

# Reproduction of the sea urchin *Loxechinus albus* across a bathymetric gradient in the Chilean Inland Sea

Reproducción del erizo *Loxechinus albus* en un gradiente batimétrico en el mar interior chileno

Carlos Molinet<sup>1,2</sup>, Carlos A. Moreno<sup>3</sup>, Edwin J. Niklitschek<sup>4</sup>, Manira Matamala<sup>5</sup>,  
Mónica Neculman<sup>4</sup>, Alejandra Arévalo<sup>3</sup>, José Codjambassis<sup>1</sup>,  
Patricio Diaz<sup>1</sup> and Manuel Diaz<sup>1</sup>

<sup>1</sup>Programa de Investigación Pesquera, Instituto de Acuicultura, Universidad Austral de Chile, Los Pinos S/N balneario Pelluco, Puerto Montt, Chile. cmolinet@uach.cl

<sup>2</sup>Centro Trapananda, Universidad Austral de Chile, Portales 73, Coyhaique, Chile

<sup>3</sup>Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Campus Isla Teja, Valdivia, Chile

<sup>4</sup>Centro I-mar, Universidad de Los Lagos, Camino a Chiquihue Km. 6, Puerto Montt, Chile

<sup>5</sup>Consultora Pupelde, Regimiento 1312, Puerto Montt, Chile

**Resumen.-** La distribución batimétrica reportada para erizos de interés comercial va desde el intermareal hasta cientos de metros, aunque estudios reportados a profundidades mayores que 25 m son escasos. Se espera que erizos que habitan sitios someros tengan acceso a más alimento y desplegar un mayor desarrollo gonádico que aquellos erizos de hábitat más profundos. Los erizos en hábitat profundo pueden jugar un rol importante para mejorar la resiliencia de las poblaciones explotadas ubicadas en hábitat someros. El objetivo de este estudio fue verificar la existencia de parches del erizo *Loxechinus albus* reproductivamente activos en un gradiente batimétrico desde 0 a 100 m de profundidad en dos áreas de pesca del mar interior chileno. Para esto se evaluó el índice gonádico (IG) y el desove inducido con KCl en ejemplares adultos de *L. albus* recolectados entre la superficie y los 100 m de profundidad entre septiembre de 2008 y marzo de 2009. Los erizos fueron relativamente abundantes hasta 15 m de profundidad, escasos hasta 60 m de profundidad y sólo un parche de erizos fue encontrado entre 60 y 100 m de profundidad. Se observó una asincronía en el IG y el desove inducido entre estratos y áreas de muestreo, lo que sugiere que los erizos ubicados entre 30 y 100 m podrían estar reproductivamente activos y desovar en distintos periodos, aunque se desconoce su potencial aporte en la dinámica poblacional de *L. albus*. Futuros estudios deberían enfocarse en estudiar el rol de las escasas agregaciones profundas de *L. albus* sobre la dinámica de la población de este recurso, particularmente en áreas donde la presión de pesca es intensa.

**Palabras clave:** Parches profundos, capacidad reproductiva, desove inducido

**Abstract.-** The reported bathymetric distribution of commercial sea urchin species varies globally from the intertidal zone down to a depth of a hundred meters or more, although few studies have been conducted at depths >25 m. Urchins that inhabit shallow sites are expected to have access to more food and to display greater gonad development than those from deeper habitats. The latter could, however, play an important reproductive role by enhancing the resilience of the exploited populations. The objective of this study was to verify the existence of deep reproductively active patches of the edible sea urchin *Loxechinus albus* in two fishing areas of the Chilean Inland Sea, and compare the main reproductive features of these patches over the 0-100 m bathymetric gradients. We evaluated the gonadic index (GI) and KCl-induced spawning in adult *L. albus* collected between the surface and 100 m depth between September 2008 and March 2009. Urchins were relatively abundant up to 15 m depth, few to 60 m depth and only one patch of urchins was found between 60 and 100 m depth. Asynchrony was observed in the GI and induced spawning between strata and sampling areas, suggesting that urchins located between 30 and 100 m may be reproductively active and may asynchronously spawn during the breeding season, although their potential contribution to the population dynamic is unknown. Future studies should examine the role of the scarce deep-water aggregations for the regional population dynamics of *L. albus*, in particular in areas where shallow populations have been heavily fished.

**Key words:** Deep patches, reproductive capacity, induced spawn

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## INTRODUCTION

Sea urchins *Loxechinus albus* (Molina, 1782) are among the key benthic herbivores in Chilean coastal waters (*e.g.*, Vásquez *et al.* 1984, Guisado & Castilla 1987, Moreno & Vega 1988, Vásquez 2001, Kino & Agatsuma 2007, Pérez *et al.* 2010), and sustain the largest sea urchin fishery in the world (Andrew *et al.* 2002, Moreno *et al.* 2006, Moreno *et al.* 2011). The geographic distribution of *L. albus* runs from northern Peru (6°S) to Tierra del Fuego (55°S) and its bathymetric range extends from the shoreline to a depth of several hundred meters (Larraín 1975). The highest abundances and the commercial fisheries for this and other related species, in Chile as elsewhere, are limited to the first 20 to 30 m of the depth range (Inostroza *et al.* 1983, Keats *et al.* 1984, Vásquez *et al.* 1984, Gage & Tyler 1985, Lawrence 2001, Basch & Tegner 2007, Moreno *et al.* 2011).

Sea urchin preference for shallower habitats seems to be related to its herbivorous diet, which is heavily dependent upon kelp and other seaweed species (Vásquez *et al.* 1984, Agatsuma *et al.* 2000, Lawrence 2001, Vásquez 2001, Villouta *et al.* 2001, Burdett-Coutts & Metaxas 2004, Senaratna *et al.* 2005, Shpigel *et al.* 2005, Vanderkluft & Kendrick 2005). Thus, higher food consumption, growth rates, early maturation schedules and higher reproductive output would be expected in more productive shallower habitats (Keats *et al.* 1984, Byrne 1990, Lamare *et al.* 2002). However, in shallow waters it is likely to expect a higher mortality rate than in deeper areas due to both the effect of predation and fisheries.

Since sea urchins can also feed on encrusting algae, benthic microalgae, phytodetritus and small invertebrates (Kelly *et al.* 2001), they can survive in deeper habitats (Gage & Tyler 1985). Moreover, there are zones where macrophyte detritus may represent an important source of energy, capable of sustaining productive communities in deep habitats (Harrold *et al.* 1998, Vetter & Dayton 1998, Dierssen *et al.* 2009).

Despite their low abundances and slow individual growth rates, patches inhabiting sub-optimal habitats can play a fundamental role in the persistence of the population in space and time (Basch & Tegner 2007, Kerr *et al.* 2010a). These areas may provide higher environmental stability, resulting in higher survival rates compared to populations living in shallower waters affected by overfishing.

While the reproductive schedule of *L. albus* changes over its latitudinal range (Bay-Schmith *et al.* 1981, Guisado

& Castilla 1987, Zamora & Stotz 1994, Arias *et al.* 1995, Guisado *et al.* 1998), two seasonal peaks of gonadic maturation have been described: a first and larger peak during mid-spring, followed by a secondary peak in late summer (Bay-Schmith *et al.* 1981, Kino & Agatsuma 2007). According to Bay-Schmith *et al.* (1981) and Bückle *et al.* (1977), only the first maturation peak produces a massive spawning event, while the secondary peak may be reabsorbed to conserve energy for other physiological demands during the following autumn and winter. This reabsorption process has also been described for other sea urchin species in temperate climates (Byrne 1990). Differences in both the gonad maturation schedule and fecundity have been observed over the bathymetric gradient down to 25 m and are related to decreasing food availability with depth as observed in other sea urchin species and habitats (Keats *et al.* 1984, Byrne 1990, Rogers-Bennett *et al.* 1995, Basch & Tegner 2007).

The current abundance of deep *L. albus* patches (deeper than 20-30 m) and their relative contribution as a source of eggs and larvae that may maintain the viability of populations exploited by hookah divers in shallow habitats (above 30 m) has been matter for strong debate by the stakeholders involved in the Chilean *L. albus* fishery. Information on the abundance and reproductive biology of populations inhabiting deeper waters is, however, very scarce.

The inland seas of southern Chile (41°S to 56°S) correspond to a large archipelagic region dominated by fjords and channels, which receive substantial freshwater inputs from coastal regions. Circulation patterns in the Chilean inland sea have been described as being highly influenced by tides, winds, density gradients and local topographic features such as sills, constrictions, channels and embayments (*e.g.*, Silva *et al.* 1998, Valle-Levinson & Blanco 2004, Cáceres *et al.* 2006, 2008, Aiken 2008). All these factors interact to form retention and dispersion zones of high biological value (*e.g.* Valle-Levinson *et al.* 2001, Molinet *et al.* 2006, Castro *et al.* 2011). Considering these oceanographic features it is possible to hypothesize the existence of deep-sea urchin patches reproductively active in Chilean inland seas.

The objectives of this study were (i) to verify the existence of deep and reproductively active *L. albus* patches in two fishing areas within the Chilean Inland Sea, and (ii) compare their reproductive features over the 0-100 m bathymetric gradient, including gonadic index, spawning and reproductive capacity for egg production.

## MATERIALS AND METHODS

### STUDY AREA

The study was conducted in two areas of the Northwest Patagonian inland sea (Fig. 1A): the southeast portion of Chiloé Island ( $43^{\circ}08'S$ - $43^{\circ}25'S$ ) close to Quellón, the most important landing port of the northwest Chilean Inland Sea *L. albus* fishery (hereafter Quellón), and the Guaitecas Archipelago ( $43^{\circ}54'S$ - $44^{\circ}S$ ), close to Melinka, the second largest landing port of this fishery in the area.

Quellón is a system formed by three main channels, with a main depression within the Laitec Channel, which reaches a maximum depth of 110 m and covers about 2 km<sup>2</sup> (about 5% of this system). A particular alternation of upwelling and downwelling fluxes over a rise in this depression has been identified by Cáceres *et al.* (2008). Guaitecas is a system formed by several channels with maximum depths of around 80 m. Both systems have a layered water column with salinities between 27 and 33 in the top 50 m (Silva *et al.* 1998, Cáceres *et al.* 2008, Molinet *et al.* 2008), and exhibit abrupt changes in their coastal morphology and bathymetry (Gobierno de Chile 2005, Quiroz & Duhart 2006).

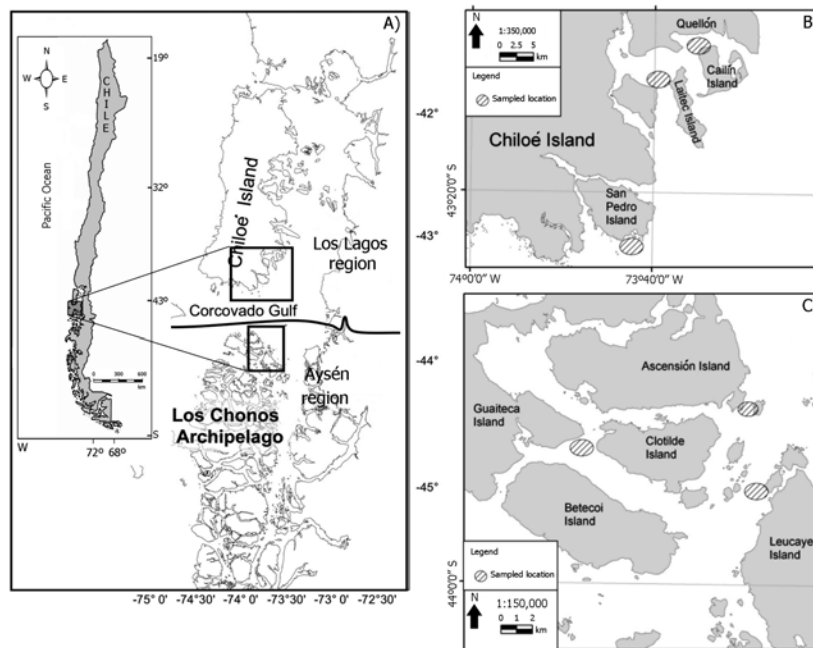
After an exploratory survey (described below) three fixed stations were selected in Quellón: Canal Chaiguao,

Laitec depression (in the Laitec Channel) and south of San Pedro Island (Fig. 1B), and three others in Guaitecas: Westhoff Island, west of Leucayec Island, and west of Clotilde Island (Fig. 1C). The criteria applied for selecting fixed stations for further biological sampling was defined as a minimum average of 30 individuals per exploratory transect of 100 m.

### EXPLORATORY SURVEY

In order to achieve our objective of finding deep sea urchin patches in the study areas, exploratory surveys were carried out based upon a minimum of four 100-m long video counting transects per station, conducted by means of a towed SeaViewer video camera (resolution: 520 lines), equipped with a variable intensity LED lighting system. The camera was connected to a console at the surface for visualization and recording. Nominal towing speed ranged between 1 and 2 knots. The depth and the start and end points of each transect were registered using a Garmin 492s GPS-sounder. The distance traveled was obtained by recording the navigation track of each transect from the GPS, marking the start and end point for each depth stratum, as well as landmarks such as the first appearance and end point of each sea urchin patch. The field of view width, and therefore the segment sampled, was estimated based on light levels at each depth as well

**Figure 1.** A) Study area in southern Chile highlighting Quellón area (frame located north of Corcovado Gulf) and Guaitecas area (frame located south of Corcovado Gulf). B) and C) show Quellón and Guaitecas at 1:150,000, for details of sampled stations. Dashed circles are sampling stations. Dashed circle on the Laitec channel corresponds to the Laitec depression. The line that crosses the Corcovado Gulf defines the regional administrative political border between the Los Lagos and Aysén regions / A) América del Sur, destacando en gris el territorio Chileno y la ubicación del área de estudio en un recuadro. B) Área de estudio en la Isla de Chiloé e Islas Guaitecas. C) Estaciones de muestreo en la zona de Quellón y D) estaciones de muestreo en Guaitecas. Círculos con líneas diagonales muestran los sitios específicos de muestreo en cada área. La línea a través del Golfo Corcovado indica el límite administrativo de las regiones de Aysén y de Los Lagos



as the presence of sea urchins that were collected and subsequently measured. The estimation was: one meter wide for stratum 1 (0-10 m) and stratum 2 (11-30 m), 0.5 m for stratum 3 (31-60 m) and 0.3 m for stratum 4 (61-100 m). The abundance in each transect was estimated considering the number of urchins and the area swept by the camera per transect.

#### SAMPLING FOR REPRODUCTIVE STUDIES

Four depth strata were defined at each sampling station: 0-15 m, 16-30 m, 31-60 m, and 61-100 m depth. Between 100 and 150 individuals were collected at each of the three deepest strata, whenever possible, by means of a 'chain sweep' trawl with a 1 m<sup>2</sup> mouth and 2 m length (Campagna *et al.* 2005), which was towed over a distance of 100-200 m. Samples from the 0-15 m stratum were collected by artisanal fishermen divers, because the irregular bottom did not allow for the proper use of the chain sweep trawl. Divers randomly collected all sea urchin individuals (irrespective of their sizes) visible in the sampled area until a net bag designed to accommodate approximately 40 kg of urchins was filled.

None of the Guaitecas stations had sea urchin patches below 50 m in sufficient abundance to fulfill the previously established criteria. A small group of 5 individuals was nonetheless collected from a depth of 70 m in November 2008 and included in the induced spawning experiments of that month.

Four sampling surveys were carried out at 45-60 day intervals (September 2008, November 2008, January 2009, and March 2009). This period corresponded to the *L. albus* spawning season, as described in the literature (Bay-Schmith *et al.* 1981, Guisado 1995, Kino & Agatsuma 2007). The samples collected were stored in labeled polyethylene bags and transported live to the laboratory where they were processed and where spawning assays were conducted.

#### SAMPLE PROCESSING

All individuals collected were measured for test diameter with a knife-edged caliper (0.1 mm precision) and wet weighed with a digital balance (0.1 g precision). From each sample, a total of 40 adult individuals were selected, using a minimum size criterium of 55 mm test diameter (TD), considering that at this TD at least 80% of the urchins are reproductively mature according to Bay-Schmith *et al.* (1981) and Lozada & Bustos (1984). Thirty of these 40 individuals were sexed and the wet weight of

their gonads was determined. The gonadic index (GI) was individually calculated using the following relationship: GI = Gonad wet weight / Total wet weight (Gonor 1972).

Sex determination was carried out on fresh gonad smears, under a microscope at a magnification of 100x. Spawning was induced in the remaining 10 individuals from each sub-sample. Individuals were rinsed with seawater, measured, weighed and put into individual transparent flasks of 100 to 300 mL. Each individual was then injected with 6 mL of KCl 0.5 M via the peristomal membrane, and left for 90 min (Zamora & Stotz 1994, Bustos & Olave 2001, Barahona *et al.* 2003). After this period, three 10-20 µL sub-samples were taken from the flask, and deposited in a Sedgewick Rafter counting chamber, where oocytes were counted under a microscope at 200x. The total number of released oocytes per spawned female ( $N_o$ ) was estimated using the following formula:

$$N_o = \frac{\bar{X} V_T}{v}$$

where  $\bar{X}$  is the average of the three counts in the Sedgewick Rafter chamber,  $V_T$  is the total volume of the flask in which the female spawned, and  $v$  is the volume of the sample observed in the Rafter chamber. For standardization purposes,  $N_o$  was divided by the wet weight of the individual sea urchin before the statistical analysis. When spawning induction failed, individuals were dissected and sexed.

#### DATA ANALYSIS

Because *L. albus* from the deepest stratum were only sampled on a regular basis in Quellón, and in order to keep sampling period and location as fixed effects, two designs for each analysis were utilized: (i) a model that included the three most shallow strata in both sampled areas (Quellón and Guaitecas) for studying GI variability, the success/failure of spawning and the number of oocytes g<sup>-1</sup> of urchin, and (ii) a model which included all the strata only for area Quellón to study the variables described in (i).

The gonadic index data, being a proportion, were transformed by applying an arcsine transformation. Then, normality of residuals and homogeneity of variances of the transformed variable was assessed using the Shapiro-Wilk test (Zar 1999), and an ANOVA was used to test differences between zone, month, sex and stratum means (Zar 1999).



The binary response variable spawning induction success/failure was analyzed using as predictors the variables depth strata, month, and location by applying a GLM binomial model (link logit), and the variable providing the best fit was chosen according to Akaike's information criterion (AIC) (Akaike 1974). The AIC is an estimator of expected relative Kullback-Leibler information based on the maximized log-likelihood function, corrected for asymptotic bias (Burnham & Anderson 2004). The selected model is one that has a lower value of AIC, defined by:

$AIC = (-2) \log(\text{maximized likelihood}) + 2$  (the asymptotic bias correction term).

When September 2008 data on spawning induction success were available, they were only included in the binomial model, where they helped to assess the degree of synchrony between depth strata and locations.

The statistical conclusions from GI and spawning induction models were verified by visually exploring a graphical display of the fitted values and residuals: (i) a plot of deviance residuals versus the fitted values, (ii) a plot of the square root of the absolute deviance residuals versus the linear predictor values, (iii) a plot of the response *versus* the fitted values, and (iv) a normal quantile plot of the Pearson residuals (q-q plots) (McCullagh & Nelder 1989).

In the case of the spawning induction results, the large number of zero values made it impossible to apply standard ANOVA or mean comparison approaches, as normality assumptions had been severely violated. If zeros had been ignored a relevant part of the information would have been lost. Moreover, both the spawning induction success and the number of oocytes released were variables of interest. Hence we used a delta-gamma general linear model (GLM) approach (sensu Stefansson 1996) based upon the Aitchison-Pennington method (Aitchison 1955, Pennington 1983). Here the observable positive density response (number of oocytes  $g^{-1}$  of urchin) ( $\hat{d}$ ) is considered a random variable with a spike in probability mass at the origin. As a consequence, ( $\hat{d}_p$ ) is calculated as a conditional mean, by ignoring null observations. The latter are, however, used to produce an independent estimate of the probability of spawning success in each sample ( $\hat{p}$ ) and then combined into a corrected estimate for the response variable  $\hat{d}_c$  following the relationships:  $\hat{d}_c = \hat{p} \times \hat{d}$ , and their variance:

$$v\hat{d}_c = \hat{p}^2 \times v(\hat{d}_p) + v(\hat{p}) \times \hat{d}_p^2$$

Corrected means ( $\hat{d}_c$ ) were calculated using a general linear model procedure (Wolfinger & O'Connell 1993), by assuming a gamma distribution of errors and using a log-link function. The gamma distribution of errors was selected because greater flexibility in accommodating non-normal datasets (McCullagh & Nelder 1989). A log-link function was needed to fulfill distribution assumptions.

Spawning success/failure data from our samples were analyzed as a dichotomous variable (0/1) used to estimate  $\bar{p}$  ( $d > 0$ ) within a general linear model procedure. For this, we assumed a binomial distribution of errors and used a logit-link function (Kleinbaum *et al.* 1998).

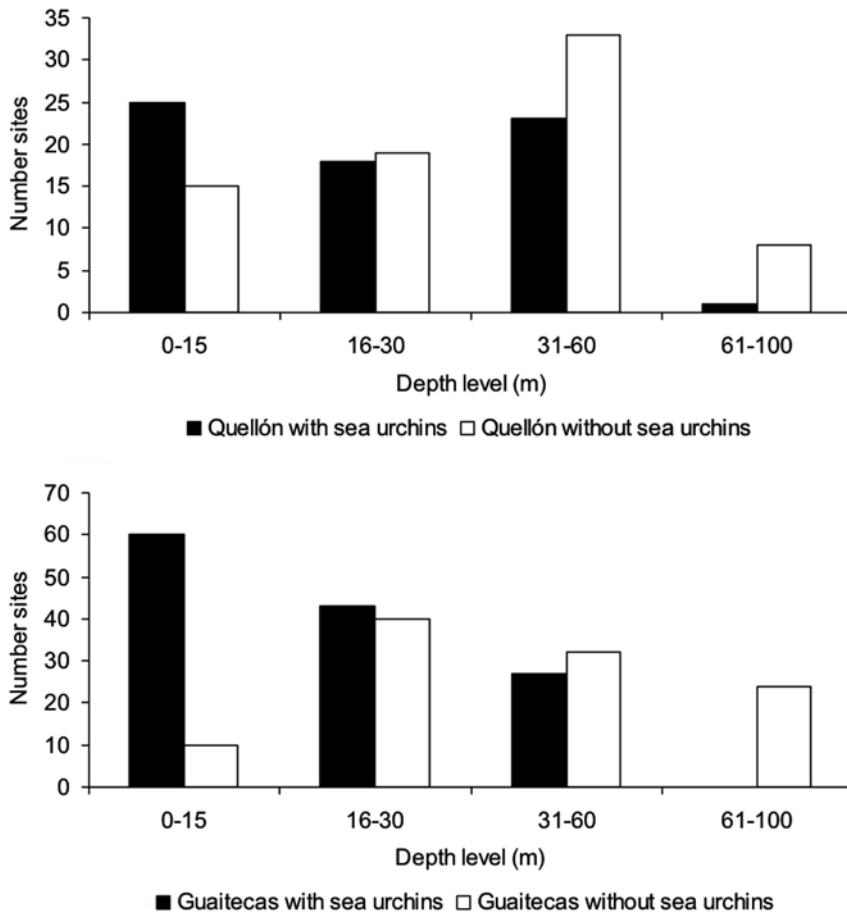
Alternative models based upon competing explanatory variables were selected as those yielding the smallest sum of Akaike's information criteria (AIC) computed from the binomial and gamma models that corresponded to each set of variables being tested. These models were assessed through a likelihood ratio test using the *lmer* package in R 2.1.13 (Zeileis & Hothorn 2002). All general linear models were constructed and tested using the statistical and programming software R 2.1.13 (Venables & Ripley 2002, Fox & Sanford 2010).

## RESULTS

We explored a total of 49 stations in Quellón and 78 stations in Melinka (Fig. 2). Given the bathymetric characteristics of the study area (higher proportion of shallow versus deeper zones), a greater number of transects were carried out between 0 and 60 m depth (see Moreno *et al.* 2011). As a result of these explorations higher urchin abundances were observed in Guaitecas area and in shallow habitats (Table 1). Only one sea urchin patch (around 54,000 individuals) was found at a depth greater than 60 m, which occurred in the Canal Laitec depression and represented about 0.2% of the total estimated abundance in Quellón Area. Molinet *et al.* (2009) and Moreno *et al.* (2011) provide detailed abundance, size distribution data, and substratum types inhabited by *L. albus* at different depths within the studied fishing areas.

### GONADIC INDEX

The GI for the first analysis (0-60 m depth, all months and both areas) showed significant differences between areas, depth strata, months, and sex (ANOVA,  $P < 0.05$ ). The highest GI median value corresponded to females sampled from the shallowest strata at Quellón, during September



**Figure 2.** Number of samples with presence and absence of *L. albus* during the exploratory survey by sampling area and depth strata. Each sample corresponds to a video-counting transect / Número de muestras por área de muestreo y estrato de profundidad en las que se observó presencia y ausencia de *L. albus* en los muestreos realizados. Cada muestra corresponde a una transecta que fue grabada en imágenes de video

**Table 1.** *Loxechinus albus* estimated abundance (number of sea urchins) and percentage of urchins on each depth strata, and study area (from Molinet *et al.* 2009) / *Loxechinus albus*, abundancia estimada (número de erizos) y porcentaje de erizos en cada estrato de profundidad y área de estudio (según Molinet *et al.* 2009)

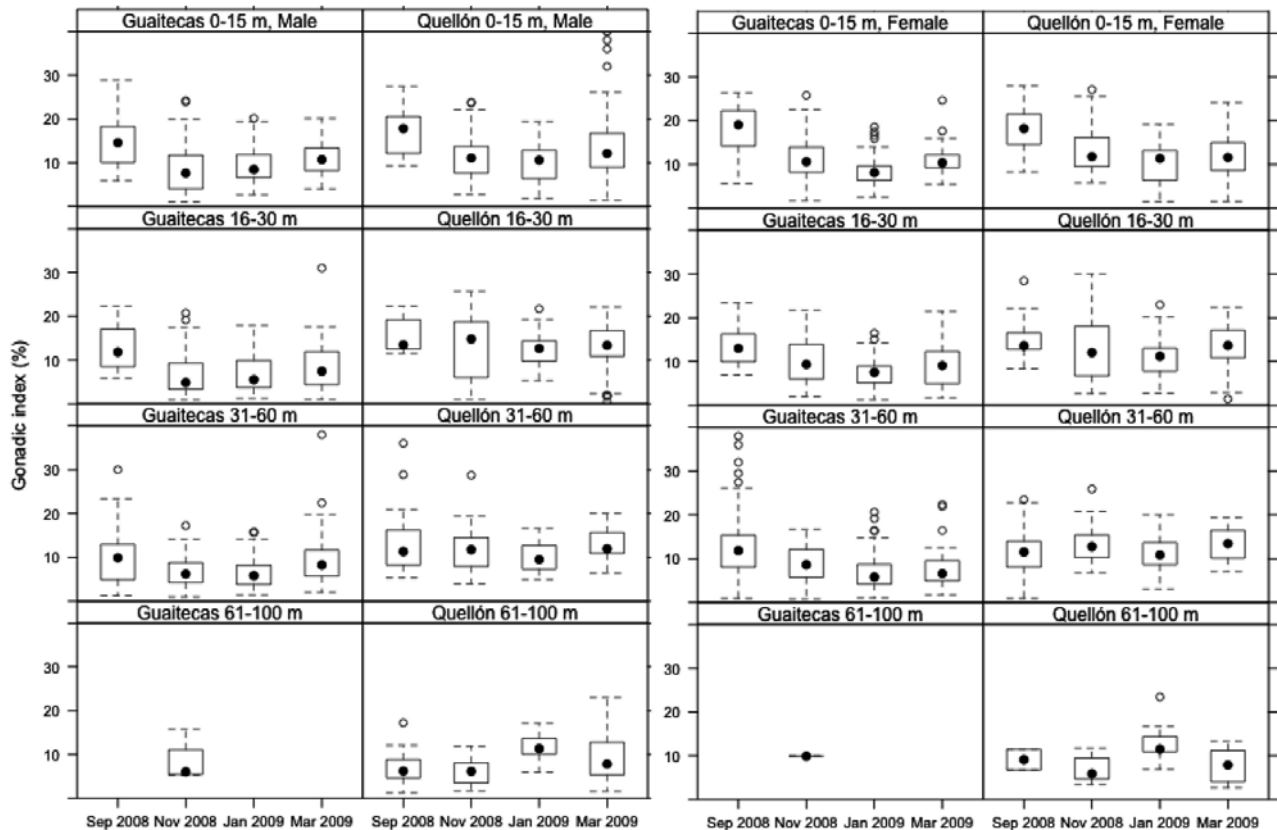
Area		Observed abundance per depth stratum			
		0 to 10 m	11 to 30 m	31 to 60 m	61 to 100 m
Quellón	Abundance	65,870,694	15,773,764	740,402	54,342
	Percentage	79.90	19.03	0.50	0.02
Guaitecas	Abundance	347,756,380	7,218,463	649,957	546
	Percentage	97.79	2.03	0.18	0.00

2008. The lowest median value was observed in the same area and month, but at the deepest strata (Fig. 3, Table 2). The GI for the second analysis (only the Quellón area, sex, all the depth strata and months) showed significant differences (ANOVA,  $P < 0.05$ ), where the median GI in samples from 31-60 m showed significant differences with respect to all other strata (Table 2). No significant differences in male/female ratios were observed (ANOVA,  $P > 0.05$ ) in the first three strata (0-60 m). Nevertheless, significant differences were observed (ANOVA,  $P < 0.05$ ) in the proportion of females (30%) to males (70%) found in samples from Quellón collected from the 60-100 m depth stratum (Fig. 4, Table 2).

### SPAWNING

Induced spawning success for the first three strata was

significantly affected by month, sampling area, test diameter and the interactions between month and depth strata, and between month and sampling area (Table 3, Fig. 5). The results indicated that the spawning success was scarce in September, while the greatest spawning success occurred between November and March, depending upon month, depth strata and sampling area. *Loxechinus albus* from Guaitecas did not respond to induction in September (Fig 5), but showed a similar pattern to Quellón during the rest of the season. Spawning induced in Quellón showed an asynchrony between depth strata, where the highest success ratios tended to occur later in the season at the deepest strata (Fig. 5, Table 3). Sex was not a significant factor in explaining induced spawning success variability.



**Figure 3.** Boxplot of the gonad index of *L. albus* (separated by males and females) per study area and depth strata. Black dots indicate medians; boxes indicate percentiles 25 and 75. Whiskers indicate 5<sup>th</sup> and 95<sup>th</sup> percentiles. White dots indicate outliers / Box plot de la variación del índice gonádico de *L. albus* (separados para machos y hembras) por área y estrato de profundidad. Puntos negros indican la mediana, cuadros representan los percentiles 25 y 75, barras de error muestran el percentil 5 y 95%. Puntos blancos indican valores fuera de rango

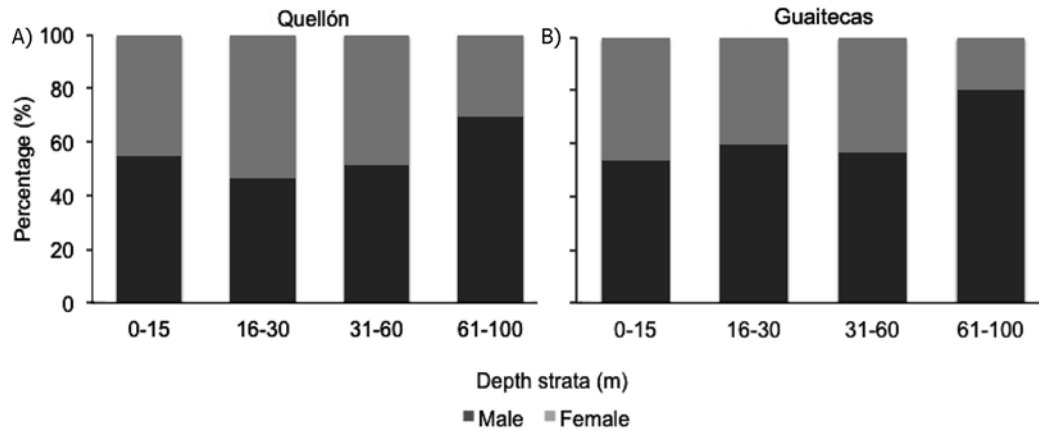
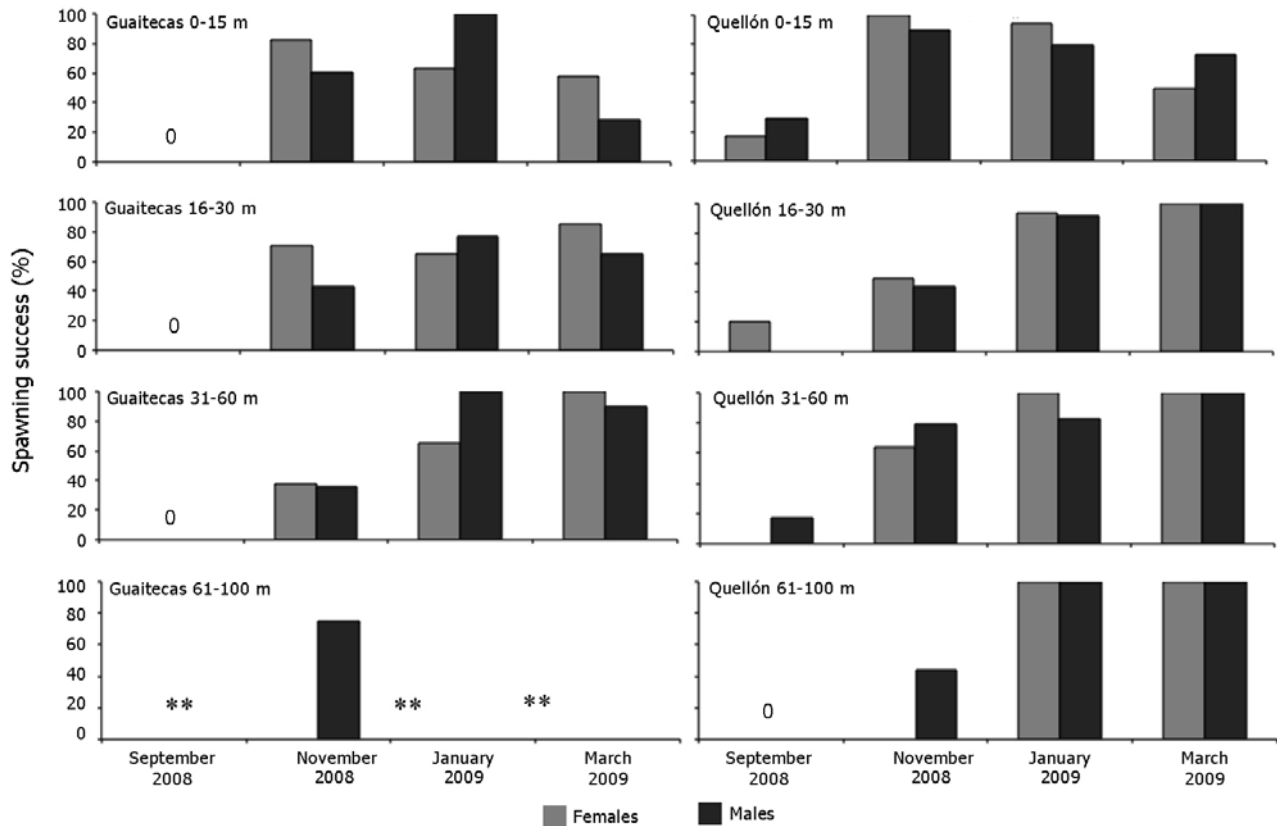


Figure 4. Sex ratios for *L. albus* per area and depth strata for the whole sampling period from A) Quellón and B) Guaitecas/ Proporción de sexos para *L. albus* por área y estrato de profundidad para todo el periodo de muestreo de A) Quellón and B) Guaitecas

Table 2. ANOVA table for the variation in arcsine transformed gonadic index observed in *Loxechinus albus* sampled between September 2008 and March 2009. Significant effects are highlighted with asteriks / ANOVA para la variación del índice gonádico, transformado usando la función Arcoseno, en *Loxechinus albus* muestreados entre septiembre de 2008 y marzo de 2009. Efectos significativos son destacados con asterisco

<i>Loxechinus albus</i> GI	Degree of freedom	Sum of square	Mean square	F	<i>P</i> (>F)
0-60 m depth					
Depth strata	2	0.4158	0.20791	29.3	2.68E-13*
Area	1	1.5038	1.50376	211.921	2.20E-16*
Sex	1	0.1736	0.17357	24.46	8.11E-07*
Month	3	1.748	0.58268	82.116	2.20E-16*
Residuals	2389	16.952	0.0071		
0-100 m depth from Quellón					
Depth strata	3	0.4627	0.154217	22.0159	6.90E-14*
Sex	1	0.0091	0.009051	1.2922	0.2559
Month	3	0.2421	0.080685	11.5186	1.90E-07*
Residuals	1223	8.5669	0.007005		





**Figure 5. Spawning induction success in *L. albus* females and male per area, depth strata, for all sampling periods. Zero indicates spawning failure, while double asterisk indicates no urchins were available for spawning induction experiments / Éxito en la inducción al desove en machos y hembras de *L. albus* por área y estrato de profundidad para todo el periodo de muestreo. Ceros indican fracaso en la inducción al desove, mientras que doble asterisco indica que no fueron recolectadas hembras para los experimentos de inducción al desove**

**Table 3. Deviance analysis of the general linear model (binomial family, logit link) used to evaluate spawning induction success in *Loxechinus albus*, injected with KCl. Two designs for each analysis are show: Spawning success between 0-60 m depth, for the entire study period and both study areas, and spawning success for *L. albus* from Quellón over the entire bathymetric gradient. The best model is one that shows highest likelihood ratio relative to other models and their  $\chi^2 P < 0.05$ / Análisis de Desviación del modelo general lineal (familia binomial, link logit) usado para evaluar el éxito en la inducción al desove en *Loxechinus albus* inyectados con KCl. Se muestran dos diseños por cada análisis: éxito de desove entre 0-60 m de profundidad, para todo el periodo de estudio y ambas áreas de estudio, y éxito de desove para erizos de Quellón en el gradiente batimétrico 0 a 100 m de profundidad. El mejor modelo muestra un mayor valor de razón de verosimilitud y su  $\chi^2 P < 0,05$**

<i>Loxechinus albus</i> spawning success	Likelihood-ratio	$\chi^2$ Degree of freedom	$P(>\chi^2)$
<b>0-60 m depth</b>			
Month	276.521	3	2.20E-16*
Depth strata	0.516	2	0.772697
Area	24.796	1	6.37E-07*
Test diameter	9.251	1	0.0023*
Month * Depth strata	57.254	6	1.62E-10*
Month * Sampled area	9.6	3	0.0222*
<b>0-100 m depth from Quellón</b>			
Month	153.45	3	2.20E-16*
Depth strata	1.685	3	0.6402
Test diameter	5.867	1	0.01543*
Month * Depth strata	52.188	9	4.17E-08*

As released oocytes were not estimated for the first spawning induction experiments (September 2008), related variables were only available for November 2008, January 2009, and March 2009. The greatest numbers of released oocytes/female were recorded in March in both areas, at most sampling strata, with a maximum average of nearly 5 million oocytes/female in Quellón (Laitec depression), at the 16-30 m depth stratum (Table 4). In November and January, the average number of released oocytes/female ranged between 280,000 and 797,000 across areas and depth strata, except at the Quellón 31-60 m depth stratum where they reached the value of 1,483,000 released oocytes/female (Table 4).

The delta-gamma general linear model, which included only the three shallower strata in Quellón and Guaitecas, built to explain variability in the number of oocytes·g<sup>-1</sup>, showed that month and depth strata, explained significant proportions of observed variability (Table 5). On the other hand, the delta-gamma general linear model which included all the strata in Quellón showed that only month explained a significant proportion of the observed number of oocytes·g<sup>-1</sup> variability (Table 6), showing that corrected number of oocytes·g<sup>-1</sup> were highest in March 2009 (Fig. 6A). It was possible to observe general pattern

characterized by a induced spawning success that started earlier in Quellón and at shallower depths and increased in March, at intermediate depths, both in Quellón and Guaitecas (Fig 6A and 6B). Corrected number of oocytes·g<sup>-1</sup> in urchins from the deepest depths of the Quellón depression was recorded only from January to March 2009 (Fig. 6C), but the delta-gamma model results showed that depth was significant only for the spawning success (Table 6), and the number of oocytes was only affected by month.

## DISCUSSION

Most *L. albus* patches were confined to shallow areas (0-10 m depth), patches between 30 and 60 m depth were rare, and only one patch was found below 60 m (Laitec patch). Regardless of the depth strata, densities were low across the whole study area at the time this survey was carried out, ranging between 1 and 15 individuals·m<sup>-2</sup> (Molinet *et al.* 2009, Moreno *et al.* 2011). These low densities could be the result of the high fishing pressure that affects the study area, with recorded landings between 3,000 and 4,500 ton year<sup>-1</sup> in Quellón, and between 1,800 and 2,500 ton year<sup>-1</sup> in Guaitecas in the last 5 years (Molinet *et al.* 2009, Moreno *et al.* 2011).

**Table 4. Mean numbers of oocytes spawned (thousand of oocytes ± standard deviation) by *Loxechinus albus* females induced to spawn by KCl injection by depth, month and area / Promedio de ovocitos desovados (miles de ovocitos ± desviación estandar) por área y por mes para hembras de *Loxechinus albus* inducidas al desove por inyección de KCl**

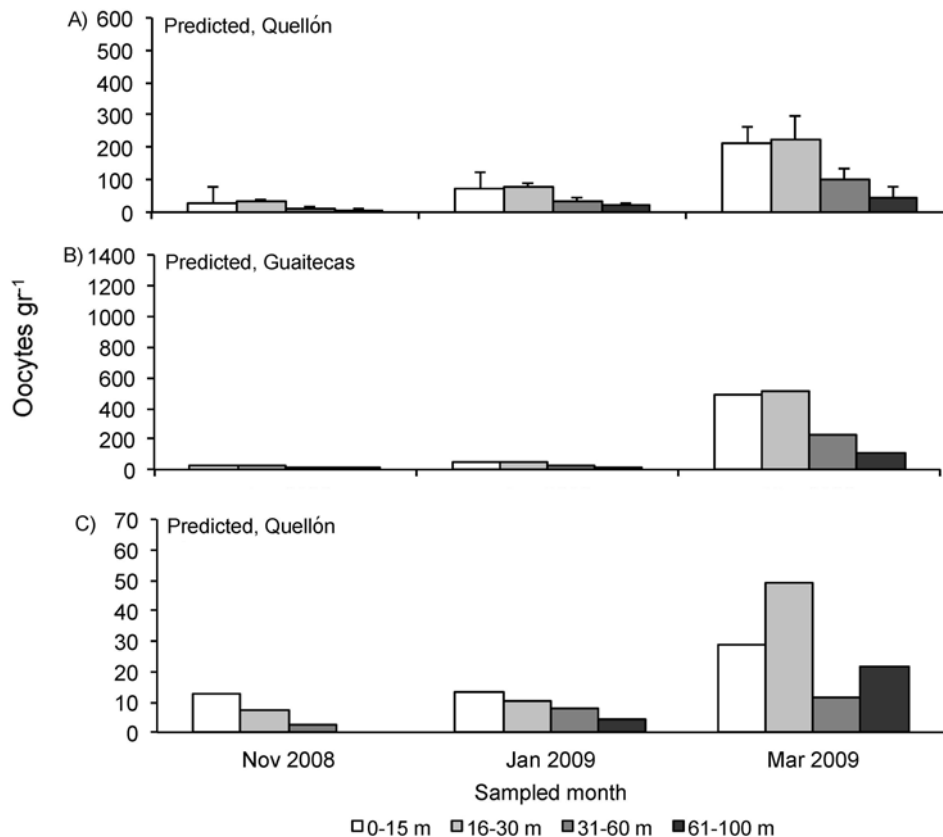
Depth stratum (m)	Month	Guaitecas	Quellón
0 - 15	September 2008		
	November 2008	367 ± 488	683 ± 740
	January 2009	345 ± 749	588 ± 707
	March 2009	2,402 ± 4,554	1,536 ± 1,852
16 - 30	September 2008		
	November 2008	419 ± 576	797 ± 1603
	January 2009	280 ± 301	748 ± 745
	March 2009	3,603 ± 4,064	4,993 ± 5,517
31 - 60	September 2008		
	November 2008	105 ± 201	326 ± 540
	January 2009	376 ± 529	1,483 ± 1042
	March 2009	1,793 ± 2,943	720 ± 85
61 - 100	September 2008		
	November 2008	0	0
	January 2009		753 ± 1181
	March 2009		1,305 ± 177

**Table 5. Likelihood ratios and  $\chi^2$  test for explanatory variables selected by the delta-gamma general linear model (GLM) approach used to explain variability in spawning induction results, in both study areas, from November 2008 to March 2009, and between 0-60 m depth. Results are presented for the logistic sub-model applied to the dichotomous success/failure results and for the log-gamma sub-model applied to the conditional ( $n>0$ ) number of released oocytes  $g^{-1}$ . The best model is one that shows highest likelihood ratio relative to other models and their  $\chi^2 P < 0.05$ / Relaciones de verosimilitud y test  $\chi^2$  para las variables explicatorias seleccionadas por la aproximación delta-gama usada para evaluar la variabilidad en los resultados de inducción al desove en ambas áreas de estudio entre noviembre de 2008 y marzo de 2009 en los estratos 0-15, 15-40 y 40-60 m de profundidad. Los resultados muestran (arriba) el submodelo aplicado a la dicotomía éxito/fracaso en el desove y (abajo) el submodelo log-gamma, aplicado a la condición ( $n > 0$ ) número de ovocitos liberados por gramo de hembra. El mejor modelo muestra un mayor valor de razón de verosimilitud y su  $\chi^2 P < 0,05$**

<i>Loxechinus albus</i>	Likelihood-ratio	$\chi^2$ Degree of freedom	$P (>\chi^2)$
Spawning induction success between 0-60 m depth			
Month	3.2464	2	0.197
Depth strata (3 strata)	0.016	2	0.992
Area	9.3608	1	0.002*
Month * Depth strata	22.8801	4	0.0001*
Month * Area	5.928	2	0.051
Positive number of oocytes $g^{-1}$ between 0-60 m depth			
Month	97.036	2	2.20E-16*
Depth strata (3 strata)	16.509	2	0.00026*
Area	1.452	1	0.2281613
Month * Depth strata	6.134	4	0.1893828
Month * Area	4.831	2	0.089306

**Table 6. Likelihood ratios and  $\chi^2$  test for explanatory variables selected by the delta-gamma general linear model (GLM) approach used to explain variability in spawning induction results, in Quellón, from November 2008 to March 2009, and over the entire bathymetric gradient 0-100 m depth. Results are presented for the logistic sub-model applied to the dichotomous success/failure results and for the log-gamma sub-model applied to the conditional ( $n > 0$ ) number of released oocytes  $g^{-1}$ . The best model is one that shows highest likelihood ratio relative to other models and their  $\chi^2 P < 0.05$ / Relaciones de verosimilitud y test  $\chi^2$  seleccionadas por el modelo GLM delta-gamma utilizado para evaluar la variabilidad en la inducción al desove y el número de ovocitos en Quellón desde noviembre de 2008 a marzo de 2009 en el gradiente batimétrico de 0 a 100 m de profundidad. Los resultados muestran el submodelo aplicado a la dicotomía éxito/fracaso en el desove y el submodelo log-gamma, aplicado a la condición ( $n > 0$ ) número de ovocitos liberados por gramo de hembra. El mejor modelo muestra un mayor valor de razón de verosimilitud y su  $\chi^2 P < 0,05$**

<i>Loxechinus albus</i>	Likelihood-ratio	$\chi^2$ Degree of freedom	$P (>\chi^2)$
Spawning induction success between 0-100 m depth from Quellón			
Month	11.3114	2	0.003*
Depth strata (4 strata)	0.2601	3	0.967
Month * Depth strata	21.5997	6	0.001*
Positive number of oocytes $g^{-1}$ between 0-100 m depth from Quellón			
Month	30.9918	2	1.86E-07*
Depth strata (4 strata)	6.3388	3	0.096
Month * Depth strata	6.1469	5	0.29218



**Figure 6.** Corrected mean number of oocytes  $g^{-1}$  estimated for *L. albus* females induced by KCl injection from A) Quellón and B) Guaitecas areas in the first three strata and between November 2008 and March 2009. C) Corrected mean number of oocytes  $g^{-1}$  estimated for *L. albus* females induced by KCl injection from the four strata studied at Quellón. Error bars show standard errors / Promedio corregido del número de ovocitos  $g^{-1}$  estimado para hembras de *L. albus* inducidas al desove utilizando KCl en las áreas de A) Quellón y B) Guaitecas en los primeros tres estratos, entre noviembre de 2008 y marzo de 2009. C) Promedio corregido del número de ovocitos  $g^{-1}$  estimado para hembras de *L. albus* inducidas al desove en el área de Quellón en los cuatro estratos estudiados. Las barras de error muestran los errores estándar

We found spatial and temporal differences in GI and spawning induction results. Median GI observed for *L. albus* showed higher median values during September, except for samples collected below 30 m in Quellón, where these indices peaked during January. The GI pattern observed in shallower patches was the same as that reported in the literature for shallow patches of this species in the study area (Bay-Schmith *et al.* 1981, Kino & Agatsuma 2007).

The temporary increase in GI observed in January for the 60-100 m depth stratum in the Laitec patch may reflect either a reproductive or an energy storage process, as gonad development has been described to serve the later function in sea urchins (Bay-Schmith *et al.* 1981). Nonetheless, the positive response to spawning

induction in January and March, matched by an evident decrease in median GI between January and March suggests that natural spawning may be occurring at this depth. Furthermore, we did not find significant differences in the corrected number of oocytes  $g^{-1}$  between deep and shallow patches in the Laitec patch, which suggests that a similar reproductive contribution per individual existed along the entire bathymetric gradient, but a delayed maturity process occurred at this deeper depression.

The observed spatial and temporal heterogeneity in GI and induced spawning success suggests an asynchronous reproductive maturity schedule between the northern and southern sectors of the Corcovado Gulf and across depth strata. Spatial differences in reproductive processes of the urchin *L. albus* were

previously observed by Bay-Schmith *et al.* (1981) between the same areas (north and south of the Corcovado Gulf), suggesting that temperature effects could explain these differences. As the temperature throughout the water column of the Laitec Depression is homogeneous (C. Molinet unpubl. data), delayed reproductive maturity in this depression can not be explained by temperature effects. We hypothesize that vertical differences in reproductive timing could result from differential access to an adequate food supply. Persistence, growth and reproductive dynamics of deeper sea urchin patches might depend partially or completely upon top-down pathways driven by saprophyte detritus. Therefore, food supply to deep patches in southern Chile may depend upon two main processes. First, the removal of coastal seaweed by seasonal storms (Moreno & Sutherland 1982, Buschmann *et al.* 2004, Hinojosa *et al.* 2007, 2010), and, second, the interactions between local currents, hollows and rises that can induce significant modifications in the residual flow, as observed in the Laitec Depression by Cáceres *et al.* (2008). These interactions could promote downwelling and convergence over the hollow as described by Park & Wang (1991) and Salas-Monreal & Valle-Levinson (2009) in other systems, supplying organic detritus to deep areas where seaweeds are scarce. These pathways have been described for deep-sea environments adjacent to productive near-shore habitats such as seagrass meadows or kelp forests, where macrophyte detritus removed from these habitats may be transported offshore to deep-sea benthic communities via bottom currents (Harrold *et al.* 1998, Vetter & Dayton 1998).

The potential importance of macrophyte detritus as a food supply to the Laitec patch is supported by incidental observations, obtained during two exploratory surveys conducted in September and December 2008 (pers. obs.). While we did not observe detached seaweeds during the first exploratory survey in September, we observed and recorded images with abundant detached seaweeds (*Macrocystis pyrifera*) down to a depth of 90 m in the Laitec Depression in December.

The reasons for the observed deviation from a 1:1 sex ratio in the deepest strata of the Laitec patch remains unclear, although it could be related to a higher selective predation on females, as observed in *Paracentrotus lividus* (Lamarck, 1816) by Gianguzza *et al.* (2009). Testing this or other alternative hypotheses deserves further study.

We found evidence of *L. albus* reproductive capacity

over the entire studied bathymetric gradient (0-100 m depth), although urchin patches deeper than 30 m represent less than 1% of the studied population. However, given the reported maturity curve of *L. albus* in the study area (Bay-Schmith *et al.* 1981, Lozada & Bustos 1984), and of smaller individuals from shallower habitats as observed by Moreno *et al.* (2011) it is important to examine the reproductive contribution of these deep sea urchins found in the Laitec Depression, and whether that contribution may explain the persistence of patches as heavily exploited as it happens around Quellón.

Considering our results and scientific literature worldwide, at least three hypotheses can be proposed: First, results allow us to propose that recruitment to heavily exploited patches in shallower strata might be partly subsidized by unfished spawning patches from deeper habitats, which could explain the presence of urchin aggregations between 60 and 100 m depth in Laitec channel. The actual importance of such subsidies would depend, however, upon several factors, besides the mere presence and abundance of reproductively active adults in deep areas. It is possible to identify two main factors, which would be strongly regulated by local oceanographic processes (Cáceres *et al.* 2008): (i) the amount and timing of food imports (kelp debris) from upper strata, and (ii) the strength and direction of transporting fluxes affecting larvae originated from deep water spawners.

Second, these deeper habitats may not constitute a source, but a sink habitat for local populations (*sensu* Pulliam 1988), which are colonized by either stochastic dispersal mechanisms or from density-dependent expansions of the population into less suitable habitats (MacCall 1990). In spatially limited environments such active dispersion from source habitats can maintain large populations in distant habitats, which become stable in evolutionary terms (Pulliam 1988). Nonetheless, sub-populations in sink habitats would not be, by definition, self-sufficient. Thus, they would tend to gradually disappear, as shallower areas are over-exploited.

Third, it might be that shallower and deeper patches play complementary roles in increasing the resilience of the population to environmental variability (Kerr *et al.* 2010a). Under this portfolio effect hypothesis (Secor *et al.* 2009), sub-populations inhabiting less suitable, but more stable habitats would make marginal contributions to population dynamics during 'good years', where productivity was maximized at more suitable (but variable)



habitats. Nonetheless, these sub-populations would play a key role as a valuable population reservoir, able to sustain re-colonization of optimal habitats after catastrophic years.

While our findings are far from conclusive regarding which of the three hypotheses previously discussed explain the relationships between shallow and deep sea urchin patches in southern Chile, they do emphasize the precautionary value of protecting areas where sea urchins form extensive patches over a wide bathymetric gradient in southern Chile. This is a relevant component of an urgently needed management strategy that should be implemented to protect the over-exploited shallow-water sub-populations in the area and allow for their recovery.

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