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Prey selection by *Larus belcheri atlanticus* in Mar Chiquita lagoon, Buenos Aires, Argentina: a possible explanation for its discontinuous distribution

Selección de presas por *Larus belcheri atlanticus* en la laguna de Mar Chiquita, Buenos Aires, Argentina: una posible explicación para su distribución discontinua

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ABSTRACT

The diet of the gull *Larus belcheri atlanticus* in Mar Chiquita Lagoon (Buenos Aires Province, Argentina) was studied through the analysis of pellets regurgitated in resting places during the non-reproductive season. This gull inhabits with low densities this brackish-water lagoon in winter (June to November) and preys on two grapsid crabs: *Chasmagnathus granulata* and *Cyrtograpsus angulatus*, species which are similarly used as food items. Rarely, remains of an ocypodid crab, *Uca uruguayensis*, birds, fishes and insects were found. Sex ratio and size of available grapsid prey were compared to data obtained from pellets. This gull preys selectively on females of both crab species but males of *C. granulata* are included in its diet to a certain extent. A selection for a definite prey size is observed. Although many gulls present a generalized trophic spectrum, *L. belcheri atlanticus* is a specialized feeder during most of the time spent in its wintering habitat.

Key words: Sea gull, crabs, salt marshes, coastal lagoons, Argentina.

RESUMEN

Se estudió la dieta de la gaviota *Larus belcheri atlanticus* en la laguna de Mar Chiquita, Provincia de Buenos Aires, Argentina, a partir del análisis de egagrópilas regurgitadas en lugares de descanso durante la estación no reproductiva. La gaviota habita esta laguna de aguas salobres en invierno (junio a noviembre), con baja densidad. Sus principales presas son dos cangrejos grápsidos, *Chasmagnathus granulata* y *Cyrtograpsus angulatus*, los que son utilizados de manera similar como alimento. Raramente se encontraron restos de un cangrejo ocipódido, *Uca uruguayensis*, aves, peces e insectos. Se compararon las proporciones de sexos y las tallas de los grápsidos disponibles como presas con los datos obtenidos de las egagrópilas. La gaviota depreda selectivamente sobre hembras de ambas especies de cangrejos pero su dieta incluye, en menor medida, machos de *C. granulata.* Se observó selección a favor de un tamaño definido de presa. A pesar de que muchas gaviotas presentan un espectro trófico generalizado, *L. belcheri atlanticus* es especialista en cuanto a su alimentación durante la mayor parte del tiempo que pasa en su hábitat invernal.

Palabras claves: gaviota, cangrejos, marismas, lagunas costeras, Argentina.

INTRODUCTION

Larus belcheri atlanticus breeds on the Atlantic coast at San Blas Island, Argentina (40°34'S, 62°15'W) and migrates off north towards Punta del Este, Uruguay (35°00'S, 59°58'W) and south to Puerto Deseado, Argentina (47°42'S, 65°54'W) during winter (Fig. 1) (Harrison 1985, Olrog 1967). This gull was described as a subespecies of *Larus belcheri*, a species confined to the coasts of South America (Harrison 1985), but it appeared morphologically too distinct from the Pacific *Larus belcheri belcheri* for this arrangement to be warranted (Devillers 1977). Moreover, differences in habitat and feeding habits have been determined (Olrog 1967, Devillers 1977).

Larus belcheri atlanticus has a discontinuous distribution, restricted to salt marshes or the mouth of rivers (Escalante

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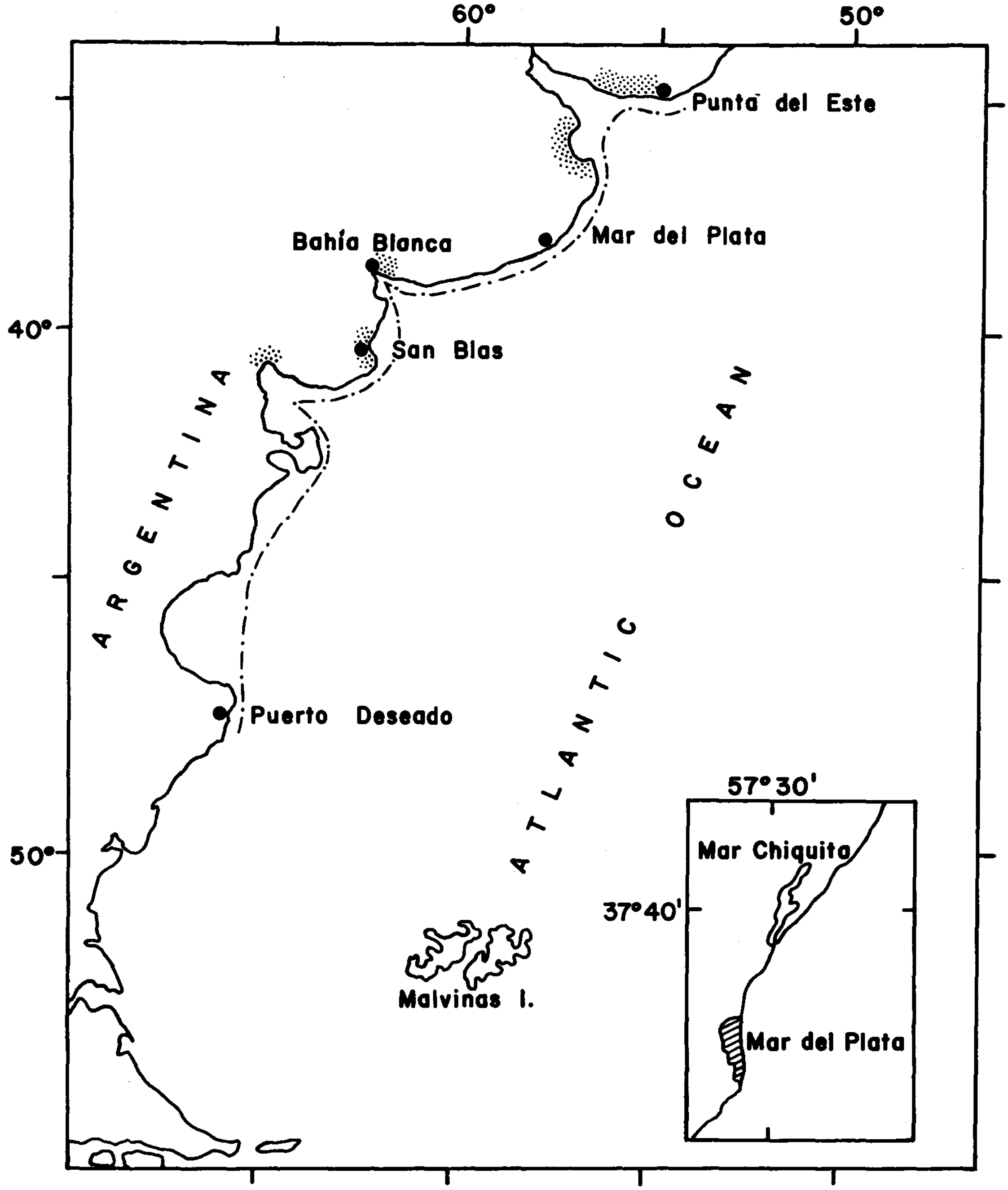

Fig. 1: Geographic distribution of *Larus belcheri atlanticus* (.........). Dotted areas indicate presence of dense grapsid crab assemblages. Insert: Mar Chiquita Lagoon and study area.

Distribución geográfica de *Larus belcheri atlanticus* (............). Las áreas punteadas indican la presencia de densas concentraciones de cangrejos grápsidos. Detalle: laguna de Mar Chiquita y área de estudio.

1966, Olrog 1967), and has never been seen in large numbers on the sea coast or "near the sewers of coastal cities or at the sea following in the wake of fishing boats" (Escalante 1966). Every winter, a number of *L. belcheri atlanticus* (adults, subadults and juveniles) arrive at Mar Chiquita Lagoon (37°46'S, 57°27'W), a body of brackish water which flows into the Atlantic Ocean 35 km north of Mar del

Plata (Fig. 1). In this estuarine habitat, gulls can be seen feeding on crabs from June to November.

Four species of crabs live in Mar Chiquita Lagoon: *Cyrtograpsus altimanus, Cyrtograpsus angulatus, Chasmagnathus granulata* (Grapsidae), and *Uca uruguayensis* (Ocypodidae). *Cyrtograpsus altimanus* and juvenile *C. angulatus* are found in the intertidal zone, under stones that form small moles. Juveniles of the latter species are also found on *Phycopomatus enigmaticus* "reefs". As *C. angulatus* grows, its distributional range gradually expands to subtidal muddy areas. However, during the annual reproductive period (from September to February), adults concentrate in dense clusters in intertidal muddy beaches (Gavio & Spivak, unpublished results). The most striking detail of the biology of *C. angulatus* is the high incidence of walking leg autotomy in adults, mainly in females, and the effect of predators has been postulated as a possible cause (Spivak & Politis 1989). *Chasmagnathus granulata* and *U. uruguayensis* are burrowing semi-terrestrial crabs always observed in intertidal muddy areas bordering *Spartina densiflora* grasslands (Boschi 1964). Adults of *C. granulata* leave their burrows when they are covered by water, although many of them remain in shallow waters even during low tides. *Uca uruguayensis* is active only during low tides, remaining in the vicinity of burrows. Crabs quickly run into their burrows when disturbed (Spivak *et al.* 1991).

Crabs are the main food item for *L. belcheri atlanticus* (Daguerre 1933, Escalante 1966, 1970, 1984, Devillers 1977). This latter author hypothesized that the concentration of gulls on or near rivers and lagoons is correlated with a specialized animal diet. However, this hypothesis is refuted by reports of omnivorous and scavenger feeding habits of gulls observed in Mar del Plata Fishing Harbor and in Puerto Belgrano, Argentina (Escalante 1984, Palmerini, unpublished results).

Gulls are conspicuous inhabitants (year round residents or seasonally abundant) of intertidal muddy or sandy flats, but scarce attention has been paid to their feeding ecology on these areas and few studies quantify the impact of their predation on prey populations. The present study was designed to estimate the importance of predation on crabs by *L. belcheri atlanticus* feeding on the salt marshes of Mar Chiquita Lagoon. Here, we document quantitatively the prey items utilized by this gull (crab species, size and sex) through analysis of regurgitated pellets. Finally, we examine the suggested relationships between the diet of *L. belcheri atlanticus* and its discontinuous distribution.

MATERIAL AND METHODS

The study area was located near the mouth of Mar Chiquita Lagoon, Buenos Aires Province, Argentina (37°46'S, 57°27'W), a coastal body of brackish water of 46 km^2 affected by tides and characterized by mud flats bordered by *Spartina densiflora* grasslands (Olivier *et al.* 1972a, Fasano *et al.* 1982). Samples (all available pellets regurgitated by gulls) were collected at different intervals between June and November 1988 in the upper horizontal surface of several moles where gulls, but no other birds, rested before and after feeding. Moles are usually covered by high tides, so pellets were certainly casted during the preceding 12 hours before collection. The contents of pellets were subsequently analyzed in the laboratory. The prey items present were sorted as follows: 1) insects (Carabidae and Curculionidae), 2) fishes, 3) birds, 4) crab chelae (*C. angulatus, C. granulata* and *U. uruguayensis*), and 5) crab mandibles (*C. angulatus* and *C. granulata*). One crab was counted per two chelae or mandibles, right and left, which differred less than 0.2 mm, and per one unilateral chela or mandible. The higher count in each pellet was taken as representative of the number of crabs present in it. The maximum width of each mandible in the broad terminal lobe (Snodgrass 1935) and the length and height of the *propodus* were measured with Vernier calipers to 0.1 mm. The sex of crabs was determined by comparing the length and height of each chela with the regression lines of these variables calculated for male and female *C. angulatus* and *C. granulata* (Table 1, Gavio & Spivak, Zagarese & Gómez, unpublished results). Crabs size (CW: carapace width) were independently estimated from mandible widths and chela lengths, using previously calculated and specific linear regressions of mandible versus carapace width (Table 1, *C. granulata* n = 74 and r = 0.99, *C. angulatus* n = 91 and r = 0.99) and of chela length versus carapace width (Table 1, Gavio & Spivak, Zagarese & Gómez, unpublished results). The mean number of crabs of each species and sex per sample and their mean CW were calculated and used for comparisons among samples.

Data on sex ratio, size (CW) and natural history of *C. angulatus* (Spivak & Politis 1989, Gavio & Spivak, unpublished results) and of *C. granulata* (Pérez, Rivero D'Andrea, unpublished results) were used to estimate prey availability[1].

RESULTS

Pellet analysis

The total number of collected pellets was 216; 105 were intact and had a mean weight (± SD) of 4.48 ± 2.07 g and they did not differ significantly among samples (ANOVA, $F_{(7,97)} = 1.92$, $0.1 > P > 0.05$). Out of those 216 pellets, 60 had remains of *Chasmagnathus granulata*, 20 of *Cyrtograpsus angulatus*, and 127 of both *C. granulata* and *C. angulatus*. Pellets with different composition were seldom found: 4 included remains of *C. granulata* and *C. angulatus* plus birds or the ocypodid crab *Uca uruguayensis*, 2 included remains of *C. granulata* plus insects or fishes and 3 included remains of insects and/or fishes (Table 2). The proportion of pellets containing remains of one or both grapsid crab species expected by chance (considering the 213 pellets with remains of crabs and the total number of identified crabs) was: 71.3 pellets with *C. granulata*, 37.8 pellets with *C. angulatus* and 103.9 pellets with both species. The observed proportion differed significantly from that expected by chance: more pellets contained both species and fewer only on of them (Table 2, Goodness of a fit tests, $X^2 = 16.3$, $P < 0.001$).

Mandibles or chelae found in gull's pellets allowed identification of 548 *Chasmagnathus granulata* and 399 *Cyrtograpsus angulatus*. The relative number of *C. granulata* and *C. angulatus* identified varied along the sampling period (Table 2). The X^2 tests rejected the null hypothesis of independence between the number of *C. granulata* and *C. angulatus* found during this study ($X^2 = 100.7$, d.f. = 14, $P < 0.001$). The mean number of crabs per pellet also varied significantly among samples, in both species (ANOVA, *C. granulata*, $F_{(14\text{-}197)} = 7.4$, $P < 0.01$; *C. angulatus*, $F_{(14\text{-}197)} = 4.2$, $P < 0.01$). Student's t-tests showed that there were more *C. granulata* than *C. angulatus* per pellet when the whole sampling period was considered, but only in six samples differences between their numbers were significant: in five of them dominated *C. granulata* and in the remainder (corresponding to 25 September) dominated *C. angulatus* (Table 2).

Remains of mandibles were found in 194 pellets and allowed to estimate the CW of 307 *C. granulata* and 336 *C. angulatus*. In most cases, estimates did not differ significantly among pellets of each sample, so mean CW values per sample were used for comparisons (ANOVA tests, Table 3). Crab's CW varied significantly along the sampling period (Table 3, ANOVA, *C. granulata*, $F_{(14\text{-}292)} = 6.2$, $P < 0.01$; *C. angulatus*, $F_{(14\text{-}321)} = 6.9$, $P < 0.01$).

Chelae, which allowed to determine sex, were found in 137 pellets. This way,

[1] Most of the mentioned "unpublished results" cocorrespond to Licenciatura Theses presented to the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Argentina (ML Coccia 1984, RD Palmerini 1988, A Pérez 1988, I Rivero D'Andrea 1989, M Rognone 1984) and to Seminars of the Summer Marine Biology Course, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina (HE Zagarese & SE Gómez 1982).

TABLE 1

Regression equations used to estimate size and sex of *Chasmagnathus granulata* and *Cyrtograpsus angulatus* from remains found in regurgitated pellets of *Larus belcheri atlanticus*. QW: chela width; QL: chela length; MW: mandible width; CW: carapace width. Authors: 1: Zagarese & Gómez (unpublished results); 2: Gavio & Spivak (unpublished results).

Ecuaciones de regresión usadas para estimar tamaño y sexo de *Chasmagnathus granulata* y *Cyrtograpsus angulatus* a partir de restos encontrados en egagrópilas de *Larus belcheri atlanticus*. QW: ancho de la quela; QL: largo de la quela; MW: ancho de la mandíbula; CW: ancho del caparazón. Autores: 1: Zagarese & Gómez (resultados no publicados); 2: Gavio & Spivak (resultados no publicados).

Species	Sex	Regression	Authors	Estimation of
Chasmagnathus granulata	Male	log QW = 1.107 log QL – 0.364	1	sex
	Female	log QW = 1.088 log QL – 0.400	1	sex
	Male	log QL = 1.368 log CW – 0.611	1	size
	Female	log QL = 1.108 log CW – 0.412	1	size
	---	MW = 0.143 CW – 0.206	this paper	
Cyrtograpsus angulatus	Male	ln QL = 1.235 ln QW + 0.899	2	sex
	Female	ln QL = 1.028 ln QW + 0.855	2	sex
	Male	ln QL = 1.235 ln CW – 1.374	2	size
	Female	ln QL = 1.028 ln CW – 0.977	2	size
	---	MW = 0.112 + 0.056	this paper	

TABLE 2

Number and type of regurgitated pellets of *Larus belcheri atlanticus* and number of crabs identified. Mean number of crabs of each species per sample were compared by Student's t-tests. *Cg: Chasmagnathus granulata, Ca: Cyrtograpsus angulatus*, d.f.: degrees of freedom. Significance: ns = non significant; * = 0.05 > P > 0.01; ** = 0.01 > P > 0.001; *** = P < 0.001.

Número y tipo de egagrópilas de *Larus belcheri atlanticus* y número de cangrejos determinados. El número promedio de cangrejos de cada especie por muestra fue comparado por pruebas t de Student. *Cg: Chasmagnathus granulata, Ca: Cyrtograpsus angulatus*, d.f.: grados de libertad. Significación: ns = diferencias no significativas; * = 0.05 > P > 0.01; ** = 0.01 > P > 0.001; *** = P < 0.001.

Date	Number of pellets					Number of crabs						
						Per sample		Per pellet (± SD)				
	Cg	*Ca*	Both	Other	Total	*Cg*	*Ca*	*Cg*	*Ca*	t	d.f.	
June 6	5	1	4	0	10	27	17	2.70 ± 2.00	1.70 ± 2.11	1.09	18	ns
June 14	9	1	1	0	11	30	4	2.73 ± 1.68	0.36 ± 0.92	4.10	20	***
June 20	3	1	6	0	10	36	14	3.60 ± 2.50	1.40 ± 1.50	2.39	18	*
June 29	4	1	10	0	15	28	32	1.87 ± 1.50	2.13 ± 2.39	0.36	28	ns
August 10	7	2	14	0	23	37	31	1.68 ± 1.13	1.41 ± 1.40	0.70	42	ns
August 11	3	2	10	0	15	30	27	2.00 ± 1.51	1.80 ± 1.57	0.36	28	ns
August 18	6	1	7	0	14	45	14	3.21 ± 1.67	1.00 ± 1.71	3.46	26	**
September 6	1	0	8	0	9	65	33	7.22 ± 2.95	3.67 ± 3.08	2.50	16	*
September 11	5	0	15	0	20	61	40	3.05 ± 1.79	2.00 ± 1.86	1.82	38	ns
September 25	0	3	18	0	21	34	63	1.62 ± 1.07	3.05 ± 1.50	3.55	40	***
October 17	2	2	8	0	12	20	36	1.67 ± 1.15	3.00 ± 2.52	1.66	22	ns
October 23	1	3	19	0	23	53	64	2.30 ± 1.89	2.74 ± 1.60	0.85	44	ns
October 26	4	2	0	0	6	11	5	1.83 ± 1.94	0.83 ± 1.33	1.04	10	ns
November 15	1	1	7	0	9	20	15	2.22 ± 1.48	1.67 ± 1.12	0.89	16	ns
November 23	11	0	4	3	18	51	4	3.40 ± 1.18	0.27 ± 0.59	9.19	28	***
Total observed	62	20	131	3	216	548	399	2.58 ± 2.00	1.88 ± 1.92	3.67	422	***

TABLE 3

Number and size (CW: carapace width) of crabs identified from mandibles found in pellets of *Larus belcheri atlanticus*. Estimated CWs within and among pellets were compared by ANOVA. NP: number of pellets, NC: number of crabs, d.f.: degrees of freedom. Significance: ns = non significant; * = 0.05 > P > 0.01; ** = 0.01 > P > 0.001; *** = P < 0.001.

Número y tamaño (CW: ancho del caparazón) de los cangrejos identificados a partir de mandíbulas encontradas en egagrópilas de *Larus belcheri atlanticus*. Los CW estimados fueron comparados dentro y entre las egagrópilas de cada muestra por medio de ANOVA. NP: número de egagrópilas, NC: número de cangrejos, d.f.: grados de libertad. Significación: ns = diferencias no significativas; * = 0.05 > P > 0.01; ** = 0.01 > P > 0.001; *** = P < 0.001.

Date	*Chasmagnathus granulata*						*Cyrtograpsus angulatus*					
	NP	NC	Mean CW ± SD (mm)	F	d.f.		NP	NC	Mean CW ± SD (mm)	F	d.f.	
June 6	7	12	30.2 ± 3,2	0.78	6-5	ns	5	16	27.9 ± 4.0	2.13	4-11	ns
June 14	10	25	28.6 ± 3.0	3.91	9-15	**	2	3	34.2 ± 3,3	1.61	1-1	ns
June 20	6	13	25.7 ± 3.2	2.83	5-7	ns	4	7	27.5 ± 4.7	0.48	3-3	ns
June 29	10	13	30.5 ± 2.4	0.35	9-3	ns	9	26	28.7 ± 4.1	3.22	8-17	*
August 10	14	18	28.2 ± 2.2	1.01	13-4	ns	14	29	30.0 ± 5.1	1.64	13-15	ns
August 11	8	15	28.4 ± 2.7	0.56	7-7	ns	9	22	29.4 ± 4.1	4.48	8-13	**
August 18	10	26	25.3 ± 2.9	3.26	9-16	*	5	13	27.5 ± 2.3	0.36	4-8	ns
September 6	7	12	26.1 ± 2.4	1.07	6-5	ns	6	25	27.9 ± 3.1	2.43	5-19	ns
September 11	17	44	25.5 ± 3.5	1.77	16-27	ns	14	33	26.8 ± 3.6	0.63	13-19	ns
September 25	13	18	25.8 ± 4.6	5.12	12-5	*	18	59	25.3 ± 3.8	0.95	17-41	ns
October 17	8	14	25.7 ± 3.8	0.81	7-6	ns	10	27	26.0 ± 2.4	3.29	9-17	*
October 23	16	33	26.7 ± 2.7	1.27	15-17	ns	20	53	24.7 ± 2.5	0.84	19-33	ns
October 26	3	9	25.0 ± 2.1	1.09	2-6	ns	2	5	25.6 ± 0.9	0.09	1-3	ns
November 15	8	20	24.6 ± 3.4	0.90	7-12	ns	8	15	25.4 ± 2.1	0.77	7-7	ns
November 23	13	35	25.5 ± 2.5	0.39	12-22	ns	3	3	23.3 ± 5.0	–	–	–
Total		307						336				

58 males and 91 females of *C. granulata* and 2 males and 75 females of *C. angulatus* were identified. The percentage of females, respect to total number of identified crabs, was significantly higher than that of males in both species (*C. granulata*, equality of two percentages test, $t = 2.92$, $P < 0.001$). The mean number of crabs per sample varied significantly in males, but not in females, of *C. granulata* (Table 4, ANOVA, males $F_{(14\text{-}86)} = 2.5$, $P < 0.01$; females, $F_{(13\text{-}85)} = 1.3$, $P > 0.1$). Student's t-tests showed that, in this species, there were more females than males when the whole sampling period was considered, although only three of the samples showed significant differences between the mean number of crabs of both sexes (Table 4). The mean number of females determined per sample varied significantly along the sampling period in *C. angulatus* (Table 5, ANOVA, $F_{(13\text{-}41)} = 3.6$, $P < 0.01$). Few males were determined in two of the samples, whose mean number did not differ significantly from that of females (Table 5, Student's t-test).

Chelae remains were also used for an independent estimate of CW in each sex. The mean CW of crabs differed significantly among samples in *C. granulata* males without a definite trend, and in *C. angulatus* females with size decreasing along the sampling period (Table 4, ANOVA, $F_{(13\text{-}45)} = 3.0$, $P < 0.01$; Table 5, ANOVA, $F_{(13\text{-}64)}$ x 4.1, $P < 0.01$). Differences were not significant among CW estimates of *C. granulata* females (Table 4, ANOVA, $F_{(13\text{-}17)} = 1.0$, $P > 0.1$). Student's t-tests showed significant differences between mean CW of males and females of *C. granulata* preyed upon by gulls in only two samples (Table 4).

Prey availability

Although total density of these two crabs in Mar Chiquita lagoon has not been yet determined, both of them are extremely abundant (Boschi 1964) and their availability to the small number of gulls observed at once in the feeding site (no more than 30) was considered similar. However, dense clusters of *C. angulatus* adults have been observed several times in spring and summer in the study area (Spivak & Politis 1989). This behavior, probably related to mating, is especially intense at the beginning of spring and may temporarily modify the ratio between these two crab species in this area. The phenomenon was observed on 25 September, 1988 by Gavio & Spivak (unpublished results); pellets collected on that day differed from the observed dominance of *C. granulata* in *L. belcheri atlanticus* diet: they showed more *C. angulatus* remains (Table 2).

The existence of size-related spatial segregation of crabs has been described for *C. granulata* and *C. angulatus* (Table 6). In the first species, smaller individuals are usually found in burrows located in the upper intertidal zone, and larger individuals, adults of both sexes, are found wandering in muddy shores or shallow waters (Rivero D'Andrea unpublished results). Mean CW's estimated from remains found in pellets (male and female CW's from chelae, total crab from mandibles) were compared with data from crabs collected in different habitats at the same time or no more than a week after or before (Table 6). Student's t-tests showed

TABLE 4

Number and size (CW: carapace width) of females and males *Chasmagnathus granulata* identified from chelae found in pellets of *Larus belcheri atlanticus*. Mean number and size of males and females per sample were compared by Student's t-tests. NP: number of pellets, NC: number of crabs, Fe: females, Ma: males, d.f.: degrees of freedom.
Significance: ns = non significant; * = 0.05 > P > 0.01; ** = 0.01 > P > 0.001; *** = P < 0.001.

Número y tamaño (ancho del caparazón) de hembras y machos de *Chasmagnathus granulata* identificados a partir de quelas encontradas en egagrópilas de *Larus belcheri atlanticus*. El número y tamaño promedios de machos y hembras por muestra fueron comparados por pruebas t de Student.
NP.: número de egagrópilas, NC: número de cangrejos, Fe: hembras, Ma: machos, d.f.: grados de libertad.
Significación: ns = diferencias no significativas; * = 0.05 > P > 0.01; ** = 0.01 > P > 0.001; *** = P < 0.001.

Date	NP	NC		Mean number ± SD					Mean CW ± SD (mm)				
		Fe	Ma	Fe	Ma	t	d.f.		Fe	Ma	t	d.f.	
June 6	6	5	5	0.83 ± 0.75	0.83 ± 1.17	0.00	10	ns	29.7 ± 3.6	29.0 ± 3.4	0.34	8	ns
June 14	7	3	8	0.43 ± 0.53	1.14 ± 0.69	2.16	12	ns	28.8 ± 4.3	30.9 ± 3.1	0.94	9	ns
June 20	5	2	4	0.40 ± 0.55	0.80 ± 0.45	1.26	8	ns	29.7 ± 2.0	31.8 ± 1.3	1.29	4	ns
June 29	2	0	3		1.50 ± 0.71					33.9 ± 2.8			
August 10	3	2	1	0.67 ± 0.58	0.33 ± 0.58	0.72	4	ns	28.6 ± 1.1	28.8	0.17	1	ns
August 11	5	4	1	0.80 ± 0.45	0.20 ± 0.45	2.12	8	ns	31.7 ± 6.8	35.0	0.43	3	ns
August 18	10	13	3	1.30 ± 0.67	0.30 ± 0.48	3.81	18	**	27.2 ± 2.8	28.2 ± 3.0	0.55	14	ns
September 6	8	12	11	1.50 ± 0.93	1.37 ± 1.06	0.25	14	ns	29.8 ± 5.2	28.0 ± 1.9	1.07	21	ns
September 11	15	12	7	0.80 ± 0.68	0.47 ± 0.52	1.50	28	ns	27.5 ± 3.9	31.9 ± 3.4	2.45	17	*
September 25	10	9	1	0.90 ± 0.32	0.10 ± 0.32	5.66	18	***	29.5 ± 3.9	28.5	0.24	8	ns
October 17	3	2	2	0.67 ± 0.56	0.67 ± 0.56	0.00	4	ns	26.9 ± 2.0	29.6 ± 0.5	1.87	2	ns
October 23	10	12	2	1.20 ± 1.13	0.20 ± 0.42	2.61	18	*	29.4 ± 3.4	22.6 ± 7.1	2.23	12	*
October 26	3	2	2	0.67 ± 0.56	0.67 ± 0.56	0.00	4	ns	28.4 ± 0.5	28.7 ± 1.8	0.23	2	ns
November 15	4	3	3	0.75 ± 0.96	0.75 ± 0.50	0.00	6	ns	26.0 ± 2.0	24.3 ± 4.0	0.67	4	ns
November 23	10	10	5	1.00 ± 0.82	0.50 ± 0.53	1.63	18	ns	26.3 ± 4.0	28.7 ± 3.9	1.13	13	ns
Total	101	91	58	0.92 ± 0.75	0.57 ± 0.70	3.37	101	**					

TABLE 5

Number and size (CW: carapace width) of females and males *Cyrtograpsus angulatus* identified from chelae found in pellets of *Larus belcheri atlanticus*. Mean number of males and females per sample were compared by Student's t-tests. NP: number of pellets, NC: number of crabs, Fe: females, Ma: males, d.f.: degrees of freedom. Significance: ns = non significant; * = $0.05 > P > 0.01$; ** = $0.01 > P > 0.001$; *** = $P < 0.001$.

Número y tamaño (ancho del caparazón) de hembras y machos de *Cyrtograpsus angulatus* identificados a partir de quelas encontradas en egagrópilas de *Larus belcheri atlanticus*. El número promedio de machos y hembras por muestra fue comparado por pruebas t de Student. NP: número de egagrópilas, NC: número de cangrejos, Fe: hembras, Ma: machos, d.f.: grados de libertad. Significación: ns = diferencias no significativas; * = $0.05 > P > 0.01$; ** = $0.01 > P > 0.001$; *** = $P < 0.001$.

Date	NP	NC		Mean number ± SD					Mean CW ± SD (mm)	
		Fe	Ma	Fe	Ma	t	d.f.		Fe	Ma
June 6	1	2	0	2.00					35.5 ± 3.1	
June 14	2	3	0	1.50 ± 0.71					42.1 ± 9.3	
June 20	1	1	0	0.50					30.7	
June 29	2	2	0	1.00					31.5 ± 10.1	
August 10	4	13	0	3.25 ± 1.71					37.9 ± 7.6	
August 11	4	5	0	1.25 ± 0.50					38.2 ± 13.7	
August 18	0	0								
September 6	3	4	0	1.33 ± 0.58					29.4 ± 3.3	
September 11	5	5	0	1.00					28.5 ± 8.5	
September 25	15	18	0	1.20 ± 0.42					28.4 ± 3.8	
October 17	4	6	0	1.50 ± 0.58					28.0 ± 6.7	
October 23	8	12	0	1.50 ± 0.53					27.8 ± 2.7	
October 26	1	1	0	1.00					29.0	
November 15	3	2	1	0.67 ± 0.56	0.33 ± 0.58	0.72	4	ns	27.4 ± 1.7	20.3
November 23	2	1	1	0.50 ± 0.71	0.50 ± 0.71	0.00	2	ns	21.9	20.1
Total	55	75	2							

that mean CW of *C. granulata* estimated from pellets were significantly larger than those of crabs found in burrows on 18 August. Mean CW estimated from chelae of this species found on 23 November did not differ significantly from the mean CW of crabs found in muddy shores and shallow waters on 30 November, although differences were significant when mandibles were used for estimations. The same tests showed that on 17 October and on 9-15 November, estimated mean CW of *C. angulatus* females in pellets were significantly smaller than the mean CW of females found wandering in shores or in shallow waters. Smaller *C. angulatus* (mean CW ± SD = 16.0 ± 6.2 mm was recorded in April 1987 by Spivak & Politis, 1989) are found beneath stones, at least during low tides. They seldom contributed to gull's diet.

Sex ratio –male to female– of *C. granulata* in Mar Chiquita Lagoon was estimated as 1:1 (Pérez, unpublished results) but it actually varies according to habitat (Table 7). The overall sex ratio of *C. granulata* from pellets is significantly different from adults found in the muddy shore and shallow waters (Chi-square test, $X^2 = 81.2$, $P < 0.001$). Females of *C. angulatus* were always dominant in pellets. Although the sex ratio of juvenile crabs living under stones was approximately 1:1, this value is extremely variable in adults found in winter and spring in shallow waters of the study area (Table 7).

TABLE 6

Mean carapace width (CW) of crabs found in pellets and in field samples collected in different habitat. Field sample data are from Rivero D'Andrea (1) and Gavio & Spivak (2), unpublished results. Student's t-test for difference in means, d.f.: degrees of freedom. CW from pellets were estimated from chelae (CL) for each sex or from mandibles (MW) without sex determination. NC: number of crabs. Significance: ns = non significant; * = $0.05 > P > 0.01$; ** = $0.01 > P > 0.001$; *** = $P < 0.001$.

Ancho promedio del caparazón de cangrejos encontrados en egagrópilas y en muestras de terreno recolectadas en diferentes hábitat. Los datos de muestras de terreno provienen de Rivero D'Andrea (1) y Gavio & Spivak (2), resultados no publicados. Pruebas t de Student para diferencias entre las medias, d.f.: grados de libertad. Los CW en las egagrópilas fueron estimados a partir de quelas (CL) para cada sexo o de mandíbulas (MW) sin determinación del sexo. NC: número de cangrejos. Significación: ns = diferencias no significativas; * = $0.05 > P > 0.01$; ** = $0.01 > P > 0.001$; *** = $P < 0.001$.

Date	Sex	Crabs found in	NC	Mean CW ± SD (mm)	t	d.f.	
Chasmagnathus granulata							
August 18	males	burrows (1)	64	18.7 ± 6.1			
August 18	males	pellets (CL)	4	28.2 ± 3.0	4.39	48	***
August 18	–	pellets (MW)	26	25.3 ± 2.9	5.31	88	***
August 18	females	burrows (1)	37	18.4 ± 7.0			
August 18	females	pellets (CL)	13	27.2 ± 2.8	3.06	66	**
August 18	–	pellets (MW)	26	25.3 ± 2.9	4.80	61	***
November 30	males	muddy shores-shallow waters (1)	101	27.9 ± 3.5			
November 23	males	pellets (CL)	6	28.7 ± 3.9	0.57	105	ns
November 23	–	pellets (MW)	35	25.5 ± 2.5	3.67	134	***
November 30	females	muddy shores-shallow waters (1)	26	28.2 ± 3.1			
November 23	females	pellets (CL)	9	26.3 ± 4.0	1.51	33	ns
November 23	–	pellets (MW)	35	25.5 ± 2.5	3.79	59	***
Cyrtograpsus angulatus							
October 17	females	muddy shores-shallow waters (2)	72	30.9 ± 3.5			
October 17	–	pellets (MW)	27	26.0 ± 2.4	6.72	97	***
November 9	females	muddy shores-shallow waters (2)	176	31.4 ± 3.3			
November 15	–	pellets (MW)	15	25.4 ± 2.1	6.79	189	***

TABLE 7

Sex ratio (male: female) of crabs found in pellets and in field samples collected in different habitats. Field sample data are from Rivero D'Andrea (1) and Gavio & Spivak (2), unpublished results; and from Spivak & Politis, 1989 (3).

Proporción de sexos (macho: hembra) de cangrejos encontrados en egagrópilas y en muestras de terreno recolectadas en diferentes hábitat. Los datos de muestras en el terreno provienen de Rivero D'Andrea (1) y Gavio & Spivak (2), resultados no publicados; Spivak & Politis, 1989 (3).

Species	Sex ratio (male: female)	Crabs found
Chasmagnathus granulata	0.63:1	in pellets
	1.15:1	in burrows (1)
	2.53:1	in muddy shores and shallow waters (1)
Cyrtograpsus angulatus	0.02:1	in pellets
	from 0.46:1 to 14.40:1	in muddy shores and shallow waters (2)
	from 0.69:1 to 1.63:1	beneath stones (3)

DISCUSSION

Gulls (Laridae) are generalized foragers that utilize many kinds of food items, forage over a large range of available habitats and use a wide variety of feeding techniques (Hunt & Hunt 1973). In the Northern Hemisphere, several gull species feed on mudflats macroinfauna (Harris 1965, Spaans 1971, Hunt & Hunt 1973, Ambrose 1986). Crabs are an important prey for at least one of them (*Larus argentatus*), but they are mainly captured on intertidal mussel beds or sand banks (Verbeek 1977, Sibly & McCleerly 1983). In Mar Chiquita Lagoon, three species of Laridae can be observed: *Larus dominicanus, L. maculipennis* and *L. belcheri atlanticus.* The first one has never been seen feeding in this area; it obtains its food on the sea coast and in Mar del Plata Harbor (Mariano Martínez, personal communication, 1990). Interestingly, in an undisturbed Central Chilean rocky shore, intertidal crustaceans form part of *L. dominicanus* diet (Bahamondes & Castilla 1986), although this species forages mainly on molluscs in this temperate area as well as in subantarctic and antarctic intertidal and nearshore communities (Branch 1985, Castilla & Rozbaczylo 1985, Hockey 1988). Crab remains were sometimes found in gut samples of *L. maculipennis* (Olivier *et al.* 1972b). By contrast, *L. belcheri atlanticus* preys mainly on a restricted part of the macroinfaunal community. This gull eats almost only crabs, and concentrates on a narrow fringe of the demographic spectra of *Chasmagnathus granulata* and *Cyrtograpsus angulatus.* Only occasionally, other mudflat crabs (*Uca uruguayensis*) are found in regurgigated pellets.

During winter, *L. belcheri atlanticus* feeding in Mar Chiquita Lagoon had both grapsid crab species always available and they were indeed taken as food. However, their ratio varied, probably as a consequence of temporary changes in *C. angulatus* density in the gull's feeding area due to mating behavior. In late spring, shortly before leaving the lagoon, insects and fishes were incorporated to its diet. An insect spring bloom was described in grasslands near the Lagoon (Coccia, unpublished results). However, by this time only juvenile gulls remain in their wintering habitat. Juvenile shorebirds had been found to feed less efficiently than adults, owing to their inexperience (O'Connor 1981), suggesting the possibility of a more generalistic trophic spectrum.

The gull tended to concentrate its feeding activity on adult crabs of both species that wander in shallow waters or in muddy shores and selected prey by size of, at least, *C. angulatus* females (Table 6). Along the sampling period the mean CW of preyed upon crabs decreased in both species. This fact coincides with the observed input of relatively smaller mature individuals to adult recruiting areas. These smaller crabs, recruited in summer and early fall, lasted until spring in protected areas, in burrows or under stones according to the habitat requeriments of each species (Spivak & Politis 1989, Gavio & Spivak, unpublished results). However, the possibility of a differential prey size selection among adult and juvenile gulls should be taken into account.

Female crabs were selected as food, partially in *C. granulata* and almost entirely in *C. angulatus* Several factors explaining prey sex selection by crustacean predators, that could be applied here, have been mentioned in the literature: 1) males have an aggressive behavior related to territoriality (Howard & Lowe 1984), 2) females consume more food and spend more time searching for it before egg production, thus increasing their probability of being caught, and 3) females have a reduced avoidance ability when ovigerous (Stein 1977). *Chasmagnathus granulata* and *Cyrtograpsus angulatus* are sexually dimorphic and males have larger chelae than females. Although males of the former species tend to escape off shore when disturbed, they defend themselves with their chelae when captured. Males of the latter species display a defensive behavior common to several crab species known as "aufbaumreflex" which may decrease its availability to predators. Further, ovigerous females of *C. granulata* were found from October to March in Mar Chiquita Lagoon (Pérez, unpublished results). In the sea coast near the Lagoon, *C. angulatus* ovigerous females were found the year round, but their proportion was higher from June to October (Rognone, unpublished results). In Mar Chiquita Lagoon, this crab showed a sex and size dependent high incidence of limb autotomy; the highest values were detected for females between 25 and 29.9 mm of carapace width (Spivak & Politis 1989). These data clearly agree with the size and sex of *C. angulatus* apparently selected by *L. belcheri atlanticus* (Table 5).

Extremely dense assemblages of grapsid crabs ("cangrejales") are widely distributed in the warm temperate coastal zones of the southwestern Atlantic. Crabs inhabiting mudflats are an apparently unlimited resource in Argentine and Uruguayan coasts: few birds may be considered to compete for them, at least in Mar Chiquita Lagoon: *Haematopus ostralegus* (Martínez, personal communication, 1990), *Himantopus melanurus* and *Larus maculipennis* (Olivier *et al.*, 1972b), and *L. belcheri atlanticus.* However, crab density is enormous and interference between predators for these prey has never been recorded. The presence of these abundant crab assemblages may explain why *L. belcheri atlanticus* –a potential generalist feeder (Escalante 1984)– has a discontinous distribution along the southern Atlantic coasts.

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