VI.5b. Introduced species
2. *Basilichthys bonariensis* (The "Pejerrey")

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Basilichthys bonariensis (Valenciennes, 1835), locally known as the "pejerrey." is a member of the Atherinidae, originating from estuarine and riverine habitats in Argentina, Uruguay and southern Brazil, from Bahía Blanca in the south as far as the Río da Prata in the north (Lahille, 1929; Fowler, 1954 and Buen, 1959). It penetrates inland several hundred kilometres, since it is one of the main commercial species in the Rosario region, Paraná (Welcomme, 1979, citing Vidal, 1969). Because of its commercial value and its good adaptability it has been introduced in numerous natural and artificial lakes from Argentina to Chile and Brazil (Huet, 1978), and also in Israel and Japan (Bardach *et al.*, 1972). As far as Bolivia is concerned, examples may have been released in 1946 into Lake Poopo by an angling club (Bustamante and Treviño, 1977), but according to Everett (1971), the introduction probably took place a little later into the lake of Oruro. Whichever the case, the pejerrey ascended the Río Desaguadero and entered Lake Titicaca in 1955 or 1956. It invaded the entire lake, including the inflow rivers, where it is at present abundant in all suitable habitats. It is very probably the most important species from an economic point of view in the lake region, as *Orestias agassii* has a lower market value and *Salmo gairdneri* (rainbow trout) is now less common after a period of abundance in the 1960s.

According to Bustamante and Treviño (*op. cit.*) it can attain a fork length of 56 cm and a weight of 2.5 kg. Huet (1978) gave 50 cm and 3 kg. The records in our captures are only 50 cm standard length and 1.65 kg. Individuals of over a kilogram are rare.

Taxonomy

The species *bonariensis* was described for the first time in 1835 by Valenciennes in Cuvier and Valenciennes, *Histoire naturelle des Poissons*, 10, p.

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469, under the genus *Atherina* Linné 1758. Nowadays it is generally placed in the genus *Basilichthys* Girard 1854, but *Odontesthes* Evermann and Kendall 1906 is still sometimes used, for example by Nion (1977), Huet (1978) and Pinto Paiva and Scheffer (1983). Bertin and Arambourg (1958) and Ringuelet and Aramburú (1961) used the genus *Austromenidia* Hubbs 1918. The name *Odontesthes basilichthys* has even been used (Bardach *et al.*, 1972; Pillay and Dill, 1979) ! The latest revision of the Atherinidae seems to be that of Schultz (1948), who placed the species in the genus *Odontesthes*. However, several characters recorded by us on pejerrey from Lake Titicaca do not correspond with this genus, nor with those of the genera *Austromenidia* and *Basilichthys*, according to the key given by this author. Fowler (1954) considered the three genera to be synonyms, but gave no reasons for this decision. The problem as to which genus the Lake Titicaca pejerrey belongs therefore remains unresolved. While waiting for a resolution we retain the most commonly employed name, *Basilichthys bonariensis* (Valenciennes, 1835).

At the subspecies level, Cabrera (1962) believed he could distinguish between an estuarine population from the Río de la Plata and a riverine population in the Paraná, but the argument proposed – a difference in the length-weight curves, based on a small number of individuals – would appear to be precarious. More recently Freyre *et al.* (1983) designated the pejerrey from a reservoir on the Río Tercero as *B. bonariensis bonariensis*. Finally Linarès (1979) (*non vidi*) named the Peruvian pejerrey as *Basilichthys bonariensis* var. *titicacaensis*. It is then possible that there are several forms.

As far as the pejerrey introduced to the Bolivian Altiplano are concerned, two questions can be posed: firstly, what is the origin of the stock from which they are derived, origin which unfortunately it seems very difficult to retrace; and secondly, what special adaptations have they been able to acquire over the thirty years since they have been isolated from the original stock ? The answer to these questions requires a detailed comparison of the various estuarine and inland populations occurring around the tropic of Capricorn, whether native or introduced.

Age determination and growth

As scale reading, study of the length distribution of fish captured or mark-recapture were methods which proved to be too difficult in Lake Titicaca (Loubens and Osorio, 1988), the growth rates of *Basilichthys bonariensis* are only known from works carried out in Chile and Argentina. Burbridge *et al.* (1974) worked on pejerrey in the region of Valparaiso (33°S) using Petersen's method and scale reading. For the first method, the captures made did not appear to be a representative sample of the population. In the case of scale reading, no indication was given of the nature of the rings nor of their chronology of appearance. It is not impossible that they could be used, given that there is a rather pronounced winter at this latitude. The annual growth rate given (total length) was 107 mm for the first year, 111 for the second, 126 for the third, 84 for the fourth and 45 for the fifth. With the exception of the first year these were based on a small number of observations.

Wurtsbaugh *et al.* (in press) report on works carried out in Argentina that we have not been able to consult directly: *Basilichthys bonariensis* reached 20 cm in the first year (Ringuelet and Aramburú, 1961); 28 cm in 1 year and 39 cm in 3 years (Boschi and Fuster, 1959). Lake Lobos near Buenos Aires and a reservoir on the Río Tercero near Córdoba were sampled using beach seines of shallow depth and a few gill nets (Freyre, 1976; Freyre *et al.*, 1983). The recorded size distributions reflected mainly the selectivity of the fishing gear. In the case of the Río Tercero, the standard length was 18.5 cm at one year, 22.3 at 2 years, 25 at 3 years, 27 at 4 years etc. Freyre *et al.* were not able to observe annual rings on the scales, although the latitude was comparable to that of Valparaiso, but report on spawning marks on large individuals.

Sex and reproduction

Sex ratio

We have not recorded any external sexual dimorphism, so the sex and sexual condition was recorded by observation of the gonads, which are recognizable from a body length of about 15 cm.

There are significantly more males than females among young individuals, then as from 18 to 24 cm the sex-ratio is even. The percentage of males then continues to decrease until a minimum of 10%, after which there seems to be a slight rise, although this is not statistically significant, because of the small number of observations. For all pejerrey collected of more than 30 cm there was 1 male for 4 females, for individuals of more than 37 cm there was only one male for 7 females.

The progressive decrease with size in the percentage of males is probably explicable by a slower growth rate, but this could not be proved as the age was unknown.

Wurtsbaugh *et al.* (*op. cit.*) recorded a similar change in sex-ratio with size in their samples from the northern part of the lake.

Stages of sexual maturity and maturation

The development of the ovaries during the life of a female pejerrey can be divided into 6 successive stages, starting with the juvenile stage (stage 1), with a low gonado-somatic index (0.1%) through to individuals which have just spawned in which the gonado-somatic index varies between 1.5 and 4% (stage 6). Each stage is characterised by a particular ovarian morphology. Only three stages have been distinguished in the development of the testes (Loubens and Osorio, 1988).

Table 1. Length at sexual maturity. F, female; M, male; A, adult; +gametogenesis; 1, immature or sexually inactive adult.

L	Females		Males					
	F	% F.A.	M	M1	M+	M.A1	M.A	% M.A.
135	68	0.0	54	50	4	2	6	11.1
160	134	0.0	174	135	39	19	58	33.3
185	165	0.0	176	98	78	39	117	66.5
210	138	2.2	151	64	87	43	130	86.1
235	112	6.3	109	43	66	33	99	90.8
260	82	22.0	70	26	44	22	66	94.3
285	69	59.4	41	15	26	13	39	95.1
310	62	77.4	26	10	16	8	24	92.3
335	47	87.3	21	7	14	7	21	100.0
360	58	98.3	18	5	13	5	18	100.0
385	68	100.0	8	3	5	3	8	100.0
410	55	100.0	9	2	7	2	9	100.0
> 410	26	100.0	6	3	3	3	6	100.0
L.S.M.: 280 mm Minimum size of maturation : 201 mm			L.S.M.: 180 mm Minimum size of maturation : 140 mm					

Size at sexual maturity

The size at sexual maturity is that at which 50% of individuals are immature and 50% adult. The ability to reproduce, which typifies adults, is considered to have been reached when the gonads are clearly mature.

In the case of females, all individuals of more than 35 cm length show clear signs of more or less active gametogenesis irrespective of the season (% A.F., Table 1). For males, the calculation is a little more complicated because, even among large males, there is a certain proportion of individuals with reduced gonads (M1) which may either be adults or immatures. We have assumed that all the males measuring at least 335 mm are adult, which enables us to calculate a value of 0.50 for the proportion of adult males with resting gonads (M.A1) compared to mature males (M+), which was then applied to size classes of less than 335 mm.

Plots of the percentage adults against length give values for the length at sexual maturity (L.S.M.) of 280 mm for females and 180 mm for males, the minimum length for maturity being 201 mm for females and 140 mm for males. The largest immature female recorded being 344 mm, the range of lengths at sexual maturity is therefore 201–344 mm.

By using the alternative method of the relationship between gonado-somatic index and length, the value of 285 mm for the L.S.M. in females was obtained, a value very close to the first.

Wurtsbaugh *et al.* gave the following minimum lengths for advanced mat-

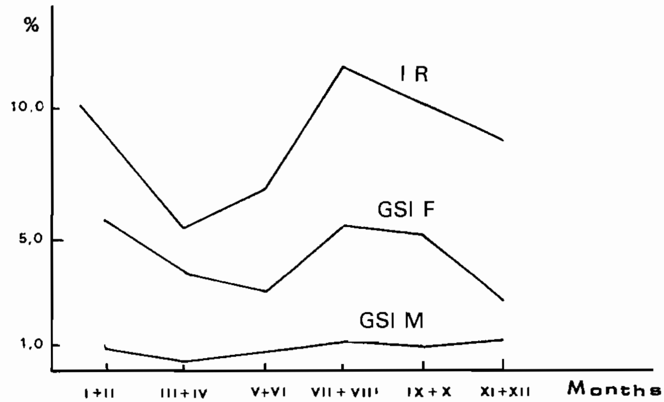

Figure 1. Bimonthly changes in GSI and reproductive index, RI.

uration for pejerrey from the north of the lake, based on a small number of observations: 25 cm for females and 17 cm for males. Pinto Paiva and Scheffer (1982), working on *B. bonariensis* in the Río Jacui (Río Grande do Sul State, Brazil, 30°S), were successful in artificial spawning with fish of 25 cm total length and over, or 21 cm standard length. This accords well with our observations. Finally, Burbidge *et al.* (*op. cit.*) found a distinct group of fish among their sample ranging in length between 19 and 30 cm and which were all adults.

Maturation cycle and period of reproduction

Tables 2 and 3 and Fig. 1 give the percentages of males and females in each two-month period at the various stages of gonadal development, and the corresponding mean GSI values. In addition, an index known as the reproductive index RI has been calculated (last column of Table 3), which is intended to represent in a single value all the observations made of the GSI of both males and females. As the GSI of the females is on average 5.5 times greater than that of the males, the RI value is equal to GSI female + 5.5 GSI male. In interpreting this figure it should be noted that if in a particular season all the adults returned to sexual quiescence, the IR would be equal to about 1.5.

The reproductive season covers the entire year, the mean GSI values and reproductive indices being high throughout the year. A slight downturn in March to June is all that can be noted. As with *Orestias agassii*, the cycles of maturation of individual fish are not synchronised, because of the remarkable constancy of the main physico-chemical and biological properties of the lake.

It is interesting to compare these results with those of *Basilichthys bonariensis* living in their original habitat of estuaries and lowland rivers at between

Table 2. Percentage of females at various stages of maturation and seasonal changes in mean GSI for individuals of at least 300 mm

Months	N	% of the stages 1 + 2	3 + 4	5	6	G.S.I.
I + II	96	12	30	20	38	5.7
III + IV	45	4	33	7	56	3.7
V + VI	125	3	41	13	43	3.0
VII + VIII	31		48	19	32	5.4
IX + X	10		60	30	10	5.1
XI + XII	6	33	33	33		2.6
I to XII	313					4.23

Table 3. Percentage of males at various stages of maturation and seasonal changes in mean GSI and reproductive index RI for individuals of at least 200 mm

Months	N	% of the stages 1	2	3	G.S.I.	R.I.
I + II	157	43	21	36	0.8	10.1
III + IV	47	62	36	2	0.3	5.4
V + VI	136	25	30	35	0.7	6.9
VII + VIII	18	17	22	61	1.1	11.5
IX + X	29	55	14	31	0.9	10.1
XI + XII	57	40	16	44	1.1	8.7
I to XII	444				0.77	

30°S and 40°S. These habitats show much more pronounced fluctuations in temperature, salinity and in water level. The information that we have been able to find in the literature is, however, brief and contradictory. Buen (1953) indicated that the species spawned in the spring, i.e. from October to December, but according to Boschi and Fuster (1959), sexually mature individuals occur throughout the year in Argentina and especially from September to November. Iwaszkiw and Freyre (1980) considered there to be two periods of reproduction, the first from August to November and the second during the southern autumn. According to Pinto Paiva and Scheffer (1982), spawning takes place from May to July in southern Brazil. These indications need to be confirmed and strengthened by detailed studies allowing comparisons to be made on a solid basis, and in particular providing an insight into how the chronology of maturation has changed after thirty years spent in a stable environment.

The problem of spawning

The pejerrey would appear to experience problems with spawning in Lake Titicaca. We have in fact encountered a significant proportion of mature females at all seasons which appear not to have been able to spawn or not able to complete spawning. Their ovaries contain large quantities of mature eggs beginning to become atretic and sometimes forming enormous hernias from which the eggs could obviously not escape. Some ovaries were also filled with an aqueous liquid.

The main difference in comparison with the original habitat is the water temperature. The slight salinity of Lake Titicaca (1 g l^{-1}), its good oxygenation and its abundant vegetation cover are all favourable factors. In contrast, the temperature of the surface 10 m of water in which the pejerrey live, remains at between 10°C and 14°C, with a maximum in December to February (Lazzaro, 1985), whereas the authors cited above all agree that the temperature range favourable for reproduction and egg development is between 15 and 21°C, with an optimum of 17–18°C. The slightly too cold waters of Lake Titicaca probably constitute a major obstacle for the reproduction of this subtropical species, but the fact that reproduction occurs throughout the year enables this obstacle to be overcome. Nevertheless, strong annual variations in recruitment are to be expected, given that the fish are at their lower limit of temperature tolerance. This seems to be confirmed by the remarks of Bustamante and Treviño (*op. cit.*) on the pejerrey of Lago Pequeño, based on observations made in 1976–1977: "this fish was formerly abundant in Lago Pequeño, but at present it is only rarely captured." After a period of abundance in 1970, the pejerrey became rare in Lago Pequeño and then became abundant again in the period of our observations (October 1979–November 1981).

Are there several cycles of maturation per year for each individual? In mature ovaries, in addition to ripe eggs measuring 1.6 to 1.8 mm, there also occur maturing oocytes of up to 0.7 to 0.8 mm, corresponding to stage 3. A second cycle during the course of a single year would therefore appear to be possible, since the total time taken for maturation from stage 1 to stage 5 is in general of the order of a few months in many species of fish.

The GSI of mature females is very variable, values ranging from 2 and 36%, without any pronounced modal value, which indicates fractional spawning, or perhaps interrupted spawning because of the temperature problem described above.

The number of eggs laid per female in a year is very difficult to estimate. Wurtsbaugh *et al.* recorded a mean of 3570 mature eggs in the ovaries of 6 females of 24 to 28 cm caught in the north of Lake Titicaca. Iwaszkiw and Freyre (1980) working on *B. bonariensis* in a reservoir on the Río Tercero, counted the mature eggs in the ovaries of 80 females of between 20 and 31 cm long, and gave the following relationship between the number of eggs N and the standard length L in mm: $N = 0.0188\ L^{2.2955}$. For L = 260 mm, N = 6572, that is much higher than Wurtsbaugh *et al.*

Study of condition

The condition of the pejerrey in the lake was studied using the various factors described by Le Cren (1951) after having overcome several methodological problems described in detail in Loubens and Osorio (1988). This led us to draw up a condition index C, calculated from the means of the condition

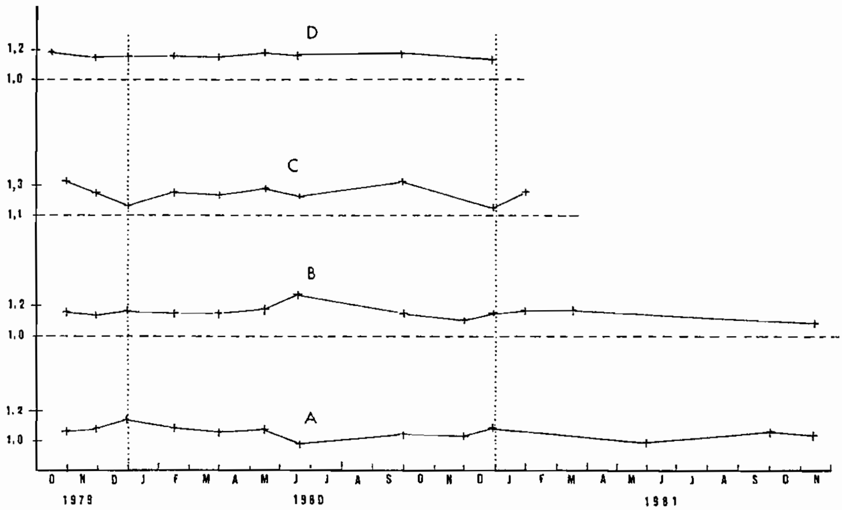

Figure 2. Seasonal changes in condition factor of pejerrey of 100 to 249 mm length. A, changes in K for fish of 100 to 149 mm; B, 150 to 199 mm; C, 200 to 249 mm; D, changes in condition index C for fish of 100 to 249 mm length.

factors K calculated for three size classes (100–149, 150–199 and 200–249 mm). The condition factor $K = 10^5\ PL^{-3}$, where P is the weight in grams and L is the standard length in mm. For fish of over 250 mm, because of the small sample, the relative condition factor K′ was used: $K' = P \times \mathbf{P}^{-1}$, where **P** is the weight estimated from the length weight relationship for Lake Titicaca pejerrey.

The most complete results are those for the Lago Pequeño (Fig. 2, Table 4). There is no apparent seasonal cycle in condition, even if some samples have a mean significantly different from those of others. These occasional differences can be attributed to the samples being too small compared to the rather large variance of this variable. The value of the overall index of condition C was particularly stable from October 1979 to December 1980. For large individuals the results are incomplete but do not reveal any major variation. With *Basilichthys bonariensis* the same stability in condition is therefore found as that already demonstrated for another biologically very different species, *Orestias agassii* (Loubens and Sarmiento, 1985). This stability and the reproduction season lasting throughout the entire year are very rare biological characteristics, reflecting the extreme constant environmental conditions, which it would appear have only been found elsewhere in the East African lakes (Loubens and Sarmiento, *op. cit.*).

The results for the Lago Grande are incomplete (Table 5). They do however reveal a tendency for the fish of greater than 150 mm to have a better condition than those in the Lago Pequeño. The difference is significant for large individuals. The large pelagic pejerrey of the Lago Grande have available very abundant prey in the form of shoals of *Orestias ispi*, a small

Table 4. Seasonal changes in condition factor K and condition index C for pejerrey from the Lago Pequeño; V = variance of K

Date	100 – 149 mm			150 – 199 mm			200 – 249 mm			
	K	v x 10²	n	K	v x 10²	n	K	v x 10²	n	C
30/10/79	1.06	0.59	130	1.15	1.07	72	1.33	2.21	10	1.18
27/11/79	1.08	0.67	169	1.13	0.50	123	1.25	0.87	14	1.15
1/01/80	1.13	0.84	113	1.17	1.04	136	1.17	1.17	21	1.16
17/02/80	1.09	0.65	108	1.15	0.52	126	1.25	2.05	26	1.16
1/04/80	1.07	0.39	11	1.14	0.66	20	1.23	0.57	9	1.15
13/05/80	1.07	0.41	11	1.18	0.63	23	1.28	1.37	40	1.18
19/06/80	0.97	0.20	10	1.27	0.87	11	1.23	0.71	40	1.16
27/09/80	1.04	0.90	300	1.14	1.03	40	1.32	1.35	20	1.17
28/11/80	1.02	0.40	50	1.10	0.63	57				
26/12/80	1.09	0.46	33	1.15	0.74	93	1.15	0.52	13	1.13
1/02/81				1.17	0.72	43	1.25	1.09	70	
12/03/81				1.17	0.35	10				
28/05/81	0.99	0.78	40							
1/10/81	1.05	1.55	14							
12/11/81	1.04	0.71	83	1.04	0.87	10				

pelagic species usually living in deep water and therefore rarely present in the southern part of the Lago Pequeño.

It is interesting to compare the pejerrey from Lake Titicaca with those from Argentina and Chile for which there are some publications (Table 6). The condition factor has not however been calculated in these works, but rather the length-weight relationship which can be used when it is really representative of the parent populations. This requires that a wide range of lengths has been taken into account – otherwise the regression lines are biased – and that equal weight has been accorded to the various length classes, which is the case in the works we have selected. The relationships

Table 5. Seasonal changes in condition factor K for pejerrey from the Lago Grande

Length groups (mm)	Date	K	v x 10²	n
100 - 149	10/05/80	0.95	0.58	12
	22/07/81	1.01	1.10	20
150 - 199	28/03/80	1.15	0.73	15
	10/05/80	1.21	1.24	52
	30/10/80	1.20	0.27	10
	26/02/81	1.21	0.82	22
200 - 249	28/03/80	1.28	0.87	40
	10/05/80	1.29	1.12	65
	25/06/80	1.29	0.89	23
	10/12/80	1.34	2.33	24
	26/02/81	1.25	1.39	49
	23/09/81	1.26	0.84	14

Table 6. Length-weight relationships for some pejerrey populations

Parameters	Burbidge *et al.*, 1974 Peñuelas lake, Valparaíso Chile	Freyre, 1976 De Lobos lake Buenos Aires Argentina	Freyre *et al.* 1983 Tercero lake Córdoba Argentina	Loubens and Osorio Lake Titicaca Bolivia
a x 10^6	2.023	3.766	5.046	2.918
b	3.2525	3.2125	3.1629	3.2669
Length (mm)	Weigth (g)			
200	110	93	96	96
300	406	342	345	361
400	1028	861	857	924

are regression lines, and reduced major axes would have been preferable for making comparisons, but the correlation coefficients are very high and all the lines very similar for sets of data.

In the case of the Chilean pejerrey, the data are given for the total length which is related to standard length by the relationship $LT = 1.177L + 4$ (Burbidge *et al.*, 1974). The regressions obtained for the Bolivian and Argentine fish are very similar – the larger Bolivian pejerrey are perhaps slightly heavier – but the difference is probably not significant as the variability in body weight is great among large individuals. In contrast, the Chilean pejerrey are considerably heavier at all lengths. However these results need to be strengthened by additional observations on larger samples, standardised in terms of measurement and analysis.

Transfer of body reserves, gonadal development and condition

Methods

During the life of a fish body reserves can be stored in various organs to be reused at a later date, particularly for the formation of sexual products. These transformations and transfers can provoke sometimes major variations in the relative weights of these organs. In fish, the body reserves are mainly in the form of lipids, glycogen only representing a very low percentage of total weight, at most 0.3% according to Jacquot (1961).

In terms of lipids, two types of fish are traditionally distinguished: the non-oily fish, such as *Gadus*, where the fat reserves are concentrated essentially in the liver (the HSI, hepato-somatic index, is maximum during the early stages of gonad maturation and then decreases as GSI increases), and the oily fish such as the female *Mullus*, in which lipids accumulate in the skin, muscles and peritoneum (the HSI is low, varies little and is not time-lagged with the GSI) (Bougis, 1952; Bertin, 1958 a and b; Hureau, 1970; Lagler *et al.*, 1977, amongst others).

We have attempted to study these transfers in *Basilichthys bonariensis* by measuring 4 ratios or indices of which 3 are well known, the GSI, HSI and condition factor (K for L $\leq$ 300 mm K′ for L $\geq$ 300 mm), and the fourth must be defined. In numerous species of fish lipids can be deposited in the abdominal cavity, sometimes in large quantities. This is easy to remove by pulling on the peritoneum to which it adheres, this can then be weighed and the PSI calculated, being the ratio between the weight of peritoneal fat to body weight. The weight of the peritoneum itself being very low, this ratio correponds to almost pure adipose tissue. This has been calculated for about 750 pejerrey. The lipids contained in the muscles and skin could not be measured simply. Changes in condition could however, by difference, give an approximate estimate of the quantity of these stored.

Results

The simplest case is that of the males (Table 7, Fig. 3). The HSI varies between 2.0 and 3.1%, being significantly correlated with size and with maturation of the testes. It increases with increasing length up to to the 200–249 mm size class and then remains stable. The influence of sexual maturation is slight but clear, since it leads to a decrease of 0.5 to 0.6% in the HSI, irrespective of size. The PSI is about twice as great as the HSI and undergoes similar, but more pronounced changes, the difference between resting males and maturing males reaching 2.5% of body weight in the largest individuals. K or K′ also decreases slightly but significantly in maturing males.

If an attempt is made to draw up a balance for males measuring at least 300 mm, K′ equals 1.06 for resting males and 0.99 for others, or a difference in weight of 7%. 3% of this difference corresponds to a decrease in hepatic and peritoneal reserves. The rest of the body therefore loses at least 5%, taking into account the GSI of maturing males, to which must be added the unknown losses due to release of sperm.

Similar results are obtained for females (Table 8, Fig. 3). In immature and pre-adult fish, in which the GSI remains low, the HSI and PSI values increase with length to reach 3.5 and 7.2% respectively. In this stage, growth and accumulation of body reserves predominate. Ovarian development also leads to a decrease in the relative weight of the liver and partial utilisation of the peritoneal fat. In individuals having spawned, the HSI and PSI values are only 2.2 and 3.3%, respectively. As in males the values of K and K′ vary little, even in females in the last stage of maturation.

Several remarks can be made on this series of results. In terms of the liver, this certainly plays a lipid storage role, but this is rather limited in

Table 7. Changes with size and IGS of some variables relating to body reserves in males. S = GSI + HSI + PSI; x = mean; v = variance

Individus categories		GSI	HSI	PSI	S	K or K'
Prepubescents	x	~ 0.1	2.56	3.83	6.5	1.180
140–199 mm	v		0.3537	2.0481		0.0155
GSI < 0.3 %	N		30	20		30
Young adults	x	1.33	2.03	3.61	7.0	1.190
140–199 mm	v	0.7840	0.2646	2.3032		0.0089
GSI > 0.3 %	N	14	15	9		15
Prepubescents	x	0.16	3.14	6.04	9.3	1.292
200–249 mm	v	0.0064	0.6353	1.9419		0.0127
GSI < 0.3 %	N	39	59	42		59
Young adults	x	1.38	2.48	4.19	8.1	1.242
200–249 mm	v	0.6175	1.0830	3.2218		0.0161
GSI > 0.3 %	N	75	71	53		74
Adults	x	0.11	3.13	7.14	10.4	1.023
250–299 mm	v	0.0054	0.8272	2.1637		0.0079
GSI < 0.3 %	N	26	34	32		33
Adults	x	1.28	2.54	5.79	9.6	0.965
250–299 mm	v	0.3229	0.6020	6.1196		0.0114
GSI > 0.3 %	N	47	46	42		47
Adults	x	0.11	3.13	7.03	10.3	1.063
300 mm	v	0.0046	1.3400	4.1400		0.0159
GSI < 0.3 %	N	21	27	27		27
Adults	x	1.24	2.60	4.52	8.4	0.991
300 mm	v	0.4332	0.9950	4.5757		0.0099
GSI > 0.3 %	N	42	42	42		42

terms of the overall balance of energy reserves, most of which come from elsewhere. This tends to lead *Basilichthys bonariensis* being placed among the oily fish, even though the maximum HSI value in any given fish precede that of the GSI. The physiological shock of reproduction would appear to be slight, given that noteworthy quantities of reserves remain and that the condition only drops slightly. In any case this shock is nowhere like as great as that suffered by numerous species of fish, in which the adults are exhausted or die after spawning. Here again the pejerrey is well adapted to its new environment, the only point against it remaining the excessively cold water at the time of spawning.

Finally, the results demonstrate the role played by the peritoneum as a

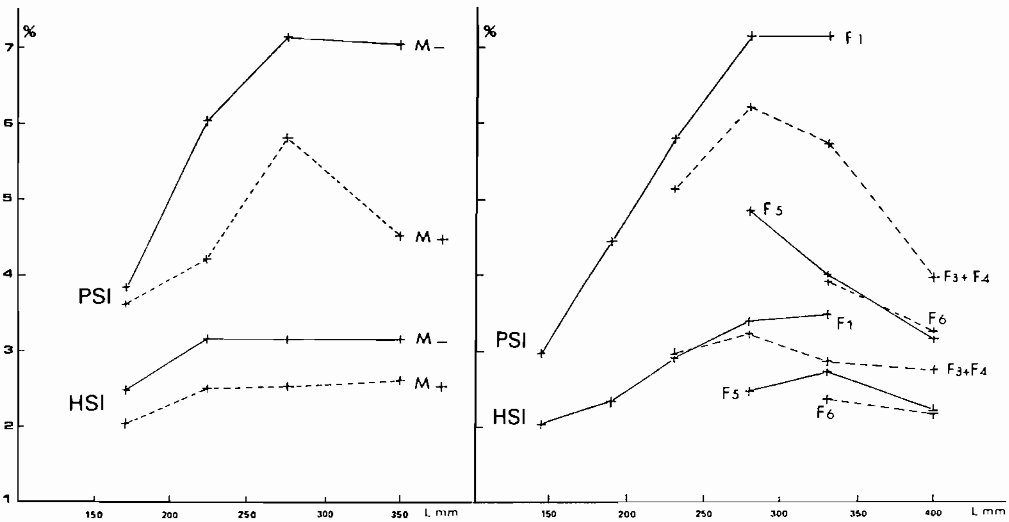

Figure 3. Changes in HSI and PSI in males (left) and females (right) in relation to length and sexual state. M+ maturing or mature males; M− juvenile or sexually inactive male.

lipid store, a role already known, but rarely measured. This role is very important in the pejerrey since the PSI exceeds 7% before start of gonadal maturation. It would be of value to divide the oily fish species into several types depending on the relative importance of the various lipid storage organs. If, for example, *Basilichthys bonariensis* is compared with *Polydactylus quadrifilis*, an amphibious species from the Gulf of Guinea (Loubens, 1966), the combined liver and peritoneal weight accounts for 10% of body weight in pre-adults in the former, so that the concentration of lipids in the muscles is probably rather low and constant. In the latter, the hepatic and peritoneal lipids are of little importance (HSI varies little at around 0.5%, PSI varying between 0.5 to 1.5%), the concentration of lipids in the muscles being undoubtedly higher and more variable. This could have an influence on the market value of fish, depending on local tastes, and in the latter case could lead to seasonal fluctuations in price.

Trophic relations

The diet of *Basilichthys bonariensis* in Lake Titicaca has been studied in detail by Wurtsbaugh *et al.* who examined the stomach contents of several hundred individuals caught in the northern part of the lake in 1973 and 1974. However they only examined a very small number of fish of over 25 cm standard length. For this reason, after a brief report on their main results, we will provide some additional information on the diet of large pejerrey caught in the southern part of the Lago Pequeño.

Table 8. Changes with size and IGS of some variables relating to body reserves in females. S = GSI + HSI + PSI; **x** = mean; v = variance

Sexual development Stage and length (mm)		GSI	HSI	PSI	S	K or K′
F1	**x**	~0.1	2.05	2.97	5.1	1.060
120 – 169	v		0.1719	0.6976		0.0054
	N		17	18		19
F1	**x**	0.14	2.35	4.45	6.9	1.214
170–209	v	0.0171	0.2348	1.2212		0.0135
	N	23	47	32		59
F1 + F2	**x**	0.13	2.94	5.81	8.9	1.273
210 + 254	v	0.0099	0.4237	1.8890		0.0128
	N	82	95	73		127
F3 + F4 + F5	**x**	2.65	2.99	5.16	10.8	1.390
210 – 254	v	7.9744	0.8632	3.4398		0.0476
	N	14	9	8		14
F1 + F2	**x**	0.18	3.42	7.18	10.8	1.365
255 – 299	v	0.012	1.0434	2.1736		0.0199
	N	51	63	57		71
F3 + F4	**x**	2.23	3.26	6.23	11.7	1.346
255 – 299	v	5.5688	1.9660	3.2233		0.0371
	N	34	34	34		34
F5	**x**	7.61	2.53	4.89	15.0	1.407
255–299	v	43.85	0.6981	5.0029		0.0193
	N	10	10	10		10
F1 + F2	**x**	0.28	3.52	7.19	11.0	0.995
300 – 369	v	0.0194	1.408	1.5781		0.0176
	N	28	28	28		28
F3 + F4	**x**	2.42	2.90	5.76	11.1	1.016
300–369	v	5.7410	0.9958	5.4281		0.0271
	N	45	45	45		45
F5	**x**	9.19	2.75	4.03	16.0	1.037
300 – 369	v	53.68	0.8755	2.9656		0.0131
	N	23	23	22		22
F6	**x**	3.12	2.40	3.95	9.5	0.988
300–369	v	5.6248	0.3624	2.4561		0.0188
	N	25	25	25		25
F3 + F4	**x**	4.26	2.80	4.02	11.1	1.054
≥370	v	7.9768	0.5166	3.4701		0.0231
	N	41	41	40		42
F5	**x**	11.60	2.25	3.20	17.0	1.042
≥370	v	41.35	0.4985	5.5121		0.0170
	N	25	25	24		25
F6	**x**	2.80	2.22	3.31	8.3	0.975
≥370	v	4.4640	0.2813	1.8807		0.0171
	N	62	62	62		62

Table 9. Diet of small and medium-sized pejerrey; percentage by volume of the main prey in relation to fish size (from Wurtsbaugh *et al.* in press)

Preys	Standard length sizes (cm) of the predator			
	5-9	9 - 13.5	13.5 - 18	18-27
Amphipoda	27.5	39.2	31.2	17.9
Chironomides	39.1	15.2	3.5	2.2
Copepods	19.7	33.2	25.8	10.3
Cladocerans	1.5	5.4	7.0	4.1
Orestias mooni			1.3	32.3
Other fishes	5.6	2.4	24.7	27.4

Small individuals less than 9 cm long feed mainly on benthic organisms (Table 9), particularly amphipods and chironomids, as would expected from what is known of their habitat. At a slightly larger size the benthos still remains dominant, but zooplankton represents 39% of the diet in terms of volume. At around 25 cm, the three prey categories, amphipods, zooplankton and fish, are equally important. Finally at around 20–25 cm fish become dominant.

Our results (Table 10) complete the sequence and confirm the increasing predominance of fish in the diet with increasing size of the predator. Zooplankton disappear as from 35 cm, whereas the percentage occurrence of amphipods diminishes to become very low in individuals of more than 40 cm. *Basilichthys bonariensis* therefore exploits all the main groups of animals available in the upper 10 m of water in Lake Titicaca, during the various stages of its development. As a species it can be considered as polyphagous, even though the different stages of development have marked preferences.

As far as the species of prey fish are concerned, Wurtsbaugh *et al.* mainly found a small fish known locally as *ispi* and which they attributed to the species *mooni*. It is very likely that this was *Orestias ispi*, a species described in 1981 by Lauzanne, from numerous specimens of ispi from the Lago Pequeño. In the stomachs of pejerrey from the Lago Pequeño, we have found a few *Orestias olivaceus* and numerous *O. agassii*. In contrast, Vaux *et al.* (*op. cit.*) found no fish in the stomach contents of about forty specimens of 12 to 26 cm long caught in open water at the entrance to Puno Bay, in an area where *O. ispi* were nevertheless abundant. These differences can be explained as follows.

Generally there are few *O. ispi* in the surface water layers, the species being in contrast abundant at a depth of 25–30 m. The pejerrey captured by Vaux *et al.* therefore had to content themselves with zooplankton. If Wurtsbaugh *et al.* found *O. ispi* in the stomach contents of littoral pejerrey this was because the prey species approaches the coast to spawn in the belt of vegetation and then finds itself exposed to the surface water predator, *Basilichthys bonariensis*. Finally, the absence of *O.ispi* in our own results

Table 10. Diet of large pejerrey: percentage occurrence of the main prey categories and relationship between length of prey fish and that of predators

Preys		Groups of standard length (cm) of the predator			
		25–30	30 - 35	35 - 40	> 40
Fish, unidentified		47.2	40.0	39.3	50.0
Orestias, unidentified		5.6	16.7	7.1	15.0
Orestias agassii		8.3	13.3	42.9	30.0
Orestias olivaceus		5.6			
Total fish		69.4	70.0	89.3	95.0
Amphipods		19.4	26.7	10.7	5.0
Zooplankton		13.9	10.0		
Insects		2.8			
Number of stomachs		36	30	28	20
Forage fish	L'	4.6	6.0	7.0	7.7
	v	0.72	1.52	2.19	2.39
	N	18	28	26	12
Predator	L	26.8	32.9	37.5	42.4
	v	0.82	2.76	1.54	2.51
	N	9	10	16	10
L /L'		5.8	5.5	5.4	5.5

can be explained by the very sporadic occurrence of this species in the southern part of the Lago Pequeño from where most of our large specimens of pejerrey originate. In its behaviour *B. bonariensis* can therefore be classed as an opportunist, but this opportunism does not go as far as altering its behaviour so that it descends into deep water to take advantage of the abundant prey at 25–30 m.

By measuring the fish found in the stomach contents, a fairly constant relationship is found between the size of the predator and that of its prey, the relationship between the the standard lengths always being close to 5.5. Such a relationship is not usually so clear cut as in this case, where there was only one prey species, *Orestias agassii* and only one habitat, the southern part of the Lago Pequeño.

Finally, it is interesting to note the complete absence of *Salmo gairdneri* from the prey. It is certain that the data are still incomplete, because Wurtsbaugh *et al.* worked only on *B. bonariensis* less than 30 cm and perhaps only the large pejerrey capture *S. gairdneri*. In our study we obtained about 400 *B. bonariensis* of more than 30 cm, but nearly all came from the Lago Pequeño where the population levels of rainbow trout are very reduced. There are however some indications suggesting that predation by *B. bonariensis* on *S. gairdneri*, if it exists, would not be very important. In contrast, *S. gairdneri* does feed partly on *B. bonariensis*: in twenty full stomachs examined, 4 contained young pejerrey of 8 to 12 cm.

In terms of the main species of zooplankton prey, *Daphnia pulex* is most important for pejerrey of less than 20 cm, and the copepod *Boeckella titicacae* in those of 20 to 26 cm (Vaux *et al.*, *op. cit.*). In contrast, according to the results provided by Wurtsbaugh *et al.*, Cladocera are of little importance. This no doubt results from the structure of the zooplankton populations which varies with habitat and season.

Burbidge *et al.* (1974) gave the composition of the stomach contents of 40 young pejerrey of 6 to 9 cm from Lake Peñuelas, Valparaiso, Chile. The diet consisted essentially of zooplankton, with 93% Copepoda and 6% Cladocera. Cabrera (1962) and Cabrera *et al.* (1973) studied the diet of about 300 *B. bonariensis* from the Buenos Aires region. They demonstrated the existence of a very varied diet composed of numerous zooplanktonic and benthic components, but also predominantly fragments of aquatic higher plants. This last item is surprising, since despite the abundance of vegetation in Lake Titicaca, neither Wurtsbaugh *et al.* nor ourselves have ever found the slightest trace of such a component, in spite of the large number of observations. These Chilean and Argentine observations confirm the omnivorous diet of *Basilichthys bonariensis*.

Conclusions

These preliminary results on the biology of *Basilichthys bonariensis* in Lake Titicaca show that this species is very well adapted to conditions of life rather different from those occurring in its original habitat. Coming from a lowland, subtropical riverine environment with fairly marked seasonality, the pejerrey fairly quickly colonised the entire Lake Titicaca basin. The main aspects of their successful acclimatisation are the continuous reproduction, the abundance of young stages in the vast nurseries constituted by the littoral macrophyte beds and of adults in the superficial pelagic zone, the varied diet using the main resources available, the formation of body reserves which always remains considerable and the constancy in body condition.

Considerable gaps remain in the knowledge of the biology of the species. These include: age determination, growth, demographic structure and knowledge of the populations occurring in rivers. On the last point, all that is known from Wurtsbaugh *et al.* is that the pejerrey penetrates fairly far up the inflow rivers in the form of individuals of 10 to 22 cm. It would also be very important to test if the low water temperature is the real cause for the aborted spawnings recorded in many females from Lago Pequeño. More detailed information is also needed on the relationships with native species and *Salmo gairdneri*. Finally, monitoring is required of the impact of fishing on the pejerrey in the lake. Ten years ago captures were of the order of 1700 tonnes for a habitable area (depth zone of less than 50 m) of about

3000 km^2, or a yield of 5.7 kg ha^{-1}. This does not seem very great, but the quantity captured at present is unknown, as is the impact of fishing on the various ecophases. It is probable that fishing mainly affects spawning congregations, as we have recorded in Guaqui Bay in 1981, and in this case, in spite of a relatively modest tonnage captured, fishing could be a major factor for the depletion of the stocks of *Basilichthys bonariensis* in Lake Titicaca.

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