

Endoparasites of the blue whiting, *Micromesistius poutassou* from north-west Spain

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Abstract

The communities of metazoan endoparasites of blue whiting, *Micromesistius poutassou*, in waters of north-west Spain were analysed and a geographical comparison made with other localities. Four hundred blue whiting collected in July 1999 and September 2000 were examined for parasites, excluding the head and gills. Six species were found: *Anisakis simplex* s.l. (L3), *A. physeteris* (L3), *Hysterothylacium aduncum* (L2 and L3), *Stephanostomum lophii* (metacercaria), *S. pristis* (adult), and *Proisorhynchus crucibulum* (metacercaria). The latter is a new host record, and *A. physeteris* is reported for the first time in blue whiting from the north-east Atlantic. Host gender was not a significant predictor of abundance of any helminth species, and host length was only weakly and positively related to the abundance of *A. simplex*. Infracommunities were species-poor, with 56% of fish harbouring only one parasite species, and 92% up to two species. Infracommunities were strongly dominated by *A. simplex* (389 fish) or *S. lophii* (6 fish). Fish length or gender, and the year of capture, did not affect species richness nor the degree of dominance. There were no significant pair-wise associations between species. Infracommunities were basically composed of several allogenic parasites with different life histories that converge in the blue whiting through the local food web. The parasite fauna of blue whiting in the study area was poor and distinctive compared with that of other localities in the north-east North Atlantic. These peculiarities might primarily be related to the composition of the local community of definitive hosts, although there might also be some influence of the geographical distribution of parasites.

Introduction

The blue whiting, *Micromesistius poutassou* Risso, 1826 is a pelagic gadoid fish broadly distributed in the north-east Atlantic. This species has frequently been analysed for parasites in several localities of this region, particularly in the waters off the Faroe Islands (e.g. Gaevskaya, 1978; Grabda, 1978; Szuks *et al.*, 1978; MacKenzie, 1979; Højgaard, 1980; Koie, 1993a, 2000). In the north-western waters of Spain, most parasitological surveys have

dealt with specific groups of parasites (nematodes: Sanmartín *et al.*, 1989, 1994; Viu *et al.*, 1996; De la Torre *et al.*, 2001; digeneans: Quinteiro *et al.*, 1988, 1993). Common to all these studies is the lack of a community perspective. At infracommunity level, basic infection data such as mean intensities or mean abundances of parasite species are seldom provided, and other parameters such as the mean number of species or species co-occurrences are not available from any study. At component community level, Karasev (1990) attempted a comprehensive geographical comparison of parasite faunas, but he did not include data from some areas, e.g. north-west Spain. In the present paper, the helminth fauna of blue

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whiting from north-west Spain are analysed from a large sample of fish. Our aim is to provide information on the communities of metazoan endoparasites of blue whiting in this area and to make a geographical comparison with data from other localities.

Materials and methods

Fish were captured by bottom trawling in September 1999 and July 2000 in a fishing ground of Rías Bajas (42°15'N, 9°25'W), Galicia, Spain (depth range 250–350 m). A total of 400 fish (200 each year) were measured, weighed and sexed. Fish length varied significantly between years: in 1999, mean length (in cm) \pm SD (range) was 22.8 ± 1.2 (17.4–26.5); in 2000, 21.8 ± 0.9 (19.7–25.3); *t*-test, *t* = 9.63, 398 df, *P* < 0.0001. Therefore, the variable 'year' was taken into account as a potential confounding variable of 'fish size' in further analyses (see below).

In each fish, the epaxial and hypaxial muscles, abdominal cavity, liver, intestine and intestinal caeca, stomach, swimbladder, gonads and heart, but not the head and gills, were examined for metazoan parasites. Viscera were examined under a stereomicroscope by pressing them with a Petri dish, so that parasites were first observed by transparency, then the viscera were opened and the parasites collected. Hypaxial and epaxial muscles were examined by candling under a stereomicroscope. All parasites were washed in 9% saline, fixed in 70% ethanol and identified. Nematodes were cleared with lactophenol for morphological identification; no electrophoretic diagnosis was attempted. Adult digeneans were stained with boracic carmine, and metacercariae with iron acetocarmine following Georgiev *et al.* (1986). Voucher material is deposited at The Natural History Museum, London, UK, with the following accession numbers: *Anisakis simplex* sensu lato BM(NH) 2002.2.7.1–5; *Anisakis physeteris* BM(NH) 2002.2.7.6; *Hysterothylacium aduncum* L2 BM(NH) 2002.2.7.7–8; *Hysterothylacium aduncum* L3 BM(NH) 2002.7.19.321–323; *Stephanostomum lophii* metacercariae BM(NH) 2002.2.7.9–13; *Stephanostomum pristi* BM(NH) 2002.2.7.14–15; *Proserhynchus crucibulum* metacercariae BM(NH) 2002.2.7.16–20.

The abundance of each helminth species, and several features of the infracommunities, i.e. species richness, total abundance and dominance, were investigated relative to gender and length of the fish and the year of capture. Dominance was calculated using the Berger-Parker dominance index $d = N_{\max}/N_t$, where N_{\max} is the total number of helminths belonging to the dominant species, and N_t is the total number of helminth individuals in the infracommunity (Esch *et al.*, 1988). For statistical comparisons standard non-parametric tests (Spearman rank correlation and Mann-Whitney tests) were applied (Sokal & Rohlf, 1981). The influence of host gender and length was examined for each year separately. A test for significant pair-wise associations between species was performed for the species occurring in at least ten hosts. For prevalence data, the null probability *p* that two helminth species share the number of hosts where they are observed to co-occur was calculated, according to the formula given

by Simberloff (1990):

$$p = \frac{\binom{S_j}{X} \binom{N - S_j}{S_i - X}}{\binom{N}{S_i}},$$

where S_i and S_j are the number of host where parasite species *i* and *j* occur, respectively (by convention, $S_i \leq S_j$), X is the number of hosts where species *i* and *j* co-occur, and N is the total number of hosts analysed. If $P < 0.05$, there is statistical evidence that the species are not arranged independently over the hosts (Simberloff, 1990). We also calculated Spearman correlations with intensity data using only the hosts where species *i* and *j* co-occur. This allowed to explore more specific hypotheses, i.e. that one species facilitates the establishment of another (Lotz & Font, 1994). Since pair-wise comparisons are not independent, the sequential Bonferroni procedure was used to correct *p*-values according to the total number of comparisons (Rice, 1989).

Species richness was compared at component community and infracommunity levels between our blue whiting sample and the available data from other geographical localities of the north-east Atlantic. Data for ectoparasites and species inhabiting mainly the gills or head of the host (e.g. metacercariae of *Proserhynchoides gracilescens*) were excluded. The mean species richness based on infracommunity data was not available from the published surveys and, therefore, it was calculated as $\sum p_i$, where p_i is the proportion of species *i* in the sample (Lotz & Font, 1991). Since our fish sample size was notably larger than that of other studies, we calculated the minimum sample size necessary to detect, with a 95% probability, a given parasite species in our sample (Martin *et al.*, 1987). This procedure served to deal with the effect of sampling effort. Ecological terminology follows Bush *et al.* (1997). Since parasite distribution among hosts is aggregated, we report mean and median values of abundance to maximize meaningful information about infections.

Results

Only nematodes and digeneans, six species in total, were found in the blue whiting (table 1). *Stephanostomum pristi* was the only species found as adults; other digeneans were found as metacercariae, and all nematodes usually as third-stage (L3) larvae (table 1). Four individuals of *H. aduncum* occurred as second-stage (L2) larvae. There were no significant differences in the abundance of the parasite species between genders (Mann-Whitney tests, $P \geq 0.05$). There was a weak, statistically significant relationship between fish length and the abundance of *A. simplex* in both years (in 1999: $r_s = 0.142$, $n = 200$, $P < 0.05$; in 2000: $r_s = 0.173$, $n = 200$, $P = 0.01$), but it was not significant for other helminth species. Likewise, only the abundance of *Anisakis simplex* differed significantly between years ($U = 15,722$, $n = 400$, $P < 0.001$; see also table 1).

All but three fish individuals were infected with at least one helminth species. Two species occurred in single hosts, *A. physeteris* and *S. pristi* (table 1). Data of infracommunity parameters are shown in table 2. Communities were species-poor: 56% of fish harboured only one parasite species, and 92% up to two species.

Table 1. Species, developmental stage, habitat, total number, prevalence and intensity of metazoan parasites collected from 400 blue whiting *Micromesistius poutassou* collected off Galician coasts in 1999–2000.

Species	Site	Total number		Prevalence (%) (95% C.I.)			Mean intensity \pm SD (median)		
		1999	2000	1999	2000	Total	1999	2000	Total
Nematoda									
<i>Anisakis simplex</i> s.l. (L3)	Viscerae and musculature	2398	2022	99 (97–100)	99.5 (98–100)	99.3 (97–100)	12.1 \pm 10.9 (10)	10.2 \pm 12 (8)	11.1 \pm 11.5 (9)
<i>A. physeteris</i> (L3)	Peritoneum	1	0	0.5 (0–2.5)	0	0.25 (0–1)	1	0	1
<i>Hysterothylacium aduncum</i> (L2 and L3)	Viscerae	52	22	13.5 (9.5–19.5)	8.5 (5.5–13)	11 (7–15)	1.9 \pm 4.4 (1)	1.4 \pm 1.2 (1)	1.7 \pm 3.5 (1)
Digenea									
<i>Stephanostomum lophii</i> (metacercaria)	Musculature	130	220	26.5 (20–32.5)	36 (28–43)	31.3 (26.5–36)	2.5 \pm 2.4 (2)	3.1 \pm 3.7 (1)	2.8 \pm 3.2 (1)
<i>Prosorhynchus crucibulum</i> (metacercaria)	Musculature	18	27	8.5 (13–5.5)	9.5 (6–15)	9 (6–15)	1.0 \pm 0.2 (1)	1.4 \pm 1.6 (1)	1.3 \pm 1.2 (1)
<i>S. pristis</i> (adult)	Intestinal caeca	0	8	0	0.5 (0–2.5)	0.25 (0–1)	0	8	8

Table 2. Mean values (\pm SD) [median] of parasite infracommunity parameters of 400 blue whiting *Micromesistius poutassou* collected off Galician coasts in 1999–2000.

Year	Species richness	Total abundance	Dominance
1999	1.48 \pm 0.69 [1.00] (0–4)	13.0 \pm 12.5 [11.0] (0–157)	0.94 \pm 0.10 [1.00] (0.55–1.00)
2000	1.55 \pm 0.66 [1.00] (0–4)	11.5 \pm 12.6 [9.0] (0–134)	0.90 \pm 0.14 [1.00] (0.44–1.00)
Total	1.51 \pm 0.68 [1.00] (0–4)	12.3 \pm 12.5 [10.0] (0–147)	0.92 \pm 0.12 [1.00] (0.44–1.00)

Total abundance was low: over 90% of fish harboured up to 20 worms, and over 99% of fish, less than 45 worms. Infracommunities were strongly dominated by two species: *A. simplex* was the dominant species in 389 fish, *S. lophii* in six fish, and both species were co-dominant in two fish. The high average dominance index (table 2) resulted in part from the large number of fish with a single species. However, the dominance index was still high (0.82 \pm 0.13, median: 0.86) considering only infracommunities with two or more species ($n = 173$). Fish length or gender, and the year of capture, had no effect on species richness or the degree of dominance ($P \geq 0.05$). However, total abundance increased weakly with fish length (in 1999: $r_s = 0.125$, $n = 200$, $P < 0.05$; in 2000: $r_s = 0.121$, $n = 200$, $P < 0.05$), and differed significantly between years ($U = 16,800$, $n = 400$, $P = 0.006$). Community composition changed between years only regarding rare species: *A. physeteris* and *S. pristis* were found in 1999 and 2000, respectively (table 1). Regarding species associations, only the pair *S. lophii*–*P. crucibulum* had a nominal $P < 0.05$ using prevalence; however, after the correction for multiple comparisons, this value was not statistically significant. All correlations involving pair-wise intensities in co-infected hosts were not

significant (r_s ranged from -0.24 to 0.42 , n from 16 to 125, and nominal P from 0.10 to 0.87).

A geographical comparison of data on species richness at component community and infracommunity levels is shown in table 3. Fish sample sizes were less than 100 except in the present study and in one study in which 250 fish were partially analysed for parasites. Overall, data indicate that the parasite communities of blue whiting analysed in this study are particularly species-poor (table 3). At component community level, a minimum of 25 fish would be necessary to detect four parasite species, and at least 311 fish to detect five or six species. Controlling for sampling effort, most surveys indicate that in other localities the blue whiting harbours richer component communities, richer infracommunities, or both (table 3).

Discussion

Prosorhynchus crucibulum is the only parasite species that is new for the blue whiting. The life cycle of *P. crucibulum* appears to be associated with the benthic fauna of coastal waters (Matthews, 1973). The conger eel *Conger conger* is considered to be its main definitive host (Bray, 1973), whereas several species of teleosts, including gadids, would act as second intermediate or accidental hosts (e.g. Matthews, 1973; Radujkovic *et al.*, 1989; Grau *et al.*, 1999). The blue whiting seems to move especially close to the coast in the summer (Quinteiro *et al.*, 1993), and occurs near the bottom during the day (Cohen *et al.*, 1990), which might facilitate contacts with the cercariae of *P. crucibulum*. In localities close to the study area, *P. crucibulum* was not found in 67 blue whiting collected during the winter (Quinteiro *et al.*, 1988), but *Prosorhynchus* sp. (probably *P. crucibulum*) was found in a sample collected throughout one year (Quinteiro *et al.*, 1989). The apparent absence of infections in the winter might be related to the movement of fish into more

Table 3. Comparative data for parasite species richness at component community and infracommunity level of metazoan parasite fauna of blue whiting *Micromesistius poutassou* off North Atlantic areas (including the present study). Parasites from the head and gills are excluded from the calculations (see text for details).

Locality	Sample size	Species richness	
		Component community	Infracommunity
North Scotland (1)*	30	7	3.45
North Scotland (1)	20	6	2.55
West Scotland (1, 2)†	24	6	1.46
	20	9	1.85
Faroe Islands (2)	20	5	5.00
Faroe Islands (3)	49	7	1.97
Faroe Islands (4)	30	5	2.80
Faroe Islands (5)	10	4	2.80
Norwegian Sea (4)‡	78	6	2.56
Spitzbergen and Faroe Islands (6)	70	8	>1.90 (Spitzbergen)§ >1.70 (Faroe)
Spitzbergen (7)	25	6	–
Barents Sea (7)	10	9	–
Biscay Bay (7)	65 + 250	10	–
Azores Islands (7)	19	4	–
North Ireland (8)	50¶	3	1.70
Galicia (9, 10)#	67	4	1.32
Galicia (11)	?	11	1.80
Galicia (12)	400	6	1.51
	<311**	4	1.51

* 1. McKenzie (1979); 2. Raitt (1968); 3. Højgaard (1980); 4. Kusz & Treder (1980); 5. Køie (1993a, 2000); 6. Szuks *et al.* (1978); 7. Karasev (1990); 8. Grabda (1978); 9. Quinteiro *et al.* (1988); 10. Sanmartín *et al.* (1989); 11. Quinteiro *et al.* 1989; 12. This study.

† Raitt (1968) includes unpublished data by Kabata, and McKenzie (1979) includes data apparently from the same source. However, there are slight differences between the two datasets so we have included both.

‡ Parasites from viscerae only.

§ Prevalence data are given for two species only and, therefore, species richness is calculated as a minimum value.

|| Partial parasitological analysis in 250 fish.

Only digeneans and nematodes are included in the survey.

¶ Parasites from the interior of the gut are excluded.

** Minimum sample size to detect four species.

offshore waters (Quinteiro *et al.*, 1993) or to seasonal effects on the parasite's life cycle.

Both *A. simplex* and *H. aduncum* infect the blue whiting throughout its geographical range (Karasev, 1990), including Galician waters (Sanmartín *et al.*, 1989; Quinteiro *et al.*, 1989). However, *A. physeteris* has been reported only in blue whiting from the western Mediterranean, also with low numbers (Valero *et al.*, 2000). Abollo *et al.* (2001) recently recorded *A. simplex* sensu stricto and *A. pegreffii* in blue whiting and other meso- and benthopelagic fish from the north-west Atlantic waters of Spain, which is suggested to be the boundary area of sympatry between both species (Mattiucci *et al.*, 1997). Therefore, it is likely that our sample of *A. simplex* s.l., contain both species. Most individuals of *H. aduncum* from our sample were L3, except four L2. In a close locality, Sanmartín *et al.* (1989) found L3s in blue whiting collected in the winter, but Quinteiro *et al.* (1989) found L4 and adults in a sampling over a year. L4 and adults have also been found in samples of blue whiting from North Atlantic waters (see, e.g. MacKenzie, 1979; Køie, 1993a). Sanmartín *et al.* (1989) and Quinteiro *et al.* (1989) suggested that the adult stage of *H. aduncum* might be most common in the summer,

but this is not supported by our data. Køie (1993b) suggested that L3 of *H. aduncum* would develop to adult depending on the length of the recruited larva, which varies according to the type of prey consumed. Perhaps the blue whiting have a different diet, thus play a different role for the transmission of *H. aduncum*, according to the local food web.

Stephanostomum pristis is the most frequent of the three to four species of this genus reported in the blue whiting (references in Bartoli & Bray, 2001). Quinteiro *et al.* (1988, 1989) found this species in other localities off Galician coasts, also with a low abundance. Køie (1978) considered that the number of circum-oral spines is the single criterion that enables separation of *S. pristis* (with 2 rows of 18 spines) from *S. caducum* (with 2 rows of 24–25 spines). The later species was considered as a junior synonym of *S. pristis* because in a large sample of *Stephanostomum* specimens identified as *S. pristis* the number of circum-oral spines ranged from 2 × 18 to 2 × 26 (Køie, 1984). However, Bartoli & Bray (2001) argued that the number of spines in *S. pristis* is constant (2 × 18 spines) and suggested that Køie's (1984) sample perhaps contained both *S. pristis* and *S. caducum*. In our study, only one of the eight specimens conserved all

circum-oral spines, and the number was 2×18 . Since the other specimens were found along with this specimen and were morphologically similar, we assumed that they also belong to the same species. The life-cycle of *S. pristis* sensu Køie (1984) include, in the North Atlantic, the gastropod *Natica alderi* as the first intermediate host, gobies as the second intermediate hosts, and gadids, cod in particular, as the definitive hosts. The scarcity of infections in the blue whiting might partly be accounted for by the fact that blue whiting feeds mainly on crustaceans (Bailey, 1982). The other species of *Stephanostomum* found in this study, *S. lophii*, uses gadids as the main second intermediate hosts, the definitive host being the anglerfish *Lophius piscatorius* (Quinteiro *et al.*, 1993). So far *S. lophii* have only been reported from Galicia (Quinteiro *et al.*, 1993).

There was a weak but statistically significant increase of the abundance of *A. simplex* with host length. In addition, the abundance of *A. simplex* was significantly higher in 1999 than in 2000 but, since fish were significantly larger in 1999 than in 2000, annual differences in infection levels can be confounded by the effect of size. Positive relationships between host size and abundance of *A. simplex* have been reported in many fish species (Bratley & Bishop, 1992, and references therein), and can theoretically be accounted for by three factors (Wootton & Waddell, 1977): (i) larvae of *A. simplex* are apparently long-lived and tend to accumulate in older fish (age effect); (ii) larger fish tend to eat more, increasing the recruitment rate of the parasite (size effect); (iii) that larger and older fish can consume larger, presumably more infected, prey (mixed age-size effect). The range of sizes in our fish sample is fairly narrow (17.4–26.5 cm, for a species reaching as adult over 40 cm) and, based on length, the range of ages could be estimated roughly as 1–4 years (Raitt, 1968). Since the observed accumulation of *A. simplex* is weak, the pattern might especially depend on a pure age effect (see Bussman & Enrich, 1979).

Helminth infracommunities of blue whiting in the study area were depauperate and showed little variation among hosts. Species richness was unaffected by host length and sex, or year of capture; species composition changed only in minor elements between years, and all infracommunities were strongly dominated by a single species, generally *A. simplex*. The significant changes of total parasite abundance with fish length and year of capture merely reflect the changes observed in the abundance of *A. simplex*. On the other hand, the four common species did not show any statistically significant pair-wise associations. When prevalences are very low or very high (e.g. that of *A. simplex*), it may be difficult to construct proper null hypotheses and, therefore, biological and ecological information become crucial to decide whether meaningful associations exist in these cases (see Janovy *et al.*, 1995). Based on statistical grounds, there is little evidence that parasite species exclude one another, that there are facilitation processes between parasites, or that parasites have a strong dependence on the same intermediate hosts for transmission. The latter is also supported by the available evidence on life cycles. In short, infracommunities are composed of several allogenic parasites with different life histories that converge

in the blue whiting through the local food web. Additionally, a generalist parasite occurs as adult in very low numbers. This pattern is common to blue whiting from higher latitudes in the northern North Atlantic (references in table 3). Excluding parasites from the head or gills, the most important groups in this region are larval nematodes (*A. simplex* and *H. aduncum*) followed by larval cestodes of marine mammals (*Diphyllobothrium*), larval cestodes of elasmobranchs (*Monorygma*, *Grillotia*, *Scolex pleuronectis*) and, in lower numbers, adult digeneans and acanthocephalans of teleosts, some of which infect especially gadids (*S. pristis*, *Hemiurus lewini*, *Lecithaster gibbosus*, *Derogetes varicus* and *Echinorhynchus gadi*) (references in table 3; see also Karasev, 1990). All these taxa appear to be regionally frequent (Karasev, 1990) and locally abundant (references in table 3). However, most of these elements are absent from the blue whiting analysed in this study or occur with unusually low abundance (*H. aduncum*). Therefore, the low species richness observed at both component community and infracommunity levels might be related to geographical factors. However, a previous survey carried out in the Ría de Arousa (about 50 km away from our study area) reported as many as 11 parasite species, many of which typically occur in blue whiting from higher latitudes (Quinteiro *et al.*, 1989; table 3). Although differences in parasite composition are likely to reflect, to some extent, the geographic distribution and relative abundance of intermediate or definitive hosts (e.g. in the case of *Diphyllobothrium*), it appears that local conditions, particularly the composition of the host community, seem to be of paramount importance in determining major features of parasite communities.

Acknowledgements

We are grateful to Victoria Herreras and Juan Rodríguez, for their assistance in processing the fish and identifying the parasites. Special thanks are due to Dr Aneta Kostadinova for their help in identification of parasites and revision of the manuscript. We also want to thank Casildo León (Mercadona), Alejandro Cadabal, Manuel González and the crew of the *Ficha* for providing the fish. This study was supported by projects 1FD97-1147, REN-2003-01758 from the Spanish Government (funded by FEDER); and HPMD-2000-0037 from the European Commission. M. Fernández and F.J. Aznar benefit from a 'Ramón y Cajal' contract from the Ministry of Science and Technology, Spain.

References

- Abollo, E., Gestal, C. & Pascual, S. (2001) *Anisakis* infestation in marine fish and cephalopods from Galician waters: an updated perspective. *Parasitology Research* **87**, 492–499.
- Bailey, R.S. (1982) The population biology of blue whiting in the North Atlantic. *Advances in Marine Biology* **19**, 257–355.
- Bartoli, P. & Bray, R.A. (2001) Contribution to the knowledge of species of the genus *Stephanostomum* Looss, 1899 (Digenea: Acanthocolpidae) from teleosts

- of the Western Mediterranean, with the description of *S. gaidropsari* n. sp. *Systematic Parasitology* **49**, 159–188.
- Bratley, J. & Bishop, C.A.** (1992) Larval *Anisakis simplex* (Nematoda: Ascaridoidea) infection in the musculature of Atlantic cod, *Gadus morhua*, from Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2635–2647.
- Bray, R.A.** (1973) Some digenetic trematodes in fishes from the bay of Biscay and nearby waters. *Bulletin of the British Museum (Natural History) Zoology* **26**, 151–183.
- Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W.** (1997) Parasitology meets ecology in its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.
- Bussmann, B. & Enrich, S.** (1979) Investigations on infestation of blue whiting (*Micromesistius poutassou*) with larval *Anisakis* sp. (Nematoda: Ascaridida). *Archiv für Fischereiwissenschaft* **29**, 155–165.
- Cohen, D.M., Inada, T., Iwamoto, T. & Scialabba, N.** (1990) FAO species catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. *FAO Fisheries Synopsis* **10**, 1–442.
- De la Torre, R., Pérez Aparicio, J., Hernández Bienes, M., Jurado Pérez, R., Martínez Ruso, A. & Morales Franco, E.** (2001) Anisakiasis en pescados frescos comercializados en norte de Córdoba. *Revista Española de Salud Pública* **74**, 517–526.
- Esch, G.W., Kennedy, C.R., Bush, A.O. & Aho, J.M.** (1988) Patterns in helminth communities in freshwater fish in Great Britain: alternative strategies for colonization. *Parasitology* **96**, 519–532.
- Gaevskaya, A.V.** (1978) The parasitofauna of blue whiting (*Micromesistius poutassou*) in the northeast Atlantic. ICES CM 1978/H, 20 pp.
- Georgiev, B.B., Biserkov, V.Y. & Genov, T.** (1986) In toto staining method for cestodes in iron acetocarmine. *Helminthologia* **23**, 279–281.
- Grabda, J.** (1978) Studies on parasitic infestation of blue whiting (*Micromesistius* sp.) with respect to the fish utilization for consumption. *Acta Ichthyologica et Piscatoria* **8**, 29–41.
- Grau, A., Riera, F. & Carbonell, E.** (1999) Some protozoan and metazoan parasites of the amberjack from the Balearic Sea (western Mediterranean). *Aquaculture International* **7**, 307–317.
- Højgaard, D.P.** (1980) Parasitter hos blåhvilling, *Micromesistius poutassou* (Risso, 1810). MSc thesis, University of Bergen, Norway 70 pp.
- Janovy, J. Jr., Clopton, R.E., Clopton, D.A., Zinder, S.D., Efting, A. & Krebs, L.** (1995) Species density distributions as null models for ecologically significant interactions of parasite species in an assemblage. *Ecological Modelling* **77**, 189–196.
- Karasev, A.B.** (1990) Ecological and geographical analysis of the northeast Atlantic blue whiting parasitic fauna. Proceedings of the fourth Soviet–Norwegian Symposium. Section Parasites, mortality and migration. Bergen, pp. 307–318.
- Koie, M.** (1978) On the morphology and life-history of *Stephanostomum caducum* (Loos 1901) Manter 1934 (Trematoda: Acanthocolpidae). *Ophelia* **17**, 121–133.
- Koie, M.** (1984) Digenetic trematodes from *Gadus morhua* L. (Osteichthyes: Gadidae) from Danish and adjacent waters, with special reference to their life-histories. *Ophelia* **23**, 195–222.
- Koie, M.** (1993a) Nematode parasites in teleosts from 0 to 1540 m depth off the Faroe Islands (the North Atlantic). *Ophelia* **38**, 217–243.
- Koie, M.** (1993b) Aspects of the life cycle and morphology of *Hysterothylacium aduncum* (Rudolphi, 1802) (Nematoda, Ascaridoidea, Anisakidae). *Canadian Journal of Zoology* **71**, 1289–1296.
- Koie, M.** (2000) Metazoan parasites of teleost fishes from Atlantic waters off the Faroe Islands. *Ophelia* **52**, 25–44.
- Kusz, W. & Treder, A.** (1980) Parasitic fauna of European blue whiting, *Micromesistius poutassou* (Risso, 1810). *Acta Ichthyologica et Piscatoria* **10**, 45–47.
- Lotz, J.M. & Font, W.F.** (1991) The role of positive and negative interspecific associations in the organization of communities of intestinal helminths of bats. *Parasitology* **103**, 127–138.
- Lotz, J.M. & Font, W.F.** (1994) Excess positive associations in communities of intestinal helminths of bats: a refined null hypothesis and a test of the facilitation hypothesis. *Journal of Parasitology* **80**, 398–413.
- Martin, S.W., Meek, A.H. & Willeberg, P.** (1987) *Veterinary epidemiology. Principles and methods*. Ames, Iowa, Iowa State University Press.
- Matthews, R.A.** (1973) The life-cycle of *Prosorhynchus crucibulum* (Rudolphi, 1819) Odhner, 1905, and a comparison of its cercaria with that of *Prosorhynchus squamatus* Odhner, 1905. *Parasitology* **66**, 133–164.
- Mattiucci, S., Nascetti, G., Cianchi, R., Paggi, L., Arduino, P., Margolis, L., Bratley, J., Webb, S., D'Amelio, S., Orecchia, P. & Bullini, L.** (1997) Genetic and ecological data on the *Anisakis simplex* complex, with evidence for a new species (Nematoda, Ascaridoidea, Anisakidae). *Journal of Parasitology* **83**, 401–416.
- McKenzie, K.** (1979) Some parasites and diseases of blue whiting, *Micromesistius poutassou* (Risso), to the North and West of Scotland and at the Faroe Islands. *Scottish Fisheries Research Report* **17**, 1–14.
- Quinteiro-Alonso, P., Martínez-Ubeira, F., Fernández, J.A. & Sanmartín Durán, M.L.** (1988) Helminthofauna de peces de interés comercial capturados en el Noroeste de España. I. Trematoda (Digenaea). *Revista Ibérica de Parasitología* **48**, 139–144.
- Quinteiro, P., Iglesias, R., Estevez, J.M., Santamarina, M.T.** (1989) Helminth parasites of some commercially important fish from N.W. Spanish waters. IV EAFP International Conference, Santiago de Compostela, p. 173.
- Quinteiro, P., Tojo, J., Núñez, A., Santamarina, M.T. & Sanmartín, M.L.** (1993) *Stephanostomum lophii* sp. nov. (Digenaea: Acanthocolpidae), intestinal parasite of *Lophius piscatorius*, with reference to seasonal fluctuations of metacercariae in intermediate second hosts (Gadidae). *Journal of Fish Biology* **42**, 421–433.
- Radujkovic, B.M., Orecchia, P. & Paggi, L.** (1989) Parasites des poissons marins du Montenegro: digenes. *Acta Adriatica* **30**, 1–2.

- Raitt, D.F.S.** (1968) Synopsis of biological data on the blue whiting *Micromesistius poutassou* (Risso, 1810). *FAO Fisheries Synopsis* **54**, 1–39.
- Rice, W.R.** (1989) Analyzing tables of statistical tests. *Evolution* **43**, 223–225.
- Sanmartín Durán, M.L., Quinteiro, P. & Ubeira, F.M.** (1989) Nematode parasites of commercially important fish in NW Spain. *Diseases of Aquatic Organisms* **7**, 75–77.
- Sanmartín, M.L., Quintero, P., Iglesias, R., Santamaría, M.T., Leiro, J. & Ubeira, F.M.** (1994) *Nematodos parásitos en peces de las costas gallegas*, 80 pp. Madrid, Díaz de Santos.
- Simberloff, D.** (1990) Hypotheses, errors, and statistical assumptions. *Herpetologica* **46**, 351–357.
- Sokal, R.R. & Rohlf, F.J.** (1981) *Biometry* 2nd edn. New York, Freeman.
- Szuks, H., Lorenz, H. & Stedling, D.** (1978) Parasitierung des Blauen Wittlings, *Micromesistius poutassou* (Risso, 1810). *Wissenschaftliche Zeitschrift der Pädagogischen Hochschule "Liselotte Herrmann" Güstrow Aus der Mathematisch-Naturwissenschaftlichen Fakultät* **1**, 143–151.
- Valero, A., Martín-Sánchez, J., Reyes-Muelas, E. & Adroher, F.J.** (2000) Larval anisakids parasitizing the blue whiting, *Micromesistius poutassou*, from Motril Bay in the Mediterranean region of southern Spain. *Journal of Helminthology* **74**, 361–364.
- Viu, M., Sánchez-Acedo, C., del Cacho, E., Quílez, J. & López-Bernard, F.** (1996) Occurrence of anisakid larvae (Nematoda: Ascaridida) in fresh market fish from Zaragoza (Spain). *Research and Review in Parasitology* **56**, 25–28.
- Wootton, R. & Waddell, I.F.** (1977) Studies on the biology of larval nematodes from the musculature of cod and whiting in Scottish waters. *Journal du Conseil International pour l'Exploration de la Mer* **37**, 266–273.

(Accepted 10 September 2004)

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