Parasite fauna and community structure of bathydemersal fishes: *Notacanthus bonaparte* (Osteichthyes), *Etmopterus spinax* and *Deania profundorum* (Chondrichthyes)

Tesis doctoral por Wolf Isbert

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Programa de doctorado:
3059 Recursos Marinos

Universitat de València

Facultat de Ciències Biològiques

Valencia, mayo 2017

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Doctoral Thesis

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Valencia, mayo 2017

Front and back cover concept and design by Autun Purser
PhD book design and realisation by Antonio Secilla

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CERTIFICAN que D **Wolf Isbert** ha realizado bajo nuestra dirección, y con el mayor aprovechamiento, el trabajo de investigación recogido en esta memoria y que lleva por título “**Parasite fauna and community structure of bathydemersal fishes: *Notacanthus bonaparte* (Osteichthyes), *Etmopterus spinax* and *Deania profundorum* (Chondrichthyes)**”, para optar al grado de Doctor en Ciencias Biológicas.

Y para que así conste, en cumplimiento de la legislación vigente, expedimos el presente certificado en Valencia a 30 de mayo de 2017.

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…con un tren a las 7 empezó todo…
para Cova

Agradecimientos

En primer lugar quiero agradecer a mis tres directores de tesis Francisco E. Montero Royo (Paco), Maite Carrassón López de Letona (Maite) y Ana Pérez del Olmo (Ana), su apoyo y paciencia durante todo este proceso. Esta tesis doctoral es el resultado del trabajo en equipo y sin vuestra ayuda y apoyo constante, no hubiera sido posible. Os agradezco muchísimo vuestra disposición a compartir vuestro gran conocimiento sobre la ecología de los peces y sobre las comunidades de parásitos. Gracias por todas las discusiones que hemos tenido a lo largo de estos años sobre todos estos temas y de las cuales he aprendido muchísimo. Gracias también por transmitirme siempre vuestra positividad y vuestros ánimos y es que…vuestro esfuerzo y ayuda ha ido mucho más allá de lo que yo esperaba de mis directores ¡MUCHAS GRACIAS!

Quiero dar las gracias a los miembros del tribunal Pablo Abaunza, Javier Aznar, Lutz Bachmann, Mercedes Fernández, Paolo Merella e Izaskun Preciado por su disponibilidad e interés en evaluar este trabajo y también por su presencia el día de la defensa en Valencia.

El trabajo de esta tesis doctoral se ha realizado dentro de varios proyectos de investigación y agradezco a las/los investigadoras/es principales el facilitarme las muestras que han sido la base de este trabajo ‘BIOMARE’ (CTM2006-13508-C02-01MAR), ‘ANTROMARE’ (CTM2009-12214-C02-02-MAR; ‘DEEPCON’ (CGL2010-16690), EU LIFE+ Project ‘INDEMARES: Inventory and designation of marine Natura 2000 areas in the Spanish sea’ (07/NAT/E/000732).

Muchísimas gracias por su gran apoyo durante estos años a “mis” dos grupos de trabajo en la Universidad de Valencia (Cavanilles) y en la Universidad Autònoma de Barcelona. Gracias por acogerme en el laboratorio cuando he realizado estancias de trabajo en Valencia y Barcelona. Siempre me he sentido muy bien, muy acogido y he disfrutado el clima de trabajo en ambos sitios. Gracias especialmente a Natalia y Raúl que me han ayudado siempre con mis preguntas sobre el papeleo. Muchas gracias al jefe del grupo, Antonio Raga, de Valencia, donde he realizado las estancias más largas durante estos años, por acogerme y apoyar mi trabajo.

Recordando mi tiempo en La República Checa, quiero darle las gracias a Tomáš Scholz por hacer posible mi estancia en České Budějovice, y también por el apoyo económico que me brindó. También quiero dar las gracias a todo el grupo de trabajo por su apoyo y acogida en el Biology Centre, Academy of Sciences of the Czech Republic de České Budějovice! Děkuji! Además me gustaría agradecer a David González Solís por su gran ayuda y por el placer de haber trabajado juntos en el artículo de *Dichelyne* durante mi estancia en České Budějovice. David, nuestras largas discusiones sobre estos bichos y tus respuestas a mis preguntas sobre los nematodos son cosas que no olvidaré y te agradezco enormemente. In relation to this article, I would like to thank Roman Kuchta for providing us with his samples for the description of the new species, this helped us a lot.

Merci beaucoup à Armelle Jung et Cécile Brigaudeau Des Requins et De Hommes (DRDH) pour leur disponibilité, leur collaboration et leur aide lors de mon séjour à Brest. Je vous remercie pour votre aide, en espérant pouvoir développer nos projets. Merci beaucoup également à Madame Lebourges-Dhaussy et Monsieur Ragueneau, ainsi que le laboratoire LEMAR de Brest, qui ont soutenu nos travaux de recherche.

Vielen Dank auch Claudia Junge und Timon Brüggemann!! Danke Claudia für die Organisation meines Aufenthalts in Oslo, und Dein unermüdlicher Eifer an diesem Thema weiter zu arbeiten. Ich hoffe,

wir schaffen es u.a. mit Armelle und Cécile was auf die Beine stellen zu können! Danke Timon für Deine grosse Hilfe im Labor und die langen Nächte zwischen Eingeweiden und Parasiten!! Many thanks to Dr. Vøllestad and the CEES, Oslo for supporting our laboratory work.

Thanks a lot, Rudolf Svensen, for providing me with these beautiful *Etmopterus spinax* images and allowing me to use them during several presentations and in the final PhD document. Thank you also for the provided information on this shark from the Norwegian fjords.

Muchas gracias a los colegas de OCEANA en España, especialmente a Pilar Marín que me proporcionó unas fotografías submarinas fantásticas de las especies estudiadas en este trabajo.

Thank you very much Autun for your great work on the book front and back cover! I am proud to have an original 'Purser' as cover page and I am very grateful for your effort as I know you have some other work to do ;-)

Muchísimas gracias también a Antonio por la maquetación de este trabajo y su ánimo especialmente en las últimas semanas, a lo largo de las cuales….siempre había cambios;-)

Muchas gracias a Cesar, Noemí, Jorge y Beatriz a los que también quiero agradecer el haber estado siempre presentes, especialmente por vuestra ayuda y apoyo durante los tiempos que tuvimos que vivir en Santander y por ayudarnos a sobrellevar esa situación con más calma ¡e incluso con humor! Muchísimas gracias también a Rosa y Joserra por su ayuda y apoyo durante nuestro tiempo en Santander, que tuvo de bueno conocer a mucha gente estupenda. Muchas gracias al equipo de laboratorio del IEO, Santander por tantas conversaciones divertidas durante nuestro trabajo "en el sótano".

Muchas gracias a la gente del COB: Xisco, María, Beatriz, Vanessa, Olga, Teresa, Lucía….por vuestra ayuda y apoyo en diferentes "frentes" durante estos últimos años. Gracias a Vasco por compartir la afición al fútbol y ¡por "sacarme de casa" para ver algún partido juntos!

Muchas gracias a Ale y Vero por haber estado siempre ahí, ¡por recibirnos siempre en vuestra casa! También Vero por tu ayuda y disposición costeándome algunos de mis viajes a Valencia en el barco lo que además me permitió disfrutar de ver bichos, contar medusas y …¡algunos de los restos de nuestra 'civilización' en el Mediterráneo!

Danke an die Freunde in Bremen (Düsseldorf) und umzu (Lola, Jürgen, Andrés, Kai, Irene (Vielen Dank fürs Asyl!!), Walter, Silvia, Sascha, Janne, Nils, Andrea, Pitty, Jeannette, Tilman) für Euer Interesse und Zeit, und die teilweise langen Abende/Nachmittage am Weserdeich oder im Stadion!!! Vielen Dank auch den Freunden in NRW (Dirk, Okie, Anne, Markus, Mechthild, Carsten und Sarah) für Eure Zeit und Flexibilität sich auch mal kurzfristig zu treffen. Danke Dirk für lange Nächte und Spaziergänge am 'Tag danach'!

Muchas gracias a Jacob por sus consejos para mi trabajo y presentaciones para congresos y por ayudarme a ver la vida con un poco más de relax ;-) Gracias también por tu confianza en incluirme en uno de tus trabajos.

Gracias Juanchete por ayudarme profundizar mi conocimiento del castellano y aprender un castellano de verdad… …y por el concierto de Barón Rojo ¡claro!

Enrique…me faltan palabras para agradecerte lo que has hecho por mí a lo largo de estos años…¡¡Muchísimas gracias por darme un asilo de lujo todo este tiempo!! ¡¡Siempre me dejaste ocupar parte de tu piso sin más!! Puedes estar seguro esta tesis es en buena parte tuya pues sin tu apoyo hubiese sido imposible realizar las largas estancias que he podido hacer en Valencia. ¡¡Muchísimas gracias por toda tu ayuda y amistad!! …y segundas gracias a Lola…

Johannes, ich danke Dir für die Jahre während des Bio-Studiums in D´dorf! Und natürlich auch für Dein beständiges Interesse am Leben und an unserer Arbeit hier! Danke für die vielen Unterhaltungen beim Bier, im Garten oder in der DB, mit der obligatorischen Flucht vorm Schaffner…. Danke für diese Jahre!!

Natürlich möchte ich auch meinen Eltern (Isi und Jane) und dem Rest der Familie (Maren, Lisa, Werner und Hans) danken, für all Ihre Unterstützung in den letzten Jahren und während des Studiums in den Jahren davor!! Vielen Dank für alles!
Esto se refiere también a mi segunda familia en Madrid (Enrique, Teresa, Almu, Javi e Irene) y Francia (Bego, Cristophe, Inés y Diego), muchas gracias por vuestro apoyo y acogida como miembro de la familia.

Gracias a Alba por sus sesiones gratuitas de “terapia autogénica” y por distraerrme.

…Cova, no tengo palabras para decir cómo te agradezco tu apoyo, paciencia y amor. ¡GRACIAS Chata, por todo!

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Summary

The deep-sea is the largest biome on earth, but it is also still the less studied (Ramirez-Llodra et al. 2010). While in former times the deep-sea was considered as highly ‘stable’ with low variations below the permanent thermocline, more recent research clearly indicates to a more dynamic environment (Gage 2003, Ramirez-Llodra et al. 2010). Natural effects exerted on deep-sea habitats arise from different factors which comprise e.g. the horizontal movement of huge water masses driven by circum-global currents, which can change salinity and temperature regimes. Additionally, topographic underwater features such as seamounts and canyons interact with these currents and create environmental conditions distinctly different to the continental slope or deep-sea plains, which can enhance the food supply and diversity in the deep-sea on a local scale (Levin & Dayton 2009 and references therein). Therefore, the high spatial heterogeneity of deep-sea habitats together with the spatial and temporal limitations of food supply in their communities (Snelgrove & Grassle 1995) can result in a high variability of the diversity, even in very small spatial scales (Levin & Dayton 2009).

The current knowledge on these deep-sea dynamics and its habitats is still scarce and negligible when compared to the knowledge of costal and shallow water ecosystems (Ramirez-Llodra et al. 2010, Snelgrove et al. 2016). This applies also to the deep-sea fishes for which knowledge is often limited to species of commercial value and targeted in specific areas (Snelgrove et al. 2016). Therefore, based on this unbalanced study effort, it is recommended to consider assumptions about common patterns in the deep-sea with caution (Snelgrove et al. 2016).

The scant overall information lacks knowledge on several ecological and biological traits of deep-sea fishes, including their parasites. Several aspects of parasites, such as their life cycles and distribution patterns in the deep-sea are often assumed based on the knowledge from shallow water fishes. The few data available on parasites in deep-sea fishes show similarities to shallow waters, where a certain relation between parasite communities and host related factors exists. Parasite life cycles in the deep-sea ecosystems are often not known. Available studies show that the diversity of certain parasite groups seems to be distinctly lower compared to shallow waters (Klimpel et al. 2009). This lower diversity is partly explained in some higher taxa, such as Digenea, by the fact that few parasites followed and coevoluted with their hosts in the deep. Further, a lower host density in the deep-sea and the inappropriate life cycles may impede a successful colonization of this habitat (Campbell et al. 1980, Bray et al. 1999, Klimpel et al. 2006).

Increasing knowledge on fish parasite communities from the deep-sea would not only provide more data on the parasites, but even indicate to host related ecological and biological traits, as parasites can be used as biological indicators. This would also provide an insight in the transmission pathways of parasites in extreme environments with often lower host diversity and density (Leung et al. 2015).

In particular, the use of parasites as biological indicators is recommended for rare species or species difficult to sample (MacKenzie & Abaunza 1998), which is partly the case for the three species studied in this work: *Notacanthus bonaparte* Risso, 1840 (Notacanthiformes: Notacanthidae), *Etmopterus spinax* L., 1758 (Squaliformes: Etmopteridae), and *Deania profundorum* Smith & Radcliffe, 1912 (Squaliformes: Centrophoridae).

The data available for deep-sea habitats and their fish fauna clearly indicate to life history traits with slow growth, late maturity and low fecundity which make deep-sea fishes less resilient to anthropogenic impacts such as fisheries (Koslow et al. 2000, Bergstad et al. 2013). This also applies to the three species studied here, and although all have a low or no commercial value, they suffer fishery impacts due to partly high by-catch mortalities.

Notacanthus bonaparte is 'grazing' on benthic fauna and in some areas may exhibit high abundances. However, the particular role of *N. bonaparte* in ecosystems is not known, and it can only be speculated if a depletion would have cascading effects in the ecosystem. Regarding the shark species (*E. spinax* and *D. profundorum*), their role/importance in deep-sea ecosystem is not clear but as predators of higher trophic levels (Cortés 1999) it is suggested, that their depletion or extinction could have profound consequences for the local community and ecosystem stability.
The specific objectives of this work are:

1. To contribute to the knowledge on the parasite fauna of the three selected species *N. bonaparte*, *E. spinax* y *D. profundorum*.

2. To describe species new to science.

3. To describe the parasite communities of *N. bonaparte*, *E. spinax* and *D. profundorum*.

4. To generate information on the composition and abundance of parasite species which may be used as potential indicators.

5. To analyse potential relationships between the detected parasite communities with the diet and trophic ecology of the host.

Annotated checklist of parasites recorded from the species of the three families of deep-sea fish: Centrophoridae, Etmopteridae and Notacanthidae

A compilation of data currently available on recorded parasites for the three host families (Centrophoridae, Etmopteridae and Notacanthidae) which comprise the three model species, has been performed (Table 4.1). A thorough literature search has been conducted consulting different databases (e.g. Google Scholar, Web of Knowledge, World of Copepods, Global Cestode Database and Host-parasite database of the Natural History Museum, London), but also the comprehensive checklist compiled by Klimpel et al. (2009). The information found by means of a web search engine, was verified with the original source (publication) when available.

All three fish families exhibited a different number of valid species, where some species are still under discussion. The total number of valid fish species (82) is distributed over these three families as follows: 20 centrophorids, 51 etmopterids and 11 notacanthids.

The found publications dealing with parasites species described in these host families are low in number compared to shallow water or commercially important species, but an increasing study effort is observable since the 70's (Fig. 4.1). Further, the publications reveal a clear geographical bias with most studies conducted in the Northeast Atlantic followed by the Northwest Atlantic, the Southwest Pacific, and the Mediterranean Sea.

Several families of different parasite higher taxa groups were found with varying importance with respect to elasmobranchs and teleost hosts. These taxa were: Cestoda, Monogenea, Trematoda (Digenea), Nematoda, Copepoda, Isopoda, Cirripedia and Amphipoda (Fig. 4.2). In both elasmobranch species most parasites recorded were assigned to the cestodes followed by the copepods, while in Notacanthidae digeneans were the most diverse group followed by monogeneans. These are patterns which were already observed for other elasmobranchs and osteichthyes (Campbell et all. 1980, Cribb et al. 2002, Caira & Healy 2004). Amphipods and cirripeds were detected in etmopterids only (Fig. 4.4, 4.5). The lower overall diversity in monogeneans may hint to sampling artefacts or a general low presence in the deep-sea as previously suggested (De Buron & Morand 2004).

The parasite taxa detected in these fish families partly represent families which were already found frequently in other fishes from the deep-sea (Fig. 4.3). The proportions between specialist and generalist species of all parasite groups were different between all three fish families, where the notacanthids showed the highest proportion of specialist species (almost 58%) followed by etmopterids (50%) and centrophorids (30%) (Fig. 4.6). Specialists were not only found among monogeneans, but also digeneans (in Notacanthidae) and cestodes (both in elasmobranchs). As previously suggested, generalist feeders may be infected by a more diverse parasite fauna with more generalist species (Klimpel et al. 2006, Chambers 2008); the differences between the fish families are partly explained by the different feeding habits with often broader ranges of prey items in sharks. In comparison notacanthids show a more limited range of prey items and are partly highly specialised.

The proportions of heteroxenous and monoxenous parasite taxa were similar for all three families; the highest proportion of heteroxenous parasites was detected in notacanthids, probably in part due to their strict benthic diet. In etmopterids, monoxenous parasite taxa had a higher contribution, in part owing to two taxa found exclusively in this fish family. This might also be related to the higher proportion of adult parasite stages recorded for etmopterids, while in centrophorids the proportion is almost balanced. In etmopterids, more monoxenous species were recorded which mostly infect their host as adult stage (except e.g. Gnathiidae). The high proportion of adults in notacanthids is mainly represented by digeneans which may hint to its specialised, benthic feeding habit. Interestingly the high amount of larval stages in centrophorids, which is the family with largest body sizes of all three fish families, indicates to an important role as intermediate or at least paratenic host. Consequently, predators of these species, having at least the same size of these sharks, might exist in their habitats. Though, further studies are needed to analyse whether some larval cestodes may occur only in smaller, younger sharks and diminish in adults.

A new species of *Tinrovia* Mamaev, 1987 (Monogenea: Microcotylidae) from the deep-sea fish *Notacanthus bonaparte* Risso (Notacanthiformes: Notacanthidae) in the western Mediterranean and the Northeast Atlantic

During the analysis of the parasite communities from the shortfin spiny eel, *Notacanthus bonaparte* Risso, 1840, a new monogenean species was detected and described. The parasite fauna of the deep-sea fish *N. bonaparte* is poorly studied and to date only two species have been described: the trematode *Steringovermes notacanthi* Bray, 2004 and the cestode *Bathycestus brayi* Kuchta & Scholz, 2004.

This new microcotylid, *Tinrovia mamaevi* n. sp. (Monogenea: Polyopisthocotylea), is described from the gills of 165 specimens sampled in the western Mediterranean and Northeast Atlantic. The obtained specimens were used for a detailed morphological study by means of light

and confocal laser scanning microscopy. The morphological traits observed in the analysed monogenean specimens from both areas justify their classification belonging to the same species. This species is allocated to the subfamily Syncoelicotylinae Mamaev & Zubchenko 1978 due to the possession of a symmetrical haptor with two separate frills. This species is assigned to the genus *Tinrovia* which includes the type- and only other species *T. papiliocauda* Mamaev, 1987.
Tinrovia mamaevi differs from *T. papiliocauda*, in having a narrower haptor with a lower number of clamps. Clamps are also smaller in the new species, testes more numerous, the genital atrium smaller with a lower number of spines, and the eggs have a short and a long filament (Table 5.1).

The clamps in *T. mamaevi* n. sp. are of the 'microcotylid' type, arranged in two distinct lateral haptoral frills (Fig. 5.1). Previous publications suggested that clamps of Syncoelicotylinae have to be considered 'massive' (Mamaev & Zubchenko 1978, Mamaev 1987, Mamaev & Brashovian 1989) however, clamps of *T. mamaevi* were slightly smaller than in *T. papiliocauda*, especially their sclerites were slender and more delicate. Therefore, in these cases descriptions could be ambiguous and should be referred to total clamp size in relation to the body size or to the relative sizes of the sclerites. This applies also to the description of the haptor made for two species of Syncoelicotylinae.

In the present study we could observe an overall smaller haptor in *T. mamaevi* compared to *T. papiliocauda*, and the lateral frills appear to be relatively smaller and narrower. In the generic diagnoses of two species of the genera, *Syncoelicotyle* and *Tinrovia,* the haptor is described as 'butterfly-shaped', meaning wide, separated haptor frills (Mamaev & Zubchenko 1978, Mamaev 1987) (Figs. 5.1, 5.2). We suggest that this description in the diagnoses of these species of Syncoelicotylinae can be controversial. Firstly, we observed overall narrower lateral frills suggesting the wide shape as no longer valid for diagnostic of this genus. Secondly, we suggest using a more generic term to refer to characters such as 'wide haptor frill', as descriptions referring to peculiar shapes can be misinterpreted depending on the observer.

Along with the lower spine number, the genital atrium in *T. mamaevi* is smaller and exhibits a different pattern of armed muscular pads compared to the genital organ described for *T. papiliocauda*. However, owing to the difficulties describing complex traits the supposedly different genital atrium lobulation should be interpreted with caution. The here applied confocal techniques were highly useful to interpret especially the 3D- structure of the genital atrium (Fig. 5.3). The use can help to diminish controversies about the correct interpretation of traits and enhance the reliability for diagnostics. In the present study, eggs also differed to the diagnosis of the genus (two short filaments); and branched caeca, usually described as anastomosed, could not be observed due to dense vitelline follicles. The description of these characters are known to be controversial in other polyopisthocotyleans, therefore both morphological traits are unreliable for taxonomical diagnoses.

We suggest an emended diagnosis of the genus *Tinrovia*: as in Mamaev (1987) except for: Haptor with two lateral frills not joining posteriorly, markedly winged when frills wide; eggs with two filaments (short or long).

Dichelyne (*Cucullanellus*) *romani* n. sp. (Nematoda: Cucullanidae) in notacanthid fishes from the Northeast Atlantic and western Mediterranean

A new nematode, *Dichelyne* (*Cucullanellus*) *romani* n. sp. (Nematoda: Cucullanidae), is described from the digestive tract of two notacanthid fishes, *Notacanthus chemnitzii* Bloch, 1788 and *N. bonaparte* Risso, 1840 (Notacanthiformes: Notacanthidae), from the Northeast Atlantic Ocean and western

Mediterranean Sea. Currently, the helminth fauna of both notacanthids is poorly studied and to date one cucullanid nematode has been detected in *N. chemnitzii*, while for *N. bonaparte* no nematode record exists (Gibson et al. 2005, Soares 2007). This is the first species of *Dichelyne* Jägerskiöld, 1902 in a notacanthid fish and one of the only two records in deep-sea fish species, and the fourth *Dichelyne* (*Cucullanellus*) species described for the Mediterranean Sea.

A detailed morphological study of these specimens was performed by means of light and scanning electron microscopy. The individuals of this nematode species possess a precloacal sucker, ten pairs of caudal papillae, and an intestinal caecum, typical features for species belonging to *Dichelyne* (*Cucullanellus*) (Figs. 6.1–6.3). The new species differs from other members of this subgenus, recorded in other fish species from different geographical areas including the Atlantic Ocean and the Mediterranean Sea, in different morphological traits. The new species has a larger body size, smaller spicule/body length ratio, and differs in the position of deirids and excretory pore, and in the distribution of caudal papillae (Table 6.1).

Interestingly, in the present study, specimens taken from the Mediterranean Sea were smaller than from the Atlantic Ocean and additionally males found in *N. bonaparte* had a smaller body size than male specimens obtained from *N. chemnitzii*, both hosts from the Atlantic Ocean. Despite the biometric differences, nematode specimens from both hosts and areas were considered to belong to the same species because most body ratios and other values were identical among them. These here detected differences in the nematode development agree with other studies and supposedly are related to different biological and environmental factors such as host species, host size and condition, and temperature (Sasal et al. 2000, Timi et al. 2009). Considering previous publications of differences in fish sizes between the Northeast Atlantic Ocean and the Mediterranean Sea (Stefanescu et al. 1992) it is supposed that the lower host body size of *N. bonaparte* from the latter area affects the size of these nematodes (Poulin 1998).

In the present study we could also observe a broad intraspecific variability in certain aspects of the morphological traits, in particular considering the presence/absence of the intestinal caecum and the distribution of the papillae in the caudal region of the males. The latter trait is one of the key diagnostic features to identify species of this subgenus. Cases of high intraspecific variability in these morphological traits were also detected in other *Dichelyne* spp. (De & Maity 1995, Li et al. 2014). The differences in the distribution of papillae recorded in the present study were partly detected on the same specimen (both sides of the tail) (Fig 6.1J, K). Along with differences which might be related to the fixation procedure or the examination of material from fresh or frozen hosts, in this case we suggest simple intraspecific variabilities which seem to occur quite frequently.

The revision of the described species for *Dichelyne* (*Cucullanellus*) spp. revealed many uncertainties of their validity and a profound revision would be necessary, especially when considering the morphological variabilities observed here and elsewhere.

Seasonal variation of parasite communities of *Notacanthus bonaparte* Risso, 1840 (Notacanthiformes: Notacanthidae) over the Northwest Mediterranean slope

The short-fin spiny eel *Notacanthus bonaparte* Risso, 1840 was first described from the Western basin of the Mediterranean Sea, and its distribution extends to the Northeast Atlantic (Froese & Pauly 2017). Few studies exist on this species and available data comprise its spatial and depth-related distribution, reproduction and diet (e.g. Stefanescu et al. 1992, Coggan et al. 1998, Rodríguez-Romeu et al. 2016). The aim of this study is to provide detailed information on the parasite communities of *N. bonaparte* from different seasons and depth ranges of the slope in the western Mediterranean. Further, we want to assess the potential effects on the parasite communities imposed by the factors depth, season, host size and sex, trying to detect links between environmental parameters from this area and the parasite communities.

The analyses were performed on the parasite communities of 150 specimens of *N. bonaparte* sampled in the western Mediterranean Sea (Balearic Sea, Spain) from three bathymetric strata between 600 and 2,000 m over the seasons in 2007/08 and 2011 (Fig. 7.1). The depth was separated in three depth strata: 600–1,000 (D1), 1,000–1,400 (D2) and 1,400–1,800 (D3). Each depth range was joined with the season (winter (W), spring (Sp), summer (S), autumn (A)) of sampling (Table 7.1). The potential effects by these 'DepthSeason' combinations on the parasite communities and on single parasites were tested including also the cofactors sex and status of maturity (fish size). We tested the effect of 'DepthSeason' combinations with co factors (fish size, sex) on parasite infracommunity parameters, such as richness and diversity, and on the abundance and prevalence of single parasite species (common species prevalence >5%). Latter analyses were repeated using samples from different depth strata where samples were taken in a particular season (D1 and D2, summer; D1–D3, autumn). Seasonal variation in prevalence and abundance were tested for D1, where samples from all seasons were available, including also the cofactors. The potential effect on parasite community composition and structure was assessed considering the factor 'DepthSeason', or 'season' and 'depth' separately. Finally, the potential impact of environmental variables (temperature, salinity, oxygen, turbidity) imposed on the parasite communities was tested.

Overall, parasite communities of *N. bonaparte* in this area are poor, especially when considering its benthic feeding habit, supposedly exposed to the many benthic parasite life cycles. Almost all analysed *N. bonaparte* specimens were infected by at least one parasite species (overall prevalence 94.7%), while the overall mean abundance was 94.3±112.6. The infracommunity composition is defined by the factors, depth, maturity status (size) and sex. The infracommunity richness and Margalef Species Richness revealed significant differences between 'DepthSeason' combinations, where samples taken in spring showed a higher richness (Table 7.2). Margalef Species Richness and Brillouin's diversity were signifcantly different between sexes, where mean values for both indices were signifcantly higher in males.

We detected five taxa, all of them recorded for the first time in *N. bonaparte* (Table 7.3): a larval cucullanid which could not be identified to species level, the monogenean *Tinrovia mamaevi* **a**nd the nematode *Dichelyne (Cucullanellus) romani*; the other two taxa were larval stages of *Hysterothylacium aduncum* and Tetraphyllidea fam. gen. sp. and showed overall prevalences below 5%, supposedly being accidental infections.

The parasite *D.* (*C.*) *romani* did not show any pattern considering any of the tested factors. In contrast, the most abundant taxon, the cucullanid larva, showed significant differences between 'DepthSeasons' and between depths, fish size and sex. This parasite seems to be accumulated during host life showing higher abundances in larger fish of deeper waters (on the middle and lower slope) and is more abundant in larger sized females. The monogenean *T. mamaevi* was recorded in the upper slope mainly during the spring season. The abundance of this parasite differed significantly among all 'DepthSeason' combinations with highest values in D1, but without any effect by fish size or sex. Abundance and prevalence of this monogenean were signifcantly different between the four seasons from D1. The prevalence for spring was significantly higher compared to summer and autumn. Both taxa were slightly related to measured environmental parameters: cucullanid larvae to turbidity and *T. mamaevi* to temperature and salinity (Fig. 7.2).

Communities were richer in shallower waters (D1) owing to the presence of *T. mamaevi* and both uncommon taxa, *H. aduncum* and Tetraphyllidea gen. sp., while cucullanid larvae showed lower abundances. Higher abundances of cucullanid larvae were detected in larger mature specimens, indicating an accumulation of this parasite during host growth. Further, females showed higher abundances of this parasite which can be explained by their larger sizes, compared to males. The lower abundance in males might partly explain the higher Margalef Species Richness and Brillouin diversity indices calculated in males. Although not for the present study, a bigger-deeper trend for this species has been reported (Coggan et al. 1998, Rodríguez-Romeu et al. 2016), which also explains the higher abundances of this nematode observed in deeper waters. We suggest that 3rd stage larvae of this cucullanid nematode are free-living, which has been observed for another cucullanid (Køie 2000), and after hatching they sink to the bottom and survive a certain period in the sediment. As sediment has been recorded in stomach (Rodríguez-Romeu et al. 2016), we argue that cucullanid larvae can infect fish when they are ingested with sediments or while fish feeds on benthic organisms. The high infection rate by this larval parasite may hint to the important role of this species as intermediate host. In case of the species *D.* (*C.*) *romani* the life cycle is still unknown and further studies are needed to identify the intermediate hosts.

The monogenean *Tinrovia mamaevi* was recorded in the upper slope mainly during the spring season. Usually, several studies observed monogeneans in ‘shallower’ waters of the deep ocean only (up to 1,000 m) (De Buron & Morand 2004) and the overall diversity is considered to be lower compared to shallow coastal waters (Rohde 1988). In this study, the higher prevalence at the upper slope could be related to higher host densities observed in these depths, but also to temperature and salinity. Though, the measured variations for these parameters between depth strata were marginal therefore, we argue that additionally other abiotic parameters may influence its spatial and temporal distribution.

Finally, the samples obtained for this study contribute to the description of two parasite species new to science, and substantially enhance the knowledge on the parasite fauna of *N. bonaparte*.

Metazoan parasite communities and diet of the velvet belly lanternshark *Etmopterus spinax* (Squaliformes: Etmopteridae): a comparison of two deep-sea ecosystems off northern Spain

The first data on metazoan parasite communities and diet composition in *Etmopterus spinax* at the Galicia Bank and the Avilés Canyon (northwestern Spain, southern Bay of Biscay) are provided in this study. Both areas are topographic underwater features which were included recently in the ‘Natura 2000’ network (Fig. 8.1). This comparative approach focussed on the variation at the level of individual fish hypothesizing that both, parasites and diet, would be informative at detecting differences between the populations of *E. spinax* in these deep-sea ecosystems. The aim of this study was to combine the examination of stomach contents with the structure of parasite communities, yielding a snapshot of the most recent trophic niche utilisation and reflecting a long-term feeding niche to get more comprehensive information on the role of this shark species in the two local food webs.

Parasite communities and diet of 59 specimens of the velvet belly lantern shark, *E. spinax*, sampled in two underwater features in the Northeast Atlantic off northwestern (Galicia Bank, GB) and northern (Avilés Canyon, AC) Spain have been analysed. Samples of this shark species were taken in summer months of 2010, at 558 (GB) and 855 m (AC) depth.

Parasite infracommunity parameters (richness, total abundance, diversity and dominance, parasite abundance) and the number of detected prey items were tested for potential differences between both localities, including host size as covariate. Data on parasite and prey abundance were tested for a potential relationship with host size. The effect of the factor locality and the covariate host size on the composition and structure of the parasite community and diet assemblages were assessed. This was followed by the identification of key taxa mostly contributing to similarities within and dissimilarities between both sampled localities.

As far as is known, this study provides the first comparative parasite infracommunity data for a deep-sea shark species. The overall prevalence of infection in *E. spinax* was 76.3%; overall prevalences and abundances in both areas were not signifcantly different (overall prevalence: GB: 86.7% *vs* AC: 65.5%; total mean abundance GB: 5.30 *vs* AC: 9.52). Overall eleven parasite taxa were recovered from both areas, and the majority of taxa was represented by larval stages (84.4%) (Table 8.1). Three species are recorded for the first time in *E. spinax*: the cestodes *Ditrachybothridium* cf. *macrocephalum* Rees, 1959 (Diphyllidea) and *Sphyriocephalus* sp. (Trypanorhyncha), and the digenean *Otodistomum* cf. *cestoides* (van Beneden, 1871) (Hemiuroidea).

Fishes from the GB were significantly larger than in the AC and size could be associated with the abundance of four taxa in the GB and two in the AC, where most correlation were positive except for the monogenean *Squalonchocotyle spinaci*, which revealed a negative association with host size.

We detected nine taxa (6 larval and 3 adult stages) at the GB and seven taxa (5 larval and 2 adult stages) at the AC, while five taxa (3 larval and 2 adult stages) occurred in both localities. The component parasite communities in *E. spinax* were relatively rich for both areas, whereas the infracommunities were rather depauperate, with similar low diversity at both localities (Table 8.2).

The differentiation of parasite community composition and structure could be associated with locality (Fig. 8.2), but also indicated that these parameters are affected by host size. The key discriminating taxa contributing to the high dissimilarity (82%) between both localities (GB and AC) were *Anisakis* sp. (Type I *sensu* Berland, 1961), larval tetraphyllideans and the monogenean *Squalonchocotyle spinaci*. While *Anisakis* sp. was significantly more abundant in samples from the AC, *S. spinaci* was detected in samples from the GB only.

Of the 59 specimens examined 40.7% had empty stomachs. In both areas main prey items consisted of crustaceans, mainly carideans and euphausiids, and fishes, whereas squid and echinoderms were of minor importance (Table 8.3). While sharks from the GB mostly preyed on carideans and bathypelagic fishes, at the AC euphausiids and carideans had the highest contribution to the diet, followed by bathy- and benthopelagic fishes. At the GB host size could not be associated with prey abundance while abundances of euphausiaceans in the AC showed significant negative correlations with host size. The composition and relative abundance of prey was partly explained by locality and host size, where euphausiaceans, carideans and fishes were the key discriminating prey items contributing to the dissimilarity (92.5%) between sampling localities. The total abundance of euphausiids was signifcantly different between both localities, as it was absent in GB.

The significant differences in the composition and structure of both parasite communities and prey assemblages indicate differential effects of the two deep-sea ecosystems (GB and AC) on both long-term and most recent trophic niches of *E. spinax*. The here observed relatively high richness of component communities, and the depauperate infracommunities in *E. spinax,* which are strongly dominated by a single species (Table 8.1), may represent a characteristic feature of small sharks. Host size played a certain role with respect to the detected differences in parasites and diet between both localities. Larval cestodes and nematodes were accumulated during host growth with high abundances in larger sharks.

This study revealed clear variations in the diet on a very small spatial scale. Euphausiids were of higher importance for smaller shark specimens in the AC, while in the GB these crustaceans exhibited a lower abundance. This also indicates to the already observed opportunistic feeding habits of *E. spinax* (e.g. Dimech et al. 2012), feeding on most abundant prey items. But it also indicates that larger specimens alter their diet, which was already observed in previous studies, in order to meet higher energetic requirements.

The higher abundance of the nematode *Anisakis* sp. in the AC might be explained by the higher numbers of its definitive hosts detected in the southern Bay of Biscay (López et al. 2004), especially piscivorous and teuthivorous toothed whales (López pers. com.), and probably, to the high amount of discards (fish and viscera) due to enhanced fishing effort in that area (Punzón et al 2010). This may facilitate the infection of all host types by this nematode. The detection of concordant differences in the abundances of euphausiids and *Anisakis* sp. in the Aviles Canyon linked both most recent and long-term trophic niches. Free-living larvae of monogeneans such as *S. spinaci* depend on several abiotic factors (Grutter 1998) and the physical-chemical conditions of the GB seabed could be more suitable for this monogenean. Additionally potential schooling behaviour, especially of younger sharks, may promote parasite transmission (Raeymaekers et al. 2008, Jacoby et al. 2011).

The presented results underline the importance of the use of multivariate analyses for the assessment of geographical variation in shark populations based on parasites and diet data. This study could serve as a starting point for future studies focussing on potential migration and population connectivity of *E. spinax* within this geographical area and between the GB and AC. This would also help to define the importance of these protected deep-sea areas (Natura 2000 network) for small sized deep-sea shark populations.

First insight into the diet and parasite communities of the deep-sea shark *Deania profundorum* (Smith & Radcliffe, 1912) from the Avilés Canyon (southern Bay of Biscay): shedding light on host's role?

Owing to the partly high importance of elasmobranchs in the deepwater communities in areas of the southern Bay of Biscay (Sánchez et al. 2008), this study shall provide an insight into the role of the centrophorid *Deania profundorum* within the community of the Avilés Canyon (AC) combining the description of the recent trophic niche (stomach contents) and the long-term feeding niche utilization (parasite communities).

We present information on the parasite communities and diet of the arrowhead dogfish, *D. profundorum*, sampled in an underwater canyon system in the Northeast Atlantic off northern Spain. The samples of this shark species were taken in the Avilés Canyon (AC) (Fig. 9.1), which is part of the 'Natura 2000' network, in June 2010 and May 2011 at 580 and 1,260 m depth. The host size was tested for a potential relation to parasite abundances and prey item number. The potential effect imposed by the factors, years and host sex, on several infracommunity parameters (abundance, richness, diversity, dominance, parasite abundance) and diet were tested including host size as covariate. Community similarity analyses and multivariate analyses were performed to assess the potential effects of sampling years and host sex, including host size as covariate, on the composition and structure of parasite communities and diet assemblages.

This is the first comprehensive study on the parasite community and diet of this species in the Northeast Atlantic. We examined 29 specimens of *D. profundorum* which exhibited an overall prevalence of 89.7% and a total mean abundance of 42.2±71.6. Nine parasite species were detected, of these five were found as larval stage comprising the majority of all identified parasite individuals (88.7%) (Table 9.1). Six out of nine taxa are recorded for the first time in *D. profundorum* and one species (*Squalotrema* sp.) could be a species new to science.

Both sampling years did not differ in sex ratio, host size, or parasite infracommunity parameters, therefore the comparison between sexes were performed with pooled data of both years. Host size was associated with infracommunity parameters (abundance, richness, diversity) and with abundances of three taxa (*Deanicola* sp., Lacistorhynchidae gen. sp. and *Anisakis* sp. (Type I *sensu* Berland, 1961)) showing a positive correlation (Fig. 9.2).

The sex ratio was balanced, and males were only slightly larger. Infracommunity parameters did not reveal significant differences between sexes (Table 9.2). Host sex was also not affecting the community similarity, where host size explained a part of the variations observed. However, GLMs analyses indicate that two parasite species, larval *Anisakis* sp. (Type I sensu Berland, 1961) and lacistorhynchid larvae were significantly more abundant in males (Fig. 9.3).

Of the 29 examined specimens 37.9% had empty stomachs. The diet of *D. profundorum* consisted of fishes, crustaceans (carideans) and squid – with bentho- and bathypelagic fishes as most abundant prey (Table 9.3). None of the prey items could be related to host size and factors years and host sex did not show any effect on the composition of the diet assemblage.

The high representation of larval stages of cestodes and nematodes indicates that this shark has an intermediate position in the local food-web, which is also supported by the composition of its diet mentioned above.

Host size clearly influenced the parasite community with increasing load observed for larger shark specimens indicating an accumulation during growth. This pattern was already observed in other studies, where parasite abundance and richness increased with host size (e.g. Timi & Poulin 2003, Bagge et al. 2004), as parasites are acquired and accumulated over the life span (Barber & Poulin 2002). The comparison with conspecific, congeneric and other shark species partly indicated the same pattern of increasing parasite load, while the observed different parasite diversity and richness indicate, amongst other parameters, to distinct species related feeding habits (e.g. Dallarés 2016). The host size also explains the differences observed for single parasite species between sexes, where slightly larger males exhibited higher abundances of larval *Anisakis* sp. and lacistorhynchid larvae. These differences between sexes may indicate to potentially distinct feeding habits of both sexes which could not be discerned by the diet analysis.

This study highlights the previous suggestions on the importance of using parasites as biological indicators to identify potential prey items of past feeding events, and the assessment of the host role in marine communities. Further, this survey on the diet and metazoan parasite communities of this shark provides the first data from this area and adds some new data to the scant information available for this genus. Future studies could clarify the potential role of underwater features (canyons, seamounts) on the diet and parasite community of benthopelagic shark species, especially when comparing these parameters from areas without these topographic features.

Resumen

El mar profundo es el mayor bioma de la tierra y el menos estudiado (Ramirez-Llodra et al. 2010). Si bien inicialmente el mar profundo se consideró como un ambiente muy estable con variaciones muy leves por debajo de la termoclina permanente, los estudios realizados en las últimas décadas indican que el mar profundo es un ambiente más dinámico de lo que se pensaba (Gage 2003, Ramirez-Llodra et al. 2010). La variabilidad natural de los procesos que tiene lugar en los hábitats del mar profundo tiene su origen en diferentes factores entre los que se encuentran las corrientes horizontales de masas de agua de grandes dimensiones dirigidas por las corrientes circunglobales, las cuales pueden dar lugar a modificaciones en los regímenes de temperatura y salinidad. Por otro lado los accidentes topográficos sumergidos, como por ejemplo las montañas y los cañones submarinos, interaccionan con dichas corrientes dando lugar a unas condiciones ambientales diferentes de las que tienen lugar en el talud continental o en las llanuras abisales; las condiciones específicas que se dan en estas formaciones favorecen el incremento del alimento disponible y también de la diversidad en el mar profundo a escala local (Levin & Dayton 2009 y referencias dentro de este trabajo). Por lo tanto, la alta heterogenidad espacial que pueden presentar los hábitats en el mar profundo, junto con la limitación espaciotemporal del aporte de alimento en estas comunidades (Snelgrove & Grassle 1995) puede dar lugar a una alta variabilidad en la diversidad, incluso a pequeña escala espacial (Levin & Dayton 2009).

El conocimiento actual sobre las dinámicas del mar profundo y de sus hábitats es todavía muy limitado y en algunos casos casi inexistente, sobre todo comparado con el conocimiento que se tiene de los ecosistemas costeros y de aguas someras (Ramirez-Llodra et al. 2010, Snelgrove et al. 2016). Esta afirmación es también válida cuando hablamos de las especies ícticas del mar profundo sobre las que existe un conocimiento muy limitado, restringido a aquellas que tienen un valor comercial y que son especies objetivo en zonas determinadas (Snelgrove et al. 2016). Por consiguiente, debido al gran desequilibro en el número de estudios realizados en zonas profundas, se recomienda considerar con cautela las extrapolaciones sobre patrones comunes en el mar profundo (Snelgrove et al. 2016).

Dentro de esta información generalmente escasa sobre los ecosistemas profundos, hay una gran falta de conocimiento en lo que respecta a las características de los peces de aguas profundas, incluyendo su parasitofauna. Muchos de los aspectos de la biología de los parásitos, tales como sus ciclos de vida y patrones de distribución en el mar profundo a menudo se han extrapolado basándose en conocimientos preexistentes sobre peces de aguas someras. Los pocos datos existentes sobre los parásitos de los peces de profundidad muestran similitudes con los de las aguas someras, existiendo una cierta relación entre las comunidades parasitarias y las características de los hospedadores. Los ciclos de vida de los parásitos en aguas profundas son a menudo desconocidos. Los estudios existentes parecen mostrar que la diversidad de ciertos grupos de parásitos es claramente menor que la que muestran especies de peces de aguas someras (Klimpel et al. 2009). La menor diversidad puede explicarse parcialmente en algunos taxones superiores, como los digeneos, por el hecho de que pocos parásitos han conseguido seguir y coevolucionar con sus hospedadores hacia las profundidades oceánicas. Además, la menor densidad de hospedadores en el mar profundo, junto a la inadecuación de ciclos de vida, podrían haber impedido una exitosa colonización de este hábitat (Campbell et al. 1980, Bray et al. 1999, Klimpel et al. 2006).

El aumento del conocimiento de la fauna parasitaria de especies ícticas del mar profundo no solo proporciona mayor información sobre los parásitos en sí, también proporciona información sobre las características biológicas y la ecología de los hospedadores, por lo que los parásitos pueden emplearse como indicadores biológicos. Este conocimiento contribuye además a mejorar la comprensión del las vías de transmisión de los parásitos en condiciones ambientales extremas con a menudo baja diversidad y densidad de hospedadores (Leung et al. 2015).

En particular, el uso de los parásitos como indicadores biológicos es recomendable para especies de hospedadores raras o difíciles de muestrear (MacKenzie & Abaunza 1998), que es en buena parte el caso de las tres especies estudiadas en este trabajo: *Notacanthus bonaparte* Risso, 1840 (Notacanthiformes: Notacanthidae), *Etmopterus spinax* L., 1758 (Squaliformes: Etmopteridae), y *Deania profundorum* Smith & Radcliffe 1912 (Squaliformes: Centrophoridae).
La información existente sobre los hábitats profundos y su ictiofauna apunta claramente a 'historias de vida' caracterizadas por un crecimiento lento, madurez retardada y baja fecundidad lo que hace que los peces del mar profundo sean en general menos resilientes ante impactos antropogénicos como es el caso de la pesca (Koslow et al. 2000, Bergstad et al. 2013). Estas características son comunes a las tres especies estudiadas en este trabajo, y a pesar de que las tres tienen un bajo valor comercial, todas ellas sufren el impacto de la pesca debido en parte a las altas tasas de mortalidad experimentadas por las especies debido al *bycatch*.

Notacanthus bonaparte se alimenta de organismos bentónicos y en algunas zonas presenta abundancias elevadas. Sin embargo el papel concreto de *N. bonaparte* en el ecosistema no se conoce, y solo puede especularse que una disminución en sus densidades tendría un 'efecto cascada' en el ecosistema. En lo que respecta a las especies de tiburones (*E. spinax* and *D. profundorum*), su papel/importancia en los ecosistemas profundos no se conoce con precisión, sin embargo, dadas sus características como especies predadoras y pertenecientes a altos niveles tróficos (Cortés 1999), se ha sugerido que su disminución o extinción podría tener importantes consecuencias para la comunidad local y para la estabilidad del ecosistema.

Objetivo principal y específicos

El principal objetivo de esta tesis es contribuir al conocimiento de la parasitofauna de peces de profundidad del Mediterráneo y Atlántico nororiental. En concreto se pretende conocer la diversidad, estructura y composición de las comunidades, información imprescindible para la realización de estudios en los que se utilicen a los parásitos como indicadores de diferentes aspectos de la biología y ecología de sus hospedadores y de los ecosistemas en los que habitan.

Con este fin se han seleccionado tres especies de peces modelo: un representante de los osteíctios (la anguila de Bonaparte, *Notacanthus bonaparte* (Teleostei: Notacanthiformes)) y dos condríctios (el negrito, *Etmopterus spinax* y el tollo flecha *Deania profundorum* (Chondrichthyes: Squaliformes)).

Para la consecución del objetivo general, se han marcado como objetivos específicos:

1. Estudiar la parasitofauna de *N. bonaparte*, *E. spinax* y *D. profundorum* en el Mediterráneo occidental y el Atlántico nororiental, identificando las especies encontradas y haciendo una revisión bibliográfica detallada de los parásitos encontrados en estos hospedadores y otras especies próximas.

2. Describir especies de parásitos nuevas para la ciencia (*N. bonaparte*).
3. Describir las comunidades de parásitos de *N. bonaparte*, *E. spinax* y *D. profundorum*, e investigar los factores biológicos que influyen en su composición y estructura.

4. Contribuir al conocimiento sobre la composición y abundancia de las especies de parásitos para su uso como posibles indicadores de los patrones de distribución y conectividad en especies de peces, tanto en el marco de las variaciones estacionales y batimétricas (hospedador modelo *N. bonaparte*), como geográficas (hospedador modelo *E. spinax*).

5. Analizar la relación entre la fauna parasitaria y la dieta/ecología trófica del hospedador (hospedadores modelo *E. spinax* y *D. profundorum*).

Listado con anotaciones de los parásitos citados en las especies de tres familias de peces de profundidad: Centrophoridae, Etmopteridae and Notacanthidae

Se presenta una revisión de la información existente hasta la fecha de los parásitos documentados hasta ahora para las tres familias de hospedadores (Centrophoridae, Etmopteridae and Notacanthidae) a las que pertenecen las tres especies modelo (Tabla 4.1). Se ha realizado un búsqueda detallada consultando diferentes bases de datos (p.ej. *Google Scholar, Web of Knowledge, World of Copepods, Global Cestode Database* y *Host-parasite database of the Natural History Museum, London*) así como la amplia revisión realizada por Klimpel et al. (2009). La información encontrada mediante motores de búsqueda de internet fue además verificada con la Fuente original (la publicación) cuando ésta estuvo disponible.

Las tres familias presentan un número diferente de especies válidas, estando algunas especies todavía en discusión. El número total de especies de peces válidas (82) se distribuye entre las tres familias de la siguiente manera: 20 centrofóridos, 51 etmoptéridos y 11 notacántidos.

Las publicaciones encontradas sobre las especies de parásitos descritas para las tres familias de los tres hospedadores objeto de este estudio son pocas en comparación con las existentes para peces de aguas someras o especies de interés comercial, aunque se detecta un aumento en el número de publicaciones a partir de la década de los setenta (Fig. 4.1). Por otro lado, las publicaciones muestran un claro sesgo geográfico, correspondiendo la mayor parte de los estudios al Noreste Atlántico, seguidos por los estudios en el Noroeste Atlántico, en el Suroeste Pacífico y en el Mar Mediterráneo.

El análisis de la información muestra que varias familias de parásitos pertenecientes a diferentes grandes grupos taxonómicos, tienen una relevancia diferente en los hospedadores elasmobranquios y en los teleósteos. Estos grupos taxonómicos fueron: Cestoda, Monogenea, Trematoda (Digenea), Nematoda, Copepoda, Isopoda, Cirripedia y Amphipoda (Fig. 4.2). En las dos especies de elasmobranquios la mayoría de parásitos documentados eran cestodos, seguidos por los copépodos, mientas que en los notacántidos los digeneos fueron el grupo más diverso, seguido de los monogeneos. Se trata de patrones que ya han sido observados en otros elasmobranquios y osteíctios (Campbell et al. 1980, Cribb et al. 2002, Caira & Healy 2004). Los anfípodos y cirrípedos solo se detectaron en los etmoptéridos (Fig. 4.4, 4.5). En general la baja diversidad de monogeneos puede deberse a artefactos asociados al muestreo o a una presencia en general baja de este grupo en el mar profundo, como ya han sugerido otros autores (De Buron & Morand 2004).

Los parásitos detectados en las familias de peces analizadas representan parte de las familias que se encuentran con frecuencia en otros peces del mar profundo (Fig. 4.3). Las proporciones de especialistas y generalistas de todos los grupos de parásitos fueron diferentes entre las tres familias de hospedadores, donde los notacántidos mostraron la proporción más elevada de especies especialistas (casi un 58%), seguidos de los etmoptéridos (50%) y los centrofóridos (30%) (Fig. 4.6). Los parásitos especialistas no solo se encontraron en los monogeneos, sino también en los digeneos (en Notacanthidae) y cestodos (en las dos familias de elasmobranquios). Como se ha sugerido previamente, los organismos generalistas, a través de la dieta, pueden infectarse por una fauna parasitaria más diversa con más especies generalistas (Klimpel et al. 2006, Chambers 2008); las diferencias entre las familias de hospedadores se pueden explicar en parte por los diferentes hábitos alimenticios de las mismas, dado que los tiburones presentan, en general, un espectro mayor de presas. En comparación, los notacántidos muestran un espectro de presas más limitado y son también en parte especies de dietas más especializadas.

La proporción de parásitos heteroxenos y monoxenos fue similar en las tres familias. La proporción más elevada de parásitos heteroxenos fue detectada en notacántidos, probablemente debido en parte a su dieta estrictamente bentónica. En etmoptéridos, los taxones de parásitos monoxenos contribuyeron en mayor medida, en parte debido a dos taxones encontrados exclusivamente en esta familia de peces. Este hecho puede también estar relacionado con el hecho de que haya registrado una mayor proporción de parásitos adultos en etmoptéridos, mientras que en los otros tiburones, los centrofóridos, la proporción de heteroxenos y monoxenos fue prácticamente la misma. En etmoptéridos se detectaron más especies monoxenas que infectan a sus hospedadores mayoritariamente en estado adulto (excepto Gnathiidae). La mayor proporción de adultos en notacántidos está representada mayoritariamente por digeneos, lo que puede estar relacionado con su dieta bentónica especializada. Cabe destacar el elevado número de estadios larvarios detectados en los centrofóridos, la familia que presenta mayores tamaños corporales, indicando un papel importante de la misma como hospedador intermediario o, por lo menos, paraténico. Consecuentemente, deben de existir depredadores de estos centrofóridos, de al menos un tamaño similar, en sus hábitats. Se necesitan más estudios para analizar si algunas larvas de cestodos podrían parasitar exclusivamente a tiburones pequeños y/o jóvenes, siendo menos frecuentes en hospedadores adultos.

Una nueva especie de *Tinrovia* Mamaev, 1987 (Monogenea: Microcotylidae) en el pez de profundidad *Notacanthus bonaparte* Risso (Notacanthiformes: Notacanthidae) en el Mediterráneo occidental y el Noreste Atlántico

Durante el análisis de las comunidades parasitarias de la anguila de Bonaparte, *Notacanthus bonaparte* Risso, 1840, una nueva especie de monogeneo fue detectada y descrita. La fauna parasita del pez de profundidad *N. bonaparte* es poco conocida y hasta la fecha solo se han descrito dos especies: el trematodo *Steringovermes notacanthi* Bray, 2004 y el cestodo *Bathycestus brayi* Kuchta & Scholz, 2004.

Este nuevo microcotílido, *Tinrovia mamaevi* n. sp. (Monogenea: Polyopisthocotylea), se describió en las branquias de especímenes muestreados en el Mediterráneo occidental y el Noreste Atlántico. Los especímenes obtenidos se emplearon para realizar un análisis morfológico detallado mediante microscopio óptico y confocal. Las características morfológicas observadas en los especímenes de monogeneos analizados de las dos áreas justifican su clasificación como una única especie. Esta especie se asigna a la subfamilia Syncoelicotylinae Mamaev & Zubchenko 1978 debido a la posesión de un háptor asimétrico con dos salientes longitudinales separados. Esta especie se incluye en el género *Tinrovia* que incluye únicamente a la especie tipo *T. papiliocauda* Mamaev, 1987.

Tinrovia mamaevi se diferencia de *T. papiliocauda* por la presencia de un háptor más estrecho, con un menor número de pinzas. Las pinzas son menores en esta nueva especie, los testículos más numerosos, el atrio genital es menor y con un menor número de espinas y los huevos tienen un filamento largo y uno corto (Tabla 5.1).

Las pinzas en *T. mamaevi* n. sp. son de tipo 'microcotílido', organizadas sobre dos salientes longitudinales laterales (Fig. 5.1). Las publicaciones previas sobre Syncoelicotylinae han sugerido que sus pinzas son robustas (Mamaev & Zubchenko 1978, Mamaev 1987, Mamaev & Brashovian 1989), sin embargo las pinzas de *T. mamaevi* son ligeramente menores que las de *T. papiliocauda* y sus escleritos son delgados y más delicados. Por ello si bien en estos casos las descripciones pueden ser ambiguas, deben referirse al tamaño total de la pinzas en relación con el tamaño del cuerpo o al tamaño relativo de los escleritos. Esto también es aplicable a la descripción del haptor hecha para dos especies de Syncoelicotylinae.

En este estudio hemos podido observar un háptor menor en *T. mamaevi* comparado con *T. papiliocauda*, mientras que los salientes laterales parecen ser relativamente menores y más estrechos. En la diagnosis genérica de dos especies de los géneros *Syncoelicotyle* y *Tinrovia,* el háptor se describe como 'con forma de mariposa', es decir, compuesto por salientes anchos y separados (Mamaev & Zubchenko 1978, Mamaev 1987) (Figs. 5.1, 5.2). Sugerimos que las descripciones de estas especies de Syncoelicotylinae hacen referencia a aspectos que pueden ser controvertidos. En primer lugar se observa, que los salientes del háptor de la nueva especie no son anchos, sugiriendo que este carácter no es ya válido para la diagnosis de todo el género *Tinrovia*. En segundo lugar, sugerimos el uso de un término más genérico para hacer referencia a caracteres como salientes laterales del háptor anchos, dado que descripciones que hacen referencia a una forma muy particular pueden ser mal interpretados dependiendo del observador.

Junto con el menor número de espinas, el atrio genital en *T. mamaevi* es menor y presenta un patrón diferente de almohadillas musculares armadas en comparación con el órgano genital descrito para *T. papiliocauda*. Sin embargo, debido a las dificultades para describir estas estructuras de arquitecturas complejas, se recomienda interpretar con cautela a la supuesta diferencia en la lobulación del atrio genital. Las técnicas aplicadas empleando el microscopio confocal fueron muy útiles, especialmente para interpretar la estructura tridimensional del atrio genital (Fig. 5.3). El uso de estas técnicas puede ayudar a reducir las posibles controversias en la interpretación de las características e incrementar la fiabilidad de los diagnósticos. En este estudio se observó que los huevos de la nueva especie (con un filamento polar largo y uno corto) no se correspondían con la descripción en la diagnosis del género (dos filamentos cortos). No se pudieron distinguir la anastomosis de los ciegos ramificados, supuestamente características de este género, debido a la elevada densidad de los folículos de las glándulas vitelógenas. Las descripciones de estos caracteres son típicamente controvertidas en otras descripciones de poliopistocotileos, por ello son, en general, aspectos morfológicos poco fiables para diagnósticos taxonómicos.

Sugerimos la siguiente diagnosis corregida para el género *Tinrovia*: como en Mamaev (1987) excepto por el háptor con dos salientes laterales que no se unen posteriormente, marcadamente alados cuando éstos son anchos, y huevos con dos filamentos (cortos o largos).

Dichelyne (*Cucullanellus*) *romani* n. sp. (Nematoda: Cucullanidae) en especies de notacántidos del Noreste Atlántico y del Mediterráneo occidental

Se describe un nuevo nematodo, *Dichelyne* (*Cucullanellus*) *romani* n. sp. (Nematoda: Cucullanidae), en el tracto digestivo de dos peces notacántidos, *Notacanthus chemnitzii* Bloch, 1788 y *N. bonaparte* Risso, 1840 (Notacanthiformes: Notacanthidae), del Noreste Atlántico y del Mediterráneo occidental. En la actualidad, la fauna parasitaria de estos notacántidos se conoce muy poco y, hasta la fecha, se ha registrado un solo cuculánido en *N. chemnitzii*, mientras que no existe ningún nematodo citado en *N. bonaparte* (Gibson et al. 2005, Soares 2007). Esta es la primera especie de *Dichelyne* Jägerskiöld, 1902 descrita en un notacántido, uno de los dos únicos registros en especies de mar profundo, y la cuarta especie de *Dichelyne* (*Cucullanellus*) descrita para el Mar Mediterráneo.

El estudio morfológico detallado de estos especímenes se realizó mediante el uso de microscopía óptica y electrónica de barrido. Los individuos de esta especie de nematodo poseen una ventosa precloacal, 10 pares de papilas caudales y un ciego intestinal, todas éstas, características típicas para especies pertenecientes a *Dichelyne* (*Cucullanellus*) (Figs. 6.1 – 6.3). La nueva especie se diferencia de otros miembros de este subgénero, registrado en otras especies de peces de áreas geográficas del Océano Atlántico y el Mar Mediterráneo, por las siguientes características morfológicas: la nueva especie tiene un cuerpo más largo, una relación entre longitud de la espícula y cuerpo menor, la posición de los deiridios y el poro excretor, así como en la distribución de las papilas caudales (Tabla 6.1).

Cabe destacar que en el presente estudio los especímenes recolectados en el Mar Mediterráneo fueron menores que los del Océano Atlántico, así mismo los machos encontrados en *N. bonaparte* eran de menor tamaño que los obtenidos para la especie *N. chemnitzii*, siendo ambos atlánticos. A pesar de las diferencias biométricas, los especímenes encontrados en ambos hospedadores y áreas fueron considerados como pertenecientes a la misma especie, dado que la mayoría de las proporciones corporales y otros valores fueron idénticos entre ellos. Las diferencias detectadas en este trabajo sobre el desarrollo de los nematodos concuerdan con otros estudios, estando dichas diferencias supuestamente relacionadas con diferentes factores biológicos y ambientales como, por ejemplo, la especie hospedadora, el tamaño y la condición del hospedador, así como la temperatura (Sasal et al. 2000, Timi et al. 2009). Teniendo en cuenta las publicaciones previas en el Noreste Atlántico y el Mar Mediterráneo (Stefanescu et al. 1992), se supone que el menor tamaño de *N. bonaparte* en el Mediterráneo afectaría también al tamaño de los nematodos (Poulin 1998).

En este estudio hemos observado un amplio rango de variabilidad intraespecífica en ciertas características morfológicas, en particular en lo referente la presencia o ausencia de un ciego intestinal y la distribución de las papilas en la región caudal de los machos. Esta última característica es una de las características diagnósticas clave para identificar las especies de este subgénero. También se han detectado casos de una gran variabilidad intraespecífica en estas características morfológicas en otras especies de *Dichelyne* (De & Maity 1995, Li et al. 2014). Las diferencias en la distribución de papilas registradas en este estudio fueron parcialmente detectadas en un mismo ejemplar (a ambos lados de la cola) (Fig 6.1 J, K). Junto con las diferencias que pueden deberse a artefactos asociados a los procesos de fijación o al examen de material fresco o congelado, en este caso también parecen existir variaciones intraespecíficas naturales que parecen suceder con frecuencia en determinados ejemplares.

La revisión de las especies descritas de *Dichelyne* (*Cucullanellus*) spp. muestra numerosas incertidumbres sobre su validez, lo que hace necesaria una revisión en profundidad, especialmente considerando las variaciones morfológicas observadas.

Variaciones estacionales de las comunidades de parásitos de *Notacanthus bonaparte* Risso, 1840 (Notacanthiformes: Notacanthidae) a lo largo del talud continental del Mediterráneo noroccidental

La anguila de Bonaparte, *Notacanthus bonaparte* Risso, 1840, fue descrita por primera vez en la cuenca occidental del Mar Mediterráneo, aunque posteriores estudios han mostrado que su distribución se extiende por el Atlántico nororiental (Froese & Pauly 2017). Los pocos estudios disponibles sobre esta especie tratan sobre su distribución geográfica y batimétrica, así como su reproducción y dieta (p.ej. Stefanescu et al. 1992, Coggan et al. 1998, Rodríguez-Romeu et al. 2016). El objetivo de este estudio es proporcionar información detallada sobre las comunidades de parásitos de *N. bonaparte* en diferentes estaciones del año y en rangos batimétricos del talud continental del Mediterráneo noroccidental. Además, se analizaron los efectos potenciales en las comunidades de parásitos de varios factores (profundidad, estación del año, tamaño del hospedador y sexo), con el fin de detectar posibles relaciones entre parámetros ambientales en el área de estudio y las comunidades de parásitos. Se analizaron las comunidades de parásitos de 150 especímenes de *N. bonaparte* muestreados en el Mediterráneo noroccidental (Mar Balear, España) en tres estratos batimétricos comprendidos entre los 600 y los 2.000 metros y a lo largo de los años 2007/2008 y 2011 (Fig. 7.1).

Las profundidades se separaron en los siguientes estratos: 600–1.000 (D1), 1.000–1.400 (D2) and 1.400–1.800 (D3). Cada rango de profundidad fue analizado a lo largo de las diferentes estaciones del año en que se muestreó (invierno (W), primavera (Sp), verano (S), otoño (A)) (Tabla 7.1). Se analizaron los efectos potenciales de la combinación Profundidad-Estación del año (‘Profundidad-Estación’) en las comunidades de parásitos y en los parásitos tratados de forma individual, incluyendo también como cofactores el sexo y el grado de madurez del hospedador (tamaño del pez). Se analizó el efecto ‘Profundidad-Estación’ con los cofactores ‘tamaño del pez’ y ‘sexo’ en la riqueza y diversidad de las infracomunidades, así como en la abundancia y prevalencia de las especies de parásitos (especies consideradas comunes con prevalencias >5%). Este análisis se repitió empleando muestras provenientes de los diferentes estratos de profundidad para una estación en concreto (D1 y D2, verano; D1–D3, otoño). Se analizaron las variaciones estacionales en la prevalencia y abundancia de los parásitos para el estrato D1, para el cual había muestras a lo largo de todas las estaciones del año, incluyendo también los cofactores. El efecto potencial en la composición y estructura de las comunidades de parásitos se analizó considerando el factor ‘Profundidad-Estación’, o separadamente ‘Estación del año’ y ‘Profundidad’. Finalmente, se analizó el impacto potencial de las variables ambientales (temperatura, salinidad, oxígeno y turbidez) en las comunidades de parásitos.

En general las comunidades de parásitos de *N. bonaparte* en el área de estudio son pobres, especialmente teniendo en cuenta que su dieta es bentónica, por lo que se supone que están expuestos a numerosos ciclos de vida bentónicos. Casi todos los especímenes analizados de *N. bonaparte* estaban infectados por al menos un parásito (prevalencia total 94,7%), mientras que la abundancia media general fue 94,3±112,6 (SD). La composición de la infracomunidad queda definida por los factores profundidad, estado de madurez (tamaño) y sexo. La riqueza de la infracomunidad y el índice de riqueza de especies de Margalef mostraron diferencias significativas entre las combinaciones de ‘Profundidad-Estación’, mostrando una mayor riqueza en muestras tomadas en primavera (Tabla 7.2). El índice de Margalef y el de diversidad de Brillouin mostraron diferencias significativas entre sexos, siendo los valores medios de ambos índices significativamente mayores en los machos.

Se detectaron cinco taxones, todos ellos registrados por primera vez en *N. bonaparte* (Tabla 7.3) entre los cuales se encontraban una larva de cuculánido que no pudo ser identificada a nivel de especie, el monogeneo *Tinrovia mamaevi* y el nematodo *Dichelyne* (*Cucullanellus*) *romani*. Los otros dos taxones eran estadíos larvarios de *Hysterothylacium aduncum* y Tetraphyllidea fam. gen. sp. que mostraron prevalencias por debajo del 5%, por lo que se supone que son infecciones accidentales.

El parásito *D.* (*C.*) *romani* no mostró ninguna tendencia respecto a los factores analizados. Por el contrario, el taxón más abundante, las larvas de cuculánidos, mostraron diferencias significativas en 'Profundidad-Estación', así como entre profundidades, tamaño de pez y sexo. Este parásito parece ir acumulándose a lo largo de la vida del hospedador mostrando mayores abundancias en peces de mayor tamaño que habitan en aguas más profundas (zonas media y baja del talud continental), siendo más abundante en las hembras de mayor tamaño. El monogeneo *T. mamaevi* se registró en la parte superior del talud continental, fundamentalmente durante la primavera. La abundancia de este parásito mostró diferencias significativas en todas las combinaciones 'Profundidad-Estación', con los mayores valores en D1, pero sin ningún efecto de los factores tamaño de pez o sexo. La abundancia y prevalencia de este monogeneo eran significativamente diferentes entre las cuatro estaciones del año para D1. La prevalencia para primavera fue significativamente mayor en comparación con verano y otoño. Los dos taxones resultaron estar ligeramente relacionados con parámetros ambientales: la larva de cuculánido con la turbidez y *T. mamaevi* con temperatura y salinidad (Fig. 7.2).

Las comunidades resultaron más ricas en los estratos más someros (D1) debido a la presencia de *T. mamaevi* y de los dos taxones poco comunes *H. aduncum* y Tetraphyllidea gen. sp., mientras que la larva de cuculánido mostraba una baja abundancia. Las mayores abundancias de larvas de cuculánidos se detectaron en individuos maduros y de mayor tamaño, indicando una acumulación de este parásito a lo largo de la vida del hospedador. Además, las hembras mostraron abundancias más elevadas de este parásito, lo cual puede explicarse por sus mayores tamaños comparados con los tamaños de los machos. Las bajas abundancias en los machos pueden explicar parcialmente los elevados valores de los índices de riqueza Margalef y de diversidad de Brillouin. Aunque no se analizó en este estudio, la tendencia 'mayor tamaño-mayor profundidad' ('*bigger-deeper trend*') se ha confirmado para esta especie, lo cual explica también las mayores abundancias de este nematodo observadas en aguas profundas (Coggan et al. 1998, Rodríguez-Romeu et al. 2016). Sugerimos que el tercer estadío larvario de este cuculánido es de vida libre (como ya se ha sugerido en otros cuculánidos, ver Køie 2000), y, tras eclosionar, se deposita en el sedimento, donde sobrevive durante un periodo indeterminado. Dado que se ha encontrado sedimento en el estómago del hospedador (Rodríguez-Romeu et al. 2016), consideramos que la larva de cuculánido puede infectar al pez al ser ingerida con el sedimento o impregnando a los organismos bentónicos de la dieta. La alta tasa de infección por parte de esta larva puede apuntar a un importante papel de esta especie como hospedador intermediario. En el caso de la especie *D.* (*C.*) *romani*, el ciclo de vida todavía no se conoce y son necesarios más estudios para poder identificar al hospedador intermediario.

El monogeneo *Tinrovia mamaevi* se detectó en la parte más superficial del talud continental, fundamentalmente en primavera. Normalmente, los monogeneos parecen estar restringidos a los estratos superiores de los mares profundos (hasta 1.000 m) (De Buron & Morand 2004) y su diversidad se considera en general menor en comparación con las aguas costeras someras (Rohde 1988). En este estudio, su elevada prevalencia en la parte superior del talud puede estar relacionada con las mayores densidades del hospedador observadas en esas profundidades, así como con la temperatura y la salinidad. Cabe mencionar que las variaciones medidas para estos últimos parámetros en los diferentes estratos de profundidad resultaron ser marginales, por lo que consideramos que otros parámetros abióticos pueden estar también influyendo en su distribución temporal y espacial.

Finalmente, las muestras obtenidas en este estudio han contribuido a la descripción de dos especies de parásitos nuevas para la ciencia y han aumentado de forma considerable el conocimiento de la parasitofauna de *N. bonaparte*.

Comunidades de metazoos parásitos y dieta del tiburón de profundidad 'negrito' *Etmopterus spinax* (Squaliformes: Etmopteridae): una comparación de dos ecosistemas profundos del Norte de España

Se proporcionan los primeros datos de comunidades de metazoos parásitos y de la composición de la dieta de *Etmopterus spinax* en el Banco de Galicia y el Cañón de Avilés (Noroeste de España y Sur de la Golfo de Vizcaya respectivamente). Ambas áreas son formaciones topográficas recientemente incluidas en la red 'Natura 2000' (Fig. 8.1). Este estudio comparativo está enfocado en la variación a nivel individual entre especímenes, hipotetizando que ambos, parásitos y dieta, pueden contribuir a detectar diferencias entre las poblaciones de *E. spinax* en estos ecosistemas profundos. El objetivo de este estudio es combinar el análisis de los contenidos estomacales con la estructura de las comunidades de parásitos, proporcionando información tanto sobre el uso del nicho trófico reciente ('foto instantánea') como a largo plazo, con el fin de contar con información lo más completa posible para poder entender el papel de esta especie de tiburón en las redes tróficas locales.

Las comunidades de parásitos y la dieta de 59 especímenes de tiburón 'negrito', *E. spinax*, se muestrearon y analizaron posteriormente, provenientes de dos formaciones topográficas sumergidas en el Noreste Atlántico, una de ellas en el Noroeste (Banco de Galicia, GB) y la otra en el Norte de España (Cañón de Avilés, AC). Se tomaron muestras de esta especie de tiburón en ambas áreas en los meses de verano del año 2010, a 558 (GB) y 855 metros (AC) de profundidad.

Los parámetros de la infracomunidad (riqueza, abundancia total, diversidad y dominancia abundancia de parásitos) y el número de presas encontradas fueron analizados con el fin de detectar posibles diferencias entre las dos localidades de muestreo, incluyendo el tamaño del hospedador como covariable. Los datos de abundancia parásitos y presas se analizaron con el fin de detectar la posible relación con el tamaño del hospedador. Se analizó también el efecto del factor 'localidad' y la covariable 'tamaño del hospedador' en la composición y estructura de la comunidades de parásitos y los ensamblajes de dieta. Posteriormente se identificaron los taxones clave que contribuían a las similitudes en cada localidad y disimilitudes entre las dos localidades de muestreo.

Este trabajo presenta, según la información disponible actualmente, el primer estudio comparativo de la infracomunidad para una especie de tiburón de profundidad. La prevalencia general de infección en *E. spinax* fue 76,3%, no habiendo sido detectadas diferencias significativas en la prevalencia general y abundancia total entre ambas áreas (prevalencia general: GB: 86,7% *vs* AC: 65,5%; abundancia media total GB: 5,30 *vs* AC: 9,52). En total se encontraron once taxones de parásitos para ambas áreas y la mayoría de ellos estuvieron representados por estadíos larvarios (84,4%) (Tabla 8.1). Tres especies se documentaron por primera vez en *E. spinax*: los cestodos *Ditrachybothridium* cf. *macrocephalum* Rees, 1959 (Diphyllidea) y *Sphyriocephalus* sp. (Trypanorhyncha), y el digeneo *Otodistomum* cf. *cestoides* (van Beneden, 1871) (Hemiuroidea).

Los peces del GB fueron significativamente más grandes que los de AC lo cual puede contribuir a explicar la abundancia de cuatro taxones en GB y de dos en AC, donde la mayoría de las correlaciones fueron positivas excepto para el monogeneo *Squalonchocotyle spinaci*, el cual presentó una relación negativa con el tamaño del hospedador.

Se detectaron nueve taxones (6 larvas y 3 estadíos adultos) en GB y siete taxones (5 larvas y 2 estadíos adultos) en AC, mientras que cinco taxones (3 larvas y 2 estadíos adultos) estaban presentes en ambas localidades. Las comunidades de parásitos de *E. spinax* resultaron ser relativamente ricas para ambas áreas, mientras que las infracomunidades resultaron ser bastante pobres, siendo los valores de diversidad similarmente bajos para ambas zonas (Tabla 8.2).

Las diferencias en la composición de las comunidades de parásitos y su estructura pueden estar asociadas con la localidad (Fig. 8.2), pero también indican que esos parámetros pueden estar influidos por el tamaño del hospedador. Los taxones clave que contribuyen a la elevada disimilitud (82%) entre ambas localidades (GB y AC) fueron *Anisakis* sp. (Tipo I *sensu* Berland, 1961), estadíos larvarios de tetrafilideos y el monogeneo *S. spinaci*. *Anisakis* sp. fue significativamente más abundante en muestras procedentes de AC, mientras que *S. spinaci* se detectó solo en muestras de GB.

De los 59 especímenes examinados, 40,7% no contenían presas en sus estómagos. En las dos zonas de estudio las presas más frecuentes fueron crustáceos, fundamentalmente carideos, eufausiáceos y peces, mientras que calamares y equinodermos fueron menos abundantes (Tabla 8.3). Si bien los tiburones de GB fundamentalmente capturaban carideos o peces batipelágicos, en AC, los eufausiáceos y carideos fueron las presas más abundantes en la dieta, seguidos por peces bati- y bentopelágicos. En GB el tamaño de los hospedadores no pudo asociarse con la abundancia de las presas encontrados en los mismos, mientras que en AC se encontró una relación negativa significativa entre la abundancia de eufausiáceos y el tamaño del hospedador. La composición y abundancia relativa de las presas se pudo explicar parcialmente para cada localidad y tamaño del hospedador, constatándose que eufausiáceos, carideos y peces eran las presas clave más importantes, contribuyendo a la disimilitud (92,5%) entre las dos localidades de muestreo. Las abundancias totales de eufausiáceos fueron significativamente diferentes en las localidades, no estando presentes en el GB.

Las diferencias significativas en la composición y estructura de las dos comunidades de parásitos y grupos de presas, indican una influencia diferente por parte de los dos ecosistemas profundos estudiados (GB y AC), tanto a largo plazo como en los nichos tróficos recientes de *E. spinax*. La relativamente alta riqueza de las comunidades componentes observada en este estudio, y las infracomunidades depauperadas en *E. spinax*, claramente dominadas por una única especie (Tabla 8.1), pueden representar una característica típica de los tiburones de pequeño tamaño. El tamaño del hospedador juega un cierto papel en relación a las diferencias detectadas en los parásitos así como en la dieta en las dos localidades de estudio. Las larvas de cestodos y nematodos se acumulan a lo largo de la vida del hospedador con elevadas abundancias en los tiburones más grandes.

Este estudio ha revelado variaciones claras en la dieta a pequeña escala espacial. Los eufausiáceos fueron una presa importante para los tiburones de pequeños tamaño en AC, mientras que en GB estos crustáceos mostraron una abundancia menor. Estas diferencias coinciden también con el carácter generalmente oportunista descrito para los hábitos alimenticios de *E. spinax* (e.g. Dimech et al. 2012), que se alimenta de las presas más abundantes. Sin embargo, ello también indica que especímenes de gran tamaño modifican su dieta, algo ya observado en estudios previos, con el fin de poder cubrir sus elevadas necesidades energéticas.

La mayor abundancia del nematodo *Anisakis* sp. en AC puede explicarse por el abundante número de hospedadores definitivos detectados en el Sur de la Golfo de Vizcaya (López et al. 2004), especialmente odontocetos piscívoros y teutófagos (López com. pers.) y también probablemente por el elevado número de descartes (peces y vísceras) asociadas al elevado esfuerzo pesquero en el área (Punzón et al 2010). Este hecho podría favorecer las infecciones por este nematodo a todos los diferentes tipos de hospedadores. La detección de diferencias concordantes en las abundancias de eufausiáceos y *Anisakis* sp. en el Cañón de Avilés asoció los nichos tróficosreciente y de largo plazo. Las larvas de vida libre de los monogeneos como *S. spinaci* están influidas por numerosos factores abióticos (Grutter 1998), las condiciones físico-químicas de los fondos marinos del GB podrían ser más favorables para este monogeneo. Adicionalmente, el potencial comportamiento de agrupación, especialmente de los tiburones más jóvenes, podría promover la transmisión entre tiburones (Raeymaekers et al. 2008, Jacoby et al. 2011).

Los resultados presentados muestran la importancia del uso de los análisis multivariados para el estudio de las variaciones geográficas en las poblaciones de tiburones basados en sus parásitos y en su dieta. Este estudio puede suponer un punto de partida para futuros trabajos centrados en las posibles migraciones y la conectividad entre poblaciones de *E. spinax* dentro de cada área geográfica concreta y también entre GB y AC. Ello puede también ayudar a definir la importancia de la protección de estas zonas profundas (Red ‘Natura 2000’) para poblaciones de pequeños tiburones de profundidad.

Primera aproximación al estudio de la dieta y las comunidades de parásitos del tiburón de profundidad *Deania profundorum* (Smith & Radcliffe, 1912) en el Cañón de Avilés (Sur del Golfo de Vizcaya): un vistazo a su papel como hospedador

La supuesta importancia descrita para los elasmobranquios en las comunidades profundas en zonas del Sur del Golfo de Vizcaya (Sánchez et al. 2008), justifica este estudio que ofrece una primera aproximación sobre el papel del centrofórido *Deania profundorum* dentro de la comunidad del Cañón de Avilés, combinando la descripción de su nicho trófico reciente (contenidos estomacales) y el uso del nicho trófico a largo plazo (comunidades de parásitos).

Se presentan datos sobre las comunidades de parásitos y la dieta de tiburones tollo flecha, *D. profundorum*, muestreados en las aguas de un sistema de cañones submarinos situado en el Noreste Atlántico, al Norte de España. Las muestras de esta especie de tiburón se tomaron en el Cañón de Avilés (AC) (Fig. 9.1), que es parte de la red ‘Natura 2000’, en los meses de junio del 2010 y mayo del 2011, a 580 y 1.260 metros de profundidad respectivamente. El tamaño del hospedador se analizó para comprobar su posible relación con la abundancia de parásitos y el número de presas. Se analizó el efecto potencial de los factores ‘año de muestreo’ y ‘sexo del hospedador’, en varios parámetros de la infracomunidad (abundancia, riqueza, diversidad y dominancia, abundancia de sus parásitos) y su dieta; en el análisis se incluyó el tamaño del hospedador como covariable. El análisis de similitud de las comunidades, así como el análisis multivariado, se efectuaron para probar los efectos potenciales de los diferentes años de muestreo y sexo del hospedador, incluyendo tamaño del hospedador como covariable, en la composición y estructura de las comunidades de parásitos y los ensamblajes de la dieta.

Este es el primer estudio completo sobre las comunidades de parásitos y la dieta de esta especie en el Noreste Atlántico. Los 29 especímenes examinados de *D. profundorum* mostraron una prevalencia general de 89,7% y una abundancia total media de 42,2±71,6 (SD). Se detectaron nueve especies de parásitos, cinco de ellas fueron encontradas en fases larvarias, incluyendo la mayoría de todos los parásitos identificados (88,7%) (Tabla 9.1). Seis de los nueve taxones fueron registrados por primera vez en *D. profundorum* y una especie (*Squalotrema* sp.) podría ser nueva para la ciencia.

Los análisis realizados comparando los dos años de muestreos no mostraron diferencias significativas en la proporción de sexos, el tamaño de los hospedadores, ni los parámetros de la infracomunidad, por ello en la comparación realizada entre los sexos se unieron los datos de ambos años de muestreo. El tamaño del hospedador se encontraba relacionado con algunos parámetros de la infracomunidad (abundancia, riqueza y diversidad) y con las abundancias de tres taxones (*Deanicola* sp., Lacistorhynchidae gen. sp. y *Anisakis* sp. (Tipo I *sensu* Berland, 1961)), mostrando una correlación positiva (Fig. 9.2).

La proporción de sexos fue equilibrada, siendo los machos ligeramente mayores en tamaño. Los parámetros de la infracomunidad no mostraron diferencias significativas entre los sexos (Tabla 9.2). El sexo del hospedador no afectó tampoco a la similitud de la comunidad, donde el tamaño del hospedador explicó parte de las variaciones observadas. Sin embargo, los análisis GLM realizados, indicaron que dos especies de parásitos, las larvas de *Anisakis* sp. (Tipo I *sensu* Berland, 1961) y las de lacistorrínquidos, fueron significativamente más abundantes en los machos (Fig. 9.3).

De los 29 especímenes examinados, 37,9% no presentaron ninguna presa en los estómagos. La dieta de *D. profundorum* consiste en peces, crustáceos (carideos) y calamares, siendo los peces bentónicos y batipelágicos las presas más abundantes (Tabla 9.3). Ninguna de las abundancias de las presas encontradas puede relacionarse con el tamaño del hospedador y los factores ‘año de muestreo’ y ‘sexo del hospedador’.

La gran representación de estadíos larvarios de cestodos y nematodos indica que este tiburón tiene una posición intermedia en las redes tróficas locales, lo que también está apoyado por la composición de su dieta mencionada previamente.

El tamaño del hospedador tiene una clara influencia en las comunidades de parásitos, cuya carga es mayor en los tiburones de mayor tamaño, indicando una acumulación a lo largo del crecimiento del hospedador. Este patrón se ha observado previamente en otros estudios en los que se describió que la abundancia y riqueza se incrementaban con el tamaño del hospedador (e.g. Timi & Poulin 2003, Bagge et al. 2004), ya que los parásitos se adquieren y acumulan a lo largo de la vida del pez (Barber & Poulin 2002). La comparación con especies coespecíficas, congenéricas, así como con otras especies de tiburones, apunta parcialmente al mismo patrón de incremento de la carga parasitaria, mientras que las diferencias observadas en la diversidad de parásitos y su riqueza indican, junto a otros parámetros, que los hábitos alimenticios son diferentes para cada especie (e.g. Dallarés 2016). El tamaño del hospedador también explica las diferencias observadas para las especies de parásitos entre sexos, donde los machos ligeramente mayores presentan mayores abundancias de estadios larvarios de *Anisakis* sp y de lacistorrínquidos. Estas diferencias entre sexos pueden indicar potenciales diferencias en los hábitos alimenticios de ambos sexos, sin embargo, esto no ha podido discernirse a través del análisis de la dieta.

Este estudio apoya trabajos previos en los que ya se sugería la importancia del uso de los parásitos como indicadores biológicos para identificar potenciales presas o eventos de alimentación antiguos, así como para abordar el papel del hospedador en las comunidades marinas. Además, el análisis de la dieta y las comunidades de parásitos metazoos de este tiburón, proporcionan los primeros datos para esta zona, añadiendo además nuevos datos a la escasa información existente sobre este género. Es necesario realizar más estudios para clarificar el papel potencial de determinados accidentes topográficos submarinos (cañones, montañas, etc.) en la dieta y las comunidades de parásitos de las especies de tiburones bentopelágicas; la comparación de estos aspectos con áreas sin este tipo de accidentes sería especialmente informativo.

Conclusiones

1- El análisis de las citas de especies parásitas en tres familias de peces de aguas profundas (Notacanthidae, Centrophoridae y Etmopteridae) ha revelado que no se han citado parásitos en cerca de un 67% de las especies reconocidas. El número de citas en la única familia de teleósteos fue mayor que las de elasmobranquios: 64% frente a 35 y 25%, respectivamente.

2- Las pocas citas disponibles indican que en ambas familias de elasmobranquios existe una mayor cantidad de cestodos, mientras que los digeneos fueron el grupo taxonómico más diverso en la familia de telósteos. Este hecho puede estar asociado a las diferencias entre los hábitos alimenticios: Los notacántidos son mayoritariamente bentónicos (es decir, próximos a los hospedadores intermediarios) mientras que los elasmobranquios son más bentopelágicos.

3- Los taxones parásitos en notacántidos son principalmente especialistas, reflejando, probablemente, un rango de presas más restringido. Por el contrario, los centrofóridos, familia que incluye a los peces de mayor tamaño, mostraron el número más bajo de parásitos especialistas, los que puede deberse a su dieta generalmente más diversa y oportunista. La proporción equilibrada entre especialistas y generalistas en los etmoptéridos podría estar relacionada con el mayor número de ectoparásitos y su alimentación oportunista.

4- Los parásitos heteroxenos fueron más frecuentes que los monoxenos en las tres familias de peces; sin embargo, cerca del 40% eran monoxenos en los etmoptéridos. Los tiburones de ambas familias ocupan generalmente un nivel medio en las redes tróficas, lo que podría explicar la mayor cantidad de parásitos larvarios. En etmoptéridos, el elevado número de especies monoxenas implica un mayor número de parásitos adultos, que acaban siendo más numerosos que los larvarios. Las mayores proporciones de parásitos adultos en notacántidos podrían verse explicada por la supuesta baja depredación por peces que puedan actuar de hospedadores definitivos potenciales.

5- *Tinrovia mamaevi* Isbert, Carrassón, Pérez-del-Olmo & Montero 2017, descrita en este trabajo por primera vez, es el primer monogeneo descrito en el pez de profundidad *Notacanthus bonaparte*. Se sugiere una diagnosis corregida para el género *Tinrovia*. Los salientes laterales del háptor se describen como ‘alados’ y no como ‘con forma de mariposa’, ya que pueden estrechos o amplios. Los huevos de *Tinrovia* spp. pueden llevar filamentos polares cortos y/o largos, y no solo cortos, como indica la descripción original del género.

6- El uso de microscopía confocal ha sido muy útil para interpretar las estructuras tridimensionales del atrio genital y el órgano copulador, así como el vestíbulo bucal de *Tinrovia mamaevi*. Gracias a esta metodología se ha observado que muchas estructuras pueden ser interpretadas de forma muy diferente según la condición del ejemplar, lo que debe de ser tenido en cuenta en futuras descripciones taxonómicas.

7- *Dichelyne* (*Cucullanellus*) *romani* Isbert, Montero, Carrassón & González-Solis 2015, nueva especie de nematodo, es el primer cuculánido descrito en notacántidos. Este nematodo se detectó en *Notacanthus bonaparte* y *N. chemnitzii* del Noreste Atlántico y en *N. bonaparte* del Mediterráneo occidental. Es uno de los dos únicos registros de Dichelyne Jägerskiöld, 1902 en especies del mar profundo y se trata de la cuarta especie de Dichelyne (Cucullanellus)descrita en el Mar Mediterráneo.

8- Este estudio confirma las publicaciones previas que ya observaron una alta variabilidad intraespecífica en los rasgos morfológicos de las especies de este género. La amplia variabilidad intraespecífica de ciertos aspectos morfológicos remarca la necesidad de clarificar el estatus de algunas especies del subgénero *Dichelyne* (*Cucullanellus*), siendo recomendable reexaminar a los ejemplares tipo.

9- El presente estudio sobre la parasitofauna de *Notacanthus bonaparte* es el primer análisis detallado de sus comunidades de parásitos, incluyendo datos estacionales y de estratos de profundidad. De las cinco especies de parásitos descritas, dos han sido nuevas para la ciencia y tres representaron nuevas citas de hospedador.

10- Las comunidades de parásitos de *Notacanthus bonaparte* son pobres, con solo tres especies de consideradas como comunes. Este hecho podría estar apoyado por las observaciones previas que indican que tienen un rango limitado de depredadores. Las comunidades son más rica en el rango de profundidad más superficial (600–1.000 m).

11- El parásito más abundante en *Notacanthus bonaparte* (la larva de cuculánido), especie más abundante en las profundidades más bajas, parece acumularse durante el crecimiento del hospedador. El rango de profundidades observado para esta especie se explica en parte por la tendencia 'más grande a más profundidad', en la que los peces mayores se encuentran en las aguas más profundas. Se sugiere que las larvas de cuculánido son ingeridas directamente por *N. bonaparte* al alimentarse de sus presas habituales, organismos bentónicos sésiles o de movimiento lento. Los principales periodos de infección podrían estar ligados a la mayor actividad de alimentación de *N. bonaparte* (primavera/verano), cuando se han detectado los mayores valores de turbidez del agua cerca de los fondos marinos. La turbidez podría estar relacionada con la prevalencia de las larvas de cuculánidos, ya que las fases larvarias de vida libre parecen acumularse en el sedimento.

12- La presencia de *Tinrovia mamaevi* en *Notacanthus bonaparte* de las profundidades superiores se explica en parte por la mayor densidad de hospedadores. Se observa además una débil relación entre su prevalencia y los factores abióticos (temperatura, salinidad).

13- Se ha realizado la primera descripción detallada de las comunidades de parásitos y la dieta de *Etmopterus spinax*, incluyendo a ejemplares juveniles y adultos. Las comunidades componentes de parásitos de *E. spinax* del Atlántico nororiental fueron ricas, mientras que sus infracomunidades eran pobres y poco diversas. Este estudio aporta los primeros datos comparativos de infracomunidades de parásitos de una especie de tiburón de profundidad, citando a tres nuevas citas de hospedador entre las once especies detectadas.

14- La localidad y el tamaño del hospedador explicaron las diferencias en la composición y estructura de las comunidades de parásitos de *Etmopterus spinax* encontradas entre una montaña submarina (Banco de Galicia) y un cañón (Cañón de Avilés). La asociación entre el tamaño del hospedador y la abundancia de *Squalonchocotyle spinaci* podría estar asociada al comportamiento de agregación de los individuos juveniles de *E. spinax*, probablemente debido a la evasión ante los posibles depredadores. La presencia en el Banco de Galicia podría estar asociada a los efectos de condiciones abióticas y variables ambientales. La elevada abundancia de *Anisakis* sp. (Tipo I *sensu* Berland, 1961) en el Cañón de Avilés podría reflejar las mayores abundancias de hospedadores definitivos, así como unas mayores tasas de pesca y descarte en esta área.

15- La dieta de *Etmopterus spinax* mostró claras diferencias geográficas, con carideos y teleósteos en el Banco de Galicia, y carideos y eufausiáceos en el Cañón de Avilés como presas principales. El tamaño de los tiburones del Cañón de Avilés solo se asoció a los eufausiáceos. La detección de diferencias concordantes en las abundancias de eufausiáceos y *Anisakis* sp. en el Cañón de Avilés asoció los nichos tróficos recientes y de largo plazo.

16- El presente estudio reveló un efecto diferente de los dos ecosistemas del mar profundo sobre el nicho trófico de *Etmopterus spinax*, a largo plazo y en un momento reciente. Además, se subraya la utilidad de las aproximaciones estadísticas multivariantes para explorar las variaciones geográficas en poblaciones de tiburones en base a las presas y los datos parasitológicos.

17- Este estudio aporta el primer análisis exhaustivo de las infracomunidades de parásitos y la composición de la dieta del tiburón de profundidad *Deania profundorum* en el Atlántico nororiental. La presencia de parásitos adultos y larvas (especialmente cestodos) y el hecho de que la dieta consistiera principalmente en peces, crustáceos y cefalópodos bento- y batiplágicos indica que estos tiburones ocupan una posición intermedia en la red trófica local del Cañón de Avilés.

18- La talla de *Deania profundorum* tiene un claro impacto sobre los parámetros de la infracomunidad y las abundancias de *Deanicola* sp., Lacistorhynchidae gen. sp. y *Anisakis* sp. (Tipo I *sensu* Berland, 1961); además, los niveles de infección de las dos últimas especies también variaron entre sexos. Este hecho podría estar asociado a los machos de un tamaño ligeramente mayor, los cuales podrían tener hábitos alimenticios diferentes, alimentándose de presas mayores o en más cantidades, de forma que se infectarían más. El análisis de la dieta no reveló estas diferencias ligadas al sexo y el tamaño del hospedador, subrayando la utilidad de los parásitos como indicadores biológicos para estudiar hábitos alimenticios.

Chapter 1 Introduction

1.1 THE DEEP-SEA: THE LAST FRONTIER

The deep-sea has been and is still considered as the 'most remote and seemingly difficult of environments for life on Earth' (Gage & Tyler 1991). This remote realm has several characteristics distinct from other marine and terrestrial ecosystems making it 'unique for the entire planet' (Ramirez-Llodra et al. 2010). Traditionally, in terms of topography, the largest biome on earth (Ramirez-Llodra et al. 2010) is considered to start at the continental shelf breaks, at about 200 meter (m) depth, extending down into the ocean basins (Gage & Tyler 1991, Glover et al. 2017), and reaching the largest depths, recorded for the Mariana Trench with 10,924 m depth. In terms of hydrography the deep-sea is considered to start below the permanent thermocline, where temperatures decline rapidly with depth, until temperature gradients become low reaching values below 4°C; the thermocline is considered to 'isolate' the deep-sea from changing surface parameters and usually it can be found between 800 and 1,300 m (Gage & Tyler 1991). Following the classification of Marine Ecoregions of the World (MEOW) (Spalding et al. 2007), more recent schemes of the categorization of the deep-sea also define a deeper boundary between coastal and shelf areas extending down to 800 m (Glover et al. 2017). The biogeographic classification following the Global Open Oceans and Deep Seabed (GOODS) considers depths between 300 and 800 m as upper bathyal (the shallowest deep-sea), mostly at the continental margins (UNESCO 2009, Watling et al. 2013, Glover et al. 2017). These categorizations are adopted as criterion for the WoRDSS database (The World Register of Deep-Sea Species) of deep-sea species, where species usually have to be sampled in depths below 500 m (Glover et al. 2017).

From the 71% of the earth covered by the oceans, 90% is beyond the shallow margins of the continents (<200 m depth) (e.g. Snelgrove et al. 2016) and about 50% is below 3,000 m (Ramirez-Llodra et al. 2010). However, although research in the deep-sea increased and new discoveries have been made in the last decades, the scientific knowledge of the ocean depths is still scarce, and up to date only 5% of the deep-sea has been explored, which is less than 0.001% of the total (Ramirez-Llodra et al. 2010, Snelgrove et al. 2016).

The deep-sea is characterized by increasing hydrostatic pressures (1 bar per 10 m) and varying current speeds. The lack of solar radiation implies a distinctly lower seasonal influence on this biome compared to shallow waters. Parameters such as temperature or salinity are considered to be more stable below the permanent thermocline. Bottom temperatures in the deep-sea usually show geographical variations between -1°C and 4°C (Gage & Tyler 1991 and references therein, Ramirez-Llodra et al. 2010), and even between 12.0-14.5°C in the Mediterranean Sea (Cartes et al. 2004a, Sardà et al. 2004). Similarly, common values for salinity below 2,000 m in most ocean basins are close to 34.8‰ (Gage & Tyler 1991 and references therein), whereas in the Mediterranean Sea higher salinities between 38.4 and >39.0‰ occur (Ramirez–Llodra et al. 2010). In general, oxygen concentrations are considered saturated in the deep-sea except for some regions with low concentrations (e.g. North Pacific, South East Atlantic, Black Sea) (Gage & Tyler 1991 and references therein). Gage & Tyler (1991) indicated that temperature and salinity are not completely constant below the permanent thermocline, where for example water masses often origin from the Arctic Ocean (in case for the northern Atlantic). Therefore, sinking surface waters have to be colder or saltier to reach the sea floor and induce variations in temperature and salinity below the thermocline (Gage & Tyler 1991). Large volumes of water masses with partly high current speeds, such as the Mediterranean Outflow Water (MOW), can also influence the physical properties of the water close to the bottom (Candela 2001). Research carried out in the last and current decade also indicates to the deep-sea as a more dynamic environment than previously thought (Gage 2003, Ramirez-Llodra et al. 2010), demonstrating that the influence of horizontal currents, tides or storms can affect high depths. This new knowledge has been acquired thanks to the technological advances using instruments for long periods at great depths, and allowing to obtain a more precise and comprehensive idea on the dynamics of the deep-sea.

Nowadays we know that geomorphological features such as submarine canyons and seamounts, or deep trenches close to the continental shelves, can enhance the local and regional productivity by promoting primary production and facilitating the deposition of detritus (‘deep-sea snow’ or ‘marine snow’) in the deep-sea. These processes also impose (even if delayed in time) a sort of ‘seasonal pattern’ on deep-sea populations and communities (e.g. Cartes et al. 2004b, Bray 2005, Fernández-Arcaya 2017). Further, the sinking and sedimentation of dead organisms (from phyto- and zooplankton to large vertebrates) periodically provides the bathyal and abyssal benthic communities with food resources that can trigger biological processes in the deep-sea, such as reproduction (Ramirez-Llodra et al. 2010). These enhanced processes hint to the importance of deep-sea features such as canyons and seamounts as hotspots for migrating species (small pelagic, sharks, dolphins, whales) (e.g. Clark et al. 2010, Vetter et al. 2010).

The species diversity in the deep-sea started to be considered as high during the 60’s (Hessler & Sanders 1967) and in the 90’s deep-sea diversity was regarded to be as high as in rain forests with many rare species (Snelgrove & Grassle 1995). Deep-sea habitats can show high spatial heterogeneity and the food supply in these communities can be limited ‘in space and time’ (Snelgrove & Grassle 1995); this can result in a high variability of the diversity even in very small spatial scales (Levin & Dayton 2009). Some scientists suggest that 91% of the species in the deep-sea are not described yet (Mora et al. 2011). Diversity studies in the deep sea have been increasing in the last 20–25 years, using morphological and molecular approaches. Marine invertebrates are still the largest portion of the biome diversity less studied, although parasites are an exception among invertebrates, as new parasite species are continuously described when new host species (mostly fish) from unstudied deep-sea areas are found (examples of new species Kuchta & Scholz 2004, 2008, Pérez-i-García et al. 2015, Pérez-del-Olmo et al. 2014). Despite these continuous discoveries of new species, a search in the Web of Knowledge with the words ‘deep-sea’, ‘fish’ and ‘parasite’ results in only 17 entries, with the first one in 1973. Moreover, even though studies on biodiversity of marine parasites are still fairly scarce, knowledge on its ecological role is almost unknown (but see for instance Constenla et al. 2015, Ñacari & Oliva 2016).

1.2 MARINE PARASITES, DEEP-SEA PARASITES: A WORLD WITHIN A WORLD

The first circumnavigation research expedition was conducted on board the H.M.S. ‘Challenger’ (1872-1876) (Fig. 1.1); this voyage is considered as a milestone not only for deep-sea science, but also for the oceanography of those past times (Gage & Tyler 1991). One of the famous citations referring to this expedition is from Moseley (1880) indicating that even in the remote and vast deep-sea the organisms are infected by parasites: ‘…The unhappy deep-sea animals have not escaped their parasites in their cold and gloomy retreat...’ (Moseley 1880). This citation is often included in papers dealing with studies in the deep-sea and especially when parasites are one of the topics (e.g. Bray et al. 1999, McClain et al. 2006).

These and the following pioneer studies on the deep-sea fauna also revealed data on parasites; for example the ‘Ingolf’ expedition (around Iceland, 1895-96), where improved sieving techniques were used, small free-living crustaceans and parasitic copepods could be found (Wolff 2008 and references therein). Even though parasitological studies on deep-sea fishes were done to a lesser extent than on commercially important species from shallower areas, the first studies provided important data on parasite infection patterns, as well as on types and taxonomy in deep-sea fish species (e.g. Manter 1934, Noble 1973, Campbell et al. 1980, Mauchline & Gordon 1986, Gartner & Zwerner 1989).

The metazoan parasite taxa most commonly found in the deep-sea fish are Platyhelminthes (Cestoda, Monogenea and Trematoda), Nematoda, Acanthocephala and Crustacea (i.e. Isopoda, Copepoda). The overall knowledge on the deep-sea parasite life cycles is limited and especially scarce for invertebrates, which are potential intermediate hosts for many fish parasites (Leung et al. 2015). With regard to

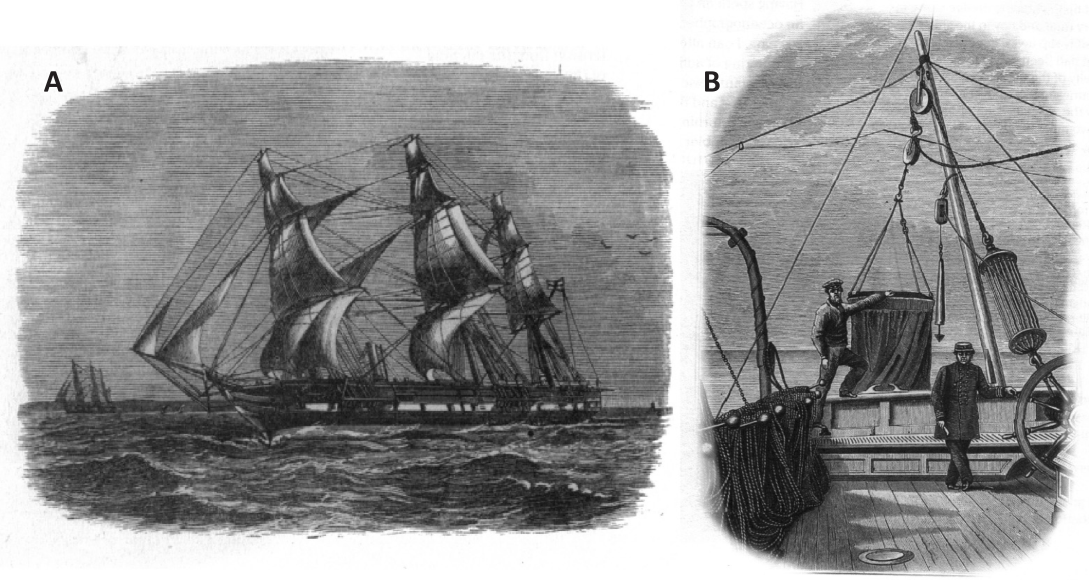

Fig. 1.1 - Prints on pioneer oceanographic expeditions. The ‘Challenger under sail’ (A) (source: Koslow 2007). Dredging on board the ‘Porcupine’ during the Porcupine expedition in the NE Atlantic (B) (source: “The depths of the Sea”, CW Thomson, 1874, copyright Dr. David Bossard).

parasite communities in invertebrates of cold seeps and hydrothermal vents, Leung et al. (2015) stressed that studies in environments with often lower species diversity are necessary for understanding transmission pathways of parasites in extreme environments. Available knowledge on deep-sea parasites (including taxonomical, biological and ecological knowledge) is ‘virtually’ based on different stages of parasite life cycles observed in fishes (Bray 2005) which are often commercially important fish species (Klimpel et al. 2009).

Caira et al. (2012) indicated that for elasmobranchs from shallow and deep waters, cestodes exhibit the highest species diversity (Fig. 1.2). In contrast, Campbell et al. (1980) suggested that parasite communities in deep-sea teleosts are mainly characterized by the presence of Nematoda, Digenea and Cestoda. In 52 benthic and demersal fish species, nematodes were found in 54% of all specimens examined, followed by digeneans (48%), cestodes (12%), monogeneans (13%), copepods (5%) and acanthocephalans (4%). The dominance of these groups in deep-sea teleosts has been partially confirmed by other studies: for example, Heath (1987) found that digeneans were the most common parasite group at species level (62.2%), followed by nematodes and cestodes each with >50% occurrence. Although digeneans (parasites with intermediate hosts) are considered to be less diverse in the deep-sea than in shallow waters (Bray et al. 1999), available data indicates that they are the most important metazoan parasite group in deep-sea teleosts (Heath 1987, Bray 2005).

Parasite species richness and diversity in a community can be affected by several host

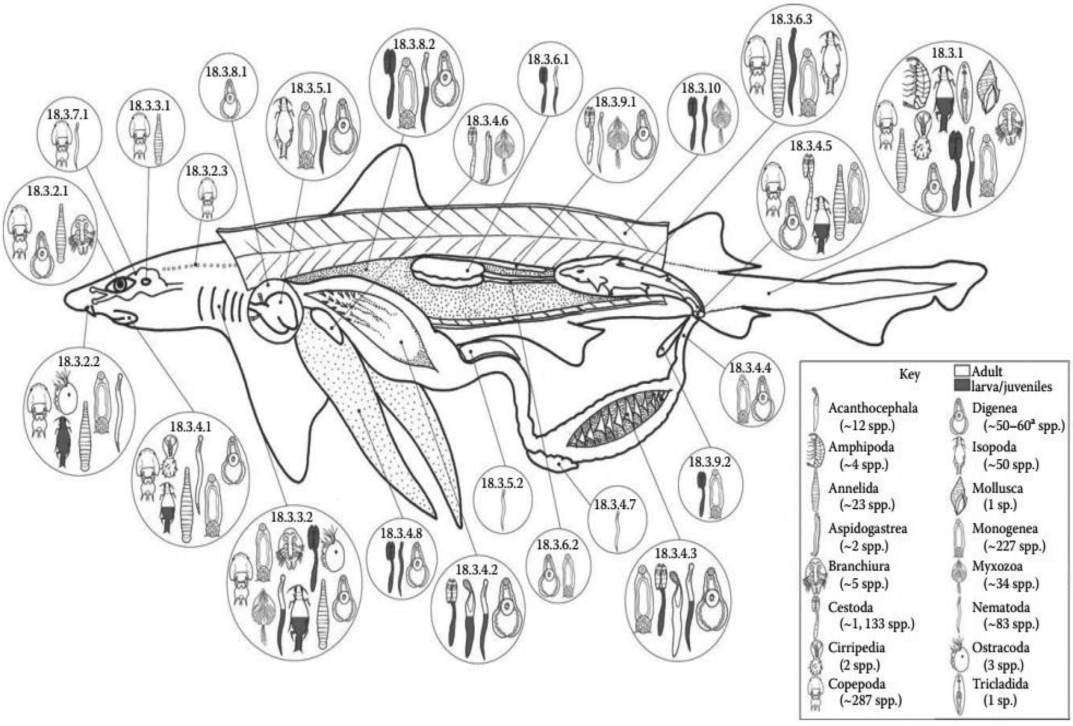

Fig. 1.2 - Higher taxa groups of parasites showing the potential diversity which could be found in a selachian (source: Caira et al. 2012).

related factors (geographic distribution, home range, diet, local habitat use, size, behaviour, etc) as well as by the parasite environmental tolerance (e.g. Sasal et al. 1997, Begg & Waldman 1999, Barber & Poulin 2002). Parasite communities in shallow water fishes are considered to show higher species richness compared to deep-sea parasite communities. Average values for parasite species per fish calculated over all checklists published so far (including shallow water species), results in three to four parasite species per fish species (Palm 2004). In contrast, Klimpel et al. (2001), based on 421 deep-sea fish species, calculated a mean value of 1.5 metazoan parasite species per species. However, these data need to be taken with caution as most of the studies refer only to the North Atlantic (Rohde 2002) and the calculations by Klimpel et al. (2001) are based on less than 15% of the known deep-sea fish species (Klimpel et al. 2009).

1.3 SOME ASPECTS ON THE BIOLOGY AND ECOLOGY OF DEEPWATER PARASITES

Life cycles of parasites are classified by the number of hosts involved in the cycle. A parasite with direct life cycle (‘monoxenous’) infects a single host. This is the case for instance of ectoparasites as monogeneans, isopods and most copepods. In contrast, parasites with indirect life cycle (‘heteroxenous’) need to infect multiple host species; this is the case for most endoparasites such as cestodes, digeneans and nematodes. These parasites can be transmitted via the food web or by penetration, very often having free-living larval stages. Monoxenous and heteroxenous free-living parasites have to cope with different biotic and abiotic factors which affect their reproductive success and transmission. The influence of abiotic parameters such as temperature can even be different between larval and adult stage of the same species. For instance, a free-living larva will be more affected by temperature changes than the adult being in the digestive tract of the host. The parasite richness of heteroxenous parasites is largely related to the diversity of available prey (intermediate hosts) ingested by the fish host (Cirtwill 2016). While parasite infections in fishes decrease in the deep layers of the water column, diversity and intensity of infection increase again in areas close to the seafloor owing to the higher availability of intermediate hosts in benthic habitats and along the benthic boundary layer (Campbell et al. 1980, Marcogliese 2002, Klimpel et al. 2010). Further, infection rates can also vary in small spatial scales, for instance Campbell et al. (1980) observed that deep-sea fishes sampled in a submarine canyon had a higher parasite load and diversity than those from outside the canyon sampled at the same depths.

In the following paragraphs parasite groups that can be found in deep waters are presented including traits of their life cycles and developmental stages in order to gauge the possible effects of deep-sea conditions.

1.3.1 Phylum Platyhelminthes

Class Monogenea

Generally, the monogeneans are considered as the most ‘host specific parasites’ very often infecting a single host species (Whittington 2005 and references therein). This class is divided in two subclasses, the Monopisthocotylea and the Polyopisthocotylea which mainly differ in the complexity of the attachment structures, the infection sites and their diet (Hayward 2005). They can be found on different vertebrates (e.g. teleosts, chondrichthyans) mainly on skin and gills, but also in other habitats such as the nasal cavity (Kearn 2014, Caira et al. 2012). These parasites attach by hooks, clamps, and suckers of the attachment organ, the haptor, and these are highly adapted to particular anatomical features of the host such as gill secondary lamellae (Kearn 2014). Most monogeneans are oviparous, while some gyrodactylids giving birth to unciliated juveniles (Kearn 2014). But mostly, in the life cycles of monogeneans, eggs often have long appendages to attach by entanglement or to form a long string with other eggs which can entangle or remain in the water column (Hayward 2005, Kearn 2014). Short-lived (1-3 days) ciliated larvae (oncomiracidium) hatch from the egg, and swim in the seawater or sink to the seafloor (Hayward 2005, Whittington 2005, Whittington & Kearn 2011).

The monogeneans can be found from polar regions to the tropics, and on fishes from coastal and oceanic waters, and also in the deep-sea. In the deep-sea they are considered less diverse compared to the fauna observed in the shallow waters (Whittington 2005) and published studies indicated that below 1,000 m only 2% of all parasites were monogeneans (De Buron & Morand 2002), which in part is explained by the supposed lower host densities in the deep-sea (Campbell et al. 1980). Most species found in the deep-sea are assigned to the Diclidophoridae, which may be due to their hosts which are widespread in this biome (gadiforms, and in particular macrourids) (Bray 2005). Furthermore, species of 11 families were recorded: Acanthocotylidae, Capsalidae, Chimaericolidae, Dactylogyridae, Discocotylidae, Hexbothriidae, Mazocraeidae, Microcotylidae, Monocotylidae, Plectanocotylidae and Tetraonchoididae.

Class Trematoda

The class Trematoda comprises two subclasses, the Aspidogastrea and the Digenea, both parasitizing marine fishes. The former is a small group of parasites present in different groups of host with few infecting also chondrichthyans. Nevertheless, the Digenea is a more diverse group with adult stages usually infecting a variety of vertebrates. The adult specimens of digeneans or flukes are usually characterized by the presence of an anterior and a ventral sucker (Cribb 2005). In 1999, Bray et al. indicated that even if the life cycles of deep-sea digeneans are understudied, it can be assumed that they are similar to those of the shallow waters. Considering the available information from shallow areas, the life cycles of digeneans exhibit an alternation of sexual and asexual phases. They have two or three hosts during its life cycle, mostly infecting a bivalve or gastropod as first intermediate host (Bray et al. 1999). Usually the short-lived ciliated larva (miracidium) hatches from the egg and it has to attach to the first intermediate host within hours, but in some orders eggs have to be ingested by the first intermediate host. The larva penetrates the host tissue, developing a sporocyst (a sac containing germinal cells), which is considered as the first generation in the mollusc. This first stage of parthenogenetic generation produces a second ‘intra-molluscan’ generation that could comprise multiple daughter sporocysts or multiple rediae. These reproduce asexually producing free-living larval forms called cercariae (Cribb 2005), which usually have a tail, suckers and cystogenous glands. This larval stage emerges actively and infects other hosts. The following host can be the definitive one (as in Aporocotylidae) or, more usually act as second intermediate host where a metacercaria is developed. This second intermediate host must be preyed by the definitive host in order to close the life cycle (Bray et al. 1999, Cribb 2005), as the metacercariae develop into adults and reproduce sexually. It is suggested that the asexual-sexual alternating form of reproduction is the basis of the great success that digeneans have achieved infecting a wide range of invertebrates and vertebrates (Cribb 2005). Several families of digenean trematodes were recorded in the deep-sea, but they vary in the maximum recorded depths. For instance Lepocreadiidae, Lepidapedidae, Fellodistomidae, Derogenidae and Hemiuridae were found in hosts from >4,000 m depths, whereas Lecithasteridae, Zoogonidae and Opecoelidae exhibit ‘truly deep-water forms’ and can be found >3,000 m (Bray 2004). Several other families occur >200 m such as Accacoeliidae, Bucephalidae, Monorchiidae and Aporocotylidae (Bray et al. 1999, Bray 2004). For most of these families 2-3 host life cycles are supposed with molluscs as first intermediate host, such as amongst others Lepocreadiidae, Opecoelidae, Zoogonidae, Hemiuridae (with gastropods as first intermediate host) and e.g.

Fellodistomidae and Bucephalidae (bivalves) (Bray et al. 1999). A potential adaptation to the deep was observed in the family Lepidapedidae, where larval and adult stages have no eye spots (Bray et al. 1999).

Bray et al. (1999) stressed that none of the common flukes currently known from the deep-sea were 'basal' for digenean phylogeny and they are distinct from the ones of the shallow waters. Therefore, no digenean taxa supposedly emerged in the deep-sea (Bray et al. 1999), but it is a parasite group which has developed successfully in that habitat (Campbell et al. 1980, Cribb et al. 2002). In this way, according to Palm & Klimpel (2008), the origin of deep-sea digeneans may derive from generalist digeneans infecting gadiform fish in the shallow waters and which invaded the deep-sea 'onboard' of the macrourid species.

Class Cestoda

Cestodes are separated in two main subclasses: Cestodaria and Eucestoda (Caira & Reyda 2005). Eucestoda are characterized by the presence of a scolex, the anterior attachment region, and proglottids, repeated segments with one or more reproduction organs of both sexes; Cestodaria lack a scolex and they have only 1 set of reproductive organs per individual (Caira & Reyda 2005). Three orders, predominantly marine, comprise the highest species numbers: Pseudophyllidea, Trypanorhyncha and Tetraphyllidea (in all 1190 species, Caira & Reyda 2005). Scolices vary in their morphology: in pseudophyllideans they have two bothria (grooves of the scolex, usually longitudinal) often weakly muscular; in tetraphyllideans they have four muscular bothridia (sessile or pedunculated outgrowths) sometimes muscular; in trypanorhynchs scolices have two or four bothridia, sometimes weakly muscular and four hooked retractable tentacles at the apex (Khalil 1994, Caira & Reyda 2005). Tentacles are lacking in the species of the trypanorhynch genus *Aporhynchus* (Noever et al. 2010). Adult cestodes infect the digestive tract of terrestrial, freshwater and marine vertebrates, while larvae (metacestodes) are usually free or encapsulated in tissues.

Caira & Reyda (2005) stressed that temperature is a key factor for the geographical distribution of this group as it highly influences the development of the eggs and the embryonation. Nevertheless, some species could adapt to the cold water environments as in subarctic regions, especially spathebothriideans, pseudophyllideans and tetrabothriideans, but also diphyllideans, tetraphyllideans and trypanorhynchs (Caira & Reyda 2005). The deep-sea cestode fauna is considered as less diverse but equal in prevalence and intensity, when compared to shallow waters. The limited data on deep-sea cestodes has revealed that the three most diverse orders (tetraphyllideans, trypanorhynchs and pseudophyllideans) also dominate this environment (Caira & Reyda 2005, Klimpel et al. 2009). Adult trypanorhynchs and tetraphyllideans parasitize chondrichthyans, while adult pseudophyllideans (Bothriocephalidae, Philobythiidae, Echinophallidae, Triaenophoridae) are in osteichthyans (Khalil 1994, Caira & Reyda 2005, Caira & Pickering 2013). Cestodes occur especially in benthic communities as in horizontal life cycles transmission of larvae is facilitated and less diluted than in the open water column (Caira & Reyda 2005, Caira & Pickering 2013).

Life cycles of cestodes pass through the food web, with different kinds of larvae which can vary greatly among and within orders. All life cycles of eucestodes begin with a hexacanth larva (having six hooks) which in most cases remains in the egg, but sometimes hatches and survives as free-living larva, until it is ingested by an appropriate host. Aquatic life cycles can involve three to five hosts, sometimes including paratenic hosts (as in several tetraphyllideans). The hexacanth (free or in egg) is ingested by a small invertebrate (copepod, euphausiid or mollusc) as first intermediate host and it develops to a procercoid. After being preyed by the second intermediate host (fish, euphausiid), they grow to a larger metacestode (plerocercus, plerocercoid, merocercoid, depending on the group), with the incipient scolex forming an encapsulated blastocyst in the host tissues (Palm 2004 and references therein). Merocercoids are able to survive a passage though more than one paratenic hosts (Caira & Reyda 2005). Definitive hosts are marine mammals and large fishes (elasmobranchs mostly) (Caira & Reyda 2005, Klimpel et al. 2009, Jensen & Bullard 2010 and references therein).

1.3.2 Phylum Nematoda

This phylum currently consists of four classes Adenophorea, Chromadorea, Enoplea and Secernentea (Eisendle-Flöckner et al. 2017) with free-living and symbiotic species, many of them parasitic. Parasitic nematodes of the Chromadorea y Enoplea are found widespread in the marine environment with species of the genera such as *Ascarophis*, *Anisakis*, *Cucullanus*, *Capillaria* and *Paracapillaria*. This group is described to be shaped as 'elongate cylinder', tapered at the anterior and posterior body end with mouth and tail with anus, respectively, and bilaterally symmetrical. Nematodes are ecdysozoans (with cuticle that requires moulting to grow), with pseudocoelom acting as a hydroskeleton, and mostly sexually dimorphic (McClelland 2005).

Parasitic nematodes are recorded from a wide range of invertebrate and vertebrate hosts and are partly described as unspecific concerning their intermediate, paratenic and definitive hosts (fishes, marine birds, mammals). The knowledge on the larval morphogenesis and life cycles of Nematoda is fragmentary and often unknown, and the identification of the larvae is impossible when based solely on morphological characteristics (Moravec et al. 2016). In their definitive hosts nematodes can be mostly found in the digestive tract. In the following examples two frequent life cycles are described briefly.

The life cycle of ascaridids (anisakids and raphidascarids) includes four larval stages (L1–L4). Larvae 4 and adults live in the digestive tract of their definitive hosts, such as pinnipeds and cetaceans (see Fig. 1.3) or large fin fish (Anderson 2000, Klimpel & Palm 2011, Kuhn et al. 2016). The eggs are released and the hatched larvae 3 are ingested by small crustaceans (as copepods), considered as intermediate (obligate) hosts. This first host is ingested by several paratenic hosts (from small euphausiids, carideans, teleosts to larger fishes, squid, etc.) as larvae are capable of encysting and re-infecting these hosts without further moulting (Abollo et al. 2001, Klimpel et al. 2004, Klimpel & Palm 2011 and references therein, Gregori et al. 2015).

The life cycle of some *Cucullanus* spp. (Cucullanidae) may include three ways to reach the definitive host. Larva 3 stage hatches from the egg in the seawater and can be consumed by a copepod, or by larger hosts such as small benthic fishes like gobies, or even directly by codlings, the fry of the definitive host (the latter infection way will be a direct life cycle). Infected copepods and small fishes can also act as paratenic or intermediate hosts, respectively, carrying the larvae to the definitive hosts (cods), which is often the case in more complex paratenic life cycles within the food webs (Køie 2000).

Bray (2005) stressed that relatively few nematode species were recorded in the deep-sea. The families Capillariidae (Trichinellida), Anisakidae, Cucullanidae, Cystidicolidae, Gnathostomatidae, Philometridae, Raphidascaridae, Rhabdochonidae (Rhabditida) have been reported in deep-sea fishes (Bray 2005, Klimpel et al. 2009). The checklist by Klimpel et al. (2009) revealed that especially *Anisakis* spp., *Hysterothylacium* spp., *Contracaecum* sp. and *Ascarophis* sp. were recorded frequently in different deep-sea fish species.

1.3.3 Phylum Acanthocephala

This phylum comprises three classes (Archiacanthocephala, Eoacanthocephala, Palaeacanthocephala), most marine taxa belong to the latter order (WoRMS 2004, Taraschewski 2005). Acanthocephalans are described as more or less tubiform worms with a trunk (metasoma) being inside the intestinal lumen, and an armed proboscis and neck (presoma) attached in the intestinal wall (Taraschewski 2005). This parasite group has no intestine and nutrients are absorbed by crypts (invaginations) of the 'outer membrane of the metasoma from the intestinal lumen'.

The egg with the first larva (acanthor) is covered with up to five layers, each with a different composition and function, enabling for example the egg to attach to food substrate visited by the intermediate host, or the activation of the hatching (Taraschewksi 2005). Within the haemocoel of the intermediate hosts (e.g. amphipods) the larva develops to the cystacanth, which is infective for the definitive host. Several fishes may act as paratenic hosts, being infected by cystacanths. When cystacanths infect the definitive hosts they establish in the lumen of the digestive tract and develop to adult males and females. Adults can be found in several vertebrates (marine mammals, birds, turtles, fish) (Taraschewski 2005, Caira et al. 2012). Generally, acanthocephalans are considered as accidental or unusual in elasmobranchs and it is supposed that this parasite group does not 'tolerate the high levels of urea' present in elasmobranchs species (Caira et al. 2012 and references therein).

This group is cosmopolitan occurring in warmer to temperate and cold geographical regions. Most common species in deep-sea belong to the families Echinorhynchidae, Polymorphidae and Rhadinorhynchidae, while species of the Heteracanthocephalidae and Hypoechinorhynchidae are less common. Arhythmacanthidae, Cavisomidae, Diplosentidae, Plagiorhynchidae, Polymorphidae and Neoechinorhynchidae are also reported (Bray 2005, Klimpel et al. 2009). The life cycles of these parasites are often not-restricted to the deep-sea, such as polymorphids which adults live in marine mammals (cetaceans, pinnipeds) (Bray 2005).

1.3.4 Phylum Arthropoda

Subclass Copepoda

Copepods are small maxillopodan crustaceans, with short, cylindrical segmented body. The head and the first one or two pereion segments are fused, and the remaining three to five pereionites are articulated with limbs. Cephalic appendages include two pairs of antennae, mandibles, maxillae and a first pair of pereiopods modified in maxillipeds. The abdomen is typically narrower, without any appendages, except for the distal rami. Paired egg sacs are carried by the females. Many parasitic copepods have lost several taxonomical traits due to fusion, reduction or loss during their evolution (Boxshall 2005). Most parasitic parasites exhibit sexual dimorphism with females growing larger than males (even dwarf).

As ectoparasites, copepods can be found on the skin, fins, gills, nostrils, eyes. They attach to the hosts with appendages transformed into clamps, suckers, adhesion pads (Boxshall 2005); some copepods are motile while others are sessile, attached by imbedding part of the body transformed into anchor-like structures or cephalic holdfasts. The typical life cycle described by Boxshall (2005) begins with a nauplius larva hatching from the egg, and comprises a maximum of six (NI – NVI) naupliar stages, which are lecitho- or planktothrophic. The last nauplius stage moults in the copepodid (the infective stage), with up to five copepodid stages. After this stage, copepods moult into adult males and females (Boxshall 2005). Life cycles are often shorter, including fewer larval stages or larvae hatching as copepodids. Some parasitic copepods (e.g. pennellids) are heteroxenous, where copepodids first infect an intermediate host, a demersal static fish and develop into other copepodid stages until they release and find the definitive host (Matthews 1998).

Species of the following families have been recorded on deep-sea fish: Bomolochidae, Caligidae, Chondracanthidae, Eudactylinidae, Hatschekiidae, Hyponeoidae, Lernaeopodidae, Lernaeosoleidae, Lernanthropidae, Naobranchiidae, Pandaridae, Pennellidae, Philichthyidae, Sphyriidae, Trebiidae (Klimpel et al. 2009). Chondracanthidae, Lernaeopodidae and Sphyriidae, are more frequently found in the deep-sea, mostly on benthic/demersal species. It is suggested that often species of these families can be found on fishes of widely distributed families in the deep-sea, what may facilitate their life cycle in high depths with low host densities. Sexual dimorphism (with dwarf males) observed in these families may also increase encounter options as large females attach and attract dwarf males which become hyperparasites of the female (Boxshall 1998).

Infraclass Cirripedia

Cirripeds are maxillopodan crustaceans highly modified to sessile life when adults (stalked or not). In this infraclass two main superorders exist, the Rhizocephala and the Thoracica, comprising parasitic and epizoic species. The former are strictly parasites infecting other crustacean species, where females are attached to crab hosts with dwarf males living within the female; the larvae is the only free-living stage. The few parasitic species of Thoracica infect polychaeta and dogfish; for instance *Anelasma squalicola* is detected on several etmopterid sharks, often close to the fins or dorsal spines. This species is an highly modified barnacle, as the stalk is modified into a root-like structure in order to anchor in the host and absorb nutrients (Høeg et al. 2005, Rees et al. 2014), keeping the morphology of the mouth appendages and gut, although these structures are supposed to have lost their feeding function (Ommundsen et al. 2016). *Anelasma squalicola* is hermaphroditic and often this species is found in pairs in order to ease reproduction (Rees et al. 2014). Other species of Thoracica were observed as epizootic on corals, anemones, echinoderms, sea turtles, etc., but these are considered suspension feeders, not ectoparasites, still using their mouthparts for food intake (Rees et al. 2014), although some damage can be provoked by their high often tough attachment and high numbers, covering surfaces and/or affecting the motility of their carriers (e.g. Félix et al. 2006).

Order Isopoda

Isopods are one of the most diverse crustacean taxa, with many terrestrial and aquatic species (about 50% of each), and many of them adapted to parasitic or micropredatory life. They belong to the class Malacostraca and they are typically characterized by their dorso-ventrally flattened body, articulated with several highly sclerotized segments in pereion and pleon. The isopod suborder Cymothoida comprises several taxa which are considered to occur as ectoparasites. Within the Cymothoida, Epicaridea (infraorder) are recorded from crustaceans as immature and adults, while some families of the Cymothooidea (superfamily) parasitize marine fish as larvae and adults (Cymothoidae, Aegidae, Cirolanidae) or as larval stages only (Gnathiidae) (Lester 2005, WoRms 2011, Smit et al. 2014). Cymothooideans are mostly found in warm water fishes, where they are attached to the body surface, or within the orobranchial cavity. Morphological adaptations to the parasitic life mode are observed in the modifications of their periopods (hook-like); some species (Aegidae) show fewer modifications and keep their 'free-swimming capability', even as adults (Lester 2005). In isopods with adults as parasites, after hatching and several moults (two or more times), larvae leave the parent as 'manca' (larva 'pullus II') stage having six pairs of legs, large eyes and being able to swim rapidly (Lester 2005). After a period of free-living they become parasitic and have to a find a host within two days. Some species attach and detach several times from hosts after taking blood, in order to moult on the seabed, and then reattach to the next host, until reaching adulthood. Other species are more sedentary and remain attached on the preferred host site from a manca or juvenile stage to adulthood (e.g. on tongue). As protandous hermaphrodites the first male attaching to a fish individual change to a female, while the second remains as male (Lester 2005).

Gnathiidae infect marine teleosts and elasmobranchs as larval stage while adults are free-living in the benthos, supposedly without feeding (Lester 2005). A 'zuphea I' (unfed larva) hatches from the egg, attaches to a fish host and feeds on blood (as 'praniza I' stage). After a certain period (depending on species and temperature) it detaches, sinks to the bottom and moults in the 'zuphea II'. After several reinfections, the 'praniza III' leaves the last host to mature. Lester (2005) compares the alternating mode of micropredator and free-living stages with terrestrial ticks.

The few available data on isopod families from the deep-sea comprise two records for a parasitic Cymothooidea species only (Klimpel et al. 2009), while others indicate the occurrence of cymothoids (>10 species) beyond 500 m depth (Smit et al. 2014). In general, isopod records are few in higher latitudes (Smit et al. 2014); this low presence probably points to a lower adaptation to colder waters, such as commonly found in the deep-sea.

Order Amphipoda

Amphipods are not as diverse as isopods (both peracarids, phylogenetically close), exclusively adapted to aquatic life. They are laterally flattened with a segmented body, composed by several pereionites and pleonites. The few parasitic amphipods belong to the suborders Hyperiidea and Senticaudata. Hyperiidea have large a 'cephalothorax' and large eyes, with most species occurring in the open ocean, in temperate and tropical waters and some in the Polar regions and in meso-, bathy- and abyssopelagic water layers. They highly depend on gelatinous zooplankton as medusae or salps, which they parasitize or predate. Most of the parasitic Senticaudata belong to the family Cyamidae which, exceptionally among the amphipods, are dorsoventrally flattened amphipods with reduced/rudimentary posterior part of the body. Cyamids are found on marine mammals such as whales, dolphins, porpoises (Lützen 2005).

Tendency to parasitic life also exists in other Senticaudata, as the species of the genera *Lafystius* or *Trischizostoma* (Gammaridea), described as parasites of fish species due to morphological modifications in the mouthpart and gnathopod I (Bousfield 1987, Freire & Serejo 2004). *Lafystius* spp. have been described on several benthopelagic elasmobranchs and fin fishes at different depths, while *Trischizostoma* spp. were ectoparasites of pelagic and bathypelagic fishes in depths down to >3,600 m (e.g. *Etmopterus spinax* Bousfield 1987, *Bathypterois phenax*, Freire & Serejo 2004).

1.4 PARASITES ECOLOGICAL ROLE IN THE DEEP-SEA REALM

Although parasites are widely present in terrestrial and marine ecosystems and their life traits are considered as the most common consumer strategy, their role within communities and ecosystem is often unknown, or has been underestimated or regarded as 'trivial' (Hudson et al. 2006, Lafferty al. 2008). However, nowadays scientists begin to include parasites in their ecosystem-models (e.g. food web, demography) and their importance in the ecosystem is clearly acknowledged. Some authors consider that parasite impacts on the host have further implications on the local communities and ecosystems (Marcogliese et al. 2003). Thieltges et al. (2013) argued that parasites could contribute to enhance food-web paths and ecosystem stability, while Goater et al. (2014) proposed to consider parasites as 'ecosystem engineers' (*sensu* Jones et al. 1994), due to their profound influence to provoke changes on the community and ecosystem structures. Due to the current lack of knowledge on deep-sea parasites, it can only be speculated that they may have an impact similar to those observed in shallow waters.

Based on the connection of parasites with the marine organisms and the whole ecosystems, together with the host-parasite co-evolution, it has been considered that parasites are useful as

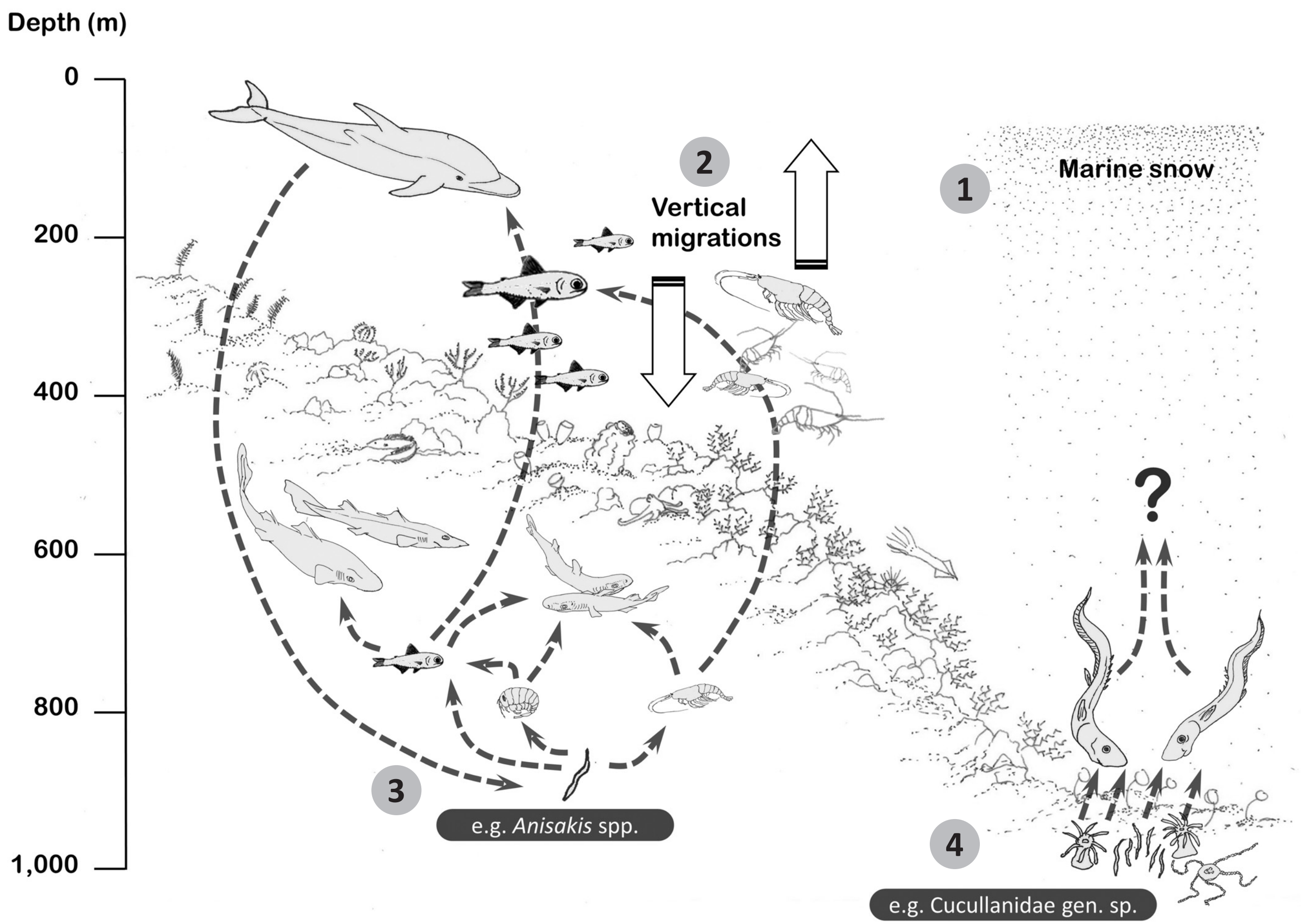

Fig. 1.3 - Ideal scheme presenting the parasite life cycles of nematodes in the deep-sea ecosystems. 1. ‘marine snow’: sinking and sedimentation of dead organisms (comprising phyto- and zooplankton to large vertebrates) food source for pelagic and benthic organisms; 2. Meso-bathypelagic fish and crustacean (copepods, euphausiids, decapods) exhibiting vertical migration and may act frequently as important intermediate hosts for adult parasites found in the deep-sea; 3. Life cycle of ascaridids; 4. Life cycle of cucullanids.

biological indicators for several aspects of the host ecology and biology (Campbell et al. 1980, Caira 1990, Williams et al. 1992, Marcogliese 2005). The use of parasites as indicators can, amongst others, indicate predator-prey interactions in the local or regional food webs, as heteroxenous parasites pass through the food web infecting different intermediate and definitive host species (Marcogliese 2002). The combined study of prey items and parasites in fish provide comprehensive information including short (prey item) and long-term (parasites) feeding habits, respectively, of the host species (Lafferty et al. 2008, Knudsen et al. 2010). On the other hand, monoxenous parasites provide insight in connectivity between certain fish stocks/populations (MacKenzie et al. 2008). Parasites can also reveal preferred depths of their host or seasonality patterns owing to the presence of their intermediate host, vertical migration events of hosts or food supply (Marcogliese 2002, 2005). Currently, most studies using parasites as biological indicators have been made on teleost species and their use in elasmobranchs is still scarce (MacKenzie 2002, Yamaguchi et al. 2003). The use of parasites as indicators has already been recommended for deep-sea and rare marine species (MacKenzie & Abaunza 1998), where direct information is difficult to be obtained due to low samples sizes, and the remoteness of the areas.

1.5 WHY IS IT WORTH TO STUDY THESE HOST SPECIES?

Nowadays it is acknowledged that the increased fishery efforts, which are turning to deeper waters since the 50-60’s (Morato et al. 2006), can have similar or even more severe impacts on the deep-sea fauna and habitats than in shallow waters (Koslow et al. 2000). A sustainable effective management and the implementation of proper protection measures in the deep-sea highly depend on the available information on these ecosystems and their fauna. Along with the scarce data on deep-sea dynamics and its habitats, knowledge on deep-sea organisms is often limited to species of commercial value and targeted in specific areas (Ramirez-Llodra et al. 2010, Snelgrove et al. 2016). Therefore, based on often scarce and unbalanced study efforts, it is recommended to consider assumptions about common patterns in the deep-sea with caution (Snelgrove et al. 2016).

Some deep-sea fishes have commercial value (e.g. *Phycis blennoides*), but most of them are of low or no value. This applies also to most deep-sea chondrichthyans, which can be considered as one of the less studied groups and indeed the published data on the life history of most deep-sea chondrichthyans is particularly scarce (Simpfendorfer & Kyne 2009). Data on the current status of the commercially used deep-sea stocks are frequently scant and there are only few available stock assessments for some elasmobranch populations; moreover these studies indicate to mostly depleted and/or overfished populations for most of the deep-sea shark species (Campana et al. 2016).

Regarding deep-sea osteichthyans, they frequently exhibit slow growth, high longevity, late maturity and low fecundity (‘K-selected’, Koslow et al. 2000, Bergstad et al. 2013), presenting life history traits rather similar to chondrichthyans, in general, and marine mammals than to other fin fish inhabiting shallower waters. These life traits are more pronounced in deep-sea chondrichthyans, showing an even lower productivity and overall low resilience to anthropogenic impacts such as fisheries (Kyne & Simpfendorfer 2007, Coelho & Erzini 2008). Indeed, for the deepwater elasmobranchs, rates of population growth are less than a half of those observed for shelf species and it is suggested that depleted stocks partly may need at least decades to recover (Simpfendorfer & Kyne 2009) making them highly susceptible even to lower fishing impacts (Walker 1998).

The three species studied in this work (*Notacanthus bonaparte*, *Etmopterus spinax* and *Deania profundorum*) are non-commercial species, even though *Deania* spp. (in particular *D. calcea*) were recorded to be landed for their liver and meat in the Northeast Atlantic (Clarke et al. 2002). However, it is supposed that *D. profundorum* and *E. spinax* are mostly discarded as bycatch and often they are not registered in official fishery statistics (Clarke et al. 2002, Coelho 2007). In the case of the bony fish, *N. bonaparte* is also considered as bycatch species and usually is discarded (Gordon et al. 1996). Coggan et al. (1998) supposed that commercial trawls are not appropriate to catch spiny eels due to the wide mesh size and the anguilliform shape of fish; the authors argued that most probably, when the spiny eels escape through the trawl-meshes, they might suffer physical damage even leading to mortality.

Considering the life history traits of the studied species, severe impacts by deep-sea fisheries, at least in a regional/local scale with high fishing effort, could lead to depletion of populations and even to species extinctions (García et al. 2008). In the case of elasmobranchs, knowledge from shallow waters indicate that consequences of shark removals from the ecosystem are often complex and unpredictable (Stevens et al. 2000); other authors suggested profound changes within the community structure and the local food-web, resulting in a community which is less resilient to other perturbations (Campana et al. 2016 and references therein). Sharks play particularly key roles often being positioned at the top or at least mid-ranked within the food web (apex or meso predator, Heupel et al. 2014). This applies also to the sharks analysed in the present work, where trophic levels for *D. profundorum* and *E. spinax* assign them to upper trophic positions as tertiary (trophic level 4.2) and secondary consumers (3.8), respectively (Cortés 1999). The relative importance of the role of these species in their ecosystems can also be estimated on the basis of their local abundance. Based on available data obtained during a long term study, the abundance of *E. spinax* in the Cantabrian Sea exhibited partly high values per hectare (0.6 – 29.1 Ind./ha) depending on the depth strata (Serrano et al. 2011). A more recent isolated sampling in 2014, indicate overall lower abundances of this species (5.7 Ind. /haul) (Ruiz-Pico et al. 2015), but also showed a patchy distribution with peaks of biomass along the northern Spanish coast. For *D. profundorum*, with less available information, scientific surveys indicate to low biomass values in the same area (0.03 Ind./haul) (Ruiz-Pico et al. 2015).

The role of *N. bonaparte* in ecosystems is still understudied. However, its benthic feeding habits, grazing mostly on epibenthic sessile or slow moving prey, has been described as highly specialised (Rodríguez-Romeu et al. 2016). *Notacanthus bonaparte* can be quite abundant in certain areas and depth ranges, often being among the 10 most abundant fish species (Gordon et al. 1996, Coggan et al. 1998). In the western Mediterranean Sea, scientific survey data on this species showed maximum values of 23 Ind./ha (data from 46 hauls) (Rodríguez-Romeu et al. 2016). Interestingly, despite the partly high abundances, to date no record is available for any potential predator and it is possible that this species does not play a major role as prey.

Chapter 2

Main Aim and Specific Objectives

The overall aim of this PhD thesis is to contribute to the knowledge on the parasite fauna of deep-sea fishes in the Mediterranean Sea and the Northeast Atlantic. In particular, to gain knowledge on the diversity, structure and composition of the parasite communities which is essential for potential future studies using parasites as biological indicators; this will also contribute to increase the knowledge in different biological and ecological aspects of their hosts and the ecosystems where those occur.

For this purpose three species were selected as "model species": one representative of the Osteichthyes (the shortfin spiny eel, *Notacanthus bonaparte* (Teleostei: Notacanthiformes)) and chondrichthyans (the velvet belly lantern shark, *Etmopterus spinax* and the arrowhead dogfish *Deania profundorum* (Chondrichthyes: Squaliformes)).

The objectives for this work are:

1. Contributing to the knowledge on the parasite fauna of the three selected species *N. bonaparte*, *E. spinax* y *D. profundorum* from the Mediterranean Sea and the Northeast Atlantic, respectively. Detected parasite taxa will be identified and a comprehensive bibliographical work will be conducted on the parasites found in these hosts and relative species.

2. Describing species new to science if necessary.

3. Describing the parasite communities of *N. bonaparte*, *E. spinax* and *D. profundorum*, analysing the biological factors which might influence the composition and structure of these communities.

4. Generating information on the composition and abundance of parasite species which may be used as potential indicators for patterns in the distribution and connectivity of the analysed fishes. This shall be done considering seasonal and bathymetric variations (host model *N. bonaparte*) and with respect to geographical variations/differences (host model *E. spinax*).

5. Analysing potential relationships between the detected parasite communities with the diet and trophic ecology of the host and assessing trophic position of the hosts in local food webs (host models (*N. bonaparte*, *E. spinax* and *D. profundorum*).

Chapter 3

General Material and Methods

In this section the study areas as well as the different methods used in this study are briefly presented. Details on the methodologies applied can be found in the specific chapters.

3.1 STUDY AREAS

In the following paragraphs descriptions of the study areas are presented briefly.

3.1.1 The Mediterranean Sea

The Mediterranean Sea exhibits maximum depths of over 5,000 m with an average depth of 2,500 m harbouring submarine canyons, seamounts and deep trenches (Cartes et al. 2004a). The Strait of Sicily separates the two main basins: the Western basin and the Central-Eastern basin (Fig. 3.1a,b). Due to the limited exchange with the Atlantic Ocean by the Strait of Gibraltar, and with the Red and Black Sea, by the Suez Channel and the Bosphorus Strait respectively, the Mediterranean is considered as a semi-closed sea (Sardà et al. 2004, Tanhua et al. 2013).

Following Gage & Tyler (1991) regions off the continental shelf beginning at the shelf break, are considered 'deep-sea' zones. This can be at *c*. 500 m, such as in some parts of the Antarctic shelf, but in most cases begins at *c*. 200 m, as in the Mediterranean Sea. Temperatures are known to decrease and salinities to increase in deep-sea waters of the Atlantic Ocean, whereas in the Mediterranean deep-sea basins temperatures and salinities seem to be less affected and remain relatively uniform (12–14.5°C and 38.4–39.0‰, respectively) (Cartes et al. 2004a, Sardà et al. 2004). The water exchange with the Atlantic Ocean along the sill of Gibraltar is nearly balanced: intermediate depth water from almost the Mediterranean (the so called Mediterranean Outflow Water, MOW), exhibiting higher temperatures and salinity, is exported below the inflowing water body from the Atlantic Water (AW) (Tanhua et al. 2013). This described anti-estuarine circulation contributes to the overall oligotrophic environment of the Mediterranean Sea, with a net export of nutrients throughout the MOW which is not compensated by inflowing surface AW that is lower in nutrient concentrations (Huertas et al. 2012). A negative hydrographic balance exists in the Mediterranean Sea resulting from a high net evaporation exceeding the precipitation, which in this area is the dominating source for freshwater followed by river discharges (Tanhua et al. 2013).

The Balearic Sea

Part of the research conducted in this work focus on the Western Mediterranean Basin, specifically in the so called Balearic Sea (International Hydrographic Organisation (IHO 2017) (Fig. 3.1c). In particular, samples were taken on the slope along the coast of northeastern Spain. Details are provided under section 3.3 and in the corresponding chapters.

The Balearic Sea is considered as a transitional region connecting the Liguro-Provençal Basin in

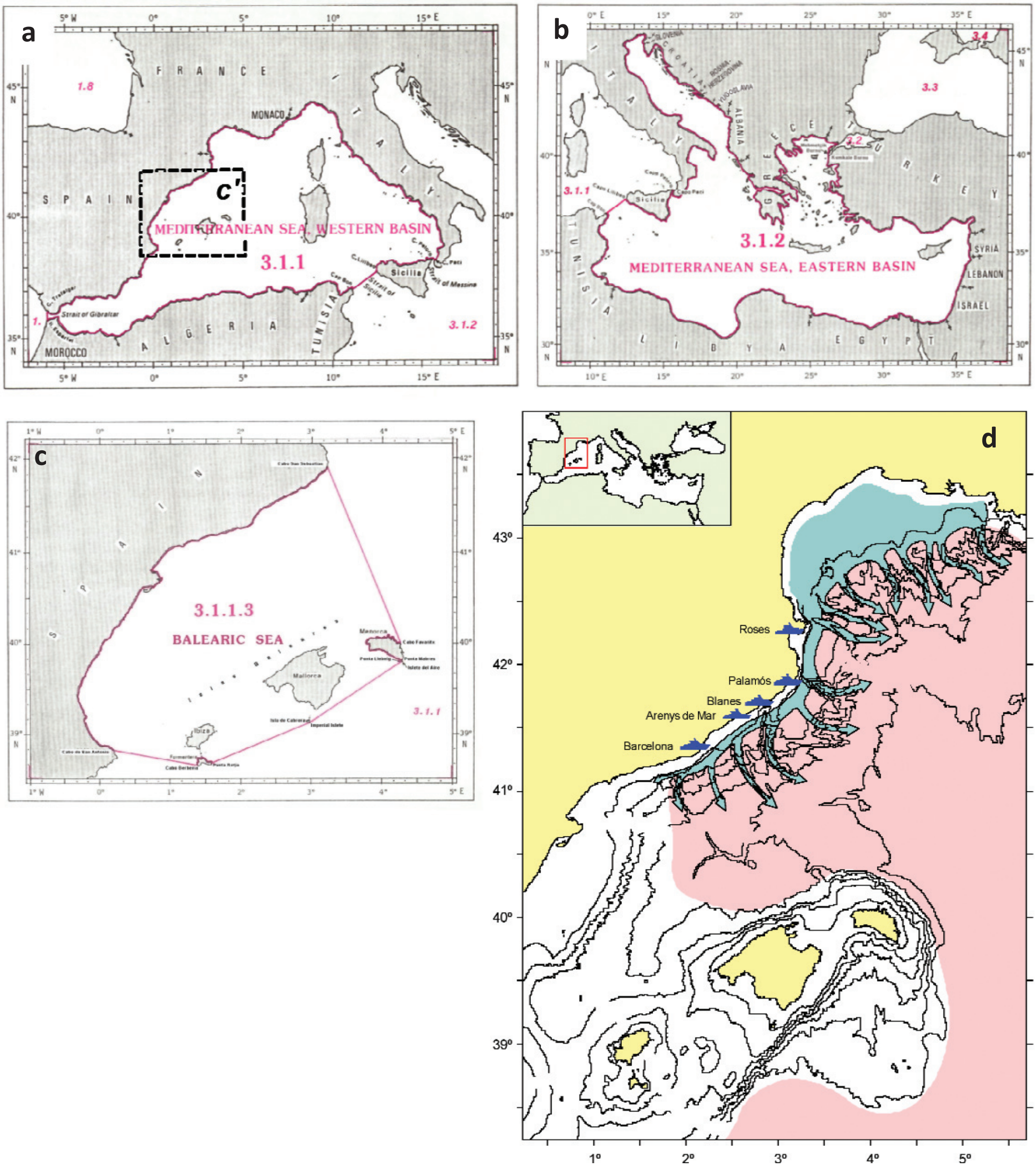

Fig. 3.1 - The Mediterranean basins and the Balearic Sea. Western basin, with the Balearic Sea (*c'*) squared with dashed line (a); Central-Eastern basin (b); limits of the Balearic Sea (c). Map of the northwestern Mediterranean showing the Balearic Sea (d); the pale blue arrows in d indicate the pathway of the dense shelf water cascading mechanism extending from the Gulf of Lions along and across the continental slope. The pink area represents the region affected by the thermohaline and turbidity anomaly observed in the Western Mediterranean Deep Water after the 1999 and 2005 major cascading events.(sources: a-c, International Hydrographic Organisation 2017; d, modified from Company et al. 2008).

the North, with the Algerian Basin in the South (Astraldi et al. 1999). It is suggested, that channels located in the Balearic Sea play an important role in diverting inflowing Atlantic water into the northern regions of the western Mediterranean Sea (Astraldi et al. 1999).

The continental margin of the western Mediterranean Sea, and in particular in the Balearic Sea, is characterized by deep submarine canyons incising the continental shelf and slope in depths below 1,000 m close to the coast (Sardà et al. 1994). Submarine canyons are considered to play an important role channelling particulate organic matter (POM) from surface waters of the shelf into the bathyal zone. The transport of organic material into the deep-sea is subjected to seasonal variability, where primary production in the northwest Mediterranean Sea peaks in a surface bloom in late winter, while deep chlorophyll maxima were observed in the periods of open water column stratification, registered from April to November (Estrada 1996, Papiol et al. 2013 and references therein). In this area, the advective fluxes (in April and October) channel organic matter from the shelf into the deep-sea, resuspend and deposit particles on the bottom, affecting the food availability (Nittrouer et al. 2006). In part, these processes have been registered by the high bottom turbidity in these periods (Palanques et al. 2006, Papiol et al. 2012 and references therein). This can be associated with discharges of continental run-offs and/or by cascading events, as it has been documented in the northwestern Mediterranean Sea (Canals et al. 2006), where part of the study areas of this work are included (Fig 3.1d). Seasonal variations of river discharges and cascading events are associated with increased precipitations and the development of dense shelf water layers which sink down the slope into the deep (Canals et al. 2006). Strong currents of cold and turbid waters from the shelf can have negative direct impacts on some species living in the slope area (Company et al. 2008) but on the other hand, the same authors argued that in short and medium terms these events can be positive and important promoting biological processes within the deep-sea communities (Company et al. 2008).

Seasonal variations in the distribution of nutrients on the slopes of the western Mediterranean is supposed to induce migrations of deep-sea organisms. Changes in temperature and salinity in the water masses, especially within the Levantine Intermediate Water (LIW), are linked with movements of deep-sea fishes (Aguzzi et al. 2013, Cartes et al. 2013a). Generally it is suggested, that bathymetric shifts of the species distributions through seasons are a result of the prey movement followed by their predators (Aguzzi et al. 2013 and references therein).

Parameters such as water turbidity, temperature and O_2 concentration in water fluxes can increase the abundances of primer consumers, as observed for copepods in the slopes of the western Mediterranean deep-sea (Cartes et al. 2013a); this applies also to mesopelagic organisms (e.g. euphausiids, small myctophids). This could be related to temporal changes in the composition of the deep-sea fish assemblages in the northwestern Mediterranean Sea (Stefanescu et al. 1993), as euphausiids and small myctophids are direct prey species of the demersal fish assemblages, and they also enrich deep-sea sediments with detritus.

3.1.2 The Northeast Atlantic Ocean

The second part of the studies has been conducted in two specific features located in the Northeast Atlantic: the Avilés Canyon system (southern Bay of Biscay) and the Galicia Bank (northwestern Iberian shelf). The Northeast Atlantic is described as a deep basin on one side of the Mid Atlantic Ridge, with depths down to 5,000 m (Johnsen et al. 2002). Tides and wind predominantly generate currents in the shelf areas of European countries whereas the main water flow is from south to north (Johnsen et al. 2002). Usually, temperature and salinity measured in deep waters of the Northeast

Atlantic are between 5.5 to 7.5°C and *c*. 35.0‰ (Johnsen et al. 2002).

The Bay of Biscay and the Iberian shelf can be considered as part of the ocean margins entering in the deep basin of the Northeast Atlantic. Usually ocean margins are influenced by several forces (atmospheric, continental, oceanic) promoting a high hydrographic variability on the structure of the food webs (Llope et al. 2006 and references therein). Water masses in the Bay of Biscay originate predominantly from the North Atlantic and the deep Mediterranean Outflow Water (MOW) (Pollard et. al 1996). These water masses consist of different water layers, where the Eastern North Atlantic Central Water (ENACW) can be found as surface water extending to depths of up to 800 m (Fontanier et al. 2002, González-Pola et al. 2006, Flögel et al. 2014). At these depths the ENACW exhibits a minimum salinity (35.6‰) (Flögel et al. 2014) while salinity increases below 800 m owing to the influence of the MOW (up to 1,200–1,500 m) (Fontanier et al. 2002, González-Pola et al. 2006, Flögel et al. 2014). The MOW exhibits high salinities (35.80–36.2‰) and lowest oxygen values (3.8 to 4.4 ml/l) (Fontanier et al. 2002 and references therein, Flögel et al. 2014), and forms a contour current along the continental margin. The deepest parts of the Bay of Biscay represent water masses belonging to the North Atlantic Deep Water (NADW) at depths between 1,500 and 3,000 m (Fontanier et al. 2002, Flögel et al. 2014). Generally, upwelling and other exchanging processes between coastal and deep waters within the Bay of Biscay are limited by dense and cold water layers on the continental shelf occurring in spring and summer, which impede the advection of sub-surface water (Fontanier et al. 2002 and reference therein).

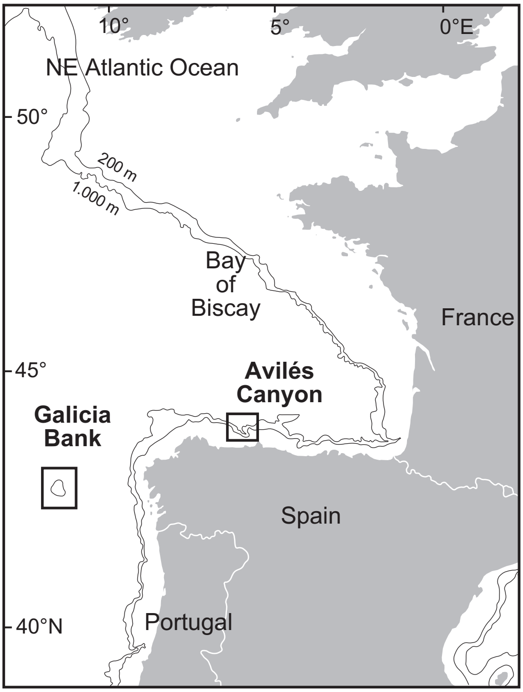

Fig. 3.2 - Map showing the location of both main sampling areas in the Northeast Atlantic: the Avilés Canyon (AC) and the Galicia Bank (GB).

The Avilés Canyon system

The Avilés submarine canyon system (AC) is a topographic feature located in the Cantabrian Sea (southern Bay of Biscay) very close to the coast of Asturias (*c*. 7 nautical miles, NM) which receives continental input of sediments and organic matter by freshwater runoff (González-Quirós et al. 2003, Louzao et al. 2010). The canyon intersects the narrow Cantabrian continental shelf (Fig. 3.2), opening at 140 m depth and reaching deep areas of almost 4,700 m.

The AC morphology is narrow and steep, exhibiting 15 km width in the 200 m isobath and a length of 32 km (González-Quirós et al. 2003, Ruiz-Villarreal et al. 2004a). The temperatures measured in this area range from 12.5°C at the surface in winter to 2.0°C at maximum depth. Different water masses generate variations in temperature within the water column varying from 10°C at 700–1,400 m (MOW) to 4°C below 1,800 m Labrador Sea water (LSW) (Sánchez et al. 2014).

The high local faunal biodiversity observed in the Cantabrian Sea (southern Bay of Biscay), and in particular in the AC, is partly explained because this sea is a boreal/subtropical transition zone of the Northeast Atlantic with boreal and south temperate species (Louzao et al. 2010 and references therein, Cartes et al. 2013b, Sánchez et al. 2014). Biodiversity hotspots in this canyon system were observed associated with key habitats, like reef-forming corals and sea-pens forming three dimensional complex habitats (Louzao et al. 2010). Additionally, these authors linked the high diversity also with coastal upwelling events of colder, nutrient rich water, which promotes the primary production followed by the sinking of dead phytoplankton nourishing and affecting the composition and structure of benthic communities in the deep (e.g. Cartes et al. 2004b). As topographic features, submarine canyons effectively induce flow modifications promoting exchange of water masses between the shelf and slope (González-Quirós et al. 2004). These underwater features can locally modify the described seasonal pattern of low water mass exchanges between coastal and deep waters due to dense water layers on the shelf (Fontanier et al. 2002). For this area, including the AC, two main seasons regarding their hydrographic conditions were established: a 'down-welling season' (October to March) and an 'upwelling season' (April to September) (Ruiz-Villarreal et al. 2006). Further, pole- and equatorward currents through winter and summer months, respectively, are associated with high salinity, forcing saline stratification in coastal areas due to river run-offs, where plankton distribution is influenced by the fronts of these water masses (González-Quirós et al. 2003, Ruiz-Villarreal et al. 2004a). Primary production is enhanced by mesoscale processes, such as wind driven upwelling events in summer (Llope et al. 2006), in post-bloom phases with high biomass of zooplankton (González-Quirós et al. 2003). By means of these upwelling events surface waters already depleted of nutrients by spring primary production, are supplied with essential nutrients enhancing another primary production event which benefits the production of high zooplankton biomass. Consequently, all these processes together are considered of high importance by intensifying the energy transfer though the whole food web to the highest trophic levels (González-Quirós et al. 2003, 2004).

The Galicia Bank seamount

The Galicia Bank (GB) is a seamount 120 NM away from the coast (Fig. 3.2) with a summit located between 620 to 1,800 m depth, separated from the Iberian continental margin by deep trenches *c.* 2,500–3,000 m, with maximal depths in the GB region of *c.* 5,000 m (Duineveld et al. 2004, Ercilla et al. 2011, Somoza et al. 2014). Usually, the 'plateau-like' top of the GB is covered by thick layers of planktonic foraminifera ooze and sand with low fine sediment fraction, biomass and low organic particles forming small and occasional mega-current ripples (Duineveld et al. 2004). The area is under the influence of many different water masses from the Atlantic and the MOW, resulting in high current velocities and mobile sediments (Pollard et al. 1996, Ruiz-Villareal et al. 2004b, Duineveld et al. 2004). Further, as also described for the AC, the circulation of water masses is northward during autumn and winter (Iberian Poleward Water – IPC) and southward (Equatorward) in spring and summer (Ercilla et al. 2011). Below surface waters (up to 100 m) the ENACW, followed by the MOW are the dominating water masses where latter reaches up to *c.* 1,600 m depth exhibiting salinity maxima at 800 m and 1,200 m depths. Water masses below the MOW result from density dependent mixing of water bodies with the LSW and the NADW, which carries water masses from the Arctic Seas (up to *c.* 4,000 m), and the Lower Deep Water (LDW) (Ercilla et al. 2011 and references therein).

The temperature and salinity in the seamount summit (~ 770 m) revealed a mean of 11.2°C and a salinity maximum on the top of the bank (700–900 m) with values of *c.* 36.0‰ due to the influence of the MOW (Duineveld et al. 2004). Drastic decreases of oxygen were measured in depths where the MOW has been detected

(800–1,200 m close to the bank summit), while values on top of the bank (600–750 m) outside the influence of the MOW core revealed higher oxygen values and lower salinity (Somoza et al. 2014). The MOW is considered as one of the most important forces, erosive and depositional, in this area, forming bottom currents in depths between 620 to 1,750 m including the top of the GB (Ercilla et al. 2011). The GB presents a rich and diverse benthic community inhabiting this area (Cartes et al. 2013b, de la Torriente et al. 2014) and in part the composition and structure of assemblages is clearly influenced by water masses occurring in this area. In the specific case of the GB, Ruiz-Villarreal et al. (2004b) suggested a trapping mechanism on the top of the bank which could be caused by circulation patterns of the MOW. The generation of the own hydrographic conditions and the enhancement of the local productivity by trapping zooplankton are aspects generally supposed for seamounts (White et al. 2007). The analysed decapod communities from the GB consisted of species with southern origin in depths influenced by the MOW, while northern species were found in the cold and deeper waters of the LSW (Cartes et al. 2013b). The higher diversity of smaller crustaceans (decapods) and euphausiceans has been suggested to be associated with higher oxygen and phytoplankton concentration in the water column above the bank (Cartes et al. 2013b).

3.2 HOST SPECIES

In the present work three deep-sea fish species were studied, one finfish and two sharks; we analyzed the parasite fauna for all three species. Additionally, the stomach content of both elasmobranchs was studied. The known aspects on the biology and ecology of all three species are detailed below.

3.2.1 The shortfin spiny eel, *Notacanthus bonaparte*

The shortfin spiny eel, *Notacanthus bonaparte* Risso, 1840 (Notacanthiformes, Notacanthidae) (Fig. 3.3A) is a bathydemersal deep-sea fish (Sulak 1986). It has a Northeast Atlantic-Mediterranean distribution (Fig. 3.3B), ranging from the most northern record (Faroe Islands) to the most southern ones (Mauritania) (Froese & Pauly 2017), and with presence in the western and central Mediterranean Sea (Lozano Cabo 1952, McDowell 1973); however, recent publications indicated its presence even in the East Mediterranean basin (e.g. Deval 2013, Farrag 2017).

Notacanthus bonaparte usually occurs in depths between 500 and 2,500 in the Northeast Atlantic, and from 200 to 2,200 m in the Mediterranean Sea (Moranta et al. 1998, Coggan et al. 1998, D'Onghia et al. 2004, Rodríguez-

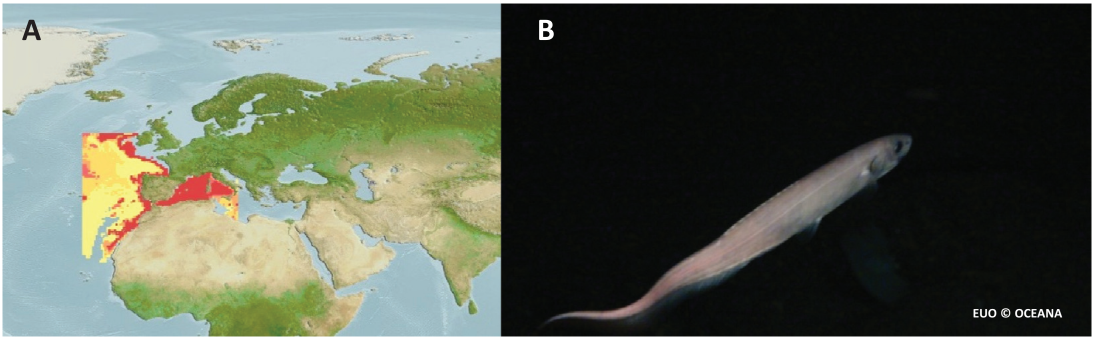

Fig. 3.3 - Distribution map of *Notacanthus bonaparte*, obtained by AquaMaps in Froese & Pauly (2017) (A); the shortfin spiny eel, *N. bonaparte* (B) (source: Oceana).

Romeu et al. 2016). The maximum abundances in the Northeast Atlantic have been documented between 500 –1,000 m (Coggan et al. 1998) and for the western Mediterranean between 1,000–1,450 m and 580–1,000 m (Stefanescu et al. 1992, Rodríguez-Romeu et al. 2016). Maximum size provided by Froese & Pauly (2017) is 26 cm (male), while in the Mediterranean Rodríguez-Romeu et al. (2016) measured 28 cm and for the Atlantic 50 cm were observed (R. Kuchta pers. com). The diet descriptions for *N. bonaparte* show marked benthic feeding habits for this species, in the Atlantic Ocean and the Mediterranean Sea. The diet comprise ophiuroideans, actinians, hydrozoans, bryozoans, polychaetes, amphipods, while also rests of fish and polyps of corals were observed in the Mediterranean (Lozano Cabo 1952, Macpherson 1981, Coggan et al. 1998, Rodríguez-Romeu et al. 2016, Preciado et al. 2017).

3.2.2 The velvet belly lantern shark, *Etmopterus spinax*

The velvet belly lantern shark *Etmopterus spinax* (L. 1758) (Squaliformes, Etmopteridae) (Fig. 3.4A) has an East Atlantic distribution, from Iceland and Norway to southern Africa and also occurs in the Western Mediterranean Basin (Coelho & Erzini 2008) (Fig. 3.4B); more recent publications also recorded this species in the Levantine Mediterranean Sea (Basusta 2016).

This deep-sea shark has been recorded from the outer continental and insular shelves and on upper to lower slopes close or at the sea floor at depths between 70 and 2,000 m but its presence is more common in the dept range 200 to 500 m (Compagno 1984). The depth with highest abundances vary, as in the Northeast Atlantic highest abundances were detected at 500 m while in the Mediterranean Sea the largest aggregations have been recorded at 700 m (Coelho et al. 2010). *Etmopterus spinax* shows a clear sexual dimorphism with larger females which mature at higher ages compared to males (4 to 4.5 years) and display larger body sizes. *Etmopterus spinax* is an aplacental viviparous species and the reproductive season (mating) is considered to take place in summer (Coelho & Erzini 2008). The ovarian fecundity is low but increases with larger body sizes (reaching 1 to 21 embryos); a 2–3 years reproduction cycle is supposed for the species (Coelho & Erzini 2008). Although there are still uncertainties with respect to the reproductive cycle, it is known that even when this is a small-sized shark species, the population dynamics are comparable to many larger sized elasmobranchs (e.g. late maturity, slow growth), resulting in a high susceptibility to fishery impacts (Coelho et al. 2015). The maximum size is 60 cm, specimens above 45 cm being rare (Compagno 1984).

This species exhibits ontogenic shifts in its diet, gradually becoming more piscivorous with

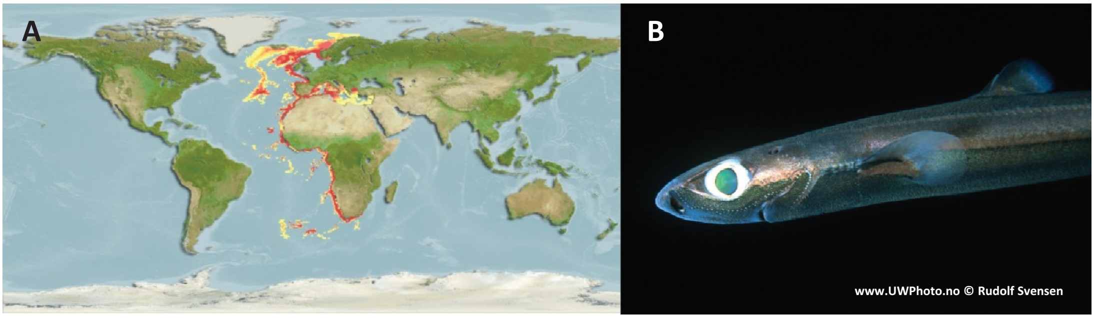

Fig. 3.4 - Distribution map of *Etmopterus spinax* obtained from AquaMaps in Froese & Pauly (2017) (A); the velvet belly lanternshark, *E. spinax* (B) (source; R. Svensen).

increased size (Klimpel et al. 2003, Neiva et al. 2006, Fanelli et al. 2009). As this species is an opportunistic feeder its diet may vary spatially. Considering the available data from the Atlantic and the Mediterranean *E. spinax* feeds mostly on crustaceans (decapods, euphausiids), cephalopods, small meso- and benthopelagic fishes (myctophids, engraulids), and in some cases scavenging has been observed (e.g. Macpherson 1981, Bergstad et al. 2003, Neiva et al. 2006, Preciado et al. 2009, Fanelli et al. 2009, Valls et al.2011).

3.2.3 The arrowhead dogfish *Deania profundorum*

The arrowhead dogfish shark *Deania profundorum* (Smith & Radcliffe, 1912) (Squaliformes, Centrophoridae) (Fig. 3.5A) is a benthopelagic species. Its geographical distribution ranges from the West to the East in the North and South Atlantic Ocean, with the Bay of Biscay considered as the northernmost distribution area for this species in the Northeast Atlantic (Sanjuán et al. 2012). *Deania profundorum* was also recorded in the south Pacific and in the Indian Ocean (Compagno 1998, Nelson 2006, Froese & Pauly 2017) (Fig. 3.5B). As observed for relative species (e.g. *Deania calcea*) it is supposed that this species is confined to bathyal habitats a (Musick et al. 2004) and can be found usually on or close to the seabed, in depths between 270 and 1,800 m (Compagno 1984).

Data on the reproduction of *D. profundorum* reveals sexual dimorphism, with females reaching larger sizes than males, and maturing at larger sizes (Sousa et al. 2009). As for many other species in its family, there is scarce knowledge on their biology and ecology (Sousa et al. 2009), therefore some assumptions on its biology are made on the basis of relative species. As other Centrophoridae species, *D. profundorum* is ovoviviparous. The current available information for *Deania* species regarding reproductive traits and reproductive cycle mostly refer to the species *D. calcea*: late maturity, low litter size, and a two- or three year non-continuous reproductive cycle (Clarke et al. 2002, Irvine et al. 2012). Sousa et al. (2009) partially confirmed that *D. profundorum* have similar life traits, as they also recorded a low litter size in specimens from the Northeast Atlantic (11 embryos). Like in other centrophorids, the very low lifetime fecundity indicate a high susceptibility to even very low fishing mortality (Kyne & Simpfendorfer 2010 and references therein, Irvine et al. 2012). Maximum sizes for this species were recorded with 109 and 110 cm (Compagno 1984, Sousa et al. 2009). The scant available data on the diet of this shark indicate a benthopelagic feeding habits, preying on crustaceans, cephalopods and different fish species (Compagno 1984, Ebert et al. 1992), however, no data on its diet exists for the Northeastern Atlantic.

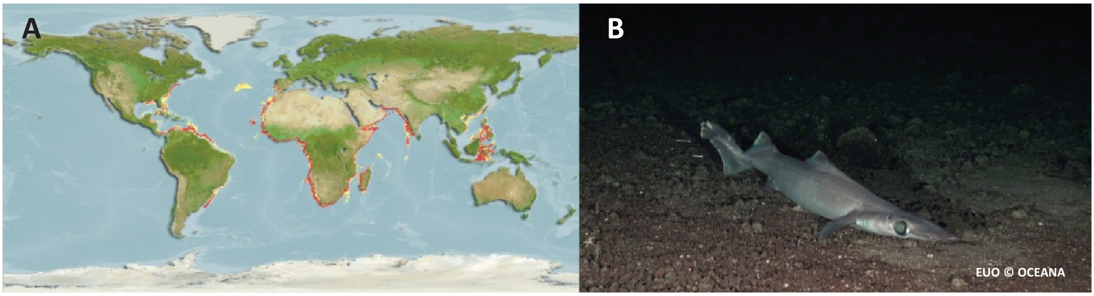

Fig. 3.5 - Distribution map of *Deania profundorum* obtained by AquaMaps in Froese & Pauly (2017) (A); the arrowhead dogfish, *D. profundorum* (B) (source: Oceana).

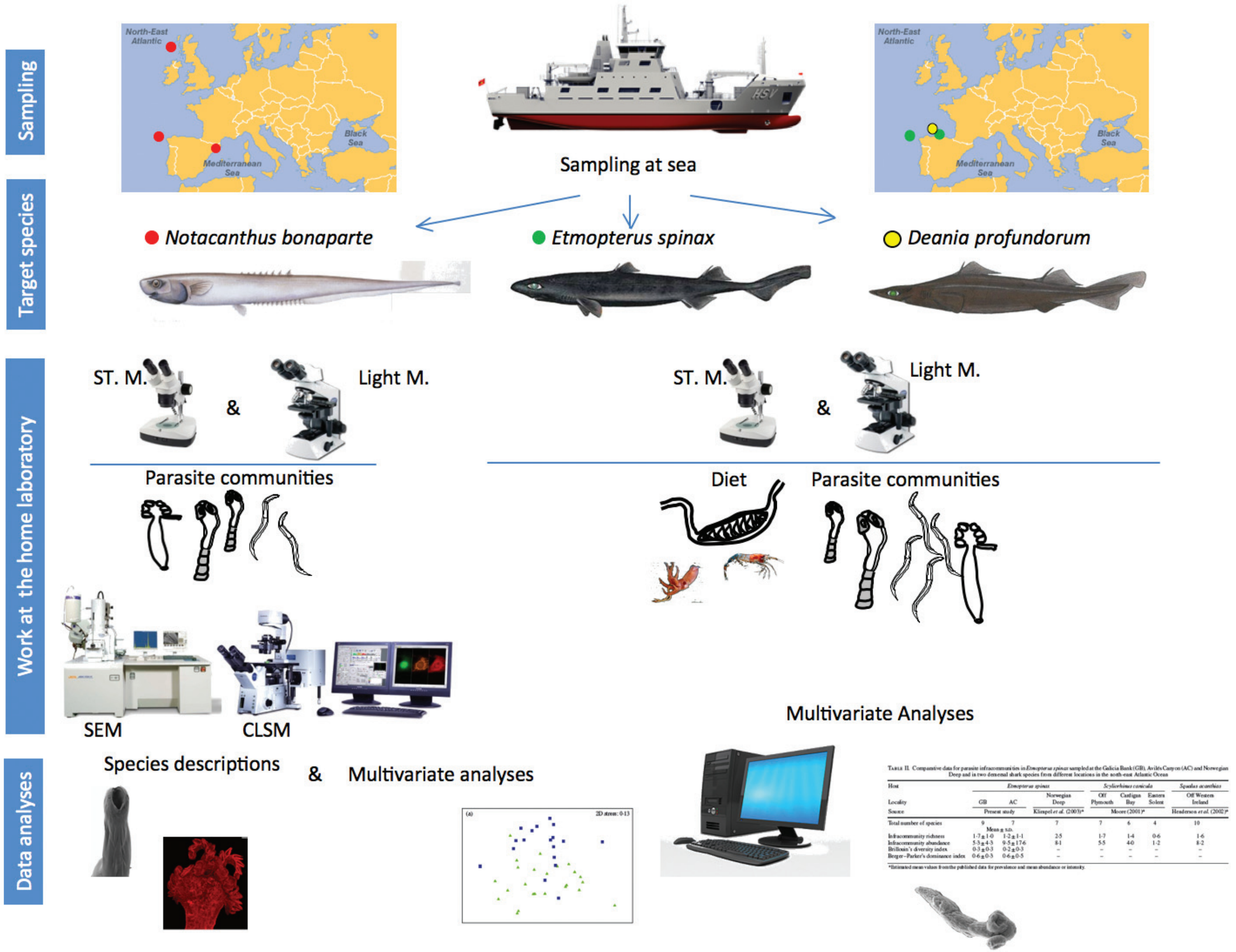

TABLE II. Comparative data for parasite infracommunities in *Etmopterus spinax* sampled at the Galicia Bank (GB), Avilés Canyon (AC) and Norwegian Deep and in two demersal shark species from different locations in the north-east Atlantic Ocean

Host	*Etmopterus spinax*			*Scyliorhinus canicula*			*Squalus acanthias*
Locality	GB	AC	Norwegian Deep	Off Plymouth	Cardigan Bay	Eastern Solent	Off Western Ireland
Source	Present study		Klimpel *et al.* (2003)*	Moore (2001)*			Henderson *et al.* (2002)*
Total number of species	9	7	7	7	6	4	10
	Mean ± S.D.						
Infracommunity richness	1·7 ± 1·0	1·2 ± 1·1	2·5	1·7	1·4	0·6	1·6
Infracommunity abundance	5·3 ± 4·3	9·5 ± 17·6	8·1	5·5	4·0	1·2	8·2
Brillouin's diversity index	0·3 ± 0·3	0·2 ± 0·3	–	–	–	–	–
Berger–Parker's dominance index	0·6 ± 0·3	0·6 ± 0·5	–	–	–	–	–

*Estimated mean values from the published data for prevalence and mean abundance or intensity.

Fig. 3.6 - Schematic overview on the sampling areas, targeted species and methods used in the studies conducted in this PhD work.

3.3 SAMPLING PROCEDURE

Comprehensive and detailed descriptions of the sampling methods are provided in the separated chapters. Methods are described briefly with references to the appropriate chapters (see Fig. 3.6 for a brief scheme on the sampling and data processing).

3.3.1 Sampling of *Notacanthus bonaparte*

Specimens of *Notacanthus bonaparte* were collected during several scientific surveys in the western Mediterranean on the slope off Catalonia (Spain) in the Balearic Sea at depths between 620 and 1,750 ('BIOMARE 1' – 'BIOMARE 5' all seasons 2007-2008, 'ANTROMARE 2' and 'ANTROMARE 3' June and October 2011, respectively). Onboard, morphometrical data was recorded and fish specimens were deep frozen (-25°C) for later inspection for parasites in the laboratory. Additional *N. bonaparte* specimens were sampled in the GB (Northeast Atlantic Ocean) during the 'INDEMARES-0710-BANGAL' cruise in August 2010 at depths between 771 and 837 m. The procedure onboard was the same as described above.

Further specimens of *N. bonaparte* and *N. chemnitzii* were taken off the Outer Hebrides (Northeast Atlantic) in depths between 400 to 1,800 m during a scientific survey in August/September 2004. In this case, after taking the morphometric data of the specimens, the fish samples were dissected immediately onboard and detected parasites were collected and preserved in buffered 4% formalin by Dr. R. Kuchta (Institute of Parasitology, Academy of Science of the Czech Republic).

The specimens of *N. bonaparte* sampled in the western Mediterranean were integral part for the studies developed in: **Chapter 5** ("A new species of *Tinrovia* Mamaev, 1987 (Monogenea: Microcotylidae) from the deep-sea fish *Notacanthus bonaparte* Risso (Notacanthiformes: Notacanthidae) in the Western Mediterranean and the North East Atlantic"); the **Chapter 6** ("*Dichelyne* (*Cucullanellus*) *romani* n. sp. (Nematoda: Cucullanidae) in notacanthid fishes from the Northeast Atlantic and Western Mediterranean"), and **Chapter 7** ("Seasonal variation of parasite communities of *Notacanthus bonaparte* Risso, 1840 (Notacanthiformes: Notacanthidae) over the northwest Mediterranean slope") of this work. **Chapter 5** includes samples of *N. bonaparte* taken in the GB (Northeast Atlantic Ocean). The **Chapter 6** also includes the samples of both *Notacanthus* spp. taken off the Outer Hebrides.

3.3.2 Sampling of *Etmopterus spinax* and *Deania profundorum*

Specimens of *E. spinax* were sampled in the AC and the GB (both areas located as described in the previous section in the Northeast Atlantic) during the surveys 'INDEMARES-AVILÉS 0710' and 'INDEMARES-0710-BANGAL' conducted in July and August in 2010 respectively. Samplings were conducted at depths between 200 and 1,250 m. Onboard, morphometrical data was recorded and fish specimens were deep frozen (-25°C) for later inspection for parasites and diet in the laboratory. The specimens of *D. profundorum* were sampled in the AC only, in the surveys 'INDEMARES-AVILÉS 0710' and 'INDEMARES-AVILÉS 0511' conducted in July 2010 and May 2011 respectively, in depths between 580 and 1,260 m. The procedure onboard was the same as described above.

The specimens collected from these two shark species were the basis for the study conducted in **Chapter 8** ("Metazoan parasite communities and diet of the velvet belly lanternshark *Etmopterus spinax* (Squaliformes: Etmopteridae): a comparison of two deep-sea ecosystems") and in **Chapter 9** ("First insight into the diet and parasite fauna of the deep-sea shark *Deania profundorum* (Smith & Radcliffe, 1912) from the Avilés Canyon (southern Bay of Biscay, Northeast Atlantic): shedding light on host's role?"), respectively.

3.4 SAMPLE PROCESSING AT THE LABORATORY

3.4.1 Dissection of host specimens for parasite and diet extraction

In the laboratory, prior to examination and dissection, thawed fish were measured and weighed. External surfaces and fins were inspected. Gills and all internal organs were removed and preserved separately in physiological saline. In the case for both elasmobranchs where diet was analysed, the stomach was weighed (full and empty). Organs and body parts examined were: mouth, brain, eyes, nasal cavity/lamellae, gills, all internal organs and body cavity. All parts and organs were examined for the presence of parasites by means of a stereomicroscope. After the inspection of the organs, the entire body musculature was sliced and examined using glass plate compression method and inspection was conducted under a stereomicroscope. All metazoan parasites and all prey items detected were collected and cleaned in physiological saline. Parasites were preserved in 70% ethanol for subsequent identification; some specimens were preserved in 100% ethanol for molecular analyses. Prey items from the stomach were separated, counted and identified to the lowest possible taxonomic level using a stereomicroscope, or preserved in 70% ethanol for subsequent identification.

3.4.2 Techniques applied for parasite analyses and host diet

Adult platyhelminths were stained with iron acetocarmine (Georgiev et al. 1986), dehydrated in an ethanol series, cleared in dimethyl-phthalate and mounted in Canada balsam for further inspection under a light microscope. Larval cestodes and nematodes were examined in light microscopy observation in physiological saline or in glycerine mounts after dehydration in a graded glycerine-ethanol series. Preliminary identifications up to the minimum taxonomic level (genus when possible) were based on specialized bibliography: Khalil et al. 1994 and Palm 2004 for cestodes; Gibson et al. 2002, Jones et al. 2005, Bray et al. 2008 for trematodes; Yamaguti 1963 for monogeneans; and Petter 1974, Moravec 1994, and Anderson 2000 for nematodes.

Regarding the molecular analyses, we failed to obtain sequences for *Tinrovia mamaevi* ex. *Notacanthus bonaparte* (Chapter 5). The molecular analyses of specimens of the nematode *Dichelyne* (*Cucullanellus*) *romani* were performed at the Zoology Unit of the Autonomous University of Barcelona for further studies.

For the studies focussed on the descriptions of the species *Tinrovia mamaevi* and *Dichelyne* (*C.*) *romani* (**Chapters 5** and **6**) where a detailed morphological study was needed, parasite specimens were analysed by means of confocal laser scanning microscopy (CLSM) or with scanning electron microscopy (SEM). Details on these both techniques can be found in the **Chapters 5** and **6**, respectively.

The diets of the host species *Etmopterus spinax* and *Deania profundorum* were analysed and used for the chapters dedicated to the study of the parasite communities of *Etmopterus spinax* (**Chapter 8**), and the chapter dedicated to the study of the parasite communities of *Deania profundorum* (**Chapter 9**), respectively. For the preliminary identification of the prey items literature on the marine fauna was used (e.g. Hayward & Ryland 1990).

3.5 DATA ANALYSIS

3.5.1 Quantitative description of the parasite communities

The ecological terminology follows Bush et al. (1997). Population parameters used for the quantitative description of found parasite communities were: prevalence (%P; with 95% confidence intervals), mean abundance (MA), and mean intensity (MI) for each single taxa; calculations for MA and MI include the standard deviation (SD). Calculations have been performed using the software Quantitative Parasitology (QP 3.0; Rozsa et al. 2000). Parasites were considered common when exhibiting a prevalence >5%; uncommon parasites (P%<5%) were not included in detailed analyses. Data treatment is explained in detail in **Chapters 5, 6, 7, 8** and **9**.

In the **Chapters 7, 8** and **9,** metazoan parasite richness (Margalef species richness index) and diversity (Brillouin diversity index) were calculated using the software PRIMER v6 (Anderson et al. 2008). The total abundance, infracommunity richness and Berger Parker dominance index were calculated on raw data in EXCEL.

3.5.2 Quantification of prey items of the host

This data treatment has been performed in **Chapters 8** and **9:** the frequency of occurrence (%F) for the prey encountered in the host stomachs, as well as the percentage by number (%N) and percentage by mass (%W) for each prey item was calculated following the methodology of Hyslop (1980). The quantitative importance of each prey item was defined with the index of relative importance I_{RI} (Pinkas et al. 1971) which was calculated in order to facilitate the comparison of the results with previous studies. Further, the number of prey items per species or higher taxon in individual fish was used in the quantitative diet comparisons. More details can be found in **Chapters 8** and **9**.

3.5.3 Statistical analyses

In **Chapters 7, 8** and **9** the parasite communities of the hosts were analysed with respect to a range of factors. For this purpose, the parasite infrapopulations (all parasites of a given species in an individual fish specimen) and infracommunities (all infrapopulations in an individual fish specimen), and the prey item assemblages were used as replicate samples. All data sets where univariate analyses have been performed were tested for normality and homoscedasticity, in order to assess if the data complied with the requirements to perform parametric statistical tests. In the cases where normality and variance homogeneity were not achieved, non-parametric tests were conducted. When necessary data was ln (x +1) or square root transformed prior to analyses.

The statistical analyses used in this work are indicated in detail in each chapter. Several statistical methods have been used and the following software and statistical programs have been applied: SPSS Statistics 17.0; Statistica 9.0 (StatSoft, Inc.); XLSTAT Evaluation 18.06 (Addinsoft); and PERMANOVA+for PRIMER v6 software.

3.6 BIBLIOGRAPHIC RESEARCH. METADATA COMPILATION FOR THE CHECKLIST OF PARASITES RECORDED FROM THE THREE HOST FAMILIES

In **Chapter 4** a compilation was performed including published available data on the metazoan parasite fauna in species of the three families which include the host species of this work: Notacanthidae (*Notacanthus bonaparte*), Etmopteridae (*Etmopterus spinax*), and Centrophoridae (*Deania profundorum*). A comprehensive literature search has been conducted consulting different databases (e.g. Google Scholar, Web of Knowledge, World of Copepods, Global Cestode Database, Host-parasite database of the Natural History Museum London). The search was conducted using the names of the fish families and/or the single species names along with several keywords: “parasite”, “ectoparasite”, “endoparasite”, and higher taxa groups (e.g. “Cestoda”, “Monogenea” etc.). Additionally, the comprehensive checklist compiled by Klimpel et al. (2009) was consulted. Scientific names of host species and parasite species were verified in the World Register of Marine species (WORMS) and shark-references (Pollerspöck & Straube 2016). The information found by means of a web search engine, was verified with the original source (publication) when available.

Chapter 4

Annotated checklist of parasites recorded from the species of the three families of deep-sea fish: Centrophoridae, Etmopteridae and Notacanthidae

The fish fauna comprises more than 33,000 fish species globally (Froese & Pauly 2017) and it is suggested that 10-15% of these species (3,100-4,600) can be found in the deep-sea, including chondrichthyans and osteichthyes (Klimpel et al. 2009). Klimpel et al. (2009 and references therein) estimated an overall mean of 1.5 parasite species per deep-sea fish which is lower than what is assessed as average over all fish species (3–4 parasite species). The pioneer studies on the parasitic assemblages in the deep-sea fish fauna (e.g. Manter 1934, Noble 1973, Campbell et al. 1980, Gartner & Zwerner 1989) were followed by a slightly increasing number of studies on this issue in more recent decades; though, most studies are specifically dedicated to certain deep-sea fish species or parasite groups (amongst others: Bray & Campbell 1995, Bray et al. 1999, Bray 2004a, Klimpel et al. 2006a, Caira & Pickering 2013). These and the former studies were the basis for the possibly most comprehensive compilation of data and checklists by Klimpel et al. (2009) which was an update of Klimpel et al. (2001). However, Klimpel et al (2009) indicated that only about 15 % of all known deep-sea fish species had been studied on parasites, which also reflects the general dearth of information for many organisms in these habitats (Kyne & Simpfendorfer 2007, Norse et al. 2012). The available data on deep-sea fish parasites is scarce which can be explained firstly by the difficulties/constraints to obtain samples from the deep-sea (e.g. high costs, often low sample sizes), and secondly by the lack of interest in species of low or no commercial value.

In the following chapter a revision of the literature has been conducted in order to compile a complete checklist of the parasite species of three fish families with species which are mostly considered of ‘low or no commercial value’, the chondrichthyans Centrophoridae and Etmopteridae, and the osteichthyan Notacanthidae, along with their distributional range (Table 4.1). The total number of valid fish species (82) is distributed differently among the three families: 20 centrophorids, 51 etmopterids and 11 notacanthids; although to date, especially for the two elasmobranch families, there are still several taxonomical uncertainties with respect to the validity of already described species and the existence of possible cryptic species (Straube et al. 2011a, White et al. 2013).

In the following paragraphs all three families are presented shortly to describe their main traits and biology. It is important to highlight that the information on these three families is often restricted to few species (Kyne & Simpfendorfer 2007) and this data cannot always be extrapolated to related species as biological parameters can vary greatly (Rochowski et al. 2015).

4.1 STUDIED FISH FAMILIES

Centrophoridae

The Centrophoridae Bleeker, 1859 (Elasmobranchii: Squaliformes) comprises 20 valid species of sharks: 16 of the genus *Centrophorus*

Müller & Henle, 1837, and four of the genus *Deania* Jordan & Snyder, 1902. The validity of four of the *Centrophorus* species is still under discussion and revision (see: Ebert et al. 2013, White et al. 2013, Wienerroither et al. 2015, Weigmann et al. 2016). These 'gulper sharks' are small to medium fishes, characterized by having strong, grooved spines in both dorsal fins, larger teeth in the lower jaw, and the absence of precaudal pits and lateral keels on the caudal peduncle (Nelson 2006, Lloris 2015). The maximum body size may reach 101–300 cm (*Deania calcea*, Clarke et al. 2002a, *Centrophorus granulosus*, Bañon et al. 2008, Musick et al. 2004). Maximum ages were calculated between 11–36 years for *D. calcea* (Clarke et al. 2002a, Irvine et al. 2012) and 21–70 years for *C. squamosus* (Clarke 2002b). Some shark species may exhibit sexual dimorphism (Clarke et al. 2002b, Irvine et al. 2012) and generally show late maturity, e.g. the estimation of the total length at 50% maturity ($TL_{50\%}$ maturity) for *C. squamosus* from Northeast Atlantic was 102–128 cm (Clarke et al. 2002b). Age at maturity was calculated as more than 15.5 to 25 years for *D. calcea* (males and females, respectively) and could even reach 8.5 to 30 years and 16.5 to 35 years in *Centrophorus* spp. males and females, respectively (Kyne & Simpfendorfer 2007 and references therein). These sharks are ovoviviparous (Paiva et al. 2012) with low litter sizes (6–17 pups in *C. granulosus* and *Deania* spp., Bañon et al. 2008, Clarke et al. 2002a, Irvine et al. 2012). For *Deania* spp. it is recognised that the reproductive cycle is non-continuous with alternating two- or three-year cycles (Kyne & Simpfendorfer 2007; Irvine et al. 2012). *Centrophorus* spp. are considered as the most unproductive chondrichthyan species with very low fecundities and small litter sizes (Kyne & Simpfendorfer 2007).

Species of this family occur in warm temperate to tropical waters on continental and insular shelves and slopes from the upper to the middle bathyal depths in the Atlantic Ocean, and the Indian and Pacific Ocean, except the eastern North Pacific (Musick et al. 2004, Nelson 2006). All centrophorids are benthopelagic species (Musick et al. 2004) and available data on the diet reveal prey items mainly consisting of teleosts (meso-bathypelagic and demersal) and cephalopods (in part deepwater squids), while smaller specimens also feed on crustaceans (Yano et al. 1991, Ebert et al. 1992, Saldanha et al. 1995, Dunn et al. 2013, Costa et al. 2014 and references therein) which could indicate an ontogenic shift as observed in other sharks.

Species of this family are partly exploited for human consumption and livers are used for oil extraction, mostly on a more local scale (Clarke et al. 2002a,b, Clarke et al. 2005, Costa et al. 2014). However, usually they are considered of no commercial value and often discarded (Clarke et al. 2002a, 2005).

Etmopteridae

The Etmopteridae Fowler, 1934 (Elasmobranchii: Squaliformes), commonly known as lantern sharks, comprises five genera with 51 valid species. Three genera are monotypic (*Aculeola* de Buen, 1959, *Miroscyllium* Shirai & Nakaya, 1990, and *Trionognathus* Mochizuki & Ohe, 1990), while seven species are assigned to *Centroscyllium* Müller & Henle, 1841, and 41 to *Etmopterus* Rafinesque, 1810. The validity of some species is still under discussion (e.g. *Miroscyllium* sp.) and revisions are necessary especially for the genus *Etmopterus*. Diversity for this genus is supposed to be higher due to cryptic species (Straube et al. 2011a), as reflected also by several recent species descriptions (see also: Ebert et al. 2013, 2016, 2017, Straube et al. 2015, Vázquez et al. 2015, Weigmann et al. 2016). The monotypic species and the *Centroscyllium* spp. are restricted to local and regional geographical distributions, and species of the latter genus 'have been recorded from seamounts and oceanic islands' (Musick et al. 2004). Although this family comprises many endemic species, some wide-ranging species exist with global distribution (Kyne & Simpfendorfer 2007).

Etmopterids are small deepwater sharks (maximum lengths <90 cm, with some species even <50 cm), having two dorsal fins, with the second being larger, both with grooved spines. The mouth is small, with teeth smaller in the upper jaw. Lateral keels or pits on the caudal peduncle are absent, but the caudal fin has a subterminal notch (Musick et al. 2004, Nelson 2006, Lloris 2015, Froese & Pauly 2017). Species of this family, e.g. the majority of the genus *Etmopterus*, usually have luminous organs on the body (Claes et al. 2015). Sexual dimorphism was observed for some species (e.g. *Etmopterus spinax, E. princeps, Centroscyllium fabricii*) (Jakobsdottir 2001, Aranha et al. 2009, Mourato et al. 2010) and the size range of sexual maturity was for example between 28–36 cm for *E. spinax* (Aranha et al. 2009). Some authors observed mature specimens of *E. spinax*, the most studied species, with 43–50% and 80% of the maximum observed size (Coelho & Erzini 2008a, Porcu et al. 2014).

In general fecundity is considered to be low with usually a two- or three-year reproductive cycle (Coelho & Erzini 2008a). Species of this family are aplacental viviparous, with litter sizes of 10 in *Aculeola nigra*, 1–21 in *Etmopterus* spp. or 40 for *C. fabricii* (Kyne & Simpfendorfer 2007 and references therein, Coelho & Erzini 2008a, Porcu et al. 2014, Cotton et al. 2015). The few available data for age estimates in this family suggests maximum ages ranging from 8 to 57 years (Kyne & Simpfendorfer 2007, Coelho & Erzini 2008a). Maximum longevity (57 years) was detected in *E. baxteri*, with $TL_{50\%}$ maturity of 20–30 years (Kyne & Simpfendorfer 2007 and references therein).

The Etmopteridae are distributed regionally around the world in deep waters of the tropics to temperate latitudes. They can be found on the continental and insular slopes, and seamount regions in depths between 200 to 2,500 m (Nelson 2006, Straube et al. 2011b, Froese & Pauly 2017). The species of this family are considered benthopelagic (Musick et al. 2004), with a diet composition consisting mostly of crustaceans (decapods, euphausiids), cephalopods and teleosts (e.g. myctophids, gadids). These species often are described as opportunistic feeders, exhibiting also scavenging habits and ontogenic shifts were observed in some species (Jakobsdottir 2001, Neiva et al. 2006, Fanelli et al. 2009, Preciado et al. 2009, Hallet et al. 2011, Valls et al. 2011, Xavier et al. 2012, Dunn et al. 2013 and references therein).

Etmopterids are species without commercial value considering their meat and even their liver, which is too small or of less value with respect to the squalene content (Cotton et al. 2015). Nevertheless, they suffer high by-catch mortalities, being caught and discarded in high numbers in trawl and longline fisheries around the world (e.g. Jakobsdottir 2001, Coelho & Erzini 2008b, Aranha et al. 2009, Cotton et al. 2015).

Notacanthidae

The fin fish family Notacanthidae Rafinesque, 1810 (Actinoptertygii: Elopomorpha: Notacanthiformes) comprises 11 valid species: one of the genus *Lipogenys* Goode & Bean, 1895, six in *Notacanthus* Bloch, 1788, and four in *Polyacanthonotus* Bleeker, 1874. Notacanthids have long, slender anguilliform bodies, with dorsal isolated spines distinct in numbers (6–36), which is the key character for their common name 'deep-sea spiny eels' (Coggan et al. 1998, Lloris 2015). Some species have also spine-like rays on each pelvic fin. Notacanthids exhibit an inferior/subterminal mouth. Sexual dimorphism was recorded for the *Notacanthus* spp. only. Maximum lengths between these species vary greatly between 10 to 120 cm (*P. rissoanus*, *N. chemnitzii*, respectively; Froese & Pauly 2017). Available data on the age of notacanthids is scant, but recently specimens of *Notacanthus chemnitzii* from the North Atlantic revealed ages ranging from 11 to 26 years, and the authors supposed a maximum age of 30 years (Vedishcheva et al. 2016).

All species of this family are oviparous (Coggan et al. 1998, Nelson 2006, Lloris 2015, Froese & Pauly 2017), probably, as other elopomorph species, including leptocephalus larva during their development (Coggan et al. 1998 and references therein). For some species a protracted reproductive season is described, with mature individuals found in deeper waters (e.g. *N. bonaparte*, *P. rissoanus*; Coggan et al. 1998, Rodríguez-Romeu et al. 2016).

Many aspects of their life history are not well known and many details can be speculated only e.g. considering the migration behaviour and connectivity between populations (Coggan et al. 1998). The family exhibits a circumglobal distribution with partly overlapping horizontal and vertical distributions between species (Crabtree 1985, Nelson 2006 and reference therein). The extension of distribution varies between species; for instance, *Notacanthus chemnitzii* exhibits a circumglobal distribution, whereas *N. sexspinis* seems to occur on the southern hemisphere only, and *N. bonaparte* is restricted to the Northeast Atlantic and the Mediterranean Sea (Froese & Pauly 2017). Species of this family inhabit deep waters between 200–3,700 m (Nelson 2006). These bathydemersal fishes, feed on different small benthic invertebrates (hydrozoans polychaetes, bryozoans, crustaceans, echinoderms) and small nektonic crustaceans (Macpherson 1981, Coggan et al. 1998, Carrassón and Matallanas 2002). In some species a piscivorous habit was recorded (Coggan et al. 1998, Rodríguez-Romeu et al. 2016). Some species were observed to feed in an 'inclined attitude', feeding on epibenthic organisms while others use their premaxillary teeth to crop benthic prey from the bottom (Crabtree et al. 1985, Carrasson & Matallanas 2002 and references therein). In some geographical areas, notacanthid species have been reported to be 'among the most 10 abundant species' in research trawls (Coggan et al. 1998, Carrassón & Matallanas 2002). They are of no value for commercial fisheries and they are part of the discarded by-catch (Coggan et al. 1998).

4.2 CHRONOLOGICAL AND GEOGRAPHICAL DISTRIBUTION, AND METHODOLOGICAL CONSTRAINTS

The overall number of studies conducted on parasites of these families is very low, but shows a steady upward trend since the 1970s, although still in low numbers (Fig. 4.1a). This might be explained by the technological developments during the last 40 years, which promoted deep-sea research (Ramirez-Llodra et al. 2010). However, the pattern observed for these studies concerning the geographical areas also shows that, although an overall increase in deep-sea research exists, this kind of research seems to be conducted in stocks and by countries with a certain interest for industrial fisheries. Most studies are from the Northeast Atlantic followed by the Northwest Atlantic, the Southwest Pacific, and the Mediterranean Sea (Fig. 4.1b). This pattern has been reported for certain taxonomic groups such as parasitic copepods, isopods and digeneans with often more comprehensive information for the northern Atlantic than for other geographical areas (Boxshall 1998, Bray & Kuchta 2006, Smit et al. 2014, Bray et al. 2016).

No parasites have been recorded in 68.3% of the fish species assigned to the three families; the percentage of host species with at least one parasite varies between the families: 35.0% in centrophorids, 25.3% in etmopterids and 63.6% in notacanthids. However, the overall low number of records does not necessarily imply a low parasite infection in these families, but a low number of studies that were focussed on few host species. Studies on the parasite fauna of deep-sea fishes are scarce when compared with studies on commercially important species, especially from coastal and shelf waters (Klimpel et al. 2009). For example, a search in 'Web of Knowledge' for publications having 'Atlantic cod' and 'parasite' in the title revealed a result of 345 publications for the period from 1900 to 2017. Comprehensive information on the parasite fauna is more abundant for few deep-sea fish taxa like macrourids, which are exploited by fisheries (Palm & Klimpel 2008). Along with the lack of commercial interest, the low number of records can also be explained by the fact that scientific surveys in the deep-sea are hampered by logistical constraints, high costs, frequently few species and low sample availability (Cailliet et al. 2001, Klimpel et al. 2009). Additionally, even though notacanthids are considered a quite abundant fish family in some regions, they are fairly difficult to catch with deep-sea trawls owing to their elusive eel-like body shape, which impedes obtaining representative samplings (Coggan et al. 1998). The very low proportion of records of etmopterid species with at least one parasite species is also due to the higher number of species assigned to this family compared to the two other ones.

The low percentage of records herein reported may also be a result of an underestimation of studies as very few authors publish 'negative' results (no parasites found). The few studies presenting 'negative' results were mostly based on surveys with many host species but often low sample sizes (<10). Moreover, these surveys were conducted in order to find particular

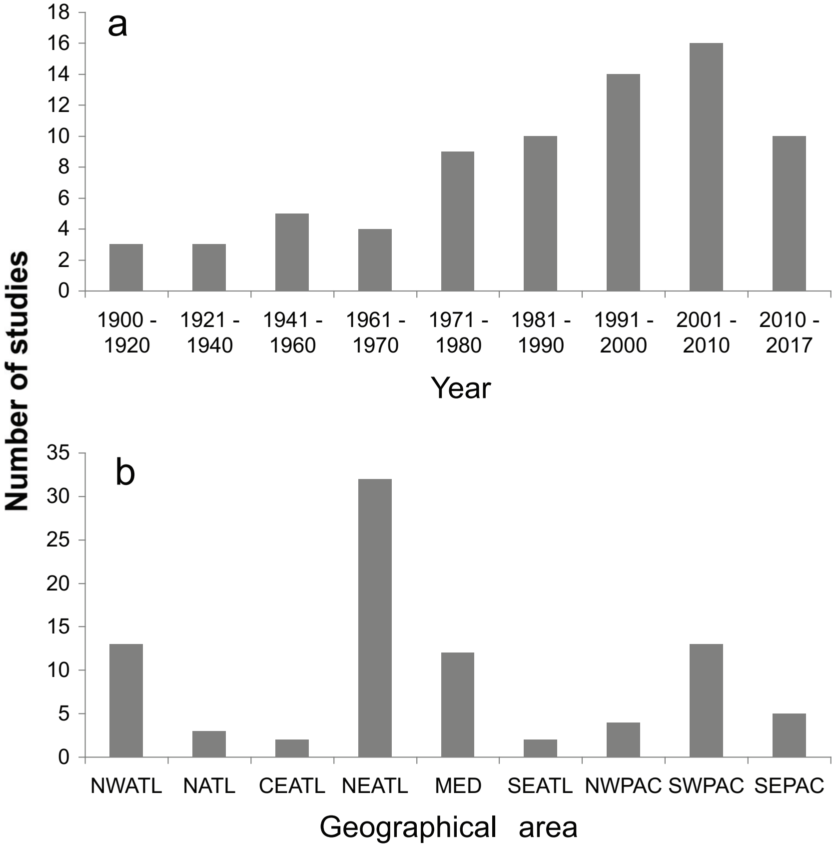

Fig. 4.1 - Published studies on parasites of fish hosts assigned to the families Centrophoridae, Etmopteridae and Notacanthidae, over the last century (a); among geographical areas within the same time frame (1900–2017) (b). Abbreviations: NWATL, Northwest Atlantic, NATL, North Atlantic, CEATL, Central Atlantic, NEATL, Northeast Atlantic, MED, Mediterranean Sea, SEATL, Southeast Atlantic, NWPAC, Northwest Pacific, SWPAC, Southwest Pacific, SEPAC, Southeast Pacific.

parasites or groups of parasites, or to examine particular sites or organs. For example, Bullard et al. (2006) analysed the heart of 17 shark species from the Gulf of Mexico for blood flukes (Trematoda: Aporocotylidae) and detected two shark species only, infected by these parasites. Among the 15 sharks species without aporocotylids two were etmopterids (*E. gracilispinis* and *E. hillianus*) which have not been found to be surveyed in any other study. A similar case is the study by Trilles & Justine (2004) on the presence of isopods (Aegidae) on deepwater shark species from New Caledonia, where *E. molleri* was recorded as 'not infected'. Some taxa listed in Table 4.1 were also recorded with 'negative results' in other studies (Rees 1946, Carvajal 1974, Pascoe 1987, Bullard et al. 2006, Caira & Pickering 2013, Kheddam et al. 2016). In general, 'negative results' are helpful to complete the information on the geographical distribution of parasites. The resulting dearth of information hampers to assess if the apparent poor parasite richness derives from impoverished parasite faunas or from an artefact arising from a low research effort. The publication of this kind of data would be useful as they do not only provide information about non-infected species, but also that a certain species was surveyed for parasites.

Along with environmental conditions which are discussed below, the low representation by external parasites may also partially be affected by parameters such as the sampling procedures, which could provoke their dislodgement (Kvach et al. 2016, Quattrini & Demopoulos 2016). This applies especially to fisheries such as trawls (Ross et al. 2001), where parasites could be lost easily through physical abrasion during the haul procedure, especially in commercial boats where hauls have to be processed quickly. However, this impact may vary between parasite taxa. Kalman (2006) indicated that the sampling on different demersal shallow water fish performed with trawls may have resulted in the low abundances of monogeneans and leeches observed on fish. In contrast, Rohde (1988) did not report any evidence for a loss of monogeneans during the haul procedures using trawls. Kalman (2006 and references therein) also concluded, that while samplings by trawls may bias the infrapopulations of parasitic isopods, copepods may be less affected as these are attached more firmly to the host. However, there are isopods living in the mouth or on gills (e.g. Cymothoidae) which are retained within the orobranchial chamber, while others detach rapidly after host capture (Gnathiidae, Lester 2005). Moreover, adaptations to the parasitic life, such as the thickened and calcified cuticule of cymothoids (Smit et al. 2014) probably make them less susceptible to pressure changes during sampling. Some authors also hint to fish stress related factors, which could have implications on the found ectoparasites observed on fish hosts (Kvach et al. 2016). Grutter (1995 and references therein) showed that some parasites detach from the host on capture and indicated that handling and capture can result in biochemical changes in the host which are likely to affect their parasites.

4.3 HIGHER TAXA GROUPS AND DOMINATING PARASITE FAMILIES

The three fish families exhibit fairly different proportions of taxonomic groups, where chondrichthyans were proportionally dominated by cestode species (59.4% Centrophoridae; 40.5% Etmopteridae), while in notacanthids digeneans represented half (50%) of all species recorded (Fig. 4.2 provides total numbers of species recorded). This agrees with suggestions made by other authors, who emphasized the exceptional difference between parasite faunas of elasmobranchs and teleosts, where former are dominated by cestodes whereas teleosts reveal a huge variety of monogeneans and digeneans (Campbell et al. 1980, Cribb et al. 2002). Cestodes are of minor importance in notacanthids (12.5%), similar to digeneans in chondrichthyan families (no species, 8.1%). Monogenean species are recorded in all fish families with lowest proportion of all recorded parasite species in Centrophoridae (6.3%) and the highest in Notacanthidae (16.7%). Nematodes show similar proportions of recorded species between the three families [from 12.95% (Centrophoridae) to 16.7% (Notacanthidae)]. No copepods have been recorded in notacanthids, while species of this taxon represent 15.6% and 21.6% of recorded species for centrophorids and etmopterids, respectively. Similarly, isopods are detected in all families in low proportions [from 2.7% (Etmopteridae) to 6.3% (Centrophoridae)] while cirripedian (barnacles) and amphipods are represented in Etmopteridae only.

With respect to the parasite families, all three fish groups show a distinctly different composition considering the six most represented taxa groups (Fig. 4.3). But in all fish families ectoparasitic families are less numerous than the endoparasitic ones. Reviewing studies on marine parasites in deep-sea fishes and invertebrates, de Buron & Morand (2004) reported that monogeneans have been recorded only in waters in depths up to 1,000 m. Copepods show a distinctly higher diversity and were also recorded in depths up to 6,000 m (de Buron & Morand 2004) and some isopods were detected in > 3,000 m (Quattrini & Demopoulos 2016). Factors such as host density, schooling behaviour, susceptibility to infection, and cleaner fish density can influence the degree of infection by monogeneans or other ectoparasites (Grutter 1998, Sasal 2003, Raeymaekers et al. 2008, Sikkel et al. 2009).

Usually, monogeneans are considered as particularly scarce in deeper waters (Campbell et al. 1980, Campbell 1990). Host densities and abundances and to a lesser extent environmental conditions are regarded as main factors for the observed lower abundance and diversity of monogeneans in the deep-sea (Bray et al. 1999). Considering monogenean families, the Hexabothriidae (restricted to chondrichthyans according to Boeger & Kritsky 1989) are found in both shark families, being the only monogenean family reported in centrophorids.

Three more families with one taxon each are recorded in etmopterids. Cribb et al. (2002) listed eight families of monogeneans occurring regularly in chondrichthyans, including Hexabothriidae, Microbothriidae and Monocotylidae, all three recorded for etmopterids (Table 4.1, Fig. 4.3). The Microbothriidae are regarded as specialist

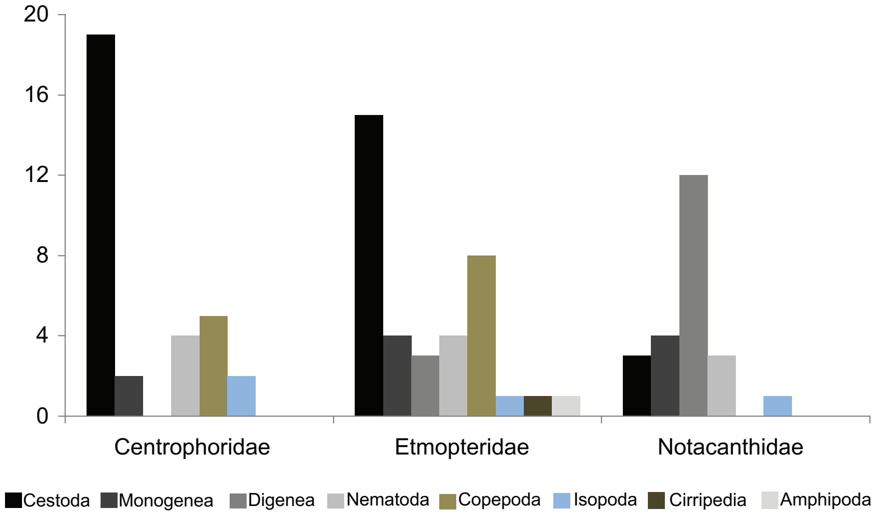

Fig. 4.2 - Species number for taxonomic higher parasite groups observed in the three fish families.

parasites infecting the placoid scales in elasmobranchs, whereas the Monocotylidae are described as ectoparasites on skin, gills and nasal cavities but also as endoparasites in cloaca or rectal glands (Cribb et al. 2002 and references therein). One species of Diclidophoridae has been reported in etmopterids and another in notacanthids. In

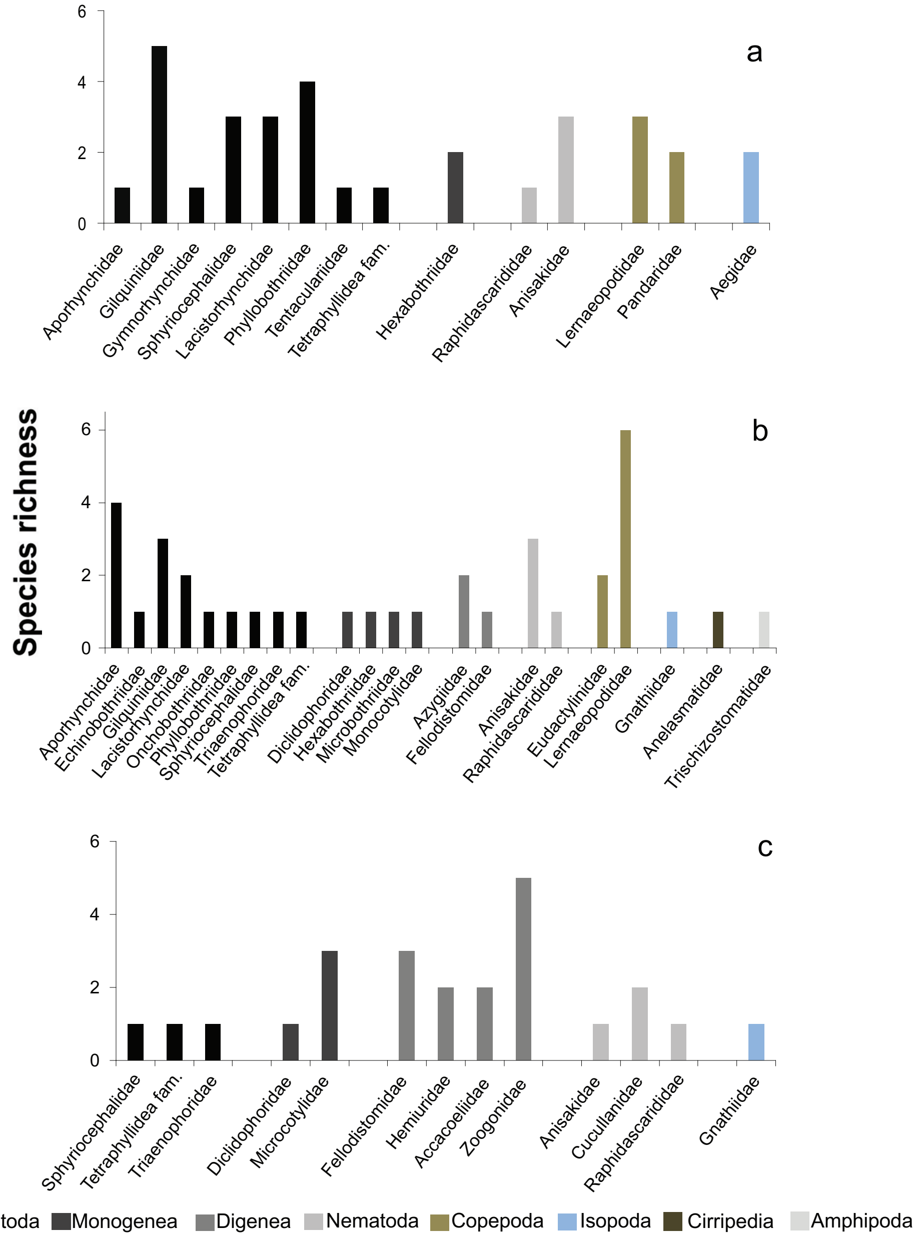

Fig. 4.3 - Total number of records for each parasite family observed in host species of the families Centrophoridae, (a); Etmopteridae, (b); Notacanthidae, (c).

distinct surveys from different geographical areas, species of the Diclidophoridae were found most frequently in deep-sea fishes (e.g. Campbell et al. 1980, Rohde 1988, Ñacari & Oliva 2016). Finally, three microcotylids parasitize notacanthids, a group of parasites only recorded in marine teleosts (Yamaguti 1963, Mamaev 1986).

Most species of copepods observed in the two chondrichthyan families are assigned to the Lernaeopodidae, which confirms the suggestion by Boxshall (1998) that amongst others, this family is most commonly encountered on deep-sea fishes (fin fishes and chondrichthyans), although it is represented by few genera. Underwater videos by Remote Operated Vehicle (ROV) surveys in the deep-sea of the northwestern Atlantic confirmed the frequent occurrence of Lernaeopodidae (Quattrini & Demopoulos, 2016). Boxshall (1998) referred especially to the lernaeopodid genera *Lernaeopodina* and *Clavella*, where species of the former are recorded on different chondrichthyans and one Alepocephalidae (fin fish), whereas species of *Clavella* occur on the more abundant fin fish family, Macrouridae (Castro & González 2009). Altogether, the Lernaeopodidae exhibit an overall wide range of hosts in the deep-sea, which explains also the records on centrophorids and etmopterids presented in this chapter. No copepods are reported in nothacanthids. Boxshall (1998) already indicated that, curiously no copepods have been recorded in the Halosauridae, despite this is a fish family highly represented in the deep-sea; interestingly together with Notacanthidae this family constitutes the order Notacanthiformes. In general, Boxshall (1998) suggested that in order to compensate the low host densities, copepods may benefit from host behaviour aggregating during mating or around food resources. This could apply to deep-sea sharks which partly feed opportunistically or scavenge (Jones et al. 2003, Cartes et al. 2016). However, in case of notacanthids, due to their feeding habits, a similar behaviour is not expected.

Other ectoparasites recorded in all three fish families were isopods, represented by the families Aegidae and Gnathiidae (Table 4.1). During their deep-sea surveys with ROVs Quattrini & Demopoulos (2016) also observed Aegidae and Gnathiidae, occurring most frequently on diverse deepwater fishes, together with Cymothoidae. The authors stressed that the Gnathiidae were observed even in deepest sampling stations (>3,000 m) and argued that this family infects a wide range of diverse deep-sea fishes, both chondrichthyans and ostheichthyans, as in present study (in etmopterids and notacanthids). The single record of a Cymothoidae in the mouth of *Etmopterus* sp. was considered as accidental infection (Williams et al. 2010). Aegidae and Gnathiidae are often considered as micropredators or commensals rather than parasites (Grutter & Poulin, 1998, Smit et al. 2014), however many symbiotic relationships are difficult to assign to a certain category (Leung & Poulin 2008).

Parasitation by species of two peculiar ectoparasite groups have been reported in the Etmopteridae, as they belong to crustacean taxa not often reported as fish parasites: amphipods and cirripeds. The amphipod *Trischizostoma raschi* is frequently observed on *Etmopterus spinax* in Norwegian fjords with one or more specimens attached mainly to the head or fins (R. Svensen pers. com. Fig. 4.4 A, B), while reports from other locations are scarce (Bousfield 1987). The barnacle *Anelasma squalicola* (Cirripedia, Fig. 4.5 A, B) is considered as mesoparasite recorded for species of the genus *Etmopterus*. Other specimens of *Anelasma* sp. were recorded also from *Centroscyllium* spp., although they were not classified to species level (Yano & Musick 2000, Rees et al. 2014).

With respect to the endoparasitic families the cestodes represent the most diverse group within the two chondrichthyan families, whereas in notacanthids they were of minor importance (Table 4.1, Fig. 4.3). Only one cestode species is described as adult in notacanthids, *Bathycestus brayi* Kuchta & Scholz, 2004 (Triaenophoridae), and the remaining ones are larval stages, which are generalist found in deep-sea fishes and invertebrates (e.g. Klimpel et al. 2008, Klimpel et al. 2009, Mateu et al. 2014, Constenla et al. 2015, Dallarés et al. 2017). Cestodes are suggested to be the most diverse metazoan parasite group in elasmobranchs (Caira & Healy 2004) and here they showed the highest species representation in the Centrophoridae and Etmoperidae with the trypanorhynchs Aporhynchidae, Gilquiniidae and Lacistorhynchidae and larval Tetraphyllidea fam. gen. sp. Most cestode families found in both elasmobranch families are assigned to the order Trypanorhyncha (73%) which agrees with Caira & Pickering (2013). These authors already observed dominance of this order among the poor cestode fauna in squaliform deep-sea sharks, being gilquiniids and aporhynchids the most frequent, together with larval tetraphyllideans. Considering its phylogeny, Palm et al. (2009) indicated that lacistorhynchids (Trypanorhyncha) are present in the deep-sea due to host switching from their second intermediate hosts in more shallow waters, gadids, to those mainly in deeper waters, macrourids, which also results in infections of deep-sea squaliforms.

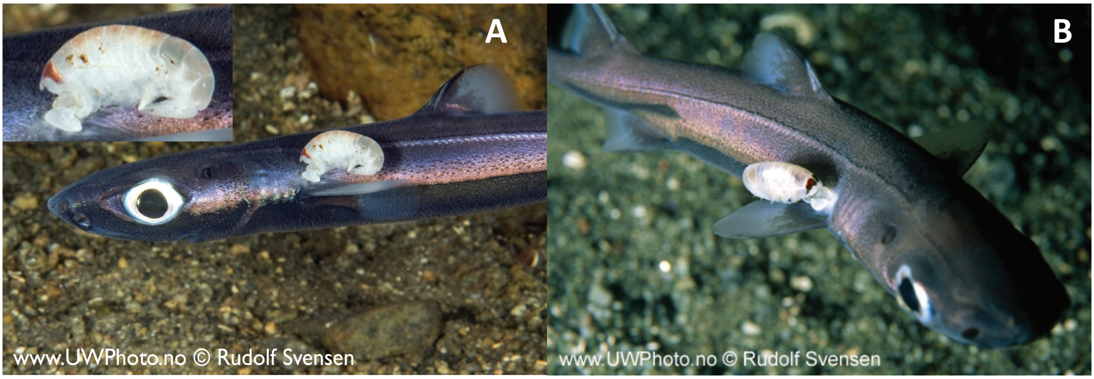

Fig. 4.4 - *Trischizostoma raschi* (Amphipoda) on two *Etmopterus spinax*, Norway. Lateral (A) and anterolateral views (B), with detail of the parasite in 'A'. Source: R. Svensen.

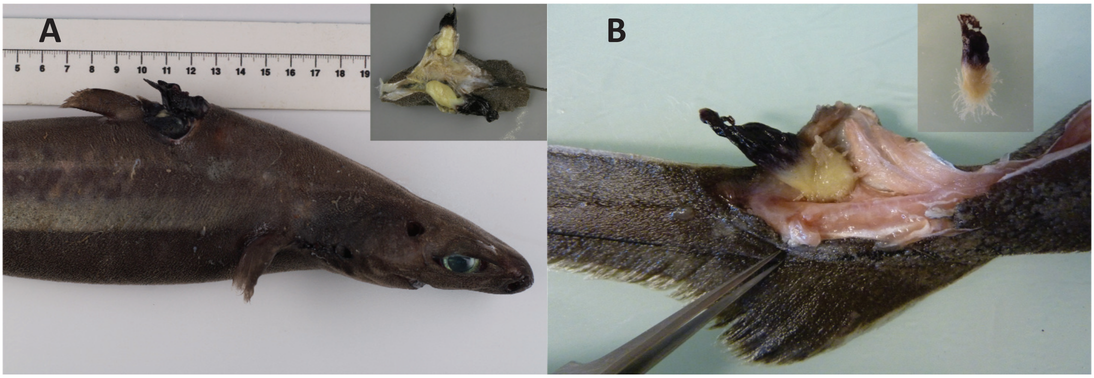

Fig. 4.5 - *Anelasma* sp. (Cirripedia) on *Etmopterus spinax*, off Ireland (A) (Image by C. Rodríguez-Cabello, W. Isbert) and off Scotland (B) (Image by W. Isbert).

Most of the studies on trematodes in deep-sea fish refer to digeneans, which also include most of the species of the class. The subclass Aspidogastrea includes very few species, not recorded in any of the three families analysed in this chapter. Similar to the high diversity of cestodes in chondrichthyans, digeneans are the dominating endoparasites in deep-sea teleosts (Campbell et al. 1980, Cribb et al. 2002), although several authors suggest that digeneans are even more diverse in shallow waters (Bray et al. 1999, Bray 2004a). The reports regarding digeneans in notacanthids include four different families, with the Zoogonidae representing the highest species number (Fig. 4.3). Overall, this agrees with the observations from previous publications including Zoogonidae as one of the families present in the deep-sea. Others such as as Hemiuridae and Fellodistomidae also found in notacanthids, are reported as even more frequent in this environment (Campbell et al. 1980, Bray et al. 1999) (Table 4.1, Fig. 4.3). Centrophorids did not had any digenean taxon, while for etmopterids very few species of two families (Azygiidae and Fellodistomidae) were reported, with most of the individuals assigned to the genus *Otodistomum* (Azygiidae). Revising different aspects of this subclass, Cribb (2005) commented that few families of digeneans are found in chondrichthyans and, some of them are considered accidental (Bray & Cribb 2003, Caira & Healy 2004). Cribb (2005) also noted that one of the more common families recorded in this fish group are the Azygiidae. Other authors confirmed this and considered Azygiidae together with four other families as ‘long-term’ parasites occurring regularly in elasmobranchs (Cribb et al. 2002, Bray & Cribb 2003). The low representation of digeneans in elasmobranchs was also recorded when revising all infections by digenean species in the Mediterranean fish fauna (192 species in 76 families) (Pérez-del-Olmo et al. 2016). Over all infected fishes, elasmobranch species infected by a digenean accounted for 6.6 % only.

The nematode families reported in all three families comprise the same taxa (Anisakidae, Raphidascaridae), with an additional family (Cucullanidae) in notacanthids (Table 4.1, Fig. 4.3). All three parasite families can occur regularly in elasmobranchs and teleosts, even from the deep-sea (e.g. Caira & Healy 2004, Klimpel et al. 2009, Moravec & Justine 2011). The occurrence of anisakids is still considered to be rare or accidental in elasmobranchs however, records for this family in this fish group are increasing probably due to the increasing number of studies in the last two decades (e.g. Palm & Schröder 2001, Henderson et al. 2002, Klimpel et al. 2003, Costa et al. 2014). Overall, in all three families the nematodes were poorly represented, which agrees with the observations in some deep-sea teleosts (*Halosauropsis macrochir* Halosauridae, *Lepidopus caudatus* Trichiuridae; Klimpel et al. 2006b, 2008). However, nematodes have been found to be more diverse in other deep-sea teleosts and elasmobranchs as *Macrourus berglax* (Macrouridae) or *Galeus melastomus* Pentanchidae) (Klimpel et al. 2006a, Dallarés 2016). The single record of specimens of the Schistorophinae (Acuariidae) in centrophorids from the Great Meteor Bank (Palm & Schröder 2001) is probably accidental, as definitive hosts are fish-eating birds (Moravec 1994), and gulper sharks would be a dead-end for the parasite life cycle.

4.4 SPECIALISTS *VS* GENERALISTS

The specialist or generalist strategy of a parasite species is defined by the narrower o wider range of host species which it can infect (Lymbery 1989 in Sasal et al. 1999). In this study a parasite species has been defined as specialist when it occurs in one host species, and a genus specialist would be those recorded in more than one host species of the same genus. The family generalist would define a parasite recorded from at least two species of the same family but distinct genera, whereas a generalist parasite would not be restricted to a single species, genus or family. In regard to the overall proportions of specialist and generalist parasite taxa among the fish families herein studied are fairly distinct: more than half (57.9%) are specialists in Notacanthidae, more than two thirds (69.6%) are generalist species in Centrophoridae, and in Etmopteridae the ratio between specialist (including genus specialist) and generalist is balanced (50%)(Fig. 4.6).

More generalist parasites are expected in the deep-sea as host densities are supposedly lower than in shallow waters. However, for some ectoparasite taxa such as copepods the deep-sea seems not to be a challenge, as their specificity levels are comparable to those found in coastal or shelf waters (Boxshall 1998). Quattrini & Demopoulos (2016) also observed that in deep-sea fishes copepods were more specific than other crustaceans such as the gnathiid isopods, which are considered generalists. For both authors these observations mirror the patterns recorded for these taxa in shallow waters, and do not exhibit a modified specialist-generalist ratio as a result of the distinct environment. Regarding Gnathiidae, the status of host specificity is unclear as some species apparently are more specific in elasmobranchs (Grutter & Poulin 1998).

Occurrence and diversity of monogeneans decrease from shallow coastal to deep waters (Rohde 1988); fish host densities from the lower slope downwards are supposed to be too low for a successful transmission of monogeneans (Campbell et al. 1980). However, in this study monogeneans contribute to the high quantity of specialists reported for notacanthids and both elasmobranchs, and species of these taxa usually are considered to be highly host specific (Sasal et al. 1999 and references therein). Some authors pointed to the higher richness of host specific monogeneans in long-lived hosts exhibiting a stable life history (Sasal et al. 1999), which is also the case for many species of the three families studied here. Additionally, Cribb et al. (2002 and references therein) hint to the close association between monogeneans and the many different fish host microhabitats, which allow fish to harbour several highly specialised parasites. For example, in gill monogeneans (e.g. hexabothriids or microcotylids) clamp size and shape is highly adapted to the gill topography (Hayward 2005). Further, some species of these families are specialised on placoid scales or nasal cavities of elasmobranchs, or even to uncommon sites for monogeneans as cloaca or, inner wall of body cavity (Cribb 2005).

Digeneans are considered fairly host specific in the adult stage (Campbell 1990 and references therein) and in the present study, they are

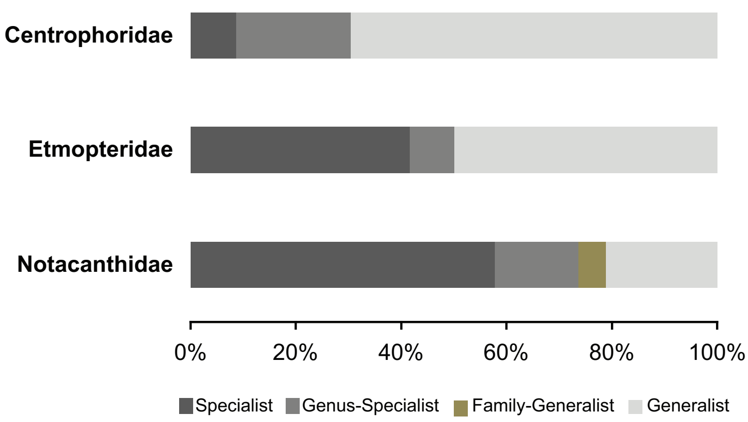

Fig. 4.6 - Proportion (in per cent) over all species between levels of specificity for each fish family.

represented by several specialist taxa particularly recorded for notacanthids. As stated above, digenean species dominate in the records for this family mostly being specialists (63.6%), or at least genus specialist (18.2%) and few taxa were family generalist and generalist (9.1% each). In part, this is comparable with studies on other deep-sea fin fishes where the majority of host specific parasites were digeneans (Palm & Klimpel 2008, Klimpel et al. 2008). Life cycles of digeneans can also be favoured in benthic habitats as they generally include gastropods and bivalves as obligate first intermediate hosts (Cribb 2005). Notacanthids have mainly epi- and suprabenthic feeding habits, where they get close to wide range of potential second intermediate benthic hosts (Campbell et al. 1980, Klimpel et al. 2008), as suggested for other fishes e.g. macrourids (Palm & Klimpel 2008).

The main part of specialists or genus specialists found for the chondrichthyans are adult cestodes. Records on cestodes within the Etmopteridae indicate a balanced proportion between species and genus specialists (45.5 and 9.0%) and generalists (45.5%). This is mainly due to the trypanorhynch contribution in this family: firstly, the Aporhynchidae with four specialists (*Aporhynchus* spp.), which infect three *Etmopterus* spp., showing a strong link between host and parasite genera; secondly, gilquiniid species which infect hosts from different genera, found here as larvae and adults in both elasmobranchs. This proportion is fairly different compared to the Centrophoridae, where very few specialists were recorded (5.9%) and genus specialist and generalists showed the highest proportions (35.3 and 58.8%, respectively). Especially the species of the genus *Deanicola* (Gilquiniidae) infect several host species from the same genus. The lower proportion of specialists detected in centrophorids compared to etmopteridae could partly be explained by cestodes infecting sharks of this family as larvae, and these stages often show a distinctly lower host specificity than adult stages. In regard to the adult cestodes, Campbell et al. (1980) indicated that when comparing parasite communities of elasmobranchs they showed low indices of similarity owing to the high host specificity of adult cestodes. This might be supported by the fact that seven tapeworm orders of the valid 17 are parasitizing elasmobranchs as adult (Caira et al. 2012). This is somewhat different when referring to larval stages, even to final metacestodes such as plerocercoids, plerocerci or merocercoids as these are considered to be less host specific (Palm & Caira 2008) infecting a huge range of fin fish and elasmobranchs. The representation of more generalist taxa in centrophorids could also reflect a more benthopelagic and opportunistic feeding habits, which is suggested for some shark species of this family (Preciado et al. 2009, Costa et al. 2014). Further, these species often grow larger than etmopterids (see above) providing a broader prey range due to gape size and potentially larger home ranges (Marcogliese 2002, Cirtwill et al. 2016 and references therein). The association between generalist feeders and low host specific parasite species was already observed for fish species in the Arctic deep-sea (Klimpel et al. 2006a, Chambers 2008). The latter author indicated that this tendency occurs for large numbers of generalist feeders in areas, such as the Arctic deep-sea, where the presence of prey species is low and where a lesser niche specialisation exists. Moreover the proportion of non-host specific parasites in deep-sea fishes is supposed to be related to their proximity to the sea bed, where benthopelagic fishes are supposed to feed on more diverse prey and being infected by a larger number of non-host specific parasites than the more strictly benthic species (Chambers & Dick 2005). Therefore, the supposedly more diverse diet in species of both elasmobranch families might explain the higher proportions of generalist parasites, mainly larval cestodes and nematodes. As larval stages, both parasite groups often infect a broad range of invertebrates, teleosts and chondrichthyans as intermediate or paratenic host. Along with the larval tetraphyllideans, also found in notacanthids, larval trypanorhynchs can be found frequently in elasmobranchs (Costa et al. 2014, Dallarés 2016; see also **Chapters 7, 8** and **9**).

Nematodes are recorded for all three fish families, with cucullanids listed only for the notacanthids, while Anisakidae or Raphidascaridae are found in all fish families. Both nematode families have been recorded more frequently in centrophorids and etmopterids occurring as larval stages. Several fish species from the deep-sea with pelagic and benthopelagic feeding habits exhibit larval stages of these very host unspecific nematode families, mainly represented by *Anisakis* spp. and *Hysterothylacium* spp. (e.g. Klimpel et al. 2008, Mateu et al. 2014, Constenla et al. 2015, Pérez-i-García et al. 2015).

4.5 MONOXENOUS *VS* HETEROXENOUS AND DEFINITIVE *VS* INTERMEDIATE

Concerning their life cycle complexity of the parasites of the three fish families in Table (4.1), the composition of the parasite communities is similar; the majority of parasites are heteroxenous: 73.3 heteroxenous *vs* 26.7% monoxenous in Centrophoridae, 61.2 *vs* 38.8% in Etmopteridae and 79.2 *vs* 20.8% in Notacanthidae (both chondrichthyan families combined 65.6 *vs* 35.4%). Most heteroxenous parasites infecting these fishes are transferred via trophic web (Locke et al. 2014). The overall higher proportion of monoxenous parasites in Etmopteridae compared to both other fish families is partly explained by the higher diversity of parasite groups (9 families) with direct life cycles, two of them exclusive of the Etmopteridae (see above in 4.3).

As already stressed in former studies, the diversity and number of parasite species found in a host in part depends on ecological factors such as host size, prey selectivity, number of consumed prey, habitat or host range (Poulin 2000, Cirtwill et al. 2016). Monoxenous parasites are mostly external and, as previously stated, these parasites are especially scarce in the deep-sea. At the same time, a higher parasite richness and diversity of heteroxenous parasites is often considered as strongly associated with a broader diet range in contrast to narrow prey ranges (e.g. Locke et al. 2014, Cirtwill et al. 2016 and references therein). Further, in relation to the trophically transmitted parasites, Marcogliese (2002) suggested that fish species being positioned towards the middle food-web should exhibit the highest parasite diversity as they can act as intermediate and definitive hosts. Trophic levels calculated for some species of the centrophorids and etmopterids assign them to upper trophic positions as secondary to tertiary (trophic level 3.5–4.2) consumers, where other families e.g. Hexanchidae and Lamnidae had higher values (4.7 and 4.5, respectively) (Cortés 1999). Further, the abundance and richness of heteroxenous parasites in a host is explained by the diversity of possible intermediate hosts sharing heteroxenous life cycles (Cirtwill et al. 2016 and references therein). It is supposed that these parameters are higher in hosts from benthic and benthopelagic habitats, compared to more pelagic species (Marcogliese 2002). These patterns agree with the higher percentage of heteroxenous parasites in all three families, and especially for the notacanthids, with more benthic habits than centrophorids or etmopterids. However, although nothacantids show mostly benthic feeding habits, they seem to be less susceptible to be infected by a wide range of parasites than other benthic fishes. This might be due to their particular specialised diet, with mainly epi- or suprabenthic preys, many of them not frequently found as intermediate hosts in parasite life cycles (actinians, coral polyps, echinoderms) (Coggan et al. 1998, Carrassón & Matallanas 2002, Rodríguez-Romeu et al. 2016). This low contribution to parasite life cycles is interesting especially when considering that notacanthids have often been reported as most common at local/regional scale (Coggan et al. 1998, Carrassón & Matallanas 2002). Compared to this, species of both elasmobranchs families show a

Table 4.1 - Checklist of the metazoan parasites of Centrophoridae, Etmopteridae, Notacanthidae. **Abbreviations:** M-monoxenous, H-heteroxenous, L-Larva, A-Adult **(life cycle and life stage)**; S-specialist, GS-genus specialist; FG-family generalist; G-generalist (**host specificity)**; bc-buccal cavity, gi-gills, in-intestine, inw-intestine wall, cla-clasper, liv-liver, mo-mouth, mus-muscle, nc-nasal cavity, pc-pyloric caeca, spin-spiral intestine, sto-stomach, stow-stomach wall, sk-skin **(site of infection)**; CEA-Central East Atlantic Ocean, CAN-Central North Atlantic Ocean, CWA-Central West Atlantic Ocean, CWP-Central West Pacific Ocean, CMed-Central Mediterranean Sea, Med-Mediterranean Sea, NA-North Atlantic Ocean, NEA-Northeast Atlantic Ocean, NOS-North Sea, NWA-Northwest Atlantic Ocean, NWP-Northwest Pacific Ocean, SAIO-Southern Atlantic Ocean/Indian Ocean, SEA-Southeastern Atlantic Ocean, SEP-Southeastern Pacific Ocean, SO-Southern Ocean, SWP-Southwestern Pacific Ocean, WMed-Western Mediterranean (**locality area).**

Host species	Classification		Parasite species	Life cycle	Life stage	Host specificity	Site of infection	Locality	Source
Squaliformes: Centrophoridae									
***Centrophorus* sp.**	Platyhelminthes: Cestoda	Gymnorhynchidae Dollfus, 1935	*Chimaerarhynchus rougetae* Beveridge & Campbell, 1989	H	A (immature)	S	spin	CEA (Senegal)	Beveridge & Campbell 1989
		Gilquiniidae Dollfus, 1935	*Gilquinia minor* Beveridge & Justine, 2006	H	A	GS	spin	SWP (New Caledonia)	Beveridge & Justine 2006
			Sagittirhynchus aculeatus Beveridge & Justine, 2006	H	A	GS	spin	SWP (New Caledonia)	Beveridge & Justine 2006
		Fam. incertae sedis	Tetraphyllidea fam. gen. sp.	H	A	-	spin	SWP (New Caledonia)	Beveridge & Justine 2006
Centrophorus granulosus (Bloch & Schneider, 1801)	Platyhelminthes: Cestoda	Phyllobothriidae Braun, 1900	*Calyptrobothrium riggii* Monticelli, 1893	H	A	-	spin	CMed	*Bilocularia hyperapolytica* Obersteiner, 1914
		Sphyriocephalidae Pintner, 1913	*Sphyriocephalus viridis* (Wagner, 1854) Pintner 1913	H	A	G	sto	global distribution	Dallares et al. 2017
	Platyhelminthes: Monogenea	Hexabothriidae Price, 1942 Price, 1942	*Squalonchocotyle centrophori* Maillard, 1970	M	A	S	gi	Med	Maillard 1970 in Kheddam et al. 2016
	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	*Neoalbionella longicaudata* (Hansen, 1923)	M	A	-	sk	NEA (off northern Spain)	Fernández-Ovies 1992
			Eudactylina vilelai Nunes-Ruivo, 1956	M	A	G	-	SEA (Angola)	Nunes-Ruivo 1956 (in Dippenaar 2005)
Centrophorus moluccensis (Bleeker, 1860)	Platyhelminthes: Cestoda	Gilquiniidae Dollfus, 1935	*Gilquinia robertsoni* Beveridge, 1990	H	A	G	spin	SO (South Australia)	Beveridge 1990
Centrophorus squamosus (Bonnaterre, 1788)	Platyhelminthes: Cestoda	Lacistorhynchidae Guiart, 1937	*Grillotia erinaceus* (van Beneden, 1858) Guiart, 1927	H	L	G	spin	NEA (Porcupine; prob. global distribution)	Rees & Llewellyn 1941
		Lacistorhynchidae Guiart, 1937	*Grillotia dolichocephala* Guiart, 1935 (species inquerenda in WORMS)	H	L	G	-	NEA (Bay of Biscay)	Beveridge & Campbell 2013
		Tentaculariidae Poche, 1926	*Tentacularia coryphaenae* Bosc, 1802	H	L	G	sto	NEA (Portugal, Madeira)	Costa et al. 2014
		Gilquiniidae Dollfus, 1935	Gilquiniidae gen. sp.	H	L	-	sto, spin	NEA (Portugal, Madeira)	Costa et al. 2014
		Fam. incertae sedis	Trypanorhyncha fam. gen. sp.	H	L	-	sto	NEA (Portugal, Madeira)	Costa et al. 2014
		Fam. incertae sedis	Tetraphyllidea fam. gen. sp.	H	A (immature)	-	sto, spin	NEA (Portugal, Madeira)	Costa et al. 2014
	Nematoda: Ascaridoidea	Anisakidae Skrjabin & Karokhin, 1945	*Anisakis simplex* (Rudolphi, 1809)	H	L	G	sto	NEA (Portugal, Madeira)	Costa et al. 2014
			Pseudoterranova ceticola (Deardorff & Overstreet, 1981)	H	L	G	sto	NEA (Portugal, Madeira)	Costa et al. 2014
	Nematoda (incertae sedis)	Fam. incertae sedis	Nematoda fam. gen. sp.	H	L	-	sto	NEA (Portugal, Madeira)	Costa et al. 2014
	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	*Lernaeopodina longibrachia* (Brian, 1912)	M	-	G	-	Med	Brian (1913) in Boxshall 1998
		Pandaridae Milne Edwards, 1840	*Dinemoura ferox* (Krøer, 1938)	M	-	G	-	NEA (Iceland)	Stephensen 1940 in Ho et al. 2003
	Crustacea: Cymothooidea	Aegidae White, 1850	*Aega monophthalma* Johnston, 1834	M	-	-	-	NEA / North and Baltic Sea*/ Greenland†	Hansen (1916)†, Nierstrasz & Stekhoven (1930)* (all from Moreia & Sadowsky 1978)
			Aega bicarinata Leach, 1818	M	-	-	-	NEA / North and Baltic Sea* / Iceland/Greenland†	Hansen (1916)†; Nierstrasz & Stekhoven (1930)*; Stephensen (1937) †(all from Moreira & Sadowsky 1978)
Centrophorus uyato (Rafinesque, 1810)	Platyhelminthes: Monogenea	Monocotylidae Taschenberg, 1879	*Calicotyle* sp. (most probably *C. palombi*)	M	A	accidental infec.	rec, cl	WMed	Euzet & Williams, 1960 (see also Chisholm et al. 1997)
	Crustacea: Siphonostomatoida	Pandaridae Milne Edwards, 1840	*Echthrogaleus coleoptratus* (Guérin-Méneville, 1837)	M	-	G	-	Med / prob. global distribution (Pratt et al. 2010)	Raibaut et al. 1998

Table 4.1 - (cont.)

Host species	Classification		Parasite species	Life cycle	Life stage	Host specificity	Site of infection	Locality	Source
Squaliformes: Centrophoridae									
Deania calcea (Lowe, 1839)	Platyhelminthes: Cestoda	Phyllobothriidae Braun, 1900	*Clistobothrium carcharodoni* Dailey & Vogelbein, 1990	H	L	G	spin	NEA (Azores)	Caira & Pickering 2013
			Clistobothrium montaukensis Ruhnke, 1993	H	L	G	spin	NEA (Azores)	Caira & Pickering 2013
		Gilquiniidae Dollfus, 1935	*Deanicola minor* Beveridge, 1990	H	A	GS	spin	SWP (New Zealand)	Beveridge 1990
			Deanicola minor Beveridge, 1990	H	A	GS	spin	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
			Deanicola protentus Beveridge, 1990	H	A	GS	spin	SWP (New Zealand)	Beveridge 1990
			Deanicola sp.	H	A	-	spin	NEA (Azores)	Caira & Pickering 2013
		Sphyriocephalidae Pintner, 1913	*Hepatoxylon megacephalum* (Rudolphi, 1819)	H	L	G	bc, in	SWP (New Zealand)	Waterman & Sin 1991
			Hepatoxylon trichiuri Holten, 1802	H	L	G	bc, in	SWP (New Zealand)	Hewitt & Hine 1972, Waterman & Sin 1991
		Tentaculariidae Poche, 1926	*Tentacularia coryphaenae* Bosc, 1802	H	L	G	sto, stow	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
		Fam. incertae sedis	Cestoda fam. gen. sp.	H	-	-	spin	NEA	Hennemann 1985
	Nematoda: Ascaridoidea	Anisakidae Skrjabin & Karokhin, 1945	*Anisakis* sp.	H	L	-	sto	SWP (New Zealand)	Hewitt & Hine 1972, Hine et al. 2000
			Anisakis sp. Type I (Type: Koyama et al. 1969)	H	L	-	sto, stow	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
	Nematoda (incertae sedis)	Fam. incertae sedis	Nematoda fam. gen. sp.	H	-	-	stomach	NEA	Mauchline & Gordon 1984
Deania hystricosa (Garman, 1906)	Platyhelminthes: Cestoda	Gilquiniidae Dollfus, 1935	*Deanicola minor* Beveridge, 1990	H	A	GS	spin	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
			Deanicola protentus Beveridge, 1990	H	A	GS	spin	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
		Lacistorhynchidae Guiart, 1937	*Grillotia acanthoscolex* Rees, 1944	H	L	G	sto, inw, mus	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
		Phyllobothriidae Braun, 1900	*Crossobothrium* sp.	H	A	-	in	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
	Platyhelminthes: Monogenea	Hexabothriidae Price, 1942	Hexabothriidae gen. sp.	H	A	-	gi	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
	Nematoda: Ascaridoidea	Anisakidae Skrjabin & Karokhin, 1945	*Anisakis* sp. Type I & II (Type: Koyama et al. 1969)	H	L	-	sto, stow, in	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
	Nematoda: Acuarioidea	Acuariidae: Schistorophinae	Schistorophinae gen. sp.	H	L	-	stow	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
	Crustacea: Isopoda	Fam. incertae sedis	Cymothooidea fam. gen. sp. (reported as Flabellifera fam. gen. sp.)	M	L	-	gi	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
Deania profundorum (Smith & Radcliffe, 1912)	Platyhelminthes: Cestoda	Gilquiniidae Dollfus, 1935	*Deanicola minor* Beveridge, 1990	H	A	GS	spin	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
			Deanicola protentus Beveridge, 1990	H	A	GS	spin	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
			Deanicola sp.	H	A	-	sto, spin	NEA (off northern Spain)	present study
		Lacistorhynchidae Guiart, 1937	*Grillotia meteori* Palm & Schröder, 2001 (species inquerenda in WORMS)	H	L	GS	stow, inw, mus, liv	CEA (Great Meteor Bank)	Palm & Schröder 2001 (junior syn. Beveridge & Campbell 2013)
			Grillotia acanthoscolex Rees, 1944	H	L	G	stow, inw	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
			Grillotia sp.	H	L	-	stow, inw, mus, liv	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
		Tentaculariidae Poche, 1926	*Tentacularia coryphaenae* Bosc, 1802	H	L	G	stow	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
		Aporhynchidae Poche, 1926	*Aporhynchus* cf. *menezesi* Noever, Kuchta, Caira, Desjardins, 2010	H	A (immature)	S	spin	NEA (off northern Spain)	present study
			Aporhynchus sp.	H	A (immature)	S	spin	NEA (Azores)	Caira & Pickering 2013

Table 4.1 - (cont.)

Host species	Classification		Parasite species	Life cycle	Life stage	Host specificity	Site of infection	Locality	Source
Squaliformes: Centrophoridae									
Deania profundorum (Smith & Radcliffe, 1912)	Platyhelminthes: Cestoda	Sphyriocephalidae Pintner, 1913	*Sphyriocephalus* sp.	H	L	-	sto	NEA (off northern Spain)	present study
		Lacistorhynchidae Guiart, 1937	Lacistorhynchidae gen. sp	H	L	-	sto, spin, mus	NEA (off northern Spain)	present study
		Fam. incertae sedis	Tetraphyllidea fam. gen. sp.	H	L	-	liv, spin	NEA (off northern Spain)	present study
	Platyhelminthes: Monogenea	Hexabothriidae Price, 1942	*Squalonchocotyle spinaci* (Goto, 1894)	M	A	S	gi	NEA (off northern Spain)	present study
		Monocotylidae Taschenberg, 1879	*Squalotrema* sp.	M	A	-	nc	NEA (off northern Spain)	present study
	Nematoda: Ascaridoidea	Anisakidae Skrjabin & Karokhin, 1945	*Anisakis* sp. Type I (*sensu* Berland, 1961)	H	L	-	liv, mus, stow, inw, go, ki	NEA (off northern Spain)	present study
			Anisakis sp. Type I (sensu Koyama et al., 1969)	H	L	-	stow, inw, spinw	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
		Raphidascarididae Hartwich, 1954	*Hysterothylacium* sp.	H	L	-	sto, spin	NEA (off northern Spain)	present study
	Nematoda: Acuarioidea	Acuariidae: Schistorophinae	Schistorophinae gen. sp.	H	L	-	stow	CEA (Great Meteor Bank)	Schröder 1999, Palm & Schröder 2001
D. cf. profundorum	Platyhelminthes: Cestoda	Gilquiniidae Dollfus, 1935	*Deanicola* sp.	H	A (immature)	-	spin	NEA (Azores)	Caira & Pickering 2013
Squaliformes: Etmopteridae									
Aculeola nigra de Buen, 1959	Crustacea: Siphonostomatoida	Eudactylinidae Wilson, 1932	*Eudactylina chilensis* Ho & McKinney, 1981	M	-	S	gi	SEP (Chile)	Ho & McKinney 1981
Centroscyllium fabricii (Reinhardt, 1825)	Platyhelminthes: Cestoda	Gilquiniidae Dollfus, 1935	*Gilquinia* sp.	H	A	-	spin	NEA (Azores)	Caira & Pickering 2013
			Gilquinia squali (Fabricius, 1794)	H	-	G	-	NWA (West Greenland)	Chambers 2008
		Trianeophoridae	*Philobythos* sp.	H	-		-	NWA (West Greenland)	Chambers 2008
		Fam. incertae sedis	Cestoda fam. gen. sp.	H	-		-	NWA (West Greenland)	Chambers 2008
	Platyhelminthes: Monogenea	Diclidophoridae Fuhrmann, 1928	*Macruricotyle newfoundlandiae* Campbell, Correia & Haedrich, 1982	M	-		-	NWA (West Greenland)	Chambers 2008
	Platyhelminthes: Trematoda	Azygiidae Lühe, 1909	*Otodistomum cestoides* (Van Beneden, 1871) Odhner,1911	H	-	G	-	NWA	Margolis & Arthur 1979
			Otodistomum plunketi Fyfe, 1953	H	A	G	bc	NEA	Bray & Cribb 2003
		Fellodistomidae Nicoll, 1909	*Fellodistomum fellis* (Olsson, 1868) Nicoll, 1909	H	-		-	NWA (West Greenland)	Chambers 2008
		Fam. incertae sedis	Trematoda fam. gen. sp.	H	-	-	bc	NEA	Hennemann 1985
	Nematoda: Ascaridoidea	Anisakidae Skrjabin & Karokhin, 1945	*Anisakis simplex* (Rudolphi, 1809)	H	L	G	-	NWA (West Greenland)	Chambers 2008
			Pseudoterrnova decipiens	H	L	G	-	NWA (West Greenland)	Chambers 2008
			Anisakidae gen. sp.	H	-	-	-	NWA (West Greenland)	Chambers 2008
	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	*Neoalbionella centroscyllii* (Hansen, 1923)	M	A	S	fin (dorsal)	NWA (Newfoundland)	Rubec & Hogans 1988
			Neoalbionella centroscyllii (Hansen, 1923)	M	A	S	-	NWA	Margolis & Arthur 1979 and reference therein
			Neoalbionella fabricii (Rubec & Hogans, 1988)	M	A	S	gi	NWA (Newfoundland)	Rubec & Hogans 1988
	Crustacea: Cymothooidea	Gnathiidae Leach, 1814	Gnathiidae gen. sp.	M	L	-	-	NWA (New England, seamount chain)	Quattrini & Demopoulos 2016
	Crustacea: Cirripedia	Anelasmatidae Gruvel, 1905	*Anelasma* sp.	M	A	-	fin	NWA (West Greenland)	Yano & Musick 2000
Centroscyllium granulatum Günther, 1887	Platyhelminthes: Cestoda	Gilquiniidae Dollfus, 1935	*Gilquinia squali* (Fabricius, 1794)	H	A	G	-	SEP (Chile)	Carvajal 1974
Centroscyllium nigrum Garman, 1899	Crustacea: Cirripedia	Anelasmatidae Gruvel, 1905	*Anelasma* sp.	M	A	-	fin (dorsal)	SEP (Chile)	Long & Waggoner 1993
***Etmopterus* sp.**	Platyhelminthes: Cestoda	Lacistorhynchidae Guiart, 1937	*Grillotia amblyrhynchus* Campbell & Berveridge, 1993	H	L	-	stow	CWP (Indonesia)	Palm 2004
	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	*Neoalbionella etmopteri* (Yamaguti, 1939)	M	-	-	-	SA / SI (off South Africa)	Kensley & Grindley 1973 (in Dippenaar 2005)
			Lernaeopoda sp.	M	-	-	sk	SWP (New Zealand)	Hine et al. 2000

Table 4.1 - (cont.)

Host species	Classification		Parasite species	Life cycle	Life stage	Host specificity	Site of infection	Locality	Source
Squaliformes: Etmopteridae									
***Etmopterus* sp.**	Crustacea: Cymothooidea	Cymothoidae Leach, 1818	*Elthusa raynaudii* (H. Milne Edwards, 1840)	M	A	accidental infec.	mo	NWP (Taiwan)	Williams et al. 2010
Etmopterus baxteri Garrick, 1957 (species is considered as synonym of *E. granulosus*; Straube et al. 2011)	Platyhelminthes: Cestoda	Gilquiniidae Dollfus, 1935	*Plesiorhynchus etmopteri* Beveridge, 1990	H	A	GS	spin	SWP (Australia, Tasmania)	Beveridge 1990
		Aporhynchidae Poche, 1926	*Aporhynchus tasmaniensis* Beveridge, 1990	H	A	S	spin	SWP (Australia, Tasmania)	Beveridge 1990
	Platyhelminthes: Trematoda	Azygiidae Lühe, 1909	*Otodistomum plunketi* Fyfe, 1953	H	A	G	spin	SWP (New Zealand)	Hine et al. 2000, Bray & Cribb 2003
	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	*Neoalbionella* sp.	M	-	-	sk, nc	SWP (New Zealand)	Hine et al. 2000
	Crustacea: Cirripedia	Anelasmatidae Gruvel, 1905	*Anelasma squalicola* Darwin, 1852	M	A	GS	mus (head)	SWP (New Zealand)	Kazachenko & Feshchenko 2016
			Anelasma sp.	M	A	GS	skin	SWP (New Zealand)	Hine et al. 2000
Etmopterus granulosus (Günther, 1880)	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	*Neoalbionella* sp.	M	A	-	fin	SEP (Chile)	Rodríguez, Luque & George-Mascimento 2010
	Crustacea: Cirripedia	Anelasmatidae Gruvel, 1905	*Anelasma* sp.	M	A	-	fin	SWP (Australia, Tasmania)	Yano & Musick 2000
Etmopterus lucifer Jordan & Snyder, 1902	Platyhelminthes: Cestoda	Gilquiniidae Dollfus, 1935	*Plesiorhynchus etmopteri* Beveridge, 1990	H	A	GS	spin	SWP (Australia, Tasmania)	Beveridge 1990
	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	*Neoalbionella etmopteri* (Yamagutii, 1939)	M	A	GS	sk, fin	NWP (Japan)	Benz 1991
Etmopterus princeps Collett. 1904	Platyhelminthes: Cestoda	Gilquiniidae Dollfus, 1935	*Plesiorhynchus brayi* Palm, 2004	H	A	S	-	NA	Palm 2004
			Plesiorhynchus brayi Palm, 2004	H	A	S	spin	NEA (Azores)	Caira & Pickering 2013
			Gilquinia sp.	H	A	-	spin	NEA (Azores)	Caira & Pickering 2013
		Aporhynchidae Poche, 1926	*Aporhynchus* sp.	H	A (immature)	-	spin	NEA (Azores)	Caira & Pickering 2013
	Platyhelminthes: Monogenea	Microbothriidae Price, 1936	*Asthenocotyle azorensis* Kearn, Whittington & Thomas 2012	M	A	S	sk, sc	NEA (Azores)	Kearn et al. 2012
	Platyhelminthes: Trematoda	Azygiidae Lühe, 1909	*Otodistomum plunketi* Fyfe, 1953	H	A	G	bc	NWA	Gibson & Bray 1977
	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	*Ommatokoita* sp.	M	A	-	sk, mus	NWA	Hogans & Brattey 1986
	Crustacea: Cirripedia	Anelasmatidae Gruvel, 1905	*Anelasma squalicola* Darwin, 1852	M	A	GS	sk, mus	NEA (off British Isles)	Hennemann 1985
			Anelasma sp.	M	A	-	mus (head)	CNA	King et al. 2006
			Anelasma sp.	M	A	-	mo, fin	NEA	Yano & Musick 2000
	Crustacea (incertae sedis)	Fam. incertae sedis	Crustacea fam. gen. sp.	M	A	-	fin	NEA (off British Isles)	Hennemann 1985
Etmopterus pusillus (Lowe, 1839)	Platyhelminthes: Cestoda	Aporhynchidae Poche, 1926	*Aporhynchus pickeringae* Noever, Kuchta, Caira, Desjardins, 2010	H	A	S	spin	NEA (Azores)	Noever et al. 2010
			Aporhynchus pickeringae Noever, Kuchta, Caira, Desjardins, 2011	H	A	S	spin	NEA (Azores)	Caira & Pickering 2013
	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	*Lernaeopodina longibrachia* (Brian, 1912)	M	A	G	-	Med	Brian (1912) in Boxshall 1998
		Eudactylinidae Wilson, 1932	*Eudactylina epaktolampter* Deets, 1994 (nomen nudum in WORMS)	M	A	-	gi	NEA / NW	Deets 1994
Etmopterus schultzi Bigelow, Schroeder & Springer, 1953	Crustacea: Cirripedia	Anelasmatidae Gruvel, 1905	*Anelasma* sp.	M	A	-	-	CWA	Causey 1957 in Yano & Musick 2000
Etmopterus spinax Rafinesque , 1810	Platyhelminthes: Cestoda	Onchobothriidae Braun, 1900	*Acanthobothrium coronatum* (Rudolphi, 1819)	H	x	G	-	-	Williams 1969 in Pollerspöck & Straube 2016
		Aporhynchidae Poche, 1926	*Aporhynchus menezesi* Noever, Kuchta, Caira, Desjardins, 2010	H	A	S	spin	NEA (Azores)	Noever et al. 2010
				H	A	S	spin	NEA (Azores)	Caira & Pickering 2013

Table 4.1 - (cont.)

Host species	Classification		Parasite species	Life cycle	Life stage	Host specificity	Site of infection	Locality	Source
Squaliformes: Etmopteridae									
Etmopterus spinax Rafinesque , 1810	Platyhelminthes: Cestoda	Aporhynchidae Poche, 1926	*Aporhynchus menezesi* Noever, Kuchta, Caira, Desjardins, 2010	H	A	S	spin	NEA (off northern Spain)	present study
		Aporhynchidae Poche, 1926	*Aporhynchus norvegicus* (Olsson, 1868)	H	A	S	-	NEA (west of Ireland, Porcupine)	Rees & Llewellyn 1941
				H	A	S	spin	NEA (Ireland; Portugal; Scandinavia)	Beveridge 1990
				H	A	S	sto, spin	NOS (Skagerrak)	Klimpel et al. 2003
				H	A	S	spin	WMed (Balearic Sea)	Dallares 2016
				H	A	S	spin	NEA (Azores)	Caira & Pickering 2013
			Aporhynchus cf. *norvegicus* (Olsson, 1868)	H	A	S	spin	NEA (off northern Spain)	present study
		Lacistorhynchidae Guiart, 1937	*Lacistorhynchus tenuis* (van Beneden, 1858) Pintner, 1913	H	L	G	bc	NOS (Skagerrak)	Klimpel et al. 2003
		Sphyriocephalidae Pintner, 1913	*Sphyriocephalus* sp.	H	L	-	sto	NEA (off northern Spain)	present study
		Phyllobothriidae Braun, 1900	*Phyllobothrium squali* Yamaguti, 1952	H	x	G	in	NEA (off British Isles)	Williams 1959
		Echinobothriidae Perrier, 1897	*Ditrachybothridium macrocephalum* Rees, 1959	H	A (immature)	G	spin	NEA (off northern Spain)	present study
		Fam. incertae sedis	Trypanorhyncha fam. gen. sp.	H	L	-	mus, stow	NEA (off northern Spain)	present study
			Pseudophyllidea fam. gen. sp.	H	L	-	spin	NOS (Skagerrak)	Klimpel et al. 2003
			Tetraphyllidea fam. gen. sp.	H	L	-	spin	NEA (Azores)	Caira & Pickering 2013
			Tetraphyllidea fam. gen. sp.	H	L	-	liv, spin	NEA (off northern Spain)	present study
			Tetraphyllidea fam. gen. sp.	H	L	-	liv, spin	WMed (Balearic Sea)	Dallares 2016
		Fam. incertae sedis	Cestoda fam. gen. sp.	H	L	-	sto	NEA	Mauchline & Gordon 1984
	Platyhelminthes: Monogenea	Hexabothriidae Price, 1942	*Squalonchocotyle spinaci* (Goto, 1894)	M	A	S	gi	WMed (Thyrrenian Sea)	Di Cave et al. 2003
				M	A	S	gi	NOS (Skagerrak)	Klimpel et al. 2003
				M	A	S	gi	NEA (off northern Spain)	present study
			Squalonchocotyle sp.	M	A	-	gi	Med	Orecchia & Paggi 1978 (in Strona et al. 2010)
		Monocotylidae Taschenberg, 1879	Monocotylidae gen. sp. (most probably Squalotremasp.)	M	A	-	nc	NOS (Skagerrak)	Klimpel et al. 2003
	Platyhelminthes: Trematoda	Azygiidae Lühe, 1909	*Otodistomum* sp.	H	L	G	in	NEA (off northern Spain)	present study
		Fam. incertae sedis	Trematoda fam. gen. sp.	H	-	-	bc	NEA (off British Isles)	Hennemann 1985
	Nematoda: Ascaridoidea	Anisakidae Skrjabin & Karokhin, 1945	*Anisakis simplex* (Rudolphi, 1809)	H	L	G	stow, bc	NOS (Skagerrak)	Klimpel et al. 2003
			Anisakis sp. Type I (*sensu* Berland, 1961)	H	L	G	liv, mus, stow, inw, go	NEA (off northern Spain)	present study
			Contracaecum sp.	H	L	-	sto, spin	NEA (off northern Spain)	present study
		Raphidascarididae Hartwich, 1954	*Hysterothylacium aduncum* (Rudolphi, 1802)	H	L	G	sto, spin	NOS (Skagerrak)	Klimpel et al. 2003
			Hysterothylacium sp.	H	L	-	sto	NEA (off northern Spain)	present study
	Nematoda (incertae sedis)	Fam. incertae sedis	Nematoda fam. gen. sp.	H	-	-	sto	NEA	Mauchline & Gordon 1984
	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	Lernaeopodina longibrachia (Brian, 1912)	M	A	G	-	Med	Raibaut et al. 1998
			Lernaeopodina spinacis (Brian, 1908) taxon inquirendum (Kabata 2004)	M	-	-	-	Med	Raibaut et al. 1998
	Crustacea: Cirripedia	Anelasmatidae Gruvel, 1905	*Anelasma squalicola* Darwin, 1852	M	A	GS	sk, mus	NEA (off British Isles)	Hickling 1963
				M	A	GS	sk, mus	NEA (off British Isles)	Hennemann 1985
				M	A	GS	sk, mus	NEA (off northern Spain)	Fernández-Ovies 1995 (in Yano & Musick 2000)
	Crustacea: Lysianassoidea	Trischizostomatidae Lilljeborg, 1865	*Trischizostoma raschi* Esmark & Boeck, 1861	M	A	G	-	NEA (Norway)	Bousfield 1987 and references therein

Table 4.1 - (cont.)

Host species	Classification		Parasite species	Life cycle	Life stage	Host specificity	Site of infection	Locality	Source
Squaliformes: Etmopteridae									
Etmopterus unicolor) (Engelhardt, 1912	Crustacea: Siphonostomatoida	Lernaeopodidae Milne Edwards, 1840	*Lernaeopoda* sp.	M	A	-	cla	NWP (Japan)	Abe 1965
	Crustacea: Cirripedia	Anelasmatidae Gruvel, 1905	*Anelasma* sp.	M	A	-	cla, fin, mo	SWP (New Zealand; Australia; Tasmania)	Yano & Musick 2000
Notacanthiformes: Notacanthidae									
Notacanthus abbotti Fowler, 1934	Platyhelminthes: Trematoda	Fellodistomidae Nicoll, 1909	*Steringophorus furciger* (Olsson, 1867) Odhner, 1905	H	A	G	in	NWP	Machida 1988
		Zoogonidae Odhner, 1902	*Koiea notacanthi* Bray & Campbell, 1995	H	-	GS	-	SWP	Korotaeva 1994
Notacanthus bonaparte Risso, 1840	Platyhelminthes: Cestoda	Triaenophoridae Lönnberg, 1889	*Bathycestus brayi* Kuchta & Scholz, 2004	H	A	S	in	NEA	Kuchta & Scholz 2004
		Fam. incertae sedis	Tetraphyllidea fam gen. sp.	H	L	G	pc	WMed	Present study
	Platyhelminthes: Monogenea	Microcotylidae Taschenberg, 1879	*Tinrovia mamaevi* Isbert et al., 2017	M	A	S	gi	Wmed / NEA	Present study
	Platyhelminthes: Trematoda	Fellodistomidae Nicoll, 1909	*Steringovermes notacanthi* Bray, 2004	H	A	S	in	NEA	Bray 2004b
	Nematoda: Ascaridoidea	Raphidascarididae Hartwich, 1954	*Hysterothylacium* sp.	H	L	G	sto, in, go	WMed	Present study
	Nematoda: Seuratoidea	Cucullanidae Cobbold, 1864	*Dichelyne* (*Cucullanellus*) *romani* Isbert et al., 2015	H	A	GS	pc, sto, in	Wmed / NEA	Present study
		Cucullanidae Cobbold, 1864	Cucullanidae gen. sp.	H	L	-	pc, sto, in	WMed	Present study
Notacanthus chemnitzii Bloch, 1788	Platyhelminthes: Trematoda	Zoogonidae Odhner, 1902	*Koiea notacanthi* Bray & Campbell, 1995	H	A	GS	in	NWA	Bray & Campbell 1995
			Panopula spinosa (Zubchenko, 1978) Bray & Gibson 1986	H	A	S	in	*NEA (Iceland) / ‡NWA	*Zubchenko 1978, *‡Bray & Gibson 1986
		Hemiuridae Looss, 1899	*Lecithophyllum euzeti* Gibson & Bray, 2003	H	A	FG	sto	NEA	Gibson et al. 2003
	Platyhelminthes: Monogenea	Microcotylidae Taschenberg, 1879	*Syncoelicotyle polyorchis* Mamaev & Zubchenko, 1978	M	A	S	gi	NEA	Mamaev & Zubchenko 1978
		Diclidophoridae Fuhrmann, 1928	*Atlanticotyle notacanthi* Mamaev & Zubchenko, 1978	M	A	S	gi	NEA	Mamaev & Zubchenko 1978
	Nematoda: Seuratoidea	Cucullanidae Cobbold, 1864	*Dichelyne* (*Cucullanellus*) *romani* Isbert et al., 2015	H	A	GS	pc, sto, in	Wmed / NEA	Present study
	Crustacea: Cymothooidea	Gnathiidae Leach, 1814	Gnathiidae gen. sp.	M	L	-	gi	NWA	Quattrini & Demopoulos 2016
Notacanthus sexpinis Richardson, 1846	Platyhelminthes: Cestoda	Sphyriocephalidae Pintner, 1913	*Hepatoxylon trichiuri* (Holten, 1802)	H	L	G	in	SEP	Pardo-Gandarillas et al. 2008
	Platyhelminthes: Monogenea	Microcotylidae Taschenberg, 1879	*Tinrovia papiliocauda* Mamaev, 1987	M	A	S	gi	SWP	Mamaev 1987
	Platyhelminthes: Trematoda	Hemiuridae Looss, 1899	*Dinosoma* sp.	H	A	-	sto, in	SEP	Pardo-Gandarillas et al. 2008
		Accacoeliidae Odhner, 1911	*Accacladium* sp.	H	L	-	sto, in	SEP	Pardo-Gandarillas et al. 2008
			Paraccacladium leontjevae (Korotaeva, 1976) Bray & Gibson, 1977	H	-	S	in	SWP	Korotaevea 1976 in Hine et al. 2000
	Nematoda: Ascaridoidea	Anisakidae Skrjabin & Karokhin, 1945	*Anisakis* sp.	H	L	-	sto, in	SEP	Pardo-Gandarillas et al. 2008
Polyacanthonotus africanus Gilchrist & von Bonde, 1924	Platyhelminthes: Cestoda	Fam. incertae sedis	Cestoda fam. gen. sp.	H	-	-	sto	NEA	Mauchline & Gordon 1984
Polyacanthonotus challengeri (Vaillant, 1888)	Platyhelminthes: Trematoda	Hemiuridae Looss, 1899	*Lecithophyllum euzeti* Gibson, Bray, Combe & Jourdane 2003	H	A	FG	sto	NEA	Gibson et al. 2003
		Zoogonidae Odhner, 1902	*Brachyenteron rissoanum* Bray & Campbell, 1995	H	A	GS	in	NWA	Bray & Gibson 1998
Polyacanthonotus rissoanus (De Filippi & Vérany, 1857)	Platyhelminthes: Cestoda	Fam. incertae sedis	Cestoda fam. gen. sp.	H	-	-	sto	NEA	Mauchline & Gordon 1984
	Platyhelminthes: Trematoda	Zoogonidae Odhner, 1902	*Brachyenteron rissoanum* Bray & Campbell, 1995	H	A	GS	sto	NWA	Bray & Campbell 1995

Table 4.1 - (cont.)

Host species	Classification		Parasite species	Life cycle	Life stage	Host specificity	Site of infection	Locality	Source
Notacanthiformes: Notacanthidae									
Polyacanthonotus rissoanus (De Filippi & Vérany, 1857)	Platyhelminthes: Trematoda	Zoogonidae Odhner, 1902	Brachyenteron campbelli Bray & Gibson, 1986	H	A	S	in	NEA	Bray & Gibson 1986
			Panopula bridgeri Bray & Gibson, 1986	H	A	S	in	NEA	Bray & Gibson 1986
		Fellodistomidae Nicoll, 1909	*Prudhoeus nicholsi* Bray & Gibson, 1980	H	A	S	in	NEA	Bray & Gibson 1980

wider range of prey items and these are often part of parasite life cycles (crustaceans, squid, fin fish).

Proportions between parasite species infecting as adults or larvae are similar in notacanthids (69.6 *vs* 30.4%) and etmopterids (70.0 *vs* 30.0%), while for centrophorids the proportion of adult – larvae is balanced (51.9 *vs* 48.1%). The occurrence as adult or larvae and their proportion in these fish families depend on several factors, which influence their representation in this environment and hosts. Generally, it is suggested that predators preying on more diverse species have more trophically transmitted adult heteroxenous parasites, while infections by larval parasites increase especially in fish preyed by a higher diversity of predators (Locke et al. 2014). This general pattern is difficult to apply to the deep-sea environment, as trophic webs are known to be particular, with a restricted diversity. Moreover, although it can be supposed that elasmobranchs are generally predators with a wide prey range, etmopterids and centrophorids are small, medium to large sized sharks, with more limited prey ranges; this could partly explain why adult stages of their heteroxenous parasites are not predominant, with proportions of 50 and 40.9%, respectively. Considering the species of the three studied families as possible preys, in the deep-sea the range of their predators seems also to be limited, as very few records exist (Dunn et al. 2010, Cortés 1999, Heithaus 2004), reducing the number of larval stages mostly to quite specific hosts. However, the presence of many opportunistic and/or scavenging species in this habitat must also be taken into account.

The main parasite groups differ distinctly in their life cycles. Larval stages are predominant among the cestodes parasitizing the elasmobranch families, while the presence of cestodes in notacanthids is rare (see table 4.1). The frequently detected unspecific larval cestodes in the elasmobranch hosts point to non-accidental infections by parasites widely spread in the deep-sea trophic webs, where both elasmobranch families are preyed by other shark species (Cortés 1999, Palm & Schröder 2001, Klimpel et al. 2003, Heithaus 2004, Dunn et al. 2010). The here observed high importance of shark species as intermediate and paratenic hosts for cestode taxa is astonishing considering the partly relatively large body sizes which can be attained especially by some Centrophoridae (*Centrophorus* spp.: up to 300 cm; *Deania* spp. up to 150 cm, Musick et al. 2004). Consequently, predators of these species would have to be of the same size at least to prey on them. Further studies are necessary to analyse if some larval cestodes may occur only in smaller, younger sharks and diminish in adults.

While adult and larval nematodes have been detected in notacanthids, in both elasmobranch families, only larval stages have been reported. The nematode species mostly found as larvae in these families, both *Anisakis* spp. and *Hysterothylacium* spp., are widespread and exhibit a broad range of intermediate hosts. Species of both genera were also found in *Galeus melastomus* (Dallarés 2016) from the western Mediterranean, but this shark exhibited a more diverse nematode community comparable to shallow water sharks with nematodes from other families and as adult stages (Moore 2001, Dallarés 2016). Interestingly, in the case of cucullanids, the notacanthids can act as intermediate and definitive hosts depending on the parasite species. Cucullanids are supposed to be common parasites of elasmobranchs (Caira et. al. 2012), but they are not present in the families herein studied. Most parasite taxa reported in the notacanthids were digeneans recorded as adults, while only one larval stage was documented (*Accacladium* sp.). Although notacanthids show a benthic feeding habit and consequently most of their life are located close to several potential first intermediate hosts living at the sea bed (e.g. gastropods), they are not exploited by digenean larvae. Regarding the monoxenous parasites, they are mostly reported as adults as they mature in the fish, except for the case of the gnathiid isopods whose adults are free-living, while larvae are blood-feeders in fish (Grutter & Poulin 1998). As previously stated the presence of monoxenous parasites has been reported to be generally lower than heteroxenous species.

In all, the here presented Table 4.1 reflects what is generally supposed to influence the parasite species diversity. The composition of parasite faunas depend amongst others on the feeding and general behaviour of the host, the presence of intermediate and definitive hosts in the environment, biogeography, depth and environmental tolerances of parasites (Begg and Waldman 1999, Klimpel et al. 2006a). Many hypotheses explaining the patterns and distribution of parasites in deep-sea fishes remain speculative and based on knowledge on shallow waters as the records are very limited and patchy in this environment. As previously stated, only a slight increase of the number of studies on deep-sea species and their parasite communities can be observed in the last 40 years, mainly made in certain geographical and commercially interesting areas and species. Some authors stress that there is a high discovery rate of habitats and species in the deep-sea, but currently the proportion sampled and investigated in detail is still very low (Ramirez-Llodra et al. 2010). Increasing knowledge on the parasite fauna of these kinds of deep-sea organisms can be achieved by conventional methods (scientific surveys, commercial fishing) but also be complemented by new methods such as underwater videos (ROV) which are applied regularly in the deep-sea (Priede et al. 1994, Jones et al. 2003, Ross et al. 2001, Morris et al. 2014, Quattrini & Demopoulos 2016). These methods are applied to study organisms from shallow and deep-sea waters assessing e.g. densities and abundances, behaviour and owing to the progress made in processing digital photos and films of high quality, now this method can be used to evaluate infection patterns of ectoparasites (Quattrini & Demopoulos 2016). All these kinds of studies can enhance our knowledge on parasites, but also on the ecology and biology of hosts in this huge biome, when using parasites as biological indicators such as proposed especially for rare species or species difficult to obtain (MacKenzie & Abaunza 1998).

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Notacanthus bonaparte

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Chapter 5

A new species of *Tinrovia* Mamaev, 1987 (Monogenea: Microcotylidae) from the deep-sea fish *Notacanthus bonaparte* Risso (Notacanthiformes: Notacanthidae) in the western Mediterranean and the Northeast Atlantic

Systematic Parasitology (2017)
doi: 10.1007/s11230-017-9727-3

ABSTRACT

A new microcotylid, Tinrovia mamaevi n. sp. (Monogenea: Polyopisthocotylea), is described from the gills of *Notacanthus bonaparte* Risso (Notacanthiformes: Notacanthidae), sampled in the western Mediterranean and Northeast Atlantic. This species is allocated to the subfamily Syncoelicotylinae Mamaev & Zubchenko, 1978 due to the possession of a symmetrical haptor with two separate frills. The clamps in *T. mamaevi* n. sp. are of the ´microcotylid type, arranged in two distinct lateral haptoral frills; the genital atrium and the copulatory organ are armed and the vaginal pore is unarmed. The new species differs from the type- and only species of the genus, *T. papiliocauda* Mamaev, 1987, in having a shorter and narrower haptor with a smaller number of clamps. Clamps are also smaller in the new species, testes are more numerous, the genital atrium is smaller, divided into two lateral lobes (instead of five) with a smaller number of spines and the eggs have a short and a long filament (instead of two short filaments). The host species and locality of *T. mamaevi* n. sp. also differ as *T. papiliocauda* was recorded in Notacanthus sexspinis Richardson from the South Pacific.

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INTRODUCTION

The fish family Notacanthidae Rafinesque (Notacanthiformes: Notacanthidae) has a global distribution and includes species inhabiting the deep-sea between depths of 200–3,500 m (Nelson 2006). These fishes, commonly known as deep-sea spiny eels, are benthopelagic, feeding mainly on different small benthic invertebrates and nektonic crustaceans (Macpherson 1981, Coggan et al. 1998, Carrassón & Matallanas 2002). One of the nominal species belonging to this family is the shortfin spiny eel *Notacanthus bonaparte* Risso exhibiting a distribution restricted to the Northeast Atlantic off Faroe Islands to Mauritania and western Mediterranean Sea (Froese & Pauly 2016). The poorly studied parasite fauna of this fish comprises two species only: the trematode *Steringovermes notacanthi* Bray, 2004, the cestode *Bathycestus brayi* Kuchta & Scholz, 2004.

No monogenean species have been recorded to date in *N. bonaparte*; however other species of *Notacanthus* Bloch were reported to harbour monogeneans in gills: *Atlanticotyle notacanthi* Mamaev & Zubchenko, 1978 (Diclidophoridae) ex *N. chemnitzii* Bloch; and two representatives of the Syncoelicotylinae Mamaev & Zubchenko, 1978 (Microcotylidae), *Syncoelicotyle polyorchis* Mamaev & Zubchenko, 1978 ex *N. chemnitzii* and *Tinrovia papiliocauda* Mamaev, 1987 ex *N. sexspinis* Richardson.

During studies on parasitic helminths of marine deep-sea fishes from the western Mediterranean and the Northeast Atlantic, specimens of a microcotylid monogenean were recovered from the gills of *N. bonaparte*. Detailed morphological study of these specimens by light and confocal laser scanning microscopy revealed that they represent a species new to science, *Tinrovia mamaevi* n. sp. which is described here.

MATERIAL AND METHODS

A total of 150 specimens of *N. bonaparte* [total length (TL) 13.5–29.0 cm] was sampled during two projects (BIOMARE, ANTROMARE) carried out in the Balearic Sea in the western Mediterranean during 2007/2008 and 2011. Additionally, we examined 15 specimens (TL 22.4–38.0 cm) caught in the Galicia Bank (Northeast Atlantic) during 2010 within the framework of the INDEMARES EU-Life+project. All fish specimens were measured and weighed, and in case of the surveys in the Mediterranean Sea, the gills were removed from some specimens and preserved in 10% formal saline. All other specimens were frozen at -25°C; examination for the presence of parasites was later conducted in the laboratory. Monogeneans isolated from gills preserved in 10% formal saline or from thawed fish, were washed in physiological saline and preserved in 70% ethanol. Partially bent specimens were gently flattened in saline under a coverslip with a 2 g scale weight overnight in a refrigerator.

For morphological examination, monogeneans were stained with iron acetocarmine (Georgiev et al. 1986), dehydrated in an ethanol series, cleared in dimethyl phthalate and mounted in Canada balsam. Specimens were examined morphologically under a light microscope equipped with differential interference contrast (DIC). Drawings were made with the aid of a drawing tube. When available, measurements of all body parts were taken from specimens with relaxed bodies which had been removed from frozen fish. However, in order to increase the sample size, some additional measurements were made from those traits which were not affected by body contraction in specimens formerly preserved in formal saline. The type-material was deposited in the British Museum (Natural History) Collection of the Natural History Museum, London, UK (NHMUK) and in the Helminthological Collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences (IPCAS), České Budějovice, Czech Republic. Voucher material was deposited in the Marine Zoology Collection of the Cavanilles Institute of Biodiversity and Evolutionary Biology (ICBiBE) of the University of Valencia, Spain.

All measurements are presented as the range followed by the mean in parentheses. The mean length and width of some characters were calculated, when possible, from a maximum of ten measurements (testes, clamps and spines of the genital atrium) and from both buccal suckers of each specimen. One specimen was dissected in order to extract the egg and measure and illustrate its filaments. The terminology follows Rubec & Dronen (1994) and terms for the description of the microcotylid clamps follow Boeger & Kritsky (1993).

Additionally, images of some body parts from selected specimens were taken by means of a confocal laser scanning microscopy (CLSM) to obtain a better insight into details which were not well/completely visible under light microscopy. For CLSM, specimens stained in iron acetocarmine and mounted in Canada balsam were used. Samples were examined with an Olympus FV1000 (inverted IX81) confocal microscope using the following objectives: Super Apochromat UPLSAPO 10´ 2 (numerical aperture 0.40) and UPLFLN 40´ (oil) (numerical aperture 1.30). Laser emission wave length was 603 nm, BF position 570 nm, BF range 100 nm. Images were processed with the software FLUOVIEW Ver. 4.2a Viewer (FV10-ASW Version 04.02.02.09).

RESULTS

Family Microcotylidae Taschenberg, 1879
Subfamily Syncoelicotylinae Mamaev & Zubchenko, 1978
Genus *Tinrovia* Mamaev, 1987

Tinrovia mamaevi n. sp.

Type-host: *Notacanthus bonaparte* Risso (Notacanthiformes: Notacanthidae).

Type-locality: Balearic Sea, western Mediterranean; 40°10'N, 01°30'E – 41°12'N, 02°26'E; depth 620–1,009 m (mean 741 m).

Other localities: Galicia Bank, Northeast Atlantic; 42°43'N, 11°40'W – 42°47'N, 11°47'W; depth 771–837 m (mean 828 m).

Type-material: Holotype and 3 paratypes (NHMUK 2017.4.13.1 – NHMUK 2017.4.13.4), 2 paratypes (Cat. No. IPCAS M-579) and 8 vouchers (ICBiBE UV/ZOOMAR/*N. bonaparte*/ 12734–12741).

Site on host: Gill filaments.

Prevalence and intensity: Balearic Sea: 8.7% (13 infected out of 150 examined); 1–4 (1.5) monogeneans per infected fish (fish total length: 19.4–29.0 cm); Galicia Bank (Northeast Atlantic): 40.0 % (6 infected out of 15 examined); 1–3 (1.8) monogeneans per infected fish (TL: 23.9–36.4 cm).

ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Tinrovia mamaevi* n. sp. is urn:lsid:zoobank.org:act: E5B52C99-0731-4625-927F-CD88778E11CE.

Etymology: The new species is named after the late Dr Yuri L. Mamaev, of the Institute of Biology and Pedology of the Russian Academy of Sciences, Vladivostok, Russia in recognition to his invaluable contribution to the knowledge of the monogeneans.

Description (Figs. 5.1–5.3)

[Based on 12 adult whole-mounted specimens from the Balearic Sea; see Table 5.1 for measurements.] Body variably elongated, digitiform, dorsoventrally flattened, with rounded anterior extremity (Fig. 5.1A). Posterior extremity with relatively short, well-defined haptor; mean haptor length/ total body length ratio 22%. Haptor differentiated from body, symmetrical, winged formed by 2 slightly expanded lateral frills, bearing clamps (Figs. 5.1A, B, 5.2A); anterior ends of each frill forming

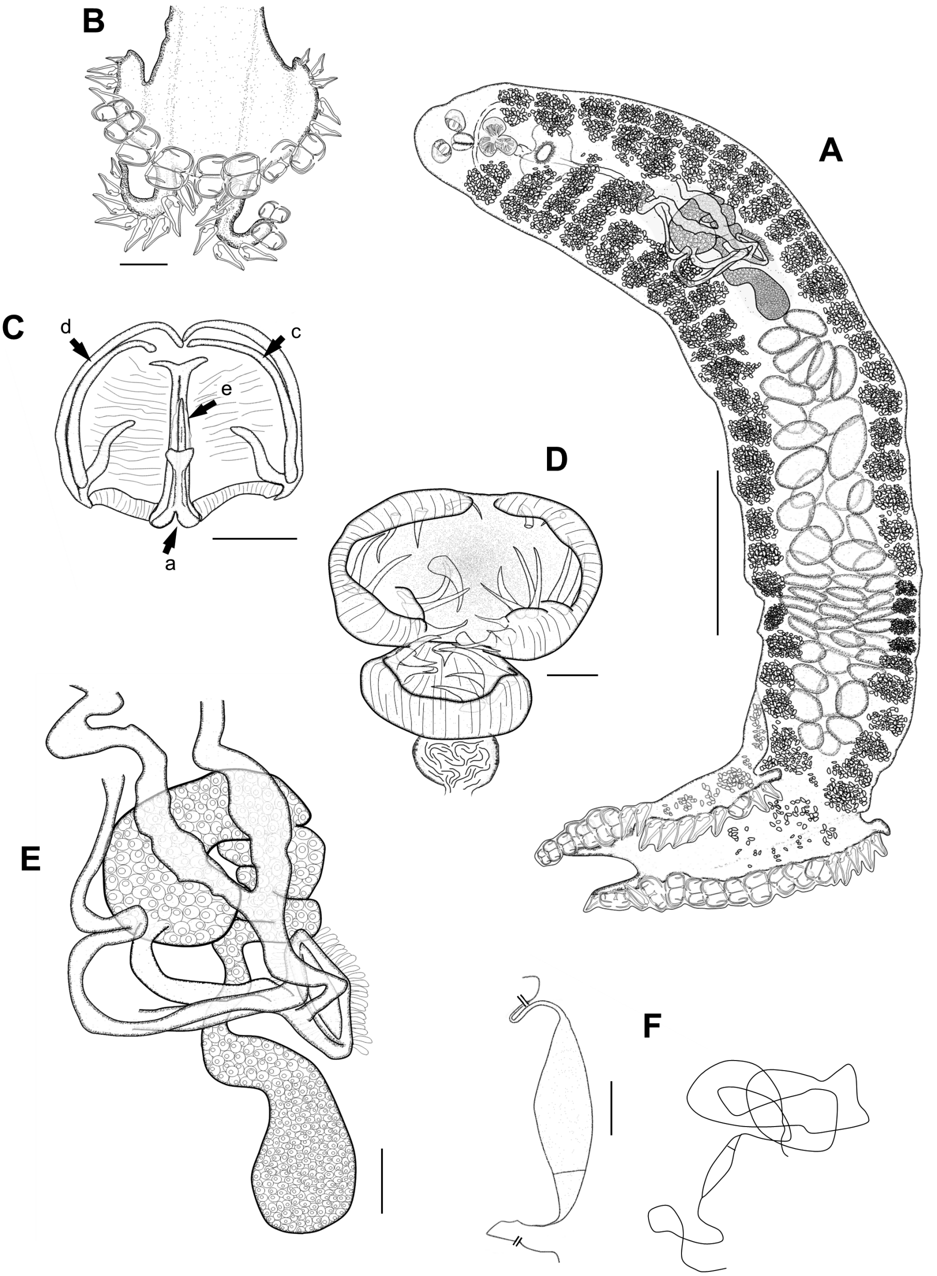

Fig. 5.1 - *Tinrovia mamaevi* n. sp. type-material ex *Notacanthus bonaparte*. A, Whole-mount (composite, ventral view); B, Haptor with frills bent at medial level (paratype, dorsal view); C, Clamp (anterior view: a, anterior mid-sclerite; c, antero-lateral sclerite; d, postero-lateral sclerite; e, accessory sclerite); D, Genital atrium with copulatory organ (paratype, ventral view); E, Proximal female genitalia, ventral view; F, Egg with detail of egg capsule (ex voucher specimen). Drawings from the holotype except otherwise indicated. *Scale-bars*: A, 500 μm; B, E 100 μm; C, D, F, 50 μm.

Table 5.1 - Morphometric data for *Tinrovia mamaevi* n. sp. from the western Mediterranean and the Northeast Atlantic and *T. papiliocauda*.

Species	*Tinrovia mamaevi* n. sp.		*T. mamaevi* n. sp.	*T. papiliocauda* Mamaev, 1987
Host	*Notacanthus bonaparte* Risso		*N. bonaparte* Risso	*N. sexspinis* Richardson
Locality	western Mediterranean		Northeast Atlantic	West Pacific
Source	Present study		Present study	Mamaev (1987)
	Range (Mean)	n	(n = 2)	(n = 1)
Total Total length (TL)	2,094–4,885 (3,333)	8	3,985	4,700
Maximum width	234–671 (491)	8	491	580
Haptor length (HL)	504–1,052 (798)	6	618, 683[a]	1,100
Ratio HL to TL (%)	16–29 (22)	6	14, 19	23
Haptor width	322–797 (512)	6	423, 647	1,400
Haptor median groove depth	163–258 (217)	6	284, 355	1,240[b]
Haptor frill width	89–193 (128)	6	-	360[b]
Clamp number	32–40 (36)	10	34, 36	45
Clamp length	64–110 (84)	10	66–90 (78)	120–140
Clamp width	81–133 (102)	10	99–111 (105)	110–130
Buccal sucker length	47–78 (60)	6	47	79
Buccal sucker width	39–67 (51)	6	60	63
Pharynx length	36–68 (50)	6	-	93
Pharynx width	29–79 (51)	6	72	65
Ratio buccal sucker-pharynx length	0.8–1.7 (1.3)	6	-	-
Gential atrium to anterior extremity	137–227 (200)	6	223	-
Genital atrium length	61–101 (89)	6	98	140
Genital atrium width	59–114 (86)	6	99	110
No. of spines (genital atrium)	11–30 (23)	10	31	81
No. of spines (copulatory organ)	7–11 (9)	10	8	14
Total no. of genital spines	22–39 (32)	10	39	95
Spine length (genital atrium)	17–26 (21)	10	27	24–32
Spine width (genital atrium)	2.0–2.4 (2.2)	10	1.9	-
Spine length (copulatory organ)	10–18 (15)	10	16	20
Spine width (copulatory organ)	2.8–4.7 (3.6)	10	3.2	-
Testes area length	980–1,488 (1,251)	6	1,662	-
Testes area maximum width	161–334 (234)	6	166	-
Testes length	54–159 (108)	6	116	-
Testes width	39–113 (73)	6	63	-
Testes number	41–53 (50)	6	44	25
Vaginal pore to anterior extremity	258–491 (382)	6	-	-
Germarium length	650–1,578 (1,058)	6	-	-
Germinal area length	101–311 (205)	6	-	-
Germinal area width	63–218 (123)	6	-	-
Egg length	78–279 (142)	6	-	230
Egg width	13–30 (18)	6	-	80
Egg filament length (opercular)	1,092	1	-	120[b]
Egg filament length (abopercular)	293	1	-	113[b]

[a] In the case of two measurements, the values are separated by a comma; [b] Calculated from the published figure

1 lobe; posterior extremities of frills not joining posteriorly, forming broad median groove. Larval hooks absent. Clamp number equal on both sides (32–40). Clamps of 'microcotylid' type, with very short peduncles, wider than long; smallest clamps located on anterior and posterior extremities of haptoral frills. Clamp sclerites: lateral sclerites (c, d) slender, middle sclerite (a) thick, with longitudinal grooves (Figs. 5.1C, 5.2B–D, Online Resource 5.1); accessory sclerite (e) single-pointed on apical part of middle sclerite, deeply grooved under DIC light microscopy (Figs. 5.1C, 5.2C, D). Clamp musculature slender, extended at basis of jaws.

Mouth ventral, subterminal; vestibule cup-like, with 2 oval, septate buccal suckers with mid-ventral, ellipsoidal aperture (Figs. 5.1A, 5.2E, F, Online Resource 5.2). Pharynx as long as wide (Fig. 5.1A); mean ratio buccal sucker to pharynx length 1.3. Oesophagus short. Intestinal bifurcation just anterior to or at level of genital atrium. Caeca with lateral internal and external ramifications overlapped by vitelline follicles (caeca not distinguished at haptor level).

Testes numerous, sub-ellipsoidal, flattened, post-germarial, intercaecal, pre-haptoral or slightly extending into haptoral region; arranged in 2 overlapped dorso-ventral levels. Vas deferens submedial, sinuous, ascending dorsal to uterus, terminating in small seminal vesicle (Fig. 5.3A–C, Online Resource 5.3, 5.4). Common genital pore midventral. Genital atrium posterior to pharynx, muscular, armed with numerous spines (Figs. 5.1A, D, 5.3B, C, Online Resource 5.3); divided into 2 lateral semi-circular lobes with armed muscular pads, each often apparently separated in 2 regions: proximal thick and distal thin (Figs. 5.1D, 5.3A–C, Online Resource 5.3); spines numerous, slender, often contorted and/or slightly hooked. Copulatory organ formed by medial tongue-shaped muscular pad with thick, rose-thorn-shaped spines.

Germarium in anterior half of body, elongated, question-mark shaped, with globular posterior germinal area, with distal part directed posteriorly (Fig. 5.1E). Oviduct oriented sinistro-posteriorly, straight or slightly coiled ending in oötype. Oötype sinistral to germarium; Mehlis' gland well developed. Genito-intestinal duct connected to oötype, dextrally oriented. Uterus originating from oötype, directed to right, looping anteriorly, continuing in slightly sinuous ventromedial duct terminating in common genital pore (Fig. 5.1A, E). Vagina posterior to level of copulatory organ (Fig. 5.1A); vaginal pore single, dorsal, unarmed, sub-elliptical, surrounded by tegumentary wrinkles, leading to wide vaginal atrium with 2 anterolateral chambers; vaginal duct connection wide, duct not observed. Vitelline follicles extending from level of copulatory organ into haptor, anterolaterally in variably irregular intercaecal fields; follicles scarce in haptor, reaching approximately to its midlevel. Vitelline ducts wide Y-shaped, variably coiled, joining in common duct at level of germarium. Intrauterine eggs not numerous, elliptical, with very long opercular filament and shorter needle-shaped abopercular filament (Fig. 5.1F); filament ends pointed.

Remarks

Apart from *Tinrovia*, the subfamily Syncoelicotylinae includes three species only within two genera, all having symmetrical haptor with two separate lobes (Mamaev 1986): *Syncoelicotyle polyorchis* Mamaev & Zubchenko, 1978 in *Notacanthus chemnitzii* Bloch from Reykjanes Ridge Seamount (North Atlantic Ocean); and two species of *Syncoelicotyloides*, *S. macruri* Mamaev & Brashovian, 1989 in *Macrourus holotrachys* Günther [most probably *M. carinatus* (Günther) according to Rubec et al. 1995] from the Walvis Ridge (Southeast Atlantic) and *S. zaniophori* in *Coryphaenoides zaniophorus* (Vaillant) in the DeSoto Canyon in the Gulf of Mexico (western central Atlantic).

The morphological traits of *Tinrovia mamaevi* n. sp. clearly justify the inclusion of the specimens from the western Mediterranean and Northeast Atlantic within the genus *Tinrovia* Mamaev, 1987: two-lobed differentiated haptor ('butterfly-shaped' *sensu* Mamaev, 1987; see

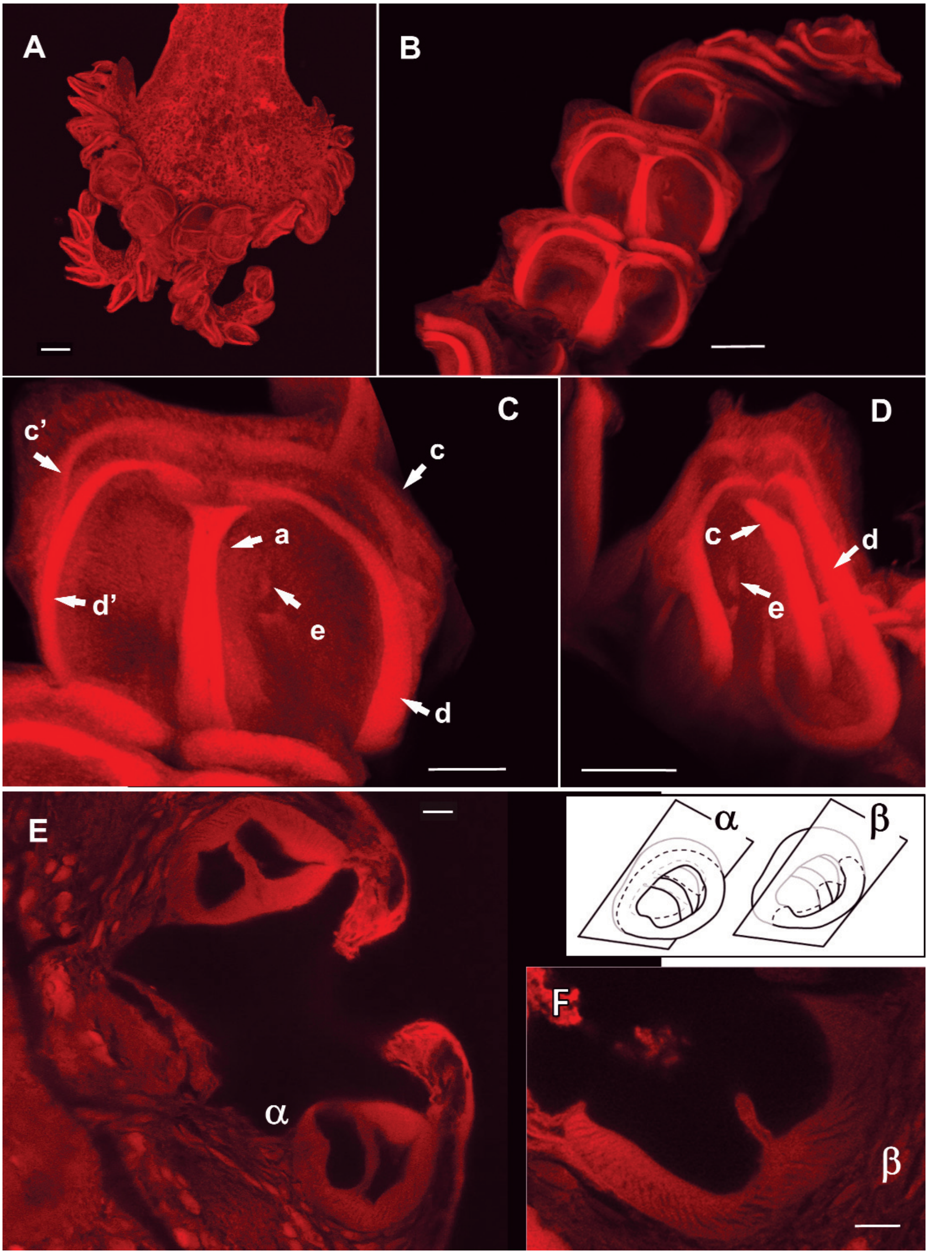

Fig. 5.2 - *Tinrovia mamaevi* n. sp. type-material ex *Notacanthus bonaparte*, confocal laser scanning micrographs of haptoral and mouth regions. A, Haptor with frills bent at medial level (dorsal view, paratype); B, Row of clamps on lateral frill (posterior view); C, D, Details of clamps, ventral and lateral view, respectively (a, anterior mid-sclerite; c, antero-lateral sclerite; d, postero-lateral sclerite; e, accessory sclerite); E, Section of buccal suckers and mouth vestibule (paratype); F, Section of buccal sucker (paratype). α and β represent diagrammatic figures of the section plain of buccal suckers in Figs. E and F, respectively. *Scale-bars*: A, 50 μm; B, 30 μm; C, 15 μm; D, 20 μm; E, F 10 μm.

also discussion), complex genital atrium and a single unarmed vagina (Mamaev 1987, Mamaev & Brashovian 1989, Rubec et al. 1995). The new species differs from the type- and only other species in this genus, *T. papiliocauda*, in the lower number of clamps (36 *vs* 45; see also Table 5.1). Clamps are also smaller in the new species (64–110 *vs* 120–140 µm); and as a consequence its haptor is always shorter (1,051 *vs* 1,100 µm) even in worms with similar length (4,885 *vs* 4,700 µm); additionally, the haptor of *T. mamaevi* n. sp. is narrower (797 *vs* 1,400 µm) and the lateral frills appear to be relatively smaller. Testes of the new species are notably more numerous than those of the type-species. *Tinrovia mamaevi* n. sp. exhibits a smaller genital atrium despite the total body length of the holotype of *T. papiliocauda* lies within the length range of the new species. The number of spines in *T. mamaevi* n. sp. is distinctly smaller in both, the genital atrium (23 *vs* 81) and copulatory organ (9 *vs* 14). The musculature of the genital atrium in *T. mamaevi* n. sp. is divided into two lateral semi-circular lobes with armed muscular pads forming an incomplete circle anterior to the medial, armed, tongue-shaped copulatory organ. In contrast, Mamaev (1987) described the genital atrium of *T. papiliocauda* as a complex organ consisting of five lobes with muscular spined pads surrounding one central armed circular pad. The eggs of both species are two-filamented, but in *T. mamaevi* n. sp. one filament is short and the other is very long whereas *T. papiliocauda* has short filaments on both poles of the egg. Furthermore, *T. mamaevi* n. sp. differs in the type-host species and locality; *T. papiliocauda* was described from *Notacanthus sexspinis* Richardson collected close to New Zealand. *Notacanthus sexspinis* and *N. bonaparte* exhibit different and non-overlapping geographical distributions (South Atlantic, to the Indian and the South Pacific Ocean *vs* Northeast Atlantic and western Mediterranean; Mamaev 1987, Mundy et al. 2011 and references therein, Froese & Pauly 2016).

DISCUSSION

The previous studies and descriptions of species of the Syncoelicotylinae were based on few parasite individuals collected from very few host specimens. Parasites are often lost during the sampling procedures from deep waters (Bray et al. 1999). Commonly monogeneans are considered as particularly scarce in deep waters (Campbell 1980, Rohde 2005); in a review of studies on marine parasites in deep-sea fishes and invertebrates, de Buron & Morand (2004) reported that monogeneans have been recorded only in shallower waters at depths up to 1,000 m, while copepods showed a distinctly higher diversity and were also recorded at depths up to 6,000 m. The scarcity of some parasites such as monogeneans in deep waters has been related mostly to the lower density of their host species (Campbell 1980, de Buron & Morand 2004) and, to a lesser extent, to environmental conditions (Bray et al. 1999). Notwithstanding the difficulties complicating the collection of parasite samples from deep-sea fish, future studies on Syncoelicotylinae, and in particular on *Tinrovia*, obtaining more specimens would be extremely useful to clarify questions concerning taxonomic issues.

The diagnoses of the species of Syncoelicotylinae refer to some characters which can be controversial in view of the species described to date (Mamaev & Zubchenko 1978, Mamaev 1987, Mamaev & Brashovian 1989, Rubec et al. 1995, present study). In the generic diagnoses of *Syncoelicotyle* and *Tinrovia* the haptor is described as ‘butterfly-shaped’, meaning wide, separated haptor frills (Mamaev & Zubchenko 1978, Mamaev 1987) whereas in contrast, the genus *Syncoelicotyloides* was partly differed by having a ‘haptor undifferentiated as a separate organ’ and not ‘butterfly-like’ shaped (Mamaev & Brashovian 1989, Rubec et al. 1995). The lateral frills of the haptor in *Tinrovia mamaevi* n. sp. are narrower than observed in the type-species *T. papiliocauda* (see Table 5.1); therefore this

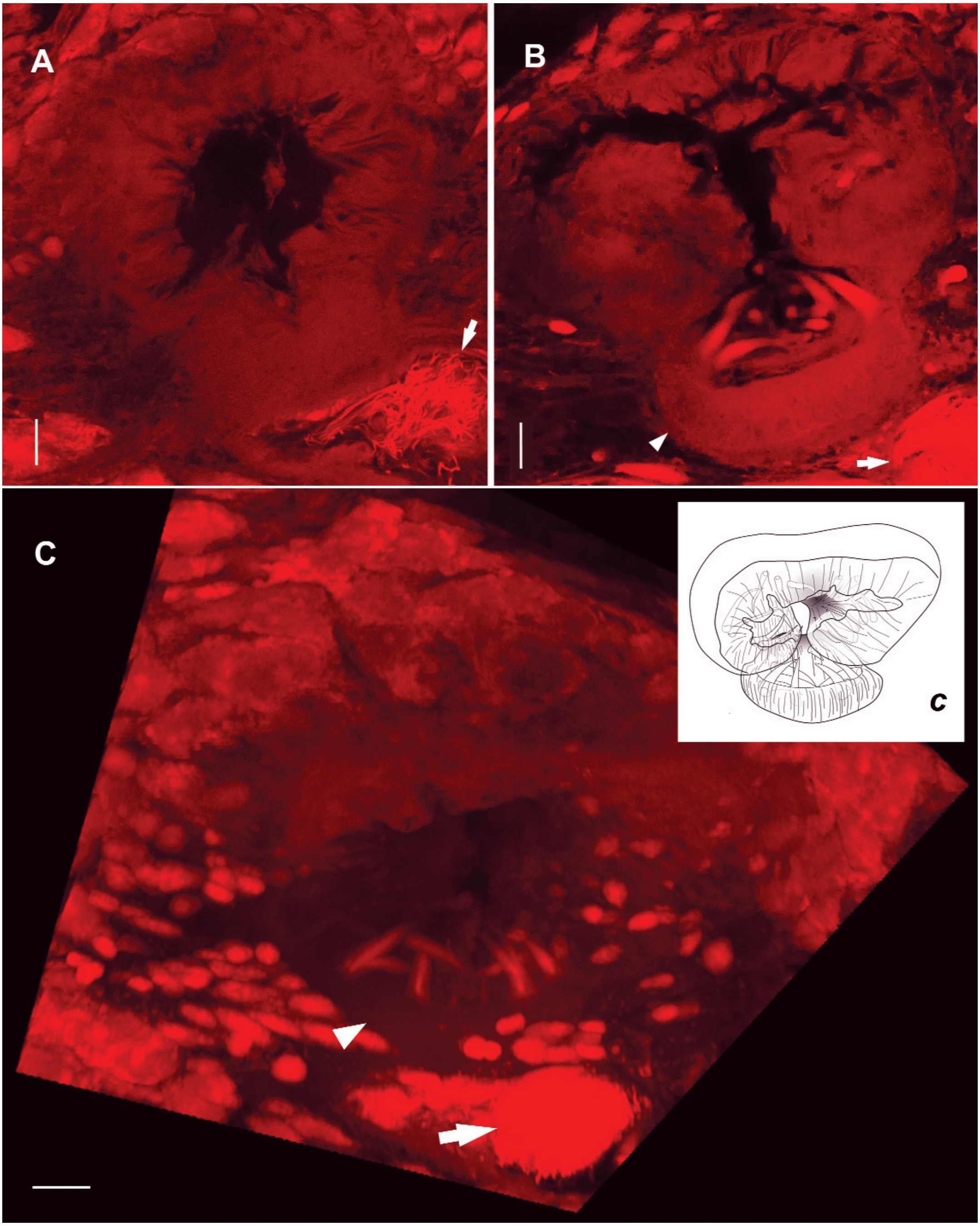

Fig. 5.3 - *Tinrovia mamaevi* n. sp. ex *Notacanthus bonaparte*. Paratype, confocal laser scanning micrographs of genital atrium, ventral views. A, Ventralmost section, close to genital pore; B, Mid-level section; C, 3D micrograph with diagrammatic reconstruction (*c*). *Arrows* indicate seminal vesicle; *arrowheads* indicate copulatory organ with spines. *Scale-bars*: 10 μm.

character cannot be longer diagnostic for the genus. Moreover, morphological characters are often affected by sampling and fixation conditions as already observed in studies on other platyhelminths (e.g. CCME 2011, Ahuir-Baraja et al. 2015). Formalin is considered an appropriate fixative for monogeneans with respect to their morphological preservation (e.g. Snyder & Clopton 2005, Strona et al. 2009). Parasites of the present study were preserved in formalin or frozen, subsequently fixed in ethanol. Comparisons of specimens fixed by both procedures did not reveal morphometric differences; however, the haptors bent laterally at medial level could be observed in two *T. mamaevi* n. sp. specimens only preserved frozen and subsequently fixed in ethanol. Due to the medial folding each frill appeared to be two-lobed in dorsal view, which could be described at first glance as 'butterfly-like shape' (Figs. 5.1B, 5.2A). We suggest using the more generic term 'winged' to refer to the wide haptor frills in species of *Tinrovia* and *Syncoelicotyle* as descriptions referring to peculiar shapes can be misinterpreted depending on the observer.

Clamps in species of the Syncoelicotylinae described to date were considered 'massive' (Mamaev & Zubchenko 1978, Mamaev 1987, Mamaev & Brashovian 1989). This description could be ambiguous as it could be referred to the total size of clamps in relation to body size, or to the relative size of the sclerites. Clamps in *T. mamaevi* n. sp. were not only relatively smaller than those in *T. papiliocauda*, but their sclerites were also apparently slender and delicate as well. This fact might also reflect the overall smaller host species *N. bonaparte*, which in part shows a generally lower body size (present study max. 38 cm) compared to the type-host of *T. papiliocauda* (maximum body size of *N. sexspinis*, 60 cm; Froese & Pauly 2016). Hayward (2005) indicated that host size, and consequently the size of the gill lamellae, can determine the maximum clamp size.

Caeca of the species of Syncoelicotylinae have been described to date as profusely branched and anastomosed, reaching the posterior part of the haptor; Mamaev (1987) also included this feature to characterise the subfamily. The caeca could not be observed at haptor level in the 14 specimens analysed in the present study. Traits referred to the arrangement and extension of the caeca are often difficult to be distinguished in polyopisthocotyleans, as the dense vitelline follicles often obscure the caeca impeding the observations of the anastomosis.

The genital atrium of *T. papiliocauda* was described with five lobes whereas *T. mamaevi* n. sp. possesses an atrium divided into two lobes. The different genital atrium lobulation should be interpreted with caution as the two lateral muscular pads of *T. mamaevi* n. sp. seem to be divided into distal and proximal regions which, together with the copulatory organ, may give the appearance of five slightly notched lobes in some specimens. Confocal techniques applied in the present study were very useful for the interpretation of the 3D-structure of the genital atrium and especially the arrangement and dimensions of the copulatory organ within the atrium. In general, this technique provides great support for the three dimensional interpretation of chambers or empty spaces which could hardly be described by conventional light microscopy alone, such as those of the mouth vestibule (Fig. 5.2E, Online Resource 5.2) or the genital atrium with the copulatory organ (Fig. 5.3A–C, Online Resource 5.3, 5.4).

The six eggs observed in the specimens of *T. mamaevi* n. sp. (see Table 5.1) were found at different degrees of development, showing an extended range of length and width. The short abopercular and the long opercular filaments could be distinguished in one mature egg only dissected out of the genital atrium. This observation differs from the diagnosis of the genus, as eggs of the type-species were described as bearing two short filaments (Mamaev 1987). The presence and length of filaments has also been used to characterise the genus *Syncoelicotyloides* (see Mamaev & Brashovian 1989) while no eggs were found in

Syncoelicotyle polyorchis (see Mamaev & Zubchenko 1978). This trait often seems to be insufficiently reliable and unavailable in these monogeneans, consequently the use of egg morphology in generic diagnoses should be treated with caution.

In view of some morphological traits of *Tinrovia mamaevi* n. sp. differing from those of the type-species of the genus, *T. papiliocauda*, some aspects on the generic diagnosis should be emended.

Emended diagnosis of the genus *Tinrovia*: as in Mamaev (1987) except for: Haptor with two lateral frills not joining posteriorly, markedly winged when frills wide; eggs with two filaments (short or long).

Acknowledgements
The authors thank the participants and staff on board during the BIOMARE and ANTROMARE oceanographic campaigns for their assistance. We thank the staff of the Central Service for Experimental Research (SCSIE) of the University of Valencia for technical assistance, in particular to Enrique Navarro Raga for his support. We are grateful to Aneta Kostadinova (Institute of Parasitology, Czech Academy of Sciences) for the translation of the Russian publications. We thank two anonymous reviewers and the editor for their constructive criticisms and helpful corrections improving the manuscript.

Funding
This study was supported by the Spanish Ministry of Science and Innovation (MICINN) projects BIOMARE (CTM2006-13508-C02-01-MAR), ANTROMARE (CTM2009-12214-C02-02-MAR). Part of the samples was collected within the frame of the EU LIFE+Project 'INDEMARES: Inventory and designation of marine Natura 2000 areas in the Spanish sea' (07/NAT/E/000732)

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

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SUPPLEMENTARY ELECTRONIC MATERIAL

Online Resource 5.1 *Tinrovia mamaevi* n. sp. type-material ex *Notacanthus bonaparte,* confocal laser scanning three-dimensional image of a row of clamps on lateral frill (posterior view)

Online Resource 5.2 *Tinrovia mamaevi* n. sp. paratype ex *Notacanthus bonaparte,* consecutive sections of confocal laser scanning micrographs from mouth region

Online Resource 5.3 *Tinrovia mamaevi* n. sp. paratype ex *Notacanthus bonaparte*, confocal laser scanning three-dimensional image of the genital atrium

Online Resource 5.4 *Tinrovia mamaevi* n. sp. paratype material ex *Notacanthus bonaparte,* consecutive sections of confocal laser scanning micrographs from the genital atrium

Chapter 6

Dichelyne (*Cucullanellus*) *romani* n. sp. (Nematoda: Cucullanidae) in notacanthid fishes from the Northeast Atlantic and western Mediterranean

Systematic Parasitology (2015)
doi: 10.1007/s11230-015-9556-1

ABSTRACT

A new cucullanid, *Dichelyne* (*Cucullanellus*) *romani* n. sp. (Nematoda: Cucullanidae), is described from the digestive tract of two notacanthid fishes, *Notacanthus chemnitzii* Bloch and *N. bonaparte* Risso (Notacanthiformes: Notacanthidae), from the Northeast Atlantic and western Mediterranean. The presence of a precloacal sucker and ten pairs of caudal papillae in males allocates it to the subgenus *Cucullanellus* Törnquist, 1931. The new species differs from other members of this subgenus in its larger body size, smaller spicule/body length ratio, the distribution of caudal papillae, and the position of deirids and excretory pore. Both notacanthid fishes act as definitive hosts with slightly larger nematode specimens detected in *N. chemnitzii*. A wide intraspecific variability was found in the distribution of caudal papillae, and in some specimens the position of deirids, excretory pore and length of intestinal caecum also varied. A complete list of all assigned species of the subgenus *Cucullanellus* is presented and discussed as there are several uncertainties regarding the validity and synonymy of some species. This is the first species of *Dichelyne* Jägerskiöld, 1902 in a notacanthid fish and one of the only two records in deep-sea fish species.

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D. González-Solís

INTRODUCTION

The fish family Notacanthidae (Elopomorpha: Notacanthiformes) has a global distribution and includes species inhabiting deep waters between 200–3,500 m (Froese & Pauly 2014). These benthopelagic fishes, commonly known as deep-sea spiny eels, feed on different small benthic invertebrates (crustaceans, echinoderms, polychaetes, bryozoans, hydrozoans) and small nektonic crustaceans (Macpherson 1981, Coggan et al. 1998, Carrassón & Matallanas 2002). Two of the nominal species belonging to this family are the snub-nosed spiny eel *Notacanthus chemnitzii* Bloch with a worldwide distribution, except in tropical waters and the Mediterranean, and the shortfin spiny eel *N. bonaparte* Risso which is restricted to the eastern Atlantic and western Mediterranean (Froese & Pauly 2014).

The knowledge about the parasite fauna of these fish species is scarce. Currently, the known helminth fauna of *N. chemnitzii* comprises seven metazoan parasites: two monogeneans (*Atlanticotyle notacanthi* Mamaev & Zubchenko, 1978 and *Syncoelicotyle polyorchis* Mamaev & Zubchenko, 1978), four trematodes (*Antorchis spinosus* Zubchenko, 1978; *Lecithophyllum euzeti* Gibson & Bray, 2003; *Koiea notacanthi* Bray & Campbell, 1995 and *Panopula spinosa* Zubchenko, 1979) and one nematode (*Cucullanus* sp.) (Gibson et al. 2005, Soares 2007). One trematode (*Steringovermes notacanthi* Bray, 2004), and one cestode (*Bathycestus brayi* Kuchta & Scholz, 2004) species have been recorded in *N. bonaparte* in the Atlantic (Bray 2004, Kuchta & Scholz 2004), and the monogenean, *Tinrovia mamaevi* Isbert, Carrassón, Pérez-del-Olmo & Montero, 2017, was detected in specimens from the Atlantic and the Mediterranean.

During recent studies on the parasitic helminths of marine fishes from the Northeast (NE) Atlantic and western (W) Mediterranean several nematodes were recovered from the digestive tract of *N. chemnitzii* and *N. bonaparte*. On the basis of a detailed morphological study of these specimens by using light and scanning electron microscopy, a new species of *Dichelyne* (*Cucullanellus*) is proposed and described herein. Moreover, the number of species in the subgenus *Cucullanellus* Törnquist, 1931 was revised and a comprehensive list comprising valid, invalid and questionable species assignations is provided.

MATERIAL AND METHODS

Ten individuals of *N. chemnitzii* [total body length (TL) 40.0–100.0 cm] and 21 *N. bonaparte* (TL 25.0–50.0 cm) from the NE Atlantic were collected during a survey off Outer Hebrides in August and September 2004 at depths between 400 and 1,800 m. A total of 156 specimens of *N. bonaparte* (TL 13.5–29.0 cm) was sampled during two projects (BIOMARE, ANTROMARE) carried out in the western Mediterranean.

All fish specimens were measured and weighed; fishes from the NE Atlantic collected by R. Kuchta (Institute of Parasitology, Biology Centre of the Czech Academy of Sciences) were immediately examined for parasites; nematodes collected were washed in physiological saline and preserved in buffered 4% formalin. Fish samples from the western Mediterranean were frozen at -25°C; examination for the presence of parasites was later conducted in the laboratory. Nematodes isolated from these fishes were washed in physiological saline and preserved in 70% ethanol for morphological examination and in 100% ethanol for molecular analysis. For light microscopy, nematodes were cleared in a mixture of glycerine and water in different concentrations. For scanning electron microscopy (SEM), specimens were postfixed in 1% osmium tetroxide (in phosphate buffer), dehydrated through a graded acetone series, critical-point-dried and sputter-coated with gold and examined using a JEOL JSM-7401F scanning electron microscope (JEOL, Tokyo, Japan) at an accelerating voltage of 4 kV (GB low mode). Drawings were made with the aid of a drawing tube. All measurements are given in micrometres, unless otherwise indicated. Nomenclature of the caudal papillae follows Petter (1974).

After morphological identification, the mid-body parts of three adult individuals were dissected out and used for molecular analysis. DNA from all samples was extracted with Qiagen TM (Valencia, California) DNeasy® Blood & Tissue Kit. The partial 18S rRNA gene fragment was amplified by polymerase chain reaction (PCR) using the primers ERIB1 (forward: 5'-ACC TGG TTG ATC CTG CCA G-3') and ERIB10 (reverse: 5'-CTT CCG CAG GTT CAC CTA CGG-3') (Barta et al. 1997). PCR was performed in an Applied Biosystems Veriti 96 Well thermal cycler under the following conditions: initial denaturation of 95°C for 3 min, followed by 35 amplification cycles of 50 s at 94°C (denaturation), 50 s at 56°C (annealing), 80 s at 72°C (extension) and a final extension step for 4 min at 72°C. The rDNA internal transcribed spacer cluster ITS1-5.8S-ITS2 was amplified by PCR using the primers A (forward: 5'-GTC GAA TTC GTA GGT GAA CCT GCG GAA GGA TCA-3') and B (reverse: 5'-GCC GGA TCC GAA TCC TGG TTA GTT TCT TTT CCT-3') (D'Amelio et al. 2000). PCR was performed under the following conditions: initial denaturation of 94°C for 5 min, followed by 30 amplification cycles of 30 s at 94°C, 30 s at 55°C, 70 s at 72°C and a final incubation for 7 min at 72°C. PCR products were purified using a Qiagen TM (Valencia, California) MinElute® PCR Purification Kit. PCR fragments were sequenced by Macrogen (Amsterdam, Netherlands) for both strands using the PCR primers. Sequences were aligned using BioEdit 7.0.1 (Hall 1999) and variable sites were checked visually for accuracy.

RESULTS

Family Cucullanidae Cobbold, 1864
Genus *Dichelyne* Jägerskiöld, 1902

Dichelyne (*Cucullanellus*) *romani* n. sp.

Type-host: Snub-nose spiny eel *Notacanthus chemnitzii* Bloch (Notacanthiformes: Notacanthidae).
Other hosts: Shortfin spiny eel *Notacanthus bonaparte* Risso (Notacanthiformes: Notacanthidae).
Type-locality: Northeast Atlantic, off Outer Hebrides (56°10'N, 09°34'W – 58°44'N, 08°10'W).
Other localities: western Mediterranean, off Spain (40°10'N, 01°30'E – 41°12'N, 02°26'E).
Site in host: Digestive tract (pyloric caeca, stomach, intestine).
Prevalence and mean intensity: Ex *N. chemnitzii* from the NE Atlantic: 40% (4 infected out of 10 examined); 4 nematodes per infected fish. Ex *N. bonaparte* from the NE Atlantic: 29% (6 infected out of 21); 4 nematodes per infected fish. Ex *N. bonaparte* from the W Mediterranean: 46% (71 infected out of 156); 2 nematodes per infected fish.
Specimens deposited: Holotype and allotype ex *N. chemnitzii* and two paratypes ex *N. bonaparte* (collected in August 2004, depth range: 1,400–1,500 m) are deposited in the Helminthological Collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice (Cat. No. IPCAS N-1066); two paratypes ex *N. bonaparte* are deposited in the National Helminthological Collection, UNAM, Mexico (CNHE No. 9369).
Representative sequences: 18S rDNA (KP699577); ITS1-5.8S-ITS2 (KP699576).
Etymology: The new species is named in honour of Dr Roman Kuchta from the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice.

Description (Figs. 6.1–6.3)

General. Large-sized nematodes. Cuticle finely transversely striated. Lateral alae absent. Anterior end rounded, dorsoventrally expanded (Figs. 6.1A–C, 6.2D). Cephalic extremity with 2 pairs of prominent submedian cephalic papillae and a pair of lateral amphids surrounding mouth. Mouth slit-like, dorsoventrally elongated, with an inner collarette armed with numerous triangular denticles (89–108 in number) (Fig. 6.2A–C). Oesophagus expanded in its anterior part, forming a distinct buccal capsule (oesophastome), with

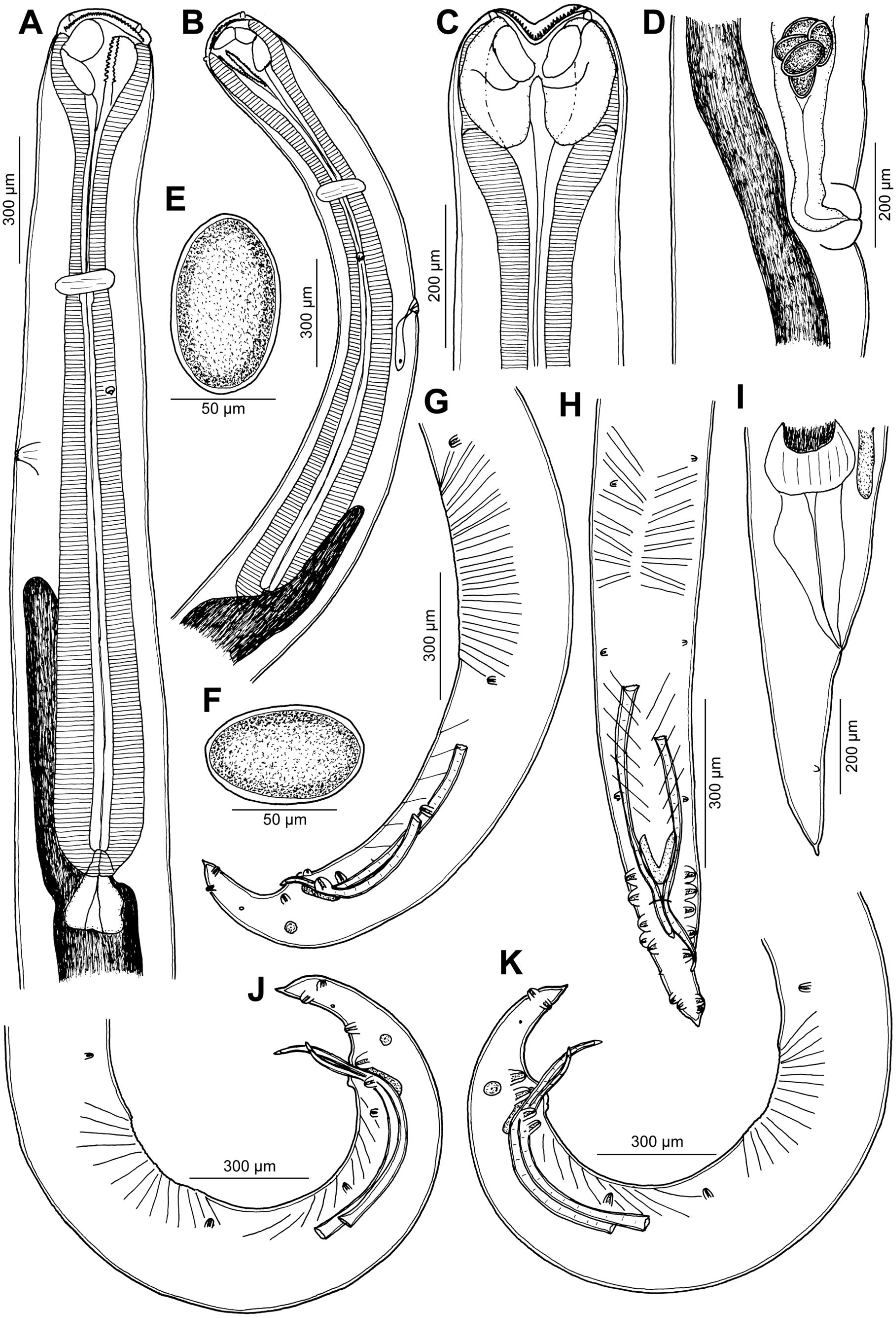

Fig. 6.1 - *Dichelyne* (*Cucullanellus*) *romani* n. sp. ex *Notacanthus chemnitzii*. A, B, Anterior end of body, lateral views, different specimens; C, Cephalic end, dorsoventral view; D, Region of vulva, lateral view; E, F, Egg; G, H, Posterior end of male, lateral and ventral views, respectively; I, Posterior end of female, lateral view; J, K, Posterior end of male, lateral views, both sides of the same specimen to illustrate the variability of papillae.

internal cuticular lining and dorsal denticulate surface (Fig. 6.1A–C). Nerve-ring surrounding oesophagus at it first third. Posterior end of oesophagus broad, opens into intestine through small valve. Ventral intestinal caecum anteriorly directed, extends below level of excretory pore (Fig. 6.1A, B). Caecum absent or poorly-developed in some specimens. Deirids relatively large, posterior to nerve-ring (Figs. 6.1A, B, 6.2D, E), at level of nerve-ring in one specimen. Excretory pore posterior to deirids, clearly anterior to posterior end of oesophagus (Fig. 6.1A, B). Postdeirids asymmetrical, right postdeirid almost equatorial, left postdeirid close to tail. Tail conical, with sharp tip (Figs. 6.1G–K, 6.2G, 6.3B, E).

Male [Based on 4 specimens ex *N. chemnitzii*; measurements of holotype in parentheses. Measurements for 17 specimens ex *N. bonaparte* are provided in Table 6.1.] Body 18.46–21.98 (20.53) mm long, with maximum width 313–395 (360). Oesophagus 1.78–2.00 (1.98) mm long, 8–10% (10%) of body length, 177–219 (200) wide at base; buccal capsule 196–221 (215) wide. Intestinal caecum 520–636 (586) long, intestinal caecum to oesophagus length ratio 29–32% (30%). Nerve-ring, deirids and excretory pore 570–649 (649), 840–971 (889) and 1,109–1,176 (1,176), respectively, from anterior extremity. Right and left postdeirid 3.33–7.28 (3.33) mm and 8.63–10.79 (8.63) mm, respectively, from posterior extremity. Ventral precloacal sucker present (Fig. 6.1G, H), difficult to observe in smaller specimens, variable in size according to the development of males. Distance from ventral precloacal sucker to posterior end 1.56–1.94 (1.78) mm. Ventral muscular bands well developed, starting posterior to ventral precloacal sucker, almost reaching cloacal opening (Fig. 6.1G, H, J, K). Caudal alae absent. Cloaca with slightly elevated lips (Fig. 6.3B, C). Ten pairs of caudal papillae (Fig. 6.1H, J, K): 3 subventral precloacal pairs (pair 1 slightly anterior to ventral precloacal sucker, pair 2 posterior to it, pair 3 between precloacal sucker and cloaca), 5 adcloacal pairs (pair 4 lateral and slightly posterior to cloaca, located between pairs 7 and 8; pairs 5–6 subventral and anterior to cloaca, pairs 7–8 subventral and posterior to cloaca), and 2 postcloacal pairs (pair 9 subdorsal, pair 10 subventral, both near tail tip). In some specimens, pair 1 far anterior to ventral precloacal sucker, almost on anterior border or above it (Fig. 6.1G, H, J); pair 2 near or above posterior border of precloacal sucker (Fig. 6.1H, J, K). Adcloacal papillae in some specimens close to each other on one side and spread out on opposite side (Fig. 6.1J, K). Pairs 4 and 8 fused together in some specimens (Fig. 6.3A, C, D); pair 7 lacking on left side of one specimen (Fig. 6.1G). Pair 9 anterior or posterior to pair 10, the latter near phasmids in one specimen. Additional medioventral unpaired papilla present anterior to cloacal opening (Figs. 6.1G, J, 6.3C). Spicules similar, equal, with proximal end expanded and distal end pointed (Fig. 6.1G, H, J, K); right spicule 608–1,187 (1,187) long, left spicule 527–1,063 (985) long, spicule length 3–8% (5%) of body length. Gubernaculum Y-shaped (Fig. 6.1H), well sclerotised, 171–254 (224) long. Tail 446–594 (540) long. Small, lateral papilla-like outlets (probably representing phasmids) posterior to last pair of adcloacal papillae, situated at 217–295 (295) from posterior extremity (Figs. 6.1G, H, J, K, 6.3D, E).

Female [Based on 5 specimens ex *N. chemnitzii*; measurements of allotype in parentheses Measurements for 20 specimens ex *N. bonaparte* are provided in Table 6.1.] Body 16.94–25.21 (23.13) mm long, with maximum width 306–462 (421). Oesophagus 1.75–2.04 (2.04) mm long, 7–10% (9%) of body length, 153–238 (217) wide at base; buccal capsule 187–253 (246) wide. Intestinal caecum 532–821 (693) long, intestinal caecum to oesophagus length ratio 29–43% (34%). Nerve-ring, deirids and excretory pore 590–618 (614), 855–1,093 (935) and 1,092–1,189 (1,164), respectively, from anterior extremity. Right postdeirid anterior to vulva, left postdeirid posterior to it, at 9.07–15.13 (13.68) mm and 3.81–6.94 (5.56) mm, respectively, from posterior extremity. Vulva with elevated lips (Figs. 6.1D, 6.2F), slightly postequatorial, 10.99–16.03 (14.91) mm from anterior extremity, representing 58–68%

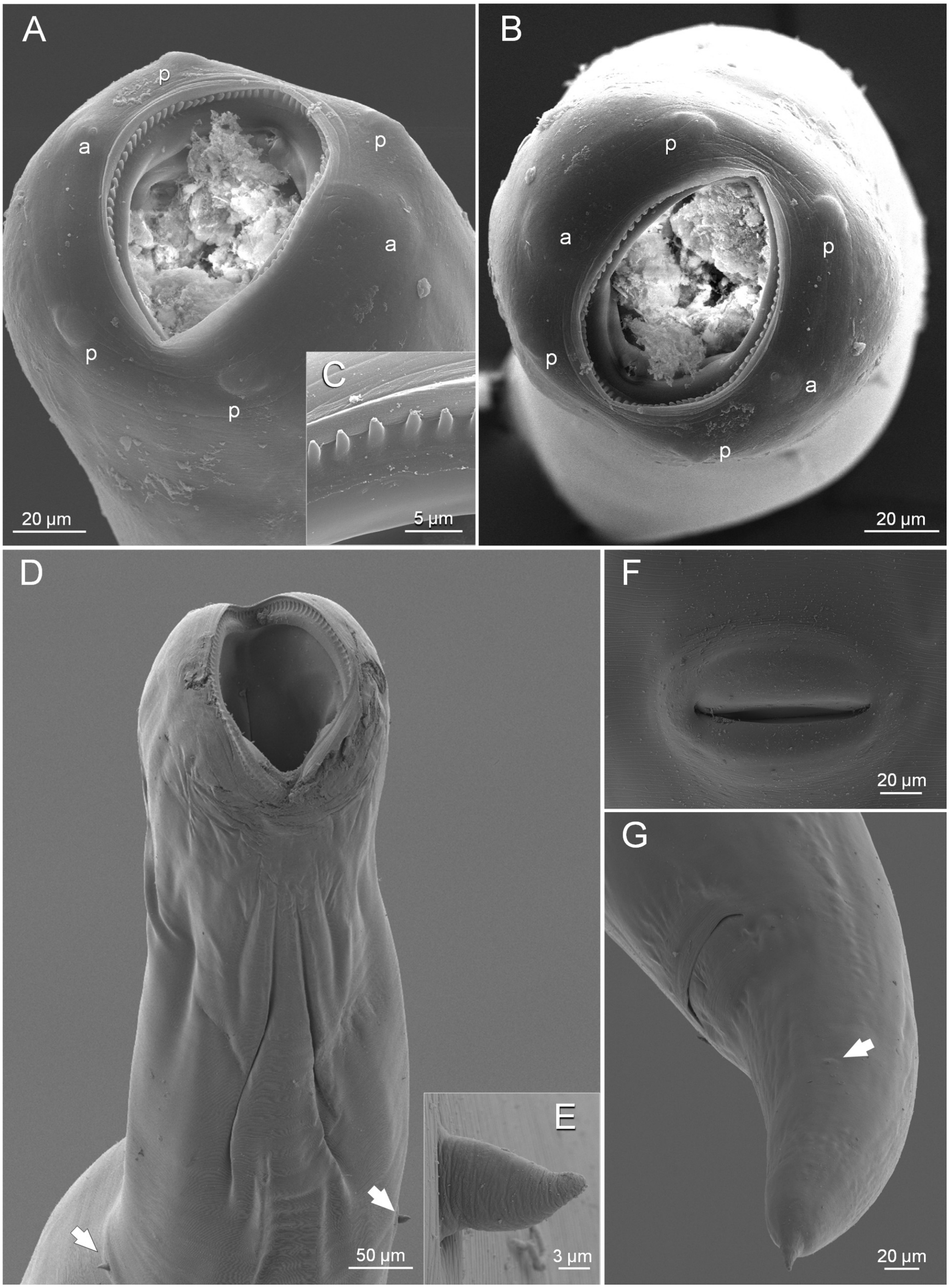

Fig. 6.2 - *Dichelyne* (*Cucullanellus*) *romani* n. sp., scanning electron micrographs (A–C ex *Notacanthus bonaparte*; D–G ex *Notacanthus chemnitzii*). A, Cephalic end, sub-apical view; B, Cephalic end, apical view; C, Detail of teeth; D, Anterior end of body, dorsoventral view (*arrows* indicate deirids); E, Deirid; F, Vulva, ventral view; G, Tail of female, sublateral view (*arrow* indicates phasmid). *Abbreviations*: a, lateral amphid; p, cephalic papillae.

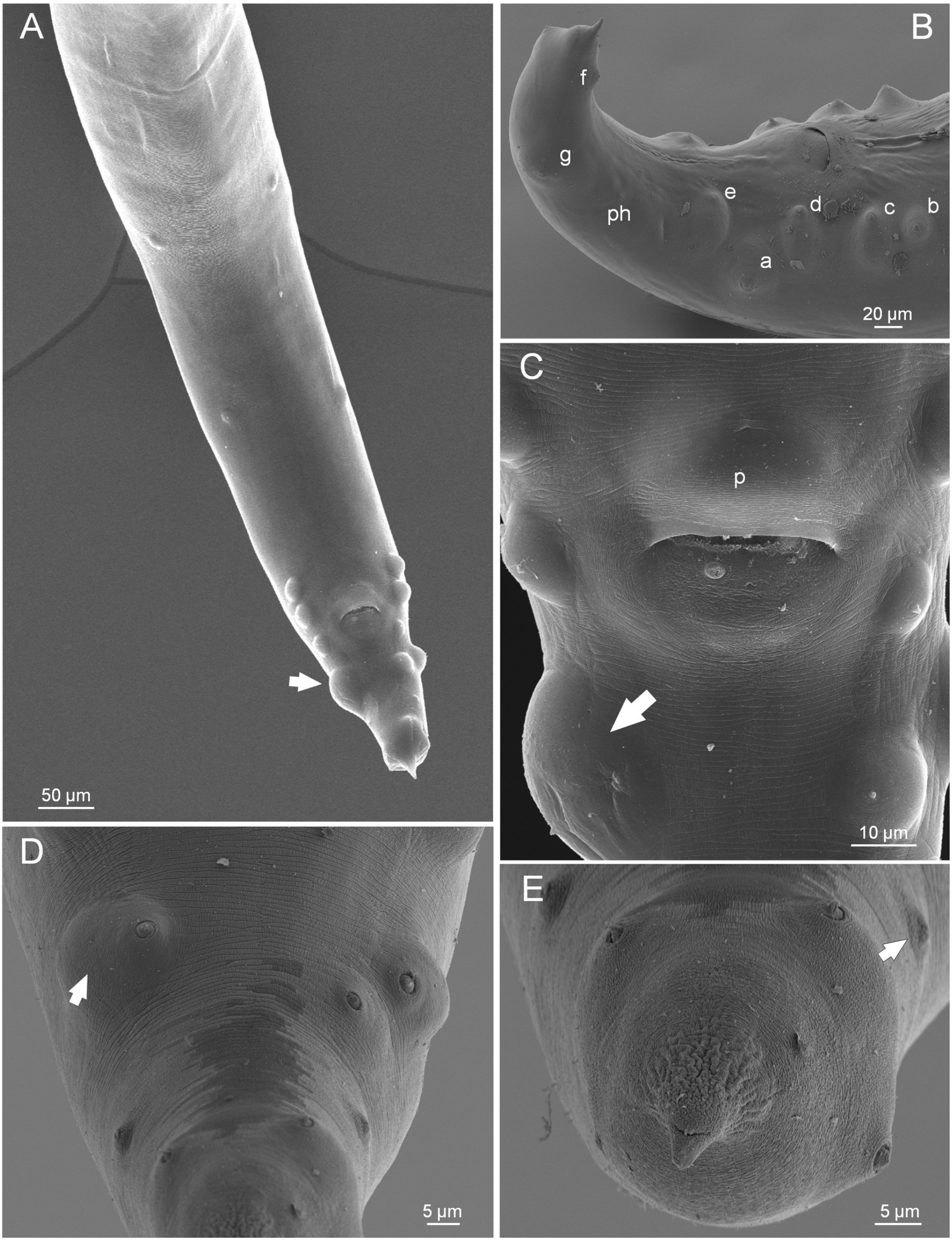

Fig. 6.3 - *Dichelyne* (*Cucullanellus*) *romani* n. sp., scanning electron micrographs of male (A, C–E ex *Notacanthus bonaparte*; B ex *Notacanthus chemnitzii*). A, Posterior end, ventral view (*arrow* indicates fused papillae); B, Tail, subventral view (a–g, papillae 4–10; ph, phasmid); C, Region of cloaca, ventral view (*arrow* indicates fused papillae; p, unpaired medioventral papilla); D, Caudal region, ventral region (*arrow* indicates fused papillae); E, Tail tip, apical view (*arrow* indicates phasmid).

(64%) of body length. Vagina anteriorly directed from vulva (Fig. 6.1D). Uteri amphidelphic. Ovaries extending from just posterior to oesophago-intestinal junction to near anus (Fig. 6.1I). Eggs in utero oval, partly embryonated, 62–94 ´ 43–55 (94 ´ 43) (Fig. 6.1E, F). Tail 357–630 (384) long, with pair of caudal papillae (phasmids) at its mid-length, situated at 170–385 (192) from posterior extremity (Figs. 6.1I, 5.2G).

DISCUSSION

The nematode family Cucullanidae Cobbold, 1864 is mainly characterised by the presence of a buccal capsule (Moravec 1994) and includes parasites of marine, brackish- and freshwater fishes throughout the globe, occasionally occurring in turtles (Petter 1974). To date, six genera are considered in this family, namely: *Cucullanus* Müller, 1777, *Dichelyne* Jägerskiöld, 1902, *Neocucullanus* Travassos, Artigas & Pereira, 1928, *Campanarougetia* Le Van Hoa & Pham-Ngoc-Khue, 1967, *Oceanicucullanus* Schmidt & Kunz, 1969 and *Truttaedacnitis* Petter, 1974 (Petter 1974, Anderson et al. 2009). However, some authors consider the latter genus a subgenus of *Cucullanus* (e.g. Moravec 1979). The genus *Dichelyne* includes three subgenera: *Dichelyne*, *Cucullanellus*, and *Neocucullanellus* Yamaguti, 1941 (Petter 1974, Anderson et al. 2009). The present nematodes possess a precloacal sucker, ten pairs of caudal papillae, and an intestinal caecum, typical features for species belonging to *Dichelyne* (*Cucullanellus*).

To date, the number of recognised species within the genus *Dichelyne* is not completely clarified, but there is an estimation of over 40 nominal species (Li et al. 2014) of which 28 have been assigned to the subgenus *Cucullanellus* (Table 6.2). Of these, *D.* (*C.*) *abbreviatus* (Rudolphi, 1819) should be considered a *species inquirenda* due to its poor description (see Moravec & Justine 2011), *D.* (*C.*) *diplocaecum* Chandler, 1935 cannot be assigned to the subgenus because males are unknown (Petter 1974, Crites & Overstreet 1997, Moravec & Justine 2011) and *D.* (*C.*) *amaruincai* (Freitas, Ibañez & Vicente, 1969) was synonymised with *D.* (*C.*) *elongatus* (Törnquist, 1931) by Vicente et al. (1989), but recent studies considered it as a valid species (Alarcos et al. 2006, Timi et al. 2009). Timi et al. (2009) indicated that this applies only to the nematodes detected in *Paralonchurus peruanus* (Steindachner) from Brazil (Pinto et al. 1992).

Even though the status of *D.* (*C.*) *rodriguesi* (Pinto, Fábio & Noronha, 1970) was confirmed by Vicente et al. (1989), re-examination of the type-material by Timi et al. (2009) revealed that an intestinal caecum is lacking, thus indicating that the specimens may belong to the genus *Cucullanus*, although the bad condition of the material did not allow to clarify its identity (see Timi et al. 2009 for details).

Zdzitowiecki & Cielecka (1996) mentioned that *D.* (*C.*) *dichelyneformis* (Szidat, 1950) shows apparently high similarity and might be conspecific with *D.* (*C.*) *fraseri* (Baylis, 1929), but the type-specimens were not examined; therefore we consider these species distinct. The nomination of *D.* (*C.*) *yvonnecampanae* Timi, Lanfranchi, Tavares & Luque, 2009 is rather questionable since it was not based on the examination of the type-specimens, but just on the brief original description provided by Campana-Rouget (1957). Timi et al. (2009) differentiated this species from its congeners by the closeness of pairs 2 and 3 of the caudal papillae. However, as we have shown, the variability of the caudal papillae might be very high. Therefore, the number of recognised species within the subgenus *Cucullanellus* should be 26, although a careful revision of the type-specimens of several species should be carried out in order to elucidate their status.

Out of the recognised species, none has so far been described for notacanthid fishes (Table 6.2). Apparently, there is only one record of a cucullanid nematode in *N. chemnitzii* from the NE Atlantic (Soares 2007). In general, records of species of *Dichelyne* are scarce in the North

Table 6.1 - Morphometric data for *Dichelyne* (*Cucullanellus*) *romani* n. sp.

Host	***N. chemnitzii***		***N. bonaparte***		***N. bonaparte***	
Locality	**Northeast Atlantic**		**Northeast Atlantic**		**western Mediterranean**	
	males (n = 4)	**females (n = 5)**	**males (n = 2)**	**females (n = 6)**	**males (n = 15)**	**females (n = 14)**
Total length (mm)	18.46-21.98	16.94-25.21	14.83-15.71	17.55-24.95	3.53-12.01	3.96-14.16
Maximum width	313-395	306-462	263-290	89-433	127-268	103-323
Oesophagus length (mm)	1.78-2.00	1.75-2.04	1.80-1.93	1.84-2.29	0.56-1.28	0.48-1.30
Oesophagus length/ total length (%)	8.45-9.65	7.38-10.34	11.47-12.98	9.04-10.46	9.56-17.73	8.77-14.79
Oesophagus width at base	177-219	153-238	161-170	131-230	56-174	52-167
Buccal capsule width	196-221	187-253	182-191	180-243	66-177	60-180
Buccal capsule length	255-302	225-331	317-319	283-376	121-215	126-241
Intestinal caecum length	520-636	532-821	410-675	533-830	136-414	153-524
Intestinal caecum width	89-105	73-113	43-89	69-94	30-64	23-69
Intestinal caecum length/ oesophagus length (%)	29.21-31.93	29.18-42.74	22.75-35.06	29.03-36.32	13.76-38.98	16.13-46.25
Nerve-ring to anterior end	570-649	590-618	541-565	574-691	225-446	209-451
Excretory pore to anterior end	1,109-1,176	1,092-1,189	908-941	1,005-1,369	404-890	416-992
Right deirid to anterior end	866-971	880-952	754-755	901-1,021	335-636	306-669
Left deirid to anterior end	840-940	855-1,093	753-781	674-961	339-684	348-663
Right deirid to posterior end (mm)	8.63-10.79	9.07-15.13	6.54	9.58-12.20	2.07-5.80	2.27-7.53
Left deirid to posterior end (mm)	3.33-7.28	3.81-6.94	3.21	4.56-6.33	0.9-3.62	1.32-6.81
Ventral precloacal sucker to cloaca (mm)	1.08-1.33	-	0.77-0.90	-	0.33-0.80	-
Ventral precloacal sucker to posterior end (mm)	1.56-1.94	-	1.11-1.32	-	0.47-1.11	-
Right spicule length	608-1,187	-	728-744	-	253-597	-
Left spicule length	527-1,063	-	675-727	-	255-546	-
Spicule length/ total body length (%)	2.63-6.09	-	4.46-4.96	-	2.70-7.79	-
Gubernaculum length	171-254	-	163-178	-	52-118	-
Vulva to anterior end (mm)	-	10.99-16.03	-	11.06-15.93	-	2.76-9.60
Vulva length/ total body length (%)	-	57.88-67.62	-	63.00-65.63	-	56-73
Ovary to anterior end (mm)	-	2.48-3.35	-	2.65-8.36	-	1.21-4.98
Ovary to posterior end (mm)	-	0.46-1.09	-	0.51-3.75	-	0.32-1.58
Egg length	-	62-94	-	62-74	-	65-66
Egg width	-	43-55	-	48-54	-	45-50
Tail length	446-594	357-630	315-433	332-481	139-311	180-375
Phasmid to posterior end	217-295	170-385	160-163	141-211	63-145	81-188

Atlantic and especially in the Mediterranean, since most studies have been carried out on shallow-water perciform fishes of different families and geographical regions, such as the Southwestern and western Atlantic (e.g. Szidat 1950, Zdzitowiecki & Cielecka 1996, González-Solís et al. 2002, Timi & Sardella 2002, Alarcos et al. 2006, Timi et al. 2009, Paschoal et al. 2014) or Pacific Ocean (e.g. Moravec & Justine 2011, Li et al. 2014) (Table 6.2).

Table 6.2 - Nominal species of *Dichelyne* (*Cucullanellus*) along with their type-hosts, host families and original geographic distribution.

Species	Type-host	Host family	Locality	Reference
D. (*C.*) *abbreviatus* (Rudolphi, 1819)	*Umbrina cirrosa* (Linnaeus)	Sciaenidae	Mediterranean, off Italy	Petter (1974
D. (*C.*) *adriaticus* (Törnquist, 1931)	*Sparus aurata* (Linnaeus)	Sparidae	Mediterranean, off Italy	Petter (1974)
D. (*C.*) *amaruincai* (Freitas, Ibañez & Vicente, 1969)	*Paralonchurus peruanus* (Steindachner)	Sciaenidae	Southeast Pacific, off Peru	Petter (1974)
D. (*C.*) *branchiostegi* (Yamaguti, 1941)	*Branchiostegus japonicus* (Houttuyn)	Malacanthidae	West Pacific, off Japan	Paschoal et al. (2014)
D. (*C.*) *bullocki* Stromberg & Crites, 1972	*Fundulus heteroclitus heteroclitus* (Linnaeus)	Fundulidae	Northwest Atlantic, off USA	Baker (1984)
D. (*C.*) *cnidoglanis* (Johnston & Mawson, 1945)	*Cnidoglanis macrocephalis* (Valenciennes)	Plotosidae	South Pacific, off South Australia	Paschoal et al. (2004)
D. (*C.*) *cotylophora* (Ward & Magath, 1917)	*Perca flavescens* Mitchill	Percidae	Northwest Atlantic, off USA	Moravec et al. (2011)
D. (*C.*) *dichelyneformis* (Szidat, 1950)	*Eleginops maclovinus* Cuvier	Eligonosidae	South Atlantic, off Argentina	Zdzitowiecki & Cielecka (1996)
D. (*C.*) *diplocaecum* Chandler, 1935	*Ictalarus furcatus* (Valenciennes)	Ictaluridae	Gulf of Mexico, off Texas, USA	Moravec & Justine (2011)
D. (*C.*) *elongatus* (Törnquist, 1931)	Unknown sciaenid fish	Sciaenidae	South Pacific, off Chile	Petter (1974)
D. (*C.*) *fastigatus* Chandler, 1935	*Sciaenops ocellatus* (Linnaeus)	Sciaenidae	Gulf of Mexico, off Texas, USA	Moravec et al. (2011)
D. (*C.*) *fraseri* (Baylis, 1929)	*Chaenocephalus aceratus* (Lönnberg)	Channichthyidae	West Antarctic, off South Georgia	Petter (1974)
D. (*C.*) *hardellus* Khera, 1954	*Hardellus thurjii* (Gray)	Geoemydidae	Uttar Pradesh, off North India	Petter (1974)
D. (*C.*) *kanabus* Walder & Arai, 1974	*Cymatogaster aggregata* Gibbons	Embiotocidae	Northeast Pacific, off Canada	Walder & Arai (1974)
D. (*C.*) *jialaris* Luo, Guo, Fang & Hang, 2004	*Pagrus major* (Temminck & Schlegel)	Sparidae	Taiwan Strait, off China	Luo et al. (2004)
D. (*C.*) *mariajuliae* Alarcos, Timi, Etchegoin & Sardella, 2006	*Pogonias cromis* (Linnaeus)	Sciaenidae	Mar Chiquita, off Argentina	Alarcos et al. (2006)
D. (*C.*) *minutus* (Rudolphi, 1819)	*Platichthys flesus* (Linnaeus)	Pleuronectidae	Baltic Sea	Moravec (1994)
D. (*C.*) *pleuronectidis* (Yamaguti, 1935)	*Pleuronichthys cornutus* (Temminck & Schlegel)	Pleuronectidae	West Pacific, off Japan	Li et al. (2014)
D. (*C.*) *rodriguesi* (Pinto, Fábio & Noronha, 1970)	*Micropogonias* sp. (probably *M. furnieri*; Desmarest)	Sciaenidae	Southwest Atlantic, off Brazil	Petter (1974)
D. (*C.*) *romani* n. sp.	*Notacanthus chemnitzii* Bloch	Notacanthidae	Northeast Atlantic, off Scotland	Present study
D. (*C.*) *sciaenidicola* Timi, Lanfranchi, Tavares & Luque, 2009	*Umbrina canosai* Berg	Sciaenidae	Southwest Atlantic, off Argentina and Brazil	Timi et al. (2009)
D. (*C.*) *sheardi* (Johnston & Mawson, 1944)	*Chironemus maculosus* (Richard)	Chironemidae	South Pacific. off Australia	Paschoal et al. (2014)
D. (*C.*) *szidati* Timi & Sardella, 2002	*Acanthisthius brasilianus* (Cuvier)	Serranidae	Southwest Atlantic, off Argentina	Timi & Sardella (2002)

Table 6.2 - (Continued).

Species	Type-host	Host family	Locality	Reference
D. (*C.*) *travassosi* (Guimarães & Cristofaro, 1974)	*Balistes vetula* (Linnaeus)	Balistidae	Southwest Atlantic, off Brazil	Vicente et al. (1989)
D. (*C.*) *trionyxi* Chakravarty & Majumdar, 1961	*Nilssonia gangetica* (Cuvier)	Trionychidae	Indian Ocean, off eastern India	Chakravarty & Majumdar (1961)
D. (*C.*) *tripapillatus* (Gendre, 1927)	*Diplodus cervinus* (Lowe)	Sparidae	East Atlantic, off Mauritania	Petter (1974)
D. (*C.*) *tornquisti* Paschoal,Vieira, Cezar & Luque, 2014	*Orthopristis ruber* (Cuvier)	Haemulidae	Southwest Atlantic, off Brazil	Paschoal et al. (2014)
D. (*C.*) *wallagoni* Chakravarty & Majumdar, 1961	*Wallago attu* (Bloch & Schneider)	Siluridae	Indian Ocean, off eastern India	Chakravarty & Majumdar (1961)
D. (*C.*) *yvonnecampanae* Timi, Lanfranchi, Tavares & Luque, 2009	*Umbrina canariensis* Valenciennes	Sciaenidae	Eastern Atlantic, off West Africa	Timi et al. (2009)

Dichelyne (*C.*) *szidati* Timi & Sardella, 2002, *D.* (*C.*) *mariajuliae* Alarcos, Timi, Etchegoin & Sardella, 2006, *D.* (*C.*) *sciaenidicola* Timi, Lanfranchi, Tavares & Luque, 2009 and *D.* (*C.*) *tornquisti* Paschoal, Vieira, Cezar & Luque, 2014, reported from the Southwestern Atlantic (Argentinean waters) (Table 6.2), can be clearly differentiated from *D.* (C.) *romani* n. sp. in the position of the excretory pore and deirids near to or at posterior end of oesophagus, and the greater spicule to body length ratio (8–22 *vs* 5%). Similarly, *D.* (*C.*) *pleuronectidis* (Yamaguti, 1935) from the East China Sea has deirids at the posterior third of oesophagus or anterior to the oesophago-intestinal junction, excretory pore anterior to deirids, and greater spicule to body length ratio (15%) (Li et al. 2014).

In the Mediterranean, three species have been reported, i.e. *D.* (*C.*) *adriaticus* (Törnquist, 1931), *D.* (*C.*) *minutus* (Rudolphi, 1819), and *D.* (*C.*) *tripapillatus* (Gendre, 1927), though the latter two were originally described from other geographical areas (see Table 6.2) (Törnquist 1931, Gibson 1972, Moravec 1994, Ternengo et al. 2009). The new species differs from *D.* (*C.*) *minutus* in having larger body size (males: 3.53–21.98 *vs* 2.62–4.60 mm; females: 3.96–25.21 *vs* 2.53–4.90 mm), excretory pore located distinctly anterior to the posterior end of oesophagus, smaller spicule to body length ratio (2.6–7.8 *vs* 22%) and in parasitising species of different fish family (Notacanthidae *vs* Pleuronectidae) (Moravec 1994). *Dichelyne* (*C.*) *adriaticus* originally described from a sparid fish has a smaller body size (males 1.90–2.68 mm; females 2.43–3.70 mm) (Törnquist 1931) than the new species described here. Although some specimens of *D.* (*C.*) *romani* n. sp. have a comparable body size as *D.* (*C.*) *adriaticus*, they exhibit a larger distance from the nerve-ring to the anterior extremity and a longer oesophagus and tail. *Dichelyne* (*C.*) *tripapillatus* differs from the new species in having two intestinal caeca (Li et al. 2014).

There are three species of *Dichelyne* from deep-sea or cold-water fishes. *Dichelyne* (*D.*) *etelidis*

Moravec & Justine, 2011, described from the deepwater red snapper *Etelis carbunculus* Cuvier (Lutjanidae) in the South Pacific Ocean (Moravec & Justine 2011), belongs to a different subgenus. *Dichelyne* (*C.*) *dichelyneformis* described from fishes off Tierra del Fuego, Argentina (Szidat 1950), differs from *D.* (*C.*) *romani* n. sp. in having deirids and excretory pore allegedly situated anterior to nerve-ring, smaller body length (males and females: 4.10 mm) and greater spicule to body length ratio (26%). *Dichelyne* (*C.*) *fraseri* collected from sub-Antarctic and Antarctic fishes (Baylis 1929, Zdzitowiecki & Cielecka 1996) has a similar position of the excretory pore, deirids, and distribution of the caudal papillae as the new species, but smaller body size (males: 3.06–5.55, females: 3.34–7.34), and larger spicule to body length ratio (22%).

In the present study the number of the NE Atlantic fish samples was smaller in comparison to those collected in the Mediterranean, though the better condition of these samples from the former area facilitated the morphological analysis and the selection of the type- and paratype specimens. Although the number of nematodes measured from the Atlantic and Mediterranean was different, it is noteworthy to indicate that there exist differences in their body size from both regions and hosts. Specimens from the Mediterranean were distinctly smaller than those from the Atlantic, where male nematodes from *N. bonaparte* were also smaller than those from *N. chemnitzii* (14.83–15.71 *vs* 18.46–21.98 mm) (see Table 6.1 for ranges).

Despite the biometric differences, nematode specimens from both hosts and areas were considered to belong to the same species because most body ratios and other values were identical among them (see Table 6.1). Differences in the development of nematodes related to host species have also been observed in other cucullanid nematodes, such as *D.* (*C.*) *sciaenidicola*, which attained a larger body size in one of the sciaenid host species studied (*Micropogonias furnieri* [Desmarest]) than in *Umbrina canosai* Berg (Timi et al. 2009). Parasite body size can be affected by biological-environmental parameters, such as temperature, host species, host size and condition (Poulin 1998, Timi et al. 2009, Sasal et al. 2000), as well as biochemical factors (e.g. lipid content in host tissue) or the infection site (Strømnes & Andersen 2003). Moreover, larger hosts offer more resources and feeding places, thus allowing parasites to grow better (Sasal et al. 2000). The larger size of Atlantic notacanthids in comparison to Mediterranean fish is a common phenomenon occurring in deep-sea fish of the two regions (Stefanescu et al. 1992, Massuti et al. 2004). Apparently, latitudinal gradients and ecological factors (e.g. temperature, limited resources) might affect the body size of deep-sea fish (Stefanescu et al. 1992), thus affecting host physiology and producing cascading effects on the nematodes (Poulin 1998).

A broad intraspecific variability was observed in the new species, especially in the distribution of the caudal papillae and in relation to the presence of intestinal caecum. This variation was not only observed among specimens from different hosts and geographical regions, but also within the specimens from the same host specimen. De & Maity (1995) observed similar variations in *D.* (*D.*) *alatae* De & Maity, 1995 parasitising a percoid fish (Sillaginidae) from West Bengal, India and detected an additional pre- and postcloacal papilla on one side of the body of two different specimens, respectively. More recently, Li et al. (2014) showed strong morphological differences in *D.* (*C.*) *pleuronectidis* and, on the basis of molecular analysis, confirmed that observed differences in the number of intestinal caeca (one, two or absent) and the position of deirids (at the level of posterior third of oesophagus or oesophago-intestinal junction) can be considered as intraspecific variability. Sometimes, such differences could be related to the fixation procedure or the examination of material from fresh or frozen hosts.

This is the first report of a species of the subgenus *Cucullanellus* in a notacanthid fish and the fourth species recorded in the Mediterranean.

Acknowledgements

The authors thank the staff of the Laboratory of Electron Microscopy, Institute of Parasitology, Biology Centre of the Academy of Sciences of the Czech Republic, České Budějovice for technical assistance, and Blanka Škoríková from the same institution for her help in preparing drawings and plates. We thank David Pérez-i-García and Anna Soler-Membrives for the molecular characterization of specimens. We also thank Tomáš Scholz for his financial support during WI stay in the above-mentioned institute. This study was supported by the Spanish Ministry of Science and Innovation (MICINN) projects BIOMARE (CTM2006-13508-C02-01MAR), ANTROMARE (CTM2009-12214-C02-02) and the Czech Science Foundation (Project No. P505/12/G112).

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Chapter 7

Seasonal variation of parasite communities of *Notacanthus bonaparte* Risso, 1840 (Notacanthiformes: Notacanthidae) over the Northwest Mediterranean slope

ABSTRACT

In the last decades fishing activities have spread from coastal to deeper waters with serious impacts on the deep-sea ecosystems and its fauna, which is highly susceptible to these impacts owing to its life history traits. The implementation of protection measures is necessary, but the knowledge on this biome is scant, and often limited to species of commercial value. Here we present information on the parasite communities of *Notacanthus bonaparte* sampled from three bathymetric strata between 600 and 1,800 m in the western Mediterranean Sea (Balearic Sea, Spain). Samples were taken over the four seasons in the years 2007-2008 and in 2011. The aim of this work was to assess the effect of host specific parameters as well as environmental conditions and spatial and temporal variation on the composition and structure of the parasite communities. To the best of our knowledge, this study is the first survey to analyse and describe complete parasite communities of the deep-sea fish *N. bonaparte*. We found poor parasite communities usually rather described for bathypelagic fishes, than for fishes with benthic feeding habits such as *N. bonaparte*, with two out of five species considered as accidental infections. The infracommunity composition is defined by the factors, depth, maturity status (size) and sex. The most abundant dominating species, cucullanid larvae, seem to be accumulated during host life showing higher abundances in larger fish of deeper waters on the middle and lower slope, and in larger sized females. As larvae of some cucullanids are supposed to survive as free-living stages in the sediment, *N. bonaparte* might ingest this parasite when feeding on sessile or slow moving benthic organisms. It is suggested that *N. bonaparte* acts as important intermediate host for this larvae and that infected fish would be preyed by larger predators that feed in this deep-sea area. The single monogenean species *Tinrovia mamaevi* was recorded in the upper slope mainly during the spring season. Its higher prevalence in the shallowest depth range could be related to higher host densities observed in these depths. Prevalences of this parasites species was related to temperature and salinity, but measured variations for these parameters were marginal. Therefore temporal and depth-related distribution patterns may also be driven by additional abiotic factors. Under consideration of previously published diet data this study indicates potential pathways other than expected for heteroxenous parasites using *N. bonaparte* as intermediate and definitive host.

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INTRODUCTION

Even though the network of deep-sea ecosystems is considered as the largest biome within the global biosphere, the knowledge on its pelagic and benthic biodiversity is still scant (Gage & Tyler 1991, Ramirez-Llodra et al. 2010). In the 19th century investigations of the deep-sea fauna and their habitats began and, especially in the last 30 years, this research advanced also driven by technological developments (Ramirez-Llodra et al. 2010). Though, obtaining samples of deep-sea organisms to study their biology and ecology is still a major obstacle due to the expense of the research expeditions, logistical constraints, and frequently few species and small sample sizes available (Cailliet et al. 2001, Klimpel et al. 2009). Consequently, even entering the 21st century basic knowledge is lacking for many aspects in this ecosystem concerning e.g. temporal processes, species richness and distribution, and biological composition in the different habitats (Glover et al. 2010, Tittensor et al. 2010). This applies also to the deep-sea fish fauna where it was already indicated that scientific knowledge clearly lags behind the development of commercial deep-sea fisheries and its impact on the ecosystem (Haedrich et al. 2001, Devine et al. 2006). Often, this lack of knowledge is demonstrated even more clearly in non-commercial species as these are of lower research priority (Damalas et al. 2010, Thomsen et al. 2012, Wiecaszek et al. 2015).

The fish family Notacanthidae (Elopomorpha: Notacanthiformes) is represented by non-commercial species and exhibits a global distribution comprising species which inhabit deep waters between 200–3,700 m (Nelson 2006). These benthopelagic fishes, commonly known as deep-sea spiny eels and bathydemersal, feed on different small benthic invertebrates (crustaceans, echinoderms, polychaetes, bryozoans, hydrozoans) and small nektonic crustaceans (Macpherson 1981, Coggan et al. 1998, Carrassón & Matallanas 2002). The short-fin spiny eel, *Notacanthus bonaparte* Risso, 1840, was first described from the Western basin of the Mediterranean Sea, and its distribution ranges from the Northeast Atlantic off Faroe Islands to Mauritania (Froese & Pauly 2017), including also the Eastern basin of the Mediterranean Sea (Basusta et al. 2002, Deval 2013). While this species is found in depth ranges between 200–2,200 m in Mediterranean Sea (Moranta et al. 1998, D'Onghia et al. 2003, 2004, Rodríguez-Romeu et al. 2016), maximum abundances in the western Mediterranean were detected in depths between 580–1,450 m where catches were made from 580 to 2,250 m (Stefanescu et al. 1992, Rodríguez-Romeu et al. 2016).

Studies focussing on this species are scarce and available information partly derived from surveys exploring the occurrence and distribution of fish assemblages. Therefore, along with the information on its spatial and depth-related distribution and its proportional representation within the fish community (e.g. Stefanescu et al. 1992, Moranta et al. 1998, D'Onghia et al. 2003, 2004), the biological data currently available comprise some information on its reproduction (Coggan et al. 1998, Fernandez-Arcaya et al. 2013, Rodríguez-Romeu et al. 2016) and diet from the Northeast Atlantic and the western Mediterranean Sea (Lozano Cabo 1952, Macpherson 1981, Coggan et al. 1998, Rodríguez-Romeu et al. 2016, Preciado et al. 2017).

Considering the limited range of issues covered concerning this species, information on its parasite fauna is very scarce and to the best of our knowledge no study exist which explored the parasite communities of this host species. To date, only a few studies reporting occasional presence of parasites in this fish have been published and mostly include descriptions of individual parasite species (Bray 2004, Kuchta & Scholz 2004, Isbert et al. 2015, 2017). The overall scarce data on the parasites corresponds to the common consideration that available data and scientific information on the parasite diversity in oceanic regions and habitats such as the deep-sea, is practically non-existent (Rohde 2016). Though, recent publications dealing with parasites of deepwater fishes from the Northeast Atlantic Ocean (e.g. Klimpel et al. 2008a, 2010, Palm & Klimpel 2008), and the western Mediterranean Sea (e.g. Mateu et al. 2014, Constenla et al. 2015, Pérez-i-García et al. 2015, Dallarés et al. 2016) reflect the increased effort to gain insight in the parasite communities of deep-sea fishes and partly using parasites as biological indicators.

Parasites are used as natural tags and are considered as powerful tool providing insights in different aspects of life history and ecological traits of marine organisms such as fishes (Campbell et al. 1980, Marcogliese 2005). Their study has been recommended especially for deep-sea and rare marine species (MacKenzie & Abaunza 1998), where often information is difficult to obtain e.g. due to remote and hardly accessible areas. In particular, trophic relationships in marine communities are reflected by heteroxenous parasites where different parasite life stages pass through the food web by infecting intermediate and definitive hosts species. Parasites can reveal information on the food web structure and predator-prey interactions (Marcogliese 2002), and indicate the past food acquisition of individual hosts providing valuable information on long-term feeding habits and diet niches of the species in a given ecosystem (Lafferty et al. 2008, Knudsen et al. 2010). The presence of parasites in their hosts can reflect depth and seasonality owing e.g. to the presence of their intermediate hosts, seasonal vertical migration or food supply, as their life cycles are adapted to repetitive seasonal patterns (Marcogliese 2002, 2005 and references therein). It is suggested that phytodetritus originating from primary production processes and remains of animals descending from the surface waters partly represent an important seasonal food supply for the deep-sea communities (Bray 2005). The potentially different supply of organic matter into the deep-sea is supposed to influence also the variability observed in parasite communities (Dallarés et al. 2014).

The aim of the present study is to provide, for the first time, detailed information on the parasite communities of *N. bonaparte* from different seasons and depth ranges of the slope in the western Mediterranean Sea. Furthermore, we will assess the link between parasite community composition and structure and measured environmental parameters from this area, to detect potential seasonal and depth related variability in these communities.

MATERIAL AND METHODS

Sample collection

A total of 150 specimens of *Notacanthus bonaparte* was sampled during two projects (BIOMARE, ANTROMARE) carried out on the slope off Catalonia (Spain) in the Balearic Sea (Northwestern Mediterranean Sea) at depths between 620 and 1,750 m in 2007–2008 and 2011 during all four seasons (Fig. 7.1, Table 7.1). The fishing hauls were conducted with a semi-balloon otter-trawl (OTSB-14) for demersal sampling (Merrett & Marshall 1981). Environmental parameters (temperature in ºC, salinity in psu, oxygen concentration in mL/L and turbidity in voltage units) were recorded by casts with a SBE25 CTD profiler at 5 m above the sea bottom.

Morphometrical data (total length (TL)) were taken from individual fish immediately on board and was recorded to the nearest 0.1 cm. The specimens were frozen at -25ºC for posterior inspection of parasite load.

Parasitological examination

In the laboratory, prior to examination and dissection, each fish specimen was thawed, viscera were removed and gonad weight were recorded to the nearest 0.1 mg. External and internal body surfaces were inspected and gills and all organs were examined separately for the presence of metazoan parasites by means of a

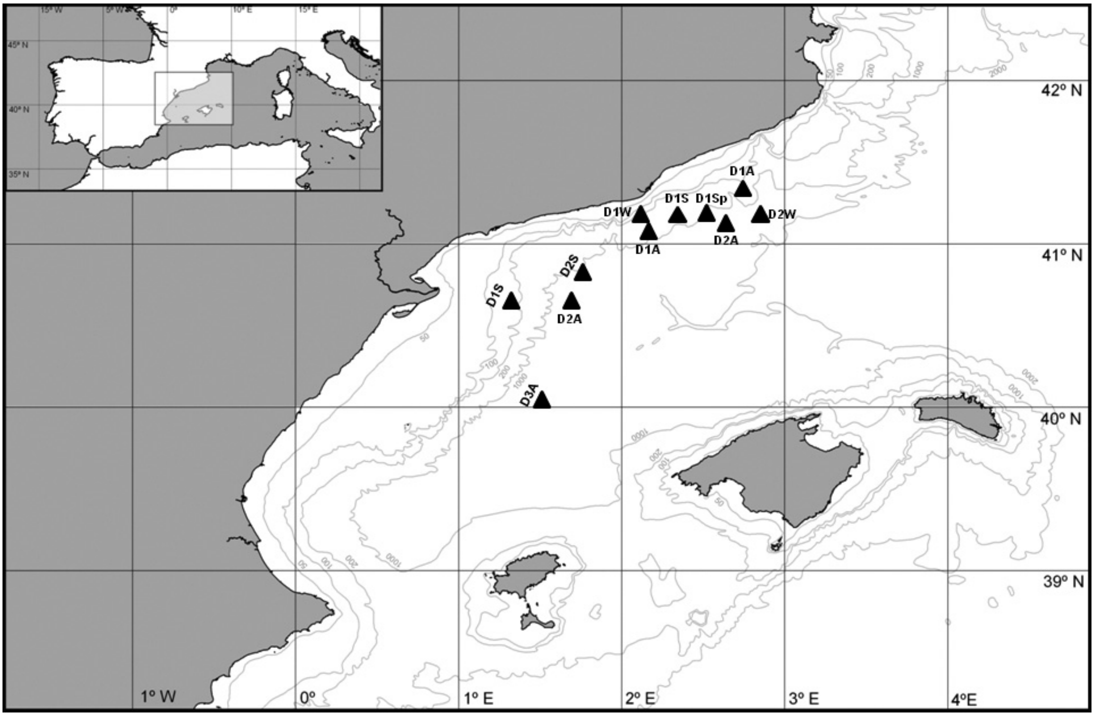

Fig. 7.1 - Study area with sampling sites and depths within the slopes of the Norteastern Iberian peninsula. Abrreviations for survey and DepthSeason combinations: D1 at 600–1,000 m, D2 at 1,000–1,400 m, D3 at 1,400–1,800 m; Seasons: W–winter, Sp-spring, S-summer, A–autumn).

stereomicroscope. Further, the entire body musculature was sliced and examined using glass plate compression method under stereomicroscope. Metazoan parasites were collected and preserved in 70% ethanol for subsequent identification, except for some specimens which were fixed in saline formalin for additional morphological studies. Some larval and adult nematodes were fixed in 100% ethanol for molecular identification analyses. In order to identify the specimens to the lowest possible taxonomic level, different techniques, according to the different groups have been applied. Platyhelminths were stained with iron acetocarmine (Georgiev et al. 1986), dehydrated in an alcohol series, cleared in dimethyl-phthalate and mounted in Canada balsam for further inspection with a light microscope. Nematodes were examined in saline solution or in glycerine mounts after dehydration in a graded glycerine-ethanol series. All parasites were identified to the lowest possible taxonomic level and counted.

Data analysis

The ecological terms for parasite communities used and the prevalence (%P) and mean abundance (MA) calculated in this work, follow Bush et al. (1997). Infracommunity parameters such as mean parasite species number (infracommunity richness), parasite richness (Margalef Species Richness) and diversity (Brillouin’s diversity index) were also calculated.

In the analysis of the parasite communities of N. *bonaparte,* data were grouped into two size categories related to the maturity status of fish

Table 7.1 - Haul data with date, mean depths, coordinates, number auf caught specimens, code for DepthSeason combinations and environmental parameters measured during each haul. DepthSeason combinations: Depth range: D1 at 600–1,000 m, D2 at 1,000–1,400 m, D3 at 1,400–1,800 m (Seasons: W-winter, Sp-spring, S-summer, A-autumn). Environmental variables: T: temperature, S: salinity, O: oxygen concentration, Turb: turbidity.

Trawl	Date	Mean depth (m)	Coordinates		*n*	DepthSeason	*T* (°C)	*S* (psu)	*O* (mL/L)	Turb (V)
			Latitude	Longitude						
B1O2	25/02/2007	797.5	41°09.93 N	2°19.38 E	8	D1W	13.19	38.51	4.12	1.10
B2O2	28/04/2007	650	41°11.11 N	2°25.31 E	3	D1Sp	13.29	38.53	5.76	0.27
B2O3	28/04/2007	796.5	41°09.85 N	2°26.23 E	1	D1Sp	13.24	38.52	5.77	0.44
B2O4	29/04/2007	808.5	41°09.84 N	2°26.18 E	1	D1Sp	13.24	38.52	5.77	0.44
B2O5	29/04/2007	660.5	41°14.50 N	2°27.56 E	1	D1Sp	13.29	38.53	5.76	0.27
B3O3	30/06/2007	804	41°08.50 N	2°23.37 E	2	D1S	13.18	38.51	5.78	0.08
B3O4	01/07/2007	1071	41°07.13 N	2°22.49 E	9	D1S	13.18	38.51	5.78	0.08
B3O6	05/07/2007	666.5	41°05.82 N	2°13.04 E	3	D1S	13.41	38.53	3.95	0.40
B3O7	05/07/2007	802.5	41°03.76 N	2°10.17 E	4	D1S	13.17	38.50	5.78	0.09
B4O3	02/10/2007	810.5	41°13.84 N	2°36.18 E	2	D1A	13.18	38.51	8.25	0.18
B4O4	03/10/2007	1025	41°12.17 N	2°41.41 E	2	D2A	13.18	38.51	8.25	0.18
B5O1	24/02/2008	1094	41°09.70 N	2°40.89 E	2	D2W	13.12	38.48	8.27	0.06
B5O5	26/02/2008	996.5	41°15.54 N	2°50.09 E	4	D2W	13.12	38.48	8.27	0.06
A201	18/06/2011	639	40°34.50 N	1°26.51 E	8	D1S	13.14	38.50	4.16	1.03
A202	18/06/2011	646	40°34.45 N	1°26.43 E	2	D1S	13.14	38.50	4.16	1.03
A204	19/06/2011	627	40°54.39 N	1°34.60 E	1	D1S	13.12	38.50	4.14	0.24
A205	19/06/2011	627.5	40°54.71 N	1°34.80 E	1	D1S	13.12	38.50	4.14	0.24
A206	19/06/2011	648	40°54.32 N	1°34.82 E	3	D1S	13.12	38.50	4.14	0.24
A207	20/06/2011	620	40°41.00 N	1°26.44 E	4	D1S	13.08	38.49	4.20	0.00
A208	20/06/2011	631.5	40°40.85 N	1°26.44 E	6	D1S	13.08	38.49	4.20	0.00
A210	22/06/2011	623.5	40°40.89 N	1°26.44 E	2	D1S	13.10	38.49	4.17	0.00
A212	23/06/2011	1060	40°47.22 N	1°35.23 E	4	D2S	13.10	38.49	4.17	0.00
A213	23/06/2011	1052	40°55.87 N	1°50.32 E	15	D2S	13.10	38.49	4.17	0.00
A301	14/10/2011	650	41°05.88 N	2°13.33 E	8	D1A	13.28	38.54	3.91	0.33
A302	14/10/2011	650	41°07.85 N	2°05.31 E	14	D1A	13.38	38.55	3.86	0.64
A303	15/10/2011	1009	40°50.80 N	1°43.94 E	19	D2A	13.11	38.49	4.21	0.24
A304	15/10/2011	1200	40°41.95 N	1°37.46 E	2	D2A	13.12	38.48	4.25	0.28
A305	16/10/2011	1500	40°10.20 N	1°38.25 E	1	D3A	13.18	38.49	4.32	0.21
A306	16/10/2011	1750	40°09.65 N	1°30.22 E	14	D3A	13.18	38.49	4.32	0.21
A309	17/10/2011	1050	39°23.12 N	1°18.45 E	2	D2A	13.07	38.49	4.29	0.25
A313	21/10/2011	1500	40°57.99 N	1°02.87 E	2	D3A	13.12	38.49	4.31	0.22

Table 7.2 - Calculated means and standard deviations for host TL and parasite infracommunity parameters in total and for the eight DepthSeason combinations. DepthSeason combinations: Depth range: D1 at 600-1,000 m, D2 at 1,000-1,400 m, D3 at 1,400-1,800 m (Seasons: W-winter, Sp-spring, S-summer, A-autumn).

	Total	**D1W**	**D1Sp**	**D1S**	**D1A**	**D2W**	**D2S**	**D2A**	**D3A**
	n = 150	**n = 8**	**n = 6**	**n = 45**	**n = 24**	**n = 6**	**n = 19**	**n = 25**	**n = 17**
TL (cm)	21.76±2.22	21.99±1.91	22.83±1.58	22.42±1.92	20.05±1.94	21.67±1.11	23.21±1.07	20.47±2.75	22.51±1.73
Infracommunity abundance	94.34±112.56	65.63±90.81	71.17±57.65	67.93±118.87	67.54±102.50	92.67±100.61	141.26±74.67	82.04±64.54	190.00±165.71
Infracommunity richness	1.58±0.62	1.71±0.76	2.67±0.82	1.61±0.59	1.50±0.51	1.33±0.51	1.58±0.51	1.60±0.65	1.25±0.45
Margalef Species Richness	0.17±0.21	0.17±0.17	0.47±0.29	0.23±0.27	0.15±0.16	0.10±0.17	0.12±0.11	0.16±0.18	0.06±0.11
Brillouin diversity index	0.08±0.13	0.08±0.08	0.19±0.16	0.11±0.18	0.07±0.10	0.06±0.10	0.04±0.05	0.10±0.16	0.02±0.06

hosts (further referred to as fish size): immature (64 individuals) (size 1; standard length < 220 mm) and mature individuals (83 individuals) (size 2; standard length ≥ 220 mm) (Lozano Cabo 1952), while three individuals could not be determined and were not considered in analyses focussed on the factor fish size. Eight categories (DepthSeason) were established in cases where samples were available from one of the three depth categories [600–1,000 (D1), 1,000–1,400 (D2) and 1,400–1,800 (D3)] which were combined with the different seasons (winter (W), spring (Sp), summer (S), autumn (A)). Species with an overall prevalence of at least >5% across all fish examined were considered common and used for analyses. Parasite infrapopulations (all parasites of a given species in an individual fish) and infracommunities (all infrapopulations in an individual fish) were used as replicate samples in all analyses.

All data was tested for normality and homoscedasticity in order to comply with requirements and only infracommunity richness and Margalef Species Richness values were ln (x+1) -transformed prior to the analysis. Significant relationships between fish TL and fish sex were tested by means of General Linear Models (GLM). Possible effects of the factor DepthSeason, using fish size or sex as cofactor, were tested for parasite infracommunity parameters (infracommunity richness, Margalef Species Richness and Brillouin's diversity index) using the general linear model (GLM), with post-hoc pairwise comparisons (Tukey).

Differences in abundance and prevalence of the parasite species of the common species (%P >5) were tested using Generalized Linear Model (GZM) with post-hoc pairwise comparisons (Tukey) for the factor DepthSeason, using fish size and sex as cofactors (applying negative-binomial model for abundance and logistic model for prevalence). GZM analyses were repeated using samples from summer and autumn separately, collected in different depths (D1–D2 and D1–D3, respectively). These analyses were conducted in order to test depth variability in prevalence and abundance of common parasites together with the effect of the cofactors fish size and sex. Similarly, seasonal samples from depth strata 1 (D1) were used to test seasonal variability in prevalence and abundance for all common species, also including the cofactors fish size and sex.

Community similarity analyses were carried out with PERMANOVA+for PRIMER v6 software (Anderson et al. 2008). Permutational multivariate analyses of variance (PERMANOVA; Anderson 2001) with the fixed factors DepthSeason, or season and depth separately were used to assess the effects of these factors on the composition and structure of the parasite communities. Parasite abundance data were square-root transformed and permutation P-values were obtained under unrestricted permutation of raw data with 9,999 permutations and the SUM OF SQUARES TYPE I (sequential) in all cases. PERMANOVA provides estimated components of variation (ECV) indicating the relative importance of each factor included in the analysis; here it is provided as [ratio (%) = (estimated magnitude of variance for each factor)/(sum of estimated variances)*100]. SIMPER procedure was also used in order to identify the species mostly contributing to dissimilarity of communities between the different factors.

A multivariate Canonical Correspondence Analysis (CCA) (Ter Braak 1986) was applied to assess the potential impact of environmental variables (temperature, oxygen, salinity, turbidity) on the prevalence of the common parasite species. Environmental variables were ln (x+1) -transformed prior to the analysis. Arrows in CCA plots represent explanatory variables and they are proportional in length to their importance on the explained variable. The arrow points in the direction of maximum change in the value of the associated variable.
Metazoan infracommunity richness, Margalef Species Richness and Brillouin's diversity index were calculated with PRIMER v6 (Anderson et al. 2008). GLM and GZM were conducted by means of SPSS Statistics 17.0 and the CCA plot using XLSTAT Evaluation 18.06 (Addinsoft).

RESULTS

The total length of *N. bonaparte* specimens exhibited significant differences between sexes (male: 21.8±1.8; female: 22.8±1.6; GLM: $F_{7,96}$ = 6.96; P = 0.01) and DepthSeason (GLM: $F_{7,96}$ = 2.69; P = 0.01). Fish samples from D2S were significantly larger than those collected at D1A (P = 0.04) (Table 7.2).

All analysed *N. bonaparte* specimens, except eight individuals, were infected by at least one parasite species (overall prevalence 94.7%). Overall mean abundance and mean intensity values were 94.3±112.6 and 99.7±113.4, respectively. The 14,151 parasite individuals collected belong to five species: the cucullanid nematode *Dichelyne* (*Cucullanellus*) *romani* Isbert, Montero, Carrassón & González Solís, 2015; larval stages of a cucullanid nematode (Cucullanidae), the monogenean *Tinrovia mamaevi* Isbert, Carrassón, Pérez-del-Olmo, Montero, 2017; the nematode *Hysterothylacium aduncum* (Rudolphi, 1802), and plerocercoids of tetraphyllidean cestodes (Tetraphyllidea fam. gen. sp.) known collectively as *Scolex pleuronectis* (Müller, 1788) (Table 7.3). With respect to both cucullanids recorded in the present study, molecular analyses revealed that both are distinct from each other, so that they were treated as separate species. *Dichelyne* (*Cucullanellus*) *romani*, larval cucullanids and *T. mamaevi* were considered as common owing to their overall prevalence above 5%. The two former species were represented over all depth ranges and seasons with larval cucullanids as the most frequent and abundant of all detected parasites (Table 7.3). *Tinrovia mamaevi* was mostly observable in the shallow depth range and was not present in D3.

Infracommunity descriptors showed no interaction between DepthSeason groups, fish size and sex in all cases. No GLMs between these

Table 7.3 - Comparative data for parasites detected in *Notacanthus bonaparte* from the samples collected in the Western Mediterranean. Developmental stage, site, prevalence (%P) and mean abundance (MA±SD) for each species are presented overall and for each of the eight DepthSeason combinations. DepthSeason combinations: Depth range: D1 at 600–1,000 m, D2 at 1,000–1,400 m, D3 at 1,400–1,800 m (Seasons: W–winter, Sp–spring, S–summer, A–autumn). Abbreviations: cv – body cavity, g – gills, go – gonad, i – intestine, k– kidney, pc – pyloric caeca, l – liver, ms – mesentery, s – stomach.

			Total n = 150		D1W n = 8		D1Sp n = 6		D1S n = 45		D1A n = 24		D2W n = 6		D2S n = 19		D2A n = 25		D3A n = 17	
	Stage	**Location**	**%P**	**MA ±SD**	**%P**	**MA ±SD**	**%P**	**MA ±SD**	**%P**	**MA ±SD**	**%P**	**MA ±SD**	**%P**	**MA ±SD**	**%P**	**MA ±SD**	**%P**	**MA ±SD**	**%P**	**MA ±SD**
Monogenea																				
Tinrovia mamaevi	ad	g	8.7	0.13 ±0.50	25.0	0.25 ±0.46	66.7	1.00 ±1.10	11.1	0.18 ±0.65	4.7	0.08 ±0.41	-	-	-	-	4.0	0.04 ±0.20	-	-
Nematoda																				
Dichelyne (*C.*) *romani*	L4/ad	i, k, ms, pc, s	48.0	0.913 ±1.3	37.5	0.88 ±1.3	83.3	1.00 ±0.63	55.6	1.13 ±1.56	33.3	0.50 ±0.93	50.0	1.17 ±1.60	57.9	1.16 ±1.42	52.0	1.04 ±1.49	23.5	0.35 ±0.70
Cucullanidae	L3	cv, go, i, k, l, ms, pc, s	90.7	93.26 ±112.64	8.5	64.50 ±89.69	100.0	69.00 ±57.44	80.0	66.62 ±118.88	91.7	66.88 ±102.44	83.3	91.50 ±100.97	100.0	140.11 ±74.98	100.0	80.84 ±64.79	94.1	189.65 ±165.69
Hysterothylacium aduncum	L3	go, i, s	1.3	0.03 ±0.26	12.5	0.13 ±0.35	-	-	-	-	-	-	-	-	-	-	4.0	0.12 ±0.60	-	-
Cestoda																				
Tetraphyllidea fam. gen. sp.	L	pc	1.3	0.01 ±0.12	-	-	-	-	-	-	8.3	0.08 ±0.28	-	-	-	-	-	-	-	-

factors and infracommunity abundance were conducted as the very high and dominating abundance of the larval cucullanids would greatly influence these results. Infracommunity parameters did not reveal any significant difference between fish size. The infracommunity richness and Margalef Species Richness revealed significant differences between DepthSeason combinations (GLM; $F_{7,147}$ = 2.15 and 2.92; $P < 0.05$). The infracommunity richness exhibited a significant higher value for D1Sp compared to D3A ($P = 0.004$) and the Margalef Species Richness differed in D1Sp compared to all other depth strata (D2W, D2S, D2A, D3A) (all $P < 0.03$) (Table 7.2). Margalef Species Richness and Brillouin's diversity were significant different between sexes (GLM; $F_{1,97}$ = 6.98 and 4.95; $P < 0.03$), where mean values for both indices were significant higher in males, while infracommunity richness did not differ between sexes.

Prevalence and abundance of the three common species (%P>5) showed no interaction between fish size or sex and DepthSeason. The prevalence and abundance of the *D.* (*C.*) *romani* neither differed significantly between the DepthSeason combinations, the two fish size groups nor sex. Further, contrasting prevalence and abundance of *D.* (*C.*) *romani* between all three depth ranges (D1–D3) sampled in autumn and between D1 and D2 in the summer, and among seasons for D1 did not reveal any significant difference.

The prevalence of cucullanid larvae did not show any significant effect of the factors fish size and sex and also did not differ significantly between DepthSeason combinations. A GZM with abundance data of this parasite species showed a significant difference between the DepthSeason combinations (GZM DepthSeason, $\chi^2_{7,147} = 14.43$, $P < 0.05$) but not for fish size and sex. Depth range 3 in autumn (D3A) showed a significant higher abundance compared to most DepthSeason combinations from D1 and the combination D2A (GZM pairwise, all $P < 0.05$; Table 7.3). Prevalence of cucullanid larvae from samples taken in autumn over all three depth strata (D1–D3) showed no significant differences for the factors depth, host size and sex. In contrast, abundance in autumn differed significantly between depths (GZM depth, $\chi^2_{2,37} = 6.19$, $P < 0.05$), sex (GZM sex, $\chi^2_{1,37} = 11.54$, $P < 0.01$) and size (GZM size, $\chi^2_{1,66} = 6.05$, $P < 0.05$) been significantly higher in females and mature host. Pairwise comparisons revealed significant higher abundances in D3 compared to D1 and D2 ($P = 0.01$ and $P = 0.03$ respectively). For summer data, prevalence of cucullanid larvae showed no differences between D1 and D2, whereas abundances were significantly higher in D2 than D1 (140.1±74.9 and 66.6±118.8, respectively) (GZM depth, $\chi^2_{1,46} = 6.27$, $P = 0.01$). For both analyses the cofactors fish size and sex showed no effect on the abundance. Further, contrasting prevalence and abundance of cucullanid larvae between all four seasons at D1 did not reveal any significant difference.

The prevalence of *Tinrovia mamaevi* did not differ significantly between the DepthSeason combinations including the factors fish size and sex. The abundance of *T. mamaevi* did not differ significantly between fish size or sex while the factor DepthSeason revealed an overall significant difference in abundance (GZM DepthSeason, $\chi^2_{4,147} = 10.54$, $P = 0.03$), where abundance in D1S was significantly higher than in three DepthSeason combinations (D2W, D2S, D3A) where *T. mamaevi* could not be detected (all $P = 0.01$) (Table 7.3). *Tinrovia mamaevi* was detected in all four seasons in D1 exhibiting the highest abundance for D1Sp but without revealing a significant difference to the other DepthSeason combinations which probably results from the low sample size (Table 7.3). No significant differences could be detected when contrasting prevalence and abundance data of this species between autumn samples from depth ranges D1 to D3 and from summer in D1 and D2 including the three factors depth, fish size and sex. The prevalence and abundance of *T. mamaevi* were significant different over all 4 seasons in D1 (GZM season, $\chi^2_{3,82} = 11.31$, $P < 0.01$; GZM season, $\chi^2_{3,83} = 8.78$, $P < 0.01$, respectively). Posthoc pairwise comparisons revealed no significant differences for abundance whereas significant higher prevalence for spring when contrasted with summer and autumn samples was observed ($P = 0.005$; $P = 0.001$, respectively).

The PERMANOVA analysis performed using infracommunities as replicate samples showed a significant effect of the factor DepthSeason ($\text{Pseudo-F}_{7,146} = 3.92$; $P_{(perm)} = 0.0001$; 9,908 unique permutations) explaining 29.2% of the variation while the residual variation was substantial (70.8%). The post hoc pairwise comparisons did not show a tendency with respect to seasons or depths when contrasting single DepthSeason combinations. PERMANOVA analyses with depth and season factors separately show not significant effect of the factor season. However, this analysis revealed that depth significantly affected the infracommunity structure ($\text{Pseudo-F}_{2,146} = 9.63$; $P_{(perm)} = 0.0001$; 9,956 unique permutations) explaining 30.6% of the variation with a residual variation of 69.4%. Pairwise comparisons showed significant differences between infracommunities of D1 and D2 ($t = 3.74$, $P_{(perm)} < 0.001$; 9,951 unique permutations) and D1 and D3 ($t = 2.70$, $P_{(perm)} < 0.01$; 9,941 unique permutations), whereas infracommunities of D2 and D3 were similar. SIMPER analysis revealed varying dissimilarities between the depth strata (D1-D2 46.4%; D1-D3 53.6%, D2-D3 37.1%) and in all cases the cucullanid larvae contributed mostly to these dissimilarities (> 85%) followed by *D.* (*C.*) *romani* (8.5-12%) and *T. mamaevi* (0.2-2.1%).

The CCAs relating the prevalence of common parasites with environmental variables explained 100% of the total variance (Fig. 7.2). The prevalence of *T. mamaevi* was linked to high near bottom salinity and temperature coinciding with hauls from shallower waters (mainly D1). The prevalence of cucullanid larvae was slightly associated with turbidity coinciding with the deeper depth ranges (D2/D3) in summer and autumn.

DISCUSSION

In the northwestern Mediterranean Sea *Notacanthus bonaparte* is infected by a relatively poor metazoan parasite community which comprises helminthic larval and adult forms (only two of five species were adult). Within the five taxa two have been described as new species to science: *Dichelyne* (*C.*) *romani* and *Tinrovia mamaevi*. Further, the other three species are recorded for the first time in *N. bonaparte*, but two of them are considered uncommon due to their low prevalence (< 5%): *Hysterothylacium aduncum* (Rudolphi, 1802) and Tetraphyllidea fam. gen. sp. Previously only two parasite species were described in this host, one trematode (*Steringovermes notacanthi* Bray, 2004) and one cestode (*Bathycestus brayi* Kuchta & Scholz, 2004) therefore, this study substantially enlarge the number of species described for this host.

Parasite infracommunity parameters of *N. bonaparte* revealed differences between the tested factors as significant higher values have been detected in the DepthSeason D1Sp for

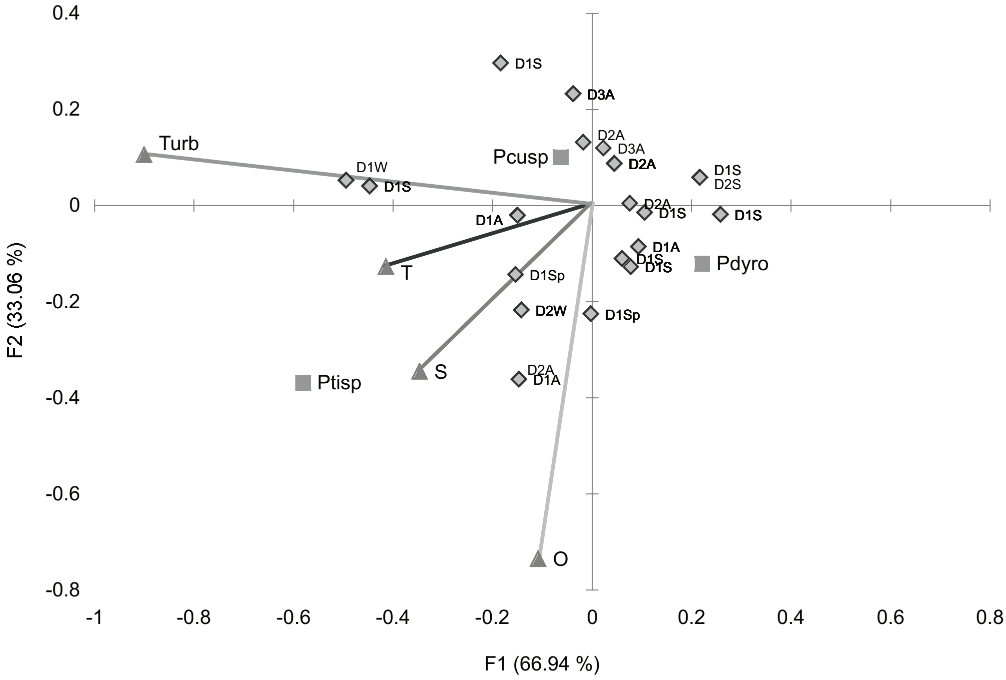

Fig. 7.2 - Canonical correspondence analysis (CCA) showing relationships between the prevalence of the three common parasites (%P>5%) in *Notacanthus bonaparte* and environmental data. Abbreviations for parasites names: Pcusp: Cucullanidae larvae; Pdyro: *Dichelyne* (*C.*) *romani*, Ptisp: *Tinrovia mamaevi*. Abbreviations for environmental variables: LS, salinity; LT, temperature; Lturb, turbidity; LO, oxygen. DepthSeason combinations (as defined in Table 7.1

infracommunity richness and Margalef Species Richness. These higher values might be due to the stronger representation of the monogenean *T. mamaevi* and the presence of uncommon taxa *H. aduncum* and Tetraphyllidea gen. sp. in this DepthSeason combination compared to the other combinations. Further, the Margalef Species Richness and Brillouin's diversity indices were higher in males which can be explained by a lower parasite burden of cucullanid larvae compared to females (see below).

The detection of depauperate parasite communities in *N. bonaparte* agrees with results for *Notacanthus sexspinis* from the south-eastern Pacific regarding the overall prevalence, low diversity and richness (Pardo-Gandarillas et al. 2008). These results can be considered robust due to the number of specimens analysed (35 *N. sexspinis*) since most of the previous studies on notacanthids were conducted on distinctly lower sample sizes and furthermore were focused on specific parasite taxa (e.g. Mamaev & Zubschenko 1978, Mamaev 1987, Bray 2004, Kuchta & Scholz 2004).

The host feeding habits might contribute to explain the poor parasite community of *N. bonaparte*. The most recent publications on this species described it as one of the most specialized predators within the bathypelagic and –benthic feeders. These recent studies confirmed its assignation as bathydemersal (Sulak 1986), with benthic feeding habits preying mostly on sessile or slow moving benthic organisms such as asteroideans, actinians (Rodríguez-Romeu et al. 2016) and ophiuroideans (Preciado et al. 2017). The infracommunity abundance and richness of heteroxenous parasites are largely related to the diversity of available preys (intermediate hosts) ingested by the fish host (Cirtwill 2016). The life cycles of these heteroxenous parasites depend directly on the abundance of free-living species, which affects the overall infection by these parasites and usually decreases with depth. However, while meso- and bathypelagic fishes exhibit an impoverished parasite fauna, due to mainly planktonic preys, diversity and intensity of infection increase in deep living benthic fish taxa owing to the higher availability of intermediate hosts in benthic habitats and along the benthic boundary layers (Campbell et al. 1980, Marcogliese 2002, Klimpel et al. 2010). This has been demonstrated for species such as *Phycis blennoides* and *Mora moro*, with benthopelagic/benthic and pelagic to benthic feeding habits, respectively, exhibiting high total parasite species numbers (14 and 18, respectively, Table 7.4) (Dallarés et al. 2014, 2016). However, *P. blennoides* and *M. moro* have a distinctly broader diet range, which results in a higher infracommunity richness and diversity (*P. blennoides*: 6.2 and 1.1; *M. moro*: max. values 5.0 and 0.9) than observed for *N. bonaparte*, which has a distinctly narrower prey range. The lower parasite richness and diversity of *N. bonaparte* associated with the narrow prey range agrees with previous suggestions made by e.g. Locke et al. (2014) and Cirtwill et al. (2016 and references therein). Consequently, although *N. bonaparte* is a benthic feeder, it's highly specialised feeding habits prevent the infection by more diverse and richer parasite communities, resembling those usually found in meso- and bathypelagic species.

Dichelyne (*Cucullanellus*) *romani* was one of the two cucullanid nematode taxa detected herein. To date there was only one other record of a cucullanid in a notacanthid, *Notacanthus chemnitzii* from the Northeast Atlantic, but without any further taxonomic description (Soares 2007). Therefore, to the best of our knowledge *D.* (*C.*) *romani* represents the first described cucullanid species for the genus *Notacanthus* Bloch, 1788. This species exhibited a partly high prevalence but low abundance, and no clear pattern has been observed in *N. bonaparte*, which relates its occurrence to any of the tested factors. With respect to its life cycle no detailed conclusions can be drawn as potential intermediate hosts are unknown. Along with main prey items mentioned above, stomach contents of *N. bonaparte* from the western Mediterranean Sea often comprised mud,

Table 7.4 - Number and composition of metazoan parasite taxa detected in different deep-sea teleosts in studies from different geographical areas. The composition of parasite community is indicated as number of species per taxa in the following order: Acanthocephala/Cestoda/Monogenea/Digenea/Nematoda/Copepoda/Isopoda.

Number Parasite taxa	Parasite taxa	Geographical Area	Host species	Host (N)	Prey	Study
8	0/1/1/1/5/0/0	western Mediterranean Sea	*Alepocephalus rostratus* Risso, 1820	82	pelagic	Pérez-i-García et al. (2015)
2	0/1/0/1/1/0/0	East Greenland Sea, Irminger Sea North Atlantic	*Argentina silus* (Ascanius, 1775)	40	pelagic	Klimpel et al. (2006)
5	0/1/0/3/1/0/0	Mid-Atlantic Ridge (North Atlantic)	*Bathylagus euryops* Goode & Bean, 1896	86	pelagic	Busch et al. (2008)
9	1/2/0/4/3/0/0	Mid-Atlantic Ridge (North Atlantic)	*Halosauropsis macrochir* (Günther, 1878)	42	benthic, benthopelagic	Klimpel et al. (2008b)
5	0/1/0/1/1/1/0	western Mediterranean Sea	*Bathypterois mediterraneus* Bauchot, 1962	170	pelagic	Mateu et al. 2014
20	1/3/1/5/7/2/0	East Greenland Sea, Irminger Sea North Atlantic	*Macrourus berglax* Lacepède, 1801	35	benthic, benthopelagic	Klimpel et al. (2006)
16	0/2/1/6/6/1/0	Mid-Atlantic Ridge (North Atlantic)	*Coryphaenoides mediterraneus* (Giglioli, 1893)	38	benthic, benthopelagic	Kellermanns et al. 2009
2	0/1/0/0/0/1/0	Mid-Atlantic Ridge (North Atlantic)	*Scopelogadus beanii* (Günther, 1887)	35	pelagic	Klimpel et al. (2010)
18	1/3/0/5/9/0/0	western Mediterranean Sea	*Mora moro* (Risso, 1810)	62	pelagic, benthopel., benthic	Dallares et al. (2014)
4	0/1/0/2/1/0/0	Mid-Atlantic Ridge (North Atlantic)	*Myctophum punctatum* Rafinesque, 1810	89	pelagic	Klimpel et al. (2008a)
4	0/1/0/2/1/0/0	Mid-Atlantic Ridge (North Atlantic)	*Notoscopelus kroyeri* (Malm, 1861)	74	pelagic	Klimpel et al. (2008a)
3	0/2/0/0/0/1/0	Mid-Atlantic Ridge (North Atlantic)	*Benthosema glaciale* (Reinhardt, 1837)	70	pelagic	Klimpel et al. (2010)
4	0/2/0/4/1/1/0	southeastern Pacific	*Notacanthus sexspinis* Richardson, 1846	35	benthic, benthopelagic	Pardo-Gandarillas et al. (2008)
5	0/1/1/0/3/0/0	western Mediterranean Sea	*Notacanthus bonaparte* Risso, 1840	150	benthic	present study
20	1/2/1/6/13/1/1	western Mediterranean Sea	*Phycis blennoides* (Brünnich, 1768)	188	benthic, benthopelagic	Dallares et al. (2016)
2	0/1/0/1/0/0/1	East Greenland Sea, Irminger Sea North Atlantic	*Chauliodus sloani* Bloch & Schneider, 1801	21	pelagic	Klimpel et al. (2006)

decaying gelatinous and teleost remains, partly difficult to identify (Rodríguez-Romeu et al. 2016). Thus, further studies are needed in order to assess if *N. bonaparte* incorporates *D.* (*C.*) *romani* by scavenging and which of the prey items play a crucial role in the life cycle of this nematode.

Larval individuals of the Cucullanidae Cobbold, 1864, were the most frequent and abundant parasite detected in *N. bonaparte*. Although it was not possible to identify the specimens to the genus level yet, molecular analyses confirmed that they are genetically distinct from *D.* (*C.*) *romani* (unpublished data) and further analysis is necessary for a more detailed identification. These larvae showed quite similar high prevalences with varying abundances between seasons and a clear trend to deeper waters.

Life cycles of cucullanids are not fully understood yet, but it is supposed that most cucullanids have invertebrates and vertebrates as intermediate hosts, such as crustaceans, polychaetes and teleosts (Køie 2000, 2001). Laboratory experiments and the analysis of natural infection patterns in copepods and sand gobies from the Baltic Sea, revealed infections by the 3rd larval stage of the nematode, *Cucullanus cirratus*, in both hosts (Køie 2000). The author suggested that the 3rd free larval stage could be ingested either by copepods, considered as paratenic hosts, or directly by sand gobies as intermediate host. While in copepods the larvae did not grow, they grew larger in the intermediate fish host but did not molt. This intermediate host is considered obligate for the infection of large cods, which are the definitive hosts and frequently prey on sand gobies. These results agree with our findings since the larvae observed in *N. bonaparte* were not encapsulated but free in the intestinal mucosa, as those detected in sand gobies.

In the present study, the prevalence of cucullanids was related to the turbidity conditions measured in the study area. The increased turbidity in deeper waters in the study area is linked to seasonal advective fluxes due to peaks in river discharge (April, October), resuspending and depositing particles on the bottom (Palanques et al. 2006, Papiol et al. 2012 and references therein). Further, it is supposed that organic matter and particles are channelled into the deep-sea and increase the food availability (Cartes & Maynou 1998, Palanques et al. 2006, Papiol et al. 2012 and references therein). Turbidity is supposed to promote the increase of zooplankton communities in the western Mediterranean (Cartes et al. 2013) and some authors argued that this may also influence the load of certain parasite species in different host taxa from the western Mediterranean (Dallarés et al. 2014, Constenla et al. 2015). Indeed, the positive relationship between the occurrence of cucullanids and turbidity was already detected in *Alepocephalus rostratus* in the same geographical region (Pérez-i-García et al. 2015). Additionally, for *N. bonaparte* a positive association between high turbidity events and gut fullness maxima (spring-summer) has been recorded (Rodríguez-Romeu et al. 2016). These maxima were positively correlated with Chlorophyll a maxima in the surface waters 2–3 months before sampling of fishes and one month after high river discharge. However, a study by Rodríguez-Romeu et al. (2016) on the feeding habits of *N. bonaparte* in the western Mediterranean Sea (which included some specimens from our study) showed a low importance of pelagic and suprabenthic prey items (e.g. copepods, amphipods), supporting the results from previous studies from the Mediterranean and the Northeast Atlantic (Lozano-Cabo 1952, Macpherson 1981, Mauchline & Gordon 1986, Coggan et al. 1998, Preciado et al. 2017). The main preys recorded for *N. bonaparte* are sessile or slow moving benthic organisms (e.g. actinians, echinoderms, coral polyps), and also organic remains (sediment, particulate organic matter (POM)). Rodríguez-Romeu et al. (2016) suggested that when *N. bonaparte* feeds on the sessile prey, it ingests sediment and POM. Køie (2000) observed that the free-living 3rd stage larvae of *C. cirratus* survived for two months under laboratory conditions, being inactive on the bottom unless these were disturbed. Therefore, we suggest that *N. bonaparte* could ingest the already hatched larvae in the sediment when preying on benthos.

The here observed higher burden of cucullanid larvae shows a clear trend to the deeper depth range independently if all data is considered or samples of particular seasons. The specifically high abundances for lower depth strata in summer and autumn, respectively, could indicate a higher previous ingestion of parasites induced by enhanced feeding activity as observed in other studies (e.g. Dallarés et al. 2014). Additionally, the abundance of nematode larvae could also be related to fish size, as in our study mature individuals presented a higher burden than immature specimens, indicating an accumulation during host lifetime (Poulin 2000, Dallarés et al. 2014). Furthermore, differences between sexes resulted from a higher burden in females which are also bigger than males. Although no significant differences have been detected in the mean TL among the three depth strata we analysed, a clear bigger-deeper trend for this fish was observed by Rodríguez-Romeu et al. (2016).

Considering the role of *N. bonaparte* in this larval cucullanid life cycle, in view of their high prevalence and abundance, we argue that *N. bonaparte* might act as an important intermediate host. Though, to the best of our knowledge no information is available for any potential predator and there exists only one record for detected remains of the notacanthid *N. sexspinis* in the sebastid *Helicolenus percoides* from the southern Pacific. The same data indicated that notacanthids are very rare prey for this predator (Blaber & Bulman 1987), however, presence of *N. bonaparte* in the diet of predators can be underestimated due to the very small size of its otoliths (e.g. 0.5mm diameter in 25cm fish; Tuset et al. 2008). Therefore, it can be assumed that larger predators in this deep-sea area could be the potential definitive host; for instance *P. blennoides* or *Conger conger* which exhibit adult stages of cucullanids (Radujkovic & Raibaut 1989, Dallarés et al. 2016). Considering the here presented data on this parasite in *N. bonaparte* it represents one of few parasites found as larval stage in notacanthids. Generally, due to the low infection of notacanthids by larval stages, it can be supposed that this group does not play a crucial role as common prey item for other predators. The conclusions drawn on the potential life cycle of the cucullanid larvae as well as *D.* (*C.*) *romani*, and the role of the shortfin spiny eel are speculative at best. Future molecular analyses of these larvae, compared with data from adult cucullanids detected in potential deep-sea predators, may help to identify the possible ‘common’ predator of *N. bonaparte*.

This is the first record of a monogenean in *N. bonaparte*. *Tinrovia mamaevi* (Mircocotylidae Taschenberg, 1879) is the second species described for this genus and the type species *Tinrovia papiliocauda* Mamaev, 1987, was detected in another notacanthid, *N. sexspinis*, from the Pacific. *Tinrovia mamaevi* is an ectoparasite with a direct life cycle supposedly infecting a single host species. Eggs of monogeneans are released by adults and sink to the bottom, where the larvae will hatch following different strategies of hatching triggered by distinct cues (e.g. environmental, chemical factors, mechanical disturbance) (Whittington & Kearn 2011). The usually ciliated larvae (oncomiracidium) hatch from the egg and swim freely in the water column searching a new host. Several studies observed monogeneans in ‘shallower’ waters of the deep ocean only (up to 1,000 m) (De Buron & Morand 2004), while the overall diversity is considered lower compared to shallow coastal waters (Rohde 1988). Consequently, monogeneans seem to be more successful in shallower waters, while from the lower slope downwards fish (host) densities are supposed to be too low for successful transmission (Campbell et al. 1980). Data from the western Mediterranean Sea indicate that average abundances of *N. bonaparte* are higher in the middle slope (1,000–1,300 m) (Papiol et al. 2012, Fanelli et al. 2013) or at least in the lower part of the upper slope (840 m, Cartes et al. (2009); 940 m, Rodríguez-Romeu et al. (2016)). These depths match with the shallower depths where most specimens of *T. mamaevi* were recorded in the present study (D1; 600–1,000 m). Therefore, these findings confirm the assumptions of a depth related distribution pattern in monogeneans and also indicate, that higher host densities could promote higher infection rates by this monoxenous parasites (Sasal 2003).

Highest prevalence and abundances of *T. mamaevi* were detected in spring followed by winter and summer, though pairwise comparisons with other DepthSeason combinations were not significant for spring and winter due to the lower sample size. In addition to parameters such as host density, transmission of ectoparasites is also influenced by host behaviour (Raeymaekers et al. 2008 and references therein). The higher infection rate by *T. mamaevi* observed in spring might hint to host specific behaviour during this season; as indicated above, feeding activity of *N. bonaparte* was highest in spring and summer, which may increase their mobility above the bottom (independently on the depth strata) and the contact with the benthos, enhancing the possibility to be infected by this ectoparasite (Grutter 1998). The CCA related the prevalence of *T. mamaevi* to temperature and salinity, especially in the upper and middle slope. With respect to the free-living larval stage, it is suggested that the lifespan of larvae and the period to find a new host is limited due to low energy reserves (Whittington & Kearn 2011). Previous studies on shallow water organisms demonstrated the impact of temperature and salinity on the life cycle, where monogeneans exhibited a faster growth, higher hatching success and reduced time to reach sexual maturity, when they were kept in environments with relatively high temperatures and salinities (Ernst et al. 2005, Brazenor & Hutson 2015). Therefore, environmental parameters apparently influence the life cycles of monogeneans, but in our study temperature and salinity exhibited marginal variations among the DepthSeason combinations (Table 7.1). Therefore, further abiotic parameters (e.g. substratum, currents; Grutter 1998, Sikkel et al. 2009), which may change over the depth range and seasons could influence the survival of the monogenean larvae.

The two species presenting low prevalences in the shortfin spiny eel are generalist parasites which were recorded globally in many fish species from shallow and deep waters (Gibson et al. 2005, Klimpel et al. 2009). Both species were mainly detected in the shallow depth strata contributing to the higher richness in D1. The Tetraphyllidea fam. gen. sp. is a collective group of larval cestodes where the identification of the larvae ‘remains indeterminate at all levels’ without molecular evidence due to lacking ‘morphological clues’ (Jensen & Bullard 2010). These tetraphyllidean larvae are found in various intermediate hosts such as different invertebrates and fish species (Cake 1977, Klimpel et al. 2009, Jensen & Bullard 2010 and references therein), whereas elasmobranchs are considered as definitive hosts (Euzet, 1994). Owing to the very low prevalence we suggest an accidental infection of *N. bonaparte* also regarding its main prey, which is not recorded as common intermediate hosts for this collective group.

The nematode *Hysterothylacium aduncum* is described as unspecific concerning its intermediate and paratenic hosts being found in planktonic and benthic invertebrates (e.g. copepods, amphipods, chaetognaths and polychaetes) (Køie 1993, Marcogliese 1996, Klimpel & Rückert 2005, Klimpel et al. 2009). This might explain the low infection by this species observed in *N. bonaparte* as these potential intermediate hosts are of none or minor importance in its diet. Adult specimens of this species were observed in the gut of different benthic and pelagic fish species (Køie

1993, Navone et al. 1998). Potential definitive hosts in these depths and area could be common species such *P. blennoides*, *M. moro* or *C. conger* which are infected by adult *Hysterothylacium* spp. (Radujkovic & Raibaut 1989, Dallarés et al. 2014, 2016). Regarding the very low prevalence observed in the present study, we suppose that the spiny shortfin eel is not a common paratenic host and this may be an accidental infection. Nevertheless, the infection of *N. bonaparte* does not necessarily imply a dead end for this parasite, but still provides a chance to reach the definitive host such as *P. blennoides*, *M. moro* or *C. conger*.

In conclusion, the overall depauperate parasite communities detected in *N. bonaparte* could be mostly associated with the feeding habits described for this species in that area. Communities were richer in shallow water (D1) owing to the presence of *T. mamaevi* and both uncommon taxa *H. aduncum* and Tetraphyllidea gen. sp., while cucullanid larvae showed lower abundances. While turbidity can increase zooplankton abundances in these waters the prevalence of cucullanid larvae could only be indirectly linked to this aspect. We suggest that cucullanid larvae might be present as free-living stage in the sediment being ingested by *N. bonaparte* when it preys on sessile and slow moving organisms. The accumulation of cucullanid larvae by *N. bonaparte* during lifetime resulted in higher burden in larger mature fishes and females; latter exhibited a lower parasite diversity compared to smaller sized males. This aspect and the observed bigger-deeper trend of *N. bonaparte* explain the here observed higher infection rates of cucullanid larvae in deeper waters. The high infection rate by this larval parasite supports the idea of its role as intermediate host, being potentially preyed by larger predators feeding opportunistically in this deep-sea area that could act as definitive hosts. The observed temporal and depth-related distribution pattern of *T. mamaevi* is associated to higher host densities in D1. Furthermore, temperature and salinity and other abiotic parameters could also affect the distribution of this monogenean species. Finally, the samples obtained for this study contribute to the description of two parasite species new to science, and substantially enhance the knowledge on the parasite fauna of *N. bonaparte*.

ACKNOWLEDGMENTS

This study was supported by the MICYT projects “BIOMARE (CTM2006-13508-C02-C01/MAR) and “ANTROMARE” (CTM2009-12214-C02-02-MAR). We thank all participants on BIOMARE and ANTROMARE cruises and the staff of the Department of Animal Biology, Vegetal Biology and Ecology of the Universitat Autònoma de Barcelona (Spain) for their assistance during the oceanographic campaign and in the laboratory work. We thank David Pérez-i-García and Anna Soler-i-Membrives for the molecular characterization of specimens.

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Etmopterus spinax

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Chapter 8

Metazoan parasite communities and diet of the velvet belly lantern shark *Etmopterus spinax* (Squaliformes: Etmopteridae): a comparison of two deep-sea ecosystems off northern Spain

Journal of Fish Biology (2014)
doi: 10.1111/jfb.12591

ABSTRACT

By combining an examination of stomach contents yielding a snapshot of the most recent trophic niche and the structure of parasite communities reflecting a long-term feeding niche, this study aimed at gaining more comprehensive information on the role of the small-sized deepwater velvet belly lantern shark *Etmopterus spinax* in the local food webs of the Galicia Bank and the canyon and valley system of the Avilés Canyon, which have been both proposed for inclusion in the 'Natura 2000' network of protected areas. As far as is known, this study provides the first comparative parasite infracommunity data for a deep-sea shark species. Component parasite communities in *E. spinax* were relatively rich, whereas the infracommunities were rather depauperate, with similar low diversity at both localities. The significant differences in the composition and structure of both parasite communities and prey assemblages indicate differential effects of the two deep-sea ecosystems on both long-term and most recent trophic niches of *E. spinax*. The results underline the importance of the use of multivariate analyses for the assessment of geographical variation in shark populations based on parasites and diet data.

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INTRODUCTION

The enhanced movement of fisheries into the deep-sea had raised concerns regarding sustainability and the threats of overfishing in deep-sea habitats (Morato et al. 2006, Norse et al. 2012). Deepwater sharks exhibit slow growth rates, late maturity and low fecundity resulting in extremely low rebound potentials and high susceptibility to fishing mortality. Consequently, loss of these predators may induce changes at the ecosystem level (Simpfendorfer & Kyne 2009). Given the intrinsic vulnerable life cycle of deep-sea elasmobranchs and the paucity of previous investigations, studies on this group are required to understand their ecology and shed more light on their role within the deep-sea community.

The genus *Etmopterus* Rafinesque 1810 is comprised of small benthopelagic species that occur in all oceans and are confined to bathyal habitats (Musick et al. 2004). The velvet belly lantern shark *Etmopterus spinax* (L. 1758) occurs in the eastern Atlantic Ocean from Iceland and Norway to southern Africa and in the Mediterranean Sea (Coelho & Erzini 2008 and references therein). This small-sized deepwater shark is found on the outer continental and insular shelves and on upper to lower slopes near or at the bottom at depths between 70 and 2000 m but usually at 200–500 m (Compagno 1984).

The velvet belly feeds on crustaceans, small fishes and cephalopods (Compagno 1984) but seem to gradually become piscivorous with increased size (Klimpel et al. 2003, Neiva et al. 2006, Fanelli et al. 2009). Stomach content studies have also revealed spatial variations in the diet of this species. Euphausiids were shown to be of major importance in *E. spinax* in the Skagerrak (Bergstad et al. 2003), off Algarve, Portugal (Santos & Borges 2001, Neiva et al. 2006) and Le Danois Bank, Cantabrian Sea (Preciado et al. 2009), whereas carideans (shrimp) were found to play a major role in the Mediterranean (Macpherson 1981, Fanelli et al. 2009, Valls et al. 2011). Fishes detected in the diet of *E. spinax* mostly comprise meso-, bentho- and bathypelagic species of different families (Bergstad et al. 2003, Neiva et al. 2006, Fanelli et al. 2009, Preciado et al. 2009) with engraulids being of major importance in the Mediterranean (Macpherson 1981). Previous studies have shown that cephalopods represent variable proportions in the diet and that the occurrence of large species implies potential scavenging behaviour of *E. spinax* (see Bergstad et al. 2003, Neiva et al. 2006). However, the data on the diet of this species in the northern Spanish waters are limited (Preciado et al. 2009).

The use of parasites as natural biological tags is considered a powerful tool shedding light on different aspects of fish life (Caira 1990, Williams et al. 1992) and their study has been recommended especially for deep-sea and rare marine species (MacKenzie & Abaunza 1998). Food-web transmitted parasites are related to the past food acquisition of individual hosts and thus can provide valuable information on the relatively long-term feeding habits and diet niches of the species in a given ecosystem (e.g. Lafferty et al. 2008, Knudsen et al. 2010). Furthermore, knowledge on the life cycle pathways and transmission patterns of parasites provides information on food web structure (Marcogliese 2002). However, data on the parasite fauna of elasmobranchs in general (MacKenzie 2002, Caira & Healy 2004) and of *E. spinax* in particular, are still scarce. Although isolated records of parasite species in this host exist (Klimpel et al. 2009 and references therein, Caira & Pickering 2013) there is a single survey on the parasite fauna of this host based on examination of juvenile fish from the Norwegian Deep (Klimpel et al. 2003).

The present study was carried out in two different deep water ecosystems of the North East Atlantic (off northern Spain), the seamount Galicia Bank and the canyon and valley system Avilés Canyon (Fig. 8.1). These areas are of specific interest because oceanic features harbour faunal communities distinct from the

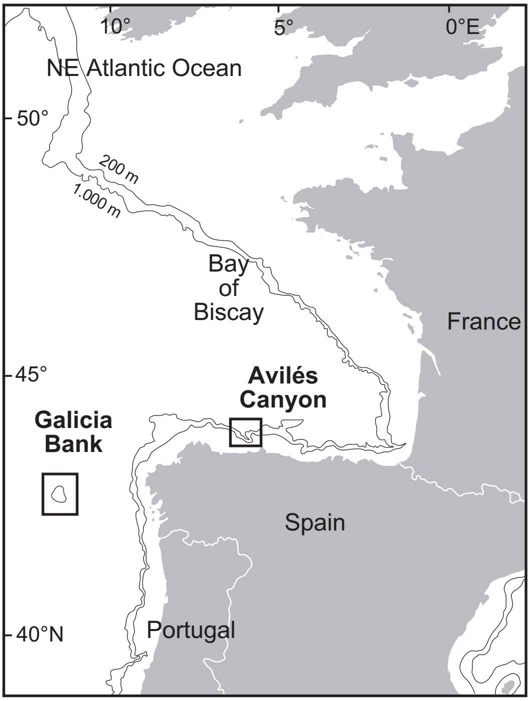

Fig. 8.1 - Map showing the location of the areas of sampling of *Etmopterus spinax*: the Galicia Bank and the Avilés Canyon.

surrounding areas such as the continental shelves and slopes and can aggregate higher level consumers, e.g. migrating vertebrates, due to the different hydrographic conditions providing enhanced biological production (Morato et al. 2008, Clark et al. 2010, Vetter et al. 2010). Previous studies on deep-sea chondrichthyans conducted in the study areas have provided information on biological aspects such as the bathymetric range, length distribution, fecundity or feeding habits of some species (Bañon et al. 2006, 2008, Preciado et al. 2009) or have dealt with entire fish communities in the context of spatial distributions and fishery impacts (Piñeiro et al. 2001, Rodríguez-Cabello et al. 2005, Sánchez et al. 2008). Consequently, these two topographic features have been proposed for inclusion in the Natura 2000 network of protected areas. A comprehensive knowledge of these ecosystems, their vulnerable habitats and the biology and ecology of potential key species, e.g. deep-sea sharks, is required for the establishment of proper protection and management measures.

This paper provides the first data on metazoan parasite communities and diet composition in this shark species at the Galicia Bank and Avilés Canyon. The comparative approach focused on the variation at the level of individual fish hypothesising that both parasites and diet would be informative at detecting differences between the populations of *E. spinax* in these deep-sea ecosystems. By combining an examination of stomach contents, which yields a snapshot of the most recent trophic niche utilisation (i.e. reflecting diet use at the time of catch), and the structure of parasite communities, which reflect a long-term feeding niche, this study was aimed at gaining more comprehensive information on the role of this shark species in the two local food webs.

MATERIAL AND METHODS

Study area

This study profited from a recent deep-sea survey conducted on board of RV *Thalassa* within the framework of the INDEMARES EU-Life+ project which supplied representative samples of *E. spinax*. Fish were sampled in two deepwater topographic features located in the North East Atlantic off Spain separated by *c.* 250 nautical miles, the Galicia Bank (further referred to as GB) and Avilés Canyon (further referred to as AC) (Fig. 8.1). The GB is a seamount located at *c.* 120 nautical miles from the north-western coast of Spain. It is separated from the shelf by a c. 2,500 m deep channel and is characterised with a summit reaching 620 m from the surface and a maximal depth of about 5,000 m (Ercilla et al. 2011). This area is influenced by water masses from the Atlantic and Mediterranean Outflow Water resulting in high current velocities and mobile sediments (Ruiz Villarreal et al. 2006, Ercilla et al. 2011). The AC is a submarine canyon system in the southern Bay of Biscay with a very steep and narrow morphology, situated very close to the coast (*c*. 7 nautical miles). It intersects the continental shelf at depth of 140 m and ranges to nearly 4,700 m in depth. This area is characterised by continental input of sediments and organic matter by freshwater runoff, and seasonal poleward and equatorward currents inducing phytoplankton blooms (González-Quirós et al. 2003, Ruiz Villarreal et al. 2004).

A total of 59 *E. spinax* was sampled during two surveys conducted in 2010 (July: AC, 43°49′, N 6º09′ W; August: GB, 42°39′ N, 11°43′ W) (Fig. 8.1). Samples were collected with a bottom trawl net (GOC-73, mesh size 10 mm, haul duration 30 min) and a beam trawl (3.5 m width, 10 mm, 15 min). Hauls were conducted at depths between 200 and 1,250 m. Specimens of *E. spinax* collected at depths between 558 and 855 m, were identified on board and frozen at -25˚C for further parasitological and diet examination. Prior to examination and dissection, each fish individual was thawed and morphometric data including total length (TL) and stomach wet weight were recorded to the nearest 0.1 cm and 0.01 g, respectively.

Parasites and diet

In the laboratory, external and internal body surfaces were inspected and gills, olfactory organs and the gastrointestinal tract were examined for the presence of parasites separately. The entire body musculature was sliced and examined using glass plate compression method under a stereomicroscope. All metazoan parasites were collected and preserved in 70% ethanol or fixed in 4% borax-buffered formalin for subsequent identification. Monogeneans, digeneans and cestodes were stained with iron acetocarmine (Georgiev et al. 1986), dehydrated in an alcohol series, cleared in dimethyl phthalate and mounted in Canada balsam. Nematodes were examined in glycerine mounts after dehydration in a graded glycerine-ethanol series. All parasites were identified to the lowest possible taxonomic level and counted. Ecological terms for parasite populations and communities follow Bush et al. (1997). Prevalence (*%P*) is the number of hosts infected with a particular parasite taxon divided by the number of hosts examined; mean abundance (MA) is the total number of individuals of a particular parasite taxon divided by the number of hosts examined; mean intensity (MI) is the average of the total number of individuals of a particular parasite taxon found in a sample divided by the number of hosts infected with this taxon.

The stomach contents were analysed for prey items. Stomachs of individual fish were weighed (wet weight) and prey items were separated and identified to the lowest possible taxonomic level using a stereomicroscope. The contribution of each prey item to the diet was expressed as frequency of occurrence (*%F*), percentage by number (*%N*) and percentage by weight (*%W*) following Hyslop (1980). The frequency of occurrence was determined as the number of stomachs with prey item i divided by the number of all full stomachs (stomach with food/prey items). The numerical and weight percentages were calculated as the number/weight of prey item i divided by the total number/ weight of all prey items. To facilitate comparisons between different samples or studies, the index of relative importance, I_{RI} was calculated as follows $I_{RI} = (\%N + \%W) \times \%F$, to determine the quantitative importance of each prey item (Pinkas et al. 1971). In the present study this index is expressed as the sum of I_{RI} indices of all prey items: $I_{RI} = (I_{RIi}\ \Sigma I^{-1}_{RIi})$. Otoliths found in the stomach contents were identified consulting the AFORO web (Lombarte et al. 2006).

Data Analysis

Parasite infrapopulations (all parasites of a given species in an individual fish) and infracommunities (all infrapopulations in an individual fish) were used as replicate samples in all analyses. For both locations, the means for parasite richness and abundance, Brillouin's diversity and Berger-Parker dominance index of the infracommunities were calculated and compared. The number of prey items per species/higher taxon in individual fish were used in the quantitative diet comparisons. All data were ln (x+1) transformed and General Linear Model (GLM) analyses were performed to assess possible differences between the samples from the two localities using fish total length as a covariate. Parasite taxa with prevalence lower than 5% were excluded from these analyses. Additionally, non-parametric tests [Spearman rank correlations (r_s) and Chi-square (χ^2) test] were applied. Parasite prevalences were compared with Fisher's exact test. Analyses were carried out using Statistica 9.0 (StatSoft, Inc., Tulsa, OK, USA) and the programme Quantitative Parasitology (QP 3.0, Rozsa et al. 2000).

Community similarity analyses were carried out with PERMANOVA+ for PRIMER v6 software (Anderson et al. 2008). Multidimensional scaling (MDS) based on Bray-Curtis similarities was performed to obtain an ordination of infracommunities/prey assemblages in individual fish from both sampling locations. Permutational multivariate analysis of covariance (PERMANCOVA, Anderson 2001) with locality as a fixed factor and fish total length as a covariate was used to assess the effects of locality on the composition and structure of parasite communities/prey assemblages accounting for the effect of fish size. Permutation *P*-values were obtained under a reduced model of permutation of raw data (9,999 permutations). Parasite and prey abundance data were square root transformed and fish length data were ln-transformed. Following the PERMANCOVA test for between location differences, the SIMPER procedure was used to identify key discriminating taxa on the basis of the overall percent contribution of each parasite/prey species or higher-level taxonomic group to the average dissimilarity between sampling locations.

RESULTS

Parasite communities

A total of 59 specimens of *Etmopterus spinax* collected at depths between 558-855 m was examined (30 at GB and 29 at AC). The overall sex ratio was 1:1.27 in favour of females; no significant sex ratio differences were detected between the fish sampled at GB (1:1.73) and AC (1:0.93) ($\chi^2 = 0.81$, df = 1, $P > 0.05$). Fish total length ranged from 15.3 to 45.9 cm; fish sampled at GB were significantly larger ($F_{(1,57)} = 4.983$, $P < 0.05$) than fish from AC (TL range: 17.0 – 44.2 *vs* 15.3 – 45.9 cm; mean ± SD: 31.1 ± 7.9 *vs* 26.6 ± 8.3 cm). Furthermore, fish size was significantly associated (all $P < 0.05$) with the abundance of four parasite taxa at GB (*Sphyriocephalus* sp., $r_s = 0.528$; *Squalonchocotyle spinaci* (Goto 1894), $r_s = -0.566$; Tetraphyllidea fam. gen. sp., $r_s = 0.499$; and *Contracaecum* sp., $r_s = 0.370$) and two taxa at AC (*Anisakis* sp. ascribed to morphotype *Anisakis* Type I *sensu* Berland (1961), $r_s = 0.812$ and Tetraphyllidea fam. gen. sp., $r_s = 0.492$). Therefore, all comparisons of parasite populations and communities between locations were carried out with fish total length as a covariate.

The overall prevalence of infection in *E. spinax* was 76.3% (95% CI: 63–86%). There were no significant differences between the samples from GB and AC with respect to the overall prevalence of infection (86.7 *vs* 65.5%, respectively; Fisher's exact test, $P > 0.05$) and total parasite abundance (mean 5.30 *vs* 9.52; $F_{(1,57)} = 1.615$, $P = 0.209$). A total of 11 parasite taxa was recovered in the samples of *E. spinax* from GB and AC: six cestodes, three nematodes, one monogenean and one digenean (Table 8.1). Of these, three species are recorded for the first time in *E. spinax*: the cestodes *Ditrachybothridium* cf. *macrocephalum* Rees 1959 (Diphyllidea) and *Sphyriocephalus* sp. (Trypanorhyncha) and the digenean *Otodistomum* cf. *cestoides* (van Beneden 1871) (Hemiuroidea). Six of the 11 taxa were represented by larval stages which comprised the majority of the individuals (84.4%) (Table 8.1). Fish were infected with nine taxa (six larval and three adult stages) at the GB and with seven taxa (four larval and three adult stages) at the AC; five taxa (three larval and two adult stages) occurred in both localities. A GLM

Table 8.1 - Comparative data for parasites [prevalence, %P (95% C.I.); mean abundance ± S.D., MA; mean intensity, ± S.D., MI] in component communities of *Etmopterus spinax* at the Galicia Bank and Avilés Canyon.

Parasites		**Galicia Bank** (n = 30)			**Avilés Canyon** (n = 29)		
	Site in host	**P% (CI)**	**MA ± SD**	**MI ± SD**	**P% (CI)**	**MA ± SD**	**MI ± SD**
MONOGENEA							
Squalonchocotyle spinaci *	gi	43.3 (25.4-62.6)	1.7 ± 3.2	3.9 ± 3.9	-	-	-
CESTODA							
Aporhynchus menezesi *	si	10.0 (2.8-26.3)	0.2 ± 0.5	1.7 ± 0.6	17.2 (7.1-36.0)	0.2 ± 0.5	1.2 ± 0.4
Aporhynchus norvegicus *	si	6.7 (0.8-22.8)	0.1 ± 0.3	1,0	3.4 (0.1-17.7)	0.1 ± 0.4	2,0
Ditrachybothridium cf. *macrocephalum* †	si	-	-	-	3.4 (0.1-17.7)	0.03 ± 0.2	1,0
Sphyriocephalus sp. †	st	16.7 (5.6-34.7)	0.3 ± 0.8	2.0 ± 0.7	-	-	-
Tetraphyllidea fam. gen. sp. †‡	l, si, st	53.3 (34.3-71.6)	2.4 ± 3.3	4.5 ± 3.3	27.6 (12.7-47.7)	1.0 ± 3.0	3.6 ± 5.1
Trypanorhyncha fam. gen. sp. †‡	m, st	6.7 (0.8-22.8)	0.1 ± 0.3	1,0	13.8 (3.8-31.7)	0.2 ± 0.5	1.3 ± 0.5
NEMATODA							
Anisakis sp. (Type I *sensu* Berland, 1961) †‡	st, si, l, m, go	26.7 (12.3-45.9)	0.4 ± 0.3	1.6 ± 0.9	48.3 (29.4-67.5)	8.0 ± 15.1	16.6 ± 18.4
Contracaecum sp. †§	st, si	6.7 (0.8-22.8)	0.1 ± 0.4	1.5 ± 0.7	-	-	-
Hysterothylacium sp. †‡	mo	3.3 (0.1-17.2)	0.03 ± 0.2	1,0	-	-	-
TREMATODA							
Otodistomum cf. *cestoides* †‡	st	-	-	-	3.4 (0.1-17.7)	0.03 ± 0.2	1

*Adult parasites. †Larval stages. ‡Encapsulated larvae. §Transient parasite.
Abbreviations: gi, gills; go, gonads; l, liver; m, muscles; mo, mouth; si, spiral intestine; st, stomach.

Table 8.2 - Comparative data for parasite infracommunities in *Etmopterus spinax* sampled at the Galicia Bank (GB), Avilés Canyon (AC) and Norwegian Deep and in two demersal shark species from different locations in the north-east Atlantic.

Host	***Etmopterus spinax***			***Scyliorhinus canicula***			***Squalus acanthias***
Locality	**Galicia Bank**	**Avilés Canyon**	**Norwegian Deep**	**Off Plymouth**	**Cardigan Bay**	**Eastern Solent**	**Off Western Ireland**
Source	**Present study (Mean ± SD)**		**Klimpel et al. (2003)***	**Moore (2001)***			**Henderson et al. (2002)***
Total number of species	9	7	7	7	6	4	10
Infracommunity richness	1.7 ± 1.0	1.2 ± 1.1	2.5	1.7	1.4	0.6	1.6
Infracommunity abundance	5.3 ± 4.3	9.5 ± 17.6	8.1	5.5	4.0	1.2	8.2
Brillouin's diversity index	0.3 ± 0.3	0.2 ± 0.3	-	-	-	-	-
Berger-Parker's dominance index	0.6 ± 0.3	0.6 ± 0.5	-	-	-	-	-

*Estimated mean values from the published data for prevalence and mean abundance or intensity.

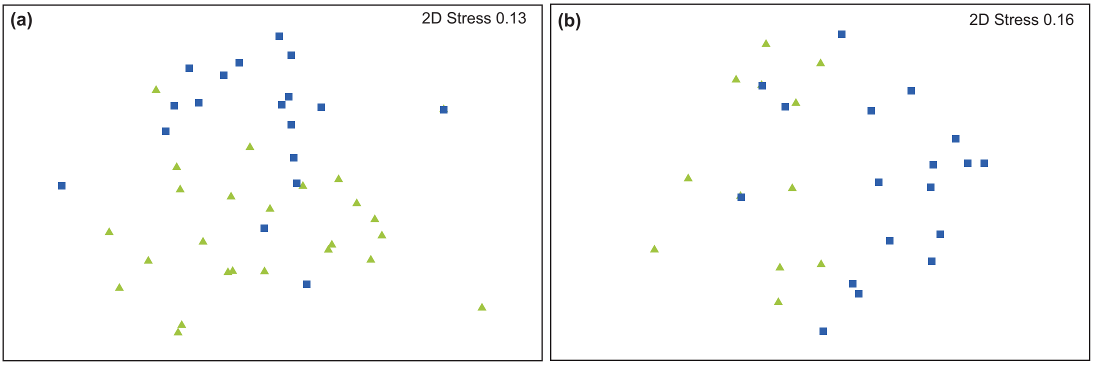

Fig. 8.2 - Non-metric multidimensional scaling ordination based on Bray-Curtis similarities (data square root transformed) of the parasite infracommunity (a) and prey items (b) in *Etmopterus spinax* from the Galicia Bank (squares) and the Avilés Canyon (triangles).

constructed for the total infracommunity abundance of larval and adult stages with fish size as a covariate revealed significant differentiation with respect to locality, the larval stages being significantly more abundant in the fish sampled at AC and the adult stages in the fish sampled at GB ($F_{(1,56)} = 10.61$, $P < 0.01$; $F_{(1,56)} = 11.42$, $P < 0.01$, respectively).

Fish size was not associated with infracommunity parameters at GB (range for r_s = 0.101-0.248, all $P > 0.05$) but was significantly correlated with species richness ($r_s = 0.737$), abundance ($r_s = 0.862$), diversity ($r_s = 0.475$) and dominance ($r_s = 0.427$) at AC (all $P < 0.05$). This was due to the wider host size variation in the sample from AC with a larger proportion of smaller fish which were either uninfected or harboured more depauperate infracommunities. Parasite infracommunities at GB exhibited somewhat higher richness, diversity and dominance whereas those at AC had higher abundance (Table 8.2). However, a GLM in which the effect of fish size was partialled out, revealed no significant differentiation with respect to locality for the four measures of infracommunity structure and diversity (richness, $F_{(1,56)} = 1.612$, $P > 0.05$; abundance, $F_{(1,56)} = 0.623$, $P > 0.05$; diversity, $F_{(1,56)} = 1.873$, $P > 0.05$; dominance, $F_{(1,56)} = 0.001$, $P > 0.05$).

The MDS ordination of infracommunities based on their relative similarities (Fig. 2a) showed a good separation of the communities sampled at GB and AC (2D stress 0.13). The PERMANCOVA with fish total length as a covariate provided strong support for the differentiation of parasite community composition and structure associated with locality (*Pseudo-*$F_{(1,55)} = 9.55$, $P_{(perm)} < 0.001$). Additionally the analysis revealed a significant effect of fish TL on community similarity (*Pseudo-*$F_{(1, 55)} = 6.212$, $P_{(perm)} < 0.001$). The factor locality explained 30.9% while TL explained 16.8% of the variation and there was a substantial residual variation (49.3%) probably reflecting the overall low similarity levels within each locality (mean similarity: GB, 30%; AC, 32%). The SIMPER procedure revealed that larval tetraphyllidean cestodes and the larval nematode *Anisakis* sp. had strong contribution to the similarity among infracommunities at the GB and AC respectively (54.4 and 76.0% contribution, respectively) whereas the second most contributing species were the monogenean *S. spinaci* at the GB (31.3% contribution) and the tetraphyllidean cestodes at AC (12.9% contribution). The overall dissimilarity between parasite communities sampled at the GB and AC was high (82%) with the three taxa contributing most to the community similarity at each locality being identified as key discriminating taxa between locations: *Anisakis* sp. (35.9%

Table 8.3 - Comparative data for diet composition (per cent frequency of occurrence, %*F*; percent by number, %*N*; per cent by mass, %*W*; index of relative importance of detected prey items, I_{RI} of *Etmopterus spinax* from the Galicia Bank (GB) and the Avilés Canyon (AC).

Prey items / Locality	**Galicia Bank**				**Avilés Canyon**			
	%*F*	**%*N***	**%*W***	**I_{RI}**	**%*F***	**%*N***	**%*W***	**I_{RI}**
Crustacea	76.5	61.5	41.0	7,841.6	100	85.5	85.2	17,068.6
Lophogastrida	5.9	3.9	1.6	32.1	-	-	-	-
Gnathophausia zoea	5.9	3.9	1.6	32.1	-	-	-	-
Euphausiacea	-	-	-	-	66.7	61.8	22.7	5,635.8
Euphausiacea unid.	-	-	-	-	16.7	9.2	3.5	212.2
Meganyctiphanes norvegica	-	-	-	-	61.1	52.6	19.2	4,388.3
Decapoda	76.5	57.7	39.4	7,424.0	77.7	23.7	62.5	6,700.5
Decapoda unid.	5.9	3.9	3.8	45.2	-	-	-	-
Brachyura unid.	-	-	-	-	5.6	1.3	0.5	9.9
Munida spp.	-	-	-	-	5.6	1.3	0.1	7.8
Caridea	70.6	53.9	35.6	6,310.6	72.2	21.1	61.9	5,992.1
Caridea unid.	52.9	42.3	18.9	3,239.2	27.8	6.6	11.4	498.2
Pasiphaea sivado	-	-	-	-	16.7	4.0	24.1	467.9
Pasiphaea multidentata	5.9	3.9	8.6	73.1	-	-	-	-
Pasiphaea spp.	11.8	7.7	8.1	185.8	33.3	7.8	19.4	911.3
Processa spp.	-	-	-	-	5.6	1.3	1.9	18.0
Penaeoidea	-	-	-	-	5.6	1.3	5.1	35.5
Solenocera membranacea	-	-	-	-	5.6	1.3	5.1	35.5
Echinodermata	5.9	3.9	0.4	24.8	5.6	1.3	0.1	8.0
Ophiuroidea unid.	5.9	3.9	0.4	24.8	5.6	1.3	0.1	8.0
Mollusca	5.9	3.9	2.5	37.6	-	-	-	-
Cephalopoda unid.	5.9	3.9	2.5	37.6	-	-	-	-
Actinopterygii	47.1	30.8	56.1	4,089.3	50.0	13.2	14.7	1,394.9
Actinopterygii unid.	35.3	23.1	32.5	1,960.3	38.9	9.2	8.9	702.53
Phycis blennoides	-	-	-	-	5.6	1.3	4.7	33.2
Xenodermichthys copei	5.9	3.9	18.4	130.9	-	-	-	-
Centrolophus niger	5.9	3.9	5.3	54.0	-	-	-	-
Ceratoscopelus maderensis	-	-	-	-	5.6	1.3	0.6	10.7
Myctophidae unid.	-	-	-	-	5.6	1.3	0.6	10.7

contribution to the dissimilarity between locations), larval tetraphyllideans (22.7% contribution), and *S. spinaci* (17.0% contribution). However, the GLMs constructed for the key taxa showed that locality significantly explained the abundance of two taxa after controlling for fish size: *Anisakis* sp. ($F_{(1,\ 56)}$ = 26.11, P < 0.001) showing significantly higher abundance in the fish sampled at AC and *S. spinaci* ($F_{(1,56)}$ = 20.62, P < 0.001), a species that was only recovered in the fish sampled at GB.

Diet

Of the 59 specimens examined 40.7% had empty stomachs (43.3% and 37.9% of the fish sampled at the GB and AC, respectively). In both areas fish diet consisted of crustaceans, mainly carideans and euphausiids, and fishes, whereas molluscs and echinoderms were of minor importance (Table 8.3). Carideans, chiefly represented by decapods *Pasiphaea* spp., were the most abundant prey of fish sampled at the GB in terms of %*F*, %*N* and I_{RI}. However, fishes including the bathypelagic species *Centrolophus niger* (Gmelin

1789) and *Xenodermichthys copei* (Gill 1884) showed the highest relative weight in the overall diet (Table 8.3). No significant correlations between the distributions of fish TL and prey abundance were found at the GB. Crustaceans, especially euphausiids and carideans, had the highest contribution to the diet of the fish sampled at the AC by means of %F, %N and IRI (Table 8.3). Crustaceans were chiefly represented by *Meganyctiphanes norvegica* (Sars 1857) and *Pasiphaea* spp. the latter being the most representative species group of carideans. Relatively high significant negative correlations were found between fish TL and the abundance of *M. norvegica* (r_s = -0.596, $P < 0.05$), and the total abundance of the euphausiids (r_s = -0.580, $P < 0.05$).

The MDS ordination based on Bray-Curtis similarity derived from the distributions of abundance of the prey taxa in individual fish revealed an overall good separation of the fish sampled at GB and AC (2D stress 0.16; Fig. 8.2b). The differences in composition and relative abundance of prey taxa/higher-level taxonomic groups in fish from the two study areas were confirmed by PERMANCOVA run with fish size (TL) as a covariate ($Pseudo\text{-}F_{(1,55)} = 4.392$, $P_{(perm)} < 0.01$). The analysis also revealed a significant effect of fish TL on the differentiation of prey assemblages in individual fish with respect to locality ($Pseudo\text{-}F_{(1,55)} = 6.417$, $P_{(perm)} < 0.001$). The factors locality" and TL explained 11% and 9.4% of the variation, respectively, the residual variation being of substantial importance (31%) probably reflecting the overall extremely low similarity levels within each locality (mean similarity: GB, 10%; AC, 14%). The SIMPER procedure revealed an overall high dissimilarity (92.5%) between the prey assemblages in fish from the GB and AC. The total abundance of the euphausiids (including *M. norvegica*) contributed most to the observed dissimilarity (27.0%), followed by the unidentified carideans (23.0%), unidentified Actinopterygii (17.5%) and *Pasiphaea* spp. (14.4%). GLM constructed for abundance of the four key discriminating prey taxa in individual fish using TL as a covariate, revealed no significant differentiation with respect to studied areas except for euphausiids ($F_{(1,56)} = 9.428$, $P < 0.01$) due to the lack of this prey item in the fish sampled at GB.

DISCUSSION

To the best of our knowledge, this study provides the first comparative parasite infracommunity data for a deep-sea shark species. The data revealed relatively rich component parasite communities and depauperate, with homogeneously low diversity infracommunities in *E. spinax*. The significant differences in the composition and structure of both parasite communities and prey assemblages indicate differential effects of the two deep-sea ecosystems on both long-term and most recent trophic niche of *E. spinax* and underline the importance of the use of multivariate analyses for the assessment of geographical variation in shark populations based on parasite and prey abundance data.

Obtaining deep-water samples is a major obstacle for studying trophic interactions of sharks and other deep-sea fishes due to the expense of the research expeditions, logistical constraints, and frequently few species and small sample sizes are available (Cailliet et al. 2001, Klimpel et al. 2009). Consequently, even for commercially targeted deep-sea species there is a lack of information on life history and ecological traits (Norse et al. 2012) and there is very limited information for most deep-sea chondrichthyans (Simpfendorfer & Kyne 2009) including data for parasites (Klimpel et al. 2003). However, in spite of the sampling constraints, this study reports *E. spinax* as a new host record for three parasite species: the cestodes *Sphyriocephalus* sp. and *Ditrachybothridium* cf. *macrocephalum* and the digenean *Otodistomum* cf. *cestoides*.

Post-larvae of *Sphyriocephalus* sp. (Trypanorhyncha: Sphyriocephalidae) were recovered in *E. spinax* at the GB only. Large migrating pelagic sharks

(Lamniformes) are suggested as definitive hosts of *Sphyriocephalus* spp. (Klimpel et al. 2006) and larval stages have been recorded in epi- and mesopelagic deep-water species (Klimpel et al. 2009 and references therein). Lamniform sharks such as the shortfin mako shark *Isurus oxyrinchus* Rafinesque 1810 and the porbeagle *Lamna nasus* (Bonnaterre 1788) are recorded in northern Spanish waters (ICES 2008, Lorance et al. 2009) and it is suggested that this kind of sharks aggregate close to seamounts (Morato et al. 2008, Oliver et al. 2011); higher densities of the definitive hosts may have facilitated the transmission of *Sphyriocephalus* sp. at GB.

The detection of a single encysted plerocercoid of *Ditrachybothridium* cf. *macrocephalum* also represents a new host record. Diphyllidean cestode larval stages have been recorded in molluscs, crustaceans and elasmobranchs, the later likely being infected by predation on infected invertebrates (Bray & Olson, 2004; Tyler, 2006). Plerocercoids, immature and non-gravid specimens of *Ditrachybothridium macrocephalum* (Diphyllidea: Ditrachybothriidae) have been recorded in the scyliorhinids *Scyliorhinus canicula* (L. 1758) and *Apristurus laurussonii* (Saemundsson 1922) and in the rajids *Leucoraja fullonica* (L. 1758), *Leucoraja circularis* (Couch 1838) and *Rajella bigelowi* (Stehmann 1978) (Rees 1959, Bray & Olson 2004). Bray & Olson (2004) also reported one fully mature early-gravid specimen from *Galeus melastomus* Rafinesque 1810. This study is the first to record a plerocercoid in an etmopterid thus indicating that *Ditrachybothridium* spp. may be widely distributed among different elasmobranch groups. Considering that *Galeus* spp. cannot be regarded as conventional predators of *E. spinax* (Ebert et al. 1996, Fanelli et al. 2009, Preciado et al. 2009) it is likely that the new host record is a result of accidental parasitism.

The single metacercaria of *Otodistomum* cf. *cestoides* (Azygiidae) recovered from the stomach of *E. spinax* in the AC had poorly developed anlagen of the reproductive organs and a sucker ratio of 1:1.38. Metacercariae of *Otodistomum* spp. have been reported encysted in teleosts, chimaeras, a ray and carcharhiniform sharks (Gibson & Bray 1977); these authors also considered the vast majority of the records of immature encysted *Otodistomum* spp. in the North East Atlantic to belong to *Otodistomum cestoides* (van Beneden 1871), a species that matures in rays (*Raja* spp.) and occasionally in sharks (*Centroscymnus* spp.). Three larval *Contracaecum* sp. were found freely in the digestive tract of two *E. spinax*. These are likely transient parasites (i.e. from a fish prey item) and thus reflecting most recent feeding history of the individual shark.

The richness of parasite component communities in *E. spinax* observed at both locations is comparable to that recorded in studies of other small demersal shark species (range 4–10 species, Moore 2001, Henderson et al. 2002, Klimpel et al. 2003, see Table 8.2). It is worth noting that these data come from species in shallow waters (usually < 200 m; see Moore 2001, Henderson et al. 2002) and juvenile *E. spinax* (see Klimpel et al. 2003). Previous studies on other small-sized deep-sea shark species report similar total richness e.g. Palm & Schröder (2001) recorded nine and seven species in the rough longnose dogfish *Deania hystricosa* (Garman 1906) and in the arrowhead dogfish *D. profundorum* (Smith & Radcliffe 1912), respectively, and Chambers (2008) found eight species in the black dogfish *Centroscyllium fabricii* (Reinhardt 1825).

In spite of this relatively high richness of component communities, the infracommunities in *E. spinax* were depauperate, with low diversity and strongly dominated by a single species (Table 8.2). This may represent a characteristic feature of small sharks, the estimated mean richness in juvenile *E. spinax* examined by Klimpel et al. (2003) (see Table 8.2) being somewhat higher; however, no other data are currently available to assess this prediction. Although parasite communities at both localities exhibited homogeneity in relation to the species richness, abundance, diversity and dominance, infracommunities in fish from the GB and the AC differed regarding the species composition and structure and these differences were especially associated with the distribution and abundance of three key discriminating taxa: the larval nematodes *Anisakis* sp., the larval tetraphyllideans and the monogenean *S. spinaci*.

Anisakis sp. contributed strongly to the dissimilarity between the infracommunities from the two localities studied due to the higher abundance in the fish from the AC. All collected larval *Anisakis* spp. were found encysted in the wall of the digestive tract, gonads or liver and were identified as *Anisakis* Type I of Berland (1961). This morphotype has been recorded (with molecular confirmation of the identification) in hake *Merluccius merluccius* (L. 1758) and horse mackerel *Trachurus trachurus* (L. 1758) (Mattiucci et al. 2004, Mattiucci et al. 2008) and in sharks from the North East Atlantic (Moore 2001, Palm & Schröder 2001, Henderson et al. 2002, Klimpel et al. 2003). *Anisakis* spp. utilise pelagic life cycles with invertebrate and vertebrate intermediate and paratenic hosts, respectively, and cetaceans as definitive hosts (Anderson et al. 2000). The higher abundance of *Anisakis* sp. in the AC may be associated with the abundance of the other hosts in the life cycle e.g. the presence and abundance of toothed whales. The southern Bay of Biscay (Fig. 8.1) harbours a high cetacean diversity (López et al. 2004, Laborde Basto d'Andrade 2008) and surveys in the AC observed higher numbers of piscivorous and teuthivorous toothed whales compared to the GB (López personal communication). However, to the best of our knowledge the benthopelagic *E. spinax* has not been recorded as a common prey of cetaceans and due to the pelagic life cycle of *Anisakis* spp. this infection can be considered accidental and a dead end for the parasite.

The higher abundance of *Anisakis* sp. at the AC may also be associated with the higher fishery efforts at this locality (Rodríguez-Cabello et al. 2005, Punzón et al. 2010) compared with the GB (Piñeiro et al. 2001). Fishing pressure has been shown to have a negative effect on the diversity and abundance of parasites with complex life cycles (Wood & Lafferty 2014). However, one aspect of the interplay between fishing and transmission pathways of *Anisakis* spp. deserves further exploration. Fish discard rates in the North East Atlantic off the Iberian Peninsula are very high (c. 90%; see MRAG, 2007) as are the evisceration practices on board; the latter may result in release of large quantities of viable *Anisakis* spp. accumulated in the viscera due to their lipid content (Strømnes & Andersen 2003). The disposal of infected discards to opportunistic scavengers such as *E. spinax* and related species (Hallett & Daley 2011, Dimech et al. 2012) may facilitate the transmission and thus increase the infection levels of *Anisakis* spp. in the fish paratenic hosts (Abollo et al. 2001, Blanco et al. 2007). Consequently, the distinctly higher abundance of *Anisakis* sp. observed in fish from the AC may also be associated with the higher fishing and discard rates at this locality compared with the GB.

Unidentified larval tetraphyllideans also contributed to the discrimination of the infracommunities in *E. spinax* studied at GB and AC perhaps due to the higher prevalence at GB (no significant differences in abundance were detected). These are usually assigned to *Scolex pleuronectis*, a collective group name for larval cestodes presumed to be members of the order Tetraphyllidea (Jensen & Bullard 2010). However, the identification of these larvae 'remains indeterminate at all levels' (Jensen & Bullard 2010) and no inference can be made about possible transmission pathways without molecular evidence.

The monogenean *Squalonchocotyle spinaci* (Diclybothriidea: Hexabothriidae) contributed to the dissimilarity of parasite communities at the GB and the AC due to its presence in the former locality only. Since *S. spinaci* is a directly transmitted parasite, its distribution and transmission are subjected to potential effects of the abiotic conditions (Grutter 1998, Bagge et al. 2004). In particular, the benthic stages of the monogenean life cycle (egg and oncomiracidium) can be affected by environmental variables such as the nature of the substrate or strong currents resulting in variations of infection rates between areas (Grutter 1998, Sikkel et al. 2009 and references therein). Sediments on the plateau of the GB are represented mainly by medium sand whereas medium to fine sand were observed in the AC (Sánchez et al. 2010, Serrano et al. 2010). Further, during the sampling in 2010 a large part of the plateau of the GB was covered with a layer of dead pteropods (Thecosomata), which may also act as suitable substrate for benthic stages of parasites (Serrano et al. 2010). It is therefore possible that environmental conditions (e.g. substrate) are more advantageous for the establishment and spread of *S. spinaci* in the GB compared with the AC.

Additionally, biotic factors such as host schooling behaviour, density and susceptibility to infection, and cleaner fish density, can affect monogenean transmission contributing to variations in parasite abundance between locations (Grutter 1998, Sasal 2003, Raeymaekers et al. 2008, Sikkel et al. 2009) where, amongst other factors, parasite infection co-varies with fish host schooling behaviour and density (Sasal 2003 and references therein). Monogeneans are usually strictly host specific and the oncomiracidia are short-lived, so that the transmission of these parasites is strongly associated with local host abundance (Wood et al. 2013). Although the data are scarce, aggregation behaviour in different shark species, both adult and juveniles, has been suggested (Heithaus 2004, Jacoby et al. 2011) including some *Etmopterus* spp. (see Reif 1985). It is possible that younger (smaller) *E. spinax* exhibit aggregation behaviour that is likely driven by predation avoidance (as indicated for elasmobranchs by Jacoby et al. 2011). This may have facilitated the transmission of *S. spinaci* at GB, especially among host individuals of smaller body size; this suggestion is supported by the significant negative correlation between the abundance of *S. spinaci* and fish size. The four other parasite taxa that exhibited correlations (positive) with host size in either GB or AC, were larval cestodes and nematodes which tend to be accumulated with fish age (Poulin 2000). This significant correlation could also be related to higher ingestion rates of larger hosts.

The present data on food composition indicate that *E. spinax* exhibits opportunistic feeding habits, capturing the available benthopelagic prey of suitable size and exploiting aggregations of organisms as described by Mauchline & Gordon (1986). This is the first study to provide information on the diet of this species at GB and AC. The main prey items recorded here were also reported in previous studies on *E. spinax* and related species (Santos & Borges 2001, Bergstad et al. 2003, Neiva et al. 2006, Fanelli et al. 2009, Preciado et al. 2009, Valls et al. 2011, Xavier et al. 2012). It is worth noting that whereas these studies revealed variations in the diet composition over large spatial scales, the present data provide an insight into similar variations but at distinctly smaller spatial scale.

No significant effect of fish size on the abundance of prey taxa/higher-level taxonomic groups was found in the diet of fish from the GB, but the analysis of the sample with a wider range of TL collected at AC revealed a negative correlation between host size and the abundance of *M. norvegica* and the total abundance of euphausiids. A similar tendency was observed in specimens studied in the Norwegian Deep (Bergstad et al. 2003, Klimpel et al. 2003) and in the diet composition of *E. spinax* from off Algarve (Neiva et al. 2006). Larger specimens tend to alter their feeding habits to larger prey (e.g. fishes, cephalopods), thus, changes in feeding habits with body size could be associated to the need to meet higher energetic requirements for growth and reproduction in larger fish (Neiva et al. 2006).

Although a high variability in the similarity of prey composition in individual fish within each locality was found, the multivariate analysis revealed a significant geographical differentiation in prey composition with three prey taxa contributing most to the observed dissimilarity (i.e. euphausiids, carideans and actinopterygians). Euphausiids showed higher abundances in the ecosystem of AC than in the GB (IF, unpublished data) where *E. spinax* was found to prey on benthopelagic decapods. In contrast, euphausiids were reported as the dominant prey of this shark species in the Skagerrak, the Bay of Biscay, the southern Portuguese slope (Santos & Borges 2001, Bergstad et al. 2003, Neiva et al. 2006, Preciado et al. 2009) and in juvenile specimens from the Norwegian Deep (Klimpel et al. 2003) whereas carideans were shown to play a major role in the diet of *Etmopterus* spp. in Portuguese waters (Saldanha et al. 1995, Xavier et al. 2012) and in the Mediterranean (Macpherson 1981, Fanelli et al. 2009, Valls et al. 2011). The dominance of different crustacean preys observed in GB and AC, could be due to contrasting environmental conditions such as topography, oceanography and sedimentation (Preciado et al. 2009) which could influence the vertical stratification of prey that affects its availability (Neiva et al. 2006).

Following current knowledge on parasite life cycles, the prey items found in this study represent potentially important intermediate hosts. Crustaceans in particular, are considered to play important roles as intermediate hosts of fish parasites (Marcogliese 2002), and are involved in the life cycles of the cestodes and nematodes recorded in the present study. Thus, the presence of euphausiids in AC could be linked to the corresponding higher abundances of *Anisakis* sp. in the sharks from this location (see e.g. Smith 1983, Brickle et al. 2006, Hojgaard 1999).

In conclusion, the multivariate approach applied in this study revealed differences in the parasite community structure and diet of *E. spinax* that indicate variation in both the environmental characteristics and communities of free-living organisms in the parasite- and food sub-webs associated with *E. spinax* in the ecosystems of Galicia Bank and Avilés Canyon. Although several parasites complete their life cycles in these two ecologically important topographic features, the quantitative comparisons suggest differential effects on parasite abundance and community similarity of the definitive hosts as indicated by the distribution within infracommunities of the three key discriminating taxa. Of particular importance is the detection of concordant differences in the most recent trophic niche utilisation by individual fish from the two localities and the life cycle link between two of the key discriminating taxa, the euphausids and *Anisakis* sp., explaining the higher abundance of this larval nematode in the AC. The present data may serve as a starting point for future analyses of population connectivity and potential migration of *E. spinax* between GB and AC and adjacent areas using parasites and diet as biological indicators. Of particular importance would be their use in comparative analyses of adult fish populations from other areas in the North East Atlantic that would help assess the importance for shark populations of these two ecosystems considered for inclusion in the Natura 2000 network.

ACKNOWLEDGMENTS

We are grateful to A. López (Coordinadora para el Estudio de los Mamíferos Marinos, CEMMA, Spain), A. Henderson (Sultan Qaboos University, Oman) and A. Moore (RSK Environment Ltd., UK) for their help providing information on additional data and sampling depth of published studies and A. Kostadinova (Institute of Parasitology, Academy of Sciences of the Czech Republic) for her very useful comments. We thank the anonymous reviewers and the editor for their constructive criticisms and helpful corrections. We thank C. Junge for improving the English of the manuscript and R. Mendiguchia for her great support providing the bibliography. Thanks are due to the scientific staff and crew onboard the research vessels RV Thalassa and RV Cornide de Saavedra for their help during the collection of material. This study was conducted in the frame of the projects: 'DEEPCON: Study of the connectivity between marine deepwater ecosystems based on elasmobranch populations' (CGL2010-16690;

financed by the Spanish Ministry for Science and Innovation, MICINN) and the EU LIFE+ Project 'INDEMARES: Inventory and designation of marine Natura 2000 areas in the Spanish sea' (07/NAT/E/000732).

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Deania profundorum

Chapter 9

First insight into the diet and parasite communities of the deep-sea shark *Deania profundorum* (Smith & Radcliffe, 1912) from the Avilés Canyon (southern Bay of Biscay): shedding light on host's role?

ABSTRACT

The life-history traits of deep-sea elasmobranchs make them less resilient to the increasing scale of anthropogenic impacts such as fisheries. The necessity for proper management measures is hampered by the scant knowledge on these taxa and its biology. Here we studied the metazoan parasite fauna and diet of the arrowhead dogfish, *Deania profundorum*, from the Avilés Canyon system in the southern Bay of Biscay (Northeast Atlantic, Spain). To the best of our knowledge this study provides the first comprehensive insight in the parasite infracommunities and diet data of the deep-sea shark *Deania profundorum* in the Northeast Atlantic. The present study revealed a rich parasite infracommunity dominated by cestode species. The high representation of larval stages of cestodes and nematodes indicates that this shark has an intermediate position in the local food-web. The composition and structure of parasite communities did not reveal differences between sampling years and host sex, while the abundance, richness and diversity of the infracommunity could be related to host size. The abundance of two cestodes, adults of *Deanicola* sp. and larval Lacistorhynchidae gen. sp., and of one larval nematode, *Anisakis* sp. Type I (*sensu* Berland, 1961), increased with host size and revealed a higher parasite burden in larger males. These differences between host sex may hint to potentially distinct feeding habits. The diet of the fish sampled consists mainly of bentho-, bathypelagic fishes, crustaceans and cephalopods. No significant differences were observed in prey composition and structure associated neither to sex nor to host size. This study highlights the previous suggestions of the importance using parasites as biological indicators to identify potential prey items of past feeding events and the assessment of the host role in marine communities.

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INTRODUCTION

Species of the family Centrophoridae (Squaliformes) are distributed from the tropics to warm temperate waters on continental and insular shelves and slopes. They have been recorded from upper to middle bathyal depths in the Atlantic, the Indian and the Pacific Ocean, except the eastern North Pacific (Musick et al. 2004, Nelson 2006). Usually centrophorids are considered benthopelagic (Musick et al. 2004) preying mostly on teleosts (mesopelagic and benthic), squids, while smaller specimens also feed on crustaceans (Yano et al. 1991, Ebert et al. 1992, Saldanha et al. 1995, Dunn et al. 2013, Costa et al. 2014 and references therein). The genus *Deania* Jordan & Snyder, 1902 represented by four species is distributed in all oceans (Musick et al. 2004). The arrowhead dogfish, *Deania profundorum* (Smith & Radcliffe, 1912) was recorded from the Pacific and the Indian Ocean and from both sides of the North and South Atlantic Ocean (Compagno 1998, Nelson 2006, Froese & Pauly 2017) with the Bay of Biscay (Cantabrian Sea) considered as the northernmost extension in the Northeast Atlantic (Sanjuán et al. 2012). This species usually occurs in habitats on or near the seabed, in depths between 270 and 1,800 m (Compagno 1984). For most species of the Centrophoridae knowledge on the taxonomy as well as their ecology and biology is scarce and this also applies to *D. profundorum* (Sousa et al. 2009).

The interest to fisheries for species of this genus is considered moderate (FAO 2012) and in most areas of the Northeast Atlantic these species are of no commercial value and even though livers are retained sometimes for oil extraction carcasses are often discarded (Clarke et al. 2002). Although effort restrictions and total allowable catch (TAC) implemented by the European Union are maintained for years (Council Regulation (EU) No 1359/2008; Council Regulation (EU) 2016/2285 of 2016) high by-catch impacts imposed by mixed fisheries still exist (Clarke et al. 2015, Neat et al. 2015). The discards of moribund or already dead specimens can be quite high especially in deep-sea trawl fisheries (Neat et al. 2011) but often are not quantified (Neat et al. 2015). Owing to their life history traits (e.g. slow growth, late maturity, low fecundity) deep-water sharks exhibit a low resilience to fishery impacts and can be affected profoundly especially by non selective deep-sea fisheries (Simpfendorfer & Kyne 2009, Dunn et al. 2010). However, the current dearth of relevant information on chondrichthyans impedes the development of proper management measures and their effective implementation to protect these predators of deepwater ecosystems (Dunn et al. 2010, Kyne & Simpfendorfer 2010, Gallagher et al. 2012).

The few aspects on the biology of *D. profundorum* published to date are mainly focused on reproduction and diet (Ebert et al. 1992, Sousa et al. 2009). Along with observed sexual dimorphism where females grow larger than males (Sousa et al. 2009), it is supposed that *D. profundorum* exhibits typical k-selective characteristics such as a two- or three- year non-continuous reproductive cycle, as observed for other species of this genus (Clarke et al. 2002, Kyne & Simpfendorfer 2010, Irvine et al. 2012). Knowledge on the diet and feeding habits is still scarce for many sharks (Wetherbee & Cortés 2004) and especially for deepwater species due to low catch rates and often empty stomachs (Dunn et al. 2010 and references therein). Scant available data refer to teleosts, cephalopods and crustaceans as main prey of *D. profundorum* (Compagno 1984) which was also recorded for samples from off western South Africa (Ebert et al. 1992), but no data on its diet exists for the Northeast Atlantic. The removal of predators like sharks can affect the composition and diversity of the local fish assemblages; therefore, studies on trophic interactions of chondrichthyans are recommended (Stevens et al. 2000).

Along with the data on its diet more information on feeding habits could also be revealed by analysing its parasite communities (Caira 1990, Begg & Waldman 1999, MacKenzie 2002). Long-term feeding habits and diet niches of host species can be analysed via food-web transmitted parasites, as these indicate past food acquisition of host individuals (Lafferty et al. 2008, Knudsen et al. 2010). The knowledge on the life cycle pathways and transmission patterns of parasites provide valuable information on food-web structure (Marcogliese 2002) and consequently, parasites are suggested as useful biological indicators especially for deep-sea and rare species (Caira 1990, MacKenzie & Abaunza 1998). Along with food-web transmitted parasites, directly tranmitted parasites such as monogeans could indicate migratory behaviour or could be related to density patterns of their host (e.g. Grutter 1998, Sasal 2003).

Some information on parasites found in species of the genus *Deania* is available from the Pacific Ocean, the Northeast and central East Atlantic and recorded parasites comprised cestodes, nematodes and few monogeneans (Schröder 1999, Palm & Schröder 2001, Klimpel et al. 2009). Information on parasites recorded for *D. profundorum* exist from the central East Atlantic only and even though based on very few specimens, it indicated a prospective rich parasite fauna (Schröder 1999, Palm & Schröder 2001), which point to the fact that its parasites could be potentially excellent indicators of host biology (MacKenzie 1987, Caira 1990, MacKenzie 2002).

The present study area, the Avilés Canyon system (southern Bay of Biscay, Northeast Atlantic, Spain), is included in the Natura 2000 network (Fig. 9.1) and reveals a rich fauna and communities are considered to be distinctly different to those of the surrounding continental shelf (Louzao et al. 2010 and references therein). In general, topographic underwater features such as canyons modify the flow regime in the area and facilitate the water exchange between the shelf and the slope, and can promote the primary production by enhanced upwelling of cold and nutrient rich water (González-Quirós et al. 2003, 2004, Ruiz-Villarreal et al. 2004). The enhanced primary production is usually followed by the sinking of dead phytoplankton cells nourishing pelagic communities in the water column but also affects the composition and structure of benthic communities in the deep and promotes an increased diversity (e.g. Cartes et al. 2004).

Few surveys were conducted on deep-sea elasmobranchs of this area focusing on distribution patterns (Sánchez et al. 2008), potential fishery impacts imposed on these species (Sánchez et al. 2005), the analysis of diet (Preciado et al. 2009, Isbert et al. 2015) and parasite communities (Isbert et al. 2015). Therefore, owing to the supposed importance of elasmobranchs in the deepwater communities in other areas of the southern Bay of Biscay (Sánchez et al. 2008), the present study shall provide an insight into the role of *D. profundorum* within the community of the Avilés Canyon combining the description of the recent trophic niche (stomach contents) and the long-term feeding niche (parasite communities) utilization. Further, this survey on the diet and metazoan parasite communities of this shark species will provide the first data from this area and add some new data to the scant information available for this genus.

MATERIAL AND METHODS

Study area and sampling

This work has been developed in the Avilés Canyon system, located in the Northeast Atlantic, very close to the northern Spanish coast (*c.* 7 miles) (Fig. 9.1), exhibiting a very steep and narrow morphology. The canyon intersects the continental shelf at *c.* 140 m depth and ranges to *c.* 4,700 m depth. Due to its proximity to the coast, this area is characterized by continental input of sediments and organic matter by freshwater runoff, poleward currents in winter and equatorward currents in spring/summer producing upwelling events and phytoplankton blooms (González-Quirós et al. 2003, Ruiz-Villarreal et al. 2004, Louzao et al. 2010).

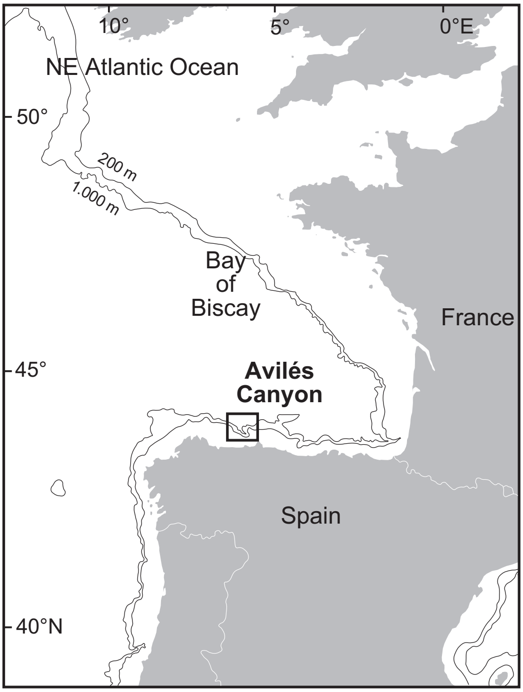

Fig. 9.1 - Sampling area (Avilés Canyon system) of *Deania profundorum* in the southern Bay of Biscay in the Northeast Atlantic, Spain.

Specimens of *Deania profundorum* were sampled during scientific surveys carried out in the Avilés Canyon in July 2010 and May 2011 (between 43°49'00''N, 06°21'00''W and 43°58'00''N, 05°28'00''W). Sampling of specimens was conducted with a bottom trawl net (GOC-73, mesh size 10 mm, haul duration 30 min) in depths between 580 and 1,260 m. Shark specimens were identified on board and frozen at -25°C for further inspection. In the laboratory, prior examination and dissection, each specimen was defrosted, sexed, and total length (TL) was recorded to the nearest 0.1 cm.

Parasitological examination

In the laboratory the external and internal body surfaces of the fish specimens were inspected. The gills, olfactory organs and the gastrointestinal tract were removed, preserved separately in seawater and examined for parasites. The entire musculature was sliced and squeezed between glass plates and examined under the stereomicroscope. All metazoan parasites were collected and preserved in 70% ethanol or fixed in 4% borax-buffered formalin for subsequent identification. Monogeneans and cestodes were stained with iron acetocarmine (Georgiev et al. 1986), dehydrated in alcohol series, cleared in dimethyl phthalate, and mounted in Canada Balsam. Nematodes were examined in 100% glycerine after dehydration in graded glycerine ethanol series. All parasites were identified to the lowest possible taxonomic level using identification keys and counted.

Ecological terminology for the quantitative description of the parasite populations and communities follow Bush et al. (1997). Prevalence (%P) is the number of hosts infected with a particular parasite species divided by the number of hosts examined and expressed as a percentage; mean abundance (MA) is the total number of individuals of a particular parasite species divided by the number of hosts examined; mean intensity (MI) is the average of the total number of individuals of a particular parasite species found in a sample divided by the number of hosts infected with this species.

Diet examination

The stomach contents were analysed for prey items. The stomach was weighed (wet weight), dissected and prey items were separated and identified to the lowest possible taxonomic level using a stereomicroscope. The contribution of each food item to the diet was expressed as frequency of occurrence (%F), percentage by number (%N) and percentage by mass (%W) following Hyslop (1980). The frequency of occurrence was determined as the number of stomachs with prey item "i" divided by the number of all full stomachs (stomachs with food and prey items). The (%N) and (%W) were calculated as the number or mass of prey item ("i") divided by the total number or mass of all prey items, expressed as percentage. The index of relative importance I_{RI} (Pinkas et al. 1971) was calculated to facilitate comparisons between

Table 9.1 - Site of infestation in the host, prevalence [%P (95% C.I.)], mean abundance (MA ± S.D.) and mean intensity [MI ± S.D. (range)] of parasite species recovered in *Deania profundorum* from the Avilés Canyon (southern Bay of Biscay).

Parasite	Site in host	%P	MA	MI
Monogenea				
Squalonchocotyle spinaci	gi	3.4 (0.0–17.7)	0.03±0.2	1
Squalotrema sp.	nc	13.8 (3.8–31.7)	0.2±0.5	1.3±0.5 (1-2)
Cestoda				
Aporhynchus cf. *menezesi*	si	10.3 (2.2–27.4)	0.1±0.3	1
Deanicola sp.	st, si	75.9 (56.5-89.7)	4.4±6.0	5.9±6.2 (1–27)
Lacistorhynchidae gen. sp.†‡	st, si, m, go	79.3 (60.3-92.0)	4.3±5.0	5.4±5.0 (1–18)
Sphyriocephalus sp.†	st	6.9 (0.8–22.7)	0.1±0.3	1
Tetraphyllidea fam. gen sp. †‡	l, si	13.8 (3.9-31.7)	0.4±1.4	3.3±2.6 (1–7)
Nematoda				
Anisakis sp. (Type I sensu Berland, 1961)†‡	l, sp, k, go, st, si, m	79.3 (60.3–92.0)	32.5±69.6	41.0±76.1 (1–276)
Hysterothylacium sp.†‡	st, si	10.3 (2.2–27.4)	0.1±0.3	1

gi, gills; go, gonads; k, kidney; l, liver; m, muscle; nc, nasal cavity; si, spiral intestine; sp, spleen; st, stomach.
†Larval stages
‡Encapsulated larvae

samples of other studies. This index is expressed as the sum of I_{RI} indices in all prey: $I_{RI} = (I_{RIi}\ \Sigma I^{-1}_{RIi})$. Otoliths found in the stomach contents were identified by consulting the AFORO web (http://www.cmima.csic.es/aforo/; Lombarte et al. 2006).

Data analysis

Morphometric host data (i.e. TL) were tested for normality and variance homogeneity (Kolgomorov-Smirnov-test, F-test) and, depending on the obtained results, parametric or non-parametric tests were applied. Sex ratio, TL and its potential relation to the total parasite load or detected number of prey items were tested with non-parametric tests except in the case of normal distribution.

Parasite infrapopulations (all individuals of a given parasite species in an individual fish) and infracommunities (all infrapopulations in an individual fish) were used as replicate samples in all analyses performed using parasites. For both sampling years and host sex, the means of infracommunity richness and abundance, Brillouin's diversity and Berger–Parker dominance index for the infracommunities were calculated and compared. The number of prey items per species or higher taxon in individual fish was used in the quantitative diet comparisons. Parasite and diet data were ln (x + 1) transformed. General linear model (GLM) analyses were performed to assess possible differences between the samples of both sampling years or host sex using TL as a covariate if not stated otherwise. Parasite taxa with %P<5% were excluded from these analyses. Due to the overall low numerical representation of single prey taxa for the GLMs prey items were summarized to higher-level taxonomic groups. Parasite prevalences and total mean abundances between years or sexes were compared with Fisher's exact test and Bootstrap two-sample t-test, respectively. Analyses were carried out using Statistica 9.0 (StatSoft, Inc.; www.statsoft.com) and Quantitative Parasitology (QP 3.0; Rozsa et al. 2000).

Community similarity analyses were carried out with PERMANOVA+for PRIMER v6 software (Anderson et al. 2008). Permutational multivariate analyses of covariance (PERMANCOVA; Anderson 2001) with TL as a covariate were conducted with years or host sex as a fixed factor to assess the effects of these two factors on the composition and structure of parasite communities and prey assemblages accounting for the effect of fish size. Permutation P-values were obtained under a reduced model of permutation of raw data 9,999 permutations and the SUM OF SQUARES TYPE I (sequential). Parasite and prey abundance data were square-root transformed and TL data were ln-transformed.

RESULTS

Parasite communities

In the present study 29 specimens of *Deania profundorum* were examined and a total of 1,224 parasite individuals belonging to nine different taxa were found. Overall prevalence (P) was 89.7% (C.I.: 72.7–97.1), with a total mean abundance of 42.2±71.6 (range 0–292).

All detected parasites belong to the three main groups: Cestoda, Monogenea, and Nematoda (Table 9.1). Five of the nine taxa were represented by larval stages which comprised the majority of all identified parasite individuals (88.7%). Nematodes and monogeneans were represented by larval and adult stages, respectively, while cestodes showed a balanced ratio between larval and adult stages (51.5 to 48.5%). Six out of nine taxa are recorded for the first time in *D. profundorum*: the cestodes *Aporhynchus* cf. *menezesi* Noever, Caira, Kuchta & Desjardins, 2010 (Trypanorhyncha, Aporhynchidae), *Sphyriocephalus* sp. (Trypanorhyncha, Sphyriocephalidae), Tetraphyllidea fam. gen. sp., a nematode of the genus *Hysterothylacium* (Ascaridoidea, Raphidascaridae) and two monogeneans, *Squalonchocotyle spinaci* (Goto 1894) and *Squalotrema* sp. (Monopisthocotylea, Monocotylidea).

Both years of sampling (July 2010 and May 2011) did not differ significantly neither in TL nor in sex ratios. Overall prevalence and total mean abundance of parasites did not differ significantly between both years (2010: %P 76.9% (48.0–93.4), MA 32.2±60.8; 2011: %P 100.0% (79.2–100.0), MA 50.3±80.4). The GLMs in which the effect of fish size was partialled out, revealed no significant differentiation with respect to the sampling years for all four infracommunity parameters. Therefore the subsequent analyses were performed with pooled data from the two different years.

Considering all fish individuals, the mean value for TL was 41.5±11.1cm. The fish size was significantly associated with the infracommunity abundance ($r_s = 0.874$, $P < 0.0001$), richness ($r_s = 0.639$, $P = 0.0002$) and Brillouin's diversity index ($r_s = 0.419$, $P = 0.03$), whereas Berger Parker's dominance index showed no relation to body size (Fig. 9.2). The abundances of three parasite taxa were significantly associated to fish size (*Anisakis* sp. ascribed to morphotype Type I *sensu* Berland (1961), $r_s = 0.888$, $P < 0.0001$; Lacistorhynchidae gen. sp. $r_s = 0.622$, $P = 0.0003$ and *Deanicola* sp. $r_s = 0.451$, $P = 0.01$). Moreover, these three parasite taxa exhibited the highest infection levels (Table 9.1).

The sex ratio for all specimens examined was 1:0.9 in favour of males. Mean values for TL of two sexes did not differ significantly but males were slightly larger (males: 44.1±12.6 cm; females: 38.7±9.0 cm). Overall prevalence and total mean abundance of samples did not show significant differences between sexes (males: %P 80.0 (53.4–94.3), MA 56.1±86.8; females: %P 100.0 (76.8–100.0), MA 27.4±49.8). The GLM in which the effect of fish size was partialled out did not reveal significant differences with respect to host sex for the four infracommuity parameters (Table 9.2).

The PERMANCOVA with fish TL as covariate did not show significant differentiation in the composition and structure of the parasite infracommunities between sexes. Though, the analysis showed a significant effect of fish TL on community similarity (pseudo-$F_{1,25} = 16.04$ $P_{(perm)} = 0.0001$) but without interaction. The GLMs constructed for all species with P%>5% showed that sex significantly explained the abundance of two of eight species after controlling for TL: *Anisakis* sp. ($F_{1,26} = 36.79$, $P < 0.0001$), and Lacistorhynchidae gen. sp. ($F_{1,26} = 6.73$, $P = 0.004$)

where each species revealed higher mean abundances in males (Fig. 9.3), while all other species showed no significant differences.

Diet

Of the 29 examined specimens 37.9% had empty stomachs and none of the stomachs was regurgitated. The number of detected prey items

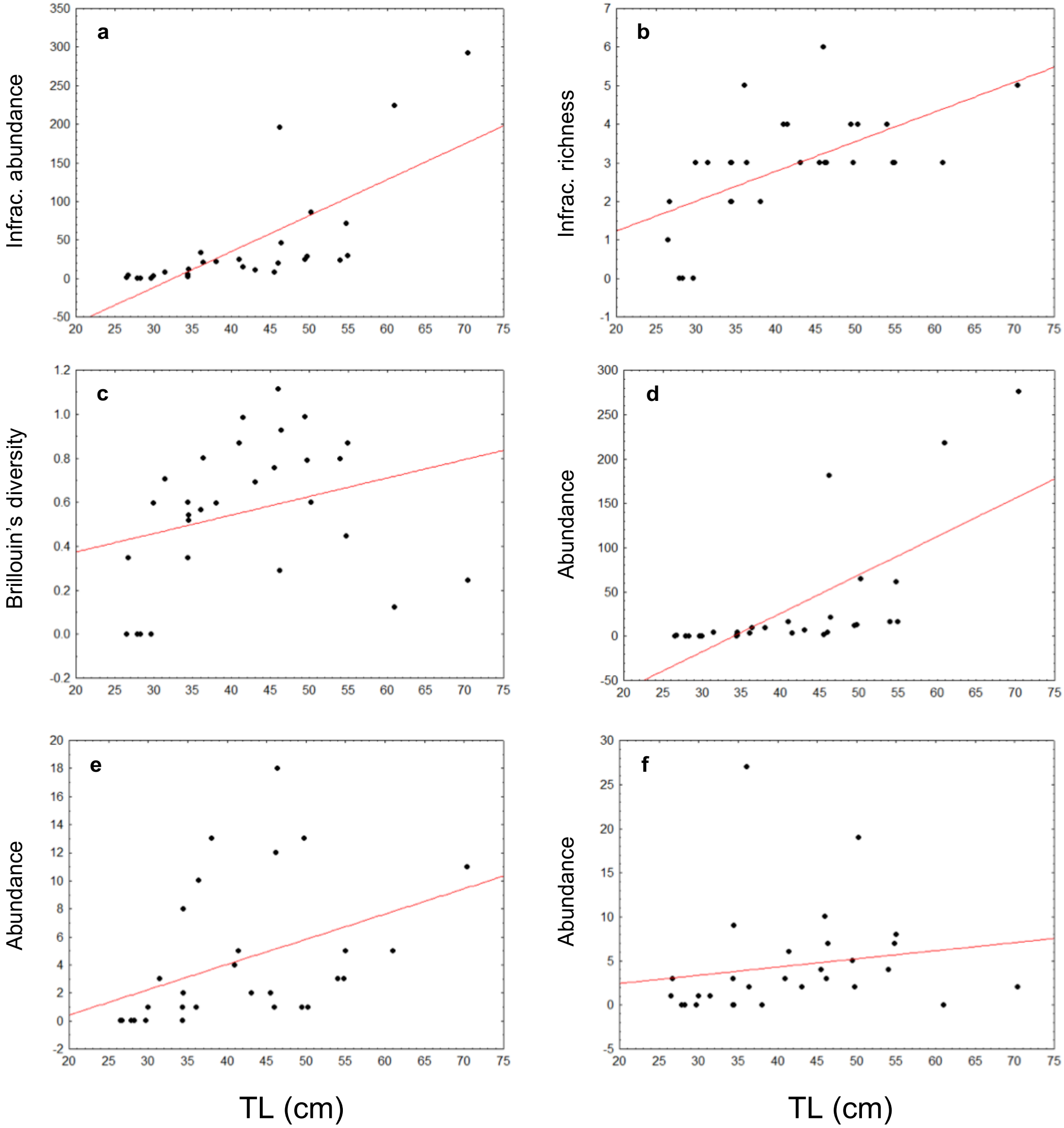

Fig. 9.2 - Relationship between the body size (TL), and the infracommunity parameters and abundances of most abundant single taxa found in *Deania profundorum* from the Avilés Canyon (southern Bay of Biscay). a: infracommunity abundance; b: infracommunity richness; c: Brillouin's diversity; d: *Anisakis* sp. Type I (*sensu* Berland, 1961); e: Lacistorhynchidae gen. sp.; f: *Deanicola* sp.

Table 9.2 - Comparative data for parasite infracommunity parameters for the total number of analysed specimens, male and female of *Deania profundorum* from the Avilés Canyon (southern Bay of Biscay) [data provided as mean +/- standard deviation (S.D.)].

	Total Mean±S.D.	**Male** Mean±S.D.	**Female** Mean±S.D.
Infracommunity richness	2.9±1.4	2.7±1.8	3.1±1.0
Infracommunity abundance	42.2±71.6	56.0±86.7	27.4±49.8
Brillouin's diversity index	0.6±0.3	0.5±0.4	0.6±0.3
Berger-Parker's dominance index	0.6±0.3	0.5±0.3	0.6±0.2

in the examined specimens with full stomachs was low: one and two prey items were found in 61.1% and 33.3% of stomachs, respectively, whereas only one individual (5.6%) exhibited three different prey items in its stomach.

Overall, the diet of *D. profundorum* consisted of fishes, crustaceans and molluscs – with fishes as most abundant prey in terms of %F, %N, %W and I_{RI} (Table 9.3). This prey group was represented by bentho- and bathypelagic species, mostly Myctophidae such as *Myctophum punctatum* Rafinesque, 1810, but also Gadidae (*Micromesistius poutassou* (Risso, 1827)) and Lotidae (*Molva macrophthalma* (Rafinesque, 1810)) were identified. The crustaceans exhibited the second highest I_{RI} among the detected prey items and were chiefly represented by carideans of the genus *Pasiphaea*. In the diet molluscs were slightly less important than crustaceans and solely represented by cephalopods.

No significant correlation was found between the distributions of TL and number of higher-level taxonomic groups (i.e. fish prey, carideans, cephalopods and total number of prey items). The PERMANCOVA run with TL as covariate did not reveal any significant difference in the composition and relative abundance of the prey taxa neither for the factors years and host sex, nor for TL. A GLM constructed for abundance of prey taxa controlling for TL as covariate did not show a significant differentiation with respect to the sampling years or host sex.

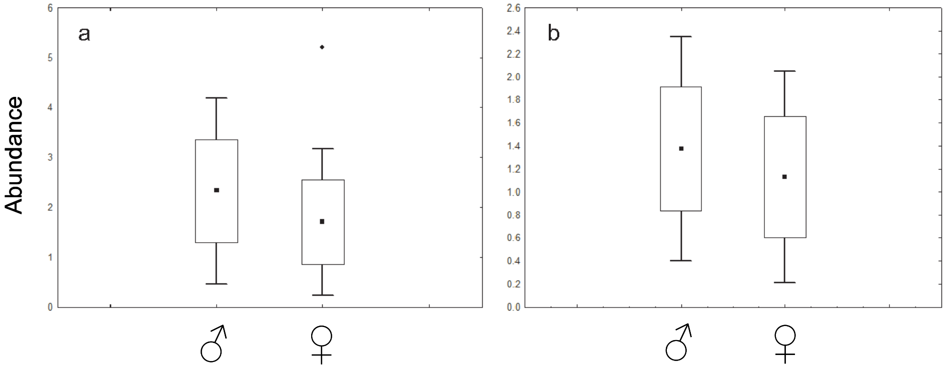

Fig. 9.3 - Box-Whisker plots showing significant differences between mean abundance of *Anisakis* sp. (a) and Lacistorhynchidae gen. sp. (b) in males and females of *Deania profundorum* form the Avilés Canyon (southern Bay of Biscay) (Box: mean+/-SD; Whisker: mean+/-95% C.I.)

Table 9.3 - Data for diet composition: per cent frequency of occurrence (%F), per cent by number (%N), per cent by mass (%W), index of relative importance of detected prey items (I_{RI}) in the stomachs of *Deania profundorum* from the Avilés Canyon (southern Bay of Biscay).

Prey items	**%F**	**%N**	**%W**	I_{RI}
CRUSTACEA	33.33	29.63	6.34	1198.89
Euphausiacea				
Meganyctiphanes norvegica	5.56	3.7	0.07	20.97
Caridea	27.78	22.22	5.8	778.28
Pasiphaea multidentata	5.56	3.7	2.25	33.09
Pasiphaea sivado	5.56	3.7	3.1	37.83
Pasiphaea sp.	11.11	7.41	0.13	83.72
Caridea unid.	11.11	7.41	0.31	85.75
Isopoda				
Natatolana borealis	5.56	3.7	0.47	23.19
MOLLUSCA				
Cephalopoda unid.	16.67	11.11	24.42	592.13
ACTINOPTERYGII	72.22	55.56	68.99	8995.05
Micromesistius poutassou	5.56	3.7	23.75	152.51
Molva macrophthalma	5.56	3.7	0.41	22.83
Lobianchia gemellarii	11.11	7.41	9.87	191.99
Myctophum punctatum	11.11	7.41	9.2	184.56
Stomiidae unid.	5.56	3.7	20.37	133.76
Myctophoidea unid.	11.11	7.41	2.76	113
Actinopterygii unid.	33.33	22.22	2.63	828.31
OTHERS				
Unidentified	5.56	3.7	0.26	22.04

DISCUSSION

To the best of our knowledge the present study provides the first comprehensive insight in the parasite infracommunities and diet of the deep-sea shark *Deania profundorum*. Moreover, 66.7% of the parasite species recovered in the present study were recorded for the first time in this shark species, as well as a possible new species of monopisthocotylean monogenean, identified as *Squalotrema* sp. (Monocotylidae, Merizocotylinae). The logistical constraints and the high costs of research expeditions often complicate the sample collection for studies on deep-water organisms and frequently few species and small sample sizes are available only (Cailliet et al. 2001, Klimpel et al. 2009). Considering the dearth of biological and ecological data and the necessity of proper management measures for deep-sea areas under anthropogenic impacts, even studies with lower sample sizes are crucial for enhancing the current knowledge on deep-water species.

The infracommunity parameters observed in *D. profundorum* were partly comparable with conspecific and congeneric specimens and also with species of other selachian genera. Specimens of *Galeus melastomus* Rafinesque, 1810 (Pentanchidae) from the Mediterranean Sea showed similar values (40.8) whereas *Centroscymnus coelolepis* Barbosa du Bocage & de Brito Capello, 1864 (Somniosidae) from the same area had a distinctly higher mean infracommunity abundance (920.0) compared to the one observed in the present study. In part this might show distinct feeding habits especially

Table 9.4 - Total parasite species richness and composition of parasite community in selachians from different geographical areas. The composition of parasite community is indicated as number of species per taxa in the following order: Cestoda/Monogenea/ Digenea/Nematoda/Copepoda/Isopoda. [N]-number of examined specimens; [S]-shallow water species; [D]-deepwater species.

No. parasite taxa	Community composition	Host species [N]	Habitat	Geographical area	Source
11	8/0/0/1/2/0	*Mustelus manazo* (Bleeker, 1855) [1038]	benthopelagic [S]	Off Japan / Taiwan, W Pacific	Yamaguchi et al. 2003
10	2/1/0/2/5/0	*Squalus acanthias* Linnaeus, 1758 [254]	benthopelagic [S]	Off Ireland (NE Atlantic)	Henderson et al. 2002
10	2/2/1/3/2/0	*Scyliorhinus canicula* (Linneaus, 1758) [101]	benthic [S]	Off Brit. Isles (NE Atlantic)	Moore 2001
9	4/1/0/3/0/1	*Deania hystricosa* (Garman, 1906) [8]	benthopelagic [D]	Great Meteor Bank (central NE Atlantic)	Palm & Schröder 2001
9	5/2/0/2/0/0	*Deania profundorum* (Smith & Radcliffe, 1912) [29]	benthopelagic [D]	Avilés Canyon (NE Atlantic)	present study
9	5/1/0/3/0/0	*Etmopterus spinax* (Linneaus, 1758) [30]	benthopelagic [D]	Galicia Bank (NE Atlantic)	Isbert et al. 2015
8	3/1/1/3/0/0	*Centroscyllium fabricii* (Reinhardt, 1825) [40]	benthopelagic [D]	Canada (NW Atlantic)	Chambers 2008
8	6/0/0/2/0/0	*Centroscymnus coelolepis* Barbosa du Bocage & de Brito Capello, 1864 [10]	benthopelagic [D]	Balearic Sea (W Mediterranean Sea)	Dallares 2016
7	5/0/1/1/0/0	*Etmopterus spinax* (Linneaus, 1758) [29]	benthopelagic [D]	Avilés Canyon (NE Atlantic)	Isbert et al. 2015
7	5/0/0/2/0/0	*Deania profundorum* (Smith & Radcliffe, 1912) [2]	benthopelagic [D]	Great Meteor Bank (central NE Atlantic)	Palm & Schröder 2001
7	3/2/0/2/0/0	*Etmopterus spinax* (Linneaus, 1758) [37]	benthopelagic [D]	Skagerrak (NE North Sea)	Klimpel et al. 2003
6	3/1/1/1/0/0	*Heptranchias perlo* (Bonnaterre, 1788) [10]	benthopelagic [D]	Great Meteor Bank (central NE Atlantic)	Palm & Schröder 2001
3	2/0/0/1/0/0	*Deania calcea* (Lowe, 1839) [2]	benthopelagic [D]	Great Meteor Bank (central NE Atlantic)	Palm & Schröder 2001
2	2/0/0/0/0/0	*Etmopterus spinax* (Linneaus, 1758) [11]	benthopelagic [D]	Balearic Sea (W Mediterranean Sea)	Dallares 2016

of *C. coelolepis*, which preys on squid and carrion while the prey of *G. melastomus* is similar to *D. profundorum* consisting of fish, squid and crustaceans (Dallarés 2016). The extremely higher mean infracommunity abundance of *C. coelolepis* could also be related to an increased ingestion of prey and probably of larger prey items, which are already highly infected (Iyaji et al. 2009 and references therein). In contrast, mean infracommunity abundance recorded in the present study was similar to those in *D. profundorum* and *D. hystricosa* (30.5 and 35.3) from the Great Meteor Bank (Schröder 1999, Palm & Schröder 2001). Interestingly, compared to the present study, all three *Deania* species studied from the Great

Meteor Bank had a larger body size, but only *D. calcea* had an higher mean infracommunity abundance (153.0). However, the sample number from the Great Meteor Bank were low (2–8 specimens) and a larger sample size probably would result in more pronounced differences. Additionally, other important factors such as geographical differences in the diversity of preys that act as intermediate hosts could also explain these observed differences (Cirtwill et al. 2016).

The used dominance and diversity infracommunity indices (i.e. Berger Parker and Brillouin) consider abundances of single parasite species and overall abundances. In this study three species (*Anisakis* sp. Type I *sensu* Berland, 1961, *Deanicola* sp., *Lacistorhynchidae* gen. sp.) exhibited similar MA in most of the fish examined. In contrast, infracommunities of several area-season combinations in *G. melastomus* were dominated by single species, while infracommunities of *C. coelolepis* were strongly dominated by one cestode species and most of the remaining parasite taxa showed low infection levels (Dallarés 2016). For both species the author recorded a higher dominance (do) and lower diversity (di) value compared to the present study (*G. melastomus* 0.9(do), 0.07(di) and *C. coelolepis* 0.9(do), 0.3(di) *vs* *D. profundorum* 0.6(do), 0.6(di)). The lower dominance and higher diversity values in *D. profundorum* may be explained by infracommunities dominated by three species with similar abundances.

The here observed mean infracommunity richness (Table 9.2) is slightly higher than in other benthic and benthopelagic selachians: such as *C. coelolepis* (2.5; Dallarés 2016), *G. melastomus* (0.6; Dallarés 2016), *Etmopterus spinax* (0.7–2.5; Isbert et al. 2015, Dallarés 2016), and even higher compared to sharks commonly found in shallower waters (<200m) such as *Scyliorhinus canicula* and *Squalus acanthias* (0.6–1.7 and 1.6, respectively; Isbert et al. 2015). These differences in infracommunity richness in *D. profundorum* could partly reflect the diverse predatory feeding habits assigned to this species and its relatives (Ebert et al. 1992, Preciado et al. 2009). High infracommunity richness (3.0 to 5.0) described for *Deania* spp. from the offshore seamount Great Meteor Bank might support this assumption (Schröder 1999; values estimated from published data). These fairly high values were even obtained from low sample sizes (2–8 specimens) but overall mean body size was higher (90 cm) than in the present study, probably indicating a potential enrichment of the parasite community with host size. Further, underwater features such as seamounts and submarine canyons are considered as hotspots for aggregations of higher-level consumers due to enhanced biological production caused by favorable hydrographic conditions (Morato et al. 2008, Clark et al. 2010, Vetter et al. 2010). This could affect the presence of intermediate hosts resulting in higher parasite richness as observed in *D. profundorum* from the Avilés Canyon and in *Deania* spp. from the Great Meteor Bank. Similarly, the increased infracommunity richness observed in *G. melastomus* was explained by the potential influence of a submarine canyon in the western Mediterranean (Dallarés 2016). Though, no final conclusion can be drawn as it lacks knowledge on the parasite community of *D. profundorum* in localities which are not under the influence of such underwater features.

The total parasite richness in *D. profundorum* from the Avilés Canyon is comparable with most other benthic and benthopelagic shark species from deeper and coastal waters (Table 9.4). Further, independently of the geographic area and of the sample size, most species revealed a parasite community dominated by species of cestodes. This agrees with this study and supports the assumption made by Caira & Healy (2004) that tapeworms are the most diverse metazoan parasites found in elasmobranchs. According to these studies on benthic and benthopelagic sharks, nematodes are usually found in nearly all species and localities, whereas the presence of ectoparasites varies between shallow and deepwater sharks (Table 9.4).

Commonly monogeneans are considered as particularly scarce in deeper waters, related to the mostly lower density of their host species, while copepods are supposed to show higher diversities and to occur in greater depths (Campbell 1980, de Buron & Morand 2004). Caira et al. (2012) indicated that in elasmobranchs copepods and monogeneans exhibit the highest diversity in ectoparasites and latter show partly high specificity for gills and skin (Caira et al. 2012). The few studies on shallow water and deep-sea selachians (Table 9.4) show a different picture without any copepod recorded in a deep-sea species, while monogeneans were well presented in these species (five out of seven). The low representation of ectoparasites observed might be also related by the procedure of sampling which could provoke the dislodgement of these parasites which are fixed between scales, skin or gills of its host (e.g. Moore 2001, Quattrini & Demopoulos 2016).

In the present study one specimen of the monogenean *Squalonchocotyle spinaci* Goto, 1894 was found. This species belongs to the Hexabothriidae, a monopisthocotylean family with species restricted to chondrichthyan hosts (Caira & Healy 2004, Martorelli et al. 2008, Justine 2011) and being described previously only in *Etmopterus spinax* from different areas including the Northeast Atlantic (Di Cave et al. 2003, Klimpel et al. 2003, Isbert et al. 2015). Apart from some exceptions, monogeneans are considered as highly host specific (Hayward 2005), consequently, and in view of the very low infection observed in *D. profundorum*, it can be regarded as accidental. This is not supposed for *Squalotrema* sp. (Monocotylidae, Merizocotylinae), with almost 14% prevalence. This species is morphologically different to the only species of this genus described to date, *Squalotrema llewellyni* Kearn & Green, 1983, based on remarkable differences in the haptoral sclerites. The nasal cavities of sharks and rays are regularly inhabited by Monocotylidea (Klimpel et al. 2003, Justine 2009, Chisholm & Whittington 2012) and even are suggested as primary site for the attachment of monocotylid species (Caira & Healy 2004 and references therein). Several studies have proved that monogeneans could accumulate during host life (Lo et al. 1998, Morand et al. 2002, Pérez-del-Olmo et al. 2008). The lack of correlation of *Squalotrema* sp. with host size could be related to the relatively narrow host size range sampled or even to the low sample size. As monoxenous parasite, this parasite might be useful as biological indicator considering studies on connectivity or migration between populations however, larger samples sizes from different localities would be needed to assess these aspects.

The herein found prey and its composition did not reveal any significant difference between the factors years or sex, and no effect by TL could be detected. The prey composition observed agrees with other studies on *Deania* spp. (Yano 1991, Ebert et al. 1992, Saldanha et al. 1995, Cortés 1999, Preciado et al. 2009); this and other relative species are considered as opportunistic feeders (Mauchline & Gordon 1986), described as active benthopelagic predators with high trophic level and preying above the substratum and in the water column (Musick et al. 2004, Preciado et al. 2009). Further, the detection of a single isopode *Natatolona borealis* could hint to opportunistic scavenging habits by *D. profundorum*, as supposed for most elasmobranchs (Heithaus 2004) also from the deep-sea (e.g. Neiva et al. 2006).While formerly this isopod was considered to be parasitic on teleosts and sharks, nowadays this species is considered as benthic micropredator and scavenger (Bruce 1986 & references therein). This species was observed to scavenge on netted, moribund fishes and is highly attracted to baited fishing traps (Johansen 2000) and the present finding could indicate an accidental ingestion by *D. profundorum* when preying on dead or moribund fish.

In the specimens analysed we detected a relatively high degree of empty stomachs which partly agrees with other studies on deep-sea elasmobranchs (Ebert et al. 1992, Wetherbee & Cortés 2004, Preciado et al. 2009). It is suggested that teleosts and elasmobranchs especially from deeper water frequently regurgitate prey items during the haul process to the surface (Bowman 1986). Nevertheless, regurgitation is not always the reason for empty stomachs in sharks and could not be detected in herein analysed specimens. Similarly, very low numbers of specimens revealed signs of regurgitation in other studies on teleosts and deep-sea sharks (Preciado et al. 2009, Preciado et al. 2017). These empty stomachs could hint to intermittent feeding habits, observed in other elasmobranchs where feeding in short bouts alternates with long periods of low or no feeding activity (Yano 1991, Wetherbee & Cortés 2004, Preciado et al. 2009). Considering these described circumstances, heteroxenous parasites can be fairly useful for assessing the host role in the local food-web, as they can be related to past feeding events (Lafferty et al. 2008) and they are less susceptible to be lost during the sampling procedure. For example, larval stages of the herein detected tetraphyllidean and trypanorhynch taxa clearly indicate that *D. profundorum* is not a top-predator but rather a prey for larger taxa in the local food-web. These cestodes usually mature in elasmobranchs (e.g. Palm 1997, Klimpel et al. 2008a), but in the present study more than half of the cestode species found were larval stage confirming previous suggestions that elasmobranchs can also act as intermediate host for cestodes (e.g. Palm & Schröder 2001, Klimpel et al. 2003).

The detected larvae of Tetraphyllidea fam. gen. sp. cannot be identified to species level simply by means of morphological traits, consequently, they have been assigned to a compendium of species, as *Scolex pleuronectis* or *S. polymorphus* (Jensen & Bullard 2010). Potential second intermediate hosts of these larvae are supposed to be euphausiids, teleosts and cephalopods (Caira & Reyda 2005, Jensen & Bullard 2010 and references therein), which in part were also an important part of the here detected prey items. Elasmobranchs are suggested to be the definitive hosts of this cestode group (Caira & Healy 2004), and different larger demersal or benthopelagic sharks probably preying on *D. profundorum* were recorded on the continental shelf, slope and surrounding deeper waters close to the Avilés Canyon system (Serrano et al. 2011).

Trypanorhynch cestodes showed the highest taxa number in *D. profundorum* and were represented by adult and larval stages. For the families Aporhynchidae, Sphyriocephalidae and Gilquiniidae an oceanic life cycle is supposed, where copepods are the first, and euphausiids or large decapods, schooling and other kinds of fish are second intermediate hosts, while fishes and cephalopods may also act as paratenic hosts (Palm 2004 and references therein). All these potential second intermediate hosts were observed as prey items in *D. profundorum* even though with different degree of importance (Table 9.3). Along with larval and adult stages of trypanorhynchs we also found immature specimens of a cestode identified as *Aporhynchus* cf. *menezesi* (Trypanorhyncha: Aporhynchidae) according to body size and scolex morphology (Noever et al. 2010). Previous publications described this genus only from Etmopteridae sampled in different geographical areas, therefore, considering the definitive hosts described to date and the fact that here found specimens were immature the infection of *D. profundorum* is supposed to be accidental.

The post-larvae of *Sphyriocephalus* sp. (Trypanorhyncha: Sphyriocephalidae) were found in the stomach of *D. profundorum* adding a new record to previous findings where plerocerci were found in different epi- and mesopelagic, and deep-water teleosts, as well as benthic and benthopelagic selachii (e.g. Lester et al. 1988, García et al. 2011, Dallarés et al. 2017). *Sphyriocephalus viridis* (Wagener, 1854) Pintner, 1913 is described from the Northeast Atlantic and the present finding could indicate the occurrence of potential definitive hosts in the study area, e.g. *Dalatias licha* (Dalatiidae) (Dallarés et al. 2017 and references therein). This species has been recorded in the study area (Serrano et al. 2011), and *D. profundorum* can be part of the diet of *D. licha* (Matallanas 1982, Dunn et al. 2010), acting as intermediate or paratenic host and thus facilitating the completion of the life cycle of this parasite species.

Adults of the trypanorhynch cestode *Deanicola* Beveridge, 1990 (Trypanorhyncha: Gilquiniidae) were detected in the digestive tract of the specimens studied. Usually species of this family are found as plerocerci and adults in different species of selachians: Centrophoridae, Etmopteridae, Squalidae and Scyliorhinidae (Beveridge 1990, Beveridge & Justine 2006, Klimpel et al. 2009, Costa et al. 2014 and references therein) and two species, *Deanicola minor* and *D. protentus*, were reported in previous studies on *Deania* spp. including *D. profundorum* (Beveridge 1990, Schröder 1999, Palm & Schröder 2001). The presence of gilquiniids recorded in different centrophorid species and the comparable infection levels (prevalence 38–100%) observed in previous studies from the Northeast Atlantic (Schröder 1999, Palm & Schröder 2001) let us suggest that *D. profundorum* is a common definitive host for *Deanicola* sp. in the Avilés Canyon system. The abundance of this species is related with host size which probably indicates an accumulation of this parasite during lifetime of the host. This may contradict the supposedly minor importance of euphausiids in the diet, as it is the obligate intermediate host for this parasite (Palm 2004 and references therein). However, the lack of euphausiids in the analysed stomachs does not imply that euphausiaceans are not part of the diet. Usually it is supposed that several sharks exhibit an opportunistic feeding habit exploiting available local prey, and the lack of euphausiids in the analysed stomachs may hint to low abundance in the environment before fishes were caught (Dunn et al. 2013). Additionally, the single study on the diet of *D. profundorum* revealed fishes and cephalopods as main prey items, which is similar to studies on relative species, *D. calcea* and *D. crepidalbus* (Yano 1991, Preciado et al. 2009, Dunn et al. 2013). However, most specimens in these studies were larger than in the present study, whereas Saldanha et al. (1995) detected crustaceans (decapods) in the diet of smaller *D. calcea* specimens probably indicating a higher importance of crustaceans in smaller exemplars. Generally, as studies on deep-sea sharks are hampered by often low samples sizes and empty stomachs (Dunn et al. 2010), it is supposed that diets of deep-sea sharks might be more diverse than suggested by analysing available small sample sizes (Dunn et al. 2013). For example, Dunn et al. (2013) indicated a potential bias relating the absence of crustaceans to a small sample size. Under these conditions parasites can be a useful tool reflecting previous feeding habits and additionally may even indicate feeding habits/prey items not even described yet. The here detected infection rate by *Deanicola* sp. may also be explained by intermittent feeding habits on larger prey species such as teleosts which can be intermediate or paratenic hosts bridging the gap to the definitive host, *D. profundorum*. Several marine fish species including myctophids are listed to harbour larval gilquiniids, which are potential preys of *D. profundorum* in the Avilés Canyon (Gibson et al. 2005).

Lacistorhynchidae gen. sp. larvae (Trypanorhyncha) were detected in *D. profundorum* but it still lacks a more detailed identification. However, the infection sites of tissue are consistent with findings of other lacistorhynchid larvae such as *Grillotia meteori* Palm & Schröder, 2001 and *G. acanthoscolex* Rees, 1944 in *D. profundorum* and *D. hystricosa* from the central Northeast Atlantic (Palm & Schröder 2001). Along with the intermediate hosts described above for the other trypanorhynchs, the life cycles of lacistorhynchids involve an obligate predatory fish species as third intermediate host (Palm 2004). *Deania profundorum* could be considered necessary for completion of the larval development and the main site of infection (78% of the larval individuals removed were encysted in musculature) of these larvae confirms previous assumptions: forming a large blastocyst deep within the muscle tissue of the host structurally is rather enabled by larger hosts than by small fish species (Palm 2004). Almost all the lacistorhynchid larvae were detected in the musculature of the caudal fin which confirms similar observations made for trypanorhynch larvae in *Etmopterus spinax* from different geographical areas (pers. observation) and *Galeus melastomus* from the western Mediterranean (Dallarés 2016). Considering the strong association between body size of *D. profundorum* and abundance of lacistorhynchid larvae observed here it may indicate an accumulation of larvae during lifetime. This accumulation of plerocerci in a preferred site such as the tail region could have certain impacts on swimming speed and performance as suggested in previous studies (Palm et al. 1994). Together with a supposed longevity of some cestode species (Hassan et al. 2002) this could facilitate the predation of heavily infested fish, enhancing the chance of transmission to the potential definitive hosts

Three larvae 3 of *Hysterothylacium* sp. Ward & Magath, 1917 (Ascaridoidea: Raphidascarididae) were removed encysted from the serosa of the digestive tract. The species of this genus are described as highly unspecific in the larval stage and are reported in a wide range of intermediate and paratenic hosts, invertebrates and fishes (Anderson 2000), whereas adult specimens are parasites of the digestive tract mostly of marine fish families from pelagic and benthic deep-sea habitats (Navone et al. 1998, Klimpel et al. 2009, Moravec et al. 2016). The low prevalence observed in this work and the lack of information on potential teleost predators of *D. profundorum* indicates that this shark species is not a common host and the infection may be a ‘dead-end’ for the parasite.

In this study identified larval nematodes were exclusively represented by ascaroids and nearly all individuals (99.6%) belonged to the genus *Anisakis*. The larvae 3 of *Anisakis* Type I (*sensu* Berland, 1961) (Ascaridoidea: Anisakidae) were found encysted in mesenteries of different organs and tissues. This morphotype has been recorded and its identification confirmed by molecular analysis in hake *Merluccius merluccius* (L. 1758), horse mackerel *Trachurus trachurus* (L. 1758) (Mattiucci et al. 2004, 2008) and in sharks from the Northeast Atlantic Ocean (Moore 2001, Palm & Schröder 2001, Henderson et al. 2002, Klimpel et al. 2003). Similar to a part of the cestode families above, life cycles of *Anisakis* spp. are considered pelagic (Klimpel et al. 2004, Klimpel & Palm 2011 and references therein), but larval stages of these nematodes are less specific and can be found in a huge variety of intermediate and paratenic hosts in marine invertebrates (e.g. copepods, euphausiaceans, cephalopods) (Abollo et al. 2001, Gregori et al. 2015) and predatory vertebrates such as benthic/benthopelagic teleosts (e.g. Busch et al. 2008, Klimpel et al. 2008b) and sharks, even from the deep-sea (e.g. Palm & Schröder 2001, Costa et al. 2014). Adult stages of *Anisakis* spp. parasitize the digestive tract of pinnipeds and cetaceans (Anderson 2000, Kuhn et al. 2011). The overall infection rate by *Anisakis* sp. in a certain area is influenced by the presence of its definitive hosts (Klimpel et al. 2010). The Bay of Biscay, including the Cantabrian Sea, is an area with high cetacean diversity in the Northeast Atlantic (Ruano Álvarez et al. 2007, Laborde Basto d’Andrade 2008) with frequent strandings and sightings of toothed and baleen whales in northern Spain (López et al. 2004, de la Maza et al. 2007). The high presence of definitive hosts could promote a regular trophic transfer of this parasite, increasing the prevalence and abundance of this nematode in all host types within the food-web, including *D. profundorum*. This suggestion is supported by high prevalence and abundances of *Anisakis* sp. observed in *E. spinax* specimens from the same area (Isbert et al. 2015). Consequently, the here observed very strong association between *Anisakis* sp. abundance and fish size may reflect an accumulation of this parasite with host age, which could further be fostered by an increased ingestion of larger already infected hosts from the water column (e.g. myctophids, squid) during short bouts of feeding. Although, the role of *D. profundorum* for *Anisakis* sp. is unclear, the fact that the parasites were encysted and the high infection rates observed may indicate a rather suitable paratenic host than being an accidental infection. As far as it is known, this benthopelagic shark has not been recorded as a common prey of cetaceans but it may bridge a gap to the definitive hosts, remaining a host path with highly uncertain outcome for the parasite.

The fish size imposed a significant effect on community structure which is mainly due to the most abundant taxa, larval stages of *Anisakis* sp. Type I (*sensu* Berland, 1961), and Lacistorhynchidae gen. sp., and adults of *Deanicola* sp. These may accumulate during host growth influencing the community parameters such as total parasite abundance, richness and diversity. Other studies already showed that parasite abundance and richness increases with host size (e.g. Timi & Poulin 2003, Bagge et al. 2004, Pérez-del-Olmo et al. 2008), as parasites are acquired and accumulated over the life span, and larger individuals can have a more numerous and diverse diet (Barber & Poulin 2002).

Neither the four infracommunity parameters nor the composition and structure of the community differed between sexes. Differences observed between both sexes are associated with the abundance of *Anisakis* sp. Type I (*sensu* Berland, 1961) and Lacistorhynchidae gen. sp. larvae, where both showed higher mean abundances in males even differences were more pronounced in the previous species. Both taxa infect their hosts *via* the food-web and under consideration that prey of fishes is partly influenced by host size the herein slightly larger body size of males might explain the distinct parasite burden observed for both parasite taxa between sexes. This infection pattern might change during life time, as usually females of this genus grow larger than males (Yano 1991, Sousa et al. 2009), and this can result in higher infections by females. In the present study the prey composition and structure did not differ between sexes, and none of the prey items could be related to the body size, neither any ontogenic shift in the diet was observable, which in part may be due to the low sample size. We suggest a higher sample number with a wider range of host size could result in differences between sexes.

In conclusion, *D. profundorum* from the Avilés Canyon system is considered to occupy an intermediate position in the local food-web, as it exhibits adult as well as larval parasite stages. Its diet consists mainly of bentho-, bathypelagic fishes, crustaceans and cephalopods without detectable differences between sexes and size. The infracommunities are comparable to other sharks, while the composition and structure of parasite communities did not reveal differences between sexes. However, the parasite abundance, richness and diversity of the infracommunity could be related to host size and abundances of single taxa increased with fish length. Larval Lacistorhynchidae gen. sp. and *Anisakis* sp. Type I (*sensu* Berland, 1961) revealed a higher parasite burden in larger males indicating to potentially distinct feeding habits between sexes. This could not be discerned by the diet analysis and highlights previous suggestions of the importance using parasites as biological indicators to identify potential prey items of past feeding events and for the assessment of the host role in marine communities. This is recommendable especially in studies on rare species difficult to obtain and often with low samples sizes. Further studies of this kind from the continental shelf and areas without the influence of underwater features would be helpful to support our results.

ACKNOWLEDGEMENTS

The authors are very grateful to all participants and crew onboard the research vessels ‘RV Thalassa’ (IFREMER-IEO) and ‘RV Vizconde de Eza’ (SGM) for their help in collecting the samples. We are also indebted to Antoni Lombarte (CSIC) for his help with otolith identification. This work has been supported by the EU-project “LIFE+INDEMARES” (07/NAT/E/000732) and the project "DEEPCON" (CGL2010-16690) funded by the Spanish Ministry of Science and Innovation (MICINN).

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Chapter 10 Conclusions

1- The analysis of available records for the parasite species of three deep-sea fish families (Notacanthidae, Centrophoridae and Etmopteridae) revealed that for almost 67% of them no parasite record exists. The amount of records in the only teleost family is larger than in the elasmobranchs: 64% *vs* 35 and 25%, respectively.

2- The few available data indicate a higher diversity of cestodes in both elasmobranch families, while digeneans were the most diverse group in the teleost family. This could be associated to the differences in the feeding habits: notacanthids are mostly benthic (i.e. close to intermediate hosts) while elasmobranchs are more benthopelagic.

3- Parasite taxa in notacanthids were mostly specialists, probably reflecting a more restricted range of prey items. In contrast, centrophorids, comprising the largest fishes of all three families, showed a lower number of specialist parasites, which may hint to a more diverse diet with opportunistic feeding habits. The balanced ratio between specialist and generalists in etmopterids could be related to a higher number of specialist ectoparasites and an opportunistic feeding pattern.

4- Heteroxenous were more frequent than monoxenous parasites in species of all families; however, close to 40% were monoxenous in etmopterids. Sharks of both families commonly occupy middle level in food webs, what explains the high number of larval parasites. In etmopterids the high number of monoxenous species increases the relative number of adult parasites, which become proportionally more numerous than larvae. Higher proportions of adult parasites in nothacanthids could be explained by the supposedly low predation by fish that act as potential definitive hosts.

5- The herein described new species, *Tinrovia mamaevi* Isbert, Carrassón, Pérez-del-Olmo & Montero 2017 is the first recorded monogenean in the deep-sea fish *Notacanthus bonaparte*. An emended generic diagnosis of *Tinrovia* is suggested. Lateral separated frills of the haptor are described as ‘winged’ and not as ‘butterfly-like’, as they can be narrow or wide. Eggs of *Tinrovia* spp. can bear short and/or long filaments, and not only short ones, as the generic description indicated.

6- The application of confocal microscopy has been helpful to interpret the 3D-structure of the genital atrium and the copulatory organ as well as for the mouth vestibule of *Tinrovia mamaevi*. In view of this methodology a note of caution must be added for further taxonomical descriptions as traits can be interpreted differently depending on the condition of each specimen.

7- The herein described new nematode species *Dichelyne* (*Cucullanellus*) *romani* Isbert, Montero, Carrassón & González-Solis 2015 is the first cucullanid described for notacanthids. This nematode was detected in *Notacanthus bonaparte* and *N. chemnitzii* from the northeastern Atlantic Ocean and in *N. bonaparte* from the western Mediterranean Sea. It is the fourth species of *Dichelyne* (*Cucullanellus*) in the Mediterranean Sea and the fourth species of the genus *Dichelyne* recorded from deep or cold waters.

8- This study confirms previous publications which also observed a high intraspecific variability in morphological traits of species of this genus. The broad intraspecific variability of some morphological traits underpins the need of clarifying the status of some species of the subgenus *Dichelyne* (*Cucullanellus*) and further re-examination of type-specimens is recommended.

9- The present study on the parasite fauna of *Notacanthus bonaparte* is the first comprehensive analysis and description of its parasite communities, including data from different seasons and depth strata. Of the five parasite species detected two were new to science and three represent new host records.

10- The parasite community of *Notacanthus bonaparte* is depauperate with only three species considered common. This may be supported by previous observations of a limited prey range. The community is richer in the upper depth range (600–1,000 m).

11- The most abundant parasite in *Notacanthus bonaparte* (cucullanid larvae), which is more abundant in the lower depth ranges, seems to be accumulated during host growth. The depth-range pattern observed for this species is partly explained by the bigger-deeper trend, where larger fish are found in deeper waters. Cucullanid larvae are suggested to be directly ingested by *N. bonaparte* when feeding on its main type of prey, sessile or slow moving benthic organisms. The main infection periods might be linked to the highest feeding activities of *N. bonaparte* (spring/summer), when highest turbidity values are measured close to the seabed. Turbidity could be related to cucullanid larvae prevalence, as free-living larvae are supposed to accumulate in the sediment.

12- The presence of *Tinrovia mamaevi* in *Notacanthus bonaparte* from the upper depth range is mainly explained by a higher host density, while a weak relationship between its prevalence and abiotic factors (temperature, salinity) has been detected.

13- The first comprehensive description of the parasite communities and diet of *Etmopterus spinax* comprising juvenile and adult specimens has been performed. Parasite component communities of *E. spinax* from the northeastern Atlantic were rich, while the infracommunities were depauperate with low diversity. This study provides the first comparative parasite infracommunity data for a deep-sea shark species and reports *E. spinax* as a new host record for three of the eleven parasite species detected.

14- Locality and host size explained the detected differences in the composition and structure of the parasite communities of *Etmopterus spinax* between a seamount (Galicia Bank) and a canyon (Avilés Canyon). The host size association with the abundance of *Squalonchocotyle spinaci* may be linked to aggregation behaviour of younger *E. spinax* likely driven by predation avoidance; while its presence in Galicia Bank could be associated to potential effects of the abiotic conditions and environmental variables. The high abundance of *Anisakis* sp. (Type I *sensu* Berland, 1961) in the Avilés Canyon may reflect the higher abundances of definitive hosts but also a higher fishing and discard rates at this area.

15- Diet of *Etmopterus spinax* showed clear geographical differences, with carideans and fin fish in the Galicia Bank, and carideans and euphausiids in the Avilés Canyon, as main prey items. Shark body size from specimens of the Aviles Canyon was associated with euphausiids only. The detection of concordant differences in the abundances of euphausiids and *Anisakis* sp. in the Aviles Canyon linked both most recent and long-term trophic niches.

16-The present study revealed a differential effect of the two deep-sea ecosystems on both long-term and most recent trophic niche of *Etmopterus spinax*. Furthermore, it underlines the usefulness of multivariate statistical approach for assessing geographical variations in shark populations based on parasite and prey abundance data.

17-This study provides the first comprehensive insight in the parasite infracommunities and diet assemblages of the deep-sea shark *Deania profundorum* in the Northeast Atlantic. The presence of larval and adult parasites (especially cestodes) and the diet consisting mainly of bentho- and bathypelagic fish, crustaceans and squid indicate that his shark species seems to occupy an intermediate position in the local food-web of the Avilés Canyon.

18-Host size of *Deania profundorum* has a clear impact on the infracommunity parameters and the abundance of *Deanicola* sp., Lacistorhynchidae gen. sp. and *Anisakis* sp. (Type I *sensu* Berland, 1961); infection levels for both latter species also differed between both sexes. This could be linked to slightly larger males that may have differing feeding habits, preying on larger or more items and getting more infected. The diet analysis did not reveal these sex and host size related differences highlighting the usefulness of parasites as biological indicators to assess feeding habits.

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"I don't know why I don't care about the bottom of the ocean, but I don't."

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