Journal of the Marine Biological Association of the United Kingdom

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Seawater warming favours the northward range expansion of Lessepsian species in the Mediterranean Sea: the cephalaspidean *Lamprohaminoea ovalis*

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Abstract

Monitoring the spread of non-indigenous species is fundamental to study global warming effects on marine biodiversity. A valuable tool is represented by the continuous updating of the geographic range expansion of non-indigenous species. *Lamprohaminoea ovalis* is a Lessepsian mollusc initially recorded in the Mediterranean Sea in 2001. This paper reports its range expansion over the last 20 years related to water warming. The first record of *Lamprohaminoea ovalis* from the Ligurian Sea (NW Mediterranean) is also reported. Two individuals (about 10 mm length) were observed on a sub-vertical rocky bottom at 26 m depth displaying potential trailing behaviour. This recent finding extends the currently known distributional range of *Lamprohaminoea ovalis*, representing the northernmost occurrence of this non-indigenous species in the western Mediterranean Sea.

Marine Record

Cite this article: Azzola A, Furfaro G, Trainito E, Doneddu M, Montefalcone M (2022). Seawater warming favours the northward range expansion of Lessepsian species in the Mediterranean Sea: the cephalaspidean *Lamprohaminoea ovalis*. *Journal of the Marine Biological Association of the United Kingdom* **102**, 167–173. https://doi.org/10.1017/S0025315422000339

Received: 20 December 2021
Revised: 1 May 2022
Accepted: 10 May 2022
First published online: 28 July 2022

Key words:
Climate change; *Heterobranchia*; Ligurian Sea; non-indigenous species; species range expansion

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As a result of global warming, the spread of non-indigenous species is one of the major drivers of change in marine ecosystems, with drastic consequences on their biodiversity (Bonanno & Orlando-Bonaca, 2019). Considering the number of non-indigenous species and the rate of introduction, the Mediterranean is one of the most affected seas by biological invasions (Zenetos *et al.*, 2010). Spatio-temporal information on non-indigenous species and monitoring their geographic range expansion represent valuable tools for conservation of marine ecosystems and biodiversity (Katsanevakis *et al.*, 2020).

Following a taxonomic revision of the Order Cephalaspidea, *Haminoea cyanomarginata* Heller & Thompson, 1983 was described from individuals of the Red Sea (Heller & Thompson, 1983; Dekker & Orlin, 2000) and initially considered junior synonym of *Lamprohaminoea cyanomarginata* (Oskars & Malaquias, 2019). Further taxonomic studies demonstrated that both *H. cyanomarginata* and *L. cyanomarginata* are junior synonyms of *Lamprohaminoea ovalis* (Pease, 1868; Oskars & Malaquias, 2020). This heterobranch, characterized by highly variable body colour pattern, was first described from Tahiti (French Polynesia, France). Nowadays it is widespread from the Red Sea to the Indo-West Pacific. Its fairly recent records from Greece, Turkey, Malta, Italy, Cyprus, Croatia and Spain, more than 20 years after its first finding in the Red Sea, suggest that it is an invasive Lessepsian species that entered and established in the Mediterranean Sea via the Suez Canal (Rizgalla *et al.*, 2018; Oskars & Malaquias, 2020). Nowadays, *L. ovalis* has been reported from the whole Mediterranean basin (Mifsud, 2007; Crocetta & Vazzana, 2009; Zenetos *et al.*, 2010; Fernández-Vilert *et al.*, 2018 and reference therein; Ragkousis *et al.*, 2020), except from the Gulf of Lion and the Ligurian Sea.

With the aim of investigating *L. ovalis* range expansion in the Mediterranean Sea in the last 20 years, all available records have been collected. The expansion rate of *L. ovalis* has been evaluated by measuring the geographic distances (kilometres) between the location of its first record in 2001 and the locations of the following new records from other Mediterranean areas. The expansion rate of the species has been compared with change in time of the sea surface temperature (SST), to evaluate if the spread of this non-indigenous species is a direct consequence of seawater warming. The first record of *L. ovalis* from the Ligurian Sea (NW Mediterranean) has also been reported.

The first occurrence of *L. ovalis* in the Mediterranean Sea was reported at Porto Germano (Greece) in 2001 (Zenetos *et al.*, 2003) (Figure 1A, Table 1). In the following years this species remained confined to the eastern basin of the Mediterranean, where Lessepsian species more typically settle (Gambi *et al.*, 2009). Since the second half of the 2010s the species crossed the 20° meridian East, reaching the westernmost portions of the Mediterranean, and since 2014 it

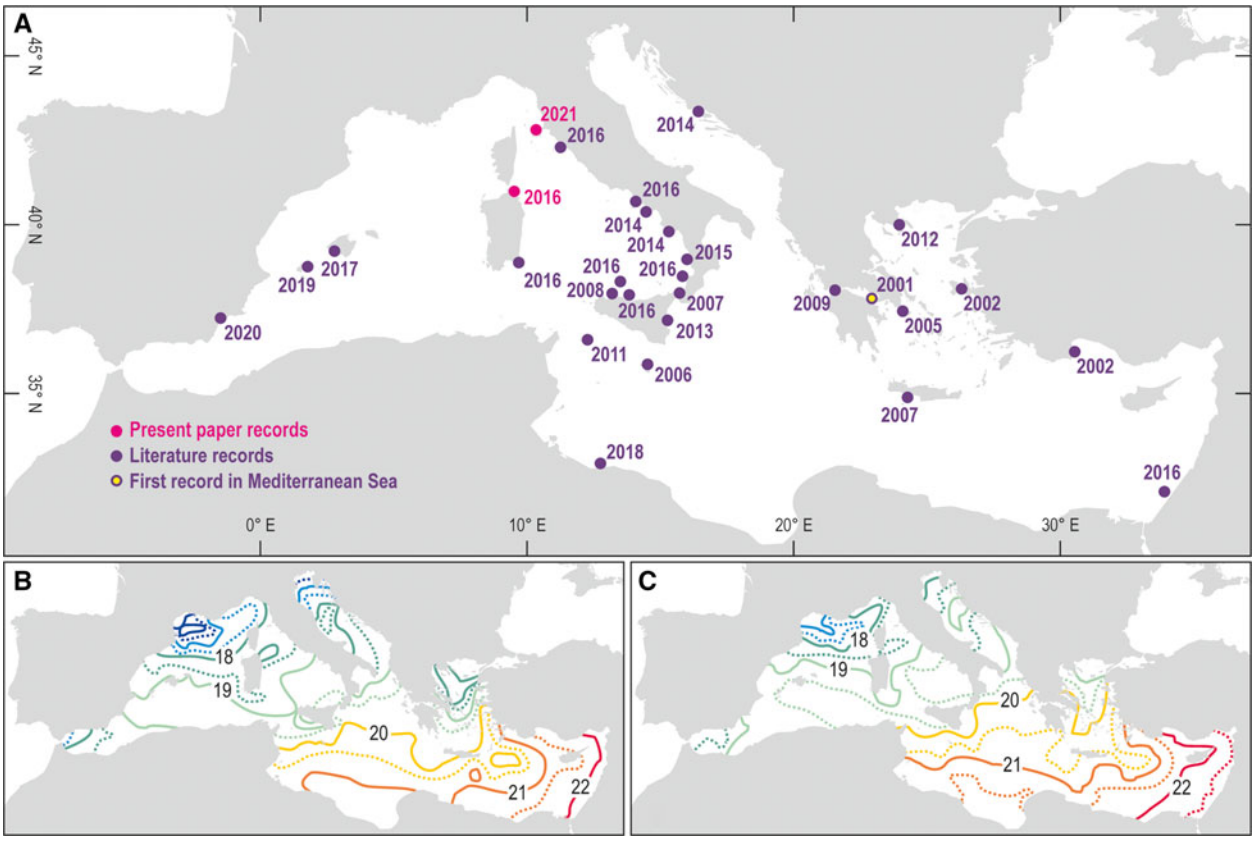

Fig. 1. Map of the available records of *Lamprohaminoea ovalis* in the Mediterranean Sea (a). Yearly mean SST from 1994 to 2005 (b) and from 2006 to 2018 (c) (modified from Pisano *et al.*, 2020).

crossed the 40° parallel North, starting to approach the northernmost and coldest sectors of the basin (Figure 1A, Table 1). During the last 20 years the yearly mean SST continuously increased, and the isotherms shifted northwards (Pisano *et al.*, 2020) (Figure 1B, C), favouring the north-western expansion of *L. ovalis* (Bianchi, 2007).

Since 2016 the geographic range of *L. ovalis* expanded northward in the Tyrrhenian Sea (NW Mediterranean) and an individual has been recorded in 2016 at Porto Ercole, Tuscany (Figure 1A, Table 1). In the same year the species has been observed multiple times by the authors in the Tavolara-Punta Coda Cavallo Marine Protected Area (MPA), which represents its first record in North Sardinia (Tyrrhenian Sea) (Figure 1A, Table 1). Four individuals have been observed at Reulino (Isola Rossa) at 13 m depth in a mixed habitat with rocks, detritus and algae (Figure 2A). In the following years two other individuals have been observed in the MPA, one at 30 m depth on a coralligenous outcrop at Punta Papa (Tavolara Island), and one at Porto San Paolo at 3 m depth (Figure 2B). In the subsequent years *L. ovalis* became common in the MPA along the southeastern coast of Tavolara Island.

On 21 October 2021, during a scientific expedition conducted by the University of Genova in collaboration with Greenpeace to monitor non-indigenous species, two *L. ovalis* individuals of about 10 mm in length were observed and photographed at Portoferraio, Elba Island (Ligurian Sea) (Figures 1A & 2C, D, Table 1). The individuals were found at 26 m depth on a subvertical rocky bottom, covered by photophilic algae and *Posidonia oceanica*. They were observed in potential trailing behaviour. In Heterobranchia trailing action is aimed at reproduction: an individual follows the mucous trail of a conspecific and keeps contact with it by touching the tail. In this way, rows of up to four individuals can be formed (Betti *et al.*, 2011; Rizgalla *et al.*, 2018). The unambiguous determination of the species from the photographs taken in Sardinia and at Elba Island has been possible thanks to the distinctive unornamented bubble shell and body colour pattern. The mantle bordered with purple perfectly matches the '*L. cyanomarginata* purple morph' (Figure 3) reported in the recent systematic revision of the genus *Lamprohaminoea* Habe, 1952 and ascribed to *L. ovalis* species (Oskars & Malaquias, 2020).

The expansion rate of *L. ovalis* showed a significant increasing trend since 2001 (Figure 4A), and two distinct phases can be identified: (i) 2001–2013, when the species spread slowly westward; and (ii) 2014–2021, when its spread was faster and northward (Figures 1A & 4A). The mean distance 'travelled' by *L. ovalis* in the second period (2014–2021) was significantly higher than in the first one (Figure 4A). This species increased its range expansion in correspondence of a warming phase of the SST started in 2014 (Bianchi *et al.*, 2019). As it is known that high summer temperatures favour the spread of alien species and mild winter temperatures allow for their establishment (Osland *et al.*, 2021), both minimum and maximum mean SST in the two considered periods showed the same significant increase as *L. ovalis* expansion rate (Figure 4C, D). Although this close analogy does not represent a correlation, it is suggestive that the new thermal regime is making the Mediterranean Sea increasingly receptive to species of tropical origin.

The expansion of non-indigenous species is a growing and recurrent phenomenon, so that the Mediterranean Sea is going towards a phase of tropicalization (Bianchi & Morri, 2003). In the Ligurian Sea, one of the northernmost portions of the Mediterranean Sea, reports of thermophilic southern species are becoming frequent (Parravicini *et al.*, 2015; Bianchi *et al.*, 2018). The continuous observations of *L. ovalis* in the Mediterranean, particularly after the year 2014, demonstrate

https://doi.org/10.1017/S0025315422000339 Published online by Cambridge University Press

Table 1. List of records of *Lamprohaminoea ovalis* in the Mediterranean Sea (see also Figure 1)

First record	Locality	Lat. (N)	Long. (E)	Reference	Author of the record
2001	Porto Germano, Greece	38.155064	23.222459	Zenetos *et al.* (2003; CIESM)	Ernesto Mollo
2002	Üç Adalar, Antalya, Turkey	36.459593	30.549790	Sea Slug Forum – http://www.seaslugforum.net	Adnan Buyuk
2002	Çeşme, Izmir, Turkey	38.326670	26.294391	Sea Slug Forum – http://www.seaslugforum.net	Namzi Kural
2003	Üç Adalar, Antalya, Turkey	36.459593	30.549790	Sea Slug Forum – http://www.seaslugforum.net	Baki Yokes
2004	Üç Adalar, Antalya, Turkey	36.459593	30.549790	Sea Slug Forum – http://www.seaslugforum.net	
2005	Çeşme, Izmir, Turkey	38.326670	26.294391	Sea Slug Forum – http://www.seaslugforum.net	Aziz Saltik
2005	Saronikos Kolpos, Greece	37.768312	23.895814	Sea Slug Forum – http://www.seaslugforum.net	Panaiotis Ovalis
2006	Rdum id-Delli, Malta	35.951865	14.338688	Mifsud (2007)	
2006	Fomm ir-Rih Bay, Malta	35.907289	14.339596	Mifsud (2007)	
2006	Ġnejna Bay, Malta	35.920942	14.342461	Mifsud (2007)	
2007	Cirkewwa, Malta	35.983213	14.332776	Sea Slug Forum – http://www.seaslugforum.net	Patricia Peels
2007	Schinaria, Plakias, Creta, Greece	35.166232	24.421272	Sea Slug Forum – http://www.seaslugforum.net	Jim Anderson
2007	Saline Joniche, Italy	37.937922	15.707796	Crocetta and Vazzana (2009)	
2008	Castellammare del Golfo, Italy	38.036258	12.876490	Stasolla *et al.* (2014)	Santo Tirnetta and Anna Macaluso
2009	Lazzaro, Italy	37.971763	15.662174	Crocetta *et al.* (2009)	
2009	Salamis, Attiki, Greece	37.934791	23.466596	NMR_Mollusca – http://www.marinespecies.org	Joop Trausel and Frans Slieker
2009	Golfo di Patrasso, Greece	38.317006	21.642224	Medslugs – http://www.medslugs.de	George Tryfonopoulos
2011	Scauri, Pantelleria, Italy	36.765097	11.969795	Stasolla *et al.* (2014)	Maria Ghelia and Francesco De Marchi
2012	Kalogrias Beach, Chalkidiki, Greece	40.177022	23.714886	Social media – Facebook	Nicholas Samaras
2013	Saline Joniche, Italy	37.937922	15.707796	Stasolla *et al.* (2014)	Domenico Tripodi
2013	Acicastello, Italy	37.554525	15.150620	Stasolla *et al.* (2014)	Alessandro Pagano
2013	Scilla, Italy	38.258340	15.715148	Stasolla *et al.* (2014)	Domenico Tripodi
2014	Mgarr, Gozo, Malta	36.027588	14.308428	Medslugs – http://www.medslugs.de	Silke Baron
2014	Baia di Puolo, Massa Lubrense, Italy	40.626660	14.341940	Katsanevakis *et al.* (2014)	Fabio Russo
2014	Acicastello, Italy	37.554525	15.150620	Social media – Facebook	Alessandro Pagano
2014	Casteldaccia, Palermo, Italy	38.057863	13.542987	Social media – Facebook	Dario Messina
2014	Palinuro, Italy	40.029065	15.266873	Tiberti *et al.* (2015)	Fabio Barbieri
2014	Uvala Travna, Šolta, Croatia	43.368852	16.267800	Social media – Facebook	Jakov Prkic
2015	Ammouliani island, Greece	40.313241	23.944508	Social media – Facebook	Yiannis Iliopoulos
2015	Praiano, Italy	38.930623	16.209802	Social media – Facebook	Raffaele Livornese
2016	Porto Ercole, Grotta Azzurra, Italy	42.370636	11.188660	Social media – Facebook	Gabriele Ziino

(*Continued*)

Table 1. (*Continued.*)

First record	Locality	Lat. (N)	Long. (E)	Reference	Author of the record
2016	Lago Faro, Italy	38.269288	15.637137	Vitale *et al.* (2016)	
2016	Munxar, Gozo, Malta	36.021566	14.218147	Social media – Facebook (Nudibranch lovers)	Vera Wittenberg
2016	Agios Minas, Greece	40.587246	22.881911	Underwater Photography in Greece – http://www.greeceme.com	Tasos Drosopoulos
2016	Costa Rei, Muravera, Sardegna, Italy	39.249898	9.579118	Social media – Facebook	Giorgio Zara and Silvia Crippa
2016	Nemesis wreck, Protraras, Cyprus	32.049633	34.0366	Yokes *et al.* (2018)	Fabio Crocetta and Vasilis Andreou
2016	Ammouliani island, Greece	40.313241	23.944508	Underwater Photography in Greece – http://www.greeceme.com	Yiannis Iliopoulos
2016	Greben Štit, southern side, Croatia	42.77166	17.33250	Chartosia *et al.* (2018)	Branko Dragicevic, Marija Despalatovic and Jakov Dulcic
2016	Capo Vaticano, Italy	38.618792	15.825806	Social media – Facebook	Francesco Pacienza
2016	Ustica, Italy	38.705300	13.196120	Social media – Facebook	Jonathan Cecchinel
2016	Ischia Island	40.737956	13.853602	Personal communication	Paolo Mariottini and Giulia Furfaro
2016	Secca della Formica, S. Flavia, Italy	38.083431	13.550167	Social media – Facebook	Giovan Ombrello
2016	Isola Reulino, AMP Tavolara, Italy	40.877310	9.673453	Present paper	Egidio Trainito
2016	Kašuni, Split, Croatia	43.510980	16.400696	Social media – Facebook	Jakov Prkic
2016	Praiano, Italy	38.930623	16.209802	Social media – Facebook	Francesco De Rosa
2017	Reggio Calabria, Italy	38.104215	15.626211	Social media – Facebook	Domenico Tripodi
2017	Porto Ercole, Grotta Azzurra, Italy	42.370636	11.188660	Social media – Facebook	Gabriele Ziino
2017	Argentario Promontory, Italy	42.400000	11.091666	Personal communication	Giulia Furfaro
2017	Capo Figari, Golfo Aranci, Italy	40.991111	9.6577778	Personal communication	Renato Romor
2017	Porto Santo Stefano, Italy	42.444388	11.114297	Social media – Facebook	Flavio Mattucci
2017	Punta Papa, AMP Tavolara, Italy	40.911873	9.743434	Present paper	Egidio Trainito
2017	Porto San Paolo, Italy	40.881635	9.637065	Present paper	Egidio Trainito
2017	Illa del Toro, Mallorca, Spain	39.462182	2.471748	Fernandez-Vilert *et al.* (2018)	Rubén Castrillo
2018	Tripoli, Lybia	32.854028	13.054639	Rizgalla *et al.* (2018)	
2019	Ibiza, Spain	39899546	1.429359	Ragkousis *et al.* (2020)	Miquel Pontes, Fabio Crocetta and Ro Ba
2020	Nova Tabarca Island, Alicante, Spain	38.172250	−0.483639	Ragkousis *et al.* (2020)	Miquel Pontes and Fabio Crocetta
2020	Gozo, Malta			Social media – Facebook (nudibase)	Flow Curlebee
2020	AMP Tavolara, Italy	40.896533	9.707200	Present paper	Egidio Trainito
2021	Porto Ferraio, Elba Island, Italy	42.821707	10.328733	Present paper	Annalisa Azzola and Monica Montefalcone

Fig. 2. Individuals of *Lamprohaminoea ovalis* observed at: (a) Isola Rossa in 2016 (Sardinia, Tyrrhenian Sea), (b) Porto San Paolo in 2017 (Sardinia, Tyrrhenian Sea), (c, d) Elba Island (Tuscany, Ligurian Sea). Photo credit: Egidio Trainito (a, b), Lorenzo Moscia (c), Monica Montefalcone (d).

Fig. 3. An individual of *Lamprohaminoea ovalis* collected at 10 m depth at Cala Grande, Argentario (Tuscany, Tyrrhenian Sea) in October 2017 and photographed in laboratory. Photo credit: Giulia Furfaro.

https://doi.org/10.1017/S0025315422000339 Published online by Cambridge University Press

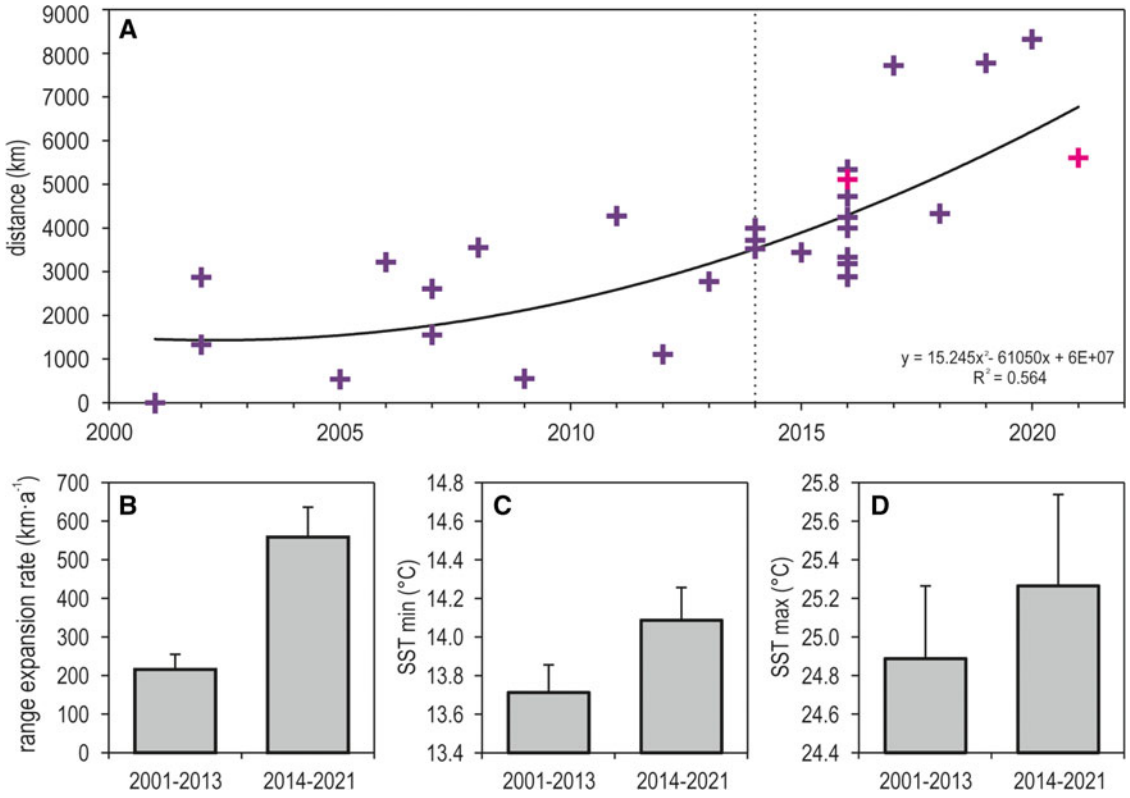

Fig. 4. Expansion rate of *Lamprohaminoea ovalis* in the Mediterranean Sea since its first record in 2001 (a). Mean range expansion rate in the two investigated time periods: 2001–2013 and 2014–2021 (b). SST minimum (c) and maximum (d) yearly mean in the two investigated time periods 2001–2013 and 2014–2021.

that its spread is mainly favoured by seawater warming. In the coldest Mediterranean sectors, where the yearly mean SST is still around 18°C or lower, this species is not yet widespread. Nevertheless, the first observation of *L. ovalis* in the Ligurian Sea reported in this paper represents the northernmost record of occurrence of this non-indigenous species in the Western Mediterranean Sea, providing further important evidence of the ongoing global water warming also in the coldest sectors of the Mediterranean.

Acknowledgements. Authors would like to dedicate this work in the memory of Professor Riccardo Cattaneo-Vietti, for his valuable contribution to marine biology and to the knowledge of the heterobranchs. Annalisa Azzola and Monica Montefalcone are grateful to Professor Carlo Nike Bianchi, a continuous source of inspiration and suggestions. Giulia Furfaro would like to thank the Italian Ministry of Education, University and Research (MIUR, PON 2014-2020, grant AIM 1848751-2, Linea 2) for support. Andrea Romoli and Nicola Rozzi (Il Careno Diving Center) and Marco Sartore (ElbaTech SRL) provided logistic support during field activities at Elba Island.

Financial support. Part of this work has been supported by Greenpeace within the framework of the project 'Mare Caldo' (contract no. 1959.2021) for monitoring global warming effects on marine benthic habitats.

Conflict of interest. The authors declare that they have no competing interests.

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https://doi.org/10.1017/S0025315422000339 Published online by Cambridge University Press