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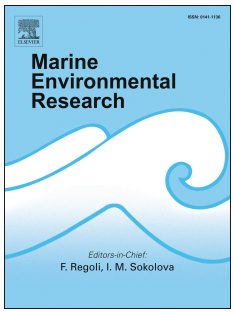

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Digenean parasites as novel tracers of predation on jellyfish

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Abstract

Cnidarian medusae and ctenophores were long considered trophic dead ends due to their low nutritional value and they are often overlooked in in the digestive tracts of predators. Traditional and emerging methods of analysing diets, including gut content analysis, stable isotopes, and metabarcoding, have limitations in identifying jellyfish consumption. This review explores the potential of using endoparasitic trematodes as novel trophic tracers of jellyfish predation. Trematodes, which require multiple hosts to complete their life cycles, can serve as natural dietary tags, with their presence in definitive hosts reflecting consumption of infected intermediate hosts, including jellyfish. First, we systematically compiled published records of trematode metacercariae in jellyfish and supplemented these with new, unpublished records from off eastern Australia. To identify potential jellyfish predators, we then examined the published literature for reports of definitive hosts of trematode species known to infect jellyfish as metacercariae. We identified 230 definitive host-parasite associations involving 64 putative trematode species. Molecular and morphological analyses linked these parasites to 140 fish species across 48 families, confirming some known predators of jellyfish (e.g. some carangids) and identifying some previously unrecognised potential jellyfish predators (e.g. some scombrids). While host

specificity of digeneans in jellyfish and fish hosts varies, some trematodes show strong potential as indicators of jellyfish predation. However, the accurate identification of metacercariae (to the level of individual species) remains a key limitation, underscoring the need for integrative taxonomic approaches that incorporate molecular data. This review highlights the promise of trematodes as powerful tools for elucidating jellyfish predation and improving our understanding of marine food webs.

Keywords: diet, medusivory, Cnidaria, Ctenophora, medusae, comb jellyfish, fish, Trematoda

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Introduction

Jellyfish (defined as cnidarian medusae and siphonophores, and ctenophores) often comprise a large proportion of the pelagic biomass. Due to their very high water content (Pitt et al., 2013) and low calorific content (Doyle et al., 2007), jellyfish have historically been assumed to be a poor source of food that are regularly consumed by just a few large and specialised predators (e.g. leatherback turtles and ocean sunfish; Verity and Smetacek, 1996). This understanding was seemingly confirmed by the fact that jellyfish tissue is rarely observed in, and infrequently positively identified in, the digestive tracts of predators. As a result, jellyfish have been routinely interpreted as trophic 'dead ends' and research on the trophic ecology of jellyfish has, therefore, focused disproportionately on their role as predators in marine food webs; their potential importance as prey has, until recently (Hays et al., 2018), been largely overlooked.

A diverse array of techniques has been used to assess animal diets, including gut content analyses, biochemical tracers such as stable isotopes and fatty acids, metabarcoding of gut contents and faeces, and animal-borne cameras (Hays et al., 2018). However, the unusual biology and ecology of jellyfish provides some unique challenges that limit the ability of many methods to detect jellyfish in the diets of predators. The tissues of most jellyfish are transparent, fragile, contain few or no distinctive structures, and are usually macerated during ingestion; all these factors render jellyfish almost impossible to identify in gut content analyses (but see Mianzan et al., 1996). The high-water content of their tissues (>96%; Lucas et al., 2011) facilitates rapid digestion, further decreasing the likelihood that gelatinous tissue will be detected and identified. Most jellyfish also exhibit extreme variations in their spatial and temporal distributions. Few animals, therefore, are likely to be obligate consumers of jellyfish, and those that are typically consume jellyfish in significant amounts at specific times and places. Hence, approaches such as gut content analyses, which provide a 'snapshot' of recent feeding, may only detect consumption of jellyfish if the sampling program is temporally and spatially comprehensive. Stable isotopes and fatty acid tracers offer advantages over traditional gut content analyses by providing time-integrated analyses of diet. However, these analyses can only provide a broad overview of dietary sources and experiments (e.g., where prey enriched with isotopes are fed to predators) are required to identify the species involved in specific trophic links (Pitt et al., 2009).

Emerging technologies have greatly improved the ability to detect jellyfish in diets (Hays et al., 2018). Metabarcoding of gut contents and faeces has enabled more accurate identification

of gelatinous tissue and has revealed some novel predators, including penguins (Jarman et al., 2013; Lamb et al., 2017). However, like traditional gut content analyses, metabarcoding still only indicates recent feeding. Moreover, although faeces may be readily collected from seabirds or mammals that return to land, they are challenging to collect from most marine predators. Animal-borne cameras have observed penguins (Sutton et al., 2015) and turtles (Fukuoka et al., 2016) ingesting jellyfish, but they are limited to predators to which cameras can be attached and retrieved. Whilst these technologies have expanded our knowledge of predation on jellyfish and helped challenge the "trophic dead-end" paradigm (Hays et al., 2018), they still have significant limitations. New approaches, preferably ones that integrate dietary signals over time, are needed to identify predators of jellyfish and to improve understanding of marine food webs.

Parasites are ubiquitous in the marine environment and are estimated to account for almost half of all species on Earth (Poulin and Morand, 2000). Many endoparasites, including trematode flukes (Digenea) infect multiple hosts during their life cycles (Box 1). Typically, the final (definitive) host, usually a vertebrate, acquires parasites by consuming intermediate hosts that are infected with metacercariae (second stage trematode larvae). The parasites that infect any specific definitive host, therefore, reflect the host's diet and, potentially, temporal and spatial patterns in the distribution of food sources. Thus, parasites may act as natural tags that can be used to address ecological questions regarding movement, habitat use and diet of the host (Williams et al., 1992). For example, spatial and temporal variations in parasite communities within fish have been used to indicate habitat use and movements of juvenile fish at small spatial scales (i.e.,10s of kms; see Durieux et al., 2010), to assess population structure (Catalano et al., 2014; Feki et al., 2018) and to identify migration routes (Groot et al., 1989).

Parasites are estimated to be involved in 75% of food web links (Dobson et al., 2008) and, therefore, hold great potential as tracers of diet. Parasites may be particularly valuable trophic tracers because they usually survive for weeks to months in definitive hosts, thereby providing an indication of their diet over time (Davidsen et al., 2017; Knudsen et al., 2014). The utility of parasites to inform aspects of diet has been demonstrated by studies that have correlated parasite communities of fish with the prey they have consumed. For example, seasonal changes in intestinal parasite communities of lake salmonids mirrored the seasonal changes in the types of prey consumed (Prati et al., 2020). Parasite communities also reflected different feeding specialisations within populations of Arctic char, *Salvelinus*

alpinus; those that fed in benthic habitats consistently consumed different intermediate hosts and were infected by different parasites than those that fed in limnetic zones (Curtis et al., 1995). Moreover, parasites have proved valuable for examining various food web properties. For example, fish with the broadest diet (as determined by analysis of gut contents) also hosted the greatest diversity of parasites (Prati et al., 2020). Hence, endoparasites appear to be robust and useful tracers of diet and may prove a useful tool for identifying predators of jellyfish (Briz et al., 2016; Briz et al., 2012).

There are several key requirements for a parasite to be a useful trophic tracer of predation on jellyfish. First and most importantly, the transmissible forms of the parasite should be common and prevalent in jellyfish. Second, the parasites that infect jellyfish need to be accurately identified to species level and their life cycle linked to the adult parasite in the definitive hosts that consume jellyfish. Third, the degree of host specificity of the parasite in the jellyfish should be known, to help determine whether its presence in a definitive host reflects feeding on one or multiple species of jellyfish, or other groups of animals as well.

In the recently published literature, there have been six clear examples of parasites being used to identify predators of jellyfish, one using morphological data in isolation and five that incorporated molecular data. Kondo et al. (2016) morphologically matched adult trematodes in three species of juvenile fish that associate with jellyfish with metacercariae in the respective host jellyfishes, thus providing evidence that these fishes preyed on their jellyfish hosts. The five studies that used molecular approaches (Browne et al., 2020; Cribb et al., 2024; Duong et al., 2022; Louvard et al., 2024; Yong et al., 2025) confirmed the diet of some fish that had been suspected to feed on jellyfish (such as scombrids; Browne et al., 2020; Cribb et al., 2024; carangids; Yong et al., 2025 and *Mola mola*; Louvard et al., 2024) but also suggested novel predators of jellyfish, including tropical pomacentrid damselfishes (Duong et al., 2022) and a monodactylid (Cribb et al., 2024). These studies provide a strong foundation for expanding the use of parasites as trophic tracers of predators of jellyfish.

The aim of this review is to assess the potential of endoparasitic trematodes as novel trophic tracers of predation on jellyfish. First, we assembled all published reports of trematode metacercariae in jellyfish and supplemented these with new records from specimens collected by the authors. We used these data to assess 1) whether digenean metacercariae commonly infect jellyfish hosts and 2) the specificity of jellyfish/trematode associations. We then searched for reported definitive hosts of the trematodes that were found to infect jellyfish, to assess whether the trematode life cycles involving jellyfish were known, and to identify

potential predators of jellyfish. Finally, we discuss how endoparasites could be used to inform trophic ecology, beyond the simple identification of jellyfish predators.

Methods

Reports of trematode parasites infecting jellyfish were compiled by exhaustively searching the published literature. ISI Web of Knowledge, Google Scholar, and the Biodiversity Heritage Library were searched using the broad search terms "jellyfish* OR medusa* OR ctenophore* OR siphonophore* AND parasite*". Additional references not listed in online databases were identified following citations found in papers. Currently accepted species names and higher classifications follow those of the World Register of Marine Species (http://www.marinespecies.org) and the taxonomic literature.

Published reports were supplemented with new records of digenean metacercariae collected by the authors during oceanographic voyages on RV Investigator in eastern Australia in 2019 and 2021 and from samples collected in coastal waters of southeast Queensland, Australia. Collection and fixation methods for these samples were reported in Duong et al. (2023) and Cribb et al. (2024). For trematode identification, precedence was given to generating molecular data over preparing permanent morphological preparations. However, where specimens were large enough, hologenophores were prepared and deposited in the Queensland Museum (QM). Morphological specimens were prepared according to the protocols of Cribb et al. (2024). Some hologenophores were drawn with a camera lucida fitted to an Olympus BX-53 compound microscope and subsequently digitised using a drawing pad and Adobe Illustrator 2025 software. ITS2 rDNA and *cox*1 mtDNA sequences were generated using the same primers as Cribb et al. (2024). Sequences were visualised with NJ trees, and distance matrices were generated for each family or superfamily. Sequences were considered as representative of separate species based on the levels of difference discussed for each family. All sequences were subject to BLAST analysis through GenBank in search of identifications based on identical or close matches.

Definitive hosts of parasites from jellyfish that had been identified to the taxonomic level of species were compiled by searching the species name of the trematode using ISI Web of Knowledge and references to unpublished data held in the collections of the Queensland Museum Marine Parasitology Group. Literature was searched using both currently accepted names and unaccepted names, if the unaccepted name was used when the parasite was first

reported in the jellyfish host. The names used in the original papers, and the currently accepted names are presented throughout.

Results

New records of digenean metacercariae infecting gelatinous zooplankton

New records of digenean metacercariae from Australian jellyfish are presented in detail in Supplementary Information Section 1 and Supplementary Table 1. These records are interpreted to relate to two species of Accacoeliidae, 14 species of Didymozoidae, four species of Hemiuridae, two species of possible Lecithophyllidae, one species of Sclerodistomidae, and one species of Fellodistomidae.

Diversity of jellyfish/trematode associations

Based on the literature and new records reported here, 230 plausible records (here defined as distinct host/parasite/report combinations) of jellyfish being infected by digenean parasites were identified (Supplementary Table 1). Metacercariae have been reported in 61 species of cnidarian medusae, including in 44 Hydrozoa, 16 Scyphozoa and 1 Cubozoa, and in eight species of ctenophores (four each in the Nuda and Tentaculata) (Table 1). Metacercariae in jellyfish were dominated by just three trematode superfamilies: Hemiuroidea (six families) representing 70 (30%) reports; Lepocreadioidea (two families) representing 121 (53%) reports; Gymnophalloidea (two families) representing 26 (11%) reports. Species belonging to Microphallidae or not convincingly identifiable to family represented ~6% of all records. Sixty-four putative digenean species (including those identified only to supraspecific taxa) have been reported in jellyfish (Table 2; Supplementary Table 1).

Specificity of host/parasite relationships

Host-specificity of metacercariae in jellyfish varies dramatically. Many host/parasite relationships were reported as non-specific. For example, *Monascus filiformis* (Fellodistomidae) infects 17 species of hydrozoan medusae and *Opechona bacillaris* (Lepocreadiidae) infects at least 11 species of jellyfish across two phyla (Supplementary Table 1). In total, 12 nominal species of digeneans were reported to infect both cnidarians and ctenophores (Table 2). In contrast, from the present sequencing of samples from Australian jellyfish (Supplementary Information) there is also evidence that several species of

metacercariae are specific to or at least are concentrated in individual species of jellyfish. For example, Sclerodistomidae species A occurred in seven individual *Hormiphora* sp. (Ctenophora) but in no cnidarians; Didymozoidae Type 1 was sequenced from 23 *Hormiphora* sp. individuals but only three cnidarians; *Lecithocladium* species 4 was found in five *Aldersladia magnificus* but in no other cnidarians or ctenophores (Supplementary Table 1). In previous work (Cribb et al., 2024) metacercariae of *Prodistomum keyam* (Lepocreadiidae) were found in only one intermediate jellyfish host (*Pukia falcata*), despite extensive sampling within the study region.

Some jellyfish species were infected by many trematode species (Table 1); the ctenophores *Mnemiopsis leidyi* and *Pukia falcata* were infected by at least six and seven species respectively and the cnidarians *Aldersladia magnificus* and *Chrysaora pentastoma* hosted 17 and six species respectively (Supplementary Table 1). These high figures of richness probably reflect the fact that these species have been well-studied. However, there is some evidence of jellyfish that are poor hosts; for example, we examined ten *Catostylus mosaicus* (Scyphozoa) from Moreton Bay without finding any infections.

Reliability of species assignment in metacercariae

Of the 230 recorded host/parasite combinations, 145 identified metacercariae using only morphology and 85 integrated molecular sequencing with morphological analyses (Supplementary Table 1). Seventy-eight of the 145 records of metacercariae identified solely from morphology assigned the metacercariae to species, and 32 of the 85 metacercariae identified using integrative taxonomy were assigned to species, with the rest designed as type species whose taxonomy is not fully resolved. The degree to which reports of incompletely identified species overlap with each other and with fully identified species is uncertain. Species counts and proportions are, therefore, only estimates.

Definitive hosts of trematodes that infect jellyfish

Definitive hosts were located for 36 of the 56 (Table 1) species of metacercariae that infect jellyfish (including species of metacercariae designated as type-species using integrative taxonomy; Supplementary Table 2). We identified 48 families and 138 species of fish as definitive hosts of digenean species that infect jellyfish as metacercariae (Table 3). Numbers of fish species recorded from the infected families differ dramatically. The Carangidae,

Pleuronectidae, Pomacentridae and Scorpaenidae each had >9 species infected, whereas no other family had more than seven infected; 26 families had only one infected species. These rarely infected families included some that are exceptionally rich (e.g. Gobiidae =1957 species; Labridae n=569 species; Liparidae n=435 species). Numbers of nominal digenean species per fish family are also heavily skewed. By far the most heavily infected is the Scombridae (13 digenean species) followed by the Carangidae, Gadidae and Pleuronectidae, each of which were infected by six digenean species (Table 3). Despite the richness of jellyfish-infecting digeneans in scombrids, just five of the 54 species of scombrid were infected (four species of *Scomber* and *Rastrelliger kanagurta* (Cuvier, 1816)); by contrast, according to our unpublished records, other trematodes are known from at least 51 of the 54 recognised scombrid species. Similarly, infections of digeneans that occur as metacercariae in jellyfish have been reported in only 14 of 147 species of carangids and in 9 of 62 species of Pleuronectidae; members of both of these families are infected by a diverse fauna of trematode species.

Discussion

Parasitological evidence of jellyfish in fish diet

The results of the literature searches combined with our new records demonstrate that digenean metacercariae are widespread and diverse in jellyfish, and that many jellyfish are infected by digeneans. The ubiquity of jellyfish/trematode associations make digeneans potentially useful for tracing trophic relationships, and especially for identifying species of fish that have never been reported to ingest jellyfish. However, the utility of digeneans as tracers of diet is at least partially hindered by two aspects: 1) the difficulty in accurately identifying metacercariae and thus linking the metacercariae to adults in definitive hosts, and 2) the range of specificity in host parasite relationships.

Taxonomic challenges and elucidating life cycles

Accurate taxonomic identification of the different life history stages of parasites is fundamental to elucidating life cycles and to parasites being used as trophic tracers. Less than half the metacercariae reported in jellyfish, however, were identified to species, many based on morphology and thus subject to molecular verification. Metacercariae are typically morphologically simple compared with their adult forms, having undergone only minor

development in characters used to identify adults (e.g., oral and ventral suckers, reproductive organs, terminal genitalia) and can often only be reliably identified to genus or family. Hence, records where species have been identified based on only morphology (which represent most of the records) need to be interpreted cautiously. DNA sequencing has revolutionised our ability to identify metacercariae (e.g. Jousson et al., 1999), and to elucidate life cycles by linking metacercariae to other life history stages in first-intermediate and definitive hosts. Indeed, molecular approaches are now used in >90% of taxonomic and systematic studies of trematodes (Blasco-Costa et al., 2016). Despite the wide-spread adoption of molecular approaches in the field of digenean taxonomy, DNA sequencing has only been applied in studies of jellyfish metacercariae since 2020.

A further complexity in using trematodes as trophic tracers of diet is that the adult forms of many species are yet to be described. The World Register of Marine Species shows that about 30 new marine trematode species have been described every year for the past decade. Molecular techniques are also revealing a high degree of diversity, through evidence of cryptic speciation (Cutmore et al., 2023; Diaz et al. 2015) that had been masked by studies that identified trematodes using morphology alone (e.g. Cribb et al., 2022; Cutmore et al., 2023). There is also considerable activity in splitting and recombining (synonymising) species. Together, these factors imply that when metacercariae in jellyfish are found, it is by no means certain that the digenean in question has a formal name.

Specificity of trematode/jellyfish associations

In general, digeneans will provide the most unambiguous indication of predation by a definitive host on an intermediate host when the host/parasite relationship is highly specific; if a digenean species infects only one species of intermediate host, the definitive host can be reliably inferred to have consumed that species. Our thorough review, however, revealed that most species of digeneans appear to infect numerous jellyfish hosts and some also infect phyla other than cnidarians and ctenophores. For example, *O. bacillaris* infects jellyfish but also chaetognaths (*Sagitta* spp; Køie, 1975) and the pelagic polychaete *Tomopteris helgolandica* (Reimer et al. 1971 cited in Køie, 1975). Estimates of host specificity are likely to be highly sensitive to sampling effort and even seemingly specific relationships may be revealed to be non-specific if increasing sampling effort reveals additional hosts; in this area the issue of ‘absence of evidence’ vs. ‘evidence of absence’ is highly problematic.

Conversely, molecular analyses may also reveal that parasite/host relationships may be much more specific than currently realised. For example, six species of trochid gastropods (first intermediate hosts) were thought to be infected by a single trematode morphotype; molecular sequencing of this morphotype revealed that the infections comprised three distinct clades (and probable species) of trematodes, some of which infected a single molluscan host (Donald et al., 2004). Molecular exploration of digenean larvae in jellyfish hosts can be expected to reveal comparable cases of a higher degree of host specificity than are currently recognised. However, it should not be assumed that molecular characterisation will prove complexes of species and high specificity; many trematodes have been shown to have high specificity at the first and definitive stages and genuinely low specificity at the second intermediate stage (Locke et al., 2010). Such low specificity appears common for those species that infect jellyfish as metacercariae.

Overall, sampling effort has probably been insufficient to allow reliable conclusions about patterns of host-specificity for most species. While trematodes usually have lower specificity for second intermediate hosts than for definitive hosts, the low specificity in jellyfish may be an artifact of failure to identify species accurately to the level of species and even genus. The available evidence, however, suggests that the role of jellyfish in the transmission of digeneans to marine fishes covers a spectrum from obligate (or at least critical) involvement to relatively insignificant occasional transmission for species in which other hosts are more important, to some possible transmission dead-ends (where a parasite infects a host that does not contribute to the continuation of the parasite's life cycle). The details require further attention in almost every case. In general, however, the presence of these digeneans in fishes stands as an indicator of the potential role of jellyfish in the diet and the consequent value in exploring this possibility further.

The utility of digeneans as trophic tracers of jellyfish predators

Despite limitations regarding current understanding of digenean taxonomy and life cycles, and the low specificity of some jellyfish/digenean relationships, we consider that digenean trematodes hold considerable promise for identifying predators of jellyfish. As molecular taxonomy becomes more affordable and mainstream, our ability to accurately identify metacercariae in jellyfish, and to accurately link the metacercariae to adult forms in definitive hosts will improve. However, this relies on genetic data being made available through

archiving in public databases (such as GenBank) and linking those data to morphological voucher specimens.

Additional information on the prevalence and intensity of infections and distributions of parasites and hosts can also overcome some of the challenges associated with low host/parasite specificity. Ultimately, digeneans that infect single species of jellyfish intermediate hosts may be quite rare because paratenic hosts (those in which the parasite does not develop but that may transport the parasite to another host) and accidental hosts are proving reasonably common. The prevalence and intensity of infection in paratenic and accidental hosts, however, can be expected to be much lower than in obligate hosts. Hence, when assessing the utility of a particular parasite as a trophic tracer, the prevalence and intensity of infection should be considered in addition to the total number of hosts. This is because if a parasite occurs predominantly and/or abundantly in one host species and only occasionally and in small numbers in other host species, then it is most likely that definitive hosts acquired their parasites by preying on the common rather than paratenic or accidental hosts. Patterns of geographical distribution may also help elucidate trophic links of some parasites that exhibit low host specificity. For example, a widely distributed parasite might infect multiple hosts, but if the distribution of the definitive host overlaps with only one or some of the intermediate hosts, the parasite might still be useful for interpreting trophic links.

The use of digenean trematodes to identify predators of jellyfish provides several benefits over traditional trophic elucidation techniques. Most importantly, this approach can utilise existing information from the field of marine fish parasitology, which has been documenting the digenean fauna of fishes for >100 years and lodging molecular sequences of fish digeneans in public repositories, such as a GenBank, for several decades. Thus, once a metacercaria from a jellyfish has been reliably identified, there is a reasonable chance that it can be linked to a digenean in a definitive host; indeed, we identified definitive hosts for 36 of the 56 species of metacercaria reported in jellyfish. Identifying the hosts of adult digeneans from existing literature and data repositories negates the need to kill large numbers of potential predators, as is usually required for gut content analyses. The technique also provides precise taxonomic information about which species of predator consume which species of jellyfish prey; this is an advantage over stable isotope analyses, which broadly distinguish types of food sources, but cannot readily identify individual species of prey. Finally, digeneans are readily observed and easily extracted from jellyfish; particularly small and translucent species (Box 2) and molecular sequencing is now routine. Hence specialised

equipment and facilities are not required. Since digeneans tend to occur in the mesoglea of jellyfish (pers. obs.), this approach may under-estimate predation by predators that selectively target the gonads or mucus of jellyfish (e.g. Milisenda et al. 2014), although such predators are likely to be opportunistic, rather than major predators of jellyfish.

Proof of concept

Notwithstanding our concerns regarding the reliability of the species level identifications of metacercariae and specificity of host/parasite relationships, as proof-of-concept, we searched for indications of previously unrecognised predators of jellyfish by identifying definitive hosts of the species of metacercariae reported to infect jellyfish. From the 230 reports of digeneans infecting jellyfish, we identified 140 species of fish from 48 families as candidate predators of jellyfish. Using information on prevalence and intensity of infections and knowledge of the digenean fauna of the fish, we suggest that the infections in these fishes can be considered in four (overlapping) categories:

1. Infections in fishes that are already considered significant predators of jellyfish. Good examples in this category include known or suspected predators of jellyfish, such as the carangid, *Trachurus trachurus* (see Tilves et al., 2018) and the ocean sunfish, *Mola mola*. For *M. mola*, infection by the accacoeliid *Accacoelium contortum* that occurs in *Porpita porpita* (Louvard et al., 2024) is consistent with this species feeding predominantly on gelatinous zooplankton (Chang et al. 2024). Strikingly, *M. mola* hosts a rich fauna of at least ten accacoeliid species (World Register of Marine Species). The fact that only one of these species has so far been found as a metacercaria in jellyfish may relate to *M. mola* being a relatively uncommon fish and that its parasites are large, perhaps long-lived, and, therefore, uncommon in jellyfish.

2. Infections in fishes not presently considered significant predators of jellyfish but likely to be so. The four species of *Scomber* together with *Rastrelliger kanagurta* shared the richest community of digenean species known to infect jellyfish as metacercariae. These digeneans included multiple didymozoids and lepocreadiids, a hemiurid, and a fellodistomid. The abundance and richness of this fauna, concentrated in these closely related fishes, suggests strongly that jellyfish are a regular and significant part of the diet of these fishes that has been largely overlooked, as they are variously characterised as planktivorous or as eating a range of invertebrates.

Other fish species identified as potential novel predators of jellyfish included *Aldrichetta forsteri* (Mugilidae; see Jones, 1978), *Micropogonias furnieri* (Sciaenidae; see Pereira et al., 2000), and several pomacentrids, including *Abudefduf sexfasciatus* (see Duong et al., 2022). *Abudefduf sexfasciatus* is planktivorous (Frédérich et al., 2009) and *Aldrichetta forsteri* and *Micropogonias furnieri* are generalist predators, predominantly of invertebrates (Platell et al., 2006; Ruiz et al., 2001), so predation on jellyfish is plausible.

3. Infections in fishes that may reflect occasional ingestion of jellyfish or complex life cycles that involve other intermediate hosts in addition to jellyfish. This category reflects many host/parasite associations with insufficient information to allow understanding of how the life cycle works. A good example is *Derogenes varicus* which infects at least 20 families of fishes. Metacercariae of this species have been reported from ctenophores (Künne 1952; Lauckner 1980) but also from copepods (Køie, 1979). Køie (1979) also showed that infections could be transferred as immatures by the ingestion of smaller fish by larger fish. As a result of these observations, it is presently impossible to know the dominant patterns of transmission and the relative importance of jellyfish.

4. Infections in fishes which, despite the identity of the parasites, seem improbable as the result of the direct ingestion of jellyfish. *Coryphaena hippurus* and *Pomatomus saltatrix* are large, fast swimming carnivores that seem improbable as regular predators of jellyfish. However, coryphaenids are infected by an accacoeliid and two hemiurids known as metacercariae in jellyfish and *P. saltatrix* hosted a hemiurid and a lepocreadiid that infect jellyfish. This discrepancy points either to jellyfish as dead-end hosts for this species or, perhaps more likely, that the digeneans have complex life cycles that involve facultative transfer of parasites from ingested host to host until final infection of the definitive host. Facultative transmission between members of the pleuston community was inferred by Louvard et al. (2024). In this kind of pattern of transmission, jellyfish may be a significant part of the life cycle without being eaten directly by the definitive host.

Trophic information provided by digeneans, beyond simple predator prey relationships

Using parasites as trophic tracers is likely to provide information on diet beyond simple identification of predators and prey. Parasites may provide useful measures of fundamental food web properties, such as niche width. This is because definitive hosts that prey on diverse intermediate hosts are likely to encounter, and potentially be infected by, a greater diversity

of parasites than those that specialise on fewer types of prey. Indeed, populations of sharks that had more diverse diets also hosted the greatest diversity of cestodes (Rasmussen and Randhawa, 2018). Intraspecific specialisation in diet may also be revealed. For example, Arctic charr (*Salvelinus alpinus*) that fed on zooplankton were infected with parasites transmitted by pelagic copepods, whereas benthic-feeding individuals hosted parasites transmitted by benthic amphipods (Knudsen et al., 2014).

Knowledge of the residence time of digeneans within definitive hosts could greatly enhance their utility as trophic tracers. For example, residence times could inform the timing of predation, in a similar way to the 'isotopic clock' concept in stable isotope ecology, whereby analyses of tissues with different turnover times of isotopes are used to infer timing of predation events (Fry, 2006). The occurrence of short-lived parasites in a host (i.e. those that persist for days to weeks) will reflect recent feeding, whereas long-lived parasites may have been acquired by the host by feeding long ago or more recently. Hence, short-lived parasites will be very useful for studying short-term and seasonal changes in diet, whereas long-lived parasites may broadly indicate a food source but not the timing of feeding (although logically it must have occurred within the lifespan of the parasite). Hence, knowledge of the lifespan of digeneans would be extremely useful for interpreting dietary trends.

Ontogenetic changes in diets may be revealed if parasites infect hosts of particular ages or sizes (e.g. Munster et al., 2015). Switches to or from prey may be detected (e.g. Randhawa and Brickle, 2011) but switches away from a prey source (as indicated by the intensity of infection decreasing as the host ages) could only be detected for parasites that are short-lived relative to their host. In contrast, the appearance of a new parasite in a host at a particular age could indicate a switch to a new source of prey, and such changes could be detected, regardless of the longevity of the parasite.

The key impediment to determining residence times is that endoparasites (particularly helminths) lack structures that record their age (*cf.* otoliths in fish). Longevity is, therefore, determined experimentally (e.g. Bailey et al., 1989), inferred through changes in size distributions of adult parasites (e.g. Giæver et al., 1991), or by comparing the timing of infection and shedding of parasites (Meskal, 1967). Estimates of residency are available for only few taxa, appear to be quite variable, and are often inexact, especially when parasites persist within hosts beyond the duration of the experiment (e.g. Bailey et al., 1989). Most intestinal helminths are thought to persist for < 1 year (Bailey et al., 1989; Scott, 1969) but

there are exceptions; the hemiurid *Tubulovesicula lindbergi* lives for >31 months in the stomach of chum salmon *Oncorhynchus keta* (Margolis and Boyce, 1969).

The demographics of parasites within a host may also provide clues about their residency. For example, parasites with long residence times (e.g. multiple years) probably accumulate in hosts as they age (Amundsen et al., 2003), those that persist for weeks to months may occur seasonally within a host (Amundsen et al., 2003) and those with intermediate longevity (i.e. many months to a year) may display intensities of infection that are independent of the age of the host due to the continual turn-over of parasites. Studies comparing intensity of infection to host age may, therefore, be particularly informative for inferring longevity of parasites. Jellyfish could be ideal experimental models for such studies, since metacercariae can be easily seen within the tissues of living jellyfish species that have transparent tissues.

Coupling multiple trophic tracers to elucidate diet

As with most trophic tracers, combining multiple approaches is likely to provide the most robust evidence of trophic pathways, particularly for parasites that have not been sequenced and whose identities cannot be confirmed. For example, Kondo et al. (2016) identified metacercariae in jellyfish hosts using morphology and matched them to adult trematodes in juvenile fish that associated with the jellyfish. Greater confidence in trophic links identified using these digenean matches was provided by also analysing the $\delta^{13}C$ and $\delta^{15}N$ values of fish and jellyfish and by examining the guts of the fish and identifying the presence of jellyfish tissue and nematocysts. The results of the three different methodologies were mostly consistent and provided robust evidence that two of the three species of fish both associated with and fed on the jellyfish.

Conclusion

Digeneans hold great promise as a tool for studying the trophic ecology of jellyfish and, particularly for identifying novel predators of jellyfishes. Several challenges, however, need to be solved before digeneans can be widely adopted as a tool for trophic ecology. Most important is to improve the accuracy with which metacercariae are identified. This is already happening as taxonomists progressively move towards using integrative taxonomic approaches that incorporate molecular data. The study of digeneans parasitising jellyfish

517 needs to expand beyond the relatively localised regions that have been sampled so far, to
518 better resolve biodiversity and biogeographical patterns, and to better understand the
519 residence times of adult digeneans in definitive hosts. Nonetheless, digeneans hold great
520 promise and, if coupled with other trophic tracers, such as stable isotopes, will be a powerful
521 tool for identifying the nature and significance of trophic links.
522
523 **BOX 1**
524 **Trematode life cycles**

525 The life cycles of trematodes comprise parasitic and free-living stages (Fig. 1). Typical
526 trematode life cycles have three hosts (two intermediates and one definitive (final)), with
527 some cycles having two hosts (an intermediate and definitive host), and a few having four
528 (three intermediates and the definitive host). The first intermediate host is usually a mollusc,
529 and definitive hosts are usually vertebrates (including fishes, amphibians, reptiles, birds and
530 mammals). Adult trematodes in definitive hosts produce eggs that pass to the environment in
531 faeces and hatch into motile ciliated larvae (miracidia). Miracidia seek out and burrow into
532 the first intermediate molluscan host and develop into a mother sporocyst that reproduces
533 asexually, producing a second intra-molluscan generation of multiple daughter sporocysts or
534 rediae. This second asexual generation may produce more daughter sporocysts, rediae or
535 cercariae. Cercariae are morphologically diverse but almost always have a tail. They emerge
536 from their mollusc host and drift or actively swim before infecting either a second
537 intermediate host (three and four host life cycles) or the definitive host directly (two host life
538 cycle). In second intermediate hosts the cercariae develop into metacercariae, a stage that has
539 lost the cercarial tail and typically developed towards the form of the sexual adult to some
540 extent. Metacercariae are transferred to the definitive host when the definitive host preys on
541 the second intermediate host, in which they develop into sexually reproducing adults.
542

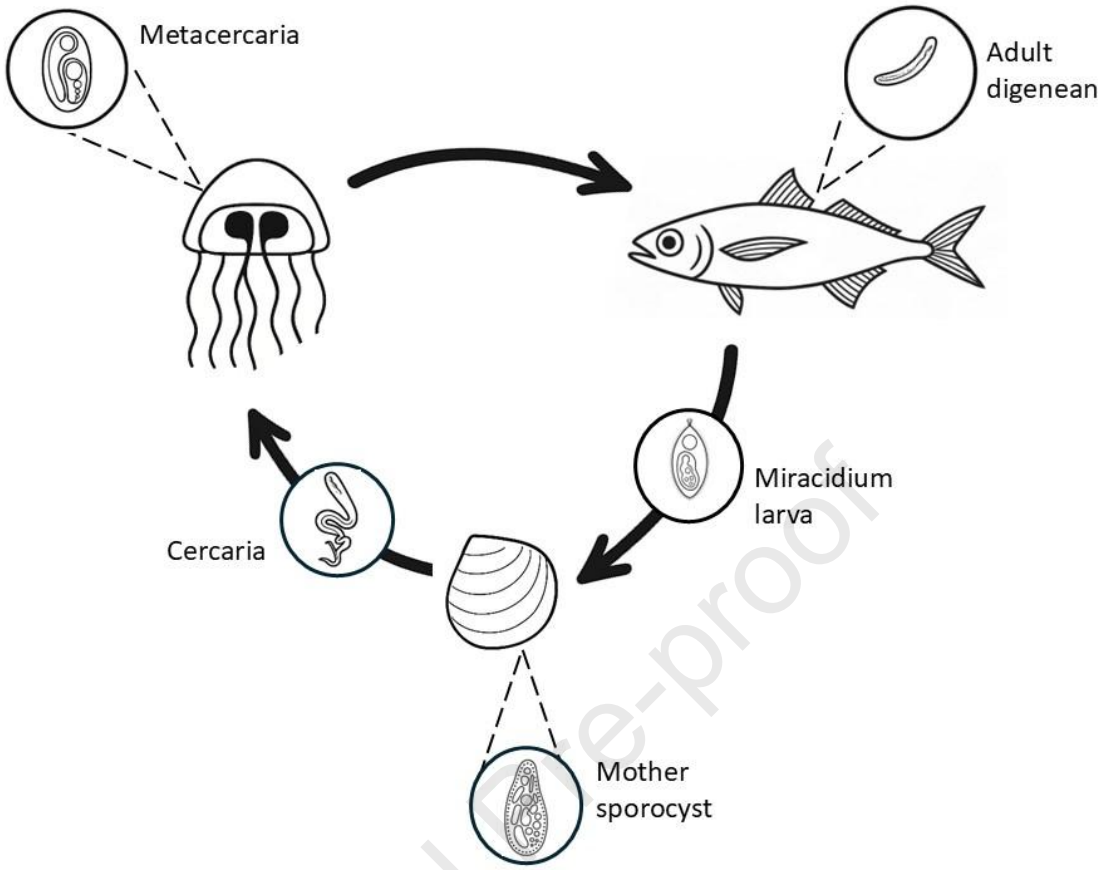

Fig. 1. Typical life cycle of digenean trematode involving a mollusc as the first intermediate host, a medusa as a second intermediate host, and a fish as a definitive host.

First intermediate hosts are always obligate hosts (i.e. necessary for the trematode to complete its life cycle). Most trematode life cycles incorporate second intermediate hosts, and they are typically obligate components of the cycle. Where third intermediate hosts are involved, it is not always clear if the infection is obligate (essential for transmission) or facultative (effectively a "transfer host" that enables transmission but is not strictly essential). A final category of host can be defined as "accidental hosts", those in which infections occur but that do not lead to the parasite completing its life cycle and effectively form a "dead-end" for the parasite. Identifying infections as dead-ends or accidental is problematic; even in host/metacercaria combinations that are capable of leading to infection in a definitive host, probably the great majority of trematode individuals fail to be transmitted.

BOX 2

Sampling and processing metacercariae from jellyfish

The metacercariae that infect jellyfish are typically small (e.g. <500 µm) but the translucent properties of many jellyfish enable them to be readily located using a dissecting microscope. Once located (usually in the mesoglea), metacercariae can be gently excised using fine needles (e.g. entomological pins). Extracted specimens are transferred using a pipette into near boiling vertebrate saline (one part seawater with three parts tap water; Cribb and Bray, 2010). Heat fixation causes the worms to extend and adopt a uniform shape, optimal for morphological characterisation and, importantly, does not interfere with molecular analyses. Fixed specimens are preserved in 80% ethanol, which is suitable for both molecular and morphological analyses. Extracting metacercariae from small, translucent jellyfish is straightforward, but the process becomes exponentially more difficult for large jellyfish, especially those with opaque tissues. Large and opaque jellyfish generally need to be sectioned to enable parasites to be located, which is very time consuming. As genetic sequences of metacercariae infecting jellyfish become increasingly available, metabarcoding of macerated jellyfish tissue might be a means to identify digeneans infecting jellyfish, although this method has not been tested. Metabarcoding could, in theory, accurately identify metacercariae parasitising jellyfish, but it would only provide information on the presence or absence of species; intensity of infection could not be quantified.

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Table 1. Number of independent reports of jellyfish being infected by digenean families. Details are only reported for jellyfish that were identified to species. Digeneans recorded as "Digenea" were not identified beyond the taxonomic level of Subclass. More details re available in Supplementary Table 1.

Jellyfish host species	Accacoeliidae	Baccigeridae	Derogenidae	Didymozoidae	Fellodistomidae	Hemiuridae	Lepidapdidae	Lecithophyllidae	Lepocreadiidae	Sclerodistomidae	Digenea	Total
Ctenophora, Nuda												
Beroe beroe									1			1
Beroe cucumis				1					1			2
Beroe ovata											1	1
Beroe rufescens											1	1
Ctenophora, Tentaculata												
Mnemiopsis leidyi		1			2	1			5		1	10
Pleurobrachia globosa											1	1
Pleurobrachia pileus			2	1	1	4	1		9		1	19
Pukia falcata				2	1	1		1	2			7
Cnidaria, Cubozoa												
Carybdea marsupialis											2	2
Cnidaria, Hydrozoa												
Aegina citrea				6								6
Aequorea forskalea									4			4
Aequorea pensilis						1						1
Aglantha digitale									1		1	2
Aglauropsis kawari					2							2
Aldersladia magnificus				10		3			9			22
Benthocodon pedunculatus						1						1
Bougainvillia carolinensis									4			4
Bougainvillia pagesi									2			2
Clytia hemisphaerica					1				3		1	5
Clytia lomae					1							1
Clytia simplex		1			1				1			3
Coryne eximia									2			2
Cosmetira pilosella									1			1
Cosmetirella davisii					1							1
Dimophyes arctica											1	1
Eirene lactea									1			1
Eirene tenuis									1			1
Eucheilota maculata									1			1
Eucheilota ventricularis		1			2	1			1			5
Eutonina indicans									1			1
Geryonia proboscidalis				1					2			3
Gonionemus vertens									1			1
Halopsis ocellata					1							1
Hippopodius hippopus									1			1
Leuckartiara octona					2				5			7
Liriope tetraphylla	1	1			2	1			2			7
Melicertum octocostatum									2			2

Mitrocomella 2rownie				1						1
Nemopsis bachei							2			2
Octobulbacea brachymera							1			1
Octobulbacea brachymera							1			1
Olindias sambaquiensis							2			2
Parateclaia norvegica							1			1
Phialella falklandica							1			1
Podocoryna carnea							2			2
Polyorchis penicillatus							2			2
Porpita porpita			3		2		1	1		7
Proboscidactyla mutabilis				2	2		2			6
Rhacostoma atlanticum							1			1
Tima bairdii							1			1
Velella velella	1		1		1			1		4
Cnidaria, Scyphozoa										
Aurelia aurita							3			3
Chrysaora kynthia							3			3
Chrysaora lactea							3			3
Chrysaora pacifica							3			3
Chrysaora pentastoma			1		1		4			6
Chrysaora quinquecirrha							2		1	3
Cotylorhiza tuberculata									1	1
Cyanea annaskala							1			1
Cyanea nozakii							3			3
Lobonemoides sewelli									1	1
Lychnorhiza lucerna							2			2
Pelagia noctiluca	1						1			2
Pseudorhiza haeckeli							1			1
Rhizostoma octopus									1	1
Rhizostoma pulmo							1			2
Stomolophus meleagris									1	1

Table 2. Digenean species reported to occur as metacercariae within Phylum Cnidaria and Ctenophora. Numbers are the number of independent reports. SF = Superfamily; G = Superfamily Gymnophalloidea; M = Superfamily Microphalloidea P.S. = present study. Only digeneans identified to species (or specific types) are reported. More details in Supplementary Table 1.

			Cnidaria			Ctenophora		Total
SF	Digenean Family	Digenean Species	Scyphozoa	Hydrozoa	Cubozoa	Tentaculata	Nuda	
G	Fellodistomidae	*Cercaria laevicardium*				1		1
	Fellodistomidae	*Coomera brayi*				1		1
	Fellodistomidae	*Lintonium vibex*				1		1
	Fellodistomidae	*Monascus filiformis*		19				19
Hemiuroidea	Accacoeliidae	Accacoeliidae species A (P.S.)		1				1
	Accacoeliidae	*Accacoelium contortum*		1				1
	Accacoeliidae	*Accacoelium pelagiae*	1					1
	Accacoeliidae	*Tetrochetus coryphaenae*		3				3
	Derogenidae	*Derogenes varicus*				2		2
	Didymozoidae	Didymozoid Species A (P.S.)		2		1		3
	Didymozoidae	Didymozoid Species J (P.S.)		1				1
	Didymozoidae	Didymozoid Species K (P.S.)		2				2
	Didymozoidae	Didymozoid Species L (P.S.)		2		1		3
	Didymozoidae	Didymozoid Species M (P.S.)		1				1
	Didymozoidae	Didymozoid Species N (P.S.)		1				1
	Didymozoidae	Didymozoid Species B (P.S.)		3		1		4
	Didymozoidae	Didymozoid Species C (P.S.)		1				1
	Didymozoidae	Didymozoid Species D (P.S.)		2		1		3
	Didymozoidae	Didymozoid Species E (P.S.)		1		1		2
	Didymozoidae	Didymozoid Species F (P.S.)		1		2		3
	Didymozoidae	Didymozoid Species G (P.S.)		1				1
	Didymozoidae	Didymozoid Species H (P.S.)	1					1
	Didymozoidae	Didymozoid Species I (P.S.)		1				1
	Didymozoidae	Didymozoidae sp. A		1				1
	Didymozoidae	Didymozoidae sp. B		1				1
	Didymozoidae	*S*pecies 4 (P.S.)		2				2
	Hemiuridae	*Dinurus tornatus*		3				3
	Hemiuridae	Hemiuridae sp. A		1				1
	Hemiuridae	*Hemiurus communis*				1		1
	Hemiuridae	*Lecithocladium* Species A (P.S.)				1		1
	Hemiuridae	*Lecithocladium* Species B (P.S.)		1				1
	Hemiuridae	*Lecithocladium* Species C (P.S.)	1					1
	Hemiuridae	*Lecithocladium* Species D (P.S.)		2				2
	Hemiuridae	*Lecithocladium excisum*				3		3
	Lecithophyllidae	Lecithophyllidae Species A		1		2		3
	Lecithoophyllidae	Lecithophyllidae Species B		1				1
	Sclerodistomidae	Sclerodistomidae sp. A		2				2
	Sclerodistomidae	Species A (P.S.)				1		1
Lepocreadoidea	Lepidapedidae	*Lepidapedon rachion*				1		1
	Lepocreadiidae	*Cephalolepidapedon saba*	5	2				7
	Lepocreadiidae	*Cephalolepidapedon warehou*	2					2
	Lepocreadiidae	*Lepocreadium areolatum*		2		2	1	5
	Lepocreadiidae	*Lepocreadium setiferoides*	1					1
	Lepocreadiidae	*Lepotrema clavatum*	3					3
	Lepocreadiidae	*Opechona bacillaris*		16		7		23
	Lepocreadiidae	*Opechona* cf. *kahawai*		2				2
	Lepocreadiidae	*Opechona* cf. *olssoni*	2	2				4
	Lepocreadiidae	*Opechona kahawai*		2				2
	Lepocreadiidae	*Opechona olssoni*	3					3
	Lepocreadiidae	*Opechona pyriformis*	2	10		2		14
	Lepocreadiidae	*Opechonoides opisthoporus*				3		3
	Lepocreadiidae	*Prodistomum*		4		1		5
	Lepocreadiidae	*Prodistomum keyam*				1		1

	Lepocreadiidae	*Proalstomum orientale* (Type 1)	2	4	1	7
M	Microphallidae	*Microphallus basodactylophallus*			1	1
	Unknown	*Distoma carinariae*	1			1

Table 3: Families of fishes infected by digenean trematodes reported to infect jellyfish - number of fish species infected within each fish family, number of species of fish in each family (in parentheses) as reported on Fishbase, and number of digenean species reported from each fish family. More details in Supplementary Table 2.

Family	Number of infected fish species	Number of digenean species
Acipenseridae	1 (27)	1
Alosidae	2 (32)	1
Ammodytidae	1 (34)	3
Anarhichadidae	1 (5)	1
Anguillidae	1 (20)	2
Balistidae	4 (42)	3
Belonidae	1 (49)	1
Carangidae	14 (147)	6
Centrolophidae	3 (31)	4
Cepolidae	1 (46)	1
Channichthyidae	2 (25)	1
Clupeidae	3 (15)	3
Congridae	1 (226)	1
Coryphaenidae	2 (2)	3
Cottidae	4 (294)	3
Gadidae	7 (22)	6
Gobiidae	3 (1957)	2
Kyphosidae	1 (16)	1
Labridae	1 (569)	1
Liparidae	1 (435)	1
Macrouridae	1 (378)	1
Merlucciidae	2 (17)	2
Molidae	1 (5)	1
Monacanthidae	4 (109)	3
Monodactylidae	1 (4)	2
Moronidae	1 (6)	1
Mugilidae	2 (78)	2
Mullidae	2 (104)	1
Nototheniidae	2 (56)	1
Osmeridae	1 (15)	1
Pleuronectidae	9 (62)	6
Pomacentridae	14 (428)	2
Pomatomidae	1 (1)	2
Salmonidae	4 (240)	2
Scatophagidae	1 (4)	1
Sciaenidae	1 (299)	1
Scombridae	5 (54)	13
Scophthalmidae	1 (9)	1
Scorpaenidae	9 (239)	1

Sebastidae	4 (133)	1
Soleidae	2 (184)	1
Sparidae	5 (163)	4
Stromateidae	2 (17)	1
Syngnathidae	1 (383)	1
Tetraodontidae	4 (206)	3
Trachinidae	1 (9)	1
Triglidae	2 (131)	1
Zanclorhynchidae	1 (3)	1

Declaration of interests

☐ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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