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Research paper

Spatial and vertical distribution of the genus *Amphistegina* and its relationship with the indigenous benthic foraminiferal assemblages in the Pelagian Archipelago (Central Mediterranean Sea)



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ABSTRACT

A serious threat affecting the Mediterranean Sea is the migration of Indo-Pacific marine species through the Suez Canal following its opening in 1869. This phenomenon gives extreme causes for concern as many non-indigenous species are highly invasive and seriously threaten native biodiversity. Particularly insidious are small-size taxa such as benthic foraminifera, which are able to invade wide areas un-noticed.

The objective of this study is to evaluate the stage of invasion of non-indigenous foraminifer *Amphistegina lobifera* and the re-colonization of *Amphistegina lessonii* in two islands of the Pelagian Archipelago (Central Mediterranean) where both species were first recorded in 2005.

Absolute abundances quantified in seabed and algal samples collected in 2014 were compared with those detected in 2005 and 2009. Results show that, in the innermost part of the neritic environment, amphisteginids were so abundant and widespread as to have replaced native benthic foraminifera just a few years after earlier reports.

On Lampedusa Island, Amphisteginids seem to compete mainly with other symbiont-bearing foraminifera, such as the milioliid *Peneroplis pertusus* and *Peneroplis planatus*; we hypothesize that the different algal symbionts housed by the invasive species could play an important role in the invasion success in the Mediterranean Sea. In the most severe case of amphisteginid invasion, as seen around the volcanic island of Linosa, the accumulation of their carbonatic remains is causing a sedimentation switch: increasing the content of white carbonatic sands and replacing the black volcanic substrates, as already observed in Indian Ocean atolls.

1. Introduction

In recent years, several non-indigenous species (NIS) have entered the Mediterranean Sea from the Atlantic Ocean through the Strait of Gibraltar, and from the Red Sea through the artificial Suez Canal (such as *Percnon gibbesi, Ocypode cursor, Siganus luridus, Caulerpa taxifolia, C. racemosa, Amphistegina lobifera*). NIS are considered a serious threat to Mediterranean marine ecosystems as they may compromise native biodiversity, affecting anything from the single species to the entire community (Katsanevakis and Crocetta, 2014; Servello et al., 2019).

The colonization process by NIS in the Mediterranean was facilitated on the one hand by the increase in maritime traffic with continuous new introductions, and, on the other, by sea surface temperature increases due to global warming, which has favoured the migration and subsequent proliferation of tropical/subtropical species (i.e., Guastella et al., 2021 and references therein). The entry of NIS from the Red Sea and Indian Ocean was triggered in 1869 by the opening of the Suez Canal, phenomenon known as "Lessepsian Migration" after Ferdinand De Lesseps, responsible for developing the canal (Por, 1978). Since the canal provided direct access, a large number of fishes, crustaceans, cnidarians, molluscs, algae, soft corals and also protozoa of Indo-Pacific origin have progressively colonized the Mediterranean Sea (i.e., Azzurro et al., 2007; Zenetos et al., 2010; Lodola et al., 2012; Langer et al., 2012; Bariche et al., 2013; Caruso and Cosentino, 2014a; Ahnelt, 2016; Guastella et al., 2019; Weinmann et al., 2023; Nativ et al., 2023; Guastella et al., 2023).

The detection, identification and origin of the larger non-indigenous organisms has been far more rapid, undoubtedly due to their

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macroscopic size, which favoured the initial identification also by nonspecialist people (Perzia et al., 2023). In contrast, the detection of smallsize taxa, such as unicellular foraminifera, occurred later as requiring specialized study, in particular by micropaleontologists (Langer et al., 2012; Guastella et al., 2019). Of these hidden invaders, larger benthic foraminifera play an important role in Lessepsian colonization, particularly in the Eastern Mediterranean (Blanc-Vernet, 1969; Langer and Hottinger, 2000; Hyams et al., 2002; Langer, 2008; Meriç et al., 2008; Triantaphyllou et al., 2009; Koukousioura et al., 2010; Zenetos et al., 2010; Çinar et al., 2011; Langer et al., 2012, 2013; Mouanga and Langer, 2014), Central Mediterranean Sea (Caruso and Cosentino, 2014a; El Kateb et al., 2018; Guastella et al., 2019, 2021), along Tunisian coasts (Blanc-Vernet et al., 1979) as well as in the southern Adriatic Sea (off Albania; Langer and Mouanga, 2016).

Amphistegina lobifera (Larsen 1976) is a large symbiont-bearing foraminifera (LBF) of Indo-Pacific origin with diatom endosymbionts (Leutenegger, 1984; Reiss and Hottinger, 1984). It prefers shallow-waters at a depth of <20 m (Hallock, 1984; Hallock, 1999; Langer and Hottinger, 2000) and is widely distributed in warm tropical and sub-tropical areas of the central and western Pacific Ocean, Indian Ocean and Red Sea (Langer, 2008; Förderer et al., 2018). This genus thrives at temperatures above 14°C (winter isotherm; Langer, 2008 and reference therein).

In addition, thanks to its high dispersal capability (Prazeres et al., 2020; Raposo et al., 2023), *A. lobifera* is now highly invasive in the Eastern and Central Mediterranean Sea (Langer and Hottinger, 2000; Hyams et al., 2002; Yokeş et al., 2007; Hyams-Kaphzan et al., 2008; Meriç et al., 2008; Triantaphyllou et al., 2009; Koukousioura et al., 2010; Caruso and Cosentino, 2014a; El Kateb et al., 2018; Guastella et al., 2019, 2021). Recently, Raposo et al. (2023) performed genetic analysis on living *A. lobifera* specimens from Sicily documenting the abandonment of sexual reproduction as strategy for faster colonization: a mechanism that could have increased the invasion success of the species. In addition, Mancin et al. (2023) backdated the first arrival of *A. lobifera* in the Maltese archipelago at the beginning of the 20th century, making this small Lessepsian invader one of the earliest NIS in the Mediterranean Sea.

The Pelagian Islands (Fig. 1) are located in the centre of the Sicilian Channel (Central Mediterranean Sea) where water masses from western and eastern basins exchange fluxes; the islands also represent one of the largest Marine Protected Areas in the Mediterranean. Due to their geographic position, far enough away from strong sources of anthropogenic pollution, these islands are characterized by a high level of marine biodiversity (Zavattari, 1960); a genuine hot spot that also attracts different NIS, such as fishes (Pizzicori et al., 2000; Castriota et al., 2002; Azzurro et al., 2007), crabs and bivalves (Lodola et al., 2012), green algae (Serio et al., 2006; Lodola et al., 2012) and foraminifera (Caruso and Cosentino, 2014a) both Indo-Pacific and Atlantic in origin.

Amphistegina lobifera and congeneric *A. lessonii* were recorded for the first time in the Pelagian Island waters in 2005 (Caruso and Cosentino, 2014a). In 2009 and 2014, subsequent sampling campaigns were carried out to document the amphisteginid colonization process.

This work aims to evaluate the invasion stage of the genus *Amphistegina* and possible impacts on native benthic foraminiferal assemblages in the marine sediments around Lampedusa and Linosa a few years after the first finding in 2005. For this purpose, absolute abundances quantified in sea-bed and algal samples (collected in 2014 but not analysed until now) were compared with abundances quantified in samples collected in 2005 and 2009 and previously published (Caruso and Cosentino, 2014a). The collected results help to integrate the distribution and abundance frame presented by Guastella et al. (2019) and to furnish a solid base for data that will be collected in 2024, when a new sampling campaign will take place. This will make the Pelagian Archipelago one of the most monitored places in the Central Mediterranean regarding the invasion of *A. lobifera*, crucial in order to understand how the benthic foraminiferal ecosystem has changed over time.

2. Study area

The Pelagian archipelago is located in the Central Mediterranean Sea, within the bounds of Sicilian Channel, and comprises three islands: the larger islands of Lampedusa and Linosa, and the small islet of Lampione, rather more of a rock in the middle of the sea (Fig. 1). On the surface of the Sicilian Channel, Modified Atlantic Water (MAW) flows eastwards on the deeper Levantine Intermediate Water (LIW), moving in the opposite direction between 200 and 600 m water depth (Pinardi and Masetti, 2000; Kubin et al., 2019). During winter, the surface temperature of the sea does not fall below 15,5 $^\circ\text{C}$; during summer, however, water temperatures over 28 - 29can soar °C to (ref. MEDSEA REANALYSIS PHY 006 0099).

The Pelagian Archipelago became an Italian Marine Protected Area in 2002, encompassing both the islands and surrounding seabed. It is known around the world for the many nesting sites favoured by protected turtle species, *Caretta caretta* above all, on the beaches of "Isola dei Conigli" (Lampedusa) and "Pozzolana di Ponente" (Linosa).



Fig. 1. Location of the studied area (Mediterranean Sea, Pelagian Islands). Sampling sites: A) Lampedusa Island; B) Linosa Island.

2.1. Lampedusa Island

Lampedusa Island (Fig. 1A) has a sedimentary origin; it is subrectangular in shape, almost flat and paleogeographically belongs to the African Plateau (Grasso et al., 1985). The sedimentary cover comprises mostly carbonatic successions, aged in the Miocene, Quaternary and the Recent. To the north, coasts are steep and characterized by high cliffs, tens of meters thick, while to the south, coasts gently slope down to the sea, forming small sandy bays. The seabed sediments are essentially constituted by carbonatic sands of biogenic origin, rich in mollusc, echinoid and bryozoan remains and foraminiferal tests.

The underwater morphological profile mirrors the subsurface geological setting: in the southern part of the island, the seabed gradually deepens to 50 m, widening out due to the gentle tilting Miocene strata wich roll southwards (Fig. 1A). To the southeast, a discontinuous *Posidonia oceanica* meadow covers the seabed.

By contrast, in the northern part of the island, the seabed deepens abruptly and large blocks of stone which have crumbled from the cliffs above accumulate at the base of the escarpment forming an irregular sea bottom. These blocks are often covered by a thin layer of sand, and, at times, algae as *Dyctiota linearis* and *Dyctiota dichotoma* can be found blanketing the blocks. In the shallow water around Lampedusa, *Posidonia oceanica* meadows are missing or are patchy, especially in the southern part of the island where *Cymodocea nodosa* can be found. However, *P. oceanica* meadows increase in abundance at depths of over 30 m, covering the shelf and become profuse down to 50 m. Around the island the non-indigenous Indo-pacific algae *Caulerpa racemosa* is relatively plentiful, living on the blocks forming the seabed of the northern part, while rare on the sandy bottoms to the south.

2.2. Linosa Island

The Island of Linosa is volcanic in origin; it is almost circular in shape due to the volcanic cone (Fig. 1B) and is formed by basalts and pyroclastic deposits (Rossi et al., 1996) which erupted between 1.06 and 0.5 Ma (i.e., Romagnoli et al., 2020). The water depth of the seabed varies with the morphology of the volcanic cone. It slopes gently to 10 m and then plummets with large rocky blocks of basalts, sometimes columnar, sprouting up as necks. The large volcanic blocks are covered by green and brown algae, scattered in the soft sediment in the first depths 10-15 m, whilst in the southern part steeper coasts characterise the landscape. To the south-east, located at approx. 250 m from the coast, a submerged basaltic neck, named "Secchitella", forms a shoal, which descends from 6 m depth to 60 m. The rocky seabed is covered by extremely coarse, dark-black sands, mostly formed by pyroxenes and olivines and other silicatic grains derived from the erosion of basalts (Grasso et al., 1991). Mixed with these dark, coarse-grained sediments a large amount of white carbonatic foraminiferal shells have accumulated, bestowing a typical "salt and pepper" aspect to the sea bottom (Caruso and Cosentino, 2014a). Basalt blocks are often covered by several algal species (i. e., Haloptersis scoparia, Laurentia sp., Dyctiota linearis, D. dichotoma, C. racemosa). Among these, C. racemosa is the most abundant and creates a dense grid that prevent the growth of the other algae.

The submerged "Secchitella" rock to the southeast has a vertical morphology and thus constitutes a good place to study the vertical distribution of benthic foraminifera.

The shoal was defined by Jacqueas Cousteau as "the best scuba diving place in the Mediterranean for the biodiversity present in the area". Here, the submerged cliff is largely colonized by the madrepore species Astroides calicularis, which covers the basalts rocks down to a depth of 37 m. This is an exceptional place along the coasts of central Mediterranean, where *A. calicularis* habitually colonizes the upper 10–15 m below the sea surface. This is due to the sea water temperature which, in Linosa, does not fall below 17 °C during the winter. The gorgoniid species *Paramuricea clavata* colonizes the cliff from a depth 25 m to 53 m. *C. racemosa* persists down to 25 m in depth.

3. Materials and methods

A total of 36 samples were collected during a scuba diving expedition in June 2014.

Fourteen surficial soft bottom sediment samples were collected offshore Lampedusa and three surficial soft sediment were collected off the coasts of Linosa following the FOBIMO protocol (Schönfeld et al., 2012). Sampling sites, depths, geographic coordinates, and types of sample collected are reported in Table 1.

For the collection of each sediment sample, a cylindrical polyethylene hand corer (\emptyset 5.5 cm) was inserted approximately 1.5 cm into the soft bottom sediment, obtaining a sediment volume of ~35 cm³. At each sampling site, three replicates of soft sediment sample were collected at a 2 m distance one from the other; this distance was also subject to the presence of rocky blocks that prevented sampling. Furthermore, around Lampedusa, at depths of over 25 m, dense *P. oceanica* meadows cover the seabed, inhibiting sampling of the sandy substrate.

In the waters around Linosa, 19 algal samples were also collected from the hard rocky substrate (Table 1). Sampled algae had a squared area of approx. 7 cm² and 5 cm height; in this way, a volume of \sim 35 cm³ was obtained for each algal sample. Samples were collected at several sites (14 in Lampedusa and 12 in Linosa) and at varying water depths (from a minimum depth of 0 to a maximum of 60 m) (Table 1). The site labelled as LI 14–7 corresponds to the submerged "Secchitella" rock, where five samples (labelled from LI 14–7a to LI 14–7e) were collected at different water depths (Table 1).

Following collection, sediments and algae were stored immediately in polyethylene bottles and stained with buffered Rose Bengal dye (2 g of Rose Bengal in 1 L of ethanol). This solution allows us to distinguish living (stained) from dead (unstained) foraminifera (Walton, 1952). The shells with the last chamber coloured pink were considered as living individuals. The five algal samples collected offshore Linosa were stored in ethanol to classify algal taxa. All samples were then placed in an iced cooler.

After 14 days sediment samples were gently washed in a 63 μ m sieve; the washed residues were then oven-dried at 40 °C for 48 h and weighed. Residues were stored in plastic jars until microscopic analysis. Qualitative and quantitative analyses of the total benthic foraminiferal assemblages (distinguishing living from dead foraminifera, i.e., stained and unstained) were carried out in the fraction >63 μ m. An Otto microsplitter was used to obtain a statistically valid count of the benthic foraminifera for each washed residue. All benthic foraminifera contained in the split fraction were identified and counted, separating stained (living) from unstained (dead) individuals. In this study, we focus our attention on living assemblages.

Subsequent to taxonomic classification, the algal samples were dried at 40 $^{\circ}$ C and weighed; all foraminiferal specimens were then isolated, taxonomically identified and counted. In samples treated with ethanol, the living individuals were recognized thanks to the presence of pseudopods around the opening and the brown colour of the cell present in the last chamber of the test.

Benthic foraminiferal census counts, both for sediment and algal samples, are reported as number of specimens per gram of dry sediment (Ng^{-1}) , or per gram of dry algae (Ng_a^{-1}) (Tables 2A and 2B). Furthermore, as suggested by Schönfeld et al. (2012), abundance has also been normalized to a standard volume of 50 cm³ (Tables 2A and 2B).

Benthic foraminiferal species were identified following Loeblich and Tappan (1987), Cimerman and Langer (1991) and Hottinger et al. (1993). The species *Amphistegina lobifera*, is here considered as non-indigenous (exotic) invasive, whilst the species *A. lessonii, Amphisorus hemprichii* and *Coscinospira arietina* were considered as cryptogenic (e.g., Guastella et al., 2019 and references therein).

Moreover, some small-sized specimens, characterized by a highly flattened spiral side and a much more pronounced carina (classified as *A*. cf. *lessonii* in Caruso and Cosentino, 2014a) were considered a

Table 1

Geographic coordinates and bathymetries of the sampling sites. Around Lampedusa only sediments were collected; around Linosa algae and sediments were collected.

Sampling sites	Depth (m)	Latitude	Longitude	Sample	Sample treatment
Lampedusa Island					
LAMP 14-1	14	35°31′075″	12°31'170″	sediment	Rose Bengal
LAMP 14-2	11	35°30'920"	12°31'697″	sediment	Rose Bengal
LAMP 14-3	12.5	35°30'851"	12°32'008"	sediment	Rose Bengal
LAMP 14-4	11	35°30'706"	12°33'141″	sediment	Rose Bengal
LAMP 14-5	12.4	35°30'571"	12°33'726"	sediment	Rose Bengal
LAMP 14-6	9.4	35°30′565″	12°34'005″	sediment	Rose Bengal
LAMP 14-7	17.6	35°30'224"	12°34′622″	sediment	Rose Bengal
LAMP 14-8	5.4	35°29'639″	12°36′554″	sediment	Rose Bengal
LAMP 14-9	18	35°29′580″	12°36'959″	sediment	Rose Bengal
LAMP 14-10	13	35°29'657″	12°37′485″	sediment	Rose Bengal
LAMP 14-11	18.4	35°29'691″	12°37′996″	sediment	Rose Bengal
LAMP 14-12	17.6	35°30′594″	12°37′664″	sediment	Rose Bengal
LAMP 14-13	15	35°30'824″	12°37′664″	sediment	Rose Bengal
LAMP 14-14	34.5	35°31′492″	12°34′579″	sediment	Rose Bengal

Sampling sites	Depth (m)	Latitude	Longitude	Sample	Name of algal species	Sample treatment
Linosa Island						
LI 14-1	1.5	35°52′045″	12°52'907″	algae	Halopteris scoparia, Cystoseira sp.	formaldehyde
LI 14-2	1	35°52′042″	12°52'922″	algae	Cystoseira sp.	Rose Bengal
LI 14-3	0.6	35°52′018″	12°52′911″	algae	Cystoseira sp.	formaldehyde
LI 14-4	4.5	35°52′297″	12°52′802″	sediment		Rose Bengal
LI 14-5a	3	35°51′402″	12°52'380"	sediment		Rose Bengal
LI 14-5b	3	"	"	algae	Halopteris scoparia, Dyctiota linearis	Rose Bengal
LI 14-6	1	35°51′388″	12°52'316″	algae	Cystoseira sp.	Rose Bengal
LI 14-7a	7	35°51′279″	12°52′105″	algae	Halopteris scoparia	Rose Bengal
LI 14-7b	18	"	"	algae	Halopteris scoparia	Rose Bengal
LI 14-7c	21	"	"	algae	Halopteris scoparia	Rose Bengal
LI 14-7d	26	"	"	algae	Dyctiota linearis, D. dichotoma	Rose Bengal
LI 14-7e	60	"	"	sediment		Rose Bengal
LI 14-8a	1	35°51′816″	12°51′228″	algae	Cystoseira sp.	Rose Bengal
LI 14-8b	3	"	"	algae	Halopteris scoparia	Rose Bengal
LI 14-8c	4	"	"	algae	Halopteris scoparia	Rose Bengal
LI 14-9a	3	35°51′310″	12°51′630″	algae	Halopteris scoparia	Rose Bengal
LI 14-9b	6.4	"	"	algae	Cystoseira sp.	Rose Bengal
LI 14-10a	5	35°52′515″	12°51′897″	algae	Halopteris scoparia	formaldehyde
LI 14-10b	6.5	"	"	algae	Halopteris scoparia	Rose Bengal
LI 14-11	0	35°52′496″	12°51′885″	algae	Cystoseira sp., Laurentia sp.	formaldehyde
LI 14-12a	7	35°52′507″	12°52′481″	algae	Halopteris scoparia, Caulerpa racemosa	formaldehyde
LI 14-12b	10	"	"	algae	Halopteris scoparia	Rose Bengal

morphotype of *Amphistegina*. Due to the small size it was impossible to attribute these individuals to *A. lessonii* or *A. lobifera*, thus they were counted separately and indicated in figures and tables as *Amphistegina* morphotype alfa.

Four diversity indexes were calculated using Paleontological

Statistics Data Analysis (PAST) software (Hammer et al., 2001): 1) Species richness (S); 2) Dominance (D); 3) Shannon index (H); and 4) Fisher- α index, (Fisher et al., 1943; Shannon, 1948; Murray, 1973). Statistical analysis using ORIGIN pro2017–64 bit software for the crosscorrelation matrix (Pearson's correlation coefficient) was performed

Table 2A

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Data of the studied sam	ples from Lampedusa	(weight, volum	e of sediment samples	, toraminiteral dens	sifies).
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Lampedusa Island	Dry sample weight (g)	Number of split	Split weight (g)	Number of living specimens counted	Total specimens	Forams/gram sediment (Ng ⁻¹)	Sediment sample volume (cm ³)	Forams/ cm ³ sediment	Normalized to 50 cm ³ sediment volume
LAMP 14-1	34.11	1/32	0.60	153	4896	143.52	35.6	137.45	6872.66
LAMP 14-2	34.44	1/32	0.46	67	2144	62.25	35.6	60.19	3009.60
LAMP 14-3	32.07	1/32	1.30	52	1664	51.88	35.6	46.72	2335.81
LAMP 14-4	25.91	1/32	0.84	78	2496	96.33	35.6	70.07	3503.71
LAMP 14-5	31.34	1/16	2.05	68	1088	34.72	35.6	30.55	1527.26
LAMP 14-6	37.61	1/32	1.27	76	2432	64.66	35.6	68.28	3413.87
LAMP 14-7	21.12	1/16	1.04	87	1392	65.90	35.6	39.08	1953.99
LAMP 14-8	26.60	1/64	0.31	137	8768	329.59	35.6	246.16	12307.91
LAMP 14-9	25.44	1/8	2.27	106	848	33.34	35.6	23.81	1190.36
LAMP 14-10	24.99	1/16	1.28	149	2384	95.40	35.6	66.93	3346.49
LAMP 14-11	27.80	1/4	5.56	154	616	22.16	35.6	17.29	864.70
LAMP 14-12	32.49	1/64	0.38	74	4736	145.77	35.6	132.96	6648.07
LAMP 14-13	23.64	1/64	0.54	147	9408	398.00	35.6	264.13	13206.30
LAMP 14-14	19.48	1/64	0.55	73	4672	239.82	35.6	131.16	6558.23

Table 2B		
Data of the studied samples from Linosa (weight,	volume of algae and sediment sample	es, foraminiferal densities).

Linosa Island	Dry sample weight (g)	Number of split	Split weight (g)	Number of living specimens counted	Total specimens	Total weight (algae + foram) (g)	Foraminifera weight (g)	Forams/ gram sediment (Ng ⁻¹)	Sediment sample volume (cm ³)	Forams/ cm ³ sediment	Normalized to 50 cm ³ sediment volume	Algal sample volume (cm ³)	Forams/ cm ³ algae	Normalized to 5 0 cm ³ algal volume	Number foram/ g of algae (Nga ¹)	Biomass
LI 14-1	-	-	-	3	-	0.82	0.00					37.5	0.08	4.00	3.64	0.39
LI 14-2	-	-	-	30	-	0.78	0.02					37.5	0.80	40.00	38.39	2.66
LI 14-3	-	-	-	78	-	0.75	0.06					37.5	2.08	104.00	104.11	7.46
LI 14-4	26.49	1/8	2.95	171	1368	-	-	51.64	35.62	38.41	1920.30					
LI 14-5a	18.74	1/2	10.05	283	566	-	-	30.20	35.62	15.89	794.51					
LI 14-5b	-	-	-	398	-	2.17	0.18					37.5	10.61	530.67	183.11	8.14
LI 14-6	-	-	-	247	-	1.68	0.08					37.5	6.59	329.33	146.92	4.93
LI 14-7a	-	-	-	45	-	2.15	0.04					37.5	1.20	60.00	20.96	1.98
LI 14-7b	-	-	-	478	-	3.21	0.46					37.5	12.75	637.33	148.75	14.41
LI 14-7c	-	-	-	1444	-	3.77	1.15					37.5	38.51	1925.33	382.61	30.52
LI 14-7d	-	-	-	86	-	1.52	0.08					37.5	2.29	114.67	56.48	5.36
LI 14-7e	11.16	1/16	0.44	100	1600	-	-	143.35	35.62	44.92	2245.97					
LI 14-8a	-	-	-	1	-	1.56	0.01					37.5	0.03	1.33	0.64	0.84
LI 14-8b	-	-	-	1669	-	1.86	0.14					37.5	44.51	2225.33	895.47	7.42
LI 14-8c	-	-	-	502	-	2.65	0.08					37.5	13.39	669.33	189.51	3.10
LI 14-9a	-	-	-	165	-	2.76	0.06					37.5	4.40	220.00	59.89	2.08
LI 14-9b	-	-	-	410	-	2.95	0.27					37.5	10.93	546.67	139.11	9.22
LI 14-10a	-	-	-	472	-	2.30	0.28					37.5	12.59	629.33	205.04	12.06
LI 14-10b	-	-	-	848	-	3.63	0.50					37.5	22.61	1130.67	233.76	13.83
LI 14-11	-	-	-	50	-	0.74	0.09					37.5	1.33	66.67	67.34	12.74
LI 14-12a	-	-	-	289	-	3.53	0.17					37.5	7.71	385.33	81.85	4.95
LI 14-12b	-	-	-	586	-	3.89	0.22					37.5	15.63	781.33	150.74	5.63



Fig. 2. Diversity indexes calculated for living benthic foraminiferal assemblages around Lampedusa.

only on living species with abundances >2%.

4. Results

A total of 63 different living species, belonging to 5 orders, 13 superfamilies, 27 families and 37 genera were recognized in the samples; 60 species offshore Lampedusa and 42 offshore Linosa. The complete list of benthic foraminifera is reported on the Supplementary File S1.

Data on the living assemblage for each sample have been reported in pie charts; when taxa were below 2%, were grouped together and reported as "other species". Census counts of dead assemblages (as a percentage) were also reported in Supplementary File S1.

4.1. Lampedusa Island

The highest number of species and genera, together with foraminiferal density, were found in the samples around Lampedusa. In particular, the richest sample was LAMP 14–13 with 398 Ng⁻¹ of sediment and 13206.3 N/50 cm³ sediment volume. In contrast, the lowest values were counted in sample LAMP 14–11 (22.1 Ng⁻¹ of sediment). These two samples were collected not far from each other and at similar depth (–15 and – 18.4 m, respectively; see Table 2A).

Species richness (S) ranged from 12 in LAMP 14–2 to 27 in LAMP 14–13, while dominance (D) varied from 0.074 in LAMP 14–8 to 0.38 in LAMP 14–10. The Shannon index shows values ranging from 1.71 in LAMP 14–10 to 2.84 in LAMP 14–8. The Fisher- α index varies from 3.7 in LAMP 14–2 to 11.44 in LAMP 14–12 (Fig. 2).

Pie charts of Fig. 3 report living benthic foraminiferal relative abundances in samples collected around Lampedusa, at water depths varying from 5.4 m to 34.5 m. *Amphistegina lobifera* is the species with the highest percentages at LAMP 14–10 (60.4%), at LAMP 14–11 (55.2%), at LAMP 14–1 (54.9%), and at LAMP 14–9 (50.9%). *Amphistegina lessonii* continuously recorded lower percentages, as in samples LAMP 14–2 (14.9%), LAMP 14–1 (9.8%) and LAMP 14–14 (6.9%); in the other samples it was extremely rare (<2%), or absent. *Amphistegina* morphotype alfa is usually less abundant than the other two species; it

was found in some samples with percentages <7%: 6.7% (LAMP 14–10), 4.7% (LAMP 14–9), 3.2% (LAMP 14–1), 1.9% (LAMP 14–11),2.3% (LAMP 14–7), 1.4% (LAMP 14–2), 1.3% (LAMP 14–6) and 0.7% (LAMP 14–8). In the other samples, the morphotype was found to be absent. This morphotype co-occurs in samples where typical *A. lessonii* was present, with the exception of the site LAMP 14–6, where only very rare *Amphistegina* morphotype alfa (1.3%) was documented.

The accompanying foraminiferal assemblage was characterized by several epiphytic and epilithic foraminifera belonging to the orders Rotaliida and Miliolida; among these latter, the most abundant genera were *Peneroplis* and *Quinqueloculina*. *Peneroplis pertusus* increased progressively from LAMP 14–1 (5.8%) to LAMP 14–6 (28.9%), whilst scarce between LAMP 14–7 and LAMP 14–11, increasing again in the eastern part of the island in samples LAMP 14–12 (16.2%) and LAMP 14–13 (24.5%).

Coscinospira arietina was found to be rare and present only in three samples with percentages of 0.73%, 1.28% and 3.27% in samples LAMP-8, LAMP 14-4 and LAMP 14-1, respectively. It was found, in general, to be more abundant in the dead assemblages. Amphysorus hemprichii was rare or absent in several sites, and reached its highest percentages in LAMP 14-10 (4%), LAMP 14-2 (5.97%) and LAMP 14-7 (12.6%). Among the epiphytes, the species with the highest percentages were Lobatula lobatula, Asterigerinata mamilla, Hanzawaia boueana, Rosalina bradyi, Rosalina macropora, Rosalina floridensis and Rosalina globularis. Lobatula lobatula reached percentages of up to 23.9% in LAMP 14-2, 23% in LAMP 14-12, 16.1% in LAMP 14-8, 15.6% in LAMP 14-13 and 15.1% in LAMP 14-4, whilst abundances fell below 8% in the other samples. Asterigerinata mamilla reached abundances of 23.1% in LAMP 14-3, 13.2% in LAMP 14-5 and 13.7% in LAMP 14-14. Hanzawaia boueana recorded percentages between 2% and 8.9% in samples LAMP 14-1, LAMP 14-2, LAMP 14-4, LAMP 14-5 and LAMP 14-13, whilst the species was <2% in the other samples. The epiphytic genus *Rosalina* was common showing the highest percentages with Rosalina bradyi and R. macropora at 7.7% in LAMP 14-3, and Rosalina floridensis and R. globularis at 6.4% and 7.7%, respectively, in LAMP 14-4, respectively. The genus Ammonia was present in eight samples and with constantly



Fig. 3. Pie charts with living (L) benthic foraminiferal percentages in Lampedusa samples.



Fig. 4. Diversity indexes calculated for living benthic foraminiferal assemblages around Linosa.

low percentages, with the exception of site LAMP 14–6 where an unusual assemblage was found. This assemblage was constituted by *Ammonia beccarii* (19.7%), *A. parkinsoniana* (9.2%) and *A. tepida* (2.6%).

4.2. Linosa Island

The highest and the lowest foraminiferal density values in Linosa were found in the same site (LI 14–8) but at different depths (samples a-c, Table 1): 2225.3 N/50 cm³ algae volume at -3 m (LI 14–8b) and 1.33 N/50 cm³ algae volume at -1 m (LI 14–8a) (Table 2B).

Species richness (Fig. 4) ranged from 1 to 18, in LI 14–8a and LI 14–7e, respectively. Dominance shows the lowest value in sample LI 14–7e (0.107) and the highest value in sample LI 14–8a (1), as only one living individual was found. The Shannon index is 0 in sample LI 14–8a, while its highest value of 2.52 was recorded in sample LI 14–7e (Fig. 4). The Fisher- α index varies from 0, in samples LI 14–1 and LI 14–8a to 6.4 in sample LI 14–7e.

Pie charts in Figs. 5, 6 and 7 show percentages of living benthic foraminifera in samples collected off the shore of Linosa. Samples LI 14–1and LI 14–8a have an excessively low number of living individuals (3 in the first and 1 in the second). Thus, pie charts of these last two samples have been not plotted and not considered in the discussion.

The most abundant species found was *Amphistegina lobifera*, which recorded higher percentages with respect to samples from Lampedusa and was present in all the samples, with percentages that often exceeded 60% and rarely fell below 40%. *Amphistegina lessonii* was present in almost all the samples, the highest percentage was found in LI 14–9a (7.9%). *Amphistegina* morphotype alfa was considered, rare and with percentages of up to 3.4% (LI 14–9b) and it did not co-occur with *A. lessonii*.

The other living benthic foraminifera were essentially constituted by miliolids and rotalids living as epiphytes on algea and marine plants (Figs. 5–6). *Peneroplis pertusus* occurred in a lot of samples, sometimes with high percentages (up to 90% in LI 14–8b and 73% in LI 14–8c), followed by *P. planatus* (up to 29.1% in LI 14–6 and 20.6% in LI 14–12b)

with the only exception being sample LI 14–12b, where *P. planatus* (20.6%) was more abundant than *P. pertusus* (14.3%).

Coscinospira arietina was rare and present only in a few sites with percentages of 1% or lower (LI 14–5a). *A. hemprichii* was present only in one site at different water depths and extremely low abundances: 1% (LI 14–12a) and 1.8% (LI 14–12b), respectively. The genus *Quinqueloculina* was discontinuously distributed and characterized by low percentages. The most abundant species were *Q. agglutinans* and *Q. disparilis* at site LI 14–4 with relative abundances of 4.6% and 2.9%, respectively. Among epiphytes, the most frequent species were *Hanzawaia boueana*, *Lobatula lobatula* and *Planorbulina acervalis*.

At site "Secchitella" LI 14–7 (samples a-e; Fig. 7), the most abundant species was *Amphistegina lobifera* with percentages varying between 75.6% and 91.6%, whilst at –60 m (LI 14–7e) the most abundant species was L. *lobatula* (23%), followed by *A. lobifera* (14%), *M. subrotunda* (10%) and other Miliolida (*Pyrgo* sp., *P. pertusus* and *Q. bradyana*) and epiphytes (*R. bradyi*, *R. globularis*, *H. bouweana*).

Pearson' correlation matrix show a statistical significant negative correlation between *A. lobifera* and *P. pertusus*, with values of r = -0.70149 and *p*-value = 0.00518 (Lampedusa), and r = -0.81069 and p-value = 0.04753 (Linosa) (Supplementary File S2).

5. Discussion

5.1. Foraminiferal distribution in the study area

Despite similar bathymetries, the benthic foraminiferal assemblages are substantially different for the two islands, and their abundances are strictly tied to the geomorphological and geological peculiarities of two islands. This aspect undoubtedly influenced the sampling methodologies used in the two cases, well evident in the underwater morphological profiles of the seabed (i.e. seabed, substratum, presence/absence of algae, etc.)

A higher number of foraminiferal species were found off the coasts of Lampedusa (60) compared to Linosa (42), coupled with a greater



Fig. 5. Pie charts with living (L) benthic foraminiferal percentages in Linosa samples.

number of genera, 36 in Lampedusa and 26 in Linosa. These data, however, do not mirror what we would expect to find in samples taken within a marine protected area, where native assemblages should be more diverse and abundant due to the pristine environment, little affected by human activities. However, the occurrence of an invasive alien species, *A. lobifera*, has been documented in the Pelagian Archipelago since 2005. Its continuously increasing abundance over time may have caused a significant loss in the indigenous benthic foraminiferal assemblages, thus representing a genuine threat, as also reported by Guastella et al. (2023). The decrease in foraminiferal diversity is greater in the waters off Linosa where *A. lobifera* dominates the assemblage at almost all stations indicating that the invasive species is



Fig. 6. Pie charts with living (L) benthic foraminiferal percentages in Linosa samples.



Fig. 7. Bathymetric profile of the studied samples at the Secchitella shoal (Linosa) with relative pie charts of living (L) benthic foraminiferal percentages.

able to replace native benthic foraminifera. Other inner-shelf areas of Sicily, where the invader is absent, such as the Gulfs of Palermo and Termini, show higher native diversity with more than double the number of benthic foraminiferal species (for more details see Caruso et al., 2011a, 2011b; Caruso and Cosentino, 2014a, 2014b). In the studied samples, *A. lobifera* is the most abundant species living as

epiphytes attached to algae, especially around Linosa, where in several sites it exceeded 70%. On the contrary, in Lampedusa, it occurs on firm rocky substrate and rarely exceeded 50% with abundance variations in samples collected at similar water depths. It is reasonable to assume that the difference in the adopted sampling method may have influenced the abundance percentages recorded in the samples, suggesting that



Fig. 8. SEM photographs: A- Amphistegina morphotype alfa, ventral side (LI 09 4), B- particular of photo A, C- diatoms near the aperture in the ventral side of Amphistegina lobifera (LI 09 1), D- Amphistegina lobifera, ventral side (LI 09 8), E- particular of photo D in which diatoms are well visible.

amphisteginids can live as epiphytes on algae, as well as on firm substrates.

The high percentages of amphisteginids recorded in the south-west cape of Lampedusa may be related to local surface water circulation connected with the morphology of the inner shelf, which favours an increase in nutrient supply around the island. This local nutrient enrichment may facilitate diatom blooming: amphisteginids feed on diatoms (Fig. 8) and also use them as photosymbionts (Lee, 1995).

In the Mediterranean Sea, peaks of *A. lobifera* have been reported at very shallow depths (<5 m, Triantaphyllou et al., 2012, Guastella et al., 2023). Amphisteginids are symbiont-bearing foraminifera (Hallock, 1999) that proliferates in oligotrophic waters. Mediterranean waters are usually considered as oligotrophic (D'Ortenzio and Ribera D'Alcalà, 2008 and references therein); however, it is known that in some limited areas of the Sicilian Channel, rising waters which are rich in nutrients influence the trophic chain, leading to a series of consequences for marine organisms.

Our study shows that, in the Pelagian archipelago, this species is also capable of colonizing deeper environments. Extremely high percentages of *A. lobifera* were, in fact, found in samples up to -18,4 m off the coast of Lampedusa (55%), and up to -26 m off Linosa (86%). Around Linosa *Amphistegina lobifera* is common in seabed sediments surrounding the island at 60 m depth (14%). It is worth noting that, in Linosa samples, Ferraro et al. (2020) described 140 species found at -39 m to -407 m, reporting only extremely low percentages of *A. lobifera* and *A. lessonii* at these greater water depths (-39 m and -53 m).

Also noteworthy is the fact that the genus *Peneroplis* and, in particular, the species *P. pertusus* is abundant in shallow water samples (depth < 20 m) where *A. lobifera* is rare or missing (e.g., samples 14–4 L, 14–5 L and 14–6 L) indicating a probable competition for the same habitat and trophic resources. The higher percentages of peneroplids with respect to other benthic foraminifera may be related to the presence of

rhodophyceans (genus *Porphyridium*) that live as photosymbionts within their shells (Leutenegger, 1984). The hypothesis of an antagonistic behaviour between *A. lobifera* and *P. pertusus* is supported by statistical data: the abundances of *A. lobifera* and *P. pertusus* are negatively correlated in both the Lampedusa and Linosa samples (see Supplementary file S2).

According to Cimerman and Langer (1991), in the Tyrrhenian and Adriatic seas P. pertusus colonizes depths of 0 to -20 m, while P. planatus prefers deeper habitats, down to -50 m or - 80 m. Different ecological limitations could explain why P. pertusus seems to suffer direct competition from A. lobifera. Our data highlights that, at the "Secchitella" shoal (Linosa), P. pertusus colonizes water depths down to -60 m (Li 14–7e). This is probably due to the transparency of the sea water (see Fig. 3 in Innangi et al., 2024) and higher temperatures. The sample collected at -60 m has the highest specific diversity, probably due to a lower presence of A. lobifera, thus other species occupy the ecological niche and become more abundant. Furthermore, though if P. planatus may prefer deeper water conditions compared to P. pertusus, in some sites, it has become more abundant. In our opinion, local environmental variables may contribute to small percentage changes in benthic foraminiferal assemblages, above all when there are comparable values. This is due to the fact that, moving laterally, percentages may change as a result of local factors that affect sampling (i.e., shape of the rocks, granulometry, algae, predators).

Nevertheless, peneroplids are opportunistic taxa (Ćosović et al., 2016); in fact, in the samples from Linosa island, where the invader *A. lobifera* is particularly abundant and widespread, Peneroplids seem to survive in the assemblage, whilst other species (e.g., *L. lobatula*, *R. bradyi* and *Quinqueloculina* spp.) greatly decrease in their abundance or disappear. This type of impact has also been observed in Malta and the Corfu islands, where *A lobifera* is today so abundant as to cause a loss of biodiversity in native benthic foraminiferal assemblages (Weinmann



Fig. 9. Comparison between samples collected in 2005 (Lampedusa), 2009 (Linosa) and 2014 (Lampedusa and Linosa).

et al., 2023; Guastella et al., 2023).

A natural pool (6-m wide and 5-m deep) lies along the coastline of Linosa, in front of site LI 14–12, excavated into the basaltic rock. During the winter storms, the wave motion and wind snatch foraminiferal tests from algae (almost exclusively amphisteginids) and transport them over 100 m away from the coastline. The progressive accumulation of the foraminiferal remains is creating a carbonatic sandy layer that is gradually covering the basaltic rocks behind the pool. This particular carbonate deposition is modifying the normal littoral sedimentation, with the formation of small dunes (few centimetres high), as occurs in tropical volcanic islands (Resig, 2004; Narayan et al., 2021). Until now in temperate areas, such as the Mediterranean Sea, the accumulation of biogenic carbonatic sands, formed by amphisteginid remains, has only been observed in submerged environments (Blanc-Vernet, 1969; Meriç et al., 2008; Guastella et al., 2023), never along the coasts in transitional and emerged areas.

5.2. Comparison between samples collected in 2005–2009 and 2014

Here, we compare collected data with those previously published by Caruso and Cosentino (2014a) that refer to sampling take in 2005–2009 (Fig. 9). It should be remembered that during the 2005–2009 sampling, only sediment samples were collected, the samples were treated with Rose Bengal, however, owing to the low number of living individuals, data discussed in Caruso and Cosentino (2014a) referred to the entire (living plus dead) assemblage. In the 2014 sampling, both sediment and algae samples were collected and treated with Rose Bengal and counts were carried out separating living from dead assemblages. To compare data of the present study with the previous one, pie charts in Fig. 9 show total (dead plus living) counted specimens.

The collected results show that, within relatively few years, both the absolute abundance and the number of invaded sites have increased around both islands, albeit more severely in Linosa (Fig. 9). Here, change in the type of sedimentation is clearly observable, visible not only on the sea bottom (Fig. 10) but also in the coastal environment, as commonly occurs in tropical areas.

In samples from Lampedusa collected in 2005, amphisteginids occurred only in three of the twelve sampled sites; abundances were relatively low, <5%, with a maximum of approx. 30% at a single site in the eastern part of the island (Fig. 9). In contrast, samples collected in 2014 showed amphisteginids widespread distributed, present at more than half of the sampled sites, also with higher relative abundances (varying between 10% and 50%; Fig. 9).

In samples from Linosa collected in 2009, amphisteginids occurred in 11 of the total 14 sites; the abundances varied between <5% and over 90%, with a maximum of approx. 95% in two sites in the northern part of the island (Fig. 9). In contrast, samples collected in 2014 recorded amphisteginids in all the sampled sites, together with higher relative abundances. It is worth noting that *A. lessonii* was also more abundant in the 2009 samples, with percentages varying between 0 and 45%, and an



Fig. 10. Underwater photographs taken offshore of Linosa island. A) LI 09 13 - sediment samples; the large amount of carbonatic shells of *Amphistegina* gives a typical "salt and pepper" coloration to the black volcanic sediment; B) LI 09 6 - living specimens of *Amphistegina* attached on algae (arrows), carbonatic shells of *Amphistegina* are well visible in the picture; C) LI 09 5 - the algae *Padina pavonica* (Pp) and *Caulerpa racemosa* (Cr) with living *Amphistegina lobifera* (arrows); D) LI 09 12 - *Caulerpa racemosa* and living *Amphistegina lobifera* (arrows).

average value of 7,7% whilst in 2014 samples had decreased (0–6,2%), probably due to greater proliferation of *A. lobifera* (Fig. 9).

In 2014 amphisteginids were the dominant foraminifera in the sites around Linosa, thus the foraminiferal assemblages from most of the sites and water depths were very impoverished, indicating that as levels of abundance rise beyond a certain level, even the deeper sites, although less preferred by amphisteginids and particularly by *A. lobifera*, were found to be invaded. Weinmann et al. (2023) suggest a 20% abundance of *A. lobifera* is already capable of causing an impact on native assemblages. In the investigated samples from Linosa, this abundance threshold is widely exceeded in 18 of the 22 sampled sites.

5.3. Environmental and geographical considerations

Undoubtedly, the progressive colonization of *A. lobifera* is strictly tied to the opening of the Suez Canal, which enabled Lessepsian migration. Before the construction of the Canal, migration was prevented by a natural geographical barrier. The small, salty lakes were connected during the construction of the Suez Canal in 1869, which initiated the passage of surface waters from the Red Sea to the Mediterranean, further facilitated by the passage of large container ships. This caused the mixing of surface waters and consequent lowering of salinity. This phenomenon started at the end of 19th century and accelerated during the second world war. Lessepsian migration slowed during the late 60s during the Arab-Israeli war, which led to the closure of the Canal between 1967 and 1975. Now the Suez Canal constitutes the most important route for trade and the transport of oil, and in 2015 it

was enlarged, thereby amplifying the problem. This has facilitated the migration of organisms (i.e. larvae), travelling in bilge waters or attached to the hulls of ships. We are now witnessing one of the most important biological revolution events affecting Mediterranean biodiversity in the last 6 million years, following that of the Messinian salinity crisis. This phenomenon is amplified by the increase in sea surface temperatures (SST) of the Mediterranean Sea (Guastella et al., 2021; Mancin et al., 2023).

Today, Eastern Mediterranean SST are indeed similar to those of the northern part of the Red Sea, the problem will be understanding what this biological revolution could lead to. What will happen to species separated by millions of years of evolution? Who will succeed? Who will become extinct? Will ecological competition and environmental factors be able to control and mitigate the effects? The earth throughout its history, and the evolutionary history of species, has always reacted with innumerable extinctions and with evolution into new species. Scientists are witnessing these events; however, any human intervention is unpredictable and may cause even further imbalances which Earth, with its dynamic ecosystems, may take hundreds or even thousands of years to readjust.

6. Conclusion

This work documents the invasion stage of the genus *Amphistegina* in the Pelagian Islands. The collected data shows that in 2014, a few years after the first discovery in 2005, the invasion is at an advanced stage in the water around both Lampedusa and Linosa islands, particularly in

those of Linosa.

Where Amphistegina spp. is particularly abundant and dominates the assemblages, the native diversity of benthic foraminifera is significantly compromised even in those deeper sites (below 20 m depth), where in other places in the Central Mediterranean (e.g., Malta) the impact appears still moderate. It is likely that, in the Pelagian Islands Amphistegina lobifera has managed to colonize deeper aquatic environments than that reported in literature for other areas of the Mediterranean due to specific environmental and ecological conditions (higher temperature and sea water transparency) present in these small Mediterranean islands. Around Linosa, its proliferation is so intense that it is changing black volcanic sands into white biogenic carbonate sands, formed by the accumulation of amphisteginids, as previously described in Indo-Pacific atolls. Furthermore, around Lampedusa, Peneroplids are the major ecological competitor of Amphisteginids and we hypothesize that diverse algal symbionts housed can play an important role in the dynamics of foraminiferal population.

Finally, this invasion is amplified by increases in the Mediterranean SST (Guastella et al., 2021).

The results presented in this work show worrying conditions already back in 2014, which, 9 years later, have undoubtedly worsened.

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CRediT authorship contribution statement

Claudia Cosentino: Writing – original draft, Investigation, Formal analysis, Data curation. **Roberta Guastella:** Investigation, Formal analysis. **Nicoletta Mancin:** Writing – review & editing, Methodology. **Antonio Caruso:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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