

Predicting the distribution of a portunid crab in Patagonian coastal waters

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ABSTRACT: *Ovalipes trimaculatus* is a commercially important, cosmopolitan portunid crab. However, environmental conditions that drive its distribution have never been studied. Thus, we aimed to assess the habitat preferences of this species in northern Patagonia by developing a species distribution model. We obtained spatial quantitative data of the crab and its prey species from a benthic survey performed prior to commercial fishing in the area. We used measurements of environmental condition, biomass, richness and evenness of its prey as predictors, and modeled the density of *O. trimaculatus* through a delta-gamma model, and produced a map of its predicted biomass. Prey biomass, depth and substrate type were the most important variables for predicting the distribution of *O. trimaculatus*. The model predicts a restricted depth range, with maximum crab density at 10 m (the shallowest depth sampled) in bottom substrates of relatively fine granulometry, such as silty sand and silt. Prey biomass does not determine crab presence, but, where the crab is present, higher prey biomass correlates with higher crab abundance. Our results accurately predicted 1 of the 2 actual fishing grounds; hence, the model may be a useful tool for local fishers and managers.

KEY WORDS: *Ovalipes trimaculatus* · Biotic predictors · San Matías Gulf · Species distribution model

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1. INTRODUCTION

Management of marine systems is changing, with an increasing use of tools that depend on spatial information for establishing marine protected areas, spatial planning and ecosystem-based management (Freitag et al. 2018, Janßen et al. 2018). As a consequence, the need for species and habitat distribution maps has also been on the rise (Maxwell et al. 2009). However, the need for assessing the status of a fishery is generally not acknowledged until after the sys-

tem has already been impacted, making it difficult to understand to what extent it has changed. For this reason, it is relevant to recover information that was generated before the system was impacted (Pauly 1995) and that can be modeled. Novel methods can then be used to reconstruct the history of a given stock or system to understand its present status. This information is especially useful if the data were systematically gathered.

Species distribution models (SDMs) have been used successfully to predict the distributions of several eco-

nominically important species (e.g. Jones et al. 2015, Weatherdon et al. 2016). However, few studies have used SDMs to predict the distribution of crustaceans, despite the economic relevance of this taxonomic group (FAO 2018), even though marine benthic invertebrates present several attributes well suited for this technique (Robinson et al. 2011). In the available models, bathymetry and substrate characteristics have shown to be good predictors of the presence and abundance of marine invertebrates (e.g. Serrano et al. 2008, Pierrat et al. 2012) and crustaceans species in particular (Gogina & Zettler 2010, Drewnik et al. 2017). In a recent study, sea bottom temperature, sea bottom salinity and sediment type were important predictors of the distributions of 3 portunid crab species (Luan et al. 2018). Environmental variables are clearly important drivers of the distributions of marine macroinvertebrates such as crabs, but biological variables are rarely evaluated (Reiss et al. 2015), even though calls have been made for the inclusion of interspecific interactions as predictors (Paine 2010, Zarnetske et al. 2012). Trophic interaction is a good candidate in this sense (Reiss et al. 2015).

The portunid crab *Ovalipes trimaculatus* (De Haan 1833) occurs in temperate waters of the Atlantic (Vinueza 2005, de Melo 2010), Pacific (Retamal 1981) and Indian Oceans (Schoeman & Cockcroft 1993). As with other portunid crabs, *O. trimaculatus* is commercially fished in Chile (Haye et al. 2012) and Ar-

gentina (Boschi 1997, de la Barra et al. 2019). Despite the economic importance of the species, the variables that drive its distribution have never been specifically studied. It has been observed to occur in sandy bottoms (Fenucci & Boschi 1975), ranging from 3 to 100 m depth at different latitudes and regions (Boschi et al. 1992, Retamal & Arana 2000). However, the probability of occurrence within a depth range or in different substrates has never been systematically studied. Moreover, its preference for other environmental variables relevant for the distribution of benthic species, such as seabed slope (e.g. Compton et al. 2013, Basher et al. 2014), has not yet been described.

In the San Matías Gulf of Argentina (41° S), a fishery for *O. trimaculatus* has existed since 2007 (de la Barra et al. 2019). Although the fishery has been growing since its inception, after 10 yr it is still fairly small in terms of activity, size of vessels (around 8 fiberglass motor boats of 6.5–9.5 m), number of fishers and catch levels (de la Barra et al. 2019). It is a surface-supplied diving fishery in which divers fish in previously baited areas, shallower than 20 m (de la Barra et al. 2019). Crabs are collected by hand and stored in a net bag. The fishery occurs along the north-western coast of the gulf, in 2 distinct fishing grounds (hereafter referred to as 'eastern' and 'western' according to their relative positions in the gulf, Fig. 1). Each fishing ground is associated with a land-

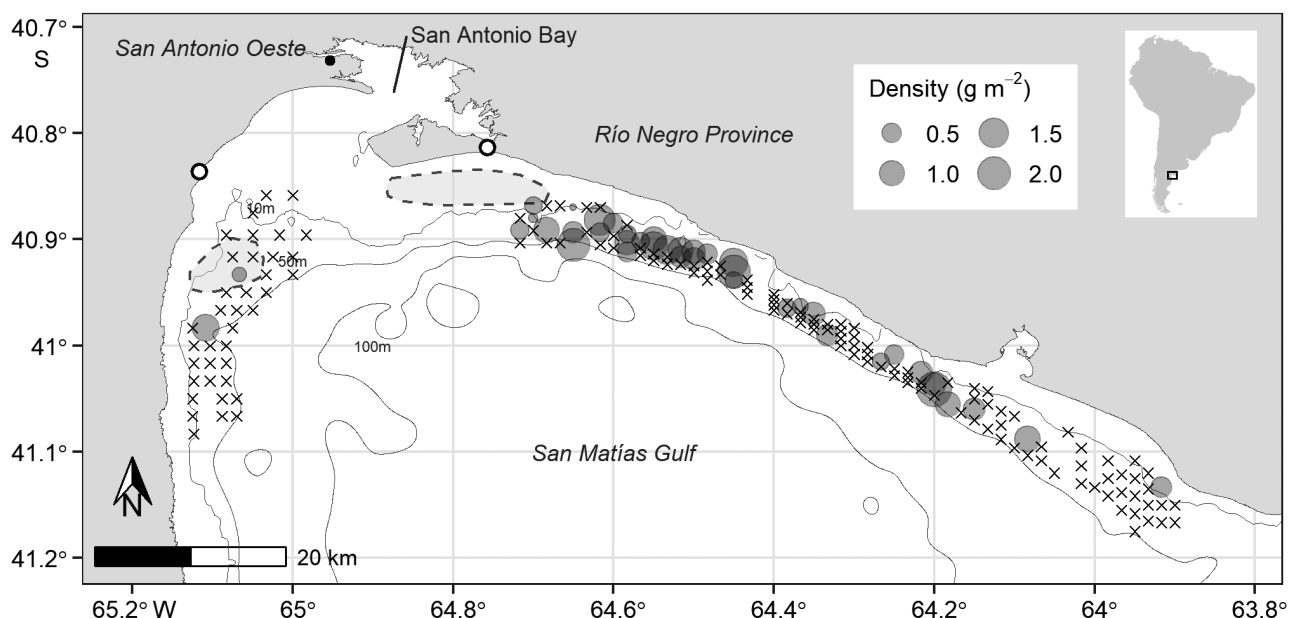


Fig. 1. Sampling stations. Circles indicate hauls where at least 1 *Ovalipes trimaculatus* was captured; circle size is proportional to the biomass of *O. trimaculatus* captured per area swept. Crosses indicate hauls where *O. trimaculatus* were not captured. Areas enclosed by dashed lines are fishing grounds used between 2008 and 2013. Open circles on the coast indicate where commercial fishery vessels are launched

ing point on the coast (Fig. 1) with no specific infrastructure (ports or marinas, de la Barra et al. 2019). To launch the vessels, fishers have farm tractors parked on the beach. The fishery takes place throughout the year, with effort depending mainly on wind conditions (de la Barra et al. 2019).

Adequate management of this fishery requires an understanding of the biological and ecological aspects of the target population, but because of its small scale, along with political decisions, there are neither specific management measures for the fishery, nor monitoring of the population.

As *O. trimaculatus* has a generalist carnivore diet (de la Barra et al. 2018), we expect the biomass of prey species to be a good predictor of the distribution of *O. trimaculatus*, independently of prey identity. However, locations with higher prey abundance may not be necessarily the more energetically profitable (Elner & Hughes 1978) or offer all the nutrients that adult *O. trimaculatus* need (Pulliam 1975). Environments with a high variety of prey species could represent high profitability and a broad offering of different nutrients. For this reason, the richness and evenness of prey species could also be good biological predictors of the distribution of *O. trimaculatus*.

Given this background, the aim of our study was to assess the distribution of *O. trimaculatus* in the north of the San Matías Gulf, taking advantage of information gathered during a systematic survey of the benthic community, prior to the beginning of the crab fishery. These surveys were independent of the crab fishery, and thus provide information about the system before it was impacted by fishing. We tested the hypothesis that the distribution of *O. trimaculatus* depends on depth, substrate type, seabed slope, water temperature and the biomass, richness and evenness of its prey. Through the use of SDMs, we aimed to generate a baseline of spatial information about the species in the San Matías Gulf and to identify the variables that may drive its distribution during the cold season.

2. MATERIALS AND METHODS

2.1. Study area

The San Matías Gulf is a temperate system located in the Patagonian Shelf Large Marine Ecosystem (Argentina). The seabed of the gulf is mainly composed of sediment of different grain size (SHN 1974). The gulf does not receive sufficient freshwater input to have any noticeable effect on salinity. During the

survey, salinity remained relatively homogeneous throughout the study area, ranging from 33.92 to 34.45‰.

2.2. SDM

During June and July 2006 (approximately 1 yr before the beginning of the crab fishery), 200 stations (survey hauls) were sampled in the north of the San Matías Gulf using a 1.6 m wide-mouth dredge (maximum weight of 50 kg, more details in Narvarte et al. 2011) as a means of estimating the abundance of different benthic resources. The survey was performed during the cold season. In other swimming crab fisheries, using dredges during the time of the year when the species is less active has proven to be a better way of estimating abundance (Vølstad et al. 2000).

The survey had a quasi-regular design covering different benthic environments between the 10 and 60 m isobaths (depth range that includes most of the described bathymetric distribution of *Ovalipes trimaculatus*). The design consisted of groups of 2 to 5 sampling stations each, located along a transect perpendicular to the coast extending between the 10 and 60 m isobaths (Fig. 1).

During the survey, each haul was tracked using GPS to calculate the area swept by the dredge. For each haul, the total weight of each species captured was measured. As Narvarte et al. (2011) observed that the efficiency of the dredge was very high (over 90 % for mussels, sea urchins and ophiuroids), whenever the dredge was lifted empty it was considered that it had not worked correctly (e.g. the dredge must have not touched the ground, or had not been properly deployed), and as a result, these hauls were not used in the subsequent analysis. Of the 129 species captured, 72 were identified as potential prey of *O. trimaculatus* following de la Barra et al. (2018). These included a selection of: bivalves, gastropods, chitons, cephalopods, crustaceans (mainly decapods), echinoids, ophiuroids, asteroideans and polychaetes (for a comprehensive list of prey species recorded, see List S1 in the Supplement at www.int-res.com/articles/suppl/m638p095_supp.pdf).

We obtained a climatological layer of sea surface temperature (SST) for June constructed from AVHRR (NOAA) satellite images for the period 2000–2008 (processing details of satellite images are found in Williams et al. 2010). The resolution of the SST images (0.01° sides, ca. 1.1 km²) was applied to all raster layers used in this study for consistency. We constructed a depth map of the area by interpolating

bathymetric points from a nautical chart of the Naval Hydrographic Service of Argentina (SHN 2000) using an ordinary kriging function (all of the following statistical analyses and maps were generated in R version 3.5.0, R Core Team 2018, and using the ordinary kriging function of the package 'gstat,' Pebesma 2004). The nautical chart had between 1 and 10 *in situ* measures of depth for each pixel of the map generated by us. From the depth map, we obtained a slope map by assigning, to each pixel, the maximum slope observed between that pixel and its 8 neighboring pixels. A map of the substrate types was obtained by rasterizing a sedimentology map of the area (SHN 1974) using QGIS (QGIS Development Team 2016). The sedimentology map had a coarser resolution (only 65 survey points in the study area) and was used as an indicator of the different large substrate habitats in the area. At 108 stations, covering the full extent of the survey area, *in situ* measures of water temperature were collected at 10 m depth using a handheld multiparameter probe (YSI556). With this information, we constructed a bottom temperature layer by interpolating these measurements with an ordinary kriging function. We considered temperature at 10 m a good proxy of sea bottom temperature because during this time of the year the water column is well mixed (Rivas & Beier 1990). Finally, we assigned values of depth, slope, SST and temperature at 10 m depth to each haul using the coordinates of the beginning of each haul and the raster layers of the variables using the R package 'raster' (Hijmans 2019).

For each haul, 3 estimators of the availability of prey of *O. trimaculatus* were calculated: biomass, richness and evenness of prey species. Biomass was calculated as the aggregated biomass of all the prey species per area swept by the dredge (g m^{-2}). Richness was derived via the Chao species estimator for abundance data (Gotelli & Colwell 2011) using the 'Chao1' function in R (Oksanen et al. 2019), and evenness was calculated as the probability of inter-specific encounter (PIE, Hurlbert 1971). The PIE index is a measure of species evenness, but it is also dependent on species richness, and, unlike richness, is not sample-size dependent (Gotelli 2008).

Pearson correlation coefficients were calculated among all variables (both environmental and biological) in order to check that they were not highly correlated ($r_{\text{pearson}} > 0.75$). We also checked for collinearity between predictors considering that if the variance inflation factor between 2 variables was higher than 3 then there was collinearity between these predictors (Zuur et al. 2010) and thus 1

variable would be omitted. However, no strong correlation was detected between any pairs of variables (Fig. S2), and the variance inflation factor showed that there was also no collinearity between any predictors; thus, all variables were retained in the analyses.

We tested the hypothesis that the distribution of *O. trimaculatus* depends on depth, substrate type, seabed slope, temperature at 10 m, SST and the biomass, richness and evenness of its prey through a delta generalized linear model (Shelton et al. 2014). This kind of model is widely used in fisheries studies as it deals with zero inflated continuous distributions, therefore allowing the study of the biomass of a species in addition to its presence/absence patterns (Shelton et al. 2014, Garofalo et al. 2018). For the delta generalized linear model, the observed catches were divided into 2 sub-models: one describing the presence or absence of *O. trimaculatus* (hereafter 'Presence sub-model'), and one for the distribution of catches conditioned on the presence of *O. trimaculatus* (hereafter 'Biomass sub-model'). We used a logit-link function and a binomial error distribution for the Presence sub-model, and a logarithmic-link with gamma error distribution for the Biomass sub-model, using the biomass per area of *O. trimaculatus* (g m^{-2}) as the response variable. Once the parameters of the model were estimated (as described in the next paragraph), we multiplied the Presence sub-model by the Biomass sub-model to obtain the delta generalized linear model that predicts the most likely biomass density of *O. trimaculatus* (SDM). The spatial autocorrelation of this final model was then tested using Moran's *I* coefficient (Moran 1950).

To evaluate the global and nested models for the Presence sub-model and the Biomass sub-model, we used an information theoretical approach. This was done independently for each sub-model (i.e. the analysis of the Presence sub-model did not affect the analysis of the Biomass sub-model). For each case, we analyzed 512 nested models (Tables S1 & S2 in the Supplement). Akaike's information criterion corrected for small sample size (AICc) was calculated for all nested models (Burnham & Anderson 2002). The nested models were then compared through ΔAICc , which is the difference between the lowest AICc value of the suite of all models (i.e. best of suitable models) and the AICc of each nested model. The AICc weight of a model (w_i) is the relative likelihood that a specific model is the best of a suite of models. Hence, we evaluated the support for each explanatory variable by summing w_i from the models where the variable was included (parameter likelihood,

Burnham & Anderson 2002). Finally, parameter estimates were calculated using model-averaged parameter estimates through the R package 'MuMin' (Barton 2018), based on w_i from the top-ranked models ($\Delta AICc < 2$). To supplement parameter-likelihood evidence of important effects, we also calculated 95 % confidence intervals (CI).

The Presence sub-model was trained using 70 % of the data, while the remaining 30 % were used to test its predictive performance through the area under the receiver operating characteristic curve (AUC) using the R package 'pROC' (Robin et al. 2011). The AUC is a threshold independent measure representing the relationship between sensitivity and the corresponding proportion of false positives. It varies between 0 and 1; values greater than 0.9 represent an excellent prediction, between 0.7 and 0.9 a good prediction, between 0.5 and 0.7 a weak prediction and below 0.5 a prediction comparable to random outcomes (Hosmer et al. 2013).

To generate a predictive map of the density of *O. trimaculatus*, we used the raster layers of the explanatory variables for the entire area (Fig. S1 in the Supplement) as input for the delta generalized linear model. Raster layers of prey biomass, richness and evenness (Fig. S1A–C) were developed through kriging (ordinary kriging of the package 'gstat' in R, Pebesma 2004). For depth, substrate type, slope, SST and temperature at 10 m depth, we used the raster layers previously mentioned in this section (Fig. S1D–H). All rasters had almost the same extent as the survey (between 1 and 60 m isobaths).

We also constructed response curves of the biomass per area of *O. trimaculatus* to all the explanatory variables. To achieve this, we calculated the mean value of each of the numeric explanatory variables and used them together with the estimated parameters (Table 1) to construct the curve of the mean predicted density of *O. trimaculatus* relative to each predictor.

3. RESULTS

From the 200 hauls performed during the survey, 13 presented no catch and 4 had an area swept that was smaller than expected ($<100 \text{ m}^2$) and were discarded due to likely deployment error. The hauls occurred on 4 types of substrate: sand, silt, silty sand and gravel. In total, we analyzed 183 hauls with an area swept of $343.8 \pm 107.2 \text{ m}^2$ (mean \pm SD). In 40 of these hauls, at least 1 individual of *Ovalipes trimaculatus* was caught (Fig. 1). The depths of the analyzed hauls ranged between 12 and 58 m, seabed slope ranged between 0.03 and 1.55° , SST ranged from 12.81 to 14.58°C , and temperature at 10 m depth ranged from 11.7 to 12.97°C . Prey of *O. trimaculatus* were found in all the hauls analyzed, with biomass ranging from 0.11 to 45.3 g m^{-2} , species richness ranged from 1 to 54, and the PIE ranged from 0 to 0.83.

For the Presence sub-model, 6 models had $AIC < 2$ (Table S1) and were therefore averaged. The averaged Presence sub-model included substrate type, depth, richness and SST as explanatory variables (Table 1). Specifically, depth and substrate type had a higher likelihood of explaining presence (Table 1). This model obtained an AUC of 0.74, with 95 % CI ranging from 0.51 to 0.97, and we considered the model to have acceptable predictive power on the presence of *O. trimaculatus*. The Presence sub-model explained 26.15 % of the deviance of the presence/absence data.

For the Biomass sub-model, 5 models were averaged to explain the density of *O. trimaculatus* conditioned on its presence (Table S2). The variables included in the averaged Biomass sub-model were depth, prey biomass, SST, evenness and slope, the latter 3 having a lower likelihood to explain changes in biomass density (Table 1). The Bio-

Table 1. Parameter likelihoods, estimates and 95 % confidence intervals (CI) for explanatory variables describing variation in probability of presence of *Ovalipes trimaculatus*, and biomass density given that it is present. *Italics*: explanatory variables with CI excluding 0. SST: sea surface temperature

Explanatory variable	Parameter likelihood	Parameter estimate \pm SE	CI	
			Lower	Upper
Presence				
Intercept		5.22 ± 7.44	-9.37	19.81
Substrate (Sand)	1	-19.04 ± 1679.76	-3311.31	3273.24
Substrate (Gravel)	1	-1.07 ± 0.71	-2.47	0.32
Substrate (Silt)	1	-0.57 ± 0.57	-1.69	0.56
Depth	1	-0.04 ± 0.02	-0.08	-0.00
Richness	0.59	-0.04 ± 0.05	-0.16	0.01
SST	0.38	-0.28 ± 0.55	-2.06	0.59
Biomass				
Intercept		-2.60 ± 4.07	-10.58	5.37
Depth	1	-0.03 ± 0.01	-0.06	-0.01
Prey biomass	1	0.04 ± 0.02	0.01	0.07
SST	0.47	0.23 ± 0.31	-0.06	1.02
Evenness	0.46	-0.42 ± 0.56	-1.87	0.06
Slope	0.11	0.04 ± 0.14	-0.27	0.93

mass sub-model explained 30.54 % of the deviance of the biomass data. Through the multiplication of the averaged Presence and the averaged Biomass sub-models, we obtained the SDM (Fig. 2). Between 10 and 60 m depth, the SDM predicted an average biomass density of *O. trimaculatus* of 0.30 g m^{-2} , with a maximum density of 1.29 g m^{-2} . The higher densities of *O. trimaculatus* were predicted at the lower depths along the northern coast of the gulf (Fig. 2). The model did not present spatial autocorrelation (Moran test $p = 0.15$).

Depending on substrate type, the response curve of the SDM showed clear differences: silt and silty sand presented a higher density of *O. trimaculatus*, compared to sand or gravel (Fig. 3A–F). Depth and prey species richness showed a negative relationship with *O. trimaculatus* density (Fig. 3B,C), while prey biomass presented a positive relationship (Fig. 3F). However, their effect was much lower when the substrate type was sand (Fig. 3B,C,F). Evenness, slope and SST had a very small effect on *O. trimaculatus* density (Table 1, Fig. 3A,D,E), and *in situ* temperature at 10 m depth was not retained in the final model.

4. DISCUSSION

Our model suggests that the distribution of *Ovalipes trimaculatus* in the north of San Matías Gulf is likely influenced by substrate type, depth and prey

biomass. Seabed slope, SST, prey species richness and prey species evenness were retained in the model, but confidence in their importance was lower, as the confidence intervals included zero. We are aware of only one other published paper modeling the distribution of portunid crabs (Luan et al. 2018). Unlike that study, our work was conducted over a smaller area but at a much higher spatial resolution. Furthermore, our study includes proxies of trophic interactions as predictors of the distribution of these crabs for the first time, shedding new light on how they may be modulating the population's distribution.

Depth is a reliable predictor of crustacean distributions (Gogina & Zettler 2010, Drewnik et al. 2017). In this study, we determined that the depth range within the studied area was quite restricted, with the maximum predicted density of crabs at 10 m (the shallowest depth sampled). Moreover, in bottom trawl surveys carried out in deeper areas of the San Matías Gulf between 30 and 170 m depth, in different years and seasons, *O. trimaculatus* has never been found (Ocampo-Reinaldo 2005a,b, Ocampo-Reinaldo et al. 2008, Maggioni et al. 2010). This may be because depth may be an indirect estimator of different environmental variables, such as substratum, temperature, light, wave energy and salinity (Reiss et al. 2015). While we tested substrate type and temperature, we did not consider salinity because the spatial variation of this variable in the north of San Matías Gulf is minimal (Rivas & Beier 1990), with no appre-

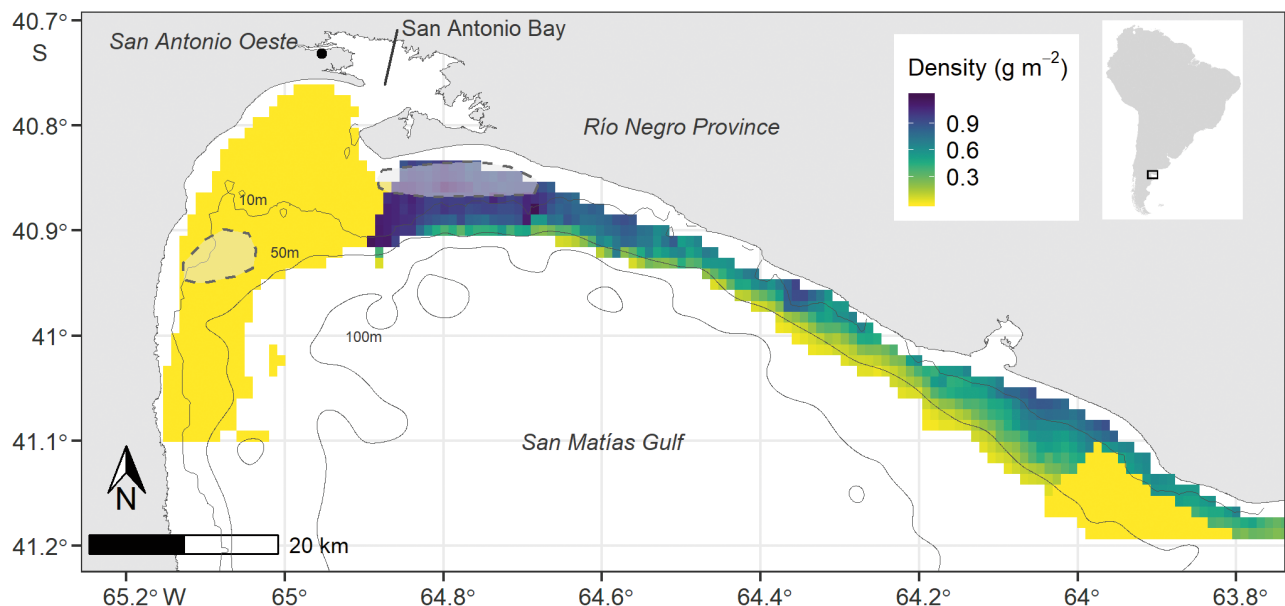


Fig. 2. Predicted biomass density of *Ovalipes trimaculatus*. The species distribution model was extrapolated between 0 and 60 m depth. Areas enclosed by dashed lines are fishing grounds used between 2008 and 2013

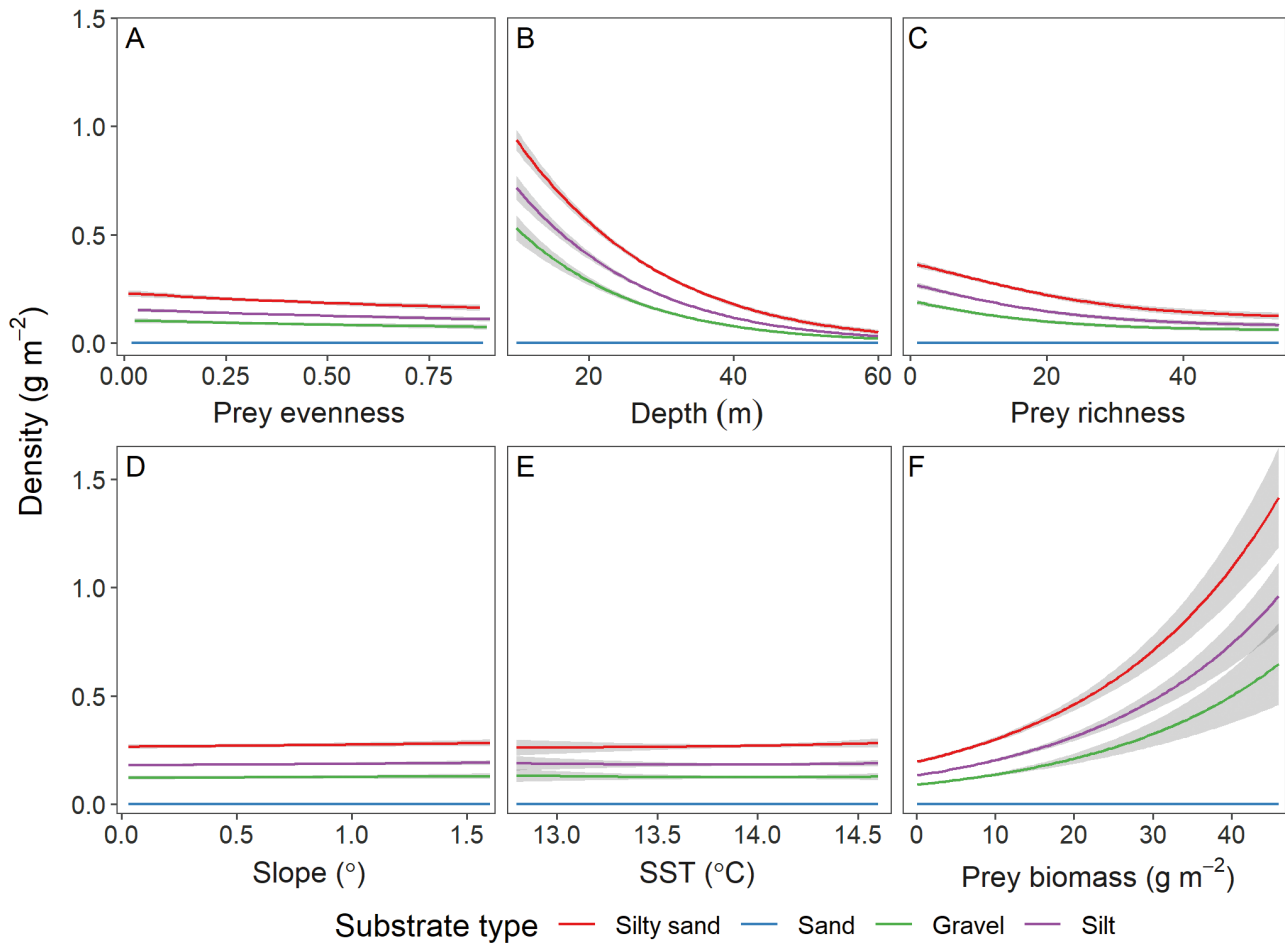


Fig. 3. Averaged response curves of the *Ovalipes trimaculatus* species distribution model to the predictors. Response curves to (A) evenness (probability of interspecific encounter, PIE), (B) depth, (C) prey species richness, (D) seabed slope, (E) sea surface temperature (SST) and (F) prey species biomass. Grey ribbons represent standard errors

ciable freshwater input (i.e. there are no stream flows into the gulf), and the extent of the study area is quite small. In our study, depth might only be an indirect driver of the *O. trimaculatus* distribution. However, the structuring nature of bathymetry makes it difficult to replace depth in distribution modeling (Reiss et al. 2015).

Our model predicts that in the San Matías Gulf, *O. trimaculatus* mainly occurs in bottom substrate of relatively fine granulometry, such as silt and silty sand. Until now, it was assumed that *O. trimaculatus* mainly occurs on sandy bottoms (Fenucci & Boschi 1975). We found that contrary to some literature, sandy bottoms were the least favorable for *O. trimaculatus*, even less favorable than gravel. Sandy bottoms occur in the western area of the gulf (Fig. S1B), and *O. trimaculatus* was only caught in 2 hauls from that area. However, an important fishing ground occurs there, thus it is likely that the SDM underestimated the density of *O. trimaculatus* in sandy bot-

toms. As substrate type may influence the efficiency of the dredge, it is also possible that the low biomass of *O. trimaculatus* in sandy bottoms is due to a lower catchability of the species in that type of substrate. Trawling gear may have a different efficiency in catching crustaceans depending on the kind of gear, the substrate type and the species' habitat preference (e.g. Reiss et al. 2006, Somerton et al. 2013). However, for *Callinectes sapidus*, another portunid crab, the efficiency of dredges is the same in muddy and sandy bottoms during winter as crabs present a quasi-hibernation behavior—they spend most of the time buried in the sediment (Zhang et al. 1993). Given the similarity in season and bottom substrate type, we do not expect our case to be too different.

Sea bottom temperature was one of the main predictors of portunid crab distributions in a large bay in China (Luan et al. 2018). In our models, *in situ* bottom temperature was not a good predictor for crab presence or density, and climatological SST provided

only a moderate contribution to the final model (Fig. 3). Because *in situ* temperature did not influence the distribution of *O. trimaculatus*, we do not consider that water temperature directly constrains its distribution in the gulf by influencing physiology or behavior. Instead, the correlation with SST may indicate a preference of this crab for the productive waters of San Antonio Bay, which during this time of the year are colder than the adjacent waters of the gulf (Fig. S1G, Esteves et al. 1996).

Although environmental variables (substrate type, depth and SST) were the most important for predicting the distribution of *O. trimaculatus*, biological variables (prey biomass, richness and evenness) were all retained in the SDM, and we can therefore affirm that they improved the prediction of the crab's distribution. Co-occurrence of predators and their prey is commonly observed in terrestrial (e.g. Fernández et al. 2003), freshwater (e.g. Godin & Keenleyside 1984) and benthic marine environments (e.g. Stewart & Jones 2001). However, benthic invertebrates are considered to be more dependent on environmental variables than marine apex predators, which have a wider span of homeostasis and are therefore more capable of moving among different environmental conditions to find their prey (Robinson et al. 2011). Moreover, some authors have suggested that in the soft sedimentary benthos, environmental variables dominate over biological interactions in driving the distribution of macroinvertebrates (i.e. predation, Woodin 1983, Wilson 1990). Hence, the effect of prey on the distribution of marine macroinvertebrates is generally not evaluated (e.g. see review by Snickars et al. 2014), particularly in sedimentary environments. Portunid crabs are benthic macroinvertebrates, but also are active predators and thus need to at least partially share their distribution with their prey.

Using prey biomass as a predictor of predator abundance assumes that energy availability is the main constraint to the predator's diet, and that access to prey is equal across the study area (Trainor & Schmitz 2014). In our SDM, biomass of prey species was retained as a predictor in the Biomass sub-model, but not in the Presence sub-model. This means that the amount of prey biomass does not determine the presence of *O. trimaculatus*, but, where the species is present, higher prey abundance will correlate with higher biomass of *O. trimaculatus* (Table 1). Given that *O. trimaculatus* is a generalist consumer, it makes sense that prey biomass is not a limiting factor for its presence, as it is likely that individuals will find prey in most places. This conclusion is supported by the fact that every haul in the sampling survey

presented some amount of prey biomass. However, this is not always the case for consumers that prey upon benthic invertebrates. Hines et al. (1997) and Schwemmer et al. (2016) observed, in eagle rays and wading birds, respectively, that prey density must reach a certain limit for it to be a good predictor of predator presence. Using prey biomass as a predictor of predator abundance also assumes that accessibility to prey is the same in every area where predator and prey co-occur (Trainor & Schmitz 2014). This assumption may not be realistic when the abundance of prey species does not reflect the likelihood that a predator finds and successfully captures one of them (Trainor & Schmitz 2014). As mentioned before, the predation rate of crabs may be affected by substrate type; in particular, larger particle size diminishes their foraging efficiency (Liu et al. 2019). The results of the SDM suggest that something similar could be happening in the San Matías Gulf. We observed a positive effect of prey biomass mainly within substrate types that favored the distribution of *O. trimaculatus* (silt and silty sand), but a lower effect of prey biomass in sub-optimal substrate types (sand, Fig. 3F).

The metabolic system of a consumer requires different proportions of key nutrients, and hence, the food items that maximize energetic intake may not satisfy the rest of the nutritional needs of the consumer (Pulliam 1975). In a wide variety of taxa, including arthropods, a mixed diet enhances various fitness indicators in comparison with a monospecific diet (Lefcheck et al. 2013). Therefore, patches where various prey species occur should have a higher biological value for a generalist consumer than areas with high dominance of one or a few prey species. However, according to the SDM, higher evenness and richness negatively affect the distribution of *O. trimaculatus* (Fig. 3A,C), the latter having a larger effect. In coastal sedimentary environments, at a larger scale, benthic species richness positively correlates with depth (Gray 2002, and references therein). However, species richness had a low correlation with depth in our study area (Fig. S2 in Supplement 2). Therefore, we assume that species richness in San Matías Gulf may be affected by an un-measured variable that negatively affects the distribution of *O. trimaculatus*. For example, species richness has been observed to be positively correlated with habitat complexity (Gratwicke & Speight 2005), and it is possible that *O. trimaculatus* prefers simpler habitats with large sedimentary plains, where it can bury itself. Birch (1981) observed that in sedimentary habitats, dominance and richness are positively correlated as well. On the other hand, Gray (2002) pro-

posed that the patterns of species richness in benthic marine sedimentary environments reflect complex processes: a combination of the availability of food resources (i.e. patches of microbial communities) and the spatial and temporal heterogeneity in a given area. However, it is not clear how these processes may affect the distribution of *O. trimaculatus*.

Our results accurately predicted 1 of the 2 fishing grounds, as the highest biomass values for *O. trimaculatus* were obtained within the eastern fishing ground. This was in spite of the relatively low explained deviance obtained, and no sampling stations were located inside this fishing ground. The prediction for the western fishing ground, on the other hand, showed very low biomass of *O. trimaculatus*, likely due to the lower sampling effort in that area, or due to a lower efficiency of the dredge in that substrate type, as discussed before.

The correlative approach used in this study prevents us from establishing causal relationships between the distribution of *O. trimaculatus* and the environmental and biological variables studied. More complex approaches would be required to adequately deal with this causation. Mechanistic niche modeling, for example, allows integration of mechanistic links between functional traits of organisms and their environments into SDMs (Kearney & Porter 2009). Hybrid datasets combine the inferential power of experiments with the large scales (spatial and temporal) of observational studies (Benedetti-Cecchi et al. 2018). Nonetheless, in many cases, it is not possible to carry out an experimental approach (Mac Nally 2000). The difficulty in accessing certain environments, as well as the scarce economic resources available for research throughout the majority of the world, underline the importance that correlative approaches have (and will have for some time) in our understanding of the natural world. Although unable to indicate causality, correlative approaches are a useful tool to select and refine candidate variables for experimental approaches to progress our understanding of potential mechanisms (Kearney & Porter 2009).

In conclusion, the present distribution model of *O. trimaculatus* achieved acceptable predictive power for the north of the San Matías Gulf, where a fishery has recently been established targeting this species. Considering the cosmopolitan nature of the species, the environmental and biological variables that constrain its distribution in the San Matías Gulf could also be relevant in other regions, and thus, substrate type, depth, SST, and prey biomass, evenness and richness may be useful candidate variables in future studies. Considering the small scale of the fishery,

the exploration of the gulf with the objective of understanding the distribution of *O. trimaculatus* would impose an unaffordable economic cost upon the fishery managers (local government). Not even the fishers can afford to invest time in finding new fishing grounds (de la Barra et al. 2019). Hence, a map of the species distribution may be a useful tool for managers (Maxwell et al. 2009) as a reference of the areas where they should focus their efforts.

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