DEPARTAMENT DE ZOOLOGIA

BIODIVERSITY AND STRUCTURE OF PARASITE COMMUNITIES IN *BOOPS BOOPS* (TELEOSTEI: SPARIDAE) FROM THE WESTERN MEDITERRANEAN AND OFF THE NORTH EAST ATLANTIC COASTS OF SPAIN

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INSTITUT CAVANILLES DE BIODIVERSITAT I BIOLOGIA EVOLUTIVA

Biodiversity and structure of parasite communities in *Boops boops* (Teleostei: Sparidae) from the Western Mediterranean and off the North East Atlantic coasts of Spain

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TESIS DOCTORAL

Valencia, Febrero 2008

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TESIS DOCTORAL

POR

ANA PÉREZ-DEL-OLMO

DIRECTORES

JUAN ANTONIO RAGA ESTEVE

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VALENCIA, FEBRERO DE 2008

JUAN ANTONIO RAGA ESTEVE, Profesor Titular del Departamento de Zoología de la Facultad de Ciencias Biológicas de la Universitat de Vàlencia,

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Certifican: que Ana Pérez-del-Olmo ha realizado bajo nuestra dirección, y con el mayor aprovechamiento, el trabajo de investigación recogido en esta memoria, y que lleva por título: 'Biodiversity and structure of parasite communities in *Boops boops* (Teleostei: Sparidae) from the Western Mediterranean and off the North East Atlantic coasts of Spain', para optar al grado de Doctora en Ciencias Biológicas.

Y para que así conste, en cumplimiento de la legislación vigente, expedimos el presente certificado en Paterna, a 26 de Febrero de 2008

Juan Antonio Raga Esteve

Mª Mercedes Fernández Martínez

Aneta Kostadinova

A mis aitas,
Felipe y Mª Carmen

Foto portada: José Rafael García-March

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SUMMARY

Parasites provide excellent opportunities for comparative analyses of patterns of community organisation at several hierarchical levels depending of the physical scale selected for the study. Although two lines of research, taxonomic initiated in the 18th Century and continuing, and parasite inventory studies carried out especially on Mediterranean fish, have provided an overall sound taxonomic and faunistic basis for the development of ecological studies on marine fish parasites, these are virtually lacking in the Mediterranean and NE Atlantic.

The present study carried out a detailed assessment of the metazoan parasite fauna in *Boops boops* (L.) (Teleostei: Sparidae) along the Spanish coasts off the Western Mediterranean and North East Atlantic, which provided a large taxonomically consistent dataset comprising three levels of parasite community organisation (i.e. infracommunities, component communities and local faunas), and allowed questions regarding the structure of parasite communities in the model host-parasite system to be addressed.

The model host was selected based on its non-migratory behaviour, wide distribution and abundant populations in both the Mediterranean and North East Atlantic. The intermediate trophic position and omnivorous diet of *Boops boops* would ensure the development of rich and diverse parasite communities and its site fidelity indicates that parasite communities would reflect the structure of local food webs and allow meaningful comparisons at a larger geographical scale. *B. boops* which hosts a relatively large number of metazoan parasites with different transmission strategies and its parasite fauna is relatively well studied in the Mediterranean, where large samples of fish have been investigated. Finally, the availability of fish samples collected before the *Prestige* oil-spill in November 2002 provided the unique opportunity to assess the changes in parasite communities in this host after the disturbance event.

The following objectives were targeted in the study:

1. An exhaustive revision of the metazoan parasite fauna of *B. boops* from the Western Mediterranean and off the North East Atlantic coasts of Spain. Identification of the parasites on the basis of a detailed morphological and taxonomical study. Compilation of a complete checklist of parasites of *B. boops* throughout its distributional range.

2. An evaluation of the effect of host size on the development of parasite communities in *B. boops*. Examination of the patterns of composition and structure of parasite communities along a gradient of fish sizes and identification of the underlying processes.
3. An assessment of the geographical and temporal variations in parasite community composition and structure. Test of the hypothesis of the decay of similarity between communities with distance using original, taxonomically consistent data at two nested spatial scales (parasite faunas and component communities). Test for synchrony in seasonal patterns of community similarity-distance relationship. Evaluation of the importance of species abundance-distribution relationships and identification of the parasite species that contribute substantially to the observed patterns.
4. A comparative study, in a 'before-after' design, on the structure and composition of metazoan parasite communities in *B. boops* from selected impacted localities off the North East Atlantic coast of Spain after the *Prestige* oil-spill in 2002. Evaluation of the importance of the individual parasite species and larger functional groupings in the detection of directional trends in community composition and structure that could be related to the oil-spill.

A total of 22 samples comprising 805 fish were collected in 2001-2007 from four North East Atlantic and three Mediterranean localities. All metazoan parasites were identified and counted. The diversity of the parasite fauna of *B. boops* appeared to be much higher than previously thought, as evidenced by the description of one species new to science, *Wardula bartolii* Pérez-del-Olmo, Gibson, Fernández, Sanisidro, Raga & Kostadinova, 2006, and the recovery of 53 parasite species along the NE Atlantic and the Mediterranean coasts of Spain, of which 25 represent new host records. The complete checklist of parasites of *B. boops* throughout its distributional range, developed during the course of the study, comprises information for 78 species and 365 host-parasite-area records. A group of nine species with a wide geographical distribution, consistently present in both Mediterranean and North East Atlantic fish, are identified as the core of the parasite fauna of *B. boops*.

The regional parasite fauna of *B. boops* was richest in the North East Atlantic. There was a clear separation of the North East Atlantic and Mediterranean local faunas, with that of the 'transition' location (Barbate-Atlantic) occupying an intermediate position. Local

parasite faunas were diverse, comprising *c.* 30-50% of the parasites of *B. boops* throughout its distributional range, except in Valencia and Barcelona where faunal richness was notably lower. A characteristic feature of the parasite communities in *B. boops* was the high representation of parasites with complex life-cycles that are transmitted to fish *via* food ingestion and the dominance of trematodes. The phylogenetic influence on the composition and structure of parasite communities in *B. boops* is rather weak, since generalist parasites contains a considerable part (36 species *vs* 8 strict specialists and sparid generalists) of the parasite communities both with respect to richness and abundance.

The species identified as the core of *B. boops* parasite fauna were already present in juvenile 1-year-old fish in a population off Santa Pola (Mediterranean; n=130) in spring 2005, whereas all species added to communities in larger/older fish were either rare or accidental. The observed sequence of species appearance and persistence in the developing parasite communities in *B. boops* supported the hypothesis that species with wide geographical distributions appear in the fish population earlier than rare and stochastic species. Parasite communities in *B. boops* were rich and abundant from an early age. Although community complexity and abundance tended to increase with fish size, perhaps related to an increase in feeding rates, the older fish cohorts showed no differences in parasite community parameters. Six species of the core parasite fauna of *B. boops* were identified as key parasites in developing communities in this host since they persisted as common in all size cohorts and represented the majority of the individuals.

Although no supportive evidence was found for interspecific competition, the repeatable community structure across size/age classes of *B. boops* translated into a nested subset pattern at the lowest infracommunity scale within the individual cohorts. This non-random compositional pattern could not be completely attributed to either accumulation over time or segregation of the parasite species among different size-class hosts. The small mouth size of *B. boops* coupled with suction feeding results in passive ingestion of prey restricted to small invertebrates suspended in the water column. These serve as intermediate/paratenic hosts of the key parasites as well as of an additional group of parasites. This addition to a baseline community of key parasite species results in a nested structure strongly related to the differential species abundance, thus suggesting that passive sampling could be the mechanism leading to the non-random parasite community structure observed in the developing communities in *B. boops*.

The first attempt to test the similarity-distance decay hypothesis using original taxonomically consistent data at two nested spatial scales was performed with the 22

component community samples (n= 709). The data revealed that the geographical distance and the region of origin affect the species composition and structure of parasite faunas and component communities in *B. boops*. The distance between localities/regions contributed significantly to the decay of the similarity estimated from parasite abundance at the infracommunity level. The structured spatial patterns were consistent in time but not across seasons, since only component communities sampled in spring exhibited a highly structured spatial pattern. The spatial synchrony observed was solely due to the assemblage of the 'core' species, thus supporting the hypothesis that widespread species would be strongly associated with patterns of variation in environmental conditions. The interspecific abundance-distribution patterns were recognized as the most important for the distance-decay relationship of similarity in the studied host-parasite system due to the strong correlations observed at all scales of analysis.

The comparative analyses revealed dramatic changes in community richness, abundance and structure of parasite communities and a notable alteration of both individual and functional group parasite abundance patterns in *B. boops* (n= 400) studied after the *Prestige* oil-spill. A directional trend in parasite community succession was detected. Parasite communities studied in the pilot study were largely dissimilar to those examined before the oil-spill both in terms of composition and structure. These dissimilarities decreased with time and the direction of compositional changes appeared to be towards the pre-spill situations. However, the differences were still large thus indicating that shifting pollution baselines probably affect the recovery of benthic (and parasite) communities from the *Prestige* oil-spill.

Focusing on higher taxonomic and/or functional levels provided a higher resolution in detecting directional trends in parasite community structure with respect to the two separate classes of confounded environmental variables, *i.e.* toxicants and organic enrichment. The elevated levels of monoxenous infections in the pilot study indicate that changes in immune parameters of fish due to chronic exposure to PAHs post-spill may be involved. The notable increase of heteroxenous, and the remarkable alteration in the hemiuroid abundance post-spill in particular, may have reflected an enhancement of the populations of the mollusc and copepod hosts due to organic enrichment following the *Prestige* oil-spill. The multivariate statistical approach, which facilitates an assessment of the variation of the overall community structure, proved to be very useful in studying the response of parasite communities in *B. boops* after the *Prestige* oil-spill.

RESUMEN

BIODIVERSIDAD Y ESTRUCTURA DE LAS COMUNIDADES PARÁSITAS DE *BOOPS BOOPS* (TELEOSTEI: SPARIDAE) EN LAS COSTAS ESPAÑOLAS DEL MEDITERRÁNEO OESTE Y ATLÁNTICO NORDESTE

1. INTRODUCCIÓN GENERAL

El **parasitismo** ha evolucionado independientemente en organismos de diferentes linajes y es considerado como uno de los modos de vida más exitosos. Los parásitos han evolucionado de formas muy diversas y han elaborado diferentes estrategias para sobrevivir en diversos ambientes.

Aunque los océanos hayan sido considerados evolutivamente como medios estables, uno de los grandes obstáculos para los parásitos es que deben adaptarse a un medio en el que el encuentro con sucesivos hospedadores, durante su ciclo de vida, puede ser periódico e incluso infrecuente, debido a la distribución discontinua de los mismos y la baja densidad de hospedadores intermediarios y definitivos (Marcogliese, 2005a, 2007). Aún así, la diversidad de especies parásitas en peces marinos es mayor que en los de agua dulce. Uno de los mecanismos que puede generar estas diferencias es la habitual presencia de hospedadores paraténicos en el medio marino, que aseguran la transmisión a los siguientes hospedadores en el ciclo vital. La explotación de nuevas cadenas tróficas a través de hospedadores paraténicos es más común en los parásitos marinos que en los dulceacuícolas. Asimismo, los parásitos pueden ir acumulándose en 'paquetes' debido a la predación de estos hospedadores por otros hospedadores. Otra de las razones que puede llevar a esta mayor diversidad de parásitos en el medio marino es la baja especificidad de los mismos.

Debido al gran número de **hábitats fragmentados,** los ecólogos realizan muchos estudios utilizando sistemas jerárquicos. Las comunidades parásitas son un excelente modelo para el estudio de diferentes patrones de organización a diferentes niveles, dependiendo de la escala física elegida para el estudio (Holmes y Price, 1986; Bush *et al.*, 1997; Poulin, 2005).

La escala más pequeña está representada por las infracomunidades, formadas por las infrapoblaciones de todas las especies parásitas en un único hospedador. El estudio de diferentes individuos de una misma población de hospedador nos proporciona réplicas de infracomunidades, ofreciendo la oportunidad de realizar análisis estadísticos robustos. A su vez, cada hospedador ofrece a los parásitos diferentes microhabitats para explotar. El siguiente nivel estaría formado por las comunidades componentes que comprenden todas las infracomunidades en una población de hospedador. Cada comunidad componente es, a su vez, una parte de una entidad artificial, más que ecológica, considerada como la fauna

parásita de dicho hospedador. Tanto las comunidades componentes como las faunas parásitas proporcionan la escala adecuada para realizar comparaciones macroecológicas (Poulin, 1998; Guégan *et al.*, 2005).

Dentro de la **estructura** de las comunidades parásitas en peces se puede estudiar la distribución de especies dentro de las infracomunidades o se pueden realizar estudios sobre los patrones macroecológicos. Se han detectado ciertos patrones tales como la co-ocurrencia de especies (Poulin y Valtonen, 2001; Vidal-Martínez y Poulin, 2003), el anidamiento de la infracomunidades (Worthen y Rohde, 1996; Morand *et al.*, 2002), organizaciones núcleo-satélite de las especies (Hanski, 1982; Morand *et al.*, 2002) y presencia de comunidades parásitas interactivas y aisladas (Holmes y Price, 1986; Esch *et al.*, 1990; Sousa, 1994). El número de estudios de los patrones macroecológicos ha aumentado con el creciente interés en la teoría de metapoblaciones. Unos de los patrones macroecológicos más extendidos es la relación entre las especies y el área (Kuris, 1980; Kennedy, 1990) y entre la riqueza y el aislamiento (Whittaker, 1998) (ambos muy relacionados con la teoría de biogeografía de islas de MacArthur y Wilson, 1967) o los patrones de relación entre riqueza local y regional (Price, 1980; Kennedy y Guégan, 1994; Barker *et al.*, 1996).

Sin embargo, tan importante como identificar los patrones de la estructura de las comunidades parásitas es encontrar los **procesos** que los crean. Los procesos epidemiológicos, es decir, la diferente capacidad de colonización/extinción de las especies parásitas ha sido sugerido como causante de la estructura de ciertas comunidades parásitas (Morand *et al.*, 2002). Otros estudios indican que las características de los hospedadores son las que más influyen en la estructura de las comunidades (Guégan y Hugueny, 1994). La competencia interespecífica es otro proceso que puede dar forma a las comunidades parásitas, pero resulta complicado probar la importancia de este proceso (Poulin, 2005). Por último, la estructura de las comunidades puede ser debida a la llegada de parásitos en forma de paquetes (hospedadores intermediarios con varias especies e individuos parásitos) al hospedador definitivo (Bush *et al.*, 1993; Lotz *et al.*, 1995).

Otro aspecto interesante es el estudio del **desarrollo de las comunidades** parásitas en relación al tamaño/edad del hospedador. Numerosos estudios indican que existe una correlación positiva entre el aumento del tamaño/edad de los peces y la riqueza y abundancia de parásitos. Las hipótesis planteadas para explicar esta relación son

principalmente tres. La primera de ellas está relacionada con la idea de que a mayor tamaño de hospedador mayor número de especies se pueden fijar (relacionado con la teoría de biogeografía de islas, ver Dogiel, 1964). La segunda, en cambio, considera que al aumentar la talla/edad del pez aumenta también la probabilidad de encuentro (hipótesis de acumulación, ver Lo *et al.*, 1998). Por último, existe una hipótesis que considera que los cambios tanto en el hábitat como en la alimentación de los hospedadores a lo largo de su vida influyen directamente sobre estos parámetros (Rohde *et al.*, 1998; Poulin y Valtonen, 2001).

Por último, cabe destacar la utilidad de los parásitos como **indicadores de contaminación ambiental**. Existen numerosos estudios que indican que los cambios en el ambiente se ven reflejados en la transmisión de los parásitos. Por una parte, los ectoparásitos suelen aumentar sus infecciones debido a la existencia de inmunosupresión del hospedador tras un evento contaminante (MacKenzie *et al.*, 1995; Moles y Wade, 2001; Khan, 2003). Por otra parte, los parásitos transmitidos por la red trófica pueden verse afectados disminuyendo sus poblaciones debido a cambios en su transmisión, incluso debido a mortalidad de fases larvarias (Poulin, 1992; Marcogliese y Cone, 1997)

Existen numerosas razones que justifican la selección de las comunidades parásitas de la boga, *Boops boops* (Teleostei, Sparidae), para tratar los aspectos mencionados anteriormente. Primero, los estudios ecológicos son escasos en el área del Mediterráneo y Noreste Atlántico, aunque existen numerosos estudios taxonómicos. Segundo, *B. boops* es una especie no migratoria, muy abundante en esta zona, con una posición trófica intermedia, y con una fidelidad por la zona en la que vive. Tercero, la parasitofauna de *B. boops* ha sido relativamente bien estudiada en el Mediterráneo y los estudios realizados indican que alberga numerosas especies parásitas. Por último, la disponibilidad de muestras previas al vertido del petrolero *Prestige* (Noviembre 2002) ofrecen una oportunidad única de estudiar los cambios en estas comunidades tras este evento.

Las cuestiones específicas que se plantean en este estudio son:

1. ¿Cuál es la composición taxonómica de la parasitofauna de *B. boops* en el Mediterráneo y Noreste Atlántico?

2. ¿Es la estructura de las infracomunidades parásitas predecible y se ve repetida, o es producto de infecciones independientes y al azar? ¿Hay patrones reconocibles en el desarrollo de las comunidades parásitas asociadas al tamaño/edad del hospedador?

3. ¿Hay variaciones temporales/espaciales en la estructura de las comunidades parásitas? ¿Hay alguna vinculación entre los patrones de composición de las comunidades y la relación entre la distribución espacial y la abundancia local de los parásitos?

4. ¿Es posible detectar cambios en las comunidades parásitas de *B. boops* que puedan estar relacionados con el vertido de crudo?

2. JUSTIFICACIÓN Y OBJETIVOS

La presente tesis doctoral tiene dos propósitos generales: (i) Proporcionar un mayor y detallado conocimiento de la diversidad, composición y estructura de las comunidades parásitas de la boga, *Boops boops* (Teleostei: Sparidae) a lo largo de la costa Mediterránea y Atlántica de España. (ii) Utilizar diversos parámetros de las comunidades parásitas de la boga para valorar el efecto potencial del vertido del petrolero *Prestige* sobre las comunidades costeras de 3 localidades de la costa Atlántica española afectadas por dicho vertido.

Los objetivos específicos que se plantean son cuatro:

1. Caracterización de la parasitofauna de *B. boops* del Mediterráneo y Noreste Atlántico español mediante (a) un estudio morfológico detallado de las especies parásitas para su correcta identificación taxonómica y (b) realización de una compilación de las especies de parásitos de *B. boops* a lo largo de su rango de distribución, basada en registros ya publicados y en los datos de este estudio.

2. Evaluación del efecto de la talla del hospedador, *B. boops*, en el desarrollo de sus comunidades parásitas, mediante el análisis de los patrones de composición y estructura de las comunidades parásitas a lo largo de un gradiente de talla de hospedador e identificación de los procesos subyacentes.

3. Examen de las variaciones geográficas y temporales de las comunidades parásitas de *B. boops*. Comprobar la hipótesis del declive de la similitud entre las comunidades con respecto a la distancia geográfica, utilizando datos originales a dos escalas espaciales

anidadas (faunas parásitas y comunidades componentes). Comprobación de la sincronía estacional de los patrones de relación entre la similitud de las comunidades y la distancia. Evaluación de la importancia de la relación entre la abundancia y la distribución de las especies parásitas y la identificación de las especies que contribuyen sustancialmente a los patrones observados.

4. Estudio comparativo, mediante un diseño 'antes-después', de la estructura y composición de las comunidades parásitas de *B. boops* provenientes de 3 localidades de la costa Atlántica española afectadas por el vertido del petrolero *Prestige* en 2002. Evaluación de la importancia de ciertas especies parásitas y de los grupos funcionales de parásitos en la detección de una tendencia direccional en la composición de las comunidades naturales, que podría estar relacionada con el vertido.

3. MATERIALES Y MÉTODOS

3.1. ESPECIE MODELO

La boga, *Boops boops* (L.), es un teleósteo de la familia Sparidae de distribución demersal, tendiendo a semipelágica, con hábitos no migratorios. Está distribuida por todo el Mediterráneo y el Noreste Atlántico, desde Noruega hasta Angola, siendo especialmente común desde el Golfo de Vizcaya hasta Gibraltar. Se trata de una especie gregaria que se halla a profundidades de 0 a 350 metros. Se encuentra sobre diversos fondos como rocas, praderas de *Posidonia*, fango y arena. La boga forma bancos erráticos con actividad diurna. Aunque ocasionalmente se acerca al fondo, habitualmente se encuentra en la columna de agua.

La boga puede alcanzar 36 cm de talla total pero, generalmente, miden de 15 a 20 cm. Aunque existen numerosos estudios sobre la relación talla-edad de *B. boops* (principalmente realizados en el Mediterráneo), la gran variabilidad de la tasa de crecimiento en las diferentes localidades complica la determinación de la edad de esta especie. Las estimaciones realizadas para el presente estudio están basadas en los datos correspondientes a una población del litoral de Castellón (Zúñiga, 1967).

A pesar de que *B. boops* es, posiblemente, una de las especies más abundantes en el Mediterráneo y Noreste Atlántico (Girardin, 1981; Valle *et al.*, 2003; Boyra *et al.*, 2004; Froese y Pauly, 2007), los estudios sobre su dieta son escasos y ambiguos.

3.2. MUESTREO DE PECES Y PARÁSITOS

Las muestras fueron recogidas por pescadores locales en caladeros cercanos a siete puertos a lo largo de la costa Mediterránea y Atlántica de España. En el presente trabajo dichos caladeros se nombrarán como las localidades de los puertos más cercanos. Se analizó un total de 805 peces, provenientes de 22 muestras. Las muestras se recogieron durante 2001, 2005-2007 (Tabla 3.1.) en Ondarroa, Vigo, Malpica y Barbate en el Atlántico, y en Santa Pola y Barcelona en el Mediterráneo (Figura 3.2.). Además, se recogieron dos muestras adicionales, la primera en Valencia (Mediterráneo; 13 de Noviembre de 2003) y la segunda en Malpica (12 de Mayo de 2004).

Los parásitos fueron recogidos siguiendo un protocolo estándar, y todos ellos fueron identificados y contados. Se examinó una submuestra de peces en fresco para una correcta identificación de las especies parásitas. Los parásitos encontrados se conservaron en alcohol 70%. Los trematodos, monogeneos y acantocéfalos se tiñeron con acetocarmín férrico (Georgiev *et al.*, 1986) y se montaron en bálsamo de Canadá. Los nematodos, las larvas de cestodos y los copépodos se montaron temporalmente en solución salina o glicerina y los isópodos se examinaron en solución salina. Todas las medidas de los parásitos (expresados en micrómetros) se tomaron a partir de los dibujos realizados al microscopio óptico.

Los datos referentes a los ciclos de vida y especificidad de los parásitos se recopilaron gracias a una búsqueda bibliográfica exhaustiva y a partir de la base de datos de hospedadores-parásitos (http://www.nhm.ac.uk/research-curation/projects/host-parasites /database/) y del catálogo hospedador-parásito del Museo de Historia Natural de Londres.

3.3. ANÁLISIS ESTADÍSTICO

La información sobre las comunidades parásitas se ordenaron en dos niveles jerárquicos: infracomunidad y comunidad componente. Los descriptores cuantitativos utilizados en el estudio son: la prevalencia y la abundancia media (Bush *et al.*, 1997). Las especies con una prevalencia mayor del 30% se han considerado como comunes, del 10-30% como raras y menor del 10% como accidentales.

Debido a la distribución agregada de los datos, se han realizado análisis no paramétricos. En las comparaciones a posteriori se aplicó la corrección de Bonferroni,

obteniendo datos más conservativos en las comparaciones pareadas. En los casos en los que se han aplicado análisis paramétricos, la abundancia de los parásitos se transformó logarítmicamente [ln (x+1)] (Sokal y Rohlf, 1995). Las prevalencias fueron comparadas mediante el test exacto de Fisher. Los programas empleados para estos análisis fueron el SPSS ®14.0 (SPSS Inc., Norušis, 2002) y Quantitative Parasitology (QP1.0, Rózsa *et al.*, 2000).

En cada capítulo se llevaron a cabo análisis específicos mediante los programas PRIMER v6 software (Clarke y Gorley, 2006), Nestedness Temperature Calculator (Atmar y Patterson, 1995); PAUP* 4.0 beta (Swofford, 2002) y RT 2.1 program (Western EcoSystems Technology, Inc., Cheyenne, Wyoming).

4. PARASITOFAUNA DE *B. BOOPS*

Un paso primordial antes de realizar cualquier estudio de comunidades es proceder a la correcta identificación de los individuos con los que se está trabajando. El presente estudio ha revelado que la diversidad de la fauna parasitaria de *B. boops* es mayor que lo previamente documentado.

En los 805 peces analizados (de las 22 muestras de las siete localidades) se registró un total de 54.034 individuos, pertenecientes a 53 especies. Treinta y cuatro de las especies son transmitidas mediante la cadena trófica (con una dominancia de los trematodos) y 36 presentaron una baja especificidad (parásitos generalistas frente a 8 especies especialistas o generalistas de espáridos). Los detalles de los parámetros de infección en las 22 muestras se muestran en los apéndices 1-4. En este trabajo se realizó la redescripción morfológica de nueve especies de digeneos (Figuras 4.4.; 4.7.-4.15.) (Tabla 4.2.; 4.3.): *Stephanostomum euzeti* Bartoli y Bray, 2004 (met.); *Accacladium serpentulum* Odhner, 1928; *Tetrochetus coryphaenae* Yamaguti, 1934; *Magnibursatus caudofilamentosa* (Reimer, 1971) Gibson y Køie, 1991; *Steringotrema pagelli* (van Beneden, 1871) Odhner, 1911; *Robphildollfusium martinezgomezi* López-Román, Gijón-Botella, Kim y Vilca-Choque, 1992; *Aponurus laguncula* Looss, 1907; *Lecithaster confusus* Odhner, 1905; *Lepocreadium album* Stossich, 1890. En un principio, se consideró la posibilidad de que tres de las especies descritas fueran nuevas especies (*R. martinezgomezi*, Tabla 4.2.) o nuevos registros (*L. album* y *S. pagelli*). Sin embargo, la comparación detallada de los ejemplares y la posterior ampliación de la literatura específica demostraron que no era así. Cabe resaltar que *B. boops* es el primer hospedador intermediario documentado para *S. euzeti*.

Otro claro indicativo de la gran diversidad parasitaria en la boga, previamente no documentada, fue la aparición de 25 especies consideradas como nuevos registros y la descripción de una nueva especie, *Wardula bartolii*. Además de las 6 especies descritas (*S. euzeti*, *A. serpentulum*, *T. coryphaenae*, *M. caudofilamentosa*, *A. laguncula* y *L. confusus*), 19 especies resultaron ser nuevos registros (Figuras 4.3.; 4.5.; 4.6.; 4.16.-4.30.): *Stephanostomum cesticillum* (Molin, 1858) (met.), *S. lophii* Quinteiro *et al.*, 1993 (met.); *Tormopsolus* sp. (met.); Opecoelidae gen. sp.; Renicolidae gen. sp. (met.); *Cardiocephaloides longicollis* (Rudolphi, 1819) (met.); *Echinorhynchus gadi* Zoega in Müller, 1776; *Andracantha mergi* (Lundstroem, 1941) Schmidt 1975; *Andracantha tunitae* (Weiss, 1914) Zdzitowiecki 1989; *Corynosoma* sp. (post-cystacanth); *Neoechinorhynchus agilis* (Rudolphi, 1819); *Camallanus* sp.; *Cucullanellus* sp.; *Ascarophis* sp. nº 1 Petter y Radujkovic, 1989; *Caligus* sp.; *Clavellodes* sp.; *Philichthys* sp.; Taeniacanthidae gen. sp. y *Gnathia* sp.

Durante el estudio taxonómico de los parásitos de las bogas capturadas en el Atlántico se detectó una nueva especie de digeneo, *Wardula bartolii*, perteneciente a la familia Mesometridae (subfamilia Wardulinae). Esta familia se caracteriza por carecer de ventosa ventral, bolsa del cirro y metratermo, presentar un tegumento espinoso, un sistema excretor reticular y una concavidad ventral, bien en la parte anterior, bien en todo su cuerpo, que forma un órgano de fijación (Figuras 4.1.; 4.2.). La subfamilia está representada únicamente por un género, *Wardula*, que hasta hoy sólo incluía 2 especies, *W. capitellata* (en *Sarpa salpa*) y *W. sarguicola* (en *Diplodus sargus*). El examen de las características de diagnosis de ambas especies permitió determinar que los individuos encontrados no encajaban en ninguna de ellas (Tabla 4.1.), por lo que se consideraron miembros de una nueva especie *W. bartolii*. Los miembros del género *Wardula* se han registrado casi en su totalidad en el Mediterráneo, siendo éste el tercer registro de este genéro fuera de esta área.

Como resultado de este estudio se ha realizado un compilación (Tabla 4.4.) de los parásitos de *B. boops* a lo largo de su área de distribución, incluyendo todas las citas adicionales a la publicación de Pérez-del-Olmo *et al.* (2007a). Esta compilación muestra que la parasitofauna de la boga esta formada por 78 especies (basado en 365 citas hospedador-parásito-área). Los digeneos representan el grupo más diverso dentro de los parásitos encontrados en *B. boops*. Nueve especies de metazoos, que probablemente formen

el núcleo de la parasitofauna de este hospedador, han sido citadas en las tres áreas de estudio (Mediterráneo oeste, Mediterráneo este, Noreste Atlántico): el monogeneo *Microcotyle erythrini*, los digeneos *Bacciger israelensis*, *Aphanurus stossichii*, *Lecithocladium excisum* y *Hemiurus communis*, las larvas de nematodos *Anisakis simplex s.l.* e *Hysterothylacium aduncum* y los isópodos *Ceratothoa oestroides* y *C. parallela.* Una larva tetrafilídea no identificada (conocida como *Scolex pleuronectis* Müller, 1788) ha sido también documentada en las tres áreas. Además, se ha elaborado una base de datos con los ciclos de vida conocidos de las especies citadas en la boga.

5. DESARROLLO DE LAS COMUNIDADES PARASITAS EN *B. BOOPS*

5.1. INTRODUCCIÓN

Aunque la idea de que el nivel de infección por parásitos metazoos aumenta con la edad del hospedador no es una idea nueva (Dogiel, 1958), existen evidencias empíricas recientes que sugieren que un gran número de características del hospedador, como la talla/edad (p.ej. Guégan y Hugueny, 1994; Johnson *et al.*, 2004), el hábitat y la dieta (p.ej. Muñoz *et al.*, 2006), la movilidad y capacidad de encontrarse en diferentes ecosistemas (también denominado vagilidad, ver Kennedy, 1990), el comportamiento social y la formación de cardúmenes (Bartoli *et al.*, 2000; Luque *et al.*, 2004), actúan proporcionando una determinada estructura a las comunidades parásitas de peces. Sin embargo, existen pocos estudios a nivel de población del hospedador, siendo estos necesarios para precisar el papel de la edad del hospedador *per se*.

Los análisis del anidamiento de sub-grupos (‘nested subsets analysis’) han proporcionado una valiosa herramienta para la detección de la asociación talla/edad con la heterogeneidad composicional en los ensamblajes de parásitos en peces (Guégan y Hugueny, 1994; Poulin y Valtonen, 2001; Timi y Poulin, 2003). El cambio ontogénico de la dieta y/o hábitat por parte del hospedador es un mecanismo sencillo que puede dar lugar a un patrón de anidamiento en la estructura de las infracomunidades (p.ej. Rohde *et al.*, 1998; Poulin y Valtonen, 2001). No obstante, la adición de especies parásitas que dependen de la talla del hospedador a una comunidad base formada por especies que no se ven afectadas por la talla del hospedador, podría crear también una estructura anidada, sin darse un estricto cambio de dieta (Zelmer y Arai, 2004).

En el presente estudio se aborda esta cuestión empleando la boga como especie modelo. Entre el gran número de metazoos parásitos que hospeda este pez, existe un grupo de 9 especies con una amplia distribución geográfica, las cuales forman el núcleo de su parasitofauna y que, consistentemente, se encuentran presentes en el Mediterráneo y Noreste Atlántico (Pérez-del-Olmo *et al.,* 2007a). Un estudio piloto reveló que existía una correlación negativa o positiva, dependiendo de la especie, entre la abundancia y la talla de *B. boops* (Pérez-del-Olmo *et al.*, 2004). Esta influencia de la talla de *B. boops* en la variabilidad de los parámetros de ciertas especies parásitas también ha sido observada por otros autores (Renaud *et al.,* 1980; Saad-Fares y Combes, 1992). La pregunta que surge entonces es si los parámetros observados en las comunidades parásitas de la boga son inherentes a las mismas o son un mero artefacto, debido a una heterogeneidad en el muestreo con respecto a la talla del pez.

Es importante señalar que un análisis de la estructura de las comunidades parásitas en relación a la talla del hospedador tiene una gran utilidad para posteriores estudios sobre la localización de caladeros (p.ej. Power *et al.,* 2005) o para el empleo de las comunidades parásitas de *B. boops* como bioindicadoras del potencial impacto del vertido de petróleo y la evolución de las comunidades costeras tras el mismo (p.ej. Pérez-del-Olmo *et al.,* 2007b).

En este estudio se examinaron los patrones de composición y estructura de las comunidades parásitas de *B. boops* usando un gradiente de tallas de peces provenientes de una misma población. Con este trabajo se pretendió comprobar la predicción de que las especies que forman el núcleo de la fauna, y que son responsables de la detección de estructura en las comunidades, deben aparecer en la población de peces antes que las especies raras y estocásticas (*p.ej.,* Vidal-Martínez *et al.,* 1998). Este estudio ofreció la oportunidad de estudiar el desarrollo secuencial de un sistema de metazoos parásitos en un espárido poco usual, con una alta transmisión de especies parásitas con poca especificidad, centrándose en (i) la variación de los parámetros descriptores de las comunidades, (ii) distribución de especies clave y (iii) predecibilidad de la composición de las comunidades con la edad.

5.2. MATERIALES Y MÉTODOS

Se analizó un total de 130 peces que fueron recogidos por los pescadores locales de Santa Pola (Mediterráneo). Estos peces se dividieron en cinco clases de talla arbitrariamente. Las especies de parásitos se dividieron según su modo de transmisión (D, directa; F, por la red trófica) y su especificidad por el hospedador (G, generalista; BG, generalista de espáridos; BS, especialista). Los análisis se aplicaron a tres conjuntos de datos: el total de las especies, y los ensamblajes de las especies de transmisión directa (DA) y trófica (FA). Igualmente, se comprobó si la distribución de densidades de las especies parásitas se ajustaba al modelo de no existencia de interacciones interespecíficas de Janovy *et al.* (1995).

5.3. RESULTADOS

De las 26 especies encontradas, 16 eran transmitidas por vía trófica, y existiendo una dominancia de los trematodos. Una parte considerable de las especies encontradas fue generalista (16 especies), frente a las cuatro generalistas de espáridos y tres especialistas (Tabla 5.1). De las nueve especies 'núcleo', seis (*Bacciger israelensis*, *Aphanurus stossichii*, *Hemiurus communis*, *Hysterothylacium aduncum*, *Microcotyle erythrini* y *Lecithocladium excisum*) se encontraron en todas las clases de talla, con una prevalencia relativamente alta y representando la mayor parte de individuos encontrados (Figura 5.1.). Estas especies fueron consideradas como especies clave en el desarrollo de las comunidades parásitas. La distribución de densidades de las especies en las cinco submuestras se ajustaron al modelo de no existencia de interacciones interespecíficas basado en la frecuencia de co-ocurrencias (Janovy *et al.*, 1995).

Las infracomunidades tendieron a incrementar la riqueza y la abundancia con la talla del pez (r_s=0,399 p<0,0001 y r_s=0,251 p=0,004 respectivamente). Las diferencias entre las clases de talla se debieron principalmente a los mayores niveles de infección en peces de mayor tamaño, en comparación con los de menor tamaño.

Las 130 infracomunidades formadas por todas las especies dieron lugar a una matriz anidada como lo hicieron DA y FA (Tabla 5.3). Se detectó una correlación entre la talla de los peces y el orden que tomaban en la matriz anidada, tanto para el conjunto de datos de las infracomunidades formadas por todas las especies como las formadas por FA. Este patrón anidado se observó repetidamente en cada clase de talla, excepto para DA de las clases 1 y 2, en donde no se detectó una correlación significativa entre la talla del pez y su

posición en la matriz. Las seis especies clave, por su parte, exhibieron consistentemente las posiciones más altas dentro de todas las matrices, presentando una correlación altamente significativa entre la posición que toman en la matriz y el tamaño de la comunidad componente. Salvo *M. erythrini*, todas las especies clave presentaron, además, las distribuciones más idiosincráticas.

5.4. DISCUSIÓN

Los resultados apoyan parcialmente la sugerencia de que la fauna de trematodos de espáridos tiene un importante componente filogenético (Bartoli *et al.*, 2005), ya que los parásitos generalistas transmitidos a *B. boops* por mediación de otras especies simpátricas constituyen una gran parte de la comunidad (62% de todas las especies y >50% de todos los individuos). Además, de las tres especies especialistas, sólo *B. israelensis* exhibió una abundancia sustancial.

La secuencia de infección en las diferentes clases de talla apoyan claramente la hipótesis de que las especies con una distribución geográfica más amplia infectan antes la población de peces que las raras y estocásticas.

De las seis especies clave en el desarrollo de las comunidades, cuatro fueron también observadas en otro estudio como especies persistentes en bogas de diferentes tallas (Renaud *et al.*, 1980). Saad-Fares y Combes (1992) encontraron *A. stossichii* y *B. israelensis* infectando *B. boops* desde juveniles.

Aunque la información referente a la dieta de *B. boops* es escasa, los estudios más detallados demuestran que la boga se alimenta principalmente de copépodos. Esta información es consistente con la información obtenida sobre los ciclos vitales de las especies parásitas presentes en la boga.

La única especie que presentó una notable correlación positiva entre la talla de hospedador y la prevalencia y abundancia fue el monogeneo *M. erythrini*. Este resultado es consistente con la idea de que el mayor determinante de riqueza y abundancia de los monogeneos es la talla del hospedador, debido a la mayor heterogeneidad del hábitat y superficie que ofrecen las branquias (Rohde, 1989). El aumento de la abundancia de *H. aduncum* con la talla puede ser debido a la acumulación de larvas con la edad (Poulin, 2000). La disminución de la abundancia de *H. communis* con la edad podría ser debida a

una cierta segregación batimétrica de juveniles-adultos (esta información concuerda con los datos que se han recopilado de numerosos estudios sobre las diferentes tallas de *B. boops* capturadas u observadas a diferentes profundidades).

Las infracomunidades resultaron ricas y abundantes desde una edad temprana de los peces. La complejidad de FA podría estar relacionada con la predicción de Kennedy *et al.* (1986) sobre el aumento en la diversidad de las comunidades parásitas en hospedadores que se alimentan selectivamente de presas que actúan como hospedadores intermediarios para un amplio rango de helmintos. Los mayores niveles de infección encontrados en peces de mayor tamaño quizá puedan ser un indicativo de un aumento en la cantidad de alimento ingerido.

No se encontró un cambio abrupto en la composición de las comunidades parásitas de *B. boops*, lo que sugiere que no existe un cambio ontogénico brusco en la dieta de la boga. Los datos apoyan más bien la idea de que la boga se alimentaría ocasionalmente de algas (Ruitton *et al.*, 2005).

Aunque se trata de comunidades ricas y abundantes, no se encontraron evidencias que indiquen la existencia de interacción interspecífica. De hecho, las distribuciónes de densidades de las especies parásitas observadas se ajustan a la hipótesis nula de adquisición independiente (Janovy *et al.*, 1995).

El resultado clave de este estudio es la estructuración repetida de las comunidades a lo largo de las clases de talla/edad de *B. boops*, que se ve reflejada en un patrón anidado, formado por las infracomunidades de cada clase de talla/edad. Sin embargo, este orden no puede ser totalmente atribuido a una acumulación de parásitos a lo largo del tiempo, ni a una segregación de las especies en las diferentes clases de edad. Así, aunque la correlación entre la posición de los peces en la matriz y su talla es significativa para el análisis realizado con todas las especies, la correlación para FA es mucho menor e inexistente para DA. De hecho, esta falta de correlación se ve repetida en casi todos los subgrupos. Finalmente, las especies clave contribuyen y, a su vez, reducen el anidamiento, existiendo una correlación entre la posición de las especies en la matriz y el tamaño de la comunidad componente.

Poulin y Guégan (2000) sugirieron que puede existir un posible vínculo entre un patrón no-aleatorio en la composición de las comunidades y una relación positiva entre la distribución regional y la abundancia local. El sistema en estudio representa un ejemplo de esta predicción, ya que existe una fuerte correlación positiva entre la distribución regional y la abundancia local de las especies 'núcleo', tanto a nivel de comunidad componente como de infracomunidad. Además, parte de estas especies contribuyen a la homogeinidad de la estructura encontrada en la composición de las comunidades parásitas de *B. boops* en Santa Pola.

Además del hecho de que la boga es un espárido poco usual con respecto a la especificidad de los parásitos, resulta también ser un buen candidato para comprobar si el muestreo pasivo puede ser el mecanismo responsable de una estructura no-aleatoria de las comunidades. El tamaño de la boca es uno de los determinantes en la búsqueda de alimento y, por lo tanto, en la dieta del pez (Breck, 1993; Magnhagen y Heibo, 2001). Karpouzi y Stergiou (2003) observaron que *B. boops* posee la boca más pequeña de entre 18 especies de peces mediterráneos. El cambio ontogénico de la dieta suele estar frecuentemente asociado a cambios en la estructura de la boca (Castro y Hernández-García, 1995). Sin embargo, Stergiou y Karpouzi (2002) observaron que no existía una alteración significativa en la estructura de la boca de *B. boops* con la talla. Esta información, junto con el escaso incremento del área y tamaño de la boca (Karpouzi y Stergiou, 2003), hace pensar que este pez no puede consumir presas de mayor tamaño a lo largo de su vida. Este hecho sugiere que todos los hospedadores individuales son homogéneos e igualmente accesibles a los parásitos transmitidos por la red trófica. Esta idea se ve reforzada, a su vez, por el hecho de que *B. boops* alcanza su máximo nivel trófico a una edad temprana [20 cm, clase de talla 3 (ver en Stergiou y Karpouzi, 2002)].

Por otro lado, la alimentación por succión no permite una selección activa de las presas. El pequeño tamaño/área de la boca junto con la alimentación por succión restringe el abanico de presas a pequeños invertebrados suspendidos en la columna de agua. Ello facilita la ingestión pasiva de hospedadores intermediarios/paraténicos (copépodos, quetognatos, ctenóforos y, ocasionalmente, pequeños anfípodos) de las especies clave transmitidas por la cadena trófica, lo que explicaría su presencia en todas las clases talla/edad y las pocas diferencias en sus abundancias. Sin embargo, esta forma no selectiva de alimentarse también conlleva una ingestión adicional de parásitos transmitidos por los

mismos hospedadores intermediarios. Esta adición a una comunidad base formada por las especies clave da lugar a una estructura anidada, que está más relacionada con una abundancia diferencial de parásitos que con el tamaño del pez.

6. DECLIVE DE LA SIMILITUD DE LAS COMUNIDADES PARÁSITAS DE *B. BOOPS* CON LA DISTANCIA GEOGRAFICA: LA IMPORTANCIA DE LAS ESPECIES AMPLIAMENTE EXTENDIDAS

6.1. INTRODUCCIÓN

Los hospedadores representan para las comunidades parásitas una réplica jerárquicamente estructurada de un hábitat fragmentado. Esto ofrece una oportunidad extraordinaria para un análisis comparado de la variabilidad de los patrones de organización de las comunidades a varios niveles jerárquicos (Guégan *et al.*, 2005).

Un patrón macroecológico muy reconocido por los ecólogos durante varias décadas es el declive de la similitud entre comunidades con la distancia geográfica. Recientemente, estudios sobre los sistemas de hospedador-parásito han indicado una tendencia de autocorrelación de la composición y/o riqueza a lo largo del espacio (*p.ej.* Poulin y Morand, 1999; Poulin, 2003; Fellis y Esch, 2005a). Sin embargo, el declive de la similitud de las comunidades parásitas con la distancia sólo ha sido observado en algunos hospedadores (Poulin, 2003; Oliva y González, 2005), planteándose la cuestión de cómo esta relación varía entre hospedadores. La mayoría de los estudios sobre este patrón se ha realizado con sistemas de hospedador-parásito provenientes del medio terrestre o dulceacuícola y de hábitats físicamente aislados, existiendo un único estudio sobre peces marinos (Oliva y González, 2005). Por otra parte, los estudios realizados hasta el momento se basan en datos binarios obtenidos de listados de especies previamente publicados o de datos de abundancia agrupados a nivel de población de hospedador (Poulin y Morand, 1999; Poulin, 2003; Brouat y Duplantier, 2007). Por lo tanto, no se conoce ningún estudio basado en la abundancia de parásitos a nivel de hospedador individual.

En este estudio se analizó una gran cantidad de datos de la comunidades parásitas de *B. boops* obtenidos de muestras recogidas entre 2001-2007, en siete localidades cuya situación geográfica formaba un gradiente a lo largo de las costa Noreste Atlántica y Mediterránea de España (Figura 6.1A). La elección de este gradiente se realizó para valorar cómo actúan los factores relacionados con la distribución zoogeográfica en la diferenciación de comunidades parásitas de peces marinos. *B. boops* resulta ser un modelo

muy interesante debido a la gran diversidad parasitaria y su sedentarismo, lo cual podría causar un aislamiento de las comunidades parásitas en una escala geográfica más baja.
Utilizando datos binarios y de abundancia a diferentes escalas anidadas se pretende: (i) examinar la influencia de la distancia geográfica y regional en la disimilitud de la composición y estructura de las comunidades, (ii) evaluar la importancia de las especies 'núcleo' de la parasitofauna en la diferenciación de las comunidades y (iii) estudiar la sincronía en los patrones estacionales de la relación de similitud estructural de comunidades y la distancia. Finalmente, se ha explorado la distribución espacial de los parásitos de *B. boops* a diferentes escalas anidadas con el fin de observar la conexión entre la relación positiva de abundancia-distribución y la importancia de las especies ampliamente extendidas en el declive de la similitud entre comunidades.

6.2. MATERIALES Y MÉTODOS

Se han utilizado 2 conjuntos de datos. En primer lugar, para realizar una comparación global se han empleado 22 comunidades componentes (709 peces) recolectadas en primavera e invierno de 2001, 2003 y 2004-2007. El segundo grupo de datos se ha utilizado para comprobar si los patrones observados en la muestra anterior, la cual presenta un gran ruido, se repiten en un set restringido al año 2005 (415 peces; Tabla 6.1.). En este último conjunto no se recogió ninguna muestra de Valencia, y de Ondarroa sólo se obtuvo una muestra de primavera.

Los datos fueron reunidos en dos niveles: infracomunidad y comunidad componente. Se consideraron dos escalas espaciales: las faunas locales (para la comparación global y el restringido a 2005) y la comunidad componente (datos estacionales de 2005). Las muestras fueron divididas, a su vez, según la región de la localidad de muestreo, es decir, Noreste Atlántico y Mediterráneo, excepto Barbate (Atlántico). Esta última se consideró como una región separada debido a su posición fronteriza entre las dos regiones anteriormente citadas, con el fin de probar la hipótesis de que pueda tratarse de una región de transición entre las faunas parásitas de *B. boops*.

Para el estudio de las variaciones en la composición y estructura de las comunidades parásitas con la distancia geográfica y entre las regiones, los análisis se realizaron utilizando: (i) datos de presencia-ausencia, (ii) abundancia de todas las especies y (iii) datos de abundancia de conjuntos restringidos de especies. Para la primera variante se obtuvo una

matriz de similitud por el método del vecino más próximo (NJ) (Neighbour Joining) con PAUP 4.0 beta. Para las otras dos variantes, la matriz se obtuvo calculando la distancia de Mahalanobis (MD), realizando un análisis discriminante. Los conjuntos de especies se crearon al separar, por un lado, las especies 'núcleo' y, por otro lado, el resto de especies (llamadas 'marginales' en este estudio).

Para determinar el efecto de la distancia geográfica y la región sobre la composición y estructura de las comunidades parásitas se utilizó un método de permutación (Legendre *et al.*, 1994; Poulin y Morand, 1999; Goüy de Bellocq *et al.*, 2002). Se emplearon varios modelos para valorar cual de todos ellos se adaptaba mejor a la relación distancia-disimilitud de cada variante: linear simple, exponencial y potencial (power function). La significatividad de la mejor regresión fue calculada mediante aleatorización (Manly, 1997) utilizando el programa RT 2.1, realizando 1.000 permutaciones al azar de la matriz dependiente (NJ, MD). En este análisis, las matrices independientes son las matrices de distancia geográfica (creadas en base a distancias de línea de costa entre las localidades) y matrices de distancia 'regional' (con la siguiente codificación: 0, muestras de localidades de la misma región; 1, muestras de localidades del Noreste Atlántico y Mediterráneo frente a muestras de la region Barbate; 2, Muestras del Mediterráneo frente a las de Noreste Atlántico).

6.3. RESULTADOS

Se encontraron 53 especies en las 22 muestras de la comparación global y 47 especies en las 11 muestras de 2005. Las especies generalistas formaron una proporción considerable tanto en riqueza como en abundancia. La fauna parásita más rica se encontró en el Noreste Atlántico. Se observó un mayor intercambio de taxones parásitos entre Barbate y el Mediterráneo que con el Noreste Atlántico. Las faunas parásitas locales eran generalmente diversas (20-38 especies), excepto en las localidades Mediterráneas de Valencia y Barcelona, en donde la fauna era notablemente menor (9-12 especies).

Los árboles creados a partir de los datos de presencia-ausencia indican una clara separación entre el Mediterráneo y el Noreste Atlántico. Barbate aparece agrupada con Santa Pola en la comparación global (Figura 6.1A). El conjunto de datos de 2005 presenta un patrón muy similar (Figura 6.1B), con una posición intermedia de Barbate. Cabe destacar que al separar las muestras de primavera e invierno de 2005, Vigo y Malpica (las

localidades más cercanas) se agrupan por estación y no por la localidad. Por otra parte, Barbate se agrupa con Santa Pola en primavera y con Barcelona en invierno.

La disimilitud en la composición de las comunidades parásitas aumentó con la distancia geográfica y regional, tanto para la comparación global como para el conjunto de 2005 (Table 6.2.). En relación a la composición de las muestras estacionales, sólo se observó una influencia de la distancia geográfica en la disimilitud de las muestras de primavera. Por otro lado, se detectó un aumento en las diferencias entre las comunidades parásitas y la distancia geográfica cuando se utilizaron los datos de abundancia de especies en las infracomunidades. Los datos estacionales mostraron un claro efecto de la estación, siendo únicamente visible el efecto de la distancia geográfica y de la región sobre la similitud de las comunidades en la muestras de primavera.

Los resultados de los análisis realizados exclusivamente con las especies 'núcleo' de la parasitofauna fueron estadísticamente más significativos que los obtenidos con el total de especies, tanto en la comparación global como para el conjunto de 2005 y primavera de 2005. En el caso de las especies marginales, no se detectó ninguna influencia de la distancia geográfica y regional sobre la disimilitud de las comunidades parásitas.

Los modelos exponenciales y potenciales fueron los que proporcionaron los mejores modelos de regresión entre la relación de disimilitud (calculada através de los datos de presencia-ausencia/abundancia) y la distancia geográfica/regional.

Se encontró una correlación positiva significativa entre la distribución regional de especies individuales (medida por el número de localidades donde está presente) y la abundancia local (medida por el número de comunidades componentes donde está presente) ($F_{(1, 51)}$=452,64 p<0,0001). La figura 6.2A muestra, por un lado, 14 especies (10 de ellas accidentales) que fueron encontradas sólo en una o dos comunidades componentes en una única localidad. Por otro lado, en la parte superior derecha apareció un grupo de especies que estaban presentes en la mayoría de las comunidades componentes de todas las localidades. Cuatro especies del núcleo de la parasitofauna (*Bacciger israelensis*, *Aphanurus stossichii*, *Hemiurus communis* y *Hysterothylacium aduncum*) de la boga se detectaron en todas las comunidades componentes, y *Microcotyle erythrini* se encontró en 20 de las 22 muestras. Las otras tres especies del 'núcleo' (*L. excisum*, *A. simplex* y *C. oestroides*) se situaron en esta zona superior derecha, además de las larvas *Scolex*

pleuronectis y *Cardiocephaloides longicollis* (no consideradas previamente como parte del núcleo de la parasitofauna).

Se observó una correlación positiva significativa a una escala menor, en donde la abundancia local se determinó a partir de la prevalencia y la distribución regional a partir del número de comunidades componentes donde estaba presente ($F_{(1,\ 403)}$ =345,93 p<0,0001). En la figura 6.2B puede observarse que en este caso existía una clara triangularidad, indicando una mayor variación de la abundancia local a esta escala. Aún así, el aumento de la frecuencia de casos en los dos extremos resultó evidente. La parte superior derecha presenta las mismas cuatro especies núcleo de la parasitofauna anteriormente observadas.

También se detectó una correlación positiva entre la distribución de las especies y su intensidad máxima ($F_{(1,\ 51)}$ =52,28 p<0,0001), siendo las especies 'núcleo' las que presentaron mayores intensidades y, al mismo tiempo, dominancia ($F_{(1,\ 85)}$ =55,11 p<0.0001).

6.4. DISCUSIÓN

Este estudio ha resultado ser el primero en aplicar la hipótesis del declive de la similitud con la distancia mediante la utilización de datos taxonómicos originales a dos niveles espaciales anidados.

Existen tres características del sistema hospedador-parásito aquí estudiado que tienden a homogenizar la composición de las comunidades parásitas a una escala regional superior. Primero, *B. boops* es, probablemente, una de las especies más abundantes tanto en el Mediterráneo como en el Noreste Atlántico (Valle *et al.*, 2003; Boyra *et al.*, 2004). Por lo tanto, la altas densidades y el solapamiento de las poblaciones del hospedador podría aumentar la dispersión de parásitos (Morand y Poulin, 2004). Segundo, la mayoría de los parásitos de *B. boops* utilizan los mismos hospedadores intermediarios y más de una ruta de transmisión. Tercero, la gran representación en abundancia y riqueza por parte de las especies generalistas, capaces de infectar varias especies de hospedadores que coexisten, hace que la densidad adopte un significado más amplio, al considerar la densidad total de todos los hospedadores adecuados. Además, la transmisión de las especies núcleo de la fauna parásita puede aumentar considerablemente debido a la predación de copépodos por parte de los quetognatos, acumulándose así las especies parásitas en paquetes.

Las expectativas iniciales sobre la posible homogenización en la composición de las faunas locales y comunidades componentes de los parásitos de la boga no se cumplieron, por lo que se puede sugerir que procesos a mayor escala podrían estar influyendo notablemente sobre la estructura de las comunidades locales. Esta sugerencia se vio apoyada por el aumento significativo de la disimilitud con la distancia 'regional'.

Por otra parte, se ha observado que el declive de la similitud con la distancia geográfica sigue en muchos casos un modelo potencial, lo cual implica que la disimilitud en la composición y la estructura se hace cada vez más independiente de la distancia. Sin embargo, no se ha encontrado un patrón en la presencia de cada modelo con respecto a la escala y/o a las especies consideradas.

Un resultado importante de este estudio es la falta de sincronía en la composición y la estructura, tanto del total de las especies, como las especies núcleo de la fauna parásita y las marginales en la muestra de invierno de 2005. Esto podría ser indicativo de una homogenización de las comunidades en la época fría debido a un efecto de la temperatura a nivel de hospedador intermediario. El considerable intercambio de especies y la variación estocástica en la prevalencia y la abundancia indican un aumento en la estocasticidad de las tasas transmisión de los parásitos y/o interrupción de la colonización de hospedadores.

Se ha podido observar que las especies núcleo de la fauna, las cuales presentan una notable abundancia y amplia distribución, se encuentran estructuradas a escala regional. Los análisis realizados con estas especies han indicado un claro declive de la similitud con la distancia geográfica de las localidades, por lo que parecen estar estructuradas en el espacio. Se puede sugerir que *B. boops* actúa como un muestreador pasivo (como se ha comentado anteriormente) de las poblaciones locales de parásitos y que las infracomunidades parásitas reflejan las tasas de transmisión a una escala espacial menor. Por otra parte, el ambiente local conforma las comunidades de hospedadores intermediarios, dando lugar a tasas de transmisión de los parásitos diferentes, pero que serían más similares en los lugares más cercanos. Todas estas consideraciones indican la importancia de la supracomunidad en el declive de la similitud con la distancia.

7. LAS COMUNIDADES PARASITAS DE *B. BOOPS* TRAS EL VERTIDO DEL PETROLERO PRESTIGE: UN ESTUDIO EN EL TIEMPO

7.1. INTRODUCCIÓN

El vertido del petrolero *Prestige* empezó el 13 de Noviembre de 2002 cuando este buque se partió en dos y se hundió en el Banco de Galicia. Se liberaron unas 60.000 toneladas de crudo al mar, contaminando no sólo las costas gallegas sino, en mayor o menor medida, toda la costa Cantábrica. Este vertido tuvo una dispersión geográfica muy amplia y afectó a casi todos los tipos de hábitat marinos (Albaigés *et al.*, 2006).

Estudios previos han demostrado que la recuperación de un ecosistema marino afectado por un vertido puede tardar de dos a diez años en recuperarse. Así, en un reciente estudio que examinó durante cuatro años la macrofauna béntica tras el vertido del *Aegean Sea* en 1992 en la costa gallega (A Coruña), se observó que las especies sensibles al crudo desaparecieron o disminuyeron, siendo remplazadas por especies oportunistas, como los poliquetos. Tras este brusco declive en la diversidad y biodensidad, la recuperación de las comunidades empezó a detectarse a partir del tercer año del accidente (Gómez Gesteira y Dauvin, 2005).

La contaminación ambiental afecta a las poblaciones y comunidades parásitas, tanto directamente como a través de los efectos sobre los hospedadores intermediarios o definitivos. Estudios previos coinciden en que los ectoparásitos aumentan y los endoparásitos de peces disminuyen, tanto en prevalencia como en abundancia, tras una exposición crónica a xenobióticos e hidrocarburos aromáticos policíclicos (PAHs) (MacKenzie, 1999; Khan, 2003). La causa del aumento de los ectoparásitos suele relacionarse con una inmunosupresión del hospedador. En cuanto al descenso de los endoparásitos producido por la contaminación, puede ser debido a efectos tanto directos (supervivencia de estados larvales) como indirectos (declive de los hospedadores intermediarios) (Khan, 2003 y referencias incluidas). Recientemente, se ha empezado a utilizar la proporción entre especies parásitas con un único hospedador (monoxenas) y con múltiples hospedadores (heteroxenas) en el estudio del impacto de la contaminación en los ecosistemas marinos costeros (Broeg *et al.*, 1999; Diamant *et al.*, 1999; Dzikovski *et al.*, 2003).

Una desventaja de los estudios sobre eventos catastróficos, como es el caso del Prestige, es la falta de datos previos a la perturbación. Por otro lado, aunque existen

numerosos estudios sobre el impacto del crudo de este vertido en áreas costeras directamente petroleadas, la información sobre el efecto en las aguas costeras es escaso (*p.ej*. Martínez-Gómez *et al.*, 2005; 2006; Serrano *et al.*, 2005; 2006), y refleja las dificultades para diferenciar entre el efecto físico y el tóxico del crudo sobre la plataforma continental.

El hecho de poseer tres muestras pre-vertido, junto con la rica parasitofauna que presenta este hospedador y su fidelidad por el área, nos indica que probablemente las comunidades parásitas podrían reflejar cambios en la estructura de la red trófica, así como en los niveles de infección y otras características de las localidades post-vertido a una escala geográfica más fina. El objetivo de este estudio fue determinar si existía una tendencia direccional en la composición y estructura de las comunidades parásitas que podría estar relacionada con el vertido del petrolero *Prestige* y su efecto en las comunidades costeras naturales. Para ello, fueron utilizadas tanto ciertas especies parásitas como grupos funcionales de parásitos.

7.2. MATERIALES Y MÉTODOS

Se recolectó un total de 400 peces procedentes de 11 muestras de Galicia (Malpica y Vigo) y Euskadi/País Vasco (Ondarroa) (Mapa 7.1. y Tabla 7.1. y 7.2.), entre 2001 y 2006. Los análisis de distribución y estructura se realizaron seleccionando peces de tallas similares (n=146). Los datos de las comunidades parásitas fueron analizados a nivel de infracomunidad y comunidad componente. Los análisis de similitud a nivel de comunidad componente se realizaron con los 400 peces para comprobar la consistencia de los resultados obtenidos en el rango de tallas seleccionado. Para aumentar el tamaño de muestra en este último análisis, los peces de cada muestra se separaron por grupos de talla/edad (Pérez-del-Olmo *et al.*, 2008). No se detectó ningún efecto del esfuerzo de muestreo en los parámetros de las comunidades.

Los análisis se realizaron utilizando tres conjuntos de datos: (i) un *'estudio piloto'* con las tres muestras pre-vertido de las tres localidades (2001), de Malpica (2004) y de Vigo (2005); (ii) un *'segundo estudio'*, en el que se compararon las tres muestras pre-vertido de las tres localidades (2001) con tres muestras de 2005 (coincidentes en localidad y estación), para evaluar si los cambios persistían; (iii) una *'comparación global'* con la serie

de muestras recolectadas en Vigo (2001-2005-2006) y Malpica (2001-2004-2005), para evaluar la tendencia en el tiempo de las comunidades.

Con el programa PRIMER v6 software (Clarke y Gorley, 2006) se realizaron escalamientos multidimiesionales (MDS), basados en la similitud de Bray-Curtis, un análisis ANOSIM (con el fin de probar la hipótesis de que no existían diferencias en la estructura de las comunidades debidas al factor pre- y post-vertido, corregido por la localidad, el año de muestreo o la estación) y, finalmente, el procedimiento SIMPER para identificar las especies parásitas que contribuyen a la disimilitud de las comunidades en relación a ciertos factores.

7.3. RESULTADOS

Se encontraron 43 especies de parásitos, de los cuales 18 fueron nuevos registros en este hospedador y 23 fueron solamente detectados tras el vertido. El grupo predominante fue el de los digeneos (22 especies), en especial los Hemiuroidea (11 especies). Diecinueve especies fueron consideradas comunes (15 heteroxenas y 4 monoxenas), de las cuales seis fueron únicamente encontradas después del vertido. De los 12 digeneos comunes, cinco eran hemiuroideos, grupo que generalmente presentó también las mayores abundancias.

La comunidades componentes presentaron una riqueza sustancialmente mayor en las muestras inmediatamente posteriores al vertido en comparación con las previas (28 *vs.* 12-16 especies), al igual que el rango de infecciones de cada pez individual (5-15 *vs* 2-9 especies). En general, este incremento continuó siendo visible en los años posteriores. Veintiséis especies aparecieron tras el vertido en Vigo (217 % de incremento en la riqueza de especies), 19 en Malpica (119% de incremento) y 9 en Ondarroa (71% de incremento). Esta adición de especies a las faunas locales fue principalmente registrada en los primeros años tras el vertido.

'Estudio piloto'

La prevalencia, riqueza y abundancia de las especies monoxenas y heteroxenas fue significativamente mayor en las comunidades componentes post-vertido ($p<0,0001$) en comparación con las pre-vertido, no existiendo diferencias entre las muestras pre-vertido ni entre las post-vertido. Las infracomunidades de los peces muestreados tras el vertido exhibieron una riqueza y abundancia significativamente mayor, tanto para el conjunto de

todas las especies como para el conjunto de monoxenos y heteroxenos (Tabla 7.1., 7.2.). Este incremento también fue patente en los ratios tanto de especies monoxenas frente a heteroxenas (Sm/Sh) como para los individuos monoxenos frente a los heteroxenos (Im/Ih).

El MDS indicó una relativamente buena separación entre las infracommunidades pre- y post-vertido (estrés 0,16; Figura 7.3A), obteniéndose un resultado similar cuando se aplicó el MDS sólo a las especies comunes. Cuando la suma de las abundancias de heteroxenos y monoxenos fue utilizada para construir la matriz de similitud y posteriormente el MDS se obtuvo una separación excepcional (estrés 0,05) (Figura 7.3B,C,D).

Los resultados del ANOSIM indicaron que había un gran efecto del factor 'vertido' (R=0,76 p=0,001) en la separación de las infracomunidades, así como un efecto de la 'localidad' (R=0,544 p=0,001).

'Segundo estudio'

Se obtuvieron resultados semejantes a los anteriores, excepto por la ausencia de un incremento significativo tanto de las especies monoxenas como de Im/Ih y Sm/Sh en Malpica, así como de Im/Ih y Sm/Sh en Ondarroa.

Por otro lado, once especies comunes (*Hemiurus communis*, *Bacciger israelensis*, *Wardula bartolii*, *Lecithocladium excisum, Aphanurus stossichii*, *Magnibursatus bartolii, Scolex pleuronectis*, *Cardiocephaloides longicollis*; *Stephanostomum cesticillum* y *Microcotyle erythrini*) sufrieron un incremento significativo en la abundancia en alguna de las 3 localidades tras el vertido (Tabla 7.1., 7.2.). Los cambios en la prevalencia, en cambio, no fueron tan llamativos en ninguna de las localidades.

Aunque el MDS basado en las similitudes de las infracomunidades no presentó una clara separación, el análisis del ANOSIM reveló que existían diferencias entre las infracomunidades debido al factor 'vertido' (R=0,631 p=0,001), si bien el factor localidad también tuvo una gran influencia (R=0,667 p=0,001). El procedimiento SIMPER identificó ocho especies (*H. communis*, *B. israelensis, A. stossichii*, *L. excisum*, *M. bartolii*, lepocreádidos juveniles, *Hysterothylacium aduncum* y *M. erythrini*) que contribuyeron sustancialmente a la disimilitud debido al 'vertido' y a la 'localidad'.

Los MDS obtenidos en base a los parámetros de la comunidad componente (es decir, abundancia y prevalencia) presentaron un menor estrés (0,12 y 0,09, respectivamente). El análisis con ANOSIM indicó también una mayor diferenciación debido tanto al 'vertido' (R=1 p=0,011 y R=0,868 p=0,011 respectivamente) como a la 'localidad' (R=1 p=0,002 y R=1 p=0,003 respectivamente). Las especies que contribuyeron a las diferencias entre localidades y entre pre y post-vertido fueron las mismas que para las infracomunidades en el caso de las abundancias. En cuanto a la prevalencia, sufrieron alguna variación debido a que las especies anteriormente mencionadas presentaron una elevada prevalencia en todas las localidades antes y después del vertido.

'Comparación global'

En general, las muestras post-vertido mostraron un incremento considerable en la riqueza y abundancia de las especies monoxenas y heteroxenas, en comparación con las muestras pre-vertido (Figura 7.7.). En las muestras de Malpica se detectó una tendencia hacia la disminución de estos parámetros, mientras que en las de Vigo se observó un patrón más variable.

En la muestra de **Malpica** de primavera de 2005 se observó una disminución en los parámetros de las comunidades (excepto en el número de individuos heteroxenos), así como un decrecimiento significativo en la abundancia de cinco especies (*H. communis*, *B. israelensis*, lepocreádidos juveniles, *M. erythrini* y *Ceratothoa oestroides*). Sin embargo, *H. aduncum* y *L. excisum* aumentaron en comparación con la muestra de primavera de 2004 (Tabla 7.1.).

El MDS basado en las infracomunidades no reflejó un separación muy importante (estrés 0,15), pero el ANOSIM indicó que había un efecto tanto del 'año' (R=0,556 p=0,001) como de la 'estación' (R=0,761 p=0,001) en la separación de las muestras. Las mayores diferencias encontradas entre años fueron entre 2001-2004 (R=0,937 p=0,001), aunque este cambio persistió entre 2001-2005 (R=0,469 p=0,001) y también resultó ser patente entre 2004-2005 (R=0,621 p=0,001). Las especies que contribuyeron a las diferencias debidas al 'año' y a las 'estaciones' fueron las mismas siete que habían contribuido a las diferencias entre infracomunidades del '*segundo estudio*'.

Los resultados obtenidos con el MDS a partir de la abundancia y prevalencia de las comunidades componentes revelaron una separación significativa (estrés 0,01 y 0,06

respectivamente), presentando una mayor separación de las muestras de 2001-2004, mientras que las de 2005 se encontraron en una posición intermedia. El análisis ANOSIM mostró resultados concordantes con los obtenidos con las infracomunidades pero más marcados. Por su parte, SIMPER reveló de nuevo a las mismas siete especies en relación con la abundancia y una lista más variable en relación con la prevalencia (al igual que en el '*segundo estudio'*).

En la muestras de **Vigo** se observó que seguía existiendo un aumento en los parámetros de las comunidades en 2006 respecto a 2001, con un aumento igualmente en la abundancia de cinco especies (*M. erythrini*, *H. communis*, *B. israelensis*, *M. bartolii* y *S. cesticillum*) (Tabla 7.2.). En general, entre 2005 y 2006 se observaron unos parámetros de las comunidades parecidos, con un descenso de la abundancia media de especies en total y la riqueza de heteroxenos. A su vez, diez especies exhibieron un descenso en su abundancia entre 2005 y 2006. Inesperadamente, se observó un incremento en los parámetros de comunidad y de cuatro especies entre el otoño de 2005 al 2006.

El MDS formado por las infracomunidades no reflejó una clara separación como se observó con las comunidades componentes, pero esta separación resultó evidente al realizarlo con los parámetros de comunidades. En este caso, se observó que las muestras de 2005 y 2006 se encontraban separadas de las de 2001 y muy cercanas entre sí. El análisis ANOSIM realizado con las infracomunidades y con los parámetros de comunidad (abundancia y prevalencia), indicaron un efecto tanto del 'año' como de la 'estación', presentándose las mayores diferencias entre los años 2001-2005 y 2001-2006, y no siendo tan evidentes entre 2005-2006. En este caso, las especies que más contribuyeron a la distinción debido al 'año' y a la 'estación' fueron nueve (*H. communis, A. stossichii, B. israelensis*, lepocreádidos juveniles, *Steringotrema pagelli*, *L. excisum*, *M. bartolii*, *S. cesticillum* y *M. erythrini*). Al igual que anteriormente, esta lista sufrió alguna variación al aplicar el procedimiento SIMPER con los datos de prevalencias.

7.4. DISCUSIÓN

Como se ha comentado anteriormente, los parásitos son buenos indicadores de perturbaciones en el medio debido a que reflejan interacciones complejas entre los posibles contaminantes y las formas larvarias de vida libre o las poblaciones de los hospedadores

intermediarios y definitivos. Así, una desviación de los valores normales de transmisión podría ser una advertencia de una condición ambiental adversa (MacKenzie *et al.*, 1995).

Los análisis univariantes y multivariantes nos indicaron un cambio drástico en la riqueza, abundancia y estructura de las comunidades parásitas y una notable alteración, tanto a nivel de especie como de grupo funcional. En general, podríamos decir que la comunidades parásitas de *B. boops* podrían reflejar el efecto del vertido del *Prestige* en las comunidades naturales.

El presente estudio indicó que el empleo de grupos taxonómicos de mayor rango y/o de grupos funcionales en vez de especies proporciona una mayor resolución y detecta mejor la tendencia de la estructura de las comunidades parásitas en los peces tras un vertido.

Los mayores niveles de infección por **monoxenos,** así como los altos valores de los índices Im/Ih y Sm/Sh observados justo tras el vertido, fueron indicativos de una posible respuesta a un factor de estrés. Por una parte, nuestros datos concuerdan con la idea de que los monoxenos, debido a que están en continuo contacto con el medio externo, en este caso marino, han desarrollado una flexibilidad y una resistencia a cambios naturales durante su evolución que les hace menos vulnerables al efecto de los contaminantes (MacKenzie, 1999). Por otra parte, se tiene constancia de la capacidad inmunosupresora que pueden causar los PAHs en los organismos acuáticos y esto puede originar picos de infección (Sinderman, 1983, 1993; Sures, 2004). Aunque no existe casi ningún estudio al respecto tras el vertido del *Prestige*, algunos autores han detectado un aumento en la actividad EROD en peces (Jiménez-Tenorio *et al.*, 2005; Martínez-Gómez *et al.*, 2005, 2006; Morales-Caselles *et al.*, 2006). Estos datos indican que puede haber tenido lugar una inmunosupresión en los peces que sería responsable de una elevada infección por monoxenos. Aunque apareció una elevada infección por especies monoxenas en 2004, 2005 y 2006, se observó una tendencia a la disminución, aunque esto debe considerarse con prudencia, debido al posible efecto de enmascaramiento que puede estar creando la estacionalidad.

En contra de lo esperado, no hubo una disminución de las infecciones por especies **heteroxenas** en *B. boops*. Esto sugiere que posiblemente no hubo una perturbación cualitativa en las comunidades bentónicas/pelágicas. Sin embargo, se detectó un aumento tanto en el número de especies como de individuos heteroxenos. Al igual que para las

especies monoxenas, las heteroxenas también mostraron un pico en 2004 y una tendencia al decrecimiento en años posteriores. Algunas especies de heteroxenos que se enquistan en los tejidos pueden haber sido favorecidos por el efecto de inmunosupresión tanto en el pez como en sus hospedadores definitivos. Para el aumento de las infecciones por resto de especies heteroxenas se pueden sugerir 2 hipótesis alternativas no excluyentes. Por una parte, un efecto de inmunosupresión en los hospedadores intermediarios que se vería apoyada por los altos contenidos en PAHs encontrados en el molusco *Mytilus galloprovincialis* un año después del vertido (Laffon *et al.*, 2006; Soriano *et al.*, 2006). La segunda hipótesis podría estar relacionada con un aumento del enriquecimiento orgánico tras el vertido. Esta hipótesis surge debido a la gran cantidad de poliquetos encontrados en los estómagos de *B. boops* tras el vertido y los grandes niveles de infección por hemiuroideos, que utilizan este hospedador intermediario o que, potencialmente, podrían hacerlo (Rebecq, 1965; Margolis, 1971; Bray, 1988). Se sabe que los poliquetos son especies oportunistas (Gómez Gesteira y Dauvin, 2005) y, aunque los pocos estudios que se han realizado al respecto no revelan cambios bruscos en la abundancia de este taxón en las comunidades tras el vertido, sí que se ha constatado que son un grupo dominante (Parra y Frutos, 2005; Serrano *et al.*, 2006). Un estudio en el mar Báltico (Zander y Reimer, 2002) demostró que en lugares con un alto enriquecimiento aparecían una mayor cantidad de hemiuroideos. El efecto rebote en la abundancia y distribución de las especies bentónicas y dermersales indicadoras descrito por Serrano *et al.* (2005, 2006) parece apoyar nuestra hipótesis. También se sabe que los copépodos harpacticoides pueden aumentar su biomasa tras un vertido (Celewycz y Wertheimer, 1996; Wertheimer *et al.*, 1996). Las especies de *Acartia* son calanoides oportunistas que sirven de hospedadores intermediarios a numerosos hemiuroideos (p.ej. Rebecq, 1965; Gibson y Bray, 1986; Køie, 1991, 1992, 1995) y se ha observado que dominan los sistemas marinos eutroficados del Mediterráneo los cuales también se encuentran afectados por contaminación por hidrocarburos y metales pesados (Marcus, 2004).

El presente estudio ha demostrado, por una parte, que diversos métodos multivariantes pueden ser muy útiles para detectar cambios en la composición y la estructura de las comunidades parásitas. Merece la pena destacar también que los análisis a nivel de comunidad componente han reflejado más claramente los cambios en las comunidades que a nivel de infracomunidad, los cuales presentaron una variación más estocástica. Por otra parte, las especies comunes, un grupo creado artificialmente a priori,

han resultado ser las especies que más han contribuido a las diferencias debidas al ‘vertido’ y al ‘año’.

Aunque el presente estudio muestra que las comunidades parásitas son capaces de reflejar los cambios complejos que ocurren en la cadena trófica, otras fuentes responsables de la contaminación marina pueden estar cambiando las líneas de referencia y afectando la recuperación de las comunidades parásitas tras el vertido del petrolero *Prestige* (Ruiz, 2004). Esto podría estar indicando que el estado de las comunidades parásitas encontradas en *B. boops* en 2005-2006 son los nuevos niveles de referencia a tener en cuenta en caso de ocurrir un nuevo evento contaminante.

8. CONCLUSIONES FINALES

1. La diversidad de la parasitofauna de *B. boops* es mucho mayor de lo que previamente se pensaba, como se ve evidenciado en la descripción de una nueva especie para la ciencia, *Wardula bartolii* Pérez-del-Olmo *et al.*, 2006 y la presencia de 53 especies en las siete poblaciones de peces estudiadas a lo largo del Noreste Atlántico y el Mediterráneo de la costa española, de las cuales 25 resultaron ser nuevos registros. La compilación de los parásitos de *B. boops* a lo largo de su área de distribución, realizado durante el presente estudio, comprende 78 especies a partir de 365 citas hospedador-parásito-área. Se ha encontrado regularmente un grupo de nueve especies con una amplia distribución en los peces del Mediterráneo y Noreste Atlántico, siendo considerados el núcleo de la parasitofauna de *B. boops*.

2. La parasitofauna regional de *B. boops* en el Noreste Atlántico ha resultado ser rica en especies. Existe una clara separación entre las faunas locales del Atlántico y el Mediterráneo, apareciendo una localidad de transición (Barbate-Atlántico) en una posición intermedia. Las faunas parásitas locales son generalmente diversas, comprendiendo entre el 30 y el 50% de los parásitos de *B. boops* en su área de distribución, excepto en Valencia y Barcelona (Mediterráneo), en donde la fauna es notablemente menor, comprendiendo sólo el 15% de las especies encontradas en este hospedador.

3. Las comunidades parásitas de *B. boops* se caracterizan por una gran representación de parásitos con ciclos de vida complejos, transmitidos al pez por vía trófica, y por la dominancia de los trematodos. La influencia filogenética en la composición y la estructura

de las comunidades parásitas en *B. boops* es escasa, dado que las especies parásitas generalistas comprenden la mayor parte (36 especies frente a 8 especies especialistas o generalistas de espáridos) de las comunidades parásitas, tanto en lo que respecta a riqueza como a abundancia.

4. Las especies identificadas como núcleo de la parasitofauna de *B. boops* se encuentran presentes en peces juveniles de un año de edad de una población de Santa Pola (Mediterráneo), mientras que todas las especies añadidas a las comunidades en peces de mayor tamaño, o de mayor edad, se consideran como raras o accidentales. La secuencia de aparición y la persistencia observada en el desarrollo de las comunidades parásitas de *B. boops* apoya la hipótesis de que las especies con una distribución geográfica amplia aparecen en las poblaciones de peces antes que las raras y estocásticas.

5. Las comunidades parásitas de *B. boops* son ricas y abundantes desde una edad temprana. Aunque la riqueza y abundancia tiende a incrementarse con la edad, tal vez debido a un aumento en la tasa de alimentación, no existen diferencias en la distribución de estos parámetros entre los peces de mayor tamaño. No existe un cambio abrupto en la riqueza y abundancia de las especies parásitas que pueda indicar un cambio ontogénico de la dieta del pez en el gradiente de tallas estudiado. Seis especies del núcleo de la parasitofauna de *B. boops* han sido identificadas como especies parásitas clave en el desarrollo de las comunidades en este hospedador, ya que aparecen como comunes en todas las cohortes de tallas y representan la mayoría de los individuos.

6. Aunque las comunidades parásitas de *B. boops* resultan ricas y abundantes, no se ha encontrado ninguna evidencia de competencia interespecífica. Sin embargo, la repetitiva presencia de estructura en las comunidades a lo largo de las clases de talla/edad en *B. boops* se ha traducido en una estructura anidada al nivel más bajo (infracomunidades), dentro de la cohortes de talla. Esta estructura composicional no-aleatoria, que se ha visto repetida dentro de un estrecho rango de tallas, no es completamente atribuible a una acumulación a lo largo del tiempo, ni a una segregación de especies a lo largo de las clases de talla del hospedador.

7. El pequeño tamaño de la boca de *B. boops*, junto con su alimentación por succión, da como resultado una ingestión pasiva de presas restringidas a pequeños invertebrados suspendidos en la columna de agua. Estos actúan como hospedadores

intermediarios/paraténicos de las especies clave, así como de un grupo adicional de parásitos. Esta adición a una comunidad base de especies parásitas clave da lugar a una estructura anidada, fuertemente relacionada con una abundancia diferencial de las especies, sugiriendo así que el muestreo pasivo puede ser el mecanismo que lleva a esta estructura no-aleatoria observada en el desarrollo de las comunidades parásitas de *B. boops*.

8. Este estudio ha resultado ser el primero en aplicar la hipótesis del declive de la similitud con la distancia mediante la utilización de datos taxonómicos originales a dos niveles espaciales anidados, revelando que tanto la distancia geográfica como la región de origen afectan la composición de especies y la estructura de las faunas parásitas y comunidades componentes de *B. boops*.

9. La distancia entre localidades/regiones contribuye significativamente al declive de la similitud estimada de la abundancia de los parásitos a nivel de infracomunidad. El patrón de estructura espacial es consistente en el tiempo pero no entre estaciones. Las comunidades componentes muestreadas en primavera exhiben una fuerte estructura espacial mientras que las muestreadas en invierno no se diferencian de una distribución aleatoria. Esta falta de sincronía espacial indica una mayor homogenización de las comunidades en la estación fría.

10. La sincronía espacial observada es debida a las especies ‘núcleo’ mientras que el resto de especies exhiben una estructura espacial al azar. Esto sustenta la hipótesis de que las especies más extendidas están asociadas fuertemente con patrones de variación de las condiciones ambientales. La relación de abundancia-distribución interespecífica es reconocida como el aspecto más importante en el declive de la similitud con la distancia en el sistema de hospedador-parásito estudiado, dada la significativa correlación observada en todas las escalas analizadas.

11. El análisis comparativo revela un cambio drástico en la riqueza, abundancia y estructura de las comunidades parásitas de *B. boops* y una notable alteración de los patrones de abundancia tras el vertido, tanto a nivel individual como a nivel de grupos funcionales. Esto sugiere que es posible que las comunidades parásitas en el hospedador modelo estén reflejando el efecto en las comunidades naturales a lo largo de la costa española tras el vertido del *Prestige*.

12. Se ha detectado una tendencia direccional en la sucesión de las comunidades parásitas tras el vertido del *Prestige*. Las comunidades parásitas analizadas en el estudio piloto son drásticamente disimilares a las examinadas previamente al vertido, tanto en su composición como en su estructura. Estas diferencias han disminuido con el tiempo y la dirección del cambio composicional se acerca a la situación previa al vertido. Sin embargo, el hecho de que las diferencias sigan siendo altas puede ser debido a que se estén desplazando los niveles base, afectando la recuperación de las comunidades bentónicas y parásitas tras el vertido del petrolero *Prestige*. Otras fuentes responsables de la contaminación marina pueden estar cambiando las líneas de referencia y afectando la recuperación de las comunidades parásitas tras el vertido del petrolero *Prestige*. Esto podría estar indicando que la estructura de las comunidades parásitas registrada en 2005-2006 represente los niveles de referencia que podrían ser utilizados en caso de otro evento catastrófico en la región.

13. El enfoque basado en niveles taxonómicos y funcionales mayores proporciona una mayor resolución en la detección de tendencias direccionales en la estructura de las comunidades parásitas con respecto a dos tipos de variables de confusión ambientales (toxicidad y enriquecimiento orgánico). Los altos niveles de infección de especies monoxenas en el estudio piloto indican cambios en los parámetros inmunológicos de los peces, debido tal vez a una exposición crónica a PAHs tras el vertido. Es posible que el notable aumento de especies heteroxenas y la considerable alteración en la abundancia de hemiuroideos tras el vertido esté reflejando un aumento de las poblaciones de hospedadores moluscos, poliquetos y copépodos, debido a un enriquecimiento orgánico tras el vertido.

14. La aproximación mediante análisis estadísticos multivariantes, que facilitan una evaluación de la variación de la estructura global de las comunidades, ha resultado ser muy útil en el estudio de la respuesta de las comunidades parásitas de *B. boops* tras el vertido del petrolero *Prestige*. El acuerdo entre las dos técnicas aplicadas y la consistencia en la detección de diferencias significativas en la estructura de las comunidades (en el diseño ‘antes-después’), tanto a nivel de infracomunidad como de comunidad componente, apoya esta sugerencia.

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CHAPTER 1

INTRODUCTION

At some stage of its lifetime every living organism is probably affected by parasites (Price, 1980). The parasitic mode of life has evolved independently in organisms of different lineages (Zrzavy, 2001; de Meeûs & Renaud, 2002) and is considered one of the most successful modes of life (Poulin & Morand, 2000), parasites making up over 30% of known species diversity (de Meeûs & Renaud, 2002). Metazoan parasites (*sensu stricto*) are represented in numerous phyla spread across the entire tree of life and are estimated at more than 100,000 of the approximately 1.5 million species known to exist (Poulin & Morand, 2004). This number is probably underestimated due to the differential effort in studying the taxonomy of parasitic organisms compared with free-living ones, and the existence of large number of morphologically similar cryptic species (de Meeûs & Renaud, 2002; Poulin & Morand, 2004).

Parasites have evolved diverse and elaborate strategies of ensuring their perpetuation in diverse environments. These include the diversity of life histories, the diversity of transmission strategies and the diversity of host-parasite associations. Although at an evolutionary scale the ocean may be considered as a stable environment, it poses great obstacles to parasites largely because of the scale of the habitats, *i.e.* parasites must adapt to survive in an environment where encounter between successive hosts in the life-cycle may be periodic or even rare due to the patchy distribution and low population densities of the intermediate and definitive hosts in a dilute three-dimensional environment (Marcogliese, 2005a, 2007).

However, parasite species diversity in marine fishes is greater than in freshwater fishes (Holmes, 1990), the mean number of species per individual fish and per sample of a species of fish being estimated as *c.* twofold greater in marine compared with fresh waters (Marcogliese, 2001). One of the mechanisms generating these differences between fish parasite communities in the two aquatic environments is that in the marine environments passively transmitted parasites with complex life-cycles commonly use paratenic or transport hosts to ensure their transmission to the next host in the life-cycle (*e.g.* hemiuroid trematodes, anisakid nematodes and tetraphyllidean cestodes). The exploitation of new food web pathways by parasites *via* the capacity to use paratenic hosts is more common in marine than freshwater systems. Furthermore, parasites (both parasite individuals and

species) can accumulate in extra trophic levels consisting of large invertebrate (*e.g.* zooplankters such as chaetognaths, coelenterates and ctenophores) and fish predators which then transmit parasite species to definitive hosts as packets (Marcogliese, 2002, 2005a, 2007).

Another important adaptation to the marine realm, that might account for the higher parasite diversity in marine fishes, is the low host specificity. Low specificity is a common trait among copepod/fish intermediate hosts and even definitive hosts for numerous species (Marcogliese, 2005a) and, as a result, there are many more generalist species in marine systems.

1.1. PARASITE COMMUNITIES: EXCELLENT MODEL SYSTEMS FOR ECOLOGICAL RESEARCH

Because of the patchy or fragmented structure of most habitats ecologists work with hierarchical systems, *i.e.* those in which a unit of study at one level becomes a part of a unit at a higher level. Because different mechanisms operate at different scales (or levels of the hierarchy), the scale at which pattern is clearest can suggest what mechanisms are responsible (Holmes, 2001). Parasites provide excellent opportunities for comparative analyses of patterns of community organisation at several hierarchical levels (Holmes & Price, 1986; Bush *et al.*, 1997; Poulin, 2005), depending of the physical scale selected for the study.

The smallest scale (*i.e.* lowest level) represents the parasite *infracommunity* which comprises all of the infrapopulations of all parasite species within a single host individual. Examination of host individuals from the same host population provides census of many replicate infracommunities thus offering the opportunity for robust statistical tests at this level. At the same time, each host provides different microhabitats for the parasites so patterns can be explored at an even finer scale. The next level up represents the parasite *component community*, which comprises all of the infracommunities within a given host population at a given point in time. The component community supplies the local pool of parasites forming infracommunities. Each component community is a subset of a larger collection of species referred to as the parasite *fauna* of the host species, an artificial rather than biological entity. Parasite faunas and component communities provide the relevant scales for macroecological comparisons (Poulin, 1998; Guégan *et al.*, 2005).

1.2. PATTERNS IN PARASITE COMMUNITY STRUCTURE IN FISH HOSTS

1.2.1. Distribution of species among infracommunities

There has been an exponential increase in the studies of patterns in parasite community structure in marine fish hosts in the last decade perhaps due to the higher parasite diversity in the marine environment and the wide range of variation of parasite communities which includes a diversity of community types (Poulin, 2005). A key question has been whether infracommunities represent random samples of the component community or they are stochastic samples of the supracommunity (*i.e*. parasite communities in all potential hosts as well as free-living phases in an ecosystem, see Bush *et al.*, 1997), and component communities are merely aggregates without much ecological significance (Holmes, 1990; Guégan *et al.*, 2005; Poulin, 2005).

One approach to search for structure in parasite communities is to examine species composition of infracommunities: if it departs from that expected by chance alone then infracommunities might be structured by ecological processes (Poulin, 2005). The distribution of parasite species among infracommunities can range from completely random to highly structured. Janovy *et al.* (1995) developed a multiple-kind lottery null model of no interspecific interaction. This model is used to determine whether species density distributions observed in parasite infracommunities indicate regular occurrences of species-to-species interactions. Random structure is assumed if the probability of occurrence of any parasite species in an infracommunity is equal to its prevalence in the component community (*i.e*. host population) and totally independent of the presence of other species (Janovy *et al.*, 1995).

A basic departure from randomness has been sought in some studies focused on patterns of species co-occurrence, *i.e.* testing for positive or negative associations between species present in infracommunities (*e.g*. Poulin & Valtonen, 2001a; Vidal-Martínez & Poulin, 2003) or comparing the observed pattern of parasite occurrences with that expected under random assembly of infracommunities (*e.g.* Gotelli & Rohde, 2002). However, spurious covariances can be observed due to the effect of sample size and/or species prevalence in the component community so that associations of parasite species among

infracommunities may not reflect underlying community structure (Vidal-Martinez & Poulin, 2003; Poulin, 2005).

Testing the nested subset hypothesis of Patterson & Atmar (1986), formulated to explain patterns in community structure of insular mammal faunas, has become recently a common approach to assess the departure of observed species occurrences from an expected random pattern. The hypothesis states that the species comprising a depauperate fauna should constitute a proper subset from those in richer faunas, and that an archipelago of such faunas arranged by species richness should present a nested series. Adapted to parasite systems, a nested pattern in a parasite component community would imply that the species forming species-poor infracommunities are distinct subsets of progressively richer infracommunities (Poulin, 2005).

Nested subsets analyses have been carried out extensively on infracommunities of ectoparasites in marine fish hosts (*e.g.* Worthen & Rohde, 1996; Rohde *et al.*, 1998; Morand *et al.*, 2002) and have led to the conclusion that nestedness, *i.e.* non-random assembly patterns in assemblages of this higher-level taxonomic group, is uncommon (Rohde, 2005). Studies involving both ecto- and endoparasites in various parasite communities of marine fish populations in the Southwest Atlantic and Southeast Pacific, were carried out to assess the repeatability of parasite infracommunity structure in both space and time (Timi & Poulin, 2003; Vidal-Martínez & Poulin, 2003; González & Poulin, 2005). However, most of these studies failed to detect consistency in nested patterns when comparing communities in host populations from different localities or seasons, thus leading to the conclusion that non-random patterns in parasite communities of marine fish are both ephemeral and unpredictable (Poulin, 2005).

One different kind of community order studied in free-living organisms is core-satellite organisation (Hanski, 1982; Morand *et al.*, 2002). Hanski (1982) introduced the core-satellite hypothesis as a simple null hypothesis to explain regional rarity of the species. It predicts a bimodal distribution of organisms in their environment if stochastic variation in the rates of local extinction and/or colonisation is sufficiently large. He identified two distinct types of species: ‘core’ and ‘satellite’. Core species were defined as regionally common and locally abundant, and relatively well-spaced-out in niche space, while satellite species were said to be characterised by the opposite attributes (Hanski, 1982). In an influential study Morand *et al.* (2002) investigated the relation between the two kinds of

community structure, *i.e.* nestedness and bimodal species distribution using marine fish ectoparasite assemblages as a model system. These authors found (i) a positive relationship between the mean abundance and the variance of abundance across populations of fish ectoparasites; (ii) a positive relationship between abundance and prevalence; (iii) a bimodal pattern of parasite prevalence frequency distribution; and (iv) connection between nested patterns and the latter, *i.e.* species in more nested assemblages exhibiting unimodal prevalence distribution and on the opposite, species in less ordered assemblages exhibiting core-satellite pattern (Morand *et al.*, 2002).

One of the paradigms of parasite community ecology is the interactive *vs* isolationist classification of parasite communities, *i.e.* rich assemblages of species with high colonisation rates in which interspecific interactions play an important structuring role *vs* species-poor non-interactive assemblages (Holmes & Price, 1986; Esch *et al.*, 1990; Sousa, 1994). These are now viewed as extremes of a continuum rather than a dichotomy and this view has served as a framework to interpret the large variability observed in parasite communities (Poulin & Luque, 2003). Kennedy *et al.* (1986) and Bush (1990) suggested that helminth communities are more likely to be interactive in endothermic vertebrate hosts than in fish hosts. Poulin & Luque (2003) developed an index of interactivity based on the general likelihood of species co-occurrence, and thus on the potential for interactions, and applied it to a large data set on the gastrointestinal helminth communities of marine fish from coastal Brazil. They found that helminth communities in these fish hosts potentially span the whole spectrum from isolationist to interactive, and concluded that interspecific interactions can be important structuring forces in some parasite communities in fish. However, the existence of competitive interactions can only be truly assessed if their magnitude and direction are studied in experimental infections (Poulin, 2001). Still, no study has directly linked a non-random pattern of species co-occurrences observed in a natural endoparasite community with specific data on interspecific competition obtained from the same system (Poulin, 2005). Therefore, ‘interactive’ and ‘isolationist’ communities are nowadays mostly used in a descriptive context (Poulin, 2007).

1.2.2. Macroecological patterns

There has been a marked increase in interest in the ecology of parasite populations and communities over the last decade, and this coincides with the change of focus in

mainstream ecology to metapopulation theory, habitat fragmentation, population dynamics in fragmented habitats and macroecology (Guégan *et al.*, 2005 and references therein). In particular, the development of a more synthetic approach to understanding spatial patterns in biogeography constitutes a major challenge in the field (reviewed by Gaston *et al.*, in press). There has been a recent surge of interest in revealing macroecological patterns in host-parasite systems, which appear to provide a good parallel for detection of spatial patterns due to the 'third-order scaling' of habitat fragmentation for the parasites (Guégan *et al.*, 2005).

One such regular macroecological pattern is the species-area relationship. Several studies have attempted to use island biogeographical theory (MacArthur & Wilson, 1967) as a predictor of helminth community structure in freshwater localities (Kuris *et al.*, 1980; Kennedy, 1990). Species richness on an island is determined by the balance between the rate at which species colonise the island and the rate at which existing species become extinct. Island size and island distance hypotheses have been applied to parasite communities and host species body size, age and geographical range have been suggested as good predictors of species richness (*e.g.* Dogiel, 1964; Price & Clancy, 1983; Poulin & Morand, 2004; Guégan *et al.*, 2005). However, caution is needed due to the confounding effect of some other factors such as host phylogeny (Poulin, 1998; Poulin & Morand, 2004 and references therein).

Another macroecological pattern found recently in parasite communities is the species richness-isolation relationship, based on the dependence of species diversity on the fragmentation and isolation of habitats (Whittaker, 1998). Parasites in freshwater fish were found to exhibit patterns of similarity in composition and richness depending on the geographical distance and isolation, *i.e.* species composition and richness showed a tendency to be autocorrelated over space (Poulin & Morand, 1999). Exponential rates of decay in similarity between communities with increasing geographical distance, a pattern that has been reported in plant communities, has been studied in some host-parasite systems. Poulin (2003) observed exponential decay of similarity in the species composition of communities with distance in mammals and freshwater fish. Poulin & Morand (1999) suggested that the lack of physical barriers could make the influence of geographical distance weaker due to the exchange of parasite species. Nevertheless, recently Oliva &

González (2005) detected this non-random pattern in parasite communities in three species of marine fish.

A recent interest emerged addressing the question of the effect of the spatial scale in parasite community ecology, thus recognising that regional and historical processes can strongly affect local community structure (Price, 1980; Kennedy & Guégan, 1994; Barker *et al.*, 1996). The shape of the relationship when local richness is regressed against regional richness could indicate effects of saturation at the infracommunity level, which can be related to interaction or density/biomass dependence of some species or that communities exhibit 'proportional sampling' of the regional pool (Kennedy & Guégan, 1994, 1996; Norton *et al.*, 2004). Current knowledge on host-parasite systems indicates that both regional and local factors may have important influence on the local-regional richness relationship. Thus studies on ectoparasites of marine fish have shown that local communities are unsaturated and suggested the existence of empty niches (*e.g.* Morand *et al.*, 1999), whereas studies on endoparasites in freshwater fish observed the opposite (Kennedy & Guégan, 1994).

1.3. PROCESSES SHAPING PARASITE COMMUNITIES IN FISH HOSTS

As important as identifying the patterns in parasite community structure is to find the processes that lead to the patterns observed. Characteristics of host-parasite systems, such as the usual lack of some interactions (*i.e.* predation) and the confinement of parasites in an individual host during a specific stage, make it easier to understand some regulatory mechanisms and community structures. Conversely, the physiological and immunological interactions of parasites with their host habitats provide a new field with no parallel in free-living organisms (Bush & Aho, 1990; Poulin, 2004).

Guégan *et al.* (2005) made the important notion that macroecological patterns are not independent of each other. Thus, Morand *et al.* (2002) suggested that the non-random assembly in ectoparasite assemblages in marine fish discussed above can be explained by differential colonisation/extinction processes, also called epidemiological processes, acting at the level of the individual species. They concluded that nestedness, when it occurs, is not a result of interspecific competition but characteristics of the various species (see also Rohde *et al.*, 1998). Along this line, Guégan & Hugueny (1994) suggested that host biology

determines parasite community structure and identified fish body size as a major determinant of the non-random assembly pattern overshadowing other unpredictable variables. Overall, empirical support is yet lacking for considering interspecific competition which has received much attention and debate in parasite ecology (Poulin, 1997, 1998; 2005 and references therein) as a process that can produce non-random patterns in fish parasite communities.

Another potential structuring processes that can lead to non-random associations between species in endoparasite assemblages of marine fish is the arrival of larval stages of different parasite species at the definitive host in packets. Endoparasites are transmitted *via* food chains so that intermediate, and especially paratenic hosts, that may contain several species effectively 'transfer' structure to the fish hosts (Bush *et al.*, 1993; Lotz *et al.*, 1995). Finally, nestedness can be observed as a sampling artefact if there is variation among individual fish in the studied population in either food preference or foraging habitat (*e.g.*, Rohde *et al.*, 1998; Poulin & Valtonen, 2001b). These authors suggest that nested subset structure can be produced by an ontogenetic shift in host diet and/or habitat utilisation.

1.4. PARASITE DIVERSITY AND HOST AGE

Most hosts are born free of parasites and consequently, studies based on the development of parasite communities with age of the host offer the opportunity to study the colonization and succession processes. Comparative studies on fish host-parasite systems have revealed a positive relationship between fish size/age and parasite abundance (*e.g.* Noble *et al.*, 1963; Dogiel, 1964; Kabata, 1981; Lo *et al.*, 1998) and richness (Guégan *et al.*, 1992; Poulin, 1995; Sasal *et al.*, 1997; Lo *et al.*, 1998). Several non-mutually exclusive hypotheses have been proposed to explain the relationship between parasite richness/abundance and fish size/age: (i) island size hypothesis (related to the theory of island biogeography), *i.e.* more species can settle on larger hosts (Dogiel, 1964); (ii) accumulation hypothesis, *i.e*. increased chances of acquiring new parasite species and individuals with time (age) (Lo *et al.*, 1998); (iii) changes in food intake (both qualitative and quantitative) and habitat preferences as the fish grow (Rohde *et al.*, 1998; Poulin & Valtonen, 2001b). However, Saad-Fares & Combes (1992a) examined the abundance distributions of six trematode species in the digestive tract of six sparid fishes from the Eastern Mediterranean and demonstrated variable patterns. In some host-parasite systems

infections were present in the lowest size classes and parasites exhibited a clear tendency of increase of abundance in older fish. In other systems parasites appear after some threshold size level, young fish never being infected or infection decreased with age, older fish being rarely or never infected. These authors concluded that the age structure of fish populations has a notable influence on the distribution of parasite populations. However, studies at the host population level are still few (*e.g.* Lo *et al.*, 1998).

1.5. PARASITES AS INDICATORS OF ENVIRONMENTAL PERTURBATION

In the way parasites are indicative of the biology of their hosts including diet, migration, populational differentiation and phylogeny (Williams *et al.*, 1992) they may also be good indicators of environmental contamination (*e.g.* Sures *et al.*, 1994a, b, c). Generally, parasite transmission is impeded or altered in polluted habitats (MacKenzie *et al.*, 1995; Marcogliese & Cone, 1997). Because ectoparasites are in direct contact with the polluted water, they may well reflect any direct negative effect of a pollutant on their reproduction and survival (Khan & Thulin, 1991) or their populations may increase, the latter effect usually attributed to a compromised immune response of the host (MacKenzie *et al.*, 1995; MacKenzie, 1999; Moles & Wade, 2001; Khan, 2003). On the other hand, because many parasites have complex life-cycles, their transmission can be regulated through pollution effects on both their free-living stages and intermediate hosts (Poulin, 1992; Marcogliese & Cone, 1997; MacKenzie, 1999; Marcogliese, 2005b). Parasite communities, therefore, integrate the direct effects of toxicants on the individual species and the indirect effects mediated *via* impacts of pollution on different components of the food web and the structure of the local animal community.

Because assemblages of metazoan parasites in fish may provide information on the dynamics of altered food webs (*e.g.* Cone *et al.*, 1993) a number of studies have been undertaken to assess the effects of anthropogenic impacts on parasite communities (reviewed in MacKenzie *et al.*, 1995; Williams & MacKenzie, 2003; Sures, 2004; and Marcogliese, 2005b). However, community-level analyses have only rarely been attempted and then predominantly carried out in freshwater ecosystems (Valtonen *et al.*, 2003; Sures, 2004 and references therein).

1.6. 'NON-RANDOM' SELECTION OF THE STUDY SYSTEM

The studies on fish parasites in the Mediterranean and North East Atlantic, initiated by Müller in the 18th, Century were carried out actively during the 19th Century by an extremely productive group of taxonomists (G.M.R. Levinsen, A. Looss, M.V. Lebour, E. Lönnberg, L. Molin, F.S. Monticelli, W. Nicoll, T. Odhner, P. Olsson, C.A. Rudolphi, M. Stossich and P.J. Van Beneden). These studies have resulted in the description of a substantial number of species parasitizing marine fish. This was followed by a long time gap before a determined effort was made in the 20th Century towards clarifying the position of many of the species in the early descriptions, description of new forms in the region and the development of a taxonomical framework for studying the diversity of fish parasites (P. Bartoli, L. Paggi, P. Orecchia, D.I. Gibson, R.A. Bray, J.P. Trilles, L. Euzet, M. Køie, S. Mattiucci). A number of parasite inventory studies have been carried out especially on Mediterranean fish (*e.g.* Sey, 1968; 1970; López-Román & Guevara Pozo, 1973, 1974; Papoutsouglou, 1976; López-Román & Guevara-Pozo, 1977; Orecchia & Paggi, 1978; Fischthal, 1980; Renaud *et al.*, 1980; Fischthal, 1982; López-Román & De Armas Hernández, 1989; Radujkovic & Raibaut, 1989; Radujkovic *et al.*, 1989; Anato *et al.*, 1991; Le Pommelet *et al.*, 1997; Bartoli *et al.*, 2005). The two lines of research have provided an overall sound taxonomic and faunistic basis for the development of ecological studies on marine fish parasites.

However, studies on parasite communities have flourished in areas with relatively poor or just recent taxonomic background (*e.g*. Southwest Atlantic, East Pacific and Southeast Pacific) and are virtually lacking in the Mediterranean and North East Atlantic. Thus, few studies have been conducted in the Mediterranean, focused on disparate subjects such as the determinants of parasite species richness (Sasal *et al.*, 1997; Desdevises, 2006); the structure of parasite communities in *Sciaena umbra* (Holmes & Bartoli, 1993) and trematode assemblages in sparid and labrid fishes off Corsica (Sasal *et al.*, 1999); the distribution of trematodes in relation to fish social rank in the labrid *Symphodus ocellatus* off Corsica (Bartoli *et al.*, 2000); and on specific topics such as the usefulness of parasites for distinguishing harvest location of fish and the problem of pseudoreplication in studies using parasites as tags for discrimination of fish populations (Power *et al.*, 2005; Ferrer-Castéllo *et al.*, 2007).

Rohde (2005) stated that "Authors tend to select systems for hypothesis testing not at random but only those for which expected effects are likely". Although the account above suggests that any host-parasite system with Mediterranean-Atlantic distribution would be appropriate (*i.e.* would provide novel data on parasite community patterns), the model host in the present study was not selected 'at random'. First, a host was sought whose biology and especially diet would provide a setting for the development of rich and diverse parasite communities. Secondly, a host was sought that forms abundant populations that may sustain abundant local parasite populations. Thirdly, a non-migratory species of host was sought with both Mediterranean and North East Atlantic distribution that exhibits site fidelity, which would help reveal regional patterns of variations in parasite community composition and structure. Fourthly, to ensure straightforward parasite identification, a host was sought with well-studied fauna in the region of study.

The non-migratory *Boops boops* (Teleostei: Sparidae) fulfils these requirements due to its wide distribution and abundant populations in both the Mediterranean and North East Atlantic (Valle *et al.*, 2003; Boyra *et al.*, 2004). Its intermediate trophic position and omnivorous diet would ensure the development of rich and diverse parasite communities. On the other hand, its site fidelity indicates that parasite communities would reflect the structure of local food webs and, therefore, allow meaningful comparisons at a larger geographical scale.

The parasite fauna of *B. boops* is relatively well studied in the Mediterranean, where large samples of fish have been investigated (Renaud *et al.*, 1980; Saad-Fares, 1985; Anato *et al.*, 1991) as opposed to the North East Atlantic situation (Power *et al.*, 2005). In its distributional range, *B. boops* hosts a relatively large number of metazoan parasites with different transmission strategies which utilise it as both an intermediate and a definitive host.

Finally, in a study using parasite communities as predictors of harvest location of fish (Power *et al.*, 2005), a large sample of *B. boops* was collected in 2001 from the North East Atlantic coasts of Spain. This sample provided the unique opportunity to assess the changes in parasite communities in this fish after the oil-spill which occurred a year later, on November 13th 2002, when the tanker *Prestige* sank over the Galician Bank and

released *c.* 60.000 tons of crude oil, creating an unprecedented ecological disaster along the Galician and Cantabrian coasts of Spain.

The detailed assessment of the metazoan parasite fauna in *B. boops* along the Spanish coasts of the Western Mediterranean and North East Atlantic carried out in the present study, provided a large taxonomically consistent dataset comprising three levels of parasite community organisation (*i.e.* infracommunities, component communities and local faunas) and allowed the following questions regarding the structure of parasite communities in the model host-parasite system to be addressed:

- What constitutes the parasite fauna of *B. boops* in the Mediterranean and North East Atlantic?
- Is the structure of parasite infracommunities repeatable and predictable or is it a product of the independent and random infection of host individuals by parasites? Are there recognisable patterns of parasite community development associated with hosts size/age?
- Are there spatial/temporal variations in parasite community structure? Is there a link between community compositional patterns and the relationship between the spatial distribution and local abundance of parasites?
- Is it possible to detect changes that could be related to oil-spill pollution using parasite communities in *B. boops*?

CHAPTER 2

AIM AND OBJECTIVES

2.1. AIM

The aim of the study is two-fold: (i) to provide a better understanding of the parasite diversity, and the composition and structure of parasite communities in the marine sparid teleost, *Boops boops*, along the Mediterranean and Atlantic coasts of Spain; and (ii) to attempt a parasite community approach to assessing the effects of the *Prestige* oil-spill on coastal communities in selected localities on the Atlantic coasts of Spain.

2.2. OBJECTIVES

2.2.1. An exhaustive revision of the metazoan parasite fauna of *B. boops* from the Western Mediterranean and North East Atlantic coasts of Spain. Identification of the parasites on the basis of a detailed morphological and taxonomical study. Compilation of a complete checklist of parasites of *B. boops* throughout its distributional range.

2.2.2. An evaluation of the effect of host size on the development of parasite communities in *B. boops*. Examination of the patterns of composition and structure of parasite communities along a gradient of fish sizes and identification of the underlying processes.

2.2.3. An assessment of the geographical and temporal variations in parasite community composition and structure. Test of the hypothesis of the decay of similarity between communities with distance using original, taxonomically consistent data at two nested spatial scales (parasite faunas and component communities). Test for synchrony in seasonal patterns of community similarity-distance relationship. Evaluation of the importance of species abundance-distribution relationships and identification of the parasite species that contribute substantially to the observed patterns.

2.2.4. A comparative study, in a ‘before-after’ design, on the structure and composition of metazoan parasite communities in *B. boops* from selected impacted localities on the North East Atlantic coast of Spain after the *Prestige* oil-spill in 2002. Evaluation of the importance of the individual parasite species and larger functional groupings in the detection of directional trends in community composition and structure that could be related to the oil-spill.

CHAPTER 3

GENERAL MATERIALS AND METHODS

3.1. MODEL FISH

The bogue *Boops boops* (L.) (Teleostei: Sparidae) is distributed along the Mediterranean and Eastern Atlantic, from Norway to Angola, being common from Bay of Biscay to Gibraltar. It is also found in the Black Sea and in the Western Atlantic, in the Gulf of Mexico and Caribbean Sea. *B. boops* is a gregarious demersal to semipelagic non-migratory species, mostly occupying the water column (Harmelin, 1987). Bogue is found on the shelf of the coastal pelagic at a depth range 0-350 m on various bottoms such as rocks, *Posidonia* beds, mud and sand (Bauchot & Hureau, 1986; García-Rubies & Zabala, 1990; Valle *et al.*, 2001; Sánchez-Jerez *et al.*, 2002; Valle *et al.*, 2003), where it forms erratic schools with a diurnal activity and juveniles are found near the coast, at least in summer (Girardin, 1981).

B. boops possesses an elongate-fusiform body, dark blue on the top and silvery on the sides, with 3 to 5 golden lines and a black spot at the base of the pectoral fin. Bogue exhibits external body characteristics typical of planktivorous fishes such as large eyes, short snout and oblique mouth, that seem to be adaptations to feed on tiny organisms (Hobson, 1991) (Figure 3.1.). *B. boops* has only one row of short vertically disposed incisor-like teeth.

Figure 3.1. The bogue, *Boops boops* (L.).

Pectoral fins are short, ending before the anus. Bogue can reach 36 cm in total length but the usual range is 15-20 cm (Bauchot & Hureau, 1986). It is protogynous with an hermaphrodic stage occurring mostly in fish of 10-24.5 cm total length (Girardin, 1981; Erzini *et al.*, 2001). In the Gulf of Lyon bogue attains maturity at 13 cm total length (2 years-old) and its fecundity was found to increase exponentially (Girardin, 1981). Spawning occurs between March and May depending on the latitude.

A number of studies on the size-age relationship in *B. boops*, mostly carried out in the Mediterranean, exist (Navarro & Navaz, 1946; Vidalis, 1950; Andreu & Rodríguez-Roda, 1951; Matta, 1958; Zúñiga, 1967; Mouneimné, 1978; Romestand, 1978; Girardin *et al.* 1985; Anato & Ktari, 1986; Girardin & Quignard, 1986; Alegria-Hernández, 1989; Livadas, 1989; Gordo, 1996; El-Haweet *et al.*, 2005; Khemiri *et al.*, 2005). These studies have shown different growth rates in different localities in the Mediterranean and Atlantic, which complicates age determination. Estimation of age, when used in the present study, is based on data by Zúñiga (1967) from a bogue population off Castellón.

B. boops exhibits an intermediate trophic level. Bell & Harmelin-Vivien (1983) considered it to be *2*.5 for adult *B. boops* and Sánchez-Velasco & Norbis (1997) estimated it as 2.97 for the larval stages. Similar results (2.53 - 3.30) were obtained by Sterigiou & Karpouzi (2002), who considered that bogue attains its maximum trophic level early in the life span and reported no significant alteration of the trophic level with size/age (Stergiou & Karpouzi, 2002; Karpouzi & Stergiou, 2003). A part of the cetaceans, main predators of *B. boops* are *Seriola dumerili, S. rivoliana, Trachurus trachurus, T. mediterraneus, Merluccius merluccius, Phycis phycis, Sarda sarda, Scorpaena scrofa, Serranus cabrilla , S. hepatus, Sphyraena viridensis, Synodus saurus, Xiphias gladius* and *Zeus faber* (Froese & Pauly, 2007 and references therein). Marine fish-eating birds feeding on discards also consume *B. boops* (Martínez-Abraín *et al.*, 2002).

Although the bogue is perhaps one of the most abundant species in both the Mediterranean and the North East Atlantic (Girardin, 1981; Valle *et al.*, 2003; Boyra *et al.*, 2004; Froese & Pauly, 2007), data on its feeding habits are scarce and somewhat ambiguous. Thus, Bell & Harmelin-Vivien (1983), who considered *B. boops* to be microphagic carnivores, found that juveniles normally feed high in the water column but on occasions descend to browse on algae within the seagrass canopy. They recorded fairly large quantities of algae eaten by juveniles, whereas Bauchot & Hureau (1986) considered that juveniles are mostly carnivorous and adults mostly herbivorous. Harmelin (1987) classified *B. boops* as planktophagus, Linde *et al.* (2004) as suction feeding secondary planktivores, Karpouzi & Stergiou (2003) as omnivores, and Stergiou & Karpouzi (2002) as omnivorous with a preference for plant material but also feeding on a wide range of invertebrates. Finally, Fernández *et al.* (2001) suggested that *B. boops* is mainly

herbivorous whereas Ruitton *et al.* (2005) have shown that grazing on algae by bogue only occurs in the post-spawning period.

Bogue is often associated with fish farms (Boyra *et al.*, 2004; Dempster *et al.*, 2002). It is usually caught accidentally and is consistently present in large numbers in discarded fish of Spanish and Portuguese fisheries because of its low economic value (Borges *et al.*, 2001; Martínez-Abraín *et al.*, 2002; Borges & Erzini, 2003; Sánchez *et al.*, 2004). Bogue is mostly used in aquaculture as food for *e.g. Octopus vulgaris* (García-García & Aguado-Giménez, 2002; Socorro *et al.*, 2005), *Thunnus thynnus* (Vita *et al.*, 2004) and *Dicentrarchus labrax* (Navas *et al.*, 1998).

3.2. FISH SAMPLES

B. boops were collected by local fishermen at harvest locations close to seven ports along the Mediterranean and Atlantic coasts of Spain; henceforth port names will be referred to as localities. A total of 22 samples comprising 805 fish was collected during 2001, 2005-2007 (Table 3.1.) from the North East (NE) Atlantic [off Ondarroa (Basque Country), Vigo and Malpica (Galicia) and Barbate (Cádiz)] and from the Mediterranean [Santa Pola (Valencian Community) and Barcelona (Catalonia)] (see map in Figure 3.2.). Two additional single samples (not shown in Table 3.1.) were collected: (i) off Valencia (13 November 2003, n=33) and off Malpica (12 May 2004, n=30). The specific materials used in each study are described in Materials & Methods sections of the corresponding chapters (see Chapters 5-8).

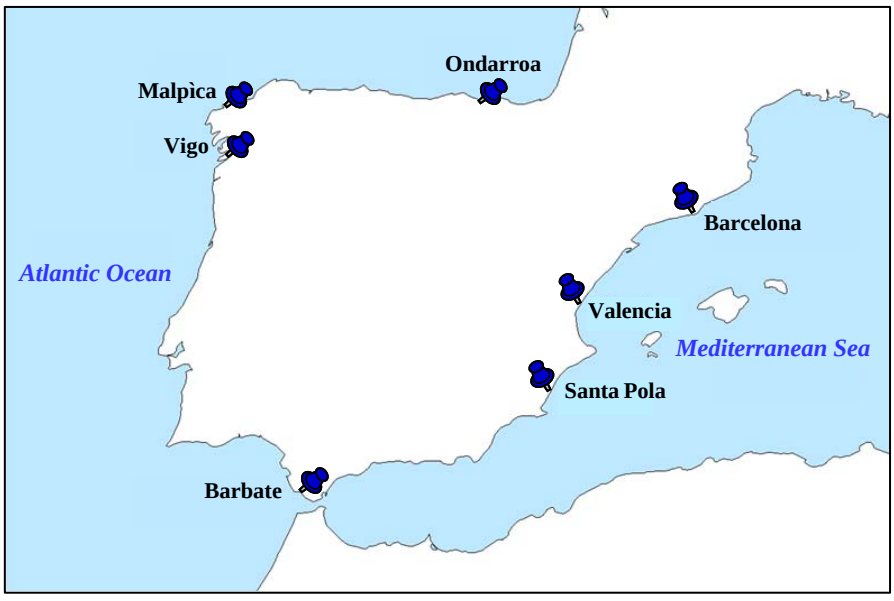

Figure 3.2. Map of Spain indicating the sampling localities.

Fish were usually caught as by-catch by different methods (*e.g.* traditional purse seine and bottom trawling) and this complicated the sampling. Fish, transferred on ice to the laboratory, were measured [total length (TL, cm), standard length (SL, cm), weight (W, g)], labelled, and packed individually before being frozen at -20°C.

Table 3.1. Samples of *B. boops* examined for parasites in the present study.

	First Sampling	**Second Sampling**	**Third Sampling**
NE Atlantic			
Ondarroa	6 June 2001 (n=30)	21 June 2005 (n=30)	-
Malpica	27 November 2001 (n=30)	24 May 2005 (n=32)	-
		24 November 2005 (n=42)	
Vigo	18 May 2001 (n=30)	11 May 2005 (n=50)	14 June 2006 (n=34)
		11 November 2005 (n=40)	20 December 2006 (n=39)
			10 January 2007 (n=20)
Barbate	-	27 June 2005 (n=30)	-
		21 February 2006 (n=30)	
Mediterranean			
Santa Pola	-	07 June 2005 (n=131)	21 June 2006 (n=29)
		1 March 2006 (n=35)	19 February 2007 (n=30)
			8 March 2007 (n=20)
Barcelona	-	22 June 2005 (n=30)	-
		8 November 2005 (n=30)	

3.3. PARASITE COLLECTION

Parasites were collected according to a standardised protocol. A sub-sample of fresh fish (5-10 fish) was examined from at least two samples per locality to obtain live parasite material for precise species identification. The remaining fish was frozen for later examination. The body surface and mouth of the fish were examined and an external body wash was collected before dissection. Fish were dissected and an internal body wash was obtained after the removal of all organs. Gills were removed, placed in saline solution and gill arches were examined separately. The intestinal tract was divided into four parts (oesophagus, stomach, pyloric caeca, and intestine) which were examined separately. Each was opened longitudinally and the contents scraped in saline solution. The heart, liver,

spleen, kidney, gonads and brain were separated and pressed between glass plates. Pectoral muscles were also examined under high magnification for the presence of encysted metacercariae. This procedure was accepted after the total examination of musculature in a large sample revealed the absence of nematode larvae.

Metazoan parasites recovered from fresh or frozen fish were fixed and stored in 70% alcohol. Trematodes, monogeneans and acanthocephalans were stained with iron acetocarmine (Georgiev *et al.*, 1986), dehydrated through an alcohol series, cleared in dimethyl phthalate and examined as permanent mounts in Canada balsam. Nematodes, larval cestodes and copepods were identified on temporary mounts in saline solution or glycerine and isopods were examined in saline solution. Measurements were taken from illustrations, made using a drawing apparatus at high magnification. All measurements are in micrometres.

All metazoan parasites were identified and counted. The type-material of *Wardula bartolii* Pérez-del-Olmo, Gibson, Fernández, Sanisidro, Raga & Kostadinova, 2006 is deposited at the Natural History Museum, London, UK. Voucher material is deposited at the Natural History Museum, London and the Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Spain.

Parasite life-cycle and host specificity data were compiled from an exhaustive search of literature sources and both the Host-Parasite Database (http://www.nhm.ac.uk/research-curation/projects/host-parasites/database/) and the Host-Parasite Catalogue compiled by the Natural History Museum, London.

3.4. STATISTICAL ANALYSES

Data were gathered at two hierarchical community levels: **infracommunity,** *i.e.* a community of parasite populations in a single host individual and **component community,** *i.e.* infrapopulations of all species in a host population sample in a given locality at a particular time. The measures of parasite infection referred in this study are: **prevalence**, which is the number of fish infected divided by the number of fish examined, expressed as a percentage, and **mean abundance**, which is the total number of individuals of a particular parasite species divided by the total number of fish examined (see Bush *et al.*, 1997).

Species with a prevalence of >30% will be referred to henceforth as common, those with a prevalence of ≤30% as rare and those with prevalence < 10% as accidental.

Due to the overall aggregated distribution of the data, non-parametric tests [Spearman rank correlations (r_s), Mann-Whitney (M-W) and Kruskall-Wallis (K-W) tests] were applied for statistical comparisons. Using a Bonferroni correction in *post hoc* tests, following the main analysis, more conservative values (data in text) were taken to indicate significance of pairwise comparisons. Where parametric tests were used, parasite abundance data were ln (x+1) transformed (Sokal & Rohlf, 1995). Prevalences were compared with Fisher's exact test. Analyses were carried out using SPSS ®14.0 (SPSS Inc., Norušis, 2002) and the programme Quantitative Parasitology (QP1.0, Rózsa *et al.*, 2000).

Specific analyses were carried out using a battery of programs: PRIMER v6 software (Clarke & Gorley, 2006); Nestedness temperature calculator (Atmar & Patterson, 1995); PAUP* 4.0 beta (Swofford, 2002); and RT 2.1 program (Western EcoSystems Technology, Inc., Cheyenne, Wyoming). The specific applications are described in Materials & Methods sections of the corresponding chapters (see Chapters 5-8).

CHAPTER 4

THE PARASITE FAUNA OF *B. BOOPS*

4.1. INTRODUCTION

The present study has revealed a much higher diversity of the parasite fauna of *B. boops* than previously known. One species new to science of the mesometrid genus *Wardula*, *W. bartolii* Pérez-del-Olmo *et al.*, 2006, was described (Pérez-del-Olmo *et al.*, 2006) which represents only the third record of the genus outside the Mediterreanean area (see Gijón-Botella & López-Román, 1989, 1996). Furthermore, *B. boops* is a new host record for 26 species.

A total of 54,032 metazoan parasites belonging to 53 species was recovered from the 805 *B. boops* collected from the 7 localities along the NE Atlantic (NEA) and the Western Mediterranean (WM) coasts of Spain. Of these, 34 are transmitted *via* food ingestion (with the dominance of trematodes) and 36 exhibit low specificity (generalist parasites). Detailed data on the infection parameters of each species in the 22 seasonal samples are presented in Appendices 1-4. Due to space limitation, this chapter includes only the description of the new species, detailed morphological redescriptions of 9 digenean species and documented records of a further 19 species found for the first time in *B. boops*. Three of the described species were initially suspected to represent either new species (*Robphildollfusium martinezgomezi* López-Román, Gijón-Botella, Kim & Vilca-Choque, 1992) or new host records [*Lepocreadium album* Stossich, 1890 and *Steringotrema pagelli* (van Beneden, 1871) Odhner, 1911]. However, detailed comparisons or subsequent retrieval of difficult to obtain references have shown the opposite. The inclusion of redescriptions of these species gives an opportunity to provide more information on the influence of the host on parasite morphology and development. *B. boops* represents the first intermediate host record for *Stephanostomum euzeti* Bartoli & Bray, 2004, recently described from the Mediterranean (see Bartoli & Bray, 2004).

As a result of the study, a complete checklist of parasites of *B. boops* throughout its distributional range [including all records additional to those published by Pérez-del-Olmo *et al.* (2007a)], comprising summarised information for 78 species and 365 host-parasite-area records, was compiled. A host-parasite/life-cycle database for further use in ecological analyses was also constructed from an exhaustive search of literature sources and both the Host-Parasite Database (http://www.nhm.ac.uk/research-curation/projects/host-parasites/database/) and the Host-Parasite Catalogue compiled by the Natural History Museum, London.

4.2. DESCRIPTION OF A SPECIES NEW TO SCIENCE

Class Trematoda Rudolphi, 1808

Family Mesometridae Poche, 1926

Genus *Wardula* Poche, 1926

***Wardula bartolii* Pérez-del-Olmo, Gibson, Fernández, Sanisidro, Raga & Kostadinova, 2006**

Prevalence: 3.3-30.0%.

Mean abundance: 0.03- 2.87.

Localities and dates of collection: NEA (off Ondarroa: 6.vi.2001, 20.vi.2005; Malpica: 12.v.2004, 23.xi.2005, 24.v.2005; Vigo: 18.v.2001, 10.vi.2005, 11.xi.2005, 14.vi.2006, 20.xii.2006, 10.i.2007).

Material studied

Specimens from *Boops boops* L. (type-host). Rectum. NE Atlantic coasts of Spain: off Malpica, Galicia (type-locality) (12.v.2004); Vigo, Galicia (18.v.2001); and Ondarroa, Basque Country (6.vi.2001).

Type-material: Holotype BMNH 2005.4.18.1; paratypes BMNH 2005.4.18.2-13, 2005.4.18.14-15.

Etymology: The new species is named for Professor Pierre Bartoli, Centre d'Océanologie de Marseille, in recognition of his major contribution to the morphology, taxonomy, life-history studies and evolution of the Mesometridae.

Description (Figures 4.1., 4.2.)

Based on 16 whole-mounted adult specimens; metrical data in Table 4.1. Body elongate, fusiform, with rounded extremities and maximum width in posterior third of body. Anterior part of body slightly narrower than and delineated from reminder of body by shallow constriction (Figure 4.1.), somewhat leaf-like and concave ventrally (concavity referred to as 'attachment organ' by Bartoli & Gibson, 1989). Tegument armed with very fine spines, observed in only few specimens as they are readily lost in fixed material. Numerous

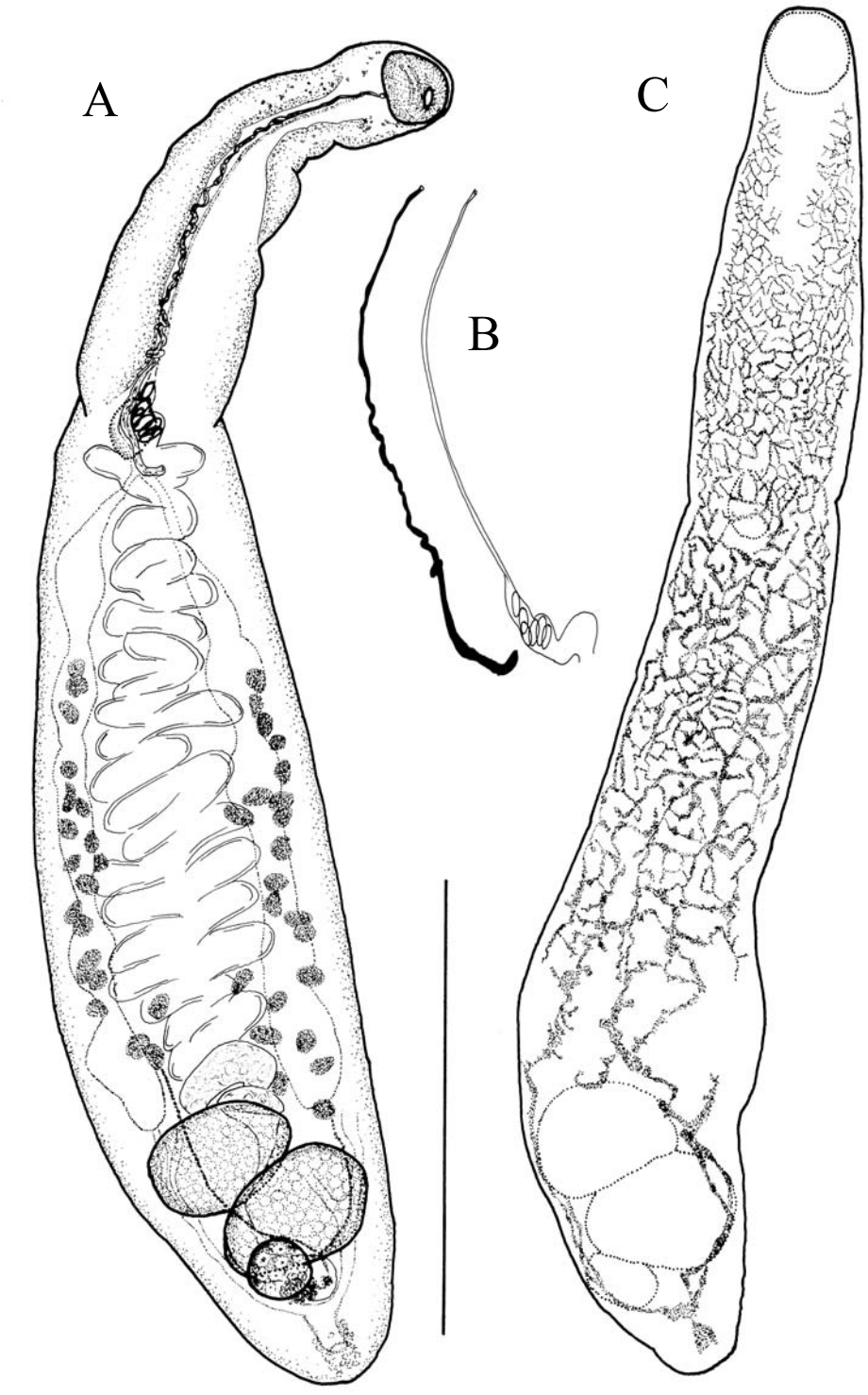

Figure 4.1. *Wardula bartolii* n. sp. ex *Boops boops*. A, Holotype, ventral view, anterior end twisted to one side partly obscuring 'attachment organ'. B, Terminal regions of male (left) and female ducts illustrated separately (uterus usually obscured by male duct). C. Excretory system. *Scale-bar*: A,C, 1000 µm.

eye-spot pigment granules dispersed in parenchyma of prepharyngeal region. Small pre-oral lobe, clearly seen in lateral view, present in most specimens. Oral sucker ventrally subterminal, subspherical, with buccal ridges furnished with blunt sclerotised denticles which appear to form 1 or 2 transverse arches in ventral view (Figure 4.2A,B). Ventral sucker absent.

Prepharynx very long (30-38% of body length), narrow, with thin wall, difficult to see. Pharynx ('oesophageal bulb') subconical, with wide lumen, enlarged to form bulb posteriorly (Figure 4.2C); inner wall sclerotised, transparent, linked to prepharynx through relatively thick projection forming tulip-like structure at junction between pharynx and prepharynx; this structure consists of 6 pieces whose lateral margins merge at mid-level of pharynx (Figure 4.2C); outer layers of pharyngeal wall comprised of fine circular muscle fibres covering layer of inner longitudinal muscles with rugged appearance. Two groups of small gland-cells surround anterior and posterior extremities of pharynx (Figure 4.2C). Oesophagus absent. Intestinal caeca 2, relatively narrow but swollen posteriorly in most specimens, end blindly close to anterior margin of anterior testis; anteriorly oriented diverticula absent.

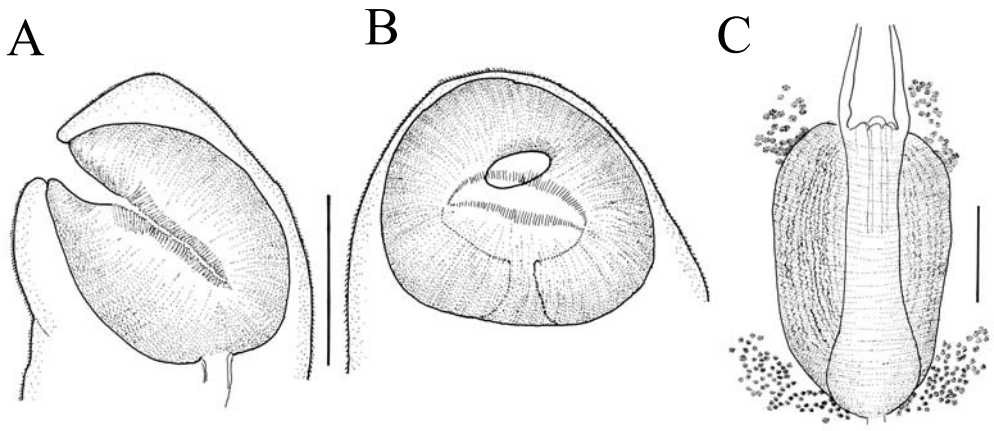

Figure 4.2. Wardula bartolii n. sp. ex *Boops boops*. A, Oral sucker, ventral view. B, Oral sucker, lateral view. C, Pharynx. *Scale-bars*: A,B, 200 µm; C, 100 µm.

Testes 2, round to transversely-oval, tandem to somewhat oblique, contiguous in posterior quarter of body. Cirrus-sac absent. Long, tubular, convoluted seminal vesicle free in parenchyma, difficult to distinguish, extends from about level of intestinal bifurcation to about anterior third of attachment organ. Pars prostatica indistinct; prostatic sac (terminology of Bartoli & Gibson, 1989) absent. Ejaculatory duct difficult to distinguish.

Genital pore mid-ventral, at level of posterior margin of oral sucker.

Ovary entire, transversely elongate-oval, contiguous with posterior testis or separated from it by loop of uterus. Mehlis' gland similar in size to ovary, contiguous with and dorsal to postero-dorsal to ovary. Uterine seminal receptacle present just anterior to testes. Uterus forms small loop ventral or slightly posterior to ovary and fills inter-caecal region of body between level of anterior testis and pharynx. Metraterm not observed. Vitellarium in 2 lateral fields of relatively small number (see Table 4.1.) of large follicles; fields mostly ventral to caeca and extend between anterior testis and some distance posterior to pharynx (Figure 4.1A). Eggs numerous, operculate, large and rather elongate.

Excretory system reticular (Figure 4.1B). Excretory pore wide, dorso-subterminal.

Remarks

The material described above belongs to the Mesometridae Poche, 1926 because of the absence of a ventral sucker and cirrus-sac, the presence of an accessory attachment organ and the reticulate excretory system (see Bartoli & Gibson, 1989). It shows affinity to the Wardulinae Paggi & Orecchia, 1964 with respect to the structure and distribution of vitellarium and the position of the testes (see Paggi & Orecchia, 1964; Bartoli & Gibson, 1989).

The worms described here exhibit similarities with both known species of *Wardula*, *i.e. W. capitellata* (Rudolphi, 1819) and *W. sarguicola* Bartoli & Gibson, 1989, but in different combinations of features. They resemble *W. sarguicola* in body dimensions and the slight extension of the uterus posterior to the ovary. However, the body of *W. bartolii* appears more robust, with a much wider attachment organ which represents a larger proportion of body length; and the oral sucker and pharynx are larger, the latter also being situated more posteriorly. Furthermore, the gonads of the specimens studied are distinctly transversely elongate (versus subspherical) and located more posteriorly, the vitelline fields overlap the caeca ventrally (versus intercaecal in *W. sarguicola*), a prostatic sac is absent, the genital pore is located at the level of the posterior margin of the oral sucker (versus well posterior to this level) and the eggs are distinctly larger (mean 84 × 40 versus 71 × 28 μm; see Table 1 for metrical data).

W. bartolii appears more closely related to *W. capitellata,* especially in the presence of buccal ridges with sclerotised denticles inside the oral sucker, the posterior location of the testes and ovary which are also contiguous, the distribution of the vitelline follicles and the location of the genital pore at the level of oral sucker. The new species can be

distinguished from this form, which has only been recorded from *Sarpa salpa* in the Mediterranean, in its distinctly smaller body (well outside the range for *W. capitellata*), resulting in the smaller dimensions (both ranges and means) for most features (*e.g.* lengths of prepharynx and both pre- and post-pharyngeal body-regions, size of gonads, etc.; see Table 4.1.). The attachment organ of *W. bartolii* is shorter and wider in relation to body length, and is not as muscular as that described for *W. capitellata* (see Bartoli, 1987a). Furthermore, the caeca lack anterior diverticula, and the more anteriorly located pharynx exhibits a peculiar sclerotised structure of the inner lining.

The peculiar inner structure of the oral sucker, *i.e.* the multidenticulate ridges which appear common in mesometrids (but see Bartoli & Gibson, 1989), has been interpreted by Bartoli (1987a) as a formation adapted to the intestinal microhabitat of the parasites (*i.e.* acting as a microfilter for an intestinal chyme dominated by algal fibres in the herbivorous *Sarpa salpa*). It is possible that the tulip-like sclerotised oesophageal structure we observed in *W. bartolii* is also related to preventing the entrance of plant material into the intestinal caeca.

4.3. SPECIES DESCRIPTIONS AND NEW HOST RECORDS

Class Trematoda Rudolphi, 1808

Family Acanthocolpidae Lühe, 1906

Genus *Stephanostomum* Looss, 1899

***Stephanostomum cesticillum* (Molin, 1858) (metacercaria)** (Figure 4.3.)

Prevalence: 3.3-76.5%.

Mean abundance: 0.05-9.41.

Localities and dates of collection: NEA (off Malpica: 12.v.2004, 24.v.2005, 23.xi.2005; Vigo: 10.vi.2005, 11.xi.2005, 14.vi.2006, 20.xii.2006, 10.i.2007; Barbate: 27.vi.2005); WM (off Santa Pola: 19.ii.2007).

Table 4.1. Comparative table for metrical data (in micrometres) of *Wardula* spp. * Estimated from published data (range, mean). ** Calculated from published drawing.

Species	***W. bartolii* n. sp.**		***W. capitellata* (Rudolphi, 1819)**		***W. sarguicola* Bartoli & Gibson, 1989**	
Host	***Boops boops***		***Sarpa salpa***		***Diplodus sargus***	
Locality	NE Atlantic (off Malpica, Spain)		Mediterranean (Scandola Nature Reserve, Corsica)		Mediterranean (Scandola Nature Reserve, Corsica)	
Source	Present study		Bartoli (1987a)		Bartoli & Gibson (1989)	
	Range	**Mean**	**Range**	**Mean**	**Range**	**Mean**
Body length	3,140-5,034	3,897	6,481-8,713	7,359	2,231-4,038	3,060
Body width at:			744-999	861	319-638	468
attachment organ	500-940	680				
posterior body	561-982	736				
Pre-oral lobe length	9-44	15	-	-	-	-
Oral sucker	167-289 × 149-298	223× 223	160-277 × 187-288	204 × 217	98-165 × 93-173	132 × 137
Prepharyngeal region length	1,052-1,859	1,330	2,550-3,549	2,877	511-1,169	839
Postpharyngeal region length	2,000-2,999	2,422	3,549-5,249	4,501	1,412-2,933	2,063
Prepharynx length	833-1,535	1,096	2,252-3,188	2,646	506-999	735
Pharynx	128-228 × 93-162	170 × 121	133-213 × 85-133	172 × 111	109-152 × 76-96	126 × 85
Anterior testis	219-360 × 267-517	279 × 368	336-533 × 384-533	434 × 470	245-394 × 245-378	291 × 300
Posterior testis	226-351 × 267-482	294 × 354	336-533 × 384-480	438 × 434	229-362 × 213-368	292 × 285
Prostatic sac	Absent	-	Absent	-	109-239 × 63-100	167 × 81
Ovary	96-197 × 104-219	150 × 147	203-256 × 165-240	229 × 214	144-213 × 149-213	175 × 179
Mehlis' gland	70-140 × 75-175	101 × 122	-	-	-	-
No. of vitelline follicles per field (right, left)	14-30, 11-20	21, 17	-	-	30 in total	-
Eggs (n=41)	75-94 × 33-47	84 × 40	72-85 × 30-43	77 × 39	65-78 × 24-35	71 × 28
Attachment organ length	1,131-1,745	1,427	-	-	630-960	764
Pretesticular field	2,438-4,192	3,087	-	-	1,470-2,550	1,913
Posttesticular field	184-406	317	-	-	309-1,039	571
Postovarian field	145-351	249	149-352	253	171-656	336
Attachment organ as % of body length	33.2-43.9	36.8	39.3-40.7* 41.5**	39.1*	22-29	25
Pretesticular field as % of body length	76.5-83.3	79.1	83.4**	-	61-65	63
Prepharynx as % of body length	29.9-37.6	34.0	39.3-40.7* 38.4**	39.1	-	-
Attachment organ width as % of body length	12.0-23.0	17.7	11.9**	-	-	-
Posterior end of pharynx to anterior testis	1,272-2,149	1,608	2,447-3719	3,018	-	-
Anterior end of anterior testis to posterior body end	684-991	821	1,084-1,594	1,294	-	-

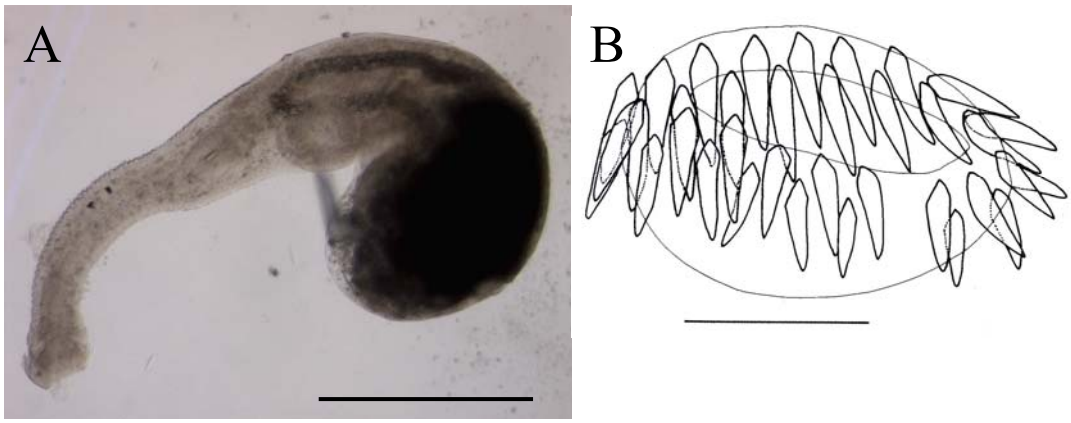

Figure 4.3. *Stephanostomum cesticillum* (Molin, 1858) Looss, 1899 (metacercaria) ex *Boops boops*. A, Ventro-lateral view. B, Crown of circumoral spines, ventral view. *Scale-bars*: A, 500 µm; B, 100 µm.

Stephanostomum euzeti **Bartoli & Bray, 2004 (metacercaria)**

Prevalence: 11.4-46.7%.

Mean abundance: 0.03- 1.28.

Localities and dates of collection: NEA (off Barbate: 27.vi.2005, 21.ii.2006); WM (off Santa Pola: 07.vi.2005, 01.iii.2006, 21.vi.2006; Barcelona: 22.vi.2005, 07.xi.2005).

Material studied

Three specimens from *Boops boops* L. Pectoral muscle. Mediterranean coast of Spain: off Burriana (9.vi.2005); off Santa Pola (7.vi.2005). Voucher material BMNH 2006.3.14.2.

Description (Figure 4.4.)

Body 2,660-3,314 long, with width of 478-641 at level of ventral sucker and 654-962 at mid-level of excretory vesicle, narrows noticeably at level of prepharynx to 234-238. Tegument covered with large spines except in region just posterior to oral sucker;

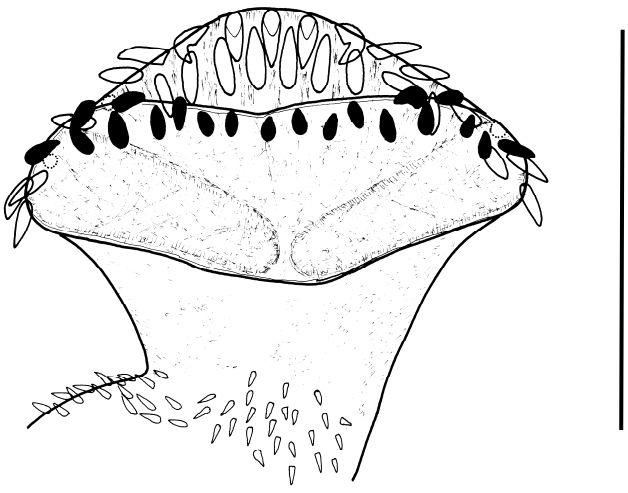

Figure 4.4. *Stephanostomum euzeti* Bartoli & Bray, 2004 metacercaria ex *Boops boops*. Anterior end, ventral view. Ventral row of spines in black; position of missing spines indicated with dotted circles. *Scale-bar*: 400 µm.

spines 20-23 × 5-8. Oral sucker terminal, transversely elongate, funnel-shaped, 256-268 × 385-516; dorsal lip with anteriorly-directed lobe; ventral lip medially concave in outline. Oral aperture very large, sub-triangular, surrounded by crown of 49-50 spines (3 missing in Figure 4.4.) in double alternating row without ventral interruption; dorsal spines 54-67 × 19-22, significantly larger than ventral, 26-34 × 16-18. Prepharynx 462-641. Pharynx elongate-oval, 205-292 × 103-115. Ventral sucker in second quarter of body, subspherical, 199-295 × 231-308. Excretory vesicle I-shaped, extends throughout length of posterior quarter of body. Uroproct not seen.

Remarks

This is the first record of a fish intermediate host for *Stephanostomum euzeti* Bartoli & Bray, 2004, which has only recently been described on the basis of adult worms from *Seriola dumerili* (Risso) in the Western Mediterranean (off Corsica, see Bartoli & Bray, 2004). The metacercariae located on the internal surface of the pectoral muscle of *B. boops* are readily distinguishable from all other forms with a Mediterranean distribution (see Bartoli & Bray, 2001; Bray & Cribb, 2003; Bartoli & Bray, 2004) due to the peculiar structure and funnel-shape of the oral sucker and the number and arrangement of the oral crown of spines.

***Stephanostomum lophii* Quinteiro *et al.*, 1993 (metacercaria)** (Figure 4.5.)

Prevalence: 2.6, 3.3% .

Mean abundance: 0.03, 0.07.

Localities and dates of collection: NEA (off Malpica: 12.v.2004; Vigo: 20.xii.2006).

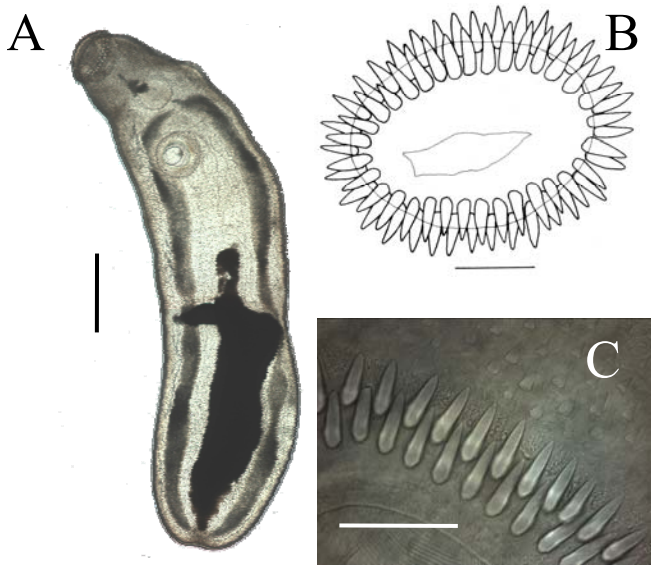

Figure 4.5. Stephanostomum lophii Quinteiro, Tojo, Nuñez, Santamaría & Sanmartín, 1993 (metacercaria) ex *Boops boops*. A, Ventral view. B, Crown of circumoral spines, apical view. C, Detail showing circumoral and tegumental spines, ventro-lateral view. *Scale-bars*: A, 500 µm; B,C, 100 µm.

Genus *Tormopsolus* Poche, 1926

***Tormopsolus* sp. (metacercaria)** (Figure 4.6.)

Prevalence: 3.1- 70.0%.

Mean abundance: 0.03-3.57.

Localities and dates of collection: NEA (off Barbate: 27.vi.2005, 21.ii.2006); WM (off Santa Pola: 07.vi.2005, 19.ii.2007, 08.iii.2007).

Figure 4.6. Tormopsolus sp. (metacercaria) ex *Boops boops*. A, Encysted, ventral view. B, Excisted, ventral view. *Scale-bars*: 500 μm

Family Accacoeliidae Odhner, 1911

Genus *Accacladium* Odhner, 1928

***Accacladium serpentulum* Odhner, 1928**

Prevalence: 3.3-10.3%.

Mean abundance: 0.03- 0.10.

Localities and dates of collection: NEA (off Malpica: 27.xi.2001; Vigo: 10.vi.2005); WM (off Santa Pola: 21.vi.2006, 08.iii.2007).

Material studied

Specimens (2) from *Boops boops* L. ?Intestine (recovered from internal body wash). One specimen, NE Atlantic (off Malpica, Galicia, Spain, 27.xi.01); second specimen from Mediterranean (off Santa Pola, Spain, 02.vii.02).

Voucher: BMNH 2005.4.18.16.

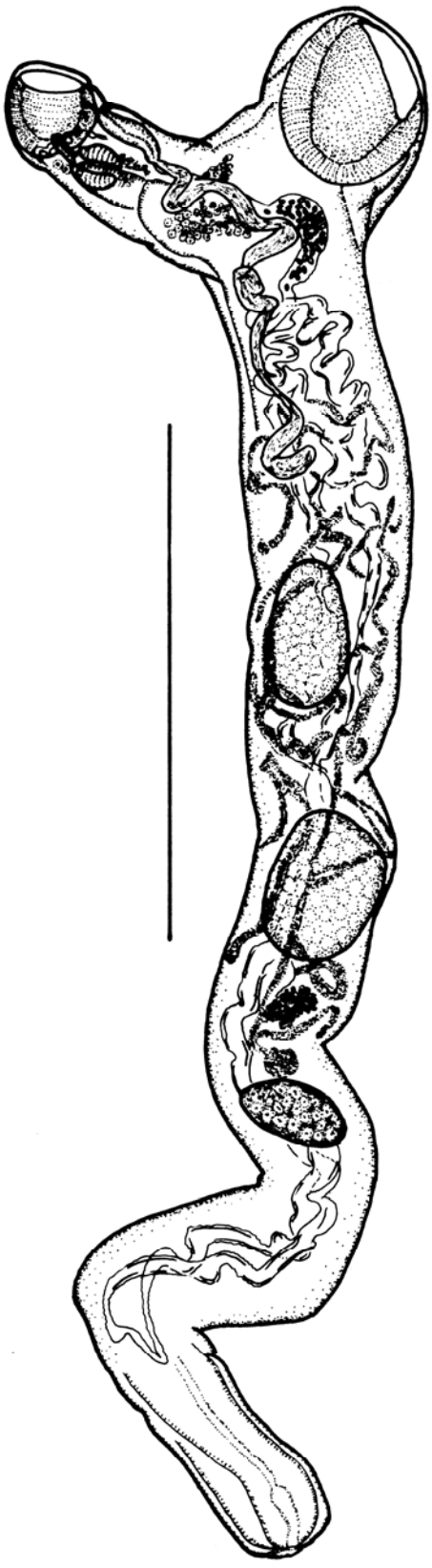

Figure 4.7. Accacladium serpentulum Odhner, 1928 ex *Boops boops*, lateral view. *Scale-bar*: 2000 µm.

Description (Figure 4.7.)

Based on 2 adult specimens (measurements for Atlantic specimen given first). Body very elongate, with almost parallel margins, 7,149 × 671; 8,163 × 690. Tegument smooth. Pre-oral lobe very small, 35; 34. Oral sucker ventrally subterminal, subglobular, 342 × 355; 345 × 259. Ventral sucker subglobular, much larger than oral sucker, 588 × 596; 647 × 422, surmounted on short peduncle, 149 × 895. Forebody 851; 776 (11.9% and 9.5% of body length). Pharynx elongate-oval, 193 × 175; 147 × 164, with additional narrow anterior region, 132 × 44; 103 × 60, projecting into lumen of oral sucker. Oesophagus short. Intestine H-shaped, with thick epithelial lining; anterior caeca reach pharyngeal region and posterior caeca unite with excretory vesicle to form uroproct at posterior extremity of body.

Testes 2, entire, elongate-oval, tandem and separated by loops of uterus, located just inside anterior half of hindbody, at 1,149; 1,327 from ventral sucker; anterior testis lies slightly dorsally, 579 × 303; 379 × 241; posterior testis lies slightly ventrally, 588 × 421; 422 × 233. Seminal vesicle long, 3,816 × 96, tubular, coiled, reaches from level of first vitelline tubules, some distance from anterior testis, to sinus-sac. Large cluster of prostatic cells mostly dorsal to seminal vesicle at level of ventral sucker; field length 395, width 399. Sinus-sac rather elongate, 298 × 83; 216 × 60.

Genital atrium distinct; genital pore mid-ventral, at about level of posterior margin of oral sucker.

Ovary post-testicular, in third quarter of body, separated from testes by loops of uterus, elongate-oval or subglobular, 443 × 237; 233 × 233; post-ovarian field 2,246; 3,620 (31.4 and 44.3% of body length). Mehlis' gland just anterior to ovary, transversely-oval, 132 × 237; 129 × 147. Uterus long, slightly coiled; descending loop reaches close to posterior extremity, extends throughout much of hindbody. Eggs numerous, 32-38 × 17-22 (mean 35 × 19). Vitellarium consists of numerous branching tubules from 2 main stems (1 ventral and 1 dorsal), extends from level of posterior end of seminal vesicle to level of ovary.

Excretory vesicle Y-shaped; arms unite anteriorly at level of pharynx, obscured by strongly stained epithelial cell lining of caeca in posterior part of body; stem narrow; distal extremity of vesicle small; pore terminal.

Remarks

The morphology of the present material generally grees with the redescription of *A. serpentulum* by Bray & Gibson (1977). However, it differs from the latter in the following: (i) the testes are entire and not contiguous; (ii) the genital pore is somewhat more anterior, at the level of oral sucker; (iii) the overlap between seminal vesicle and vitellarium is smaller; and (iv) the ovary is more posterior. The worms also exhibit substantially smaller dimensions than those previously recorded for the NE Atlantic (data from the comparative table in Bray & Gibson, 1977), except for the size of the eggs which overlaps the range of the material from Sweden described by these authors. On the other hand, the metrical data of the present material overlapped with the wide range provided for the Mediterranean worms (as *A. nematulum* Noble & Noble, 1937) given by Timon-David & Musso (1971). Bray & Gibson (1977) considered this species a synonym of *A. serpentulum*. Although the worms from *B. boops* are much smaller, with uterus not fully expanded, they appear normally developed and contained numerous eggs. The differences observed may be due to their younger age and/or poorer development in an unusual, and likely accidental, host. This is the first record of *A. serpentulum* in a fish host other than its type-host (*Mola mola*), the third record of this species in the NE Atlantic and the second in the Mediterranean.

Genus *Tetrochetus* Looss, 1912

Tetrochetus coryphaenae Yamaguti, 1934

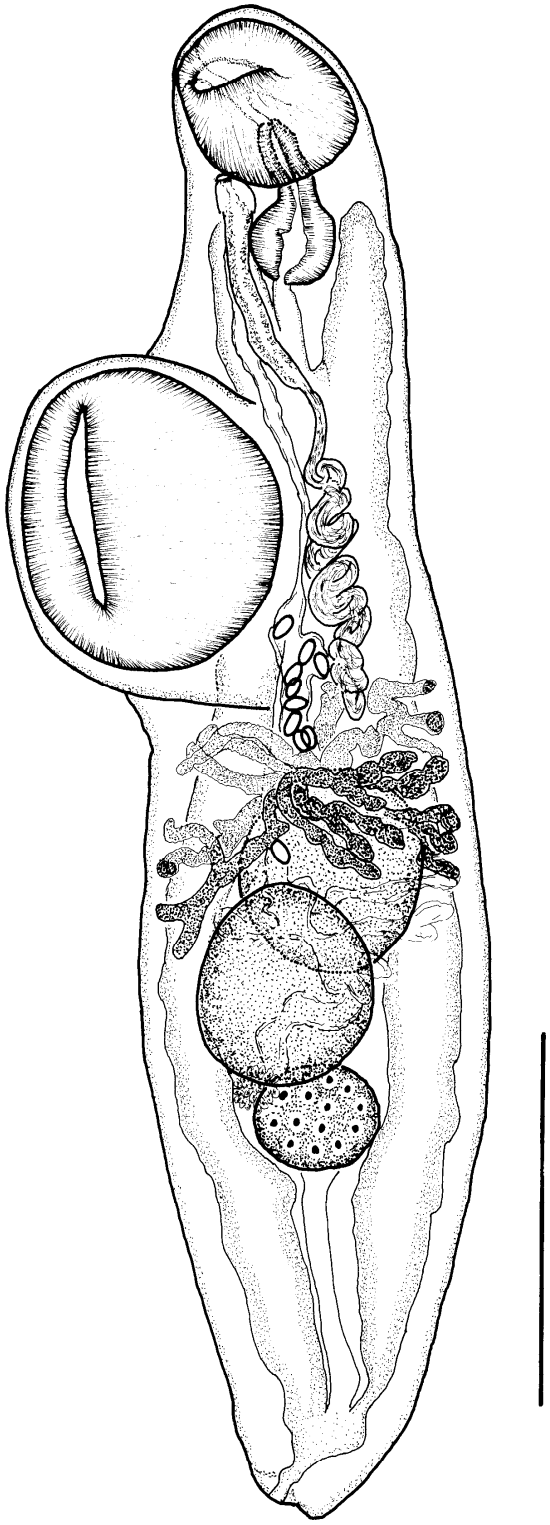

Figure 4.8.. Tetrochetus coryphaenae Yamaguti, 1934 ex *Boops boops*. Ventro-lateral view. *Scale-bar*: 400 μm.

Prevalence: 0.8- 16.7%.

Mean abundance: 0.01- 0.40.

Localities and dates of collection: NEA (off Ondarroa: 20.vi.2005); WM (off Santa Pola: 07.vi.2005, 21.vi.2006, 19.ii.2007, 08.iii.2007).

Material studied

Single specimen from *Boops boops* L. Intestine. Mediterranean coast of Spain: off Santa Pola (7.vi.2005). Voucher material BMNH 2006.3.14.9.

Description (Figure 4.8.)

Body elongate, 1,617 × 364, with prominent ventral sucker on short peduncle in second quarter of body. Tegument smooth. Oral sucker ventrally subterminal, subglobular, 190 × 169. Ventral sucker subglobular, much larger than oral sucker, 325 × 273 in sublateral aspect, surmounted on short peduncle. Forebody 395 (24.4% of body length). Prepharynx absent. Pharynx spherical, 91 × 91, with additional narrow anterior extension, 91 × 31, projecting into lumen of oral sucker. Oesophagus short. Oesophago-intestinal junction in posterior forebody. Intestine H-shaped; anterior caeca reach pharyngeal region and posterior caeca posterior extremity of body.

Testes 2, large, entire, subglobular, oblique, located in anterior half of hindbody; anterior testis 221 × 190; posterior testis 211 × 187. Seminal vesicle long, tubular, coiled, commences posteriorly to level of first vitelline tubules, some distance from anterior testis. Sinus-sac absent. Pars prostatica long, tubular, opens into base of genital atrium. Genital pore mid-ventral, at level of posterior margin of oral sucker.

Ovary post-testicular, contiguous with posterior testis, subglobular, 109 × 130. Mehlis' gland just contiguous with ovary, small, 49 × 55. Uterus not extensive, coils dorsally to testes, contains few eggs, which measure 27-30 × 16-17, forms narrow metraterm at level of oesophago-intestinal junction; metraterm appears to open directly into genital atrium. Vitellarium consists of numerous branching tubules, extends from level of ventral sucker peduncle to level of ovary.

Excretory vesicle Y-shaped; stem short, narrows distally; pore terminal.

Remarks

The single specimen found in *B. boops* exhibits all the characteristic features of *Tetrochetus* Looss, 1912, *i.e.* the absence of a detectable sinus-organ and sinus-sac and the tubular branching vitellarium on either side of the hindbody. Although having a short body (falling within the lower length range), the worm described here agrees well with the description of *T. coryphaenae* by Gibson (1976). The eggs, although not as numerous as in the material from the main coryphaenid host, are similar in size, *i.e.* 27-30 × 16-17 *vs* 26-35 (usually 28-33) μm in length (see Gibson, 1976). *B. boops* is a new host record for *T. coryphaenae*.

Family Derogenidae Nicoll, 1910

Genus *Magnibursatus* Naidenova, 1969

***Magnibursatus caudofilamentosa* (Reimer, 1971) Gibson & Køie, 1991**

Prevalence: 2.5-6.7%.

Mean abundance: 0.03-0.20.

Localities and dates of collection: NEA (off Ondarroa: 6.vi.2001, 20.vi.2005; Malpica: 12.v.2004; Vigo: 10.vi.2005, 11.xi.2005, 14.vi.2006; Barbate: 27.vi.2005).

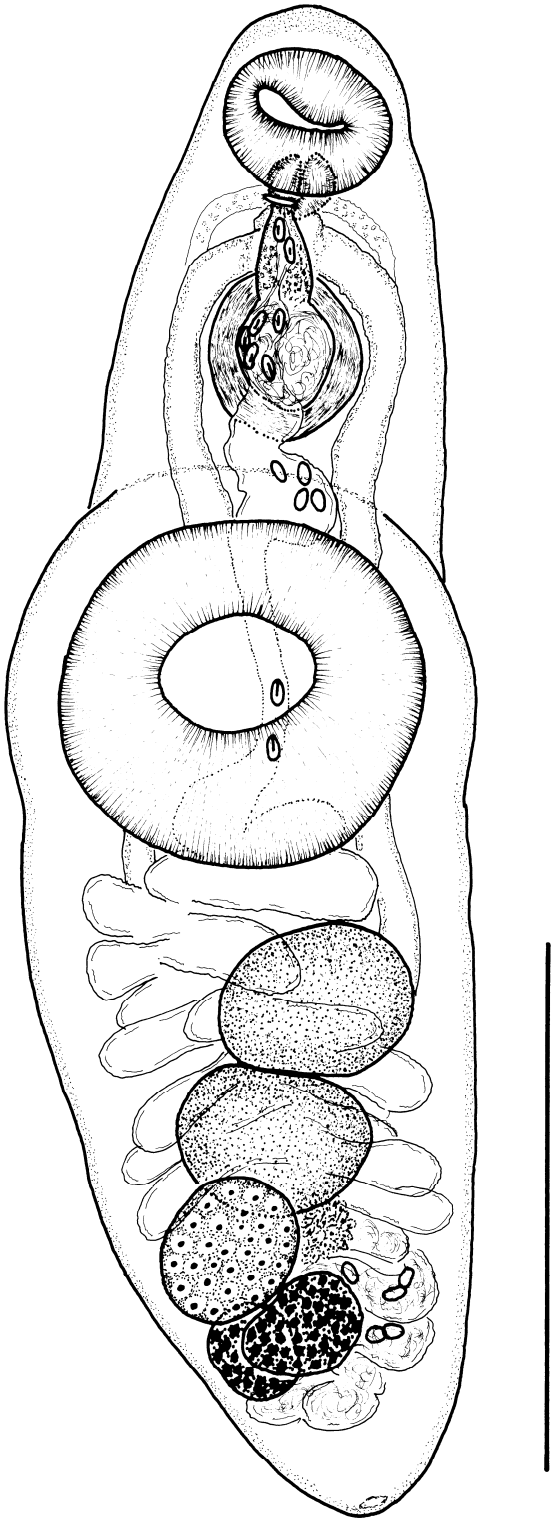

Figure 4.9. *Magnibursatus caudofilamentosa* (Reimer, 1971) ex *Boops boops*. Ventral view with uterus in outline. *Scale-bar*: 500 µm.

Material studied

Specimens (7) from *Boops boops* L. Gills. NE Atlantic coasts of Spain [Galicia: off Malpica (12.v.2004) and Vigo (11.v.2005); Basque Country: off Ondarroa (6.vi. 2001). Voucher material BMNH 2006.3.14.6-8.

Description (Figure 4.9.)

Body elongate fusiform, widest at level of ventral sucker, 920-1,472 × 296-452 (1,265 × 394). Tegument thick, unarmed. Pre-oral lobe distinct, 18-44 (30) long. Oral sucker spherical, subterminal, 107-138 × 117-164 (123 × 145). Ventral sucker muscular, substantially larger than oral sucker, 244-330 × 242-354 (282 × 313). Sucker-width ratio 1:2.28-2.39 (1:2.34); sucker-length ratio 1:1.93-2.43 (1:2.16). Forebody 309-499 (419) long [28-42% (33%) of body length]. Prepharynx absent. Pharynx subglobular, 47-68 × 47-62 (57 × 56). Oesophagus very short. Intestinal bifurcation just posterior to pharynx. 'Drüsenmagen' indistinct. Caeca with thick epithelial lining, end blindly fairly close to posterior end of body.

Testes 2, transversely oval, smooth, oblique to tandem, contiguous. Anterior testis 83-156 × 146-185 (132 × 161), adjacent to posterior border of ventral sucker or separated from it by uterine coil; distance to ventral sucker 0-68 (40), *i.e.* 0-4.8% (2.9%) of body length. Posterior testis 81-190 × 161-208 (140 × 189), at 166-364 (290) from posterior end of

body, *i.e.* 18-28% (23%) of body length. Seminal vesicle internal, wide-tubular, coiled. Pars prostatica and hermaphroditic duct short. Sinus-sac subglobular, larger than oral sucker, in middle of forebody; its posterior 2/3 with multi-layered muscular wall up to 34 thick; length (posterior margin to genital pore) 135-260 (195), maximum width 114-156 (137); male and female ducts unite within its proximal thin-walled portion. Genital atrium shallow. Permanent sinus organ not observed. Genital pore median, at level of pharynx or slightly posterior.

Ovary smaller than testes, subglobular, 75-122 × 99-148 (109 × 128), contiguous with posterior testis. Mehlis' gland lateral to postero-dorsal to ovary, 60-78 × 47-78 (70 × 62). Laurer´s canal and rudimentary seminal receptacle not seen. Uterine seminal receptacle well developed, coils from level of ovary to near posterior end of body, filled with spermatozoa. Uterine coils fill much of hindbody; uterus passes into forebody as narrow tube apparently restricted by bulk of ventral sucker, forms coil in forebody. Metraterm enters sinus-sac ventrally to male duct. Eggs small, operculate, with numerous filaments, 21-26 × 10-13 (23 × 11). Vitellarium 2 compact, entire, partly overlapping, oval to 3-4 sided masses, immediately posterior and adjacent to ovary, 60-101 × 78-101 (81 × 90).

Excretory pore terminal. Vesicle not seen; anterior arms unite dorsally to pharynx.

Remarks

Morphologically, the specimens from *Boops boops* (all fully gravid and containing numerous eggs) key down (see Kostadinova *et al.*, 2003) to and agree well with the description of *M. caudofilamentosa* by Gibson & Køie (1991) based on material from *Gasterosteus aculeatus* in eastern Danish marine waters. This is especially with regard to: (i) the large portion of the forebody occupied by the sinus-sac; (ii) the thickness of its muscular wall (in relation to the space occupied by the seminal vesicle); (iii) the ovary is not separated from the posterior testis by uterine coils; and (iv) the relatively small eggs.

The present material differs from *M. bartolii* Kostadinova, Power, Fernández, Balbuena, Raga & Gibson, 2003, which was described from *Boops boops* from the Atlantic coasts of Spain and also recovered (with a higher prevalence than *M. caudofilamentosa, i.e.* 20-50% *vs* 3.3-11.1%; see Appendix 1-4) in three of the samples reported here, in: (i) a smaller sinus-sac with a much thicker muscular wall; (ii) a shorter forebody; (iii) testes located close to the ventral sucker and contiguous with the ovary; and (iv) a smaller proportion of the uterus in the forebody. Finally, although larger, *M. bartolii* is a much

thinner, more elongate form, and, due to a strongly muscular, protuberant ventral sucker, worms invariably form from a shallow '3'-shape to a right-angle when viewed laterally, and this allows the rapid identification and discrimination from *M. caudofilamentosa* at low magnifications.

The present record extends the distributional range of *M. caudofilamentosa. B. boops* is a new host record and possibly an accidental host for *M. caudofilamentosa.* The site of the parasite indicates that it might be the result of a post-mortem migration from the stomach, a common feature of derogenids which commonly inhabit the cardiac stomach; however, the occurrence of two records suggests that this was unlikely to have been from another host species.

Family Fellodistomidae Nicoll, 1909

Genus *Steringotrema* Odhner, 1911

***Steringotrema pagelli* (van Beneden, 1871) Odhner, 1911**

Prevalence: 4.0, 32.4%.
Mean abundance: 0.84, 7.26.
Locality and dates of collection: NEA (off Vigo: 10.vi.2005, 14.vi.2006).

Material studied

Two non-gravid specimens from *Boops boops* L. Oesophagus, pyloric caeca. NE Atlantic coasts of Spain: off Vigo (11.v.2005). Voucher material BMNH 2006.3.14.10.

Description (Figures 4.10., 4.11.)

Body small, fusiform, tapered anteriorly to pointed pre-oral lobe, with maximum width at level of ventral sucker, 780-933 × 333-356. Tegument unarmed. Forebody 268-408 long (34.4-43.7% of body length). Oral sucker subterminal, elongate-oval, pointed anteriorly, 104-125 × 88-91. Ventral sucker massive, strongly muscular, in middle of body, 239-242 × 276-278. Sucker-width ratio 1:3.03-3.16. Prepharynx apparently absent. Pharynx elongate-oval, with wide lumen, 78-99 × 57-60. Oesophagus 39-91 long, 23-29 wide. Caeca with thick glandular walls, terminate just posterior to testes.

Testes 2 large, smooth, elongate-oval, symmetrical, contiguous or slightly separated, fairly close to or touching posterior margin of ventral sucker; right testis 94-133 × 70-104;

left testis 101-125 × 68-96. Cirrus-sac elongate-oval, just anterior to anterior margin of ventral sucker, 85-86 × 54-66, contains small bipartite seminal vesicle, wide pars prostatica and short ejaculatory duct. Genital pore medio-sinistral.

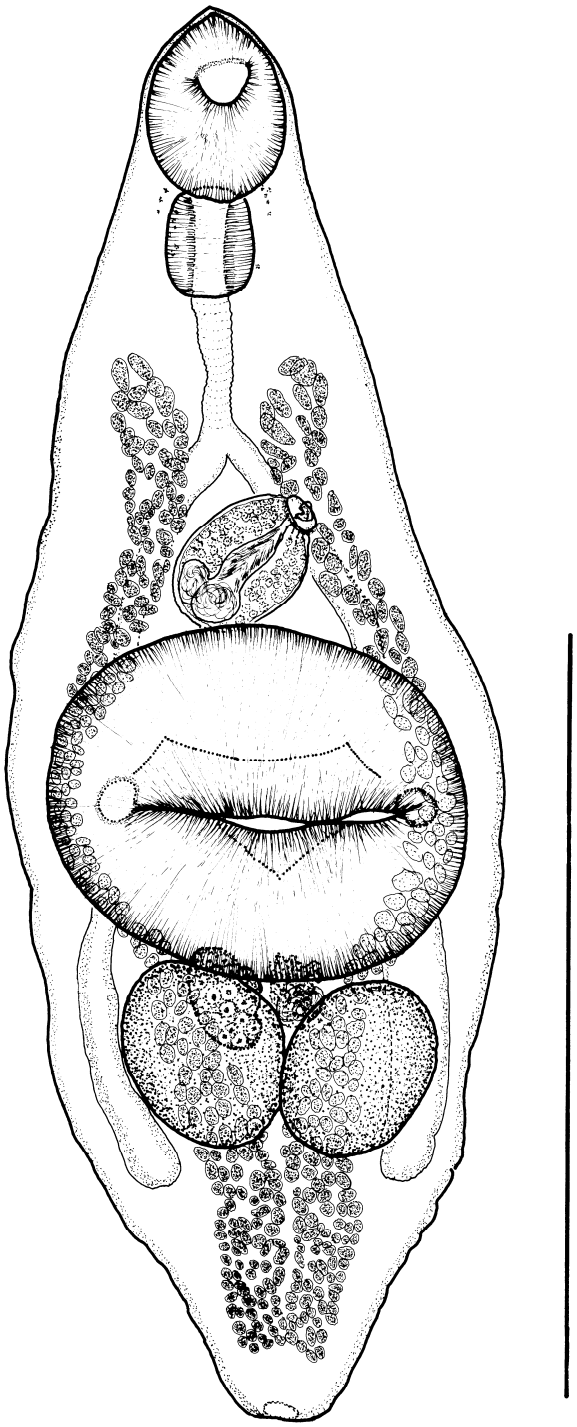

Figure 4.10. *Steringotrema pagelli* (van Beneden, 1871) ex *Boops boops*. Ventral view. *Scale-bar*: 500 μm.

Ovary small, with 3 irregular lobes, antero-dorso-medial to right testis, 42-70 × 47-52. Mehlis' gland 52 × 31-39, between testes. Laurer's canal not observed. Uterine seminal receptacle dorsal to Mehlis' gland. Vitellarium in 2 lateral fields of tightly packed vitelline follicles, which extend in forebody to just anterior to intestinal bifurcation, converge and unite posterior to testes thus forming V-shape, curved dorsally to ventral sucker.

Excretory pore wide, dorsal; other details of excretory system not observed.

Remarks

This material is morphologically very close to, and was identified as, *Steringotrema pagelli* (van Beneden, 1871). Due to the smaller size of the non-gravid worms from *B. boops,* all metrical data (with the exception of the sucker and forebody/length ratios) fall within or somewhat below the lower ranges of variation reported by Bray & Gibson (1980) for mature specimens from various hosts in the

North East Atlantic. This is the second record of *S. pagelli* in *B. boops*, which is likely an accidental host (see Parukhin, 1976; a record reiterated in Naidenova & Mordvinova, 1997).

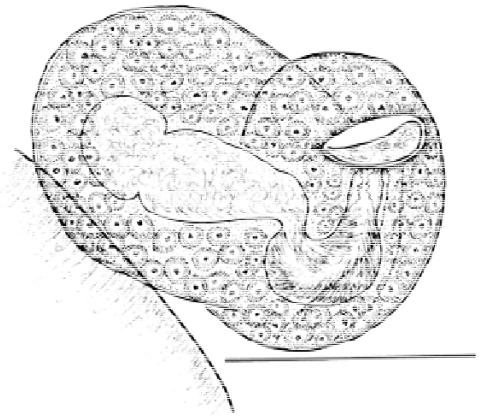

Figure 4.11. *Steringotrema pagelli* (van Beneden, 1871) ex *Boops boops*. Terminal genitalia. *Scale-bar*: 50 µm.

Family Gyliauchenidae Fukui, 1929

Genus *Robphildollfusium* Paggi & Orecchia, 1963

***Robphildollfusium martinezgomezi* López-Román, Gijón-Botella, Kim & Vilca-Choque, 1992**

Prevalence: 2.9, 3.1%.

Mean abundance: 0.03, 0.06.

Locality and dates of collection: WM (off Santa Pola: 07.vi.2005, 01.iii.2006).

Material studied

Specimens (5) from *Boops boops* L. Intestine. Mediterranean coast of Spain: off Santa Pola (7.vi.2005). Voucher material BMNH 2006.3.14.3-5.

Description (Figures 4.12., 4.13.)

Based on 5 whole-mounted adult specimens; metrical data in Table 4.2. Body elongate, fusiform, tapered at both extremities and with maximum width at level of anterior testis. Forebody longer than hindbody. Tegument unarmed. Oral sucker absent (see 'Remarks'). Ventral sucker at mid-body level or slightly posterior, subspherical, muscular; aperture a longitudinal slit. Pre-oral lobe present. Pharynx opens ventro- subterminally as mouth, strongly muscular, elongate to subcylindrical, with muscular thickening in its internal walls. Oesophagus very long, wide, sigmoid in 1 specimen, surrounded by thick mass of small

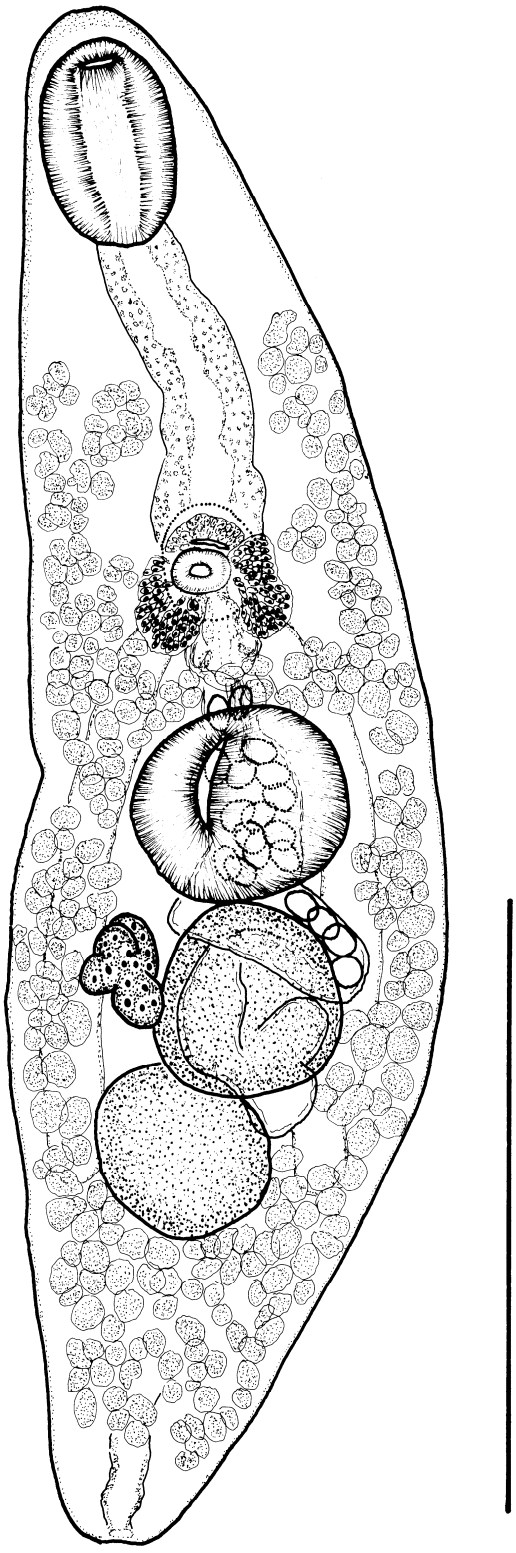

Figure 4.12. *Robphildollfusium martinezgomezi* López-Román *et al.*, 1992 ex *Boops boops*. Ventral view with uterus in outline. *Scale-bar*: 1000 µm.

gland-cells. Oesophageal bulb without discrete capsule present, subspherical, dorsal to cirrus-sac. Intestinal caeca 2, wide, end blindly close to posterior margin of posterior testis.

Testes 2, entire, round to transversely oval, slightly oblique, contiguous. Seminal vesicle external, long, wide-tubular, difficult to distinguish (obscured by strong musculature of ventral sucker). Cirrus-sac subconical; its base with thick muscular walls. Masses of large prostate cells present on either side of cirrus-sac, extending to anterior margin of ventral sucker; 2 symmetrical groups of prostatic cell ducts enter base of cirrus-sac. Ejaculatory duct short, forms short, muscular, eversible cirrus. Male and female genital pores separate (Figure 4.12.); male genital pore mid-ventral to slightly lateral, in posterior third of forebody.

Ovary small, quadri-lobed, just posterior to ventral sucker and contiguous with anterior testis. Seminal receptacle, Mehlis' gland and Laurer's canal not observed (obscured by numerous eggs in uterus). Uterus short, forms few tightly packed median intercaecal loops between cirrus-sac and posterior testis. Eggs numerous, operculate, rather wide, with point at anopercular pole. Metraterm nearly as long as cirrus-sac, strongly muscular; its terminal portion surrounded by large mass of gland-cells, delimited by fine membrane. Female genital atrium with presumably sclerotised lamellae supporting female genital pore. Female genital pore opens close to male genital pore (Figure

4.13.). Vitellarium follicular, in 2 lateral fields of large follicles between mid-level of prepharynx and posterior extremity, approaches median line just anterior to ventral sucker and confluent posterior to testes.

Excretory vesicle tubular, sinuous, with thick glandular walls. Excretory pore wide, dorsal.

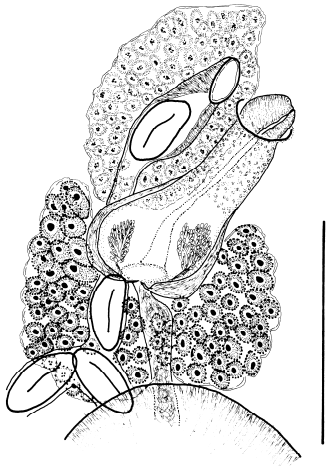

Figure 4.13. Robphildollfusium martinezgomezi López-Román *et al.*, 1992 ex *Boops boops*. Terminal genitalia. *Scale-bar*: 200 µm.

Remarks

The present material differs from *Robphildollfusium fractum* (Rudolphi, 1819), as described by Bartoli (1987a), in the presence of a much thicker muscular wall at the base of the cirrus-sac and the absence of an internal seminal vesicle. Furthermore, *R. fractum* is a significantly larger worm, with almost all measurements outside the upper range for the present material (with the exception of egg-width which is smaller).

A comparison with *R. martinezgomezi* revealed higher upper limits for almost all metrical data (except egg-width) for this species (López-Román *et al.*, 1992; see Table 4.2.). However, no substantial morphological differences between this material and the original description of *R. martinezgomezi* from *B. boops* in the NE Atlantic were found. This redescription, therefore, adds to the morphometric variability of this species, provides a more detailed picture of the terminal genitalia (*e.g.* the absence of an internal seminal vesicle; the presence of a large mass of gland-cells delimited by a fine membrane which surrounds the terminal part of the metraterm; the presence of a mass of large prostate cells on either side of the cirrus-sac; and the size of uncollapsed eggs) and extends its known range to the Mediterranean. This is the second record of *R. martinezgomezi*.

Hall & Cribb (2000) examined the type-material of *R. fractum* and, analogous to the situation in the gyliauchenids, interpreted the anterior muscular organ, through which the digestive tract opens, as a pharynx, ensuing from the combination of its 'almost dorso-ventrally symmetrical' condition with the presence of an unencapsulated oesophageal bulb. The two comb-like denticulate structures described in *R. fractum* by Bartoli (1987a) were not detected. However, the dorso-ventral symmetry of the 'anterior organ' and muscular thickening of its internal walls were observed. This has led to the decision to treat the anterior organ as a pharynx, in agreement with Hall & Cribb (2000, 2005).

Table 4.2. Comparative metrical data for *Robphildollfusium martinezgomezi* López-Román *et al.,* 1992 and *R. fractum* (Rudolphi, 1819)

Species	***R. martinezgomezi* López-Román Gijón-Botella, Kim & Vilca-Choque, 1992**		***R. martinezgomezi* López-Román Gijón-Botella, Kim & Vilca-Choque, 1992**		***R. fractum* (Rudolphi, 1819)**	
Host	***Boops boops***		***Boops boops***		***Sarpa salpa***	
Locality	Off Santa Pola (Mediterranean, Spain)		Off Azores, Canary Islands, Cape Verde Isles (NE Atlantic, Spain)		Off Corsica (Mediterranean, France)	
Source	Present study		López-Román *et al.*. (1992)		Bartoli (1987a)	
	Range	**Mean**	**Range**	**Mean**	**Range**	**Mean**
Body	2,079-2,449 × 673-805	2,226 × 734	1,818-4,545 × 697-1,606	3,405 × 1,281	3,421-4,208 × 722-1,190	3,870 × 884
Forebody length	1,010-1,135	1,069	-	-	1,445-1,998	1,770
Hindbody length	719-1,049	870	-	-	1,403-2,125	1,600
Pre-oral lobe	26-53	40	-	-	-	-
Pharynx	251-337 × 211-224	307 × 218	238-398 × 163-297	323 × 230	490-560 × 272-330	526 × 294
Ventral sucker	304-343 × 297-343	322 × 326	252-460 × 261-446	386 × 360	426-533 × 416-533	490 × 474
Oesophagus	396-416 × 191-198	406 × 193	416-916 × 48-119	638 × 88	-	-
Oesophageal bulb	145-185 × 119-177	172 × 150	119-220 × 134-238	179 × 182	213-330 × 213-330	277 × 250
Anterior testis	224-310 × 231-323	252 × 276	267-380 × 193-487	346 × 340	213-341 × 224-437	260 × 327
Posterior testis	224-310 × 244-310	255 × 285	208-413 × 285-490	354 × 340	266-373 × 203-432	334 × 308
Cirrus-sac	174-208 × 86-117	186 × 106	-	-	746-1,146 × 266-533	1,022 × 416
Cirrus width	47-106	65	-	-	-	-
Ovary	139-198 × 132-178	176 × 152	235-368 × 154-220	295 × 186	160-266 × 144-240	219 × 191
Eggs	62-73 × 39-47	66 × 44	64-80 × 33-43	72 × 38	67-74 × 26-35	70 × 30

Family Lecithasteridae Odhner, 1905

Genus *Aponurus* Looss, 1907

***Aponurus laguncula* Looss, 1907**

Prevalence: 2.5-5.0%.

Mean abundance: 0.03-0.05.

Localities and dates of collection: NEA (off Ondarroa: 20.vi.2005; Malpica 12.v.2004; Vigo: 11.xi.2005, 10.i.2007).

Material studied

Single specimen from *Boops boops* L. Stomach. NE Atlantic (off Malpica, Galicia, Spain, 12.v.2004).

Voucher: BMNH 2005.4.18.17.

Description (Figure 4.14A)

Based on 1 ovigerous specimen. Body small, fusiform, widest at level of ventral sucker, 390 × 143. Tegument unarmed. Pre-oral lobe 10. Oral sucker subterminal, spherical, 56 × 56. Ventral sucker subglobular, at mid-body, 77 × 87. Sucker-ratio 1:1.55. Forebody 42.6% of body length. Pharynx subglobular, 30 × 26. Oesophagus virtually absent. 'Drüsenmagen' distinct. Caeca wide, terminate at level of posterior vitelline follicles. Testes oval, oblique; right testis elongate-oval, overlapping ventral sucker dorsally, 69 × 41; left testis transverse-oval, just posterior to ventral sucker, 41 × 56. Seminal vesicle saccular, 41 × 29, antero-dorsal to ventral sucker. Pars prostatica narrow, slightly sinuous, *c*.47 long; prostatic cell field width 21. Sinus-sac oval, 27 × 19. Genital pore at level of posterior margin of pharynx. Ovary posterior to and contiguous with testes, spherical, 34 × 33. Seminal receptacle and Mehlis' gland not seen. Uterus with few eggs (*c*.20); eggs tanned, operculate, with pointed anopercular pole, 23-24 × 10-11. Vitellarium consists of 7 claviform follicles; overall field 79 × 49; anterior group overlapping ovary ventrally.

Remarks

Morphologically, the single specimen from *B. boops* agrees well with the redescription of *A. laguncula* by Bray & MacKenzie (1990) based on material from *Clupea harengus* L. in

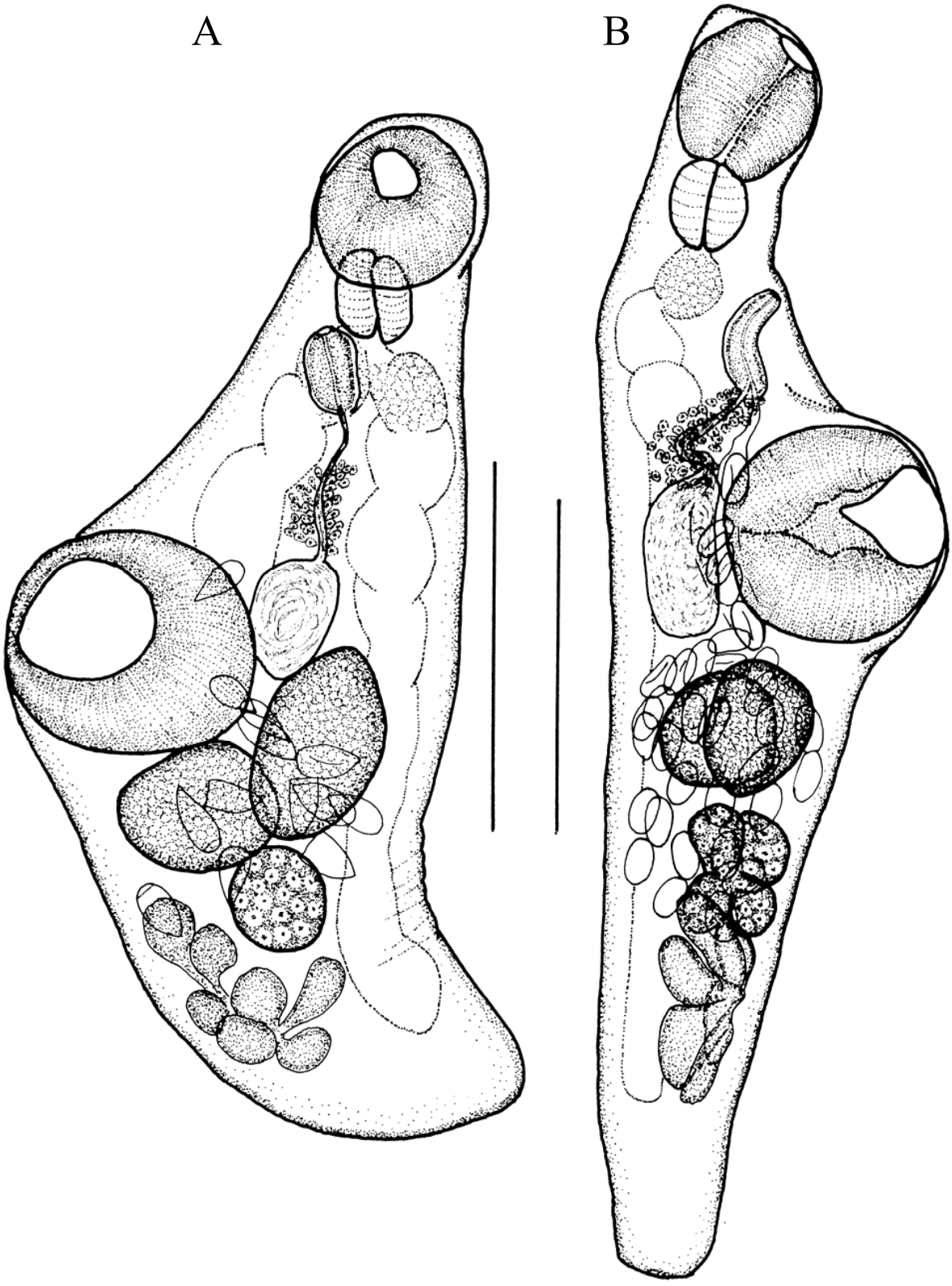

Figure 4.14. A, *Lecithaster confusus* Odhner, 1905 ex *Boops boops*, lateral view; B, *Aponurus laguncula* Looss, 1907 ex *Boops boops*, lateral view. *Scale-bars*: 100 µm.

the English Channel. This is especially with regard to the characteristic shape of the eggs which possess a narrow, pointed anopercular pole (Figure 4.14A). *B. boops* is a new host record and is probably an accidental host for *A. laguncula*.

Genus Lecithaster Lühe, 1901

***Lecithaster confusus* Odhner, 1905**

Prevalence: 2.4-4.0%.
Mean abundance: 0.02-0.04.
Localities and dates of collection: NEA (off Ondarroa: 20.vi.2005; Malpica 12.v.2004, 23.xi.2005; Vigo 10.vi.2005).

Material studied
Specimens (2) from *Boops boops* L. Intestine. NE Atlantic (off Malpica, Galicia, Spain, 12.v.2004).
Voucher: BMNH 2005.4.18.18.

Description (Figure 4.14B)
Based on 2 adult specimens. Body elongate-fusiform, 469-515 long, widest at level of ventral sucker, 117-146. Tegument unarmed. Pre-oral lobe small, 8-10. Oral sucker subterminal, spherical, 58-75 × 54-72. Ventral sucker large, subspherical, in anterior half of body, 82-96 × 85-96. Sucker-width ratio 1:1.33-1.57. Forebody 34.5-34.8% of body length. Pharynx subglobular, 35 × 30. Oesophagus absent, 'Drüsenmagen' distinct. Caeca wide, terminate at *c*.50 from posterior extremity. Testes subglobular, symmetrical, just posterior to ventral sucker, 43-51 × 40-46. Seminal vesicle saccular, elongate-oval, 64-88 × 29-40, reaches level of testes posteriorly. Pars prostatica 48-128 long; prostatic cell field width 16-43. Sinus-sac somewhat banana-shaped (Figure 4.14B), 48 × 14-19. Genital opening just posterior to level of pharynx. Ovary 4-lobed, 48-83 × 40-58. Seminal receptacle dorsal to posterior ovarian lobes, relatively small, 24 × 42. Uterine coils between vitellarium and ventral sucker. Eggs 18-19 × 10-12. Vitellarium consists of 7 tear-shaped lobes; overall field 74-77 × 56-74. Post-vitelline region 7.8-13.6% of body length.

Remarks

This material is morphologically very close to, and was identified it as, *L. confusus*. However, both worms from *B. boops,* although bearing many eggs, are rather small, and this results in all metrical data falling within the lower ranges of variation reported by Linton (1940) and Overstreet (1973) (see Table 4.3.) for specimens from the North West Atlantic. While egg-size corresponds well with the known range for *L. confusus*, the sucker-ratio is distinctly smaller, the forebody is relatively longer and the postvitelline region shorter (Table 4.3.); but these are likely allometric differences relating to the small size of the worms studied. *B. boops* is a new host record, and likely an accidental host, for *L. confusus*.

Table 4.3. Comparative data (measurements in micrometres) for *Lecithaster confusus* Odhner, 1905.

Source	**Present study** Range	**Odhner (1905)** Range	**Looss (1908)** Range	**Linton (1940)** Range	**Overstreet (1973)** Range
Body length	469-515	1,000-1,500	1,000-1,200	330-1,750	379-1,299
Body width at ventral sucker	117-146	300-500	400	180-650	155-485
Forebody length	162-179	-	-	-	-
Pre-oral lobe	8-10	-	-	-	-
Oral sucker	58-75 × 54-72	? × 130-160	? × 140-150	? × 60-160	49-126 × 55-122
Pharynx length	35 × 30	? × 70-85	-	? × 36-100	32-73 × 33-73
Ventral sucker	82-96 × 85-96	? × 230-300	? × 250-270	? × 100-280	110-252 × 102-232
Sinus-sac	48 × 14-19	80-110 × ?	-	-	29-67 × ?
Seminal vesicle	64-88 × 29-40	Posterior to level of the ventral sucker	-	-	-
Pars prostatica length	48-128	-	-	-	-
Pars prostatica field width	16-43	-	-	-	-
Right testis	43-51 × 45-46	-	-	-	44-139 × 38-133
Left testis	50 × 40	-	-	-	38-157 × 36-116
Ovary	48-83 × 40-58	Lobes of ovary elongate, similar to lobes of vitellarium	-	-	67-255 × 57-177
Seminal receptacle	24 × 42	-	-	-	-
Vitellarium field	74-77 × 56-74	? × 250 (smaller than ovary)	-	-	-
Eggs	18-19 × 10-12	15-17 × 7	15-17 × 9	12-20 × 7-13	15-23 × 9-15
Sucker width ratio	1:1.33-1.57	1: 1.75	1:2.0		1:1.7-2.3
Forebody as % of length	34.5-34.8	-	22.9*	24.4	21.0-37.0
Postvitelline region as % of length	7.8-13.6	-	26.0	17.1	6.0-28.0

Family Lepocreadiidae Odhner, 1905

Genus *Lepocreadium* Stossich, 1904

Lepocreadium album Stossich, 1890

Prevalence: 2.0-6.7%.

Mean abundance: 0.03-0.10.

Localities and dates of collection: NEA (off Ondarroa: 20.vi.2005; Malpica: 12.v.2004; off Vigo: 10.vi.2005; Barbate: 21.ii.2005).

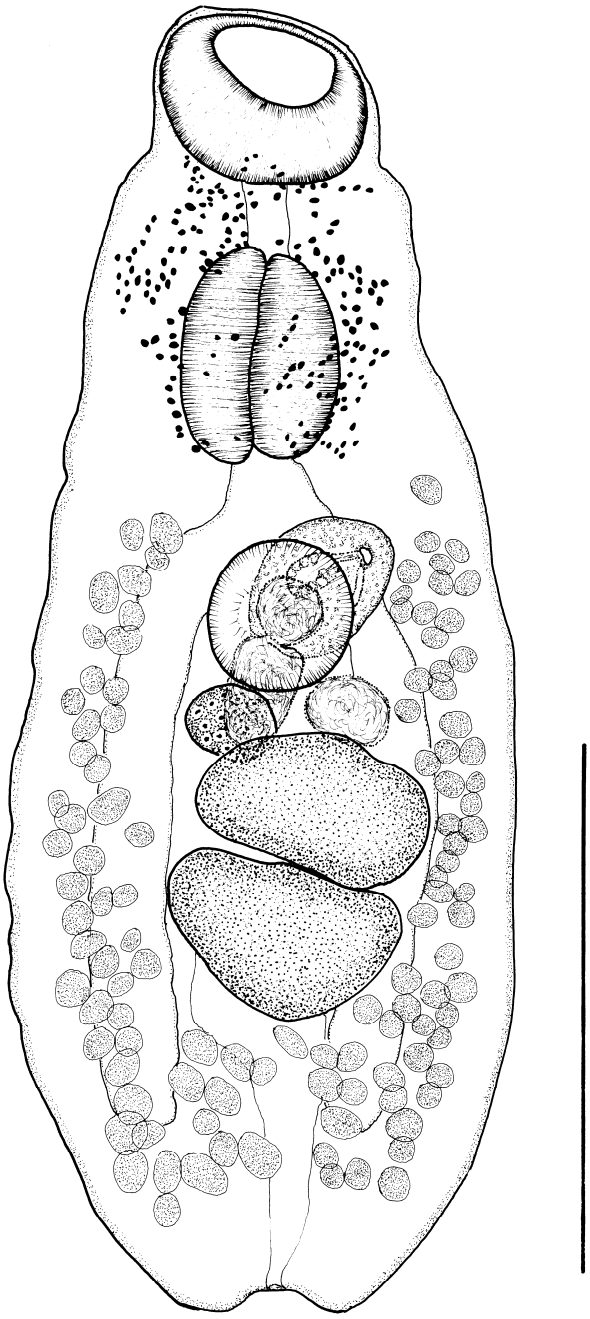

Figure 4.15. *Lepocreadium album* Stossich, 1890 ex *Boops boops*. Ventral view. *Scale-bar*: 200 μm.

Material studied

Specimens (4) from *Boops boops* L. Pyloric caeca. NE Atlantic coasts of Spain: off Malpica (12.v.2004) and Vigo (11.v.2005). Voucher material BMNH 2006.3.14.11.

Description (Figure 4.15.)

Body elongate-oval, rounded at both ends, 421-483 × 144-192. Tegument with fine spines. Sparce scattering of eye-spot pigment granules present in region of prepharynx and pharynx. Pre-oral lobe indistinct. Oral sucker subglobular, opens subterminally, 64-75 × 78. Ventral sucker round, not overly muscular, just anterior to mid-body, smaller than oral sucker, 56-64 × 53-80. Sucker-length ratio 1:0.85-0.88; sucker-width ratio 1:0.68-0.72. Forebody 152-197 (36.1-40.8% of body length). Prepharynx distinct, 24 long, with wide lumen. Pharynx elongate-oval, large, 67-82 × 59-64. Oesophagus very short. Caeca wide, terminate blindly close to posterior extremity.

Testes transversely oval, smooth or slightly irregular, in

tandem, contiguous, just posterior to ventral sucker; anterior testis 51-69 × 86-96; posterior testis 59-75 × 88-91. External seminal vesicle saccular, 38 × 26. Cirrus-sac oval, 61 × 45, antero-dorsal to and reaching to about mid-level of ventral sucker, contains small globular internal seminal vesicle, 24 × 26, scattered prostatic cells and small vesicular pars prostatica. Ejaculatory duct short, straight. Genital pore medio-sinistral, fairly close to ventral sucker. No formed cirrus seen. Ovary smoothly rounded, just posterior to ventral sucker, contiguous with or overlapping anterior testis dorsally, 27-40 × 30-34. Mehlis' gland and Laurer's canal not seen. Seminal receptacle saccular, close to ovary, 24 × 34. Uterus short, with few large eggs, 74 × 45. Metraterm shorter than cirrus-sac. Vitellarium follicular, in lateral fields which are confluent in post-testicular field and reach to relatively close to posterior extremity; anterior limit at level of oesophagus.

Excretory pore dorso-subterminal, with sphincter; vesicle I-shaped, very long.

Remarks

Apart from the fact that the specimens are much smaller, no convincing differences were detected between the material from the NE Atlantic and the descriptions of *Lepocreadium album* from the Mediterranean (Odhner, 1914; Radujkovic *et al.*, 1989; Saad-Fares & Maillard, 1990). The egg-size of uncollapsed eggs appears close to the values for the type-material and the redescription of Saad-Fares & Maillard (1990) [74 × 45 *vs* 65-72 (up to 77) × 35-46 and 65-77 × 34-40 µm] rather than to the range given by Radujkovic *et al.* (1989) (80-90 × 45-50 µm). Odhner (1914) observed that egg-production in the type-material of *L. album* starts at a worm size of 600-700 µm, whereas the present egg-bearing worms are even smaller. Although *L. album* has been recorded in a range of sparid hosts (possibly the main hosts in the Mediterranean, see also Saad-Fares, 1985; Bartoli, 1987b; Saad-Fares & Maillard, 1990; Akmirza, 1998, 2000), it is possible that the metrical differences observed in the present specimens are due to the different host and the geographically distant locality. This is the third record of *L. album* in *B. boops* (see Papoutsoglou, 1976; Akmirza, 1998).

Family Opecoelidae Ozaki, 1925

Opecoelidae gen. sp. (Figure 4.16.)

Prevalence: 0.8-2.5%.
Mean abundance: 0.01-0.03.
Localities and dates of collection: NEA (off Malpica: 24.v.2005; Vigo: 10.vi.2005, 11.xi.2005); WM (off Santa Pola: 07.vi.2005).

Family Renicolidae (Dollfus, 1939)

Renicolidae gen. sp. (metacercaria) (Figure 4.17.)

Prevalence: 2.9-16.75%.
Mean abundance: 0.03-0.78.
Localities and dates of collection: NEA (off Malpica: 27.xi.2001, 12.v.2004, 24.v.2005, 23.xi.2005; Vigo: 18.v.2001, 10.vi.2005, 11.xi.2005, 14.vi.2006, 20.xii.2006, 10.i.2007); WM (off Santa Pola: 01.iii.2006, 19.ii.2007).

Family Strigeidae Railliet, 1919
Genus *Cardiocephaloides* Sudarikov, 1959

***Cardiocephaloides longicollis* (Rudolphi, 1819) (metacercaria)** (Figure 4.18.)

Prevalence: 2.5-36.7%.
Mean abundance: 0.03-0.73.
Localities and dates of collection: NEA (off Ondarroa: 20.vi.2005; Malpica: 23.xi.2005; off Vigo: 11.xi.2005, 20.xii.2006; Barbate: 27.vi.2005, 21.ii.2006); WM (off Santa Pola: 07.vi.2005, 01.iii.2006, 21.vi.2006, 19.ii.2007, 08.iii.2007; Valencia: 13.xi.2003; Barcelona: 22.vi.2005, 07.xi.2005).

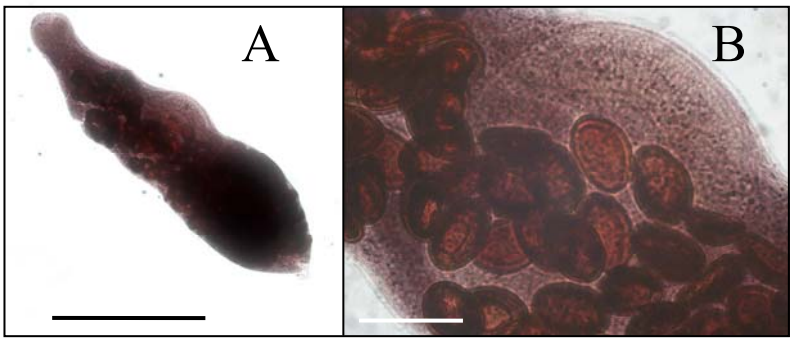

Figure 4.16. Opecoelidae gen. sp. ex *Boops boops*. A, Ventral view. B, Detail showing eggs, ventral view. *Scale-bars*: A, 500 µm;B, 100 µm.

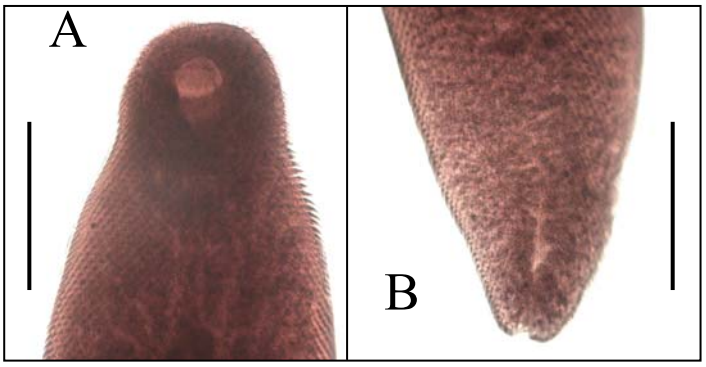

Figure 4.17. Renicolidae gen. sp. (metacercaria) ex *Boops boops*. A, Anterior end, ventral view. B, Posterior end, ventral view. *Scale-bars*: 100 µm

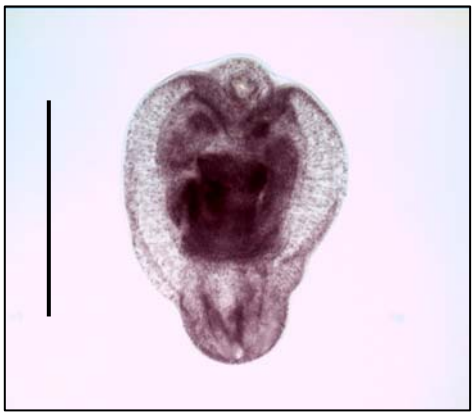

Figure 4.18. Cardiocephaloides longicollis (Rudolphi, 1819) Dubois, 1982 (metacercaria) ex *Boops boops.* Ventral view. *Scale-bar*: 500 µm

Class Palaeacanthocephala Meyer, 1931

Family Echinorhynchidae Cobbold, 1876

Genus *Echinorhynchus* Joy 1835

***Echinorhynchus gadi* Zoega in Müller, 1776** (Figure 4.19.)

Prevalence: 6.7%.
Mean abundance: 0.07.
Locality and date of collection: NEA (off Malpica: 12.v.2004).

Family Polymorphidae Meyer, 1931

Genus *Andracantha* Schmidt, 1975

***Andracantha mergi* (Lundstroem, 1941) Schmidt 1975** (Figure 4.20.)

Prevalence: 3.1%.
Mean abundance: 0.03.
Locality and date of collection: NEA (off Malpica: 24.v.2005).

***Andracantha tunitae* (Weiss, 1914) Zdzitowiecki 1989** (Figure 4.21.)

Prevalence: 2.9%.
Mean abundance: 0.03.
Locality and date of collection: NEA (off Vigo: 14.vi.2006).

Genus *Corynosoma* Lühe, 1904

***Corynosoma* sp. (post-cystacanth)** (Figure 4.22.)

Prevalence: 2.0%.
Mean abundance: 0.02.
Locality and date of collection: NEA (off Vigo: 10.vi.2005).

Figure 4.19. Echinorhynchus gadi Zoega in Müller, 1776 ex *Boops boops.* A, Male, lateral view. B, Anterior end, lateral view. *Scale-bars*: 1000 µm

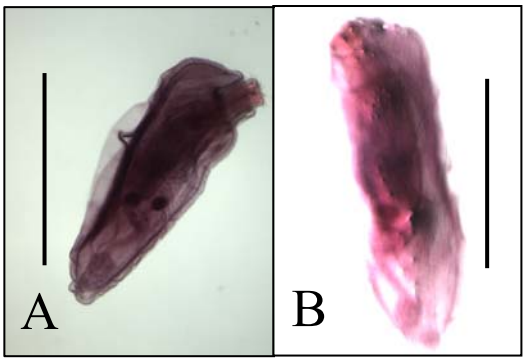

Figure 4.20. Andracantha mergi (Lundstroem, 1941) Schmidt 1975 ex *Boops boops*. A, Male, ventro-lateral view. B, Detail of ventral spines. *Scale-bars*: 1000 µm.

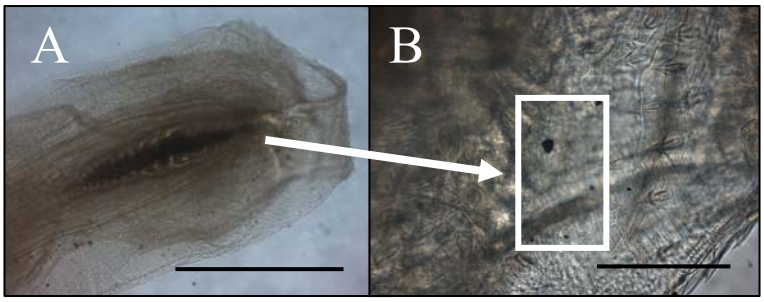

Figure 4.21. Andracantha tunitae (Weiss, 1914) Zdzitowiecki 1989 ex *Boops boops*. A, Anterior end, lateral view; B, Interruption of the spines on the trunk, ventral view. *Scale-bars*: A, 500 µm; B, 100 µm.

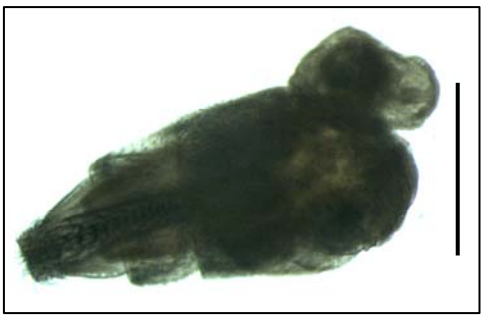

Figure 4.22. Corynosoma sp. ex *Boops boops*. Lateral view. *Scale-bar*: 1000 µm.

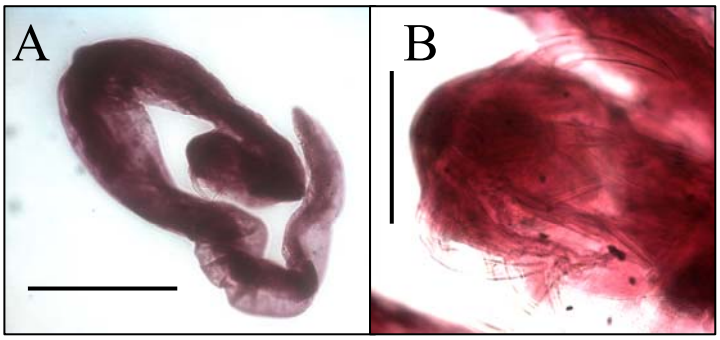

Figure 4.23. *Neoechinorhynchus agilis* (Rudolphi, 1819) ex *Boops boops.* A, Individual *in toto*; B, Proboscis, lateral view. *Scale-bars*: A, 500 µm; B, 100 µm.

Class Eoacanthocephala Van Cleave, 1936

Family Neoechinorhynchidae Ward, 1917

Genus *Neoechinorhynchus* Hamann 1892

***Neoechinorhynchus agilis* (Rudolphi, 1819)** (Figure 4.23.)

Prevalence: 3.3%.
Mean abundance: 0.03.
Locality and date of collection: NEA (off Malpica: 12.v.2004).

Phyllum Nematoda Rudolphi, 1808

Family Camallanidae Railliet & Henry, 1950

Genus *Camallanus* Railliet et Henry, 1915

***Camallanus* sp.** (Figure 4.24.)

Prevalence: 0.8%.
Mean abundance: 0.01.
Locality and date of collection: WM (off Santa Pola: 07.vi.2005).

Family Cucullanidae Cobbold, 1864

Genus *Cucullanellus* Törnquist, 1931

***Cucullanellus* sp. (juv.)** (Figure 4.25.)

Prevalence: 6.7, 0.8%.
Mean abundance: 0.10, 0.01.
Localities and dates of collection: NEA (off Barbate: 27.vi.2005); WM (off Santa Pola: 07.vi.2005).

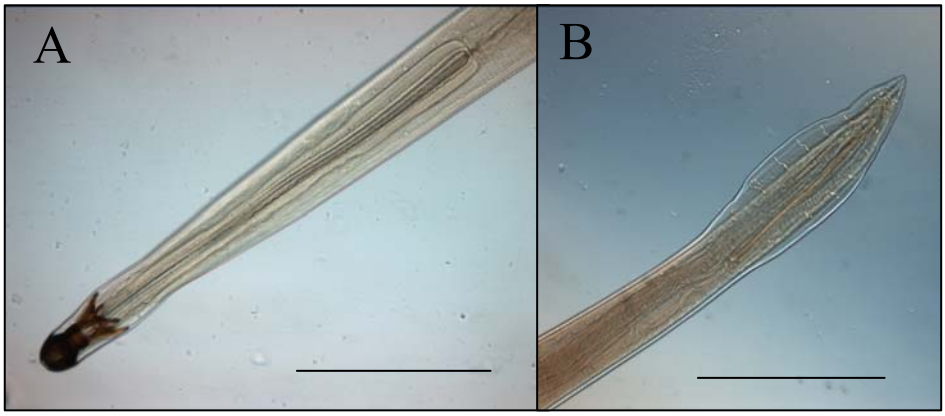

Figure 4.24. Camallanus sp. ex *Boops boops*. A, Anterior end, ventral view. B, Posterior end of a male, ventral view. *Scale-bars*: 500 µm.

Figure 4.25. Cucullanellus sp. (juv) ex *Boops boops*. Lateral view. Arrow points to the intestinal caeca. *Scale-bar*: 1000 µm.

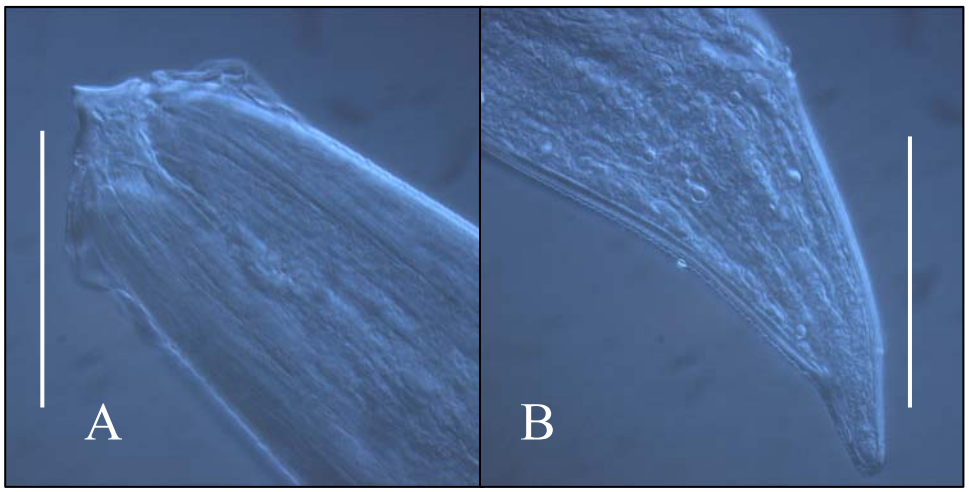

Figure 4.26. Ascarophis sp. nº 1 Petter & Radujkovic, 1989. A, Anterior end, lateral view; B, Posterior end, lateral view. *Scale-bars*: 50 µm.

Family Cystidicolidae Skrjabin, 1946

Genus *Ascarophis* van Beneden, 1870

***Ascarophis* sp. nº 1 Petter & Radujkovic, 1989** (Figure 4.26.)

Prevalence: 3.3-10.0%.

Mean abundance: 0.03-0.10.

Localities and dates of collection: NEA (off Ondarroa: 20.vi.2005; Malpica: 23.xi.2005; off Vigo: 10.vi.2005, 11.xi.2005, 20.xii.2006, 10.i.2007).

Subclass Copepoda Milne-Edwards, 1840

Family Caligidae Burmeister, 1835

Genus *Caligus* Muller, 1785

***Caligus* sp.** (Figure 4.27.)

Prevalence: 2.5-5.9%.

Mean abundance: 0.02-0.06.

Localities and dates of collection: NEA (off Ondarroa: 20.vi.2005; Malpica: 23.xi.2005; Vigo: 11.xi.2005, 14.vi.2006, 20.xii.2006, 10.i.2007).

Family Lernaeopodidae Milne Edwards, 1840

Genus *Clavellodes* Wilson, 1915

***Clavellodes* sp.**

Prevalence: 3.3%.

Mean abundance: 0.03.

Locality and date of collection: NEA (off Malpica: 12.v.2004).

Figure 4.27. Caligus sp. ex *Boops boops*. Female, dorsal view. Scale-bar: 1000 µm.

Figure 4.28. Philichthys sp. ex *Boops boops*. A, Male, dorsal view. B, Lateral view. Scale-bars: 1000 µm.

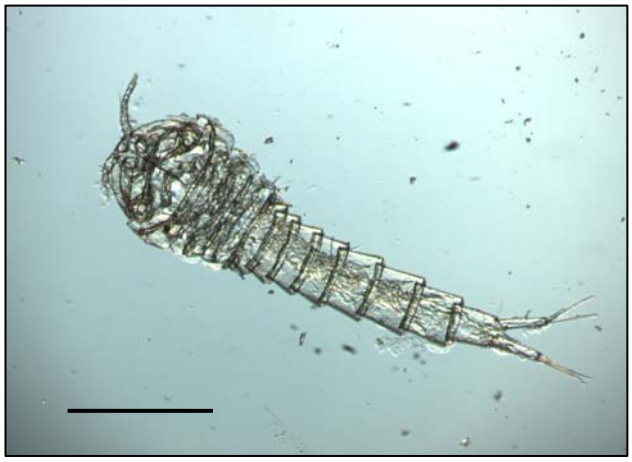

Figure 4.29. Taeniacanthidae gen. sp. (larva) ex *Boops boops*. Dorsal view. Scale-bar: 500 µm

Figure 4.30. Gnathia sp. ex *Boops boops*. A, Praniza larva, dorsal view; B, Lateral view. Scale-bars: 500 µm.

Family Philichthyidae Vogt, 1877

Genus *Philichthys* Steenstrup, 1862

***Philichthys* sp.** (Figure 4.28.)

Prevalence: 6.7%.

Mean abundance: 0.07.

Locality and date of collection: NEA (off Barbate: 21.ii.2006).

Family Taeniacanthidae Wilson, 1911

Taeniacanthidae gen. sp. (larva) (Figure 4.29.)

Prevalence: 0.8%.

Mean abundance: 0.01.

Locality and date of collection: WM (off Santa Pola: 07.vi.2005).

Order Isopoda Latreille, 1817

Family Gnathiidae Harger, 1880

Genus *Gnathia* Leach, 1814

***Gnathia* sp.** (Figure 4.30.)

Prevalence: 3.3- 26.7%.

Mean abundance: 0.07-0.40.

Localities and dates of collection: NEA (off Ondarroa: 20.vi.2005; Malpica: 12.v.2004; Vigo: 18.v.2001; Barbate: 21.ii.2006).

4.4. CHECKLIST OF METAZOAN PARASITES OF *B. BOOPS*

The parasite list in Table 4.4. includes a total of 78 species (7 monogeneans, 37 digeneans, 2 larval cestodes, 12 nematodes, 7 acanthocephalans, 7 copepods and 6 isopods) and 365 host-parasite-area records. Digeneans represent the most diverse group of parasites in *B. boops*. Nine species, which perhaps form the core of the metazoan parasite fauna of the bogue, have been consistently recorded in the three most studied areas (North East Atlantic, Western and Eastern Mediterranean): the monogenean *Microcotyle erythrini*; the digeneans *Bacciger israelensis*, *Aphanurus stossichii*, *Lecithocladium excisum* and *Hemiurus communis;* the larval nematodes *Anisakis simplex s.l.* and *Hysterothylacium aduncum*; and the isopods *Ceratothoa oestroides* and *C. parallela*. Unidentified tetraphyllidean larvae have also been recorded (as *Scolex pleuronectis* Müller, 1788) in these three areas.

Table 4.4. Checklist of the metazoan parasites of *Boops boops. Abbreviations*: NEA, North East Atlantic; SEA, South-East Atlantic; WM, Western Mediterranean; EM, Eastern Mediterranean; M, Mediterranean (no location specified); BS, Black Sea. [a]Recorded as *Allodiclidophora charcoti* (Dollfus, 1922); [b]Recorded as *Microcotyle chrysophryii* Van Beneden & Hesse, 1863; [c]Recorded as *Bacciger bacciger* (Rudolphi, 1819); [d]Recorded as *Bacciger harengulae* Yamaguti, 1934; [e]Recorded as *Haplocladus typicus* Odhner, 1911; [f]Recorded as *Proctoeces lintoni* Siddiqi & Cable, 1960.

Parasite	Area	Reference
Monogenea		
Family Diclidophoridae Cerfontaine,1895		
Cyclocotyla bellones Otto, 1821	NEA	Cordero del Campillo (1975); López-Román & De Armas Hernández (1989); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2007a,b)
	WM	Dollfus (1922); Euzet & Trilles (1961); López-Román & Guevara-Pozo (1974, 1976); Orecchia & Paggi (1978); Renaud *et al.* (1980); Cook *et al.* (1981); Anato *et al.* (1991); Mollaret *et al.* (2000); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2007a, 2008)
	M	Parukhin (1976)[a]; Naidenova & Mordvinova (1997)[a]
Family Diplectanidae Bychowsky, 1957		
Lamellodiscus elegans Bychowsky, 1957	SEA	Parukhin (1966, 1976); Gaevskaya & Aleshkina (1988)
Family Gastrocotylidae Price, 1943		
Pseudaxine trachuri Parona & Perugia, 1889	NEA	López-Román & De Armas Hernández (1989); Cordero del Campillo (1975); Cordero del Campillo *et al.* (1994); Present study
	WM	López-Román & Guevara-Pozo (1974); Orecchia & Paggi (1978); Anato *et al.* (1991); Pérez-del-Olmo *et al.* (2008)
	SEA	Lebedev (1986) cites López-Román & Guevara-Pozo (1974)
Family Microcotylidae Taschenberg, 1879		
Atrispinum salpae (Parona & Perugia, 1890)	NEA	Cordero del Campillo (1975)
	WM	López-Román & Guevara-Pozo (1973, 1974)

Table 4.4. continued

Parasite	Area	Reference
Microcotyle erythrini van Beneden & Hesse, 1863	NEA	Cordero del Campillo (1975); Cordero del Campillo *et al.* (1994); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2007a,b)
	WM	Parona & Perugia (1890); López-Román & Guevara-Pozo (1973, 1974); Cordero del Campillo (1975); Cordero del Campillo *et al.* (1994); Orecchia & Paggi (1978); Renaud *et al.* (1980); Cook *et al.* (1981); Justine (1985); Anato *et al.* (1991); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2007a, 2008)
	EM	Papoutsoglou (1976); Akmirza (1998); Brinkmann (1966)[b]
Microcotyle sargi Parona & Perugia, 1899	SEA	Parukhin (1966, 1976); Gaevskaya & Aleshkina (1988)
	M	Naidenova & Mordvinova (1997)
Microcotyle sp.	M	Parukhin (1976); Naidenova & Mordvinova (1997)
	BS	Dimitrov (1993)
Digenea		
Family Acanthocolpidae Lühe, 1906		
Stephanostomum bicoronatum (Stossich, 1883) met.	WM	Anato *et al.* (1991)
Stephanostomum cesticillum (Molin, 1858) met.	NEA	Pérez-del-Olmo *et al.* (2007a,b)
	WM	Present study
Stephanostomum euzeti Bartoli & Bray, 2004 met.	WM	Pérez-del-Olmo *et al.* (2007a, 2008)
	NEA	Present study
Stephanostomum imparispine (Linton, 1905) met.	SEA	Parukhin (1966, 1976)
Stephanostomum lophii Quinteiro *et al.*, 1993	NEA	Pérez-del-Olmo *et al.* (2007a,b)
Tormopsolus sp. met.	NEA	Present study
	WM	Pérez-del-Olmo *et al.* (2008)
Family Accacoeliidae Odhner, 1911		
Accacladium serpentulum Odhner, 1928	NEA	Pérez-del-Olmo *et al.* (2006); Pérez-del-Olmo *et al.* (2007b)
	WM	Pérez-del-Olmo *et al.* (2006)
Tetrochetus coryphaenae Yamaguti, 1934	WM	Pérez-del-Olmo *et al.* (2007a, 2008)
	NEA	Present study
Family Bucephalidae Poche, 1907		
Prosorhynchus crucibulum Rudolphi, 1819 met.	NEA	Pérez-del-Olmo *et al.* (2007a,b)
	WM	Anato *et al.* (1991); Pérez-del-Olmo *et al.* (2008)
Prosorhynchus sp. met.	SEA	Parukhin (1966, 1976)
Family Derogenidae Nicoll, 1910		
Arnola microcirrus (Vlasenko, 1931)	NEA	Pérez-del-Olmo *et al.* (2007a,b)
	WM	Kostadinova *et al.* (2004a); Bartoli *et al.* (2005); Pérez-del-Olmo *et al.* (2008)
Derogenes varicus (Müller, 1784)	NEA	Pérez-del-Olmo *et al.* (2007a,b)
	WM	Renaud *et al.* (1980); Cook *et al.* (1981); Anato *et al.* (1991); Present study
Magnibursatus bartolii Kostadinova *et al.*, 2003	NEA	Kostadinova *et al.* (2003); Pérez-del-Olmo *et al.* (2007a,b)

Table 4.4. continued

Parasite	Area	Reference
Magnibursatus bartolii Kostadinova *et al.*, 2003	WM	Pérez-del-Olmo *et al.* (2008)
Magnibursatus caudofilamentosa (Reimer, 1971)	NEA	Pérez-del-Olmo *et al.* (2007a,b)
Family Faustulidae Poche, 1926		
Bacciger israelensis Fischthal, 1980	NEA	Cordero del Campillo *et al.* (1994) [c]; Pérez-del-Olmo *et al.* (2004); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2007b)
	SEA	Parukhin (1966, 1976) [d]
	WM	Orecchia & Paggi (1978); Renaud *et al.* (1980) [c]; Cook *et al.* (1981) [c]; Lozano *et al.* (2001); Pérez-del-Olmo *et al.* (2004); Bartoli *et al.* (2005); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2008)
	EM	Sey (1970) [c]; Papoutsoglou (1976) [c]; Fischthal (1980, 1982); Saad-Fares (1985); Saad-Fares & Combes (1992a,b); Akmirza (1998) [c]; Pérez-del-Olmo *et al.* (2004)
	BS	Dimitrov & Bray (1994)
	M	Naidenova & Mordvinova (1997) [c]; Parukhin *et al.* (1971); Parukhin (1976) [c]
Family Fellodistomidae Nicoll, 1909		
Monascus filiformis (Rudolphi, 1819)	M	Naidenova & Mordvinova (1997) [e]
Proctoeces maculatus (Looss, 1901)	EM	Fischthal (1980, 1982) [f]; Le Pommelet *et al.* (1997)
Steringotrema pagelli (van Beneden, 1871)	NEA	Pérez-del-Olmo *et al.* (2007 a,b)
	M	Parukhin (1976); Naidenova & Mordvinova (1997)
Tergestia acanthocephala (Stossich, 1887)	WM	Nikolaeva & Parukhin (1969)
Family Gyliauchenidae Fukui, 1929		
Robphildollfusium fractum (Rudolphi, 1819)	WM	Bartoli *et al.* (2005)
Robphildollfusium martinezgomezi López-Román, *et al.*, 1992	NEA	López-Román *et al.* (1992); Cordero del Campillo *et al.* (1994)
	WM	Pérez-del-Olmo *et al.* (2007a, 2008)
'*Paragyliauchen boopsi*'	M	Parukhin (1976)
'*Paragyliauchen nagatyi*'	EM	Rizk et al. (1996)
Family Hemiuridae Looss, 1899		
Aphanurus stossichii (Monticelli, 1891)	NEA	Cordero del Campillo (1975); Cordero del Campillo *et al.* (1994); Pérez-del-Olmo *et al.* (2004); Kostadinova *et al.* (2004b): Power *et al.* (2005); Pérez-del-Olmo *et al.* (2007b)
	WM	López-Román & Guevara-Pozo (1974); Orecchia & Paggi (1978); Renaud *et al.* (1980); Cook *et al.* (1981); Anato *et al.* (1991); Pérez-del-Olmo *et al.* (2004); Kostadinova *et al.* (2004b): Bartoli *et al.* (2005); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2008)
	EM	Saad-Fares (1985); Saad-Fares & Combes (1992a,b); Sey (1970); Papoutsoglou (1976); Fischthal (1980; 1982); Akmirza (1998); Pérez-del-Olmo *et al.* (2004); Kostadinova *et al.* (2004b)
	BS	Dimitrov (1991); Kostadinova *et al.* (2004b)
	M	Naidenova & Mordvinova (1997); Parukhin (1976)
Hemiurus appendiculatus (Rudolphi, 1802)	EM	Fischthal (1980, 1982)

Table 4.4. continued

Parasite	Area	Reference
Hemiurus appendiculatus (Rudolphi, 1802)	M	Naidenova & Mordvinova (1997)
Hemiurus communis Odhner, 1905	NEA	Pérez-del-Olmo *et al.* (2004); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2007b)
	WM	Renaud *et al.* (1980); Cook *et al.* (1981); Anato *et al.* (1991); Pérez-del-Olmo *et al.* (2004); Bartoli *et al.* (2005); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2008)
	EM	Akmirza (1998); Pérez-del-Olmo *et al.* (2004)
Lecithochirium sp.	M	Parukhin *et al.* (1971); Naidenova & Mordvinova (1997)
Lecithocladium excisum (Rudolphi, 1819)	NEA	Pérez-del-Olmo *et al.* (2004); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2007b)
	WM	Orecchia & Paggi (1978); Pérez-del-Olmo *et al.* (2004); Power *et al.* (2005); Pérez-del-Olmo *et al.* (2008)
	EM	Saad-Fares (1985); Fischthal (1980)
	M	Parukhin (1976); Naidenova & Mordvinova (1997)
Family Lecithasteridae Odhner, 1905		
Lecithaster confusus Odhner, 1905	NEA	Pérez-del-Olmo *et al.* (2006); Pérez-del-Olmo *et al.* (2007b)
Aponurus laguncula Looss, 1907	NEA	Pérez-del-Olmo *et al.* (2006); Pérez-del-Olmo *et al.* (2007b)
Family Lepocreadiidae Odhner 1905		
Lepocreadium album Stossich, 1890	NEA	Pérez-del-Olmo *et al.* (2007a,b)
	EM	Papoutsoglou (1976); Akmirza (1998)
Juvenile lepocreadiids	NEA	Pérez-del-Olmo *et al.* (2007b)
	WM	Present study
Family Mesometridae Poche, 1926		
Wardula bartolii Pérez-del-Olmo *et al.*, 2006	NEA	Pérez-del-Olmo *et al.* (2006); Pérez-del-Olmo *et al.* (2007b)
Family Opecoelidae Ozaki, 1925		
Opecoelidae gen. sp.	NEA	Pérez-del-Olmo *et al.* (2007b)
	WM	Pérez-del-Olmo *et al.* (2008)
Renicolidae (Dollfus, 1939)		
Renicolidae gen. sp. met.	NEA	Pérez-del-Olmo *et al.* (2007b)
	WM	Present study
Family Sclerodistomidae Odhner, 1927		
'*Sclerodistomum saoudi*'	EM	Rizk *et al.* (1996)
Family Strigeidae Railliet, 1919		
Cardiocephaloides longicollis (Rudolphi, 1819) met.	WM	Pérez-del-Olmo *et al.* (2007a, 2008)
	NEA	Present study
Family Zoogonidae Odhner, 1902		
Zoogonus rubellus (Olsson, 1868)	SEA	Parukhin (1966, 1976)
Cestoda		
Family Tentaculariidae Poche, 1926		
Heteronybelinia estigmena (Dollfus, 1960)	NEA	Vassiliades (1985); Palm & Walter (2000)

Table 4.4. continued

Parasite	Area	Reference
Nybelinia lingualis Cuvier, 1817	WM	Anato *et al.* (1991)
Fam. et gen. *incertae sedis*		
Trypanorhyncha larva	M	Parukhin (1976); Naidenova & Mordvinova (1997)
	NEA	Present study
Scolex pleuronectis Müller, 1788	NEA	Pérez-del-Olmo *et al.* (2007a,b)
	WM	Joyeux & Baer (1936); Renaud *et al.* (1980); Anato *et al.* (1991); Pérez-del-Olmo *et al.* (2007a, 2008)
	EM	Akmirza (1998)
	M	Parukhin (1976); Naidenova & Mordvinova (1997)
Nematoda		
Family Anisakidae (Railliet & Henry, 1912)		
Anisakis pegreffii Campana-Rouget & Biocca, 1955 larva	NEA	Mattiucci *et al.* (1997)
	WM	Mattiucci *et al.* (1997)
Anisakis simplex (Rudolphi, 1809) *sensu lato* larva	NEA	Pérez-del-Olmo *et al.* (2007a,b)
	WM	Nascetti *et al.* (1984, 1986); Pérez-del-Olmo *et al.* (2007a, 2008)
	EM	Rizk et al. (1996); Akmirza (2000)
	M	Paggi *et al.* (1983); Orecchia *et al.* (1989)
Larval Anisakidae	NEA	Rego (1987); Power *et al.* (2005)
	WM	Renon & Malandra (1993); Power *et al.* (2005)
'Ascarididae'	WM	Anato *et al.* (1991)
Contracaecum sp. larva	NEA	Pérez-del-Olmo *et al.* (2007a,b)
	WM	Pérez-del-Olmo *et al.* (2008)
	M	Parukhin (1976); Naidenova & Mordvinova (1997)
Hysterothylacium aduncum (Rudolphi, 1802)	NEA	Pérez-del-Olmo *et al.* (2004); Pérez-del-Olmo *et al.* (2007b)
	WM	Renaud *et al.* (1980); Cook *et al.* (1981); Petter *et al.* (1984); Petter & Maillard. (1988a,b); Pérez-del-Olmo *et al.* (2004, 2008)
	EM	Sey (1970); Papoutsoglou (1976); Petter & Radujkovic (1989); Radujkovic & Raibaut (1989); Pérez-del-Olmo *et al.* (2004)
Hysterothylacium fabri (Rudolphi, 1819)	EM	Petter *et al.* (1984); Petter & Radujkovic (1989); Radujkovic & Raibaut (1989); Akmirza (1998)
Hysterothylacium rhacodes (Deardorff & Overstreet, 1978)	EM	Deardorff & Overstreet (1978); Bruce *et al.* (1994)
Hysterothylacium sp.	EM	Rizk et al. (1996)
	NEA	Costa & Biscoito (2003)
'*Porrocaecum* sp.'	SEA	Parukhin (1966, 1976)
Family Camallanidae Railliet & Henry, 1950		
Camallanus sp.	WM	Pérez-del-Olmo *et al.* (2008)
Family Capillariidae Neveu-Lemaire, 1936		
Pseudocapillaria adriatica (Nikolaeva & Naidenova, 1964) Moravec, 1982	EM	Nikolaeva & Naidenova, (1964); Naidenova & Mordvinova (1997); Moravec (2001)
	NEA	Present study
	WM	Pérez-del-Olmo *et al.* (2008)

Table 4.4. continued

Parasite	Area	Reference
Family Cystidicolidae Skrjabin, 1946		
Ascarophis sp. nº 1 Petter & Radujkovic, 1989	NEA	Present study
Family Cucullanidae Cobbold, 1864		
Cucullanellus sp. juv.	NEA	Present study
	WM	Pérez-del-Olmo *et al.* (2008)
Acanthocephala		
Family Echinorhynchidae Cobbold, 1876		
Echinorhynchus gadi Zoega in Müller, 1776	NEA	Pérez-del-Olmo *et al.* (2007a,b)
Family Neoechinorhynchidae Ward, 1917		
Neoechinorhynchus agilis (Rudolphi, 1819)	NEA	Pérez-del-Olmo *et al.* (2007a,b)
Family Polymorphidae Meyer, 1931		
Andracantha mergi (Lundstroem, 1941) Schmidt 1975 (post-cystacanth)	NEA	Present study
Andracantha tunitae (Weiss, 1914) Zdzitowiecki 1989 (post-cystacanth)	NEA	Present study
	WM	Present study
Corynosoma sp. (post-cystacanth)	NEA	Pérez-del-Olmo *et al.* (2007a,b)
Family Rhadinorhynchidae Travassos, 1923		
Rhadinorhynchus pristis (Rudolphi, 1802)	NEA	Vassiliades (1985) ; Present study
	SEA	Parukhin (1966, 1976)
Rhadinorhynchus cadenati (Golvan & Houin, 1964)	SEA	Golvan (1969)
Unidentified acanthocephalans	NEA	Costa & Biscoito (2003)
Copepoda		
Family Caligidae Burmeister, 1835		
Caligus sp.	NEA	Present study
Family Lernaeopodidae Milne Edwards, 1840		
Clavellodes sp.	NEA	Pérez-del-Olmo *et al.* (2007a,b)
Family Naobranchiidae Yamaguti,1939		
Noabranchia cygniformis (Hesse, 1863)	WM	Brian (1906); Delamare Deboutteville & Nunez (1952); Manier *et al.* (1977); Renaud *et al.* (1980); Anato *et al.* (1991); Pérez-del-Olmo *et al.* (2008)
	NEA	Present study
	M	Richiardi (1880)
Family Pennellidae Burmeister, 1835		
Lernaeolophus sultanus Nordmann, 1839	WM	Anato *et al.* (1991)
Peniculus fistula Nordmann, 1832	NEA	Pérez-del-Olmo *et al.* (2007a,b)
	WM	Renaud *et al.* (1980); Pérez-del-Olmo *et al.* (2007a, 2008)
Family Philichthyidae Vogt, 1877		
Philichthys sp.	NEA	Present study
Family Taeniacanthidae Wilson, 1911		
Taeniacanthidae gen. sp. larva	WM	Present study
Clavellodes sp.	NEA	Pérez-del-Olmo *et al.* (2007a,b)

Table 4.4. continued

Parasite	Area	Reference
Isopoda		
Family Cymothoidae Dana, 1852		
Ceratothoa parallela (Otto, 1828)	NEA	Pérez-del-Olmo *et al.* (2007a)
Ceratothoa parallela (Otto, 1828)	WM	Gilbert i Olivé (1919); Montalenti (1948); Euzet & Trilles (1961); Trilles (1964); Trilles (1968); Berner (1969); Romestand & Trilles (1979); Anato *et al.* (1991); Renaud *et al.* (1980)
	EM	Geldiay & Kocatas (1972); Trilles *et al.* (1989); Papapanagiotou & Trilles (2001)
Ceratothoa oestroides (Risso, 1826)	NEA	Costa & Biscoito (2003); Pérez-del-Olmo *et al.* (2007a)
	WM	Balcells (1953); Vu Tan Tue (1963); Trilles & Raibaut (1971); López-Román & Guevara-Pozo (1976); Renaud *et al.* (1980); Anato *et al.* (1991); Pérez-del-Olmo *et al.* (2008)
	EM	Trilles *et al.* (1989)
Ceratothoa oxyrrhynchaena Koelbel, 1878	WM	Euzet & Trilles (1961)
Ceratothoa sp.	NEA	Pérez-del-Olmo *et al.* (2007b)
Anilocra physodes (Linnaeus, 1758)	WM	Trilles (1965, 1968); Renaud *et al.* (1980); Anato *et al.* (1991); Pinnegar *et al.* (2001)
	NEA	Present study
	EM	Trilles *et al.* (1989)
Emetha audouini (Edwards, 1840)	WM	Amar (1951)
Family Gnathiidae Harger, 1880		
Gnathia sp.	NEA	Pérez-del-Olmo *et al.* (2007a)

CHAPTER 5

DEVELOPMENT OF PARASITE COMMUNITIES IN *B. BOOPS*

5.1. INTRODUCTION

Although the idea that infection by metazoan parasites increases with age in fish hosts is not new (see Dogiel *et al.,* 1958), recent empirical evidence suggests that a wide range of host traits, such as body size and/or age (*e.g.*, Guégan & Hugueny, 1994; Lo *et al.*, 1998; Vidal-Martínez *et al.,* 1998; Poulin, 2000; Johnson *et al.,* 2004), habitat and diet (*e.g.*, trophic status, feeding rates; Sasal *et al.,* 1999; Muñoz *et al.,* 2006), degree of vagility (Kennedy, 1990), social behaviour and schooling (Bartoli *et al.,* 2000; Luque *et al.*, 2004) act jointly to provide structure to fish parasite communities. However, studies at the host population level are necessary to pinpoint the role of host age *per se*, and these are still few.

Nested subsets analyses have proved a useful analytical tool to detect size/age-associated compositional heterogeneity across fish parasite assemblages (Guégan & Hugueny, 1994; Poulin & Valtonen, 2001b; Timi & Poulin, 2003). An ontogenetic shift in host diet and/or habitat utilisation is a straightforward mechanism that can produce nested patterns of infracommunity structure (*e.g.*, Rohde *et al.,* 1998; Poulin & Valtonen, 2001b). However, the addition of size-dependent parasites (*i.e.*, with prevalence increasing with size due to higher feeding rates of the host and/or accumulation of parasites) to a baseline community of size-independent parasite species can also result in a nested structure in the absence of a strict diet shift (Zelmer & Arai, 2004). Therefore, other approaches must be combined to nested subsets analyses to determine exactly how the acquisition of parasites in relation to host age serves to structure parasite communities.

Here, these questions are addressed using *B. boops* as a model species. Among the large number of metazoan parasites hosted by this host a group of nine species with a wide geographical distribution, forming the core of the bogue parasite fauna and consistently present in both Mediterranean and NE Atlantic fish was identified (see Chapter 4; Pérez-del-Olmo *et al.,* 2007a). A pilot study on bogue revealed positive or negative (depending on the parasite species) correlations of abundance with fish size (Pérez-del-Olmo *et al.*, 2004). This size-associated variability in some bogue parasites (see also Renaud *et al.,* 1980; Saad-Fares & Combes, 1992a) raises the question as to whether the observed community parameters are inherent to parasite communities in *B. boops* or merely artefacts of sampling heterogeneity with respect to fish size. Knowledge of size-related variation in parasite community composition and abundance among hosts in a fish population is essential for the

adequate application of multivariate statistical analyses of entire parasite communities as biological tags of fish populations (Williams & MacKenzie, 2003, and references therein). Therefore, a study on the demography of parasite community structure as a function of size of individual hosts in bogue has important implications for investigations seeking to establish the harvest localities of fish or to assess the effect of the *Prestige* oil-spill using bogue parasites (*e.g.*, Power *et al.*, 2005; Pérez-del-Olmo *et al.,* 2007b).

Here, using a single population sample from a single habitat, the patterns of composition and structure of parasite communities in *B. boops* were examined along a gradient of fish sizes in order to test the prediction that species forming the core of the parasite fauna and being responsible for recognisable community structure should appear in the fish population earlier than rare and stochastic species (*e.g.*, Vidal-Martínez *et al.,* 1998). This study provides novel data on the sequential development of an unusual sparid-metazoan system characterised by high transmission rates and low levels of host specificity, focusing on (i) variation in community parameters, (ii) distributions of key parasite species, and (iii) predictability of community composition with size. The data on the life-cycles, distribution and host range of the parasites in the Mediterranean, and on host biology were further explored to explain the observed patterns of parasite community structure.

5.2. MATERIALS & METHODS

A total of 130 *B. boops* was collected by local fishermen in two days in June 2005 off Santa Pola (Spanish Mediterranean coast).

Ecological terms follow Bush *et al.* (1997). Species with a prevalence of >30% will be referred to henceforth as common, those with a prevalence of ≤30% as rare and those with prevalence < 10% as accidental. Component population size refers to the total number of individuals of a given species in the total sample. Observed species density distributions within total communities in each size-class were tested for fit to the null model of no interspecific interaction (Janovy *et al.,* 1995).

The data set (SL 10.2-25.0 cm) was stratified into five size-classes with 3.0 cm intervals (ranges and means in Table 5.2.). All parasite taxa were divided into two groups (labelled ‘D’ and ‘F’ in Table 5.1.; parasite assemblages referred to as DA and FA in the

text) with respect to the mode of infection: (i) D, transmitted to fish directly or *via* cercarial penetration; and (ii) F, food-transmitted parasites. Parasites were classified into three categories with regard to their host specificity: (i) bogue specialists (BS); (ii) sparid generalists (SG); and (iii) generalists (G). Data for the regional distribution of parasites were taken from the complete checklist of parasites of *B. boops* (see Chapter 4; Pérez-del-Olmo *et al.,* 2007*a*).

Nested subset analyses were carried out for the total parasite communities and separately for the separate matrices containing either directly transmitted or food-transmitted parasites using the Nestedness Temperature Calculator Program of Atmar & Patterson (1995). The latter matrices were further stratified by size-class and subjected to analysis. Matrices were packed maximally and the nestedness metric "temperature" (T) was calculated. For each matrix, the value of T was compared with those of 1,000 random matrices generated by Monte-Carlo simulations, with no row or column constraints, to assess the probability of randomly obtaining a matrix with the same or higher degree of order.

5.3. RESULTS

5.3.1. Parasites of B. boops *off Santa Pola*

Species composition, prevalence and abundance of each parasite in each size-class sample are summarised in Table 5.1. A total of 26 parasite species was found in the 130 fish examined from Santa Pola. With respect to the mode of infection, 16 species were parasites with complex life-cycles transmitted to the final host by ingestion of the second intermediate/paratenic host. This group accounted for 84.6% of all parasites in the overall sample (range for size-class samples: 77.4 - 93.8%) and included nine species of trematode with a high representation of the superfamily Hemiuroidea (6 species, 53.5% of individuals transmitted *via* food ingestion), six nematodes and a larval cestode. The remaining ten species were parasites transmitted to fish directly (3 monogenean and 3 crustacean species) or *via* cercarial penetration (4 larval trematodes).

Table 5.1. Prevalence (P%) and abundance [mean, MA±SD (median shown if >0 only) of parasites in the sample of *Boops boops* stratified by size. *Abbreviations*: na, not applicable; BS, bogue specialist; SG, sparid generalist; G, generalist; D, transmitted *via* direct infection; F, transmitted *via* food ingestion. Hemiuroideans marked with an asterisk.

Parasite species	**Mode of infection & Specificity**	**Size-class 1**		**Size-class 2**		**Size-class 3**		**Size-class 4**		**Size-class 5**	
		P%	MA±SD (M)	P%	MA±SD (M)	P%	MA±SD (M)	P%	MA±SD (M)	P%	MA±SD (M)
MONOGENEA											
Cyclocotyla bellones	D, G	-	-	-	-	2.9	0.03±0.2	17.2	0.17±0.4	4.8	0.05±0.2
Microcotyle erythrini	D, SG	35.0	1.55±3.2	57.7	1.31±1.5 (1)	73.5	2.12±2.1 (1)	100.0	8.83±7.7 (7)	95.2	10.19±8.0 (10)
Pseudaxine trachuri	D, G	15.0	0.25±0.7	7.7	0.15±0.6	11.8	0.21±0.6	20.7	0.28±0.6	-	-
DIGENEA											
Aphanurus stossichii *	F, G	85.0	3.05±2.1 (3)	96.2	7.69±11.8 (4.5)	91.2	6.38±5.6 (5)	96.6	9.28±15.1 (5)	90.5	6.29±7.7 (4)
Arnola microcirrus *	F, SG	5.0	0.10±0.5	-	-	-	-	-	-	-	-
Bacciger israelensis	F, BS	95.0	15.25±18.1 (9)	88.5	6.58±9.2 (4.5)	94.1	10.29±9.0 (9)	82.8	16.21±19.6 (10.5)	85.7	36.19±53.9 (12)
Cardiocephaloides longicollis met.	D, G	10.0	0.20±0.7	19.2	0.31±0.7	17.7	0.18±0.4	20.7	0.28±0.6	28.57	0.43±0.8
Hemiurus communis *	F, G	100.0	21.00±17.4 (18)	96.2	9.12±7.2 (6)	94.1	13.79±22.4 (8.5)	93.1	13.93±27.3 (5)	95.2	6.76±5.9 (1)
Lecithocladium excisum *	F, G	15.0	0.20±0.5	34.6	0.42±0.6	41.2	0.65±1.0	55.2	1.21±1.8 (1)	33.3	0.43±0.7
Magnibursatus bartolii *	F, BS	-	-	-	-	-	-	3.4	0.03±0.2	4.8	0.05±0.2
Opecoelidae gen. sp.	F, na	-	-	-	-	2.9	0.03±0.2	-	-	-	-
Prosorhynchus crucibulum met.	D, G	10.0	0.20±0.7	3.9	0.15±0.8	20.6	2.29±7.4	13.8	2.34±9.67	9.5	0.14±0.5
Robphildollfusium martinezgomezi	F, BS	-	-	11.5	0.27±1.0	-	-	-	-	4.8	0.05±0.2
Stephanostomum euzeti met.	D, G	-	-	11.5	0.31±0.9	23.5	0.29±0.6	24.1	0.28±0.5	4.8	0.05±0.2
Tetrochetus corypahenae *	F, G	-	-	3.9	0.04±0.2	-	-	-	-	-	-
Tormopsolus sp. met.	D, G	5.0	0.05±0.2	-	-	5.9	0.06±0.2	3.4	0.03±0.2	-	-
CESTODA											
Scolex pleuronectis	F, G	10.0	0.15±0.5	15.4	0.15±0.4	14.7	0.21±0.5	20.7	0.72±2.1	19.0	1.67±6.8
NEMATODA											
Anisakis simplex sensu lato larva	F, G	-	-	3.9	0.04±0.2	5.9	0.06±0.2	24.1	0.24±0.4	14.3	0.33±1.1
Camallanus sp.	F, na	-	-	-	-	-	-	3.4	0.03±0.2	-	-
Pseudocapillaria adriatica	F, G	-	-	3.9	0.04±0.2	-	-	-	-	4.8	0.05±0.2
Contracaecum sp. larva	F, G	-	-	-	-	2.9	0.06±0.3	-	-	-	-
Cucullanellus sp.	F, na	-	-	3.9	0.04±0.2	-	-	-	-	-	-
Hysterothylacium aduncum larva	F, G	35.0	0.50±0.8	61.5	0.96±1.1	44.1	0.79±1.0	69.0	1.17±1.2 (1)	81.0	1.86±1.6
ISOPODA											
Ceratothoa oestroides	D, SG	5.0	0.40±1.8	-	-	2.9	0.03±0.2	-	-	4.8	0.05±0.2
COPEPODA											
Naobranchia cygniformis	D, SG	-	-	19.2	0.19±0.4	20.6	0.21±0.4	24.1	0.31±0.6	19.1	0.19±0.4
Peniculus fistula	D, G	-	-	-	-	-	-	-	-	9.5	0.10±0.3
Component community richness			13		17		18		17		18
Proportion of individuals transmitted *via* food chain			0.94		0.91		0.86		0.77		0.83
Proportion of generalist individuals			0.60		0.70		0.66		0.54		0.28

Generalist parasites comprised a considerable part of the component community in *B. boops* (16 species, 53.5% of all individuals) compared with bogue specialists (3 species, 35.4%) and sparid generalists (4 species, 11.1%). This excludes three taxa not identified to the species level but only being represented by 1 specimen each in the total sample (see Table 5.1.).

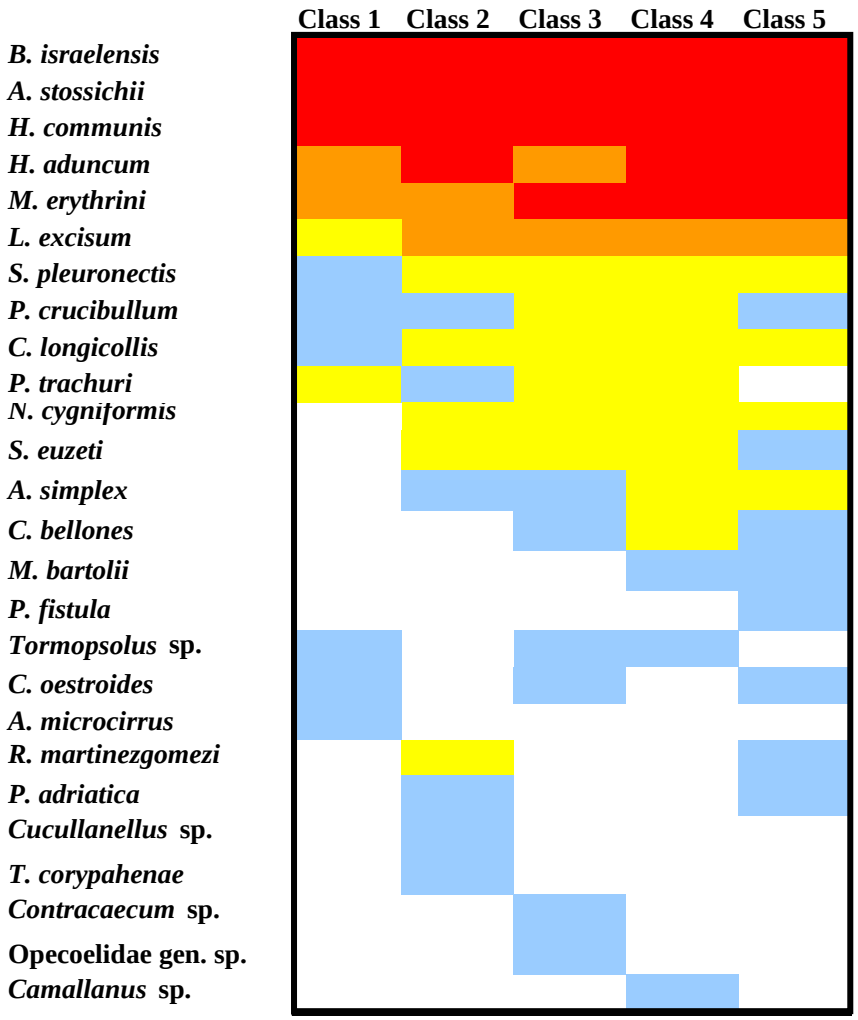

Figure 5.1. Schematic illustration of colonisation and persistence (order of appearance and prevalence status) of bogue parasites in the component communities of the five size-class samples. , prevalence > 60%; , prevalence 30-60%; , prevalence 10-30%; , prevalence < 10%.

Figure 5.1. shows the distribution of parasites in relation to their first appearance and prevalence in the size-class samples. Thirteen species colonized the fish of size-class 1. Seven species appeared for the first time in the second size-class and three, two and one species were added to the species lists of the subsequent samples, respectively.

Five groups of species can be distinguished with respect to their prevalence and persistence in the five samples stratified by size. Six species (*Bacciger israelensis*, *Aphanurus stossichii*, *Hemiurus communis*, *Hysterothylacium aduncum*, *Microcotyle erythrini* and *Lecithocladium excisum*) were found in all five samples with high prevalence (> 30%, common species; except for *L. excisum* with a prevalence of 15.0% in size-class 1). Of these, the first three species were the most frequent in all five size-class samples (prevalence: >60%, overall range: 83-100%) and represented the vast majority (78-95%) of the parasites found. Three species (*Cardiocephaloides longicollis*, *Prosorhynchus crucibulum* and *Scolex pleuronectis*) were recovered in all samples but at low prevalences (< 30%, rare species). Four species occurred at low prevalences in four samples, and six species were found with low prevalences in two or three samples. Finally, a group of seven species occurred in only one size-class and, with the exception of *Peniculus fistula*, in a single fish (accidental species). There was a highly significant negative correlation between the order of the 'arrival' of the species (coded 1-5, according to the size-class) and the prevalence at which they infected fish (r_s=- 0.643, p=0.0004; n=26).

5.3.2. Host size and parasite community descriptors

All specimens of *B. boops* examined were infected with 2-13 parasite taxa and harboured 7-245 individual parasites. Species density distributions in all five samples were found to fit the null model of no interspecific interaction based on frequency of co-occurrences (Janovy *et al.* 1995). Data on the mean parasite infracommunity richness and abundance in each size class are given in Table 5.2. Assemblages formed by the two parasite groups with different transmission strategies (direct *vs* food-transmitted) are presented as separate subsets.

Infracommunities tended to increase in richness and abundance with host size (r_s=0.399, p<0.0001 and r_s=0.251, p=0.004, respectively). This positive association was stronger in DA (r_s=0.389, p<0.0001 and r_s=0.593, p<0.0001, respectively) and significant for the number of species only in FA (r_s=0.210, p=0.017). Furthermore, there were significant differences in the distributions of species and individual parasites among the five size-classes (see Table 5.2.). These differences were largely due to the higher parasite load in the largest size-classes (4 and 5) compared to size-classes 1 and 2. With respect to the distributions of individual parasites the lowest abundance of food-transmitted parasites

Table 5.2. Community parameters of parasite assemblages, significance of differ°ences and length correlations of infracommunity richness and abundance in the five size subsamples of *Boops boops*. Abbreviations as in Material and Methods; ns, not significant ($p > 0.05$).

	Size-class 1 (n = 20)	**Size-class 2 (n = 26)**	**Size-class 3 (n = 34)**	**Size-class 4 (n = 29)**	**Size-class 5 (n = 21)**	**Significance of differences**
Fish total length [TL, range (mean) in cm]	12.8-15.1 (13.9)	15.5-18.5 (17.0)	18.3-22.0 (20.4)	21.7-27.0 (23.6)	25.5-29.6 (26.9)	-
Fish standard length [SL, range (mean) in cm]	10.2-12.9 (11.9)	13.2-15.7 (14.7)	16.0-18.9 (17.4)	19.0-21.9 (20.5)	22.0-25.0 (23.2)	-
Total communities						
Mean no. of species ± SD	4.25 ± 1.2	5.38 ± 1.5	5.74 ± 1.6	6.72 ± 1.9	6.10 ± 1.5	K-W H = 27.11 p < 0.00001
Mean no. of individuals ± SD	42.90 ± 22.1	27.77±15.1	37.68 ± 25.8	55.34 ± 44.5	64.86 ± 52.2	K-W H = 20.50 p = 0.0004
No. of species *vs* Fish length (r_s, p)	ns	r_s = 0.398 p = 0.044	ns	r_s = - 0.443 p = 0.016	ns	-
No. of individuals *vs* Fish length (r_s, p)	ns	ns	ns	r_s= - 0.380 p= 0.042	r_s = 0.511 p = 0.018	-
Assemblages resulting from food ingestion (FA)						
Total no. of species	7	11	9	9	10	-
Mean no. of species ± SD	3.45 ± 0.8	4.19 ± 1.0	3.94 ± 1.0	4.48 ± 1.3	4.33 ± 1.1	K-W H = 11.24 p = 0.0239
Mean no. of individuals ± SD	40.25 ± 21.6	25.35 ± 14.7	32.26 ± 25.5	42.83 ± 42.2	53.67 ± 51.9	K-W H = 11.75 p = 0.0193
No. of species *vs* Fish length (r_s, p)	ns	r_s = 0.405 p = 0.040	ns	ns	ns	-
No. of individuals *vs* Fish length (r_s, p)	ns	ns	ns	ns	r_s = 0.493 p = 0.023	-
Assemblages resulting from direct infection (DA)						
Total no. of species	6	6	9	8	8	-
Mean no. of species ± SD	0.80 ± 0.7	1.19 ± 0.8	1.79 ± 1.1	2.24 ± 1.18	1.76 ± 0.8	K-W H=27.15 p<0.00001
Mean no. of individuals ± SD	2.65 ± 3.9	2.42 ± 1.9	5.41 ± 7.7	12.52 ± 11.9	11.19 ± 7.7	K-W H=51.51 p<0.00001
No. of species *vs* Fish length (r_s, p)	ns	ns	ns	r_s = - 0.434 p = 0.019	ns	-
No. of individuals *vs* Fish length (r_s, p)	ns	ns	ns	ns	ns	-

in size-class 2 and the substantially higher load of directly-transmitted parasites in large fish (class 4-5) contributed to the overall significant differences for total communities by size (see Table 5.2.).

Despite the narrow range of lengths within size classes, some within-class variability was observed. Thus, there were correlations between richness or abundance and host length in some size classes (see Table 5.2. for details).

5.3.3. Key parasite species

Six species (1 bogue specialist, 1 sparid generalist and 4 generalists) were present in all size samples (most with prevalences of >60% in at least 3 samples, see Figure 5.1.), and represented the majority of the parasites recovered in each size-class (96.8, 93.9, 90.3, 91.5 and 95.2% of all individuals, respectively). Of these, *B. israelensis*, *H. aduncum* and *M. erythrini* showed a positive correlation between abundance and fish size (r_s=0.179, p=0.041; r_s=0.281, p=0.001; and r_s=0.646; p<0.0001, respectively) in contrast to *H. communis* which exhibited a negative association (r_s=-0.379; p<0. 0001). No significant relationship was found for *A. stossichii* and *L. excisum*.

A tendency for an increase in prevalence with size was detected for *H. aduncum* (χ^2=8.284; p=0.004) and *M. erythrini* (χ^2=30.954; p<0.0001). However, with the exception of the monogenean *M. erythrini*, which had distinctly higher prevalences in the largest fish (classes 4-5 as compared to 1-2), the prevalence of infection by the dominant species did not differ significantly among the 5 size-classes of fish (see Figure 5.2A). The abundance of *M. erythrini* also exhibited the most significant differences between size-classes (all p<0.00001), following the prevalence divergence pattern (Figure 5.2B). The abundance of the other key species exhibited a few significant differences among size samples (Figure 5.2B). A comparison of the within-class abundance distributions of the three most abundant trematode species showed significant differences exclusively in size-class 1 and 5. The smallest fish had more individuals of *H. communis* than *A. stossichii* and *B. israelensis* (p<0.0001; p=0.023), whereas in the largest fish, there were more individuals of *B. israelensis* (p=0.014; p=0.006).

There was a strong positive correlation (r_s=0.813, p=0.008) between the regional distribution (measured by the number of records; Pérez-del-Olmo *et al.* 2007a) and local prevalence in the total sample of nine taxa (*B. israelensis*, *A. stossichii*, *H. communis*, *L. excisum*, *H. aduncum*, *Anisakis simplex*, *M. erythrini* and *C. oestroides*, forming the core of bogue fauna, plus unidentified tetraphyllidean larva (*Scolex pleuronectis*) known from both the Mediterranean and Atlantic.

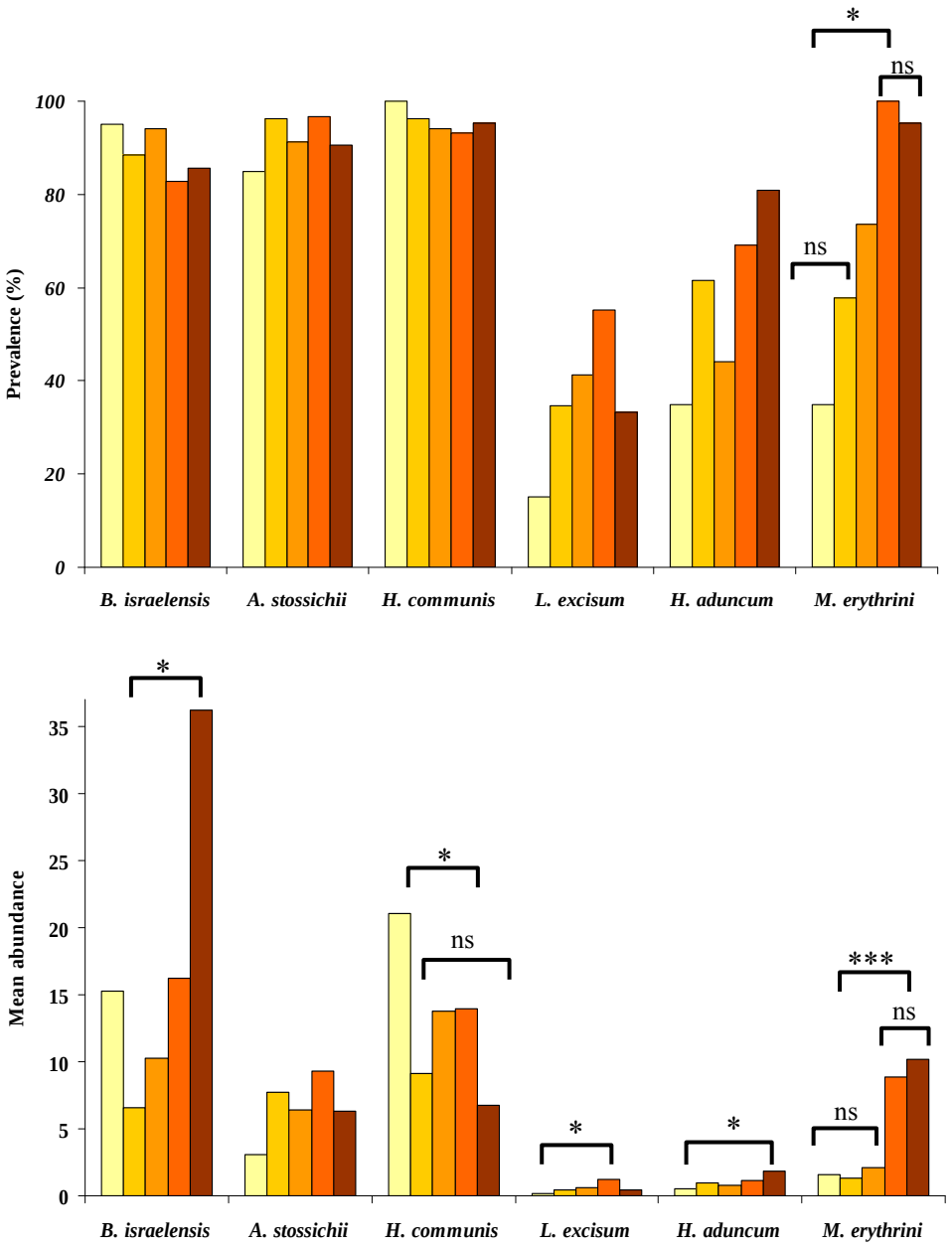

Figure 5.2. Prevalence (A) and mean abundance (B) of the key species in parasite communities of *Boops boops* off Santa Pola. Error bars omitted for clarity. Differences between host size classes (the five columns, in order) indicated by asterisks (*, p<0.05; ***, p<0.001).

5.3.4. Host size and non-random community structure

The pooled infracommunities in *B. boops* produced a significantly nested matrix, as did the assemblages resulting from food ingestion (FA) and direct infection (DA) (Table 5.3.). There were significant correlations between the standard length of individual fish and their rank order in the packed matrix in the total community and FA datasets (the latter being rather weak, with low values for both r_s and p) but not in the DA dataset. Significant nested subset patterns were observed among FA of the five size-classes, as well as among DA of the larger fish (size-classes 3-5). With the exception of class 4 DA, no significant association between the rank order and size of fish was detected (Table 5.3.).

In contrast, there was a strong association between the rank position in the matrix and component population size of parasites (total communities, r_s=-0.961, $p<0.0001$; FA, r_s=-0.949, $p<0.0001$; DA, r_s=-0.854, p=0.0016). Furthermore, the order of species in the packed matrix of total communities was not related to either the mode of transmission (direct infection *vs via* food ingestion, $p>0.05$) or host specificity (generalists *vs* specialists, $p>0.05$). The six key species exhibited consistently the highest ranks in all subsets.

With the exception of *M. erythrini*, these key species also exhibited the most idiosyncratic distributions, which resulted in a characteristic gradual increase to a peak, of idiosyncratic temperatures of the infracommunities with the lowest richness in DA subsets (pooled and size-class 2-5 sets). Generally, the 'kinds' of species contributing to 'erosion' of the uniform distributions of temperatures across hosts differed between FA and DA. Three main groups were distinguished: (i) species 'unexpectedly' present in most species-poor assemblages, (ii) species with erratic occurrence showing both unexpected absences and presences, and (iii) species with low occurrence showing a few accidental unexpected presences. The first group was only detected in FA and consisted of the three most prevalent species (*B. israelensis*, *H. communis*, and *A. stossichii*), whereas the species of the third group were mostly represented in the DA (see Table 5.3.). Species of the second group were detected in both DA (*P. crucibulum*, *C. longicollis* and *Naobranchia cygniformis*) and FA (*H. aduncum*, *L. excisum* and *S. pleuronectis*).

Table 5.3. Nested subset analyses results for the metazoan infra-assemblages in *Boops boops* from off Santa Pola (1000 Monte-Carlo simulation runs). *Abbreviations*: ns, not singnificant; AMIC, *A. microcirrus*; ASTO, *A. stossichii*; BISR, *B. israelensis*; CBEL, *C. bellones*; CLON, *C. longicollis*; COES, *C. oestroides*; HADU, *H. aduncum*; HCOM, *H. communis*; LEXC, *L. excisum*; MERY, *M. erythrini*; NCYG, *N. cygniformis*; PCRU, *P. crucibulum*; PFIS, *P. fistula*; PTRA, *P. trachuri*; SEUZ, *S. euzeti*; SPLE, *S. pleuronectis*; TORM, *Tormopsolus* sp.

Data set	Matrix temperature	Matrix fill (%)	Random temperature ± SD	P value	Correlation between host rank in packed matrix and SL	Top colonisers	Idiosyncratic species (top colonisers marked with a *)
Total metazoan communities	13.7	21.9	62.3±2.5	$3.75.10^{-62}$	r_s = -0.349; p < 0.0001	HCOM; ASTO; BISR; MERY; HADU	BISR*; HADU*; MERY*; ASTO*; LEXC; CLON; SPLE; NCYG
Assemblages resulting from food ingestion (FA)	13.1	25.6	60.6±3	$4.59.10^{-47}$	r_s = -0.191; p = 0.03	ASTO; HCOM; BISR; HADU; LEXC	BISR*; HCOM*; HADU*;LEXC*
Size-slass 1	11.8	49.2	49.2±7.9	$9.69.10^{-7}$	ns	HCOM; BISR; ASTO; HADU; LEXC	LEXC*; BISR*; HADU*; AMIC
Size-slass 2	16.7	38.1	54.6±6.5	$2.69.10^{-9}$	ns	HCOM; ASTO; BISR; HADU; LEXC	ASTO*; SPLE; BISR*; LEXC*
Size-slass 3	14.8	43.7	54.8±5.8	$3.83.10^{-12}$	ns	BISR; HCOM; ASTO; LEXC; HADU	ASTO*; HCOM*; SPLE; LEXC*
Size-slass 4	11.2	49.8	54.7±6.1	$5.05.10^{-13}$	ns	ASTO; HCOM; BISR; HADU; LEXC	BISR*; LEXC*; HADU*; HCOM*
Size-slass 5	20.2	43.3	52.9±7.0	$1.46.10^{-6}$	ns	ASTO; HCOM; BISR; HADU; LEXC	BISR*; HADU*; HCOM*; LEXC*
Assemblages resulting from direct infection (DA)	12.1	18.4	44.6±4.0	$1.86.10^{-16}$	ns	MERY; CLON; NCYG; SEUZ; PTRA	PFIS; PCRU; TORM
Size-slass 1	59.3	20.5	29.2±11.9	ns	ns	MERY; PTRA; TORM	PCRU; CLON
Size-slass 2	23.3	23.4	35.9±9.7	ns	ns	MERY; CLON; NCYG	PCRU; CLON*
Size-slass 3	13.7	23.3	41.0±7.4	$1.17.10^{-4}$	ns	MERY; SEUZ; CLON	NCYG; PCRU
Size-slass 4	15.9	28.0	45.3±7.9	9.10^{-5}	r_s = 0.407; p = 0.03	MERY; SEUZ; NCYG	PCRU; TORM; CLON
Size-slass 5	13.0	22.0	34.9±8.7	0.005	ns	MERY; CLON; NCYG	COES; CBEL

5.4. DISCUSSION

The 26 species found in this study comprised ~ 33% of the parasites of *B. boops* throughout its distributional range (78 species; see Chapter 4; Pérez-del-Olmo *et al.,* 2007a). A characteristic feature of the parasite community in *B. boops* off Santa Pola was the high representation of parasites with complex life-cycles that are transmitted to fish *via* food ingestion (16 species comprising > 80% of all parasite individuals) and the dominance of trematodes (mostly hemiuroids, comprising more than half of the individuals transmitted *via* the food chain in the total sample). The present data only partially support the suggestion for a strong phylogenetic element of the trematode fauna of sparids (Bartoli *et al.,* 2005), since generalist parasites transmitted to *B. boops* from other sympatric species comprised a large percentage of the community (62% of all species and > 50% of all individuals). Of the three bogue specialists, only *B. israelensis* exhibited substantial abundance.

The observed sequence of infection with parasites of bogue size-classes clearly supports the hypothesis that species with wide geographical distributions should appear in the fish population earlier than rare and stochastic species since all helminths (7 species) and the isopod *C. oestroides* identified as the core of the bogue parasite fauna were already present in size-class 1 comprised of juvenile 1-year-old fish. Furthermore, the six key parasites in developing communities persisted as common (prevalence typically of > 60%) in all subsequent size samples and represented the vast majority (>90%) of the individuals. Finally, all species added to communities in larger fish were either rare or accidental; only 5 persisted in subsequent size-class samples, but showing low intensities of infection.

The present observations are supported by the data on another large Mediterranean sample of *B. boops* from the Gulf of Lion, which includes fish sizes below the range of Santa Pola sample (Renaud *et al.,* 1980). These authors found that six of the 'core' bogue parasites infect fish of smaller size [juveniles as small as 11 cm (TL); 9 cm for *B. israelensis*] and are consistently present in larger fish (up to 20 cm). These include the four key species of the study (*i.e.*, *B. israelensis*, *A. stossichii*, *H. communis* and *H. aduncum*) plus the isopods *C. paralella* and *C. oestroides*. Saad-Fares & Combes (1992a) also found that *B. israelensis* and *A. stossichii* infect bogue off Lebanon at an early age (young-of-the-year juvenile fish; forklength < 10 cm).

In spite of the uncertainties regarding the diet of bogue, the most detailed surveys clearly demonstrate that copepods represent the prevailing portion of its food (55.7% and 98.0%, respectively; see Jukic, 1972 for data from Eastern Mediterranean and Bell & Harmelin-Vivien, 1983 for data from Western Mediterranean). Information on parasite life-cycles supports this notion, since calanoids (*Acartia* spp.) act as intermediate hosts for four common species (*H. communis*, *A. stossichii*, *L. excisum* and *H. aduncum*) and indicate three additional alternative routes of transmission for the key parasites of bogue: (i) ctenophores (*H. communis*, *L. excisum*, *B. israelensis* and *H. aduncum*), (ii) chaetognaths (*H. communis* and *A. stossichii*), and (iii) amphipods (*B. israelensis* and *H. aduncum*). Furthermore, the presence of seven accidental species can be also attributed to transmission *via* either the main food resource [*e.g*., harpacticoid and calanoid copepods (*Contracaecum* sp., *A. simplex*, *M. bartolii* and *Arnola microcirrus*) or chaetognaths (*Tetrochetus coryphaenae* and *A. simplex*) and plants (*Robphildollfusium martinezgomezi*)] (Rebecq, 1965; Bray & Gibson, 1980; Gibson & Bray, 1986; Køie, 1991; Køie & Gibson, 1991; Køie, 1992, 1995; Anderson, 2000)

The only species that exhibited a notable positive correlation with size and an increase in both prevalence and abundance in the larger size-classes (SL>19 cm, over 4 year-old) was the directly transmitted monogenean *M. erythrini*. This species appeared on the gills of the smallest fish (SL=10.2 cm) and persisted thereafter, but at much lower prevalence and abundance in younger fish (1-3 year-old). Host body size is perhaps the main determinant of monogenean species richness and abundance due to increased gill habitat heterogeneity and surface in larger fish (Rohde, 1989); this may explain the observed increase of infection levels of *M. erythrini* in older fish.

Overall, the correlation with size of the abundance of the other key parasites (all diet-transmitted) was either not significant (*A. stossichii* and *L. excisum*), weakly positive (*B. israelensis* and *H. aduncum*) or moderately negative (*H. communis*). Whereas the association of the abundance of *H. aduncum* and size is due to a slight larval accumulation as a function of fish age (Poulin, 2000), the differences in abundance distributions of *H. communis* between juvenile (SL 10.2-12.9 cm; 1 year-old) and larger fish (SL >13.0 cm, 2-8 year-old) may indicate differential microhabitat use. For most demersal fish species, there is a trend for fish size to increase with depth, with juveniles occurring in shallower waters

and older fish at greater depths (Cushing, 1976; MacPherson & Duarte, 1991). Studies of fish landings from different types of fishing gear in the Mediterranean support this tendency for *B. boops*, since purse seine landings off Lebanon were exclusively comprised of juvenile young-of-the-year individuals (TL 5.40-14.30 cm; Bariche *et al.,* 2006) and a discard study in North-West Mediterranean indicates that bogue collected by bottom trawl between 14 and 35 m were all small-sized juveniles (Sánchez *et al.,* 2004). Visual fish counts in the area close to Santa Pola have shown that *B. boops* were represented predominantly by fish in the larger size categories (TL 20-29 cm), with no juvenile fish being recorded at depths between 35 and 40 m where adults were found at highest abundances. On the other hand, the juvenile fish cohort (TL < 15 cm) was much less abundant in the overall counts and only observed at somewhat lower depths (30 m) where no adults were recorded (Dempster *et al.,* 2002). These data support the hypothesis of a bathymetric juvenile-mature segregation effect on the distribution of *H. communis* within the bogue population off Santa Pola.

Parasite infracommunities were rich and abundant from an early age. The observed complexity of FA, in particular, meets the prediction of Kennedy *et al.* (1986) for diverse helminth communities in hosts with selective feeding on prey which serve as intermediate hosts for a wide variety of helminths. Although infracommunities tended to increase in richness and abundance with host size, the differences in richness/abundance distributions were mostly due to the higher infection levels in older fish (SL > 19 cm, 4-8 year-old), perhaps related to an increase in feeding rates. Since trematodes encysting on vegetation and transmitted to fish *via* grazing are few (Bartoli, 1987a; Jousson & Bartoli, 1999), it could be expected that a notable decrease of both richness and abundance in older fish would support the statement made by Bauchot & Hureau (1986) that juveniles are predominantly carnivorous and adults mostly herbivorous. However, no abrupt change was observed in parameters to indicate an ontogenetic diet shift; rather, the present data suggest that plant grazing by bogue is only occasional and does not affect the assemblages of food-transmitted parasites (see also Ruitton *et al.,* 2005). The observed variability and lower abundance of infracommunities in size-class 2 might relate to increased vagility as an effect of a transition in bathymetric distribution of fish reaching maturity or to the presence of 1 year-old fish in this sample.

Although bogue parasite communities and those of gastrointestinal parasites, in particular, were rich and abundant, no supportive evidence was found for interspecific competition. The present results indicate a neutral structure in all five size-class sub-samples, since no departures from the null model of independent acquisition were observed in the species density distributions (Janovy *et al.,* 1995). Species co-existence in this host-parasite system appears to be favoured by the different microhabitats utilised by the parasites. Indeed, the most abundant and prevalent species in this study did not exhibit substantial microhabitat overlap. *M. erythrini* is a gill parasite, *A. stossichii* inhabited the oesophagus and anterior stomach, whereas *H. communis* and *L. excisum* were found predominantly in the posterior stomach, and *B. israelensis* in the caeca.

A key result was the recognition of repeatable community structure across size/age cohorts of *B. boops* which translated into a nested subset pattern at the lowest scale, *i.e*., infracommunities within the individual cohorts. This was not unexpected, considering previous studies on developing communities (Poulin & Valtonen, 2001b; Timi & Poulin, 2003; Vidal-Martínez & Poulin, 2003) and the high richness and abundance of infracommunities in bogue resulting from lowered specificity and the presence of several species utilising more than a single route of transmission. However, the higher-level order that delineates predictability of parasite community structure in Santa Pola's bogue could not be completely attributed to either accumulation over time or segregation of species among different size-class hosts. Thus, although the total communities exhibited significant moderate correlation between host rank positions in the packed matrix and size, the two assemblages (FA and DA) differed. FA exhibited a weak correlation with size, whereas no significant correlation was detected in DA. Furthermore, nested patterns were repeated in virtually all size-class subsets within a fairly narrow size range and in the absence of significant correlations between host rank positions and fish size. Finally, key parasites both contributed to and reduced nestedness, and there was a strong association between the rank position in the matrix and component population size of parasite species.

Poulin & Guégan (2000) suggested a possible link between non-random community compositional patterns and a positive relationship between spatial distribution and local abundance of faunas. The present study system seems to provide an illustration of this prediction. Thus, the strong positive correlation between the regional distribution and local abundance of the 'core' species of bogue fauna observed at both component and

infracommunity levels, and the fact that these largely contributed to the homogeneity in parasite community structure and composition in Santa Pola's bogue population, both support the prediction.

In addition to being an unusual sparid, with respect to the specificity of its parasites, bogue appears to be the best candidate (at least among the Mediterranean omnivorous fishes) to provide a setting for the action of passive sampling as a mechanism leading to non-random parasite community structure. Mouth size is one of the most important factors determining foraging ability and consequently fish diet (Breck, 1993; Magnhagen & Heibo, 2001). Karpouzi & Stergiou (2003) have shown that bogue possesses the smallest mouth dimensions among 18 Mediterranean species (including a group of 12 omnivorous species). Ontogenetic changes in diet often are related to alterations in mouth structures (Castro & Hernández-García, 1995). However, Stergiou & Karpouzi (2002) have not reported significant alterations in mouth structures of *B. boops* with increasing body size. This information, together with the exceptionally slow increase in mouth area with length (Karpouzi & Stergiou, 2003) which does not allow consumption of large prey by *B. boops* during its life span, suggests that individual fish are homogeneous and equally accessible to food-transmitted parasites. This proposal is supported by the fact that bogue attains its maximum trophic level early in its life span [at 20 cm (size-class 3 in this study), see Stergiou & Karpouzi, 2002]. On the other hand, suction feeding does not allow for active prey selection.

The small mouth size/area in *B. boops* coupled with suction feeding, while restricting prey size to small invertebrates suspended in the water column, thus facilitates passive ingestion of substantial quantities of potential second intermediate hosts of the key food-transmitted parasite species (copepods, chaetognaths, ctenophores and occasionally small amphipods), which explains their co-occurrence in all size groups and few differences in abundance. However, this non-selective feeding pattern also leads to ingestion of a large additional suite of parasites utilising the same intermediate host groups. This addition to a baseline community of key parasite species results in a nested structure which is linked to the differential species abundance rather than fish size.

CHAPTER 6

SIMILARITY-DISTANCE DECAY RELATIONSHIP IN PARASITE COMMUNITIES OF *B. BOOPS*: THE IMPORTANCE OF WIDESPREAD SPECIES

6.1. INTRODUCTION

Hosts represent replicate, hierarchically structured, fragmented habitats for parasite communities and thus offer a remarkable opportunity for comparative analyses of the variability of community organization patterns at several hierarchical levels (*i.e.* host individuals, populations and communities) (Guégan *et al.*, 2005). One of the main advantages of the parasite community structure is that it provides a useful model for studying macroecological patterns in community diversity and differentiation, which are largely dependent on the fragmentation and isolation of habitats at several nested scales.

One such pattern that has been recognised by ecologists for several decades is the decay of community similarity with geographical distance and recent studies on host-parasite systems have indicated a tendency for species composition and/or richness to be autocorrelated over space (Poulin & Morand, 1999; Poulin, 2003; Fellis & Esch, 2005 a,b; Krasnov *et al.*, 2005; Oliva & González, 2005; Brouat & Duplantier, 2007). However, the decay in similarity of parasite communities was observed for some host species but not in others (Poulin, 2003; Krasnov *et al.*, 2005; Oliva & González, 2005; Brouat & Duplantier, 2007) and this raises the question on how the relationship varies across hosts. Most of the host-parasite systems previously examined come from freshwater and terrestrial environments and physically isolated habitats (marine fish hosts studied by Oliva & González, 2005 being an exception). On the other hand, the similarity-decay relationship in the pioneering 'spatial parasitology' studies is inferred from binary data taken from either published species lists (Poulin & Morand, 1999; Poulin, 2003; Oliva & González, 2005) or abundance data pooled at the level of host populations (Fellis & Esch, 2005 a,b; Krasnov *et al.*, 2005; Brouat & Duplantier, 2007) and no attempt has been made so far to utilise parasite abundance in the individual host patches. Further studies on host-parasite systems, from different environments and geographical gradients may, therefore, prove useful to test if the distance-decay relationship exhibits predictable variation in parasite communities.

The present study explored abundant data on parasite communities in *B. boops*, collected between 2001-2007 at seven localities along a coastal positional gradient from northern NE Atlantic to northern Mediterranean coasts of Spain. The selection of the gradient was based on the assumption that although exchanges of parasite species between communities in the marine environments, where physical barriers are absent, may appear a

common force tending to homogenise parasite communities, large-scale zoogeographical distribution factors may act towards differentiation of marine fish parasite communities. The selection of the model host species is related to its omnivorous diet, which ensures the development of rich and diverse parasite communities, and the sedentary character of its populations, which may provide sufficient isolation for the parasite communities at a lower geographical scale.

In this study, both binary and abundance compositional data at different nested scales were used to: (i) examine the influence of the geographical and regional distance on dissimilarity in community composition and structure; (ii) evaluate the importance of the species of the core fauna to community differentiation; and (iii) test for synchrony in seasonal patterns of community structural similarity-distance relationship. Finally, the spatial distribution of bogue parasites at different nested scales was explored. This revealed a link between the positive abundance-distribution relationship and the importance of widespread species to the decay of community similarity.

6.2. MATERIALS AND METHODS

6.2.1. Host-parasite system

In the course of the present study, examination of parasite community structure in the *B. boops* population from the western Mediterranean revealed a diverse parasite community, with a substantial representation of generalist parasites transmitted to this host from other sympatric host species, and indicated that six species of its core fauna are responsible for the community predictability across size/age cohorts. The combination of small mouth size and suction feeding in this host appears to provide a setting for the action of passive sampling as a mechanism leading to non-random parasite community structure (see Chapter 5; Pérez-del-Olmo *et al.*, 2008).

The above characteristics, combined with the differential abundance of the parasites comprising the hosts' core fauna observed between host populations sampled in the Mediterranean and NE Atlantic (Pérez-del-Olmo *et al.*, 2004), indicated that the rich parasite communities in this fish species may provide a useful model for studying local/regional interactions in parasite dispersal.

6.2.2. Study regions and data

Fish were sampled at seven localities (see Figure 6.1.). Two data sets were subjected to analysis. First, a global comparison was carried out with the entire dataset comprising 22 component community samples (709 fish) collected in late spring [May-June (11 samples)] and late autumn/winter [November (5 samples) and February (6 samples)] during 2001, 2003, and 2004-2007 (these will be henceforth referred to as spring and winter). Secondly, the patterns observed in this relatively noisy (including annual variation) dataset were tested on a subset restricted to communities sampled in 2005 (415 fish, see Table 6.1.). In this dataset one locality (Valencia) was not sampled and one locality (Ondarroa) was sampled in spring only.

Only adult fish within the size range 17-25 cm (SL) were used in the analyses based on results from the present study (Chapter 5; Pérez-del-Olmo *et al.*, 2008), which indicated no significant differences in community richness, abundance or composition between host age cohorts within this length range. The number of fish typically ranged from 20 to 30 per sample (50 and 73 fish were collected in spring 2005 from off Vigo and Santa Pola, respectively) and there was no correlation between sample size and component community richness in either data sets.

6.2.3. Terminology and similarity analyses

Data were gathered at two hierarchical community levels: infracommunity and component community. Two spatial scales were considered in the comparisons: local faunas (global comparison and subset 2005) and component communities (seasonal subset 2005). Although the sampled localities belong to either Mediterranean or NE Atlantic regions, Barbate (Atlantic) was treated separately due to its geographical location at the boundary between the two in order to test the hypothesis of the existence of a 'transition' region for the parasite faunas in bogue.

Parasite abundance-distribution parameters are referred to as regional at the next-highest spatial scale from the scale under consideration (*e.g.* prevalence is a measure of species local abundance at the component community level on a regional scale and a measure of species regional distribution at the infracommunity level on the lower scale).

To examine the variations of parasite species composition and structure with geographical distance among sampling localities and geographical regions, analyses were performed on the two data sets described above in three variants: (i) using presence-absence data; (ii) taking into account species abundances; and (iii) using abundance data but of restricted assemblages of species. In the first analysis geographic 'trees' (similarity networks, see Goüy de Bellocq *et al.*, 2002) were obtained using binary parasite data. A presence/absence matrix of parasite species at each locality was created to obtain distance matrices from Neighbour Joining method with PAUP* 4.0 beta (Swofford, 2002). Trees were drawn using MacClade 4.08. In the second variant, designed to test if parasite load affects community differentiation, linear discriminant analysis was run on ln (x+1) transformed abundance data, using parasite infracommunities as replicate samples and locality as a dependent variable(Sokal & Rohlf, 1995). Species infecting a single fish were considered accidental and removed from this last analysis. The latter routine was applied to restricted species assemblages [further referred to as 'core' and 'marginal' species for simplicity, with no implication to the 'core-satellite' hypothesis (Hanski, 1982)] in the third analysis in order to evaluate their importance to the spatial structure. The list of the 'core' species comprised the parasites identified as the core of the parasite fauna of bogue (*i.e.* the trematodes *Aphanurus stossichii*, *Bacciger israelensis*, *Hemiurus communis* and *Lecithocladium excisum*, larval nematodes *Anisakis simplex s.l.* and *Hysterothylacium aduncum*, the monogenean *Microcotyle erythrini* and the isopod *Ceratothoa oestroides*; see Chapter 4) whereas the remaining species were labelled as 'marginal' species.

The influence of the geographical distance between localities and regions on community compositional and structural differentiation was assessed by applying a method based on the permutation of distance matrices (Legendre *et al.*, 1994; Poulin & Morand, 1999; Goüy de Bellocq *et al.*, 2002). Simple linear (*i.e.* untransformed data), exponential (semi-ln) and power function models (ln-ln) were fitted for each dataset in order to examine the best fit of distance-dissimilarity relationship. These are labelled as model 1, 2 and 3, respectively in Table 6.2. The significance of the best regression model was tested with a randomisation approach (Manly, 1997) using the RT 2.1 program (Western EcoSystems Technology, Inc., Cheyenne, Wyoming). Regressions were performed on the values of the dependent distance matrices (Neighbour Joining in Variant 1; Mahalanobis distance from the discriminant analysis in Variants 2 and 3) and the geographical and region matrices, and based on 1,000 random permutations of the dependent variable matrix.

Linear distances along the coastal line among all pairs of localities were obtained from maps. To code region into a distance matrix, comparisons between localities of the same region were given a distance of 0; comparisons between localities from either NE Atlantic or Mediterranean and the 'transition' region (Barbate) were given a distance of 1; and comparisons between Mediterranean and NE Atlantic localities were given a distance of 2). Conventional linear regressions exploring model fit of dissimilarity-distance and local/regional richness-abundance relationship were performed with Statistica, data for the latter were ln (x+1) transformed.

6.3. RESULTS

A total of 53 species was found in the 22 parasite component communities in bogue (47 were present in the 11 communities of the 2005 subset, see Table 6.1.). Generalist parasites comprised a considerable portion of the parasite communities both with respect to richness and abundance (36 species *vs* 4 bogue specialists and 4 sparid generalists; specificity not determined for further 9 species). Local diversity of the parasite faunas in bogue was generally high (20-38 species) except in Valencia and Barcelona where it was notably lower (9-12 species). The regional fauna of bogue parasites species was richest in the NE Atlantic (43 species *vs* 26 and 31 in the 'transition' region (Barbate) and Mediterranean, respectively). There was a somewhat higher species turnover between the 'transition' region and the NE Atlantic (44% of the species shared) as compared to the Mediterranean (61%). Fifteen parasite species were only present in the NE Atlantic, three only in Barbate and three only in the Mediterranean (of these 6, 2 and 2, respectively, were considered accidental).

The geographic 'trees' showed a clear separation of the NE Atlantic and Mediterranean local faunas in bogue. The two northern Mediterranean faunas formed a separate cluster whereas Santa Pola's fauna was grouped with that of the 'transition' region (see Figure 6.1A). The latter occupied an intermediate position between the two regions in the 2005 subset (Figure 6.1B). A pattern similar to that of the 2005 dataset was observed in the trees constructed with component community data (Figure 6.1C) except that communities of the two closest localities in the NE Atlantic (Malpica and Vigo) were grouped by season. Trees constructed separately for the spring and winter of 2005 (not shown) revealed that component communities sampled in the 'transition' region

Table 6.1. Prevalence (P%) and mean abundance (MA, in parentheses) of parasites in component communities of *Boops boops* sampled in 2005 from five localities along the Mediterranean – NE Atlantic coastal gradient.

Locality	**Ondarroa**	**Malpica**		**Vigo**		**Barbate**		**Santa Pola**		**Barcelona**	
Season	**Spring**	**Spring**	**Winter**	**Spring**	**Winter**	**Spring**	**Winter**	**Spring**	**Winter**	**Spring**	**Winter**
	P (MA)	P (MA)	P (MA)	P (MA)	P (MA)	P (MA)	P (MA)	P (MA)	P (MA)	P (MA)	P (MA)
MONOGENEA											
Cyclocotyla bellones	4.3 (0.04)	9.4 (0.13)	4.9 (0.05)	12.0 (0.14)	2.7 (0.03)			9.0 (0.09)	2.9 (0.03)	6.7 (0.07)	
Microcotyle erythrini	69.6 (1.91)	53.1 (1.56)	7.3 (0.12)	86.0 (3.64)		33.3 (1.77)	10.3 (0.1)	92.3 (7.09)	5.7 (0.06)	76.7 (2.43)	
Pseudaxine trachuri						3.3 (0.07)		12.8 (0.19)	11.4 (0.11)		
DIGENEA											
Accacladium serpentulum				2.0 (0.02)							
Arnola microcirrus	17.4 (0.74)	12.5 (0.13)		4.0 (0.04)							
Aponurus laguncula	4.3 (0.04)				2.7 (0.03)						
Aphanurus stossichii	95.7 (22.26)	100 (46.72)	97.6 (27.9)	100 (34.54)	97.3 (28.89)	96.7 (53.63)	96.6 (23.07)	92.3 (7.68)	88.6 (6.34)	83.3 (3.2)	90.0 (11.5)
Bacciger israelensis	91.3 (18.22)	90.6 (14.84)	80.5 (7.73)	82.0 (10.84)	75.7 (7.19)	90.0 (28.17)	65.5 (8.17)	87.2 (19.27)	100 (16.77)	90.0 (6.5)	63.3 (4.2)
Derogenes varicus		9.4 (0.09)	17.1 (0.24)	44.0 (0.98)	24.3 (0.32)	3.3 (0.03)			2.9 (0.03)		
Hemiurus communis	100 (61.22)	100 (44.66)	78 (3.05)	100 (44.22)	67.6 (2.84)	93.3 (9.4)	75.9 (9.38)	93.6 (12.03)	17.1 (0.69)	20.0 (0.20)	33.3 (0.43)
Lecithocladium excisum		71.9 (1.66)	85.4 (24.9)	82.0 (2.68)	89.2 (5.51)	30.0 (0.5)	13.8 (0.17)	47.4 (0.83)	11.4 (0.34)	36.7 (0.47)	70 (3.03)
Lepocreadium album	4.3 (0.04)			2.0 (0.06)			6.9 (0.10)				
Lecithaster confusus	4.3 (0.04)		2.4 (0.02)	4.0 (0.04)							
Magnibursatus bartolii	95.7 (18.65)	31.3 (0.78)	9.8 (0.63)	44.0 (1.46)	35.1 (0.81)	20.0 (0.2)	10.3 (0.10)	2.6 (0.03)			
Magnibursatus caudofilamentosa	8.7 (0.17)			4.0 (0.06)	2.7 (0.03)	3.3 (0.03)					
Opecoelidae gen. sp.		3.1 (0.03)		2.0 (0.02)	2.7 (0.03)			1.3 (0.01)			
Robphildollfusium martinezgomezi								1.3 (0.01)	2.9 (0.03)		
Steringotrema pagelli				4.0 (0.84)							
Tetrochetus coryphaenae	4.3 (0.04)										
Cardiocephaloides longicollis met.	39.1 (0.87)		4.9 (0.07)		2.7 (0.03)	23.3 (0.23)	20.7 (0.24)	21.8 (0.28)	20.0 (0.26)	23.3 (0.43)	20.0 (0.33)
Lepocreadiidae gen. sp. met.	13 (0.17)	21.9 (0.44)		74.0 (5.1)	29.7 (0.46)	3.3 (0.03)	10.3 (0.21)				
Renicolidae gen. sp. met.		15.6 (0.69)	17.1 (0.49)	22.0 (0.78)	10.8 (0.43)				2.9 (0.03)		
Prosorhynchus crucibulum met.		18.8 (0.31)	7.3 (0.1)	12.0 (0.18)	18.9 (0.32)	93.3 (14.9)	69.0 (5.41)	15.4 (3.82)	2.9 (0.14)		
Stephanostomum euzeti met.						46.7 (0.8)	3.4 (0.03)	19.2 (0.23)	11.4 (0.11)	33.3 (0.50)	3.3 (0.13)
Stephanostomum cesticillum met.		9.4 (0.13)	4.9 (0.05)	38.0 (0.5)	13.5 (0.38)	3.3 (0.07)					
Tormopsolus sp. met.						43.3 (0.87)	72.4 (3.69)	3.8 (0.04)			
Wardula bartolii	34.8 (0.96)	9.4 (0.25)	9.8 (0.15)	20.0 (0.32)	27.0 (0.51)						
CESTODA											
Scolex pleuronectis fam. gen. sp. larva	34.8 (0.43)	6.3 (0.06)	17.1 (0.41)	10.0 (0.1)	5.4 (0.11)	23.3 (0.53)	34.5 (1.1)	17.9 (0.78)	34.3 (1.86)		3.3 (0.03)
Trypanorhyncha fam. gen. sp. larva						3.3 (0.03)					
NEMATODA											
Anisakis simplex sl larva		40.6 (0.72)	24.4 (0.76)	20.0 (0.2)	54.1 (1.16)	23.3 (0.23)	3.4 (0.1)	16.7 (0.22)	11.4 (0.14)		3.3 (0.03)
Ascarophis sp. larva	4.3 (0.04)		9.8 (0.1)	4.0 (0.04)	5.4 (0.08)						
Camallanus sp.								1.3 (0.01)			
Pseudocapillaria adriatica					2.7 (0.03)			1.3 (0.01)	2.9 (0.03)		
Contracaecum sp. larva					2.7 (0.03)				2.9 (0.03)		
Cucullanellus sp. larva						6.7 (0.1)					
Hysterothylacium aduncum larva	26.1 (0.43)	87.5 (2.38)	78.0 (1.66)	42.0 (0.78)	59.5 (1.14)	66.7 (1.63)	27.6 (0.31)	65.4 (1.24)	48.6 (0.71)	86.7 (2.5)	90.0 (3.47)
ACANTHOCEPHALA											
Andracantha mergi		3.1 (0.03)									
Corynosoma sp. (post-cystacanth)				2.0 (0.02)							
Rhadinorhynchus pristis						30.0 (0.7)					
ISOPODA											
Ceratothoa oestroides	13 (0.17)		19.5 (0.37)	14.0 (0.22)	13.5 (0.19)		3.4 (0.03)	1.3 (0.01)	5.7 (0.06)		
Ceratothoa parallela				2.0 (0.02)							
Gnathia sp.	26.1 (0.43)						3.4 (0.14)				
COPEPODA											
Caligus sp.			2.4 (0.02)		2.7 (0.03)						
Naobranchia cygniformis						6.7 (0.07)	6.9 (0.17)	21.8 (0.25)	5.7 (0.06)		3.3 (0.03)
Peniculus fistula			4.9 (0.05)	14.0 (0.24)	5.4 (0.05)			1.3 (0.01)	2.9 (0.03)		
Philichthys sp.							3.4 (0.03)				
Taeniacanthidae gen. sp. larva								1.3 (0.01)			

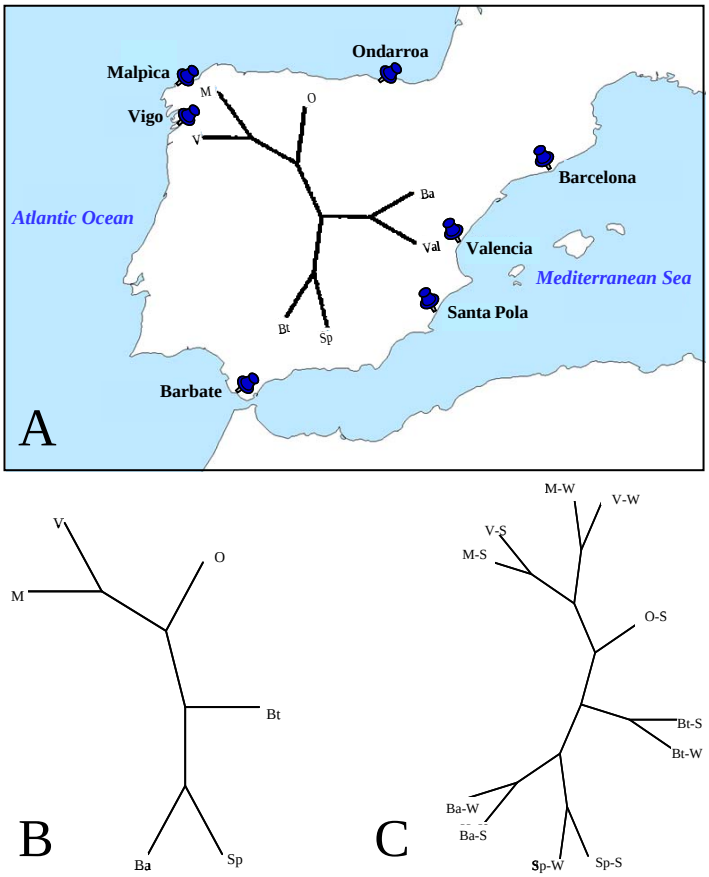

Figure 6.1. Geographic 'trees' obtained from binary parasite data for parasite faunas (A, global comparison; B, 2005 dataset) and component communities (C, 2005 dataset). *Abbreviations*: Ba, Barcelona; Bt, Barbate; M, Malpica; O, Ondarroa; Sp, Santa Pola; V, Vigo; Val, Valencia; S, spring; W, winter.

interchange position (forming a cluster with those from Santa Pola in spring and with Barcelona in winter).

The composition of the local parasite faunas in bogue showed a significant increase in dissimilarity with geographical and 'regional' distance, whereas component communities (seasonal data of 2005 subset) exhibited spatial autocorrelation in spring only (geographical distance only, see Table 6.2.). On the other hand, analyses based on distinctness inferred from infracommunity abundance data revealed a significant increase in faunal/community structural dissimilarity with geographical distance. The effect of region was only significant in the global comparison and in the spring 2005 subset (Table 6.2.).

Regressions with component comunity data (spring/winter 2005 subsets) indicated a clear seasonal effect. Component communities sampled in spring exhibited a highly structured spatial pattern whereas those sampled in winter did not differ from random distribution. Both geographical distance and region contributed significantly to the dissimilarity in community structure observed in spring along the positional gradient (Table 6.2.). There was a noteworthy species turnover between component communities sampled in spring and winter at each locality. On average, 26% of the species in the spring lists disappeared while a similar number of species (23% of the total species number in spring) appeared in the fish populations in winter.

The dissimilarity in the structure of the assemblages comprised of the species of bogue core fauna increased significantly with both geographical and 'regional' distance in the global comparison and the 2005 dataset. Overall, the significance of the influence of these independent variables was statistically stronger in the former analysis. However, in the seasonal comparison a significant pattern was observed in spring only. When assemblages of the 'marginal' species were tested separately, no significant pattern was observed at all scales (Table 6.2.).

The relationship between faunal/community dissimilarity and geographical/'regional' distance in the datasets studied was found to agree with three different models. Of the significant regressions both exponential and power function models most frequently provided the best regression models (Table 6.2.). A simple linear function provided the best fit only for the 'core' species assemblages relationship with geographical distance in the global comparison.

Using individual species' regional distribution (measured as the number of localities where present) and local abundance (measured as the number of component communities where present) as independent observations, a highly significant positive correlation was found between these two variables ($F_{(1, 51)} = 452.64$, $p < 0.0001$, see Figure 6.2A). Generally the species formed a continuum with a large group at the lower abundance-distribution pole. This group comprised fourteen rare species (10 accidental) which were only found in one and two component communities in a single locality. On the other hand, the upper pole represented species which were present in a substantial proportion of the component

Table 6.2. Regression statistics for the effect of distance and region on distinctness of parasite communities in *B. boops*. *Abbreviations:* r^2, coefficient of determination, F, F-ratio; p, significance level; MD, Mahalanobis distance; NJ, neighbour joining distance.

Dataset	Analysis variant	Geographical distance					Region				
		Model	Slope	r^2	F	p	Model	Slope	r^2	F	p
Global comparison	Presence/absence (NJ)	2	0.070	0.256	5.88	0.022	2	0.137	0.273	7.12	0.013
	Abundance (MD)										
	All species	3	0.624	0.479	17.5	0.004	3	0.832	0.256	6.53	0.038
	‘Core’ species	1	0.005	0.533	21.67	0.001	2	0.637	0.486	17.97	0.001
	‘Marginal’ species	3	0.579	0.177	4.07	ns	3	0.695	0.076	1.57	ns
Subset 2005	Presence/absence (NJ)	3	0.201	0.408	8.94	0.019	3	0.323	0.362	7.4	0.043
	Abundance (MD)										
	All species	3	0.451	0.313	5.93	0.034	3	0.392	0.081	1.15	ns
	‘Core’ species	3	0.688	0.703	30.76	0.01	2	0.534	0.487	22.26	0.001
	‘Marginal’ species	2	4.024	0.072	1.02	ns	1	-0.787	0.003	0.04	ns
Spring	Presence/absence (NJ)	3	0.196	0.469	7.07	0.021	3	0.389	0.485	7.52	ns
	Abundance (MD)										
	All species	2	0.001	0.431	6.06	0.043	3	0.814	0.482	7.44	0.036
	‘Core’ species	2	0.001	0.773	26.23	0.017	2	0.636	0.562	10.28	0.017
	‘Marginal’ species	2	0.962	0.007	0.06	ns	3	0.442	0.042	0.35	ns
Winter	Presence/absence (NJ)	3	0.219	0.368	4.67	ns	3	0.407	0.332	3.98	ns
	Abundance (MD)										
	All species	3	0.303	0.196	1.95	ns	3	0.554	0.171	1.65	ns
	‘Core’ species	3	0.437	0.549	9.74	ns	3	0.729	0.409	5.34	ns
	‘Marginal’ species	1	-0.003	0.054	0.46	ns	3	0.453	0.038	0.32	ns

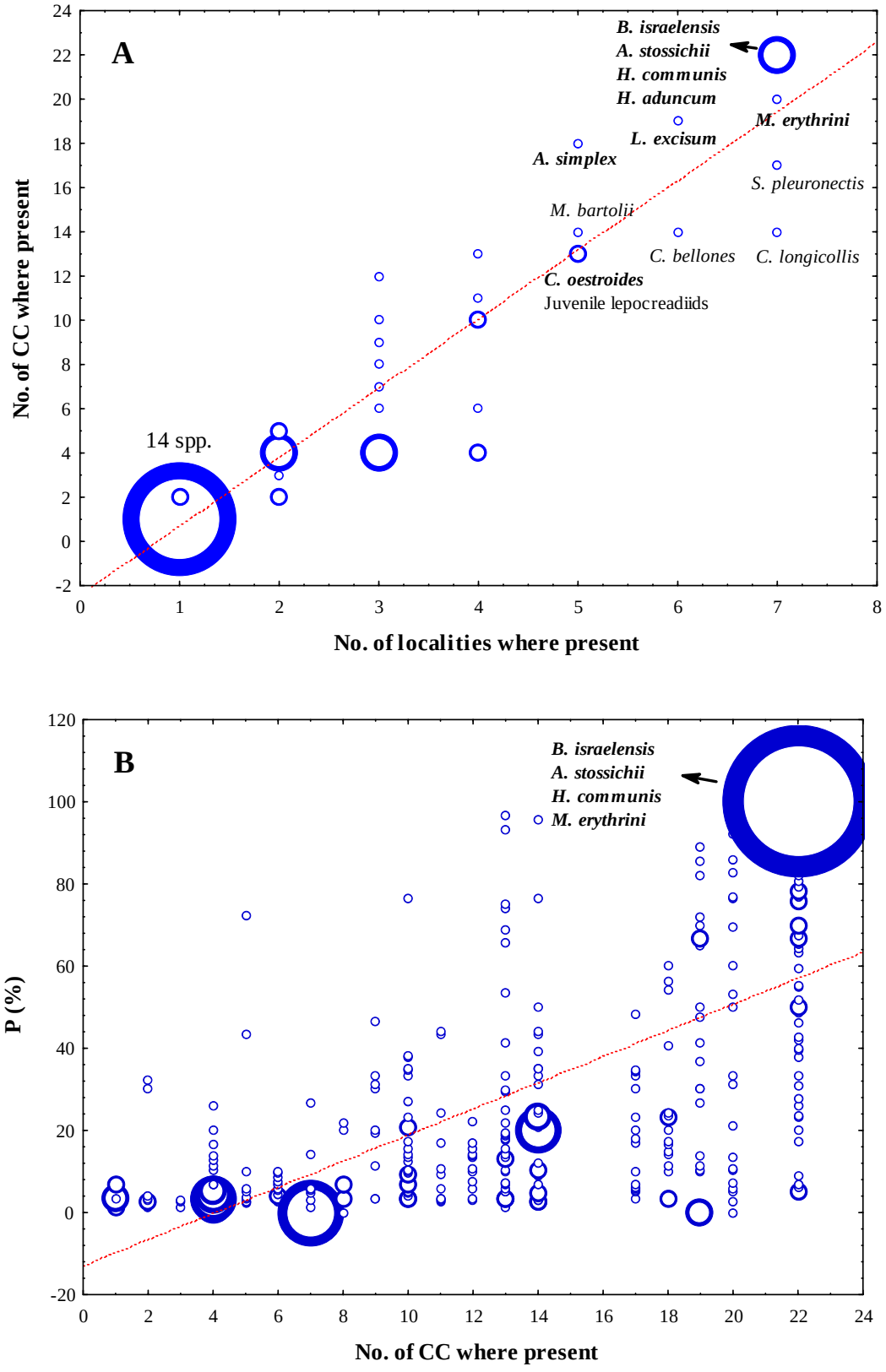

Figure 6.2. Abundance-distribution relationship in parasites of *B. boops* at two higher level scales. A, Local faunas. B, Component communities. 'Bubbles' indicate the relative frequencies of the number of points represented by a single plot position. *Abbreviations*: CC, component communities; P, prevalence.

communities in all localities. Four of the 'core' species (*B. israelensis*, *A. stossichii*, *H. communis* and *H. aduncum*) were present in all component communities and *M. erythrini* was found in 20 component communities (Figure 6.2A). The other three 'core' species (*L. excisum*, *A. simplex* and *C. oestroides*) were closely associated with the upper pole. Notably, two larval forms (unidentified tetraphyllideans *Scolex pleuronectis* and the trematode *Cardiocephaloides longicollis*) not assigned to the 'core' species group were also present in a large proportion of the component communities in all localities.

There was a highly significant correlation between species local abundance and regional distribution (*i.e* prevalence *vs* the number of component communities where present) at the lower spatial scale ($F_{(1, 403)}$ =345.93, p<0.0001, see Figure 6.2B). In contrast to the tight pattern of the distribution-abundance plot at the higher regional-local scale (Figure 6.2A), the plot in Figure 6.2B exhibited a roughly triangular shape which indicates a higher variation of local abundance at this scale. However, the increased frequencies at both distribution-abundance poles were similar. Notably, the same four 'core' species exhibited maximum prevalence or occupied the highest prevalence range. Of these, *B. israelensis*, *A. stossichii* and *H. communis* had a prevalence of 100% in a large proportion of component communities (14, 10 and 9 respectively, see Figure 6.2B) and *M.. erythrini* attained the maximum prevalence in one community. Moreover, these species were well represented in the cluster of points associated with the upper pole, *i.e.* with prevalence > 60% (a boundary line shown for 'core' species category, see Bush & Holmes, 1986) in most communities: *B. israelensis* in 17 component communities, *A. stossichii* in 13, *H. communis* in 7 and *M. erythrini* in 6. Two other 'core' species were also present in the cluster (*H. aduncum* in 9 component communities and *L. excisum* in 8) whereas *A. simplex* and *C. oestroides* exceeded 60% prevalence in a single community each. Finally, only four of the remaining 35 parasite species were present in the upper prevalence–distribution group (juvenile lepocreadiids in 3 component communities, *Magnibursatus bartolii* in 2 and the metacercariae of *Stephanostomum cesticillum* and *Tormopsolus* sp. in 1 community each).

A strong positive relationship was found between species distributional range and maximum intensity of infection ($F_{(1, 51)}$=52.28, p<0.0001, see Figure 6.3A). The most widely distributed 'core' species not only attained the highest maximum intensity levels but

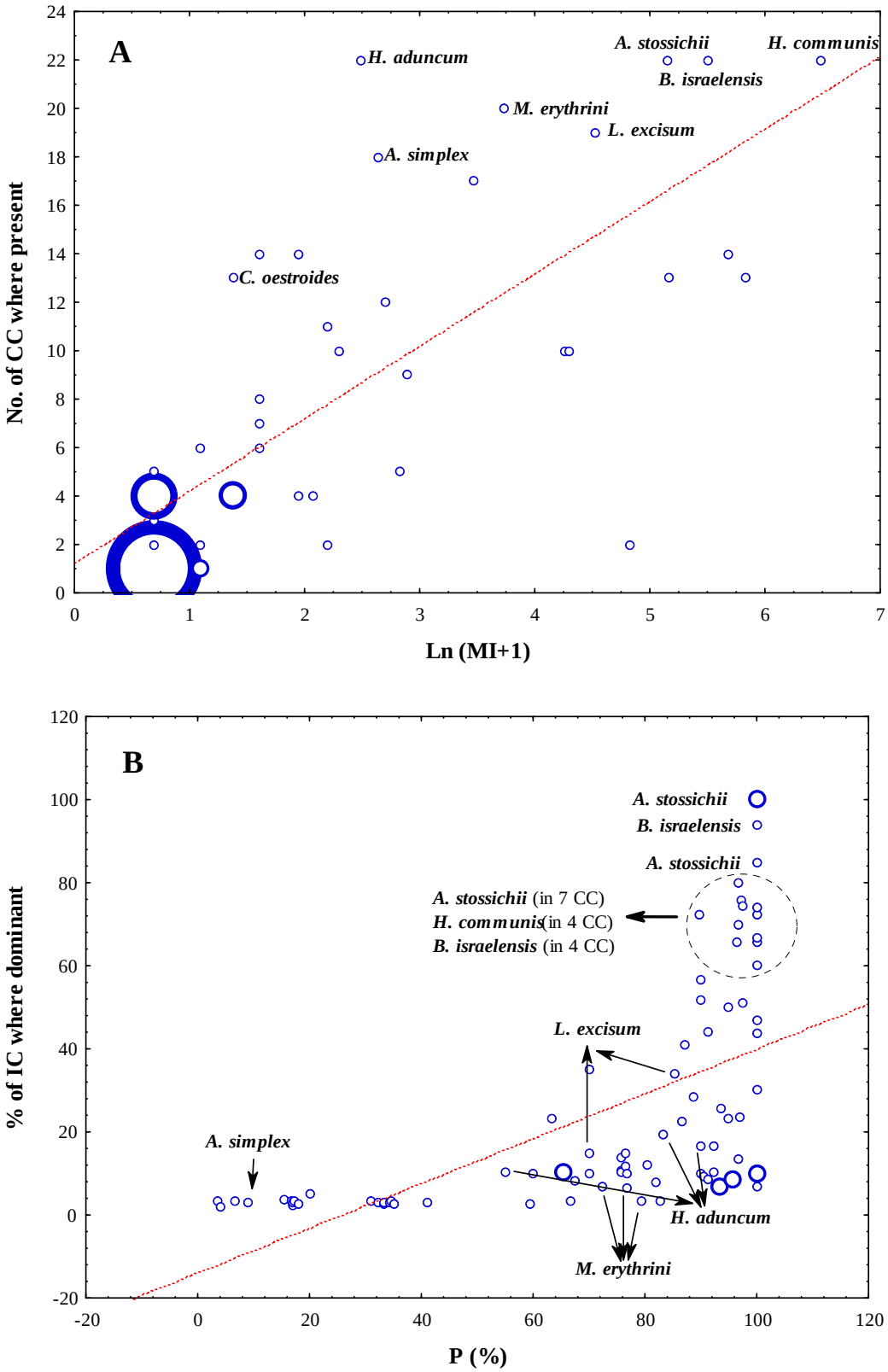

Figure 3. Distribution-maximum parasite intensity (A) and abundance-distribution relationship (B) in parasites of *B. boops* at the lowest (infracommunity) scale. 'Bubbles' indicate the relative frequencies of the number of points represented by a single plot position. *Abbreviations*: CC, component communities; IC, infracommunities; MI, maximum intensity; P, prevalence.

dominated a substantial proportion of infracommunities ($F_{(1, 85)}$=55.11, p<0.0001, see Figure 6.3B). Thus the abundance-distribution relationship at this lowest scale of comparison effectively echoed the patterns observed at the higher spatial scales. There was a significant effect of region (p<0.026) but not season (p>0.05) on the prevalence of the species dominating infracommunities (ANOVA, $F_{(2, 83)}$ =3.825), the prevalence being lower in communities sampled in the Mediterranean.

6.4. DISCUSSION

6.4.1. A multitude of patterns

The present study appears to be the first attempt to test the similarity-distance decay hypothesis using original, taxonomically consistent data at two nested spatial scales (*i.e.* parasite faunas and component communities) and the first to infer the relationships from abundance data gathered at the lowest scale of parasite community organisation.

Three characteristics of the studied system are expected to act towards homogenising the composition of parasite communities in bogue at higher regional scales. First, *B. boops* is perhaps one of the most abundant species in both the Mediterranean and the NE Atlantic (Valle *et al.*, 2003; Boyra *et al.*, 2004). High densities and overlaps of the host populations may, therefore, enhance parasite dispersal and persistence over long distances due to the general link between host population density and parasite transmission rates (see Morand & Poulin, 2004 and references therein). Secondly, a substantial number of bogue parasites utilise the same intermediate hosts and more than two alternative routes of transmission (see Chapter 5; Pérez-del-Olmo *et al.*, 2008). Copepods which represent the prevailing portion of bogues' food (Jukic, 1972; Bell & Harmelin-Vivien, 1983) are prey which serve as intermediate hosts for a wide variety of parasites (including 5 of the 6 'core' species). Thirdly, for generalist parasites, capable of infecting several coexisting host species, host density adopts a wider meaning *i.e.* the total density of all suitable hosts (Morand & Poulin, 2004). Generalist parasites dominated parasite communities in bogue both with respect to richness and abundance. This observation based on a single community studied off Santa Pola (see Chapter 5; Pérez-del-Olmo *et al.*, 2008) was confirmed in the present, relatively long-term survey on a wide geographical extent. Since the transmission and persistence of generalist parasites is associated with a multiple array of hosts they may have more opportunities to expand their geographical range (Poulin, 2003). The present

data provides strong support for this prediction since, with the exception of *B. israelensis*, the few bogue specialists exhibited narrow distributional range and low abundance whereas generalist species (including the other 7 'core' species) were widespread and abundant at all scales of the study.

Furthermore, the transmission of the 'core' species is perhaps fuelled by predation of copepods by chaetognaths, which thus may accumulate and transfer species in 'packets' (*e.g.* hemiuroids and larval anisakids) to communities of the final fish hosts. The above host and parasite characteristics which are not, however, exceptional for marine fish host-parasite systems, would tend to favour parasite community homogenisation over time and space.

However, the initial expectations of a substantial compositional homogenisation of local faunas and component communities of bogue parasites were not met, thus indicating that larger-scale processes may have a strong influence on local community structure (*i.e.* top-down effect, see Poulin,1998; Poulin *et al.* 2000; Guégan *et al.*, 2005). This suggestion is also supported by the significant increase of dissimilarity with increased 'regional' distance observed in the majority of the comparisons. A number of bogue parasite species exhibited specific regional distributions restricted to a single region and the three regional faunas differed in richness and species turnover and this might have contributed to the observed relationship. Interestingly, the hypothesis that Barbate can be considered as 'transition' region between the Mediterranean and Atlantic parasite faunas of bogue is supported by the present results probably due to the higher interchange of parasite species with the Mediterranean.

This is a second marine example to show decline in compositional similarity with distance. Oliva & González (2005), using presence/absence parasite data, found a similarity-distance decay relationship in three of four fish species studied in the eastern Pacific. In addition to the substantially higher rates of increase of community dissimilarity with distance (range for slopes in presence-absence data regressions 0.07-0.201 *vs* 0.0001-0.0003) a diversity of relationships in terms of best model fit was observed, varying among datasets and species being analysed. In particular, the power function model fit was unexpected and to the best of our knowledge not yet reported. This model implies that faunal/community dissimilarity becomes increasingly independent of distance (*e.g.* global

comparison, all species and both distance variables). However, no clear pattern was found in the occurrence of the two most frequent models, *i.e.* the power and exponential function with respect of the scale and/or parasite species in the analysis.

One important observation in the present study is the seasonal variation in the dissimilarity-distance relationship depicted at the lower scale of the analysis (seasonal 2005 subset). The lack of spatial synchrony in the structure of both component communities and assemblages of the 'core' and 'marginal' species in the winter 2005 comparison indicates higher homogenization of communities in the cold season probably due to the temperature effect on parasite intermediate hosts. The considerable species turnover (50% change on average) and the stochastic variations in both prevalence and abundance (see Table 6.1.) indicate an increased stochasticity in transmission rates of parasites and/or interruption of host colonisation for some species.

6.4.2. How to be important?

The extent to which particular patterns are shaped by spatial or environmental changes in the contribution of different clades to an assemblage is an important issue in understanding spatial patterns of assemblage composition (Gaston *et al.*, in press). These authors suggested that although the extent to which more widespread species shape assemblage patterns remains unknown, the latter may account for patterns based on summed abundances of species in an area due to the general positive interspecific abundance-distribution relationship (Gaston *et al.*, 2000; Gaston, 2003). The present results, although not inferred from summation, validate this prediction.

The idea that the rate of decline in similarity might be related to the 'kinds' of parasite species of which communities are comprised is not new. Poulin & Morand (1999) and Karvonen & Valtonen (2004) were the first to assume that the nature of the constituent species (*e.g.* generalist/specialist and autogenic/allogenic parasites) may affect the similarity-distance relationship. However, only one study has so far explicitly tested the hypothesis of the rates of distance decay of similarity among parasite communities in a freshwater fish as a result of parasite dispersal abilities using the autogenic/allogenic proxy (Fellis & Esch, 2005 a,b). These authors have shown that the similarity of allogenic species assemblages decays exponentially with geographical distance whereas autogenic similarity decays linearly.

Instead of using a dichotomy related to parasite life-cycle or specificity patterns, a different assessment of the dispersal ability of the parasites was attempted by testing the hypothesis that interspecific abundance-distribution patterns should be most important for the distance-decay relationship of similarity. Although the 'core' species were *a priori* identified based on their distributional range in published records (Chapter 4; Pérez-del-Olmo *et al.,* 2007a), the detailed abundance-distribution comparisons fully supported this selection at all community scales. The 'core' species were also found to infect bogue populations earlier than rare and stochastic species (Chapter 5; Pérez-del-Olmo *et al.,* 2008).

The patterns observed sustain the idea that widespread species would be strongly associated with patterns of variation in environmental conditions since the spatial synchrony was solely due to the assemblage of the 'core' species (see Table 6.2.), whereas the remaining species exhibited a random spatial structure. Interestingly, this assemblage also exhibited substantially higher rates of decrease in similarity as the 'regional' distance increases. This indicates that colonisation rates of the 'core' species are spatially structured on a regional scale. On the other hand, the fact that although these species were virtually 'everywhere', the significant declines of similarity with geographical distance indicate that their persistence on a local scale is also spatially structured.

Although a final host characteristic emerges as a major determinant for this pattern it is in no way preventing generalisation across fish hosts. Bogue utilises suction feeding (Linde *et al.,* 2004) which does not allow for active prey selection. This host, therefore, acts as a passive sampler of the local parasite populations and parasite infracommunities reflect closely parasite transmission rates on a small spatial scale. On the other hand, local environmental conditions shape communities in intermediate host populations thus leading to differential transmission rates (and persistence) of the individual species across sites, which appear more similar in close localities, thus strengthening the spatial synchrony among parasite communities in bogue and its decline with distance. All these considerations stress the importance of the parasite supracommunity (*sensu* Bush *et al.,* 1997) to the decay of similarity with distance.

In conclusion, the results of the present study reveale that: (i) geographical and 'regional' distance affects the species composition in the system studied at both scales; (ii) the distance between localities/regions contributes significantly to the decay of the similarity estimated from parasite abundance at the lowest scale (*i.e.* infracommunities); (iii) the shape of these relationships differ between datasets and analyses; (iv) the structured spatial patterns are consistent in time but not across seasons; and (v) the 'core' species of bogue parasite fauna contribute substantially to the observed patterns of both community homogenisation and differentiation due to the strong relationship between species local-regional distribution and abundance.

CHAPTER 7

PARASITE COMMUNITIES IN *B. BOOPS* AFTER THE *PRESTIGE* OIL-SPILL: A FOLLOW-UP STUDY

7.1. INTRODUCTION

The *Prestige* oil-spill started on 13th November 2002 when this oil tanker carrying crude oil began leaking, broke in two and sank over the Galician Bank, *c.* 103 miles off the Spanish coast. The release of 60,000 tons of crude oil into the sea contaminated, to some degree, large areas of the Galician and Cantabrian Sea. Because of its huge geographical spread, the spill reached virtually all types of marine habitat (Albaigés *et al.*, 2006).

Previous experience has shown that the recovery of impacted marine ecosystems may take from as little as two years to over a decade following an oil-spill. Thus, a recent study examining changes in the benthic macrofauna after the 1992 *Aegean Sea* spill in Galician waters (off A Coruña) over a four-year period compared with pre-spill data, found that, during the first 12 months, most of the species sensitive to crude oil disappeared or declined to be replaced by opportunistic species (mostly polychaetes). This sudden decrease in biodiversity and biodensity was followed by a three-year low, until the original communities begin to re-emerge (Gómez Gesteira & Dauvin, 2005).

Environmental pollution affects parasite populations and communities, both directly and through effects on intermediate and final hosts. Previous studies support the view that ectoparasites increase and endoparasites decrease in prevalence and abundance in fish after chronic exposure to xenobiotics and polycyclic aromatic hydrocarbons (PAHs), in particular (MacKenzie, 1999; Khan, 2003). Host immunosuppression has been suggested as one of the main causes contributing to an increase of ectoparasites. On the other hand, the decrease of endoparasites might be associated with both direct (low survival of larval forms) and indirect (a decline in intermediate hosts) effects of pollutants (see Khan, 2003 and references therein). Recently, the ratio between single-host (monoxenous) and multiple-host (heteroxenous) parasite species, which basically reflects the above findings, has been used in analyses of impacted coastal marine ecosystems (Broeg *et al.*, 1999; Diamant *et al.*, 1999; Dzikovski *et al.*, 2003).

One of the drawbacks of follow-up studies of catastrophic events, such as the *Prestige* oil-spill, is the absence of pre-disturbance data. On the other hand, whereas a wealth of studies on the effects of the oil-spill on marine communities concerns the coastal areas (intertidal and subtidal

habitats) directly oiled by the spill (http://otvm.uvigo.es/vertimar2005) the information on possible effects offshore, in shelf communities is still scarce (*e.g.* Martínez-Gómez *et al.*, 2005, 2006; Serrano *et al.*, 2005, 2006) and reflects the difficulties to identify major physical (*e.g.* sediment contamination) and toxicological (*e.g.* PAH bioaccumulation) impacts in the continental shelf.

In the course of a pilot study, using parasite communities as predictors of harvest location of fish (Power *et al.*, 2005), a large sample of bogue, *Boops boops* (L.), was collected in 2001 from the NE Atlantic coasts of Spain. Three of the localities originally sampled were re-sampled after the *Prestige* oil-spill. The rich parasite fauna combined with the site fidelity of bogue, indicated that parasite communities are likely to reflect local food web structure, as well as levels of infection and other characteristics of the localities of sampling (*e.g.* oil-spill impact) at a finer geographical scale.

This chapter presents the results from a comparative study on the structure and composition of metazoan parasite communities in *B. boops*, using a series of seasonal samples collected between 2004-2006 from three impacted localities on the Atlantic coast of Spain. The study is focused on the distribution of both individual parasite species and larger functional groupings in order to test their usefulness to detect directional trends in community composition and structure that might be related to the *Prestige* oil-spill disturbance of the natural coastal communities.

7.2. MATERIALS & METHODS

7.2.2. Fish & parasite samples

A total of 400 fish were analyzed comprising 11 samples collected from Galicia (off Malpica and Vigo) and the Basque Country (off Ondarroa) (see map in Figure 7.1. and Tables 7.1. and 7.2. for sampling details). Three pre-spill samples collected in 2001 provided comparative data on the variations in parasite community structure in *B. boops* populations from NE Atlantic and were used in 'before-after' contrasts. Due to the ban on fishing in 2002 and 2003 and the erratic fishing practices in the affected zones, there were difficulties in obtaining post-spill samples (see Tables

7.1., 7.2.). Ondarroa was originally selected as a control site in order to carry out a BACI (before-after-control-impact) design. Unfortunately, this locality was also oil-contaminated in January 2003 assisted by the action of Poleward Current (Navidad current, see Garcia-Soto, 2004). Fish were examined for both ecto- and endoparasites. Parasites were recovered according to a standardised protocol by the present author. All metazoan parasites were identified and counted.

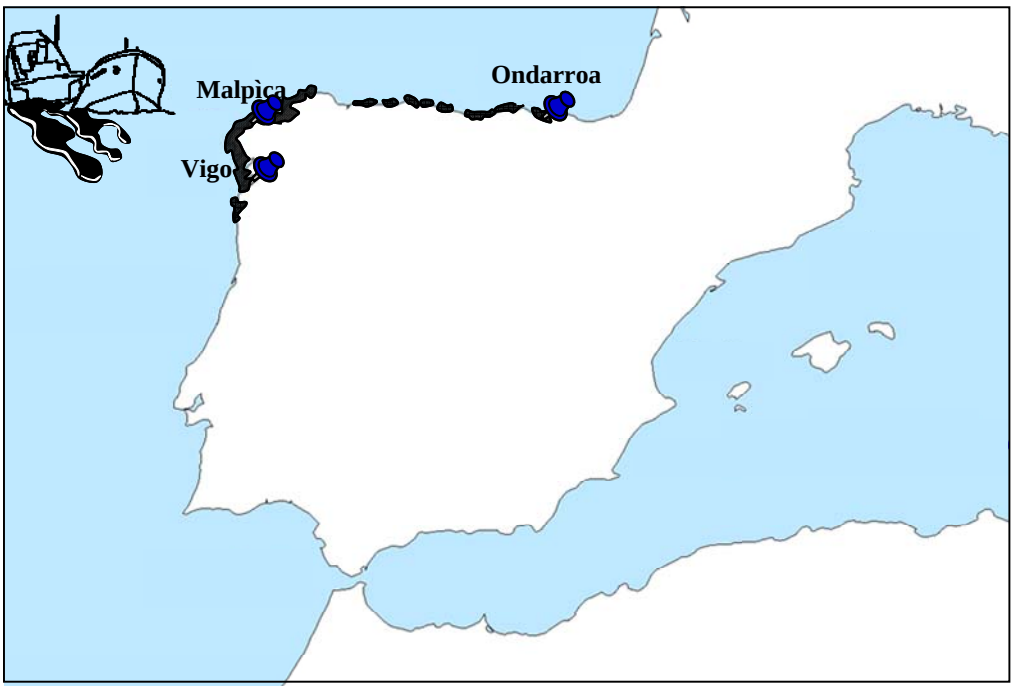

Figure 7.1. Map indicating the affected areas (in black) along the NE Atlantic coasts of Spain and the sampling localities.

7.2.3. Statistical analyses

Patterns of parasite distribution and infracommunity structure were based on fish of matched size (SL=19-23 cm in fish off Vigo and Malpica; SL=21-27.5 cm in fish off Ondarroa). Thus, only adult fish were used in before-after oil-spill comparisons based on results from a previous study, which indicated no significant differences in community richness, abundance and composition between host age cohorts within this length range (see Chpater 5; Pérez-del-Olmo *et al.*, 2008). Parasite community data were analysed at two hierarchical community levels: infracommunities and component communities (see Chapter 3). Similarity analyses at the component level were carried out on the total dataset (400 fish) in order to test the consistency of the results based on

size-restricted samples (*i.e.* infracommunity level, 146 fish). To increase sample size in the component community comparisons, fish within each sample were pooled by size class (corresponding to 3 size-classes in Chapter 5; Pérez-del-Olmo *et al.*, 2008). No effect of the sampling effort on community parameters was detected.

Following the approach of Pérez-del-Olmo *et al.* (2007b), all parasite taxa were split into two groups with respect to the mode of reproduction: (i) monoxenous (single host life-cycle); and (ii) heteroxenous (multiple-host life-cycle). The monoxenous/heteroxenous species ratio was calculated for each infracommunity in two variants: (i) Sm/Sh index is the species richness ratio; and (ii) Im/Ih is the ratio between sums of monoxenous/heteroxenous individuals in each infracommunity.

Three sets of data were analysed using communities in individual fish as replicate samples. First, in a pilot study pre-spill samples were compared with the first samples obtained post-spill (off Malpica: spring 2004; off Vigo: spring 2005). Secondly, matched seasonal samples from off Malpica, Vigo and Ondarroa collected in 2005 were contrasted to the pre-spill samples collected in 2001 in order to evaluate if changes in parasite communities in *B. boops* registered in the pilot study persist. Thirdly, sample series collected during 2001-2006 were examined to reveal the overall follow-up trends of community composition and structure in two impacted localities (Malpica, 2001-2004-2005; Vigo, 2001-2005-2006).

Community composition analyses were carried out with PRIMER v6 software (Clarke & Gorley, 2006), which provides a range of graphical and multivariate procedures for analyzing species/samples abundance matrices. First, the low-dimentional relationships between communities was visualised by non-metric multi-dimensional scaling (MDS) ordination based on Bray-Curtis similarity matrix derived from the square root transformed abundance/prevalence. Square root transformation was selected to provide deeper community comparison by a moderate down-weighting the contribution of the numerically dominant taxa. Secondly, the ANOSIM procedure (2-way crossed layout) performing randomization tests on the similarity matrices (Bray-Curtis index), was used to test the null hypothesis of no differences in parasite community structure due to ‘treatment’ (*i.e.* before-after the oil-spill) allowing for the locality of collection differences in the first and second analysis. In the third analysis the null hypothesis of no

differences in parasite community structure due to 'treatment' (*i.e.* year of sampling) allowing for the season of collection differences was tested. Sample series from the two localities were treated separately in this analysis.

The ANOSIM procedure calculates the R-statistic, which indicates the magnitude of the difference among/between conditions and a significance level that corresponds to the alpha level (probability of Type I error) in traditional ANOVA. The R-statistics ranges from 0 to 1; $R>0.75$ indicates a substantial difference in overall community structure (*i.e.* strong separation) whereas values for $R<0.25$ indicate little separation; intermediate R values reflect varying degrees of overlap but generally different community structure. In the few cases when $p>0.05$, more weight was given to R-values (Clarke & Gorley, 2006). The analyses were carried out at the infracommunity and component community levels using both species abundance and prevalence data in the latter. Following the ANOSIM test, the SIMPER procedure was used to identify 'key discriminating' species on the basis of the overall percent contribution of each species to the average dissimilarity of communities between conditions.

Parasite abundance and community structure data were analysed by Generalized Linear Models (GLM) after normalization of the data by $Ln(x+1)$ transformation. Non-parametric tests were carried out on original data.

7.3. Results

7.3.1. Structure of parasite communities in B. boops

A total of 43 species was found in the 400 fish from the 11 samples of *B. boops* examined in the course of the study. Of these, 18 represented new host records (Pérez-del-Olmo *et al.*, 2007b; present study) and 23 were only recovered in the post-spill samples. The predominant group of parasites was trematodes (22 species), with a high representation of the superfamily Hemiuroidea (11 species); other groups were represented by one to six species (2 monogeneans, 1 larval cestode, 5 larval nematodes, 6 acanthocephalans, 4 isopods and 3 copepods). Nineteen species were considered common (15 heteroxenous and 4 monoxenous, see Tables 7.1., 7.2.). Of these six species (*Steringotrema pagelli*, *Cardiocephaloides longicollis*, *Prosorhynchus crucibulum*, *Stephanostomum cesticillum*, *Scolex pleuronectis* and *Peniculus fistula*) were only found in the

Table 7.1. Summary statistics for parasite communities, mean abundance (± SD) of the common species and the significance of difference of the temporal contrasts in Ondarroa and Malpica data series (↑ indicates an increase and ↓ indicates a decrease in the parameter under comparison in the second year of the contrast). *Steringotrema pagelli* was absent in both localities. Number of species in the total sample in parentheses.

Locality	**Ondarroa**			**Malpica**						
Year/Statistical comparison	**2001**	**2005**	**2001 *vs* 2005**	**2001**	**2004**	**2005**	**2005**	**2001 *vs* 2004**	**2001 *vs* 2005**	**2004 *vs* 2005**
Season	**Spring**	**Spring**	**Spring**	**Autumn**	**Spring**	**Spring**	**Autumn**		**Autumn**	**Spring**
Sample size	19	30		20	25	22	21			
Total no. of species	14 (14)	21 (21)	14 *vs* 21	15 (16)	25 (28)	18 (19)	16 (21)	15 *vs* 25 (16 *vs* 28)	15 *vs* 16 (16 *vs* 21)	25 *vs* 18 (28 *vs* 19)
Mean no. of species	4.58±1.57	6.83±1.76	0.0001 ↑	4.45±1.88	8.68±1.68	6.73±1.83	5.86±1.46	0.0001 ↑	0.008 ↑	0.0009 ↓
Mean no. of individuals	54.00±36.95	121.4±46.90	0.0001 ↑	43.10±30.52	350.60±245.15	122.55±57.51	84.52±36.52	0.0001 ↑	0.0003 ↑	0.0001 ↓
Mean no. of monoxenous species	0.58±0.84	1.20±0.89	0.007 ↑	0.25±0.44	2.36±1.11	0.59±0.67	0.29±0.64	0.0001 ↑	ns	0.0001 ↓
Mean no. of monoxenous individuals	1.00±1.60	2.43±2.19	0.006 ↑	0.45±0.83	7.44±4.73	1.55±2.18	0.38±0.92	0.0001 ↑	ns	0.0001 ↓
Mean no. of heteroxenous species	4.00±1.25	5.63±1.50	0.0001 ↑	4.20±1.91	6.32±1.31	6.14±1.58	5.57±1.03	0.0001 ↑	0.004 ↑	ns
Mean no. of heteroxenous individuals	53.00±37.23	118.97±46.12	0.0001 ↑	42.65±30.66	343.16±244.71	121.00±57.98	84.14±36.66	0.0001 ↑	0.0003 ↑	0.0004 ↓
Sm/Sh	0.15±0.22	0.23±0.20	ns	0.11±0.25	0.39±0.20	0.10±0.12	0.04±0.09	0.0001 ↑	ns	0.0001 ↓
Im/Ih	0.05±0.17	0.02±0.02	ns	0.02±0.03	0.03±0.03	0.02±0.03	0.01±0.01	0.0001 ↑	ns	0.002 ↓
COMMON SPECIES										
Hemiurus communis	2.37±2.7	58.13±36.8	0.0001 ↑	1.55±1.6	164.24±160.3	52.73±42.1	4.43±5.4	0.0001 ↑	0.003 ↑	0.0003 ↓
Aphanurus stossichii	14.95±17.5	21.43±12.7	0.029 ↑	34.25±25.7	31.60±18.8	50.36±40.6	34.05±29.4	ns	ns	ns
Lecithocladium excisum	0.16±0.4	-	0.025	1.85±2.7	0.56±1.3	1.36±1.6	33.62±20.9	ns	0.0001 ↑	0.024 ↑
Derogenes varicus	-	-	-	0.20±0.5	0.64±1.0	0.14±0.4	0.29±0.6	ns	ns	ns
Magnibursatus bartolii	1.21±3.5	15.00±25.5	0.0001 ↑	0.05±0.2	8.64±34.0	1.00±2.2	1.19±4.2	0.003 ↑	ns	ns
Bacciger israelensis	32.84±34.7	20.73±32.6	ns	1.95±3.3	49.96±60.9	10.59±8.8	7.48±7.7	0.0001 ↑	0.001 ↑	0.0003 ↓
Wardula bartolii	0.05±0.2	0.83±1.5	0.026 ↑	-	3.40±14.5	0.09±0.3	0.29±0.7	ns	0.043 ↑	ns
Juvenile lepocreadiids	0.26±0.7	0.17±0.5	ns	0.20±0.7	81.12±93.7	0.50±1.2	-	0.0001 ↑	ns	0.0001 ↓
Stephanosomum cesticillum	-	-	-	-	0.20±1.0	0.14±0.5	0.05±0.2	ns	ns	ns
Cardiocephaloides longicollis	-	0.73±1.3	0.006 ↑	-	-	-	-	ns	ns	ns
Prosorhynchus crucibulum	-	-	-	-	-	0.36±1.0	-	ns	ns	ns
Scolex pleuronectis	-	0.67±1.1	0.002 ↑	-	0.36±1.3	-	-	ns	ns	ns
Anisakis simplex s.l. larvae	0.58±1.1	-	0.003	0.30±0.8	0.64±2.0	0.59±1.1	0.14±0.5	ns	ns	ns
Hysterothylacium aduncum larvae	0.37±0.6	0.40±0.9	ns	1.60±1.7	0.36±0.8	2.23±2.0	2.05±1.7	0.003 ↓	ns	0.0001 ↑
Microcotyle erythrini	0.79±1.1	1.80±1.7	0.02 ↑	0.20±0.6	5.32±4.3	1.45±2.0	0.05±0.2	0.0001 ↑	ns	0.0001 ↓
Cyclocotyla bellones	0.11±0.3	0.03±0.2	ns	-	0.68±1.1	0.09±0.3	0.05±0.2	0.022 ↑	ns	ns
Ceratothoa oestroides	0.11±0.5	0.17±0.5	ns	0.20±0.6	0.88±0.9	-	0.24±0.6	0.021 ↑	ns	0.002 ↓
Peniculus fistula	-	-	ns	-	0.40±0.6	-	0.05±0.2	ns	ns	ns

Table 7.2. Summary statistics for parasite communities, mean abundance (± SD) of the common species and the significance of difference of the temporal contrasts in Vigo data series (↑ indicates an increase and ↓ indicates a decrease in the parameter under comparison in the second year of the contrast). Number of species in the total sample in parentheses.

Year/Statistical comparison	**2001**	**2005**	**2005**	**2006**	**2006**	**2001 *vs* 2005**	**2001 *vs* 2006**	**2005 *vs* 2006**	**2005 *vs* 2006**
Season	**Spring**	**Spring**	**Autumn**	**Spring**	**Autumn**	**Spring**	**Spring**	**Spring**	**Autumn**
Sample size	10	46	26	19	44				
Total no. of species	11 (12)	26 (28)	24 (25)	21 (24)	23 (25)	11 *vs* 26 (12 *vs* 28)	11 *vs* 21 (12 *vs* 24)	26 *vs* 21 (28 *vs* 24)	24 *vs* 23 (25 *vs* 25)
Mean no. of species	4.70±0.95	8.26±1.79	7.27±2.27	8.42±3.02	6.05±1.84	0.0001 ↑	0.001 ↑	ns	0.032 ↑
Mean no. of individuals	43.80±18.26	108.65±42.20	56.38±21.68	80.47±46.78	39.25±22.39	0.0001 ↑	0.030 ↑	0.010 ↓	0.001 ↑
Mean no. of monoxenous species	0.30±0.48	1.28±0.78	0.23±0.51	1.16±0.96	0.86±0.88	0.0001 ↑	0.035 ↑	ns	0.003 ↑
Mean no. of monoxenous individuals	0.50±0.97	4.39±3.86	0.27±0.60	2.79±2.68	1.48±1.58	0.0001 ↑	0.022 ↑	ns	0.001 ↑
Mean no. of heteroxenous species	4.40±0.97	6.98±1.57	7.04±2.16	7.26±2.47	5.18±1.69	0.0001 ↑	0.003 ↑	0.013 ↓	0.0005 ↑
Mean no. of heteroxenous individuals	43.30±18.35	104.26±41.99	56.12±21.79	77.68±45.82	37.77±22.76	0.0001 ↑	0.037 ↑	ns	0.0007 ↑
Sm/Sh	0.08±0.13	0.19±0.12	0.03±0.07	0.16±0.14	0.19±0.21	0.023 ↑	ns	ns	0.001 ↑
Im/Ih	0.01±0.03	0.05±0.05	0.01±0.02	0.04±0.04	0.06±0.07	0.003 ↑	ns	ns	0.0009 ↑
COMMON SPECIES									
Hemiurus communis	18.90±11.6	44.65±19.90	3.42±4.7	5.53±3.8	0.61±1.9	0.0001 ↑	0.003 ↑	0.0001 ↓	0.0002 ↑
Aphanurus stossichii	13.10±8.4	34.43±24.70	32.58±20.9	16.21±15.9	19.84±12.2	0.0001 ↑	ns	0.0001 ↓	0.014 ↑
Lecithocladium excisum	-	2.67±2.56	6.19±5.2	0.63±1.0	1.98±3.4	0.0001 ↑	ns	0.0002 ↓	0.0001 ↑
Derogenes varicus	0.10±0.3	1.00±1.62	0.38±0.9	0.16±0.5	0.02±0.2	ns	ns	0.032 ↓	ns
Magnibursatus bartolii	1.30±3.8	1.37±2.64	1.00±2.0	7.42±23.3	0.55±1.5	ns	0.031 ↑	0.046 ↓	ns
Bacciger israelensis	2.90±3.3	10.96±14.22	7.38±9.1	23.58±24.9	11.09±19.4	ns	0.005 ↑	0.036 ↓	ns
Steringotrema pagelli	-	0.91±5.24	-	9.37±28.5	-	ns	ns	0.044 ↓	ns
Wardula bartolii	0.10±0.3	0.30±0.76	0.58±0.9	0.89±1.6	0.27±0.7	ns	ns	ns	ns
Juvenile lepocreadiids	6.00±10.7	5.35±7.82	0.62±1.0	2.84±6.2	0.20±0.8	ns	ns	0.023 ↓	ns
Stephanosomum cesticillum	-	0.46±0.66	0.42±1.6	9.00±9.3	0.59±1.02	ns	0.001 ↑	ns	ns
Cardiocephaloides longicollis	-	-	0.04±0.2	-	-	ns	ns	ns	ns
Prosorhynchus crucibulum	-	0.11±0.38	0.27±0.6	0.63±1.2	0.20±0.6	ns	ns	0.0001 ↓	ns
Scolex pleuronectis	-	0.11±0.31	0.15±0.6	-	0.02±0.2	ns	ns	ns	ns
Anisakis simplex s.l. larvae	0.10±0.3	0.15±0.36	1.12±1.2	0.42±0.7	0.82±1.1	ns	ns	ns	ns
Hysterothylacium aduncum larvae	0.50±0.7	0.67±1.01	1.19±1.1	0.26±0.5	0.75±0.9	ns	ns	ns	ns
Microcotyle erythrini	0.50±1.0	3.80±3.24	-	2.16±2.2	0.07±0.3	0.0003 ↑	0.031 ↑	0.047 ↓	ns
Cyclocotyla bellones	-	0.11±0.31	0.04±0.2	0.16±0.4	0.32±0.7	ns	ns	ns	ns
Ceratothoa oestroides	-	0.20±0.54	0.15±0.5	0.26±0.7	1.05±1.0	ns	ns	ns	0.0008 ↑
Peniculus fistula		0.26±0.77	0.04±0.2	0.11±0.5		ns	ns	ns	ns

post-spill samples. Five of the 12 common digenean species belonged to the superfamily Hemiuroidea. Hemiuroids in general also exhibited high relative abundance in all samples (57-90% of the heteroxenous parasites), except in that off Ondarroa (spring 2001, 31%) and Vigo (spring 2006, 37%).

All fish were infected with 2-15 species. Parasite component communities in the first post-spill samples of the pilot study showed a substantially higher richness than in pre-spill samples (28 *vs* 12-16 species) the range of parasites in individual fish being also higher in the former (5-15 *vs* 2-9 species). Overall, this remarkable increase in parasite species richness after the *Prestige* oil-spill kept steady in the follow-up samples. Twenty six species (20 heteroxenous and 6 monoxenous species) appeared for the first time in the fish sampled off Vigo post-spill (217 % increase in species richness); 19 species (15 heteroxenous and 4 monoxenous) were added to parasite communities in fish off Malpica (119% increase) and nine new species (7 heteroxenous and 2 monoxenous) appeared in the communities in fish off Ondarroa (71% increase). This addition of parasite species to the local faunas of *B. boops* occurred mostly in the first years after the oil-spill. Thus, at Vigo 65.4% of the species were added to the local fauna of *B. boops* in spring 2005, 19.2% in autumn 2005 and 7.7% in spring and autumn of 2006 each. Data for Malpica followed a similar trend (68.4% in spring 2004; 15.8% in spring and autumn 2005 each).

7.3.2. A pilot study: Two impacted localities

Due to the erratic fishing practices in the affected zones, the first post-spill samples were collected in May 2004 (Malpica) and 2005 (Vigo). The pilot study was, therefore, focused on a comparison of parasite communities in these samples with those collected before the oil-spill, also including comparative data for the pre-spill sample from Ondarroa. The prevalence of monoxenous parasites in the post-spill samples did not differ significantly and was substantially higher ($p<0.0001$) than in all pre-spill samples, which did not show significant variation (Figure 7.2.). Copepods were absent in the pre-spill samples whereas 3 species were found in the post-spill samples. Of the three higher taxa forming the monoxenous grouping, the monogeneans exhibited significantly higher prevalence ($P<0.0001$) in the post-spill samples. These prevalence

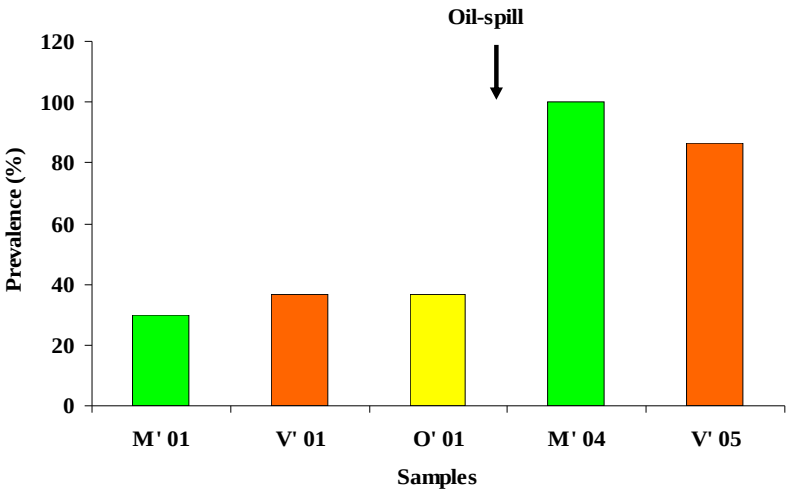

Figure 7.2. **Pilot study**. Prevalence of monoxenous parasites of *Boops boops* sampled before and after the *Prestige* oil-spill. Matched locality samples indicated by the same pattern. *Sample abbreviations*: M'01, off Malpica (2001); V'01, off Vigo (2001); O'01, off Ondarroa (2001); M'04, off Malpica (2004); V'05, off Vigo (2005).

patterns reflected in the higher levels of both mean species richness and abundance of the monoxenous parasite assemblages in both post-spill samples. There was no correlation between the fish size and infracommunity parameters. Infracommunities in fish sampled post-spill exhibited significantly higher richness and abundance of the total and both monoxenous and heteroxenous species assemblages ($p<0.0001$), Sm/Sh and Im/Ih indices (see Tables 7.1., 7.2.). The post-spill communities showed substantially higher levels of relative representation of monoxenous parasites (both in terms of species and individuals) and this was in contrast to all pre-spill samples, which have also shown no significant variation with respect to this index. There were no differences between the post-spill samples in the total and heteroxenous species richness. The Malpica 2004 sample, however, exhibited higher levels of all other community parameters.

The MDS run on total communities provided a relatively good separation (stress 0.16) between post-spill and pre-spill communities. Figure 7.3A shows the two dimensional configuration of communities sampled off Vigo and Malpica with the four samples labelled individually. A similar plot with a close stress value (0.15) was obtained using similarities between common species only (data not shown). An exceedingly low stress value (0.05) was obtained when the summed abundances of monoxenous parasites and hemiuroid trematodes only

were used to construct the similarity matrix. Figure 7.3B illustrates a clear separation between infracommunities sampled pre- and post-spill which indicates a stress effect on these parasite functional groups. The same plot with superimposed abundances shows a large representation of both monoxenous species (Figure 7.3C) and hemiuroids (Figure 7.3D) in the post-spill samples.

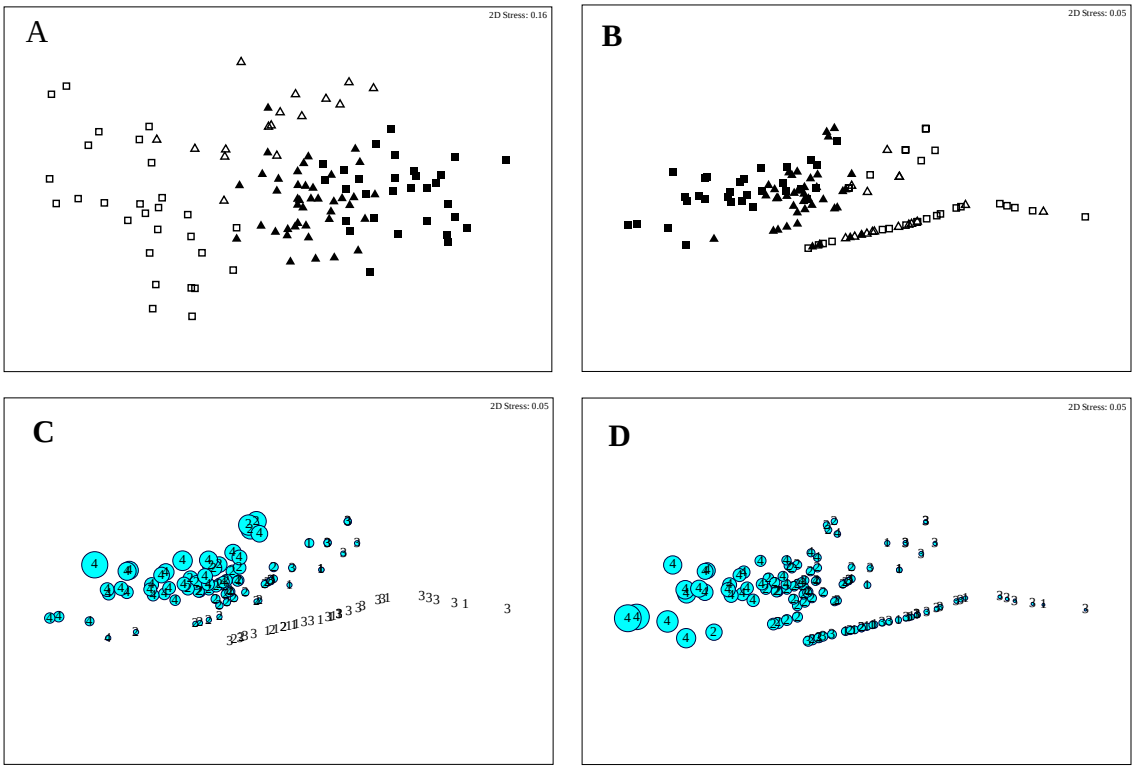

Figure 7.3. **Pilot study**. A, Two-dimensional MDS configuration of the fish sampled off Malpica (squares) and off Vigo (triangles) based on similarity in parasite infracommunity structure. Post-spill samples in black. B, MDS solution based on summed abundance data for monoxenous species and hemiuroid trematodes only. Labels as in 7.3A. C-D, The same MDS plot but with superimposed circles whose size is directly proportional to the abundance of the monoxenous species (C) and hemiuroids (D) in each infracommunity. The four samples labelled individually: 1, Vigo 2001; 2, Vigo 2005; 3, Malpica 2001; 4, Malpica 2004.

A 2-way crossed layout was used in the ANOSIM procedure in order to separate the effect from geographical/seasonal variation from any changes resulting from disturbance (*i.e.* oil-spill). The R value obtained (R=0.76, p=0.001) indicates that communities in *B. boops* collected before and after the oil-spill differ consistently. On the other hand, the hypothesis for no block (*i.e.* 'locality') effect, allowing for the fact that there are disturbance differences, was also rejected (but with a lower R, R=0.544, p=0.001). Similar results were obtained when the analysis was run using a subset comprising common species only (R=0.777 and R=0.562; both p=0.001).

7.3.3. Second survey: Three impacted localities

'Before-after' analyses on community composition carried out with the samples from Vigo and Malpica separately revealed similar ordination patterns and dissimilarity levels related to disturbance, the latter exhibiting much lower stress values and higher levels of distinction of the post-spill infracommunities (Pérez-del-Olmo *et al.*, 2007b). However, the post-spill sample from Malpica was collected in spring (*vs* autumn in 2001). Therefore, these data were treated with caution because a possible superimposed temporal effect on parasite populations contributing to the higher degree of community dissimilarity between samples from this locality could not be ruled out.

A 'before-after' comparison was, therefore, conducted using matched seasonal samples from off Malpica, Vigo and Ondarroa collected in 2005. Parasite communities in these samples were contrasted to the pre-spill samples collected in 2001 in order to evaluate if changes in parasite communities in *B. boops* registered in the pilot study persist. Tables 7.1. and 7.2. present summary statistics for parasite community data and the mean abundance of the common species in the pre- and post-spill samples. Parasite communities in the post-spill samples examined at the three localities in 2005 showed a significant increase in mean parasite richness and abundance (Figure 7.4). With the exception of the assemblages of monoxenous species in fish sampled off Malpica which did not show a significant change in complexity, this trend was similar for the assemblages of both heteroxenous and monoxenous species (range for p 0.023-0.0001). However, Sm/Sh and Im/Ih indices did not show significant differences in 'before-after' comparisons of Malpica and Ondarroa samples.

A number of common species appeared to be significantly affected by the oil-spill. Four heteroxenous species (*Hemiurus communis*, *Bacciger israelensis*, *Wardula bartolii* and *Lecithocladium excisum*) increased significantly in abundance in the post-spill sample from Malpica (Table 7.1.). In Ondarroa seven species exhibited significant increase in abundance after the oil-spill: one monoxenous (*Microcotyle erythrini*) and six heteroxenous species (*Aphanurus stossichii*, *Magnibursatus bartolii*, *H. communis*, *W. bartolii*, *S. pleuronectis* and *C. longicollis*; the latter two appeared after the oil-spill). On the other hand, *Anisakis simplex* and *L. excisum* which were present in the pre-spill sample, were not recovered at this locality in

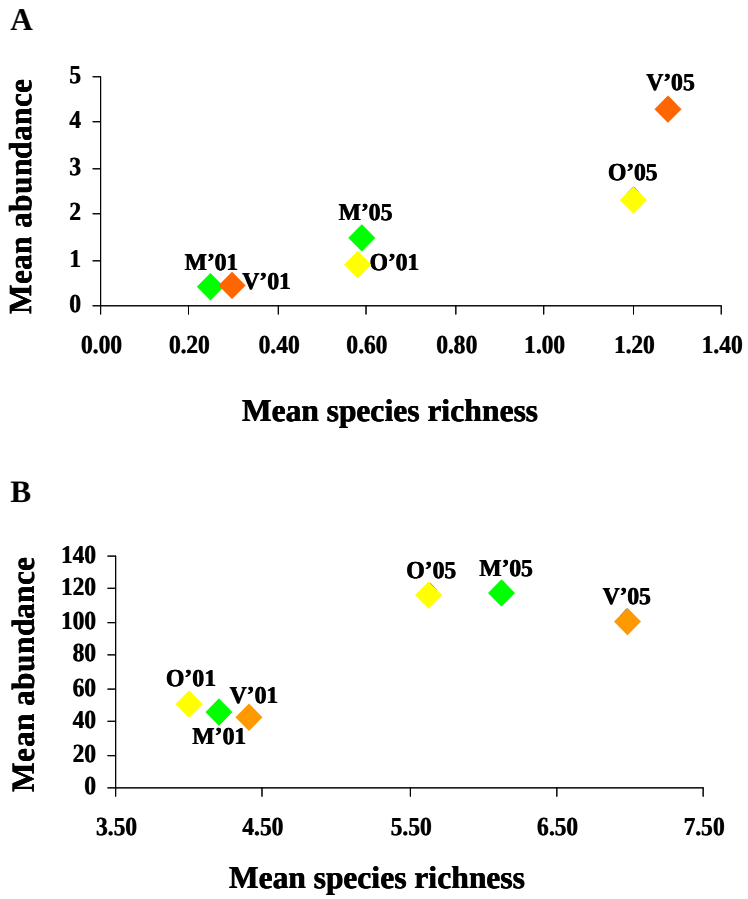

Figure 7.4. **Second survey**. Richness and abundance of parasite assemblages in fish sampled before and after the *Prestige* oil-spill. A, Monoxenous species. B, Heteroxenous species. *Sample abbreviations*: M'01, off Malpica (2001); V'01, off Vigo (2001); O'01, off Ondarroa (2001); M'05, off Malpica (2005); V'05, off Vigo (2005); O'05, off Ondarroa (2005).

2005 (Table 7.1). In the Vigo post-spill sample the abundances of *M. erythrini* and four heteroxenous species (*A. stossichii*, *H. communis*, *L. excisum* and *S. cesticillum*; the latter two appeared after the oil-spill) had significantly higher values (Table 7.2.). Prevalences of the species that were common for the pre- and post-spill samples did not show many changes. These include the significant increase of the prevalence of *B. israelensis* and *L. excisum* in the sample off Malpica (p=0.001); of *H. communis* and *M. bartolii* in the sample off Ondarroa (p=0.044 and p=0.0001, respectively); and of *M. erythrini* in the sample off Vigo (p=0.003).

The MDS performed on infracommunity data showed a high stress (0.22) with no clear separation (Figure 7.5A). ANOSIM analysis separated the effect from geographical variation from the change due to the disturbance. Although the infracommnunities in fish sampled at the three localities differed in composition and structure (R=0.667, p=0.001) a significant 'treatment' effect was detected (R=0.631, p=0.001).

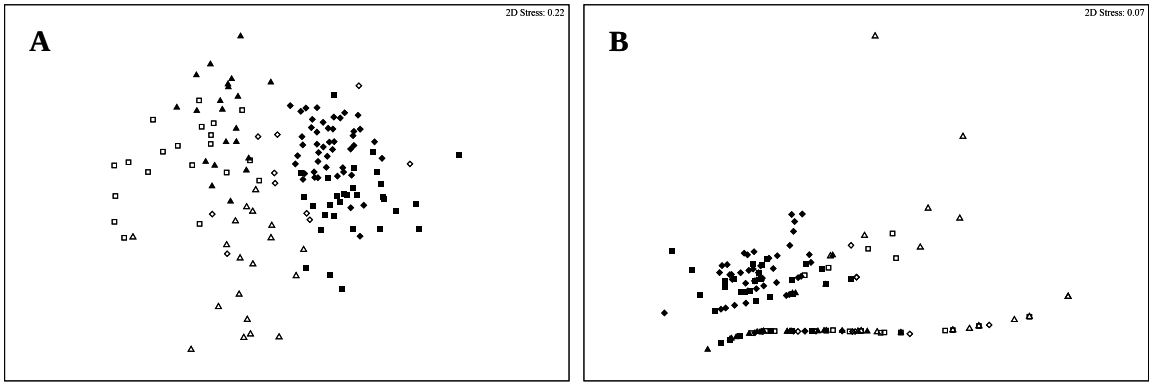

Figure 7.5. **Second survey.** A, MDS plot for infracommunities sampled off Malpica (squares), off Vigo (triangles) and off Ondarroa (diamonds). Post-spill samples in black. B, MDS plot based on summed abundance data for monoxenous species and hemiuroid trematodes only. Labels as in 7.5A.

SIMPER procedure identified eight species (*H. communis*, *B. israelensis*, *A. stossichii*, *L. excisum*, *M. bartolii*, juvenile lepocreadiids, *H. aduncum* and *M. erythrini*) which contributed substantially to the dissimilarity between infracommunities before and after the oil-spill (51.08%), as well as among localities (range 43.96-59.75%). An excellent ordination with a very low stress value (0.07) was obtained when the similarity matrix was calculated on summed abundances of monoxenous parasites and hemiuroid trematodes (Figure 7.5B). Infracommunities from the three localities exhibited different composition with respect to these two groups before and after the oil-spill (R=0.631, p=0.001), although they also differed between localities (R=0.150, p=0.001).

Figure 7.6. presents the ordination of component communities based on a similarity matrix derived from species abundance (stress 0.12). Component community sub-samples from the three localities exhibited clear grouping with respect both the disturbance and season effect. MDS based on species prevalence data

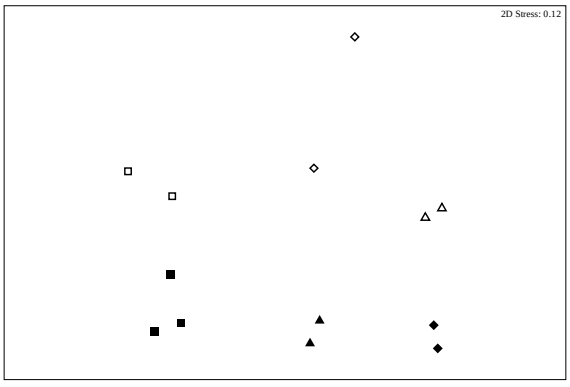

Figure 7.6. **Second survey**. MDS plot for component communities sampled off Malpica (squares), off Vigo (triangles) and off Ondarroa (diamonds). Post-spill samples in black.

showed even better stress value (0.09). ANOSIM procedure on abundance data indicated a perfect differentiation for both disturbance and locality effect (R=1, p=0.011 and R=1, p=0.002, respectively). Overall, the species contributing to the dissimilarity at the infracommunity level were responsible for the separation at the component community level [*i.e.* dissimilarity due to oil-spill (37.27%) and locality (37.86-48.89%)].

The separation of communities was similar when using prevalence data (R=0.868, p=0.011 and R=1, p=0.003, for 'oil-spill' and 'locality' factors, respectively). However different species had a significant contribution to community separation. In addition to *M. bartolii* and *L. excisum* mentioned above, five species (*Derogenes varicus*, *W. bartolii*, *A. simplex*, *S. pleuronectis* and *C. longicollis*; the latter two found only after the oil-spill) were associated to the dissimilarity due to oil-spill (32.46%). Juvenile lepocreadiids, *Ceratothoa oestroides*, *Arnola microcirrus*, renicolid metacercariae, *M. erythrini* and *H. aduncum* in addition to the above mentioned *D. varicus*, *A. simplex*, *M. bartolii* and *L. excisum* were found to contribute to community dissimilarities between localities.

7.3.4. Global comparison: Two impacted localities over time

Figure 7.7. illustrates the relative increase (compared with the pre-spill levels) in mean species richness and abundance of monoxenous (Figure 7.7A) and heteroxenous (Figure 7.7B) assemblages in the series of communities examined at Vigo and Malpica. Overall, the post-spill samples exhibited substantially higher richness and abundance of both parasite groups. There was a trend of decrease of the relative mean richness and abundance of communities sampled at Malpica, whereas the pattern of change in communities sampled off Vigo was more variable.

GLM analysis carried with fish standard length as a covariable revealed an overall highly significant effect of both factors ('oil-spill' and 'season') on all community parameters and on the worm burdens of a number of common species ('oil-spill': *H. communis*, *L. excisum*, juvenile lepocreadiids, *M. erythrini* and *C. oestroides*; 'season': *H. communis*, *L. excisum*, juvenile lepocreadiids, *H. aduncum*, *C. bellones* and *M. erythrini*). However, four community parameters (mean number of individuals, mean number of heteroxenous individuals and the mean number of monoxenous species and individuals) and the abundance of *A. stossichi* were subject to a 'season*oil-spill' interaction, being generally lower in the communities sampled in spring.

Comparative analyses for the variation of parasite communities over the period of study were, therefore, restricted to matching seasonal samples at each locality.

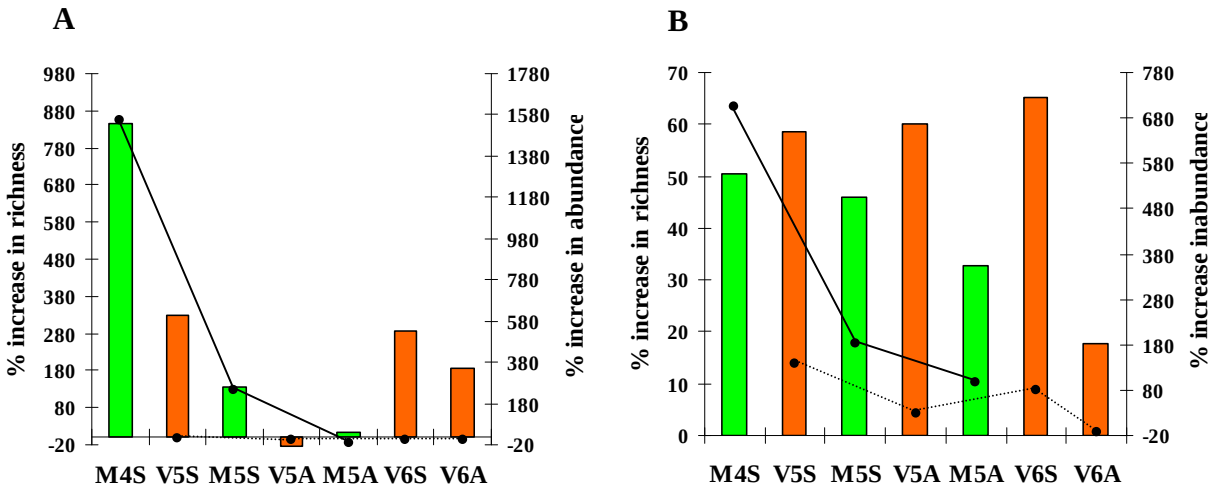

Figure 7.7. **Global comparison**. A, Percent increase in richness and abundance of monoxenous species assemblages in the sample series off Malpica and Vigo. B, Percent increase in richness and abundance of heteroxenous species assemblages. *Sample abbreviations*: M, Malpica; O, Ondarroa; V, Vigo; S, spring; A, autumn; 1, year 2001; 4, 2004; 5, year 2005; 6, year 2006.

7.3.4.1. Malpica

There was a significant decrease in community parameters, with the exception of the number of heteroxenous species in the spring 2005 samples off Malpica, compared with those collected in the same season in 2004 (Table 7.1.). The abundance of five common species (*H. communis, B. israelensis,* juvenile lepocreadiids, *M. erythrini* and *C. oestroides*) also decreased significantly, whereas *H. aduncum* and *L. excisum* showed a substantial increase in the spring sample of 2005.

The MDS ordination of infracommunities of Malpica showed intermediate stress levels (0.15, not shown). ANOSIM analysis showed a significant effect on infracommuty composition of both factors [‘season’ (R=0.761, p=0.001); ‘year’ (R=0.556, p=0.001)]. Post-spill infracommunities sampled in 2004 revealed high level of compositional distinction as compared to the pre-spill data (R=0.937, p=0.001). Communities sampled in 2005 still exhibited compositional differences compared to those sampled pre-spill (year 2001, R=0.469, p=0.001); these were, however, more pronounced in the 2004-2005 comparison (R=0.621, p=0.001). SIMPER procedure indicated that the same eight species that contributed to the dissimilarity in

the infracommunities of the second survey were contributing to the dissimilarity between years (47.46-49.60%) and seasons (49.70%).

The MDS run on component communities (similarity based on mean abundance) exhibited a strong separation (stress 0.01, see Figure 7.8A). Communities in fish from the first sample after the oil-spill (year 2004) exhibited the highest separation from those in the pre-spill sample, whereas communities in the seasonal samples of 2005 showed an intermediate position. A similar ordination with very low stress value (0.06) was obtained with similarities based on species prevalence data. ANOSIM applied to both mean abundance and prevalence data exhibited similar results for the effect of 'year' and 'season' on compositional variation of component communities (abundance: R=1, p=0.033 and R=1, p=0.10; prevalence: R=0.827, p=0.033 and R=0.833, p=0.2, respectively). Although the p-levels for the seasonal effect were not significant due to the low number of possible permutations in this analysis, the differentiation between spring and autumn samples was apparent (see also Figure 7.8.A). The pairwise comparisons revealed completely different composition of communities sampled in 2004 compared with 2001 (R=1, p=0.33). Communities sampled in 2005 showed strong dissimilarity compared to 2004 (R=0.855, p=0.048). Finally, the R-level in 2005-2001 comparison was low (R=0.291, p=0.14) thus indicating overlapping composition of component communities. Similar results were obtained in pairwise comparisons based on prevalence data. SIMPER analysis based on abundance data revealed the importance for the dissimilarity between component communities across years (32.57-39.94%) and seasons (77.78%) of the same seven 'key discriminating' species which contributed to infracommunity differenciation. Analyses with prevalence data identified an overall different list of species (*A. simplex*, *S. pleuronectis*, *D. varicus*, *Ascarophis* sp., *L. excisum*, *M. bartolii*, *A. microcirrus*, *P. crucibullum*, *C. oestroides*, juvenile lepocreadiids, *C. bellones*, *H. aduncum*, *D. varicus* and *M. erythrini*) which contributed to community distinctness with respect to 'year' (27.11-30.77%) and 'season' (27.32%) factors.

7.3.4.2 Vigo

The summary statistics for parasite community data of the samples off Vigo (Table 7.2.) revealed significantly higher levels for most community parameters in communities sampled in 2006 as compared to 2001, a pattern also observed in the 2001-2005 comparison (see above). Five species

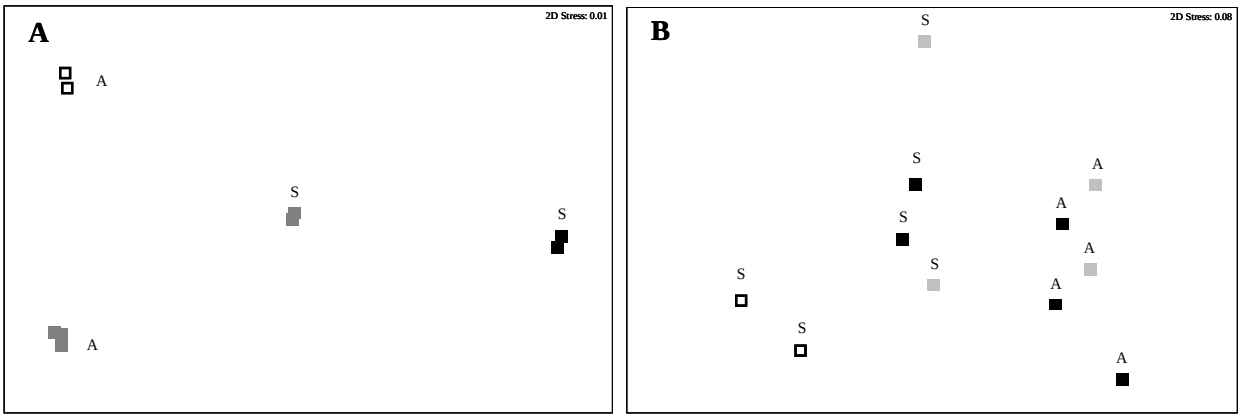

Figure 7.8. **Global comparison.** A, MDS plot for component communities sampled off Malpica 2001 (open squares), 2004 (black squares) and 2005 (grey squares). B, MDS plot for component communities sampled off Vigo 2001 (open squares), 2005 (black squares) and 2006 (grey squares).

exhibited significantly higher abundance (*M. erythrini* and the heteroxenous *H. communis*, *B. israelensis*, *M. bartolii* and *S. cesticillum*). The spring samples of years 2005-2006 had overall similar community parameters with a decrease in the total mean abundance and heteroxenous species richness in 2006. A large number of the common species (9 heteroxenous and 1 monoxenous species, see Table 7.2.) exhibited significant decrease in mean abundance in 2006. Unexpectedly, there was an increase in all community parameters and the mean abundance of *H. communis L. excisum*, *A. stossichii* and *C. oestroides* in communities sampled in the autumn sample of 2006 (compared with autumn 2005 sample).

MDS ordination of the infracommunities sampled at Vigo did not show clear separation (stress 0.22). ANOSIM procedure indicated different composition with respect to both year and season of collection (R=0.478 and R=0.664, respectively; both p=0.001). Pairwise comparisons revealed higher compositional similarity between samples of 2001 and 2006 (R=0.423, p=0.001) and 2005-2006 (R=0.459, p=0.001), whereas those in the 2001-2005 comparison exhibited different composition (R=0.658, p=0.001). The SIMPER procedure indicated that nine species (*H. communis*, *A. stossichii*, *B. israelensis*, juvenile lepocreadiids, *Steringotrema pagelli*, *L. excisum*, *M. bartolii*, *S. cesticillum* and *M. erythrini*) mostly contributed to community distinctness between years (45.31-55.70%) and seasons (54.57%).

Component communities sampled off Vigo post-spill formed a separate cluster in the MDS based on mean abundance data (stress 0.08) The ordination also indicated a seasonal grouping along the first axis (Figure 7.8B). The plot based on prevalence showed a similar grouping (stress 0.07). ANOSIM analysis showed an effect of both 'year' and 'season' factors on component community composition in the analyses based on both mean abundance (R=0.426, p=0.053 and R=0.615, p=0.033, respectively) and prevalence (R=0.541, p=0.027 and R=0.540, p=0.06, respectively). Communities sampled in 2005 and 2006 revealed a different composition compared to the pre-spill sample (R=0.727, p=0.048 and R=0.786, p=0.067, respectively). However the differences between communities sampled in 2005 and 2006 were negligibly small (R=0.113, p=0.238) indicating an overlapping composition. Pairwise comparisons based on prevalence data showed similar results. SIMPER procedure revealed the same list of nine discriminating species that contributed at the infracommunity level (see above). However this list was expanded to *D. varicus*, *A. simplex*, *P. fistula*, *A. microcirrus*, *C. oestroides*, *P. crucibullum*, *W. bartolii* and renicolid metacercariae when prevalence data were used.

7.4. Discussion

Parasite communities may appear good indicators of environmental disturbance because they reflect complex interactions between a possible stressor and either free-living larval stages or populations of their intermediate and final hosts. Thus, a significant deviation either way from a normal rate of transmission may be a warning of adverse environmental conditions (MacKenzie *et al.*, 1995). On the other hand, parasite communities encompass species with different phylogenies exploiting a diversity of life-cycle strategies, and this offers the opportunity to search for a common theme in a wider array of differential responses to perturbation. Because most of parasites are trophically transmitted, the observed responses may reflect alterations in the local food webs (Marcogliese, 2005b). Not surprisingly, recent studies on anthropogenic impacts on marine ecosystems and pollution monitoring focus on the entire parasite community rather than on single species populations (*e.g.* Broeg *et al.*, 1999; Diamant *et al.*, 1999; Dzikovski *et al.*, 2003) by attempting a multivariate approach to community patterns (see also Valtonen *et al.*, 2003).

A similar strategy was adopted in the present study. Both univariate and multivariate analyses revealed dramatic changes in community richness, abundance and structure of parasite communities and a notable alteration of both individual and functional group parasite abundance patterns in the model fish species studied post-spill. Further, these differences in component community structure reflected consistently in the change in infracommunity compositional patterns which were amenable to statistical tests. Overall, the present comparative analyses suggest that parasite communities in *B. boops* may have reflected a disturbance effect on the natural communities along the NE Atlantic of Spain following the *Prestige* disaster.

Anthropogenic discharges into marine environments include in general two separate classes of confounded environmental variables, *i.e.* toxicants and organic enrichment. This dual character of petroleum hydrocarbon releases is apparent in virtually every study of environmental effects of oil-spills and natural petroleum seeps (see Peterson *et al.*, 1996). Although it is difficult to disentangle the causation of the above confounded environmental variables, the results of this study have shown that focusing on higher taxonomic and/or functional levels, rather than species, provided a higher resolution in detecting directional trends in parasite community structure in the fish following the oil-spill. This opens the possibility of reducing the identification effort in follow-up impact analyses of parasite community responses to perturbation. Furthermore, it appears that the variations in the diversity and abundance of the selected life-cycle groupings exhibit a differential response with respect to the confounded environmental variables.

As expected, the substantially higher levels of infection with monoxenous parasites, resulting in significantly higher levels of Sm/Sh and Im/Ih indices observed in the first post-spill samples (pilot study), are indicative of a stress response. Parasites with direct life-cycles are normally ectoparasites, which are in constant contact with external environment and have developed a flexibility and resistance to certain natural changes in the course of their evolution. Therefore, their populations are expected to be less affected by pollution (MacKenzie, 1999). The present data also indicate that this group may appear better adapted for survival in a polluted environment. Thus, isopods were more prevalent and abundant and copepods were only found in the fish sampled in 2004-2005. Furthermore, the monogenean *M. erythrini*, the prevailing species in the monoxenous species group, was identified among the key contributors to infracommunity

dissimilarity between pre- and post-spill samples. Whereas the main evidence on enhanced population growth comes from studies on monopisthocotylean monogeneans (Khan, 1987; Khan & Kiceniuk, 1988; Moles & Wade, 2001), this study provides the third example for increased levels of infection with polyopisthocotylean monogeneans (*M. erythrini* and *C. bellones*) in oil polluted areas (see Paperna & Overstreet, 1981; Williams & MacKenzie, 2003).

On the other hand, PAHs are known immune suppressors. Impaired immunofunction due to pollutant stress may lead to infectious disease outbreaks in aquatic organisms (Sinderman, 1983, 1993; Sures, 2004). Hydrocarbon exposure in demersal fishes often results in an increase in gill parasites (and monogeneans in particular, see Khan & Thulin, 1991; MacKenzie *et al.*, 1995) and a recent study in sediments (Moles & Wade, 2001) provides evidence relating host immunosuppression with the increase in gill parasites at the concentrations of crude oil that might be encountered following an oil-spill. Chronic exposure to contaminants has also been shown to lead to gill hyperplasia and excessive mucus secretion in both laboratory experiments and field studies (Khan & Kiceniuk, 1988; Khan, 1990, 2003), including one subsequent to the *Amoco Cadiz* spill off the Brittany coast of France (Haensly *et al.*, 1982). On the other hand, pollutants have been shown both to stimulate secretion and coagulate mucus. Khan (1987) suggested that toxicants create a habitat, enhancing parasite rates of infection by some mechanism impairing the defensive nature of mucus secretion. Although data on fish exposure to PAHs after the *Prestige* oil-spill are far too scarce, both bioassay (see Jiménez-Tenorio *et al.*, 2005) and field studies (see Martínez-Gómez *et al.*, 2005, 2006) indicate elevated levels of hepatic detoxicating enzymes (EROD activity) in fish. Experimental tests on the effect of sediment samples collected from localities affected by *Prestige* oil-spill on juveniles of another sparid fish, *Sparus aurata*, also revealed increased EROD activities (Morales-Caselles *et al.*, 2006). It is, therefore, possible that changes in immune parameters of bogue due to chronic exposure to PAHs post-spill have resulted in the elevated levels of monoxenous infections observed in the pilot study. Although the richness and abundance of monoxenous parasite assemblages were higher in the following samples (2005-2006) some tendency was observed towards a decrease. This should be treated with caution due to the possible seasonal effects on monoxenous infections.

In contrast to the initial expectations, no impoverishment in the endoparasite fauna of *B. boops* collected post-spill was observed, since no species from the 2001 samples was missing in the post-spill samples. This suggests no substantial qualitative perturbation of the benthic/pelagic communities or at least the ones associated with *B. boops* trophic interactions. However, the parasite species lists of the post-spill samples were more than twice as large and included 18 new host records and, of the 19 common species, six were only found in the post-spill samples. Furthermore, a substantially higher richness and abundance of heteroxenous parasites (mostly trematodes) than previously found in the Atlantic *B. boops* was observed (see also Power *et al.*, 2005 for data covering a wider size range). Overall, the richness and abundance of heteroxenous parasite assemblages exhibited a marked peak in communities of the pilot study and were notably higher in all post-spill samples, although some tendency of a decrease in abundance was noted after spring 2005. The hemiuroids, mostly represented by generalist parasites that are shared with many marine fish species (see Gibson & Bray, 1986 and NHM Host-parasite database, www.nhm.ac.uk/research-curation/projects/host-parasites/database), comprised up to 90% of the heteroxenous parasites in the post-spill samples and strongly contributed to the observed patterns of richness and abundance. These observations largely depart from the initial hypothesis that the two model groups of parasites selected for a comparative study would exhibit an opposing response to the post-spill situation. Whereas the presence of the tissue heteroxenous parasites in the post-spill samples (the metacercariae of *Stephanostomum* spp. and *Prosorhynchus* sp., *C. longicollis*, unidentified renicolid; the post-cystacanths of *Corynosoma* sp. and *Andracantha* spp.; and larval anisakids) might be related to the inmunosupression of the fish, no published evidence could be found for a positive effect of PAHs (or other xenobiotics) on trematode populations in their final hosts. Previous work, on the contrary, suggests that pollution (including oil and heavy metals) is toxic to adult trematodes in the fish hosts (*e.g.* Overstreet & Howse, 1977; Khan & Kiceniuk, 1983; Overstreet, 1988; Khan & Thulin, 1991) and lethal to free-living stages as well as to mollusc intermediate hosts, thus compromising the transmission of the heteroxenous species by blocking the completion of their life-cycles (Dzikowski *et al.*, 2003 and references therein; but see Powell *et al.*, 1999).

Two mutually non-exclusive hypotheses can be suggested for the remarkable increase in both the diversity and abundance of heteroxenous parasites observed in *B. boops* sampled after

the *Prestige* oil-spill. The first, and an obvious prediction, is that increased levels of infection reflect compromised health (*e.g.* reduced immunological capabilities), following chronic exposure to contaminated sediments, of the benthic mollusc populations serving as first intermediate hosts for trematodes, rendering them more susceptible to parasitism (*e.g.* McDowell *et al.*, 1999; Powell *et al.*, 1999). This, in turn would lead to increased transmission rates and higher levels of infection of fish hosts (*e.g.* gadoids, the main hosts of hemiuroids, but also other fishes, *e.g. B. boops*). Although evidence is largely wanting, preliminary bioassay studies with *Prestige* fuel oil have shown 'no great influence on mussel (*Mytilus galloprovincialis*) immune status' (Ordás *et al.*, 2005). Field collections of *Mytilus edulis* from localities north and south of the Costa da Morte (including Malpica and Vigo) 3 and 7 months after the oil-spill exhibited PAH concentration levels similar to those observed before oil-spill in 2000 (Viñas *et al.*, 2005). These data, however limited, do not seem to provide support for the first prediction (see above). Recently published data have shown an increase of PAHs concentrations in *M. galloprovincialis* one year after the *Prestige* oil-spill due to the adverse meteorological conditions that disturbed the sea bottom and dispersed the oil accumulated in the sediments (Laffon *et al.*, 2006; Soriano *et al.*, 2006, 2007).

A second hypothesis can be suggested, namely that endoparasite communities in *B. boops* reflect a notable change in the composition and abundance of the benthic fauna in the localities sampled post-spill due to organic enrichment after the *Prestige* oil-spill. One apparent, though purely qualitative change in the post-spill communities related to a structural alteration in the local food webs, is the accidental appearance of mature lepocreadiids in *B. boops* (*i.e. L. album*), which was coupled with a consistent presence of the juvenile lepocreadiids and the generalist hemiuroid *D. varicus* in the post-spill samples. These species use polychaetes as second intermediate hosts (Rebecq, 1965; Margolis, 1971; Bray, 1988). Polychaetes are not particularly sensitive to toxic substances and also include species with opportunistic life histories and feeding types that render them capable of proliferation following organic pollution and oil-spills and seeps in particular (Peterson *et al.*, 1996). It is worth noting that the polychaetes were found to dominate, accounting for more than 40% of the total number of species in the macrobenthic community in a short-term study after the *Aegean Sea* oil-spill in Galician waters (Gómez Gesteira & Dauvin, 2005). The preliminary results on infaunal and benthic communities on the

Galician continental shelf suggest that no important changes of the bioindicator (opportunistic or sensitive to oil pollution) species, comparable to the *Aegean Sea* oil-spill situation, were seen between 2002-2004. However, the polychaetes were found to be the dominant group accounting for 70-77% of the abundance in all strata (*i.e.* 71-120m, see Parra & Frutos, 2005; Serrano *et al.*, 2006). All fish sampled off Vigo in the pilot study contained mostly polychaetes in their stomachs. Inferring from the life-cycle data and the observations in the course of the study, it can be suggested that the post-spill increase in polychaete abundance has fuelled the transmission of the lepocreadiids and *D. varicus* in the affected localities and perhaps has contributed to an additional transmission route for the hemiuroids in general (by analogy with the life-cycle pattern of *D. varicus*). It could be predicted, therefore, that a substantial enhancement of the populations of these parasites has occurred in the communities of their main fish hosts in the impacted localities.

The most apparent changes in parasite communities from the localities sampled post-spill comprised the marked increases in the diversity and abundance of the hemiuroid trematodes, a situation strikingly similar to that observed by Zander & Reimer (2002) in the ecosystems of the Baltic Sea. These authors related the predominance of the hemiurids to the eutrophication of the systems studied. For parasites with complex life-cycles, such as hemiuroids, transmission thresholds are directly related to the abundance of the benthic fauna (Campbell *et al.*, 1980; Dobson & May, 1987). The results of the present study, therefore suggest that the notable increase of the infection levels with hemiuroid trematodes indicates an enhancement of the populations of their first intermediate hosts due to organic enrichment following the *Prestige* oil-spill. The rebound effect in the distribution and abundance of benthic and demersal indicator species observed in the Galician continental shelf in 2004 (Serrano *et al.*, 2005; 2006) tends to support this hypothesis.

Furthermore, the remarkable alteration in the hemiuroid abundance in the post-spill samples may have reflected an increase in the abundance of the harpacticoid copepods. Celewycz & Wertheimer (1996) reported significantly greater biomass of harpacticoid copepods in oiled than in non-oiled locations in the Prince William Sound in 1990, and Wertheimer *et al.* (1996) showed increased abundance of harpacticoid copepods in response to direct and indirect impacts

of the *Exxon Valdez* oil-spill on their intertidal habitats during the year after the spill. *Acartia* spp. are opportunistic copepods which are known to serve as second intermediate hosts of a number of hemiuroids [*e.g. D. varicus* (Rebecq, 1965), *M. caudofilamentosa* (Køie & Gibson, 1991) and perhaps by analogy, *M. bartolii, H. communis* (Rebecq, 1965; Gibson & Bray, 1986; Køie, 1995), *Lecithocladium excisum* (Køie, 1991, 1992), *Lecithaser confusus* (Rebecq, 1965)]. *Acartia clausii* (second intermediate host of the 'key discriminating' parasite in the fish sampled post-spill, *H. communis*) is associated with organic enrichment, and was found to dominate in the eutrophic marine systems in the Mediterranean which had also experienced hydrocarbon and heavy metal pollution (Marcus, 2004). Therefore, the characteristic raise of the hemiuroids observed post-spill can be attributed to an increased abundance of the calanoid copepods following organic enrichment in the affected localities thus fuelling the transmission of these generalist fish parasites in the area.

The multivariate statistical approach of this study, which took into account both the overlap in the taxa among communities and the differing abundance of each taxon in each community, thereby facilitating an assessment of the variation of the *overall* community structure, proved to be very useful in studying the response of parasite communities post-spill. Furthermore, there was good agreement between the two techniques applied, MDS and ANOSIM and both effectively revealed some degree of within-season consistency and among-treatment (*i.e.* time post-spill) differences in overall community structure, particularly in the global comparison at the two impacted localities, Malpica and Vigo. Multivariate analyses also detected significant differences in community structure between pre- and post-spill samples at both hierarchical levels (infra- and component communities) and the results obtained at the two levels were consistent irrespective of the sacrificed sample size in infracommunity analyses. It appears that analyses at component community level depict overall clearer picture of community change than infracommunities, the latter exhibiting higher stochastic variation.

One important result of the present four-year study is the detection of a directional trend in parasite community succession after the *Prestige* oil-spill. Parasite communities studied in the pilot study were largely dissimilar to those examined before the oil-spill in terms of both composition and structure. The remarkable dissimilarities have decreased with time reaching

negligibly small levels indicating an overlapping composition of communities in 2006. However, although the direction of compositional changes appeared to be towards the pre-spill situations, the differences were still large. Due to the overwhelming abundance of the heteroxenous parasites, the monoxenous-heteroxenous indices failed to detect changes and are probably not useful in host-parasite systems with dissimilar representation of these parasite groupings. Notably, the common species, an artificial *a priori* defined group, were identified by the similarity analyses as 'key discriminating' species with a significant contribution to community dissimilarities due to the oil-spill disturbance, season and locality effects. Analyses of component communities using prevalence data revealed the importance of some additional discriminating species with generally lower prevalence and abundance.

Overall, results on the compositional and structural changes in parasite communities in *B. boops* tend to indicate a synergistic effect of the two separate classes of confounded environmental variables, *i.e.* toxicants and organic enrichment. A note of caution, however, is necessary. Ruiz (2004) stressed the difficulties to demonstrate cause-and-effect relationships following a contaminant pulse such as an oil-spill due to the background environmental degradation (*e.g.* shifting chronic toxicity levels). Of particular relevance to the present study is his estimation of the toxic substances introduced by shipping in the Finisterre Traffic Separation Scheme, *i.e.* pulse contamination resulting from PAHs in the *Prestige* oil-spill as 10% *vs* 100% background toxicity set by antifouling paints (Ruiz, 2004). Although the present study has shown that parasite communities may well reflect the complex changes in the marine food webs following an effect as small as suggested above, the results indicate that shifting baselines probably affect the recovery of benthic (and parasite) communities from the *Prestige* oil-spill. It may appear that the state of parasite communities recorded in 2005-2006 is the new baselines to be used in case of another catastrophic event.

CHAPTER 8

CONCLUSIONS

The following conclusions can be drawn as a result of the present study:

8.1. The diversity of the parasite fauna of *B. boops* is much higher than previously thought, as evidenced by the description of one species new to science, *Wardula bartolii* Pérez-del-Olmo *et al.*, 2006, and the recovery of 53 parasite species in the seven fish populations studied along the North East Atlantic and the Mediterranean coasts of Spain, of which 25 represent new host records. The complete checklist of parasites of *B. boops* throughout its distributional range, developed during the course of the study, contains information for 78 species and 365 host-parasite-area records. A group of nine species with a wide geographical distribution, consistently present in both Mediterranean and North East Atlantic fish, are identified as the core of the parasite fauna of *B. boops*.

8.2. The regional parasite fauna of *B. boops* is richest in the North East Atlantic. There is a clear separation of the North East Atlantic and Mediterranean local faunas, with that of the 'transition' location (Barbate-Atlantic) occupying an intermediate position. Local parasite faunas are generally diverse, comprising *c.* 30-50% of the parasites of *B. boops* throughout its distributional range, except in two Mediterranean localities (off Valencia and Barcelona), where faunal richness is notably lower and comprises *c.* 15% of all species found in this host.

8.3. A characteristic feature of the parasite communities in *B. boops* is the high representation of parasites with complex life-cycles that are transmitted to fish *via* food ingestion and the dominance of trematodes. The phylogenetic influence on the composition and structure of parasite communities in *B. boops* is rather weak, since generalist parasites comprise a considerable part (36 species *vs* 8 strict specialists and sparid generalists) of the parasite communities with respect to both richness and abundance.

8.4. The species identified as the core of *B. boops* parasite fauna were already present in juvenile 1-year-old fish in the population off Santa Pola (Mediterranean), whereas all species added to communities in larger/older fish were either rare or accidental. The observed sequence of species appearance and persistence in the developing parasite communities in *B. boops* supports the hypothesis that species with wide geographical distributions appear in the fish population earlier than rare and stochastic species.

8.5. Parasite communities in *B. boops* were rich and abundant from an early age. Although community complexity and abundance tended to increase with fish size, perhaps related to an increase in feeding rates, the older (or larger size) fish cohorts showed no differences in the distributions of the parasite community parameters. No abrupt change that might indicate an ontogenetic diet shift was observed in these parameters along the fish size gradient studied. Six species of the core parasite fauna of *B. boops* were identified as key parasites in developing communities in this host since they persisted as common in all size classes and represented the majority of the individuals.

8.6. Although parasite communities in *B. boops* were rich and abundant no supportive evidence was found for interspecific competition. However, the repeatable community structure across size/age classes of *B. boops* translated into a nested subset pattern at the lowest infracommunity scale within the individual cohorts. This non-random compositional pattern, which was repeated within a fairly narrow size range, could not be completely attributed to either accumulation over time or segregation of the parasite species among different size-class hosts. The 'key' parasites both contributed to and reduced nestedness.

8.7. The small mouth size of *B. boops* coupled with suction feeding results in passive ingestion of prey restricted to small invertebrates suspended in the water column. These serve as intermediate/paratenic hosts of the key parasites as well as of an additional group of parasites. This addition to a baseline community of key parasite species results in a nested structure strongly related to the differential species abundance, thus suggesting that passive sampling could be the mechanism leading to the non-random parasite community structure observed in the developing communities in *B. boops*.

8.8. The first attempt to test the similarity-distance decay hypothesis using original taxonomically consistent data at two nested spatial scales revealed that both, the geographical distance and the region of origin, affect the species composition and structure of parasite faunas and component communities in *B. boops*.

8.9. The distance between localities/regions contributed significantly to the decay of the similarity estimated from parasite abundance at the infracommunity level. The structured spatial patterns were consistent in time but not across seasons. Component communities sampled in spring exhibited a highly structured spatial pattern whereas those sampled in

winter did not differ from random distribution. This lack of spatial synchrony indicates higher homogenization of communities in the cold season.

8.10. The spatial synchrony observed was solely due to the assemblage of the 'core' species whereas the remaining species exhibited a random spatial structure. This supports the hypothesis that widespread species would be strongly associated with patterns of variation in environmental conditions. The interspecific abundance-distribution patterns were recognized as the most important for the distance-decay relationship of similarity in the studied host-parasite system due to the strong correlations observed at all scales of analysis.

8.11. The comparative analyses revealed dramatic changes in species richness, abundance and structure of parasite communities and a notable alteration of both individual and functional group parasite abundance patterns in *B. boops* studied after the *Prestige* oil-spill. This suggests that parasite communities in the model host may have reflected a disturbance effect on the natural communities along the Spanish coasts following the oil-spill.

8.12. A directional trend in parasite community succession after the *Prestige* oil-spill was detected. Parasite communities studied in the pilot study were largely dissimilar to those examined before the oil-spill both in terms of composition and structure. These dissimilarities have decreased with time and the direction of compositional changes appeared to be towards the pre-spill situations. The fact that the differences were still large indicates that shifting pollution baselines probably affect the recovery of benthic (and parasite) communities from the *Prestige* oil-spill. It is possible, therefore, that parasite community structure registered in 2005-2006 represents the new baseline to be used in case of another catastrophic event in the region.

8.13. Focusing on higher taxonomic and/or functional levels provided a higher resolution in detecting directional trends in parasite community structure with respect to the two separate classes of confounded environmental variables, *i.e.* toxicants and organic enrichment. The elevated levels of monoxenous infections in the pilot study indicate that changes in immune parameters of fish due to chronic exposure to PAHs post-spill may be involved. The notable increase of heteroxenous, and the remarkable alteration in the hemiuroid abundance post-spill in particular, may have reflected an enhancement of the populations of the

mollusc, polychaete and copepod hosts due to organic enrichment following the *Prestige* oil-spill.

8.14. The multivariate statistical approach which facilitates an assessment of the variation of the overall community structure, proved to be very useful in studying the response of parasite communities in *B. boops* after the *Prestige* oil-spill. The good agreement between the two techniques applied (MDS and ANOSIM) and the consistency of detection of significant differences in community structure in the 'before-after' design at both hierarchical levels, infra- and component communities, support this suggestion.

APPENDICES

Appendix 1. Prevalence (P%) and mean abundance (MA±SD) of parasites recovered in *B. boops* off Ondarroa and Malpica. *Abbreviations*: na, not applicable; BS, bogue specialist; SG, sparid generalist; G, generalist; D, transmitted *via* direct infection; F, transmitted *via* food ingestion; M, monoxenous species; H, heteroxenous species. *, *Ascarophis* nº 1 of Petter & Radujkovic, 1989.

Locality	**Mode of infection and reproduction**	**Specificity**	**Ondarroa**				**Malpica**							
Season and Year			**Spring 2001**		**Spring 2005**		**Autumn 2001**		**Spring 2004**		**Spring 2005**		**Autumn 2005**	
			P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD
MONOGENEA														
Cyclocotyla bellones	D-M	G	6.7	0.07±0.3	3.3	0.03±0.2			43.3	0.70±1.0	9.4	0.13±0.4	4.8	0.05±0.2
Microcotyle erythrini	D-M	SG	36.7	0.70±1.1	73.3	1.80±1.7	10.0	0.17±0.5	100.0	5.27±4.0	53.1	1.56±2.1	7.1	0.12±0.5
DIGENEA														
Accacladium serpentulum	F-H	G					3.3	0.03±0.2						
Aphanurus stossichii	F-H	G	96.7	12.53±15.0	96.7	21.43±12.7	96.7	28.63±23.5	100.0	30.60±18.0	100.0	46.72±37.3	97.6	28.02±24.1
Aponurus laguncula	F-H	G			3.3	0.03±0.2			3.3	0.03±0.2				
Arnola microcirrus	F-H	SG	6.7	0.13±0.6	13.3	0.57±1.7	13.3	0.13±0.3	6.7	0.13±0.6	12.5	0.13±0.3		
Bacciger israelensis	F-H	BS	96.7	34.10±42.1	90.0	20.73±32.6	43.3	1.60±2.8	100.0	47.43±56.7	90.6	14.84±16.2	81.0	7.57±8.4
Cardiocephaloides longicollis met.	D-H	G			36.7	0.73±1.3							4.8	0.07±0.3
Derogenes varicus	F-H	G					10.0	0.13±0.4	43.3	0.70±1.0	9.4	0.09±0.3	19.0	0.26±0.6
Hemiurus communis	F-H	G	80.0	2.30±2.4	100.0	58.13±36.8	70.0	1.67±1.6	100.0	175.80±156.1	100.0	44.66±37.5	78.6	3.74±6.1
Lecithaster confusus	F-H	G			3.3	0.03±0.2			3.3	0.03±0.2			2.4	0.02±v
Lecithocladium excisum	F-H	G	10.0	0.10±0.3			46.7	1.83±2.7	26.7	0.57±1.2	71.9	1.66±2.1	85.7	24.43±21.4
Lepocreadium album	F-H	SG			3.3	0.03±0.2			3.3	0.03±0.2				
Juvenile lepocreadiids	F-H	G	16.7	0.27±0.7	13.3	0.17±0.5	6.7	0.13±0.6	96.7	85.93±90.7	21.9	0.44±1.0		
Magnibursatus bartolii	F-H	BS	20.0	0.93±2.9	90.0	15.00±25.5	3.3	0.03±0.2	50.0	7.23±31.1	31.3	0.78±1.9	11.9	0.64±3.0
Magnibursatus caudofilamentosa	F-H	G	3.3	0.03±0.2	6.7	0.13±0.6			6.7	0.20±0.8				
Opecoelidae gen. sp.	F-H	na									3.1	0.03±0.2		
Prosorhynchus crucibulum met.	F-H	G									18.8	0.31±0.8	9.5	0.17±0.6
Renicolidae gen. sp. met.	D-H	G					16.7	0.33±0.9	13.3	0.83±2.8	15.6	0.69±2.2	16.7	0.48±1.5
Stephanostomum cesticillum met.	D-H	G							3.3	0.17±0.9	9.4	0.13±0.4	4.8	0.05±0.2
Stephanostomum lophii met.	D-H	G							3.3	0.07±0.4				
Tetrochetus corypahenae	F-H	G			3.3	0.03±0.6								
Wardula bartolii	F-H	BS	3.3	0.03±0.2	30.0	0.83±1.5			23.3	2.87±13.3	9.4	0.25±1.1	9.5	0.14±0.5
CESTODA														
Scolex pleuronectis	F-H	G			43.3	0.67±1.1			6.7	0.30±1.2	6.3	0.06±0.2	16.7	0.40±1.1
NEMATODA														
Anisakis simplex sensu lato larva	F-H	G	26.7	0.57±1.0			13.3	0.23±0.7	23.3	0.57±1.9	40.6	0.72±1.0	26.2	0.76±1.7
Ascarophis sp. *	F-H	na			3.3	0.03±0.2							9.5	0.10±0.3
Hysterothylacium aduncum larva	F-H	G	20.0	0.23±0.5	26.7	0.40±0.9	63.3	1.40±1.6	23.3	0.40±0.8	87.5	2.38±1.9	76.2	1.62±1.4
ACANTHOCEPHALA														
Andracantha mergi	F-H	G									3.1	0.03±0.2		
Echinorhynchus gadi	F-H	G							6.7	0.07±0.3				
Neoechinorhynchus agilis	F-H	G							3.3	0.03±0.2				
ISOPODA														
Ceratothoa oestroides	D-M	G	3.3	0.07±0.4	13.3	0.17±0.5	16.7	0.33±0.8	53.3	0.87±0.9			21.4	0.40±0.8
Ceratothoa parallela	D-M	G					3.3	0.03±0.2	3.3	0.07±0.4				
Gnathia sp.	D-M	na			26.7	0.40±0.8			6.7	0.23±1.1				
COPEPODA														
Caligus sp.	D-M	na			3.3	0.03±0.2							2.4	0.02±0.2
Clavellodes sp.	D-M	na							3.3	0.03±0.2				
Peniculus fistula	D-M	G							26.7	0.33±0.6			4.8	0.05±0.2

Appendix 2. Prevalence (P%) and mean abundance (MA±SD) of parasites recovered in *B. boops* off Vigo. *Abbreviations*: na, not applicable; BS, bogue specialist; SG, sparid generalist; G, generalist; D, transmitted *via* direct infection; F, transmitted *via* food ingestion; M, monoxenous species; H, heteroxenous species. *, *Ascarophis* nº 1 of Petter & Radujkovic, 1989.

Season and Year	Mode of infection and reproduction	Specificity	Spring 2001		Spring 2005		Autumn 2005		Spring 2006		Autumn 2006-A		Autumn 2006-B	
			P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD
MONOGENEA														
Cyclocotyla bellones	D-M	G			12.0	0.14±0.4	2.5	0.03±0.2	17.6	0.18±0.4	10.3	0.18±0.6	35.0	0.50±0.8
Microcotyle erythrini	D-M	SG	33.3	0.57±0.9	86.0	3.64±3.2			76.5	2.59±2.1	2.6	0.05±0.3	5.0	0.05±0.2
DIGENEA														
Accacladium serpentulum	F-H	G			2.0	0.02±0.1								
Aphanurus stossichii	F-H	G	100.0	9.93±6.4	100.0	34.54±24.0	97.5	29.88±22.0	97.1	14.50±13.6	97.4	17.36±10.8	100.0	20.85±12.7
Aponurus laguncula	F-H	G					2.5	0.03±0.2					5.0	0.05±0.2
Arnola microcirrus	F-H	SG	40.0	0.80±1.2	4.0	0.04±0.2			20.6	0.26±0.6	10.3	0.44±1.7	5.0	0.05±0.2
Bacciger israelensis	F-H	BS	76.7	8.17±20.0	82.0	10.84±13.7	72.5	6.75±9.5	91.2	32.56±31.7	94.9	14.62±19.9	70.0	4.90±7.5
Cardiocephaloides longicollis met.	D-H	G					2.5	0.03±0.2			2.6	0.03±0.2		
Derogenes varicus	F-H	G	3.3	0.03±0.2	44.0	0.98±1.6	22.5	0.30±0.7	5.9	0.09±0.4	2.6	0.03±0.2		
Hemiurus communis	F-H	G	100.0	26.57±13.0	100.0	44.22±19.4	67.5	2.70±4.0	88.2	4.91±3.9	30.8	0.79±2.0	5.0	0.10±0.4
Lecithaster confusus	F-H	G			4.0	0.04±0.2								
Lecithocladium excisum	F-H	G			82.0	2.68±2.5	82.5	5.10±5.2	41.2	0.71±1.1	66.7	2.38±3.7	65.0	1.80±2.4
Lepocreadium album	F-H	SG			2.0	0.06±0.4								
Juvenile lepocreadiids	F-H	G	66.7	8.83±15.3	74.0	5.10±7.6	27.5	0.43±0.8	41.2	8.38±25.5	5.1	0.13±0.7	25.0	0.45±1.1
Magnibursatus bartolii	F-H	BS	16.7	0.53±2.2	44.0	1.46±2.6	35.0	0.78±1.8	76.5	15.32±52.1	33.3	1.10±2.6	20.0	0.25±0.6
Magnibursatus caudofilamentosa	F-H	G			4.0	0.06±0.3	2.5	0.03±0.2	5.9	0.06±0.2				
Opecoelidae gen. sp.	F-H	na			2.0	0.02±0.1	2.5	0.03±0.2						
Prosorhynchus crucibulum met.	F-H	G			12.0	0.18±0.6	17.5	0.30±0.8	29.4	0.53±1.0	17.9	0.33±0.9	5.0	0.05±0.2
Renicolidae gen. sp. met.	D-H	G	16.7	0.20±0.5	22.0	0.78±2.3	12.5	0.53±1.8	5.9	0.24±1.0	7.7	0.38±1.5	10.0	0.30±1.1
Stephanostomum cesticillum met.	D-H	G			38.0	0.50±0.7	12.5	0.35±1.3	76.5	9.41±14.3	33.3	2.33±11.2	35.0	0.40±0.6
Stephanostomum lophii met.	D-H	G									2.6	0.03±0.2		
Steringotrema pagelli	F-H	G			4.0	0.84±5.0			32.4	7.26±22.5				
Wardula bartolii	F-H	BS	3.3	0.03±0.2	20.0	0.32±0.8	27.5	0.50±1.0	20.6	0.53±1.2	15.4	0.26±0.7	10.0	0.10±0.3
CESTODA														
Scolex pleuronectis	F-H	G			10.0	0.10±0.3	7.5	0.13±0.5	5.9	0.06±0.2	5.1	0.05±0.2		
NEMATODA														
Anisakis simplex sensu lato larva	F-H	G	3.3	0.03±0.2	20.0	0.20±0.4	50.0	1.08±1.4	23.5	0.68±2.3	56.4	1.00±1.1	60.0	1.15±1.4
Ascarophis sp. *	F-H	na			4.0	0.04±0.2	5.0	0.08±0.3			7.7	0.08±0.3	10.0	0.10±0.3
Contracaecum sp. larva	F-H	G					2.5	0.03±0.2			2.6	0.03±0.2	20.0	0.20±0.4
Hysterothylacium aduncum larva	F-H	G	36.7	0.47±0.7	42.0	0.78±1.1	55.0	1.05±1.2	23.5	0.24±0.4	46.2	0.69±0.9	55.0	0.80±0.9
Pseudocapillaria adriatica	F-H	G					2.5	0.03±0.2						
ACANTHOCEPHALA														
Andracantha tunitae	F-H	G							2.9	0.03±0.2				
Corynosoma sp.	F-H	G			2.0	0.02±0.1								
Rhadinorhynchus pristis	F-H	G									2.6	0.03±0.2		
ISOPODA														
Anilocra physodes	D-M	G							2.9	0.06±0.3				
Ceratothoa oestroides	D-M	G			14.0	0.22±0.6	15.0	0.23±0.6	17.6	0.26±0.6	33.3	0.62±0.9	75.0	1.40±1.0
Ceratothoa parallela	D-M	G			2.0	0.02±0.1					2.6	0.08±0.5		
Gnathia sp.	D-M	na	3.3	0.07±0.4										
COPEPODA														
Caligus sp.	D-M	na					2.5	0.03±0.2	5.9	0.06±0.2	2.6	0.03±0.2	5.0	0.05±0.2
Peniculus fistula	D-M	G			14.0	0.24±0.7	5.0	0.05±0.2	5.9	0.09±0.4				

Appendix 3. Prevalence (P%) and mean abundance (MA±SD) of parasites recovered in *B. boops* off Santa Pola. *Abbreviations*: na, not applicable; BS, bogue specialist; SG, sparid generalist; G, generalist; D, transmitted *via* direct infection; F, transmitted *via* food ingestion; M, monoxenous species; H, heteroxenous species.

Season and Year	**Mode of infection and reproduction**	**Specificity**	**Spring 2005**		**Autumn 2005**		**Spring 2006**		**Autumn 2006-A**		**Autumn 2006-B**	
			P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD
MONOGENEA												
Cyclocotyla bellones	D-M	G	5.3	0.05±0.2	2.9	0.03±0.2					25.0	0.25±0.4
Microcotyle erythrini	D-M	SG	74.0	4.81±6.5	5.7	0.06±0.2	82.8	1.90±1.4	13.3	0.20±0.6	60.0	2.35±4.5
Pseudaxine trachuri	D-M	G	11.5	0.18±0.6	11.4	0.11±0.3	3.4	0.03±0.2				
DIGENEA												
Accacladium serpentulum	F-H	G					10.3	0.10±0.3			5.0	0.05±0.2
Aphanurus stossichii	F-H	G	92.4	6.85±9.9	88.6	6.34±6.0	79.3	3.34±3.8	76.7	3.17±4.5	70.0	8.35±11.6
Arnola microcirrus	F-H	SG	0.8	0.02±0.2			3.4	0.03±0.2				
Bacciger israelensis	F-H	BS	89.3	15.73±26.6	100.0	16.77±14.0	89.7	12.62±11.1	96.7	14.40±16.6	95.0	13.05±19.8
Cardiocephaloides longicollis met.	D-H	G	19.1	0.27±0.6	20.0	0.26±0.6	10.3	0.10±0.3	23.3	0.27±0.5	20.0	0.30±0.7
Derogenes varicus	F-H	G			2.9	0.03±0.2						
Hemiurus communis	F-H	G	95.4	12.80±19.2	17.1	0.69±3.2	55.2	2.24±4.2	6.7	0.07±0.3	5.0	0.05±0.2
Lecithocladium excisum	F-H	G	38.2	0.62±1.1	11.4	0.34±1.3	10.3	0.10±0.3	66.7	1.10±1.0	10.0	0.10±0.3
Juvenile lepocreadiids	F-H	G							3.3	0.03±0.2		
Magnibursatus bartolii	F-H	BS	1.5	0.02±0.1								
Opecoelidae gen. sp.	F-H	na	0.8	0.01±0.1								
Prosorhynchus crucibulum met.	F-H	G	13.0	2.53±16.2	2.9	0.14±0.8	3.4	0.90±4.8	6.7	0.47±2.2		
Renicolidae gen. sp. met.	D-H	G			2.9	0.03±0.2			3.3	0.03±0.2		
Robphildollfusium martinezgomezi	F-H	BS	3.1	0.06±0.5	2.9	0.03±0.2						
Stephanostomum cesticillum met.	D-H	G							6.7	0.10±0.4		
Stephanostomum euzeti met.	D-H	G	14.5	0.21±0.6	11.4	0.11±0.3	31.0	1.28±3.4	30.0	0.50±0.9	20.0	0.30±0.7
Tetrochetus corypahenae	F-H	G	0.8	0.01±0.1			13.8	0.17±0.5	16.7	0.40±1.3	5.0	0.05±0.2
Tormopsolus sp. met.	D-H	G	3.1	0.03±0.2					3.3	0.10±0.5	10.0	0.10±0.3
CESTODA												
Scolex pleuronectis	F-H	G	16.8	0.54±2.9	34.3	1.86±4.4	48.3	0.69±0.9	20.0	0.63±1.6	30.0	0.30±0.5
NEMATODA												
Anisakis simplex sensu lato larva	F-H	G	10.7	0.14±0.5	11.4	0.14±0.4	17.2	0.24±0.6	10.0	0.33±1.3	15.0	0.15±0.4
Camallanus sp.	F-H	na	0.8	0.01±0.1								
Contracaecum sp. larva	F-H	G			2.9	0.03±0.2						
Cucullanellus sp.	F-H	na	0.8	0.01±0.1								
Hysterothylacium aduncum larva	F-H	G	58.8	1.07±1.2	48.6	0.71±0.9	51.7	0.97±1.5	66.7	1.50±1.7	40.0	0.55±0.8
Pseudocapillaria adriatica	F-H	G	0.8	0.01±0.1	2.9	0.03±0.2						
ACANTHOCEPHALA												
Neoechinorhynchus agilis	F-H	G	0.8	0.01±0.1								
ISOPODA												
Ceratothoa oestroides	D-M	G	1.5	0.07±0.7	5.7	0.06±0.2					10.0	0.10±0.3
COPEPODA												
Naobranchia cygniformis	D-M	SG	17.6	0.19±0.4	5.7	0.06±0.2	6.9	0.10±0.4	3.3	0.03±0.2	20.0	0.35±0.8
Peniculus fistula	D-M	G	0.8	0.01±0.1	2.9	0.03±0.2						
Taeniacanthidae gen. sp. larva	D-M	na	0.8	0.01±0.1								

Appendix 4. Prevalence (P%) and mean abundance (MA±SD) of parasites recovered in *B. boops* off Barbate, Valencia and Barcelona. *Abbreviations*: na, not applicable; BS, bogue specialist; SG, sparid generalist; G, generalist; D, transmitted *via* direct infection; F, transmitted *via* food ingestion; M, monoxenous species; H, heteroxenous species.

Locality			**Barbate**				**Valencia**		**Barcelona**			
Season/Year	**Mode of infection and reproduction**	**Specificity**	**Spring**	**2005**	**Autumn**	**2005**	**Autumn**	**2003**	**Spring**	**2005**	**Autumn**	**2005**
			P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD	P (%)	MA±SD
MONOGENEA												
Cyclocotyla bellones	D-M	G					3.0	0.03±0.2	6.7	0.07±0.3		
Microcotyle erythrini	D-M	SG	33.3	1.77±4.5	10.0	0.10±0.3	21.2	0.30±0.7	76.7	2.43±3.5		
Pseudaxine trachuri	D-M	G	3.3	0.07±0.4								
DIGENEA												
Aphanurus stossichii	F-H	G	96.7	53.63±35.4	96.7	22.67±17.3	6.1	0.06±0.2	83.3	3.20±2.7	90.0	11.53±12.5
Bacciger israelensis	F-H	BS	90.0	28.17±37.2	63.3	7.90±19.1	100.0	7.27±7.5	90.0	6.50±6.6	63.3	4.20±5.7
Cardiocephaloides longicollis met.	D-H	G	23.3	0.23±0.4	23.3	0.27±0.5	24.2	0.27±0.5	23.3	0.43±0.9	20.0	0.33±0.7
Derogenes varicus	F-H	G	3.3	0.03±0.2								
Hemiurus communis	F-H	G	93.3	9.40±9.2	73.3	9.07±10.2	9.1	0.18±0.6	20.0	0.20±0.4	33.3	0.43±0.7
Lecithocladium excisum	F-H	G	30.0	0.50±0.9	13.3	0.17±0.5	30.3	0.67±1.5	36.7	0.47±0.7	70.0	3.03±3.6
Lepocreadium album	F-H	SG			6.7	0.10±0.4						
Juvenile lepocreadiids	F-H	G	3.3	0.03±0.2	10.0	0.20±0.7						
Magnibursatus bartolii	F-H	BS	20.0	0.20±0.4	10.0	0.10±0.3						
Magnibursatus caudofilamentosa	F-H	G	3.3	0.03±0.2								
Prosorhynchus crucibulum met.	F-H	G	93.3	14.90±14.8	70.0	5.60±7.1						
Stephanostomum cesticillum met.	D-H	G	3.3	0.07±0.4								
Stephanostomum euzeti met.	D-H	G	46.7	0.80±1.1	3.3	0.03±0.2			33.3	0.50±0.8	3.3	0.13±0.7
Tormopsolus sp. met.	D-H	G	43.3	0.87±1.3	70.0	3.57±4.7						
CESTODA												
Scolex pleuronectis	F-H	G	23.3	0.53±1.2	33.3	1.07±2.4	33.3	0.58±1.2			3.3	0.03±0.2
Larval trypanorhyncha	F-H	G	3.3	0.03±0.2								
NEMATODA												
Anisakis simplex sensu lato larva	F-H	G	23.3	0.23±0.4	3.3	0.10±0.5					3.3	0.03±0.2
Cucullanellus sp.	F-H	na	6.7	0.10±0.4								
Hysterothylacium aduncum larva	F-H	G	66.7	1.63±1.8	26.7	0.30±0.5	39.4	0.42±0.6	86.7	2.50±2.5	90.0	3.47±2.1
ACANTHOCEPHALA												
Rhadinorhynchus pristis	F-H	G	30.0	0.70±1.6								
ISOPODA												
Ceratothoa oestroides	D-M	G			3.3	0.03±0.2						
Gnathia sp.	D-M	na			3.3	0.13±0.7						
COPEPODA												
Naobranchia cygniformis	D-M	SG	6.7	0.07±0.3	6.7	0.17±0.7					3.3	0.03±0.2
Philichthys sp.	D-M	na			6.7	0.07±0.3						

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