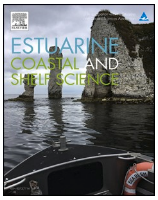
Estuarine, Coastal and Shelf Science 319 (2025) 109283

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss



Comprehensive insights into *Pseudo-nitzschia* research in the Adriatic Sea: Diverse perspectives and emerging discoveries

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ARTICLE INFO

Keywords:
Pseudo-nitzschia
Adriatic
Diversity
Ecology

ABSTRACT

Pseudo-nitzschia, a globally distributed diatom genus, dominates phytoplankton communities in biomass and abundance, with some species producing domoic acid (DA), the neurotoxin responsible for Amnesic Shellfish Poisoning (ASP). The Adriatic Sea has become a hub of *Pseudo-nitzschia* research over the past 15 years. This review synthesizes multidisciplinary research across Adriatic sub-basins, integrating morphological, genetic, and ecological data. While ASP has never been documented in the Adriatic, DA was occasionally detected in shellfish. The production was linked to toxic species such as *P. multistriata*, *P. calliantha*, and *P. galaxiae*, which were found to produce DA in cultures from Adriatic isolates. Despite progress, LM-based monitoring remains prevalent, underestimating species complexity and toxigenic potential. Electron microscopy and genetic barcoding have nonetheless revealed new insights into the species composition of this genus in Adriatic. A total of 14 species have been reported so far with prominent regional disparity: the northern and middle Adriatic host higher diversity, contrasting with the southern Adriatic, where only five species were confirmed, and research remains sparse. Seasonal dynamics show summer-autumn peaks in abundance, though interannual and regional variability is notable. We present recent advances from the Adriatic including the discovery of *Pseudo-nitzschia*-infecting viruses, population genomic insights in *P. multistriata*, and metabarcoding-driven revelations of cryptic diversity. Finally, we highlight critical knowledge gaps, including the ecological drivers of toxicity and the impacts of oligotrophication on community shifts. Collaborative, high-resolution methodologies (e.g., omics, automated imaging) are urged to address emerging challenges under climate change and anthropogenic pressures.

1. Introduction

The Adriatic Sea (AS) is the northernmost part of the Mediterranean Sea and is divided into three sub-basins: the northern (NA), the middle (MA) and the southern Adriatic (SA), which differ in depth, temperature, salinity and nutrient concentration and are each characterized by cyclonic eddies at the surface (Cushman-Roisin et al., 2001 and references cited therein). The same cyclonic circulation pattern is repeated in the deeper layers of the Adriatic, where the Adriatic Deep Water, which forms in the shallow NA and in the SA Pit, flows into the Ionian Sea, while in the intermediate layer the Levantine Intermediate Water enters

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This article is part of a special issue entitled: The Adriatic blue growth published in Estuarine, Coastal and Shelf Science.

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https://doi.org/10.1016/j.ecss.2025.109283
Received 30 October 2024; Received in revised form 7 March 2025; Accepted 27 March 2025

Glossary

ASP (Amnesic Shellfish Poisoning) – A vertebrate illness caused by consuming shellfish contaminated with domoic acid, a neurotoxin produced by certain *Pseudo-nitzschia* species. Symptoms include memory loss, gastrointestinal distress, and neurological damage

Barcoding sequencing of phylogenetic marker genes (e.g., ribosomal RNA genes 18S, 28S, ITS, or plastid-encoded *rbcL* and *COI* genes) often after amplification with specific primers with the polymerase chain reaction (PCR). Sequencing is mainly performed with the classical Sanger or new Sanger approaches that are low throughput but less error prone. Lately, high-throughput platforms such as the Oxford Nanopore and PacBio Revio are also used for this purpose

Metabarcoding – barcoding specific regions of marker genes mainly in a community context, that involves the extraction of environmental (bulk) DNA (eDNA). This approach requires high-throughput next generation sequencing platforms such as Illumina MiSeq, PGM Ion-Torrent etc.

Morphological species group (MSG) – Classification system for *Pseudo-nitzschia* based on the width of the transapical axis (TA) of *Pseudo-nitzschia* frustules and typically used in light microscopy determination. Two MSGs are distinguished the *P. delicatissima* MSG (TA$<$ 3 μm) and the *P. seriata* MSG (TA $>$ 3 μm). It was shown that this classification is paraphyletic and largely ecologically irrelevant, however it is still used due to data continuity

Species complex – a phylogenetic classification that is also rooted in morphology. Within the *P. delicatissima* MSG two species complexes are recognized based on the way cells ends overlap in girdle view the '*P. delicatissima*' and the '*P. pseudodelicatissima*' species complexes, which seem to be monophyletic

the Adriatic on the eastern side (Civitarese et al., 2023; Cushman-Roisin et al., 2013; Raicich, 1996). This exchange of water masses between the Adriatic and Ionian Seas influences the circulation of the Northern Ionian Gyre, which operates on a decadal scale through the bimodal Adriatic–Ionian Oscillation System (BiOS) (Gačić et al., 2010). BiOS has a strong influence on the thermohaline and biogeochemical properties in the AS, including a significant impact on the distribution of primary producers, on the structure of the pelagic food web and ultimately on biodiversity in the Adriatic (Civitarese et al., 2010, 2023). Furthermore, the AS is an area with heavy maritime traffic and aquaculture activities that have favoured the ingression of a large number of non-indigenous species, most of which are invertebrates, but there are cases of microalgae deemed introduced as well, such as *Ostreopsis* cf. *ovata, Chaetoceros bacteriastoides, Skeletonema tropicum* and also, tentatively, *Pseudo-nitzschia multistriata* (Corriero et al., 2015). The political landscape of the Adriatic, which currently includes six EU and non-EU countries (Italy, Slovenia, Croatia, Bosnia and Herzegovina, Montenegro and Albania), and the fact that it has historically been a place of political turmoil, has made scientific cooperation difficult in the past. This has now improved, particularly with EU cross-border and transnational collaboration and exchange (e.g. Interreg IPA Adrion and Interreg Med projects among many). Besides, several Adriatic institutions through their national consortium are partners in European research infrastructure LifeWatch ERIC for investigating biodiversity and ecosystem functions.

The diatom genus *Pseudo-nitzschia* comprises planktonic, chain-forming species distributed throughout the world's oceans (Trainer et al., 2012). They have attracted particular scientific attention because some species of the genus produce domoic acid (DA) (Bates et al., 2018; Lelong et al., 2012). This neurotoxin can accumulate in the trophic web and cause Amnesic Shellfish Poisoning (ASP) at higher trophic levels such as birds, marine mammals and humans (see Lelong et al., 2012; Trainer et al., 2012). Despite their ecological importance and the potential impact on human health, the identification of these organisms at the species level in routine monitoring programs is very problematic. Indeed, by light microscopy (LM), *Pseudo-nitzschia* is often categorized into two morphological species groups, as described below, based on paraphyletic morphometric characteristics (valve width), completely losing the information on the toxic species that may be present. Another problem that has emerged recently is that certain very common species, such as the toxic *Pseudo-nitzschia galaxiae*, have been completely overlooked in the monitoring datasets (Turk Dermastia et al., 2023) because they have inconspicuous cells that are difficult to identify. Most *Pseudo-nitzschia* species are characterized by ultrastructural features visible only under the electron microscope or by genetic barcoding (Bates et al., 2018; Lim et al., 2018). Historically, *Pseudo-nitzschia* species were categorized into two paraphyletic Morphological Species Groups (MSGs) based on the dimension of the transapical axis (TA), the *P. delicatissima* MSG (TA$<$ 3 μm) and the *P. seriata* MSG (TA $>$ 3 μm) (Hasle and Syvertsen, 1997). The paraphyly can be exemplified by *P. fraudulenta* and *P. subfraudulenta* that have traditionally been grouped into the *P. seriata* MSG. However, they are genetically distinct from the *P. seriata sensu stricto* clade and have some features that place them outside this group, such as the presence of the central interspace (Lim et al., 2018). Later, two species complexes were defined within the *P. delicatissima* MSG based on the way cells ends overlap in girdle view, the '*P. delicatissima*' and the '*P. pseudodelicatissima*' species complexes, each comprising a number of cryptic species (Ajani et al., 2018; Gai et al., 2018; Huang et al., 2019; Li et al., 2017; Lim et al., 2012; Lundholm et al., 2003, 2006, 2012; Percopo et al., 2016; Quijano-Scheggia et al., 2009; Teng et al., 2016). In truth, the phylogeny of this genus is still the subject of ongoing research, but great progress has been made in the last decade, with new species and phylogenetic relationships discovered and several phylogenetic markers tested (Bates et al., 2018; Lim et al., 2018; Turk Dermastia et al., 2020). Six phylogenetic clades are now known, which are also reflected in the microstructure of the frustules (Lim et al., 2018).

The environmental conditions favouring the proliferation of *Pseudo-nitzschia* have also been studied in the AS, particularly in the northwestern area, where shifts in the nutrient regime, especially oligotrophication and decreasing phosphorus concentrations, have affected phytoplankton communities (Giulietti et al., 2021a; Mozetič et al., 2010; Ninčević Gladan et al., 2020). However, the ecology of *Pseudo-nitzschia* species and the factors contributing to their occurrence/blooming remain open research questions, with conflicting evidence for certain species from different oceanographic regions. For example, the Northeast Pacific shares many *Pseudo-nitzschia* species with the AS (Bates et al., 2018) but the seasonal timing of similar environmental conditions differs between these regions – for instance, summer Sea Surface Temperature (SST) in the Pacific, particularly during upwelling, may resemble winter SST in the Adriatic. As a result, the ecological profiles and seasonal patterns of species occurrence in these regions vary significantly. This variation is likely due to differences in environmental conditions that define specific times of the year in each geographic area. These discrepancies highlight the challenge of generalizing species' seasonal distributions, as what is considered "winter" or "summer" varies by location, and similar environmental conditions may occur at different times of the year in different regions. In addition, autecology is often difficult to determine, as studies often do not provide exact species identification, but report on the ecology of MSGs. Depending on the location and timing of the study, MSGs may contain different species, making comparisons across regions and time periods more complex. In many cases, this variability is not a major issue, as researchers often categorize phytoplankton into broader taxonomic or functional groups based on their ecological roles. However, in the case of *Pseudo-nitzschia*, this approach poses a challenge because it is a potentially toxic and harmful genus. The toxicity of *Pseudo-nitzschia* depends not only on the species present but also on the specific environmental conditions in which the population occurs. As a result, distinguishing species within this genus is critical for assessing ecological and toxicological risks.

In this review, we highlight the enormous efforts that have been undertaken along the Adriatic coastal and open waters in relation to the potentially toxic diatoms of the genus *Pseudo-nitzschia*. The main reason for this review is that many researchers and institutions throughout the Adriatic have conducted at least some research on this genus, but the data are scattered across various journals, datasets, reports and proceedings. Our search in Google Scholar using keywords *Pseudo-nitzschia* and *phytoplankton* in association with *Adriatic* or country names (*Slovenia, Croatia, Italy, Albania, Bosnia, Montenegro*) revealed 54 relevant sources used to make this review. Our first goal is to provide an updated and integrated picture of the *Pseudo-nitzschia* species recorded in Adriatic waters. We also try to summarize the patterns of occurrence of the different species, if available, and to identify environmental factors that seem to favour the occurrence of one species over another. As several studies have also investigated the toxicity of the Adriatic strains as well as environmental conditions and concentrations of domoic acid in shellfish, in the final section we provide an overview of these studies and provide information on HAB threats from *Pseudo-nitzschia* diatoms in the Adriatic Sea.

2. History of *Pseudo-nitzschia* research in the Adriatic sea

The presence of species of the genus *Pseudo-nitzschia* in the AS has been known for decades, thanks to the research activities of marine institutions in the Adriatic, some of which are among the oldest in the

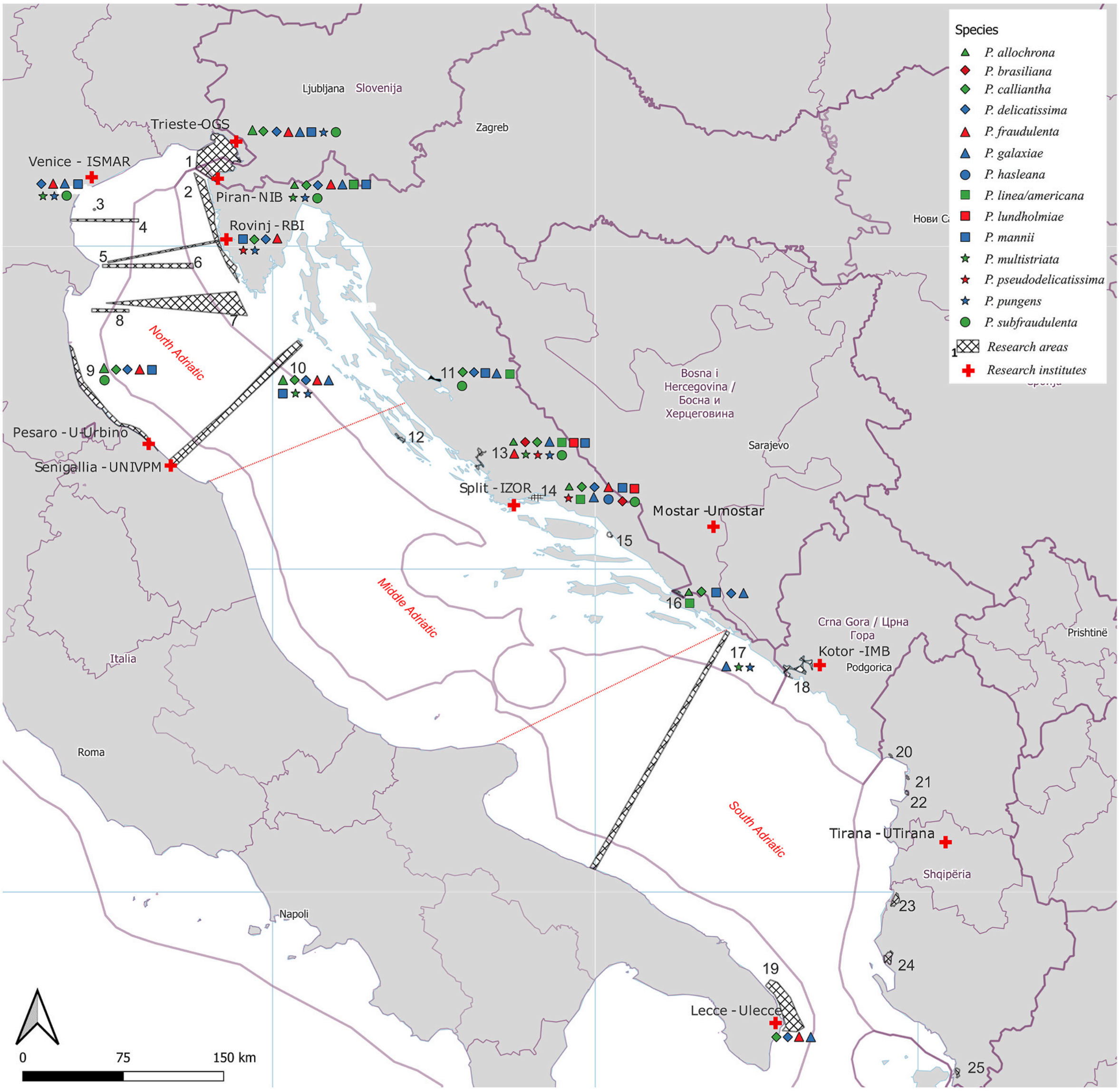

Fig. 1. Locations of *Pseudo-nitzschia* research in the Adriatic Sea along with reported species. The shredded numbered areas are the rough locations of sampling areas, with the research institution conducting research in parentheses: 1: LTER Gulf of Trieste (OGS-Miramare, NIB-Vida). 2,5,7: Western Istria Coast and Northern Adriatic Sea transects (RBI). 3: LTER Acqua Alta Oceanographic Tower - AAOT (ISMAR). 4,6,8: Gulf of Venice and Po River delta transects (ISMAR). 9: Emilia Romagna Coast (U-Urbino). 10: LTER Senigallia-Susak transect (UNIVPM). 11: Velebit Channel. 12: Telaščica National Park (RBI). 13: Krka River Estuary (IZOR). 14: Kaštela Bay. 15: Makarska Coast (U-Mostar). 16: Neum and Mali Ston Bays (IZOR, U-Mostar). 17: Bari-Dubrovnik transect (ISMAR, UNIVPM). 18: Bay of Kotor (IMB). 19: Otranto Channel Transects (ULecce). 20: Vilunit Lagoon. 21: Lezhe Lagoon. 22: Patouk Lagoon. 23: Karavasta Lagoon. 24: Vlore Lagoon. 25: Butrinti Lagoon. 20–25 (U-Tirana).

world (Cattaneo-Vietti and Russo, 2019) and/or are part of the European Long Term Ecological Research (eLTER) network. Nevertheless, some areas of the Adriatic remain understudied, such as coasts of Adriatic islands and offshore areas, which have mainly been studied in NA (Fig. 1) (Neri et al., 2022). Most *Pseudo-nitzschia* research is therefore confined to certain protected bays and areas where aquaculture is practiced, or to areas that are most susceptible to the introduction of non-native species or the spread of autochthonous harmful species (e.g. harbours, coastal lagoons). These include the Gulf of Trieste and Lim Bay (NA), the Krka and Zrmanja estuaries, Kaštela Bay (MA) and the Bay of Kotor (SA), as well as twelve Adriatic ports surveyed for the purposes of the Ballast Water Management Convention (Kraus et al., 2019). Offshore surveys were conducted only on the west coast of Istria (NA) (Godrijan et al., 2013; Marić et al., 2011, 2012), along a transect from Senigallia to Susak Island (NA) (Giulietti et al., 2021a) and a transect from Bari to Dubrovnik (SA) (Cerino et al., 2012) (Fig. 1).

To our knowledge, the first species to be identified in the Adriatic was *P. calliantha* in 1995 from Slovenian and Croatian samples using TEM (Lundholm et al., 2003). Soon after, this species was also found in the southwestern AS, together with *P. delicatissima* and *P. fraudulenta* identified by TEM (Caroppo et al., 2005). The first integrated study combining 28S barcoding and electron microscopy was performed on only 3 strains of *P. multistriata*, *P. pseudodelicatissima* and *P. fraudulenta* (Pistocchi et al., 2012), while in the same period a comprehensive barcoding and toxicity study was performed on several species (Penna et al., 2013). A thorough multigenic and morphological study was conducted on *P. mannii* from Telašćica Bay (MA) (Grbin et al., 2017). However, integrated taxonomic approaches combining molecular and morphological methods were not common until the early 2020s. The study by Turk Dermastia et al. (2020) was one of the first substantial integrated taxonomic studies that aimed to describe the entire *Pseudo-nitzschia* assemblage by combining 3 phylogenetic markers (ITS, 28S and *rbcL*) and examining over 80 isolated strains from 8 species. Following this study, several similar investigations were conducted (Arapov et al., 2023; Bonačić et al., 2025; Giulietti et al., 2021a, 2021b; Smodlaka Tanković et al., 2022). These studies not only provided a great insight into the actual species composition of Adriatic waters and the seasonal distribution of species but also contributed significantly to the global understanding of the population genetics of *Pseudo-nitzschia*.

3. Genetic and morphological diversity of Adriatic *Pseudo-nitzschia* species

With the increase in the accessibility of technology such as electron microscopy, which reveals the fine details of diatom frustules used for species identification, and genetic barcoding, species-level identification of *Pseudo-nitzschia* (and many other phytoplankton taxa) became reliable and commonplace about 20 years ago in the AS, allowing researchers to conduct accurate diversity assessments. Lately, high-throughput sequencing techniques, commonly known as metabarcoding, enabled us to probe even deeper into the intra and interspecific genetic diversity of *Pseudo-nitzschia*, which has provided us yet another layer of understanding of this genus.

To date, 14 species of *Pseudo-nitzschia* have been identified in the AS. The full list is summarized in Table 1, including the techniques used to identify each species to emphasize the reliability of the assignments. Most species were identified using both electron microscopy and molecular methods. The exceptions are *P. lundholmiae* and *P. brasiliana*, which were identified by electron microscopy only.

The locations of records are described in the text only for the Adriatic sub-basins, but for a more detailed occurrence of species see Fig. 1. It's unclear whether the observed lower species diversity in the Southern Adriatic (SA) is due to limited research or to different environmental conditions. Indeed, the SA has received the least scientific attention, yet studies in the nearby Ionian Sea suggest a similar and relatively low species diversity (Moschandreou and Nikolaidis, 2010; Moschandreou

Table 1
List of Pseudo-nitzschia species detected in the Adriatic Sea. Toxicity (NT: not tested, -: no toxicity, +:toxic, O: some strains toxic, some not). Methods (LM – light microscopy, TEM: transmission electron microscopy, SEM: scanning electron microscopy; ITS,28S, rbcL refers to PCR barcoding using these marker genes). Regions (NA: northern Adriatic, MA: middle Adriatic, SA: southern Adriatic).

Species	Toxicity	Methods	Region	First record (Year)	Reference
P. allochrona$^{1\ d,d}$	NT	LM, TEM, ITS, *rbcL,* 28S	NA, MA	2017	(Arapov et al., 2020a; Giulietti et al., 2021b; Pugliese et al., 2017; Turk Dermastia et al., 2023)
P. brasiliana ^{s}	NT†	SEM	MA	2022	(Arapov et al., 2023)
P. calliantha ^{d,pd}	+	LM, SEM, TEM, ITS, 28S, *rbcL*, 18S	NA, MA, SA	1995	(Arapov et al., 2017; Bonačić et al., 2025; Bosak et al., 2010; Caroppo et al., 2005; Lundholm et al., 2003; Marić et al., 2011; Marić et al., 2018; Penna et al., 2013; Turk Dermastia et al., 2020)
P. delicatissima ^{d,d}	O	LM, SEM, TEM, ITS, 28S, 18S, *rbcL*	NA, MA, SA	1995	(Arapov et al., 2017; Bernardi Aubry et al., 2022; Bonačić et al., 2025; Caroppo et al., 2005; Cerino et al., 2012; Giulietti et al., 2021a; Neri et al., 2024; Penna et al., 2013; Turk Dermastia et al., 2020)
P. fraudulenta ^{s}	-†	LM, SEM, TEM, ITS, 28S, *rbcL*, 18S	NA, MA, SA	1995	(Arapov et al., 2017; Bernardi Aubry et al., 2022; Bonačić et al., 2025; Caroppo et al., 2005; Cerino

(*continued on next page*)

Table 1 (*continued*)

Species	Toxicity	Methods	Region	First record (Year)	Reference
					et al., 2012; Giulietti et al., 2021a; Ljubešić et al., 2011; Marić et al., 2018; Turk Dermastia et al., 2020)
P. galaxiae [d,d]	+	LM, SEM, TEM, ITS, 28S, *rbcL*	NA, MA, SA	2019	(Arapov et al., 2023; Caroppo et al., 2005; Cerino et al., 2012; Giulietti et al., 2021b, Turk Dermastia et al., 2020)
P. hasleana [d,pd]	–	LM, SEM, ITS, 28S	MA	2022	(Arapov et al., 2023)
P. linea [s]	NT	LM, *rbcL,* SEM	NA, MA	2022	(Turk Dermastia et al., 2023; Arapov et al., 2023)
P. lundholmiae [d,pd]	NT	SEM	MA	2020	(Arapov et al., 2020a)
P. mannii [d,pd]	–	LM, SEM, TEM, ITS, 28S, *rbcL, 18S*	NA, MA	2011	(Bonačić et al., 2025; Grbin et al., 2017; Giulietti et al., 2021a; Ljubešić et al., 2011; Marić et al., 2018; Turk Dermastia et al., 2020)
P. multistriata [s]	+	LM, SEM, TEM, ITS, 28S, *rbcL*	NA, MA, SA	2012	(Arapov et al., 2020a; Bonačić et al., 2025; Cerino et al., 2012; Turk Dermastia et al., 2020)
P. pseudodelicatissima [d,pd]	NT	TEM, SEM, 28S, *rbcL,* 18S	NA, MA	2012	(Arapov et al., 2017; Bonačić et al., 2025; Bosak et al., 2010; Giulietti et al., 2021a; Ljubešić et al., 2011; Marić et al., 2018; Neri et al., 2024; Pistocchi et al., 2012; Smodlaka Tanković et al., 2022)
P. pungens [s]	-[†]	LM, SEM, TEM, ITS, 28S, *rbcL,* 18S	NA, MA, SA	1995	(Bernardi Aubry et al., 2022; Caroppo et al., 2005; Cerino et al., 2012; Giulietti et al., 2021a; Ljubešić et al., 2011; Arapov et al., 2016; Marić et al., 2018; Neri et al., 2024; Turk Dermastia et al., 2020)
P. subfraudulenta [s]	-[†]	LM, SEM, TEM, ITS, 28S, *rbcL*	NA, MA	2017	(Arapov et al., 2017; Bernardi Aubry et al., 2022; Bonačić et al., 2025; Bosak et al., 2010; Penna et al., 2013; Turk Dermastia et al., 2020)

[1] Defined as maximum contribution to the cumulative annual abundance calculated for each year. The mode of the entire series is reported.

[s] Species commonly assigned to the *Pseudo-nitzschia seriata* MSG.

[d,d] Species commonly assigned to the *Pseudo-nitzschia delicatissima* MSG, and occasionally to the *Pseudo-nitzschia delicatissima sensu lato* species complex.

[d,pd] Species commonly assigned to the *Pseudo-nitzschia delicatissima* MSG, and occasionally to the *Pseudo-nitzschia pseudodelicatissima sensu lato* species complex.

[†] Potentially toxic species as per Bates et al. (2018).

et al., 2012) compared to the rare studies in the SA (Caroppo et al., 2005). This could be due to the oligotrophic environment unfavourable to diatoms in general, even though at least *P. delicatissima* MSG is a dominant member of these communities (Matek et al., 2023). Research scope also varies based on methodology—SA remains the least studied part of the Adriatic and the only region where *Pseudo-nitzschia* species have been identified solely using light microscopy (LM), except for Caroppo et al. (2005), who analysed samples from 1995 to 1997 and used TEM. Consequently, species inventories and seasonal profiles from SA remain scarce. In Albania and Bosnia and Herzegovina, for instance, only a few species or the genus level has been reported (Mozetič et al., 2019; Saracino and Rubino, 2006; Talić et al., 2020). Overall species composition appears similar across regions (Fig. 1), despite some species being recorded in only a few locations. This could be due to the different research efforts and expertise of Adriatic taxonomists. As a result, records based on LM may differ considerably between institutions due to this bias. Records of species new for the Adriatic continue to be found, but this is probably largely due to increased vigilance, expertise, and use of novel techniques rather than to introduction from other areas. For some species, such as *P. multistriata*, the debate about their non-indigenous status is still ongoing. The debate has arisen because this species has a typical sigmoidal morphology that is easily distinguishable with LM methods, while Mediterranean taxonomists while Mediterranean taxonomists have only begun to observe it regularly in water samples since the late 1990s (Zingone et al., 2021). Recent genomic evidence shows that Mediterranean strains, including those from the AS, are phylogenomically closer to strains from the Gulf of Mexico but distinct from Pacific strains from New Zealand (Mager et al., 2025). It is therefore still unclear whether the species recently arrived from another Atlantic region and has already sufficiently evolved to form a distinct phylogenomic clade, or whether the species was already present but overlooked in the past.

While the phylogenomic investigation on *P. multistriata* is the most advanced study on the intraspecific diversity of the Adriatic *Pseudo-nitzschia* (Mager et al., 2025), other studies have probed the intraspecific diversity of other species. For example, Turk Dermastia et al. (2020) revealed that the high intraspecific diversity within the *P. galaxiae* species complex was reflected at both genetic and morphological levels. In a later work based on the metabarcoding method, it was shown that different haplotypes, probably corresponding to different morphotypes, coexisted within the same population, but were nevertheless seasonally separated in terms of abundance, suggesting that they have different ecological preferences (Turk Dermastia et al., 2023). Thus, they could well be different species, although no compensatory base changes – one of the key genetic signatures of speciation – were observed in the secondary structure of the ITS-2 RNA (unpublished data). Alternatively, these different types of *P. galaxiae* could instead represent distinct populations in the process of sympatric speciation. As there are clear size differences between these populations, authors hypothesized that they are unable to interbreed, as cells of the larger population may be above the critical size for sexual reproduction. However, this has yet to be determined in cross strain reproduction studies. These results complemented similar observations made in the Gulf of Naples (Cerino et al., 2005; Ruggiero et al., 2022). Adriatic studies also showed that haplotypes of *Pseudo-nitzschia* exhibit species-specific differentiation patterns. *P. delicatissima, P. calliantha, P. fraudulenta* and *P. mannii* showed a high dominance of certain haplotypes with some much less frequent auxiliary haplotypes (Giulietti et al., 2021b; Pistocchi et al., 2012; Turk Dermastia et al., 2020). This finding was also supported by metabarcoding, which has a much higher detection power and deeper coverage compared to the isolation of individual strains (Turk Dermastia et al., 2023). Based on ITS1-5.8S sequences, Penna et al. (2013) highlighted that the Adriatic strains of *P. delicatissima* exhibit little geographic differentiation compared to other Mediterranean strains (Catalonia, Tyrrhenian Sea), yet together they form a distinct clade compared to the Atlantic strains. The opposite is true for *P. calliantha* and *P. pungens*, although the haplotypes found in the Adriatic also occur in other Mediterranean and non-Mediterranean regions. Turk Dermastia et al. (2020) extended these results to *P. fraudulenta*, *P. subfraudulenta* and *P. multistriata,* all of which showed that the dominant haplotypes of the Adriatic strains are similar to those within and outside the Mediterranean. Based on *rbcL* and ITS-2, this study also showed that despite the great variability of *P. galaxiae*, these haplotypes occur in both the Adriatic and Tyrrhenian Seas. A new cryptic species, previously described as *P.* cf. *delicatissima* from the Tyrrhenian Sea (Lamari et al., 2013) was also identified and isolated in the NA (Giulietti et al., 2021b; Pugliese et al., 2017) and described as *P.* cf. *arenysensis*. Its presence was also confirmed in metabarcoding samples by *rbcL* (Turk Dermastia et al., 2023). It is now assumed that all these records belong to *P. allochrona* (Percopo et al., 2022), which has so far only been reported in the Mediterranean region.

Significant progress has also been made in the morphological study of *Pseudo-nitzschia* species in the Adriatic region. Electron microscopy investigation in *Pseudo-nitzschia* isolates has provided morphometric information on strains from several Adriatic sites. We now have detailed information on: *P. allochrona, P. calliantha, P. delicatissima, P. fraudulenta, P. galaxiae, P. mannii, P. multistriata, P. pseudodelicatissima, P. pungens, P. subfraudulenta* from the NA (Giulietti et al., 2021b; Ljubešić et al., 2011; Marić et al., 2018; Turk Dermastia et al., 2020); on *P. allochrona, P. brasiliana, P. calliantha, P. delicatissima, P. fraudulenta, P. linea, P. lundholmiae, P. mannii, P. multistriata, P. pseudodelicatissima, P. subfraudulenta* from the MA (Arapov et al., 2017, 2020b; Bonačić et al., 2025); and for *P. calliantha, P. delicatissima* and *P. fraudulenta* and *P. galaxiae* from the SA (Caroppo et al., 2005). The morphometrics of species are generally very similar across the basin, particularly when average values are considered. The only notable differences can be seen in the maximum apical axis lengths of *P. delicatissima* reported in the MA (94 μm) compared to 70 μm in the NA and SA, and in the relatively small *P. fraudulenta* cells reported in the MA (60–88 μm), compared to the larger cells in the NA and SA (72–108 μm and 76–114 μm, respectively). However, the values reported in the MA were similar to those recorded in the Ionian and Aegean Seas (Moschandreou and Nikolaidis, 2010).

Dedicated morphological studies of individual species were also carried out. The above-mentioned morphotypes of *P. galaxiae* have been thoroughly studied in the Gulf of Trieste, including a toxicological analysis (Turk Dermastia et al., 2020, 2022), similarly to studies carried out in the Tyrrhenian Sea (Cerino et al., 2005). An in-depth morphological study on the intraspecific morphological variability of *P. pungens* was also conducted (Accoroni et al., 2020). This study showed that the old classification of *Pseudo-nitzschia* based on valve width is outdated not only because the groups are paraphyletic, but also because *P. pungens*, which is usually classified as a species of the *P. seriata* MSG, shows a large intraspecific variability that includes cells with valve widths below this arbitrary threshold (Accoroni et al., 2020). In addition, the strains examined in this study showed great variability in many other morphometric traits normally considered for discriminating morphological varieties within this species. Despite these differences, the strains were genetically very similar when considering the ITS1-5.8S-ITS2 region. The relatively conserved nature of the marker used may mask morphological intraspecific differences among clades. In fact, a clade does not necessarily correspond to a morphological variety and *vice versa* (Accoroni et al., 2020). This aligns with the well-known morphometric variability of diatoms, particularly in *Pseudo-nitzschia*, where frustule plasticity complicates taxonomic distinctions despite interspecific differences often remaining sufficient for species identification (Round et al., 1990). The evolutionary and ecological role of frustule morphology remains debated. Frustules influence light harvesting (e.g., valve ultrastructure optimizes light capture efficiency), sinking rates, hydrodynamic properties, and defence mechanisms (De Tommasi et al., 2017). Environmental factors such as light and nutrient availability can modulate frustule architecture (Smith et al., 2016; Soler et al., 2010), though genetic determinants dominate interspecific differences (De Tommasi et al., 2017). Notably, morphometric shifts occur during the asexual life cycle (e.g., progressive size reduction) and are reset during sexual reproduction, further complicating species delineation based solely on morphology.

In summary, the genus *Pseudo-nitzschia* appears to be highly diversified in the AS, particularly in the coastal regions of the northern and middle sub-basins, similarly to other Mediterranean areas like the Greek Aegean Archipelago, where 14 species have been identified (Moschandreou and Nikolaidis, 2010). This diversity is slightly lower compared to the Gulf of Naples in the Tyrrhenian Sea, where 17 species have been identified (Ruggiero et al., 2022), and somewhat higher compared to the Catalan Coast in the NW Mediterranean where 11 species have been recorded (Quijano-Scheggia et al., 2010). Notably, species commonly found elsewhere in the Mediterranean, such as *P. arenysensis, P. dolorosa* and *P. caciantha*, have not been yet recorded in the AS, while *P. lundholmiae* has only been found here (Arapov et al., 2020b). Overall, the Adriatic *Pseudo-nitzschia* diversity is lower than that recorded around Malaysian islands or Chinese coasts (Huang et al., 2019), which host the highest recorded *Pseudo-nitzschia* diversity, numbering 26 species in both regions (Dong et al., 2020; Teng et al., 2016). Moreover, it is also lower than in some other temperate regions, such as the Australian SE coasts (Ajani et al., 2021 and references therein), but comparable to the California Current Ecosystem (Bates et al., 2018; Brunson et al., 2024). With new research and techniques, particularly in underexplored areas, the species lists will likely improve and grow, although we can say that considerable effort has already been made.

4. Spatial and temporal distribution of the genus in the Adriatic sea

4.1. Long term trends

The genus *Pseudo-nitzschia* is a widespread and ecologically important pennate diatom. In the AS, its cell abundances have been consistently monitored using LM, typically reporting the two MSGs, the *P. delicatissima* group and the *P. seriata* group. In some cases, *P. delicatissima* has been further divided into the *P. delicatissima* and *P. pseudodelicatissima* species complexes based on the way cell ends overlap in girdle view (Bernardi Aubry et al., 2004, 2006, 2012, 2022; Vascotto et al., 2021). However, the ecological relevance of categorizing species into these MSGs and interpreting their distribution and occurrence in relation to environmental variables remains disputed. Recent evidence from the AS shows that some species traditionally considered as members of one group may exceed the arbitrary threshold of 3 μm separating the two groups (Accoroni et al., 2020), as described in the previous section. Nevertheless, in most cases, and especially in local surveys where the species composition is relatively well known, these data are useful and can provide insights into the variability and ecology of the genus. In addition, the long-term data we have are based on quantifying the MSGs using LM, providing a guideline for drawing past and future ecological scenarios.

One of the most complete assessments of *Pseudo-nitzschia* comes from a 37-year phytoplankton time series (1972–2009) on the west coast of Istria, combining data from coastal and offshore stations (Marić et al., 2012). The study identified two periods within this nearly 40-year time frame that were separated by a change in the nutrient and salinity regime in 2000 and drastically different ecological conditions. This regime shift is also documented in other studies (Cabrini et al., 2012; Mozetič et al., 2010; Totti et al., 2019). The study of Marić et al. (2012) revealed differences in the frequency of the two MSGs between the two time periods (pre 2000 and post 2000). The frequency of occurrence of *P. delicatissima* MSG increased in the second period in both coastal and off-shore stations (coastal: 62.5–82.1 % of samples; offshore: 56.6–68.7 % of samples), but with roughly 50 % lower average and maximum abundance values (coastal: $\max_1 = 1.08 \times 10^6$ cells/L, $\text{avg}_1 = 52.2 \times 10^3$ cells/L; $\max_2 = 4.3 \times 10^5$ cells/L, $\text{avg}_2 = 26.6 \times 10^3$ cells/L; offshore: $\max_1 = 2.12 \times 10^6$ cells/L, $\text{avg}_1 = 65.2 \times 10^3$ cells/L; $\max_2 = 3.78 \times 10^5$ cells/L, $\text{avg}_2 = 41 \times 10^3$ cells/L). On the contrary, *P. seriata* MSG showed a decrease in frequency of occurrence (coastal: 19.2to 12.5 % of samples; offshore: 22.8 to 12.5 % of samples) and maximum abundance in both stations (coastal: $\max_1 = 1.14 \times 10^6$ cells/L, $\text{avg}_1 = 23.3 \times 10^3$ cells/L; $\max_2 = 4.3 \times 10^5$ cells/L, $\text{avg}_2 = 26.6 \times 10^3$ cells/L; offshore: $\max_1 = 1.8 \times 10^6$ cells/L, $\text{avg}_1 = 46.4 \times 10^3$ cells/L; $\max_2 = 6.1 \times 10^5$ cells/L, $\text{avg}_2 = 80.9 \times 10^3$ cells/L). Cabrini et al. (2012), who analysed a long-term data set (1986–2010) from the Gulf of Trieste, also showed that before 2000, the spring bloom was often dominated by *P. delicatissima* MSG and *Skeletonema marinoi*, while the autumn bloom was often dominated by *P. seriata* MSG. This dominance largely shifted to *Chaetoceros* spp. in both the spring and autumn blooms after the regime change. A more recent study from the same area, 2005–2017, did not show as clear a shift in the seasonal dominance of blooming species as reported by Cabrini et al. (2012). Instead, after the severe drought (2002–2007) (Cozzi et al., 2012) and the onset of variable environmental conditions, a transition from a more predictable to a more erratic phytoplankton community dynamic was observed, driven largely by 'ephemeral' spring-blooming species. Nevertheless, *P. delicatissima* MSG remained the dominant autumn taxa (Vascotto et al., 2021). A general decreasing trend in *Pseudo-nitzschia* spp. abundance was recorded in the open and coastal between 2007 and 2020 (Skejić et al., 2024). In a similar period (2014–2018) in coastal aquaculture areas, a trend of increasing abundance of *Pseudo-nitzschia* spp. occurred in the NA and MA and found to be positively correlated with higher precipitation (Ninčević Gladan et al., 2020). While clear trends in *Pseudo-nitzschia* abundance (either genus or MSGs) are hard to establish given the sometimes-conflicting data that is reported in the literature, it is clear that *Pseudo-nitzschia* occasionally dominate phytoplankton communities in the AS and that they are important phytoplankton constitutes. Long-term Adriatic studies have also shown that greater river discharge and precipitation positively correlate with *Pseudo-nitzschia* abundance and that *Pseudo-nitzschia* can tolerate higher turbulence and prefer mixed water columns (Ninčević Gladan et al., 2020). These data also concur with observations in upwelling system of the US Pacific (Trainer et al., 2007) and South Africa (Lucas et al., 2014), and in the English Channel (Husson et al., 2016). However, the genus seems to be opportunistic with abundance peaks both in summer and winter across the basin. This is likely due to very different requirements of species within the genus (and within MSGs), which makes it overall successful in exploiting different ecological niches. Therefore, data on individual species, where available, are highly valuable for disentangling the complexity behind the ecology of the whole genus.

4.2. Light microscopy derived occurrence and distribution data

We have compiled time series data from eLTER sites in the northern Adriatic, such as the Slovenian and Italian LTER sites in the Gulf of Trieste (stations 000F and C1, respectively) (Cabrini et al., 2012; Vascotto et al., 2021), the LTER Aqua Alta Oceanographic Tower (AAOT) in the Gulf of Venice (Bernardi Aubry et al., 2022), the LTER Senigallia-Susak Transect (Neri et al., 2022; Totti et al., 2019) and studies focused on regions of special interest such as mussel farming areas (Bužančić et al., 2012; Godrijan et al., 2013; Ljubešić et al., 2011; Marić et al., 2011, 2012; Ninčević Gladan et al., 2020; Skejić et al., 2024; Xhulaj et al., 2007) (Table 2). To normalize data, we defined the bloom periods as the time of the year where the percentage of *Pseudo-nitzschia* (either genus or MSG) is highest over its cumulative annual abundance to normalize data, since the number of samples, sampled depths and the number of phytoplankton classes that are identified in different time series varies. The mode of seasonal preference for all examined years was then reported, or in the case of a bimodal or random distribution this is also stated. The data show that the genus *Pseudo-nitzschia* represents on average 10–30 % of the diatom community and the majority falls into the *P. delicatissima* MSG. These proportions can in some cases reach almost 100 % of the total phytoplankton during the bloom period, emphasizing the ecological importance of the genus in the AS. The highest abundance ever measured since 1972 was 5×10^6 cells/L in the Gulf of Trieste (C1-LTER) and 6.2×10^6 in the Gulf of Venice (AAOT LTER). Interestingly, even within a very close geographic range such as the C1 and 000F stations in the Gulf of Trieste, the bloom periods differed, even though the data period was very similar (Table 2). At C1 the prevailing bloom period was spring, whereas at 000F it was autumn with far greater maximum percentages, although at C1 the distribution was bimodal, and autumn peaks were also recorded albeit with lower maximum percentages (Table 2, unpublished data). This finding exacerbates the variability of data and the influence of unaccounted factors for the perceived seasonal preference of *Pseudo-nitzschia* spp. The cells of *P. seriata* MSG rarely exceeded 10^5 cells/L, but there are cases in offshore NA and Albanian coastal lagoons where they exceeded 10^6 cells/L

Table 2
Seasonal distribution of the genus Pseudo-nitzschia and commonly light microscopy monitored MSGs: P. delicatissima MSG and P. seriata MSG. NR – Not reported.

Research Area	Region	Data period	*Pseudo-nitzschia* genus bloom period (*maximum contribution in period*)[2]	*Pseudo-nitzschia* genus (average % of diatom community)	*Pseudo-nitzschia* genus peak abundance (cells/L)	*Pseudo-nitzschia delicatissima* MSG peak period[1]	*Pseudo-nitzschia delicatissima* MSG mean/max abundance (cells/L)	*Pseudo-nitzschia seriata* MSG peak period[1]	*Pseudo-nitzschia seriata* MSG mean/max abundance (cells/L)
Gulf of Venice (AAOT station)[3]	NA	2011–2022	Summer-Autumn (*74 %, Sep 2018*)	18 %	6.2×10^6 (Sep 2018)	Summer-Autumn	6.2×10^6 (max) 1.7×10^5 (mean)	No clear preference	1.3×10^5 (max) 3.6×10^3 (mean)
Gulf of Trieste (C1 station)[2]	NA	2006–2022	Spring (*40 %, Apr, 2011*); Autumn[4]	15 %	5×10^6	Spring; Autumn	5×10^6 (max) 6.2×10^4 (mean)	Spring	2.6×10^6 (max) 1.4×10^4 (mean)
Gulf of Trieste (000F station)[2]	NA	2005–2023	Autumn (*91 %, Sep 2008*)	14 %	3.8×10^6 (Nov 2010)	Autumn	3.7×10^6 (max) 5.1×10^4 (mean)	Autumn	2.3×10^5 (max) 3.3×10^3 (mean)
Senigallia-Susak (coastal and offshore stations)[2]	NA	1988–2022	Spring (*74 %, May 2009*)	10 %	4.1×10^6	Spring	4.1×10^6 (max) 6.9×10^4 (mean)	Spring	3.4×10^5 (max) 1.7×10^3 (mean)
Krka Estuary[5]	MA	2005	Winter (*Jan 59 %*)	21 %	1.2×10^6 (Jan 2005)	/	/	/	/
Kaštela Bay[6]	MA	2007–2020	Spring (*71 %, Mar 2010*); Summer-Autumn (*66 %, Oct 2015*)	33 %	3.0×10^6 (Mar 2010 2.0×10^6 (Aug 2013)	Spring	3.0×10^6 (max) 7.6×10^5 (mean)	Summer	2.7×10^5 (max) 1.5×10^4 (mean)
Istria west coast[7]	NA	2002–2008	Summer	24 %	1.6×10^6	Summer-Autumn	1.6×10^6	Winter	NR
Istria offshore west coast[8]	NA	1972–2009	NR	NR	1.2×10^6	Summer-Autumn	1.2×10^6 (max)	Winter	4×10^4 (mean) 1.1×10^6 (max)
Albanian Adriatic Lagoons	SA	2006–2007	NR	NR	NR	NR	7.2×10^4 (mean)	Winter	2×10^6 (max) 3.4×10^5 (mean)
Bay of Kotor[2]	SA	2008–2009	45 %			Summer	1.2×10^5 (max)		

1 This species was previously regarded as either *P.* cf. *delicatissima* or *P.* cf. *arenysensis*.
2 Unpublished (data from authors of this review).
3 Spring more common with more pronounced blooms.
4 Bužančić et al. (2012).
5 Skejić et al. (2024).
6 Ljubešić et al. (2011), Marić et al. (2011).
7 Godrijan et al. (2013), Marić et al. (2011, 2012).

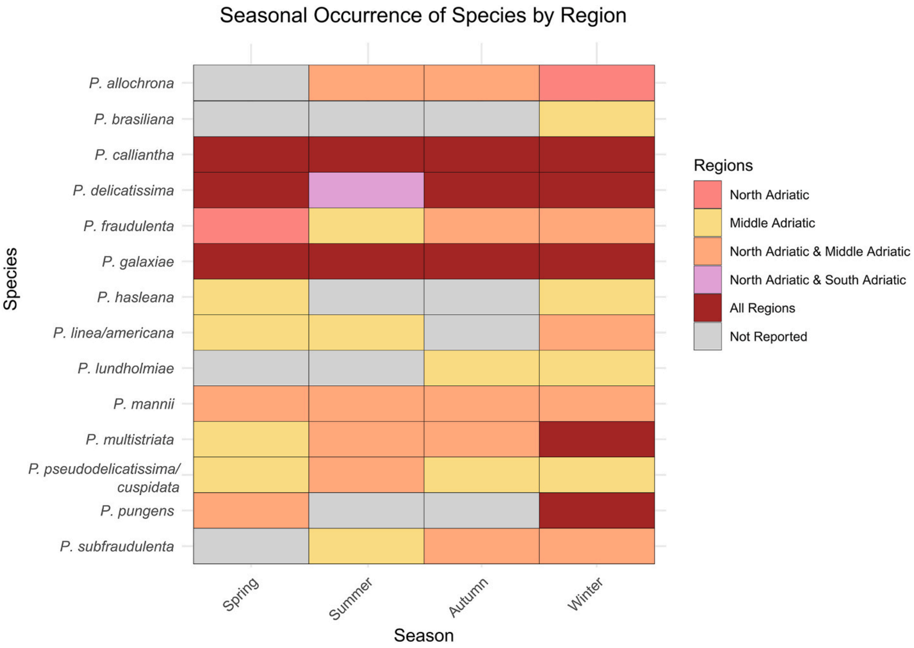

Fig. 2. Seasonal distribution of *Pseudo-nitzschia* species across the Adriatic sub-basins. Seasonality data are not available for some species reported from the AS. The occurrence data is based on either TEM, isolate with genetic ID, or metabarcoding data. Occurrence from LM only where applicable (e.g. *P. multistriata*, *P. galaxiae*).

(Godrijan et al., 2013; Marić et al., 2012; Xhulaj et al., 2007). Both *P. delicatissima* and *P. seriata* MSGs usually peak in autumn or late summer, although there are certain areas where the peak in *P. delicatissima* MSG occurs in spring (Table 2). In some cases, such as the Gulf of Venice *P. seriata* did not have a clear seasonal preference with bloom peaks in winter occurring 5 times, in spring four times, in autumn 6 times, and in summer 2 times in the 12-year time series.

4.3. Occurrence and distribution of individual species

Most taxonomic surveys that have focused on *Pseudo-nitzschia* have also addressed their ecological requirements and the environmental factors that influence the occurrence and abundance of individual species. These assessments are somewhat unreliable, especially if proper species identification is not carried out, which has been a common problem in the past. Therefore, reports on the ecological preference of individual species are often inconsistent (Thorel et al., 2017). However, for certain species we can recognize common patterns of occurrence as they also have identifiable features under LM. Species classified under the *P. seriata* MSG appear to be more common in the Adriatic during the colder months (from autumn to early spring) (Fig. 2). For example, it was demonstrated that *P. subfraudulenta* and *P. fraudulenta* have a quite specific autumn-winter occurrence in the Adriatic (Arapov et al., 2020b; Giulietti et al., 2021a; Turk Dermastia et al., 2020), with some reports of occurrence in late summer in the MA (Arapov et al., 2020b). This distribution is also typical for other Mediterranean areas (Quijano-Scheggia et al., 2008; Ruggiero et al., 2015). This rather specific occurrence window was also confirmed by a metabarcoding study in NA (Turk Dermastia et al., 2023). Similarly, *P. pungens* also has a restricted winter-spring occurrence in the whole Adriatic. In the SA it only recorded once in February (Cerino et al., 2012), similarly to the Gulf of Naples, where it also appears to be rare (Ruggiero et al., 2022). Since there are three recognized clades of *P. pungens*, each demonstrating different ecophysiological characteristics (Kim et al., 2015), and the ones in the Mediterranean cluster with the cold-adapted clade (Turk Dermastia et al., 2020), we can speculate that the higher winter temperatures in the SA and the Gulf of Naples, compared to the NA and MA, make these habitats suboptimal for this species (Kim et al., 2015) *P. linea*, another member of the *P. seriata* MSG, also occurs mainly in winter and spring in the Adriatic, with a single cell recorded in summer in MA (Arapov et al., 2023). *P. multistriata* seems to have an autumn-winter restricted occurrence in the NA with autumn peaks in the NW and winter peaks in the NE (Giulietti et al., 2021a; Turk Dermastia et al., 2020), although there is also a single summer report from the Lagoon of Venice (Bernardi Aubry et al., 2022). In the MA, it has also been documented in spring, but with peak abundance in autumn (Arapov et al., 2020b), similar to the Tyrrhenian Sea (Ruggiero et al., 2022). In the SA it was only recorded in winter (Cerino et al., 2012). Interestingly, although *P. multistriata* is a less widespread and relatively rare species in the Adriatic with low abundances, it was recognized as a significant autumn indicator species between 2007 and 2017 in the NW Adriatic (Totti et al., 2019). In the Gulf of Trieste, the species was observed only very rarely after repeated occurrences in 2019–2021 (unpublished data), and it was not recorded in metabarcoding data (Turk Dermastia et al., 2023). Cells were observed again in the winter 2023 and the autumn 2024 (unpublished data). Finally, *P. brasiliana* reported only in the MA, was restricted to winter months with low temperatures of the water column (Arapov et al., 2023).

The species classified into the *P. delicatissima* MSG by LM typically have their abundance peaks during late summer and autumn (Fig. 2). While this data is not commonly reported these peaks are mostly driven by members of the *P. pseudodelicatissima* species complex and *P. galaxiae*. A spring peak of the *P. delicatissima* species complex is also common, sometimes driving the bloom mode to this period (Table 2). This was shown for the *P. delicatissima* species complex, which typically blooms in early spring in NA and reaches abundances of over 10^6 cells/L (Cabrini et al., 2012; Giulietti et al., 2021a; Totti et al., 2019), but also produces summer peaks in the Gulf of Venice (unpublished data). Within this species complex, *P. galaxiae* can be distinguished by LM. It was found in all regions year-round with peak abundances in summer and early in autumn in the NA and SA (Bernardi Aubry et al., 2022; Cerino et al., 2012; Giulietti et al., 2021a; Turk Dermastia et al., 2020) and in the summer and winter in the MA (Arapov et al., 2023). In a study comparing the Lagoon of Venice (enclosed lagoon) and Gulf of Venice (open sea) Bernardi Aubry et al. (2022) established that *P. galaxiae* is among the "generalists" species as it was consistently recorded in both habitats. Another *P. delicatissima* species complex member – *P. allochrona* (reported previously as *P.* cf. *arenysensis*) as identified by TEM - was responsible for a late-summer high-abundance bloom in the Krka River estuary (MA) (Arapov et al., 2020a), while in NA it was detected only in autumn and winter by qPCR and metabarcoding (Pugliese et al., 2017; Turk Dermastia et al., 2023). In another NA study, it was found only in summer similar to the Krka River estuary (Giulietti et al., 2021b). *P. delicatissima sensu stricto* is indistinguishable from *P. allochrona* by LM, but isolate (with genetic and morphological determination), TEM and metabarcoding data suggests this species has a year-round presence with peak abundances in spring and an absence of summer occurrence in the MA (Bonačić et al., 2025; Caroppo et al., 2005; Giulietti et al., 2021a; Turk Dermastia et al., 2020, 2023). These findings can guide future studies, as it seems that these two phylogenetically very close species demonstrate a temporal separation with *P. delicatissima* preferring winter-spring periods and *P. allochrona* preferring summer-autumn periods. The lack of overlap was also demonstrated by metabarcoding in the Gulf of Trieste (Turk Dermastia et al., 2023).

The *P. pseudodelicatissima* species complex seems to drive the observed preference of the *P. delicatissima* MSG of summer-early autumn periods in the NA as it is consistently observed to peak, and sometimes dominate the diatom community in this time (Giulietti et al., 2021a; Ljubešić et al., 2011; Totti et al., 2019). This was also evident in Boka Kotorska Bay (MA) with a relatively high abundance of the *P. pseudodelicatissima* species complex (1.2 × 10^5 cells/L (Bosak et al., 2012)). In contrast in the MA and SA, members of the *P. pseudodelicatissima* species complex, such as *P. calliantha* were more abundant in winter (Arapov et al., 2020b; Caroppo et al., 2005). Mixed blooms of *P. calliantha* and *P. mannii* with abundances reaching over 10^6 cells/L were common in August and September in NA (Giulietti et al., 2021a; Marić et al., 2011; Turk Dermastia et al., 2020). *P. calliantha* is also the only species recorded in all subregions in all seasons (Fig. 2). Both in the NA and MA, *P. mannii* has a year-round occurrence, although the patterns differ from study to study. In the NW the species was found in winter and spring (Giulietti et al., 2021a), while in other the NE it was restricted to the warmer months in summer and early autumn (Grbin et al., 2017; Turk Dermastia et al., 2020, 2023). In a recent MA study, it was the only species present in all examined locations with year-round occurrence (Bonačić et al., 2025). Three other species in the *P. pseudodelicatissima* species complex were identified by TEM and are restricted to the MA. These include *P. pseudelicatissima/cuspidata* which is common year-round in the MA sites (Arapov et al., 2020b), and two rare and cold-water restricted species *P. lundholmiae* and *P. hasleana* (Arapov et al., 2023). Note that only *P. hasleana* was confirmed also with molecular methods.

Based on the available data, we can say that species belonging to the *P. seriata* MSG proliferate in colder mixed waters in the AS, while members of the *P. delicatissima* MSG generally prefer stable and warmer waters. This is evident from both long-term time-series analyses (Cabrini et al., 2012; Marić et al., 2012) and limited reliable autecological evidence, such as for *P. fraudulenta* and *P. pungens*, which were significantly correlated with increasing DIN:PO_4 ratios and negatively correlated with increasing temperature, while silicate played no role in this respect (Giulietti et al., 2021a). Negative correlations were observed for silicate concentrations and the abundance of *Pseudo-nitzschia* species (Arapov et al., 2020b; Turk Dermastia et al., 2020), suggesting that *Pseudo-nitzschia* can tolerate silicate variations. However, this correlation could also stem from silicate depletion during bloom events (Marić et al., 2011), which has also been observed in other studies (Marchetti et al., 2004; Thorel et al., 2017). Linking the occurrence of individual species to environmental conditions is therefore a challenging task, especially because many factors, such as interspecific interactions and pathogens, are rarely considered. The contradictory findings regarding the factors that drives the distribution and abundance of different species are, therefore, not surprising.

4.4. Toxicity of Adriatic Pseudo-nitzschia

The Adriatic *Pseudo-nitzschia* have not been shown to pose a major threat to marine animals or human health (Accoroni et al., 2024; Henigman et al., 2024; Zingone et al., 2021). Although neither ASP outbreaks nor concentrations of DA in shellfish above the legal limit have been recorded in the basin to date (Zingone et al., 2021), detectable levels of DA occasionally occur in mussels. For example, DA was detected in mussel samples from the coast of Emilia-Romagna and the Gulf of Trieste in 2000 and 2002 (Ciminiello et al., 2005), and from the Istrian peninsula (north-eastern Adriatic) in 2006–2008 (Ujević et al., 2010). In the area of Boka Kotorska Bay (MA), there have been no records of toxicity events, nor has the presence of DA been detected so far (Pestorić et al., 2019). To date, four species of Adriatic *Pseudo-nitzschia* have been confirmed as toxic to varying degrees (Table 1). The most toxic species was *P. multistriata* with up to 160 fg/cell of particulate DA and 80 ng/ml of dissolved DA in the cultures tested (Turk Dermastia et al., 2022). These values were similar to some *P. multistriata* strains from the Tyrrhenian Sea (Amato et al., 2010). Less toxic strains of *P. multistriata* (3 fg/cell) were also found in the northwestern Adriatic (Pistocchi et al., 2012). In addition, the *dabA* gene presence, which is involved in DA biosynthesis, was also confirmed by PCR in the Adriatic *P. multistriata*, but not in other examined species (Turk Dermastia et al., 2022). However, *P. multistriata* is a less common and relatively rare species in the Adriatic (Arapov et al., 2020b; Giulietti et al., 2021a; Turk Dermastia et al., 2020), so it is unlikely that this species can be associated with increased toxin concentrations in shellfish. Toxicity was also confirmed in three other species. *P. delicatissima* was found to be mildly toxic with intracellular concentrations ranging from 0.063 fg/cell (Penna et al., 2013) to 1.5 fg/cell (Turk Dermastia et al., 2022). Toxicity was also determined in certain strains of *P. galaxiae*. Although intracellular quantification was not possible, the results showed DA concentrations in culture media ranging from 5 to 24.8 ng/ml (Turk Dermastia et al., 2022). These concentrations are high, but we must note that they were measured in a highly stressful batch culture environment and thus may not reflect field conditions. The species most commonly associated with shellfish toxicity in the Adriatic Sea is *P. calliantha* (Arapov et al., 2016; Marić et al., 2011), although its toxicity was only recently confirmed in culture conditions, with toxin concentrations ranging from 5 to 85 fg/cell (Arapov et al., 2020c). Given that the abundance of this diatom in the environment can be quite high ($>10^6$ cells/L), these concentrations suggest that it could indeed be associated with the detected DA in mussel samples. Finally, there are other species present in the AS that have tested negative for DA but have been found to be toxigenic in other areas worldwide (Table 1). These include *P. brasiliana*, *P. fraudulenta, P. pungens* and *P. subfraudulenta*, which could contribute to DA found in AS shellfish. Testing for DA in cultures may yield ambiguous results, especially if conducted at single points, rather than across different growth stages, which are known to influence the amount of DA produced (Lelong et al., 2012). We cannot ignore the toxigenic potential of these species particularly in the light of changing environmental conditions.

4.5. Emerging fields in Adriatic (and global) Pseudo-nitzschia research

Although the diversity of the genus *Pseudo-nitzschia* has been significantly elucidated over the past decade, the difficulties in establishing ecological profiles of individual species and species complexes are likely to persist in future ecological surveys. This is because most long-term data come from continuous monitoring, which is still based on MSGs and LM. Several cross-basin projects (e.g. INTERREG-MED SHAREMED) have attempted to introduce higher resolution methods, such as metabarcoding, into water monitoring programs. Such progress takes time, as additional resources and manpower are often not available. However, high-throughput analyses such as metabarcoding have great potential to reveal new patterns of species occurrence. For example, the study by Turk Dermastia et al. (2023) has shown an overwhelming dominance of *P. galaxiae* in the *Pseudo-nitzschia* assemblage throughout the year, with the highest relative abundance in winter in the Gulf of Trieste. This was attributed to both the prevalence of this species and a possible amplification bias – the low silicification state of *P. galaxiae* cells and their small size could render them more prone to lysis during DNA extraction potentially resulting in higher relative abundance in sequencing – while diatoms were generally not very abundant in winter in this study, as shown by the light microscopy counts. The fact that the dominance of this species was not previously recorded was partly attributed to the inconspicuousness of the small morphotype of *P. galaxiae*. It was shown that the average apical axes length in MA *P. galaxiae* was indeed the lowest in January (Arapov et al., 2023). The small morphotype can hardly be classified as a *Pseudo-nitzschia* species and was often ignored in LM monitoring until recently. On the other hand, the large morphotype of this species can also easily be confused with other very common species in the Adriatic, such as *Cylindrotheca closterium* and *Nitzschia gobbii* (Giulietti et al., 2021c).

Ecophysiological studies on *Pseudo-nitzschia*, which were so far rare in the Adriatic area, are also moving into the high-throughput era. Recently, a regional diatom transcriptome database for NA was published, which also contains transcriptomes of *P. mannii*. These transcriptomes will become invaluable resources as they are tailored to regional ecological conditions characterized by ongoing phosphorus limitation. This database will serve as a reference for future (meta) transcriptomic studies and can be extended to other species (Knjaz et al., 2024). Adriatic strains of *P. multistriata* were included in a population genomic study of the species, elucidating that functional genes for the domoic acid biosynthetic pathway are present in non-toxic strains (Mager et al., 2025). This is an important step forward in our understanding of the role and evolution of the DA biosynthetic cluster and demonstrates that even strains that are believed to be non-toxic have the toxigenous machinery. The same study also demonstrated that genomic distance correlates with geographic distance, suggesting that *P. multistriata* is a native species in the Mediterranean region, and that sex-related genes described in *P. multistriata* are likely to be subject to selection pressure (Mager et al., 2025).

Pathogens and symbionts such as fungi and bacteria are known to influence bloom dynamics and toxin production in this genus (Bates et al., 1995; Hanic et al., 2009), while the role of viruses has not yet been investigated as no viruses were known. The first virus infecting *Pseudo-nitzschia* was isolated in the Gulf of Trieste (Turk Dermastia et al., 2024). The ssRNA virus PnGalRNAV, which infects *P. galaxiae*, is similar to some other diatom-infecting viruses. In the same study, the authors reported another virus infecting *P. calliantha*, although the virus was not characterized. The isolated viruses will allow experiments in controlled and natural environments to better understand the role of virus infection in the ecology of *Pseudo-nitzschia* and possibly even toxin production. These findings have wider implications as viruses are now known to be intricately related to biogeochemical cycles as they influence the cycling of organic carbon (Zimmerman et al., 2020). Since *Pseudo-nitzschia* is a key phytoplankton genus not just in the AS, the discovery of its viruses is of wider scientific interest. Experiments with *Pseudo-nitzschia* and their viruses to study impacts on aggregation, carbon cycling and the microbial loop have been and will be conducted in the future.

5. Conclusions and future perspectives

The AS has emerged as a significant center for *Pseudo-nitzschia* research, with increasing efforts dedicated to elucidating the species diversity, distribution, and ecological dynamics of this key diatom genus. Despite the relatively low risk of Amnesic Shellfish Poisoning (ASP) in the region, the genus remains ecologically crucial, significantly contributing to phytoplankton community structure and primary productivity. However, gaps in our knowledge persist—particularly regarding the SA, which remains a largely unexplored frontier.

Remarkable progress in species identification has been made in the last 15 years, yet much of the research has been concentrated on the NA and certain bays and estuaries of the MA. This geographic bias highlights the urgent need for expanded monitoring programs, particularly in understudied regions. Future research should integrate novel omics-based methodologies to refine our understanding of species-specific physiological responses to environmental fluctuations. High-throughput sequencing, transcriptomics, and population genomics will be instrumental in uncovering adaptive strategies, niche differentiation, and potential evolutionary trajectories of *Pseudo-nitzschia* species under shifting oceanographic conditions.

A particularly promising avenue of research is the interplay between *Pseudo-nitzschia* and its associated microbiome, including bacteria, fungi, and recently discovered viruses. The first isolation of *Pseudo-nitzschia*-infecting viruses in the Gulf of Trieste opens a new chapter in the study of diatom-virus interactions. These findings provide a foundation for investigating how viral infections influence carbon cycling, bloom dynamics, competitive interactions, and possibly even toxin production. Given the broader implications of virus-mediated biogeochemical cycling, future studies should aim to integrate viral ecology into broader models of *Pseudo-nitzschia* population dynamics.

Beyond fundamental ecological research, applied studies will be crucial in refining monitoring and mitigation strategies. Climate change, eutrophication, and altered nutrient regimes are reshaping phytoplankton communities globally, and the AS is no exception. A proactive approach—incorporating molecular tools into routine monitoring programs—will be essential for early detection of harmful species and for predicting future shifts in bloom patterns. Additionally, fostering transnational collaborations and data-sharing initiatives across Adriatic and Mediterranean research institutions will be pivotal in addressing regional knowledge gaps and implementing standardized methodologies.

In conclusion, while significant strides have been made in understanding *Pseudo-nitzschia* ecology in the AS, much remains to be explored. The integration of classic microscopy method with more advanced molecular techniques, the expanded geographic monitoring, and interdisciplinary research frameworks will be key to unravelling the complex ecological roles of this genus. These efforts will not only advance our fundamental knowledge but also contribute to the sustainable management of marine ecosystems in the face of ongoing environmental change.

CRediT authorship contribution statement

Timotej Turk Dermastia: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition, Data curation, Conceptualization. **Janja Francé:** Writing – review & editing, Methodology, Funding acquisition. **Jasna Arapov:** Writing – review & editing, Methodology, Data curation. **Francesca Neri:** Writing – review & editing, Validation, Methodology. **Stefano Accoroni:** Writing – review & editing, Supervision, Data curation. **Cecilia Totti:** Writing – review & editing, Validation, Supervision, Data curation. **Federica Cerino:** Writing – review & editing, Validation, Methodology, Data curation. **Maria Immacolata Ferrante:** Writing – review & editing, Methodology, Data curation. **Fabrizio Bernardi Aubry:** Writing – review & editing, Methodology, Funding acquisition, Data curation. **Stefania Finotto:** Writing – review & editing, Methodology. **Jelena Godrijan:** Writing – review & editing, Data curation. **Dragana Drakulović:** Writing – review & editing, Data curation. **Patricija Mozetič:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Data curation.

Funding

Slovenian Research and Innovation Agency (research core funding No. P1-0237). National monitoring program financed by the Slovenian Environment Agency of the Ministry of Environment, Climate and Energy.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Part of the time series analysed in this paper was collected within the national (LTER-Italy and LTER-Slovenia) networks for Long-Term Ecosystem Research (LTER), which are grouped under the umbrella of the European (LTER-Europe) and international (ILTER) networks. The authors would like to thank Daniela Fornasaro for *Pseudo-nitzschia* count in LM at station C1-LTER. The text was edited with the help of InstaText writing assistant.

Data availability

Data will be made available on request.

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