ICES Journal of Marine Science
April 2006; 63(3) : 476-484
http://dx.doi.org/10.1016/j.icesjms.2005.05.022

Upstream migration and reproductive patterns of a population of allis shad in a small river (L'Aulne, Brittany, France)

M.L. Acolas[a], V. Véron[b], H. Jourdan[a], M.L. Bégout[c*], M.R. Sabatié[a] and J.L. Baglinière[a]

[a]UMR INRA-Agrocampus Ecobiologie et Qualité des Hydrosystèmes Continentaux, 65 rue de Saint Brieuc, CS 84215, F-35042 Rennes Cedex, France
[b]Institut d'aménagement de la Vilaine, Boulevard de Bretagne, BP 11, 56130 La Roche-Bernard, France
[c]Centre de Recherche sur les Ecosystèmes Marins et Aquacoles, UMR CNRS/Ifremer, BP 5, F-17137 L'Houmeau, France

*: Corresponding author : tel: +33 546 500695; fax: +33 546 500600. mlbegout@ifremer.fr

Abstract: The characteristics and activity of adult allis shad [Alosa alosa (L.)] were analysed during the last part of their upstream migration in the L'Aulne, a small river in Brittany, and during reproduction on a unique spawning ground downstream of an insurmountable dam. The age of the spawners ranged from three to seven years, females being larger and older than males. Population-level migration and reproduction were studied by counting the number of migrating fish, by estimating the sex ratio, and by counting the number of nocturnal spawning acts for three consecutive years starting in 2000. The influence of the environment, especially water temperature and discharge, was highlighted: temperature during migration may supplant the influence of water flow, although high flow could allow passage over the dam. Such factors partly explain the annual pattern of migration and reproduction during the spawning season. The study showed that the biological features and characteristics of this population of allis shad in a small river were similar to those of western Atlantic stocks in large rivers.

Keywords: allis shad; anadromous migration; biological features; reproduction; small river

Introduction

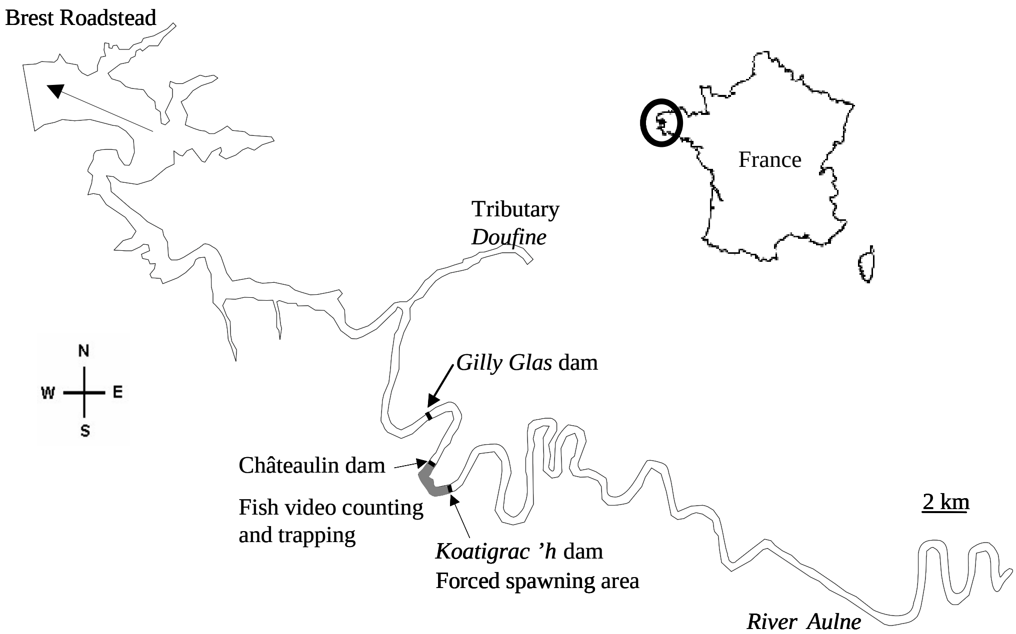
Originally, the distribution of allis shad (*Alosa alosa* (L)) extended to the Atlantic coast from Norway to Morocco (Baglinière, 2000). The fish has a pelagic sea life and migrates to the higher middle watercourse of rivers to spawn. Currently, this species is classified as vulnerable in Europe because of the reduction in its distribution and the threats to its freshwater habitat due to dams, pollution and deterioration of the spawning grounds (Baglinière *et al*., 2003). The actual northern limit would be the River Loire in France (Baglinière, 2000) and the southern limit the rivers Mondego and Vouga in Portugal (Baglinière *et al*., 2003) following on from the extinction of the populations in Morocco in 1992 (Sabatié and Baglinière, 2001). However, allis shad has not disappeared or has reappeared in small French rivers and recent studies have revealed perennial populations and functional spawning grounds (Véron *et al*., 2001; Baglinière *et al*., 2003). In France, research on the biology and conservation status of this fish has mainly focused on populations in large river systems, such as the Loire (Mennesson-Boisneau and Boisneau, 1990), the Garonne (Cassou-Leins *et al*., 2000), the Gironde (Taverny *et al*., 2000) and Adour (Prouzet *et al*., 1994). Studies on the migratory behaviour have focused only on the first phases of upstream migration and less work has been carried out on the last phase, namely the arrival of spawners on the spawning grounds (Mennesson-Boisneau *et al.*, 2000a). A detailed study of this last phase using acoustic tracking was conducted at the same time (Acolas *et al*., 2004) as the present ecological study of the population. It highlighted the existence of a separate resting, pre-spawning area and the limited visiting of the spawning ground that was partly dependent on physical (temperature and water flow) and biotic factors (sex) as well as individual variability in spawning behaviour. The purposes of this multi-year survey were to provide a detailed description of this last phase of the migration and the reproduction activity on a forced spawning ground of the population of allis shad in the River Aulne, a small human-impacted stream in Brittany, and to compare its characteristics to the populations of larger rivers.

Materials and Methods

Study site

The catchment of the River Aulne (1875 km^2 in surface) is the third-largest coastal river in Brittany. The source is on granite, and the river then penetrates the schist of Châteaulin before arriving at the roadstead of Brest after vast meanders for 145 km, of which 70 km have been channelled since 1836 (Figure 1). There are 28 dams to maintain a depth of 2 m for navigation. Average water flow of the river is 9 m^{3}s^{-1} with a maximum value of 80 m^{3}s^{-1}. Water quality is lowered by fish-farm effluents and nitrates from agriculture activity. Poor water quality is associated with low summer flow and the multitude of dams that lead to eutrophication in the channelled areas. The first dam met by upstream migrating fish (Gilly Glas) is about 30 km from the river mouth and can be crossed by a fish pass at high tides (Figure 1). The second dam is located in Châteaulin at the limit of tidal influence. This sill has a fish pass with vertical slits that allows the passage of the migrating fish species present: allis shad, eels (*Anguilla anguilla* (L.)), sea lamprey (*Petromyzon marinus* (L.)), Atlantic salmon (*Salmo salar* (L.)), and sea trout (*Salmo trutta* (L.)). The pass is equipped with a trap and a video system that has allowed the number of migrating fish to be counted since 2000.

Figure 1: Map of study site within the River Aulne, in Brittany, France (The coordinates of the Brest roadstead are 48°23’N 04°29’W.).



The study area included 2.3 km of channelled river located between the dams of Châteaulin and Koatigrac'h, the latter being insurmountable by allis shad because of an unsuitable fish pass (Figure 1). The channel has a sandy-silty bottom and the average depth varies between 1.80 and 2.15 m according to water-discharge level. The spawning area of allis shad is located just downstream Koatigrac'h dam and covers an area of 3000 m^2. Its physical habitat is characterized by mobile coarse gravel on a schist bed and depths range between 0.1 and 1.9 m. Those two characteristics are similar to those described for natural spawning areas in larger rivers (Boisneau *et al.*, 1990; Cassou-Leins *et al.*, 2000). However, the spawning-area width (25-50 m) and water-current speeds observed (0.1-1.3 m s^{-1} in 2001, 0.3-0.9 m s^{-1} in 2002) were on average lower than typical values recorded for natural spawning grounds (50-200 m wide, 0.9-2.0 m s^{-1}) (Cassou-Leins *et al.*, 2000). Moreover, the “forced” character of the spawning ground was reinforced by the presence of a pool with a relatively slow current (0.2-0.4 m s^{-1} in 2002) while typical spawning grounds are usually followed downstream by a shallow, fast running zone (Cassou-Leins *et al.*, 2000). The characteristics of the spawning site contrasted with those of the channel, with reference to bottom type and water current, because of its rocky bottom habitat and. a narrow jet of water flow created by an island which allowed the current to accelerate.

Protocol for migration and reproduction assessment

The number of migrating allis shad was counted by the aquatic observatory of Châteaulin (SMATAH). Fish sampling was done during the second half of the 2001 migration (74 individuals) and during the whole 2002 migration period (239 individuals) at the rate of three to four times per week using the trap system. Sex was determined by gentle pressure on the abdomen (males were all ripe, with running milt): total length (Lt ± 5 mm) and weight (Mf ± 50 g) were measured. A scale sample was taken from the optimum zone to estimate age (Baglinière *et al.*, 2001). Population reproduction was documented during one month in 2000, and during all the spawning seasons in both 2001 and 2002 (Table 1). An observer was positioned on a jetty in the middle of the spawning area, to count spawning events by seeing and hearing them or just hearing them (Cassou-Leins and Cassou-Leins, 1981; Boisneau *et al.*, 1990). Reproduction acts were counted every night between 22:00 and 6:00 (U.T. +2) in 2000 and 2001 and for three nights a week in 2002. A spawning act was defined, according to Boisneau *et al.* (1990) as a fast, nocturnal circular movement at the water surface (1-1.2 m in diameter during 2 to 10 s) of two spawners minimum side by side. Its sound intensity at a distance of 1 m was measured between 35 and 50 dB (Cassou-Leins *et al.*, 2000). Further, surface current speed was visually estimated. When water turbidity was low and fish were close enough to the observer, the number of fish participating in a spawning act was noted.

Water flow was measured by Brittany DIREN (Direction Régionale de l'Environnement). Water temperature on the spawning area was recorded hourly by a datalogger (Minilog, Vemco Ltd).

Table 1: Studied migration and reproduction periods

Year	Migration period	Total number of migrants	Number of migrants sampled	Reproduction period	Number of spawning acts counted	Maximum of spawning acts counted in one night
2000	07/04-08/08	2182	0	13/05-16/06*	2917	306
2001	16/04-22/07	4325	74	12/05-11/07	16851	675
2002	06/04-15/08	2331	239	24/04-11/07	6310	531

* In 2000 reproduction was partially followed

Data analysis

Statistical analysis of migration and spawning patterns were performed with EXCEL and SPAD®. Migration and reproduction trends were evaluated by calculating a 7-day moving average. Average daily temperature was calculated for each study year. A sex-ratio expressed by the sampled males number/females number was calculated in 2001 and 2002.

To study the environmental factors that influence migration, the migrating population was considered as closed (total number of migrants known) and was expressed by the percentage of migrating individuals per day (Xj) in relation to the number of migrants remaining.

Percentage of migrants per day: $$Xj = Nj \Bigg/ \left(\sum_{i=1}^{n} Ni - \sum_{j=1}^{j-1} Nj - i \right)$$

(j=date of the day; i=day between 1 and n with n=total number of days; N=number of migrants.)

For the analysis of migration activity, the study period was reduced by removing 2% of the total duration of the migration period at the beginning and the end. Thus the following periods were considered: 29/04-18/06 in 2000, 27/04-30/06 in 2001, 20/04-19/06 in 2002.

In 2001 and 2002, the evolution of the daily migrants and reproductive activity were analysed with an ANOVA and a global linear model (GLM). The Fisher test was used to indicate the significance of some of the results. Temperature, water flow and tidal influences on migration were monitored using the following variables:

Daily average temperatures and water flow and derived variables

Daily average of the two highest tide coefficients

Spawning activity was analysed using the following variables:

Daily average temperature and water flow and derived variables

The number of migrants of the day before

For each year, the number of spawning acts per female was estimated by using the number of spawning acts counted on the spawning area and the number of migrants counted at Châteaulin pass following the assumptions of Cassou-Leins *et al.* (2000) viz.

1) Spawners visit only one spawning ground.
2) A balanced sex-ratio of the population exists.
3) There is only one spawning act per night per female, and
4) One act corresponds to only one female.

Based on these assumptions, Cassou-Leins *et al*. (2000) considered a female could spawn between 5 to 7 times during a reproduction season.

Results

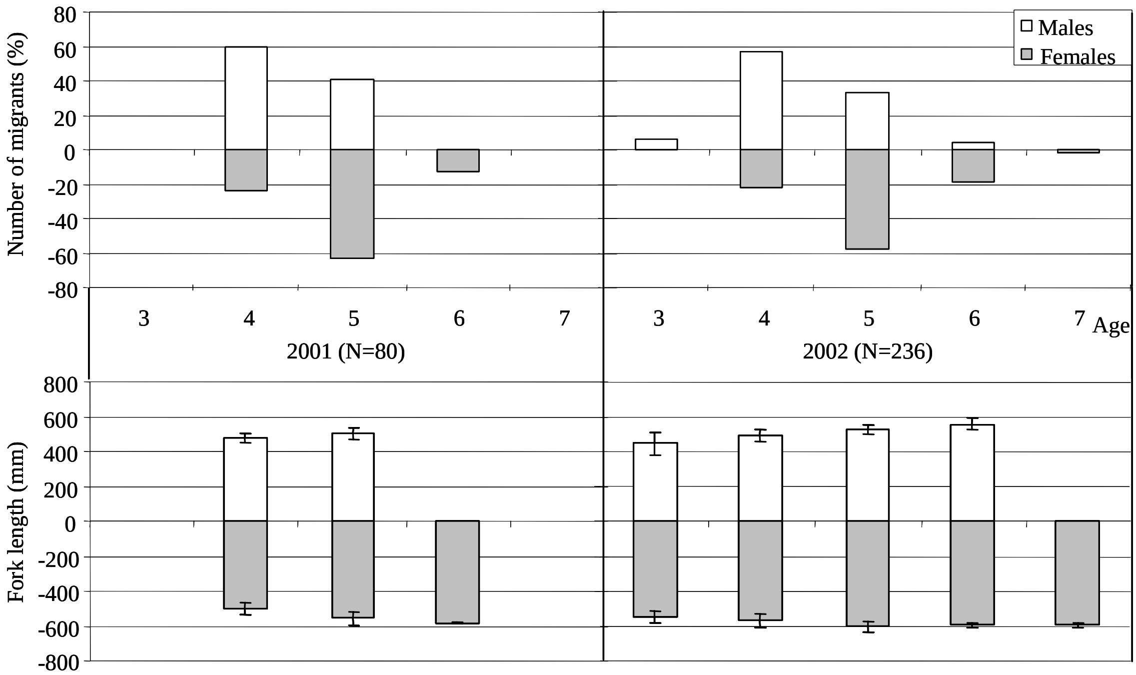
Upstream Migration

Demographic characteristics

In 2001, a sex-ratio of 1.51 in favour of females was observed in a sample of 1.7 % of the population (N=74) during the second half of the migration period. In 2002 the sex-ratio was estimated over the whole migration period in a sample of 10.2% of the population (N=239). It tended to be in favour of males at the beginning (sex-ratio=1.3 in April, N=52) and at the end of the migration (sex-ratio=1.2 in June, N=28) whereas it was in favour of female in the middle of the migration period (sex-ratio=0.6 in May, N=150). According to those values, the population in 2002 has a total sex ratio of 0.92 and was estimated to be composed of 1103 males and 1195 females.

Sampled individuals in 2001 and 2002 were between 3 and 7 years old (3-6 y. for males and 4-7 y. for females). In males, sizes and weights ranged from 370 to 585 mm and from 510 to 2000 g respectively. In females, sizes and weights were higher ranging from 445-670 mm and from 600-3100 g respectively (Figure 2). Otherwise the percentage of multispawners was very low (2.1 % - 2.5 %).

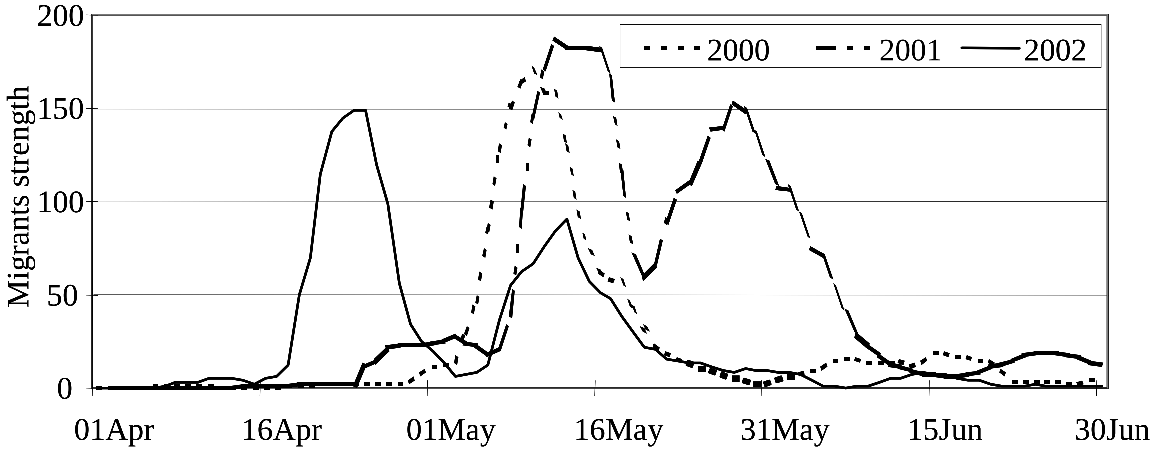
Figure 2: Age and length-at-age according to sex of allis shad sampled in 2001 and 2002.



Period and trends

During the three years upstream migration occurred between April 6 and August 15. The main movement took place between April 29 and June 18 in 2000 (96 % of the migrants), between April 25 and June 16 in 2001 (94 % of the migrants) and between April 19 and May 27 in 2002 (91 % of the migrants). The total number of migrants in 2001 was twice that observed in 2002 (Table 1). Migration trends calculated on as a 7-day moving average were uni-modal in 2000 and bi-modal in both 2001 and 2002 (Figure 3).

Figure 3: Trends in upstream migration of Allis shad for three consecutive years (weekly moving averages of the daily number of migrants).



Environmental influence

Over the three years the temperature observed during the migration varied between 10.5°C and 23°C. The temperature threshold under which migration would be inhibited seemed to be close to 11°C and was recorded in 2001 only. In the same period the observed water flows varied strongly during upstream migration (2.7 - 86.7 $m^3 s^{-1}$) (Table 2).

Table 2: Water temperature, water flows and current speed variations during migration and reproduction

Year	T observed during migration period Min-Max	T Migration activity started	T Migration activity stopped	T during reproduction period Min-Max	T during reproduction activity Min-Max	Water flows (m^3s^{-1}) during migration period Min-Max	Water flows (m^3s^{-1}) during reproduction period Min-Max	Water flows (m^3s^{-1}) during reproduction activity Min-Max	Current speed (ms^{-1}) during reproduction period Min-Max	Current speed (ms^{-1}) during reproduction activity Min-Max
2000	11.8-21.9	-	-	13.3-17.2*	13.9-17.2	10.1-86.7	10.1-47.6	26.6-47.6	-	-
2001	10.5-23.0	11,3	10,7	14.0-23.0	14.3-23.0	2.7-64.0	2.7-26.9	20.5-26.3	0.10-1.25	0.10-0.80
2002	11.6-19.9	11,7	-	13.4-19.3	13.9-19.3	5.6-44.3	5.6-44.3	8.3-19.9	0.30-1.50	0.30-0.75

T=Water Temperature; *In 2000 reproduction was partially followed (Cf. Table 1)

The analysis of migration activity in 2001 and 2002 showed an increase in activity during the continuous increase in temperature associated with a decrease in the water flow whereas it dropped when the temperature decreased with or without a decrease in water flow (Figure 4).

In 2001, the water-temperature derived variable “difference of temperature with the day before” explained the highest variance of the model (49%) followed by the daily average temperature (45%) water flow (39%) and tide coefficient (21%). In 2002, the water-temperature derived variables “temperature 5 days before” and “difference of temperature with the day before” explain the highest variance (54 and 44%), the next highest being water flow (34%) (Table 3).

Figure 4: Percentage of migrating individuals per day (Xj,) in relation to the number of migrants remaining in relation to temperature and water flow in 2001 and 2002.

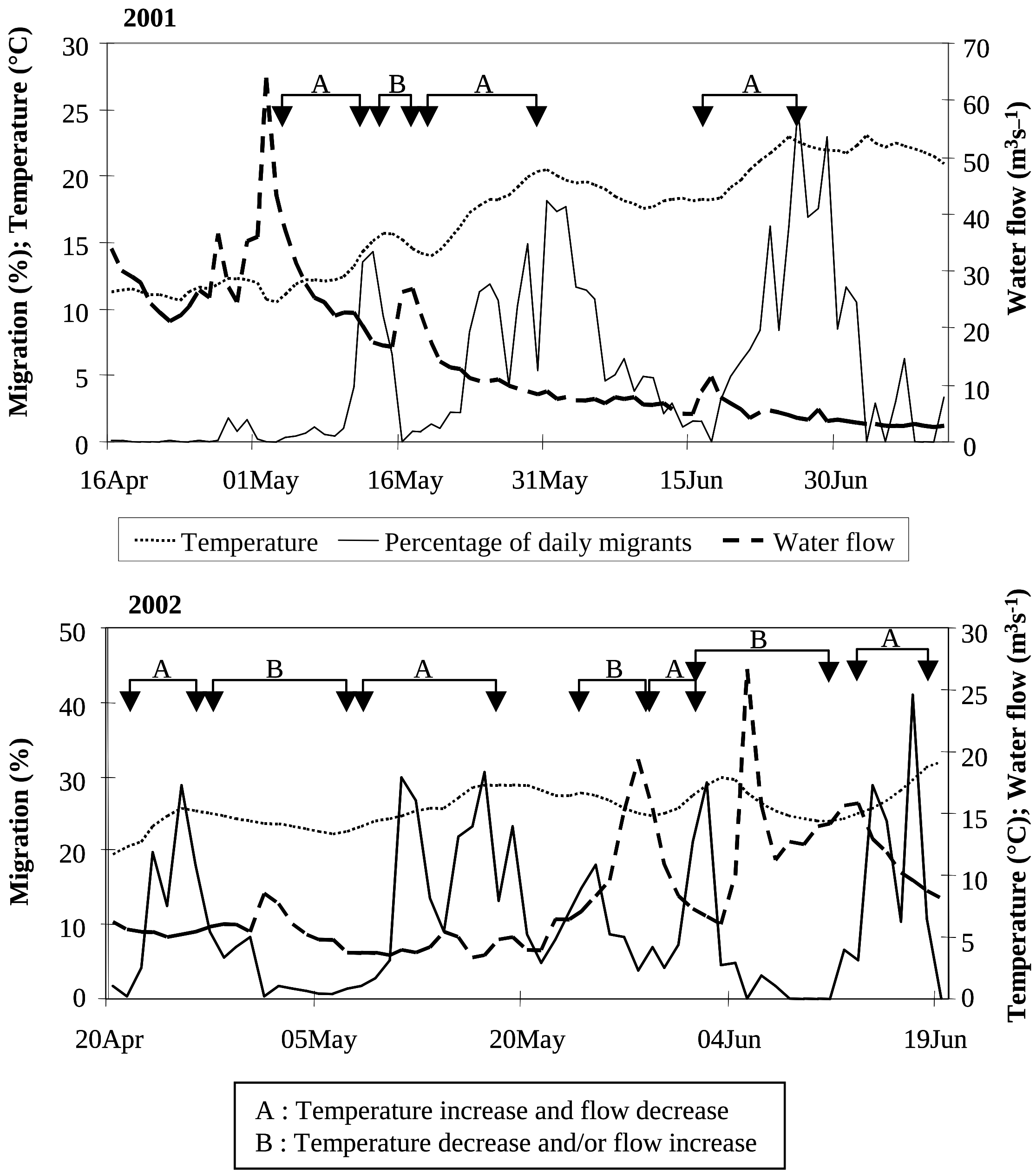


Table 3: ANOVA analysis of environmental factors on migration and reproduction activity
DF=Degrees of freedom; Probability level: ****:p<0.001; ***: p<0.01; **: p<0.05; *: p<0.1
Derived variables:
T1=difference of temperature with the day before
T5=temperature 5 days before
Wf1=difference of water flow with the day before
Wf3=difference of the water flow of the day and 3 days before

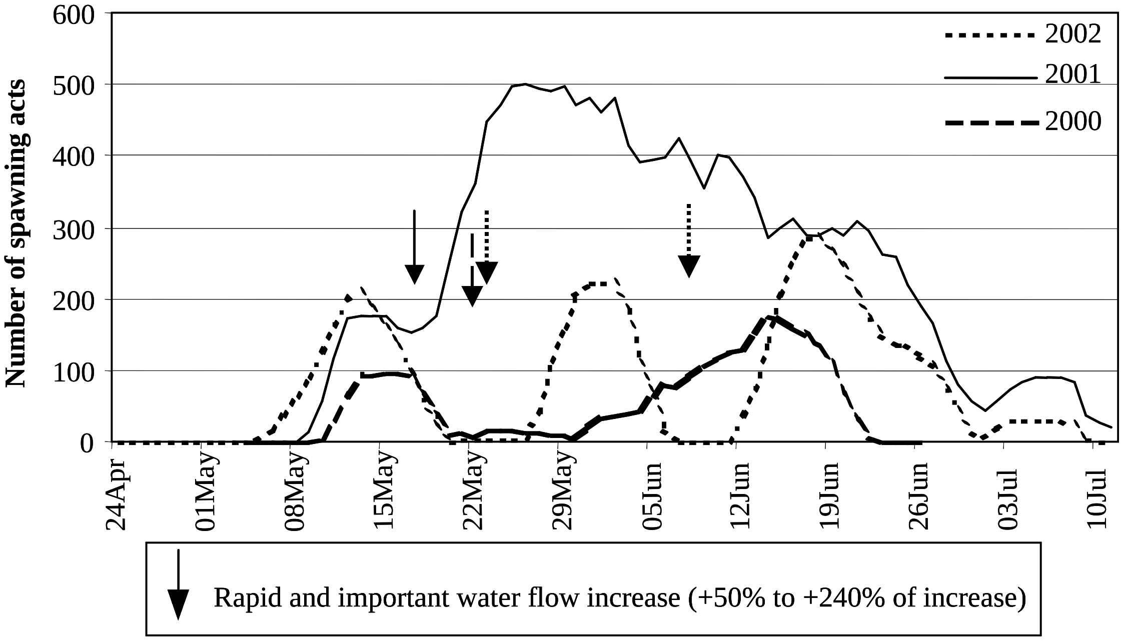
	Year	Tested variable	DF	Variance explained (%)	Probability level (test "f" of Fisher)
Migration	2001	Total	99		
		Temperature	6	45	****
		Water flow	6	39	****
		Tide coefficient	4	21	****
		T1	5	49	****
	2002	Total	73		
		Temperature	4	23	****
		Water flow	5	34	****
		Tide coefficient	4	25	****
		T5	4	54	****
		T1	5	44	****
Reproduction	2001	Total	99		
		Temperature	6	72	****
		Water flow	6	78	****
		Migration	4	60	****
		Wf1	6	81	****
	2002	Total	25		
		Temperature	3	33	**
		Water flow	5	52	***
		Migration	4	33	*
		Wf3	5	75	****

Spawning activity

Period and trends

Reproduction took place between April 24th and July 11th. The total number of spawning acts was highest in 2002 and lowest in 2000 when spawning was only partially followed (Table 1). Temporal trends in spawning activity, calculated on a 7-days, moving-mean basis, were clearly bi-modal in 2000, uni-modal to bi-modal in 2001 and tri-modal in 2002 (Figure 5). In 2001, the occasional presence of allis shad downstream of Châteaulin dam resulted in the observation of some spawning acts.

Figure 5: Trends in spawning activity of allis shad for three consecutive years (weekly moving averages of the daily number of nocturnal spawning acts counted on site) in relation to water flow.



Environmental factors

Over the study period, the temperatures observed during spawning period varied over the range 13.3-23°C (Table 2). The minimum temperature below which reproduction activity seemed to be inhibited was between 13.9 and 14°C. No maximum temperature threshold was recorded. Temperature explained 72% of the variance model in 2001 and 33% in 2002 (Table 3).

Water flows observed during the spawning period over the three years varied between 2.7 and 47.6 $m^3 s^{-1}$. In 2001 and 2002, current surface speeds ranged between 0.1 and 1.5 $m s^{-1}$ (Table 2). Generally, spawning activity ceased when water discharges were higher than 0.75-0.80 $m s^{-1}$. In 2001, the water-flow derived variable “difference of water flow with the day before” explained the highest variance of the model (81%) water flow *per se* (78%) was the next most important factor. In 2002, the water-flow derived variable “difference of water flow between the day and three days before” explained the highest variance of the model (75%) and was again followed by the water flow *per se* (52%) (Table 3).

During 2001 and 2002, the hourly distribution of spawning acts fluctuated during the spawning period but 50% of the spawning acts were observed in a short period of time (2:00 to 4:00 U.T +2) (Figure 6). Otherwise, water temperature reduced the length of the nocturnal spawning activity by progressively shifting the reproduction peak towards the end of the night (between 4:00 to 5:00 U. T. +2) (Figure 7).

Figure 6: Hourly distribution of spawning acts counted in 2001 and 2002.

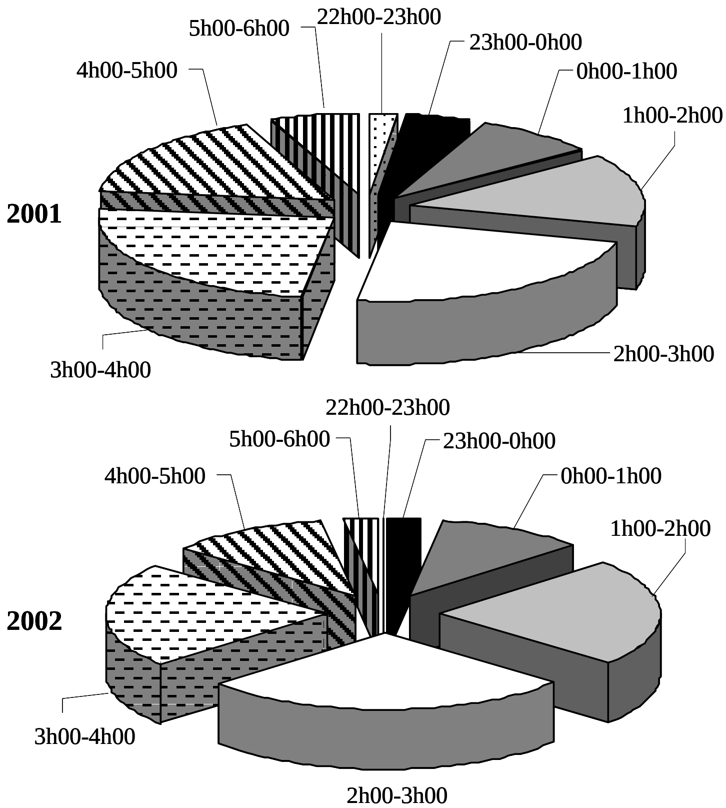
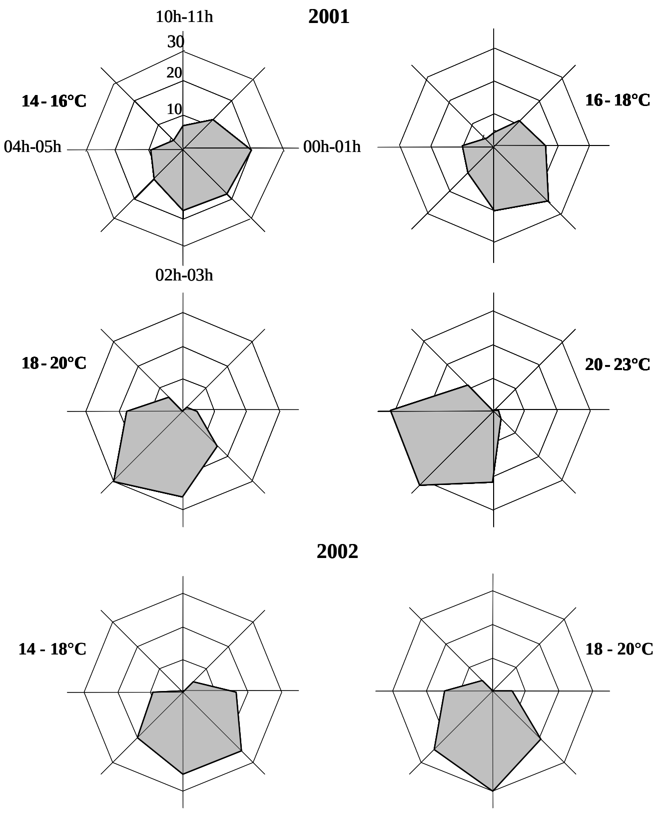


Figure 7: Distribution of spawning acts in relation to time of the day and to water temperature fluctuations (N = Number of spawning acts counted on site) for 2001 and 2002 study years.

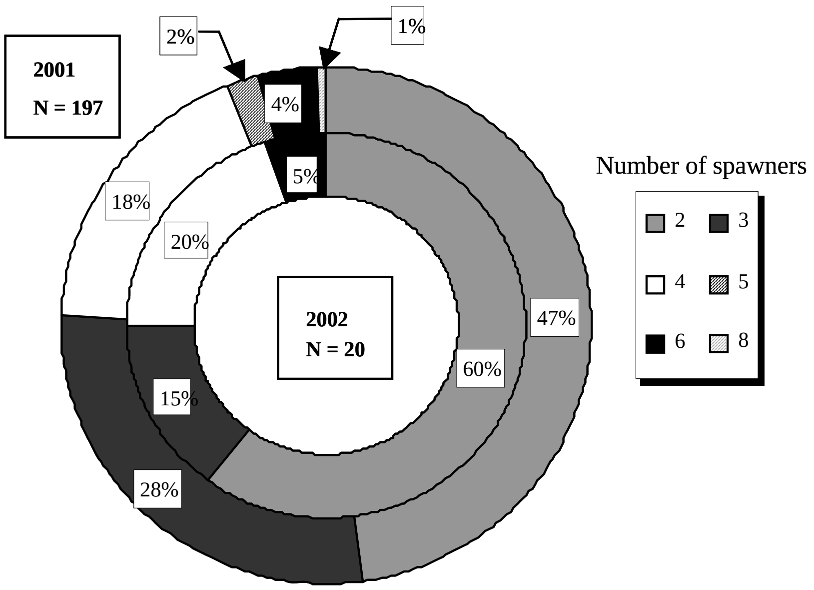


Number of spawning acts per female and of spawners by act

In 2000, the reproductive activity was documented only at its beginning (the first month, mid-April/mid-May) and the number of spawning acts per female was estimated at 2.3 assuming a sex-ratio of 1:1. In 2001, the average number of spawning acts per female was estimated at 7.7, assuming a sex ratio of 1:1, and 9.9 if we used the calculated sex ratio (1.5). In 2002, the average number of spawning acts per female estimated for the whole spawning season was 5.2 considering the calculated sex-ratio (0.9)

During the 2001 reproduction period, the number of spawners was >2 for 52.3% of the spawning acts (197 observations). In 2002, water turbidity limited the number of observations to 20 resulting in a possible overestimation of the spawning acts involving two spawners. However, the trend observed in 2002 was similar to that observed in 2001 (Figure 8).

Figure 8: Number of observed spawners participating in spawning act in 2001 (external annular) and 2002 (internal annular).



Discussion

Biological characteristics

Life history traits (first maturity age) and biological features (age range, older females having higher growth than in males, semelparous character) in the population of allis shad on the River Aulne were similar to western Atlantic populations and may be closer to those of the Loire stock (Mennesson–Boisneau *et al.*, 2000b).

Upstream migration

In the River Aulne, upstream migration of allis shad took place between early April and mid-August. The early migration was similar to that described in the Loire (end of March/mid-April) (Mennesson-Boisneau *et al.*, 2000a) and in the Garonne (Cassou-Leins and Cassou-Leins, 1981; Bellariva, 1998). The number of migrating fish recorded during the three years in the River Aulne was much lower than the number of migrants observed in larger rivers like the Dordogne and the Garonne at the dams at Tuillère (by a factor of 45) and Golfech (by a factor of 8) (Bellariva, 1998).

The observation of a bi-modal migration trend in 2001 and 2002 might be explained by lower flows during those two years compared to 2000. Moreover, in the Loire system, Mennesson-Boisneau *et al.* (1993) noticed that migration tended to be uni-modal in years of medium flow and to become bi-modal to dissymmetrical in years of low flow. A temperature decrease would also modify migration trend toward a bi-modal or tri-modal distribution (Mennesson-Boisneau *et al.*, 2000a; Rochard, 2001).

The significant influence of temperature on upstream migration with the presence of a minimum threshold (10-11°C) for migration activity was confirmed (Sabatié, 1993; Mennesson-Boisneau *et al.*, 2000a). The effects of water temperature and its variations were highlighted during 2001 and 2002. On the other hand, the influence of water discharge on migration activity was low except during spates when a decrease in migration activity was observed, as was also shown by Mennesson-Boisneau and Boisneau (1990). An extreme flow threshold for migration did not seem to exist while water flow varied between 2.7 and 86.7 m^3s^{-1}. In 2001, high flow increase (+161 and +62 %) induced negative temperature variations and caused a decrease of migration activity. In 2000, the increase in water flow (+240%) led to better hydraulic condition in that there were no changes of temperature. This helped the passage of allis shad. Temperature may supplant the influence of water flow although high flow could make dam passage easier. Migration activity appeared slightly related to tide height (coefficient) as observed by Mennesson-Boisneau *et al*. (2000b).

Reproduction

General characteristics

In the Aulne, the beginning of the shad spawning period (late April /mid-May) was close to that observed in larger rivers (Bellariva, 1998; Mennesson-Boisneau and Boisneau, 1990). Overall, spawning activity showed trends modulated by variations of water flow and temperature as in larger rivers (Mennesson-Boisneau *et al*., 2000a). There was no correspondence between peak periods of upstream migration and peak periods of spawning. This might be explained by first, a different influence of environmental factors on the two activities, second, a greater influence of biological and internal factors (maturity state) as showed by Mennesson-Boisneau and Boisneau (1990) during the end of upstream migration and, finally, a possible impact of the forced spawning zone resulting in a high concentration of spawners and an increase in individual interactions.

According to Cassou-Leins *et al.* (2000), water temperature would be an important factor that initiated and then controlled reproductive activity but the threshold values would vary according to year and river. In the River Aulne, the temperature threshold of this activity was observed at 14° C and confirmed by the telemetry study conducted in 2001 and 2002 (Acolas *et al*., 2004). Water flow influence and its variations were highlighted during the two years of complete observation.

Spawning activity

Because further upstream migration to potential spawning grounds is rapidly obstructed in the downstream course of the river, the forced spawning ground described is the only permanent spawning area in the River Aulne for the population of allis shad at present. However, a temporary spawning ground was observed downstream of the Châteaulin dam in 2001 probably in relation to low water and migration delay due to the dam as observed in other rivers (Mennesson-Boisneau *et al*., 1993).

The hourly distribution of spawning acts during all the spawning season was similar to that observed in the River Loire (Mennesson-Boisneau and Boisneau, 1990) and the River Garonne (Cassou-Leins and Cassou-Leins, 1981). However, we noticed that the timing of the spawning acts varied during the reproduction period, a phenomenon not previously documented. A reduction in duration of the reproductive activity and a shift in time of peak spawning were observed. This shift was coincident with the daily average water-temperature increase suggesting that shad were seeking a thermal optimum during the night for spawning.

In 2001 and 2002, the visual observation of the number of spawners participating in a spawning act showed that >2 individuals were involved in 45 % of the spawning acts. The proportion of spawning acts involving only two spawners (55 %) in the River Aulne was lower than that observed in the River Loire (78 %) (Boisneau *et al.*, 1990). The increase in the number of spawners participating to a spawning act might be due to the forced character of the spawning zone that induced a higher concentration of spawners. Otherwise, this observation would suggest a reconsideration of the method of estimating total spawners based on the counting of spawning acts over the whole spawning season under the assumptions proposed by Cassou-Leins *et al*. (2000). Nevertheless, in 2002, the one year when the sex ratio has been estimated over the whole migration period, the average number of spawning acts per female during the reproduction period was included in the values range recorded in larger rivers (5 to 7) (Cassou-Leins *et al*., 2000). This estimation was not in accordance with that obtained at the same time using acoustic tracking (1 to 2 spawning acts per tagged female) (Acolas *et al*., 2004). This difference could be explained by the variability of individual behaviour, the limited surveyed area and the small number of tracked fish. Moreover, the sex-ratio on the spawning zone seemed to vary according to river, year and during spawning season though this could be due to the difficulty to estimate it accurately during upstream migration of shad (Mennesson-Boisneau *et al.*, 2000b).

Overall it seems to us that the many similarities that exist between the population of allis shad in the River Aulne, a small channelled river at the northern limits of the species distribution, and larger

Atlantic rivers regarding biological and ecological characteristics suggests a large homogeneity in European populations of this species.

Acknowledgements

This study was developed in the framework of the Ph. D of Véronique Véron. It was carried out with the financial support of the Conseil Régional de Bretagne, Direction Régionale de l'Environnement de Bretagne, Agence de l'Eau de Loire-Bretagne, Ministère de l'Ecologie et du Développement Durable and Conseil Général du Département du Finistère. We wish to thank the SMATAH representatives who allowed us to trap shad at Châteaulin, the members of the APPMA of Châteaulin for links with the fishermen, the rowing club of Châteaulin and the assistance of field students: P.-Y. Brioche and R. Keller. We thank John E. Olney for helpful comments on an earlier version of this manuscript.

References

Acolas, M.L., Bégout Anras, M.L., Véron, V., Jourdan, H., Sabatié, M.R., and Baglinière, J.L. 2004. Assessment of upstream migration and reproductive behaviour of allis Shad (*Alosa alosa* (L.)) using acoustic tracking. ICES Journal of Marine Science, 61: 1291-1304.

Baglinière, J.L. 2000. Le genre Alosa. *In* Les aloses (*Alosa alosa* et *Alosa fallax spp*.) : Ecobiologie et variabilité des populations, pp. 3-30. Ed. by Baglinière, J.L., and Elie, P. Inra-Cemagref, Paris. 275pp.

Baglinière, J.L., Sabatié, M.R., Aprahamian, M.W., Alexandrino, P., Aprahamian, C.D., Assis, C.A., Cassou-Leins, J.J., Le Corre, M., Mennesson-Boisneau, C., Martin-Vandembulcke, D., Rochard, E., and Teixeira, C. 2001. Guide pour l'interprétation des écailles et l'estimation de l'âge chez les aloses (*Alosa spp*.) de la façade Atlantique–Est et de la Méditerranée-Ouest (français et anglais). Bulletin Français de Pêche et Pisciculture, 357/360: 485-531.

Baglinière, J.L., Sabatié, M.R., Rochard, E., Alexandrino, P., and Aprahamian, M.W. 2003. The allis shad (*Alosa alosa*): Biology, Ecology, Range, and Status of Populations. *In* Biodiversity, Status and Conservation of the World's Shad. Ed. by K.E. Limburg, and J.R. Waldman. American Fisheries Society Symposium, 35: 85-102.

Bellariva, G. 1998. Contribution à l'étude du déroulement de la migration et de la reproduction de la grande alose (*Alosa alosa* L.) en Garonne. Etude prospective de la dévalaison des juvéniles. Thèse de doctorat, Institut National Polythechnique de Toulouse, 114 p.

Boisneau, P., Mennesson-Boisneau, C., and Baglinière, J.L. 1990. Description d'une frayère et comportement de reproduction de la grande Alose (*Alosa alosa*, L.) dans le cours supérieur de la Loire. Bulletin Français de Pêche et Pisciculture, 316: 15-23.

Cassou-Leins, J.J., and Cassou-Leins, F. 1981. Recherche sur la biologie et l'halieutique des migrateurs de la Garonne et principalement de l'Alose : *Alosa alosa* L. Thèse de doctorat, Institut National Polytechnique de Toulouse, 393 p.

Cassou-Leins, J.J., Cassou-Leins, F., Boisneau, P., and Baglinière, J.L. 2000. La reproduction. *In* Les aloses (*Alosa alosa* et *Alosa fallax spp*.) : Ecobiologie et variabilité des populations, pp. 73-92. Ed. by Baglinière, J.L., and Elie, P. Inra-Cemagref, Paris. 275pp.

Mennesson-Boisneau, C., Aprahamian, M.W., Sabatié, M.R., and Cassou-Leins, J.J. 2000a. Remontée migratoire des adultes. *In* Les aloses (*Alosa alosa* et *Alosa fallax spp*.) : Ecobiologie et variabilité des populations, pp. 55-72. Ed. by Baglinière, J.L. and Elie P. Inra-Cemagref, Paris. 275pp.

Mennesson-Boisneau, C., Aprahamian, M.W., Sabatié, M.R., and Cassou-Leins, J.J. 2000b. Caractéristiques des adultes. *In* Les aloses (*Alosa alosa* et *Alosa fallax spp*.): Ecobiologie et variabilité des populations, pp. 33-53. Ed. by Baglinière, J.L. and Elie P. Inra-Cemagref, Paris. 275pp.

Mennesson-Boisneau, C., and Boisneau, P. 1990. Recherches sur les aloses du bassin de la Loire : Migration, Reproduction, Caractéristiques biologiques et taxonomiques des Aloses (*Alosa sp*.). Thèse de doctorat (*document de synthèse*), Université de Rennes et de Paris Val de Marne, 143p.

Mennesson-Boisneau, C., Boisneau, P., and Baglinière, J.L. 1993. Migration de reproduction des aloses dans le bassin de la Loire : Incidences des obstacles. Bulletin Scientifique et Technique, Département Hydrobiologie et Faune sauvage, INRA, 1-23.

Prouzet, P., Martinet, J.P., and Badia, J. 1994. Biological characteristics and catch variation of allis shad (*Alosa alosa*) from commercial catches in the Adour River (Pyrénées Atlantiques, France). Aquatic Living Ressources, 7: 1-10.

Rochard, E. 2001. Migration anadrome estuarienne des géniteurs de grande Alose, allure du phénomène et influence du rythme des marées. Bulletin Français de Pêche et Pisciculture, 362-363: 853-867.

Sabatié, M.R. 1993. Recherches sur la biologie et l'écologie des aloses du Maroc (*Alosa alosa*, Linné, 1758 and *Alosa fallax* Lacépède, 1803) : Exploitation et taxonomie des populations atlantiques, Bioécologie des aloses de l'oued Sébou. Thèse de doctorat, Université de Bretagne occidentale, Brest, 326 p.

Sabatié, M.R., and Baglinière, J.L. 2001. Some ecobiological traits in morrocan shads; a cultural and socio-economic value interest which has disappeared. Bulletin Français de la Pêche et de la Pisciculture, 362/363: 903-917.

Steinbach, P., Gueneau, P., Autuoro, A., and Broussard, D. 1986. Radio-pistage de Grandes Aloses adultes en Loire. Bulletin Français de Pêche et Pisciculture, 302: 106-117.

Taverny, C., Cassou-Leins, J.J., Cassou-Leins, F., and Elie, P. 2000. De l'œuf à l'adulte en mer. *In*: Les aloses (*Alosa alosa* et *Alosa fallax spp*.): Ecobiologie et variabilité des populations, pp. 93-126. Ed. by Baglinière, J.L. and Elie P. Inra-Cemagref, Paris. 275pp.

Véron, V., Sabatié, M.R., Baglinière, J.L., and Alexandrino, P. 2001. Première caractérisation morphologique, biologique et génétique des populations de grande alose (*Alosa alosa*) et d'alose feinte (*Alosa fallax spp*.) de la Charente (France). Bulletin Français de Pêche et Pisciculture, 362/363: 1037-1057.