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Reproductive cycle of *Loxechinus albus* (Echinodermata: Echinoidea) in two areas of the Magellan region (53°S, 70-72°W), Chile*

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SUMMARY: The reproductive cycle of the Chilean edible sea urchin, *Loxechinus albus*, was studied in two areas of the Magellan region, the Cockburn Channel (53°43'S, 70°42'W) and Dawson Island (53°43'S, 72°00'W). Eleven monthly samplings were carried out from April 1996 to May 1997 in each area and samples of between 88 and 100 organisms were collected. Test diameter, total wet weight, and wet gonad weight was measured for each organism. Sex, gonad index, maturity index and gametogenic condition were estimated for each organism through histological analyses. The results indicate that *L. albus* in the Magellan region has an annual reproductive cycle in which the temporal sequence of different gametogenic processes can not be distinguished accurately due to the rapid and continuous gonadal recovery and gamete production after the spawning period. Although mature organisms were present most of the year, simultaneous spawning of males and females occurred from August to September in Dawson Island and from July to September in the Cockburn Channel. Gametes of those organisms that became mature after the spawning period were resorbed by nutritive phagocytes. Results from this study suggest that small-scale variability of spawning period in the Magellan region is an exception to the latitudinal pattern of spawning period reported for most of the Chilean coast. This large-scale variability may be explained by the simultaneous occurrence of low temperatures and short days during late winter and early spring.

Key words: Loxechinus albus, sea urchin, reproductive cycle, Magellan region, marine benthic resources.

RESUMEN: CICLO REPRODUCTIVO DE *LOXECHINUS ALBUS* EN DOS ÁREAS DE LA REGIÓN DE MAGALLANES, CHILE. – El ciclo reproductivo del erizo comestible chileno, *Loxechinus albus*, fue estudiado en dos áreas en la región de Magallanes, Canal Cockburn (53°43'S, 70°42'W) e Isla Dawson (53°43'S, 72°00'W). Entre abril de 1996 y mayo de 1997 se realizaron 11 muestreos por área en los cuales se recogieron entre 88 y 100 individuos cada mes. De cada individuo se midió el diámetro de testa y se determinó el peso total húmedo y el peso húmedo de las gónadas, sexo, se estimó el índice gonádico, el índice de madurez y la condición gametógenica a través de análisis histológico. Los resultados indican que *L. albus* en la región de Magallanes tiene un ciclo reproductivo anual, en el cual no es posible distinguir claramente la secuencia temporal de los distintos procesos gametogénicos debido a la rápida y contínua recuperación y producción de gametos después del desove. Aunque se observaron individuos maduros durante todo el año, el desove simultáneo de machos y hembras ocurriría entre agosto y septiembre en Isla Dawson, y entre julio y septiembre en Canal Cockburn. Los gametos de individuos que maduraron después del período de desove fueron reabsorbidos por fagocitos nutritivos. La continuidad de la actividad gametogénica a través del año, y las variaciones en el período de desove entre las áreas estudiadas se explican considerando las diferencias en la disponibildad y tipo de alimento presente en las áreas de estudio. Estos resultados también indican que la región de Magallanes constituye una excepción al patrón latitudinal observado para el período de desove en gran parte de la costa chilena. Tales diferencias se explicarían considerando que las temperaturas más bajas y días más cortos ocurren simultáneamente durante el final de invierno y principio de primavera.

Palabras clave: Loxechinus albus, erizo de mar, ciclo reproductivo, región de Magallanes, recurso marino bentónico.

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INTRODUCTION

The Chilean edible sea urchin, *Loxechinus albus* (Molina, 1782) (Echinodermata: Echinoidea), is distributed throughout the Chilean coast, from Arica (18°S) to Tierra del Fuego (55°S). In southern Chile, specifically in the Magellan region (53°S), this resource has become the region's most valuable fishery, contributing 51% to the national fishery of *L. albus*.

Variation in timing and duration of the spawning period for sea urchin populations distributed along a large latitudinal range have been attributed to variations in water temperature (Byrne, 1990) and photoperiod (Bay-Schmith and Pearse, 1987). In Chile, the main reproductive period for L. albus occurs later in the year as latitude increases (Zamora and Stotz, 1992). However the exceptions to this pattern are Mejillones Peninsula (23°S), where sea urchin populations reproduce later in the year (November-December; Gutiérrez and Otsú, 1975), despite being located in northern Chile; and the Punta Arenas area (53°S) where the reproductive period extends from September to October (Bay-Schmith et al., 1981), despite being located in southern Chile. In addition to the latitudinal pattern, variations in the reproductive period have been reported for sea urchin populations inhabiting adjacent areas (Byrne, 1990; Zamora and Stotz, 1992). These small-scale geographic variations may be more important in the Magellan region due to its spatial heterogeneity. The Magellan region has a highly complex hydrographic regime due mainly to the complexity of the coast line. It is indented by numerous fjords and secondary channels leading to a complex web of waterways and embayments in the Pacific Ocean sector. In addition, the Magellan region is strongly modulated by its seasonal climatic characteristics (Endlicher and Santana, 1988).

These particular characteristics suggest that timing and periodicity of the reproductive cycle of *L*. *albus* in the Magellan region may be different from northern Chile populations, and they also suggest that there may exist differences among populations inhabiting the Magellan region. Specific information about the reproductive cycle of *L. albus* populations inhabiting the Magellan region and its relationships with environmental and habitat characteristics would allow the improvement of legislation concerning lower size limits and seasonal closures for this species. Thus, future management plans would be based on sound information and would

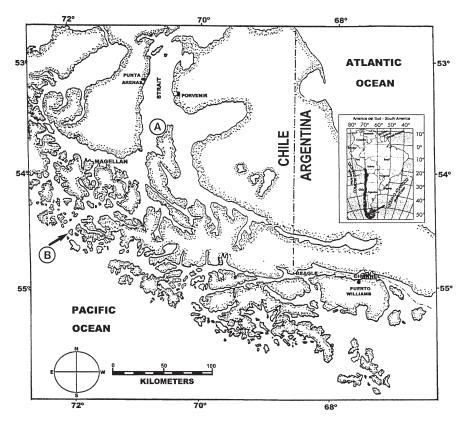


FIG. 1. - Map showing the sampling sites. (A) Dawson Island, Magellan Straits, Chile; (B) Cockburn Channel, Brecknock Peninsula, Chile.

contribute to the development of a sustainable exploitation of this fishery in the Magellan region.

In this context the main goal of this study was to determine the annual cycle of gonadal growth of the sea urchin, *Loxechinus albus*, inhabiting two contrasting sites located in the Magellan region. Additional information regarding environmental and habitat characteristics was obtained to search for relationships with the reproductive cycle results.

MATERIAL AND METHODS

Sampling sites

Reproduction of Loxechinus albus was examined at two sites located in Magallanes, XII Región, Chile. "Cockburn Channel" refers to an exposed bay located north of Aguirre Island, Cockburn Channel, Brecknock Peninsula (53°43'S, 70°42'W) (Fig. 1). "Dawson Island" (53°43'S, 72°00'W) is a small sheltered embayment west of Dawson Island, Magellan Straits (Fig. 1). Eleven monthly samplings were carried out at both sites from April 1996 to March 1997 in Cockburn Channel, and from June 1996 to May 1997 in Dawson Island. Between 88 and 100 organisms equal to or larger than 7 cm of test diameter were collected from both sites by SCUBA diving and taken to the laboratory. Simultaneously, surface sea temperature (°C), salinity (parts per thousand) and phytoplankton biomass (as chlorophyll-a) were measured at both sites (Parsons et al., 1984).

Laboratory procedures

Each organism was weighed to 0.1 g of precision and its maximum test diameter measured to 0.01 cm of precision. Gonads were removed and weighed to 0.0001 g of precision and then preserved in 10% formaldehyde (final conc.). Sex, Gonad Index (GI), and Maturity Index (MI) (Yoshida, 1952) were estimated for each organism. Five males and five females from each monthly sampling were chosen to determine gametogenic condition through histological analysis (GC). Histological procedure utilized to determine sex, MI and gametogenic condition was applied on the middle region of gonad number two (Larraín, 1975). Preserved gonads were dehydrated, embedded in paraffin and sectioned at 7 μ m. Between 4 and 6 paraffin sections from each organism were stained with haematoxylin and eosin

according to Martoja and Martoja-Pierson (1967).

Gonad Index (GI) for males and females was calculated separately as:

GI = (wet weight gonads / total wet weight) * 100

To estimate the Maturity Index (MI), cualitative microscopic analysis was made of paraffin sections of each organism to determine the gonad stage according to the relative scale for gonad maturation proposed by Fuji (1960), and recently applied by Byrne (1990) and Zamora and Stotz (1992). This scale identifies the following stages for males and females: spawned (I), recovery (II), growing (III), premature (IV) and mature (V). Information provided by this analysis was used to calculate MI proposed by Yoshida (1952):

$$MI = \left(\sum nF\right) / N$$

where MI is the Maturity Index, F is the gametogenic stage (I-V), n is the number of organisms in stage F, and N is the total number of organisms in the sample.

To determine Gametogenic Condition (GC), in each section of the five females 40 oocytes and/or ova were measured according to Holland (1967). Non-spherical oocytes were measured along their longest and shortest axes and the sum of these measures was halved to calculate the diameter. Data from these measurements were pooled and used to determine oocyte and ova size frequency distributions. For males, gonad condition was not homogeneous since mature ascini were observed throughout the year. Although for most echinoids measuring only one ascinus allows determination of the lobe stage (Holland, 1967), for L. albus it was necessary to measure ascini for the five paraffin sections of each organism. These measurements allowed estimation of relative abundance of the lobes in different stages in each organism and for all organisms analyzed during a given month.

RESULTS

Description of sampling sites

The substrate in Dawson Island was dominated by sand and boulder patches to which *Macrocystis pyrifera* were attached. In contrast, the substrate in Cockburn Channel was dominated by boulders and

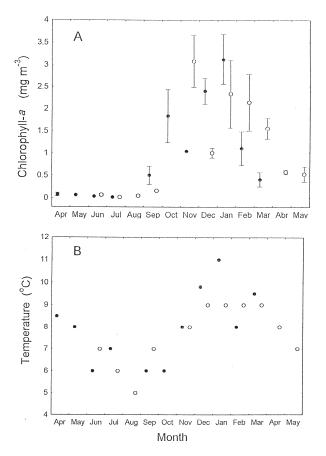


FIG. 2. – (A) Monthly values of phytoplankton biomass as mg clorophyll-a m⁻³ for Dawson Island (open circles) and Cockburn Channel (closed circles). (B) Monthly values of surface water temperature (°C) for Dawson Island (open circles) and Cockburn Channel (closed circles).

several macroalgae species were observed (Macrocystis pyrifera, Desmarestia sp., Lessonia sp., Gigartina skottsbergii, Rodhimenia sp., and Callophyllis variegata. In both sites, Dawson Island and Cockburn Channel, samples were collected from depths of 2 to 15 m. Sea surface temperature showed a clear seasonal pattern fluctuating from 5-6°C in winter and early spring to 9 and 11°C during late spring and summer in Dawson Island and the Cockburn Channel, respectively (Fig. 2). Sea surface salinity values ranged from low values of 31.5 to 34 ppt at both sites, without showing a clear seasonal pattern. Seasonal dynamics of phytoplankton biomass in both sampling sites varied from values lower than 0.5 mg chl.-a m⁻³ during the austral autumn and winter to maximum values of 2-3 mg chl.-a m-3 during late spring and early summer (Fig. 2).

Description of reproductive cycles

Males - Dawson Island. During June there was a high number of organisms in growing and prematurity. First mature organisms appeared in July and maximum percentage was observed in August along with the beginning of the spawning which extended until November (Fig. 3A and 4A). In December there was a high percentage of males in the spawned stage, and as a consequence MI continued to decrease during this month suggesting that the

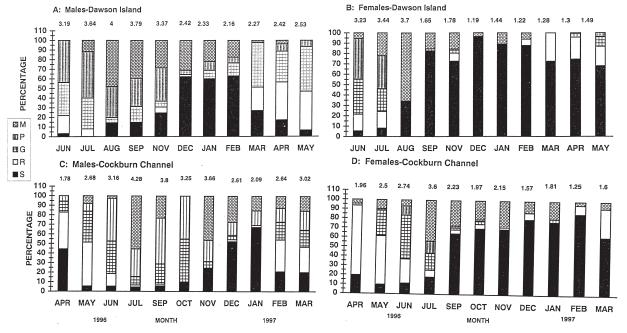


FIG. 3. – Percentage of males (A) and females (B) of *L. albus* collected in Dawson Island, and percentage of males (C) and females (D) collected in Cockburn Channel in stages of maturity (M), prematurity (P), growing (G), recovery (R), and spawned (S). Values on top of bars correspond to Maturity Index.

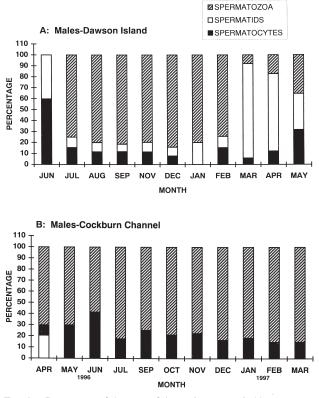


FIG. 4. – Percentage of the area of the ascinus occupied by spermatocytes, spermatids, and spermatozoa during the reproductive cycle of *L. albus* off Dawson Island (A) and Cockburn Channel (B).

spawned period could extend until December. However, the decrease of the MI occurred simultaneously with an increase of the GI (Fig. 3A and 5B), which suggests that the high percentage of spawned organisms in December was not due to gamete evacuation but to resorption of gametes. From late December to February there was a resting period in which no spermatogenic activitity was observed. Gonad recovery for the next cycle started during March with a high percentage of organisms in the recovery stage, and an increased number of spermatids and spermatozoa in the ascini (Fig. 3A and 4A). Mature organisms occurred throughout the year, which made gonad maturation not homogeneous. This continuous spermetazoa production did not conclude in a spawning event since GI continued to increase and no change in MI occurred. Thus, spermatozoa would be resorbed by nutritive phagocytes (Fig. 3A, 4A and 5B).

Females - Dawson Island. During June and July organisms in all stages were observed and as a consequence cell diameter fluctuated from 20 to120 μ m. The maximum percentage of mature females occurred during August, when aproximately 35% of the cells had a diameter of 80 μ m. The spawning

period started in August associated to both a decreasing number of cells of 80 μ m, and fluctuations of MI and GI (Fig. 3B, 5B and 6). Since no sampling was carried out during October, the end of the spawning period could have occurred in September or October. During November and January additional mature females were observed and caused an increase in MI, but this was not followed by a decrease of the GI (Fig. 3B and 5B). These secondary periods of mature females were followed by a vacuolization of the ova which suggests that this new maturation period did not conclude in a spawning. Although during December and January there was a small percentage of mature organisms and large cells, these gametes were not produced by new gametogenic activity, but they were the remaining mature organisms from previous months (Fig. 3B and 6). Gonad recovery for the next cycle started in March with abundant cell division which caused the dominance of oocytes less than 70 μ m. Gonad recovery for females was slower than for males.

Males - Cockburn Channel. The April-June period was characterized by an active gametogenesis

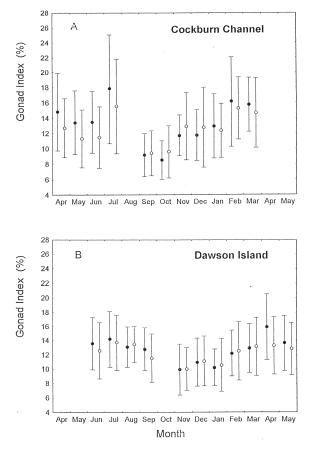


FIG. 5. – Monthly values of the Gonad Index for males (closed circles) and females (open circles) collected off Cockburn Channel (A) and Dawson Island (B).

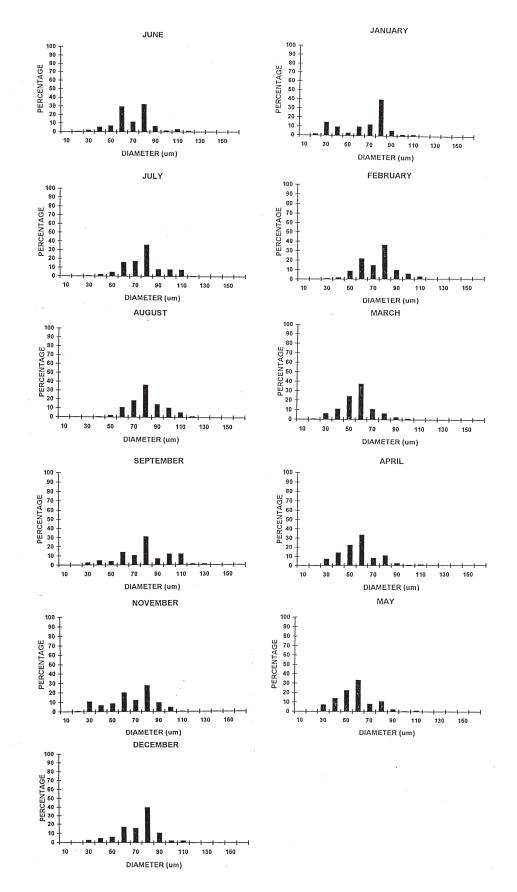


FIG. 6. - Frequency distribution of the diameter of oocytes and/or ova expressed as percentage for organisms collected off Dawson Island.

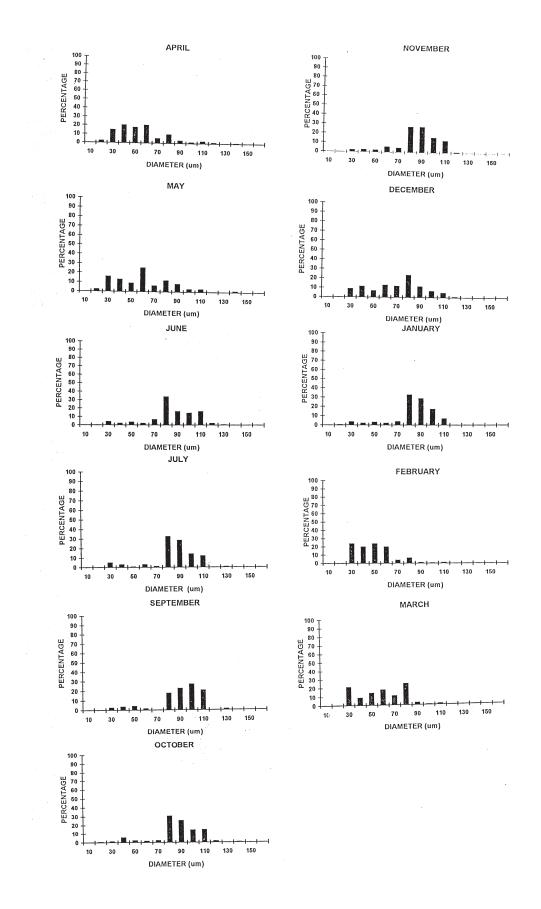


FIG. 7. - Frequency distribution of the diameter of oocytes and/or ova expressed as percentage for organisms collected in Cockburn Channel.

starting with a high number of organisms in recovery stage followed, in May, by organisms in growing, prematurity and in maturity stages (Fig. 3C and 4B). The maximum percentage of mature organisms and the beginning of the spawning period occurred during July, one month earlier than in Dawson Island and reached its maximum and end during October. During November additional mature organisms were observed increasing the values of GI and MI. However, since during December the two indices behaved inversely, the gametes produced by these additional mature organisms could have been resorbed and not spawned (Fig. 3C and 5A). The resting period is short and would occur in January when only one organism in recovery and none in the growing stage were observed. In February there was a sudden decrease of spawned organisms, and an important increase in the number of organisms in recovery and growing stages, which suggested the beginning of a new cycle (Fig. 7). In this site, as was observed in Dawson Island, mature organisms occurred throughout the year.

Females - Cockburn Channel. Gonad growth occurred from April to June associated to abundant cells smaller than 70 μ m. As in males, the maximum number of mature organisms occurred during July along with the beginning of the spawing period when MI and GI decreased simultaneously and cell diameter was equal to or larger than 80 μ m (Fig. 3D, 5A and 7). The spawning period of females ended during September. During the following months MI fluctuated due to the occurrence of mature organisms. However, ovary histology indicated that although these organisms became mature (cell diameter equal or larger than 80 μ m), their ova showed cytoplasm vacuolization, which along with the absence of a decrease of the GI during this period (Fig. 5A) suggests that ova would be resorbed by nutritive phagocytes to store energy for the next cycle. The resting period occurred during November when only one female in the recovery stage and none in growing stages were observed. Gonad recovery started in February and gametogenesis was slower than for males, since only females in the recovery stage with cell diameter equal to or smaller than 80 μ m were observed (Fig. 3D and 7).

The spawning period of males and females in both studied areas was not completely synchronic. In Dawson Island spawned females and males were observed from August to November and from August to September, respectively (Fig. 3A and 3B). In Cockburn Channel spawned females and males were observed from July to September and from July to October, respectively (Fig. 3C and 3D). Thus, the simultaneous spawning period for urchins collected in Dawson Island and Cockburn Channel would be August-September and July-September, respectively.

DISCUSSION

The reproductive cycle of L. albus in Cockburn Channel seems to be distinct from that of Dawson Island for having an earlier and longer spawning period as a consequence of an extended period of gametogenic activity which is revealed by the short resting and rapid recovery periods. This rapid and continuous gonad recovery and gamete production makes it difficult to distinguish the temporal sequence of different gametogenic processes. For most echinoids the different stages occur in a seasonal sequence, and the recovery period takes several months because of the urchin's gonad utilization for storing nutrients to produce gametes only before the spawning period (Byrne, 1990). However, the short recovery period and the continuous gamete production observed in this study is not an exception on the Chilean coast. This situation has also been reported for Tetrapigus niger in Punta Lagunillas and Herradura Bay in the IV region, Chile (30°05'S), and for Arbacia spatuligera in Concepción Bay (37°S) (Bay-Schmith, 1982). The presence of mature organisms during long periods has been related to food availability (Pearse, 1981). Keats et al. (1984) reported that urchins feeding on macroalgae have greater gonad development than those feeding on calcareous algae. Since the dominant food items found in the two study sites were macroalgae, it is probable that food availability for these populations allows them to support a continuous gamete production. However, the absence of both a continuous spawning and a resting period during which L. albus would store nutrients suggests that gametes are being resorbed by nutritive phagocytes in the gonads as a mechanism to supply energetic demands. Bernard (1977) indicated that gametogenesis in Strongylocentrotus franciscanus during starvation, with normal gonad index, continues for 3-4 weeks, then phagocytosis exceeds gamete production, and the gonad degenerates to a dark brown mass.

Timing and duration of spawning period for *Lox*echinus albus is variable among adjacent areas (small-scale variability) and along the Chilean coast (large-scale variability). At the small-scale, our study reports the beginning of the spawning period in Cockburn Channel one month earlier than Dawson Island. Bay-Schmith et al. (1981) found that in Punta Arenas the spawning period would occur during September-October. Arana et al. (1996) grouping samples from several areas surrounding Punta Arenas determined a spawning period between August and September. These three studies conducted in the Magellan region are coincident that spawning period would finish at the most by the end of October. However, the beginning of the spawning period varies among the studies, which makes the spawning period shorter or longer for the different sites. Such small-scale differences in urchin populations have been reported for several sea urchin species (Andrew, 1986; Byrne, 1990; Zamora and Stotz, 1993). The main factor suggested as being responsable for variability in reproductive cycle, and also in the magnitude of spawning, has been food quality and availability. In Ireland, Paracentrotus lividus belonging to different populations showed different gonadal growth which was explained considering the differences in food availability among areas (Byrne, 1990). These differences have also been explained considering differences in population density. Andrew (1986) reported that for Evechinus chloroticus populations there was an inverse relationship between gonad size and population density under the same conditions of food availability, which suggested a limited food situation. The degree of exposition was mentioned by Zamora and Stotz (1993) to explain differences in the spawning period of Tetrapigus niger belonging to populations geographically close to each other. However, there is no quantitative information regarding the relative importance of this factor.

According to observations made in our study regarding the composition of macroalgal communities at both sites it is possible that the food type available for urchins may influence the length of the spawning period. *Desmarestia* sp., which has been reported as one of the preferred food items for other urchin species (Keats *et al.*, 1984), was also observed in Cockburn Channel where the spawning period was longest. In contrast, the most abundant macroalga in Dawson Island was *Macrocystis pyrifera* which was found to be distributed in patches. Lemire and Himmelman (1996) demonstrated a positive correlation between preferred algae by urchin and gonad production. Vadas (1977) reported that urchins in habitats containing preferred macroalgae had larger Gonad Indices than those collected in habitats with non-preferred macroalgae. Thus, Cockburn Channel may represent a more favorable habitat for urchins in terms of food type and availability. This condition in Cockburn Channel may be the cause of both, the more extended spawning period and the more active reproductive cycle compared to Dawson Island. Marín *et al.* (1997) reported that urchins collected in Cockburn Channel had a larger mean reproductive potential (11.36%) than those collected at Dawson Island (5.93%). This result was explained considering differences in availability of food items.

The large-scale variability in spawning period of urchin populations along Chilean coast was well presented by Zamora and Stotz (1992). They reported that the spawning period occurs later in the year as latitude increases. For example, in Caleta Coloso (23°S) the spawning period occurs in June (Zegers et al., 1983), in Punta Lagunillas (30°S) during the period June-August (Zamora and Stotz, 1992), in Valparaíso and Quisco (32-33°S) during August-November (Buckle et al., 1978; Guisado and Castilla, 1987), and in Chiloé and Guaitecas Islands (42-45°S) during the period November-December (Bay-Schmith et al., 1981). Urchin populations inhabiting areas surrounding Punta Arenas (53°S) are an exception to this pattern since their spawning period occurs from July to September (this study), September-October (Bay-Schmith et al., 1981) and August-September (Arana et al., 1996). Thus, spawning period would be closer to the middle of the year and not late in the year as would be expected according to the pattern described by Zamora and Stotz (1992).

Urchin populations inhabiting Herradura Bay, Chile showed a main spawning period during the advection of low temperature water (9-11°C) associated with phytoplankton blooms and short days during the winter (Zamora and Stotz, 1992; 1993). Phytoplankton concentration has also been reported as a factor triggering spawning in sea urchins. Starr et al. (1990) demonstrated experimentally that high phytoplankton concentrations trigger spawning in the green sea urchin, Strongylocentrotus droebachiensis. These authors conclude that phytoplankton blooms may be a more reliable signal of favourable conditions than temperatures at the time of spawning, since they integrate various environmental parameters indicating favourable conditions for larval success. Results from our study indicate that the spawning period in the two sampled sites was related to low

temperatures (5-7°C) and short days (average: 8 h of daylight during winter) (Santana, 1996), as was concluded by Zamora and Stotz (1992). Spawning in these urchin populations had no relation to phytoplankton blooms. Phytoplankton concentration began to increase during October and reached the maximum during the period November-January, which is two and three months after the beginning of spawning in Dawson Island and Cockburn Channel, respectively. If larval development of L. albus in the Punta Arenas area takes 30 days, as has been indicated for L. albus inhabiting the northern Chilean coast, the larvae would have no food to survive until settlement. The lack of correspondence between spawning time and phytoplankton blooms has been reported for Antarctic asteroids (Pearse et al., 1991). In these organisms, spawning begins three to four months before the pulse of plytoplankton. Larvae of these species begin to feed actively when they are one or two months old and feed on bacterioplankton. Time delay between spawning and phytoplankton blooms suggests that larvae of L. albus in the Magellan region may have a development pattern similar to that described for Antarctic asteroids.

Differences in urchin reproductive cycle and those that may occur at the larval stage between urchins inhabiting the Magellan region and those inhabiting the northern Chilean coastline suggest that the Magellan region should be treated differently regarding management strategies. Results from this study suggest that spatial heterogeneity in both, environmental conditions and food availability for urchins in the Magellan region, needs to be considered in future management plans to ensure both protection of urchin populations inhabiting the region and the development of a sustainable exploitation. Future studies should consider investigating the reproductive cycle of populations inhabiting areas located north and south of the Magellan Straits to determine the geographical extension of variability in the reproductive cycle and to investigate larval dynamics in the plankton, settlement and recruitment of sea urchins.

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REFERENCES

- Andrew, N.L. 1986. The interaction between diet and density in influencing reproductive output in the echinoid *Evechinus chlorticus* (Val.). J. Exp. Mar. Biol. Ecol., 97: 63-79.
- Arana, P., S. Palma, E. Bay-Schmith, M. Monardes and M. Galvez. – 1996. Aspectos biológicos y pesqueros del erizo (*Loxechinus albus*) en la Región de Magallanes. *Univ. Católica Valparaíso*, *Informe Final*, 23: 83-139.
 Bay-Schmith, E., C. Werlinger and J. Silva. – 1981. Ciclo anual de
- Bay-Schmith, E., C. Werlinger and J. Silva. 1981. Ciclo anual de reproducción del recurso erizo Loxechinus albus entre la X y XII Región. Informe final. Proyecto de Investigación, Subsecretaria de Pesca, Univ. Concepción: 1-66.
- Bay-Schmith, E. 1982. Estado actual de las principales pesquerías nacionales. Bases para un desarrollo pesquero. Complementación. Informe Inst. Fomento Pesq., Chile, 1-52.
- Bay-Schmith, E. and J.S. Pearse. 1987. Effect of fixed lengths on the fotoperiod regulations of gametogenesis in the sea urchin *Strongylocentrotus purpuratus*. *Invert. Reprod. Develop.*, 11: 287-294.
- Bernard, F.R. 1977. Fishery and reproductive cycle of the red sea urchin, *Strongylocentrotus franciscanus*, in British Columbia. J. Fish. Res. Board Can., 34 (5): 604-610.
- Buckle, F., C. Guisado, E. Tarifeño, A. Zuleta, L. Córdova and C. Serrano. – 1978. Biological studies on the Chilean sea urchin *Loxechinus albus* (Molina) (Echinodermata: Echinoidea). IV Maturation cycle and seasonal changes in the gonad. *Cienc. Mar.*, 5 (1): 1-15.
- Byrne, M. 1990. Annual reproductive cycle of the commercial sea urchin *Paracentrotus lividus* from an exposed intertidal and a sheltered subtidal habitat on the west coast of Ireland. *Mar. Biol.*, 104: 275-289.
- Endlicher, W. and A. Santana. 1988. El clima del sur de la Patagonia y sus aspectos ecológicos. Un siglo de mediciones climatológicas en Punta Arenas. Ans. Inst. Pat. Ser. Cs. Nat., Punta Arenas (Chile), 18: 57-86.
- Fuji, A. 1960. Studies on the biology of the sea urchin. II Size at first maturity of two sea urchins, *Strongylocentrotus mudus* and *S. intermedius*. *Bull. Fac. Fish. Hokkaido Univ.*, 11: 1-4.
- Guisado, C.B. and J.C. Castilla. 1987. Historia de vida, reproducción y avances en el cultivo del erizo comestible chileno Loxechinus albus (Molina, 1972) (Echinoidea: Echinidae). In: P. Arana (ed.), Manejo y Desarrollo Pesquero, pp. 59-68. Escuela de Ciencias del Mar, Univ. Católica de Valparaíso, Valparaíso.
- Gutiérrez, J. and I. Otsú. 1975. Periodicidad en las variaciones biométricas de Loxechinus albus Molina. Rev. Biol. Mar., Valparaíso, 15(2): 179-199.
- Holland, N.D. 1967. Gametogenesis during the annual reproductive cycle in a cidaroid sea urchin (*Stylocidaris affinis*). Biol. Bull., 133: 578-590.
- Keats, D.W., D.H. Steele and G.R. South. 1984. Depth-dependent reproductive output of the green sea urchin, *Strongylocentrotus droebachiensis* (OF Muller), in relation to the nature and availability of food. J. Exp. Mar. Biol. Ecol., 80: 77-91.
- Larraín, A. 1975. Los equinoideos fósiles y recientes de Chile. Gayana Zool., 35: 1-189.
- Lemire, M. and J.H. Himmelman. 1996. Relation of food preferences to fitness for the green sea urchin, *Strongylocentrotus droebachiensis*. Mar. Biol., 127: 73-78.
- Marín, S.L., S.T. Oyarzún, J.L. Iriarte and C. Valladares. 1997. Aspectos biológicos pesqueros recurso erizo XII Región. Univ. Magallanes, Informe Final: 1-127.
- Martoja, R. and M. Martoja-Pierson. 1967. Inition aux Techniques de l'Histologie Animale. Masson et Cie, Editeurs, Paris.

- Parsons, T.R., Y. Maita and C.M. Lalli. 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, New York.
- Pearse, J.S. 1981. Synchronization of gametogenesis in the sea urchins Strongylocentrotus purpuratus and S. franciscanus. In: W.H. Clark and T.S. Adams (eds.), Advances in Invertebrate Reproduction, pp. 53-68. Elsevier North Holland, Amsterdam.
- Pearse, J.S., J.B. McClintock and I. Bosch. 1991. Reproduction of Antarctic benthic marine invertebrates: tempos, modes, and timing. Amer. Zool., 31: 65-80.
- Santana, A. 1996. Resumen meteorológico año 1995, Estación Jorge C. Schythe. Ans. Inst. Pat. Ser. Cs. Nat., Punta Arenas, (Chile), 24: 97-104.
- Starr, M.J.H. Himmelman and J.C. Therriault. 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science*, 247: 1071-1074.

- Vadas, R.L. 1977. Preferential feeding: an optimization strategy in sea urchin. *Ecol. Monogr.*, 47: 337-371.
- Yoshida, M. 1952. Some observations on the maturation of the sea urchin, *Diadema setosum. Annot. Zool. Japan*, 25: 265-271.
- Zamora, S. and W. Stotz. 1992. Ciclo reproductivo de Loxechinus albus (Molina 1782) (Echinodermata: Echinoidea) en Punta Lagunillas, IV Región, Coquimbo, Chile. Rev. Chil. Hist. Nat., 65: 121-133.
- Zamora, S. and W. Stotz. 1993. Ciclo reproductivo de *Tetrapygus* niger (Molina 1782) (Echinodermata: Echinoidea) en dos localidades de la IV Región, Coquimbo, Chile. *Rev. Chil. Hist. Nat.*, 66: 155-169.
- Zegers, J.M. Oliva, C. Hidalgo and L. Rodriguez. 1983. Crecimiento de Loxechinus albus (Molina, 1982) (Echinodermata: Echinoidea) en sistemas de jaulas suspendidas a media agua. Mem. Asoc. Latinoamer. Acuicult., 5: 369-378.