The impact of size truncation on reproductive success in the southern king crab (*Lithodes santolla*)

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ABSTRACT

Sex-biased fishing mortality caused by male-only fishing may result in sperm limitation and recruitment overfishing. These effects can be observed by studying the size at functional reproduction (SFR) of lithodid females. We studied changes in the ratio of males to females, size truncation, and changes in SFR in the southern king crab (SKC) in two areas experiencing different fishing pressures in southern Chile. SFR was estimated with the Richards Function, a generalized 4-parameter logistic model. The shrinking of SFR of females may occur due to the proportional shrinking of reproductive and non-reproductive females and/or because the shape of the ogive changes, setting the inflection point back to smaller sizes. In the region with low fishing pressure the functional reproductive ogive was symmetric ($\gamma = 1$, and the asymptote was ~1, indicating a balance in male availability. In the region with high fishing pressure γ was 82 % lower and the asymptote was 23 % lower, an indicator of sperm limitation. The symmetric shape of the logistic curve, which is widely assumed when fitting maturity ogives, is not the most appropriate assumption in SKC and possibly in other males-only crab fisheries. More general shapes of the ogive should be estimated and studied.

1. Introduction

Sex-biased fishing mortality occurs in crab fisheries because fishers seek to catch larger-sized males and/or because regulations prohibit the landing of females or berried females (Di Salvatore et al., 2021; Kruse, 1993; Otto, 2014). When sex-biased fishing is strong and females prefer to mate with larger males, the reproductive success of stocks may be hampered due to sperm limitation caused by the inability to find suitable mates (Baker et al., 2022; Lovrich et al., 2002; Ogburn, 2019; Sato, 2012; Sato et al., 2007, 2005). Although unbalanced sex ratios have been observed in a number of crustacean fisheries, the impact of these biased sex ratios on reproductive success remains unknown in the majority of cases (Ogburn, 2019; Ogburn et al., 2014; Rains et al., 2018, 2016). Furthermore, spatial variations in fishing pressure may lead to dissimilar degrees of unbalanced sex ratio and sperm limitation in

different areas (Sato, 2012; Ogburn, 2019; Di Salvatore et al., 2021). This article examines the aforementioned phenomenon in southern king crab (SKC) (*L. santolla)* by comparing a generalized functional reproduction model for females in two distinct fishing areas with contrasting fishing pressures and size-truncated stocks in southern Chile.

Because female lithodid crabs attach their fertilized eggs to their pleopods, it is possible to directly monitor reproductive success by observing the presence of eggs in a wide size range of females, which is termed size at functional reproduction (SFR) (Di Salvatore et al., 2021). Accordingly, it is also possible to estimate model parameters of functional reproduction in females as a function of size (Kruse, 1993, Lovrich and Tapella, 2014). The estimation of size-maturity or reproduction models in female crustaceans is performed using logistic models that generally consider three parameters: one that represents the maximum ratio of mature individuals, and two that determine the shape of the

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logistic curve (Di Salvatore et al., 2021; Firpo et al., 2017; Jewett et al., 1985; Olson et al., 2018; Restrepo and Watson, 1991; Roa et al., 1999; Somerton, 1980; Webb, 2014). The variability in the forms that the fitted functions acquire for the different crustacean species studied, in addition to the temporal and spatial variability of the parameters obtained for the same species, have not been discussed in detail. The exception is Di Salvatore et al. (2021) who suggested the existence of at least two detectable phases within the *L. santolla* fishery in Argentina: a first phase of sperm limitation due to the exclusive extraction of males; and a second phase characterized by a low ratio of ovigerous females and an increase in SFR, but with no changes in the individual fecundity, resulting in recruitment overfishing. However, these phases have not been directly associated with a quantitative indicator or parameter. On the other hand, except for parameters representing mean size at maturity (such as size at 50 % maturity), few results have been reported on i) the relationship between the parameters obtained and the reproductive biology of the species studied; ii) the criteria used to assign the stage of maturity; and iii) the selectivity of the fishing method used (Aguirre--Villaseñor et al., 2022). Further connections of sexual maturity with molting and growth in the SKC have been clarified by Lovrich and Tapella (2014): in the Beagle Channel and Golfo San Jorge gonadal maturity is attained between 65 and 75 mm CL (Following Vinuesa 1984). After the gonad maturity males probably molt twice a year until they are 100 mm CL, then they could molt annually and males larger than 130 mm LC could molt biennially. Females could molt annually since their maturity, because of the 10-month egg-bearing.

This article explores the effects of changes in the ratio of males and females and size truncation on alterations in reproductive success and the quantification thereof in SKC fisheries in two areas with different fishing pressures in southern Chile. We studied the SFR in female SKC by applying a generalized 4-parameter logistic model, known as the Richards Function (Giraldo et al., 2002). It is argued that parameters of the generalized logistic maturity models serve as indicators of the reproductive health status of the population studied.

2. Methodology

2.1. Study area and fishery description

The study area included *L. santolla* fisheries located on the continental shelf (oceanic zone) and in the north Patagonian channels and fjords between 41° 30′ S and 46° S, which includes the Los Lagos and Aysén Regions (zones 117, 118, 121 and 122, see Fig. 1). Samples were collected from this area from: i) fishery sampling, which included on-board scientific observers (zones 117, 118 and 122), and ii) fishery-independent sampling (zones 121 and 122).

The bathymetry of the fjords and inland channels in the study area is heterogeneous, with trenches of more than 200 m in depth and bottom temperatures varying between 9 and 11° C (Rodríguez et al., 2020). On the continental shelf, the fishing grounds extend to ~250 m in an area intersected by several trenches that drop steeply to over 2000 m (Fig. 1). Fishing activity is concentrated between 50 and 250 m both in the fjords and inland channels and on the continental shelf. Both fishery and fishery-independent sampling used cone traps, as described by Lovrich and Tapella (2014).

Molinet et al. (2020) described the expansion and characteristics of the SKC fishery in the Los Lagos and Aysén Regions of southern Chile, which increased landings by a magnitude of 6–8 times between 2010 and 2018, with more intense fishing in the northern fishing grounds of Los Lagos than in the southern Aysén. Between 2018 and 2019, catches and fishing trips increased in Aysén, coinciding with a decrease in catches and fishing trips in Los Lagos, which began in 2017 (Fig. 2). The fishery is managed in Chile according to the well-known 3 S rule (sex, size, season: males only, minimum size at 100 mm, and 50 days of closed season) (Molinet et al., 2020; Otto, 2014) and, to date, no stock assessment has been conducted for the fishery in the study area.
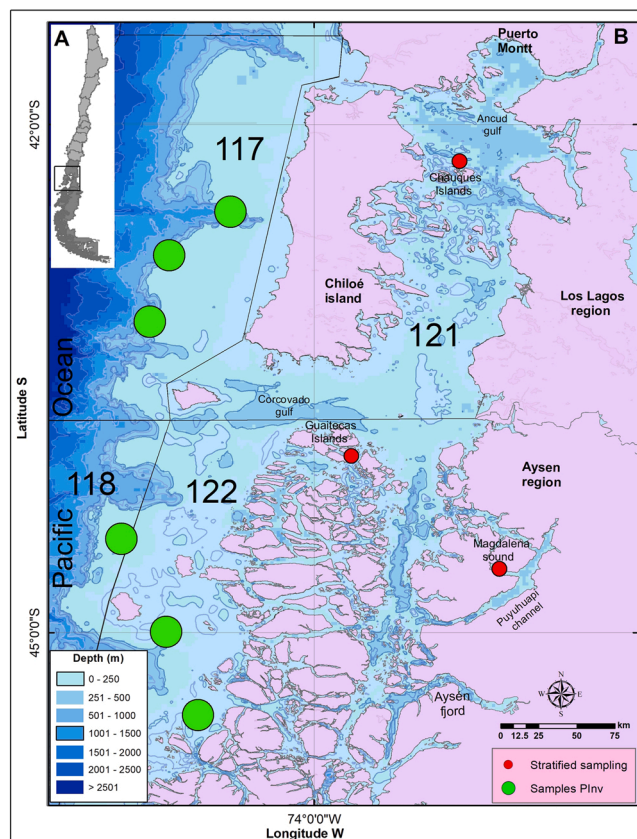

Fig. 1. A) Study area in southern Chile. B) Los Lagos (zones 117 and 121) and Aysén regions (zones 118 and 122). Red dots show areas with fishery-independent sampling. Green dots show areas with fishery sampling.
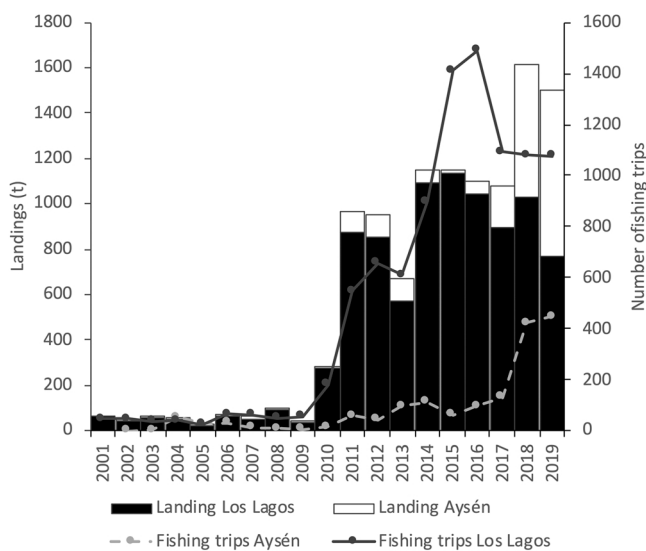

Fig. 2. Landings and the number of fishing trips in the Los Lagos and Aysén regions, southern Chile, between 2001 and 2019.

2.2. Sample collections from fishing vessels

Monthly sampling of *L. santolla* was conducted between May 2018 and December 2019. To record information and collect samples, scientific observers embarked on fishing vessels that operated in both the Los Lagos and Aysén Regions. The frequency of embarkation was subject to that of the fishing vessel departures (between one to two trips per month

in Los Lagos and more sporadically in Aysén) as well as their availability to transport a scientific observer. These observers recorded carapace length (CL), sex of specimens and the presence of eggs from a sample of at least three traps per line (10–18 lines per boat). In addition, up to 20 females per trip were collected at random. Samples were transferred to the laboratory where they were measured, weighed and, in the case of ovigerous females, fecundity was estimated.

2.3. Fishery-independent sample collection

Between January 2018 and December 2019, samples of *L. santolla* were collected in Seno Magdalena, Guaitecas Islands (Aysén Region) and Chauques Islands (Los Lagos Region) (Fig. 1). In each sector, 12–15 traps were used on a monthly basis, with each one deployed for a period of ~24 h. In every sector, all SKC specimens that entered each trap were collected, weighed, measured and sexed, and all ovigerous females were identified and registered. Up to a maximum of 60 individuals per sector and month were then sampled at random and transferred to the laboratory, where they were measured and weighed once more and the fecundity, in the case of ovigerous females, was estimated. Animal`s manipulation in laboratory were realized fulfilling the legal requirements of Chile, and the Ethical Committee of the Universidad Austral de Chile.

2.4. Fecundity

Egg development stages were classified as follows: i) initial stage 1, with homogeneous yolk and no eyespot; ii) intermediate stage 2, between ¼ and ½ of the yolk consumed and with a slightly visible eyespot; iii) final stage 3, with ¾ of the yolk consumed and well-developed eyespot of the prezoea (Gebauer et al., 2007; Lardies et al., 2004; Wehrtmann, 1990). Finally, stage 4 classified ovigerous masses in which eggs were hatching.

The number of eggs from each ovigerous female was estimated in four steps. First, the total weight of the ovigerous mass was recorded, using a digital balance (Snowrex model EJ-1200), with 0.01 g accuracy. Second, 600 eggs from the total sample were carefully separated into groups of 100 eggs and placed in Eppendorf tubes (having been previously labeled). Third, these were weighed (wet weight) using an analytical balance (Shimadzu model AUX 220), with 0.1 mg precision. Finally, the weight of the 100 eggs was averaged and the fecundity was calculated as follows:

$$F = \frac{100 eggs}{Weight_{100 eggs}} x (Ovigerous mass weight - Pleopdos weight)$$

2.5. Data analysis

2.5.1. Cohort composition and model selection

To determine the number of cohorts from the size frequency data, a mixture distribution analysis was performed for each year of data collected at intervals of 1 mm carapace length, and undertaken separately for males and females (Orensanz et al., 2007; Roa-Ureta, 2010). In the mixture distribution analysis, each component is assumed to correspond to an annual age class or cohort with size distribution of each cohort well approximated by the normal density function. Part of this assumption is supported by knowledge of the biology of the stock, which indicates that the stock is composed of annual cohorts (Lovrich and Tapella, 2014). For the estimation of these models, the ratios of each cohort in the mixture were conditioned to add up to 1, mean lengths were in certain cases conditioned to be different and incremental, and the standard deviations were in some cases conditioned to be higher than 0. These constraints are similar to those set by MacDonald and Pitcher (1979, Appendix C) and are grounded on mathematical and biological considerations. Nevertheless, both mean lengths and standard deviations were estimated in an unrestricted manner in the majority of

the fits.

Since the data correspond to counts in each one of the multiple length categories, its distribution was modeled as multinomial, and therefore the log-likelihood function to maximize as a function of the parameters was:

$$L = n \sum_{1}^{D} P_l log(H(l, \delta))$$

where n is the total number of measured crabs, D is the total number of length categories, P is the proportion of crabs observed in the length category l, and $H(l,\delta)$ is a mixture of J normal distributions of length values grouped into bins of 2δ width. Each one of these normal distributions represent a distinct year class, and they have three parameters each: proportion of participation in the mixture, mean length and standard deviation of length. Since the number of year classes J is unknown, several models were fitted for each length frequency data set, with a minimum number of two-year classes and a maximum number of seven. To determine which of all the fitted models that converged for each length frequency examined was the most appropriate, the Akaike information criterion (AIC) was used (Akaike, 1974; Burnham and Anderson, 2004). Statistical fitting was performed in the AD Model Builder v 12.3 programming environment (Fournier et al., 2012), while data and fitting results were processed using the vcdExtra package (Friendly, 2021) in the R programming environment version 4.1.0. (Anon, 2021).

2.5.2. Size at functional reproduction

To study female SFR, a generalized, 4-parameter logistic ogive model was applied, known as the Richards Function (Giraldo et al., 2002):

$$P(l) = \frac{\alpha}{\left(1 + 10^{\beta(\lambda - l)}\right)^\gamma}, \tag{1}$$

where P is the ratio of functionally mature females, l is the carapace length, α is the asymptotic or saturation ratio of functional reproductive females, β is the gradient of the rise in the ratio of mature females as size increases, λ is the midpoint of the maturity progression along the length axis, and γ is the symmetry of the logistic progression of reproduction. The location of the point of inflection, which is the point on a curve at which the curvature changes from convex to concave or vice versa, serves for the assessment of the symmetry of the curve (Giraldo et al., 2002). This functional reproduction progression model can be made more general by adding a further parameter to establish the minimum ratio of mature females at the lowest carapace length although, on the basis of biological principles, it is assumed that this 'base' ratio of mature females is zero. Under the generalized maturity progression model, the length at 50 % functional reproduction is found by making the model in Eq. (1) equal to 0.5 and solving for l,

$$l_{50\%} = \lambda - \frac{1}{\beta} \left[log_{10} \left((2\alpha)^{\frac{1}{\gamma}} - 1 \right) \right] \tag{2}$$

This model is characterized by allowing an objective comparison of the saturation of functional reproduction α in females between regions and years with different fishing intensities, which could be explained by a different degree of the removal of males. It is expected that the Los Lagos Region will register a less than complete saturation of functionally mature females because of the more intense removal of males in the area. This makes it harder for females to find males large enough with which to mate, in contrast to the less intensively exploited Aysén Region. Furthermore, this model allows for an examination of the potential shrinking in the SFR of females, not only by displacing the ogive to smaller crab sizes but also by changing its shape by means of the symmetry parameter γ. Thus, in the model, the shrinking of functionally reproductive female crabs may occur due to the proportional shrinking of reproductive and non-reproductive females (i.e., a retreat in $l_{50\%}$

without a change in the shape of the ogive) and/or because the shape of the ogive changes, setting the inflection point back to smaller sizes.

We fitted this model to the proportion of functionally reproductive females and length using data collected between January and March 2019, under the assumption that this is a post-mating period (following Campodónico, 1974). This is reflected in the extrusion of eggs in developmental stage one. This sub setting of the data had the goal of reducing the chances that other variables might affect the presence of ovigerous females. Furthermore, to test for significant differences in maturity progression with size between the two regions, data from both Los Lagos and Aysén regions were analyzed as a single group (both regions together) and as separate data sets. We used 95 % confidence tests for the CL at 50 % maturity (CL_{50}) and goodness of fit statistics consistent in the correlation between observed and predicted values of proportion mature at size. Under the hypothesis of no significant difference, confidence intervals for this parameter CL_{50} from grouped data, Los Lagos region data and Aysén region data, should overlap, and the goodness of fit statistic should be higher for grouped data. We used the R package *nplr* (n-parameter logistic regression) version 0.1–7 (Commo and Bot, 2016) in R version 4.1.0 (Anon, 2021). We implemented some minor editing of the code of the *nlpr* function and associated classes of objects to report the Hessian matrix in the object containing results. This was done to be able to calculate standard errors of estimates. The models for each region were fitted to the data by minimizing the weighted sum of squares (equivalent to maximizing a weighted profile likelihood function based on the normal distribution), with the weights *W* defined by

$$W(l) = \frac{s_l}{\sum_{l=l_{min}}^{l=l_{mx}} s_l}, \qquad (3)$$

where s_l is the sample size per length category (at intervals of 1 mm carapace length). The minimum and maximum length categories for modelling were 66 and 102 mm in Los Lagos (471 females) and 60 and 143 mm (2263 females) in Aysén.

2.5.3. Fecundity

Variation in fecundity between regions was evaluated using carapace length, egg development stage and year as predictor variables, while linear models and generalized linear models were applied (McCullagh and Nelder, 1989). The most informative model was selected using the AIC. All statistical procedures were performed in R version 4.1.0 (R Development Core Team, 2021), using the *car* (Fox and Sanford, 2010) and *lmtest* (Zeileis and Hothorn, 2002) packages.

3. Results

During the study period, 21,522 specimens of *L. santolla* were sampled in the Los Lagos region (67 % males, 33 % females) and 5316 specimens in the Aysén region (46 % males, 54 % females), 80 % of which were obtained from the fishery (see Table A1, Appendix). In Aysén, data from the fishery were obtained between January and March 2019, while in Los Lagos the data were recorded between May 2018 and December 2019.

For fecundity estimation in the laboratory, 495 females were captured in Los Lagos and 406 females in Aysén (see Table A2, Appendix). In Los Lagos, the catch between April and July consisted primarily of males, while a more balanced ratio of males and females was observed between August and January, (Fig. 3A). In Aysén, where fishery-independent sampling was more common, catches consisted primarily of females, although in the months of January to March 2019 (mainly fishery data) a pattern similar to that observed in Los Lagos was recorded (Fig. 3B).

In both study years (2018 and 2019) the highest ratio of ovigerous females was observed between January and September, with eggs in developmental stage 1 predominating between January and April, in
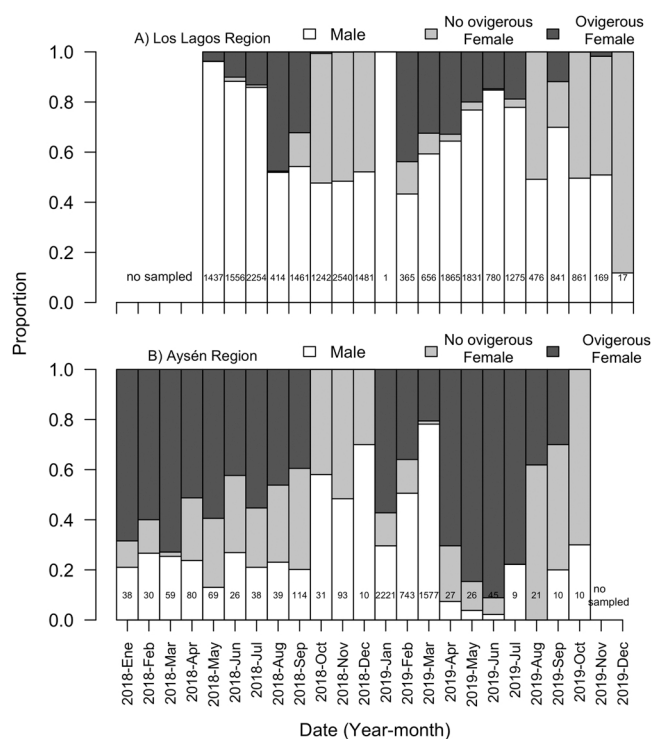

Fig. 3. Monthly ratio of males, non-ovigerous females and ovigerous females in A) Los Lagos region, B) Aysén region. Numbers at the bottom of the bar show the total sampled specimens.

stage 2 between May and July, and in stage 3 between August and September (Fig. 4).

3.1. Year class composition

The model selection for year class composition using length frequency data is shown in the appendix (Figs. A1–A6). For females captured in Los Lagos, a range of between 50 and 118 mm was observed in both years studied, with a mode of ~83 mm LC. The most informative model enabled the identification of 5 year classes in both years studied, although one year class (mean= 83.3 mm LC) accounted for 89 % of the sampled catch in 2019 (Fig. 5A and C, Table 1). For the catches in Aysén, only the data from 2019 was analyzed, since too few records were obtained in 2018 to apply the model. The size range of females captured in Aysén was 40–150 mm LC and the most informative model identified six year classes, three of which were larger (mean = 77 [14.6 %], 100 [49.7 %] and 113 [30.7 %] mm LC) (Table 1, Fig. 5E).

For males captured in Los Lagos in 2018 and 2019 and in Aysén in 2019, the model with lesser AIC values was composed of 5 year classes, although differences in AIC between 5 and 6 year classes in 2019 were less than two units (Fig. A4, Appendix). Furthermore, the composition of year classes identified between both years and regions differed (Table 2, Fig. 5B, D and F). In males recorded in Los Lagos, a distribution mode shift was observed from ~95 mm LC in 2018–83 mm LC in 2019, with a decrease from ~31 % to ~20 % of the year class proportion that sustain the fishery (Table 2). In Aysén, the analysis identified 5 major year classes, with a more homogeneous representation of males between ~70 and 150 mm LC (Fig. 5F, Table 2).

3.2. Size at functional reproduction

In Los Lagos, where the SKC fishery is older and more intense (Molinet et al., 2020, Fig. 2), the best working model was the one that included 5 parameters. The inflection point was located at 64.2 mm, below the midpoint, implying a value of asymmetry of 0.018 (Fig. 6A,
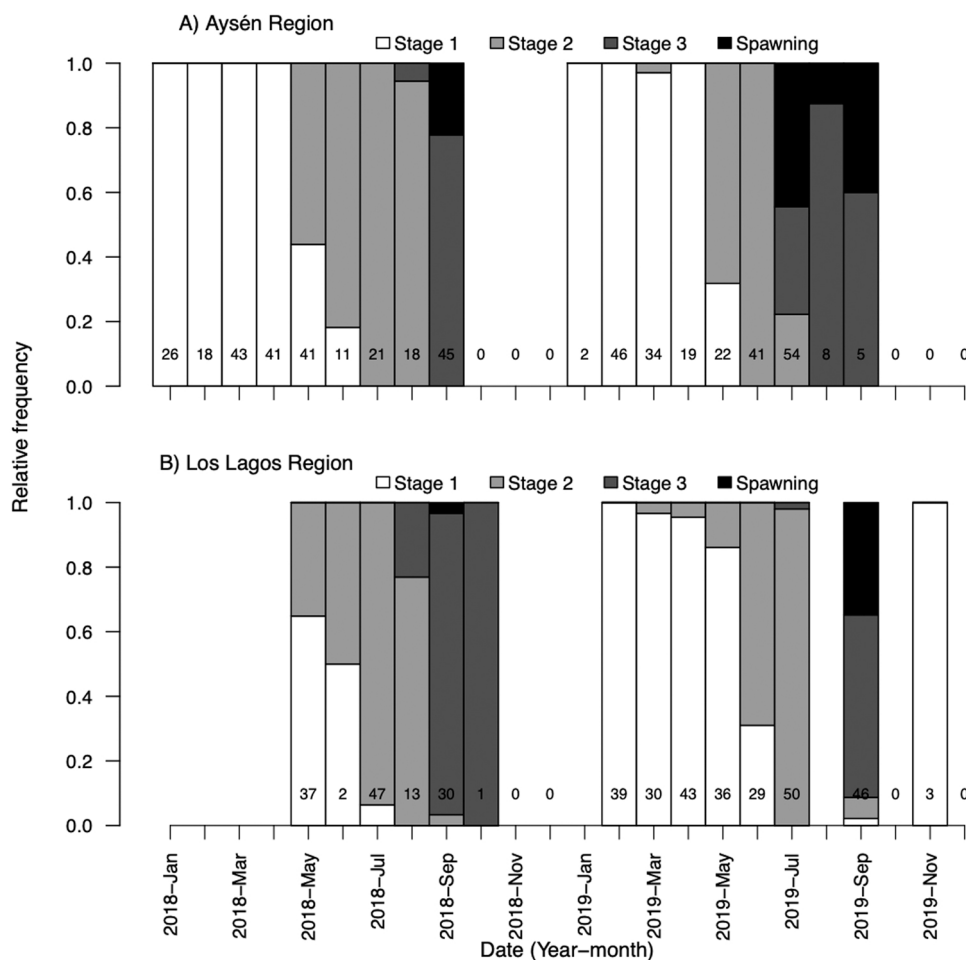
Fig. 4. Maturity stage of eggs sampled on a monthly basis in A) the Los Lagos and B) Aysén regions, between 2018 and 2019. The ratio of females spawning is included, to differentiate from stage 3 eggs. Numbers at the bottom of each bar indicate the total ovigerous females sampled.

Table 3). Furthermore, the asymptote (or saturation) only reached 87 %, while the slope was steep (1.21 1/mm) (Fig. 6A). It was also observed that the ratio of functionally reproductive females tended to decrease at sizes larger than 90 mm LC, which coincided with the absence of males > 105 mm LC, although with a higher ratio of males than females in the mating period studied (January to March 2019) (Fig. 6B).

Conversely, in Aysén, where the fishery is newer, the best model included four parameters, with a 100 % saturation of functionally mature females (Fig. 6C, Table 3). Interestingly, female SKC showed a symmetric ogive curve (midpoint (x50) =inflection point) in the selected period. Female crabs larger than 100 mm CL reached complete functional reproduction and attained 50 % maturity at 86 mm CL (Fig. 6C). This coincided with: i) a decrease in the ratio of male/females between approximately 60 and 110 mm LC; and ii) an increase in male/ female ratio in individuals > 110 mm (Fig. 6D).

For grouped data (Los Lagos and Aysén, 2019), the best working model was the one that included 5 parameters. The inflection point was located at 84.7 mm, below the midpoint, implying a value of asymmetry of 0.02 (Fig. 6E, Table 3). The asymptote reached 100 %, while the slope was moderate (Fig. 6E). It was observed that the ratio of functionally reproductive females tended to increase almost linearly between the minimum values and ~90 mm LC.

None of the three 95 % confidence intervals for CL_{50} overlapped and the highest goodness of fit was obtained with the model with Aysén region data and the lowest with Los Lagos region data (Table 3). This shows that there are significant differences in maturity progression at size in females of the two regions. The data and model fit from Los Lagos

region show some pathological features because of not observing sufficient numbers of small immature females. Another result is that only the model for Aysén data produced standard error for all its parameters. In the other two cases, involving data from Los Lagos region, numerical optimization in R failed to calculate some standard errors. All these results together allow to conclude that there are differences between the two regions in the maturity process and that Los Lagos region is a special case.

3.3. Fecundity

The number of eggs was estimated in 336 females captured in Los Lagos and in 363 females captured in Aysén, with a range of between ~1000 and 38,000 eggs/female (Fig. 7). Carapace length and egg developmental stages contributed to the most informative model in terms of explaining the observed fecundity (Table 4), therefore, larger females carried out more eggs, while females with eggs in stage 1 and 2 carried out more eggs than females in stage 3 (Fig. 7). The region and year variables did not contribute to improving fecundity predictions, thus the lower fecundity in Los Lagos (8876 and 6584 eggs/female in stage 1–2 and 3 respectively) compared with fecundity in Aysén (11792 and 9159 eggs/female in stage 1–2 and 3, respectively) can be explained by the smaller size of females recorded therein (Figs. 5 and 7).

4. Discussion

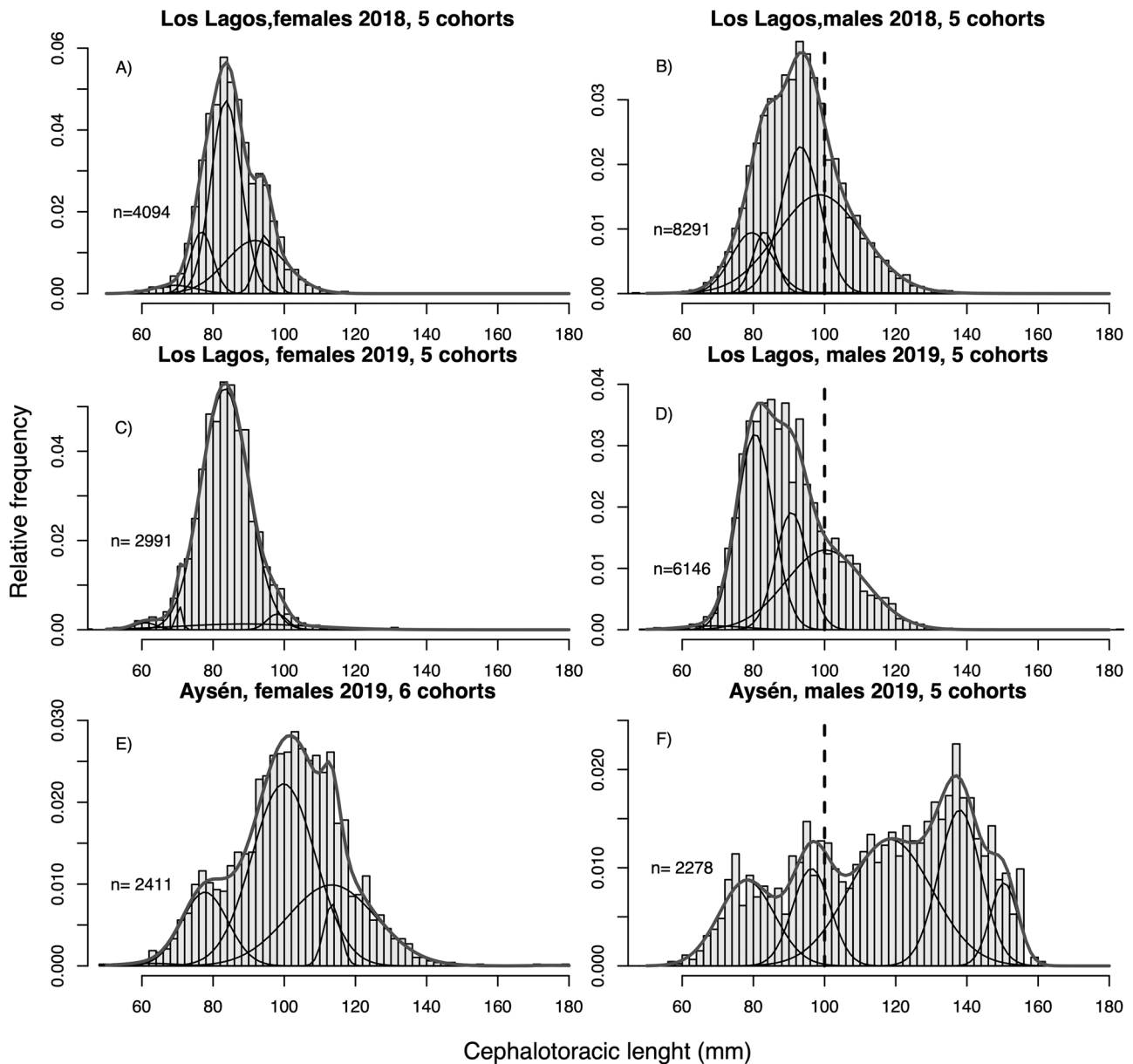The contrasting differences observed in the size distribution of male

Fig. 5. Size distribution (bars) and fitted mixture models (grey dashed line) of *L. santolla* females (A, C, E) and males (B, D, F) collected with traps in the Los Lagos and Aysén regions, between 2018 and 2019. Each normal distribution (black dashed lines) represents one cohort. Vertical dashed lines show the minimum legal size in males. n indicates the sample size.

and female *L. santolla* caught in the Los Lagos and Aysén regions resulted in distinct functional reproduction patterns of the females from each region, as well as differential fecundity between regions due to the size differences of females. A response through the Richards function was observed, most likely caused by the different fishing histories and intensities between the regions. In the more pristine conditions of the *L. santolla* fishery in Aysén the rate of growth of functional reproduction of females with length is accurately represented by a parabola of symmetrical shape ($\gamma = 1$) while in the more exploited region of Los Lagos the shape of the parabola becomes asymmetrical, with maximum at smaller lengths ($\gamma = 0.018$). On the other hand, the combined analysis of SFR females data from both stocks masked the decrease in α in the intensively exploited stock, smoothed the slope but kept the symmetry < 1. Therefore, caution is suggested in the spatial and/or temporal pooling of SFR data and their subsequent interpretation.

The observed size truncation in males and females SKC from Los Lagos is coincident with an upswing of its fishery in this region reported

by Molinet et al. (2020) and data from Fig. 2, and could affect the interpretation of cohorts estimates in this region. Also, Lovrich and Tapella (2014) and Vinuesa (1984) proposed than males < 100 mm CL (which correspond to the largest proportion of males SKC recorded in Los Lagos region) could molt twice a year, making more difficult the interpretation of these results and, therefore, we suggest that further studies are required for a better understanding.

Males are known to be larger than females among Lithodidae and this size difference only increases as they grow (Kruse, 1993; Webb, 2014; Lovrich, 2002; Lovrich and Vinuesa, 2016; Lovrich and Tapella, 2014). In contrast, significant fishing efforts that target larger male crabs produce selection pressures on faster growing individuals (Baker et al., 2022; Kruse, 1993; Mullowney and Baker, 2021) and can even affect size at maturity. In this regard, Sato et al., (2005, 2007) reported that in *Paralithodes brevipes*, the removal of larger males decreases the probability of encounters between larger females and functionally reproductive males. It was observed in this work that the ratio of males increases

Table 1
Parameters derived from cohort analysis in all the females sampled. * Shows the proportions estimated in last position in each adjustment made (number of cohorts) in ADMB, and therefore these result from the subtraction of the proportions of the cohorts previously estimated, minus 1.

	Los Lagos Region				Aysén Region	
Parameter	Female 2018	standard error	Female 2019	standard error	Female 2019	standard error
Proportion 1	0.030	0.000	0.012	0.005	0.006	0.031
Proportion 2	0.119	0.149	0.011	0.005	0.146	0.080
Proportion 3	0.498*		0.891	0.021	0.497	0.000
Proportion 4	0.268	0.141	0.060*		0.043	0.022
Proportion 5	0.085	0.033	0.025	0.015	0.307	0.068
Proportion 6					0.001*	
Mean 1	69.2	1.17	61.0	1.12	62.4	36.10
Mean 2	76.8	2.09	70.5	0.37	77.7	1.57
Mean 3	83.7	1.35	83.3	0.21	99.8	1.14
Mean 4	91.8	3.50	89.1	2.63	113.4	0.76
Mean 5	94.4	0.45	98.0	1.25	113.3	3.62
Mean 6					175.0	3.19
St. deviation 1	6.0	0.82	3.1	1.07	7.7	10.16
St. deviation 2	3.1	0.87	0.8	0.25	6.5	2.55
St. deviation 3	4.2	0.94	6.6	0.23	8.9	1.42
St. deviation 4	8.2	0.48	18.3	1.70	2.3	0.70
St. deviation 5	2.4	0.92	2.9	1.20	12.4	1.49
St. deviation 6					4.5	2.26

Table 2
Parameters derived from cohort analysis in males.

	Los Lagos Region				Aysén Region	
	Male 2018	standard error	Male 2019	standard error	Male 2019	standard error
Proportion 1	0.136	0.110	0.014	0.025	0.16971	0.015
Proportion 2	0.078	0.066	0.407	0.000	0.13191	0.035
Proportion 3	0.315	0.074	0.216	0.085	0.37864	0.084
Proportion 4*	0.01*		0.363*		0.082085	0.000
Proportion 5	0.460	0.093	0.001	0.000	0.2377*	
Mean 1	79.563	3.81	69.0	16.02	78.132	1.0
Mean 2	83.103	0.81	80.5	0.49	96.309	0.8
Mean 3	93.242	0.84	90.7	0.59	118.47	2.1
Mean 4	97.072	4.37	100.3	3.13	150.41	0.5
Mean 5	98.613	2.07	146.0	31.11	137.98	0.7
St. deviation 1	5.7597	1.46	8.9	5.32	7.7825	0.6
St. deviation 2	3.2308	0.83	5.1	0.17	5.3123	0.8
St. deviation 3	5.5296	0.69	4.5	0.82	11.73	2.6
St. deviation 4	25.512	5.56	11.1	1.19	3.8666	0.3
St. deviation 5	12.01	0.69	30.6	20.68	5.9701	0.8

with increasing CL relative to females, although marked differences were noted between the two regions (Fig. 6B and D). The more intensively exploited Los Lagos region has an almost vertical upward trend (from ~95 mm) that rapidly reaches a maximum ~105 mm CL, while the less intensively exploited Aysén region shows a less accelerated upward ratio of males, from ~110 mm CL to a maximum of approximately 140 mm CL.

Therefore, we propose that in the less exploited Aysén fishery, the value asymmetry = 1 for functional reproduction in females, reflects a situation of balance in relation to the availability of males (in size and ratio) for the reproductive success of the population. In turn, a value of asymmetry < 1 could be used as an indicator of sperm limitation resulting from the degree of development of the fishery and the corresponding cumulative removal of larger sized males. Furthermore, it could be an indicator of the first phase of the SKC fishery proposed by Di Salvatore et al. (2021), who suggest that the exclusive extraction of males (of larger sizes) results in sperm limitation, following Sato (2012) and Ogburn (2019). Currently, there is sharp contrast between the assymetry parameter between Los Lagos and Aysén, with the former presenting an 82 % reduction with respect to the latter. Further research is needed to estimate intermediate drops in assymetry. The accumulation of estimates could point to the definition of critical values indicative of a qualitative change in the condition of crustacean males-only

fisheries such as the fishery for the SKC.

Coincidentally, the size at which the male/female ratio begins to increase in the less exploited region (110 mm) of Aysén corresponds to the minimum legal size in Argentina, where the fishery shows improved reproductive status indicators (at least in the Golfo San Jorge) (Di Salvatore et al., 2021) compared to the Los Lagos fishery in this study. This suggests that the minimum size of 100 mm LC in the area studied in this research should be increased to at least 110 mm LC.

The saturation parameter (α) of the functional reproduction of females is substantially less than 1 in Los Lagos. We suggest that the α value could be associated with the second phase in the exploitation of the SKC fishery proposed by Di Salvatore et al. (2021), which is evidenced by the occurrence of a low proportion of ovigerous females. A value of α less than 0.99 should be avoided and considered a warning signal. Accordingly, the estimate from Los Lagos (0.87) could be considered as clearly threatening reproductive success of the population. The case of the inland sea in Los Lagos, where only 24–40 % of ovigerous females (relative to females >70 mm) were recorded between 2014 and 2017 (Molinet et al., 2020) may indicate a serious overfished condition.

Spatial variations in the SFR of female crabs have been observed, for example in *Chionoecetes opilio* and *Paralithodes camtschaticus* in the northern hemisphere, and attributed to temperature variations
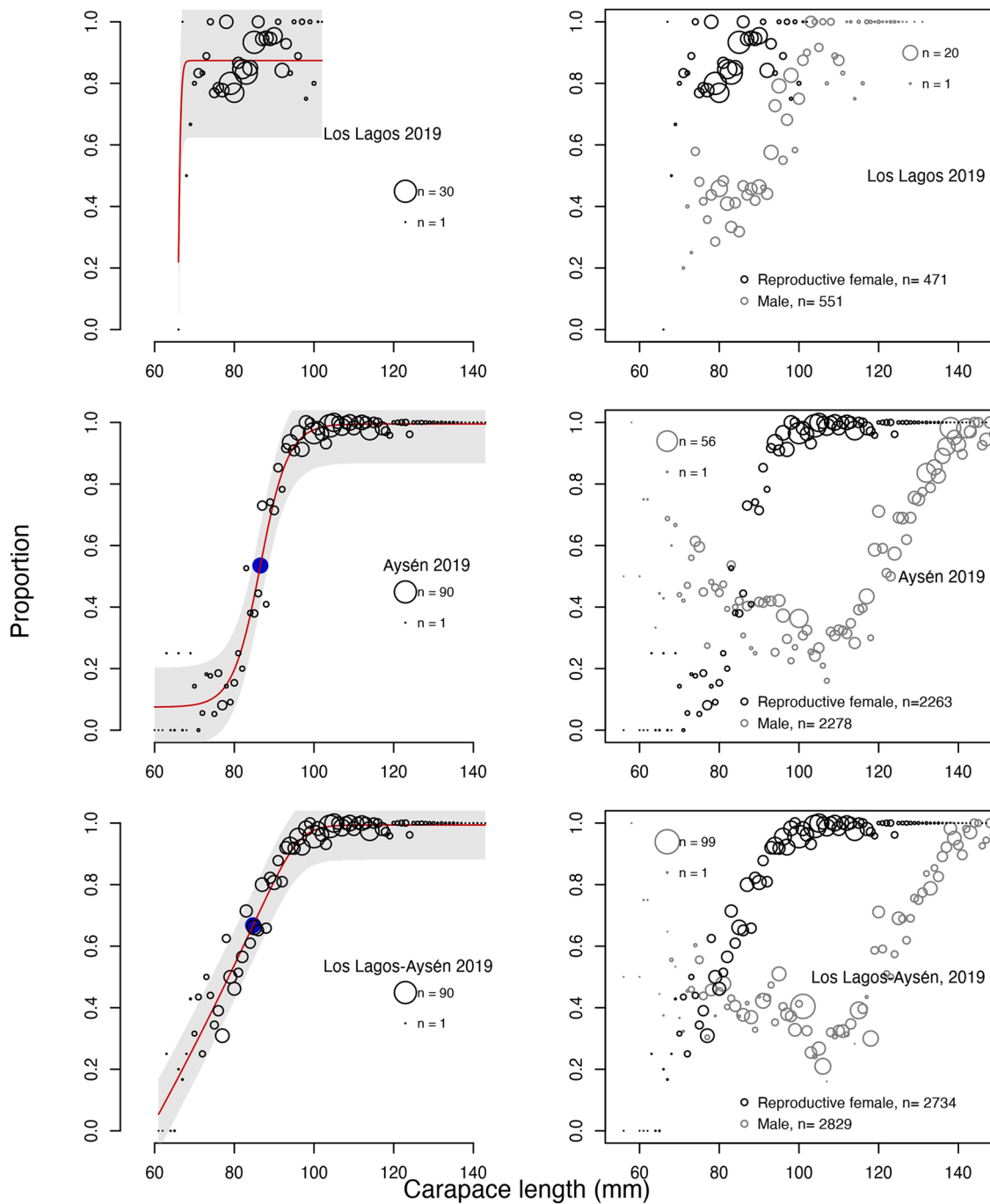
Fig. 6. A) Maturity ogive of female southern king crab in the Los Lagos (heavy fishing pressure), C) Aysén (low fishing pressure) regions of southern Chile, and E) Aysén and Lagos data grouped. The blue dot is the inflection point. Ratio of males and females by length category in B) the Los Lagos, D) Aysén regions of southern Chile, and F) Aysén and Lagos data grouped. Size of circles show the observations frequency (n maximum and n minimum) at intervals of 1 mm carapace length for reproductive females (A, C, and E) and males (B, D, F).

(Orensanz et al., 2007, Jewett et al., 1985). However, Olson et al. (2018) found that the variables of depth, temperature and fishing history had no effect on the maturity of *Lithodes aequispina*. In this study area, a relatively homogeneous bottom temperature has been reported between Los Lagos and Aysén (Rodríguez-Villegas et al., 2021), while the fishing depth in both areas has also been similar. Consequently, it appears that fishing intensity is the most important variable in explaining the variations observed between the regions studied, although in the case of *L. santolla* there are no systematic studies into geographic variations in sexual maturity.

One of the main consequences of highly intense fishing in Los Lagos

would be the lower fecundity of *L. santolla* recorded in our study, which is explained by the smaller average size of the females collected. Furthermore, it coincides with the relationships between size and fecundity reported by other authors (Díaz et al., 2021; Militelli et al., 2019; Varisco et al., 2019). In addition, higher fishing intensity is expected to elevate the frequency in which ovigerous females are caught and discarded and, thus, increase the likelihood of egg loss because of handling, as reported by Di Salvatore et al. (2019) and Gowland-Sainz et al. (2015), although the percent loss seems high compared to red king crab *P. camtschaticus* (Swiney et al., 2012).

The narrow size distribution observed in females collected in Los

Table 3

Results of the generalized 4-parameter logistic ogive model applied (Giraldo et al., 2002) to study female size at functional reproduction. Goodness of fit is the correlation between observed and predicted values. CL50 is the size at 50 % maturity. NE, not estimated.

Model	Parameters	Standard error [95 % Confidence interval]
Los Lagos	α = 0.874	0.11
	β = 1.21 1/mm	NE
	λ = 66.17 mm	NE
	γ = 0.018	0.009
	Goodness of fit= 0.570	[66.1, 66.7]
	CL50 = 66.3 mm	
Aysén	α = 0.99	0.10
	β = 0.12 1/mm	0.13
	λ = 86.5 mm	4.18
	γ = 1	[84.1, 87.9]
	Goodness of fit= 0.974	
	CL50 = 86.0 mm	
Los Lagos and Aysén grouped	α = 0.99	0.11
	β = 0.15 1/mm	0.58
	λ = 95.8 mm	10.4
	γ = 0.02	NE
	Goodness of fit= 0.967	[74.5, 82.5]
	CL50 = 78.6 mm	

Lagos shows a truncation of sizes greater than 100 mm LC. This suggest the following: i) the probable removal of females despite regulations against it, as observed by Campodónico et al. (1974) in the southern-most Magallanes region; ii) an eventual increase in mortality due to the discard frequency, given the intensive nature of the fishery (Gowland-Sainz et al., 2015; Di Salvatore et al., 2019); and iii) selective male culling may increase female mortality during molting, since there are not enough males in the population to participate in the precopulatory

Table 4

Results of the application of a general linear, negative binomial model to evaluate the effect of the variables: carapace length, egg development stage, year and region, on fecundity, and the multiple comparisons of levels of the variable stage of egg development.

| Response: Fecundity			
Predictors	Likelihood ratio (Chisq)	Degree of freedom	Probability (>Chisq)
Carapace length	226.269	1	< 2e-16
Egg development stage	83.792	2	< 2e-16
Year	0.629	1	0.4278
Region	1.232	1	0.267
Multiple comparisons of levels of the variable egg development stage			
Linear Hypotheses:	Estimate	Std. Error	z value	Probability (>|z|)
Stage 2–1 == 0	-0.07153	0.03699	-1.934	0.128
Stage 3–1 == 0	-0.40687	0.04359	-9.333	< 0.001
Stage 3–2 == 0	-0.33534	0.04497	-7.458	< 0.001
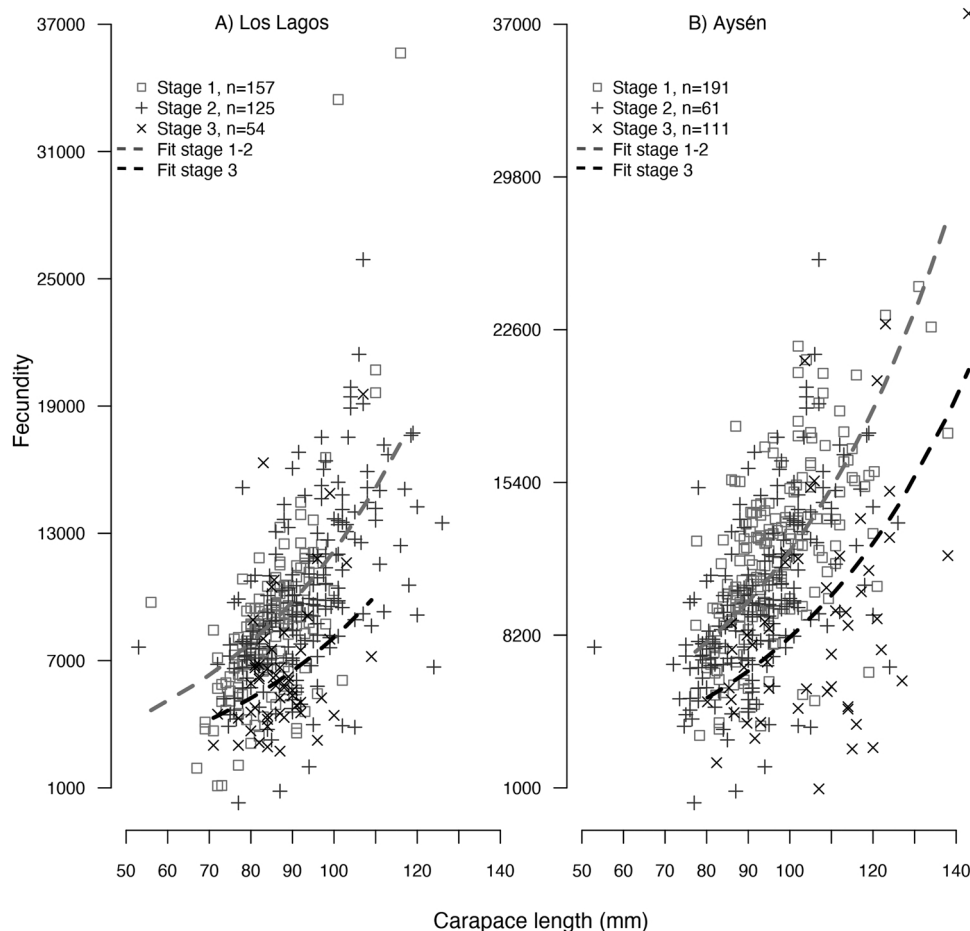
Fig. 7. Observed (points) and predicted (lines, based on model from Table 4) fecundity of *L. santolla* in the Los Lagos and Aysén regions at egg development stages 1, 2 and 3. n indicates the number of females sampled per stage.

embrace and protect females from predators (Di Salvatore et al., 2021).

5. Conclusions

We study the female functional reproduction ogive in two stocks of SKC in southern Chile. The northern more intensively exploited of Los Lagos region stock shows size truncation in both males and females, in addition to diminished fecundity. In contrast, the southern less exploited stock of Aysén region shows a robust size distribution in both male and female components. The four parameters Richards Function for the maturity ogive in the less exploited stocks is symmetrical ($\gamma = 1$, inflection point=midpoint), therefore reflects a balanced male availability. On the other hand, in the intensively fished Los Lagos fishery, γ is 0.018 and $\alpha = 87$, suggesting sperm limitation, and a deteriorated condition of the fishery. The symmetric shape of the logistic curve, widely assumed when fitting maturity ogives in fished populations (Jewett et al., 1985; Webb, 2014; Firpo et al., 2017; Olson et al., 2018; Di Salvatore et al., 2021), needs to be replace with more complex logistic models. We propose that the asymmetry and asymptote of the Richards Function of female SFR could be used as an indicator of reproductive health in males-only crustacean fisheries.

CRediT authorship contribution statement

All authors contributed to the study conception and design, Data collection was performed by: Carlos Molinet, Katherine Espinoza, Manuel Diaz, Patricio Díaz, Thamara Matamala, José Valenzuela, Yohnatan Jaramillo, Sampling and fecundity were performed by: Paulina Gebauer, Oscar de Lázaro, Thamara Matamala, Katherine Espinoza, Daniela Uribe, Data analysis and modelling were performed by: Carlos Molinet, Rubén Roa-Ureta, Jorge Henríquez, The first draft of the manuscript was written by: Carlos Molinet, Rubén Roa-Ureta, Paulina Gebauer, Andrés Olguín and Kurt Paschke. All authors read and approved the final manuscript."

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

We declare that the submission to Ices Journal of Marine Science implies that materials described in the manuscript, including all relevant raw data, will be freely available to any researcher wishing to use them for non-commercial purposes, without breaching participant confidentiality.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2022.106522.

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