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Biogeographic Spread of the Non-Indigenous Copepod *Pseudodiaptomus marinus* in Italian Waters—Insights by the Marine Strategy Framework Directive Surveys

Stefano Corona¹  | Érica Caroline Becker^{2,3}  | Ylenia Carotenuto¹  | Alessandra de Olazabal²  | Iole Di Capua^{1,4}  | Alenka Goruppi²  | Valentina Tirelli^{2,4}  | Marco Uttieri^{1,4} 

¹Stazione Zoologica Anton Dohrn, Naples, Italy | ²National Institute of Oceanography and Applied Geophysics—OGS, Trieste, Italy | ³Universidade Do Estado de São Paulo, São Paulo, SP, Brazil | ⁴NBFC, National Biodiversity Future Center, Palermo, Italy

Correspondence: Valentina Tirelli (vtirelli@ogs.it)

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ABSTRACT

Aim: This research investigates the distribution of the non-indigenous calanoid copepod *Pseudodiaptomus marinus* Sato, 1913 in Italian coastal waters as retrieved by the data collected in the Marine Strategy Framework Directive (MSFD) programme in the 2015–2023 time window.

Location: Italian marine coastal waters, Mediterranean Sea.

Taxon: *Pseudodiaptomus marinus* Sato, 1913 (Copepoda, Calanoida).

Methods: The occurrence of *P. marinus* along the Italian coasts was checked in the Italian MSFD database, focusing on Descriptor 1 (D1: marine biodiversity) and Descriptor 2 (D2: non-indigenous species). The temporal and seasonal patterns at a key site (port of Civitavecchia) were also examined.

Results: The MSFD records account for a ~15% increase in the number of *P. marinus* occurrences in Italian waters, expanding the documented range of this species. Records were more abundant in ports and coastal sites, and copepodites dominated the observations. In addition, the seasonal analysis at the port of Civitavecchia showed late-summer peaks, indicating recurrent recruitment and establishment.

Main Conclusions: These findings demonstrate the ongoing expansion and successful establishment of *P. marinus* along the Italian coasts and confirm the role of coastal infrastructures as primary introduction pathways. This study highlights the importance of constant monitoring of the coastal areas to assess the introduction and establishment of non-indigenous species, and underlines the pivotal role of broad-scale initiatives like the MSFD to solicit transnational initiatives.

1 | Introduction

Biological invasions are major drivers of biogeographical change in marine ecosystems, reshaping community structure

and altering ecosystem functioning (Briggs 2007; Katsanevakis et al. 2014). The Mediterranean Sea is a global hotspot for marine bioinvasions due to intense maritime traffic and multiple introduction pathways (e.g., Suez Canal, shipping, aquaculture)

Valentina Tirelli and Marco Uttieri co-last authors.

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(Galil et al. 2018). Within the Mediterranean Sea, Italy is the most invaded EU country currently hosting 282 non-indigenous species (NIS) and ranking third at basin scale following Israel (457 NIS) and Türkiye (437) (Galanidi et al. 2023). The number of NIS in Italy has increased over the years (Occhipinti-Ambrogi 2002; Occhipinti-Ambrogi et al. 2011; Servello et al. 2019), following the same trend reported at the Mediterranean and global scale (Richardson et al. 2025).

Zooplankton invaders are increasingly recognised as sensitive indicators of ecosystem change and shifting biogeographical boundaries (Dexter and Bollens 2020). Among Crustacea, the second most abundant taxon following macrophyta, nine non-indigenous copepods have been recorded in Italian waters to date, including the calanoid *Pseudodiaptomus marinus* Sato, 1913 (Servello et al. 2019). This species was recognised as one of the 26 top-priority NIS in a horizon-scanning study performed at European level (Tsiamis et al. 2020), and is included in the information systems AquaNIS—Aquatic Non-Indigenous and Cryptogenic Species (AquaNIS 2025) and EASIN—European Alien Species Information Network (EASIN 2025). However, due to its small dimensions and the taxonomic expertise required to identify it, this species is presently not ranked among the 18 ones suitable for risk assessment (Tsiamis et al. 2020). In Italy, *P. marinus* has been recorded since 2007, first in the North Adriatic Sea (de Olazabal and Tirelli 2011) and then progressively in all Italian seas over a time interval of approximately 18 years (Sabia et al. 2015; Uttieri et al. 2020, 2023), raising questions about its establishment success, seasonal population dynamics and dispersal pathways. These previous records come from heterogeneous sampling efforts, including periodic long-term samplings and oceanographic cruises (as reviewed in: Uttieri et al. 2020, 2023). As such, these datasets differ in spatial coverage and sampling methodology, limiting their ability to provide a unified view of invasion patterns.

The constant monitoring of coastal areas is pivotal in the assessment of ecosystem biodiversity, in particular with reference to the introduction and establishment of NIS (Galil et al. 2018), one of the major human-derived pressures in the global ocean (Georgian et al. 2022). The European Water Frame Directive (2000/60/EEC) was committed to achieve Good Ecological Status (GES) in the water bodies of the Member States, but it did not explicitly mention NIS, which were indirectly and generically accounted for as ‘other significant anthropogenic impacts’ (Council of the European Communities 2000). Later on, NIS formally became a key descriptor for the assessment of GES in the Marine Strategy Framework Directive (MSFD) (Boon et al. 2020). The MSFD offers a unique opportunity to overcome the above limitations by applying standardised methods across a national coastline. In particular, Descriptor 2 (D2) of the MSFD (non-indigenous species; European Commission 2010) boosted the overall knowledge about the time of arrival, introduction pathway, potential invasiveness and establishment success of NIS at European scale (e.g., Tsiamis et al. 2019, 2018; Zenetos et al. 2010; Zenetos, Tsiamis, et al. 2022).

In this study, the MSFD data collected in Italy over the 2015–2023 window were systematically used to integrate and expand upon the distribution of *P. marinus* along the Italian coastline (Sabia et al. 2015; Uttieri et al. 2020, 2023). The new records

presented in this contribution provide a more exhaustive view of the presence of this NIS in Italian waters, witnessing a significant expansion of *P. marinus* in new areas, while at the same time assessing the successful establishment of this NIS in numerous previously introduced sites. In addition, they provide insight into the relationship between the presence of this species and environmental parameters (salinity, temperature and sea depth), as well as into the interannual seasonal patterns of abundance of this species at a key site. Through this approach, we aim to advance knowledge of the introduction trajectory of *P. marinus* in the Mediterranean Sea and to demonstrate the central role of transnational programmes, such as the MSFD, to monitor biological invasion biogeography in near real time.

2 | Methods

2.1 | Zooplankton Sampling and Taxonomic Analysis

Zooplankton data collected along the Italian coasts between 2015 and 2023 under the MSFD programme were downloaded from the publicly available ISPRA (Italian Institute for Environmental Protection and Research) repository (<http://www.db-strategiamarina.isprambiente.it/app/#/datiMonitoraggio20182023>). In particular, the attention was focused here on Descriptor 1 (D1: marine biodiversity) and Descriptor 2 (D2: non-indigenous species) to improve the monitoring of the occurrence of *Pseudodiaptomus marinus* along the Italian coastline. The analysis of the zooplankton community in terms of taxa composition and abundance was carried out for Descriptor 1 (D1: marine biodiversity) and Descriptor 2 (D2: non-indigenous species), presented as Module 1 and 3 on the website, respectively. Zooplankton samples were collected through vertical hauls using a WP2 plankton net (200 µm mesh size). The net was towed from –50 m to the surface in coastal areas, and from –100 m to the surface in offshore ones. If the site depth was < 50 m, the net was towed starting 1 m above the bottom (SNPA 2024).

The sampling strategy differed between the two descriptors. For D1, samples were collected at three sites located at 3, 6 and 12 miles off the coast along a series of transects (between two and seven for each administrative region, according to the mapping provided in SNPA 2024), every 3 months. For D2, samples were collected at a minimum of two sampling stations in each administrative region in highly impacted locations, namely in ports (docks for loading/unloading of goods; areas for the discharge of ballast waters) and in proximity of shellfish farming (but sufficiently distant from port areas), every 2 months (SNPA 2024). No D2 sampling was carried out in the Basilicata and Molise regions. In the following sections, the term ‘location’ is used to define the geographic toponym of the surveyed area, whereas ‘sampling station ID’ refers to the actual site where the samples have been collected (Table 1). Details on the sampling stations and dates are summarised in the Table S1 and Figure S1.

Mesozooplankton samples were immediately preserved in 70% ethanol solution, stored at 4°C and preferentially analysed within 2 weeks to avoid organism deterioration (SNPA 2024). For abundance and taxonomic composition, zooplankton individuals were

TABLE 1 | List of all *Pseudodiptomus marinus* finds during the 2015–2023 MSFD campaign.

D	Location (Sampling Station ID)	Lat (°N)	Lon (°E)	Y	M	ind. m ⁻³	Stage	<i>P. marinus</i> status
1	Gaeta (IT_m1lt01_12)	41.039	13.604	2019	7	1.23	A	N
1	Gaeta (IT_m1lt01_3)	41.198	13.611	2019	7	11.76	A	N
1	Gaeta (IT_m1lt01_6)	41.152	13.608	2019	6	2.23	A	N_nE
1	Gaeta (IT_m1lt01_6)	41.152	13.608	2019	6	2.23	C	N_nE
1	Gaeta (IT_m1lt01_6)	41.152	13.608	2019	7	3.42	A	N_nE
1	Gulf of Olbia (0129-MS00730_TR03)	40.963	9.626	2016	1	0.70	A	N
1	Ladispoli (IT_m1rm03_6)	41.863	11.996	2019	8	4.97	A	N
1	Lido di Tarquinia (IT_m1vt04_3)	42.208	11.637	2018	11	3.33	A	N_E
1	Lido di Tarquinia (IT_m1vt04_3)	42.208	11.637	2019	6	12.00	C	N_E
1	Lido di Tarquinia (IT_m1vt04_3)	42.208	11.637	2022	10	4.66	C	N_E
1	Lignano Sabbiadoro (ITA06SMLG1)	45.643	13.181	2015	11	11.33	A	E
1	Lignano Sabbiadoro (ITA06SMLG1)	45.643	13.181	2016	7	4.71	A	E
1	Lignano Sabbiadoro (ITA06SMLG1)	45.643	13.181	2016	11	1.49	A	E
1	Lignano Sabbiadoro (ITA06SMLG1)	45.643	13.181	2017	7	2.83	C	E
1	Lignano Sabbiadoro (ITA06SMLG1)	45.643	13.181	2020	7	13.05	C	E
1	Lignano Sabbiadoro (ITA06SMLG1)	45.643	13.181	2020	11	6.52	C	E
1	Lignano Sabbiadoro (ITA06SMLG1)	45.643	13.181	2023	11	0.88	C	E
1	Lignano Sabbiadoro (ITA06SMLG2)	45.608	13.233	2016	7	2.57	A	E
1	Lignano Sabbiadoro (ITA06SMLG3)	45.55	13.318	2016	7	4.04	A	E
1	Ofanto river mouth (3FO02bis)	41.404	16.235	2022	2	5.86	A	N
1	Pellestrina island (50530)	45.288	12.38	2019	7	0.18	A	N_E ^a
1	Pellestrina island (50530)	45.288	12.38	2021	7	0.61	A	N_E ^a
1	Pellestrina island (60530)	45.285	12.45	2017	11	0.23	A	N_nE
1	Pellestrina island (60530)	45.285	12.45	2021	7	0.85	A	N_nE
1	Pellestrina island (70530)	45.278	12.592	2017	7	0.22	A	N_E
1	Pellestrina island (70530)	45.278	12.592	2017	7	0.05	C	N_E
1	Pellestrina island (70530)	45.278	12.592	2020	6	0.05	C	N_E
1	Pellestrina island (70530)	45.278	12.592	2021	7	0.08	C	N_E
1	Rimini (2017)	44.209	12.812	2021	12	0.60	A	E
1	Rimini (617)	44.113	12.636	2022	11	0.85	C	E
1	Rosolina Mare (50720)	45.098	12.417	2017	7	0.39	A	E
1	Rosolina Mare (50720)	45.098	12.417	2018	7	1.78	A	E
1	Rosolina Mare (50720)	45.098	12.417	2018	7	7.11	C	E
1	Rosolina Mare (50720)	45.098	12.417	2021	7	0.07	C	E
1	Rosolina Mare (60720)	45.122	12.482	2021	7	0.36	A	N
1	Rosolina Mare (60720)	45.122	12.482	2021	7	22.74	C	N
1	Rosolina Mare (70720)	45.168	12.606	2017	11	0.28	A	nE
1	Rosolina Mare (70720)	45.168	12.606	2018	1	0.72	A	nE

(Continues)

TABLE 1 | (Continued)

D	Location (Sampling Station ID)	Lat (°N)	Lon (°E)	Y	M	ind. m ⁻³	Stage	<i>P. marinus</i> status
1	Salerno (M1GS6)	40.566	14.735	2021	7	2.51	A	E
1	Trieste (ITA06SMTS1)	45.649	13.695	2015	11	46.90	C	E
1	Trieste (ITA06SMTS1)	45.649	13.695	2016	7	3.53	A	E
1	Trieste (ITA06SMTS1)	45.649	13.695	2016	11	23.56	A	E
1	Trieste (ITA06SMTS1)	45.649	13.695	2017	5	1.66	A	E
1	Trieste (ITA06SMTS1)	45.649	13.695	2021	7	7.07	C	E
1	Trieste (ITA06SMTS1)	45.649	13.695	2023	11	2.69	C	E
1	Trieste (ITA06SMTS2)	45.638	13.626	2016	7	2.83	A	E
1	Trieste (ITA06SMTS2)	45.638	13.626	2016	11	5.93	A	E
1	Trieste (ITA06SMTS2)	45.638	13.626	2017	7	3.77	C	E
1	Trieste (ITA06SMTS2)	45.638	13.626	2021	11	1.55	C	E
1	Trieste (ITA06SMTS2)	45.638	13.626	2022	11	1.66	C	E
1	Trieste (ITA06SMTS2)	45.638	13.626	2023	11	9.42	C	E
1	Trieste (ITA06SMTS3)	45.615	13.487	2015	11	11.00	C	E
1	Trieste (ITA06SMTS3)	45.615	13.487	2016	11	2.98	A	E
1	Trieste (ITA06SMTS3)	45.615	13.487	2019	7	3.53	C	E
1	Trieste (ITA06SMTS3)	45.615	13.487	2021	7	2.83	C	E
1	Trieste (ITA06SMTS3)	45.615	13.487	2022	7	1.57	C	E
1	Trieste (ITA06SMTS3)	45.615	13.487	2023	11	1.13	C	E
1	Volturno mouth (M1FV3)	40.996	13.869	2021	7	0.20	A	N
2	Gioia Tauro (M3T2A)	38.443	15.898	2019	9	3.59	A	nE
2	Gioia Tauro (M3T2B)	38.455	15.904	2018	12	6.68	A	nE
2	La Spezia (SPNIS1)	44.071	9.857	2023	10	1.10	A	N
2	Marina di Ravenna (RAOUT)	44.489	12.315	2015	11	11.50	A	E
2	Marina di Ravenna (RAOUT)	44.489	12.315	2018	7	2.60	A	E
2	Marina di Ravenna (RAOUT)	44.489	12.315	2022	11	6.06	C	E
2	Pellestrina island (50530)	45.288	12.38	2015	12	0.52	A	N_E ^a
2	Pellestrina island (50530)	45.288	12.38	2017	7	0.39	A	N_E ^a
2	Pellestrina island (50530)	45.288	12.38	2017	11	0.30	A	N_E ^a
2	Pellestrina island (50530)	45.288	12.38	2021	7	0.42	A	N_E ^a
2	Pellestrina island (80530)	45.302	12.501	2015	12	2.81	A	E
2	Pellestrina island (80530)	45.302	12.501	2016	9	0.45	A	E
2	Pellestrina island (80530)	45.302	12.501	2017	5	0.44	A	E
2	Pellestrina island (80530)	45.302	12.501	2017	7	0.41	A	E
2	Pellestrina island (80530)	45.302	12.501	2017	11	0.20	A	E
2	Pellestrina island (80530)	45.302	12.501	2021	7	0.22	A	E
2	Port of Brindisi (M3_BR02)	40.649	17.967	2020	9	7.00	A	N
2	Port of Brindisi (M3_BR02)	40.649	17.967	2022	7	179.00	A	N

(Continues)

TABLE 1 | (Continued)

D	Location (Sampling Station ID)	Lat (°N)	Lon (°E)	Y	M	ind. m ⁻³	Stage	<i>P. marinus</i> status
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2015	11	7.73	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2015	11	7.73	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2016	2	7.12	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2016	2	7.12	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2016	9	12.29	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2016	9	841.90	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2017	1	1.43	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2017	2	3.61	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2017	11	0.91	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2017	11	40.19	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2018	1	2.00	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2018	1	11.00	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2018	10	74.00	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2018	10	864.54	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2018	11	115.00	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2018	11	118.00	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2019	2	4.92	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2019	5	18.11	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2019	9	8.00	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2019	12	12.88	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2020	1	2.44	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2020	5	41.96	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2020	7	74.79	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2020	11	155.40	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2021	4	22.07	C	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2022	1	15.45	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2022	6	6.76	A	E
2	Port of Civitavecchia (IT_m3rm1)	42.099	11.777	2023	1	23.66	A	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2015	11	5.30	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2016	9	5.41	A	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2016	9	600.20	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2017	3	4.74	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2017	11	24.14	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2018	10	4.00	A	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2018	10	219.00	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2018	11	2.00	A	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2018	11	97.00	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2019	2	1.25	C	E

(Continues)

TABLE 1 | (Continued)

D	Location (Sampling Station ID)	Lat (°N)	Lon (°E)	Y	M	ind. m ⁻³	Stage	<i>P. marinus</i> status
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2019	3	10.01	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2019	5	4.19	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2019	8	3.98	A	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2019	9	7.14	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2019	12	1.80	A	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2019	12	1.80	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2020	5	120.80	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2020	7	42.49	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2020	11	204.60	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2021	4	86.30	C	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2022	9	15.90	A	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2023	1	23.33	A	E
2	Port of Civitavecchia (IT_m3rm2)	42.104	11.768	2023	3	1.57	A	E
2	Port of Naples (M3PN1)	40.837	14.264	2021	5	0.22	A	N
2	Port of Naples (M3PN2)	40.827	14.261	2021	7	6.69	A	N
2	Port of Salerno (M3PS1)	40.67	14.749	2022	9	50.16	A	N
2	Port of Taranto (M3_TA01)	40.468	17.19	2023	3	5.00	A	nE
2	Porto Corsini (RAIN)	44.495	12.294	2022	9	1.00	C	E
2	Porto Corsini (RAIN)	44.495	12.294	2022	11	33.83	M	E
2	Porto Corsini (RAIN)	44.495	12.294	2023	1	1.23	A	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2015	7	0.77	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2015	9	0.59	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2015	11	1.77	A	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2015	11	31.04	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2016	1	1.87	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2016	7	3.24	A	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2016	9	1.26	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2016	11	1.26	A	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2016	11	8.08	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2017	9	0.16	A	E

(Continues)

TABLE 1 | (Continued)

D	Location (Sampling Station ID)	Lat (°N)	Lon (°E)	Y	M	ind. m ⁻³	Stage	<i>P. marinus</i> status
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2017	11	0.50	A	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2020	7	0.54	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2020	9	1.36	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2020	11	5.96	A	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2021	7	4.71	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2021	11	7.49	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2022	1	0.27	A	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2022	7	0.50	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2022	11	0.50	C	E
2	Sacchetta Trieste basin (ITA06SMNI1)	45.652	13.756	2023	11	3.53	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2015	9	0.24	A	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2015	9	0.94	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2015	11	1.47	A	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2015	11	13.84	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2016	1	0.94	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2016	7	1.99	A	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2016	9	0.34	A	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2016	9	1.01	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2016	11	14.41	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2017	5	0.44	A	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2017	7	2.45	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2017	9	1.33	A	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2017	11	0.47	A	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2018	11	0.44	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2019	7	0.25	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2019	11	0.27	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2020	7	0.81	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2020	9	6.80	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2020	11	2.29	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2021	7	15.08	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2021	11	4.91	C	E

(Continues)

TABLE 1 | (Continued)

D	Location (Sampling Station ID)	Lat (°N)	Lon (°E)	Y	M	ind. m ⁻³	Stage	<i>P. marinus</i> status
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2022	7	0.98	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2022	9	1.35	C	E
2	Settimo Trieste (ITA06SMNI2)	45.623	13.747	2023	11	9.98	C	E

Note: The first column (D) reports in which descriptor the record was scored. For each find, information on the location and sampling station (with MSFD ID) together with its coordinates (latitude, Lat; longitude, Lon) are reported, along with year (Y) and month (M) of sample. The ind. m⁻³ column reports the density of individuals found, while the S column describes the stage composition (adults, A; copepodites, C; or a mix of both, M). The information on whether the record in that sampling station was new, established or not established following Zenetos, Albano, et al. (2022) is reported in the last column (N = new find, N_E = New and Established, N_nE = New and not Established, nE = not Established).

^aPellestrina island (50530) sampling site was surveyed both in D1 and D2. The records from both descriptors were merged for the assessment of the introduction status *sensu* Zenetos, Albano, et al. (2022).

counted at the stereoscope and identified to the lowest taxonomic level (mainly genus or species level) using taxonomic keys from the literature and on line references (e.g., <https://copepodes.obs-banyuls.fr/en/>). For both descriptors, out of the total volume (200–500 mL), subsamples (5 mL each) or fractions (1/2, 1/4, 1/8 or 1/16) of the entire sample were taken, always ensuring the counting of at least 800–1000 individuals for eutrophic/mesotrophic areas, and a minimum of 400 individuals for oligotrophic areas (or when the sample was collected in seasons of low abundance). In addition, samples collected for D2 were entirely examined to check the presence of NIS. Mesozooplankton abundance was expressed as the number of individuals per cubic metre (ind. m⁻³). More details on the quali-quantitative analysis of the samples are reported in SNPA (2024) and references therein.

Copepods were often identified at species level and distinguished as copepodites and adults. For *P. marinus*, only in two cases sample counts were labelled as a mix of both stages, and in a minority of samples young stages were labelled as ‘*Pseudodiaptomidae* copepodites’; since to date only *P. marinus* is known to be present in Italian waters, these records were here assigned to this NIS.

2.2 | Quality Assurance/Quality Control Procedures

All datasets for the different descriptors, years and geographic sub-regions (Western Mediterranean Sea, MWE; Ionian Sea and the Central Mediterranean Sea, MIC; Adriatic Sea, MAD; following the description by the European Environment Agency 2020) were merged into a single dataset. During this process, formatting inconsistencies and typographical errors in the raw files were fixed, including: different column header names between files, allocation of information in the wrong column (e.g., species name in the class name, latitude instead of longitude). The occurrence of *P. marinus* was assessed for each region and compared to previous literature (Sabia et al. 2015; Stefanni et al. 2018; Uttieri et al. 2020, 2023). First records (considering either copepodites, adults or a mix of the two stages) were flagged as ‘new’, while ‘not established’ or ‘established’ referred to records confirmed at the same site up to two or more than three times, respectively, as per the definition by Zenetos, Albano, et al. (2022) (‘ESTABLISHED: this includes species with more than two records distributed in space and time, indicating self-sustaining populations and locally established species.’). When both adults and copepodites were scored at the same site during the same sampling, the record was considered only once for the flagging scheme. All the records were

then merged with earlier ones for the same geographical area based on previous literature (Sabia et al. 2015; Stefanni et al. 2018; Uttieri et al. 2020, 2023; Varrella et al. 2025) and used to generate an updated map of occurrences for the Italian regions using QGIS v3.38.3 (QGIS.org 2025). The projection used for all maps was spherical (orthogonal method).

2.3 | Statistical Analyses

The median abundance across all years and months and the corresponding inter-quartile range were plotted for each sampling station, descriptor and stage as barplots. Different variables (temperature, salinity and sea bottom depth) were tested to explore their effect on the abundance and number of finds measuring their correlation. Of all MSFD sites, the port of Civitavecchia was the one with the highest number of *P. marinus* finds and the one with samples from most months. In order to explore the seasonal distribution of *P. marinus*, the D2 abundance data from the port of Civitavecchia (sampling stations ID: IT_m3rm1 and IT_m3rm2, Table 1 and Table S1) were log₁₀-transformed and plotted against months. Individual values were displayed over boxplots, which show the corresponding median values (horizontal black line), inter-quartile range (the box itself) and the 5th/95th percentiles (bottom and top whiskers) (Tukey 1977). To investigate the seasonal abundance distribution, a polynomial regression model was fitted between copepod abundance (dependent variable, calculated as ind. m⁻³) and months (independent variable), across all years and for both stages separately. The degree chosen for the polynomial regression was 3 ($y = a + bx^3 + cx^2 + dx$), based on the lowest AIC value (125.38) among different degrees (Akaike 1973), and the residuals resulted normally distributed ($p > 0.05$ following Shapiro–Wilk test; Shapiro and Wilk 1965). Boxplots were produced also to describe the distribution of salinity and temperature values recorded across all samples of the 2015–2023 MSFD campaign. All analyses and plots were made with R Statistical Software (v4.4.1; R Core Team 2021).

3 | Results

The analysis of the occurrence of *Pseudodiaptomus marinus* in the 2015–2023 MSFD dataset permitted an update of the distribution of this NIS in Italian waters (Figure 1). Compared to previous reviews (Sabia et al. 2015; Uttieri et al. 2020, 2023) (Figure 1a), the data presented here confirmed the establishment

of *P. marinus* in a number of already introduced areas, but they also highlighted the first record of this NIS in specific areas from both D1 and D2 (Figure 1b,c), resulting in a general increase in the occurrence of this species in Italian coastal waters (Figure 1d). All detailed information on stations, coordinates, months and years, and corresponding abundance of *P. marinus* (differentiating between adults, copepodites and mix of stages, depending on available information) is reported in Table 1 and Table S1.

Overall, over the 2015–2023 MSFD campaign *P. marinus* was recorded 178 times: ~32% of finds were recorded in D1 and ~68% in D2 (Table 1 and Table S1). Specifically, it was found in 23 sampling sites (out of 181, ~13% of total sites) over 12 locations in D1, and in 16 sampling sites (out of 44, ~36% of total sites) over 12 localities in D2 (Table 1 and Table S1). A total of 17 new unique sampling stations (12 in D1 and 6 in D2 over 8 and 5 locations, respectively) were scored, with Pellestrina island station (ID: 50530) shared between the two descriptors. This resulted in a ~15% increase in the number of *P. marinus* occurrences in Italian waters compared to the latest review (Uttieri et al. 2023). A total of 4684 ind. m⁻³ have been found across 16% of all stations, with a maximum value of 864.50 ind. m⁻³ and a median value of 2.83 ind. m⁻³ [IQR: 7.12] considering both copepodites and adults. ~5% of total ind. m⁻³ were counted in D1 and ~95% in D2. Overall, copepodites represented the majority of ind. m⁻³ (~85%; Figure 2).

Following Zenetos, Albano, et al. (2022), the analysis of the 2015–2023 MSFD dataset (Figure 3) showed that among all records of *P. marinus*: 45% confirmed a previous establishment of this NIS at the sampled sites; 47% represented new introductions, of which 10% (relative to all stations with *P. marinus* records) were subsequently followed by establishment; 37% of stations indicated an occurrence without evidence of establishment. These proportions revealed the spreading distribution of *P. marinus*, distinguishing between confirmed establishments, recent introductions and transient occurrences.

Regarding the salinity and temperature ranges across all samples of the 2015–2023 MSFD campaign collected in both D1 and D2, median values of 37.8 [IQR: 1.2] for salinity and 17.5°C [IQR: 6.9] for temperature were detected (Figure 4). The ranges of salinity and temperature in which *P. marinus* was found were 33–39 and 9°C–27°C, respectively. Average sea depth differed between the two descriptors: ~40 m in D1 (maximum value: 145 m; minimum value: 11 m) and ~17 m in D2 (maximum value: 35 m; minimum value: 6 m). *P. marinus* abundance or number of records never significantly correlated with either salinity, temperature or sea depth (not shown).

A description of the MSFD records for each administrative region, as grouped following the European Environment Agency (2020), is here given. All details are presented in Table 1.

3.1 | Western Mediterranean Sea (MWE)

For the first time (as per literature), *P. marinus* was found along the coastline of Liguria near an aquaculture mussel farm at La Spezia (D2) in October 2023.

Pseudodiaptomus marinus was not detected along the Ligurian Sea coast of Tuscany, where it had been previously recorded near Massa di Carrara and Livorno (Uttieri et al. 2023). No *P. marinus* was tallied along the Tyrrhenian coasts of Tuscany as well. In Lazio, new finds of *P. marinus* were recorded in three locations: (1) in the most coastward site of the Lido di Tarquinia transect (D1), where it was found in November 2018, June 2019 and October 2022; (2) in the central site of the Ladispoli transect (D1), in August 2019; and (3) at all three sites of the transect off the coast of Gaeta (D1) between June and July 2019 (Figure 5a). Compared to Uttieri et al. (2023) and Varrella et al. (2025), the establishment status of *P. marinus* in Lazio was reconfirmed in the port of Civitavecchia (D2), where it was found each year and month from 2015 to 2023, setting the highest abundances recorded across the whole period with 938.54 ind. m⁻³ (74.00 adults and 864.54 copepodites m⁻³) in October 2018 and 854.19 ind. m⁻³ (12.29 adults and 841.90 copepodites m⁻³) found in September 2016. The presence of *P. marinus* was not recorded at San Felice Circeo station (D1), where it had been scored previously (Uttieri et al. 2020).

In Campania, *P. marinus* was found for the first time at 3 nautical miles from the Volturno river mouth (D1) in July 2021 (Figure 5a). In the Gulf of Naples, *P. marinus* was found only in proximity of the port of Naples (D2) for the first time in May and July 2021 (Figure 5a). No other finds were recorded in the rest of the basin, despite its presence was considered well established according to previous literature (Uttieri et al. 2023) (Figure 5a). In the Gulf of Salerno, *P. marinus* was found at a density of 50.16 ind. m⁻³ in the port area (D2) for the first time in September 2022; in addition, the NIS was found in the second station of the transect off the coast (D1) in July 2021, in the same area where it had already been recorded in September 2019 (Uttieri et al. 2023) and in February 2021 (Montalbano and Di Capua 2025) (Figure 5a), thus being considered as ‘established’ *sensu* Zenetos, Albano, et al. (2022).

In Calabria, *P. marinus* was found inside the port of Gioia Tauro (D2) in December 2018 (as previously reported in Uttieri et al. 2020) and in September 2019.

The first record of the NIS in Sardinia was reported in the Gulf of Olbia in January 2016 (D1), at the site located 3 nm from the coast.

3.2 | Ionian Sea and Central Mediterranean Sea (MIC)

In this basin, *P. marinus* was found only along the Ionian coast of Apulia, in the port of Taranto (D2) in March 2023. This record confirmed previous occurrences in the same area as from taxonomic identification (July 2022) and eDNA metabarcoding (October 2022) (Varrella et al. 2025).

3.3 | Adriatic Sea (MAD)

Pseudodiaptomus marinus was newly recorded along the Adriatic coast of Apulia too: in the port of Brindisi (D2), making it the southernmost record in the Adriatic Sea, in

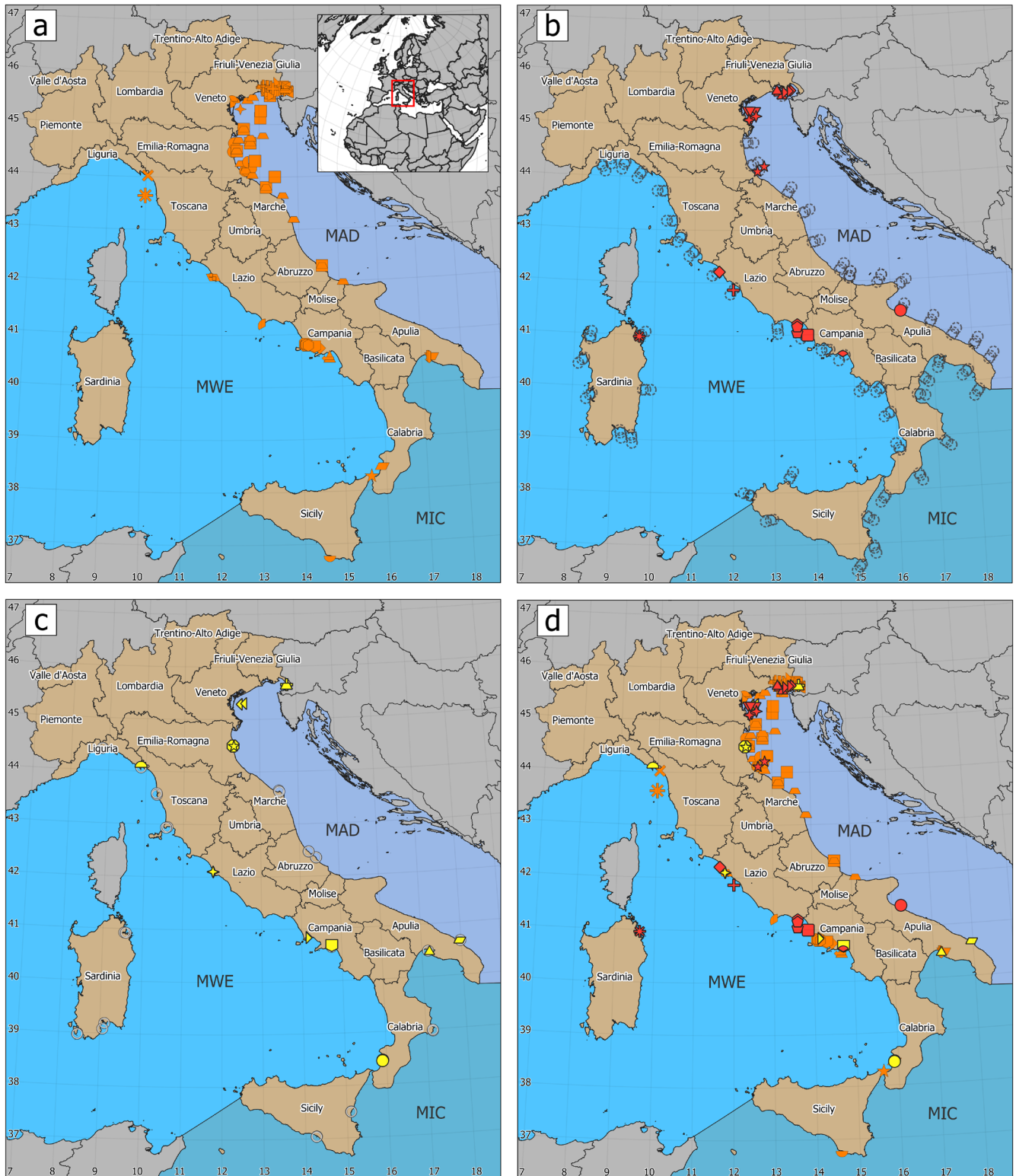


FIGURE 1 | *Pseudodiaptomus marinus* records along the Italian coastlines: (a) presence of *P. marinus* according to previous literature; (b) records of *P. marinus* presence (red symbols) and absence (dashed empty grey circles) based on Descriptor 1 (marine biodiversity) samplings from 2015 to 2023 MSFD; (c) records of *P. marinus* presence (yellow symbols) and absence (empty grey circles) based on Descriptor 2 (non-indigenous species) samplings from 2015 to 2023 MSFD; (d) integrated reconstruction of the presence of *P. marinus* along the Italian coasts based on panels (a–c). Labels on land refer to Italian administrative regions, labels on the sea refer to the different basins: Western Mediterranean Sea (MWE); Ionian Sea and Central Mediterranean Sea (MIC); Adriatic Sea (MAD). The projection of all maps is spherical (orthogonal method). References for panel a: Fiori et al. (2019)¹; Stefanni et al. (2018)²; Uttieri et al. (2020)³; Sabia et al. (2015)⁴; Uttieri et al. (2023)⁵; Margiotta et al. (2020)⁶; Pansera et al. (2014)⁷; Zagami and Brugnano (2013)⁸; Karuza et al. (2016)⁹; de Olazabal and Tirelli (2011)¹⁰; Vidjak et al. (2019)¹¹; Varrella et al. (2025)¹²; Montalbano and Di Capua (2025)¹³.

MWE

Previous records

- ▲ Civitavecchia³
- ▲ Gioia Tauro and Strait of Messina³
- ▲ Gulf of Naples⁵
- ▲ Gulf of Naples - LTER_EU_IT_061⁴
- ▲ Gulf of Naples - Sarno River⁵
- ▲ Gulf of Naples - Torre del Greco⁵
- ▲ Gulf of Naples⁴
- ▲ Gulf of Pozzuoli⁵
- ▲ Gulf of Pozzuoli⁶
- ▲ Gulf of Salerno⁵
- ★ Lake Faro and Lake Ganzirri^{4,7,8}
- ▲ Lake Fusaro⁴
- ★ Leghorn⁵
- ✕ Marina di Carrara⁴
- ▲ San Felice Circeo³
- ▲ Venice Lagoon³
- ▲ Civitavecchia¹²
- ▲ Gulf of Salerno¹³

Descriptor 1

- ▲ Gaeta
- ▲ Ladispoli
- ▲ Lido di Tarquinia
- ▲ Salerno
- ▲ Volturno mouth
- ★ Gulf of Olbia
- *P. marinus* not found

Descriptor 2

- ▲ Gioia Tauro
- ▲ La Spezia
- ★ Port of Civitavecchia
- ▲ Port of Naples
- ▲ Port of Salerno
- *P. marinus* not found

MIC

Previous records

- ▲ Mar Piccolo di Taranto⁹
- ▲ Ragusa⁵
- ▲ Taranto¹²

Descriptor 2

- ▲ Port of Taranto
- *P. marinus* not found

MAD

Previous records

- ▲ Adriatic Sea - Emilia Romagna¹
- ▲ Adriatic Sea²
- ▲ Adriatic Sea³
- ▲ Gulf of Trieste - LTER_EU_IT_056³
- ▲ Gulf of Trieste⁵
- ▲ Gulf of Trieste³
- ▲ Gulf of Venice³
- ▲ Marano and Grado Lagoon⁵
- ▲ Monfalcone¹⁰
- ▲ Port of Trieste¹¹
- ▲ Port of Venice¹¹
- ▲ Rimini¹⁰
- ▲ Venice Lagoon³
- ▲ Trieste¹²

Descriptor 1

- ▲ Lignano Sabbiadoro
- ▲ Ofanto river mouth
- ▲ Pellestrina island
- ★ Rimini
- ★ Rosolina Mare
- ▲ Trieste
- *P. marinus* not found

Descriptor 2

- ★ Marina di Ravenna
- ▲ Pellestrina island
- ▲ Port of Brindisi
- ▲ Porto Corsini
- ▲ Sacchetta Trieste basin
- ▲ Settimo Trieste
- *P. marinus* not found

FIGURE 1 | (Continued)

September 2020 and July 2022, in this latter case registering a relatively great abundance (179.00 ind. m⁻³); and at the sampling station closest to the coast at the mouth of the Ofanto river (D1) in February 2022.

In Molise, Abruzzo and Marche *P. marinus* was not recorded in the 2015–2023 period compared to previous scores collected in September 2014 (Stefanni et al. 2018).

In Emilia-Romagna (Figure 5b), individuals of *P. marinus* were found in Porto Corsini (D2) in 2022 (September and November) and 2023 (January), at Marina di Ravenna in November 2015, July 2018 and November 2022 (D2), and off the coast of Rimini (D1) in December 2021 and November

2022. *P. marinus* was previously found in the proximity of all these locations (Fiori et al. 2019; Stefanni et al. 2018; Uttieri et al. 2020), hence confirming its establishment. However, *P. marinus* was not recorded at other sites where it had been scored previously (Fiori et al. 2019; Stefanni et al. 2018; Uttieri et al. 2020) (Figure 5b).

In Veneto (Figure 5c), both stages of *P. marinus* were found: in the transect off the coast of Rosolina Mare (D1; new records) in 2017 (July and November), in 2018 (January and July), and 2021 (July); in the transect (D1) and in the D2 sites off the coast of Pellestrina island, in 2015 (December), in 2016 (September), in 2017 (May, July and November), and from 2019 to 2021 (June and July), all representing new sites with the only exception of

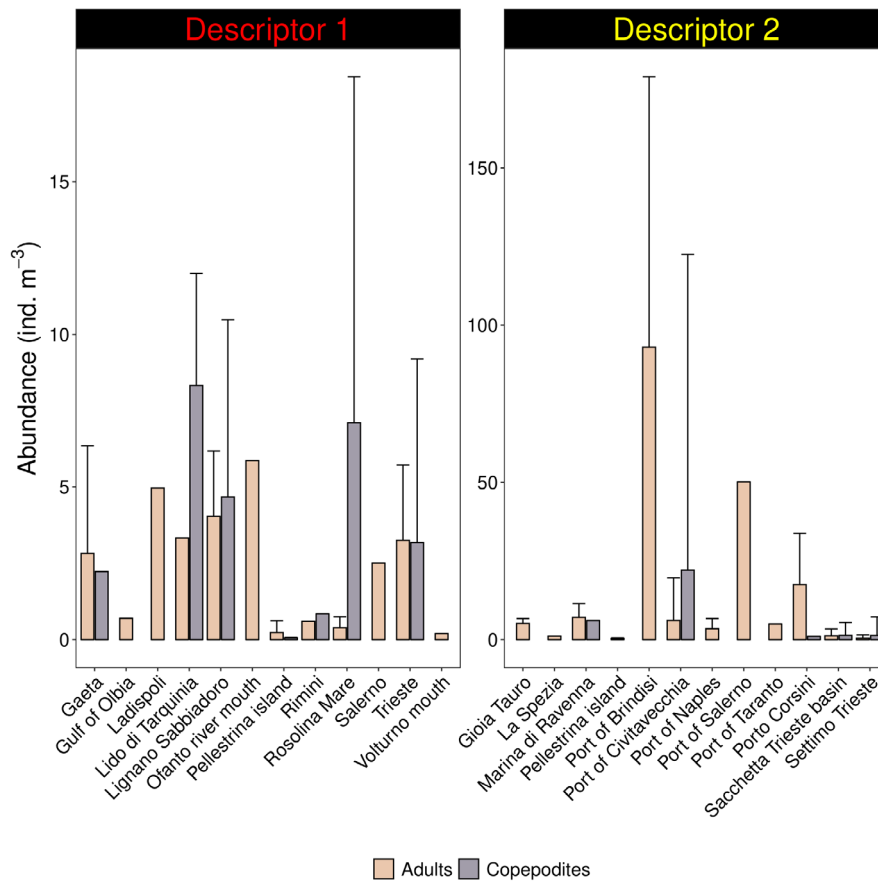


FIGURE 2 | Abundance of *Pseudodiaptomus marinus* in the 2015–2023 MSFD: median abundance (vertical bar; ind. m⁻³) and IQR (vertical black line) of adults and copepodites (colour indexed as in the legend at the bottom) at each station and separately for each descriptor. Note the different range scale between the abundance of individuals in the two descriptors.

the most offshore D2 site where *P. marinus* had been previously found (Uttieri et al. 2020).

In Friuli Venezia Giulia (Figure 5d) *P. marinus* was recorded in locations where its presence was already assessed (Stefanni et al. 2018; Uttieri et al. 2020, 2023; Varrella et al. 2025): copepodites were found in all three sampling stations of the Lignano Sabbiadoro transect (D1) in 2015, 2016, 2017, 2020 and 2023, and in all three sampling stations of the transect off the coast of Trieste (D1) in 2016, 2017, 2019, 2021, 2022 and 2023. The establishment of *P. marinus* was confirmed in the port area of Trieste too: in Sacchetta Trieste basin (D2), individuals were found between 2015 and 2023, in different months depending on the year, and off the coast of Settimo Trieste (D2) over the whole 2015–2023 period, in several months depending on the year.

3.4 | Abundance and Seasonality

Abundance data from the port of Civitavecchia site showed a late summer/early autumn-centred distribution (Figure 6). More specifically, copepodites peaked between August and September, whereas adults showed their peak the following months, roughly between September and October. This was based on the abundance peak described by the 3rd degree polynomial fitting line between abundance (y) and months (x), whose equations are

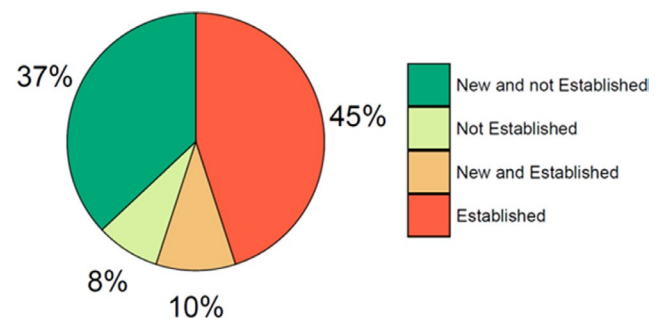


FIGURE 3 | *Pseudodiaptomus marinus* status along Italian coasts: the pie chart shows the percentage of finds among all four different statuses as per Zenetos, Albano, et al. (2022). ‘Established’ refers to occurrences with more than two records distributed in space and time, indicating self-sustaining populations and locally established species. ‘New’ refers to finds in locations where *P. marinus* had not been recorded previously.

here reported: $y = 0.85 + 0.02x^3 - 0.15x^2 - 0.77x$ for adults and $y = 1.31 - 1.59x^3 - 2.06x^2 - 1.15x$ for copepodites.

4 | Discussion

The Mediterranean Sea is considered the most invaded basin worldwide (Bailey et al. 2020; Tsiamis et al. 2018), with 1006

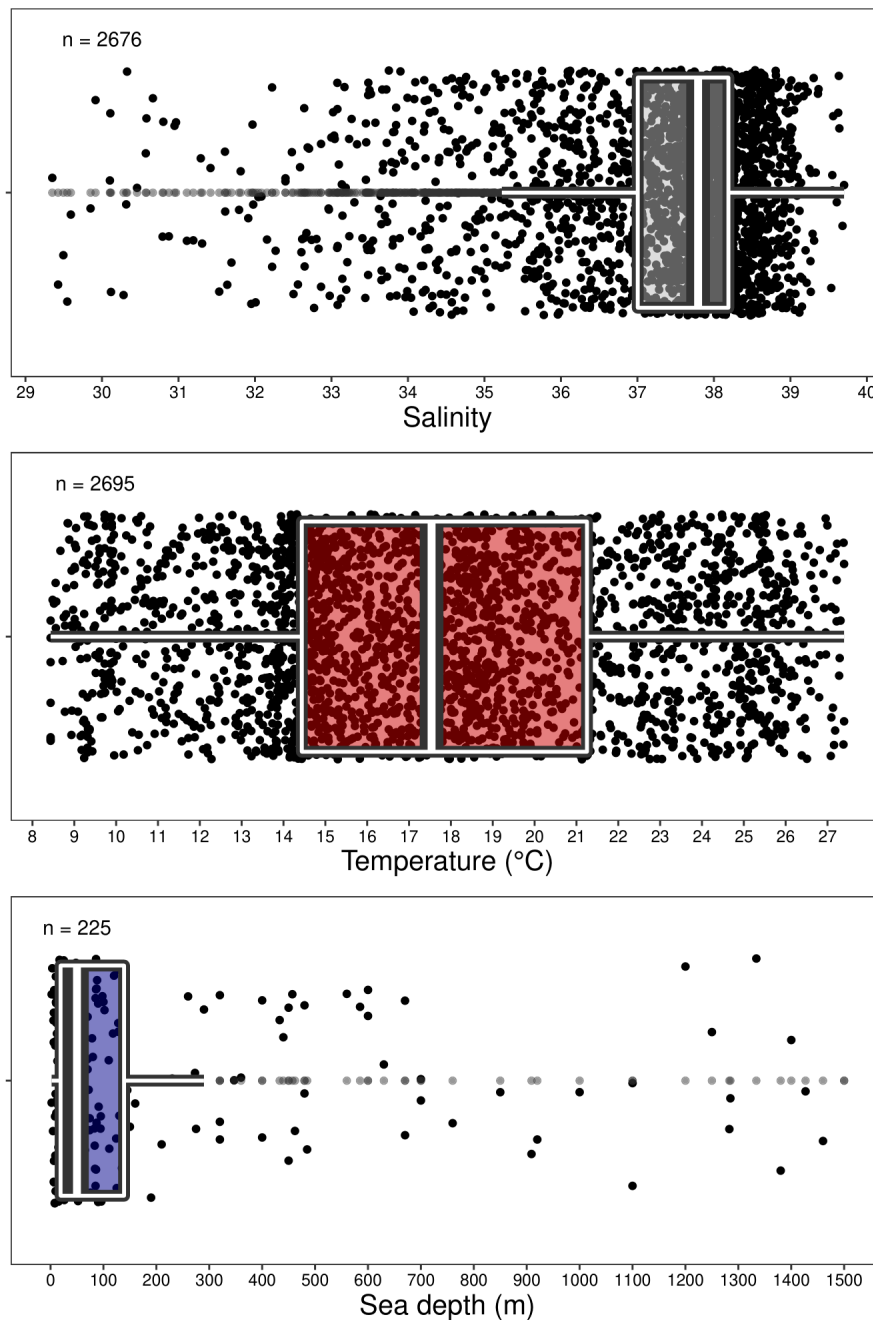


FIGURE 4 | Salinity, temperature and depth distribution of *Pseudodiptomus marinus* records from the 2015 to 2023 MSFD: the horizontal box-plots indicate the 5th and 95th percentiles (left and right ends of white horizontal lines, respectively), the 25th and 75th percentiles (left and right ends of the rectangle) and the median (central vertical white line). Black points indicate each measurement (n) across the whole 2015–2023 MSFD campaign.

certified records as of December 2020 (Galanidi et al. 2023). National NIS inventories are available only for some European countries (Katsanevakis et al. 2023), among which Italy (Occhipinti-Ambrogi et al. 2011; Servello et al. 2019), setting a baseline for the ecosystem diversity and assessing the introduction of new species. A host of reasons may affect NIS recording both in terms of correct species identification and time of introduction (Ojaveer et al. 2018, 2014), including different sampling methodologies and the need for specialist taxonomic expertise. The data presented here, collected within the framework of the Italian 2015–2023 MSFD monitoring for the descriptors D1 and D2, used standardised sampling protocols, uniform levels of

taxonomic description and a common list of taxa, and aimed to achieve uniform levels of taxonomic identification through national training courses for analysts, providing a unique opportunity to investigate the presence of NIS at national level.

The MSFD records provide an updated distribution of *P. marinus* along the Italian coasts. Although the number of locations in which this species was found was equal between both descriptors, ~95% of individuals were found in D2, highlighting the importance of targeted surveys in more impacted areas, such as aquaculture farms, ports and highly trafficked ship routes where NIS may be introduced by the discharge of ballast waters.

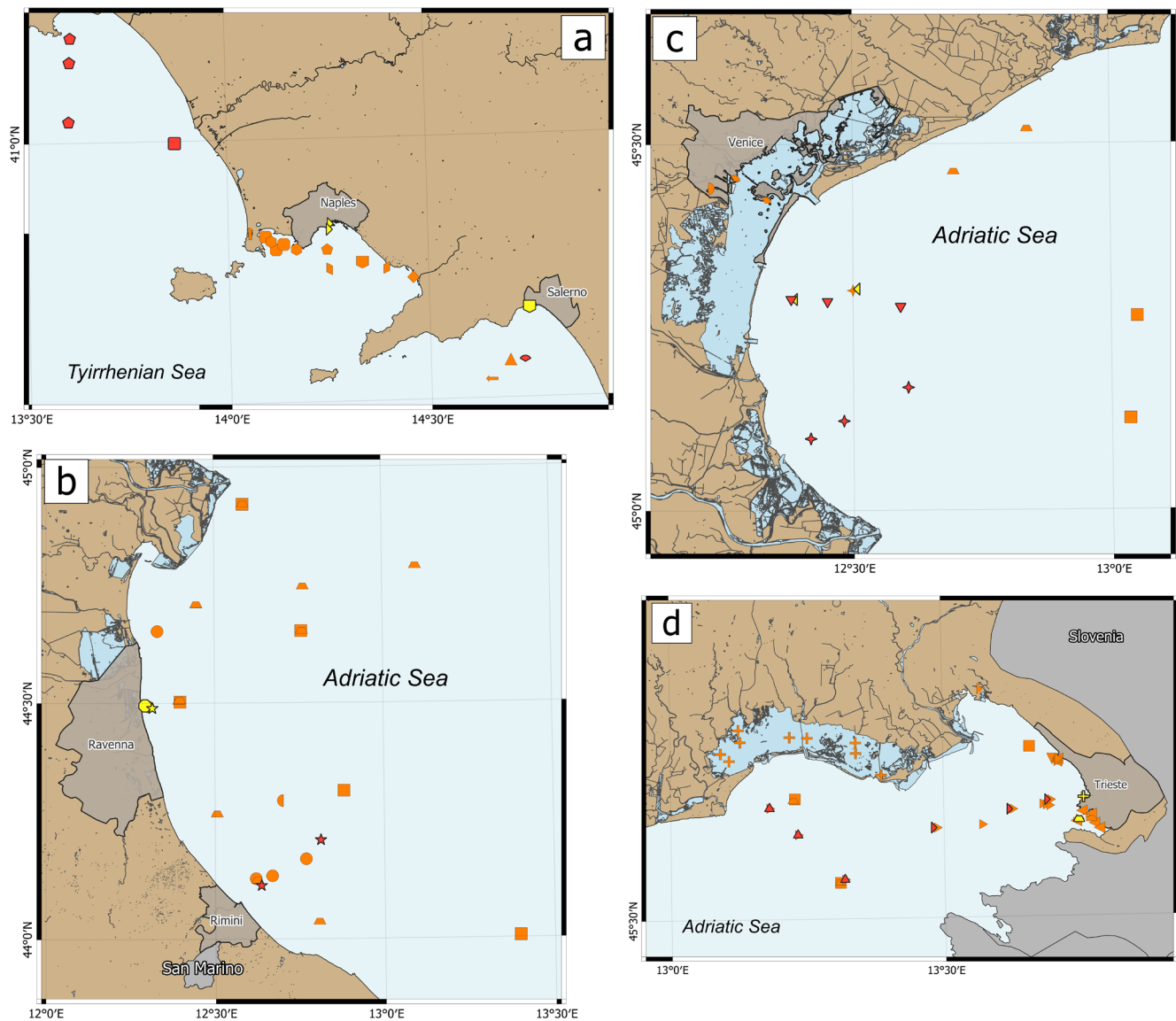


FIGURE 5 | Geographic insets of Campania (a), Emilia Romagna (b), Veneto (c) and Friuli Venezia Giulia (d). Detailed descriptions of the presence of *Pseudodiaptomus marinus* in the four administrative regions. Symbols and colour codes according to the legend of Figure 1. The projection of all maps is spherical (orthogonal method).

In both descriptors, the majority of individuals were represented by copepodites (~85%), similar to previous studies (Deschutter et al. 2018; Gubanova et al. 2020; Liang and Uye 1997; Seregin and Popova 2023).

As previously reported (Sabia et al. 2015; Uttieri et al. 2020), the demersal behaviour of *P. marinus* during daylight can reduce capture efficiency in morning vertical tows (procedure used also in the framework of the MSFD), potentially leading to its underestimation. While in the vast majority of the cases the abundance of this NIS was very low, episodic high values were reported, reaching values of hundreds of ind. m^{-3} , always in port areas (Table 1). Although no specific annotations on the MSFD datasheet were associated with these scores, such abundances seem to confirm previous evidence by Lučić et al. (2015), who hypothesized that the manoeuvre by tugboats led to the resuspension of individuals lying on the bottom during daytime.

Another aspect deserving attention is the mesh size used for the collection of the zooplankton samples. Specifically for *P. marinus*, uncertainties may derive from the use of different nets, which may lead to differences in sampling effectiveness (e.g., Kourkoutmani and Michaloudi 2022; Pansera et al. 2014; Uttieri et al. 2020). The adoption of common protocols in the Italian MSFD (WP2 net with 200 μm mesh size) provides a common ground for a sound comparison among sites, but the use of nets equipped with finer meshes could provide better insight into the abundance of juvenile stages (Pansera et al. 2014).

Approximately 50% of *P. marinus* detections occurred in the MAD basin, for the most part in its northern sector. The presence of this species in this basin is well proven (Uttieri et al. 2023), and these new records indicate that this area is particularly favourable to its establishment. Nonetheless, its actual occurrence in Italian waters may still be, at least in part, underestimated, considering the sampling criticalities

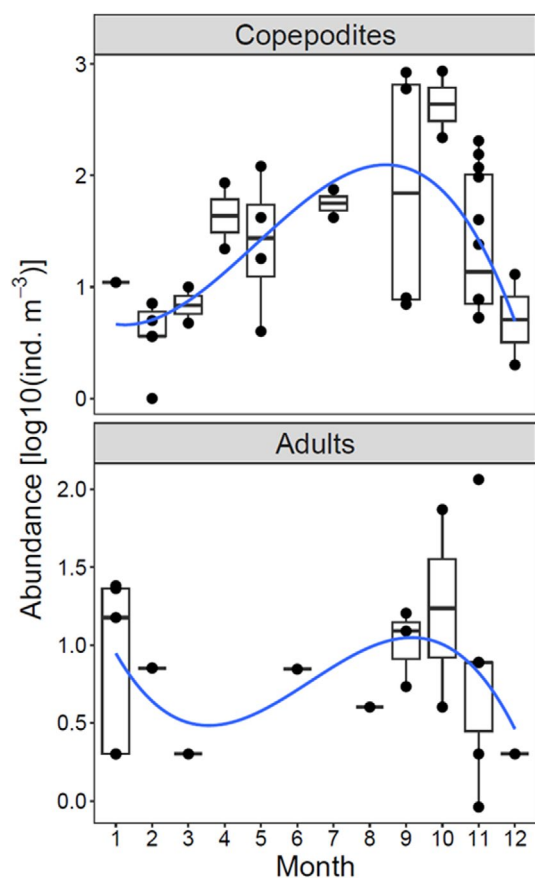


FIGURE 6 | Seasonal abundance distribution of *Pseudodiaptomus marinus* at Civitavecchia: abundance values are reported on the y-axis as $\log_{10}(\text{ind. m}^{-3})$ and are scattered against months (on the x-axis) for copepodites (above) and adults (below). Observations are depicted as black points on boxplots. Blue lines indicate the polynomial regression lines (see text for equations).

discussed above. This could also explain the evidence that this species has not been scored in numerous areas where it had been previously recorded (e.g., at several sites in Emilia-Romagna, Marche, Abruzzo), as clear from the comparison of the panels in Figure 1. An alternative interpretation of this outcome may be that at given sites the previous records have not been followed by a stable establishment of this NIS. Additional future sampling efforts in selected areas may raise the curtain on this aspect.

The great amount of *P. marinus* finds and abundance in D2 allowed to visualise the seasonal distribution of this species in a single and very impacted location, the port of Civitavecchia, which showed a peak of abundance of adult individuals between September and October. This is consistent with the unimodal seasonal distribution reported in other introduced sites (Deschutter et al. 2018; Gubanov et al. 2020; Seregin and Popova 2023), with a major peak in late summer/early autumn. Interestingly, studies from the native area of this species (Inland Sea of Japan) had detected a bimodal seasonal distribution with a major peak in early summer (around June) and a secondary peak around October (Liang and Uye 1997; Uye et al. 1982). It is important to note that studies on the seasonality of *P. marinus* are primarily based on data from a limited number of years (up

to five). Therefore, additional data from long-term monitoring such as the MSFD time series at fixed stations are essential to gain a deeper understanding of the ecology of this species as well as of other NIS.

In Italy, the major vector of NIS primary introductions is shipping, followed by aquaculture (Nunes et al. 2014; Solak-Fiskin et al. 2025). Interestingly, the occurrence of *P. marinus* has been scored both in D1 (23/181 sampling stations, 12.7%) and D2 (16/44 sampling stations, 34.1%), indicating that this species is not restricted to areas subject to intense anthropic stress like those surveyed in D2. The results presented here point not only to human-mediated introductions (e.g., by ballast waters in port areas; Cabrini et al. 2019; Lawrence and Cordell 2010), but also to possible mechanisms of secondary introduction at play supporting the further spread of this NIS, which is catalogued as polyvetic (Uttieri et al. 2020).

Beyond documenting new occurrences, the spatial pattern observed along the Italian coastline illustrates key invasion biogeographic processes underlying the establishment of *P. marinus*. Its presence in areas subject to intense human activities points to an initial phase dominated by anthropogenic vectors, enabling establishment in introduction hubs (e.g., Cabrini et al. 2019; Vidjak et al. 2019). The recurrent detections in less impacted coastal areas suggest subsequent natural secondary spread, consistent with invasion stage progression from initial introduction to wider spatial integration (Zenetos, Albano, et al. 2022). Although the expansion is not directly quantified in our study, the proportion of sites classified as introduction (37%; Figure 3) and establishment (45%; Figure 3) suggests a system trending towards broader expansion (Zenetos, Albano, et al. 2022). Such continued spread is expected, as many marine NIS show no sign of having reached their full potential allochthonous range and display instead accelerating expansion rates worldwide (Richardson et al. 2025).

Under the main umbrella of the MSFD targets, each country adopts specific actions for monitoring and conservation purposes (García-Barón et al. 2019; Pierson et al. 2021). As for zooplankton, the mandatory parameters do not include the analysis of the community composition (Uusitalo et al. 2016). However, the effort to characterise the species composition of the pelagic habitat carried out in the Italian implementation of the MSFD has recently allowed the use of zooplanktonic NIS for the assessment of the GES (<https://strategiamarina.isprambiente.it/report-comunitari/msfd-paper-report-2024/>). The integration of literature data and MSFD surveys was used to determine an updated baseline of NIS new introductions, following the primary criterion D2C1 of the Decision 2017/848/UE aiming to minimise their presence. This step is fundamental to apply the breakpoint analysis, by which identifying abrupt shifts in the rate of NIS introductions over time (Magliozzi et al. 2025).

The present study represents one of the first attempts to use MSFD data to witness the expanding distribution and establishment of a benthopelagic NIS (*P. marinus*). In a wider perspective, the approach used in this work could be extended to other planktonic species present in the MSFD database thus significantly ameliorating our understanding of the invasion processes.

The use of molecular tools is strongly advocated not only as a support to the taxonomical identification of NIS, but also as an early-warning detection system and to investigate introduction pathways (Brown et al. 2016; Katsanevakis et al. 2023; Ojaveer et al. 2014; Stefanni et al. 2018; Varrella et al. 2025). With the aim of retrieving a more exhaustive description of the zooplankton community, future monitoring programmes should include the metabarcoding of the bulk samples and/or the analysis of eDNA from both aqueous and sediment matrices, as recently discussed in Varrella et al. (2025) and in Tagliabue et al. (2026). In combination with the morphological examination of the net-collected samples, the molecular investigations may help reveal the hidden diversity of the zooplankton assemblage, as recently discussed in Di Capua et al. (2023). Molecular analyses would be particularly supportive in the identification of rare species and meroplanktonic taxa, whose presence in bulk zooplankton samples may be underestimated. Specifically for *P. marinus*, an increasing number of sequences using different molecular markers is being made available (Di Capua et al. 2022, 2021; Guy-Haim et al. 2022; Sabia et al. 2017), facilitating its identification and the reconstruction of their phylogeographic connections. However, more sequences from different regions worldwide, including both native and introduced areas, are advocated to improve the knowledge of this NIS.

Very recently, *P. marinus* was found in the gut content of European sardines (*Sardina pilchardus*) from the Thessaloniki Bay (Syrri et al. 2025), showing the presence of this species in the food web in an introduced area. Future efforts may be devoted to investigating the trophic role of this NIS using not only morphological analyses but also molecular approaches, which may provide further insights into complex trophic relationships as demonstrated for the European hake (*Merluccius merluccius*) (Riccioni et al. 2018). It is worth noting that *P. marinus* alternates an epibenthic phase during the morning with a pelagic phase at night, a behaviour that could severely underestimate its presence (Tirelli et al. 2024; Uttieri et al. 2020, 2023). Nocturnal samplings are difficult to carry out but could be of crucial importance to record hyperbenthic taxa as in the case of the Japanese NIS *Metacalanus acutioperculum* Ohtsuka, 1984, recently found in the Gulf of Trieste (Bariche et al. 2025).

The study of biological invasions can benefit from the integration of biogeography and ecology (Briggs 2007). Future climate scenarios will increasingly support the spread and establishment of organisms that can more effectively adapt to stressful conditions (e.g., Glamuzina et al. 2024; Sarà et al. 2018). Monitoring programmes can shed light on the response of marine ecosystems to changes in local and global stressors (Chiba et al. 2018), and provide a near real-time assessment of the arrival of NIS (e.g., Zenetos et al. 2010). The knowhow acquired through the MSFD programme can set a baseline for future transnational actions, by which getting up-to-date information on the status of coastal systems.

Author Contributions

Conceptualisation: V. Tirelli and M. Uttieri. Data curation: S. Corona, V. Tirelli and M. Uttieri. Formal analysis: S. Corona and M. Uttieri. Funding acquisition: V. Tirelli and M. Uttieri. Investigation: all authors.

Methodology: all authors. Project administration: V. Tirelli and M. Uttieri. Supervision: V. Tirelli and M. Uttieri. Visualisation: S. Corona. Writing – original draft: S. Corona, M. Uttieri. Writing – review and editing: all authors.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The complete data sets used in this work are freely available at the URL: <http://www.db-strategiamarina.isprambiente.it/app/#/datiMonitoraggi020182023>.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** plots summarising the mesozooplankton sampling dates in the 2015–2023 MSFD campaign for each marine basin (reported on the right; MAD, Adriatic Sea; MIC, Ionian Sea and Central Mediterranean; MWE, Western Mediterranean Sea), with years on the x-axis and months on the y-axis for both Descriptors (reported on top). White cells correspond to sampling months, with coloured dots highlighting *P. marinus* finds. Grey cells indicate months in which sampling was not done. **Table S1:** list of information (descriptor, region, station ID, station name, coordinates, bottom depth) of each sampling station of both descriptors for all Italian administrative regions, as reported in the MSFD dataset. Text is in bold when referring to a station where *P. marinus* has been found.