

Seasonal variations in somatic condition, hepatic and gonad activity of sand smelt *Atherina boyeri* (Teleostei, Atherinidae) in the Mar Menor coastal lagoon (SE Iberian Peninsula)

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Abstract. Seasonal changes in somatic condition, hepatic and gonad activity, as well as their effects with age and sex were examined in *Atherina boyeri* from the Mar Menor coastal lagoon (SE Spain). Seasonal cycles of somatic condition, hepatic and gonad activity were similar in both sexes, consisting of three phases. Somatic condition increased during summer, remained constant from autumn to mid-spring and decreased from mid-spring to the beginning of summer, coinciding with reproduction. Hepatic activity remained constant from mid-summer to winter, increased sharply from winter to spring and decreased during the spawning period, which lasted 4–5 months (similar to other Mediterranean locations). These cycles suggest that the species is well adapted to local conditions, ensuring reproductive success without endangering individual survival.

Key words: condition residual index, hepatosomatic residual index, gonadosomatic residual index, life history

Introduction

The sand smelt, *Atherina boyeri* Risso, 1810, is a small, short-lived, euryhaline atherinid species that mainly inhabits coastal and estuarine waters, including coastal lagoons (Henderson & Bamber 1987). Sand smelt fisheries are amongst the most important on the Spanish Mediterranean coast and one of the main fishing resources in the Mar Menor (Pérez-Ruzafa 2003), a Mediterranean saline coastal lagoon located on the south eastern coast of Iberian Peninsula (37°38' N, 0°42' W). However, published work on the species in the Mar Menor is limited to two studies, one on life history traits (Andreu-Soler et al. 2003) and one on the species' contribution to ichthyoplankton composition (Pérez-Ruzafa et al. 2004).

Knowledge of the seasonal variations in growth and reproduction of exploited fish stocks is crucial for identifying critical periods so as to aid in the sustainable management of the populations (Reznick & Braun 1987, Jesbu et al. 1991, Karlsen et al. 1995). The aim of the present study was to determine the pattern of seasonal variation in somatic condition, hepatic and gonad activity in the populations of sand smelt in the Mar Menor.

Study Area

The Mar Menor (Fig. 1) has a maximum depth of 6 m and an area of 135 km², which makes it one of the largest lagoons of the Mediterranean basin (Pérez-Ruzafa et al. 1987). The lagoon is separated from the Mediterranean Sea by a sand bar of 100 to 1500 m width, with several narrow channels to the sea, and the bottom is covered in part by dense mixed beds of *Caulerpa prolifera* Lamouroux and *Cymodocea nodosa* (Ucria) Ascherson. Some

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temporary water courses, which drain the adjacent agricultural catchment, discharge into the lagoon, which acts as a concentration basin in which evaporation largely exceeds rainfall and run-off and the water's salinity ranges from 39 to 45 ‰ (Pérez-Ruza et al. 1987, 1989, Gilbert 2001). From a morphological and hydrodynamic point of view (*sensu* Kjerve (1994), the lagoon can be classified as 'choked lagoon, with restricted circulation and long flushing times'. Besides sand smelt, the lagoon supports important commercial fisheries, mainly European eel *Anguilla anguilla* (Linnaeus), flathead mollet *Mugil cephalus* Linnaeus, gilthead sea bream *Sparus aurata* Linnaeus and crustaceans (Pérez-Ruza et al. 2004). It is under a great pressure from human activities, which have resulted in high contaminant levels, overfishing and poor management of the water resources, which favour tourist demands over ecological integrity (Pérez-Ruza et al. 2000, 2002).

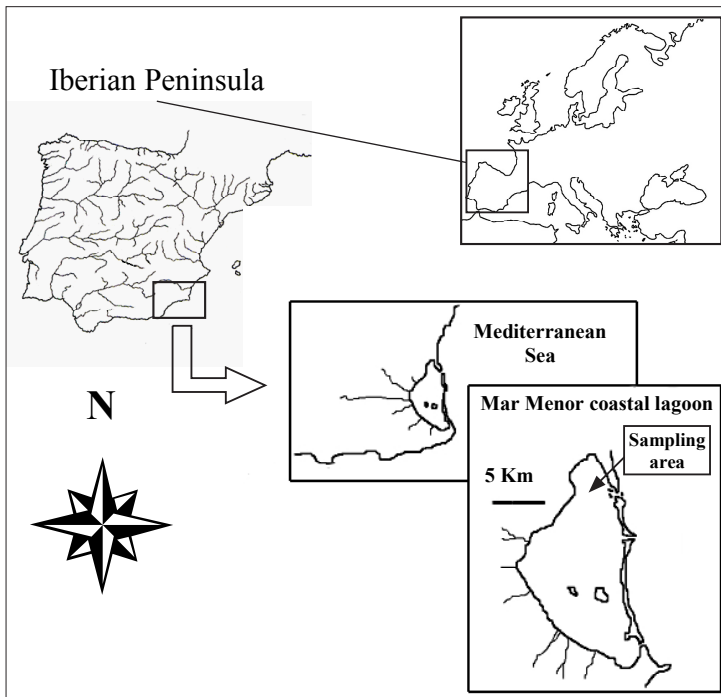


Fig. 1. Geographical location of the sampling site into the Mar Menor coastal lagoon in the Iberian Peninsula (Spain).

Material and Methods

A total of 1936 fish were collected either weekly or fortnightly by fishermen between November 1997 and September 1998 using traditional fishing gear, i.e. fyke nets (11 mm mesh size, 100 m length). The fish were preserved in buffered formaldehyde solution (7%) and transported to the laboratory, where they were measured for fork length (FL) and standard length (SL) to the nearest mm and weighed (± 0.001 g) for total body mass (TW). Following evisceration, gonad (GW), liver (LW) and carcass (EW) weight were measured, and sex was determined by visual inspection of the gonads.

Age was estimated both from scales and from modal analysis of the length frequency distributions (see details in Andreu-Soler et al. 2003). The linear relationships of

log-transformed SL and EW were analysed separately for males and females. The somatic condition index (IKr) was taken as the residuals from these regressions (Sutton et al. 2000), so that body length effects were removed. Hepatosomatic (IHr) and gonadosomatic (IGr) indices were studied using the standardized residuals from the least-squares regressions of LW and GW, respectively, on SL. Analysis of co-variance (ANCOVA), analysis of variance (ANOVA), Pearson' correlation, Kruskal-Wallis and Tukey-Kramer tests were carried out using SPSS® software package (v. 11) to determine whether values differed significantly ($P < 0.05$) between periods, sex and age classes (Sokal & Rohlf 1981).

Results

All captured sand smelt were sexually mature, with no specimens less than age 1+ observed and ranging in size from 39 to 94 mm FL (age classes 1+ to 3+). Sexual dimorphism was observed in the relationships between SL and EW of sand smelt (ANCOVA, $F = 7.99$, $df = 1$, 1934, $P = 0.005$, slope), but no differences between sampling dates were observed in either sex when season was used as a factor (ANCOVA, males: $F = 1.75$, $df = 3$, 855, $P = 0.153$, slope; females: $F = 2.03$, $df = 3$, 1078, $P = 0.106$, slope). Therefore, the SL-EW relationships for all males ($b = 3.11 \pm 0.02$, 95% CL, $r^2 = 0.97$, $F = 28442.97$, $df = 1$, 855, $P < 0.0005$) and all females ($b = 3.04 \pm 0.02$, 95% CL, $r^2 = 0.97$, $F = 32966.54$, $df = 1$, 1078, $P < 0.0005$) were used separately to obtain the standardized residuals.

Somatic condition

Somatic condition varied significantly over time (Kruskal-Wallis test, males: $H = 128.77$, $df = 32$, $P < 0.0005$; females: $H = 256.82$, $df = 32$, $P < 0.0005$), with both sexes demonstrating a similar cycle (Pearson correlation, $r = 0.714$, $P < 0.01$; Fig. 2). Three phases could be identified in the condition cycle: Phase I (high residual values) took place from autumn to mid-spring, reaching maximum values in November (males IKr = 0.90 ± 0.19 ; females IKr = 0.97 ± 0.28) and at the beginning of April (males IKr = 0.70 ± 0.40 ; females IKr = 0.90 ± 0.28); Phase II (decreased residual values) took place from mid-spring to the beginning of summer, coinciding with the species' spawning period in this lagoon, IKr decreased to reach a minimum at the end of June in females and at the beginning of July in males (males IKr = -0.70 ± 0.25 ; females IKr = -0.77 ± 0.32); Phase III (increased residual values) took place during summer, when condition gradually recovered.

A comparison of fish condition between sexes in each phase revealed significant differences. In Phase I, females had significantly higher residual values than males (males IKr = 0.23 ± 0.10 ; females IKr = 0.45 ± 0.10 ; two-way ANOVA, $F = 8.35$, $df = 1$, 542, $P = 0.004$). During Phase II, differences in condition between the sexes were not significant (two-way ANOVA, $F = 3.33$, $df = 1$, 690, $P = 0.068$). Finally, during Phase III, males showed a greater ability to recover their condition than females (males IKr = -0.01 ± 0.11 ; females IKr = -0.31 ± 0.53 ; two-way ANOVA, $F = 10.94$, $df = 1$, 855, $P = 0.001$). Within females (Table 1), only age 3+ fish presented values significantly lower than younger females (1+, 2+) during Phase I (Tukey test, $P < 0.0005$). In males no differences were observed between any age classes during the studied period. Between sexes by each age class, younger females (1+, 2+) showed a significantly higher condition than males of the same age in Phase I. During the reproductive period (Phase II), there were no significant differences in condition between the sexes. Whereas, during Phase III (increased condition), 1+ females showed lower values than 1+ males (Table 2).

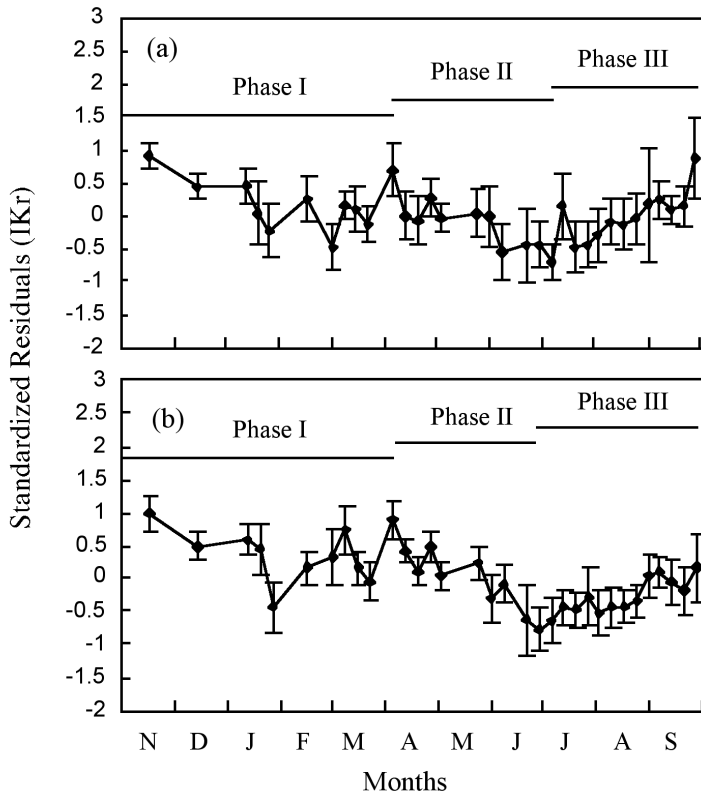


Fig. 2. Temporal pattern in somatic condition residual index for (a) males and (b) females of sand smelt *Atherina boyeri* in the Mar Menor (mean \pm 95% CL of SL-EW relationship of standardized residuals).

Hepatosomatic index

The relationships between SL and LW revealed significant differences between males and females (ANCOVA, $F = 12.57$, $df = 1$, 1935, $P < 0.0005$, slope), including between seasons (ANCOVA, males: $F = 8.12$, $df = 3$, 856; females: $F = 19.93$, $df = 3$, 1078, $P < 0.0005$, slope). These differences were marked apparent in the winter but not in spring, summer and autumn were detected (ANCOVA, males: $F = 2.15$, $df = 2$, 741, $P = 0.115$, slope; females: $F = 1.87$, $df = 2$, 944, $P = 0.152$, slope). Therefore, the SL-LW relationship was used for all males captured in spring, summer and autumn ($b = 2.97 \pm 0.06$, 95% CL, $r^2 = 0.74$, $F = 2113.45$, $df = 1$, 741, $P < 0.0005$), males captured in winter ($b = 1.96 \pm 0.21$, 95% CL, $r^2 = 0.45$, $F = 91.02$, $df = 1$, 114, $P < 0.0005$), females captured in spring, summer and autumn ($b = 3.42 \pm 0.07$, 95% CL, $r^2 = 0.70$, $F = 2253.61$, $df = 1$, 944, $P < 0.0005$) and females captured in winter ($b = 1.94 \pm 0.22$, 95% CL, $r^2 = 0.34$, $F = 80.22$, $df = 1$, 133, $P < 0.0005$) separately to obtain the standardized residuals.

Significant changes were observed in the temporal variation of residuals (Kruskal-Wallis test, males: $H = 178.88$, $df = 32$, $P < 0.0005$; females: $H = 4876.48$, $df = 32$, $P < 0.0005$) and a similar cycle was evident in both sexes (Pearson correlation, $r = 0.647$, $P < 0.0005$; Fig. 3). Three phases were identified in hepatic activity: Phase I (stable residual values) took place from mid-summer (July in males and 1 month later in females) to winter (February in males

Table 1. Residuals for age classes in each seasonal phase of IK_r, IH_r and IG_r (sexes separately) of sand smelt in the Mar Menor coastal lagoon (phase mean values, 95% CL) (ANOVA, $P < 0.05$).

Age	Males						Females						
	1+	2+	3+	F	df	P	1+	2+	3+	F	df	P	
IK _r	Phase I	0.388	0.135	0.027	2.880	2, 161	0.059	0.769	0.472	0.008	9.513	2, 182	<0.0005
	Phase II	-0.135	0.007	-0.478	1.726	2, 157	0.181	0.003	0.120	-0.109	0.642	2, 229	0.527
	Phase III	-0.150	0.007	-0.335	1.021	2, 196	0.362	-0.372	-0.221	-0.392	0.257	2, 225	0.774
IH _r	Phase I	-0.151	-0.131	-0.600	2.893	2, 375	0.057	-0.256	-0.244	-0.557	4.351	2, 396	0.014
	Phase II	0.323	0.306	-0.313	2.368	2, 54	0.103	0.704	0.870	0.202	7.985	2, 104	0.001
	Phase III	0.376	0.810	1.254	2.148	2, 80	0.123	0.411	0.897	1.087	7.143	2, 76	0.001
IG _r	Quiescence	-0.717	-1.241	-0.899	4.814	2, 149	0.009	-0.641	-1.416	-0.931	13.039	2, 172	<0.0005
	Maturation	-0.432	-0.157	-0.314	0.799	2, 114	0.452	-0.600	-0.881	-0.750	1.121	2, 124	0.329
	Spawning	0.323	0.748	0.888	11.519	2, 80	<0.0005	0.464	0.871	0.689	6.285	2, 316	0.002

and 1 month earlier in females); Phase II (increased residual values) took place from winter to spring, reaching a maximum at the end of April in females and at the beginning of June in males (males IHr = 1.14 ± 0.42 ; females IHr = 1.12 ± 0.24); Phase III (decreased residual values) took place from spring to summer, reaching a minimum at the end of July in females and 1 month earlier in males (males IHr = -1.02 ± 0.29 ; females IHr = -0.81 ± 0.28).

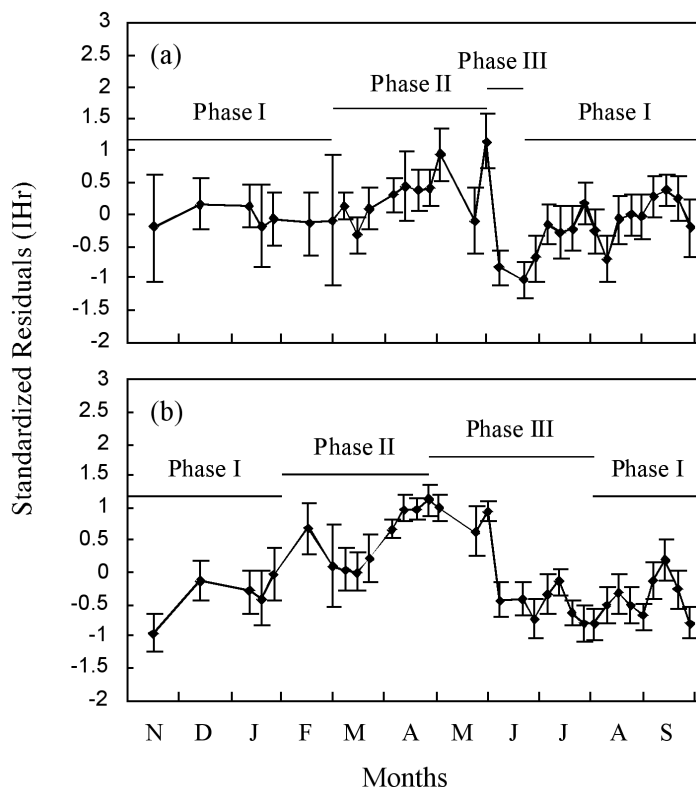


Fig. 3. Temporal pattern in hepatosomatic residual index for (a) males and (b) females of sand smelt in the Mar Menor (mean \pm 95% CL of SL-LW relationship of standardized residuals).

Differences between sexes with respect to the residual hepatosomatic index depended on the phase under consideration. In Phase I, males showed significant higher residual values than females (males IHr = 0.00 ± 0.09 , females IHr = -0.49 ± 0.07 ; two way ANOVA, $F = 32.74$, $df = 1$, 949, $P < 0.0005$). Females had significantly higher residuals than males during Phase II (males IHr = 0.22 ± 0.10 , females IHr = 0.51 ± 0.08 ; two way ANOVA, $F = 17.80$, $df = 1$, 815, $P < 0.0005$) and Phase III (males IHr = -0.45 ± 0.20 , females IHr = 0.07 ± 0.15 ; two way ANOVA, $F = 16.82$, $df = 1$, 259, $P < 0.0005$). During Phases I and II, older females (3+) presented significantly lower residual values than younger females (1+, 2+) (Tukey test, $P < 0.05$). In Phase III females 3+ showed significantly higher values than females 1+ (Tukey test, $P = 0.001$). In males, no differences were observed between any age classes (Table 1). During Phase I (Table 2), younger males (1+) presented significantly higher hepatosomatic residual values than females of the same age. In Phase II younger females (1+, 2+) showed significantly higher values than males of the same age. During Phase III (decreased), there were no differences in residual values between the sexes.

Table 2. Results of ANOVA tests between sexes in each seasonal phase of IKr, IHr and IGr (age classes separately) of sand smelt in the Mar Menor coastal lagoon, Spain.

		Age	F	df	P
IKr	Phase I	1+	5.769	1, 116	0.018
		2+	8.225	1, 149	0.005
		3+	0.075	1, 78	0.785
	Phase II	1+	1.169	1, 219	0.281
		2+	0.047	1, 81	0.829
		3+	2.146	1, 86	0.147
	Phase III	1+	4.817	1, 317	0.029
		2+	1.067	1, 46	0.307
		3+	0.030	1, 58	0.862
IHr	Phase I	1+	4.601	1, 457	0.032
		2+	0.705	1, 185	0.402
		3+	0.042	1, 112	0.838
	Phase II	1+	5.980	1, 73	0.017
		2+	6.271	1, 48	0.016
		3+	2.189	1, 37	0.147
	Phase III	1+	0.013	1, 75	0.910
		2+	1.126	1, 27	0.298
		3+	2.894	1, 43	0.096
IGr	Quiescence	1+	0.495	1, 220	0.482
		2+	0.695	1, 68	0.408
		3+	0.011	1, 33	0.919
	Maturation	1+	0.337	1, 63	0.564
		2+	7.134	1, 85	0.009
		3+	2.609	1, 60	0.111
	Spawning	1+	2.892	1, 342	0.090
		2+	0.815	1, 97	0.369
		3+	1.286	1, 101	0.259

Gonadosomatic index

The relationship between SL and GW revealed significant differences between males and females (ANCOVA, $F = 12.56$, $df = 1, 1935$, $P < 0.0005$, slope), although no time-related differences were observed in this relationship when the season was used as a factor (ANCOVA, males: $F = 1.48$, $df = 3, 856$, $P = 0.217$, slope; females: $F = 1.35$, $df = 3, 1078$, $P = 0.256$, slope). Therefore, the SL-GW relationships for all males ($b = 2.73 \pm 0.20$, 95% CL, $r^2 = 0.18$, $F = 183.59$, $df = 1, 856$, $P < 0.0005$) and all females ($b = 3.65 \pm 0.17$, 95% CL, $r^2 = 0.31$, $F = 482.55$, $df = 1, 1078$, $P < 0.0005$) were used separately to obtain the standardized residuals.

Significant changes were observed in the temporal variation of residual values for the gonadosomatic index (Kruskal-Wallis test, males: $H = 606.71$, $df = 32$, $P < 0.0005$; females: $H = 678.16$, $df = 32$, $P < 0.0005$) and both sexes showed a similar cycle (Pearson correlation, $r = 0.945$, $P < 0.0005$) (Fig. 4). Three phases were identified in gonad activity: the onset of gonad maturation (increased residual values), which took place between January and February for ovaries and in December for testes. Although the greatest increase in both sexes occurred in March, older fish began to mature earlier (December-January); the onset

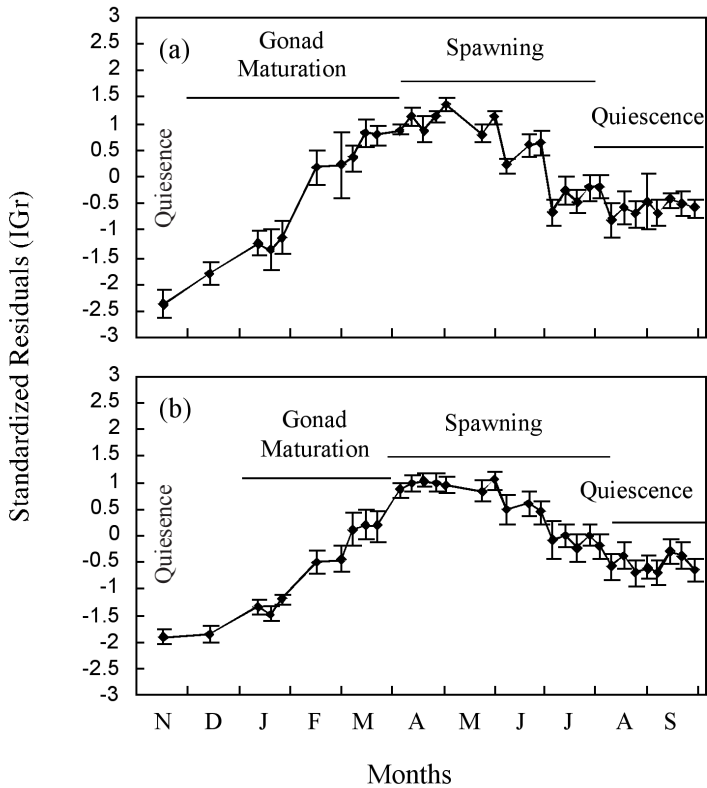


Fig. 4. Temporal pattern in gonado-somatic residual index for (a) males and (b) females of sand smelt in the Mar Menor (mean \pm 95% CL of SL-GW relationship of standardized residuals).

of spawning (high residual values) took place from the beginning of spring (March) to the mid-summer (July-August), reaching a maximum at the end of April in males and at the end of May in females (males IGr = 1.38 ± 0.12 ; females IGr = 1.06 ± 0.17); the onset of quiescence (stable residual values) took place from mid-summer to the end of autumn (August-December). Thus, females showed a quiescent period of five months (August-December) and males a period of four months (August-November), with a minimum observed in both sexes in November (males IGr = -2.39 ± 0.26 ; females IGr = -1.90 ± 0.15). Younger fish stopped reproducing before older ones; 1+ fish stopped reproducing in August and > 1+ fish from September. A comparison of residual values between sexes in each phase showed significant differences. During the gonad maturation phase, males presented significantly higher residual values than females (males IGr = -0.01 ± 0.15 , females IGr = -0.48 ± 0.12 ; two-way ANOVA, $F = 22.56$, $df = 1$, 368 , $P < 0.0005$). Nevertheless, there were no significant differences between sexes during spawning (two-way ANOVA, $F = 0.004$, $df = 1$, 689 , $P = 0.95$) and quiescence (two-way ANOVA, $F = 3.49$, $df = 1$, 841 , $P = 0.06$).

During gonad maturation, males and females showed no differences between any age classes. During spawning, 2+ females showed significantly higher values than younger females (1+) (Tukey test, $P = 0.003$), but significantly lower values during quiescence (Tukey test, $P < 0.0005$). During spawning, 1+ males presented significantly lower values than older males (2+, 3+) (Tukey test, $P < 0.005$). Finally, during quiescence, 2+ males

presented significantly lower values than younger males (1+) (Tukey test, $P = 0.006$) (Table 1). During gonad maturation, 2+ males had significantly higher values than females of the same age (Table 2).

Discussion

The age and length at first maturity of sand smelt in the Mar Menor have been reported as 1+ and 39–42 mm, respectively (Andreu-Soler et al. 2003), which correspond to fish younger and smaller than those examined in the present study. Seasonal cycles in body condition, hepatic and gonad activity are common among temperate fish species and are usually related to temporal variations in exogenous factors and to variations in endogenous factors within the species (Wotton 1998).

In the present study, the seasonal cycle of somatic condition was similar in both sexes of sand smelt, as reported in other populations (Marfin 1982, Fernández-Delgado et al. 1988, Trabelsi & Kartas 1989), with active somatic energy accumulation and maintenance from summer until mid-spring (Phases III and I, respectively), and a clear somatic energy depletion phase from mid-spring to the beginning of summer (Phase II); this coincided with the spawning period and could be related to reproductive stress (Fernández-Delgado et al. 1988).

Several authors have suggested that somatic condition in *A. boyeri* declines with longevity (e.g. Fernández-Delgado et al. 1988, Creech 1992, Leonards 2001). In the present study, the oldest females showed significantly lower condition values than younger fish during gonad maturation. The Gonad maturation period coincides with Phase I in the seasonal condition variation and with the non-growing period detected in all age classes for this population (Andreu-Soler et al. 2003). In this context, reproductive stress during pre-spawning could be responsible for the non-vegetative period (Henderson & Bamber 1987, Fernández-Delgado et al. 1988) and, probably, as a consequence responsible for the low condition in 3+ individuals. This suggests the existence of a trade-off between the energy devoted to reproduction and that devoted to maintenance or growth (Herrera & Fernández-Delgado 1994).

The seasonality of hepatic activity of *A. boyeri* was significant in both sexes, although there were differences in the duration of identified phases: a phase of stable values, which was more longer in males, a phase of substantially increased values, with a similar duration but with a month's difference between sexes, and a phase of clear decline, which lasted longer in females, coinciding with the spawning period. The trend for liver mass to decrease more in older than in younger fish between January and March was consistent with early gonad maturation in older fish. This seasonal pattern could be a consequence of a change in the quality and amount of food ingested as well as to a variation in the metabolic rate. Thus, in the studied population, liver reserves seemed to be primarily used for reproduction, while high IHR values before spawning period and significant decreases during spawning have been reported in several populations of the same species (Trabelsi & Kartas 1989, Roscchi & Crivelli 1992, Tomasini et al. 1999).

As regards between sex differences, the IHR values were higher for females during phase II, coinciding with gonad maturation and spawning, while the same values in phase III did not differ between sexes, the fall in IHR values from phase II to phase III being more pronounced in females. This might reflect greater effort and lower status in females during

and after spawning, respectively. Moreover, as regards the overall hepatic cycle, longevity affected the liver mass in a much more variable way in females. A pattern of decline in hepatic activity during quiescence and gonad maturation associated with female longevity has also been suggested by Marfin (1981), who related this pattern with a lower growth rate in the oldest individuals. Moreover, the studied populations had shown a negative correlation between longevity and growth rates (Andreu-Soler et al. 2003).

Depending on environmental factors and energy accumulation, the reproductive effort in atherinid species is more or less important during the spawning season (Tomasi ni et al. 1996). The spawning period of *A. boyeri* in the Mar Menor coastal lagoon lasts 4–5 months, as observed in other Mediterranean localities (Marfin 1981, Sostoa 1983, Rosecchi & Crivelli 1992). *A. boyeri* generally has a long spawning season, which extends earlier and longer as latitude decreases (Tomasi ni et al. 1996). Such a long spawning period appears to be a feature of the biology of *A. boyeri* (Henderson & Bamber 1987, Fernández-Delgado et al. 1988, Creech 1992, Tomasi ni et al. 1996, Tomasi ni & Laugier 2002, among others). Probably, the long breeding season in the Mar Menor was promoted by the favourable water temperature, since prolonged breeding seasons are typical of repeat spawners and fish living in variable and highly productive environments (Tomasi ni et al. 1996).

As with populations from other areas (Fernández-Delgado et al. 1988, Creech 1992, Rosecchi & Crivelli 1992, Tomasi ni et al. 1996, 1999, Tomasi ni & Laugier 2002), older fish start spawning earlier and stop later than younger ones in the Mar Menor coastal lagoon. Hence younger fishes, for which growth starts earlier (Andreu-Soler et al. 2003) and overwintering is a more critical period (Markevich 1977), must improve their condition earlier and consistently stop reproducing before older fishes.

Based on the present study, sand smelt may be included in the group of fish species that spawn at the end of spring and during summer, with a quiescent period during autumn and winter (Wootton 1998). In this group, gonad development is related to increased daylight periods, water temperature and food supply. This suggests that sand smelt in the Mar Menor coastal lagoon optimize reproductive success by improving their condition (Tomasi ni et al. 1996, 1999) prior to the end of spawning, which in younger fish is a rapidly process of storing reserves as soon as spawning ends. This is a so-called “energy-sparing strategy” (Tomasi ni et al. 1996) at the end of the breeding season.

LITERATURE

- Andreu-Soler A., Oliva-Paterna F.J., Fernández-Delgado C. & Torralva M. 2003: Age and growth of the sand smelt, *Atherina boyeri* (Risso 1810), in the Mar Menor coastal lagoon (SE Iberian Peninsula). *J. Appl. Ichthyol.* 19: 202–208.
- Creech S. 1992: A study of the population of *Atherina boyeri* Risso, 1810 in Aberthaw Lagoon, on the Bristol Channel, in south Wales. *J. Fish Biol.* 41: 277–286.
- Fernández-Delgado C., Hernando J.A., Herrera M. & Bellido M. 1988: Life-history patterns of the sand smelt *Atherina boyeri* Risso, 1810 in the Estuary of the Guadalquivir River, Spain. *Estua. Coast. Shelf Sci.* 27: 697–706.
- Gilbert J. 2001: Seasonal plankton dynamics in Mediterranean hypersaline coastal lagoon: the Mar Menor. *J. Plankton Res.* 23: 207–217.
- Henderson P.A. & Bamber R.N. 1987: On the reproductive biology of the sand smelt *Atherina boyeri* Risso (Pisces: Atherinidae) and its evolutionary potential. *Biol. J. Linnean Soc.* 32: 395–415.

- Herrera M. & Fernández-Delgado C. 1994: The age, growth and reproduction of *Chondrostoma polylepis willkommii* in a seasonal stream in the Guadalquivir River basin (southern Spain). *J. Fish Biol.* 44: 11–22.
- Karlsen Ø., Holm J.C. & Kjesbu O.S. 1995: Effects of periodic starvation on reproductive investment in first-time spawning Atlantic cod (*Gadus morhua* L.). *Aquaculture* 133: 159–170.
- Kjerfve B. 1994: Coastal Lagoon Processes. *Elsevier Oceanography Series No. 60*.
- Kjesbu O.S., Klungsøyr J., Kryvi H., Witthames P.R. & Walker M.G. 1991: Fecundity, artresia and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. *Can. J. Fish. Aquat. Sci.* 48: 2333–2343.
- Leonardos I.D. 2001: Ecology and exploitation pattern of a landlocked population of sand smelt, *Atherina boyeri* (Risso, 1810), in Trichonis Lake (western Greece). *J. Appl. Ichthyol.* 17: 262–266.
- Marfin J.P. 1981: Biologie de l'Athérine : *Atherina boyeri* Risso, 1810 (Poissons Téléostéen) dans trois milieux saumâtres du Roussillon (Leucate, Canet, Bourdigou). *PhD Thesis, University of Perpignan, Montpellier, France*.
- Marfin J.P. 1982: Alimentation et condition de l'athérine *Atherina boyeri* Risso, 1810 durant un cycle annuel. *J. Rech. Océanog.* 7: 12–40.
- Markevich N.B. 1977: Some morphophysiological indices of the silverside, *Atherina mochon pontica*, in the Aral Sea in connection with the age structure of its population. *J. Ichthyol.* 17: 618–626.
- Pérez-Ruzafa A. 2003: Los recursos pesqueros en la Región de Murcia. In: Esteve M.A., Llorens M. & Martínez C. (eds), Los recursos naturales de la Región de Murcia, un análisis interdisciplinar. *Servicio de Publicaciones de la Universidad de Murcia, Spain: 412–417 (in Spanish)*.
- Pérez-Ruzafa A., Marcos C., Pérez-Ruzafa I.M. & Ros J.D. 1987: Evolución de las características ambientales y de los poblamientos del Mar Menor. *Anales de Biología* 12: 53–65.
- Pérez-Ruzafa A., Navarro S., Barba A., Marcos C., Cámara M.A., Salas F. & Gutiérrez J.M. 2000: Presence of pesticides throughout trophic compartments of the food web in the Mar Menor Lagoon (SE Spain). *Mar. Pollu. Bull.* 40: 140–151.
- Pérez-Ruzafa A., Gilabert J., Gutiérrez J.M., Fernández A.I., Marcos C. & Sabah S. 2002: Evidence of a planktonic food web response to changes in nutrient input dynamics in the Mar Menor coastal lagoon, Spain. *Hydrobiologia* 475/476: 359–369.
- Pérez-Ruzafa A., Quispe-Becerra J.I., García-Charton J.A. & Marcos C. 2004: Composition, structure and distribution of the ichthyoplankton in a Mediterranean coastal lagoon. *J. Fish Biol.* 64: 202–218.
- Reznick D.N. & Braun B. 1987: Fat cycling in the mosquitofish (*Gambusia affinis*): fat storage as a reproductive adaptation. *Oecologia* 73: 401–413.
- Rosecchi E. & Crivelli A.J. 1992: Study of a sand smelt (*Atherina boyeri* Risso, 1810) population reproducing in fresh water. *Ecol. Freshwat. Fish* 1: 77–85.
- Sokal R.R. & Rohlf F.J. 1981: Biometry. *Freeman, W. H. & Company, New York*.
- Sostoa A. 1983: Las comunidades de peces del delta del Ebro. *PhD Thesis, University of Barcelona, Spain (in Spanish)*.
- Sutton S.G., Bult T.P. & Haedrich R.L. 2000: Relationships among fat weight, body weight, water weight and condition factors in wild salmon parr. *Trans. Amer. Fish. Soc.* 129: 527–538.
- Tomasini J.A., Collart D. & Quignard J.P. 1996: Female reproductive biology of the sand smelt in the brackish lagoons of southern France. *J. Fish Biol.* 49: 594–612.
- Tomasini J.A., Collart D. & Quignard J.P. 1999: Reserve management strategy for the sand smelt from brackish lagoons in southern France. *J. Mar. Biol. Ass. U.K.* 79: 145–151.
- Tomasini J.A. & Laugier T. 2002: Male reproductive strategy and reserve allocation in sand smelt from brackish lagoons of southern France. *J. Fish Biol.* 60: 521–531.
- Trabelsi M. & Kartas F. 1989: La reproduction de l'athérine *Atherina boyeri* Risso, 1810 en milieux marin et lagunaire. *Bulletin de l'Institut National Scientifique et Technique d'Océanographie et de Pêche de Salammbô* 16: 79–101.
- Wootton R.J. 1998: Ecology of Teleost fishes. *Kluwer Academic Publishers, The Netherlands*.