



Contribution to the Theme Section 'Small pelagic fish: new research frontiers'

REVIEW

Parasites of small pelagics reflect their role in marine ecosystems

Kym C. Jacobson^{1,*,#}, David J. Marcogliese^{2,4,#}, Ken MacKenzie^{3,#}

¹National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center, Newport, Oregon 97365, USA

²Aquatic Contaminants Research Division, Water Science and Technology Directorate, Science and Technology Branch, Environment and Climate Change Canada, St. Lawrence Centre, Montreal, Quebec H2Y 2E7, Canada

³School of Biological Sciences (Zoology), University of Aberdeen, Aberdeen AB24 2TZ, UK

⁴Present address: St. Andrews Biological Station, Fisheries and Oceans Canada, St. Andrews, New Brunswick E5B 0E4, Canada

ABSTRACT: Small pelagics occupy an intermediate trophic level in marine ecosystems, serving as prey for a variety of predators and thus playing a very important role in these ecosystems. This review collates information gleaned from parasitological studies of small pelagics (fish, squid and euphausiids) and describes the valuable biological information they can provide. We describe why parasitology studies are important and how they have contributed to our understanding of the role of small pelagics in marine ecosystems. Pertinent general patterns in marine parasite ecology relevant to trophic interactions in small pelagics, including variations in parasite faunas with features such as host size, depth distribution and feeding behaviour are synthesized. With their relatively long life spans relative to stomach contents and stable isotopes, trophically transmitted parasites can provide a unique dietary history for the host. Therefore, we summarize the trophically transmitted parasites found most frequently in small pelagics and assess the potential of different parasite taxa as indicators of host diet. The use of multiple techniques, including stomach contents and stable isotopes, along with parasites, are evaluated to better reveal fish diets. Parasites provide complementary, and additional, information compared to other techniques. Furthermore, we discuss how the presence of certain parasites in small pelagics can be used to infer their main predators and emphasize the neglected but important role of parasites in elucidating a host's role in marine food webs. Lastly, we identify important gaps in our knowledge of the parasites of small pelagics and what can be done to fill these gaps.

KEY WORDS: Trophically transmitted parasites · Fish · Euphausiids · Squid · Diet · Predators · Food web

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Small pelagics, fishes and many invertebrates, are integral to the structure and function of coastal and marine ecosystems, transferring energy from phytoplankton and zooplankton up the food web to piscivorous fish, birds and mammals. Despite this impor-

tant ecosystem function (Pikitch et al. 2012), their trophic role in many cases is relatively poorly understood (Boldt et al. 2022). For example, Boldt et al. (2022) mapped 50 yr (1970–2020) of scientific literature on 11 species of small pelagic fishes found in a number of Canadian fisheries and identified the diet of small pelagic fishes among the most important

*Corresponding author: kym.jacobson@noaa.gov

#All authors contributed equally

[§]Advance View was available March 7, 2024

knowledge gaps. Their review also pointed out that as nations move toward implementing more ecosystem-based fisheries management, the tools required to do so rely on understanding trophic linkages. Trophic information is also fundamental to understanding the responses of small pelagic populations to bottom-up processes (Peck et al. 2021). In systems where diet is difficult to ascertain (for various reasons), parasites have been used to indicate trophic relationships. However, in major recent syntheses of trophic studies on small pelagics, there was no mention of parasites (Peck et al. 2021, Boldt et al. 2022). In this review, we include squid and euphausiids based on their similar roles to small pelagic fin fishes in the marine food web and their inclusion in some fishery management plans (e.g. US Mid-Atlantic Fishery Management Council and Pacific Fishery Management Council).

The use of parasites as indicators of fish diet was described and reviewed by Williams et al. (1992), among numerous others. Trophically transmitted parasites make their way upwards through the food chain towards their ultimate target — a suitable final host in which they can mature and reproduce (Fig. 1). The different developmental stages of these parasites occur at different levels within a food web and can reveal dietary connections between hosts. Parasites use different approaches to infect a host depending upon the parasite taxa and the complexity of their life cycles. Parasites with a direct life cycle do not require an intermediate host and often capitalize on direct contact between hosts, with free-swimming infective stages attaching to or penetrating a host. Parasites with complex life cycles have one or more intermediate hosts that are required for development. Although some of these parasites will infect fish by penetration of the skin or via a blood-sucking vector, parasites with complex life cycles will often use trophic transmission by predation on an intermediate host to infect subsequent hosts. Many parasites at some point in their life cycles may also use paratenic (transport) hosts, which are not required for growth or development but, by acquiring and hosting larval parasite stages, can help transport them to their definitive hosts when consumed (Fig. 1) (Marcogliese 1995, 2007). Given sufficient information on their life cycles and degree of host specificity, their presence in a fish can reveal evidence

of its dietary history, possibly going back months or even years in the case of some long-lived helminth larvae (MacKenzie 1985). This is in contrast to the examination of stomach contents, which only reveals items more recently consumed by the fish. Even in fish with otherwise empty stomachs or unrecognizable prey, parasites can imply past feeding history. Indeed, parasites can reveal that soft-bodied animals such as coelenterates, which are not normally found in the gut contents of fishes, are more common prey items than previously believed (Marcogliese 2005).

The parasite fauna of small pelagic fishes encompasses a broad range of taxa, including both Protozoa and Metazoa. Examples of protozoans found in small pelagics include ciliates, apicomplexans, microsporidians and parasites in the class Mesomycetozoa (a causative agent of epizootics in small pelagic fishes; Jones 2005), which sits between the plants and animals in recent classifications (Mendoza et al. 2002). The Metazoa include Myxozoa, Arthropoda and the helminth taxa Nematoda, Trematoda, Monogenea, Cestoda and Acanthocephala. Most small pelagics, including squid and euphausiids, occupy an intermediate level in a food web, so they serve as important intermediate or transport hosts for helminth larval stages. Parasitic larval stages found in small pelagics include nematode larvae, cestode plerocercoids, acanthocephalan cystacanths and trematode metacercariae. These larval parasites use different

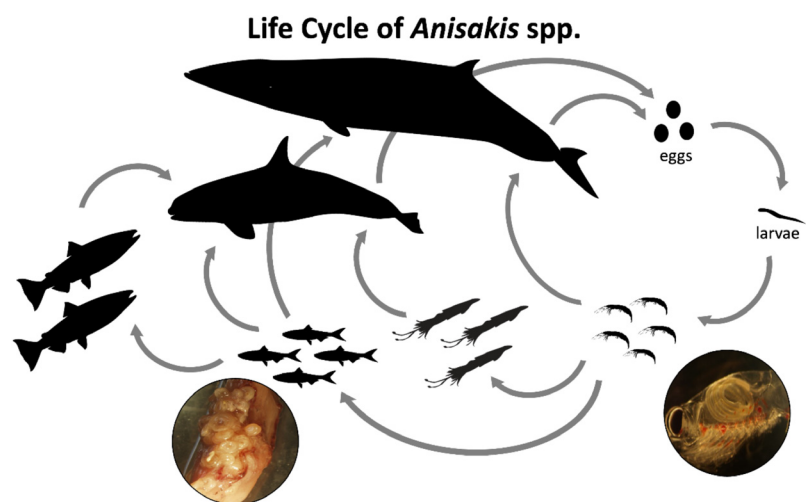


Fig. 1. Anisakid nematodes are among the most ubiquitous parasites in the marine food web. Adult worms mature and reproduce in the stomachs of cetaceans. Their eggs are released with feces and hatched larvae are consumed by intermediate host euphausiids (note right inset photograph of larva inside euphausiid). Parasites may pass directly to baleen whales feeding on euphausiids or to paratenic (transport) hosts, including forage fish, predatory fish and squid (note left inset photograph of larvae encysted on outside of digestive tract of a fish). Whales and dolphins feeding on these hosts also acquire infection

organisms, mostly small invertebrates, as first intermediate hosts and can thus indicate the relative importance of these organisms in the diet of small pelagics. Adult gastrointestinal helminths, in contrast, for which small pelagic fishes serve as final hosts, are useful indicators of the second intermediate or paratenic hosts on which the fish have fed (Fig. 2).

The goals of this review are thus to provide a global perspective of parasitological studies of small pelagics and how they have contributed to our understanding of their role in marine ecosystems. To achieve these goals, we discuss and analyse the results of studies that utilized parasites of small pelagic fin fishes, squid and euphausiids to infer their hosts' diets, in addition to those comprehensive parasitological studies from which such information can be derived. Furthermore, we compare studies that have used coordinated efforts, combining analyses of parasites with stomach contents and/or stable isotopes. Lastly, we discuss how parasites in small pelagic fishes may be indicators of their predators and their roles in local food webs.

2. GENERAL PATTERNS IN MARINE PARASITE ECOLOGY

There are several important metrics of parasite assemblages for ecologists. For individual parasite species in a sample of hosts, these include prevalence (the percentage of hosts infected), mean abundance (the mean number of parasites recovered from all hosts examined) and mean intensity (the mean number of parasites recovered from infected hosts only) (Bush et al. 1997). For communities of parasites, species richness and other diversity metrics are as informative as they are for free-living communities. For many groups of vertebrate hosts, parasite species richness can be predicted by certain ecological factors of the hosts, including population density, body size, distributional range and/or latitude (Poulin 2007). However, results can be inconsistent when controlling for host phylogeny, as evolutionary relationships between host and parasite species are also a driving factor (Poulin 2007). Among marine fishes in particular, parasite diversity depends on feeding behaviour, the availability of other hosts in parasite life

cycles, depth distribution and host migration (Klimpel et al. 2006a).

While to our knowledge there are no studies of patterns of parasite species richness specifically in marine small pelagic fishes, there are a few that examine trophically transmitted endoparasites of marine fishes in general that are illuminating. In a comprehensive study examining the effects of host length, diet, habitat and latitude, length was positively correlated with gastrointestinal parasite species richness in freshwater and marine fish (Poulin 1995). Parasite species richness also increased with the proportion of animal food in the host diet. Presumably, larger hosts consume more prey and are thus exposed to more trophically transmitted parasites, thereby providing more space and resources for parasites (Poulin 1995). In a detailed study of 50 species of coastal marine fish off Brazil, body length was positively correlated with total parasite species richness, and piscivorous fish had higher total richness than planktivores, although the latter relationship was lost when controlling for phylogeny (Luque et al. 2004). Furthermore, benthic and benthopelagic fishes had greater total parasite species richness than pelagic planktivores. When considering endohelminths only, predatory feeding was associated with greater parasite taxonomic distinctness, a measure of diversity, but not parasite species richness (Luque et al. 2004). Luque & Poulin (2004) examined the effects of ecological factors on species richness and abundance of larval helminth parasites

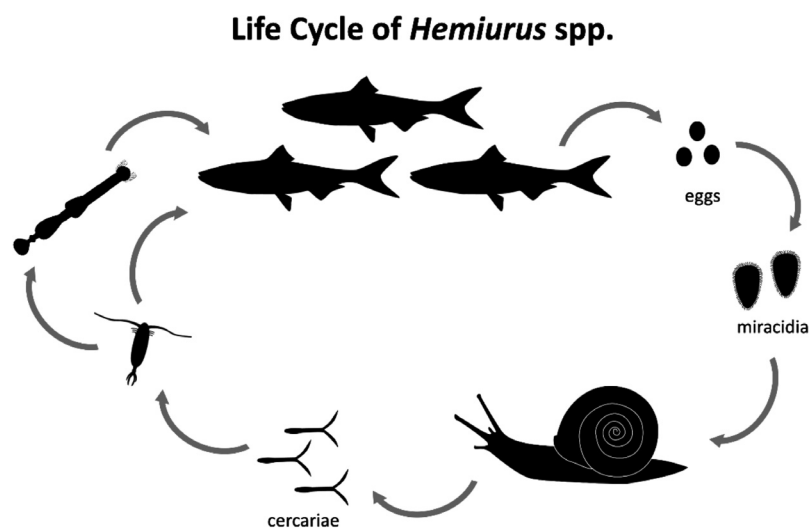


Fig. 2. Trematodes in the genus *Hemiurus* mature and reproduce in fish, including small pelagic species. Their eggs are released with feces and hatch into free-swimming miracidia, which penetrate mollusks that serve as first intermediate hosts. Asexually produced free-swimming cercariae released from the mollusk are ingested by calanoid copepods. These are eaten by a fish or a chaetognath, which transfers the parasite to fish when consumed. The adult parasite may also be transmitted between fish by predation

across the same 50 host species as Luque et al. (2004) and found that larval parasite abundance was positively associated with host length, after accounting for host phylogeny.

Parasite faunas of marine fishes are also affected by bathymetry (Poulin 2007). In the open ocean, the water column is divided into epipelagic, mesopelagic (200–1000 m) and bathypelagic (>1000 m), and pelagic fishes are categorised according to which zone they occupy (Madin & Madin 1995). From the diet point of view, however, categorising fish according to depth zone is complicated by the fact that many demersal marine fishes undertake diurnal vertical migrations to feed on pelagic organisms (Campbell 1983, Houston & Haedrich 1986, Nacari et al. 2022). Many pelagic species also migrate between oceanic and continental shelf waters; such species are categorised as pelagic–neritic (Froese & Pauly 2023). Furthermore, other species change habitats with ontogeny and only the adult stages are categorised by depth. Nevertheless, parasite diversity generally decreases with depth in pelagic fishes due to the decrease in pelagic biomass or prey availability at greater depths, which means there are fewer prey organisms to serve as intermediate hosts for fish feeding in these zones (Campbell 1983, Gartner & Zwerner 1989, Marcogliese 2002). Total species richness and the intensity of parasitic infections are highest in the epipelagic and benthic zones, decrease in vertically migrating mesopelagics and are lowest in deep non-migratory mesopelagic and bathypelagic fishes (Marcogliese 2002).

George-Nascimento (1987) and Marcogliese (2002) predicted that small fish situated in the middle of the food web will have richer parasite communities than those higher up or lower down because they serve as intermediate, paratenic and definitive hosts for a variety of parasites. In a study of 182 species of marine fish, the highest species richness of both endo- and ectoparasites was seen in small and mid-sized fishes (Poulin et al. 2011). In a comprehensive study that combined 303 species of both freshwater and marine fishes, maximum fish length was a better predictor of larval endohelminth species richness than trophic level, although both were strongly positively correlated with each other (Poulin & Leung 2011). The proportion of larval parasite taxa in fish less than 20 cm was double the proportion in fish greater than 100 cm. This proportion drops as host maximum body size and trophic level increase (Poulin & Leung 2011). In general, smaller fish species appear to host more species of larval parasites than do larger fish species, supporting their important central role in the aquatic food webs.

3. PARASITES OF SMALL PELAGICS: THEIR LIFE CYCLES AND POTENTIAL AS INDICATORS OF HOST DIET

Tables 1 & 2 summarize current knowledge of the life cycles of parasites of small pelagics. Table 1 shows examples of parasites that use small pelagics as second intermediate or transport hosts, while Table 2 shows examples of parasites that use small pelagics as definitive (final) hosts. The small pelagic species listed in these tables are those that have been the subjects of the most parasitological studies, which also includes those species targeted by important fisheries worldwide. The hosts listed represent merely a subset of the total number of small pelagic species in the world's oceans, most of which have either not, or only rarely, been examined for parasites.

Based on the information in these tables, the potential of parasites as indicators of the diet of small pelagics can be assessed. With few exceptions, most trophically transmitted adult helminth parasites have life spans of up to about 1 yr in the alimentary tract of their fish hosts, so they can provide a better overall picture of dietary differences between host species than the more transient dietary items. Larval helminths, with life spans extending to several years in their intermediate hosts, can be useful as indicators of diet over even a much longer time period.

The major parasite taxa best represented in Table 1 are the Cestoda (tapeworms) and Nematoda (roundworms) that use small pelagics as second intermediate or paratenic hosts to facilitate progress from their invertebrate first intermediate (precursor) hosts to the definitive hosts in which they will mature. Tetraphyllidean cestodes in particular are frequently reported from many species of teleost fish and are amongst the most common parasites of small mesopelagic fishes such as those in the families Myctophidae and Paralepididae (see Klimpel et al. 2001, 2010). Most of the cestodes infecting small pelagics are acquired through feeding on a variety of crustaceans, although tetraphyllideans also use other organisms as first intermediate hosts. The wide range of first intermediate hosts used by cestodes limits their use as indicators of the diet of their fish second intermediate hosts.

In the Nematoda, the taxon in Table 1 with the greatest number of host species listed is the genus *Anisakis*. This genus represents one of the most abundant groups of marine parasites. Euphausiids serve as obligate first intermediate hosts, reflecting the important role of these crustaceans in the diet of small pelagic fish. Piscivorous small pelagic fish and squid may also serve as paratenic hosts when they eat

Table 1. Examples of trophically transmitted parasites infecting selected small pelagic species as second intermediate or transport (paratenic) hosts. Only parasite taxa for which life cycle information is available are shown. These parasites may be used to determine diet of the pelagic hosts. In addition, predators of the fishes may be inferred from the parasite life cycles. Fish scientific names and common names listed are according to Froese & Pauly (2023)

Parasite	Precursor (first intermediate and paratenic host(s))	Small pelagic hosts	Definitive hosts	Key references
Acanthocephala Polymorphidae (<i>Corynosoma</i> , <i>Bolbosoma</i>)	Peracaridan crustaceans, mainly amphipods	<i>Clupea harengus</i> <i>Clupea pallasii</i> <i>Engraulis anchoita</i> Euphausiids (krill) <i>Hypomesus pretiosus</i> <i>Mallotus villosus</i> <i>Osmerus eperlanus</i> <i>Osmerus mordax</i> <i>Trachurus trachurus</i>	Marine mammals	Leidenberger et al. (2020)
Cestoda Bothriocephalidean plerocercoids (<i>Eubothrium</i> spp.)	Copepods	<i>Osmerus eperlanus</i> <i>Clupea harengus</i>	Salmonid fish	Saksvik et al. (2001), Vik (1963)
Diphyllidean plerocercoids	Crustaceans	Euphausiids (krill)	Elasmobranchs	Tyler (2006)
Diphyllbothriid plerocercoids	Copepods	<i>Clupea harengus</i> <i>Clupea pallasii</i> <i>Engraulis anchoita</i> <i>Hypomesus pretiosus</i> <i>Mallotus villosus</i> <i>Maurolicus muelleri</i> Myctophidae <i>Scomber japonicus</i> <i>Scomber scombrus</i> <i>Trachurus trachurus</i>	Marine mammals	Kuchta & Scholz (2017)
Tetraphyllidean plerocercoids (also reported as <i>Scolex pleuronectis</i> and <i>S. polymorphus</i>)	Gastropod and bivalve molluscs, hermit crabs, <i>Amphioxus</i>	<i>Ammodytes tobianus</i> <i>Chauliodus sloanei</i> <i>Clupea harengus</i> <i>Clupea pallasii</i> <i>Cololabis saira</i> <i>Engraulis anchoita</i> <i>Engraulis encrasicolus</i> <i>Engraulis mordax</i> <i>Mallotus villosus</i> <i>Maurolicus muelleri</i> Myctophidae <i>Osmerus mordax</i> Paralepididae <i>Sardina pilchardus</i> <i>Sardinops sagax</i> <i>Scomber scombrus</i> <i>Sprattus sprattus</i> <i>Trachurus trachurus</i>	Elasmobranchs	Holland & Wilson (2009), Jensen & Bullard (2010), McDermott et al. (2010)
Phyllobothriid plerocercoids	Crustaceans	<i>Clupea pallasii</i> <i>Cololabis saira</i> Myctophidae Paralepididae (barracudinas) <i>Scomber japonicus</i> Squid	Elasmobranchs	Ruhnke et al. (2017)
Trypanorhynch plerocercoids <i>Nybelinia</i> spp.	Euphausiids and possibly other crustaceans	<i>Engraulis mordax</i> Myctophidae Paralepididae (barracudinas) <i>Scomber japonicus</i> Squid	Carcharinid sharks	Shimazu (1999)

(Table 1 continued on next page)

Table 1. (continued)

Parasite	Precursor (first intermediate and paratenic host(s))	Small pelagic hosts	Definitive hosts	Key references
<i>Grillotia</i> spp.	Calanoid copepods	<i>Clupea harengus</i> <i>Clupea pallasii</i> <i>Osmerus eperlanus</i> <i>Sardina pilchardus</i> <i>Scomber scombrus</i> <i>Trachurus trachurus</i>	Elasmobranchs (Rajidae)	Ruszkowski (1934)
<i>Hepatoxylon</i> spp.	Crustaceans	Myctophidae <i>Scomber japonicus</i> Squid	Pelagic sharks	Palm (2004)
<i>Lacistorhynchus</i> spp.	Harpacticoid copepods	<i>Clupea harengus</i> <i>Clupea pallasii</i> <i>Scomber scombrus</i> <i>Trachurus trachurus</i>	Triakid sharks	Sakanari & Moser (1985)
<i>Tentacularia coryphaenae</i>	Crustaceans	<i>Sardinops sagax</i> <i>Scomber scombrus</i> Squid <i>Trachurus trachurus</i>	Sharks, especially carcharinids	Palm (2004)
Nematoda <i>Anisakis</i> spp.	Euphausiids	<i>Allosmerus elongatus</i> <i>Ammodytes dubius</i> <i>Argentina silus</i> <i>Bathylagus euryops</i> <i>Borostomias antarcticus</i> <i>Chauliodus sloani</i> <i>Clupea harengus</i> <i>Clupea pallasii</i> <i>Cololabis saira</i> <i>Engraulis anchoita</i> <i>Engraulis encrasicolus</i> <i>Engraulis mordax</i> Euphausiids <i>Hypomesus pretiosus</i> <i>Mallotus villosus</i> <i>Maurollicus muelleri</i> Myctophidae <i>Osmerus eperlanus</i> <i>Osmerus mordax</i> Paralepididae <i>Sardina pilchardus</i> <i>Sardinops sagax</i> <i>Scomber japonicus</i> <i>Scomber scombrus</i> <i>Sprattus sprattus</i> Squid <i>Trachurus trachurus</i>	Cetaceans	Smith (1983), Klimpel & Palm (2011)
<i>Ascarophis</i> spp.	Decapod and amphi- pod crustaceans	<i>Engraulis anchoita</i> <i>Mallotus villosus</i> Myctophidae <i>Osmerus eperlanus</i> <i>Osmerus mordax</i> Squid	Teleosts	Uspenskaya (1953), Jackson et al. (1997)
<i>Hysterothylacium</i> spp.	Copepods, amphi- pods, euphausiids, crab larvae	<i>Ammodytes tobianus</i> <i>Argentina silus</i> <i>Clupea harengus</i> <i>Clupea pallasii</i>	Teleosts	Køie (1993)

(Table 1 continued on next page)

Table 1. (continued)

Parasite	Precursor (first intermediate and paratenic host(s))	Small pelagic hosts	Definitive hosts	Key references
		<i>Engraulis anchoita</i> <i>Engraulis encrasicolus</i> <i>Engraulis mordax</i> <i>Hypomesus pretiosus</i> <i>Mallotus villosus</i> <i>Maurollicus muelleri</i> Myctophidae <i>Osmerus eperlanus</i> <i>Osmerus mordax</i> <i>Sardina pilchardus</i> <i>Sardinops sagax</i> <i>Scomber japonicus</i> <i>Scomber scombrus</i> <i>Sprattus sprattus</i> <i>Trachurus trachurus</i>		
<i>Contracaecum osculatum</i> s.l.	Calanoid copepods, <i>Balanus</i> larvae, gammarids	<i>Ammodytes tobianus</i> <i>Clupea harengus</i> <i>Mallotus villosus</i> <i>Osmerus eperlanus</i> <i>Osmerus mordax</i> <i>Sprattus sprattus</i>	Pinnipeds	Køie & Fagerholm (1995), Pawlak et al. (2019)
<i>Porrocaecum</i> sp(p).	Annelids	Squid	Birds	Anderson (1992)
<i>Spinitectus</i> sp(p).	Crustaceans, insects	Squid	Teleost fish	Anderson (1992)
Trematoda				
Didymozoidae	Planktonic invertebrates	<i>Clupea harengus</i> <i>Engraulis mordax</i> Myctophidae Squid	Teleosts, especially scombroids	Pozdnyakov & Gibson (2008), Louvard et al. (2021)
Opecoelidae				
<i>Pseudopecoelus japonicus</i>	Unknown	Euphausiids	Teleosts	Shimazu (1971)
Syncoelidae				
<i>Paronatrema</i> sp.	Unknown	Euphausiids	Elasmobranchs	Shimazu & Kagei (1978)
<i>Copiatestes</i> sp.	Unknown	Euphausiids	Teleosts	Morales-Ávila et al. (2015)
<i>Syncoelium</i> sp.	Unknown	Euphausiids	Elasmobranchs	

infected prey (Fig. 1) (Køie et al. 1995, Measures 2014, Palomba et al. 2021). The importance of euphausiids and other small pelagic and benthic crustaceans in the diet of small pelagic fish is further illustrated by the frequent occurrence of species of other nematode genera such as *Hysterothylacium* and *Contracaecum*. For *Hysterothylacium*, Table 1 only includes those host species that have been confirmed as hosting third-stage larvae (fourth-stage larval and adult *Hysterothylacium* spp. are more commonly found in larger piscivorous teleosts).

Small pelagics are also common hosts for Acanthocephala (thorny-headed worms) of the family Polymorphidae. Small pelagics acquire these infections by feeding on the crustacean (mainly amphipod) first

intermediate hosts of these acanthocephalans (Leidenberger et al. 2020). Trematoda are poorly represented in Table 1. Most trematodes that use small pelagics as second intermediate hosts infect them by active penetration or, rarely, by ingestion of the free-swimming cercarial stage. Therefore, these cannot be used as indicators of host diet. However, some species in the trematode families Didymozoidae, Opecoelidae and Syncoelidae do use small pelagics, particularly squid and euphausiids, as paratenic hosts (Shimazu 1971, Shimazu & Kagei 1978, Shukhgalter & Nigmatullin 2001, Morales-Ávila et al. 2015). In the case of didymozoids, small pelagics may serve as third intermediate hosts that become infected by eating the unknown invertebrate second intermediate

Table 2. Examples of trophically transmitted parasites infecting selected small pelagic species as definitive hosts. Only parasite taxa for which life cycle information is available are shown. These parasites may be used to determine diet of the pelagic hosts. Fish scientific names and common names listed are according to Froese & Pauly (2023)

Parasite	First intermediate host(s)	Second intermediate and paratenic hosts(s)	Small pelagic hosts	Key references
Acanthocephala				
<i>Echinorhynchus gadi</i>	Amphipods	None	<i>Clupea harengus</i> <i>Clupea pallasii</i> <i>Mallotus villosus</i> <i>Osmerus mordax</i> <i>Scomber scombrus</i>	Valtonen et al. (1983)
<i>Echinorhynchus borealis</i> <i>Echinorhynchus cinctulus</i> <i>Echinorhynchus salmonis</i> <i>Pomphorhynchus laevis</i>	Freshwater amphipods	None	<i>Clupea harengus</i> <i>Osmerus eperlanus</i>	Van Maren (1979)
<i>Rhadiorhynchus</i> spp.	Euphausiids	None	<i>Allosmerus elongatus</i> <i>Clupea pallasii</i> <i>Cololabis saira</i> <i>Hypomesus pretiosus</i> Myctophidae Paralepididae <i>Sardina pilchardus</i> <i>Sardinella aurita</i> <i>Sardinops sagax</i> <i>Scomber japonicus</i> <i>Scomber scombrus</i> <i>Trachurus trachurus</i>	Gregori et al. (2012)
Cestoda				
<i>Eubothrium parvum</i>	Copepods	None	<i>Mallotus villosus</i>	Kennedy (1979)
<i>Proteocephalus tetrastomus</i>	Copepods	None	<i>Osmerus mordax</i>	Scholz (1999)
Nematoda				
<i>Hysterothylacium</i> spp.	Copepods, amphipods, mysids, isopods	Ctenophores, chaetognaths, polychaetes and ophiuroids	<i>Ammodytes dubius</i> <i>Argentina silus</i> <i>Clupea pallasii</i> <i>Mallotus villosus</i> <i>Scomber scombrus</i> <i>Trachurus trachurus</i>	Køie (1993), Marcogliese (1995)
Trematoda				
<i>Bacciger bacciger</i>	Lamellibranch molluscs	Amphipods	<i>Engraulis encrasicolus</i> <i>Sardina pilchardus</i> <i>Sardinella aurita</i>	Palombi (1934), Bartoli & Gibson (2007)
<i>Brachyphallus crenatus</i>	Gastropod mollusc <i>Retusa obtusa</i>	Calanoid copepods	<i>Ammodytes dubius</i> <i>Ammodytes tobianus</i> <i>Clupea harengus</i> <i>Mallotus villosus</i> <i>Osmerus eperlanus</i> <i>Osmerus mordax</i> <i>Scomber scombrus</i>	Køie (1992)
<i>Derogenes varicus</i>	Gastropod molluscs (genus <i>Natica</i>)	Calanoid and harpacticoid copepods	<i>Ammodytes dubius</i> <i>Ammodytes tobianus</i> <i>Argentina silus</i> <i>Clupea harengus</i> <i>Mallotus villosus</i> <i>Osmerus eperlanus</i> <i>Osmerus mordax</i> <i>Scomber scombrus</i> <i>Sprattus sprattus</i> <i>Trachurus trachurus</i>	Køie (1979)

(Table 2 continued on next page)

Table 2. (continued)

Parasite	First intermediate host(s)	Second intermediate and paratenic hosts(s)	Small pelagic hosts	Key references
<i>Hemiurus levinseni</i>	Gastropod mollusc <i>Cylichna alba</i>	Copepods and chaetognaths	<i>Allosmerus elongatus</i> <i>Argentina silus</i> <i>Clupea harengus</i> <i>Clupea pallasii</i> <i>Hypomesus pretiosus</i> <i>Mallotus villosus</i>	Krupenko et al. (2020)
<i>Hemiurus luehei</i>	Gastropod mollusc <i>Philine denticulata</i>	Calanoid copepods	<i>Ammodytes tobianus</i> <i>Clupea harengus</i> <i>Sardina pilchardus</i> <i>Scomber scombrus</i>	Køie (1990)
<i>Lecithaster gibbosus</i>	Gastropod mollusc <i>Brachystomia eulimoides</i>	Calanoid copepods	<i>Ammodytes dubius</i> <i>Ammodytes tobianus</i> <i>Clupea harengus</i> <i>Clupea pallasii</i> <i>Engraulis encrasicolus</i> <i>Engraulis mordax</i> <i>Hypomesus pretiosus</i> <i>Mallotus villosus</i> <i>Osmerus mordax</i> <i>Sardina pilchardus</i> <i>Sardinops sagax</i> <i>Scomber scombrus</i> <i>Sprattus sprattus</i> <i>Trachurus trachurus</i>	Køie (1989)
<i>Opechona bacillaris</i>	Gastropod molluscs (genus <i>Nassarius</i>)	Ctenophores, chaetognaths and medusae	<i>Ammodytes tobianus</i> <i>Clupea harengus</i> <i>Scomber scombrus</i> <i>Sprattus sprattus</i> <i>Trachurus trachurus</i>	Køie (1975)
<i>Parahemiurus merus</i>	Unknown	Chaetognaths	<i>Anchoa tricolor</i> <i>Cetengraulis edentulus</i> <i>Clupea pallasii</i> <i>Engraulis anchoita</i> <i>Engraulis encrasicolus</i> <i>Engraulis japonicus</i> <i>Engraulis mordax</i> <i>Opisthonema libertate</i> <i>Opisthonema oglinum</i> <i>Sardina pilchardus</i> <i>Sardinella aurita</i> <i>Sardinella brasiliensis</i> <i>Sardinops sagax</i>	Almeida et al. (2009)
<i>Prodistomum</i> spp.	Unknown	Ctenophores	<i>Engraulis encrasicolus</i> <i>Engraulis japonicus</i> <i>Sardina pilchardus</i> <i>Scomber japonicus</i> <i>Scomber scombrus</i> <i>Trachurus trachurus</i>	Duong et al. (2022)

hosts (Louvard et al. 2022). Until the life cycles of more members of these trematode families are fully elucidated, their use as indicators of the diet of their fish hosts remains limited.

In contrast to those taxa that use small pelagics as intermediate and paratenic hosts, the major parasite

taxon using small pelagics as definitive hosts is the Trematoda (Table 2), with members of the superfamily Hemiuroidea being particularly prominent. Hemiuroids generally have a planktonic life cycle, with calanoid copepods, chaetognaths and ctenophores serving as second intermediate and/or para-

tenic hosts (Køie 1979, 1989, 1990, 1992, Almeida et al. 2009, Krupenko et al. 2020). The range of possible second intermediate hosts is thus relatively wide, which limits the use of hemiurids as precise indicators of definitive host diet. This is further complicated by the possibility of direct fish-to-fish transmission by some hemiurids (Køie 1979, Gibson & Bray 1986). Some trematode species in Table 2, such as *Bacciger bacciger*, have more benthic life cycles, with benthic amphipods as second intermediate hosts (Palombi 1934, Bartoli & Gibson 2007). The occurrence of such species indicates benthic feeding by the fish host, further evidence of which is derived from the occurrence of some adult acanthocephalans with benthic amphipods as first intermediate hosts (*Echinorhynchus* spp. and *Pomphorhynchus laevis*). Four of the acanthocephalan species listed in Table 2 are freshwater and brackish water species, so their presence in small pelagic fish in purely marine waters indicates previous feeding in freshwater or brackish water. Adult forms of cestodes and nematodes are rarely found in small pelagics, which usually serve as intermediate hosts for these parasites.

The above assessment shows that parasites, particularly those with narrower intermediate host ranges, have the potential to be useful indicators of the diet of small pelagics. A recurring theme is the limitations imposed by the wide host range of many larval helminths. However, in any chosen ecosystem, the likely sources of infection of a particular parasite can be reduced by comparing infections in different invertebrate intermediate hosts with examinations of the stomach contents of the fish hosts. For example, Klimpel & Rückert (2005) used this approach to identify planktonic hyperiid amphipods as the obligatory intermediate hosts for the nematode *Hysterothylacium aduncum* in the North Sea.

4. USE OF MULTIPLE TECHNIQUES TO DOCUMENT DIET

While numerous ecological studies of fish parasites infer host diets based on the life cycles of their constituent parasites (Tables 1 & 2), comparatively few studies evaluate fish diets using multiple techniques that include parasites. Typically, diet and trophic position are inferred from stomach contents, stable isotopes and morphometrics. Stomach contents, parasites and stable isotopes have been examined in birds (Aponte et al. 2014) and freshwater fish (Johnson et al. 2004, Bertrand et al. 2011, Locke et al. 2013, Rochat et al. 2022). Stomach contents, parasites and morpho-

metrics have been examined in freshwater fish to determine trophic position and habitat selection (Bertrand et al. 2008). All tools provided useful and complementary information in these studies, although variations in diet and prey importance were detected among them.

There are no individual studies that make use of both stable isotopes and parasites to evaluate the diet of small pelagic fishes. The only study involving the use of both stomach contents and stable isotopes that also included parasites to estimate diet in a marine fish was on the benthic shorthorn sculpin *Myoxocephalus scorpius* from Frobisher Bay, Canada (Dick et al. 2009). Larger sculpin had a greater diversity of parasites and higher nitrogen stable isotope ($\delta^{15}\text{N}$) values, indicating more diverse prey occurring higher up the food chain (Dick et al. 2009). An integrated approach was taken in a large-scale study to examine trophic relationships among pelagic fishes in the northern California Current off California and Oregon, USA (Miller & Brodeur 2007, Miller et al. 2008, 2010, Jacobson et al. 2012). Individual fish of 10 pelagic species, including 6 small pelagics, were examined in this collaborative set of studies in which many of the same fish specimens were shared for analyses of stomach contents, trophically transmitted parasites and stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). Even though some temporal analyses and species differed in the final analyses, several generalities were consistent among the techniques. Parasites, diet and $\delta^{13}\text{C}$ identified similar cross-shelf trends in feeding ecology, one being similarities between Pacific saury *Cololabis saira* and jack mackerel *Trachurus symmetricus*, both offshore species. In another similarity, $\delta^{15}\text{N}$ (used to identify trophic position) and parasites grouped some fish taxa similarly (e.g. Pacific herring *Clupea pallasii* and Pacific hake *Merluccius productus*). Finally, all analyses grouped juvenile salmon *Oncorhynchus* spp. together, potentially due to their omnivory. These studies highlight not only the value of using parasites to infer the diet of their hosts but also the value of using multiple techniques to evaluate a fish's diet.

A variety of studies have examined stomach contents and parasites to evaluate the diet of small pelagic fishes from a variety of habitats in both brackish and marine waters (Table 3). Most of these showed conformity between the 2 techniques, and authors subsequently were able to assign fishes to their respective feeding categories. Some large-scale studies provide good opportunities to examine broader patterns and trends among fish species. Woodstock et al. (2020) examined the stomach contents and parasites of 18 species of mesopelagic fishes from the Gulf

Table 3. Studies of diets of small pelagic forage fishes and squids evaluated by both gastrointestinal tract contents and trophically transmitted parasites. Fish scientific names, common names and habitats listed are according to Froese & Pauly (2023). MAR: Mid-Atlantic Ridge; ND: Norwegian Deep

Host	Habitat	Location	Conclusions	Reference
<i>Ammodytes tobianus</i> (small sandeel)	Brackish, demersal	Wadden Sea	Feeds on calanoid copepods and cypris larvae. Hemiurids dominant trematodes. Many bird parasites	Groenewold et al. (1996)
<i>Hyperoplus lanceolatus</i> (great sandeel)	Brackish, demersal	Wadden Sea	Feeds on small sandeel and copepods. Hemiurids dominant trematodes. Many bird parasites	Groenewold et al. (1996)
<i>Sprattus sprattus</i> (European sprat)	Brackish, pelagic–neritic	Wadden Sea	Feeds on calanoid copepods and cypris larvae. Hemiurids dominant trematodes. Many larval parasites, including parasites of birds and marine mammals	Groenewold et al. (1996)
<i>Sardina pilchardus</i> (European pilchard) and <i>Engraulis encrasicolus</i> (European anchovy)	Marine, brackish, pelagic–neritic	Adriatic Sea	Relative abundance of <i>Parahemiurus merus</i> and <i>Hysterothylacium aduncum</i> related to differences in diet contents, although could not determine specific prey from parasites	Zorica et al. (2016)
<i>Scomber japonicus</i> (chub mackerel)	Pelagic–neritic	Argentine Sea	Higher levels of <i>Corynosoma australe</i> from feeding more on crustaceans; adult <i>Hysterothylacium</i> sp. from feeding on Argentine anchovy (<i>Engraulis anchoita</i>)	Cremonte & Sardella (1997)
<i>Myctophum punctatum</i> (spotted lanternfish)	Marine, bathypelagic	5 sites, European waters	Diet reflects parasite fauna and species richness from different areas	Kleinertz et al. (2012)
<i>Notoscopelus kroyeri</i> (lancet fish)	Marine, pelagic–oceanic	MAR	Feed on small pelagic crustaceans. Acquires infections of <i>Anisakis</i> spp.	Klimpel et al. (2008)
<i>Neolatus tripes</i> (black snake mackerel)	Marine, bathypelagic	Canary Current System	Feeds on small pelagic fish. Parasites show trophic relationships typical for mesopredators from subtropical epi- and mesopelagic waters	Alt et al. (2018)
<i>Maurollicus muelleri</i> (silvery lightfish)	Marine, bathypelagic, mesopelagic	MAR, ND	Feeds on copepods and other crustaceans in MAR, copepods and euphausiids in ND. More parasite species and trematodes at ND	Klimpel et al. (2007)
<i>Oncorhynchus kisutch</i> (coho salmon) <i>O. tshawytscha</i> (Chinook salmon)	Marine, pelagic, benthopelagic Also freshwater and brackish	Oregon and California coast	Parasites and stomach contents show that fish, euphausiids and hyperid amphipods are main prey	Baldwin et al. (2008)
<i>Johnius borneensis</i> (sharpnose hammer croaker) <i>Upeneus asymmetricus</i> (asymmetrical goatfish) <i>U. moluccensis</i> (goldband goatfish)	Marine, brackish, benthopelagic; Marine, demersal; brackish, reef	Java	All fish mainly feed on smaller fish. Strong association between diet category based on stomach contents and parasite species composition	Koepper et al. (2022)
<i>Etmopterus spinax</i> (velvet belly) bathy-demersal	Marine	ND	Cestode larvae linked to euphausiids in stomach contents, anisakid nematodes to fish	Klimpel et al. (2003a)
<i>Agonus cataphractus</i> (hooknose) <i>Enchelyopus (= Rhinonemus) cimbrius</i> (fourbeard rockling)	Marine, demersal	North Sea	Both species classed as benthopelagic based on stomach contents and parasites	Klimpel et al. (2003b)
<i>Champsocephalus gunnari</i> (mackerel icefish) and <i>Chaenodraco wilsoni</i> (Spiny icefish)	Marine, benthopelagic	Antarctic Peninsula	Both species have similar parasite communities and specialize on euphausiids	Kuhn et al. (2018)

(Table 3 continued on next page)

Table 3. (continued)

Host	Habitat	Location	Conclusions	Reference
Myctophidae (3 species) Melamphaidae (3 species) Stromiidae (1 species)	Bathypelagic except <i>Benthoosema glaciale</i> (pelagic)	MAR	Most species have low infections acquired by feeding on crustaceans. Only one fed on fish	Klimpel et al. (2010)
<i>Chauliodus sloani</i> (Sloane's viperfish) and <i>Stomias boa ferox</i> (dragonfish)	Marine, bathypelagic	Norfolk Submarine Canyon	Presence of <i>Nybelinia</i> spp. and <i>Anisakis</i> spp. attributed to occurrence of <i>Cerato- scopelus maderensis</i> (Madeira lantern- fish) in diet. Lanternfish fed on euphausiids	Gartner & Zwerner (1989)
18 mesopelagic species	Various	Gulf of Mexico	Six different feeding guilds based on stomach contents. Parasite assemblages differ among guilds	Woodstock et al. (2020)
31 species	Marine, brackish and freshwater	Bothnian Bay	Five species classified as planktivores and 7 as omnivores. Mean number of para- sites positively correlated with number of prey taxa. Highest diversity of parasites and prey in omnivores. Predators inferred from parasites	Valtonen et al. (2010)
<i>Ommastrephes bartramii</i> (neon flying squid)	Marine, nektonic	Southeastern Pacific	Feeds on small fishes, squids, crusta- ceans. Parasites are larval helminths that use planktonic invertebrates, small fish and squids as intermediate and paratenic hosts	Nigmatullin et al. (2009)
<i>Illex coindetti</i> (short-finned squid)	Marine	Adriatic Sea	Seasonal variation in <i>Anisakis pegreffii</i> and <i>Phyllobothrium</i> sp. coincided with <i>M. muelleri</i> in diet	Petrić et al. (2011)
<i>Doryteuthis (=Loligo) gahi</i> (longfin Patagonian squid)	Marine	Falkland Islands	Presence of <i>Anisakis</i> sp. and larval tetra- phyllidean cestodes attributed to euphausiids in diet	Brickle et al. (2001)

of Mexico. Based on stomach contents, the authors divided the fishes into 6 feeding guilds: (1) copepods, (2) copepods/mesozooplankton, (3) copepods/ostracods, (4) gelatinous zooplankton, (5) generalist mesozooplankton and (6) fish and other organisms from higher trophic levels. Importantly, the parasite assemblages differed significantly among the 6 guilds, and the abundances of various types of parasites also differed among them.

Another extensive study of parasites and stomach contents of 31 fish species in Bothnian Bay, Finland, a low-saline habitat inhabited by freshwater, brackish and marine fishes, illustrates the usefulness of combining multiple techniques to evaluate fish diets (Valtonen et al. 2010). These authors classified the fishes as planktivores, omnivores (consuming both invertebrates and vertebrates), benthivores and piscivores based on stomach contents. Using stomach contents alone, the occurrence of small fragile crustaceans such as copepods as well as oligochaetes in the diet was seriously underestimated compared to that esti-

mated from parasites. By contrast, insects, bivalves and teleosts were observed in stomach contents more often than inferred from the occurrence of parasites (Valtonen et al. 2010). There was a positive correlation between the number of prey taxa in a fish's diet and the total number of parasites in a fish among the species. Omnivores had the highest diversity of both parasites and prey items in the diet. Importantly, the mean number of prey taxa per fish was 12.5 using stomach contents, 15.8 using parasites and 24.5 using both parasites and diet items, illustrating the value of utilizing both methods combined rather than either in isolation (Valtonen et al. 2010).

5. LARGE PREDATOR INFERENCE FROM PARASITES

Given that small pelagics reside at an intermediate level within food webs, they are important in transferring energy from lower trophic levels to larger pred-

ators (Peck et al. 2021, Boldt et al. 2022). However, questions remain concerning not only their role within different food webs but also the impact of predators including large fishes, seabirds and marine mammals on their standing stocks (Peck et al. 2021, Boldt et al. 2022). While trophically transmitted parasites provide direct evidence of a host's diet, they also can be used to infer predators of that host when it acts as an intermediate or paratenic host (Campbell 1983, Marcogliese & Cone 1997, Marcogliese 2003, Lafferty et al. 2008). Thus, the presence of larval stages of trophically transmitted parasites reflects the relative role of those fishes in parasite transmission (Zander et al. 1993, Groenewold et al. 1996), so consideration of parasites in a host leads to an improved understanding of predator–prey relationships (Poulin 2010). Parasite life cycles have evolved along with their hosts and they are adapted to long-standing trophic relationships developed over evolutionary time (George-Nascimento 1987, Marcogliese 2004). Therefore, the common occurrence of a trophically transmitted parasite in a host may suggest long-term stable predator–prey relationships in that ecosystem (Overstreet et al. 1996, Marcogliese & Cone 1997, Marcogliese 2003). For example, the high infection levels of *Contracaecum osculatatum* s.l. in the Weddell seal *Leptonychotes weddellii* and its fish prey have been interpreted as a sign of trophic web stability in Antarctica (Mattiucci & Nascetti 2008).

All of the parasites listed in Table 1 are potential indicators for predators of small pelagic fishes. However, there is another set of parasites indicative of predation on small pelagic fishes not included in Table 1 that must be considered. The presence of trematode metacercariae in fish is not a result of trophic transmission, but penetration by free-swimming infective cercariae. These metacercariae then are transmitted to their definitive hosts through predation of the infected fish. A common and widespread example is *Cryptocotyle* spp., a bird parasite whose metacercariae causes blackspot on inshore fishes, the second intermediate hosts, before being consumed by birds (Fig. 3; see also below).

There are a limited number of studies that actually use larval parasites in a host to infer direct predation of a fish host (Table 4). However, in one large-scale study of fish trophic ecology, predators of 31 species of fish were eluci-

dated using both gut contents and parasites in the Bothnian Bay, Finland (Valtonen et al. 2010). For example, smelt *Osmerus mordax* and three-spined sticklebacks *Gasterosteus aculeatus* were inferred to be preyed upon by both birds and seals in addition to fish, based on their parasites (Valtonen et al. 2010). Using the Bothnian Bay data set mentioned above along with published records, Locke et al. (2014) inferred the predators of 31 fish species in the Bothnian Bay based on their parasites' life cycles to evaluate vulnerability to predation, with three-spined sticklebacks *G. aculeatus* being the most vulnerable species to predation. Furthermore, predator diversity was correlated with larval parasite diversity in prey species (Locke et al. 2014). Also, Alt et al. (2018) noted that variations in the prevalence of *Anisakis typica* in fishes off NW Africa reflect the distribution of the definitive hosts (delphinids) along coastal habitats. The abundant occurrence of tetraphyllidean cestode larvae in black snake mackerel *Nealotus tripes* in the Canary Current suggested that these fish were prey to pelagic sharks, while the presence of *Anisakis phyceteris* indicated they may be consumed by squid (Alt et al. 2018). The prevalence and abundance of the nematode *Hysterothylacium* sp. and the trematode *Cryptocotyle lingua* in sprat and the small sandeel *Ammodytes tobianus* implied that these fish were important prey for both piscivorous fish and sea birds in the Wadden Sea (Groenewold et al. 1996). Similarly, most larval parasites occurring in sandeels off western Ireland were parasites of sea birds and marine

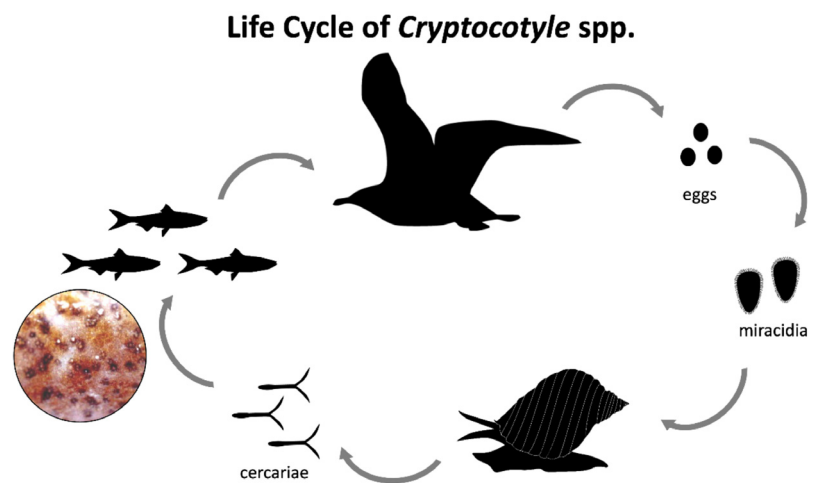


Fig. 3. Trematodes in the genus *Cryptocotyle* mature and reproduce in fish-eating birds. Their eggs are released with feces and hatch into free-swimming miracidia, which penetrate the molluscan host. As with all trematodes, mollusks serve as first intermediate hosts. Asexually produced free-swimming cercariae released from the mollusk penetrate the skin of fish where they encyst as metacercariae resulting in 'black-spot' disease (inset photograph). Infected fish transfer the parasites to birds by predation

Table 4. Parasites of small pelagic forage fishes and squids that were used to infer predation by their definitive hosts. Fish scientific names and common names listed are according to Froese & Pauly (2023)

Host forage fish	Location	Parasite	Predator	Comments	Reference
<i>Ammodytes tobianus</i> (small sandeel)	Wadden Sea	<i>Hysterothylacium</i> sp.	Piscivorous fish	Fish play important role in parasite transmission	Groenewold et al. (1996)
<i>Sprattus sprattus</i> (European sprat)		<i>Cryptocotyle lingua</i>	Sea birds		
<i>Ammodytes tobianus</i>	Western Ireland	Larval helminths	Sea birds, marine mammals		O'Connell & Fives (2004)
<i>Sprattus sprattus</i>	European waters	Larval helminths	Piscivores	Sprat is important intermediate host	Kleinertz et al. (2012)
<i>Etropterus spinax</i> (velvet belly)	Norwegian Deep	Tetraphyllidean and trypanorhynch larvae	Sharks, piscivorous fish		Klimpel et al. (2003a)
<i>Nealotus tripes</i> (black snake mackerel)	Canary Current off NW Africa	<i>Anisakis typica</i> <i>Anisakis physeteris</i> Tetraphyllidean larvae	Small toothed whales Squid Sharks	Distribution reflects that of delphinids along coast	Alt et al. (2018)
<i>Centropomus nigrescens</i> (black snook)	Mexican lagoons	<i>Echinocephalus</i> sp. <i>Sebakia</i> sp.	Elasmobranchs Crocodiles		Violante-González et al. (2010)
<i>Anchoa mitchilli</i> (bay anchovy)	Mississippi Sound, USA	<i>Bucephalus scomberomorous</i> , <i>Didymocystis scomberomori</i> , <i>Hysterothylacium fotalezae</i> <i>Phoreobothrium</i> sp., <i>Acanthobothrium</i> sp.	<i>Scomberomorus maculatus</i> (Spanish mackerel), <i>Rhizoprionodon terraenovae</i> (Atlantic sharpnose shark)	Prevalence and abundance of parasites reflects timing of predator migration into sound	Andres et al. (2016)
<i>Osmerus mordax</i> (smelt)	Bothnian Bay, Finland	8 of 11 helminth species	<i>Lota lota</i> (burbot)	Both pelagic species in stomach contents of burbot	Valtonen & Julkunen (1995)
<i>Gasterosteus aculeatus</i> (three-spined stickleback)		9 of 15 helminth species			
<i>Osmerus mordax</i> <i>Gasterosteus aculeatus</i>	Bothnian Bay, Finland	Various parasites	Sea birds and marine mammals		Valtonen et al. (2010)
<i>Liza</i> spp. (grey mullets)	Santa Gilla Lagoon, Sardinia	<i>Phagicola</i> spp.	Foxes	Also, parasites of demersal fishes indicate predation by seabirds and migrating piscivorous fishes	Culurgioni et al. (2015)
<i>Mugil cephalus</i> (flathead grey mullet)		Various trematodes	<i>Dicentrarchus labrax</i> (European sea bass), <i>Anguilla anguilla</i> (European eel)		
<i>Illex coindetii</i> (short-finned squid)	Off coast of Spain	Larval tetraphyllideans and trypanorhynchs, and larval anisakid nematodes	Sharks	Absence of larval didymozoid trematodes implied that squid were not preyed upon by xiphoid fishes	Pascual et al. (1996)
<i>Todaropsis eblanae</i> (short-finned squid)			Marine mammals		
<i>Dosidicus gigas</i> (jumbo squid)	Pacific Ocean	Larval helminths	Sharks, whales and xiphoid fishes	Relative abundance suggests predator abundance varies regionally	Shukhgalter & Nigmatullin (2001)
<i>Histioteuthis bonnelli</i> (umbrella squid)	Tyrrhenian Sea	<i>Anisakis physeteris</i>	Sperm whales (Physeteridae) Swordfish (<i>Xiphias gladius</i>)	Transmission to whales occurs across the Mediterranean Sea	Palomba et al. (2021)

mammals, suggesting their importance as sandeel predators (O'Connell & Fives 2004), while the abundance of larval helminths in sprat led Kleinertz et al.

(2012) to suggest that sprat were important intermediate hosts for piscivorous predators in European waters.

Off the coast of Spain, short-finned squid *Illex coindetii* was infected with larval tetraphyllideans and trypanorhynchs (Cestoda), suggesting that this squid was preyed upon by sharks, which are the definitive hosts of these parasites. In contrast, another short-finned squid, *Todaropsis eblanae*, was infected with anisakid nematodes, suggesting that it was consumed by marine mammals (Pascual et al. 1996). Furthermore, the absence of larval didymozoid trematodes implied that these squids were not preyed upon by tuna, swordfish or sailfish, the definitive hosts for these trematodes. The parasites provided useful information about the local food web, which might not have been apparent from definitive hosts' diets alone. In Pacific waters, parasites of the jumbo squid *Dosidicus gigas* demonstrated that predation intensity by various predators varied between regions. Based on their larval parasites' relative abundance and life cycles, the parasite fauna suggested that predation by sharks, whales and xiphoid (swordfish) fishes off Peru was more intense than in the East Equatorial Pacific (Shukhgalter & Nigmatullin 2001).

For numerous logistical reasons, much less work has been completed on parasites of large predators. There are a few studies that incorporated multiple techniques, including stomach contents and parasites, of predators of small pelagics such as elasmobranchs (Santoro et al. 2022), various teleost fishes (Houston & Haedrich 1986, Gartner & Zwerner 1989, Klimpel et al. 2006b, Koepper et al. 2022) and marine mammals (reviewed in Cipriani et al. 2022) to infer parasite life cycles and transmission patterns (Table 5). Others used fecal pellets to extract the diet and parasites of seabirds (Garbin et al. 2019) or stable isotopes and parasites to infer the diet of seals (Sini-salo et al. 2006). In their extensive study of deep demersal fishes on the continental slope off Newfoundland, Canada, Houston & Haedrich (1986) utilized both stomach contents and parasites to conclude that feeding on pelagic fishes and euphausiids was a common practice by vertically migrating demersal fishes.

Some studies have used parasites of large predators on their own to demonstrate that they feed upon small pelagics. Numerous examples of these predators, including seabirds, teleosts and elasmobranchs, are included in Table 5. For example, the infection of *C. lingua* in herring gulls *Larus argentatus* demonstrated that these birds fed on inshore coastal marine fishes, primarily at an early age before they dispersed to other feeding grounds (Threlfall 1967). One unusual study noted the occurrence of remains of a parasitic copepod *Pennella* sp., which is not troph-

ically transmitted but specific to its pelagic fish host, in the intestine of thresher sharks *Alopias vulpinus* caught off southern California to inform that they feed on Pacific saury *Cololabis saira* (Prete et al. 2020). Parasites of various tunas have been studied extensively off Madeira and used to infer their diets (Cavaleiro et al. 2018, Hermida et al. 2018, 2019). Variations in abundance of the nematode *Hysterothylacium* spp. in various swordfish species have been linked to differences in foraging, especially on deep-sea squids, in different areas (Palomba et al. 2023). Using molecular techniques in an intensive and ambitious survey encompassing 31 species of seabird, 40 teleosts, 9 elasmobranchs, 1 marine mammal and 87 invertebrate species from the Otago coastal marine ecosystems, Bennett et al. (2023) linked parasites in intermediate host prey to numerous piscine and avian definitive hosts, establishing routes of parasite transmission via predation for most of the trophically transmitted helminth taxa in the ecosystem. In the process, they elucidated an extraordinary diversity of predator–prey relationships that included many large predatory species.

6. PARASITES AND THE ROLE OF HOSTS IN THE FOOD WEB

Given that parasites reflect the diet of their hosts and can be used to infer predators as well, parasites may be used to elucidate the role of a particular host in the food web (Marcogliese & Cone 1997, Marcogliese 2002, 2003, 2004). Yet food web studies initially neglected parasites (Marcogliese & Cone 1997). Huxham et al. (1995) were the first to use parasites of various organisms in the Ythan estuary to infer their predators in the absence of diet data in the construction of a food web. This practice of using parasite life cycles to determine predator–prey links has become more widespread as more studies continue to include parasites in food webs (e.g. Lafferty et al. 2006a, Morton & Lafferty 2022). A summary of marine food webs that have incorporated parasites is provided in Table 6. Most of these are estuarine, from different geographical regions, and many include small pelagic fishes. Generally, these food webs focus on other trophic levels or guilds and do not highlight the role of small pelagic fishes, but some relevant patterns emerge. In the Wadden Sea food web, host taxa that were highly connected as both predators and prey within the food web also had high parasite diversity (Thompson et al. 2013). In the Carpenteria Salt Marsh food web, animals occurring at mid-trophic levels were the most

Table 5. Selected representative examples of studies that use trophically transmitted parasites of large predators to infer small pelagic prey in their diets. (A) Studies that use multiple techniques to evaluate diet, including parasites. Note that unless indicated otherwise, techniques used stomach contents and parasites. (B) Studies that relied only on parasites. Fish scientific names and common names listed are according to Froese & Pauly (2023)

Predator	Location	Parasite(s)	Pelagic prey	Comment	Reference
(A) Studies that include both stomach contents and parasites					
<i>Scyliorhinus stellaris</i> (nursehound shark)	Gulf of Naples Mediterranean Sea	Intestinal cestodes	Squids most important prey, plus fish and octopus	Fairly specialized diet resulted in low parasite diversity	Santoro et al. (2022)
<i>Lepidopus caudatus</i> (silver scabbard fish)	Great Meteor Seamount (North Atlantic)	9 species of helminths	Myctophid fishes and euphausiids most important prey, plus other crustaceans, chaetognaths and squids	Rich parasite fauna reflects high diversity of mesopelagic prey	Klimpel et al. (2006b)
<i>Trichiurus lepturus</i> (largehead hairtail)	West Java, Indonesia	Nematodes, trema- todes, cestodes	Predominantly a piscivore	Evenly distributed parasite fauna among groups reflects piscivorous diet	Koepper et al. (2022)
<i>Coryphaenoides rupestris</i> (roundnose grenadier)	Upper continental slope, Newfoundland	Mainly trematodes, especially <i>Stering- ophorus</i> sp.	Copepods and other crustaceans, in- cluding euphausiids	Bathypelagic fish that vertically migrates to feed	Houston & Haedrich (1986)
<i>Synaphobranchus kaupii</i> (Kaup's arrowtooth eel)	Upper continental slope, Newfoundland	<i>Hysterothylacium</i> sp., <i>Contraecum</i> sp. (Nematoda)	Myctophid fishes, euphausiids	Bathydemersal fish that vertically migrates to feed	Houston & Haedrich (1986)
<i>Physeter macrocephalus</i> (sperm whale)	Tyrrhenian Sea, Central Mediterranean	<i>Anisakis physeteris</i> (Nematoda)	Squids (<i>Histio- teuthis bonnellii</i> , <i>Histioteuthis reversa</i>)		Cipriani et al. (2022)
<i>Phalacrocorax atriceps</i> (imperial shag)	Santa Cruz Province, Argentina	<i>Contraecum</i> spp. (Nematoda)	<i>Engraulis anchoita</i> (Argentine anchovy)	Parasites and prey determined using fecal pellets	Garbin et al. (2019)
<i>Phalacrocorax gaimardi</i> (red-legged cormorant)	Santa Cruz Province, Argentina	<i>Contraecum</i> spp. (Nematoda)	<i>Sprattus fueguensis</i> (Falkland sprat), <i>Ramnogaster arcuate</i> (Jenyns's sprat)	Parasites and prey determined using fecal pellets	Garbin et al. (2019)
<i>Phoca hispida botnica</i> (ringed seal)	Bothnian Bay, Finland	<i>Schistocephalus solidus</i> (Cestoda)	<i>Gasterosteus aculeatus</i> (three-spined stickleback)	Prey determined using stable isotopes and parasites	Sinisalo et al. (2006)
(B) Studies that infer diet from parasites alone					
<i>Larus argentatus</i> (herring gull)	North Wales	<i>Cryptocotyle lingua</i> (Trematoda)	Inshore coastal fishes		Threlfall (1967)
Alcid seabirds	Holarctic	<i>Alcataenia</i> spp. (Cestoda)	Euphausiids		Hoberg (1986)
<i>Antimora rostrata</i> (blue antimora)	New York Bight	Mainly trematodes	Benthopelagic invertebrates	Bathypelagic fish that feeds on pelagic prey	Campbell et al. (1980)
<i>Alopias vulpinus</i> (thresher shark)	Southern California	<i>Rhadinorhynchus cololabis</i> (Acanthocephala)	<i>Cololabis saira</i> (Pacific saury)	Remains of the parasitic copepod (<i>Pennella</i> sp.) also indicate feeding on <i>C. saira</i>	Preti et al. (2020)
<i>Katsuwonus pelamis</i> (skipjack tuna) <i>Seriola dumerili</i> (greater amberjack)	Madeira	<i>Oncophora melano- cephala</i> (Nematoda)	<i>Scomber colias</i> (Atlantic chub mackerel)	Abundant and common prey of tunas in the region	Hermida et al. (2019), Cavaleiro et al. (2018)

(Table 5 continued on next page)

Table 5. (continued)

Predator	Location	Parasite(s)	Pelagic prey	Comment	Reference
<i>Katsuwonus pelamis</i> (skipjack tuna)	Madeira	<i>Anisakis</i> sp. (Nematoda)	<i>S. colias</i> <i>Trachurus picturatus</i> (bluejack mackerel)	These fishes are common prey of skipjack tuna	Hermida et al. (2018)
Seabirds, seals, teleost fishes	Bothnian Bay, Finland	Helminths	Multiple pelagic prey		Valtonen et al. (2010)
Elasmobranchs, teleosts, seabirds	Otago coastal marine ecosystem, New Zealand	Helminths	Multiple pelagic prey	Determined life cycle pathways of helminths within ecosystem	Bennett et al. (2023)

vulnerable to natural enemies, including both predators and parasites (Lafferty et al. 2006a). In a number of ecosystems, small pelagic fishes such as sprats and smelt had the most larval parasite species, suggesting their importance as prey in those systems (Valtonen et al. 2010, Bennett et al. 2023; see also below).

Overall, network analysis permits the determination of general patterns within food webs and insight into ecosystem function (Poulin 2010). Not only can parasites be used to account for missing links within a food web (Runghen et al. 2021) but they may also be used to trace co-evolved sub-webs, also referred to as compartments or modules (George-Nascimento 1987, Marcogliese 2003). These consist of groups of species that interact more with each other than other species within the food web or network (Bellay et al. 2013). This includes trophic interactions within a cluster of species that form the module. A network analysis of the Hackensack Meadowlands in New Jersey found that parasite diversity was highest in those hosts with a broad diet as well as those situated in species-rich

compartments within the network (Anderson & Sukhdeo 2011). In a broader network analysis of 3 marine food webs, the following general patterns emerged that are directly relevant herein: first, a host with high parasite species richness tends to have a broad diet; and second, a host highly vulnerable to predation is important for parasite transmission (Chen et al. 2008). Following a network analysis of parasite records of 303 species of freshwater and marine fish, the percentage of larval parasites among all parasites in a host was best explained by trophic level or body size. Furthermore, the smallest size classes of fish had the highest proportion of larval parasites, suggesting their importance in parasite transmission (Poulin & Leung 2011). An analysis of 5 food webs, mostly marine, showed that (1) the number of parasite species infecting a host species was positively correlated with the number of prey species consumed by that host and (2) there was a significant positive relationship between the number of predator species feeding on an intermediate host and the proportion of those

Table 6. Estuarine and marine food webs that include parasites

Food web	Location	Reference
Bothnian Bay ^a	Finland	Valtonen et al. (2010)
Ythan estuary	United Kingdom	Huxham et al. (1995)
Company Bay, Otago Harbour	New Zealand	Thompson et al. (2005)
Carpinteria salt marsh	California, USA	Lafferty et al. (2006a,b)
Sylt tidal basin	Wadden Sea	Thieltges et al. (2011)
Sylt–Rømø Bight	Wadden Sea	Thompson et al. (2013)
Estero de Punta Banda	California, USA	Hechinger et al. (2011)
Bahía Falsa	California, USA	Hechinger et al. (2011)
Flensburg Fjord	Germany and Denmark	Zander et al. (2011)
Tuckerton salt marsh	New Jersey, USA	Rossiter & Sukhdeo (2011)
Hackensack Meadowlands	New Jersey, USA	Anderson & Sukhdeo (2011)
Palmyra Atoll	South Pacific	McLaughlin et al. (2020)
Kelp forest, Santa Barbara Channel	California, USA	Morton et al. (2021), Morton & Lafferty (2022)

^aFood web interactions containing only fish, their predators and their prey

predator species infected by parasites (Rossiter & Sukhdeo 2011).

In the Otago coastal marine ecosystem in New Zealand, an extensive examination of invertebrates, elasmobranchs, teleosts and seabirds for helminth parasites, and subsequent molecular analyses of the parasites found, led to the establishment of transmission networks for each of the major helminth groups. Furthermore, results demonstrated the importance of small pelagics in the transmission of trophic parasites within those networks (Bennett et al. 2023). Among all the transmission pathways, those using the New Zealand blueback sprat *Sprattus antipodum* and the arrow squid *Nototodarus sloanii* were among the most important, hosting the highest number of larval parasites, suggesting their important role as intermediate hosts. The thorough and extensive evaluation also uncovered other small pelagics serving as important intermediate hosts (and thus prey for larger predators), including the Australian anchovy *Engraulis australis*, New Zealand sprat *Sprattus muelleri* and euphausiids *Nyctiphanes australis*. The New Zealand sprat was the most important intermediate host for nematodes, including those infecting seabirds, while the arrow squid was the most important intermediate host for cestode parasites (Bennett et al. 2023). The study further emphasized key predators of pelagic fishes. For example, 3 species of seabird served as definitive hosts for acanthocephalans infecting *S. antipodum*. While not a traditional food web analysis, as diet contents were not examined, this study is perhaps the most comprehensive in evaluating trophic transmission pathways in a marine habitat. Taken together, these results and those above suggest that small pelagics are highly vulnerable to predation, that these animals are key hosts for parasites and that various parasites can be used to demonstrate their trophic connections within food webs.

7. SUMMARY AND THE WAY FORWARD

Both larval and adult trophically transmitted parasites may be used as indicators of diet in fishes. Because adult parasites reside in a host's alimentary tract for periods of weeks to years, they provide longer-term indicators than stomach contents or stable isotopes. Larval parasites also provide long-term information on a host's diet that reflects their feeding habits over a period of a year or more. Numerous examples of larval and adult parasites that provide information on the diet of small pelagics are included and summarized. While we have presented

only a subset of parasitological information on common fishes of the Northern Hemisphere (Tables 1 & 2), there are a multitude of additional studies available presenting this information. Indeed, as long as the parasite life cycles are known, inferences on prey can be made from any parasitological survey. Given that parasites can be used to discriminate fish stocks (Williams et al. 1992), and have been used to do so extensively (Timi & MacKenzie 2015 and papers within), these studies can also be used to inform fishery managers what those individual stocks are consuming. In contrast to studies documenting just parasites, interdisciplinary studies examining both parasites and stomach contents from the same individual small pelagic fish also are much rarer, with only 18 studies found globally (Table 3). These studies originate from diverse areas ranging from the inshore to deep waters. Surprisingly, few of these deal with common fishes or even common historic fishing grounds, and many concern deepwater fishes. While parasites and prey items from stomach contents demonstrate comparable results, parasites also provide complementary information on prey that do not turn up often in stomach contents due to their easily digestible fragile nature, or when stomachs are completely empty, and provide evidence on different time scales, highlighting the value of incorporating multiple techniques to evaluate diet. The same applies for parasites and stable isotopes, although only a single series of studies on small pelagics using parasites also included stable isotopes. Thus, there is a huge avenue for future collaborative and interdisciplinary research on small pelagics' feeding involving parasitology, especially on important commercial small pelagic fisheries, where so little has been done in this regard. Furthermore, larval trophically transmitted parasites in a fish may also be used to infer piscine, mammalian and avian predators on that host. Directed studies that look at this question are rarer still, with only 13 found (Table 4). While a number come from diverse areas of the globe, most of these are European and inshore. Again, inferences on predators can be made from any parasitological survey, as long as life cycles are known (e.g. see Table 2). Similar to parasites as diet indicators, results from parasitological stock discrimination studies can also contribute knowledge of predation on individual fish stocks. Examination of parasites of predators of small pelagics also provides useful information on predation pressures. While a comprehensive survey of parasites of these predators is beyond the scope of this study, the evidence presented indicates that parasites help to demonstrate the wide variety of predators that prey on small pelagics,

many of which have potential population impacts. Together, larval and adult parasites that rely on predation for transmission can indicate the host's position and role within a food web. There is enormous potential for multidisciplinary work that includes parasitology. Fisheries scientists and managers would benefit from multidisciplinary approaches that incorporate parasitology into their various research programs on stock discrimination and migration, fish feeding and growth studies, population studies, and investigations into anthropogenic effects and climate change on small pelagics (Marcogliese 2008).

Acknowledgements. The authors thank Dr. Ric Brodeur for his assistance with this project, Su Kim at the Northwest Fisheries Science Center for help with graphics and Rachel Pleuthner for the photo of the infected euphausiid. Dr. Laurie Weitkamp and anonymous reviewers provided helpful comments on earlier drafts of the manuscript. This review is a contribution to the Working Group on Small Pelagic Fish started jointly by ICES (WGSPF) and PICES (WG43) to continue world-wide collaboration to advance knowledge of the drivers of populations of small pelagics.

LITERATURE CITED

- Almeida FM, Barquete V, Pereira J Jr (2009) Progenetic metacercariae of *Parahemiurus merus* (Platyhelminthes, Digenea, Hemiuridae) infecting *Parasagitta friderici* (Chaetognatha) from southern coast Brazil. *Atlântica* 31:35–38
- Alt KG, Kuhn T, Miinster J, Klapper R, Kochmann J, Klimpel S (2018) Mesopredatory fishes from the subtropical upwelling region off NW-Africa characterised by their parasite fauna. *PeerJ* 6:e5339
- Anderson RC (1992) Nematode parasites of vertebrates: their development and transmission. CAB International, Wallingford
- Anderson TK, Sukhdeo MVK (2011) Host centrality in food web networks determines parasite diversity. *PLOS ONE* 6:e26798
- Andres MJ, Peterson MS, Anderson EJ, Hendon JR, Higgs JM (2016) Connecting anchovies to pelagic predators by their parasites. In: Proc 69th Gulf and Caribbean Fisheries Institute, 7–11 November 2016, Grand Cayman, p 339–340 (extended Abstract)
- Aponte V, Locke SA, Gentes ML, Giroux JF, Marcogliese DJ, McLaughlin D, Verreault J (2014) Effect of habitat use and diet on the gastrointestinal parasite community of an avian omnivore from an urbanized environment. *Can J Zool* 92:629–636
- Baldwin RE, Miller TW, Brodeur RD, Jacobson KC (2008) Expanding the foraging history of juvenile Pacific salmon: combining stomach-content and macroparasite-community analyses for studying marine diets. *J Fish Biol* 72:1268–1294
- Bartoli P, Gibson DI (2007) Synopsis of the life cycles of Digenea (Platyhelminthes) from lagoons of the northern coast of the western Mediterranean. *J Nat Hist* 41: 1553–1570
- Bellay S, de Oliveira EF, Almeida-Neto M, Lima DP, Takemoto RM, Luque JL (2013) Developmental stage of parasites influences the structure of fish–parasite networks. *PLOS ONE* 8:e75710
- Bennett J, Presswell B, Poulin R (2023) Tracking life cycles of parasites across a broad taxonomic scale in a marine ecosystem. *Int J Parasitol* 53:285–303
- Bertrand M, Marcogliese DJ, Magnan P (2008) Trophic polymorphism in brook charr revealed by diet, parasites and morphometrics. *J Fish Biol* 72:555–572
- Bertrand M, Cabana G, Marcogliese DJ, Magnan P (2011) Estimating the feeding range of a mobile consumer in a river–flood plain system using $\delta^{13}\text{C}$ gradients and parasites. *J Anim Ecol* 80:1313–1323
- Boldt JL, Murphy HM, Chamberland JM, Debertain A and others (2022) Canada's forage fish: an important but poorly understood component of marine ecosystems. *Can J Fish Aquat Sci* 79:1911–1933
- Brickle P, Olson PD, Littlewood D, Bishop A, Arkhipkin AI (2001) Parasites of *Loligo gahi* from waters off the Falkland Islands, with a phylogenetically based identification of their cestode larvae. *Can J Zool* 79:2289–2296
- Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *J Parasitol* 83:575–583
- Campbell RA (1983) Parasitism in the deep sea. In: Rowe GT (ed) *The sea*, Vol 8: Deep-sea biology. John Wiley & Sons, New York, NY, p 473–552
- Campbell RA, Haedrich RL, Munroe TA (1980) Parasitism and ecological relationships among deep-sea benthic fishes. *Mar Biol* 57:301–313
- Cavaleiro B, Hermida M, Saraiva A (2018) Parasites of amberjacks from the archipelago of Madeira, eastern Atlantic. *Dis Aquat Org* 131:133–142
- Chen HW, Liu WC, Davis AJ, Jordan F, Hwang MJ, Shao KT (2008) Network position of hosts in food webs and their parasite diversity. *Oikos* 117:1847–1855
- Cipriani P, Palomba M, Giulietti L, Marcer F and others (2022) Distribution and genetic diversity of *Anisakis* spp. in cetaceans from the Northeast Atlantic Ocean and the Mediterranean Sea. *Sci Rep* 12:13664
- Cremonte F, Sardella NH (1997) The parasitofauna of *Scomber japonicus* Houttuyn, 1782 (Pisces: Scombridae) in two zones of the Argentine Sea. *Fish Res* 31:1–9
- Culurgioni J, Figus V, Cabiddu S, De Murtas R, Cau A, Sabatini A (2015) Larval helminth parasites of fishes and shellfishes from Santa Gilla lagoon (Sardinia, western Mediterranean), and their use as bioecological indicators. *Estuar Coast* 38:1505–1519
- Dick T, Chambers C, Gallagher CP (2009) Parasites, diet and stable isotopes of shorthorn sculpin (*Myoxocephalus scorpius*) from Frobisher Bay, Canada. *Parasite* 16:297–304
- Duong B, Cutmore SC, Cribb TH, Pitt KA, Wee NQX, Bray RA (2022) A new species, new host records and life cycle data for lepecreadiids (Digenea) of pomacentrid fishes from the Great Barrier Reef, Australia. *Syst Parasitol* 99: 375–397
- Froese R, Pauly D (eds) (2023) FishBase. www.fishbase.org (accessed 28 March 2023)
- Garbin L, Diaz JI, Morgenthaler A, Millones A, Kuba L, Fuchs D, Navone GT (2019) Cormorant pellets as a tool for the knowledge of parasite–intermediate host associations and nematode diversity in the environment. *Helminthologia* 56:296–302
- Gartner JV, Zwerner DE (1989) The parasite faunas of meso- and bathypelagic fishes of Norfolk Submarine Canyon, western North Atlantic. *J Fish Biol* 34:79–95

- George-Nascimento M (1987) Ecological helminthology of wildlife animal hosts from South America: a literature review and a search for patterns in marine food webs. *Rev Chil Hist Nat* 60:181–202
- Gibson DI, Bray RA (1986) Hemiuridae (Digenea) of fishes from the north-east Atlantic. *Bull Br Mus Nat Hist Zool* 51:1–125
- Gregori M, Aznar FJ, Abollo E, Roura Á, González ÁF, Pascual S (2012) *Nyctiphanes couchii* as intermediate host for the acanthocephalan *Bolbosoma balaenae* in temperate waters of the NE Atlantic. *Dis Aquat Org* 99:37–47
- Groenewold S, Berghahn R, Zander CD (1996) Parasite communities of four fish species in the Wadden Sea and the role of fish discarded by the shrimp fisheries in parasite transmission. *Helgol Meeresunters* 50:69–85
- Hechinger RF, Lafferty KD, McLaughlin JP, Fredensborg BL and others (2011) Food webs including parasites, biomass, body sizes, and life stages for three California/Baja California estuaries. *Ecology* 92:791
- Hermida M, Cavaleiro B, Gouveia L, Saraiva A (2018) Parasites of skipjack, *Katsuwonus pelamis*, from Madeira, eastern Atlantic. *Parasitol Res* 117:1025–1033
- Hermida M, Cavaleiro B, Gouveia L, Saraiva A (2019) Seasonality of skipjack tuna parasites in the eastern Atlantic provide an insight into its migratory patterns. *Fish Res* 216:167–173
- Hoberg EP (1986) Evolution and historical biogeography of a parasite–host assemblage: *Alcataenia* spp. (Cyclophyllidae, Dilepididae) in Alcidae (Charadriiformes). *Can J Zool* 64:2576–2589
- Holland ND, Wilson NG (2009) Molecular identification of larvae of a tetraphyllidean tapeworm (Platyhelminthes: Eucestoda) in a razor clam as an alternative intermediate host in the life cycle of *Acanthobothrum brevissime*. *J Parasitol* 95:1215–1217
- Houston KA, Haedrich RL (1986) Food habits and intestinal parasites of deep demersal fishes from the upper continental slope east of Newfoundland, Northwest Atlantic Ocean. *Mar Biol* 92:563–574
- Huxham M, Raffaelli D, Pike A (1995) Parasites and food web patterns. *J Anim Ecol* 64:168–176
- Jackson CJ, Marcogliese DJ, Burt MDB (1997) Role of hyperbenthic crustaceans in the transmission of marine helminth parasites. *Can J Fish Aquat Sci* 54:815–820
- Jacobson KC, Baldwin RE, Reese DC (2012) Parasite communities indicate effects of cross-shelf distributions, but not mesoscale oceanographic features on northern California Current mid-trophic food web. *Mar Ecol Prog Ser* 454:19–36
- Jensen K, Bullard SA (2010) Characterisation of a diversity of tetraphyllidean and rhinebothriidean cestode larval types, with comments on host associations and life-cycles. *Int J Parasitol* 40:889–910
- Johnson MW, Hesslein RH, Dick TA (2004) Host length, age, diet, parasites and stable isotopes as predictors of yellow perch (*Perca flavescens* Mitchell), trophic status in nutrient poor Canadian Shield lakes. *Environ Biol Fishes* 71:379–388
- Jones B (2005) Transmission of marine parasites. In: Rohde K (ed) *Marine parasites*. CSIRO Publishing, Collingwood, p 371–374
- Kennedy CR (1979) The distribution and ecology of the cestode *Eubothrium parvum* in capelin, *Mallotus villosus* Pallas in the Barents Sea, and its use as a biological tag. *J Fish Biol* 15:223–236
- Kleinertz S, Klimpel S, Palm HW (2012) Parasite communities and feeding ecology of the European sprat (*Sprattus sprattus* L.) over its range of distribution. *Parasitol Res* 110:1147–1157
- Klimpel S, Palm HW (2011) Anisakid nematode (Ascaridoidea) life cycles and distribution: Increasing zoonotic potential in the time of climate change? In: Mehlhorn H (ed) *Progress in parasitology. Parasitology research monographs*, Vol 2. Springer, Berlin, p 201–222
- Klimpel S, Rückert S (2005) Life cycle strategy of *Hysterothylacium aduncum* to become the most abundant anisakid fish nematode in the North Sea. *Parasitol Res* 97:141–149
- Klimpel S, Seehagen A, Palm HW, Rosenthal H (2001) Deep-water metazoan fish parasites of the world. Logos Verlag, Berlin
- Klimpel S, Palm HW, Seehagen A (2003a) Metazoan parasites and food composition of juvenile *Etmopterus spinax* (L., 1758) (Dalatiidae, Squaliformes) from the Norwegian Deep. *Parasitol Res* 89:245–251
- Klimpel S, Seehagen A, Palm HW (2003b) Metazoan parasites and feeding behaviour of four small-sized fish species from the central North Sea. *Parasitol Res* 91:290–297
- Klimpel S, Palm HW, Busch MW, Kellermanns E, Rückert S (2006a) Fish parasites in the Arctic deep-sea: poor diversity in pelagic fish species vs. heavy parasite load in a demersal fish. *Deep Sea Res I* 53:1167–1181
- Klimpel S, Rückert S, Piatkowski U, Palm HW, Hanel R (2006b) Diet and metazoan parasites of silver scabbard fish *Lepidopus caudatus* from the Great Meteor Seamount (North Atlantic). *Mar Ecol Prog Ser* 315:249–257
- Klimpel S, Kellermanns E, Palm HW, Moravec F (2007) Zoogeography of fish parasites of the pearlside (*Maurollicus muelleri*), with genetic evidence of *Anisakis simplex* (s.s.) from the Mid-Atlantic Ridge. *Mar Biol* 152:725–732
- Klimpel S, Kellermanns E, Palm HW (2008) The role of pelagic swarm fish (Myctophidae: Teleostei) in the oceanic life cycle of *Anisakis* sibling species at the Mid-Atlantic Ridge, Central Atlantic. *Parasitol Res* 104:43–53
- Klimpel S, Busch MW, Sutton T, Palm HW (2010) Meso- and bathy-pelagic fish parasites at the Mid-Atlantic Ridge (MAR): low host specificity and restricted parasite diversity. *Deep Sea Res I* 57:596–603
- Koepper S, Nuryati S, Palm HW, Wild C, Yulianto I, Kleinertz S (2022) Metazoan endoparasite fauna and feeding ecology of commercial fishes from Java, Indonesia. *Parasitol Res* 121:551–562
- Køie M (1975) On the morphology and life-history of *Opechona bacillaris* (Molin, 1859) Looss, 1907 (Trematoda, Lepocreadiidae). *Ophelia* 13:63–86
- Køie M (1979) Morphology and life-history of *Derogenes varicus* (Muller, 1784) Looss, 1901 (Trematoda, Hemiuridae). *Z Parasitenkd* 59:67–78
- Køie M (1989) On the morphology and life-history of *Lecithaster gibbosus* (Rudolphi, 1802) Luhe, 1901 (Digenea, Hemiuroidea). *Parasitol Res* 75:361–367
- Køie M (1990) On the morphology and life-history of *Hemurus luehei* Odhner, 1905 (Digenea, Hemiuridae). *J Helminthol* 64:193–202
- Køie M (1992) Life-cycle and structure of the fish digenean *Brachyphallus crenatus* (Hemiuridae). *J Parasitol* 78:338–343
- Køie M (1993) Aspects of the life cycle and morphology of

- Hysterothylacium aduncum* (Rudolphi, 1802) (Nematoda, Ascaridoidea, Anisakidae). *Can J Zool* 71:1289–1296
- ✦ Køie M, Fagerholm HP (1995) The life cycle of *Contracaecum osculatum* (Rudolphi, 1802) sensu stricto (Nematoda, Ascaridoidea, Anisakidae) in view of experimental infections. *Parasitol Res* 81:481–489
- ✦ Køie M, Berland B, Burt MDB (1995) Development to third-stage larvae occurs in the eggs of *Anisakis simplex* and *Pseudoterranova decipiens* (Nematoda, Ascaridoidea, Anisakidae). *Can J Fish Aquat Sci* 52:134–139
- ✦ Krupenko DY, Gonchar A, Kremnev G, Uryadova A (2020) On the life cycle of *Hemiurus levinseni* Odhner, 1905 (Digenea: Hemiuridae). *Invertebr Zool* 17:205–218
- Kuchta R, Scholz T (2017) Diphyllbothriidea Kuchta, Scholz, Brabec & Bray, 2008. In: Caira JN, Jensen K (eds) Planetary diversity inventory (2008–2017): tapeworms from vertebrate bowels of the earth. Special Publication No. 25. The University of Kansas Natural History Museum, Lawrence, KS, p 167–189
- ✦ Kuhn T, Zizka VM, Münster J, Klapper R, Mattiucci S, Kochmann J, Klimpel S (2018) Lighten up the dark: metazoan parasites as indicators for the ecology of Antarctic crocodile icefish (Channichthyidae) from the north-west Antarctic Peninsula. *PeerJ* 6:e4638
- ✦ Lafferty KD, Dobson AP, Kuris AM (2006a) Parasites dominate food web links. *Proc Natl Acad Sci USA* 103:11211–11216
- Lafferty KD, Hechinger RF, Shaw JC, Whitney K, Kuris AM (2006b) Food webs and parasites in a salt marsh ecosystem. In: Collinge S, Ray C (eds) Disease ecology: community structure and pathogen dynamics. Oxford University Press, Oxford, p 119–134
- ✦ Lafferty KD, Allesina S, Arim M, Briggs CJ and others (2008) Parasites in food webs: the ultimate missing links. *Ecol Lett* 11:533–546
- ✦ Leidenberger S, Boström S, Wayland MT (2020) Host records and geographical distribution of *Corynosoma magdalenii*, *C. semerme* and *C. strumosum* (Acanthocephala: Polymorphidae). *Biodivers Data J* 8:e50500
- ✦ Locke SA, Bulté G, Forbes R, Marcogliese DJ (2013) Estimating diet in individual pumpkinseed sunfish *Lepomis gibbosus* using stomach contents, stable isotopes and parasites. *J Fish Biol* 82:522–537
- ✦ Locke SA, Marcogliese DJ, Valtonen ET (2014) Vulnerability and diet breadth predict larval and adult parasite diversity in fish of the Bothnian Bay. *Oecologia* 174:253–262
- ✦ Louvard C, Cutmore SC, Yong RQY, Dang C, Cribb TH (2022) First elucidation of a didymozoid life cycle: *Saccularina magnacetabula* n. g. n. sp. infecting an arcid bivalve. *Int J Parasitol* 52:407–425
- Luque JL, Poulin R (2004) Use of fish as intermediate hosts by helminth parasites: a comparative analysis. *Acta Parasitol* 49:353–361
- ✦ Luque JL, Mouillot D, Poulin R (2004) Parasite biodiversity and its determinants in coastal marine teleost fishes of Brazil. *Parasitology* 128:671–682
- ✦ MacKenzie K (1985) The use of parasites as biological tags in population studies of herring (*Clupea harengus* L.) in the North Sea and to the north and west of Scotland. *J Cons Int Explor Mer* 42:33–64
- Madin LP, Madin KAC (1995) Diversity in a vast and stable habitat: midwater is one of Earth's least explored environments. *Oceanus* 38:20–24
- ✦ Marcogliese DJ (1995) The role of zooplankton in the transmission of helminth parasites to fish. *Rev Fish Biol Fish* 5: 336–371
- ✦ Marcogliese DJ (2002) Food webs and the transmission of parasites to marine fish. *Parasitology* 124:S83–S99
- Marcogliese DJ (2003) Food webs and biodiversity: Are parasites the missing link? *J Parasitol* 89(Suppl):106–113
- ✦ Marcogliese DJ (2004) Parasites: small players with crucial roles in the ecological theatre. *EcoHealth* 1:151–164
- Marcogliese DJ (2005) Transmission of marine parasites. In: Rohde K (ed) Marine parasites. CSIRO Publishing, Collingwood, p 280–286
- ✦ Marcogliese DJ (2007) Evolution of parasitic life in the ocean: paratenic hosts enhance lateral incorporation. *Trends Parasitol* 23:519–521
- Marcogliese DJ (2008) Interdisciplinarity in marine parasitology. In: Afonso-Dias I, Menezes G, MacKenzie K, Eiras JC (eds) Proceedings of the international workshop on marine parasitology: applied aspects of marine parasitology, 21–24 May 2006, Arquipélago: life and marine sciences, Vol 6. University of the Azores, Ponta Delgada, p 7–14
- ✦ Marcogliese DJ, Cone DK (1997) Food webs: a plea for parasites. *Trends Ecol Evol* 12:320–325
- ✦ Mattiucci S, Nascetti G (2008) Advances and trends in the molecular systematics of anisakid nematodes, with implications for their evolutionary ecology and host–parasite co-evolutionary processes. *Adv Parasitol* 66:47–148
- ✦ McDermott JJ, Williams JD, Boyko CB (2010) The unwanted guests of hermits: a global view of the diversity and natural history of hermit crab parasites. *J Exp Mar Biol Ecol* 394:2–44
- McLaughlin JP, Morton DN, Lafferty KD (2020) Parasites in marine food webs. In: Behringer DC, Silliman BR, Lafferty KD (eds) Marine disease ecology. Oxford University Press, Oxford, p 45–70
- ✦ Measures LN (2014) Anisakiosis and pseudoterranovosis. Circular No. 1393. United States Geological Survey, Reston, VA
- ✦ Mendoza L, Taylor JW, Ajello L (2002) The class Mesomyxozoa: a group of microorganisms at the animal–fungal boundary. *Annu Rev Microbiol* 56:315–344
- Miller TW, Brodeur RD (2007) Diets of and trophic relationships among dominant marine nekton within the northern California Current ecosystem. *Fish Bull* 105:548–559
- ✦ Miller TW, Brodeur RD, Rau GH (2008) Carbon stable isotopes reveal relative contribution of shelf-slope production to the northern California Current pelagic community. *Limnol Oceanogr* 53:1493–1503
- ✦ Miller TW, Brodeur RD, Rau G, Omori K (2010) Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. *Mar Ecol Prog Ser* 420:15–26
- ✦ Morales-Ávila JR, Gomez-Gutierrez J, del Prado-Rosas M del CG, Robinson CJ (2015) Larval trematodes *Paronatrema mantae* and *Copiatestes* sp. parasitize Gulf of California krill (*Nyctiphanes simplex*, *Nematoscelis difficilis*). *Dis Aquat Org* 116:23–35
- ✦ Morton DN, Lafferty KD (2022) Parasites in kelp-forest food webs increase food-chain length, complexity, and specialization, but reduce connectance. *Ecol Monogr* 92: e1506
- ✦ Morton DN, Antonino CY, Broughton FJ, Dykman LN, Kuris AM, Lafferty KD (2021) A food web including parasites for kelp forests of the Santa Barbara Channel, California. *Sci Data* 8:99
- ✦ Nacari LA, Escribano R, Oliva ME (2022) Endoparasites and diet of the 'bigeye grenadier' *Macrourus holotrachys*

- Gunther, 1878 from the deep sea in the Southeastern Pacific Ocean. *Deep Sea Res I* 190:103903
- ✦ Nigmatullin CM, Shchetinnikov AS, Shukhgalter OA (2009) On feeding and helminth fauna of neon flying squid *Ommastrephes bartramii* (Lesueur, 1821) (Cephalopoda: Ommastrephidae) in the southeastern Pacific. *Rev Biol Mar Oceanogr* 44:227–235
- ✦ O'Connell MP, Fives JM (2004) Helminth communities of the lesser sandeel *Ammodytes tobianus* L. off the west coast of Ireland. *J Parasitol* 90:1058–1061
- Overstreet RM, Hawkins WE, Deardorff TL (1996) The western mosquitofish as an environmental sentinel: parasites and histological lesions. In: Servos MR, Munkittrick KR, Carey JH, Van der Kraak GJ (eds) *Environmental fate and effects of pulp and paper mill effluents*. St. Lucie Press, Delray Beach, FL, p 495–509
- Palm HW (2004) *The Trypanorhyncha* Diesing, 1863. PKSPL-IPB Press, Bogor
- ✦ Palomba M, Mattiucci S, Crocetta F, Osca D, Santoro M (2021) Insights into the role of deep-sea squids of the genus *Histioteuthis* (Histioteuthidae) in the life cycle of ascaridoid parasites in the Central Mediterranean Sea waters. *Sci Rep* 11:7135
- ✦ Palomba M, Marchiori E, Tedesco P, Fioravanti M and others (2023) An update and ecological perspective on certain sentinel helminth endoparasites within the Mediterranean Sea. *Parasitology* 150:1139–1157
- Palombi A (1934) *Bacciger bacciger* (Rud.) Trematode digenetic: fam. Steringophoridae Oehner: Anatomia, sistematica e biologia. *Pubbl Staz Zool Napoli* 13:438–488
- ✦ Pascual S, Gonzalez A, Arias C, Guerra A (1996) Biotic relationships of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda, Ommastrephidae) in the Northeast Atlantic: evidence from parasites. *Sarsia* 81:265–274
- ✦ Pawlak J, Nadolna-Altyn K, Szostakowska B, Pachur M, Bańkowska A, Podolska M (2019) First evidence of the presence of *Anisakis simplex* in *Crangon crangon* and *Contracaecum osculatum* in *Gammarus* sp. by *in situ* examination of the stomach contents of cod (*Gadus morhua*) from the southern Baltic Sea. *Parasitology* 146:1699–1706
- ✦ Peck MA, Alheit J, Bertrand A, Catalán IA and others (2021) Small pelagic fish in the new millennium: a bottom-up view of global research effort. *Prog Oceanogr* 191:102494
- ✦ Petrić M, Mladineo I, Sifner SK (2011) Insight into the short-finned squid *Illex coindetii* (Cephalopoda: Ommastrephidae) feeding ecology: Is there a link between helminth parasites and food composition? *J Parasitol* 97:55–62
- Pikitch E, Boersma PD, Boyd IL, Conover D, Cury PM, Essington TE, Heppell SS (2012) *Little fish, big impact: managing a crucial link in ocean food webs*. Lenfest Ocean Program, Washington, DC
- ✦ Poulin R (1995) Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecol Monogr* 65: 283–302
- Poulin R (2007) *Evolutionary ecology of parasites*, 2nd edn. Princeton University Press, Princeton, NJ
- ✦ Poulin R (2010) Network analysis shining light on parasite ecology and diversity. *Trends Parasitol* 26:492–498
- ✦ Poulin R, Leung TLF (2011) Body size, trophic level, and the use of fish as transmission routes by parasites. *Oecologia* 166:731–738
- ✦ Poulin R, Guilhaumon F, Randhawa HS, Luque JL, Mouillot D (2011) Identifying hotspots of parasite diversity from species–area relationships: host phylogeny versus host ecology. *Oikos* 120:740–747
- Pozdnyakov SE, Gibson DI (2008) Family Didymozoidae Monticelli, 1888. In: Bray RA, Gibson DI, Jones A (eds) *Keys to the Trematoda*, Vol 3. CAB International and Natural History Museum, London, p 631–734
- ✦ Preti A, MacKenzie K, Spivey KA, Noble LR, Jones CS, Appy RG, Pierce GJ (2020) Spiral valve parasites of blue and common thresher sharks as indicators of shark feeding behaviour and ecology. *J Fish Biol* 97:354–361
- ✦ Rochat EC, Paterson RA, Blasco-Costa I, Power M, Adams CE, Greer R, Knudsen R (2022) Temporal stability of polymorphic Arctic charr parasite communities reflects sustained divergent trophic niches. *Ecol Evol* 12:e9460
- ✦ Rossiter W, Sukhdeo MVK (2011) Exploitation of asymmetric predator–prey interactions by tropically transmitted parasites. *Oikos* 120:607–614
- Ruhnke TR, Caira JN, Pickering M (2017) Phyllobothriidea. In: Caira JN, Jensen K (eds) *Planetary biodiversity inventory (2008–2017): tapeworms from vertebrate bowels of the earth*. Special Publication No. 25. The University of Kansas Museum of Natural History, Lawrence, KS, p 305–326
- ✦ Rungghen R, Poulin R, Monlleo-Borrull C, Llopis-Belenguer C (2021) Network analysis: ten years shining light on host–parasite interactions. *Trends Parasitol* 37:445–455
- Ruszkowski JS (1934) Études sur le cycle évolutif et sur la structure des Cestodes de mer. III-e partie. Le cycle évolutif du Tétrarhynque *Grillotia erinaceus* (Van Beneden 1858). *Mém Acad Polon Sci Lettr Class Sci Math Nat Sér B. Sci Nat* 1934:1–10
- ✦ Sakanari J, Moser M (1985) Infectivity of, and laboratory infection with, an elasmobranch cestode, *Lacistorhynchus tenuis* (Van Beneden, 1858). *J Parasitol* 71:788–791
- ✦ Saksvik M, Nylund A, Nilsen F, Hodneland K (2001) Experimental infection of Atlantic salmon (*Salmo salar*) with marine *Eubothrium* sp. (Cestoda: Pseudophyllidea): observations on the life cycle, aspects of development and growth of the parasite. *Folia Parasitol* 48:118–126
- Santoro M, Bellisario B, Fernandez-Alvarez FA, Crocetta F, Palomba M (2022) Parasites and prey of the nursehound shark *Scyliorhinus stellaris* (Linnaeus, 1758): insights into hidden trophic web interactions in the Mediterranean Sea. *J Fish Biol* 102:271–280
- ✦ Scholz T (1999) Life cycles of species of *Proteocephalus*, parasites of fishes in the Palearctic Region: a review. *J Helminthol* 73:1–19
- Shimazu T (1971) Description of the progenetic metacercaria of *Pseudopecoelus japonicus* (Allocreadiidae: Trematoda) from *Euphausia similis* (Euphausiacea: Crustacea) of Suruga Bay. *Jpn J Parasitol* 20:83–86
- Shimazu T (1999) Plerocercoids with blastocysts of the trypanorhynch cestode *Nybelinia surmenicola* found in the euphausiid crustacea *Euphausia pacifica*. *Otsuchi Mar Sci* 24:1–4
- Shimazu T, Kagei N (1978) A metacercaria of the genus *Paronatrema* (Trematoda: Syncoeliidae) parasitic in *Euphausia pacifica* (Crustacea: Euphausiidae) from the East China Sea. *Zool Mag* 87:158–161
- ✦ Shukhgalter OA, Nigmatullin CM (2001) Parasitic helminths of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) in open waters of the central east Pacific. *Fish Res* 54:95–110
- ✦ Sinisalo T, Valtonen ET, Helle E, Jones RI (2006) Combining stable isotope and intestinal parasite information to evaluate dietary differences between individual ringed seals (*Phoca hispida botnica*). *Can J Zool* 84:823–831

- ✦ Smith JW (1983) *Anisakis simplex* (Rudolphi, 1809, det. Krabbe, 1878) (Nematoda: Ascaridoidea): morphology and morphometry of larvae from euphausiids and fish, and a review of life-history and ecology. *J Helminthol* 57: 205–224
- ✦ Thieltges DW, Reise K, Mouritsen KN, McLaughlin JP, Poulin R (2011) Food web including metazoan parasites for a tidal basin in Germany and Denmark. *Ecology* 92: 2005
- ✦ Thompson RM, Mouritsen KN, Poulin R (2005) Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *J Anim Ecol* 74:77–85
- ✦ Thompson RM, Poulin R, Mouritsen KN, Thieltges DW (2013) Resource tracking in marine parasites: Going with the flow? *Oikos* 122:1187–1194
- ✦ Threlfall W (1967) Studies on helminth parasites of the herring gull *Larus argentatus* Pontopp., in Northern Caernarvonshire and Anglesey. *Parasitology* 57:431–453
- ✦ Timi JT, MacKenzie K (2015) Parasites in fisheries and mariculture. *Parasitology* 142:1–4
- Tyler GAT II (2006) Tapeworms of elasmobranchs. II. A monograph on the Diphyllidea (Platyhelminthes, Cestoda). *Bull Univ Nebr State Mus* 20:1–143
- Uspenskaya AV (1953) Life cycle of nematodes of the genus *Ascarophis* Van Beneden (Nematodes-Spirurata). *Zool Zh* 32:828–832 (in Russian)
- ✦ Valtonen ET, Julkunen M (1995) Influence of the transmission of parasites from prey fishes on the composition of the parasite community of a predatory fish. *Can J Fish Aquat Sci* 52:233–245
- Valtonen ET, Van Maren MJ, Timola O (1983) A note on the intermediate hosts of *Echinorhynchus gadii* Acanthocephala in the Baltic Sea. *Aquilo (Zool)* 22:93–98
- ✦ Valtonen ET, Marcogliese DJ, Julkunen M (2010) Vertebrate diets derived from trophically transmitted fish parasites in the Bothnian Bay. *Oecologia* 162:139–152
- ✦ Van Maren MJ (1979) Amphipod *Gammarus fossarum* Koch (Crustacea) as intermediate host for some helminth parasites, with notes on their occurrence in the final host. *Bijdr Dierkd* 48:97–110
- Vik R (1963) Studies of the helminth fauna of Norway. IV. Occurrence and distribution of *Eubothrium crassum* (Bloch, 1779) and *E. salvelini* (Schrank, 1790) (Cestoda) in Norway, with notes on their life cycles. *Nytt Mag Zool* 11: 47–73
- ✦ Violante-González J, Mendoza-Franco EF, Rojas-Herrera A, Gil Guerrero S (2010) Factors determining parasite community richness and species composition in black snook *Centropomus nigrescens* (Centropomidae) from coastal lagoons in Guerrero, Mexico. *Parasitol Res* 107:59–66
- ✦ Williams HH, MacKenzie K, McCarthy AM (1992) Parasites as biological indicators of the population biology, migrations, diet, and phylogenetics of fish. *Rev Fish Biol Fish* 2: 144–176
- ✦ Woodstock MS, Blonar CA, Sutton TT (2020) Diet and parasites of a mesopelagic fish assemblage in the Gulf of Mexico. *Mar Biol* 167:184
- ✦ Zander CD, Strohbach U, Groenewold S (1993) The importance of globies (Gobiidae, Teleostei) as hosts and transmitters of parasites in the SW Baltic. *Helgol Meeresunters* 47:81–111
- ✦ Zander CD, Josten N, Detloff KC, Poulin R, McLaughlin JP, Thieltges DW (2011) Food web including metazoan parasites for a brackish shallow water ecosystem in Germany and Denmark. *Ecology* 92:2007
- ✦ Zorica B, Kec VC, Vidjak O, Mladineo I, Balic DE (2016) Feeding habits and helminth parasites of sardine (*S. pilchardus*) and anchovy (*E. encrasicolus*) in the Adriatic Sea. *Mediterr Mar Sci* 17:216–222

Editorial responsibility: Susana Garrido (Guest Editor),
Lisbon, Portugal
Reviewed by: Z. Zilz and 2 anonymous referees

Submitted: March 31, 2023
Accepted: January 8, 2024
Proofs received from author(s): March 3, 2024