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Reserve management strategy for the sand smelt from brackish lagoons in southern France

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Visceral fat content, liver weight and carcass weight changes in female sand smelt *Atherina boyeri* from three brackish lagoons of southern France were studied throughout the year 1993. Each of these three parameters showed a peak in autumn, the visceral fat content peak occurring earlier in the season. Moreover, when ovary weight was maximal, maturing and ripe fish exhibited a second liver weight peak in April, at the beginning of the reproductive season which extended from late February to late August. Reserves were stored in flesh, liver and the abdominal cavity after the end of reproduction and were utilized from late autumn to early summer to overwinter and reproduce. At the onset of the breeding season, visceral fat content and eviscerated weight in larger fish, which started reproducing earlier and stopped later than smaller ones, were relatively higher. From April onwards, as reproductive effort was at its highest, liver and ovary weights decreased. However, eviscerated weight in smaller fish and visceral fat content in larger ones rose slightly before they ceased breeding. It is suggested that the strategy, especially in younger fish, is to avoid complete exhaustion in reproduction. This reduces the risk of subsequent overwintering mortality and increases the chance of reproduction in the future.

INTRODUCTION

Atherina boyeri Risso, 1810 is a small euryhaline fish ranging from the north-eastern Atlantic to the Mediterranean Basin, Caspian and Aral Sea (Kiener & Spillman, 1969; Quignard & Pras, 1986). The reproductive biology of the sand smelts from our study area has been examined in a previous paper (Tomasini et al., 1996). The breeding season of this resident population inhabiting brackish lagoons of southern France is protracted and extends from late February, or early March, to late August, or early September. As with populations from other areas (Fernandez-Delgado et al., 1988; Creech, 1992; Rosecchi & Crivelli, 1992), larger fish start spawning earlier and stop later than smaller ones. From February to April, the proportion of maturing and ripe females increases and proportions generally increase with fish length (Tomasini et al., 1996). In April, all the adult females, irrespective of their size, are reproducing. From June, smaller females cease reproducing and gradually disappear from the spawner stock. Batch fecundity increases with fish length and weight. Fecundity and relative fecundity are at their highest in April, May and June. Ripe oocyte size is not related to body length and steadily declines from April to June or August.

In the present study, energy storage and expenditure were investigated by examining liver weight, visceral fat content and carcass weight changes throughout the year. In animals, energy devoted to maintenance, reproduction and growth is provided by food resources. Another resource allocation is storage. Storage is an important function because it represents a way of buying a degree of independence from the environment (Reznick & Braun, 1987). Thus if material supply from the environment and demand, for instance reproduction or overwinter maintenance, do not occur at the same time, energy stored when resources are abundant can be used when they are scarce. The management of available energy is important in the life history of fish. It may affect survival and reproductive success. Various energy allocation strategies can be followed by fish. Some fish partition energy both to ensure maintenance during periods of food scarcity and successful reproduction. In other fish, egg production is sacrificed in favour of growth and/or to reduce the risk of mortality. Conversely, some fish favour the reproduction at the expense of their condition.

The aim of the present study was to determine the patterns of annual variation in energy content in female sand smelt and to establish differences between younger and older fish. Indeed, it can be hypothesized that it is not in the interest of fish of different age groups to follow the same strategy. Thus, the reproductive success of the population can be optimized. According to the age of the fish, it may be more advantageous either to devote the available energy to reproductive effort, at the expense of survival, or to do the opposite.

MATERIALS AND METHODS

Samples were collected several times a month in 1993 from local fishermen's catches. Fish were captured by nets, named 'capechades', which are composed of several hoop-nets of 5-mm mesh. Specimens were preserved for several months in 10% formalin. After establishing sex by macroscopic examination of the gonads, 2113 females of *Atherina boyeri* measuring from 30 to 108 mm total length (TL) were examined. Each female was measured to the nearest 1 mm for total length and standard length (SL)

Table 1. *Coefficients from monthly relationships* $LnW_f = a\ Ln\ W_e + b$ *for stages A and D females and results of ANCOVA.*

Stage	Month	N	a	b	s_e^2
Stage A	Jan & Dec	293	1.1773^1	-3.8045^4	0.17847
	Feb	187	1.1773^1	-4.3093	0.47990
	Mar	99	1.1773^1	-4.5112	0.51008
	Aug & Oct	371	1.3286^2	-3.3920^5	0.16326
	Sep	92	1.3286^2	-3.2242	0.05742
	Nov	242	1.1319	-3.4902	0.11243
Stage D	Apr	82	1.0188	-4.7977	0.33252
	May	83	0.7188	-4.5737	0.27980
	Jun	98	1.4670^3	-5.3015	0.58554
	Jul	64	1.4670^3	-4.9559	0.69050

F_{slope}: [1], F=1.4887, $P=0.2165$; [2], F=1.4605, $P=0.2332$; [3], F=3.0804, $P=0.0812$. $F_{intercept}$: [4], F=0.1559, $P=0.6933$; [5], F=0.0783, $P=0.7798$. W_f, visceral fat weight (g); W_e, eviscerated weight (g); N, number of value pairs; s_e^2, residual variance.

(conversion relationship: SL=0.866 TL−1.073, $r=0.999$) and weighed to the nearest 0.001 g for total body weight (W_t), ovary weight (W_o), carcass weight (W_e) after the organs were removed, liver weight (W_l) and visceral fat weight (W_f). Somatic weight (W_s) was calculated as $W_t - W_o$ and ovarian development quantified by the gonadosomatic index, $GSI = 100\ W_o W_s^{-1}$. Hepatosomatic index (HSI) and lipidosomatic index (LSI) were estimated as followed:

$$HSI = 100\, W_l\, W_e^{-1} \quad (1)$$

$$LSI = 100\, W_f W_e^{-1} \quad (2)$$

Females were separated into four categories; A, B, C and D. Stage A females showed only one group of tiny, non-maturing oocytes within their ovary. In stage B there were several oocyte groups and the largest oocytes were maturing, but they exhibited no attachment filaments over their surface. In stage C, attachment filaments tightly wrapped around the periphery of the largest oocytes were distinguishable. In stage D, the largest oocytes had outspread attachment filaments arising from their surface. These oocytes were about to be released. Stage A females were defined in this paper as non-maturing females, stages B and C as maturing females and stage D as ripe females.

Ratio indices, GSI, LSI and HSI, were not used for statistical analysis. As suggested by Jakob et al. (1996), they were only calculated for their descriptive values. Indeed, various authors have shown that ratio indices have critical flaws, especially when allometric variation prevails, which can result in improper conclusions (Packard & Boardman, 1987; Cone, 1989; Jakob et al., 1996). So, the analysis of covariance (ANCOVA) was used to study changes in visceral fat, liver, ovary and carcass weights. Monthly relationships between these parameters were obtained by the least squares method. The best relationships being power relationships, data were Ln transformed to homogenize the variance. Relationships were estimated in the months when the number of fish in our samples were not too small, namely from August to March in stage A, and from April to July in stage D. When there was no difference in intercept and/or in slope between some months, common regression or regressions with common slope were calculated. Relationships and results of ANCOVA are given in Tables 1, 2, 3 and 5.

To confirm some changes in eviscerated weight, the residual index suggested by Jakob et al. (1996) was also used. In this method, the residual for each individual is its condition.

In some comparisons fish were grouped in 1 cm length-classes (TL).

Study area

The studied *A. boyeri* population lived in three brackish lagoons along the Gulf of Lion, near Montpellier city. The Méjean and Pérols lagoons are extensively connected (546 ha; mean depth 0.55 m) and connected with Mauguio Lagoon (3166 ha; mean depth 0.8 m) by a channel. These lagoons receive water both from the sea and rivers and abiotic conditions varied in space and time from 2–32 psu salinity and 0–31°C temperature. These variable and unstable habitats are highly eutrophic, and summer dystrophic crisis commonly occur resulting in fish kills.

RESULTS

Seasonal visceral fat content change

Irrespective of reproductive stage, monthly increases of visceral fat content W_f were correlated to eviscerated weight W_e. These parameters were related by power relationships. Monthly relationships $LnW_f - LnW_e$ from August to March for stage A and from April to July for the stage D are given in Table 1.

Regression analysis showed that for stage A females the visceral fat content increased from August to a maximum in September (Table 1), then decreased until March. From August to March, monthly lipidosomatic index means in stage A females varied from 1.24±0.08% (mean±SE) in March and 5.10±0.14% in September (Figure 1A). From February, the first ripe females were found in the samples. At the beginning of the breeding season, not many fish were reproducing. Only some fish from the middle and large length-classes had ripe oocytes (Tomasini et al., 1996). Comparison in February and March between maturing (stage B) and stage A females, from the length range with both stage A and B individuals, showed that

Table 2. *Coefficients from monthly relationships* $LnW_l = a\ Ln\ W_e + b$ *for stages A and D females and results of ANCOVA.*

Stage	Month	N	a	b	s_e^2
Stage A	Jan	170	0.8776^{1}	−3.5491	0.06474
	Feb	187	1.0702	−3.7657	0.09964
	Mar	99	0.9120^{1}	−3.7808	0.07693
	Aug & Sep	234	1.1164^{2}	−3.8286^{5}	0.09109
	Oct	229	1.0006	−3.6069	0.09293
	Nov	242	0.8776^{1}	−3.3656	0.07171
	Dec	123	0.8776^{1}	−3.8204	0.07810
Stage D	Apr	82	1.1183^{3}	−3.2898	0.05772
	May	82	1.1183^{3}	−3.4897	0.04245
	Jun	98	1.2611^{4}	−3.8026	0.04246
	Jul	64	1.2611^{4}	−4.0168	0.05522

F_{slope}: ^{1}, F=2.5309, P=0.0806; ^{2}, F=0.4297, P=0.5128; ^{3}, F=0.1822, P=0.6701; ^{4}, F=0.6626, P=0.4169. $F_{intercept}$: ^{5}, F=0.0624, P=0.8030. W_l, liver weight (g); W_e, eviscerated weight (g); N, number of value pairs; s_e^2, residual variance.

Table 3. *Coefficients from monthly relationships* $LnW_e = a\ Ln\ TL + b$ *for stages A and D females and results of ANCOVA.*

Stage	Month	N	a	b	s_e^2
Stage A	Jan	170	3.0785	−12.2934	0.00502
	Feb & Mar	286	3.1773^{1}	−12.7211^{3}	0.00927
	Aug	142	3.0721	−12.2687	0.00593
	Sep	92	2.8557	−11.3546	0.00356
	Oct	229	3.0985	−12.3446	0.00553
	Nov	242	3.0156^{2}	−11.9644	0.00438
	Dec	123	3.0156^{2}	−12.0215	0.00576
Stage D	Apr	82	3.0537	−12.2260	0.00605
	May	83	2.8862	−11.5075	0.00398
	Jun	98	2.9990	−11.9528	0.00456
	Jul	64	2.8557	−11.3546	0.00496

F_{slope}: ^{1}, F=0.0262, P=0.8716; ^{2}, F=2.2655, P=0.1332. $F_{intercept}$: ^{3}, F=0.3128, P=0.5767. W_e, eviscerated weight (g); TL, total body length (mm); N, number of value pairs; s_e^2, residual variance.

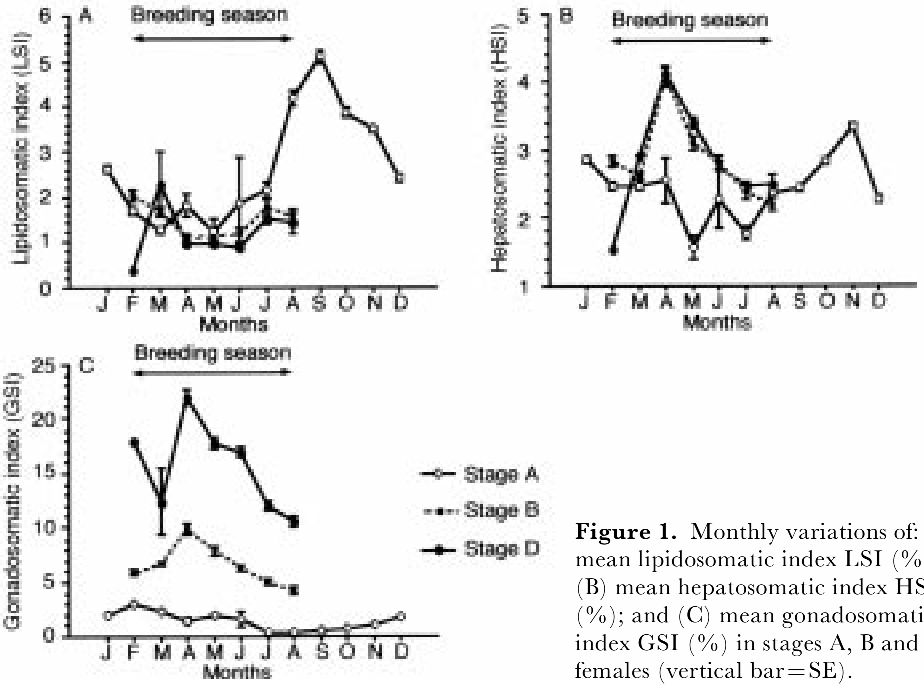

Figure 1. Monthly variations of: (A) mean lipidosomatic index LSI (%); (B) mean hepatosomatic index HSI (%); and (C) mean gonadosomatic index GSI (%) in stages A, B and D females (vertical bar=SE).

Table 4. *Mean condition indices in stage A females from September to December (estimation from* $Ln W_e$ *and* $Ln TL$ *by the method of Jakob et al., 1996).*

	September	October	November	December
Residuals	−0.0138	0.0194	0.0519	0.0103
SE	0.0069	0.0049	0.0045	0.0072

visceral fat content tended to be higher in stage B than in stage A in females larger than ~64 mm and 55 mm in February and March respectively (ANCOVA: February, $F_{1,182}=4.8571$, $P=0.0288$; March, $F_{1,108}=4.5050$, $P=0.0361$). The difference in W_f was higher in the larger fish. From April to May, visceral fat content in stage D females was low. From May onwards, abdominal fat content sharply decreased in smaller ripe females and increased in larger ones (Table 1). Lipidosomatic index LSI mean values in ripe females were 0.97% ± 0.06 in April, 0.99 ± 0.06% in May, 0.90 ± 0.06% in June, 1.53 ± 0.13% in July and 1.43 ± 0.22% in August (Figure 1A). As soon as they stopped reproducing, fish rapidly stored fat in their abdominal cavity. In July, the only month when both stage A and stage D females were numerous enough to be compared, a significant difference was found in LnW_f between these two stages in the length-classes [55] and [65], the only two with both stages A and D in this month (ANCOVA: $F_{1,47}=5.0316$, $P=0.0001$). Fish which just ceased breeding (adjusted LnW_f mean $= -3.22 \pm 0.10$; LSI = 2.95 ± 0.25%) displayed more perivisceral fat content than ones which still reproduced (adjusted LnW_f mean $= -4.63 \pm 0.15$; LSI = 1.69 ± 0.34%).

Seasonal liver weight change

Like the visceral fat content, the liver weight was positively correlated with carcass weight (Table 2).

In females which stopped breeding, liver weight increased to a maximum in November. This increase was most marked for smaller fish (Table 2). A dot-plot of W_l vs W_e or W_l vs TL showed that W_l values in large females were very scattered from low to very high values, and obviously some large fish stored relatively little reserves in the liver during these months. Moreover, in our samples, fish >81 mm disappeared from the stock in December. From November to December, W_l sharply declined. During the interspawning season, HSI mean values ranged from 3.34 ± 0.06% (November) to 2.26 ± 0.06% (December) (Figure 1B). In ripe females, liver weight reached a maximum value in April, and next it declined throughout the breeding season (Figure 1B). The decrease was higher in smaller fish than in larger ones between May and June (Table 2). From April to August, HSI mean values varied from 4.12 ± 0.11% (April) to 2.45 ± 0.07% (July). In July, comparison between stages A and D in pooled length-classes [55] and [65] did not reveal any differences in LnW_l ($F_{1,47}=0.0086$, $P=0.9264$). At that time, HSI mean values were 2.18 ± 0.13% and 1.89 ± 0.15% in stages D and A respectively.

Seasonal eviscerated weight change

Concerning W_e changes, LnW_e–$LnTL$ relationships seemed similar, but tests revealed significant differences (Table 3). Some features were worth noting, though monthly changes in eviscerated weight were weak. After breeding stopped, stage A females showed an upward trend in W_e to November, then it decreased in December and remained low throughout the winter. This trend with maximal W_e value occurring in November, then decreasing in December, was confirmed by using the method suggested by Jakob et al. (1996) (ANOVA: $F_{7,1276}=32.2837$, $P=0.0001$) (Table 4). At the very start of the breeding season, W_e tended to be slightly lower in the stage A than in the stage B fish in February ($F_{1,183}=7.4084$, $P=0.0071$; stage A: adjusted LnW_e mean $=0.704 \pm 0.076$, stage B: adjusted LnW_e mean $=0.737 \pm 0.076$). During the breeding season, W_e seemed to increase, especially between April and May in small ripe fish, this increase occurring between May and June in larger ones (Table 3). Comparison in July between stages A and D in length-classes [55] and [65] showed no significant differences ($F_{1,47}=0.5827$, $P=0.4491$).

Seasonal ovary weight change

Relationships LnW_o–LnW_e were given in Table 5.

Ovary weight continually increased from the end of the breeding season to the beginning of the next one (Figure 1C). From August to March, monthly GSI mean values in stage A females ranged from 0.39 ± 0.02% (August) to 2.94 ± 0.10% (February). In stage B fish,

Table 5. *Coefficients from monthly relationships* $LnW_o = a\ LnW_e + b$ *for stages A and D females and results of ANCOVA.*

Stage	Month	N	a	b	s_e^2
Stage A	Jan	170	1.6166^1	−4.1345	0.21565
	Feb	187	1.6166^1	−3.7296	0.22429
	Mar	99	1.6166^1	−3.5923	0.24187
	Aug & Sep	234	1.2847^2	-5.5579^4	0.12318
	Oct	229	1.0955	−5.0056	0.17785
	Nov	242	1.1899	−4.6379	0.07630
	Dec	123	1.0744	−3.9814	0.05296
Stage D	Apr	82	1.2005^3	−1.5719	0.10416
	May & Jun	181	1.2005^3	-1.8145^5	0.08527
	Jul	64	1.2005^3	−2.2769	0.08289

Fslope: ^{1}, $F=2.0911$, $P=0.1247$; ^{2}, $F=1.0694$, $P=0.3022$; ^{3}, $F=1.3646$, $P=0.2536$. Fintercept: ^{4}, $F=3.2049$, $P=0.0747$, ^{5}, $F=1.0609$, $P=0.3044$. W_o, ovary weight (g); W_e, eviscerated weight (g); N, number of value pairs; s_e^2, residual variance.

which appeared in February, its values were 5.87 ± 0.24% and 6.68 ± 0.20% in February and March respectively. Ovary weight rose sharply in ripe females in April, then it declined to the end of the spawning season. Values of the GSI in these females were 21.95 ± 0.73% in April, 12.02 ± 0.42% in July and 10.59 ± 0.58% in August when only a few large individuals were still reproducing.

DISCUSSION

During the annual cycle of *Atherina boyeri* from the Mauguio, Méjean and Pérols lagoons, three main periods could be roughly distinguishable: (i) a protracted reproduction period with energy expenditure through spring and summer; (ii) an energy storage period in late summer and autumn; and (iii) a depletion of stored material in autumn and especially in winter.

In ripe females, hepatosomatic index was at its highest in April, at the same time as gonadosomatic index (Figure 1B,C). High HSI values when GSI was at a maximum have been observed by various authors in sand smelts (Markevich, 1977; Trabelsi & Kartas, 1989; Rosecchi & Crivelli 1992) and in other fish species (Htun-Han, 1978; Clearwater & Pankhurst, 1994; Sayer et al., 1995). However, in many fish, the HSI peak occurs before the spawning season (Tyler & Dunn, 1976; Joyeux et al., 1992; Fouda et al., 1993; Milton et al., 1994). In the population studied here, some fish >63 mm were ripe as early as February (Tomasini et al., 1996) and there were no maturing fish <51 mm before April. The early-maturing fish were probably those for which condition was the best. Consequently, these fish were not too depleted to mature their oocytes by investing the remaining reserves in reproduction. However, available reserves were still low in these individuals and their fecundities were low at this period (Tomasini et al., 1996). Their low energy content and feeding levels prevented small fish from investing in reproduction in February and March. They reproduced later as food supply increased. In southern France, Marfin (1982a) pointed out that sand smelt from the Bourdigou Estuary fed heavily in spring and autumn but little in winter and summer. Henderson et al. (1988) have noticed in *A. boyeri* from the UK that older individuals built up more reserve than younger ones in summer and autumn. At the end of the winter, reserves of the latter were almost completely exhausted while fat content of the former was still high. Thus, larger fish from this population could allocate this energy to reproduction and their gonads started to mature at the beginning of March. From April to the end of the breeding season (late August), liver reserves were assigned, largely at least, to the gonad and liver weight steadily decreased in ripe females (Figure 1B, Table 2). Declining liver reserves were often observed during the spawning period in *A. boyeri* (Kohler, 1976; Trabelsi & Kartas, 1989, Rosecchi & Crivelli, 1992) and many other fish species (Htun-Han, 1978; Chellappa et al., 1989; Joyeux et al., 1992; Lenhardt, 1992; Fouda et al., 1993; Ruchon et al., 1993). As liver weight declined, ovary weight did likewise (Figure 1C, Table 5). Clearly there was not enough material to maintain high reproductive effort throughout the breeding season, because either food intake was not high enough or material was partly utilized for functions other than reproduction. As a result, fecundity, relative fecundity and ripe oocyte diameter decreased from May (Tomasini et al., 1996). Between May and June visceral fat content sharply declined in smaller ripe females and their liver weight exhibited a higher decrease than in larger ones (Tables 1 & 2). So, all the adult females, irrespective of their size, were reproducing only from April to June. From July, fish <56 mm disappeared from the spawning stock, the minimum size of the maturing and ripe females increased and only fish >60 mm still reproduced in August, the proportions of reproducing females increasing with length. Small fish directed their available energy towards growth. According to Marfin (1982b), younger sand smelts from southern France renewed their growth in spring, earlier than older ones in which it was postponed to autumn. Before they ceased breeding, smaller fish began improving W_c while larger fish showed a W_f increase. As soon as fish stopped reproducing, they stored reserves in their liver, flesh and abdominal cavity. Visceral fat in particular sharply increased (peak in September) whereas liver and carcass weight did not increase so steeply (peaks in November). From the September peak to December, W_f dropped all the more sharply as fish were larger, very likely because of the growth renewal in large fish. Through winter, as mean water temperature decreased and available food was scarce, stored reserves were used in maintenance and declined. This commonly occurred in many fish (Guillemot et al., 1985; Reznick & Braun, 1987; Wallace, 1991; Griffiths & Kirkwood, 1995). Various authors have noted this winter decrease in *A. boyeri* (Marfin, 1982a; Henderson & Bamber, 1987; Henderson et al., 1988). Energy was also partly allocated to ovary growth. Indeed, from September onwards GSI rose (Figure 1C). This ovarian development was consistent with the pattern of species spawning in late winter and spring (Wootton, 1979).

The strategy followed by *A. boyeri* in our study area was both to optimize reproductive success and to avoid endangering too many of the reproducers, especially younger ones, and progeny survival. During the breeding season, the strategy was to avoid reproduction which could result in the complete exhaustion of fish. Before they stopped breeding, spawners began improving their condition instead of tiring themselves by spending a lot of energy maintaining high batch fecundity and there was no trade-off between egg number and egg size, both of which declined (Tomasini et al., 1996). Tyler & Dunn (1976) have shown that the reproductive choice of *Pseudopleuronectes americanus* in poor food condition, was to sacrifice egg production and maintain body weight for future reproduction. Depletion due to high reproductive expenditure may result in postspawning mortality (Chellappa et al., 1989; Jonsson et al., 1991; Sandström et al., 1995). In our sand smelt population, the most intensive reproductive effort occurred from April to June. At this time, all the adult females reproduced and exhibited high fecundity values, which consequently resulted in many broods with many eggs. Their spawning of numerous young early in the season is a good strategy to maximize reproductive success. Indeed, the fitness of young born earlier is greater than young born later (Reznick & Braun, 1987). Larvae hatched from the first clutches encountered better environmental conditions, especially temperature and feeding conditions. They could grow and store reserve for a longer time before overwintering. Younger spawners by ceasing reproduction earlier than older spawners did likewise. To store reserves and grow as much as possible is advantageous for younger individuals because overwintering is a more critical period for smaller fish than larger ones. The risk of mortality during the approaching winter may be reduced by growth in size and the accumulation of reserves. In various fish species, a decrease in winter fat content below a critical level causes fish death (Newsome & Leduc, 1975; Griffiths & Kirkwood, 1995). In the Aral Sea, sand smelt <4 cm die in winter because they do not store enough fat to successfully overwinter (Markevich, 1977). Henderson & Bamber (1987) have shown that the younger *A. boyeri* had a greater possibility of starvation in winter than older ones. These fish had to achieve a minimum size to hold sufficient fat reserves to survive the winter, and fish born too late were unlikely to reach this size (Henderson et al., 1988). Moreover, fecundity being positively related to body size (Tomasini et al., 1996), growth to a large size by the next reproductive season allows production of more eggs. Furthermore, because of instability and variability in our lagoons, catastrophic events endangering population survival could occur at any time. It is advantageous to allocate energy to growth and condition improvement, and quickly become robust enough to survive adverse conditions. Older fish stopped reproducing later than younger ones, because the former probably did not gain by ceasing as early as the latter. As fish grow older, reduced growth makes growth cost smaller. Moreover, as fish get older, life expectancy decreases and potential for future reproduction declines. So, it is prudent for the oldest females to protract the breeding season longer and to invest more in spawning than younger spawners.

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