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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<sup>2</sup>. An average abundance of 11,000 m<sup>-2</sup>, a biovolume of 487 cm<sup>3</sup> m<sup>-2</sup>, and a biomass of 35.5 g dry organic weight m<sup>-2</sup> 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<sup>2</sup>, 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.

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### 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<sup>2</sup>, 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

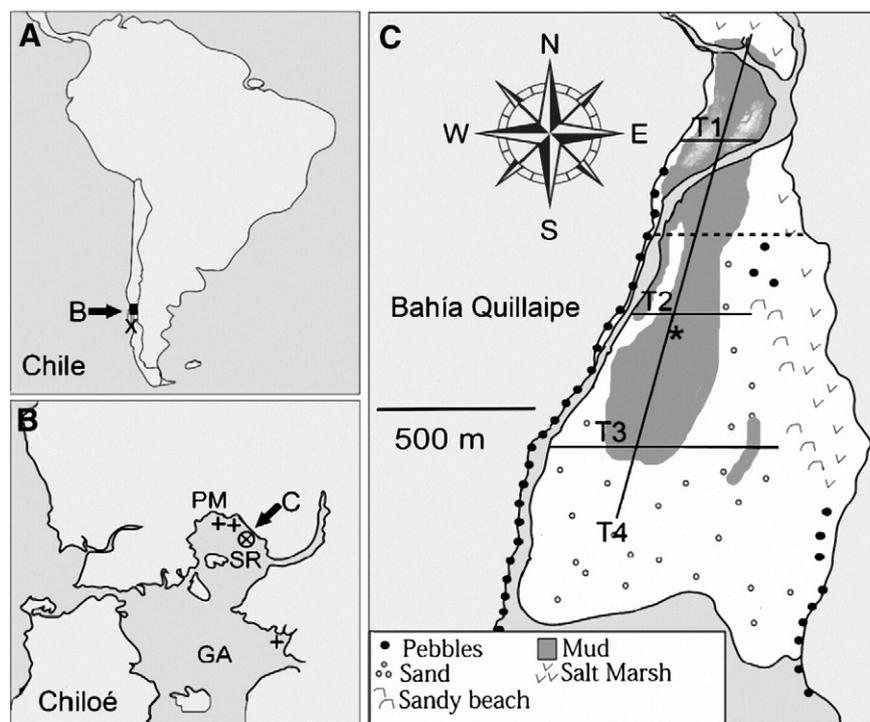
We observed *Anthopleura hermaphroditica* at several tidal flats in southern Chile over a distance of 80 km along the eastern shore of the Seno de Reloncaví and Golfo de Ancud, e.g. Chamiza-West (41°29'30" S 72°52'03" W), Chamiza-East (41°30'12" S 72°48'27" W), Bahía Quillaiepe (41°32'30" S 72°44'35" 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 Quillaiepe near Puerto Montt (Fig. 1). Bahía Quillaiepe is a narrow, sheltered bay comprising 1.4 km<sup>2</sup> 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<sup>3</sup> h<sup>-1</sup> 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 Quillaiepe (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.

tide pool with *A. hermaphroditica* attained a temperature of up to 31 °C in January.

## 2.2. Species description

Observations on outer morphology were done in the field and under a dissecting microscope in 2008.

### 2.2.1. Identification, morphology and brooding

Species identification was done by Riemann-Zürneck on the basis of a few individuals in 1989, and repeated by the authors due to the similarity of *A. hermaphroditica* and *Gyactis hermafroditica* (Carlgren, 1959) (Sanamyan et al., 2009) in 2008. The anatomy was studied of about 200 individuals differing in size and coloration.

80 individuals selected haphazardly were dissected under a stereo microscope and the internally brooded young were counted and measured. The brooding rate was estimated in January 1989 (austral summer) and in April 2008 (austral autumn). In 1989, 36 *A. hermaphroditica* of average size were kept in petri dishes over 10 days on a window sill with daily exchange of seawater. In 2008, this experiment was repeated with 56 individuals.

### 2.2.2. Shape, size and biomass

After breaking sediment open with a spade, burrowing depth and shape of anemones were directly measured as well as from photographs of sediments sectioned in specific depth horizons. Individuals removed from the sediment contracted to balls and then the diameter was measured to the nearest mm to get the size frequency distribution. This measurement was done in 1989 ( $n=763$ ) and 2008 ( $n=274$ ). For comparison, the diameter of 29 contracted *Paranthus niveus* (Lesson, 1830) was also measured which co-exist with *A. hermaphroditica* near low tide level in the mouth of Bahía Quillaípe.

A total of eight batches with each of 100 randomly selected individuals were used to determine the mean body volume by underwater weighing. Subsequently the samples were dried at 60 °C for 72 h and combusted at 500 °C for 6 h to estimate average dry weight (DW) and ash free dry weight biomass (AFDW).

## 2.3. Distribution

Sampling of *A. hermaphroditica* was done along three parallel transects across the bay with a total of 54 stations in January 1989 and 55 in April 2008 (Fig. 1C, T1–T3). Additional sampling along a perpendicular line with a total of 16 stations was done in 2008 (Fig. 1C, T4). The effects of time and sediment type on actinian abundance were examined using ANOVA. If required, data were  $\ln(x+1)$  transformed before testing, with homogeneity of variance examined using a Levene's test (Levene, 1960). For the analysis 15 mud or muddy sand stations and 15 sandy stations were selected randomly to obtain equal cell frequencies.

At the innermost transect (Fig. 1C, T1) in 1989, 6 samples of 87 cm<sup>2</sup> were taken with a sediment corer at each of 13 equidistant stations. At all other transects, corers of 10 cm<sup>2</sup> cross section were pushed 5 cm into the sediment. At each station 10 random replicates were taken within an area of 100 m<sup>2</sup>. Distances between stations varied between 50 and 200 m, depending on topography and substrate homogeneity. Within one day, sediment samples were washed through a 1-mm mesh. Sieve residues were transferred to dishes (12×36 cm) and specimen were sorted alive. In total, 1.80 m<sup>2</sup> had been sieved for *A. hermaphroditica* at Bahía Quillaípe. In addition, the distribution was recorded by observing tentacular crowns under water or characteristic holes in the sediment during tidal exposure. 10 random replicates (10 cm<sup>2</sup>) were taken within an area of 100 m<sup>2</sup> in each of the bays, Chamiza-West, Chamiza-East and Caleta de Manzano in 1989.

## 2.4. Behavioural experiments

### 2.4.1. Salinity

Because of intermittent low salinities in the bay due to freshwater runoff after heavy rainfall, a laboratory experiment was conducted with *A. hermaphroditica* subjected to diluted seawater in steps of 5, ranging from 30 to 0 salinity (7 treatments with 10 replicates). This was controlled with a hand refractometer. Ten individuals for each treatment were kept individually in small petri dishes (30 mm across) for 12 h, and then were supplied with new seawater with a salinity of 30 and observed for another 9 h. This design was chosen to simulate a rainfall event. Individuals with fully extended tentacular crowns were counted.

### 2.4.2. Burrowing

Most observations on behavior and organisms offered for prey capture were obtained from a mud flat site with plenty of low tide puddles (Fig. 1, asterisk). Here also a few preliminary field experiments were conducted. To measure the ability of *A. hermaphroditica* to rebury, 24 individuals were washed out of the sediment and then placed in parallel on the mud surface covered by 20 mm of water during low tide. In January 1989, positions of these sea anemones were recorded at 10 min intervals until 1 h had elapsed.

### 2.4.3. Response to re-suspended mud

Based on accidental observations we hypothesized that sediment in suspension may trigger sea anemones to extend tentacles to capture infaunal prey. The stinging tentacles of *A. hermaphroditica* are all extended above the mud surface, while potential prey organisms dwell below the surface. In an attempt to unravel this paradox, we re-suspended sediment in the field by trampling a few seconds in mud submerged by 20 mm of water, and observed the response of sea anemones downstream. On plots of 400 cm<sup>2</sup> at a distance of 0.3 m from our feet, we counted extended tentacular crowns before (1 min) and after (5 and 15 min) trampling. This was replicated 7 times in January 1989.

## 2.5. Associated fauna and prey capture

Sampling of the associated infauna was done in 1989, whereas the food catching area and a small experiment to study the potential prey of *A. hermaphroditica* were conducted in 2008.

### 2.5.1. Infauna

Cores of 87 cm<sup>2</sup> were taken to study associated infauna at a muddy site in the centre of the bay where abundance of *A. hermaphroditica* was high (Fig. 1, asterisk). Five such samples were divided into an upper core of 5 cm deep, washed through a 0.5 mm mesh, and a lower core from 5 to 20 cm, washed through 1 mm meshes. In addition, 5 samples of 2 cm<sup>2</sup> to a depth of 2 cm were suspended in seawater and corophiid amphipods were forced out of their branched tube system. Two samples of 1 cm<sup>2</sup> to a depth of 1 cm were also suspended in seawater to pipette meiofauna under a dissecting microscope at 30× magnification.

### 2.5.2. Prey capture

We offered potential prey items to sea anemones in the field to see whether these were captured. To obtain observations and capture rates under more standardized conditions, we supplied small aquaria (87 cm<sup>2</sup> cross section) with mud cores containing natural densities of *A. hermaphroditica*, and covered these gently with a layer of 25 mm of stagnant seawater (salinity 30, temperature about 11 °C). Associated macrobenthic invertebrates were offered individually by releasing the potential prey into the water column above the sea anemones. Responses of sea anemones and the fate of released prey had been recorded for up to 10 min under daylight conditions in April 2008.

### 2.5.3. Catching area

The distance that tentacles extend in relation to oral disc diameter of individual *A. hermaphroditica* was estimated with the software ImageJ vers. 1.40. A Nikon Coolpix 5000 digital camera was placed on a small tripod vertically over the sediment and photos were taken in macro mode at a distance of about 10 cm. To minimize lens distortion effects, only the central part of each image were analyzed (1200×900 pixel from 2560×1920 available). A total of 80 individuals were measured.

## 3. Results

### 3.1. Species description

The two species, *Gyrcactis hermaphroditica* and *A. hermaphroditica* are extremely similar in most features. However, in contrast to examinations made earlier (Reise, 1991), all specimens identified belong without doubt to *A. hermaphroditica*. On the basis of only a few specimens examined in 1989 they may seem to belong to both species mentioned above or only to *G. hermaphroditica*. However, after examining numerous samples in 2008 again the features used for identification could be regarded as species-specific for *A. hermaphroditica*.

#### 3.1.1. Identification, morphology and brooding

In the material examined from Bahía Quillaiepe, true acrorhagi are present in some specimens on the inner surface of larger marginal spherules of the first and second cycles and contain numerous holotrichous nematocysts. Up to 12 acrorhagi were present in some specimens while others had only 1–2 or none developed. Although the presence of acrorhagi is listed in the diagnosis of the genus *Anthopleura*, these structures are not invariably present in every specimen belonging to this genus.

According to England (1987: 239) “the best character by which *Anthopleura* can be distinguished from *Gyrcactis* (*Bunodactis*) is the presence of heterotrichs in the ectoderm of column”. Heterotrichs were present in the lower part of the column in all specimens examined in the present study.

*A. hermaphroditica* is a small and delicate sea anemone. We found it occasionally attached to hard substrate (usually mussels) but most frequently buried in sediment without any attachment. The tentacular crown is opened above the sediment when submerged (Fig. 2). Oral disc, tentacles and the upper part of the column is colored olive-green to brown, owing to the presence of zooxanthellae. The lower part of the column is paler and cream colored, lacking symbiotic dinoflagellates. Small white markings may be present on the oral disk and tentacles, forming distinctive patterns when fully developed.

Brooded young specimens encountered in the body cavity of the adults ranged between 0.5 and 2 mm in width, with a mean of 1.4 mm ( $n = 29$ ). These were found in 80 individuals cut open, mostly in the larger specimen. In one individual of 7 mm of contracted width, 4 young of 2 mm were observed. Most anemones contained one brooded young of 1 mm and the mean width of contracted brooders was 4.5 mm ( $n = 19$ ). Contracted individuals of <1 mm in width were not found free-living.

Brooding of *A. hermaphroditica* was notable during austral summer in 1989. 36 *A. hermaphroditica*, kept in petri dishes, brooded in total 20 juveniles over 10 days. Thus, doubling time under these conditions was approximately 13 days. When the experiment was repeated with 56 individuals in austral autumn 2008 only one additional individual was encountered after 10 days.

#### 3.1.2. Shape, size and biomass

Considering individuals buried in sediment, we found the width to length ratio of extended anemones to be about 1:6, while contracted individuals attain a ratio of 1:1.3. In the sediment, average column length was about 9 mm and width 1.5 mm over most of the column

length. Depth of burrows mostly ranged between 4 and 13 mm (mean  $9 \pm 3$  mm,  $n = 35$ ) however a single individual was found at a depth of 34 mm. The slender column is widest near the oral disc and gradually tapers off downward but then begins widening again shortly before the limbus, forming an anchor with an often swollen pedal disc.

Contracted anemones form stout cylinders. Normally contraction is incomplete and a tuft of tentacles remains visible. The pedal disc is occasionally swelled which either might be related to attempts of burrowing or it may serve to increase buoyancy. The pigmented region covers the upper third of the column with a length 2–3 mm in extended individuals. The size distribution of *A. hermaphroditica* was unimodal but right-skewed (Fig. 3). The 3-mm size class dominated, both in January 1989 and April 2008, with a mean width of 2.9 and 3.6 mm, respectively. A larger sea anemone co-existing with *A. hermaphroditica* near low tide level at the mouth of Bahía Quillaiepe was *Paranthus niveus* with a diameter  $9.5 \pm 2.0$  mm of 29 contracted individuals.

The individual mean biovolume of *A. hermaphroditica* was  $44.29 \pm 4.93$   $\mu\text{l}$ . Dry weight biomass was  $6.154 \pm 1.605$  mg and individual ash-free dry weight was  $3.224 \pm 0.713$  mg. Mean dry weight and ash-free dry weight of *A. hermaphroditica*  $\text{m}^{-2}$  in 1989 and 2008 for all mud and muddy sand sites were similar. Total number of stations in 1989 was 19 out of 54 and in 2008 it was 24 out of 71. In 1989, mean DW  $\text{m}^{-2}$  was  $67.69 \pm 21.53$  g, mean AFDW  $\text{m}^{-2}$  was  $35.47 \pm 11.28$  g, the biovolume was  $487.21 \pm 155.02$   $\text{cm}^{-3}\text{m}^{-2}$ , and the number of individuals was  $11,000 \pm 3,500$   $\text{m}^{-2}$ . In 2008, mean DW  $\text{m}^{-2}$  was  $65.23 \pm 50.46$  g, mean AFDW  $\text{m}^{-2}$  was  $34.17 \pm 26.44$ , the biovolume was  $469.49 \pm 363.20$   $\text{cm}^{-3}\text{m}^{-2}$ , and the number of individuals was  $10,600 \pm 8,200$   $\text{m}^{-2}$ .

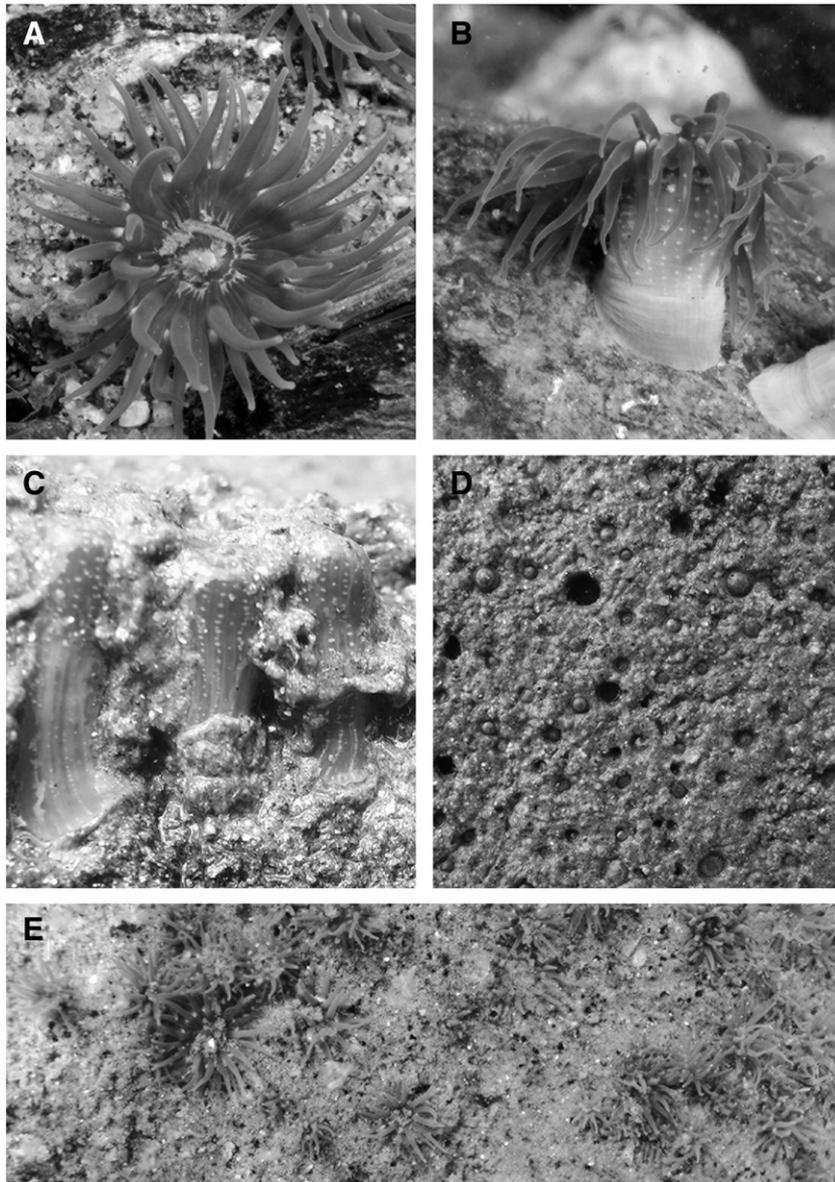
### 3.2. Distribution

Over a distance of 80 km along the eastern shore of the Seno de Reloncaví and Golfo de Ancud, the density of *A. hermaphroditica* was estimated at 4 localities from sites with muddy sand. Mean abundance was  $21.0 \pm 12.2$  individuals  $10\text{ cm}^{-2}$  at Chamiza-West ( $41^{\circ}29'30\text{ S } 72^{\circ}52'03\text{ W}$ ),  $11.6 \pm 5.4$  individuals  $10\text{ cm}^{-2}$  at Chamiza-East ( $41^{\circ}30'12\text{ S } 72^{\circ}48'27\text{ W}$ ),  $15.4 \pm 7.6$  individuals  $10\text{ cm}^{-2}$  at Bahía Quillaiepe ( $41^{\circ}32'30\text{ S } 72^{\circ}44'35\text{ W}$ ), and  $17.2 \pm 7.1$  individuals  $10\text{ cm}^{-2}$  at Caleta de Manzano ( $42^{\circ}00'50\text{ S } 72^{\circ}39'45\text{ W}$ ).

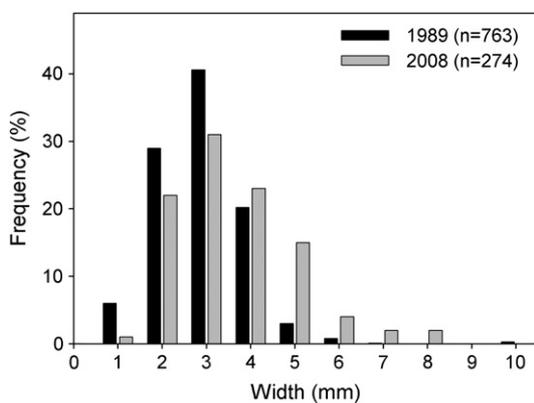
Total average abundance was  $16,300\text{ m}^{-2}$ . Similarly high abundance was also noted at the south eastern shores of the island of Chiloé.

Individuals of *A. hermaphroditica* are easily visible, either as tentacular crowns when submerged or as circular holes when retracted during tidal exposure. This allowed a bay-wide qualitative survey in Bahía Quillaiepe. Together with quantitative data from transects (Figs. 1 and 4), the following aspects of distribution and abundance are derived from Bahía Quillaiepe:

- (1) *A. hermaphroditica* occurred in sediments from mean low tide line up to neap high tide level. It was not encountered in salt marsh habitats, sandy and shingle beaches positioned between neap and spring high tide level, and remained absent from elevated sand waves or firm clay ridges overgrown with filamentous cyanobacteria in the upper intertidal.
- (2) Transects showed that abundance of *A. hermaphroditica* increased from sand to muddy sand and mud in Bahía Quillaiepe. It was most abundant in soft mud around mid tide level ( $34.8 \pm 7.6$  individuals  $10\text{ cm}^{-2}$ ;  $n = 10$  in 2008). A 2-way ANOVA was used to test whether changes in the abundance of *A. hermaphroditica* occurred depending on sediment type. All data were  $\ln(x + 1)$  transformed, and Levene's test of equality of error variances was used ( $F = 1.335$ ,  $p = 0.272$ ). In muddy sand and mud *A. hermaphroditica* was significantly more abundant ( $F = 199.183$ ,  $p < 0.001$ ) than on sand, however total abundance did not vary significantly between 1989 and 2008

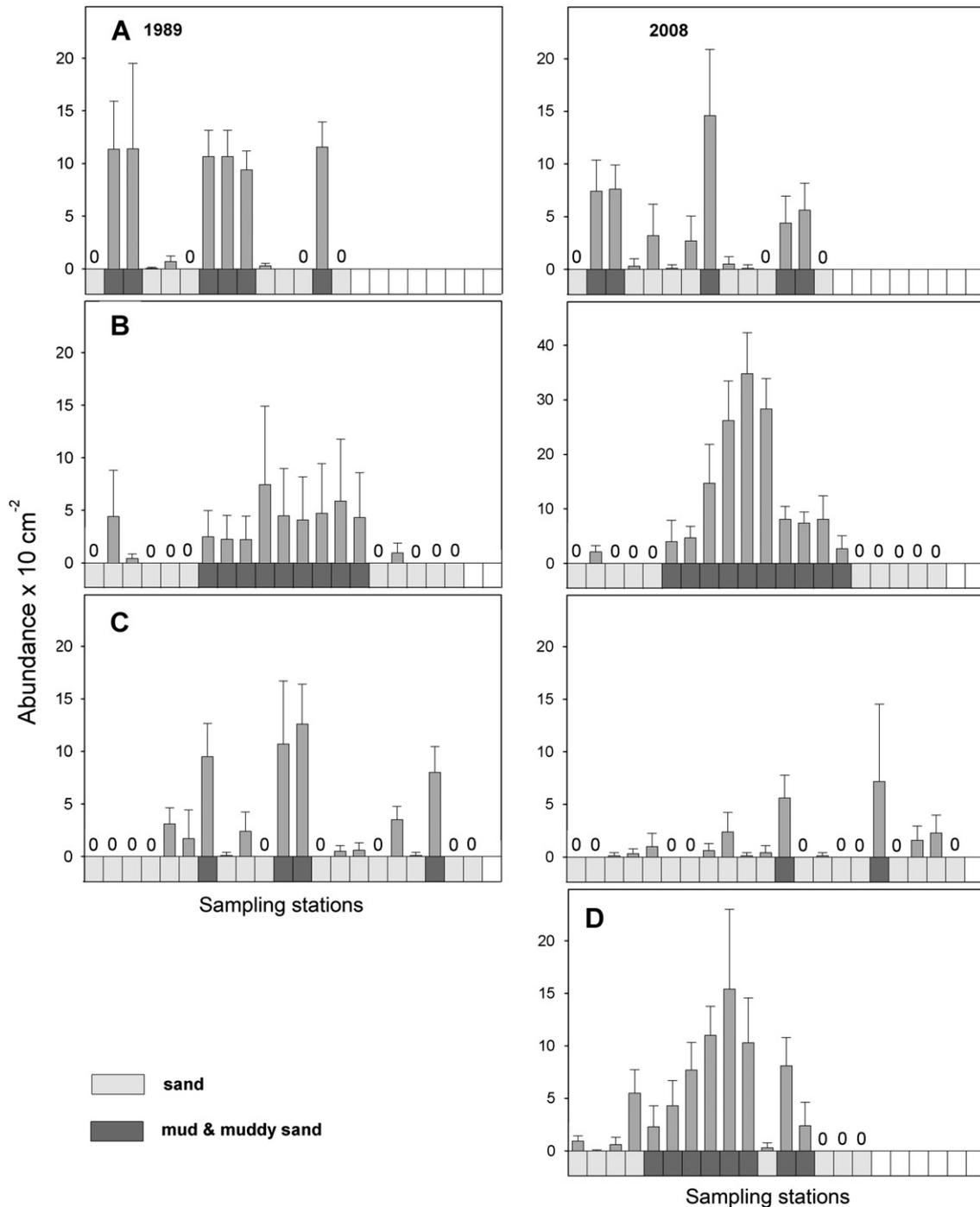


**Fig. 2.** *Anthopleura hermaphroditica* seen from above with extended tentacles (A) and inside view (B) with olive-green to brown color owing to zooxanthellae. Note the pale column in the lower part, and up to 24 longitudinal rows of endocoelic veruciae marked by white dots. Vertical position in oxidized ambient sediment (C), contracted individuals during low tide (D), and high density with extended tentacles in a low tide puddle (E).



**Fig. 3.** Size-frequency distribution of *Anthopleura hermaphroditica* in 1989 (n=763) and 2008 (n=274). The width ( $\emptyset$ ) of contracted individuals was measured to the nearest mm.

- ( $F=0.156$ ,  $p=0.694$ ). Interaction was not found ( $F=0.000$ ,  $p=0.939$ ).
- (3) *A. hermaphroditica* was rare or absent in rippled sand but where sediment was stabilized by mussels and/or tubes of chaetopterid worms it reappeared. Within hummocks generated by such tube worms, abundance was significantly higher than  $\geq 0.3$  m outside ( $4.8 \pm 2.1$  versus  $0.1 \pm 0.3$  individuals  $10 \text{ cm}^{-2}$ ,  $n=10$ ; Mann-Whitney U test,  $p<0.05$ ).
  - (4) Tidal channels carrying freshwater during part of the ebbing phase were devoid of *A. hermaphroditica*.
  - (5) In troughs of deltaic tidal channels at the mouth of the bay, *A. hermaphroditica* partly overlapped with a larger infaunal actinian, *Paranthus niveus*. Maximum abundance of that species was lower than for *A. hermaphroditica*. At spring low tide level, up to  $241 \text{ m}^{-2}$  were observed ( $2.1 \pm 2.0$  individuals  $87 \text{ cm}^{-2}$ ,  $n=10$ ), and at slightly higher tidal level in a zone of overlap abundance was  $103 \text{ m}^{-2}$  ( $0.9 \pm 0.7$  *P. niveus* versus  $8.3 \pm .3$  *A. hermaphroditica*  $87 \text{ cm}^{-2}$ ).



**Fig. 4.** Abundance of *Anthopleura hermaphroditica* along three transects in 1989 (left) and four transects in 2008 ( $n=10$  for each station, mean  $\pm$  1SD, except A in 1989: see Methods). Distance between sampling stations varied between 50 and 200 m. Dark shaded boxes below columns indicate stations with mud or muddy sand. Transect A–C are shown from West (left) to East (right), transect D from South (left) to North (right).

(6) Density of *A. hermaphroditica* in January 1989 and April 2008 was strikingly similar for 30 randomly chosen stations used for the statistical analysis mentioned under (2). In mud and muddy sand station,  $11.1 \pm 3.7$  and  $12.3 \pm 9.7$  individuals  $10 \text{ cm}^{-2}$  were present, respectively. In the sandy stations only  $1.1 \pm 3.0$  and  $0.6 \pm 1.1$  individuals  $10 \text{ cm}^{-2}$  were found in 1989 and 2008, respectively. In 1989, 19 of 54 stations were categorized as mud and muddy sand, and in 2008, 16 stations from transects A–C and 8 stations from transect D (see Figs. 1 and 4) were considered as mud and muddy sand. Nearly 90% of all *A. hermaphroditica* were found in these habitats.

### 3.3. Behavioural experiments

#### 3.3.1. Salinity

Salinity has a strong effect on activity. On a mudflat area of  $10 \times 30 \text{ m}$  with residual water in 6 shallow puddles with salinities of 10 to 16, actinians had their tentacles retracted, while in 6 other puddles, slightly deeper and with salinities of 20 to 26, actinians had their tentacles extended. This sensitivity to salinity was confirmed with an experiment in petri dishes with 10 individuals per treatment. At salinities  $\leq 20$  at least 4 individuals ( $S=20$ ) or all individuals of *A. hermaphroditica* had retracted tentacles after 2 h. After 11 h at least 7

individuals or all individuals extended their tentacles at salinities  $\geq 15$ , whereas all tentacles of *A. hermaphroditica* exposed to freshwater or a salinity of 5 or 10 remained retracted. When after 12 h, salinity of 30 had been reestablished, only those actinians subjected to freshwater before had not recovered completely after 9 h, and 2 individuals remained retracted.

Behavioral response of *A. hermaphroditica* subjected to salinities between 0 and 30 by diluting seawater with freshwater in petri dishes with 10 individuals per treatment. Given are numbers of individuals with their tentacular crowns fully extended after 2 and 11 h. After 12 h all were transferred back to a salinity of 30 and numbers with their tentacles extended were counted again after 1 and 9 h.

### 3.3.2. Burrowing

We found no evidence that buried anemones move laterally. During low tide exposure oral parts are retracted, remain level with the sediment surface or the entire individual retracts down the burrow when the surface sediment gets dry. In that case, circular holes indicate the position of the sea anemone in the sediment. In a tide pool with a layer of about 20 mm of water, 24 *A. hermaphroditica* were placed upon the mud surface. After 40 min, 19 had anchored themselves with the pedal disc and stood upright. After 1 h, only 3 were still lying on the mud surface.

### 3.3.3. Response to re-suspended mud

*A. hermaphroditica* extended its tentacles when we trampled for a few seconds in mud covered by about 20 mm of water. We counted the number of individuals before and after trampling within plots of 400 cm<sup>2</sup> at a distance of 0.3 m. Mean initial crown density before trampling was  $19.4 \pm 9.5$ . Five minutes after trampling, visible crown numbers had increased to  $76.3 \pm 31.1$ , and after 10 more minutes had declined somewhat to  $50.1 \pm 24.4$ . The increase was significant ( $n = 7$ , Mann–Whitney U test,  $p < 0.05$ ).

### 3.4. Associated fauna, prey capture and potential predators

The sediment fauna was studied in 1989 and 2008, whereas prey capture, catching area and potential predators were only studied in 2008.

#### 3.4.1. Infauna

Hardly any studies on the benthos of the sediment fauna from southern Chile have been published to date (Hartmann-Schröder, 1991), thus species identification was limited. Sediment fauna associated with abundant *A. hermaphroditica* in mud at mid tide level was rather poor in meiofauna, particularly in copepods and also comprised relatively few annelids (Table 1). Small and young mollusks were absent altogether. Superabundant was a small (<5 mm) corophiid amphipod, *Monocorophium acherusicum*, dwelling within a communal tube system in the upper 5 mm of the sediment. Tips of their antennae were occasionally observed at tube openings but these amphipods were never observed upon or above an undisturbed sediment surface. Also in sorting dishes, these amphipods rarely left their tubes unless forced out with needles or forceps. A relatively abundant nereid polychaete was never observed outside the sediment neither, not in the field nor in the aquaria with undisturbed mud. The only member of the benthic fauna observed swimming and crawling on the sediment surface was the robust isopod *Exosphaeroma lanceolata* which does not seem to be affected by the dense tentacular mesh.

#### 3.4.2. Prey capture

Field observations demonstrated that some tentacles of *A. hermaphroditica* were always in move. As soon as potential prey had touched one, others began to move as well and reached towards the prey. Tentacles to which the prey adhered retracted and transferred

**Table 1**

Abundance (individuals 10 cm<sup>-2</sup>) of zoobenthos in mud at mid tide level associated with *Anthopleura hermaphroditica*. Calculated from differently treated samples to account for the full spectrum body sizes: A: 1 cm<sup>2</sup>/0–1 cm depth,  $n = 2$ , sediment suspended, January 1989; B: 2 cm<sup>2</sup>/0–2 cm depth,  $n = 5$ , sediment suspended, April 2008; C: 87 cm<sup>2</sup>/0–5 cm depth, sieved through 0.5-mm mesh size, 5–20 cm depth, sieved through 1.0-mm mesh size,  $n = 5$ , April 2008; nc = taxon not counted. Meiofauna and macrofauna organisms are separated by dashed line.

Type of sample	A	B	C
Foraminifera	43	Nc	nc
Plathelminthes	123	Nc	nc
Nematoda	570	Nc	nc
Copepoda (post-naupliar stages)	133	Nc	nc
Ostracoda	273	Nc	nc
Halacaridae indet. (Acari)	25	Nc	nc
<i>Anthopleura hermaphroditica</i> (Actiniaria)	30	44	28.2
<i>Lineus</i> spec. (Nemertini)	0	0	0.1
Naididae indet. (Oligochaeta)	10	nc	nc
Capitellidae indet. (Polychaeta)	40	0	0
<i>Perinereis vallata</i> (Polychaeta)	0	3	2.6
Terebellidae indet. (Polychaeta)	0	2	1.9
<i>Scoloplos tribulosus</i> (Polychaeta)	3	0	0.3
Spionidae indet. (Polychaeta)	0	0	0.1
<i>Exosphaeroma lanceolata</i> (Isopoda)	0	3	0.4
<i>Monocorophium acherusicum</i> (Amphipoda)	243	147	nc
Haustoriidae indet. (Amphipoda)	0	0	<0.1
Gammaridae indet. (Amphipoda)	0	0	<0.1

the prey into the mouth. A few minutes later most tentacles were extended again. Stirring up sediment in low tide puddles caused anemones to open their tentacle crowns. When submerged and undisturbed, regardless of day and night, tentacles in *Anthopleura* were extended in all directions laterally and upwards but were never laid upon the sediment and were not probing within (Fig. 2). When subjected to flow, all tentacles point downstream. The presence of zooxanthellae and their crowding in the endoderm layer suggests that exudates of the photosynthetic symbionts contribute at least during summer months to the nutrition of *A. hermaphroditica*.

Microscopic analysis of feces collected from the oral opening showed abundant dinoflagellate zooxanthellae and a few diatoms. The zooxanthellae seemed to have been liberated into the coelenteron. Also setae of polychaetes and skeletal remains of amphipods were found in the feces. These feces were difficult to obtain and numbers were too low for a quantitative analysis. The coelenterons were usually found empty.

Benthic invertebrates coexisting with *A. hermaphroditica* were individually tested whether captured and consumed or not. The potential invertebrate prey was released in the water column of aquaria 25 mm above sediment densely inhabited by *A. hermaphroditica*. 24 individuals of small corophiid amphipod *M. acherusicum*, 2–4 mm in size, were rapidly taken and eaten. The 3 polychaete species offered did not swim and were captured immediately. 10 individuals of *Perinereis vallata*, 10–40 mm in size, became captured by several actinians at a time and fall into pieces, most of which were consumed. 2 terebellid individuals, 10–30 mm in size, were captured and eaten. 6 individuals of *Scoloplos tribulosus*, 10–20 mm in size, were captured, but then rejected. They did not survive. The small and agile isopod, *E. lanceolata*, was the only tested invertebrate which was swimming right through the tentacles and was not caught ( $n = 10$ , size 3–4 mm). Cannibalism in *A. hermaphroditica* was not observed. 10 small individuals were placed right upon the oral disc or between tentacles of larger individuals; there was no attempt to catch the offered sea anemones.

#### 3.4.3. Catching area

A dense net of *A. hermaphroditica* tentacles is widely spread over the mud flat areas. The diameter of opened oral discs without tentacles varied between 0.9 and 5.7 mm (mean  $2.7 \pm 0.9$ ,  $n = 40$ ) and with tentacles from 3.4 to 13.3 mm (mean  $7.0 \pm 2.0$ ,  $n = 40$ ), thus

increasing its area of prey capture by the factor  $7.3 \pm 2.8$ . The mean catching area of fully expanded individuals with tentacles covered  $42.2 \pm 25.2 \text{ mm}^2$  ( $n = 80$ ), which corresponds to a circular area of  $7.3 \pm 5.7 \text{ mm}$  in diameter. Considering a mean density of  $16,300 \text{ ind. m}^{-2}$  in muddy sand and mud at all locations studied, indicate that about 69% of the surface can be controlled by *A. hermaphroditica*. At Bahía Quillaie ( $11,000 \text{ ind. m}^{-2}$ ) nearly half of the muddy sediment surface is covered by the stinging tentacles of *A. hermaphroditica*.

#### 3.4.4. Predation

We were unable to identify any predator on *A. hermaphroditica* in the benthos. Attempts to catch nekton with a sweeping net of 7 mm mesh size in May 2008 were in vain, and no shrimp and crabs were observed on or above the mud surface where *A. hermaphroditica* was abundant. The brachyuran *Hemigrapsus crenulatus* was encountered in burrows at clay ridges or at mussel beds but not on bare mud or muddy sand where *A. hermaphroditica* was abundant.

Few birds were observed foraging on *Anthopleura* flats. Whimbrel, *Numenius phaeopus*, was probing deep into the mud, apparently searching for nereid worms. Dotterel, *Charadrius modestus*, also foraged on nereid worms, usually higher in the tidal zone than where *A. hermaphroditica* was common. One Chilean Flamingo, *Phoenicopterus chilensis*, stayed in May 2008 at Bahía Quillaie but its feeding scars were not observed on *Anthopleura* flats. A flock of dabbling ducks (*Anas flavirostris*) was only once observed feeding in puddles on the mudflat. The only bird possibly feeding on *A. hermaphroditica* was the Kelp Gull, *Larus dominicanus*. They followed the tide line but we could not identify the items these gulls were picking at on the mudflat. However, most of these gulls aggregated at mussel beds which were encountered close to low tide line, and not where *A. hermaphroditica* was common.

## 4. Discussion

In this study, the sea anemone *Anthopleura hermaphroditica*, endemic to southern Chile, is shown to populate estuarine intertidal mudflats at densities as high as  $30,000 \text{ m}^{-2}$  or on average about  $16,300 \text{ m}^{-2}$  ( $11,000 \text{ m}^{-2}$  Bahía Quillaie). Continuous brooding throughout the year as known from other members of the genus *Anthopleura* (Isomura et al., 2003) and observed by María Díaz (pers. comm.), may enable this anemone to stay at such high abundances. Intermittent low salinities are endured. The small actiniid is stuck in the sediment without any hard substrate for attachment and readily reburies when excavated.

Observations in the field and lab suggest that most of the typical zoobenthos, known from other South Chilean mudflats (Clasing et al., 1994), is kept away from the sediment by the extended tentacles forming a stinging umbrella above the sediment, and which is estimated to control almost half of the sediment surface. Although not measured, we suppose that *A. hermaphroditica* is potentially able to prevent settlement of pelagic larvae as *Nematostella vectensis* does (Hand and Uhlinger, 1992). Sea anemones are often euryphagous predators and several closely related intertidal species to *A. hermaphroditica* behave in this way (Tsurpalo and Kostina, 2003).

Predators of sea anemones are often fish, sea stars, gastropods, pantopods and polychaetes (Mercier and Hamel, 1994; Ottaway, 1977), but we could not detect any predation on *A. hermaphroditica*. Thus, our preliminary results indicate that a small actinian seems to prevent the establishment of a more diverse benthic fauna as a potential food source for fish and birds visiting intertidal mudflats in southern Chile.

#### 4.1. Why is *A. hermaphroditica* so successful in intertidal mud?

While sea anemones commonly occur at high densities on rocky shores, their densities in coastal sediments are usually low and have no

general effects on community structure and function. How does *Anthopleura hermaphroditica* manage to break this rule and what makes it different from *Nematostella vectensis*? Is the success of both species to be explained by unique adaptations of these sea anemones not found in other species? A similar question has been raised by Peterson and Black (1986) when discussing the abundance of the actinian *Heteractis malu* in low intertidal to shallow subtidal sand of a shore in Western Australia. With only about 6 individuals  $\text{m}^{-2}$  this sea anemone was not nearly as abundant as *A. hermaphroditica* in Chilean mud with an average density of  $16,000 \text{ ind. m}^{-2}$  and *N. vectensis* with an abundance of  $12,572 \text{ ind. m}^{-2}$  in an English marsh tide pool (Williams, 1983). However, due to its larger size (4–6 cm diameter and an average volume of  $16 \text{ cm}^3$ ) the total biovolume per  $\text{m}^2$  is only 20% of what has been estimated for *A. hermaphroditica*. Peterson and Black (1986) recognized an attachment problem as well as an energetic paradox for the observed prominence of *H. malu* in the benthos.

The attachment problem is solved by *H. malu* by attaching to abundant shell fragments and *Posidonia* rhizomes in the sand. Three other intertidal brooding species of the genus *Anthopleura* behave similar (Dunn, 1978; Yanagi and Daly, 2004), all of them attaching to small shell fragments, mussels or stones in the intertidal as does *Paranthus niveus* in the Chilean mud and sandflats (own observation). *A. hermaphroditica* and *N. vectensis* have gone a step further in this respect. These sea anemones do not require shell fragments or any other large objects for attachment. They burrow in mud and with their widened pedal discs form kind of an anchor. Once pushed out of the sediment both species are capable to rebury themselves rather quickly. Thus, *A. hermaphroditica* and *N. vectensis* are capable to colonize sedimentary areas independently of the availability of shell fragments and the like. While this is a general feature of the Edwardsiidae to which *N. vectensis* belongs, it may be unique among intertidal Actiniidae and may constitute a major reason for the success of *A. hermaphroditica* on the Chilean mudflats. The strong population fluctuations of *N. vectensis* (Hand, 1957; Kneib, 1985; Posey and Hines, 1991) are in contrast with our observation on the population of *A. hermaphroditica*. In Bahía Quillaie mean population density has changed only marginally over a time period of twenty years.

The absence of *A. hermaphroditica* from rippled sand unless stabilized by mussels or tube worms, however, points to the limitations of its burrowing performance. Wave-disturbed, rippled bottoms or strongly bioturbated sand flats are unsuitable for *A. hermaphroditica*; here it seems to become washed away due to limited anchorage strength.

How can we explain the stable communities of *A. hermaphroditica* in Southern Chile and the up and downs of *N. vectensis* in English marsh pools? A striking difference between both species is the presence of endosymbiotic zooxanthellae in *A. hermaphroditica* observed all year long. Most probably dense colonies of *N. vectensis* are running out of food in temperate regions whereas *A. hermaphroditica* receive a significant amount of its respiratory carbon requirement from its endosymbiotic zooxanthellae throughout the year. As feeding is impossible at low tide, heterotrophic consumption is restricted to high tide for *A. hermaphroditica* and photosynthesis become an alternative pathway for nutrition as long as the sediment surface does not completely dry out. The related sea anemone, *Anthopleura elegantissima*, receives at least 34–42% of their respiratory carbon requirements from their endosymbiotic zooxanthellae. Indeed, this value decreases to 17% when intertidal sea anemones are exposed to air for 15 h and the anemone retracts its tentacle and contracts its marginal sphincter (Shick and Dykens, 1984). The benefits of symbiotic algae to the *A. hermaphroditica* may be evident on different temporal scales. During winter months it contributes only to a smaller amount to sea anemone nutrition, but in summer months zooxanthellae production may contribute directly to the reproduction of *A. hermaphroditica*.

*A. hermaphroditica* has been shown in this study to be eury- to polyhaline with an ability to endure intermittent low salinities.

Nevertheless, estuaries in southern Chile with salinities below 20 over extended periods of time seem to lack *A. hermaphroditica* (i.e., Quijón and Jaramillo, 1996; Quijón et al., 1996; Jaramillo et al., 2001; Duarte et al., 2006). Martin et al. (1996) noticed that *A. elegantissima* expelled symbiotic algae under hyposaline stress and this entailed bleaching. Although we noticed that *A. hermaphroditica* retracts its tentacles when subjected to salinity below 20, expulsion of zooxanthellae was not observed and tentacles were expanded once salinity increased again. Sensitivity to low salinity and sediment mobility should be explored further as possible key variables to the distribution of *A. hermaphroditica* in southern Chile.

*N. vectensis* is adapted to lower salinities, the anemone is usually found in brackish marsh pools with salinities of 10 to 25 but it has been recorded in salinities of 9 to 52 (Williams, 1983). It is demonstrably an eurythermal, euryhaline animal (Hand and Uhlinger, 1994), but is restricted to estuaries, whereas *A. hermaphroditica* inhabits the intertidal and subtidal from the mudflat to the rocky shore even if not in high densities. Hand and Uhlinger (1994) suppose that predation restricts *N. vectensis* to less saline portions of estuaries.

#### 4.2. Reproduction and dispersal

The ability to brood and to release young at a spherical diameter of 1–2 mm which may immediately bury throughout the year, could also contribute to the success of *A. hermaphroditica*. However, brooding as well as asexual division by longitudinal fission or pedal laceration is not uncommon in actinarians (Manuel, 1988; Buchsbaum Pearse, 2007) especially in the genus *Anthopleura*, where at least four internally brooding intertidal species are known (Yanagi and Daly, 2004). If such a mode of reproduction would be a key to dense populations in sediments, *A. hermaphroditica* would presumably not be the only sea anemone realizing this niche. However, relative to other actiniids and members of the genus *Anthopleura*, this species is unusually small and may represent a case of progenesis, truncating ontogeny by early brooding which may be interpreted as an r-strategy to quickly occupy new habitats and to persist by high numbers rather than by individual longevity (see Gould, 1977). This may be advantageous on estuarine mudflats. Brooding animals were found in January 1989 and April 2008, but expulsion of juveniles was much higher in January than in April. We suppose that brooding time is extremely short during austral summer when plenty of food is available and symbiotic zooxanthellae contribute a large portion of their photosynthate to the host and extended under less favorable conditions, but further research is needed.

*Nematostella vectensis* shows sexual reproduction after only 55 d (see review by Hand and Uhlinger, 1994). Reproduction in *N. vectensis* is often asexually by transverse fission and many populations consist of one sex (probably clones) only (Hand and Uhlinger, 1994). Besides sexual and asexual reproduction, *N. vectensis* has extensive capacity for regeneration. It can undergo complete bidirectional regeneration following bisection: the oral half will regenerate a new foot and the aboral half will regenerate a new head (Darling et al., 2004).

We do not know whether the brooded young in the coelenterons of *A. hermaphroditica* are genetically identical to the parent and the products of parthenogenesis. Both male and female gametes may be present simultaneously in perfect mesenteries of the same individual but were generally poorly developed (own observations). Thus, it remains unknown whether clones or outcrossing, brooding or larval dispersal prevails in *A. hermaphroditica*. However, up to now there is no evidence for the latter, and from the unimodal size distributions in January and April it may be inferred that continuous production by brooded young seems to be the ordinary mode of reproduction.

Natural dispersal of contracted individuals with tidal currents was not observed but could be easily initiated by trampling in the mud during submergence. Contracted individuals with swollen pedal discs swiftly rolled along with the currents. This behavioral mode was

earlier observed for the burrowing actinarian *Sagartia troglodytes* by Riemann-Zürneck (1969). However, in *A. hermaphroditica* natural means of dispersal seem to be limited to short distances.

We conclude that early brooding may help *A. hermaphroditica* to persist on Chilean mudflats in high abundance, whereas reproductive and developmental plasticity allows *N. vectensis* to populate tide marshes. However, these adaptations are not sufficiently unique to explain why elsewhere other actinians do not achieve similar abundances on intertidal mudflats. May be essential is the combination with anchoring in the mud without requiring any hard substrate for adherence, whereas the presence of zooxanthellae are a requirement for a stable and high population density.

#### 4.3. Trophic position

Functionally, *Anthopleura hermaphroditica* may be regarded as a primary producer, whereas *Nematostella vectensis* lacks any phototrophic symbionts. *A. hermaphroditica* hosts innumerable zooxanthellae in its tissue and exposes its tentacle crown to the sun when covered by water with a salinity >20. On most days turbidity is low in Bahía Quillaie. Davy et al. (1996) reported that *A. ballii* covers 73% of its daily respiratory carbon requirements at 1.5 m depth on sunny days by photosynthesis and *A. elegantissima* receives at least 34–42% of their respiratory carbon requirements from their endosymbiotic zooxanthellae under favourite conditions (Shick and Dykens, 1984). *A. elegantissima* hosts two phylogenetically different symbiotic microalgae, a dinoflagellate *Symbiodinium zooxanthellae* and a chlorophyte (Verde and McCloskey, 2002). In *A. hermaphroditica* the olive-green to brown colored individuals contained only dinoflagellates. The magnitude of carbon translocation from the zooxanthellae to *A. hermaphroditica* in Bahía Quillaie is under investigation and will be reported on later (Schubert et al., in prep.). Up to 140 µg Chl a g<sup>-1</sup> tissue fresh weight suggest that under clear sky conditions zooxanthellae may be able to largely satisfy the daily respiratory carbon requirements of their hosts.

While *N. vectensis* is an important euryphagous predator (Frank and Bleakney, 1978; Posey and Hines, 1991), the Australian actiniid *H. malu* bears zooxanthellae and is abundant in shallow sandy bottoms with a low turbidity in the water above (Peterson and Black, 1986). These authors argue that the contribution of photosynthetic products to the nutrition of the sea anemone may solve the apparent energetic paradox of the prominence of a carnivore in a zoobenthic assemblage with relatively few prey items found in the coelenterons. It supports also our assumption, that *N. vectensis* is not able to maintain stable populations at high densities because of food limitation.

We found remains of prey in the feces of *A. hermaphroditica* but rarely observed sea anemones with prey caught by the tentacles unless this was offered by us experimentally. Coelenterons were not filled with detritus as it occurs in the estuarine *Sagartia troglodytes*, regarded as a detritus feeder by Riemann-Zürneck (1969). Our preliminary experiments suggest that *A. hermaphroditica* feeds rather unselectively on prey organisms which happen to touch their tentacles. Only an orbiniid polychaete was rejected and an isopod was never caught.

The trophic position of *A. hermaphroditica* seems strange. With *A. hermaphroditica* there is an abundant and potent predator on benthic fauna but we found little evidence that this fauna contributes significantly to its nutrition. As an explanation we suggest avoidance behavior by the potential prey. Although capable of swimming, the superabundant tube-dweller *Monocorophium acherusicum* was never observed swimming or crawling outside its communal tube system. An abundant nereid polychaete lives in burrows which extend well below the layer of the sea anemones, and we never observed it moving on the sediment surface as other nereid species often do. In both cases, this may be an avoidance behavior in response to the stinging tentacles of the sea anemone. While the corophiids

reproduce within their burrows, the mode of reproduction in *Perinereis vallata* is not known and the question remains open how these worms colonize *Anthopleura* flats.

The composition of the mudflat benthos is rather poor in species and unusual in being devoid of mollusks. These were only found outside *Anthopleura* flats, either in the form of mussel beds (*Mytilus edulis* associated with *Perumytilus purpuratus*, *Siphonaria lessoni* and *Tegula atra*) or several endobenthic bivalves with *Tagelus dombeii* being particularly abundant in sand or the gastropods *Nassarius gayi* and *Caecum chilense* also dwelling in sand of the lower tidal zone where zoobenthic diversity is much higher (see Reise, 1991).

Considering a density of *A. hermaphroditica* with 1–3 individuals per cm<sup>2</sup> and each covering 0.4 cm<sup>2</sup> with its tentacular crown in the muddy sediments, there is little chance for potential prey organisms to settle without being caught before. The same argument used Hand and Uhlinger (1994) for *N. vectensis*, which tentacle crown is of a similar size (8–10 mm in diameter) and densities are in the same order.

We suggest that larval or juvenile settlement of mollusks is prevented or reduced by both sea anemones when they are present in high densities although the general importance of larval capture by predators such as sea anemones is questioned by Lindquist (1996). Possibly also other early juvenile stages may be affected by dense populations of *A. hermaphroditica* and *N. vectensis*. McKenzie (1977) reports significant predation of the sea anemone *Diadumene leucolena* on oyster larvae, and concludes that it substantially limits the abundance of oysters in the Maryland portion of Chesapeake Bay.

As predators on sea anemones, fish, crabs, shrimp, nudibranchs, some prosobranchs, starfish, polychaetes and pycnogonids have been mentioned (see (Lizama and Blanquet, 1975; Ottaway, 1977; Manuel, 1988)). None of these were observed by us preying on *A. hermaphroditica* or they were not present at all. We also looked for birds and found no particular evidence that they foraged on sea anemones. Although we admit that more attention needs to be given to potential predators, we conclude that the mudflat population of *A. hermaphroditica* is unaffected by predation or may have found a refuge devoid of predators. The latter argument can be used also for *N. vectensis*. Hand and Uhlinger (1992) recorded asexual divisions in salinities of 7 to 42 and successful sexual reproduction in salinities of 12 to 34 and reported also its eurythermy. However, high densities of *N. vectensis* are restricted to tidal salt marshes. Both species are reported to occur at low abundance from a variety of habitats in their natural environment, e.g. lagoons and other intertidal habitats in case of *N. vectensis* (Darling et al., 2004) and mussel beds, the intertidal and subtidal rocky shore in case of *A. hermaphroditica* (Carlgren, 1899, 1927; Häussermann and Foerster, 2005 and own observations). Predation may be the reason for the limited success in these habitats, but further research is needed.

#### 4.4. Conclusions

We scratched with our preliminary experiments only at the surface of a phenomenon observed for the first time on intertidal mudflats in southern Chile and compared it to a similar species observed in the northern hemisphere. The ability of the small brooder *A. hermaphroditica* to burrow and anchor in soft mud and muddy sand without solid objects seems to be unique among shallow-water actiniid sea anemones, but is shared with the edwardsiid sea anemone *N. vectensis*. However, the symbiosis with dinoflagellates allows it to maintain high population densities without relying on an ample supply of prey and makes it different from *N. vectensis*. Nevertheless, both species seem to relegate most associated zoobenthos to a life below surface and may prevent the settlement of larvae by other species such as bivalves. The sea anemones, in turn, may enjoy a refuge from predation on the intertidal mudflats (*A. hermaphroditica*) and intertidal salt marshes (*N. vectensis*). While several studies have

been conducted on *N. vectensis*, further work is needed to understand the trophic role of *A. hermaphroditica* and its mixotrophic mode of life.

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#### References

- Baird, D., Asmus, H., Asmus, R., 2004. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. *Mar. Ecol. Prog. Ser.* 279, 45–61.
- Buchsbaum Pearce, V., 2007. Sea anemones. In: Denny, M.D., Gaines, S.D. (Eds.), *Encyclopedia of tidepools & rocky shores*. Univ. California Press, Berkeley, pp. 486–491.
- Buhr, K.-J., Winter, J.E., 1977. Distribution and maintenance of *Lanice conchilega* association in the Weser estuary (FRG), with special reference to the suspension-feeding behaviour of *Lanice conchilega*. In: Keegan, B.F., Ceidigh, P.O., Boaden, P.J.S. (Eds.), *Biology of benthic organisms*. Pergamon Press, Oxford, pp. 101–113.
- Carlgren, O., 1899. Zoantharien. Ergebnisse der Hamburger Magalhaensischen Sammelreise, 4. L. Friederichsen & Co., Hamburg, pp. 1–47. 1.
- Carlgren, O., 1927. Actiniaria and Zoantharia. In: Odhner, T. (Ed.), *Further zoological results of the Swedish Antarctic Expedition 1901–1903*, 2. Norstedt, P.A., Söner, Stockholm, pp. 1–102. 3.
- Carlgren, O., 1959. Corallimorpharia and Actiniaria with description of a new genus and species from Peru. Reports of the Lund University Chile Expedition 1848–49, 38. Lunds Universitets Arsskrift. (N.F.) Adv 2, 56 (6), 1–39.
- Clasing, E., Brey, T., Stead, R., Navarro, J., Ascencio, G., 1994. Population dynamics of *Venus antiqua* (Bivalvia, Veneracea) in the Bahía de Yaldad, Isla de Chiloé, Southern Chile. *J. Exp. Mar. Biol. Ecol.* 177, 171–186.
- Darling, J.A., Reitzel, A.R., Finnerty, J.R., 2004. Regional population structure of a widely introduced estuarine invertebrate: *Nematostella vectensis* Stephenson in New England. *Mol. Ecol.* 13, 2969–2981.
- Dauvin, J.C., Desroy, N., 2005. The food web in the lower part of the Seine estuary: a synthesis of existing knowledge. *Hydrobiologia* 540, 13–27.
- Davy, S.K., Lucas, I.A.N., Turner, J.R., 1996. Carbon budgets in temperate anthozoan-dinoflagellate symbioses. *Mar. Biol.* 126, 773–783.
- Di Castri, F., Hajek, E.R., 1976. *Bioclimatología de Chile*. Editorial de la Universidad Católica de Chile, Santiago, Chile.
- Duarte, C., Jaramillo, E., Contreras, H., Figueroa, L., 2006. Community structure of the macrofauna in the sediments below an intertidal mussel bed (*Mytilus chilensis* (Hupe)) of southern Chile. *Rev. Chil. Hist. Nat.* 79 (3), 353–368.
- Dunn, D.F., 1978. *Anthopleura handi* n. sp. (Coelenterata, Actiniaria), an internally brooding, intertidal sea anemone from Malaysia. *Wasmann J. Biol.* 35, 54–64.
- England, K.W., 1987. Certain Actiniaria (Cnidaria, Anthozoa) from the Red Sea and tropical Indo-Pacific Ocean. *Bull. Br. Mus. (Nat. Hist.) (Zool.)* 53(4), 205–29.
- Fager, E.W., 1968. A sand-bottom epifaunal community of invertebrates in shallow water. *Limnol. Oceanogr.* 13, 448–464.
- Frank, P., Bleakney, J.S., 1978. Asexual reproduction, diet, and anomalies of the anemone *Nematostella vectensis* in Nova Scotia. *Can. Field-Nat.* 92, 259–263.
- Gould, S.J., 1977. *Ontogeny and phylogeny*. Belknap Press of Harvard Univ. Press, Cambridge.
- Hand, C., 1957. Another sea anemone from California and the types of certain California species. *J. Wash. Acad. Sci.* 47, 411–414.
- Hand, C., Uhlinger, K.R., 1992. The culture, sexual and asexual reproduction, and growth of the sea-anemone *Nematostella vectensis*. *Biol. Bull.* 182, 169–176.
- Hand, C., Uhlinger, K.R., 1994. The unique, widely distributed, estuarine sea anemone, *Nematostella vectensis* Stephenson: A review, new facts, and questions. *Estuaries* 17, 501–508.
- Hartmann-Schröder, G., 1991. Beitrag zur Polychaetenfauna der Bahía Quillaípe (Süd-Chile). *Helgoländer Meeresunters* 45, 39–58.
- Häussermann, V., Foerster, G., 2005. Distribution patterns of Chilean shallow-water sea anemones (Cnidaria: Anthozoa: Actiniaria, Corallimorpharia), with a discussion of the taxonomic and zoogeographic relationships between the actinofauna of the South East Pacific, the South West Atlantic and the Antarctic. *Sci. Mar.* 69 (suppl.2), 91–102.
- Isomura, N., Hamada, K., Nishihira, M., 2003. Internal brooding of clonal propagules by a sea anemone, *Anthopleura* sp. *Invert. Biol.* 122, 293–298.
- Jaramillo, E., Contreras, H., Quijón, P., 2001. Seasonal and interannual variability in population abundances of the intertidal macrofauna of Queule river estuary, south-central Chile. *Rev. Chil. Hist. Nat.* 74, 455–468.
- Kneib, R.T., 1985. Predation and disturbance by grass shrimp, *Palaemonetes pugio* Holthius, in soft-substratum benthic invertebrate assemblages. *J. Exp. Mar. Biol. Ecol.* 93, 91–102.
- Kuris, A.M., et al., 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* 454, 515–518.

- Leguerrier, D., Niquil, N., Boileau, N., Rzeznik, J., Sauriau, P., Moine, O.L., Bacher, C., 2003. Numerical analysis of the food web of an intertidal mudflat ecosystem on the Atlantic coast of France. *Mar. Ecol. Prog. Ser.* 246, 17–37.
- Lesson, R.P., 1830. Voyage Autour du Monde, Execute par Ordre du Roi, sur la Corvette de La Majeste, La Coquille, pendant les annees 1822, 1823, 1824, et 1825, sous le ministere et conformement aux instructions de S. E. M. de Marquis de Clermont-Tonnerre, ministre de la marine. Chapter: XVI, Vol.2, part 2 (zoophytes), Arthus Bertrand, Paris, 67–83.
- Levene, H., 1960. Robust tests for equality of variances. In: Olkin, I., Hotelling, H., et al. (Eds.), *Contributions to Probability and Statistics: Essays in Honor of Harold Hotelling*. Stanford University Press, pp. 278–292.
- Lindquist, N., 1996. Palatability of invertebrate larvae to corals and sea anemones. *Mar. Biol.* 126, 745–755.
- Lizama, J., Blanquet, R.S., 1975. Predation on sea anemones by the amphinomid polychaete, *Hermodice carunculata*. *Bull. Mar. Sci.* 25, 442–443.
- Manuel, R.L., 1988. In: Kermack, D.M., Barnes, R.S.K. (Eds.), *British Anthozoa*. Synopsis of the British Fauna. : New Series 18. Brill and Backhuys, Leiden.
- Martin, K.L.M., Lawson, M.C., Engebretson, H., 1996. Adverse effects of hyposalinity from storm water runoff on the aggregating anemone, *Anthopleura elegantissima*, in the marine intertidal zone. *Bull. South Calif. Acad. Sci.* 95, 46–51.
- McKenzie Jr., C.L., 1977. Sea anemone predation on larval oysters in Chesapeake Bay (Maryland). *Proc. Natl Shellfish. Assoc.* 76, 113–117.
- McLusky, D.S., Elliott, M., 2004. *The estuarine ecosystem*. Oxford Univ. Press, Oxford.
- McMurrich, J.P., 1904. The Actiniae of the Plate collection (Fauna Chilensis 3). *Zoologische Jahrbücher Jena, Suppl.* 6, 215–305.
- Mercier, A., Hamel, J.F., 1994. Deleterious effects of a pycnogonid on the sea anemone *Bartholomea annulata*. *Can. J. Zool.* 72, 1362–1364.
- Ottaway, J.R., 1977. Predators of sea anemones. *Tuatara* 22, 213–221.
- Peterson, C.H., Black, R., 1986. Abundance patterns of infaunal sea anemones and their potential benthic prey in and outside seagrass patches on a western Australian sand shelf. *Bull. Mar. Sci.* 38, 498–511.
- Piersma, T., de Goeij, P., Tulp, I., 1993. An evaluation of intertidal feeding habitats from a shorebird perspective: Towards relevant comparisons between temperate and tropical mudflats. *Neth. J. Sea Res.* 31, 503–512.
- Posey, M.H., Hines, A.H., 1991. Complex predator-prey interactions within an estuarine benthic community. *Ecology* 72, 2155–2169.
- Quijón, P., Jaramillo, E., 1996. Seasonal vertical distribution of the intertidal macroinfauna in an estuary of South-Central Chile. *Estuar. Coast. Shelf Sci.* 43, 653–663.
- Quijón, P., Jaramillo, E., Pino, M., 1996. Macroinfaunal assemblages associated with mussel and clam beds in an estuary of southern Chile. *Estuaries* 19, 62–74.
- Raffaelli, D., 2000. Trends in food web research. *J. Exp. Mar. Biol. Ecol.* 250, 71–79.
- Reise, K., 1985. Tidal flat ecology. *Ecological studies*. Springer, Berlin.
- Reise, K., 1991. Macrofauna in mud and sand of tropical and temperate tidal flats. In: Elliott, M., Ducrotoy, J.-P. (Eds.), *Estuaries and Coasts: Spatial and temporal intercomparisons*. Olsen and Olsen, Fredensborg, pp. 211–216.
- Reise, K. (Ed.), 2001. *Ecological comparisons of sedimentary shores*. Ecological Studies 151. Springer, Berlin.
- Reitzel, A.M., Darling, J.A., Sullivan, J.A., Finnerty, J.R., 2008. Global population genetic structure of the starlet anemone *Nematostella vectensis*: multiple introductions and implications for conservation policy. *Biol. Invasions* 10, 1197–1213.
- Riemann-Zürneck, K., 1969. *Sagartia troglodytes* (Anthozoa) Biologie und Morphologie einer schlickbewohnenden Aktinie. *Veröff. Inst. Meeresforsch. Bremerh.* 12, 169–230.
- Sanamyan, N.P., Sanamyan, K.E., Schories, D., 2009. On authorship of Chilean anemone '*Bunodactis hermafroditica*' (Cnidaria: Actiniaria) and its generic assignment. *Zoosystematica Rossica* 18, 320–322.
- Shick, J.M., Dykens, J.A., 1984. Photobiology of the symbiotic sea anemone *Anthopleura elegantissima*: photosynthesis, respiration, and behavior under intertidal conditions. *Biol. Bull.* 166, 608–619.
- Stephenson, T.A., 1935. *The British Sea Anemones*. Ray Society, London.
- Tsurpalo, A.P., Kostina, E.E., 2003. Feeding characteristics of three species of intertidal sea anemones of the South Kuril Islands. *Russ. J. Mar. Biol.* 29, 31–40.
- Verde, E.A., McCloskey, L.R., 2002. A comparative analysis of the photobiology of zooxanthellae and zoochlorellae symbiotic with the temperate clonal anemone *Anthopleura elegantissima* (Brandt). *Mar. Biol.* 141, 225–239.
- Williams, R.B., 1983. The starlet sea anemone: *Nematostella vectensis*. In: Wells, S.M., Pyle, R.M., Collins, N.M. (Eds.), *The IUCN Invertebrate Red Data Book*. IUCN, Gland, Switzerland, pp. 43–46.
- Yanagi, K., Daly, M., 2004. The hermaphroditic sea anemone *Anthopleura atodai* n. sp. (Anthozoa : Actiniaria : Actiniidae) from Japan, with a redescription of *A. hermafroditica*. *Proc. Biol. Soc. Wash.* 117, 408–422.