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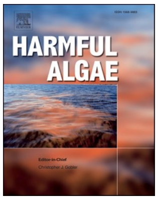

Review

The Adriatic Sea mucilage: The history of a hidden harmful dinoflagellate bloom

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ABSTRACT

Mucilage events, characterized by the accumulation of gelatinous, polysaccharide-rich organic aggregates in seawater, are irregularly occurring phenomena in the northern Adriatic Sea. While mucilage in other seas is typically linked to blooms of a single phytoplankton or phytobenthic species, Adriatic events have been mostly attributed to complex biogeochemical processes, rapidly leading to the formation of extensive gelatinous masses. Long-term studies on Northern Adriatic phytoplankton communities have revealed a consistent association, since the 1990s, between mucilage events and blooms of a non-toxic dinoflagellate. Originally identified as *Gonyaulax fragilis*, the ongoing debate regarding its definitive classification leads us to refer to the species as *Gonyaulax* cf. *hyalina*. Generally, this species acts as the primary biological trigger for these phenomena, which subsequently develop into a distinct, recurrent mucilage-associated microbial ecosystem. This review provides a comprehensive synthesis of the taxonomic debate, the main hypotheses proposed over the years, historical and recent evidence leading to *G.* cf. *hyalina* as the mucilage causative organism, and the ecological and economic impacts of these outbreaks. Regarding the interannual variability of the events, a link with specific environmental conditions could not be assessed; however, based on *G.* cf. *hyalina* growth and nutrient dynamics, we speculate about the importance of specific nutritional requirements (i.e., phosphate inputs or still unknown organic compounds) and of competitive interactions. This review would contribute to increasing knowledge on the most recurrent mucilage phenomenon in the Mediterranean Sea, opening the question on the inclusion of the investigated species in the list of harmful algal species.

1. Introduction

"The extraordinary phenomenon whereby the surface of the sea is covered for a few days with substances of a dark gray or yellowish color and of an uncertain nature…" are the words used by Castracane (1873) to describe a mucilage event occurred in the Adriatic Sea in 1872. The term mucilage is widely used to indicate a phenomenon irregularly recurring in several coastal and pelagic areas around the world, characterized by the presence of gelatinous foams of organic origin in seawater, thus drawing public attention and concern for its impact on the ecosystem and on human activities (e.g., fisheries, tourism). One of the most affected areas where the phenomenon has been reported since the 18th century is the Adriatic Sea (Fig. 1), mainly in its northern part. Here, these mucilage formations are rich in polysaccharides and appear particularly viscous and gelatinous, to such an extent that they were referred to with colorful names as "dirty sea", "sea snot", "sea slime", or even with local dialectal names as "onto del mar", "mare sporco", "bromo/brommo".

In most of the other seas, this production has been linked to a single phytoplankton or phytobenthic species proliferation, while the appearance of the mucilage in the Adriatic Sea has been mainly explained as the result of complex biogeochemical processes starting at the microbial level in the early stage, then resulting in the almost sudden formation of large masses. Briefly, most of the proposed hypotheses assumed that the

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carbohydrate pool, an important part of the organic matter in all the seas (Alldredge, 1999; Azam et al., 1999; Myklestad, 1999), accumulates during water column stratification, becoming the main precursor of mucilage masses, particularly because of the inter-bridging properties of these molecules (Ahel et al., 2005; Giani et al., 2005d). The north-western part of the Adriatic Sea is a thoroughly studied basin, having at least one or more fixed sampling stations in each of the Italian regions facing it; among these regions, Emilia-Romagna (Italy) has a network of 35 sampling stations for the regular coastal monitoring plus several dozens of sampling stations for sanitary control of the mussel farms, with sampling activities performed since 1976, well before the first mucilage event of the modern era in 1988. The authors of this review are affiliated with Institutions that have conducted long-term studies, spanning over 35 years, on the phytoplankton communities of the northern Adriatic Sea (ARPAE, 2025; Pistocchi et al., 2005a; Zoffoli et al., 2025), a region of significant economic and touristic relevance. Within this framework, research has extensively addressed mucilage events during peak occurrences, demonstrating a consistent association between these phenomena and the proliferation of a dinoflagellate that, in previous studies was named *Gonyaulax fragilis* (Schütt) Kofoid (Honsell et al., 1992; Pistocchi et al., 2005a; Pompei et al., 2003); however, the ongoing debate on the taxonomy of this species regarding its similarity to *G. hyalina* (see further for details), has ascertained that *G. fragilis* is not the species associated with mucilage in the Adriatic Sea (Gómez et al., 2025). According to some authors (Carbonell-Moore and Mertens, 2019; Chirdon et al., 2025), the mucilage producer should be identified with *G. hyalina;* nevertheless, as the debate doesn't appear to be completely resolved, we will refer to the organism as *G.* cf. *hyalina*. Our hypothesis on the primary role of this dinoflagellate in mucilage production in the Adriatic Sea has been increasingly supported by other researchers working on the western Adriatic phytoplankton, especially in light of the extensive mucilage event recorded in several coastal regions in summer 2024 (Totti and Ubaldi, 2024; Ubaldi et al., 2026). Nonetheless, it has to be noticed that, in the recent past, other authors have assigned a predominant role to various diatoms in mucilage formation (see, for example, Demir-Yilmaz et al., 2023; Kraus and Ivošević DeNardis, 2023), and also recently Vlašiček et al. (2025) have suggested the role of *Cerataulina pelagica* in the event that occurred in 2024. This

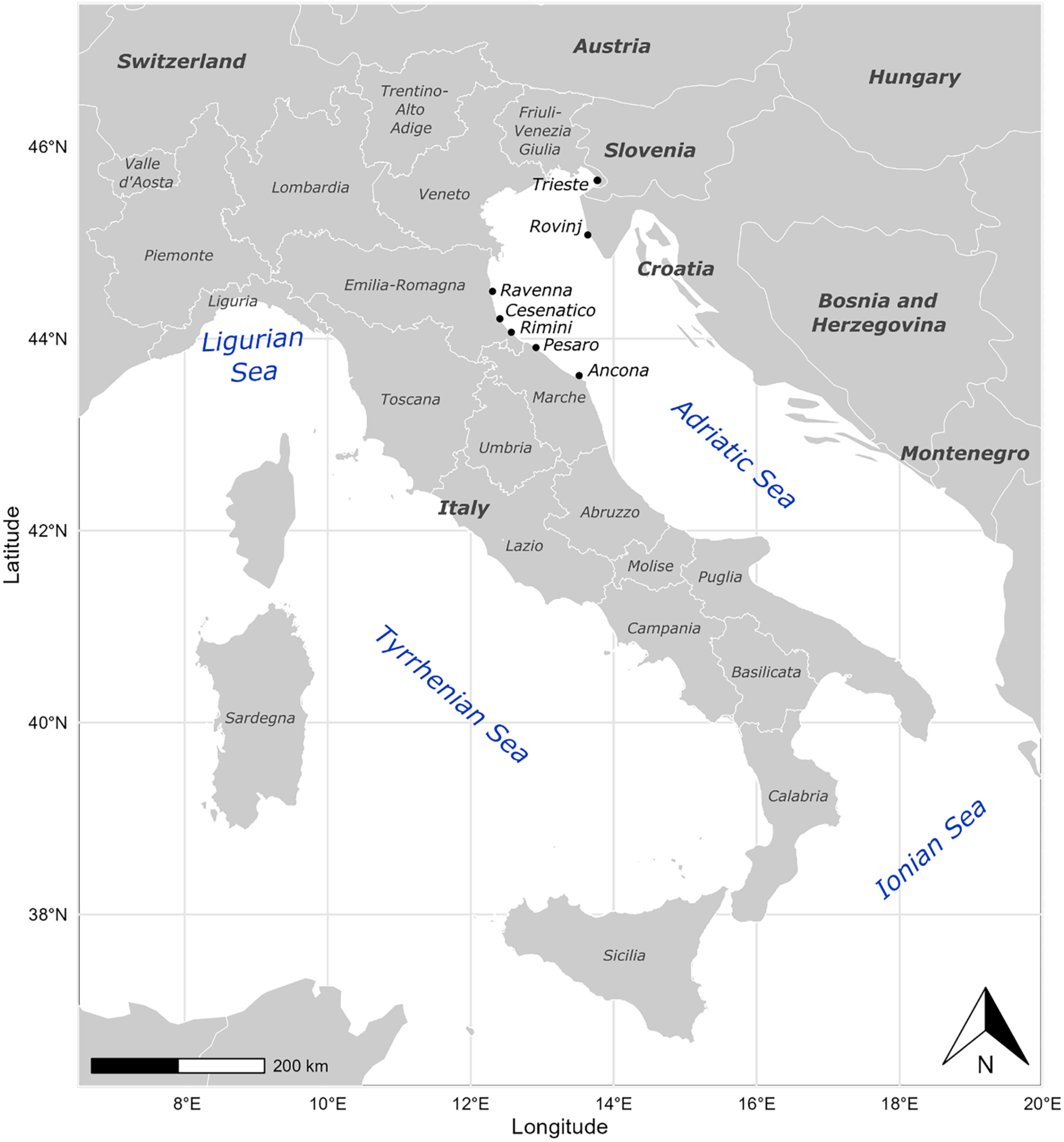

Fig. 1. Map of the study area highlighting the Italian regions and locations referenced in the text.

review summarizes key findings, spanning from early historical records to the most recent investigations, highlighting the remarkable seasonal timing and chemical consistency of the mucilage phenomenon in the Adriatic Sea. Such repeatability strongly supports the role of a single-species bloom as the initial trigger, which in turn drives a cascade of ecological and chemical processes culminating in the formation of a distinct and recurrent mucilage-associated microbial ecosystem.

2. The 2024 mucilage event

The mucilage event that occurred in the Adriatic Sea in the summer of 2024 was arguably the most extensive and prolonged one since the first scientific description nearly 150 years ago. It covered approximately 20,000 km^2, lasting over three months from June to September in the northern part, with a southward extension. This event has been extensively characterized through satellite observations and oceanographic data acquisition (Hadjal et al., 2025; Vilibić et al., 2025; Vlašiček et al., 2025) (Fig. 2). For the first time, the 2024 mucilage phenomenon was described by Croatian scientists as unfolding in three distinct stages: the most pronounced phase occurred between 31st May and 9th June, followed by subsequent episodes around 12-14th July and 28th July-8th August (Paliaga et al., 2024; Vilibić et al., 2025). All three phases were closely connected with intense phytoplankton blooms triggered by successive outbursts of the Po River (i.e., the longest river in Italy), with the riverine outflow advected across the northern Adriatic towards the Istrian coast. Interestingly, each event followed the typical progression of mucilage development: initial formation of gelatinous aggregates, subsequent accumulation at the pycnocline, and sedimentation on the seabed as the biomass aged, attesting that the event sequence does not require a long time (e.g., months) to occur.

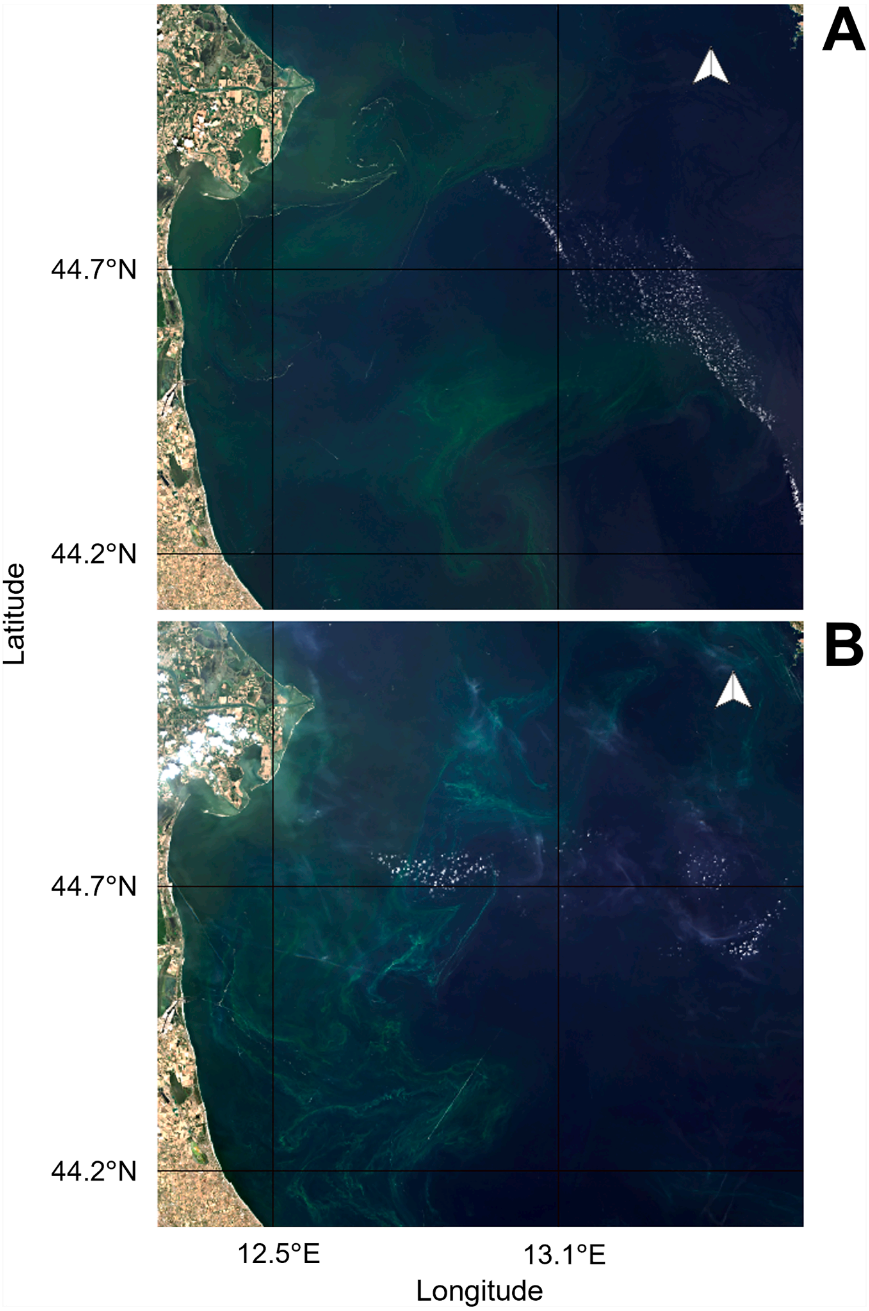

Fig. 2. Sentinel 2 L2A satellite images of the 2024 mucilage event in the north-western Adriatic Sea, near the coast of the Emilia-Romagna region (Italy) in two selected dates: (A) 28th July and (B) 7th August (provided by Riccardo Bentivogli).

Accordingly, each time the Po River plume arrived close to the Istrian coast, the event coincided with elevated chlorophyll concentrations and a rapid increase in primary production, clearly evidencing the activity of mucilage-producing organisms (Vilibić et al., 2025). The first and most intense mucilage event on the Istrian coast was observed near Rovinj on 6th June; the phenomenon then extended towards the northwestern Adriatic Sea, reaching the Italian coasts of the regions Friuli-Venezia Giulia and Veneto by 19th June. By the end of June, it reached the Emilia-Romagna coastline (Fig. 3), followed by further southward expansion reaching as far south as Puglia in August (ARPAE, 2024). Since the 19th century, several observations have indicated that mucilage formation typically begins in the northeastern Adriatic Sea, particularly along the coasts of the Istrian Peninsula and the Gulf of Trieste. The phenomenon then spreads westward, following the well-known anticlockwise surface current circulation of the basin (Giani et al., 2012; Molin et al., 1992; Stachowitsch et al., 1990). Nevertheless, this pattern is not always consistent, as previously testified during an event occurred in 1989, for which satellite observations revealed that the mucilage first appeared along the Emilia-Romagna coast and then expanded to the northern Adriatic; on that occasion, it was also observed to predominantly occur along density gradients and frontal structures generated by riverine outflow (Zambianchi et al., 1992). In fact, large-scale mucilage accumulations are recorded more frequently near the Po River delta, as evidenced by a comprehensive study by Hadjal et al. (2025). This research provides maps based on the integration of four months (June to September) of remote sensing data, covering all affected years from 1988 to 2024.

Regarding the phytoplankton composition of the 2024 mucilage event, two detailed studies were recently published (Ubaldi et al., 2026; Vlašiček et al., 2025). The first one is related to the Istrian coast with observation starting after the first mucilage appearance: *G. fragilis* (= *G.* cf. *hyalina*) was observed only before the second and third mucilage phase, while high diatom numbers, i.e., *Cerataulina pelagica, Cylindrotheca closterium* and *Thalassionema* sp., were observed in concomitance with the first, second and third phase, respectively; however, the sampling period may not have allowed to detect the dinoflagellate initial growth. The study by Ubaldi et al. (2026) is related to two sites, one in the north (Gulf of Trieste) and one in the central Adriatic coast (Ancona); *G. fragilis* (or *G.* cf. *hyalina*) was observed since the beginning of the mucilage event (June 6th) and resulted abundant at the onset and during the phenomenon (peak numbers in the order of 10^6 cells L^{-1} were counted in the second week of July), then decreasing. Diatoms were also abundant in mucilage samples (4.4 to 6.6 × 10^7 cells L^{-1}), and the most present species were *Thalassionema nitzschoides, Nitzschia gobbii,* and *Cylindrotheca closterium,* while *Cerataulina pelagica* presence was scarce. The phytoplankton monitoring activities performed in Italy by various Regional Environment Protection Agencies (ARPA), confirmed the presence of *Gonyaulax* cf. *hyalina* all along the Italian Adriatic coast where mucilaginous masses were observed; in Puglia, the southernmost region, only occasionally affected by mucilage events, a peak of 1.8 × 10^5 cells L^{-1} was observed in July during a coastal monitoring (Ciciriello P., ARPA Puglia, Centro Regionale Mare, personal communication).

In Emilia-Romagna *G.* cf. *hyalina* was detected during the regular water monitoring in mussel farming areas (Fig. 4), where the water is collected through hose samplers designed for integrated water column samplings (Zoffoli et al., 2025), although the sampling sites do not necessarily coincide with those affected by mucilage events. Nonetheless, as shown in Fig. 4, a clear spatial and temporal pattern of *G.* cf. *hyalina* abundance in Emilia-Romagna was observed across 3 different zones arranged along a north-south gradient (Ravenna, Cesenatico, and Rimini). Cell densities rose simultaneously, but patterns diverged among zones: the northern (Ravenna) and central (Cesenatico) zones showed two peaks (late June and early August), matching the Istrian trend, while the southern coastal zone (Rimini) recorded only a single, delayed peak. The aforementioned Po River water outburst was a consequence of a major flooding event, characterized by extensive overbank flows from numerous tributary rivers, which occurred in May. This event resulted in markedly elevated freshwater outflows that persisted until June, reaching a peak flow of 5,151 $m^3 s^{-1}$ in May, compared with an average discharge of 1,473 $m^3 s^{-1}$ calculated from 2017 to 2023 (ARPAE, 2024). The delayed growth observed in Emilia-Romagna could potentially be ascribed to the great strength of the water outflow from the Po River. This higher discharge, compared to more distant zones, likely created instability that inhibited *G.* cf. *hyalina* growth during June.

Another relevant aspect observed during the summer of 2024 was the persistence of elevated coastal water temperatures, with sea surface values ranging between 28.5 and 30.1°C, recorded from July to August within a 10 km range offshore. On multiple occasions, the thermocline was absent. A notable instance was recorded on 5th August 3 km off the coast of Cesenatico, where surface and bottom temperatures measured

Fig. 3. Mucilage event affecting the north-western Adriatic Sea in July 2024. Aggregates observed along the Emilia Romagna coast: (A) offshore (by Daphne II oceanographic vessel); (B) along the pier of Cesenatico (by Rossella Pistocchi).

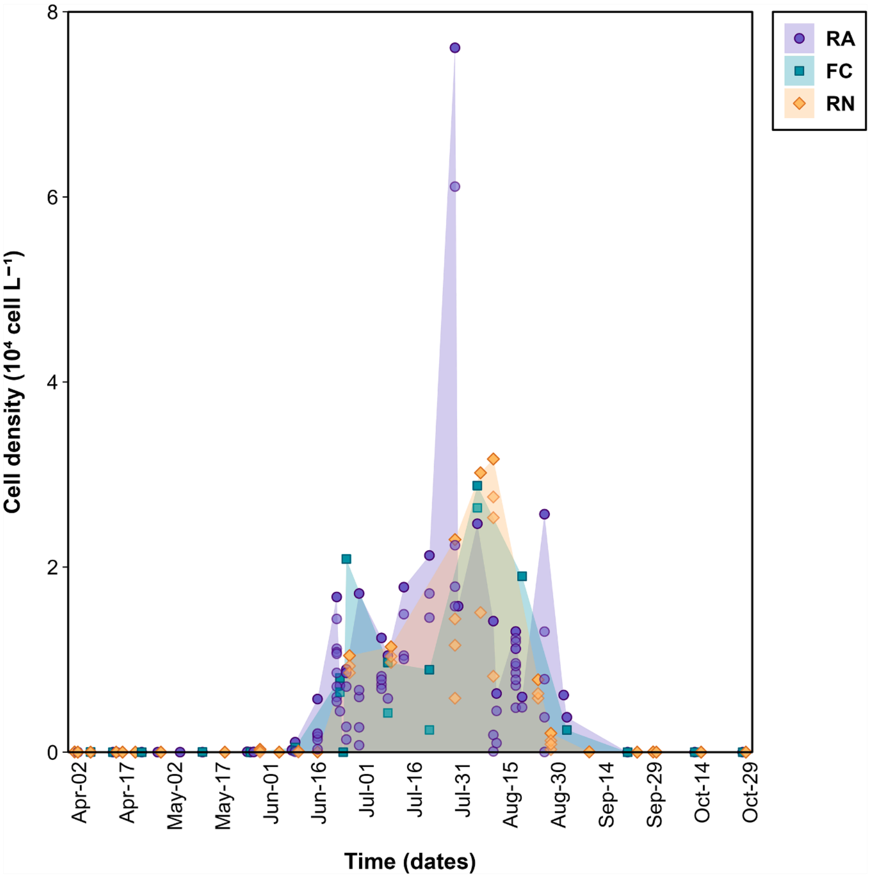

Fig. 4. *G.* cf. *hyalina* cell densities in surface water sampled in 42 mussels' farms along the Ravenna (RA), Cesenatico (FC) and Rimini (RN) coastal area (Italy) in 2024.

28.7 and 28.3°C, respectively, indicating significant vertical homogeneity of the water column. This condition may have facilitated extensive algal proliferations even in nearshore areas, as suggested by bioluminescence events reported by local bathers and media sources. Typically, *G.* cf. *hyalina* blooms develop in the water column and only superficial creamy or gelatinous layers, composed predominantly of senescent or dead cells, are subsequently transported to the shore via winds or currents.

3. *Gonyaulax fragilis* and *G. hyalina* taxonomy debate: morphological and molecular insights

Since its first detection in the Adriatic Sea, the species observed in high abundance within the mucilage aggregates was identified as *Gonyaulax* cf. *hyalina* (Cabrini et al., 1992) and then as *G. fragilis* (Honsell et al., 1992). However, the latter authors reported a certain difficulty in the two species classification due to contradictions among the descriptions reported in the available literature (as detailed in Honsell et al., 1992), highlighting the need for a taxonomic reassessment, as also previously noted (Balech et al., 1984). In the following years, most authors referred to the species detected in the Adriatic Sea as *G. fragilis* or *G.* cf. *fragilis* while similar organisms associated with mucilage formation in other geographical areas were more often identified as *G. hyalina* (MacKenzie et al., 2002; Nikolaidis et al., 2008). When cultures of strains from the Adriatic, Tyrrhenian, and New Zealand seas were established, a comparative study among these strains was performed (Escalera et al., 2018). Morphological and molecular analyses confirmed shared features across all the strains, and the authors therefore proposed, based on these results and on a revision of the taxonomic history of the two taxa, that *G. fragilis* and *G. hyalina* are the same species and gave priority to the name *Gonyaulax fragilis* (Escalera et al., 2018). The classification of both species was then studied by Carbonell-Moore and Mertens (2019): through examination of field samples from different parts of the World Ocean, they demonstrated that the external morphology of *G. fragilis* and *G. hyalina* is different enough to keep them as separate taxa and stated that the three strains (i.e., the isolates from Adriatic, Tyrrhenian and New Zealand seas) belonged to the same species that was instead identified as *G. hyalina.* Notable differences between the two species included cell size, with *G. hyalina* being generally smaller (24–53 µm long, n = 14) compared to *G. fragilis* (41–83 µm long, n = 7), although these dimensions did not align with the original holotype description (92 µm) (Ostenfeld and Schmidt, 1902). Additional morphology-based distinctions among the two species were observed in the thecal plate ornamentation and arrangement. They therefore concluded that the SEM images and/or the plate ornamentation reported in Escalera et al. (2018) and in Honsell et al. (1992) agree with the description of *G. hyalina*; however, according to Carbonell-Moore and Mertens (2019), a light microscope image of a typical *G. fragilis* cell is reported in the work of Honsell et al. (1992); this evidence may suggest the potential coexistence of both species in the Adriatic Sea.

A further contribution to this ongoing taxonomic debate was provided by Gómez et al. (2025), who focused their studies on live cells of *G. fragilis* from the Mediterranean Sea and from the southwestern Indian Ocean, along with preserved material from the open North Atlantic Ocean. They conducted both morphological observations and molecular phylogenetic analyses attesting that the plate formula of *G. fragilis* aligns more closely with most members of the family Protoceratiaceae, rather than *Gonyaulax* species. Phylogenetic analyses of rDNA/ITS sequences further supported this view, showing that *G. fragilis* clustered with full support within the Protoceratiaceae, while the sequences from Italy and New Zealand grouped within the Gonyaulacaceae. Consequently, Gómez et al. (2025) suggested reinstating the genus *Steiniella,* which had been dismantled by Kofoid (1911), when *S. fragilis* and *S. mitra* were transferred to the genus *Gonyaulax*. They proposed renaming *G. fragilis* as *Steiniella fragilis,* reflecting its greater phylogenetic distance from *G. hyalina.* The authors (Gómez et al., 2025) concluded that the species proliferating in the Adriatic Sea is neither *G. fragilis,* nor is the one originally described by Ostenfeld and Schmidt (1902), but instead a new species; this observation is supported by the relevant differences in their habitat (eutrophic coastal waters versus open ocean) and in size, being the original description of *G. hyalina* related to a larger-sized cell with respect to those reported in literature (Carbonell-Moore and Mertens, 2019; Escalera et al., 2018).

Another contribution was provided by Chirdon et al. (2025), who focused their studies on strains of *G. hyalina* newly isolated from the Gulf of Aden (Western Indian Ocean), Korea, and Viet Nam. Morphological results confirmed that all shared the same characteristics, i.e., the same plate pattern reported by Escalera et al. (2018) and Carbonell-Moore and Mertens (2019) for *G. hyalina*, thus confirming the distinction from *G. fragilis* (or *S. fragilis* according to Gómez et al. 2025). Interestingly, the molecular analysis revealed the existence of two ribotypes among the different *G. hyalina* strains sharing the same morphological characteristics, with ribotype A including the newly isolated strains from Indian and Pacific Ocean (Chirdon et al., 2025) and ribotype B including the studied strains of the Adriatic Sea, Tyrrhenian Sea and New Zealand (Escalera et al., 2018; Riccardi et al., 2010). This aspect, evidencing the existence of cryptic species, raises several open questions to the point of reinforcing the hypothesis of a new species, an aspect that we support on the basis of our observations that cells found over the years in field samples, although smaller in size, often exhibit a morphology resembling *G. fragilis*, but have the distinct plate striae typical of *G. hyalina* (Cangini M., personal communication). In conclusion, in the following paragraphs, we will refer to the mucilage producer found in the Mediterranean areas and to the clones used in our studies as *G.* cf. *hyalina.*

4. History of mucilage occurrences in the Adriatic Sea and main proposed theories

The first ever report concerning the presence of gelatinous masses on the Adriatic Sea surface dates back to 1729, and at that time, it was explained with theories such as earthquake shocks (Forti, 1906). Historical reviews on all the events occurring since then are reported by several authors (Fonda-Umani et al., 1989; Giani et al., 2005a; Molin et al., 1992); briefly, the past events described in scientific literature occurred in 1873, 1880, 1881, 1892, 1893, 1903, 1905, 1906, 1920, 1928, 1930 and 1931, while those of the modern era which have been the most deeply studied occurred from 1988, after an interval of nearly 60 years, to date. The events' chronology reported in Table 1 refers to observations made along the Emilia-Romagna coast (the timing and length of the phenomenon could have been slightly different in other Adriatic areas), and what stands out is the marked year-to-year variability of the phenomenon.

Since the 19th century, all the hypotheses proposed on mucilage formation have been focused on the involvement of microalgae as causative organisms and were mainly characterized by a dispute on the major contribution of diatoms (either benthic or planktonic) or of dinoflagellates. Table 2 summarizes the main steps of the dispute with the corresponding hypothesis.

Table 1
Day and maximum *G.* cf. *hyalina* cell density recorded during the coastal monitoring program of the Emilia-Romagna region performed by ARPAE (1998-2024), and in discrete sampling of mucilage (in selected dates) during a specific study or project campaign. In bold are indicated the years and the months affected by mucilage.

Year	Mucilage	Regular monitoring of water column		Mucilage sampling	
		Max cell density (cell L^{-1})	Observed peak (date)	Max cell density (x 10^6 cell L^{-1})	
1988	**Aug-Sept**	**-**		**6.1**	Honsell et al. (1992)
1989	**Jul**	**-**			
1990	Absence	-			
1991	**Jul-Aug**	**-**			
1992-96	Absence	-			
1997	**Aug-Sept**	**-**		**1.3**	Boni et al. (2000)
1998	**Jun**	**3,861**	**30-Jul**		
1999	Absence	0	-		
2000	**Jun-Jul**	**112,115**	**03-Jul**	**6.6**	Pompei et al. (2003)
2001	**Jul**	**2,908**	**03-Jul**		
2002	**Jul-Aug**	**54,510**	**19-Aug**	**5.2**	Mazziotti et al. (2004)
2003	**Jun**	**1,480**	**23-Jun**		
2004	**Jun-Jul**	**136,675**	**05-Jul**	**1.5**	Riccardi et al. (2010)
2005	Absence	40	04-Jul		
2006	**Nov-Dec**	**4,640**	**28-Nov**		
2007	Absence	1,200	21-Aug		
2008	Absence	240	14-Jul		
2009	Absence	1,840	03-Aug		
2010	Absence	2,080	02-Aug		
2011	Absence	400	01-Aug		
2012	Absence	400	02-Jul		
2013	Absence	5,040	03-Sep		
2014	**Aug**	**13,200**	**05-Aug**		
2015	Absence	1,600	17-Aug		
2016	Absence	1,920	03-Aug		
2017	Absence	240	01-Aug		
2018	**Jul-Aug**	**29,949**	**06-Aug**		
2019	Absence	3,480	03-Jul		
2020	Absence	600	10-Aug		
2021	Absence	900	07-Jul		
2022	Absence	0	-		
2023	Absence	800	01-Aug		
2024	**Jun-Jul-Aug-Sept**	**67,820**	**05-Aug**	**2.2**	Ubaldi et al. (2026)
2025	Absence	80	01-Jul		

The theories of the 80s-90s on the importance of diatoms as causative agents of mucilage were fostered by several studies that emerged at the end of the 1970s, showing that in diatom cells a fraction of organic carbon exceeding cell storage capacity would be excreted as a normal process by healthy cells (Fogg, 1977; Sharp, 1977). A large amount of polysaccharides was observed to be excreted by living and healthy diatom species (Haug and Myklestad, 1976; Myklestad, 1995, 1974; Myklestad et al., 1989, 1972), including species from the Adriatic Sea (Guerrini et al., 2000, 1998; Pistocchi et al., 2005c, 1997; Urbani et al., 2005), especially under phosphorus deficiency (Myklestad, 1977; Myklestad and Haug, 1972; Obernosterer and Herndl, 1995). Benthic species, e.g., *Achnanthes* (Pistocchi et al., 2005c) and *Licmophora* sp. (Stachowitsch et al., 1990), were identified as the most prolific producers, and some of them were predominant in mucilage phenomena occurring in the eastern part of the Adriatic Sea from 1983 to 1989, such as the Gulf of Trieste, Gulf of Kvarner (Rab Island), and near the island of Vis (Dalmatia) (Pucher-Petkovic and Marasovic, 1987; Stachowitsch et al., 1990). These species, however, were not considered able to produce huge masses which displayed a quite clear pelagic origin (Stachowitsch et al., 1990).

Regarding planktonic diatoms, a single causative organism was never clearly identified, although *Cylindrotheca closterium* (= *Nitzschia closterium*) was often addressed as an important contributor due to its constant presence and high abundances in mucilage, being, therefore, the subject of several studies (Alcoverro et al., 2000; Degobbis et al., 1999; Kovač et al., 2005; Monti et al., 1995; Najdek et al., 2005;

Table 2
A summary of the major postulated hypotheses on mucilage formation in the Adriatic Sea.

Mucilage event	Hypotheses issued	References
1872	**benthic diatoms** are involved and then transported to the surface by entrapped gas bubbles	Castracane (1873)
1872	**dinoflagellates** are the producers of mucilage that is then colonized by diatoms	Cori (1906)
1905	**dinoflagellates** should be involved due to the observed bioluminescence, a bentho-neritic origin is excluded, and **planktonic species** (maybe of different genera) should grow inside the mucilage	Forti (1906)
1929	**benthic diatoms** are involved, and dinoflagellates are entrapped later	Zanon (1931)
1988-89	organic matter from **decaying diatom blooms** aggregates above the pycnocline with the increase of time and random collisions	Herndl et al. (1992)
1988-89	**diatom growth** (e.g. *Cylindrotheca closterium*) produces mucilage with the concurrence of cyanobacteria, virus, and heterotrophic bacteria	Degobbis et al. (1999)
1988-89	involvement of the **dinoflagellate** *G. fragilis* is supposed as high abundances were found in different samples collected in Italian regions	Honsell et al. (1992)
2000-01-02	**different phytoplankton species** are the cause, with a prevalent role of diatoms and an important contribution of bacteria and meteoclimatic conditions, so that: i) polysaccharides are copiously exuded or released by the lysis of diatoms (Myklestad, 1995) during scarce riverine inputs (Degobbis et al., 1995) and in the presence of unbalanced nutrient availability (Kaltenböck and Herndl, 1992; Obernostererr and Herndl, 1995), low grazing pressure (Bochdansky and Herndl, 1992; Najdek, 1997), and ii) with bacteria playing multifaced and dominant roles in the production of long-lived dissolved and colloidal polysaccharides (Azam et al., 1999)	as described e.g. in Del Negro et al. (2005); Giani et al. (2005a)
2000-01-02-04	A bloom of the **dinoflagellate** *G. fragilis* (now *G.* cf. *hyalina*) is the triggering event	Pistocchi et al. (2005a); Pompei et al. (2003)

Pletikapić et al., 2011; Radić et al., 2011; Svetličić et al., 2011). Recently, the role of diatoms (i.e., *Cerataulina pelagica*) has also been proposed by Vlašiček et al. (2025). Overall, different diatoms were present in conjunction with different mucilage episodes (Degobbis et al., 1995; Forti, 1906; Honsell et al., 1992; Totti et al., 2005), including the 2024 event (Ubaldi et al., 2026; Vlašiček et al., 2025); noteworthy, the species composition was reported to be similar both inside the mucilage and in the water column, and also did not differ in periods with and without mucilage events (Del Negro et al., 2005; Revelante and Gilmartin, 1991; Totti et al., 2005). Therefore, according to some authors' opinion, the mucilage was of phytoplankton polysaccharide origin with no species-specific attribution and with the support of a highly active microbial community (Fogg, 1995).

In the 1990s, in light of this perspective and corroborated by the cited studies, research focused primarily on the potential key role of meteo-climatic and environmental and trophic conditions favoring phytoplankton growth. During the late 80s outbreaks (Molin et al., 1992; Rinaldi et al., 1995) and especially from 1999 to 2002, when monthly meteorological observations were performed in the course of the "Mucilage of the Adriatic and Tyrrhenian Seas" (MAT) project (https://www.sciencedirect.com/journal/science-of-the-total-environment/vol/353/issue/1), many studies were performed on the environmental conditions favoring diatoms growth, polysaccharide excretion and aggregates formation. Results suggested that anomalies in temperature, total rainfall, and rainy-day frequency were not directly correlated with the mucilage outbreaks; however, in mucilage years, both vertical and horizontal thermohaline gradients were more pronounced, and stratification was increased by the intrusion of dense and cold water (Russo et al., 2005). With regard to the nutrient status, it was observed that dense algal blooms, as those occurring in the 70s (Pompei et al., 2018), and mucilage accumulations were mutually exclusive, suggesting that mucilage formation was not directly linked to eutrophication. Nevertheless, in that period, an important role was attributed to the increase in N/P ratio (mean spring values >100, with values also >1,000) which occurred after the Emilia-Romagna region introduced legislation to reduce polyphosphate content in detergents in 1985. Also for this ratio, a direct correlation with mucilage events was not stated, as occurred in 1989 when the ratio measured in offshore stations was <5, indicating that phosphorus was not used up and available (Rinaldi et al., 1995).

Later on, approximately at the beginning of this century, it became evident that polysaccharide production was not a diatom prerogative. Several dinoflagellate species are likewise capable of releasing large quantities of polysaccharides, generating networks that entrap their own cells along with other microorganisms. Besides *G.* cf. *hyalina,* frequently implicated in the pelagic mucilage formations, notable examples include the benthic species *Ostreopsis* cf. *ovata*, which proliferates along numerous Mediterranean coasts and, to a lesser extent, in other regions, forming dense brown mucilaginous mats that cover and compromise the health of many benthic plant and animal organisms (Barone, 2007; Honsell et al., 2013; Pezzolesi et al., 2014). Additional dinoflagellates, *Gymnodinium* (former *Gyrodinium*) *impudicum* and *Margalefidinium* (former *Cochlodinium*) *polykrikoides*, are recognized for producing high amounts of sulphated exopolysaccharides, compounds of interest for their antiviral properties (Hasui et al., 1995; Yim et al., 2004). Historical accounts also document the occurrence of foamy and mucilaginous formations in the Adriatic Sea, in particular those following an intense bloom of the dinoflagellate *Lepidodinium* (former *Gymnodinium*) *chlorophorum* in 1984; floating yellowish agglomerates were also observed in August 1990 when two athecate species, *Margalefidinium* (former *Cochlodinium)* and *Nematodinium,* were present (Rinaldi et al., 1995). Another example is *Noctiluca scintillans,* a dinoflagellate frequently causing high biomass accumulation in the Adriatic Sea, which undergoes a color shift from reddish to yellowish during senescence and decay, acquiring an appearance reminiscent of mucilage (Hadjal et al., 2025; Rinaldi et al., 1995).

5. Mucilage phenomena linked to *Gonyaulax* spp. detection occurring in the Tyrrhenian and other Seas

The recurrent mucilage events affecting the Tyrrhenian Sea have provided valuable insight into the existence of two distinct phenomena within the Mediterranean Sea, thereby helping to outline some fundamental underlying mechanisms; in fact, in the summer 1991 two distinct mucilage forms (i.e., pelagic and benthic) were reported, each exhibiting different characteristics (Innamorati, 1995; Rinaldi et al., 1995).

The benthic mucilage formations resembled those observed in the Adriatic Sea but were generally less extended and, unlike the pelagic forms, were characterized by the complete absence of suspended mucus in the overlying water. Various studies have attributed such events to five filamentous macroalgal species: the free-living forms of two brown algae, *Tribonema marinum* J. Feldmann and *Acinetospora crinita* (Carmichael ex Harvey) Kornmann (Giani et al., 2016; Sartoni et al., 1993; Sartoni and Sonni, 1991), along with three fast-growing benthic chrysophytes, *Nematochrysopsis marina* (J. Feldmann) Billard, *Chrysonephos lewisii* (Taylor), and *Chrysophaeum taylorii* Lewis & Bryan (Caronni et al., 2017, 2016; Sartoni et al., 2008, 1995). More recently, mucilage formations associated with *A. crinita* have also been observed in the Adriatic Sea, along the Istrian coast (northwestern basin) and near the Tremiti Islands (southeastern basin) (Giani et al., 2016; Ivеša et al., 2021), both characterized by rocky bottoms, differently from the northwestern part.

Pelagic mucilage events in the Tyrrhenian Sea were not known until 1991, when the entire basin, from the Toscana Archipelago to Sicilia, was affected by a major event that coincided with the outbreak in the Adriatic Sea (Innamorati, 1995; Rinaldi et al., 1995). Interestingly, although no previous published reports of pelagic mucilage events were available, a survey conducted among fishermen and scuba divers revealed that the phenomenon was widely recognized locally. The pelagic mucilage occurred as sporadic banks and contained only phytoplankton, some zooplankton, and bacteria; the microalgal community was more typical of a spring period, dominated by diatoms, mainly of the genus *Nitzschia* (Innamorati, 1995), along with *Chaetoceros* and dinoflagellates of the genera *Gymnodinium* and *Gonyaulax* (Rinaldi et al., 1995). The surrounding water column hosted a typical summer planktonic assemblage, characterized by a heterogeneous composition of phytoplankton classes and high species diversity. Pelagic mucilage events in the Tyrrhenian Sea were also reported in 2000 (Giani et al., 2005a) and 2012 (Escalera et al., 2018). In the latter event, the mucus aggregations present in the Gulf of Naples were observed to contain dense populations of *G. hyalina* (Escalera et al., 2018).

Beyond the Adriatic and Tyrrhenian Seas, mucilage outbreaks have been described in other parts of the Mediterranean Sea, particularly in the coastal regions of Spain, Greece, and Turkey, experiencing recurrent episodes (see Table 3). In all these events, *Gonyaulax fragilis/hyalina* was among the major components of microalgal assemblages; in a few cases, it was reported as the dominant species, although without being acknowledged as the causative organism of the mucilaginous event.

Outside the Mediterranean Sea, mucilage phenomena have also been documented as recurrent pelagic formations along the North Sea coast (Lancelot, 1995), the English Channel (Boalch, 1984; Boalch and Harbour, 1977), and the New Zealand coast (MacKenzie et al., 2002). These events share a common feature: each has been attributed to the proliferation of a single phytoplankton species, although of different taxonomic groups. Among them, only the mucilage occurring in New Zealand has been linked to *G.* cf. *hyalina* proliferation, also sharing many similarities with events of the Adriatic Sea (MacKenzie et al., 2002). One common aspect is the interannual variability. New Zealand mucilage events have in fact been documented at 20-year intervals since 1860, and the outbreaks were described as vast, buoyant slime masses, sustained at the surface by abundant gas bubbles, extending down to 30 m depth above the thermocline and emitting nocturnal bioluminescence, as well as causing fish mortality and disruptions of local fisheries. While no causative species was identified during the 1981 outbreak, subsequent field and laboratory investigations performed during the 2000 event demonstrated that the mucus formation was driven by proliferations of the dinoflagellate *G.* cf. *hyalina* (MacKenzie et al., 2002).

Table 3
Coastal areas around the world (excluding the Adriatic Sea) where mucilage events associated with *Gonyaulax* spp. were observed.

Coastal area	Occurrence	References
Catalan coast, Spain, NW Mediterranean Sea	2006	(Sampedro et al., 2007)
	2013	(Carnicer et al., 2015)
Thessaloniki Bay, Greece, NW Aegean Sea	1982-1993	(Gotsis-Skretas, 1995)
	2004	(Nikolaidis et al., 2008)
	2017	(Genitsaris et al., 2019)
Sea of Marmara, Turkey	2007	(Aktan et al., 2008; Tüfekçi et al., 2010)
	2020-21	(Akcaalan et al., 2023; Yurga, 2022)
Tasman Bay, New Zealand	Since 1860, at intervals 1981, 2000	(MacKenzie et al., 2002)
Gulf of Aden, W Indian Ocean	2023	(Chirdon et al., 2025)

It is worth mentioning that in the Gulf of Aden (Western Indian Ocean), where recent studies on *G. hyalina* have been performed, aggregates of mucilaginous material were observed during a bloom occurring in June 2023. Previous observations are not available as specific monitoring activities are not performed in that area (Chirdon et al., 2025).

6. *G.* cf. *hyalina* as the causative agent of mucilage and as a blooming and harmful organism

6.1. *Constant association and timing of G. cf. hyalina with mucilage occurrence*

G. cf. *hyalina* (formerly *G. fragilis*) presence during mucilage outbreaks in the Adriatic Sea was first documented during the late 1980s (Cabrini et al., 1992; Honsell et al., 1992; Totti et al., 1993); however, there are historical reports indicating the bioluminescence within the mucilage (Forti, 1906; Giani et al., 1992), pointing to an important presence of dinoflagellates. Interestingly, before 1988, the species was rarely detected (Honsell et al., 1992; Pompei et al., 2003). In previous studies, a consistent temporal pattern linking *G.* cf. *hyalina* proliferation with mucilage formation had already been reported. Specifically, the species was observed among the phytoplankton population only during years characterized by mucilage formation, and, in addition, its cell densities in seawater increased 20–30 days prior to the first appearance of mucilaginous strings and cobweb-like structures (Mazziotti et al., 2004; Pompei et al., 2003). Our results have been refined using data from long-term, high-frequency monitoring of the Emilia-Romagna coastal waters, conducted weekly or fortnightly (Table 1). We have observed that, regardless of the presence or absence of mucilage events, *G.* cf. *hyalina* is relatively always present in summer with maximum cell densities roughly spacing between 100-1,000 cell L^{-1}; however, it is worth mentioning that high cell densities (10^3-10^5 cell L^{-1}) were only counted during years when the mucilage events were recorded. In addition, although in Table 1 only the highest peak numbers are shown, we have observed that only in the years of mucilage outbreaks, cell numbers started to increase, exceeding 1,000 cells L^{-1} already in June (data not shown).

Other authors have observed that only a limited number of taxa exhibited significantly higher abundances during mucilage events; among these, *G.* cf. *hyalina* alongside a few but varying diatom species, was consistently enriched within mucilaginous aggregates relative to the surrounding water column (Totti et al., 2005); it was found in higher abundances in fresh mucilage samples (Del Negro et al., 2005) and recorded at several stations along three transects from the western to the eastern Adriatic coast during the outbreak of the year 2000 (Pistocchi et al., 2005a; Totti et al., 2005). Despite this, *G.* cf. *hyalina* presence was often overlooked in many investigations over recent decades (e.g., Flander-Putrle and Malej, 2008; Najdek et al., 2002; Revelante and Gilmartin, 1991) or was not considered a dominant component (Cabrini et al., 1992). This underrepresentation is likely attributable to two factors. First, proliferating cells tend to aggregate, resulting in relatively low concentrations in the surrounding water column, outside of mucilaginous clouds and creamy layers (Pompei et al., 2003). Second, surface mucilage layers, frequently targeted for sampling but typically representing aged accumulations (Giani et al., 2005b), contain predominantly broken or degraded cells, which are often unidentifiable morphologically (Del Negro et al., 2005; Mazziotti et al., 2004; Pompei et al., 2003). Observations during the 1999-2002 MAT project further corroborated this association. Mucilage samples, consisting of semi-degraded surface layers and the water immediately below, as the one in Fig. 5A, emanated bioluminescence consistently at night from the water beneath the thick

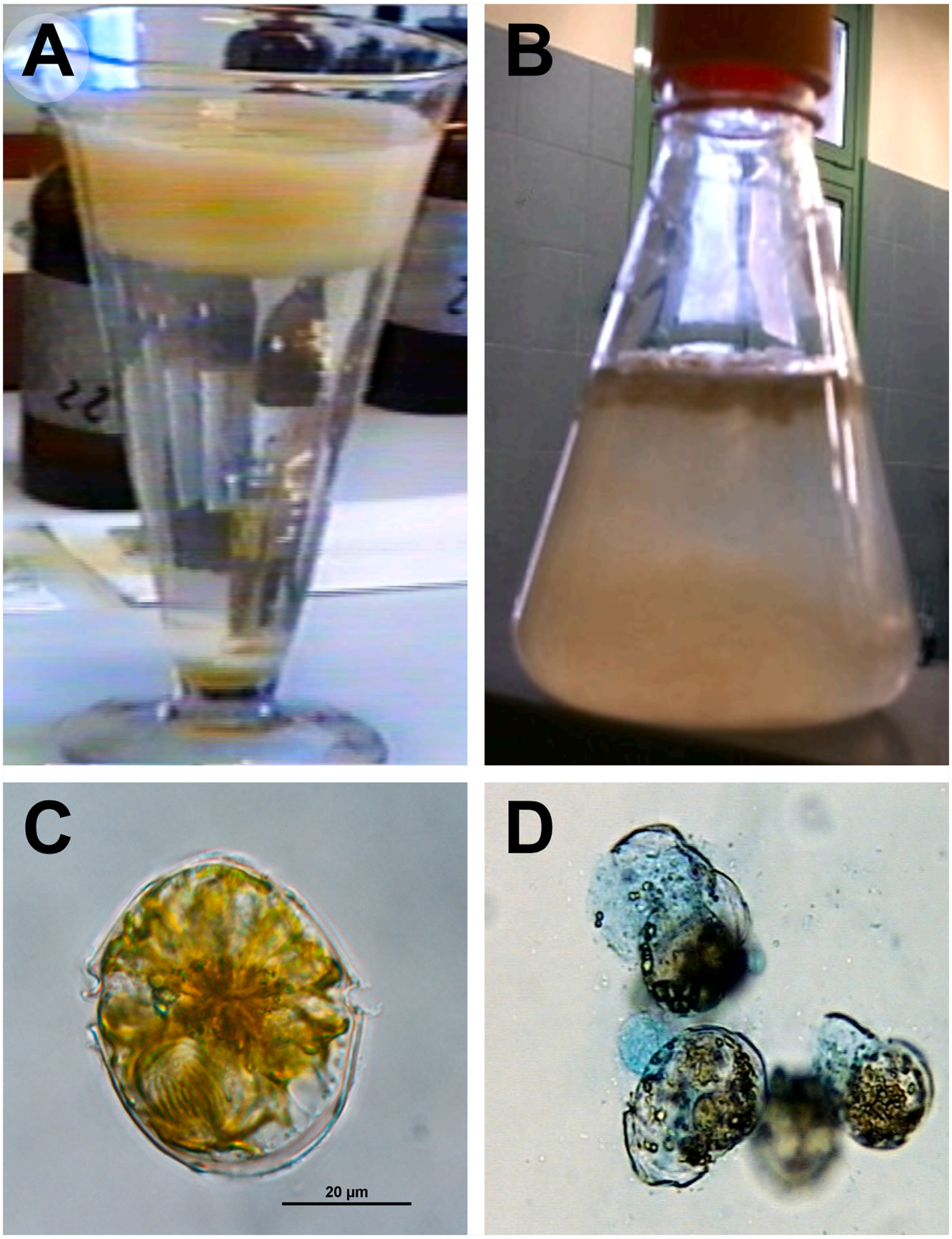

Fig. 5. (A) A field sample collected during a mucilage event in the context of the 1999-2002 MAT project. (B) *G.* cf. *hyalina* culture with an old mucilage formation floating on the surface and a cloud-like formation underneath containing algal cells; (C) *G.* cf. *hyalina* living cell observed from a sample collected in 2024 from the Adriatic Sea; (D) *G.* cf. *hyalina* cells found in a field mucilage sample releasing their content (polysaccharides are stained with Alcian Blue).

mucilage layer, where numerous viable *G.* cf. *hyalina* cells were thriving (Pistocchi R., personal observation). Even in senescent formations, *G.* cf. *hyalina* DNA could be reliably detected using species-specific primers (Riccardi et al., 2010). Similarly, Akcaalan et al. (2023), through environmental DNA analyses during the 2021 mucilage event in Turkey (Table 3), reported high sequence reads of *Alexandrium margalefii* and *G. fragilis* (or *G.* cf. *hyalina*) at several locations where dinoflagellate cysts were commonly found. This finding, if confirmed, could further support the association of this species with mucilage events in Turkey and raises questions on the possible presence of cysts in its life cycle, although never reported in the literature.

The persistent temporal and spatial correlation between elevated *G.* cf. *hyalina* cell densities and mucilage structures is difficult to interpret as a mere coincidence or the result of opportunistic colonization, as it was initially hypothesized.

6.2. High *G. cf. hyalina* densities in mucilage masses

Cell densities of *G.* cf. *hyalina* during significant mucilage events were exceptionally high, in the order of 10^6 cells L^{-1} (Table 1), to which a substantial number of disrupted cells, also in the same order (Mazziotti et al., 2004), should be added. The exceptionally high cell densities recorded during mucilage events indicate the occurrence of a bloom, as well as the spreading of the cells across vast areas (e.g., from the western to the eastern Adriatic coast and, in 2024, also from the northern to the southern Italian coastal regions). Like other dinoflagellates, the proliferation of this species depends on a narrow “window” of favorable environmental conditions, which typically constrain its growth to a specific period of the year. Historically, the largest mucilage formations in the northern Adriatic have consistently developed within the same seasonal timeframe, dating back several centuries (Forti, 1906). While the onset may occasionally be detected as early as June, peak occurrences are most frequently observed between late June and early August (Giani et al., 2005c; Hadjal et al., 2025; Precali et al., 2005; Stachowitsch et al., 1990) (see also Table 1). Climate change may now be contributing to an extension of this seasonal timeframe, potentially amplifying bloom intensity and duration.

6.3. *Linking the growth and composition of G. cf. hyalina to mucilage formations*

6.3.1. *Growth dynamics and constitutive mucous polysaccharide production*

Once monospecific cultures of *G.* cf. *hyalina*, isolated from the Adriatic Sea (formerly *G. fragilis*), were established in the early 2000s, experimental studies allowed for the characterization of the growth pattern and extracellular polysaccharide production.

In terms of growth performance, cultured *G.* cf. *hyalina* displayed a relatively low growth rate (max growth rate = 0.330 ± 0.003 day^{-1}) compared to other dinoflagellates, which in culture typically achieve cell densities of an order of magnitude higher than those recorded in natural environments. This limited growth is likely attributable to the organism's metabolic allocation strategy, whereby a significant proportion of the photosynthetically fixed carbon is not directed towards biomass accumulation but rather to the synthesis of extracellular carbohydrates. The highest cell yield was observed in GP medium characterized by a low N/P ratio and the presence of selenium (Pistocchi et al., 2005a). All the studied strains were tolerant to a broad salinity range (25-35 psu) but were more sensitive to light conditions, as maximum cell yields were obtained under the intermediate irradiance tested (90 μmol photons m^{-2} s^{-1}). Lower and higher light levels resulted in reduced cell densities; moreover, exposure to higher light intensities led to a marked increase in extracellular carbohydrates production (Pompei et al., 2003).

Further investigations, specifically on *G.* cf. *hyalina* nutrient dynamics, were later carried out aimed at deepening insight into its ecophysiology (Pistocchi et al., 2005b). Results of nutrient analyses evidenced a remarkably slow consumption pattern: after approximately 44 days of cultivation only 33% of the initial N amount resulted assimilated (Fig. 6A), while complete nitrogen depletion occurred solely in the treatment where the initial N concentration was reduced by a factor of ten; an even lower P uptake rate was observed, with depletion occurring only in the low-P treatments (ten times lower respect to controls) (Fig. 6B). Notably, when phosphate was supplied at a concentration three times higher than the standard GP medium (i.e., 300 μM), a rapid initial uptake occurred until concentrations equilibrated with those present in the standard condition. These results align with prior observations and attest that *G.* cf. *hyalina* cultures can be maintained for up to 4 months without medium renewal (Pistocchi R., personal observations), although presumably this long persistence is also related to a mutualistic relationship with bacteria. Nutrient dynamics data suggest that this species exhibits a pronounced ability for phosphorus luxury uptake and intracellular storage, with phosphate limitation appearing to be the primary factor constraining growth (data not shown).

Polysaccharide extrusion by *G.* cf. *hyalina* appeared to be a constitutive physiological trait. Consequently, higher growth rates and increased cell density correlate with elevated extracellular polysaccharide (EPS) concentrations in the surrounding medium or water column. Actively dividing cultures, particularly following medium renewal, produced visible white foamy clouds suspended within the flask. As the cultures aged, this material progressively floated to the surface, eventually darkening and turning brown, indicating oxidative processes (Fig. 5B). These observations provide direct experimental support for the organism's ability to generate mucilage-like matrices under controlled conditions, reinforcing its role in natural mucilage events.

Although other algae also produce and release extracellular EPS, such production in *G.* cf. *hyalina* is higher than those of different phytoplankton species (Myklestad and Haug, 1972; Pompei et al., 2003; Urbani et al., 2005) being, in late exponential phase, in the order of 500-800 μM C (Pistocchi et al., 2005a, 2005c) and in line with those previously reported for TOC measured in mucilage aggregates (i.e., stringers, cobweb, ribbons, clouds) ranging from about 400 to 3000 μM C (Del Negro et al., 2005). In addition, distinct differences can be observed microscopically and in culture: many EPS-producing species are embedded within loosely structured mucilaginous substances, often forming organic flocs visible in culture flasks. In contrast, true mucilage-forming species, such as *G.* cf. *hyalina,* generate an opaque, dense, highly viscous, and gel-like substance within culture vessels (Fig. 5B) to such an extent that it can be collected by hand, closely resembling the environmental mucilage. This distinction is also evident in field observations. For instance, mucilage-like accumulations originating from coastal waters and/or canals were documented in 2011; although these shared some features with typical mucilage (e.g., aggregated behind boat trails), they did not persist further than 30 km offshore. ARPAE analyses reported a lack of viscosity in this material compared to classic mucilage and identified diatom species, such as *Chaetoceros* spp., *Dactyliosolen fragilissimus, Cerataulina pelagica,* and *Asterionellopsis glacialis,* as potential EPS producers (ARPAE, 2011). The

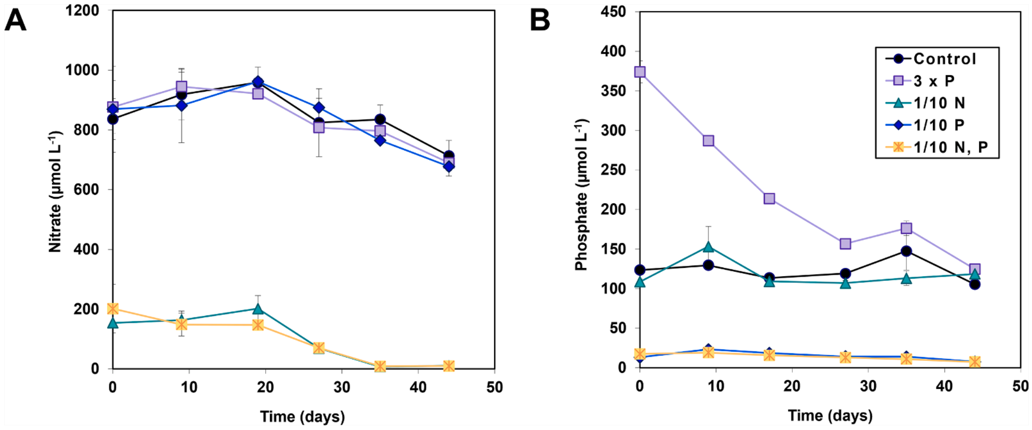

Fig. 6. Consumption of (A) Nitrate (N-NO$_3$) and (B) phosphate (P-PO$_4$) in *G.* cf. *hyalina* cultures grown under different nutrient conditions at 20°C, light intensity of 90 μmol photons m^{-2} s^{-1}, and a light/dark period of 16:8 h. Control = GP medium; 3xP = 3 times the P amount of the control; 1/10 N, P or N,P = one tenth the corresponding nutrient amount of the control. The *G.* cf. *hyalina* strain was isolated from mucilage samples collected in coastal waters of the northern Adriatic Sea (Emilia-Romagna, Italy). Details Nutrient measurements were performed by ARPAE using an autoanalyzer (Seal Analytical Quaatro39) after filtering the samples through 0.45 μm Millipore filters.

difference between the two types of organic matter was later confirmed also by means of satellite observations (Hadjal et al., 2025).

6.3.2. *Consistency of mucilage organic matter and polysaccharide monomeric composition*

An additional argument supporting *G.* cf. *hyalina* as a primary contributor to mucilage formation is the consistency observed in the chemical composition of mucilage across multiple samples analysed over the course of several decades. Although this composition evolves temporally, characteristic biochemical “fingerprints” attributable to specific organisms, including *G. hyalina,* remain detectable throughout the mucilage’s development, also helping in understanding its evolution over time.

Main components of the mucilage organic fraction (mean 54% d.w.) are carbohydrates (26.0% d.w.) and proteins (around 19.2% d.w.), with carbohydrates becoming less abundant in the surface mucilages and in sedimented aggregates (Giani et al., 2005b); the same pattern was reported for C/N ratio (Giani et al., 2005a; Pettine et al., 1993). Analysis of the monomeric composition of the polysaccharides extracted from various Adriatic mucilage samples revealed a consistent enrichment in galactose, as the dominant sugar (35-54%), followed by other sugars, such as glucose, xylose, mannose, fucose, rhamnose, ribose, and arabinose (Giani et al., 2005b; Marchetti et al., 1989; Pistocchi et al., 2005a). The similarity in monosaccharide profiles across multiple events, even in samples collected over a decade apart, strongly suggested a common marine origin of the aggregates (Giani et al., 2005b) in accordance with the theory of a single causative organism. These compositional profiles can be compared with polysaccharides derived from different diatoms and mucilaginous species, which generally contain galactose in relatively low proportions with respect to glucose, sometimes increasing under nutrient deficiency, but never exceeding 30% (De Angelis et al., 1993; Magaletti et al., 2004; Metaxatos et al., 2003; Myklestad and Haug, 1972; Urbani et al., 2005). In contrast, polysaccharides produced by *G. fragilis* cultures were characterized by galactose as the dominant monomer (ranging from 30.5 to 52.0%), and the other monomers matched the profile of mucilage field samples, although with some variability attributed to culture media differences (Pistocchi et al., 2005a).

6.3.3. *Consistency of mucilage lipid profile*

While the monosaccharide composition of mucilage polysaccharides can serve as an indicator of specific events and associated organismal growth, lipid profiles result even stronger taxonomic markers, as they have long been employed to differentiate microalgae, macroalgae, and prokaryotes, particularly in terms of fatty acids and sterols (Mansour et al., 1999; Napolitano et al., 1997; Russell and Nichols, 1999; Volkman et al., 1998). Analyses of mucilaginous formations sampled across multiple years (2001, 2002, 2004) (Pistocchi et al., 2005c; Riccardi et al., 2010) evidenced a general constancy in lipid composition. Conversely, the organic matter collected on 13th June 2002 after the massive *Noctiluca scintillans* growth displayed a distinct fatty acid profile compared to "real" mucilage, even though their general chemical and biochemical compositions were similar (Giani et al., 2005b). Assessing the precise contributions of different phytoplankton groups to mucilage organic matter production remains challenging, as community composition evolves over time. Enumeration of species in aged samples is often unreliable due to the abundance of dead or degraded cells, and comparisons with cultured strains are further complicated by variability in their biochemical profiles under different growth conditions. Analysis of fatty acid profile in mucilage samples revealed a variable correspondence with diatom presence, in some cases more evident (Blažina et al., 2005; Najdek et al., 2002; Viviani et al., 1995), in others less clear (Pistocchi et al., 2005c). Lipid markers indicative of exponential diatom growth were observed during the aging of the mucous matrix, concurrent with increasing colonization by opportunistic species such as *Cylindrotheca closterium* (Blažina et al., 2005; Najdek et al., 2002).

The sterol fraction of the mucilage showed additional similarities to *G.* cf. *hyalina,* both being characterized by the same dominant sterols (i.e., desmethylsterols, cholesterol, and β-sitosterol); in addition, 4α-methylsterols, which are recognized biomarkers for dinoflagellates, were detected in both samples with a similar profile (Riccardi et al., 2010). Bacterial contribution to mucilage formation was indicated by the occurrence of uneven C15 and C17 fatty acids (Blažina et al., 2005; Pistocchi et al., 2005c).

The above-reported chemical studies were performed nearly two decades ago, requiring extensive sampling and laboratory analyses. Advances in remote sensing now enable comparable insights to be achieved more rapidly. For instance, Hadjal et al. (2025) utilized NOAA’s OCView medium-resolution satellite imagery to identify surface aggregations of unidentified materials in the northern Adriatic Sea. Through spectral reflectance analysis, they demonstrated the ability to discriminate between *Noctiluca scintillans* massive presence and mucilage events, which both periodically affect the basin, although with distinct seasonal windows: *N. scintillans* primarily in spring (March–May) with occasional events in late February or June, while *G.* cf. *hyalina* in summer (June-September).

6.4. *Mucilage effects on human activities and the marine ecosystem*

Although *Gonyaulax* cf. *hyalina* is a nontoxic species, its blooms have been repeatedly associated with significant negative impacts on both human activities and the marine ecosystem, justifying its potential inclusion among harmful algal species (IOC list).

Outbreaks of marine mucilage significantly disrupt fishing operations by fouling and damaging gear. Although historical records (Zanon, 1931) describe similar occurrences, the presence of *G.* cf. *hyalina* during that period remains unreported. Nevertheless, comparable events have occurred recurrently since 1988. The tourism sector is even more severely impacted, since mucilage occurs during the summer season and the wind-driven mucilage masses on coastal beaches lead to high physical discomfort for bathers, as the sticky aggregates adhere to the skin and become irritating upon drying. Trade associations of tourism operators reported notable economic damage following the 1988-1989 mucilage events, because of a sustained reduction in vacationers’ presence. This decline persisted for several years, largely due to extensive negative coverage in European media (Giani et al., 2005a).

Environmental consequences for marine fauna have also been documented. During the 1988 and 1989 mucilage events, despite the absence of anoxic conditions in bottom waters, the settlement of mucilaginous material led to suffocation and mortality of numerous benthic organisms, such as mollusks, coelenterates, and crustaceans (Rinaldi et al., 1995). Additionally, negative effects were observed on eggs and larval stages of demersal fish species such as those of the *Gobius* genus (Rinaldi et al., 1995). According to Stachowitsch et al. (1990), stringers and clouds can cover multiple species in a cobweb-like network or massive layer, determining the interruption of suspension feeding and hindering locomotion. A zooplankton survey performed in the Gulf of Trieste for three months in 1989 revealed two distinct minima of community “evenness” indices coinciding with the presence of gelatinous masses with protozoans, particularly tintinnids, being preeminently affected (Milani and Fonda Umani, 1992).

Further episodes reinforce these observations. In 1997, mass mortality of farmed oysters was reported (Giani et al., 2005a). In 2000, a reduction in macrobenthos community density was observed, though it was not possible to clearly attribute it to mucilage accumulation or to a concurrent peak in Po River discharge (Occhipinti-Ambrogi et al., 2005). A study assessing mucilage effects on macrozoobenthic community and on farmed mussel (Cornello et al., 2005), found no significant changes in species richness or density of the macrozoobenthic community; however, a significant reduction was detected in mussel growth in the period June-July 2000 and July-August 2002. On the contrary, during an event occurring in the summer of 2004 on the rocky

Istrian coast, after approximately 20 days of mucilage impact with a coverage from 40% to 90%, the effects on selected macrobenthic species were species dependent. Mucilage caused partial necrosis of the sponge *Verongia aerophoba* (from 7% to 56% of the colony surface), while the impact was lethal for the mollusk *Arca noae,* which experienced death of 5-45% of the population (Devescovi and Ivеša, 2007).

During the 2024 event, an unprecedented mortality of wild mussels (*Mytilus galloprovincialis*) was reported along the Conero Riviera (Marche region) towards the end of the mucilage event and attributed to a combined effect of mucilage-induced hypoxia and unusually high temperatures (Totti and Ubaldi, 2024). Damage to nets and problems for fisheries have been reported by the local press in several regions, such as Friuli, Veneto, Emilia Romagna, Molise, Abruzzo, and Puglia. In Istria, widespread deterioration of macroalgal assemblages was observed one week after the mucilage outbreak, during a long-term monitoring campaign performed every year since 2010 (Pistocchi R., personal observation).

In addition to ecosystem functioning impairment and economic damage, mucilage events may also pose a threat to human health. These blooms are frequently associated with high abundances of bacteria and viruses, among which pathogenic species may be further concentrated compared to clear seawater (Danovaro et al., 2009; Volterra et al., 1992). Recently, *G. fragilis* has been included in the IOC-UNESCO list of non-toxigenic marine microalgal species associated with animal kills or health impairment (last version v 1.2, October 2025) (Zingone and Escalera, 2025), following an episode of fish mass mortality that occurred in the NW Aegean Sea, Greece (Harmful Algae Event Database-HAEDAT reference code GR-17-001). Nonetheless, in the database report, the causative species for this event is named *G. hyalina,* once again highlighting the need to better clarify the taxonomic position of these two species both morphologically and molecularly.

7. From the hidden *G.* cf. *hyalina* bloom to mucilage formation

After years of observations and the analysis of the characteristics of the 2024 long-lasting event, our proposed hypothesis still aligns with the one previously published (Pompei et al., 2003) and with the theory briefly outlined by Totti and Ubaldi (2024). Nevertheless, the long-term monitoring of phytoplankton communities and of seawater quality in Emilia-Romagna, combined with mucilage chemical features highlighting the biochemical fingerprints of various organisms over time, allows us to refine this view with additional details. The primary triggering mechanism for mucilage formation appears to be associated with the proliferation of the dinoflagellate *G.* cf. *hyalina* (Fig. 5C). Its growth is presumably stimulated by a combination of factors occurring below the surface and above the thermocline (ARPAE, 2025), often at depths of about 5-6 meters where mucilage is often reported to start growing (Cori, 1906; Gotsis-Skretas, 1995; Precali et al., 2005; Rinaldi et al., 1995) and where strings and cloudy aggregates gradually formed, marking the earliest stages of mucilage (Giani et al., 2005c). These initial aggregates, however, are not consistently detected during routine coastal monitoring, making the use of underwater video cameras essential. In certain years, such as 2001 and 2014, these early-stage masses did not follow the usual migration to the surface and subsequent maturation, likely due to meteorological and climatic factors that created turbulence in the water column and dispersed the developing aggregates.

Generally, following its initial occurrence, which is most frequently observed in June, *G.* cf. *hyalina* population requires approximately one month to achieve a substantial increase in cell density and to synthesize and excrete significant amounts of polysaccharides. The ecological function of this polysaccharide production remains speculative; however, several hypotheses consistent with those proposed by Reynolds (2007) can be considered. Given that the exuded material consists predominantly of carbohydrates and incurs minimal metabolic costs, even under nitrogen- and phosphorus-limited conditions, it may provide multiple adaptive advantages to the slow-growing *G.* cf. *hyalina* cells. These benefits could include protection against high irradiances (as supported by culture-based studies) by reducing the necessity for photoacclimation mechanisms, facilitation of passive vertical transport within the water column, thereby conserving ATP, and deterrence of predation through the entrapment of zooplankton (Pezzolesi et al., 2010). Furthermore, the polysaccharide matrix fosters mutualistic interactions with bacteria, which are consistently abundant within mucilage aggregates, exhibiting higher densities compared to the surrounding water (Blažina et al., 2005; Pistocchi et al., 2005c; Volterra et al., 1992). These bacterial communities display elevated enzymatic activities (Del Negro et al., 2005) and undergo temporal shifts in their dominant taxa from those adapted to elevated nutrient concentrations and readily assimilable organic carbon, to populations capable of hydrolyzing high-molecular-weight compounds, including complex polysaccharides (Blažina et al., 2005), suggesting dynamic ecological interactions within the mucilage environment. During mucilage formation, numerous *G.* cf. *hyalina* cells undergo lysis (as suggested by the species epithet *G. fragilis* or *G. hyalina: in nomen omen*!), releasing their cytoplasmic contents along with substantial amounts of polysaccharides (see Fig. 5D). This process contributes significantly to the accumulation of organic matter, leading to the characteristic biochemical fingerprints of mucilage. All the other mechanisms usually described, which consider the mucilage “as a build-up of organic material entrapped in a matrix, generated primarily by the gelling of phytoplankton polysaccharide exudate” (Giani et al., 2005d), in our opinion, occur specifically inside the polysaccharide matrix produced by *G.* cf. *hyalina.* As the built-up masses oscillate vertically through the water column and undergo maturation, they incorporate diverse organic particles (e.g., TEPs, DOC, marine snow, fecal pellets) and living organisms, including diatoms, bacteria, cyanobacteria (many of which release polysaccharides as well), and zooplankton. Several organisms perish due to the extreme conditions within the mucilage matrix, promoting biogeochemical decomposition, intense nutrient recycling, and bacterial proliferation, which, concurrently, change the properties of organic matter by rendering it more refractory. Only a limited number of opportunistic diatom taxa are able to grow under these conditions together with cyanobacteria and other flagellates (Totti et al., 2005; Ubaldi et al., 2026; Vanucci, 2003). With regard to diatoms, those initially observed are species already present in the surrounding water column, which may bloom as well or remain entrapped, reaching high cell abundances and contributing to the organic matter accumulation; however, the dominant taxa inside the mucus are typically tychoplanktonic and opportunistic species adapted to elevated nutrient concentrations, particularly spring-blooming forms previously documented in similar events (Innamorati, 1995). These species thrive within the mucilage due to the formation of a “false bottom” and the nutrient enrichment with respect to the water column (Mazziotti et al., 2004; Rinaldi et al., 1995); simultaneously, aggregates tend to sediment to the pycnocline or to the bottom or to ascend to the surface. Within this aged mucilage, *G.* cf. *hyalina* cells are no longer visible, and diatoms become the predominant organism as frequently observed (Flander-Putrle and Malej, 2008; Totti et al., 2005); nevertheless, numerous *G.* cf. *hyalina* cells persist just below the dense mucilage layers or within the adjacent water column.

The mechanisms triggering *G.* cf. *hyalina* growth remain poorly understood. Broader drivers such as climate change or anthropogenic environmental alterations cannot be implicated, given that present-day conditions differ substantially from those documented between the 18th and early 20th centuries. Some meteorological and hydrological conditions, including water column stability, specific nutrient inputs, and elevated temperatures, can indeed facilitate the proliferation of *G.* cf. *hyalina.* From this perspective, ongoing climate change raises concerns regarding a potential amplification of the phenomenon. However, as reported by Hadjal et al. (2025), the occurrence of only two major outbreaks between 2004 and 2024 does not substantiate the hypothesis of a sustained increase in mucilage occurrence in the Northern Adriatic

Sea.

Competitive interactions with other phytoplankton species cannot be excluded. Notably, the first major mucilage outbreak in the late 1980s coincided with the decline of large red tides that had characterized the coastal area of Emilia-Romagna from 1975 to 1987, a decline determined by the implementation of phosphate reduction directives issued in 1985. The red tides were caused by diatoms and by non-toxic but fast-growing dinoflagellates, such as *Ceratium* spp., *Diplopsalis lenticula, Prorocentrum micans, Lingulaulax polyedra,* and *Lepidodinium chlorophorum* (Pompei et al., 2018). They belong to the Gymnodinioids, Prorocentroids, Ceratians species, i.e., the type I-III phytoplankton (according to Smayda and Reynolds, 2003), characterized by the C-strategy (=colonist), being generally invasive, small, competitive, fast growing, and having a preference for high nutrient levels, although with a certain variability. From 1988 in the Adriatic Sea, among the dinoflagellates, there were *Gonyaulax* cf. *hyalina* and toxic species such as *Dinophysis* spp. and *G. spinifera,* which caused the first outbreak of DSP in 1989 (Boni et al., 2000) and high levels of yessotoxins in mussels from 1995 (Zoffoli et al., 2025), respectively. Both *Dinophysis* spp. and *G.* cf. *hyalina* share some characteristics in appearing nutrient stress tolerant and thus representing S-strategists: "typically very large species, often highly ornamented, and capable of depth-keeping by means of motility or auto-regulated buoyancy" (i.e., the mucous in the case of *G.* cf. *hyalina*), in addition, they are slow growing and capable of supplementing their photo-autotrophy by mixotrophy (or mutualistic behaviour in the case of *G.* cf. *hyalina*) (Smayda and Reynolds, 2003). The changed conditions may have provided a temporal niche for the slow-growing *G.* cf. *hyalina,* although it is also very difficult to explain the interannual variability and the coexistence with very high diatom abundances, as often documented. Specific nutrient dynamics are likely to play a critical role. In 2024, the Po River discharges due to the previously mentioned flooding event in the Pianura Padana carried elevated nitrogen and phosphorus loads with average values higher than in 2023 and, from July to September, coupled with low N/P ratio values (ARPAE, 2024). Additionally, the Po River overflow could have carried out a wide array of substances, such as fertilisers, animal-derived organic waste, stored foodstuffs, and micronutrients, washed from warehouses, farms, and urban areas. Such extraordinary conditions, as seen in 2024, may provide valuable insights into the mechanisms underlying mucilage formation. Anomalous events can also be informative, for example, *G.* cf. *hyalina* presence is recorded almost every year in the summer period, culminating in mucilage phenomena only in certain years, as reported in Table 1, where maximum cell numbers, recorded from 1998 to 2024, are summarized. However, small growth increments were sometimes observed in autumn (from 160 to 5,200 cells L^{-1}), leading to a late mucilage event only in November 2006. This event occurred concurrently with unusually warm winter conditions (Danovaro et al., 2009), preceded by elevated phosphate concentrations during the summer months (ARPAE, 2006). Overall, we suggest increased attention to phosphate inputs, which have also been implicated as a trigger for the dinoflagellate *Ostreopsis* cf. *ovata* blooms (Accoroni et al., 2015). Given the pronounced phosphate demand of *G.* cf. *hyalina*, this nutrient may represent a key driver, potentially challenging the prevailing paradigm that high N/P ratios are the primary stimulus for mucilage formation.

8. Conclusion

For over 35 years, each mucilage event in the Adriatic Sea has been accompanied by media narratives portraying the phenomenon as mysterious and inexplicable. In past centuries, when similar phenomena were observed from a scientific perspective well before the advent of modern monitoring technologies, the presence of a floating organic mass in the water column was associated with phytoplankton proliferation. Indeed, in all the cases here discussed, whether in the Adriatic or in other Seas, organic aggregations have been associated with the proliferation of a single organism. Overall, despite the socio-economic and environmental impacts caused by the Adriatic mucilages, these events are not officially acknowledged as HABs; nevertheless, such extensive formation of mucilaginous aggregates should be referred to as a "white tide". In our opinion, they are unequivocally linked to the presence and growth of a *Gonyaulax* species, already known to produce nuisance blooms, although its taxonomic position remains uncertain and needs to be further addressed.

Recognizing *G.* cf. *hyalina* as the causative organism opens new research and management perspectives. Unfortunately, there is still a lack of knowledge about many important biological features of *Gonyaulax* cf. *hyalina* cytology, life cycle, and ecophysiology that could be achieved through a combination of culture-based studies and field observations. A deeper understanding of the conditions promoting *G.* cf. *hyalina* growth and mucilage production could be instrumental in advancing our ability to forecast these phenomena, and ultimately in reducing their impacts on ecosystems and human activities in the Adriatic Sea.

CRediT authorship contribution statement

Rossella Pistocchi: Writing – original draft, Formal analysis, Data curation, Conceptualization. **Franca Guerrini:** Writing – review & editing, Visualization, Data curation. **Mara Simonazzi:** Writing – review & editing, Visualization. **Silvana Vanucci:** Writing – review & editing, Visualization. **Monica Cangini:** Writing – review & editing, Investigation. **Stefania Milandri:** Writing – review & editing, Investigation. **Cristina Mazziotti:** Writing – review & editing, Investigation. **Laura Pezzolesi:** Writing – review & editing, Supervision, Methodology.

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.

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Data availability

Data will be made available on request.

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