

Parasites as biological tags for stock identification of Atlantic horse mackerel *Trachurus trachurus* L.

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Abstract

Forty-five different parasite taxa were recorded from 1919 Atlantic horse mackerel *Trachurus trachurus* caught at 20 stations in a study area from off the coast of Morocco to south-west Norway, and throughout the Mediterranean Sea. Eleven taxa are new host records, and one is probably a new species. The geographical distribution and biology of each parasite and its value for the stock identification of *T. trachurus* are described and discussed. The most effective biological tags were the larval nematodes *Anisakis* spp. and *Hysterothylacium aduncum*. The distinctive pattern of infection with these nematodes observed in samples from the single North Sea station clearly distinguishes this from all other stations and supports the current management strategy which treats the North Sea population as a separate stock. The distinction between the putative “western”, “southern” and “mauritanian” stocks is less clear, with evidence of considerable mixing between them. The highly localised distributions of some parasites in the Mediterranean part of the study area suggest that *T. trachurus* populations there appear to comprise three main stocks—western, central and eastern. There is also strong evidence of the migration of fish from Atlantic populations into the extreme western part of the Mediterranean.

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1. Introduction

The basic principle underlying the use of parasites as biological tags in population studies of marine fish is that a fish can become infected with a parasite only when it is within the endemic area of that parasite. The endemic area is that geographical region in which conditions are suitable for the transmission of the parasite and the completion of its life cycle and is determined by the existence of suitable environmental conditions, primarily temperature and salinity, and the presence of all the required intermediate and definitive hosts. If a fish is found infected with a parasite outside the endemic area of that parasite, we can infer that the fish had been within the endemic area at some time in its past history. Knowledge of the maximum life

span of the parasite in the fish host can enable us to estimate the period of time since the fish left the parasite's endemic area. Parasites can also be used as tags within their endemic areas, where differences in the behaviour and feeding habits of different host populations or in the abundance of intermediate hosts can give rise to significantly different levels of infection in different parts. The more parasites with different endemic areas that can be used, the more information can be obtained about the past movements and stock structure of the fish populations sampled. The main factor limiting the use of marine parasites as biological tags is insufficient information on their complex biology and ecology, but as research adds to our knowledge the interpretation of parasite infection data in terms of fish population biology becomes increasingly more efficient and reliable.

The steadily increasing frequency of publications referring to the actual or potential use of parasites as biological tags in population studies of marine fish reflects the increasing recognition of the value of this method. These publications include

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several reviews, the most recent of which are those of Lester (1990), Moser (1991), Williams et al. (1992), Arthur (1997) and MacKenzie (2002). MacKenzie and Abaunza (1998, 2005) published a guide to the procedures and methods involved in the use of parasites for stock discrimination of marine fish.

The present study was carried out as part of the multidisciplinary international project HOMSIR (QLK5-Ct1999-01438) aimed at clarifying the stock structure of the Atlantic horse mackerel *Trachurus trachurus* L. in European waters. An integral part of this project was the use of parasites as biological tags. The only previous biological tag studies on *T. trachurus* are those of Gaevskaya and Kovaleva (1980b,c) and Abaunza et al. (1995), but there have also been some recent studies on other species of the genus *Trachurus* in other parts of the world (George-Nascimento, 2000; George-Nascimento and Arancibia, 1992; Avdeev, 1992; Aldana et al., 1995). A checklist of the protozoan and metazoan parasites reported from *T. trachurus* was published by MacKenzie et al. (2004).

2. Materials and methods

Parasitological examinations were carried out on the same specimens of *T. trachurus* used for genetic and other biological studies (see Abaunza et al., 2008). Samples of fish were caught at predetermined sampling stations (Fig. 1) by research or commercial fishing vessels and deep-frozen in individually labelled bags at sea. The samples were then transferred to the laboratories of the partners responsible for parasitological examinations (University of Aberdeen, Scotland; IPIMAR, Lisbon, Portugal; Institute of Parasitology, Rome, Italy). In the laboratory the fish were thawed individually and examined according to the following procedure. The fish was first measured, then photographed with the fins pinned out for morphological measurements. The visceral cavity was opened and a sample of liver removed and frozen at -70°C for genetic analysis. A complete autopsy was then carried out. All host organs and tissues were examined under a dissecting microscope for metazoan parasites

and smears were examined at $300\text{--}500\times$ for myxozoan and protozoan infections. The numbers of metazoan parasites and their sites of infection in each fish were recorded. Anisakid nematodes were washed in saline solution and stored at -70°C for genetic studies. Other parasites were preserved in either 70% alcohol or 10% formalin.

All parasites found were first examined unstained under a dissecting microscope for larger metazoan parasites and/or at higher magnifications under a research microscope, using phase contrast microscopy, for protozoans and myxozoans. Some helminths were stained with borax carmine to make identification easier, and preparations of stained specimens mounted in DePeX were made as representative specimens of each species. Some of the monogenean and digenean species are delicate and many of these deep-frozen specimens proved difficult to identify. Nematodes, acanthocephalans and crustaceans were examined in temporary mounts, cleared with glycerine jelly or beechwood creosote, before permanent mounts were prepared. A spreadsheet was prepared in which details of all parasites recorded from each individual fish were recorded. *Anisakis* larvae collected from all the sampling stations were sent to the Institute of Parasitology in Rome, Italy, where they were identified by means of multilocus electrophoresis. The methods are described by Mattiucci et al. (2008).

The measures of parasitic infection referred to in this report are: *prevalence*, which is the number of fish infected divided by the number of fish examined, expressed here as a percentage; *mean intensity*, which is the total number of parasites of a particular taxon found divided by the number of infected fish; and *mean abundance*, which is the total number of parasites of a particular taxon found divided by the total number of fish examined (see Bush et al., 1997).

Two main approaches to the use of parasites as biological tags were recognised by MacKenzie and Abaunza (1998, 2005). In one, a small number of parasite taxa are selected according to established criteria and data on individual taxa are analysed separately; in the other, entire parasite assemblages are analysed using multivariate statistical techniques. Three features of our data presented difficulties with the parasite assemblage approach: (1) although a wide range of parasite taxa was found in this study, most of them occurred only rarely; (2) the fish examined had a wide age range (from 1 to 29 years) and the occurrence of some of the more common parasites is age-related; and (3) the samples were taken at different seasons over a period of from February to December, although in the majority of areas the aim was to sample during the spawning season. A further complication was that female horse mackerel of any given age group and year class tended to be larger and to have heavier larval nematode burdens than males. In the second year's sampling we also decided not to record adult gut digeneans from some samples because they are short-lived, widely distributed and relatively uncommon, and so not very effective as biological tags. We therefore focused on selected individual parasite taxa. Two genera of anisakid nematode larvae, *Anisakis* and *Hysterothylacium*, which were by far the most common parasites found in our samples, proved to be of particular value. The relative proportions of these two genera in samples from different sta-

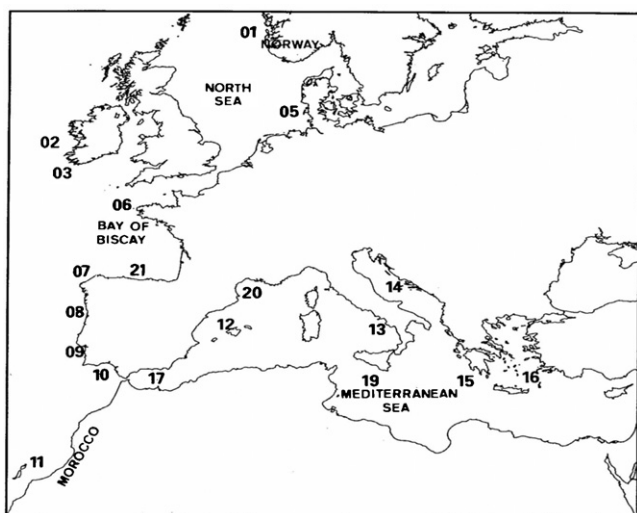


Fig. 1. Chart of the study area showing sampling stations.

tions varied enormously and showed considerable potential as a means of distinguishing between different stocks of *T. trachurus*, particularly in the Atlantic area. As these nematodes are long-lived (life spans measured in years) and cumulative with age, we analysed and compared data from the same limited age ranges from different samples to obtain valid comparisons.

3. Results

3.1. General

A total of 1919 fish from 38 samples were examined. Forty-five different parasite taxa were recorded, 37 of which were identified to species level (Table 1). Ten parasites appear to be new host records for *T. trachurus*: *Kudoa* sp., *Myxobolus spinicurvatura*, the unidentified monogenean, the digenean *Bathycereadum elongatum*, the acanthocephalans *Corynosoma strumosum* and *C. wegneri*, the pseudophyllidean cestode plerocercoids, the larval nematodes *Pseudoterranova decipiens* and *Anisakis* sp., and the branchiuran *Argulus purpureus*. *Kudoa* sp. may be a new species. The greatest number of parasite taxa found in one sample was 14, from sample 01.00 from south-west of Norway. Sample prevalences and mean intensities of infection are shown in Tables 2–5.

3.2. Apicomplexa

One species of this phylum of Protozoa, *Goussia cruciata*, occurred commonly in most samples. Prevalence of infection varied greatly and ranged from 0 to 98% in individual samples. In the Atlantic region prevalence was over 50% in most samples except for those at the northern and southern extremes of the study area (01 and 11); in the Mediterranean prevalence was highest in the central part.

3.3. Myxosporea

Five species were found, the most common being two allopatric species of *Alataspora* infecting the gall bladders. *A. serenum* was found in samples 02, 03 and 06 to the south and west of the British Isles, but was also recorded in one fish from sample 11 off Mauritania. The gall bladders of fish from samples 08, 09 and 10 from off the coast of Portugal were not examined, and no infected fish were found in samples 07 and 21 from off the north coast of Spain. *Alataspora solomoni* was found only in samples 15 and 16 from the eastern Mediterranean. Four fish, from stations 07 and 11, were infected with *Kudoa nova*, and three fish in sample 03.01 were infected with an unknown species of *Kudoa*. The liver of one fish, from sample 16.01 in the eastern Mediterranean, was infected with a myxosporean tentatively identified as *M. spinicurvatura*.

3.4. Monogenea

Five species were found, four of them parasitic on the gill filaments. The most common was *Gastrocotyle trachuri*, the prevalence of which ranged from 0 to 86% in individual samples,

Table 1

Parasites recorded from Atlantic horse mackerel in the present study

Parasite	Site of infection
Apicomplexa	
<i>Goussia cruciata</i> (Thélohan, 1892)	Liver
Myxosporea	
<i>Alataspora serenum</i> (Gaevskaya & Kovaleva, 1979)	Gall bladder
<i>Alataspora solomoni</i> (Yurakhno, 1988)	Gall bladder
<i>Kudoa nova</i> (Naidenova, 1975)	Musculature
<i>Kudoa</i> sp.	Gall bladder
<i>Myxobolus spinicurvatura</i> (Maeno et al., 1990)	Liver
Monogenea	
<i>Cemocotyle trachuri</i> (Dillon & Hargis, 1965)	Gills
<i>Gastrocotyle trachuri</i> (van Beneden & Hesse, 1863)	Gills
<i>Heteraxinoides atlanticus</i> (Gaevskaya & Kovaleva, 1979)	Gills
<i>Pseudaxine trachuri</i> (Parona & Perugia, 1889)	Gills
Unidentified polyopisthocotylean monogenean	Gills
<i>Paradiplectanotrema trachuri</i> (Kovaleva, 1970)	Stomach, oesophagus
Digenea	
<i>Bathycereadum elongatum</i> (Maillard, 1970)	Intestine
<i>Derogenes varicus</i> (Müller, 1784)	Stomach
<i>Ectenurus lepidus</i> (Looss, 1907)	Stomach
<i>Hemiurus communis</i> (Odhner, 1905)	Stomach
<i>Lasiotocus tropicus</i> (Manter, 1940)	Intestine
<i>Lasiotocus typicus</i> (Nicoll, 1912)	Intestine
<i>Lecithocladium excisum</i> (Rudolphi, 1819)	Intestine
<i>Monascus filiformis</i> (Rudolphi, 1819)	Intestine
<i>Opechona pyriforme</i> (Linton, 1900)	Intestine
<i>Pseudopoceloides chloroscombi</i> (Fischthal & Thomas, 1970)	Intestine
<i>Prodiumum polonii</i> (Molin, 1859)	Intestine
<i>Tergestia laticollis</i> (Rudolphi, 1819)	Intestine
Cestoda (all metacestodes)	
<i>Nybelinia lingualis</i> (Cuvier, 1817)	Visceral cavity
<i>Scolex pleuronectis</i> (Müller, 1788)	Intestine
<i>Grillotia</i> sp.	Visceral cavity
Pseudophyllidean plerocercoids	Visceral cavity
Acanthocephala	
<i>Corynosoma strumosum</i> (Rudolphi, 1802) juveniles	Visceral cavity
<i>Corynosoma wegneri</i> (Heinze, 1934) juveniles	Visceral cavity
<i>Rhadinorhynchus cadenati</i> (Golvan & Houin, 1964)	Intestine
Nematoda	
<i>Anisakis simplex</i> (Rudolphi, 1809) (s.s.) larvae	Visceral cavity
<i>Anisakis pegreffii</i> (Campana-Rouget & Biocca, 1955) larvae	Visceral cavity
<i>Anisakis physeteris</i> (Baylis, 1923) larvae	Visceral cavity
<i>Anisakis typica</i> (Diesing, 1860)	Stomach, intestine
<i>Hysterothylacium aduncum</i> (Rudolphi, 1802) adults	Visceral cavity
<i>H. aduncum</i> (Rudolphi, 1802) larva	Musculature
<i>Pseudoterranova decipiens</i> (Krabbe, 1878) larvae	Visceral cavity
Unidentified nematode larva	Visceral cavity
Crustacea	
<i>Argulus purpureus</i> (Risso, 1826)	Skin
<i>Caligus elongatus</i> (Nordmann, 1832)	Skin
<i>Caligus pelamydis</i> (Krøyer, 1863)	Mouth
<i>Peniculus fistula</i> (Nordmann, 1832)	Fins
<i>Lernanthropus trachuri</i> (Brian, 1903)	Gills
<i>Ceratothoa oestroides</i> (Risso, 1826)	Mouth
Praniza gnathiid isopod larva	Skin

with intensities of up to 46 worms per fish. The heaviest infections were in samples of small fish. *Pseudaxine trachuri* was less common, with prevalence ranging from 0 to 34% and with intensities of up to seven per fish. Of the remaining two gill parasites, *Heteraxinoides atlanticus* was found in fish from seven stations, all in the Atlantic region except for two infected fish in sample

Table 2
Prevalence (%) of different parasites in stations sampled in 2000

Parasite	Sample number																	
	01	02	03	05	06	07	08	09	10	12	13	15	17	18	19	20	21	
<i>G. cruciata</i>	10	38	64	98	68	50	98	96	74	6	71	0	36	95	22	4	64	
<i>A. serenum</i>	0	0	2	0	2	0	–	–	–	0	–	0	0	–	–	0	0	
<i>A. solomoni</i>	0	0	0	0	0	0	–	–	–	0	–	5	0	–	–	0	0	
<i>K. nova</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Kudoa</i> sp.	0	0	0	0	0	0	–	–	–	0	–	0	–	–	–	0	0	
<i>Myxobolus spinicurvatura</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Gastrocotyle trachuri</i>	14	0	4	23	0	0	31	50	73	0	18	9	6	57	20	54	2	
<i>Pseudaxine trachuri</i>	2	0	4	13	0	0	2	9	29	0	0	27	0	0	0	16	0	
<i>Heteraxinoides atlanticus</i>	6	0	2	0	0	0	10	2	0	0	0	0	4	0	0	0	2	
<i>Paradiplectanotrema trachuri</i>	0	0	0	0	0	0	0	0	0	4	0	0	0	52	0	0	0	
<i>Cemocotyle trachuri</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Lasiotocus typicus</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	
<i>B. elongatum</i>	0	0	0	0	0	0	0	0	0	0	9	0	0	0	2	0	0	
<i>Lasiotocus tropicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>D. varicus</i>	4	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>E. lepidus</i>	0	0	2	11	0	0	0	27	42	4	0	0	32	0	0	14	0	
<i>Hemiurus communis</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	
<i>Lecithocladium excisum</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Monascus filiformis</i>	2	0	0	0	0	0	0	0	0	0	0	0	12	0	0	12	0	
<i>Opechona bacillaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	0	
<i>Pseudopoeoeloides chloroscombri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
<i>Prodistomum polonii</i>	0	0	0	2	0	4	0	0	0	16	0	0	12	0	0	4	0	
<i>Tergestia laticollis</i>	8	6	0	19	2	0	0	0	0	4	0	0	0	0	0	0	4	
<i>Grillotia</i> sp.	4	0	4	0	0	0	0	0	0	0	0	0	0	5	2	0	0	
<i>N. lingualis</i>	0	2	2	7	0	0	0	0	0	0	0	0	0	0	0	2	4	
Pseudophyllidean plerocercoids	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>S. pleuronectis</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	4	
<i>C. strumosum</i>	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>C. wegneri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>R. cadenati</i>	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	
<i>Anisakis</i> spp.	100	100	90	70	64	96	88	71	48	0	100	77	24	100	100	0	100	
<i>H. aduncum</i> larvae	84	66	90	100	100	92	22	4	5	60	9	0	0	0	12	42	90	
<i>H. aduncum</i> adults	2	16	4	30	0	0	0	0	0	0	0	0	0	0	0	0	10	
Unidentified nematode larva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>P. decipiens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Argulus purpurea</i>	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	
<i>Caligus elongatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Caligus pelamydis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Peniculus fistula</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	
<i>L. trachuri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	5	8	0	0	
<i>Ceratothoa oestroides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Praniza larva	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	

17.00 from the extreme western part of the Mediterranean, while single infections of *Cemocotyle trachuri* were found in one fish from sample 01.00 and in one from sample 09.01. The endoparasitic monogenean *Paradiplectanotrema trachuri* was found in Mediterranean samples only and was most common in fish from stations 18 and 19.

3.5. Digenea

Twelve species were found, all of them adult forms. None was particularly common, the most frequently encountered species being *Ectenurus lepidus* and *Tergestia laticollis*, with sample prevalences of up to 42% and 20%, respectively. *B. elongatum* is a new host record for *T. trachurus* and was found only in fish from stations 13 and 19 in the central Mediterranean. *Pseu-*

dopoeoeloides chloroscombri was found only in fish from station 21 off the north coast of Spain in both years. None of the other digeneans showed any clear regional distribution.

3.6. Cestoda

Four species were found, all of them metacestodes. None was common, the most frequent being *Grillotia* sp., found in 14 fish from northern samples in the Atlantic part of the study area. Another trypanorhynch, *Nybelinia lingualis*, was found in eight fish from the same region and in one from sample 20.00 in the Mediterranean. Fourteen fish in samples 15.01 and 16.01 from the eastern Mediterranean were infected with pseudophyllidean plerocercoids, while *Scolex pleuronectis* was found in only one fish from station 09.

Table 3
Mean intensities of the more common parasites from stations sampled in 2000, with 95% confidence limits in parentheses for anisakid nematode larvae

Parasite	Sample number																		
	01	02	03	05	06	07	08	09	10	12	13	15	17	18	19	20	21		
<i>Gastrocoyle trachuri</i>	1.6	0	2.0	2.6	0	0	3.3	2.6	4.9	0	1.0	1.0	4.0	3.3	1.7	3.0	1.0		
<i>Pseudaxine trachuri</i>	1.0	0	0	1.3	0	0	2.0	1.2	1.3	0	0	1.2	0	0	0	1.0	0		
<i>Heteraxinoides atlanticus</i>	1.7	0	1.0	0	0	0	1.0	1.0	0	0	0	0	1.0	0	0	0	1.0		
<i>Paradiplectanotrema trachuri</i>	0	0	0	0	0	0	0	0	0	1.0	0	0	0	1.5	0	0	0		
<i>B. elongatum</i>	0	0	0	0	0	0	0	0	0	0	2.3	0	0	0	1.0	0	0		
<i>Lastioncus tropicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>D. varicus</i>	1.0	0	0	8.0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>E. lepidus</i>	0	0	1.0	5.8	0	0	0	1.3	1.7	1.0	0	0	1.8	0	0	1.1	0		
<i>Hemirius communis</i>	1.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.1	0		
<i>Monascus filiformis</i>	1.0	0	0	0	0	0	0	0	0	0	0	0	1.8	0	0	1.2	0		
<i>O. bacillaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.0	0		
<i>Prodistomum polonii</i>	0	0	0	7.0	0	1.5	0	0	0	1.9	0	0	1.2	0	0	1.0	0		
<i>Tergestia latcollis</i>	1.3	1.3	0	2.8	2.0	0	0	0	0	1.5	0	0	0	0	0	0	1.0		
<i>Grillotia</i> spp.	0	0	6.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Anisakis</i> spp. larvae	55.3 (±15.3)	96.6 (±33.3)	67.6 (±22.4)	31.2 (±26.3)	11.7 (±6.0)	8.0 (±6.3)	6.9 (±4.5)	2.9 (±0.6)	1.5	0	54.1 (±14.3)	2.8	5.4 (±3.9)	81.7 (±13.6)	95.7 (±30.6)	0	124.5 (±37.1)		
<i>H. aduncum</i> larvae	12.4 (±13.1)	17.2 (±13.3)	58.5 (±28.7)	196.5 (±29.5)	54.9 (±10.0)	12.0 (±5.7)	1.6 (±8.0)	1.0	1.0	2.1	1.0	0	0	0	1.0	1.8	75.1		
<i>H. aduncum</i> adults	1.0	1.8	1.5	2.8	0	0	0	0	0	0	0	0	0	0	0	0	1.8		
<i>L. trachuri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	1.0	0	0		

3.7. Acanthocephala

Three species were found. One fish in sample 05.00 was infected with two juvenile specimens of *C. strumosum*, and one fish from sample 03.01 had one juvenile specimen of *C. wegneri*. Two fish from sample 10.00 had single adult specimens of *Rhadinorhynchus cadenati* in their intestines.

3.8. Nematoda

Eight species were found. *Hysterothylacium aduncum* was present mostly in larval form but a few adult worms were also found. The other seven species were present as larvae only. Five were members of the genus *Anisakis* and were identifiable to species level only by the application of genetic-molecular biology techniques, as described in Mattiucci et al. (2008). The species of *Anisakis* identified were: *A. simplex* (*sensu stricto*), *A. pegreffii* (a sibling species of the *A. simplex* complex), *A. typica*, *A. physeteris* and *Anisakis* sp. For the main data analyses these congeneric species are here grouped together as *Anisakis* spp. The geographical distribution of each species is described in Mattiucci et al. (2008).

In some samples several hundred *Anisakis* spp. larvae were found in individual fish, which led to our estimating the numbers present in the most heavily infected fish of the first year's samples. However, when we realised the potential of these nematodes as biological tags, exact numbers were recorded in the second year's samples. The most heavily *Anisakis*-infected fish, with 795 nematodes, was from sample 15.01 in the eastern Mediterranean. The other common nematode was *H. aduncum*, larvae of which were found in most samples, but which were particularly abundant in fish from the North Sea station 05, where the heaviest single infection of 1083 larvae was recorded in 2001. In the Mediterranean, *H. aduncum* was present in significant numbers only in samples from stations 12 and 20 in the western part; elsewhere, nematode infections were dominated by *Anisakis* spp. Samples from station 05 in both years were characterised by heavy infections of *H. aduncum* (several hundred) and light infections of *Anisakis* spp. (<10). In contrast, fish from stations 02 and 03 to the west and south-west of Ireland were characterised by heavy infections of *Anisakis* spp. (several hundred) and light infections of *H. aduncum* (<10) (Figs. 2–5). Fish sampled in 2000 from station 21 in the southern Bay of Biscay had a similar pattern of nematode infection to those from stations 02 and 03, but in 2001 they were very different and had a pattern almost identical to those from station 07 off north-west Spain, with light infections of both nematodes.

Some anomalous individual fish could be clearly distinguished from all other fish in the same sample by their markedly different patterns of nematode infection. In sample 05.00, three fish with heavy infections of *Anisakis* spp. (>300 worms) stood out starkly from all the other lightly infected fish. Other anomalous individuals found were: one in sample 01.01 from off south-west Norway, one in sample 02.00 to the west of Ireland, and two in sample 03.00 southwest of Ireland, all identified by nematode infections more typical of station 05.

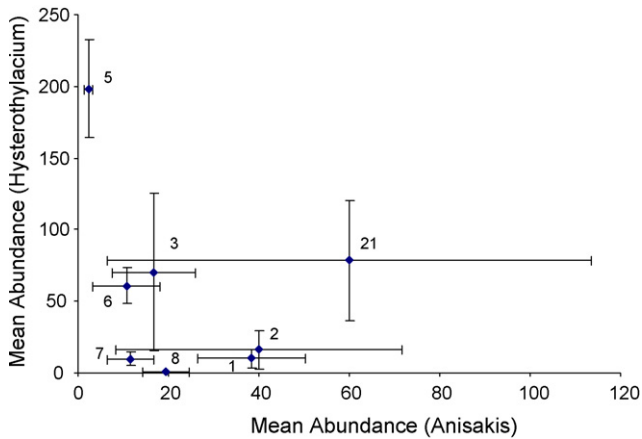


Fig. 2. Relative mean abundances of *Anisakis* and *Hysterothylacium* larvae in horse mackerel aged from 5 to 9 years from Atlantic samples taken in 2000. Lines are 95% confidence limits.

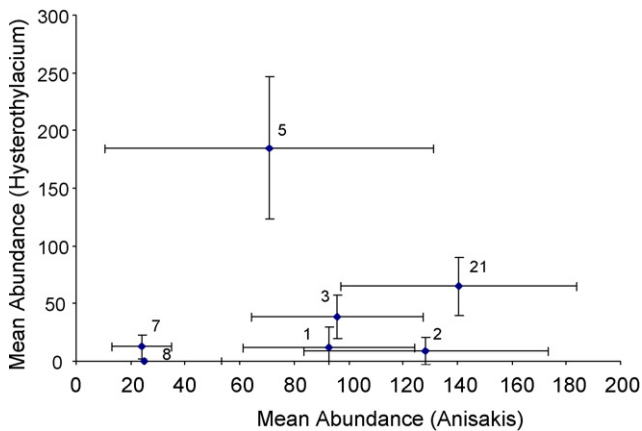


Fig. 3. Relative mean abundances of *Anisakis* and *Hysterothylacium* larvae in horse mackerel aged 10 years and older from Atlantic samples taken in 2000.

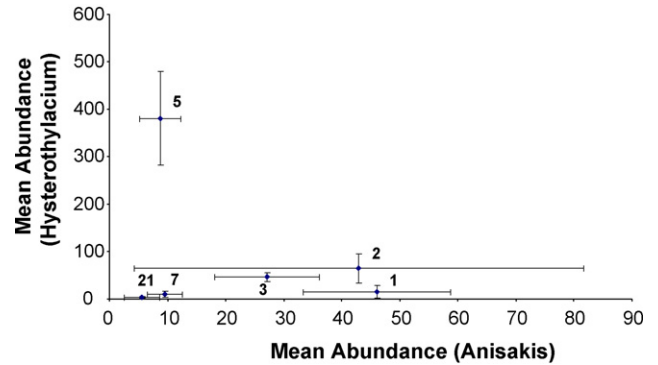
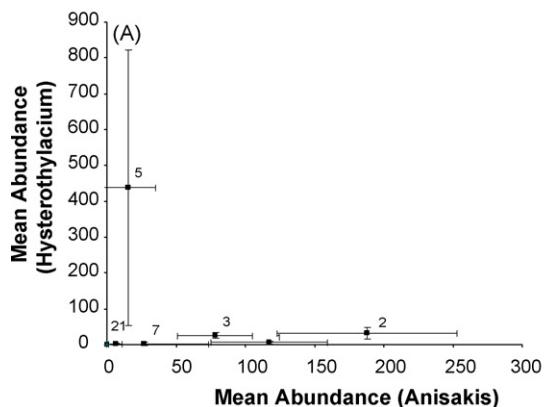


Fig. 5. Relative mean abundances of *Anisakis* and *Hysterothylacium* larvae in horse mackerel aged 11 years and older from Atlantic samples taken in 2001. A, showing all samples; B, to larger scale for *Hysterothylacium* and excluding sample 05.01. Lines are 95% confidence limits.

Fig. 4. Relative mean abundances of *Anisakis* and *Hysterothylacium* larvae in horse mackerel aged from 6 to 10 years from Atlantic samples taken in 2001. Lines are 95% confidence limits.

Single larvae of *P. decipiens* and an unidentified nematode larva were found in samples 12.01 and 16.01, respectively.

3.9. Crustacea

Seven species of crustacean parasites were found, comprising four copepods, two isopods and one branchiuran. None was common, the most frequently recorded being the copepod *Lernanthropus trachuri*, found as single infections on five fish from samples 18.00 and 19.00 taken in the south-central Mediterranean. Single infections of another copepod, *Caligus elongatus*, were found on two fish, and single specimens of each of two other copepods, *Caligus pelamydis* and *Peniculus fistula*, were recorded. Single specimens were recorded of a praniza larva of a gnathiid isopod, the adult isopod *Ceratothoa oestroides* and the branchiuran *Argulus purpureus*.

4. Discussion

4.1. Apicomplexa

Prevalence of the coccidian *G. cruciata* differed significantly between samples within both the Atlantic and Mediterranean

Table 4
Prevalence (%) of different parasites in stations sampled in 2001

Parasite	Sample number																			
	01	02	03	05	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	
<i>G. cruciata</i>	2	53	77	90	52	86	90	85	2	33	58	35	52	36	28	76	50	22	48	
<i>A. serenum</i>	0	21	15	0	0	–	–	–	2	0	–	–	0	0	–	–	–	0	0	
<i>A. solomoni</i>	0	0	0	0	0	–	–	–	0	0	–	–	14	22	0	–	–	0	0	
<i>K. nova</i>	0	0	0	0	2	0	0	0	6	0	0	0	0	0	0	0	0	0	0	
<i>Kudoa</i> sp.	0	0	6	0	0	–	–	–	0	0	–	–	0	0	0	–	–	0	0	
<i>Myxobolus spinicurvatura</i>	0	0	0	0	0	–	–	–	0	0	–	–	0	2	0	–	–	0	0	
<i>Gastrocotyle trachuri</i>	2	0	6	62	26	62	79	86	40	2	0	29	18	36	4	44	38	47	24	
<i>Pseudaxine trachuri</i>	0	0	1	18	2	12	27	34	4	0	0	0	2	0	0	2	0	4	4	
<i>Heteraxinoides atlanticus</i>	0	0	0	0	0	10	8	2	0	0	0	0	0	0	0	0	0	0	0	
<i>Paradiplectanotrema trachuri</i>	0	0	0	0	0	0	0	0	0	0	4	0	7	0	0	6	32	0	0	
<i>Cemocotyle trachuri</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Lasiotocus typicus</i>	0	3	1	0	0	–	–	–	0	0	0	0	0	0	0	0	0	2	2	
<i>B. elongatum</i>	0	0	0	0	0	–	–	–	0	0	0	0	0	0	0	0	2	0	0	
<i>Lasiotocus tropicus</i>	0	0	0	0	0	–	–	–	0	0	0	0	0	0	0	0	0	0	0	
<i>D. varicus</i>	0	0	0	26	0	–	–	–	0	0	0	0	0	0	0	0	0	0	4	
<i>E. lepidus</i>	0	0	0	6	0	–	–	–	6	0	0	0	7	4	0	0	0	8	14	
<i>Hemiurus communis</i>	0	0	0	12	0	–	–	–	0	0	0	0	0	0	0	0	0	0	0	
<i>Lecithocladium excisum</i>	0	0	0	0	0	–	–	–	0	0	0	0	0	0	0	0	0	0	0	
<i>Monascus filiformis</i>	0	0	0	6	0	–	–	–	0	2	0	0	0	0	0	0	0	8	2	
<i>Opechona bacillaris</i>	0	0	0	0	0	–	–	–	0	0	0	0	0	0	0	0	0	0	0	
<i>Pseudopoeoeloides chloroscomberi</i>	0	0	0	0	0	–	–	–	0	0	0	0	0	0	0	0	0	0	22	
<i>Prodistomum polonii</i>	0	0	0	0	2	–	–	–	0	2	0	0	2	0	0	0	0	2	2	
<i>Tergestia laticollis</i>	0	12	9	26	0	–	–	–	0	6	0	0	0	2	0	0	0	2	4	
<i>Grillotia</i> sp.	2	0	11	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>N. lingualis</i>	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Pseudophyllidean plerocercoids	0	0	0	0	0	0	0	0	0	0	0	0	20	10	0	0	0	0	0	
<i>S. pleuronectis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>C. strumosum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>C. wegneri</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>R. cadenati</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Anisakis</i> spp.	100	95	100	90	88	86	37	39	4	2	100	100	100	92	30	100	98	2	78	
<i>H. aduncum</i> larvae	78	95	98	100	68	0	0	0	16	21	12	20	2	22	0	6	4	22	64	
<i>H. aduncum</i> adults	2	2	4	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Unidentified nematode larva	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	
<i>P. decipiens</i>	0	3	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	
<i>Argulus purpurea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Caligus elongatus</i>	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	
<i>Caligus pelamydis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Peniculus fistula</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>L. trachuri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ceratothoa oestroides</i>	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	
Praniza larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

regions. Stations 01 and 11 had significantly lower levels of infection than all other Atlantic samples, while stations 15 and 20 (in both years) had significantly lower levels than all other Mediterranean samples. Prevalence of infection does not appear to be related to host length or age, but levels of infection or the occurrence of different developmental stages may vary seasonally, so we can consider this parasite only as a potential biological tag pending further information on its life cycle and ecology.

4.2. Myxosporea

Given more information on their geographical distributions at different times of the year, the two myxosporean species

Alataspora serenum and *A. solomoni* could be used to follow migrations of *T. trachurus* and to estimate the extent of mixing between stocks. *A. serenum* was found only in Atlantic samples, mainly from the Celtic Sea area, while *A. solomoni* was found only in the eastern Mediterranean. *A. solomoni* was originally described from *T. mediterraneus ponticus* in the Black Sea by Yurakhno (1988), who recorded a prevalence of 42% in this host near Sevastopol. We have no information on the occurrence of either parasite in the central and western Mediterranean and off the coast of Portugal. Examinations of samples from these areas would provide the information needed to use these myxosporeans as biological tags. *M. spinicurvatura* was originally described by Maeno et al. (1990) from mullet *Mugil cephalus* in Japan.

Table 5
Mean intensities of the more common parasites from stations sampled in 2001, with 95% confidence limits in parentheses for anisakid nematode larvae

Parasite	Sample Number																				
	01	02	03	05	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21		
<i>Gastrocoyle trachuri</i>	1.0	0	1.5	3.1	1.4	4.7	8.7	6.7	1.7	2.0	0	1.5	1.5	2.2	2.0	2.7	2.3	4.3	1.4		
<i>Pseudaxine trachuri</i>	0	0	1.0	1.4	1.0	1.3	1.4	2.1	1.0	0	0	0	1.7	0	0	1.0	0	1.5	1.5		
<i>Heteraxinoides atlanticus</i>	0	0	0	0	0	1.5	1.3	1.0	0	0	0	0	0	0	0	0	0	0	0		
<i>Paradiplectanotrema trachuri</i>	0	0	0	0	0	0	0	0	0	0	1.0	0	1.0	0	0	1.0	1.6	0	0		
<i>B. elongatum</i>	0	0	0	0	0	—	—	—	0	0	0	0	0	0	0	0	1.0	0	0		
<i>Lastiocus tropicus</i>	0	0	0	0	0	—	—	—	0	0	0	0	0	0	0	0	0	0	0		
<i>D. varicus</i>	0	0	0	2.7	0	—	—	—	0	0	0	0	0	0	0	0	0	1.0	0		
<i>E. lepidus</i>	0	0	0	7.0	0	—	—	—	1.7	0	0	0	1.3	1.0	0	0	0	1.3	1.2		
<i>Hemiramus communis</i>	0	0	0	8.0	0	—	—	—	0	0	0	0	0	0	0	0	0	0	0		
<i>Monacrus filiformis</i>	0	0	0	5.0	0	—	—	—	0	4.0	0	0	0	0	0	0	0	2.5	1.0		
<i>O. bacillaris</i>	0	0	0	0	0	—	—	—	0	0	0	0	0	0	0	0	0	0	0		
<i>Prodistomum polonii</i>	0	0	0	0	1.0	—	—	—	0	2.0	0	0	1.0	0	0	0	0	1.0	1.0		
<i>Tergestia latifollis</i>	1.0	7.0	3.0	3.5	0	—	—	—	0	1.3	0	0	0	1.0	0	0	0	1.0	2.5		
<i>Grillotia</i> sp.	2.0	0	1.7	1.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Anisakis</i> spp. larvae	84.5 (±25.1)	135.2 (±49.2)	40.6 (±10.7)	12.8 (±4.8)	11.5 (±5.1)	18.3 (±3.9)	2.2	1.4	1.5	1.0	72.8 (±12.1)	153.3 (±44.9)	217.5 (±54.6)	129.4 (±25.1)	46.7 (±13.7)	80.7 (±3.7)	25.8 (±7.3)	1.0	7.2 (±3.1)		
<i>H. aduncum</i> larvae	13.1 (±8.2)	48.2 (±16.6)	41.1 (±6.2)	323.3 (±81.8)	10.2 (±6.4)	0	0	0	1.9	2.4	1.2	1.4	3.0	2.6 (±1.0)	0	1.0	1.0	1.1	5.5 (±1.6)		
<i>H. aduncum</i> adults	1.0	0	1.0	1.8	0	0	0	0	360	0	1.2	0	0	0	0	0	0	0	0		

4.3. Monogenea

Heteraxinoides atlanticus was found in over 5% of fish from stations 08, 09 and 10 taken off the coast of Portugal and was also found in fish from stations 01, 03, 17 and 21. This monogenean is a characteristic parasite of *Trachurus* spp. caught off the west coast of Africa to the south of the present study area. Gaevskaya and Kovaleva (1979) reported 20–40% prevalence of *Heteraxinoides atlanticus* in *T. trachurus* caught in an area off West Africa to the south of our southernmost station 11. The same authors (Gaevskaya and Kovaleva, 1980b) failed to find it in samples of the same host caught further north as far as the North Sea. Gaevskaya and Kovaleva (1980a) reported it from *T. capensis* caught off the southwest coast of Africa, and Gaevskaya and Kovaleva (1985) reported it from *T. picturatus* caught off Western Sahara but not from the same host caught around the Azores. The records of *Heteraxinoides atlanticus* from the present study indicate migrations of *T. trachurus* from West Africa northwards as far as southwest Norway and into the extreme western part of the Mediterranean.

Cemocotyle trachuri is also more characteristic of *Trachurus* spp. caught outside the HOMSIR study area. Gaevskaya and Kovaleva (1979) reported it from 24% of *T. trachurus* caught off Western Sahara and in 1–2% of *T. capensis* caught off Namibia. The same authors (Gaevskaya and Kovaleva, 1980b) also reported a single specimen in a *T. trachurus* caught in the northwestern North Sea, some distance to the west of our North Sea station 05 and closer to our station 01, where we found one of the only two specimens recorded in the present study. Gaevskaya and Kovaleva (1985) found *Cemocotyle trachuri* in *T. picturatus* caught off Western Sahara and at the Azores. Our two records of this monogenean from off southwest Norway and off the coast of Portugal are thus further evidence of migrations of *T. trachurus* from West Africa into European waters.

The endoparasitic monogenean *Paradiplectanotrema trachuri* was found in Mediterranean samples only and was most common in fish from stations 18 and 19. Its occurrence in *T. trachurus* and *T. mediterraneus* was reported by Kovaleva (1970), while Dimitrov (1991) reported it from *T. mediterraneus ponticus* in the Black Sea, and Gaevskaya and Kovaleva (1980b, 1985) from *T. trachurus* and *T. picturatus* from Gibraltar southwards along the coast of Africa to 23°N. The latter authors found no infections in samples of *T. trachurus* taken north of Gibraltar.

4.4. Digenea

The only digenean of any significance as a biological tag is *B. elongatum*, because it was found only in fish from stations 13 and 19 in the central Mediterranean. This is the first record of this species from *T. trachurus*, and its occurrence in this host only in the central Mediterranean probably reflects the different feeding habits of *T. trachurus* in this area.

4.5. Cestoda

The only cestodes of any significance as biological tags are the pseudophyllidean plerocercoids, because they were

found only in samples 15 and 16 from the eastern Mediterranean.

4.6. *Acanthocephala*

Two specimens of *R. cadenati* found in fish from sample 10.00 provide evidence of northward migrations of *T. trachurus* from West Africa. Gaevskaya and Kovaleva (1980a) reported the occurrence of this acanthocephalan in *T. trachurus* caught off West Africa and the same authors (Gaevskaya and Kovaleva, 1985) reported it from *T. picturatus* caught off Western Sahara and the Azores. Ours is the first record of *R. cadenati* from European waters. *R. cadenati* also parasitises a wide range of other teleost fish species off West Africa (see Golvan, 1969).

4.7. *Nematoda*

The most effective biological tags to emerge from this study are the larval nematodes *Anisakis* spp. and *H. aduncum*. The distinctive pattern of infection with these nematodes observed in samples from the North Sea station 05 clearly distinguishes it from the nearest stations 01, 02, 03 and 06, and supports the current management strategy which treats the North Sea population as a separate stock. The three anomalous fish in sample 05.00, identified by infections more characteristic of fish from the putative ‘western’ stock area, indicate that some migration does occur from western areas into the North Sea and provides a means of estimating the extent of such migration. The fact that these were three of the oldest fish in the sample at ages 12, 18 and 18 years may also be significant. The distinction between the ‘western’ and ‘southern’ stocks is less clear. The significant differences in levels and patterns of nematode infection in the two samples from station 21 suggests that the southern Bay of Biscay is an area of mixing between these two stocks. Sample 21.00 had a similar pattern of nematode infection to samples 02.00 and 03.00, whereas sample 21.01 was markedly different from 02.01 and 03.01 but almost indistinguishable from 07.01 from northwest Spain. The geographical distributions of the different species of *Anisakis* also provide useful clues to horse mackerel stock structure (see Mattiucci et al., 2008).

4.8. *Crustacea*

The copepod *L. trachuri* was found only in fish from stations 18 and 19 in the central Mediterranean. It was originally described from *T. trachurus* caught in the Ligurian Sea off the coast of Italy (Brian, 1903), but has also been reported from *T. picturatus* caught off Western Sahara and the Azores by Gaevskaya and Kovaleva (1985), and from *T. capensis* caught off Namibia by Piasecki (1982).

5. Conclusions

1. In the Atlantic part of the HOMSIR study area, there is strong evidence from the occurrence of the larval nematodes *Anisakis* spp. and *H. aduncum* that the North Sea population of *T. trachurus* should continue to be treated as a

separate stock, but there is also evidence of some migration from areas to the west of the British Isles into the North Sea, possibly restricted to older fish. The distinction between the putative ‘western’, ‘southern’ and ‘mauritanian’ stocks is less clear, with evidence of considerable mixing between populations. The occasional occurrence in some of our northern samples of parasites known to be more common in *Trachurus* spp. populations off West Africa indicates migration of *T. trachurus* from West Africa as far north as south-west Norway. These indicator parasites are the monogeneans *Heteraxinoides atlanticus* and *Cemocotyle trachuri* and the acanthocephalan *R. cadenati*. It is also possible, however, that the monogeneans could have been carried into European waters with northward migrating *T. picturatus* and cross-infection of *T. trachurus* could have occurred there. This is possible because the two monogeneans have direct single-host life cycles. This caveat does not apply to the acanthocephalan *R. cadenati*, which has an indirect life cycle involving unknown crustacean intermediate hosts. The southern endemic area for *R. cadenati* is determined by environmental factors, the major one probably being temperature, and by the geographical distribution of its intermediate hosts. The *T. trachurus* from our study could therefore only have become infected through feeding within this southern area.

2. The localised distributions of *A. solomoni*, *Paradiplectanotrema trachuri*, *B. elongatum*, pseudophyllidean plerocercoids and *L. trachuri* suggest the existence of three distinct subpopulations of *T. trachurus* in the Mediterranean Sea—western, central and eastern. There is also strong evidence from the distribution of the monogenean *Heteraxinoides atlanticus* of migration of fish from Atlantic populations into the extreme western part of the Mediterranean. Further support for this conclusion comes from the fact that the two fish from sample 17.00 (western Mediterranean) infected with *Heteraxinoides atlanticus* were also two of only four fish in that sample infected with the nematode *Anisakis simplex sensu stricto*, which is characteristic of Atlantic horse mackerel (see Mattiucci et al., 2008).

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Appendix A

There are relevant new data from two short follow-up studies (thesis dissertations from Sylianteng and Macdonald, The University of Aberdeen, UK, personal communication) since this paper was completed. In the first, a sample of 25 *T. trachurus* caught at station 08 off the west coast of Portugal in July 2004 were examined for parasites. Three fish from this sample were infected with the acanthocephalan *R. cadenati*, thereby lending further support to the hypothesis that some *T. trachurus* found in this area are migrants from West Africa. In the second, a sample of 70 *T. trachurus* caught off the village of Larache on the north-

ern Atlantic coast of Morocco in February 2004, were examined. Thirty-nine fish from this sample (55.7%) were infected with a total of 106 *R. cadenati* (mean intensity 2.7), providing further support for the same hypothesis by showing that fish from this area do carry moderately heavy infections of this acanthocephalan, and also supporting the current placement of the boundary between the Southern and Moroccan-Saharan stocks. The fish in the Moroccan sample were significantly larger than those in sample 11 from off Mauritania, and showed a pattern of increasing prevalence and intensity of infection of *R. cadenati* with length, which possibly explains the absence of this parasite from sample 11.

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