEM pictures by Chimenz Gusso *et al*. (2014). The wall structure and some morphological details of this species were described by Gordon & Grischenko (1994) from Hayward's material. The colonies examined by Hayward (1975), Unsal & d'Hondt (1978-1979) and Chimenz Gusso *et al*. (2014) were small, poorly calcified, growing on *Posidonia* leaves. In contrast, the Lebanese colonies were robust, well calcified, with rounded ramifications, growing on shaded hard substrata (Fig. 3A). Despite these zoarial and habitat differences, the Lebanese colonies were considered to be conspecific with *C. posidoniae* in having significant morphological similarities at zooidal level: primary orifice with a wide, low sinus, peristomial complex bearing a proximo-lateral avicularium with a proximal process delimiting a pseudosinus and a triangular, slightly hooked rostrum, and ovicell with two ectooecial foramina (Figs. 3B-C). However, a taxonomic reassessment of all *Cellepora* species from the Atlanto-Mediterranean region would be advisable.

Hippaliosina depressa (Fig. 4A) was recorded at 12 localities from Tripoli Islands to Tyre (5-42m depth). *Lepralia depressa* Busk, 1854 was originally described from the Aegean Sea, where its frequency was noticed by Harmelin (1968-1969) and Hayward (1974). It was recorded from the same area by Ünsal (1975) and Morri *et al.* (1999), and from the Levantine Basin, in Israel (d'Hondt, 1988; Sokolover, 2014), Egypt (Abdelsalam, 2014), Northern Cyprus (Koçak *et al.*, 2002), and Lebanon (Bitar & Kouli-Bitar, 2001). Records of this species beyond the Eastern Mediterranean are scarce: Tunisia, Gulf of Gabes (David & Pouyet, 1979), SE Sicilia (Rosso *et al.*, 2012), Corsica (Calvet, 1902; Gautier, 1962). The record by Powell (1969) at Acre, Haifa Bay of *H. acutirostris* Canu & Bassler, 1929, a species from Philippines, is doubtful and most likely concerns *H. depressa*.

Monoporella bouchardi (Fig. 4B) was particularly common along the coasts of Lebanon, as already pointed out by Harmelin (2014a). It was found at 13 localities (2-

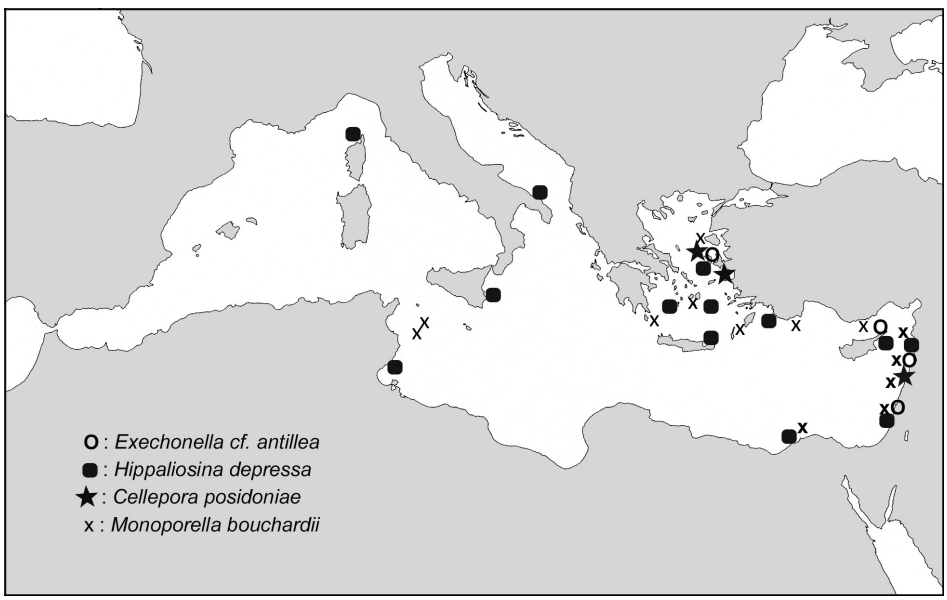

Fig. 2: Geographical range of four 'southern' species, *Exechonella cf. antillea, Hippaliosina depressa, Cellepora posidoniae and Monoporella bouchardii* according to records by Calvet (1902), O'Donoghue & De Watteville (1939), Harmelin (1968-1969, 2014a + unpublished data), Hayward (1974, 1975), Ünsall (1975), David & Pouyet (1979), d'Hondt (1988), Morri et al. (1999), Koçak *et al.,* (2002), Rosso *et al.* (2012).

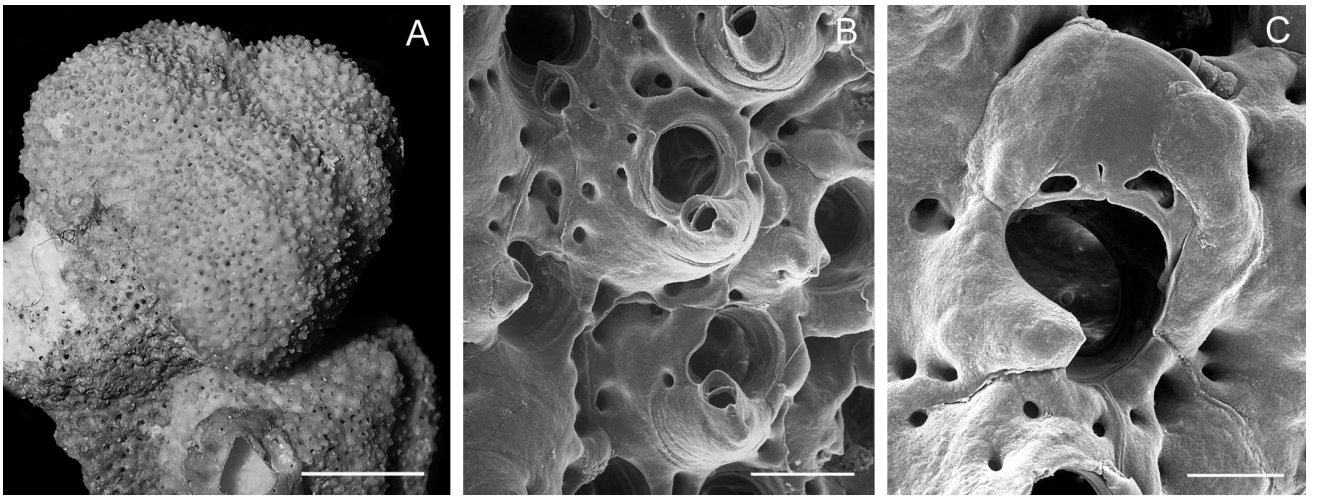

Fig. 3: *Cellepora posidoniae,* Selaata, 8 m. A: nodular colony. B: non ovicellate autozooids. C: ovicellate zooid. Scale bars, A: 5 mm, B: 200 µm, C: 100 µm

36m depth) from Tripoli Islands to Tyre. The geographical range of this Mediterranean endemic mostly covers the Eastern Mediterranean, although a few records are available from the Central Mediterranean (Harmelin, 2014a).

Exechonella cf. *antillea* (Fig. 4C) was present at 10 localities from 3 to 36m depth and in all samples from shaded walls from Selaata (3-35m depth). Its frequency in Lebanon contrasts with the scarcity of previous records, which are restricted to a few places in the Eastern Mediterranean (Fig. 2): Chios (Hayward, 1974: a single colony, first Mediterranean record), Cyprus (Koçak *et al.*, 2002; on *Posidonia* rhizomes), Israel, Akhzov canyon (Sokolover, 2014). This distribution pattern raises the question of the biogeographical status of this species: is it actually native to the Mediterranean or a cryptogenic species (*sensu* Carlton, 1996)? This species belongs to a worldwide "*E. antillea"* complex including, inter alia, the Caribbean *E. antillea* and species from W Africa (Cook & Bock, 2004). Several *Exechonella* species were recorded from the Red Sea at Safaga Bay (Ostrovsky *et al.*, 2011) including *E. tuberculata* (MacGillivray, 1883), *E. brasiliensis* Canu & Bassler, 1928 and three unnamed species.

Adeonella pallasii is another typical 'southern' species endemic to the Mediterranean. Unlike the preceding species, it was recorded from a single locality, Selaata, where colonies were aggregated on overhangs and cave walls at 20-35m depth. Its occurrence is worth noting as it is the only species in this collection with large, rigid, erect colonies. This species is common in the Aegean Sea, also present in the Ionian Sea (Rosso, 2003; Rosso & Novosel, 2010), and particularly abundant in the Adriatic Sea on shaded walls and cave entrances (Hayward & McKinney, 2002; Novosel *et al.*, 2004; Rosso & Novosel, 2010; JGH, pers. observ.), where it replaces the 'northern' *A. calveti* (Canu & Bassler, 1930) in the same ecological niche.

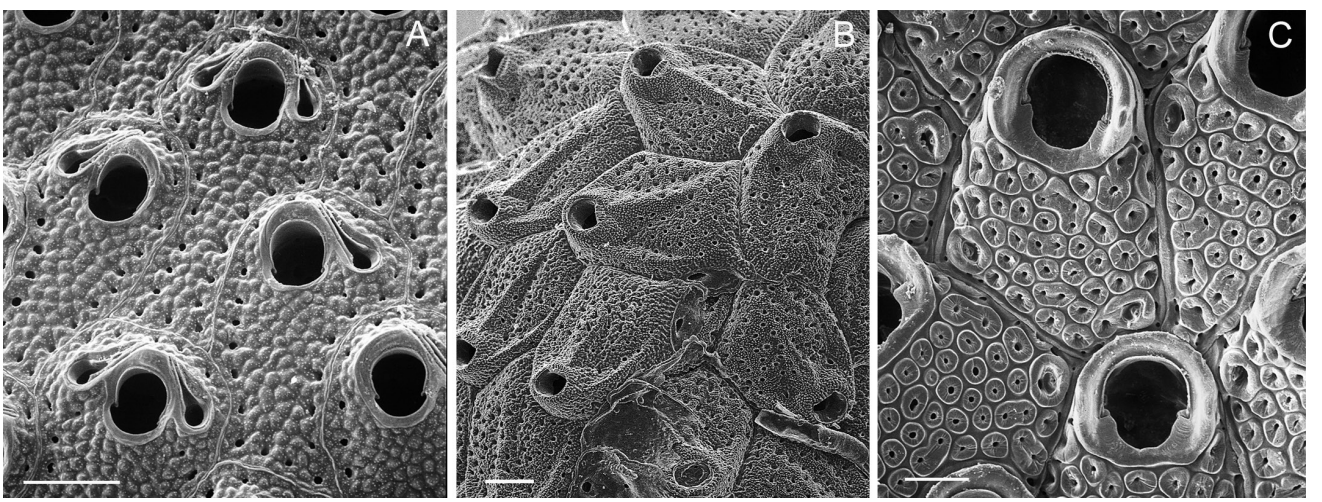

Fig. 4: Three 'southern' cheilostomes common in Lebanon. A: *Hippaliosina depressa,* B: *Monoporella bouchardii,* C: *Exechonella* cf. *antillea.* Scale bars: 200 µm.

Table 2. List of bryozoan species and families recorded in Lebanon in two northern (Tripoli: TR, Batroun: BA) and two southern (Beirut: BE, Tyre: TY) areas. Oc.: rank of occurrence frequency in 18 localities (A >50%, B: 26-50%, C: 10-25%, D <10%). NIB: non-indigenous species, including two cryptogenic species: *). En.: Mediterranean endemic species.

	TR	BA	BE	TY	Oc.	NIB	En.
CYCLOSTOMATA							
Annectocymidae							
Proboscina boryi (Audouin, 1826)	X	X	.	.	B	?	?
Annectocyma sp. 1, creeping	.	X	X	X	B	.	.
Annectocyma sp. 2, erect	.	X	.	.	C	.	.
Entalophoroecia sp.	.	X	.	.	D	.	.
Tubuliporidae							
Idmidronea atlantica (Forbes) in Johnston, 1847	.	X	.	.	C	.	.
Diastoporidae							
Liripora amphorae (Harmelin, 1976)	X	.	.	.	D	.	.
Frondiporidae							
Frondipora verrucosa (Lamouroux, 1821)	X	X	.	X	B	.	.
Crisiidae							
Crisia recurva Heller, 1867	X	.	X	X	C	.	X
Crisia sp.	X	.	.	X	C	.	.
Lichenoporidae							
Patinella radiata (Audouin, 1826)	X	X	X	.	B	.	.
Disporella hispida (Flemming, 1828)	X	X	X	X	A	.	.
Disporella sp.	X	X	.	.	C	.	.
CTENOSTOMATA							
Pherusellidae							
Pherusella tubulosa (Ellis & Solander, 1786)	X	X	X	X	B	.	.
Vesiculariidae							
Amathia verticillata (delle Chiaje, 1822)	.	X	X	.	C	X	.
CHEILOSTOMATA							
Aeteidae							
Aetea sica *(Couch, 1844)*	X	X	X	.	B	.	.
Calloporidae							
Copidozoum tenuirostre (Hincks, 1880)	.	X	.	.	D	.	.
Crassimarginatella sp	X	.	X	.	C	.	.
Retevirgula akdenizae Chimenz *et al.,* 1997	.	X	.	.	D	.	X
Anthroporidae							
Akatopora leucocypha (Marcus, 1937)	X	.	.	X	C	X	.
Bugulidae							
Bugula neritina (Linnaeus, 1758)	X	.	X	.	C	X	.
Beaniidae							
Beania cf. *hirtissima* (Heller, 1867)	X	.	.	X	C	.	.
Beania magellanica (Busk, 1852)	.	X	X	.	C	.	.
Candidae							
Licornia jolloisii (Audouin, 1826)	.	X	X	.	B	X	.
Cradoscrupocellaria bertholletii (Audouin, 1826)	.	X	X	.	C	.	.
Cradoscrupocellaria macrorhyncha Gautier, 1962	X	.	.	.	D	.	X
Cradoscrupocellaria cf. *ellisi* Vieira & Spencer-Jones, 2012	X	.	.	.	D	.	.
Microporidae							
Calpensia nobilis (Esper, 1796)	X	.	.	X	C	.	.
Mollia circumcincta (Heller, 1867)	X	X	.	.	C	.	X
Monoporellidae							
Monoporella bouchardi (Audouin, 1826)	X	X	X	X	A	.	X
Onychocellidae							
Onychocella marioni Jullien, 1881	X	X	X	X	A	.	.
Onychocella vibraculifera Neviani, 1895	X	X	X	.	B	.	X
Rectonychocella disjuncta (Canu & Bassler, 1930)	X	.	.	.	D	.	.
Thalamoporellidae							
Thalamoporella harmelini Soule *et al.,* 1999	.	.	X	.	C	X*	.
Thalamoporella rozieri (Audouin, 1826)	.	X	.	.	D	X	.
Chlidoniidae							
Chlidonia pyriformis (Bertolini, 1810)	X	.	.	.	D	.	.
Cribrilinidae							
Collarina balzaci (Audouin, 1826)	.	X	.	.	D	.	.
Puellina pedunculata Gautier, 1956	X	X	.	.	C	.	X
Puellina picardi Harmelin, 1988	X	X	X	.	A	.	X
Puellina radiata (Moll, 1803)	.	.	X	.	D	.	X
Puellina setosa Waters, 1899	X	.	.	.	D	.	.
Hippothoidae							
Hippothoa flagellum Manzoni, 1870	X	X	.	X	C	.	.
Chorizoporidae							
Chorizopora brongnarti (Audouin, 1826)	.	X	.	.	C	.	.

(continued)

Table 2 *(continued)*

Trypostegidae							
Trypostega venusta (Norman, 1864)	X	X	.	X	B	.	.
Exochonellidae							
Exechonella cf. *antillea* (Osburn, 1927)	X	X	X	X	A	.	.
Adeonidae							
Reptadeonella violacea (Johnston, 1847)	X	X	X	X	A	.	.
Adeonellidae							
Adeonella pallasii (Heller, 1867)	.	X	.	.	D	.	X
Lepraliellidae							
Celleporaria labelligera Harmer, 1957	X	X	X	.	B	X	.
Celleporaria cf. *sherryae* Winston, 2009	.	X	X	.	C	X	.
Celleporaria cf. *brunnea* (Hincks, 1884)	.	.	X	.	D	X	.
Celleporaria vermiformis (Waters, 1909)	X	.	.	.	D	X	.
Drepanophora birbira Powell, 1967	X	X	.	X	C	X	.
Smittinidae							
Parasmittina egyptiaca (Waters, 1909)	X	X	X	X	A	X	.
Parasmittina protecta (Thornely, 1905)	.	.	X	.	C	X	.
Parasmittina raigii (Audouin, 1826)	.	X	.	.	D	.	.
Parasmittina rouvillei (Calvet, 1902)	X	X	X	X	C	.	X
Parasmittina spondylicola Harmelin *et al.,* 2009	X	X	X	.	C	X	.
Parasmittina serruloides Harmelin *et al.,* 2009	X	X	X	.	B	X	.
Smittina nitidissima (Hincks, 1880)	X	X	X	X	B	X	.
Watersiporidae							
Watersipora subtorquata (d'Orbigny, 1852)	X	X	X	.	A	X	.
Schizoporellidae							
Schizoporella errata (Waters, 1878)	X	X	X	X	A	.	.
Schizoporella cf. *tetragona* (Reuss, 1848)	.	.	X	.	C	.	X
Schizobrachiella sanguinea (Norman, 1868)	X	X	.	X	B	.	.
Margarettidae							
Margaretta cereoides (Ellis & Solander, 1786)	X	X	.	.	B	.	X
Hippaliosinidae							
Hippaliosina depressa (Busk, 1854)	X	X	X	X	A	.	.
Hippopodinidae							
Hippopodina ambita (Hayward, 1974)	.	X	.	.	D	.	X
Cheiloporinidae							
Hagiosynodos hadros Hayward & McKinney, 2002	.	.	.	X	D	.	X
Hagiosynodos kirchenpaueri (Heller, 1867)	X	X	X	.	B	.	X
Cryptosulidae							
Cryptosula pallasiana (Moll, 1803)	.	.	X	.	D	.	.
Microporellidae							
Microporella browni Harmelin *et al.,* 2011	.	.	X	.	D	X	.
Microporella cf. *ciliata* (Pallas, 1766)	.	X	X	.	C	.	.
Microporella coronata (Audouin, 1826)	X	X	.	X	B	X	.
Microporella genisii (Audouin, 1826)	X	X	X	X	B	X	.
Microporella harmeri Hayward, 1988	.	X	.	.	D	X	.
Petraliellidae							
Micropetraliella thenardii (Audouin, 1826)	.	.	.	X	D	X	.
Escharinidae							
Escharina vulgaris (Moll, 1803)	X	X	X	X	A	.	.
Therenia rosei Berning *et al.,* 2008	.	X	X	.	B	.	X
Colatooeciidae							
Trematooecia ligulata Ayari & Taylor, 2008	.	X	X	X	C	.	X
Romancheinidae							
Hippomenella mucronelliformis (Waters, 1899)	X	X	.	.	C	.	X
Celleporidae							
Buskea cf. *dichotoma* (Hincks, 1862)	.	X	.	X	C	.	.
Cellepora posidoniae (Hayward, 1974)	X	X	X	X	A	.	X
Celleporina bitari Harmelin, 2014	.	X	.	.	D	X	.
Celleporina canariensis Aristegui, 1989	X	X	X	X	A	.	.
Celleporina mangnevillana (Lamouroux, 1816)	.	X	.	.	C	.	X
Celleporina sp.	X	X	.	.	C	.	.
Predanophora longiuscula (Harmer, 1957)	.	.	X	X	C	X	.
Scorpiodinipora costulata (Canu & Bassler, 1929)	X	X	X	X	B	X	.
Phidoloporidae							
Dentiporella sardonica (Waters, 1879)	.	X	.	.	D	.	.
Plesiocleidochasma mediterraneum Chimenz Gusso & Soule, 2003	X	.	.	X	D	.	X
Reteporella grimaldii (Jullien, 1903)	X	X	.	.	C	.	.
Rhynchozoon neapolitanum Gautier, 1962	X	X	X	.	B	.	X
Rhynchozoon pseudodigitatum Zabala & Maluquer, 1988	.	X	.	X	C	.	X
Schizoretepora hassi Harmelin *et al.,* 2007	X	X	X	X	B	X*	.
N species	**57**	**68**	**48**	**37**		**27**	**25**

Missing native taxa

An obvious peculiarity of the sampled assemblages was the absence of certain families, genera, or of some large, conspicuous species which are among the most common bryozoans in coastal habitats of other parts of the Mediterranean. These missing taxa include cyclostomes such as *Tubulipora spp., Diplosolen obelia, Plagioecia spp.*. Among the Cheilostomata, the most obvious absences concern families such as Cellariidae (*Cellaria*), Bitectiporidae *(Hippoporina, Metroperiella, Schizomavella*, *Pentapora*), Romancheinidae (*Escharella*, *Escharoides*, *Hemicyclopora*, *Hippopleurifera*), Myriaporidae (*Myriapora*), Bugulidae (only represented by the non-indigenous *Bugula neritina*). Genera such as *Callopora, Hincksina, Fenestrulina, Smittoidea*, *Turbicellepora* are also missing.

The absence of *Schizomavella* species is all the more surprising in that this genus is one of the most species-rich in the Mediterranean (Rosso, 2003; Reverter-Gil *et al*., 2016) and that several species [e.g. *S. mamillata* (Hincks, 1880), *S. cornuta* (Heller, 1867)] are major components of the landscape of coastal rocky bottoms in the western Mediterranean. This genus was not recorded from Israel by Sokolover (2014), but is not entirely excluded from the Levantine Basin. In Egypt, a *Schizomavella* species was recorded from Alexandria as *S. auriculata* (probably misidentified) by O'Donoghue & de Watteville (1939), and recently, *S. triangularis* Reverter & Fernandez-Pulpeiro was found in the same area by Abdelsalm (2014).

Other large bryozoans which contribute significantly to the Mediterranean coastal landscapes were also missing, such as *Schizoporella dunkeri* (Reuss, 1848), normally very common with *Reptadeonella violacea* on shallow hard substrata, and the large erect species *Myriapora truncata* (Pallas, 1766), *Smittina cervicornis* (Pallas, 1766), *Pentapora fascialis* (Pallas, 1766) and *Turbicellepora avicularis* (Hincks, 1860). Some other species playing the same landscaping role in other parts of the Mediterranean, such as *Dentiporella sardonica* and *Parasmittina rouvillei,* were present but with few, small colonies.

Non-indigenous bryozoans

All non-indigenous bryozoans (NIB) identified in the present collection, except *Bugula neritina* s.l. and *Amathia verticillata*, were recorded previously and described in taxonomic works (Harmelin *et al.*, 2007, 2009, 2011, 2012; Harmelin, 2014b). With the addition of *B. neritina* s.l. and *A. verticillata* (see below), this NIB pool comprises 27 species, including two cryptogenic species (*Schizoretepora hassi*, *Thalamoporella harmelini*), all belonging to the order Cheilostomata (Table 2) except for *A. verticillata* (Ctenostomata). This pool might also include *Exechonella* cf. *antillea* considering that it is closely related with a species group from tropical waters (see above) and its range in the Mediterranean is restricted to the eastern basin and is very limited (Fig. 2). However, pending a taxonomic re-assessment of the whole species group, this species has been provisionally left in the native group. Among the 16 cheilostome genera that composed the NIB pool, eight occurred in the Mediterranean Sea only with alien species: *Akatopora* Davis, 1934, *Drepanophora* Harmer, 1957, *Licornia* van Beneden, 1850, *Mucropetraliella* Stach 1936, *Predanophora* Tilbrook, 2006, *Scorpiodinipora* Balavoine, 1959, *Thalamoporella* Hincks, 1887 and *Celleporaria* Lamouroux, 1821. The latter and two other genera, *Parasmittina* Osburn, 1952 and *Microporella* Hincks, 1877, contributed particularly to the NIB pool, each with four species. No Cyclostomata species was considered as NIB.

The proportion of NIB reached 31.4 % in the bryozoan fauna as a whole and 33.8 % in the cheilostome assemblage (Table 3). The contribution of NIB was variable in the four areas sampled along the coast of Lebanon (Fig. 1). It was higher in the two southern areas, particularly in the Beirut area where the proportion of alien species reached 43 % of the cheilostome assemblage. However, the number of non-indigenous cheilostome species in this area was only marginally higher than in the adjacent Batroun area (18 vs. 17 species), while the number of native cheilostomes was clearly lower in the Beirut area than in the Batroun area (24 vs. 39 species). Therefore, the higher percentage of NIB observed in the Beirut area is explained by the lower diversity in native cheilostomes. In the Tyre area, which was the focus of a lower sampling effort than the other areas, species richness was relatively low (37 species in total), but the proportion of NIB (35.5 % of the cheilostome assemblage) was also higher than in the two northern areas.

Table 3. Number of bryozoan species recorded in the northern and southern regions and along the whole coast of Lebanon within the following categories: cyclostomes, ctenostomes, cheilostomes, species identified at species level, native cheilostomes, endemic cheilostomes and non-indigenous species (NIB); percentage of endemic cheilostomes (relative to native cheilostomes); percentage of NIB species relative to (1) whole assemblage identified at species level, (2) whole cheilostome assemblage identified at species level.

	N Lebanon	S Lebanon	Whole coast
Whole assemblage	82	66	93
Cyclostomes	12	6	12
Ctenostomes	2	2	2
Cheilostomes	68	58	79
Identified species	75	63	86
Native cheilostomes	46	35	51
Endemic cheilostomes	21	15	24
% Endemic cheilost.	45.7	42.9	47.1
NIB species	21	23	27
% NIB (1)	28.0	36.5	31.4
% NIB (2)	30.3	38.6	33.8

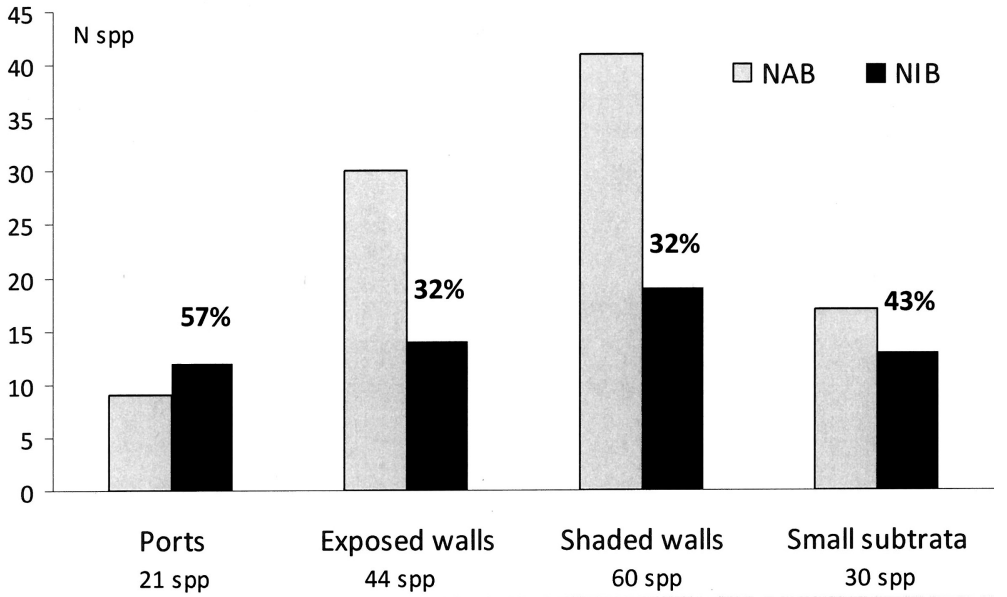

Fig. 5: Number of native (NAB) and non-indigenous (NIB) cheilostome species recorded in four habitat categories (histogram bars), total number of cheilostome species in each habitat and corresponding percentage of NIB species.

The distribution of the cheilostome species richness in the four habitat categories (Fig. 5) shows that the highest number of NIB species was found on shaded walls and the lowest in ports. On the other hand, in terms of the ratio between indigenous and non-indigenous species, the highest proportions in NIB were found in ports and small substrata. The great majority (81 %) of the 27 NIB species were reported from the 5-15 m depth range, as a result, at least in part, of the higher sampling effort made in this depth range (Table 4). The other depth categories harboured similar NIB diversity.

Eleven NIB species, i.e. 40.7 % of the NIB pool, were recorded in class A (7.4 %) and class B (33.3 %) of occurrence frequency (Table 2). These widespread species occurred predominantly in natural habitats on various substrates (rock walls, bioconcretions, shells, coral and erect bryozoan skeletons), from shallow (3-9 m) to deep (34-42 m) stations (Table 4). In particular, *Celleporaria labelligera, Microporella genisii, Parasmittina egyptiaca* (Fig. 6)*, Smittina nitidissima*, *Schizoretepora hassi* and *Watersipora subtorquata* were among the most frequent bryozoans recorded in Lebanon and were distributed across a wide depth range (Table 4). In constrast, 9 NIB species were recorded exclusively in a single area and, in some cases, at a single station. Four of these species, *Thalamoporella rozieri, Microporella harmeri*, *Celleporina bitari* and *Mucropetraliella thenardii*, were found in moderately anthropized localities (Batroun, Selaata and El Kasmieh-Tyre) without large ports. The five other species (*Thalamoporella harmelini, Celleporaria* cf. *brunnea, C. vermiformis, Parasmittina protecta, Microporella browni*) were collected off Beirut city or in

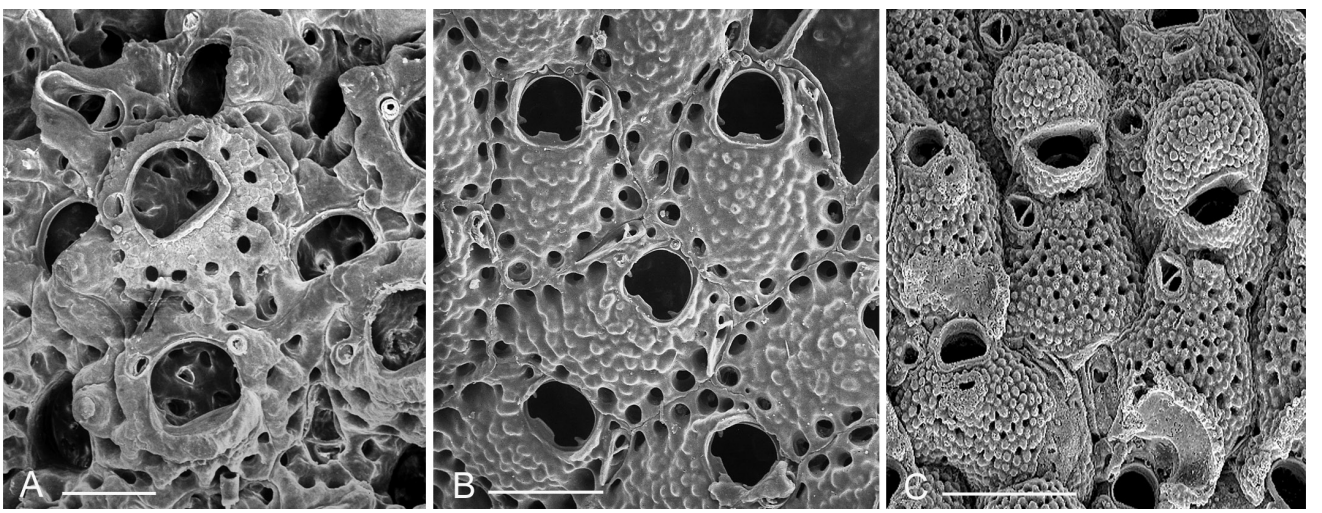

Fig. 6: Three non-indigenous bryozoans common in Lebanon. A: *Celleporaria labelligera.* B: *Parasmittina egyptiaca.* C: *Microporella genisii.* Scale bars: 200 µm.

ports and harbours (Tripoli and Beirut main ports, Beirut airport marine infrastructures, Khalde Villamar marina).

Discussion

Diversity of the native bryozoan assemblages

Paucispecificity, high endemism and strong presence of southern species are the most striking features of the native bryozoan assemblages of the Lebanese coastal bottoms.

Species richness of the native cheilostomes recorded in Lebanon represents only 14 % of the diversity of this group in the Mediterranean as a whole, as compiled by Rosso (2003). This deficit is less pronounced at generic (27 %) and family (48 %) levels. The paucispecificity of this native assemblage is also evident when compared with other Mediterranean regional assemblages from the same depth range (Tab. 5). Therefore, the bryozoans of Lebanon clearly illustrate the extreme end of the well-known eastward depletion of marine biodiversity in the Mediterranean (Fredj, 1974; Bianchi & Morri, 2000; Boudouresque, 2004; Coll *et al.*, 2010).

The exclusion of conspicuous components of Mediterranean hard substrata communities is quite surprising, especially since these missing taxa have been recorded in the Aegean Sea (Harmelin, 1968-1969; Hayward, 1974; Ünsal, 1975; Morri *et al.*, 1999). Similarly, the temperate-boreal species are almost entirely excluded while this category is well represented in the Aegean Sea (23 %: Hayward, 1974). In assemblages of hydroids from Lebanon, Atlanto-Mediterranean species were also lacking (Morri *et al.*, 2009). This phenomenon of regional exclusion raises the question of whether it reflects a natural, biogeographical distinctive feature of the Lebanese coastal area, recent environmental degradation or cases of species displacement by invasive aliens.

Biogeographical particularity hypothesis**.** A most obvious bionomic feature of the coastal communities in this part of the Levantine coasts, which includes Lebanon and Israel, is the absence of the endemic sea-grass *Posidonia oceanica*, which is widespread throughout the rest of the Mediterranean. The absence of this major ecosystem engineer species in this area (Celebi *et al.*, 2006; Pergent *et al.*, 2014) may be relatively recent as it was recorded in 1977 (Bitar, 2010). However, the ab-

Table 4. Depth distribution of non-indigenous bryozoan species recorded in Lebanese waters according to four depth categories. N-Re: number of records. In bold, the 11 most frequent species. *: cryptogenic species.

	<5m	5-15m	16-25m	>25m	N-Re
Amathia verticillata	■				2
Akatopora leucocypha		■			3
Bugula neritina s.l.	■	■			4
Licornia jolloisii		■	■	■	7
Thalamoporella harmelini *	■	■			3
Thalamoporella rozieri	■				1
Watersipora subtorquata	■	■	■	■	11
Celleporaria cf. *brunnea*		■			1
C. labelligera	■	■			9
C. vermiformis	■				1
C. cf. *sherryae*		■		■	2
Drepanophora birbira		■	■		4
Parasmittina egyptiaca	■	■	■	■	16
P. protecta	■	■		■	7
P. serruloides		■	■		6
P. spondylicola			■		2
Smittina nitidissima		■	■	■	16
Microporella browni	■	■			2
M. coronata		■			7
M. genisii		■	■	■	5
M. harmeri		■			1
Mucropetraliella thenardii				■	1
Celleporina bitari			■	■	2
Predanophora longiuscula		■	■	■	3
Scorpiodinipora costulata	■	■	■		**8**
Rhynchozoon larreyi		■	■	■	8
***Schizoretepora hassi** *	■	■	■	■	14
Number of species (27)	12	21	13	12	
Number of stations (33)	7	17	5	6	

Table 5. Species richness of native bryozoan regional pools recorded from different parts of the Mediterranean. Data from Harmelin (1976, part): Table I, species from Precoralligenous, Coralligenous and semi-dark caves. n.r.: not recorded.

Geographical area (source)	Cyclostomata	Cheilostomata
Lebanon (present collection)	**7**	**51**
Aegean Sea (Harmelin, 1968-1969)	14	85
Aegean Sea, Chios (Hayward, 1974)	n.r.	101
Aegean Sea, Milos (Morri *et al.*, 1999)	12	70
Tunisia (Ben Ismail *et al.*, 2012)	13	73
N Adriatic (Hayward & McKinney, 2002)	19	79
Adriatic Sea (Novosel *et al.*, 2004)	9	68
Balearic Islands, Cabrera (Zabala, 1993)	26	109
NW Mediterranean, Provence (Harmelin, 1976, part)	23	83

sence of remaining dead matte, a remarkably persistent component of *Posidonia* beds (Pergent *et al.*, 2014), in recently surveyed sites (this study and RAC/SPA-UNEP/MAP, 2014) suggests that *P. oceanica* was restricted to very small areas. Our field surveys also showed that several conspicuous and normally common invertebrates were lacking, such as gorgonians and zoanthids among the Cnidaria, and many large echinoderms (unpublished data). The subtropical thermal regime occurring in the SE Mediterranean (Abboud-Abi Saad *et al.*, 2004; Nykjaer, 2009) enhanced by global warming, is the most likely ecological driver (Celebi *et al.*, 2006) of this regional exclusion process. The exploration of deep-water habitats below 50-60 m depth, where thermal conditions are cooler all year round (Abboud-Abi Saad *et al.*, 2004), might perhaps reveal the occurrence of several taxa missing at shallower depths, including bryozoans.

Habitat degradation hypothesis. The Lebanese coast is highly urbanized and exposed to multiple human stressors (e.g. Nakhlé, 2003; Shaban, 2008; Bitar, 2008, 2010). Unfortunately, references to the past status of the benthos of the Levantine area are very limited, except for some taxa, such as bivalves (Crocetta *et al.*, 2013a). Some investigations suggest that the quality of coastal habitats has severely declined over the last decades, in parallel to alien invasions (Basson *et al.*, 1976; Bitar & Kouli-Bitar, 1995). The marked difference in cyclostome diversity observed between the northern and the southern regions may conceivably be attributed to differences in environmental quality, as suggested by the decline of cyclostome diversity observed along a gradient of increasing pollution in Provence (Harmelin & Capo, 2002).

Displacement hypothesis. The establishment of highly competitive exotic species is one of the major threats suffered by marine communities, with a dramatic impact on interspecific relationships (e.g. Occhipinti Ambrogi, 2001; Galil, 2007). Profound changes caused by exotic species due to competitive exclusion were observed in Lebanese coastal communites. Two obvious examples are provided by remarkably successful Lessepsian species. Firstly, in the guild of herbivorous fishes, the native sparid *Sarpa salpa* was driven out by two invasive lessepsian rabbit-fishes, *Siganus luridus* and *S. rivulatus* (Bariche *et al.*, 2004). Secondly, in the mediolittoral zone of the same area, the native mussel *Mytilus galloprovincialis* was replaced by the lessepsian species *Brachidontes pharaonis* (Bitar, 2010; Crocetta *et al.*, 2013a). In the present bryozoan collection, the native *Watersipora cucullata* (Busk, 1854), originally described from the Aegean Sea, was not recorded while the alien *W. subtorquata* was frequent (Harmelin, 2014b). However, the hypothesis that the latter is responsible for the exclusion of the former would appear to be doubtful. No invasive trend was observed among the non-indigenous bryozoans collected in Lebanon (see below) and there was no evidence of a displacement phenomenon by other alien sessile organisms in the sampled habitats.

The particular occurrence of 'southern' species is another spectacular feature of the native assemblage. These species confirm the observation by Rosso (2003) that the native Mediterranean bryozoan fauna includes species which are predominantly or exclusively distributed in the eastern basin, or even only in the Levant Sea. The geographical distribution pattern of these species is most likely related to their thermophilic character and shaped by particular winter thermal thresholds (e.g. February surface isotherm at 16°C), as suggested by the distribution of other biota (Bianchi, 2007; Coll *et al.*, 2010; Bianchi *et al.*, 2012). These thermophilic species might be remnants of the tropical-subtropical fauna present during the Pleistocene interglaciations (Taviani, 2002). The same assumption was made for lithistid sponges from a Lebanese submarine cave (Pérez *et al.*, 2004). 'Southern' cheilostomes could thus become good indicators of the effects of global warming on the geographical range of species.

The high degree of endemicity noted within the assemblage of native cheilostomes (47 %) contrasts with lower rates observed for this group in the western Mediterranean (32 %: Gautier, 1962 in Hayward, 1974) and the Aegean Sea (36 %: Hayward, 1974). This high endemicity was unexpected as it is not consistent with

the general pattern of endemicity in the Mediterranean, which shows an eastward decreasing trend (e.g. Fredj, 1974; Coll *et al*., 2010). Consistently with this trend, a low proportion of endemic species was noted by Morri *et al.* (2009) among hydroids collected at the same Lebanese localities as the bryozoans. The paradoxically high proportion of bryozoan endemics probably originates from the climatic discrimination which particularly affects the Atlanto-Mediterranean species not adapted to the warm conditions of this corner of the Mediterranean, and thus increases the proportion of endemic species, including the 'southern' ones restricted to the eastern Mediterranean.

Non-indigenous species: Lebanon, a hot-spot of bryozoan xenodiversity

The present results confirm that cheilostomes have a remarkable capacity for dispersal using human-mediated vectors, and attest that the coastal zone of Lebanon is a bioinvasion hotspot. A recent survey of bryozoans along the Mediterranean coast of Israel also showed a high, albeit lower, proportion of NIB (Sokolover, 2014: about 25%). The strong presence of NIB in Levantine coastal waters contrasts with low numbers of alien bryozoans recorded in other parts of the eastern Mediterranean (e.g. only two species reported from Turkey: Koçak & Aydin Önen, 2014). However, the report of a low occurrence of alien bryozoans may result from insufficient sampling and a lack of taxonomic expertise. This bias is not specific to bryozoans and may affect the validity of comparisons of regional invasion rates. If the exotic bryozoans recorded in Lebanon are added to the list compiled by Zenetos *et al.* (2010, 2012) for the whole of the Mediterranean, the amended list comprises 40 species, including 5 Ctenostomata and 35 Cheilostomata. Thus, the Lebanese NIB species represent 74 % of the whole Mediterranean pool of exotic cheilostomes. Moreover, the actual occurrence of several species of this pool needs to be reassessed as they were recorded without explanation despite serious taxonomic problems [e.g. *Celleporaria fusca* (Busk, 1854) in d'Hondt, 1988]. The list of NIB recorded in Lebanon itself, will probably be adjusted by future taxonomic revisions. In particular, the actual geographical range of the two cryptogenic species is still a pending issue. A cause of underestimation of the bioinvasion by bryozoans was the sampling design of the studied collection. A more intensive sampling effort on microhabitats particularly rich in bryozoans, such as empty shells and other small substrates, and in deep-water habitats, would probably have provided more records of NIB species. Moreover, the present list was based on relatively old samples, the most recent being from 2003. Therefore, considering the intensification of the colonization of the Mediterranean by non-indigenous species during the last decades (e.g. Ben Rais Lasram & Mouillot, 2009; Boudouresque & Verlaque, 2012; Galil & Goren, 2014), it is highly probable that the NIB fauna established in the Lebanese waters is now significantly richer than what is presented here.

The proportion of NIB observed in Lebanon exceeds the highest proportions of non-indigenous species recorded in other groups from the same area, except for the opisthobranch fauna (37% of exotic or cryptogenic species: Crocetta *et al.*, 2013b). According to Lakkis (2012), the highest percentages of alien species in Lebanese waters was observed among crustaceans (less copepods: 30 %) and zooplankton (18 %). Among bivalves from Lebanon, alien species account for ca. 16% (Crocetta *et al.*, 2013a). The same proportion (15.8 %) of exotic species was found among hydroids sampled together with the bryozoans studied here (Morri *et al.*, 2009). At Lebanese coastal localities similar to those sampled for bryozoans, the bony fish assemblages censused by diving comprised 13 % of introduced species (Harmelin-Vivien *et al.*, 2005). The highest proportion of alien species recorded in Levantine waters (56%) was found in an assemblage of 16 serpulid species from SE Turkey (Çinar, 2006).

Among the most abundant and widespread NIB in Lebanon (class A), only the worldwide invader *Watersipora subtorquata* was known from other parts of the Mediterranean Sea (Harmelin, 2014b), while *Smittina nitidissima* was the only one already known from the Levantine coasts (recorded as *S. malleolus*: d' Hondt, 1988). Other particularly frequent NIB species were never recorded before in the Mediterranean, such as *P. egyptiaca,* although it was an early colonizer of artificial structures in the southern part of the Suez Canal (Hastings, 1927; Ghobashy *et al.*, 1980). The lack of previous records of these frequent exotic species may be due to misleading identifications and more generally to poor knowledge of the bryozoan fauna of the SE Mediterranean and also of the Red Sea, despite recent efforts (Ostrovsky *et al.*, 2011). The cryptogenic status (Carlton, 1996) attributed to *T. harmelini* and *S. hassi*, two species described from Lebanese material and afterwards only recorded in Israel (Sokolover, 2014), is another example of gaps in our knowledge. Their extremely limited known range may also be a case of stenoendemicity or an indication that these species are native to poorly known non-Mediterranean areas. The remarkable diversity of *Parasmittina, Microporella* and *Celleporaria* in the NIB pool may be explained by the fact that they are among the most species-rich cheilostome genera in warm waters (cf. species lists in Bock, 2015).

The absence of cyclostomes in the NIB pool is worth noting. This lack may result from the poor dispersal capacity of larvae in this group (e.g. Hayward & Ryland, 1985) and probably also from a low tolerance of conditions of vessel fouling and shipping transfer. It is noticeable that cyclostomes were similarly absent from a pool of alien bryozoans recorded in Australia (Campbell *et al.*, 2003) and only one species was recorded by Gordon & Mawatari (1992) among fouling bryozoans in New Zealand ports. However, obvious taxonomic difficulties and

poor knowledge of the cyclostome fauna from both the eastern Mediterranean and the Red Sea may also explain in part this absence. For instance, *Proboscina boryi*, to which some small specimens were provisionally ascribed, was considered here as native although this species is very poorly known and its origin, Mediterranean or Red Sea, was not indicated by Audouin (1826).

The wide spatial and habitat distribution of many NIB species in Lebanon (Table 4, Fig. 1) is a strong indication of a relatively old colonization and good acclimatation to the Levantine environment. On the other hand, the restricted range of species recorded in a single area or at a single station can be diversely interpreted. The record of a species apparently well established in a single port (e.g. *C. vermiformis* at Tripoli) may correspond to a primary recipient area directly supplied by shipping. In contrast, single records of inconspicuous colonies from moderately anthropized localities (e.g. *M. thenardii* and *C. bitari*) are more likely attributable to deficient sampling.

Geographical range of the Lebanese NIB and inferred pathways

The geographical range of the NIB species recorded in Lebanon was compiled from recent relevant sources and categorized according to the biogeographical classification proposed by Spalding *et al.* (2007), with slight modifications (Table 6). As noted in previous descriptions of the Lebanese NIB species (Harmelin *et al.*, 2007, 2009, 2011, 2012; Harmelin, 2014b), knowledge of the actual range of many of them is hampered by taxonomic uncertainties involving sibling species. However, some clear trends can be evidenced.

Historical introductions. The Lebanese pool of non-indigenous cheilostomes includes three of the most widespread aliens in tropical to temperate seas, whose occurrence in anthropized sites in the Mediterranean has been known for a long time: *Amathia verticillata* (= *Zoobotryon verticillatum*: cf. Waeschenbach *et al*., 2015 for generic change), *Bugula neritina* and *Watersipora subtorquata*.

The non-indigenous status of *A. verticillata* in the European waters has been recognized only recently (Galil & Gevili, 2014; Ferrario *et al*., 2014; Marchini *et al.*, 2015). This ctenostome, often confused with an algae, is widely distributed in tropical and subtropical regions, whereas in the Mediterranean it is confined to ports and marinas (e.g. Prenant & Bobin, 1956). A recent taxonomic revision (Vieira *et al.*, 2014) of *W. subtorquata,* originally described from Brazil and often confused with other *Watersipora* species, has clarified its actual range, which includes the Mediterranean. Its occurrence in this sea only at anthropized sites (Chimenz Gusso *et al*., 2004; Harmelin, 2014b) strongly suggests a man-induced introduction. For the same reasons, we consider that *B. neritina* s.l. is not indigenous to the Mediterranean. This *Bugula* is widespread in Mediterranean ports and marinas, fouling artificial structures and ship hulls (e.g. Gautier, 1962; Prenant & Bobin, 1966), most probably since several centuries ago, as indicated by its first record in this sea (Linnaeus, 1758 in Ryland *et al.*, 2011). Molecular data (Mackie *et al*., 2006; Fehlauer-Ale *et al*., 2014) have shown that *B. neritina* is a complex of three cryptic biological species but, unfortunately, Mediterranean populations were not considered in these genetic studies. The current data do not allow the designation with any confidence of the native region of type S, the most widely distributed haplotype, which occurs in the English Channel and Galicia, but the south-western Atlantic and California may be two possible alternatives (Fehlauer-Ale *et al*., 2014).

It is conceivable that transoceanic transportation on ship hulls of these three non-indigenous species may have started with the first voyages of discovery and trade between Europe and the rest of the world, an historical pathway that should not be underestimated (Bianchi & Morri, 2000). It is thus quite likely that their Mediterranean populations reflect very complex introduction histories with multiple imports from different geographical sources.

Suez Canal corridor. Most NIB recorded in Lebanon also occur in the Red Sea (85% with two disputable records: Table 6) and many of them were recorded in the Gulf of Suez and northern Red Sea (Balavoine, 1959; Ostrovsky *et al*., 2011) and the Suez Canal (Hastings, 1927; Eitan, 1972b; Ghobashy *et al*., 1980). The Indo-Pacific realm is also well represented, particularly the western Indo-Pacific region (Table 6). About 15 NIB species were also recorded in other areas of the Levantine coast, particularly Israel (Powell, 1969; d' Hondt, 1988; Sokolover, 2014). This distribution pattern stresses the major contribution of the Suez Canal as a pathway to the colonisation of the Levantine coasts by non-indigenous bryozoans, and is consistent with results for other groups (reviews in Streftaris *et al.*, 2005; Galil, 2007; Çinar *et al*. 2011; Zenetos *et al*., 2012). Bryozoan translocation through the Suez Canal involves both transportation (i.e. shipping and rafting) and migration (see below). The Suez Canal is not only a two-way transit route for thousands of vessels each month, but also a place where barges and tugs are working all year round, in contact with fouled quays and immersed structures. As stressed by Fox (1926), Galil (2007) and Mineur *et al*. (2012) when fouled, these craft are probably important vectors of introduction, functioning as moving relays from spot to spot along the Canal. For instance, *P. egyptiaca* was recorded on barges at Port Taufiq (southern end of the Suez Canal) by Hastings (1927).

Gibraltar gateway. Long-distance vessels coming from the Atlantic via Gibraltar Strait can be vectors of introduction of alien species ("herculean" introductions) in both the Levantine Basin and the Red Sea. This scenario probably concerns first Atlantic species native to tropical and warm-temperate areas, such as *Smittina nitidissima*,

Table 6. Geographical distribution of non-indigenous bryozoan species (NIB) recorded in Lebanon (*: cryptogenic species). 1: Other Levant localities (a: from N. Sokolover, 2014, with some taxonomic changes). 2: Rest of the Mediterranean. 3: Red Sea, including the Gulf of Aden. 4: W Indo-Pacific. 5: Central Indo-Pacific. 6: Warm-temperate NE Pacific. 7: Tropical W Atlantic. 8: Warm-temperate W Atlantic. 9: Temperate W Atlantic. 10: Tropical E Atlantic. 11: Warm-temperate E Atlantic (including Canaries Is. and S Lusitanian region). 12: Temperate E Atlantic. (x): uncertain.

	1	2	3	4	5	6	7	8	9	10	11	12
Amathia verticillata	X	X	X	X	X		X				X	
Akatopora leucocypha	(x)		(x)				X	X	X			
Bugula neritina s.l.	X	X	X	X	X	X	X	X	X	X	X	X
Licornia jolloisii	X		X				X	X				
Thalamoporella harmelini *	X (a)											
Thalamoporella rozieri	X (a)		X	X			(x)					
Watersipora subtorquata	X	X	X	X	X	X	X	X	X	X		
Celleporaria cf. *brunnea*	X	X				X					X	X
C. labelligera			X		(x)							
C. vermiformis			X		(x)							
C. cf. *sherryae*	X (a)		(x)				(x)	X				
Drepanophora birbira	X (a)		X									
Parasmittina egyptiaca	X (a)		X									
P. protecta	X (a)		X	X						X	X	
P. serruloides				X			(x)					
P. spondylicola			X	X								
Smittina nitidissima	X		X				X			X	X	
Microporella browni			X	X								
M. coronata	(x)	(x)	X									
M. genisii			X	X							X	
M. harmeri	X (a)		X	X	X						X	
Mucropetraliella thenardii	X(a)		X	(x)								
Celleporina bitari			X		(x)							
Predanophora longiuscula			X	(x)								
Scorpiodinipora costulata			X	X	X		X			X		
Rhynchozoon larreyi	X		X		(x)							
Schizoretepora hassi *	X (a)											

Akatopora leucocypha and *Celleporaria* cf. *sherryae*, but also species from other seas, such as *Celleporaria* cf. *brunnea*. The invasive range of this species, possibly native to California, now includes the NE Atlantic (Portugal, Cascais: Canning-Clode *et al.*, 2013; France, Arcachon: André *et al.*, 2014), the western Mediterranean (Italy, several ports: Lodola *et al.*, 2015), the central Mediterranean (Gulf of Tarento, fouling near aquaculture farm: Lezzi *et al*., 2015) and the eastern Mediterranean (Turkey: Koçak, 2007; Lebanon: Harmelin, 2014b).

Means of translocation and spreading processes

The colonisation of Levantine waters by NIB species results from two modes of translocation at different spatial scales, functioning both through the Suez Canal and within the Mediterranean, i.e. transportation and natural spread (Fig. 7). Transportation of colonies is realized by attachment to moving substrata, mainly vessels and, occasionally, drifting items. Natural spread consists in an alternation between short-distance dispersal of propagules in the flow (essentially larvae), and attached stages (sexually mature colonies established on natural or artificial substrata). The distribution of NIB along the Levantine coasts most likely results from the linkage of transportation with natural spread using stepping stone habitats. Other vectors, such as release from shellfish aquaculture and aquaria, appear to be negligible in this regional context.

Shipping is a major but heterogeneous vector of species introduction, which includes both transcontinental exchanges by large vessels and coastal navigation by smaller merchant vessels, fishing boats or recreational craft. The maritime traffic across the Mediterranean is among the most intensive in the world (Dobler, 2002; Flagella *et al*., 2006; Abdulla & Linden, 2008) and is a major source of alien introduction (Zibrowius, 2002; Galil *et al.*, 2008, Nunes *et al*., 2014). It is well known to be the most powerful vector of introduction of bryozoans, (Ryland, 1965; Gordon & Mawatari, 1992; Watts *et al*., 1998), chiefly by hull fouling. However, settlement of colonies in less exposed niche areas of vessels, such as 'sea-chests' (Jackson, 2008), may be an even more ef-

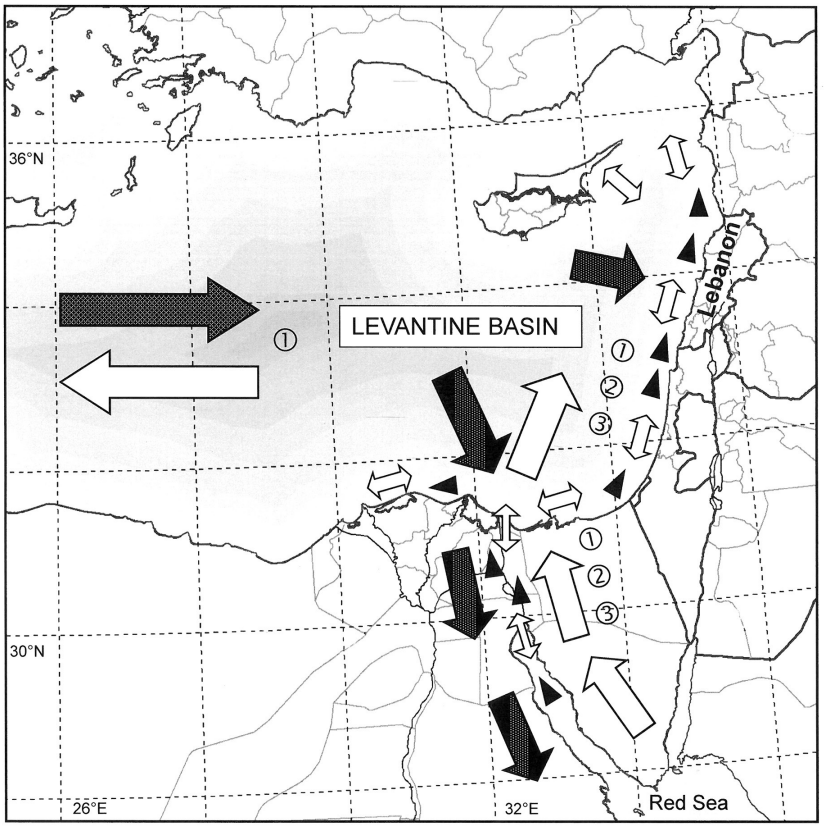

Fig. 7: Introduction processes and spread of alien bryozoans in the Levantine basin. Large arrows: main shipping routes; small double arrows: coastal shipping and working boats in the Suez Canal; black triangles: step by step spread of alien bryozoans by larval dispersal and colony settlement. 1: colony transfer by shipping; 2: colony transfer by rafting; 3: larval dispersal.

ficient introduction pathway for bryozoans. Moreover, if ballast waters cannot be vectors of direct transfer of bryozoan lecithotrophic larvae, given their short life duration and the length of the voyage, it might be possible that some larvae loaded with ballast water may occasionally settle on the walls of ballast tanks. This might concern especially sciaphilic species with short life cycles, such as several NIB recorded in Lebanon. If this occurs despite ballast water management (e.g. Endresen *et al*. 2004), this 'interior hull fouling' (Drake *et al*., 2005) would lead to the development of fertile colonies and the possible production of larvae released into the sea during the ballast discharge.

Rafting on drifting substrata, either natural (e.g. algae: pelagic *Sargassum*) or artificial (e.g. plastic debris), allows sessile organisms, including bryozoans, to be transported over long distances (Winston *et al.*, 1977; Barnes *et al.*, 2009). The Mediterranean is severely polluted by vast amounts of plastic debris (Galgani *et al.*, 1995; Galil *et al.*, 1995; Suaria & Aliani, 2014). The abundance and nature of the debris along the Lebanese coasts, both of local and distant origin (pers. observ.), suggest that their role as vector of the dispersal of NIB along the Levantine coast should be considered.

Apart from the rare transfer of colony fragments of light erect species, propagules responsible for the spread of bryozoan local populations are free larvae released by fertile colonies. Most gymnolaemate bryozoans (all species recorded here) produce short-lived lecithotrophic larvae (Ryland, 1981; Jackson, 1986) which settle short distances from the parents, as confirmed by population genetics (Goldson *et al.*, 2001). However, exceptional hydrological events may occasionally extend the dispersal range of these larvae. In any case, the geographical spread of a bryozoan population depends for the most part on the intensity of larvae production and the availability of habitats suitable for the settlement of larvae. Species whose life-history is characterized by an early and abundant production of larvae are particularly well suited to active step-by-step spread, including an opportunistic occupation of ephemeral and/or artificial substrata. This is in particular the case of *Celleporina bitari, Smittina nitidissima*, *Parasmittina serruloides* and *P. spondylicola*, small colonies of which are formed almost entirely of ovicellate zooids (Harmelin, 2014b; Harmelin *et al*., 2009).

Why are there so many alien bryozoans in Lebanese waters?

The conditions that foster the establishment of exotic species in native marine communities and their successful spread have been widely discussed in the literature (for the Mediterranean, e.g. Zibrowius, 1992; Boudouresque, 1999b; Occhipinti-Ambrogi, 2001; Streftaris *et al.*, 2005; Galil, 2007). Clearly, the exceptional success of NIB in Lebanese coastal waters mainly results from

the combination of two conditions: a highly favourable local context and strong propagule pressure from species well-adapted to this environment.

The geographical position of Lebanon in the Mediterranean is the key feature of the particular suitability of this area for colonisation by NIB species as it combines proximity to the Suez Canal, permanent circulation of surface waters favouring linkages with the Canal and warm climate. Other local features reinforce the invasibility of the Lebanese coasts, such as intensive shipping activity converging on the ports of Beirut and Tripoli and proximity to routes to the Canal entrance, Turkish ports and the Black Sea, and benthic communities combining naturally low diversity and poor conditions.

Oceanographical context. The permanent flow direction of the Atlantic surface waters flowing off the eastern Levantine coasts is northerly (Hamad *et al.*, 2006). This surface circulation can thus be a powerful vector of supply of alien propagules (essentially free stages of larvae), released at or near the Mediterranean mouth of the Suez Canal, i.e. about 400-600 km upstream of Lebanon. However, this dispersal route is subject to fluctuations due to mesoscale anticyclonic eddies (Hamad *et al.*, 2006) and, as in any coastal system, local factors (e.g. wind, shoreline geography, underwater topography, etc.) increase the stochasticity of dispersal and recruitment. Currents are also vectors of transfer of drifting objects that may be colonized by non-indigenous sessile organisms.

Climatic context of Lebanese coastal waters. The marine water bodies of the south-east Levantine basin are the warmest of the Mediterranean Sea, as clearly seen on satellite thermal images of surface water (e.g. Hamad *et al.*, 2006; Taupier-Letage, 2008). Temperature profiles recorded in Lebanon (Abboud-Abi Saad *et al*, 2004) show that within the 0-40m depth range, the mean temperature does not fall below 16.9°C in winter and reaches 30°C in summer. These thermal conditions, intensified by the effect of global climate change on the Mediterranean Sea water temperature (Nykjaer, 2009), are thus particularly favourable to subtropical and tropical invaders (Occhipinti-Ambrogi, 2007; Lejeusne *et al*., 2009; Por, 2010; Raitsos *et al*., 2010).

Condition of benthic communities. The naturally poor diversity of the native bryozoan assemblages, and more generally of the native sessile benthos in the south-eastern Mediterranean, might be favourable to the colonisation of NIB species able to occupy poorly exploited niches. The assumption that the naturally species poor Levantine area serves as a 'Godot' basin waiting for colonizers (Taviani, 2002; Oliviero & Taviani, 2003), has often been argued to explain the massive biotic invasion of the Levantine Basin (e.g. Galil, 2000). According to Boudouresque & Verlaque (2012), this hypothesis remains questionable, as counter-examples exist in the Mediterranean. The decline of Lebanese benthic communities due to pollution (Nakhlé, 2003; Shaban, 2008), responsible in part for their low diversity, may favour the settlement of resistant NIB species. Experiments with fouling assemblages in New-Zealand ports involving native and non-native bryozoans have shown that increased pollution resulted in the decline of native species diversity and percentage cover while non-native species were not affected (Piola & Johnston, 2008). The occurrence of *Celleporaria* cf. *brunnea* in the port of Beirut (Harmelin, 2014b) confirms the aptitude of this species to occupy port and anthropized habitats, already noted in California by Soule & Soule (1981) and indicated by records in the Mediterranean (Turkey: Koçak, 2007; Italy: Lezzi *et al.*, 2015, Lodola *et al*., 2015) and eastern Atlantic (Portugal: Canning-Clode *et al*., 2013).

Status of alien bryozoans in Lebanese communities

According to Zenetos *et al.* (2005, 2010), alien species can be classified as *established* (naturalized species with self-perpetuating populations), *casual* (recorded only once, presumed to be non-established), *questionable* (for taxonomic or other reasons) and *cryptogenic*. How may these categories be applied to the NIB recorded here, and more generally to bryozoans? Galil (2007) noted that it may be difficult to judge from a single record whether the occurrence of a new alien species reveals an on-going colonization or only an ephemeral intrusion. This doubt is reasonable, particularly when this record involves a species of which the individuals are able to move over long distances at the adult stage, such as fishes. In the present collection, only two NIB, *Celleporaria vermiformis* and *C.* cf. *brunnea,* were represented by a single colony. However, for *C. vermiformis*, the available sample was a fragment of a large fertile colony growing among many others on a jetty block (H. Z. observation), while *C.* cf. *brunnea*, also collected on a jetty, also occurs in other Mediterranean ports (see above). Therefore, these species are considered as established in Lebanese ports. More generally, as already stressed (Harmelin, 2014b), the actual spatial distribution and local abundance of bryozoan species are all the more likely to be underestimated as field sampling is not focused on bryozoans. This was the case for the studied collection, the initial purpose of which was a general overview of the Lebanese benthos. Therefore, all NIB recorded in Lebanon are considered to be established with self-reproducing populations. Moreover, considering that these NIB species have apparently no adverse impact on the recipient communities, they are considered to be non-invasive. This assessment refers to the concept of 'invasive' as implying the occurrence of harmful changes and biodiversity damage in the recipient ecosystems caused by the spread of alien species (e.g. IUCN, 1999, Boudouresque & Verlaque, 2002).

Expected trends in the Levantine basin

We have shown from a relatively old series of samples that the bryozoan assemblages of Lebanon reflect particularly well the peculiarities of this region, i.e. poorly di-

verse communities, warm climate favouring thermophilic species and high incidence of alien species illustrated by an unexpectedly high proportion of non-indigenous species among cheilostomes. The current situation, 12 years after the last sampling survey, is most likely worse, with an increased number of NIB species established in the coastal zone. In the near future, the intensification of surface water warming and increased shipping activity through the Suez Canal and the Mediterranean will boost the introduction of new alien species, leading to drastic changes in the structure of bryozoan assemblages. In particular, the new expansion of the Suez Canal, inaugurated in August 2015, that aims to significantly increase the shipping activity, will result in the intensification of both the direct transfer of propagules from the Red Sea and the ship-mediated import of non-indigenous warm-water colonizers, with catastrophic consequences for the Mediterranean ecosystems well beyond the Levantine basin. Bryozoans thus provide a fascinating model of future trends with regard to the marine fauna in other regions under the impact of global and local changes.

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