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Invading the Greek Seas: Spatiotemporal Patterns of Marine Impactful Alien and Cryptogenic Species

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Abstract: The Greek Seas are greatly exposed to the proliferation of marine alien species. At least 242 alien species have been reported within Greek territorial waters, three-quarters of which are considered established, while their rate of introduction is increasing. Some of these species exhibit high invasiveness, imposing severe impacts on native ecosystems and ecosystem services. The spatiotemporal proliferation of these species outside their natural boundaries depends on several parameters, including their biological characteristics, native distribution range, introduction pathway, and time of initial introduction. Knowing the current and potential alien species distribution is essential for the implementation of effective management actions. To investigate the distribution of impactful cryptogenic and alien species (ICAS) in the Greek Seas, we combined all records available until the end of 2020 from eight types of data sources: (1) scientific literature, (2) grey literature, (3) offline databases, (4) online scientific databases, (5) personal observations of independent researchers, (6) communications with divers and diving centers, (7) in situ underwater sampling, and (8) social networks. The results of 5478 georeferenced records refer to 60 marine ICAS belonging to 16 taxonomic groups. The number of records and the overall number of ICAS present an increasing trend from the northern to the southern parts of our study area, and there is a clear distinction in community composition between the northern and southern subregions. This latitudinal gradient is mainly due to the large number of thermophilous Lessepsian species of West Indo-Pacific origin, which reach the southern parts of the study area through unaided dispersal. On the other hand, transport stowaways appear to be more prevalent in areas located near large ports, which show significant differences in ICAS numbers and community composition compared to sites located far from ports. Most records (>40% of the total) were associated with rocky reefs, partly reflecting the preference of divers for this habitat type but also the presence of conspicuous, reef-associated impactful fish. The number of published records, as well as the number of reported ICAS, shows a dramatic increase with time, highlighting the urgent need for immediate proactive management actions and scientifically informed control measures.

Keywords: bioinvasions; exotic species; Mediterranean; biodiversity

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1. Introduction

Alien species, i.e., species accidentally or deliberately introduced in areas beyond their native distribution range by human agency, represent one of the main drivers of global change and native biodiversity loss across all terrestrial, freshwater, and marine biogeographic realms [1,2]. In particular, established alien species can become invasive, with profound effects on biodiversity, ecosystem services, and human well-being [3–5]. For this reason, the Convention on Biological Diversity (CBD) [6] and regional policy instruments, such as the EU Regulation on Invasive Alien Species [7] and the Marine Strategy Framework Directive (MSFD) [8], highlight the urgent need for the adoption of appropriate management actions to control invasive populations and minimize their impacts. However, to develop and adopt effective mitigation strategies, it is essential to compile and systematically update existing information on the spatiotemporal distributions of invasive alien species and their introduction pathways. Such information forms the basis for tracking the spatiotemporal dynamics of invasive species, conducting impact and risk assessments, and building well-informed regional or national strategies for the prevention or control of invasive species [9–12].

In addition to the most frequently reported negative impacts, many well-established alien species may have positive impacts on biodiversity or ecosystem services through a variety of mechanisms, e.g., providing food for native species or humans, controlling invasive species, creating novel habitats, and sequestering carbon [5,13]. In the Eastern Mediterranean, these positive impacts can be very important for halting the loss of ecosystem functioning and securing the flow of ecosystem services, particularly in the context of climate change, and thus marine managers need to be realistic and adaptive, understanding the role of alien species in novel Mediterranean ecosystems [5,14,15].

Although the field of invasion biology is less than 50 years old, human-aided relocations of species beyond their natural distribution range are as old as humanity itself [16]. For instance, in the Greek Seas, the presence and impact of one such species can be traced to the times of Aristophanes: "Soon shall age these timbers eat, and give the worms a lasting treat" (Knights. 1300–1310), referring to a trireme being eaten by shipworms, now known as the naval shipworm *Teredo navalis* [17]. In addition, at a global scale, alien species have been associated with the extinction of several species as far back as 1500 [2,18].

At present, climate change is a major driver of biological invasions and alien species establishment, and the Mediterranean is a fast-warming sea that is going through major ecological shifts leading to its tropicalization [19–23]. The rising sea temperatures, acting in concert with other human interventions, enhance the distribution expansion of thermophilous species throughout the Mediterranean. In the western parts of the basin, Atlantic species of sub-tropical affinity move into the Mediterranean Sea through the Gibraltar Strait (i.e., neonative species *sensu* [24]), and, in the eastern parts of the basin, Red Sea species (the so-called Lessepsian immigrants) may enter the Mediterranean unaided through the Suez Canal. Human activities, such as marine traffic and fishing, further exacerbate the secondary expansion of alien and neonative species across the basin. According to relevant assessments, the four main pathways of alien species introductions into the Mediterranean are: (a) unaided movement through the Suez Canal (corridor; 53.9%), (b) stowaways on vessels (44.9%), (c) aquaculture runaways (11.6%), and (d) pet-trade escapees/releases (2.0%) [25]. The rate of alien species introductions in the Mediterranean has been increasing since the 1970s and has grown by 40% within the last 11 years, resulting in a significant restructuring of native ecosystems [26,27]. At the same time, native species suffer mass mortalities during extreme events related to recurrent marine heatwaves [28]. The problem is more pronounced in the eastern and warmer parts of the basin, where alien species dominate in terms of biomass over native taxa [29,30], while several native species have gone locally extinct [31,32]. This decline of high-temperature-sensitive Mediterranean species further promotes the expansion of alien species, as the loss of native biota leaves empty functional niches for the alien species to fill and exploit [30].

Located in the NE part of the Mediterranean Sea, the Greek waters of the Aegean, Levantine, Ionian, and Adriatic Seas (hereafter collectively referred to as the Greek Seas) are increasingly being affected by the expansion of alien species. By 2020, out of a total of 1001 marine alien species recorded in the Mediterranean [26,27], 242 had been reported within the Greek coastal waters [33]. The highest numbers of alien species are generally observed in the warmer southeastern areas, as most of the alien species in the Greek Seas are thermophilous Lessepsian immigrants [34,35]. The presence of alien species in this region is continuously being monitored over the last two decades. The first list of species was published in 2005 and has been updated several times thereafter [34,36–39]. The Ellenic (Hellenic) Network on Aquatic Invasive Species (EASIN) [40] and citizen science initiatives [41] are collecting and reporting spatial information on aquatic alien species systematically. New first records are published regularly (e.g., [42,43]), and large datasets of georeferenced alien species records have recently become available [10,44].

Nevertheless, the spatial distributions of impactful Mediterranean cryptogenic (i.e., species of unknown biogeographic status) [45,46] and alien species—hereafter collectively called ICAS, including species with negative or positive impacts—that are present in the region has never been quantitatively assessed. The present work aimed to compile and analyze all spatiotemporal ICAS data available along the Greek coastline until 2020.

2. Materials and Methods

The study area covers all coastal waters of the Aegean, Levantine, Ionian, and Adriatic Seas that are included within the Greek reporting obligations under the Marine Reporting Units (MRUs) of the MSFD [8] of the European Union Seas (hereafter collectively referred to as the Greek Seas; Figure 1).

Figure 1. Map of the study area featuring the four marine ecoregions forming the Greek Seas (the Aegean Sea, the Levantine Sea, the Ionian Sea, and a small part of the Adriatic Sea) along with seven major commercial ports (black triangles). Ecoregions are delimited according to the Marine Reporting Units (MRUs) of the Marine Strategy Framework Directive (MSFD) [8].

A catalog of ICAS in the Greek Seas was compiled based on species classified as of high impact in the European Alien Species Information Network (EASIN) [47] or as invasive or of high impact in recent review papers [5,13,48–50], and a thorough search was conducted for information on the presence of these species in the study area. Specifically, spatiotemporal data until the end of 2020 were collected through the following seven types of data sources: (1) published scientific literature; (2) gray literature (e.g., theses, technical reports, and newspaper reports); (3) offline databases, including records from past projects of universities and research institutes, the ELNAIS database, and citizen science initiatives;

(4) online scientific or citizen science databases: Algaebase, GBIF, OBIS, and iNaturalist (only research-grade data); (5) unpublished independent observations by marine scientists; (6) interviews with fishers and divers; (7) in situ underwater sampling during the ALAS project [51] (Supplementary Figure S1 and Table S1); and (8) social networks (e.g., Instagram and Facebook). Information from social networks refers to websites of diving centers, which were thoroughly checked for images of ICAS, and, once relevant images were found, the corresponding information was further validated through direct communication with the authors.

The biogeographic status (alien or cryptogenic) of the target species was defined based on the work of Tsirintanis et al. [5], as was their native distribution range according to Tsiamis et al. [52], following the ecoregional classification of Spalding et al. [53]. The primary pathways of introduction into the Mediterranean Sea were assessed using the six broad categories of the CBD classification [54] based on information retrieved from the literature. To depict the spatiotemporal distribution of ICAS records, species richness, and the spatial patterns of records based on the ICAS native distribution range and primary pathway of introduction into the Mediterranean, heatmaps were produced using the 10 × 10 km quadrat of the European Environmental Agency (EEA) reference grid and the ArcGIS software.

To investigate the total number of ICAS recorded within the Greek Seas through time (from the 1880s until 2020), a model was created that best fitted the relationship between the number of records gathered and time. The tested models were the sixth-order polynomial, the exponential, and the double exponential. The respective analyses were carried out in Statgraphics Centurion XVI.

To look at the spatial patterns of ICAS composition, the study area was further divided into 11 marine subregions (Figure 2). Within each subregion, five sites containing relevant spatial data were randomly selected. In this case, a site was defined as a 10 × 10 km quadrat using the EEA reference grid. Species presence within each site was retrieved from our full ICAS dataset. Presence/absence data were used to construct a similarity matrix based on the Jaccard coefficient. To identify spatial patterns, a Hierarchical Cluster Analysis was carried out and a corresponding dendrogram was constructed using the unweighted pair-group method with arithmetic means. In addition, to look at the spatial clustering of the different subregions, a non-Metric Multidimensional Scaling (nMDS) analysis was conducted. To test for significant differences in the observed patterns of community composition among subregions, a Permutational Multivariate Analysis of Variance (PERMANOVA) was performed.

To investigate the potential effect of ports on ICAS distribution, a total of seven major commercial ports (i.e., one for each distinct subregion, if available) were selected (Figure 2). For each port, data were retrieved from three randomly selected sites (i.e., 10 × 10 km quadrats of the EEA reference grid) that were located within or close to the port (i.e., on a cell including the port and two neighboring cells) and from three sites located far (i.e., between 50 and 100 km) from the port (Figure 2). In all cases, no other important port was found close to the focal port. Data on species presence/absence within each site were retrieved from our ICAS database. To test for differences in community composition between sites located within/close to and far from large ports, a similarity matrix was created using the Jaccard coefficient, and a two-factor PERMANOVA test was run using port (seven levels) and location (two levels: close and far) as fixed factors. To investigate differences in the number of species found within/close to and far from port areas, a similarity matrix based on Euclidean distances was created, and a two-factor PERMANOVA test was run using the same design as above. PERMANOVA tests were conducted using 9999 permutations of residuals under a reduced model and type III sum of squares. The Hierarchical Cluster, n-MDS and PERMANOVA analyses were carried out using Primer 6 Version 6.1.16 with the Permanova+ Version 1.0.6 add-on from PRIMER–E Ltd 2013, Plymouth, UK [55].

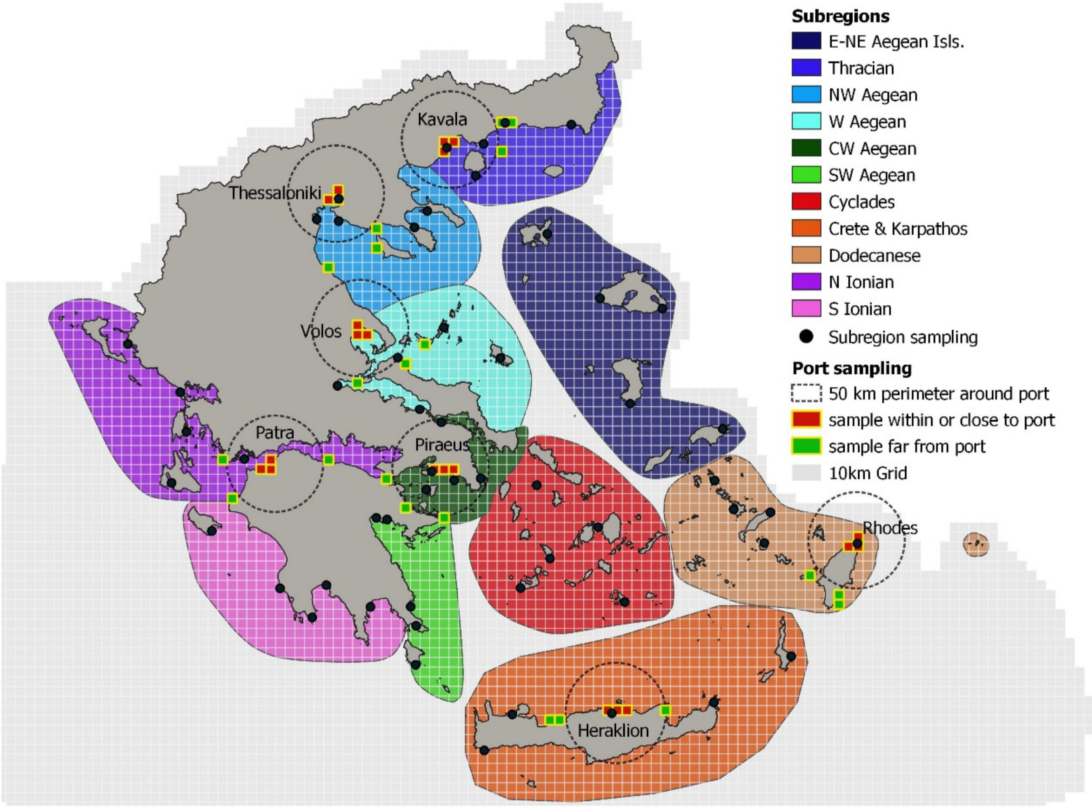

Figure 2. Map of the study area depicting the eleven subregions and the seven largest commercial ports that were used for the spatial analysis regarding community structure and number of reported ICAS in the Greek Seas. Grid cells were produced using the 10 × 10 km European Environmental Agency (EEA) reference grid.

3. Results

Out of a total number of 89 Mediterranean ICAS [5], our search revealed 60 marine ICAS (56 alien and 4 cryptogenic) belonging to 14 phyla with reported presence in the Greek Seas (Table 1). The taxonomic group with the highest richness was fish (Chordata–Teleostei: 16 species), followed by Mollusca (14), Arthropoda (7), Ascidiacea (Chordata–Tunicata: 6), Rhodophyta (4), Chlorophyta (3), and Annelida, Bryozoa, and Echinodermata (2 species each), while Ochrophyta, Tracheophyta, Foraminifera, Cnidaria, Porifera, and Ctenophora had 1 species each. Of the recorded ICAS, 58 species appeared in the Aegean Sea (54 in the S Aegean and 45 in the N Aegean), 49 in the Levantine, 32 in the Ionian, and 9 in the Adriatic. The total species richness, as well as fish species richness, per 100 km^2 followed a decreasing trend from southern/southeastern to northern/northwestern areas (Figure 3a,b, respectively), and the highest values for species richness of invertebrates (including tunicates) were displayed in areas close to the large ports of Piraeus, Heraklion, Rhodes, and Thessaloniki (Figure 3c), whereas macrophyte richness was relatively uniform throughout the study area (Figure 3d).

The resulting dataset consisted of 5478 records: 61.5% from the Aegean Sea, 19.6% from the Levantine Sea, 18.6% from the Ionian Sea, and 0.3% from the Adriatic. The majority of the records were retrieved from the published scientific literature (47.4%), followed by offline databases (25.6%), in situ underwater sampling during the ALAS project (11.4%), independent observations (7.3%), social media (4.9%), online databases (1.9%), communications with divers (0.7%), and grey literature (0.7%).

Table 1. Number of records of the investigated impactful cryptogenic and alien species (ICAS) per phylum, along with information on their biogeographic status (alien or cryptogenic); origin (i.e., native distribution range—WIP: Western Indo-Pacific, TA: Tropical Atlantic, Tau: Temperate Australasia, TNP: Temperate Northern Pacific, TNA: Temperate Northwest Atlantic, CIP: Central Indo-Pacific, TEP: Tropical Eastern Pacific, EIP: Eastern Indo-Pacific, UNK: Unknown); primary introduction pathway into the Mediterranean, if known (TS: Transport Stowaway, TC: Transport Contaminant, CR: Corridor, EC: Escape from Confinement, REL: Release into Nature, UNA: Unaided, UNK: Unknown) [54]. Numbers within parentheses indicate the total number of records per phylum. Grey highlights: most commonly recorded species (>100 records each).

Phylum, Class	Species	Status	Native Distribution Range	Pathway	Number of Records
Ochrophyta (66)	*Stypopodium schimperi*	Alien	WIP	CR	66
Chlorophyta (403)	*Caulerpa cylindracea*	Alien	TAu	EC/TS	365
	Caulerpa taxifolia var. distichophylla	Alien	TAu	EC/TS	15
	Codium fragile subsp. fragile	Alien	TNP	TC/TS	23
Rhodophyta (448)	*Asparagopsis* spp.	Alien	WIP/TAu	TS	103
	Ganonema farinosum	Cryptogenic	WIP/TNA	CR/TS	67
	Lophocladia lallemandii	Alien	WIP/CIP/TNP	CR/TS	243
	Womersleyella setacea	Alien	WIP/CIP/EIP	EC/TS	35
Tracheophyta (154)	*Halophila stipulacea*	Alien	WIP	CR/TS	154
Foraminifera (30)	*Amphistegina lobifera*	Alien	WIP	CR	30
Porifera (3)	*Paraleucilla magna*	Alien	TA	TS	3
Cnidaria–Anthozoa (71)	*Oculina patagonica*	Cryptogenic	TA/TNA	TS	71
Cnidaria–Scyphozoa (10)	*Rhopilema nomadica*	Alien	WIP	CR	10
Ctenophora (82)	*Mnemiopsis leidyi* *	Alien	TNA	TS/UNA	82
Bryozoa (21)	*Amathia verticillata*	Cryptogenic	WIP	TS	20
	Tricellaria inopinata	Alien	TNP	TS	1
Mollusca (559)	*Anadara transversa*	Alien	TA	TS	1
	Brachidontes pharaonis	Alien	WIP	CR/TS	34
	Bursatella leachii	Alien	WIP/CIP/TA	CR	72
	Chama pacifica	Alien	WIP	CR/TS	10
	Conomurex persicus	Alien	WIP	TS	152
	Crepidula fornicata	Alien	TNA	TC/TS	26
	Dendostrea cf. *folium*	Alien	WIP	CR/TS	33
	Fulvia fragilis	Alien	WIP	CR/TS	27
	Magallana sp.	Alien	TNP	EC	3
	Mya arenaria	Alien	TNA	TC/TS	4
	Petricolaria pholadiformis	Alien	TA/TNA	TS	5
	Pinctada radiata	Alien	WIP	CR/REL	187
	Rapana venosa	Alien	TNP	TC/UNA	3
	Spondylus spinosus	Alien	WIP	CR/TS	2
Annelida (46)	*Ficopomatus enigmaticus*	Alien	TAu	TS	19
	Hydroides elegans	Alien	WIP/CIP/TAu	TS	27
Arthropoda (523)	*Callinectes sapidus*	Alien	TA/TNA	TS	132
	Matuta victor	Alien	CIP/EIP	CR	3
	Paracerceis sculpta	Alien	TEP/TNP	TC/TS	6
	Penaeus aztecus	Alien	TA/TNA	EC/TS	67
	Penaeus pulchricaudatus	Alien	WIP/CIP/TNP	CR	10
	Percnon gibbesi	Cryptogenic	TA/TEP/TNA	UNK	283
	Portunus segnis	Alien	WIP	CR	22

Table 1. *Cont.*

Phylum, Class	Species	Status	Native Distribution Range	Pathway	Number of Records
Echinodermata (202)	*Diadema setosum*	Alien	WIP/CIP	CR	136
	Synaptula reciprocans	Alien	WIP	CR	66
Chordata–Ascidiacea (42)	*Ciona robusta*	Alien	UNK	TS	2
	Herdmania momus	Alien	WIP/CIP	CR/TS	12
	Styela plicata	Alien	TNP	TS	28
Chordata–Teleostei (2818)	*Apogonichthyoides pharaonis*	Alien	WIP	CR	11
	Atherinomorus forskali	Alien	WIP	CR	6
	Etrumeus golanii	Alien	WIP	CR	47
	Fistularia commersonii	Alien	WIP/CIP/EIP	CR	192
	Lagocephalus sceleratus	Alien	WIP/CIP	CR	265
	Nemipterus randalli	Alien	WIP	CR	2
	Parupeneus forsskalli	Alien	WIP	CR	61
	Pempheris rhomboidea	Alien	WIP	CR	30
	Pterois miles	Alien	WIP	CR	511
	Sargocentron rubrum	Alien	WIP/CIP	CR	97
	Saurida lessepsianus	Alien	WIP	CR	6
	Siganus luridus	Alien	WIP	CR	849
	Siganus rivulatus	Alien	WIP	CR	532
	Torquigener flavimaculosus	Alien	WIP	CR	172
	Upeneus moluccensis	Alien	WIP	CR	14
	Upeneus pori	Alien	WIP	CR	19

* Arrived via shipping in the Black Sea and dispersed unaided in the Mediterranean Sea.

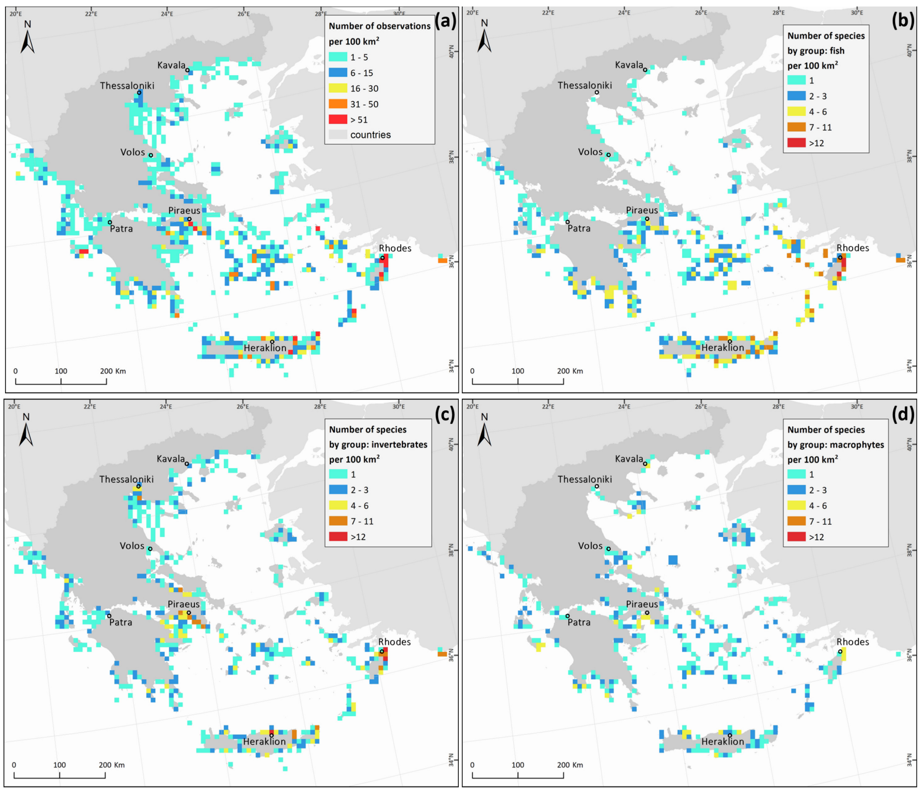

Figure 3. Maps of the Greek Seas depicting the total number of records (**a**) as well as the total number of ICAS belonging to different taxonomic groups, i.e., fishes (**b**), invertebrates (**c**), and marine macrophytes (**d**). Grid cells were produced using the 10 × 10 km European Environmental Agency (EEA) reference grid.

At the phylum level, Chordata (mainly fishes) accounted for 52.2% of the total number of records, followed by Mollusca (10.2%), Arthropoda (9.6%), Rhodophyta (8.2%), and Chlorophyta (7.4%), with the remaining phyla representing less than 5.0% of the records each (Table 1). At the species level, 15 taxa with more than 100 records each accounted for 78% of the records and presented the most widespread distribution throughout the Greek Seas (Table 1). Based on their numbers of records, in decreasing order, these taxa were: *Siganus luridus, S. rivulatus, Pterois miles, Caulerpa cylindracea, Percnon gibbesi, Lagocephalus sceleratus, Lophocladia lallemandii, Fistularia commersonii, Pinctada radiata, Torquigener flavimaculosus,* Halophila stipulacea, Conomurex persicus, Diadema setosum, Callinectes sapidus, and *Asparagopsis* spp. (including *A. armata*: 25 records, *A. taxiformis*: 72 records, and unidentified *Asparagopsis* sp.: 7 records).

In terms of their native distribution range (Table 1), the majority of species (38 species) originate in the Western Indo-Pacific (WIP, Figure 4a), 11 are from the Central Indo-Pacific (CIP, Figure 4b), 9 are from the Temperate Northwest Atlantic (TNA, Figure 4c), 8 are from the Temperate Northern Pacific (TNP, Figure 4d), 7 are from the Tropical Atlantic (TA, Figure 4d), 5 are from Temperate Australasia, 3 are from the Eastern Indo-Pacific, 2 are from the Tropical Eastern Pacific, and 1 is of unknown origin. Nineteen of these species are native to more than one ecoregion. Species of Indo-Pacific origin presented high richness levels in the southeastern Greek Seas, declining towards northwestern marine areas, whereas no such pattern was observed for species of other origins (Figure 4a,b).

Regarding the primary pathway of introduction (Table 1), 35 of the species entered the Mediterranean through the Suez Canal and then spread unaided into the Greek Seas (CR, Figure 5a), 31 were introduced as transport stowaways (including ship/boat ballast water or hull fouling) (TS, Figure 5b), 5 were escapees from aquaculture or mariculture confinement (EC), and 5 were transport contaminants (TC) on animals (Figure 5d), while 2 species entered unaided (UN) from the neighboring Black Sea (where they are invasive), 1 entered through release into nature (REL), and 1 is of an unknown pathway of introduction (UKN). Species introduced by shipping have richness hotspots in several large ports (Piraeus, Heraklion, Rhodes, and Thessaloniki), whereas Lessepsian species display high richness in the southeastern areas, declining towards the northwest.

Of the 5478 records, only 42.9% specified the habitat type in which the ICAS were recorded. Of the 2352 records reporting habitat type, 58.0% referred to rocky substrata, 23.0% to mobile substrata (i.e., including mud, sand, and small pebbles), 8.6% to mixed substrata (combining rock with sand or seagrasses), 3.8% to marine caves, 3.2% to seagrasses, and 2.1% to artificial substrata, while the water column and coastal lagoons accounted for less than 1% of records each. The habitat types with the highest numbers of species were the mobile (37 species) and rocky substrata (35), followed by mixed substrata (24), artificial substrata and marine caves (17 species each), seagrasses (12), the water column (2), and coastal lagoons (2) (Figure 6a).

Regarding the progress of records through time, 96.5% of the total records were accompanied by temporal information, covering a period between 1893 and 2020 (Figure 6b). Of these records, 38 records of 9 species were recovered up to 1960 (Figure 7a), which added up to 88 records of 17 species by 1980 (Figure 7b), 284 records of 37 species by 2000 (Figure 7c), and 5288 records of 60 species by 2020 (Figure 7d). The model that best fitted the relationship between the number of records and time ($R^2 = 83.9\%$) was the double exponential:

$$y = e^{e^{(0.501+0.0345(x-1979))}}$$

where y is the number of records and x is the corresponding year (Figure 5b).

The sixth-order polynomial ($R^2 = 81.0\%$) and the simple exponential ($R^2 = 58.0\%$) performed worse.

The PERMANOVA results regarding the ICAS community composition in the different marine subregions indicated that there were significant differences between most sites of the northern and southern coasts, but also among several sites of the Northern Aegean subregions (Table 2). These spatial patterns were also reflected in the n-MDS plot (Figure 5c; but see also the corresponding dendrogram in Supplementary Figure S2), according to which there was a clustering of sites of the Southern Aegean islands (i.e., the Cyclades, Crete & Karpathos, and the Dodecanese) along with those of the mainland SW Aegean and S Ionian coasts, whereas those of the northern coasts (both of the Aegean and the Ionian Seas) were more spread out and those of the CW Aegean coasts were positioned in between.

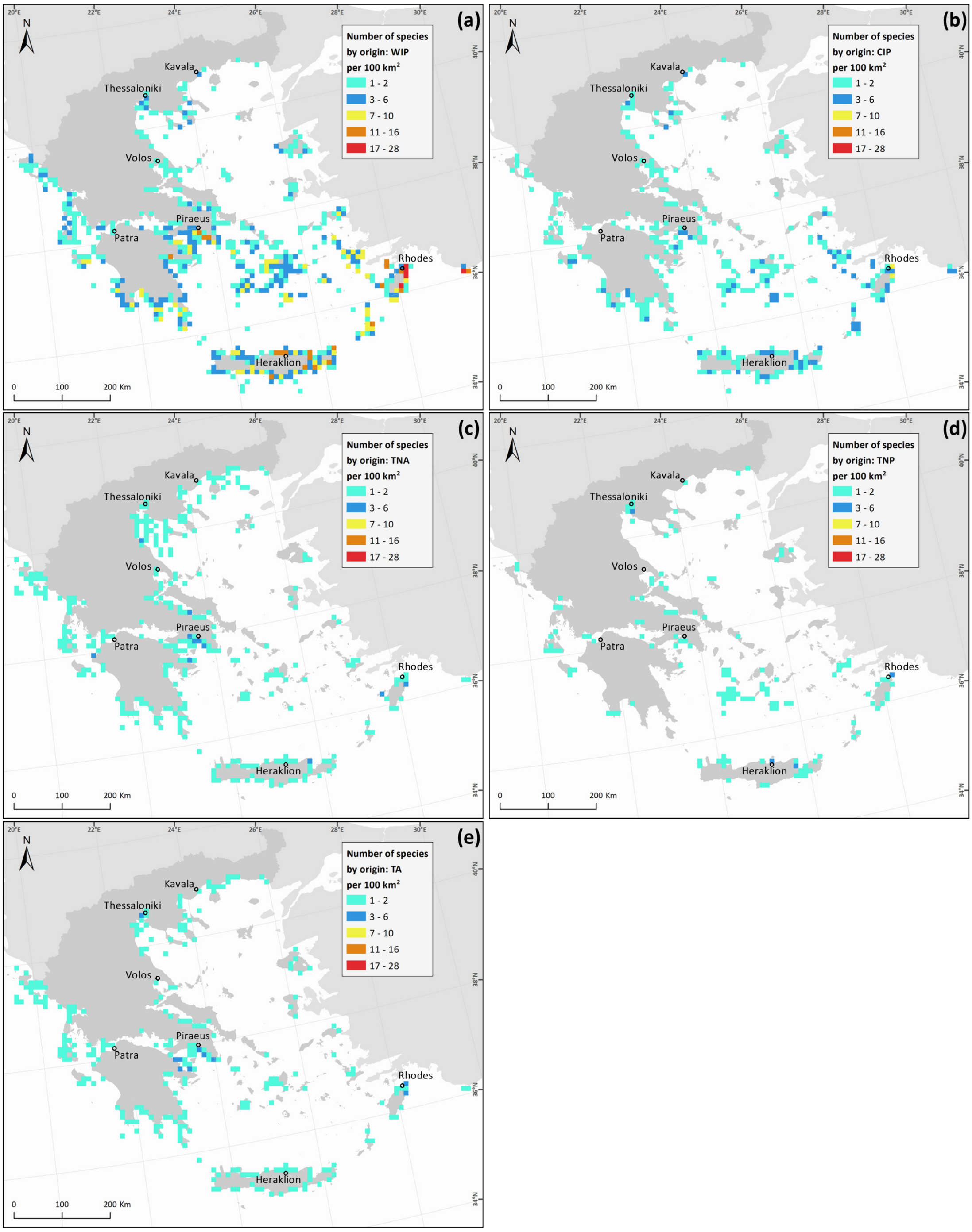

Figure 4. Map of the Greek Seas depicting the total number of ICAS according to their native distribution range—WIP: Western Indo-Pacific (**a**), CIP: Central Indo-Pacific (**b**), TNA: Temperate Northwest Atlantic (**c**), TNP: Temperate Northern Pacific (**d**), TA: Tropical Atlantic (**e**). Grid cells were produced using the 10 × 10 km EEA reference grid.

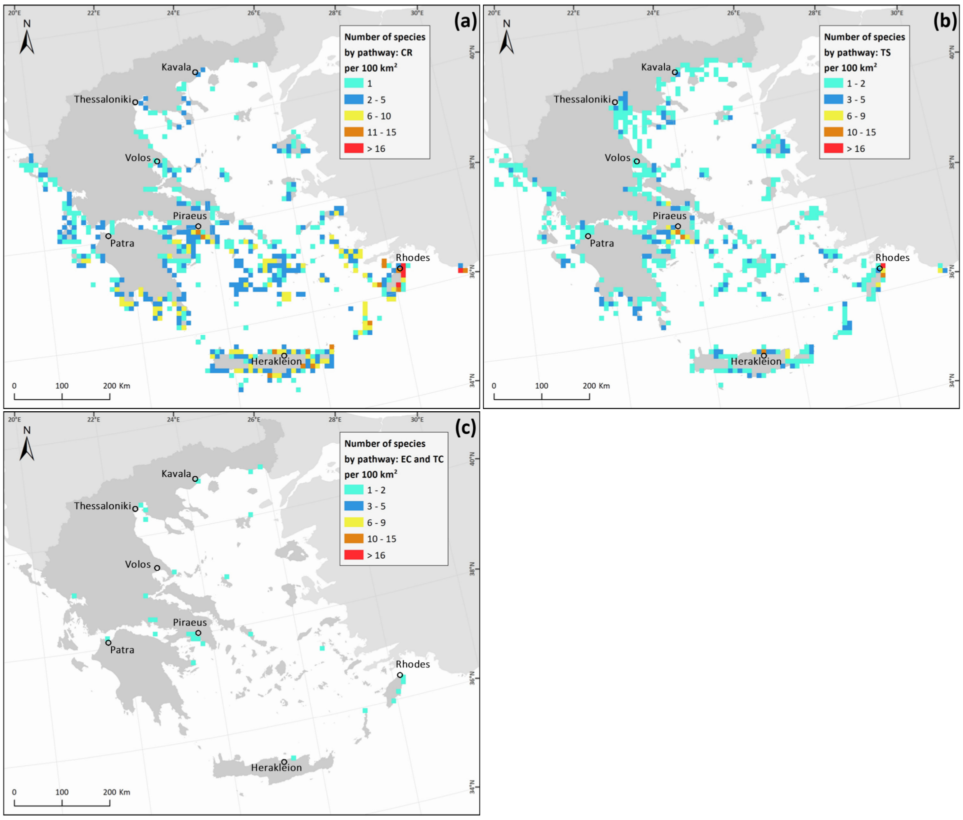

Figure 5. Map of the Greek Seas depicting the total numbers of ICAS according to their primary introduction pathways into the Mediterranean: (**a**) via corridors—CR, (**b**) as transport stowaways—TS, (**c**) via escape from aquaculture or mariculture confinement—EC—and as transport contaminants on animals—TC. Grid cells were produced using the 10 × 10 km EEA reference grid.

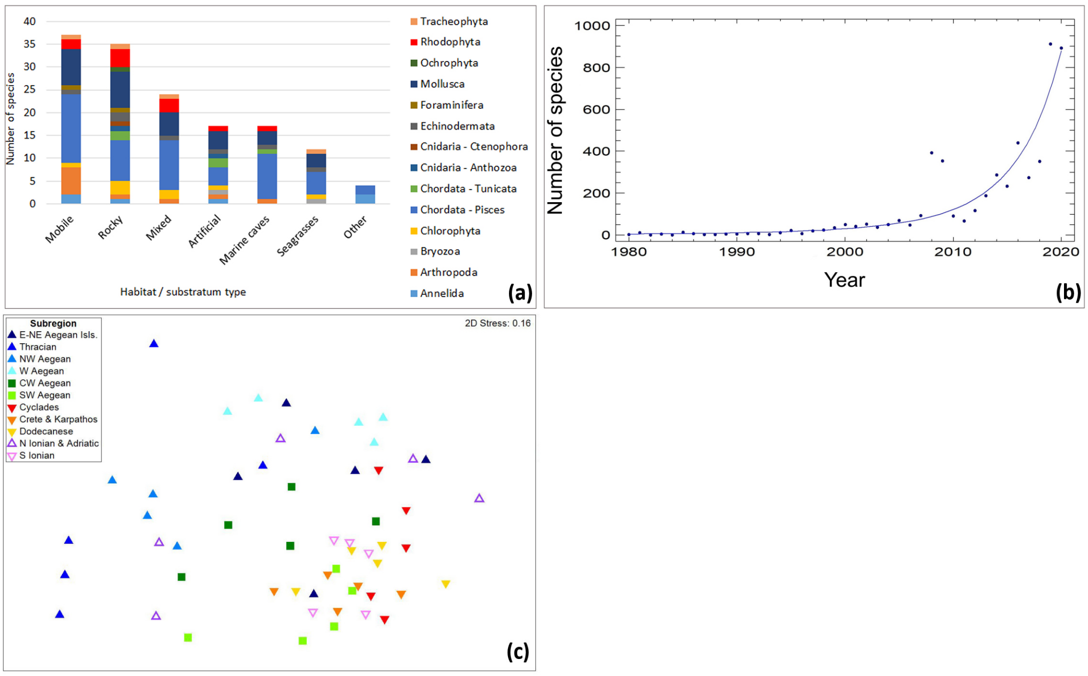

Figure 6. Charts depicting the number of ICAS per habitat or substratum type (**a**) and the numbers and trend of ICAS recorded per year (**b**) and the n-MDS plot presenting the spatial patterns in the ICAS community composition across sites in the 11 subregions of the study area (**c**).

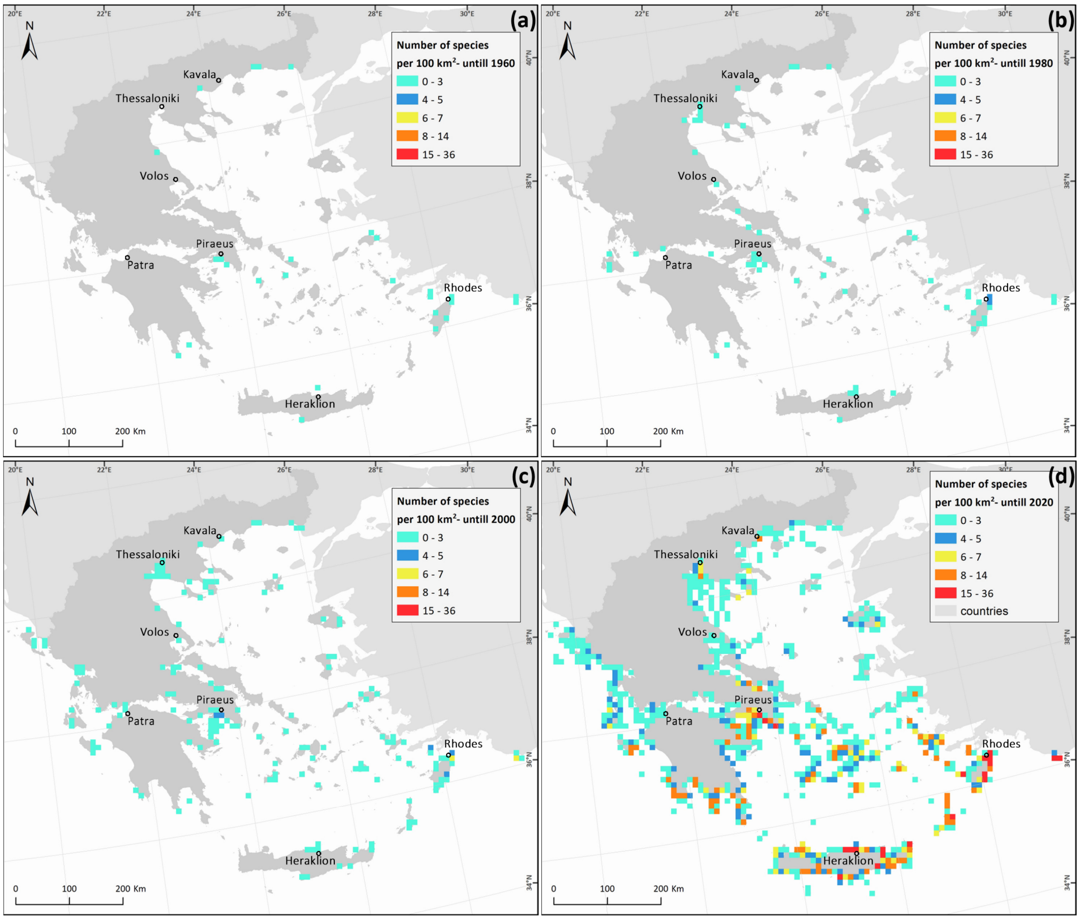

Figure 7. Map of the Greek Seas depicting the total number of ICAS recorded until 1960 (**a**), 1980 (**b**), 2000 (**c**), and 2020 (**d**). Grid cells were produced using the 10 × 10 km EEA reference grid.

Table 2. Significant differences in ICAS community composition between the different subregions of the Greek Seas according to the PERMANOVA results. Colors denote different marine areas: Red—Southern Aegean Islands, Blue—Northern Aegean, Green—Western Aegean, Purple/Pink—Ionian, Black—Not applied. Significance levels: * $p \leq 0.05$, ** $p \leq 0.01$.

Subregions	Cyclades	Crete and Karpathos	Dodecanes	E-NE Aegean Isls.	Thracian	NW Aegean	W Aegean	CW Aegean	SW Aegean	N Ionian	S Ionian
Cyclades					*	**	*				
Crete and Karpathos					*	**	**			*	
Dodecanese					**	**	**	*	*	*	
E-NE Aegean Isls.						*					*
Thracian	*	*	**				*		*		**
NW Aegean	**	**	**	*			*	*	**		**
W Aegean	*	**	**		*	*			**		**
CW Aegean			*			*					
SW Aegean			*		*	**	**				
N Ionian		*	*								*
S Ionian				*	**	**	**			*	

When comparing ICAS communities within/close to and far from port areas, the total number and the mean number of species were overall higher within ports (55 species; 8.8 ± 8.7) than outside ports (37 species; 5.0 ± 4.7). The PERMANOVA results referring to the number of ICAS indicated significant differences among ports (degrees of freedom—d.f. = 6, Pseudo-F = 8.9, p-value < 0.0001), in further support of the spatial heterogeneity reported among subregions and also among locations (i.e., within/close to or far from the ports) (d.f. = 1, Pseudo-F = 7.2, p-value < 0.01), but not in the interaction of the two factors (Supplementary Table S2). Similarly, community composition within/close to and far from major ports indicated significant differences among ports (d.f. = 6, Pseudo-F = 2.2, p-value < 0.0001) and among locations (d.f. = 1, Pseudo-F = 1.8, p-value < 0.04), but not in the interaction of the two factors (Supplementary Table S2).

4. Discussion

The four most commonly reported species in this study (in order of decreasing number of records) were the fishes *S.luridus, S. rivulatus*, and *P. miles* and the green alga *C. cylindracea*. These are amongst the most widespread alien species within the Mediterranean [10,43] with well-documented negative impacts [5]. They have also been classified as invasive in the study area in previous assessments [35,39] and are included among the 22 marine species in the Greek national list of invasive alien species (HELLAS-ALIENS) [56] that has been compiled in accordance with the provisions of Article 12 of the EU Regulation on the management of invasive alien species [7].

ICAS can be found across the entire Greek coastline, but species richness and records are more abundant in the southeastern parts of the study area and in certain hotspots, such as areas close to large ports. Apart from the introduction pathway, the spatial distribution of distinct ICAS is greatly related to the species' biology and ecology, as these have been shaped by evolutionary processes in the species' native range. Hence, species-specific characteristics, such as lifestyle and traits, hold predictive power with respect to their establishment success and spread in a new environment [57–59]. For example, a warm-water species has a low probability of successful invasion and expansion if introduced into a new cold-water environment ([60] and references therein). Specific traits, such as preferred temperature and habitat type, maximum reported length, and infinite length, are considered the most important predictors in the establishment process of Red Sea fishes [59]. Likewise, the biological characteristics of a species determine the likelihood of its introduction pathway. For example, a marine species with no planktonic life phase is not likely to be transported as a stowaway in ballast water [9].

The warmer waters of the southern areas in the Greek Seas [61] appear to provide suitable conditions for the fast establishment of thermophilous species (such as most Lessepsian migrants). In contrast, the cooler N Aegean and N Ionian waters present natural obstacles, preventing or delaying the establishment of several alien species (e.g., *S. luridus*). Overall, the latitudinal gradient in the number of ICAS records is mainly driven by fishes (51.5% of all records), most of which originate from the warm waters of the Western Indo-Pacific, entered the Mediterranean Sea through the corridor of the Suez Canal, and dispersed unaided into other parts of the basin; hence, within our study area, they have mainly proliferated in the warm southern parts of the Greek Seas. This is why there is a high similarity in the spatial patterns among the maps displaying the total number of fish species (Figure 3b), the total number of species originating from the Western Indo-Pacific (Figure 4a), and the number of species whose introduction pathway is through corridors (Figure 5a). In all these maps, most records are concentrated in the southern areas. On the contrary, most invertebrate species (Figure 3c), many of which have been introduced into the Mediterranean as transport stowaways from distant oceans, such as the Temperate Northern Pacific (Figure 4d) and the Tropical Atlantic (Figure 4e), are mainly found around large Greek ports (Figure 5b). Zenetos et al. [62] documented that 54% of all alien species in the Saronikos Gulf (i.e., the wider area around Piraeus port) have been introduced by vessels, while most of them are invertebrates, especially Mollusca. The density of records of macrophyte ICAS exhibits a relatively uniform distribution throughout the study area, possibly because of the introduction of most species as transport stowaways, the diversity of thermal niches in the study area, and the capacity of many species (e.g., *C. cylindracea*, *L. lallemandii*, and *H. stipulacea*) to reproduce via fragmentation and spread easily [63–65].

The ICAS community structure analysis across the distinct subregions of our study area indicated that, whereas a more homogenized community characterizes the southern parts of the Greek Seas, in the northern subregions ICAS communities are more variable.

These patterns in community composition can be attributed to both the different introduction pathways described above and the differences in environmental conditions that characterize the Greek subregions. Whereas the southern areas present more uniform and annually stable environmental conditions in terms of temperature, salinity, and nutrient availability, the northern areas, with a greater inflow of cool freshwater from large rivers and low-salinity water from the Black Sea, present wider variability in environmental conditions [61,66,67]. Thus, southern areas provide more stable warm-water environments for many thermophilous Lessepsian migrants, while northern areas provide a patchier environmental canvas with variable conditions where ICAS of different origins may establish. However, given the continuous sea warming, some of the thermophilous marine ICAS are gradually expanding their distribution range into the Northern Aegean [33].

The temporal aspect of ICAS records indicates continuous increases in new introductions and successful establishments over the last 20 years, but also reflects the intensification of research efforts focusing on marine alien species over the same time frame. The increased vigilance of the scientific community and enhanced public awareness, along with the evolution of new technologies (e.g., underwater digital cameras, smartphones) and social media which have increased the ability of non-scientists to contribute to data collection through the direct sharing of their observations [41], has resulted in a double exponential increase in the number of records over the last 20 years, with new or previously unpublished sightings continuously being reported (e.g., [43]). According to Zenetos et al. [62], citizen scientists alone have contributed substantially to the detection of new non-indigenous species in the Saronikos Gulf (42%), especially molluscan taxa (24 out of 29 species).

However, research efforts are unevenly distributed across our study area. For example, the identification of an ICAS hotspot in the Bay of Laganas Zakynthos Island—S Ionian Sea, with a total of 14 recorded ICAS accounting for 4% of total records, is due to the systematic monitoring that is being conducted by the management body of the National Marine Park of Zakynthos. Similarly, the increased numbers of records within the Saronikos Gulf (8.8% of total records) and Thermaikos Gulf (2%), especially compared to nearby areas, are related to the occurrence of large ports but also to the presence of research institutes and universities which conduct systematic marine research in these locations. The extensive research efforts in these areas provide a better understanding of the true extent of biological invasions therein compared to the rest of the Greek Seas, where research efforts are uneven and information is greatly based on unsystematic, opportunistic observations, mainly focusing on large, iconic species. In contrast, more remote areas, especially offshore, are rarely investigated, both within the Greek Seas and across the Mediterranean [9]. Furthermore, certain taxa, especially those that are hard to spot or identify due to their dubious morphological characters, small size, or elusive behavior, are less commonly recorded than the more conspicuous or emblematic ones [33,41]. For example, within our ICAS dataset, the majority of records (>40% of the total) are associated with rocky reefs, partly reflecting the preference of divers for this habitat type, as well as the presence of conspicuous reef-associated impactful fish (e.g., the siganids and *P. miles*) that are easy to spot by citizen scientists. All these effort-related biases may result in the unrealistically low representation of some taxa in the datasets (e.g., *Amphistegina lobifera*) and their underestimation in the respective assessments [68].

Information on ecological context, such as habitat type and depth, was missing from most records. Successful invasions depend on the interaction between the biological and ecological traits of a species that define its potential invasiveness, but also on the habitat's suitability and susceptibility (invasibility) to the establishment and proliferation of invasive species [69]. Hence, information related to habitat type is essential to understand what makes specific habitats and ecosystems susceptible to bioinvasions [70,71], assess the impacts of invasive species [9,72,73], and interpret the responses of habitats and ecosystems to bioinvasions to inform conservation planning [74–76].

As bioinvasions in the Greek Seas continue to grow, improving the existing monitoring capacity is essential, since data quality is the cornerstone of well-informed management decisions and the implementation of area-specific prevention and mitigation actions at various spatial scales. This is particularly important considering that the Greek Seas are acting not just as recipients but also as donors of marine ICAS, as they provide an important crossroad for the further distribution expansion of ICAS westwards into the Mediterranean, northwards into the Black Sea, but also to more distant areas through transfer via commercial activities (e.g., [77,78]). The use of *in situ* collected data based on systematic scientific methods may provide more reliable and detailed information with regard to the numbers and taxonomic identities of alien species present, their population density/cover, their habitat characteristics/status, and potential impacts. However, scientific surveys cannot cover the entire spatial scale of the Greek Seas due to cost restrictions. The engagement of citizens and selected stakeholder groups, such as fishers and NGOs, in the reporting process has been proven to be a precious tool (e.g., [41,79], data presented herein), especially when considering an area of great geomorphological complexity, such as the coastlines of the Greek Seas. To enhance the continuous updating of existing data, it is crucial to boost funding for monitoring, impact assessment, and citizen science training projects related to alien species. Moreover, building a unified national data repository with free and easy access for all is essential for the fast exchange and use of available information. Finally, it is crucial to develop simplified scientifically based field protocols to be used both by scientists and citizens. Alongside basic spatial information, these protocols should also incorporate predefined metrics that will enable the quantification and characterization of marine alien species populations, their preferred habitat types, and their potential impacts. All of the above will enable the acquisition of more systematic information and will enhance the monitoring and assessment efforts related to ICAS.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15030353/s1, Figure S1: Map of the study area depicting all sampling stations that were assessed through scientific diving surveys in the framework of the ALAS project. Table S1: List of stations covered through scientific diving surveys along with their geographic coordinates and the habitat type investigated. Figure S2: Dendrogram of the Hierarchical Cluster Analysis depicting the level of similarity between distinct marine subregions in the Greek Seas based on ICAS community composition. Table S2: PERMANOVA results regarding the total number of ICAS and ICAS community composition located within/close to and far from large ports of the Greek Seas.

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