Feeding and nutritional ecology of the edible sea urchin *Loxechinus albus* in the northern Chilean coast

Ecología nutricional y alimenticia del erizo comestible *Loxechinus albus* en el norte de Chile

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ABSTRACT

The red sea urchin *Loxechinus albus*, an economically important species occurring along the Chilean littoral benthic systems, has been heavily exploited by artisanal fisheries in recent decades. However, basic knowledge of its trophic biology is still scarce. Studies of this kind are critical to the successful development of farming techniques as an alternative to the harvest of natural populations. The aims of this study were to quantify the composition of *L. albus*' natural diet, to determine the assimilation efficiency of the most important dietary components, and to experimentally examine the species' trophic selectivity. Adult and juvenile specimens were sampled in spring 1993 and summer, fall and winter 1994 from the shallow subtidal zone of Iquique, northern Chile. Neither juveniles nor adults showed significant seasonal differences in dietary composition. The main items in the diet were the green alga *Ulva* sp. for juveniles and the kelp *Lessonia* sp. for adults. In adults, assimilation efficiency (as percentage of the total organic matter ingested) was not significantly different among individuals that consumed *Lessonia* sp. (48.7 %), *Ulva* sp. (44.6 %) and *Macrocystis* (38.1 %), whereas in juveniles assimilation efficiency was significantly higher for individuals fed on the chlorophyte *Ulva* sp. (55.4 %), followed by *Lessonia* sp. (35.0 %) and *Macrocystis* (25.5 %). These results suggest that *L. albus* undergoes an ontogenetic shift in the diet, consisting of a differential foraging strategy between juveniles and adults.

Key words: assimilation efficiency, *Loxechinus*, natural diet, trophic selectivity.

RESUMEN

El erizo *Loxechinus albus* (Molina, 1782) es un recurso de gran importancia económica en los sistemas bentónicos costeros, y que se encuentra bajo una fuerte presión de explotación. Sin embargo, los antecedentes sobre diversos aspectos básicos de su biología trófica son aún escasos. Estudios de esta naturaleza son importantes en razón a que constituyen la base para el desarrollo de técnicas de cultivo exitosas, alternativa a la explotación de poblaciones naturales. Los objetivos del presente trabajo fueron: determinar cuantitativamente la composición dietaria de *L. albus*, el grado de selectividad trófica, y las tasas de asimilación de los componentes de su dieta. Especímenes adultos y juveniles fueron muestreados en la primavera de 1993 y el verano, otoño e invierno de 1994 en la zona submareal de Iquique, norte de Chile. No se detectaron diferencias en la composición de la dieta de adultos y juveniles entre las estaciones muestreadas. El principal ítem alimentario de los juveniles y adultos fueron el alga verde *Ulva* sp. y el alga parda *Lessonia* sp., respectivamente. En experimentos de selección trófica se observó que los juveniles y adultos prefieren el ítem que es más abundante en su dieta natural. Estos resultados muestran un cambio ontogenético en la dieta de esta especie, sugiriéndose una estrategia de forrajeo diferencial entre juveniles y adultos.

Palabras clave: eficiencia de asimilación, *Loxechinus*, dieta, selectividad trófica.

INTRODUCTION

The red sea urchin, *Loxechinus albus* (Molina 1782), is distributed along the South Pacific coast, from northern Peru (6°53'50" S) to Tierra del Fuego (53°15' S) (Clark 1948, Bernasconi 1953). It is a gregarious, sedentary species inhabiting crevices and ledges in coastal shallow waters (Viviani 1975). It is also a benthic littoral resource of great social and economic importance along the Chilean coast, where it has been intensively exploited over the last decades by artisanal fisheries. Recent studies have shown that exploitation of *L. albus* has significantly increased, with a total catch of about 300,000 tons between 1984 and 1994 (Vásquez 2001). This amounts to over 20 % of the global sea urchin catch, making it the most heavily exploited echinoderm species in the world (Sernapesca 2006). Its commercial exploitation has virtually led to the extinction of the natural populations along the Chilean coast, where this fishery is currently operating with a closed season and size restriction. Therefore, mass cultivation (hatchery) of *L. albus* and subsequent repopulation in the wild is a viable alternative to prevent the species extinction and maintain it as an important economic resource. Despite the species' commercial value, basic biological aspects – from the physiological to the community level– remain poorly known (Vásquez 2001), which poses a constraint on the implementation of management strategies and successful hatchery technology.

In most animals, feeding and digestion are two interdependent stages of a single process by which most organisms obtain the nutrients and energy necessary to meet their metabolic demands (Penry & Jumars 1986). Accordingly, the mechanisms involved in searching for prey, feeding and digesting are of vital importance because they determine the organisms' nutritional status and reproductive performance (Vadas 1977, Karasov 1990, Penry 1993). Although several factors have been shown to affect the fitness of a predator exploiting a given prey resource, the nutritional value of the prey and handling cost for the predator are the most important in optimal foraging models (Pyke 1984).

The aim of this study was to describe the feeding behavior and nutritional ecology of juveniles and adults of *L. albus* in the northern Chilean coast by: (1) determining their natural feeding patterns; (2) exploring relationships between food preferences, nutrient values and assimilation efficiency, and (3) determining their feeding strategies.

MATERIAL AND METHODS

Collection of specimens

Individuals of *L. albus* were collected from Caleta Los Verdes (20°25' S, 70°08' W), approximately 30 km south of Iquique (northern Chile). Individuals were captured manually by diving in shallow subtidal waters, in spring 1993 and summer, autumn and winter 1994. On each occasion a total of 100 sea urchins were haphazardly collected. They were weighed to the nearest 0.1 g and their test diameter was measured to the nearest 0.01 mm. The urchins were classified into juveniles and adults according to the relationship between sexual maturity and body size, as defined by Bückle et al. (1978).

Diet composition

The gastrointestinal tracts of both juveniles and adults were removed, placed in plastic bags in a solution of 10% formalin with sea water, and transported to the laboratory where the contents were adjusted to a volume of 60 ml. Three 5 ml aliquots were distributed at random on a Petri dish with 30 intersection points and analyzed under a stereoscopic microscope (Castilla & Moreno 1982, Vásquez et al. 1984, Klumpp et al. 1993). Prey items were identified to the lowest taxonomic resolution possible. Kendall's Coefficient of Concordance was used to evaluate seasonal variations in the dietary composition of adults and juveniles (Siegel & Castellan 1988). Ontogenic changes in the diet were evaluated by means of the Spearman's rank correlation coefficient (r_s), using frequency of food item in the diet as the dependent variable and body weight as the independent variable.

Prey choice experiments

Juvenile and adult individuals of *L. albus* were collected from the study site and transported

live to the laboratory in aerated seawater, where they were acclimated in seawater running systems under a natural photoperiod and at an average water temperature of 17 °C.

To evaluate ecologically realistic food selectivity, multiple prey choice experiments were conducted. Among juveniles, 10 specimens of 35.0 ± 2.4 mm ($\overline{X}$ ± SE) of test diameter (TD) were offered 10 g of the most abundant items in their diet: the brown algae *Lessonia nigrescens* (Bory 1826), *L. trabeculata* (Villouta & Santelices 1986), *Glossophora kunthii* (C. Agardh; J. Agardh, 1822), *Macrocystis integrifolia* (Bory, 1826), and the green alga *Ulva* sp. In adults, a group of 10 specimens of 64.62 ± 3.39 mm ($\overline{X}$ ± SE) of TD were offered 20 g of the same algal species offered to juveniles. The kelp *Macrocystis integrifolia* was included in these experiments because it was an abundant algal component in the northern Chilean coast until it was wiped out during a strong ENSO event in 1982-1983 (Soto 1985), and because it has been reported as an important component of *L. albus*'s natural diet in other Chilean sites (Bückle et al. 1980, Vásquez et al. 1984). All these experiments were replicated three times.

Before each experiment, juvenile and adult urchins were starved until no feces were observed in the tanks (72 h) (Larson et al. 1980, Hay et al. 1986). Each experiment lasted 24 h under a natural photoperiod. At the end of the experiments, the remaining algae were removed and weighed to calculate total consumption rates. Statistical differences between consumption of the different items were evaluated using Friedman's non-parametric test (Siegel & Castellan 1988, Manly 1993).

Digestibility and nutritional food values

To evaluate the assimilation digestibility efficiency of organic matter of the most important items in the diet of *L. albus*, four groups composed of 10 juveniles and 10 adults each, were fed with 30 g of each of the algae most frequently consumed in the prey choice experiments. Before each experiment, the urchins were starved for 72 h. After 24 h. the feces produced during each experiment were siphoned out onto Whatman N 1 filter paper and dried. Assimilation efficiency was determined by an indirect method (Montgomery & Gerking 1980, Targett & Targett 1990, Benavides et al 2005), which compares organic and ash content in food and feces, using ash as a non-absorbed reference marker. Assimilation efficiency was calculated using the following formula: [1 - (% ash in food / % ash in feces)] x 100%. The differences between the items assayed were evaluated using a Kruskal-Wallis non-parametric ANOVA, and an a-posteriori test (Siegel & Castellan 1988).

Energy content of each algal item used in the experiments was determined in a Parr 1261 computerized calorimeter. Two replicates were determined to be ash free and reliable when the difference between two measurements was less than 1 %. Protein content was measured by a modification of the method used by Lowry et al. (1951). The percentage of ash content in the algal samples was determined by heating 3 sub-samples at 650 °C for 4 h in a muffle furnace.

RESULTS

Test diameter in both adults and juveniles of *L. albus* did not show seasonal variation (Kruskal-Wallis ANOVA, H = 3.75, P = 0.29; H = 2.02, P = 0.57 for adults and juveniles, respectively) and ranged between 21.9 and 126.9 mm, 33.2 mm being the average diameter for juveniles and 70.8 mm for adults (Table 1). Body weight, however, showed seasonal variations (Kruskal-Wallis ANOVA, H = 15.42, P < 0.01; H = 23.91, P < 0.01 for juveniles and adults, respectively). The greatest mean body weight for adults and the lowest weight for juveniles were observed in winter (Table 1).

Dietary analysis

The analysis of the diet of *L. albus* showed that this is a strictly herbivorous species. Algae comprised 100% of the items found in the guts in all seasons. The most frequent dietary items found in *L. albus* were: three phaeophytes (*Lessonia* sp., *Halopteris* sp., and *Glossophora* sp.), two chlorophytes (*Ulva* sp. and *Enteromorpha* sp.) and three rhodophytes (*Gelidium* sp., *Centroceras* sp., and *Polysiphonia* sp.). Of these algae, *Ulva* sp., *Lessonia* sp. and *Halopteris* sp., comprised

TABLE 1

Body weight (g) and test diameter (mm) of juveniles (A) and adults (B) of *Loxechinus albus* collected between spring 1993 and winter 1994 (X ± SE) at Caleta Los Verdes, Iquique, northern Chile

Peso corporal (g) y diámetro de testa (mm) de juveniles (A) y adultos (B) de *Loxechinus albus* colectados entre la primavera de 1993 y el invierno de 1994 en Caleta Los Verdes, Iquique, norte de Chile

(A) Juveniles					
Trait	Spring	Summer	Fall	Winter	Total
Body weight (g)	24.07(2.20)	16.64(1.79)	18.80(1.70)	13.33(0.70)	18.21(0.84)
Test diameter (mm)	34.52(0.93)	32.13(1.15)	33.77(0.93)	32.47(0.92)	33.22(0.49)
Replicates (n)	24	21	25	25	95
(B) Adults					
Trait	Spring	Summer	Fall	Winter	Total
Body weight (g)	110.41(4.04)	113.58(5.30)	116.99(5.73)	150.03(8.38)	122.75(3.02)
Test Diameter (mm)	70.15(1.40)	70.17(1.88)	70.52(2.37)	72.39(1.86)	70.81(0.95)
Replicates (n)	76	79	75	75	305

over 98 % of the diet of *L. albus* juveniles and adults. No significant seasonal differences were detected in the diet (Kendall's coefficient of concordance, W = 1, P < 0.01; W = 0.925, P < 0.01 for adults and juveniles, respectively).

In adults, the brown algae *Lessonia* sp. and *Halopteris* sp. were the most abundant food items in all seasons sampled, comprising 72.5 and 17.7 % of the average gut contents, respectively, followed by the green alga *Ulva* sp. with 7.7 % (Table 2). *Ulva* sp. was the most important food item (49.2 %) in juveniles' diet, followed by *Lessonia* sp. and *Halopteris* sp. (26.3 and 21.4 %, respectively; Table 2).

During its ontogeny, *L. albus* showed marked dietary differences. The relative abundance of *Ulva* sp. in the diet decreased sharply as *L. albus'* body size increased. A similar trend was observed for *Halopteris* sp. In contrast, *Lessonia* sp., showed a marked increase with *L. albus'* increasing body size (Sperman's rank correlation, rs = -0.47, P < 0.01 for *Ulva* sp.; rs = -0.29, P < 0.01 for *Halopteris* sp.; rs = 0.55, P < 0.01 for *Lessonia* sp.).

Prey choice experiments

The results of multiple prey choice experiments reject the null hypothesis of no prey selection in both juvenile and adult urchins (Friedman test, X^2 = 14.61, P < 0.05 for juveniles; X^2 = 12.43, P < 0.05 for adults). Of the six items

offered to juveniles, *Ulva* sp. was the preferred alga, whereas *Halopteris hordacea* and *Glossophora kunthii* were the least consumed items. In contrast, in adults the preferred item was *Macrocystis integrifolia*, whereas *H. hordacea* and *G. kunthii* were less consumed (Fig. 1).

TABLE 2

Dietary composition (%) of juvenile and adult individuals of *Loxechinus albus* at Caleta Los Verdes, northern Chile

Composición dietaria (%) de juveniles y adultos de *Loxechinus albus* en Caleta Los Verdes, norte de Chile

Prey item	Juveniles	Adults
PHAEOPHYTES	49.53	91.74
Lessonia sp.	26.29	72.49
Halopteris sp.	21.44	17.75
Glossophora sp.	1.80	1.50
RHODOPHYTES	0.65	0.41
Centroceras sp.	0.05	0.15
Gelidium sp.	0.60	0.20
Polysiphonia sp.	0.00	0.06
CHLOROPHYTES	49.83	7.93
Ulva sp.	49.16	7.67
Enteromorpha sp.	0.67	0.26
Total prey	95	305

Assimilation efficiency and nutritional food values

The energy content analysis of the five most important food items in *L. albus* diet (*Lessonia nigrescens*, *Lessonia trabeculata*, *Halopteris hordacea*, *Ulva* sp., and *Glossophora kunthii*), and of the kelp *M. integrifolia*, showed that *Ulva* sp. exhibits the highest caloric value (ash free), followed by *L.* trabeculata, then by *L. nigrescens* and *G. kunthii* with similar values. The lowest values corresponded to *Macrocystis integrifolia* and *H. hordacea* (Table 3). *Lessonia trabeculata* and *L. nigrescens* had the highest protein content values (16.1 and 13.1 %, respectively). *Glossophora kunthii*, *Ulva* sp., and *H. hordacea* exhibited similar protein levels, and the lowest caloric content (3.6 %) was observed in *M. integrifolia* (Table 3).
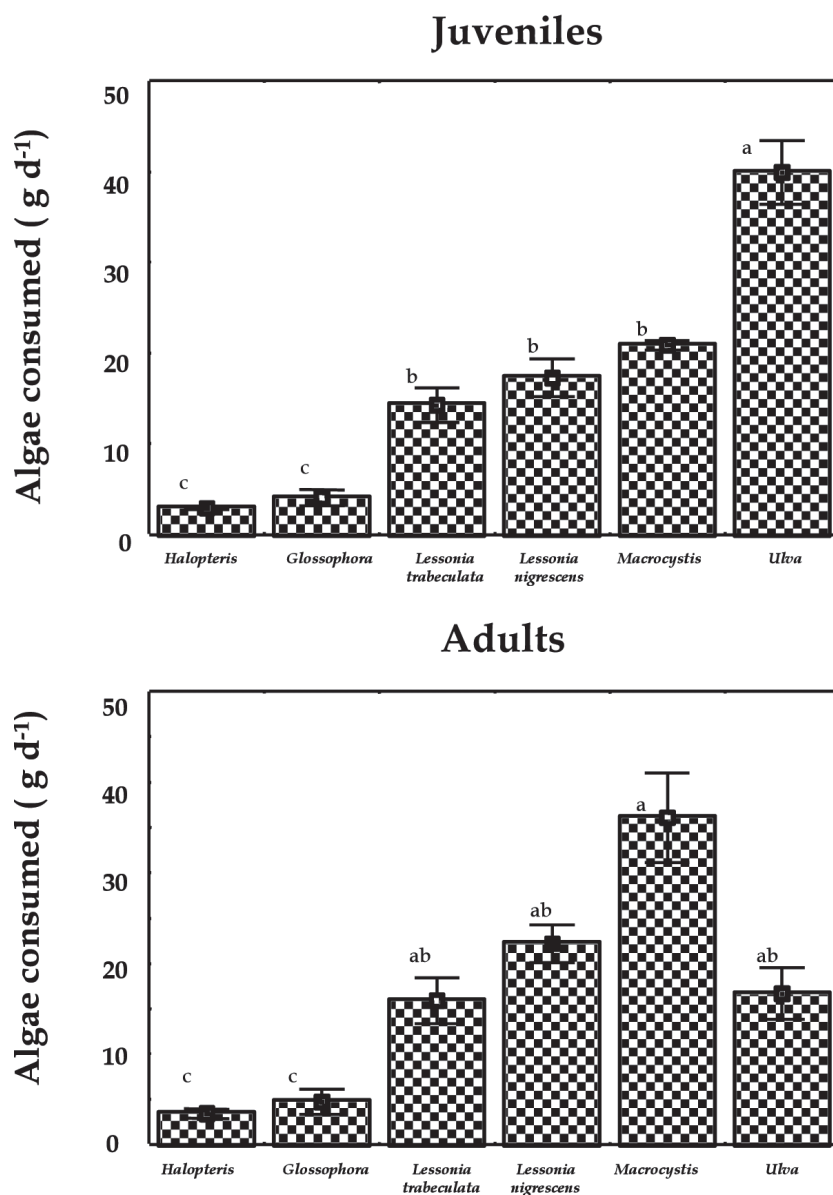
Juveniles

Adults

Fig. 1: Patterns of food selection in *Loxechinus albus* juveniles and adults at Caleta Los Verdes, Iquique (x ± SE, n = 5). Letters indicate statistically significant differences after a-posteriori tests.

Patrones de selección de alimentos en juveniles y adultos de *Loxechinus albus* en Caleta Los Verdes, Iquique. (x ± EE, n = 5). Las letras indican diferencias estadísticamente significativas luego de utilizar pruebas a-posteriori.

Assimilation efficiency in adults was not significantly different for the different algae assayed, the greater values corresponding to those individuals fed on *Lessonia nigrescens* (48.7 %), followed by *Ulva* sp. (44.6 %) and *M. integrifolia* (38.1 %) (Kuskal-Wallis test, H = 1.77, P = 0.41). On the other hand, assimilation efficiency in juveniles was significantly higher for *Ulva* sp. (55.4 %), followed by *L. nigrescens* (35.0 %), and lowest for *M. integrifolia* (25.5 %) (Kuskal-Wallis test, H = 6.48, P < 0.05) (Table 4).

DISCUSSION

Seasonal differences in individual biomass observed in *Loxechinus albus* may be related to seasonal differences in feeding rates. Previous studies on this species in central Chile reported a decrease in ingestion of plant material during the autumn-winter period, probably due to reproductive events and to fluctuations in algal availability (Bückle et al. 1980, Bay-Schmith 1982). Similarly, southern populations of this species show strong seasonal differences in energy allocation as response to food availability and reproduction (Pérez et al. 2008).

Dietary patterns

The diet of *L. albus* comprised eight algal taxa, the most important for adults being the brown algae *Lessonia* sp. and *Halopteris* sp., which together accounted for over 80% of the total diet between spring 1993 and winter 1994. These items were followed by the green alga

TABLE 3

Nutrient content of the principal dietary items of *Loxechinus albus*.

Contenido nutritivo de los principales itemes dietarios de *Loxechinus albus*

Item	Energy(kJ g^{-1})	Protein(%)	Ash(%)	Protein/energy
Lessonia trabeculata	12.73	16.09	30.27	1.26
Glossophora kunthii	12.04	9.98	36.35	0.83
Halopteris hordacea	9.55	9.36	45.02	0.98
Ulva sp.	13.27	9.66	30.49	0.73
Lessonia nigrescens	12.04	13.10	27.85	1.09
Macrocystis integrifolia	10.87	3.57	37.98	0.32

TABLE 4

Assimilation efficiency of juveniles (A) and adults (B) of *Loxechinus albus* (x ± SE, n = 4); (*) indicates statistically significant differences at P < 0.05 after the use of Kruskal-Wallis ANOVA test

Eficiencia de asimilación de juveniles (A) y adultos (B) de *Loxechinus albus* (x ± EE, n = 4) (*) indica diferencias estadísticamente significativas (P < 0,05) luego de utilizar la prueba de Kruskal-Wallis

	(A) Juveniles		
	Lessonia nigrescens	*Ulva* sp.	*Macrocystis integrifolia*
Ash in food (%)	27.85 ± 2.03	30.49 ± 1.16	37.98 ± 2.19
Ash in feces (%)	42.85 ± 5.82	68.43 ± 1.63	51.01 ± 1.82
Assimilation efficiency*	35.00 ± 3.84	55.44 ± 0.66	25.54 ± 1.89
	(B) Adults		
	Lessonia nigrescens	*Ulva* sp.	*Macrocystis integrifolia*
Ash in food (%)	27.85 ± 2.03	30.49 ± 1.16	37.98 ± 2.18
Ash in feces (%)	54.26 ± 4.46	55.08 ± 2.87	61.36 ± 5.84
Assimilation efficiency	48.67 ± 7.38	44.64 ± 4.99	38.10 ± 2.63

Ulva sp., the red algae *Centroceras* sp., *Polysiphonia* sp. and *Gelidium* sp., representing less than 1 % of the total diet. The prevalence of brown algae in the diet was also observed in others populations of *L. albus* from the central and southern Chilean coast (Bückle et al. 1980, Castilla & Moreno 1982, Vásquez et al. 1984), suggesting that brown algae are the most palatable components in the diet of adult sea urchins. This pattern can be primarily attributed to changes in digestive performance of adults probably related to the presence of enteric bacteria capable to break down the cell wall of phaeophytes, a characteristic that has been occasionally observed in sea urchins (Eppley & Lasker 1959, Harris 1993). In contrast, in juveniles, the most important item was *Ulva* sp. The prevalence of this green alga in the diet of *L. albus* has been reported earlier (Contreras & Castilla 1987, Santelices 1989, Bustos et al. 1991). This preference in juveniles for green algae could be attributed to facilitated digestion of starch over laminarin or a size effect that mechanical limits access to nutrients in a more rigid and leathery brown algae (Cáceres & Ojeda 2000).

The absence of seasonal changes in the diet of juveniles and adults may be because most of its trophic components (*Lessonia, Halopteris, Ulva, Glossophora*) are perennial and annual species that did not exhibit important seasonal fluctuations in the study site (S.J. González, personal observations). This disagrees with observations along the central and southern coast of Chile, where macroalgal communities undergo marked seasonal variations in diversity and abundance (Santelices 1989). For other Chilean species, particularly fish, these regional differences are reflected in the organisms' fitness and reproductive output (Cáceres et al. 1994).

Multiple prey choice experiments

Our results show that *L. albus* juveniles preferred *Ulva*, which was also the most important prey item in their diet during the sampling period. Similar results were obtained in other locations of the Chilean coast (Contreras & Castilla 1987, Santelices 1989, Bustos et al. 1991). Juveniles may prefer green algae because green algal compounds are more digestible than those of brown algae.

Furthermore, previous studies reported that juveniles fed on *Ulva* grew faster than those fed on *M. pyrifera* (Bustos et al. 1991). Similar results were reported for other echinoid species by Lawrence & Lane (1982) and Dafni (1992).

Loxechinus albus juveniles assimilated *Ulva* sp. more efficiently (55.4 %) than adults (44.6 %). The opposite situation was observed with the brown alga *L. nigrescens*. Such differences in assimilation efficiency may be due to ontogenic changes in the composition of the symbiotic bacterial flora in the digestive tract. These findings suggest that sea urchins have a great capacity to digest food efficiently (Fong & Mann 1980, Yano et al. 1993). Enteric bacteria would play an important role in food digestion, as in other species (Fuji 1967, Lawrence 1975, Fong & Mann 1980, Harris 1993, Yano et al. 1993, Bozinovic & Martínez del Río 1996). Neither juveniles nor adults showed preference for *Glossophora kunthii*. This trophic behavior is consistent with the natural diet found in the stomach of *L. albus* (1.8 % of *G. kunthii* in juveniles and 1.5 % in adults) and could be due to the presence of secondary metabolites in this alga that would act as a deterrent to herbivores (Arroyo et al. 1991, Martínez 1996).

The brown algae *H. hordacea* was the third most frequent (26.3 %) trophic item present in the diet of juveniles. These results together with results of multiple feeding preference experiments show that *L. albus* juveniles do not prefer *H. hordacea*, suggesting that its consumption is related to its natural availability. This is consistent with results of Vadas (1977), who showed that *Strongylocentrotus* spp. consume the alga *Agarum* in the laboratory in a lower amount than in the natural environment. The study of herbivores' diet is considered complex because of several factors: the prevalence of food items of low nutritional quality, the difficulties in selecting a balanced diet consistent with herbivores' nutritional requirements, and herbivores' need to avoid over-ingestion of the plants' secondary compounds (Lawrence 1975, Webster 1975, Hughes 1980, Krebs et al. 1983, Belovsky 1984, Pyke 1984, Stephens & Krebs 1986, Dearing & Schall 1992, Bozinovic & Martínez del Río 1996). In our study, *L. albus* clearly preferred food items with the highest protein content and energy values, hence the

highest fitness value. Results of the absorption efficiency experiments may explain the natural dietary composition patterns mentioned above. Thus, juveniles absorbed the green alga *Ulva* more efficiently than the other algae assayed. *Ulva* was the most frequently consumed item in multiple and dichotomic food preference experiments and was also the most abundant food item in the natural diet of *L. albus* juvenile stages (González 1995). Our findings are not consistent with the results of González et al. (1993), who found that juveniles of *L. albus* of southern Chile populations did not meet their metabolic requirements with *Ulva* because of higher losses of metabolic nitrogen as compared to other algae (*M. pyrifera* and *Gracilaria* sp.). The reason for such inconsistent results may be related to an effect of temperature on the physiology of this ectothermic invertebrate. For instance, Bückle et al. (1980) demonstrated that individuals of the southern Chilean coast consumed higher amounts of food and showed lower reproductive output and growth rates than those from the central coast, this suggest a lack of compensatory mechanisms against a thermal gradient. This paucity could partially explain the apparent lower incidence of *Loxechinus*' herbivory in the structure of the southern subtidal algal stand (Dayton 1985).

The metabolic requirements of an average juvenile individual would be met by consuming a lower amount of the green alga *Ulva* than of *Lessonia* or *Macrocystis*. In the study site, *Ulva* was less abundant than *Lessonia* or *Macrocystis*, suggesting that *L. albus* juveniles would act as energy maximizers (sensu Emlen 1966), i.e., they would consume the food that reports a higher energy input and nutrient gain-assuming a constant handling and searching time- thus obtaining a higher scope for growth and maintenance. On the contrary, *L. albus* adults would have a conformist behavior, foraging on a single patch of brown algae, the most abundant resource, during the necessary amount of time.

In comparison to terrestrial herbivores, specialization and co-evolutionary development of defenses are less common in marine systems (Stimson et al. 2007). This difference allows large marine invertebrates to change their dietary patterns as a plastic response to food availability and metabolic demand, and consequently are suitable models for testing predictions derived from foraging theory.

LITERATURE CITED

ARROYO P, M NORTE, JT VÁSQUEZ (1991) Absolute configuration of hydroazulenoid diterpenes based on circular dichroism. Journal of Organic Chemistry 56: 2671-2675.

BAY-SCHMITH E (1982) Erizo *Loxechinus albus* (Molina). Echinoidea, Echinoida, Echinoidae. Estado actual de las principales pesquerías nacionales. Bases para el desarrollo pesquero, Instituto de Fomento Pesquero, Gobierno de Chile, Santiago, Chile. 52 pp.

BENAVIDES AG, A VELOSO, P JIMÉNEZ[1] & MA MÉNDEZ (2005) Assimilation efficiency in *Bufo spinulosus* tadpoles (Anura: Bufonidae): effects of temperature, diet quality and geographic origin. Revista Chilena de Historia Natural 78: 295-302

BELOVSKY G (1984) Herbivore optimal foraging: a comparative test of three models. American Naturalist 124: 97-114.

BERNASCONI I (1953) Monografías de los echinoídeos argentinos. Anales del Museo Nacional de Historia Natural (Chile) 2: 17-18.

BOZINOVIC F & C MARTÍNEZ DEL RÍO (1996) Animals eat what they should not: why do they reject our foraging models? Revista Chilena de Historia Natural 69: 15-20.

BÜCKLE F, C GUISADO, C SERRANO, L CÓRDOVA, L PEÑA & E VÁSQUEZ (1978) Estudio del crecimiento en cautiverio del erizo *Loxechinus albus* (Molina) en las costas de Valparaíso y Chiloé. Anales del Centro de Ciencias del Mar y Limnología, Universidad Nacional Autónoma (México) 4: 141-152.

BÜCKLE F, K ALVEAL, E TARIFEÑO, C GUISADO, L CORDOVA, C SERRANO & J VALENZUELA (1980) Biological studies on the Chilean sea-urchin *Loxechinus albus* (Molina) (Echinodermata, Echinoidea). Food analysis and seasonal feeding rate. Anales del Centro de Ciencias del Mar y Limnología, Universidad Nacional Autónoma (México) 7: 149-158.

BUSTOS E, C GODOY, S OLAVE & R TRONCOSO (1991) Desarrollo de técnicas de producción de semillas y reproducción de recursos bentónicos. I. Investigaciones en el erizo chileno *Loxechinus albus* (Molina, 1782). Programa de las Naciones Unidas para el Desarrollo, Instituto de Fomento Pesquero, Gobierno de Chile, Santiago, Chile.

CÁCERES CW, LS FUENTES & FP OJEDA (1994) Optimal feeding strategy of the temperate herbivorous fish *Aplodactylus punctatus*: the effects of food availability on digestive and reproductive patterns. Oecologia 99: 118-123.

CÁCERES C & FP OJEDA (2000) Patrones de forrajeo en dos especies de peces intermareales herbívoros de las costas de Chile: efecto de la abundancia y composición química del alimento. Revista Chilena de Historia Natural 73: 253-260.

CASTILLA JC & C MORENO (1982) Sea urchin and *Macrocystis pyrifera*: experimental test of their ecological relations in southern Chile. In: Lawrence JM (ed) International echinoderm conference: 257-263. A.A.B. Balkema, Rotterdam, The Netherlands.

CLARK H (1948) A report on the echinoid of the warmer eastern Pacific based on the collections of the "Velero III". Allan Hancock Pacific Expedition 8: 265.

CONTRERAS S & JC CASTILLA (1987) Feeding behavior and morphological adaptations in two sympatric sea urchins species in central Chile. Marine Ecology Progress Series 38: 217-224.

DAFNI J (1992) Growth rate of the sea urchin *Tripneustes gratilla elatensis*. Israel Journal of Zoology 38: 25-33.

DAYTON PK (1985) The structure and regulation of some South American kelp communities. Ecological Monographs 55: 447-468.

DEARING D, J SCHALL (1992) Testing models of optimal diet assembly by the generalist herbivorous lizard *Cnemidophorus murinus*. Ecology 73: 845-858.

EMLEN JM (1966) The role of time and energy in food preference. American Naturalist 100: 611-617.

EPPLEY R & R LASKER (1959) Alginase in the sea urchin *Strongylocentrotus purpuratus*. Science 129: 214-215.

FONG W & K MANN (1980) Role of gut flora in the transfer of amino acids through a marine food chain. Canadian Journal of Fisheries and Aquatic Sciences 37: 88-96.

FUJI A (1967) Ecological studies on the growth and consumption of Japanese common littoral sea-urchin, *Strongylocentrotus intermedius* (A. Agassiz). Memory of Faculty of Fisheries, Hokkado University (Japan) 15: 84-160.

GONZÁLEZ S (1995) Ecología trófica del erizo comestible *Loxechinus albus*, en la zona norte de Chile. Marine Biology thesis, Universidad Arturo Prat, Iquique, Chile. 53 pp.

GONZÁLEZ ML, MC PÉREZ, DA LÓPEZ & CA PINO (1993) Effects of algal diet on the energy available for growth of juvenile sea-urchin *Loxechinus albus* (Molina, 1782). Aquaculture 11: 87-95.

HARRIS JM (1993) The presence, nature, and role of gut microflora in aquatic invertebrates: a synthesis. Microbial Ecology 25: 195-231

HAY M, R LEE & R GUIEB (1986) Food preference and chemotaxis in the sea urchin *Arbacia punctata* (Lamarck) Philippi. Journal of Experimental Marine Biology and Ecology: 96: 147-153.

HUGHES RN (1980) Optimal foraging theory in the marine context. Oceanography and Marine Biology Annual Review 18: 423-481.

KARASOV WH (1990) Digestion in birds: chemical and physiological determinants and ecological implications. Studies in Avian Biology 13: 391-415.

KREBS JD, W STEPHENS & W SUTHERLANS (1983) Perspectives in optimal foraging. In: Brush A & G Clark (eds) Perspectives in ornithology: 165-216. Cambridge University Press, New York, New York, USA.

KLUMPP D, J ESPINOSA & M FORTES (1993) Feeding ecology and trophic role of sea urchins in a tropical seagrass community. Aquatic Botany 45: 205-229.

LAWRENCE JM (1975) On the relationship between marine plants and sea urchins. Oceanography and Marine Biology Annual Review 13: 213-286.

LAWRENCE JM & JM LANE (1982) The utilization of nutrients by post-metamorphic echinoiderms. In: Jangoux M & JM Lawrence (eds) Echinoderm nutrition: 331-371. A.A. Balkema Publishers, Rotterdam, The Netherlands.

LARSON B, RL VADAS & M KESER (1980) Feeding and nutritional ecology of the sea urchin *Strongylocentrotus droebachiensis* in Maine, USA. Marine Biology 59: 49-62.

LOWRY H, N ROSENBROUGH, A FARR & R RANDALL (1951) Protein measurement with the Folin phenol reagent. Journal of Biological Chemistry 193: 265-275.

MANLY BFJ (1993) Comments on design and analysis of multiple-choice feeding-preference experiments. Oecologia 93: 149-152.

MARTÍNEZ EA (1996) Micropopulation differientiation in phenol content and susceptibility to herbivory in the Chilean kelp *Lessonia* nigrescens (Pheophyta, Laminariales). Hydrobiologia 326/327: 205-211.

MONTGOMERY WL & SD GERKING (1980) Marine macroalgae as foods for fishes an evaluation of potential food quality. Environmental Biology of Fishes 5: 143-153.

PENRY DL (1993) Digestive constraints on diet selection. In: Hughes RN (ed) Diet selection: an interdisciplinary approach to foraging behaviour: 32-55. Blackwell Scientific Publications, Oxford, United Kingdom.

PENRY DL & PA JUMARS (1986) Chemical reactor theory and optimal digestion. BioScience 36: 310-315.

PYKE GH (1984) Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics 15: 523-575.

PEREZ AF, E MORRICONI, C BOY & J CALVO (2008) Seasonal changes in energy allocation to somatic and reproductive body components of the common cold temperature sea urchin *Loxechinus albus* in a sub Antarctic environment. Polar Biology 31: 443-449.

SERNAPESCA (2006) Anuario estadística de pesca. Servicio Nacional de Pesca, Gobierno de Chile, Santiago, Chile. Xx pp.

SANTELICES B (1989) Algas marinas de Chile: distribución, ecología, utilización, diversidad. Ediciones Universidad Católica de Chile, Santiago, Chile. Xx pp.

SIEGEL S & NJ CASTELLAN (1988) Nonparametric statistics for the behavioral sciences. Second edition. McGraw-Hill, New York, New York, USA. 399 pp.

SOTO R (1985) Efectos del fenómeno El Niño 1982-83 en ecosistemas de la I Región. Investigaciones Pesqueras (Chile) 32: 199-206.

STEPHENS W & JR KREBS (1986) Foraging theory. Princeton University Press, Princeton, New Jersey, USA. 247 pp.

STIMSON J, T CUNHA & J PHILIPPOV (2007) Food preferences and related behavior of the brownsing sea urchin *Tripneustes gratilla* (Linnaeus) and its

potential for use as biological control agent. Marine Biology 151: 1761-1772.

TARGETT TE & NM TARGETT (1990) Energetics of food selection by the herbivorous parrotfish *Sparisoma radians*: roles of assimilation efficiency, gut evacuation rates, and algal secondary metabolites. Marine Ecology Progress Series 66: 13-21.

VADAS RL (1977) Preferential feeding: an optimization strategy in sea urchins. Ecological Monographs 47: 337-371.

VÁSQUEZ JA, JC CASTILLA & B SANTELICES (1984) Distributional patterns and diet of four species of sea urchin giant kelp forest (*Macrocystis pyrifera*) of Puerto Toro, Navarino Island. Chile. Marine Ecology Progress Series 19: 55-63.

VÁSQUEZ JA (2001) Ecology of *Loxechinus albus*. In: Lawrence JM (ed) Edible sea urchins: biology and ecology: 161-175. Elsevier, Amsterdam, The Netherlands.

VIVIANI CA (1975) Las comunidades marinas litorales en el norte grande de Chile. Dirección de Investigaciones Marinas, Universidad del Norte, Iquique, Chile. Xx pp.

YANO Y, Y MACHIGUCHII & Y SAKAI (1993) Digestive ability of *Strongylocentrotus intermedius*. Nippon Suisan Gakkaishi 59: 733.

WEBSTER S (1975) Oxygen consumption in echinoderms from several geographical location, with particular reference to the echinoidea. Bulletin of Marine Biology Laboratory 148: 157-180.