

Breeze conditions as a favoring mechanism of *Alexandrium taylori* blooms at a Mediterranean beach

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Abstract

A study of Santa Ponça Bay (Balearic Islands) was conducted during summer 2002 to understand further the processes controlling recurrent *Alexandrium taylori* blooms near the beach. These massive algal proliferations (10^6 cells L^{-1}) have become common in many anthropized pocket beaches of the Mediterranean during the summer season. Nearshore dissolved inorganic nutrient concentrations (DIN) are generally high near the shoreline (avg. DIN at $1.6 \mu M$), yet this factor alone is insufficient to explain harmful algal bloom (HAB) occurrences at some beaches and their absence in others. It is postulated that summer conditions, and particularly, the mild breeze conditions are key factors into understanding these nearshore blooms. The advantages of this coastal environment for a migrating dinoflagellate such as *A. taylori* are discussed. Resilience to undergo enhanced turbulence episodes, motility, day/night migration and a favorable current regime that produces shoreward transport at sea surface are regarded as concurrent mechanisms that lead to HAB generation and maintenance.

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1. Introduction

Understanding the circulation and water renewal rates of coastal waters is becoming an issue of key importance for many coastal managers. This is so, because the capacity of the coastal ecosystems to accept the impact of human activities highly relies on water flow patterns and residence time. Coastal currents are particularly critical in semi-enclosed areas, such as some Mediterranean tourist locations, where strong human pressure often concentrates around embayments and pocket beaches. The restrictions to water renewal imposed by the coastal morphology with their consequent

concentration of dissolved compounds, and the accumulation of floating debris and organisms result in loss of water quality.

Apart from the obvious direct economical impacts that the degradation of coastal water quality produces in the tourist sector, coastal and marine ecosystems are also affected. Most of these problems are enhanced during summer season when tourism occupation reaches its maximum (more than 10 times the winter population at specific sites) and when, owing to the mild weather conditions, hydrodynamic forcing is low. It is during this time of the year when problems related to the increased nutrient availability and low water renewal, such as oxygen reduction and harmful algal bloom (HAB) occurrence, arise at these locations.

The genus *Alexandrium* is the group of dinoflagellates which causes most HABs in Mediterranean coastal locations, and *Alexandrium taylori* is one of the noxious

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species (Garcés et al., 2000). The ability of *A. taylori* to produce and maintain elevated biomasses ($>10^5$ cell L^{-1}) provokes green–brown discoloration of the water during the summer months causing an evident deterioration in the quality of water for recreational uses. Although critical factors for bloom formation have been described for some species we have only a crude understanding of the mechanisms that promote and maintain harmful algal blooms.

Alexandrium outbreaks can be classified as (1) large-scale coastal blooms associated with major oceanographic processes such as shelf currents, tidal fronts, etc. (e.g. Franks and Anderson, 1992; Townsend et al., 2001) or (2) small-scale coastal blooms (Garcés et al., 1999). This second *Alexandrium* bloom model is the most commonly observed in the Mediterranean and is related to areas of restricted dynamism such as bays (Yamamoto and Seike, 2003), lagoons (Sorokin et al., 1996; Giacobbe et al., 1996), ports (Delgado et al., 1990) and estuaries. Blooms in these areas are very tightly linked in time and space environmental conditions (temperature, stratification, water renewal, etc.) that may act either dispersing the bloom or favoring cell growth and/or accumulation (Anderson, 1998).

To our knowledge, three western Mediterranean regions have been affected by summer blooms of this species: the Catalan Coast (NE Spain), the Balearic Islands and Sicily (Vulcano Island). In these regions, blooms concentrate in highly frequented bathing areas where there is evidence of blooms occurring every summer since the 1980s, with a temporal persistence of between 2 and 3 months. Although *Alexandrium taylori* is widely distributed in these regions, blooms develop at localized hot-spots. Understanding the specificities of these locations could be a way to gain inside into near-coast *A. taylori* massive occurrences.

This study explores the influence of summer breeze conditions in *Alexandrium taylori* bloom generation and maintenance in Paguera, an urban beach in the Bay of Santa Ponça (Mallorca, Spain). The location of the beach at the head of a sheltered Bay and the strong anthropogenic pressure exerted by the tourist industry settled in its vicinity make this beach the archetype of an *A. taylori* affected beach. This study is based on field observations and on numerical simulations with a 3-D hydrodynamic model which was used to understand circulation patterns that favor massive algal occurrence.

2. Materials and methods

2.1. Study site

The experiment was carried out in the Bay of Santa Ponça, a small embayment bay (about 3×4 km)

located on the southern coast of Mallorca (Balearic Islands). The bay is opened to the southwest where a depth of about 45 m is reached. The average depth is 11 m and the surface area 8.5 km². To the north a shallow embayment holds a sandy beach sustained by a groin on its western side (Peguera). The bathymetry of the area is shown in Fig. 1.

The meteorological conditions in Mallorca exhibit a strong seasonality. Storms are frequent during fall and winter, whereas breezes dominate during summer. Tides are typically mixed diurnal with a spring tidal range of less than 0.25 m (e.g. Tsimplis et al., 1995).

2.2. Moored instruments

The location of current moorings during the study is shown in Fig. 1. Vertical profiles of current velocities at 4 m depth intervals were measured at two locations (M1 and M2) with bottom mounted acoustic Doppler current profilers (1 MHz Nortek Aquadopp). The instruments were set to burst for 60 s every 10 min. Wind velocity, air temperature and atmospheric pressure were recorded at 20 min intervals on an Aanderaa weather station placed near the beach. Unfortunately, the station failed after 1 month of operation and the data had to be supplemented with records from Palma Airport supplied by INM (*Instituto Nacional de Meteorología*). Both records present a similar trend albeit with some differences that are discussed below.

2.3. Biological sampling

Alexandrium taylori bloom occurrence was monitored at three sampling stations along the beach during the development, maintenance, and end phases (May–September, 2002). Surface samples were obtained daily (over a series of 5 days) at two stations near the shoreline (St1, St2) and at a station (St3) located off the beach. The abundance of dinoflagellate species, inorganic nutrient concentration (Grasshoff et al., 1983), temperature and salinity were measured each time a water sample was withdrawn. Additionally, two HOBO loggers recorded temperature at 1.5 m depth semi-hourly, at St1 and St2. Samples for cell identification and quantification were fixated with lugol (1% final concentration), sedimented in 50 ml settling chambers and counted with an inverted microscope (Hasle, 1978).

The spatial distribution of *Alexandrium taylori* within the Bay was surveyed on 3 and 4 July 2002 afternoon (13–17 pm). Although, a number of stations throughout the bay were sampled (see Fig. 1), most of the offshore stations showed low ($>10^2$) or absence of *A. taylori* cells and thus, for the purpose of this paper, only the data from a section to distance of 3.2 km off the coast are considered. Vertical profiles of temperature, salinity and chlorophyll fluorescence were obtained with an SBE 19

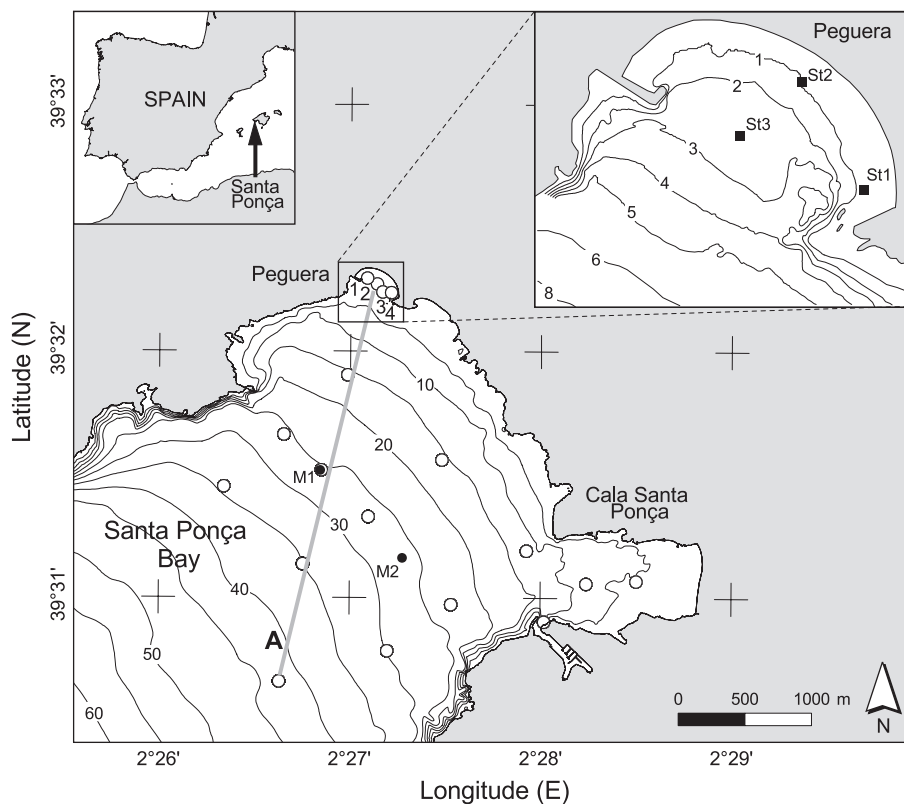


Fig. 1. Bathymetry (m) of Santa Ponça Bay showing the location of the moorings (M1 and M2), biological sampling stations (open circles) and the position of the onshore–offshore transect A.

plus CTD probe with attached Wetlabs fluorometer. Water samples for chlorophyll (Holm-Hansen et al., 1965), cell counts and nutrient analysis were taken at three depths (0, 3 and 10 m) with 5 l Niskin bottles.

A daily variation experiment of cell densities at the bloom maximum (when water discoloration occurred), was carried out at St1, and St3 between June 29th and 31st, 2001 to describe the short-time changes in the population. Water samples were withdrawn at time intervals of between 2 and 4 h for cell counts. During the same period, temperature was recorded with a moored temperature logger at 30-min intervals.

2.4. Hydrodynamic model

In order to investigate the effect of breeze on the circulation of Santa Ponça Bay a numerical circulation model has been implemented for the Bay. The algorithm selected is a linear, shallow water, sigma-coordinate, three-dimensional finite element model with spherical-polar extensions formulated in the frequency domain (FUNDY). The model solves the linearized 3-D shallow water equations, forced by tidal or other barotropic boundary conditions, wind and/or baroclinic pressure gradients. Conventional hydrostatic and Boussinesq approximations and Mellor and Yamada (1982) level 2.5 eddy viscosity closure with adjustments by Galperin

et al. (1988) and Blumberg et al. (1992) closure are employed. Solutions are obtained in the frequency domain; the limit of zero frequency represents the steady state. An older version of the model was successfully applied southern of Mallorca by Werner et al. (1993) to evaluate alongshelf circulation under different wind forcings. Details of the model are given by Lynch and Werner (1987), Lynch et al. (1992) and Greenberg et al. (1998).

The computational domain extends along the southern shelf of the island (Fig. 2). Discrete bathymetric and coastal boundary data were obtained from the nautical charts of the Instituto Hidrográfico de la Marina. Additional soundings in shallowest areas were obtained with a shipmounted Biosonics DE-4000 echosounder equipped with a 200 kHz transducer. A final bathymetry resolution of better than 50 m spacing was obtained throughout the inner shelf of the region of interest. The mesh contains 9282 elements, 5176 nodes and 11 levels in the vertical, extending along the southern Mallorcan shelf. Vertical levels are non-uniformly distributed to obtain maximum resolution near the surface and close to the bottom. Ocean boundary openings lie far from the area of interest and hence are unlikely to influence the circulation of the study site. Variable horizontal resolution is achieved with an unstructured mesh of conventional triangles.

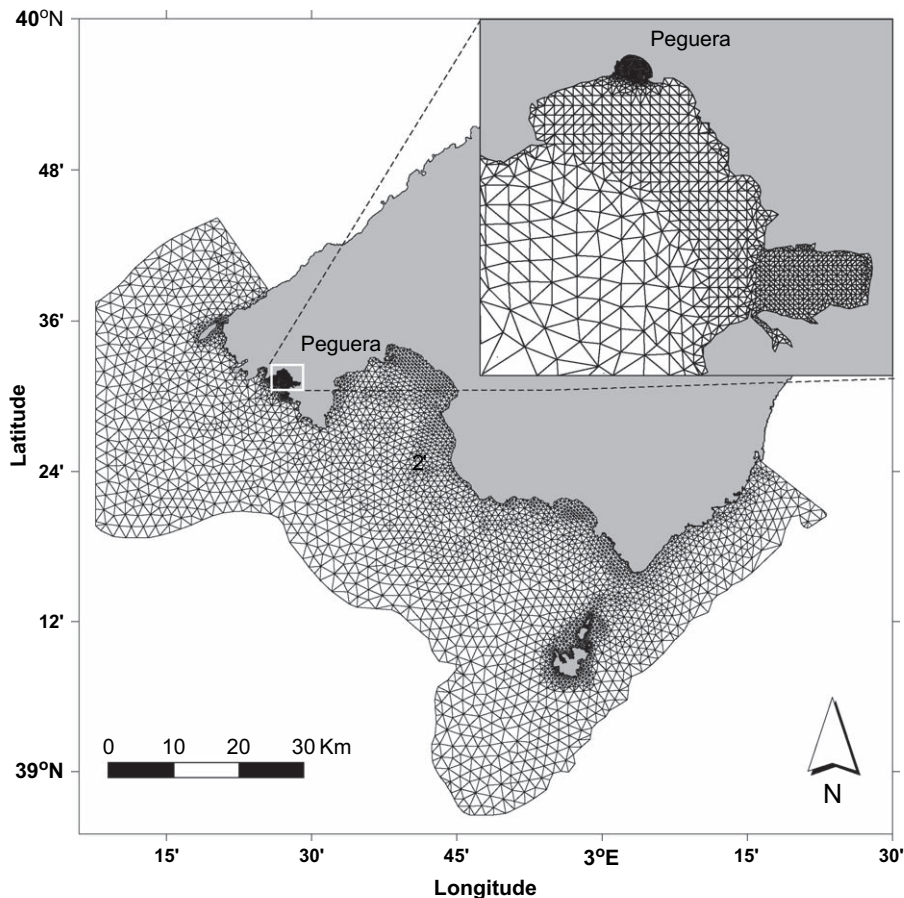


Fig. 2. Finite element grid used for the hydrodynamics and particle tracking simulations. The mesh contains 5176 nodes and 9282 elements. Maximum resolution at Peguera is approximately 25 m.

3. Experimental results

3.1. General summer conditions

Wind records from Palma Airport reveal the atmospheric conditions experienced in southern Mallorca during summer months (Fig. 3). A breeze regime with speeds rarely exceeding 6 m s^{-1} is the prevalent pattern during the summer season. This atmospheric circulation is a consequence of the contrasting thermal response of the land and the sea. Land tends to heat and cool more rapidly than sea surface and the consequent thermal difference generates sea breezes across the coast. This process reverses at night giving rise to an opposite circulation pattern, although with weaker intensity. This daily cycle has a clear 24 h signal in the wind velocity spectra. Sustained wind enhancements for periods of 1 or 2 days with N and NE components (locally called Tramontana winds) eventually occur, disrupting the summer breeze regime.

Average breeze condition values at Santa Ponça reflect the sinusoidal oscillation of the wind (Fig. 4). The flow is directed towards the coast from 9 am to 6:30 pm

(UT) with speeds increasing from 0 to $3.8 \pm 1.8 \text{ m s}^{-1}$ at 13:30, whereas the flow is reverse and weaker ($< 1 \text{ m s}^{-1}$) during the night. Sea breeze has a vector mean direction of $27 \pm 5^\circ$ whereas land breeze is directed towards $240 \pm 39^\circ$. Higher variability in land breeze direction may reflect disturbances produced by land topography at the measuring point. Winds at Palma Airport follow the same day/night pattern although, in this case, the diurnal cycle lasts for 2 h more and values above 6 m s^{-1} with an offset of 10° in the mean midday vector direction are reached.

Temperature, salinity and chlorophyll distribution along an onshore–offshore transect obtained at midday are shown in Fig. 5. The surface field is quite homogeneous for most of the bay, but two marked features are evidenced: (1) the presence of a thermocline intersecting the seabed at 25 m depth and (2) intense nearshore warming near the beach (up to 1.5°C). This temperature difference between nearshore and offshore waters is the result of diurnal heating near the beach. This difference reaches its maximum near midday and vanishes during night (not shown). Both temperature and salinity gradients are weaker at the intersection of

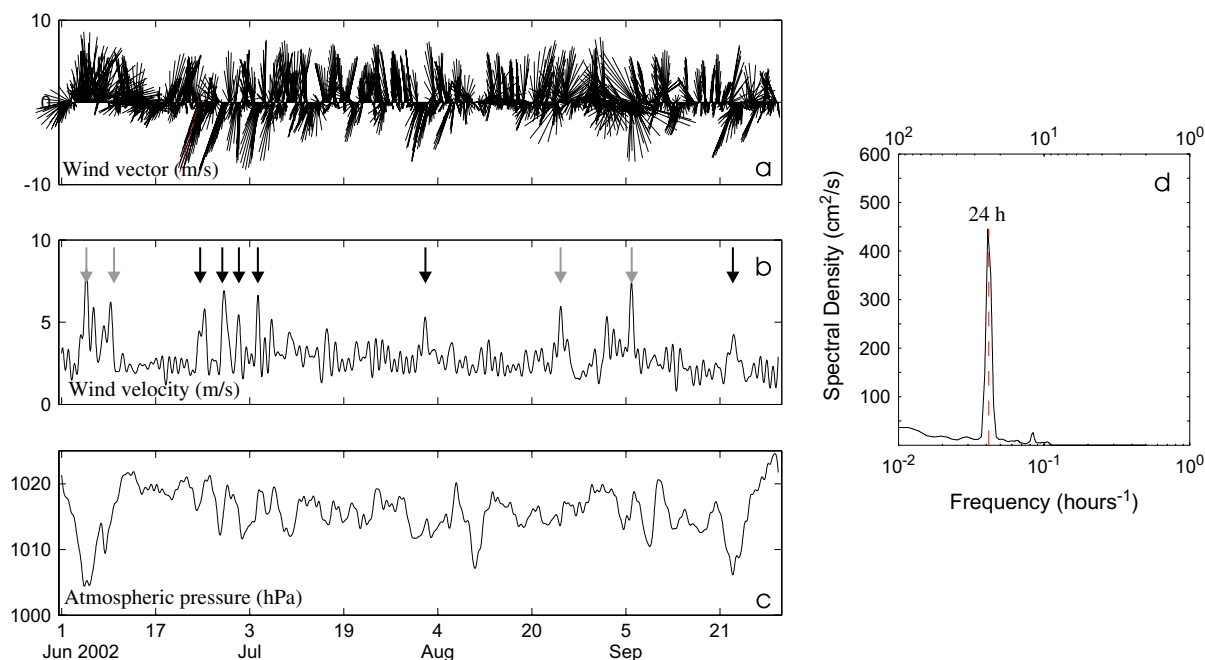


Fig. 3. Summer 2002 wind vector (a) low passed wind velocity (b) and atmospheric pressure (c). Wind vectors have been rotated 40° counter-clockwise. Episodes of Tramontana (NE) and winds from the SW are indicated with black and gray arrows, respectively. Wind speed spectral density (d) showing a clear 24 h peak.

the pycnocline with the seafloor suggesting a higher degree of mixing at this point. Chlorophyll displays shoreward enhancement reaching values $>0.4 \text{ mg m}^{-3}$ in the vicinity of the beach and a remarkable increase near the shoreline ($>5 \text{ mg m}^{-3}$) where summer DIN values average $1.6 \mu\text{M}$ (predominantly ammonia).

Records of beach (St1) and offshore (M1) temperatures near the bottom show similar low frequency variations, albeit the range is somewhat enhanced in the latter due to the presence of the thermocline (Fig. 6).

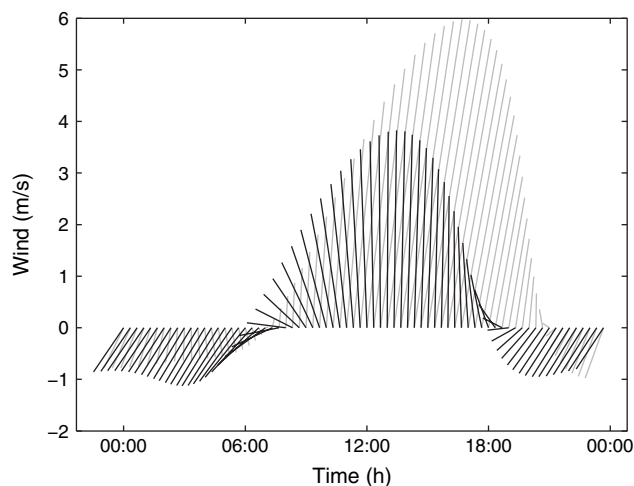


Fig. 4. Average sea breeze cycle at Santa Ponça (black) and Palma Airport (gray). Wind vectors have been rotated 27° counter-clockwise for convenience.

This similarity suggests that both systems (beach and bay) are influenced by the same general regime. Yet, at higher frequencies (periods <1 day), the registers present clear dissimilarities induced by diurnal warming in the nearshore record and by the thermocline oscillations in the near-bottom record. These differences are clearly revealed in the spectral analysis, which shows a clear peak at 24 h generated by diurnal heating and a secondary maximum at 12 h. Unlike the beach, the most energetic frequency of oscillation in the offshore temperature occurs at the local inertial frequency (18 h).

Surface (0–10 m) dissolved inorganic nitrate concentrations range from $0.10 \mu\text{M}$ at the offshore stations to $>0.6 \mu\text{M}$ near the beach (Fig. 7). Phosphate concentrations are more homogeneous, displaying average values of $0.07 \pm 0.01 \mu\text{M}$. Although *Alexandrium taylori* is present at most stations ($<100 \text{ cells L}^{-1}$), high abundances were only observed in the proximity of the beach (stations 1, 2, 3 and 4). These stations presented values ranging between 14×10^3 and $32 \times 10^3 \text{ cells L}^{-1}$.

3.2. Circulation patterns

Surface ADCP time series during breeze conditions are strongly correlated to wind records displaying a clear day/night pattern (Fig. 8). Maximum amplitudes of between 7 and 8 cm s^{-1} are reached at noon at both moorings. Complex vector correlation between M1 and M2 yields a value of 0.96 and a rotation angle of 10°. Major differences between both series occur at night;

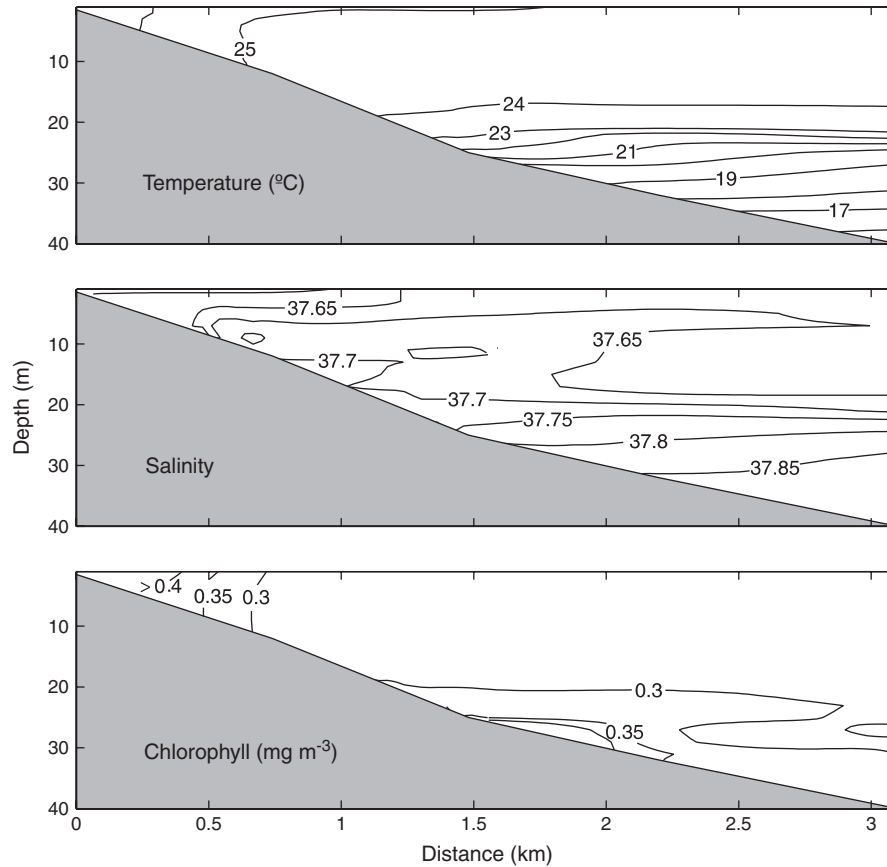


Fig. 5. Longitudinal distributions of temperature, salinity, and chlorophyll concentrations along transect A.

currents exceeding 5 cm s^{-1} are attained at M1 whereas a weaker flow ($<3 \text{ cm s}^{-1}$) is observed at M2.

Fig. 9 shows the progressive vector plots of currents measured at M1 and M2. Both moorings show a consistent net northwestward flow of 6 cm s^{-1} . This average flow is disrupted by NE–SW oscillations induced by the breeze regime. Conversely, near the bottom, both registers diverge considerably. A westward flow is observed at M1 whereas a northeastward flow is maintained at M2, suggesting cyclonic circulation.

Spectral analysis of the current meter time series shows that, near the surface, the signal peaks at diurnal and semidiurnal frequencies (Fig. 10). The diurnal signal appears even if tide is removed by performing a harmonic analysis of the series and subsequently subtracting the reconstructed tidal series. Thereby, the diurnal peak can be attributed to breeze induced oscillations. In contrast, near the bottom, the inertial signal (about 17 h) acquires greater relevance. It should be reminded that the near-bottom bin is coincident with the

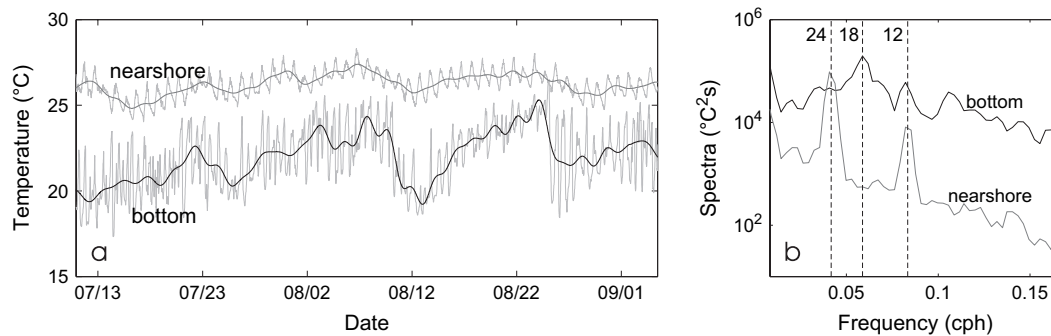


Fig. 6. (a) Time series of nearshore and near-bottom (M1) temperatures. (b) Spectra of the same registers. Dotted lines in the figure indicate diurnal, inertial, and principal lunar M2 frequencies.

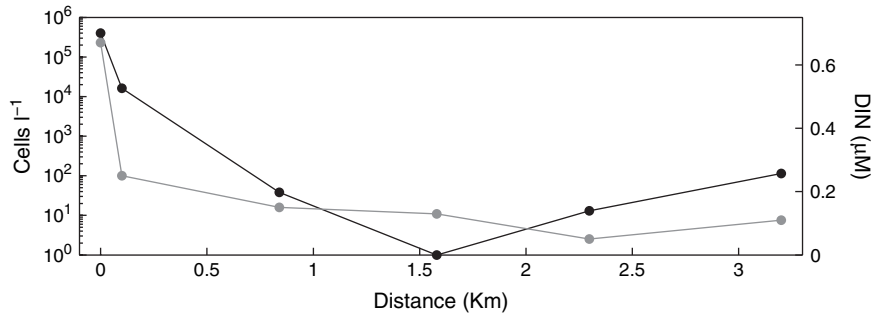


Fig. 7. Average cell abundance (black) and dissolved inorganic nitrate (gray) concentration (0–10 m were possible) along onshore–offshore transect A.

thermocline depth and, thus, it is representative of the thermocline dynamics. Indeed, these inertial oscillations are consistent with temperature variation at this level, as mentioned before.

3.3. *Alexandrium taylori* bloom

Surface cell densities at the beach (mean of St1 and St2) reveal the evolution of the bloom (Fig. 11). During June an exponential growth phase, when cells increased between 100 and 1000 cell L⁻¹, was observed. This stage was followed by a stationary phase (July–August) with values of between 10⁴ and 10⁶ cell L⁻¹, and an end phase, beginning in early September, where strong fluctuations were detected. Peak cell density values of

4×10^6 cell L⁻¹ (31 August) yielded chlorophyll values of 22 mg m⁻³. The *Alexandrium taylori* evolution pattern was paralleled by temperature variation. Temperature increased from 20 °C in May, reaching values above 26 °C in July. During the stationary phase, temperatures were relatively stable, decreasing in late September.

Regarding spatial variability, *Alexandrium taylori* cell counts were always higher near the shore (St1 and St2) with St3 reflecting the transition between the bay and near beach conditions. Values at this station rarely exceeded 10⁴ cells L⁻¹, which is two orders of magnitude less than nearshore counts, and only equalled inshore occasionally (July, 16 and August, 13 and from the beginning of September) when nearshore cell densities

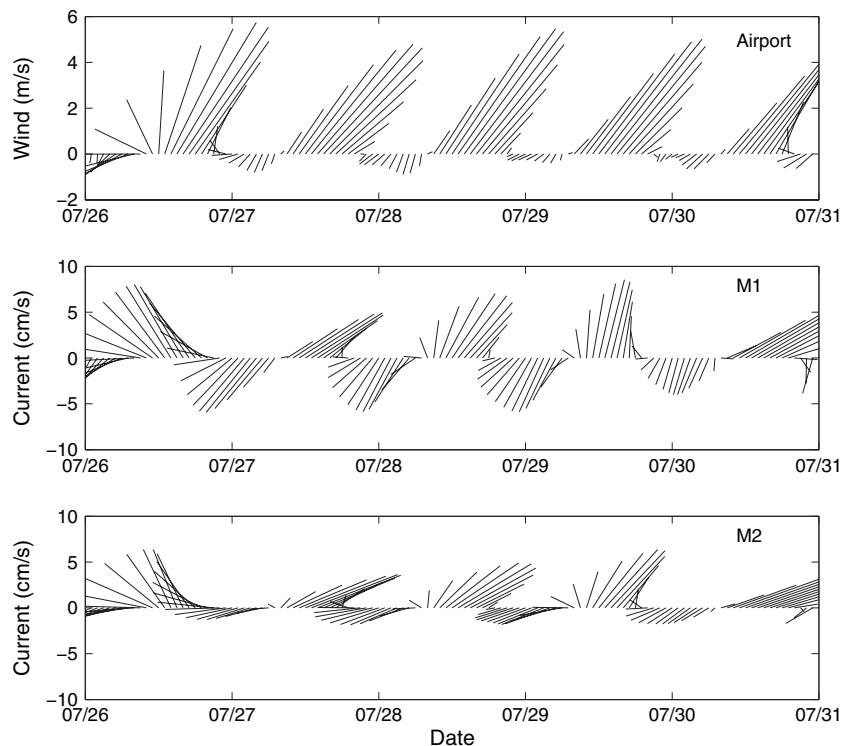


Fig. 8. Wind and surface currents (M1 and M2) stick diagrams during a 5-day breeze episode (hourly data).

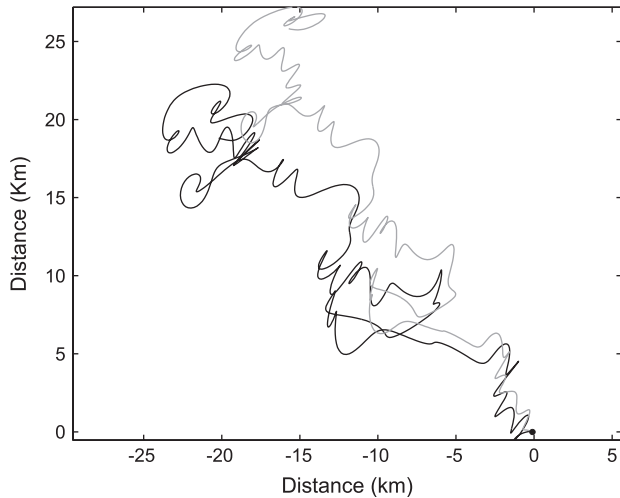


Fig. 9. Progressive vector plots of currents at M1 (black) and M2 (gray) for a selected breeze period.

decrease (10^4 cells L^{-1}). Cell abundances at St1 and St2 were similar, although higher variability was observed in the latter, particularly in the exponential phase when the bloom was restricted to a small patch. Cells in St3 were first detected in July, 1 month later, when cell densities in near shore stations rose to 10^5 cell L^{-1} . *Alexandrium taylori* was the most abundant cell in these waters. However, other dinoflagellates such as *Gymnodinium* sp. were also abundant (10^3 – 10^4 cell L^{-1}) and followed the same temporal trend as *A. taylori*.

Comparison between cell abundances and daily averaged wind intensity reveals a correspondence between certain enhanced wind episodes and decrease in surface cell abundances (Fig. 11b). This is particularly evident in the exponential and end phases, when southerly winds and swells with periods above 7.5 s took place.

3.4. Daily variations

Daily cell abundance variations at St1 are shown in Fig. 12. Vegetative cells reached maximum surface

abundances of between 10^5 and 10^6 cells L^{-1} in the afternoon and diminished during the night. Minimum values, measured at dawn, show that approximately 1% of the cells remains at surface. This value is of the same order of magnitude of the cells measured in Santa Ponça bay, off the beach. Between June 27th and 28th the daily pattern seems to be disturbed by an episode of wind intensification and a consequent temperature decrease. Cell abundances rapidly decreased to minimum values. Even though the breeze regime re-established at noon, the pattern was not re-established until the next day. During the experiment, values at St3 (not shown) were on average 65% lower than the ones observed at St1 but they equalized during the land breeze intensification of July 1. This suggests that, although advection can be occasionally important to explain daily variations, most of the observed variability can be attributed to vertical migration near the beach.

3.5. Modeling results

Wind-forced model simulations were performed for average breeze and tramontana conditions. The oscillatory nature of breeze conditions was simulated by a periodic sinusoidal signal of frequency $1/24$ h^{-1} (Werner et al., 1993) and tramontana forcing was assumed constant in time. Tidal forcing was not considered since preliminary tests showed that tidal currents contribute in a small proportion to the general circulation patterns.

Breeze-induced surface circulation patterns in Santa Ponça Bay show that water near the free surface is driven by the dominant wind shear stress and, at midday, is transported towards the coast in the direction of the wind (Fig. 13). Current velocities typically range from 5 to 6 $cm\ s^{-1}$, although clearly decrease near the coast. In the detailed figure of nearshore current intensification, this is readily observed. At night, the flow is in the opposite direction. The response of the surface currents displays a southward flow at the center of the bay, and progressive clockwise deflection of the currents off the bay following the wind stress direction.

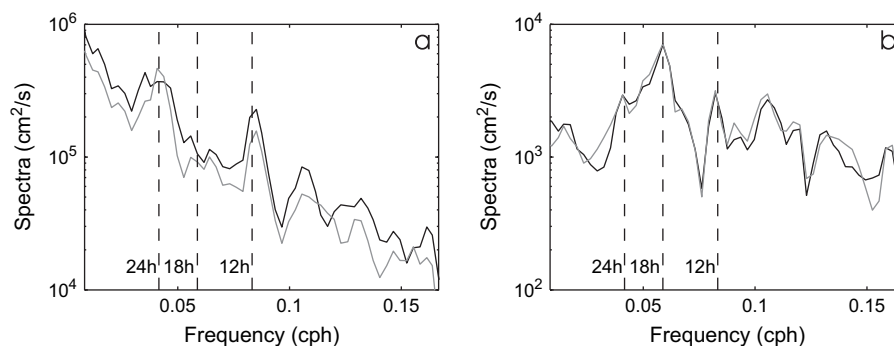


Fig. 10. Near surface (a) and bottom (b) current spectra at M1 (black) and M2 (gray). Dashed lines indicate the periods of 24, 18 and 12 h.

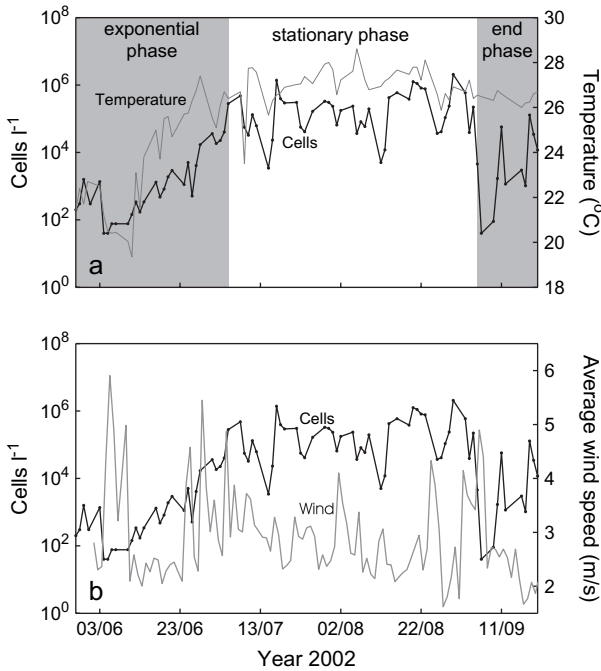


Fig. 11. Variation of cell abundance (black) and temperature (gray) near the beach during summer 2002 (a) and comparison of the evolution of cell abundance (black) and the daily averaged wind speed (b).

Simulations under tramontana forcing show a similar pattern to that under land breeze, although with a threefold enhancement of current velocities.

A particle-based model was used to estimate the areas where accumulation is favored along the coast. Fig. 14 shows the tracks of two such particles released at the surface on the offshore side of the bay. In this experiment, no allowance was made for sinking, dissolution or aggregation. Results show that, under breeze conditions, the particles present showed NE–SW oscillations following the daily breeze cycle and a consistent northeastward drift that tends to accumulate them in the vicinity of

Peguera. During tramontana conditions, particles released near the beach are directed to the southwest, requiring several days, under these conditions, to reach offshore waters. However, sustained NE forcing rarely occurs in summer.

4. Discussion

In the last decades, urbanization and intensive recreational use of the beaches have resulted in a dramatic increase of point and non-point nutrient sources along the coast, which result in massive algal bloom occurrence. This relationship between cultural over-enrichment and HABs event around the world (from which near beach *Alexandrium taylori* blooms are a further evidence), has been thoroughly reviewed by Hallegraeff (1993), Smayda (1997), Zingone and Enevoldsen (2000) and Anderson et al. (2002) among others. In spite of the generalized near-coast enrichment, dinoflagellate blooms are not ubiquitous along the coast. They can occur at the less exposed sites of pocket beaches and in shallowest waters (<3 m), where their swimming behavior allows for the maintenance of critical patches (Kierstead and Slobodkin, 1953), even at early bloom stages. The intricate coastal geomorphology of the Balearic Islands, with numerous inlets and pocket beaches provides these ideal conditions for HAB development. This characteristic is common to the other Mediterranean regions where *A. taylori* blooms have been reported (Giacobbe et al., 1996; Garcés et al., 1998; Penna et al., 2000).

Clearly, summer irradiance and temperature are also relevant for bloom dynamics, but photosynthetically available radiation in these nearshore waters exceeds *Alexandrium taylori* requirements during most of the year, and should only be limiting during sediment resuspension episodes, or at high cell densities when self

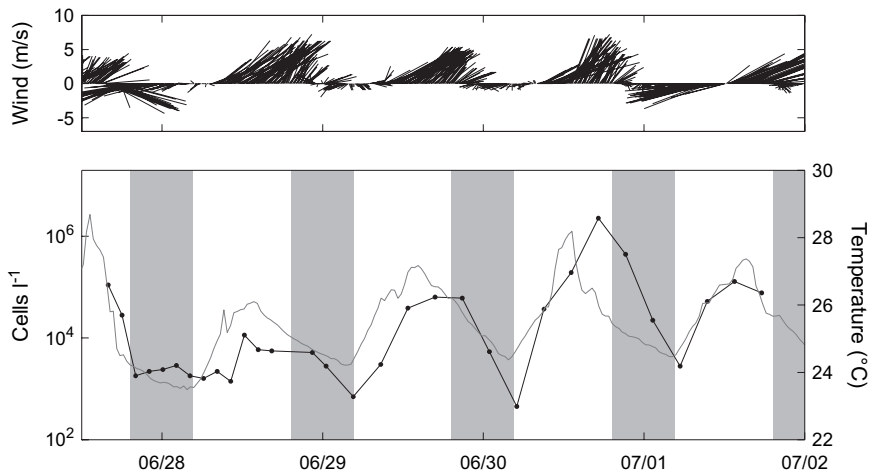


Fig. 12. Daily variations of wind, cell and temperature during breeze regime at St1.

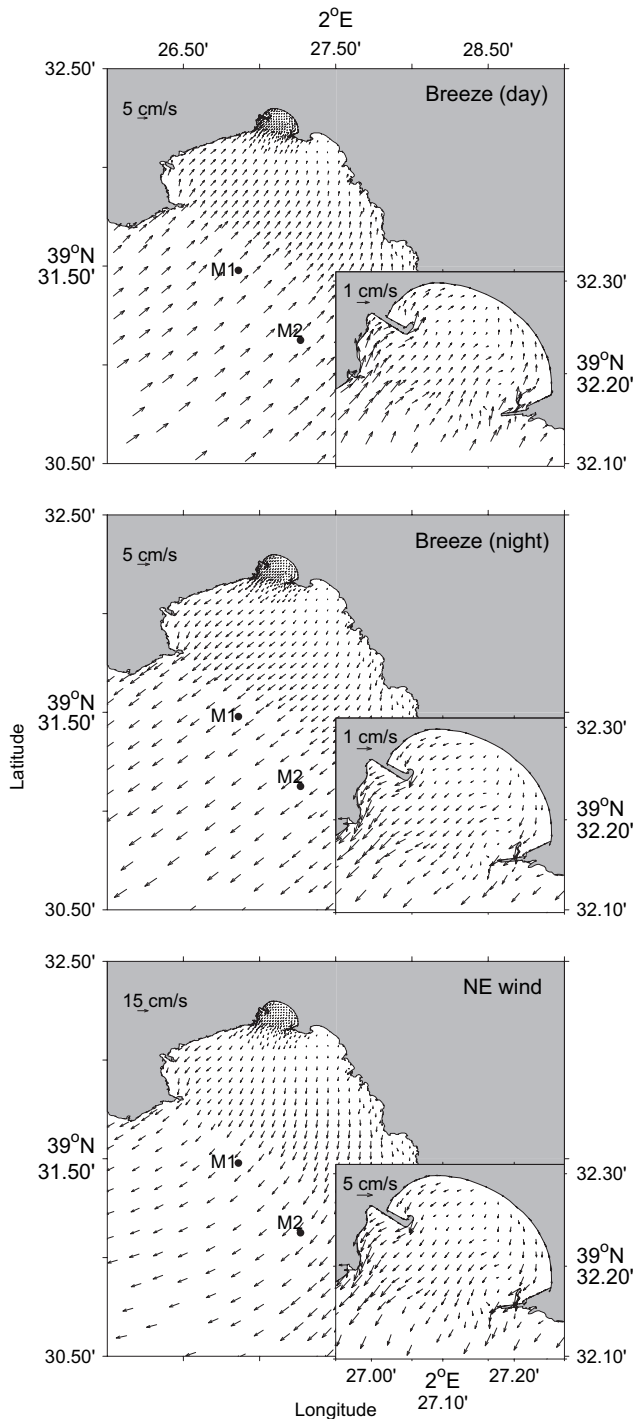


Fig. 13. Simulation of surface currents under maximum sea breeze, land breeze and tramontana situations.

shading becomes important. Turbidity is a factor that influences phytoplankton bloom dynamics and its spatial variability in shallow waters (May et al., 2003). Wave induced resuspension episodes are not rare near the beach, but low mud content and the medium granulometry of the beach ($D_{50} \sim 0.35$ mm) benefit rapid transparency recovery. In the case of temperature, we believe that it establishes a temporal frame in which

the bloom may develop (from May to October). Other *Alexandrium* species are not uncommon in the plankton during the winter in the Mediterranean (Vila et al., 2001), but this is not the case of *A. taylori* since vegetative cells have never been recorded out of the seasonal bloom occurrence. This fact, and evidence of cell aggregation in areas exposed to intense diurnal warming, suggests a thermophilic behavior of *A. taylori* cells.

The data presented here indicate the importance of summer breeze forcing and coastal circulation patterns in determining the occurrence and persistence of near-coast massive dinoflagellate blooms. The origin of massive algal growths has been generally linked to increased nearshore inorganic (Riegman, 1998) and organic nutrient loads (Carlsson and Granéli, 1998) and, possibly, to the presence of annual cysts in the sediment. However, nutrient injection is a necessary but not sufficient condition. In the present case, relatively low shear environment, shoreward transport, and reduced flushing rates are essential for this type of persistent bloom manifestation.

The inverse relationship between wind intensity and bloom formation and maintenance has been previously documented (e.g. Pollinger et al., 1988; Yamamoto et al., 2002). Pollinger and Zemel (1981) observed that winds above 3.5 m s^{-1} , similar to the average midday wind speed at Santa Ponça (3.8 m s^{-1}), disrupted dinoflagellate blooms in lake Kinneret. Dinoflagellate growth, motility, mortality and other aspects of cell biology are known to be affected by enhanced shear (White, 1976; Thomas and Gibson, 1990; Berdalet, 1992; Thomas et al., 1995; Juhl et al., 2000; Zirbel et al., 2000; Juhl and Latz, 2002). Not surprisingly, our data show that most noticeable cell abundance variations occur under the combination of enhanced winds and swells. However, the thresholds for the appearance of these negative effects are species specific (e.g. Sullivan and Swift, 2003) and, recently, it is a question into review (Smayda, 2000, 2002). Our results demonstrate that the *Alexandrium taylori* population is not severely affected by enhanced wind episodes, at least in the maintenance phase. In the nearshore zone, an intrinsically turbulent environment, this tolerance to eventual increased shear conditions is an ecological advantage that could explain the success of *A. taylori* to the detriment of other dinoflagellate species.

As mentioned before, the effect of breeze is not restricted to the turbulence issue. Coastal circulation aspects are a key factor for bloom occurrence. Breeze forced coastal flow within the bay tends to advect offshore cells towards the beach, impeding cell loss to open waters and allowing for allochthonous cell seeding near the beach. The prevailing low current velocities and the presence of near shore recirculation patterns induced by the beach geomorphology facilitate cell accumulation. Furthermore, as depicted in the daily cell density

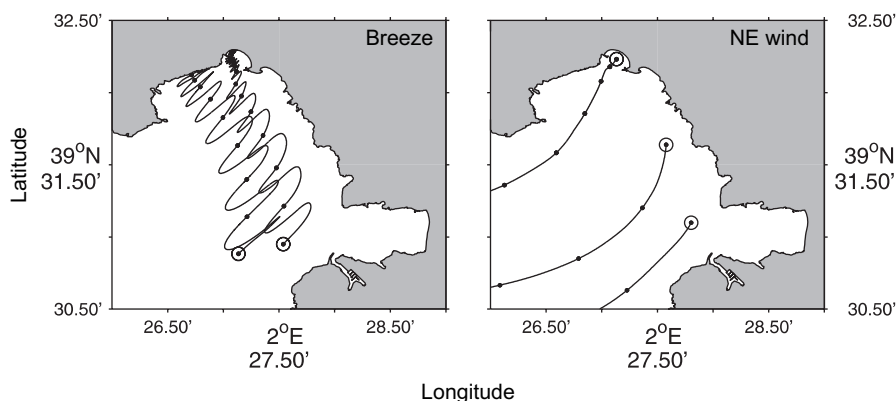


Fig. 14. Passive tracer's trajectories under breeze and tramontana forcing. Dots indicate the position every 24 h.

variation, the tight coupling between the vertical migration patterns and the wind (and current) regime further promotes accumulation in shallow waters. Cells are most abundant in the water column during sea breeze and settle when the flow reverses at night, minimizing advective losses. Settled cell resuspension at night is unlikely due to the weak wind forcing and to the small fetch that impedes significant wave formation. Even so, a stock of 10^3 cells L^{-1} remains unsettled at night, which is comparable with the values observed off the beach. This suggests that part of this unsettled stock would be advected to the outer bay seeding nearby beaches. However, surface water net transport, under breeze forcing, is directed towards the beach and, hence, mitigates cell dispersal, facilitating the eventual reincorporation of these cells to the near beach dynamics.

Shoreward transport could explain partially population recovery after some adverse situations. For example, while the population loss of June 4th, during the exponential phase, could be explained by sustained cellular growth rates of 0.3 day^{-1} , which agrees with previously reported values (Garcés et al., 1998), the rapid population recovery (2–4 days) requires growth rates exceeding reported maximum values for dinoflagellates (Smayda, 1997). These events must entail other processes such as recruitment of temporary cysts from the sediment (Garcés et al., 2002) and reincorporation of previously dispersed cells to the near beach stock, as suggested by our particle simulations.

In conclusion, the nearshore environment of intensively anthropized Mediterranean coasts provides a nutrient-rich environment for massive bloom development. Despite the fact that only the most protected pocket beaches have shown evidences of this phenomenon, this nearshore environment is relatively turbulent and exhibits low turbidity when compared to other semi-enclosed systems such as ports and lagoons. Shorewards coastal flow and coupling between physical forces and biological strategies (vertical migration) are critical for reducing population loss rates. Moreover, low water renewal benefits nutrient availability and,

possibly, certain position maintenance for species with swimming ability which enables them to avoid being washed out to the beach.

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References

- Anderson, D.M., 1998. Bloom dynamics of toxic *Alexandrium* species in the northwestern U.S. *Limnology and Oceanography* 42, 1009–1022.
- Anderson, D.M., Glibert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. *Estuaries* 25, 704–726.
- Berdalet, E., 1992. Effects of turbulence on the marine dinoflagellate *Gymnodinium nelsonii*. *Journal of Phycology* 28, 267–272.
- Blumberg, A.F., Galperin, B., O'Connor, D.J., 1992. Modeling vertical structure of open-channel flows. *ASCE Journal of Hydraulic Engineering* 118, 1119–1134.
- Carlsson, P., Granéli, E., 1998. Utilization of dissolved organic matter (DOM) by phytoplankton, including harmful species. In: Anderson, D.A., Cembella, A.D., Hallegraeff, G.M. (Eds.), *Physiological Ecology of Harmful Algal Blooms*. Springer-Verlag, Berlin, Heidelberg, pp. 509–524.
- Delgado, M., Estrada, M., Camp, J., Fernandez, J.V., Lleti, C., 1990. Development of a toxic *Alexandrium minutum* Halim (Dinophyceae) bloom in the harbour of San Carles de la Rapita (Ebro Delta, northwestern Mediterranean). *Scientia Marina* 54, 1–7.

- Franks, P.J.S., Anderson, D.M., 1992. Alongshore transport of a toxic phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the Gulf of Maine. *Marine Biology* 112, 153–164.
- Galperin, B., Kantha, L.H., Hassid, S., Rosati, A., 1988. A quasi-equilibrium turbulent energy model for geophysical flows. *Journal of Atmospheric Science* 45, 55–62.
- Garcés, E., Delgado, M., Maso, M., Camp, J., 1998. Life history and in situ growth rates of *Alexandrium taylori* (Dinophyceae, Pyrrophyta). *Journal of Phycology* 34, 880–887.
- Garcés, E., Maso, M., Camp, J., 1999. A recurrent and localized dinoflagellate bloom in a Mediterranean beach. *Journal of Plankton Research* 21, 2373–2391.
- Garcés, E., Masó, M., Vila, M., Camp, J., 2000. HABs events in the Mediterranean Sea: are they increasing? A case study the last decade in the NW Mediterranean and the genus *Alexandrium*. *Harmful Algal News* 20, 1–11.
- Garcés, E., Maso, M., Camp, J., 2002. Role of temporary cysts in the population dynamics of *Alexandrium taylori* (Dinophyceae). *Journal of Plankton Research* 24, 681–686.
- Giacobbe, M.G., Oliva, F.D., Maimone, G., 1996. Environmental factors and seasonal occurrence of the dinoflagellate *Alexandrium minutum*, a PSP potential producer, in a Mediterranean lagoon. *Estuarine, Coastal and Shelf Science* 42, 539–549.
- Grasshoff, K., Ehrhardt, M., Kremling, K., 1983. *Methods of Sea Water Analysis*. Verlag Chemie, Germany, 174 pp.
- Greenberg, D.A., Werner, F.E., Lynch, D.R., 1998. A diagnostic finite element ocean circulation model in spherical-polar coordinates. *Journal Atmospheric Oceanic Technology* 15, 942–958.
- Hallegraeff, G.M., 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32, 79–99.
- Hasle, G.R., 1978. The inverted microscope method. In: Sournia, A. (Ed.), *Phytoplankton Manual*. UNESCO, Paris, pp. 88–96.
- Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., Strickland, J.D.H., 1965. Fluorometric determination of chlorophyll. *Journal du Conseil Permanent International pour L'Exploration de la Mer* 30, 3–15.
- Juhl, A.R., Latz, M.I., 2002. Mechanisms of fluid shear-induced inhibition of population growth in a red-tide dinoflagellate. *Journal of Phycology* 38, 683–694.
- Juhl, A.R., Velazquez, V., Latz, M.I., 2000. Effect of growth conditions on flow-induced inhibition of population growth of a red-tide dinoflagellate. *Limnology and Oceanography* 45, 905–915.
- Kierstead, H., Slobodkin, L.B., 1953. The size of water masses containing plankton blooms. *Journal of Marine Research* 12, 141–147.
- Lynch, D.R., Werner, F.E., 1987. Three-dimensional hydrodynamics on finite elements. Part I: linearized harmonic model. *International Journal of Numerical Methods in Fluids* 7, 871–909.
- Lynch, D.R., Werner, F.E., Greenberg, D.A., Loder, J.W., 1992. Diagnostic model for baroclinic, wind-driven and tidal circulation in shallow seas. *Continental Shelf Research* 12, 37–64.
- May, C.L., Koseff, J.R., Lucas, L.V., Cloern, J.E., Schoellhamer, D.H., 2003. Effects of spatial and temporal variability of turbidity on phytoplankton blooms. *Marine Ecology Progress Series* 254, 111–128.
- Mellor, G.L., Yamada, T., 1982. Development of a turbulence closure model for geophysical fluid problems. *Reviews of Geophysics Space Physics* 20, 851–875.
- Penna, A., Giacobbe, M., Andreoni, F., Garcés, E., Berluti, S., Penna, N., Magnani, M., 2000. Molecular characterization of Mediterranean isolates of the HAB dinoflagellate *Alexandrium taylori*: a preliminary intra- and interspecies analysis. In: Hallegraeff, G.M., Blackburn, S.I., Bolch, C.J., Lewis, R.J. (Eds.), *Harmful Algal Blooms 2000*. UNESCO, Paris, pp. 218–221.
- Pollinger, U., Zemel, E., 1981. In-situ and experimental evidence of the influence of turbulence on cell division processes of *Peridinium cinctum* forma *Westii* (Lemm.) Lefevre. *British Phycological Journal* 16, 281–287.
- Pollinger, U., Berman, T., Kaplan, B., Scharf, D., 1988. Lake Kinneret phytoplankton: response to N and P enrichments in experiments and in nature. *Hydrobiologia* 166, 65–75.
- Riegman, R., 1998. Species composition of harmful algal blooms in relation to macronutrient dynamics. In: Anderson, D.A., Cembella, A.D., Hallegraeff, G.M. (Eds.), *Physiological Ecology of Harmful Algal Blooms*. Springer-Verlag, Berlin, Heidelberg, pp. 475–488.
- Smayda, T.J., 1997. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnology and Oceanography* 42, 1137–1153.
- Smayda, T.J., 2000. Ecological features of harmful algal blooms in coastal upwelling ecosystems. *South African Journal of Marine Science* 22, 219–253.
- Smayda, T.J., 2002. Turbulence watermass stratification and harmful algal blooms: an alternative view and frontal zones as “pelagic seed banks”. *Harmful Algae* 1, 95–112.
- Sorokin, Y.U.I., Sorokin, P.Y.U., Ravagnan, G., 1996. On an extremely dense bloom of the dinoflagellate *Alexandrium tamarense* in lagoons of the Po river delta: impact on the environment. *Journal of Sea Research* 34, 251–255.
- Sullivan, J.M., Swift, E., 2003. Effects of small-scale turbulence on net growth rate and size of ten species of marine dinoflagellates. *Journal of Phycology* 39, 83–94.
- Thomas, W.H., Gibson, C.H., 1990. Quantified small-scale turbulence inhibits a red tide dinoflagellate *Gonyaulax polyedra* Stein. *Deep Sea Research* 37, 1583–1593.
- Thomas, W.H., Vernet, M., Gibson, C.H., 1995. Effects of small-scale turbulence on photosynthesis, pigmentation, cell division, and cell size in the marine dinoflagellate *Gonyaulax polyedra* (Dinophyceae). *Journal of Phycology* 31, 50–59.
- Townsend, D.W., Pettigrew, N.R., Thomas, A.C., 2001. Offshore blooms of the red tide dinoflagellate, *Alexandrium* sp., in the Gulf of Maine. *Continental Shelf Research* 21, 347–369.
- Tsimplis, M.N., Proctor, R., Father, R.A., 1995. A two-dimensional tidal model for the Mediterranean Sea. *Journal of Geophysical Research Oceans* 100, 16223–16239.
- Vila, M., Camp, J., Garcés, E., Maso, M., Delgado, M., 2001. High resolution spatio-temporal detection of potentially harmful dinoflagellates in confined waters of the NW Mediterranean. *Journal of Plankton Research* 23, 497–514.
- Werner, F.E., Viúdez, A., Tintoré, J., 1993. An exploratory numerical study of the currents off the southern coast of Mallorca including the Cabrera Island complex. *Journal Marine Systems* 4, 45–66.
- White, A.W., 1976. Growth inhibition caused by turbulence in the toxic marine dinoflagellate *Gonyaulax excavata*. *Journal of the Fisheries Research Board of Canada* 33, 2598–2602.
- Yamamoto, T., Hashimoto, T., Tarutani, K., Kotani, Y., 2002. Effects of winds, tides and river water runoff on the formation and disappearance of the *Alexandrium tamarense* bloom in Hiroshima Bay, Japan. *Harmful Algae* 1, 301–312.
- Yamamoto, T., Seike, T., 2003. Modelling the population dynamics of the toxic dinoflagellate *Alexandrium tamarense* in Hiroshima Bay, Japan. II. Sensitivity to physical and biological parameters. *Journal of Plankton Research* 25, 63–81.
- Zingone, A., Enevoldsen, H.O., 2000. The diversity of harmful algal blooms: a challenge for science and management. *Ocean and Coastal Management* 43, 725–748.
- Zirbel, M.J., Veron, F., Latz, M.I., 2000. The reversible effect of flow on the morphology of *Ceratocorys horrida* (Peridinales, Dinophyta). *Journal of Phycology* 36, 46–58.