

Coupling planktonic and benthic shifts during a bloom of *Alexandrium catenella* in southern Chile: Implications for bloom dynamics and recurrence

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ABSTRACT

Cell abundances and distributions of *Alexandrium catenella* resting cysts in recent sediments were studied along time at two locations in the Chilean Inland Sea exposed to different oceanographic conditions: Low Bay, which is much more open to the ocean than the more interior and protected Ovalada Island. The bloom began in interior areas but maximum cyst concentrations were recorded in locations more open to the ocean, at the end of the Moraleda channel. Our results showed a time lapse of around 3 months from the bloom peak (planktonic population) until the number of resting cysts in the sediments reached a maximum. Three months later, less than 10% of the *A. catenella* cysts remained in the sediments. Maximum cyst numbers in the water column occurred one month after the planktonic peak, when no cells were present. The dinoflagellate assemblage at both study sites was dominated by heterotrophic cysts, except during the *A. catenella* bloom. CCA analyses of species composition and environmental factors indicated that the frequency of *A. catenella* blooms was associated with low temperatures, but not with salinity, chlorophyll *a* concentration, and predator presence (measured as clam biomass). However, resting cyst distribution was only related to cell abundance and location. The occurrence of *A. catenella* cysts was also associated with that of cysts from the toxic species *Protoceratium reticulatum*. By shedding light on the ecological requirements of *A. catenella* blooms, our observations support the relevance of encystment as a mechanism of bloom termination and show a very fast depletion of cysts from the sediments (<3 months), which suggest a small role for resting cyst deposits in the recurrence of *A. catenella* blooms in this area.

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1. Introduction

Dinoflagellates are best known as the source of dense and often toxic blooms, with species belonging to the genus *Alexandrium* causing serious episodes of paralytic shellfish poisoning (PSP). In South America, PSP has been recognized as an important public health risk for over a century (Hallegraeff, 1993; Balech, 1995; Lagos, 2003).

The sexual life cycle of *Alexandrium* species includes a dormant benthic stage (resting cyst). A role for benthic cysts has been cited in species dispersion, resistance to unfavorable conditions, population resilience through sexual recombination, and bloom onset and termination (Anderson et al., 1982; Anderson, 1984; Garcés et al., 1999; McGillicuddy et al., 2003). Moreover, given that the toxicity of resting cysts can be higher than that of vegetative cells, resting cyst formation must be taken into account when analyzing the possible effects of a bloom on human health (Dale et al., 1978; Lirdwitayaprasit et al., 1990; Oshima et al., 1992). The roles played by resting cysts in the life cycle and ecology of dinoflagellate species can be very different depending on the species. For example, the life cycles and encystment strategies of *Alexandrium* species are both complex and species-specific

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(for e.g. Figueroa et al., 2006, 2008). Thus, the current approach to the study of dinoflagellate ecology is to reconsider previous general assumptions, by specifically investigating each species.

Exogenous (environmental) factors mainly affect the timing and success of germination whereas endogenous (physiological) factors regulate the germination of resting cysts and determine whether this stage is involved in the short- or long-term survival of the species or serves as a bloom maintenance mechanism (see for e.g. the review by Bravo and Figueroa, 2014, and references therein). Local hydrographic and environmental factors greatly affect the strength and timing of sexual induction, and therefore the success of encystment and germination, while hydrodynamic processes determine the location of cyst deposits (Anderson et al., 2005; Keafer et al., 2005; McGillicuddy et al., 2005; He et al., 2008). Sexual events are known to depend on nutrient levels (e.g. Anderson, 1998; Ellegaard et al., 1998; Figueroa et al., 2005) and the photoperiod (Nuzzo and Montresor, 1999; Sgroso et al., 2001), but also on the mating system of the species (Kremp, 2013) and the genetic composition of the bloom (Dia et al., 2014). Within the genus *Alexandrium*, the dormancy requirements of *Alexandrium tamarense* cysts differ between deep water and shallow coastal environments (Anderson and Keafer, 1987; Matrai et al., 2005). In *Alexandrium catenella*, dormancy periods are highly variable, ranging from 28 to 97 days (Yoshimatsu, 1984; Hallegraeff et al., 1998). In Mediterranean populations of this species, they are characterized by a gradual rather than a synchronous pattern of germination (Figueroa et al., 2006) that allows for rapid cycling between benthic and planktonic stages (Hallegraeff et al., 1998).

Alexandrium catenella (Dale, 1983) is also an important causative agent of PSP in southern Chile, where it was found for the first time in 1972, in the Magallanes region (Guzmán et al., 1975). Since this report, the intensity and expansion of *A. catenella* outbreaks in Chile have increased (Guzmán et al., 2002; Molinet et al., 2003), with detrimental effects on human health and severely limiting economically important aquaculture activity in the region, which is based on shellfish production (Campodónico et al., 1995). The

most recent *A. catenella* bloom, at the end of the austral summer (February–March) of 2009, was one of the most significant with respect to geographic extent and cell density, which in the Aysén region reached up to 1.1×10^6 cells L^{-1} in late March. Sadly, this bloom was directly responsible for the death of two people.

In the present work, to gain further insights into bloom formation by this species and the role of its resting cysts on bloom recurrence, we monitored the abundance and distribution of cells and its resting cysts in both the water column and the surface sediments of two different locations in the Chilean Inland Sea: Low Bay, which is open to the ocean, and Ovalada Island, a more interior and protected area. Our results clarify bloom dynamics and add support to the role of encystment as a mechanism of *Alexandrium catenella* bloom termination. In addition, we discuss on the relevance of resting cysts deposits for the recurrence of blooms in the area, as no long-term cysts beds were found.

2. Material and methods

2.1. Study area

Low Bay ($43^{\circ}49'39''$ S– $73^{\circ}57'40''$ W) and Ovalada Island ($44^{\circ}04'08''$ S– $73^{\circ}42'32''$ W) are located in the NW portion of the Chilean Inland Sea (Fig. 1). Both sites are characterized by the presence of large natural beds of clams (*Venus antiqua*), with a total biomass estimate of 1300 and 10,000 tons, respectively (Seguel et al., 2011a). Low Bay (Fig. 1C) is much more open to the ocean than the more interiorly located and protected Ovalada Island (Fig. 1D). In general, this system is characterized by an abrupt bathymetry and a complex coastal morphology, both locations strongly shaped by the oceanic water (Pickard, 1971). The salinity gradient in the upper 50 m ranges between 27 and 33 psu and is mainly influenced by the intense seasonal rainfall, which in this region averages about 3000 mm per year (Pickard, 1971; Silva et al., 1995). Semidiurnal tides have amplitudes ranging from 2 m (neap tides) to 4 m (spring tides) (www.shoa.cl).

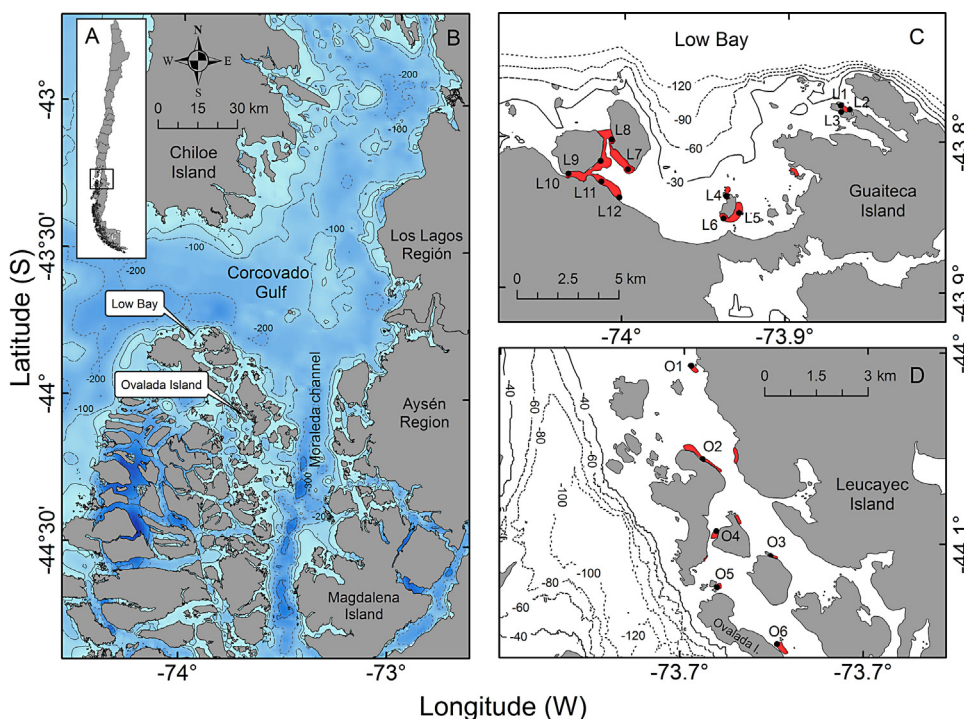


Fig. 1. (A) Study area in southern Chile (gray rectangle). (B) The map shows a section of the Chilean Inland Sea, including the location of Low Bay and Ovalada Island. (C) The 12 sampling stations of Low Bay. (D) The six sampling stations at Ovalada Island.

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