



Endemic and Indo-Pacific plankton in the Mediterranean Sea: a study based on dinoflagellate records

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ABSTRACT

Aim To investigate biogeographical patterns based on published dinoflagellate records from the Mediterranean and Black Seas, and to provide a tentative list of endemic and Indo-Pacific dinoflagellates in the Mediterranean Sea.

Location Mediterranean Sea, Black Sea.

Methods Checklists of dinoflagellates of the Mediterranean and Black Seas were compared with worldwide literature records. Only species reported in the Indo-Pacific Ocean or exclusively known in the Mediterranean Sea were selected for biogeographical analysis.

Results Dinoflagellates in the Mediterranean Sea comprised *c.* 43% of the world marine species and *c.* 88% of the dinoflagellate genera. Species richness among the Mediterranean sub-basins showed marked differences due to the less reliable records of unarmoured (athecate) and rare dinoflagellates. These differences disappeared when only the more easily identifiable taxa were considered. Of the 673 dinoflagellates cited in the Mediterranean, 87% were also reported in the Atlantic Ocean. Only 40 taxa (6% of the total) were considered to be potential Indo-Pacific species. Most were reported from the Ligurian Sea (21), and only two species from the Levantine basin. The other 48 taxa (7% of total) were known exclusively from the Mediterranean Sea, mainly from the Ligurian Sea. Half of these taxa were reported by a single author.

Main conclusions Substantial dinoflagellates species richness can be attributed, in part, to the historical tradition of taxonomic studies in the Mediterranean Sea. The list of species of both Indo-Pacific and exclusively Mediterranean species included taxa of dubious taxonomic validity or that were insufficiently known. The exclusion of these questionable taxa revealed the near absence of endemic dinoflagellates in the Mediterranean Sea compared with macroscopic organisms. This could be related to: (1) continuous replenishment of the plankton populations by the inflow of Atlantic water through the Strait of Gibraltar, (2) the possibility that species introduced during the Pliocene flooding after the Messinian salinity crisis have not had enough time to diverge from their Atlantic ancestors, and/or (3) the reliance on traditional taxonomy based on morphological characters, which precludes the detection of cryptic speciation.

Keywords

Black Sea, dinoflagellate, endemic, Erythrean invader, Indo-Pacific, Lessepsian migrant, marine biogeography, Mediterranean Sea, phytoplankton.

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INTRODUCTION

It has been estimated that *c.* 26% of the total Mediterranean marine fauna (4238 species, Fredj *et al.*, 1992) are endemic.

This rich biodiversity represents 4–18% of the total number of species in the world's oceans (Fredj *et al.*, 1992; Bianchi & Morri, 2000). The generally high biodiversity of the Mediterranean Sea may be explained by the synergy of: (i) a

historical tradition of taxonomic studies, (ii) a wide variety of climatic and hydrographic conditions, and (iii) the fluctuating hydrography of the Mediterranean Sea on a geological scale as communication with the Atlantic and Indian Oceans opened and closed due to changing sea levels and plate tectonics, serving as a type of 'diversity pump' (Fredj *et al.*, 1992; Bianchi & Morri, 2000).

The biodiversity of the Mediterranean Sea is undergoing rapid alteration within the context of a globally changing climate (Jeftić *et al.*, 1992; Bianchi & Morri, 2000). The basin has been subject to introductions of non-indigenous species by ship traffic since the opening of maritime routes five centuries ago. Since 1869 a narrow, man-made channel has connected the Mediterranean and the Indian Ocean: the Suez Canal has been considered the major gateway for the entry of invading species, and over 300 Erythrean species have established populations (Galil, 2000). This northbound migration of Erythrean invaders, formerly Lessepsian migrants, appears to have been accelerated during the past few decades by a rise in the sea temperatures as well as by the activation of the Aswan High Dam, leading to more oligotrophic conditions on the Mediterranean side of the Canal (Por, 1990). Exotic macrophytes, invertebrates and fish are found in most coastal habitats in the Mediterranean Sea. In addition to the Erythrean invaders, species are intentionally or accidentally introduced into the Mediterranean via ship fouling, ballast waters, aquaculture, trade in living bait, wrapping of fresh seafood in living algae, aquariology, and scientific research (Bianchi & Morri, 2000).

The Mediterranean Sea is a remnant of the extensive Tethys Ocean of the Triassic (*c.* 200 Ma BP). During the Cretaceous (*c.* 120 Ma BP), the Mediterranean was opened to communication with the Atlantic Ocean. Later in the Miocene (*c.* 10 Ma BP), the isthmus of Suez was formed, isolating the Mediterranean from the Indo-Pacific Ocean. Towards the end of the Miocene, the connection with the Atlantic Ocean closed again as the Messinian salinity crisis led to nearly complete evaporation of the sea. The Messinian salinity crisis occurred synchronously throughout the Mediterranean Basin *c.* 5.96 Ma BP, and caused a large fall in sea level (> 1000 m). The Messinian salinity crisis ended 5.33 Ma BP, during the Pliocene, with the reopening of the Strait of Gibraltar (Krijgsman *et al.*, 1999) which inundated the Mediterranean Basin in only 35 years (Blanc, 2002). During the Quaternary, the alternating ice ages and warm interglacial periods resulted in repopulation of the Mediterranean with boreal or subtropical species, respectively, of Atlantic origin. Bianchi & Morri (2000) separated the present marine biota into several biogeographical categories: (1) temperate Atlantic–Mediterranean, (2) cosmopolitan/panoceanic, (3) endemic, palaeoendemic (Tethyan origin) and neoendemic (Pliocenic origin), (4) subtropical Atlantic (interglacial remnant), (5) boreal Atlantic (ice-age remnants), (6) Red Sea migrants, and (7) eastern Atlantic migrants (especially in the Alborán Sea). Exchange through the Strait of Gibraltar can be considered the main source of species to the Mediterranean Sea, excluding the

Tethys relics that survived the extreme environmental changes associated with the Messinian salinity crisis. Fredj *et al.* (1992) reported that 67% of the Mediterranean fauna (excluding protists) were also known from the Atlantic Ocean.

The introduction of exotic species modifies the ecosystem: endemic species unable to tolerate this perturbation will go extinct and exotic species will flourish. Studies of this dilemma require characterization of the marine biota. Studies on Mediterranean biogeography are numerous, but nearly all are focused on macroscopic organisms, whereas studies on the biogeographical affinities of marine phytoplankton are almost non-existent. Halim (1990) reported a list of Indo-Pacific dinoflagellates. Marino (1990) concluded that it is difficult at present to quantify the number of endemic phytoplankton species.

Several authors link the changing nitrogen–silicon ratio in the Mediterranean Sea to a large increase in the number of blooms of phytoplankton species that do not require silica for their growth (a shift from diatoms to dinoflagellates) (Turley, 1999). More than 200 dinoflagellate species have a negative impact on human activity through the production of potent toxins which may accumulate in the food chain (red-tides or harmful algal blooms) (Sournia, 1995). In terms of species richness, the number of species of dinoflagellates is comparable only to that of diatoms. About 1500 diatoms (Sournia *et al.*, 1991) and 1555 dinoflagellate species comprise the marine phytoplankton in the world's oceans (Gómez, 2005).

The aims of this study are to establish the biogeographical origin of the Mediterranean dinoflagellates, and to present a checklist of species candidates considered to be endemic or Indo-Pacific taxa. The validity of these species and the low endemism compared with macroscopic groups are discussed.

METHODS

A matrix was constructed based on the checklist of dinoflagellates reported by Gómez (2003a) for each Mediterranean sub-basin, and by Gómez & Boicenco (2004) for the Black Sea. The distribution of each taxon in the world's seas was established from scrutiny of more than 1100 references. Only some references of interest are cited due to space limitations.

The species cited in the Atlantic waters were eliminated as potential endemic or Indo-Pacific taxa. The remaining group of species was divided into: (1) exclusively Mediterranean species, potential candidates as endemic species, and (2) Indo-Pacific species known exclusively from the Mediterranean and Indo-Pacific Basins.

RESULTS AND DISCUSSION

Dinoflagellates recorded from the Mediterranean Sea comprise 673 species (104 genera), a value close to the 660 species previously reported by Marino (1990) (this author did not report a species checklist). Sournia *et al.* (1991) reported that 1424–1772 species comprising *c.* 115–131 genera constitute the dinoflagellates in the world's oceans. Gómez (2005) listed 1555

species and 117 genera. Thus, although the Mediterranean represents only a small percentage of the world's ocean (0.82% by surface area and 0.32% by volume), nearly 43% of the world's marine dinoflagellate species occur there, including *c.* 88% of the dinoflagellate genera. This percentage is higher than the average value of 6.3% (4–18%) for marine macroscopic organisms in the Mediterranean Basin (Bianchi & Morri, 2000).

The species richness of dinoflagellates in the Mediterranean Basin is highly variable among its sub-basins. In the Ligurian Sea, the smallest of the Mediterranean sub-basins, 74% of the total species have been reported. The number of species cited in the Ligurian and Ionian Seas compared with other sub-basins (Alborán or Aegean Seas) substantially increases when the less reliable records of unarmoured (athecate) dinoflagellates are included. Innamorati *et al.* (1986, 1989a,b) and Skolka *et al.* (1986) cited many freshwater species and synonyms considered as separate species for the Ligurian and Ionian Seas, respectively. Also suspect among the armoured (thecate) dinoflagellates are the large number of species of *Histioneis* Stein, *Heterodinium* Kofoid and, to a lesser extent, *Oxytoxum* Stein and *Gonyaulax* Diesing, cited in the Ligurian Sea. Many of the species described by Rampi (see references in Rampi & Bernhard, 1980) and Halim (1960) have not been reported after the initial descriptions (Gómez, 2003a). These rare taxa and unarmoured forms accounted for the variable distribution of species among the Mediterranean sub-basins (Fig. 1). These unreported taxa should be interpreted as having been overlooked by non-specialist authors and/or due to the scarcity of taxonomic studies in these sub-basins, rather than as being absent.

More easily identifiable genera, such as *Ceratium* Schrank, have been the subject of several biogeographical studies (e.g. Dodge & Marshall, 1994). In the eastern Mediterranean basin, the Aegean Sea, with only half the total species richness reported in the Ionian or Adriatic Seas, had more records of *Ceratium* species than either of the aforementioned sub-basins (Gómez, 2003a). In the Alborán Sea, with about one-third of the total species cited in the Ligurian Sea, 46 species of *Ceratium* were reported, as opposed to the 52 species of the Ligurian Sea (Gómez, 2003a). If the more difficult-to-

recognize unarmoured forms and dubious taxa are disregarded, the species richness for each sub-basin is quite similar. For example, the Levantine Basin shows greater species richness than the Adriatic or Ionian Seas. High species richness in some Mediterranean sub-basins is probably due to the unequal number of studies, rather than true differences in species richness among the sub-basins.

Indo-Pacific species

Since the Miocene, communication between the eastern Mediterranean (Tethys Sea) and the Indian Sea has been closed (Maldonado, 1985). A narrow, man-made channel connecting the Mediterranean with the Red Sea was opened during the Egyptian Empire period (Sneh *et al.*, 1975). Since the completion of the Suez Canal in 1869, Erythrean species have colonized the Mediterranean marine biota (Por, 1978). It has been calculated that these species (over 300) now constitute nearly 5% of the global Mediterranean fauna and 13% of the species found in the Levantine Basin (Fredj *et al.*, 1992; Galil, 2000).

The 168 km of the Suez Canal are characterized by extreme physical and chemical conditions: high turbidity, high temperatures, and two salinity barriers represented by the hypersalinity of the Bitter Lakes in the south and the Nile freshwater dilution at the north. The residual current tends to flow from the Red Sea for 10 months, reversing in late summer. The completion of the Aswan High Dam in 1965, and the increase of the cross-sectional flow, have minimized the two salinity barriers. The progressive increase of the water fluxes (and reduction of the salinity gradients) could favour northbound migration directly through the Suez Canal (Halim, 1990). Ships navigating the Canal may likewise facilitate migration of species via transport in their ballast waters (Shefer *et al.*, 2004).

From the 673 species of free-living dinoflagellates listed by Gómez (2003a), 40 species (6% of the total) were cited exclusively from the Mediterranean Sea and Indo-Pacific Ocean (Table 1). Most of the taxa were reported from the Pacific Ocean, and only 11 species from the Indian Ocean. In this case the low number of studies in the Indian Ocean

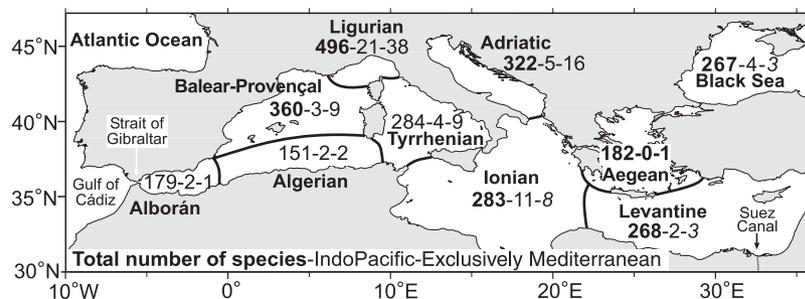


Figure 1 Map of the Mediterranean sub-basins and the Black Sea. Number of dinoflagellate species cited in each Mediterranean sub-basin and the Black Sea based on Gómez (2003a); Gómez & Boicenco (2004); number of dinoflagellate species tentatively considered as Indo-Pacific taxa (see Table 1 for species list); number of exclusively Mediterranean dinoflagellates (see Table 3 for species list).

Table 1 Species reported only in Mediterranean and Indo-Pacific waters

<i>Alexandrium insuetum</i> Balech (Tyr)	<i>Gymnodinium ovulum</i> Kofoid & Swezy (Lig)
* <i>Amphidinium curvatum</i> Schiller† (Lig, Ion, Adr, BS)	<i>Gymnodinium ravenescens</i> Kofoid & Swezy (Lig)
* <i>Amphidinium inflatum</i> Kofoid† (Alg)	<i>Gymnodinium sphaeroideum</i> Kofoid (Lig, Ion)
* <i>Amphidinium lissae</i> Schiller‡ (Lig, Adr)	<i>Gymnodinium translucens</i> Kofoid & Swezy (Lig)
* <i>Amphidinium vasculum</i> Kofoid & Swezy† (Ion)	<i>Gyrodinium acutum</i> (Schütt) Kofoid & Swezy (Bal, Tyr, Ion)
<i>Amphidoma elongata</i> Kofoid & Swezy (Alb, Alg)	<i>Gyrodinium biconicum</i> Kofoid & Swezy (Ion)
<i>Amphisolenia complanata</i> Kofoid & Skogsberg (Lig)	<i>Gyrodinium rubricaudatum</i> Kofoid & Swezy (Lig)
<i>Centrodinium elongatum</i> Kofoid (Alb)	* <i>Heterodinium crassipes</i> Schiller† (Adr)
* <i>Ceratium egyptiacum</i> Halim (Lev)	<i>Heterodinium dubium</i> Rampi¶ (Lig)
<i>Ceratoperidinium yeye</i> Margalef (Alb, Bal, Lev)	<i>Histioneis detonii</i> Rampi¶ (Lig)
<i>Cochlodinium turbineum</i> Kofoid & Swezy (Adr)	* <i>Histioneis elongata</i> Kofoid & Michener (Lev)
<i>Craspedotella pileolus</i> Kofoid (Lig)	<i>Leptodiscus medusoides</i> Hertwig (Bal, Lig, Tyr)
* <i>Gonyaulax ligustica</i> Rampi§ (Bal, Lig)	* <i>Oxytoxum areolatum</i> Rampi§ (Bal, Ion, Adr)
<i>Gonyaulax rugosum</i> Wailes (Ion)	<i>Parahistioneis acutiformis</i> Rampi¶ (Lig)
<i>Gymnodinium attenuatum</i> Kofoid & Swezy (Lig, Ion)	<i>Petalodinium porcelio</i> Cachon & Cachon (Lig)
<i>Gymnodinium canus</i> Kofoid & Swezy (Ion)	<i>Protoceratium pepo</i> Kofoid & Michener (Lig)
<i>Gymnodinium lineatum</i> Kofoid & Swezy (Ion)	<i>Protoperidinium tregouboffii</i> (Halim) Balech (Lig)
<i>Gymnodinium lira</i> Kofoid & Swezy (Lig)	<i>Scrippsiella precaria</i> Montresor & Zingone** (Tyr, Ion)
* <i>Gymnodinium multilineatum</i> Kofoid & Swezy†	<i>Tripisolenia longicornis</i> Kofoid (Lig)
* <i>Gymnodinium sulcatum</i> Kofoid & Swezy† (also BS)	<i>Warnowia pulchra</i> Schiller** (Tyr, Lig)

*Taxa cited in the Indian Ocean. Alb, Alborán; Alg, Algerian; Bal, Balear-Provençal; Lig, Ligurian; Tyr, Tyrrhenian; Ion, Ionian; Adr, Adriatic; Aeg, Aegean; Lev, Levantine; BS, Black Sea.

†From Australian waters (Wood, 1963a,b).

‡From the Red Sea (Halim, 1969).

§From the Arabian Gulf (Dorgham & Mofteh, 1986).

¶Only reported in the south Pacific Ocean (Rampi, 1948, 1950).

**Reported in the Pacific Ocean (Chihara & Murano, 1997).

compared with other major oceans should be taken into account.

Most of the Mediterranean Indo-Pacific dinoflagellates corresponded to taxa described by Kofoid and collaborators (Kofoid & Michener, 1911; Kofoid & Swezy, 1921; Kofoid & Skogsberg, 1928) from the eastern Pacific Ocean (Table 1). This literature is commonly referenced for the identification of Mediterranean species, and many authors working in the Mediterranean have assigned their observations to the Pacific taxa illustrated by Kofoid. For unarmoured dinoflagellates, despite the excellent and detailed descriptions by Kofoid & Swezy (1921) compared with other, older studies, poor fixation due to the commonly used preservatives formaldehyde and iodine hindered identification. With these preservatives, body shape and morphology often change during the process of fixation so that even determination of the genus becomes difficult (Steidinger & Tangen, 1997).

The list of Mediterranean Indo-Pacific taxa is full of dubious or poorly known species. *Ceratium egyptiacum* Halim was reported as an example of a recent Erythrean invader (Halim, 1990). The taxon shows variable morphology associated with the stress of environmental changes (salinity > 47) in the Suez Canal (Dowidar, 1972). *Ceratium egyptiacum*, which resembles *Ceratium pulchellum* Schröder, was reported only from the proximity of the Suez Canal, with no records in the Indian or Pacific Oceans. *Alexandrium insuetum* Balech is recognizable only by a few specialists; Steidinger & Tangen (1997) reported

differences in the sulcal plates between the Mediterranean and Pacific specimens. *Gonyaulax ovalis* Schiller and *Gonyaulax ovata* Matzenauer may be synonyms, and both taxa are dubious. The description of *Gonyaulax rugosum* Wailes was insufficient. *Protoperidinium tregouboffii* Halim was reported only by Balech (1962) in the Pacific Ocean. This taxon shows similarity to the cosmopolitan *Protoperidinium brachypus* (Schiller) Balech. *Ceratoperidinium yeye* Margalef (= *C. mediterraneum* Abbud Abi-Saab) has recently been reported from the Pacific Ocean (Gómez *et al.*, 2004). This taxon may be overlooked in other oceans. Halim (1969) reported *Pyrodinium bahamense* var. *compressum* (Böhm) Steidinger, Tester *et* Taylor (formerly *P. schilleri* (Matzenauer) Schiller) from Port Said, just on the Mediterranean side of the Suez Canal; however no other Mediterranean records exist of this distinctive taxon, which has been investigated extensively due to its toxicity. The Noctilucales Haeckel *Petalodinium porcelio* Cachon & Cachon and *Leptodiscus medusoides* Hertwig have been found recently in Pacific waters (Gómez & Furuya, 2005). These taxa are barely recognizable as dinoflagellates, and are probably going unnoticed in the world's oceans (Gómez & Furuya, 2004, 2005). For *Craspedotella* Kofoid, the record by Cachon & Cachon (1969) in the Mediterranean Sea differed from the description by Kofoid from the Pacific Ocean.

In the Black Sea, it is doubtful that *Amphidinium cucurbita* Kofoid *et* Swezy, *Gymnodinium radiatum* Kofoid & Swezy, *Gymnodinium sulcatum* Kofoid & Swezy and *Protoperidinium*

sinaicum (Matzenauer) Balech belong to Indo-Pacific taxa (Gómez & Boicenco, 2004).

The absence of information on dinoflagellates before the opening of the Suez Canal hinders attempts to determine the biogeographical origins of present Mediterranean species. According to Marino (1990), tropical invaders from the Red Sea only partially compensate for the lack of Atlantic species in the eastern Mediterranean Sea. Since the highest number of Indo-Pacific macroscopic species occurred in the Levantine basin (Galil, 2000), it is expected that, likewise, a majority of Indo-Pacific dinoflagellates would occur here. In the Levantine basin only the doubtful taxon *C. egyptiacum* and *Histioneis elongata* (the latter illustrated by Polat & Koray, 2002) remain as Indo-Pacific dinoflagellates. Most of these tentative Indo-Pacific dinoflagellates, however, were reported from the Ligurian Sea (21 species) (Fig. 1). The present study did not find any clear candidate Indo-Pacific species. Curiously, the toxic and distinctive dinoflagellate *Dinophysis miles* Cleve, a solid example of an Indo-Pacific species, frequently occurring even in the Red Sea, has never been reported in the Mediterranean Sea.

Halim (1990) reported a tentative list of 17 armoured Mediterranean–Indo-Pacific dinoflagellates. However the Indo-Pacific origin of these species is questionable due to the fact they were also reported in the Atlantic Ocean. Furthermore, several of the species are dubious or invalid taxa (Table 2).

According to Por (1978), Red Sea species in the Levantine Basin will increase and decline according to future climatic fluctuations. The increase of temperature and salinity in the Mediterranean Sea, associated with climate change, could facilitate the adaptation of introduced Red Sea/Indian Ocean species. The Strait of Gibraltar is another route for the entrance of tropical species. For example, *Gymnodinium catenatum*

Graham, a distinctive toxic dinoflagellate, has apparently entered the Mediterranean Sea through the Strait of Gibraltar (Gómez, 2003b). Global warming is expected to promote northward expansion of tropical species in the eastern Atlantic towards the Strait of Gibraltar. Studies on the phytoplankton composition along the coasts of Africa and the Alborán and Algerian Seas are nearly non-existent, precluding the detection of tropical phytoplankton species entering the Mediterranean Sea from the Atlantic. As most monitoring studies are carried out along the Italian coasts or in the north-west Mediterranean Sea, when tropical species are detected it is difficult to establish the biogeographical origin of the invaders. Permanent studies in key areas, including the Strait of Gibraltar, the Bosphorus–Dardanelles Straits and the surrounding waters of the Suez Canal, will be useful for monitoring the expansion of tropical species.

Exclusively Mediterranean species

Endemism, the number of species living exclusively in the Mediterranean, is expected to be high in this semi-enclosed basin (Bianchi & Morri, 2000). The semi-enclosed Mediterranean conditions are thought to have led to speciation and neoendemism of Pliocene invaders introduced during or after the Messinian salinity crisis (Furnestin, 1979). Relics of the Tethys Sea could survive the Messinian salinity crisis, as proposed for some benthic fauna (Wilke, 2003). Around 25% of the marine macroscopic species in the Mediterranean Sea are endemic (Bianchi & Morri, 2000), with > 50% endemism for some benthic fauna (Fredj *et al.*, 1992). In contrast to this general trend, Bouchet & Taviani (1992) reported that the deep fauna of the Mediterranean is characterized by a very low degree of endemism compared with the other areas of the world's oceans.

Table 2 Mediterranean–Indo-Pacific species according to Halim (1990, p. 16) and citations of these taxa from the Atlantic Ocean

Species	Records in Atlantic Ocean/comments
<i>Ceratium egyptiacum</i> Halim	= ? <i>Ceratium pulchellum</i> Schröder, see text
<i>Dinophysis giganteum</i> Kofoid <i>et</i> Michener	Closely related to <i>Dinophysis cuneus</i> (Schütt) Abé
<i>Dinophysis umbosa</i> Schiller	Wood (1968)
<i>Heterodinium dubium</i> Rampi	Reported only by the authority in the Pacific Ocean (Rampi, 1950)
<i>Heterodinium minutum</i> Rampi (?)	Non-existent, <i>Heterodinium minutum</i> Kofoid & Michener?
<i>Histioneis inclinata</i> Kofoid <i>et</i> Michener	Wood (1968), Balech (1988)
<i>Histioneis longicollis</i> Kofoid	Wood (1968), Dodge (1993)
<i>Histioneis subcarinata</i> Rampi	Balech (1971), only by Rampi (1950) in the Pacific
<i>Gonyaulax ovalis</i> Schiller	Doubtful taxa, insufficient description
<i>Oxytoxum caudatum</i> Schiller	Wood (1968), Marshall (1976), Moita & Vilarinho (1999), etc.
<i>Oxytoxum laticeps</i> Schiller	Wood (1968), Marshall (1976), Parke & Dodge (1976), Moita & Vilarinho (1999)
<i>Oxytoxum variabile</i> Schiller	Establier & Margalef (1964), Wood (1968), Margalef (1973), Marshall (1976), Parke & Dodge (1976), etc.
<i>Prorocentrum maximum</i> Matzenauer	Doubtful taxon, <i>Prorocentrum maximum</i> (Gourret) Schiller?
<i>Protoperidinium hirobis</i> Abé	Wood (1968), Balech (1971), Marshall (1976), Okolodkov (1998)
<i>Protoperidinium nipponicum</i> Abé	Steidinger <i>et al.</i> (1967), Lessard & Swift (1986), similar to <i>Protoperidinium ovum</i> Schiller
<i>Protoperidinium tregouboffii</i> Halim	See text
<i>Pyrodinium schilleri</i> (Matzenauer) Schiller	Only by Halim (1969) in the Mediterranean Sea

In the present study 48 dinoflagellate species were described and reported exclusively from the Mediterranean Sea, mainly by Rampi and Schiller in the Ligurian and Adriatic Seas, respectively (Table 3). Half these species were reported by a single author. Among the Dinophysiales Lindemann, species of the genera *Amphisolenia* Stein and *Histioneis* were poorly described and strongly resembled cosmopolitan species. In the original descriptions, based on single or few specimens, the authors failed to take into account the high morphological variability in the life cycle of Dinophysiales (Reguera & González Gil, 2001). As an example, Halim (1960) described several new species of *Histioneis* that strongly resemble immature (or damaged) specimens of a population of the cosmopolitan *Histioneis longicollis* Kofoid existing in the type locality (Fig. 2). *Ceratium brunellii* Rampi strongly resembles the cosmopolitan *Ceratium incisum* (Karsten) Jørgensen. Dodge & Saunders (1985) considered many of the species of *Oxytoxum* Stein, described by Rampi, as synonyms of common species. As occurred with other Noctilucales (Gómez & Furuya, 2004, 2005), *Cachonodinium* Kofoid goes unnoticed in the world's oceans and probably *Greuetodinium* (Greuet) Loeblich III is not a dinoflagellate.

Records of the remaining half of the exclusively Mediterranean species were reported by multiple authors, and thus are somewhat more credible. The identifications, however, were frequently based on older texts, which are imperfect. For example, Schiller (1933) described numerous unarmoured dinoflagellates of the genera *Amphidinium* Claparède &

Lachmann and *Gymnodinium* Stein. These early descriptions were insufficiently detailed, often based on specimens deformed by the fixation used, and should be interpreted with caution (Fig. 3). More recently, Sournia (1986) questioned the validity of taxa such as *Archaeosphaerodiniopsis* Rampi, *Adinimonas* Schiller or *Pachydinium* Pavillard. While the contributions of Schiller and other earlier workers in the field are important references for dinoflagellate identification, researchers who rely solely on the older literature, without considering more recent work in the field of phytoplankton taxonomy, risk inaccuracies in their species accounts.

In the case of two genera, *Protoperidinium* Bergh and *Scrippsiella* Balech, identification at species level is limited to a few experts, which may explain the scarcity of records outside the Mediterranean Basin. The complex life cycle of the genus *Pyrocystis* Murray ex Haeckel precludes the consideration of *Pyrocystis margalefii* Léger for biogeographical purposes. The poor description of *Asterodinium libanum* Abboud-Abi Saab, the high morphological variability and the unknown life cycle of the order Brachidiniales Sournia, probably morphotypes of some species of *Karenia* G. Hansen & Moestrup, also prevent consideration of this taxon as an exclusively Mediterranean species (Gómez, 2003c; Gómez *et al.*, 2005).

These questionable dinoflagellate records reported as exclusively Mediterranean represented less than 7% of the total species. These taxa should be considered as 'false endemics' due to dubious taxonomic identification or the sparse geographical information. Based on the present study,

<i>Adinimonas oviforme</i> Schiller	* <i>Heterodinium laticeps</i> Léger (Lig)
<i>Alexandrium foedum</i> Balech (Tyr)	* <i>Histioneis alata</i> Rampi (Lig)
* <i>Amphisolenia sigma</i> Halim (Lev)	* <i>Histioneis bernhardii</i> Rampi (Lig)
<i>Amphidinium conus</i> Schiller (Adr,Lig)	* <i>Histioneis elegans</i> Halim (Lig)
<i>Amphidinium stigmatum</i> Schiller (Lig,Ion,Adr)	<i>Histioneis expansa</i> Rampi (Lig,Lev)
* <i>Archaeosphaerodiniopsis verrucosa</i> Rampi (Lig)	* <i>Histioneis imbricata</i> Halim (Lig)
<i>Asterodinium libanum</i> Abboud-Abi Saab (Lig,Lev)	<i>Histioneis faouzii</i> Halim (Lig)
<i>Cladopyxis quadrispina</i> Pavillard	<i>Histioneis kofoidii</i> Forti & Issel (Tyr,Adr)
<i>Dinophysis alata</i> Jørgensen	* <i>Histioneis ligustica</i> Rampi (Lig)
* <i>Cachonodinium caudatum</i>	<i>Histioneis marchesonii</i> Rampi (Bal,Lig,Lev)
(Cachon <i>et</i> Cachon) Loeblich III (Lig)	* <i>Histioneis rampii</i> Halim (Lig)
* <i>Ceratium brunellii</i> Rampi (Lig)	* <i>Histioneis speciosa</i> Rampi (Lig)
* <i>Gonyaulax trottii</i> Rampi (Lig)	* <i>Histioneis sublongicollis</i> Halim (Lig)
* <i>Greuetodinium cylindricum</i>	* <i>Histioneis villafranca</i> Halim (Lig)
(Greuet) Loeblich III (Lig)	* <i>Oxytoxum obesum</i> Rampi (Lig)
<i>Gonyaulax elegans</i> Rampi (Lig, also in BS)	<i>Oxytoxum depressum</i> Schiller
<i>Gymnodinium caput</i> Schiller	* <i>Oxytoxum radiosum</i> Rampi (Lig)
<i>Gymnodinium najadeum</i> Schiller (also in BS)	<i>Pachydinium mediterraneum</i> Pavillard
<i>Gymnodinium neapolitanum</i> Schiller (also in BS)	* <i>Parahistioneis sphaeroidea</i> Rampi (Lig)
<i>Gymnodinium pulchrum</i> Schiller (Lig,Adr)	* <i>Prorocentrum venetum</i>
<i>Gymnodinium tridentatum</i> Schiller (Adr)	Tolomio & Cavolo (Adr)
<i>Gymnodinium voukii</i> Schiller	<i>Protoperidinium maranense</i> Tolomio (Adr)
* <i>Heterodinium balechii</i> Rampi (Lig)	<i>P. parthenopes</i> Zingone & Montresor (Tyr)
* <i>Heterodinium debeauxii</i> Rampi (Lig)	* <i>Pyrocystis margalefii</i> Léger (Lig)
* <i>Heterodinium grahamii</i> Rampi (Lig)	<i>Scrippsiella ramonii</i> Montresor (Tyr,Ion)
<i>Heterodinium kofoidii</i> Pavillard	

*Taxa reported only by the authority.

Table 3 Dinoflagellate species known exclusively from the Mediterranean Sea

Figure 2 Illustrations of (a) *Histioneis vil-lafranca* Halim; (b) *Histioneis elegans* Halim; (c) *Histioneis longicollis* Kofoid; (d) *Histioneis sublongicollis* Halim; (e) *Histioneis faouzii* Halim, adapted from Halim (1960). The new species described by Halim (1960) from single or few specimens strongly resemble the cosmopolitan *H. longicollis*. Scale bar = 20 µm.

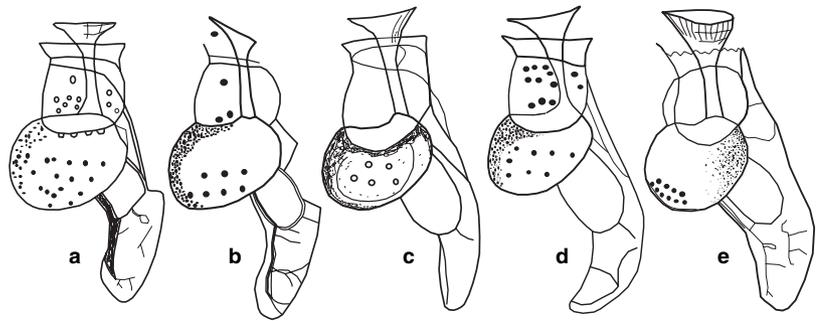
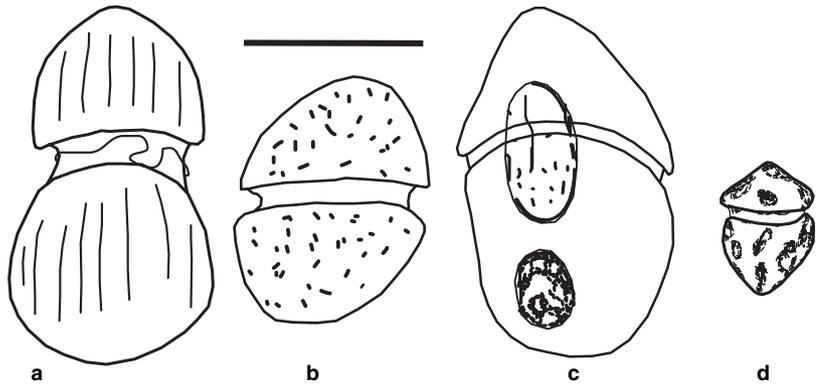


Figure 3 Illustrations of (a) *Gymnodinium caput* Schiller; (b) *Gymnodinium najadeum* Schiller; (c) *Gymnodinium neapolitanum* Schiller; (d) *Gymnodinium pulchrum* Schiller, adapted from Schiller (1933). The descriptions by Schiller (1933) are insufficiently detailed for precise identification of unarmoured taxa. Scale bar = 20 µm.



dinoflagellates show a lower percentage of endemic species compared with macroscopic or benthic species (Fredj *et al.*, 1992; Bianchi & Morri, 2000). In fact, no taxon considered in this study can be confirmed as being of exclusively Mediterranean origin. The Black Sea is an extreme case of a quasi-enclosed basin, which first came into contact with the world's oceans through the Bosphorus–Dardanelles Strait c. 12,000 yr BP (Çağatay *et al.*, 2000). Gómez & Boicenco (2004) compiled the dinoflagellate taxa cited in the Black Sea. They, likewise, concluded that no taxon could be recognized as endemic.

Neoendemism

According to van der Spoel (1994), the continuity of the marine pelagic environment provides very limited scope for isolation creating different habitats. Endemicity is difficult to prove in microscopic organisms because they are not easily recognizable: distinctive morphological features are rare compared with higher plants and animals; and the field has been distinctly understudied. Based on new molecular tools, the genetic distances in several ribosomal genes (18S rRNA for deep evolutionary divergences) are used to delimit the species. When physical barriers separate populations, as in the semi-enclosed Mediterranean Sea, the geographical isolation is expected to develop the endemism associated with genetic divergence.

If it is assumed that no species survived the extreme environmental changes that occurred during the Messinian salinity crisis and the rapid re-inundation that followed, the neoendemic taxa that entered through the Strait of Gibraltar from the Atlantic Ocean had a maximum of 5.33 Ma to diverge in gene sequence from their Atlantic ancestors. The molecular clock approach has been applied recently to marine

dinoflagellates for the first time. John *et al.* (2003) estimated 23 Ma as the average time of origin of the *Alexandrium tamarense* species complex. Estimations based on the molecular clock approach should be considered very cautiously due to the difficulties in obtaining exact and comparable molecular clock rates for the non-protein-coding 16S gene, and other factors (Ayala, 1997). Nonetheless, according to the value reported by John *et al.* (2003), the 5.33 Ma after the re-inundation of Mediterranean Basin was insufficient for the speciation of dinoflagellates such as *Alexandrium* Halim.

Hydrographic circulation through the Strait of Gibraltar, with a strong surface inflow of Atlantic water, favours the introduction of Atlantic species (Gómez *et al.*, 2000). The Atlantic waters with a residence time of 80–100 years in the Mediterranean Basin could facilitate continuous exchange of plankton of Atlantic origin. This mechanism is more limited for non-free-swimming macroscopic or benthic species. This could explain the near absence of endemic dinoflagellate species in the Mediterranean compared with macroscopic organisms. The classic taxonomy based on morphological characters is insufficient for detecting morphologically similar, but distinct, forms in the Mediterranean Sea. Consequently, the occurrence of cryptic species cannot be discounted. The application of recent molecular techniques to the biogeography of the Mediterranean phytoplankton would contribute greatly to the clarification of these aspects of phytoplankton taxonomy.

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BIOSKETCH

Fernando Gómez has dedicated his research career to unravelling phytoplankton diversity and community structure in the Mediterranean Sea, particularly the Straits of Gibraltar and Ligurian Sea, the Eastern Atlantic, and the Northern, Equatorial and Southern Pacific. His favourite research topic is the taxonomy, ecology and biogeography of marine dinoflagellates. He is currently with the Protista & Mathematics Division of the Department of Zoology, Natural History Museum, London, UK, where he is investigating the morphological and molecular diversity of marine microplankton in European waters, with financial support from the European Commission's Marie Curie Intra-European Fellowship Scheme.

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