The effect of clam grazing on phytoplankton spring blooms in the low-salinity zone of the San Francisco Estuary: A modelling approach

Richard C. Dugdale [a,*], Frances P. Wilkerson [a], Alexander E. Parker [b]

[a] Romberg Tiburon Center, San Francisco State University, 3150 Paradise Drive, Tiburon, CA 94920, USA
[b] Department of Sciences and Mathematics, California State University Maritime Academy, 200 Maritime Academy Drive, Vallejo, CA, 94590, USA

ABSTRACT

Benthic grazing by estuarine bivalves can be an important top-down process impacting pelagic food webs. In the low-salinity zone of the San Francisco Estuary mass balance calculations and models have reported that clams (especially the invasive *Potamocorbula amurensis*) suppress phytoplankton blooms. However, spring blooms frequently occur. We aimed to understand this clam paradox using a biogeochemical modelling approach to evaluate the effects of clam grazing and excretion on phytoplankton production and nutrient uptake. The conceptual framework combines both the reduction of phytoplankton biomass by grazing and the role of ammonium (from clam excretion, wastewater plant discharge and sediment efflux) in minimizing chlorophyll accumulation, since phytoplankton cannot access nitrate (the major form of available nitrogen) for growth, due to ammonium suppression of nitrate uptake. We constructed the CLAMFLOW model by adding a clam module (with pathways of nitrogen for clam grazing, clam excretion and sediment efflux) to an existing phytoplankton-nitrogen-flow model. Whatever the parameter that was varied in the model (clam abundance, grazing, excretion, sediment efflux or flow) it decreased the peak nitrate uptake by the phytoplankton and shifted the time to reach peak uptake so delaying the likelihood of bloom initiation.

Outcomes of the CLAMFLOW model were to demonstrate how clams can indirectly impact phytoplankton growth through excretion of ammonium, and to illustrate how most published laboratory filtration rates are likely too high for application in the field. There are management implications from using too high a clam grazing rate in models that may overestimate their impact on trophic estuarine and wetland productivity. We suggest that improved prediction of bloom occurrences requires the use of lower filtration rates combined with observed clam abundances, and a suitable combination of flow and ammonium source concentrations. This simple modular model (CLAMFLOW) offers portability to other ecosystems and is designed to connect with estuary scale three-dimensional circulation or numerical biogeochemical models. Our model and results are applicable to other situations, including aquaculture development and bivalve restoration efforts, where the biogeochemical effects of bivalves on phytoplankton productivity need to be quantitatively understood.

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1. Introduction

Clams located in the benthos of shallow estuarine embayments can play an important top-down role in structuring pelagic food webs, through grazing by both natural (e.g. Prins et al., 1997; Alpine and Cloern, 1992; Lonsdale et al., 2009; Lucas et al., 2016) and cultivated populations (e.g. Spillman et al., 2008; Marinov et al., 2007). Conversely, bottom-up factors affecting trophic estuarine productivity are often closely linked to nitrogen (N); an important nutrient

that occurs in various forms in these ecosystems. Understanding the interaction of clams, with N dynamics and phytoplankton productivity and accumulation is important for estuarine management and efforts to determine the impact of clam populations on water quality. This requires modelling of the clam-phytoplankton N interactions and including realistic filtration and excretion rates of the clams.

In the low-salinity zone (LSZ; salinity range 0.5–5, Kimmerer et al., 2012) of the San Francisco Estuary (SFE) (Fig. 1) the motivation to construct a clam grazing-nitrogen dynamics model arises from the need to assess the role of an invasive clam, the Asian overbite clam, *Potamocorbula amurensis,* which was reported to be the primary cause of an abrupt decrease in chlorophyll concentration
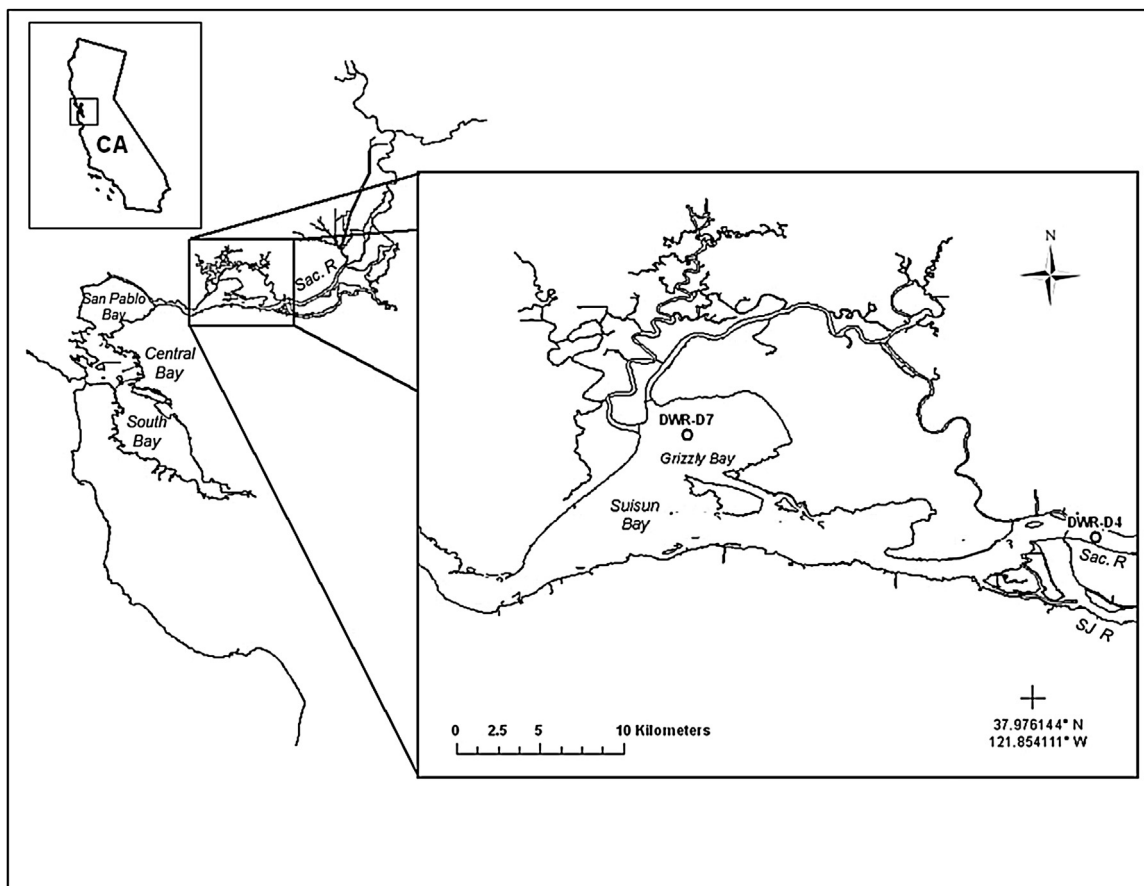
Fig. 1. Map of the low-salinity zone of the northern San Francisco Estuary showing the location of the shoal station DWR-D7 in Grizzly Bay, California, USA.

(Alpine and Cloern, 1992; Cloern and Jassby, 2012), leading to a later decline (starting in 2000) in populations of a number of fish species, including threatened species (Sommer et al., 2007). The decrease in chlorophyll in 1987 coincided approximately with the arrival and population increases of the clam (Nichols et al., 1990). However, a three-fold increase in discharge of anthropogenic nitrogen (as ammonium; NH_4) from a regional wastewater treatment plant upstream of the LSZ also occurred at that time (Jassby, 2008). The elevated NH_4 has been proposed to have a bottom-up oligotrophic (Nixon, 2009) effect on chlorophyll, through NH_4 repression of phytoplankton NO_3 uptake and minimizing bloom formation (Wilkerson et al., 2006; Dugdale et al., 2007; Glibert 2010; Glibert et al., 2011; Parker et al., 2012). Consequently, there are two alternative hypotheses to explain the present low phytoplankton biomass in the LSZ: 1) the introduction of an invasive clam, *P. amurensis* and 2) increased NH_4 discharge to the Sacramento River.

For the SFE, other than the correlations in time, the evidence for clam grazing as the causal agent of low chlorophyll is based on models using grazing rates that rely on laboratory filtration rates and measured observations of clam biomass, since direct measurements of clam grazing in nature are virtually impossible to obtain. For the LSZ of the SFE, Kimmerer and Thompson (2014) compared phytoplankton growth rates (calculated from carbon uptake) with clam and zooplankton grazing rates and concluded that only rarely in shoal habitats could growth rates exceed grazing rates and allow blooms to occur. However, phytoplankton blooms have been observed in the LSZ, including at deeper channel locations, in years when their model showed phytoplankton growth to be less than grazing rates, i.e., in 1998, 2000, 2010–2012 (Kimmerer and Thompson, 2014; Wilkerson et al., 2015). This conflict between

their modelled predictions and field observations of blooms results is a "clam paradox"; the clams should be preventing virtually all blooms according to the Kimmerer and Thompson (2014) model but blooms occur in spring quite frequently. There is little predictability of spring blooms in the LSZ from a knowledge of just clam abundance. For example, Wilkerson et al. (2015) reported a lack of correlation between blooms and clam abundance in the LSZ, with higher than average clam abundances occurring in spring 2010 and 2012, when blooms were observed.

Uncertainties that may contribute to the clam paradox include the accuracy of the laboratory filtration rates and the method of extrapolation to field grazing rates. Published laboratory filtration rates for *P. amurensis* vary. Kimmerer and Thompson (2014) used a "trimmed mean" of $383 \, L \, g \, (AFDW)^{-1} \, d^{-1}$ [AFDW = ash-free dry weight] measured in the flume study of Cole et al. (1992), in which the lowest and highest of eight measurements were eliminated. Other published rates for *P. amurensis* range over an order of magnitude, from $29 \, L \, g \, (AFDW)^{-1} \, d^{-1}$ (Paganini et al., 2010) to a maximum of $724 \, L \, g \, (AFDW)^{-1} \, d^{-1}$ (Werner and Hollibaugh, 1993). Ramifications of such variability in bivalve filtration rates were highlighted by Cranford et al. (2011) "Questions regarding the accuracy of clearance rate measurements have generated a rather fruitless debate in the literature because we cannot arbitrarily assume that any rate is more accurate than another. Accuracy may best be assessed by determining the ability of reported clearance rates to predict measured tissue growth or magnitude of phytoplankton depletion resulting from the feeding activity of a given bivalve population". Due to the difficulty of making direct measurements of grazing in the natural setting, modelling provides one avenue to assess the effect of such feeding activity.