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Research Article

Conquering the north: the recent expansion of a Lessepsian sea slug in the north-western Mediterranean Sea as a mirror of seawater warming

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Abstract

The Mediterranean Sea is strongly affected by the global warming, which favours the spread of non-indigenous species (NIS). This study analyses the range expansion of the Lessepsian sea slug *Lamprohaminoea ovalis*, linked to the increase in sea water temperatures. First recorded in Greece in 2001, *L. ovalis* has progressively spread northward, eastward and westward, recently reaching the Ligurian Sea, one of the coldest regions in the Mediterranean Sea. Thanks to the contribution of citizen science and through *in situ* surveys, this study documents thirteen new records of *L. ovalis* between 2021 and 2024 in previously unreported Mediterranean areas, including the Adriatic, Balearic, Ionian, and Ligurian seas. These recent observations reveal evidence of mating and egg-laying behaviours, indicative of successful establishment. Furthermore, *L. ovalis* exhibits biological traits that are likely to enhance its invasive potential. Temperature data from two sites in the Ligurian Sea at different latitudes (*i.e.*, Portofino Marine Protected Area and Elba Island), collected by temperature data loggers, corroborate the link between *L. ovalis* expansion and seawater warming. Finally, the present study revealed *L. ovalis* as a powerful bioindicator of climate-driven changes in marine ecosystems and emphasises the importance of continued monitoring to evaluate its ecological impact. While no negative effects on native species have been reported to date, the rapid spread and adaptive capacity of *L. ovalis* warrant further investigation to understand its long-term implications for Mediterranean biodiversity.

Key words: Mollusca, Heterobranchia, Cephalaspidea, global warming, topicalization, invasive species

Introduction

Global warming is a critical issue and emergent worldwide threat (Henson et al. 2017). Due to its nature as a semi-enclosed basin, the Mediterranean is one of the seas most affected by sea water warming, with negative effects on its marine flora and fauna (Schroeder et al. 2017). Although it covers only 0.82% of the global surface area of the oceans, the Mediterranean Sea hosts approximately 8% of the world's known marine species, of which

20–30% are endemic (Bianchi and Morri 2000). This great biodiversity is currently threatened by mass mortalities events, due to the increasing temperatures and the spread of various pathogens (also favoured by higher temperatures) (Vezzulli et al. 2010; Carella et al. 2020; Garrabou et al. 2022), and the arrival and possible establishment of non-indigenous species (NIS) (Tsirintanis et al. 2022). The expansion of NIS, which can become invasive, is a growing and recurrent pressure that is determining a shift in the Mediterranean biodiversity towards a new setting characterised by tropical species, a phenomenon known as tropicalization of the Mediterranean Sea (Bianchi and Morri 2003; Toso et al. 2022; Trainito et al. 2022; Toso and Musco 2023).

The loss of native species in favour of NIS has its maximum expression in the Levantine basin where the presence of the Suez Canal, coupled with new environmental conditions, generates continuous inflows into the Mediterranean Sea of species coming from the nearby Red Sea or from more distant areas of the Pacific and Indian oceans (Katsanevakis et al. 2014; Albano et al. 2021, 2024; Furfaro et al. 2025). However, the eastern part of the Mediterranean Sea is no longer the only one affected by the arrival and invasion of NIS: in fact this phenomenon is also widely known for the colder areas of the Mediterranean basin such as the Ligurian Sea (Bianchi 2007; Bianchi et al. 2018; Morri et al. 2019). In this area, recent changes in the biogeographical setting are increasingly evident and are promoting a new configuration of the Ligurian Sea, partly shaped by the unprecedented presence and abundance of thermophilic and exotic species (Azzola et al. 2024).

In this context, the recent arrival of a new NIS, the Lessepsian sea slug *Lamprohaminoea ovalis* (Pease, 1868), in the southernmost area of the Ligurian Sea was recently reported with the complete history of its invasion by Azzola et al. (2022). This cephalaspidean species belongs to the family Haminoeidae, a group of shelled gastropod molluscs that can show different chromatic patterns from cryptic to highly visible and aposematic ones (Oskars and Malaquias 2019). *Lamprohaminoea ovalis* was first reported in Greece (from "Porto Germano") in 2001 (Zenetos et al. 2003) and remained confined in the eastern part of the Mediterranean Sea until 2008, when it reached Castellammare del Golfo (Sicily, Italy), the western portion of this basin (Azzola et al. 2022). Since 2014, the geographic range of *L. ovalis* expanded northward into the Tyrrhenian Sea, reaching the Ligurian Sea in 2021, when it was observed on the coast of Elba Island (Azzola et al. 2022), currently considered the northernmost record of this species. Azzola et al. (2022) observed that the range expansion of *L. ovalis* in the Mediterranean Sea occurred particularly after 2014, favoured by the increasing of temperature and the shift of isotherms towards the northwest, and they also revealed that the yearly mean sea surface temperature (SST) of ~ 18 °C is the limiting temperature for this species (Azzola et al. 2022). This was of paramount importance for the early detection of changes in the marine environment and demonstrated the great ability of *L. ovalis* to function as a bioindicator of sea water warming.

On the other side, although possible impacts of *L. ovalis* on native Mediterranean species have not been reported, some biological traits of this species suggest it as potentially successful invasive species (*sensu* Carlton and Schwindt 2024). For example, as already known for other specialised heterobranchs, this mollusc can produce a chemical toxic compound (the brominated tetrahydropyran 2) with high activity as feeding deterrent that is a powerful defensive strategy from possible predators and even more from predators that are not used to interacting with this species (Mollo et al. 2008). The lack of potential predators is exacerbated by the presence of aposematic body colour patterns that help the possible new predators to avoid feeding on this newcomer, finally promoting its potential spread (Mollo et al. 2008). Considering that the way a species responds to resource availability, natural enemies, and the physical environment determines its ability to invade, its generalist diet (mainly consisting of common filamentous and brown algae and diatoms) (Crocetta and Vazzana 2009), the almost lack of predators, and the high reproductive potential of *L. ovalis* make this species a very good candidate for a successful invasion of new habitats.

For all these reasons, the main aims of the present study are to monitor possible further spreading of *L. ovalis* in the Mediterranean Sea, of paramount importance to detect as early as possible the new changes in the native communities due to further warming; and to increase knowledge on the biological link existing between this important bioindicator of sea water warming and the environmental conditions that would be extremely useful to expose patterns of changes in the sea water column.

Materials and methods

Range expansion of Lamprohaminoea ovalis

A bibliographic analysis was conducted to update the geographical range of *L. ovalis* in the Mediterranean Sea since the last review by Azzola et al. (2022). In addition, multimedia content documenting the presence of the species in the Mediterranean Sea from 2021 to December 2024 was collected from the social platforms Facebook (https://www.facebook.com), Instagram (https://instagram.com), iNaturalist (https://www.inaturalist.org) and OPK Opistobranquis (https://opistobranquis.info/en/) using specific keywords and searching directly within groups focused on marine biodiversity, conservation, recreational diving, and heterobranchs (Boldrocchi and Storai 2021 and references therein) and thanks to the contributions of the citizen scientists (*i.e.*, scuba divers and underwater photographers). Only publicly accessible contents were used, as posts from private accounts were inaccessible and did not align with our ethical protocol. Records were considered valid only when the multimedia content provided observation data, geographical location, depth of finding, and a clear image of the individual(s), allowing for accurate species identification.

The rate of expansion of *L. ovalis* was evaluated by entering the geographical coordinates of all records into the Google Earth platform (www.google.com/intl/it/earth) and measuring the geographical distances (kilometres) between the location where it was first recorded in 2001 and the first records of subsequent locations from other Mediterranean areas, taking into account the direction of the currents in this basin. Furthermore, starting from the last northernmost Mediterranean record of this species in 2021, a broad in-depth survey was conducted throughout the Ligurian Sea by *in situ* investigations and, where possible, additional data on *L. ovalis* population structure were collected. All the new records of *L. ovalis* were checked by the authors and the species identified through morphological analysis of the external diagnostic characters visible from the underwater images taken *in situ*.

Population structure

In the Portofino Marine Protected Area (MPA, Ligurian Sea), the *in situ* investigations were conducted in particular at the "Bigo" site along the so-called "Aurora" transect, where an historical data series on benthic communities has been available since the 1970s thanks to the continuous monitoring by the University of Genoa (Bavestrello et al. 2024). This site has been surveyed every month since April 2023 until October 2024 to collect data on the presence, abundance, and size of *L. ovalis*. When the species was present, individuals were photographed alongside a calliper and then measured using ImageJ software (Ferreira and Rasband 2012).

Temperature data

As the correlation between the SST increase and the range expansion of *L. ovalis* have previously been observed (Azzola et al. 2022), this study added the analysis of water column temperature data to further investigate the thermal tolerance of the species. The data were obtained from temperature data loggers (model: HOBO Water Temperature Pro v2 and HOBO TidbiT MX Temperature 400' Data Logger MX2203), placed both at Portofino MPA (since 2015) and at Elba Island (since 2020) as part of several projects (see: "Acknowledgments" section) aimed at monitoring climate-related responses in the Mediterranean MPAs. Following the T-MEDNet protocol (Garrabou et al. 2018), temperature data loggers are placed on rocky substrates at the depths of 5, 10, 15, 20, 25, 30, 35 and 40 m and data recording occurred every hour. In the present study, temperature data to a depth of 30 m (maximum bathymetry at which *L. ovalis* was sighted so far)

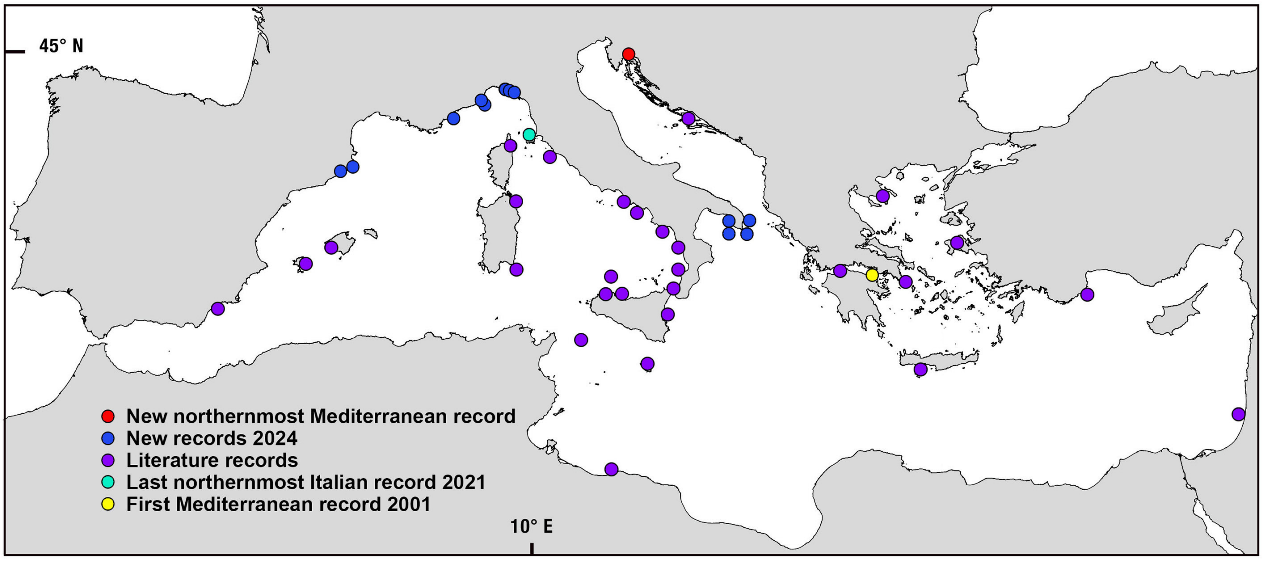

Figure 1. Map of all the known records of *Lamprohaminoea ovalis* in the Mediterranean Sea, starting from those reported in Azzola et al. (2022) and updated with all the new discoveries of this species until 14 December 2024.

were considered to compare trends at Elba Island and Portofino MPA from 2021 to 2024. The mean yearly and monthly temperature data of both areas were compared at six depths: 5, 10, 15, 20, 25, and 30 m. Data were analysed with Ocean Data View software (https://odv.awi.de).

Results

New records and geographical range expansion

The data collection was completed on 14 December 2024. Thirteen new Mediterranean records were obtained by the bibliographic analysis, multimedia contents, and from *in situ* campaigns (Figure 1, Table 1). Thanks to the contribution of the citizen science *L. ovalis* was reported from the coldest area of the Mediterranean Sea, the north Adriatic Sea, where it was observed on 14 December 2024 at Rijeka, in Croatia; this also represents the new northernmost record of *L. ovalis* in the Mediterranean (Figure 1, Table 1). Moreover, new records highlight the presence of *L. ovalis* in previously unreported areas in Italy in the Ligurian and Ionian seas, in France in the Ligurian Sea, and in Spain in the Balearic Sea. The literature record from the coast of Granada in Spain (Orenes-Salazar et al. 2024) represents the westernmost record in the Mediterranean Sea and the furthest from the very first Mediterranean record of this species in Greece (Figure 1). New records are listed and described more in detail below and in Table 1.

From the *in situ* investigations and thanks to the contribution of the citizen science *L. ovalis* was recorded in Italy in five new locations of the Ligurian Sea (Figure 1, Table 1). All these new records are further north with respect to the previous discoveries of this species (Azzola et al. 2022). The five records are listed from the southernmost to the northernmost: 1) at Capo Noli some individuals were found at the end of August 2024 at a

Table 1. List of the new unpublished Mediterranean records of *Lamprohaminoea ovalis* in Italy, Croatia, France, and Spain. The previous published Mediterranean northernmost record of *L. ovalis* (Azzola et al. 2022) is highlighted in italics.

First record	Locality	Lat. (N)	Long. (E)	Depth (m)	Author of the record
		ITALY, LIGURIAN SEA			
21/10/2021	*Italy, Tuscany, Elba Island, Porto Ferraio*	*42.821707*	*10.328733*	*26*	*Annalisa Azzola, Monica Montefalcone*
10/08/2024	Italy, Liguria, Genova, S. Margherita Ligure	44.334625	9.334625	11	Pietro Simoni
30/08/2024	Italy, Liguria, Savona, Capo Noli	44.197700	8.425301	18–22	Giacomo Marchione, Daniel Drago
11/09/2024	Italy, Liguria, Genova, Portofino, Bigo	44.299862	9.217888	11–15	Lorenzo Merotto
22/09/2024	Italy, Liguria, Genova, Paraggi	44.309924	9.211661	6–8	Daniel Drago
13/10/2024	Italy, Liguria, Savona, Bergeggi MPA	44.234450	8.444980	18	Daniel Drago
		ITALY, IONIAN SEA			
25/10/2024	Italy, Apulia, Lecce, Secche di Ponente	40.056917	17.876250	22	Elisa Manganelli
01/11/2024	Italy, Apulia, Lecce, Otranto, Porto Badisco	40.078461	18.484979	24	Romualdo Rizzo
09/11/2024	Italy, Apulia, Lecce, Santa Maria al Bagno	40.125270	17.995886	6	Romualdo Rizzo
09/11/2024	Italy, Apulia, Lecce, S. Maria di Leuca, Punta Meliso	39.793193	18.366919	15–20	Cataldo Licchelli
		CROATIA, ADRIATIC SEA			
14/12/2024	Croatia, Rijeka	45.339841	14.371782	10–12	Chiara Scrigner
		FRANCE, LIGURIAN SEA			
06/12/2024	France, Villefranche-sur-Mer	43.68940	7.30885	20–26	Pascal Girard
		SPAIN, BALEARIC SEA			
03/10/2024	Spain, Catalonia, Girona, Tossa de Mar, Mar Menuda	41.721213	2.940601	20	Oriol Basanta
27/11/2024	Spain, Catalonia, Barcellona, Matarò	41.308470	2.855000	23	Roger Punsola

depth of ~ 20 m (Figure 2A, B), and again on 17 November 2024 at a depth of 30 m on a mixed substrate; 2) at Bergeggi Marine Protected Area (MPA) several individuals was observed on 13 October 2024 on a rocky substrate at a depth of ~ 18 m on both the eastern and western sides of the island; 3) at Portofino MPA several individuals was observed on 11 September 2024 (Figure 2C), and again on 24 October 2024 (see below: "Population structure at Portofino MPA" section); 4) at Paraggi dozens of individuals were observed on 22 September 2024 on a rocky substrate mixed with sand at a depth of ~ 6–8 m, singly or paired and mating in a "head-to-tail" position (Figure 2D, E) (Rizgalla et al. 2018), and again on 29 October 2024 on a detritic substrate at a depth of 30 m; 5) at Santa Margherita several individuals were found on 10 August 2024 at a depth of 11 m (Figure 2F).

In the Apulian region, in southern Italy, *L. ovalis* was found in four localities from both side of the Salento peninsula in a depth range of 6–24 m (Figure 3, Table 1). As for the Ligurian population, also in these cases the firsts sightings were followed by further discoveries of larger numbers of individuals, highlighting the immediate expansion of these populations in the same area. Interestingly, from the dive sites "Secche di ponente" (in the open sea near Gallipoli – Apulian peninsula, Italy) and "Punta Meliso" (in the coastal sea in front of S. Maria di Leuca – Apulian peninsula, Italy), the individuals were observed and photographed during trailing and mating (Figure 3A, F) and a *L. ovalis* typical egg mass was documented from the latter site (Figure 3B).

The Croatian discover of *L. ovalis* occurred in Rijeka at 15 °C seawater temperature, at depths of 10–12 m, and ~ 20 individuals were observed crawling on a sunken summit covered by algae and epiphytic organisms (Figure 4A, B and Table 1).

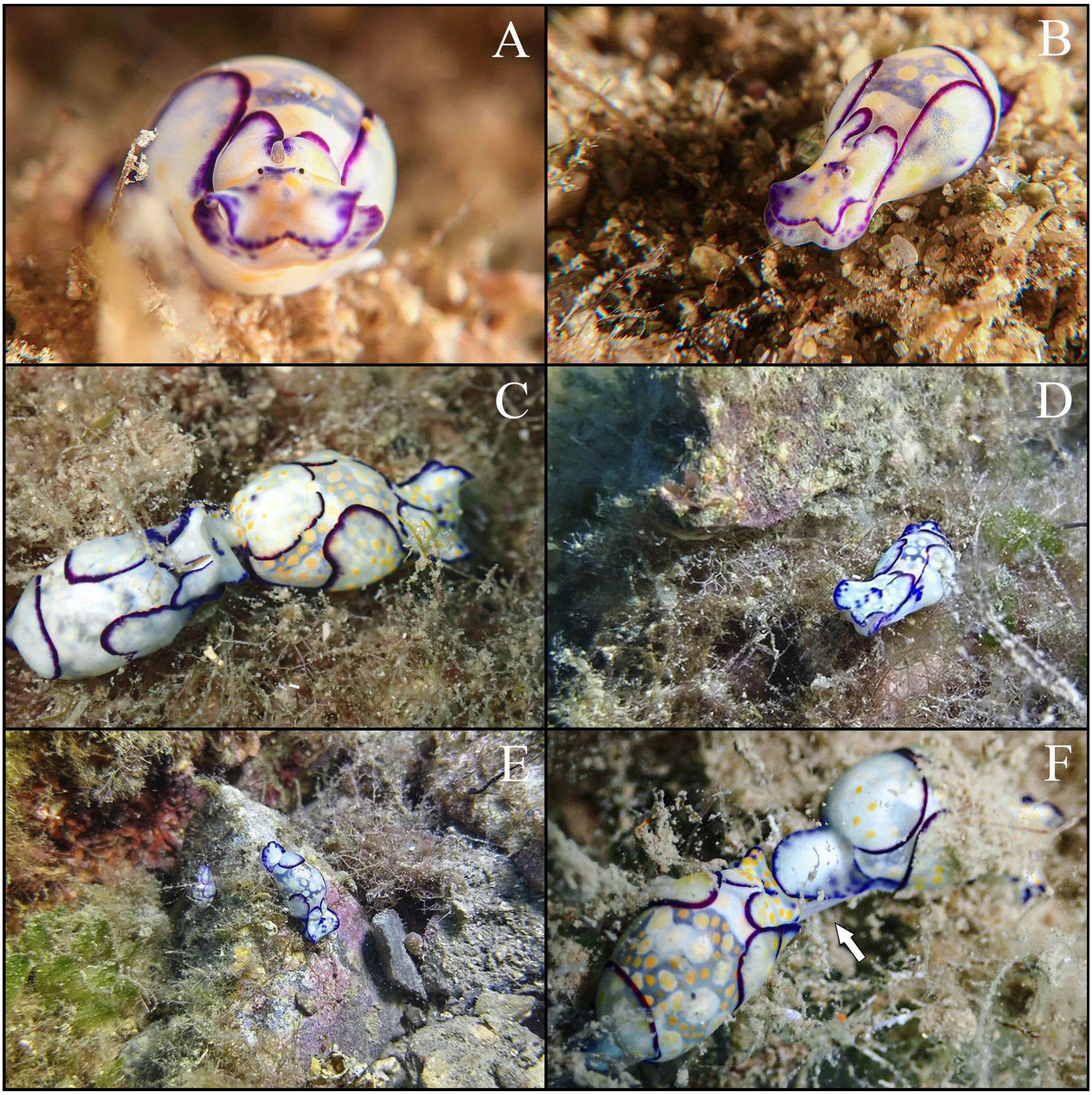

Figure 2. Individuals of *Lamprohaminoea ovalis* observed in 2024 on the Ligurian coast (Italy) in the Ligurian Sea at: (A, B) Capo Noli (Savona); (C) Portofino MPA (Genova); (D, E) Paraggi (Genova); (F) Santa Margherita (Genova). The typical trailing behaviour is visible in (C) where two individuals are aggregated in the typical 'trailing' chain, while mating between two individuals is shown in (F) where the extroverted reproductive organs are clearly visible and highlighted with a white arrow. Photo credits: Giacomo Marchione (A, B); Lorenzo Merotto (C); Daniel Drago (D, E); e Pietro Simoni (F).

Along the Mediterranean coasts of France in the Ligurian Sea, individuals of *L. ovalis* were observed at 16 °C between 20–26 m depth in Villefranche-sur-Mer, in Nizza, very close to the Italian border (Figure 4C, D and Table 1).

In Spain, this species had been previously reported from the coast of Granada (Orenes-Salazar et al. 2024), in Tossa de Mar, in Girona (Figure 4E and Table 1) and in Matarò, in Barcellona (Figure 4F and Table 1). The *L. ovalis* record from Tossa de Mar, in Girona is the easternmost Spanish record of this species. After the first discovery from this latter locality on 3 October 2024 (seawater temperature 21 °C), dozens of individuals (> 60) were

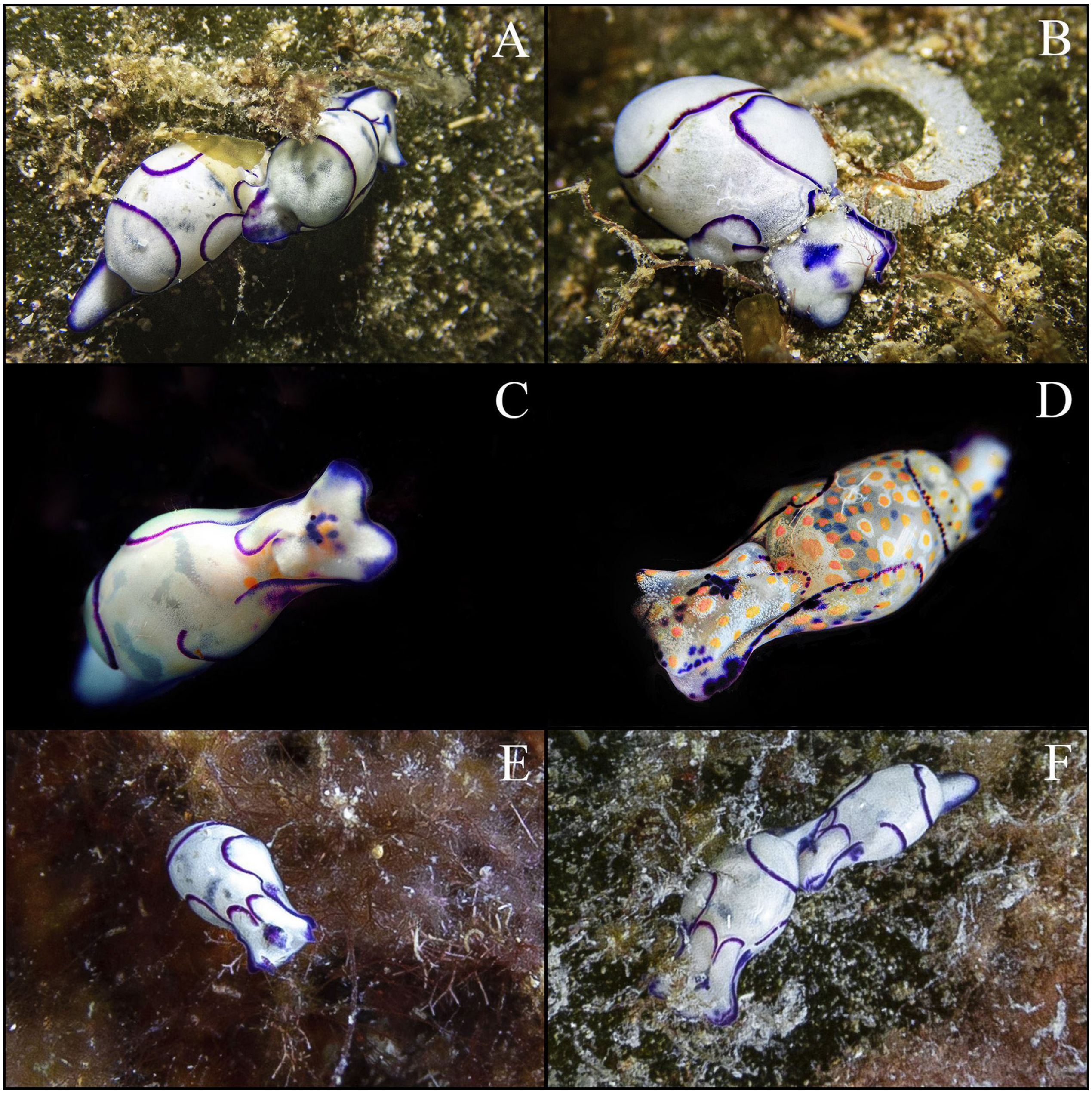

Figure 3. Individuals of *Lamprohaminoea ovalis* observed in 2024 on the Apulian coast (Italy) in the Ionian Sea at: (A, B) Secche di Ponente (Lecce); (C) Porto Badisco (Otranto); (D) Santa Maria al Bagno (Lecce); (E, F) Punta Meliso, S. Maria di Leuca (Lecce). The characteristic mating (A) and trailing behaviour (F) and the peculiar egg mass of *L. ovalis* (B) are shown. Photo credit: Elisa Manganelli (A, B); Romualdo Rizzo (C, D); Cataldo Licchelli (E, F).

observed approximately one month later (on 12 November 2024) from the same area (OB *personal observation*, Table 1) and on 27 November 2024 from Matarò, in Barcellona at about 23 m depth (Figure 4F and Table 1). According to Azzola et al. (2022) *L. ovalis* continued to expand rapidly since the last northernmost record in 2021. The mean distance travelled by *L. ovalis* every three years since 2001 increased significantly (r = 0.9554; Figure 5). In the first three years since its entry into the Mediterranean, *L. ovalis* had travelled a mean distance of 507 (± 201 SE) km, between 2013 and 2015 it travelled a mean distance of 853 (± 49 SE) km, and in the last three years from 2022 it travelled a mean distance of 1663 (± 227 SE) km (Figure 5).

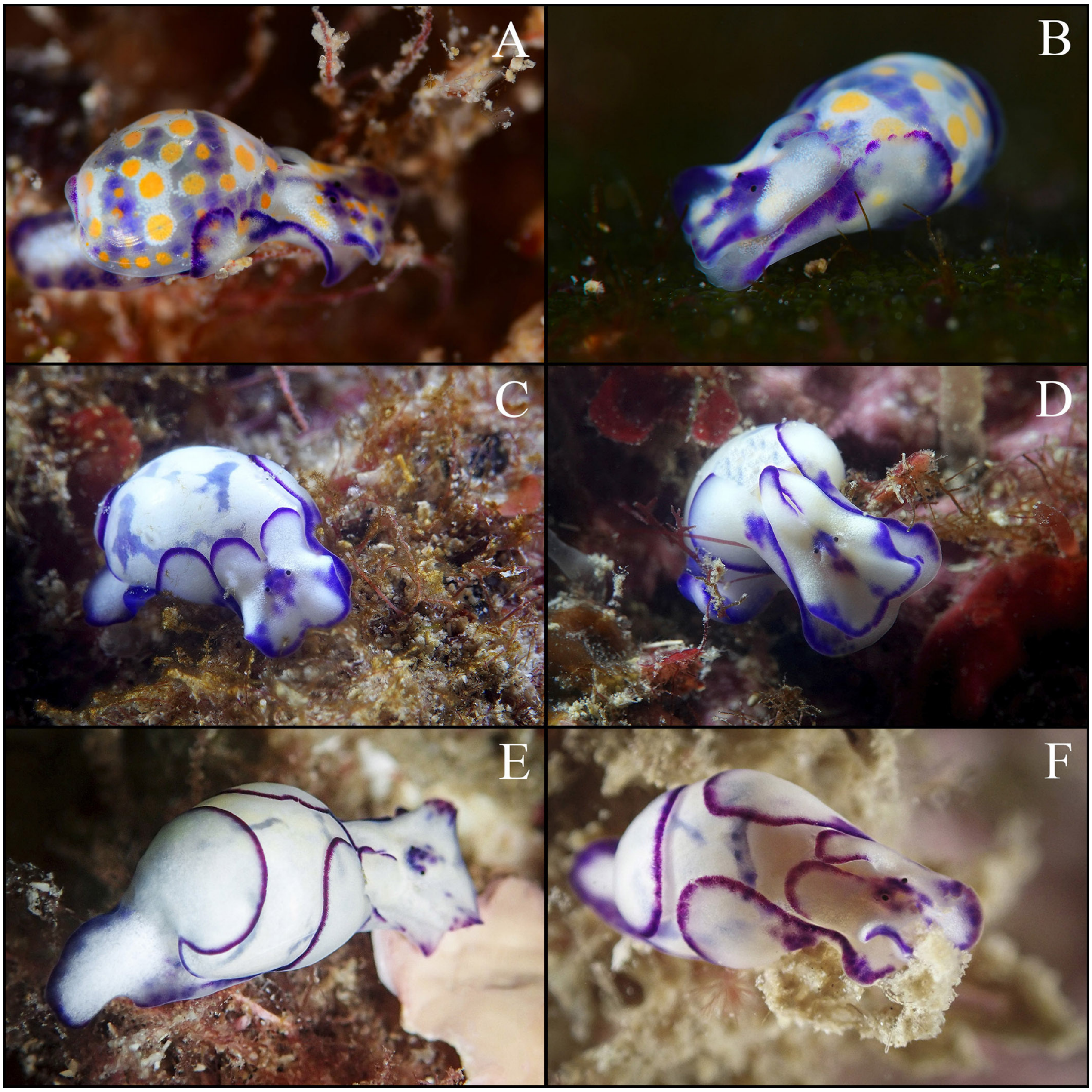

Figure 4. Individuals of *Lamprohaminoea ovalis* observed in 2024 from Croatia (Adriatic Sea), France, and Spain at: (A, B) Rijeka (Croatia); (C, D) Villefranche-sur-Mer (France); (E, F) at Tossa de Mar, Girona and Matarò, Barcellona (Spain) in the Balearic Sea, along the Catalonia coast (Spain). Photo credit: Chiara Scrigner (A, B); Pascal Girard (C, D); Oriol Basanta (E); Roger Punsola (F).

Population structure at Portofino MPA

In the Portofino MPA *L. ovalis* was found at Bigo site for the first time on 11 September 2024 and re-observed on 24 October 2024. In September, a total of 13 individuals were found at a depth of 11 m on a rocky substrate dominated by photophilic algae and divided into two groups 50 m apart. The first group consisted of 6 individuals, divided into 3 trail pairs. The second group consisted of 7 individuals. In October ~ 20 individuals were found at a depth of 15 m in an area of approximately 3–4 m^2 on the same rocky substrates. Image analysis allowed to measure 9 individuals for both periods (September and October). In September, the average size (*i.e.*,

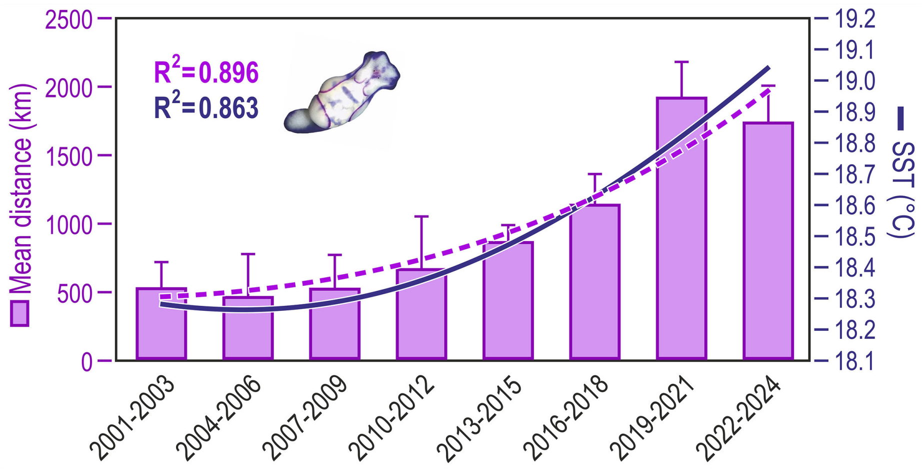

Figure 5. Three-year mean expansion rate of *Lamprohaminoea ovalis* in the Mediterranean Sea since its first recorded occurrence in 2001, shown alongside the corresponding trend line (dashed purple line with R^2 value). Sea Surface Temperature (SST) increase over the same period is also displayed (blue line with R^2 value).

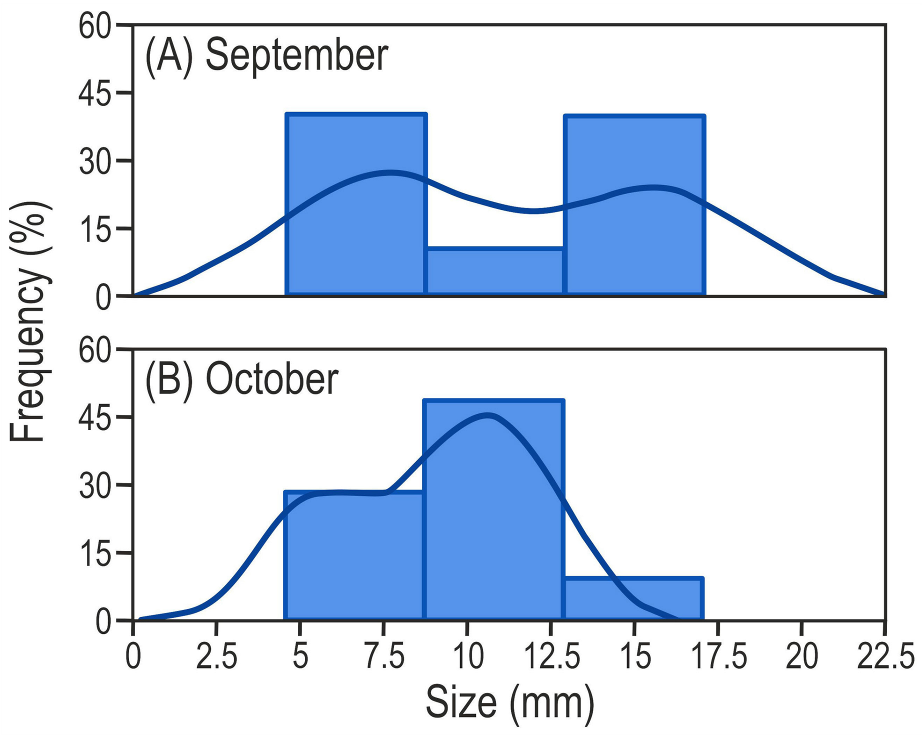

Figure 6. Population structure of *Lamprohaminoea ovalis* at Bigo site (Portofino MPA, Genova, Italy): frequency of size with kernel density estimation identifying a bi-modal trend for population on 11 September 2024 (A) and a unimodal trend on 24 October 2024 (B).

longitudinal length) was 11 (± 1.5 SE) mm with the smallest individual measured 5.6 mm and the largest 17 mm. In October, the average size was 9 (± 1.0 SE) mm, with a minimum length of 4.5 mm and a maximum of 12.9 mm. Kernel density estimation applied on the size of the individuals identified a bi-modal trend for the population observed on 11 September 2024 and a unimodal trend for that of 24 October 2024 (Figure 6).

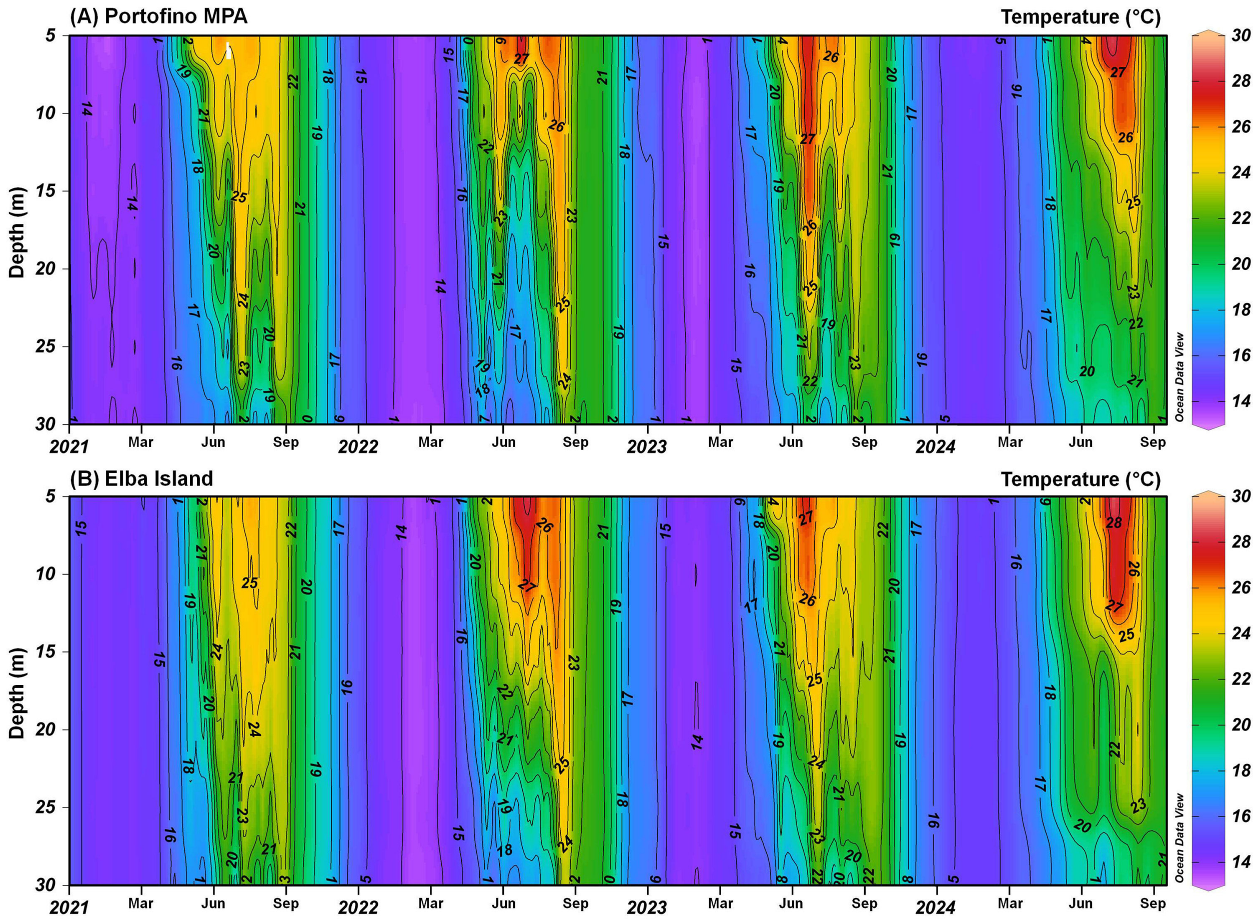

Figure 7. Temperature trend of the water column up to 30 m depth at Portofino MPA (A) and Elba Island (B) since the year 2021 (year of the first record of *L. ovalis* in the Ligurian Sea). The data were collected using temperature data loggers placed on the rocky substrates at depths of 5, 10, 15, 20, 25 and 30 m and plotted using Ocean Data View software.

Water column temperature data

The analysis of data collected with temperature data loggers from 2021 to 2024 at Elba Island and in Portofino MPA showed very similar mean annual and monthly temperature values (Figure 7, Supplementary material Tables S1, S2, S3). In particular, in 2021, the year of the first record of *L. ovalis* at Elba Island, the mean annual temperature in this area was 18.4 (± 3.5) °C, while in Portofino MPA it was 18.0 (± 3.7) °C; indeed in the year 2024 the mean annual temperature at Elba Island was 19.0 (± 3.8) °C, while in Portofino MPA it was 18.6 (± 6.6) °C (Table S1). However, considering the monthly minimum temperatures at the 6 depths considered, it can be observed that in 2021 the mean temperature in February (the month in which the lowest temperatures were recorded) at Elba Island was 14.4 (± 0.01) °C (Table S2), while in the Portofino MPA it was 13.9 (± 0.2) °C (Table S2). Similarly, in February 2022 and 2023, in Portofino MPA, the mean temperature was 14.0 (± 0.0) °C and 14.0 (± 0.1) °C, respectively (Table S3). In contrast, in February 2024 (first record of *L. ovalis* in the Portofino MPA), a monthly mean of 14.5 (± 0.1) °C was recorded (Table S3).

Discussion

Since its first record on the coast of Greece in 2001 (Zenetos et al. 2003), the non-indigenous species *Lamprohaminoea ovalis* has rapidly expanded in the Mediterranean Sea in approximately 20 years (Azzola et al. 2022). The recent records from the Spanish coast (Orenes-Salazar et al. 2024) demonstrate that this species is now widespread from east to west across nearly the entire Mediterranean Sea and has now established in almost all areas of this basin. The high number of individuals observed and reported here for the first time from different localities throughout the Adriatic and Ligurian Seas confirms the spreading of this Lessepsian species in the coldest sectors of the Mediterranean Sea. Moreover, the finding of individuals during mating activities and of the egg mass suggests that this species has well-established populations; this hypothesis is also supported by the results from the population dynamic study conducted at Portofino MPA which demonstrated the presence of different size classes (Figure 6). This evidence highlights the capacity of *L. ovalis* to adapt to different environmental conditions and to quickly invade new geographic areas.

The recent finding from northern Adriatic Sea is particularly important since this area is considered the coldest of the Mediterranean Sea and the only one where *L. ovalis* had not arrived yet. The record from Rijeka is the northernmost of the whole Mediterranean Sea and one of the very few records reported from Croatia. Additionally, the recent finding of a well-established population from Porto Badisco, in Otranto, right on the border of the southern Adriatic Sea, demonstrate this species has invaded all the Adriatic Sea from the southern area until the northernmost regions. The appearing in the late summer and following spreading of this species during the autumn season is in line with what previously reported from other southern Italian localities (Lombardo and Marletta 2021) even if a broader comparison with the seasonality showed by other populations from original geographic areas should be done to confirm the adaptation abilities of *L. ovalis* to different environmental conditions. The range expansion of *L. ovalis* in Villefranche-sur-Mer (France) and in Matarò and Tossa de Mar (Spain), geographic areas located in the same isotherm of the Ligurian and the North Adriatic seas (Azzola et al. 2022), is following the same expansion trend shown by the Ligurian population, supporting what has been said so far and confirming the connection between the range expansion of this sea slug and the seawater warming. According to this, the water column temperature data analysed in the present study showed that *L. ovalis* was able to reach the Ligurian Sea thanks to an increase not only in the mean annual temperature, but also, and primarily, thanks to that of the minimum temperatures (Figure 7). It can be assumed that the optimal mean annual temperature for the establishment of *L. ovalis* is around 18.5 °C in areas with minimum temperatures higher than 14 °C. Thus, even though other environmental factors (such as the current circulation patterns) could play a key role in the expansion of this species throughout the basin, our study confirms that temperature is one of the main drivers for the spread of this species in the Mediterranean Sea. However, further studies exploring the larval development of this species and its ability to disperse as planktonic veliger larvae by following currents could help to better outline the spreading potential of this NIS.

The *L. ovalis* ability to feed on a variety of common algae and diatoms (Crocetta and Vazzana 2009), coupled with its highly specialised chemical defensive strategy also maximised by the aposematic colouration (Mollo et al. 2008), and with the high reproductive potential being a hermaphrodite species (characterised by whitish and difficult-to-see egg mass) (Crocetta and Vazzana 2009) suggests *L. ovalis* as a successful invader for the Mediterranean Sea. To date, no negative effects of *L. ovalis* on native Mediterranean species have been reported in the literature. Its feeding habits seem to involve Mediterranean algae species with no related NI food webs (*i.e.*, food webs that involve only NI species) reported, contrary to what happened for other NI Heterobranchia recently recorded in the Mediterranean Sea (Vitale et al. 2016; Furfaro et al. 2018, 2025; Mioni and Furfaro 2022; Trainito et al. 2022). However, the speed with which it has spread warrants attention to its invasive potential, and further monitoring on a wider temporal scale will be necessary to assess its possible negative effects on Mediterranean biodiversity.

NIS usually follow four successive phases in the process of introduction to a new area: (i) the arrival, (ii) the establishment phase, until success (or fail), (iii) the expansion phase, and (iv) the persistence phase (Boudouresque 1999; Boudouresque and Verlaque 2012). It can be said that *L. ovalis* is now in the phase of expansion in some new areas of the Mediterranean Sea and in the phase of persistence in others. In these two phases the abundance of NIS fluctuates strongly, due to the new environmental conditions that they must face and due to inter-specific relationships with other species. As other NIS, *L. ovalis* could follow one of the two models of invasion kinetics: the "natural fluctuation model", characterised by a plateau-like persistence phase, or the "boom and bust model", according to which during the expansion phase (or at is end) the abundance of the introduced species naturally collapses to a very low and almost stable level (Boudouresque and Verlaque 2012). Future quantitative monitoring of *L. ovalis* will be then necessary to evaluate the future trend of its populations in the Mediterranean Sea.

Analysing the spread of non-indigenous species may be useful for understanding the negative effects of global warming that is affecting the marine biodiversity worldwide (Katsanevakis et al. 2020). In this framework, the present study represents the first example of an Heterobranchia mollusc as a powerful bioindicator of marine environmental changes.

Authors' contribution

Conceptualization A.A., G.F.; data curation A.A., E.T., F.E., G.F., L.M., M.M., M.S.; formal analysis A.A., F.E.; funding acquisition G.F., L.M., M.M., investigation A.A., E.T., F.E., G.F., L.M., M.S.; methodology A.A., F.E., G.F.; project administration G.F.; resources A.A., E.T., F.E., G.F., L.M., M.M., M.S.; software A.A., E.T., M.S.; supervision G.F.; validation A.A., E.T., F.E., G.F., L.M., M.M., M.S.; visualization A.A., E.T., F.E., G.F., M.S.; writing – original draft A.A., G.F., L.M.; writing – review and editing A.A., E.T., F.E., G.F., L.M., M.M., M.S.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Annual mean and minimum temperatures at Elba Island and the Portofino MPA.

Table S2. Monthly mean temperatures at Elba Island.

Table S3. Details monthly mean temperatures at the Portofino MPA.

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