

1 **Predicting the distribution of a Portunid crab in Patagonian coastal waters: an SDM**
2 **approach**

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14 Running page head: Predicting the distribution of Portunid crab

15 **Abstract**

16 *Ovalipes trimaculatus* is a cosmopolitan Portunid crab that is commercially important.
17 However, environmental conditions that drive its distribution have never been studied.
18 Thus, we aimed to assess the habitat preferences of the species in northern Patagonia
19 by developing a species distribution model. We obtained spatial quantitative data of the
20 crab and its prey species from a benthic survey performed prior to commercial fishing
21 in the area. We used measurements of environment condition, biomass, richness and
22 evenness of its prey as predictors, and modeled the density of *O. trimaculatus* through

1 a delta-gamma model and produced a map of its predicted biomass. Prey biomass,
2 depth and substrate type were the most important variables for predicting *O.*
3 *trimaculatus'* distribution. The model predicts a restricted depth range, with maximum
4 crab density at 10 m (the shallowest depth sampled) in bottom substrates of relatively
5 fine granulometry, as silty sand and silt. Prey biomass does not determine the crab
6 presence, but, where the crab is present, higher prey biomass correlates with higher
7 crab abundance. Our results accurately predicted one of the two actual fishing grounds,
8 hence, the model may be a useful tool for local fishers and managers.

9 Key words: *Ovalipes trimaculatus*, biotic predictors, San Matías Gulf, Species
10 distribution model

11

12 **1. Introduction**

13 Marine systems management is changing, with an increasing use of tools that depend
14 on spatial information such as marine protected areas, spatial planning and ecosystem-
15 based management (Freitag et al. 2018, Janßen et al. 2018). As a consequence, the need
16 for species and habitat distribution maps has also been on the rise (Maxwell et al. 2009).
17 However, the need for assessing the status of a fishery is generally not acknowledged
18 until after the system has already been impacted, making it difficult to understand to
19 what extent it has changed. For this reason, it is relevant to recover information
20 generated before the system has been impacted (Pauly 1995), that may be modeled,
21 and with novel methods, reconstruct the past of a stock or system, and thus understand

1 its present status. This information will be especially useful if it was systematically
2 gathered.

3 The use of Species Distribution Models (SDMs) has successfully predicted the
4 distribution of several economically important species (e.g. Jones et al. 2015,
5 Weatherdon et al. 2016). However, few studies have used SDMs to predict the
6 distribution of crustaceans, notwithstanding the economic relevance of this taxonomic
7 group (FAO 2018), even though marine benthic invertebrates present several attributes
8 well suited for this technique (Robinson et al. 2011). In the available models, bathymetry
9 and substrate characteristics have shown to be good predictors of the presence and
10 abundance of marine invertebrate species (e.g. Serrano et al. 2008, Pierrat et al. 2012)
11 and crustaceans species in particular (Gogina and Zettler 2010, Drewnik et al. 2017). In
12 a recent study, sea bottom temperature, sea bottom salinity and sediment type were
13 important predictors of the distribution of three portunid crab species (Luan et al. 2018).
14 Environmental variables are clearly important drivers of the distribution of marine
15 macroinvertebrates such as crabs, but biological variables are rarely evaluated (Reiss et
16 al. 2014), even though calls have been made for the inclusion of interspecific
17 interactions as predictors (Paine 2010, Zarnetske et al. 2012). Trophic interaction is a
18 good candidate in this sense (Reiss et al. 2014).

19 The portunid crab *Ovalipes trimaculatus* (De Haan 1833) occurs in temperate waters of
20 the Atlantic (Vinuesa 2005, Melo 2010), Pacific (Retamal 1981) and Indian Oceans
21 (Schoeman & Cockcroft 1993). As with other portunid crabs, *O. trimaculatus* is
22 commercially fished in Chile (Haye et al. 2012) and Argentina (Boschi 1997, de la Barra
23 et al. 2019). Despite the economic importance of the species, the variables that drive its

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

8 In the San Matías Gulf (41° S, Argentina), a fishery for *O. trimaculatus* has existed since
9 2007 (de la Barra et al. 2019). Although the fishery has been growing since its inception,
10 after 10 years it is still fairly small in terms of activity, size of vessels (around eight
11 fiberglass motor boats of 6.5–9.5 m), number of fishers and catch levels (de la Barra et
12 al. 2019). It is a surface-supplied diving fishery in which divers fish on previously baited
13 areas, shallower than 20 m (de la Barra et al. 2019). Crabs are picked up by hand and
14 stored in a net bag. The fishery occurs in the north-western coast of the gulf, in two
15 distinct fishing grounds (hereafter referred to as eastern and western according to their
16 relative positions in the gulf, Figure 1). Each fishing ground is associated with a landing
17 point on the coast (Figure 1) with no specific infrastructure (ports or marinas, de la Barra
18 et al. 2019). To launch the vessels, fishers have farm tractors parked on the beach. The
19 fishery takes place throughout the year, with the effort depending mainly on the wind
20 conditions (de la Barra et al. 2019).

21 Adequate management of this fishery requires an understanding of the biological and
22 ecological aspects of the target population, but because of its small scale, along with

1 political decisions, there are neither specific management measures for the fishery, nor
2 monitoring of the population.

3 As *Ovalipes trimaculatus* has a generalist carnivore diet (de la Barra et al. 2018), we
4 expect the biomass of prey species to be a good predictor of the distribution of *O.*
5 *trimaculatus*, independently of prey identity. However, locations with higher prey
6 abundance may not be necessarily the more energetically profitable (Elner & Hughes
7 1978) or offer all the nutrients that adult *O. trimaculatus* need (Pulliam 1975).
8 Environments with a high variety of prey species could represent high profitability and
9 a broad offering of different nutrients. For this reason, the richness and evenness of prey
10 species could also be good biological predictors of the distribution of *O. trimaculatus*.

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

21

22 **2. Materials and Methods**

23 **2.1 Study area**

1 The San Matías Gulf is a temperate system located in the Patagonian Shelf Large Marine
2 Ecosystem (Argentina). The seabed of the gulf is mainly composed of sediment of
3 different grain size (Servicio de Hidrografía Naval Argentino 1974). The Gulf does not
4 receive sufficient freshwater input to have any noticeable effect on salinity. During the
5 survey, salinity remained relatively homogeneous throughout the study area ranging
6 from 33.92 to 34.45‰.

7 **2.2 Species distribution model**

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

15

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

21 During the survey, each haul was tracked using a GPS to calculate the area swept by the
22 dredge. For each haul, the total weight of each species captured was measured. As
23 Narvarte et al. (2011) observed that the efficiency of the dredge was very high (over 90%

1 for mussels, sea urchins and ophiuroids), whenever the dredge was lifted empty it was
2 considered that it had not worked correctly (e.g. the dredge must have not touched the
3 ground, or had not been properly deployed), as a result these hauls were not used in
4 the subsequent analysis. Seventy two of the 129 species captured were identified as
5 potential prey of *O. trimaculatus* following de la Barra et al. (2018). These included a
6 selection of: bivalves, gastropods, chitons, cephalopods, crustaceans (mainly decapods),
7 echinoids, ophiuroids, asteroideans and polychaetes (Electronic supplement 1).

8 We obtained a climatological layer of sea surface temperature (SST) for June
9 constructed from AVHRR (NOAA) satellite images for the period 2000–2008 (processing
10 details of satellite images are found in Williams et al. 2010). The resolution of the SST
11 images (0.01° sides, ca. 1.1 km²) was applied to all the raster layers used in this study for
12 consistency. We constructed a depth map of the area by interpolating bathymetric
13 points from a nautical chart of the Naval Hydrographic Service of Argentina (SHN 2000)
14 using an ordinary Kriging function (all the following statistical analyses and maps were
15 generated in R version 3.5.0, R Core Team 2018, ordinary kriging function of the package
16 “gstat”, Pebesma 2004,). The nautical chart had between one and ten *in situ* measures
17 of depth for each pixel of the map generated by us. From the depth map, we obtained
18 a slope map by assigning, to each pixel, the maximum slope observed between itself and
19 its eight neighboring pixels. A map of the substrate types was obtained by rasterizing a
20 sedimentology map of the area (SHN 1974) using QGIS (QGIS Development Team 2016).
21 The sedimentology map had a coarser resolution (only 65 survey points in the study
22 area) and was used as an indicator of the different large substrate habitats in the area.
23 In 108 stations, covering the full extent of the survey area, *in situ* measures of water
24 temperature were collected at 10 m depth using a handheld multiparameter probe

1 (YSI556). With this information, we constructed a bottom temperature layer by
2 interpolating these measurements with an ordinary Kriging function. We considered
3 temperature at 10 m a good proxy of sea bottom temperature because during this time
4 of the year the water column is well mixed (Rivas and Beier 1990). Finally, we assigned
5 values of depth, slope, SST and temperature at 10 m depth to each haul using the
6 coordinates of the beginning of each haul and the raster layers of the variables using the
7 R package “raster” (Hijmans 2019).

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

16 Pearson correlation coefficients were calculated among all variables (both
17 environmental and biological) in order to check that they were not highly correlated
18 ($r_{\text{pearson}} > 0.75$). We also checked for collinearity between predictors considering that if
19 the variance inflation factor between two variables was higher than 3 then there was
20 collinearity between these predictors (Zuur et al. 2010) and thus one would be omitted.
21 However, no strong correlation was detected between any pairs of variables (Figure S2)
22 and the variance inflation factor showed that there was also no collinearity between any
23 predictors, thus, all variables were retained in the analyses.

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

18 To evaluate the global and nested models for the Presence sub-model and the Biomass
19 sub-model we used an information theoretical approach. This was done independently
20 for each sub-model (i.e. the analysis of the Presence sub-model did not affect the
21 analysis of the Biomass sub-model). For each case, we analyzed 512 nested models
22 (Table S1 and S2). Akaike's information criterion corrected for small sample size (AICc)
23 was calculated for all the nested models (Burnham & Anderson 2002). Then, the nested
24 models were compared through ΔAICc , which is the difference between the lowest AICc

1 value of the suit of all models (i.e. best of suitable models) and the AICc of each nested
2 model. The AICc weight of a model (w_i) is the relative likelihood that a specific model is
3 the best of a suit of models. Hence, we evaluated the support for each explanatory
4 variable by summing w_i from the models where the variable was included (parameter
5 likelihood, Burnham & Anderson 2002). Finally, parameter estimates were calculated
6 using model-averaged parameter estimates through the R package “MuMIn” (Barton
7 2018), based on w_i from the top-ranked models ($\Delta AICc < 2$). To supplement parameter-
8 likelihood evidence of important effects, we also calculated 95% confidence interval
9 limits (CL).

10 The Presence sub-model was trained using 70% of the data, while the remaining 30%
11 were used to test its predictive performance through the area under the receiver
12 operating characteristic curve (AUC) using the R package “pROC” (Robin et al. 2011). The
13 AUC is a threshold independent measure representing the relationship between
14 sensitivity and the corresponding proportion of false positives. It varies between 0 and
15 1; values greater than 0.9 represent an excellent prediction, between 0.7 and 0.9 a good
16 prediction, between 0.7 and 0.5 a weak prediction and below 0.5 prediction comparable
17 to random outcomes (Hosmer et al. 2013).

18 To generate a predictive map of the density of *O. trimaculatus*, we used the raster layers
19 of the explanatory variables for the entire area (Figure S1) as input for the delta
20 generalized linear model. Raster layers of prey biomass, richness, and evenness (Figure
21 S1 A-C) were developed through kriging (ordinary kriging of the package “gstat” in R,
22 Pebesma 2004). For depth, slope, SST, temperature at 10 m depth and substrate type

1 we used the raster layers previously mentioned in this section (Figure S1 D-H). All rasters
2 had the almost the same extent as the survey (between 1 and 60 m isobaths).
3 We also constructed response curves of the biomass per area of *O. trimaculatus* to all
4 the explanatory variables. To achieve this, we calculated the mean value of each of the
5 numeric explanatory variables and used them together with the estimated parameters
6 (Table 1) to construct the curve of the mean predicted density of *O. trimaculatus* relative
7 to each predictor.

8

9 **3. Results**

10 From the 200 hauls performed during the survey, 13 presented no catch and 4 had an
11 area swept that was smaller than the expected (less than 100 m²) and were discarded
12 due to likely deployment error. The hauls occurred on six types of substrate: sand, silt,
13 silty-sand and gravel. In total, we analyzed 183 hauls with an area swept of 343.8, 107.2
14 m² (mean, SD). In 40 of these hauls at least one individual of *O. trimaculatus* was caught
15 (Figure 1). The depths of the analyzed hauls ranged between 12 and 58 m, seabed slope
16 ranged between 0.03 and 1.55°, SST between 12.81 and 14.58 °C and temperature at 10
17 m depth ranged between 11.7 and 12.97 °C. *Ovalipes trimaculatus*' prey were found in
18 all the hauls analyzed and its biomass ranged from 0.11 to 45.3 g·m⁻², its species richness
19 ranged from 1 to 54 and the PIE ranged from 0 to 0.83.

20 For the Presence sub-model six models had $\Delta AIC < 2$ (Table S1) and were therefore
21 averaged. The averaged Presence sub-model included substrate type, depth, richness
22 and SST as explanatory variables (Table 1. a). Specifically, depth and substrate type had
23 a higher likelihood of explaining presence (Table 1. a). This model obtained an AUC of

1 0.74, with 95% CL ranging from 0.51 to 0.97, we considered the model to have
2 acceptable predictive power on the presence of *O. trimaculatus*. The Presence sub-
3 model explained 26.15% of the deviance of the presence-absence data.

4 For the Biomass sub-model, five models were averaged to explain the density of *O.*
5 *trimaculatus* conditioned on its presence (Table S2). The variables included in the
6 averaged Biomass sub-model were depth, prey biomass, SST, evenness and slope, the
7 latter three having a lower likelihood to explain the Biomass sub-model (Table 1. b). The
8 Biomass sub-model explained 30.54% of the deviance of the biomass data.
9 Through the multiplication of the averaged Presence and the averaged Biomass sub-
10 models we obtained the SDM (Figure 2). Between 10 and 60 m depth the SDM predicted
11 an average biomass density of *O. trimaculatus* of 0.30 g m⁻², with a maximum density of
12 1.29 g m⁻². The higher densities of *O. trimaculatus* were predicted at the lower depths
13 of the north coast of the gulf (Figure 2). The model did not present spatial
14 autocorrelation (Moran test $P = 0.15$).

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

23

1 4. Discussion

2 Our model suggests that the distribution of *Ovalipes trimaculatus* in the north of San
3 Matías Gulf is likely influenced by substrate type, depth and prey biomass. Seabed
4 slope, SST, prey species richness and prey species evenness were retained in the model
5 but confidence in their importance was lower as confidence intervals included zero.
6 Before this study we are aware of only one published paper modeling of the
7 distributions of portunid crabs (Luan et al. 2018). Unlike that study, our work was
8 conducted over a smaller area but at a much higher spatial resolution. Furthermore, our
9 study includes proxies of trophic interactions as predictors of the distribution of these
10 crabs for the first time, shedding new light on how they may be modulating the
11 population's distribution.

12 Depth has been found to be a reliable predictor of crustaceans' distribution (Gogina &
13 Zettler 2010, Drewnik et al. 2017). In this study, we determined that the depth range
14 within the studied area was quite restricted, with the maximum predicted density of
15 crabs at 10 m (the shallowest depth sampled). Moreover, in bottom trawl surveys
16 carried out in deeper areas of the San Matías Gulf between 30 and 170 m depth, in
17 different years and seasons, *O. trimaculatus* has never been found (Ocampo-Reinaldo
18 2005a,b, Ocampo-Reinaldo et al. 2008, Maggioni et al. 2010). This may be because depth
19 may be an indirect estimator of different environmental variables, such as substratum,
20 temperature, light, wave energy and salinity (Reiss et al. 2014). While we tested
21 substrate type and temperature, we did not consider salinity because the spatial
22 variation of this variable in the north of San Matías Gulf is minimal (Rivas and Beier
23 1990), with no appreciable freshwater input (i.e. there are no stream flows into the

1 Gulf), and the extent of the study area is quite small. In our study, depth might only be
2 an indirect driver of *O. trimaculatus*' distribution. However, the structuring nature of
3 bathymetry makes it difficult to replace depth in distribution modelling (Reiss et al.
4 2014).

5 Our model predicts that, in the San Matías Gulf, *O. trimaculatus* mainly occurs in bottom
6 substrate of relatively fine granulometry, such as silt and silty sand. Until now, it was
7 assumed that *O. trimaculatus* mainly occurs in sandy bottoms (Fenucci and Boschi 1975).

8 We found that contrary to some literature, sandy bottoms were the least favorable for
9 *O. trimaculatus*, indeed, even less favorable than gravel. This is probably because sandy
10 bottoms occur in the western area of the gulf (Figure S1 B), and *O. trimaculatus* was only
11 caught in two hauls from that area. However, an important fishing ground occurs there,
12 thus it is likely that the SDM has underestimated the density of *O. trimaculatus* in sandy
13 bottoms. As substrate type may influence the efficiency of the dredge, it is also possible
14 that the low biomass of *O. trimaculatus* in sandy bottoms is due to a lower catchability
15 of the species in that type of substrate. Trawling gear may have a different efficiency in
16 catching crustaceans depending on the kind of gear, the substrate type and the species'
17 habitat preference (e.g. Reiss et al. 2006, Somerton et al. 2013). However, for *Callinectes*
18 *sapidus*, another portunid crab, the efficiency of dredges is the same in muddy and
19 sandy bottoms during winter as crabs present a quasi-hibernation behavior – they spend
20 most of the time buried in the sediment (Zhang et al. 1993). Given the similarity in
21 season and bottom substrate type, we do not expect our case to be too different.

22 Sea bottom temperature was one of the main predictors of portunid crab distributions
23 in a big bay of China (Luan et al. 2018). In our models *in situ* bottom temperature was

1 not a good predictor for crab presence or density and climatological SST provided only
2 a moderate contribution to the final model (Figure 3). Because *in situ* temperature did
3 not influence the distribution of *O. trimaculatus*, we do not consider that water
4 temperature directly constrains its distribution in the gulf through influencing
5 physiology or behavior. Instead, the correlation with SST may be indicating a preference
6 of this crab for the water mass of San Antonio Bay which is very productive and during
7 this time of the year is colder than the adjacent waters of the gulf (Figure S1 G, Esteves
8 et. al 1996).

9 Although environmental variables (substrate type, depth and SST) were the most
10 important for predicting the distribution of *O. trimaculatus*, biological variables (prey
11 biomass, richness and evenness) were all retained in the SDM and therefore, we can
12 affirm that they improved the prediction of the crab's distribution. Co-occurrence of
13 predators and their prey is commonly observed in terrestrial (e.g. Fernández et al. 2003),
14 freshwater (e.g. Godin & Keenleyside 1984), and benthic marine environments (e.g.
15 Stewart & Jones 2001). However, benthic invertebrates are considered to be more
16 dependent on environmental variables than marine apex predators, which have a wider
17 span of homeostasis and are therefore more capable of moving among different
18 environmental conditions to find their prey (Robinson et al. 2011). Moreover, some
19 authors suggest that in the soft sedimentary benthos, environmental variables dominate
20 over biological interactions in driving the distribution of macroinvertebrates (i.e.
21 predation, Woodin 1983, Wilson 1990). Hence, the effect of prey on the distribution of
22 marine macroinvertebrates is generally not evaluated (e.g. see review by Snickars et al.
23 2014), particularly in sedimentary environments. Portunid crabs are benthic

1 macroinvertebrates, but also are active predators and thus, need to at least partially
2 share their distribution with their prey.

3 Using prey biomass as a predictor of predator abundance assumes that energy
4 availability is the main constraint to the predator's diet and that access to prey is equal
5 across the study area (Trainor & Schmitz 2014). In our SDM, biomass of prey species was
6 retained as a predictor in the Biomass sub-model, but not in the Presence sub-model.
7 This means that the amount of prey biomass does not determine the presence of *O.*
8 *trimaculatus*, but, given that the species is present, higher prey abundance will correlate
9 with higher biomass of *O. trimaculatus* (Table 1). As *O. trimaculatus* is a generalist
10 consumer, it makes sense that prey biomass is not a limiting factor to its presence, it is
11 likely that individuals will find prey in most places. This conclusion is supported by the
12 fact that every haul of the sampling survey presented some amount of prey biomass.
13 However, this was not always the case for consumers that prey upon benthic
14 invertebrates. Hines (1997) and Schwemmer (2016) observed, in eagle rays and wader
15 birds respectively, that prey density must reach a certain limit for it to be a good
16 predictor of predator presence. Using prey biomass as a predictor of predator
17 abundance also assumes that accessibility to prey is the same in every area where
18 predator and prey co-occur (Trainor & Schmitz 2014). This assumption may not be
19 realistic when the abundance of prey species does not reflect the likelihood that a
20 predator finds and successfully captures one of them (Trainor & Schmitz 2014). As
21 mentioned before, crab's predation rate may be affected by substrate type, in particular
22 larger particle size diminishes crab's foraging efficiency (Liu et al. 2019). The results of
23 the SDM suggest that something similar could be happening in the San Matías Gulf. We
24 observed a positive effect of prey biomass mainly within substrate types that favored

1 the distribution of *O. trimaculatus* (silt and silty sand), but, a lower effect of prey biomass
2 in suboptimal substrate types (sand, Figure 3 F).

3 The metabolic system of a consumer requires different proportions of key nutrients,
4 hence, the food items that maximize energetic intake may not satisfy the rest of the
5 nutritional needs of the consumer (Pulliam 1975). In a wide variety of taxa, including
6 arthropods, a mixed diet enhances various fitness indicators in comparison with a mono
7 specific diet (Lefcheck et al. 2013). Therefore, patches where various prey species occur
8 should have a higher biological value for a generalist consumer than areas with high
9 dominance of one or a few prey species. However, according to the SDM, higher
10 evenness and richness negatively affect the distribution of *O. trimaculatus* (Figure 3 A,
11 C), the latter having a larger effect. In coastal sedimentary environments, at a larger
12 scale, benthic species richness positively correlates with depth (Gray 2002, and
13 references therein). However, species richness has a low correlation with depth in our
14 study area (Figure S2). Therefore, we estimate that species richness in San Matías Gulf
15 may be affected by an un-measured variable that negatively affects the distribution of
16 *O. trimaculatus*. For example, species richness has been observed to be positively
17 correlated with habitat complexity (Gratwicke & Speight 2005) and it is possible that *O.*
18 *trimaculatus* prefers simpler habitats with large sedimentary plains, where it can bury
19 itself. Birch (1981) observed that in sedimentary habitats, dominance and richness are
20 positively correlated as well. Gray (2002), on the other hand, proposes that the patterns
21 of species richness in benthic marine sedimentary environments reflect complex
22 processes: a combination of the availability of food resources (i.e. patches of microbial
23 communities) and the spatial and temporal heterogeneity in a given area. However, it is
24 not clear how said processes may affect the distribution of *O. trimaculatus*.

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

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

1 In conclusion, the present model of *O. trimaculatus*' distribution achieved acceptable
2 predictive power for the north of the San Matías Gulf, where a fishery has recently been
3 established targeting this species. Considering the cosmopolitan nature of the species,
4 the environmental and biological variables that constrain its distribution in the San
5 Matías Gulf could also be relevant in other regions, and thus, substrate type, depth, SST,
6 and prey biomass, evenness and richness may be useful candidate variables in future
7 studies. In terms of fishery management, considering the low scale of the fishery, the
8 exploration of the gulf with the objective of understanding the distribution of *O.*
9 *trimaculatus* would impose an unaffordable economic cost. Not even the fishers afford
10 to invest time in finding new fishing grounds (de la Barra et al. 2019). Hence, a map of
11 the species distribution may be a useful tool for managers (Maxwell et al. 2009) as a
12 reference of the areas where they should focus their efforts.

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16 **Tables**

17 Table 1: Parameter likelihoods, estimates and 95% confidence interval limits (CL) for
 18 explanatory variables describing variation in (a) probability of presence of *O.*
 19 *trimaculatus*, and (b) biomass density given that it is present. Explanatory variables with
 20 CL excluding zero are in bold.

21

Response variable	Explanatory variable	Parameter likelihood	Parameter estimate ± SE	CL	
				Lower	Upper
(a)					
Presence of	Intercept		5.22 ± 7.44	-9.37	19.81

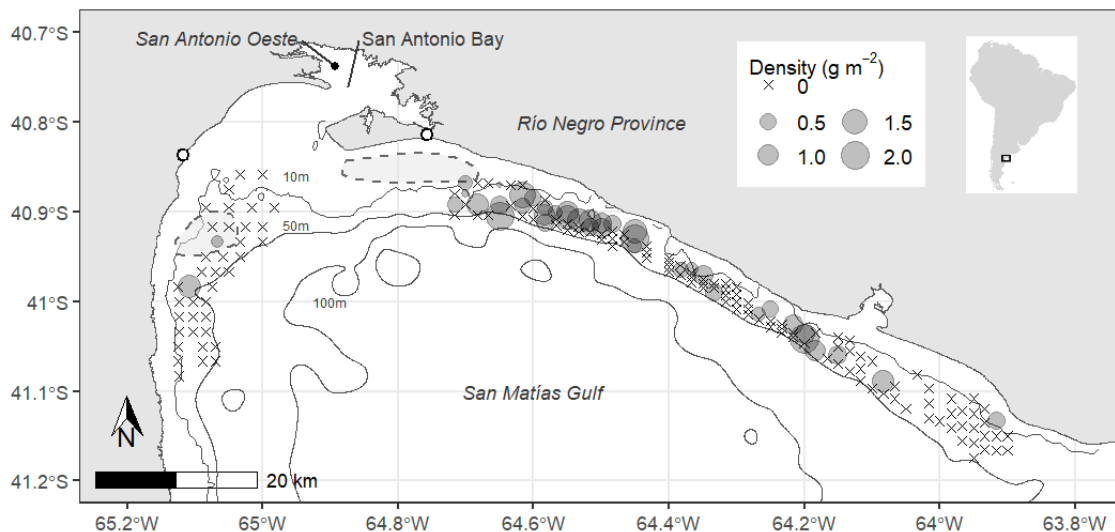
<i>O. trimaculatus</i>	Substrate (Sand)	1	-19.04 ± 1679.76	-3311.31	3273.24
	Substrate (Gravel)	1	-1.07 ± 0.71	-2.47	0.32
	Substrate (Silt)	1	-0.57 ± 0.57	-1.69	0.56
	Depth	1	-0.04 ± 0.02	-0.08	-0.00
	Richness	0.59	-0.04 ± 0.05	-0.16	0.01
	SST	0.38	-0.28 ± 0.55	-2.06	0.59

(b)

Biomass of	Intercept		-2.60 ± 4.07	-10.58	5.37
<i>O. trimaculatus</i>	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

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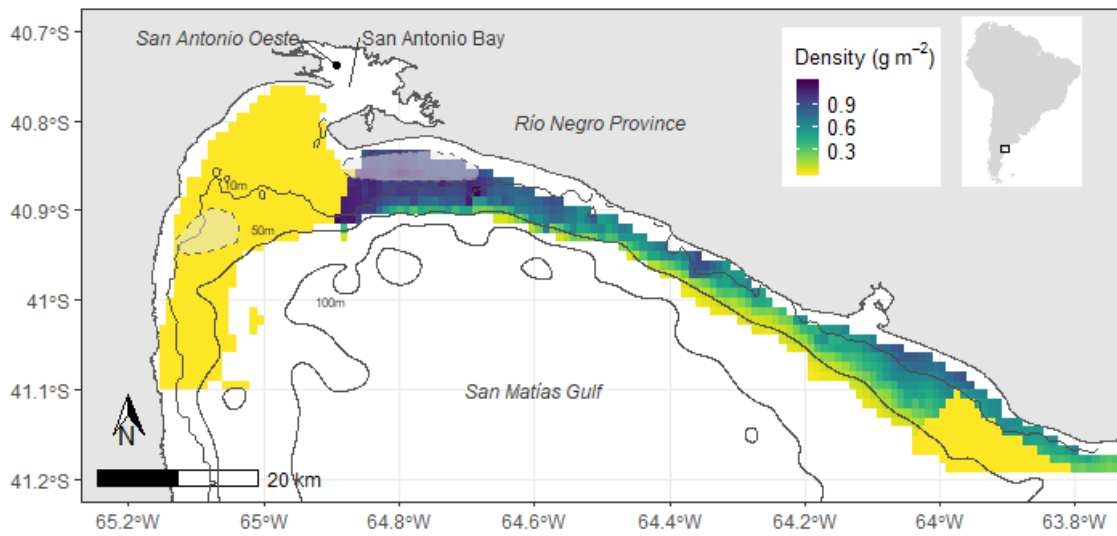
2 Figures



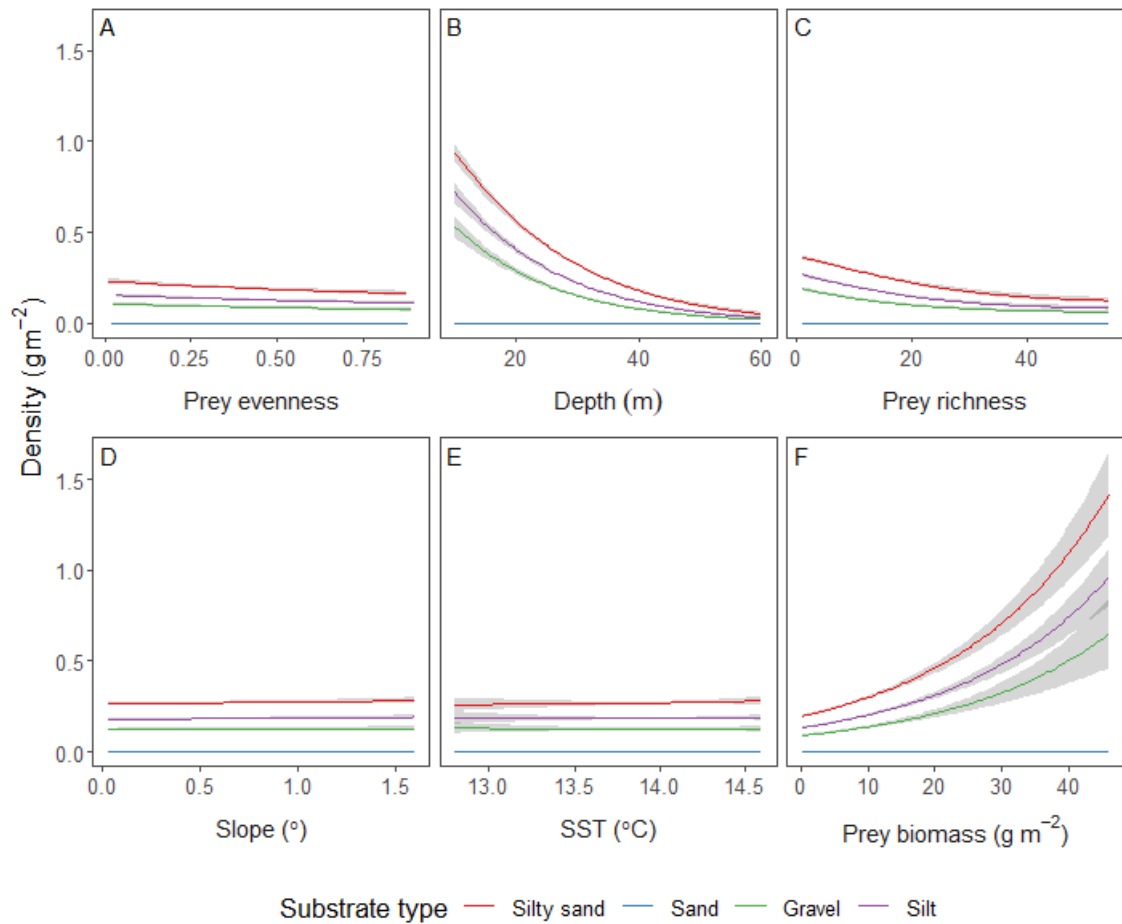
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4 Figure 1: Sampling stations analyzed. Circles indicate hauls where at least one *O.*
 5 *trimaculatus* was captured; their size is proportional to the biomass of *O. trimaculatus*

1 captured per area swept. Crosses indicate hauls where *O. trimaculatus* were not
2 captured. Areas enclosed by dashed lines are fishing grounds used between 2008 and
3 2013. Empty circles on the coast indicate where the vessels are launched.
4



5
6 Figure 2: Predicted biomass density of *O. trimaculatus*. The SDM model was
7 extrapolated between 0 and 60 m depth. Areas enclosed by dashed lines are fishing
8 grounds used between 2008 and 2013.
9



1

2 Figure 3: Averaged response curves of the SDM to the predictors. **A** Response curve to
 3 Evenness (PIE), **B** response curve to depth, **C** response curve to prey species richness, **D**
 4 response curve to seabed slope, **E** response curve to SST, **F** response curve to prey
 5 species biomass. Grey ribbons represent standard errors.

6