

Article

Spatial Patterns of the Marine Alien Gastropod *Rapana venosa* Invasion Across the Black Sea, Mediterranean, and Atlantic Europe

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Simple Summary

Rapana venosa is an invasive marine snail that has spread across several marine regions of the world. In this study, we analyzed where and how this species has expanded in western Eurasia (up to the Black Sea) by combining published records and citizen science data with spatial analysis tools. We found that the invasion is most advanced in the Black Sea, where the species is widespread and linked to brackish, nutrient-rich areas influenced by rivers. In the Mediterranean Sea, the invasion has only recently accelerated, with the north-western Adriatic Sea representing the main area of expansion. In Northwest Europe, the species is still limited to a small area and has not yet spread widely. Overall, our results suggest that environmental conditions, especially salinity and river inputs, play a key role in determining where the species can establish and spread. Coastal areas influenced by freshwater emerge as particularly important, highlighting the need for monitoring and management to reduce potential impacts.

Abstract

The invasion of the marine alien gastropod *Rapana venosa* (Valenciennes, 1846) across different basins is investigated through a spatiotemporal analysis of distribution patterns, aggregation processes, and spatial structure. Occurrence data from scientific literature and citizen science were integrated with GIS-based spatial statistics to compare invasion dynamics in the Black Sea, the Mediterranean Sea, and Northwest Europe. The Black Sea represents the most advanced invasion stage, characterized by extensive distribution, multiple aggregation zones, and strong associations with brackish, nutrient-rich areas influenced by major river outflows. In the Mediterranean, the invasion has progressed from a prolonged establishment phase to a recent acceleration, with the Adriatic Sea acting as the historical core of expansion. Here, persistent populations are concentrated near the Po River delta and lagoon systems, where reduced salinity and high nutrient loads favor both settlement and long-term persistence. In Northwest Europe, *R. venosa* remains in the establishment phase, forming a compact and localized nucleus along the French Atlantic coast without evidence of broad spatial expansion. Our analyses suggest that environmental factors, particularly salinity gradients and riverine inputs, are possibly related to the observed invasion patterns. Transitional coastal environments emerge as important areas for establishment and subsequent spread, suggesting that monitoring efforts should prioritize these environments.



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Keywords: alien rapa whelk; hotspots; invasive alien species; marine bioinvasion; spatiotemporal statistics; spread dynamics

1. Introduction

Rapana venosa (Valenciennes, 1846), commonly known as the veined rapa whelk, is a large predatory gastropod native to the temperate waters of the northwestern Pacific, including the Sea of Japan, Yellow Sea, and East China Sea. Since the mid-20th century, this species has expanded far beyond its native range, largely facilitated by maritime traffic—through transport via ballast water or as part of the hull fouling community—and the accidental transfer of egg masses associated with aquaculture activities [1]. The first record of *R. venosa* outside its native distribution occurred in 1947 in the Black Sea, in Novorossiysk Bay, misidentified as *R. bezoar* (Linnaeus, 1767) [2]. Within a decade, the species spread along the Caucasian and Crimean coasts and penetrated the Sea of Azov [3], demonstrating a remarkable capacity for rapid dispersal and establishment in new environments. Today, *R. venosa* is regarded as one of the most dangerous invasive species in both the Black Sea and the Mediterranean, owing to its intense predatory pressure on native bivalve populations and its ability to modify benthic community structure. At the same time, it has also become a valuable fishery resource in several regions, particularly within the Black Sea basin [4,5]. Although the species has been reported in the Sea of Marmara since 1966 [6] and later detected in several Mediterranean coastal regions, including parts of France, the mechanism underlying its expansion within the Mediterranean Sea remains unclear. It is nevertheless considered very likely that this distribution pattern results from multiple independent introduction events rather than from a single, continuous colonization process. In several parts of the Mediterranean Sea, however, *R. venosa* shows a more limited degree of invasion compared to its extensive and well-documented spread in the Black Sea. Parallel to its Mediterranean spread, *R. venosa* has also invaded the eastern Atlantic, where individuals have been recorded from the North Sea to the coasts of Spain, as well as in the western Atlantic, where it was first detected and established in Chesapeake Bay in 1998 [7]. A particularly successful and well-documented invasion took place in the Río de la Plata estuary (western Atlantic) beginning in 1999. Since then, the species has expanded along the Argentine and Uruguayan coasts and, more recently, into southern Brazil, where it impacts native mollusk communities and exhibits high ecological adaptability [8,9]. Globally, the invasive success of *R. venosa* is attributed to its ecological plasticity, broad dietary spectrum, high fecundity, long lifespan, strong tolerance to human-induced environmental stressors, and ability to exploit a wide range of habitats—from soft substrates to mussel and oyster beds—consistently generating significant impacts on native benthic communities and commercial fisheries [1]. As such, *R. venosa* represents an important model organism for studying marine biological invasions and for developing effective management strategies across invaded areas. Moreover, understanding the spread and ecological impact of *R. venosa* greatly benefits from the application of spatial statistics and GIS-based analyses, which enable the identification of invasion hotspots, the modeling of dispersal pathways, and the assessment of environmental drivers shaping its distribution [10–15]. In this paper, we present an analysis of the spatial distribution of *R. venosa* across the Black Sea and adjacent waters, the Mediterranean Sea, and the northwest Atlantic, with the objective of identifying the directional patterns that characterize its spread and assessing the geographic factors that may have influenced its invasion dynamics.

2. Materials and Methods

2.1. *Rapana venosa* Invasion History

To investigate the distribution of *Rapana venosa* in the Black Sea and adjacent waters (the Azov and Marmara Seas) (BS), the Mediterranean Sea (MS), and Northwest European waters (NWE), occurrence records were compiled from both the scientific literature and citizen-science archives. Relevant studies were identified using the search engines Google (google.com), Google Scholar (scholar.google.com), and ResearchGate (researchgate.net), with searches conducted up to December 2025. A range of keyword combinations was employed to ensure comprehensive coverage of the available literature. Terms such as *Rapana venosa*, its synonym *Rapana thomasi*, the misapplied name *Rapana bezoar*, and its common names “rapa whelk” and “veined rapa whelk” were used as search keywords, individually and in combination with geographical descriptors including Black Sea, Azov, Marmara, Mediterranean, and Atlantic. Additional bibliographic sources were gathered by examining the reference lists of the retrieved publications. Citizen-science archives (i.e., iNaturalist) were also consulted.

The integration of occurrence data from heterogeneous sources, including citizen-science platforms and literature, may introduce spatial and temporal biases associated with uneven sampling effort, reporting intensity, and temporal coverage. Such heterogeneity can potentially affect the robustness and interpretation of inferred invasion patterns. To reduce these limitations, a filtering protocol was applied: (i) only records with precise geographic coordinates or clearly identifiable sampling locations were retained; (ii) duplicate, doubtful, or taxonomically uncertain records were excluded; and (iii) for citizen-science data, only records accompanied by clear photographs were considered, and exclusively those documenting live individuals or specimens retaining the operculum were included.

An unpublished observation by one of the authors (LC), at coordinates 44.845398° N, 12.435761° E, was also considered.

The compiled dataset included the year of the record (or, when unavailable, the publication year), locality, country, geographic coordinates, and source.

2.2. Distribution, Aggregation Patterns, and Spatial Structure Analyses

Spatial data were processed in ArcMap 10.3 (ESRI, Redlands, CA, USA) by retaining only the earliest occurrence record within each 0.05° latitude–longitude grid cell, following the approach of Lipej et al. [16]. This procedure ensured that only a single occurrence was assigned to intensively sampled areas, thereby reducing the effects of preferential sampling and the potential bias associated with distribution analyses [16]. The resulting subset was used for all analyses, regardless of the number of individuals recorded within each grid cell.

Following Perzia et al. [11], spatial and temporal statistical analyses were performed to characterize the distribution, aggregation patterns, and spatial structure of the records to identify (i) spatial distribution patterns, (ii) temporal changes in distribution, (iii) the earliest and most recent phases of species spread, (iv) dispersal versus settlement areas, and (v) spatial outliers. Qualitative and quantitative multi-parameter modeling was carried out using the Spatial Analyst and Spatial Statistics toolboxes in ArcMap.

Data were analyzed separately for the three investigated areas—BS, MS, and NWE—due to temporal and geographical differences in the invasion process.

Invasion phases of *R. venosa* were identified from the cumulative occurrence curve, segmented by changes in slope, following Perzia et al. [11]. Regression lines were used to estimate the rate of increase and to delineate the different phases of the invasion process, i.e., arrival (Ar), establishment (Es), and expansion (Ex). The *y*-axis values also represent the expansion area, measured as the cumulative number of 0.05° latitude/longitude grid cells affected.

Spatial patterns in *R. venosa* occurrences were investigated using a combination of complementary spatial statistical approaches.

Cumulative kernel density analyses were applied to qualitatively explore temporal and spatial variations in occurrence density across different time periods [11–15,17]. Specifically, the analyses were conducted to (i) evaluate temporal and spatial increases in occurrence density, (ii) identify areas of species expansion, and (iii) detect persistently high occurrence densities.

Key distribution characteristics—center of gravity (median center), directional dispersion along the east–west axis (XStdDist) and along the north–south axis (YStdDist), and directional trends [18,19]—were calculated for each invasion phase within the study areas.

The north–south and east–west components reported in this study do not represent actual dispersal pathways but are used solely as statistical descriptors of the spatial configuration of the distribution. This approach enabled the assessment and comparison of spatiotemporal distribution changes and the evaluation of shifts in distribution shape (e.g., dispersed, compact, or elongated), thereby helping to identify patterns of species expansion and/or contraction over time [11–15].

Incremental Spatial Autocorrelation (ISA) was first conducted to determine the distance at which spatial autocorrelation in occurrence density was maximized, based on peaks in the z-score of Global Moran’s I [20]. The ISA analysis also identified the optimal distance threshold used to define the spatial scale of subsequent local analyses.

Hot spot analysis was performed using the Getis–Ord Gi* statistic (GOG*) to identify statistically significant spatial clusters of high (hot spots) and low (cold spots) occurrence densities by comparing local neighborhood values with the global spatial context [21]. Years of occurrence were used as the feature attribute, with clusters classified according to their confidence level: high-confidence hot spots indicate recent occurrence clusters, high-confidence cold spots indicate older clusters, and clusters not statistically significant indicate random spatial patterns. This approach was applied to assess spatial trends in species spread and settlement dynamics [11–15].

Finally, local spatial autocorrelation was assessed using Anselin’s Local Moran’s I (AMI) to identify statistically significant spatial outliers in species occurrence [22]. In particular, high–low and low–high outliers were detected, representing recent records located near clusters of older records, and vice versa, reflecting negative spatial autocorrelation [11–15].

Table 1 summarizes the analyses and indicators applied to the study areas (BS, MS, and NWE).

Table 1. Analyses, spatial and temporal indicators, ecological interpretation, methods, and scales (modified from Perzia et al. [15]). For the analyses, only the first records per 0.05° lat/long grid cell were considered.

Analysis/ Indicator Name	Tools	Spatial Scale	Time Scale	Ecological Meaning
Occurrence Increase rate	Evaluation of the slopes of the cumulative occurrence curve using the least squares method	Global	Temporal and spatial–temporal pattern	
			BS:	
			1947–1959; 1960–2003;	
			2004–2025	
			MS:	
			1973–1982; 1983–2019;	
			2020–2025	
			NWE:	
			1997–2019; 2020–2025	
			Identification of the invasion phases; rate of specimen increases; expansion areas	

Table 1. Cont.

Analysis/ Indicator Name	Tools	Spatial Scale	Time Scale	Ecological Meaning
Density hotspots	Kernel density BS: distance radius = 87 km MS: distance radius = 83 km NWE: distance radius = 68 km	Global	BS: 1947–1959; 1947–1983; 1947–2003; 1947–2025 MS: 1973–1982; 1973–2001; 1973–2019; 1973–2025 NWE: 1997–2004; 1997–2011; 1997–2019; 1997–2025	Nuclei of record aggregation; space–time occurrence density increase; occurrence of persistent areas; highest density areas
Key characteristics of distribution				
Center of gravity	Central tendency (median center)	Global	BS: 1947–1959; 1960–2003; 2004–2025	Species concentration center and its change over time
Directional Dispersion	XStdDist, YStdDist; (km) Standard deviational ellipse (1 standard deviation) Rotation (°)	Global	MS: 1973–1982; 1983–2019; 2020–2025	Species distribution in X and Y directions
Directional trends	Standard deviational ellipse (1 standard deviation)	Global	NWE: 1997–2003; 2005–2019; 2020–2025	Directional trend of species dispersion
Aggregation patterns and spatial structure				
Spatial autocorrelation for a series of increasing distances	Incremental spatial autocorrelation (ISA) Number of distance bands = 10	Global	All years	The distances where the clustering spatial processes are most pronounced. Distribution pattern: dispersion vs. random vs. clustering. Change in the spatial pattern over time
Statistically significant hot spots and cold spots	Getis–Ord Gi* (GOG*) BS: distance band = 87 km MS: distance band = 473 km NWE: distance band = 165 km Anselin local Moran’s I (AMI)	Local	All years	Initial and current direction of spread and identification of dispersion/settle areas
Spatial outliers	BS: distance band = 87 km MS: distance band = 473 km NWE: distance band = 165 km	Local	All years	Presence of recent records within clusters of older records (and vice versa)

3. Results

A total of 810 occurrence records of *Rapana venosa* were compiled from the Black Sea and adjacent waters (562), the Mediterranean Sea (176), and Northwest Europe (72). The full dataset is provided as Supplementary Material Table S1 [1–6,23–203].

After filtering, 453 records were retained for analysis, including 319 from BS, 95 from MS, and 39 from NWE.

Figure 1 shows the spatial distribution of records, as well as the first and most recent occurrences in each area: the Russian coast (1947) and the Bosphorus Strait (2025) in the BS area; the Adriatic Sea (1973) and Montenegro (2025) in the MS; and the French Atlantic coast (1997 and 2025) in the NWE.

3.1. Invasion History and Spatial–Temporal Patterns of *Rapana venosa* Distribution

Figure 2 shows the cumulative occurrence curves of *R. venosa* in the three invasion areas (BS, MS, and NWE), together with the cumulative number of grid cells affected by the species over time. The equations of the regression lines and the corresponding R^2 values are also reported.

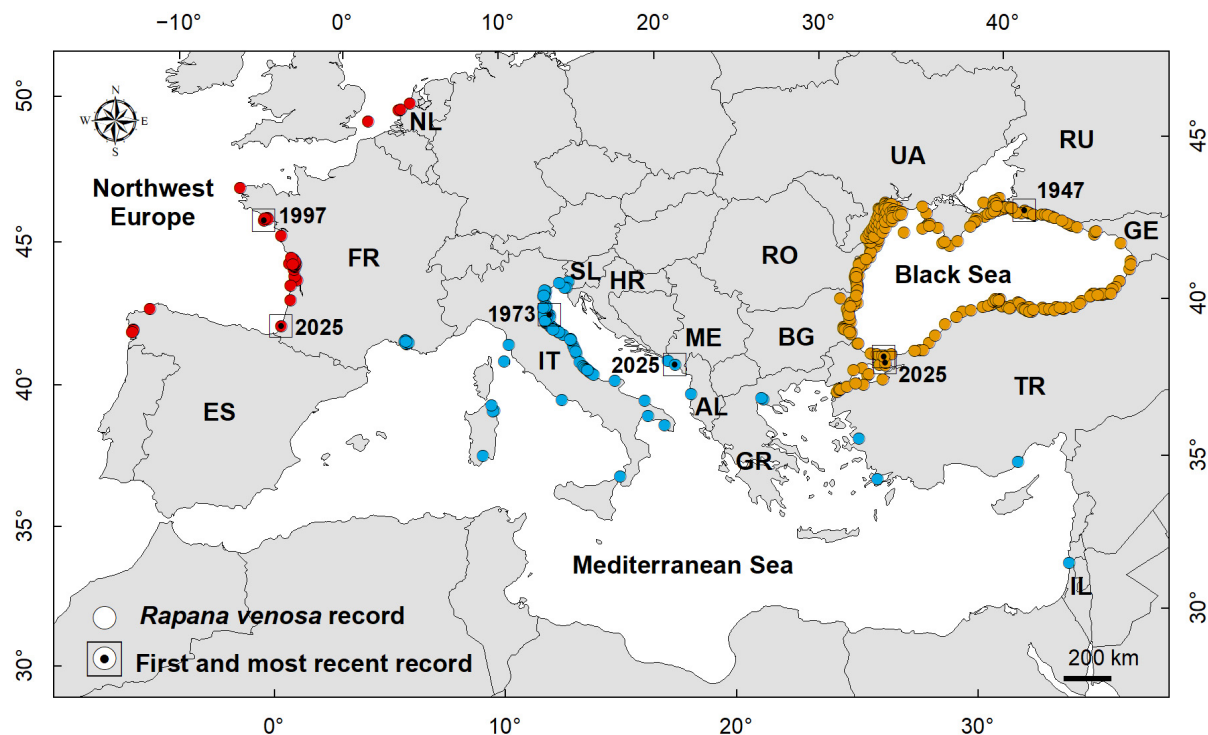


Figure 1. Distribution of *Rapana venosa* across the three invasion areas: the Black Sea and its adjacent waters (Azov and Marmara Seas) (orange dots), the Mediterranean Sea (blue dots), and Northwest Europe (red dots). The first and most recent records in each area are also reported.

In the BS area, three slope changes were identified, corresponding to the arrival phase (1947–1959), the establishment phase (1960–2003), and the expansion phase (2004–2025). The marked increase in slope values indicates that the invasion of *R. venosa* in the BS area has accelerated substantially during the last 21 years, with a slope of 9.95 ± 0.51 during the expansion phase, compared to much lower rates during the arrival (slope = 1.12 ± 0.06) and establishment phases (slope = 2.02 ± 0.06). The progressive increase in slope values indicates an acceleration of the invasion process over time, with an intensification during the most recent expansion phase.

Similarly, in the MS area, the cumulative curve displayed three clear slope changes, corresponding to: (i) the arrival phase (1973–1982; slope = 0.65 ± 0.09); (ii) the establishment phase (1983–2019; slope = 1.55 ± 0.04); and (iii) the expansion phase (2020–2025; slope = 3.97 ± 0.46). In both the BS and MS areas, the arrival phase was relatively short (12 and 9 years, respectively), followed by a long-term establishment phase, lasting 43 years in the BS and 36 years in the MS.

In the NWE area, the cumulative curve showed two distinct changes in slope, corresponding to a prolonged arrival phase (1997–2019; slope = 0.73 ± 0.05) and a subsequent establishment phase (2020–2025; slope = 1.26 ± 0.25). No expansion phase was detected in this area.

Figures 3–5 illustrate the spatiotemporal expansion of *R. venosa* in the BS, MS, and NWE areas, respectively, based on cumulative occurrence records and kernel density analysis. These showed a period-to-period variation in space and time, highlighting substantial changes in occurrences, both in terms of spread and species aggregation. The kernel density gradient (from low to high) highlights areas with increasing concentrations of records along the coastline.

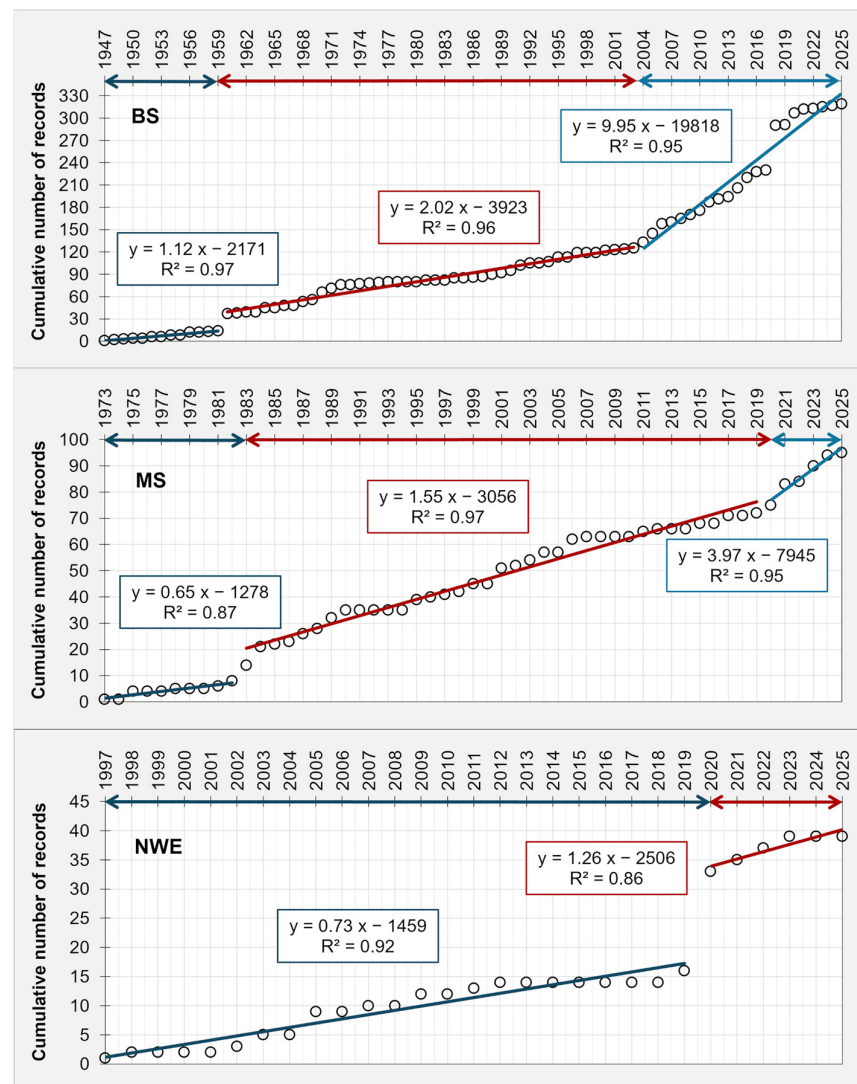


Figure 2. Cumulative curves of occurrences of *Rapana venosa* in the three invasion areas: the Black Sea and adjacent waters (the Azov and Marmara seas) (BS), the Mediterranean Sea (MS), and Northwest Europe (NWE). Only the first records within a 0.05° Lat/Long grid were considered. Arrows indicate the phases in the invasion process—arrival (blue), establishment (red), and expansion (light blue)—and mark the corresponding years for each phase.

3.1.1. Black Sea and Adjacent Waters

During the arrival phase (1947–1959; Figure 3a), occurrences were limited and mainly concentrated in the northwestern Black Sea, particularly along the Crimean coast.

After 1960, the species entered the establishment phase (Figure 3b,c). During this period, the number of records increased, and the distribution extended along a larger portion of the northwestern and western coasts, with additional occurrences appearing along the southern coastline.

The most recent cumulative map (1947–2025; Figure 3d), which includes the expansion phase of the species, shows a basin-wide coastal distribution, with higher kernel density values along extensive portions of the western and southern Black Sea coasts and additional records along the northern and eastern sectors.

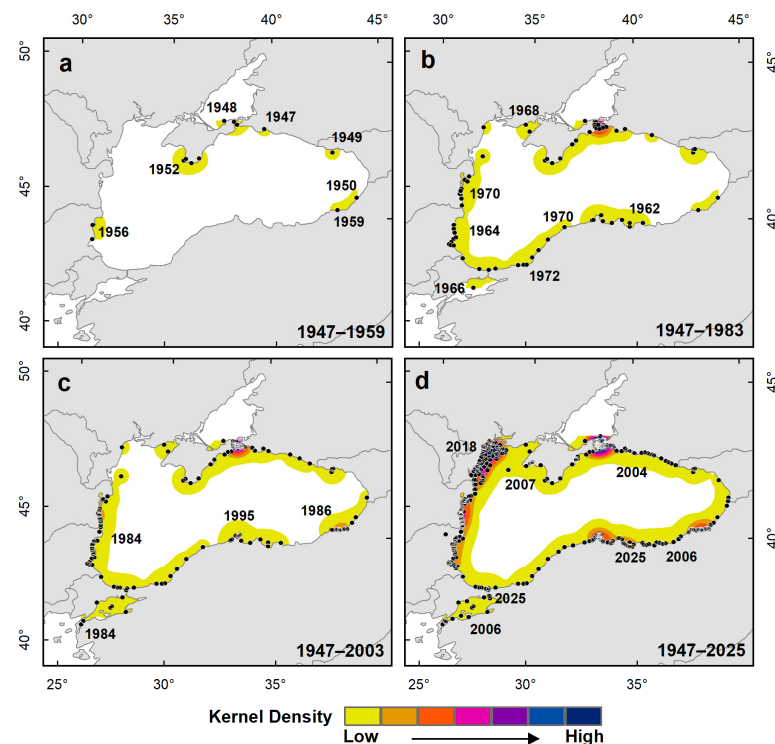


Figure 3. Cumulative kernel density maps showing the spatiotemporal expansion of *Rapana venosa* in the Black Sea and adjacent waters: (a) 1947–1959; (b) 1947–1983; (c) 1947–2003; (d) 1947–2025. Black circles indicate occurrence records of *R. venosa*.

3.1.2. Mediterranean Sea

During the arrival phase (1973–1982; Figure 4a), records are scarce and mainly concentrated in the northern Adriatic Sea, particularly along the Italian coast. An isolated occurrence is recorded in the northern Tyrrhenian Sea (1978). Kernel density values remain low and highly localized, reflecting the initial detection of the species with limited spatial spread.

In the subsequent period (1973–2001; Figure 4b), the number of records increases, and the distribution expands across much of the Adriatic basin, with additional occurrences reported in the central Mediterranean and in the eastern Mediterranean (the Aegean Sea and the south Turkish coast). Areas of higher kernel density begin to emerge along the Adriatic coasts, indicating increasing concentrations of records in this region.

In the following phase (1973–2019; Figure 4c), the spatial distribution becomes broader, with records reported throughout much of the central and eastern Mediterranean, including the Ionian Sea. The Adriatic Sea remains the main area with higher record density, while additional occurrences contribute to a more widespread distribution of records across the basin.

In the most recent cumulative phase (1973–2025; Figure 4d), higher kernel density values remain concentrated in the Adriatic Sea, while additional occurrences are reported in the western Mediterranean. Notably, the distribution of records remains largely confined to the northern Mediterranean coasts. Overall, the pattern reflects a progressive increase and spatial spread of occurrence records across the Mediterranean, while maintaining a clear concentration along its northern coastal areas.

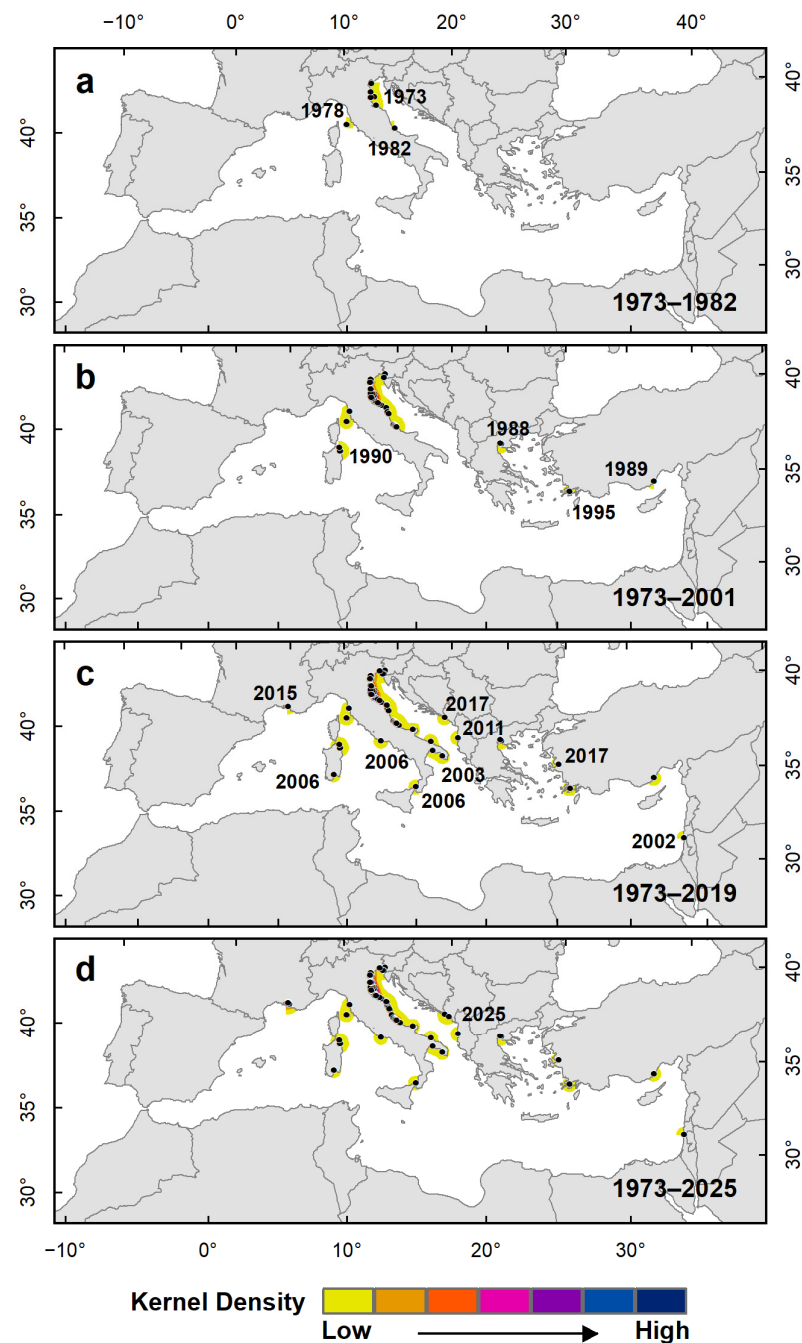


Figure 4. Cumulative kernel density maps showing the spatiotemporal expansion of *Rapana venosa* in the Mediterranean Sea. Maps (a–d) represent the invasion phases: (a) 1973–1982; (b) 1973–2001; (c) 1973–2019; (d) 1973–2025. Black circles indicate occurrence records of *R. venosa*.

3.1.3. Northwest Europe

Figure 5 shows the progressive expansion of *R. venosa* in the NWE area from the initial detection site, with increasing spatial continuity over time.

The first three maps (Figure 5a–c) represent the arrival phase. During the earliest period (1997–2004), the species was recorded at a limited number of sites along the French Atlantic coast. In the following period (1997–2011), additional records appeared in the Bay of Biscay and the English Channel, indicating a gradual expansion from the initial introduction area. By 1997–2019, the distribution extended further along the French coast and the southern Dutch coast.

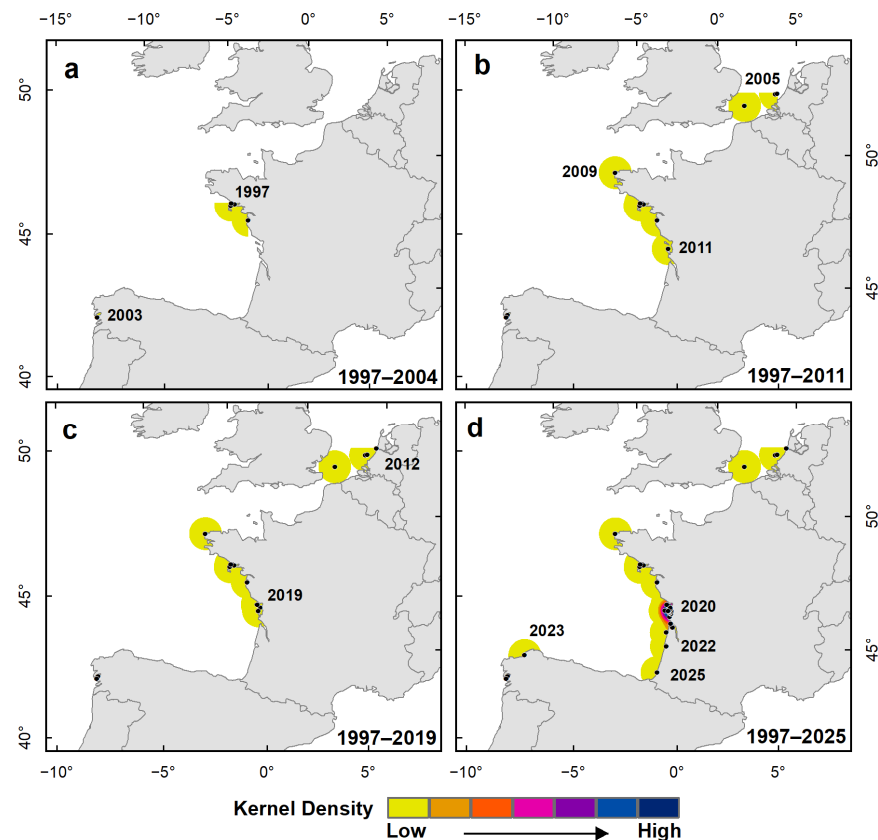


Figure 5. Cumulative kernel density maps showing the spatiotemporal expansion of *Rapana venosa* in northwestern Europe: (a) 1997–2004; (b) 1997–2011; (c) 1997–2019; (d) 1997–2025. Black circles indicate occurrence records of *R. venosa*.

The last map (1997–2025), including the recent establishment phase, shows a more continuous distribution along parts of the French Atlantic coast, with recent records confirming the continued presence of the species in the region.

3.2. Key Characteristics of Distribution

Figure 6 presents the key characteristics of the distribution of *R. venosa* in BS, MS, and NWE areas across the examined periods.

The central tendency, directional dispersion, and directional trend varied across space and time in the three investigated areas, revealing distinct changes in the spatial configuration of the invasion phases, particularly in MS and NWE. These patterns indicate area-specific trajectories, with periods of spread followed by partial contraction and, in some cases, a reorientation of the main dispersal axis.

3.2.1. Black Sea and Adjacent Waters

In the BS, dispersion was initially higher along the north–south axis ($YStdDist = 525$ km) than along the east–west axis ($XStdDist = 219$ km) in 1947–1959 (Ar phase). During 1960–2003 (Es phase), both axes remained high and relatively stable (548 km in Y; 281 km in X), reflecting sustained broad distribution. In 2004–2025 (Ex phase), $XStdDist$ increased substantially to 496 km, while $YStdDist$ decreased to 290 km, indicating a shift toward greater zonal dispersion. The directional trend remained consistent across periods (70 – 92°), suggesting a stable main orientation of spread.

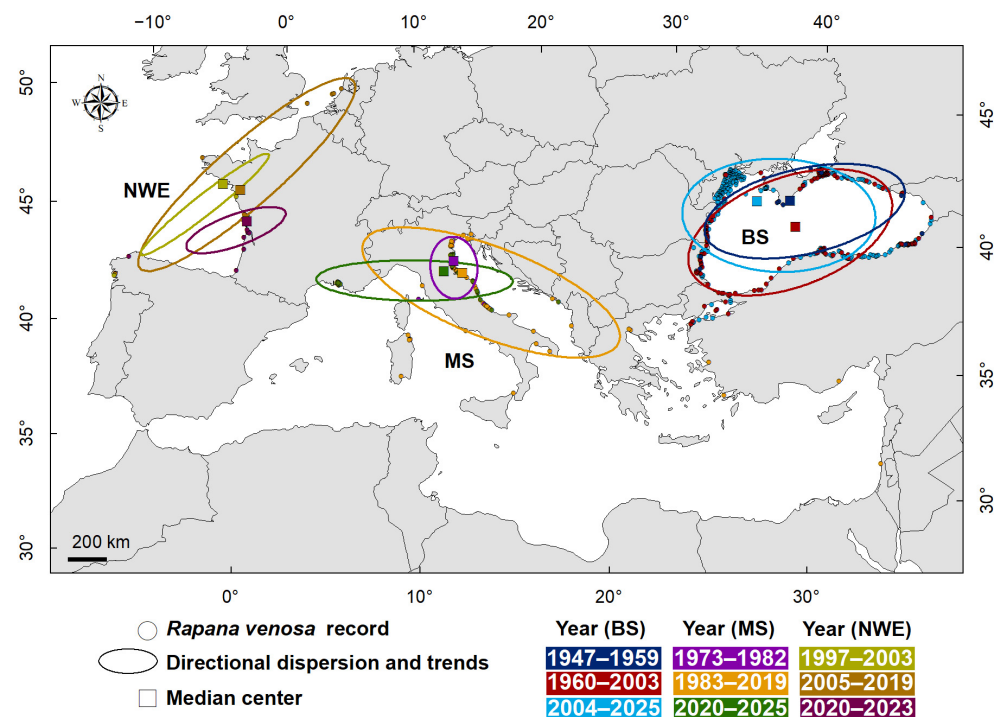


Figure 6. Key distribution characteristics of *Rapana venosa* in the three invasion areas: the Black Sea and adjacent waters (the Azov and Marmara seas) (BS), the Mediterranean Sea (MS), and Northwest Europe (NWE). Central tendency (median center), directional dispersion, and temporal trends calculated for different periods, showing changes in spatial distribution over time.

3.2.2. Mediterranean Sea

In the MS, the first period (1973–1982), corresponding to the arrival phase, was characterized by moderate and relatively balanced dispersion (159 km in X; 121 km in Y), with occurrences concentrated along the northeastern coast of Italy in the Adriatic Sea. A marked spread occurred during the 1983–2019, Es phase, when XStdDist increased to 704 km and YStdDist to 231 km, indicating a pronounced zonal dispersion. In the most recent period (2020–2025, Ex phase), both axes contracted (505 km in X and 104 km in Y), suggesting a westward spatial consolidation. The rotation angle shifted from 175° in the earliest period to 111° and then 91°, indicating a progressive reorientation of the main dispersal axis. The ellipse became elongated from Italy toward France; however, the highest number of records continued to be reported in the Adriatic Sea, where the median centers of distribution remained confined.

3.2.3. Northwest Europe

The arrival phase of *R. venosa* in the NWE area was examined in two sub-periods (1997–2003 and 2005–2019). Dispersion was consistently greater along the north–south axis than along the east–west axis throughout all periods. YStdDist increased from 417 km (1997–2003) to a peak of 728 km (2005–2019) before decreasing to 269 km in 2020–2025 (Es phase), indicating an initial longitudinal confinement followed by a pronounced meridional spread during the arrival phase and a subsequent contraction in the establishment phase. XStdDist followed a similar but less marked pattern (52 km → 160 km → 80 km). The directional trend remained relatively stable, with rotation values between 49° and 70°, indicating a persistent NE–SW orientation from France toward Spain despite changes in dispersion magnitude. The median centers for all periods were located along the western Atlantic coast of France.

3.3. Aggregation Patterns and Spatial Structure

At the global scale, the ISA revealed statistically significant positive spatial autocorrelation in all three invasion areas, as indicated by Global Moran's I values higher than the expected indices and z -scores exceeding 2.58 ($p < 0.01$). This confirms that occurrence records were spatially clustered rather than randomly distributed.

In the BS, the GMI (0.18) exceeded the expected value (-0.003), showing moderate spatial clustering. This intermediate pattern suggests the presence of identifiable aggregation zones combined with a relatively wide spatial spread.

In the MS, the GMI (0.11) was only slightly above the expected index (-0.011), indicating weaker but still significant clustering. This pattern reflects a broad and diffuse distribution.

In the NWE, the observed GMI (0.58) was markedly higher than the expected value (-0.026), indicating strong spatial clustering and a well-defined aggregation structure. This suggests that records were concentrated within specific sectors, consistent with a localized invasion nucleus and limited dispersal beyond core areas.

Overall, the results indicate significant but area-dependent clustering intensity, with moderate clustering in the BS, more diffuse spatial structure in the MS, and the strongest aggregation in the NWE.

At a local scale, the GOG* and ALM analyses revealed clear spatial structuring in the distribution of significant hot spots, cold spots, and outliers across the three invasion areas (Figure 7):

- **Black Sea and adjacent waters**—In the BS area, the earliest records are strongly clustered in the north-eastern sector (cold spot, 99%), consistent with the historical introduction area. Additional cold spots along the southern and eastern coasts denote areas of earlier establishment. Extensive and highly significant hot spots (95–99%) occur along the north-western Black Sea shelf, indicating large and persistent core zones of recent spread and ongoing expansion. The spatial arrangement of cold and hot spots supports a stepwise expansion from the north-eastern nucleus, with progressive infilling of adjacent areas and short-range dispersal processes. The presence of high outliers in the north-eastern Black Sea highlights sites with very recent records surrounded by older ones.
- **Mediterranean Sea**—In the MS, a significant cold spot (90–95%) is identified along the central–northern Adriatic coast, confirming this region as the primary aggregation area. Most other locations in the Mediterranean Sea were classified as not significant, indicating weak spatial clustering of similar occurrence years (i.e., a dispersed spatial pattern). A distinct pattern emerges along the French Mediterranean coast, where a highly significant hot spot (99%) identifies this region as the main area of recent records. The presence of high outliers is observed in the northern Adriatic.
- **Northwest Europe**—In the NWE, statistically significant cold spots were located further north, along the southern North Sea coasts, characterized by earlier records and suggesting the initial establishment area. In contrast, hot spots (95–99%) were concentrated along the French Atlantic coast, indicating that this area hosts the most recent occurrences and represents the current expansion front.

Overall, the temporal hot spot pattern demonstrates a non-random diffusion process, with distinct invasion nuclei and clear chronological gradients in all three basins: (i) the most spatially extensive and statistically robust clustering in the BS; (ii) a comparatively dispersed pattern in the MS, excluding the Adriatic Sea; and (iii) a more localized but strong nucleus in the NWE.

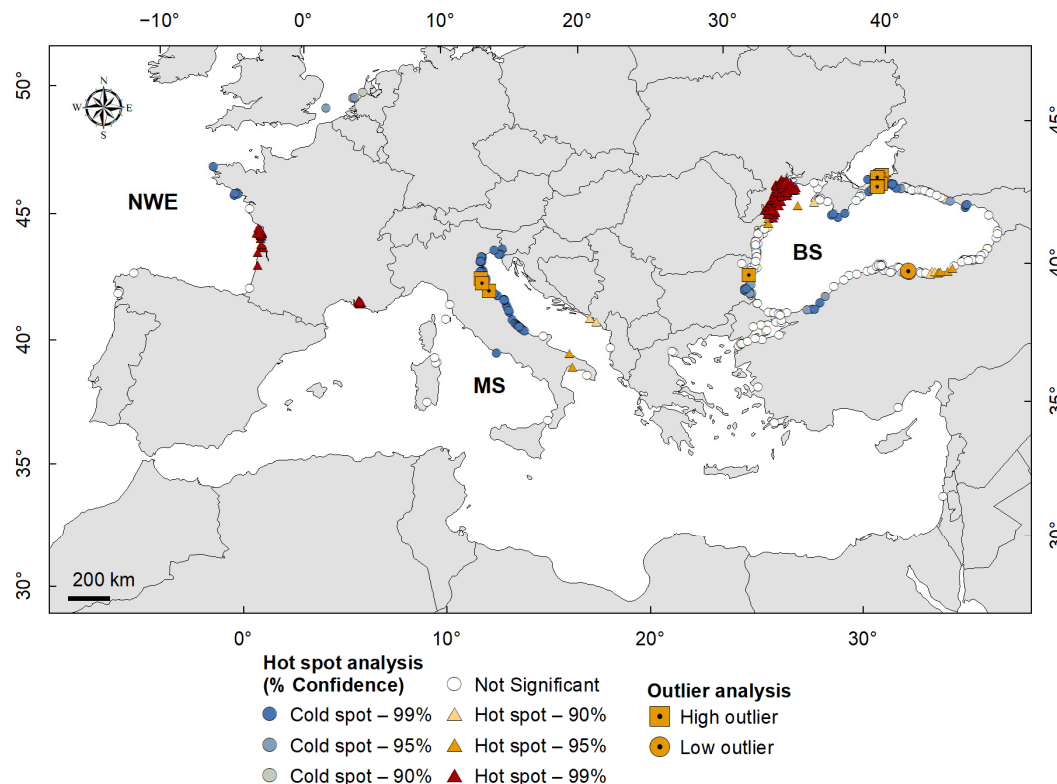


Figure 7. Results of the hot spot (Getis–Ord G_i^*) and outlier analysis (Anselin local Moran’s I) on records of *Rapana venosa* in the three invasion areas: the Black Sea and adjacent waters (the Azov and Marmara seas) (BS), the Mediterranean Sea (MS), and Northwest Europe (NWE). Areas with statistically significant spatial clustering (cold spot—blue circles; hot spot—red circles) are shown. Low outliers (yellow circles) and high outliers (yellow squares) are indicated. White circles indicate records with non-significant index values.

4. Discussion

Rapana venosa possesses a suite of biological and ecological traits that make it an exceptionally successful marine invader. It thrives across a wide range of habitats and tolerates low salinity, pollution, and oxygen-poor environments [204,205]. Its strong predatory capacity, particularly on economically and ecologically important bivalves, and adaptation to locally available prey contribute to significant declines in native benthic communities and disrupt local trophic structures [1]. Its dispersal potential is amplified by a planktonic larval stage that may remain in the water column for several days and tolerates broad salinity ranges, allowing larvae to be transported long distances in ballast water [206]. Once established, the species grows rapidly and early achieves sexual maturity [206]. High fecundity, coupled with successful egg deposition on hard substrates, ensures robust recruitment, while longevity exceeding 15 years maximizes reproductive output over time [7]. Remarkably, *R. venosa* can establish thriving populations even when introduced by very few individuals, demonstrating strong resilience and adaptability despite low genetic diversity [207]. Despite exhibiting traits typically associated with invasive species, its distribution is not uniform across the investigated area. This means that the species does not colonize all potentially suitable areas in a homogeneous way; rather, it appears concentrated in specific sites that are often isolated from one another. Such discontinuity may depend on several factors, including the availability of suitable habitats, environmental or geographical barriers, or the need for human-mediated vectors to facilitate its spread.

The Black Sea stands out as the most advanced and spatially expansive invasion case among the three basins examined. After a relatively short arrival phase in the northeast

sector and a prolonged establishment period, the species expanded rapidly over the past two decades, being recorded along almost the entire coastline, with a stronger presence in the northwest, where highly significant hot spots are concentrated. This area is directly influenced by the outflow of the Danube, Dniester, and Dnieper rivers (Figure 8), whose large freshwater input significantly reduces local salinity levels [208]. As a result, the environmental conditions shift toward brackish values that fall within the optimal tolerance range (25 to 32) evaluated for *R. venosa*, which corresponds to that of mesohaline waters [1].

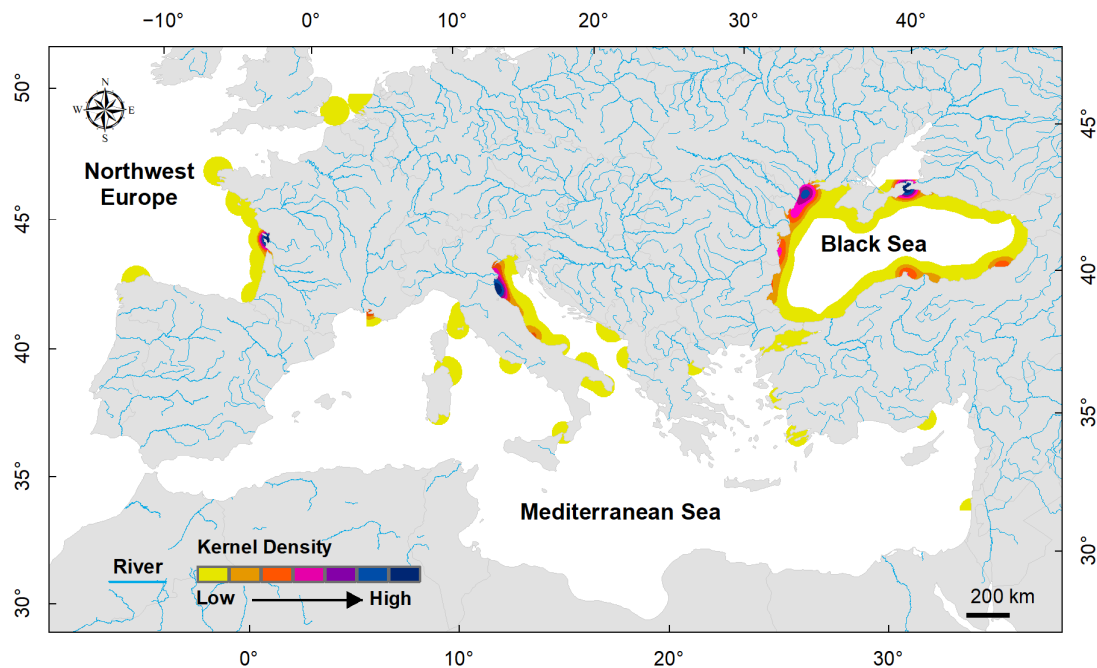


Figure 8. Cumulative kernel density maps showing the spatiotemporal expansion of *Rapana venosa* in all three study areas. Blue lines indicate the main rivers.

The lowered salinity supports the species' physiological needs and enhances its reproductive success and survival. These conditions create an ecological window that facilitates the establishment and spread of *R. venosa*, accelerating its invasion across the region. The species' success is further promoted by the absence of natural predators and by favorable environmental factors such as suitable salinity and temperature, soft-sediment habitats for burrowing, and abundant prey [209]. Overall, the configuration in the Black Sea is consistent with a mature invasion characterized by multiple aggregation zones and ongoing regional spread. This basin, with salinity about half that of the Mediterranean and relatively simple biocenoses, reflects its origin as a former freshwater lake and is characterized by the absence of animal life below ~100 m due to an expanding anoxic layer [210]. Under these conditions, the comparatively large size of *R. venosa* relative to native gastropods may have facilitated active expansion, in contrast to other European seas, where spread is typically driven by passive long-distance transport followed by local dispersal. The persistent surface outflow of low-salinity water from the Black Sea through the Sea of Marmara towards the Aegean–Mediterranean basin [211] is expected to have favored the spread of *R. venosa* into this region. However, although the species has clearly become established in the Sea of Marmara (Figure 7), the extensive and vigorous colonization that occurred in the Black Sea did not progress with the same intensity in the Aegean Sea. In this latter basin, occurrences of the species are far more sporadic, both spatially and temporally, and the populations observed so far appear to represent only the early stages of an invasion process. Such a discrepancy likely reflects differences in environmental conditions, dispersal pathways, and

local ecological pressures, which may hinder establishment and limit the species' ability to spread consistently across the Aegean, where river inputs are scarce, salinity is higher, and the fauna is more diverse, including large predatory gastropods.

In fact, while the species is euryhaline (approximately within the range of 7–30+ [1,204]) and therefore physiologically capable of withstanding broad fluctuations in salinity, its early developmental stages exhibit far narrower tolerance limits. The planktonic larvae, in particular, are highly sensitive to environmental stressors, and both elevated temperatures and high salinity—such as those characterizing large portions of the Aegean Sea—can significantly impair their survival, growth, and metamorphosis [204,212]. As a result, even though adult *R. venosa* can persist in a wide range of habitats, the combination of thermal and salinity regimes in the Aegean may constitute a substantial barrier to the establishment or expansion of self-sustaining populations.

Considering the whole Mediterranean Sea, the invasion history comprises a short arrival phase, a prolonged establishment period, and a recent expansion phase. The progressive rise in slope values over time indicates an acceleration of the invasion process, particularly after 2020, suggesting that the species remained spatially constrained for decades before undergoing a more rapid spread. The Adriatic Sea functions as the historical core area, supported by the presence of significant cold spots and persistent median centers of distribution. Even in the Adriatic Sea, as in the Black Sea, a conspicuous population nucleus can be observed near major river mouths (e.g., the Po River delta) and within lagoonal systems such as those of the northern Adriatic. In contrast, along the eastern Adriatic coast, *R. venosa* is largely absent in the northern sector, likely due to the lack of major river inputs. This spatial pattern once again highlights a certain correspondence between the distribution of *R. venosa* and the presence of brackish water environments. In these areas, the substantial freshwater input from large river systems and coastal lagoons leads to locally reduced salinity and enhanced nutrient (e.g., nitrogen and phosphorus compounds) availability—conditions that closely mirror those in which the species has successfully established and expanded in other regions [1]. However, these environmental drivers are inferred from spatial associations rather than directly tested within the present study; therefore, their role should be considered indicative rather than conclusive, as no formal analytical framework was applied to disentangle their relative contributions or to establish causal relationships. The recurring association between *R. venosa* populations and transitional waters suggests that such environments may act as ecological refugia and potential source areas, facilitating both the settlement of larvae and the persistence of adult populations. Similar considerations may be done for the Berre Lagoon (Mediterranean French coast), characterized by brackish waters, where a hotspot was detected, indicating its role as the leading edge of the ongoing expansion (Figure 7). This lagoon lies remarkably far from all other known Mediterranean invaded sites, strongly suggesting that its colonization is likely the result of anthropogenic transport rather than natural dispersal. Ultimately, this reinforces the hypothesis that brackish, nutrient-enriched zones represent key drivers in shaping the invasion dynamics of the species across different basins. The absence of self-sustaining populations at the low latitudes supports the hypothesis of thermal control acting as a barrier for the spread of the species, consistent with reports indicating that it typically survives within a temperature range of approximately 7–24 °C [1]. Prolonged exposure to elevated summer temperatures, indeed, may exceed upper tolerance thresholds of larval and juvenile stages and compromise both survival and recruitment success. Consequently, the combination of favorable salinity regimes in river-influenced areas and restrictive thermal conditions farther south helps explain why *R. venosa* forms stable populations in the northern Adriatic while failing to extend its range beyond this region. Together, these factors underscore the importance of local hydrographic and thermal regimes in

shaping the species' invasion dynamics across the Mediterranean basin. A lack of food resources can be reasonably excluded as a limiting factor. Along the Italian Adriatic coastline, indeed, eutrophic conditions are well documented [213], ensuring a continuous and abundant supply of suspended organic matter that supports dense populations of filter-feeding bivalves, such as mussels, clams, and oysters, which are the preferred food of *R. venosa* [1,214]. Moreover, the widespread presence of submerged artificial reefs, breakwaters, and other coastal defense structures provides additional hard substrate that greatly enhances larval settlement and recruitment of such organisms [215].

In Northwest Europe, the invasion history comprises a prolonged arrival phase followed by a recent establishment phase, while a distinct expansion phase has not yet emerged. The cumulative trend shows a recent increase in slope, indicating an acceleration in occurrence records but not yet a transition toward large-scale spatial spread. This suggests that the species is still consolidating its distribution rather than undergoing broad geographic expansion, as also confirmed by spatial analyses. Dispersion remained predominantly oriented along the north–south axis, maintaining a consistent NE–SW alignment from the French Atlantic coast to the Iberian Peninsula. Rather than indicating continued range expansion, the recent contraction of both axes suggests a phase of spatial consolidation and internal reorganization of the invaded area. In this context, the high Global Moran's *I* value and the concentration of significant hot spots along the French Atlantic coast point to the emergence of a core invasion nucleus, likely acting as a primary source for local spread. As observed in other basins, aggregations in the Atlantic region also tend to occur near major river mouths—such as the Gironde estuary—suggesting that transitional or nutrient-rich environments may play a facilitative role in supporting persistent populations and promoting localized spread.

5. Conclusions

The invasion dynamics of *Rapana venosa* show basin-specific trajectories across the Black Sea, the Mediterranean Sea, and Northwest Europe, reflecting differences in invasion stages and spatial patterns.

The Black Sea hosts a mature and spatially extensive invasion, the Mediterranean Sea shows a recent and ongoing expansion accompanied by changes in distributional orientation, and Northwest Europe is characterized by a more localized distribution that is still consolidating. These differences highlight the need for monitoring and management approaches tailored to regional invasion dynamics.

The largest and most persistent populations of *R. venosa* are generally associated with major river mouths, where reduced salinity and high nutrient availability may favor settlement and recruitment. These areas therefore represent strategic focal points for monitoring efforts and for the development of targeted management actions. Focusing surveillance efforts in these zones may improve the early detection of newly established populations and support actions aimed at limiting the further spread and establishment of this invasive species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/biology15131012/s1>, Table S1: *Rapana venosa* occurrence database.

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