Reproduction of the cutlassfish *Trichiurus lepturus* in the southern Brazil subtropical convergence ecosystem*

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SUMMARY: The reproduction of the cutlassfish *Trichiurus lepturus* was studied from samples collected in bottom trawl surveys on the continental shelf and shelf break off southern Brazil. The mean total length (L_T) at first gonadal maturity was 63.9 cm for males and 69.3 cm for females. Batch fecundity ranged from 3,917 in a specimen of 70 cm L_T to 154,216 in a specimen of 141 cm but the number of spawning batches in each season was not established. Spawning occurs in late spring and summer in the continental shelf and probably year round over the shelf break. High surface temperatures and moderate stratification of the water column were associated with the final stages of gonadal maturation. Seasonal and spatial differences in sex ratios, sizes, maturity stages and feeding intensities suggest that adult female *T. lepturus* remain during the cold season in the continental shelf of southern Brazil to feed, while adult males move to warmer waters northward or offshore.

Key words: Batch Fecundity, gonadal maturity, sex ratios, spawning, *Trichiurus*

INTRODUCTION

The continental shelf and slope of southern Brazil comprises the western boundary of the Subtropical Convergence and is characterized by the interactions between the oligotrophic Brazil Current, the nutrient-rich waters of the Malvinas Current, and the continental runoff of the La Plata River and the Patos Lagoon. The region is an important nursery and feeding area as well as a reproduction ground for fish stocks of subtropical and subantarctic origin, which utilize the Brazil and Malvinas Currents for long distance transport (Garcia, 1997; Castello *et al*., 1997).

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Due to the transitional character of the region, the neritic fish fauna includes a relatively large number of species (see Seeliger *et al.,* 1997 for a list) but only few of them are endemic. Furthermore, because of the high seasonal environmental variability, a small number of species is responsible for most of the biomass. The demersal bony fish fauna is dominated by the sciaenids *Micropogonias furnieri* (Desmarest, 1823), *Umbrina canosai* Berg, 1985, *Cynoscion guatucupa* (Cuvier, 1830), and *Macrodon ancylodon* (Bloch and Schneider, 1801) and by the cutlassfish, *Trichiurus lepturus* (Linnaeus, 1758) (Haimovici *et al*. 1994; Haimovici *et al.,* 1996). Cutlassfish were abundant in both mid water and bottom trawl surveys (Mello *et al.,* 1992).

Cutlassfish is a cosmopolitan fish in warm and warm-temperate shelf waters in different parts of the world (Nakamura and Parin, 1993). In the western Atlantic it occurs from Cape Cod, Massachusetts (40° N) to the La Plata River (37° S) (Fischer, 1978). In southern Brazil it is abundant despite being near the southern boundary of its distribution. Its abundance in the region was associated with its adaptations for feeding on a wide range of sizes of pelagic and benthic prey (Martins, 1992). Larvae were found on the shelf and slope generally associated with surface water temperatures over 21°C (Mafalda, 1989). Juveniles occur in coastal waters and subadults and adults from coastal waters to the shelf break (usually in relatively warm waters), while larger concentrations were frequently associated with thermal fronts (Martins and Haimovici, 1997).

Teleost fishes with pelagic eggs synchronize spawning with favorable physical conditions such as transport, horizontal advection, stability of the water column and coastal upwellings that increase the chances of released larvae to access food concentrations and avoid dispersion, consequently increasing survival rate (Bakun and Parrish 1980). Off southeastern Brazil, Nakatani *et al*. (1980) found larger concentrations of eggs and larvae of *T. lepturus* near coastal islands where the deviation of marine currents may enhance production due to local upwellings (Mann and Lazier, 1991). In southern Brazil productivity processes are of a larger scale associated with the presence during winter and early spring from cold waters of the runoff of the La Plata River and waters of subantarctic origin (Odebrecht and Garcia, 1997). The cutlassfish is absent from the cold waters, but is abundant and was found actively feeding in the frontal zone between subantarctic and warm waters of coastal or tropical origin (Martins and Haimovici, 1997; Martins, 1992). This suggests that the reproduction of the cutlassfish in southern Brazil may be associated with local productivity processes. Local upwelling events occur near the coast in summer and on the shelf break in winter (Garcia, 1997), and the cutlassfish reproduces at those sites during the corresponding time of the year. The analysis of environmental factors associated with the spawning and non-spawning regions and seasons may provide useful information on the requirements for successful reproduction of pelagic spawning fishes (Parrish *et al.,* 1983). In this paper the first maturity, batch fecundity, spawning cycle and the distribution patterns of reproductive and non-reproductive *T. lepturus* were studied in relation to the environment. Our objective was to obtain a better understanding of the reproductive strategy of the cutlassfish in the southern Brazil subtropical convergence ecosystem.

MATERIAL AND METHODS

Samples were obtained during 13 bottom trawl cruises of the R/V “Atlântico Sul” (Fig. 1). The first nine (1980 to 1983), were between Solidão (30°43’S) and Chuí (33°45’S) at the isobaths of 10 to 160 m. The last four (1986 and 1987) were from the outer shelf and upper slope between Chuí (34°30’S) and Cape Santa Marta Grande (28°40’S), at depths ranging from 124 to 587 m. *T. lepturus* occurred from the coast to the shelf break (Fig. 1). The standard duration of all hauls was 60 minutes, at 3.0 knots. All hauls were performed between dawn and dusk. After each haul, bottom and surface temperatures were recorded with inversion thermometers and profiles of temperatures were recorded with a bathythermograph. Shelf cruises were grouped in: 1) “warm water” autumn cruises with temperatures higher than 20ºC in most stations, in April 1981 and 1983; 2) “cold water” winter cruises, with bottom temperature lower than 15ºC in most stations, in August 1981 and September 1983; and 3) “inter-seasonal” spring and summer cruises in January of 1982 and November 1983 when bottom temperatures were between 15°C and 20ºC. Further details on gears, sampling, catch composition and environment are given in Haimovici *et al*. (1994, 1996) and Martins and Haimovici (1997). Samples of *T. lepturus* of the available sizes from different latitudes and depth ranges in the sampled areas were collected for reproduction studies. A total of 3,234 specimens were measured (L_T: total length in cm, between the anterior lower jaw projection and end of the caudal fin), and sexed. A total of 1,080 specimens were weighed (TW) in grams of which 916 had their testes or ovaries weighed (TG) to the nearest tenth of a gram. Maturity stages were determined macroscopically following Haimovici and Cousin (1989) as: I, virginal; II, initial development or recovering; III, in development; IV, mature; V, spawning; VI, partly spent; and VII, recovering. Ovaries in different maturity stages were fixed and preserved in buffered formalin solution at 10%. Stages III to VI were considered indicative of reproductive

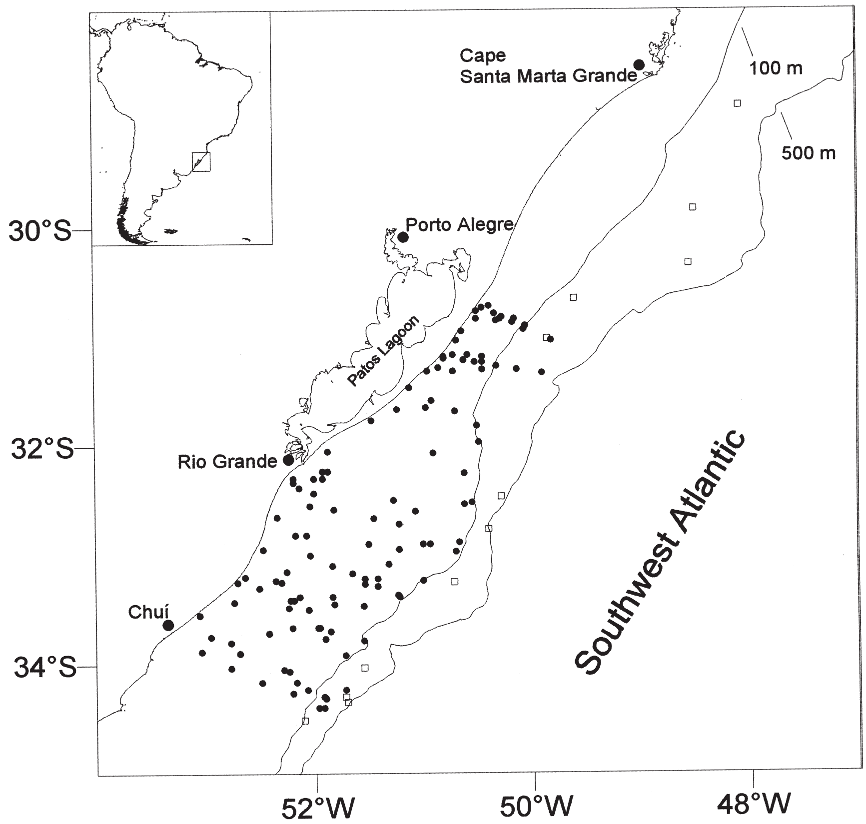

FIG. 1. – Study area, full circles (1980-83) and empty squares (1986-87) represent the bottom trawl hauls in which *Trichiurus lepturus* were collected for reproduction studies in the continental shelf and shelf break along southern Brazil.

process and the word "mature" is used in this paper to refer to individuals presenting one of these maturation stages.

The "gonadosomatic index" [$I_G = T_G x100/(T_W - T_G)$], was calculated for each specimen. To compare reproductive and feeding activities, the logarithmic rate between stomach content weight (T_E) and fish weight (T_W) was used as an index of feeding intensity ($I_{FI} = \ln (T_E/T_W - T_E) + 1$) (Hyslop, 1980).

Batch fecundity (*F*) was defined as the number of vitellogenic oocytes in maturation in the ovaries of cutlassfishes sampled at the beginning of the reproductive season. Fecundity was calculated by the gravimetric method as described by Bagenal (1978). Oocytes were counted in three samples of ca 200 μg, taken from the anterior, central and posterior part of the ovaries of each specimen.

The Student "t" test was used for means comparisons of I_G and IFI and the chi-square test was performed for sex ratio contrasts, both at 5% of probability level. Confidence intervals of means (CI, 95%) were used to describe the data dispersion. ANOVA (p<0.05) was used to test batch fecundity differences between gonadal maturity stages.

RESULTS

Gonadal maturity determination

The oocyte diameter distribution in each macroscopic maturity stage and time of the year in which they occurred in the continental shelf are shown in Figure 2. Stages II and VII show a single mode of small translucid oocytes of 0.1 mm in mean. In stages III, IV and VI two distinct modes of opaque yellow oocytes can be observed, one around 0.5 to 0.7 mm and other at around 0.8 to 1.3 mm. Stage V is characterized by a third mode of large hydrated oocytes with oil drop and diameter of around 1.8 mm. The mean I_G in different macroscopic maturity stages of males and females is shown in Figure 3a. Mean I_G of both male and female cutlassfish in advanced maturation and spawning were over 1.5 and almost all females with I_G larger than 2 were in spawning condition. The percentage of advanced maturity stages (IV and V) increased from 15-20% for I_G < 1, to 75-80% for I_G between 1 and 2 and to over 90% at I_G >2 (Fig. 3*b*). Based on these relationships, mean I_G

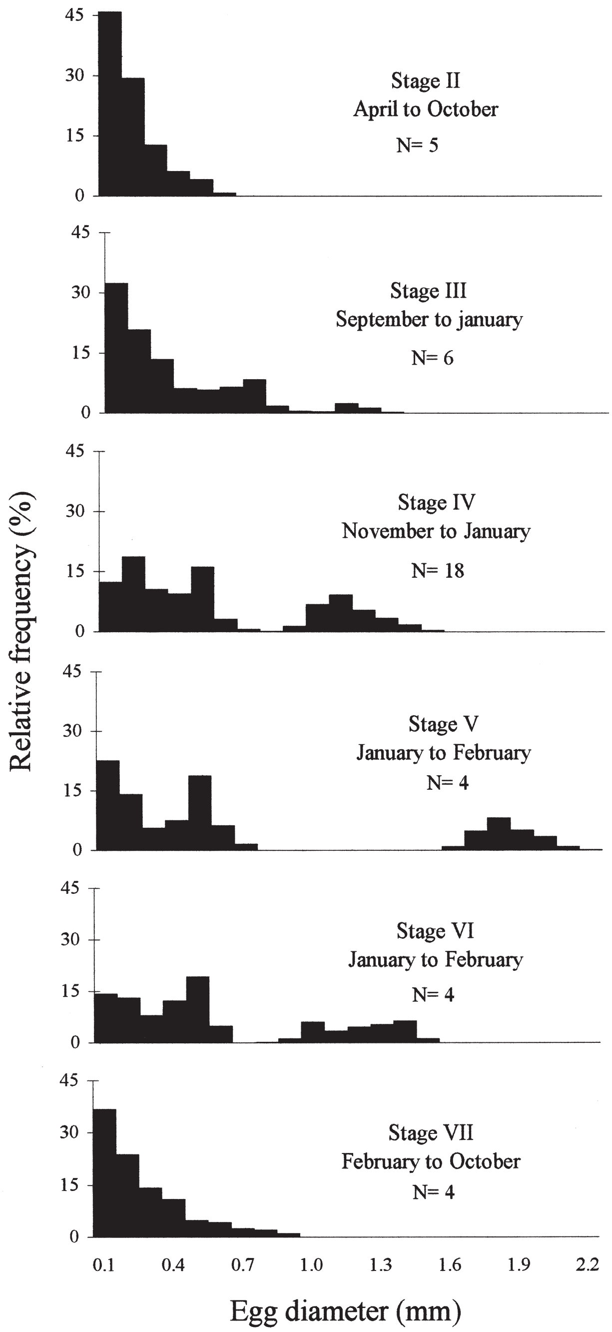

FIG. 2. – Relative frequencies of oocyte diameters in ovaries at different gonadal stages of *Trichiurus lepturus* sampled in southern Brazil. N= number of gonad samples measured.

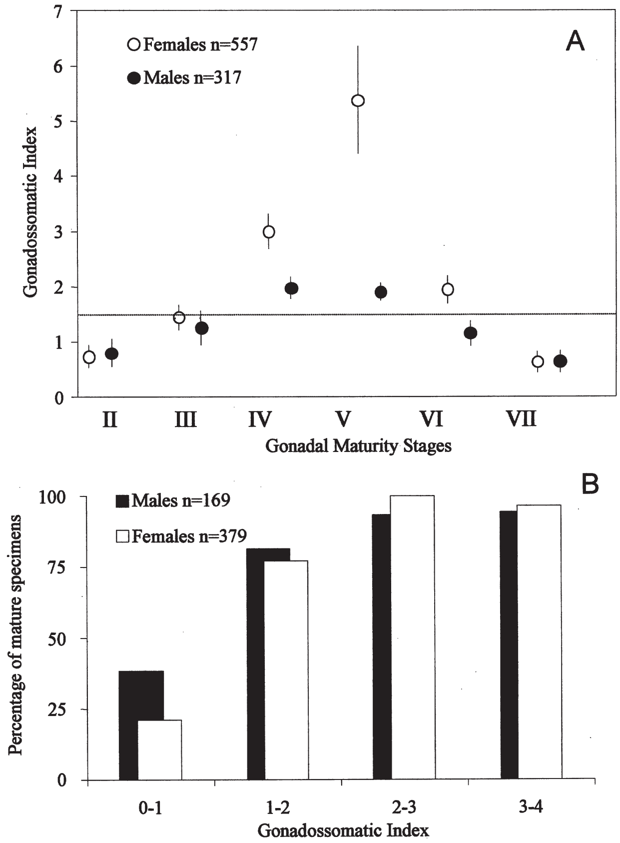

FIG. 3. – Relationship between observed macroscopic gonadal stages and gonadosomatic indices (I_G) of *Trichiurus lepturus*. (A) Mean I_G per maturity stage (B) percentage of mature specimens (stages III to VI) in different I_G classes (vertical lines represents 95% confidence intervals).

over 1.5 was considered to be indicative of advanced maturity and spawning.

As shown, oocyte diameter distributions, maturity stages and mean I_G can all be used to distinguish groups of cutlassfish in advanced maturity and spawning from those recovering and those beginning to mature. We chose mean I_G for further analysis because it could be calculated quantitatively and was amenable to statistical comparisons.

Total length of first gonadal maturity

Length at first maturity (L_{Tm}) was defined as the total length at which half of the specimens had their gonads in advanced stages of maturation during the reproductive season. To calculate L_{Tm} the logistic function $P=1/(1+\exp^{-k(LT-LTm)})$ was fitted to the proportions (P) of specimens with I_G equal or higher than 2.0 against total length in 10 cm class intervals (L_T) in the samples from November to February. The parameters k and L_{Tm} of the corresponding equations were calculated after linearization as: k=0.11378, L_{Tm} =63.962 (males) and k=0.11405, L_{Tm} =69.367 (females). Determination coefficient (r^2) of the linearized curves for both males and females were over 90% and the plots of the residuals of the observed and calculated I_G were not biased, thus it was concluded that the function adequately represented the proportion of mature specimens at each L_T (Fig. 4). Total length at first maturity (P=0.5) for males was estimated 63.9 cm and of females as 69.3 cm. All males over 105 cm and females over 110 cm were sexually mature.

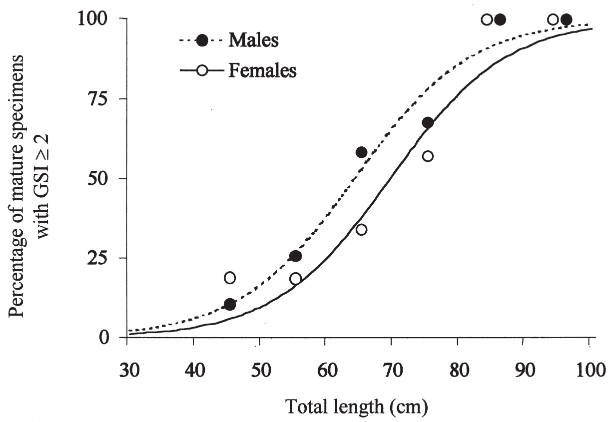

FIG. 4. – Percentages of males (n=169) and females (n=379) with I_G equal or higher than 2.0 in 100 mm in 10 cm L classes and logistic curves fit for the determination of first maturity total length (TL_m) of *Trichiurus lepturus* in southern Brazil.

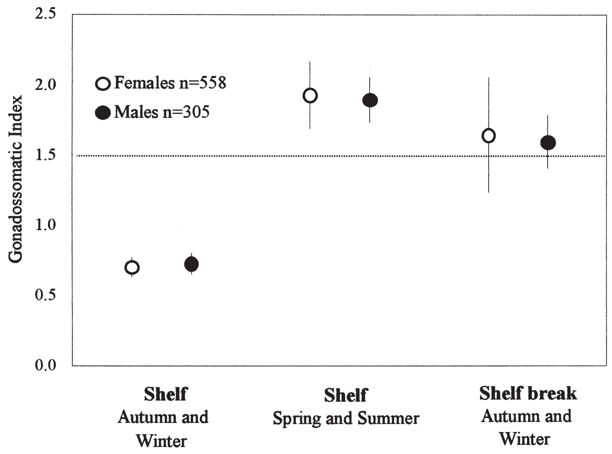

FIG. 6. – Mean gonadosomatic indices (I_G) in shelf samples and shelf break samples of *Trichiurus lepturus* in southern Brazil at different times of the year (vertical lines represents 95% confidence intervals).

Reproductive cycle

The reproductive cycle in the continental shelf (10 to 100 m depth) could be divided into three distinct seasonal phases: gonadal development from July to October, spawning from November to February and recovery from March to June (Figs. 2 and 5). A comparison of the mean I_G of adult *T. lepturus* from the continental shelf and shelf break showed different patterns. While in the shelf, I_G from April to October were low (<0.75), I_G in the shelf break from March to September were significantly higher (>1.59) and almost as high as from November to February in the shelf samples (Fig. 6). Based on the available information, it was concluded that in the continental shelf spawning takes place in late spring and summer, whereas in the shelf break spawning occurs, at least, in autumn and winter.

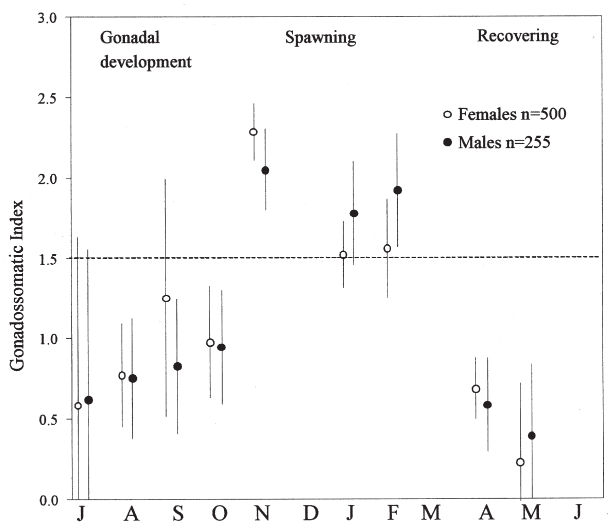

FIG. 5. – Monthly variations of mean gonadosomatic index (I_G) of *Trichiurus lepturus* in shelf surveys off southern Brazil (vertical lines represents 95% confidence intervals).

Type of spawning and batch fecundity

Polymodal oocyte diameter distributions, and ovaries in advanced maturity stages during several months, as observed for *T. lepturus* in southern Brazil, are typical of multiple spawners. Batch fecundity was estimated as the number of maturing oocytes, usually with diameter over 0.8 mm, in 56 ovaries in stages III to V selected from shelf samples obtained from September to February. Batch fecundity ranged from 3,917 in a 70 cm female to 154,215 in a 141 cm L_T female (Fig. 7). The relationship between the number of maturing oocytes (F) and total length was estimated as $F = 0.0002 \times L_T^{4.0717}$

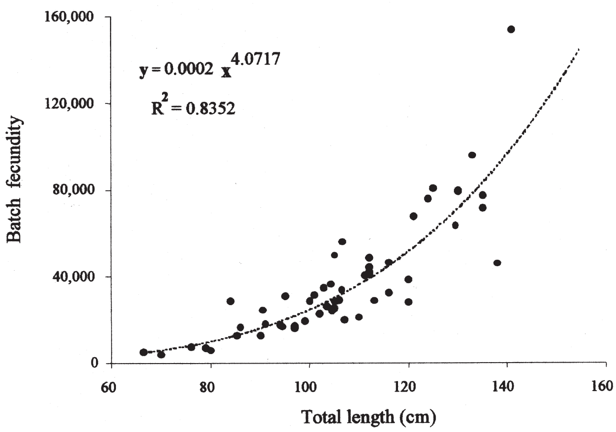

FIG. 7. – Total length batch fecundity relationship for 54 females of *Trichiurus lepturus* sampled in southern Brazil.

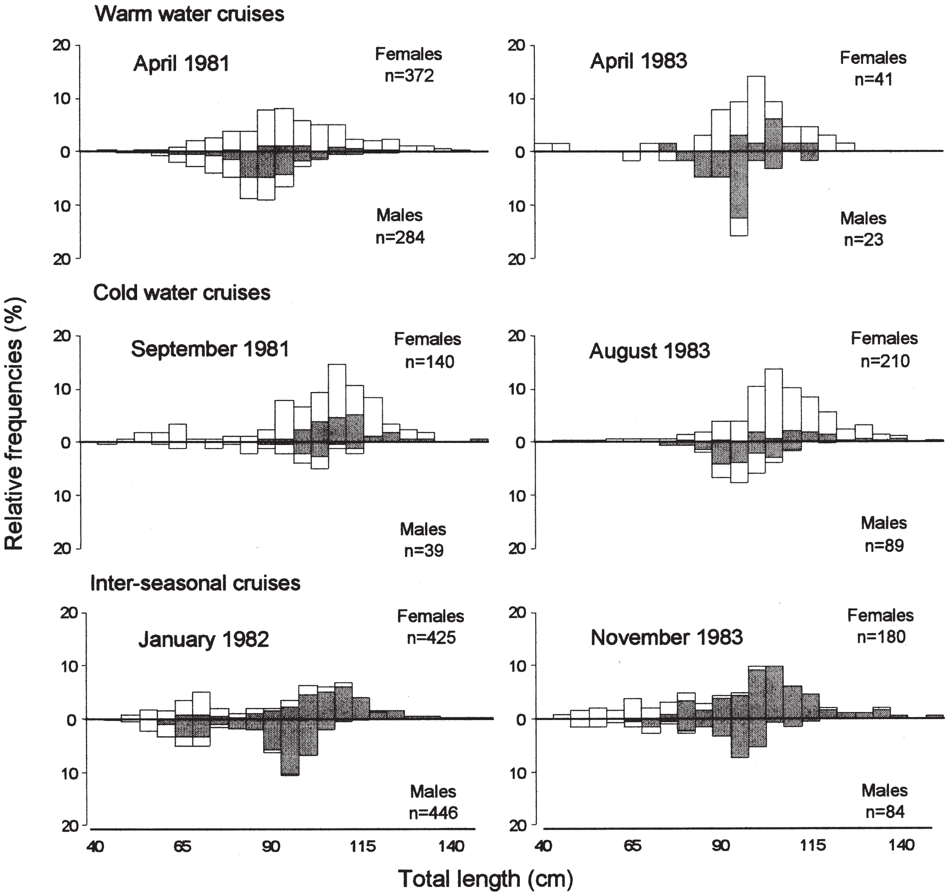

FIG. 8. – Length frequency distributions of females (upper) and males (lower) and proportions of mature (grey) and immature (white) cutlassfish *Trichiurus lepturus* in shelf bottom trawl surveys corresponding to different phases of annual reproductive cycle in southern Brazil.

($r^2 = 0.8352$). The number of maturing oocytes per gram of total weight (relative batch fecundity) ranged from 22.6 to 90.9, with an average of 45.9 (95% CI = +/- 9.1). An ANOVA test ($p<0.05$) of mean relative batch fecundity with gonadal stage (III to V) as factors did not show significant differences.

Sex ratios and maturity stages in different seasons

The numbers of mature and immature males and females (stages III to VI) in different L_T classes in samples from the continental shelf warm, inter-seasonal and cold water season cruises are shown in Fig. 8. In the warm water cruises of April 1981 and April 1983, overall sex ratios favoured females and mature females were more abundant than mature males, especially at $L_T > 90$ cm . In cold water cruises of September 1981 and August 1983 mature females were over twice the number of mature males and the overall sex ratio was strongly biased towards females. During inter-seasonal water cruises of January 1982 and November 1983, specimens with maturing or mature gonads predominated and the sex ratio of mature adults did not differ from 1:1. Chi square tests for pooled data showed that, on the shelf the percentage of mature males was higher than females in the non reproductive season but no significant differences were detected in the reproductive season.

Gonadal maturity in relation to environment and feeding intensity

Gonadosomatic indices and feeding intensity indices of adult cutlassfishes on the continental shelf were compared among the warm, cold and inter-seasonal water cruises. I_G values were higher in the inter-seasonal water cruises of November and January (Fig. 9a). Mean I_{FI} of females were significantly higher in the non-reproductive season while no differences between seasons were detected for males. Additionally, feeding intensity for females was

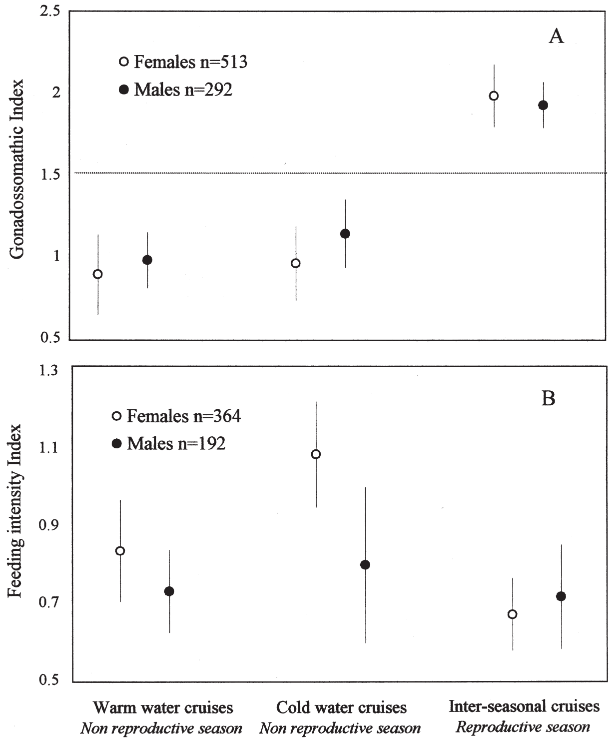

FIG. 9. – Mean gonadosomatic indices (I_G) (A) and feeding intensity index (I_{FI}) (B) of *Trichiurus lepturus* in three thermic conditions (seasons) on the continental shelf off southern Brazil (vertical lines represents 95% confidence intervals).

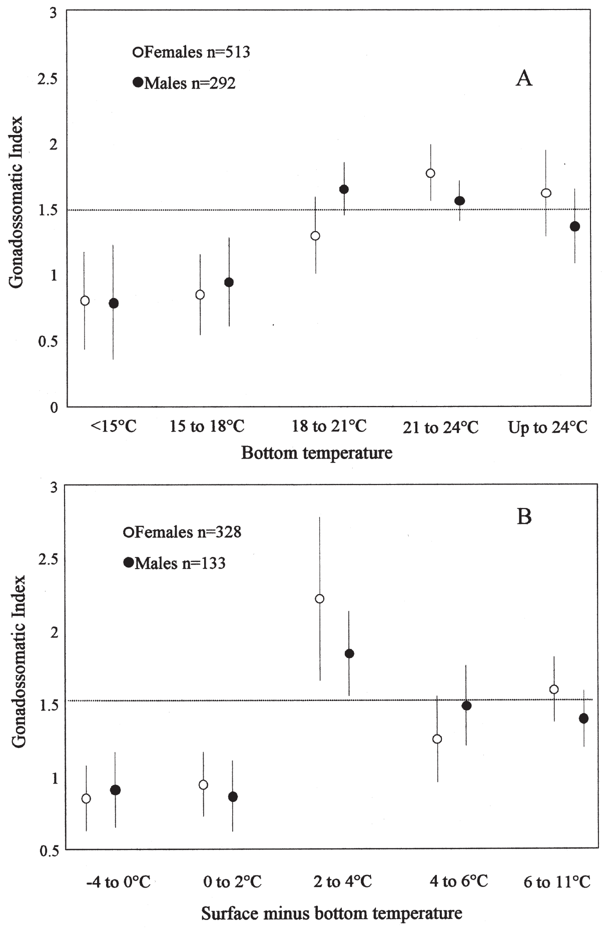

FIG. 10. – Mean gonadosomatic indices (I_G) of *Trichiurus lepturus* grouped in: classes of surface temperature (A) differences between surface and bottom temperature (B).

higher than for males in the non-reproductive season (Fig. 9b).

To investigate the environmental conditions associated with spawning on the continental shelf, the relationship between I_G with depth, surface temperature and difference between surface and bottom temperatures was calculated, the last as an indication of the degree of stratification of the water column. Males and females had higher I_G in coastal waters of depth under 20 m in reproductive season. For both sexes, I_G values were significantly lower than 1.5 at temperatures under 18°C and did not differ or were higher than 1.5 at temperatures over 18°C (Fig. 10*a*). I_G values did not differ or were significantly higher than 1.5 for surface temperatures 2°C or more warmer than bottom temperatures and were significantly lower than 1.5 for differences under 2°C. Higher I_G values were observed at surface temperatures 2° to 4°C higher than bottom temperatures (Fig. 10*b*).

Favourable environmental characteristics in the spawning season (spring and summer) on the continental shelf were found mainly in coastal waters at depth under 20 m and year round in the shelf break. In fact, in January 1982 and in November 1983, most spawning females were found nearshore and over the shelf in stratified waters at surface temperatures over 20°C. In a late winter cruise in September 1986, similar conditions prevailed over the shelf break, where some spawning females were found.

DISCUSSION

The reproductive strategy of *T. lepturus* can be characterized by its flexibility. At low latitudes and in warm regions, like in southeastern India (Tampi *et al.*, 1968), Gulf of Mexico (Sheridan *et al.*, 1984) and southeastern Brazil (Bellini, 1980), spawning has no regular periodicity. At higher latitudes (30-35°), like in the Sea of Japan, spawning takes place from late spring to summer (Munekiyo and Kuwahara, 1984). In southern Brazil both patterns coexist. On the shelf break the warm Brazil current flows year round-reproduction takes place at least in winter and spring and probably throughout the year. In the coastal shelf environment, both surface and bottom water cools down to 10 to 15°C during the winter and early spring and spawning is restricted to the warmer months. In fact, *T. lepturus* larval survival seems to be constrained by low surface temperatures, as eggs and larvae off southern Brazil were rare under 21°C and absent under 16°C (Mafalda, 1989).

Spawning off southern Brazil was also associated with medium to high water column stratification that, in turn, can be associated with coastal upwellings, owing to the strong influence of NE winds (more frequent during the late spring and summer) and to upwelling processes at the shelf break (more frequent in winter and early spring) (Garcia, 1997).

A wide range of sizes at maturity in different parts of the world demonstrate the adaptability of the cutlassfish to different environments. Mean length at first maturity (L_{Tm}) ranged from 35 cm in the Gulf of Mexico (Sheridan *et al.,* 1984) to 39 cm in southeastern Brazil (Bellini, 1980), corresponding to warm subtropical environments and from 59 cm in Japan (Munekiyo and Kuwahara 1988*b*) to 63-69 cm in southern Brazil where marked temperature cycles and lower annual mean temperatures occur. In warmer, less productive environments, smaller batch fecundity, due to smaller size, may be partly compensated by longer spawning seasons. In frontal zones where more intense feeding is associated with colder and more productive waters maturity at larger sizes and resulting larger batches compensate for a shorter reproductive season. Our results are not conclusive, but indicate that in southern Brazil both strategies occur, the first strategy prevails in coastal waters, and the second, over the shelf break.

Males and female *T. lepturus* appear to have different patterns of seasonal reproductive investment and feeding activity. The higher proportion of females among larger cutlassfishes observed in this study and growth studies by Munekiyo and Kuwahara (1988*a*) suggest that females attain larger sizes than males of the same age. Differential growth may reflect a higher reproductive investment by males. Females that remain in the colder and more productive coastal waters during winter enhance their condition and probably also grow larger. The estimated biomass of cutlassfish in autumn and winter in shelf waters was less than half of the estimated biomass in spring and early summer surveys (Martins and Haimovici, 1997) and composed mainly of large females, which are expected to contribute to the reproductive season in coastal waters. Our hypothesis for explaining this seasonal change in sex ratio is that during winter, most adult males appear to move offshore or northward, eventually spawning during a longer season or throughout the year. Females that overwinter near the coast may delay maturation. Following this conjecture, this strategy could enhance the reproductive success of larger females that should produce more eggs that will hatch during a more favourable period. Simultaneously, the population spreads out the risks of recruitment extending their spawning season in the warmer and more stable northern and offshore areas. The lack of published data on sex ratios at lower latitudes does not permit us to make definitive conclusions at this time.

The main features of the reproductive strategy of cutlassfish described in this paper were derived from fishery surveys. Because a large data set was available, it was possible to investigate how the cutlassfish takes advantage of the oceanographic process of Southern Brazilian Subtropical Convergence Ecosystem to enhance its reproductive fitness and abundance in southern Brazil.

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