

FEEDING HABITS AND CONDITION OF TWO LANDLOCKED POPULATIONS OF ALLIS SHAD (*ALOSA ALOSA*) IN PORTUGAL.

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ABSTRACT

Only three cases of landlocked populations of allis shad (*Alosa alosa* L.) were reported until the present, being two of them in Portugal. In this paper, data on the feeding habits and condition of these two populations sampled between 1998 and 1999 are presented.

Both populations are zooplanktivorous, with cladocerans (Family Daphniidae) and cyclopoid copepods (*Cyclops* sp.) as the preferential prey for both adults and juveniles from Aguieira reservoir, while in Castelo do Bode adults feed preferentially on calanoid copepods (*Copidodiaptomus albidus*) and cladocerans (Family Daphniidae).

Landlocked adults present lower condition than the migrating ones, while juveniles from the Aguieira reservoir show a better condition than the juveniles captured in the Mondego estuary.

Key-words : *Alosa alosa*, landlocked populations, feeding habits, condition, Portugal.

ALIMENTATION ET COEFFICIENT DE CONDITION DES INDIVIDUS DE DEUX POPULATIONS LACUSTRES D'ALOSE (*ALOSA ALOSA*) AU PORTUGAL.

RÉSUMÉ

Jusqu'à présent on ne connaît que trois populations d'alose (*Alosa alosa* L.) bloquées en eau douce, dont deux au Portugal. Dans cet article sont présentées les données sur les habitudes alimentaires et les coefficients de condition des individus de deux populations portugaises échantillonnées entre 1998 et 1999 dans deux lacs.

Les deux populations se nourrissaient de zooplancton. A Aguieira les proies préférentielles des adultes et des juvéniles étaient les cladocères (Famille Daphnidae) et les copépodes cyclopodes (*Cyclops* sp.), tandis qu'au réservoir de Castelo do Bode la

nourriture préférée des adultes était surtout constituée de copépodes calanoides (*Copiodiaptomus albidus*) et de cladocères (Famille Daphnidae).

Les populations adultes bloquées en eau douce avaient un coefficient de condition inférieur à celui des populations migratoires, tandis que le coefficient de condition des juvéniles du réservoir d'Agueira était meilleur que celui des juvéniles capturés dans l'estuaire du Mondego.

Mots-clés : *Alosa alosa*, populations lacustres, alimentation, condition, Portugal.

INTRODUCTION

The allis shad (*Alosa alosa*, L.) is an anadromous clupeid whose populations suffered a severe reduction in the last decades. In the beginning of the 20th century its distribution ranged from Iceland and North Europe until the Northeastern Mediterranean and the North of Africa, being nowadays rare in North Europe and British Islands, and extinct in several European rivers (QUIGNARD and DOUCHEMENT, 1991). In Portugal their populations have also decreased, especially in the rivers from the south (e.g. Tejo and Guadiana rivers) (COSTA *et al.*, 2001). One of the main factors responsible for this decline is the construction of dams and weirs (ALEXANDRINO, 1996), which obstruct their upstream migration. These obstacles have caused the reduction of spawning grounds, but on the other hand, have led to the establishment of landlocked populations of allis shad upstream those constructions, within the reservoir areas.

Although there are not many landlocked populations in the genus *Alosa*, TREWAVAS (1938) described populations from the Irish lakes (*Alosa fallax killarnensis*, Regan), and BERG and GRIMALDI (1966) worked with populations from the Italian lakes (*Alosa fallax lacustris*, Fatio). The only populations of *A. alosa* known to be locked are those from the lake El Kansera in Morocco (FURNESTIN, 1952 ; FURNESTIN and VINCENT, 1955 ; LAHAYE, 1960, 1966), and from Castelo do Bode and Agueira reservoirs in Portugal (EIRAS, 1981, 1983 ; COLLARES-PEREIRA *et al.*, 1999 ; COSTA *et al.*, 2001). The Portuguese landlocked populations of allis shad exist in the Castelo do Bode reservoir (Tagus basin) since 1951, and in the Agueira (Mondego basin) since 1981, when the dams were constructed.

As it is stressed by TAVERNY (1991), SABATIÉ (1993) and ALEXANDRINO (1996), several studies on the biology of European shads have been carried out, but only a few refer to the feeding ecology of these species (CASSOU-LEINS and CASSOU-LEINS, 1981 ; APRAHAMIAN, 1988, 1989 ; TAVERNY, 1991 ; ASSIS *et al.*, 1992 ; SABATIÉ, 1993), and there are even less for landlocked populations (BERG and GRIMALDI, 1966).

Most of the research done on the feeding ecology of landlocked populations of the genus *Alosa* deals with the effect of the alewife (*Alosa pseudoharengus*, Wilson) in the North American freshwater fishes and zooplankton communities, since this species has become established in many inland lakes of this continent (HUTCHINSON, 1971). Competition with alewives for zooplankton, or predation by alewives on eggs and larvae of native planktivorous fish have been hypothesized as causes for the decline of many of the native species (SMITH, 1970 ; BRANDT *et al.*, 1987 ; ECK and WELLS, 1987), and several authors refer that size-selective predation by alewives has restructured zooplankton communities in the North American inland lakes (WELLS, 1970 ; HUTCHINSON, 1971 ; WARSHAW, 1972 ; VIGERSTAD and COBB, 1978 ; EVANS, 1986 ; BROOKS and DODSON, 1965 ; HEWETT and STEWART, 1989).

The purpose of this work was to study the food habits of the Portuguese landlocked populations of allis shad, and to evaluate the occurrence of ontogenetic, seasonal or geographical differences on the feeding ecology of this species. The condition of these populations comparatively to the anadromous ones was also analyzed.

MATERIAL AND METHODS

The study was conducted in the Tagus and Mondego basins (Figure 1). Castelo do Bode dam, with a 3 530 ha reservoir and a gross capacity of 1100,0 hm³, is located in the River Zêzere (Tagus basin) and was constructed in 1951. MARQUES and BOAVIDA (1997) classified Castelo do Bode as oligotrophic in 1991 and mesotrophic in 1992 and 1993. Agueira dam, located in the River Mondego, was concluded in 1981 creating a reservoir with an area of 2 000 ha and gross capacity of 450 hm³. OLIVEIRA and MONTEIRO (1992) considered this one as a low productive reservoir, with phytoplankton and zooplankton communities comparable to the mesotrophic systems.

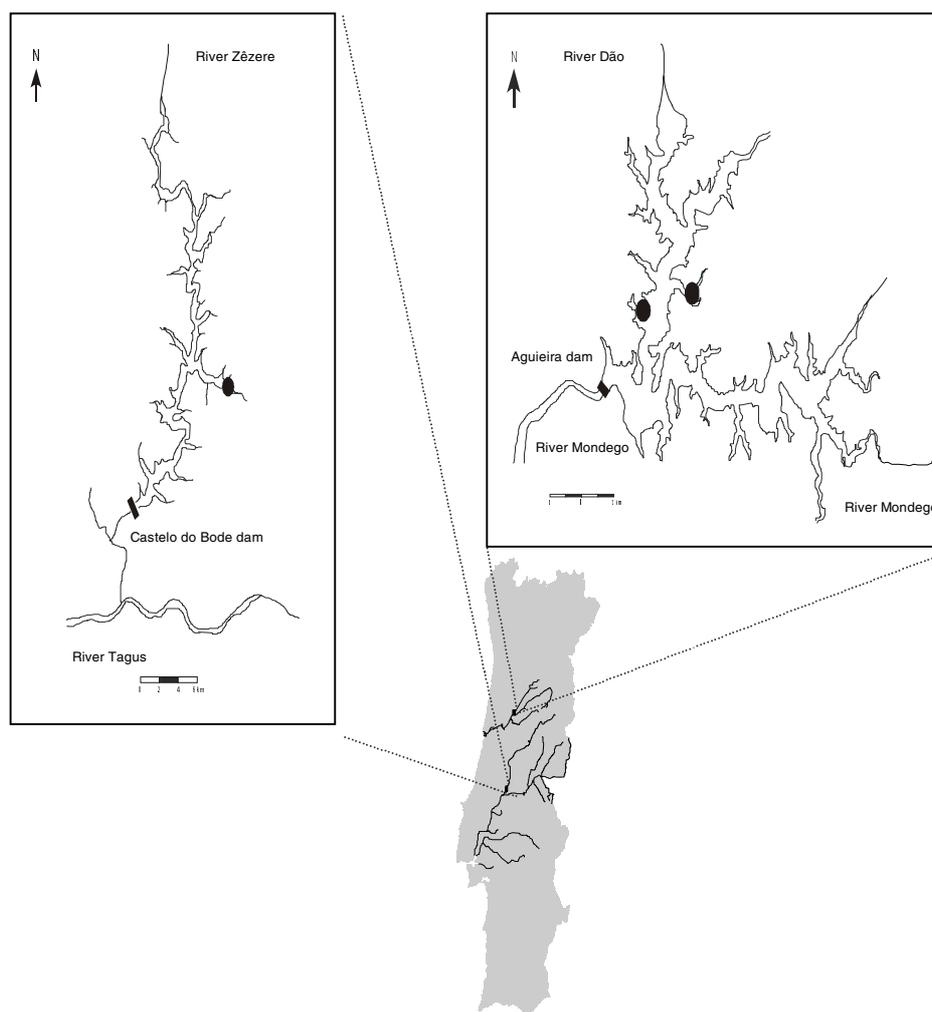


Figure 1
Map of the study area. Black dots indicate the sampling sites.

Figure 1
Carte de l'aire d'étude. Les cercles noirs marquent les sites échantillonnés.

Allis shad specimens were collected from both reservoirs using gill nets (20-200 mm knot to knot mesh size ; 2 m height ; 50 m long), set perpendicular to the shore at sunset and removed at sunrise in the following day. In Aguieira samples were taken monthly between June 1998 and May 1999, and in the Castelo do Bode collections were made in February and March 1999. After capture the fish were kept frozen. In the laboratory specimens were measured to the nearest mm (TL - total length) and weighed to the nearest g (EW - eviscerated weight). For the diet analysis a sub-sample was taken and their stomachs were removed and preserved in 70 % alcohol. Prey items were identified to the lowest taxonomic level possible.

The monthly samples from Aguieira reservoir were grouped into seasons (Winter = January-March ; Spring = April-June ; Summer = July-September ; Autumn = October-December), and sorted by length into two groups : (1) juveniles (TL \leq 260 mm) ; and (2) adults (TL > 260 mm).

To evaluate each prey's relative importance the frequency of occurrence (FO - percentage of stomachs with content in which a group of prey occurs), according to the ALBERTINI-BERHAUT (1973) method (FO \geq 50 % - preferential prey ; 10 % \leq FO < 50 % secondary prey ; FO < 10 % - occasional prey) was used. To analyze the feeding activity, the vacuity coefficient (VC) and the fullness index (FI) were calculated according to HYSLOP (1980) : VC - percentage of sample with empty stomachs ; FI = (weight stomach content / EW) x 100.

The condition factor (K) was computed according to the formula : $K = EW \times 10^5 / TL^3$ (BOLGER and CONNOLLY, 1989).

Friedman and Kruskal-Wallis tests (χ^2), Mann - Whitney test (U), independence G-test (with Williams or Yates corrections) and Spearman rank-order correlation coefficient (r), were employed in the statistical treatment of the data (SIEGEL and CASTELLAN, 1988 ; SOKAL and ROHLF, 1995). All tests were performed using a level of significance of 0,05.

RESULTS

Diet

A total of 585 specimens were caught in Aguieira and Castelo do Bode reservoirs, and a sub-sample of 200 and 83, respectively from Aguieira and Castelo do Bode reservoirs, was used in the diet analysis.

The diet of the allis shad collected from both sites was composed of zooplanktonic organisms, benthos and terrestrial and aquatic insects (Figure 2).

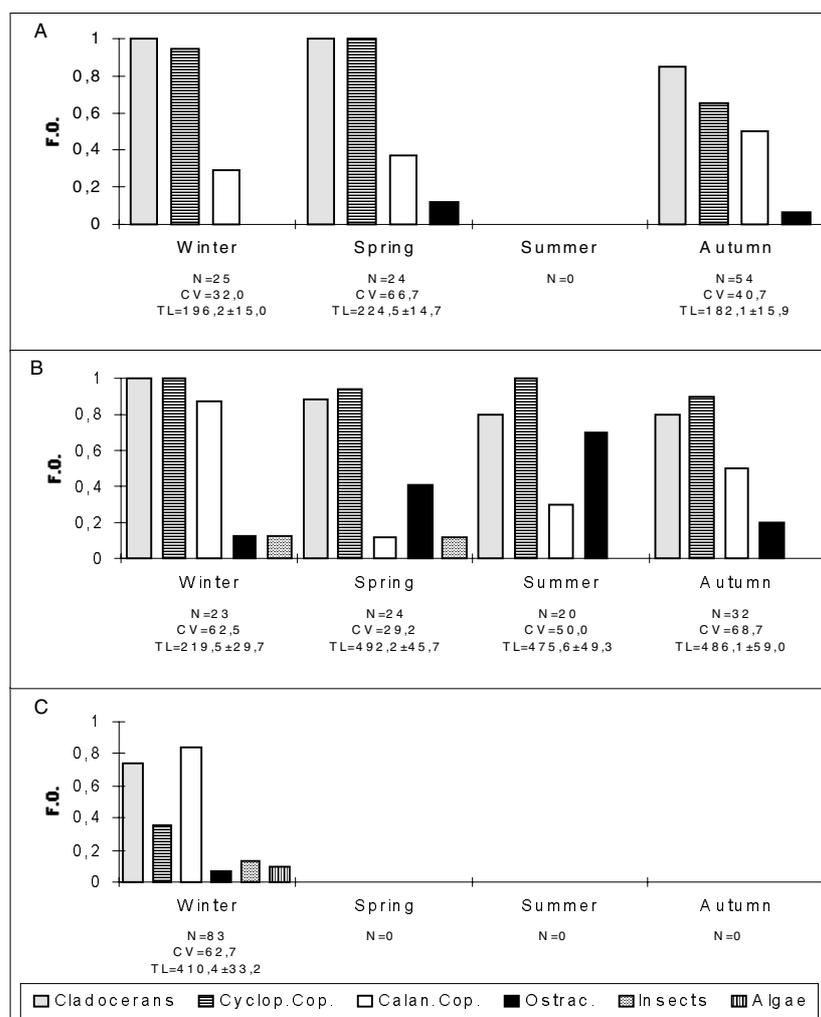


Figure 2
Frequency of occurrence (F.O.) of main prey items for juveniles (A) and adults (B) of allis shad from Aguieira, and for adults from Castelo do Bode (C).

Figure 2
Fréquence d'occurrence (F.O.) des proies pour les aloses juvéniles (A) et adultes (B) capturées à Aguieira, et pour les adultes capturés à Castelo do Bode (C).

In Aguieira reservoir the cladocerans (Family Daphniidae) and cyclopoid copepods (*Acanthocyclops* sp.) were the most frequent preys, both for juveniles and adults, while calanoid copepods (*Copidodiaptomus numedicus*) and ostracods were consumed upon less frequently, being insects rarely ingested. Globally there were no significant differences in the diet along the year, both for juveniles ($\chi^2 = 2,533$, d.f. = 2, n.s.) and adults ($\chi^2 = 3,638$, d.f. = 3, n.s.). Almost all the ingested prey had the same importance all the year in both groups, except the cyclopoid copepods which were less important in the diet of juveniles in Autumn, and the calanoid copepods and ostracods which were highly preyed upon by adults in Winter and Summer, respectively (Table I).

Table I

Results from the independence G-test to compare the absolute frequencies of each food item between seasons for the juveniles and adults of allis shad collected in Aguieira reservoir.

Tableau I

Résultats des G-tests d'indépendance, pour comparer les fréquences absolues des proies entre saisons, chez les juvéniles et adultes d'aloses capturées dans le réservoir Aguieira.

Prey items	Juveniles		Adults	
	G _{williams} ^(a)	Test results	G _{williams} ^(b)	Test results
Cladocerans	5,168	<u>Au Wi Sp</u>	2,608	<u>Au Su Sp Wi</u>
Cyclopoid copepods	9,126*	<u>Au Wi Sp</u>	1,552	<u>Au Sp Wi Su</u>
Calanoid copepods	1,948	<u>Wi Sp Au</u>	14,307*	<u>Sp Su Au Wi</u>
Ostracods	1,914	<u>Wi Au Sp</u>	7,864*	<u>Wi Au Sp Su</u>
Insects	-	-	2,840	<u>Wi Sp Su Au</u>

(a) - d.f. = 2 ; (b) - d.f. = 3 ; * significant values for $p < 0,05$.

Wi : Winter ; Sp : Spring ; Su : Summer ; Au : Autumn ; lines join non-significant sub-sets.

Adult and juvenile's diet was correlated in Winter and Autumn (respectively, $r = 0,973$, $n = 5$, $p < 0,05$ and $r = 0,900$, $n = 5$, $p < 0,05$) but not in Spring ($r = 0,789$, $n = 5$, n.s.), since adults ingested less calanoid copepods and more ostracods than juveniles in the later season. Globally the frequency of ingestion of each prey was similar between adults and juveniles, except for the ostracods which were more frequently ingested by adults (cladocerans : $G_{Yates} = 0,003$, d.f. = 1, n.s. ; cyclopoid copepods : $G_{Yates} = 3,135$, d.f. = 1, n.s. ; calanoid copepods : $G_{Yates} = 0,000$, d.f. = 1, n.s. ; ostracods : $G_{Yates} = 7,708$, d.f. = 1, $p < 0,05$; insects : $G_{Yates} = 2,696$, d.f. = 1, n.s.).

In Castelo do Bode reservoir the calanoid copepods (*Dussartius baeticus*) and the cladocerans (Family Daphniidae) were preferential prey, while cyclopoid copepods (*Acanthocyclops* sp.) played a secondary role in the diet, and ostracods, insects and algae were rarely ingested (Figure 2).

The diet of allis shad adults during the Winter period was not correlated in the two reservoirs ($r = 0,706$, $n = 6$, n.s.), especially for the frequency of ingestion of cyclopoid copepods, which was significantly higher in the adults from Aguieira (cladocerans : $G_{Yates} = 1,534$, d.f. = 1, n.s. ; cyclopoid copepods : $G_{Yates} = 9,412$, d.f. = 1, $p < 0,05$; calanoid copepods : $G_{Yates} = 0,292$, d.f. = 1, n.s. ; ostracods : $G_{Yates} = 0,031$, d.f. = 1, n.s. ; insects : $G_{Yates} = 0,031$, d.f. = 1, n.s. ; algae : $G_{Yates} = 0,084$, d.f. = 1, n.s.).

Feeding activity

The vacuity coefficient of shads from Aguieira showed some differences between seasons (Table II). Juveniles had more stomachs with food in Winter, and showed a significantly higher vacuity coefficient in Spring and Autumn, while adults, on the contrary, had more empty stomachs in Winter, Summer and Autumn, and in Spring the vacuity coefficient was significantly lower. The proportions between adults and juveniles with empty stomachs were not independent on the season (Table II).

Table II

Vacuity coefficient (VC) and fullness index (FI) of landlocked populations of allis shad, collected in Aguieira and Castelo do Bode reservoir. The results of the independence G-test and of the Kruskal-Wallis test, for comparisons along the year of the VC and FI are shown, respectively.

Tableau II

Coefficient de vacuité (VC) et indice de réplétion (FI) des populations de l'alse bloquées aux réservoirs de Aguieira et Castelo do Bode. Résultats des G-tests d'indépendance et des tests Kruskal-Wallis, pour les comparaisons saisonnières de VC et FI.

Vacuity Coefficient						
	Wi	Sp	Su	Au	G_{williams}	Test results
Aguieira						
Juveniles	32,0	66,7	-	40,7	6,567* ^(a)	Wi Au Sp
Adults	62,5	29,2	50,0	68,7	10,014* ^(b)	Sp Su Wi Au
Castelo Bode						
Adults	62,7	-	-	-		
Fullness Index						
	Wi	Sp	Su	Au	χ^2	Test results
Aguieira						
Juveniles	0,40	0,33	-	0,48	2,701 ^(c)	Sp Wi Au
Adults	0,16	0,29	0,37	0,13	4,870 ^(d)	Au Wi Sp Su
Castelo Bode						
Adults	0,12	-	-	-		

(a) : d.f. = 2 ; (b) : d.f. = 3 ; (c) : n = 102 ; (d) : n = 89 ; * significant values for $p < 0,05$.
Wi : Winter ; Sp : Spring ; Su : Summer ; Au : Autumn ; lines join non-significant sub-sets.

On the other hand, no significant differences were detected in the fullness index along the year for both juveniles and adults (Table II), although there is a similar pattern. However, despite the fact that in Spring the index was similar in both groups, juveniles had a significantly higher fullness index in Winter and Autumn, comparatively to adults (Table III).

The Castelo do Bode population had the same behaviour as the adult specimens caught in Winter in Aguieira reservoir. Both the coefficient of vacuity ($G_{\text{yates}} = 0,051$, d.f. = 1, n.s.) and the fullness index ($U = 926,000$, $n = 106$, n.s.) were similar between these populations.

Table III

Results of the independence G-test (Yates correction) and the Mann-Whitney test (U), to compare the vacuity coefficient and the fullness index between adults and juveniles from Aguieira reservoir, in each season.

Tableau III

Résultats des G-tests d'indépendance (correction de Yates) et des tests Mann-Whitney (U), pour comparer le coefficient de vacuité et l'indice de réplétion entre les juvéniles et les adultes d'aloses capturées à Aguieira, à chaque saison.

	Winter	Spring	Autumn
Vacuity Coefficient (G_{Yates}) ^(a)	4,106*	5,447*	5,320*
Fullness Index (U)	171,000* ^(b)	128,000 ^(c)	535,000* ^(d)

(a) : d.f. = 1 ; (b) : n = 48 ; (c) : n = 37 ; (d) : n = 85 ; * significant values for $p < 0,05$.

Condition of fishes

The condition factor of adult landlocked populations, namely from Aguieira reservoir, is significantly lower than the observed for the migrating adults captured in Mondego and Tejo rivers. Moreover, the Castelo do Bode population has an even lower condition than the allis shad population from Aguieira (Table IV). On the contrary, the juveniles from Mondego estuary showed a significant lower condition factor when compared with the juveniles from the Aguieira reservoir.

Table IV

Condition factor (K) of allis shad collected in Aguieira and Castelo do Bode reservoirs, and in the rivers Tejo and Mondego. Results from the Mann-Whitney (U) and Kruskal-Wallis tests to compare these values are shown.

Tableau IV

Coefficient de condition (K) des aloses capturées dans les réservoirs d'Aguieira de Castelo do Bode, et dans les fleuves Tage et Mondego. Résultats des tests Mann-Whitney (U) et Kruskal-Wallis.

Populations	K	Test results
Juveniles from Aguieira in Autumn	0,85	U = 26,000* ^(a)
Juvenile from Mondego estuary in Autumn	0,61	
A - Adults from Aguieira in Spring	0,70	$\chi^2 = 18,307$ * ^(b) A C B
B - Adults from Mondego river in Spring *	0,83	
C - Adults from Tejo river in Spring *	0,80	
Adults from Aguieira in Winter	0,64	U = 1900,000* ^(c)
Adults from Castelo Bode in Winter	0,53	

(a) : n = 94 ; (b) : d.f. = 2 ; (c) : n = 272 ; * significant values for $p < 0,05$; lines join non-significant sub-sets ; (* unpublished data).

The seasonal variation of K values in the adults from Aguieira reservoir did not present any significant change throughout the year (Table V). On the other hand, the condition of juveniles showed a variation, since the K values are significantly higher in Autumn than in Winter and Spring. Condition is always significantly higher in juveniles comparatively to adults in all seasons (Wi : U = 91,000, n = 79, p < 0,05 ; Sp : U = 38,000, n = 41, p < 0,05 ; Au : U = 401,000, n = 218, p < 0,05).

Table V

Seasonal condition values (K) of juveniles and adults of allis shad collected in Aguieira reservoir. The results of the Kruskal-Wallis tests to compare these values are also presented.

Tableau V

Valeurs saisonnières du coefficient de condition (K) des juvéniles et des adultes d'aloses capturées au réservoir d'Aguieira. Résultats des tests Kruskal-Wallis.

	Winter	Spring	Summer	Autumn	U	Test results
Juveniles	0,82	0,80	-	0,87	45,072* ^(a)	<u>Sp Wi Au</u>
Adults	0,64	0,69	0,60	0,62	6,471 ^(b)	<u>Su Au Wi Sp</u>

(a) : d.f. = 2 ; (b) : d.f. = 3 ; * significant values for p < 0,05 ; lines join non-significant sub-sets.

DISCUSSION

Diet analysis of landlocked populations of allis shad from Aguieira and Castelo do Bode reservoirs revealed that these populations are mainly zooplanktivorous, as it was observed in other studies for this and other congeneric species (BROOKS and DODSON, 1965 ; BERG and GRIMALDI, 1966 ; WELLS, 1970 ; HUTCHINSON, 1971 ; VIGERSTAD and COBB, 1978 ; EIRAS, 1981, 1983 ; HEWETT and STEWART, 1989), despite the fact that piscivory has been reported for the alewife (*Alosa pseudoharengus*) (KOHLENER and NEY, 1980 ; BRANDT *et al.*, 1987). The diet of both populations studied is based on cladocerans and copepods, prevailing the cyclopoid copepods in the population from Aguieira reservoir and the calanoid copepods in the Castelo do Bode population.

Although no studies on food selection were performed, both populations seem to consume the more abundant species reflecting each zooplankton community (CABEÇADAS *et al.*, 1980 ; OLIVEIRA and MONTEIRO, 1992 ; CARAMUJO, 1998) and some size-selection on prey should be considered since the great majority of the ingested food items have a similar size. This feature could be due to the disposition of the gill rakers, which act as a plankton sieve. Nevertheless, their feeding activity does not probably produce any effect on zooplankton community, as is was outlined by other authors (BROOKS and DODSON, 1965 ; WELLS, 1970 ; HUTCHINSON, 1971 ; WARSHAW, 1972). BROOKS and DODSON (1965) indicated that selective predation by the alewife on larger species of zooplankton was sufficient to allow smaller zooplankton species to become dominant, and WARSHAW (1972) suggested that *Alosa* predation, rather than a food decrease, caused the size decrease of zooplanktonic organisms. This effect of landlocked populations of shads on zooplankton communities is apparently null in Portuguese reservoirs, namely in Castelo do Bode, where zooplankton community has been quite stable since the construction of the dam (CABEÇADAS *et al.*, 1980 ; CARAMUJO, 1998). These differences may be related to low abundance of allis shad in Portuguese reservoirs or to specific characteristics of the species *A. alosa*.

No major ontogenetic changes in the diet of Aguieira shads' population were observed, which is in agreement with BERG and GRIMALDI (1966) studies on landlocked populations of *Alosa ficta lacustris*. Nevertheless, adults from our study showed a broader diet than juveniles. It has been reported that adult and young-of-the-year alewives exhibit spatial segregation, and this behavior conducts to different diets in the two size classes (BRANDT, 1980 ; JANSSEN and BRANDT, 1980 ; HEWETT and STEWART, 1989). BRANDT (1980) hypothesized that habitat segregation may be an effective way of reducing food competition between immature and adult alewives.

The similarity between the diet of juveniles and adults in the Aguieira reservoir suggests that they may compete for food, especially if the decrease in juvenile feeding intensity on Spring combined with an adults' increase in foraging in this season is taken into consideration. In fact, regardless the reduced seasonal changes in the specific composition of the diet of juveniles and adults, it is apparent that the former feed more actively than adults almost all the year, except during Spring, when adults probably intensify their foraging activity due to the reproductive season, and therefore may be competing directly with the immature fish. This feature could explain the decrease in juvenile's condition in this season, and the increase in the adult's condition. Since no studies on food availability, vertical distribution of both shad and zooplankton communities or even interactions of shads with other fish species were made, these considerations should be carefully regarded. Other explanations apart from competition between the two groups should be taken into consideration namely the existence of spatial segregation of shads, as observed by BRANDT (1980), combined with a differential vertical distribution of zooplankton. Another hypothesis could be a higher efficiency of adults in the filtering process, resulting from a more tight gill raker structure, since in the Spring smaller plankton is available associated with the natural blooms of the season. Finally, some negative interaction between shad juveniles and fish predators could be occurring during the Spring.

The scarcity of food available in the Aguieira and Castelo do Bode, classified as low productive reservoirs (CABEÇADAS *et al.*, 1980 ; OLIVEIRA and MONTEIRO, 1992 ; CARAMUJO, 1998), could result in the very poor condition of adults from landlocked populations when compared with anadromous fish. This has also been reported by EIRAS (1981, 1983) in the 80's referring to the population from Castelo do Bode. Besides the scarcity of food, these differences could also represent an adaptation of shads to the freshwater environment, where they do not have the energy demands that anadromous populations have for the upstream migration to the spawning grounds. It is surprising, however, that juveniles from landlocked populations have a better condition than the anadromous ones, at least in the Autumn. Considering the habitats of both populations, it is not reasonable to think that food availability is the cause to this finding, since estuaries are highly productive ecosystems. However, the juveniles inhabiting estuaries have to deal with constant changes in the salinity gradient that could cause high-energy losses with the osmoregulation process, and lead to this lower condition of fishes. This decrease in the condition factor is well documented namely for salmonids during the smolting process (MCKEOWN, 1984). On the other hand, since juveniles migrate seaward in early Autumn, with the larger individuals being the first to emigrate (APRAHAMIAN, 1988), these results could be biased and represent only the part of the juveniles, namely the smaller specimens, that have not yet gone to the sea.

Aguieira juveniles showed a better condition than adults all year round, probably due to the lowest feeding demands of the former, capable of satisfying their needs despite the scarcity of food in the reservoir. Although the adults in the reservoir could be adapted to the new environment and, as hypothesized before, have naturally a lower condition than migrating ones, despite the availability of food, the seasonal variation of condition of these fishes was in accordance with the reproductive cycle, with the maximum value in Spring, before spawning occurs, and minimum in Summer, after the spawning season.

CONCLUSION

Landlocked populations of *A. alosa* are essentially zooplanktivorous. Although some doubts about the existence of intra-specific competition within the Aguieira shad population remain, this hypothesis is consistent with the seasonal values of both feeding intensity and condition in this population.

Unfortunately the studies conducted on landlocked populations gave little importance to the condition of fishes, but this study shows that the landlocked adults have lower condition than the migrating ones. As pointed out, this could reflect the low availability of food in the reservoirs or an adaptation of these specimens to the freshwater environment, where they do not have the energy demands that anadromous populations do to reach the spawning grounds.

To clarify the unsolved questions of this study, it would be extremely important to estimate the abundance of these landlocked populations and conduct studies on selective feeding and vertical distribution of both shads and zooplankton community.

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