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Egg loss in females of two lithodid species following different return-to-the-water protocols

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ABSTRACT

Coastal waters of the southern tip of South America have sustained a mixed king crab fishery since the 1930s, with two target species: the southern king crab *Lithodes santolla* and the stone crab *Paralomis granulosa*. The fisheries are managed with the so-called 3S rule (Sex, Season, and Size) and females must be returned to the water. In king crabs, fecundity can be reduced by several mechanisms, but those related to fishing activities are only partially known. In this article, we tested experimentally whether egg loss is caused by the return of *L. santolla* and *P. granulosa* ovigerous females to the water. To do so, we performed experiments for each species with a 3 × 2 different return-to-the-water conditions: free fall, ramp, or a no-fall (control), with or without previous aerial exposure of females. Our experiments demonstrate that free fall impacts, similar to the normal practice in the fishery of the Beagle Channel, result in egg loss in both the species. Female *L. santolla* lost more eggs if females were exposed to air prior to the dropping. Also, eggs with more developed embryos were likely to be lost as a result of tumbling. In both the species, the use of a ramp for the returning of crabs to water caused an egg loss similar to those of the experimental controls. In *P. granulosa* fecundity from three areas with different fishing effort suggest that the return of females to the water may be a negative effect that could be detected at a population level. To our knowledge, this is the first study that demonstrates the egg loss of female crabs returned to the water in a fishery.

1. Introduction

In the southern tip of South America, a mixed crab fishery has developed since the 1930s. The two target species are the southern king crab *Lithodes santolla* and the false southern king crab or stone crab *Paralomis granulosa*. Both species are frequently captured in the same trap. *L. santolla* is bigger and its meat yield higher than *P. granulosa* and therefore *L. santolla* has been preferred as the target species. In Chile a fishery for *L. santolla* developed near Chiloé island (44°S) and another mixed fishery extends south of 49°S, mainly inside the numerous fjords and channels, including the Straits of Magellan and the Cape Horn area (Fig. 1). Landings of the Chilean fisheries are approximately 3000 t per year for *P. granulosa* and 4000 t per year for *L. santolla*. Argentine fisheries are less extensive geographically and hence less productive. The king crab fishery was first developed in the Beagle Channel with maximum landings of 300 and 400 t of *L. santolla* and *P. granulosa* respectively, but currently yields of *L. santolla* have cropped less than 80 t per year (Lovrich and Tapella, 2014). The current major Argentine fishery is based off the Golfo San Jorge (ca. 46°S, Fig. 1) targeting exclusively for *L. santolla* with landings of ca. 3000 t per year, during the last 2 years.

In Argentina, fisheries are managed by using the ‘3S’ rule (Sex, Season, and Size) where all females must be returned to the water. There is also a closed season and a legal minimum size of 110 mm and 80 mm of carapace length (CL) for *L. santolla* and *P. granulosa* males respectively. For decades the closed season in the Beagle Channel was November and December to protect female molting, mating and eventually the production of offspring. Female *L. santolla* attain larger sizes (140 mm CL) and reproduce once a year compared to the biennial reproductive cycle of *P. granulosa* (maximum size of 90 mm CL), resulting in *L. santolla* having much higher egg production than that of *P. granulosa* (Lovrich and Vinuesa, 1999). In both species, the abdomen completely covers the egg mass during all of the embryogenesis period. In all the South American fisheries except in continental shelf off the Golfo San Jorge, crab

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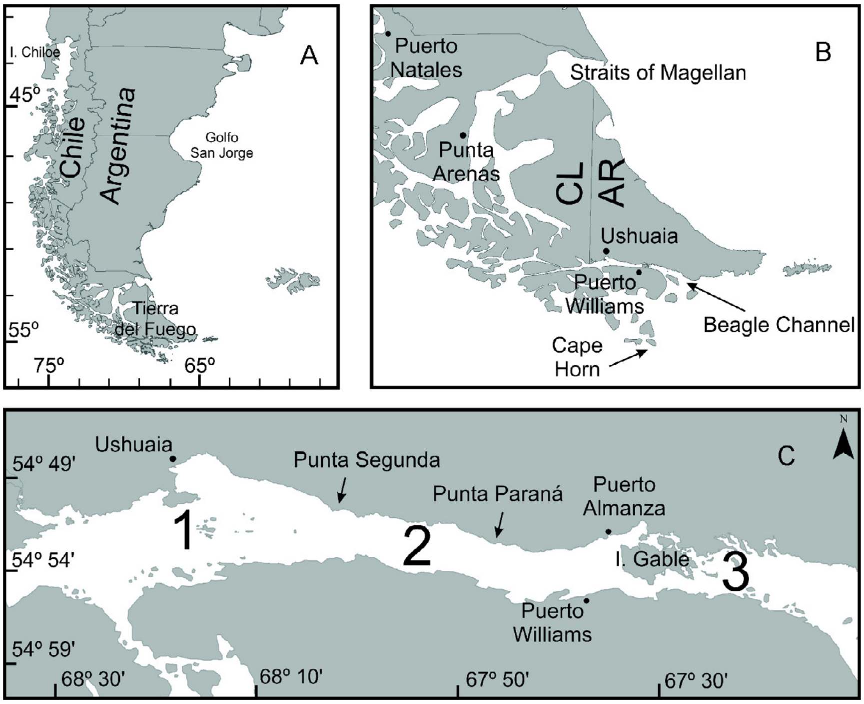

Fig. 1. Study area. Map of the southern tip of South America (A and B) and the Beagle Channel (C), with areas of different fishing pressure shown. References 1: No fishing, 2: Moderate fishing effort and 3: High fishing effort.

fishing is conducted with small boats of a maximum of 15 m length. The common practice of fishing is to empty all of the 10 truncated conical traps that constitute a fishing line on deck, to then change the bait and to redeploy the traps. Fishers then sort out the capture, retain the legal males, and return undersized males and all females to the water. Crabs spend between 0.2 and 2 h on deck exposed to the air (annual average temperature range 1–10 °C) and are returned to the water in different fashions, somewhat violent. When catches are small, animals are picked up by hand from the deck and twirled to the water. In contrast, when catches are large crabs to be discarded are dragged along the deck to the freeboard or shoveled to the water. In all cases crabs fell into the water from a height of at least 1.5 m.

Previous studies have focused on handling king crabs on deck, which can be one of the causes of injury and mortality in captured sublegal animals returned to the sea during the discarding process, (reviewed by Stoner, 2012; Stevens, 2014b). Injuries can range from onboard imperceptible physiological trauma to broken carapace or limbs (e.g., Bergmann et al., 2001; Stoner, 2012). Handling on deck and air exposure seems to be the most important mortality factors associated with crab fishing (Zhou and Shirley, 1995; Warrenchuk and Shirley, 2002). King crabs captured as bycatch of the toothfish fishery off South Georgia (ca. 55°S; 42°W) have differential mortality depending on how pots are emptied: crabs discharged down on a conveyor belt have a higher survival rate than those falling down a vertical chute (Purves et al., 2003). Extreme conditions from high latitudes, such as low temperatures and strong winds increasing the windchill, and long exposures to this environment also reduce growth, produce incomplete ecdysis, increase crab limb-loss, and mortality (Carls and O'Clair, 1989). Furthermore, crabs may become more vulnerable to predation due to impaired mobility after being exposed to air on deck and returning to water (Warrenchuk and Shirley, 2002).

In crabs, fecundity can be reduced by several reasons, but those related to fishing activities are only partially known. Predation is one of the natural causes of egg loss (Shields et al., 1989; Kuris et al., 1991). Nemerteans are the main predators of king crabs eggs of the northern hemisphere, to the point of being responsible for the loss of an entire year class in the population of *Paralithodes camtschaticus* (cf. Shields et al., 1989; Kuris et al., 1991). However, in the southern Hemisphere, there are no records of any king crab egg predators (Lovrich and Tapella, 2014). Fecundity can be variable through the years, seasons, and locations (Swiney et al., 2010; Hjelset et al., 2012; Swiney et al., 2012; Stevens, 2014a). Another source of reduction in fecundity is the male-only fishing. This practice can cause sperm limitation derived from a biased sex ratio towards females, which in turn may result in a low proportion of ovigerous females, individuals with partial clutches or low fertilization rate because fewer females have access to an appropriate sized male for mating (Paul and Paul, 1989; Sato et al., 2007; Van Son and Thiel, 2007). In lithodids, differences in fecundity during the long brooding period, between the recently extruded eggs and those near to hatch, was attributed to egg loss or brood mortality (see reviews by Kuris, 1991; Stevens, 2014a). For example egg loss account for 8–13% in *L. aequispina* (Jewett et al., 1985) and 14% in *P. granulosa* (Lovrich and Vinuesa, 1993), but the cause was never explored. In brachyuran crabs egg losses due to ventilation are substantial and are between 10% and 13% throughout the brooding period (Fernández et al., 2000). Egg losses were also verified at the time of hatching that eventually diminishes the actual birth rate and the consequent contribution of new individuals to the population, as for example it occurs in the hermit crab *Pagurus comptus* (Lovrich and Thatje, 2006) or *L. santolla* (Tapella pers. obs.).

Study or monitoring of fecundity is essential in a king crab fishery because it is indicative of the reproductive health of the population, since the presence of eggs is the direct evidence of successful mating during the last reproductive time that offspring for the season (Orensanz et al., 1998). The spatial and temporal variation in the proportion of ovigerous females can provide direct indication of the reproductive potential of the fished population and allows early detection of problems associated with fishing extraction that may have occurred during the previous reproductive season. Hence identifying the potential sources of fecundity reduction is important. In this article we tested experimentally egg loss as an effect of the return of *L. santolla* and *P. granulosa* ovigerous females to the water in two different conditions: free fall and through a ramp, and with or without previous aerial exposure. Furthermore, we compared experimentally the egg losses at two different times during the embryogenesis of *L. santolla*. In order to test the effect of female return on the fecundity of *P. granulosa*, we additionally compared the fecundity from three areas of the Beagle Channel with different fishing effort and presumably different return rates.

2. Material and methods

2.1. Tumbling experiments

Ovigerous females were captured in the Beagle Channel (Fig. 1) by means of commercial traps. Crabs were transported to the laboratory, placed in ample boxes to avoid overcrowding and without water. Air exposure is a normal practice in this fishery and no physiological damage occurs in animals during the first 6 h of air exposure (Romero et al., 2011). The time elapsed between the capture in field and re-submersion in the laboratory never exceeded 3 h. Females were kept in individual 25-l containers set up in a chilled seawater recirculation system at 6° or 8 °C in May and August, respectively. Water quality was maintained with mechanical (50 μm) and biological filters, and a UV-sterilizer. Water quality was checked every 3 days and pH, salinity, nitrite and nitrate levels were kept at 8.4 ± 0.3, 31 ± 1‰, $<0.3\,\mathrm{mg\,l^{-1}}$ and $<12.5\,\mathrm{mg\,l^{-1}}$ respectively. Crabs were fed *ad libitum* three times a week with squid mantle (*Ilex* spp.). Since king crab females tend to lose eggs in captivity (Matsuura and Takeshita, 1985), the base of the individual container was covered by a mesh of 10 mm separated 1 cm from the bottom with the aim of impeding females eating or damaging the potential detached eggs. All crabs went through an acclimation period of 4 days, the time that the egg loss was minimum, i.e., <5 lost eggs per female. During this period all containers were checked daily, cleaned, and detached eggs were removed and enumerated.

After the acclimation period, we evaluated the egg loss at two different return-to-the-water conditions performing respective experiments for each species. The experimental design consisted in a 3 × 2 different returning conditions: free fall, ramp, or a no-fall (as a control), with or without previous aerial exposure of females. In *P. granulosa* the experiment was performed once during May, with females carrying eggs in diapause stage, i.e., embryos with no ocular pigment (Lovrich and Vinuesa, 1993). To further test whether the proximity of hatching influences the egg loss in *L. santolla*, the experiment was repeated twice: one in June and again in August. Thus, eggs had 6 and 8 months of incubation and were in stages VII and VIII according to Vinuesa (1987), respectively.

Six females of each species were randomly assigned to each of the 36 combinations. Each individual female was dropped 3 consecutive times and returned to its own individual 25-l tank. We chose this number of repetitions to simulate the falling suffered when the trap is emptied on the deck, the kicking or violent classification of animals to search for legal ones, and finally the discard to the water itself. In this way we could recover from the water tank all the lost eggs because of impact, which otherwise could have been lost and difficult to enumerate. Free-fall was the tumbling from a height of 2.5 m into a 170-l tank filled with seawater (0.5 m water depth). Dropping was done in the way that females always fell in a ventral position. Immediately after the animal touched the tank bottom, the female was removed and the drop was immediately repeated. The fall through a ramp was done through a PVC hose of 0.2 m diameter, of 5.6 m length, and positioned at 2.5 m height, with the end of the hose leading to the 170-l tank, so that the angle of its slope with the horizontal plane was ca. 42°. In the no-fall treatment (control), female crabs were always left in their acclimation 25-l tanks. For the aerial exposure of crabs, water was siphoned from the acclimation tanks and covered with its plastic lid. Depending on the month when the experiment was done, animals were kept at 6° or 8 °C for 3 h previous to the drop treatment.

After the 3 tumbling trials for each female and animals returned to their individual tanks, all the detached eggs were removed from the experimental container by siphoning and enumerated (i.e., number of lost eggs at time 0). On a daily basis, all the eggs lost in the individual tanks were removed and counted. The total of detached eggs was calculated as the sum of eggs lost at the tumbling experiment until the end of the experiment, which was established when the egg losses were on average <5 eggs per day. Then, females were dissected and their egg masses individually preserved in 5% seawater formaline. Fecundity was calculated as the sum of eggs lost during acclimation, drop trials, post-drop period, and those eggs still attached to the pleopods after dissection. The number of eggs attached to pleopods was calculated by the gravimetric method (described by Lovrich and Vinuesa, 1993), by taking three subsamples of the whole brood.

2.2. Fecundity from field samples

To scrutinize in the field the potential effect of the fishery on the fecundity, we obtained samples of *P. granulosa* from three sites with different fishing pressure: null, moderate and high (Figure 1). The area with no fishing is a section of the Beagle Channel (between 68°2.0′W, i.e. Punta Segunda, and 68°35.6′W) which in 1994 was closed to fishing and has not reopened because of lack of signs of population recovery, i.e., high yields, high proportion of both ovigerous females and legal males (Lovrich and Tapella, 2014). Since currently there are no formal rules to direct differential fishing effort along the Argentine sector of the Beagle Channel, the other two areas were defined from an *ad hoc* survey performed among fishers working in the area. The adjacent section of the Beagle Channel, eastwards to the closed fishing area, between Punta Segunda and Punta Paraná (Fig. 1) was considered as having moderate fishing effort. The area of high fishing effort was between Punta Paraná and east to Isla Gable, near Puerto Almanza, where the artisanal fleet concentrates its activities. As for *L. santolla* we obtained samples at two different periods (May and August) within the area with moderate fishing pressure. This sampling permitted the comparison of the fecundity in an exploited area after 3 months of fishing activity. All crabs were obtained from commercial traps as described above.

2.3. Statistical analyses

2.3.1. Tumbling experiment

The effects of the aerial exposure and the returning condition on the number of detached eggs (DE) were tested by generalized linear models (GLM). Since DE data were overdispersed and the assumption of a Poisson error distribution could not be accomplished, we chose a negative binomial error distribution for the data (Crawley, 2012). This overdispersion of DE data and its non-normal distribution nor homoscedasticity hampered the use of a traditional factorial design such as an ANOVA. We also considered as an explanatory variable the original fecundity of the female, and for *L. santolla* the month in which each experiment was performed.

Model selection was based on information-theoretic procedures (Burnham and Anderson, 2002). We considered models with all the possible combinations of explanatory variables for the egg loss. The result was 16 and 8 candidate models for *L. santolla* and *P. granulosa*, respectively. The best models were the base of the conclusions. The Akaike's Information Criterion corrected for small sample size

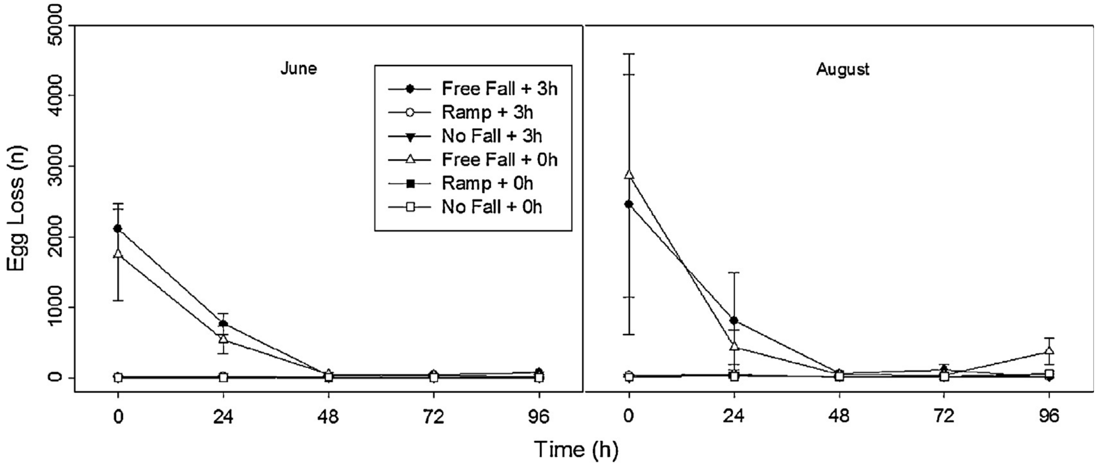

Fig. 2. *Lithodes santolla*. Average daily egg loss ± standard deviation for each combination of returning condition and aerial exposure. Left and right panels show the experiment performed at two different stages of egg brooding, in June and August, respectively.

(AICc) was calculated for each model following the information theoretic procedures, to evaluate the models that best fitted the data. Potential models were ranked using the ΔAICc i.e., the difference between the lowest AICc value and the AICc from all other models (Crawley, 2012). The AICc weight of a model (w_i) was calculated based on all candidate models. This value represents the likelihood that a particular model is the best model, given the data and the considered candidate models. The parameter likelihood for predictor variables was calculated by summing w_i across all models that contained the parameter being considered. The parameter likelihood is used as an indicator of the support for predictor variables. Thus, those predictor variables with good support have a parameter-likelihood value near 1. As a complementary evidence for the parameter-likelihood to consider or not a model with a certain predictor variable, we calculated the 95% confidence interval (CI) of parameter estimates.

2.3.2. *Fecundity from field samples*

Predictive linear regressions were calculated between the log-fecundity and the log-female size (measured as CL in mm). The effect of the fishery on fecundity was evaluated by means of an ANCOVA with fishing pressure and months as categorical explanatory variables for *P. granulosa* and *L. santolla*, respectively. By using the stepwise deletion to simplify models in each species, we first proved the slope homogeneity of the models and then we compared the intercepts (Crawley, 2012). All the statistical analyses were performed using R software (MASS and MuMIn packages) version 2.15.2 (R Development Core Team, 2011).

3. Results

3.1. *Tumbling experiments*

Within the following 5 min after the tumbling experiments and placed back to their own tanks, all crabs had normal reflexes, i.e., eye retraction, chela closure, and leg flare and movements (c.f. Stoner, 2009). No crabs died throughout or after all experiments. In both species the number of detached eggs was affected by the manner in which crabs were returned to the water. The major egg loss occurred at the time of returning animals to the water in free fall and during the first 24 h following the experiment. Overall average losses at the free fall and ramp treatments with and without air exposure were in *L. santolla* 22.0 ± 14.5% and 0.32 ± 0.36% and in *P. granulosa* 2.3 ± 2.2% and 0.05 ± 0.07% of the egg batches, respectively (Figs. 2 and 3). During the first day after the tumbling experiment, the pattern of egg loss between both species was different depending on their condition to air exposure. In *P. granulosa*, the number of lost eggs increased 24 h after the free fall experiment when females were previously exposed to the air (Fig. 3). In contrast, the number of lost eggs in females exposed to the air decreased during the first day, in a similar pattern to that exhibited by *L. santolla* in both exposure conditions (Figs. 2 and 3).

Accordingly, in *L. santolla* the number of detached eggs was also affected by the month and the aerial exposure. The best model explaining the egg loss included as explanatory variables the month, the aerial exposure and the returning condition ($w_i = 0.53$, likelihood ratio test, Table 1), and accounted for 82% of the variation. The likelihood parameter values for free fall and aerial exposure, and their confidence intervals, also support that these categorical variables are important predictors of egg loss (Table 2). The egg loss was higher in the free fall condition whereas there were almost no difference between the egg loss caused by ramp and the control (=no tumbling) treatments (Table 2 and Fig. 4). Free fall caused an egg loss ranging between 4.3% and 56.8% of the entire egg batch. In contrast, the egg loss using a ramp (between 0.02% and 1.91% of the clutch) was similar to that observed in control treatments (between 0.01% and 2.51%, Table 2). Nearer hatching,

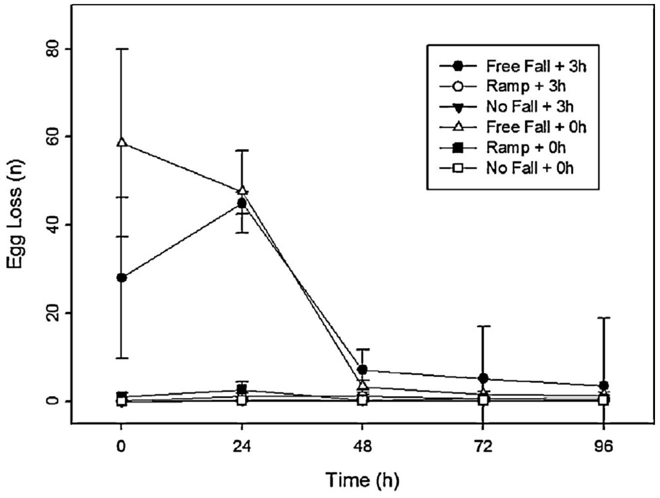

Fig. 3. *Paralomis granulosa*. Average daily egg loss ± standard deviation for each combination of returning condition and aerial exposure.

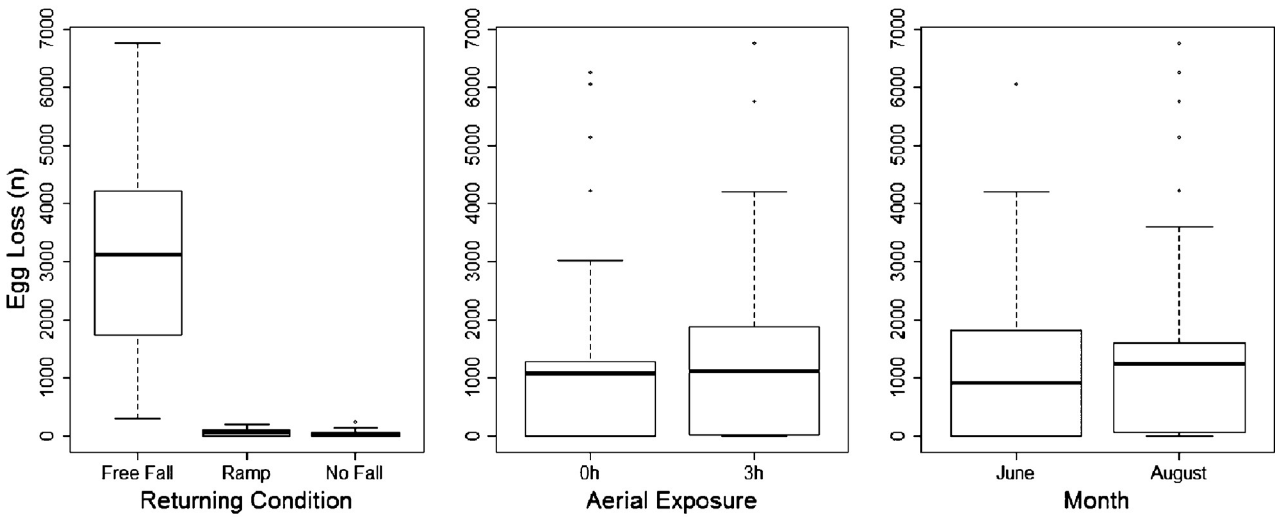

Fig. 4. *Lithodes santolla*. Modified boxplots for egg loss values for three different returning conditions (free fall, ramp and no fall), with or without aerial exposure (3 h and 0 h) and during two different times during the embryogenesis in which the experiment was carried out (June and August). The horizontal line in the boxplot represents the mean instead of the median.

Table 1
Generalized linear models explaining the variation in the egg loss of a. *Lithodes santolla* b. *Paralomis granulosa*. The null model, global model, and stronger models ($w_i > 0$) are provided and listed in decreasing order of ΔAIC_c. Ret Con = returning condition (three levels: free fall, ramp and no fall), Month (two levels: June and August), Aer Exp = aerial exposure (two levels: 0 h and 3 h), Fec = fecundity, K: number of estimated parameters, AIC_c: corrected Akaike's information criterion, W_i: AIC_c weights.

Candidate models	***K***	**AIC_c**	**ΔAIC_c**	***w_i***
Lithodes santolla				
Ret Con + Month + Aer Exp	6	902.35	0	0.53
Ret Con + Month	5	904.21	1.86	0.21
Ret Condition + Month + Aer Exp + Fec (Global Model)	7	904.55	2.2	0.18
Ret Condition + Month + Fec	6	906.21	3.86	0.08
Null Model	2	1036.9	134.53	0.00
Paralomis granulosa				
Ret Con	4	251.7	0	0.51
Ret Con + Aer Exp	5	253.5	1.84	0.20
Ret Con + Fec	5	253.6	1.9	0.20
Ret Con + Aer Exp + Fecundity (Global model)	6	255.2	3.58	0.08
Null model	2	312.1	60.45	0.00

during August, the number of detached eggs was 1.35% higher than in June (Fig. 4).

In *P. granulosa* the explanatory variable for the egg loss included in the model was also the returning condition (w_i = 0.513, likelihood ratio test, Table 1) and it also accounted for 82% of the variation. The likelihood parameter values and their confidence intervals suggest that neither aerial exposure nor fecundity affected the egg loss (Table 2). Similar to *L. santolla*, the highest values of detached eggs (2.5% of the entire egg batch) occurred in the free fall trial, whereas the egg loss caused by the ramp (0.08%) was similar to the control treatment (0.02%; Fig. 5). In free fall, the proportion of lost eggs of *P. granulosa* was lower than that in *L. santolla*.

3.2. Fecundity from field samples

In all cases fecundity increased with female size (Figs. 6 and 7; Table 3). The fecundity of *P. granulosa* seems to be affected by the fishing effort (Table 4). In the closed fishing area, fecundity was significantly higher than in the areas with moderate and high fishing effort. There were no statistical differences between the last two areas (Table 4). The adjusted fecundity in areas with moderate and high fishing effort were 16.8% and 14.8% fewer eggs than in the unfished area, respectively (Table 3). In *L. santolla*, no differences in

Table 2
Parameter likelihoods, estimates (±SE) and 95% confidence interval limits for explanatory variables for the egg loss of (a) *Lithodes santolla* and (b) *Paralomis granulosa*. Explanatory variables with confidence interval excluding zero are in bold.

Explanatory variables	Parameter likelihood	Parameter estimate ± SE	Confidence Interval	
			Lower	Upper
Lithodes santolla				
Intercept		**4.289547 ± 0.290400**	**3.711191**	**4.867902**
Ret Con (Free Fall)	1.00	**4.142761 ± 0.248500**	**3.646740**	**4.638781**
Ret Con (No Fall)		−0.239559 ± 0.248700	−0.736005	0.256886
Month (June)	1.00	**−1.058178 ± 0.212400**	**−1.481922**	**−0.634980**
Aer Exp (3 h)	0.71	**0.442466 ± 0.200600**	**0.043804**	**0.841128**
Fec	0.26	0.000015 ± 0.000023	−0.000032	0.000062
Paralomis granulosa				
Intercept		**1.500000 ± 0.474000**	**0.605300**	**2.405900**
Ret Con (Free Fall)	1.00	**3.300000 ± 0.324200**	**2.640480**	**3.960130**
Ret Con (No Fall)		**−1.270000 ± 0.402000**	**−2.084400**	**−0.447600**
Aer Exp (3 h)	0.70	−0.083000 ± 0.281100	−0.859400	0.286000
Fec	0.25	0.000026 ± 0.000082	−0.000076	0.000261

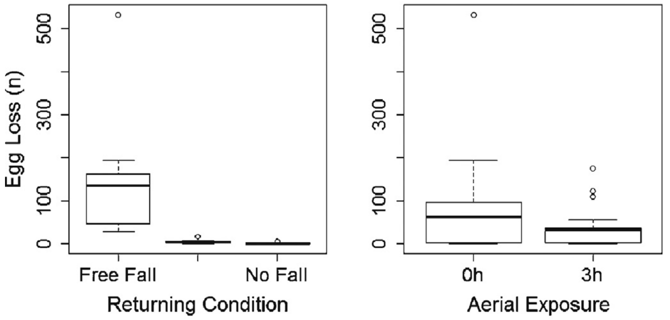

Fig. 5. *Paralomis granulosa*. Modified boxplots for egg loss values for three different returning conditions: free fall, ramp and no fall, with or without aerial exposure (3 h and 0 h). The horizontal line in the boxplot represents the mean instead of the median.

fecundity were detected in the same fishing area between May and August (Fig. 6; Table 3). Yet, the adjusted means indicate that the fecundity during August is nearly 9% lower than during May, but not statistically significant (Table 3).

4. Discussion

Our experiment demonstrates that free fall impacts, similar to those incurred in the fishery of the Beagle Channel, results in an egg loss in both the commercial species, *L. santolla* and *P. granulosa*. The main egg detachment occurs during the impact itself and during the 24 h following the drop of females to the water. Nevertheless, the egg loss pattern differs between species. The inference of multimodels indicates that *L. santolla* loses more eggs if females are exposed to air before dropping. Furthermore, the proximity of hatching likely causes a higher egg loss at the tumbling, since eggs lost in August were higher than in June. By contrast, models did not explain well the higher egg loss in *P. granulosa* of females without air exposure (Fig. 3 and see below). In both species, the use of a ramp for returning animals to the water resulted in an egg loss similar to those of the experimental controls. To our knowledge, this is the first study that shows the egg loss of female crabs returned to the water in a fishery.

Several factors may contribute to the difference in egg loss between both studied species. First, the difference of the percent egg loss was 24% and 2.6% of the whole clutch in *L. santolla* and *P. granulosa*, respectively. We attribute this variation to their different behavior during the emersion period. During a stressful situation like our experimental air exposition, *P. granulosa* females tightly contract their abdomen against their sternites so that it covers the entire egg-batch. Females also fold their pereiopods under their carapace, constituting a protection for the egg mass (c.f. Silva et al., 2007), probably avoiding desiccation. This kind of behavior in *P. granulosa* is indirectly advantageous for ovigerous females when they are returned to the water, because the number of lost eggs is lower during the impact than those during the following 24 h (Fig. 3). Furthermore, this tight contraction of abdomen and pereiopods could also be the cause of the difference in the proportion of lost eggs between the species. *L. santolla* are normally more active during air exposure and during emersion the very first reaction is to walk (pers. obs. and see Lovrich et al., 2002), probably to escape from this stressful situation. Therefore the fashion of arriving in the water, make *L. santolla* be more exposed to the impact than *P. granulosa*. Females of the former species hit the water surface flatly with the abdomen as they had opened their legs vs. folded legs protecting the abdomen in *P. granulosa*, losing more eggs due to the mechanical impact. Second, because clutch size increases with the volume of the female (Hines, 1982; Kuris, 1991), larger individuals, such as female *L. santolla*, are prone to more egg loss than a smaller species, like *P. granulosa*. Third, during our experiments eggs were in different developmental stages: *P. granulosa*

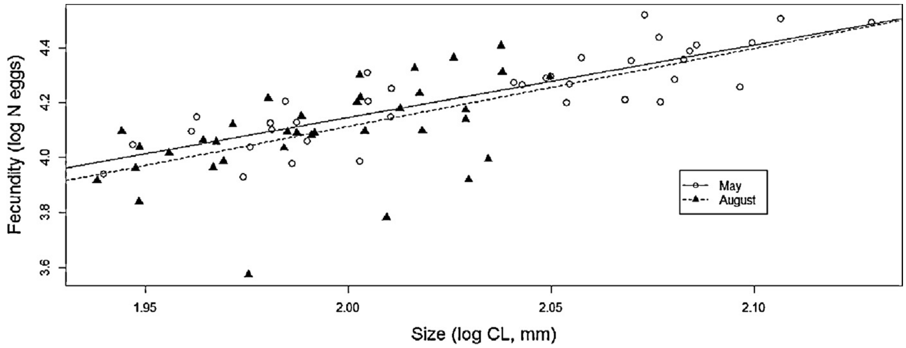

Fig. 6. *Lithodes santolla*. Linear regressions of fecundity on size in an area with moderate fishing effort in two different times of embryogenesis: June and August.

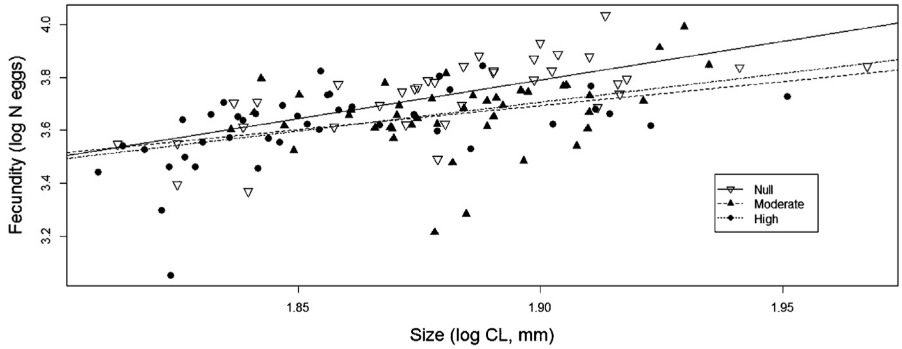

Fig. 7. *Paralomis granulosa*. Linear regressions of fecundity on size in three areas with different fishing effort (null, moderate and high). Fecundity and carapace length (CL) values are log-transformed.

Table 3
Linear regressions between the fecundity (F) and the female size (CL) for *Lithodes santolla* in the same fishing area in two different months and for *Paralomis granulosa* in three areas with different fishing pressure. Each regression is described with the number of animals sampled (N), the linear model with the log-transformed variables and the values of the slope and the intercept. Also listed are the adjusted mean of the regression, the coefficient of determination (r^2) and the level of significance of the slope (p, H_0: b ≠ 0, F). Comparison of the slopes and the intercepts of linear regressions between fecundity and female size for each field study.

Level of the categorical variable	*N*	Lineal regression	Adjusted mean	r^2	*p*
Lithodes santolla					
May	37	$\log F = 2.632 \times \log \mathrm{CL} - 1.118$	4.18	0.717	<0.001
August	36	$\log F = 2.841 \times \log \mathrm{CL} - 1.568$	4.14	0.269	<0.001
Paralomis granulosa					
Null	36	$\log F = 2.923 \times \log \mathrm{CL} - 1.763$	3.72	0.463	<0.001
Moderate	26	$\log F = 1.827 \times \log \mathrm{CL} + 0.224$	3.64	0.101	<0.05
High	27	$\log F = 2.170 \times \log \mathrm{CL} - 0.418$	3.65	0.251	<0.001
Comparison of slopes	H_0	May = August	$p = 0.785$		
		Null = Moderate = High	$p = 0.302$		
Comparison of intercepts		May = August	p = 0.502		
		Null = Moderate = High	p = 0.017		

had embryos in a diapause stage, with an embryo occupying <25% of the egg volume (Lovrich and Vinuesa, 1993), whereas embryos in *L. santolla* were in advanced stages of development, with ocular pigments and larvae clearly visible in June and August, respectively (Vinuesa, 1987). Near hatching, the egg water contents increases and hence the egg volume increases, eventually causing the larval hatching (Wear, 1974). We postulate that these changes may also affect the egg attachment to the pleopods, making the attachment weaker and easier to lose.

We hypothesize that the fishing activity can threaten the recruitment of the crab population that is the target of the fishery. First, an egg loss rate as high as 24% at a single capture and return, as it occurs in *L. santolla*, is probably important particularly in coastal populations. In southern South America fishing has developed in semi-closed systems like fjords and channels (Guzmán et al., 2004; Lovrich and Tapella, 2014), where crab movements and migrations are rather limited (Boschi et al., 1984). Moreover, crab distribution is patchy; that once they are detected by the fishers, they can follow their movements (Lovrich, pers. obs.). These facts along with evidences that crabs can be accustomed to traps (Miller, 1990) make females susceptible to be caught more than once during the 10-months fishing season, with the consequent egg loss at returning to the water. Furthermore, the population of the Beagle Channel has had the same fishing effort but yields have decreased during the last 40 years (Lovrich and Tapella, 2014). Hence, the probability of capturing the same female has increased each fishing season. In 1975 such probability was roughly 0.025 whereas in 2008 it was ca. 0.25 (calculated from the catch per unit effort data presented by Lovrich and Tapella, 2014). Therefore, the return of ovigerous females likely exacerbates the negative effect of fishing on the population recovery. Similarly, in trawl fisheries, like inside the Golfo San Jorge (Fig. 1), crabs can also be caught several times, because the normal custom is to pass through the very same spot several times until yields decrease to an unprofitable point. In this case, if females arrive on the deck in healthy conditions, returned and survive, then they likely will be caught repeatedly by trawling (Iorio et al., 2013). Furthermore, in *P. granulosa* fecundity from three areas with different fishing effort indicates that differences reach ca. 15% between the areas being fished and those not being fished (Table 3). In this species, fecundity at the end of the embryogenesis period of 18 months is 14% lower than at the initial stages of development (Lovrich and Vinuesa, 1993). These figures are comparable to values of the present study. Consequently this egg loss can likely be attributed to fishing, because the studied area at that time was subjected to intense effort, with yields varying around 180 t per year during the previous 7 years.

Table 4
Summary of the results of the lineal model log(Fecundity) ∼ log(carapace length) + fishing pressure for *Paralomis granulosa*. Written in bold are the variables that are different from those contained in the intercept.

Explanatory variables	Parameter estimate ± SE	*t* value	*p*
Intercept	−0.78468 ± 0.69510	−1.129	0.2613
Fishing pressure (moderate)	−0.01089 ± 0.02852	−0.382	0.7033
Fishing pressure (null)	**0.06545 ± 0.02954**	**2.216**	**0.0286**
Size (log(CL))	**2.36813 ± 0.37421**	**6.328**	**<0.0001**

The use of a chute from the freeboard towards the water could be useful to mitigate egg losses. In small boats of artisan fishers, we suggest the implementation of an incline attached from one side to the freeboard at the level of the deck and with a floating device at the end in contact with the water. This gadget could be compact and probably will not interfere with deck activities or stocking, either crabs or fishing material, on board. This chute can be constructed with different type of materials, through which crabs can glide down into the water. In crab handling in which similar devices are used, mortality of animals is reduced. In three *Paralomis* spp. off South Georgia, the use of a conveyor belt improves the survival of non-target crabs in 30–40% compared to that of crabs going down a vertical chute (Purves et al., 2003 and also see Stevens, 1990). Handling also produces individual damage because of the dropping and kicking on deck (Zhou and Shirley, 1995) that our suggested device will not reduce, yet a decreasing the egg loss by 1/3 probably will be a good improvement via an inexpensive and simple device.

Our study may have been subject to several biases. First, we performed a tumbling experiment by dropping each crab three times, simulating different hits that animals can suffer during their handling, e.g., falling from different heights (trap to deck) or places (kicking through deck). Even though these impacts are not the same as our three falls (c.f. Zhou and Shirley, 1995), we are confident that our estimations of egg losses are realistic, since they reflect the additive effects of concatenated impacts. Nevertheless, all handling on deck does cause egg detachment in both studied species (pers. obs.), and should be subject of further study. Moreover, the discard of non-target animals is usually done with the boat navigating and hence their impact in different positions to the water at variable speeds would be more intense than our controlled throw from a standard height. Second, our fecundity data from the field are limited in number. Data shows high variability and consequently determination coefficients (r^2) are low, yet fecundity is naturally variable, at least in *P. granulosa* (Lovrich and Vinuesa, 1993). Despite the variability, in *P. granulosa* fecundity was different in areas with different fishery effort. This is an interesting signal that deserves further study and should be monitored at the fishery scale, e.g., throughout the year or inter-annually. This monitoring could resolve whether the differences in fecundity at field are indeed produced by female discard as the experiments showed less egg detachment in this species. The population of *P. granulosa* has been harvested for several years in those areas especially since

1994 when the fishery was closed for *L. santolla*. Probably there is another factor on fecundity reduction, as sperm limitation, well described for other related species (Sato et al., 2007), which cannot be resolved by our study. Third, fecundity of female *L. santolla* in May and August was similar, albeit this species lost more eggs in our experiments. In our study, we were unable to detect the effect of fishing on fecundity of *L. santolla* probably because females were never fished nor returned to the water. During some winters fishing activities are voluntary reduced by fishers, because of male low yields after moulting in autumn. Alternatively, fishers can illegally retain females, with no effect on the fecundity.

Despite a variety of dedicated research on the subject, the cumulative evidence suggests that handling and discarding of king crabs in trap fisheries may not be a major source of mortality (Stevens, 2014b). Egg production is indicative of the reproductive potential of the population, is easily detected in the field (Orensanz et al., 1998), and is primary information for fishery management (Botsford, 1991). Any monitoring survey should consider the proportion of ovigerous females and the level of clutch repletion for better understanding the size specific contribution to population fecundity (Swiney et al., 2010). Male-only extraction with its consequent sperm limitation has been attributed as the main cause of reproductive failure (see Van Son and Thiel, 2007 for a review). Here we present that the levels of egg loss at returning the bycatch, especially in *L. santolla*, should be considered as an additional cause of the reduction in fishery productivity.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2014.06.015.

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