Challenges for assessment of cohabiting stocks of argentine shortfin squid *Illex argentinus* using parasites as biological tags

María Paz Gutiérrez [a], Delfina Canel [a], Paola E. Braicovich [a,*], Ana L. Lanfranchi [a], Manuel M. Irigoitia [a], Marcela L. Ivanovic [b], Nicolás I. Prandoni [b], Beatriz Elena [b], Juan T. Timi [a]

[a] *Laboratorio de Ictioparasitología, Instituto de Investigaciones Marinas y Costeras (IIMyC), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Funes 3350, 7600, Mar del Plata, Argentina*

[b] *Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo N°1, Escollera Norte, 7600, Mar del Plata, Argentina*

ARTICLE INFO

ABSTRACT

The Argentine shortfin squid *Illex argentinus* is one of the most important commercial species for the Argentine fisheries. The understanding of its stock structure is therefore necessary to ensure fishery sustainability and, given the relevance of squids in the regional food web, for biodiversity conservation. An overlap between parasitology and fisheries lies in the use of parasites as biological tags to identify the stock composition of exploited resources, however, the efficiency of this methodology has been questioned for stock assessment in cephalopods. In this work, the value of parasite assemblages of *I. argentinus* to discriminate between the co-occurring summer spawning stock (SSS) and south patagonic stock (SPS) in a mixing area over the Patagonian continental shelf during summer was evaluated for two cohorts. Five shortfin squid samples corresponding to SSS and SPS were examined for metazoan parasites. The squid size affected the parasite assemblage similarities, conversely, no gender effect on the infracommunities was observed. Multivariate analysis evidenced similarity in parasite assemblage composition and structure between both stocks captured in the mixing area on the same date. This similarity was related to the presence of short-lived trophically transmitted parasites, which are associated with their recently consumed food items and, indirectly, to the oceanographic conditions. The same set of host and environmental variables were identified as the most probable causes of the temporal variability observed in parasite assemblages between SPS cohorts and even intra-cohort. Despite the value of parasites as tags for discriminating squid stocks may have little value when cohabiting stocks are analysed, their variability could serve as a valuable indicator of environmental conditions. The use of parasites as biological tags to discriminate stocks needs to be verified at different spatiotemporal scales, including samples from other non-sympatric stocks in the analyses.

1. Introduction

Several approaches are available to evaluate the stock structure of marine organisms, each having its advantages and constraints, nevertheless, it is advisable to adopt integrative multiple methods (Catalano et al., 2014; Cadrin et al., 2023). One of these approaches is the use of parasites as biological tags to identify the population structure or stock composition of exploited resources (Timi and Buchmann, 2023). According to Timi and MacKenzie (2015), the use of parasites as biological tags for stock discrimination is a well-established and extensive method

for fisheries management, being a successful tool for assessing ecological stocks, with worldwide increasing acceptance.

The fishery of the Argentine shortfin squid, *Illex argentinus*, is one of the most productive in the world, representing 16.4% of global squid catch in 2020, and sustaining the major cephalopod landings in the Southwest Atlantic (FAO, 2022). Furthermore, *I. argentinus* is a key component of the marine ecosystem, as it occupies a broad range of trophic positions in the food web (Ivanovic and Brunetti, 1994; Vidal and Haimovici, 1999; Ivanovic, 2000, 2010; Santos and Haimovici, 2000; Coll et al., 2013; Rosas-Luis et al., 2016; de la Chesnais et al.,

2019).

Due to the combination of the short life cycle, variable growth rates, and a strong relationship between reproduction and recruitment with environmental conditions, Argentine shortfin squid stocks may be highly volatile (Brunetti et al., 1998b; Torres Alberto et al., 2020), and consequently, their sustainable management is a challenge (Arkhipkin et al., 2021, 2023). Therefore, stock identification, which is crucial for sustainable exploitation and ecosystem conservation (Waluda et al., 2002), is as important as it is difficult and problematic.

Four spawning stocks have been proposed in the Argentine shelf and slope (35–52°S) based on size structure, reproductive seasons and ground, and migratory patterns (Brunetti et al., 1988; 1991, 1998c; Brunetti and Ivanovic, 1991). These four stocks have remained as management units for this resource until the present. However, such stock structure is complex due to the occurrence of extensive migrations of some stocks, which pose uncertainties regarding the demographic independence between some spawning groups. Reproductive and pre-reproductive squids of two of them, the summer spawning stock (SSS) and the south patagonic stock (SPS), respectively, concentrate over the Patagonian continental shelf from December to February (austral summer) (Brunetti et al., 1998a, 1998c). This is a highly dynamic oceanographic area, dominated by two seasonal frontal systems, whose latitudinal boundaries are variable (Acha et al., 2004; Cepeda et al., 2018). There, a highly productive area is established during spring and summer (Carreto et al., 1986; Acha et al., 2004), where the hyperiid amphipod *Themisto gaudichaudii*, the main prey of shortfin squid on the Patagonian shelf (Ivanovic and Brunetti, 1994; Ivanovic, 2000, 2010), reaches its highest biomass (Sabatini and Álvarez Colombo, 2001; Padovani et al., 2015; Cepeda et al., 2018). For these reasons, this oceanographic region meets the suitable conditions and food availability, as spawning and feeding grounds for SSS and SPS shortfin squids, respectively.

These two stocks are the most important units for the shortfin squid fishery, SPS representing around 80% of the total annual catches of the Argentine fleet (Brunetti et al., 1999; Torres Alberto et al., 2020). Summer spawning stock is limited to the inner-intermediate shelf between 43 and 48°S and comprises small squids that reach maturity at small sizes. They spawn during the summer, and the paralarvae are found together with the spent individuals (Brunetti, 1988; Brunetti et al., 1998b). In contrast, members of SPS display a unique large-scale migration from 35°S to 55°S, from shelf to slope, as they pass from feeding to reproductive areas, although the location of the latter is a subject of controversy (Brunetti, 1988; Haimovici and Alvarez Perez, 1990; Brunetti et al., 1998b, 1998c; Haimovici et al., 1998; Arkhipkin, 2013; Arkhipkin et al., 2015; Torres Alberto et al., 2020; Chemshirova et al., 2021). Shortfin squids of SPS are the only that migrate to the southern part of the Patagonian shelf to feed (Hatanaka, 1988; Ivanovic and Brunetti, 1994; Ivanovic, 2000, 2010). Therefore, during the austral summer, reproductive and spawning shortfin squids of the SSS cohabit with migrating pre-adult and maturing adults of SPS (Brunetti et al., 1998b; Haimovici et al., 1998; Prandoni, 2022) in a co-occurrence area located south of 43°S, approximately (Brunetti et al., 1998b; Avigliano et al., 2020), called mixing area (Avigliano et al., 2020) that comprises most of the distribution of SSS. Both stocks remain spatially segregated for the rest of the year due to the migratory behaviour of SPS. Previous studies on cephalopod hosts have highlighted not only the ecological niche of species as the main factor in determining their parasite fauna (Rodhouse, 2001; González et al., 2003; Tedesco et al., 2020), but also geographic factors would play an important role in parasite composition and abundance (Bower and Miyahara, 2005; Tedesco et al., 2020). Therefore, the use of parasite tags for stock assessment of squids must be evaluated in relation to these host-parasite particular characteristics. Additionally, sources of variability related to specific features of the parasite taxa must also be considered when analyzing the parasite assemblages of squids (Gutiérrez et al., 2023).

Despite the economic importance of *I. argentinus* for regional

fisheries and the available information on its parasite fauna (Threlfall, 1970; Nigmatullin, 1989; Hochberg, 1990; Nigmatullin and Shukhgál-ter, 1990; Sardella et al., 1990; Vidal and Haimovici, 1999; González and Kroeck, 2000; Cipriani et al., 2019; Gutiérrez et al., 2023), studies using its parasites as biological tags are still limited (González and Kroeck, 2000; Gutiérrez et al., 2023). Therefore, this methodology needs to be validated. A recent study evaluating inter- and intra-cohort variability in the structure of parasite assemblages of *I. argentinus* showed that parasite communities of three SSS consecutive cohorts were driven by recent changes in the shortfin squid habitats and diets (Gutiérrez et al., 2023). Such results highlight the potential value of parasites as indicators of different aspects of host biology, other than stock identity, such as temporal variability, applicable to other kinds of population studies. In the present work, samples of the SPS are analysed in a similar way, but also concerning those from SSS caught simultaneously. This was promoted not only by the significantly higher numerical importance of SPS in the squid fishery but also by the temporal syntopy of SPS and SSS in the mixing area. As mixed stocks are mostly differentiated by the gonadal maturity index (Brunetti et al., 1998b), and due to the continuous nature of this process, the assignment of those squids with intermediate development to a given stock could be difficult. Thus, parasites could be complementary tools for stock assignment by providing information on previous periods in the host life cycle or their areas of provenance.

The aims of this study are, therefore, i) to evaluate the temporal variability of parasites for a highly migrating stock (SPS) and ii) to assess inter-stock differences in the mixing area when SPS and SSS cohabit using parasite tags.

2. Materials and methods

2.1. Squid and parasites sampling

The data set comprises the parasite communities of 333 specimens of *I. argentinus* caught in December 2020 (5 stations), March 2021 (1 station), and February 2022 (3 stations) at the intermediate waters of
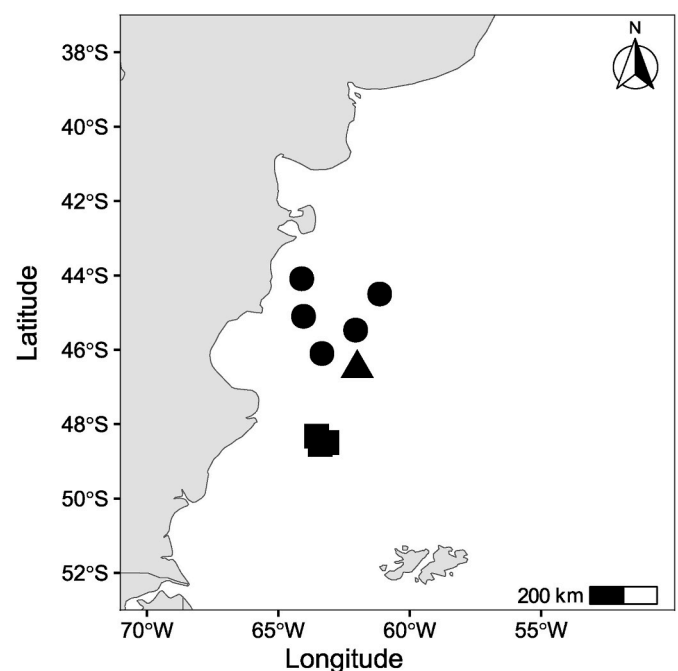

Fig. 1. Study area showing sampling sites of *Illex argentinus* in the Southwestern Atlantic. Circles: squids of SSS and SPS caught in December 2020; squares: squids of SSS and SPS caught in February 2022; triangle: squids of SPS caught in March 2021 which location is approximate.

central Patagonia (Fig. 1). Of these, 181 specimens belonging to SSS correspond to previously published data (Gutiérrez et al., 2023). Squids belonging to the same stock and date of capture were pooled as a single sample for analysis (Table 1). Samples from December and February were caught during research cruises of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). As these shortfin squids were caught at the mixing area, they were assigned to either the SPS (pre-reproductive individuals) or SSS (spawning and hatched individuals) according to sexual maturity index (Brunetti et al., 1998a, 1999). Shortfin squids from March, with maturity stages assimilable to SPS, were caught by commercial jigging vessels with a latitude/longitude estimated based on the fishing report. They were incorporated into the analysis as an additional sample representing older specimens (3 months approximately) of the same cohort to SPS Dec20, to test the extent of short-term variations in parasitism (Table 1). Shortfin squids were kept frozen in plastic bags at $-18\ °C$ until the examination. After thawing, each shortfin squid was measured for dorsal mantle length (ML, cm) and weighed. Moreover, they were cut along the ventral midline of the mantle, sexed and the gonadal maturity stage was determined according to Brunetti (1990) scale. The mantle, buccal cavity, and viscera (oesophagus, stomach, digestive caecum, intestine, digestive gland, gills, heart, kidney, and gonads) were thoroughly examined for parasites under a stereoscopic microscope. Each parasite was identified to the lowest taxonomic level possible, counted and the prevalence (percentage of the number of hosts infected divided by the number of hosts examined) and mean abundance (total number of a parasite species divided by the total number of hosts examined, including both infected and uninfected hosts) (Bush et al., 1997) were calculated for each species in each sample.

2.2. Similarity analysis

The ML was compared across samples by a 1-way univariate permutational analysis of the variance (PERMANOVA, Anderson et al., 2008) on Euclidean distances (1×5 factorial design, 'sample' as fixed factor), testing for main effects after 9999 permutations and subsequent post-hoc pairwise comparisons were made. Following Anderson et al. (2008), an unrestricted permutation of raw data was used as the method of permutation.

The similarity in parasite assemblages was computed at infracommunity level *sensu* Bush et al. (1997). Bray-Curtis index (based on abundances) and Jaccard index (based on presence/absence) were calculated for all possible pairs of hosts. Due to the large differences in parasite loads across parasite species, data were square root-transformed prior to all analyses in order to downweigh the importance of the most abundant species so that the less dominant species contribute to

Table 1
Composition of five samples of *Illex argentinus* belonging to the summer spawning stock (SSS) and the south patagonic stock (SPS).

Sample code	Date of capture	Latitude/ Longitude	N	Mantle length ±SD	Sample origin
SSS Dec20	December 2020	46° 5′– 44° 4′ S, 64° 6′– 62° 3′ W	160	20.39 ± 2.39	Gutiérrez et al. (2023)
SPS Dec20	December 2020	46° 5′– 44° 4′ S, 64° 6–62° 3′ W	60	19.50 ± 1.97	Present study
SPS Mar21	March 2021	46° 30′ S, 62° W[a]	40	29.00 ± 1.75	Present study
SSS Feb22	February 2022	48° 32′– 48° 19′ S, 63° 32′– 63° 25′ W	21	24.14 ± 2.28	Gutiérrez et al. (2023)
SPS Feb22	February 2022	48° 32′– 48° 19′ S, 63° 32′– 63° 25′ W	52	21.90 ± 2.17	Present study

N: number of shortfin squid examined; SD: standard deviation.
[a] Approximate location based on the fishing report.

determining similarity among samples (Clarke and Gorley, 2015).

The non-metric multidimensional scaling (nMDS) (Clarke and Gorley, 2015) analyses were performed between all infracommunities on both similarity matrices to evaluate if samples can be differentiated based on the abundance and composition, respectively, of their parasite assemblages. Their centroid differences were visualised by means of bootstrap averaging based on repeated resampling (with replacement, 75 iterations) from the original dataset (Clarke and Gorley, 2015). Differences between infracommunities among samples were further examined using canonical analysis of principal coordinates (CAP) (Anderson and Willis, 2003; Anderson et al., 2008). The potential for over-parameterization was prevented by choosing the number of PCO axes (m) that maximised a leave-one-out allocation success to groups (Anderson and Willis, 2003). To test for differences between infracommunities among the samples, a permutation 'trace' test (sum of squared canonical eigenvalues) was applied and a P-value was obtained after 9999 permutations. In order to estimate if shortfin squid parasite communities are useful indicators for assigning samples to their own stock, SPS Mar21 was included as a blind sample given its approximate fishing location, under the routine "add new samples'' in CAP (Anderson et al., 2008). Due to the unbalanced number of squids per group, the expected proportion of correct classification was calculated using the proportional chance criterion (Poulin and Kamiya, 2015).

Previous to comparative analyses across samples, the possible effect of sex on the structure of parasite infracommunities was tested in each sample by mean of a 1-way permutational multivariate analysis of the variance (PERMANOVA, Anderson et al., 2008) on Bray-Curtis and Jaccard similarities (1×2 factorial design, 'sex' as fixed factor). A sequential sum of squares (type I SS) was applied because samples were unbalanced (different numbers of male and female shortfin squids), testing for main effects after 9999 permutations. Following Anderson et al. (2008), an unrestricted permutation of raw data was used as the method of permutation.

The structure of parasite infracommunities was then compared between samples in a similar way under a 1×5 factorial design (samples as fixed factors). A sequential sum of squares (type I SS) was applied with host size as a covariate (ANCOVA model) because samples were unbalanced (different numbers of squids examined by sample) and testing for main effects after 9999 permutations, using Bray-Curtis and Jaccard indices. The ML was included as a covariate because of the known effect of size and age on shortfin squid parasite levels (Zelmer, 2014). Where differences were detected by PERMANOVA, pairwise comparisons were used to determine which samples differed. All similarity and distance measures, as well as multivariate analyses, were implemented in PRIMER V7 and PERMANOVA + for PRIMER package (Anderson et al., 2008; Clarke and Gorley, 2015).

3. Results

Significant differences in shortfin squid ML were found across the five samples ($F_{4,272}$: 122.08; $P_{perm}<0.01$) (Table 2), with pairwise comparisons showing significant differences for most pairs of samples (all $P_{perm}<0.01$, except for SSS Dec20-SPS Dec20, $P_{perm}<0.05$) (Fig. 2). In the three SPS samples, 88.2% of *I. argentinus* were found parasitised by at least one of the 10 parasite species, and 1428 individual parasites were recorded (Table 3). Only six of those taxa showed a prevalence >10% in at least one of the samples, with larval cestodes from the digestive tract dominating numerically the assemblages, representing 82.5% of the overall parasite load.

The bootstrap average-based nMDS ordination biplots of both Bray-Curtis (Fig. 3A) and Jaccard (Fig. 3B) were similar to each other and showed an apparent temporal separation pattern of samples between years, with a low level of stress (0.05). Shortfin squids obtained from research cruises, corresponding to different stocks captured in the same area, year and date, showed a greater overlap with each other but separated from samples of different years, especially along the first axis.

Table 2
PERMANOVA results of comparisons of mantle length, structure, and composition of parasite communities of *Illex argentinus* across five samples corresponding to the summer spawning stock (SSS) and the south patagonic stock (SPS). P-values were obtained after 9999 permutations.

Response variable	Source	d.f	SS	MS	*Pseudo* F	P (perm)
Univariate						
Mantle length	Sample	2	2639.7	659.92	122.08	0.0001
(Euclidean distance)	Residual	272	1470.3	5.4054		
	Total	276	4109.9			
Multivariate						
Infracommunity structure	Mantle length	1	79685	79685	31.018	0.0001
(Bray-Curtis similarity)	Sample	4	66195	16549	6.4419	0.0001
	Mantle length × sample	4	25585	6396.4	2.4899	0.0008
	Residual	267	$6.8591e^5$	2568.9		
	Total	276	$8.5737e^5$			
Infracommunity composition	Mantle length	1	55865	55865	20.326	0.0001
(Jaccard similarity)	Sample	4	63455	15864	5.7717	0.0001
	Mantle length × sample	4	25740	6435.1	2.3413	0.0007
	Residual	267	$7.3385e^5$	2748.5		
	Total	276	$8.7892e^5$			

d.f: degrees freedom; SS: sum of squares; MS: mean square; *Pseudo* F: pseudo-F statistic; P(perm): P-value associated with the test of a null hypothesis.
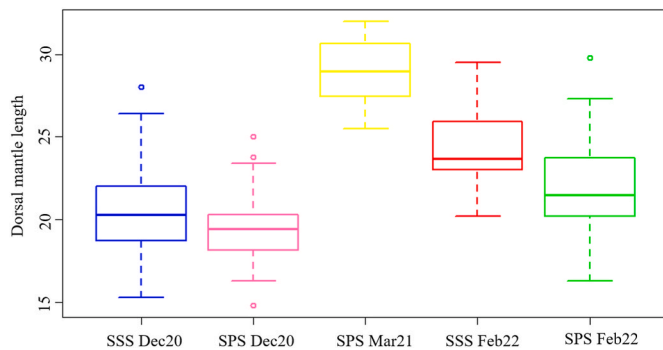

Fig. 2. Boxplot (median, minimum and maximum) of dorsal mantle length of *Illex argentinus* in five samples belonging to summer spawning stock (SSS) and the south patagonic stock (SPS). Outliers are represented by circles.

Thus, the pairs, SSS Dec20-SPS Dec20 and SSS Feb22-SPS Feb22, constituted homogeneous groups, respectively. Moreover, parasite assemblages of the sample whose location of capture is unknown, SPS Mar21, occupied a closer position to the samples SSS Feb22-SPS Feb22 on the right of the biplot but separated from shortfin squids SSS Dec20-SPS Feb20 (Fig. 3).

The CAP analysis based on abundances showed significant differences among samples (tr = 0.52471; P < 0.001). The selected orthonormal PCO axes (m = 5) described 95.08% of the variation in the data 'cloud', although the percentage of correct allocations into the pre-established groups was low (45.992%). The correct assignment by chance alone was 30.6%. Cross-validation results based on Bray-Curtis similarity (Table 4) showed that the samples SSS Feb22 and SSS Dec20 had the highest percentage of correctly allocated shortfin squids to their respective sample. Furthermore, SPS Feb22 showed a very low proportion of correctly allocated shortfin squids, most misclassified among SSS Feb22. When the Jaccard index was considered (Table 4) a similar pattern was observed, which showed significant differences between samples (tr = 0.47759; P < 0.001). The selected orthonormal PCO axes (m = 6) 99.7% of the variation in the data 'cloud', despite the low

Table 3
Prevalence (P), mean abundance (MA) with standard deviation (SD), site of infection, and stage of development of parasites of *Illex argentinus* in five samples corresponding to the summer spawning stock (SSS) and the south patagonic stock (SPS).

Parasite	Site	Stage	SSS Dec20		SPS Dec20		SPS Mar21		SSS Feb22		SPS Feb22	
			P	MA ± SD	P	MA ± SD	P	MA ±SD	P	MA ± SD	P	MA ± SD
Nematoda												
Anisakis sp.[a]	Co	L	10.6	0.3 ± 1.8	8.3	0.1 ± 0.3	32.5	0.6 ± 1.3	23.8	0.3 ± 0.6	9.6	0.1 ± 0.3
Hysterothylacium aduncum	Di	L/A	20	0.3 ± 0.6	21.7	0.2 ± 0.5	50	1.1 ± 2	14.3	0.2 ± 0.6	28.9	0.7 ± 1.4
Hysterothylacium aduncum	Co	L	3.8	0.04 ± 0.2	3.3	0.03 ± 0.2	5	0.05 ± 0.2	–	–	–	–
Rhabditida fam. gen. sp. 1[a]	Co	L	38.8	0.1 ± 1.7	35	0.8 ± 1.4	30	0.6 ± 1.1	9.5	0.1 ± 0.3	21.2	0.3 ± 0.6
Rhabditida fam. gen. sp. 2[a]	Co	L	–	–	1.7	0.02 ± 0.1	–	–	–	–	–	–
Cestoda												
Clistobothrium sp.	Di	P	30	1.5 ± 8.3	28.3	1.3 ± 6.3	100	10.4 ± 9.3	81	7.2 ± 11.5	84.5	4 ± 4.2
Dinobothrium sp. 1	Di	P	2.5	1.2 ± 14.4	1.7	0.03 ± 0.3	15	2.6 ± 11.5	57.1	9.2 ± 18.2	53.8	6.1 ± 21
Dinobothrium sp. 2	Di	P	–	–	–	–	5	0.4 ± 1.6	–	–	–	–
Lacistorhynchidae gen. sp.[a]	St	L	10.6	0.4 ± 1.9	5	0.4 ± 1.9	7.5	0.4 ± 1.7	–	–	–	–
Digenea												
Derogenes varicus s.s	Di	A	17.5	0.2 ± 0.5	10	0.1 ± 0.5	20	0.3 ± 0.9	14.3	0.2 ± 0.6	21.2	0.3 ± 0.5
Isopoda												
Gnathiidae gen. sp.	Ma	Pr	0.6	0.01 ± 0.1	–	–	–	–	–	–	–	–

[a] Long-lived parasite; A: adult; L: larvae; P: plerocercoide; Pr: praniza; Co: coelomic membrane; Di: digestive tract; Ma: mantle cavity; St: stomach wall.
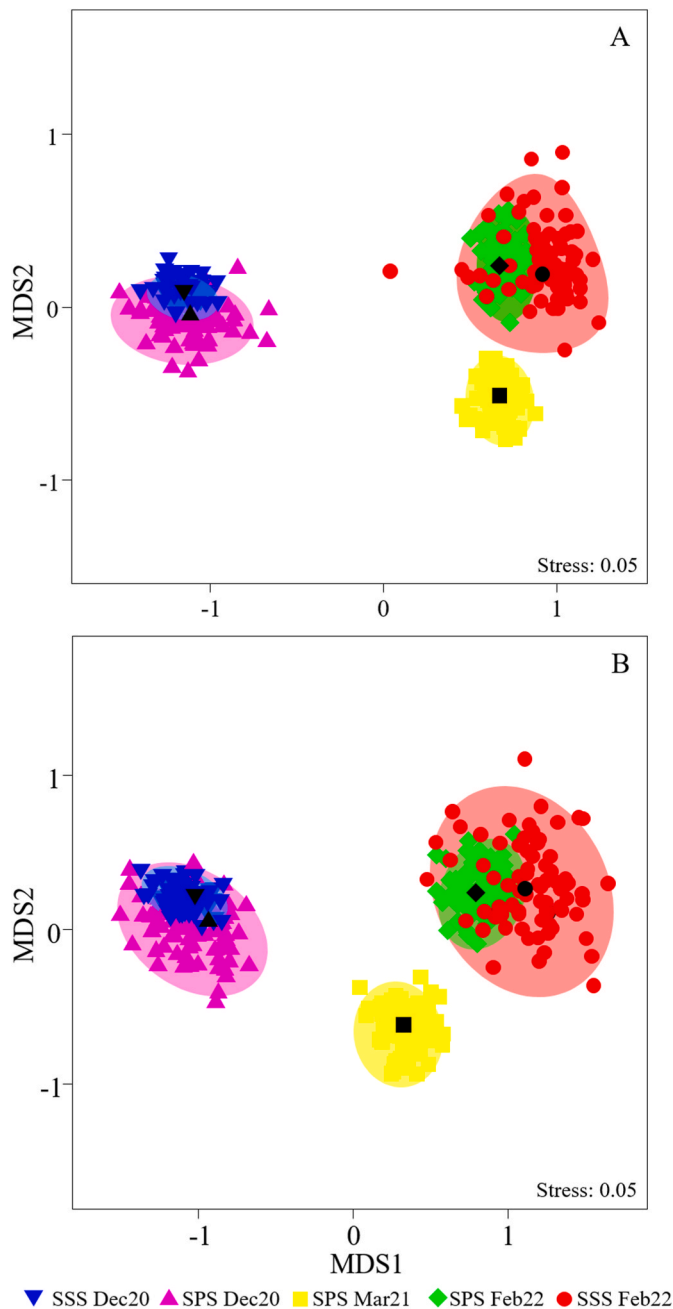
Fig. 3. Non-metric multi-dimensional scaling plot (nMDS) of bootstrap averages (75 repetitions) of parasite infracommunities of *Illex argentinus* distributed within 5 samples at intermediate waters of central Patagonia based on Bray-Curtis (A) and Jaccard (B) similarity of square root-transformed data. Individual repetitions are based on random draw and replacement of samples from the original dataset. Black symbols represent the overall centroids across all repetitions. Areas shaded in colours represent 95% confidence regions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 4

Results of the cross-validation of principal coordinate analysis (CAP) based on Bray-Curtis and Jaccard similarity (leave-one-out allocation of individual squid to one of 4 samples). Rows correspond to group memberships, including the percentage of correctly classified squid in their individual sample. Numbers in italics indicate the number of squids in four samples of spawning summer stock (SSS) and the south patagonic stock (SPS) correctly allocated to their own locality.

Original sample	SSS Dec20	SPS Dec20	SSS Feb22	SPS Feb22	Total	% (group)
Bray-Curtis						
SSS Dec20	*70*	40	3	10	123	56.91
SPS Dec20	25	*14*	1	4	44	31.82
SSS Feb22	2	0	*12*	6	20	60
SPS Feb22	2	9	26	*13*	50	26
SPS Mar21	1	15	5	19	40	–
Jaccard						
SSS Dec20	*71*	34	3	15	123	57.72
SPS Dec20	22	*12*	1	9	44	27.27
SSS Feb22	2	0	*10*	8	20	50
SPS Feb22	2	14	27	*7*	50	14
SPS Mar21	1	*25*	3	11	40	–

infracommunities, showed a significant effect of ML on both, the structure (Bray-Curtis similarity) and composition (Jaccard similarity) of assemblages, and an interaction between this variable and samples was observed (Table 2). Pairwise comparisons after taking into account the variations among samples due to shortfin squid length evidenced significant differences among most pairs of samples for Bray-Curtis and Jaccard indices (most $P_{perm} < 0.01$; comparison of SPS Mar21 with both SPS Dec20 and SSS Dec20, $0.01 < P_{perm} < 0.05$). However, the structure and composition of assemblages from the same year and date of capture, namely SSS-SPS Dec20 and SSS-SPS Feb22, were similar to each other ($P_{perm} > 0.05$). Furthermore, parasite infracommunities of SPS Mar21 were similar to those of SSS Feb22 in terms of composition and structure (both $P_{perm} > 0.05$).

4. Discussion

Parasitological examination of samples from the SPS of *I. argentinus* added only one new record for this host, a single larval nematode of the Order Rhabditida. Therefore, the infracommunities were predominantly characterised by larval gastrointestinal forms, and specifically cestodes plerocercoids dominated numerically the assemblages, as reported by Gutiérrez et al. (2023). As observed in that previous work, parasite loads were not affected by sex, due to, irrespective of gender, squids feed on the same set of available prey items and, therefore, have the same dietary composition or relative abundance (Prandoni, 2022).

As a consequence of their diet, and because most of their parasites are short-lived and trophically transmitted (Gutiérrez et al., 2023), squids of both stocks captured in the mixing area on the same date exhibited a similar structure and composition of their parasite assemblages. This was a recurrent pattern in both cohorts. The co-occurrence of both stocks is due to a combination of oceanographic features in this area that provide the appropriate thermal condition for SSS spawning, and the food availability together with the lower temperatures for the optimal growth of SPS (Brunetti, 1988; Brunetti et al., 1998c). By having complex life cycles involving more than one host, the composition of the communities of trophically transmitted parasites depends on the structure of the local food web (Marcogliese, 2002). Therefore, when SSS and SPS co-occur, they share a diet that is characterised by a very low diversity (Ivanovic and Brunetti, 1994; Ivanovic, 2000, 2010; Prandoni, 2022), determining compositionally homogeneous assemblages of trophically transmitted parasites. However, despite *I. argentinus* is an opportunistic and voracious predator, its diet appears to be influenced by the spatial-temporal availability of its prey, mostly *T. gaudichaudii*, and to a lesser extent, euphausiids (Ivanovic and Brunetti, 1994;

percentage of correct allocations (42.194%). Cross-validation results (Table 4) showed the highest proportion of correctly shortfin squids assignments in their own sample. Finally, shortfin squids corresponding to SPS Mar21 were mostly classified in their own stock, either SPS Feb22 (47.5%) or SPS Dec20 (62.5%) when Bray-Curtis and Jaccard indices were considered, respectively (Table 4).

No sex differences were observed in any sample (all $P_{perm} > 0.05$), except for SPS Mar21 which was not tested because it was mostly composed of females. The results of PERMANOVA analyses on

Ivanovic, 2000, 2010; Cepeda et al., 2018; Prandoni, 2022). This leads to temporally variable communities of short-lived parasites since their distribution depends on the population density of all the hosts involved in their life cycle (Marcogliese, 2003). Furthermore, almost all helminths found in *I. argentinus* are transient or short-lived because they live in the gut lumen of the host and persist for a few weeks (Nigmatullin and Shukhgálter, 1990; Timi and Buchmann, 2023). Consequently, transient parasites represent the food items consumed in recent times (Lester et al., 1985; Lester, 1990; Lester and MacKenzie, 2009) and, indirectly, the oceanographic conditions that affect the distribution of all hosts involved in their life cycles (Pascual et al., 2007; Cantatore and Timi, 2015), having in this case little value as indicators of stock identity. These findings are congruent with previous studies in other ommastrephid squids that yielded inconclusive results regarding their effectiveness as biological markers (Smith et al., 1981; Dawe et al., 1982; Pascual and Hochberg, 1996; Catalano et al., 2014), although none of these investigations has attempted to evaluate the capability of parasites for discriminating between sympatric stocks.

Concerning temporal comparisons, as already seen for SSS (Gutiérrez et al., 2023), SPS shortfin squids showed notorious differences between cohorts, and even intra-cohort among shortfin squids of different ages. Variability in host size across samples could be partly responsible for these differences, although temporal variations in physical and biological environmental conditions, that ultimately determine the distribution patterns of both parasites and their hosts (Timi, 2007), are also possible causes. It should be noted that shortfin squids caught during research cruises in different years were also separated by approximately 2 latitude degrees in position. As mentioned, spatially changing environmental conditions could be a source of variability in addition to the temporal one. Such geographical distance could be highly influential on shortfin squid biology since the development of *I. argentinus* is temperature-dependent at each stage of its life cycle. Indeed, it has been documented that a drop of approximately 1–2° in sea surface temperature could affect their migratory movements, especially for SPS (Moustahfid et al., 2021). Conversely, Nigmatullin and Shukhgálter (1990) observed an interannual similarity in the intensity of cestode infection, mainly *Clistobothrium* spp., suggesting a general stability of the trophic webs. The oceanographic dynamics prevailing in the mixing area, determined by the strong interannual variations in the position of its component seasonal fronts (Pisoni et al., 2015; Cepeda et al., 2018), are the main causes of the rather chaotic spatio-temporal patterns observed in parasite assemblages of *I. argentinus*, with possibly alternating variable periods of stability.

Similarly, the same causes can be attributed to the short-term processes rendering the differences between squids of the same cohort, sampled at a difference of three months, especially considering that such a period represents a significant proportion of their lifespan. That short-term variability, probably synergic with spatial one, given the imprecise location of the sample, is apparently capable of producing noticeable effects on parasite assemblages. As an example, squids of the SPS Mar21 were similar to a sample from another cohort and stock (SSS Feb22), but different to SPS Dic20 which were younger and smaller sized relatives. On the other hand, CAP analyses yielded different results mirroring the influence of host size. Despite being only slightly higher than the rate of correct classification expected by chance alone, differences in assignment success were also observed depending on the similarity index used, indicating disparate effects of host characteristics and environmental variability on the composition and abundance of the assemblages. As in the case of inter-stock differences, the transient condition of most parasites of shortfin squid enhanced the effect of temporal environmental variations.

Despite all studies that have attempted to understand the complex population structure of *I. argentinus* (Waluda et al., 2002; Avigliano et al., 2020; Chemshirova et al., 2023), to date the two stocks found its southern range of distribution remained identified as spawning stocks. A combination of traditional approaches (conventional tagging, phenotypic variation, parasites tags, and spatio-temporal fishing patterns) with advanced methods (genomics, electronic tagging, otolith, and statolith chemistry) have been recommended for population structure studies in marine fish and, to a lesser extent, in cephalopods (Carvalho and Nigmatullin, 1998; Semmens et al., 2007; Catalano et al., 2014; Cadrin et al., 2023). However, as in the case of parasites, some of these methodologies have also demonstrated limited congruence in delineating the stock of SSS and SPS in the mixing area (Roldán et al., 2014; Avigliano et al., 2020; Chemshirova et al., 2023), revealing that the structural complexity of these volatile host populations impacts negatively on the discriminating power of any methodology so far used.

Efforts to understand the stock structure should be intensified to design management strategies for *I. argentinus* that ensure sustainable fisheries and biodiversity conservation. According to previous research, multidisciplinary studies are the best approaches for such a purpose. However, the dominance of transient species and their high dependence on the variable regional environmental conditions make parasites of little value to discriminate between co-occurring stocks of *I. argentinus* in the mixing area. Consequently, their possible contribution to multidisciplinary studies needs to be verified at variable spatiotemporal scales, including samples from other stocks in the analyses.

A future challenge to the establishment of the stock composition in the Southwestern Atlantic is imposed by the ongoing climate change, whose effects have already been observed in the region and affecting several fisheries (Gianelli et al., 2019; Franco et al., 2020a), mostly through increases in water temperature (Johnson and Lyman, 2020; Franco et al., 2020b). Climate change also affects several physical processes that generate and maintain marine fronts (Acha et al., 2015), the ultimate determinants of the regional oceanographic dynamic, and their variations consequently may affect the abundance and distribution of parasites, influencing directly their free-living stages, or indirectly through effects on the physiology and ecology and abundance of their hosts (Lafferty and Kuris, 1999). Whereas the value of parasites as tags for discriminating squid stocks may remain of little value, their variability could serve as a valuable indicator of environmental conditions in this scenario of climate change, to which *I. argentinus* has been characterised as moderately sensitive (Gianelli et al., 2023).

CRediT authorship contribution statement

María Paz Gutiérrez: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Delfina Canel:** Writing – review & editing, Writing – original draft, Methodology. **Paola E. Braicovich:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Ana L. Lanfranchi:** Writing – review & editing, Methodology. **Manuel M. Irigoitia:** Writing – review & editing, Methodology. **Marcela L. Ivanovic:** Writing – review & editing, Resources. **Nicolás I. Prandoni:** Writing – review & editing, Resources. **Beatriz Elena:** Writing – review & editing, Resources. **Juan T. Timi:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

None.

References

Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M., Bava, J., 2004. Marine fronts at the continental shelves of austral South America: physical and ecological processes. J. Mar. Syst. 44, 83–105. https://doi.org/10.1016/j.jmarsys.2003.09.005.

Acha, E.M., Piola, A., Iribarne, O., Mianzan, H., 2015. Ecological Processes at Marine Fronts: Oases in the Ocean. Springer, Berlin. https://doi.org/10.1007/978-3-319-15479-4.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. Plymouth: PRIMER-E.

Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–525. https://doi.org/10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2.

Arkhipkin, A., 2013. Squid as nutrient vectors linking Southwest Atlantic marine ecosystems. Deep Sea Res. Part II Top. Stud. Oceanogr. 95, 7–20. https://doi.org/10.1016/j.dsr2.2012.07.003.

Arkhipkin, A.I., Hendrickson, L.C., Payá, I., Pierce, G.J., Roa-Ureta, R.H., Robin, J.P., Winter, A., 2021. Stock assessment and management of cephalopods: advances and challenges for short-lived fishery resources. ICES J. Mar. Sci. 78, 714–730. https://doi.org/10.1093/icesjms/fsaa038.

Arkhipkin, A.I., Nigmatullin, C.M., Parkyn, D.C., Winter, A., Csirke, J., 2023. High seas fisheries: the Achilles' heel of major straddling squid resources. Rev. Fish Biol. Fish. 33, 453–474. https://doi.org/10.1007/s11160-022-09733-8.

Arkhipkin, A., Rodhouse, P.G., Pierce, G.J., Sauer, W., Sakai, M., Allcock, L., Arguelles, J., Bower, J.R., Castillo, G., Ceriola, L., Chen, C.S., Chen, X., Diaz-Santana, M., Downey, N., González, A.F., Amores, J.G., Green, C.P., Guerra, A., Hendrickson, L.C., Ibáñez, C., Ito, K., Jereb, P., Kato, Y., Katugin, O.N., Kawano, M., Kidokoro, H., Kulik, V.V., Laptikhovsky, V.V., Lipinski, M.R., Liu, B., Mariátegui, L., Marin, W., Medina, A., Miki, K., Miyahara, K., Moltschaniwskyj, N., Moustahfid, H., Nabhitabhata, J., Nanjo, N., Nigmatullin, C.M., Ohtani, T., Pecl, G.J., Perez, A.A., Piatkowski, U., Saikliang, P., Salinas-Zavala, C.A., Steer, M., Tian, Y., Ueta, Y., Vijai, D., Wakabayashi, T., Yamaguchi, T., Yamashiro, C., Yamashita, N., Zeidberg, L. D., 2015. World squid fisheries. Rev. Fish. Sci. Aquac. 23, 92–252. https://doi.org/10.1080/23308249.2015.1026226.

Avigliano, E., Ivanovic, M.L., Prandoni, N., Méndez, A., Pisonero, J., Volpedo, A.V., 2020. Statolith chemistry as a stock tag in the Argentine shortfin squid *Illex argentinus*. Reg. Stud. Mar. Sci. 38, 102355 https://doi.org/10.1016/j.rsma.2020.101355.

Bower, J.R., Miyahara, K., 2005. The diamond squid (*Thysanoteuthis rhombus*): a review of the fishery and recent research in Japan. Fish. Res. 73, 1–11. https://doi.org/10.1016/j.fishres.2005.01.020.

Brunetti, N.E., 1988. Contribución al conocimiento biológico-pesquero del calamar argentino (Cephalopoda, Ommastrephidae, *Illex argentinus*). Facultad de Ciencias Exactas y Naturales, Museo. Universidad Nacional de La Plata 135. PhD Thesis.

Brunetti, N.E., 1990. Escala para la identificación de estadios de madurez sexual del calamar (*Illex argentinus*). Frente Marítimo 7, 45–51.

Brunetti, N.E., Ivanovic, M.L., 1991. Morfología y morfometría de los estatolitos del calamar (*Illex argentinus*). Frente Marítimo 9, 53–61.

Brunetti, N.E., Ivanovic, M.L., Elena, B., 1998a. Calamares omastréfidos (cephalopoda, ommastrephidae). In: Boschi, E.E. (Ed.), Los moluscos de interés pesquero. Cultivos y estrategias reproductivas de bivalvos y equinoideos. Instituto Nacional de Investigación y Desarrollo Pesquero INIDEP, Mar del Plata, pp. 37–68.

Brunetti, N.E., Ivanovic, M.L., Rossi, G.R., Elena, B., Pineda, S.E., 1998b. Fishery biology and life history of *Illex argentinus*. In: Okutani, T. (Ed.), Large Pelagic Squids. JAMARC, pp. 217–231.

Brunetti, N.E., Elena, B., Rossi, G.R., Ivanovic, M.L., Aubone, A., Guerrero, R., Benavides, H., 1998c. Summer distribution, abundance and population structure of *Illex argentinus* on the Argentine shelf in relation to environmental features. Afr. J. Mar. Sci. 20, 175–186. https://doi.org/10.2989/025776198784126386.

Brunetti, N.E., Ivanovic, M.L., Louge, E.B., Christiansen, H.E., 1991. Estudio de la biología reproductiva y de la fecundidad en dos subpoblaciones del calamar (*Illex argentinus*). Frente Marítimo 8, 73–84.

Brunetti, N.E., Ivanovic, M.L., Sakai, M., 1999. Calamares de importancia comercial en la Argentina. Biología, distribución, muestreo biológico. INIDEP, Mar del Plata, Argentina 45.

Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis, et al. Revisited. J. Parasitol. 83, 575–583. https://doi.org/10.2307/3284227.

Cadrin, S.X., Goethel, D.R., Berger, A., Jardim, E., 2023. Best practices for defining spatial boundaries and spatial structure in stock assessment. Fish. Res. 262, 106650 https://doi.org/10.1016/j.fishres.2023.106650.

Cantatore, D.M., Timi, J.T., 2015. Marine parasites as biological tags in South American Atlantic waters, current status and perspectives. Parasitology 142, 5–24. https://doi.org/10.1017/S0031182013002138.

Carreto, J.I., Benavides, H.R., Negri, R.M., Glorioso, P.D., 1986. Toxic red-tide in the Argentine Sea. Phytoplankton distribution and survival of the toxic dinoflagellate *Gonyaulax excavata* in a frontal area. J. Plankton Res. 8, 15–28. https://doi.org/10.1093/plankt/8.1.15.

Carvalho, G.R., Nigmatullin, ChM., 1998. Stock structure analysis and species identification. In: Rodhouse, P., Dawe, E., O'Dor, R. (Eds.), Squid Recruitment Dynamics. The Genus *Illex* as a Model, the Commercial *Illex* Species and Influences on Variability, vol. 376. FAO fisheries technical papers, Rome, pp. 199–232.

Catalano, S.R., Whittington, I.D., Donnellan, S.C., Gillanders, B.M., 2014. Parasites as biological tags to assess host population structure: guidelines, recent genetic advances and comments on a holistic approach. Int. J. Parasitol. Parasites Wildl. 3, 220–226. https://doi.org/10.1016/j.ijppaw.2013.11.001.

Cepeda, G.D., Temperoni, B., Sabatini, M.E., Viñas, M.D., Derisio, C.M., Santos, B.A., Antacli, J.C., Padovani, L.N., 2018. Zooplankton communities of the Argentine continental shelf (SW atlantic, ca. 34°–55°S), an overview. In: Hoffmeyer, M., Sabatini, M., Brandini, F., Calliari, D., Santinelli, N. (Eds.), Plankton Ecology of the Southwestern Atlantic. Springer, Cham, pp. 171–199. https://doi.org/10.1007/978-3-319-77869-3_9.

Chemshirova, I., Arkhipkin, A., Shaw, P.W., McKeown, N.J., 2023. Integrated statolith and genomic analysis reveals high connectivity in the nektonic squid *Illex argentinus*: implications for management of an international cephalopod fishery. J. Mar. Sci. 80, 1976–1990. https://doi.org/10.1093/icesjms/fsad128.

Chemshirova, I., Hoving, H.J., Arkhipkin, A., 2021. Temperature effects on size, maturity, and abundance of the squid *Illex argentinus* (Cephalopoda, Ommastrephidae) on the Patagonian Shelf. Estuar. Coast Shelf Sci. 255, 107343 https://doi.org/10.1016/j.ecss.2021.107343.

Cipriani, P., Giulietti, L., Palomba, M., Mattiucci, S., Bao, M., Levsen, A., 2019. Occurrence of larval ascaridoid nematodes in the Argentinean short-finned squid *Illex argentinus* from the Southwest Atlantic Ocean (off Falkland Islands). Int. J. Food Microbiol. 297, 27–31. https://doi.org/10.1016/j.ijfoodmicro.2019.02.019.

Clarke, K.R., Gorley, R.N., 2015. PRIMER V7: User Manual/Tutorial. PRIMER-E Ltd, Plymouth.

Coll, M., Navarro, J., Olson, R.J., Christensen, V., 2013. Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep Sea Res. Part II Top. Stud. Oceanogr. 95, 21–36. https://doi.org/10.1016/j.dsr2.2012.08.020.

Dawe, E.G., Mercer, M.C., Threlfall, W., 1982. On the stock identity of short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic. NAFO Sci. Coun. Stud. 7, 77–86.

de la Chesnais, T., Fulton, E.A., Tracey, S.R., Pecl, G.T., 2019. The ecological role of cephalopods and their representation in ecosystem models. Rev. Fish Biol. Fish. 29, 313–334. https://doi.org/10.1007/s11160-019-09554-2.

FAO, 2022. El estado mundial de la pesca y la acuicultura 2022. Hacia la transformación azul. FAO, Roma. https://doi.org/10.4060/cc0461es.

Franco, B.C., Combes, V., González Carman, V., 2020a. Subsurface ocean warming hotspots and potential impacts on marine species: the Southwest South Atlantic Ocean case study. Front. Mar. Sci. 7–563394. https://doi.org/10.3389/fmars.2020.563394.

Franco, B.C., Defeo, O., Piola, A.R., Barreiro, M., Yang, H., Ortega, L., Gianelli, I., Castello, J.P., Vera, C., Buratti, C., Pájaro, M., Pezzi, L.P., Möller, O.O., 2020b. Climate change impacts on the atmospheric circulation, ocean, and fisheries in the Southwest South Atlantic Ocean: a review. Clim. Change 162, 2359–2377. https://doi.org/10.1007/s10584-020-02783-6.

Gianelli, I., Orlando, L., Cardoso, L.G., Carranza, A., Celentano, E., Correa, P., de la Rosa, A., Doño, F., Haimovici, M., Horta, S., Jaureguizar, A.J., Jorge-Romero, G., Lercari, D., Martínez, G., Pereyra, I., Silveira, S., Vögler, R., Defeo, O., 2023. Sensitivity of fishery resources to climate change in the warm-temperate Southwest Atlantic Ocean. Reg. Environ. Change 23, 49. https://doi.org/10.1007/s10113-023-02049-8.

Gianelli, I., Ortega, L., Marín, Y., Piola, A.R., Defeo, O., 2019. Evidence of ocean warming in Uruguay's fisheries landings: the mean temperature of the catch approach. Mar. Ecol. Prog. Ser. 625, 115–125. https://doi.org/10.3354/meps13035.

González, R.A., Kroeck, M.A., 2000. Enteric helminths of the shortfin squid *Illex argentinus* in San Matías Gulf (Argentina) as stock discriminants. Acta Parasitol. 45, 89–93.

González, A.F., Pascual, S., Gestal, C., Abollo, E., Guerra, A., 2003. What makes a cephalopod a suitable host for parasite? The case of Galician Waters. Fish. Res. 60, 177–183. https://doi.org/10.1016/S0165-7836(02)00059-0.

Gutiérrez, M.P., Canel, D., Timi, J.T., Braicovich, P.E., Lanfranchi, A.L., Irigoitia, M.M., Ivanovic, M.L., Prandoni, N.I., Elena, B., 2023. Parasite assemblages in volatile host stocks: inter- and intra-cohort variability restrict their value as biological tags for squid stock assessment. Parasitology 150, 1254–1262. https://doi.org/10.1017/S0031182023001051.

Haimovici, M., Álvarez Pérez, J.A.A., 1990. Distribution and sexual maturation of the Argentinean squid, *Illex argentinus* off Southern Brazil. Sci. Mar. 54, 179–185.

Haimovici, M., Brunetti, N.E., Rodhouse, P.G., Csirke, J., Leta, R.H., 1998. Chapter 3: Illex argentinus. In: Rodhouse, P.G., Dawe, E.G., O'Dor, R.K. (Eds.), Squid Recruitment Dynamics, the Genus *Illex* as a Model, the Commercial *Illex* Species and Influences on Variability. FAO, Rome, pp. 27–58.

Hatanaka, H., 1988. Feeding migration of short-finned squid *Illex argentinus* in the waters off Argentina. Nippon Suisan Gakk 54, 1343–1349. https://doi.org/10.2331/suisan.54.1343.

Hochberg, F.G., 1990. Diseases caused by protistans and metazoans. In: Kinne, O. (Ed.), Diseases of Marine Animals. Biologische Anstalt Helgoland, Hamburg, Germany, pp. 47–200.

Ivanovic, M.L., 2000. Alimentación y relaciones tróficas del calamar *Illex argentinus* en el ecosistema pesquero. Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata 251. PhD Thesis.

Ivanovic, M.L., 2010. Alimentación del calamar *Illex argentinus* en la región patagónica durante el verano de los años 2006, 2007 y 2008. Rev. Invest. Desarro. Pesq. 20, 51–63.

Ivanovic, M.L., Brunetti, N.E., 1994. Food and feeding of *Illex argentinus*. Antarct. Sci. 6, 185–193.

Johnson, G.C., Lyman, J.M., 2020. Warming trends increasingly dominate global ocean. Nat. Clim. Change 10, 757–761. https://doi.org/10.1038/s41558-020-0822-0.

Lafferty, K.D., Kuris, A.M., 1999. How environmental stress affects the impact of parasites. Limnol. Oceanogr. 44, 925–931. https://doi.org/10.4319/lo.1999.44.3_part_2.0925.

Lester, R.J.G., 1990. Reappraisal of the use of parasites for fish stock identification. Austral. J. Mar. Freshw. Res. 41, 855–864. https://doi.org/10.1071/MF9900855.

Lester, R.J.G., Barnes, A., Habib, G., 1985. Parasites of skipjack tuna: fishery implications. Fish. Bull. 83, 343–356.

Lester, R.J.G., MacKenzie, K., 2009. The use and abuse of parasites as stock markers for fish. Fish. Res. 97, 1–2. https://doi.org/10.1016/j.fishres.2008.12.016.

Marcogliese, D.J., 2002. Food webs and the transmission of parasites to marine fish. Parasitology 124, 83–99. https://doi.org/10.1017/S003118200200149X.

Marcogliese, D.J., 2003. Food webs and biodiversity: are parasites the missing link? J. Parasitol. 89, 106–113.

Moustahfid, H., Hendrickson, L.C., Arkhipkin, A., Pierce, G.J., Gangopadhyay, A., Kidokoro, H., Markaida, U., Nigmatullin, C., Sauer, W.H., Jereb, P., Pecl, G., de la Chesnais, T., Ceriola, L., Lazar, N., Firmin, C.J., Laptikhovsky, V., 2021. Ecological-fishery forecasting of squid stock dynamics under climate variability and change: review, challenges, and recommendations. Rev. Fish. Sci. Aquac. 29, 682–705. https://doi.org/10.1080/23308249.2020.1864720.

Nigmatullin, C.M., 1989. Las especies de calamar más abundantes del Atlántico sudoccidental y sinopsis sobre la ecología del calamar (*Illex argentinus*). Frente Marítimo 5, 71–81.

Nigmatullin, C.M., Shukhgálter, O.A., 1990. Helmintofauna y aspectos ecológicos de las relaciones parasitarias del calamar (*Illex argentinus*) en el Atlántico Sudoccidental. Frente Marítimo 7, 57–68.

Padovani, L.N., Viñas, M.D., Sabatini, M.E., Álvarez Colombo, G., Mianzan, H.W., 2015. Aspectos poblacionales de *Themisto gaudichaudii*, una especie clave en la trama trófica de la plataforma patagónica austral. Rev. Invest. Desarro. Pesq. 26, 69–88.

Pascual, S., González, Á.F., Guerra, Á., 2007. Parasite recruitment and oceanographic regime: evidence suggesting a relationship on a global scale. Biol. Rev. 82, 257–263. https://doi.org/10.1111/j.1469-185X.2007.00008.x.

Pascual, S., Hochberg, F.G., 1996. Marine parasites as biological tags of cephalopod hosts. Parasitol. Today Off. 12, 324–327. https://doi.org/10.1016/0169-4758(96)40004-7.

Pisoni, J.P., Rivas, A.L., Piola, A.R., 2015. On the variability of tidal fronts on a macrotidal continental shelf, Northern Patagonia, Argentina. Deep Sea Res. Part II Top. Stud. Oceanogr. 119, 61–68. https://doi.org/10.1016/j.dsr2.2014.01.019.

Poulin, R., Kamiya, T., 2015. Parasites as biological tags of fish stocks: a meta-analysis of their discriminatory power. Parasitology 142, 145–155. https://doi.org/10.1017/S0031182013001534.

Prandoni, N.I., 2022. Alimentación del calamar argentino (*Illex argentinus*) en la región patagónica durante febrero de 2022. Inf. Invest. INIDEP 098/22, 14.

Rodhouse, P.G., 2001. Managing and forecasting squid fisheries in variable environments. Fish. Res. 54, 3–8. https://doi.org/10.1016/S0165-7836(01)00370-8.

Roldán, M.I., Planella, L., Heras, S., Fernández, M.V., 2014. Genetic analyses of two spawning stocks of the short-finned squid (*Illex argentinus*) using nuclear and mitochondrial data. C. R. Biol. 337, 503–512. https://doi.org/10.1016/j.crvi.2014.07.008.

Rosas-Luis, R., Navarro, J., Sánchez, P., Del Río, J.L., 2016. Assessing the trophic ecology of three sympatric squid in the marine ecosystem off the Patagonian Shelf by combining stomach content and stable isotopic analyses. Mar. Biol. Res. 12, 402–411. https://doi.org/10.1080/17451000.2016.1142094.

Sabatini, M.E., Álvarez Colombo, G.L., 2001. Seasonal pattern of zooplankton biomass in the Argentinian shelf off Southern Patagonia (45°–55°S). Sci. Mar. 65, 21–31. https://doi.org/10.3989/scimar.2001.65n121.

Santos, R.A., Haimovici, M., 2000. The Argentine short-finned squid *Illex argentinus* in the food webs of southern Brazil. Sarsia 85, 49–60. https://doi.org/10.1080/00364827.2000.10414554.

Sardella, N.H., Roldán, M.I., Tanzola, D., 1990. Helmintos parásitos del calamar (*Illex argentinus*) en la subpoblación Bonaerense-Norpatagónica. Frente Marítimo 7, 53–56.

Semmens, J.M., Pecl, G.T., Gillanders, B.M., Waluda, C.M., Shea, E.K., Jouffre, D., Ichii, T., Zumholz, K., Katugin, O.N., Leporati, S.C., Shaw, P.W., 2007. Approaches to resolving cephalopod movement and migration patterns. Rev. Fish Biol. Fish. 17, 401–423. https://doi.org/10.1007/s11160-007-9048-8.

Smith, P.J., Roberts, P.E., Hurst, R.J., 1981. Evidence for two species of arrow squid in the New Zealand fishery. N. Z. J. Mar. Freshw. Res. 15, 247–253. https://doi.org/10.1080/00288330.1981.9515917.

Tedesco, P., Bevilacqua, S., Fiorito, G., Terlizzi, A., 2020. Global patterns of parasite diversity in cephalopods. Sci. Rep. 10, 11303 https://doi.org/10.1038/s41598-020-68340-4.

Threlfall, W., 1970. Some helminth parasites from *Illex argentinus* (de Castellanos, 1960) (Cephalopoda: Ommastrephidae). Can. J. Zool. 48, 195–198. https://doi.org/10.1139/z70-029.

Timi, J.T., 2007. Parasites as biological tags for stock discrimination in marine fish from South American Atlantic waters. J. Helminthol. 81, 107–111. https://doi.org/10.1017/S0022149X07726561.

Timi, J.T., Buchmann, K., 2023. A century of parasitology in fisheries and aquaculture. J. Helminthol. 97, 1–18. https://doi.org/10.1017/S0022149X22000797.

Timi, J.T., Mackenzie, K., 2015. Parasites in fisheries and mariculture. Parasitology 142, 1–4. https://doi.org/10.1017/S0031182014001188.

Torres Alberto, M.L., Bodnariuk, N., Ivanovic, M.L., Saraceno, M., Acha, E.M., 2020. Dynamics of the confluence of Malvinas and Brazil currents, and a Southern Patagonian spawning ground, explain recruitment fluctuations of the main stock of *Illex argentinus*. Fish. Oceanogr. 30, 127–141. https://doi.org/10.1111/fog.12507.

Vidal, E.A.G., Haimovici, M., 1999. Digestive tract parasites in rhynchoteuthion squid paralarvae, particularly in *Illex argentinus* (Cephalopoda: ommastrephidae). Fish. Bull. 97, 402–405.

Waluda, C.M., Trathan, P.N., Elvidge, C.D., Hobson, V.R., Rodhous, P.G., 2002. Throwing light on straddling stocks of *Illex argentinus*: assessing fishing intensity with satellite imagery. Can. J. Fish. Aquat. 59, 592–596. https://doi.org/10.1139/f02-049.

Zelmer, D.A., 2014. Size, time, and asynchrony matter: the species-area relationship for parasites of freshwater fishes. J. Parasitol. 100, 561–568. https://doi.org/10.1645/14-534.1.