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Actinian dominated intertidal mudflats: A new case of an extraordinary rare phenomenon from Southern Chile

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ABSTRACT

Generally, estuarine intertidal mudflats constitute important nurseries for fish and foraging grounds for coastal birds by providing a plenitude of mollusks, worms, and crustaceans as prey, which in turn mostly feed on suspended and benthic microalgae, bacteria, and detritus. Despite the high productivity of such habitats, pronounced variability in both salinity and temperature results typically in low diversity. The only sea anemone reported from estuarine mud is the edwardsiid *Nematostella vectensis* Stephenson, 1935. It occurs widely in the northern hemisphere, and occasionally in extremely high density. Here we document another sea anemone from estuarine mud and muddy sand found in Southern Chile which has similar ecological attributes. Taxonomic confusion has impeded the reporting on this small but prominent member in a macrozoobenthic assemblage, the brooding *Anthopleura hermaphroditica* (Carlgren, 1899; Anthozoa: Actiniidae). It differs from *N. vectensis* by the presence of symbiotic algae. Average density under poly- to euhaline conditions in mud and muddy sand at around mid tide level was about 3 actinians per cm^2. An average abundance of 11,000 m^{-2}, a biovolume of 487 $cm^3 m^{-2}$, and a biomass of 35.5 g dry organic weight m^{-2} were found in mud and muddy sand in two surveys 20 years apart. The mean fishing area of fully expanded individuals covers 42 ± 25 mm^2, corresponding to a circular area with a diameter of 7.3 ± 5.7 mm. Preliminary experiments indicate that associated benthos may be relegated to life below surface by the net of tentacles above the sediment. As no predators on *A. hermaphroditica* could be found on the mudflat, the success of this mixotrophic sea anemone may entail a trophic dead end.

1. Introduction

Our prevailing perception of the ecological value and functioning of estuarine mudflats is based on a food web model where rivers and the sea supply plenty of organic carbon which is transformed into zoobenthic biomass. This in turn supports both a nursery for fish and a foraging ground for migrating birds with the changing tide (Reise, 1985; Raffaelli, 2000; Leguerrier et al., 2003; Baird et al., 2004; McLusky and Elliott, 2004; Dauvin and Desroy, 2005). In many temperate and tropical coasts, benthic fauna is primarily composed of suspension feeding and deposit feeding invertebrates, a suitable food source for consumers (i.e., Piersma et al., 1993; Reise, 2001; Kuris et al., 2008).

As an alternative to this trophic paradigm, we here first report results that a truncated food web may occur when actinians, otherwise known to abound at rocky shores, successfully establish on an intertidal mudflat. More than 1000 species of actinians have been described from the coast to the deep sea and from pole to pole, and the most populated habitat in the intertidal is the rocky shore (Buchsbaum Pearse, 2007). There actinians (1) attach with their pedal disc firmly to hard substrates but may slowly move when necessary, (2) grow slowly to large individual sizes or divide into clones of aggregated small individuals, (3) catch rather indiscriminately prey with their stinging tentacles, and (4) many have a symbiosis with unicellular algae which supply the anemones with a portion of their photosynthetic products. Many of their enemies lurk subtidally such as fish, aeolid nudibranchs, sea stars and a few others, and are scarce in the intertidal.

Only some actinians have been reported from sedimentary shores. They generally remain at much lower abundances than at rocky shores, and usually prefer the subtidal zone or where some water remains throughout low tide period (i.e., Fager, 1968; Buhr and Winter, 1977; Peterson and Black, 1986). Anchorage is often provided by mollusk shells or seagrass rhizomes buried in the sediment. An exception is a minute edwardsiid sea anemone, *Nematostella vectensis*, (Stephenson, 1935). It is found in brackish marsh pools and lagoons, may attain several thousand individuals per m^2, preys on small fauna including bivalve larvae, and is itself preyed upon by shrimp (Hand

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and Uhlinger, 1994). *N. vectensis* is native to the Atlantic coast of North America and populations along the Pacific and European coasts originate from accidental introductions, probably with shellfish imports (Reitzel et al., 2008).

We here describe the case of an actiniid sea anemone endemic to southern Chile which occurs abundantly on intertidal mudflats. Although it shares several features with *N. vectensis*, it is mixotrophic due to numerous zooxanthellae. Anecdotally, this phenomenon has been known for a long time, however, a completely muddled taxonomy stood in the way of proper reporting. Its high density has been briefly mentioned by Reise (1991), then under the name *Bunodactis hermaphroditica* (McMurrich, 1904) instead of the similar species *Anthopleura hermaphroditica* (Carlgren, 1899). We report on life history, abundance and associated fauna of *A. hermaphroditica*. Small laboratory and field experiments were conducted to explore effects of salinity and the responses to offered prey. We first visited the study site in January 1989 and then twenty years later in April/May 2008.

We ask (1) what factors favor its success, (2) what are the consequences of the actinian prevalence for the associated benthic fauna and (3) what makes *A. hermaphroditica* different from *N. vectensis* and probably more successful.

2. Materials and methods

2.1. Study site

We observed *Anthopleura hermaphroditica* at several tidal flats in southern Chile over a distance of 80 km along the eastern shore of the Seno de Reloncaví and Golfo de Ancud, e.g. Chamiza-West (41°29 30 S 72°52 03 W), Chamiza-East (41°30 12 S 72°48 27 W), Bahía Quillaipe (41°32 30 S 72°44 35 W), and Caleta de Manzano (42°00 50 S 72°39 45 W) (Fig. 1). The species was also found on the tidal flats of Southern Chiloé near Yaldad (43° 6 51 S 73°42 35 W), but this investigation was mainly focused on the Bahía Quillaipe near Puerto Montt (Fig. 1). Bahía Quillaipe is a narrow, sheltered bay comprising 1.4 km^2 of intertidal area. Our cursory mapping yielded 46% of soft mud and muddy sand. Organic content of these muddy sediments (weight loss after ignition at 520 °C) varied between 2.8 and 3.6%, and particle sizes <0.25 mm across dominated. Other habitats mapped were firm sandy flats, tidal channels, salt marshes and beaches. The bay is well sheltered and we have not observed waves of >0.2 m in height. Mean tidal range is approximately 4 m with 2 m at neap and more than 6 m at spring tides. Six freshwater streams flow into the inner bay and cause intermittent brackish conditions. The inner bay is defined as the area north of the latitude 41°32 08 S (Fig. 1C, dashed line). Mean annual rainfall is 2342 mm with a maximum in July (Di Castri and Hajek, 1976).

In January 1989, we estimated a freshwater inflow of 526 $m^3 h^{-1}$ which constitutes only about 1% of the mean tidal volume of the bay. However, during the final ebbing phase tidal gullies in the upper intertidal region contain mainly freshwater. In a main tidal channel salinity ranged between 0 and 22, above tidal flats in the inner bay between 2 and 25 and in the outer bay between 22 and 29 in January 1989.

In April 2008 salinity of 30 prevailed at high tide throughout the bay and streams contained less water. On calm days, we observed marked salinity stratification in flooding waters. In the inner zone, salinity increased from 2 at the surface to 6 at 5 cm and 30 at 10 cm below surface. In the middle zone, salinity increased from 20 at the surface to 24 at 3 cm and 30 at 6 cm below surface. As a result of this stratification, residual waters during low tide exposure in depressions <5 cm deep had a salinity of 10 to 15, while salinity was 20 to 26 in depressions of >5 cm water depth.

Air and water temperature are moderate and similar to each other. Summer average is 15.1 °C and winter average 7.7 °C (Di Castri and Hajek, 1976). Frost in winter is rare and on a sunny summer day a low

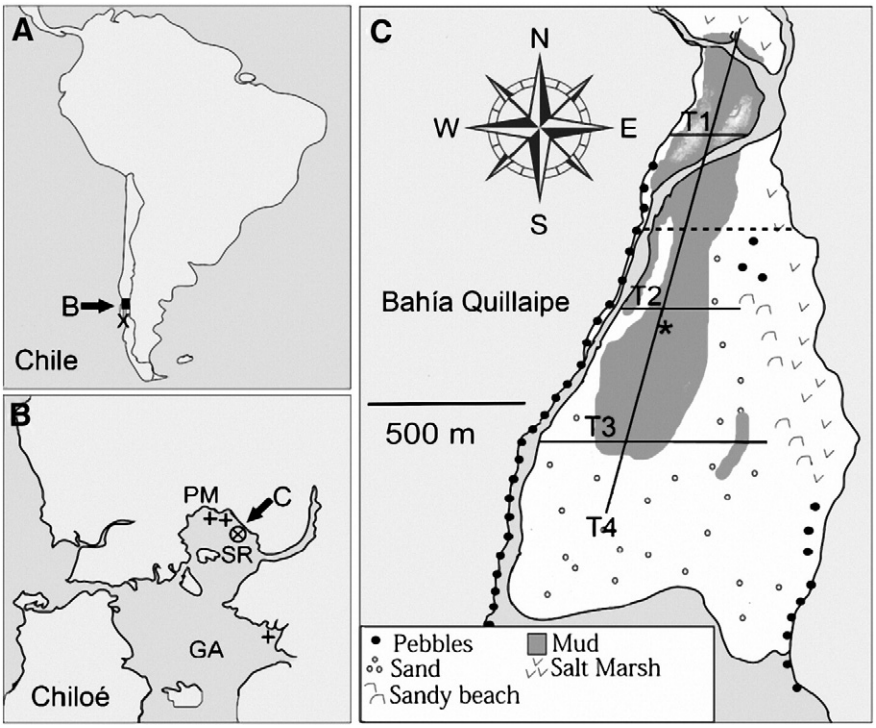

Fig. 1. The study was conducted in Southern Chile (A) in Seno de Reloncaví (B) in the intertidal Bahía Quillaipe (C). Salt marshes, beaches and sandy flats are unshaded, while an area mostly composed of mud and muddy sand is shaded in dark grey. Lines indicate transects (T1–T3 in 1989 and 2008, T4 in 2008 only) for quantitative *Anthopleura hermaphroditica* sampling. The dashed line on (C) separates the inner bay from the outer bay. Asterisk indicates the muddy site where field experiments were performed. PM = Puerto Montt; GA = Golfo de Ancud; SR Seno de Reloncaví; ⊗ indicates main study site; + indicates 3 additional sampling sites Chamiza-West, Chamiza-East, and Caleta de Manzano (from West to East); x Yaldad, Chiloé.