# Parasites of *Cynoscion guatucupa* along South American Atlantic coasts: evidence for stock discrimination

## J. T. TIMI\*†‡, J. L. LUQUE§ AND N. H. SARDELLA\*

\*Laboratorio de Parasitología, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3350, (7600) Mar del Plata, Argentina, †Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Funes 3350, (7600) Mar del Plata, Argentina and \$Departamento de Parasitologia Animal, Universidade Federal Rural de Rio de Janeiro, C.P. 74508, CEP 23851-970, Seropédica, RJ, Brazil

(Received 24 January 2005, Accepted 30 May 2005)

Two stocks of striped weakfish *Cynoscion guatucupa* in the south-west Atlantic Ocean, were identified using parasites as biological tags. A total of 297 fish caught in Brazil, Uruguay and Argentina, contained 29 species of metazoan parasites. Univariate analysis on parasite populations, as well as multivariate discriminant analysis, calculated for juvenile and adult fish separately, allowed the identification of the two stocks, one from Argentina and Uruguay and the other from Brazil, to be made. Southern samples were characterized by higher prevalences and abundance of larval endohelminths, whereas in the northern stock, gastrointestinal and ectoparasitic species were common. Discriminant analyses on parasite infracommunities of Brazilian fish showed notable differences between juvenile and adult hosts; no such trend was observed in fish from Argentina and Uruguay, despite differences between juveniles and adults at the population level. Different oceanographic conditions and their influence on the distribution of parasites as well as of other hosts involved in their life cycles could be key factors for the differences observed among stocks of *C. guatucupa*.

Key words: biological tags; Cynoscion guatucupa; south-west Atlantic; stocks.

## **INTRODUCTION**

The striped weakfish *Cynoscion guatucupa* (Cuvier) (= *C. striatus*) is a demersal sciaenid whose geographical distribution is restricted to South American Atlantic waters, from Rio de Janeiro, Brazil, to north Patagonia, Argentina (43° S) (Cousseau & Perrotta, 1998); like other sciaenids, the striped weakfish can be found in bays and estuaries during the spawning season (Cassia, 1986; Cordo, 1986; López Cazorla, 2000). Striped weakfish is carnivorous, as a juvenile and as an adult, occupying the third and fourth trophic levels in the food

<sup>‡</sup>Author to whom correspondence should be addressed. Tel.: +54 223 4752426; fax: +54 223 4753150; email: jtimi@mdp.edu.ar

chain (López Cazorla, 1996). Its main prey is fishes and crustaceans (López Cazorla, 2000).

Despite the importance of *C. guatucupa* in the regional fishery (López Cazorla, 1996), the number of populations or stocks in this area is still poorly known. Based on meristic and morphometric comparisons, Díaz de Astarloa & Bolasina (1992) suggested that striped weakfish from southern Uruguay (samples from  $34^{\circ}57'$  S;  $54^{\circ}14'$  to  $54^{\circ}15'$  W) and northern Buenos Aires Province, Argentina (samples from  $36^{\circ}12'$  to  $36^{\circ}43'$  S;  $56^{\circ}30'$  to  $56^{\circ}37'$  W) could be a single stock, isolated from those striped weakfish from El Rincón, southern Buenos Aires Province, Argentina ( $39^{\circ}05'$  to  $39^{\circ}07'$  S;  $60^{\circ}55'$  to  $61^{\circ}00'$  W). Previous studies based on fecundity (Cassia, 1986), length-mass ratios and presence of both eggs and juveniles in both zones (Cordo, 1986), support this view. No studies on stock composition of *C. guatucupa* have been carried out in Brazilian waters, although quantitative aspects of metazoan parasites of *C. guatucupa* from Rio de Janeiro have been studied (Sabas & Luque, 2003).

South American Atlantic coasts are orientated along a north-south axis. Water circulation in the south-west Atlantic Ocean is characterized by two water currents, both running parallel to the coast, the Brazil Current (warm and saline waters) and the Malvinas Current (cold, low salinity subantarctic waters) (Martos, 1989). In this area many oceanographic variables show latitudinal gradients, including water temperature which decreases southwards (Bakun & Parrish, 1991; Hoffmann *et al.*, 1997). Temperature, as a measurement of energy input, is a good predictor of latitudinal gradients in species richness and diversity (Rohde, 1992, 1999).

The thermal gradient, characteristic of the south-west Atlantic Ocean is expected to have enough influence on the structure of parasite populations and communities to allow the identification of different stocks of *C. guatucupa*, by using parasites as 'biological tags' (MacKenzie, 1983, 2002; Williams *et al.*, 1992; MacKenzie & Abaunza, 1998).

In parasite assemblages, the demographic variables of parasite species tend to be dependent of host age and size (Guégan *et al.*, 1992; Lo *et al.*, 1998; Poulin, 2000; Poulin & Valtonen, 2002; Duerr *et al.*, 2003), therefore the possible effect of host age and size on the geographical differences of parasite communities was evaluated in the present study by considering juvenile and adult fish separately.

The purpose of this study was to determine if striped weakfish, inhabiting coastal waters of Brazil, Uruguay and Argentina form a single stock.

## MATERIALS AND METHODS

A total of 297 striped weakfish were examined for parasites. Fish were caught by trawl in three zones of the south-west Atlantic Ocean: Pedra de Guaratiba, State of Rio de Janeiro, Brazil (23°01′ S; 43°38′ W) (n = 74) caught at irregular intervals between March 2002 and March 2003, Uruguayan coasts (35°38′ S; 53°19′ W) (n = 63) caught in July 1993 and Mar del Plata, Argentina (38°08′ S; 57°32′ W) (n = 160) caught at irregular intervals between July 1992 and June 2002. Fish were kept fresh, or deep frozen in plastic bags at  $-18^{\circ}$  C, until examination. After defrosting each fish was measured for total length ( $L_{\rm T}$ , cm). Parasites were recovered from the body surface, gills, branchial and body cavities and viscera after microscopic examination. Following Cassia (1986), Cordo (1986) and Vieira & Haimovici (1997) fish samples from each zone were divided into juvenile (<30 cm  $L_T$ ) and adults (>30 cm  $L_T$ ) in order to minimize the influence of host size and age on parasite burden.

Parasites were identified according to Martorelli (1992), Timi & Etchegoin (1996), Timi et al. (1997, 2001), Navone et al. (1998), Santos et al. (2002), Guagliardo (2003), Sabas & Luque (2003) and Sardella et al. (2005).

## PARASITE POPULATIONS

Ecological terms follow Bush *et al.* (1997). Prevalence and mean intensity were calculated for each parasite species in each area, for juvenile and adult fish separately. For those species with prevalence >10% in at least one of the zones (component species, Bush *et al.*, 1990),  $\chi^2$  analyses and *a posteriori* multiple comparisons for proportions, with angular transformation of each proportion, were used to test for significant differences of prevalence between zones. ANOVA and *a posteriori* Tukey tests for unequal samples on  $\log_{10}(x + 1)$  transformed data were used to analyse the effects of locality on abundance of each parasite species (Zar, 1996).

## SIMILARITY ANALYSES

Sørensen quantitative indices of similarity (Magurran, 1988), were calculated among infracommunities within and between zones.

## MULTIVARIATE ANALYSES

A discriminant analysis, based on Mahalanobis distances, was used to find differences between zones and to identify which parasite species were responsible for these differences. Analyses were computed on square root-transformed data and performed using the Brodgar 1.8 package (Brodgar, 2000). Discriminant analyses were applied to both component species and long-lived parasites.

#### RESULTS

For both juvenile and adult fish, mean  $\pm$  s.D. host  $L_{\rm T}$  from Brazil (26·45  $\pm$  1·92 cm and 40·67  $\pm$  4·31 cm, respectively), Uruguay (25·32  $\pm$  1·57 cm and 40·82  $\pm$  4·94 cm, respectively) and Argentina (26·96  $\pm$  2·88 cm and 40·65  $\pm$  5·33 cm, respectively) did not differ significantly among zones ( $F_{2,92}$ , P > 0.01 and  $F_{2,199}$ , P > 0.01, respectively).

## PARASITE POPULATIONS

Twenty-nine metazoan parasite species were found in the pooled samples, including six ectoparasites, 10 gastrointestinal and 11 larval parasites in the body cavity, with an unequal distribution among the three host populations (Table I). Two nematode species, *Hysterothylacium aduncum* and *Ascarophis marina*, were found as larvae in the stomach and intestine only when their intermediate hosts (the anchovy *Engraulis anchoita* Hubbs & Marini and the white shrimp *Peisos petrunkevitchi*, respectively) were present in the stomach contents of fish. They were considered as accidental infections and excluded from further analyses. The monogenean *Diplectanum squamatum* and the cestode

			tl	nree z	ones of the	sout	1-west Atlan	tic Oce	an	1			
			Br	azil			Uru	ıguay			Argen	tina	
		Juven	ile $(n = 41)$	Adu	ts $(n = 33)$	Juv	enile $(n = 30)$	Adu	lts $(n = 33)$	Juveni	le $(n = 24)$	Adul	s ( $n = 136$ )
Parasites	Site	Р	$\mathbf{MI}\pm\mathbf{s.d.}$	Ч	$\mathbf{MI}\pm\mathbf{s.d.}$	Ь	$MI \pm s.d.$	Ч	$\mathbf{MI}\pm\mathbf{s.d.}$	Р	$MI \pm s.d.$	Ь	$\mathbf{MI} \pm \mathbf{s.p.}$
Lobatostoma ringens (As)	In	2.4	1.0	6.1	2.0	Т	I	I	I	I	I	I	I
Pleorchis americanus (Di)	In	2.4	1.0	Ι	I	Ι	Ι	I	I	I	I	I	I
Prosorhynchus osakii (Di)	In	41.5	$11 \cdot 7 \pm 31 \cdot 1$	15.1	$13.6\pm19.1$	I	Ι	I	I	I	I	I	I
Lecithochirium microstomum (Di)	In-St	31.7	$2.8\pm5.6$	33.3	$6{\cdot}0 \pm 19{\cdot}2$	T	Ι	I	I	I	I	4-4	$3\cdot 3 \pm 5\cdot 7$
Parahemiurus merus (Di)	In	43.9	$2\cdot 3\pm 5\cdot 6$	63.6	$14{\cdot}2\pm13{\cdot}3$	I	I	I	I	I	I	I	I
Opecoeloides polynemi (Di)	In	9.8	$1{\cdot}2\pm 0{\cdot}7$	9.1	$3.7\pm0.6$	I	Ι	I	I	I	I	I	Ι
Opecoeloides feliciae (Di)	St	I	I	T	I	I	Ι	I	I	8.3	$1 \cdot 0$	2.2	$4\cdot 3\pm 2\cdot 5$
Diplectanum squamatum (Mo)	ïJ	34·1	$1.9 \pm 41.7$	100	$51 \cdot 1 \pm 31 \cdot 0$	NS	Ι	NS	I	$100^{*}$	$133.4 \pm 132.7$	$100^+$	$81{\cdot}7\pm59{\cdot}0$
Cynoscionicola jamaicencis (Mo)	ö	48.8	$4.7\pm20.5$	I	I	I	I	I	I	I	I	I	I
Hargicotyle louisianensis (Mo)	ïJ	17.1	1.0	9.1	$1{\cdot}3\pm0{\cdot}7$	I	Ι	I	I	I	I	I	I
Diclidophoridae gen. sp. (Mo)	ïJ	I	Ι	I	Ι	I	Ι	Ι	I	I	I	2.2	1.0
Progrillotia dollfusi (Ce)	Bc	26.8	$4.5 \pm 4.9$	6.06	$5 \cdot 0 \pm 4 \cdot 6$	I	Ι	I	I	I	I	I	Ι
Grillotia bothridiopunctata (Ce)	Bc	Ι	I	I	I	100	$165{\cdot}0\pm109{\cdot}8$	100	$475.3 \pm 751.9$	100	$194 \cdot 9 \pm 117 \cdot 3$	100	$371 \cdot 0 \pm 369 \cdot 7$
Callitetrarhynchus gracilis (Ce)	Bc	I	I	I	I	I	I	18-2	$1{\cdot}2\pm0{\cdot}4$	4.20	$1 \cdot 0$	21.3	$1{\cdot}6\pm1{\cdot}2$
Dasyrhynchus pacificus (Ce)	На	NS		SN		I	I	69-7	$2 \cdot 9 \pm 2 \cdot 2$	Ι	I	72.8	$8{\cdot}2\pm 6{\cdot}9$
Nvbelinia sp. (Ce)	Bc	9.8	$1 \cdot 0$	12.1	1.0	T	I	I	I	I	I	I	Ι

TABLE I. Taxonomic composition, microhabitat (site), prevalence (P) and mean intensity (MI  $\pm$  s.D.) of parasites of *Cynoscion guatucupa* in

1606

## J. T. TIMI ET AL.

Scolex polymorphus (Ce)	Pc-In	I	I	Ι	I	Ι	I	I	I	50.0	$9.1\pm8.2$	49-3	$72 \cdot 0 \pm 83 \cdot 0$
Corynosoma australe (Ac)	$\mathbf{Bc}$	2.4	$1 \cdot 0$	66.7	$5.5 \pm 6.34$	26.7	$1{\cdot}4\pm0{\cdot}5$	0.76	$11 \cdot 0 \pm 11 \cdot 7$	41-7	$2.6 \pm 2.6$	86.0	$12{\cdot}2\pm18{\cdot}4$
Corynosoma cetaceum (Ac)	$\mathbf{Bc}$	I	Ι	I	I	10.0	1.0	15.1	$1{\cdot}6\pm 0{\cdot}9$	8.3	$4.5 \pm 3.5$	31.6	$2 \cdot 4 \pm 2 \cdot 5$
Hysterothylacium aduncum (Ne)	St-In	I	Ι	I	I	I	I	I	I	I	I	$L \cdot 0$	$1 \cdot 0$
Hysterothylacium sp. (Ne)	$\mathbf{Bc}$	70.7	$11 \cdot 1 \pm 31 \cdot 8$	100	$63{\cdot}8 \pm 107{\cdot}5$	0.09	$7.3 \pm 9.2$	87.8	$14{\cdot}2\pm15{\cdot}9$	54-2	$12 \cdot 1 \pm 23 \cdot 1$	92.6	$13.7 \pm 32.8$
Terranova sp. (Ne)	$\mathbf{Bc}$	2.4	$1 \cdot 0$	21.2	2.0	3.3	1.0	6.1	$3.5 \pm 3.5$	16.7	$1 \cdot 0$	29-4	$4{\cdot}3\pm10{\cdot}7$
Contracaecum sp. (Ne)	$\mathbf{Bc}$	T	Ι	T	Ι	3.3	1.0	27-3	$3.4 \pm 4.0$	4.2	$1 \cdot 0$	22.1	$5 \cdot 0 \pm 8 \cdot 5$
Anisakis simplex s.l. (Ne)	$\mathbf{Bc}$	I	I	I	I	3.3	1.0	30-3	$1{\cdot}3\pm0{\cdot}7$	I	I	30.8	$2 \cdot 1 \pm 3 \cdot 3$
Dichelyne spinicaudatus (Ne)	In	I	I	I	Ι	I	I	I	I	4.2	3.0	7.0	$1 \cdot 0$
Cucultanus sp. (Ne)	In	T	Ι	24·2	$2.7 \pm 1.5$	T	Ι	I	Ι	I	I	1.5	$1{\cdot}5\pm0{\cdot}7$
Ascarophis marina (Ne)	St-In	I	I	I	I	I	I	I	I	I	I	19.1	$7.2 \pm 9.9$
Lernanthropus cynoscicola (Co)	:5	I	I	24·2	$3\cdot 2 \pm 3\cdot 0$	36.7	$1{\cdot}4\pm0{\cdot}7$	48.5	$3 \cdot 0 \pm 4 \cdot 0$	50.0	$1{\cdot}4\pm0{\cdot}8$	28.7	$1{\cdot}9\pm1{\cdot}3$
Caligus sp. (Co)	:5	2.4	$1 \cdot 0$	6.1	1.0	I	Ι	Ι	I	I	I	I	I
As, Aspidogastrea; Di, Digenea; M snine column: Pc, rodoric caeca, N	lo, Monog S not sam	enea; C	e, Cestoda; Ac,	Acanth	nocephala; Ne,	Nemat	toda; Co, Copep	oda; In, iı	ntestine; St, stom	ach; Gi, gi	lls; Bc, body cavi	ty; Ha, hí	temal arches of

apure commun, re, pyrone cacca, red, red sampeer. \*data based on five fish examined. <sup>+</sup>data based on six fish examined.

-, parasite absent.

1607

*Dasyrhynchus pacificus* were also excluded from analyses because fish from some zones were not searched for these two parasites.

Only three species, *Corynosoma australe*, *Hysterothylacium* sp. and *Terranova* sp. were found in both juvenile and adult fish from all the three zones. No other species were common in both Brazilian and Uruguayan samples of juvenile hosts, whereas juvenile striped weakfish from Uruguay and Argentina also shared *Grillotia bothridiopunctata*, *Corynosoma cetaceum*, *Contracaecum* sp. and *Lernanthropus cynoscicola*. Adult fish contained more species in common between zones, such as *L. cynoscicola* in all zones, *Lecithochirium microstomum* and *Cucullanus* sp. in Brazil and Argentina and *G. bothridiopunctata*, *Callitetrarhynchus gracilis*, *C. cetaceum*, *Contracaecum* sp. and *Anisakis simplex s.l.* in Argentina and Uruguay (Table I).

Thirteen and 16 parasite species reached the status of component species in at least one of the zones for juvenile and adult fish, respectively (Tables II and III). For both juvenile and adult fish, the higher number of differences in prevalence (10 and 14 parasite species, respectively) occurred between Brazil and Argentina, whereas nine and 13 species, for juvenile and adult respectively, differed between Brazil and Uruguay and only three for juvenile and one for adult respectively, between Uruguay and Argentina. Most gastrointestinal and ectoparasitic species had higher prevalences in Brazilian juvenile striped weakfish, whereas larval endohelminths showed no such trend. Similar results were observed for differences in abundance (Table II). Similarly for adult hosts most gastrointestinal species were more prevalent and abundant in Brazil, whereas the inverse was observed for larval endohelminths and no differences were observed for ectoparasites (Table III).

#### SIMILARITY ANALYSIS

A high degree of variability was observed in the analysis of similarity (Fig. 1) (see s.D.); comparisons within zones showed that Brazil was the most heterogeneous group, whereas the highest similarity was observed among striped weakfish from Uruguay [Fig. 1(a)]. Analyses between zones showed that similarity values between infracommunities from Uruguay and Argentina were higher than those involving striped weakfish from Brazil, even those within Brazil [Fig. 1(b)].

## MULTIVARIATE ANALYSES

The first two discriminant variables explained 93·26% of the variance, contributing to 78·17% (eigenvalue = 6·12) and 15·09% (eigenvalue = 1·18), respectively. A significant overall group effect was observed (Wilks' lambda = 0·04,  $F_{90,1334}$ , P < 0.01). Individual fish were distributed mainly along the first two axes (Fig. 2). Dimensionality tests for group separation showed that the zones were significantly separated in both dimensions ( $\chi^2$ , d.f. = 51, P < 0.01), although fish from Argentina and Uruguay were clumped together independently of their developmental stage [Fig. 2(a)]. Each fish was classified correctly to the six component communities with an accuracy of 64.65% (Table IV), while the percentage of correctly classified samples relative

$\chi^2$ BR-URBR-ARUGastrointestinal parasites <i>Prosorhynchus osakiiProsorhynchus osakiiProsorhynchus osakiiLecithochirium microstomum</i> 19-84*BR > UR*BR > UR*Progrillotia dolffusi16-38*BR > UR*BR > UR*BR > UR*BR > UR*Corynosoma australe15-77*BR < UR*AABR < UR*ABR < UR*BR < UR* <th>BR-UR     BR-AR       Image: Second state     Image: Second state       Image: Second state     Image: Second state</th> <th>UR-AR</th> <th>ANOVA F<sub>2,92</sub></th> <th></th> <th></th> <th></th>	BR-UR     BR-AR       Image: Second state     Image: Second state       Image: Second state     Image: Second state	UR-AR	ANOVA F <sub>2,92</sub>			
Gastrointestinal parasitesProsorhynchus osakii $27\cdot27*$ BR > UR*BR > AR*Lecithochirium microstomum $19\cdot84*$ BR > UR*BR > AR*Parahemiurus merus $29\cdot25*$ BR > UR*BR > AR*Larval helminthsScolex polymorphus $40\cdot63*$ ABR > UR*BR > AR*Drarbeniurus merus $29\cdot25*$ BR > UR*BR > AR*Draval helminthsScolex polymorphus $40\cdot63*$ ABR > UR*BR > AR*Dragillotia bothridiopunctata $95\cdot00*$ BR > UR*BR > AR*Corynosoma australe $15\cdot77*$ BR < UR*BR < AR*UR	<pre>&lt; UR* BR &gt; AR &lt; &gt; UR* BR &gt; AR &lt; &gt; UR* BR &gt; AR &lt; &gt; UR* BR &gt; AR</pre>	∀	*L7 C1	BR-UR	BR-AR	UR-AR
Toboli production $272.7$ $DR > UR*$ $BR > AR*$ $Lecithochirium microstomum19.84*BR > UR*BR > AR*Parahemiurus merus29.25*BR > UR*BR > AR*Larval helminths29.25*BR > UR*BR > AR*Larval helminths40.63*ABR < AR*Scolex polymorphus40.63*ABR < AR*Progrillotia dollfusi16.38*BR > UR*BR > AR*Grillotia bothridiopunctata95.00*BR < UR*BR < AR*Corynosoma australe15.77*BR < UR*BR < AR*$	C > UR + BR > AR C > UR + BR > AR C > UR + BR > AR	C ▼ *		80 ~ 110*	BD ∕ AD*	<
$ \begin{array}{llllllllllllllllllllllllllllllllllll$	$C > UR^* BR > AR$		6.60*	$BR > UR^*$	$BR > AR^*$	< <
$ \begin{array}{llllllllllllllllllllllllllllllllllll$		*	15.81*	$BR > UR^*$	$BR > AR^*$	V
Scolex polymorphus $40.63*$ ABR < AR*URProgrillotia dollfusi $16.38*$ BR > UR*BR > AR*Grillotia bothridiopunctata $95.00*$ BR < UR*						
Progrillotia dollfiusi $16.38^*$ BR > UR*BR > AR*Grillotia bothridiopunctata $95.00^*$ BR < UR*	A $BR < AR$	* $UR < AR^*$	27.78*	A	$BR < AR^*$	$\text{UR} < \text{AR}^*$
<i>Grillotia bothridiopunctata</i> 95-00* BR < UR* BR < AR* <i>Corynosoma australe</i> 15-77* BR < UR* BR < AR* UR	$C > UR^* BR > AR$	* A	6.39*	$BR > UR^{**}$	$BR > AR^{**}$	A
Corynosoma australe $15.77*$ BR < UR* BR < AR* UR	$C < UR^* BR < AR$	* NS	$1116.74^{*}$	$BR < UR^*$	$BR < AR^*$	NS
	$C < UR^* BR < AR$	* $UR < AR^*$	8.20*	NS	$BR < AR^*$	NS
Corynosoma cetaceum 4:92 (NS) – – –	I	I	1.97 (NS)	I	I	I
Hysterothylacium sp. 1.97 (NS) – –	1	I	1.86 (NS)	I	I	I
Terranova sp. 5-84 (NS) – – –	I	I	3.01 (NS)	Ι	I	Ι
Ectoparasites						
Hargicotyle louisianensis $7.72^*$ BR > UR* BR > AR*	$C > UR^* BR > AR$	* A	5.38*	$BR > UR^{**}$	NS	A
Cynoscionicola jamaicencis 33:37* BR > UR* BR > AR*	$C > UR^* BR > AR$	* A	17.43*	$BR > UR^*$	$BR > AR^*$	A
Lernanthropus cynoscicola $24.33*$ BR < UR* BR < AR* UR	$C < UR^* BR < AR$	* $UR < AR^*$	13.50*	$BR < UR^*$	$\mathbf{BR} < \mathbf{AR}^{\mathbf{*}}$	NS

STOCK DISCRIMINATION OF CYNOSCION GUATUCUPA

1609

-, as  $\chi^2$  tests were NS, a *posteriori* comparisons between zones were not made.

P < 0.01; \*\*0.01 < P < 0.05.

© 2005 The Fisheries Society of the British Isles, Journal of Fish Biology 2005, 67, 1603-1618

$\chi^2$ BR-URBR-ARUR-Gastrointestinal parasitesProsorhynchus osakii $26 \cdot 26^*$ BR > UR*BR > AR*NProsorhynchus osakii $26 \cdot 26^*$ BR > UR*BR > AR*NLecithochirium microstomum $32 \cdot 44^*$ BR > UR*BR > AR*NParahemiurus merus $120 \cdot 02^*$ BR > UR*BR > AR*NCucullamus sp. $31 \cdot 32^*$ BR > UR*BR > AR*NLarval helminths $31 \cdot 32^*$ BR > UR*BR > AR*NScolex polymorphus $48 \cdot 65^*$ ABR > UR*BR > AR*NCollitetrarhynchus gracilis $8 \cdot 45^*$ BR > UR*BR > AR*NNybelinia sp. $20 \cdot 00^*$ BR > UR*BR > AR*NCorynosoma australe $12 \cdot 27^*$ BR < UR*BR < AR*NHysterothylacium sp. $3 \cdot 37$ (NS) $   -$	$\begin{tabular}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{c} UR-AR\\ A\\ UR < AR*\\ A\\ NS\\ UR < AR*\\ \end{array}$	ANOVA F <sub>2,199</sub> 10-03* 24-26* 95-04* 19-62*	BR-UR BR > UR* BR > UR* BR > UR*	<b>BR-AR</b>	
Gastrointestinal parasites $Prosorhynchus osakii26 \cdot 26^*BR > UR^*BR > AR^*PR > AR^*DR < AR^*Lecithochirium nicrostonum32 \cdot 44^*BR > UR^*BR > AR^*UR < AR^*Parahemiurus merus120 \cdot 02^*BR > UR^*BR > AR^*DR < AR^*Parahemiurus merus120 \cdot 02^*BR > UR^*BR > AR^*N < AR^*Cucullanus sp.31 \cdot 32^*BR > UR^*BR > AR^*N < AR^*Cucullanus sp.31 \cdot 32^*BR > UR^*BR > AR^*N < CR^*Scolex polymorphus48 \cdot 65^*ABR > UR^*BR < AR^*N < CR^*Scolex polymorphus8.45^*BR > UR^*BR < AR^*N < CR^*N < CR^*Nybelinia bothridiopunctata202 \cdot 00^*BR < UR^*BR < AR^*N < COrynosoma australe12 \cdot 27^*BR < UR^*BR < AR^*UR < H^*Mybelinia sp.10 \cdot 30^*BR < UR^*BR < AR^*UR < H^*N < COrynosoma cetaceum16 \cdot 27^*BR < UR^*BR < AR^*UR < H^*Hysterothylacium sp.3 \cdot 37N < Corynosoma cetaceum3 \cdot 37N < Corynosoma cetaceum16 \cdot 27^*BR > 11R * AR^*R < AR^*UR < AR^*$		$egin{array}{c} A \\ UR < AR^* \\ A \\ NS \\ UR < AR^* \end{array}$	10.03* 24.26* 95.04* 19.62*	BR > UR* BR > UR* BR > UR*		UR-AR
Prosorhynchus osakii $26\cdot26^*$ $BR > UR^*$ $BR > AR^*$ $PR$ Lecithochirium microstomum $32\cdot44^*$ $BR > UR^*$ $BR > AR^*$ $UR <$ Parahemiurus merus $120\cdot02^*$ $BR > UR^*$ $BR > AR^*$ $UR <$ Parahemiurus merus $120\cdot02^*$ $BR > UR^*$ $BR > AR^*$ $VR <$ Cucullanus sp. $31\cdot32^*$ $BR > UR^*$ $BR > AR^*$ $VR <$ Larval helminths $31\cdot32^*$ $BR > UR^*$ $BR > AR^*$ $VR <$ Scolex polymorphus $48\cdot65^*$ $A$ $BR < AR^*$ $VR <$ Scolex polymorphus $48\cdot65^*$ $A$ $BR < AR^*$ $VR <$ Collitetranhynchus $8\cdot65^*$ $BR > UR^*$ $BR < AR^*$ $N$ Nybelinia bothridiopunctata $202\cdot00^*$ $BR < UR^*$ $BR < AR^*$ $N$ Nybelinia sp. $20\cdot90^*$ $BR < UR^*$ $BR < AR^*$ $N$ Nybelinia sp. $20\cdot90^*$ $BR < UR^*$ $BR < AR^*$ $NR <$ Hysterothylacium sp. $3\cdot87$ (NS) $  -$ Hysterothylacium sp. $3\cdot87$ (NS) $  -$		$\begin{array}{c} A\\ UR < AR*\\ A\\ NS\\ UR < AR*\\ \end{array}$	10-03* 24-26* 95-04* 19-62*	BR > UR* $BR > UR*$ $BR > UR*$		
$ \begin{array}{llllllllllllllllllllllllllllllllllll$		$\begin{array}{c} UR < AR* \\ A \\ NS \\ UR < AR* \\ \end{array}$	24.26* 95.04* 19.62*	$BR > UR^*$ $BR > UR^*$	$BR > AR^*$	A
Parahemiurus merus $120\cdot02*$ BR > UR*BR > AR*ACucullamus sp. $31\cdot32*$ BR > UR*BR > AR*NLarval helminths $31\cdot32*$ BR > UR*BR > AR*NScolex polymorphus $48\cdot65*$ ABR < AR*		$\mathbf{NS}$ NS UR < AR*	95.04* 19.62*	$BR > UR^*$	$BR > AR^{\ast}$	NS
Cucullamus sp. $31.32^*$ BR > UR*BR > AR*NLarval helminths $31.32^*$ BR > UR*BR > AR*UR <	$      ]R*  BR > AR* \\ BR < AR* \\ JR*  BR > AR* \\ JR*  BR > AR* \\ JR*  BR < AR* \\ R* \\ AR* \\ R* \\ AR* \\ R* \\ AR* \\ AR* \\ R* \\ $	$\begin{array}{l} NS\\ UR < AR*\\ \end{array}$	19.62*		$BR > AR^*$	A
Larval helminths $48 \cdot 65 *$ ABR < AR*UR <Scolex polymorphus $48 \cdot 65 *$ ABR < AR*	BR < AR* JR* BR > AR* JR* BR < AR*	$\mathrm{UR} < \mathrm{AR}^*$		$BR > UR^*$	BR > AR	NS
Scolex polymorphus $48.65^*$ ABR < AR*UR <Progrillotia dollfusi $180.43^*$ BR > UR*BR > AR*AGrillotia bothridiopunctata $202.00^*$ BR < UR*	$\begin{array}{ll} BR < AR* \\ \label{eq:BR} BR > AR* \\ \label{eq:BR} JR* & BR < AR* \end{array}$	$UR < AR^*$				
Progrillotia dollfusi180-43*BR > UR*BR > AR*AGrillotia bothridiopunctata202.00*BR < UR*	$JR* BR > AR* \\ JR* BR < AR* \\$	<	24.86*	A	$\mathbf{BR} < \mathbf{AR^*}$	$UR < AR^*$
$ \begin{array}{ccccc} Grillotia bothridiopunctata & 202\cdot00* & BR < UR* & BR < AR* & N\\ Callitetrarhynchus gracilis & 8\cdot45** & BR < UR* & BR < AR* & N\\ Nybelinia sp. & 20\cdot89* & BR > UR* & BR > AR* & N\\ Corynosoma australe & 12\cdot27* & BR < UR* & BR < AR* & UR < Corynosoma cetaceum & 16\cdot27* & BR < UR* & BR < AR* & UR < Hysterothylacium sp. & 3\cdot87 (NS) & - & - & - & - & - & - & - & - & - & $	$JR^* BR < AR^*$	Z	251.41*	$BR > UR^*$	$BR > AR^{\ast}$	A
Callitetrarhynchus gracilis8.45**BR < UR*BR < AR*NNybelinia sp.20.89*BR > UR*BR > AR*NCorynosoma australe12.27*BR < UR*		NS	768.34*	$BR < UR^*$	$\mathbf{BR} < \mathbf{AR^*}$	NS
Nybelinia sp. $20.89^*$ BR > UR*BR > AR*NCorynosoma australe $12.27^*$ BR < UR*	$JR^* BR < AR^*$	NS	4·02**	NS	NS	NS
Corynosoma australe12.27*BR < UR*BR < AR*UR <Corynosoma cetaceum16.27*BR < UR*	$JR^* BR > AR^*$	NS	11.48*	$BR > UR^*$	$BR > AR^*$	NS
Corynosoma cetaceum16.27*BR < UR*BR < AR*UR <Hysterothylacium sp.3.87 (NS)Torranova sn8.08**BR > 11R*BR < AR**	$JR^* BR < AR^*$	$UR < AR^*$	8.44*	$BR < UR^*$	$BR < AR^{\ast}$	NS
$Hysterothylacium$ sp. $3.87$ (NS) $  Terrmova$ sp. $8.08^{**}$ $BR > 11R^*$ $BR < AR^{**}$	$JR^* BR < AR^*$	$UR < AR^*$	*66.9	NS	$BR < AR^{\ast}$	NS
$T_{erranova}$ sin $8.08^{**}$ BR > 11R* BR < AR** 11R <	Ι	I	$31.36^{*}$	$BR > UR^*$	$BR > AR^*$	NS
	$JR^* BR < AR^{**}$	$UR < AR^*$	2·79 (NS)	I	I	I
Contracaecum sp. $9.90^{\circ}$ BR < UR* BR < AR* N	$JR^* BR < AR^*$	NS	3.47**	NS	$BR < AR^{\ast\ast}$	NS
Anisakis simplex s.l. $13.67^*$ BR < UR* BR < AR* N	$JR^* BR < AR^*$	NS	5.66*	NS	$BR < AR^{\ast\ast}$	NS
Ectoparasites						
Lernanthropus cynoscicola 5.74 (NS) – – –	I	ĺ	3.44**	NS	NS	NS

-, as  $\chi^2$  tests were NS, a *posteriori* comparisons between zones were not made.



FIG. 1. Mean  $\pm$  s.D. Sørensen similarity indices of parasite infracommunities of juvenile ( $\Box$ ) and adult ( $\blacksquare$ ) *Cynoscion guatucupa* in three zones of the south-west Atlantic Ocean: quantitative similarity (a) within each zone and (b) between zones.

to chance was 45.79%. None of the Argentinian or Uruguayan fish was assigned to Brazil, however, three hosts from Brazil were assigned to Uruguay.

The importance of each parasite species with respect to discrimination between groups [Fig. 2(b)], evaluated as the contribution of each variable to the total sum of Mahalanobis distances, showed that G. bothridiopunctata, the most important in determining the position of samples, was related to Argentinian and Uruguayan samples and directly correlated to both Scolex polymorphus and C. australe, but inversely correlated to the characteristic species of Brazilian juvenile fish (Cynoscionicola jamaicencis, Prosorhynchus osakii and Hargicotyle louisianensis). On the other hand Progrillotia dollfusi and Parahemiurus merus were important in determining the position of adult fish from Brazil, whereas Cucullanus sp. and Hysterothylacium sp. showed a position between adult fish from Brazil and those from Argentina and Uruguay, but closer to Brazilian samples. Nine species (A. simplex, Contracaecum sp., Terranova sp., Callitetrarhynchus sp., C. cetaceum, Opecoeloides polynemi, L. microstomum, L. cynoscicola and Nybelinia sp.) whose removal resulted in a small decrease in the total sum of Mahalanobis distances, were excluded from Fig. 2(b).

When only long-lived parasites were included in the analysis, the first two discriminant variables explained 94.99% of the variance, contributing to 81.59%



Discriminant function 1

FIG. 2. (a) Sample scores of the first two discriminant functions for juvenile and adult specimens of *Cynoscion guatucupa* in three zones of the south-west Atlantic Ocean. Numbers represent groups averages, circles around group means represent the 90% tolerance regions (*e.g.* 90% of the observations in a group are expected to lie in this region). 1, Argentinian juvenile; 2, Argentinian adults; 3, Uruguayan juvenile; 4, Uruguayan adults; 5, Brazilian juvenile; 6, Brazilian adults.
(b) Canonical correlations between the first two discriminant functions and the parasites. Cor, *Corynosoma australe*; Cuc, *Cucullanus* sp.; Cyn, *Cynoscionicola jamaicencis*; Gri, *Grillotia bothridiopunctata*; Har, *Hargicotyle louisianensis*; Hys, *Hysterothylacium* sp.; Par, *Parahemiurus merus*; Prog, *Progrillotia dollfusi*; Pros, *Prosorhynchus osakii*; Sco, *Scolex polymorphus*.

(eigenvalue = 3.25) and 13.40% (eigenvalue = 0.53), respectively. A significant overall group effect was observed (Wilks' lambda = 0.13,  $F_{50,1290}$ , P < 0.01). Dimensionality tests for group separation showed that the zones were

	BR juv	BR ad	UR juv	UR ad	AR juv	AR ad	Per cent*
BR juv	35	4	2	0	0	0	85.37
BR ad	3	29	1	0	0	0	87.88
UR juv	0	0	24	1	5	2	80.00
UR ad	0	0	5	23	2	3	69.70
AR juv	0	0	7	1	14	2	58.33
AR ad	0	0	17	34	18	67	49.26

 
 TABLE IV. Discriminant analysis classification showing the numbers and percentages of fish classified in each zone (rows correspond to group memberships)

BR, Brazil; UR, Uruguay; AR, Argentina. juv, juvenile; ad, adults. \*Percentage of correctly classified fish per zone.

significantly separated in both dimensions ( $\chi^2$ , d.f. = 24, P < 0.01), although fish from Argentina and Uruguay were clumped together independently of their developmental stage [Fig. 3(a)] and juvenile fish from Brazil partially overlapped southern samples, specially juvenile ones. Each fish was classified correctly to the six component communities with an accuracy of 54.17% (Table V), while the percentage of correctly classified samples relative to chance was 45.79%. None of the Brazilian fish was assigned to either Argentina and Uruguay, however two hosts from Argentina were assigned to Brazil

The importance of each parasite species with respect to discrimination between groups [Fig. 3(b)], evaluated as the contribution of each variable to the total sum of Mahalanobis distances, showed that *G. bothridiopunctata*, the most important in determining the position of samples, was related to Argentinian and Uruguayan samples and directly correlated to *C. australe, C. cetaceum, A. simplex, C. gracilis, Contracaecum* sp. and *Terranova* sp. but inversely correlated to the characteristic species of Brazilian juvenile fish (*Nybelinia* sp.). On the other hand *P. dollfusi* and *Hysterothylacium* sp. were important in determining the position of adult fish from Brazil.

#### DISCUSSION

Ideal tag parasites for fish stock identification must meet some requisites, such as life spans of >1 year and constant infection levels from year to year (MacKenzie, 2002). In the present work samples from different localities were not taken at the same time. Fish from Argentina, however, were caught over a long period of time overlapping the dates of capture of striped weakfish from both Uruguay and Brazil. The presence of many long-lived parasites, such as larval endohelminths (anisakids, juvenile *Corynosoma*, larval trypanorhynchs), which where among the most abundant and prevalent species and accounted for a high proportion of the differences among zones, overcomes the possible effects of the different years and seasons of capture on parasite community structure. Both similarity and multivariate analyses showed that Argentinian fish, sampled over a long time period (>10 years) were similar to Uruguayan fish, caught in a single catch, whereas they were more homogeneous in terms of parasite community structure than Brazilian striped weakfish, caught during a 1 year period.



FIG. 3. (a) Sample scores of the first two discriminant functions for juvenile and adult specimens of *Cynoscion guatucupa* in three zones of the south-west Atlantic Ocean based on long-lived parasites. Numbers represent groups averages, circles around group means represent the 90% tolerance regions (*e.g.* 90% of the observations in a group are expected to lie in this region). 1, Argentinian juvenile; 2, Argentinian adults; 3, Uruguayan juvenile; 4, Uruguayan adults; 5, Brazilian juvenile; 6, Brazilian adults. (b) Canonical correlations between the first two discriminant functions and the parasites. Ani, *Anisakis simplex*; Cal, *Callitetrarhynchus gracilis*; Con, *Contracaecum* sp.; Cora, *Corynosoma australe*; Corc, *Corynosoma cetaceum*; Gri, *Grillotia bothridiopunctata*; Hys, *Hysterothylacium* sp.; Prog, *Progrillotia dollfusi*; Nyb, *Nybelinia* sp.; Ter, *Terranova* sp.

Therefore, differences in sampling periods seem to have no marked effects on the parasite community structure, allowing the identification of fish stocks in the study area.

Comparisons between juvenile and adult fish showed that parasite burden was dependent on fish size or age. Prevalence and abundance of many parasite species were largely higher in adult fish. This is not surprising as a cumulative effect has been commonly reported for fish parasites in the literature. Larger fishes tend to harbour more parasites due to higher feeding rates, larger surfaces for parasite contact and attachment, a broader range of prey items (including larger ones), and higher levels of activity and vagility (with access to different areas and potentially new parasites) (Guégan *et al.*, 1992; Poulin, 2000). Some parasites, however, were markedly more prevalent in juvenile fish from Brazil

1614

AR juv

AR ad

0

2

0

0

		20110 (10 11	lived p	parasites	nemeersmp	s), moraam	g only long
	BR juv	BR ad	UR juv	UR ad	AR juv	AR ad	Per cent*
BR juv	35	6	0	0	0	0	85.37
BR ad	4	29	0	0	0	0	87.88
UR juv	0	0	19	2	9	0	63.33
UR ad	0	0	4	22	3	4	66.67

48

2

13

20

0

44

TABLE V. Discriminant analysis classification showing the numbers and percentages of fish classified in each zone (rows correspond to group memberships) including only long-

BR, Brazil; UR, Uruguay; AR, Argentina; juv, juvenile; ad, adults. \*Percentage of correctly classified fish per zone.

9

22

(i.e. P. osakii, C. jamaicencis, H. louisianensis) and Argentina (Opecoeloides feliciae, Dichelvne spinicaudatus). These parasites are probably lost in larger fishes as a consequence of changes in diet (gastrointestinal species), habitat shifts, and increase of physical constraints with host size or host immunity (ectoparasites).

Evidence from parasitological analyses clearly showed that two stocks could be identified. Striped weakfish samples from Brazil showed sufficient differences from those from southern waters to be considered a different stock. For example G. bothridiopunctata was present in 100% of fish from Uruguay and Argentina but was absent in fish from Brazil, on the other hand *P. dollfusi* was present in 90% of adult fish from Brazil, but absent in samples from Uruguay and Argentina. Thus these two parasites alone could indicate little exchange between the two regions. Some species showed differences of prevalence and abundance between Uruguayan and Argentinian samples. Differences of prevalence or abundance of a single (or a few) parasites, between zones, however, can be an unreliable indication of stock discreteness (Sardella & Timi, 2004). Both similarity and multivariate analyses yielded further evidence that two stocks (Brazil and Argentina plus Uruguay) can be differentiated in the three areas studied.

Similarity within Argentinian and Uruguayan samples was similar to those between them, indicating the integrity of the southern stock. The low values of similarity between zones involving Brazilian striped weakfish support their separation as a different stock. Analysis within Brazilian infracommunities showed low average similarity indices, even lower than those between Argentina and Uruguay. Ecological factors are important determinants of parasite community structure in hosts inhabiting the boundaries of their geographical distribution (Kennedy & Bush, 1994). Rio de Janeiro is the northern limit of distribution of C. guatucupa (Cousseau & Perrotta, 1998), and the heterogeneity in the infracommunity structure could be explained by the characteristics of the local ecosystem and its trophic web. For instance the coastal area of Rio de Janeiro is strongly influenced by upwelling systems and by the subtropical convergence (Luque et al., 2004).

35.29

54.17

Results of discriminant analysis clearly showed that striped weakfish from Brazil represented a separate stock, with evident differences between adults and juveniles, supporting the heterogeneity in these infracommunities observed in similarity analyses. Fish from Argentina and Uruguay clumped together to form another stock unit, with the expected higher similarity between fish of the same developmental stage. The parasite species that contributed most to the separation of the samples were those identified as dominant in most infracommunities within each zone, followed in importance by species with high prevalence in each area. When only long-lived parasites were included in the discriminant analysis, a similar picture was observed. Despite the differences between juvenile and adult fish from Brazil and among juveniles from all zones, the two stock units remained clearly identifiable.

It is concluded that the striped weakfish inhabiting coastal waters of Brazil are members of a stock independent of those from Uruguay and Argentina. The presence of a single stock in southern Uruguay and northern Buenos Aires Province (Argentinian-Uruguayan Common Fishing Zone) agrees with previous ichthyological studies (Díaz de Astarloa & Bolasina, 1992), which identified a third stock at El Rincón, south of Buenos Aires Province. Parasite assemblages of juvenile and adult fish show similar geographical differences, confirming the value of biological tags for stock discrimination at any stage of development.

Further studies including samples from northern Uruguay and southern Brazil are necessary to determine the boundaries between Brazilian and Uruguayan-Argentinian groups, or to determine if *C. guatucupa* inhabiting these areas constitute different stocks to those identified here.

Financial support by grants from Universidad Nacional de Mar del Plata (No. 15 E/ 225) and FONCYT (PICT 2003 No. 15192). J.L. Luque was supported by a Research fellowship from CNPq (Conselho Nacional de Pesquisa e Desenvolvimento Tecnológico).

#### References

- Bakun, A. & Parrish, R. H. (1991). Comparative studies of coastal fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the Southwestern Atlantic. *ICES Journal of Marine Science* 48, 343–361.
- Brodgar (2000). Software Package for Multivariate Analysis and Multivariate Time Series Analysis. Aberdeen: Highland Statistics Ltd.
- Bush, A. O., Aho, J. M. & Kennedy, C. R. (1990). Ecological versus phylogenetic determinants of helminth parasite community richness. *Evolutionary Ecology* 4, 1–20.
- Bush, A. O., Lafferty, K. D., Lotz, J. M. & Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* 83, 575–583.
- Cassia, M. C. (1986). Reproducción y fecundidad de la pescadilla de red, Cynoscion striatus. Publicaciones de la Comisión Técnica Mixta del Frente Marítimo 1, 191–203.
- Cordo, H. D. (1986). Estudios biológicos sobre peces costeros con datos de campañas de investigación realizadas en 1981. III. La pescadilla de red (*Cynoscion striatus*). *Publicaciones de la Comisión Técnica Mixta del Frente Marítimo* 1, 15–27.
- Cousseau, M. B. & Perrotta, R. G. (1998). *Peces marinos de Argentina. Biología, distribución, pesca.* Mar del Plata: Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP).

- Díaz de Astarloa, J. M. & Bolasina, S. N. (1992). Análisis estadístico de los caracteres morfométricos y merísticos de la pescadilla de red (*Cynoscion striatus*) en el area comprendida entre 34° y 39°30′ S. *Frente Marítimo* 11, 57–62.
- Duerr, H. P., Dietz, K. & Eichner, M. (2003). On the interpretation of age-intensity profiles and dispersion patterns in parasitological surveys. *Parasitology* **126**, 87–101.
- Guagliardo, S. E. (2003). Estudio sistemático, biológico y ecológico de los cestodes tripanorrincos (Eucestoda: Trypanorhyncha) parásitos de peces marinos en el area de Bahía Blanca. PhD Thesis, Universidad Nacional de Sur, Bahía Blanca, Argentina.
- Guégan, J.-F., Lambert, A., Lévêque, C., Combes, C. & Euzet, L. (1992). Can host body size explain the parasite species richness in tropical freshwater fishes? *Oecologia* 90, 197–204.
- Hoffmann, J. A. J., Núñez, M. N. & Piccolo, M. C. (1997). Características climáticas del Océano Atlántico Sudoccidental. In *El Mar Argentino y sus recursos pesqueros*, Tomo 1 (Boschi, E. E., ed.), pp. 163–193. Mar del Plata: Contribuciones INIDEP.
- Kennedy, C. R. & Bush, A. O. (1994). The relationship between pattern and scale in parasite communities: a stranger in a strange land. *Parasitology* **93**, 187–196.
- Lo, C. M., Morand, S. & Galtzin, R. (1998). Parasite diversity/host age and size relationship in three coral reef fishes from French Polynesia. *International Journal for Parasitology* 28, 1695–1708.
- López Cazorla, A. (1996). The food of *Cynoscion striatus* (Cuvier) (Pisces: Sciaenidae) in the Bahía Blanca areas, Argentina. *Fisheries Research* **28**, 371–379.
- López Cazorla, A. (2000). Age structure of the population of weakfisk Cynoscion guatucupa (Cuvier) in the Bahía Blanca waters, Argentina. Fisheries Research 46, 279–286.
- Luque, J. L., Mouillot, D. & Poulin, R. (2004). Parasite biodiversity and its determinants in coastal marine teleost fishes of Brazil. *Parasitology* **128**, 671–682.
- MacKenzie, K. (1983). Parasites as biological tags in fish populations studies. Advances in Applied Biology 7, 251–331.
- MacKenzie, K. (2002). Parasites as biological tags in population studies of marine organisms: an update. *Parasitology* **124**, S153–S163.
- MacKenzie, K. & Abaunza, P. (1998). Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods. *Fisheries Research* 38, 45–56.
- Magurran, A. E. (1988). *Ecological Diversity and its Measurement*. Princeton, NJ: Princeton University Press.
- Martorelli, S. R. (1992). Parasites of commercial shrimps and fishes in Argentine Sea: on the adult and metacercaria of *Opecoeloides feliciae* n. sp. *Memorias do Instituto Oswaldo Cruz* 87, 43–48.
- Martos, P. (1989). Synopsis on the reproductive biology and early life history of Engraulis anchoita, and related environmental conditions in Argentine waters. The physical environment. In Second IOC Workshop on Sardine/Anchovy Recruitment Project (SARP) in the Southwest Atlantic. Montevideo, Uruguay. Workshop Report No. 65 (Annex V), 1–2. Montivideo: Intergovernmental Oceanographic Commission, UNESCO.
- Navone, G. T., Sardella, N. H. & Timi, J. T. (1998). Larvae and adults of *Hysterothylacium aduncum* (Rudolphi, 1802) (Nematoda: Anisakidae) in fishes and crustaceans in the South West Atlantic. *Parasite* **5**, 127–136.
- Poulin, R. (2000). Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes. *Journal of Fish Biology* 56, 123–137. doi: 10.1006/jfbi.1999.1146
- Poulin, R. & Valtonen, E. T. (2002). The predictability of helminth community structure in space: a comparison of fish populations from adjacent lakes. *International Journal for Parasitology* 32, 1235–1243.
- Rohde, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65, 514–527.

<sup>© 2005</sup> The Fisheries Society of the British Isles, Journal of Fish Biology 2005, 67, 1603–1618

- Rohde, K. (1999). Latitudinal gradients in species diversity and Rapaport's rule revisited: a review of recent work and what can parasites teach us about the causes of gradients. *Ecography* 22, 593–613.
- Sabas, C. S. S. & Luque, J. L. (2003). Metazoan parasites of weakfish, Cynoscion guatucupa and Macrodon ancylodon (Osteichthyes: Sciaenidae), from the coastal zone of the State of Rio de Janeiro, Brazil. Revista Brasileira de Parasitologia Veterinária 12, 171–178.
- Santos, C. P., Timi, J. T. & Gibson, D. I. (2002). Diplectanum squamatum n. sp. (Monogenea: Diplectanidae) from the gills of Cynoscion guatucupa (Sciaenidae) in Southwest Atlantic waters. Systematic Parasitology 52, 199–204.
- Sardella, N. H. & Timi, J. T. (2004). Parasites of Argentine hake in the Argentine Sea: population and infracommunity structure as evidences for host stock discrimination. *Journal of Fish Biology* 65, 1472–1488. doi: 10.1111/j.1095-8649.2004.00572.x
  Sardella, N. H., Mattiucci, S., Timi, J. T., Bastida, R., Rodríguez, D. & Nascetti, G.
- Sardella, N. H., Mattiucci, S., Timi, J. T., Bastida, R., Rodríguez, D. & Nascetti, G. (2005). Corynosoma australe Johnston, 1937 and C. cetaceum Johnston & Best, 1942 (Acanthocephala: Polymorphidae) from marine mammals and fish in Argentinean waters: genetic differentiation and taxonomic status. Systematic Parasitology 61, 143–156.
- Timi, J. T. & Etchegoin, J. A. (1996). A new species of *Lernanthropus* (Copepoda: Lernanthropidae) parasite of *Cynoscion striatus* (Pisces: Sciaenidae), from Argentinean waters, and new records of *Lernanthropus trachuri*. *Folia Parasitologica* 43, 71–74.
- Timi, J. T., Navone, G. T. & Sardella, N. H. (1997). First report and biological considerations of *Dichelyne (Dichelyne) spinicaudatus* (Nematoda: Cucullanidae) parasite of *Cynoscions striatus* (Pisces: Sciaenidae) from the South West Atlantic Ocean. *Helminthologia* 34, 105–111.
- Timi, J. T., Sardella, N. H. & Navone, G. T. (2001). Parasitic nematodes of *Engraulis anchoita* Hubbs et Marini, 1935 (Pisces: Engraulidae) off the Argentine and Uruguayan coasts, South West Atlantic. *Acta Parasitologica* 46, 186–193.
- Vieira, P. Č. & Haimovici, M. (1997). Reprodução da pescada olhuda Cynoscion guatucupa, sin. C. striatus (Sciaenidae, Teleostei) no sul do Brasil. Atlântica 19, 133–144.
- Williams, H. H., MacKenzie, K. & McCarthy, A. M. (1992). Parasites as biological indicators of the population biology, migrations, diet, and phylogenetics of fish. *Reviews in Fish Biology and Fisheries* 2, 144–176.
- Zar, J. H. (1996). Biostatistical Analysis, 3rd edn. New Jersey: Prentice Hall Inc.