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Host feeding ecology and trophic position significantly influence isotopic discrimination between a generalist ectoparasite and its hosts: Implications for parasite-host trophic studies

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ABSTRACT

Despite being one of the most prevalent forms of consumerism in ecological communities, parasitism has largely been excluded from food-web models. Stable isotope analysis of consumers and their diets has been widely used in the study of food webs for decades. However, the amount of information regarding parasite stable isotope ecology is limited, restricting the ability of ecologists to use stable isotope analysis to study parasites in food webs. This study took advantage of distinct differences in the feeding ecology and trophic position of different species of fish known to host the same common micropredatory gnathiid isopod to study the effects of host stable isotope ecology on that of the associated micropredator. Blood engorged juvenile gnathiids were in most cases indistinguishable from their hosts' blood, but significant isotope discrimination was observed for adults. Males were generally lower in $\delta^{13}C$ and $\delta^{15}N$ than host blood whereas host-specific isotopic discrimination for females varied among the different host species. Model predictions indicated that there is a significant effect of host blood isotope ratios on the rate of carbon and nitrogen isotopic discrimination between gnathiids and their host's blood. As such, general differences in the feeding ecology and trophic positions of the different host species were reflected in their associated gnathiids, indicating that stable isotope analysis of gnathiids can provide significant details concerning previous hosts. The results presented herein have significant implications for how stable isotopes may be used as a tool to study the trophic dynamics and feeding ecology of gnathiids.

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1. Introduction

Trophic interactions between consumers and producers, and predator and prey organisms, are primarily responsible for the flow of energy through ecological communities and therefore have a major impact on community structure and dynamics (Paine, 1966; Pimm, 2002; Pascual and Dunne, 2005). An understanding of trophic relationships and dynamics is essential to understanding any community or ecosystem (Dunne et al., 2002; Calizza et al., 2015). Food-web models are a common tool used to quantify and track the transfer of energy within an ecosystem through trophic relationships (Pimm, 2002), and are thus a fundamental and essential tool in the study of ecology (Pascual and Dunne, 2005; Wood et al., 2007; Lafferty et al., 2008).

The prevalence and significance of parasites in ecological communities has been well established (Marcogliese and Cone, 1997; de Meeûs and Renaud, 2002; Lafferty and Kuris, 2002; Lafferty et al., 2008; Poulin, 2011; Jephcott et al., 2016). It is not surprising that there is a growing appreciation for their potential significance as components of food webs (Hudson et al., 2006; Lafferty et al., 2006; Wood et al., 2007; Johnson et al., 2010; Jephcott et al., 2016). Yet, in spite of this, parasites have largely been excluded from food-web models, likely a result of their complex lifestyles and cryptic nature. This omission may result in inaccurate assumptions, and thus predictions, that are generated from food-web models (Marcogliese and Cone, 1997; Lafferty et al., 2008; Sukhdeo, 2012; Jephcott et al., 2016). There have been repeated calls to amend this omission (Marcogliese and Cone, 1997; Lafferty et al., 2008; Byers, 2009; Sukhdeo, 2010), with ecologists proposing that current food-web models will need to be reconstructed from the ground up in order to accurately incorporate parasites (Sukhdeo, 2010).

A necessary first step to incorporating parasites into food-web models is to gain a comprehensive understanding of their trophic ecology and the associated energy dynamics of host-parasite interactions (Wood et al., 2007). Stable isotopes have been widely used as a tool to study food webs and trophic interactions for decades (Fry, 2006; Boecklen et al., 2011). Discrimination of stable isotopes (i.e., changes in the ratio of heavy to light stable isotope of an element) between a

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consumer and its diet are useful for inferring trophic relationships within food webs. These isotopic discriminations are, however, not always consistent as they are subject to complex biochemical and physiological factors (Krueger and Sullivan, 1984; Hobson and Clark, 1992; Hobson et al., 1993; Vanderklift and Ponsard, 2003; Robbins et al., 2005). For example, in a study of marine food webs, trophic enrichment of ^{15}N for fish and elasmobranchs ranged from 0.6 to 5.1‰ and there was a significant negative correlation between trophic level (characterized by consumer $\delta^{15}N$) and $\Delta^{15}N$ (Hussey et al., 2014). Similarly, Mill et al. (2007) observed that herbivorous tropical fish exhibit greater isotopic discrimination of ^{15}N than the generally accepted value of 3-4‰, supporting the notion that low trophic positions may be accompanied by higher than average isotopic discrimination of ^{15}N (Caut et al., 2009; Hussey et al., 2014).

Stable isotope analysis (SIA) has only recently been applied to the study of parasite trophic ecology (Pinnegar et al., 2001; Deudero et al., 2002; Stapp and Salkeld, 2009; Demopoulos and Sikkel, 2015; Nachev et al., 2017). SIA of parasites has the potential to be used as a tool to identify and measure the magnitude of their trophic interactions (Deudero et al., 2002; Fry, 2006; Stapp and Salkeld, 2009; Gómez-Díaz and González-Solís, 2010; Nachev et al., 2017) by tracking and quantifying the flow of energy (i.e., carbon) in a food web (Fry, 2006; Demopoulos and Sikkel, 2015), and reconstructing the lifetime feeding histories of parasites (Rasgon, 2008; Schmidt et al., 2011; Fritts et al., 2013). Studies thus far indicate the complex interactions between parasites and hosts yield equally complex patterns of stable isotope values (Pinnegar et al., 2001; Deudero et al., 2002; Voigt and Kelm, 2006). In particular, studies have revealed that the typical patterns of stable isotope discrimination, which are the basis for which stable isotopes are used as a tool in ecology, may not always apply to host-parasite systems (Boag et al., 1997; Pinnegar et al., 2001; Deudero et al., 2002; McCutchan et al., 2003; Stapp and Salkeld, 2009; Voigt and Kelm, 2006; Schmidt et al., 2011; Demopoulos and Sikkel, 2015). If the basic assumptions regarding isotopic discrimination cannot be confidently applied when studying parasites, then further examination into how isotopic discrimination varies for specific parasite-host combinations is required in order to make accurate predictions and inferences from stable isotope data.

Gnathiid isopods are ectoparasites of marine fishes and are ecologically similar to blood-feeding ticks, fleas and mosquitoes in that they are temporary parasites of multiple hosts, engorging themselves with blood before detaching. As such, they may be more appropriately considered as "micropredators" (Lafferty and Kuris, 2002; Raffel et al., 2008). Unlike other ectoparasites and micropredators, gnathiids are only parasitic as juveniles. Adult gnathiids do not feed; instead, they rely on the blood meal collected during their last juvenile stage to provide the energy reserves necessary for metamorphosis and reproduction. They occupy diverse habitats from polar regions to the equator (Klitgaard, 1997; Smit and Davies, 2004; Tanaka, 2008) and from shallow water coral reefs (Farquharson et al., 2012) to the deep-water abyss (Quattrini and Demopoulos, 2016). However, they are perhaps best known in tropical reef communities where they commonly infest reef fishes (Grutter, 1994; Ferreira et al., 2009; Coile and Sikkel, 2013; Santos and Sikkel, 2017). An increasing number of studies on the ecology of gnathiid isopods suggest that these parasites are an important component of benthic marine communities. In coral reef communities, they infest a wide range of hosts (Grutter, 1994; Coile and Sikkel, 2013) and are the primary food source for reef-associated cleaning organisms (Grutter, 1996; Grutter and Poulin, 1998; Arnal et al., 2000; Arnal and Côté, 2000; Whiteman and Côté, 2002). They have been found in gut contents of common reef microcarnivores (Alldredge and King, 1977; Holzman et al., 2005; Motro et al., 2005; Artim et al., 2017), and laboratory observations suggest they may be consumed when coming into contact with live coral (Artim and Sikkel, 2013). Gnathiids may be driving factors in the diel interactions of hosts with cleaners (Sikkel et al., 2004, 2005) and possibly host feeding migrations (Sikkel et al., 2017). Micropredation by gnathiids may promote increased predation on hosts by other, larger, micropredators (Stepien and Brusca, 1985), and can impact recruitment success of reef fishes (Jones and Grutter, 2008; Grutter et al., 2011; Artim et al., 2015).

Recent work on gnathiid isopods by Demopoulos and Sikkel (2015) indicates that the blood engorged juvenile (i.e., praniza, referred to as "P" hereafter) stages have, not surprisingly, similar stable isotopic values to that of their most recent fish host. The absence of significant isotopic discrimination between the fish tissue (diet) and juvenile parasite stage (consumer) appears attributed to the lack of any digestion or assimilation of the blood meal. When the juvenile gnathiid stages were allowed to digest their blood meal and undergo metamorphosis to their adult stages, there were notable shifts in both $\delta^{13}C$ and $\delta^{15}N$. There was a consistent enrichment of ^{15}N for both the male and female stages relative to the juvenile P stages and the host tissue. Discrimination of ^{13}C varied, however, with the male gnathiids having lower $\delta^{13}C$ values relative to host blood, but the female and juvenile P stages were often indistinguishable from host blood. Demopoulos and Sikkel (2015) suggested that these isotopic variations may be the result of biochemical and physiological factors associated with metamorphosis and allocation of resources.

A logical next step in the study of gnathiid isopod stable isotopes is to assess which external factors might be affecting isotopic discrimination between the micropredator and its host. This study took advantage of differences in trophic level and feeding ecology (and subsequently significant differences in $\delta^{13}C$ and $\delta^{15}N$) of nine species of reef fish that are known hosts for the gnathiid isopod *Gnathia marleyi* to determine the extent to which gnathiid stable isotope ratios are influenced by its most recent host and if there are consistent patterns of stable isotopic discrimination. We expected that among host species, the differences in feeding ecology and trophic positions of the selected host species would result in significant differences in host $\delta^{13}C$ (based on different feeding groups), and $\delta^{15}N$ (based on the different trophic levels). Based on the findings of Demopoulos and Sikkel (2015), we expected that the fed third stage juvenile P3s (i.e., engorged with host blood) would have similar $\delta^{13}C$ and $\delta^{15}N$ composition to their host blood. However, as they metamorphose into male and female stages, we expected that there will be observable isotopic discrimination of both ^{13}C and ^{15}N: male gnathiids should be depleted in ^{13}C and enriched in ^{15}N relative to fish host blood; female gnathiids should not differ from host blood $\delta^{13}C$ values, but will be enriched in ^{15}N relative to their hosts' blood. If the patterns in discrimination observed by Demopoulos and Sikkel (2015) were consistent across the different host species, we expected that gnathiids collected from hosts that are isotopically distinct would themselves be isotopically distinct.

2. Methods

2.1. Parasite and fish host collections

This study focused on the stable isotope ecology of *Gnathia marleyi*, a gnathiid isopod that infests a wide range of coral reef fish hosts in the Caribbean region (Farquharson et al., 2012; Coile and Sikkel, 2013). As with all gnathiids the life cycle of *G. marleyi* consists of three larval stages, each of which has two sub stages: zuphea (Z1-3) and praniza (P1-3) (reviewed by Smit and Davies, 2004, Tanaka, 2008). These two sub stages are distinguishable by the larvae feeding until engorged on host fluid (praniza), or non-feeding and depleted of host fluid (zuphea). In this study, *G. marleyi* were collected from fish hosts and stable isotope analyses were conducted on the final, and largest, blood-engorged juvenile stage (P3) as well as both male and female adult stages.

Nine species of coral reef fish were chosen based on their abundance at our study sites, and on their known susceptibility to infestation by *G. marleyi* (Farquharson et al., 2012, Coile and Sikkel, 2013) (Table 1). The nine species included three pelagic microinvertivores (*Abudefduf saxatilis*, *Chromis multilineata* and *Myripristis jacobus*), three reef