Parasite effects on host's trophic and isotopic niches

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Keywords: stable isotopes, host-parasite interaction, uninfected individuals

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Abstract

Wild animals are usually infected with parasites that can alter their hosts' trophic niches in food webs as can be seen from stable isotope analyses of infected versus uninfected individuals. The mechanisms influencing these effects of parasites on host isotopic values are not fully understood. Here, we develop a conceptual model to describe how the alteration of the resource intake or the internal resource use of hosts by parasites can lead to differences of trophic and isotopic niches of infected versus uninfected individuals and ultimately alter resource flows through food webs. We therefore highlight that stable isotope studies inferring trophic positions of wild organisms in food webs would benefit from routine identification of their infection status.

Parasites, resource flow and stable isotopes

Wild caught organisms should not be considered single organisms, but rather entire ecosystems, hosting a variety of microbes [1] and parasites [2,3], which can be found in virtually every tissue (see **Figure 1**). These microbes and parasites often alter the processing and routing of host dietary resources [4,5], but the impacts of these alterations remain largely unexplored in the scope of **food webs** (see **Glossary**). Accordingly, the roles of parasites in food webs still remains a significant knowledge gap [6], with few studies accounting for biomass of parasites alongside free-living organisms [7,8], or alterations to resource flows that occur due to parasite infections [9,10]. Ecosystem network modelling including parasitic interactions has identified impacts such as increased linkage density and food chain length when accounting for **parasite-host interactions** on an ecosystem scale [6,11–13]. However, these models of parasite-host and consumer-resource interactions fall short of accounting for metabolic and behavioural impacts from parasite infections on hosts, impacts that can drastically alter resource flows through food webs.

Improved delineation of changes in resource use, trophic structure, and host metabolism as a result of parasite infections will provide a more realistic picture of how parasites alter the flow of biomass and energy through food webs. New tools and frameworks are required to effectively distinguish between parasite-induced changes on host metabolism and resource use and those in host resource intake (e.g., through altered feeding), along with trying to quantify both aspects [14]. Stable carbon and nitrogen isotope analysis (**Box 1**) offers a promising approach and has already been used for characterising impacts of parasite infections on the resource use and resulting **trophic niches** of their hosts [15–17]. However, the current framing of research questions involving parasites in stable isotope ecology studies fails to account for the multiple pathways where interactions of parasites and hosts can change isotopic values of host tissues and the near ubiquitous occurrence of parasites found in wild caught organisms. Here, we present a conceptual framework of how parasite infections can alter the resource intake and the resource use of hosts and how these changes are reflected in trophic and **isotopic niches** of infected hosts. For this, we reviewed literature from separate research fields. Based on parasitological literature, we first identified different types of effects of parasites on host resource intake and resource use. We then explored the general stable isotope ecology literature

from free-living species to identify the potential consequences for the isotopic niches of infected hosts. Finally, we identified studies that explicitly investigated links between parasite infections and changes in trophic and isotopic niches of their hosts (**Table 1**). Finally, we explore how stable isotope analysis can be used to identify potential effects of parasite infections on the resource intake and use of their hosts. In addition, we discuss the methodological implications of parasite-induced changes in stable isotope patterns for food web studies and highlight outstanding research questions.

Parasites modulate host resource intake and use

In free-living organisms, external resource intake (i.e. how the energy pool is filled) and internal resource use (i.e. how the energy pool is utilised) contribute to the metabolism of an organism (**Figure 2a**) and various factors can impact these two variables. Resource intake is affected by food composition and availability within habitats, impacts on foraging habits determined by seasonally-related temperatures and environmental oxygen levels. Internal resource use is affected by energy demanding processes such as reproduction, growth, migration (habitat change), activity (e.g. dormancy), amongst others. From a food web perspective, the trophic niche that an organism occupies is defined by the resource intake in form of the proportional contribution of different resource items to its diet. This resource mix, which, depending on the organism, can span from consuming primary producers to consumers at different trophic levels, also defines the **trophic position** of this organism in a food chain (**Figure 3a**). The isotopic niche of an organism can reflect this resource intake and can thus serve as a proxy for its trophic position and the trophic niche in a food web [18,19] (**Figure 3a**) if metabolic reworking, baseline differences within habitats, and the predominant sources supporting a food web are all accounted for. Trophic and isotopic niche do not necessarily match. The isotopic values of a prey/host species can vary depending on different mechanisms such as resource use and metabolic processing, both of which may considerably differ depending on infection status.

Parasite infections can modulate both the resource intake and resource use of their hosts by altering either single or multiple processes (**Figure 2b**), which can lead to changes in the trophic niche and isotopic niches of infected individuals when compared to uninfected ones

(**Figure 3**). In the following, we discuss the two pathways for resource intake and use separately, indicating potential mechanisms that will be most affected by parasitic infections. We have therefore considered the general stable isotope ecology literature from free-living species as well as stable isotope studies that explicitly investigated infected and non-infected hosts (**Table 1**).

Parasite effects on host resource intake

Parasite infections are well known to cause behavioural, morphological or physiological changes in infected hosts that in turn alter their resource intake in quantity or quality (**Figure 2**). For example, parasite infections in fish can affect daily food consumption rates, diet composition and prey choice (e.g. [16,20,21]), and individuals infected with different parasite species have also been shown to preferentially select different habitats (e.g. trematodes in snails and fish [22,23]). Changes in habitat niche or diet quality are reflected in the stable isotope niche of free-living organisms [24,25]. However, infection-induced behavioural changes also impact resource intake in infected hosts, which can alter their trophic niche (**Figure 3b**) compared to uninfected individuals (**Figure 3a**). Given that resources are often isotopically distinct, changes in trophic niches should be reflected as a shift in the isotopic niches of infected compared to uninfected individuals stemming from changes in habitat use ([15]; **Figure 3a, b**) or prey choice [16,26]. This comparison is not often explored, but isotopic niche shifts could easily happen if, e.g., an infected fish occupies a different position in the water column and starts feeding on a different resource community (e.g. primary producer versus predatory zooplankton). For example, fish infected with eye flukes have been already shown to change from a more generalist to a more selective diet [16].

Parasite effects on host resource use

While impacts of infection-induced changes in resource intake on the trophic and isotopic niches of infected hosts are relatively well known [15], potential niche changes due to infection-induced impacts on host resource use remain largely overlooked (**Figure 2 and 3**). In this case, the trophic position or trophic niche of infected hosts does not change as long as resource intake remains the same (**Figure 3c**). However, infection-induced changes in the internal resource use

126 in infected individuals can alter their isotopic niche (**Figure 3c**) compared to uninfected ones
127 (**Figure 3a**).

128 Several mechanisms can cause a shift in the isotopic niche of infected hosts, such as
129 infection-induced host starvation (e.g. gastrointestinal parasites in ruminants, or trypanosomes in
130 bumble bees [27,28]), although some hosts can compensate (e.g. increased protein intake in
131 bovine trypanosomiasis [29]). Stable isotopes have shown a range of changes in response to host
132 starvation ([30–32], **Table 1**), with stable isotopes in parasite-host systems also reflecting this
133 wide range of responses (e.g. reduced $\delta^{15}N$ in common carp infected with cestodes, [33]; higher
134 $\delta^{15}N$ and unaltered $\delta^{13}C$ in amphipods infected with nematodes [34] and in sticklebacks with
135 cestodes [35]; higher $\delta^{15}N$ and $\delta^{13}C$ in daphnia with microsporidia [36]).

136 Resource costs of parasite infections usually imply trade-offs between immune response
137 and other nutrient-demanding processes such as growth, reproduction and thermoregulation [37]
138 being the most common impacts related to changes in growth and body condition (e.g. reduced
139 growth in trematode-infected snails or isopod-infected crabs [38,39]; see review by Sánchez *et*
140 *al.* [40]). Stable isotopes can remain unaltered despite changed physiological conditions (reduced
141 growth, increased physiological stress, reduced brain development [32]), however, other studies
142 have pointed to variations due to changes in growth and body condition (e.g. $\delta^{15}N$ increase in
143 juvenile collembolans compared to adults [31]; or variable $\delta^{15}N$ in seabird feathers [41]). Such
144 variability in stable isotopes has also been illustrated in host-parasite systems, ranging from
145 unaltered $\delta^{13}C$ and $\delta^{15}N$ values between infected and uninfected organisms ([42]; despite
146 massive pathology and reduced fish growth caused by an isopod [43]), to pronounced changes in
147 parasitized fish as a result of their lower growth and condition (higher $\delta^{15}N$ and lower $\delta^{13}C$ in
148 cestode-infected fish [44]).

149 Parasites can induce severe pathologies or mass mortalities in hosts (induced anaemia,
150 ectoparasites or isopods in fish, e.g. [45–47]) as they are able to either evade or trigger immune
151 responses (e.g. lice in salmonids [48–50]). However, the high costs to hosts required for
152 inflammatory responses or tissue repair are usually compensated by a reduction in other costs
153 such as maintenance of body condition (e.g. red grouse infected with nematodes [51]). Stable
154 isotopes have helped to confirm a similar trade-off between reproduction and wound healing by
155 showing that these two functions compete for the same resources (reptiles [52]). Furthermore,

resource costs to support immune response in infected hosts are also reflected in changes in carbon stable isotope values (e.g. higher $\delta^{13}C$ in male lizards with Salmonella [53]; higher $\delta^{15}N$ in pinworms but not whipworms in mice [54]), that impact the trophic niche of infected individuals (niche shift in fish with gill infections [55]). Impaired reproduction or castration is a common consequence of parasitic infections (trematodes in snails [56]; isopods in fish [57]; rhizocephalans in crabs [58]). Changes in stable isotopes have also been shown to reflect these effects in castrated individuals (higher $\delta^{15}N$ trematode-infected snails [59]; lower $\delta^{13}C$ in in female amphipods infected with acanthocephalans [60]).

Furthermore, host metabolic processes are also often affected by the presence of parasites, with a number of different effects that include increased thermal conductance and metabolic rate (feather-feeding lice [61]), increased respiration and decreased capacity for aerobic activity (ectoparasites [62]), or increased resting metabolic rate and diminished glucose intake (intestinal nematode [63]). In a meta-analysis, Robar *et al.* [64] showed no effects of parasites on host resting metabolic rate, but the data collected included different magnitudes of parasite-associated effects across studies. Changes in otolith chemistry in parasitized individuals has been reported (isopods in fish [65]), and increased metabolic respiration can result in changes in $\delta^{13}C$ in the deposited carbonates in invertebrate shells and fish otoliths [66–68]. However, to our knowledge, the effects of parasitism on otolith chemistry and respiration have not yet been studied with stable isotopes. Furthermore, changes in essential amino acid **turnover rates** could also reveal alterations in individual immune function or potential hidden costs of chronic and persistent infections (faster $\delta^{15}N$ and $\delta^{13}C$ turnover rates in tapeworm-infected fish [69]).

Stable isotope analyses and parasite effects on hosts: methodological implications

Given that parasite infections can cause isotopic niche shifts in infected hosts, stable isotope analyses can potentially help to identify the presence of infection-induced effects on host resource intake or use. For this, one would need to compare the isotopic niches of infected and uninfected individuals. However, identifying which of the two principal pathways (effects on resource intake or use) is underlying an observed isotopic niche shift is difficult as both

pathways can lead to different isotopic niches of infected compared to uninfected individuals (**Figure 3**).

This has important methodological implications for the use of stable isotope analyses in food web studies. Only when infections do not alter the resource intake or use of hosts can the trophic position or trophic niche of infected hosts be correctly inferred from their isotopic niche (**Figure 3a**). In contrast, when infections alter either the resource intake or the resource use of infected hosts, inferred trophic niches and trophic positions for infected hosts may lead to erroneous estimates. For example, in **Figure 3c** the isotopic niche of the infected host suggests an intermediate trophic level while infected and uninfected individuals actually feed at the same top trophic level. Given that many wild caught individuals used for stable isotope studies will likely be hosts to some variety of parasites (**Figure 1**), more studies are needed to identify the potential errors introduced into estimations of trophic niches and positions by infection-induced effects on the isotopic niches of their hosts. This is of special importance in food webs built based on stable isotopes studies, as inaccurate data due to hosts with undetected infections might allocate a species to a trophic level incorrectly, potentially affecting the food web structure (e.g. number and strength of trophic links) and leading to erroneous inferences on resources and consumers of infected hosts. Impacts from these effects probably contribute to the variability observed between individuals within wild populations and accounting for them may help to improve models of food web interactions relying on stable isotope values.

Further methodological complications arise from the fact that some parasite infections may not necessarily affect a host via one of the two pathways only but both at the same time. For example, a parasite may simultaneously affect both host resource intake and internal resource use. Such complex effects occur in the well-known host-parasite system of *Schistocephalus solidus* infecting three-spined stickleback. Heavy infections with this cestode can cause a visible bulge that may restrict stomach capacity, impair the fish's foraging ability, reduce fright response and alter resource intake (prey selection) [20,21,70], likely leading to changes in both their trophic and isotopic niches [71]. Similar simultaneous effects of infections on both host resource intake and internal resource use are likely to also occur in other parasite-host systems. However, different isotopic niches of infected and uninfected individuals would still allow to establish the presence of infection-induced effects on host resource intake and/or use. Further

controlled feeding studies will then be needed to disentangle the individual mechanisms driving the changes to their isotopic niches. The improvement of captive breeding of organisms, especially aquatic ones, together with the possibility to culture a diversity of parasite species (e.g., [72]), increases our ability to experimentally control infection levels in hosts under laboratory conditions. However, experimental studies in the field will be more difficult, also because they may become confounded by infections with other parasites than the target species. This is also a potential issue for organisms sampled in the field as they may be infected by a diversity of parasites (Fig. 1) that potentially have diverging effects on their host's stable isotope signatures. Hence, a combination of field-based host samples and experimental approaches will be most promising to disentangle the effects of single and multiple parasite infections on the isotopic niches of their hosts. In conclusion, comparing the isotopic niches of infected and uninfected organisms is a promising tool to identify the effects of parasite infections on the resource flow in food webs. Nevertheless, experimental studies using controlled diets are necessary to further disentangle underlying mechanisms in host-parasite interactions and their effects on the stable isotope values from wild-caught individuals.

Concluding remarks

As discussed above, parasite infections can affect both the resource intake and the internal resource use of their hosts and this can lead to changes in the trophic and isotopic niches of infected compared to uninfected individuals. While this offers promising methodological opportunities to quantify the effects of parasite infections on the flow of resources in food webs, there are still large gaps in our understanding of the prevalence and magnitude of infection-induced effects on host resource intake and use (see **Outstanding Questions**). This review highlights the lack of studies using stable isotope analyses on host-parasite systems, especially comparing stable isotope values of infected and uninfected individuals from the same ecosystem. More studies that compare the isotopic niches of infected and uninfected individuals are thus needed to identify the presence of infection-induced effects on host resource intake or use. To disentangle these two pathways and to identify potential complex interactive effects, further experimental studies are necessary. These should include controlled feeding regimes to separate the effects on resource intake *versus* internal resource use. Such observational and experimental

studies would also be valuable to identify the potential risk of unconsciously including infected hosts in sampling schemes from general stable isotope studies intended to infer trophic positions of organisms and food web structure.

Acknowledgments

This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 101027941 (A. B.-T.).

Declaration of interests

The authors declare that they have no competing interests.

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Glossary

Food web. Represents an ecological community through their trophic interactions, i.e. who eats whom, and includes information on the generality/specialisation of consumers (i.e. numbers of taxa they consume).

Fractionation. Difference in stable isotope composition between a consumer and its food due to different metabolic processing rates, with faster rates for the light and slower rates of the heavy isotopes, leaving consumers enriched in ^{13}C and ^{15}N relative to their food sources.

Isotopic composition. Composition of different stable isotope ratios.

Isotopic niche. Position of an organism, based on its isotopic composition, in a multivariate space created by the axes of the stable isotope ratios of the elements analysed (often C and N, $^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively, which can be represented by $\delta^{13}C$ and $\delta^{15}N$). Can be a proxy for the trophic niche of an organism.

Parasite-host interactions. Parasite-host interactions are treated as a consumer-resource interaction in food web ecology, implying that parasites predominantly feed on and metabolize their host's tissues. Nevertheless, trophic interactions of parasites are probably often more complex due to supplementary feeding on components from the pre-digested gut content of their hosts (e.g. effective routing of glucose, amino acids, fatty acids, etc.).

Stable isotope ratios. Stable isotopes are the different forms of the same atom that contain more or less neutrons than the dominant form. Their ratios are defined as the relative abundance of the rare over the common stable isotopes, comparing the abundance of the heavier isotope to the lighter one, i.e. $^{13}C/^{12}C$ or $^{15}N/^{14}N$, expressed as δ values relative an internationally defined reference value (i.e., $\delta^{13}C$ and $\delta^{15}N$). In trophic ecology, these ratios can give information about the dietary relationship between two organisms, with stable isotopes of N, C and S as most commonly applied to trophic and food web studies.

Trophic discrimination factor (TDF). The differences in isotopic composition between consumer tissue and their diet.

Trophic niche. Composition of resources that a species feeds on. A species usually feeds primarily on resources that are lower in the food chain in food webs, and can also feed on more than one trophic position.

Trophic position. Feeding position within a food chain, consisting of a succession of species that consume the species that precede them in the chain. One food chain may include a primary producer (autotrophs), a primary consumer (herbivores) and a secondary consumer (carnivores, omnivores).

Turnover rate. The rate at which stable isotopes from a diet are metabolically assimilated by the consumer. A steady turnover rate is reached after a certain time when stable isotopes ratios from the consumer's tissues, feeding on the same resource over time, become constant.

Box 1. Stable isotopes quantify resource use and trophic niche

In trophic ecology, the **stable isotope ratios (SI)** of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are used as powerful tools to determine food sources and identify the trophic interactions between organisms [73,74]. The **fractionation** and mixing of isotopes in biochemical reactions is a result of the kinetic isotope effect, which results in accumulation of more light isotopes in the final product pool and leaves relatively more heavy isotopes in the substrate pool [75]. Differences in **isotopic composition** as a result of isotopic discrimination in carbon can be used to differentiate food sources and to track metabolic processing along food chains, whereas those of nitrogen deliver insights into trophic positions of organisms in the food web. The **trophic discrimination factor (TDF)** typically found between consumers and their diet is on average 3.4‰ for $\delta^{15}N$ (bulk tissue, range 1.3‰ – 5.3‰) [74,76,77] and 0 – 1 ‰ for $\delta^{13}C$ [76,77].

The stable isotope composition of carbon and nitrogen in different tissues/organs of an organism can be affected by processes which influence an organism's food intake and metabolism, inducing isotopic shifts at the individual and/or population level (see main text). Thus, individual deviations from expected patterns or values within a population can develop or isotopic differences between different populations of the same species can occur. Isotopic changes occur more rapidly in tissues with higher turnover rates (e.g. plasma, liver). Accordingly, the stable isotope values in these tissues represent the consumer's food intake over shorter periods of time (e.g. 2 weeks to 1 month)

while other tissue types (e.g. muscle, collagen) with lower metabolic activity and turnover rate represent longer-term processes (e.g. 2 months to 10+ years [78]). Therefore, studies using bulk (whole tissue) for SI analyses should properly consider the choice of tissue that adequately covers the time range that is relevant to address the desired research questions.

Figure 1. Diversity of parasitic organisms infecting fish hosts. A parasite is considered as an organism that lives in or on another species (the host) and benefits from it, e.g. by obtaining nutrients or other resources at the expense of the host. Parasites can also impact the metabolism of their hosts, an/or specific phenotypic traits or behaviours. Depicted are the most common groups of parasites found in different tissues or organs of fish. Those marked with asterisk have been suggested to affect $\delta^{15}N$ or $\delta^{13}C$ of fish (see references in Table 1).

Figure 2. Resource intake and use in infected and uninfected organisms. In uninfected organisms (A), resource intake leads to the filling of the resource pool of individuals which is then utilised for various organismic functions. Parasite infections can alter the resource pool of infected hosts (B) by either affecting resource intake or resource use.

Figure 3. Potential consequences of the existence of an infection-induced isotopic niche shift. Parasite infections can have several outcomes on the resource intake or use of infected hosts and their feeding on primary producers (P) or consumers (C) within a food web, with different scenarios for impacts on the isotopic niches of infected hosts: A) Infections alter neither resource intake nor use, resulting in overlapping isotopic niches of infected and uninfected organisms; B) Infections alter the resource intake of infected hosts but do not affect resource use, resulting in isotopic niche shifts of infected hosts and a niche similar to other consumers feeding on an alternative resource, in this case a primary producer (assuming similar fractionations for fish and snails in the figure for simplicity, which in reality is debatable); C) Infections alter the resource use of infected hosts but do not affect resource intake, also resulting in an isotopic niche shift of infected host, with the position and shape of the niche depending on the specific

575 alteration of the resource allocation between host and parasite. Here, for simplicity, we separate
576 processes A) and B), however, in reality the two mechanisms may occur simultaneously.

577

Table 1. Different types of effects of parasites on the resource intake or use of infected hosts, the potential consequences on stable isotope composition and evidence from specific parasite-host systems for parasite-mediated effects on stable isotope composition of infected hosts.

Category	Parasite effect on host (P.)	Refs P.	Potential effects on stable isotopes (SI)	Refs SI	Evidence from parasite-host systems (P-H)	Refs P-H
Altered resource intake (same resource use)						
Prey selectivity, foraging behavior	Changes in prey selection, diet composition (e.g. lower nutritional value) or daily food consumption (cestode in stickleback, trematode in snails)	[20,21, 70,79]	$\delta^{15}N$ and $\delta^{13}C$ reflecting changes in habitat niche and diet quality (fish)	[24,25]	Higher $\delta^{13}C$ and/or $\delta^{15}N$ in inf. ind. (more selective diet, eye-fluke in fish; isopod in fish, habitat and prey change)	[16,26]
Habitat selection	Infected individuals select different habitat (cestode and isopods in fish, trematode in snails)	[22,23, 80,81]			$\delta^{15}N$, $\delta^{13}C$ reflecting niche specialization (tapeworm in fish)	[15]
Altered resource use (same resource intake)						
Host nutrition	Host starvation, reduced food intake, changes in protein uptake (nematodes in ruminants, trypanosome in bumble bee and cattle, nematodes in pigs)	[27–29,82,83]	Changes and variable $\delta^{15}N$ and $\delta^{13}C$ in starving organisms, although other studies show no effects despite physiological effects derived from food restriction (lower growth, increased physiological stress, less brain development) (e.g. fish, copepods, collembola, birds, human pregnancy)	[30–32,84–88]	Variable $\delta^{15}N$ and $\delta^{13}C$ in infected organisms (nematodes in amphipods; acanthocephalans, isopod and cestodes in fish; microsporidia in daphnia)	[33–36,89,90]

Growth and body condition	Phenotypic, growth and body condition changes (trematodes in snails, different parasites in crabs)	[38–40,91]	No isotope effect despite altered physiological conditions derived from food restriction (lower growth, increased physiological stress, less brain development in sparrows)	[32]	Higher $\delta^{15}N$ and lower $\delta^{13}C$ in parasitized individuals with lower growth and condition (cestode in fish)	[44]
			Changes in $\delta^{15}N$ and $\delta^{13}C$ (e.g. seabirds, collembola different age)	[31,41]	No differences between infected/uninfected individuals (both with same growth in fish with cestode, but also in a system with an isopod causing massive damage and reduced growth in fish)	[42,43]
			Inter-individual variability of the isotope values decreased with increasing food availability and growth (mysids)	[92]	Similar $\delta^{15}N$ and $\delta^{13}C$ isotopic ratios between infected and uninfected, but different isotopic niche in infected hosts, not related to length/age or body condition (acanthocephalan in fish)	[93]
Immune response and pathological repair	Induced immune response (e.g. lice), or immune evasion to prevent parasite clearance from the host (different parasites)	[48–50]	Amino-acid trade-off between reproduction and wound healing ($\delta^{15}N$) (reptiles)	[52]	Immunity costs, changes in $\delta^{13}C$ (Salmonella in lizards)	[53]
	Costs of immune reaction compensating from other processes (e.g. body condition)	[51]			Lower $\delta^{13}C$ with increased gene expression for immune response, $\delta^{15}N$ predominately reflects location (pinworms or whipworms in wild mice)	[54]

	Severe pathologies, induced anemia or mass mortality (ectoparasites, copepods, monogeneans, isopods in fish, nematode in birds)	[45–47,94,95]			Smaller trophic niche of infected individuals with hyperplasia and localized hemorrhaging of gill tissues (copepod in fish)	[55]
Reproduction	Impaired reproduction or castration (can drive to increased or reduced somatic growth). Lower P excretion, higher N excretion (trematodes in snails, isopods in fish)	[56,57,96,97]			Changes in $\delta^{15}N$ and /or $\delta^{13}C$ in castrated infected individuals (trematode in snails, acanthocephalans in female amphipods)	[59,60]
	Male feminization (rhizocephalan in crabs)	[58]				
Respiration / metabolic processes	Lower fat, higher resting metabolic rate and diminished glucose uptake capacity of infected hosts. Decreased energy reserves during exposure to cold (intestinal nematode)	[63]	Increased deposition of respiratory carbon into shells (molluscs)	[67]	Faster $\delta^{15}N$ and $\delta^{13}C$ turnover rates in liver and blood of inf. fish (slower $\delta^{34}S$ turnover) (tapeworm in fish)	[69]
	Increased thermal conductance and metabolic rate (feather-feeding lice), increased respiration, decreased capacity for aerobic activity (ectoparasites)	[61,62]	Metabolic effects in fish otoliths (increased contribution of $\delta^{13}C$ from diet with higher respiration)	[66,68]		

	No effect of parasites on resting metabolic rate (meta-analysis, but different magnitudes of parasite-associated effects across studies)	[64]
	Reduced metabolic rates and escape responsiveness with increased parasite load (trematode and cestode in fish)	[98]
	Changes in corticosteroids and neurotransmitters (gnaathid, brain trematode in fish)	[99,100]
	Otolith chemistry changes in parasitized individuals, suggesting an effect on metabolic and chemical processes (isopod in fish)	[65]

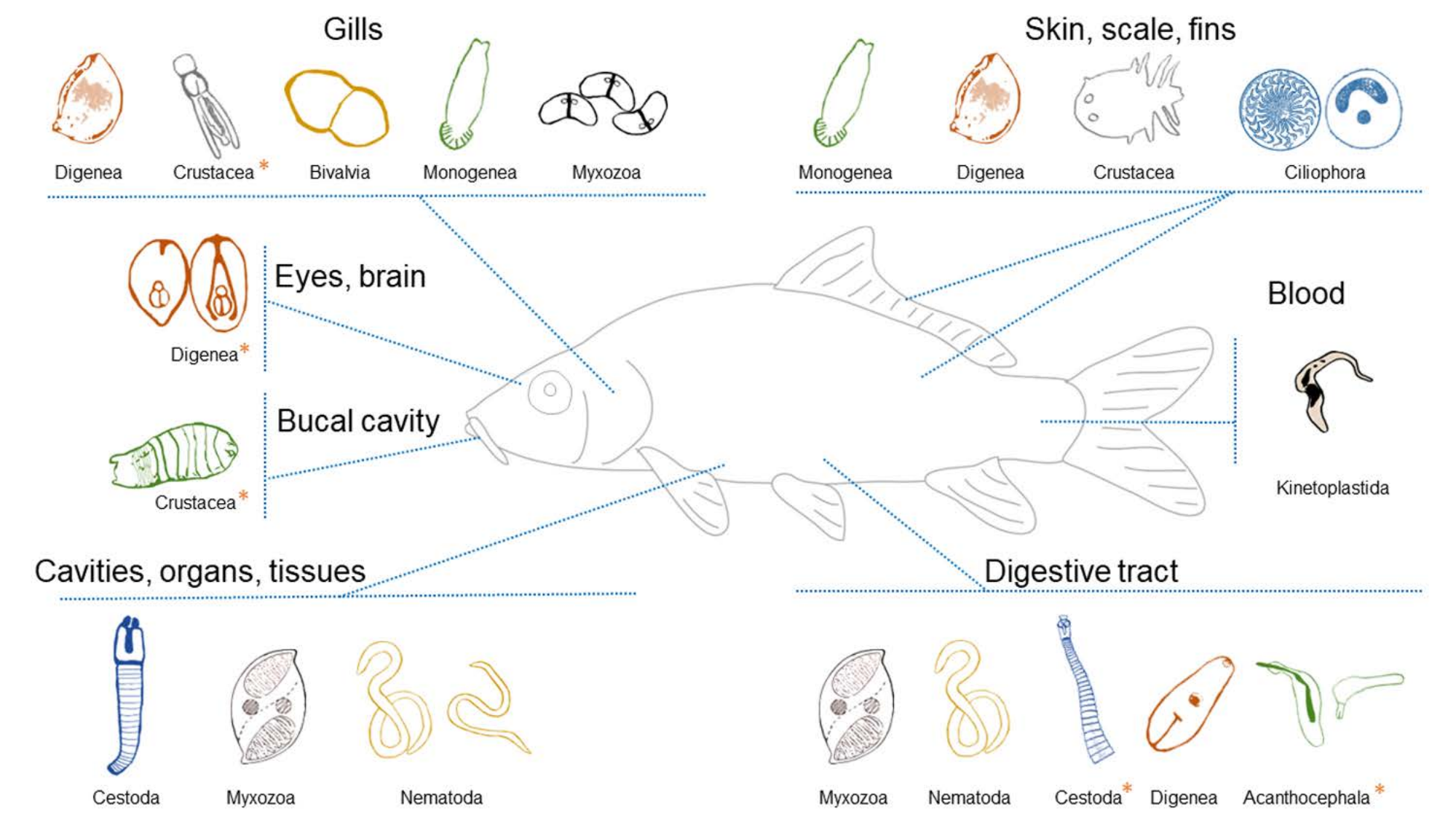
[a] Papers are assigned to the category to which they most closely apply, even though they may describe different mechanisms simultaneously.

Highlights

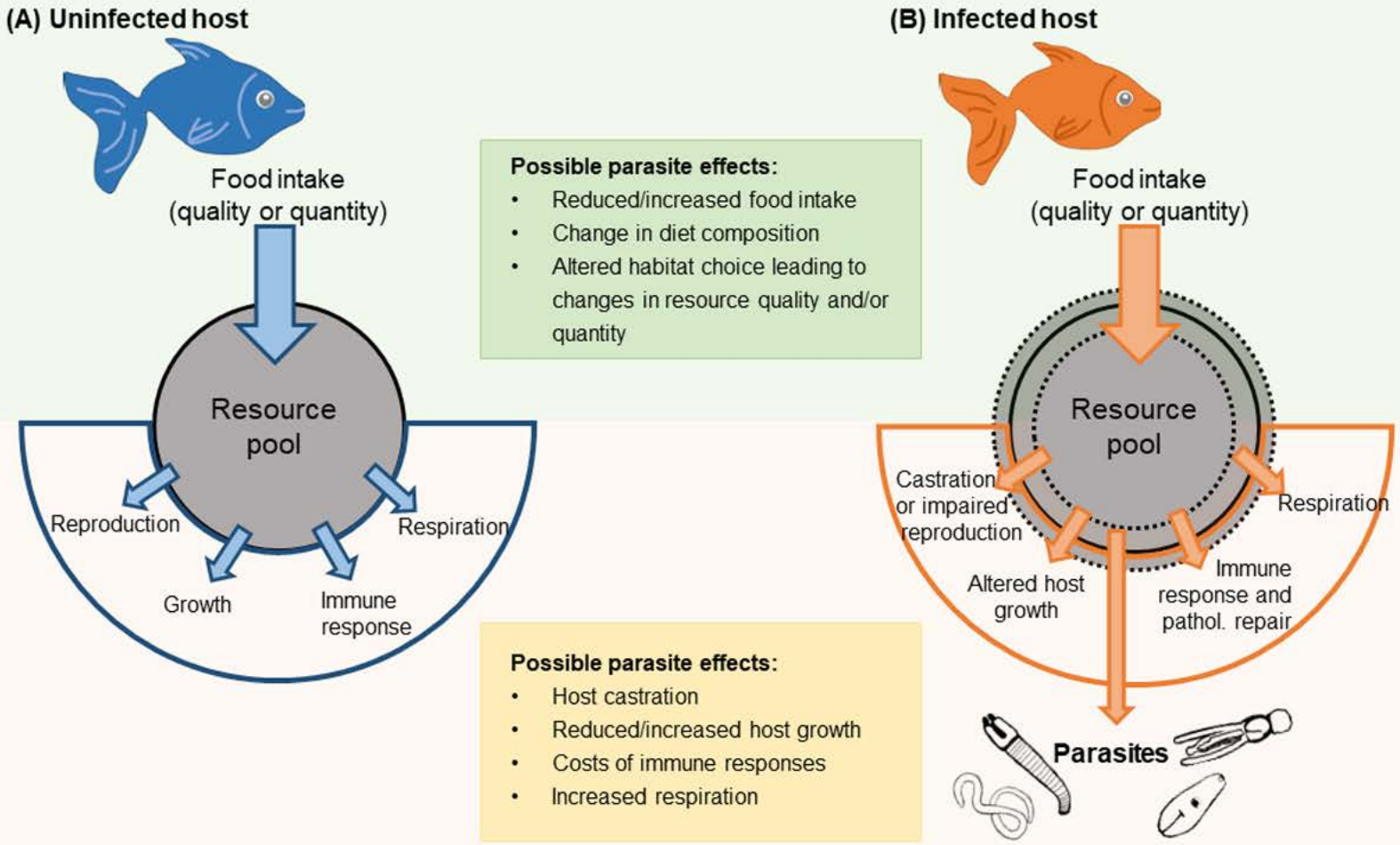
- A conceptual framework was developed to describe how parasite infections alter the resource intake and use of hosts, which could likely be reflected in the isotopic values of host tissues.
- Trophic and isotopic niches of infected and uninfected individuals may thus differ.
- The literature on stable isotope analyses in host-parasite systems is very limited, specially comparing infected and uninfected individuals.
- Experimental feeding studies comparing infected and uninfected individuals are necessary to separate parasite effects on resource intake from those on internal resource use.
- There is a need to incorporate parasites and host infection status to improve models of food web interactions based on stable isotope analyses.

Outstanding questions

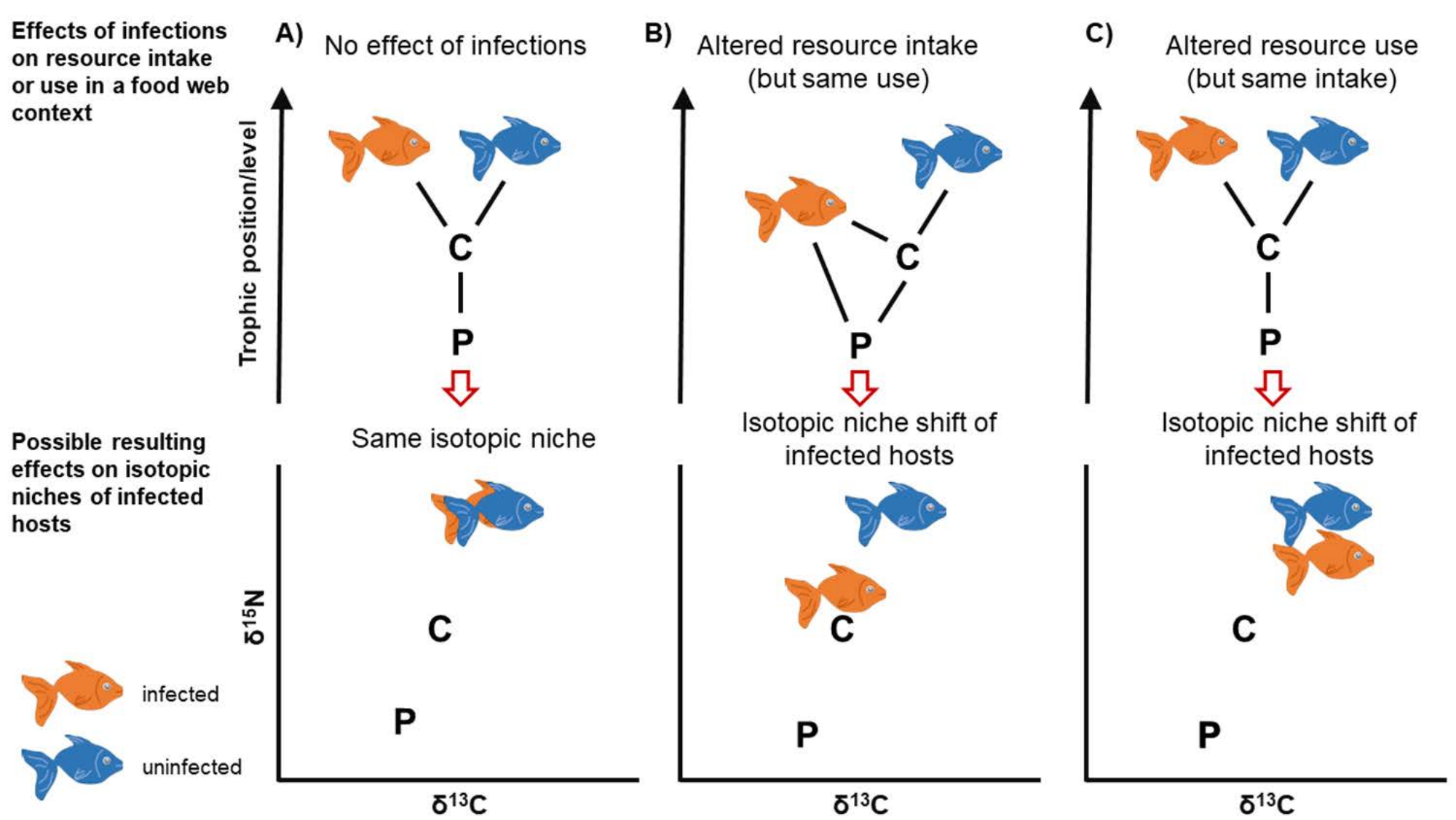
- How common is it that parasite infections alter the stable isotope values and isotopic niches of their hosts?
- Are there specific traits of parasites and/or hosts that lead to predictable changes in stable isotope values and isotopic niches of infected versus uninfected individuals?
- How do co-infections with multiple parasite species, or different infection intensities, affect the stable isotope values and trophic niches of their hosts?
- Can we use the comparison of the stable isotope compositions of infected and uninfected individuals (and parasites) to identify the energetic effects of parasites on their hosts and food webs?
- What are the methodological repercussions for using samples from wild caught organisms, possibly often containing a mix of infected and uninfected individuals, for studies that aim to determine the trophic positions of organisms and food web structure?


Gills
Digenea
Crustacea *
Bivalvia
Monogenea
Myxozoa
Skin, scale, fins
Monogenea
Digenea
Crustacea
Ciliophora
Eyes, brain
Digenea *
Bucal cavity
Crustacea *
Blood
Kinetoplastida
Cavities, organs, tissues
Cestoda
Myxozoa
Nematoda
Digestive tract
Myxozoa
Nematoda
Cestoda *
Digenea
Acanthocephala *

Resource intake – filling the energy pool



Resource use – using the energy pool


Effects of infections on resource intake or use in a food web context
A)
No effect of infections
B)
Altered resource intake (but same use)
C)
Altered resource use (but same intake)
Trophic position/level
C
P
Possible resulting effects on isotopic niches of infected hosts
Same isotopic niche
Isotopic niche shift of infected hosts
Isotopic niche shift of infected hosts
δ15N
δ13C
infected
uninfected