Homogeneity of parasite assemblages of *Dules auriga* (Serranidae) in hydrographically heterogeneous sites

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Parasite assemblages of *Dules auriga* are described for the first time from samples caught during research cruises in two localities of the Argentine–Uruguayan Common Fishing Zone (AUCFZ) and are compared with four additional samples collected by commercial catches from the same region. A total of 178 fish were examined and 13 parasite species were found. This showed low species richness, a condition observed in some other small benthic species at a low trophic level. The composition of the parasite fauna was similar to those found on other host species in the region, sharing the same set of dominant species with other sympatric fishes, which have been identified as both typical and as indicators of this ecoregion: *Grillotia carvajalregorum*, *Corynosoma australe* and *Hysterothylacium* sp. Multivariate similarity analyses at the infracommunity and the component community levels indicated that the two samples caught at different latitudes in the AUCFZ display almost identical parasite assemblages. This repeatability in assemblage structure was also observed across samples from commercial catches. The homogeneity of the parasite assemblages is considered to be an intrinsic property of fish inhabiting the AUCFZ, independent of their ecology and trophic level.

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Key words: Argentine Sea; metazoan parasites; serranids.

INTRODUCTION

The region of the northern Argentine Continental Shelf located between 33 and 37° S comprises a major proportion of the Argentine–Uruguayan Common Fishing Zone (AUCFZ). This region possesses complex hydrographical conditions, driven mainly by local freshwater inputs (Framiñan & Brown, 1996) and the influence of both modified subantarctic and subtropical shelf waters (Lucas *et al.*, 2005), but with the circulation patterns of water being mainly determined by wind and undergoing seasonal variations (Guerrero *et al.*, 1997; Palma *et al.*, 2004; Simionato *et al.*, 2004).

In this region, fish communities have been characterized as belonging to different assemblages along the environmental gradient that ranges from fresh to marine water. These fish assemblages differ significantly in their species composition that is characterized by distinct environmental conditions, with bottom salinity and temperature being the environmental variables found to be most strongly associated with

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differences observed in assemblage structure (García *et al.*, 2010). In spite of the dynamics and notable variability in the oceanographic conditions in this region, these fish assemblages show a remarkable degree of temporal persistence in species composition and geographical location, resulting in the occurrence of relatively stable boundaries (Jaureguízar *et al.*, 2006a; Lorenzo *et al.*, 2011). Consequently, according to the multispecies fisheries operating in the region, each assemblage could be considered a unit of management (Lorenzo *et al.*, 2011).

In northern Argentine waters, parasites have often been used as biological tags for the stock assessment of several fish species (Timi, 2007; Cantatore & Timi, 2015). In all cases, fishes inhabiting this region demonstrated consistent differences in parasite assemblage structure compared with other regions of the South West Atlantic, including the adjacent region of El Rincón, located in the southern coasts of the Buenos Aires province. Only two of these studies carried out, however, compared samples caught within the AUCFZ. These studies were based upon samples of the stripped weakfish *Cynoscion guatucupa* (Cuvier 1830) (Timi *et al.*, 2005) and the Brazilian flathead *Percophis brasiliensis* Quoy & Gaimard 1825 (Braicovich & Timi, 2008), which, although caught at the northern and southern limits of this region, revealed a similar composition and structure of parasite assemblages and were therefore considered to be single stocks. Given the variability in oceanographic conditions across the AUCFZ, this unexpected similarity of parasite assemblage is, however, in agreement with the homogeneity of fish host assemblages observed in the region. Nevertheless, both *C. guatucupa* and *P. brasiliensis* are highly vagile species, able to perform reproductive and ontogenetic migration (Jaureguízar *et al.*, 2006b; Barretto *et al.*, 2011) that can act to homogenize parasite assemblages across localities. Their ichthyophagous diet, composed mainly of migratory pelagic fishes such as Argentine anchovy *Engraulis anchoita* Hubbs & Marini 1935 and rough scad *Trachurus lathami* Nichols 1920 (Sardiña & López Cazorla, 2005; Milessi & Marí, 2012), is another factor that can promote the similarity of their parasite faunas at a regional level.

The homogeneity of parasite communities found in fishes inhabiting this region was investigated to determine if it is an intrinsic property of these assemblages by comparing the structure and composition of parasite communities in *Dules auriga* Cuvier 1829 from two localities of the AUCFZ. This host was selected in order to minimize the possible effect of factors that tend to homogenize parasite faunas, namely ichthyophagy and high vagility characteristic of previously studied hosts in the area. Information regarding the biology of *D. auriga* is scarce (Cussac & Molero, 1987; Militelli & Rodrigues, 2011), but from what little is known, this small benthic fish feeds mainly on benthic crustaceans, such as small prawns, crabs, amphipods and polychaetes (Cussac & Molero, 1987). These invertebrates display a restricted vagility in comparison with pelagic and migratory fishes, and are therefore expected to harbour and transmit parasite assemblages typical of their particular site of occurrence. On the other hand, serranids display sedentary habits and a high site fidelity (March *et al.*, 2010; Costa *et al.*, 2013), which makes them more suitable hosts for representing local exposure to infective stages.

Little is known about the parasite fauna of *D. auriga*, with the exception of a species of parasitic copepod (Braicovich & Timi, 2009) and some community descriptors previously published in an across-species comparative study which did not include data on individual species (Timi *et al.*, 2011). This work therefore provides the first qualitative and quantitative characterization of their parasite assemblages.

TABLE I. Composition of samples of *Dules auriga*

Sample	Locality code	Co-ordinates	Depth (m)	Date	n	Mean ± S.D. L_T (cm)
North AUCFZ	North	36° 07′−36° 28′ S, 54° 06′−55° 06′ W	56−63	7−8 November 2011	54	11·40 ± 0·67
South AUCFZ	South	38° 00′−38° 20′ S, 56° 18′−57° 16′ W	50−70	28−29 October 2011	48	13·33 ± 1·52
Mar del Plata 1	MdP1	Unknown	Unknown	31 March 2008	19	11·40 ± 1·60
Mar del Plata 2	MdP2	Unknown	Unknown	22 April 2008	24	10·70 ± 1·28
Mar del Plata 3	MdP3	Unknown	Unknown	6 June 2008	15	10·76 ± 1·92
Mar del Plata 4	MdP4	Unknown	Unknown	4 November 2008	18	11·58 ± 0·46

AUCFZ, Argentine−Uruguayan Common Fishing Zone; n, sample size; L_T, total length.

MATERIALS AND METHODS

FISH SAMPLES AND PARASITE INVENTORIES

Fish samples were obtained during a research cruise at two locations of the AUCFZ, in the outer region (shelf waters) of the la Plata Estuary in 2011 (Table I). Four additional samples of *D. auriga* taken as by-catch by commercial trawlers operating at Mar del Plata port in 2008 were included for comparative purposes (Table I). These samples were obtained from fish markets and consequently their geographical origin could not be determined. A total of 178 specimens of *D. auriga* were examined for parasites following standard procedures. Fish were either kept fresh or deep frozen at −18° C until examination. After thawing, fish were measured for total length (L_T, cm). Body surface, gills, branchial and body cavities, viscera (stomach, intestine, liver, gall bladder, spleen, heart, gonads and mesenteries), gas bladder, kidneys and musculature were examined with the aid of a stereoscopic microscope. The fish host nomenclature followed Eschmeyer (2014).

The prevalence and mean abundance (Bush *et al.*, 1997) were calculated for each parasite species in each sample, with 95% bootstrap C.I., following Rózsa *et al.* (2000), using Quantitative Parasitology 3.0 (Reiczigel *et al.*, 2013). The following community descriptors were calculated: mean total number of parasites in each infracommunity (total abundance) and species richness at component community and infracommunity level. Uninfected fish were excluded from multivariate analyses at the infracommunity level.

ANALYSES AT THE INFRACOMMUNITY LEVEL

Samples from the research cruise (north and south) were caught almost simultaneously, and consequently it is expected that their levels of similarity are not affected by the possible variability in parasite loads of short-lived species. Therefore, the differences in infracommunity structure between both samples were tested using a one-way permutational multivariate analysis of the variance (PERMANOVA, Anderson *et al.*, 2008) on the abundance values for all parasite species found, introducing host size as a covariable [analysis of covariance (ANCOVA) model]. The structures of parasite infracommunities between samples (1×2 factorial design, 'sample' as fixed factor) were compared, testing for main effects after 9999 permutations. Following Anderson *et al.* (2008), a permutation of residuals under a reduced model was used as method of permutation. A sequential sum of squares (type I SS) was applied because host length was introduced as a covariable and the samples were unbalanced (different numbers of fish examined by sample). The Bray−Curtis index was used as similarity measure. In case no effect of host length was detected by PERMANOVA, the procedure was repeated excluding this covariable and using unrestricted permutation of raw data.

Because PERMANOVA is sensitive to differences in multivariate dispersion between groups (*sensu* homogeneity of variances, which can inflate type I error even when centroids have identical locations), the same models were tested for differences in dispersion using the routine PERMDISP (Anderson *et al.*, 2008). Dispersions were measured as distance to the centroid, and each term in the analysis was tested using 9999 permutations.

Multivariate comparisons including the other four available samples (MdP1, MdP2, MdP3 and MdP4) required the selection of parasites to be included in the analyses. As these samples were caught at different seasons 3 years earlier than the samples of north and south, only long-lived parasites were considered as reliable for proper comparisons, diminishing any possible effect of season or other short-term temporal variations on parasite loads and allowing the locality effects to be more evident. This selection reduced the number of parasite species to eight, all of them larvae (one digenean, three cestodes, two nematodes and two acanthocephalans). According to the results of comparisons between both samples caught in 2011, all these fish were considered as a single sample. The PERMANOVA (1×5 factorial design, 'sample' as fixed factor) and PERMDISP analyses were repeated as in the previous section. When differences were detected by PERMANOVA, pair-wise comparisons were used to determine which samples differed.

Differences between infracommunities among samples were examined in more detail using canonical analysis of principal co-ordinates (CAPs) (Anderson & Willis, 2003; Anderson *et al.*, 2008), applied on the six samples. The potential for over-parameterization was prevented by choosing the number of axes (m) in the principal coordinates analysis (PCO) that maximized a leave-one-out allocation success to groups (Anderson & Robinson, 2003). CAPs were based on abundance data of long-lived parasites using a Bray–Curtis dissimilarity coefficient. To test for significant differences between infracommunities among the samples, a permutation trace test (sum of squared canonical eigenvalues) was applied; the *P*-value was obtained after 9999 permutations.

ANALYSES AT THE COMMUNITY LEVEL

Non-metric multidimensional scaling (MDS) (Clarke & Gorley, 2006) was performed to visualize possible geographic patterns in the composition of parasite assemblages across the six locations. MDS was conducted using the Bray–Curtis similarity index on prevalence data, restricted to long-lived species only. A hierarchical agglomerative clustering was applied to the component communities using group-average linking, and resemblance levels were overlaid on the MDS plot (Clarke & Gorley, 2006).

All multivariate analyses were implemented in PERMANOVA+ for PRIMER package (Anderson *et al.*, 2008).

RESULTS

GENERAL RESULTS

A high proportion of hosts were found parasitized in all samples (Tables II and III), although four individuals were uninfected, all of them from the commercial catches (Table IV). Fish caught in 2011 showed higher values of species richness, at both component community and infracommunity levels, as well as of total abundance (Table IV). A total of 4461 metazoan parasites belonging to 13 species were recorded in the whole sample, with an uneven distribution across samples in terms of both abundance and composition. Six of the 13 species were found in all samples, with *Grillotia carvajalregorum* and *Corynosoma australe* reaching the highest values of prevalence in all of them. *Hysterothylacium* sp. and *Hysterothylacium aduncum* also showed high values of prevalence in both samples caught in 2011, which shared nine of the 11 species found (Tables II and III).

TABLE II. Parasites of *Dules auriga* in samples from research cruises caught in 2011 in the north and south Argentine Sea, with data on its development stage, prevalence (p) and mean abundance (MA). Values in parentheses are 95% bootstrap c.i. estimated by 2000 bootstrap replicates

Parasite species	Site	Stage	North*		South*	
			p (%)	MA	p (%)	MA
Digenea						
Aponurus laguncula	S	Adult	3·7 (0·5–12·7)	>0·0 (0·0–0·09)	14·6 (6·1–27·8)	0·2 (0·0–0·3)
Bucephalidae gen sp.	G	Metacercaria	0·0	–	0·0	–
Cestoda						
Grillotia carvajalregorum	M	Plerocercus	100 (93·4–100)	28·6 (23·4–35·6)	97·9 (88·9–99·9)	24·8 (19·2–32·6)
Tentaculariidae gen. sp.	M	Plerocercoid	7·4 (2·1–17·9)	0·02 (0·0–0·1)	8·3 (2·3–20·0)	0·1 (0·0–0·2)
Unidentified cestode	M	Plerocercoid	29·6 (18·0–43·6)	1·8 (0·7–4·7)	31·2 (18·7–46·3)	0·8 (0·4–1·4)
Nematoda						
Cucullanus sp.	I	Adult	0·0	–	0·0	–
Dichelyne (Cucullanellus) szidati	I	Adult	1·8 (0·0–9·9)	>0·0 (0·0–0·1)	6·3 (1·3–17·2)	0·1 (0·0–0·1)
Hysterothylacium aduncum	M	Larva III	57·4 (43·2–70·8)	1·2 (0·9–1·6)	52·1 (32·7–66·7)	1·6 (1·1–2·3)
Hysterothylacium sp.	M	Larva III	61·1 (46·9–74·1)	1·6 (0·7–4·7)	56·3 (41·2–70·5)	1·6 (1·1–2·4)
Acanthocephala						
Corynosoma australe	M	Juvenile	98·1 (90·1–100)	8·3 (6·7–10·2)	89·6 (77·3–96·5)	4·8 (3·6–6·3)
Corynosoma cetaceum	M	Juvenile	0·0	–	4·2 (0·5–14·3)	>0·0 (0·0–0·1)
Copepoda						
Acanthochondria serrani	G	Adult	11·1 (4·2–22·6)	0·1 (0·1–1·2)	12·5 (41·2–70·5)	0·2 (0·0–0·3)
Isopoda						
Gnathia sp.	G	Praniza	1·8 (0·0–9·9)	>0·0 (0·0–0·06)	0·0	–

*, North and South Argentine-Uruguayan Common Fishing Zone; G, gills; I: intestine; M, mesenteries; S, stomach.

TABLE III. Parasites of *Dules auriga* in four commercial Mar del Plata (MdP) samples, caught in 2008 in the northern Argentine Sea, with data on its development stage, prevalence (*p*) and mean abundance (MA). Values in parentheses are 95% bootstrap c.i. estimated by 2000 bootstrap replicates

Parasite species	Site	Stage	MdP1		MdP2		MdP3		MdP4	
			p (%)	MA	*p* (%)	MA	*p* (%)	MA	*p* (%)	MA
Digenea										
Aponurus laguncula	S	Adult	5·3 (0·1–26·0)	0·05 (0·0–0·2)	12·5 (2·7–32·4)	0·4 (0·04–1·5)	6·7 (0·2–31·9)	0·1 (0·0–0·2)	11·1 (1·4–34·7)	0·2 (0·0–0·5)
Bucephalidae gen sp.	G	Metacercaria	0·0	–	4·2 (0·1–21·1)	0·04 (0·0–0·1)	0·0	–	0·0	–
Cestoda										
Grillotia carvajalregorum	M	Plerocercus	68·4 (43·4–87·4)	4·1 (1·3–9·5)	75·0 (53·3–90·2)	1·5 (1·0–2·1)	80·0 (51·9–95·7)	1·8 (1·1–2·4)	77·8 (52·4–93·6)	5·9 (2·1–19·5)
Tentaculariidae gen. sp.	M	Plerocercoid	0·0	–	0·0	–	0·0	–	5·6 (0·1–27·3)	0·1 (0·0–0·2)
Unidentified cestode	M	Plerocercoid	0·0	–	0·0	–	0·0	–	0·0	–
Nematoda										
Cucullanus sp.	I	Adult	0·0	–	0·0	–	6·7 (0·2–31·9)	0·1 (0·0–0·4)	5·6 (0·1–27·3)	0·3 (0·0–0·8)
Dichelyne (Cucullanellus) szidati	I	Adult	0·0	–	0·0	–	0·0	–	0·0	–
Hysterothylacium aduncum	M	Larva III	15·8 (3·4–39·6)	0·3 (0·1–0·7)	16·7 (4·7–37·4)	0·2 (0·04–0·3)	6·7 (0·2–31·9)	0·1 (0·0–0·2)	11·1 (1·4–34·7)	0·1 (0·0–0·2)
Hysterothylacium sp.	M	Larva III	15 (3·2–37·9)	0·2 (0·0–0·5)	16·7 (4·7–37·4)	0·2 (0·04–0·5)	20·0 (4·3–48·1)	0·3 (0·07–0·6)	22·2 (6·4–47·6)	0·3 (0·06–0·6)
Acanthocephala										
Corynosoma australe	M	Juvenile	94·7 (74–99·9)	4·8 (2·7–8·4)	75·0 (53·3–90·2)	3·0 (2·1–3·9)	60·0 (32·3–83·7)	3·3 (1·6–6·0)	72·2 (46·5–90·3)	1·8 (1·1–2·7)
Corynosoma cetaceum	M	Juvenile	0·0	–	0·0	–	6·7 (0·2–31·9)	0·1 (0·0–0·2)	5·6 (0·1–27·3)	0·1 (0·0–0·2)
Copepoda										
Acanthochondria serrani	G	Adult	21·1 (6·1–45·6)	0·3 (0·1–0·5)	25·0 (9·8–46·7)	0·3 (0·1–0·6)	26·7 (7·8–55·1)	0·3 (0·07–0·5)	5·6 (0·1–27·3)	0·1 (0·0–0·2)
Isopoda										
Gnathia sp.	G	Praniza	0·0	–	8·3 (1·0–27·0)	0·1 (0·0–0·2)	6·7 (0·2–31·9)	0·1 (0·0–0·2)	0·0	–

G, gills; I: intestine; M, mesenteries; S, stomach.

TABLE IV. Descriptors of parasite assemblages of *Dules auriga* in six samples of the northern Argentine Sea

Locality	Unparasitized hosts	Total species richness	Mean ± s.d. infracommunity species richness	Mean ± s.d. total abundance
North*	0	10	3·7 ± 1·1	41·7 ± 27·5
South*	0	10	3·7 ± 1·0	34·1 ± 26·0
MdP1	1	6	2·2 ± 1·2	9·6 ± 9·9
MdP2	1	8	2·3 ± 1·1	5·7 ± 3·8
MdP3	0	9	2·2 ± 1·0	6·1 ± 5·9
MdP4	2	9	2·2 ± 1·0	8·8 ± 14·7

*, North and South Argentine-Uruguayan Common Fishing Zone; MdP, Mar del Plata.

ANALYSES AT THE INFRACOMMUNITY LEVEL

The results of PERMANOVA analyses on all parasites of both samples, north and south, showed no effect of L_T on the response variables [$F_{1,98} = 1·27$, $P_{(perm)} > 0·05$]. After taking out the L_T as covariable, no significant variability was detected between both parasite assemblages [$F_{1,100} = 1·97$, $P_{(perm)} > 0·05$]. The results of PERMDISP showed that differences in multivariate dispersions of parasite infracommunities in terms of their deviations from centroids were not significant [$F_{1,100} = 1·96$, $P_{(perm)} > 0·05$].

The results of PERMANOVA on parasite abundance after selecting long-lived parasite species and pooling fish from samples of north and south as a single sample showed a strong effect of L_T on the response variables and therefore on the parasite community structure [$F_{1,162} = 18·48$, $P_{(perm)} < 0·01$]. The interaction of L_T with the samples showed that the nature of the relationship between the covariate and the multivariate response differed within different levels of the factor [$F_{4,162} = 2·40$, $P_{(perm)} < 0·01$]. Furthermore, taking into account the variations among samples due to L_T, significant variability was detected among the parasite assemblages [$F_{4,162} = 13·76$, $P_{(perm)} < 0·01$]. The pair-wise tests showed that there were no significant differences between pairs of samples caught in 2008 [all $P_{(perm)} > 0·05$]; however, significant differences were observed in all comparisons involving hosts caught in 2011 [all $P_{(perm)} < 0·01$].

A proportion of these differences can be attributed to differences in the multivariate dispersions of parasite infracommunities in terms of their deviations from centroids because the PERMDISP results were significant [$F_{4,167} = 3·92$, $0·01 < P_{(perm)} < 0·05$]. The pair-wise test, however, showed significant differences in the multivariate dispersions between only three pairs of samples, namely 2011-MdP1, 2011-MdP3 and MdP1-MdP3 [all $0·01 < P_{(perm)} < 0·05$].

The CAP showed significant differences among the samples (tr = 0·93, $P < 0·01$). The selected orthonormal PCO axes ($m = 6$) described 99·38% of the variation in the data cloud, with only 43·6% correct allocations. The two first canonical axes resulting from the CAP separated both groups of samples (fish caught in 2011 from those caught in 2008) (Fig. 1). Individual samples, however, were not identifiable within both groups. When vectors corresponding to the Spearman correlations of individual species were superimposed with the CAP axes (restricted to those species
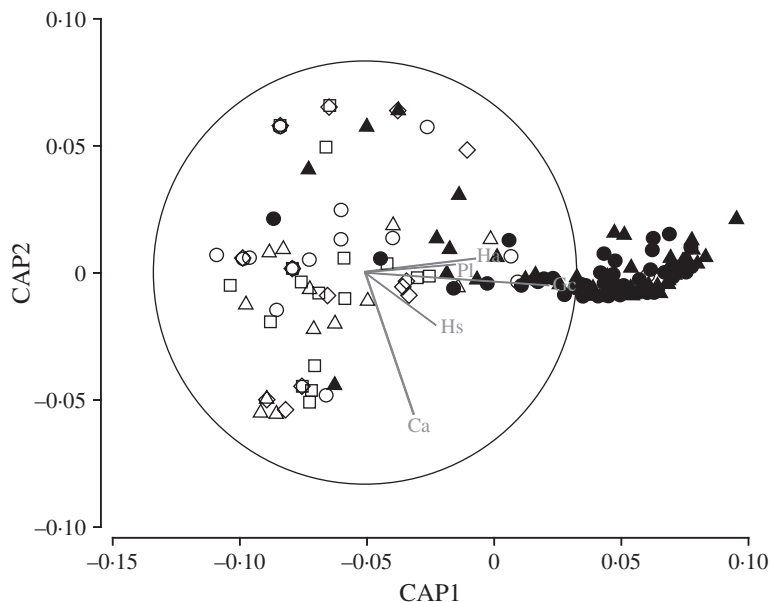
FIG. 1. Canonical analysis of principal co-ordinates (CAPs) biplot based on untransformed abundance data of long-lived parasites and Bray–Curtis dissimilarities in six samples of *Dules auriga* from the northern Argentine Sea. ●, north Argentine-Uruguayan Common Fishing Zone (AUCFZ) sample; ▲, south (AUCFZ) sample; △, sample Mar Del Plata (MdP)1; □, sample MdP2; ◇, sample MdP3; ○, sample MdP4. Vector overlay are Spearman correlations of parasite species with the CAP axes (restricted to those having $r > 0.3$): Ca, *Corynosoma australe*; Gc, *Grillotia carvajalregorum*; Ha, *Hysterothylacium aduncum*; Hs, *Hysterothylacium* sp.; Pl, unidentified plerocercoids.

with lengths >0.30), all species with the higher prevalence, namely *G. carvajalregorum*, both species of *Hysterothylacium* and the unidentified plerocercoids, were indicators of samples from the AUCFZ, whereas variability in the abundance of *C. australe* was mainly related to host dispersion of sample from 2008 along the CAP2. Cross validation of the results showed that low percentages of correctly allocated fish occurred in all samples (Table V), given mainly by misclassification of hosts to other samples caught in the same year. Indeed, when the correct allocations of fish to the year of capture were considered, the percentages increased notably (Table V), resulting in 88·2 and 87·1% of correctly classified fish from 2011 and 2008, respectively.

ANALYSES AT THE COMMUNITY LEVEL

The MDS and cluster analyses to the component communities (prevalence) revealed an apparent pattern of separation between samples caught in different years (Fig. 2), and the stress level (0·0) indicated a community composition substantially different from random. A 68·5% similarity was observed among all samples, but two groups were clearly separated at higher levels of similarity. The two samples caught during 2011 were clearly associated and showed the highest values of similarity (96·3%), whereas the four samples from 2008 clustered together at lower similarity values (86·0%), into two subgroups.

TABLE V. Discriminant analysis classification showing the number of *Dules auriga* classified in each sample using Bray–Curtis dissimilarity measures (rows correspond to group memberships), including the per cent of correctly classified fish to their sample or group (year)

	North	South	MdP1	MdP2	MdP3	MdP4	% (sample)	% (year)
North*	33	18	0	2	0	1	61·1	94·4
South*	19	20	1	0	2	6	41·7	81·3
MdP1	1	3	6	5	2	1	33·3	77·8
MdP2	0	0	4	11	4	3	50	100
MdP3	0	1	5	3	3	3	20	93·3
MdP4	1	3	0	7	2	2	13·3	69·2

*, North and South Argentine-Uruguayan Common Fishing Zone; MdP, Mar del Plata.

DISCUSSION

The parasite fauna of *D. auriga* found in this study comprised 13 metazoan species, which is a low richness value compared with other fish species studied in the region, although similar to some other small benthic species at a low trophic level (Lanfranchi *et al.*, 2009; Timi & Lanfranchi, 2009; Vales *et al.*, 2011). The parasite assemblages of *D. auriga* were, however, similar to those found on other host species in the region in terms of their composition, sharing the same set of dominant species with other sympatric fishes, namely *G. carvajalregorum*, *C. australe* and *Hysterothylacium* sp. These species have been identified as both typical and as indicators of this ecoregion (Pereira *et al.*, 2014). The presence of *H. aduncum* at high loads in the sampled fish is notable. At these latitudes, this parasite is more typical of the colder subantarctic
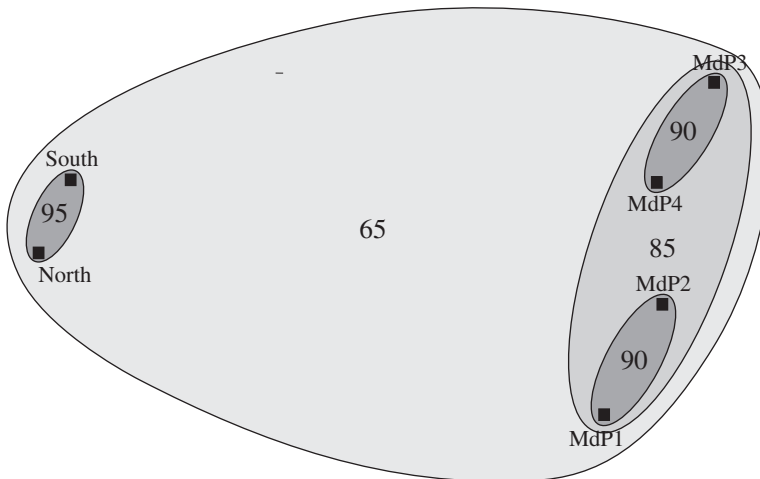

FIG. 2. Non-metric two-dimensional ordination plot and cluster analyses of parasite component communities of *Dules auriga* from six samples from the northern Argentine Sea using Bray–Curtis similarity based on untransformed parasite prevalence. Results of a hierarchical agglomerative clustering are overlaid on the multidimensional scaling plot with similarity levels represented by a grey scale and similarity values as numbers in the centre of grey areas. MdP, Mar del Plata.

waters associated with the Falkland (Malvinas) Current (Cantatore & Timi, 2015), that runs from the south-west along the continental slope.

The results of all the analyses carried out at both the infracommunity and the component community level indicated that the two samples caught at different latitudes in the AUCFZ during 2011 display almost identical parasite assemblages, despite differences being expected given the complex and variable oceanographic conditions of the region. In fact, hydrographical features are driven mainly by local freshwater inputs, in particular from the Río de la Plata discharge which drains the second largest South American basin, with a mean discharge of $22\,000\,\mathrm{m}^3\,\mathrm{s}^{-1}$ (Framiñan & Brown, 1996), and also by the advection of modified subantarctic shelf waters from the south (the Falkland, Malvinas, Current) and shelf subtropical waters from the north (the Brazil Current) (Lucas *et al.*, 2005). The circulation patterns of water are mainly determined by the winds (Palma *et al.*, 2004; Simionato *et al.*, 2004), with the balance between offshore and onshore winds affecting the extent of freshwater inflow into the continental shelf water (Guerrero *et al.*, 1997). Seasonal changes of dominant winds also produce a reversion of the outflow of fresh water towards northern Uruguayan coasts or to southern regions during cold and warm seasons, respectively (Guerrero *et al.*, 1997; Simionato *et al.*, 2004). The combination of these variable processes is expected to produce geographical heterogeneity at small geographical scale in parasite assemblages, a situation that was not observed.

The homogeneity recorded in the parasite assemblages of *D. auriga* caught during 2011 in this highly dynamic system could be explained by the existence of marine fronts in the region as a consequence of an almost permanent strong vertical stratification (Acha *et al.*, 2008), with fresh water flowing seaward on the surface while denser shelf waters intrude along the bottom towards shallower depth (Guerrero *et al.*, 1997; Piola *et al.*, 2000; Acha *et al.*, 2004). Specimens of *D. auriga* were caught at 50–70 m. Here, this sedentary species and the benthic invertebrates it consumes live in shelf waters where conditions are more stable and independent of the physical variations that occur on surface waters. Evidence of the influence of more saline shelf waters, and probably from subantarctic waters associated with the Falkland (Malvinas) Current, is also derived from the presence of *H. aduncum* at high loads. Eventually, under the influence of strong wind events, the water column can be partially or totally mixed, however, bottom fish assemblages tend not to be affected by this mixed condition (Acha *et al.*, 2008), and as such the parasite assemblages of bottom fish are found to be homogeneous across this broad region.

These results are in agreement with those of previous parasitological studies on other fish species (Timi, 2003; Timi *et al.*, 2005; Braicovich & Timi, 2008), which suggests that the homogeneity of parasite communities is an intrinsic property of fish assemblages in the region. As the distribution of parasites depends on the distribution of all the hosts involved in their life cycle, the occurrence of a homogeneous community of free living organisms should be expected in this ecosystem. Although no extensive studies have characterized the assemblages of free living organisms of this ecosystem, studies on some of their components, such as ichthyoplankton (Berasategui *et al.*, 2004), mesozooplankton (Marrari *et al.*, 2004), benthic organisms (Giberto *et al.*, 2004) and copepods (Berasategui *et al.*, 2006), have proved to be predictable in time and space, with definite limits determined by bathymetric gradients in water salinity and temperature.

The presence of significant differences in the structure and composition of parasite assemblages are typically used as evidence for discriminating fish stocks or populations

(Timi, 2007). In this sense, both samples caught in 2011 can, therefore, be considered as belonging to a single population of *D. auriga*. The same reasoning can be applied to the four samples analysed from commercial catches, given their similarity. On the other hand, the differences observed in assemblages between the two sample sets (2008 and 2011) could be indicative of the existence of distinct populations of *D. auriga* in the region. In fact, the differences observed are not considered as a result of short-term or seasonal variations in parasite burdens, as only long-lived species were included in the analyses. The possible effect of annual fluctuations in parasite transmission or in differential accumulation of parasites with age, however, cannot be disregarded as, at least partially, causes of the observed differences.

Unfortunately, the geographical provenience of commercial samples could not be determined, although two possible origins can be suggested, the AUCFZ and the southern region of El Rincón. Indeed, the coastal fleet operating from the port of Mar del Plata often changes its fishing stations depending on fishing success, resulting in vessels alternatively moving northwards to the central or north AUCFZ or sometimes southwards towards the region of El Rincón. The parasite communities of the fish inhabiting this southern region were different from those of the AUCFZ for all the host species studied so far (Cantatore & Timi, 2015). This could explain the observed differences between the two sample sets, if samples from 2008 were caught in El Rincón. Alternatively, the possibility that the samples came from the AUCFZ can neither be disregarded.

In the AUCFZ, *D. auriga* is a typical inhabitant of shelf waters at depths lower than 50 m (García *et al.*, 2010). A strong and almost permanent vertical salinity stratification is characteristic of this region with marine waters (saltier and denser) penetrating deeper into the estuary along the bottom, while fresh waters advance oceanward on the surface, forming a salt wedge (Guerrero *et al.*, 1997). The upstream reach of the salt wedge defines a bottom salinity front, whose location at about the isobath of 50 m is controlled by the topography (Guerrero *et al.*, 1997). Although fish from the research cruise were caught at deeper, cooler and more saline waters in the AUCFZ, it is possibly that those obtained from commercial catches were from shallower areas, probably at depths above the 50 m isobath point where *D. auriga* is mainly distributed and lives under different oceanographic conditions. This difference could be responsible for the variation observed between both groups of samples.

The variability of these physical conditions cannot explain the homogeneity of parasite assemblages of *D. auriga* caught at different dates in 2008 unless the captures were made in the same zone. Another possible explanation for the consistency observed in parasite assemblages across samples from 2008 is the cyclic (seasonal) occurrence of oceanographic changes (Acha *et al.*, 2008), which could result in homogeneous assemblages, especially considering that only long-lived parasites were included in the analyses.

In conclusion, this study showed evidence of the existence of at least two stocks of *D. auriga* in the region, the limits of which leaves scope for future studies including samples from El Rincón as well as from shallower and more estuarine waters of the AUCFZ. With respect to the samples obtained from the research cruise, the homogeneity of parasite assemblages observed from both sets of samples could be the result of the stable environmental conditions that dominate in deeper waters, whereas the cyclic nature of oceanographic heterogeneity in shallower waters could explain the homogeneity of commercial samples.

The data indicate that fish inhabiting northern waters of the Argentine Sea harbour parasite assemblages that display a remarkable homogeneity and repeatability which appears to be an intrinsic property of these assemblages independent of the host ecology and host trophic level.

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