



Evidences of Tropicalization of Infralittoral Communities in the Balearic Islands (Western Mediterranean) [†]

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Abstract

The Mediterranean Sea is a biodiversity and climate change hotspot. The increase in seawater temperature affects marine ecosystems causing marine species to change their distribution and abundance. Such changes lead to alterations in community composition, often characterized by an increase in warm-affinity species over time, known as tropicalization of temperate seas. Monitoring programmes are useful for understanding the consequences of the ongoing transformations driven by ocean warming. In this study, underwater visual censuses (UVC) were conducted for fish and benthic communities at 24 stations of the Balearic Archipelago in 2022 and 2025. The comparison between both periods revealed an increase in the frequency of warm-affinity species, including the fishes *Sparisoma cretense* (Teleostea, Scaridae) and *Caranx crysos* (Teleostea, Carangidae); the invertebrates *Telmatactis cricoides* (Cnidaria, Actiniaria) and *Hermodice carunculata* (Annelida, Polychaeta, Amphinomidae) and the algae *Penicillus capitatus* (Chlorophyta, Ulvophyceae). Our findings highlight the importance of monitoring programmes to identify evidence of processes such as tropicalization and to provide timely information to respond to shifting marine ecosystems.

Keywords: warm-affinity species; ocean warming; monitoring programmes; Balearic Sea

1. Introduction

The Mediterranean Sea, a global hotspot for biodiversity [1,2], is particularly vulnerable to ocean warming, with seawater temperature rising faster than the global ocean [3,4]. This increase has led to the occurrence of marine heatwaves (MHWs); a phenomenon characterized by prolonged and anomalous ocean-warming events that have increased in frequency during the last decades [5,6]. In the near future, a significant rise in MHWs duration and intensity is expected [7]. The redistribution of species is a direct consequence of climate change, which has a critical impact on marine ecosystems [7,8]. The ongoing ocean warming favours the expansion of warm-affinity species (tropicalization) in combination with the regression of cold-water species (deborealization), which notably affects native assemblages and degrades local biodiversity [9,10]. Among the aforementioned processes, tropicalization is highlighted as a relevant driving force in reshaping Mediterranean ecosystems. This process involves the expansion (specifically a northward migration), arrival and



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establishment of tropical and subtropical species whose origin ranges were once confined to Atlantic waters or to the southern parts of the Mediterranean basin [11,12]. Tropicalization, meridionalization and septentrionalization are terms used to describe the same ecological phenomenon and, hereafter, are referred to as “tropicalization”—the globally understood term [13]. It is worth noting that in this context the terms “warm-affinity” and “thermophilic” corresponds to a species that expands its geographical range into previously colder areas as consequence of ocean warming driven by climate change [14]. In many cases, these species already inhabited other regions of the Mediterranean Sea, therefore, it is not implied that they are exotic or alien species.

Even though the Western Mediterranean Sea is characterized by being colder than the Eastern Mediterranean [3], recent severe and long-lasting MHWs seem to primarily affect the Western Mediterranean (hereafter WM) [6,15,16]. Consequently, environmental factors in the WM offer optimal conditions to favour the proliferation of warm-affinity species, which were generally restricted to the Eastern Mediterranean and are recently expanding their native distribution. Hence, many tropicalization processes reported in the WM can be attributed to this migration route [2,3,13,17–23]. Altogether, tropicalization is a prominent threat to the functioning of Mediterranean marine ecosystems, challenging effective management and conservation strategies.

Monitoring programmes are important tools that enable scientists to identify marine species assemblages, to assess their status and to detect spatiotemporal environmental changes or disturbances that might influence benthic communities, such as tropicalization. Therefore, only continued monitoring will help to understand the consequences of the ongoing transformations driven by the increase in seawater temperature [17,24]. The Balearic Sea (WM) surrounding the Balearic Islands was particularly affected by the last MHWs in 2022 and 2023 [25–27]. In this study, we report evidence of tropicalization possibly as a consequence of ocean warming, based on periodic monitoring surveys conducted in several stations in the area as part of the Marine Strategy Framework Directive (MSFD) (2008/56/EC).

2. Materials and Methods

With the aim of evaluating the environmental status of Spanish Mediterranean infralittoral rocky bottoms as part of the MSFD, a group of six scientific divers conducted underwater visual censuses (UVC) at 24 stations located among the five islands of the Balearic Archipelago. Surveys were conducted in late summer 2022 and repeated at the same stations and season in 2025. To ensure that the transects of each station were deployed at the exact same location, GPS coordinates, orientation and depth were recorded. The study was restricted to rocky bottoms between 5 and 18 m depth and to daytime, between 10 am and 4 pm.

The seawater surrounding the Balearic Islands is extremely clear and allows a high amount of light penetration, enabling photophilic algae to inhabit the Balearic Sea at great depths (up to 30 m). Thus, the infralittoral zone of the Balearic Sea has a considerable bathymetric range, reaching depths of 35–43 m [28–31]. In particular, the upper infralittoral rocky bottoms (5–18 m depth) present stable abiotic conditions, resulting in homogeneous benthic assemblages along such depth gradient. In fact, due to these conditions, fish communities also remain stable in this area, and various ichthyological studies conducted in the Balearic Sea have been carried out in similar sampling depths [32–35].

At each sampling station, scuba divers surveyed fish and benthic communities along 50 m transects (four replicates per station). Divers who surveyed the fish community were the first to deploy the transect and start the census, paying attention to minimize their

disturbance to the community. The teams who surveyed benthos followed the transect line. Each survey session lasted between 60 and 80 min.

Fish were identified and their abundance was recorded within a 50 m × 5 m belt transect. Macroinvertebrates were surveyed using 50 cm × 50 cm quadrats placed every two metres along each transect. Within each quadrat, species and abundances were recorded. Finally, macroalgae coverage was measured by recording the species found every 20 cm along each transect. A schematic representation of the sampling design is shown in Figure 1.

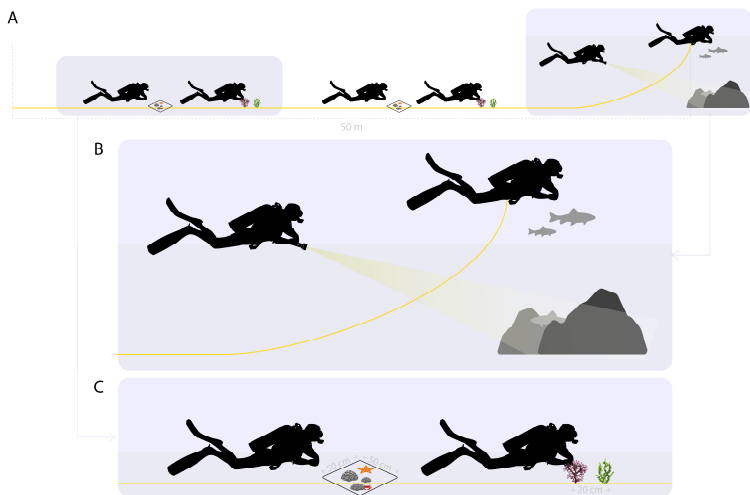


Figure 1. Schematic representation of (A) sampling design, (B) fish survey and (C) benthic survey.

Permutational univariate ANOVAs (PERMANOVAs) were used to test for differences in the abundance of warm-affinity species among years (fixed factor) and stations (random factor) [36], using PRIMER v6 with the PERMANOVA+ add-on. Data were square-root transformed, and a distance matrix was calculated using Euclidean distance.

3. Results

Survey results reflect a remarkable increase in warm-affinity species between sampling periods. While in 2022 we registered three individuals of two warm-affinity species in two sampling locations (8%), in 2025 we detected 120 individuals of five thermophilic species in 16 of the 24 (67%) stations surveyed of the Balearic Archipelago, with sightings across all islands. Data with the number of each species observed, as well as the exact location, is detailed in Table 1 and shown in Figure 2.

Table 1. Records of each warm-affinity species observed in surveys conducted in 2022 and 2025.

Species	N°	Island	2022	N°	Island	2025
			Coordinates			Coordinates
<i>Sparisoma cretense</i>	2	Menorca	39.8768° N 4.3282° E	3	Formentera	38.6637° N 1.5847° E
<i>Sparisoma cretense</i>				1	Ibiza	39.1022° N 1.5906° E
<i>Sparisoma cretense</i>				1	Ibiza	38.9843° N 1.2067° E
<i>Sparisoma cretense</i>				1	Mallorca	39.9354° N 3.0389° E
<i>Sparisoma cretense</i>				5	Mallorca	39.5728° N 2.3032° E
<i>Sparisoma cretense</i>				2	Mallorca	39.7113° N 3.4755° E
<i>Sparisoma cretense</i>				6	Mallorca	39.6335° N 3.4355° E

Table 1. Cont.

Species	N°	Island	2022 Coordinates	N°	Island	2025 Coordinates
<i>Sparisoma cretense</i>				4	Menorca	40.0682° N 4.0305° E
<i>Sparisoma cretense</i>				22	Menorca	39.8768° N 4.3282° E
<i>Sparisoma cretense</i>				16	Menorca	39.7992° N 4.2941° E
<i>Sparisoma cretense</i>				1	Menorca	40.0499° N 3.8358° E
<i>Caranx crysos</i>				18	Ibiza	38.9843° N 1.2067° E
<i>Caranx crysos</i>				1	Mallorca	39.5728° N 2.3032° E
<i>Caranx crysos</i>				4	Mallorca	39.4580° N 2.5234° E
<i>Caranx crysos</i>				22	Mallorca	39.9550° N 3.1954° E
<i>Caranx crysos</i>				1	Mallorca	39.7113° N 3.4755° E
<i>Caranx crysos</i>				2	Mallorca	39.3772° N 2.7733° E
<i>Caranx crysos</i>				1	Menorca	40.0682° N 4.0305° E
<i>Caranx crysos</i>				1	Menorca	40.0639° N 4.1309° E
<i>Telmatactis cricoides</i>	1	Mallorca	39.4580° N 2.5234° E	1	Mallorca	39.3772° N 2.7733° E
<i>Telmatactis cricoides</i>				3	Menorca	40.0639° N 4.1309° E
<i>Hermodice carunculata</i>				1	Cabrera	39.1328° N 2.9239° E
<i>Hermodice carunculata</i>				1	Menorca	39.7992° N 4.2941° E
<i>Penicillus capitatus</i>				2	Mallorca	39.3772° N 2.7733° E

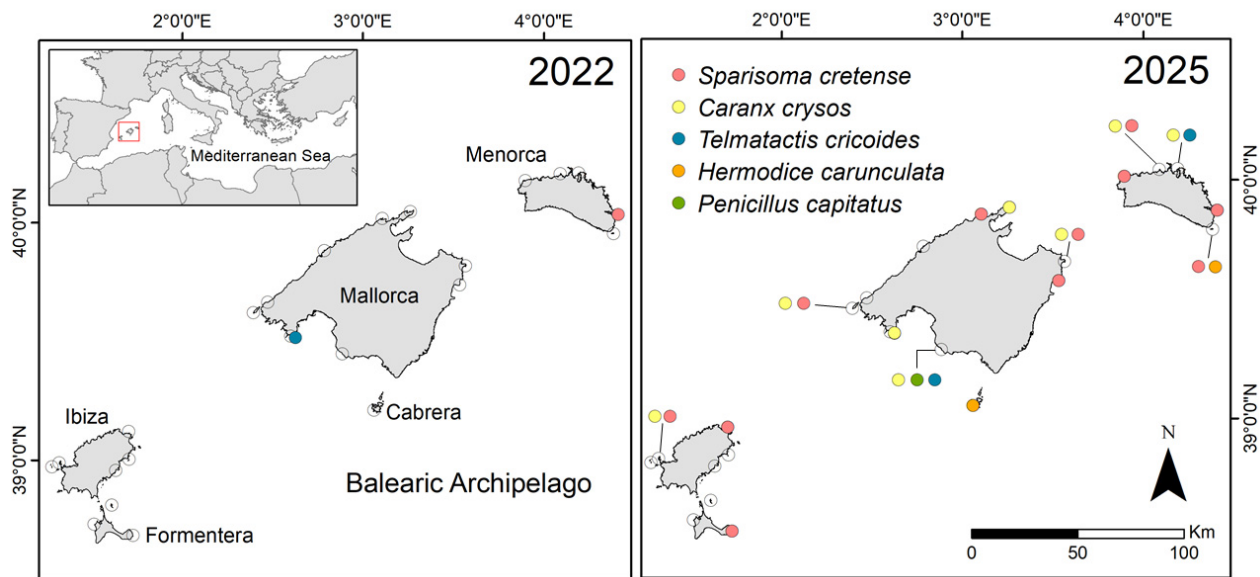


Figure 2. Distribution of sampling stations (empty circles) in Balearic Archipelago (Mediterranean Sea) in 2022 (**left**) and in 2025 (**right**). Colour-filled circles indicate sightings of warm-affinity biota; each colour represents a different species (as indicated in the legend). Colour code on the maps matches the species in the plot (Figure 3).

The total count of each species per year of study is shown in Figure 3. We observed the fish *Sparisoma cretense* and *Caranx crysos* as the species with the greatest increase in abundance when comparing the two survey periods. The invertebrate *Telmatactis cricoides* was also recorded more frequently in 2025 than in 2022, whereas *Hermodice carunculata* and the alga *Penicillus capitatus* were recorded exclusively in 2025. PERMANOVA results revealed significant differences in the abundance of *S. cretense* and *C. crysos* between sampling years (Figure 3).

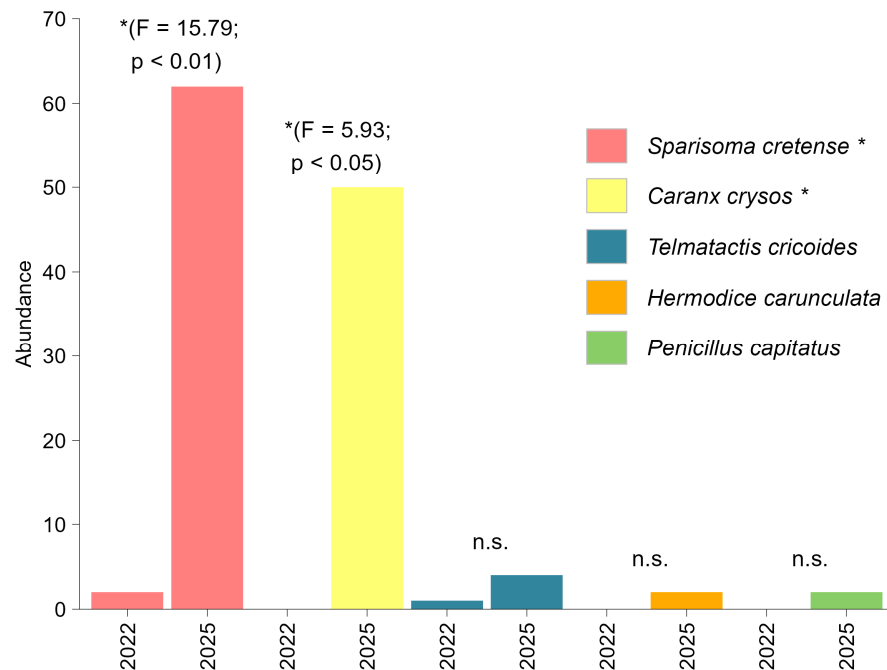


Figure 3. Bar plot showing the abundance of each species each year surveyed. The colour code on the maps (Figure 2) matches the species in the plot. Asterisks (*) indicate significant differences in species abundance between sampling years, whereas n.s. indicates absence of significant differences thereof.

4. Discussion

Monitoring programmes are essential tools to generate new information regarding the tropicalization of the Western Mediterranean Sea (WM) and contribute to the existing literature on the ongoing shifts in the distribution of warm-affinity marine organisms in an era of climate change [37]. In the present work, we compare the records of warm-affinity species in the infralittoral rocky bottoms of Balearic Archipelago, between 2022 and 2025 surveys. Our results show a significant increase in warm-affinity species over time. Of the marine heatwaves (MHWs) occurring in the WM during 2022–2023 the highest recorded temperature values, longest duration and highest number of days with temperature over 28 °C were found in Balearic islands [26,27,38]. One of the reported impacts of MHWs includes the tropicalization of marine communities [39]—an increase in the abundance of tropical and subtropical species in temperate seas [10]. This trend is consistent with the distribution expansion of the following species [40]: *Sparisoma cretense*, *Caranx crysos*, *Telmatactis cricoides*, *Hermodice carunculata* and *Penicillus capitatus* (Figure 4).

4.1. *Sparisoma cretense* (Linnaeus, 1758) (Teleostea, Scaridae)

The only native parrotfish species of the Mediterranean Sea, *Sparisoma cretense*, is associated with seagrass meadow and rocky bottom and is distributed from Southern and Eastern Atlantic, the Macaronesian archipelagos and the Mediterranean Sea from shallow waters up to a depth of 50 m [41]. It feeds on macroalgae and small invertebrates by scraping or excavating the hard substrate with its beak-like jaws [42]. While *S. cretense* was originally more common in the southern and eastern parts of the Mediterranean Sea [43], it has been rapidly expanding its distribution (toward higher latitudes and to the west) across the basin over the last decade, leading to the formation of stable populations [41,44–50]. In the present study, we detected a huge difference between the survey conducted in 2022, when we observed two individuals of *S. cretense* in a single location, and in 2025 with 62 sightings at 11 sampling stations.

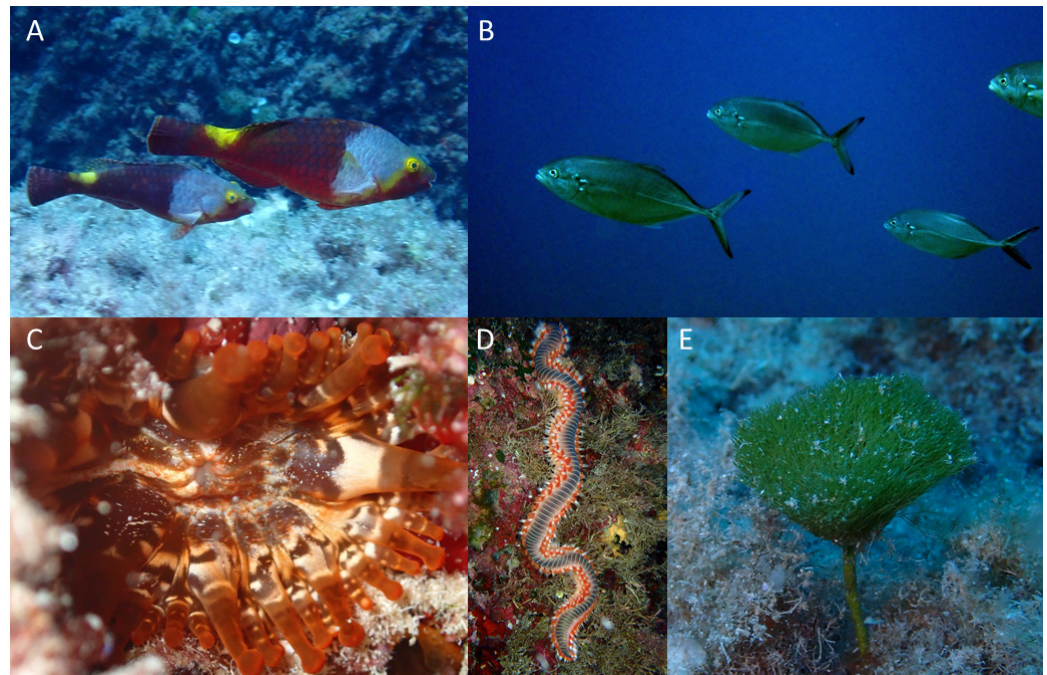


Figure 4. Images of the warm-affinity species: (A) *Sparisoma cretense*, (B) *Caranx crysos*, (C) *Telmatactis cricoides*, (D) *Hermodice carunculata* and (E) *Penicillus capitatus*.

4.2. *Caranx crysos* (Mitchill, 1815) (Teleostea, Carangidae)

The blue runner, *Caranx crysos* is a mobile predatory species found inshore at depths up to 100 m. Juveniles are commonly associated with floating debris, while adults form schools and are associated with rocky reef habitats. It is an opportunistic predator which primarily preys on pelagic species; its diet includes mainly small fish and crustaceans [51]. The blue runner shows an amphi-Atlantic distribution, including the Canary Islands [52,53]. Within the Mediterranean Sea, while its distribution has been described throughout the basin, excluding the Adriatic Sea [54], populations of *C. crysos* are found in higher frequency in the eastern and southern sectors and only sporadically in the western basin [55,56]. However, the abundance and spatial distribution of the blue runner in the Mediterranean Sea are increasing over time with a westward and northward expansion [50,56–61]. In the Spanish coasts, while *C. crysos* sightings were rare years ago, nowadays they are more frequent [22,59,62–64]. Our results support this trend, since we did not observe this species in 2022 and registered 50 sightings in the 2025 surveys located across eight different stations.

4.3. *Telmatactis cricoides* (Duchassaing, 1850) (Cnidaria, Anthozoa, Actiniaria)

The anemone *Telmatactis cricoides* inhabits rocky substrates, especially shady areas and narrow cracks, ranging from shallow waters to 40–60 m depth. The species is distributed throughout tropical and subtropical waters of the Atlantic Ocean and in the central and eastern basin of the Mediterranean Sea [65,66]. Winter temperatures in the WM seemed unfavourable to this species in previous years [66]. However, during the last decade, *T. cricoides* has been observed on the Spanish coast [20,67]. In the present study, while we observed one individual of *T. cricoides* [20] in 2022, four specimens of these anemones were sighted at two different locations in 2025.

4.4. *Hermodice carunculata* (Pallas, 1766) (Annelida, Polychaeta, Amphinomidae)

The bearded fireworm *Hermodice carunculata* is an amphinomid polychaete known for being a voracious generalist predator. The native range of this amphiatlantic species includes the Caribbean and the Gulf of Mexico, the Macaronesian archipelagos, the Mediter-

anean Sea and the Red Sea [68,69]. Recent expansion of *H. carunculata* from the southern and eastern sectors of the Mediterranean Sea towards the central region of the basin and the presence of high-density hotspots [68,69] are alarming since this is an opportunistic species able to withstand a wide range of temperature, salinity, and oxygen levels, as well as different types of pollution [70,71]. A current update describing the presence of *H. carunculata* in WM reinforces the expansion of the distribution reported for this species [23,72]. The monitoring of the Balearic Islands allowed us to observe two bearded fireworms in 2025 at two sampling stations, whereas no records were registered in 2022.

4.5. *Penicillus capitatus* (Lamarck, 1813) (Chlorophyta, Ulvophyceae, Bryopsidales)

Penicillus capitatus is a Chlorophyta macroalgae, occurring in tropical and subtropical waters of the Atlantic Ocean, the Gulf of Mexico, the Caribbean and the Mediterranean Sea. In the latter, this species is primarily present in its warmer areas: the eastern and southern basins [40,73]. *P. capitatus* exhibits two very different morphological stages, the first stage is a turf of filaments relatively common that carpets the substrate; and the second stage, which arises from the basal filaments, consists of a brush-like upper part. This second stage is quite uncommon in the WM, but its recent increased frequency in this region has been associated with global climate change [24,40,73,74]. Here, we observed the presence of *P. capitatus* in 2025 at one station, whereas we did not record sightings of this macroalgae in 2022.

Our results show five species belonging to different taxa that are increasingly observed at latitudes higher than their native geographical distribution. Since these species already inhabit other regions of the Mediterranean Sea, they cannot be considered allochthonous, and the shifts in their distribution are probably due to the increasingly warming ocean. In fact, scientists have linked the marine organisms observed in our study to tropicalization processes, as is the case with *Sparisoma cretense* [14,22,48,75,76], *Caranx crysos* [14,22,56], *Telmatactis cricoides* [20,75,77], *Hermodice carunculate* [69,78,79] and *Penicillus capitatus* [24,74,80]. Similarly, since sea temperature is a key driver of change in Mediterranean fish populations [18,21,22,81,82], distributional shifts are expected to appear earlier in nektonic groups compared to sedentary or sessile species, due to their higher motility. This hypothesis is supported by the results of our study, since fish species show a greater increase in abundance than the other warm-affinity species recorded.

Altogether, while ocean warming causes severe impacts on marine ecosystems, it can benefit the aforementioned thermotolerant species [40,72]. Species that originally inhabited the Atlantic waters, occupied the Mediterranean Sea during a warm interglacial period. Once the climate got colder such species disappeared from the western region, being confined to the warmer eastern basin. Current ocean warming could lead to these species moving back to the western region and linking eastern Mediterranean and Atlantic populations again [75,77,83]. Understanding the abilities of tropical species to adapt to environmental changes is crucial to predict ecosystem shifts in response to marine climate change. Mediterranean tropicalization could lead to biotic homogenization, biodiversity loss and reduced complexity [17]. For this reason, during the last decades there has been an increased awareness of the importance of acquiring time-series data that monitor changes in the Mediterranean Sea [3,8,21]. The methodology applied in the present work appears to be suitable to provide timely information to respond to changes in the distribution of warm-affinity species, as they can be possible indicators of tropicalization of the Mediterranean Sea [22,73,78]. Thus, we propose a continuous monitoring of the infralittoral domain to detect shifts in species range distribution and to evaluate the impacts on local biodiversity. Such monitoring studies could have a greater effect if adopted by other EU countries in order to evaluate tropicalization effects on a large scale.

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Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

The following abbreviations are used in this manuscript:

MSFD	Marine Strategy Framework Directive
MHWs	Marine Heatwaves
WM	Western Mediterranean
UVC	Underwater Visual Censuses

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