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Interactions of elasmobranchs with other taxa in Iberian waters: parasitism and agonistic relationships

TESIS DOCTORAL

Presentada por
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D. Jesús Tomás Aguirre, Profesor Contratado Doctor del Departamento de Zoología de la Facultad de Ciencias Biológicas de la Universitat de València,

CERTIFICAN que **D. Jaime Penadés Suay** ha realizado bajo nuestra dirección, y con el mayor aprovechamiento, el trabajo de investigación recogido en esta memoria, y que lleva por título "**Interactions of elasmobranchs with other taxa in Iberian waters: parasitism and agonistic relationships**", para

optar al grado de Doctor en Ciencias Biológicas.

Y para que así conste, en cumplimiento de la legislación vigente, expedimos el presente certificado en València, a 05 de enero de 2022.

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Soy fruto del esfuerzo combinado y continuado de mis padres,
ellos a la vez lo son de los suyos. Por eso lo dedico a
Josefina y Pascual, Carmen y Ramón,
Cristina y Ramón.
Ellos saben que allí dónde vaya los llevaré conmigo.

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Es difícil que en la elaboración de una tesis se dedique el tiempo suficiente a los agradecimientos. Quizás no parecen parte esencial de un trabajo científico. Sin embargo, la tesis doctoral es un esfuerzo por empujar los límites del conocimiento colectivo en un campo específico, por tanto en su misma esencia la tesis (y a tales efectos, cualquier trabajo científico) parte de lo colectivo y se nutre de ello. Yo no podría haber llegado aquí sin el trabajo de miles de personas que, alejados en el tiempo, dedicaron su atención a múltiples aspectos que permitieron empedrar el camino que un día yo me propuse recorrer. Por ser breves sin dejar de ser justos, hablaremos aquí del pasado, dos presentes claramente diferenciados y un futuro al que trato de alentar. Estos cuatro elementos se entrelazan formando un todo al que debo mi gratitud, y así espero transmitirlo en estas líneas. Si alguien no ve su nombre reflejado espero que sepa perdonar mi torpeza y entender que mi gratitud se extiende más allá de este texto.

Desde el primer humano que se preocupó en prestar atención a los procesos del mundo natural, quiero pensar que formo parte de un continuo esfuerzo que surge del pasado para lograr ese conocimiento. La llave maestra de todo se la debo a Alexandra Elbakyan, sin cuyo proyecto la mitad de las referencias que aparecen en este estudio me habrían sido vetadas o de muy difícil acceso. Abogo así por una ciencia libre de ataduras y restricciones, de fronteras y divisiones, entendida como la mayor obra emprendida por la humanidad como colectivo. A todas las personas que aparecen en las referencias, algunas de las cuales ya se asemejan a viejos conocidos aunque jamás nos hayamos encontrado, os ofrezco mi gratitud y humildemente sumo a los vuestros mi trabajo.

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La Unidad de Zoología Marina ha sido mi casa durante más de ocho años. En todo este tiempo, me he sentido arropado por todos los que formáis parte de ella. La vieja guardia siempre tendrá un lugar en mi corazón: Francesc, Patri, Ohiana, Raúl, Natalia. La ya no tan nueva guardia ha sido mi alegría diaria en estos últimos años: Olga, Rachel, Sofía, Claudia, Mar, Marta. Aunque se dediquen a los teleósteos, saben que les aprecio: Jose, María, Aïgues, Mar, Álex. Hay personas que hacen que ir al laboratorio sea más que agradable: Merche es una bomba de alegría, Paco ha tenido siempre tiempo para cualquiera de mis problemas, Isa es el motor que mueve toda la Unidad en la sombra. Eterna gratitud a Toñi por su trabajo y calidad humana, siempre con la conversación adecuada para empezar el día con ganas. A Toni le debo mi primera experiencia laboral en el mundo académico y le agradezco todos sus consejos durante este tiempo. Ha pasado tanto que algunos compañeros quedan desdibujados, pero sabed que de todos guardo un grato recuerdo.

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Por último, el futuro dirá si esta tesis y sus trabajos sirven a otros investigadores para seguir avanzando sobre el conocimiento de los elasmobranquios y sus cestodos en particular. Es a ésos investigadores a los que dirijo mi gratitud anticipada. El sacrificio que haréis sólo vosotros podréis cuantificarlo, pero de la misma manera sólo vosotros reconoceréis los frutos de vuestro trabajo. Sabed que no estáis solos y que muchos en el tiempo anduvieron caminos similares, sentiros acompañados en cada reto que tengáis que afrontar.

Gran parte de los sacrificios hechos por esta tesis han recaído en los últimos años en Alba. Gracias por asumir ésa carga no elegida de la mejor manera y ser la mejor compañera de vida. Te quiero.

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Introducción

Elasmobranquios: muy amenazados y poco estudiados

Los tiburones y las rayas se encuentran entre los grupos de animales más amenazados, incluyendo muchas especies de las que existe poca información de manera general y, particularmente, sobre su abundancia y distribución. La primera evaluación global de este grupo por la UICN (Unión Internacional para la Conservación de la Naturaleza, Dulvy et al. 2014) estimó que el 25% de las especies de tiburones estaban amenazadas de extinción (por lo tanto, clasificadas como Vulnerables, En Peligro o en Peligro Crítico de extinción - Criterios de la Lista Roja de Especies Amenazadas de la UICN), lo que convierte a los elasmobranquios en el grupo de vertebrados más amenazado después de los anfibios (Stuart et al. 2004, Hoffman et al. 2010, Dulvy et al. 2014, Pacoureau et al. 2021).

La susceptibilidad de los elasmobranquios a la sobreexplotación proviene principalmente de los rasgos que comparten muchas especies dentro del grupo: una baja productividad asociada con baja fecundidad, una tasa de crecimiento lenta y una edad tardía en la maduración sexual (Musick 1999, Dulvy et al. 2008, Pardo et al. 2016, Dulvy et al. al 2017). El alto riesgo de extinción de los elasmobranquios, junto con su importancia ecológica, exige un enfoque en profundidad para su conservación y una gestión adecuada de las poblaciones que sufren un mayor impacto por las pesquerías, que debe estar basado en la capacidad de carga de sus poblaciones y no por otros factores.

En este escenario de aparente urgencia respecto la conservación de tiburones y rayas cabe preguntarse, por una parte, cuánta cantidad de ciencia adicional es necesario aportar antes de adoptar acciones de conservación efectivas (véase, p.e., Jaramillo-Legorreta et al. 2007) y, por otra, dónde dirigir dicho esfuerzo científico. Es evidente que necesitamos mejorar nuestra comprensión sobre aspectos biológicos básicos sobre los elasmobranquios, p.e., sus dinámicas poblacionales, pero ¿por qué abordar el estudio de interacciones interespecíficas aparentemente “menores”, como las de la fauna parásita o las agresiones secundarias de algunas presas? A nuestro entender, existen varias razones de peso, que argumentamos brevemente en el siguiente apartado.

Contexto teórico de este estudio

Respecto a los parásitos cabe señalar, en primer lugar, que dichos organismos representan un componente de biodiversidad inextricablemente unido al de sus hospedadores. Esto significa que, en último término, la extinción de los hospedadores supone la coextinción de sus parásitos asociados (Koh et al. 2004). Por tanto, cualquier perspectiva taxonómica (esto es, basada en especies) de la conservación debe reconocer que los parásitos son un parte integral de la biodiversidad que tendría que considerarse explícitamente en cualquier programa de conservación (Windsor 1995, Gomper and Williams 1998, Dougherty et al. 2015). Dicho planteamiento obviamente presupone que la fauna parasitaria está bien caracterizada. Sin embargo, como explicamos más abajo, en el caso de los parásitos de elasmobranquios esto sólo ha empezado a ser una realidad en las últimas dos décadas, y es por tanto una de las razones que justifican el presente estudio.

En segundo lugar, debido a la íntima relación entre los hospedadores y sus parásitos, estos pueden arrojar luz sobre muchos aspectos sobre la biología y ecología de aquellos, incluso de gran relevancia para la conservación (véase, p.e., Williams et al. 1992, Mackenzie 2002, Whiteman and Parker 2005, Criscione et al. 2006, Nieberding and Olivieri 2007). Este papel indicador los parásitos se extiende hasta el nivel ecosistémico, ya que estos organismos juegan un papel ecológico clave, aunque tradicionalmente ignorado, en múltiples facetas del funcionamiento de los ecosistemas, especialmente las redes tróficas (p.e., Horwitz and Wilson 2005, Hudson et al. 2006, Buck and Ripple 2017, Vanatta and Minchella 2018). Los parásitos son reconocidos en todos los sistemas ecológicos por los roles cruciales que desempeñan (Huxham et al. 1995, Thompson et al. 2005, Lafferty et al. 2006, Hernández y Sukhdeo 2008, Amundsen et al. 2009); estos organismos median en la composición de especies de las comunidades de vida libre (por ejemplo, Mouritsen y Poulin 2005, Wood et al. 2007), regulan las poblaciones de hospedadores (por ejemplo, Hudson y Greenman 1998), redirigen el flujo de energía entre y dentro de las redes tróficas (por ejemplo, Lafferty y Morris 1996, Sato et al. 2012) e incluso comprenden una proporción sustancial de la biomasa total de algunos ecosistemas (por ejemplo, Kuris et al. 2008, Preston et al. 2013).

En este sentido, el análisis sobre el determinantes de la riqueza y diversidad de las comunidades de parásitos, tal y como se hará en el presente estudio, requiere preguntarse sobre aspectos tanto ecológicos (p.e., sus ciclos vitales) como evolutivos (p.e., su especificidad) que pueden ayudarnos, a largo plazo, a resolver algunas de las lagunas en nuestro conocimiento general de los elasmobranquios (particularmente en cambios ontogenéticos en el uso del hábitat y dieta, diferenciación de stocks y estructura poblacional, migración y distribuciones geográficas, salud y conectividad de las poblaciones) y los ecosistemas donde habitan. Los estudios parasitológicos pueden por tanto complementar otros estudios necesarios (principalmente sobre la dieta y la edad/rasgos reproductivos) que requieren el acceso a muestras completas en las que se pueden obtener información parasitológica.

Por último, y esto es aplicable a todas las interacciones interespecíficas tratadas en este estudio, creemos que debe reivindicarse la importancia científica de la historia natural, incluyendo su aplicación en conservación (Tewksbury et al. 2014, Barrows et al. 2016, Anderson 2017, Tosa et al. 2021). La historia natural se ha definido como "*the observation and description of the natural world, with the study of organisms and their linkages to the environment being central*" (Tewksbury et al. 2014), o más concisamente, como "*the observational study of organisms in their environment*" (Barrows et al. 2016). Un elemento implícito de estas definiciones es que la investigación en historia natural no tiene por qué hace mención explícita a teorías generalizables (Tosa et al. 2021). Para algunos autores, este énfasis en lo particular puede ir en detrimento de la "verdadera" ciencia, que debe aspirar los fenómenos naturales a partir de leyes generales (véase Gould 2002, Wilson and Armesto 2006). Sin embargo, dichas "leyes" requieren de un establecimiento previo de patrones, que emergen de grupos de observaciones (Tosa et al. 2021). La historia de la teoría ecológica y de la ciencia de la conservación están plagadas de intentos de obtener leyes generales a partir de patrones prematuros, o simplemente, no sostenibles debido a la variada idiosincrasia de los sistemas bajo estudio (véase, p.e., Hansson 2003, Sagoff 2003, Baguette 2004, Rohde 2005a, Poulin 2007a, Lindenmayer and Hunter 2010).

Es decir, el valor de la historia natural reside en que se busca la comprensión de fenómenos naturales concretos a partir de preguntas específicas. En el contexto de este estudio, las preguntas surgieron de la propia descripción de las observaciones (p.e., la extrema pobreza de las infracomunidades helmínticas de algunos de los elasmobranquios estudiados, o la detección de un fenómeno extraordinario –el empalamiento de tintoreras por peces espada). Las respuestas a estas preguntas encuentran acomodo científico como fuente de inspiración y validación de teorías ecológicos más generales (Tosa et al. 2021; véanse los capítulos correspondientes del presente trabajo), y como piezas de información relevante para la conservación de los elasmobranquios.

Elasmobranquios como hospedadores de parásitos: cestodos de elasmobranquios

Debido a que son depredadores que ocupan los niveles superiores de las redes tróficas marinas, los elasmobranquios también tienen un papel importante como hospedadores definitivos para muchos parásitos. El cuerpo de cualquier elasmobranquio ofrece una diversidad de sitios que pueden estar, y con frecuencia están, ocupados por otros animales. Pero la mayor diversidad de parásitos se encuentra en la válvula espiral (es decir, el intestino espiral) y los cestodos son los parásitos más comunes que se pueden encontrar allí.

Los cestodos son gusanos parásitos que pertenecen al filo Platyhelminthes (Clase: Cestoda). Los cestodos que parasitan a los elasmobranquios tienen representantes de nueve de los 19 órdenes de su clase, e incluyen más de 1000 especies y 202 géneros (Caira y Reyda 2005, Caira y Jensen 2017). De estos nueve órdenes, siete están constituidos por especies que parasitan exclusivamente a los elasmobranquios (con la excepción de los miembros de la familia Chimaerocestidae que parasitan taxones estrechamente relacionados, véase Williams y Bray 1984). Muchas especies de estos nueve órdenes de cestodos son altamente específicos en sus hospedadores, y algunas especies solo parasitan una sola especie de elasmobranquios (Caira 1990, Caira y Jensen 2001, Caira y Healy 2004).

El hecho de que haya solo unas pocas descripciones completas de los ciclos de vida de especies de cestodos de elasmobranquios es solo un ejemplo de lo poco que ha avanzado este campo de conocimiento y de los múltiples frentes que están abiertos para seguir estudiando. Teniendo en cuenta la importancia de los elasmobranquios como depredadores a nivel mundial, se sabe poco sobre los procesos de transmisión trófica de sus parásitos dentro de las redes tróficas marinas, hecho que se reitera cada vez que se plantea el tema (Chambers et al. 2000, Chervy 2002, Caira y Reyda 2005, Jensen y Bullard 2010, Randhawa y Poulin 2020).

Para terminar con una nota esperanzadora, nos encontramos en medio de un período de 'máximo descubrimiento de especies' tanto para los elasmobranquios (Last 2007, White y Last 2012, Randhawa et al. 2015) como para sus cestodos (Randhawa et al. 2020), en relación con lo que muestran los períodos anteriores. No podría haber un mejor momento para estudiar los cestodos de elasmobranquios.

Presente estudio

Esta tesis doctoral está dedicada al estudio de las comunidades de helmintos parásitos en elasmobranquios que se encuentran en aguas alrededor de la Península Ibérica, con comentarios sobre otras relaciones agonísticas entre una especie de este grupo, la tintorera (*Prionace glauca*), y el pez espada (*Xiphias gladius*), cuestiones que no habían sido abordadas antes en la literatura científica. En una etapa temprana de la tesis, descubrimos que aún no se habían descrito las infracomunidades de cestodos que infectan al marrajo dientuso (*Isurus oxyrinchus*), por lo que se realizó un estudio preliminar con muestras del Atlántico nororiental, en el que también se obtuvieron muestras de tintoreras (*Prionace glauca*). Algunas dificultades para obtener más muestras del Atlántico nos hicieron cambiar nuestro enfoque y buscar otros grupos de elasmobranquios que pudieran aportar algo de luz a las limitaciones que afectan a las infracomunidades de cestodos. El estudio de las rayas eléctricas (familia Torpedinidae) de las costas del Mediterráneo parecía un muy buen candidato para probar si sus particulares métodos de depredación (a través de descargas eléctricas que paralizan o matan a sus presas) podrían tener algún efecto sobre sus infracomunidades parasitarias.

Teniendo en cuenta lo aprendido al estudiar las infracomunidades de helmintos de elasmobranquios que presentaban algunas singularidades y ante la oportunidad de obtener muestras del mediterráneo, decidimos estudiar una de las especies de tiburones más cosmopolitas, el tiburón azul (*Prionace glauca*), haciendo una comparativa entre las poblaciones atlánticas y mediterráneas, junto con un análisis comparativo de lo que se sabe hasta la fecha. Aparte de estudiar sus parásitos, los estudios realizados con tiburones azules nos aportaron algunos hallazgos interesantes sobre las interacciones agonísticas entre ellos y el pez espada (*Xiphias gladius*). Durante la necropsia de un tiburón azul, se encontraron los restos de un gran rostro de pez espada atravesando el cráneo y destruyendo el cerebro, siendo descrita esta herida como la causa más probable de muerte debido al hallazgo del tiburón varado pero aún vivo.

Objetivos

Objetivo general

El presente estudio tiene como finalidad básica investigar las interacciones de cuatro especies de elasmobranquios de aguas ibéricas, esto es, el marrajo dientuso, *Isurus oxyrinchus*; la tintorera o tiburón azul, *Prionace glauca*; la tembladera, *Torpedo marmorata*, y la tembladera de lunares, *Torpedo torpedo*, con otras especies de su entorno. En concreto nos centramos, por una parte, en la investigación sobre los determinantes de la composición, diversidad y, en su caso, predecibilidad, de las comunidades de parásitos intestinales y, por otra, en las relaciones agonísticas de la tintorera con otra especie, el pez espada, que no habían sido analizadas en profundidad en la literatura.

Está dentro del objetivo general de esta tesis contribuir a líneas de trabajo ya iniciadas dentro de la comunidad científica, como cubrir enormes vacíos en la información básica sobre los elasmobranquios y su fauna parasitaria, especialmente en lo referente a los cestodos. De hecho, muchas especies de elasmobranquios nunca han sido analizadas respecto a su fauna helmíntica, y aún quedan por estudiar las asociaciones parásito-hospedador en elasmobranquios de muchas áreas geográficas. En este sentido, el presente estudio contribuirá a los incipientes esfuerzos para crear un catálogo sistemático y una estimación de la diversidad de cestodos de elasmobranquios existentes (Tapeworm Inventory Database, Cestodes of the Bowels of the Earth). Por otra parte, debido el énfasis taxonómico necesario para obtener un inventario básico de los parásitos de elasmobranquios, existen todavía muy pocos estudios que proporcionen información cuantitativa sobre las infecciones parasitarias. Resulta sorprendente que sólo existan estudios cuantitativos de las faunas intestinales completas para menos de un 5% de las especies, y que dichos estudios sólo se hayan replicado en más de una localidad en un número todavía menor. El presente trabajo contribuirá por tanto a aportar datos relevantes para futuros metaanálisis.

También pretendemos responder, siguiendo el enfoque de historia natural discutido en la Introducción, a una serie de preguntas sobre que han surgido en el transcurso del trabajo descriptivo y que son específicas para cada especie de elasmobranquio (véase más abajo). Las cuestiones relativas a la la composición, diversidad y, en su caso, predecibilidad de las comunidades de parásitos intestinales se formularán y se examinarán en un contexto comparativo amplio. Dicho enfoque permitirá: (1) contrastar hasta qué punto existen patrones generales ligados a rasgos ecológicos, geográficos y de la historia vital del hospedador que podrían explicar la variación en la diversidad y composición de sus infracomunidades parásitas, y (2) evaluar la importancia de las peculiaridades ecológicas y del ciclo de vida de cada especie para comprender las posibles desviaciones de los patrones teóricos esperables.

La segunda cuestión que se plantea en este trabajo surge de la necesidad de explicar un extraño fenómeno que detectamos durante el muestreo de una de las especies hospedadoras, esto es, el empalamiento de tintoreras por peces espada. Considerado inicialmente como un evento excepcional, la creciente detección de este fenómeno estimuló la continuación de nuestra investigación, que arrojará luz sobre su posible significado funcional e impacto poblacional.

Objetivos específicos

De acuerdo con el objetivo general anteriormente descrito, los objetivos específicos de este trabajo son los siguientes:

1. Aportar conocimiento básico sobre la fauna de cestodos del marrajo dientuso, *Isurus oxyrinchus*; la tintorera, *Prionace glauca*; la tembladera, *Torpedo marmorata*, y la tembladera de lunares, *Torpedo torpedo*, en aguas ibéricas, donde no existía información previa, proporcionando información precisa sobre parámetros de infección y descriptores de las infracomunidades.

2. Investigar la influencia potencial de factores clave ligados a cada especie hospedadora sobre la composición, diversidad y predecibilidad de las infracomunidades intestinales de cestodos, a través de un enfoque comparativo global con otros elasmobranquios. Los factores específicos son los siguientes:

    2.1. En el caso del marrajo dientuso, nos plateamos en qué medida la "dilución" potential de los estadios infectivos en un medio vasto, homogéneo y sin barreras, esto es, el dominio pelágico-oceánico, genera infracomunidades pobres y poco predecibles.

    2.2. En el caso de la tintorera, nos preguntamos cuál es el papel relativo de la especificidad de los parásitos, y el carácter cosmopolita y altamente migratorio del hospedador, a la hora de generar diferencias y similitudes locales en la composición y diversidad de las infracomunidades de cestodos.

    2.3. En el caso de las tembladeras, investigamos en qué medida el uso de descargas eléctricas por parte de estas especies para capturar sus presas podría tener un efecto negativo sobre las fases infectivas que estas contienen, generando infracomunidades depauperadas de cestodos.

3. Describir, por primera vez, los efectos del empalamiento cefálico del pez espada sobre las tintoreras, evaluando su posible significado funcional, su frecuencia en la naturaleza, y el impacto poblacional potencial sobre la tintorera que este comportamiento podría ejercer.

A continuación pasamos a desarrollar las tareas realizadas y los resultados obtenidos en la consecución de estos objetivos.

Fauna de helmintos intestinales del marrajo dientuso *Isurus oxyrinchus* (Elasmobranchii: Lamnidae) en el océano Atlántico nororiental.

Introducción

El marrajo dientuso *Isurus oxyrinchus* (Rafinesque, 1810) es un tiburón altamente migratorio de la familia Lamnidae que se encuentra muy extendido en aguas templadas y tropicales de todos los océanos desde aproximadamente 50 ° N a 50 ° S; rara vez se encuentra en aguas por debajo de los 16 ° C (Compagno 2001). Como es típico de los lamnidos, el marrajo dientuso es una especie epipelágica rápida que actúa como un depredador ápice en las redes tróficas oceánicas (López et al. 2009).

Los grandes tiburones oceánicos pelágicos, como el marrajo dientuso, representan un modelo interesante para investigar el papel del hábitat del hospedador en la estructura de sus comunidades de helmintos. Estudios previos sobre tortugas marinas (Valente et al. 2009, Santoro et al. 2010), aves marinas (Hoberg 1996, 2005), cetáceos (Balbuena y Raga 1993, Mateu et al. 2014) y teleósteos (Costa et al. 2012, Santoro et al. 2014) han sugerido que el reino oceánico pelágico puede ejercer una fuerte influencia en las infracomunidades de helmintos de grandes depredadores marinos.

La fauna de helmintos del marrajo dientuso ha sido estudiada en numerosas ocasiones (Linton 1922, Euzet 1956, Robinson 1959, Cabrera 1991, Ruhnke 1993, Caira y Bardos 1996, Knoff et al. 2002, 2007, Lyons et al. 2015). La mayoría de estos estudios, que se basan en tamaños de muestra de hospedadores pequeños (<5 hospedadores), se han llevado a cabo en los océanos Atlántico oriental o Pacífico y proporcionan principalmente datos taxonómicos.

Los marrajos dientusos se capturan regularmente en las pesquerías de palangre que operan en el Atlántico nororiental. Esta situación brindó una oportunidad única para describir la fauna de helmintos intestinales del marrajo dientuso en una región mal estudiada, y obtener parámetros tanto a nivel de infracomunidad como de comunidad componente. En particular, investigamos hasta qué punto las condiciones oceánicas influyen en la estructura de las infracomunidades de helmintos en este gran tiburón oceánico comparando nuestros resultados con los obtenidos en otros estudios parasitológicos sobre elasmobranquios.

Materiales y métodos

El marrajo dientuso no está protegido por la legislación española y las capturas tienen un interés económico. Se analizaron un total de 39 marrajos de aleta corta obtenidos en el puerto de Vigo (Galicia, España) en busca de helmintos intestinales. Los tiburones fueron capturados por pesquerías de palangre que operan en el noreste del Océano Atlántico. El intestino se almacenó a -20°C para su posterior análisis en el laboratorio. Después de descongelar, se enjuagó cada intestino con agua del grifo sobre una malla de 0,02 mm y se recogió el contenido sólido. También se examinó minuciosamente la pared del intestino en busca de helmintos adheridos.

Registramos la prevalencia (porcentaje de hospedadores en la muestra infectados por una especie de helmintos), la intensidad media (número medio de individuos de una especie de helmintos por hospedador en la muestra de hospedadores infectados con esta especie) y la abundancia media (número medio de individuos de una especie) para cada taxón de helmintos siguiendo a Bush et al. (1997). La abundancia total de helmintos, la riqueza de especies y el índice de diversidad de Brillouin se utilizaron como descriptores de infracomunidades. Se realizó una prueba de correlación de Spearman para investigar si la abundancia de cada especie de helmintos y los parámetros de la infracomunidad variaban significativamente con la longitud del hospedador, y se realizaron pruebas U de Mann-Whitney para explorar diferencias significativas en los parámetros parasitológicos de tiburones machos y hembras. La asociación general entre las especies de helmintos se investigó mediante una prueba de relación de varianza (Schluter 1984).

Se utilizaron modelos mixtos lineales generales (GLMM) para explorar si la riqueza media de especies y la abundancia total media de cestodos intestinales eran significativamente menores en marrajos dientusos y otros elasmobranquios oceánicos que en otros elasmobranquios. Nos centramos en los cestodos porque son, con mucho, el grupo de parasitos más diverso que infecta a los elasmobranquios (Caira y Jensen 2014), y muchas encuestas solo proporcionan datos de infección sobre los cestodos. En la comparación de la riqueza de especies, utilizamos la relación entre la riqueza de la infracomunidad y la riqueza de la comunidad componente como variable dependiente. De esta manera, controlamos las diferencias en la disponibilidad de cestodos locales. El tamaño de la muestra del hospedador (como medida del esfuerzo de muestreo) y el hábitat (elasmobranquios pelágicos oceánicos frente a otros elasmobranquios) se utilizaron como predictores. En todos los modelos, tratamos a las especies como observaciones independientes, es decir, no aplicamos contrastes independientes (ver, por ejemplo, Poulin 1997) porque los datos cuantitativos de las comunidades de helmintos de elasmobranquios aún son limitados.

Resultados

Se recolectaron un total de 2117 especímenes de helmintos y todos los tiburones excepto 4 fueron infectados con al menos 1 taxón de helmintos. Nematodos identificados como larvas L3 de Anisakis sp. tipo I se encontraron en el intestino de 17 tiburones, y algunos especímenes se encontraban parcialmente digeridos. También se encontraron en el intestino seis especies de cestodos de los órdenes Tetraphyllidea, Trypanorhyncha y Phyllobothriidea. Al menos algunos individuos con proglótides grávidos fueron detectados en 3 especies, incluyendo *Clistobothrium montaukensis* Ruhnke, 1993, *Gymnorhynchus isuri* Robinson, 1959 y *Ceratobothrium xanthocephalum* Monticelli, 1892*. C. montaukensis* fue el taxón más prevalente, infectando 32 tiburones; también dominó numéricamente las infracomunidades, ya que en 27 tiburones constituía más del 50% de la abundancia total de helmintos. Se encontraron un total de 21 individuos de *G. isuri* en 3 hospedadores, mientras que sólo se encontraron especímenes de *C. xanthocephalum* en 8 tiburones.

En 3 especies de cestodos, no se encontraron individuos con proglótides grávidas: *Nybelinia lingualis* (Cuvier, 1817*), Dinobothrium septaria* (Van Beneden, 1889) y *Phyllobothrium cf. lactuca* (Van Beneden, 1850). Se encontraron 39 *N. lingualis* en el intestino de 7 tiburones, mientras que solo 14 especímenes de *D. septaria* se encontraron en un solo tiburón. *P. lactuca* se encontró en 4 tiburones. En esta especie, el mal estado de conservación de los ejemplares dificultó la localización den la ventosa accesoria en el botridio y, en algunos casos, solo se pudieron observar 2 de las 4 ventosas.

No se encontró una relación significativa entre la longitud del cuerpo del hospedador y la abundancia de especies de helmintos o parámetros de infracomunidad. Además, no se detectaron diferencias significativas en la abundancia de ninguna especie de helmintos o descriptores de infracomunidad entre sexos. La prueba de varianza de Schluter no indicó una desviación significativa de la hipótesis nula de colonización aleatoria de taxones de helmintos.

La riqueza de especies a nivel de infracomunidad varió de 0 a 4 y fue baja en comparación con el número de especies a nivel de comunidad componente (7 spp.). Sin embargo, la diferencia no fue mayor que la observada en otros elasmobranquios, independientemente de su hábitat. De hecho, otros tiburones oceánicos pelágicos, es decir, el tiburón azul *Prionace glauca* y el marrajo sardinero *Lamna nasus*, no se apartan del patrón común de diferencia observado en los elasmobranquios no oceánicos. Esta conclusión fue apoyada por los resultados del GLMM. Contrariamente a lo esperado, la riqueza infracomunitaria corregida en tiburones oceánicos pelágicos fue mayor que la de otros elasmobranquios. Además, los resultados del GLMM indicaron que la abundancia total media de helmintos en los tiburones oceánicos pelágicos era más alta que la de otros elasmobranquios y cercana a ser significante. No se detectó ningún efecto significativo del tamaño de la muestra del hospedador en ningún modelo.

Discusión

La fauna parasitaria del marrajo dientuso en nuestra muestra estaba compuesta por 7 especies, todas las cuales excepto *Dinobothrium septaria* ya habían sido reportadas en este hospedador. Sin embargo, se han encontrado hasta 9 especies adicionales, todas pertenecientes al orden Trypanorhyncha, en el intestino de los marrajos a nivel mundial (Palm 2004, Randhawa y Poulin 2010, y referencias allí). Anteriormente se habían reportado 5 especies en el Atlántico Norte, pero no fueron detectadas en nuestro estudio. Todas las especies de helmintos reportadas en este estudio se encuentran casi exclusivamente en tiburones, principalmente miembros de la familia Lamnidae que habitan en aguas oceánicas. Este patrón de especificidad es común a otros elasmobranquios, cuya fauna de helmintos intestinales es peculiar y muy específica en su conjunto (Caira y Pickering 2013). Los helmintos encontrados en marrajo dientuso, con la excepción de *C. montaukensis*, tenían bajos niveles de infección, y la prueba de relación de varianza indicó colonización independiente de cada especie de helmintos. Además, no se encontró una correlación significativa entre la longitud del hospedador y la riqueza de especies o la abundancia total de helmintos intestinales. En las infracomunidades de helmintos intestinales, la ausencia de estructura se ha relacionado con la falta de interacciones competitivas entre especies (ver, por ejemplo, Curran y Caira 1995 para una especie de tiburón grande).

Contrariamente a lo que esperábamos, las infracomunidades de cestodos de marrajo dientuso y otros tiburones oceánicos pelágicos no estaban particularmente deterioradas en comparación con las de otros elasmobranquios, p. ej. *Prionace glauca*, *Squalus acanthias*, *Etmopterus spinax* y *Leucoraja naevus*; de hecho, tendían a ser más diversos. En consecuencia, parecería prematuro extraer conclusiones sólidas sobre la influencia del hábitat oceánico en el conjunto de helmintos del marrajo dientuso sobre la base de los datos disponibles. Sin embargo, creemos que los enfoques comparativos interespecíficos son necesarios para avanzar hipótesis sobre tales influencias. Este enfoque también requeriría que se publiquen los parámetros de infracomunidad adecuados en los estudios de elasmobranquios y otros vertebrados oceánicos.

Determinantes de la diversidad y la composición de la fauna de cestodos del tiburón azul (*Prionace* glauca): un análisis geográfico y de especificidad

Introducción

El tiburón azul, *Prionace glauca* (Linnaeus, 1758), es un tiburón altamente migratorio de la familia Carcharhinidae que está muy extendido en todo el mundo en aguas templadas y tropicales de todos los océanos (Compagno 2001). Actualmente está incluido en la Lista Roja de la UICN dentro de la categoría de Casi Amenazada para su evaluación global (Sims et al. 2016) pero catalogada como En Peligro Crítico para su distribución mediterránea (Rigby et al. 2019), ambas porque esta especie sufre una alta mortalidad como captura incidental de la pesquería de palangre comercial en todo el mundo.

Los cestodos son algunos de los parásitos más comunes y específicos de los tiburones (Caira y Healy 2012, Caira y Jensen 2017). Esta razón, junto con su distribución cosmopolita, los convierte en sistemas ideales para estudiar patrones e influencias en las infracomunidades parasitarias (Randhawa y Poulin 2010). Los tiburones grandes, pelágicos y cosmopolitas representan un modelo interesante para investigar el papel del hábitat del hospedador en la estructura de sus comunidades de helmintos. Los estudios anteriores carecen de muestras de todo el mundo para obtener resultados concluyentes, pero los tiburones azules del hemisferio norte se han estudiado en muchos lugares, proporcionando una imagen más detallada.

La fauna de helmintos de los tiburones azules se ha estudiado en varias ocasiones. La mayoría de estos estudios, que se basan en tamaños de muestra de hospedadores pequeños (<5 hospedadores), se han realizado en todo el mundo, a menudo en el hemisferio norte, y proporcionan principalmente datos taxonómicos. Sin embargo, existe un grupo de estudios que brindan información cuantitativa desde una perspectiva de comunidad de helmintos (Euzet 1959, Escalante 1986, Curran y Caira 1995, Henderson et al. 2002, Méndez y Galván-Magaña 2016, Preti et al. 2020), haciendo a los tiburones azules los tiburones más estudiados en cuanto a sus infracomunidades parasitarias.

Los tiburones azules se capturan regularmente en las pesquerías de palangre que operan en el Atlántico nororiental y en las pesquerías estacionales en el Mediterráneo (Mejuto et al. 2009a, 2009b). Esta situación brindó una oportunidad única (1) para describir la fauna de helmintos intestinales de la tintorera en dos regiones mal estudiadas, (2) para obtener parámetros a nivel de la infracomunidad y de la comunidad componente para compararlos con estudios previos de la infracomunidad, y (3) para estudiar la especificidad de la fauna de cestodos adultos que infecta la válvula espiral de los tiburones azules, buscando informes sobre otros hospedadores y ubicaciones, para investigar los patrones e influencias que afectan sus conjuntos parasitarios.

Materiales y métodos

La tintorera no está amparada por la ley española y las capturas tienen un interés económico, por lo que todas las muestras obtenidas de las pesquerías se sexaron y midieron (al cm más cercano) antes de que comenzara la subasta de pescado, recogiendo el estómago y el intestino (válvula espiral). Se obtuvieron un total de 16 tintoreras en el puerto de Vigo (Galicia, España), capturadas por pesquerías de palangre que operan en el Atlántico nororiental. Se capturaron trece tiburones en octubre de 2012 y tres en mayo de 2013. Otro grupo de 21 tiburones azules se obtuvo en la región de Valencia (España) y también se analizaron en busca de helmintos intestinales. Ocho tiburones fueron recuperados por la Red de Varamientos de la Comunidad Valenciana, varados en diferentes puntos del litoral regional, durante los años 2013-2021, y trece fueron capturados por pesquerías de palangre, en noviembre de 2020 y desembarcados en el puerto de Valencia. Se examinó minuciosamente el intestino en busca de helmintos adheridos. Los parásitos se recogieron bajo un microscopio estereoscópico, se lavaron en solución salina al 0,9%, se examinaron para describir sus características principales, se contaron, se fijaron y se conservaron en etanol al 70%. Se utilizó una prueba de Kruskal-Wallis para ver diferencias en la abundancia de 5 taxones de cestodos (*A. caseyi*, Tetraphyllidea sp., *P. auriculatum*, *P. armigerum*, *M. horridus*) y dos descriptores de infracomunidad (riqueza de especies e índice de diversidad de Brillouin).

Resultados

Se recolectaron un total de 2726 especímenes de helmintos, que componen un total de 9 taxones de cestodos que se encontraron en el intestino espiral de los tiburones azules. Se detectaron en la muestra especímenes adultos de *A. caseyi*, *P. auriculatum*, *P. armigerum* y *M. horridus*, pero no en el caso de Tetraphyllidea spp. y Phyllobothriinae sp. 1 y 2. Para los individuos individuales de *Scyphophyllidium* sp. y Trypanorhyncha sp. solo se pudo recolectar los escólex y, por lo tanto, no fue posible confirmar si eran sexualmente maduros.

Cinco taxones de cestodos exhibieron una prevalencia> 10%, de los cuales cuatro se compartieron entre todas las muestras de hospedadores (*A. caseyi*, *P. auriculatum*, *P. armigerum* y Tetraphyllidea sp.) Y uno ocurrió tanto en Galicia como en Valencia (S) (es decir, *M. horridus*). Los cuatro taxones de cestodos restantes se encontraron solo en Galicia. La abundancia de 4 de los 5 taxones de cestodos más comunes difirió significativamente entre las muestras de hospedadores. La comparación post hoc reveló que el patrón de diferencias no fue consistente en todos los taxones; La abundancia de *P. auriculatum* y *P. armigerum* fue significativamente mayor en Galicia en comparación con Valencia (C), mientras que la abundancia de *A. caseyi* fue mayor y menor en las dos muestras de Valencia, y la de *M. horridus* fue significativamente mayor en Valencia (S) en comparación con las otras dos muestras.

No detectamos diferencias significativas en la riqueza de especies infracomunitarias entre las muestras de tiburones. Considerando todos los taxones de cestodos, la riqueza media de especies (IC del 95%) fue de 2,69 (2,10-3,31) para Galicia, 1,75 (1,13-2,50) para Valencia (S) y 2,46 (2,00-2,92) para Valencia (C); cuando solo se seleccionaron especies con especímenes adultos, estas cifras fueron 2,13 (1,63-2,63), 1,63 (1,13-2,13) y 2,08 (1,72-2,39), respectivamente.

Aparte del presente estudio, encontramos 6 estudios que informan sobre la fauna de helmintos del intestino espiral de los tiburones azules; 2 y 1 del Océano Pacífico Norte y Sur, respectivamente, 2 del Océano Atlántico Norte y 1 del Mar Mediterráneo. Solo una especie, *P. auriculatum*, se compartió entre las 8 muestras de hospedadores, aunque con diferencias obvias en la prevalencia y la intensidad media. Se encontraron especies de *Anthobothrium* (particularmente *A. caseyi* excepto en un caso de identidad indeterminada), *Prosobothrium* (*P. armigerum* o *P. japonicum*) en todas las muestras excepto una, y especies de *Scyphophyllidium* (particularmente *S. prionacis* excepto en un caso de identidad indeterminada) en todas menos dos muestras.

Encontramos 93 registros de 15 cestodos intestinales que infectaban a la tintorera y habían sido identificados a nivel de especie. Un total de 7 especies sólo se se encontraron infectando tintoreras: un "Tetraphyllidea" (*A. caseyi*); 4 Onchoproteocephalidea (*Pla. Auriculatum*, *Pro. Armigerum*, *Pro. japonicum* y *Phoreiobothrium* sp. [= *P. lasium*]) y dos de Phyllobothriidea (*Pelichnibothrium speciosum* y *S. prionacis*). Para todas estas especies, los registros abarcaron al menos las cuencas del Pacífico y del Atlántico / Mediterráneo, excepto *Phoreiobothrium* sp. (= *P. lasium*), para el cual no se encontraron registros en el Océano Pacífico. Las otras 8 especies de cestodos que infectan a tintoreras pertenecen al orden Trypanorhyncha y son más generalistas, infectando otros elasmobranquios (de 1 a 19 spp. dependiendo de la especie), principalmente de la familia Carcharhinidae.

A nivel de género, la búsqueda bibliográfica reveló los siguientes patrones: el género monoespecífico *Pelichnibothrium* era exclusivo de los tiburones azules, *Prosobothrium* (3 spp.) infecta también a la familia Sphyrnidae (una sola especie) y *Anthobothrium* (8 spp.), *Platybothrium* (10 spp.) y *Phoreiobothrium* (18 spp.), principalmente con otros Carcharhiniidae. En el caso de *Scyphophyllidium* (51 spp.) y la mayoría de los géneros de Trypanorhyncha, la mayor parte de las especies se asignaron a Carcharhinidae, pero también se encontraron en varias otras familias de tiburones y rayas. Una excepción fue la de Molicola (3 spp.), cuyas especies solo infectan a Lamniformes y tiburones azules.

Discusión

En otras grandes especies oceánicas, se ha descrito un "efecto de dilución" de las etapas infecciosas como la razón de la ausencia de estructura en sus infracomunidades y la baja abundancia y riqueza de especies (Santoro et al. 2010, Mateu et al. 2014). Fue discutido por Penadés-Suay et al. (2017) por qué no parecía aplicarse completamente en el caso del marrajo dientuso (*Isurus oxyrinchus*) y parece ser un caso similar para los tiburones azules, ya que sus infracomunidades no están más empobrecidas que los de otros tiburones. La baja especificidad hacia los hospedadores intermediarios que muestran algunos cestodos podría ayudarlos a reducir el riesgo de no completar sus ciclos de vida, al menos en el caso de Trypanorhyncha (Marcogliese 1995, 2002; Palm y Caira 2008).

En resumen, el conjunto de helmintos de tiburones azules en todo el mundo parece presentar un grupo central de infecciones por cestodos, de origen filogenético, y un subconjunto más diverso de infecciones por cestodos inespecíficas, de la fauna parasitaria local disponible. Este podría ser un patrón general para especies de tiburones similares con un amplio rango de distribución. Sin embargo, esto es simplemente un primer paso hacia enfoques comparativos intraespecíficos para el estudio de los cestodos de elasmobranquios, abriendo un camino para proponer hipótesis futuras sobre las limitaciones e influencias en sus infracomunidades. Para que este enfoque continúe aumentando, existe la necesidad de publicaciones de parámetros de infracomunidad adecuados en encuestas de elasmobranquios.

¿Comiendo alimentos limpios? Efectos potenciales de las descargas eléctricas de *Torpedo* spp. (Torpediniformes: Torpedinidae) sobre sus parásitos de transmisión trófica.

Introducción

Los órganos eléctricos son estructuras de peces especializadas que producen un campo eléctrico fuera del cuerpo (Bennett 1971). Parece que han evolucionado de forma independiente en al menos seis linajes, lo que permite a las especies electrolocalizarse, electrocomunicarse, depredar y/o defenderse (Lissman 1958, Moller 1995, Crampton 2019). Dentro de los peces condrictios, se sabe que solo las especies del orden Torpediniformes generan fuertes descargas de con sus órganos eléctricos (EOD – Electric Organ Discharges) para la defensa, la depredación o ambas (Bennett 1971). El uso de EOD en defensa se ha observado en todas las especies torpediniformes pero, aparentemente, solo las especies de los géneros *Torpedo* e *Hypnos* utilizan EOD potentes para aturdir o matar presas potenciales (Belbenoit 1986, Lowe et al. 1994).

Una pregunta intrigante que no se ha abordado en la literatura científica previa es cómo la EOD podría afectar a las etapas infecciosas de los parásitos transmitidos tróficamente en la presa aturdida. Dado que no era posible acceder a presas infectadas en suficiente número, seleccionamos un modelo sustituto de hospedador-parásito para probar esta hipótesis. En particular, examinamos el efecto de las descargas eléctricas que imitan los EOD sobre la vitalidad de las larvas de *Anisakis* spp. que infectan a la bacaladilla, *Micromesistius poutassou* Risso, 1827. Aunque las especies de *Anisakis* son nematodos que se reproducen en cetáceos, sus larvas se encuentran en microhábitats de peces (es decir, cavidad corporal, mesenterios, hígado y músculos, ver Cruz et al. 2007) que son similares a los reportados para larvas de cestodos que infectan condrictios (Al-Zubaidy 2006, Oguz & Bray 2008, Santoro et al. 2013). Es cierto que la cutícula de los nematodos podría hacerlos más resistentes a los efectos potenciales de los EOD, por lo que nuestro modelo debe considerarse conservador.

La segunda pregunta es si los efectos de EOD realmente contribuyen a generar faunas de cestodos empobrecidas en torpedos y el género *Hypnos*. Si los EOD obstaculizan el reclutamiento de cestodos, estos peces deberían desarrollar un número menor de asociaciones hospedador-parásito como resultado de eventos de colonización. Desafortunadamente, los datos adecuados de parásitos sobre torpediniformes, especialmente en familias con "EOD débil", son extremadamente escasos y, por lo tanto, tuvimos que hacer una evaluación exploratoria utilizando a los batoideos en su conjunto.

Materiales y métodos

Para realizar el experimento con el modelo sustituto se compraron ejemplares frescos de bacaladilla, *Micromesistius poutassou*, capturados con redes de arrastre en el mar Cantábrico (Atlántico nororiental) en una lonja de pescado local de Valencia, en el este de España. En un análisis preliminar, las larvas de *Anisakis* spp. se detectaron en el hígado y la cavidad corporal de 10 peces seleccionados al azar, y la mayoría de los gusanos realizaron movimientos ondulados vigorosos cuando se pusieron en solución salina (0,90% p / v de NaCl). Luego, se asignaron aleatoriamente tres peces individuales a un grupo de control (inmersión en solución salina durante 15 segundos), o cualquiera de los 3 tratamientos, es decir, inmersión en solución salina durante 15 segundos y aplicación de una descarga eléctrica de 48 V durante 1, 5 o 10 segundos, respectivamente. La descarga se aplicó directamente al cuerpo mediante un transformador Polylux QC40 24-48V. El orden de tratamiento (incluido el control) se asignó al azar cada día. Dado que un día solo estaban disponibles 10 peces, el número final de peces por grupo fue de 14 para el grupo de control y de tratamiento de 1 segundo, y de 15 para los grupos de tratamiento de 5 y 10 segundos. Después de los tratamientos, los peces se analizaron inmediatamente en busca de larvas de Anisakis. Todas las larvas se recolectaron de cada pez individualmente con pinzas finas y se colocaron en una placa de Petri con solución salina a temperatura ambiente (20ºC) y luz natural. Se comprobó la movilidad de cada larva individual cada 30 min durante las siguientes 6 h siguiendo una secuencia aleatoria entre placas de Petri.

Verificamos si la longitud y el peso totales diferían significativamente entre los grupos de peces con ANOVA de una vía; la homogeneidad de la varianza se examinó con la prueba de Levene. Asimismo, comparamos el número de lombrices por pez entre tratamientos con la prueba de Kruskal-Wallis. Se utilizó ANOVA de medidas repetidas con contrastes polinomiales para buscar diferencias entre los tratamientos de descarga eléctrica en la proporción de larvas vivas.

Los torpedos fueron capturados por pesquerías con redes de trasmallo que operan a 1-1,5 millas náuticas de la costa a profundidades de 6 a 12 m en el Golfo de València, Mediterráneo Occidental, entre febrero y abril de 2017. Un total de 30 individuos de *T. torpedo* y 17 de *T. marmorata* se recogieron en los puertos de Valencia y Cullera. En el laboratorio, se sexó cada pez y se midió su longitud total (LT) al cm más cercano. Después de descongelar, se enjuagó cada intestino con agua del grifo bajo una malla de 0,02 mm, recogiendo el contenido sólido. Cada individuo helminto fue detectado bajo un microscopio estereoscópico, lavado en solución salina al 0,9%, identificado, contado, fijado y conservado en etanol al 70%.

Utilizamos dos fuentes bibliográficas para obtener una estimación de la riqueza de especies de cestodos por género de batoideo, excluyendo los géneros para los que nunca se han realizado análisis parasitológicos. El libro de Caira y Jensen (2017) proporciona datos, a escala de género hospedador, de la diversidad estimada de especies de cestodos que infectan a los batoideos, excepto el Trypanorhyncha. Para este último, obtuvimos registros utilizando la base de datos Shark References (https://www.shark-references.com) (Pollerspöck y Straube 2019), que proporciona una cuenta completa y actualizada sobre los parásitos que infectan a los condrictios. Resumimos las cifras de ambas bases de datos para obtener, para cada género de batoideo, la riqueza media de especies por especie hospedadora. También recopilamos datos sobre la riqueza de especies de helmintos a nivel de individuo hospedador (infracomunidad) en especies de batoideos utilizando un conjunto de datos basado en una búsqueda bibliográfica en las bases de datos Web of Science y Google Scholar, de manera similar a Rasmussen & Randhawa (2018).

Finalmente, exploramos si la fauna de helmintos comparativamente empobrecida de torpedos a nivel de infracomunidad podría estar relacionada con factores que se sabe que son significativos a nivel de la comunidad componente, específicamente para los tiburones (Randhawa y Poulin 2010, Rasmussen y Randhawa 2018). Es importante notar, desde el principio, que no estábamos interesados en investigar los factores que pudieran influir en la riqueza de especies de las infracomunidades en los batoides en su conjunto.

Resultados

La longitud y el peso totales medios de la bacaladilla fueron de 24,4 cm y 87,1 g, respectivamente. La varianza no varió significativamente entre los grupos de peces, ni tampoco la media de la longitud total o el peso. La intensidad media de *Anisakis* sp. por pez fue de 23,2 individuos y no encontramos diferencias significativas en el número de parásitos entre los grupos de peces.

No pudimos detectar diferencias en la supervivencia general entre los tratamientos de descarga eléctrica o en sus perfiles de tiempo. En los tres tratamientos, se detectó un aumento aproximadamente lineal del porcentaje de mortalidad de los parásitos (contemplada como ausencia total de movilidad ante estímulo) con el tiempo. Tomando los grupos de tratamiento en su conjunto, el porcentaje medio de mortalidad en el tiempo 0 y después de 6 h fue 1,1 (3,5)% frente a 21,2 (13,6)% (es decir, un aumento del 20,1%). En el grupo de control, el porcentaje de mortalidad fue aparentemente estable hasta las primeras 2 horas y luego aumentó (es decir, un aumento del 10,6%). No encontramos un efecto general de la descarga eléctrica sobre la supervivencia de las larvas en comparación con el grupo de control, pero hubo una interacción muy significativa entre los perfiles.

Se recolectaron un total de 474 especímenes de helmintos de 4 especies, a saber, 3 de cestodos y un ejemplar de una especie de nematodo, de la válvula espiral de *T. torpedo* y *T. marmorata*. Una sola especie, identificada como miembro del género *Acanthobothrium* van Beneden, 1849, fue compartida entre ambas especies de hospedadores y tuvo una prevalencia >10% pero una baja intensidad media de infección (<8). Un total de 8 individuos adultos de *Rhodobothrium* sp. se encontraron en 2 individuos de *T. marmorata*. En individuos de *T. torpedo* se encontraron un solo individuo inmaduro de una especie del orden Phyllobothriidea y una sola larva 3 (L3) de *Hysterothylacium* sp.

A nivel de orden, los Torpediniformes en su conjunto exhibieron los valores más bajos de riqueza de cestodos en comparación con otros batoideos. Sin embargo, dentro de este orden, las dos familias de "EOD fuerte" no mostraron valores de diversidad más bajos que las de "EOD débil"; los Hypnidae (1 spp.) tenían 2 spp. de cestodos parásitos, y los Torpedinidae (21 spp.), en promedio, 2,6 spp., mientras que los Narcinidae (30 spp.) y los Narkidae (11 spp.) albergaban 1,2 y 2, respectivamente.

El conjunto de datos de estudios previos contenía información sobre la riqueza de cestodos a nivel de infracomunidad de 3393 hospedadores individuales de 48 especies, 27 géneros y 14 familias. Dentro de los Torpediniformes, solo los datos de 3 Torpedo spp. estaban disponibles, es decir, *T. torpedo*, *T. marmorata* y *T. panthera*. A nivel de género, *Torpedo* se clasificó como el tercer género más bajo en términos de riqueza de cestodos, solo después de *Aetobatus* y *Gymnura*.

Discusión

Los resultados experimentales en un modelo sustituto de hospedador-parásito sugieren que los EOD podrían afectar negativamente las etapas infecciosas transportadas por las presas de los torpedos y el género *Hypnos*. Dado que las poblaciones de parásitos siguen una distribución binomial negativa (Anderson y May 1979), muchas oportunidades de infección podrían perderse cuando se consumieran presas poco infectadas. Sin embargo, la medida en que estos efectos EOD contribuyen a los conjuntos de cestodos pobres en especies que se observan en los torpedos es una cuestión abierta. Esta característica no puede explicarse fácilmente por factores relacionados con el hospedador que normalmente operan a una escala taxonómica amplia, como el tamaño corporal, el hábitat, el nivel trófico o diversidad en la dieta. Sin embargo, el carácter empobrecido de las faunas de cestodos parece ser compartido entre las familias de Torpediniformes "EOD fuerte" y "EOD débil", y esto obviamente requiere una mayor investigación. Los estudios futuros deben centrarse en cuatro cuestiones, a saber, (1) obtener datos adecuados de la infracomunidad, incluidos los registros de la abundancia de parásitos, de todas las familias torpediniformes, especialmente de Narcinidae y Narkidae, (2) para investigar el uso potencial del comportamiento EOD en el dos familias; (3) perfeccionar y diversificar los entornos experimentales para investigar los efectos reales de los EOD en las etapas infecciosas de los parásitos transmitidos tróficamente, y (4) replicar análisis experimentales y comparativos similares para otros peces que muestran comportamiento EOD, por ejemplo, anguilas eléctricas (ver Catania 2014).

Empalamiento fatal de un tiburón azul *Prionace glauca* por un pez espada *Xiphias gladius*

Texto principal

El pez espada (*Xiphias gladius* L.) es conocido por su comportamiento muy activo y agresivo. Hay informes de peces espada que conducen su rostro hacia una gran variedad de objetos inanimados (Fierstine y Crimmen, 1996) y animales, incluidos peces grandes (Fierstine, 1997; Fierstine et al., 1997), ballenas (Jonsgard, 1962), tortugas marinas (Frazier et al., 1994), personas (Haddad y De Figuereido, 2009; Georgiadou et al., 2010) e incluso submarinos (Zarudski y Haedrich, 1974). Este comportamiento puede resultar en una fractura transversal del rostro, dejando el segmento distal incrustado en el sustrato. Aquí, por primera vez, se presenta evidencia directa de un tiburón azul (*Prionace glauca* L.) muerto por la interacción con un pez espada.

En septiembre de 2016, una tintorera hembra adulta fue arrastrada a tierra en la costa de Valencia, España, en el Mediterráneo occidental. El animal estaba vivo cuando fue encontrado y realizó movimientos lentos de natación, pero murió poco después. Medía 247 cm de longitud total y 186 cm de longitud de horquilla. La necropsia no reveló signos de inanición ni evidencia macroscópica de enfermedad. Se detectaron dos anzuelos de pesca rodeados de tejido cicatrizado después de retirar la mandíbula, lo que indica antiguas interacciones con pesquerías. Se encontró una incisión de 35 mm de largo 11 mm anterior al ojo izquierdo. Tras un examen detenido, se descubrió un fragmento de la punta de un rostro de pez espada (18 cm de largo, 0,5 cm de ancho en sentido distal y 3 cm en sentido proximal) y se extrajo de la incisión. El fragmento estaba orientado 30º con respecto al eje longitudinal y había perforado la cabeza paralela al plano dorsoventral, atravesando la cabeza anterior a la apófisis preorbital sin causar daño aparente a la cápsula olfatoria ni al ojo. Sin embargo, había penetrado a través del cráneo provocando importantes lesiones en el cerebro. Se infirió que el daño cerebral fue la causa de la muerte.

El fragmento de rostro se identificó como perteneciente a un pez espada basándose en la siguiente combinación de características (Fierstine y Voigt, 1996): (1) apariencia aplanada en la sección transversal (es decir, profundidad menor a la mitad del ancho); (2) ausencia de dentículos en la superficie y (3) presencia de cámaras centrales en sección transversal. Para estimar la longitud total (TL) del pez espada, se calculó la relación entre la anchura máxima y la longitud del fragmento (R) proporcionando un valor de 0,169. A continuación, el punto en el que se estimó R≈ 0,169 en el rostro de dos ejemplares de pez espada conservados en la Colección Osteológica del Departamento de Zoología de la Universidad de Valencia. Suponiendo una relación isométrica, la distancia desde la punta hasta el punto de ruptura era un tercio en relación con la longitud total del rostro (TSL – Total Snout Lenght). Por lo tanto, se calculó que el TSL en nuestro espécimen de pez espada era aprox. 48 cm. La disposición de los canales de nutrientes emparejados observados en el punto de ruptura en nuestro espécimen fue similar a la que se muestra en las secciones transversales, aproximadamente a la misma distancia de la punta, en un pez espada analizado por Habegger et al. (2015). La regresión alométrica entre TSL y la longitud del cuerpo desde el post opérculo hasta la horquilla de la cola (BL) (McGowan, 1988) sugirió que el individuo tenía un BL≈ 110 cm, correspondiente a un juvenil de 1-2 años. La regresión alométrica entre BL y peso redondo (RW) (Aliçli et al., 2012) sugirió un RW≈ 20 kg.

Los tiburones azules son depredadores oportunistas que se alimentan de una amplia variedad de cefalópodos y peces (Hernández-Aguilar et al., 2015, y referencias allí citadas), incluyendo en ocasiones al pez espada en su dieta (Vaske-Júnior et al., 2009; Markaida & Sosa- Nishizaki, 2010). Sin embargo, el peso de los individuos consumidos (aproximadamente 1 kg, ver Vaske-Júnior et al., 2009) es mucho menor que el estimado para el pez espada que atravesó y mató al tiburón azul en este informe. La pregunta es, por tanto, cuál fue el tipo de interacción entre estas especies. Una posibilidad es que el tiburón azul y el pez espada chocaran accidentalmente mientras se alimentaban del mismo banco de peces. Esta razón se ha invocado para explicar el empalamiento en especies no agresivas, como las tortugas marinas (Frazier et al., 1994). En estos casos, se cree que las colisiones ocurren porque las presas objetivo de los peces espada están debajo de las tortugas, de modo que los peces espada no pueden girar o detenerse abruptamente (Frazier et al., 1994). Sin embargo, está claro que los peces espada pueden arponear a otros animales a propósito, por ejemplo, los ataques reportados a peces grandes (Starck, 1960, Cliff et al., 1990, Fierstine, 1997). Por tanto, existe la posibilidad de que, en el presente caso, el pez espada atacara al tiburón por considerarlo una amenaza (ver Fierstine, 1997).

Un punto importante para el análisis futuro es si los empalamientos mortales son anecdóticos o representan una causa importante de mortalidad de tiburones y otros animales. Los casos de empalamiento probablemente se pasen por alto, al menos por dos razones (Fierstine, 1997). En primer lugar, las "víctimas" oceánicas del apuñalamiento de peces espada pueden sufrir lesiones graves o la muerte y desaparecer sin que nadie se dé cuenta. En segundo lugar, es posible que las heridas causadas por apuñalamientos o cortes con el rostro no se detecten fácilmente o no se atribuyan al empalamiento, a menos que quede un fragmento de la espada después de la puñalada. Otra pregunta es si los peces picudos utilizan el arpón como una estrategia de defensa típica o solo como un comportamiento de último recurso. Numerosos estudios indican que la espada tiene importantes funciones hidrodinámicas y relacionadas con la alimentación (Habegger et al., 2015; Videler et al., 2016), por lo que la rotura del rostro podría ser seriamente desventajosa para los peces espada. Sin embargo, hay varios informes de peces espada aparentemente sanos con rostros dañados, malformados o incluso ausentes (Frazier et al. 1994).

Hay informes anteriores de supuestas interacciones mortales del pez espada y tortugas marinas (Frazier et al. 1996), y un informe breve que describe supuestas heridas en un tiburón zorro, *Alopias superciliosus*, similar al informado en el presente estudio (Vacchi et al. 1999). Sin embargo, el presente informe es el primero que proporciona evidencia directa de la muerte de un tiburón causada por un pez espada.

Interacciones agresivas entre juveniles de pez espada y tiburones azules en el Mediterráneo occidental: ¿un fenómeno generalizado?

Introducción

Durante las últimas décadas, se ha informado del empalamiento de objetos inanimados y organismos marinos por el pez espada (*Xiphias gladius* L.) en varias publicaciones científicas y noticias de los medios de comunicación. Hay informes de peces espada que conducen su rostro hacia objetos inanimados, como embarcaciones (Gudger 1940, Fierstine y Crimmen 1996), fardos de caucho (Smith 1956) y submarinos (Zarudski y Haedrich 1974). También hay informes de empalamiento de animales, como peces grandes (Starck 1960, Smith 1961), ballenas (Jonsgard 1962), tortugas marinas (Frazier et al. 1994 y referencias allí) e incluso personas (por ejemplo, Haddad y De Figuereido, 2009; Georgiadou et al., 2010).

El significado funcional de este comportamiento de lanza todavía está en discusión. En otros peces con rostro (marlines), casos similares se han contabilizado como colisiones accidentales. Por ejemplo, Fierstine et al. (1997) relacionaron las lesiones en otras especies de marlines con las hipotéticas colisiones producidas al alimentarse de la misma bola de cebo. En otros casos, sin embargo, el empalamiento se ha interpretado como intencional (Smith 1956, Ellis 2013, para un relato histórico detallado). La evidencia más clara de comportamiento agresivo proviene de casos que involucran humanos, particularmente cuando el pez espada es provocado o molestado (Georgiadou et al.2010, y referencias allí citadas; Romeo et al.2017, y referencias allí citadas), que a veces ha resultado en lesiones fatales (Gooi et al.2006).

Penadés-Suay et al. (2017) plantearon la cuestión de si los empalamientos por pez espada son anecdóticos y hasta qué punto el pez espada utiliza el rostro como comportamiento de defensa. La respuesta a ambas preguntas se consideró difícil porque la literatura contiene principalmente estudios de casos o revisiones de registros "fait-acommpli" dispersos durante largos períodos.

Materiales y métodos

Los cuatro ejemplares de tiburón incluidos en el presente estudio fueron encontrados varados en la playa en el momento del varamiento o poco tiempo después. Los tiburones se midieron in situ al centímetro más cercano y se examinaron visualmente en busca de lesiones externas. Se realizó una descripción detallada de las lesiones provocadas por la tribuna del pez espada, y se recogió, fotografió y midió el fragmento de la tribuna del pez espada al mm más cercano. En el tercer caso, se llevó la cabeza intacta del tiburón al laboratorio para hacerle una radiografía y tomografía computarizada (TC). Los estudios de diagnóstico por imágenes incluyeron lo siguiente:

(1) Evaluación radiográfica simple con una unidad Philips Practix 400 (Philips Medical Systems) y un sistema Kodak Direct View Classic CR (Carestream Health) con casetes Kodak de 35 × 43 cm

(2) Se realizó una TC utilizando un Somatom Volume Access (Siemens).

Los fragmentos de tribuna se identificaron como pertenecientes a un pez espada (X. gladius) según Penadés-Suay et al. 2017. Asumiendo una relación isométrica en el crecimiento del hocico, se calculó la longitud total del hocico (TSL) para cada caso en relación a la distancia desde la punta hasta el punto de ruptura. Para agregar una corrección adicional, observamos la disposición de los canales de nutrientes emparejados en el punto de ruptura, como se muestra en las secciones transversales, para compararlo con un pez espada analizado por Habegger et al. (2015). La regresión alométrica entre TSL y la longitud del cuerpo (BL), desde el opérculo hasta la horquilla de la cola, se obtuvo siguiendo a McGowan (1988).

Resultados

El 17 de febrero de 2017, un tiburón azul macho adulto muerto (TL: 236 cm) fue encontrado arrastrado a tierra en la costa de Garrucha (Almería), España. El animal presentaba una herida incisiva entre el ojo izquierdo y el hocico. Durante la necropsia, se encontró dentro del cráneo la punta rota de un pico de pez espada, que medía 180 mm de largo y 20 mm de ancho en el punto de ruptura.

El 8 de marzo de 2017, se encontró una tintorera hembra adulta (TL: 260 cm) varada en la costa de Ostia, Italia. El animal estaba vivo cuando fue encontrado, pero murió poco después. La necropsia reveló la presencia de un rostro de pez espada penetrando la carne entre la cápsula óptica y el proceso posorbitario. Al parecer, la incisión no dañó ningún órgano sensorial.

El 28 de febrero de 2018 se encontró muerta una hembra adulta de tintorera (LT: 260 cm) varada en la costa de Vera (Almería), España. Se encontró una incisión cercana al ojo derecho, entrando en la cabeza en un ángulo de 20º desde el eje anteroposterior. No se encontró ningún fragmento de factura mediante inspección visual. Tanto la radiografía como la tomografía computarizada tampoco lograron encontrar fragmentos de la espada dentro de la incisión; pero, sorprendentemente, revelaron la presencia de un fragmento distal de espada dentro de la fosa nasal derecha, anterior a la primera lesión detectada. En este caso no se observó ningún signo externo de lesión. La cavidad de la fosa nasal estaba rodeada de tejido cicatrizado.

El 2 de agosto de 2018, un tiburón azul macho adulto (TL: 293 cm) fue encontrado varado y devuelto al agua por transeúntes varias veces en una hora en la costa de Manacor (Islas Baleares), España. Cuando llegó el equipo de rescate, el tiburón estaba inmóvil en decúbito lateral cerca de la orilla, a medio metro de profundidad en el agua, sin reaccionar a ningún estímulo. Después de la eutanasia, la necropsia reveló signos de inanición y la presencia de un fragmento distal de un pico de pez espada incrustado en el hocico.

Discusión

Este estudio informa de cuatro casos de empalamiento de tiburones azules por juveniles de pez espada en el Mediterráneo occidental en menos de dos años. La pregunta que surge es hasta qué punto tales eventos son casos de colisión accidental entre ambas especies o de comportamiento intencionado. Aunque no podemos descartar la primera posibilidad, existen algunas líneas de evidencia que se ajustan a la hipótesis de que el pez espada en realidad podría haber golpeado intencionalmente a los tiburones. En primer lugar, todos los casos aquí examinados involucraron solo peces espada pequeños y tiburones azules adultos. Existe la posibilidad de que los juveniles de pez espada perciban a los grandes tiburones azules como una amenaza, dado que los tiburones azules son depredadores oportunistas que se alimentan de una amplia variedad de cefalópodos y peces (Vaske-Júnior et al.2009; Markaida y Sosa-Nishizaki 2010), y algunos estudios de su dieta incluyeron pez espada, aunque el tamaño del pez espada consumido (aproximadamente 1 kg, ver Vaske-Júnior et al. 2009) parece ser menor que el estimado para los individuos en el presente estudio. En segundo lugar, en todos los casos de empalamiento de tiburones azules reportados hasta el momento (Penadés-Suay et al. 2017; presente estudio), el ángulo de perforación indica un golpe casi horizontal con respecto al eje anteroposterior de los tiburones. Aunque no hay ninguna razón para excluir la posibilidad de una colisión accidental durante un acto de depredación contra la misma presa, se debe considerar una voluntaria del pez espada, dado que el tipo de empalamiento descrito difícilmente podría resultar de una colisión aleatoria.

En conclusión, nuestro estudio reporta tres casos dentro de un año y solo en la cuenca del Mediterráneo Occidental, lo que sugiere la relevancia de este fenómeno. A modo de ejemplo, hay un informe breve que describe supuestas heridas en un tiburón zorro, *Alopias superciliosus* (Vacchi et al. 1999), similar al caso de un tiburón azul reportado en la misma región por Penadés-Suay et al. (2017). Se necesita más atención en este asunto, buscando evidencias en todos los protocolos de necropsia e investigando este tipo de interacciones en otras especies de tiburones.

Conclusiones generales del presente estudio

Esta tesis tiene como objetivo el estudio de la fauna de cestodos en elasmobranquios, tanto pelágicos como bentónicos, así como el efecto que los rasgos ecológicos y particulares del hospedador pueden ejercer sobre las infracomunidades parásitas. También proporciona información novedosa sobre las relaciones agonísticas entre la tintorera (*Prionace glauca*) y el pez espada (*Xiphias gladius*).

Se recolectaron un total de 5371 cestodos de 18 especies diferentes de cestodos que infectaban cuatro especies distintas de elasmobranquios. En el capítulo 3 se describe por primera vez la infracomunidad intestinal de helmintos del marrajo dientuso (*Isurus* oxyrinchus). Se describen por primera vez 4 especies adultas parasitando el marrajo en aguas de Galicia (Atlántico nororiental): *Clistobothrium montaukensis*, *Gymnorhynchus isuri*, *Ceratobothrium xanthocephalum* y *Dinobothrium septaria*; de las cuales todas excepto *D. septaria* ya habían sido descritas infectando este hospedador en otras localidades. Las infracomunidades helmínticas de los marrajos no parecen estar depauperadas en comparación con las de otros elasmobranquios, poniendo en duda que el "síndrome del predador pelágico" se aplique en el caso de los tiburones.

En el capítulo 4, por primera vez se describen las infracomunidades intestinales de tintoreras (*Prionace glauca*) en dos localidades: la costa gallega (Atlántico nororiental) y la costa valenciana (Mediterráneo Occidental). Se detectaron ejemplares adultos de cuatro especies de cestodos (*Anthobothrium caseyi*, *Platybothrium auriculatum*, *Prosobothrium armigerum* y *Molicola horridus*) que constituyen primeros registros para las tintoreras en las dos localidades. No se encontraron diferencias significativas entre las dos regiones, lo que apunta a una posible conectividad de las poblaciones. Las diferencias más evidentes se encontraron entre los grupos de muestreo, lo que apunta a efectos no geográficos que ejercen su influencia en las infracomunidades. A nivel global, la helminto fauna de las tintoreras parece estar formada por un grupo de 5-6 especies que encontramos globalmente, siguiendo la distribución global de las tintoreras, junto con un grupo menos predecible de cestodos tripanorrincos.

En el capítulo 5 se describen por primera vez las infracomunidades helmínticas de *Torpedo torpedo* y *Torpedo marmorata* en el Golfo de Valencia. El hallazgo de 8 ejemplares adultos de *Rhodobothrium* sp en *T. marmorata* constituye un nuevo registro de hospedador para esta especie de cestodo. A nivel de hospedador individual la helmintofauna intestinal de las dos especies estaba extremadamente depauperada, como se ha visto en estudios previos en otras localidades. Al hacer un análisis bibliográfico, se muestra que los Torpediniformes son el orden de batoideos con los valores más bajos de diversidad de cestodos. Es un patrón que se repite a nivel de hospedador individual y que parece consistente con la teoría del efecto negativo que pueden tener las descargas eléctricas en el reclutamiento de parásitos. Dicho efecto negativo aparece en el estudio de modelo surrogado que realizamos.

Por último, en los capítulos 6 y 7, se aporta la primera evidencia directa de muertes de tiburones causadas por peces espada (*Xiphias gladius*). Se describen cinco casos de tintoreras empaladas por peces espada juveniles en el Mediterráneo Occidental en menos de tres años. Se aportan indicaciones para que los futuros protocolos de necropsias de elasmobranquios incluyan la búsqueda de evidencias de estas interacciones.

En general, esta tesis muestra cómo las comunidades de parásitos de elasmobranquios se han descuidado principalmente en el pasado, cómo sus infracomunidades son impulsadas tanto por la filogenia como por los rasgos ecológicos y los rasgos particulares de cada hospedador, y brinda puntos de referencia para estudios futuros. Asimismo, al señalar la falta de estudios ecológicos parasitarios de los elasmobranquios, hace un llamado al desarrollo de este campo de investigación, demostrando que sería beneficioso para mejorar el conocimiento actual tanto de los parásitos elasmobranquios como de sus hospedadores, contribuyendo con suerte a su adecuada conservación y asegurarse de que estén debidamente considerados.

Summary

The present study provides, for the first time, a quantitative report on the cestode fauna in four elasmobranch species, i.e., the shortfin mako shark (*Isurus oxyrhinchus*); the blue shark (*Prionace glauca*); the marbled electric ray, (*Torpedo marmorata*), and the common torpedo (*Torpedo torpedo*), in Iberian waters (Northeastern Atlantic, Galicia; Western Mediterranean, Valencia). It also investigates the role of key host species-specific traits in providing structure at infracommunity level. This study also documents unexpected, but increasingly noticed, agonistic interactions between blue sharks and swordfish (*Xiphias gladius*) over recent years, discussing their functional meaning and population impact.

Large oceanic sharks represent a suitable model to investigate the influence of a host's oceanic conditions on the structure of its helminth communities. In Chapter 03, we describe the intestinal helminth fauna, and investigate determinants of infracommunity structure, in 39 specimens of shortfin mako *Isurus oxyrinchus* collected in the NE Atlantic. Six cestode species were found in the spiral valve of makos: 3 are typical from lamnid sharks, namely, gravid specimens of *Clistobothrium montaukensis*, *Gymnorhynchus isuri* and *Ceratobothrium xanthocephalum*, and 3 are immature specimens of cestode species common to several elasmobranchs, namely, *Dinobothrium septaria*, *Nybelinia lingualis*, and *Phyllobothrium* cf. *lactuca*. In addition, L3 larvae of *Anisakis* sp. type I were detected. Infracommunities were species poor and had low total helminth abundance. The result of Schluter's variance ratio test was compatible with the hypothesis of independent colonization of helminth taxa. These results conform to previous studies on oceanic predators that have hypothesized that these hosts should have depauperate and unpredictable helminth infracommunities because oceanic conditions hamper parasite transmission. However, mean species richness and mean total abundance of cestodes of shortfin mako and other oceanic sharks did not significantly differ from those of elasmobranchs from other habitats. This suggests that the large body size and prey consumption rates of oceanic sharks offset the negative 'dilution' effect of oceanic habitat on transmission rates. Additionally, or alternatively, parasites of oceanic sharks may have expanded the use of intermediate hosts through the trophic web to spread out the risk of failure to complete their life cycles.

Over the last two decades there has been an effort to unveil community patterns of elasmobranch cestodes at a macroecological scale. In contrast, analyses at infracommunity level are still very scarce. In Chapter 04 the helminth community parasitizing 37 blue sharks (*Prionace glauca*), both juveniles and adults, is described and compared with previous studies, performing a global assessment of the relative

role of the ecological and evolutionary factors in structuring the local tapeworm assemblages of blue sharks. Shark specimens studied came from two different non previously surveyed regions: the Northeast Atlantic Ocean (Galicia, Spain) and the Western Mediterranean (Valencia, Spain). Helminths from nine different taxa, of which four presented adult specimens and have already been describe infecting blue sharks, were identified: *Platybothrium auriculatum*, *Prosobothrium armigerum*, *Anthobothrium caseyi* and *Molicola horridus*. The five other taxa only could be identified to the level of genus, order or family because of their poor condition. All six previous studies providing infracommunity data about blue sharks encountered a group of four cestode species, thus described here as the 'core' community parasitizing blue sharks worldwide. Other cestode infections in blue sharks are discussed and a checklist of adult cestodes infecting the spiral valve of blue sharks is provided. At a global geographic scale, tapeworm communities of blue sharks were composed by 10 cestode taxa, 7 of which (those belonging to the Phyllobothriidea, Onchoproteocephalidea and "Tetraphyllidea") are exclusive to this host species and share two fundamental traits: their cosmopolitan distribution and their belonging to cestode genera that typically infects carcharhinids. Thus showing that for blue sharks, and probably other elasmobranchs, the influence of ecological factors upon their tapeworm communities is highly constrained by historical factors, i.e., the strong host specificity of most of their tapeworm species.

Members of the Torpedinidae (torpedoes) and Hypnidae (coffin ray) use electric organ discharges (EOD) to stun or kill their prey before consumption. In Chapter05 we investigated whether EOD could also negatively affect the helminth larvae infecting these preys through a surrogate model: we applied electric discharges to individuals of blue whiting, *Micromesistius poutassou* that harboured live larvae of *Anisakis*. Larval mortality throughout a 6-h period was significantly higher in the treatment group, suggesting that EODs could significantly hamper helminth recruitment. We then tested whether torpedinids and hypnids ('strong-EOD' families) harboured species-poor helminth (cestode) assemblages compared with 'weak-EOD' torpediniforms (Narcidae and Narkidae) and other Batoidea. Based on comparisons on estimated species diversity and mean species richness of tapeworms at host individual level we found that (1) Torpediniformes had the lowest tapeworm diversity of all Batoidea orders; (2) *Torpedo* spp. consistently had the lowest mean cestode richness at host individual level, and this could not be related to other host factors influencing cestode diversity in chondrichthyans, i.e., body size, trophic level or dietary breath. However, a preliminary comparison between 'strong-EOD' and 'weak-EOD' torpediniforms did not detect clear differences of cestode richness. Thus, evidence supporting an unambiguous contribution of EODs to depauperate cestode assemblages requires further research.

There are numerous reports of billfishes spearing objects, marine organisms, and even humans. Whether or not this behaviour is intentional and, if so, what is its functional meaning, are open questions. In Chapter 06 we describe a case from 2016, when an adult blue shark (*Prionace glauca*) was found to be killed by a juvenile swordfish (*Xiphias gladius*) in the western Mediterranean. Following that work, in Chapter 07 we report on four more recent cases involving both species in the same area. In February 2017, an adult male blue shark was found stranded in Garrucha (Spain) with a fragment of a juvenile swordfish's rostrum (18cm long x 2cm wide at proximal end) inserted in its cranium. In March 2017, an adult pregnant female blue shark was stranded alive on the coast of Ostia (Italy) but died shortly afterwards; a fragment of a juvenile swordfish's rostrum (25x3cm) was found allocated between the eye and the cranium. In February 2018, an adult female blue shark appeared stranded in the coast of Vera (Spain), with a putative impalement injury anterior to the right eye but without an associated bill fragment. Surprisingly, X-ray and computed tomography revealed an older injury in the right nostril, with a small piece of a juvenile swordfish's rostrum (5.3x1.2cm). Finally, in August 2018, an adult male blue shark appeared stranded alive in the coast of Manacor (Spain) with a fragment of swordfish bill (6.8x1.5cm) embedded in the snout. These cases suggest that juvenile swordfish would drive their rostrum into blue sharks as a defensive or territorial strategy that is likely to be far from anecdotal. We suggest that no regular cases of these interactions are reported because they occur at high sea and evidence of them, when available, can easily be overlooked.

Overall, this thesis shows how parasite communities of elasmobranchs have been mostly neglected in the past, how their infracommunities are driven by phylogeny, ecological and particular host's traits, and gives points of reference for future studies. Also, by pointing out the lack of ecological parasitic studies of elasmobranchs, it makes a call towards the development of this research field, proving that it would be beneficial for improving the current knowledge of both elasmobranch parasites and their host, hopefully contributing to their proper conservation and making sure they are worthily validated.

Chapter 01 - General introduction

1.1 Elasmobranchs: highly endangered and poorly studied

Sharks and rays are among the most endangered groups of animals and include many species for which there is little information, particularly on their abundance and/or distribution. There are no global abundance trends for them, with only a handful of robust regional trend indicators, only about 10% of the 1197 elasmobranch species have population-level stock assessments available, which provide the most reliable index of abundance (Cortés et al. 2012, FAO 2012, Worm et al. 2013, Dulvy et al. 2014). It is a matter of concern that almost all these assessments show depleted and/or over-exploited populations. Commonly, the conservation status of elasmobranchs as a group is based on trends in reported fisheries landings, i.e. trajectories of standardized catch rates or indices of current status, most of these data being highly dependent on fisheries statistics.

The first global assessment of the IUCN (International Union for Conservation of Nature, Dulvy et al. 2014) estimated that 25% of shark species were threatened with extinction (thus being classified as Vulnerable, Endangered or Critically Endangered - IUCN Red List of Threatened Species criteria), making sharks the most threatened vertebrate group after the amphibians (Stuart et al. 2004, Hoffman et al. 2010, Dulvy et al. 2014, Pacoureau et al. 2021). Most shockingly, only 241 species (23%) were considered to be safe from any extinction threat (Least Concern category), being this the lowest fraction of safe species among all vertebrate groups studied by IUCN to date. Almost half of the examined species (47%) from the first global assessment were considered data-deficient, a value that was reduced by almost a third by the last global assessment (Dulvy et al. 2014, Dulvy et al. 2021), showing the growing interest in the study of this group in the last decade. From all elasmobranch families, the species with large body sizes were considered to be in most danger, especially species accessible to fisheries and those inhabiting shallow waters (Dulvy et al. 2014 and references therein). Nowadays, fisheries overexploitation is still the highest threat to elasmobranch populations (Dulvy et al. 2021).

The susceptibility of elasmobranchs to overexploitation comes mainly from the life history traits shared by many species within the group: a low reproduction rate associated with low fecundity, slow growth rate, and sexual maturity at late age (Musick 1999, Dulvy et al. 2008, Dulvy et al. 2017, Pardo et al. 2016). These traits make them closer or more similar to marine mammals than to the more productive teleost species (Myers and Worm, 2005), making them particularly susceptible to fishing pressures (Walker, 1998). Despite these differences between elasmobranchs and teleosts, it is the similarity of their habitat use what increases the likelihood of their capture in some fisheries aimed towards commercially valuable teleost species with similar environmental preferences. As an example, blue shark (*Prionace glauca*) seasonal distributions and fishery catch rates correlate with those of swordfish (*Xiphias gladius*), making blue sharks difficult to avoid when industrially fishing for the latter (Bigelow et al. 1999). In a similar fashion, many batoids are captured in bottom trawl fisheries targeting groundfishes, and subsequently discarded dead or sold for a low price (Graham et al. 2001, Enever et al. 2009, Damalas and Vassilopoulou 2011). Worldwide, elasmobranchs are landed for their meat, fins, gill plates and liver oil (Clarke et al. 2006, McClenachan et al. 2016), a very productive industry that had an estimated peak of 63–273 million individuals captured per year in the early 2000s, before declining due to overfishing (Davidson et al. 2016). The first signs of the concerning status of sharks were based on boom-and-bust catch patterns and the increase in the international trade of fins (Brander 1981, Manire and Gruber 1990). Following those, serious declines in many oceanic and coastal shark populations were documented (e.g. SEDAR 2016, ICCAT 2019 for the Gulf of Mexico and NW Atlantic; Dudley and Simpfendorfer 2006 for south african waters; Roff et al. 2018 for Australian waters).

Summing up, many populations of elasmobranchs are depleted, and some species face extinction due to several factors (adapted from Camhi 1998):

- life history strategies that make elasmobranchs especially susceptible to fishing over-exploitation, preventing the recovery of the already depleted populations;
- rapid growth of fisheries that are for the most part unregulated and partly driven by unrestricted international trade in shark products;
- very high levels of mortality related to incidental take (bycatch) in both marine and freshwater fisheries; and
- degradation of important nursery grounds and other critical coastal, estuarine, and freshwater habitats from development, alteration, overfishing, and pollution.

This should be a matter of great concern, because elasmobranchs are capable of offering a unique window into the state of the marine environments (both from global and local perspectives). Sharks and rays are one of the most evolutionarily distinct, functionally diverse and oldest species of all the vertebrate radiations (Stein et al. 2018, Pimiento et al. 2020). As said before, more than 1.197 species of elasmobranchs are found currently throughout the world's coastal seas, oceans, and some of the freshwater systems (Ebert et al. 2019). For at least 420 million years, elasmobranchs have persisted on Earth, forming with the chimaeras one of the three existing classes of living fishes (the Chondrichthyes). Sharks have evolved a wide range of morphological and mechanical features, including facultative parthenogenesis, embryonic diapause, bioluminescence, pockets, saws, hammers, stings, and electricity (Carrier et al. 2010, Fields et al. 2015). Also, it has been described how the vertebrate brain bauplan was first laid down in sharks and how the different brain regions remain largely unchanged across vertebrates (Yopak et al. 2010). From an ecological point of view, many species of elasmobranchs occur at or near the top of marine trophic chains, representing one of the largest radiations of predatory species. They have fundamental roles in their habitats, connecting through and across food webs, habitats and ecosystems, aggregating, integrating, and transferring energy and spreading predation risk vertically, horizontally, and temporally (Fig 1). Making difficult to detect their vertical integration role in trophic cascades because of the large spatial and temporal scale over which these predators exert their influence (Cortés 1999, Heupel et al. 2014, Hussey et al. 2014). Despite this, it is increasingly clear that the reduction of their populations can lead to predatory release and increases in smaller meso-predatory species, thus generating consequent changes throughout the ecosystem (Stevens et al. 2000, Dulvy, 2014, Grubbs et al. 2016).

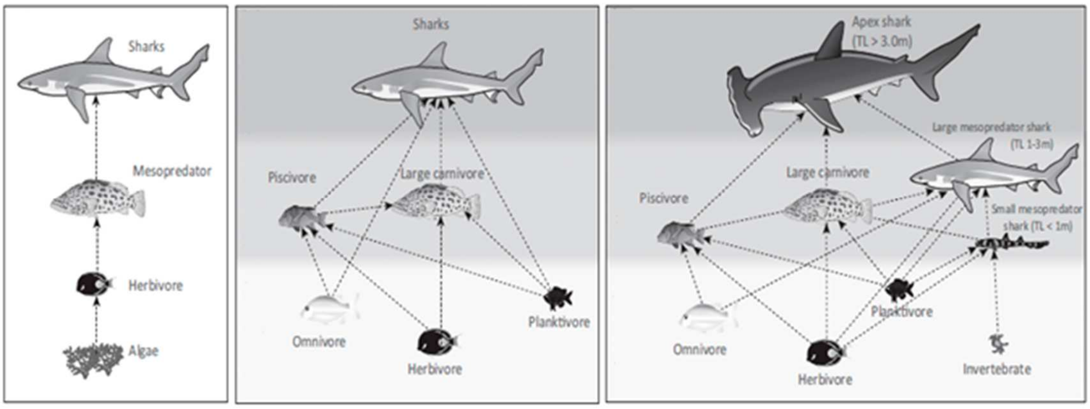

Fig. 1 Three schemes illustrating ecological importance of elasmobranchs with an increase in complexity, showing classical trophic cascades, the interconnexion between different groups and sharks in different roles (as apex predators and mesopredators), a more realistic depiction of the complex role that this diverse group plays in marine ecosystems. (Modified from Roff et al. 2016).

The high risk of extinction of elasmobranchs, together with their ecological importance, demands a serious approach towards their conservation and an adequate management of the populations. This kind of approach will require better knowledge of those aspects of their biology, ecology and life history that are yet unknown, at least for the most common populations and those cases where a species might be of particular interest due to particular traits. Following Camhi et al. (1998), studies to cover gaps in elasmobranch knowledge may include:

1. more taxonomic knowledge, including species description and genetic research into stock structure;

2. species-specific data on: reproductive characteristics (age at maturity, gestation period and average annual pups per female), critical habitats at different life stages (including mating, pupping and nursery grounds), growth rates and age structure, mortality for all age classes, stock and relative species abundance, stock structure and migration patterns, ecological relationships with other species;
3. assessment of the global and regional status of all species.

In this scenario of apparent urgency regarding the conservation of sharks and rays it is worth asking, on the one hand, how much additional science is necessary to contribute before adopting effective conservation actions (see, for example, Jaramillo-Legorreta et al. 2007) and, for another, where to direct this scientific effort. It is evident that we need to improve our understanding of basic biological aspects of elasmobranchs, e.g. their population dynamics, but why address the study of apparently “minor” interspecific interactions, such as those of parasitic fauna or the secondary aggressions of some prey? To our knowledge, there are several compelling reasons, which we briefly argue in the next section.

Theoretical context of this study

Regarding parasites, it should be noted, first, that these organisms represent a component of biodiversity inextricably linked to that of their hosts. This means that, ultimately, the extinction of the hosts implies the co-extinction of their associated parasites (Koh et al. 2004). Therefore, any taxonomic (that is, species-based) perspective on conservation must recognize that parasites are an integral part of biodiversity that would have to be explicitly considered in any conservation program (Windsor 1995, Gomper and Williams 1998, Dougherty et al. 2015). Such an approach obviously presupposes that the parasitic fauna is well characterized. However, as we explain below, in the case of elasmobranch parasites this has only begun to be a reality in the last two decades, and is therefore one of the reasons that justifies the present study.

Second, due to the intimate relationship between hosts and their parasites, they can shed light on many aspects of the biology and ecology of those, even of great conservation relevance (see, e.g., Williams et al. 1992, Mackenzie 2002, Whiteman and Parker 2005, Criscione et al. 2006, Nieberding and Olivieri 2007). This indicator role for parasites extends to the ecosystem level, since these organisms play a key ecological role, although traditionally ignored, in multiple facets of ecosystem functioning, especially food webs (e.g., Horwitz and Wilson 2005, Hudson et al. 2006, Buck and Ripple 2017, Vanatta and Minchella 2018). Parasites are recognized in all ecological systems for the crucial roles they play (Huxham et al. 1995, Thompson et al. 2005, Lafferty et al. 2006, Hernández and Sukhdeo 2008, Amundsen et al. 2009); these organisms mediate the species composition of free-living communities (e.g., Mouritsen and Poulin 2005, Wood et al. 2007), regulate host populations (e.g., Hudson and Greenman 1998), redirect the flow of energy between and within food webs (e.g. Lafferty and Morris 1996, Sato et al. 2012) and even comprise a substantial proportion of the total biomass of some ecosystems (e.g., Kuris et al. 2008, Preston et al. 2013).

In this sense, the analysis of the determinants of richness and diversity of parasite communities, as will be done in the present study, requires asking about both ecological (e.g. their life cycles) and evolutionary (e.g. their specificity) that can help us, in the long term, to solve some of the gaps in our general knowledge of elasmobranchs (particularly in ontogenetic changes in habitat and diet use, differentiation of stocks and population structure, migration and geographic distributions, health and connectivity populations) and the ecosystems where they live. Parasitological studies can therefore complement other necessary studies (mainly on diet and age / reproductive traits) that require access to complete samples from which parasitological information can be obtained.

Finally, and this is applicable to all the interspecific interactions treated in this study, we believe that the scientific importance of natural history should be claimed, including its application in conservation (Tewksbury et al. 2014, Barrows et al. 2016, Anderson 2017, Tosa et al. 2021). Natural history has been defined as “the observation and description of the natural world, with the study of organisms and their linkages to the environment being central” (Tewksbury et al. 2014), or more concisely, as “the observational study of organisms in their environment ”(Barrows et al. 2016). An implicit element of these definitions is that natural history research does not have to explicitly mention generalizable theories (Tosa et al. 2021). For some authors, this emphasis on the particular may be detrimental to "true" science, which must aspire to describe natural phenomena based on general laws (see Gould 2002, Wilson and Armesto 2006). However, these “laws” require a prior establishment of patterns, which emerge from groups of observations (Tosa et al. 2021). The history of ecological theory and conservation science are plagued with attempts to obtain general laws from premature patterns, or simply unsustainable due to the varied idiosyncrasies of the systems under study (see, e.g., Hansson 2003, Sagoff 2003, Baguette 2004, Rohde 2005, Poulin 2007, Lindenmayer and Hunter 2010).

That is, the value of natural history resides in that it seeks the understanding of specific natural phenomena from specific questions. In the context of this study, the questions arose from the description of the observations itself (e.g., the extreme poverty of the helminthic infracommunities of some of the elasmobranchs studied, or the detection of an extraordinary phenomenon - the impalement of blue shark by swordfish). The answers to these questions find scientific accommodation as a source of inspiration and validation of more general ecological theories (Tosa et al. 2021; see the corresponding chapters of this work), and as pieces of information relevant to the conservation of elasmobranchs.

1.2 Background in parasite communities

How natural systems are structured and how they function is a fundamental question underlying any ecological research. In recent decades, there has been a growing attention to previously overlooked organisms playing a key role in that question: parasites. Although frequently set aside, parasites probably contribute to more than half of the world's biological diversity, making parasitism one of the most extended (i.e. of the most successful) types of life on Earth (DeMeeus and Renaud 2002, Poulin and Morand 2004, Dobson et al. 2008). The study of parasites has had an obvious applied importance, mostly focused on parasites causing diseases in humans, livestock and wildlife worldwide (Hoberg 2002, Krauss et al. 2003, McManus et al. 2003). However, the study of parasites for their own sake has been somehow neglected as a research subject, having received fewer funds than the study of other organisms (Aznar et al. 2010, Gómez and Nichols, 2013). Despite that, the study of parasites has its own importance, not just because parasites are ubiquitously distributed, having successfully radiated into all habitats of the world. Much as commented above for the elasmobranchs, parasites are recognised in all ecological systems for the crucial roles they play (Huxham et al. 1995, Thompson et al. 2005, Lafferty et al. 2006, Hernandex and Sukhedo 2008, Amundsen et al. 2009): parasites mediate the species composition of free-living communities (e.g. Mouritsen and Poulin 2005, Wood et al. 2007), regulate host populations (e.g. Hudson and Greenman 1998), redirect energy flow among and within food webs (e.g. Lafferty and Morris 1996, Sato et al. 2012) and even comprise a substantial proportion of the total biomass in some ecosystems (e.g. Kuris et al. 2008, Preston et al. 2013). Furthermore, parasites have an intrinsic positive instrumental value by providing information on biological features of their hosts (Mackenzie 2002, Hudson et al. 2006). In fact, parasites have been used to unveil aspects of the stock identity (Balbuena et al. 1995), health condition (Aznar et al. 2005), population histories (Kaliszewska et al. 2005) and dispersal ability (Keeney et al. 2009) of different host species. Thus, a host-parasite model provides a suitable tool for studying the linkage of ecology, systematics, evolution and biogeography between organisms (Brooks and Hoberg 2000).

As in general parasitology studies, the earliest ecological studies of parasitic organisms were principally concerned with human disease agents. While the field of epidemiology considerably progressed, it had little to none impact on ecological studies of animal and plant parasites (Anderson 1981). During the the early 1960s, John Holmes published 3 papers as part of his doctoral dissertation research. On the first of these papers (Holmes 1961), he established conclusively the interaction of two species of parasites in their common environment, with such interaction being the open door to the application of the "community" concept to parasites assemblages. The beginning of modern community ecology as applied to parasitic helminths is then marked within that paper. The second paper (Holmes 1962a) further defined the nature of those interactions. But if those two papers established helminth community ecology as a rich, legitimate, and useful subdiscipline of parasitology, his next published paper (Holmes 1962b) casted a doubt over his own results, since the two parasites did not interact with one another in a similar way when infecting a different host. Therefore, these Holmes' 1962 papers told us that the secrets of symbiont interspecific relationships would not be so easily revealed and, maybe more importantly, that system-specific effects could easily be the rule rather than the exception (Janovy 2002). It was not until late in the decade the 1980s, when a couple of studies by Bush and Holmes (1986a, 1986b) triggered off the discipline of community ecology in parasites. These authors were the first to rigorously quantify the presence and the intensity of parasite species within the individual hosts, placing parasite communities into the conceptual framework of community ecology (reviewed by Goater et al. 2014). These early studies set the path to be followed by numerous authors, increasing the number of publications related to this discipline since the decade of the 1990s (Poulin and Morand 2004). Despite the different scientific origins of parasitology and ecology, their convergence has consistently provided, and will provide in the future, important contributions to the understanding of the structure and function of natural systems.

When looking at parasites in ecological terms, we establish a series of hierarchical levels: all parasites infecting a host become the parasitic infracommunity of that host, parasites infecting a community of hosts become the component community of that host and, finally, all parasites in a habitat become the local parasite fauna (see terms in Fig. 2). Also, when we collect a sample of parasites, host individuals act as natural sampling units. The collection then becomes a two-step procedure: first we collect the hosts and then we collect from them the parasite individuals. Hence, parasites are practically collected in groups, the so-called infrapopulations (Bush et al. 1997), in where group size, expressed as the number of parasite individuals, may be 0 or a positive number. The occurrence of parasites across specimens of a host sample (or the whole host population) exhibits a complex pattern that cannot be adequately described by a single measurement or index of infection, different indices are needed to capture different aspects of an infection (Reiczigel 2019). Commonly for each parasite taxon several parameters are recorded: prevalence, as the percentage of hosts in the sample infected by a parasite species; mean intensity, as the mean number of individuals of a helminth species per host in the sample of hosts infected with this species; and mean abundance, the mean number of individuals of a helminth species per host in the total sample of hosts (definitions following Bush et al. 1997).

Total abundance (considered as the number of individuals of all parasite species) and species richness (number of parasite species per individual host) are used as descriptors of infracommunities (descriptions following Reiczigel et al. 2019).

The host-specificity of a parasite species is a term that measures the number of host species that it can successfully infect, and also gives information of how closely related the different host species are (Poulin and Mouillot 2003). Host-specificity is a crucial concept in understanding the structure and diversity of a parasitic community (Kuris et al. 2007). To understand why some parasites can infect certain host species and not others, Euzet and Combes (1980) introduced a filter paradigm (later developed by Holmes 1990, Fig. 2). This paradigm states that there are three distinct steps that act as a sieve that filters out unsuitable hosts for the parasite. These are the encounter and compatibility filters (Euzet and Combes 1980, Combes 2001). The encounter filter is based on the biodiversity available and the biological traits of the host, and it simply filters out the hosts that a parasite never encounters (Combes 2001). Once a parasite has encountered a host, the infection is not completed if the parasite does not overcome the second filter: compatibility (Kuris et al. 2007). The compatibility filter excludes the hosts that do not provide an adequate habitat for the parasite. It can be caused, for example, by the lack of suitable attachment sites (Randhawa and Burt 2008). It is important to notice that these filters are not constantly fixed and selection acts on these to change their permeability over time (Poulin 2007b).

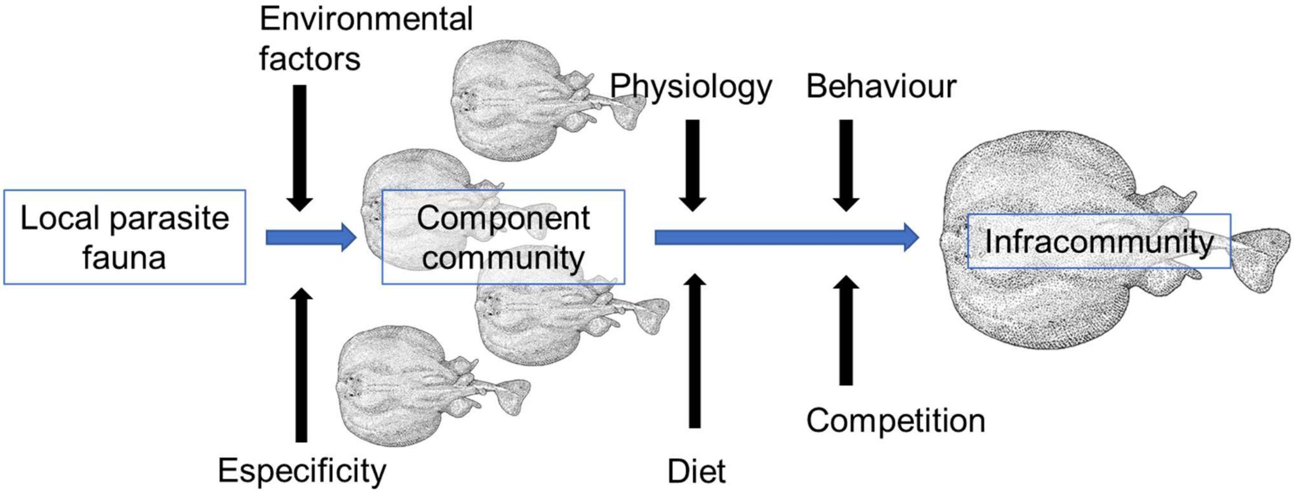

Fig 2. A scheme showing the determinants of parasite community structure. Infracommunities are a selection of parasites from the component community, as a result of a series of constraints regarding the host and the parasites themselves. In a similar fashion, component communities are a selection of parasites from the available local parasite fauna, constrained by environmental factors and the parasite’s own specificity. Adapted from Holmes (1990), to illustrate the case of parasite communities infecting elasmobranchs.

Since the beginning of life itself, all living beings are continually modified by evolutionary forces maintaining an everlasting state of flux (Darwin 1859). These evolutionary processes and selective pressures also condition the intricate relationship of hosts and their parasites (Poulin 1992). Naturally, to understand these forces has become a main goal for parasitologists and attempts to describe these processes have highlighted the key role of phylogenetic and ecological forces in determining host-parasite relationships (de Vienne et al. 2007). An great example for the study of these processes is the cestode colonization of host species such as the elasmobranchs (see next section 1.3). Several examples exist in the scientific literature that point towards the importance of ecological parameters in influencing assemblages of cestodes in a particular host species (e.g. Dunn 1963, Marcogliese 2002). As a detailed example, in a study conducted by Randhawa and Poulin (2010), host body size and foraging depth were found to be important predictors of cestode species richness in elasmobranch species. However, due to the intricated nature of host-parasite associations, it is not always possible to define a clear separation of the ecological influences that act on host species from those acting on parasite species (Penczykowski et al. 2016). For example, one may regard the availability of hosts as a characteristic of the ecology of a parasite, but the factors that enable a host availability could ultimately be attributed to the ecology of the host species itself. The nature of one cannot be understood without regarding the other.

1.3 Elasmobranchs as hosts: cestodes of elasmobranchs

Since elasmobranchs are high-trophic level predators in the marine ecosystem, they act as significant definitive hosts for many marine parasites. Elasmobranchs act often as top predators, regulating the populations of lower trophic level species (Paine 1980, Crooks and Soulé 1999, Pace et al. 1999, Duffy 2002, Myers et al. 2007, Heithaus et al. 2008, Baum and Worm 2009). Parasites with complex lifecycles exploit this process, being transmitted from one host to another through consumption, allowing the parasites to use different hosts in order to complete their lifecycles.

The body of any elasmobranch offers a diversity of sites that can be, and often are, occupied by other animals. In essence, every organ system of elasmobranchs has brought the attention of one or more groups of parasites (Caira and Healy 2004, Fig. 3). This does not mean that all sites of the body are equally parasitised. Certain organs and organ systems, such as the gills, the skin and the digestive tract, tend to host particularly diverse faunas of parasites. The highest diversity of parasites in an elasmobranch's body is encountered in the spiral valve (i.e. the spiral intestine) and cestodes are the most common parasites that can be found there (Fig. 3).

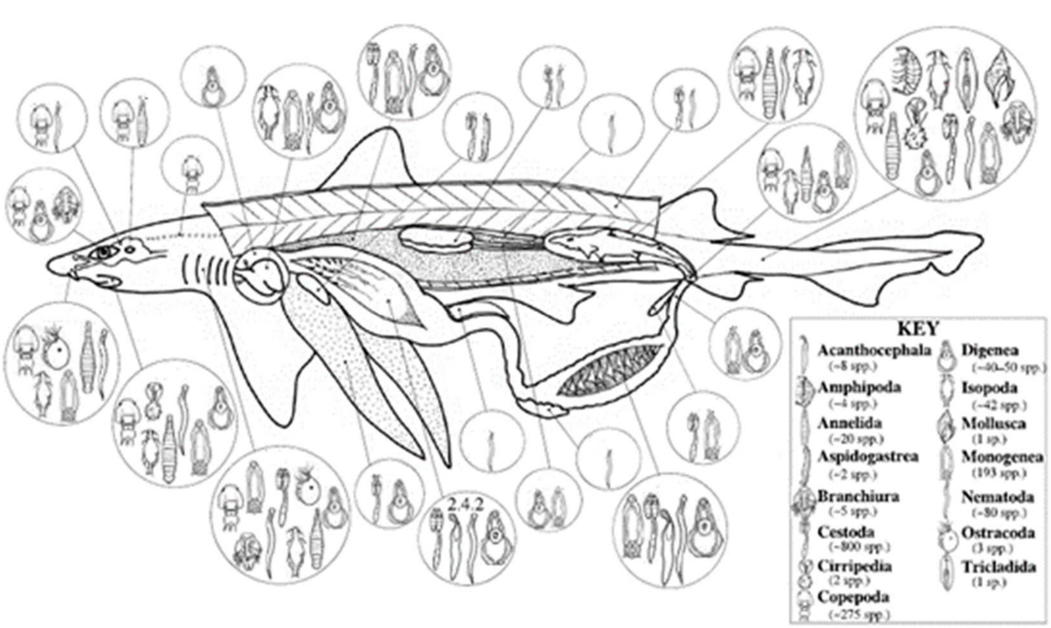

Fig 3. Overview of the sites occupied by metazoan parasites of elasmobranchs, indicating approximate number of species of each parasite group found in elasmobranchs (image adapted from Caira and Healy 2004).

Cestodes are parasitic worms belonging to the phylum Platyhelminthes (Class: Cestoda). Members of this phylum are commonly known as flatworms and cestodes are also commonly known as tapeworms. Cestodes are all parasites transmitted through the trophic chains by the ingestion of an infected prey species (Rohde 2005b). The class Cestoda is estimated to contain over 13,000 species and in theory most of them are expected to be found in the marine environment (Rohde 2005b, Strona and Fattorini 2014). There are 17 known orders of Eucestoda, or the true cestodes (hereforth referred to simply as cestodes). These include Bothriocephalidea, Caryophyllidea, Cathetocephalidea, Cyclophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Lecanicephalidea, Litobothriidea, Nippotaeniidea, Onchoproteocephalidea, Phyllobothriidea, Rhinebothriidea, Spathebothriidea, Tetrabothriidea, Trypanorhyncha and “Tetraphyllidea” (*sensu lato*) (Caira and Jensen 2017). In addition to these, there are two orders of cestodarians, Gyrocotylidea and Amphilinidea (Rohde 2005b). The subclasses of eucestodes and cestodarians can be distinguished morphologically by the presence of proglottids and scolices in eucestodes. Proglottids are a chain of repetitive compartments forming the body of the cestode, each of them containing complete sexually reproductive systems when mature. A scolex (plural: scolices) is a holdfast (i.e. an organ by which a parasitic animal attaches itself to its host) in the anterior part of the worm containing hooks, spines, tentacles, suckers, bothridia or any combination of them, for attaching to the host (Rohde 2005b).

The cestodes that parasitise elasmobranchs belong to nine of the 19 orders their class, and they include over 1000 species and 202 genera (Caira and Reyda 2005, Caira and Jensen 2017). Of these nine orders, seven are formed by species that exclusively parasitise elasmobranchs (with the exception of members of the Chimaerocestidae family which parasitise closely related taxa, the chimaeras, see Williams and Bray 1984). These different tapeworm orders vary in diversity, from fewer than ten species (e.g. Cathetocephalidea has only 7 species and 3 valid genera), to orders with tens of species (e.g. Lecanicephalidea with at least 90 species and 29 valid genera) (Caira and Jensen, 2017). In the past decades, cestodes of elasmobranchs have undergone various taxonomic revisions. Until the beginning of this century, just four orders of cestodes infecting elasmobranchs were recognised. The current nine recognised orders are largely an outcome of the establishment of new orders from former species of the order "Tetraphyllidea" (*sensu lato*) (Caira and Jensen 2014). The first order to be defined from the disentanglement of that order was the Litobothriidea (Olson and Caira 2001), followed by the Cathetocephalidea (Caira et al. 2005), and then the Rhinebothriidea (Healy et al. 2009). Finally, the last two new orders were the Phyllobothriidea and the Onchoproteocephalidea (Caira et al. 2014). Nowadays, about 30 genera and some 90 species still remain under "Tetraphyllidea" (*sensu lato*) (Caira and Jensen 2017). "Tetraphyllidea" (*sensu lato*) has always been an issue from an evolutionary perspective, largely because of the paraphyly of this group. Several of its members neither fit with any of the existing groups nor do they cluster together, avoiding any attempts to resolve the phylogeny of this order (Caira and Jensen 2014). All the other orders are considered monophyletic (Mariaux 1998, Palm et al. 2009, Caira and Jensen 2014), with the exception of the order Rhinebothriidea of which some authors argue that may not be monophyletic (Healy et al. 2009, Reyda and Marques 2011).

Many species in these tapeworm orders are host specific, with some species only parasitising a single elasmobranch species (Caira 1990, Caira and Jensen 2001, Caira and Healy 2004). But with this great diversity comes a large variation in host specificity as well. For example the order Litobothriidea is very host specific and only parasitises a subset of lamniform shark species, but species from the order Trypanorhyncha are exhibit much less host specificity, with a wide variety of elasmobranch species acting as final hosts (Palm and Caira 2008). It has been estimated that only a small fraction of the true cestode diversity has been described to date, in particular of those infecting elasmobranchs, primarily due to these parasites being overlooked for living within their definitive hosts' intestinal tract (Caira and Littlewood, 2013, Caira and Jensen 2017, Randhawa and Poulin 2020). In fact, Randhawa and Poulin (2010) gave an estimation of at least 3600 cestode species of elasmobranchs yet to be described.

One of the few complete life cycles of cestode that infecting an elasmobranch is the one studied in experimental conditions by Sakanari and Moser (1989). In this life cycle, the adult individuals of *Lacistorhynchus dollfusi* (Order Trypanorhyncha, Family Lacistorhynchidae) are found in the intestine of leopard sharks (*Triakis semifasciata)*, where they reproduce. The gravid proglottids (pieces of the worm's body) pass out with the shark's faeces and release the eggs kept inside into the water. These eggs are eaten by a copepod species, *Tigriopus californicus*, where they develop into a larval stage. These infected copepods are ingested by some teleosts species such as the white croaker (*Genyonemus lineatus*). This three-host life cycle is then closed when an infected fish is eaten by *T. semifasciata* (Sakanari and Moser 1989). This represents a typical life cycle for this group of parasite species.

The fact that there are only few complete elasmobranch cestode life cycles descriptions is just an example of how little this field of knowledge has advanced and the multiple fronts that are open to study further. Taking into account the importance of elasmobranchs as predators worldwide, little is known about the processes of trophic transmission of their parasites within marine food webs, a fact reiterated each time the subject is raised (e.g. Chambers et al. 2000, Chervy 2002, Caira and Reyda 2005, Jensen and Bullard 2010, Randhawa and Poulin 2020). Despite parasitic organisms making up a large proportion of the global diversity, the body of literature dedicated to parasites pales in comparison with that dedicated to their hosts, and this is especially true for marine ecosystems (Poulin et al. 2016). The relative scarcity of studies on the biology of parasitic organisms in general (and of elasmobranch cestodes in particular) is primarily attributable to the fact that many have yet to be discovered. Many reasons can be attributed to this. First, as explained above research efforts focusing on parasites and diseases are strongly biased towards specific host groups such as humans, livestock and particular wildlife, and second, parasites are generally discovered after their hosts (Poulin 1996). Although, there are (rare) exceptions, two of the best documented examples were parasites of the megamouth shark (*Megachasma pelagios*) described in 1983 (Taylor et al. 1983). A new genus of a parasitic copepod (Cressey and Boyle 1978) and a new family of the Trypanorhyncha (Dailey and Vogelbein 1982) were found in megamouth sharks and published before the host species itself was described. Other reason is that, organisms that occupy a wider geographical range are more likely to be discovered earlier than those with more restricted ranges (Blackburn and Gaston 1995, Gaston et al. 1995, Allsopp 1997, Collen et al. 2004, Baselga et al. 2010, Randhawa et al. 2015). For this last consideration, in the specific case of parasites, their geographical range is analogous the range of its different hosts, consequently any parasitic organisms exploiting a wider range of organisms have generally been described before than those which are restricted to fewer hosts species (Poulin and Morand 2004, Krasnov et al. 2005, Poulin and Mouillot 2005). Last, the first description of free-living organisms is generally based on their external features, overlooking the existence of endoparasites until the species are examined by a parasitologist. It is not only the fact that the hosts are poorly studied, it is that much of their parts are not accessible (evisceration before landing), and that it is not always possible to access sufficient sample sizes to study the parasitofauna of all species of elasmobranchs.

However, we are in the middle of a ‘maximum species discovery’ period for both elasmobranchs (Last 2007, White and Last 2012, Randhawa et al. 2015) and their cestodes (Randhawa et al. 2020), relative to what previous records show. Also, it seems statistically impossible to predict the global diversity of tapeworms infecting elasmobranchs, as their species accumulation curve has yet to reach an asymptote (Randhawa et al. 2020). Moreover, there are still a large number of hosts awaiting discovery (Randhawa et al. 2015), making the task of describing the world’s tapeworm diversity of elasmobranchs even a bigger task, especially if we take into account the average 127 years between the taxonomic descriptions of elasmobranchs hosts and the taxonomic descriptions of their tapeworms (Randhawa and Poulin 2020). It is then a matter of concern the fact that elasmobranchs are the most threatened group of marine fishes and one of the most endangered animal groups (Davidson and Dulvy 2017), for their extinction or decline to very low levels where parasite transmission could not be sustained would mean the consequent extinction of their parasites. Therefore, it is essential to investigate the impact of host population decline on parasites (Altizer et al. 2007, Strona 2015). There could not be a better time for studying elasmobranch cestodes.

1.4 Present study

This doctoral thesis is devoted to the study of parasite helminth communities in elasmobranchs found in Iberian waters, both in the Atlantic and the Mediterranean, with comments on the agonistic relationships between blue sharks (*Prionace glauca*) and swordfish (*Xiphias gladius*), questions that hadn’t been approached before by previous researchers. In an early stage of the thesis we realised that infracommunities of cestodes infecting shortfin makos (*Isurus oxyrinchus*) were yet to be described, so a first attempt at their study was made using samples from the northeast Atlantic. In this study we discussed the peculiarities of shortfin makos as hosts, looking onto the characteristics of the pelagic realm as drivers of their infracommunities poorness (Chapter 3). This sampling campaign also allowed to obtain some samples of bluse sharks (*Prionace glauca*), a very interesting species when considering its cosmopolitan character and the fact that it is one of the most studied species of sharks regarding it intestinal infracommunities. We obtained opportunistic samples from different regions and sources, to increase the already well-studied helminth infracommunities of blue sharks, confirming how they present a general core of four main cestode species that they carry with them around the world and clarifying previous records of cestode parasitism on blue sharks throughout the literature (Chapter 4).

Some difficulties to obtain more samples from the Atlantic made us change our approach and look for other groups of elasmobranchs that could bring some light to the constraints that affect cestode infracommunities. The study of electric rays (family Torpedinidae) from the coasts of the Mediterranean seemed a very good candidate to test whether their particular methods of predation (through electric discharges that paralyze or kill their preys) could have an effect on their parasitic infracommunities. This gave us the chance to present also the first studies of parasitic infracommunities of the common torpedo (*Torpedo torpedo*) and the marbled electric ray (*Torpedo marmorata*) for the western Mediterranean, the region of València (Chapter 5).

Finally, the studies conducted during the elaboration of Chapter 4 had brought us some interesting findings regarding agonistic interactions between blue sharks and swordfish (*Xiphias gladius*). During the necropsy of a blue shark, the remains of a large swordfish rostrum were found crossing through the skull and destroying the brain, being described as the most probable cause of death due to the shark being found stranded but still alive (Chapter 6). Looking into this issue, in the span of two years, four more cases of similar fatal interactions were described only in the western Mediterranean basin. One of them showing the tip of a swordfish rostrum already healed inside the head of the shark, indicative of a previous interaction, thus suggesting a more common occurrence of this events than previously considered by the scientific community (Chapter 7).

Chapter 02 – General and specific objectives

General Objective

The main purpose of this study is to investigate the interactions of four species of elasmobranchs from Iberian waters, that is, the shortfin mako, *Isurus oxyrinchus*; the blue shark, *Prionace glauca*; the marbled electric ray, *Torpedo marmorata*, and the common torpedo, *Torpedo torpedo*, with other species in their environment. Specifically, we focus, on the one hand, on research on the determinants of composition, diversity and, where appropriate, predictability, of intestinal parasite communities and, on the other, on the agonistic relationships of the blue shark with another species, the swordfish *Xiphias gladius*, which had not been analyzed in depth in the literature.

It is within the general objective of this thesis to contribute to lines of work already started within the scientific community, such as filling huge gaps in the basic information on elasmobranchs and their parasitic fauna, especially in relation to cestodes. In fact, many species of elasmobranchs have never been analyzed for their helminthic fauna, and parasite-host associations in elasmobranchs from many geographic areas remain unstudied. In this sense, the present study will contribute to the incipient efforts to create a systematic catalog and an estimate the diversity of existing elasmobranch cestodes (Tapeworm Inventory Database, Cestodes of the Bowels of the Earth). On the other hand, due to the taxonomic emphasis required to obtain a basic inventory of elasmobranch parasites, there are still very few studies that provide quantitative information on parasitic infections. It is surprising that there are only quantitative studies of complete gut fauna for less than 5% of species, and that such studies have only been replicated in more than one locality in even fewer. The present work will therefore contribute to provide relevant data for future meta-analyses.

We also intend to answer, following the natural history approach discussed in the General Introduction, a series of questions that have arisen in the course of the descriptive work and that are specific to each elasmobranch species (see below). Questions regarding the composition, diversity and, where appropriate, predictability of intestinal parasite communities will be formulated and examined in a broad comparative context. Said approach will allow: (1) to contrast to what extent there are general patterns linked to ecological, geographical and vital history traits of the host that could explain the variation in the diversity and composition of its parasitic infracommunities, and (2) to evaluate the importance of the ecological and life cycle peculiarities of each species to understand the possible deviations from the expected theoretical patterns.

The second question in this work arises from the need to explain a strange phenomenon that we detected during the sampling of one of the host species, that is, the impalement of blue sharks by swordfish. Initially considered an exceptional event, the increasing detection of this phenomenon stimulated the continuation of our investigation, which will shed light on its possible functional significance and population impact.

Specific Objectives

In accordance with the general objective described above, the specific objectives of this work are the following:

1. Provide basic knowledge about the cestode fauna of the shortfin mako, *Isurus oxyrinchus*; the blue shark, *Prionace glauca*; the marbled electric ray, *Torpedo marmorata*, and the common torpedo, *Torpedo torpedo*, in Iberian waters, where there was no previous information, providing precise information on infection parameters and descriptors of the infracommunities.

2. Investigate the potential influence of key factors linked to each host species on the composition, diversity and predictability of the intestinal infracommunities of cestodes, through a global comparative approach with other elasmobranchs. The specific factors are as follows:

    2.1. In the case of shortfin mako, we wonder to what extent the potential "dilution" of infective stages in a vast, homogeneous and barrier-free environment, i.e. the pelagic-oceanic domain, generates poor and unpredictable infracommunities.

    2.2. In the case of the blue shark, we wonder what is the relative role of the specificity of the parasites, and the cosmopolitan and highly migratory character of the host, in generating local differences and similarities in the composition and diversity of the infracommunities of cestodes.

    2.3. In the case of the electric rays (*Torpedo* sp.), we investigated to what extent the use of electric shocks by these species to capture their prey could have a negative effect on the infective phases they contain, generating impoverished infracommunities of cestodes.

3. Describe, for the first time, the effects of swordfish head impalement on blue sharks, evaluating its possible functional significance, its frequency in nature, and the potential population impact on blue shark that this behavior could exert.

Chapter 03 – Intestinal helminth fauna of the shortfin mako *Isurus oxyrinchus* (Elasmobranchii: Lamnidae) in the northeast Atlantic Ocean

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3.1 Abstract

Large oceanic sharks represent a suitable model to investigate the influence of a host's oceanic conditions on the structure of its helminth communities. In this study, we describe the intestinal helminth fauna, and investigate determinants of infracommunity structure, in 39 specimens of shortfin mako *Isurus oxyrinchus* collected in the NE Atlantic. Six cestode species were found in the spiral valve of makos: 3 are typical from lamnid sharks, namely, gravid specimens of *Clistobothrium montaukensis*, *Gymnorhynchus isuri* and *Ceratobothrium xanthocephalum*, and 3 are immature specimens of cestode species common to several elasmobranchs, namely, *Dinobothrium septaria*, *Nybelinia lingualis*, and *Phyllobothrium* cf. *lactuca*. In addition, L3 larvae of *Anisakis* sp. type I were detected. Infracommunities were species poor and had low total helminth abundance. The result of Schluter's variance ratio test was compatible with the hypothesis of independent colonization of helminth taxa. These results conform to previous studies on oceanic predators that have hypothesized that these hosts should have depauperate and unpredictable helminth infracommunities because oceanic conditions hamper parasite transmission. However, mean species richness and mean total abundance of cestodes of shortfin mako and other oceanic sharks did not significantly differ from those of elasmobranchs from other habitats.

This suggests that the large body size and prey consumption rates of oceanic sharks offset the negative 'dilution' effect of oceanic habitat on transmission rates. Additionally, or alternatively, parasites of oceanic sharks may have expanded the use of intermediate hosts through the trophic web to spread out the risk of failure to complete their life cycles.

3.2 Introduction

The shortfin mako *Isurus oxyrinchus* (Rafinesque, 1810) is a highly migratory shark of the family Lamnidae that is widespread in temperate and tropical waters of all oceans from about 50° N to 50° S; it is rarely found in waters below 16°C (Compagno 2001). As is typical of lamnids, the shortfin mako is a fast epipelagic species that acts as an apex predator in oceanic trophic webs (López et al. 2009). The diet of shortfin makos is generalist and mostly includes teleosts, cephalopods and crustaceans, although cetaceans, chelonians and other elasmobranchs may also be consumed (Maia et al. 2006, Preti et al. 2012, Porsmoguer et al. 2014). The shortfin mako is currently included in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species within the 'Vulnerable' category (Cailliet et al. 2012), because this species suffers heavy mortality as bycatch or as a target species of commercial longline fisheries around the world (Mejuto et al. 2009).

Large pelagic oceanic sharks such as the shortfin mako represent an interesting model to investigate the role of the host's habitat in providing structure to its helminth communities. Previous studies on sea turtles (Valente et al. 2009, Santoro et al. 2010), marine birds (Hoberg 1996, 2005), cetaceans (Balbuena & Raga 1993, Mateu et al. 2014) and teleosts (Costa et al. 2012, Santoro et al. 2014) have suggested that the pelagic oceanic realm may exert a strong influence on the helminth infracommunities of large marine predators. First, infective stages of trophically transmitted helminths are assumed to be physically more 'diluted' in the vast, isotropic pelagic environment than in demersal or benthic habitats. As noted by several authors (Collard 1970, Campbell et al. 1980, Randhawa & Poulin 2010), helminth transmission in the pelagic habitat is defined in a 3-dimensional space, whereas in benthic demersal habitats it occurs in a roughly 2-dimensional layer. Second, oceanic organisms, including both intermediate and definitive hosts of helminth parasites, exhibit lower population density, and are usually more vagile, than neritic organisms. Thus, pelagic oceanic helminths arguably face the challenge of finding hosts (Fraija-Fernández et al. 2015) and their transmission rates are expected to be low. Consequently, helminth infracommunities of large oceanic predators are predicted to be species poor, with low diversity and abundance of helminths. Also, infracommunities should harbour random subsets of the locally available helminths that are able to contact these hosts (Mateu et al. 2014).

The helminth fauna of the shortfin mako has been surveyed in numerous studies (e.g. Linton 1922, Euzet 1956, Robinson 1959, Cabrera 1991, Ruhnke 1993, Caira & Bardos 1996, Knoff et al. 2002, 2007, Lyons et al. 2015). Most of these studies, which are based on small host sample sizes (<5 hosts), have been carried out in the eastern Atlantic or Pacific oceans, and provide mainly taxonomic data. There is, however, a shortage of quantitative information from a helminth community perspective. This problem is common to parasitological studies of other large sharks because opportunistic sampling usually precludes obtaining large, homogenous host samples to analyse.

Shortfin makos are regularly caught in longline fisheries operating in the northeastern Atlantic. This situation provided a unique opportunity to describe the intestinal helminth fauna of the shortfin mako in a poorly surveyed region, and to obtain parameters at both infracommunity and component community levels. In particular, we investigated the extent to which oceanic conditions influence the structure of helminth infracommunities in this large oceanic shark by comparing our results with those obtained in other parasitological studies on elasmobranchs.

3.3 Materials and Methods

Sample collection

The shortfin mako is not protected under Spanish Law and catches have an economical interest. A total of 39 shortfin makos obtained in the port of Vigo (Galicia, Spain) were analysed for intestinal helminths. Sharks were caught by longline fisheries operating in the northeast Atlantic Ocean, between 40° N, 20° W and 35° N, 10° W (Fig. 1). Thirty-five sharks were caught in October 2012 and 4 in March 2013. Sharks were measured and sexed, collecting the stomach and the intestine (spiral valve), before the fish auction. The sample was composed of 19 males and 20 females, with total lengths ranging from 99 to 254 cm (mean ± SD: 143.9 ± 37.7 cm).

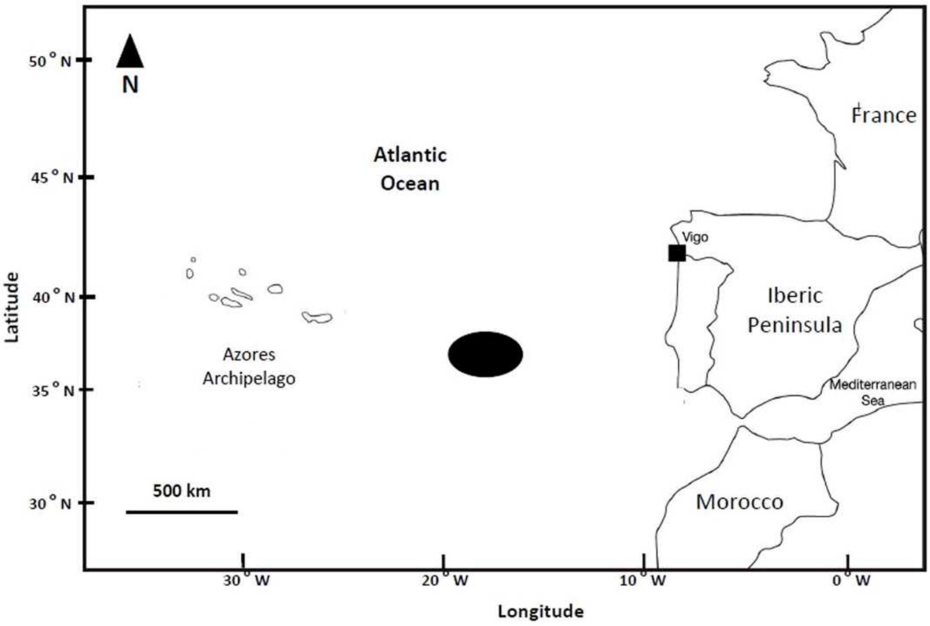

Fig. 1. Area where shortfin makos Isurus oxyrinchus were captured by longline fisheries. The oval dot indicates the area where the fishing boats were operating during the captures. The square dot indicates the port of Vigo, where the sharks were eviscerated. Modified from Porsmoguer et al. (2014)

The intestine was stored at −20°C for later analysis in the laboratory. After thawing, each intestine was rinsed with tap water over a 0.02 mm mesh and the solid contents were collected. The intestine wall was also thoroughly examined for attached helminths. Parasites were collected under a stereomicroscope, washed in 0.9% saline, counted, and fixed and preserved in 70% ethanol. Cestodes were stained with iron acetocarmine (Georgiev et al. 1986) and mounted on Canada balsam. Specimens were identified based on Khalil et al. (1994) and specific references (Ruhnke 1993, 2011, Palm 1999, Knoff et al. 2007). Larval nematodes were cleared in glycerine and examined as temporary mounts. Voucher specimens are deposited at the Natural History Museum of London with the following accession numbers: *Clistobothrium montaukensis*, NHMUK 2016.9.29.1-3; *Gymnorhynchus isuri*, NHMUK 2016.9.29.4-5; *Ceratobothrium xanthocephalum*, NHMUK 2016. 9. 29. 6-8; *Dinobothrium septaria*, NHMUK 2016.9.29.9-11; *Nybelinia lingualis*, NHMUK 2016.9.29.12-14; *Phyllobothrium cf. lactuca*, NHMUK 2016.9.29.15-17; and L3 larvae of *Anisakis* sp. type I, NHMUK 2016. 9. 29.18-20. Additional material can be found at the Collection of the Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Spain.

Statistical analyses

We recorded prevalence (percentage of hosts in the sample infected by a helminth species), mean intensity (average number of individuals of a helminth species per host in the sample of hosts infected with this species) and mean abundance (average number of individuals of a helminth species per host in the total sample of hosts) for each helminth taxon following Bush et al. (1997). Total helminth abundance, species richness and Brillouin's index of diversity were used as descriptors of infracommunities (i.e. helminth communities of individual hosts). Total helminth abundance is here considered as the number of individuals of all helminth species, and species richness as the number of helminth species per individual shark. The 95% CI for prevalence was calculated with Sterne's exact method (Reiczigel 2003). The 95% CI for mean abundance and mean intensity of each helminth taxon, as well as for mean total helminth abundance, mean species richness and mean Brillouin's index, were obtained with the biascorrected and accelerated bootstrap method using 20 000 replications (Rózsa et al. 2000).

A Spearman's correlation test was performed to investigate whether the abundance of each helminth species and infracommunity parameters varied significantly with host length, and Mann-Whitney U tests were performed to explore significant differences in parasitological parameters between male and female sharks. The overall association between helminth species was investigated using a variance ratio test (Schluter 1984). The aim of this test is to compare the observed variance in helminth species richness per shark with the variance expected assuming that the occurrence of each species is independent from that of the others (see Schluter 1984 for details). To create the null distribution under an independent colonization hypothesis, we fixed the observed value of species' occurrences per shark but randomized the occurrence of each species among sharks, assuming that the likelihood of infection of all individual hosts was equiprobable. This process was repeated 20 000 times.

General linear mixed models (GLMMs) were used to explore whether mean species richness and mean total abundance of intestinal cestodes were significantly smaller in shortfin makos and other oceanic elasmobranchs than in other elasmobranchs. We focused on cestodes because they are, by far, the most diverse helminth group infecting elasmobranchs (Caira & Jensen 2014), and many surveys only provide infection data on cestodes. Data from other host species were obtained from parasitological surveys with host sample sizes ≥10 (see the Supplement at www.int-res. com/ articles/ suppl/ d123p045 supp. xlsx). Most studies do not provide data on mean species richness or mean total abundance. In these cases, we calculated species richness by summing up prevalences (expressed as decimals) of all intestinal helminth taxa, and mean total abundance based on mean abundances of individual taxa.

In the comparison of species richness, we used the ratio between infracommunity richness and component community richness as the dependent variable. In this way, we controlled for differences of local cestode availability (for brevity we will refer to this variable as 'corrected infracommunity richness'). Host sample size (as a measure of sampling effort) and habitat (oceanic pelagic elasmobranchs vs. other elasmobranchs) were used as predictors. In some species, there was more than one survey available (see the Supplement), thus 'individual survey' was included as a random variable in the model. Type I sum of squares was used to control for sampling effort before making the contrast for habitat. In the comparison of mean total abundance, data were $\log_{10}$-transformed to achieve linearity, and the same set of predictors was used. In all models, we treated species as independent observations, i.e. we did not apply independent contrasts (see e.g. Poulin 1997) because quantitative data of helminth communities from elasmobranchs are still limited. Thus, the comparisons should be considered as preliminary, awaiting more complete analyses with data from further surveys when available.

The free software Quantitative Parasitology v.3 (www. zoologia.hu/qp/qp.html) was used to calculate infracommunity parameters and to set the 95% CIs of parameters. The free software EcoSim (www. uvm.edu/~ngotelli/ Eco Sim/ Eco Sim. html) was used to perform Schluter's test and the statistical package SPSS v.22 was used for the remaining analyses (SPSS). Statistical significance was set at $p < 0.05$.

3.4 Results

A total of 2117 helminth specimens were collected, and all sharks except 4 were infected with at least 1 helminth taxa. Nematodes identified as L3 larvae of *Anisakis* sp. type I were found throughout the intestine of 17 sharks (Table 1), some specimens being partially digested. Six species of cestode from the orders Tetraphyllidea, Trypanorhyncha and Phyllobothriidea were also found in the intestine (Table 1). At least some individuals with gravid proglottids were detected in 3 species, including *Clistobothrium montaukensis* Ruhnke, 1993, *Gymnorhynchus isuri* Robinson, 1959 and *Ceratobothrium xanthocephalum* Monticelli, 1892. *C. montaukensis* was the most prevalent taxon, infecting 32 sharks; it also numerically dominated infracommunities since in 27 sharks it made up over 50% of the total helminth abundance. A total of 21 individuals of *G. isuri* were found in 3 hosts, whereas individuals of *C. xanthocephalum* specimens were found in 8 sharks. One infection in a female shark reached 942 individuals of this cestode species (Table 1). In some sharks, the scolex was embedded in the intestinal wall and was typically surrounded by a fibrotic capsule.

In 3 cestode species, no individuals with gravid proglottids were found: *Nybelinia lingualis* (Cuvier, 1817), *Dinobothrium septaria* (Van Beneden, 1889) and *Phyllobothrium cf. lactuca* (Van Beneden, 1850) (Table 1). Thirty-nine *N. lingualis* were found in the intestine of 7 sharks, whereas only 14 specimens of *D. septaria* were found in a single shark. *P. lactuca* was found in 4 sharks. In this species, the poor state of preservation of specimens made it difficult to find the anterior accessory sucker of bothridia and, in some cases, only 2 out of the 4 suckers could be observed.

Table 1. Infection parameters of intestinal helminths found in 39 shortfin makos *Isurus oxyrinchus* from the Northeast Atlantic Ocean

Species	Prevalence (%) Overall (95% CI)	Intensity Mean (95% CI) [range]	Abundance Mean (95% CI)
Order Tetraphyllidea			
Ceratobothrium xanthocephalum	20.5 (9.7-35.7)	180.8 (47.9-536.3) [1-942]	37.1 (8.6-141)
Dinobothrium septaria	2.6 (0.2-13.6)	14 (a) [b]	0.4 (0-1.1)
Order Trypanorhyncha			
Gymnorhynchus isuri	7.7 (2.1-20.3)	7 (1-12) [1-16]	0.5 (0-2.3)
Nybelinia lingualis	17.9 (8.6-33.2)	5.6 (1.6-16.6) [1-27]	1 (0.2-3.9)
Order Phyllobothriidea			
Clistobothrium montaukensis	82.1 (66.8-91.4)	17.6 (13.8-24.5) [1-78]	14.4 (10.8-20.4)
Phyllobothrium cf. *lactuca*	10.3 (3.6-24.1)	8.5 (2.5-18.3) [2-22]	0.9 (0.2-3.2)
Order Rhabditida			
Anisakis sp. larvae 3 type I	43.6 (27.8-60.3)	8.76 (2.1-33.9) [1-110]	3.8 (0.9-15.3)

[a] Sample is too small to calculate the value
[b] Cannot be calculated with only one infection

No significant relationship between host body length and the abundance of any helminth species or infracommunity parameters was found (range of Spearman r = −0.139−0.345, $p > 0.05$). In addition, no significant differences were detected in the abundance of any helminth species or infracommunity descriptors between sexes (range of Mann-Whitney U = 90−102, $p > 0.25$). Schluter's variance test indicated no significant departure from the null hypothesis of random colonization of helminth taxa. The observed value was not significantly lower ($p = 0.958$) or higher ($p = 0.058$) than those obtained in the null distribution.

Species richness at the infracommunity level ranged from 0 to 4 (mean [95% CI]: 1.85 [1.49−2.18]), and was low compared with species number at the component community level (7 spp.). However, the difference was not higher than that observed in other elasmobranchs, regardless of their habitat (Fig. 2a,b). In fact, other pelagic oceanic sharks, i.e. the blue shark *Prionace glauca* and the porbeagle *Lamna nasus*, do not depart from the common pattern of difference observed in non-oceanic elasmobranchs (Fig. 2a,b; see also the Supplement). This conclusion was supported by the GLMM results. Contrary to what was expected, the corrected infracommunity richness in pelagic oceanic sharks was higher than that from other elasmobranchs; the associated probability was close to significance (Table 2). Brillouin's index (0.264 [0.176−0.370], range: 0−0.972) and mean total helminth abundance (58.1 [28.0−161.7], range: 0−964) were low in shortfin makos of our sample. However, values of mean total abundance tended to be higher than those observed in most elasmobranchs (Fig. 2c). Furthermore, the GLMM results indicated that mean total abundance of helminths in pelagic oceanic sharks was higher than that from other elasmobranchs and close to significance (Table 2). No significant effect of host sample size was detected in any model (Table 2).

3.5 Discussion

The parasite fauna of shortfin mako in our sample was composed of 7 species, all of which except *Dinobothrium septaria* had already been reported in this host (see below). However, up to 9 additional species, all belonging to the order Trypanorhyncha, have been found in the intestine of makos globally (Palm 2004, Randhawa & Poulin 2010, and references therein). Three species, i.e. *Nybelinia schmidti*, *N. pintneri* and *Myxonybelinia californica*, occur in South Africa and Tasmania (Palm 1999, Palm & Beveridge 2002), the Pacific Ocean (Yamaguti 1934, Heinz & Dailey 1974) and off the coast of California (Palm, 2004), respectively. Also, *Hepatoxylon megacephalum* appear to be restricted to large sharks in the Southern Hemisphere (Bates 1990, Waterman & Sin 1991, Beveridge & Campbell 1996), although there is an additional record in the nursehound *Scyliorhinus stellaris* from the Mediterranean (Hartwich & Kilias 1992).

However, 5 species have previously been reported in the North Atlantic but were not detected in our survey. Two species of the Sphyriocephalidae, i.e. *Sphyriocephalus viridis* and *Heterosphyriocephalus tergestinus*, are parasites typical from pelagic and deep-sea sharks (Dallarés et al. 2016). Although plerocercoid larvae have been detected in our study area, there is only a single record of each species in shortfin makos (Dallarés et al. 2017), suggesting that infections in makos could be infrequent. In contrast, of the other 3 non-detected species, *Gymnorhynchus gigas* and *Molicola horridus* are typical from shortfin makos (Bates 1990, Palm 2004), and *Hepatoxylon trichiuri* also occurs in other pelagic sharks (Bates 1990, Waterman & Sin 1991, Beveridge & Campbell 1996). Furthermore, there are records of these 3 species in intermediate hosts in the NE Atlantic (Heinz & Dailey 1974, Casado et al. 1999, Vázquez-López et al. 2000, Gibson et al. 2005); thus, their absence from our survey could be due to low sample numbers, particularly if prevalences are low (see also below).

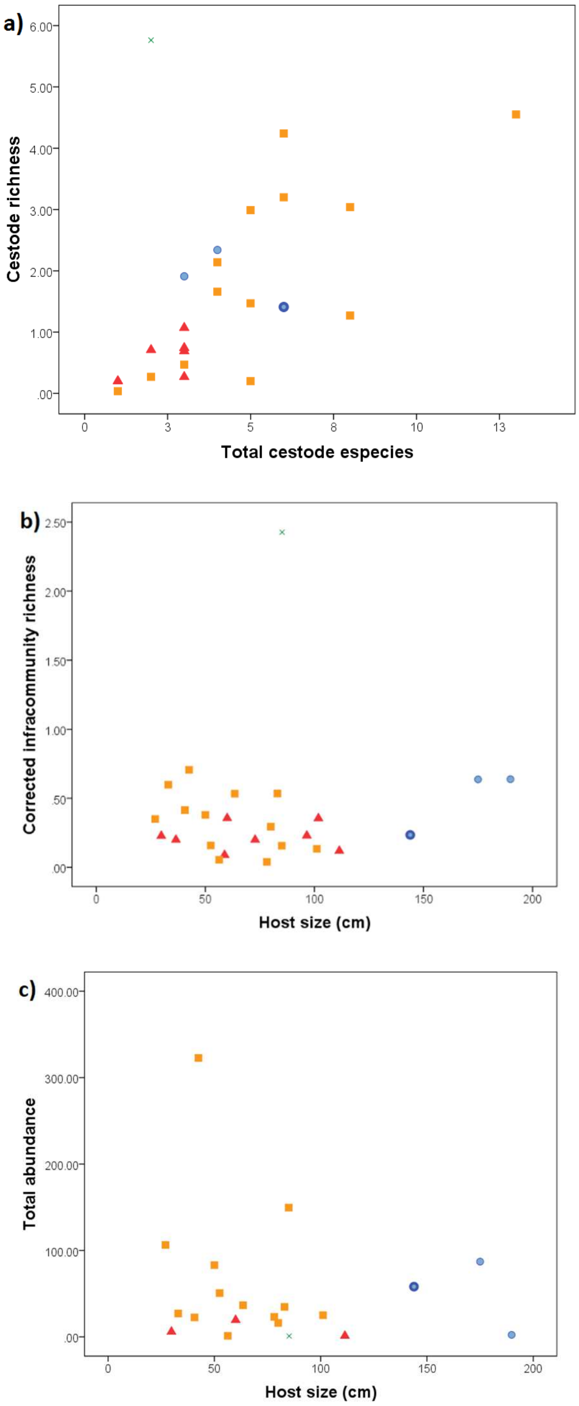

Fig. 2. Comparison of richness and mean abundance of parasite infections in elasmobranch species from different habitats. For clarity, in species with more than one survey, an average of helminth species richness and total abundance are used. Complete data can be found in the Supplement at www. int-res. com/ articles/ suppl/ d123 p045 supp. xlsx. Habitat of each species: bathydemersal (red triangles); benthopelagic (green cross); demersal (orange squares); pelagic oceanic (blue circles). Values related to our survey (shortfin mako) are circled. (a) Relationship between infracommunity cestode richness and the total number of cestode species infecting the host. (b) Relationship between corrected infracommunity richness and mean host size. (c) Relationship between total abundance of parasites with mean host size.

The L3 larvae of *Anisakis* sp. type I are ubiquitous in the oceanic realm and may correspond to any of the 6 species of *Anisakis* that have odontocete cetaceans as main definitive hosts (Mattiucci & Nascetti 2008). Two of these species, *A. simplex* (*sensu stricto*) and *A. pegreffii*, have been reported in the study area (Beverley-Burton et al. 1977, Paggi et al. 1998, Kuhn et al. 2011). The diet of the shark individuals analysed in our sample was described by Porsmoguer (2015) and includes fish and squid prey, i.e. *Histioteuthis* sp., *Xiphias gladius*, *Euthynnus alletteratus*, *Scomberesox saurus*, and *Scomber scombrus*, that are susceptible to infection with these anisakid species (Bussiéras & Baudin-Laurencin 1973, Abaunza et al. 1995, McDonald & Margolis 1995, Mattiucci et al. 1997, Culurgioni et al. 2010). It is interesting that larvae were found free in the intestine lumen of makos and not encysted in the stomach wall as commonly occurs in typical intermediate or paratenic fish hosts (Mattiucci & Nascetti 2008). This could suggest that shortfin makos likely are accidental hosts for these larvae.

Table 2. Results of the general linear mixed models to account for corrected infracommunity richness and total abundance of cestode fauna of pelagic oceanic sharks vs. elasmobranchs from other habitats. The parameter for pelagic oceanic sharks was set to zero and, therefore, the parameter for 'habitat' represents the value for other elasmobranchs.

Predictor	Parameter	SE	*t*	df	p
Infracommunity richness					
Host sample size	-0.000290	0.000562	-0.516	34.3	0.609
Habitat	-0.222	0.122	-1.823	18.7	0.084
Total abundance					
Host sample size	-0.002657	0.001564	-1.699	31.4	0.099
Habitat	-0.820	0.449877	-1.822	22.6	0.082

Species of *Clistobothrium* seem to be specific to lamnid sharks (Dailey & Vogelbein 1990, Ruhnke 1993, Randhawa & Brickle 2011). *C. montaukensis* had only been reported in the shortfin mako in the northwestern Atlantic (Ruhnke 1993), although a closely related, unidentified species of *Clistobothrium* was reported from porbeagle sharks *Lamna nasus* in the Falkland Islands (Randhawa & Brickle 2011). Molecular evidence indicates that porbeagle sharks are infected with *C. cf. montaukensis* through the squid *Doryteuthis gahi* (Randhawa & Brickle 2011). However, there is also morphological, molecular and ecological evidence that cetaceans act as intermediate hosts for species of *Clistobothrium* (Aznar et al. 2007). In fact, adults of *C. carcharodoni*, collected from great white sharks *Carcharodon carcharias* in New Zealand, were closely related to plerocercoid larvae collected in squid-feeding cetaceans from the western Mediterranean (Randhawa 2011). The diet of the shortfin makos analysed in this study included at least 7 species of oceanic squid (Porsmoguer et al. 2014), but remains of cetaceans were also found in the stomach of several individuals (Porsmoguer et al. 2015). Thus, there is the possibility that *C. montaukensis* use squids and/or cetaceans as intermediate hosts to infect shortfin makos.

Gymnorhynchus isuri has only been reported in shortfin makos, and seems to be a widespread species, with records in the north- and southwestern Atlantic (Caira & Bardos 1996, Knoff et al. 2002) and New Zealand waters (Robinson 1959). *Ceratobothrium xanthocephalum* apparently infects only species of *Lamna* and *Isurus* (Euzet 1956, 1994, Schmidt 1986). Shortfin makos accumulate the largest number of records for this cestode species, including Japan (Yamaguti 1934), New Zealand (Robinson 1959), the northeastern (Euzet 1956) and northwestern Atlantic (Olson & Caira 1999), and the Pacific coast of North America (Lyons et al. 2015). Plerocercoid larvae of *Gymnorhynchus* spp. and *C. xanthocephalum* have been reported in pelagic oceanic teleosts (Gibson et al. 2005), including some species (e.g. the swordfish *X. gladius*) that were found in the stomach contents of our mako sample (Porsmoguer 2015). Therefore, an oceanic life cycle could be inferred, with teleosts serving as second intermediate hosts.

We did not find gravid worms in 3 tapeworm species. *D. septaria* is typical of lamnid sharks, and have been found in porbeagle sharks in North Atlantic (Woodland 1927, Euzet 1956) and South Atlantic (Randhawa & Brickle 2011), and great white sharks from the North Atlantic (Woodland 1927). In our survey, only 14 individuals of this cestode were recovered from a single shark, and none had gravid proglottids, suggesting a recent or an accidental infection.

Nybelinia lingualis has been reported widely in the Atlantic and South Australia (Palm & Walter 2000) and seems to be an ecologically ubiquitous species. Plerocercoid larvae occur in a number of benthic, demersal and pelagic teleosts and cephalopods (Palm 1999, Palm & Walter 2000, Gibson et al. 2005). Adults also exhibit low host specificity and have been reported in pelagic and demersal sharks, as well as in pelagic rays (Palm & Overstreet 2000, Palm & Walter 2000, Knoff et al. 2002). There are records of adult *N. lingualis* in shortfin makos from the southwestern Atlantic (Knoff et al. 2002) and the western Mediterranean (Cabrera 1991, Palm & Walter 2000). However, none of the 39 specimens of *N. lingualis* collected from 7 sharks in this study were gravid, thus raising the question of whether or not shortfin makos are suitable hosts for this species.

Finally, the specimens of *Phyllobothrium* collected as immature specimens in 4 sharks from this study resembled *P. lactuca* but their poor state of preservation precluded an unequivocal identification at species level. *P. lactuca* typically infects elasmobranchs dwelling in shelf and upper slope waters, rarely oceanic sharks (e.g. Euzet 1956, Ruhnke 1996, Sène et al. 1999). There is an old record of this cestode in

Oxyrhina spallanzanii (= *I. oxyrhinchus*) (see Williams 1968). Records of *P. lactuca* in shortfin makos probably represent accidental infections.

In summary, all helminth species reported in this study are almost exclusively found in sharks, mainly members of the family Lamnidae inhabiting oceanic waters. This pattern of specificity is common to other elasmobranchs, the intestinal helminth fauna of which is peculiar and very specific as a whole (Caira & Pickering 2013). The helminths found in shortfin makos, with the exception of *C. montaukensis*, had low infection levels, and the variance ratio test indicated independent colonization of each helminth species. In addition, no significant correlation was found between the length of the host and species richness or total abundance of intestinal helminths. In infracommunities of intestinal helminths, an absence of structure has been related to the lack of competitive interactions between species (see e.g. Curran & Caira 1995 for a large shark species). However, a low recruitment rate of parasites has been invoked as a more likely factor accounting for independent colonization of helminths in intestinal infracommunities of oceanic vertebrates such as sea turtles (Santoro et al. 2010) or cetaceans (Mateu et al. 2014). Low recruitment would be dependent on the 'dilution' of infective stages in the oceanic habitat (Randhawa & Poulin 2010, Mateu et al. 2014), but also on a low number of infective stages transmitted with each prey. In this respect, the size of larvae could be an issue because there seems to be an inverse relationship between the size of parasites and their intensity of infection (see e.g. Randhawa & Poulin 2009 for parasites of elasmobranchs). Interestingly, the larval size for 3 of the tapeworm species infecting shortfin makos is presumably large (i.e. over 1 cm long) (see measurements for allied species in Pascual et al. 1994, Williams & Bunkley-Williams 1996).

Contrary to what we expected, the cestode infracommunities of shortfin makos and other pelagic oceanic sharks were not particularly depauperate compared with those from other elasmobranchs, e.g. *Prionace glauca*, *Squalus acanthias*, *Etmopterus spinax* and *Leucoraja naevus* (see Fig. 2); in fact they tended to be more diverse. This observation could be related to 3 potential factors. First, we cannot rule out that parameters at the infracommunity level are blurred by phylogenetic effects (i.e. the degree of diversification and specificity of cestode taxa in each host group) and/or differences in the local availability of cestodes. Nevertheless, we attempted to minimize these effects by dividing mean infracommunity richness by component community richness. For instance, bathydemersal sharks are typically infected with very few cestode species (Caira & Pickering 2013; see Fig. 2a), but corrected infracommunity richness was similar to that from other elasmobranchs (Fig. 2b).

Second, shortfin makos and other pelagic sharks are apex predators with the largest body size of all elasmobranch species in the sample (Fig. 2b,c). In addition, makos and other lamnid sharks are capable of increasing their temperature by up to 20°C (Bernal et al. 2005). Accordingly, they should have higher metabolic demands and higher rates of prey consumption, thus increasing the likelihood of contact with infective stages of many parasites (Aznar et al. 2004), particularly if they are generalist predators (Joyce et al. 2002, McCord & Campana 2003, López et al. 2009). In other words, a large body size could help offset the negative 'dilution' effect of oceanic habitat on transmission rates. Finally, it could be that the 'dilution effect' associated with oceanic conditions is inconsequential if parasites are adapted to expand the use of intermediate hosts through the trophic web. In fact, it has been suggested that many marine parasites have reduced host specificity as a strategy to spread out the risk of failure to complete their life cycles (Marcogliese 1995, 2002).

Consequently, it would seem premature to extract solid conclusions about the influence of the oceanic habitat on the helminth assemblage of shortfin makos based on the available data. However, we think that interspecific comparative approaches are necessary to advance hypotheses about such influences. This approach would also require that proper infracommunity parameters are published in surveys of elasmobranchs and other oceanic vertebrates.

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3.8 Supporting information

Appendix 1. Published surveys of intestinal helminths of elasmobranchs from which infracommunity data (i.e., mean species richness per host, mean total abundance of helminth individuals) can be obtained. (*) No data available. Table 1 shows all bibliographical data found and Table 2 shows mean values by species.

Table 1 columns are as follows:

Reference and Year: see literature cited to get the source.
Species: Host species
N: Host sample size
Habitat: Host habitat
(a) Body length: Mean host body length
(b) Species richness (I): Mean infracommunity species richness
(c) Species richness (C): Mean compound community species richness
(d) Total abundance: Mean total abundance of helminths per individual host
(e) Cestode richness: Mean infracommunity cestode richness
(f) Cestode species: number of cestode species infecting the host species
(g) Total abundance of cestodes: Mean total abundance of cestodes per individual host
Commentary: any addition that might be helpful. *=Size obtained from bibliography. $^+$=Size obtained from range of sizes.

Table 2 columns are as follows (I=infracommunity; C=compound community):

Reference and Year: see literature cited to get the source.
Species: Host species
N: Host sample size
Habitat: Host habitat
(a) Body length: Mean host body length
(b) Species richness (I): Mean infracommunity species richness
(d) Total abundance (I): Mean total abundance of helminths per individual host
(e) Cestode richness (I): Mean infracommunity cestode richness
(f) Cestode species (C): number of cestode species infecting the host species
(g) Total abundance of cestodes (I): Mean total abundance of cestodes per individual host
Commentary: *=Single study

Appendix 1 - Table 1

Reference	Species	N	Habitat	(a)	(b)	(c)	(d)	(e)	(f)	(g)	Commentary
Penadés-Suay et al. 2017	*Isurus oxyrinchus*	39	Pelagic-Oceanic	143,9	1,85	7	58,1	1,41	6	54,3	
Méndez and Galván-Magaña 2016	*Prionace glauca*	27	Pelagic-Oceanic	195	2,66	4	163,3	2,66	4	163,3	*
Henderson et al. 2002	*Prionace glauca*	94	Pelagic-Oceanic	146	0,69	3	8,7	0,69	3	8,7	+
Curran and Caira 1995	*Prionace glauca*	12	Pelagic-Oceanic	223,3	3,67	4	941	3,67	4	941	+
Randhawa and Brickle 2011	*Lamna nasus*	11	Pelagic-Oceanic	175	2,36	4	87,1	1,91	3	81,3	+
Gracan et al. 2016	*Mustelus punctulatus*	188	Demersal	78,2	1,35	9	23,2	0,2	5	0,6	
Gracan et al. 2014	*Mustelus mustelus*	15	Demersal	101,1	1,4	5	25,1	0,27	2	0,7	
Alarcos et al. 2006	*Mustelus schmitti*	20	Demersal	63,5	3,2	6	36,6	3,2	6	36,6	
Cislo and Caira 1993	*Mustelus canis*	49	Demersal	83	2,14	4	34,7	2,14	4	34,7	+
Gracan et al. 2016	*Squalus acanthias*	157	Benthopelagic	57,5	0,2	4	0,4	0,03	1	0,03	
Pickering and Caira 2014	*Squalus acanthias*	44	Benthopelagic	100	1,19	3	5,1	1,19	3	5,1	Winter, *
Pickering and Caira 2014	*Squalus acanthias*	60	Benthopelagic	100	1,02	3	3,2	1,02	3	3,2	Spring, *
Pickering and Caira 2014	*Squalus acanthias*	55	Benthopelagic	100	1,22	3	14,6	1,22	3	14,6	Summer, *
Pickering and Caira 2014	*Squalus acanthias*	58	Benthopelagic	100	1,35	3	10,9	1,35	3	10,9	Autumn, *
Henderson et al. 2002	*Squalus acanthias*	254	Benthopelagic	80,5	0,6	3	2,5	0,11	2	0,1	+
Orlowska 1979	*Squalus acanthias*	45	Benthopelagic	68,5	1,82	6	9	0,66	3	1	+
Wierzbicka and Langowska 1984	*Squalus acanthias*	55	Benthopelagic	75	0,27	3	0,4	0,07	1	0,1	Antartic survey, +
Moore 2001	*Scyliorhinus canicula*	37	Demersal	56,7	1,27	4	0,6	0,11	2	0,2	Plymouth
Moore 2001	*Scyliorhinus canicula*	49	Demersal	56,1	1,55	3	2,2	0	0	0	Cardigan Bay
Moore 2001	*Scyliorhinus canicula*	15	Demersal	56,2	1,2	3	0,7	0	0	0	Eastern Solent
Isbert et al. 2015	*Etmopterus spinax*	30	Bathydemersal	30,6	1	5	3,2	0,7	4	2,7	Galicia Bank, +
Isbert et al. 2015	*Etmopterus spinax*	29	Bathydemersal	30,6	0,69	5	9,3	0,52	4	1,3	Avilés Canyon, *+
Klimpel et al. 2003	*Etmopterus spinax*	37	Bathydemersal	21,5	1,3	3	5,4	0,92	2	2,9	+
Sanmartín et al. 2000	*Raja undulata*	74	Demersal	33	3,24	9	27	2,99	5	26,5	+

Appendix 1 – Table 1 *continued*

Reference	**Species**	**N**	**Habitat**	**(a)**	**(b)**	**(c)**	**(d)**	**(e)**	**(f)**	**(g)**	**Commentary**
Álvarez et al. 2006	*Raja microocellata*	52	Demersal	50	3,17	11	83	3,04	8	82,7	+
Álvarez et al. 2006	*Raja brachyura*	60	Demersal	52,5	1,34	11	50,7	1,27	8	50,6	+
McVicar 1977	*Leucoraja naevus*	206	Demersal	42,5	5,23	10	142,7	5,13	6	142,4	Aberdeen, +
McVicar 1977	*Leucoraja naevus*	57	Demersal	42,5	3,54	8	502,9	3,35	6	502,8	Plymouth, +
Randhawa 2012	*Leucoraja erinacea*	208	Demersal	50	2,27	5	22,6	1,66	4	19,8	*
Randhawa 2012	*Amblyraja radiata*	93	Demersal	80	1,97	6	16,2	1,47	5	13,7	*
Randhawa 2012	*Malacoraja senta*	33	Bathydemersal	60	1,28	4	19,5	1,07	3	19,3	*
Friggens and Brown 2005	*Urolophus halleri*	28	Demersal	27	4,55	13	106,3	4,55	13	106,3	+
Iannacone et al. 2011	*Rhinobatos planiceps*	36	Demersal	85	1,28	4	149,5	0,47	3	0,9	
Caira and Pickering 2013	*Deania calcea*	13	Bathydemersal	96,5	0,69	3	*	0,69	3	*	+
Caira and Pickering 2013	*Etmopterus princeps*	11	Bathydemersal	58,8	0,27	3	*	0,27	3	*	+
Caira and Pickering 2013	*Etmopterus pusillus*	15	Bathydemersal	36,5	0,2	1	*	0,2	1	*	+
Caira and Pickering 2013	*Etmopterus spinax*	23	Bathydemersal	36,5	0,83	3	*	0,83	3	*	+
Caira and Pickering 2013	*Centroscymnus coelolepis*	14	Bathydemersal	101,8	0,71	2	*	0,71	2	*	+
Caira and Pickering 2013	*Centroselachus crepidater*	10	Bathydemersal	72,8	0,2	1	*	0,2	1	*	+
In: Campbell 1983	*Rhinoptera bonasus*	20	Benthopelagic	120	*	11	*	*	*	202	*
In: Campbell 1983	*Raja eglanteria*	37	Demersal	54,5	*	3	*	*	*	42,3	*
In: Campbell 1983	*Dasyatis centroura*	19	Demersal	125	*	15	*	*	*	232	*
In: Campbell 1983	*Leucoraja erinacea*	45	Demersal	37,5	*	2	*	*	*	3,9	*
In: Campbell 1983	*Leucoraja erinacea*	19	Demersal	37,5	*	3	*	*	*	3,7	*
In: Campbell 1983	*Leucoraja erinacea*	84	Demersal	37,5	*	3	*	*	*	2	*
In: Campbell 1983	*Leucoraja ocellata*	51	Demersal	74,5	*	2	*	*	*	10,2	*
In: Campbell 1983	*Leucoraja ocellata*	27	Demersal	74,5	*	3	*	*	*	8,2	*
In: Campbell 1983	*Amblyraja radiata*	11	Demersal	80	*	1	*	*	*	46,8	*

Appendix 1 – Table 1 *continued*

Reference	Species	N	Habitat	(a)	(b)	(c)	(d)	(e)	(f)	(g)	Commentary
In: Campbell 1983	*Amblyraja radiata*	11	Demersal	80	*	2	*	*	*	3,4	*
In: Campbell 1983	*Malacoraja senta*	35	Bathydemersal	60	*	2	*	*	*	6,8	*
In: Campbell 1983	*Torpedo nobiliana*	13	Benthopelagic	40	*	2	*	*	*	27,8	*
In: Campbell 1983	*Prionace glauca*	11	Pelagic-Oceanic	195	*	4	*	*	*	2083	*
In: Campbell 1983	*Mustelus canis*	27	Demersal	100	*	3	*	*	*	38,2	*
Costa et al. 2014	*Centrophorus squamosus*	69	Bathydemersal	111,4	0,25	2	1,2	0,25	0	1,2	

Appendix 1 – Table 2

Species	N	Habitat	(a)	(b)	(d)	(e)	(f)	(g)	Commentary
Isurus oxyrinchus	39	Pelagic-Oceanic	143,9	1,85	58,1	1,41	7	54,3	*
Prionace glauca	144	Pelagic-Oceanic	189,825	2,34	2,34	2,34	3,75	799	
Lamna nasus	11	Pelagic-Oceanic	175	2,36	87,1	1,91	4	81,3	*
Mustelus punctulatus	188	Demersal	78,2	1,35	23,2	0,2	9	0,6	*
Mustelus mustelus	15	Demersal	101,1	1,4	25,1	0,27	5	0,7	*
Mustelus schmitti	20	Demersal	63,5	3,2	36,6	3,2	6	36,6	*
Mustelus canis	76	Demersal	83	2,14	34,7	2,14	3,5	36,45	*
Squalus acanthias	728	Demersal	85,19	0,95875	0,95	5,76	3,5	4,39	
Scyliorhinus canicula	101	Demersal	56,33	1,34	1,17	0,037	3,33	0,067	*
Etmopterus spinax	119	Bathydemersal	29,8	0,955	5,97	0,74	4	2,3	
Etmopterus princeps	11	Bathydemersal	58,8	0,27	*	0,27	3	*	*
Etmopterus pusillus	15	Bathydemersal	36,5	0,2	*	0,2	1	*	*
Deania calcea	13	Bathydemersal	96,5	0,69	*	0,69	3	*	*
Centroscymnus coelolepis	14	Bathydemersal	101,8	0,71	*	0,71	2	*	*
Centroselachus crepidater	10	Bathydemersal	72,8	0,2	*	0,2	1	*	*
Rhinobatos planiceps	36	Demersal	85	1,28	149,5	0,47	4	0,9	*
Rhinoptera bonasus	20	Benthopelagic	120	*	*	*	11	202	*
Dasyatis centroura	19	Demersal	125	*	*	*	15	232	*
Amblyraja radiata	115	Demersal	80	1,97	16,2	1,47	3	21,3	
Malacoraja senta	68	Bathydemersal	60	1,28	19,5	1,07	3	13,05	
Urolophus halleri	28	Demersal	27	4,55	106,3	4,55	13	106,3	*
Raja undulata	74	Demersal	33	3,24	27	2,99	9	26,5	*
Raja microocellata	52	Demersal	50	3,17	83	3,04	11	82,7	*
Raja brachyura	60	Demersal	52,5	1,34	50,7	1,27	11	50,6	*

Appendix 1 – Table 2 *continued*

Species	N	Habitat	(a)	(b)	(d)	(e)	(f)	(g)	Commentary
Raja eglanteria	37	Demersal	54,5	*	*	*	3	42,3	*
Leucoraja naevus	263	Demersal	42,5	4,385	322,8	4,24	9	322,6	
Leucoraja erinacea	177	Demersal	40,62	2,27	22,6	1,66	3,25	7,35	
Torpedo nobiliana	13	Benthopelagic	40	*	*	*	2	27,8	*
Centrophorus squamosus	69	Bathydemersal	111,4	0,25	1,2	0,25	2	1,2	*

Appendix 1 – References

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Chapter 04 – Determinants of diversity and composition of the tapeworm fauna of blue sharks (*Prionace glauca*): a geographic and host-specificity analysis

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4.1 Abstract

Over the last two decades there has been an effort to unveil community patterns of elasmobranch cestodes at a macroecological scale. In contrast, analyses at infracommunity level are still very scarce. In this work the helminth community parasitizing 37 blue sharks (*Prionace glauca*), both juveniles and adults, is described and compared with previous studies, performing a global assessment of the relative role of the ecological and evolutionary factors in structuring the local tapeworm assemblages of blue sharks. Shark specimens studied came from two different non previously surveyed regions: the Northeast Atlantic Ocean (Galicia, Spain) and the Western Mediterranean (Valencia, Spain). Helminths from nine different taxa, of which four presented adult specimens and have already been describe infecting blue sharks, were identified: *Platybothrium auriculatum*, *Prosobothrium armigerum*, *Anthobothrium caseyi* and *Molicola horridus*. The five other taxa only could be identified to the level of genus, order or family because of their poor condition. All six previous studies providing infracommunity data about blue sharks encountered a group of four cestode species, thus described here as the 'core' community parasitizing blue sharks worldwide. Other cestode infections in blue sharks are discussed and a checklist of adult cestodes infecting the spiral valve of blue sharks is provided. At a global geographic scale, tapeworm communities of blue sharks were composed by 10 cestode taxa, 7 of which (those belonging to the Phyllobothriidea, Onchoproteocephalidea and "Tetraphyllidea") are exclusive to this host species and share two fundamental traits: their cosmopolitan distribution and their belonging to cestode genera that typically infects carcharhinids. Thus showing that for blue sharks,

and probably other elasmobranchs, the influence of ecological factors upon their tapeworm communities is highly constrained by historical factors, i.e., the strong host specificity of most of their tapeworm species.

4.2 Introduction

Cestodes make up the bulk of the intestinal helminths infecting sharks (Caira and Healy 2012, Caira and Jensen 2017) and represent, for several reasons, an ideal system to investigate the role of ecological and evolutionary factors in providing structure to parasite communities (Randhawa and Poulin 2010, Rasmussen and Randhawa 2018). First, there is substantial diversity within this parasite assemblage; over 650 spp. of tapeworms from c. 180 genera and 8 orders have hitherto been reported in sharks, and the estimated diversity is close to 1500 spp. (Caira and Jensen 2017). Second, most of these species (with the exception of those belonging to the Trypanorhyncha) exhibit a high degree of host specificity, infecting a single species or a few closely-related host species (Caira and Jensen 2014). Third, since cestodes are trophically-transmitted, the contacts of infective stages with sharks must be driven by both the relative degree of exploitation of the food web by these parasites (i.e., the number of intermediate and paratenic hosts they use) and by the dietary breath of their final shark hosts (Palm and Caira 2008, Rasmussen and Randhawa 2018). In summary, both evolutionary (e.g., specificity) and ecological (e.g., passive contacts through host' diet) elements could play a variable role in defining the composition and diversity of tapeworm assemblages of sharks depending on the scale of analysis.

Over the last two decades, there has been an effort to unveil such community patterns at a global (i.e., macroecological) scale. Focusing on the component community level (i.e. samples of shark species as a whole), Randhawa and Poulin (2010) found few consistent host effects, although tapeworm species richness was significantly influenced by shark size after correcting for host phylogenetic effects. In a recent, more detailed re-analysis, a robust pattern did emerge, i.e., the diet breadth of each shark species was a strong predictor of its tapeworm species richness, with a secondary influence of other host features such as size, trophic level, taxonomic distinctness of diet, or latitudinal or depth range (Rasmussen and Randhawa 2018).

In contrast, analyses at host individual (i.e. infracommunity) level are still very scarce, mainly because few parasitological surveys of sharks report on proper infracommunity parameters (e.g., mean species richness, diversity indices, or mean abundance of each tapeworm species per host). Based on a limited dataset available, Penadés-Suay et al. (2017) recently investigated to what extent the potential “dilution” effects of infective stages of tapeworms in the pelagic-oceanic habitat could result in comparatively species-poor, low-abundance infracommunities in large oceanic sharks, regardless of the richness in the component community locally available. These authors failed to detect this specific host habitat effect, but their literature search incidentally revealed a striking finding, i.e., there were just 4 species of sharks (for a global diversity of c. 500 spp.) for which quantitative surveys of the whole tapeworm fauna had been carried out in at least two localities. This is unfortunate because the comparison of local parasitological surveys at a wide geographical range, with correspondingly varied environmental conditions, could shed much light on the ecological and evolutionary determinants of richness and composition at both component community and infracommunity levels.

The blue shark, *Prionace glauca* (Linnaeus, 1758), is likely the shark species for which more quantitative data exists on its tapeworm fauna at a global scale. Complete surveys on cestodes have been carried out in the Mediterranean Sea (Euzet 1959), the North Atlantic (Curran and Caira 1995, Henderson et al. 2002), and the North (Méndez and Galván-Magaña 2016, Preti et al. 2020) and South (Escalante 1986) Pacific. In addition, a great deal of parasitological records is available from the whole distribution range of this species (Appendix 1). Some of these studies have provided interesting insight on the microhabitat distribution of tapeworms within the spiral valve (Curran and Caira 1995), tapeworm species associations (Henderson et al. 2002), or the role of host specificity in imparting similarity to faunal composition among localities (Méndez and Galván-Magaña 2016). What is lacking, however, is a comprehensive comparative analysis that accounts for the similarities and differences in composition and diversity of the tapeworm fauna, especially at infracommunity level, across localities.

In this regard, the blue shark is also an interesting species for two reasons. First, it is a highly migratory, oceanic species which is widespread in temperate and tropical waters worldwide (Compagno 2001). Individual blue sharks typically perform large-scale movements, covering thousands of kilometres within a few months or even weeks (Vandeperre et al. 2014, Kai and Fujinami 2020), although substantial inter-individual variability in linear distances covered may occur (see, e.g., Stevens et al. 2010). Second, blue sharks are generalist predators whose diet may include, not only a number of teleost and cephalopod species, but also occasionally cetaceans, birds and crustaceans (Kohler 1987, Henderson et al. 2001, Biton-Porsmoguer et al. 2017, and references therein). The specific diet composition has been observed to change substantially among localities, likely reflecting the relative availability of prey (Markaida and Sosa-Nishizaki 2010). Thus, the tapeworm communities of blue sharks would theoretically be driven by factors tending to promote geographic similarity (i.e., a high host vagility; a narrow specificity typical from cestodes of sharks) or differentiation (a circumglobal host's geographical distribution; local variation of prey composition affecting host-parasite contacts).

Blue sharks are regularly caught by Spanish long-line fisheries operating in waters off Galicia, North East Atlantic, and Valencia, Western Mediterranean (Mejuto et al. 2009a, 2009b). This scenario provided us with the opportunity, firstly, to investigate in this study the intestinal helminth fauna of blue sharks in two new geographic areas, and to make a quantitative comparison of infracommunity data between them. Secondly, we used these data, along with those obtained for previous parasitological surveys on blue sharks worldwide, to perform a global assessment of the relative role of the ecological and evolutionary factors in structuring the local tapeworm assemblages of blue sharks.

4.3 Material and Methods

Sample collection

Sampling of blue sharks was opportunistic and included both animals stranded and captured by long-line fisheries (Table 1). The examination and collection of the intestines of the sharks captured by fisheries had to be carried out quickly, before the fish auction began, thus body length measurements of several individual fish could not always be taken (Table 1). The intestine of 16 individuals were obtained at the port of Vigo (Galicia, Spain); this sample, which we will hereafter refer to as “Galicia”, was caught by long-line fisheries operating in the NE Atlantic Ocean, between 40ºN 20ºW and 35ºN 10ºW; 13 sharks were caught in October, 2012, and three in May, 2013. Another sample of 13 sharks was caught in the W Mediterranean, in waters off the coast of Valencia (coordinates: 39°38'N 0°44'E); this sample will be identified as Valencia (C). Finally, 8 sharks were found stranded along the coast of Valencia and collected by the Valencian Community Stranding Network during the period 2013-2021; this sample will be named as Valencia (S). Blue sharks were considered juvenile when measuring less than 180 cm (males) and 220 cm (females), and adults otherwise (Compagno, 1984).

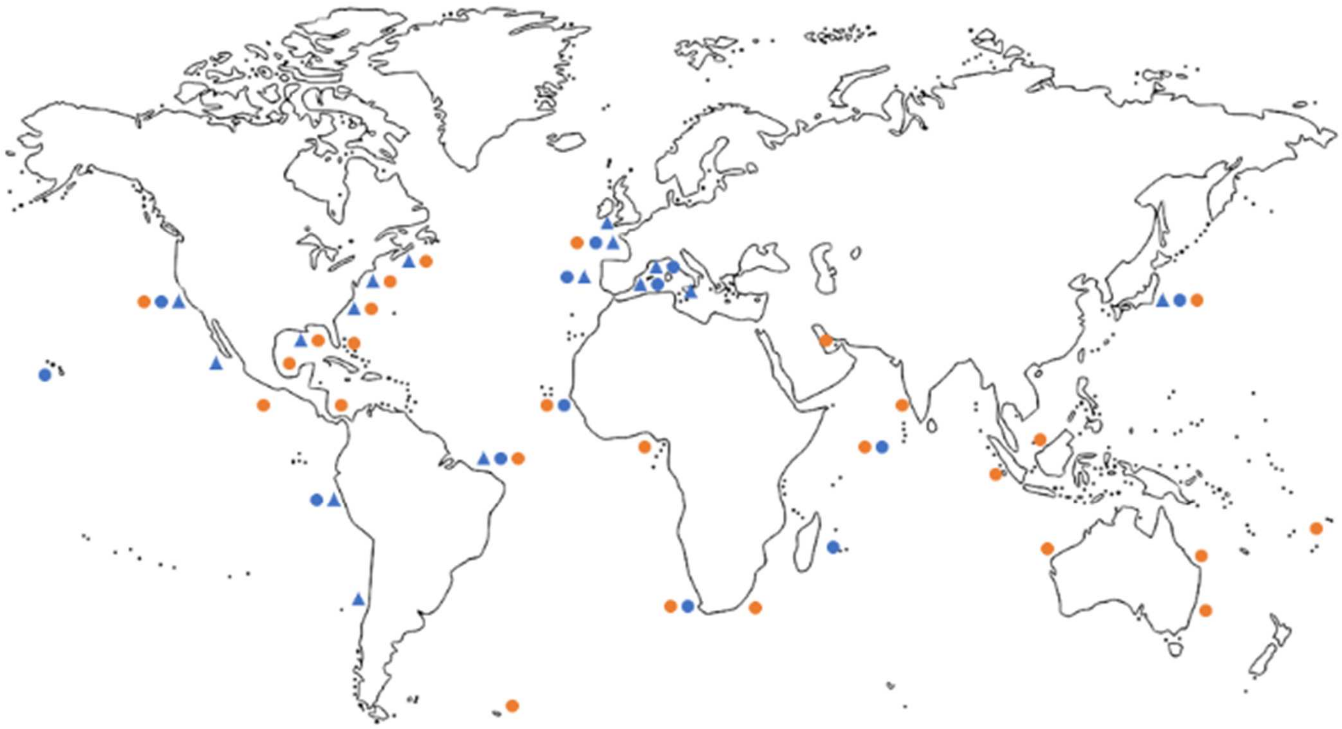


Fig. 1. Map showing the locations where adult cestode species found in the spiral valve of *Prionace glauca* have been described (see references in Appendix 1). Blue triangles indicate 'core species' found only in *P. glauca* (see text) and circles indicate species of the Trypanorhyncha that have been described infecting *P. glauca*: blue circles for when *P. glauca* acted as host and orange circles for when other shark species acted as hosts.

Table 1. Sampling features of blue sharks, Prionace glauca, collected in Iberian waters. TL: Total length (cm). Note that only the range of TL was available for the sample of sharks captured in the western Mediterranean.

	Galicia	**W Mediterranean (stranded)**	**W Mediterranean (captured)**	**Total**
n	16	8	13	37
Mean TL (SD)	202 (149.5-254.5)	247 (175.9-318.1)	[135-185]	[90-323]
[range]	[130-284]	[90-323]		
no. males (%)	12 (75.0)	4 (50.0)	11 (84.6)	27 (72.8)
no. juveniles (%)	6 (37.5)	1 (12.5)	13 (100)	20 (54.1)

Due to logistic constrains, the intestine of all sharks had to be stored at -20ºC for later analysis in the laboratory. After thawing, each intestine was rinsed with tap water under a 0.02 mm mesh and solid contents were collected. The intestine wall was also thoroughly examined for attached helminths. Parasites were collected under a stereomicroscope, washed in 0.9% saline, examined to describe their main features, counted, and fixed and preserved in 70% ethanol. Cestodes were stained with iron acetocarmine (Georgiev et al. 1986), and mounted for observation. Specimens were identified based on Khalil et al. (1994) and specific references (Healy 2003, Palm 2004, Ruhnke and Caira 2009, Ruhnke 2011). Voucher specimens are deposited at the Natural History Museum of London with accession numbers: *Anthobothrium caseyi*, XXXX.X.XX.X-X; Tetraphyllidea sp, XXXX.X.XX.X-X; *Platybothrium auriculatum*, XXX.X.XX.X-X; *Prosobothrium armigerum*, XXXX.X.XX.X-X; *Molicola horridus*, XXXX.X.XX.X-X. Additional material can be found at the Collection of the Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Spain.

Statistical analyses

For each helminth taxon, we recorded its prevalence (percentage of infected hosts in the sample), mean intensity (average number of worms in the sample of hosts infected with this taxon), and mean abundance (average number of worms in the total sample of hosts) following Bush *et al.* (1997). Total helminth abundance, species richness, and Brillouin's index of diversity were used as descriptors of infracommunities (i.e., helminth communities of individual hosts). Species richness (i.e. the number of helminth taxa per individual shark) and Brillouin's diversity index were considered as infracommunity descriptors. The 95% confidence interval (CI) for prevalence was calculated with Sterne's exact method (Reiczigel 2003). The 95% CI for mean abundance and mean intensity of each helminth taxon, as well as for mean species richness and mean Brillouin's index, were obtained with the bias-corrected and accelerated bootstrap method using 10,000 replications (Rózsa *et al.* 2000). Kruskal-Wallis tests were used to see differences between shark samples in the abundance of 5 cestode taxa (*A. caseyi*, Tetraphyllidea sp., *P. auriculatum*, *P. armigerum*, *M. horridus*) and two infracommunity descriptors (species richness and Brillouin's index of diversity).

To globally compare the infracommunity diversity and composition of cestode faunas infecting blue sharks around the world, we searched all parasitological surveys for which at least the prevalence of all tapeworm taxa found in the intestine was reported. These surveys generally did not provide data on mean species richness per host, thus we calculated this parameter by summing up prevalences (expressed as decimals) of all intestinal tapeworm taxa in each sample (Penadés et al. 2017). Differences of prevalence of specific taxa among localities were tested with exact Chi-Square tests.

We searched bibliography in the Shark References database (https://shark-references.com/species/host-parasites-list) and the Host Parasite Database of the Natural History Museum (https://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/database/index.jsp) to compile all existing records of adult cestodes infecting blue sharks. The references of each publication found were also checked for potentially missed records. We selected records in which tapeworms were identified to species level and in the spiral valve (not the stomach or the liver), excluding taxa that had been identified only to genus level or above because they were little informative to explore specificity patterns; moreover, these taxa typically concerned sexually immature forms for which blue sharks could act as putative non-hosts. Taxonomic nomenclature was updated when necessary using appropriate literature. For all compiled species, and also for their valid congeneric counterparts, we listed all hosts reported in the literature. The resulting inventory of host-parasite associations was placed on a cladogram of the elasmobranchs (adapted from: Iglésias et al. 2005, Naylor et al. 2012, Amaral et al. 2018) and visually interpreted for specificity patterns.

The software PERMANOVA+ for PRIMER (Anderson et al. 2008) was used to calculate infracommunity parameters, the free software ‘Quantitative Parasitology’ (Reiczigel *et al.* 2019) to set the 95% CIs of infection parameters, and the statistical package SPSS v. 22 for the remaining analyses (SPSS Inc., Chicago, IL). Statistical significance was set at $P<0.05$.

4.4 Results

A total of 2726 helminth specimens were collected in the spiral intestine of the 37 blue sharks, belonging to 9 cestode taxa (Table 2). All but one 278 cm-long male shark from Galicia harbored at least one cestode species. Adult specimens were detected in the sample of *A. caseyi*, *P. auriculatum*, *P. armigerum* and *M. horridus*, but not in the case of Tetraphyllidea spp. and Phyllobothriinae sp. 1 and 2. Only the scolex could be collected for single individuals of *Scyphophyllidium* sp. and Trypanorhyncha sp. and, therefore, it was not possible to confirm whether they were sexually mature.

Five cestode taxa exhibited a prevalence > 10%, of which four, *A. caseyi*, *P. auriculatum*, *P. armigerum* and Tetraphyllidea sp., were shared between the three blue shark samples, and one, *M. horridus*, occurred in both Galicia and Valencia (S) (Table 2). The remaining four cestode taxa were found only in Galicia (Table 2). The abundance of 4 of the 5 cestode taxa with adult specimens differed significantly between host samples (Table 3). The *post hoc* comparison revealed that the pattern of differences was not consistent in all taxa; the abundance of *P. auriculatum* and *P. armigerum* was significantly higher in Galicia compared with Valencia (C), whereas the abundance of *A. caseyi* was highest and smallest in the two samples from Valencia, and that from *M. horridus* was significantly higher in Valencia (S) compared with the two other samples (Table 3).

In contrast, we did not detect significant differences in infracommunity species richness among the shark samples (Table 3). Considering all cestode taxa, mean species richness (95% CI) was 2.69 (2.10-3.31) for Galicia, 1.75 (1.13-2.50) for Valencia (S) and 2.46 (2.00-2.92) for Valencia (C); when only species with adult specimens were selected, these figures were 2.13 (1.63-2.63), 1.63 (1.13-2.13) and 2.08 (1.72-2.39), respectively. In the case of Brillouin's index, significant differences did show up only when all cestode taxa were considered, with values being 0.59 (0.41-0.78), 0.19 (0.04-0.34) and 0.50 (0.36-0.63), respectively. For the subset of cestode species with adult specimens, values of Brillouin's index were 0.42 (0.27-0.56), 0.17 (0.04-0.33) and 0.43 (0.31-0.54).

Table 2. Prevalence (P) expressed as percentage, and mean intensity (MI) of the cestode taxa found in the spiral valve of blue sharks, *Prionace glauca*, collected in Iberian waters. Values between brackets and parentheses indicate ranges and 95% ICs, respectively.

	Galicia (n=16)		Valencia (stranded) (n=8)		Valencia (captured) (n=13)		TOTAL (n=37)	
	P	MI	P	MI	P	MI	P	MI
Tetraphyllidea								
Anthobothrium caseyi	62.5	11.6 [3-24]	37.5	183 [5-519]	100	87.7 [4-332]	70.3	69.4 [3-519]
	(37.2-82.2)	(7.1-17.1)	(11.1-71.1)	(5.0-354.0)	(77.5-100)	(53.7-156.0)	(54.1-82.8)	(37.9-139)
Tetraphyllidea fam. gen. sp.	31.2	13.2 [3-25]	12.5	19	38.5	14.2 [2-41]	29.7	14.2 [2-41]
	(13.2-56.4)	(6.2-20.2)	(0.6-50.0)		(16.6-65.8)	(5.4-28.8)	(17.2-45.9)	(9.0-22.7)
Onchoproteocephalidea								
Platybothrium auriculatum	62.5	9.9 [3-27]	12.5	5	23.1	3.3 [1-8]	37.8	8.1 [1-27]
	(37.2-82.2)	(5.4-16.4)	(0.6-50.0)		(6.6-52.0)	(1.0-5.7)	(23.4-54.1)	(4.7-13.1)
Prosobothrium armigerum	68.8	18.5 [1-143]	37.5	21 [12-34]	84.6	26.9 [8-63]	67.6	22.5 [1-143]
	(43.6-86.8)	(4.5-68.4)	(11.1-71.1)	(12.0-28.3)	(56.6-97.2)	(19.3-37.4)	(51.3-81.5)	(14.8-41.9)
Phyllobothriidea								
Scyphophyllidium sp.	6.2	1	-	-	-	-	2.7	1
	(0.3-30.5)						(0.1-14.4)	
Phyllobothriinae gen. sp. 1	6.3	6	-	-	-	-	2.7	6
	(0.3-30.5)						(0.1-14.4)	
Phyllobothriinae gen. sp. 2	6.3	10	-	-	-	-	2.7	10
	(0.3-30.5)						(0.1-14.4)	
Trypanorhyncha								
Molicola horridus	18.8	3 [1-5]	75	10.3 [3-35]	-	-	24.3	7.9 [3-35]
	(5.3-43.6)	(1.0-4.3)	(36.5-95.4)	(4.3-24.7)			(13.0-40.5)	(3.9-18.6)
Trypanorhyncha fam. gen. sp.	6.2	1	-	-	-	-	2.7	1
	(0.3-30.5)						(0.1-14.4)	

Table 3. Results of the Kruskal-Wallis test for differences in abundance of 5 cestode taxa, and two infracommunity descriptors, between three samples (corresponding to 2 degrees of freedom) of blue sharks, *Prionace glauca*, collected from Iberian waters, captured in Galicia (n= 16) and Valencia (C) (n= 13), and stranded along the coast of Valencia (S). The comparison of species richness and diversity are made considering all cestode taxa and only the species for which at least one adult worm was found.

Descriptor	**H**	**p**	***Post hoc* difference (<0.05)**
Abundance			
Anthobothrium caseyi	14,733	0.001	Valencia (C) vs. Valencia (S) and Galicia
Platybothrium auriculatum	8,296	0.016	Valencia (C) vs. Galicia
Prosobothrium armigerum	7,606	0.022	Valencia (C) vs. Galicia
Scyphophyllidium sp.	1,169	0.559	
Molicola horridus	16,633	<0.001	Valencia (S) vs. Valencia (C) and Galicia
Infracommunity			
All species			
Species richness	4.285	0.117	
Brillouin's index of diversity	8.584	0.014	Valencia (S) vs. Galicia
Species with adult specimens			
Species richness	2.215	0.330	
Brillouin's index of diversity	5.228	0.073	

Aside from the present study, we found 6 surveys reporting on the tapeworm fauna of the spiral intestine of blue sharks; 2 and 1 from the North and South Pacific Ocean, respectively, 2 from the North Atlantic Ocean and 1 from the Mediterranean Sea (Table 4). Overall, 11 nominal taxa were reported, and there were significant differences between the 8 host samples in all of them (exact Chi-Square, p< 0.05). Only one species, i.e., *Platybothrium auriculatum*, was shared among all host samples, although with obvious differences in prevalence and mean intensity (Table 4). Species of *Anthobothrium* (particularly *A. caseyi* except in one case of undetermined identity), *Prosobothrium* (*P. armigerum* or *P. japonicum*) were found in all but one sample, and species of *Scyphophyllidium* (particularly *S. prionacis* except in one case of undetermined identity) in all but two samples. Two other taxa, i.e., *Phoreiobothrium lasium* and *Molicola horridus*, occurred more idiosyncratically (Table 4). Although mean infracommunity species richness ranked from 0.69 to 3.67 spp./host, values were remarkably similar in 6 of the 8 surveys, around 2-2,7 spp./host (Table 4).

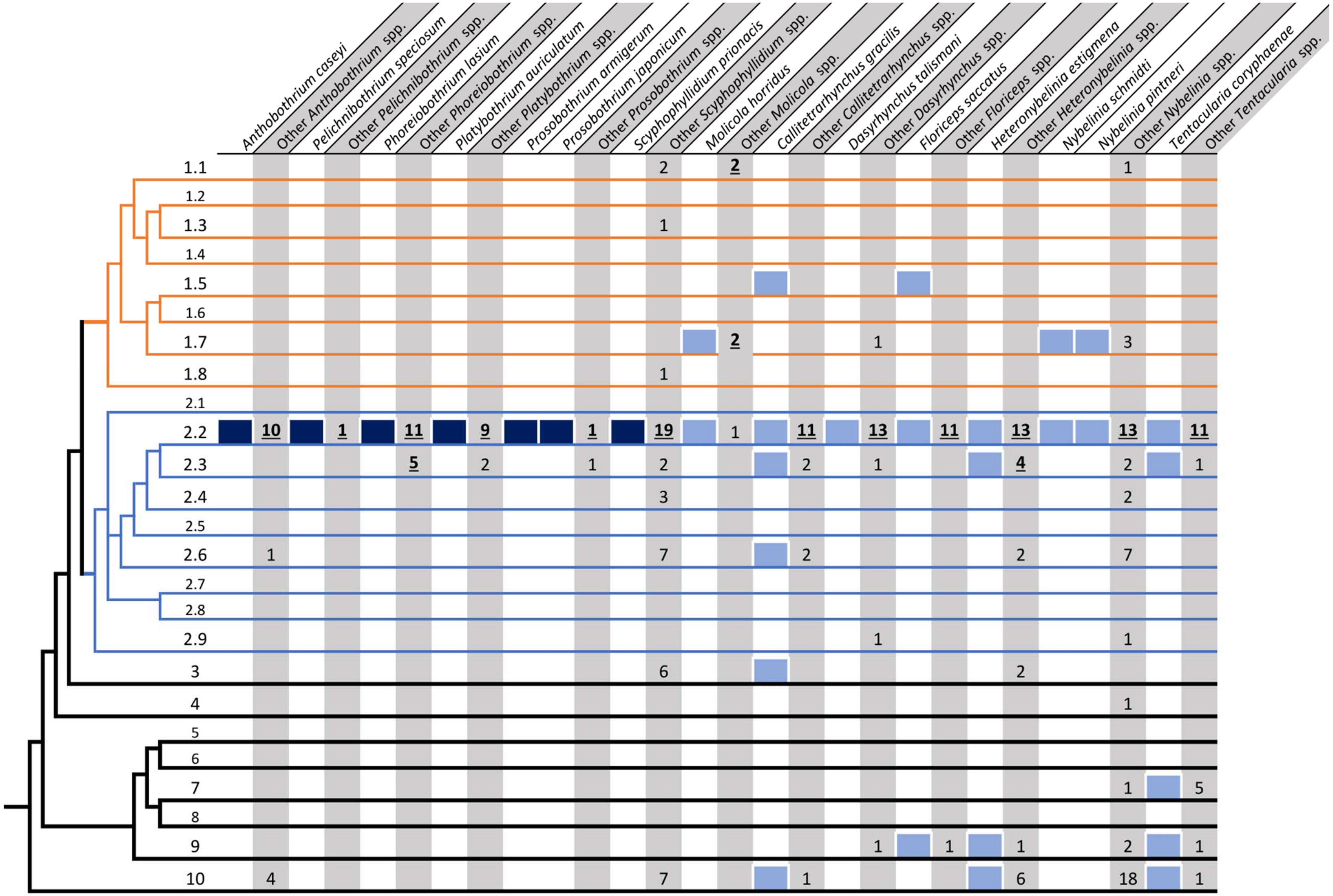
Table 4. Comparison of infection parameters, and species richness, of cestode fauna found in the spiral valve of blue sharks, *Prionace glauca*, collected all over the world. na: Information not available.

Region (Reference) [n]	NE Pacific (1) [27]		NE Pacific (2) [18]		SE Pacific (3) [8]		NW Atlantic (4) [12]		NE Atlantic (5) [159]		NE Atlantic (6) [16]		W Mediterranean (7) [22]		W Mediterranean (6) [21]	
	P	**IM**	**P**	**IM**	**P**	**IM**	**P**	**IM**	**P**	**IM**	**P**	**IM**	**P**	**IM**	**P**	**IM**
Anthobothrium																
A. caseyi	59	70	-	-	-	-	92	216	13	9	63	12	95	na	76	106
Anthobothrium sp.	-	-	78	69	-	-	-	-	-	-	-	-	-	-	-	-
Platybothrium auriculatum	85	71	67	12	100	na	100	401	13	11	63	10	23	na	19	4
Prosobothrium																
P. armigerum	-	-	-	-	-	-	92	39	43	18	69	19	23	na	67	26
P. japonicum	56	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prosobothrium sp.	-	-	67	28	-	-	-	-	-	-	-	-	-	-	-	-
Scyphophyllidium																
S. prionacis	67	80	-	-	100	na	83	354	-	-	-	-	55	na	-	-
Scyphophyllidium sp.	-	-	22	39	-	-	-	-	-	-	6	1	-	-	-	-
Phoreiobothrium lasium	-	-	-	-	-	-	-	-	-	-	-	-	9	na	-	-
Molicola																
M. horridus	-	-	-	-	-	-	-	-	-	-	19	3	-	-	29	10
Molicola sp.	-	-	11	3	-	-	-	-	-	-	-	-	-	-	-	-
Species richness	2.66		2.45		2.00		3.67		0.69		2.10		2.10		1.91	

References: 1. Méndez and Galván-Magaña (2016); 2. Preti et al. (2020); 3. Escalante (1986); 4. Curran and Caira (1995); 5. Henderson et al. (2002); 6. This study; 7. Euzet (1959).

We found 93 records of 15 intestinal cestodes infecting blue sharks that had been identified to species level (Appendix 1). A total of 7 species, including 1 of "Tetraphyllidea" (*A. caseyi*); 4 of Onchoproteocephalidea (*Pla. auriculatum*, *Pro. armigerum*, *Pro. japonicum* and *Phoreiobothrium* sp. [= *P. lasium*]) and 2 of Phyllobothriidea (*Pelichnibothrium speciosum* and *S. prionacis*), were reported only from blue sharks. For all these species, records encompassed at least the Pacific and Atlantic / Mediterranean basins, except *Phoreiobothrium* sp. (= *P. lasium*), for which records from the Pacific Ocean were not found (Fig. 1, Appendix 1). In contrast, the 8 spp. of Trypanorhyncha ever found in blue sharks were also reported from a wide range of elasmobranchs (from 1 to 19 spp. depending on the species), mainly of the family Carcharhinidae (Appendix 1). These species are also geographically widespread in tropical and temperate waters worldwide (Fig. 1). Of note, one of the two species of *Nybelinia* infecting blue sharks have been reported only in the shortfin mako shark, *Isurus oxyrinchus* (Lamnidae), and the other in *I. oxyrinchus* and the milk shark, *Rhizoprionodon acutus* (Carcharhinidae).

At genus level, the literature search revealed the following patterns (Fig. 2, Appendix 2): the monospecific genus *Pelichnibothrium* was exclusive to blue sharks, *Prosobothrium* (3 spp.) was shared with Sphyrnidae (a single species), and *Anthobothrium* (8 spp.), *Platybothrium* (10 spp.) and *Phoreiobothrium* (18 spp.), mostly with other Carcharhiniidae. In the case of *Scyphophyllidium* (51 spp.) and most genera of the Trypanorhyncha, the bulk of species were allocated in the Carcharhinidae, but also occurred in a number of other families of sharks and skates (Fig. 2, Appendix 2). An exception was that of *Molicola* (3), whose species only infect Lamniformes and blue sharks.



	Anthobothrium caseyi	Other Anthobothrium spp.	Pelichnibothrium speciosum	Other Pelichnibothrium spp.	Phoreiobothrium lasium	Other Phoreiobothrium spp.	Platybothrium auriculatum	Other Platybothrium spp.	Prosobothrium armigerum	Prosobothrium japonicum	Other Prosobothrium spp.	Scyphophyllidium prionacis	Other Scyphophyllidium spp.	Molicola horridus	Other Molicola spp.	Callitetrarhynchus gracilis	Other Callitetrarhynchus spp.	Dasyrhynchus talismani	Other Dasyrhynchus spp.	Floriceps saccatus	Other Floriceps spp.	Heteronybelinia estigmena	Other Heteronybelinia spp.	Nybelinia schmidti	Nybelinia pintneri	Other Nybelinia spp.	Tentacularia coryphaenae	Other Tentacularia spp.
1.1													2		**2**											1		
1.2																												
1.3													1															
1.4																												
1.5																▨				▨								
1.6																												
1.7														▨	**2**				1					▨	▨	3		
1.8													1															
2.1																												
2.2	■	**10**	■	**1**	■	**11**	■	**9**	■	■	**1**	■	**19**	▨	1	▨	**11**	▨	**13**	▨	**11**	▨	**13**	▨	▨	**13**	▨	**11**
2.3						**5**		2			1		2			▨	2		1			▨	**4**			2	▨	1
2.4													3													2		
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3													6			▨							2					
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5																												
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7																										1	▨	5
8																												
9																			1	▨	1	▨	1			2	▨	1
10		4											7			▨	1					▨	6			18	▨	1

← **Fig. 2.** Specifity of adult cestode taxa infecting intestines of blue sharks, *Prionace glauca*, from the literature. The phylogenetic tree of elasmobranchs (adapted from Iglésias et al. 2005, Naylor et al. 2012a, Amaral et al. 2017), shows families of Lamniforms and Carcharhiniforms, along with the other orders of sharks and, below in a general group, the Batoidea. For species described infecting *P. glauca*: dark blue boxes indicate that the cestode is specific of *P. glauca*, light blue boxes indicate other hosts besides *P. glauca* (see Appendix 2). For genera of species described from *P. glauca*, the boxes indicate number of other hosts described within the family, order or superorder: bold underlined numbers indicate groups that are considered the parasitic genus common hosts(see Appendix 2). In the phylogenetic tree: 1. Lamniforms (in orange: 1.1 Alopiidae 1.2 Odontaspididae 1.3 Pseudocarchariidae 1.4 Megachasmidae 1.5 Carchariidae 1.6 Cetorhinidae 1.7 Lamnidae 1.8 Mitsukurinidae) 2. Carcharhiniformes (in blue: 2.1 Pentanchidae 2.2 Carcharhinidae 2.3 Sphyrnidae 2.4 Hemigaleidae 2.5 Leptochariidae 2.6 Triakidae 2.7 Pseudotriakidae 2.8 Proscylliidae 2.9 Scyliorhinidae) 3. Orectolobiformes 4. Heterodontiformes 5. Squatiniformes 6. Pristiophoriformes 7. Squaliformes 8. Echinorhiniformes 9. Hexanchiformes 10. Batoidea.

4.6 Discussion

In this study we surveyed the intestinal parasites of blue sharks in Iberian waters, where no previous records exist. None of the taxa identified at least to genus level is new for this host species, but as many as 4 tapeworm taxa could only be assigned to sub-familial level at best. A potential concern is therefore, whether freezing of spiral valves could have damaged cestode specimens hampering a proper identification (e.g., Preti et al. 2020). We are aware that freezing of organs is not recommended for taxonomic work on helminths, especially when dealing with delicate forms such as tapeworms. However, sampling of large sharks is often opportunistic and subject to trade-off with the stakeholders (fishers, staff of stranding networks). Perhaps not surprisingly, other parasitological surveys on blue sharks have also dealt with frozen samples (Henderson et al. 2002, Preti et al. 2020). Fortunately, the tapeworms from this study that could only be assigned to coarse taxonomic groups contained just immature specimens lacking diagnostic traits and for which the blue shark are putative non-hosts. We interpret that these immature forms are likely specific to other elasmobranchs and do not reproduce in blue sharks; thus, they could be considered as accidental parasites such as, e.g., *Anisakis* spp. are in other sharks (Penadés-Suay et al. 2017).The degree of preservation of samples of the remaining tapeworm taxa, all containing adults, allowed reliable specific identifications (see below) except for *Scyphophyllidium* sp. for which a single scolex could be collected. In any event, the voucher specimens deposited at the Natural History Museum of London will afford researchers further taxonomic re-examination if necessary, e.g., via molecular markers.

The “true” tapeworm communities of blue sharks in Iberian waters were thus composed of 3-5 species (depending on whether *Scyphophyllidium* sp. is included). Three species were common to the three host samples analyzed, being cosmopolitan parasites specific to blue sharks (Appendix 1). *A. caseyi* can be differentiated from other congeneric species by their proglottid laciniations, which are approximately as long as wide (Ruhnke and Caira 2009); *Pla. auriculatum*, by the acutely recurved base of the medial hook on the scolex (see Healy 2003), and *Pro. armigerum* by its scolex formed by four glandular sessile discs (Khalil et al. 1994). Two other cosmopolitan species of the order Phyllobothriidea have been reported exclusively in blue sharks, *Scyphophyllidium prionacis* and *Pelichnibothrium speciosum* (Appendix 1), but none of them were verified in this study. The scolex of the specimen assigned to *Scyphophyllidium* sp. superficially resembled that of *S. prionacis* but was in a very poor state of conservation, and the lack of proglottids precluded an unequivocal identification. Finally, we detected specimens of *Molicola horridus* in two of the three shark samples. This species had previously been detected in blue sharks from other Atlantic and Mediterranean localities (Appendix 1), and can be told from other species of the genus by its sequence of 8-10 macrohooks at the base of the tentacles (Palm 2004).

Little geographic signal emerged when we compared the tapeworm assemblages of Atlantic and Mediterranean blue shark samples. This would be at odds with recent evidence showing certain degree of potential isolation of Mediterranean blue shark populations (Leone et al. 2017). First, there were not obvious differences in species composition at component community level. Even if we assume that the specimen of *Scyphophyllidium* collected in Galicia actually is a “true” member of the community, i.e. *S. prionacis*, its absence in the Mediterranean samples could hardly result from a true biogeographic gap, since Euzet (1959) reported *S. prionacis* in other localities from the western Mediterranean with high prevalence. Second, the geographical comparison of species richness or diversity at infracommunity level failed to be significant. Admittedly, the power of tests was low because host sample sizes were small, but we did detect significant differences when looking at infection parameters of most cestode species. However, these individual differences neither show a consistent geographical pattern.

Certainly, sampling heterogeneity could have blurred any potential geographical signal. For instance, *M. horridus* exhibited the highest infections in the Valencia (S) sample, which contained the largest, and presumably oldest, blue shark specimens; infections were intermediate in Galicia, which included a combination of both juvenile and adult sharks; and this parasite did not appear in the Valencia (C) sample, which was composed only of juveniles. It is therefore tempting to suggest that the host size/age influenced the likelihood of infection with *M. horridus*. In fact, this parasite has been reported as plerocercoid in the liver of large pelagic teleosts, including the sunfish, *Mola mola*, and swordfish, *Xiphias gladius* (e.g. Palm 2004, Fernández et al. 2016, Ahuir-Baraja et al. 2017), which are prey of large blue sharks (e.g. Bornatowski and Schwingel 2008, Pope et al. 2010, Markaida and Sosa-Nishizaki, 2010) but that can hardly be consumed by juvenile sharks.

In any event, inter-sampling heterogeneity in infection levels has not only been observed in this study, it is indeed a salient feature of our broad-scale geographical comparison. We observed that infracommunity species richness tended to be similar across localities, but infection levels of all cestode species showed significant, sometimes extreme variations. As expressed by Henderson et al. (2002), this variability seems inevitable because infection rates are determined by a multitude of biotic and abiotic factors. Of particular significance are the local differences in the diet of blue sharks (see, e.g., references in Markaida and Sosa-Nishizaki 2010 and Loor-Andrade et al. 2017), and in the number of intermediate / paratenic hosts available. We know that cephalopods and teleosts are the key prey groups of blue sharks (Markaida and Sosa-Nishizaki 2010, Hernández-Aguilar et al. 2016, Córdova-Zavaleta et al. 2018). Both teleosts and cephalopods have also been reported as hosts for larvae of *Anthobothrium* spp. (Dollfus 1923, Jensen and Bullard 2010, Schwerdt 2015, Tedesco et al. 2020); *Prosobothrium* spp. (Avdeeva 1989, Williams and Bunkley-Williams 1996, González and Kroeck 2000); and *Scyphophyllidium* spp. (Schuhgalter 1992, Gaevskaya and Schuhgalter 1992, Jensen and Bullard 2010). However, it is not possible to morphologically identify the larval stages to species level, except for the Trypanorhyncha (Palm 2004, Palm and Caira 2008) and, therefore, this precluded a quantitative assessment of the potential communities of intermediate / paratenic hosts at a local or even regional scale. In this context it is worth mentioning that as many as one quarter of species for the Trypanorhyncha seems to use only 1-2 prey species as intermediate / paratenic hosts (Palm and Caira 2008). Accordingly, local variation in the consumption of these prey can generate dramatic differences in the infection rates of the definitive host.

At a global geographic scale, tapeworm communities of blue sharks were composed by c. 10 cestode taxa, 7 of which (those belonging to the Phyllobothriidea, Onchoproteocephalidea and "Tetraphyllidea") are exclusive to this host species, corroborating the general pattern of specificity observed for these orders (Caira and Jensen 2014). These exclusive species share two fundamental traits. First, they appear to have a cosmopolitan distribution as their host species. The only exception is the enigmatic *Phoreiobothrium* sp., which has apparently only been cited in the Mediterranean. The species was identified as *P. lasium*, but re-examination of the specimens suggests that it is an exclusive species infecting blue sharks yet to be described (Euzet 1959, Caira et al. 2005). Second, all the cestode species unique to blue sharks belong to genera whose bulk diversity appears in carcharhinids with diverse ecologies.

These patterns would suggest that a coevolved key group of cestode species has geographically "accompanied" the blue sharks with apparently little diversification (with perhaps the exception of *P. japonicum* in the Pacific Ocean). As noted above, blue sharks are highly migratory and exhibit limited genetic structure across populations sampled from disparate oceanic regions (Madigan et al. 2021). Accordingly, this pool of tapeworm species would potentially appear, in any sampling location, with greater or lesser prevalence and intensity, thus providing similarity to infracommunity composition and diversity, such as observed. The additional occurrence of trypanorhynchan cestodes in these communities would be less predictable depending on both the composition of the local elasmobranch community and the patterns of cestode exchange through the food web. Conversely, the quantitative differences in tapeworm faunas across localities would result from (i) the variability of the local transmission rate of each cestode species (which, in part, will depend on the host diet and the density of intermediate / paratenic hosts) and (ii) the mobility of blue sharks with respect to the life span of the parasites. This factor is important because satellite tracking data indicate that blue sharks can travel thousands of kilometres in a few months (Vandeperre et al. 2014, Kai and Fujinami 2020), which means that parasites acquired in a specific region could be transported to very remote sampling areas.

As a final remark it is interesting to note that, for the cestode order with a more catholic pattern of host preference, i.e., the Trypanorhyncha, there are two putative instances of host-switching, i.e., *Molicola horridus* and *Nybelinia schmidti*. Both species reproduce in two phylogenetically unrelated hosts, i.e. the blue shark and the shortfin mako shark, two cosmopolitan species which share prey in a common oceanic habitat. The salient point of this example is that, for blue sharks, and probably other elasmobranchs, the influence of ecological factors upon their tapeworm communities is highly constrained by historical factors, i.e., the strong host specificity of most of their tapeworm species. Such historical idiosyncrasy could explain why only a few generalizations have been found on the ecological factors that provide structure to tapeworm communities of sharks (Randhawa and Poulin 2010, Rasmussen and Randhawa 2018).

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4.9 Supporting information

Appendix 1 Data from studies describing adult cestodes in the spiral valve of blue sharks, *Prionace glauca*, and other hosts described for those parasites in their adult stages and also in the spiral valve.

Appendix 1 – Table 1

"Tetraphyllidea"

Anthobothrium caseyi Key taxonomic reference: Ruhnke and Caira (2009)

	Valid name	Used name	Geographical region	Reference
1	*Anthobothrium caseyi*	*Anthobothrium laciniatum*	*Not included*	Linton (1924)
2	*Anthobothrium caseyi*	*Anthobothrium laciniatum*	NE Atlantic (US)	Riser (1955)
3	*Anthobothrium caseyi*	*Anthobothrium laciniatum* var. *brevicolle*	NE Atlantic (France)	Euzet (1959)
4	*Anthobothrium caseyi*	*Anthobothrium laciniatum* var. *brevicolle*	W Mediterranean (France)	Euzet (1959)
5	*Anthobothrium caseyi*	*Anthobothrium laciniatum*	NW Atlantic (US)	Curran and Caira (1995)
6	*Anthobothrium caseyi*	*Anthobothrium laciniatum*	NW Atlantic (US)	Caira et al. (1999)
7	*Anthobothrium caseyi*	*Anthobothrium laciniatum*	NE Atlantic (Ireland)	Henderson et al. (2002)
8	*Anthobothrium caseyi*		NW Atlantic (US)	Ruhnke and Caira (2009)
9	*Anthobothrium caseyi*		NW Atlantic (US)	Ruhnke and Caira (2009)
10	*Anthobothrium caseyi*		NE Pacific (US)	Ruhnke and Caira (2009)
11	*Anthobothrium caseyi*		NE Pacific (Mexico)	Méndez et al. (2016)
12	*Anthobothrium caseyi*		NE Atlantic (Spain)	This study
13	*Anthobothrium caseyi*		W Mediterranean (Spain)	This study
14	*Anthobothrium* sp.		NE Pacific (US)	Preti et al. (2020)

Appendix 1 – Table 1 *continued*

Onchoproteocephalidea

Platybothrium auriculatum Key taxonomic reference: Healy (2003)

	Valid name	Used name	Geographical region	Reference
15	*Platybothrium auriculatum*		*Not included*	Wagener (1854)
16	*Platybothrium auriculatum*	*Platybothrium baeri*	Mediterranean (Italy)	Euzet (1952)
17	*Platybothrium auriculatum*		NW Pacific (Japan)	Yamaguti (1952)
18	*Platybothrium auriculatum*	*Cylindrophorus posteroporus*	NE Pacific (US)	Riser (1955)
19	*Platybothrium auriculatum*		NE Atlantic (France)	Euzet (1959)
20	*Platybothrium auriculatum*		W Mediterranean (France)	Euzet (1959)
21	*Platybothrium auriculatum*		SE Pacific (Chile)	Carvajal (1974)
22	*Platybothrium auriculatum*		CW Atlantic (Brasil)	Rego&Mayer (1976)
23	*Platybothrium auriculatum*		SE Pacific (Peru)	Escalante (1986)
24	*Platybothrium auriculatum*		NW Atlantic (US)	Curran&Caira (1995)
25	*Platybothrium auriculatum*		NW Atlantic (US)	Olson&Caira (1999)
26	*Platybothrium auriculatum*		NE Atlantic (Ireland)	Henderson et al. (2002)
27	*Platybothrium auriculatum*		NE Pacific (US)	Healy (2003)
28	*Platybothrium auriculatum*		NE Pacific (Mexico)	Healy (2003)
29	*Platybothrium auriculatum*		NW Atlantic (US)	Healy (2003)
30	*Platybothrium auriculatum*		NW Atlantic (US)	Healy (2003)
31	*Platybothrium auriculatum*		NE Pacific (Mexico)	Méndez et al. (2016)
32	*Platybothrium auriculatum*		NE Pacific (US)	Preti et al. (2020)
33	*Platybothrium auriculatum*		NE Atlantic (Spain)	This study
34	*Platybothrium auriculatum*		W Mediterranean (Spain)	This study

Appendix 1 – Table 1 *continued*

Onchoproteocephalidea

Prosobothrium armigerum/japonicum Key taxonomic reference: Risser (1955), Curran and Caira (1995)

	Valid name	Used name	Geographical region	Reference
34	*Prosobothrium armigerum*		? (France)	Joyeux&Baer (1936)
35	*Prosobothrium armigerum*		NE Pacific (US)	Riser (1955)
36	*Prosobothrium armigerum*		NE Atlantic (France)	Euzet (1959)
37	*Prosobothrium armigerum*		W Mediterranean (France)	Euzet (1959)
38	*Prosobothrium armigerum*		SE Pacific (Peru)	Rivera&Sarmiento (1990)
39	*Prosobothrium armigerum*		NW Atlantic (US)	Curran&Caira (1995)
40	*Prosobothrium armigerum*		NE Atlantic (Ireland)	Henderson et al. (2002)
41	*Prosobothrium armigerum*		NE Atlantic (Spain)	This study
42	*Prosobothrium armigerum*		W Mediterranean (Spain)	This study
43	*Prosobothrium japonicum*		NW Pacific (Japan)	Yamaguti (1934)
44	*Prosobothrium japonicum*		NE Pacific (US)	Riser (1955)
45	*Prosobothrium japonicum*		NE Pacific (Mexico)	Méndez et al. (2016)
46	*Prosobothrium* sp.		NE Pacific (US)	Preti et al. (2020)

Appendix 1 – Table 1 *continued*

Onchoproteocephalidea

***Phoreiobothrium* sp.** Key taxonomic reference: Caira et al. (2005)

	Valid name	Used name	Geographical region	Reference
47	*Phoreiobothrium* sp.	*Phoreiobothrium lasium*	NE Atlantic (France)	Euzet (1959)
48	*Phoreiobothrium* sp.	*Phoreiobothrium lasium*	W Mediterranean (France)	Euzet (1959)

Phyllobothriidea

Pelichnibothrium speciosum Key taxonomic reference: Scholz et al. (1998)

	Valid name	Used name	Geographical region	Reference
49	*Pelichnibothrium speciosum*		NW Pacific (Japan)	Yamaguti (1934)
50	*Pelichnibothrium speciosum*		NW Pacific (Japan)	Yamaguti (1952)
51	*Pelichnibothrium speciosum*		W Mediterranean (France)	Euzet (1959)
52	*Pelichnibothrium speciosum*		NW Pacific (Japan)	Yamaguti (1959)
53	*Pelichnibothrium speciosum*	*Prionacestus bipartitus*	SW Indian Ocean	Mete et al. (1996)
54	*Pelichnibothrium speciosum*		W Indian Ocean	Scholz et al. (1998)

Appendix 1 – Table 1 *continued*

Phyllobothriidea

Scyphophyllidium prionacis **Key taxonomic reference:** Ruhnke (1994, 2011),Caira et al. (2020)

	Valid name	Used name	Geographical region	Reference
55	*Scyphophyllidium prionacis*	*Crossobothrium angustum*	NW Atlantic (US)	Linton (1924)
56	*Scyphophyllidium prionacis*	*Phyllobothrium prionacis*	NW Pacific (Japan)	Yamaguti (1934)
57	*Scyphophyllidium prionacis*	*Anthobothrium minutum*	*Not provided*	Guiart (1935)
58	*Scyphophyllidium prionacis*	*Crossobothrium angustum*	NE Pacific (US)	Riser (1955)
59	*Scyphophyllidium prionacis*	*Crossobothrium angustum*	NE Atlantic (France)	Euzet (1959)
60	*Scyphophyllidium prionacis*	*Crossobothrium angustum*	W Mediterranean (France)	Euzet (1959)
61	*Scyphophyllidium prionacis*	*Crossobothrium angustum*	SE Pacific (Peru)	Carvajal (1974)
62	*Scyphophyllidium prionacis*		SW Atlantic (Brasil)	Rego&Mayer (1976)
63	*Scyphophyllidium prionacis*	*Crossobothrium angustum*	SE Pacific (Chile)	Escalante (1986)
64	*Scyphophyllidium prionacis*		NW Atlantic (EEUU)	Curran&Caira (1995)
65	*Scyphophyllidium prionacis*	*Paraorygmatobothrium prionacis*	NW Atlantic (US)	Ruhnke (1994)
66	*Scyphophyllidium prionacis*	*Paraorygmatobothrium prionacis*	NW Atlantic (US)	Ruhnke (1994)
67	*Scyphophyllidium prionacis*		NE Pacific (Mexico)	Mendez et al. (2016)
68	*Scyphophyllidium* sp.		NE Pacific (US)	Preti et al. (2020)
69	*Scyphophyllidium* sp.		NE Atlantic (Spain)	This study

Appendix 1 – Table 1 *continued*

Trypanorhyncha

Callitetrarhynchus gracilis Key taxonomic reference: Heinz and Dailey (1974), Palm (2004)

Valid name	**Used name**	**Geographical region**	**Reference**
70 *Callitetrarhynchus gracilis*	*Callitetrarhynchus gracilis*	NE Pacific (California)	Heinz and Dailey (1974)

Other host species	**Geographical region**	**Reference**	**Comments**
Carcharias sp.	Indian Ocean	Pinto et al. (2006)	
Carcharhinus amblyrhynchoides	SW Pacific (Australia)	Beveridge et al. (2014)	
Carcharhinus amblyrhynchoides	SW Pacific (Australia)	Palm (2004)	
Carcharhinus amboiensis	SW Pacific (Australia)	Palm (2004)	
Carcharhinus dussumieri	Persian Gulf	Haseli et al. (2010)	Used host: *Carcharhinus* cf *dussumieri*
Carcharhinus fitzroyensis	SW Pacific (Australia)	Palm (2004)	
Carcharhinus leucas	SW Pacific (New Caledonia)	Beveridge et al. (2014)	
Carcharinus leucas	Nicaragua	Pinto et al. (2006)	
Carcharinus leucas	Caribbean (Costa Rica)	Watson & Thorson (1976)	
Carcharinus leucas	Gulf of Mexico (Mississippi)	Palm (2004)	
Carcharinus leucas	Costa Rica	Palm (2004)	
Carcharinus leucas	Mexican Gulf (Mexico)	Méndez&Gonzalez (2013)	Used parasite: *Callitetrarhynchus* cf *gracilis*
Carcharhinus limbatus	NW Atlantic (Florida)	Palm&Overstreet (2000)	
Carcharhinus limbatus	Mexican Gulf (Mexico)	Owens (2008)	Used parasite: *Callitetrarhynchus* cf *gracilis*
Carcharhinus melanopterus	SW Pacific (Queensland)	Olson et al. (2001)	In: Palm (2004)
Carcharhinus melanopterus	SW Pacific (Australia)	Beveridge et al. (2014)	
Carcharhinus melanopterus	SW Pacific (Queensland)	Palm (2004)	
Carcharhinus melanopterus	SW Pacific (Australia)	Palm et al. (2009)	
Carcharhinus obscurus	NW Pacific (Japan)	Nakajima&Egusa (1972)	In: Palm (2004)
Carcharhinus obscurus	*Not described*	Yamaguti 1959	Used parasite: *Callotetrarhynchus gracilis*
Carcharhinus obscurus	NW Atlantic (North Carolina)	Linton (1905)	Used parasite: *Rhynchobothrium speciosum*

Appendix 1 – Table 1 *continued*

Trypanorhyncha

Callitetrarhynchus gracilis (continued)

Other host species	**Geographical region**	**Reference**	**Comments**
Carcharhinus sorrah	Persian Gulf	Haseli et al. (2010)	Used host: *Carcharhinus* cf *sorrah*
Dasyatis fluviorum	SW Pacific (Queensland)	Palm (2004)	Used host: *Dasyatis fluviorum*
Lamiopsis tephrodes	IndoWest Pacific and Australia	Schaeffner&Beveridge (2014)	
Mustelus canis	SW Atlantic (Brasil)	Sao Clemente et al. (1989)	
Mustelus canis	SW Atlantic (Brasil)	Sao Clemente et al. (1991)	
Mustelus mosis	Persian Gulf	Mhaisen et al. (2013)	
Negaprion brevirostris	NW Atlantic (Florida)	Yamaguti 1959	Used host: *Hypoprion brevirostris* Used parasite: *Callotetrarhynchus gracilis*
Negaprion brevirostris	NW Pacific (Japan)	Nakajima&Egusa (1972)	In: Palm (2004)
Rhizoprionodon acutus	SW Indic Ocean (S. Africa)	Palm (2004)	
Rhizoprionodon acutus	NW Pacific (Japan)	Nakajima&Egusa (1972)	In: Palm (2004)
Rhizoprionodon acutus	Persian Gulf	Haseli et al. (2010)	
Rhizoprionodon acutus	IndoWest Pacific and Australia	Schaeffner&Beveridge (2014)	
Rhizoprionodon terraenovae	Gulf of Mexico (Mississippi)	Palm (2004)	
Rhizoprionodon terraenovae	NE Atlantic (Senegal)	Palm (2004)	
Sphyrna lewini	Gulf of Mexico (Mississippi)	Palm (1995)	
Sphyrna zygaena	NW Pacific (Japan)	Nakajima&Egusa (1972)	In: Palm (2004)
Triakis scyllium	NW Pacific (Japan)	Bates (1990)	In: Palm (2004)

Appendix 1 – Table 1 *continued*

Trypanorhyncha

Dasyrhynchus talismani Key taxonomic reference: Beveridge and Campbell (1993), Palm (2004)

	Valid name	Used name	Geographical region	Reference
71	*Dasyrhynchus talismani*		NE Atlantic (Senegal)	Dollfus (1935)
72	*Dasyrhynchus talismani*		NE Atlantic (Senegal)	Dollfus (1942)
73	*Dasyrhynchus talismani*		NW Pacific (Japan)	Nakajima&Egusa (1972)

Other host species	Geographical region	Reference	Comments
Carcharhinus brachyurus	SW Pacific (New South Wales)	Beveridge&Campbell (1993)	
Carcharhinus brachyurus	SW Pacific (Australia)	Palm (2004)	
Carcharhinus leucas	NW Atlantic (Nicaragua)	Watson&Thorson (1976)	In: Palm (2004)
Carcharhinus longimanus	NE Pacific (Mexico)	Heinz and Dailey (1974)	
Carcharhinus sp.	Southern Ocean (South Georgia)	Beveridge&Campbell (1993)	
"Shark"	Guinean Gulf (Ghana)	Beveridge&Campbell (1993)	

Appendix 1 – Table 1 *continued*

Trypanorhyncha

Floriceps saccatus Key taxonomic reference: Palm (2004)

	Valid name	Used name	Geographical region	Reference
74	*Floriceps saccatus*		Central Pacific (Kiribati)	Pintner (1929)
75	*Floriceps saccatus*		NW Pacific (Japan)	Yamaguti (1934)
76	*Floriceps saccatus*		NW Pacific (Japan)	Iwata (1939)
77	*Floriceps saccatus*		NE Atlantic (France)	Dollfus (1942)
78	*Floriceps saccatus*		NW Pacific (Japan)	Nakajima&Egusa (1972)
79	*Floriceps saccatus*		SW Atlantic (Brasil)	Knoff et al. (2002)
80	*Floriceps saccatus*		SW Atlantic (Brasil)	Pinto et al. (2006)

Other host species	Geographical region	Reference	Comments
Carcharinus limbatus	NE Pacific (Mexico)	Heinz and Dailey (1974)	
Carcharinus limbatus	California	Pinto et al. (2006)	
Carcharinus obscurus	NW Atlantic (Massachusetts)	Linton (1921)	In: Palm (2004)
Carcharinus obscurus	NW Atlantic (Massachusetts)	Pintner (1929)	In: Palm (2004)
Carcharinus obscurus	NE Atlantic (France)	Dollfus (1942)	
Carcharinus obscurus	NW Pacific (Japan)	Nakajima&Egusa (1972)	In: Palm (2004)
Carcharinus obscurus	NW Atlantic	Pinto et al. (2006)	
Carcharinus plumbeus	NW Pacific (Japan)	Iwata (1939)	In: Palm (2004)
Carcharinus plumbeus	NW Pacific	Pinto et al. (2006)	
Negaprion brevirostris	NE Pacific (Mexico)	Palm (2004)	
Negaprion brevirostris	Mexico	Pinto et al. (2006)	
Notorynchus cepedianus	NE Pacific (Mexico)	Heinz and Dailey (1974)	Used host: *Notorynchus maculatus*
Notorynchus cepedianus	Mexico	Pinto et al. (2006)	Used host: *Notorynchus maculatus*
Carcharias sp.	India	Pinto et al. (2006)	

Appendix 1 – Table 1 *continued*

Trypanorhyncha

Heteronybelinia estigmena Key taxonomic reference: Palm (2004)

	Valid name	**Used name**	**Geographical region**	**Reference**
81	*Heteronybelinia estigmena*	*Heteronybelinia estigmena*	SW Pacific (Australia)	Palm (2004)

Other host species	**Geographical region**	**Reference**	**Comments**
Beringraja binoculata	NW Pacific (California)	Palm (2004)	Used host: *Raja binoculata*
Beringraja inornata	NW Pacific (California)	Palm (2004)	Used host: *Raja inornata*
Beringraja rhina	NW Pacific (California)	Palm (2004)	Used host: *Raja rhina*
Carcharhinus amblyrhynchoides	SW Pacific (Australia)	Palm&Beveridge (2002)	
Carcharhinus amblyrhynchoides	SW Pacific (Australia)	Palm (2004)	
Carcharhinus brevipinna	SW Pacific (New Caledonia)	Beveridge et al. (2014)	
Carcharhinus leucas	IndoPacific (Malasian Borneo)	Borucinska&Caira (2006)	
Carcharhinus leucas	Caribbean (Costa Rica)	Watson & Thorson (1976)	Used parasite: *Nybelinia bisulcata*
Carcharhinus leucas	SW Indic (South Africa)	Palm (1999)	
Carcharhinus leucas	NW Atlantic (Florida)	Palm&Walter (2000)	
Carcharhinus leucas	NW Atlantic (Florida)	Palm (2004)	
Carcharhinus leucas	South Africa	Palm (2004)	
Carcharhinus leucas	Mexico Gulf (Mississippi)	Palm (2004)	
Carcharhinus leucas	IndoWest Pacific and Australia	Schaeffner&Beveridge (2014)	
Carcharhinus limbatus	SW Pacific (Australia)	Palm&Beveridge (2002)	
Carcharhinus limbatus	Mexico Gulf (Mississippi)	Palm (1995)	Used parasite: *Nybelinia alloiotica mihi*
Carcharhinus limbatus	SE Atlantic (South Africa)	Palm (1999)	
Carcharhinus limbatus	NW Atlantic (Florida)	Palm&Overstreet (2000)	Used parasite: *Nybelinia* cf. *bisulcata*
Carcharhinus limbatus	SW Pacific (Australia)	Palm&Beveridge (2002)	
Carcharhinus limbatus	SW Pacific (Australia)	Palm (2004)	
Carcharhinus limbatus	South Africa	Palm (2004)	Used parasite: *Nybelinia* cf. *bisulcata*
Carcharhinus limbatus	Indopacific (Australia)	Schaeffner&Beveridge (2014)	

Appendix 1 – Table 1 *continued*

Trypanorhyncha

Heteronybelinia estigmena (continued)

Other host species	**Geographical region**	**Reference**	**Comments**
Carcharhinus obscurus	NW Atlantic (Massachusetts)	Linton (1889)	Used parasite: *Rhynchobothrium bisulcatum*
Carcharhinus obscurus	NE Atlantic (Senegal)	Palm&Walter (2000)	
Carcharhinus obscurus	NW Atlantic (North Carolina)	Linton (1905)	Used parasite: *Tetrarhynchus bisulcatus*
Carcharhinus obscurus	NE Atlantic (Senegal)	Palm (2004)	
Carcharhinus plumbeus	NW Atlantic (North Carolina)	Linton (1905)	Used parasite: *Tetrarhynchus bisulcatus*
Carcharhinus sp	SW Pacific (Australia)	Beveridge et al. (2014)	
Notorynchus cepedianus	SW Atlantic (Brasil)	Sao Clemente&Gomes (1992)	Used host: *Notorhynchus pectorosus* Used parasite: *Nybelinia bisulcata*
Rhizoprionodon terraenovae	NW Atlantic (North Carolina)	Linton (1905)	Used host: *Scoliodon terraenovae* Used parasite:*Tetrarhynchus bisulcatus*
Sphyrna zygaena	*Not included*	Maccallum (1921)	Used host: *Cestracion zygaena* Used parasite: *Tetrarhynchus bisulcatum*
Sphyrna zygaena	*Not included*	Yamaguti (1959)	Used parasite: *Nybelinia bisulcata*

Appendix 1 – Table 1 *continued*

Trypanorhyncha

Molicola horridus Key taxonomic reference: Palm (2004)

	Valid name	Used name	Geographical region	Reference
82	*Molicola horridus*		Mediterranean	Dollfus (1942)
83	*Molicola horridus*		SW Atlantic (Brasil)	Knoff et al. (2002)
84	*Molicola horridus*		SW Atlantic (Brasil)	Knoff et al. (2004)
85	*Molicola horridus*		NE Atlantic (Spain)	This study
86	*Molicola horridus*		W Mediterranean (Spain)	This study
87	*Molicola* sp.		NE Pacific (California)	Preti et al. (2020)

Other host species	Geographical region	Reference	Comments
Isurus oxyrinchus	SW Atlantic (Brasil)	Diesing (1850)	In: Palm (2004)
Isurus oxyrinchus	SW Atlantic (Brasil)	Diesing (1863)	In: Palm (2004)
Isurus oxyrinchus	SW Atlantic (Brasil)	Pintner (1930)	In: Palm (2004)
Isurus oxyrinchus	NW Pacific (Japan)	Yamaguti (1934)	In: Palm (2004)
Isurus oxyrinchus	Mediterranean	Dollfus (1942)	In: Palm (2004)
Isurus oxyrinchus	NE Pacific (California)	Heinz&Dailey (1974)	
Isurus oxyrinchus	SW Atlantic (Brasil)	Palm (2004)	
Carcharodon carcharias	Indic Ocean (Sri Lanka)	Palm (2004)	

Appendix 1 – Table 1 *continued*

Trypanorhyncha

Nybelinia pintneri Key taxonomic reference: Palm (2004)

	Valid name	Used name	Geographical region	Reference
88	*Nybelinia pintneri*		NW Pacific (Japan)	Yamaguti (1934)
	Other host species	**Geographical region**	**Reference**	**Comments**
	Rhizoprionodon acutus	*Not included*	Bates (1990)	Used host: *Carcharias acutus*
	Rhizoprionodon acutus	Indian Ocean	Pawar (2018)	
	Isurus oxyrhynchus	NE Pacific (California)	Heinz&Dailey (1974)	
	Isurus oxyrhynchus	NE Pacific (Oregon)	Yamaguti (1934)	

Trypanorhyncha

Nybelinia schmidti Key taxonomic reference: Palm (2004)

	Valid name	Used name	Geographical region	Reference
89	*Nybelinia schmidti*		SE Atlantic (South Africa)	Palm et al. (1999)
	Other host species	**Geographical region**	**Reference**	**Comments**
	Isurus oxyrinchus	SW Pacific (Australia)	Palm&Beveridge (2002)	
	Isurus oxyrinchus	Tasmania (Australia)	Palm (2004)	

Appendix 1 – Table 1 *continued*

Trypanorhyncha

Tentacularia coryphaenae Key taxonomic reference: Palm (2004)

	Valid name	Used name	Geographical region	Reference
90	*Tentacularia coryphaenae*		NW Pacific (Japan)	Dollfus (1942)
91	*Tentacularia coryphaenae*		NW Pacific (Japan)	Yamaguti (1934)
92	*Tentacularia coryphaenae*		NW Pacific (Japan)	Yamaguti (1959)
93	*Tentacularia coryphaenae*		SE Pacific (Peru)	Cattan et al. (1979)
94	*Tentacularia coryphaenae*		SW Atlantic (Brasil)	Knoff et al. (2002)
95	*Tentacularia coryphaenae*		SW Atlantic (Brasil)	Knoff et al. (2004b)
96	*Tentacularia coryphaenae*		NW Atlantic (Massachusetts)	Borucinska&Dunham (2000)
97	*Tentacularia coryphaenae*		NW Atlantic (New York)	Borucinska&Dunham (2000)

Other host species	Geographical region	Reference	Comments
Carcharhinus falciformis	IndoWest Pacific and Australia	Schaeffner&Beveridge (2014)	
Carcharhinus galapagensis	NE Pacific (Hawai)	Carvajal et al. (1976)	
Carcharhinus limbatus	NE Pacific (Mexico)	Heinz&Dailey (1974)	Used parasite: *Tentacularia coryphaena*
Carcharhinus longimanus	SW Atlantic (Brasil)	Rego (1977)	In: Palm (2004), Alves (2017), Muniz-Pereira (2019)
Carcharhinus longimanus	NE Pacific (Mexico)	Heinz&Dailey (1974)	Used parasite: *Tentacularia coryphaena*
Carcharhinus longimanus	SW Atlantic (Brasil)	Knoff et al. (2002)	
Carcharhinus longimanus	SW Atlantic (Brasil)	Knoff et al. (2004b)	
Carcharhinus melanopterus	Australia	Palm (2004)	
Carcharhinus melanopterus	South Africa	Palm (2004)	
Carcharhinus obscurus	NW Atlantic (Massachusetts)	Linton (1924)	In: Palm (2004)
Carcharhinus obscurus	NW Atlantic (Massachusetts)	Wenninger (1939)	Used parasite: *Stenobothrium macrobothrium*

Appendix 1 – Table 1 *continued*

Trypanorhyncha

Tentacularia coryphaenae

Other host species	**Geographical region**	**Reference**	**Comments**
Carcharhinus obscurus	SW Atlantic (Brasil)	Knoff et al. (2002)	
Carcharhinus obscurus	SW Atlantic (Brasil)	Knoff et al. (2004b)	
Carcharhinus plumbeus	NW Atlantic (Massachusetts)	Wenninger (1939)	Used host: *Carcharhinus milberti* Used parasite: *Stenobothrium macrobothrium*
Carcharhinus plumbeus	NW Atlantic (Massachusetts)	Palm (2004)	
Carcharhinus signatus	SW Atlantic (Brasil)	Muniz-Pereira et al. (2009)	Misprint? The record appears on the summary of host/parasite species but nowhere else
Carcharodon carcharias	SW Atlantic (Brasil)	Dollfus (1942)	In the stomach (Love&Moser 1983), but cited by other authors (e.g. Palm 2004)
Galeocerdo cuvier	NW Atlantic (Massachusetts)	Dollfus (1942)	In: Palm (2004)
Rhizoprionodon acutus	NW Pacific (Japan)	Yamaguti (1934)	Used host: *Scoliodon walbeehmi*; In: Palm 2004
Rhizoprionodon acutus	NW Pacific (Japan)	Yamaguti 1959	Used host: *Scoliodon walbeehmi*
Sphyrna zygaena	NW Pacific (Japan)	Dollfus (1942)	In: Palm (2004)

TAXONOMIC NOTES

1. Riser (1955) considered *Prosobothrium japonicum* as conspecific with *P. armigerum.*
2. Caira et al. (2005) considered that the specimens of *Phoreiobothrium* collected from blue sharks by Euzet (1959) belong to a new species yet to be described.
3. *Crossobothrium angustum* is here considered as synonym of *Scyphophyllidium prionacis* after evidence shown by Williams (1968), Schmidt (1986), Ruhnke (1994, 1996, 2011) and Caira et al. (2020).

Appendix 1 – Table 1 *REFERENCES*

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Appendix 2. Associations of genera of cestodes described as adults infecting the spiral valve of blue sharks, Prionace glauca, detailing the common groups (families, orders) that act commonly as final hosts and other reported hosts.

Table 1 columns are as follows:

Cestode genus:
Ns: number of species in the genus
Nh: number of final hosts described for the cestode genus
Common hosts: most described final hosts for the cestode genus
Other hosts: other described final hosts for the cestode genus

Table 2 columns are as follows:

Species: cestode species
Ns: number of species of final hosts described
Ng: number of genera of final hosts described
Families: name of the families described as final hosts
Nf: number of families of final hosts described
Orders: name of the orders described as final hosts
No: number of orders of final hosts described
N: number of studies describing final hosts for the species
1st: year of the first study
Last: year of the last study

Appendix 2 – Table 1 Summary

Associations from cestode genera infecting *Prionace glauca*				
Genus	**Ns**	**Nh**	**Common hosts (no. spp.)**	**Other hosts (no. spp.)**
Anthobothrium	8	15	Carcharhinidae (10)	Rajidae (2), Gymnuridae (1), Dasyatidae (1), Triakidae (1)
Platybothrium	10	11	Carcharhinidae (9)	Sphyrnidae (2)
Prosobothrium	3	2	*Prionace glauca*	Sphyrnidae (1)
*Phoreiobothrium**	18	16	Carcharhinidae (11)	Sphyrnidae (5)
Pelichnibothrium	1	1	*Prionace glauca*	
Scyphophyllidium	51	47	Carcharhinidae (19)	Triakidae (7), Hemiscyllidae (3), Hemigaleidae (3), Alopiidae (2), Orectolobidae (2), Potamotrygonidae (2), Sphyrnidae (2), Glaucostegidae (1), Mitsukurinidae (1), Pseudocarcharidae (1), Rhinidae (1), Rhinobatidae (1), Dasyatidae (1), Rajidae (1)
Callitetrarhynchus	2	16	Carcharhinidae (11)	Sphyrnidae(2), Triakidae (2), Dasyatidae (1)
Dasyrhynchus	5	17	Carcharhinidae (13)	Hexanchidae (1), Lamnidae (1), Scyliorhinidae (1), Sphyrnidae (1)
Floriceps	2	12	Carcharhinidae (11)	Hexanchidae (1)
Heteronybelinia	15	28	Carcharhinidae (13)	Rajidae (4), Sphyrnidae (4), Triakidae (2), Arhynchobatidae (1), Ginglymostomatidae (1), Hemiscyllidae (1), Hexanchidae (1), Rhinidae (1)
Molicola	3	5	Alopiidae (2), Lamnidae (2)	*Prionace glauca*
Nybelinia	31	53	Carcharhinidae (13)	Rajidae (8), Triakidae (6), Dasyatidae (5), Lamnidae (3), Sphyrnidae (3), Hemigalidae (2), Hexanchidae (2), Myliobatidae (2), Rhinopteridae (2), Alopiidae (1), Arhynchobatidae (1), Dalatiidae (1), Heterodontidae (1), Mobulidae (1), Scyliorhinidae (1), Trygonorhinidae (1)
Tentacularia	1	19	Carcharhinidae (11)	Centrophoridae (4), Hexanchidae (1), Rajidae (1), Somniosidae (1), Sphyrnidae (1)

* The specimens infecting blue sharks described by Euzet (1959) possibly belong to a new species yet to be described (Caira et al. 2005)

Appendix 2 – Table 2 All available data

Cestode species	**Definitive hosts**							**Studies**		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
"TETRAPHYLLIDEA"										
Anthobothrium										
Anthobothrium altavelae	*Gymnura altavela*	1	1	Gymnuridae	1	Myliobatiformes	1	1	2002	2002
Anthobothrium caseyi	*Prionace glauca*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	2009	2016
Anthobothrium cornucopia	*Amblyraja radiata, Carcharhinus leucas, Dasyatis pastinaca, Galeorhinus galeus, Leucoraja ocellata*	5	5	Rajidae, Carcharhinidae, Dasyatidae, Triakidae	4	Rajiformes, Carcharhiniformes, Myliobatiformes	3	5	1934	2003
Anthobothrium galeorhini	*Galeorhinus galeus*	1	1	Triakidae	1	Carcharhiniformes	1	2	2002	2017
Anthobothrium laciniatum	*Carcharinus leucas, C. longimanus, C. obscurus, Negaprion brevirostris, Rhizoprionodon acutus, R. terraenovae*	6	3	Carcharhinidae	1	Carcharhiniformes	1	17	1890	2021
Anthobothrium lesteri	*Carcharhinus melanopterus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2004	2004
Anthobothrium lyndoni	*Carcharhinus plumbeus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2009	2009
Anthobothrium spinosum	*Carcharhinus limbatus, Rhizoprionodon acutus*	2	2	Carcharhinidae	1	Carcharhiniformes	1	1	1955	1955

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	**Definitive hosts**							**Studies**		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
ONCHOPROTEOCEPHALIDEA										
Platybothrium										
Platybothrium angelbahiense	*Carcharhinus leucas*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	2003	2016
Platybothrium auriculatum	*Prionace glauca*	1	1	Carcharhinidae	1	Carcharhiniformes	1	12	1952	2021
Platybothrium cervinum	*Carcharhinus obscurus, C. plumbeus, Galeocerdo cuvier*	3	2	Carcharhinidae	1	Carcharhiniformes	1	4	1890	2003
Platybothrium coshtaprum	*Carcharhinus plumbeus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2003	2003
Platybothrium harpago	*Negaprion brevirostris*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	1953	2003
Platybothrium hypoprioni	*Carcharhinus leucas, Galeocerdo cuvier, Rhizoprionodon terraenovae*	3	3	Carcharhinidae	1	Carcharhiniformes	1	5	1937	2004
Platybothrium jondoeorum	*Carcharhinus melanopterus, Negaprion acutidens*	2	2	Carcharhinidae	1	Carcharhiniformes	1	1	2003	2003
Platybothrium kirstenae	*Carcharhinus obscurus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2003	2003
Platybothrium spinulifera	*Galeocerdo cuvier*	1	1	Carcharhinidae	1	Carchariniformes	1	3	1925	2017
Platybothrium tantulum	*Sphyrna lewini, S. zygaena*	2	1	Sphyrnidae	1	Carchariniformes	1	2	2003	2016
Prosobothrium										
Prosobothrium adherens	*Sphyrna zygaena*	1	1	Sphyrnidae	1	Carchariniformes	1	1	1955	1955
Prosobothrium armigerum	*Prionace glauca*	1	1	Carcharhinidae	1	Carcharhiniformes	1	6	1955	2021
Prosobothrium japonicum	*Prionace glauca*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	1934	2016

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	Definitive hosts							Studies		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
ONCHOPROTEOCEPHALIDEA										
Phoreiobothrium										
Phoreiobothrium anticaporum	*Negaprion brevirostris*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	2005	2020
Phoreiobothrium blissorum	*Carcharhinus plumbeus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	2005	2017
Phoreiobothrium exceptum	*Sphyrna zygaena*	1	1	Sphyrnidae	1	Carcharhiniformes	1	3	1924	2017
Phoreiobothrium golchini	*Rhizoprionodon acutus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2019	2019
Phoreiobothrium jahki	*Rhizoprionodon acutus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	2015	2017
Phoreiobothrium lasium	*Carcharhinus leucas, C. obscurus, C. plumbeus, Galeocerdo cuvier, Rhizoprionodon terraenovae*	5	3	Carcharhinidae	1	Carcharhiniformes	1	9	1889	2017
Phoreiobothrium lewinense	*Sphyrna lewini*	1	1	Sphyrnidae	1	Carcharhiniformes	1	2	2005	2017
Phoreiobothrium manirei	*Sphyrna mokarran*	1	1	Sphyrnidae	1	Carcharhiniformes	1	2	1996	2017
Phoreiobothrium nadiae	*Rhizoprionodon acutus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	2015	2017
Phoreiobothrium pectinatum	*Sphyrna zygaena*	1	1	Sphyrnidae	1	Carcharhiniformes	1	3	1924	2017
Phoreiobothrium perilocrocodilus	*Negaprion acutidens*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	2005	2017
Phoreiobothrium puriensis	*Eusphyra blochii*	1	1	Sphyrnidae	1	Carcharhiniformes	1	2	1982	2017
Phoreiobothrium robertsoni	*Carcharhinus brachyurus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	2005	2017
Phoreiobothrium rozatii	*Carcharhinus macloti*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2019	2019
Phoreiobothrium sorrahcola	*Carcharhinus sorrah*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2020	2020
Phoreiobothrium swaki	*Rhizoprionodon acutus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	2015	2017
Phoreiobothrium tiburonis	*Sphyrna tiburo*	1	1	Sphyrnidae	1	Carcharhiniformes	1	3	1982	2017
Phoreiobothrium sp.	*Prionace glauca*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	1959	2005

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	**Definitive hosts**							**Studies**		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
PHYLLOBOTHRIIDEA										
Pelichnibothrium										
Pelichnibothrium speciosum	*Prionace glauca*	1	1	Carcharhinidae	1	Carcharhiniformes	1	4	1934	1998
Scyphophyllidium										
Scyphophyllidium alopias	*Alopias vulpinus*	1	1	Alopiidae	1	Lamniformes	1	3	1952	2011
Scyphophyllidium angustum	*Alopias vulpinus, Carcharhinus melanopterus, C. obscurus, Rhizoprionodon terraenovae*	4	3	Alopiidae, Carcharhinidae	2	Lamniformes, Carcharhiniformes	2	7	1905	2019
Scyphophyllidium arnoldi	*Negaprion acutidens*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	2006	2020
Scyphophyllidium bai	*Mustelus mustelus*	1	1	Triakidae	1	Carcharhiniformes	1	3	2008	2020
Scyphophyllidium barberi	*Triakis semifasciata*	1	1	Triakidae	1	Carcharhiniformes	1	3	1994	2020
Scyphophyllidium bullardi	*Carcharhinus acronotus, C. brevipinna, C. limbatus*	3	1	Carcharhinidae	1	Carcharhiniformes	1	2	2020	2020
Scyphophyllidium campbelli	*Rhizoprionodon terraenovae*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	2020	2020
Scyphophyllidium chiloscyllii	*Chiloscyllium griseum, Glaucostegus granulatus, Rhinobatos schlegelii, Rhinchobatos djiddensis*	4	4	Hemiscyllidae, Glaucostegidae, Rhinidae, Rhinobatidae	2	Orectolobiformes, Rhinopristiformes	2	2	1955	2020
Scyphophyllidium christopheri	*Carcharhinus sorrah*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	2017	2020
Scyphophyllidium deburonae	*Carcharhinus brevipinna, C. isodon, C. limbatus, Rhizoprionodon terranovae*	4	2	Carcharhinidae	1	Carcharhiniformes	1	2	2020	2020
Scyphophyllidium exiguum	*Alopias vulpinus*	1	1	Alopiidae	1	Lamniformes	1	4	1935	2020
Scyphophyllidium filiforme	*Alopias vulpinus*	1	1	Alopiidae	1	Lamniformes	1	4	1952	2020

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	Definitive hosts							Studies		
	Species	Ns	Ng	Families	Nf	Orders	No	N	1st	Last
PHYLLOBOTHRIIDEA										
Scyphophyllidium										
Scyphophyllidium floraformis	*Carcharhinus sorrah*	1	1	Carcharhinidae	1	Carcharhiniformes	1	4	1912	2020
Scyphophyllidium giganteum	*Amblyraja radiata, Brevitrygon walga, Galeorhinus galeus*	3	3	Rajidae, Dasyatidae, Triakidae	3	Myliobatiformes, Rajiformes, Carcharhiniformes,	3	3	1949	1968
Scyphophyllidium gobelinus	*Mitsukurina owstoni*	1	1	Mitsukurinidae	1	Lamniformes	1	3	1993	2020
Scyphophyllidium guariticus	*Paratrygon aiereba, P.*cf. *Castexi*	2	2	Potamotrygonidae	1	Myliobatiformes	1	4	2001	2020
Scyphophyllidium harti	*Carcharhinus leucas*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	2017	2020
Scyphophyllidium haselii	*Carcharhinus dussumeri*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	2011	2020
Scyphophyllidium janineae	*Hemipristis elongata*	1	1	Hemigaleidae	1	Carcharhiniformes	1	3	2006	2020
Scyphophyllidium kelleyae	*Chiloscyllium indicum*	1	1	Hemiscyllidae	1	Orectolobiformes	1	3	2006	2020
Scyphophyllidium kirstenae	*Hemigaleus microstoma*	1	1	Hemigaleidae	1	Carcharhiniformes	1	3	2006	2020
Scyphophyllidium latipi	*Scoliodon macrorhynchus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	2006	2020
Scyphophyllidium leuci	*Carcharhinus leucas*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	1976	2020
Scyphophyllidium lorettae	*Chiloscyllium* cf. *punctatum*	1	1	Hemiscyllidae	1	Orectolobiformes	1	3	2006	2020
Scyphophyllidium mattisi	*Carcharhinus brevipinna, C. limbatus, Rhizoprionodon terraenovae*	3	2	Carcharhinidae	1	Carcharhiniformes	1	2	2020	2020
Scyphophyllidium mobedii	*Carcharhinus dussumeri*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	2010	2020
Scyphophyllidium mukahensis	*Chiloscyllium indicum*	1	1	Hemiscyllidae	1	Orectolobiformes	1	3	2006	2020
Scyphophyllidium musculosum	*Rhizoprionodon acutus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	4	1955	2020
Scyphophyllidium musteli	*Mustelus canis, M. mustelus*	2	1	Triakidae	1	Carcharhiniformes	1	4	1850	2020
Scyphophyllidium nicaraguensis	*Carcharhinus leucas*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	1976	2020
Scyphophyllidium orectolobi	*Orectolobus maculatus, O. ornatus*	2	1	Orectolobidae	1	Orectolobiformes	1	5	1987	2020

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	**Definitive hosts**							**Studies**		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
PHYLLOBOTHRIIDEA										
Scyphophyllidium										
Scyphophyllidium paulum	*Galeocerdo cuvier*	1	1	Carcharhinidae	1	Carcharhiniformes	1	4	1897	2020
Scyphophyllidium prionacis	*Prionace glauca*	1	1	Carcharhinidae	1	Carcharhiniformes	1	6	1934	2017
Scyphophyllidium randyi	*Chiloscyllium hasselti*	1	1	Hemiscyllidae	1	Orectolobiformes	1	3	2006	2020
Scyphophyllidium roberti	*Negaprion brevirostris*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	2006	2020
Scyphophyllidium rodmani	*Mustelus antarcticus*	1	1	Triakidae	1	Carcharhiniformes	1	3	2008	2020
Scyphophyllidium sinclairtaylori	*Carcharhinus amboiensis, C. leucas, C. obscurus, C. sorrah, Sphyrna mokarran*	5	2	Carcharhinidae, Sphyrnidae	2	Carcharhiniformes	1	1	2017	2017
Scyphophyllidium sinuspersicense	*Carcharhinus dussumeri*	1	1	Carcharhinidae	1	Carcharhiniformes	1	3	2010	2020
Scyphophyllidium taylori	*Hemigaleus australiensis*	1	1	Hemigaleidae	1	Carcharhiniformes	1	3	2009	2020
Scyphophyllidium timvickiorum	*Pseudocarcharias kamoharai*	1	1	Pseudocarchariidae	1	Lamniformes	1	1	2020	2020
Scyphophyllidium triacis	*Triakis scyllium*	1	1	Triakidae	1	Carcharhiniformes	1	4	1952	2020
Scyphophyllidium tyleri	*Chiloscyllium punctatum*	1	1	Hemiscyllidae	1	Orectolobiformes	1	3	2006	2020
Scyphophyllidium typicum	*Rhizoprionodon acutus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	4	1955	2020
Scyphophyllidium ullmanni	*Carcharhinus amboiensis, C. cautus*	2	1	Carcharhinidae	1	Carcharhiniformes	1	3	2017	2020
Scyphophyllidium uruguayense	*Mustelus mento*	1	1	Triakidae	1	Carcharhiniformes	1	2	1999	2017
Scyphophyllidium sp. 1	*Carcharhinus cautus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2017	2017
Scyphophyllidium sp. 2	*Sphyrna lewini*	1	1	Sphyrnidae	1	Carcharhiniformes	1	1	2017	2017
Scyphophyllidium sp. 3	*Carcharhinus amboiensis*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2017	2017
Scyphophyllidium sp. 4	*Carcharhinus limbatus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2017	2017
Scyphophyllidium sp. 5	*Rhizoprionodon taylori*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2017	2017
Scyphophyllidium sp. 6	*Alopias pelagicus*	1	1	Alopiidae	1	Lamniformes	1	1	2017	2017

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	**Definitive hosts**							**Studies**		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
TRYPANORHYNCHA										
Callitetrarhynchus										
Callitetrarhynchus gracilis	*Carcharhinus amblyrhynchoides, C. amboinensis, C. fitzroyensis, C. leucas, C. limbatus, C. melanopterus, C. obscurus, Hemitrygon fluviorum, Mustelus canis, Galeocerdo cuvier, Prionace glauca, Rhizoprionodon acutus, R. terraenovae, Sphyrna lewini, S. zygaena, Triakis scyllium*	16	8	Carcharhinidae, Dasyatidae, Sphyrnidae, Triakidae	4	Carcharhiniformes, Myliobatiformes	2	17	1905	2017
Callitetrarhynchus speciosus	*Carcharhinus obscurus, Galeocerdo cuvier*	2	2	Carcharhinidae	1	Carcharhiniformes	1	5	1938	2017
Dasyrhynchus										
Dasyrhynchus basipunctatus	*Carcharhinus amblyrhynchos, C. brachyurus, C. melanopterus, C. plumbeus*	4	1	Carcharhinidae	1	Carcharhiniformes	1	3	1976	2014
Dasyrhynchus giganteus	*Carcharhynus leucas, C. limbatus, C. melanopterus, C. plumbeus, Galeocerdo cuvier, Rhizoprionodon terraenovae*	6	3	Carcharhinidae	1	Carcharhiniformes	1	6	1942	2004
Dasyrhynchus pacificus	*Carcharhinus brachyurus, C. limbatus, C. obscurus, C. plumbeus, Notorhynchus cepedianus, Scyliorhinus haeckelii, Sphyrna lewini*	7	4	Carcharhinidae, Hexanchidae, Scyliorhinidae, Sphyrnidae	4	Carcharhiniformes, Hexanchiformes	2	4	1925	2017

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	**Definitive hosts**							**Studies**		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
TRYPANORHYNCHA										
Dasyrhynchus										
Dasyrhynchus talismani	*Carcharhinus brachyurus, C. leucas, C. longimanus, Prionace glauca*	4	2	Carcharhinidae	1	Carcharhiniformes	1	2	1993	2004
Dasyrhynchus variouncinatus	*Carcharhinus amblyrhynchoides, C. amblyrhynchos, C. falciformis, C. leucas, C. limbatus, C. plumbeus, Carcharodon carcharias, Galeocerdo cuvier*	8	3	Carcharhinidae, Lamnidae	2	Carcharhiniformes, Lamniformes	2	4	1976	2004
Floriceps										
Floriceps minacanthus	*Carcharhinus amblyrhynchos, C. amboinensis, C. brachyurus, C. leucas, C. melanopterus, Triaenodon obesus*	6	2	Carcharhinidae	1	Carcharhiniformes	1	4	1987	2014
Floriceps saccatus	*Carcharhinus limbatus, C. obscurus, C. plumbeus, Galeocerdo cuvier, Notorhynchus cepedianus, Prionace glauca*	6	4	Carcharhinidae, Hexanchidae	2	Carchariniformes, Hexanchiformes	2	5	1921	2017

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	**Definitive hosts**							**Studies**		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
TRYPANORHYNCHA										
Heteronybelinia										
Heteronybelinia australis	*Carcharhinus amboinensis, C. brachyurus, Chiloscyllium punctatum*	3	2	Carcharhinidae, Hemiscyllidae	2	Carcharhiniformes, Orectolobiformes	2	3	2002	2014
Heteronybelinia estigmena	*Beringraja binoculata, B. inornata, B. rhina, Carcharhinus amblyrhynchoides, C. brevipinna, C. leucas, C. limbatus, C. obscurus, C. plumbeus, Notorhynchus cepedianus, Prionace glauca, Rhizoprionodon terranovae, Sphyrna zygaena*	13	6	Rajidae, Carcharhinidae, Hexanchidae, Sphyrnidae	4	Carcharhiniformes, Hexanchiformes, Rajiformes	3	15	1905	2019
Heteronybelinia eureia	*Mustelus canis*	1	1	Triakidae	1	Carcharhiniformes	1	2	2000	2004
Heteronybelinia heteromorphi	*Eusphyra blochii, Sphyrna mokarran*	2	2	Sphyrnidae	1	Carcharhiniformes	1	3	1999	2019
Heteronybelinia mattisi	*Sympterygia bonapartii*	1	1	Arhynchobatidae	1	Rajiformes	1	3	2013	2017
Heteronybelinia nipponica	*Carcharhinus signatus, Rhynchobatus djiddensis, Sphyrna lewini, S. zygaena*	4	3	Carcharhinidae, Rhinidae, Sphyrnidae	3	Carcharhiniformes, Rhinopristiformes	2	5	1992	2017
Heteronybelinia overstreeti	*Carcharhinus limbatus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	1	2004	2004
Heteronybelinia palliata	*Mustelus canis, Notorhynchus cepedianus, Sphyrna zygaena*	3	3	Triakidae, Hexanchidae, Sphyrnidae	3	Carcharhiniformes, Hexanchiformes	2	3	1942	2004
Heteronybelinia perideraeus	*Glyphis gangeticus, Nebrius ferrugineus, Notorhynchus cepedianus, Rhynchobatus djiddensis, Scoliodon laticaudus*	5	5	Carcharhinidae, Ginglymostomatidae, Hexanchidae, Rhinidae	4	Carcharhiniformes, Hexanchiformes, Orectolobiformes, Rhinopristiformes	4	4	1996	2017

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	Definitive hosts							Studies		
	Species	Ns	Ng	Families	Nf	Orders	No	N	1st	Last
TRYPANORHYNCHA										
Heteronybelinia										
Heteronybelinia robusta	*Bathytoshia centroura, Beringraja inornata, Carcharhinus limbatus, Mustelus asterias, Rajella leoparda*	5	5	Dasyatidae, Rajidae, Carcharhinidae, Triakidae	4	Carcharhiniformes, Rajiformes, Myliobatiformes	3	4	1999	2019
Heteronybelinia yamagutii	*Carcharhinus signatus, Sphyrna lewini*	2	2	Carcharhinidae, Sphyrnidae	2	Carcharhiniformes	1	5	1999	2019
Molicola										
Molicola horridus	*Carcharodon carcharias, Isurus oxyrhinchus, Prionace glauca*	3	3	Lamnidae, Carcharhinidae	2	Lamniformes, Carcharhiniformes	2	4	2004	2021
Molicola uncinatus	*Alopias vulpinus*	1	1	Alopiidae	1	Lamniformes	1	2	1952	2004
Molicola walteri	*Alopias superciliosus*	1	1	Alopiidae	1	Lamniformes	1	1	2004	2004
Nybelinia										
Nybelinia aequidentata	*Brevitrygon walga, Hemitrygon akajei, Rhinoptera neglecta*	3	3	Dasyatidae, Rhinopteridae	2	Myliobatiformes	1	3	2004	2009
Nybelinia africana	*Alopias superciliosus, Carcharhinus leucas, C. melanopterus, C. obscurus, Lamiopsis temminckii, L. tephrodes, Mustelus canis, Scylliogaleus quecketti*	8	5	Alopiidae, Carcharhinidae, Triakidae	3	Carcharhiniformes, Lamniformes	2	5	1999	2019
Nybelinia anthicosum	*Heterodontus francisci, Triakis semifasciata*	2	2	Heterodontidae, Triakidae	2	Heterodontiformes, Squaliformes	2	3	1974	2016
Nybelinia balinensis	*Mobula japanica*	1	1	Mobulidae	1	Myliobatiformes	1	1	2019	2019
Nybelinia bilobata	*Sphyrna lewini*	1	1	Sphyrnidae	1	Carchariniformes	1	1	2004	2004
Nybelinia bisulcata	*Notorhynchus cepedianus*	1	1	Hexanchidae	1	Hexanchiformes	1	2	1889	1992

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	Definitive hosts							Studies		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
TRYPANORHYNCHA										
Nybelinia										
Nybelinia gopalai	*Sphyrna lewini, S. zygaena*	2	1	Sphyrnidae	1	Carchariniformes	1	1	2004	2004
Nybelinia goreensis	*Maculabatis pastinacoides, Rhinoptera jayakari, Sphyrna lewini*	3	3	Dasyatidae, Rhinopteridae, Sphyrnidae	3	Carcharhiniformes, Myliobatiformes	2	3	2000	2014
Nybelinia hemipristis	*Hemipristis elongata*	1	1	Hemigaleidae	1	Carcharhiniformes	1	2	2002	2004
Nybelinia indica	*Alopias superciliosus, Carcharhinus leucas, C. limbatus, Glyphis gangeticus, Rhizoprionodon acutus, Squaliolus laticaudus, Taeniura lymma, Triaenodon obesus*	8	7	Alopiidae, Carcharhinidae, Dalatiidae, Dasyatidae	3	Carcharhiniformes, Lamniformes, Myliobatiformes	3	6	1996	2019
Nybelinia jayapaulazariahi	*Rhizoprionodon terraenovae*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	1999	2004
Nybelinia lingualis	*Beringraja binoculata, B. inornata, Carcharhinus. leucas, C. limbatus, C. obscurus, C. plumbeus, Carcharodon carcharias, Dipturus batis, Hexanchus griseus, Isurus oxyrinchus, Leucoraja fullonica, Mustelus canis, M. schmitti, Notorhynchus cepedianus, Pteroplatytrygon violacea, Raja brachyura, R. clavata, R. microocellata, Squaliolus laticaudus, Scyliorhinus canicula, Sympterygia bonapartii, Zearaja nasuta*	22	15	Rajidae, Carcharhinidae, Lamnidae, Hexanchidae, Triakidae, Scyliorhinidae, Dasyatidae, Dalatiidae, Arhynchobatidae	8	Carcharhiniformes, Hexanchiformes, Lamniformes, Myliobatiformes, Rajiformes	5	11	1989	2017

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	**Definitive hosts**							**Studies**		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
TRYPANORHYNCHA										
Nybelinia										
Nybelinia manazo	*Mustelus manazo*	1	1	Triakidae	1	Carcharhiniformes	1	2	1952	2004
Nybelinia mehlhorni	*Hemigaleus microstoma, Taeniura lymma*	2	2	Dasyatidae, Hemigalidae	2	Carcharhiniformes, Myliobatiformes	2	3	2002	2014
Nybelinia mobulicola	*Mobula japanica*	1	1	Mobulidae	1	Myliobatiformes	1	1	2019	2019
Nybelinia pintneri	*Prionace glauca*	1	1	Carcharhinidae	1	Carcharhiniformes	1	2	1934	2004
Nybelinia queenslandensis	*Carcharhinus melanopterus*	1	1	Carcharhinidae	1	Carcharhiniformes	1	4	1998	2014
Nybelinia riseri	*Beringraja binoculata*	1	1	Rajidae	1	Rajiformes	1	2	2000	2004
Nybelinia schmidti	*Isurus oxyrinchus, Prionace glauca*	2	2	Carcharhinidae, Lamnidae	2	Carcharhiniformes, Lamniformes	2	4	1999	2019
Nybelinia sphyrnae	*Sphyrna lewini, S. zygaena*	2	1	Sphyrnidae	1	Carchariniformes	1	4	1952	2014
Nybelinia strongyla	*Sphyrna tudes*	1	1	Sphyrnidae	1	Carchariniformes	1	1	2004	2004
Nybelinia surmenicola	*Hexanchus griseus, Lamna ditropis*	2	2	Hexanchidae, Lamnidae	2	Hexanchiformes, Lamniformes	2	2	2004	2007
Nybelinia syngenes	*Sphyrna zygaena*	1	1	Sphyrnidae	1	Carchariniformes	1	1	2004	2004
Nybelinia thyrsites	*Aptychotrema vincentiana, Carcharhinus brachyurus, Galeorhinus galeus, Mustelus antarcticus*	4	4	Trygonorhinidae, Carcharhinidae, Triakidae	3	Carcharhiniformes, Rhinopristiformes	2	2	2002	2004

Appendix 2 – Table 2 All available data *(continued)*

Cestode species	**Definitive hosts**							**Studies**		
	Species	**Ns**	**Ng**	**Families**	**Nf**	**Orders**	**No**	**N**	**1st**	**Last**
TRYPANORHYNCHA										
Tentacularia										
Tentacularia coryphaenae	*Carcharhinus falciformis, C. galapagensis, C. limbatus, C. longimanus, C. melanopterus, C. obscurus, C. plumbeus, C. signatus, Centrophorus moluccensis, C. squamosus, Centroscymnus coelolepis, Deania calcea, D. profundorum, Galeocerdo cuvier, Heptranchias perlo, Prionace glauca, Rajella caudaspinosa, Rhizoprionodon acutus, Sphyrna zygaena*	19	10	Carcharhinidae, Centrophoridae, Somniosidae, Hexanchidae, Rajidae, Sphyrnidae,	7	Carcharhiniformes, Squaliformes, Hexanchiformes, Rajiformes	4	10	1934	2017

Appendix 2 – Table 1,2 *REFERENCES*

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Chapter 05 – Feeding on clean food? Potential effects of electric organ discharges by *Torpedo* spp. (Torpediniformes: Torpedinidae) on their trophically transmitted parasites

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5.1 Abstract

Members of the Torpedinidae (torpedoes) and Hypnidae (coffin ray) use electric organ discharges (EOD) to stun or kill their prey before consumption. We investigated whether EOD could also negatively affect the helminth larvae infecting these preys through a surrogate model: we applied electric discharges to individuals of blue whiting, *Micromesistius poutassou* that harboured live larvae of *Anisakis*. Larval mortality throughout a 6-h period was significantly higher in the treatment group, suggesting that EODs could significantly hamper helminth recruitment. We then tested whether torpedinids and hypnids ('strong-EOD' families) harboured species-poor helminth (cestode) assemblages compared with 'weak-EOD' torpediniforms (Narcidae and Narkidae) and other Batoidea. Based on comparisons on estimated species diversity and mean species richness of tapeworms at host individual level we found that (1) Torpediniformes had the lowest tapeworm diversity of all Batoidea orders; (2) *Torpedo* spp. consistently had the lowest mean cestode richness at host individual level, and this could not be related to other host factors influencing cestode diversity

in chondrichthyans, i.e., body size, trophic level or dietary breath. However, a preliminary comparison between ‘strong-EOD’ and ‘weak-EOD’ torpediniforms did not detect clear differences of cestode richness. Thus, evidence supporting an unambiguous contribution of EODs to depauperate cestode assemblages requires further research.

5.2 Introduction

Electric organs are specialized fish structures that produce an electric field outside the body (Bennett 1971). They appear to have independently evolved in at least six lineages, allowing species to electrolocate, electrocommunicate, predate and/or defend themselves (Lissman 1958, Moller 1995, Crampton 2019). Within chondrichthyan fishes, only species of the order Torpediniformes are known to generate strong Electric Organ Discharges (EODs) for defence, predation, or both (Bennett 1971). This order is composed of 63 species of 4 families including Hypnidae (the coffin ray, 1 sp.), Narcinidae (numbfishes, 30 spp.), Narkidae (sleeper rays, 11 spp.) and Torpedinidae (torpedoes, 21 spp.) (Caira & Jensen 2017). The EOD potential in these species ranges from 26 to 56V (Belbenoit 1986, Bennett 1988, Lowe *et al.* 1994, Macesic & Kajiura 2009); larger reported values (e.g., 200V, Jawad 2017) have never been proved. The use of EOD in defence has been observed in all torpediniform species but, apparently, only torpedoes and the coffin ray use powerful EODs to stun or kill potential prey (Belbenoit 1986, Lowe *et al.* 1994). Observations of predatory behaviour of torpedoes indicate that they engulf whole prey that have been stunned using EODs (Bray & Hixon 1978, Belbenoit 1986, Lowe *et al.* 1994). This specific use of EODs can also be inferred from dietary studies: torpedoes and the coffin ray feed mainly on benthic and benthic-demersal fishes and cephalopods (Bray & Hixon 1978, Abdel-Aziz 1994, Jacobsen & Bennett 2013, Frost *et al.* 2017), whereas numbfishes and sleeper rays rely on slow-moving invertebrates (Menni & Stehmann 2000, Moreno *et al.* 2009, Jacobsen & Bennett 2013, Spath *et al.* 2016).

An intriguing question that has never been addressed is how EOD could affect the infective stages of trophically-transmitted parasites in the stunned prey. Chondrichthyans typically harbour a rich intestinal cestode fauna (Caira & Jensen 2017). Existing species-specific surveys, or meta-analyses, that have investigated potential predictors of diversity and composition of these cestode communities have focused on general host-related features, e.g., body size, dietary breath, phylogeny, and/or environmental or geographic factors (Randhawa & Poulin 2010, Rasmussen & Randhawa 2018). Although these predictors are valuable to ascertain general trends, similarly as in other vertebrates (see Morand 2015 for a review), they cannot unveil peculiarities that are important to understand diversity patterns at taxon-specific level. In particular, EODs could stun or kill not only prey, but also the infective stages of the cestodes they carry, and this may result in very depauperate cestode faunas in torpedoes and coffin rays.

In this paper we address this issue based on combined experimental and comparative approaches. The first question is, obviously, whether EOD affects the vitality of infective stages of cestodes within fish that are potential prey for torpedoes and coffin rays. Since it was unfeasible to obtain these (infected) prey, we selected a surrogate host-parasite model to test this hypothesis. In particular, we examined the effect of electric discharges that mimicry EODs on the vitality of larvae of *Anisakis* spp. infecting blue whiting, *Micromesistius poutassou* Risso, 1827. Although species of *Anisakis* are nematodes that reproduce in cetaceans, their larvae occur in fish microhabitats (i.e., body cavity, mesenteries, liver and muscles, see Cruz et al. 2007) that are similar to those reported for larvae of cestodes infecting chondrichthyans (Al-Zubaidy 2006, Oguz & Bray 2008, Santoro *et al.* 2013). Admittedly, the cuticle of nematodes could make them more resistant to the potential effects of EODs, thus our model should be viewed as conservative.

The second question is whether EOD effects indeed contribute to generate depauperate cestode faunas in torpedoes and coffin rays. If EODs hamper cestode recruitment, these fish should develop a lower number of host-parasite associations resulting from colonization events. In other words, there would be a smaller pool of cestode taxa that developed historical associations with torpedoes and coffin rays, and also smaller numbers and abundances of generalist cestodes ‘borrowed’ from other batoids in contemporary settings. A suitable test for these predictions, controlling for phylogenetic effects, should be to compare the diversity and abundance of cestodes between torpedoes and coffin rays (‘strong-EOD’ families) vs. other torpediniforms (i.e. narcinids and narkids, ‘weak-EOD’ families), which apparently do not use EODs to stun prey. Unfortunately, proper parasite data on torpediniforms, especially on ‘weak-EOD’ families, is extremely scarce and, therefore, we had to make an exploratory assessment using the Batoidea as a whole.

First, we carried out a parasitological survey on two *Torpedo* species, i.e., *T. torpedo*, Linnaeus, 1758 and *T. marmorata*, Risso, 1810, in eastern Spain to increase the amount of parasitological data of at least ‘strong-EOD’ species. Second, we compared cestode diversity between batoid families based on published estimates (Caira & Jensen 2017); being our expectation that ‘strong-EOD’ families (hypnids and torpedinids) should exhibit comparatively low values. Third, we made a comparison of cestode species richness at the host individual level (i.e., the infracommunity) between ‘strong-EOD’ species and those from other species of the Batoidea. We focused only on mean species richness per individual host because data on parasite abundance were not reported in most studies. We further assessed the influence of other host-related, potentially confounding factors, i.e., size, habitat, trophic level, and diet breadth (Randhawa & Poulin 2010, Rasmussen & Randhawa 2018).

5.3 Materials and methods

Experimental model

Fresh individuals of blue whiting, *Micromesistius poutassou*, captured by trawling nets in the Cantabric Sea (NE Atlantic Ocean) were bought in a local fish market from Valencia, eastern Spain. In a preliminary analysis, larvae of *Anisakis* spp. were detected in the liver and the body cavity of 10 randomly selected fish, with most worms performing vigorous wavy movements when put in saline (0.90% w/v of NaCl).

The experiment was set as follows. In each of 5 consecutive days, we obtained 12 fish of similar length and weight (see the Results), except in one day when only 10 fish were available. Each fish was weighed (to the nearest 0.1 g) and its total length measured (to the nearest mm). Then, three individual fish were randomly assigned to a control group (immersion in saline for 15 seconds), or any of 3 treatments, i.e., immersion in saline for 15 seconds and application of a 48V electric shock for 1, 5 or 10 seconds, respectively. The discharge was applied directly to the body using a Polylux QC40 24-48V transformer. The order of treatment (including the control) was randomly assigned each day. Since one day only 10 fish were available, the final numbers of fish per group were 14 for the control and 1-sec treatment group, and 15 for the 5- and 10-sec treatment groups.

After treatments, fish were immediately analyzed for larvae of *Anisakis*. All larvae were collected from each individual fish with fine forceps and put on a Petri dish with saline at room temperature (20ºC) and natural light. Mobility of each individual larvae was checked every 30 min for the next 6 h following a random sequence among Petri dishes. If larvae were observed to be immobile, they were gently touched with a probe pin to elicit activity. Larvae were classified as dead when they did not respond to tactile stimuli in at least two consecutive 30-min checks.

We checked whether total length and weight differed significantly between fish groups with one-way ANOVA; equality of variances was examined with Levene's test. Likewise, we compared the number of worms per fish among treatments with Kruskal-Wallis test. Repeated-measures ANOVA with polynomial contrasts was firstly used to look for differences between electric shock treatments on the proportion of live larvae. 'Treatment' was used as a 'between-subject' factor, 'time' as a 'within-subject' covariate, and the proportion of live larvae per fish as the dependent variable. The latter variable was subject to an arcsine transformation prior to analysis to achieve normality and improve homoscedasticity of residuals (Zar 2009). A second repeated-measures ANOVA with polynomial contrasts was set to test the average effect of the three treatments compared with the control. These specific contrasts were built for SPSS v. 26 following Haans (2018).

Parasitological survey of T. torpedo *and* T. marmorata

Torpedoes were caught by trammel net fisheries operating 1-1.5 nautical miles from the coast at depths of 6 to 12 m in the Gulf of València, Western Mediterranean, between February and April, 2017. A total of 30 individuals of *T. torpedo* and 17 of *T. marmorata* were collected at the ports of València and Cullera. In the lab, each fish was sexed and its total length (TL) measured to the nearest cm. The sample of *T. torpedo* was composed of 12 females, with mean TL (± SD) [range] of 34.1 ± 4.9 cm [25 - 41], and 18 males with mean TL: 35.4 ± 3.2 cm (TL: [29 - 44]. All individuals of *T. marmorata* were female with TL: 42.0 ± 7.6 cm [23 - 54]. Due to logistic constraints, the intestines had to be stored at -20ºC for later examination.

After thawing, each intestine was rinsed with tap water under a 0.02 mm mesh, collecting the solid contents. Each helminth individual was detected under a stereomicroscope, washed in 0.9% saline, identified, counted, fixed and preserved in 70% ethanol. Cestodes were stained with iron acetocarmine (Georgiev *et al.* 1986) and drawn using a light microscope to identify them based on Khalil *et al.* (1994) and specific references (Campbell & Carvajal 1979, Healy et al. 2009, Caira & Jensen 2014). The single nematode larva found was cleared in glycerine and examined as a temporary mount. Voucher specimens have been deposited at the Natural History Museum of London with accession numbers: *Acanthobothrium* sp. ex *Torpedo torpedo* NHMUK.2020.12.10.1-3; *Acanthobothrium* sp. ex *Torpedo marmorata* NHMUK.2020.12.10.4-6; *Rhodobothrium* sp. ex *Torpedo marmorata* NHMUK.2020.12.10.7. Additional material can be found at the Collection of the Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Spain.

We recorded prevalence (percentage of hosts in the sample infected by a helminth species), intensity (number of individuals of a helminth species in an infected host), and mean abundance (average number of individuals of a helminth species in a sample of hosts, regardless of whether they are infected) of each helminth taxon following Bush *et al.* (1997). Species richness and Brillouin's index of diversity were used as overall descriptors of infracommunities (i.e., parasite communities in individual hosts). Species richness is here considered as the number of helminth species harboured by each individual ray. The 95% confidence interval (CI) for prevalence was calculated with Sterne's exact method (Reiczigel 2003). The 95% CI for mean abundance and mean intensity of each helminth taxon, mean species richness and mean Brillouin's index was obtained with the bias-corrected and accelerated bootstrap method using 20,000 replications (Rózsa *et al.* 2000). The free software Quantitative Parasitology v. 3 (Reiczigel & Rózsa, 2005) was used to calculate all infracommunity parameters.

Comparison of cestode species richness of 'strong-EOD' families vs. other Batoidea

We used two bibliographic sources to obtain an estimate of cestode species richness per batoid genus, excluding genera for which parasitological analysis have never been carried out. The book by Caira and Jensen (2017) provides data, at the scale of host genus, of the estimated diversity of cestode species infecting batoids, except the Trypanorhyncha. For the latter, we obtained records using the Shark References database (https://www.shark-references.com) (Pollerspöck & Straube 2019), which provides a thorough and updated account on parasites infecting chondrichthyans. We summed up figures from both databases to obtain, for each batoid genus, mean species richness per host species. For instance, according to Caira & Jensen (2017), the estimated diversity of cestodes, excluding trypanorhynchans, for the genus *Aetobatus* is 68 spp., and there are additional records of 10 spp. of Trypanorhyncha (Appendix 1). Since there are 6 spp. of *Aetobatus*, the mean richness of cestodes per species for this genus would be (68+10)/6 = 11.14 (Appendix 1). A box and whisker plot were used to visually compare the distribution of mean cestode richness between genera of the 'strong-EOD' families and of other Batoidea.

We also gathered data on helminth species richness at host individual (infracommunity) level in species of Batoidea using a dataset based on a bibliographical search on the Web of Science and Google Scholar databases, similarly as Rasmussen & Randhawa (2018). For every extant genus of the Batoidea, four different search strings were tried, using the name of the genus followed by the terms 'cestode', 'helminth', 'parasite' or 'tapeworm'. Most studies did not provide data on mean species richness per individual host, thus we calculated it by summing up prevalences (expressed as decimals) of all intestinal helminth taxa reported (Penadés-Suay et al. 2017). Given the scarcity of appropriate surveys, we included those in which the number of examined hosts was ≥ 3 (see Appendix 2). For brevity, we will refer to this dataset as 'surveys'.

In the 'surveys' dataset, mean values of infracommunity richness per batoid species were averaged to get values per batoid genera which, in turn, were averaged to obtain values per batoid families. These figures were placed on a cladogram of the Batoidea and interpreted visually. The cladogram included all genera for which parasitological data were available and was built based on the most recent phylogenetic studies using morphology and molecular markers (Aschliman 2011, Gaitán-Espitia et al. 2016, Da Cunha et al. 2017, Last et al. 2016, Marramà et al. 2018, Villalobos-Segura & Underwood 2020).

Finally, we explored whether the comparatively depauperate helminth fauna of torpedoes at infracommunity level (see the Results) could be related to factors known to be significant at component community level, specifically for sharks (Randhawa &

Poulin 2010; Rasmussen & Randhawa 2018). It is important to notice, from the outset, that we were not interested in investigating factors that could influence infracommunity species richness in batoids as a whole. Therefore, we just explored patterns of associations via Spearman's correlation tests and examined crude associations between helminth species richness and predictors to pinpoint whether or not torpedoes fitted well to any of the global patterns. In this analysis, helminth species richness per host species was considered as the dependent variable, and five predictors were selected, and measured as described by Rasmussen & Randhawa (2018): (1) host sample size, as a measure of sampling effort; (2) host total length, measured as the maximum recorded length for each species; (3) host habitat, defined by 7 potential categories: reef-associated, demersal, pelagic-oceanic, pelagic-neritic, bentho-pelagic, bathypelagic, bathy-demersal; (3) trophic level, and (4) diet breadth, measured as the total number of prey families in a host species' diet. Data on predictors were obtained directly from recent species records listed on FishBase in April 2020 (Froese & Pauly 2019) except for host sample size and diet breadth. To calculate diet breadth, we followed the criteria described by Rasmussen & Randhawa (2018). Raw data of this predictor, per host species, are shown in Appendix 2.

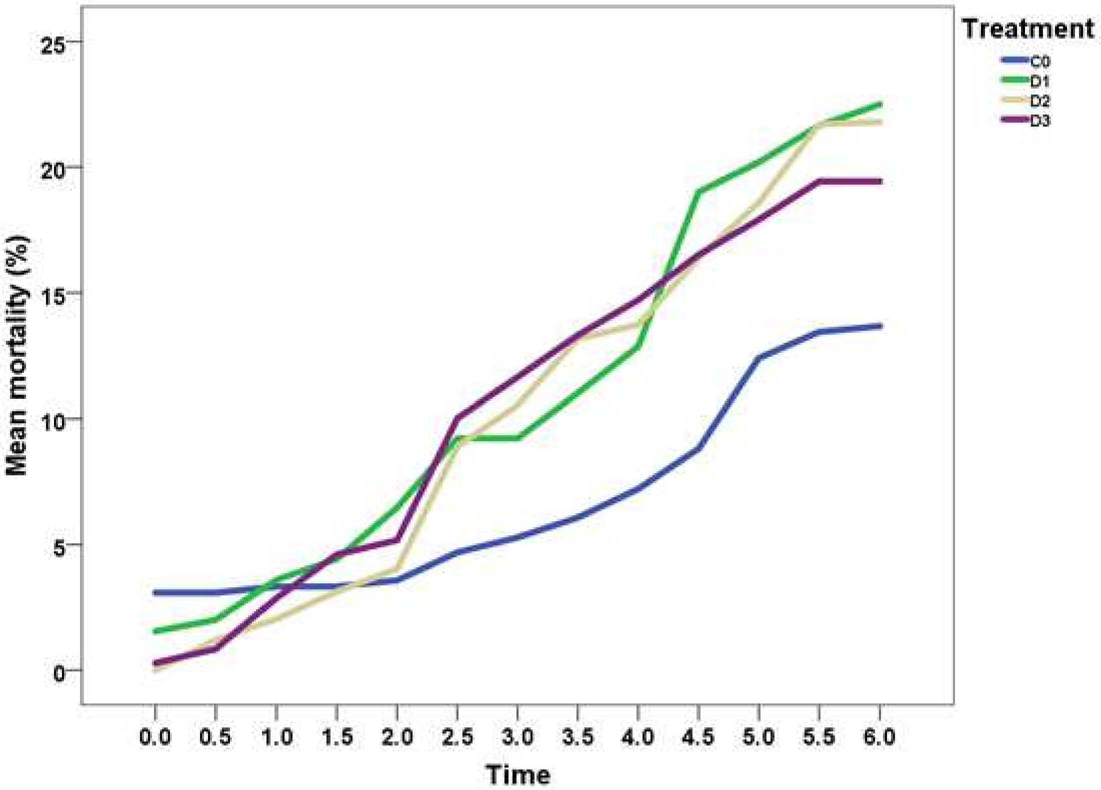

Figure 1. Mean mortality of *Anisakis* sp. over time in infected blue whiting, *Micromesistius poutassou*, treated with electric discharges of 48 V. Error bars are omitted for clarity. Blue line indicates control group (C0); green (D1), brown (D2) and purple (D3) lines indicate one, five and ten seconds treatment, respectively. The differences between the control and treatments were highly significant ($p < 0.001$).

5.4 Results

Experimental model

The average total length and weight (± S.D.) of blue whiting were 24.4 ± 1.4 cm (range: 21.0-28.2) and 87.1 ± 18.1 g (range: 52.0-133.2), respectively. The variance did not varied significantly between fish groups (Levene test, p>> 0.05), neither did mean total length (one-way ANOVA, $F_{(3,\ 54)}$= 1.081 p= 0.365), or weight ($F_{(3,\ 54)}$= 1.078 p= 0.366). The mean intensity [95% IC] of *Anisakis* sp. per fish was 23.2 [19.6-27.1] individuals, and we found no significant differences in the number of parasites between fish groups (Kruskal-Wallis test, H= 0.327, 3 d.f., p= 0.955).

The profiles of mean percent of live larvae within 6 h after collection from fish are shown in Fig. 1. We failed to detect differences of overall survival between electric shock treatments ($F_{(2,\ 41)}$= 0.075, p= 0.928) or in their time profiles (interaction treatment*time; linear polynomial contrast, $F_{(2,\ 41)}$= 0.303, p= 0.740; all upper contrasts, p>> 0.05). In the three treatments, a roughly linear increase of percent mortality with time was detected (Fig. 1). Taking the treatment groups as a whole, mean percent mortality (± S.D.) in time 0 and after 6 h was 1.1 (3.5)% vs. 21.2 (13.6)% (i.e., a 20.1% increase). In the control group, percent mortality was apparently stable up to the first 2 hours, then raised (Fig. 1). Here, mean percent mortality in time 0 and after 6 h was 3.1 (6.2)% vs. 13.7 (10.5)% (i.e., a 10.6% increase). We did not find an overall effect of electric shock on larval survival compared with the control group ($F_{(1,\ 54)}$= 1.515, one-tailed p= 0.112), but there was a highly significant interaction between the profiles (interaction treatment*time; linear polynomial contrast, $F_{(1,\ 54)}$= 9.153, one-tailed p= 0.001; quadratic contrast, $F_{(1,\ 54)}$= 3.433, one-tailed p= 0.035; all upper contrasts, p>> 0.05) (Fig. 1).

Parasitological survey of T. torpedo and T. marmorata

A total of 474 helminth specimens of 4 species, namely, 3 cestodes and 1 nematode, were collected from the spiral valve of *T. torpedo* and *T. marmorata* (Table 1). A single species, i.e., identified as a member of the genus *Acanthobothrium* van Beneden, 1849 was shared between both species and had a prevalence > 10% but a low mean intensity of infection (< 8 ind./infected hosts). A total of 8 adult individuals of *Rhodobothrium* sp. were found in 2 individuals of *T. marmorata*. A single immature individual of a species from the order Phyllobothriidea, Caira, Jensen, Waeschenbach, Olson & Littlewood 2014, and a single larva 3 (L3) of *Hysterothylacium* sp., were found in individuals of *T. torpedo* (Table 1). These specimens could not be identified at the species level due to their poor state of preservation.

Mean species richness (95% IC) per host individual was 0.90 (0.77-1.03) (n= 30) in *T. torpedo* and 0.53 (0.29-0.82) (n = 17) in *T. marmorata*, with a range from 0 to 2 in both species; Brillouin's index was 0.027 [0.000-0.054] (n = 25) and 0.148 [0.000-0.295] (n = 7), respectively.

Table 1. Infection parameters of the cestodes found in 30 individuals of *T. torpedo* and 17 individuals of *T. marmorata* from the Gulf of València, Spain. Numbers in parentheses and brackets are 95% confidence intervals and ranges, respectively.

Host species	**Cestode species**	**Infection parameters**		
		Prevalence (%)	**Mean Intensity**	**Mean abundance**
Torpedo torpedo				
	Acanthobothrium sp.	83.3 (65.2-93.2)	7.5 (4.6-12.1) [1-36]	6.2 (3.7-10.5)
	Phyllobothriidean cestode	3.3 (0.2-17.7)	1	0.03 (0-0.1)
Torpedo marmorata				
	Acanthobothrium sp.	41.2 (19.6-65)	6.4 (3.9-10.3) [1-15]	2.6 (1,1-5,4)
	Rhodobothrium sp.	11.8 (2.1-35)	4 [2-4]	0.5 (0-18)

Cestode richness in 'strong-EOD' families vs other batoids

At order level, the Torpediniformes as a whole exhibited the lowest values of cestode richness compared with other batoids (Fig. 2, Appendix 1). However, within this order, the two 'strong-EOD' families did not exhibit lower diversity values than the 'weak-EOD' ones; the Hypnidae (1 sp.) had 2 tapeworm spp., and the Torpedinidae (21 spp.), on average, 2.6 spp., whereas the Narcinidae (30 spp.) and the Narkidae (11 spp.) harboured 1.2 and 2, respectively (Fig. 2, Appendix 1).

The 'surveys' dataset contained information on cestode richness at infracommunity level from 3393 individual hosts from 48 species, 27 genera and 14 families (Appendix 2). Within the Torpediniformes, only data from 3 *Torpedo* spp. were available, i.e., *T. torpedo*, *T. marmorata* and *T. panthera* (Appendix 2). At genus level, *Torpedo* ranked the third lowest genus in terms of cestode richness, only after *Aetobatus* and *Gymnura* (Fig. 3). Interestingly, *T. panthera* was the only species in the dataset in which no single parasite was found in 96 individuals analysed (Appendix 2,

Fig. 3). No significant positive relationship was found between host sample size and helminth species richness (r_S= -0.281, n= 27, one-tailed p= 0.922).

The relationship between helminth species richness and four predictors is shown in Fig. 4. Note that, in the case of diet breadth, a strong log-log relationship was found between number of stomachs with food and number of prey families (r= 0.826, n= 43, p< 0.0001). Thus, we used the residuals of diet breath after correcting for sampling effort (Rassmusen & Randawha 2018). None of the covariates was found to have significant relationships with helminth species richness (Spearman's correlation, minimum p> 0.202). The three *Torpedo* spp. did not show obvious segregation from other host species (Fig. 4A-C), except for trophic level, which had maximum values in these species (Fig. 4D).

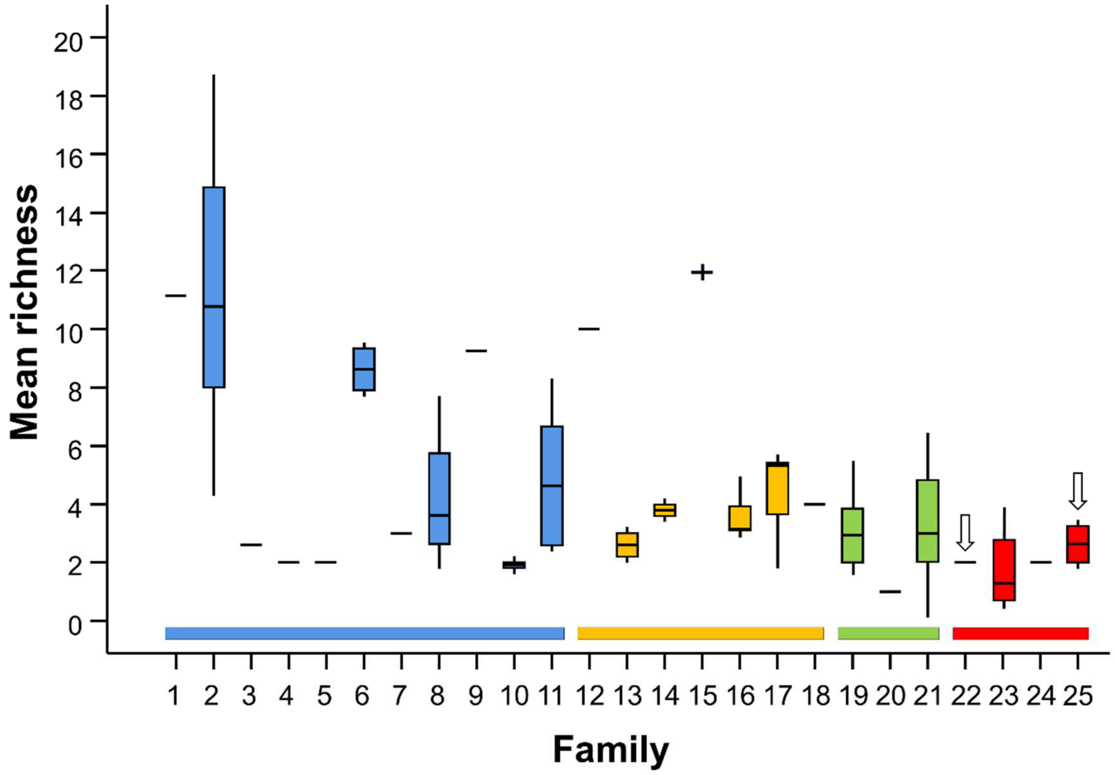

Figure 2. Box and whisker plot showing the distribution of mean richness of cestodes at genus level between families of the Batoidea. Family codes: MYLIOBATIFORMES (blue). 1. Aetobatidae; 2. Dasyatidae; 3. Gymnuridae; 4. Hexatrygonidae; 5. Mobulidae; 6. Myliobatidae; 7. Plesiobatidae; 8. Potamotrygonidae; 9. Rhinopteridae; 10. Urolophidae; 11. Urotrygonidae. RHINOPRISTIFORMES (orange). 12. Glaucostegidae; 13. Platyrhinidae; 14. "Pristidae"; 15. Rhinidae; 16. "Rhinobatidae"; 17. Trygonorrhinidae; 18. Zanobatidae. RAJIFORMES (green). 19. Arhynchobatidae; 20. Gurgesiellidae; 21. Rajidae. TORPEDINIFORMES (red). 22. Hypnidae; 23. Narcinidae; 24. Narkidae; 25. Torpedinidae. Arrows pin point the two 'strong-EOD' families. Data can be consulted in Appendix 1.

5.5 Discussion

EOD effects on larvae vitality

The use of EOD during predation has been studied only in a few torpediniform species, including *Tetronarce nobiliana* (see Wilson 1953), *Torpedo californica* (Bray & Hixon 1978, Lowe *et al.* 1994) and *Torpedo marmorata* (Belbenoit 1986, Belbenoit & Bauer 1972). In general, EODs are reported to produce in prey muscle rigidity, tetanization, immobilization, quivering, and even breaking of the vertebral column and death (Wilson 1953, Belbenoit 1986). If electricity causes these effects on muscles and internal organs, the infective stages of cestodes that typically infect elasmobranchs and are located there (e.g., Al-Zubaidy 2006, Oguz & Bray 2008, Santoro *et al.* 2013) could suffer similar detrimental effects. Evidence from our surrogate experimental model support this hypothesis. Although our results did not indicate a global effect of EOD on survival of *Anisakis* larvae, a significantly higher mortality rate was observed over time in the treatment group. Furthermore, our model likely was conservative because nematodes are protected by a thick cuticle (Lee 1972); thus, stronger detrimental effects could be expected on cestode larvae because their outer membrane-bound neodermis make them much more delicate. However, the post-EOD effects on larvae were monitored in Petri dishes with saline at room temperature, and whether these effects could be reduced or enhanced during the actual digestion of prey in torpedoes is an open question. Interestingly, the effects of the electric shock were noticeable within 3-6 hours after the simulated EOD under *in vitro* conditions. Although research on digestion time in elasmobranchs is extremely scarce, it is assumed that food emptying from the stomachs takes considerably longer than in teleosts, i.e., at least a day (Wetherbee & Cortés 2004). This opens the possibility that the putative effects of EOD on the ability of at least some infective stages to establish in the final host could be impaired when digestion is already in progress.

According to these findings, we would expect EODs to hamper the establishment of infective stages of trophically-transmitted helminths to a variable degree; the impact on viability would possibly depend on their identity and specific location within prey. In what follows, we discuss the extent to which EODs may play a role in generating depauperate cestode faunas in torpedoes and the coffin ray.

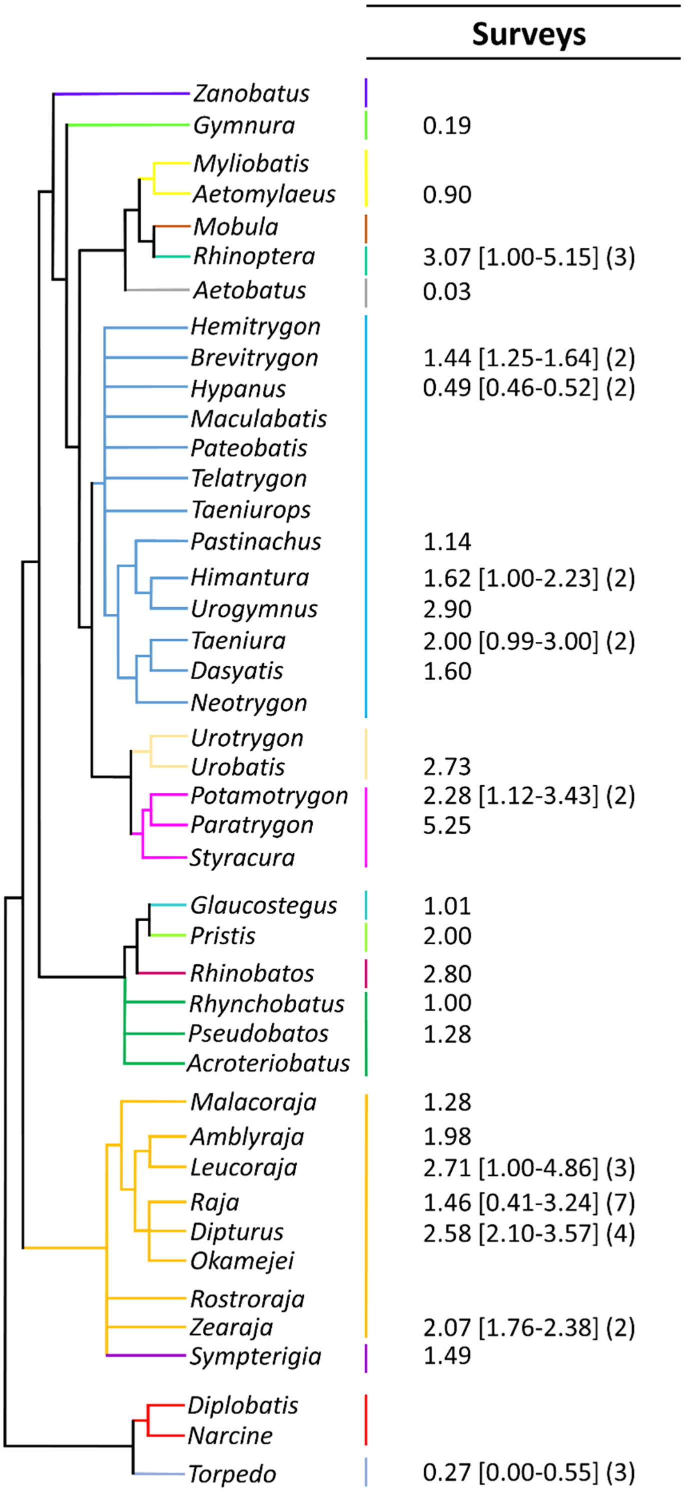

Figure 3. Values of cestode species richness at host individual level (i.e., infracommunity) for genera of the Batoidea in a phylogenetic context. Values obtained from published parasitological surveys (see Appendix 2). When data were available for several species within a genus, the mean value, range (in brackets) and sample size (number of species, in parentheses) are provided.

Inter-familial comparison of cestode richness among the Batoidea

We detected three cestode and one nematode species in the samples of *T. torpedo* and *T. marmorata* from Spain. Individuals of the genus *Acanthobothrium*, including adult specimens, occurred in both host species. Our specimens were tentatively assigned to this genus based on an elongated posterior portion of the scolex, bothridia showing three loculi and one pair of distally bifurcated hooks (Khalil et al. 1994). However, at least 3 species of *Acanthobothrium* have additionally been reported from *T. torpedo* or *T. marmorata* in the Mediterranean, including *A. benedeni*, *A. coronatum* and *A. zschokkei* (Zaragoza-Tapia et al. 2020). The finding of 8 adult specimens of *Rhodobothrium* sp. in two individuals of *T. marmorata* represent a new host record. Species of *Rhodobothrium* typically infect batoids such as the eagle ray, *Myliobatis aquila* (Campbell & Carvajal 1979, Healy et al. 2009, Caira & Jensen 2014). Eagle rays include teleosts in their diet (e.g., *Gobius* sp., *Callionymus* sp. and *Blennius* sp.), which could act as intermediate hosts for this parasite (Jardas et al. 2004). The only specimen of the order Phyllobothriidea found in *T. torpedo* was immature. Only seven of the 69 valid species of phyllobothriideans have been described parasitizing batoids and, of those, only the genus *Calyptrobothrium* Monticelli, 1893 was described infecting Torpediniforms (Caira & Jensen 2017). Our specimen lacked accessory suckers on the bothridia, one of the diagnostic traits of the genus. The specimens could not be identified further due to their poor state of preservation. Finally, species of *Hysterothylacium* sp. typically reproduce in large teleosts that feed on smaller fish (Li *et al.* 2007, Rossin *et al.* 2011); thus the single larvae we found in *T. torpedo* can likely be considered as an accidental infection.

At host individual level, the intestinal helminth fauna in both *T. torpedo* and *T. marmorata* was extremely depauperate, with only 0.90 and 0.53 species, respectively, with mean intensities ranging just from 4 to 7.5 worms per host. These patterns can hardly result just from local effects affecting the availability of potential parasites because similar figures have been obtained in previous surveys on *Torpedo* spp. In the Tyrrhenian Sea, Di Cave *et al.* (2003) reported single species, i.e., *Anthobothrium auriculatum* and *Calyptobothrium riggii*, in 112 individuals of *T. torpedo* and 4 of *T. marmorata*, respectively; each host species harboured on average 0.08 and 0.75 helminth species per host. In the Aegean Sea, Akmirza (2013) reported only two cestodes, *Acanthobothrium coronatum* and *Anthocephalum gracile* from 8 individuals of *T. marmorata* (just 0.5 species per individual host). Admittedly, these surveys only involve samples of *T. torpedo* and *T. marmorata* from the Mediterranean Sea. However, Saoud & Hassan (1981) were unable to find intestinal parasites in any of 96 individuals of *T. panthera* collected from the eastern Mediterranean and Red Sea.

When we put these data on a broader comparative context, two apparent patterns emerge. First, at order level, the Torpediniformes seem to exhibit the lowest diversity of cestodes within the Batoidea. It is unlikely that this pattern may have resulted from uneven sampling effort, since all orders contain both poorly and thoroughly sampled species (see Caira & Jensen 2017) and, among the latter, species of *Torpedo* still place in the segment of lowest cestode diversity (Fig. 2). Second, this pattern is repeated at host individual level: as many as 3 species of *Torpedo* consistently harbour very depauperate cestode infracommunities in the 'surveys' dataset. Admittedly, there were also single reports of low species richness for other Batoidea, e.g., for species of *Gymnura* and *Aetobatus* in the parasitological surveys (Fig. 3). However, the lack of replication makes it unclear if this is a local peculiarity of the surveyed host populations or an apparent "genus-level" trait as in *Torpedo* spp.

The above patterns would be consistent with the hypothesis that the negative effects of EODs on parasite recruitment may contribute to depauperate cestode communities. But, contrary to expectations, we failed to detect clear differences in cestode richness between 'strong-EOD' and 'weak-EOD' families of torpediniforms. This observation could be accounted for by several alternative factors. First, the low sampling effort for species of Hypnidae, Narcinidae and Narkidae largely decrease the precision of cestode diversity estimates for these families (see Caira & Jensen 2017), and so does the extreme paucity of parasite data available at infracommunity level. In other words, perhaps the lack of differences is partly due to a sampling artefact. Second, the possibility that narcinids and narkids do use low-voltage EODs to weaken large invertebrate prey (e.g., long polychaetes), also stunning the parasite larvae they carry, should not be ruled out. Third, it is possible that the Torpediniformes have historically developed few specific associations with cestodes, and this is reflected in their low present-day diversity which, in turn, would result in the species-poor assemblages at host individual level that we observe, at least in torpedoes. Here, one could speculate that EODs may have played a historical role in the scarce development of cestode-torpediniform associations. On the one hand, the family Torpedinidae is basal within the Torpediniformes (Marramà et al. 2018 and references therein), thus EODs could be an ancestral trait. On the other hand, it is surprising that nearly all cestode species recorded in species of the Torpedinidae are shared with other rays and/or sharks (Pollerspöck & Straube 2019), i.e., they apparently lack a bulk of specialist taxa, contrary to most batoids.

Finally, it is possible that the depauperate cestode faunas observed in the Torpediniformes have nothing to do with EODs. Indeed, there are other chondrichthyan groups for which very few cestodes have been reported, i.e., the Squaliformes and Scyliorhinidae (Caira et al. 2017). In this context, we examined 5 factors that could alternatively help explain the species-poor cestode faunas in torpedoes at infracommunity level, but we did not find any obvious relationship with 4 of them, i.e., host sampling effort, size, habitat or diet breath. However, torpedoes did combine the highest trophic level and the lowest helminth species richness of all batoids analysed. Overall, these results are at odds with the purported positive effect of trophic level, or dietary breath, on parasite richness based on theoretical grounds (Rasmussen & Randhawa 2018). One could speculate that the consumption of large prey such as teleosts might result in a reduced rate of food intake, hence of infective stages, compared with batoids feeding on invertebrates. However, teleost should also tend to accumulate more infective stages, and the Torpediniform families that feed on invertebrates (narcinids, narkids) also harboured species-poor cestode faunas.

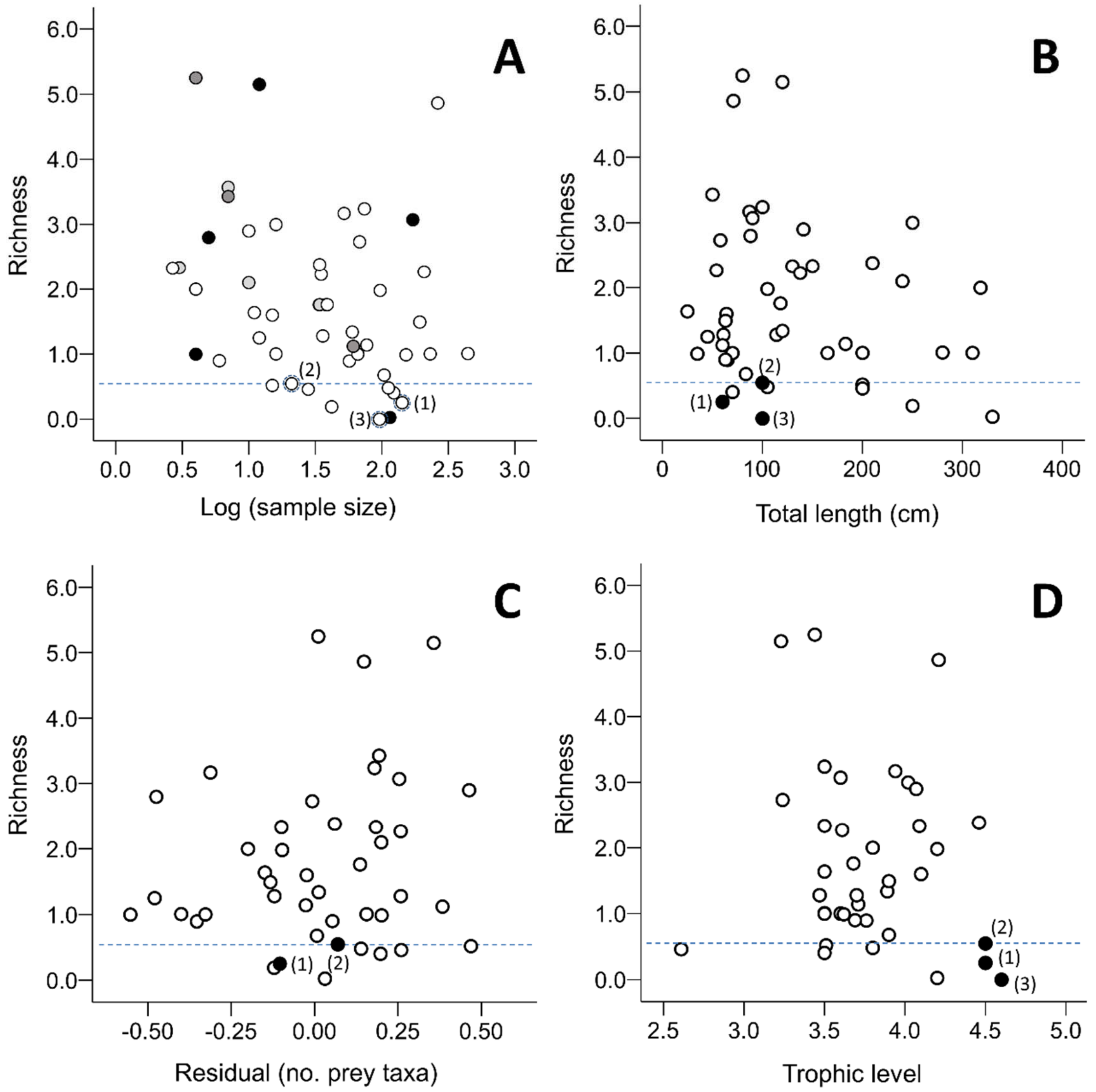

Figure 4. Scatterplots depicting the relationship between intestinal helminth species richness of species of the Batoidea, and several potential predictors. Torpedo species are pinpointed with a combination of numbers (1. *T. torpedo*, 2. *T. marmorata*, 3. *T. panthera*) and colors (blue dashed or black dots). The blue dashed horizontal lines mark the maximum value of richness recorded for torpedoes. (A). Host sample size and host habitat: demersal (white); bathydemersal (light grey); freshwater (dark grey); benthopelagic (black). (B) Host length. (C) Residuals of diet breath after correction for the number of full stomachs analyzed (see the Results). (D) Trophic level. All data can be consulted in Appendix 2.

5.6 Conclusions

Experimental results on a surrogate host-parasite model suggest that EODs could negatively affect the infective stages carried by prey of torpedoes and the coffin ray. Since parasite populations follows a negative binomial distribution (Anderson & May 1979), many infection opportunities could thus be missed when low infected prey were consumed. However, the extent to which these EOD effects contribute to the species-poor cestode assemblages observed in torpedoes is an open question. This feature cannot be readily accounted for by host-related factors that typically operate at a broad taxonomic scale such as body size, habitat, trophic level or dietary breath. However, the depauperate character of cestode faunas seems to be shared between 'strong-EOD' and 'weak-EOD' families of Torpediniformes, and this obviously begs further investigation. Future studies should focus on four issues, namely, (1) to obtain proper infracommunity data, including records of parasite abundance, from all torpediniform families, especially from the Narcinidae and Narkidae, (2) to investigate the potential use of EOD behaviour in the two families; (3) to refine and diversify the experimental settings to investigate the actual effects of EODs on infective stages of trophically-transmitted parasites, and (4) to replicate similar experimental and comparative analyses for other fish showing EOD behaviour, e.g., electric eels (see Catania 2014).

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5.9 Supporting information

Appendix 1. Number of species described and estimated for 6 orders of Cestoda infecting all extant genera of the Batoidea according to Caira and Jensen (2017), plus species of the Trypanorhyncha recorded in the 'Shark References' database (see the text for details). Total diversity (described and estimated) per host genus, mean diversity per host species (i.e., total diversity / no. host species), and median value per family are also provided. The systematics of the Batoidea follows Caira and Jensen (2017).

Table 1 columns are as follows:
Family: batoid family
Genus: batoid genus
N: number of host species
(a): Diphyllidea
(b): Lecanicephalidea
(c): Onchoproteocephalidea
(d): Phyllobothriidea
(e): Rhinebothriidea
(f): “Tetraphyllidea” relics
(g): Trypanorhyncha
(h): Total diversity
(i): Mean diversity
(j): Median value per family

Appendix 1 – Table 1

Family	Genus	N	(a)		(b)		(c)		(d)		(e)		(f)		(g)	(h)		(i)		(j)
			D	E	D	E	D	E	D	E	D	E	D	E	R	D	E	D	E	
MYLIOBATIFORMES																				
Aetobatidae	*Aetobatus*	7	2	3	30	40	9	21					2	4	10	53	78	7,57	11,14	11,14
Dasyatidae	*“Bathytoshia”*	3			4	10	3	9	1	3	8	15			15	31	52	10,33	17,33	10,00
Dasyatidae	*Brevitrygon*	5	1	5	6	15	3	7			3	15			14	27	56	5,40	11,20	
Dasyatidae	*Dasyatis*	5			3	13	3	15			4	20			13	23	61	4,60	12,20	
Dasyatidae	*Fluvitrygon*	3	2	3			2	3			5	9				9	15	3,00	5,00	
Dasyatidae	*Fontitrygon*	4	0	2	2	6	1	4			5	8			1	9	21	2,25	5,25	
Dasyatidae	*Hemitrygon*	10	1	5	7	28	8	30	1	5	3	20			8	28	96	2,80	9,60	
Dasyatidae	*Himantura*	8	1	8	38	44	9	24			3	24	2	8	17	70	125	8,75	15,63	
Dasyatidae	*Hypanus*	12			8	24	13	36			13	48			15	49	123	4,08	10,25	
Dasyatidae	*Maculabatis*	13	3	13	38	62	6	39			7	39	2	26	17	73	196	5,62	15,08	
Dasyatidae	*Megatrygon*	1			2	2	0	3			0	2			1	3	8	3,00	8,00	
Dasyatidae	*Neotrygon*	13	4	13	9	27	4	26			5	22			19	41	107	3,15	8,23	
Dasyatidae	*Pastinachus*	6	4	10	32	39	10	2			2	12	11	18	12	71	93	11,83	15,50	
Dasyatidae	*Pateobatis*	7	3	7	20	32	6	21			2	21	1	7	16	48	104	6,86	14,86	
Dasyatidae	*Pteroplatytrygon*	1			0	2	2	2			2	3			1	5	8	5,00	8,00	
Dasyatidae	*Taeniura*	5	4	8	26	31					8	16			15	53	70	10,60	14,00	
Dasyatidae	*Taeniurops*	2	0	1	1	4	1	2			1	2				3	9	1,50	4,50	
Dasyatidae	*“Telatrygon”*	4	1	4	5	11	3	12			2	8			4	15	39	3,75	9,75	
Dasyatidae	*Urogymnus*	7			22	34	11	21			9	14	1	7	10	53	86	7,57	12,29	
Gymnuridae	*Gymnura*	15	1	2	5	13	8	20					1	1	3	18	39	1,20	2,60	2,60
Hexatrygonidae	*Hexatrygon*	1			0	1	1	1								1	2	1,00	2,00	2,00
Mobulidae	*Mobula*	8			3	6					2	8			2	7	16	0,88	2,00	2,00
Myliobatidae	*Aetomylaeus*	9	5	9	27	35	4	9					7	29	2	45	84	5,00	9,33	8,62

Appendix 1 – Table 1 *continued*

Family	**Genus**	**N**	**(a)**		**(b)**		**(c)**		**(d)**		**(e)**		**(f)**		**(g)**	**(h)**		**(i)**		**(j)**
			D	**E**	**D**	**E**	**D**	**E**	**D**	**E**	**D**	**E**	**D**	**E**	**R**	**D**	**E**	**D**	**E**	
MYLIOBATIFORMES																				
Myliobatidae	*Myliobatis*	11	5	11	6	10	9	20			4	15	4	14	17	45	87	4,09	7,91	
Plesiobatidae	*Plesiobatis*	1	0	1	0	1	0	1								0	3	0,00	3,00	3,00
Potamotrygonidae	*Styracura*	2					4	4			4	4			7	15	15	7,50	7,50	3,63
Potamotrygonidae	*Paratrygon*	1					1	1	1	1	2	2				4	4	4,00	4,00	
Potamotrygonidae	*Plesiotrygon*	2					2	4								2	4	1,00	2,00	
Potamotrygonidae	*Potamotrygon*	27					12	27			11	59			2	25	88	0,93	3,26	
Rhinopteridae	*Rhinoptera*	8	5	8	20	24					1	8	11	32	2	39	74	4,88	9,25	9,25
Urolophidae	*Trygonoptera*	6			1	5	1	6							1	3	12	0,50	2,00	1,90
Urolophidae	*Urolophus*	21	2	8	0	2	7	24							4	13	38	0,62	1,81	
Urotrygonidae	*Urobatis*	6	1	3	1	2	3	6			9	18			11	25	40	4,17	6,67	4,63
Urotrygonidae	*Urotrygon*	12	0	3			3	12			1	12			4	8	31	0,67	2,58	
RHINOPRISTIFORMES																				
Glaucostegidae	*Glaucostegus*	9	9	9	24	36	3	14	2	6	3	14			11	52	90	5,78	10,00	10,00
Platyrhinidae	*Platyrhina*	5	1	2	0	2	0	2			1	5				2	11	0,40	2,20	2,60
Platyrhinidae	*Platyrhinoidis*	1	1	1			1	1							1	3	3	3,00	3,00	
“Pristidae”	*Anoxypristis*	1			1	1									3	4	4	4,00	4,00	3,80
“Pristidae”	*Pristis*	5			4	5	3	5	2	5					3	12	18	2,40	3,60	
Rhinidae	*Rhina*	1			5	6	0	1					1	1	4	10	12	10,00	12,00	11,94
Rhinidae	*Rhynchobatus*	8			12	24	12	34	2	4			2	16	17	45	95	5,63	11,88	
“Rhinobatidae”	*Acroteriobatus*	8	1	8	0	2	1	7			1	8				3	25	0,38	3,13	3,13
“Rhinobatidae”	*Pseudobatos*	8	4	8			4	16			1	8			6	15	38	1,88	4,75	
“Rhinobatidae”	*Rhinobatos*	16	3	7	2	14	3	16			0	8			4	12	49	0,75	3,06	

Appendix 1 – Table 1 *continued*

Family	**Genus**	**N**	**(a)**		**(b)**		**(c)**		**(d)**		**(e)**		**(f)**		**(g)**	**(h)**		**(i)**		**(j)**
			D	**E**	**D**	**E**	**D**	**E**	**D**	**E**	**D**	**E**	**D**	**E**	**R**	**D**	**E**	**D**	**E**	
RHINOPRISTIFORMES																				
Trygonorrhinidae	*Aptychotrema*	3	1	2	0	3	5	8			1	3				7	16	2,33	5,33	5,33
Trygonorrhinidae	*Trygonorrhina*	2	0	1	0	2	3	6							2	5	11	2,50	5,50	
Trygonorrhinidae	*Zapteryx*	3	1	2			2	3							1	4	6	1,33	2,00	
Zanobatidae	*Zanobatus*	2			3	5	1	2			1	1				5	8	2,50	4,00	4,00
RAJIFORMES																				
Arhynchobatidae	*Atlantoraja*	3	0	2			1	3			1	3			1	3	9	1,00	3,00	2,94
Arhynchobatidae	*Bathyraja*	57	2	20			2	57	3	56	3	84			3	13	220	0,23	3,86	
Arhynchobatidae	*Brochiraja*	9	0	2			0	5					1	9		1	16	0,11	1,78	
Arhynchobatidae	*Psammobatis*	8	1	4			1	8			1	8			3	6	23	0,75	2,88	
Arhynchobatidae	*Rioraja*	1	0	1			0	1								0	2	0,00	2,00	
Arhynchobatidae	*Sympterygia*	4	1	2			1	4			2	8			7	11	21	2,75	5,25	
Gurgesiellidae	*Cruriraja*	8	1	8												1	8	0,13	1,00	1,00
Rajidae	*Amblyraja*	9	2	5			0	5	1	11	5	18			3	11	42	1,22	4,67	3,00
Rajidae	*Beringraja*	6	2	6			2	6	1	2					4	9	18	1,50	3,00	
Rajidae	*Dipturus*	52	2	18			4	52	5	52	8	14			6	25	142	0,48	2,73	
Rajidae	*Leucoraja*	13	5	10			2	13	2	13	5	26			4	18	66	1,38	5,08	
Rajidae	*Malacoraja*	4	0	2			0	2			1	4	1	4		2	12	0,50	3,00	
Rajidae	*Okamejei*	12	1	4	1	4	0	6							1	3	15	0,25	1,25	
Rajidae	*Orbiraja*	3					0	1								0	1	0,00	0,33	
Rajidae	*Raja*	17	10	22			17	26	2	17	12	34			7	48	106	2,82	6,24	
Rajidae	*Rajella*	20	0	5			0	9			1	20			3	4	37	0,20	1,85	

Appendix 1 – Table 1 *continued*

Family	Genus	N	(a)		(b)		(c)		(d)		(e)		(f)		(g)	(h)		(i)		(j)
			D	**E**	**D**	**E**	**D**	**E**	**D**	**E**	**D**	**E**	**D**	**E**	**R**	**D**	**E**	**D**	**E**	
RAJIFORMES																				
Rajidae	*Rostroraja*	10	1	10			4	10							2	7	22	0,70	2,20	
Rajidae	*Spiniraja*	1	0	1			1	1							3	4	5	4,00	5,00	
TORPEDINIFORMES																				
Hypnidae	*Hypnos*	1					1	1							1	2	2	2,00	2,00	2,00
Narcinidae	*Diplobatis*	4	1	1			3	3								4	4	1,00	1,00	1,20
Narcinidae	*Discopyge*	2					0	1								0	1	0,00	0,50	
Narcinidae	*Narcine*	15	1	1	3	12	5	45							1	10	59	0,67	3,93	
Narcinidae	*Narcinops*	5			0	2	0	5								0	7	0,00	1,40	
Narkidae	*Narke*	3			1	2	2	3					0	1		3	6	1,00	2,00	2,00
Narkidae	*Typhlonarke*	1					0	1					1	1		1	2	1,00	2,00	
Torpedinidae	*Tetronarce*	9					0	5	2	9					4	6	18	0,67	2,00	2,63
Torpedinidae	*Torpedo*	12					4	12	1	12	1	12			3	9	39	0,75	3,25	

Appendix 2. Data from surveys on Batoidea for which calculations on cestode species richness could be obtained for individual hosts (i.e., infracommunities). Note that, for some species, data have been pooled from several surveys (see the references included), thus infracommunity richness have been weighed by host sample size. The references used to obtain predictor values are also provided (see also Materials and Methods). Yellow cells indicate that no data on predictors were available.

Table 1 columns are as follows:

Family: batoid family
Genus: batoid genus
Species: batoid species
N: host sample size
Habitat: batoid species habitat
(a): Infracommunity richness
(b): Trophic level
(c): Total number of prey families
(d): Number of stomachs
(e): Maximum total length registered for the batoid species

Table 2 columns are as follows:

Species: batoid species
Genus: batoid genus
Diet [References]: family of their prey items with corresponding references in brackets
No. Fam.: number of families described as prey items
No. Ref.: number of references describing prey items
Stomachs: number of stomachs with prey items examined

Appendix 2 – Table 1

Family	Genus	Species	N	Habitat	(a)	(b)	(c)	(d)	(e)
MYLIOBATIFORMES									
Aetobatidae	*Aetobatus*	*Aetobatus narinari*	115	Benthopelagic	0,0261	4,2	18	120	330
Dasyatidae	*Brevitrygon*	*Brevitrygon imbricata*	11	Demersal	1,6382	3,5	13	144	25
Dasyatidae	*Brevitrygon*	*Brevitrygon walga*	12	Demersal	1,2500	-	5	97	45
Dasyatidae	*Dasyatis*	*Dasyatis pastinaca*	15	Demersal	1,6000	4,1	32	503	64
Dasyatidae	*Himantura*	*Himantura uarnak*	231	Demersal	1,0044	3,6	15	46	200
Dasyatidae	*Himantura*	*Himantura* sp.	35	Demersal	2,2300	-	-	-	137,8
Dasyatidae	*Hypanus*	*Hypanus americanus*	15	Demersal	0,5200	3,51	21	21	200
Dasyatidae	*Hypanus*	*Hypanus guttatus*	28	Demersal	0,4600	2,61	40	209	200
Dasyatidae	*Taeniura*	*Taeniura grabata*	16	Demersal	3,0000	4,02	-	-	250
Dasyatidae	*Taeniura*	*Taeniura lymma*	152	Demersal	0,9900	3,62	18	54	35
Dasyatidae	*Pastinachus*	*Pastinachus sephen*	77	Demersal	1,1409	3,71	8	30	183
Dasyatidae	*Urogymnus*	*Urogymnus granulatus*	10	Demersal	2,9000	4,07	8	3	141
Gymnuridae	*Gymnura*	*Gymnura poecilura*	42	Demersal	0,1912	-	5	18	250
Myliobatidae	*Aetomylaeus*	*Aetomylaeus nichofii*	57	Demersal	0,8956	3,76	1	2	65
Potamotrygonidae	*Paratrygon*	*Paratrygon aiereba*	4	Freshwater	5,2500	3,44	6	14	80
Potamotrygonidae	*Potamotrygon*	*Potamotrygon falkneri*	61	Freshwater	1,1213	-	12	10	60
Potamotrygonidae	*Potamotrygon*	*Potamotrygon motoro*	7	Freshwater	3,4300	-	28	138	50
Rhinopteridae	*Rhinoptera*	*Rhinoptera bonasus*	12	Benthopelagic	5,1500	3,23	54	244	120
Rhinopteridae	*Rhinoptera*	*Rhinoptera javanica*	4	Benthopelagic	1,0000	3,6	-	-	165
Rhinopteridae	*Rhinoptera*	*Rhinoptera steindachneri*	171	Benthopelagic	3,0713	3,6	19	47	90
Urotrygonidae	*Urobatis*	*Urobatis halleri*	68	Demersal	2,7324	3,24	26	304	58

Appendix 2 – Table 1 *continued*

Family	Genus	Species	N	Habitat	(a)	(b)	(c)	(d)	(e)
RHINOPRISTIFORMES									
Glaucostegidae	*Glaucostegus*	*Glaucostegus granulatus*	444	Demersal	1,0090	3,5	8	174	280
"Pristidae"	*Pristis*	*Pristis clavata*	4	Demersal	2,0000	3,8	2	4	318
Rhinidae	*Rhynchobatus*	*Rhynchobatus djiddensis*	16	Demersal	1,0025	3,6	10	195	310
"Rhinobatidae"	*Pseudobatos*	*Pseudobatos planiceps*	36	Demersal	1,2800	3,7	19	46	114
"Rhinobatidae"	*Rhinobatos*	*Rhinobatos* cf. *punctifer*	5	Benthopelagic	2,8000	-	4	60	88
RAJIFORMES									
Arhynchobatidae	*Sympterygia*	*Sympterygia bonapartii*	193	Demersal	1,4933	3,9	10	78	63
Rajidae	*Amblyraja*	*Amblyraja radiata*	97	Demersal	1,9815	4,2	87	5482	105
Rajidae	*Dipturus*	*Dipturus innominatus*	10	Bathydemersal	2,1000	-	42	306	240
Rajidae	*Dipturus*	*Dipturus* n. sp.	7	Bathydemersal	3,5710	-	-	-	-
Rajidae	*Dipturus*	*Dipturus oxyrinchus*	3	Bathydemersal	2,3340	3,5	36	241	150
Rajidae	*Dipturus*	*Dipturus pullopunctatus*	3	Demersal	2,3330	4,09	12	97	130
Rajidae	*Leucoraja*	*Leucoraja circularis*	66	Demersal	1,0000	3,5	2	21	70
Rajidae	*Leucoraja*	*Leucoraja erinacea*	208	Demersal	2,2700	3,61	54	389	54
Rajidae	*Leucoraja*	*Leucoraja naevus*	263	Demersal	4,8637	4,21	36	285	71
Rajidae	*Malacoraja*	*Malacoraja senta*	33	Bathydemersal	1,2800	3,47	12	107	61
Rajidae	*Raja*	*Raja asterias*	123	Demersal	0,4050	3,5	42	309	70
Rajidae	*Raja*	*Raja brachyura*	60	Demersal	1,3400	3,89	32	424	120
Rajidae	*Raja*	*Raja clavata*	112	Demersal	0,4810	3,8	118	3353	105
Rajidae	*Raja*	*Raja microocellata*	52	Demersal	3,1700	3,94	26	1277	87
Rajidae	*Raja*	*Raja miraletus* complex	6	Demersal	0,9000	3,69	50	870	63
Rajidae	*Raja*	*Raja montagui*	104	Demersal	0,6790	3,9	62	1679	83,5

Appendix 2 – Table 1 *continued*

Family	Genus	Species	N	Habitat	(a)	(b)	(c)	(d)	(e)
RAJIFORMES									
Rajidae	*Raja*	*Raja undulata*	74	Demersal	3,2400	3,5	22	90	100
Rajidae	*Zearaja*	*Zearaja chilensis*	34	Demersal	2,3820	4,46	55	1024	210
Rajidae	*Zearaja*	*Zearaja nasuta*	38	Demersal	1,7618	3,68	12	32	118
TORPEDINIFORMES									
Torpedinidae	*Torpedo*	*Torpedo marmorata*	21	Demersal	0,5476	4,5	15	69	100
Torpedinidae	*Torpedo*	*Torpedo panthera*	96	Demersal	0,0000	4,6	-	-	100
Torpedinidae	*Torpedo*	*Torpedo torpedo*	142	Demersal	0,2532	4,5	20	281	60

Appendix 2 – Table 1 *REFERENCES for cestode infracommunity surveys of batoids*

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Appendix 2 – Table 2

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Aetobatus narinari	*Aetobatus*	Veneridae [3], Lucinidae [3], Arcidae [3], Solecurtidae [3], Naticidae [3], Strombidae [3], Diogenidae [42], Ocypodidae [42], Polychaeta [42], Ophiuroidea [42], Trochidae [42], Cerithiidae [42], Strombidae [43], Olividae [43], Turbinellidae [43], Fasciolariidae [43], Pinnidae [43], Diogenidae [43],	18	3	120
Aetomylaeus nichofii	*Aetomylaeus*	Dendrobranchiata [57],	1	1	2
Amblyraja radiata	*Amblyraja*	Acanthephyridae [53], Acanzonotozomatidae [61], Agonidae [53,61,71], Ammodytidae [53,61,71], Anarhichadidae [53,71], Atelecyclidae [61], Axiidae [61], Bathypolypodidae [53], Benthesicymidae [53], Bothidae [61], Buccinidae [53], Callionymidae [61], Capitellidae [61], Caprellidae [53], Carcinidae [61], Ceratiidae [53], Cirolanidae [61], Clupeidae [61,71], Corystidae [63], Cottidae [53,61,71], Crangonidae [53,61,71], Cyclopteridae [71], Epialtidae [61], Eunicidae [61], Euphausiidae [61], Gadidae [53,61,71], Gadilidae [71], Galatheidae [53,61], Glyceridae [61], Gobiidae [61], Gonatidae [71], Gonostomatidae [53], Hippolytidae [61], Histioteuthidae [53], Hyperiidae [61], Idoteidae [61], Inachoididae [61], Lampropidae [61], Liparidae [53], Lithodidae [53,61], Lophiidae [53], Lotidae [53,61], Lysianassidae [61], Macrouridae [53,71], Majidae [61], Maldanidae [61], Melitidae [61], Moridae [53], Myctophidae [53,71], Mysidae [61], Nematocarcinidae [61], Nephtyidae [61], Nereididae [61], Ommastrephidae [53,71], Opheliidae [61], Ophiuridae [61], Oregoniidae [53,61,71], Osmeridae [53,71], Paguridae [61,71], Pandalidae [53,61,71], Paralepididae [53], Pasiphaeidae [53], Pholidae [61], Phycidae [53], Pleuronectidae [53,61,71], Polybiidae [61], Portunidae [61], Priapulidae [61], Processidae [61], Pseudocumatidae [61], Psychrolutidae [53], Rajidae [53,61], Scomberesocidae [53], Scophthalmidae [61], Scorpaenidae [71], Sebastidae [53], Sepiolidae [53], Sergestidae [53,71], Serrivomeridae [53,71], Soleidae [61], Spionidae [61], Sternoptychidae [61], Stichaeidae [53,61], Stomiidae [53], Thoridae [53,61,71], Triglidae [61], Zoarcidae [53,71],	87	4	5482

Appendix 2 – Table 2 *continued*

Species	**Genus**	**Diet [References]**	**No. Fam.**	**No. Ref.**	**Stomachs**
Brevitrygon imbricata	*Brevitrygon*	Apogonidae [55], Cynoglossidae [55], Engraulidae [55], Lysmatidae [55], Myctophidae [55], Nereididae [55], Octopodidae [55], Palaemonidae [55], Penaeidae [55], Sepiidae [55], Sergestidae [55], Solenoceridae [55], Squillidae [55],	13	1	144
Brevitrygon walga	*Brevitrygon*	Gastropoda [33], Loliginidae [75], Mysidae [75], Polychaeta [33], Squillidae [75],	5	2	97
Dasyatis pastinaca	*Dasyatis*	Alpheidae [39,50], Annelidae [21], Bothidae [50], Brachyura [21], Carangidae [37,39,50], Carcinidae [37], Caridea [21], Cepolidae [39], Citharidae [50], Crangonidae [37,50], Engraulidae [37], Galatheidae [39], Gobiidae [39], Grapsidae [32], Inachidae [39], Leiognathidae [50], Mullidae [37,50], Munididae [39], Octopodidae [50], Ommastrephidae [39], Penaeidae [21,50], Polybiidae [37,39], Polychaeta [32], Portunidae [50], Processidae [39], Sepiidae [50], Sepiolidae [39], Scyllaridae [32], Sparidae [39], Squillidae [21,39,50], Upogebiidae [37,39,50], Veneridae [37],	32	5	503
Dipturus innominatus	*Dipturus*	Arhynchobatidae [68], Bramidae [68], Campylonotidae [68], Carangidae [68], Centriscidae [68], Centrophoridae [68], Chimaeridae [68], Congiopodidae [68], Congridae [68], Crangonidae [68], Etmopteridae [68], Euphausiidae [68], Galatheidae [68], Goneplacidae [68], Hoplichthyidae [68], Macrouridae [68], Majidae [68], Merlucciidae [68], Moridae [68], Myctophidae [68], Nematocarcinidae [68], Nephropidae [68], Ommastrephidae [68], Ophidiidae [68], Oplophoridae [68], Oreosomatidae [68], Pandalidae [68], Pasiphaeidae [68], Percophidae [68], Pleuronectidae [68], Polychelidae [68], Salpidae [68], Scombridae [68], Sebastidae [68], Sepiadariidae [68], Sergestidae [68], Solenoceridae [68], Squalidae [68], Sternoptychidae [68], Syngnathidae [68], Trichopeltariidae [68], Uranoscopidae [68],	42	1	306
Dipturus n. sp.	*Dipturus*	-	-	-	-

Appendix 2 – Table 2 *continued*

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Dipturus oxyrinchus	*Dipturus*	Alpheidae [73], Argentinidae [73], Aristeidae [73], Axiidae [73], Carangidae [73], Congridae [73], Crangonidae [73], Eledonidae [73], Euphausiidae [73], Eusiridae [73], Geryonidae [73], Goneplacidae [73], Lophogastridae [73], Lotidae [73], Merlucciidae [73], Munididae [73], Myctophidae [73], Mysidae [73], Octopodidae [73], Ommastrephidae [73], Pandalidae [73], Parthenopidae [73], Pasiphaeidae [73], Peristediidae [73], Phronimidae [73], Phycidae [73], Polybiidae [73], Polychelidae [73], Processidae [73], Pseudosquillidae [73], Rajidae [73], Scophthalmidae [73], Scyllaridae [73], Sepiolidae [73], Solenoceridae [73], Squillidae [73],	36	1	241
Dipturus pullopunctatus	*Dipturus*	Calappidae [65], Callionymidae [65], Cynoglossidae [65], Lophiidae [65], Merlucciidae [65], Myctophidae [65], Parapaguridae [65], Penaeidae [65], Polychelidae [65], Sebastidae [65], Sepiidae [65], Squillidae [65],	12	1	97
Glaucostegus granulatus	*Glaucostegus*	Aristeidae [76], Cynoglossidae [76], Engraulidae [76], Nemipteridae [76], Sergestidae [76], Solenoceridae [76], Squillidae [76], Trichiuridae [76],	8	1	147
Gymnura poecilura	*Gymnura*	Clupeidae [33], Haemulidae [33], Mullidae [33], Nemipteridae [33], Synodontidae [33],	5	1	18
Himantura uarnak	*Himantura*	Amphipoda [54], Annelida [31,54], Bivalvia [31,54], Brachyura [31,54], Congridae [54], Copepoda [54], Euphausiidae [54], Gastropoda [31,54], Penaeidae [31,54], Octopoda [54], Priapulidae [31,54], Sepiida [54], Spionidae [54], Stomatopoda [54], Teuthida [54],	15	2	46
Himantura sp	*Himantura*	-	-	-	-
Hypanus americanus	*Hypanus*	Albuneidae [52], Alpheidae [52,74], Branchiostomidae [67], Crangonidae [62], Diogenidae [74], Gobiidae [52], Gonodactylidae [52], Hippolytidae [52], Labridae [52], Majidae [52], Munididae [62], Octopodidae [52], Ovalipidae [62], Palaemonidae [74], Pasiphaeidae [52], Penaeidae [52,74], Portunidae [52,62,74], Processidae [52], Raninoidae [52], Scaridae [52], Squillidae [52], Strombidae [52], Tellinidae [67],	23	4	21

Appendix 2 – Table 2 *continued*

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Hypanus guttatus	*Hypanus*	Albuneidae [19], Anguilliformes [19], Ariidae [19], Calappidae [19], Callianassidae [19], Caridea [19], Clupeidae [19], Cumacea [19], Cynoglossidae [19], Dactylopteridae [19], Disciadidae [19], Gammaridea [19], Engraulidae [19], Flabelifera [19], Goniadidae [19], Glyceridae [19], Haemulidae [19], Hippidae [19], Mysidacea [19], Ogyrididae [19], Onuphidae [19], Palaemonidae [19], Palinuridae [19], Parthenopidae [19], Pasiphaeidae [19], Penaeidae [19], Penaeoidea [19], Pinnotheridae [19], Portunidae [19], Processidae [19], Rissoidae [19], Sabellidae [19], Sciaenidae [19], Sergestidae [19], Sipuncula [19], Squillidae [19], Tellinidae [19], Thalassinidae [19], Trichiuridae [19], Upogeniidae [19],	40	1	209
Leucoraja circularis	*Leucoraja*	Caproidae [56], Decapoda [56],	2	1	21
Leucoraja erinacea	*Leucoraja*	Ammodytidae [70], Ampeliscidae [70], Aoridae [70], Arenicolidae [70], Axiidae [70], Bolinosidae [70], Callianassidae [70], Cancridae [70], Caprellidae [70], Carangidae [70], Cheirocratidae [70], Clupeidae [70], Collumbellidae [70], Corophiidae [70], Crangonidae [70], Engaulidae [70], Euphausiidae [70], Flabelligeridae [70], Gammaridae [70], Glyceridae [70], Idoteidae [70], Ischyroceridae [70], Littorinidae [70], Loliginidae [70], Maldanidae [70], Merlucciidae [70], Myidae [70], Mysidae [70], Mytilidae [70], Nephropidae [70], Nereidae [70], Nereididae [70], Oedicerotidae [70], Oenonidae [70], Ogyrididae [70], Onuphidae [70], Paguridae [70], Pandalidae [70], Pandoridae [70], Panopeidae [70], Paraonidae [70], Parthenopidae [70], Pharidae [70], Pinnotheridae [70], Polynoidae [70], Portunidae [70], Scophthalmidae [70], Serranidae [70], Solecurtidae [70], Sparidae [70], Squillidae [70], Stromateidae [70], Upogebiidae [70], Veneridae [70],	54	1	389

Appendix 2 – Table 2 *continued*

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Leucoraja naevus	*Leucoraja*	Ammodytidae [16,60,61], Ampeliscidae [61], Aphroditidae [49], Bivalvia [16], Callionymidae [60,61], Cirolanidae [16], Clupeidae [16,60,61], Copepoda [16], Crangonidae [16,49,60,61], Cumacea [16], Echinodermata [16], Euphausiidae [61], Gadidae [16,60,61], Gastropoda [16], Gobiidae [61], Loliginidae [16,61], Lophogastridae [16,49], Lysianassidae [61], Malacostraca [16], Melitidae [61], Munididae [16], Mysidae [61], Nephtyidae [16,61], Nereididae [60,61], Octopodidae [60], Ommastrephidae [16], Opheliidae [61], Pandalidae [16,60,61], Paguridae [61], Phronimidae [49], Pleuronectidae [61], Polybiidae [49,61], Processidae [16,49,61], Regalecidae [49], Soleidae [61], Solenoceridae [16,49], Spionidae [61], Tryphosidae [16],	36	4	285
Malacoraja senta	*Malacoraja*	Cancridae [62], Caprellidae [53], Crangonidae [53,62], Euphausiidae [62], Liparidae [53], Mysidae [62], Oregoniidae [53], Osmeridae [53], Paguridae [62], Pandalidae [53,62], Sergestidae [53], Sternoptychidae [53], Thoridae [53],	12	2	107
Paratrygon aiereba	*Paratrygon*	Ostracoda [58], Insecta [58], Characidae [58], Loricariidae [58], Palaemonidae [58], Prochilodontidae [58],	6	1	14
Pastinachus sephen	*Pastinachus*	Acropomatidae [33], Bivalvia [33], Crustacea [33], Cephalopoda [33], Gastropoda [33], Leiognathidae [33], Ophiuridae [33], Polychaeta [33],	8	1	30
Potamotrygon falkneri	*Potamotrygon*	Ampullariidae [44], Baetidae [44], Bivalvia [44], Chironomidae [44], Gomphidae [44], Hydrobiidae [44], Hydrospsychidae [44], Leptoceridae [44], Libellulidae [44], Loricariidae [44], Naucoridae [44], Odontoceridae [44],	12	1	10
Potamotrygon motoro	*Potamotrygon*	Anelida [6], Decapoda [6], Characiformes [6], Clupeiformes [6], Gymnotiformes [6], Perciformes [6], Siluriformes [6], Coleoptera [6], Ephemeoptera [6], Hymenoptera [6], Odonata [6], Orthoptera [6], Veneroida [6], Caenogastropoda [6], Unionoida [6], Ampullariidae [44], Hydrobiidae [44], Palaemonidae [44], Elmidae [44], Chironomidae [44], Baetidae [44], Naucoridae [44], Pyralidae [44], Cordullidae [44], Gomphidae [44], Hydropsychidae [44], Leptoceridae [44], Ontoceridae [44],	28	2	138
Pristis clavata	*Pristis*	Mugilidae [66], Decapoda [66],	2	1	4

Appendix 2 – Table 2 *continued*

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Pseudobatos planiceps	*Pseudobatos*	Aethridae [77], Arenicolidae [77], Blepharipodidae [77], Callianassidae [77], Cancridae [77], Donacidae [77], Engraulidae [77], Hippidae [77], Mactridae [77], Mytilidae [77], Onuphidae [77], Paguridae [77], Panopeidae [77], Petricolidae [77], Pilumnoididae [77], Platyxanthidae [77], Sciaenidae [77], Semelidae [77], Xanthidae [77],	19	1	46
Raja asterias	*Raja*	Alpheidae [34,47], Argentinidae [51], Bregmacerotidae [51], Callionymidae [10], Cancridae [34], Carangidae [10,50], Cepolidae [47], Cerethiidae [34], Chlorophthalmidae [50], Crangonidae [34,59], Cupleidae [10,24], Dorippidae [34], Eledonidae [51], Engraulidae [34], Eriphiidae [10], Ethusidae [47], Gadidae [59], Geryonidae [47], Gobiidae [34,47], Goneplacidae [10,34], Leucosiidae [34], Loliginidae [34,47,59], Mullidae [10], Nannosquillidae [34], Paguridae [47], Palaemonidae [34], Pandalidae [50,59], Penaeidae [34], Pilumnidae [34], Polybiidae [10,34,47], Sepiidae [47], Sepiolidae [34,51], Serranidae [47], Soleidae [34,47,59], Sparidae [34], Solenoceridae [10,34], Squillidae [34,47], Sternaspidae [47], Trachinidae [34], Triglidae [34], Upogebiidae [34,47], Varunidae [34],	42	7	309
Raja brachyura	*Raja*	Alpheidae [16], Ammodytidae [9,14,16,18,60], Amphipoda [9], Brachyura [9], Callionymidae [16], Carangidae [16,18], Citharidae [16], Clupeidae [16,60], Crangonidae [14,16,60], Euphausiacea [14,60], Gadidae [16,60], Galatheidae [16], Gobiidae [14], Loliginidae [16,18], Mysidacea [9,14], Mysidae [16], Natantia [14], Nephtyidae [16], Nereidae [14,60], Ommastrephidae [16], Ostracoda [9], Pandalidae [16,60], Polybiidae [16], Porcellanidae [60], Processidae [16], Scophthalmidae [16], Sigalionidae [16], Soleidae [18,60], Sparidae [9,18], Thiidae [16], Trachinidae [16,18], Triglidae [18],	32	5	424

Appendix 2 – Table 2 *continued*

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Raja clavata	*Raja*	Alpheidae [15,16,40,49,51], Agonidae [61], Ammodytidae [14,60,61], Ampeliscidae [16], Amphipoda [14], Aphroditidae [14,49], Argentinidae [14,15,16,24,49], Atelecyclidae [14,16,49], Axiidae [14], Belonidae [16,24], Brachyura [2], Bothidae [15], Buccinidae [14,60], Calanidae [61], Calappidae [28,49], Callianassidae [14,16], Callionymidae [14,49,60], Cancridae [2,14,60,61], Caproidae [28], Carangidae [11,15,16,24,28,36,40], Carcinidae [2], Centracanthidae [24,49], Cepolidae [49], Champsodontidae [51], Chlorophthalmidae [15,50], Cirolanidae [16], Citharidae [15,24,49], Congridae [15,24], Corystidae [14,16,61], Cottidae [61], Crangonidae [2,11,14,15,16,36,49,60,61], Clupeidae [14,15,24,36,40,49,60,61], Cynoglossidae [49], Diogenidae [28,49], Dorippidae [24], Dromiidae [24], Eledonidae [14,16,24,40,49,51], Engraulidae [11,15,36], Epialtidae [61], Ethusidae [49], Euphausidae [14,49], Gadidae [11,14,15,16,36,40,49,60,61], Galatheidae [14,16,28,40,49,60], Glyceridae [16], Gobiidae [11,15,16,36,40,49,60], Goneplacidae [14,15,16,24,49],Hippolytidae [61], Hirudinea [14], Histiotheutidae [16], Homolidae [28], Inachidae [14], Isopoda [14], Labridae [24], Laomediidae [14], Leucosiidae [14], Loliginidae [14,15,16,24,49,61], Lophogastridae [16,40,49], Lotinae [14], Macroramphosidae [28], Macrouridae [15], Majidae [14,16,24,60], Melitidae [61], Merlucciidae [15,16,24,49], Mollusca [2], Moridae [28], Mullidae [24,28,36], Munididae [16,40,49], Muricidae [36], Myctophidae [28], Mysidae [14,40,61], Natantia [14], Nephropsidae [14,60], Nephtyidae [16], Nereidae [60,61], Ommastrephidae [15,16,40], Octopodidae [24,28,60], Ophichthidae [49], Ophiidae [49], Oregoniidae [14], Paguridae [2,14,16,28,49,60,61], Palaemonidae [40], Palinuridae [49], Pandalidae [14,15,16,28,49,60,61], Pandaridae [14], Panopeidae [14], Parthenopidae [28,40], Pasiphaeidae [14,16], Pectinidae [28,60], Penaeidae [15,24,28,51], Pharidae [14], Pholidae [14,61], Phronimidae [49], Phycidae [49], Pilumnidae [14,15], Pleuronectidae [14,49,61], Polybiidae [2,14,15,16,28,36,40,49,61], Pomacentridae [28], Porcellanidae [60], Portunidae [28,49,60,61], Processidae [15,16,28,40,49,51,61], Rajidae [14], Sabellidae [60], Scombridae [2,16,24,28], Scyliorhinidae [15,24], Scyllaridae [28,49], Scyoniidae [24], Sebastidae [15,49],	128	13	3861

Appendix 2 – Table 2 *continued*

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Raja clavata (continued)	*Raja*	Sepiidae [15,16,60], Sepiolidae [14,24,40,49,51], Serranidae [24,49], Sigalionidae [16], Soleidae [2,14,15,24,61], Solenidae [60], Solenoceridae [16,28,40,49], Sparidae [24,28,40], Squillidae [15,24,40,49], Sternoptychidae [40], Stichaeidae [14], Syngnathidae [36], Talassinoidea [14], Thiidae [16], Trachinidae [49], Triglidae [16,49], Upogebiidae [11,14,36,40], Uranoscopidae [36], Vibiliidae [28], Xanthidae [14,49],	128	13	3861
Raja microocellata	*Raja*	Ammodytidae [35], Ampeliscidae [35], Atherinidae [35],3 Buccinidae [35], Cancridae [2], Callionymidae [2,35], Carcinidae [2], Cirolanidae [35], Cottidae [35], Crangonidae [2,35], Donacidae [35], Gadidae [2], Gobiidae [2], Inachidae [35], Loliginidae [35], Mactridae [35], Mysidae [35], Paguridae [35], Pharidae [35], Pleuronectidae [2], Polybiidae [2,35], Polychaeta [2], Sepiolidae [35], Soleidae [2,35], Thiidae [35], Triglidae [2],	26	2	1277
Raja miraletus	*Raja*	Alpheidae [41,45], Ammodytidae [49], Anguilliformes [18], Aphroditidae [49], Atelecyclidae [18], Bregmacerotidae [45], Calappidae [45], Callionymidae [45], Caprellidae [18], Carangidae [25], Centracanthidae [49], Congiopodidae [45], Crangonidae [18,45,49], Cumacea [18], Cupleidae [25], Cynoglossidae [45], Dromeidae [45], Engraulidae [45], Flabellifera [18], Gadidae [41], Galatheidae [41], Gammaridea [18], Gobiidae [25,41,45], Goneplacidae [45], Inachidae [41], Leucosiidae [18,45], Loliginidae [18,25,45], Lophogastridae [18,41], Merlucciidae [45], Mysidae [18,41], Nereididae [25], Ommastrephidae [18], Ovalipidae [45], Penaeidae [25], Phronimidae [49], Polybiidae [18,41,49], Pomacentridae [41], Processidae [18,41,45,49], Scyonidae [25], Sepiidae [25], Sepiolidae [18,41,49], Serranidae [25], Soleidae [25], Solenoceridae [18,49], Sparidae [25,41], Sternoptychidae [41], Tanaidacea [18], Thiidae [45], Thoridae [40], Upogebiidae [41,45],	50	5	870

Appendix 2 – Table 2 *continued*

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Raja montagui	*Raja*	Acoetidae [16], Alcyoniidae [14], Alpheidae [16], Ammodytidae [14,16,60,61], Ampeliscidae [16,61], Amphipoda [14], Argentinidae [16], Atelecyclidae [14,16], Bothidae [16], Cancridae [2], Callionymidae [60], Carangidae [16], Carcinidae [2,16], Cirolanidae [16], Clupeidae [16,60,61], Corystidae [14,61], Crangonidae [2,14,16,60,61], Diastylidae [61], Eledonidae [14], Euphausiidae [61], Gadidae [14,16,60,61], Galatheidae [14,60,61], Glyceridae [16], Gobiidae [14], Goneplacidae [16], Hippolytidae [61], Isopoda [14], Loliginidae [14,16,61], Lophogastridae [16], Lysianassidae [61], Majidae [60], Melitidae [61], Munididae [14,16], Mysidacea [14,16], Mysidae [60,61], Natantia [14], Nephtyidae [16,61], Nereididae [14,60,61], Octopodidae [60], Oedicerotidae [61], Opheliidae [61], Ophiuroidea [14], Oregoniidae [14], Paguridae [2,14,60,61], Pandalidae [14,16,60,61], Pasiphaeidae [14], Pleuronectidae [14], Polybiidae [2,14,16,61], Porcellanidae [60], Portunidae [60], Processidae [16,61], Pseudocumatidae [61], Scyllaridae [16], Sepiidae [60], Sepiolidae [14], Sigalionidae [16], Solenoceridae [16], Thalassinoidea [14], Thiidae [16], Trachinidae [16,60], Tryphosidae [16], Upogebiidae [14], Xanthidae [14],	62	5	1679
Raja undulata	*Raja*	Ammodytidae [29], Ampeliscidae [29], Atelecyclidea [29], Bothidae [29], Cirolanidae [29], Crangonidae [29], Gobiidae [29], Goneplacidae [29], Leucosiidae [29], Loliginidae [29], Merluccidae [29], Mysidae [29], Penaeidae [29], Pilumnidae [29], Processidae [29], Polybiidae [29], Portunidae [29], Scyllarinae [29], Sparidae [29], Trachinidae [29], Upogebiidae [29], Xanthidae [29],	22	1	90
Rhinobatos punctifer	*Rhinobatos*	Acropomatidae [33], Crustacea [33], Mullidae [33], Polychaeta [33],	4	1	60

Appendix 2 – Table 2 *continued*

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Rhinoptera bonasus	*Rhinoptera*	Acteocinidae [78], Alpheidae [5], Ampeliscidae [78], Amphipoda [4], Anthuridae [78], Arcidae [4], Assimineidae [78], Bodotriidae [78], Branchiostomidae [78], Callianassidae [4,5], Capitellidae [4,78], Caridea [8], Chaetopteridae [4], Columbellidae [78], Crangonidae [62], Crassatellidae [78], Donacidae [4,5], Echinoidea [4], Engraulidae [62], Glycymerididae [78], Goniadidae [78], Haminoeidae [78], Haustoridae [5], Idoteidae [78], Isopoda [4], Lingulidae [78], Mactridae [4,78], Marginellidae [4], Mellitidae [4], Myidae [46], Mysidae [62,78], Mytilidae [4,46,78], Nassaridae [4,78], Nereididae [78], Nuculidae [4], Oedicerotidae [78], Opheliidae [78], Ophiuroidea [4], Ostreidae [46,78], Panaeidae [4], Pandalidae [62], Pectinariidae [78], Phyllodocidae [78], Pinnotheridae [4,5], Polychaeta [5], Portunidae [4,5], Sipuncula [8], Solecurtidae [46,63,78], Spionidae [78], Squillidae [5], Strombidae [78], Tellinidae [4,46,78], Veneridae [4,46,78], Xanthidae [4,5],	54	6	244
Rhinoptera javanica	*Rhinoptera*	-	-	-	-
Rhinoptera steindachneri	*Rhinoptera*	Ampeliscidae [30], Arcidae [30], Cancellaridae [30], Cephalaspidea [79], Engraulidae [30], Fasciolariidae [30], Majidae [30], Mysidae [79], Ogyrididae [30], Onuphidae [30], Ophiuroidea [30], Palaemonidae [30], Pectinidae [30], Processidae [30], Pseudomelatomidae [30], Sicyoniidae [30], Solenoceridae [30], Squillidae [30], Terebridae [30],	19	2	47
Rhynchobatus djiddensis	*Rhynchobatus*	Bregmacerotidae [80], Engraulidae [80], Gobiidae [80], Palaemonidae [80], Palinuridae [80], Penaeidae [80,81], Sciaenidae [80], Sergestidae [80,81], Synodontidae [80], Squillidae [80,81],	10	3	195
Sympterygia bonapartii	*Sympterygia*	Cumacea [27], Engraulidae [27], Gammaridea [27], Glyceridae [27], Malacostraca [27], Penaeidae [27], Pinnotheridae [27], Sergestidae [27], Serolidae [27], Solenoceridae [27],	10	1	78
Taeniura grabata	*Taeniura*	-	-	-	-

Appendix 2 – Table 2 *continued*

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Taeniura lymma	*Taeniura*	Amphipoda [54], Bivalvia [54], Brachyura [54], Congridae [54], Copepoda [54], Eucarida [54], Euphausiidae [54], Gastropoda [54], Oligochaeta [54], Penaeidae [54], Phyllodocida [54], Polychaeta [54], Priapulidae [54], Sabellidae [54], Spionidae [54], Stomatopoda [54], Terebellida [54], Teuthida [54],	18	1	54
Torpedo marmorata	*Torpedo*	Anguillidae [1], Atherinidae [1], Brachyura [1], Clupeidae [1], Decapodiformes [1], Gadidae [1], Gobiidae [1], Mullidae [1], Octopoda [1], Polychaeta [1], Rajidae [1], Serranidae [1], Soleidae [1], Sparidae [1], Trachinidae [1],	16	1	69
Torpedo panthera	*Torpedo*	-	-	-	-
Torpedo torpedo	*Torpedo*	Anguillidae [1], Brachyura [1], Caridea [1], Clupeidae [1,13], Decapodiformes [1], Gadidae [1], Gobiidae [1,13], Hirudinea [1], Merlucciidae [13], Mullidae [1,13], Octopoda [1], Polychaeta [1], Rajidae [1], Sepiidae [13], Serranidae [1], Soleidae [1], Sparidae [1,13], Stomatopoda [1], Trachinidae [1], Trichuridae [1],	20	2	281
Urobatis halleri	*Urobatis*	Amphipoda [17], Bothidae [17,48], Brachyura [17], Calappidae [48], Caridea [17], Congridae [48], Diogenidae [48], Euphausiidae [17], Eurysquillidae [48], Glyceridae [48], Goniadidae [48], Isopoda [17], Mollusca [17], Ogyrididae [17,48], Ophichthydae [48], Paralichthydae [48], Penaeidae [17,48], Portunidae [17,48], Processidae [17,48], Raninidae [48], Serpullidae [17], Sicyoniidae [48], Solenoceridae [48], Squillidae [17,48], Stomatopoda [17], Xanthidae [17],	26	2	304
Urogymnus granulatus	*Urogymnus*	Blenniidae [63], Calappidae [63], Gobiidae [63], Labridae [63], Octopodidae [63], Pomacentridae [63], Siganidae [63], Sipunculidae [63],	8	1	3

Appendix 2 – Table 2 *continued*

Species	Genus	Diet [References]	No. Fam.	No. Ref.	Stomachs
Zearaja chilensis	*Zearaja*	Agonidae [69], Arbaciidae [64], Arhynchobatidae [64,69], Atelecyclidae [69], Batrachoididae [64], Bovichtidae [69], Carangidae [69], Centrolophidae [64], Chaetopteridae [69], Cheilodactylidae [69], Cirolanidae [69], Congiopodidae [64,69], Congridae [64,69,72], Eledonidae [64], Engraulidae [64], Enteroctopidae [64], Epialtidae [64], Eunicidae [64,69], Euphausiidae [69], Galatheidae [69], Glyceridae [69], Hyperiidae [69], Inachidae [64], Lithodidae [64], loliginidae [69], Majidae [69], Merlucciidae [64,69,72], Munididae [64], Myxinidae [64,69], Narcinidae [69], Nephropidae [69], Nototheniidae [64,69,72], Octopodidae [69], Ommastrephidae [64,69,72], Onuphidae [69], Ophidiidae [64,69,72], Paguridae [69], Pandalidae [69], Paralichthyidae [64,65], Platyxanthidae [69], Polyprionidae [64], Rajidae [64,69], Scyliorhinidae [69], Sebastidae [64], Sepiolidae [64,69], Sergestidae [64,69], Serolidae [64,69], Solenoceridae [64,69], Squillidae [64,69], Stromateidae [64], Terebellidae [69], Trichiuridae [69], Trichopeltariidae [64], Volutidae [69], Zoarcidae [64,69],	55	3	1024
Zearaja nasuta	*Zearaja*	Ovalipidae [7], Squillidae [7], Pandalidae [7], Majidae [7], Goneplacidae [7], Clupeidae [7], Ophidiidae [7], Pleuronectidae [7], Carangidae [7], Merlucciidae [7], Octopoda [7], Cranchiidae [7],	12	1	32

Appendix 2 – Table 2 *REFERENCES for diet surveys of batoids*

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Chapter 06 – Fatal impalement of a blue shark *Prionace glauca* by a swordfish *Xiphias gladius*

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6.1 Abstract

In September, 2016, an adult female blue shark (*Prionace glauca*) 247 cm long stranded alive on the coast of Valencia (Spain, Western Mediterranean) but died shortly afterwards. The necropsy revealed an ongoing pregnancy, with 65 embryos in the early stages of development, and a healthy condition with no signs of starvation. Two fishing hooks surrounded by scarred tissue were detected in the mandible, indicating past interaction with fisheries. In addition, a fragment of the tip of a swordfish (*Xiphias gladius*) rostrum (length: 18 cm long, width: 0.5 cm (distal) and 3 cm (proximal)) was removed from the animal. The fragment had pierced the head producing an incision of 3.5 cm width close to the left eye, crossing the head anterior to the pre-orbital process. No apparent damage was observed in the olfactory capsule or the eye, but the fragment had penetrated both sides of the skull causing extensive lesions in the brain, which were inferred to be the cause of death. Allometric analysis suggested that the swordfish was ca. 110 cm long, corresponding to a juvenile only 1-2 years old. Swordfish had previously been reported driving their rostrum into pelagic sharks, allegedly as a defensive strategy. However, this is the first report of impalement as the direct cause of death in blue sharks.

6.2 Main text

Swordfish (*Xiphias gladius* L.) are known for their highly active and aggressive behaviour. There are reports of swordfish driving its rostrum into a great variety of inanimate objects (e.g., Fierstine & Crimmen, 1996) and animals, including large fishes (e.g. Fierstine, 1997; Fierstine *et al.*, 1997), whales (Jonsgard, 1962), marine turtles (e.g., Frazier *et al.*, 1994), people (e.g., Haddad & De Figuereido, 2009; Georgiadou *et al.*, 2010) and even submarines (Zarudski & Haedrich, 1974). This behaviour may result in a transverse fracture of the bill, leaving the distal segment embedded in the substratum. Here, for the first time, direct evidence is presented of a blue shark (*Prionace glauca* L.) killed by the interaction with a swordfish.

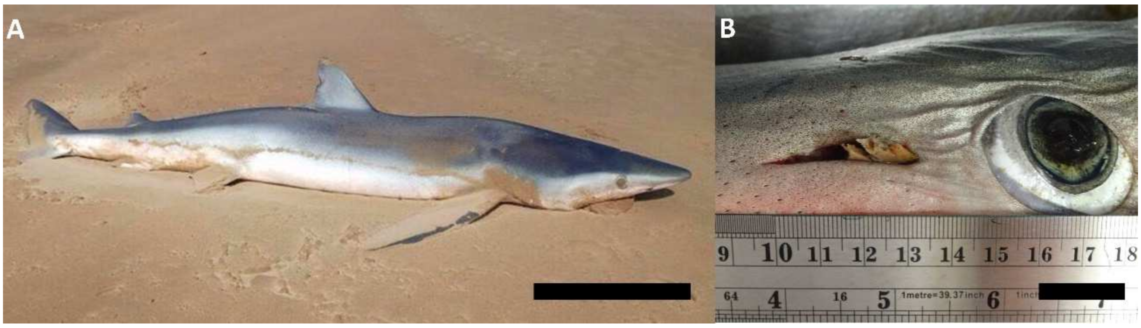

Fig 1. 'A': Picture of a blue shark (*Prionace glauca* L.) which appeared stranded in the coast of Valencia province (East Spain, western Mediterranean) with a swordfish (*Xiphias gladius* L.) rostrum pierced in its skull. Scale indicates 50 cm. 'B': details of the bill's incision close to the left eye. Scale bar indicates 2 cm.

In September, 2016, an adult female blue shark was washed ashore on the coast of Valencia, Spain, in the western Mediterranean (39.55536º N, -0.28942º W). The animal was alive when found and performed slow swimming movements, but died shortly afterwards (Fig. 1A). It measured 247 cm in total length and 186 cm in fork length. The necropsy revealed no signs of starvation or macroscopic evidence of disease. Two fishing hooks surrounded by scarred tissue were detected after removing the mandible, indicating old interactions with fisheries. The shark was in the early stages of pregnancy, having 33 less developed embryos in the left uterus and 32 more developed embryos in the right uterus. An incision 35 mm long was found 11 mm anterior to the left eye (Fig. 1B). Upon close examination, a fragment of the tip of a billfish rostrum (length 18 cm, width 0.5 cm distally and 3 cm proximally) was discovered and removed from the incision. The fragment was orientated 30º with respect to the longitudinal axis and had pierced the head parallel to the dorsoventral plane, crossing the head anterior to the pre-orbital process without causing apparent damage to the olfactory capsule or the eye (Fig. 2A, B, C). However, it had penetrated through the skull causing significant lesions in the brain (Fig. 2A, B, C). Brain damage was inferred to be the cause of death.

The rostrum fragment (Fig. 3A) was identified as belonging to a swordfish based on the following combination of features (Fierstine & Voigt, 1996): (1) flattened appearance in cross-section (i.e., depth less than half of width); (2) absence of denticles on the surface, and (3) presence of central chambers in cross-section. To estimate the total length (TL) of the swordfish, the ratio of maximum width to length of the fragment (R) was calculated providing a value of 0.169 (Fig. 3b). Then, the point in which R≈ 0.169 was estimated in the rostrum of two swordfish specimens conserved at the Osteological Collection of the Department of Zoology, University of Valencia (Fig. 3B). Assuming an isometric relationship, the distance from the tip to the breaking point was one-third relative to total snout length (TSL). Thus, TSL in our swordfish specimen was calculated to be *ca*. 48 cm. The arrangement of the paired nutrient canals observed at the breaking point in our specimen was similar to that shown in cross-sections, at roughly the same distance from the tip, in a swordfish analysed by Habegger *et al.* (2015). The allometric regression between TSL and body length from post operculum to tail fork (BL) (McGowan, 1988) suggested that the individual had a BL≈ 110 cm, corresponding to a juvenile 1-2 years old. The allometric regression between BL and round weight (RW) (Aliçli *et al.*, 2012) suggested a RW≈ 20 kg.

Blue sharks are opportunistic predators that feed on a wide variety of cephalopods and fishes (Hernández-Aguilar *et al.*, 2015, and references therein), sometimes including swordfish in their diet (Vaske-Júnior *et al.*, 2009; Markaida & Sosa-Nishizaki, 2010). However, the weight of consumed individuals (*ca.* 1 kg, see Vaske-Júnior *et al.*, 2009) is by far smaller than that estimated for the swordfish that speared and killed the blue shark in this report. The question is, therefore, what was the type of interaction between these species. One possibility is that the blue shark and the swordfish accidentally collided while feeding through the same school of fish. This reason has been invoked to explain the impalement by billfishes on non-aggressive species, such as marine turtles (Frazier *et al.*, 1994). In these cases, it is believed that collisions occur because the target preys of billfishes are under the turtles so that the billfishes cannot turn or stop abruptly (Frazier *et al.*, 1994). It is clear, however, that billfishes can spear other animals on purpose, e.g., the reported attacks on large fishes (Starck, 1960, Cliff et al., 1990, Fierstine, 1997). Thus, there is the possibility that, in the present case, the swordfish attacked the shark because it was considered a threat (see Fierstine, 1997).

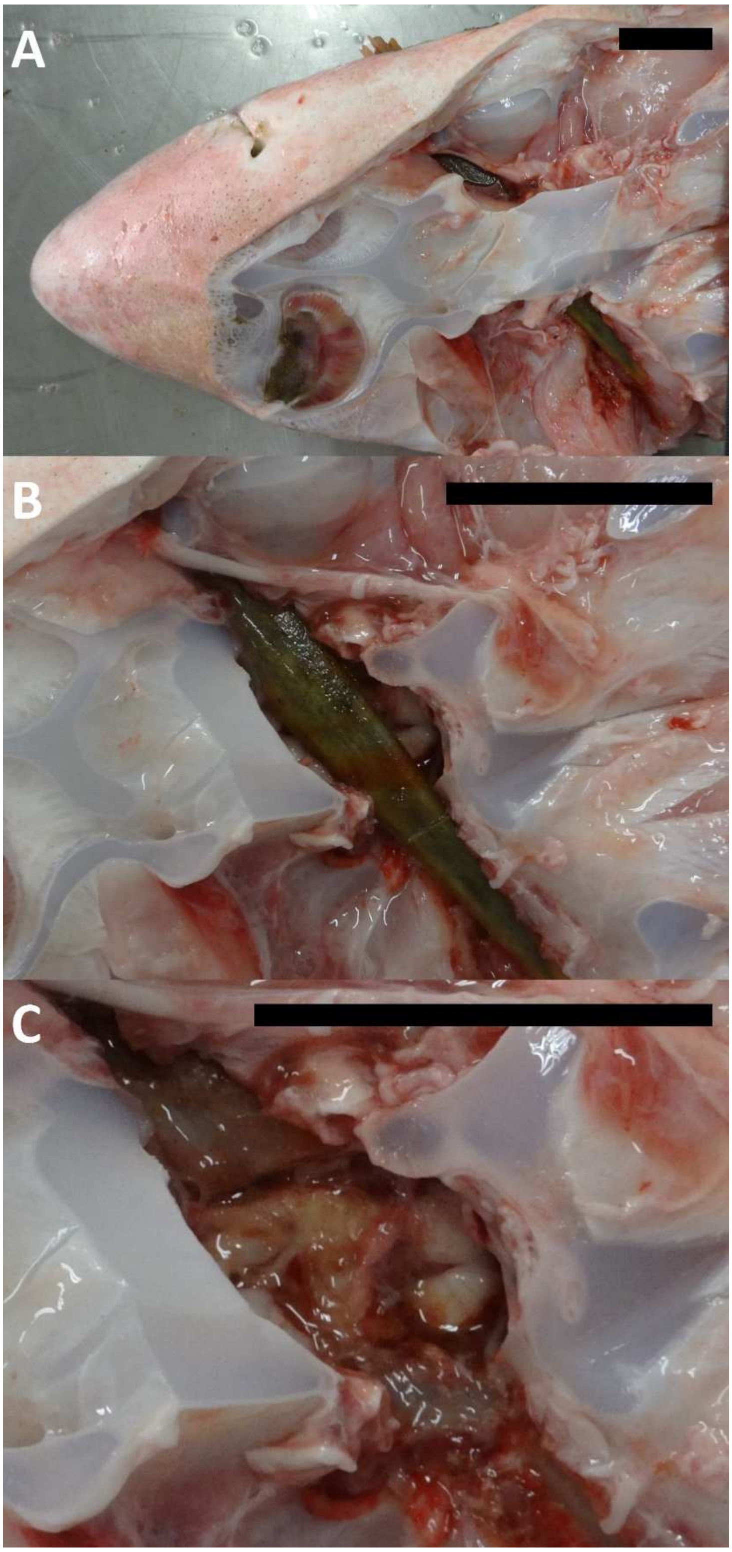

Fig 2. Pictures showing the injury inflicted by a swordfish's bill to a blue shark: 'A' ventral view of the wound showing the bill perforating both sides of the skull, 'B' ventral view of the injury showing the bill's trajectory crossing the skull, 'C' ventral view of the lesion with the bill removed. Scale bars indicate 5 cm in all pictures.

Fig 3. The fragment of the swordfish (*Xiphias gladius* L.) rostrum found impaled in a blue shark (*Prionace glauca* L.) skull, in comparison to a bill from the Osteological Collection of the Zoology Department from the Universitat de València (Spain). 'A': distal fragment of the swordfish rostrum in the blue shark skull. Scale bar indicates 2 cm. 'B': Comparison with the specimen labelled as "J. L. Granel" which measured 83 cm (TSL). Scale bar indicates 15 cm.

An important point for future analysis is whether fatal impalements are anecdotal or represent a significant cause of mortality of sharks and other animals. Cases of impalement are probably overlooked, at least for two reasons (Fierstine, 1997). Firstly, oceanic 'victims' of billfish stabbing may suffer severe injuries or death and disappear without being noticed. Secondly, wounds caused by stabbing or slashing with the rostrum may not be easily detected or attributed to impalement unless a fragment of the rostrum remains after stabbing. Another question is whether billfishes use spearing as a typical defence strategy or only as a last resort behaviour. Numerous studies indicate that the bill has important hydrodynamic and feeding-related functions (Habegger *et al.*, 2015; Videler *et al.*, 2016), thus bill breakage could be seriously disadvantageous for billfishes. However, there are several reports of apparently healthy billfishes with damaged, malformed or even missing rostra (Frazier *et al.*, 1994).

There are previous reports of putative deadly interactions of swordfish and marine turtles (Frazier *et al.*, 1996), and one short report describing putative wounds in a bigeye thresher, *Alopias superciliosus*, similar to that reported in the present study (Vacchi et al. 1999). However, the present report is the first providing direct evidence of a shark death caused by a swordfish.

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Chapter 07 – Aggressive interactions between juvenile swordfish and blue sharks in the western Mediterranean: a widespread phenomenon?

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7.1 Abstract

There are numerous reports of billfishes spearing objects, marine organisms, and even humans. Whether or not this behaviour is intentional and, if so, what is its functional meaning, are open questions. In 2016, an adult blue shark (*Prionace glauca*) was found to be killed by a juvenile swordfish (*Xiphias gladius*) in the western Mediterranean. Here we report on three more recent cases involving both species in the same area. In February 2017, an adult male blue shark was found stranded in Garrucha (Spain) with a fragment of a juvenile swordfish's rostrum (18cm long x 2cm wide at proximal end) inserted in its cranium. In March 2017, an adult pregnant female blue shark was stranded alive on the coast of Ostia (Italy) but died shortly afterwards; a fragment of a juvenile swordfish's rostrum (25x3cm) was found allocated between the eye and the cranium. In February 2018, an adult female blue shark appeared stranded in the coast of Vera (Spain), with a putative impalement injury anterior to the right eye but without an associated bill fragment. Surprisingly, X-ray and computed tomography revealed an older injury in the right nostril, with a small piece of a juvenile swordfish's rostrum (5.3x1.2cm). Finally, in August 2018, an adult male blue shark

appeared stranded alive in the coast of Manacor (Spain) with a fragment of swordfish bill (6.8x1.5cm) embedded in the snout. These cases suggest that juvenile swordfish would drive their rostrum into blue sharks as a defensive or territorial strategy that is likely to be far from anecdotal. We suggest that no regular cases of these interactions are reported because they occur at high sea and evidence of them, when available, can easily be overlooked.

7.2 Introduction

Over the last decades, impalement of inanimate objects and marine organisms by swordfish (*Xiphias gladius* L.) has been reported in a number of scientific publications and media news. There are reports of swordfish driving its rostrum into inanimate objects, such as vessels (Gudger 1940, Fierstine and Crimmen 1996), bales of rubber (Smith 1956) and submarines (Zarudski and Haedrich 1974). There are also reports of impalement on animals, such as large fishes (Starck 1960, Smith 1961), whales (Jonsgard 1962), marine turtles (Frazier *et al.* 1994 and references therein) and even people (e.g., Haddad and De Figuereido, 2009; Georgiadou *et al.*, 2010). Usually, these interactions are detected by the presence of the distal segment of the bill embedded in the substratum, which results from a transverse fracture of the bill due to the stress of the impact.

The functional meaning of this spearing behaviour is still under discussion. Carey and Robinson (1981) reported evidence of intraspecific spearing events. In other billfishes similar cases have been accounted for accidental collisions. For instance, Fierstine *et al.* (1997) linked the injuries in other billfish species to the hypothetical collisions produced while feeding on the same bait ball. Likewise, impalement of marine turtles would occur when swordfish try to prey on the fishes that use shadow beneath turtles as cover (Frazier *et al.* 1994). In other cases, however, impalement has been interpreted as intentional (Smith 1956, Ellis 2013, for a detailed historical account). The clearest evidence of aggressive behaviour comes from cases involving humans, particularly when swordfish are provoked or disturbed (Georgiadou *et al.* 2010, and references therein; Romeo *et al.* 2017, and references therein), which has sometimes resulted in fatal spearing (Gooi *et al.* 2006). Descriptions of some of the events indicate that swordfish usually try to pierce its ‘enemy’ with the bill (Romeo *et al.* 2017).

Penadés-Suay *et al.* (2017) recently reported the case of a blue shark (*Prionace glauca* L.) apparently killed by a swordfish. An adult female blue shark stranded alive but died shortly afterwards, and the necropsy revealed a fragment of the tip of a young swordfish’s rostrum that caused significant lesions in the brain. Penadés-Suay *et al.* (2017) raised the question whether or not impalements by swordfish are anecdotal, and to what extent swordfish uses spearing as defence behaviour. The answer to both questions deemed difficult because the literature contains mostly case studies, or reviews of ‘fait-acommpli’ records scattered over long periods.

In the present paper we report evidence of four additional cases of impalement of blue sharks by swordfish that occurred between February 2017 and February 2018 in the western Mediterranean. Based on the new evidences, we suggest that impalement of blue sharks could be far from anecdotal and might represent an overlooked behaviour within the defensive or territorial strategy of juvenile swordfish.

7.3 Materials and Methods

The four shark specimens included in the present study were found stranded on the beach at the moment of stranding or shortly afterwards. The sharks were measured *in situ* to the nearest cm and visually examined for external lesions. In two cases, a standard necropsy was carried out on the stranding beach (Figs. 1, 2). A detailed description of the injuries provoked by the swordfish rostrum was performed, and swordfish rostrum fragment was collected, photographed and measured to the nearest mm. In the third case (Fig. 3), the intact head of the shark was carried out to the laboratory for X-ray and computed tomography (CT). Diagnostic imaging studies included the following:

(1) Plain radiographic evaluation with a Philips Practix 400 unit (Philips Medical Systems) and a Kodak Direct View Classic CR System (Carestream Health) with 35 × 43 cm Kodak cassettes (Kodak PQ Storage Phosphor Screen Regular and 100 Microns, Carestream Health) in dorsal-ventral (DV) and lateral-lateral (LL) projections. Focal distance was 1 m, using exposure values 75 kV and 7.2 mAs based on animal size. Digital images were processed afterwards with Kodak Acquisition Software (Onyx-RAD Diagnostic Viewer) for better visualization and image interpretation.

(2) A CT was done using a Somatom Volume Access (Siemens). Acquisition parameters through head exploration of the blue shark were 5 mm slice thickness and 5 mm slice interval, with 0.5 mm retro-recon acquisition under lung and mediastinal algorithms. Images were post-processed with Osirix software version 3.3.1 (Pixmeo).

Fig 1. ‘A’: Picture of a blue shark (*P. glauca* L.) stranded in the coast of Garrucha (East Spain, western Mediterranean) with a swordfish (*Xiphias gladius* L.) rostrum in its skull. Scale indicates 50 cm. ‘B’: details of the bill stuck close to the left eye. Scale bar indicates 5 cm. ‘C’: details of the fractured swordfish rostrum. Scale bar indicates 2 cm.

Fig 2. ‘A’: blue shark (*P. glauca* L.) stranded in the coast of Ostia province (West Italy, western Mediterranean) with a swordfish (*Xiphias gladius* L.) rostrum pierced in its skull. Scale bar indicates 50 cm. ‘B’: details of the bill’s incision close to the right eye. Scale bar indicates 5 cm. ‘C’: details of the fractured swordfish rostrum. Scale bar indicates 2 cm.

Fig 3. 'A': blue shark (*P. glauca* L.) stranded in the coast of Vera (East Spain, western Mediterranean) with a swordfish (*Xiphias gladius* L.) rostrum pierced in its skull. Scale indicates 50 cm. 'B': details of the bill's incision close to the right eye. Scale bar indicates 5 cm. 'C': details of the fractured swordfish rostrum. Scale bar indicates 2 cm.

Rostrum fragments were identified as belonging to a swordfish (*X. gladius*) based on the following combination of features (Fierstine and Voigt 1996, Penadés-Suay et al. 2017): (1) flattened appearance in cross-section (i.e., depth less than half of width); (2) absence of denticles on the surface, and (3) presence of central chambers in cross-section. To estimate swordfish total body length (TL), the ratio of maximum width to length of the fragment (R) was calculated. Then, the rostrum of two swordfish specimens conserved at the Osteological Collection of the Department of Zoology, University of Valencia, were used to obtain the points in which the value of R was equal to the value obtained in each case (Penadés-Suay et al. 2017). Assuming an isometric relationship in the growth of the snout, total snout length (TSL) was calculated for each case in relation to the distance from the tip to the breaking point. To add further correction, we observed the arrangement of the paired nutrient canals at the breaking point, as shown in cross sections, to compare it with a swordfish analysed by Habegger et al. (2015). The allometric regression between TSL and body length (BL), from post operculum to tail fork, was obtained following McGowan (1988).

7.4 Results

Case 1: Garrucha (Spain)

On the 17th of February, 2017, a dead adult male blue shark (TL: 236 cm) was found washed ashore on the coast of Garrucha (Almería), Spain, 37.18833333º N 1.81555556º W (Fig. 1A). The animal had an incisive injury between the left eye and the snout. During the necropsy, the broken tip of a swordfish bill, measuring 180 mm long and 20 mm wide at the breaking point, was found inside the cranium (Fig. 1B). The bill entered the skull at 30º angle from the anteroposterior axis. The lesion was assumed to be the cause of death due to the associated brain damage. The broken tip found (Fig. 1C) could be part of a *ca*. 404 mm long snout, corresponding to a juvenile swordfish.

Fig 4. 'A': blue shark (*P. glauca* L.) stranded on the coast of Manacor (Balearic islands, western Mediterranean) with a swordfish (*Xiphias gladius* L.) rostrum piercing its snout. Scale indicates 1 m. 'B': details of the bill's incision close to the centre of the snout. Scale bar indicates 5 cm. 'C': details of the fractured swordfish rostrum. Scale bar indicates 1 cm.

Case 2: Ostia (Italy)

On the 8th of March, 2017, an adult female blue shark (TL: 260 cm) was found stranded on the coast of Ostia, Italy, 41.70861111º N 12.32638889º E (Fig. 2A). The animal was alive when found, but died shortly afterwards. The shark showed an advanced state of pregnancy, with five developed embryos inside her uterus, and no sign of starvation or disease. An incision was visible between the first gill slit and the right eye. The necropsy revealed the presence of a swordfish bill penetrating the flesh between the optic capsule and the post-orbital process (Fig. 2B). Apparently, the incision did not damage any sensory organ. The swordfish fragment (Fig. 2C) was 250 mm long and 30 mm wide at its proximal end, corresponding also to a juvenile swordfish (*ca.* 505 mm long snout).

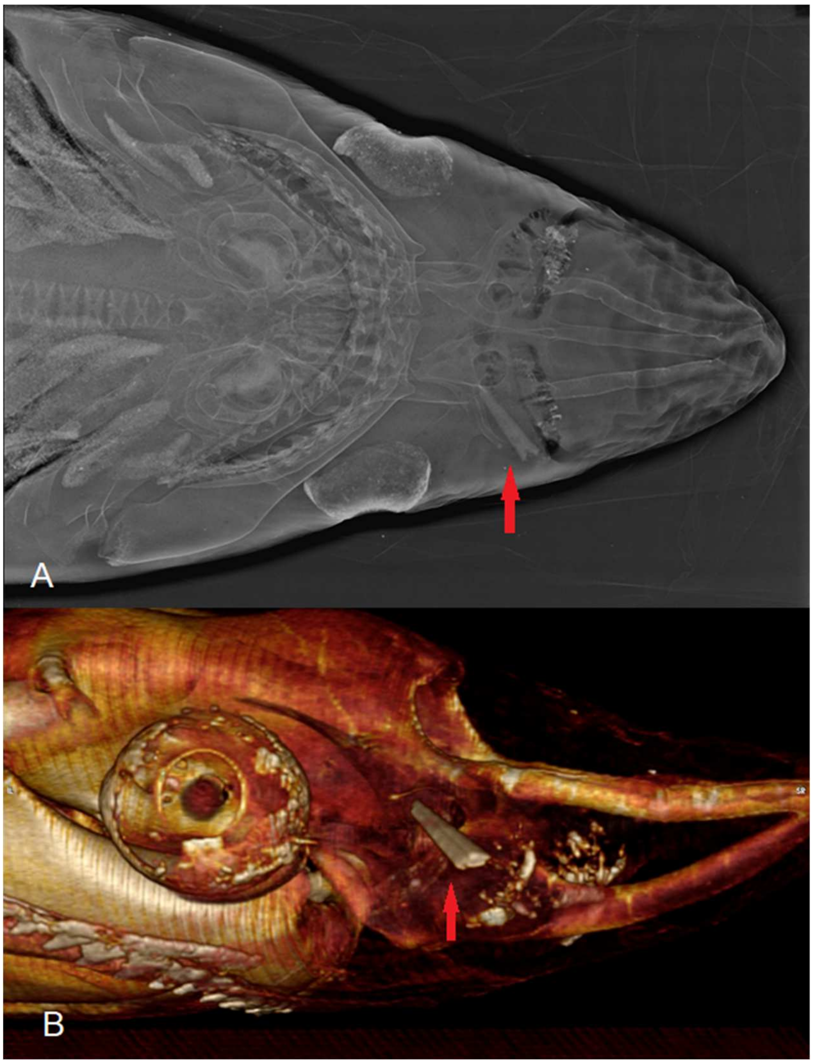

Fig 5. Pictures showing the injury inflicted by a swordfish's bill to a blue shark stranded in Vera (Spain): 'A' ventral view of the injury with X-rays, showing the fractured bill allocated inside the nostril. 'B' lateral view of the wound using Computed Tomography, showing the bill perforating the nostril. Red arrows indicate the location of the swordfish' fractured bill in both pictures.

Case 3: Vera (Spain)

On the 28th of February, 2018, an adult female blue shark (TL: 260 cm) was found dead stranded in the coast of Vera (Almería), Spain, 37.19388889º N 1.81361111º W (Fig. 3A, 3B). An incision close to the right eye was found, entering the head at 20º angle from the anteroposterior axis. No fragment of bill was found by visual inspection. Both X-ray (Fig. 5A) and CT (Fig. 5B) also failed to find fragments of bill inside the incision but, surprisingly, revealed the presence of a distal fragment of swordfish bill inside the right nostril, anterior to the firstly detected injury. No external sign of injury was apparent in this case. The cavity of the nostril was surrounded by scarred tissue (Fig. 5). The broken tip of the bill (Fig. 3C) measured 53 mm long and 12 mm wide at its proximal end, corresponding also to a juvenile swordfish (*ca.* 242 mm long snout).

Case 4: Manacor (Spain)

On the 2nd of August, 2018, an adult male blue shark (TL: 293 cm) was found stranded and returned to the water by bystanders several times within an hour in the coast of Manacor (Balearic Islands), Spain, 39.457296º N 3.277984º W (Fig. 4A). By the time the rescue team arrived, the shark was motionless in lateral decubitus close to the shore, half meter deep in the water, without reacting to any stimulus. After euthanasia, the necropsy revealed signs of starvation and the presence of a distal fragment of a swordfish bill embedded in the snout (Fig. 4B). The fragment (Fig. 4C), measuring 68 mm long and 15 mm wide at its proximal end, had entered the centre of the snout from the right posterior side in a close angle to the anteroposterior axis of the shark and was identified as belonging to a juvenile swordfish (ca. 303 mm long snout).

7.5 Discussion

This survey reports four cases of impalement of blue sharks by juvenile swordfish in the western Mediterranean in less than two years. The question that arises is the extent to which such events are instances of accidental collision between both species or of purposeful behaviour. Although we cannot rule out the first possibility, there are some lines of evidence that conform to the hypothesis that swordfish could actually have intentionally hit sharks. Firstly, all cases here examined involved only small swordfish and adult blue sharks. There is the possibility that juvenile swordfish perceive large blue sharks as a threat, given that blue sharks are opportunistic predators that feed on a wide variety of cephalopods and fishes (Vaske-

Júnior *et al.* 2009; Markaida and Sosa-Nishizaki 2010), and some studies of their diet included swordfish, although the size of swordfish consumed (ca. 1 kg, see Vaske-Júnior *et al.* 2009) seems to be smaller than that estimated for individuals in the present study. As noted above, swordfish frequently displays pugnacious behaviour, even towards *prima facie* non-threatening species, including humans (Smith 1956, Georgiadou *et al.* 2010, Ellis 2013). Secondly, in all cases of impalement on blue sharks reported so far (Penadés-Suay *et al.* 2017; present study), the angle of piercing indicates a nearly horizontal strike with respect to the sharks' anteroposterior axis. Although there is no reason to exclude the possibility of an accidental collision during an act of predation to the same prey, a voluntary offense to the blue shark by juvenile swordfish is to be considered, given that the type of impalement described could hardly result from random collisions. Finally, at least the shark stranded in the coast of Vera showed signs of two diverse interactions with swordfish happened at different times, which would refer to two swordfish interactions.

In this context, one may wonder if swordfish use spearing as a typical defence strategy/territoriality aggression or only as a last resort behaviour against blue sharks. This is difficult to ascertain. On one hand, several studies suggest that the swordfish' bill has important hydrodynamic and feeding-related functions (Habegger *et al.* 2015, Videler *et al.* 2016) thus bill breakage could be seriously disadvantageous for swordfish. On the other hand, at least in billfishes, there are several reports of apparently healthy individuals with damaged, malformed or even missing rostra (Frazier *et al.* 1994). This raises the possibility that juvenile swordfish may experience a trade-off between the benefits of repelling a perceived serious threat and the potential impairment of swimming performance if the bill eventually breaks.

A third important question concerns the frequency of such intentional impalements. The present study, and that by Penadés-Suay *et al.* (2017), report on stabbings that were inflicted on the head and, in some cases, resulted in the death of the victim. However, blue sharks are oceanic predators that only exceptionally are washed ashore when moribund or dead (hence the lack of studies reporting these events, see Neto *et al.* 2013). In general, most carcasses of large marine vertebrates disappear at sea (Carretta *et al.* 2016 and references therein). Hence, there is the possibility that many cases of fatal impalement of blue sharks have gone undetected because carcasses were consumed by scavengers or sank before they could be discovered. On the other hand, non-fatal impalement lesions could easily be overlooked. Blue sharks are target species of long-line fishery and, therefore, many individuals are visually exposed in fish markets. Also, the fact that only fragments from juvenile swordfish were found leaves the question on whether they are more prone to breakage than those of adults, giving then an added difficulty to finding evidence of the collisions in those cases. However, our study shows that not all impalements result in a breakage of the swordfish' bills, thus leaving only a small external incision that is difficult to draw attention or even to be noticed unless it is a specific target for examination. Moreover, old lesions are not visible externally, even when bill fragments remain in the scarred tissue, unless sophisticated technologies (X-rays, CT) are used, and only a deep, thorough necropsy could reveal the evidence of such past interactions. In fact, the finding of an old impalement in shark 3 in our study was serendipitous.

In conclusion, our study reports four cases within a year and only in the Western Mediterranean basin, suggesting the relevance of this phenomenon. As an example, there is one short report describing putative wounds in a bigeye thresher *Alopias superciliosus* (Vacchi *et al.* 1999), similar to the case of a blue shark reported in the same region by Penadés-Suay *et al.* (2017). More attention on this matter is needed, looking for evidences in all necropsy protocols and investigating this kind of interactions in other shark species.

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Conclusions

The present study provides, for the first time, a quantitative report on the cestode fauna in four elasmobranch species, i.e., the shortfin mako shark (*Isurus oxyrhinchus*); the blue shark (*Prionace glauca*); the marbled electric ray, (*Torpedo marmorata*), and the common torpedo (*Torpedo torpedo*), in Iberian waters, and investigates the role of key host species-specific traits in providing structure at infracommunity level. This study also documents unexpected, but increasingly noticed, agonistic interactions between blue sharks and swordfish (*Xiphias gladius*) over recent years, discussing their functional meaning and population impact.

As the outcome of this study, the following conclusions have been reached:

1. The parasite fauna of the shortfin mako in the North East Atlantic (Galicia) was composed of 6 species, namely: *Clistobothrium montaukensis*, *Gymnorhynchus isuri, Ceratobothrium xanthocephalum*, *Nybelinia lingualis*, *Dinobothrium septaria* and *Phyllobothrium cf. lactuca*. Adult specimens were detected in the samples of *C. montaukensis*, *G. isuri* and *C. xanthocephalum*. *Dinobothrium septaria* represents a first record for makos, but it likely constitutes an accidental infection.

2. The helminth infracommunities of the shortfin mako are described for the first time. Infracommunities were depauperate and composed of random combinations of cestode species. These two observations apparently conform to theoretical expectations for large, vagile oceanic predators. In particular, transmission rates of trophically-transmitted parasites should be hampered by a ‘dilution’ effect of infective stages in the oceanic habitat, coupled with a high mobility of the definitive hosts. However, a comparison of mean species richness and mean total abundance of cestodes per host did not significantly differ between shortfin mako and other oceanic sharks when compared with elasmobranchs from other habitats. Perhaps the large body size and high prey consumption rates of oceanic sharks offset the above-mentioned ‘dilution’ effects. Additionally, or alternatively, parasites of oceanic sharks may have expanded the use of intermediate hosts through the trophic web to spread out the risk of failure to complete their life cycles.

3. The parasite fauna of the blue shark is described from samples collected in fisheries from the NE Atlantic (Galicia) and W Mediterranean (Valencia), and

for sharks stranded along the coasts of the Valencian region (central Mediterranean coast). Four tapeworm taxa were common to all samples, i.e. *Anthobothrium caseyi*, *Platybothrium auriculatum*, *Prosobothrium armigerum* and Tetraphyllidea fam. gen. sp.; one was shared between fish from Galicia and Valencia (stranded), i.e. *Molicola horridus*, and 4 were found only in Galicia, i.e. *Scyphophyllidium* sp., Phyllobothriinae gen. sp. 1 and 2, and Trypanorhyncha fam. gen. sp. Adult specimens were found only for *A. caseyi*, *Pla. auriculatum*, *Pro. armigerum* and *M. horridus*.

4. Cestode infracommunities of blue sharks in Iberian waters show three apparent features: (1) mean species richness and mean Brillouin's index did not differ between shark samples; (2) differences in community composition concerned rare immature forms (for which blue sharks likely are non-hosts) and *M. horridus*, which could be absent from the sample of juvenile blue sharks captured in Valencia because they cannot consume the large fish prey that act as intermediate hosts for this parasite; (3) there were significant differences of abundance for all common tapeworm species, but with little geographical signal. A comparison at a global geographical scale using data from 5 additional surveys largely replicated the above patterns, i.e., remarkable similarity in richness and species' composition of infracommunities across localities, but significant variability of infection levels for all common species.

5. These results were interpreted based on a thorough examination of global patterns of specificity for the 15 tapeworm species that have been reported as adults in blue sharks. In summary, the cestode fauna of blue sharks is composed of a core group of 5-6 exclusive species with the potential to appear in any locality due to the enormous vagility to this species. The occurrence of generalist species of Trypanorhyncha is less predictable depending on the sympatric comunity of elasmobranchs, and makes a minor contribution to community composition. Local infection levels of particular species will largely be driven by the frequency of consumption of intermediate and/or paratenic hosts. Overall, the influence of ecological factors upon the tapeworm communities of blue sharks, and probably other elasmobranchs, is highly constrained by historical factors, i.e., the strong host specificity of most of their tapeworm species. Such historical idiosyncrasy could defy broad generalizations for elasmobrachs as a whole.

6. The helminth parasite fauna of marbled electric rays, *Torpedo marmorata*, and common torpedoes, *T. torpedo*, is described from samples obtained from accidental captures in artisanal fisheries of the Gulf of Valencia

(western Mediterranean). We detected three cestode species in the samples: *Acanthobothrium* sp., *Rhodobothrium* sp. and Phyllobothriidea gen. sp.. Infracommunities were very depauperated, Individuals of the genus *Acanthobothrium*, including adult specimens, occurred in both host species. The finding of 8 adult specimens of *Rhodobothrium* sp. in two individuals of *T. marmorata* represent a new host record. At host individual level, the intestinal helminth fauna in both species was extremely depauperate, with only 0.90 and 0.53 species per host, respectively, with mean intensities ranging just from 4 to 7.5 worms per host. A comparison with previous surveys indicated that these features appear to be common to *Torpedo* spp.; as many as 3 species of *Torpedo* consistently harbour extremely depauperate cestode infracommunities regardless of locality.

7. An investigation was carried out to test whether the electric organ discharges (EOD) that torpedoes use to stunt their prey could impair the infective stages of the trophically-transmitted parasites that prey harbour. Using a surrogate experimental model, i.e., *Anisakis* larvae in blue whiting (*Micromesistius poutassou*), a global effect of EOD on survival of larvae was not detected, but a significantly higher mortality rate was observed over time in the treatment group. Accordingly, EODs would be expected to hamper the establishment of infective stages to a variable degree, the impact being possible higher in worms devoid of a cuticle, such as tapeworms. This is the description of a novel effect of EOD in the animal kingdom.

8. A comparison on estimated species diversity and mean species richness of tapeworms at host individual level revealed (1) Torpediniformes had the lowest tapeworm diversity of all Batoidea orders; (2) *Torpedo* spp. consistently had the lowest mean cestode richness at host individual level, and this could not be related to other host factors influencing cestode diversity in chondrichthyans, i.e., body size, trophic level or dietary breath. However, contrary to our expectations, little differences of cestode richness were found between ‘strong-EOD’ (Torpedinidae and Hypnidae) and ‘weak-EOD’ (Narcidae and Narkidae) torpediniforms. Thus, evidence supporting an unambiguous contribution of EODs to depauperate cestode assemblages requires further research.

9. At least five cases of impalement of blue sharks by juvenile swordfish are reported in the western Mediterranean in less than three years. In all cases injuries appeared on the head and were considered to be the primary cause of death. On one occasion, there was unequivocal evidence of previous

non-lethal injuries of the same nature. Overall, the evidence suggests that juvenile swordfish drive their rostrum into blue sharks as a defensive or territorial strategy that is likely to be far from anecdotal. The actual frequency of these interactions is difficult assess but it is likely underestimated because they occur at high sea and evidence of them, when available, can easily be overlooked. More attention to this phenomenon is needed because of its potential role as a mortality factor.

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