*Journal of Helminthology* (2018) **92**, 90–99
doi:10.1017/S0022149X17000104

# Helminth parasites of the chub mackerel *Scomber colias* off the Tunisian coast and their use in stock discrimination

**M. Feki*, M. Châari, L. Neifar and L. Boudaya**

Laboratoire de Biodiversité et Ecosystèmes Aquatiques, Département des
Sciences de la Vie, Faculté des Sciences de Sfax, Université de Sfax,
BP 1171, 3000 Sfax, Tunisie

(Received 5 September 2016; Accepted 24 January 2017; First published online 20 February 2017)

## Abstract

Nine helminth parasites were used as biological tags to discriminate diverse areas of *Scomber colias* Gmelin, 1789. During three seasons, a total of 369 fish were examined in four zones off the Tunisian coast, including Bizerte in the north, Kelibia and Mahdia in the centre and Zarzis in the south. Discriminant analyses were used to identify distinct areas of *S. colias*. Fish from Bizerte were grouped as one area and were correlated negatively with the monogenean *Grubea cochlear* and the digenean *Lecithocladium excisum*. Specimens from Kelibia and Mahdia were grouped together and were characterized by the ectoparasite *Pseudokuhnia minor* and by endoparasites *Prodistomum orientalis*, *Monascus filiformis* and anisakid larvae. Fish from Zarzis were grouped as one area and were positively correlated with the monogenean *G. cochlear* and the digenean *L. excisum*. These results were corroborated by comparing the prevalence and mean abundance of parasites among zones. Results of other discriminant analyses used for the classification of *S. colias* between localities after pooling specimens from the central areas of Kelibia and Mahdia also allowed the identification of three distinct areas: one in the north, correlated negatively with *G. cochlear* and *L. excisum;* one in the centre, characterized by *P. minor*, *P. orientalis*, *M. filiformis* and anisakid larvae; and one in the south, from Zarzis, characterized by *G. cochlear* and *L. excisum*. Results of comparisons of infection parameters between seasons and those of seasonal discrminant analyses showed a seasonal stability of communities from the northern and the southern areas. Specimens from the central regions showed variability between seasons, suggesting migratory movements.

## Introduction

The chub mackerel *Scomber colias* Gmelin, 1789, is a small pelagic fish with great commercial importance in Tunisia. According to the national fishery statistics of Tunisia, this species has a high economic value, with a production of approximately 4725 tons in 2011, and it constitutes a considerable biomass, with a potential fishery resource of ∼11,750 tons in 2009. *Scomber colias* is widely distributed in Tunisian waters, but this distribution varies between localities and seasons (Ben Abdallah & Gaamour, 2004). Catches have undergone several fluctuations during the present decade in various areas of Tunisia (Ben Abdallah & Gaamour, 2004). Indeed, the highest production was recorded in the eastern region, while the lowest was reported in the northern area. Seasonal variability of the distribution of *S. colias* is related to the seasonal variation of the activity of the fishing fleets and the availability of resources (Ben Abdallah & Gaamour, 2004). This species, like many pelagic fishes, migrates in search of spawning grounds and optimal conditions for larvae (Binet, 1995; Pauly, 1997).

---

*E-mail: Feki_mariam@yahoo.fr

The parasite fauna of *S. colias* from the Mediterranean Sea has been studied by several authors. Akmirza (2013) reported the monogeneans *Grubea cochlear* (Diesing, 1858), *Kuhnia scombri* (Kuhn, 1829) and *Pseudokuhnia minor* (Rhode and Watson, 1985). Bray & Gibson (1997) recorded the digeneans *Prodistomum orientalis* (Layman, 1930), *Opechona bacillaris* (Molin, 1859), *Monascus filiformis* (Rudolphi, 1819) Loss, 1907 and *Lecithocladium excisum* (Lûhe, 1901), *Ectenurus lepidus* Looss, 1907 and *Tergestia acanthocephala* (Stossich, 1887). Oliva *et al.* (2008) found the nematodes *Hysterothylacium aduncum* (Rudolphi, 1802) and *Anisakis simplex* (Rudolphi, 1809).

Using parasites as biological tags to provide information regarding the stock discreteness of their fish hosts is an established methodology, and is broadly accepted as a tool for use in resolving fishery management problems (Lester, 1990; Williams *et al.*, 1992; MacKenzie & Abaunza, 1998; MacKenzie, 2002). It is also a promising tool for predicting harvest locations and can be used as an aid in combating illegal fishing (Power *et al.*, 2005). This method is more appropriate for studies of small pelagic fishes such as Scombridae (Costa *et al.*, 2011), because it is inexpensive and eliminates doubts concerning the possible abnormal behaviour of artificially tagged hosts (Williams *et al.*, 1992; Arthur, 1997). Parasites have been used mainly in fish population studies (MacKenzie & Abaunza, 2005; Mackenzie *et al.*, 2008; Marcogliese & Jacobson, 2015; Timi & Mackenzie, 2015). Discriminating between distinct populations of the same species of commercially exploited fish is essential, not only to determine their dynamics and manage their long-term sustainability but also to identify violations of fishing rights (Hilboran & Walters, 1992). The stock discrimination of *S. colias* from the Atlantic and the Mediterranean Sea has been studied using parasitological, biometric, genetic and fishery methods (Roldán *et al.*, 2000; Tzong-Der & Shean-Yahyeh, 2007; Oliva *et al.*, 2008; Crone *et al.*, 2009).

In Tunisia, most studies have determined the biology of this species. Hattour (2000) studied its growth, its cycle of reproduction, its biometry and the composition of its diet. Derbel *et al.* (2012) investigated its parasites and collected only digeneans. Ktari-Chakroun & Azouz (1971), Ben Othman (1973), Hattour (2000), Hattour *et al.* (2004) and Ben Abdallah & Gaamour (2004) studied the geographical distribution and the estimation of the biomass of *S. colias* along the Tunisian coast in different seasons, using acoustic methods, and they showed geographical and seasonal variability of this species. Despite its importance in the regional fishery, no study investigated the diverse areas of this species.

The aim of the present study was to assess the occurrence of seasonal and geographical variability using parasites as biological tags for identifying distinct areas for *S. colias* off the Tunisian coast.

## Materials and methods

### *Study area and examination of samples*

A total of 369 specimens of *S. colias* from 12 distinct fish samples were collected between September 2010 and August 2011 at four fishing localities off the coast of Tunisia, i.e. Bizerte (37°16′N, 9°52′E) in the north, Kelibia (36°50′N, 11°10′E) and Mahdia (35°30′ N, 11°5′E) in the centre and Zarzis (33°40′N, 10°30′E) in the south. Samples were obtained during three seasons (summer, spring and autumn–winter). Only one sample was released in the autumn for the autumn–winter season. Indeed, *S. colias* was not available for landing in the winter, due to bad meteorological conditions. Samples were kept fresh, or deep frozen in plastic bags at −10°C, until examination in the laboratory.

After defrosting, the total length of each fish was measured; mean total lengths of fish from Bizerte, Kelibia, Mahdia and Zarzis were 170.5 ± 1.03 mm; 171 ± 1.03 mm, 171.2 ± 1.04 mm and 167 ± 1.51 mm, respectively. Each specimen was systematically examined for parasites. For ectoparasites, the body of the fish was observed under a stereomicroscope with incident light. Fins, buccal cavity, nasal pits and eyes were thoroughly examined. Gill arches were separated by incision, removed, rinsed and examined individually. Finally, for endoparasites, the internal organs (heart, liver, spleen, gall bladder and gonads) were separated and examined individually. The stomach, pyloric caeca and intestine were separated, opened longitudinally and their contents rinsed into beakers where they were allowed to settle to remove endoparasitic helminths.

### *Data analysis*

Prevalence and mean abundance were calculated following Bush *et* al. (1997) for each parasite. Non-parametric analyses were performed to evaluate the characteristics of the infections at the population and community levels. A univariate analysis was performed to evaluate the infections at infrapopulation levels for parasites with a prevalence >5%. Chi-square analyses and *a posteriori* multiple comparisons for proportions were used to test for significant differences in prevalence between seasons in each locality and between zones. Kruskall–Wallis and *a posteriori* Dunn's tests or Mann–Whitney tests were used to analyse the effects of season in each locality and between zones on abundance of each parasite species (Zar, 1996). Analysis of variance (ANOVA) and *a posteriori* Tukey tests for unequal samples on $\log_{10}(x + 1)$ transformed data were used to analyse the effects of locality on the total length of *S. colias* (Zar, 1996). Discriminant analyses, based on Mahalanobis distances, were used to find differences between zones and to identify which parasite species were responsible for these differences. Indeed, for each group of our sample, we can determine the position of the average representative point of all variables in the multivariate space defined by the variables in the model. These points are called centroids of groups or centres of gravity. For each case, we can then calculate the Mahalanobis distances (respective observations) at each of the centres of gravity. Again, we will classify cases in the group they are closest to, that is to say with the weakest Mahalanobis distance (Highland Statistics, 2000). This was applied using the software package SPSS 18 (SPSS Inc., Chicago, Illinois, USA).

## Results

The mean values of host total lengths from the four samples landed at Tunisian coasts ranged from 16.7 to

Table 1. The prevalence and mean abundance of infection of *Scomber colias* with helminth species in four localities off the coast of Tunisia; mean values are given ± standard deviation.

| | Prevalence (%) | | | | Mean abundance | | | |
|---|---|---|---|---|---|---|---|---|
| | Bizerte | Kelibia | Mahdia | Zarzis | Bizerte | Kelibia | Mahdia | Zarzis |
| Monogenea | | | | | | | | |
| *Kuhnia scombri* | 0 | 12.76 | 14.44 | 10.52 | 0 | 0.12 ± 0.33 | 0.33 ± 0.98 | 0.1 ± 0.37 |
| *Pseudokuhnia minor* | 0 | 7.44 | 6.66 | 3.15 | 0 | 0.07 ± 0.26 | 0.11 ± 0.43 | 0.03 ± 0.17 |
| *Grubea cochlear* | 0 | 7.44 | 3.33 | 26.31 | 0 | 0.07 ± 0.26 | 0.03 ± 0.18 | 0.44 ± 0.84 |
| Digenea | | | | | | | | |
| *Prodistomum orientalis* | 0 | 17.02 | 18.88 | 8.42 | 0 | 0.26 ± 0.81 | 0.22 ± 0.51 | 0.08 ± 0.27 |
| *Opechona bacillaris* | 14.44 | 7.44 | 18.88 | 7.36 | 0.14 ± 0.35 | 0.2 ± 0.83 | 0.86 ± 2.45 | 0.23 ± 0.85 |
| *Lecithocladium excisum* | 10.00 | 42.55 | 54.44 | 68.42 | 0.10 ± 0.30 | 1.58 ± 2.85 | 2.18 ± 3.03 | 1.84 ± 1.85 |
| *Monascus filiformis* | 0 | 13.82 | 9.67 | 0 | 0 | 0.14 ± 0.38 | 0.09 ± 0.30 | 0 |
| Acanthocephala | | | | | | | | |
| *Rhadinorhynchus* sp. | 8.88 | 5.31 | 16.66 | 6.31 | 0.08 ± 0.28 | 0.05 ± 0.22 | 0.16 ± 0.37 | 0.06 ± 0.24 |
| Nematoda | | | | | | | | |
| Anisakid larvae | 21.11 | 34.04 | 46.66 | 20.00 | 0.43 ± 0.94 | 0.7 ± 1.26 | 1.00 ± 1.21 | 0.35 ± 0.79 |

17.12 cm and were not significantly different between zones ($F = 2.66$, $P > 0.05$).

A total of 1113 helminth parasites belonging to nine species were found infecting *S. colias* (table 1). Three monogeneans *Grubea cochlear* (Diesing, 1858), *Kuhnia scombri* (Kuhn, 1829) and *Pseudokuhnia minor* (Rhode and Watson, 1985) were collected from the gills. Four digeneans *Prodistomum orientalis* (Layman, 1930), *Opechona bacillaris* (Molin, 1859), *Monascus filiformis* (Rudolphi, 1819) Loss, 1907 and *Lecithocladium excisum* (Lûhe, 1901), one acanthocephalan *Rhadinorhynchus* sp. and nematode anisakid larvae were found from the digestive tract. All parasite species with a prevalence >5% in at least one season and one zone were included in the analyses of classification of *S. colias* between seasons and between localities.

Infection parameters of parasites showed seasonal differences in each locality (table 2). Prevalence and mean abundance of six and five parasites species varied between seasons in Kelibia and Mahdia, respectively, while only one parasite species showed significant seasonal differences in both infection parameters in Zarzis and Bizerte. Some parasites were absent in one season and present in another.

In seasonal multivariate parasitological analysis, all sampled specimens collected in each locality were separated into three seasons, giving 12 groups in total (locality–season). This analysis, used to identify distinct areas of *S. colias* between locality–season, was carried out according to traditional procedures and showed a significant difference between groups (Wilks' lambda = 0.229, $F = 9.08$, $\chi^2 = 529.6$, df = 66, $P < 0.01$) (fig. 1a). Fish were classified correctly to the 12 component areas with an accuracy of 30%. Three groups were discriminated: one including fish from Bizerte in the three seasons, specimens from Kelibia in summer, and those from Mahdia in autumn–winter and in summer correlated negatively with monogeneans *G. cochlear* and *P. minor*, and endoparasites *L. excisum*, *O. bacillaris*, *P. orientalis*, and anisakid larvae; one grouped specimens from Kelibia and Mahdia in spring related to digeneans *O. bacillaris* and *L. excisum*, and anisakid larvae; and one grouped fish from Zarzis in three seasons and those from Kelibia in autumn–winter correlated positively with *G. cochlear* (fig. 1b).

In each locality, all sampled specimens collected in three seasons were pooled. We did not find monogeneans *G. cochlear*, *K. scombri* and *P. minor* or digeneans *P. orientalis* and *M. filiformis* in *S. colias* from Bizerte. In specimens from Zarzis, we did not record *M. filiformis* (table 1). The comparisons of infection parameters for parasites present in the four chub mackerel populations studied showed that all parasite species vary significantly in both prevalence and mean abundance of infection between localities. The prevalence or the mean abundance of more than three parasites differed significantly among localities. Of the areas studied, Bizerte showed the greatest variation in infection parameters of helminth parasites. The prevalence and mean abundance of these species were less in Bizerte than in other localities.

A multivariate parasitological analysis used to identify distinct areas of *S. colias* between localities was carried out according to traditional procedures and showed a significant difference between groups (Wilks' lambda = 0.583, $F = 11.88$, $\chi^2 = 195.66$, df = 18, $P < 0.01$) (fig. 2a). Fish were classified correctly to the four component areas with an accuracy of 49.9%. Three groups were separated: one including fish from Bizerte correlated negatively with *G. cochlear* and *L. excisum*; one grouped specimens from Kelibia and Mahdia related to anisakid larvae, *P. orientalis* and *L. excisum*; and one grouped fish from Zarzis correlated positively with *G. cochlear* and *L. excisum* (fig. 2b).

A multivariate parasitological analysis used for the classification of *S. colias* between localities after pooling specimens from Kelibia and Mahdia was carried out according to traditional procedures and showed a significant difference between groups (Wilks' lambda = 0.623, $F = 16.04$, $\chi^2 = 171.85$, df = 12, $P < 0.01$) (fig. 3a). Fish were classified correctly to the three component areas with an accuracy of 69.3%. The same three groups were identified: one group from the north was correlated negatively with *G. cochlear* and *L. excisum*; one group from the centre was related to *P. minor*, *P. orientalis*, *M. filiformis* and anisakid larvae; and one group from the south was characterized by *G. cochlear* and *L. excisum* (fig. 3b).

Table 2. Comparisons of the prevalence and mean abundance of selected helminth parasites from *Scomber colias* at four localities in each season off the Tunisian coast; mean values are given ± standard deviation; BI, Bizerte; KE, Kelibia; MH, Mahdia; ZA, Zarzis.

| | | Prevalence (%) | | | | Mean abundance | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Seasons | Bi | KE | MH | ZA | BI | KE | MH | ZA |
| *Kuhnia scombri* | Autumn-Winter | 0 | 12.9 | 0 | 10 | 0 | 0.129 ± 0.34 | 0 | 0.13 ± 0.43 |
| | Spring | 0 | 9.67 | 43.33 | 6.66 | 0 | 0.09 ± 0.30 | 1 ± 1.50 | 0.1 ± 0.40 |
| | Summer | 0 | 15.15 | 0** | 8.57 | 0 | 0.15 ± 0.36 | 0** | 0.08 ± 0.28 |
| *Pseudokuhnia minor* | Autumn–Winter | 0 | 0 | 0 | | 0 | 0 | 0 | |
| | Spring | 0 | 0 | 20 | | 0 | 0 | 0.33 ± 0.71 | |
| | Summer | 0 | 21.21** | 0** | | 0 | 0.21 ± 0.41** | 0** | |
| *Grubea cochlear* | Autumn–Winter | 0 | 0 | 10 | 25.52 | 0 | 0 | 0.1 ± 0.30 | 0.4 ± 0.82 |
| | Spring | 0 | 0 | 0 | 26.66 | 0 | 0 | 0 | 0.5 ± 0.93 |
| | Summer | 0 | 21.21** | 0** | 26.81 | 0 | 0.21 ± 0.41** | 0* | 0.5 ± 0.9 |
| *Prodistomum orientalis* | Autumn–Winter | 0 | 32.25 | 13.33 | 6 | 0 | 0.61 ± 1.30 | 0.13 ± 0.34 | 0.06 ± 0.25 |
| | Spring | 0 | 0 | 23.33 | 10 | 0 | 0 | 0.33 ± 0.71 | 0.1 ± 0.30 |
| | Summer | 0 | 18.18** | 20 | 8.57 | 0 | 0.18 ± 0.39** | 0.2 ± 0.40 | 0.08 ± 0.28 |
| *Opechona bacillaris* | Autumn–Winter | 6.66 | 6.45 | 13.33 | 6 | 0.06 ± 0.25 | 0.22 ± 0.88 | 0.13 ± 0.34 | 0.26 ± 1.01 |
| | Spring | 13.3 | 16.12 | 43.33 | 6.66 | 0.13 ± 0.34 | 0.38 ± 1.16 | 2.46 ± 3.78 | 0.23 ± 0.89 |
| | Summer | 23.3** | 0** | 0** | 8.57 | 0.23 ± 0.43 | 0 | 0** | 0.2 ± 0.67 |
| *Lecithocladium excisum* | Autumn–Winter | 20 | 67.74 | 16.66 | 66.6 | 0.2 ± 0.40 | 2.96 ± 3.46 | 0.26 ± 0.69 | 1.5 ± 1.45 |
| | Spring | 10 | 51.61 | 90 | 73.33 | 0.1 ± 0.30 | 1.74 ± 2.99 | 5.2 ± 3.44 | 2.4 ± 1.99 |
| | Summer | 0** | 9** | 56.66** | 65.71 | 0* | 0.09 ± 0.29** | 1.1 ± 1.24** | 1.65 ± 1.98 |
| *Monascus filiformis* | Autumn–Winter | 0 | 19.35 | 0 | 0 | 0 | 0.22 ± 0.49 | 0 | 0 |
| | Spring | 0 | 9.67 | 0 | 0 | 0 | 0.09 ± 0.30 | 0 | 0 |
| | Summer | 0 | 12.12 | 0 | 0 | 0 | 0.12 ± 0.33 | 0 | 0 |
| *Rhadinorhynchus* sp. | Autumn–Winter | 0 | 0 | 16.66 | 0 | 0 | 0 | 0.16 ± 0.37 | 0 |
| | Spring | 10 | 0 | 6.66 | 6.66 | 0.1 ± 0.30 | 0 | 0.06 ± 0.25 | 0.06 ± 0.25 |
| | Summer | 16.66* | 12.12** | 26.66** | 13.33* | 0.16 ± 0.37 | 0.12 ± 0.33* | 0.26 ± 0.44 | 0.13 ± 0.32 |
| Anisakid larvae | Autumn–Winter | 0 | 12.9 | 50 | 6 | 0 | 0.19 ± 0.54 | 1.23 ± 1.40 | 0.06 ± 0.25 |
| | Spring | 23.33 | 64.51 | 50 | 23.33 | 0.43 ± 0.89 | 1.41 ± 1.65 | 1.13 ± 1.25 | 0.4 ± 0.81 |
| | Summer | 40** | 24.24** | 40 | 33.33** | 0.86 ± 1.25** | 0.48 ± 1.03** | 0.63 ± 0.88 | 0.66 ± 1.00* |

**, Level of significance with $P < 0.01$; *, level of significance with $P > 0.01$.

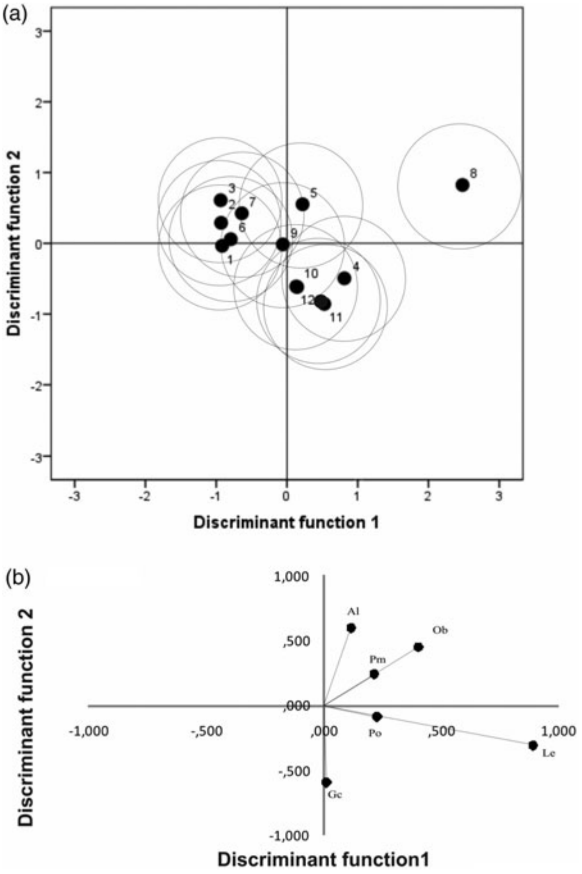

Fig. 1. (a) Sample scores of the first two discriminant functions for specimens of *Scomber colias* from (1) Bizerte in autumn–winter, (2) Bizerte in spring, (3) Bizerte in summer, (4) Kelibia in autumn–winter, (5) Kelibia in spring, (6) Kelibia in summer, (7) Mahdia in autumn–winter, (8) Mahdia in spring, (9) Mahdia in summer, (10) Zarzis in autumn–winter, (11) Zarzis in spring, (12) Zarzis in summer; lettering on the axes represents group averages surrounded by circles to show 90% tolerances. (b) Canonical correlations between the first two discriminant functions and the parasite species between localities in each season. Gc, *Grubea cochlear*; Pm, *Pseudokuhnia minor*; Po, *Prodistomum orientalis;* Le, *Lecithocladium excisum*; Ob, *Opechona bacillaris*; Al, anisakid larvae.

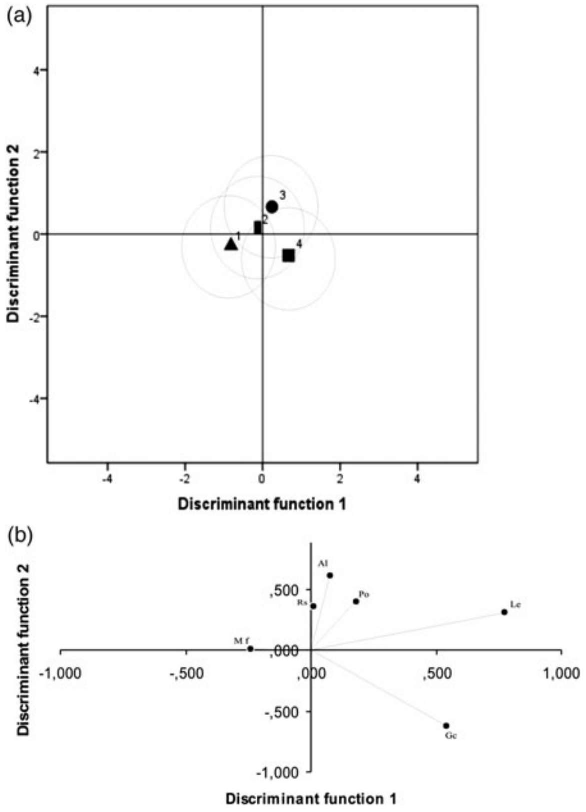

Fig. 2. (a) Sample scores of the first two discriminant functions for specimens of *Scomber colias* from (1) Bizerte, (2) Kelibia, (3) Mahdia and (4) Zarzis; lettering on the axes represents group averages surrounded by circles to show 90% tolerances. (b) Canonical correlations between the first two discriminant functions and the parasite species between localities. Mf, *Monascus filiformis;* Gc, *Grubea cochlear*; Po, *Prodistomum orientalis;* Le, *Lecithocladium excisum*; Rs, *Rhadinorhynchus* sp.; Al, anisakid larvae.

## Discussion

To use parasites as biological tags for stock identification, two aspects related on quantitative and qualitative differences in the parasite fauna are evident (Love, 1980; Scott, 1988; Stanley *et al.*, 1992). In our study, qualitative and quantitative differences in the structure of nine helminth parasites found on *S. colias* from the coast off Tunisia allowed the identification of three distinct areas: one in the north from Bizerte, one in the south from Zarzis, and one in the centre from Kelibia and Mahdia.

The seasonal samples at Bizerte and at Zarzis were homogeneous, justifying their grouping as representatives of two distinct areas (fig. 2a, b; table 2). Our results showed that monogenean parasites were totally absent in the north (Bizerte), and present with high infection parameters of the monogenean *G. cochlear* in the south (Zarzis). Undoubtedly, parasites with a direct life cycle are the simplest to use for stock discrimination. The parasite must be present in one area and absent in others. Infection is ensured through close contact between infected and non-infected fishes (MacKenzie & Abaunza, 1998).

The absence of monogeneans in the north and their presence in the south could be explained by local abiotic factors, such as salinity, temperature and depth, that affect the completion of the life cycle of the parasite (Williams & Jones, 1994). The northern marine zone was characterized by strong and very rugged currents and by a straight continental shelf that gave way to a steep slope. This can prevent the attachment of the oncomiracidium on its host. Also, in this region, the salinity and the water temperature had a zonal distribution, with values that generally increased from northwest to southeast off the coast of Tunisia. In the north, the minimum salinity of 36.8 psu was detected in the Atlantic current, which flows at a

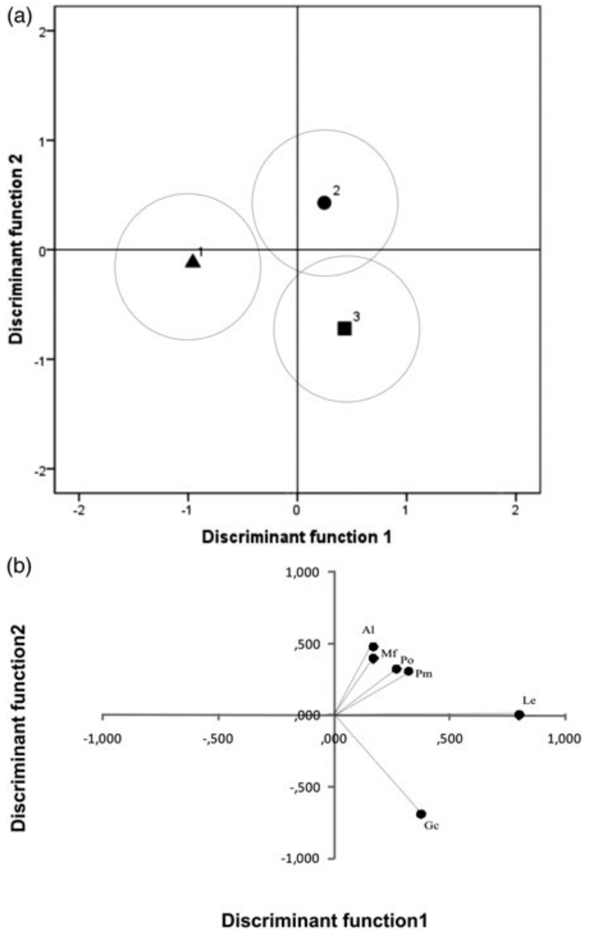

Fig. 3. (a) Sample scores of the first two discriminant functions for specimens of *Scomber colias* from (1) Bizerte, (2) Kelibia and Mahdia pooled and (3) Zarzis; lettering on the axes represents group averages surrounded by circles to show 90% tolerances. (b) Canonical correlations between the first two discriminant functions and the parasite species between localities. Po, *Prodistomum orientalis*; Le, *Lecithocladium excisum*; Pm, *Pseudokuhnia minor*; Al, anisakid larvae; Mf, *Monascus filiformis*; Gc, *Grubea cochlear*.

depth between 90 and 250 m in summer and between 40 and 50 m in autumn (Brandhorst, 1977; Alioua & Harzallah, 2008). The maximum water temperature was 13.6°C in winter and 24.8°C in summer (Gaamour *et al.*, 2004). In the south, the water temperature reached 14.6°C in winter and >29°C in summer (Gaamour *et al.*, 2004). The salinity was high (>39 psu) due to the high evaporation occurring over shallow water (Brandhorst, 1977; Alaoui & Harzallah, 2008). In the southern region, the success of the transmission of the monogenean *G. cochlear* in Zarzis may be related to the high values of the temperature and salinity of water, and to the important density of the host population of *S. colias*. Indeed, monogeneans can propagate rapidly on schools of host fish in warm water. The temperature promotes the rapid development of their life cycle and the salinity could be a factor conditioning the presence or absence of some monogeneans (Antonelli & Marchand, 2012). Furthermore, the transmission of monogeneans may also be related to differences in the density of the host population in different areas. Off the Tunisian coast, the abundance of *S. colias* was very low and consisted of a few dispersed specimens in the north, while in the south there were many dense schools (Ben Abdallah & Gaamour, 2004). Several studies have shown that infection parameters of monogenean ectoparasites depend on the water temperature, salinity and depth (Munroe *et al.*, 1981; Blažek *et al.*, 2008; Blahoua *et al.*, 2009; Antonelli & Marchand, 2012).

The northern region was also characterized by the absence of the digeneans *P. orientalis* and *M. filiformis*, and the southern area was characterized by the total absence of the digenean *M. filiformis* and the high prevalence of the digenean *L. excisum.* The absence of endoparasites can be explained by the distribution of their intermediate hosts in these zones. The high transmission of *L. excisum* in Zarzis could be due to the proliferation of its intermediate hosts and the fast completion of its life cycle. Pérez-del Olmo *et al.* (2007) proved that the predominance of digeneans is linked to the proliferation of their intermediate hosts.

The seasonal samples at Kelibia and at Mahdia are not homogeneous, justifying their seasonal variability combined with geographical origin (fig. 2 a, b; table 2). This could shed light on possible migratory patterns of specimens of *S. colias* from the central region. Indeed, the majority of parasite species collected from *S. colias* at Kelibia and Mahdia showed a seasonal variation. Fish from Kelibia in the autumn–winter and in the spring, and those from Mahdia in spring and in summer, were correlated positively with anisakid larvae and *L. excisum*. The latter species were negatively correlated with specimens from Kelibia in summer and those from Mahdia in autumn–winter. These differences can be explained by horizontal migration between fish of Kelibia and Mahdia. Changes in the infection levels of parasites can provide information about the migratory movements of the host. A decrease in the level of infection in a particular area could be the result of the immigration of another host population with a lower level of infection (MacKenzie & Abaunza, 1998).

Geographical analysis showed that there were no significant differences between Kelibia and Mahdia in the global prevalence or mean abundance of monogeneans *G. cochlear*, *P. minor* and *K. scombri*, digeneans *L. excisum, P. orientalis* and *M. filiformis* and anisakid larvae, but there were significant differences in the infection parameters of the digenean *O. bacillaris* and the acanthocephalan. The similarity and the high level of infection with monogeneans *K. scombri* and *P. minor* in Kelibia and Mahdia from the central area may be related to the adaptation of these species to the optimum ecological factors in this area. This zone was characterized by moderate hydrological conditions. The temperature was between 14.3 and 14.7°C and the salinity was relatively low throughout the year, at 37 psu (Ben Othman, 1973; Brandhorst, 1977; Alaoui & Harzallah, 2008). The currents were weak and had no effect on sedentary dynamics (Ben Mustapha & Afli, 2001). The similarity of endoparasites at Kelibia and Mahdia can be related to the distribution and the abundance of their intermediate hosts. Consequently, the qualitative diet composition of *S. colias* may be similar in both regions, although the quantity of ingested prey was likely to be different, as we recorded a significant difference between infection parameters of *Rhadinorhynchus* sp. and *O. bacillaris*. It appears that intermediate hosts of *Rhadinorhynchus* sp. and of the Lepocreadiidae *O. bacillaris*, which involves *Nassarius pygmaeus* as a first intermediate host and the cnidarian *Podocoryne minima*, the ctenophore *Pleurobrachia pileus*, a chaetognath (Bray & Gibson, 1999) or medusa (Diaz-Briz *et al.*, 2012) as second intermediate hosts (Koie, 1975), may be more abundant in Mahdia. The qualitative and quantitative diet composition of *S. colias* from the four regions was different since we have not collected the same parasite species and we showed significant differences between prevalence and mean abundance. Specific habits of fish species and the differential availability of prey species can account for the heterogeneity in parasite burdens observed among geographical zones (Braicovich & Timi, 2008). Infection parameters of digeneans depend on the structure of the food web (Marcogliese, 2002) and host feeding habits (Luque *et al.*, 2004). Oliva (2001) showed that the difference in infection parameters suggest a selectivity in the diet between localities, or lower availability of food items that are intermediate hosts for those parasites and, consequently, the distribution and the abundance of intermediate hosts, which were influenced by physical factors such as temperature, salinity, depth, and the bottom habitat and substrates (Esch & Fernândez, 1993).

The ability to differentiate stocks on the basis of their parasites reflects the variations in ecological and environmental conditions in the regions that the hosts inhabit, resulting in non-uniform distributions and abundances of the parasites' final and intermediate hosts. Differences in feeding habits may also account for the observed differences in infection between regions (Boje *et al.*, 1997).

The results of two discriminant analyses used for the separation of *S. colias* between localities (before and after pooling together specimens from the central area) were similar. *Grubea cochlear* and *L. excisum* were correlated negatively with specimens from Bizerte, in the north. *Pseudokuhnia minor*, *P. orientalis*, *M. filiformis* and anisakid larvae were characteristic of specimens from Kelibia and Mahdia in the centre. *Grubea cochlear* and *L. excisum* were correlated positively with fish of Zarzis from the south. The accuracy of classifying fish incorrectly in their ecological community can be explained by the seasonal migration of *S. colias* from inshore and offshore waters. These movements of migration can be induced by the reproduction and the search for the optimal hydrological conditions. Indeed, currents or water masses play an important role in the spatial distribution, movement and isolation of pelagic fish stocks (Tzeng, 1988; Allen *et al.*, 1990). Indeed, Čikeš Keč & Zorica (2012) showed that *S. colias* is a migratory species which usually dwells at depths between 0 and 250–300 m. From April to September, it migrates towards the coastline and channel areas for spawning. After spawning, adults and their offspring migrate to the deeper and colder offshore areas. Driven by feeding activities, chub mackerel is also well adapted to daily vertical migrations (Maigret & Ly, 1986).

In this study, the parasite species *L. excisum*, *P. orientalis*, *M. filiformis*, *G. cochlear*, *P. minor*, *K. scombri* and anisakid larvae contributed most to the separation of samples from the four localities into three distinct areas, demonstrating that they satisfy the criteria of good biological tags for stock discrimination. Indeed, adult hemiurid digeneans are good biological tags for discriminating stock of anchovy from Argentinian waters (Timi, 2003), of *Sardinella aurita* from Tunisian waters (Feki *et al.*, 2016) and of cod from waters off Greenland (Boje, 1987). Moreover, Kabata *et al.* (1988) used digeneans from the families Fellodistomatidae and Hemiuridae to distinguish the offshore seamount stock and the continental slope stock of *Anoplopoma fimbria* from the west coast of Canada. Monogenean parasites (mainly polyopisthocotyleans) have been widely used biological tags as a source of information on the discreteness of their fish host stocks (Oliva & Ballôn, 2002; Oliva *et al.*, 2004). Oliva (1999) showed that the monogenean *Cemocotyle trachuri* was a good biological tag to discriminate specimens of *Trachurus murphyi* between different localities from Peru and Chile. Rohde (1980) proved that *K. scombri* was a good biological tag to separate specimens of *Scomber japonicus* between the Mediterranean Sea and the Atlantic. Also, anisakid larvae that remained for a long time in the host were good biological tags in stock discrimination (MacKenzie, 1987). These helminth larvae were used as biological tags in stock discrimination of *Sebastes* spp. from the North Atlantic herring (*Clupea harengus*, Clupeidae) and mackerel (*Scomber scombrus*, Scombridae) (Bourgeois & Ni, 1984; Scott, 1985, 1988; Chenoweth *et al.*, 1986; Dumke, 1988; Eltink, 1988; Avdeev & Avdeev, 1989; Lang *et al.*, 1990; Moser, 1991a, b). Boje (1987) used adults of *Hysterothylacium aduncum* as biological tags to separate cod stocks.

The present work improves our understanding of the population structure of an important economic and commercial species such as *S. colias* off the coast of Tunisia. It provides useful information both to the scientific community, and to the fisheries industry and managers from the Mediterranean Sea in general. Using the geographical variability of helminth parasites as a reliable tool to recognize the discrimination of specimens of the chub mackerel, *S. colias*, off the coast of Tunisia allowed the identification of three distinct areas.

## Conflict of interest

None.

## References

**Akmirza, A.** (2013) Monogeneans of fish near Gökçeada, Turkey. *Turkish Journal of Zoology* **37**, 441–448.

**Alioua, M. & Harzallah, A.** (2008) Imbrication d'un modèle de circulation des eaux près des côtes tunisiennes dans un modèle de circulation de la mer Méditerranée. *Bulletin de l'Institut National des Sciences et Technologies de la Mer* **35**, 169–176.

**Allen, M.J., Wolotira, R.J., Sample, T.M., Noel, S.F. & Iten, C.R.** (1990). *West Coast of North America Coastal* *and Oceanic Zones Strategic Assessment: data atlas. Invertebrates and fish*. Seattle, Washington, NOAA.

**Antonelli, L. & Marchand, B.** (2012) Metazoan parasites of the European Sea Bass *Dicentrarchus labrax* (Linnaeus 1758) (Pisces: Teleostei) from Corsica. Chapter 2 *in* Carvalho, E.D., David, G.S. & Silva, R.J. (*Eds*) *Health and environment in aquaculture*. InTech. Available at http://www.intechopen.com/books/health and-environment-in-aquaculture/metazoan-parasites-of-cultured-european-sea-bass-dicentrarchus-labraxlinneaus-1758-from-corsica.

**Arthur, J.R.** (1997) Recent advances in the use of parasites as biological tags for marine fish. pp. 141–154 *in* Flegel, T.W. & MacRae, I.H. (*Eds*) *Diseases in Asian aquaculture III*. Manila, Philippines, Fish Health Section, Asian Fisheries Society.

**Avdeev, V.V. & Avdeev, G.V.** (1989) The study of population pattern and migration route of the Sea of Okhotsk pollock by parasitologic indication technique. pp. 67–75 *in Investigation in parasitology*. Collection of Papers, Academy of Sciences of the USSR, Far East Branch, Institute of Biology and Pedology, Vladivostock,.

**Ben Abdallah, L. & Gaamour, A.** (2004) Répartition géographique et estimation de la biomasse des petits pélagiques des côtes tunisiennes. *Bulletin de l'Institut National des Sciences et Technologies de la Mer* **5**, 28–38.

**Ben Mustapha, K. & Afli, A.** (2001) Quelques traits de la biodiversité marine de la Tunisie. Proposition d'aires de conservation et de gestion. *Bulletin de l'Institut National des Sciences et Technologies de la Mer* **5**, 32–55.

**Ben Othman, S.** (1973) Le Sud Tunisien (Golfe de Gabès): hydrologie, sédimentologie, flore et faune. PhD thesis, University of Tunis, Tunisia.

**Binet, D.** (1995) Hypotheses accounting for the variability of *Sardinella* abundance in the northern Gulf of Guinea. pp. 98–133 *in* Bard, F.X. & Koranteg, K.A. (*Eds*) *Dynamique et usage des ressources en sardinelles de l'upwelling côtier du Ghana et de la Côte d'Ivoire*. Paris, Orstom.

**Blahoua, K.G., N'Douba, V., Kone, T. & Kouassi, N J.** (2009) Variations saisonnières des indices épidémiologiques de trois Monogènes parasites de *Sarotherodon melanotheron* (Pisces: Cichlidae) dans le lac d'Ayamé I (Côte d'Ivoire). *Science & Nature* **6**, 39–47.

**Blažek, R., Jarkovský, J., Koubková, B. & Gelnar, M.** (2008) Seasonal variation in parasite occurrence and microhabitat distribution of monogenean parasites of gudgeon *Gobio gobio* (L.). *Helminthologia* **45**, 185–191.

**Boje, J.** (1987) Parasites as natural tags on Cod (*Gadus morhua* L.) in Greenland waters. pp. 94–101 *in* Stenmark, A. & Malmberg, G. (*Eds*) *Parasites and diseases in natural waters and aquaculture in Nordic countries*.

**Boje, J., Riget, F. & Køie, M.** (1997) Helminth parasites as biological tags in population studies of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)), in the north-west Atlantic. ICES. *Journal of Marine Science* **54**, 886–895.

**Bourgeois, C.E. & Ni, H.I.** (1984) Metazoan parasites of Northwest Atlantic redfishes (*Sebastes* spp.). *Canadian Journal of Zoology* **62**, 1879–1885.

**Braicovich, P.E. & Timi, J.T.** (2008) Parasites as biological tags for stock discrimination of the Brazilian flathead in the South West Atlantic. *Journal of Fish Biology* **73**, 557–571.

**Brandhorst, W.** (1977) Les conditions du milieu au large de la côte tunisienne. *Bulletin de l'Institut National des Sciences et Technologies de la Mer* **4**, 129–220.

**Bray, R.A. & Gibson, D.I.** (1997) The Leporeadiidae Odhner, 1905 (Digenea) of fishes from the north-east Atlantic: summary paper, with keys and checklists. *Systematic Parasitology* **36**, 223–228.

**Bray, R.A. & Gibson, D.I.** (1999) The Lepocreadiidae (Digenea) of fishes of the north-east Atlantic: review of the genera *Opechona* Looss, 1907 and *Prodistomum* Linton, 1910. *Systematic Parasitology* **15**, 159–202.

**Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W.** (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Parasitology* **83**, 575–583.

**Chenoweth, J.H., McGladdery, S.E., Sindermann, C.J., Sawyer, T.K. & Bier, J.W.** (1986) An investigation into the usefulness of parasites as tags for herring (*Clupea harengus*) stocks in the western North Atlantic, with emphasis on use of the larval nematode *Anisakis simplex*. *Journal of Northwest Atlantic Fishery Science* **7**, 25–34.

**Čikeš Keč, V. & Zorica, B.** (2012) The reproductive traits of *Scomber japonicas* (Houttuyn, 1987) in the Eastern Adriatic Sea. *Journal of Applied Ichthyology* **28**, 15–21.

**Costa, G., Cavallero, S., D'Amelio, S., Paggi, L., Santamaria, M.T.G., Perera, C.B., Santos, M.J. & Khadem, M.** (2011) Helminth parasites of the Atlantic chub mackerel, *Scomber colias* Gmelin, 1789 from Canary Islands, Central North Atlantic, with comments on their relations with other Atlantic regions. *Acta Parasitologica* **56**, 98–104.

**Crone, P.R., Hill, K.T., McDaniel, J.D. & Lo, N.C.H.** (2009) *Pacific mackerel* (Scomber japonicus) *stock assessment for USA management in the 2009–10 fishing year*. Portland, Oregon, Pacific Fishery Management Council.

**Diaz-Briz, L., Martorelli, S., Genzano, G. & Mianzan, H.** (2012) Parasitism (Trematoda, Digenea) in medusae from the southwestern Atlantic Ocean, medusa hosts, parasite prevalences, and ecological implications. *Hydrobiologia* **690**, 215–226.

**Derbel, H., Châari, M. & Neifar, L.** (2012) Digenean species diversity in teleost fishes from the gulf of Gabes, Tunisia (Western Mediterranean). *Parasites* **19**, 129–135.

**Dumke, A.** (1988) Investigations on the occurrence of *Anisakis* sp. larvae within the muscle flesh from blue whiting (*Micromesistius poutassou*, Risso) of the Northeast Atlantic. International Council for the Exploration of the Sea (ICES) C.M. 1988/H:67.

**Eltink, A.** (1988) Anisakis larvae (Nematoda: Ascaridida) in mackerel (*Scomber scombrus* L.) in ICES Sub-areas IV, VI, VII, and VIII in 1970–71 and 1982–84. International Council for the Exploration of the Sea (ICES) C.M./ H:23.

**Esch, G.W. & Fernândez, J.C.** (1993) *A functional biology of parasitism*. London, Chapman & Hall.

**Feki, M., Chaari, M. & Neifar, L.** (2016) Spatial variability of helminth parasites and evidence for stock discrimination in the round sardinella, *Sardinella aurita* (Valenciennes, 1847), off the coast of Tunisia. *Journal of Helminthology* **90**, 353–358.

**Gaamour, A., Ben Abdallah, L., Khemiri, S. & Mili, S.** (2004) Etude de la biologie et de l'exploitation des petits pélagiques en Tunisie. *Bulletin de l'Institut National des Sciences et Technologies de la Mer* **5**, 6–19.

**Hattour, A.** (2000) Contribution à l'étude des poissons pélagiques des eaux tunisienne. PhD Thesis, University of Science of Tunis in Tunisia.

**Hattour, A., Ben Abdallah, L. & Guennegan, Y.** (2004) Abondance relative et estimation de la biomasse des petits pélagiques des eaux tunisiennes. *Bulletin de l'Institut National des Sciences et Technologies de la Mer* **31**, 1117–1121.

**Highland Statistics**. (2000) *Brodgar Software package for multivariate analysis and multivariate time series analysis*. Aberdeen, Highland Statistics Ltd.

**Hilborn, R. & Walters, C.J.** (1992) *Quantitative fisheries stock assessment: Choice, dynamics, and uncertainty*. New York, Chapman & Hall.

**Kabata, Z., McFarlane, G.A. & Whitaker, D.J.** (1988) Trematoda of Sablefish *Anoplopoma fimbria* (Pallas, 1911), as possible biological tags for stock identification. *Canadian Journal of Zoology* **66**, 195–221.

**Køie, M.** (1975) On the morphology and life history of *Opechona bacillaris* (Molin, 1859) Looss, 1907 (Trematoda: Lepocreadiidae). *Ophelia* **13**, 63–86.

**Ktari-Chakroun, F. & Azouz, A.** (1971) Les fonds chalutables de la région sud-est de la Tunisie (Golfe de Gabès). *Bulletin de l'Institut National des Sciences et Technologies de la Mer* **2**, 5–48.

**Lang, T., Damm, U., Weber, W., Neudecker, T. & Kuhlmorgen-Hille, E.** (1990) Infestation of herring (*Clupea harengus* L.) with *Anisakis* sp. larvae in the western Baltic. *Archiv für Fischereiwissenschaft* **40**, 101–117.

**Lester, R.J.G.** (1990) Reappraisal of the use of parasites for fish stock identification. *Australian Journal of Marine & Freshwater Research* **41**, 855–864.

**Love, M.S.** (1980) Isolation of olive rockfish, *Sebastes serranoides*, populations off Southern California. *Fishery Bulletin* **77**, 975–983.

**Luque, J.L., Mouillot, D. & Poulin, R.** (2004) Parasite biodiversity and its determinants in coastal marine teleost fishes of Brazil. *Journal of Parasitology* **128**, 671–682.

**MacKenzie, K.** (1987) Parasites as indicators of host populations. *International Journal of Parasitology* **17**, 345–352.

**MacKenzie, K.** (2002) Parasites as biological tags in population studies of marine organisms: an update. *Journal of Parasitology* **124**, 153–163.

**MacKenzie, K. & Abaunza, P.** (1998) Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods. *Fisheries Research* **38**, 45–56.

**MacKenzie, K. & Abaunza, P.** (2005) Parasites as biological tags. pp. 211–226 *in* Cadrin, S.X., Friedland, K.D. & Waldman, J.R. (*Eds*) *Stock identification methods. Applications in fisheries science*. San Diego, USA, Elsevier Academic Press.

**MacKenzie, K., Campbell, N., Mattiucci, S., Ramos, P., Pinto, A.L. & Abaunza, P.** (2008) Parasites as biological tags for stock identification of Atlantic horse mackerel *Trachurus trachurus* L. *Fisheries Research* **89**, 136–145.

**Maigret, J. & Ly, B.** (1986) *Les poissons de mer de Mauritanie*. Science Natural Compiègne.

**Marcogliese, D.J.** (2002) Food webs and the transmission of parasites to marine fish. *Journal of Parasitology* **124**, 83–99.

**Marcogliese, D.J. & Jacobson, K.C.** (2015) Parasites as biological tags of marine, freshwater and anadromous fishes in North America from the tropics to the Arctic. *Parasitology* **142**, 68–89.

**Moser, M.** (199la) Biological tags for stock separation in Pacific herring (*Clupea harengus pallasi* Valenciennes) and the possible effects of 'El Nino' currents on parasitism. *Proceedings of the International Herring Symposium*, Anchorage, Alaska, October 1990, pp. 245–254. Fairbanks, Alaska, Alaska Sea Grant Program Report No. 91-01, University of Alaska.

**Moser, M.** (1991b) Parasites as biological tags. *Parasitology Today* **7**, 182–185.

**Munroe, T.A., Campbell, R.A. & Zwerner, D.E.** (1981) *Diclidophora Nezumiae* sp. n. (Monogenea: Diclidophoridae) and its ecological relationships with the Macrourid fish *Nezumia bairdi* (Goode and Bean, 1877). *The Biological Bulletin* **161**, 281–290.

**Oliva, M.E.** (1999) Metazoan parasites of the jack mackerel *Trachurus murphyi* (Teleostei, Carangidae) in a latitudinal gradient from South America (Chile and Peru). *Parasite* **6**, 223–230.

**Oliva, M.E.** (2001) Metazoan parasites of *Macruronus magellanicus* from southern Chile as biological tags. *Journal of Fish Biology* **58**, 1617–1622.

**Oliva, M.E. & Ballôn, I.** (2002) Metazoan parasites of the Chilean hake *Merluccius gayi* as a tool for stock discrimination. *Fisheries Research* **56**, 313–320.

**Oliva, M., González, M. & Acuria, E.** (2004) Metazoan parasites of *Sebastes capensis* from two localities in northern Chile as tools for stock identification. *Journal of Fish Biology* **64**, 170–175.

**Oliva, M., Valdivia, I.M., Costa, G., Freitas, N., Pinheiro De Carvalho, M.A., Sánchez, L. & Luque, J.L.** (2008) What can metazoan parasites reveal about the taxonomy of *Scomber japonicas* Houttuyn in the coast of South America and Madeira Islands? *Journal of Fish Biolology* **72**, 545–554.

**Pauly, D.** (1997) *Méthodes pour l'évaluation des ressources halieutiques*. p. 288 *in* Moreau, J. (*Ed.*) Adaptation Française. Toulouse, Cepadues.

**Pérez-del Olmo, A., Raga, J.A., Kostadinova, A. & Fernández, M.** (2007) Communities in *Boops boops* (L.) (Sparidae) after the Prestige oil-spill: detectable alterations. *Marine Pollution Bulletin* **54**, 266–276.

**Power, A.M., Balbuena, J.A. & Raga, J.A.** (2005) Parasite infracommunities as predictors of harvest location of bogue (*Boops boops* L.): a pilot study using statistical classifiers. *Fisheries Research* **72**, 229–239.

**Rohde, K.** (1980) Comparative studies on microhabitat utilization by ectoparasites of some marine fishes from the North Sea and Papua New Guinea. *Zoologischer Anzeiger* **204**, 27–63.

**Roldán, M.I., Perrotta, R.G., Cortey, M. & Pla, C.** (2000) Molecular and morphologic approaches to discrimination of variability patterns in chub mackerel, *Scomber japonicus*. *Journal of Experimental Marine Biology and Ecology* **5**, 63–74.

**Scott, J.S.** (1985) Occurrence of alimentary track helminth parasites of pollack (*Pollachius virens* L.) on the Scotian Shelf. *Canadian Journal of Zoology* **63**, 1695–1698.

**Scott, J.S.** (1988) Helminth parasites of redfish (*Sebastes fasciatus*) from the Scotian Shelf, Bay of Fundy, and eastern Gulf of Maine. *Canadian Journal of Zoology* **66**, 617–621.

**Stanley, R.D., Lee, D.L. & Whitaker, D.J.** (1992) Parasites of yellowtail rockfish, *Sebastes flavidus* (Ayres, 1862) (Pisces: Teleostei), from the Pacific coast of North America as potential biological tags for stock identification. *Canadian Journal of Zoology* **70**, 1086–1096.

**Timi, J.T.** (2003) Parasites of Argentine anchovy in the Southwest Atlantic: latitudinal patterns and their use for discrimination of host populations. *Journal of Fish Biology* **63**, 90–107.

**Timi, J.T. & Mackenzie, K.** (2015) Parasites in fisheries and mariculture. *Parasitology* **142**, 1–4.

**Tzeng, W.N.** (1988) Availability and population structure of spotted mackerel, *Scomber australasicus*, in the adjacent waters of Taiwan. *Acta Oceanographica Taiwanica* **19**, 132–145.

**Tzong-Der, T. & Shean-Yahyeh, J.** (2007) Morphological variation in the common mackerel (*Scomber japonicus*) off Taiwan. *Journal of the Fisheries Society of Taiwan* **34**, 197–205.

**Williams, H. & Jones, A.** (1994) *Parasitic worms of fish*. London, Taylor and Francis.

**Williams, H.H., MacKenzie, K. & McCarthy, A.M.** (1992) Parasites as biological indicators of the population biology, migrations, diet, and phylogenetics of fish. *Reviews in Fish Biology and Fisheries* **2**, 144–176.

**Zar, J.H.** (1996) *Biostatistical analysis*. 3rd edn. Upper Saddle River, New Jersey, Prentice-Hall.