REVIEW

Parasites of small pelagics reflect their role in marine ecosystems

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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

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 important 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

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 Mesomycetazoea (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
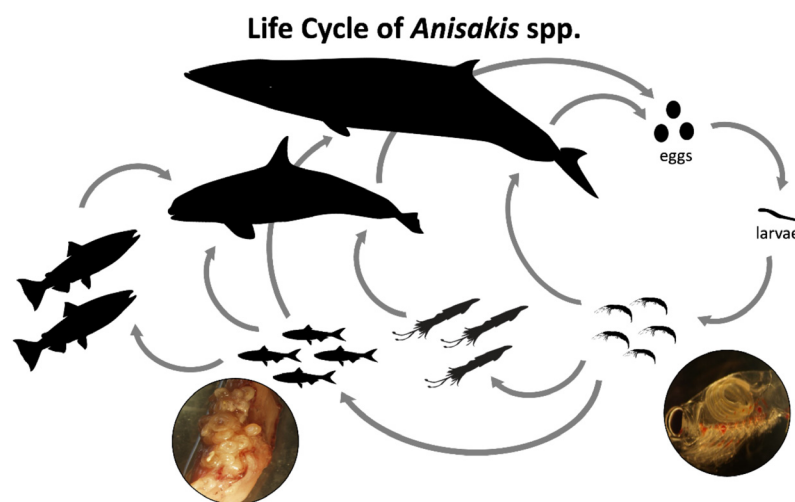

Life Cycle of *Anisakis* spp.

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

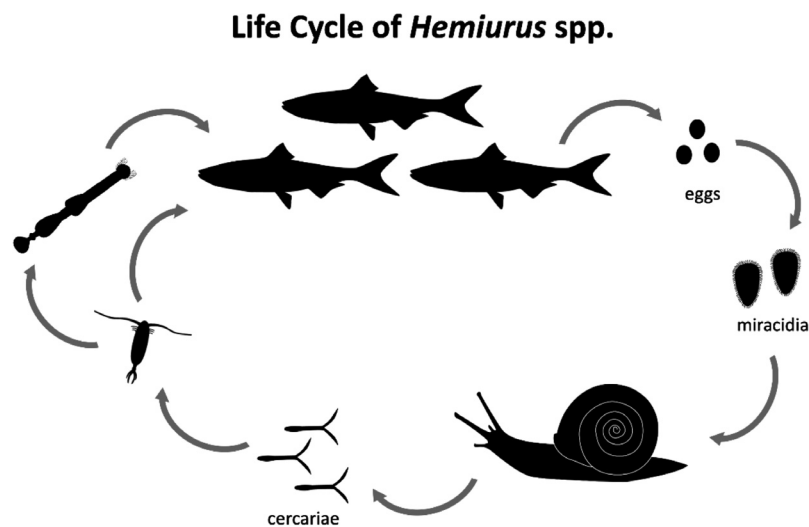## Life Cycle of *Hemiurus* spp.

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

Table 1. (continued)

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

Table 1. (continued)

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

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

Table 2. (continued)

Parasite	First intermediate host(s)	Second intermediate and paratenic hosts(s)	Small pelagic hosts	Key references
Hemiurus levinseni	Gastropod mollusc *Cylichna alba*	Copepods and chaetognaths	*Allosmerus elongatus* *Argentina silus* *Clupea harengus* *Clupea pallasii* *Hypomesus pretiosus* *Mallotus villosus*	Krupenko et al. (2020)
Hemiurus luehei	Gastropod mollusc *Philine denticulata*	Calanoid copepods	*Ammodytes tobianus* *Clupea harengus* *Sardina pilchardus* *Scomber scombrus*	Køie (1990)
Lecithaster gibbosus	Gastropod mollusc *Brachystomia eulimoides*	Calanoid copepods	*Ammodytes dubius* *Ammodytes tobianus* *Clupea harengus* *Clupea pallasii* *Engraulis encrasicolus* *Engraulis mordax* *Hypomesus pretiosus* *Mallotus villosus* *Osmerus mordax* *Sardina pilchardus* *Sardinops sagax* *Scomber scombrus* *Sprattus sprattus* *Trachurus trachurus*	Køie (1989)
Opechona bacillaris	Gastropod molluscs (genus *Nassarius*)	Ctenophores, chaetognaths and medusae	*Ammodytes tobianus* *Clupea harengus* *Scomber scombrus* *Sprattus sprattus* *Trachurus trachurus*	Køie (1975)
Parahemiurus merus	Unknown	Chaetognaths	*Anchoa tricolor* *Cetengraulis edentulus* *Clupea pallasii* *Engraulis anchoita* *Engraulis encrasicolus* *Engraulis japonicus* *Engraulis mordax* *Opisthonema libertate* *Opisthonema oglinum* *Sardina pilchardus* *Sardinella aurita* *Sardinella brasiliensis* *Sardinops sagax*	Almeida et al. (2009)
Prodistomum spp.	Unknown	Ctenophores	*Engraulis encrasicolus* *Engraulis japonicus* *Sardina pilchardus* *Scomber japonicus* *Scomber scombrus* *Trachurus trachurus*	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 hemiuroids as precise indicators of definitive host diet. This is further complicated by the possibility of direct fish-to-fish transmission by some hemiuroids (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 (δ^{15}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 (δ^{15}N and δ^{13}C). Even though some temporal analyses and species differed in the final analyses, several generalities were consistent among the techniques. Parasites, diet and δ^{13}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, δ^{15}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
Ammodytes tobianus (small sandeel)	Brackish, demersal	Wadden Sea	Feeds on calanoid copepods and cypris larvae. Hemiurids dominant trematodes. Many bird parasites	Groenewold et al. (1996)
Hyperoplus lanceolatus (great sandeel)	Brackish, demersal	Wadden Sea	Feeds on small sandeel and copepods. Hemiurids dominant trematodes. Many bird parasites	Groenewold et al. (1996)
Sprattus sprattus (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)
Sardina pilchardus (European pilchard) and *Engraulis encrasicolus* (European anchovy)	Marine, brackish, pelagic—neritic	Adriatic Sea	Relative abundance of *Parahemiurus merus* and *Hysterothylacium aduncum* related to differences in diet contents, although could not determine specific prey from parasites	Zorica et al. (2016)
Scomber japonicus (chub mackerel)	Pelagic—neritic	Argentine Sea	Higher levels of *Corynosoma australe* from feeding more on crustaceans; adult *Hysterothylacium* sp. from feeding on Argentine anchovy (*Engraulis anchoita*)	Cremonte & Sardella (1997)
		5 sites, European waters	Diet reflects parasite fauna and species richness from different areas	Kleinertz et al. (2012)
Myctophum punctatum (spotted lanternfish)	Marine, bathypelagic	MAR	Feed on small pelagic crustaceans. Acquires infections of *Anisakis* spp.	Klimpel et al. (2008)
Notoscopelus kroyeri (lancet fish)	Marine, pelagic—oceanic			
Neolatus tripes (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)
Maurolicus muelleri (silvery lightfish)	Marine, bathypelagic, mesopelagic	MAR, ND	Feeds on copepods and other crustaceans in MAR, copepods and euphausids in ND. More parasite species and trematodes at ND	Klimpel et al. (2007)
Oncorhynchus kisutch (coho salmon) *O. tschawytscha* (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)
Johnius borneensis (sharpnose hammer croaker) *Upeneus asymmeticus* (asymmetrical goatfish) *U. moluccensis* (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)
Etmopterus spinax (velvet belly) bathy-demersal	Marine	ND	Cestode larvae linked to euphausids in stomach contents, anisakid nematodes to fish	Klimpel et al. (2003a)
Agonus cataphractus (hooknose) *Enchelyopus* (=*Rhinonemus*) *cimbrius* (fourbeard rockling)	Marine, demersal	North Sea	Both species classed as benthopelagic based on stomach contents and parasites	Klimpel et al. (2003b)
Champsocephalus gunnari (mackerel icefish) and *Chaenodraco wilsoni* (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 *Benthosema glaciale* (pelagic)	MAR	Most species have low infections acquired by feeding on crustaceans. Only one fed on fish	Klimpel et al. (2010)
Chauliodus sloani (Sloane's viperfish) and *Stomias boa ferox* (dragonfish)	Marine, bathypelagic	Norfolk Submarine Canyon	Presence of *Nybelinia* spp. and *Anisakis* spp. attributed to occurrence of *Cerato-scopelus maderensis* (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)
Ommastrephes bartramii (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)
Illex coindetti (short-finned squid)	Marine	Adriatic Sea	Seasonal variation in *Anisakis pegreffi* and *Phyllobothrium* sp. coincided with *M. muelleri* in diet	Petrić et al. (2011)
Doryteuthis (=*Loligo*) *gahi* (longfin Patagonian squid)	Marine	Falkland Islands	Presence of *Anisakis* 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 transfer-ring 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 osculatum* 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 physeteris* 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
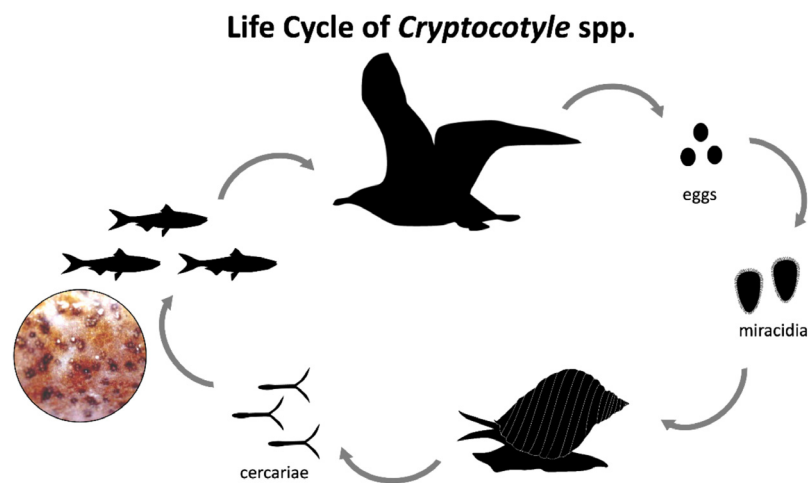

Fig. 3. Trematodes in the genus *Cryptocotyle* mature and reproduce in fish-eating birds. Their eggs are released with feces and hatch into free-swimming miracidia, which penetrate the molluscan host. As with all trematodes, mollusks serve as first intermediate hosts. Asexually produced free-swimming 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
Ammodytes tobianus (small sandeel)	Wadden Sea	*Hysterothylacium* sp.	Piscivorous fish	Fish play important role in parasite transmission	Groenewold et al. (1996)
Sprattus sprattus (European sprat)		*Cryptocotyle lingua*	Sea birds		
Ammodytes tobianus	Western Ireland	Larval helminths	Sea birds, marine mammals		O'Connell & Fives (2004)
Sprattus sprattus	European waters	Larval helminths	Piscivores	Sprat is important intermediate host	Kleinertz et al. (2012)
Etropterus spinax (velvet belly)	Norwegian Deep	Tetraphyllidean and trypanorhynch larvae	Sharks, piscivorous fish		Klimpel et al. (2003a)
Nealotus tripes (black snake mackerel)	Canary Current off NW Africa	*Anisakis typica* *Anisakis physteris* Tetraphyllidean larvae	Small toothed whales Squid Sharks	Distribution reflects that of delphinids along coast	Alt et al. (2018)
Centropomus nigrescens (black snook)	Mexican lagoons	*Echinocephalus* sp. *Sebakia* sp.	Elasmobranchs Crocodiles		Violante-González et al. (2010)
Anchoa mitchilli (bay anchovy)	Mississippi Sound, USA	*Bucephalus scomberomorous,Didymocystis scomberomori, Hysterothylacium fotalezae Phoreobothrium* sp., *Acanthobothrium* sp.	*Scomberomorus maculatus* (Spanish mackerel), *Rhizoprionodon terraenovae* (Atlantic sharpnose shark)	Prevalence and abundance of parasites reflects timing of predator migration into sound	Andres et al. (2016)
Osmerus mordax (smelt) *Gasterosteus aculeatus* (three-spined stickleback)	Bothnian Bay, Finland	8 of 11 helminth species 9 of 15 helminth species	*Lota lota* (burbot)	Both pelagic species in stomach contents of burbot	Valtonen & Julkunen (1995)
Osmerus mordax *Gasterosteus aculeatus* *Liza* spp. (grey mullets) *Mugil cephalus* (flathead grey mullet)	Bothnian Bay, Finland Santa Gilla Lagoon, Sardinia	Various parasites *Phagicola* spp. Various trematodes	Sea birds and marine mammals Foxes *Dicentrarchus labrax* (European sea bass), *Anguilla anguilla* (European eel)	Also, parasites of demersal fishes indicate predation by seabirds and migrating piscivorous fishes	Valtonen et al. (2010) Culurgioni et al. (2015)
Illex coindetii (short-finned squid) *Todaropsis eblanae* (short-finned squid)	Off coast of Spain	Larval tetraphyllideans and trypanorhynchs, and larval anisakid nematodes	Sharks Marine mammals	Absence of larval didymozoid trematodes implied that squid were not preyed upon by xiphoid fishes	Pascual et al. (1996)
Dosididicus gigas (jumbo squid)	Pacific Ocean	Larval helminths	Sharks, whales and xiphoid fishes	Relative abundance suggests predator abundance varies regionally	Shukhgalter & Nigmatullin (2001)
Histioteuthis bonnelli (umbrella squid)	Tyrrhenian Sea	*Anisakis physeteris*	Sperm whales (Physeteridae) Swordfish (*Xiphias gladius*)	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 *Dosididicus 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 (Sinisalo 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* (Preti 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					
Scyliorhinus stellaris (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)
Lepidopus caudatus (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)
Trichiurus lepturus (largehead hairtail)	West Java, Indonesia	Nematodes, trematodes, cestodes	Predominantly a piscivore	Evenly distributed parasite fauna among groups reflects piscivorous diet	Koepper et al. (2022)
Coryphaenoides rupestris (roundnose grenadier)	Upper continental slope, Newfoundland	Mainly trematodes, especially *Steringophorus* sp.	Copepods and other crustaceans, including euphausiids	Bathypelagic fish that vertically migrates to feed	Houston & Haedrich (1986)
Synaphobranchus kaupii (Kaup's arrowtooth eel)	Upper continental slope, Newfoundland	*Hysterothylacium* sp., *Contracaecum* sp. (Nematoda)	Myctophid fishes, euphausiids	Bathydemersal fish that vertically migrates to feed	Houston & Haedrich (1986)
Physeter macrocephalus (sperm whale)	Tyrrhenian Sea, Central Mediterranean	*Anisakis physeteris* (Nematoda)	Squids (*Histioteuthis bonnellii*, *Histioteuthis reversa*)		Cipriani et al. (2022)
Phalacrocorax atriceps (imperial shag)	Santa Cruz Province, Argentina	*Contracaecum* spp. (Nematoda)	*Engraulis anchoita* (Argentine anchovy)	Parasites and prey determined using fecal pellets	Garbin et al. (2019)
Phalacrocorax gaimardi (red-legged cormorant)	Santa Cruz Province, Argentina	*Contracaecum* spp. (Nematoda)	*Sprattus fueguensis* (Falkland sprat), *Ramnogaster arcuate* (Jenyns's sprat)	Parasites and prey determined using fecal pellets	Garbin et al. (2019)
Phoca hispida botnica (ringed seal)	Bothnian Bay, Finland	*Schistocephalus solidus* (Cestoda)	*Gasterosteus aculeatus* (three-spined stickleback)	Prey determined using stable isotopes and parasites	Sinisalo et al. (2006)
(B) Studies that infer diet from parasites alone					
Larus argentatus (herring gull)	North Wales	*Cryptocotyle lingua* (Trematoda)	Inshore coastal fishes		Threlfall (1967)
Alcid seabirds	Holarctic	*Alcataenia* spp. (Cestoda)	Euphausiids		Hoberg (1986)
Antimora rostrata (blue antimora)	New York Bight	Mainly trematodes	Benthopelagic invertebrates	Bathypelagic fish that feeds on pelagic prey	Campbell et al. (1980)
Alopias vulpinus (thresher shark)	Southern California	*Rhadinorhynchus cololabis* (Acanthocephala)	*Cololabis saira* (Pacific saury)	Remains of the parasitic copepod (*Pennella* sp.) also indicate feeding on *C. saira*	Preti et al. (2020)
Katsuwonus pelamis (skipjack tuna) *Seriola dumerili* (greater amberjack)	Madeira	*Oncophora melanocephala* (Nematoda)	*Scomber colias* (Atlantic chub mackerel)	Abundant and common prey of tunas in the region	Hermida et al. (2019), Cavaleiro et al. (2018)

Table 5. (continued)

Predator	Location	Parasite(s)	Pelagic prey	Comment	Reference
Katsuwonus pelamis (skipjack tuna)	Madeira	*Anisakis* sp. (Nematoda)	*S. colias* *Trachurus picturatus* (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	Multipe 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)

[a]Food 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).

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