

## Sex ratio and sexual dimorphism of the anchovy *Anchoa januaria* (Actinopterygii, Engraulidae) in a tropical bay in south-eastern Brazil

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Sex ratio and morphological traits of a very abundant anchovy *Anchoa januaria* were described in a tropical bay in south-eastern Brazil. The aim was to test the hypothesis that sexual dimorphism occurs due to the different reproductive roles of the sexes. A fish sampling programme was carried out between September 1998 and August 1999 at six sites: four sandy beaches and two lower-river sites. Population structure at river sites comprised adults only, ranging from 60 to 80 mm total length ( $L_T$ ), while at sandy beaches both juveniles and adults were found, ranging from 32 to 80 mm  $L_T$ . Well-balanced 'spawning school' at river sites during reproduction were detected, while female-dominated schools occurred in the bay feeding areas. Males had relatively longer pectoral fins, slightly larger hearts and more somatic mass than females. Females outnumbered males at sizes  $>67$  mm  $L_T$  and had significantly longer intestines and heavier livers than males. The largest size reached by females was probably related to a higher growth rate as they have a larger intestinal absorbing area for nutrients. The prediction of higher energetic investment in reproduction by females that should have larger organs associated with food acquisition and processing to produce energy-rich eggs was confirmed for *A. januaria* in Sepetiba Bay.

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Key words: anchovies; Brazil; reproduction; sexual selection; size structure.

### INTRODUCTION

Sexual dimorphism, especially sexual size dimorphism (SSD), and variation in the size of body organs are widespread among animals. Different male and female body sizes can produce differences in reproductive, foraging or predator evasion behaviour between the sexes (Hilton *et al.*, 2000). Therefore, sexual dimorphism may play an important role in enhancing reproductive success in fishes. Traits that increase reproductive success, such as body size may compromise survival, leading to opposing pressures of natural and sexual selection

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(Shine, 1989; Blanckenhorn, 2005). Rapid growth requires aggressive foraging, which may increase susceptibility to predators (Holtby & Healey, 1990). Thus, sex-specific selection appears to produce life-history strategies peculiar to each sex.

Differences in the reproductive roles of the sexes can be associated with differences in internal and external organs (Casselmann & Schulte-Hostedde, 2004), and selective pressures experienced by the sexes can result in the evolution of sexual dimorphism of morphological traits (Andersson, 1994). Hence, the magnitude and direction of sexual dimorphism of characters can be predicted by examining the reproductive roles of the sexes within a species. According to Randall *et al.* (2000), female reproductive roles predict that females should have larger organs associated with food acquisition and processing to support the production of energy-rich eggs. The intestine and liver are critical for the absorption of nutrients and the processing of fats, respectively. Differences in intestine size can result in growth differences between sexes, since the larger the intestine the larger is the absorption area for nutrients possibly influencing growth rate. Males from some species tend to show morphological characters associated with male–male competition and mating acquisition, while females tend to have greater energy reserves for the production of eggs (Kokita & Mizota, 2002).

The anchovy *Anchoa januaria* (Steindachner) is a small pelagic fish widely distributed in embayment areas of the south-east Brazilian coast. At present, there is little information on the reproductive ecology of this species and it is believed that it occurs in less saline water of the bays, migrating to lower rivers reaches to spawn (Esper, 1982; Silva & Araújo, 2000), usually being found in salinities between 7.9 and 31.3 (Cervigón, 1969). Funamoto & Aoki (2002) found that the spawning frequency of onshore migrant populations of Japanese anchovy *Engraulis japonicus* Temminck & Schlegel was higher than that of inshore populations and that the spawning frequency of onshore populations varied in response to sex ratio. *Engraulis ringens* Jenyns females with hydrated ovaries that were ready to spawn seemed to attract males and to form male-dominated ‘spawning schools’ by segregating from ‘normal schools’ (Alheit *et al.*, 1984).

Some species of engraulids change sex ratio according to life cycle. Vouglitois *et al.* (1987) found that *Anchoa mitchilli* (Valenciennes) showed more females (1.93:1) than males in Barnegat Bay, while in Chesapeake Bay the sex ratio was 1.16:1. Newberger & Houde (1995) reported that sex ratios for this species are not well understood. Unbalanced sex ratios (female or male favoured) have been found in other engraulids, although there is no clear explanation for this phenomenon (Lapolla, 2001). The regional fluctuation of sex ratio in engraulids may relate to their physiological state: either the spawning period on one side and the inactivity period of the sexual cycle on the other (Sinovic, 2000).

Understanding factors that influence reproduction such as sexual dimorphism and sex ratio are important issues in fish ecology. The present work describes aspects of sexual dimorphism and the sex ratio of *A. januaria* in Sepetiba Bay. The following questions were asked: (1) Is there sexual segregation during part of the life cycle? (2) If so, is such segregation caused by reproductive behaviour? (3) Is there any morphological sexual dimorphism associated with this process?

## MATERIALS AND METHODS

Sepetiba Bay is a sedimentary embayment (22°54'–23°04' S; 43°34'–44°10' W) caused by extensive sand deposition, which forms a barrier beach along its southern boundary. The bay has a surface area of *c.* 450 km<sup>2</sup>, a mean depth of 8.6 m, a maximum depth of 30 m and a drainage area of 2700 km<sup>2</sup>. The tidal range is *c.* 1 m. Annual rainfall varies between 1000 and 2100 mm (Barbieri & Kronemberger, 1994), but does not cause great changes in the salinity of the bay because the rivers and channels that drain into the inner part of the bay are small (Fig. 1).

Fish were collected between September 1998 and August 1999, using beach seines (10 m × 2 m, with 7 mm mesh). Four sandy beaches: Pedra de Guaratiba (B1), Sepetiba (B2), Coroa Grande (B3) and Muriqui (B4) and two lower-river sites: São Francisco channel (R1) and Guarda river (R2) were sampled. All fish anaesthetized in benzocaine hydrochloride (25–100 mg l<sup>-1</sup>) and fixed in 10% formalin and preserved in 70% alcohol. For each fish, measurements (±0.05 mm) were taken of total length ( $L_T$ ) and left pectoral fin. Total body mass ( $M$ ) and somatic mass (±0.01 g) were measured; somatic mass was measured as the eviscerated carcass mass. Liver and heart were carefully dissected out and weighed (±0.001 g), while the length of the intestine was measured (±0.05 mm). ANCOVA was used to compare the sexes for a given trait, after controlling for body size. The  $L_T$  was used as the covariate (body size) in the analyses. Bonferroni correction was applied to the analyses. A  $\chi^2$ -test was performed to test for sex ratio differences by sites and by 10 size classes ranging from 32 to 82 mm  $L_T$ .

Gonads of 269 individuals were removed and weighed ( $M_G$ ), separating the right from the left, and sex was determined. The gonado-somatic index ( $I_G$ ) was determined according to the following:  $I_G = 100M_G(M - M_G)^{-1}$ . Ovaries of 198 individuals (91 in beaches and 107 in rivers) were classified according to a macroscopic scale of gonadal development, taking into account how much they filled the abdominal cavity and the size of oocytes. According to these characteristics, the following classification was used: immature, mature, ripe and spent (Vazzoler, 1996).

The degree of stomach fullness was estimated visually, considering four categories: empty, <50% full, half-full (50–75%) and full (>75%). The repletion index ( $I_R$ ) was determined according to the following:  $I_R = 100M_{sc}M^{-1}$ , where  $M_{sc}$  is the stomach content mass.

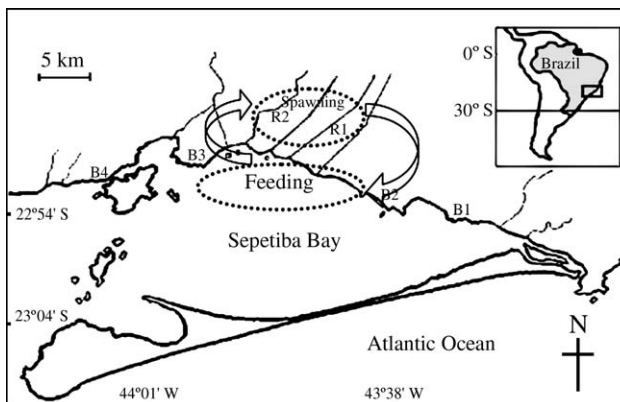


FIG. 1. Study area: Sepetiba Bay, Rio de Janeiro, Brazil, with sampling sites shown: sandy beaches = B1, B2, B3 and B4; river sites = R1 and R2.

In order to describe sexual dimorphism, 30 males and 30 females, ranging from 60 to 77  $L_T$ , were selected. A narrow size class of both males and females was used to avoid allometric influences that could mislead interpretation of sexual dimorphism.

## RESULTS

### SIZE STRUCTURE AND SEX RATIO

A total of 713 anchovies were examined (389 females, 293 males and 31 unidentified). Size ranged from 32.1 to 80.2 mm  $L_T$  for females and from 32.1 to 76.9 mm  $L_T$  for males.

Differences in size structure of the populations between the two types of habitat (beaches v. river sites) were found. Individuals sizes from river sites ranged from 60 to 80.2 mm at R1 and from 60.1 to 69.0 mm  $L_T$  at R2 and comprised only adults (Table I). At the beach sites, sizes ranged from 32.1 to 80.1 mm  $L_T$ , consisting of both juveniles and adults (Table I); the lowest size variability was recorded at B3 (45.2–61.29  $L_T$ ) where most fish were juveniles, while the largest size variability occurred at B2 (32.1–79.0 mm  $L_T$ ) where both juveniles and adults occurred (Table I).

Sex ratio differed significantly ( $P < 0.05$ ) between the two types of habitats (Fig. 2), with a predominance of females at the beach sites B2 (1.79 females: 1 male,  $\chi^2$ ,  $P < 0.05$ ), B3 (4.13:1,  $\chi^2$ ,  $P < 0.05$ ) and B4 (1.78:1,  $\chi^2$ ,  $P < 0.05$ ). The only exception was B1 where a non-significant male-biased sex ratio was found (1:1.07,  $\chi^2$ ,  $P > 0.05$ ). Considering all the beaches pooled (Table II), males outnumbered females in September (1:2.36), and the reverse of this situation occurred in October (3.88:1), December (1.74:1), March (2.78:1), June (2.33:1) and August (2.33:1), with differences being significant ( $P < 0.05$ ).

At the river sites, fish were recorded in June and July only (Table II), and no significant differences in sex ratio were found ( $P > 0.05$ ). In July, when all fish were collected at R2, the sex ratio was well balanced (1.05:1).

Significant differences ( $P < 0.05$ ) in sex ratios were found for individuals at sizes  $>67$  mm  $L_T$  (Table III), with higher number of females than males. The overall sex ratio for *A. januaria* in Sepetiba Bay (all sites pooled) was significantly female-biased (1.35:1).

TABLE I. Total length ( $L_T$ ) measurements of *Anchoa januaria* by sites at beach and river sites (see Fig. 1) in Sepetiba Bay, 1998–1999

Sites	$L_T$ (mm)		
	$n$	Mean $\pm$ S.E.	Range
Beach 1	139	61.58 $\pm$ 0.70	32.30–71.70
Beach 2	156	63.26 $\pm$ 0.80	32.10–79.00
Beach 3	41	54.90 $\pm$ 0.56	45.20–61.29
Beach 4	111	62.76 $\pm$ 1.17	36.00–80.10
River 1	108	66.24 $\pm$ 0.47	60.00–80.20
River 2	127	63.20 $\pm$ 0.26	60.01–69.00

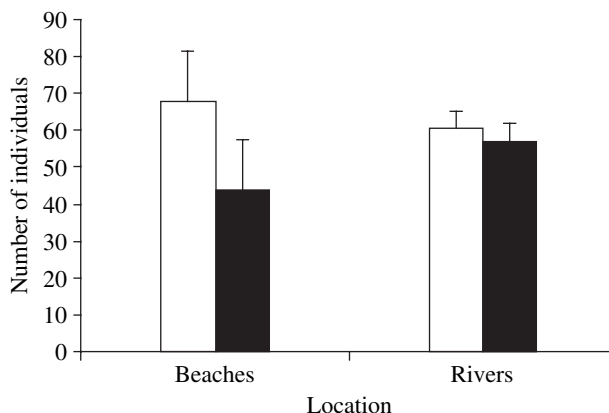


FIG. 2. Mean + s.e. number of individuals for *Anchoa januaria* in Sepetiba Bay, 1998–1999: females (□) and males (■).

### STAGES OF SEXUAL MATURATION AND GONADO-SOMATIC INDEX

Four gonadal stages were determined: immature, mature, ripe and spent (Fig. 3). Ripe females predominated in rivers (73.83%) and were scarce at beaches (4.4%) where most fish were immature, mature or spent.

The  $I_G$  showed seasonal variations for both males and females, peaking in winter and with decreased values in summer (Fig. 4). Significant differences were found for both male and female  $I_G$  between rivers and beaches ( $F_{1,265}$ ,  $P < 0.001$ ) with higher values in the rivers, between sexes ( $F_{1,265}$ ,  $P < 0.001$ ) and with higher values for females, and between seasons ( $F_{3,265}$ ,  $P < 0.001$ ).

TABLE II. Numbers ( $n$ ) of females and males and  $\chi^2$ -tests for *Anchoa januaria* sex ratio comparisons by month at beach and river sites (see Fig. 1) in Sepetiba Bay, 1998–1999

Months	Beaches					Rivers				
	Females $n$	Males $n$	Total $n$	Expected frequency	$\chi^2$	Females $n$	Males $n$	Total $n$	Expected frequency	$\chi^2$
September 1998	25	59	84	42.0	6.88*	—	—	—	—	—
October	31	8	39	19.5	13.56*	—	—	—	—	—
November	37	23	60	30.0	1.63	—	—	—	—	—
December	54	31	85	42.5	6.22*	—	—	—	—	—
January 1999	13	9	22	11.0	0.73	—	—	—	—	—
February	2	1	3	1.5	1.33	—	—	—	—	—
March	25	9	34	17.0	7.52*	—	—	—	—	—
April	—	—	—	—	—	—	—	—	—	—
May	21	19	40	20.0	0.05	—	—	—	—	—
June	32	8	40	20.0	14.4*	56	52	108	54.0	0.15
July	—	—	—	—	—	65	62	127	63.5	0.07
August	28	12	40	20.0	6.40*	—	—	—	—	—
Total	268	179	447	223.5	17.72*	121	114	235	117.5	0.21

\* $P < 0.05$ .

TABLE III. Number of females and males ( $n$ ) and  $\chi^2$ -tests for *Anchoa januaria* sex ratio comparisons by total length classes ( $L_T$ ) in Sepetiba Bay, 1998–1999

$L_T$ classes (mm)	Females $n$	Males $n$	Sex ratio	Total $n$	Expected frequency	$\chi^2$
Juveniles						
32–37	4	4	1.00:1	8	4.0	0.00
37–42	15	13	1.15:1	28	14.0	0.14
42–47	12	10	1.20:1	22	11.0	0.18
47–52	8	7	1.31:1	15	7.5	0.07
52–57	23	16	1.44:1	39	19.5	1.26
Adults						
57–62	63	71	1:1.13	134	67.0	0.48
62–67	114	101	1.1:1	215	107.5	0.56
67–72	101	62	1.63:1	163	81.5	9.33*
72–77	30	5	6.00:1	35	17.5	17.86*
77–82	19	4	4.75:1	23	11.5	9.78*
Total	389	293	1.33:1	682	341	12.96*

\* $P < 0.05$ .

This trend suggests that spawning takes place in the river because  $I_G$  declines from spring, when fish are captured only at beach sites.

#### REPLETION INDEX AND STOMACHS FULLNESS

Fish with empty or less than half-full stomachs predominated in the rivers (11.9% and 54.76%, respectively). On the other hand, most fish at beach sites were half-full (45.1%) or full (35.3%) (Fig. 5). The mean  $I_R$  differed significantly ( $t$ -test,  $n = 87$ ,  $P < 0.05$ ) between the two type of habitats, showing higher values for beaches (Fig. 6)

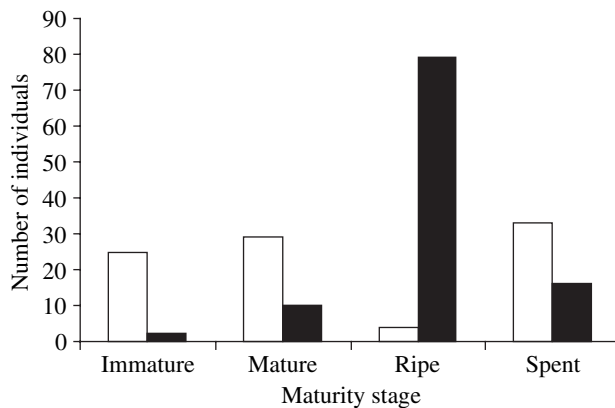


FIG. 3. Gonad maturation stages for *Anchoa januaria* in Sepetiba Bay, 1998–1999: beaches (□) and rivers (■).

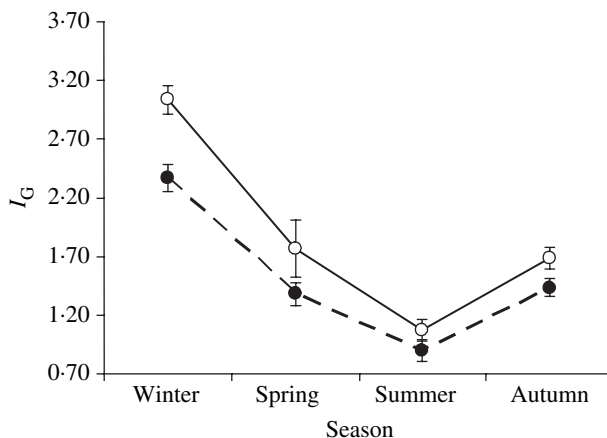


FIG. 4. Mean  $\pm$  s.e. gonado-somatic index ( $I_G$ ) for *Anchoa januaria* in Sepetiba Bay, 1998–1999: females (○) and males (●).

### SEXUAL DIMORPHISM

The mean external and internal morphological measurements for males and females are shown in Table IV. Males and females did not differ with respect to  $L_T$  and  $M$  ( $t$ -tests, both d.f. = 58,  $P > 0.05$ ). Males had more somatic mass (total mass minus internal organs and visceral fat mass) than females, after controlling for  $L_T$  (Table IV). When corrected for body size, males had longer pectoral fin lengths than females. Females had longer intestines and a greater mass of liver than males. Females had heavier livers than males for both winter and summer periods (Table IV). ANCOVA showed that, after controlling for  $L_T$ , males had a greater mass of heart than females, although this difference was rendered non-significant after Bonferroni correction (Table IV).

Slopes for male *v.* female external morphology and internal traits were homogeneous for all measurements ( $P > 0.05$ ) (Fig. 7).

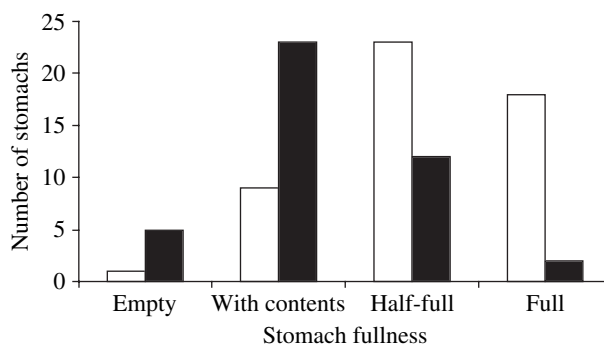


FIG. 5. Stomach fullness for *Anchoa januaria* in Sepetiba Bay, 1998–1999: beaches (□) and rivers (■).

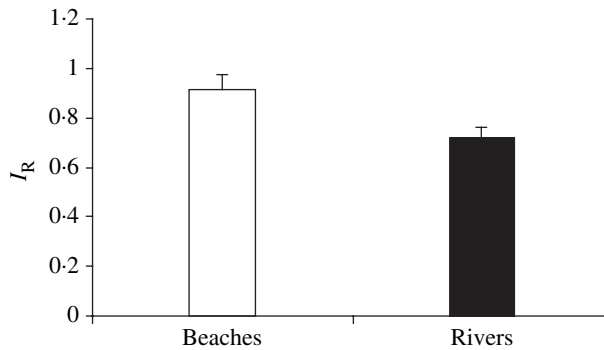


FIG. 6. Mean + s.e. repletion index ( $I_R$ ) for *Anchoa januaria* in Sepetiba Bay, 1998–1999.

## DISCUSSION

A well-marked sexual dimorphism of the internal and external morphology of *A. januaria* in Sepetiba Bay was shown in the present study. Females reach larger sizes and had larger intestines and heavier livers than males. On the other hand, males had longer pectoral fins and a heavier somatic mass than females. Although Kokita & Mizota (2002) suggest that sex differences may occur in external traits such as fin size of fishes because males with large fins tend to be more successful at mate acquisition and male–male competition due to increased speed and manoeuvrability, this is unlikely to be the case in *A. januaria* because they form large schools where male–male competition is hardly feasible. Differences in pectoral fin size may be associated with stability and control of swimming (Videler, 1993). Such differences may help *A. januaria* males position themselves optimally relative to females during spawning in order to maximize the fertilization success.

According to Casselman & Schulte-Hostedde (2004), differences in the reproductive roles occupied by the sexes should influence patterns of selection and

TABLE IV. Raw mean  $\pm$  s.e. and least squares mean (in parentheses) of external and internal morphological traits for male ( $n = 30$ ) and female ( $n = 30$ ) *Anchoa januaria*, and results of ANCOVA on sex differences in relative size (using total length,  $L_T$ , as a continuous predictor)

	Males	Females	$F_{1,57}$	$P$
$L_T$ (mm)	70.30 $\pm$ 0.73	70.40 $\pm$ 0.71	—	—
Pectoral fin length (mm)	9.50 $\pm$ 0.04 (9.51)	9.20 $\pm$ 0.04 (9.23)	26.10	0.000*
Intestine length (mm)	20.40 $\pm$ 0.09 (20.45)	22.10 $\pm$ 0.09 (22.08)	163.8	0.000*
Total mass (g)	2.40 $\pm$ 0.07 (2.35)	2.30 $\pm$ 0.07	2.5	0.12
Somatic mass (g)	1.90 $\pm$ 0.06 (1.89)	1.80 $\pm$ 0.05 (1.79)	11.3	0.001*
Liver mass (g) winter	0.0157 $\pm$ 0.0005 (0.0154)	0.0217 $\pm$ 0.0005 (0.0209)	74.71	0.000*
Liver mass (g) summer	0.0166 $\pm$ 0.0005 (0.0160)	0.0203 $\pm$ 0.0004 (0.0195)	32.178	0.000*
Heart mass (g)	0.0095 $\pm$ 0.0003 (0.0095)	0.0089 $\pm$ 0.00023 (0.0089)	4.04	0.043

Differences between the sexes for traits marked with\* remained significant after Bonferroni correction ( $\alpha = 0.05/07 = 0.0071$ ).



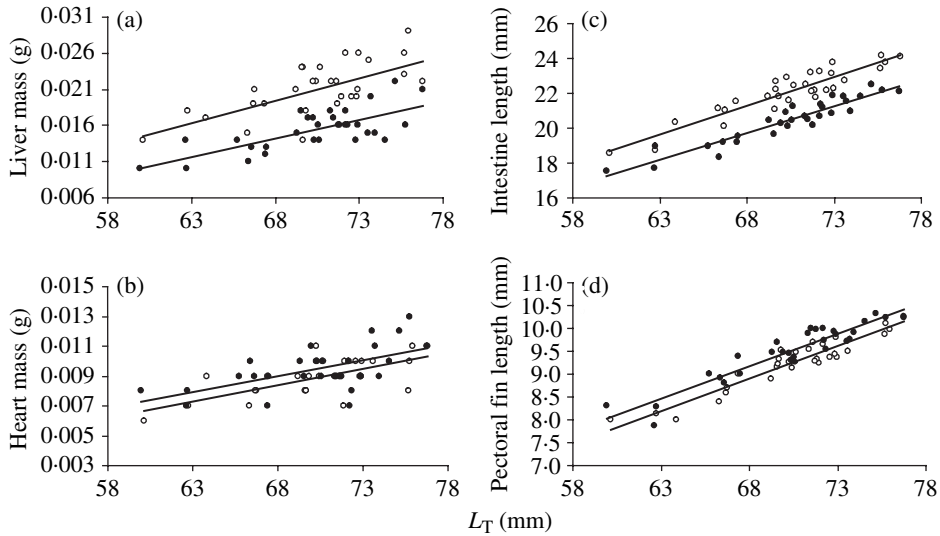


FIG. 7. Sexual dimorphism (○, females and ●, males) of (a) liver mass, (b) heart mass and (c) intestine length (internal traits) and (d) pectoral fin length (external trait) in relation to total length ( $L_T$ ) in *Anchoa januaria*. The curves were fitted by: (a) female  $y = 0.0006x - 0.0227$  ( $r^2 = 0.4202$ ,  $n = 30$ ) and male  $y = 0.0005x - 0.0211$  ( $r^2 = 0.529$ ,  $n = 30$ ), (b) female  $y = 0.0002x - 0.0055$  ( $r^2 = 0.3431$ ,  $n = 30$ ) and male  $y = 0.0002x - 0.0066$  ( $r^2 = 0.4615$ ,  $n = 30$ ), (c) female  $y = 0.331x - 1.2154$  ( $r^2 = 0.8538$ ,  $n = 30$ ) and male  $y = 0.3064x - 1.1218$  ( $r^2 = 0.8886$ ,  $n = 30$ ) and (d) female  $y = 0.1422x - 0.7711$  ( $r^2 = 0.9016$ ,  $n = 30$ ) and male  $y = 0.1424x - 0.5114$  ( $r^2 = 0.8753$ ,  $n = 30$ ).

thus should ultimately lead to sexual differences in morphology. They found sexual dimorphism for the lake whitefish *Coregonus clupeaformis* (Mitchill) in Lake Ontario, with females having heavier livers than males, whereas males have longer jaws and pectoral and pelvic fins, larger hearts and more muscle than females. One of the most interesting results from this study was the sexual dimorphism in the relative size of internal organs, such as the larger intestine and liver in females compared with males. These findings are in accordance with several small mammal species (Norrie & Millar, 1990), indicating some generality in this pattern. The intestine is critical for the absorption of nutrients and thus females should have larger intestines than males (Randall *et al.*, 2000). Therefore, selection should favour an enlarged intestine in females for the production of large numbers of eggs.

The larger intestine size in females with a larger area to absorb nutrients may also contribute to an increase in their growth rate and attainment of larger sizes compared with males. The significant female-bias sex ratio for *A. januaria* at sizes  $>67$  mm  $L_T$  could be due to a higher growth rate associated with the larger intestine. The opposite trend is apparent in males, which reach maturity at a younger age and smaller size. The male strategy consists of earlier sexual differentiation and earlier maturity over a small size and age range. Sexual size dimorphism (SSD) occurs in many species, and several studies have suggested or demonstrated that SSD is attributable to sex-specific selection on body size (Quinn & Foote, 1994; Tamate & Maekawa, 2004). Breeding selection favouring a larger body size for females than for males in *A. januaria* probably requires

that females undertake more intensive foraging behaviour with its greater inherent risks, but faster growth rates. It seems likely that selection is the ultimate cause of the female-biased size dimorphism. For breeding success of females in salmonids, larger body sizes are advantageous, mainly because of the increased fecundity of larger females (Van Den Berghe & Gross, 1989; Fleming & Gross, 1994). Thus, sex-specific selection appears to produce life-history strategies peculiar to each sex and *A. januaria* is an example of such a pattern.

According to Perrin (1992), variation in size of body organs is thought to be adaptive because allocation of resources to growth and maintenance of specific body organs entails trade-offs with other aspects of organism survival and reproduction. The evolutionary advantage of sexual dimorphism of organs in *A. januaria* seems to be a strategy to maximize lifetime reproductive success, not instantaneous reproductive success at any single spawning season. A major problem is the general difficulty of separating causes generating a particular body size and SSD over evolutionary time and their consequences for behaviour and ecology. Studies on this subject are still sparse and more research is required.

According to Randall *et al.* (2000), the variable size and structure of the gut are dynamic, since they change with energy demand and the amount of available food in most animals. There is little evidence that male and female *A. januaria* differ qualitatively with respect to diet (Sergipense *et al.*, 1999) and so differences in reproductive roles have probably led to the present results. According to Nikolsky (1963), larger numbers of females occur in sites with plenty of food. *Anchoa januaria* feeds mainly on zooplankton (Sergipense & Sazima, 1995) and use Sepetiba Bay beaches as feeding areas (Silva *et al.*, 2004), where there is plenty of organic matter brought by tributaries, favouring zooplankton production. Therefore, a female-biased sex ratio in the beaches could be attributed to food availability and high reproductive investment.

Spatial changes in the *A. januaria* sex ratio in Sepetiba Bay seem to be related to population behaviour with movements between feeding areas (beaches), where there is a female-biased population, and reproduction areas (rivers) where the population shows a balanced sex ratio (1:1). Fish with a low amount of food (empty and <half-full) predominated at river sites, while those showing half-full and full stomachs were common at beach sites. Furthermore, repletion indices were significantly higher at the beach sites confirming the use of the beaches in the bay as feeding areas. Most ripe females and the highest  $I_G$  values were recorded in specimens captured in river sites only during the winter, the probable spawning season for this species. In the remaining seasons, this species occurred only at beach sites where only 4.4% of all females were ripe. These findings did not agree with those from southern Brazil, where spawning is reported to occur in spring (Esper, 1990). Esper (1982) found this species performing regular seasonal movements into rivers to spawn, using the bay areas during sexual inactivity and reaching first maturity at 65 mm  $L_T$ . All fish recorded in river reaches (R1 and R2) were adults ( $L_T > 60$  mm), probably in the process of spawning.

According to Aka *et al.* (2004), the regional fluctuation of sex ratio for populations of *Engraulis encrasicolus* (L.) in Turkish seas is related to their physiological state, in the spawning period on the one hand and in the inactivity period of the sexual cycle on the other. They found that males were predominant

in the spawning period, whereas females dominated in the inactivity period of the reproductive cycle. Overall, there is no agreement on which sex dominates at a given physiological state, but some relationship between physiological state and sex ratio seems to exist. According to Alheit *et al.* (1984), physiological stages play an important role in spawning with *E. ringens* females containing hydrated oocytes apparently attracting males, which form segregated male-dominated schools during which most fishery activities occur. An unbalanced sex ratio during the reproductive period does not imply that the maximum reproduction yield is not reached, since it depends on the number of individuals involved in each reproduction period (Edwards, 1998). The well-balanced sex ratio for *A. januaria* at the river sites suggests that this could represent the maximum reproductive yield for this population in Sepetiba Bay.

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