







ORIGINAL RESEARCH

Distribution, abundance, and size structure of the Pacific cupped oyster *Magallana gigas* in northern Patagonia

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ABSTRACT. In the 1980s, the Pacific oyster *Magallana gigas* (Thunberg, 1783) was deliberately introduced in the southern region of the Province of Buenos Aires (Bahía Anegada, BA), Argentina. In 2004, its presence expanded 80 km south of the Río Negro estuary along the coast of El Cóndor (EC). Although oysters have demonstrated dispersal capability, there is limited data as regards the EC population since 2011. This research focusses on the present *M. gigas* population encompassing distribution, abundance, and size structure along a 180-km coastal line from EC to San Antonio Este (SAE). Subsequently, we compared these data with those for the BA population. The presence of *M. gigas* in the Province of Río Negro was detected in four sites: three of them near the Río Negro estuary (EC, Piedras Verdes PV, and El Pescadero); and the last one in San Antonio Bay. Estimated average abundances near the estuary were lower (range $1.8 \cdot 10^{-3} \pm 0.6 \cdot 10^{-3}$ and $9 \cdot 10^{-2} \pm 3.4 \cdot 10^{-2}$ ind. m^{-2}) than BA (105 ± 2 ind. m^{-2}). Presence in SAE was only limited to one site and three adults *M. gigas*. The BA oyster population exhibited a multimodal distribution, with a significant number of recruits, whereas the PV site displayed a trimodal structure dominated by large specimens. In EC, owing to the limited number of individuals, modal components were less discernible, but small oysters predominated. The current abundance of *M. gigas* in EC was considerably lower than that in 2011, indicating a population decline. Despite this, the presence of juvenile oysters suggests recent recruitment, emphasizing species resilience. These results show that *M. gigas* faces challenges when attempting to establish itself in this specific region. Studying the underlying causes would help to understand the factors that limit the expansion of a species considered to be a global invader.



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Key words: Invasive species, population dynamics, intertidal, ecosystem engineer, recruitment.

Distribución, abundancia y estructura de tamaño de la ostra cóncava del Pacífico, *Magallana gigas*, en el norte de la Patagonia

RESUMEN. En la década de 1980, la ostra del Pacífico, *Magallana gigas* (Thunberg, 1783), fue introducida deliberadamente en la región sur de la Provincia de Buenos Aires (Bahía Anegada, BA), Argentina. En 2004, su presencia se expandió 80 km al sur del estuario del Río Negro, a lo largo de la costa de El Cóndor (EC). Si bien las ostras han demostrado capacidad de dispersión, existen datos limitados sobre la población de EC desde 2011. Esta investigación se centra en la población actual de *M. gigas* que abarca la distribución, abundancia y estructura de talla a lo largo de una línea costera de 180 km desde EC hasta San Antonio Este (SAE). Posteriormente, comparamos estos datos con los de la población de BA. La presencia de *M. gigas* en la Provincia de Río Negro se detectó en cuatro

sitios: tres de ellos cerca del estuario del Río Negro (EC, Piedras Verdes PV y El Pescadero); y el último en la Bahía de San Antonio. Las abundancias promedio estimadas cerca del estuario fueron menores (rango $1,8 \cdot 10^{-3} \pm 0,6 \cdot 10^{-3}$ y $9 \cdot 10^{-2} \pm 3,4 \cdot 10^{-2}$ ind. m^{-2}) que en BA (105 ± 2 ind. m^{-2}). La presencia en SAE solo se limitó a un sitio y tres individuos adultos de *M. gigas*. La población de ostras de BA exhibió una distribución multimodal, con un número significativo de reclutas, mientras que el sitio PV mostró una estructura trimodal dominada por especímenes grandes. En EC, debido al número limitado de individuos, los componentes modales fueron menos discernibles, pero predominaron las ostras pequeñas. La abundancia actual de *M. gigas* en EC fue considerablemente menor que en 2011, lo que indica una disminución de la población. A pesar de esto, la presencia de ostras juveniles sugiere un reclutamiento reciente, lo que enfatiza la resiliencia de la especie. Estos resultados muestran que *M. gigas* enfrenta desafíos cuando intenta establecerse en esta región específica. Estudiar las causas subyacentes ayudaría a comprender los factores que limitan la expansión de una especie considerada invasora global.

Palabras clave: Especies invasoras, dinámica poblacional, intermareal, ingeniero ecosistémico, reclutamiento.

INTRODUCTION

Human actions facilitate certain species to reach previously inaccessible regions, establish self-sustaining populations, and spread to novel environments, a phenomenon known as biological invasions (Elton 1958). In marine and estuarine environments, oysters represent a significant example of invasive species (Carlton 1992; Reise 1998), acting as ecosystem engineers that modify physical and chemical environments, influencing populations, communities, and food webs through the creation of biogenic reefs in soft-sediment marine landscapes (Ruesink et al. 2005). Aquaculture has been a key driver for oyster introductions since the 1950s, often aimed at replacing declining native populations or developing new export products (Shatkin et al. 1997; Ruesink et al. 2005).

The Pacific oyster, *Magallana* (= *Crassostrea*) *gigas* (Thunberg, 1783), native to the northwest Pacific coast, has been introduced to at least 45 ecoregions worldwide (Molnar et al. 2008). While deliberate introductions account for many of these occurrences, the species has also expanded its range through unintentional transport and natural dispersal from established populations, as evidenced in Scandinavian waters including Denmark, Norway, and Sweden (Dolmer et al. 2014), as well as in New Zealand (Dinamani 1991). Although *M. gigas* has demonstrated considerable success in

colonizing new environments, its establishment patterns vary significantly across regions (Carrasco 2012). In some areas, environmental constraints have either precluded successful establishment or resulted in intermittent recruitment dynamics, characterized by periodic population pulses that correspond with favorable environmental conditions (Diederich et al. 2005).

In Argentina, this species was introduced for commercial purposes in 1982 in Bahía Anegada, in the southern area of the Province of Buenos Aires ($39^{\circ} 00' S$ to $40^{\circ} 40' S$ and $62^{\circ} 10' W$), where it established a wild population (Orensanz et al. 2002). Since then, the species have spread northwards to the Bahía Blanca estuary (Dos Santos and Fiori 2010) and southwards to El Cóndor, in the area influenced by the Río Negro estuary, which constitutes the administrative boundary between the provinces of Buenos Aires and Río Negro (González et al. 2005) (Figure 1). The success of the species in this region is attributed to several factors, including suitable water temperatures for gonad maturation and spawning (Castaños et al. 2009), availability of appropriate substrates, and its ability to recruit on various surfaces (Carrasco et al. 2018). These established populations have created shallow intertidal reefs that have significantly altered local community structure by providing habitat for invertebrates and affecting shorebird feeding patterns (Escapa et al. 2004; Bazterrica et al. 2022), demonstrating ecological implications of oyster invasions in the region.

A monitoring effort that began in 2008 tracked *M. gigas* distribution along the northern coast of the Province of Río Negro. Findings indicated higher densities near El Cóndor's central beach and a 30-km western expansion, reaching near the eastern limit of San Matías Gulf (Roche et al. 2010) (Figure 1). However, the program ceased in 2011, leaving the current species distribution unknown in an area that encompasses four protected natural zones and a crucial provincial fishing reserve (Provincial laws 1960, 2519, 3222, 2670, 2669; <http://www.legisrn.gov.ar>). Since impacts of invasive species depend on distribution, abundance, and other ecological factors (Markert et al. 2010), assessing these parameters for *M. gigas* an initial step to evaluate its potential effects in the area. Environmental conditions at the invasion front that affect the survival and individual growth of

colonizing individuals can profoundly influence the establishment and subsequent dispersal of the invasive species (Burton et al. 2010). The original monitoring of the cupped oyster in the Province of Río Negro (Roche et al. 2010) and a preliminary survey carried out in April 2019 in El Cóndor revealed the persistence of the species in the area, although in relatively very low abundance (approximately 0.1 ind. m⁻²) in comparison with those reached in other natural environments in the world and Argentina (Bahía Anegada: 90 ind. m⁻², Escapa et al. 2004; Las Toninas: 131 ind. m⁻², Gilberto et al. 2012; Sylt, Wadden Sea: 125.8 ind. m⁻², Diederich et al. 2005). In other locations where *M. gigas* was introduced, lag phases were observed. For example, in Sylt, Wadden Sea, the first established populations emerged 17 years post-commercial introduction (Wehrmann et al. 2000), while in

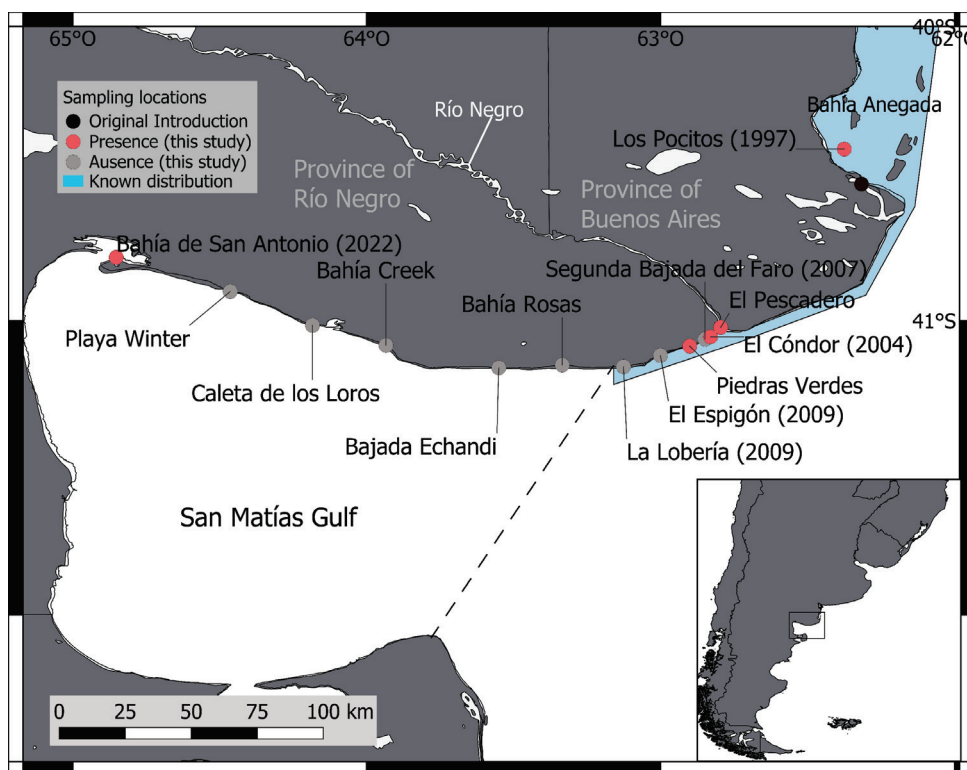


Figure 1. Distribution of *Magallana gigas* on the northern coast of the Province of Río Negro, Argentina. Years in brackets indicate first report in the corresponding site.

South Africa, a lag span of 51 years was observed (Robinson et al. 2005). Typically, these lag phases coincide with suboptimal temperatures and/or salinities for larval development, or unfavorable hydrological regimes that prevent postlarvae settlement by carrying them to unsuitable substrates (Guy and Roberts 2010). Until now, no studies have explored environmental conditions in El C ndor and their connection to *M. gigas* invasive patterns. Assessing physicochemical factors (temperature, dissolved oxygen, salinity, turbidity, wave energy) and food availability through a comparison with established population zones provides insights into impediments to the establishment of new population.

This study aimed to evaluate the distribution, abundance and size structure of *M. gigas* at the invasion forefront on the northern coast of the Province of R o Negro. Additionally, it sought to identify environmental factors influencing its potential expansion.

MATERIALS AND METHODS

Distribution

In October 2020, a one-time comprehensive survey was conducted between El C ndor (41  3.30' S, 62  49.81' W) and Caleta de los Loros (41  0.98' S, 64  11.5' W), following recommendations for monitoring frequency during early invasion stages (Guy and Roberts 2010). At each site, two parallel transects of 1,000 m each were surveyed (totaling 2,000 m per site) along the low-tide line in the lower intertidal zone. To distinguish *M. gigas* from native oysters (*Ostrea spreta* d'Orbigny, 1845 and *O. puelchana* d'Orbigny, 1842), morphological features were examined (Borges 2006). The most evident diagnostic character between genera is the absence of interlocking teeth and sockets in the hinge of *M. gigas*, which is typical of the Genus *Ostrea*. Additionally, the upper or right valve is

flat in native oysters (flat oysters), whereas it is curved in *M. gigas* (cupped oyster) (Borges 2006). *Magallana gigas* valves are also distinctive by being robust, irregularly shaped, with a nacreous interior; the hinge presents a central ligament and deep folds that are not observed in native species of the Genus *Ostrea* (Evseev et al. 1996; Borges 2006).

Transects involved daily low-tide surveys at sites with previous *M. gigas* records (El C ndor, Segunda Bajada del Faro, El Espig n, and La Lober a) and in areas of potential ongoing invasion (Bajada Echandi, Bah a Rosas, Bah a Creek, and Caleta de los Loros). The latter sites were selected to provide uniform coverage along the 120 km of coastline extending from the R o Negro estuary, while ensuring accessibility to sampling areas. Access to this predominantly cliff-lined coast is limited to man-made descents (Bajada Echandi and Bah a Creek) and natural embayment (Bah a Rosas and Caleta de los Loros). Caleta de los Loros, a protected area characterized by reduced wave exposure, was of particular interest since this environmental feature could potentially influence oyster settlement. Moreover, based on information from local fishermen and divers about the presence of *M. gigas* at the mouth of the R o Negro (El Pescadero) and San Antonio Este port, two sampling surveys were carried out in April and September 2022, respectively. The objective was to map the distribution of the species in this region (Figure 1).

Abundance

The abundance of *M. gigas* was assessed at Los Pocitos (LP), a site within Bah a Anegada characterized by dense oyster reefs, and two sites in the Province of R o Negro (El C ndor EC, and Piedras Verdes PV), where oyster distribution primarily consisted of dispersed solitary individuals on abrasion platforms. In each scenario, despite challenges in comparability across sites, distinct sampling techniques were employed. While plot sampling is recommended for high-density populations, the more efficient linear distance sampling

approach was employed for populations with dispersed individuals (Buckland et al. 2005; Miller et al. 2019).

In LP, the abundance estimation involved random 0.25 m² quadrats. The process began by outlining the study area, which comprised the rock abrasion platform of the lower and middle intertidal zone near the fishermen's walkway (7,688 m²). Google Earth was used to place 35 random spots. At each point, a quadrat was positioned, and all individuals within it were collected and subsequently transported to the laboratory for counting. The mean number of oysters *per* quadrat in the site was estimated using a generalized linear model performed with the package MASS in R (Venables and Ripley 2002; Bolker et al. 2009; R Core Team 2020) using the number of oysters *per* quadrat as the response variable.

In EC and PV, the density was estimated by means of linear distance sampling (Buckland et al. 2005). To achieve this, linear transects were established along the lower and middle intertidal zone using a rope with lengths ranging from 20 to 30 m, depending on the irregularities of terrain. Under good visibility conditions, divers assisted in covering 50-m subtidal transects (n = 6) in San Antonio Este port, estimating a surveyed area of roughly 900 m². Oysters were searched for along these transects and all perpendicular distances between detected individuals and the transects were recorded. These distances were used to build a detection probability model as a function of the distance to the observer (detection function). Finally, with the detection function, the density of oysters at each site was estimated. The analysis was performed with the package Distance in R (Miller et al. 2019; R Core Team 2020).

Size structure

Individuals collected during the abundance surveys were brought to the Laboratorio de Biodiversidad y Servicios Ecosistémicos (Escuela de Ciencias Marinas, Universidad Nacional del Comahue)

where they were weighed and their length, height, and width were measured. In addition, the volume of each individual was recorded using the water displacement method (Lawrence and Scott 1982). Given the great variability in the relationships between linear measurements, i.e. the variable morphology between individuals, the volume was used as a global measure of size to construct size-frequency histograms (6 ml interval). Subsequently, size-frequency distributions were decomposed into modal components using the Bhattacharya method, which was validated using the Normsep tool within the Fisat II software application (Pauly and Caddy 1985; Gayanilo et al. 2002). Recruits were defined as individuals with a height less than 30 mm (Fey et al. 2010; Lagarde et al. 2017).

Environmental variables

Substrate availability in study sites

The mouth of the Río Negro extends along 12.5 km of the Atlantic coastline of the Argentine Patagonia (del Río et al. 1991). Sediments from the Río Negro cliff contribute to a littoral drift towards the northeast, estimated at 900,000 m³ annually, accumulating over intertidal sandbanks and resulting in an accretion of 50 m per year (del Río et al. 1991; Etcheverría et al. 2006; Vergara Dal Pont et al. 2017). Thus, fine, well-sorted sands make up the predominantly granulometry (del Río et al. 1991), resulting in a scarcity of hard substrates for oyster settlement. The primary substrates available for oyster settlement in the inner estuary include gravel in areas of increased current speed and the roots and stems of *Sporobolus* (*Spartina*) *alterniflora* and *S. densiflora* (Alberti et al. 2007; Isaac et al. 2014). On the western coast of the estuary, the extensive sand beach of El Cóndor is interrupted by abrasion platforms composed mainly of fine-grained sandstones of the Río Negro Formation (Etcheverría et al. 2006; Mendez et al. 2015). To the southwest of the Río Negro mouth, erosion features dominate, characterized by cliff profiles and wave abrasion platforms, primarily composed

of fine-grained sandstones alternating with gray-green sandstones, vulcanogenic deposits, earthy limestones, and red claystone (Etcheverría et al. 2006; Vergara Dal Pont et al. 2017).

Los Pocitos is situated within Anegada Bay, characterized by a vast tidal flat with a gradual decline towards the east (Etcheverría et al. 2006). *Salicornia* and *Sporobolus* patches are scattered across the fine-grained sandy marsh of the intertidal zone, while valves and coarse sand buildup on the distal beach show the effects of storms (Isla and Bertola 2003). The most recent sedimentary layers consist of fine silt-clayey deposits of grayish-brown hue, dominated by crab burrows (Etcheverría et al. 2006). Occasionally, abrasion platforms formed by cohesive sediments of the Río Negro Formation are found (Cuadrado and Gómez 2010).

Physicochemical and biological environment

Seawater environmental parameters that typically have relevance for the settlement of bivalve larvae on substrates were selected. To survey these environmental variables, monthly samples were collected from three sites (LP, EC, PV) between October 2020 and November 2021. Temperature was measured *in situ*, while for the rest of the parameters, subsurface samples (~ 15 cm depth, 3 m from the shore) were collected in plastic bottles that were immediately transferred to the laboratory in ice-cold coolers. Conductivity and pH were taken from 200 ml samples with a multiparameter sensor (AtlasScientific™ Hydroponics Kit). Chlorophyll-*a* samples were collected by filtering between 300 and 750 ml of water through 47 mm diameter glass fiber filters (0.7 µm pore), which were stored in a freezer at -20 °C and then extraction with ethanol was performed for 12 h (Lorenzen 1967). Chlorophyll-*a* concentration was determined by spectrophotometry before and after acidification with 0.1 N hydrochloric acid to correct for pheopigments. Absorbances were taken with a UV-Vis spectrophotometer (Persee T7S), while chlorophyll-*a* concentrations were calculated following the equation of Marker et al. (1980).

For the estimation of suspended solids, a volume of 250 ml of seawater was filtered through fiber-glass filters of 47 mm in diameter and 0.7 µm pore previously muffled at 300 °C and weighed. Then, they were dried in an oven at 60 °C and the concentration was obtained by applying the gravimetric method (APHA 2005). The inorganic fraction was measured after burning the filters at 500 °C in a muffle for 3 h.

Comparisons between environments were performed by means of a principal component analysis where all measured environmental variables were included, previously eliminating variables that presented a strong correlation (Pearson correlation coefficient greater than 0.8 or between 0.5 and 0.8 with significant correlation, $\alpha = 0.05$).

RESULTS

Distribution

Magallana gigas individuals were found in four of the ten surveyed sites on the north coast of the Province of Río Negro. Sites with presence corresponded mostly to the estuary and the area of influence by the Río Negro (El Cóndor, El Pescadero and Piedras Verdes) (Figure 1), where the species had been previously reported. The finding in San Antonio Bay (three individuals in Puerto del Este) constitutes the first record of the species within the San Matías Gulf.

Abundance

Abundances in the Río Negro estuary and its surrounding area were notably lower, spanning between five to six orders of magnitude less than those observed in LP (Table 1). Variations were also evident among sites along the invasion front, with the highest abundance detected in the estuary (El Pescadero) and the lowest in EC. In San Antonio Bay, only three individuals were located within

a single transect out of the six surveyed, rendering the density calculation unfeasible.

Size structure

The population at LP exhibited a multimodal size structure, notably featuring a substantial percentage of small individuals (25% of individuals with a volume of 8.22 ± 1.60 ml, approximately 40 mm in height). Conversely, at PV, three modal components were discerned, all representing larger sizes (> 78 ml, approximately 90 mm in height). In EC, modal components could not be identified due to the limited number of individuals, but recruits prevailed (74% of individuals with volumes

less than 12 ml, approximately 28 mm in height) (Table 2).

Environmental variables

Temperatures ranged from 8.1 °C to 24.9 °C (Table 3). In EC and PV, the highest temperatures were recorded in February (EC: 22.9 °C, PV: 21.5 °C), while the lowest occurred in August (EC: 9 °C, PV: 8.1 °C) (Appendix, Table A1). In LP, temperatures exhibited a different pattern, with values exceeding 23 °C from November to February and the lowest temperature occurring in July (9.1 °C). Salinity levels differed as expected among the sites due to the influence of the Río Negro. The EC had the lowest

Table 1. Abundances of *Magallana gigas* in three sites on the northern coast of the Province of Río Negro (El Cóndor, El Pescadero, Piedras Verdes) and Los Pocitos (Bahía Anegada, Province of Buenos Aires).

Site	Density (ind. m ⁻²)	
	Mean \pm SD	95% CI
El Cóndor	$1.8 \cdot 10^{-3} \pm 0.6 \cdot 10^{-3}$	$0.9 \cdot 10^{-3}$ - $3.5 \cdot 10^{-3}$
El Pescadero	$9.2 \cdot 10^{-2} \pm 3.4 \cdot 10^{-2}$	$4.1 \cdot 10^{-2}$ - $20.77 \cdot 10^{-2}$
Piedras Verdes	$1.35 \cdot 10^{-2} \pm 0.35 \cdot 10^{-2}$	$0.80 \cdot 10^{-2}$ - $2.27 \cdot 10^{-2}$
Los Pocitos	104.71 ± 1.35	61.22-201.05

Table 2. Mean volume, standard deviation (SD), number of individuals (N) and separation index (SI) of the modal components (cohorts) identified for *Magallana gigas* populations in the studied sites.

Site	Cohort	Volume (ml)		N	SI
		Mean	SD		
Los Pocitos	C1	8.22	1.60	173	n. a.
	C2	23.74	9.78	345	2.73
	C3	41.38	13.51	315	2.01
	C4	80.63	11.03	18	3.20
Piedras Verdes	C1	78.46	17.25	19	n. a.
	C2	114.64	7.83	11	2.89
	C3	138.68	9.78	5	2.73

Table 3. Annual means \pm SD along with the number of monthly samples taken (in parentheses in the same line) of the measured environmental variables at three locations along the Argentine maritime coast (Los Pocitos, El C3ndor, and Piedras Verdes) from October 2020 to November 2021. Maximum and minimum values are displayed in parentheses below.

Site	Temperature (°C)	Salinity	pH	Suspended solids (mg l ⁻¹)				Chl- <i>a</i> (µg l ⁻¹)
				Total	Inorganic	Organic		
Los Pocitos	18.0 \pm 5.7 (13) (9.1-24.9)	29.8 \pm 1.2 (13) (28.1-32.3)	8.21 \pm 0.1 (13) (7.9-8.4)	240 \pm 180 (13) (84-727)	210 \pm 157 (13) (72-633)	30.2 \pm 22 (13) (12-93)	2.25 \pm 1.6 (13) (0.18-5.38)	
El C3ndor	16.7 \pm 4.4 (13) (9.0-22.9)	25.6 \pm 1.5 (13) (22.4-27.9)	8.20 \pm 0.0 (13) (8.1-8.4)	451 \pm 231 (13) (170-1,103)	400 \pm 210 (13) (152-1,003)	51.6 \pm 22 (13) (21-100)	8.87 \pm 7.6 (14) (1.27-28.67)	
Piedras Verdes	16.4 \pm 4.9 (12) (8.1-23.3)	28.8 \pm 1.0 (12) (27.1-31.1)	8.21 \pm 0.1 (12) (7.9-8.4)	207 \pm 70 (12) (92-345)	182 \pm 63 (12) (84-305)	24.6 \pm 8.9 (12) (8-40)	3.70 \pm 3.2 (13) (0.73-10.07)	

salinity (25.6 ± 1.5), followed by PV (28.8 ± 1.0), and LP (29.8 ± 1.2). In terms of suspended solids, EC exhibited the highest values, with an average of 400 mg l^{-1} (ranging from 170 to 1,103 mg l^{-1}). On the other hand, PV and LP displayed lower and similar values, both in the range of approximately 200 mg l^{-1} (Table 3). Chlorophyll-*a* concentration also followed this pattern of differences between sites since they were significantly correlated with suspended solids (Pearson correlation coefficient = 0.81 ; $p < 0.001$).

Principal component analysis (for which the variables chlorophyll-*a* and organic and inorganic suspended solids were excluded due to their high correlation with salinity and total suspended solids, Appendix, Table A2) showed that the first two components together explained 69.2% of the data variability (Table 4). The first component was mainly associated with the concentration of suspended solids and salinity and allowed samples from EC to be separated from those from the other two sites, since these samples presented a higher concentration of total solids and a lower salinity (Figure 2). The second component was mainly associated with temperature and comprised the temporal (seasonal) variability between samples.

DISCUSSION

Our study aimed to update essential population data for the Pacific cupped oyster, *M. gigas*, along the northern coast of Río Negro. Despite its initial report 19 years ago (2004), its distribution continues to be restricted to the sector of the mouth of the Río Negro and its vicinity. Its presence in San Antonio Bay, 100 km west from the estuary, suggests a separate introduction event, although our data cannot definitively rule out natural dispersal. Current results show a notable abundance difference between Bahía Anegada and Río Negro populations. While BA maintains high densities ($105 \pm 2 \text{ ind. m}^{-2}$), RN populations exhibit signif-

Table 4. Principal component analysis carried out from the environmental variables measured in the three study sites (Los Pocitos, El Cónдор and Piedras Verdes). Correlation values between each independent variable and principal components (PC) are shown. Additionally, descriptive statistical values for each principal component (standard deviation, proportion of the variance explained, and accumulated variance) are included.

	PC1	PC2	PC3	PC4
Temperature	-0.01	0.83	0.30	0.46
pH	-0.37	-0.31	0.87	-0.01
Salinity	-0.64	0.40	-0.14	-0.64
Total suspended solids	0.67	0.22	0.36	-0.62
Standard deviation	1.25	1.10	0.93	0.60
Variance ratio	0.39	0.30	0.22	0.09
Variance accumulated	0.39	0.69	0.91	1.00

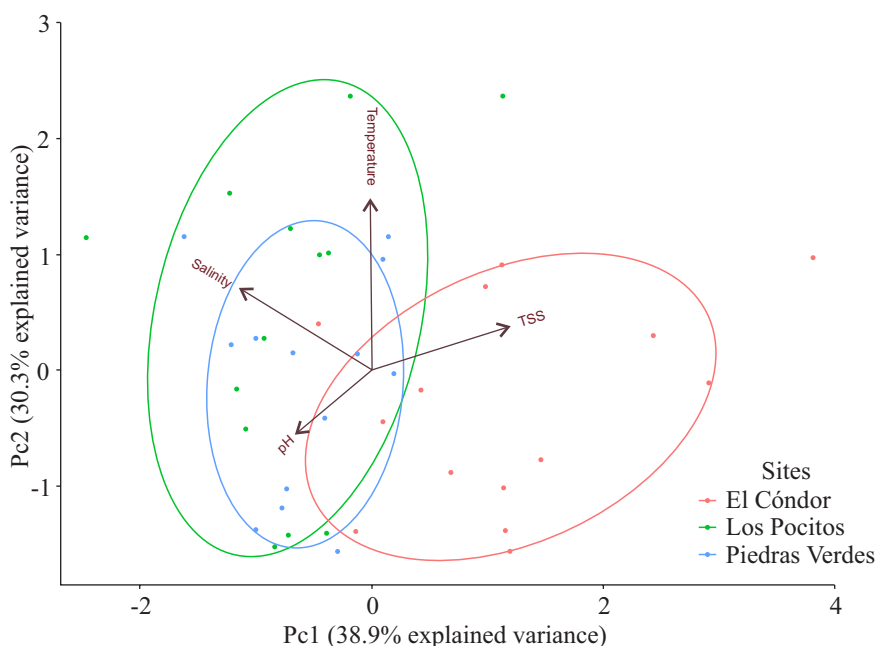


Figure 2. Biplot of principal components analysis carried out with environmental variables surveyed in the three study sites: Los Pocitos, El Cónдор, and Piedras Verdes. TSS: total suspended solids.

icantly lower values ($1.8 \cdot 10^{-3} \pm 0.6 \cdot 10^{-3}$ ind. m^{-2}). The persistence of the species in the area, characterized by low population densities and few modal components in the size-frequency distribution, indicates a pattern typical of peripheral populations. Difficulties in establishing the species may be due

to a combination of intrinsic population factors, such as the Allee effect and the low gamete encounter rate, along with external factors such as unfavorable environmental conditions. Even in challenging environments, this latency stage has resulted in significant population growth in other

parts of the world. However, the unpredictable nature of the population trajectory of *M. gigas* prevents future projections. Therefore, annual monitoring of populations is suggested as a useful tool for assessing population trends in this area.

The establishment of a new population of *M. gigas* at a given location depends on the successful completion of several stages: larval production, larval transport, initial settlement, and subsequent survival (Dolmer et al. 2014). Environmental conditions, particularly salinity and temperature, play a crucial role in these stages of establishment, as does the availability of settlement substrata. Gametogenesis initiates at 10 °C with salinities ranging from 15 to 32, while gamete release occurs at 16 °C between salinities of 23 and 28 (Dolmer et al. 2014). Within this study area, salinity and temperature fall within these ranges (Table 3). As a result, individuals can complete their reproductive cycle once established, as previously confirmed in the area by Roche et al. (2010).

Additionally, food availability (indicated by chlorophyll-*a* concentration and the composition of algal community) influences the entire process (Brown 1988; Brown and Hartwick 1988). Chlorophyll-*a* concentrations along the coast of the Province of Río Negro were similar or even exceeded those in Bahía Anegada, and suspended organic solids (a food source for suspension feeders like oysters; Brown 1988; Mitchell 2001) were higher, reflecting that food availability is not a limiting factor. However, high concentrations of suspended inorganic solids reduce filtration efficiency and can damage the gills (Dutertre et al. 2009; Barille et al. 2011). Laboratory experiments showed that *M. gigas* ceases filtration activity above 196 mg l⁻¹, but there are wild populations in areas with even higher solid concentrations, resulting in changes of oyster's internal organs (gills and palps) and reduced filtering efficiency (Dutertre et al. 2009). In France, for instance, noticeable effects from suspended solids occur at concentrations of 156 mg l⁻¹, while environments with concentrations of 600 mg l⁻¹ are considered highly turbid for oyster farming

(Dutertre et al. 2009). In El Cóndor, mean annual values exceeding this threshold were found. This suggests that the concentrations in El Cóndor could indeed pose challenging conditions for the growth of oysters.

Other factors such as substrate availability and hydrological conditions impact oyster larval settlement and growth (Pogoda et al. 2011; Graham et al. 2020). For instance, Guy and Roberts (2010) showed that strong currents and wave energy action could potentially dilute and flush away oyster larvae before they have the opportunity to settle on substrates. Information about hydrodynamic conditions in the area is limited, and this aspect has generally received little attention concerning oyster reefs formation. The scarce information available indicates that the Río Negro estuary and nearby zone experiences semidiurnal tides with average amplitudes of 2.84 m and maximum amplitudes of 4.31 m (SHN 2023), with tide currents ranging from 3.7 to 9.3 km h⁻¹, predominantly flowing in northeast or southwest directions (del Río et al. 1991; Isla and Bertola 2003). In contrast, the Bahía Anegada area, specifically Los Pocitos site, has comparatively smaller tidal amplitudes, wave heights, and periods, measuring 1.61 m, 0.1 m, and 5 s, respectively (Isla and Bertola 2003; SHN 2023). This suggests that hydrological conditions in the estuary may pose greater challenges for oyster establishment compared to Bahía Anegada, although more targeted studies would be required to verify this hypothesis.

The size structure at Los Pocitos displayed several modal components, with a significant proportion of juveniles, suggesting frequent recruitment events and a periodically replenished population. In contrast, few modes were observed at sites close the southern distribution limit within the Province of Río Negro, such as in Piedras Verdes, or no modal components could be distinguished due to a low number of individuals, such as in El Cóndor. In Piedras Verdes, collected individuals were mostly large, indicating the absence of recent successful recruitments. In contrast, El Cóndor showed a pre-

dominance of small individuals, indicating recent recruitment. Latency periods have been documented in several regions worldwide (Wehrmann et al. 2000; Robinson et al. 2005; among others) marked by sporadic recruitment, as seen in Germany with over 18 years and 6 successful recruitment events (Holm et al. 2015). When reproductive success is inconsistent and population trends are unpredictable, with years of decline followed by occasional increases, it is referred to peripheral population dynamics (Lewis et al. 2022). Outlying populations of *M. gigas* at the southern edge of their range are susceptible to population decline and potential extirpation due to ongoing changes in climate and habitat, coupled with a low recruitment rate. Nevertheless, it is plausible that low detectability poses a common challenge when researching these peripheral populations, rendering abundance estimates less precise.

Finally, it is worth noting the record of the presence of the species in San Antonio Bay, representing the first report within San Matías Gulf. Given the great distance between this site and the closest ones with the presence of the oyster, and the prevailing eastward currents along San Matías Gulf northern coast, the arrival of larvae by drift seems unlikely. This hypothesis is further supported by multiple factors: the considerable geographical distance (100 km west from the estuary), the population decline in the estuarine area (evidenced by its absence from previously occupied sites like El Espigón and La Lobería), and the low population density near the river mouth. Sampling was conducted in San Antonio Este port, identified as the site with the highest likelihood of invasive species occurrence in San Antonio Bay. This has been attributed to the regional marine traffic, where numerous invasive species have been detected in ballast water and through biofouling (Schwindt et al. 2014). Another potential source could be a former flat oyster (*O. puelchana*) farming operation that was abandoned around 20 years ago, and where bags containing illegally introduced *M. gigas* were discovered (2023 R González and MA Narvarte pers. observ.). This venture was located 600 m of the

site where oysters were found, and it is unknown whether it allowed the establishment of breeding individuals in a nearby area that would eventually generate recruitment in San Antonio Bay. In this specific area, six 50-m transects were covered and only three adhered individuals were discovered. As a precautionary measure, it is recommended to conduct yearly monitoring to identify the existence of *M. gigas* and assess its population trajectory, even if oysters are not very abundant and their origin is unknown. A study examining mollusk larvae currents and drift could be beneficial in identifying areas with high chances of species establishment, enabling efforts to be concentrated in those regions.

Given the current low abundance and limited dispersal of *M. gigas* in the Province of Río Negro, this early invasion stage presents an opportunity for implementing preventive control measures. While complete eradication may be challenging, targeted removal in key areas, particularly near protected reserves, could help manage population growth. Previous studies have shown that early intervention in non-native oyster populations can be effective (Guy and Roberts 2010). Based on our findings of concentrated populations near El Cóndor and Piedras Verdes, we recommend focusing monitoring and removal efforts in these areas. Additionally, considering the species' proven ability for rapid growth in other invaded areas, the establishment of an early warning system through regular surveys could help detect and respond to sudden population increases.

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Author contributions

Leandro A. Hünicken: conceptualization; methodology; investigation; formal analysis; writing-original draft; visualization funding acquisition. Raúl González: conceptualization; methodology; investigation; resources; writing-review and editing; supervision; project administration; funding acquisition. Dennis Landete: investigation. Maité A. Barrena: investigation. Juan F. Saad: formal analysis; resources; writing-review and editing. Maite A. Narvarte: conceptualization; methodology; investigation; resources; writing-review and editing; supervision; project administration; funding acquisition.

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APPENDIX

Table A1. Values of environmental variables measured in the three study sites where the presence of the oyster *Magallana gigas* was detected. TSS: total suspended solids; TIS: total inorganic solids; TOS: total organic solids; Chl-*a*: chllorophyll-*a*.

Site	Date	Temp (°C)	pH	Salinity	TSS (mg l ⁻¹)	TIS (mg l ⁻¹)	TOS (mg l ⁻¹)	Chl- <i>a</i> (µg l ⁻¹)
Piedras Verdes	11/18/2020	19.2	7.88 ± 0.02	28.73 ± 0.10	92 ± 22	84 ± 22	8 ± 2	1.69 ± 0.68
	12/16/2020	18	8.30 ± 0.00	30.08 ± 0.11	260 ± 17	224 ± 19	35 ± 3	2.54 ± 1.03
	01/28/2021	20.3	8.09 ± 0.17	28.58 ± 0.06	255 ± 18	223 ± 17	31 ± 2	9.56 ± 2.54
	02/24/2021	21.5	8.41 ± 0.00	28.61 ± 0.62	170 ± 8	150 ± 5	20 ± 5	3.65 ± 0.52
	03/18/2021	18.5	8.28 ± 0.02	27.17 ± 0.12	345 ± 3	305 ± 21	40 ± 0	10.0 ± 2.22
	04/13/2021	17.8	8.19 ± 0.01	28.03 ± 0.02	237 ± 3	208 ± 3	28 ± 3	3.17 ± 0.41
	05/14/2021	13.7	8.15 ± 0.04	28.61 ± 0.61	165 ± 5	143 ± 5	21 ± 2	2.72 ± 1.36
	06/16/2021	10.6	8.20 ± 0.02	28.98 ± 0.08	146 ± 6	126 ± 4	20 ± 4	2.64 ± 0.65
	07/15/2021	9.3	8.19 ± 0.05	29.14 ± 0.04	136 ± 4	120 ± 4	16 ± 0	2.79 ± 0.57
	08/12/2021	8.1	8.20 ± 0.02	27.99 ± 2.21	185 ± 8	161 ± 10	24 ± 4	7.25 ± 1.36
	09/15/2021	12	8.35 ± 0.04	28.05 ± 0.26	126 ± 8	114 ± 6	12 ± 4	0.90 ± 0.31
10/27/2021	17.3	8.27 ± 0.02	29.50 ± 0.25	273 ± 5	253 ± 5	20 ± 0	0.72 ± 0.31	
11/26/2021	23.3	8.36 ± 0.00	31.10 ± 0.36	220 ± 43	190 ± 43	30 ± 0	0.36 ± 0.31	
El Condor	10/21/2020	14.7	8.26 ± 0.00	24.66 ± 0.49	386 ± 58	343 ± 55	43 ± 3	10.7 ± 2.23
	11/18/2020	18.5	8.09 ± 0.04	25.46 ± 0.11	1,103 ± 102	1,003 ± 92	100 ± 1	28.6 ± 1.74
	12/16/2020	18.1	8.38 ± 0.00	26.58 ± 0.10	356 ± 5	306 ± 5	50 ± 1	17.9 ± 1.09
	01/28/2021	20.09	8.12 ± 0.01	27.04 ± 0.01	416 ± 23	360 ± 17	56 ± 5	8.52 ± 1.66
	02/24/2021	22.9	8.32 ± 0.00	27.01 ± 0.19	170 ± 5	151 ± 2	18 ± 2	3.55 ± 1.08
	03/18/2021	19.2	8.13 ± 0.01	22.40 ± 0.09	600 ± 45	523 ± 40	76 ± 5	15.6 ± 2.17
	04/13/2021	19.6	8.07 ± 0.01	23.84 ± 0.08	526 ± 35	473 ± 30	53 ± 5	11.7 ± 1.79
	05/14/2021	15.3	8.20 ± 0.02	24.46 ± 0.36	410 ± 51	363 ± 40	46 ± 1	3.47 ± 1.45
	06/16/2021	11.6	8.25 ± 0.02	24.47 ± 0.19	376 ± 11	330 ± 10	46 ± 5	3.62 ± 0.51
	07/15/2021	9.1	8.20 ± 0.01	27.86 ± 0.01	226 ± 15	205 ± 16	21 ± 2	2.98 ± 0.33
	08/12/2021	9	8.26 ± 0.00	26.79 ± 0.07	576 ± 12	504 ± 10	72 ± 2	8.76 ± 0.26
09/15/2021	14	8.26 ± 0.01	26.09 ± 0.04	370 ± 20	326 ± 25	43 ± 5	4.66 ± 1.94	
10/27/2021	18.3	8.25 ± 0.03	26.33 ± 0.09	313 ± 5	280 ± 10	33 ± 5	1.27 ± 0.41	
11/26/2021	21.3	8.10 ± 0.00	26.70 ± 0.09	410 ± 10	356 ± 15	53 ± 5	2.54 ± 0.62	
Los Pocitos	10/21/2020	17.2	8.19 ± 0.01	29.81 ± 0.03	151 ± 5	128 ± 6	22 ± 1	1.63 ± 0.47
	11/18/2020	24.2	7.88 ± 0.03	30.46 ± 0.06	144 ± 8	128 ± 8	16 ± 0	2.99 ± 1.69
	12/16/2020	23.1	8.33 ± 0.00	30.21 ± 0.05	390 ± 26	340 ± 26	50 ± 0	3.74 ± 2.12
	01/28/2021	23.1	8.38 ± 0.01	32.28 ± 0.02	84 ± 1	71 ± 1	12 ± 2	2.79 ± 1.90
	02/24/2021	22.9	8.06 ± 0.02	30.73 ± 0.02	726 ± 37	633 ± 41	93 ± 5	3.62 ± 3.27
03/18/2021	19.5	8.19 ± 0.01	30.42 ± 0.65	373 ± 15	330 ± 10	43 ± 5	5.38 ± 0.53	

Table A1. Continued

Site	Date	Temp (°C)	pH	Salinity	TSS (mg l ⁻¹)	TIS (mg l ⁻¹)	TOS (mg l ⁻¹)	Chl- <i>a</i> (µg l ⁻¹)
	04/13/2021	20.3	8.15 ± 0.01	29.74 ± 0.12	253 ± 17	222 ± 10	31 ± 7	3.90 ± 0.56
	05/14/2021	14.8	8.20 ± 0.03	30.06 ± 0.02	113 ± 2	100 ± 4	13 ± 2	0.48 ± 0.83
	06/16/2021	9.9	8.25 ± 0.02	28.2 ± 0.07	124 ± 4	104 ± 8	20 ± 4	0.78 ± 0.45
	07/15/2021	9.1	8.24 ± 0.02	28.42 ± 0.14	101 ± 2	89 ± 2	12 ± 0	0.24 ± 0.27
	08/12/2021	9.4	8.23 ± 0.00	28.09 ± 0.06	200 ± 10	178 ± 10	21 ± 2	2.72 ± 0.81
	09/15/2021	16	8.32 ± 0.02	28.67 ± 0.00	125 ± 2	110 ± 2	14 ± 2	0.18 ± 0.18
	10/27/2021	24.9	8.37 ± 0.01	31.06 ± 0.01	340 ± 17	296 ± 5	43 ± 1	0.82

Table A2. Correlation matrix showing relationships between physicochemical parameters and chlorophyll-*a* in the three study sites where the presence of the oyster *Magallana gigas* was detected (Los Pocitos, El Cóndor and Piedras Verdes). Values represent Pearson's correlation coefficients (*r*). NA: indicates no correlation was calculated. TSS: total suspended solids; TIS: total inorganic solids; TOS: total organic solids; Chl-*a*: chlorophyll-*a*.

	Temperature	pH	Salinity	TSS	TIS	TOS	% TIS	% TOS	Chl- <i>a</i>
Temperature	1	NA	NA	NA	NA	NA	NA	NA	NA
pH	NA	1	0.12	-0.2	-0.2	-0.16	-0.24	0.24	-0.15
Salinity	NA	0.12	1	-0.47	-0.47	-0.43	-0.23	0.23	-0.58
TSS	NA	-0.2	-0.47	1	1	0.96	0.16	-0.16	0.81
ISS	NA	-0.2	-0.47	1	1	0.95	0.18	-0.18	0.82
OSS	NA	-0.16	-0.43	0.96	0.95	1	-0.05	0.05	0.74
% ISS	NA	-0.24	-0.23	0.16	0.18	-0.05	1	-1	0.15
% OSS	NA	0.24	0.23	-0.16	-0.18	0.05	-1	1	-0.15
Chl- <i>a</i>	NA	-0.15	-0.58	0.81	0.82	0.74	0.15	-0.15	1

