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Research Article

Spatial variation in biometric parameters and condition index of *Modiolus capax* in contrasting coastal environments in the Gulf of California

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ABSTRACT. The biometric parameters and organismal condition of marine bivalves are strongly influenced by environmental conditions such as temperature, food availability, and anthropogenic disturbance. Using biometric parameters, the condition index (CI), and weight-length relationships (WLR), this study evaluated spatial variation in the organismal condition of *Modiolus capax* at coastal sites with contrasting environmental conditions in the Gulf of California, Mexico. Mussels from the Santa Rosalía (SR) mining port, a site historically impacted by mining activities and characterized by lower temperatures and higher food availability (chlorophyll-*a*), exhibited larger shell sizes and greater visceral mass, along with negative allometric growth patterns associated with shell elongation. In contrast, mussels from the La Paz Bay sites with higher temperatures and lower food availability, and with different types and intensities of anthropogenic influence (thermoelectric plant and phosphorite mine), were consistently smaller and lighter. Biometric parameters, CI, and WLR revealed clear spatial variation, indicating marked differences in morphological responses and somatic growth patterns among sites. However, at SR, shell elongation altered growth allometry and skewed condition-index interpretations based on shell length, artificially lowering CI values despite high visceral mass. These differences indicate that local environmental conditions strongly modulate biometric parameters across sites and suggest that morphological responses may mask organismal condition when conventional indices are applied without accounting for shell shape variation associated with potentially stressful conditions. Overall, this study highlights the value and limitations of biometric and condition indices as integrative indicators of population dynamics, providing a baseline to integrate future biometric assessments with physiological and biochemical biomarkers in historically impacted coastal systems.

Keywords: *Modiolus capax*; environmental heterogeneity; anthropogenic impacts; morphological plasticity; allometric growth, Mexico

INTRODUCTION

In marine ecosystems, environmental variation influences the dynamics that govern ecosystem structure and functioning (Doney et al. 2012, Assan et al. 2020). These variations create favorable conditions for some species or populations, such as optimal temperatures and greater food or nutrient availability, which optimize physiological regulation and reduce competition and predation (Johan et al. 2015, Canosa & Bertucci

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2023). However, when environmental conditions fluctuate beyond the normal range of variability, the resulting stress causes suboptimal physiological performance, leading to adverse consequences, such as decreased growth, smaller body size, lower reproductive capacity, and, in extreme cases, increased mortality (Doney et al. 2012, Johan et al. 2015). Therefore, anthropogenic impacts substantially alter organisms' natural habitats, exacerbating environmental stress (Brander et al. 2010, Moullec et al. 2021). These impacts, combined with low food availability and abrupt temperature changes outside the optimal range, significantly deteriorate marine populations (Assan et al. 2020, Horwitz et al. 2020). However, some species have developed adaptation mechanisms that allow them to tolerate extreme environmental conditions (Przeslawski et al. 2005), as do intertidal bivalves, which inhabit the intertidal zone, one of the most stressful habitats (Gosselin & Chia 1995). For this reason, bivalves are considered resilient to fluctuating environmental conditions (Chelyadina et al. 2022, Sampaio et al. 2022, Sepúlveda et al. 2024), so studying them allows detection of adverse impacts before they become irreversible (Helmholz et al. 2016).

Somatic indices, biometric parameters, and weight-length relationships (WLR) are key diagnostic tools for assessing organisms' physiological health in response to environmental changes. Their sensitivity to habitat conditions and their capacity to reflect essential physiological processes (growth, reproduction, and others) in organisms (Mercado-Silva 2005, Ramesha & Sophia 2015) make them essential methodological approaches in ecotoxicology, conservation, and management of aquatic resources since they provide information on stressful conditions caused by environmental factors and the effects of pollution on biota (Lucas & Beninger 1985, Filgueira et al. 2013).

Mussels, particularly species belonging to the genera *Mytilus* and *Modiolus*, are known for their high tolerance to stress conditions, such as low food availability, temperature fluctuations, and pollution (Anestis et al. 2008, Muñoz-Barbosa & Huerta-Díaz 2013, Clark et al. 2021). These bivalves are widely distributed in the Gulf of California (GC), a region of high biological, oceanographic, and geochemical relevance, recognized for its elevated primary productivity and diversity of marine habitats (Álvarez-Borrego 2010, Páez-Osuna et al. 2017). The GC has remarkable environmental heterogeneity driven by spatial and temporal variability in temperature, oxygen concentration, salinity, and nutrient availability, which promotes habitat and microhabitat formation and shapes the structure and species composition of biological communities (Brusca 2010, Brusca & Hendrickx 2010). Additionally, several areas of the GC have been impacted by anthropogenic activities, including mining and metal ore processing, industrial discharges, municipal effluents, and thermoelectrical plants (Páez-Osuna et al. 2017). Among the benthic communities inhabiting this region is the mussel *Modiolus capax*, a species of local commercial and subsistence importance (local fishermen, *pers. comm*.). The biology of *M. capax* has been extensively studied in the GC, with research addressing its reproductive biology, recruitment patterns, capacity to bioaccumulate pollutants, and environmentally driven morphological variability (Gutiérrez-Galindo et al. 1999, Muñoz-Barbosa & Huerta-Díaz 2013, López-Carvallo et al. 2017, García-Corona et al. 2018, García-Domínguez et al. 2018, Roldán-Wong et al. 2020, Góngora-Gómez et al. 2022). However, studies evaluating the combined effects of environmental variability and pollutant exposure on *M. capax* biological responses along the western coast of the GC remain limited.

By assessing biometric parameters, condition index (CI), and WLR, this study evaluated spatial variation in the physiological condition of *M. capax* across contrasting coastal environments driven primarily by differences in temperature, food availability, and pollutant exposure. The research was conducted at four sites along the western coast of the GC: the mining port of Santa Rosalía (SR), characterized by elevated metal concentrations in sediments, lower water temperatures, and higher food availability, and three sites within La Paz Bay (LPB), characterized by higher temperatures, lower food availability, and different types and intensities of anthropogenic influence.

MATERIAL AND METHODS

Study area

The study was conducted at four sites within the GC (Fig. 1) between 2017 and 2020. SR (27°20'N and 112°16'W) is a mining port intensively impacted by copper exploitation since the late 19th century, with approximately 370 million tons of waste disposed on land and into adjacent coastal waters (Shumilin et al. 2011). This long-term anthropogenic impact has resulted in high concentrations of metals in sediments, such as Cu (3,856 mg kg^{-1} dry weight), Zn (2,599 mg kg^{-1}), Co (635 mg kg^{-1}), Mn (6,906 mg kg^{-1}), Pb (236 mg kg^{-1}), Cd (240 mg kg^{-1}) and U (11.8 mg kg^{-1}),

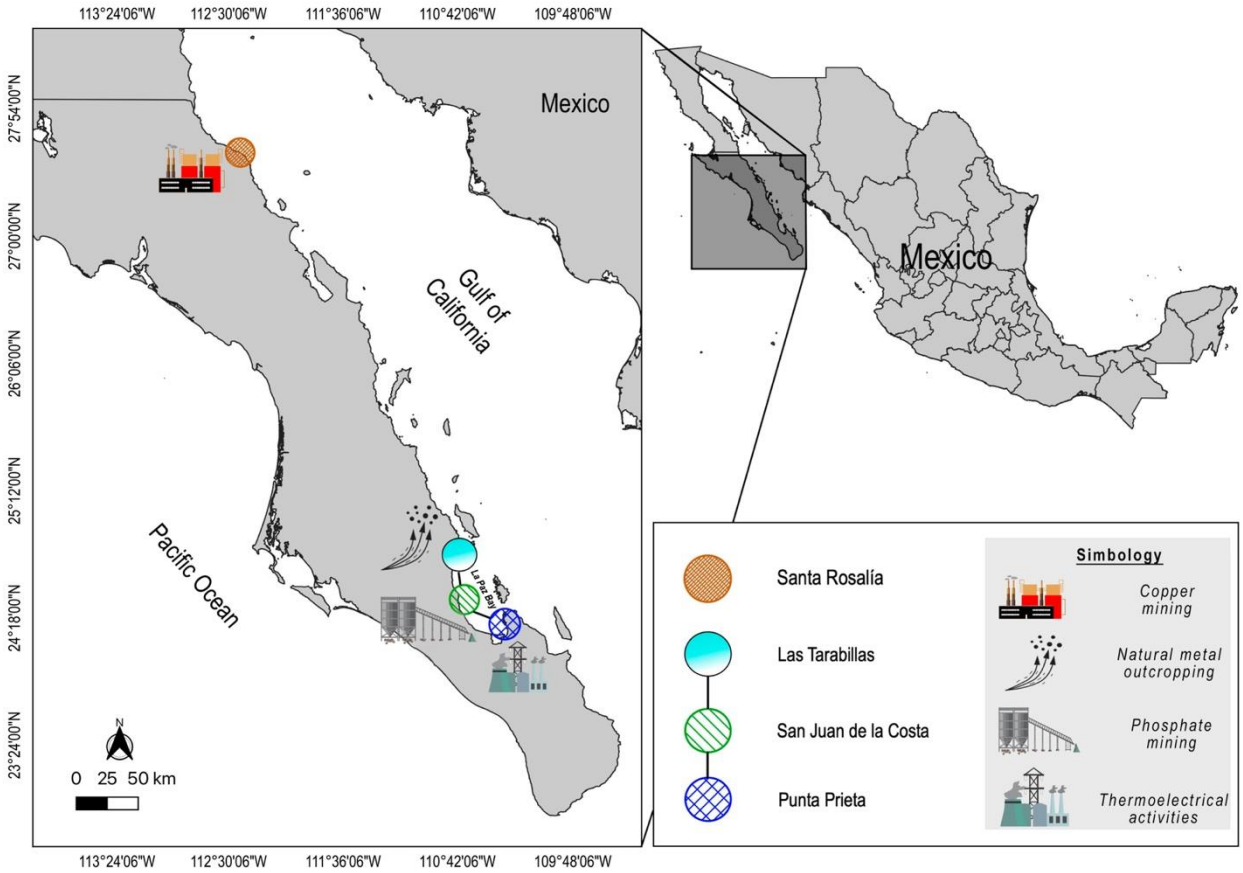


Figure 1. Geographic location of the study sites of the mussel *Modiolus capax* in the Gulf of California. La Paz Bay includes Las Tarabillas, San Juan de la Costa, and Punta Prieta.

exceeding established ecotoxicological quality guidelines (Shumilin et al. 2013, Jonathan et al. 2016). In addition, numerous studies have documented elevated concentrations of metals in the tissues of marine species from this site (Gutiérrez-Galindo et al. 1999, Cadena-Cárdenas et al. 2009, Muñoz-Barbosa & Huerta-Díaz 2013, Roldán-Wong et al. 2018, Yee-Duarte et al. 2018, 2024, 2020, Martínez-Ayala et al. 2022, Eraso-Ordoñez 2023, Pintueles-Tamayo et al. 2025), including the target species of the present study, which has been reported to accumulate up to 11 times higher concentrations of various elements compared to organism from less impacted areas (Gutiérrez-Galindo et al. 1999). Consistently, geoaccumulation index assessments categorize this area as strongly and extremely polluted (classes 4 to 6) for elements such as Mn, Ba, Cd, Co, Mo, Pb, Sr, and Zn, reflecting the long-term influence of historical mining and smelting activities in the area (Jonathan et al. 2016). The local climate is arid, with a mean annual temperature and precipitation of 23.4°C and 117.2 mm, respectively (Rodríguez-Figueroa 2004). The mean sea surface temperature (SST) is 22.4°C, with a mean pH of 8.04 (Góngora-Gómez et al. 2022), and chlorophyll-*a* (Chl-*a*) concentrations ranging from 0.84 to 10.21 mg m^{-3} (Yee-Duarte 2017).

Second, we considered three sites in LPB: a) Punta Prieta (PP) (24°22'N and 110°30'W), an area adjacent to a thermoelectric plant and a port for fuel unloading and storage, in which high concentrations of total polycyclic aromatic hydrocarbons (PAHs) have been reported (Roldán-Wong et al. 2020); b) San Juan de la Costa (SJC) (24°39'N and 110°68'W) an area with Cd, Pb, Fe, Ni, Cu, and Zn in sediments derived from phosphorite mining, which is still in operation to date, the mouth of the San Juan river, and natural deposits located northwest of San José Island (Escobedo-Fregoso 2006, Méndez et al. 2006, Rodríguez-Castañeda et al. 2006, Cadena-Cárdenas et al. 2009, SGM 2019); c) Las Tarabillas (TS) (24°64'N and 110°69'W), a site with the presence of Cd and other metals as a result of the upwelling of the seafloor

towards the surface as a natural process due to its proximity to the San Gregorio rock formation (Segovia-Zavala et al. 2003, Méndez et al. 2006, Cantú-Medellín et al. 2009). The LPB climate is desert, with mean annual precipitation below 200 mm (Coen & Cruz-Bello 2019). The mean sea temperature in LPB is 26.5°C, with a mean pH of 7.95 (Góngora-Gómez et al. 2022), while Chl-*a* concentrations range from 0.8 to 2.1 mg m^{-3} (Coria-Monter et al. 2017).

Specimen collection

At each site, mussel specimens were collected by free diving at depths of 2-5 m between 8:00 and 10:00 h during February, June, September, and November in the period 2017-2020. Subsequently, we transported the specimens in seawater to the laboratory for processing, following bioethical and regulatory guidelines for marine animals used in scientific research (Crook & Walters 2011, Crespi-Abril & Rubilar 2021).

Upon arrival at the laboratory, the biometric data of each mussel was recorded, including shell length (SL, maximum distance along the anterior-posterior axis). (± 0.1 mm), total weight (TW), wet weight (WW, weight without shell), and shell weight (SW) (± 0.1 g).

Size frequency, condition index, and weight-length relationship

The size distribution of *M. capax* at each site was analyzed by constructing frequency histograms from SL. The nutritional status, as a physiological condition of a specimen, was evaluated using the CI with the following equation (Mouneyrac et al. 2008):

$$CI = (WW / TW) \times 100$$

To improve CI estimation and comparison among sites, only organisms in the size range of 6.3 to 9.6 cm SL were used; this range was represented at each site.

As an additional indicator of the health status of *M. capax*, the type of growth of mussels was evaluated by relating the weight (TW, WW, SW) of each specimen to its length, through a WLR analysis using the potential model $P = \alpha L^b$ (Le Cren 1951) and adjusting the parameters for maximum likelihood from the logarithmic transformation:

$$Ln(P) = Ln(a) + b \times Ln(SL)$$

where a is the intercept or initial growth coefficient, b is the slope or allometry coefficient that indicates the type of growth (Gaspar et al. 2001, Froese 2006); P is TW, WW, or SW (in their respective model), and SL is shell length.

Environmental characterization

Data on SST (°C) and Chl-*a* concentration (mg m^{-3}) were obtained through the NASA GIOVANNI application using the MODIS Aqua instrument at a spatial resolution of 4 km. To assess similarity and differences in SST and food availability among study sites, interannual time series spanning 2017-2020 were plotted for each site.

The influence of anthropogenic and natural contamination at each site was characterized using published information documenting long-term environmental conditions in the region, including evidence of historical mining activities, reported trace metal concentrations, and other contaminants in sediments and biota from previous studies. This information was used to provide an environmental context for each site and to support comparisons among sites with contrasting disturbance scenarios. SST, Chl-*a* concentrations, and documented pollution sources were treated as descriptive environmental variables and used as a preliminary framework to interpret spatial differences in mussel organismal condition.

Statistical analysis

Data normality was assessed using the Kolmogorov-Smirnov test with Lilliefors correction and homoscedasticity with Levene's test (Zar 2010). All statistical comparisons among sites, relationships, Chl-*a* concentrations, temperatures, and indices were performed using the Kruskal-Wallis test followed by Dunn's multiple comparison test. To detect and remove outliers, a graph was constructed for each comparison, which improved the estimation of the WLR (Froese 2006, De la Hoz et al. 2016) and the other analyses without altering the data distribution.

Regarding the WLR, a Student's *t*-test was used to determine whether there was a significant difference between the allometry coefficient (b) and the growth hypothesis (H_0: $b = 3$, H_1: $b \neq 3$) (Zar 2010). Confidence intervals were calculated for a and b with a 95% confidence level using the accelerated bootstrap method with bias correction, and 1,000 resamples (Efron 1987, Zar 2010). Additionally, the degree of association among the variables was determined using the coefficient of determination (R^2) to measure goodness of fit (De la Hoz et al. 2016). All statistical tests were performed in R (R Core Team 2022), at a 95% significance level (Zar 2010).

RESULTS

Environmental variables

Although some fluctuations were observed, the statistical analyses revealed no significant interannual differences in SST or Chl-*a* concentrations within individual sites ($P > 0.05$). Therefore, the mean values calculated throughout the study period were used to represent the environmental conditions at each site in subsequent comparisons. Significant differences in mean SST were detected among sites ($H_{(3)} = 13.1$, $P = 0.004$). SR showed the lowest temperature of all sites ($\bar{x} = 24.3 \pm 4.5$ºC) with ranges of 16 to 31ºC, whereas PP (26.0 ± 3.2ºC), SJC (26.5 ± 3.2ºC), and TS (26.2 ± 3.3ºC) were statistically similar ($P > 0.05$), with ranges between 21 and 32ºC.

On the other hand, significant differences in mean Chl-*a* concentration were detected among sites ($H_{(3)} = 71.37$, $P < 0.001$). SR exhibited the highest Chl-*a* concentration ($\bar{x} = 1.61 \pm 0.87$ mg m^{-3}), followed by PP (0.99 ± 0.38 mg m^{-3}, $P < 0.001$). In contrast, SJC and TS showed the lowest concentrations and did not differ significantly from each other (0.78 ± 0.49, 0.69 ± 0.41 mg m^{-3}, respectively) ($P > 0.05$) (Fig. 2).

Mussel size

A total of 691 specimens were collected, distributed as follows: 272 from SR, 136 from SJC, 167 from PP, and 116 from TS. Significant differences among sites were recorded in all the *M. capax* biometric parameters evaluated ($H_{(3)} = 241.49$, $P < 0.001$). Significantly larger (SL) and heavier (TW) specimens were collected at SR ($\bar{x} = 9.4 \pm 1.5$ cm SL; $\bar{x} = 117.0 \pm 52.8$ g TW, respectively), followed by SJC (7.8 ± 2.0 cm; 75.9 ± 48.3 g) and TS (7.4 ± 1.2 cm; 64.6 ± 28.1 g). On the other hand, the mussels collected at PP were the smallest and lightest ($\bar{x} = 6.7 \pm 1.4$ cm; $\bar{x} = 46.6 \pm 27.4$ g). The heaviest mussels (WW) were recorded in SR ($\bar{x} = 25.9 \pm 10.0$ g WW), followed by those collected at SJC ($\bar{x} = 16.7 \pm 9.9$ g), while those with the lowest biomass were collected at TS (12.6 ± 5.8 g), followed by PP (10.0 ± 5.9 g) (Fig. 3).

Size frequency, condition index, and weight-length relationship

The size-frequency distribution of *M. capax* by site is shown in Figure 4. Most mussels with sizes greater than 8.5 cm SL were collected in SR, followed by those collected in SJC (7.4 to 9.6 cm SL), while most specimens collected in PP and TS had sizes between 4.1 and 8.5 cm SL.

The variation in the *M. capax* CI showed significant differences among the study sites ($H_{(3)} = 65.67$, $P < 0.001$). Mussels from SR (CI = 24.1 ± 5.76%) and SJC (23.2 ± 4.79%) showed the best nutritional status, followed by PP (21.7 ± 3.77%), while TS specimens had the lowest nutritional status (18.9 ± 2.95%) (Fig. 5).

The analysis of the WLR of *M. capax* showed isometric growth (H_0: $b = 3$, i.e. a proportional increase in length and weight) in most sites (Student's *t*-test, $P > 0.05$), except in SR and TS, where one of the WLRs (TW-SL, WW-SL, and SW-SL) showed a greater increase in length than in WW (negative allometric growth). PP was the only site where *M. capax* showed negative allometric growth ($b < 3$) in all WLR (Student's *t*-test, $P < 0.05$) (Table 1). The coefficient of determination (R^2) was greater than 0.9, confirming the strong relationship between weight and length.

DISCUSSION

Temperature and food availability are key environmental factors that regulate multiple physiological responses in organisms (Storero et al. 2012). Additionally, anthropogenic disturbance and local habitat quality can influence organismal condition through complex pathways (Cajaraville et al. 2000, Rouabhi et al. 2019). Mussels are widely recognized as effective biological models for environmental studies because they are sessile, widely distributed, long-lived, can accumulate pollutants, and are sensitive to environmental variation (Widdows et al. 2002, Dellali et al. 2023).

The present study recorded marked spatial differences in the biometric parameters (SL, TW, WW) of *M. capax* across the study sites, allowing the identification of three distinct groups. Mussels from SR were consistently the largest and heaviest, followed by SJC and TS mussels, while PP mussels were the smallest and lightest. These spatial differences align with contrasting environmental conditions among sites. SR recorded the highest Chl-*a* concentrations (1.61 mg m^{-3}) and the lowest temperature (24.3°C, with a minimum of 16°C) compared with the other study sites. In bivalves, such as *Mytilus galloprovincialis*, temperatures between 10 and 20°C combined with elevated food availability enhance filtration rates and promote somatic growth (Filgueira et al. 2009, Kholodov et al. 2017, Joyce et al. 2019), allowing organisms to increase visceral mass and improve nutritional condition (Mathieu & Lubet 1993, Lee et al.

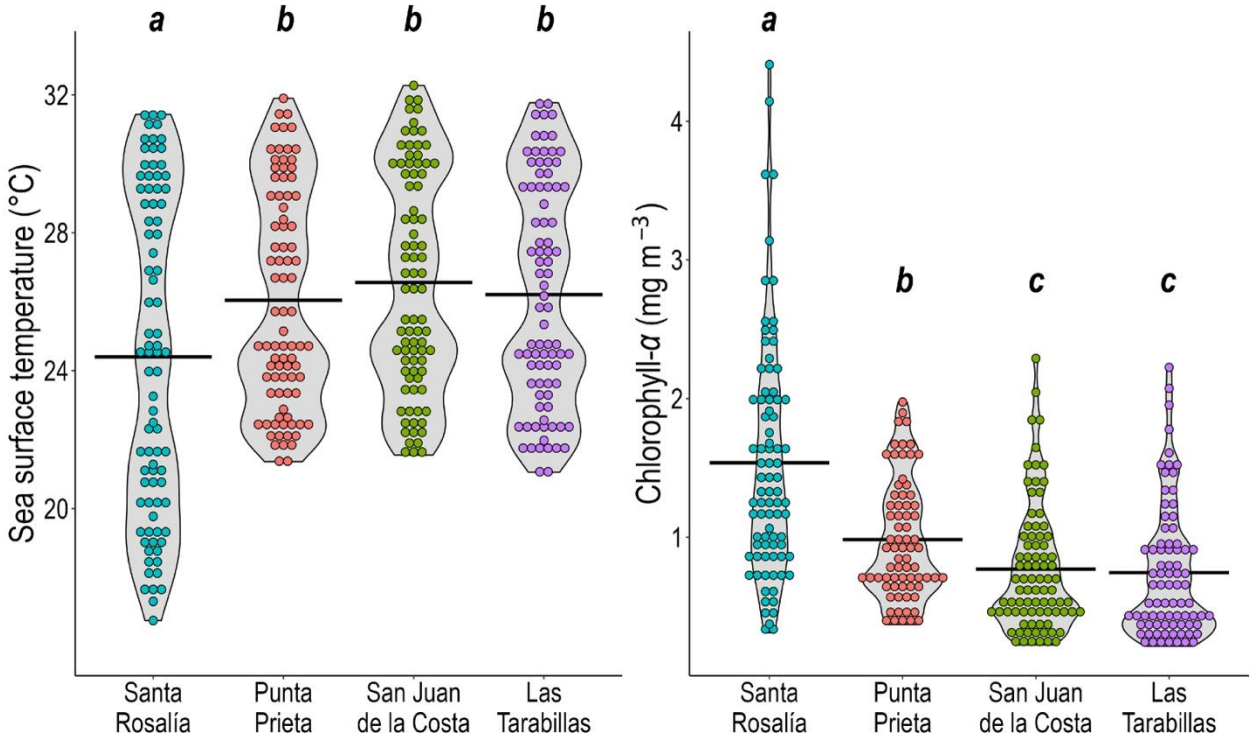


Figure 2. Variation in sea surface temperature and chlorophyll-*a* concentrations across study sites of *Modiolus capax* in the Gulf of California during the period 2017-2020. Data distributions are shown with violin plots. Black horizontal lines indicate the mean, and colored circles show data scatter. Different letters denote statistically significant differences among sites based on Dunn's *post-hoc* test ($P < 0.05$).

2015). This pattern matches the highest WW (25.9 g) recorded in SR. However, despite their greater visceral mass, mussels from SR showed a negative allometric relationship between visceral mass and SL, reflected in a more elongated shell morphology and a lower proportional visceral mass. Shell shape influences biometric relationships and may affect CI estimates, as discussed below.

In contrast, sites in LPB (SJC, TS, and PP) had higher temperatures, lower Chl-*a* concentrations, and smaller, lighter mussels. Notably, despite broadly similar temperatures and food availability conditions across LPB sites, significant differences in biometric parameters were still detected among them. Mussels from SJC and TS had comparable shell sizes and TWs; however, SJC specimens showed higher biomass than those from TS and even PP, a site with slightly higher food availability than SJC and TS. This difference may relate to the high phosphorus levels in SJC's coastal waters, attributed to its proximity to the phosphorite mine (Cantú-Medellín et al. 2009, Chávez-Sánchez et al. 2017), which produces up to 15,000 t (SGM 2019). Although nutrients were not directly measured in this study, the higher visceral mass and isometric growth recorded in SJC mussels suggest a distinct nutrient enrichment pattern relative to TS, where negative allometry between visceral mass and SL was recorded. In this sense, similar relationships among phosphorus availability, visceral mass, and reproductive investment have been reported for other mussel species, including *Lampsilis radiata siliquoidea* (Nalepa et al. 1991) and *M. demissus* (Kuenzler 1961), indicating that nutrient enrichment may influence visceral mass condition and growth patterns in bivalves.

However, although PP had the second-highest Chl-*a* concentration, only surpassed by SR, mussels from this site were the smallest and lightest (lowest visceral mass weight) of all sites analyzed. This apparent decoupling between food availability and biometric performance suggests that factors other than trophic conditions may be constraining overall size at this site. One potential factor influencing mussel size and visceral yield at PP is local population density. Field observations during sampling indicated high mussel densities in a relatively small area, a condition known to intensify intraspecific competition for food and space,

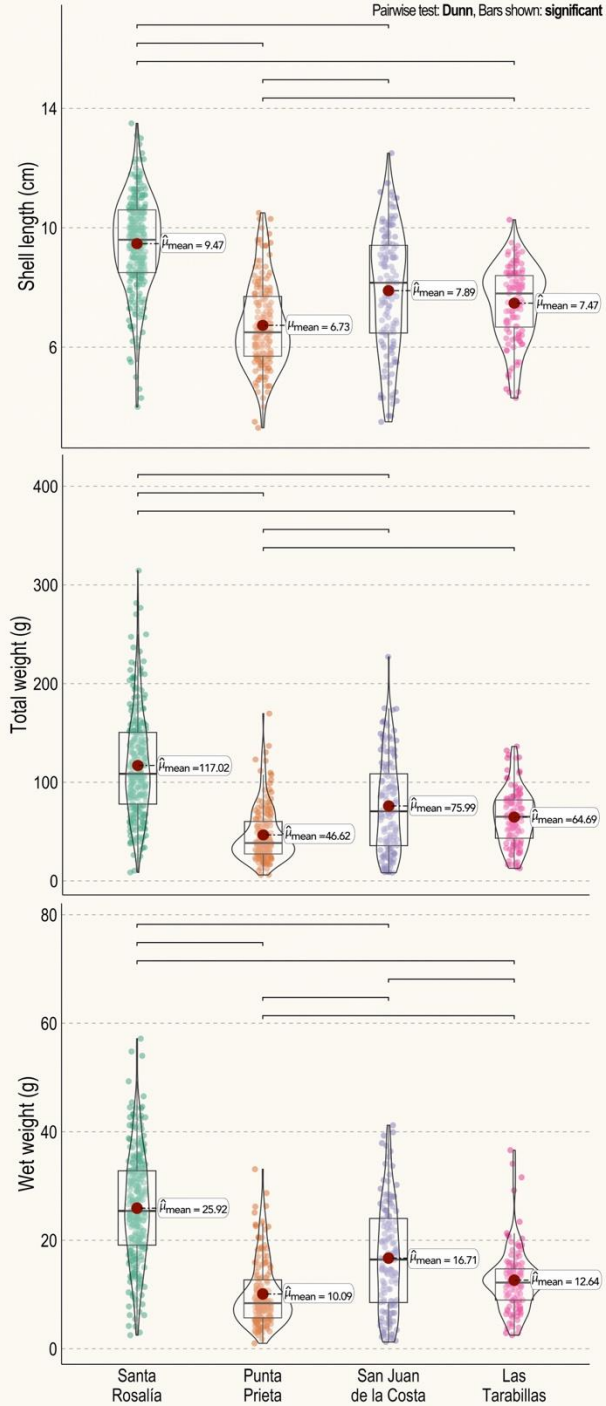


Figure 3. Biometric parameters of *Modiolus capax* across study sites in the Gulf of California. Boxplots and violin charts, along with colored circles representing individual data points for each locality, display data distributions. Within each box, the horizontal line represents the median and the central circle indicates the mean. Horizontal bars at the top denote statistically significant differences among sites based on Dunn's *post-hoc* test ($P < 0.05$).

generate overcrowding, and negatively affect somatic growth in bivalves (Mallet & Carver 1991, Alunno-Bruscia et al. 2001, Chelyadina 2018). This scenario is consistent with the lower biomass observed for a given SL and with the negative allometric relationships recorded across all weight-length parameters at PP. Other mussel populations have shown similar density conditions (Lauzon-Guay et al. 2005).

In addition to biological interactions, local thermal conditions may also contribute to the reduced biometric performance at PP. This site is near a thermoelectric power plant that discharges heated cooling water into a coastal environment, a process documented in other coastal regions (Martínez-Córdoba 1985, Cardoso-Mohedano et al. 2015). Such thermal discharges can produce abrupt fluctuations in SST, potentially inducing acute thermal stress in resident organisms (Masanja et al. 2023). In this regard, elevated temperatures and thermal variability reduce somatic growth (Hiebenthal et al. 2012, Rahman & Rahman 2021) and induce sublethal or lethal effects in bivalves (Masanja et al. 2023, Smith et al. 2023). Evidence from other regions of the GC supports the sensitivity of *Modiolus* species to extreme thermal conditions. For instance, thermal discharges from the Puerto Libertad thermoelectric plant have been associated with localized seawater temperature rises above 34°C and with massive mortalities of *Modiolus* spp. At the same time, other benthic invertebrates (clams and cirripedia) persisted under similar conditions (Martínez-Córdoba 1985). These observations suggest that mussels may be more vulnerable to acute thermal variations relative to other invertebrate taxa.

Chemical stressors may also contribute to the environmental context at PP. Previous studies have reported elevated concentrations of polycyclic aromatic hydrocarbons (PAHs) in mussels from this site, with levels (173.39 ng g^{-1} dw) exceeding those measured in surrounding sediments (Roldán-Wong et al. 2020) and comparable to values reported for moderately impacted coastal environments (see Table 3 in Baumard et al. 1998). In this context, the co-occurrence of thermal alterations, documented chemical exposure, and high population density suggests that mussels at PP are exposed to a complex set of environmental pressures. Collectively, these factors provide a plausible framework for interpreting the reduced biometric performance observed at PP, without attributing the observed patterns to any single stressor.

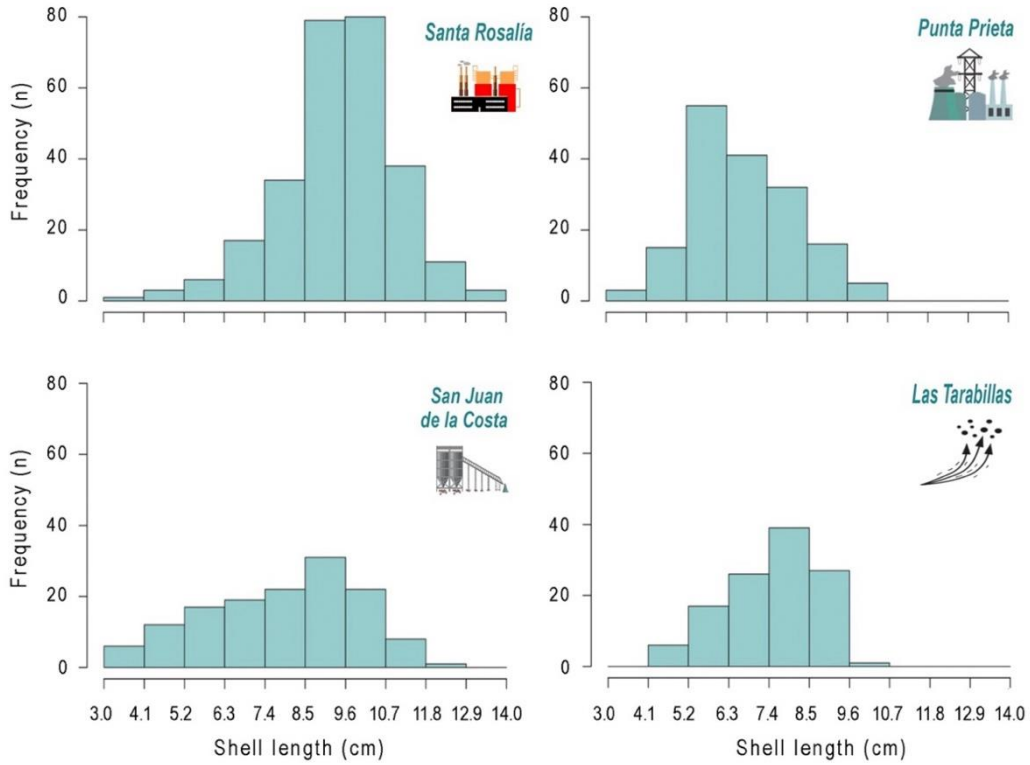


Figure 4. Size frequency distributions of *Modiolus capax* across study sites in the Gulf of California.

Chronic metal exposure is another important environmental baseline across these sites, as at least three study areas have documented elevated metal concentrations (Méndez et al. 2006, Shumilin et al. 2013). At SR, tissue copper levels in *M. capax* have been reported to exceed other regions of the Baja California peninsula baselines up to 11-fold (Gutiérrez-Galindo et al. 1999); nevertheless, SR mussels maintained the largest shell sizes and visceral masses in this study, indicating that chronic metal presence does not necessarily result in stunted somatic growth. Other mussel species in polluted environments have shown similar patterns, where somatic growth and size structure did not decline in parallel with contaminant loads (Chelomin et al. 1998). Such responses are consistent with the physiological and anatomical features that contribute to regulation and detoxification of trace elements, including highly specialized organs involved in metal binding and clearance, such as the kidney and the byssal gland system (through the byssus) (Yonge 1962, Lobel 1986, Szefer et al. 2002, Yap et al. 2003, Chelyadina et al. 2022). The relevance of these traits becomes evident when contrasting *M. capax* with other bivalves co-occurring at SR, such as *Megapitaria squalida* (Yee-Duarte et al. 2017) and *Dosinia ponderosa* (Eraso-Ordoñez 2023), which possess a much smaller kidney (*pers. obs.*) and lack the byssal gland (Yonge 1962), exhibiting deteriorated condition and stunted somatic growth under similar environmental conditions.

The above suggests that the reduced biometric parameters of mussels collected from LPB sites are more related to the high temperatures and low food availability than to previously reported metal concentrations in SJC (Escobedo-Fregoso 2006, Méndez et al. 2006, SGM 2021) and near TS (between 3 and 8 km) (Segovia-Zavala et al. 2003, Méndez et al. 2006, Cantú-Medellín et al. 2009). However, as noted above, findings of PP mussels with high total PAH concentrations (Roldán-Wong et al. 2020) highlight the need for additional studies to investigate the combined effects of these chemicals and thermal stress at this site.

Morphological plasticity in shell shape has been documented in bivalves exposed to contrasting environmental conditions, including sites with elevated metal concentrations, where variation in shell proportions or convexity has been reported (Chelyadina & Popov 2018, Chelyadina et al. 2022, Sepúlveda et al. 2024). A remarkable example was reported for *Macoma balthica*, in which greater elongation and convexity were observed in organisms that bioaccumu-

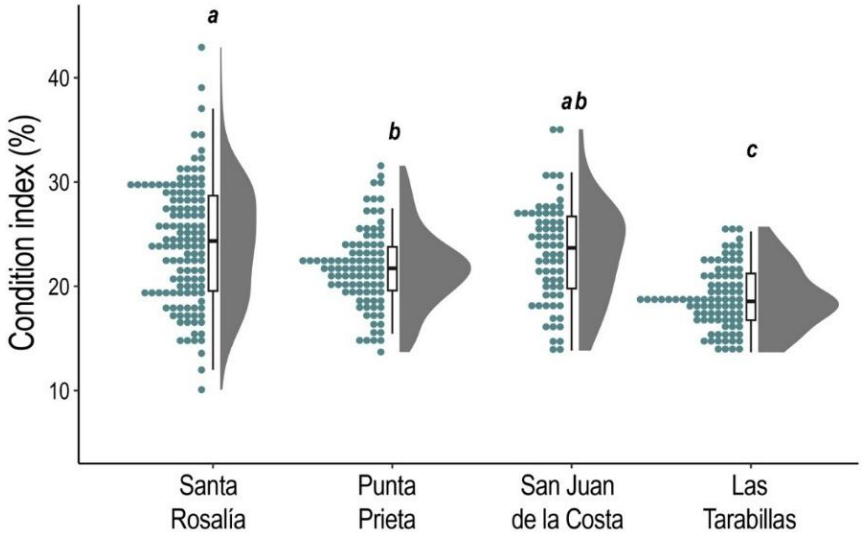


Figure 5. Spatial variation in the condition index of *Modiolus capax* across study sites in the Gulf of California. Data distributions are shown using raincloud plots that combine individual observations (dotplots), boxplots, and kernel density plots for each locality. Different letters denote statistically significant differences among sites based on Dunn's *post-hoc* test ($P < 0.05$).

Table 1. Type of growth of *Modiolus capax* from each study site in the Gulf of California. TW: total weight, SL: shell length, WW: wet weight, SW: shell weight. Bold numbers indicate allometric growth (H_1: $b \neq 3$, Student's *t*-test).

Locality	Relationship	Confidence Interval				Confidence Interval		R^2	Growth type	*P*-value
		a	**Lower**	**Upper**	***b***	**Lower**	**Upper**			
Santa Rosalía	TW-SL	0.28	0.21	0.38	2.63	2.50	2.76	0.94	Isometry	0.097
	WW-SL	0.09	0.07	0.12	**2.45**	2.34	2.57	0.93	Allometry (-)	0.003
	SW-SL	0.18	0.13	0.26	2.71	2.56	2.87	0.91	Isometry	0.178
Punta Prieta	TW-SL	0.32	0.27	0.38	**2.54**	2.45	2.63	0.97	Allometry (-)	0.031
	WW-SL	0.06	0.05	0.08	**2.59**	2.45	2.72	0.95	Allometry (-)	0.008
	SW-SL	0.23	0.18	0.29	**2.58**	2.47	2.70	0.96	Allometry (-)	0.024
San Juan de la Costa	TW-SL	0.25	0.21	0.30	2.68	2.59	2.77	0.98	Isometry	0.137
	WW-SL	0.05	0.04	0.07	2.66	2.53	2.80	0.97	Isometry	0.145
	SW-SL	0.18	0.15	0.22	2.71	2.61	2.81	0.98	Isometry	0.189
Las Tarabillas	TW-SL	0.26	0.17	0.39	2.70	2.50	2.89	0.93	Isometry	0.098
	WW-SL	0.11	0.07	0.18	**2.28**	2.04	2.51	0.90	Allometry (-)	0.011
	SW-SL	0.17	0.11	0.26	2.78	2.58	2.99	0.91	Isometry	0.216

lated high concentrations of metals in their tissues, such as Cu (~100 mg kg^{-1}), Zn (~690 mg kg^{-1}), Ag (~3 mg kg^{-1}), and As (~11 mg kg^{-1}) (Sokolowski et al. 2002). In the present study, mussels from SR were not only the largest and heaviest overall but also showed a negative allometric relationship between biomass and SL, indicating that soft-tissue accumulation did not keep pace with SL, a pattern consistent with shell elongation and geometric shape changes previously associated with metal exposure. This decoupling between visceral mass and shell elongation affects CI estimation because conventional biometric indices assume isometric or proportional growth between internal cavity volume and visceral mass; therefore, shell shape modifications, such as elongated shell morphology, can artificially yield lower CI values in SR mussels despite their large

visceral mass. Consequently, these findings highlight the need to account for shell morphological variation and length-weight allometric relationships when using biometric indices as proxies for organismal condition in metal-impacted environments. The results indicate that *M. capax* maintains high biometric performance despite chronic exposure to metal concentrations associated with historical mining activity that exceed ecotoxicological guidelines at SR (Shumilin et al. 2013, Jonathan et al. 2016). Paradoxically, mussels from this site were consistently the largest and heaviest among all sites analyzed, contrasting with acute experimental observations. For instance, although Strömgren (1982) documented reduced SL and high mortality in *M. edulis* exposed to high Cu and Zn concentrations, those results were derived from small mussels (19-29 mm SL) under short-term exposure (10-22 days), conditions that differ markedly from chronic, lifelong exposure experienced by adult mussels in wild environments.

This discrepancy suggests that large, heavy *M. capax* individuals persist at SR due to population-level acclimation or phenotypic plasticity, traits widely documented in intertidal bivalves (Bayne 2004, Sousa et al. 2007) under fluctuating and anthropogenically altered environments (Sampaio et al. 2022, Góngora-Gómez et al. 2024). These observations highlight the need to distinguish acute experimental responses from chronic, field-based patterns when assessing organismal sensitivity at polluted sites. Future studies integrating physiological, biochemical, and molecular biomarkers will be necessary to identify tolerance thresholds, detoxification pathways, and potential trade-offs that define the balance between resilience and vulnerability in *M. capax* under multi-stressor coastal environments.

CONCLUSION

This study shows that spatial variability in biometric parameters and organismal condition in *M. capax* across GC coastal environments is driven primarily by the interplay between environmental factors (SST and food availability) and localized anthropogenic pressures. Our findings indicate that shell morphological alterations (such as elongation) induced under potentially stressful anthropogenic conditions decouple visceral mass accumulation from SL. This decoupling suggests a critical methodological limitation, showing that conventional length-based condition indices may artificially underestimate organismal condition unless morphological shape alterations are accounted for. Consequently, WLR, allometric patterns, and morphometrically adjusted condition indices serve as robust, non-invasive ecological baselines for evaluating bivalve population status across coastal environments. Finally, to establish direct cause-effect mechanisms under complex multi-stressor scenarios, future research should integrate these population-level biometric baselines with physiological and biochemical biomarkers in anthropogenically impacted marine ecosystems.

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Credit author contribution

F.A. Aguilar-Santana: conceptualization, data curation, formal analysis, investigation, methodology, validation, writing-original draft, writing-review and editing, A.R. Rivera-Camacho: methodology, fieldwork, I.S. Racotta: validation, writing-review and editing, M. Arellano-Martínez: conceptualization, formal analysis, funding acquisition, methodology, project administration, resources, supervision, validation, writing-original draft, writing-review and editing.

Conflict of interest

The authors declare no conflicts of interest.

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