Bivalve grazing causes substantial mortality to an estuarine copepod population

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ABSTRACT

The escape responses of planktonic copepods to grazing by introduced clams in the San Francisco Estuary were estimated for several copepod species, and resulting loss rates were compared with overall mortality for one species. Experiments were conducted to determine the escape responses of both nauplii and copepodites to entrainment in the siphons of clams (*Potamocorbula amurensis*) and artificial siphons. Copepod nauplii escaped both classes of siphon about 75% of the time and copepodites were more capable of escaping than were nauplii. Escape probabilities were combined with field-based data on clam grazing rates to estimate the impact of clam grazing on copepod survival in the low-salinity region of the San Francisco Estuary. Clams removed nauplii of *Eurytemora affinis* at a rate of ~10% d^{-1} with a seasonal pattern from 5% d^{-1} in spring to 20% d^{-1} in summer–fall and considerable interannual variability. This range of loss rates was similar to the estimated range of total mortality rates for nauplii. Furthermore, the annual estimates of loss rate were negatively correlated with an index of decline in the annual cycle of the copepod population. By combining an understanding of copepod escape capabilities with extensive data on copepod abundance and clam grazing, this paper shows that clam grazing has persisted as a dominant control on the estuarine ecosystem and is implicated in the long-term depression in abundance of food organisms for several fish species that are also in decline.

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1. Introduction

Grazing by bivalves can exert a dominant influence on productivity of freshwater, marine, and estuarine ecosystems (Kimmerer, 2006; Strayer et al., 2004). The ability of bivalves to graze down phytoplankton biomass in the overlying water column is well established (Alpine and Cloern, 1992; Cloern, 1982; MacIsaac et al., 1999; Prins et al., 1998). The reduction in phytoplankton production often manifests as an increase in water clarity where turbidity is largely of algal origin (Phelps, 1994), and a shift from a predominantly pelagic to a benthic foodweb (Higgins and Vander Zanden, 2010).

Direct effects of bivalve grazing on zooplankton also have been reported, which can be termed "incidental predation." Bivalves can consume soft-bodied forms such as larvae and rotifers (Andre et al., 1993; MacIsaac et al., 1991; Mileikovsky, 1974), as well as copepod eggs and nauplii (Kimmerer et al., 1994; Lonsdale et al., 2007; Pace et al., 1998). Motile zooplankton is generally less vulnerable than phytoplankton to siphoning by bivalves because zooplankton may be larger (especially later life stages), have escape responses, or avoid the bottom. Bivalve grazing should generally select for smaller organisms that can enter siphons more readily and have weaker escape responses (Lehane and

Davenport, 2002, 2006). In addition, zooplankton may be ingested but subsequently egested bound in mucus from which they cannot escape (Davenport et al., 2000). Although bivalves may gain relatively little nutrition from consuming zooplankton, this consumption can devastate zooplankton populations (Pace et al., 1998).

Escape responses of adult copepods are relatively well known (Fields and Yen, 1997; Paffenhöfer et al., 1996). Much less is known about escape responses of nauplii, which have weaker swimming capabilities and possibly higher thresholds of disturbance to elicit escape behavior (Bradley et al., 2013; Fields and Yen, 1997), and should therefore be more vulnerable than adults to clam siphons. Escape responses of nauplii can vary among taxa (Titelman and Kiørboe, 2003) and by nauplius age (Buskey, 1994). Escapes of copepod nauplii from an artificial siphon included jumps of at least 130 body lengths s^{-1} oriented away from the flow (Titelman and Kiørboe, 2003).

Escape responses reduce the effective grazing rate of bivalves on zooplankton well below that on phytoplankton. However, zooplankton has generally lower population turnover rates than phytoplankton, so that a population of zooplankton can maintain itself only at a much lower mortality rate than a population of phytoplankton. Because of the complex life cycle of zooplankton, the effects of grazing on abundance of zooplankton populations can be difficult to estimate. Furthermore, bivalves can both prey on zooplankton and compete with them for particulate food, making effects of competition and predation difficult to distinguish.

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When an introduction causes a rapid change in both competition and predation on zooplankton, the effects of both can become clear. Such an event occurred in the San Francisco Estuary with the introduction of the "overbite" clam *Potamocorbula amurensis* and its subsequent spread through the estuary in 1987 (Carlton et al., 1990). This clam produced a sharp decline in chlorophyll in brackish waters of the estuary that has not been reversed (Alpine and Cloern, 1992; Kimmerer and Thompson, 2014). *P. amurensis* also consumes bacteria (Werner and Hollibaugh, 1993), copepod nauplii (Kimmerer et al., 1994), and other microzooplankton (Greene et al., 2011). Before *P. amurensis* arrived, the calanoid copepod *Eurytemora affinis* was abundant year-round, particularly in summer (Kimmerer and Orsi, 1996). Since then, *E. affinis* has been abundant only in winter–spring, declining precipitously during May–July and remaining nearly absent in summer (Kimmerer and Orsi, 1996).

Although the effects of *P. amurensis* seemed clear enough in the years immediately after its introduction, subsequent events have muddied the waters. Several species of copepod have invaded the low-salinity region, some of them within a few years after *P. amurensis* had become established (Orsi and Ohtsuka, 1999; Orsi and Walter, 1991). These include the copepod *Pseudodiaptomus forbesi*, introduced in 1987 and now very abundant in freshwater and moderately abundant in the low-salinity habitat of *E. affinis*. This species is similar in size and general life history to *E. affinis* (Orsi and Walter, 1991) and therefore could be competing for food with *E. affinis* where and when they overlap. In addition, clam abundance has not always seemed sufficient to explain the annual decline in *E. affinis*, raising the possibility that other introductions, notably that of *P. forbesi*, have contributed to this decline.

Calculating the rate of incidental predation by bivalves on nauplii requires spatially and temporally extensive data on bivalve grazing rates. Without such data, predation can be estimated only crudely (Kimmerer et al., 1994). Recently, estimates of biomass of the clams *P. amurensis* and *Corbicula fluminea* from spatially-intensive and long-term sampling programs in the upper San Francisco Estuary have been used to provide estimates of clam grazing rates on phytoplankton (Kimmerer and Thompson, 2014). This paper combines these data with experimental data on escape probabilities of copepod nauplii in order to estimate mortality due to grazing by clams and compare it with estimates of total mortality. The focus is mainly on the low-salinity zone (LSZ, defined by salinity of ~0.5–6, practical salinity scale) of the San Francisco Estuary and on the calanoid copepod *E. affinis*, although escape responses of other copepod species and life stages were determined when these species were abundant. All copepods investigated in this study carry their eggs so the most vulnerable life stage is the nauplius. Vertical distributions of nauplii were also investigated because they can influence vulnerability of nauplii to clams. Consumption of microplankton by the *P. forbesi* population, was also investigated to determine whether competition with this copepod may have contributed to the annual decline of *E. affinis*.

2. Methods

The escape probabilities of nauplii and copepodites were estimated in a series of experiments that determined the removal rate of nauplii by clams or by artificial siphons. The grazing impact on nauplii was calculated from data on clam grazing rates and copepod abundance from spatially-intensive studies in 2006–2008 and from long-term monitoring.

Pumping rate is defined here as the flow rate of water through a clam's siphon when it is filtering (volume time^{-1}); filtration rate as the rate at which a filtering clam removes passive particles of a suitable size (time^{-1}); grazing rate as the estimated rate at which a clam or assemblage of clams removes particles of interest (here, copepods; time^{-1}); and clearance rate as grazing rate divided by the ambient density of particles (volume time^{-1}). These terms are applied if copepods

are killed by entering clam siphons, whether the copepods are ingested or not.

2.1. Grazing experiments

Clams (*P. amurensis*) were obtained using Ponar grabs at various locations in the northern San Francisco Estuary (SFE) with a similar salinity to that planned for experiments. Clams were sorted from sediments and returned to the laboratory, where they were maintained in water of the same salinity and fed a mixture of cultured phytoplankton (mainly *Rhodomonas salina*, *Skeletonema costatum*, *Thalassiosira weisflogii*, and *Isochrysis galbana*).

Copepods were collected by gentle subsurface tows with a 53-μm mesh, ½-m diameter net and diluted into an insulated bucket of surface water (Table 1). Samples were size fractionated to obtain mostly nauplii using upward filtration through a series of PVC cylinders with mesh of various apertures glued over the ends. Experiments were opportunistic in examining species and life stages that were abundant at the time and place of collection, although most collections targeted *E. affinis* (Table 1). Some experiments focusing on *E. affinis* used cultures (Kimmerer and Gould, 2010; Sullivan and Kimmerer, 2013) to minimize sorting time or when this species was not abundant.

Grazing experiments were conducted in a constant-temperature room at temperatures close to ambient and at salinity close to that at which copepods were collected (Table 1). Experiments were conducted in the dark to mimic conditions near the bottom in this turbid estuary and to minimize experimental artifacts that might be caused by phototaxis of the nauplii. Clams were acclimated to experimental conditions for at least one week before experiments; this species is highly euryhaline and therefore insensitive to changes in salinity (Nicolini and Penry, 2000).

Experiments measured disappearance of prey over time. Commonly, such experiments are run either with random samples of water containing small prey such as phytoplankton or by sorting known numbers of larger prey into experimental containers. In this study the former method was used for convenience and to minimize time spent sorting, which may be stressful to the nauplii. This permitted the use of large numbers of nauplii to ensure a strong signal, but required the use of control containers to account for variability in the numbers of nauplii as well as any mortality not due to clams.

Experimental containers were 1-L beakers with magnetic stirrers running at minimum speed (ca. 100 rpm). Samples of copepods were taken by stirring the container of nauplii and dipping with a 250-mL beaker, distributing the samples among the experimental beakers, which were then randomly assigned to treatments. Experiments were started by suspending two to eight small clams, with a target total live weight of 1 g (actual range 0.6–1.9 g) at the sides of half of the beakers in small acrylic cylinders with 500-μm mesh bottoms. Control beakers contained no clams. After ~24 h the contents of the beakers were rinsed and concentrated through a 35-μm mesh sieve and preserved in 2% formaldehyde. The entire contents of experimental and control beakers were counted and identified to species and gross life stage.

Clearance rate of clams on phytoplankton was measured as a necessary input to calculations of escape response (see Section 2.2). In vivo fluorescence was measured over the first 2–5 h of each experiment using a Turner Designs model 10 AU fluorometer. In some experiments cultured phytoplankton was added to increase the fluorescence signal.

In some experiments artificial clam siphons were used to mimic clam siphons (Singarajah, 1969; Titelman and Kiørboe, 2003), simplifying subsequent analysis (Section 2.2). Siphons were made of silicone tubing of 0.55 mm inside diameter, a size similar to that of clam siphons (J. Thompson, USGS, pers. comm.). These siphons were set up with ~1 m of head, which resulted in a siphon rate of about 45 mL h^{-1}, similar to the pumping rate of individual clams (Greene et al., 2011). The siphons were allowed to flow into separate ("discharge") beakers until approximately 200 mL remained in the source beakers. Nauplii were then