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Reconstructing populations dynamics: Mortality and recruitment of the southern geoduck *Panopea abbreviata*

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ABSTRACT

In the development of management measures for sustainable fisheries, estimating the natural mortality rate and recruitment are fundamental. In northern Patagonia, Argentina, the southern geoduck, *Panopea abbreviata*, a long-lived clam that forms spatially disjunct subpopulations, supports an unregulated fishery. In this study, we estimate natural mortality. We studied the age structure of beds within the northern Patagonia gulfs, San Matías Gulf (SMG) and San Jose Gulf (SJG), and we estimated a time series for back-reconstructed recruitment to explore spatial coherence in relation to local oceanographic conditions and to elucidate its population dynamics.

We constructed a cumulative frequency distribution of the age of dead shells collected and used the exponential and Weibull models to model mortality. Live geoducks were sampled from six populations between 2000 and 2006. Age-frequency distributions and mortality models were used to back-calculate the time series of recruitment for each population. The recruitment time series was analysed using continuous wavelet transform.

The value of natural mortality estimated by the exponential model was 0.054 $years^{-1}$, whereas those estimated by the Weibull model were $\alpha = 0.00085$ $years^{-1}$ and $\beta = 2.1$. For the latter, M values for cohorts were 0.01 for 10 years, 0.02 for 20 years, 0.04 for 30 years and 0.05 for 40 years. The Weibull model was observed to be the best fit to the data. The natural mortality rate of *P. abbreviata* estimated in this study was lower than that estimated in a previous work for populations from SMG.

The back-calculated time series for recruitment demonstrated considerable yearly variation, suggesting that local conditions have an important role in recruitment regulation. At a decadal temporal scale, a clear increasing recruitment trend was evident over the last 20 years in all populations. Populations in SMG were settled > 60 years ago. In contrast, no individuals older than 30 years were observed in the populations from SJG.

P. abbreviata has several characteristics, such as longevity and low instantaneous natural mortality rate, which require attention in any resource planning. However, this species also has positive characteristics for fishery development, as historical recruitment trends indicate that populations are expanding and are part of a widely distributed metapopulation, suggesting that sustainable exploitation is possible.

1. Introduction

Fisheries conservation management aims at achieving a balance between the harvest and the productivity of a resource (Kenchington, 2014). Productivity is determined by the relationship between the loss (mortality) and increase in biomass (recruitment and individual growth) (Skalski et al., 2010). Therefore, estimations of the natural mortality rate (*M*) and recruitment are essential and are required by stock assessment models to define biological reference points (Hamel, 2015). A confident estimation is difficult to obtain (Hewitt et al., 2007) and uncorrected estimates of *M* can lead to incorrect estimates of stock size and *F*% (fishery mortality rate), which, in turn, can lead to inappropriate estimation in quotas (Clark, 1999; Williams, 2002). *F*% is more sensitive to estimates of *M* than to other life history parameters (e.g., growth, sexual maturity schedules) (Bradbury and Tagart, 2000).

In marine bivalves, *M* can be estimated by a wide range of methods. These methods can be classified as direct methods, where the estimation is made using information strictly pertaining to the species of interest, and indirect methods, where the estimation is made using life history ratios of many species (e.g., *M*/relative growth rate parameter from the von Bertalanffy model) (Pauly, 1980; Then et al., 2014). Direct methods are often data-intensive but may enable more reliable

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estimations. In addition, these methods can be classified as cohort-specific (following a cohort through its life time) or time-specific (age-structure-based). Cohort-specific methods are the most direct methods to estimate *M* but are highly difficult to use in a long-lived species. Time-specific methods can be either vertical life tables (e.g., constructed from the age structure of a population) or depositional life tables (e.g., constructed from the frequency of ages of death of shells accumulated over time as a result of natural causes) (Skalski et al., 2005). The former assume that recruitment is either constant or compensated by a great number of year classes. In the latter, sources of bias are related to the post-mortem dynamics of shells: the rate of diagenesis (breakage by physical and chemical changes occurring in sediments) of the buried shells can vary with the age of the individual at the time of death, or shells can be removed from the sediment by waves or storms and transported outside the area.

Recruitment is a complex process determined by many factors operating and interacting on multiple time and spatial scales in several environments (Roughgarden et al., 1988; Nakaoka, 1993; Eckman, 1996). Similar to that observed in other marine benthic invertebrates with pelagic larvae, the recruitment variability of bivalve species can be considered the primary factor affecting abundance fluctuations of discrete local populations that are connected by larval dispersal (Defeo, 1996). Connectivity between populations is strongly affected by local oceanographic conditions. In long-lived species, the impact of recruitment variability is buffered by the large number of year-classes present in a population, which can give a false sense of population stability and the sustainability of the fisheries that they support could be more apparent than real (Valero et al., 2004; Orensanz et al., 2006).

The southern geoduck, *Panopea abbreviata* (Valenciennes, 1839), is an endemic long-lived clam distributed from Rio de Janeiro in Brazil (23° S) to Nuevo Gulf in Argentina (43° S) (Ageitos de Castellanos, 1967; Signorelli and Alfaya, 2014) (Fig. 1), which has supported an artisanal diving fishery in northern Patagonian waters (San Matías Gulf [SMG] and San José Gulf [SJG]) since 1999. Due to the low fishing effort and apparent sustainability, this fishery is unregulated. Annual landings vary between 1.8 t and 15.6 t. This species lives deeply buried in sand and mud substrates down to 40 cm and is distributed in spatially discontinuous beds from shallow waters to a depth of 75 m. The gametogenic cycle is continuous with no resting period (Van der Molen et al., 2007; Zaidman et al., 2012) and individual growth, modelled in six beds, shows variability dependent on local oceanographic conditions and thermohaline fronts (Morsan and Ciocco, 2004; Zaidman and Morsan, 2015). Longevity has been estimated at 86 years (Morsan et al., 2010). The natural mortality rate of *P. abbreviata*, estimated by different methods, such as mean age, maximum age, and catch curve method derived from the age frequency distribution of three beds in SMG, has been observed to range from 0.062 to 0.233 years^{-1}, depending on the method used (Morsan et al., 2010). Within the genus *Panopea*, *P. abbreviata* demonstrates intermediate mortality rate and longevity (Breen and Shields, 1983; Sloan and Robinson, 1984; Bradbury and Tagart, 2000; Orensanz et al., 2000; Gribben and Creese, 2005; Cortez-Lucero et al., 2011).

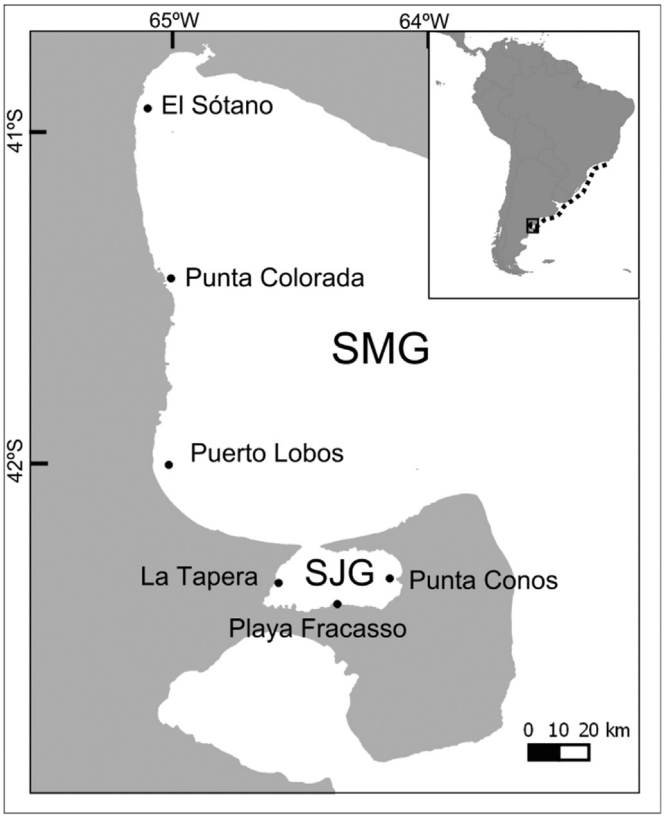

Fig. 1. Map of San Matías Gulf (SMG) and San José Gulf (SJG), showing the study site.

The insert indicates the distribution of *Panopea abbreviata* along the Atlantic coast of South America, denoted with dotted lines.

The spatial arrangement of *P. abbreviata* within SMG and SJG is equivalent to the metapopulation conceptual model, composed of several disjunct subpopulations following the coastline. Such subpopulations are affected by different local oceanographic conditions, thereby offering the opportunity to investigate the geographical coherence of long-term recruitment trends at fine spatial resolution. In this sense, the information needed are a "snapshot" of the age composition of the subcomponent of the metapopulation and an independent estimation of natural mortality. In this study, we used the dead shell assemblage of *P. abbreviata* to estimate age of death and natural mortality. We studied the age structure of all known beds within SMG and SJG, and estimated a time series for back-reconstructed recruitment to explore spatial coherence in relation to local oceanographic conditions and attempt to elucidate population dynamics of *P. abbreviata*.

2. Materials and methods

2.1. Study area

SMG is a semi-enclosed basin partially connected to the open sea through a shallow sill (60 m deep) (Rivas and Beier, 1990). SMG's surface is 19,700 km^2, and its maximum depth is 180 m (Mazio and Vara, 1983). During the spring and summer, the circulation in the gulf is dominated by one cyclonic eddy in the NW and two anticyclonic eddies in the south (Tonini, 2010). In these seasons, an intense SW-NE oriented thermohaline front divides two water masses with different oceanographic conditions (Fig. 1): south of the front, waters are relatively cold-fresh, similar to open shelf waters (high concentration of nitrates and phytoplankton dominated by diatoms), while north of the front, waters are warm-salty (low concentration of nitrates and phytoplankton dominated by dinoflagellates) (Piola and Scasso, 1988; Williams, 2011). The bottom sediment is dominated by sand near the coastline and gradually mixed with shell hash, gravel, and mud. Muddy sediments are predominant beyond 50 m.

SJG is a sub-elliptic, shallow and semi-enclosed water body (mean depth 30 m; 817 km^2), which opens to the north into SMG through a narrow (6.9 km) mouth (Fig. 1) (Amoroso et al., 2011). Tides and strong winds are the main drivers of circulation (Amoroso and Gagliardini, 2010). SJG has high productivity due to the nutrients originating from the Valdes Frontal System that enter the Gulf from the continental shelf. The distribution of suspended sediments and temperature show that SJG is split longitudinally into two areas by a well-defined thermal front during most of the year. Circulation in the west of SJG is dominated by the water exchange with the southern area of SMG, and the eastern area shows closed circulation during summer (Gagliardini and Rivas, 2004). During this time, the east of SJG operates

as a trap for nutrients and as a larval retention zone (Amoroso and Gagliardini, 2010).

2.2. Sampling

Shells of dead geoducks ("cluckers") (N = 432 shells) that remained on the substrate at El Sótano in SMG (40° 56′S, 65° 07′W) were collected to estimate the age of death. The El Sótano population was chosen to estimate natural mortality because it was established > 100 years ago (Morsan et al., 2010). A total of 322 cluckers were used to determine age. To avoid bias caused by the under-representation of younger ages in the samples, we used individuals older than five years for model estimation (315 shells).

Live geoducks were sampled in six populations along the coast of SMG and SJG, between 2000 and 2006 (Fig. 1): El Sótano, Punta Colorada (41°44′S, 65° 00′W), Puerto Lobos (42° 00′S, 65° 03′W), La Tapera (42°21′S, 64°33′W), Playa Fracasso (42°24′S, 64°30′W) and Punta Conos (42°20′S, 64°06′W). At each sampling site, between 300 and 500 geoducks were randomly obtained by scuba divers using a water jet pump. Although the sampling method could be size selective, *P. abbreviata* has fast growth (Morsan et al., 2010); therefore, the probability of being captured is the same for all individuals older than 5 years old. A total of 2731 geoducks from six sampled populations were used to determine age.

2.3. Age

Right valves were used to determine the age of clams, applying the methodology developed by Shaul and Goodwin (1982) and used by Morsan and Ciocco (2004) for *P. abbreviata*. Thin sections were obtained by cutting the valves with a low-speed diamond observed across the hinge plate. The internal section of the valve obtained from the first cut was ground and polished on a platform with variable speed using very fine grain sandpaper (4000 grit). The polished surface was mounted on a microscope slide, using cyanoacrylate adhesive. A thin section of 0.5 mm was obtained from a second cut. The thin section was ground and polished again with medium grain (1000 grit) and very fine grain (4000 grit) sandpaper until adequate thinness and texture were obtained. Small individuals with fragile valves were embedded in epoxy resin before proceeding as described previously. The preparation thus obtained was observed under a stereoscopic microscope with transmitted light to establish the optical pattern of the internal growth bands. The sections were observed twice and, if they were identical, recorded. When the two observations were not in agreement, we performed a third observation. If it was equal to one of the two previous observations, we used this as our result, whereas if it was different from the two previous observations, we discarded the individual.

The seasonality of the internal growth bands was validated for *P. abbreviata* by Morsan and Ciocco (2004). Based on the degree of transparency of the shell margins of young (< 8 years old) geoducks, which were sampled in different months of the year, the authors established that the periodicity of deposition of the internal translucent (winter) and opaque (spring–fall) bands corresponds to one year. Our age interpretation is based on the assumption that this pattern remains stable within the geographic range studied.

Because sampling in each site was conducted over more than two years, we corrected ages by subtracting the years passed between the year of each sample and the year of the first sample of each population from the age observed. Years were defined from October to September of the next year.

2.4. Mortality

The natural mortality rate was estimated using the methodology developed by Orensanz et al. (2000) for *P. generosa*. From the estimated age of the cluckers (age of death), we constructed a cumulative frequency distribution:

$$N_t = \sum_{a=t}^{A} n_a$$

where t indexes age, A is the maximum age, n_a is the number of shells of age a in the sample, and N_t is the number of shells of individuals who died at age a or older (i.e., that reached at least age a). This distribution provides a schedule of average survival.

Two candidate models were used to model the southern geoduck mortality:

The exponential model considers that the mortality rate is constant over time (Skalski et al., 2005).

$$N_t = N_0 * e^{-M*t} + \varepsilon$$

where N_t is the number the individuals of age t, N_0 is the number the individuals of age 0, M is the instant natural mortality rate, and ε is an error ($\sim N(0, \sigma^2)$).

The Weibull model considers that the mortality rate varies over time and that age-specific survival decreases over the lifetime (Skalski et al., 2005).

$$N_t = N_0 * e^{-\alpha * t^{\beta}} + \varepsilon$$

where N_t is the number the individuals of age t, N_0 is the number of individuals of age 0, α and β are the parameters of natural mortality, and ε is an error ($\sim N(0, \sigma^2)$).

The two models were fitted with non-linear least squares (nl-LS) with iterations by means of the Levenberg-Marquardt algorithm and using the "minpack.lm" package in R (Elzhov et al., 2013) (R Development Core Team 2012).

The model selection and the estimation of model selection uncertainty were based on the information theory approach (Burnham and Anderson, 2002). The small-sample bias-corrected form of the Akaike information criterion (*AICc*) was used for model selection because the ratio of sample size to the number of parameters of the model was small (< 40) (Burnham and Anderson, 2002).

$$AIC_c = AIC + \frac{2r(r+1)}{n-r-1}$$

where for least squares:

$$AIC = n * \log(\sigma^2) + 2z$$

and:

$$\sigma^2 = \frac{RSS}{n}$$

where *RSS* is the residual sum of squares, n the number of observations and r is the total number of estimated regression parameters including σ^2 (i.e., the number of parameters in the model equation plus 1). Normally distributed deviations with constant variance were assumed. The model with the smallest AIC_c value ($AIC_{c,\ min}$) was selected as the "best" of the models tested.

2.5. Recruitment

Age-frequency distributions and mortality estimation models were used to back-calculate recruitment time series for each population. Two models were used for calculations of relative recruitment:

Exponential model:

$$N_0 = \frac{N_t}{e^{-M*t}}$$

Weibull model:

$$N_0 = \frac{N_t}{e^{-\alpha * t^{\beta}}}$$

where N_0 is the number the individuals incorporated into population t

years ago, N_t is the number the individuals of age t, and M, α and β are the estimated parameters. Relative recruitment was calculated for the 1950–2003 year-classes. This window was chosen to avoid bias caused by the under-representation of younger ages in the samples.

The recruitment time series was analysed using continuous wavelet transform. Wavelet analysis is a tool to analyse a time series according to different scales or resolutions (Martínez and Gilabert, 2009). The idea of the wavelet transform is the decomposition of a signal at different spatial or time scales onto a set of basis functions called wavelets (Lau and Weng, 1995). The wavelet function has a non-dimensional "time" parameter and must have zero mean and be localized in both time and frequency space (Torrence and Compo, 1998). We chose the Mexican hat (DOG) wavelet, which is the second derivative of the Gaussian function:

$$\psi_0(\eta) = \frac{2}{\sqrt{3}}\pi^{-\frac{1}{4}}(1-x^2)e^{-x^2/2}$$

This wavelet provides good detection and localization of patch and gap events (Mi et al., 2005). The Mexican hat wavelet is a real value and captures both the positive and negative oscillations of the time series as separate peaks in wavelet power (Torrence and Compo, 1998). The Python package scipy.signal¶ was used for the continuous wavelet transform of recruitment trend. For more detail on the analysis of wavelets, see (Lau and Weng (1995); Torrence and Compo (1998).

Since the recruitment series showed a trend, the continuous wavelet transform was performed on the residuals previously detrending with a polynomial function.

The recruitment time series and sea surface temperature (SST) were scaled to a maximum of 1 in order to allow comparisons between indexes with different units and ranges.

3. Results

3.1. Age

From the total valves collected in the six populations, 260 valve sections were broken during the processing, 153 sections were discarded due to unclear pattern of internal growth bands and 133 valve sections were discarded because the three observations were different. The percentage of ages discarded on the basis of non-identical observations, although low (5%), shows an increasing tendency with respect to the average age of the three observations (Fig. A.1). Appendix Table A1 shows the age observed before the corrected the ages for the sample year.

3.2. Mortality

Clucker age ranged from 3 to 65 years. (Fig. 2 left). The value of M estimated by the exponential model was 0.054 years^{-1} (SE = 0.002 years^{-1}), whereas those estimated by the Weibull model were α = 0.00085 years^{-1} (SE = 0.00011 years^{-1}) and β = 2.1 years (SE = 0.036). Fig. 2 (right) shows how mortality rate varies over time. The Weibull model was found to be the best fit to the data (Weibull AIC = 168.04 vs Exponential AIC = 364.88).

3.3. Age structure

Age ranged from 1 to 60 years, but the ranges and maximum recorded age differed between populations (Fig. 3). The oldest geoduck in the populations from SMG ranged from 42 to 60 years old, whereas all populations from SJG were composed of individuals younger than 25 years. Individuals aged from 5 to 20 years old predominated in all populations.

3.4. Recruitment

The results of recruitment trends were different depending on the model used for the estimation (Fig. 4). Despite such differences, the trends observed were similar.

The back-calculated recruitment time series showed a fluctuating but increasing trend since the 1990s (Fig. 4). The trend was more evident in populations in SJG than in those from SMG. The wavelet analysis showed a slight biennial periodicity with alternating strong negative and positive correlations (blue and red respectively) over the biennial period in recruitment since the 1990s in El Sótano and Punta Conos and since the 1980s in Punta Colorada and Playa Fracasso (Fig. 5).

When the recruitment series were compared between populations, no relationships were found. Peaks of recruitment in one population in one particular year did not match with those that occurred in the same year in another population. This mismatch was also observed in the analysis of wavelets. However, all of the populations had the same increasing trend over recent years.

When we studied the relationship between the annual mean SST and recruitment in each population, we did not observe any clear pattern.

4. Discussion

Estimated natural mortality rate of *P. abbreviata* in this study was 0.054 years^{-1}, a value lower than that estimated in a previous work for populations in SMG (0.062–0.233 years^{-1}) (Morsan et al., 2010). The mortality rate was higher than that estimated for *P. generosa*, similar to that estimated for *P. zelandica*, and lower than that estimated for *P. globosa* and is consistent with the maximum age of these species (131 years for *P. generosa*, 86 years for *P. zelandica* and 27 years for *P. globosa*) (Breen and Shields, 1983; Sloan and Robinson, 1984; Bradbury and Tagart, 2000; Orensanz et al., 2000; Gribben and Creese, 2005; Cortez-Lucero et al., 2011). In most of these studies, the mortality rate was estimated by methods based on the age frequency distributions (catch curve methods), which rely on the assumption of constant recruitment. The age frequency distributions described in the present study does not seem to fulfil this assumption. Previous study of three populations of *P. abbreviata* in El Sótano, Punta Colorada and Puerto Lobos found the same pattern of age frequency distributions, suggesting

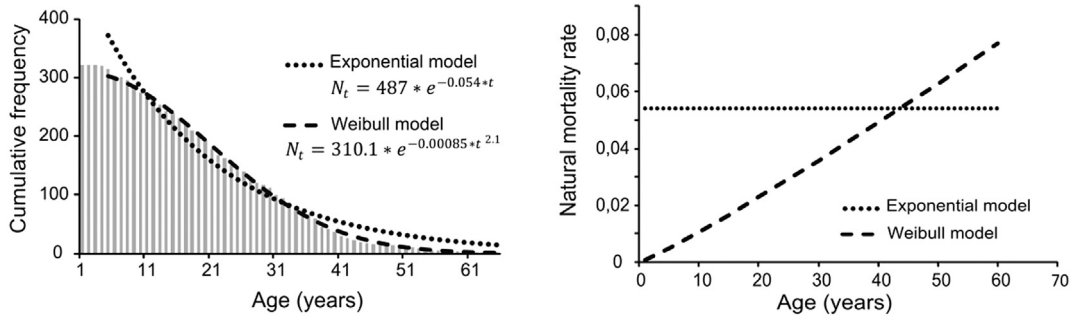

Fig. 2. Left: Cumulative age frequency of *P. abbreviata* cluckers with two mortality fitted models. Right: Variation in natural mortality rate as a function of age.

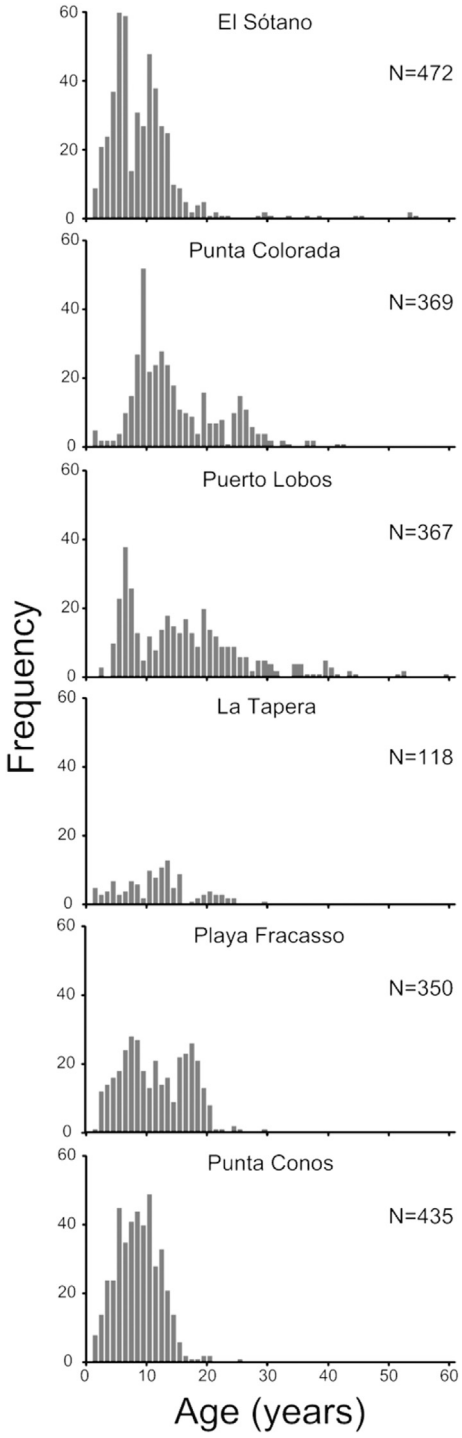

Fig. 3. Age frequency distribution of *P. abbreviata* in six populations of SMG (El Sótano, Punta Colorada and Puerto Lobos) and SJG (La Tapera, Playa Fracasso and Punta Conos).

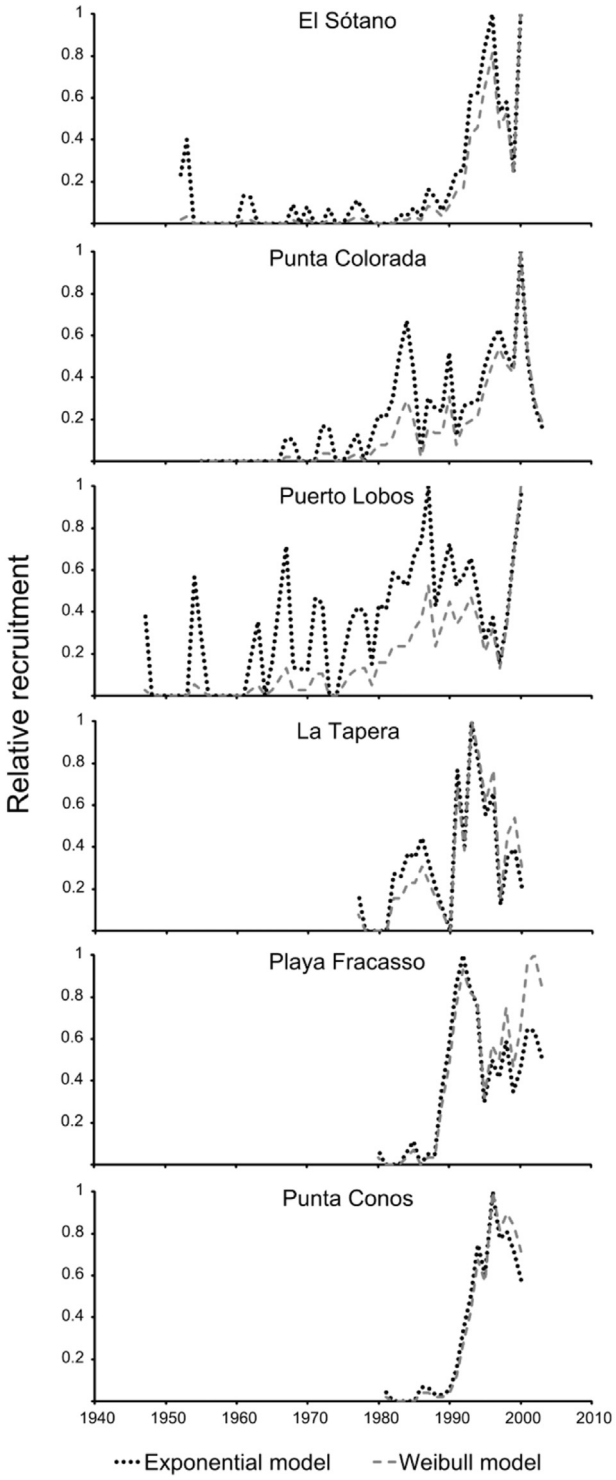

Fig. 4. Estimates of relative recruitment of *P. abbreviata* for six populations from SMG (El Sótano, Punta Colorada and Puerto Lobos) and SJG (La Tapera, Playa Fracasso and Punta Conos).

that recruitment is variable over time (Morsan et al., 2010). An alternative approach for this study could be to combine several populations into a single one, assuming that the temporary variability of recruitment to each population can be compensated by the coexistence of a large number of age classes and a wide geographical range. However, in the present case, the long-term recruitment trends of the six populations suggested that such compensation does not occur, and an estimation of natural mortality derived from the catch curve method could be biased due to the difference in maximum age between the populations in SMG and SJG. The alternative method based on records of the age of dead shells accumulated over time as a result of natural causes assumes that the population is stable and stationary in the period during which shells were deposited, that each shell has the same probability of selection and that all ages can be recorded accurately (Skalski et al., 2005). Variations in recruitment could affect these assumptions and lead to a misinterpretation of the estimated mortality rate. However, the shells were collected in a population where the individuals could have settled over > 100 years (Morsan et al., 2010), allowing us to assume that short-term variations in the recruitment were buffered by the long

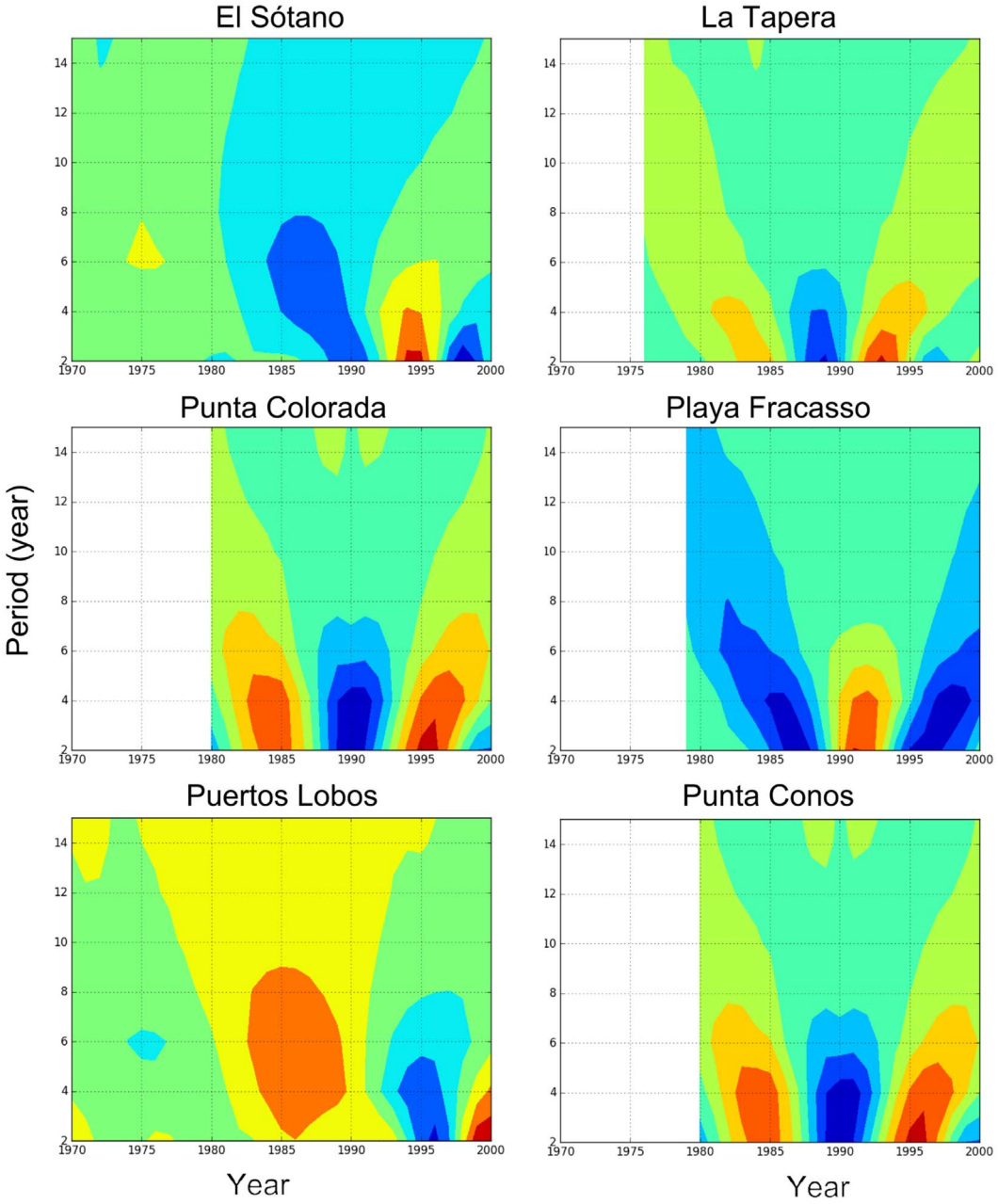

Fig. 5. Wavelet analysis for the characterization of periodic frequencies of relative recruitment of *P. abbreviata* for six populations from SMG and SJG. The colour intensity represents signal power, and the colour indicate the direction of the correlation (red = positively phased; blue = negatively phased).

period of shell deposition.

The estimation of natural mortality using clucker age was independent of fishing mortality. Fishing is undertaken by scuba divers following a visually guided procedure: identifying the siphon tips on the substrate and removing the clams individually with a hand-held water jet pump fitted with a nozzle. It is assumed that this fishing differentially targets older individuals, which can modify the population age structure. Natural mortality rate estimation could be directly affected if age structure is used in the estimation, or indirectly affected if the increased turbidity produced by digging or other injury can affect the survivorship of remaining clams. When the age of the dead shells accumulated over time is used, fishing prior to sampling can reduce the frequency of older individuals. In this study, we did not identify indirect effects of fishing on the natural mortality because until 2006 fishing trips to gather geoduck were occasional. Since then, the fishery has become stable with regular trips at El Sótano (the only population under exploitation), but the mortality estimated is prior to 2006; therefore, we can assume that fishing does not alter the estimate.

The Weibull model performed better than the exponential model to describe the trend in age of death in *P. abbreviata*. Similar results have been found in *P. generosa* (Orensanz et al., 2000). In contrast with the natural mortality rate estimated by the exponential model, that estimated by the Weibull model was variable. Several studies suggest that the mortality rate varies through the life course (Walker, 1984; Lorenzen, 1996; Deroba and Schueller, 2013). Differences in the mortality rate of *P. abbreviata* can be associated with predation of younger individuals, and occasional storms that remove geoducks from the sediment which are unable to reburrow.

The recruitment time series derived from age structures showed a large degree of yearly variation in all populations and suggests that local conditions have an important role in recruitment regulation. Similar results have been found in previous studies of other species

(Connell, 1985; Raimondi, 1990; Valero et al., 2004). Davis et al. (1997) found that density-independent processes – such as local changes in the nutritional conditions from year to year – explain yearly and spatial variation in recruitment for the bivalve *Spisula ovalis*. Studies in *P. generosa* also found spatial heterogeneity in recruitment (Valero et al., 2004). The differences in recruitment between sites can be due to a mix of physical factors, such as coastal morphology and geology; and biological factors, such as predation or competition (Connell, 1985).

In *P. abbreviata*, however, over a wide temporal scale (decadal), a clear increasing recruitment trend was evident over the last 20 years in all the populations studied. Several aspects of this pattern need to be considered: i) geoduck populations inhabit the coastal fringe, exposed to highly variable local conditions; ii) the connectivity between the populations along the coastal fringe is unknown and very difficult to explore, but there is high connectivity between the two gulfs, mediated by tidal currents (Amoroso and Gagliardini, 2010); iii) spawning is extended throughout the year, which favours larval supply (Van der Molen et al., 2007; Zaidman et al., 2012); iv) recruitment intensity does not seem to be related to SST; v) if a population increases in abundance, the probability of affecting recruitment in neighbouring beds also increases; and vi) despite the rising trend in recruitment observed over the last two decades, density did not increase sufficiently to lead to negative density-dependent interaction in recruitment.

Black et al. (2008) found that ageing error can affect the estimation of recruitment. The age determination can be influenced by the cut of the calcified structures; by the age of individuals, especially if the age exceeds 30 years; and the subjectivity of observers (Campana, 2001). We found that the percentage of individuals discarded by non-identical observations has an increasing tendency with age. Black et al. (2008) found, for *P. generosa*, an underaging bias that increased with geoduck age, and this effect was more pronounced in geoducks older than 100 years. In *P. abbreviata*, this effect has not been studied because the ages of *P. abbreviata* observed in the present work are lower than the ages of *P. generosa* (Black et al., 2008), and only the 1.5% of the clams exceed 30 years of age. For this reason, we did not consider underaging bias relevant in the present study. Nevertheless, if the demographic composition of the population changes, further studies about the ageing bias using cross dating would be important to fully clarify this point.

Populations from SMG were settled > 60 years ago (Morsan et al., 2010). In contrast, no individuals older than 30 were found in the populations from SJG. One hypothesis to explain the observed difference in longevity is the higher mortality rate in SJG compared to the SMG population. However, there do not seem to be any environmental or ecological factors that can explain such a difference in natural mortality rates between the two gulfs. A more consistent hypothesis supposes that the populations from SJG arose from larvae generated by populations in SMG, which gradually colonized the coast. This expansion is consistent with the strong presence of individuals younger than 30 years in the population structure of SMG mixed among older geoducks. Doldan et al. (2014) observed a similar expansion of *Ostrea puelchana* populations in SJG. In a recent study, de Jesús Suárez-Moo et al. (2016) found that *P. generosa* is genetically homogeneous along the northeast Pacific (thousands of km), which suggests larval flow between the populations. There are no studies about the genetic flow of *P. abbreviata* and future research on this topic is needed. Elucidating the extent and direction of population connectivity is important for fisheries management (Orensanz et al., 1991).

Recruitment is a complex process determined by many factors operating and interacting on multiple time and spatial scales in numerous environments (Roughgarden et al., 1988; Nakaoka, 1993; Eckman, 1996; Pineda et al., 2009). Over recent decades, the populations of the southern geoduck have been expanding, probably influenced by each other. Yearly variations in recruitment, both in and between sites, suggest that recruitment is modulated by regional environmental conditions that vary at different geographic scales, affecting the two gulfs.

The development of management measures for a sustainable *P. abbreviata* fishery should take into account their high longevity associated with a low rate of natural mortality. However, there are population characteristics, such as the increasing recruitment trend and high density that suggest that sustainable exploitation is possible under a co-management regime, which involves all fishery stakeholders. Sustainable exploitation should be based on spatially explicit measures (e.g., rotation of areas, closed areas) that take into account the variability observed among the populations. The spatial allocation of fishing effort and catch monitoring is currently being studied in order to develop management measures.

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Appendix A. Appendix

Table A1
Ages observed in the valve sections before the age correction for the year of sample. Site identifies the population, n identifies the individual, ob1 – ob2 – ob3 identifies the observations, and final the age estimated.

Site	n	ob1	ob2	ob3	final
El Sótano	1	10	10	NA	10
El Sótano	2	9	9	NA	9
El Sótano	3	11	10	10	10
El Sótano	4	4	4	NA	4
El Sótano	5	19	18	19	19
El Sótano	6	9	9	NA	9
El Sótano	7	11	11	NA	11
El Sótano	8	13	13	NA	13
El Sótano	10	7	6	6	6
El Sótano	11	11	11	NA	11
El Sótano	12	5	6	5	5
El Sótano	13	10	10	NA	10
El Sótano	14	32	33	33	33

El Sótano	15	11	11	NA	11
El Sótano	16	22	22	NA	22
El Sótano	17	6	5	6	6
El Sótano	18	6	7	7	7
El Sótano	20	5	5	NA	5
El Sótano	21	4	4	NA	4
El Sótano	22	11	11	NA	11
El Sótano	23	5	6	6	6
El Sótano	25	10	10	NA	10
El Sótano	26	4	4	NA	4
El Sótano	27	4	4	NA	4
El Sótano	28	4	4	NA	4
El Sótano	30	13	13	NA	13
El Sótano	31	6	5	6	6
El Sótano	32	6	6	NA	6
El Sótano	33	7	7	NA	7
El Sótano	34	10	10	NA	10
El Sótano	35	8	8	NA	8
El Sótano	36	11	12	12	12
El Sótano	38	6	6	NA	6
El Sótano	39	5	5	NA	5
El Sótano	40	5	5	NA	5
El Sótano	41	5	5	NA	5
El Sótano	42	5	5	NA	5
El Sótano	43	15	15	NA	15
El Sótano	44	8	9	7	NA
El Sótano	46	54	54	NA	54
El Sótano	48	5	5	NA	5
El Sótano	49	5	5	NA	5
El Sótano	50	7	7	NA	7
El Sótano	52	11	11	NA	11
El Sótano	53	4	5	5	5
El Sótano	54	7	7	NA	7
El Sótano	55	7	7	NA	7
El Sótano	57	13	13	NA	13
El Sótano	58	15	14	14	14
El Sótano	59	2	2	NA	2
El Sótano	61	2	2	NA	2
El Sótano	62	13	13	NA	13
El Sótano	64	9	9	NA	9
El Sótano	65	14	15	14	14
El Sótano	66	7	7	NA	7
El Sótano	67	11	11	NA	11
El Sótano	68	12	13	13	13
El Sótano	69	6	6	NA	6
El Sótano	70	11	11	NA	11
El Sótano	73	11	12	12	12
El Sótano	74	14	15	15	15
El Sótano	75	14	15	14	14
El Sótano	76	11	8	11	11
El Sótano	77	10	12	12	12
El Sótano	78	10	10	NA	10
El Sótano	79	5	5	NA	5
El Sótano	80	11	11	NA	11
El Sótano	82	7	7	NA	7
El Sótano	83	12	12	NA	12
El Sótano	84	5	5	NA	5
El Sótano	85	5	5	NA	5
El Sótano	86	5	5	NA	5
El Sótano	88	16	14	15	NA
El Sótano	89	13	13	NA	13
El Sótano	90	11	11	NA	11
El Sótano	91	14	14	NA	14
El Sótano	92	3	3	NA	3
El Sótano	93	4	4	NA	4
El Sótano	94	7	7	NA	7

El Sótano	95	5	5	NA	5
El Sótano	96	13	13	NA	13
El Sótano	97	19	19	NA	19
El Sótano	98	11	11	NA	11
El Sótano	99	2	2	NA	2
El Sótano	100	7	7	NA	7
El Sótano	101	13	13	NA	13
El Sótano	102	4	4	NA	4
El Sótano	103	12	13	12	12
El Sótano	104	7	7	NA	7
El Sótano	105	4	4	NA	4
El Sótano	106	6	6	NA	6
El Sótano	107	5	5	NA	5
El Sótano	108	5	5	NA	5
El Sótano	109	3	3	NA	3
El Sótano	110	31	30	30	30
El Sótano	111	13	13	NA	13
El Sótano	112	7	7	NA	7
El Sótano	113	9	9	NA	9
El Sótano	114	7	7	NA	7
El Sótano	115	13	13	NA	13
El Sótano	116	12	12	NA	12
El Sótano	117	14	14	NA	14
El Sótano	119	12	12	NA	12
El Sótano	120	39	40	39	39
El Sótano	121	14	15	14	14
El Sótano	122	11	11	NA	11
El Sótano	123	13	13	NA	13
El Sótano	124	9	9	NA	9
El Sótano	125	11	13	11	11
El Sótano	127	11	11	NA	11
El Sótano	128	8	8	NA	8
El Sótano	129	9	10	9	9
El Sótano	130	13	13	NA	13
El Sótano	131	17	18	18	18
El Sótano	132	9	9	NA	9
El Sótano	133	11	11	NA	11
El Sótano	134	11	11	NA	11
El Sótano	135	32	31	31	31
El Sótano	136	14	14	NA	14
El Sótano	137	12	11	11	11
El Sótano	138	7	7	NA	7
El Sótano	140	11	11	NA	11
El Sótano	142	13	12	13	13
El Sótano	143	3	3	NA	3
El Sótano	144	14	14	NA	14
El Sótano	145	10	10	NA	10
El Sótano	146	9	9	NA	9
El Sótano	147	16	16	NA	16
El Sótano	148	14	14	NA	14
El Sótano	149	11	11	NA	11
El Sótano	150	13	13	NA	13
El Sótano	151	3	3	NA	3
El Sótano	152	19	19	NA	19
El Sótano	153	14	14	NA	14
El Sótano	155	5	4	4	4
El Sótano	157	11	12	11	11
El Sótano	158	24	24	NA	24
El Sótano	159	9	9	NA	9
El Sótano	160	13	12	13	13
El Sótano	161	6	6	NA	6
El Sótano	162	6	6	NA	6
El Sótano	164	6	6	NA	6
El Sótano	165	10	10	NA	10
El Sótano	166	3	3	NA	3
El Sótano	167	9	10	9	9

El Sótano	168	11	10	10	10
El Sótano	169	5	5	NA	5
El Sótano	170	46	47	46	46
El Sótano	171	9	9	NA	9
El Sótano	173	12	12	NA	12
El Sótano	174	12	12	NA	12
El Sótano	175	12	12	NA	12
El Sótano	176	19	19	NA	19
El Sótano	177	21	21	NA	21
El Sótano	178	7	7	NA	7
El Sótano	180	12	12	NA	12
El Sótano	181	5	5	NA	5
El Sótano	182	12	12	NA	12
El Sótano	183	12	12	NA	12
El Sótano	184	6	6	NA	6
El Sótano	185	21	21	NA	21
El Sótano	186	30	30	NA	30
El Sótano	187	12	12	NA	12
El Sótano	189	7	7	NA	7
El Sótano	190	15	15	NA	15
El Sótano	191	8	8	NA	8
El Sótano	192	6	6	NA	6
El Sótano	193	8	8	NA	8
El Sótano	194	11	11	NA	11
El Sótano	195	6	6	NA	6
El Sótano	196	10	10	NA	10
El Sótano	197	19	18	18	18
El Sótano	198	4	4	NA	4
El Sótano	199	21	21	NA	21
El Sótano	200	5	5	NA	5
El Sótano	201	8	8	NA	8
El Sótano	202	10	10	NA	10
El Sótano	203	7	7	NA	7
El Sótano	204	7	7	NA	7
El Sótano	205	7	7	NA	7
El Sótano	206	7	7	NA	7
El Sótano	207	1	1	NA	1
El Sótano	208	1	1	NA	1
El Sótano	209	2	2	NA	2
El Sótano	210	11	11	NA	11
El Sótano	211	11	11	NA	11
El Sótano	212	5	5	NA	5
El Sótano	213	7	7	NA	7
El Sótano	214	15	16	15	15
El Sótano	215	7	6	7	7
El Sótano	216	9	9	NA	9
El Sótano	217	6	6	NA	6
El Sótano	218	8	8	NA	8
El Sótano	219	13	13	NA	13
El Sótano	220	12	12	NA	12
El Sótano	221	7	7	NA	7
El Sótano	222	9	9	NA	9
El Sótano	224	13	13	NA	13
El Sótano	225	12	12	NA	12
El Sótano	226	11	11	NA	11
El Sótano	227	5	5	NA	5
El Sótano	228	9	9	NA	9
El Sótano	229	46	47	46	46
El Sótano	230	11	11	NA	11
El Sótano	231	8	8	NA	8
El Sótano	232	5	5	NA	5
El Sótano	233	5	5	NA	5
El Sótano	234	6	6	NA	6
El Sótano	235	12	13	12	12
El Sótano	236	12	12	NA	12
El Sótano	237	8	8	NA	8

El Sótano	238	15	15	NA	15
El Sótano	239	13	13	NA	13
El Sótano	240	9	9	NA	9
El Sótano	242	11	11	NA	11
El Sótano	243	13	14	14	14
El Sótano	244	18	17	16	NA
El Sótano	245	3	NA	3	3
El Sótano	247	14	14	NA	14
El Sótano	248	17	17	NA	17
El Sótano	249	4	4	NA	4
El Sótano	250	15	14	15	15
El Sótano	251	10	10	NA	10
El Sótano	252	12	12	NA	12
El Sótano	254	15	15	NA	15
El Sótano	256	16	15	14	NA
El Sótano	257	15	15	NA	15
El Sótano	258	16	16	NA	16
El Sótano	259	10	10	NA	10
El Sótano	263	10	10	NA	10
El Sótano	265	12	11	12	12
El Sótano	266	9	9	NA	9
El Sótano	268	8	8	NA	8
El Sótano	269	7	6	6	6
El Sótano	270	10	10	NA	10
El Sótano	271	55	56	55	55
El Sótano	273	8	8	NA	8
El Sótano	274	10	10	NA	10
El Sótano	275	6	6	NA	6
El Sótano	276	13	13	NA	13
El Sótano	277	15	15	NA	15
El Sótano	279	10	10	NA	10
El Sótano	280	10	10	NA	10
El Sótano	281	12	12	NA	12
El Sótano	282	13	13	NA	13
El Sótano	283	12	12	NA	12
El Sótano	284	12	12	NA	12
El Sótano	286	13	13	NA	13
El Sótano	287	14	13	14	14
El Sótano	290	5	5	NA	5
El Sótano	291	10	10	NA	10
El Sótano	292	8	8	NA	8
El Sótano	294	11	11	NA	11
El Sótano	295	22	22	NA	22
El Sótano	296	7	7	NA	7
El Sótano	297	10	10	NA	10
El Sótano	298	4	4	NA	4
El Sótano	299	5	5	NA	5
El Sótano	300	8	8	NA	8
El Sótano	302	8	9	9	9
El Sótano	303	5	5	NA	5
El Sótano	304	12	12	NA	12
El Sótano	305	11	10	11	11
El Sótano	306	5	5	NA	5
El Sótano	307	5	5	NA	5
El Sótano	308	8	8	NA	8
El Sótano	309	14	14	NA	14
El Sótano	310	6	5	6	6
El Sótano	311	5	5	NA	5
El Sótano	312	5	6	6	6
El Sótano	313	6	5	6	6
El Sótano	315	6	6	NA	6
El Sótano	317	6	6	NA	6
El Sótano	318	6	6	NA	6
El Sótano	320	6	6	NA	6
El Sótano	321	6	5	6	6
El Sótano	323	6	6	NA	6

El Sótano	324	5	5	NA	5
El Sótano	325	5	5	NA	5
El Sótano	326	6	5	5	5
El Sótano	327	3	3	NA	3
El Sótano	328	2	2	NA	2
El Sótano	329	3	3	NA	3
El Sótano	330	2	2	NA	2
El Sótano	331	14	14	NA	14
El Sótano	332	15	15	NA	15
El Sótano	333	14	14	NA	14
El Sótano	334	11	11	NA	11
El Sótano	336	11	12	12	12
El Sótano	337	13	14	12	NA
El Sótano	338	6	6	NA	6
El Sótano	339	13	13	NA	13
El Sótano	340	12	12	NA	12
El Sótano	341	14	14	NA	14
El Sótano	342	14	14	NA	14
El Sótano	343	14	14	NA	14
El Sótano	344	5	5	NA	5
El Sótano	345	7	7	NA	7
El Sótano	348	13	13	NA	13
El Sótano	349	7	7	NA	7
El Sótano	350	7	7	NA	7
El Sótano	351	18	18	NA	18
El Sótano	352	11	11	NA	11
El Sótano	353	11	11	NA	11
El Sótano	354	8	8	NA	8
El Sótano	355	10	10	NA	10
El Sótano	356	8	7	10	NA
El Sótano	359	10	10	NA	10
El Sótano	360	13	13	NA	13
El Sótano	361	7	7	NA	7
El Sótano	362	19	19	NA	19
El Sótano	364	15	15	NA	15
El Sótano	365	12	13	12	12
El Sótano	366	8	8	NA	8
El Sótano	367	11	11	NA	11
El Sótano	368	16	16	NA	16
El Sótano	369	12	11	12	12
El Sótano	370	8	8	NA	8
El Sótano	371	10	10	NA	10
El Sótano	373	10	10	NA	10
El Sótano	374	18	18	NA	18
El Sótano	375	12	12	NA	12
El Sótano	376	12	13	12	12
El Sótano	377	8	8	NA	8
El Sótano	379	15	15	NA	15
El Sótano	381	14	14	NA	14
El Sótano	382	7	7	NA	7
El Sótano	383	10	10	NA	10
El Sótano	385	13	13	NA	13
El Sótano	386	17	17	NA	17
El Sótano	387	7	7	NA	7
El Sótano	388	16	16	NA	16
El Sótano	389	8	8	NA	8
El Sótano	390	16	16	NA	16
El Sótano	391	5	5	NA	5
El Sótano	392	3	3	NA	3
El Sótano	393	5	5	NA	5
El Sótano	394	16	15	15	15
El Sótano	395	6	6	NA	6
El Sótano	399	6	5	5	5
El Sótano	400	5	5	NA	5
El Sótano	401	4	7	5	NA
El Sótano	402	6	6	NA	6

El Sótano	406	9	12	10	NA
El Sótano	408	9	8	9	9
El Sótano	411	5	5	NA	5
El Sótano	412	5	5	NA	5
El Sótano	414	3	4	4	4
El Sótano	415	15	15	NA	15
El Sótano	418	6	6	NA	6
El Sótano	419	15	15	NA	15
El Sótano	420	8	9	9	9
El Sótano	421	6	6	NA	6
El Sótano	422	6	6	NA	6
El Sótano	423	11	10	11	11
El Sótano	424	8	9	8	8
El Sótano	425	6	6	NA	6
El Sótano	426	10	11	11	11
El Sótano	427	11	11	NA	11
El Sótano	428	18	17	18	18
El Sótano	429	5	5	NA	5
El Sótano	430	11	11	NA	11
El Sótano	431	8	8	NA	8
El Sótano	432	15	15	NA	15
El Sótano	433	8	8	NA	8
El Sótano	434	6	6	NA	6
El Sótano	436	5	5	NA	5
El Sótano	438	11	12	12	12
El Sótano	439	9	10	10	10
El Sótano	440	21	21	NA	21
El Sótano	441	11	10	10	10
El Sótano	442	5	6	6	6
El Sótano	444	6	6	NA	6
El Sótano	445	11	11	NA	11
El Sótano	446	9	16	16	16
El Sótano	447	53	54	54	54
El Sótano	448	11	11	NA	11
El Sótano	449	6	7	6	6
El Sótano	450	6	7	6	6
El Sótano	457	6	6	NA	6
El Sótano	458	5	5	NA	5
El Sótano	459	6	7	8	NA
El Sótano	460	11	10	11	11
El Sótano	461	5	6	5	5
El Sótano	462	40	36	36	36
El Sótano	463	6	6	NA	6
El Sótano	464	6	5	5	5
El Sótano	465	5	7	5	5
El Sótano	466	12	11	11	11
El Sótano	467	7	7	NA	7
El Sótano	469	7	8	7	7
El Sótano	470	9	12	9	9
El Sótano	471	11	10	10	10
El Sótano	472	11	11	NA	11
El Sótano	476	13	13	NA	13
El Sótano	477	12	14	12	12
El Sótano	478	6	7	7	7
El Sótano	479	6	6	NA	6
El Sótano	481	6	6	NA	6
El Sótano	482	10	10	NA	10
El Sótano	484	16	16	NA	16
El Sótano	485	4	6	4	4
El Sótano	486	6	6	NA	6
El Sótano	488	9	9	NA	9
El Sótano	489	6	6	NA	6
El Sótano	491	10	10	NA	10
El Sótano	492	6	7	6	6
El Sótano	493	8	7	7	7
El Sótano	494	4	4	NA	4

El Sótano	495	11	11	NA	11
El Sótano	496	7	7	NA	7
El Sótano	498	6	6	NA	6
El Sótano	499	14	14	NA	14
El Sótano	501	12	13	12	12
El Sótano	502	6	6	NA	6
El Sótano	504	7	6	6	6
El Sótano	505	10	10	NA	10
El Sótano	506	11	11	NA	11
El Sótano	507	6	5	6	6
El Sótano	508	7	7	NA	7
El Sótano	509	11	11	NA	11
El Sótano	510	2	2	NA	2
El Sótano	511	4	3	4	4
El Sótano	512	2	3	2	2
El Sótano	513	4	4	NA	4
El Sótano	514	15	15	NA	15
El Sótano	515	7	10	7	7
El Sótano	516	3	3	NA	3
El Sótano	517	5	4	5	5
El Sótano	519	14	14	NA	14
El Sótano	521	15	15	NA	15
El Sótano	522	12	12	NA	12
El Sótano	523	12	12	NA	12
El Sótano	525	7	7	NA	7
El Sótano	527	11	12	11	11
El Sótano	528	13	13	NA	13
El Sótano	529	4	4	NA	4
El Sótano	531	6	8	6	6
El Sótano	532	16	19	20	NA
El Sótano	533	11	11	NA	11
El Sótano	536	11	11	NA	11
El Sótano	537	20	20	NA	20
El Sótano	538	16	16	NA	16
El Sótano	539	10	13	10	10
El Sótano	540	4	4	NA	4
El Sótano	541	13	13	NA	13
El Sótano	542	6	6	NA	6
El Sótano	543	5	5	NA	5
El Sótano	544	10	10	NA	10
El Sótano	545	5	4	4	4
El Sótano	547	22	23	22	22
El Sótano	548	7	7	NA	7
El Sótano	549	4	4	NA	4
El Sótano	550	4	3	3	3
El Sótano	551	3	4	4	4
El Sótano	552	5	5	NA	5
El Sótano	553	3	3	NA	3
El Sótano	554	6	5	5	5
El Sótano	555	3	3	NA	3
El Sótano	556	2	2	NA	2
El Sótano	557	3	3	NA	3
El Sótano	558	6	5	5	5
El Sótano	559	5	5	NA	5
El Sótano	560	15	15	NA	15
El Sótano	561	2	2	NA	2
El Sótano	562	3	3	NA	3
El Sótano	563	5	6	5	5
El Sótano	564	4	4	NA	4
El Sótano	565	14	14	NA	14
El Sótano	566	2	2	NA	2
El Sótano	567	2	2	NA	2
El Sótano	568	6	6	NA	6
El Sótano	569	6	7	6	6
El Sótano	570	30	30	NA	30
El Sótano	571	6	6	NA	6

El Sótano	572	8	7	7	7
El Sótano	573	8	8	NA	8
El Sótano	574	5	5	NA	5
El Sótano	575	4	3	3	3
El Sótano	576	3	3	NA	3
El Sótano	577	3	3	NA	3
Punta Colorada	1	14	14	NA	14
Punta Colorada	2	45	40	43	NA
Punta Colorada	3	8	8	NA	8
Punta Colorada	4	16	15	16	16
Punta Colorada	5	9	9	NA	9
Punta Colorada	6	4	4	NA	4
Punta Colorada	7	13	13	NA	13
Punta Colorada	8	8	8	NA	8
Punta Colorada	9	9	9	NA	9
Punta Colorada	10	6	6	NA	6
Punta Colorada	11	8	8	NA	8
Punta Colorada	12	21	32	25	NA
Punta Colorada	13	13	13	NA	13
Punta Colorada	14	10	10	NA	10
Punta Colorada	15	14	14	NA	14
Punta Colorada	16	13	15	14	NA
Punta Colorada	17	5	5	NA	5
Punta Colorada	18	9	9	NA	9
Punta Colorada	19	19	17	18	NA
Punta Colorada	20	9	9	NA	9
Punta Colorada	21	9	9	NA	9
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Punta Colorada	31	56	49	53	NA
Punta Colorada	32	10	10	NA	10
Punta Colorada	33	13	13	NA	13
Punta Colorada	34	7	7	NA	7
Punta Colorada	35	13	13	NA	13
Punta Colorada	36	5	5	NA	5
Punta Colorada	37	12	12	NA	12
Punta Colorada	38	9	9	NA	9
Punta Colorada	39	15	15	NA	15
Punta Colorada	40	14	14	NA	14
Punta Colorada	41	7	7	NA	7
Punta Colorada	42	9	9	NA	9
Punta Colorada	43	9	9	NA	9
Punta Colorada	44	8	8	NA	8
Punta Colorada	45	9	9	NA	9
Punta Colorada	46	6	6	NA	6
Punta Colorada	47	9	9	NA	9
Punta Colorada	49	6	6	NA	6
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Punta Colorada	53	9	9	NA	9
Punta Colorada	54	9	9	NA	9
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Punta Colorada	63	8	8	NA	8
Punta Colorada	64	5	5	NA	5
Punta Colorada	65	9	9	NA	9

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Punta Colorada	68	7	7	NA	7
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Punta Colorada	71	6	6	NA	6
Punta Colorada	72	7	7	NA	7
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Punta Colorada	75	8	8	NA	8
Punta Colorada	76	6	6	NA	6
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Punta Colorada	79	9	9	NA	9
Punta Colorada	81	14	16	15	NA
Punta Colorada	82	6	6	NA	6
Punta Colorada	83	8	8	NA	8
Punta Colorada	84	9	9	NA	9
Punta Colorada	85	13	13	NA	13
Punta Colorada	86	8	8	NA	8
Punta Colorada	87	6	6	NA	6
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Punta Colorada	93	1	1	NA	1
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Punta Colorada	95	8	8	NA	8
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Punta Colorada	98	14	14	NA	14
Punta Colorada	99	14	14	NA	14
Punta Colorada	100	15	15	NA	15
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Punta Colorada	102	13	13	NA	13
Punta Colorada	103	12	12	NA	12
Punta Colorada	104	29	29	NA	29
Punta Colorada	105	27	25	28	NA
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Punta Colorada	109	12	12	NA	12
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Punta Colorada	112	20	19	19	19
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Punta Colorada	117	9	9	NA	9
Punta Colorada	119	10	10	NA	10
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Punta Colorada	121	10	10	NA	10
Punta Colorada	122	19	17	17	17
Punta Colorada	123	33	32	32	32
Punta Colorada	124	24	25	24	24
Punta Colorada	125	25	25	NA	25
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Punta Colorada	127	41	41	NA	41
Punta Colorada	128	13	12	12	12
Punta Colorada	129	15	15	NA	15
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Punta Colorada	131	27	26	27	27
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Punta Colorada	133	25	24	24	24
Punta Colorada	134	12	12	NA	12
Punta Colorada	135	19	19	NA	19
Punta Colorada	136	25	25	NA	25

Punta Colorada	137	25	25	NA	25
Punta Colorada	138	10	10	NA	10
Punta Colorada	139	10	11	10	10
Punta Colorada	140	34	33	33	33
Punta Colorada	141	9	10	9	9
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Punta Colorada	149	9	9	NA	9
Punta Colorada	150	25	25	NA	25
Punta Colorada	151	13	12	13	13
Punta Colorada	152	13	13	NA	13
Punta Colorada	153	7	7	NA	7
Punta Colorada	154	9	9	NA	9
Punta Colorada	155	14	14	NA	14
Punta Colorada	156	19	19	NA	19
Punta Colorada	158	19	19	NA	19
Punta Colorada	159	22	22	NA	22
Punta Colorada	160	8	8	NA	8
Punta Colorada	161	18	18	NA	18
Punta Colorada	162	22	22	NA	22
Punta Colorada	163	9	9	NA	9
Punta Colorada	164	25	25	NA	25
Punta Colorada	165	26	27	26	26
Punta Colorada	166	14	14	NA	14
Punta Colorada	167	26	26	NA	26
Punta Colorada	169	11	11	NA	11
Punta Colorada	170	24	25	25	25
Punta Colorada	171	21	24	23	NA
Punta Colorada	172	13	13	NA	13
Punta Colorada	173	13	13	NA	13
Punta Colorada	174	26	26	NA	26
Punta Colorada	176	13	13	NA	13
Punta Colorada	177	12	12	NA	12
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Punta Colorada	187	25	25	NA	25
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Punta Colorada	189	10	10	NA	10
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Punta Colorada	192	12	12	NA	12
Punta Colorada	193	9	9	NA	9
Punta Colorada	194	9	9	NA	9
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Punta Colorada	205	18	18	NA	18
Punta Colorada	207	6	6	NA	6
Punta Colorada	208	21	20	21	21
Punta Colorada	209	12	12	NA	12
Punta Colorada	210	12	12	NA	12

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Punta Colorada	214	9	9	NA	9
Punta Colorada	215	28	29	29	29
Punta Colorada	216	13	13	NA	13
Punta Colorada	217	13	13	NA	13
Punta Colorada	218	10	10	NA	10
Punta Colorada	219	9	9	NA	9
Punta Colorada	220	24	24	NA	24
Punta Colorada	221	25	25	NA	25
Punta Colorada	222	29	29	NA	29
Punta Colorada	223	20	20	NA	20
Punta Colorada	224	24	25	25	25
Punta Colorada	225	17	17	NA	17
Punta Colorada	226	28	27	27	27
Punta Colorada	227	6	6	NA	6
Punta Colorada	228	15	14	15	15
Punta Colorada	229	12	12	NA	12
Punta Colorada	230	24	24	NA	24
Punta Colorada	231	20	21	20	20
Punta Colorada	232	12	12	NA	12
Punta Colorada	234	11	11	NA	11
Punta Colorada	235	16	16	NA	16
Punta Colorada	236	9	9	NA	9
Punta Colorada	237	21	21	NA	21
Punta Colorada	238	8	8	NA	8
Punta Colorada	239	11	11	NA	11
Punta Colorada	240	25	26	26	26
Punta Colorada	241	16	16	NA	16
Punta Colorada	242	20	19	20	20
Punta Colorada	243	16	15	15	15
Punta Colorada	244	16	16	NA	16
Punta Colorada	245	27	28	27	27
Punta Colorada	246	19	19	NA	19
Punta Colorada	247	14	14	NA	14
Punta Colorada	248	11	11	NA	11
Punta Colorada	249	24	26	26	26
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Punta Colorada	251	17	16	16	16
Punta Colorada	252	8	8	NA	8
Punta Colorada	253	9	9	NA	9
Punta Colorada	254	19	18	19	19
Punta Colorada	255	10	10	NA	10
Punta Colorada	256	22	22	NA	22
Punta Colorada	257	8	8	NA	8
Punta Colorada	258	11	11	NA	11
Punta Colorada	260	11	11	NA	11
Punta Colorada	261	22	22	NA	22
Punta Colorada	262	10	10	NA	10
Punta Colorada	263	25	25	NA	25
Punta Colorada	264	28	28	NA	28
Punta Colorada	265	25	25	NA	25
Punta Colorada	266	8	8	NA	8
Punta Colorada	267	20	19	19	19
Punta Colorada	268	9	9	NA	9
Punta Colorada	269	11	11	NA	11
Punta Colorada	270	12	12	NA	12
Punta Colorada	271	19	19	NA	19
Punta Colorada	272	12	12	NA	12
Punta Colorada	273	19	20	19	19
Punta Colorada	274	14	14	NA	14
Punta Colorada	275	12	12	NA	12
Punta Colorada	276	19	18	19	19
Punta Colorada	277	12	12	NA	12
Punta Colorada	278	10	10	NA	10
Punta Colorada	279	8	8	NA	8

Punta Colorada	280	12	12	NA	12
Punta Colorada	282	11	11	NA	11
Punta Colorada	283	12	12	NA	12
Punta Colorada	284	38	37	37	37
Punta Colorada	285	14	14	NA	14
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Punta Colorada	288	9	9	NA	9
Punta Colorada	289	17	17	NA	17
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Punta Colorada	292	12	12	NA	12
Punta Colorada	293	24	24	NA	24
Punta Colorada	294	25	27	26	NA
Punta Colorada	295	13	13	NA	13
Punta Colorada	296	9	9	NA	9
Punta Colorada	297	14	14	NA	14
Punta Colorada	298	26	26	NA	26
Punta Colorada	299	26	26	NA	26
Punta Colorada	300	14	14	NA	14
Punta Colorada	301	21	21	NA	21
Punta Colorada	302	13	13	NA	13
Punta Colorada	303	9	9	NA	9
Punta Colorada	304	11	11	NA	11
Punta Colorada	305	11	11	NA	11
Punta Colorada	306	7	7	NA	7
Punta Colorada	308	15	15	NA	15
Punta Colorada	309	27	27	NA	27
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Punta Colorada	311	14	14	NA	14
Punta Colorada	312	16	12	14	NA
Punta Colorada	313	8	8	NA	8
Punta Colorada	314	30	36	32	NA
Punta Colorada	315	10	10	NA	10
Punta Colorada	316	9	10	9	9
Punta Colorada	317	25	25	NA	25
Punta Colorada	318	16	15	16	16
Punta Colorada	319	24	24	NA	24
Punta Colorada	320	11	11	NA	11
Punta Colorada	321	30	28	30	30
Punta Colorada	322	13	13	NA	13
Punta Colorada	323	13	13	NA	13
Punta Colorada	324	11	11	NA	11
Punta Colorada	325	28	28	NA	28
Punta Colorada	326	26	26	NA	26
Punta Colorada	327	19	20	19	19
Punta Colorada	328	20	16	18	NA
Punta Colorada	329	15	15	NA	15
Punta Colorada	330	14	13	13	13
Punta Colorada	331	20	20	NA	20
Punta Colorada	332	19	19	NA	19
Punta Colorada	333	14	14	NA	14
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Punta Colorada	335	9	9	NA	9
Punta Colorada	336	8	8	NA	8
Punta Colorada	337	20	20	NA	20
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Punta Colorada	339	15	15	NA	15
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Punta Colorada	341	24	22	24	24
Punta Colorada	342	11	11	NA	11
Punta Colorada	343	22	22	NA	22
Punta Colorada	345	25	26	25	25
Punta Colorada	346	11	11	NA	11
Punta Colorada	347	9	9	NA	9
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Punta Colorada	349	7	7	NA	7

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Punta Colorada	351	20	20	NA	20
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Punta Colorada	353	12	13	13	13
Punta Colorada	354	10	10	NA	10
Punta Colorada	355	21	20	21	21
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Punta Colorada	358	14	14	NA	14
Punta Colorada	360	11	11	NA	11
Punta Colorada	361	21	21	NA	21
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Punta Colorada	363	9	9	NA	9
Punta Colorada	364	12	12	NA	12
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Punta Colorada	366	15	15	NA	15
Punta Colorada	367	16	16	NA	16
Punta Colorada	368	15	17	17	17
Punta Colorada	369	8	8	NA	8
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Punta Colorada	377	12	12	NA	12
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Punta Colorada	380	10	10	NA	10
Punta Colorada	381	36	36	NA	36
Punta Colorada	382	23	24	24	24
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Punta Colorada	384	8	8	NA	8
Punta Colorada	385	7	7	NA	7
Punta Colorada	386	19	19	NA	19
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Punta Colorada	390	8	8	NA	8
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Punta Colorada	394	8	8	NA	8
Punta Colorada	395	20	20	NA	20
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Punta Colorada	397	7	7	NA	7
Punta Colorada	398	10	10	NA	10
Punta Colorada	399	9	9	NA	9
Punta Colorada	400	9	9	NA	9
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Punta Colorada	402	10	10	NA	10
Punta Colorada	403	18	18	NA	18
Punta Colorada	404	23	23	NA	23
Punta Colorada	405	22	22	NA	22
Punta Colorada	406	3	3	NA	3
Punta Colorada	407	2	2	NA	2
Punta Colorada	408	1	1	NA	1
Punta Colorada	409	37	37	NA	37
Punta Colorada	410	15	15	NA	15
Punta Colorada	411	36	36	NA	36
Punta Colorada	412	12	12	NA	12
Puerto Lobos	1	2	2	NA	2
Puerto Lobos	2	5	5	NA	5
Puerto Lobos	3	5	5	NA	5
Puerto Lobos	4	5	5	NA	5
Puerto Lobos	5	5	5	NA	5
Puerto Lobos	6	5	5	NA	5

Puerto Lobos	7	6	6	NA	6
Puerto Lobos	8	6	6	NA	6
Puerto Lobos	9	6	6	NA	6
Puerto Lobos	10	6	6	NA	6
Puerto Lobos	11	6	6	NA	6
Puerto Lobos	12	6	6	NA	6
Puerto Lobos	13	6	6	NA	6
Puerto Lobos	14	5	6	7	NA
Puerto Lobos	15	6	6	NA	6
Puerto Lobos	16	6	6	NA	6
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Puerto Lobos	31	6	6	NA	6
Puerto Lobos	32	8	8	NA	8
Puerto Lobos	33	11	11	NA	11
Puerto Lobos	34	11	11	NA	11
Puerto Lobos	35	12	12	NA	12
Puerto Lobos	36	12	12	NA	12
Puerto Lobos	37	13	13	NA	13
Puerto Lobos	38	14	13	16	NA
Puerto Lobos	39	15	15	NA	15
Puerto Lobos	40	15	15	NA	15
Puerto Lobos	41	17	15	16	NA
Puerto Lobos	42	16	16	NA	16
Puerto Lobos	43	16	16	NA	16
Puerto Lobos	44	18	18	NA	18
Puerto Lobos	45	19	19	NA	19
Puerto Lobos	46	21	21	NA	21
Puerto Lobos	47	27	23	24	NA
Puerto Lobos	48	30	30	NA	30
Puerto Lobos	49	30	31	31	31
Puerto Lobos	50	38	34	34	34
Puerto Lobos	57	19	19	NA	19
Puerto Lobos	58	4	4	NA	4
Puerto Lobos	59	5	5	NA	5
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Punta Conos	13	17	17	NA	17
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