

A global meta-analysis of temperature effects on marine fishes' digestion across trophic groups

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Abstract

Aim: The temperature constraint hypothesis proposes that marine herbivorous fishes are rare at high latitudes relative to carnivorous fishes because low temperatures impair the digestion of plant material. To test this hypothesis, we compared the effects of temperature on the digestive performance and investment in digestion of marine fishes across trophic groups.

Location: Global marine ecosystems.

Major taxa studied: Marine fishes.

Methods: We analysed data from 304 species consuming a range of diets to quantify the effects of temperature on three indicators of digestive performance and investment: gut passage time, absorption efficiency, and gut length.

Results: Decreasing temperatures increase gut passage time in fishes consuming macroalgae more than fishes consuming other fish or invertebrates. Low temperatures do not impair absorption efficiency in fishes regardless of diet, but herbivores have lower absorption efficiencies than carnivores overall. Gut length decreases with decreasing temperature in all trophic groups.

Main conclusions: Our analyses reveal limited evidence to support the temperature constraint hypothesis. Low temperatures slow digestion more in fishes consuming macroalgae than those consuming animal prey; however, this may not reflect a meaningful disadvantage for herbivores but rather could be explained by greater representation of fishes relying on microbial fermentation at high latitudes. Herbivorous fishes absorb nutrients and energy from their food in similar proportions regardless of temperature, in contrast to the expectations of the temperature constraint hypothesis. Decreased gut length was associated with decreasing temperature across all trophic groups, likely due to improved food quality at high latitudes, which should benefit all trophic groups by reducing their required investment in gut tissues. Altogether, our findings run counter to the general hypothesis that low temperatures disadvantage the digestion of plant material and suppress the diversity and abundance of herbivorous fishes at high latitudes.

KEYWORDS

absorption efficiency, diversity, fishes, gut length, gut passage time, herbivory, latitudinal gradient, marine, nutrients, temperature

1 | INTRODUCTION

Temperature imposes physiological constraints on taxa, and these constraints can drive global patterns of phylogenetic and functional biodiversity (Brown et al., 2004; Chown et al., 2004). Physiological constraints resulting from different thermal regimes may disproportionately favour taxa with certain traits and can spur novel adaptations that permit colonization and diversification by specific phylogenetic groups (Clarke & Johnston, 1996; Espinoza et al., 2004; Grady et al., 2019). Understanding how physiological constraints contribute to patterns of biodiversity is crucial, particularly given the rapid pace of climate change and species introductions that are reshaping biodiversity worldwide (Sardain et al., 2019; Sunday et al., 2015; Vergés et al., 2019).

It has been proposed that thermal constraints drive global patterns of fish biodiversity based on the observation that the abundance and diversity of herbivorous fishes relative to all fishes decline with increasing latitude and decreasing temperature (Ferreira et al., 2004; Floeter et al., 2004, 2005; Gaines & Lubchenco, 1982; Meekan & Choat, 1997). This relationship between temperature and the distribution of herbivorous fishes is of critical interest because of herbivorous fishes' potential to have profound impacts on community structure and ecosystem function, as shown by recent poleward expansions in the distribution of marine herbivorous fishes and the 'tropicalization' of marine ecosystems (Hyndes et al., 2016; Vergés et al., 2014, 2016, 2019; Zarco-Perello et al., 2020, 2017). A commonly invoked explanation for the relative rarity of herbivorous fishes at high latitudes is the temperature constraint hypothesis, which proposes that herbivorous fishes have greater difficulty than carnivorous fishes meeting their nutritional requirements with decreasing temperature due to constraints on digestion (Ferreira et al., 2004; Floeter et al., 2004, 2005; Gaines & Lubchenco, 1982; Harmelin-Vivien, 2002).

However, physiological evidence for the temperature constraint hypothesis from case studies and targeted observations appears inconsistent. In support of the temperature constraint hypothesis, observational and experimental evidence from several species of omnivore indicates that low temperatures disadvantage plant consumption (Behrens & Lafferty, 2007, 2012; González-Bergonzoni et al., 2016; Vejříková et al., 2016), and a comparison of feeding and metabolic rates of a tropical surgeonfish suggests that this species is limited by nutrient uptake at the cold end of its range (Floeter et al., 2005). In contrast, there are a variety of successful cold-water herbivores (Clements et al., 2009; Johnson et al., 2020; Knudsen et al., 2019) that appear to belie the hypothesis that cold waters disadvantage herbivory in fishes. For example, the temperate herbivore *Odax pullus* exhibits patterns of growth, demography and abundance across its thermal range that mirror those of a phylogenetically related carnivore (Trip et al., 2014). Some Antarctic notothenioids include plant material in their diet, showing that plant consumption occurs even at extreme thermal lows (Barrera-Oro, 2002; Barrera-Oro & Casaux, 1990; Casaux et al., 2003; Iken et al., 1997). These various findings suggest that at a minimum, any negative effects of

low temperatures on the digestion of plant material are not sufficient to exclude all clades and functional groups of herbivorous fish from cold regions. Possibly, they indicate that the role of temperature has been overstated and that thermal constraints are not a consequential driver of latitudinal patterns of fish herbivory (Clements et al., 2009). If this is the case, future efforts to identify the processes driving this gradient might more profitably focus on evolutionary explanations that do not depend on thermal constraints (Harmelin-Vivien, 2002).

These apparently contradictory findings on the effects of low temperatures on fish herbivory could be accounted for by the phylogenetic and functional diversity of herbivorous fishes. Herbivory has arisen multiple times in fishes, in both tropical (Egan et al., 2018; German et al., 2010; Lobato et al., 2014) and extratropical waters (Knudsen et al., 2019). As such, herbivorous fishes are a diverse group, and different species feed on biochemically distinct foods that vary substantially in nutritional content and digestibility (Horn, 1989; Montgomery & Gerking, 1980). Moreover, there are a variety of mechanisms and strategies employed by herbivores for digesting food, including mechanical grinding, acid lysis, endogenous enzymes, and fermentation (Horn, 1989; Horn & Messer, 1992). It is thus possible that the digestive performance of herbivorous species across temperatures is contingent on the type of plant material ingested or the digestive mechanism used, and that specific lineages or functional groups of herbivores experience thermal constraints where others do not. However, the effects of temperature on digestive performance, and whether those effects differ depending on species' diets or digestive physiology, are poorly understood due to a lack of systematic comparisons across species.

Although digestion in fishes is a complex process that integrates across physiology, morphology, behaviour and ecology, gut passage time and absorption efficiency are two indicators of digestive performance that have been widely reported. Gut passage time (the time required for food to pass through the digestive tract) potentially constrains the maximum feeding rate of fishes (Clements et al., 2009; Pandian & Vivekanandan, 1985); fishes can require upwards of 50 hr to digest a meal (e.g. Benavides et al., 1994). Gut passage time is expected to increase with decreasing temperature for all fishes (Edwards, 1971; Horn & Gibson, 1990), as decreasing temperature generally slows biological rates (Brown et al., 2004), but it is unclear whether the rate of increase differs between herbivores and carnivores. If gut passage time increases more for herbivores than carnivores with decreasing temperature, it could disproportionately constrain nutrient uptake in herbivorous fishes by limiting their intake of plant material. Alternatively, it could indicate a shift in digestive mechanisms: herbivores relying on microbial fermentation are thought to have longer gut passage times than herbivores relying on endogenous enzymes (Clements et al., 2014), but the distribution of species dependent on microbial fermentation across latitudes is unclear. Absorption efficiency is the proportion of nutrients retained during digestion; decreasing absorption efficiency reduces nutrient uptake from a given food item as more nutrients are lost to egestion (Ireland & Horn, 1991; Montgomery & Gerking, 1980; Pillans

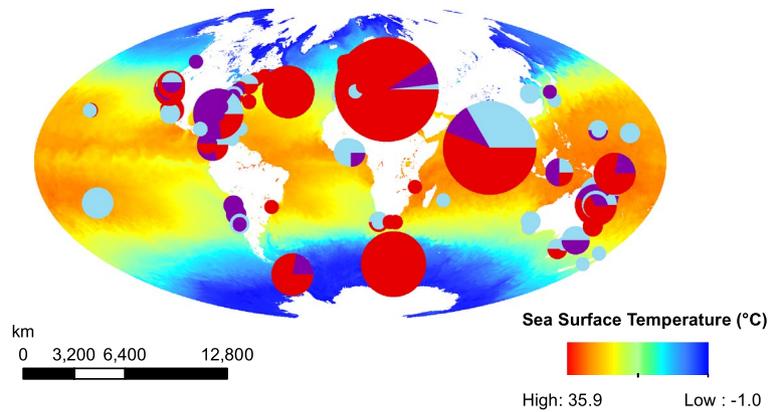


FIGURE 1 World map (Aitoff's projection) showing the locations of all studies included in the analysis. The size of each point is proportional to the number of species in each study (range: 1–56 species), and colours show the proportion of herbivorous (blue), omnivorous (purple) and carnivorous (red) species. Data shown on map are from all three primary response variables (gut passage time, absorption efficiency, and gut length). Sea surface temperature data provided by the Naval Oceanographic Office (2008) [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2004). Herbivores are expected to have lower absorption efficiencies than carnivores due to the lower nitrogen content in their food (Pandian & Marian, 1985), but it is unknown whether decreasing temperatures exacerbate this disparity in absorption efficiencies.

Gut length (generally measured as the length of the digestive tract from oesophagus to anus) is not a direct measure of digestive performance, but rather investment in digestion. Resources invested in the maintenance and function of gut tissue cannot be used for growth or reproduction, and as such, gut length should be optimized to maximize nutrient uptake while minimizing tissue investment (Horn & Messer, 1992). Herbivorous fishes typically have longer guts than carnivores because of the lower nutrient concentrations and greater refractory material in an herbivorous diet (Horn & Messer, 1992; Karachle & Stergiou, 2010a, 2010b). To our knowledge, the effects of temperature on gut length have not been systematically tested, though a case study has demonstrated that with decreasing temperature, gut length increases as enzyme activity decreases in the Malabar blood snapper (*Lutjanus malabaricus*; Mazumder et al., 2018). Similarly, we suggest that cold-water herbivorous fishes living at low temperatures could have longer guts to offset any negative effects of low temperature on nutrient uptake and allow them to meet their nutritional demands.

In this study we conducted the first broad-scale test of physiological mechanisms that could underlie the temperature constraint hypothesis by analysing the effects of temperature and diet on digestive performance and investment in marine fishes. Specifically, we quantified the effects of temperature on the gut passage time, absorption efficiency, and gut length of herbivorous, omnivorous and carnivorous fishes using a global dataset compiled from the primary literature. Our analyses tested whether decreasing temperatures are associated with disproportionate (a) increases in gut passage time, (b) decreases in absorption efficiency, and/or (c) increases in gut length in herbivorous fishes, relative to carnivorous fishes. To address the possibility that low temperatures impede digestion in some functional groups of herbivores but not others, we

distinguished among fishes consuming different types of herbivorous diets (e.g. macroalgae, seagrass, diatoms, etc.) in our analyses. Furthermore, although insufficient data were available to systematically classify species based on the type of digestive mechanism used, we discuss the role that reliance on these different mechanisms may play in shaping digestive performance across temperature.

2 | METHODS

2.1 | Literature search

We searched Web of Science, JSTOR, and Google Scholar for estimates of gut passage time, absorption efficiency and gut length. We also included data that were found in relevant review papers and in publications that cited, or were cited in, the papers discovered in our database search, as well as papers found incidentally. Our efforts resulted in a set of 99 studies that were included in the final analysis (Figure 1, Appendix, Supporting Information Appendix S1). These studies include 89 estimates of gut passage time (across 40 species), 500 estimates of absorption efficiency (across 50 species), and 358 estimates of gut length (across 249 species). Data for carnivores were available across a wider thermal range (0.2–30°C) than data for herbivores (9–30°C).

2.2 | Selection criteria and data extraction

We collected quantitative estimates of gut passage time, absorption efficiency and gut length from the studies resulting from our literature search. Data from figures were extracted using DATATHIEF (Tummers, 2006). We only accepted data for fish species that are marine or estuarine and non-larval. We did not accept data on primarily detritivorous or corallivorous species. We also did not accept data from aquaculture studies that optimized food composition

using artificial ingredients as these studies represent too large a departure from natural consumer–resource relationships and could introduce a bias towards higher absorption efficiencies. We also did not accept data if the focal species was force-fed a species of algae not typically consumed in the wild, as this could bias the data towards lower absorption efficiencies. For absorption efficiency, we accepted data for all nutrients (e.g. protein, carbohydrates) and dietary components (e.g. organic content, energetic content) as long as we were able to find a minimum of five papers that reported absorption efficiency data for that category. Additionally, we collected estimates of nutrient concentrations from these papers if the study used food items present (or similar to those present) in the focal species' natural diet. We collected temperature and diet as predictor variables, as well as body length, since many biological traits scale with size (Brown et al., 2004). If body mass but not length was reported, we used species-specific length–weight relationships to estimate length. If temperature was not given for a study, we used sea surface temperatures of the study location and time as reported by the COBE-SST2 dataset provided by the National Oceanic and Atmospheric Administration Physical Sciences Laboratory (<https://psl.noaa.gov/>).

We classified species' diets into the following categories: fish, invertebrates, zooplankton, macroalgae, turf algae, diatoms, a mix of detritus, algae and other plant material (herbivore-detritivore), or a mix of plant and animal material (omnivore). We accepted the diet characterization reported for each species in the original study, but if the species' diet was not clearly characterized, we searched the literature for other descriptions. Not all categories are represented in all analyses due to insufficient sample sizes. Few experiments on gut passage time and absorption efficiency fed fish an omnivorous diet, so we did not include omnivores in analyses of those response variables, unless the omnivorous species was fed an exclusively plant- or animal-based meal. In that event, the species was included in our analysis and classified based on the food type used in the experiment. For the analysis of gut passage time, only two estimates were obtained for piscivores, so we collapsed piscivores and invertivores into a single category. For the analysis of gut length, we created an additional category for species that feed on a mixture of invertebrates and fish.

2.3 | Statistical analysis

We analysed our dataset using multilevel generalized linear models that were built with the 'brms' package in R version 3.4.4 (Bürkner, 2017; R Core Team, 2019). Gut passage time was modelled using the gamma distribution, absorption efficiency and nutrient concentrations using the beta distribution, and gut length using the lognormal distribution. To determine if the digestive performances of herbivores and carnivores respond differently to temperature, we built sets of competing models for each response variable that tested different combinations of predictor variables including temperature, diet, and a temperature*diet interaction. For absorption efficiency,

we tested for an effect of the nutrient or component being absorbed, as well as the method used to quantify absorption (marker or total collection). Body length (ln-transformed) was included in our analyses of gut length, but earlier modelling efforts showed that body length was not a meaningful predictor for gut passage time or absorption efficiency. For gut passage time, we accounted for repeat sampling in the data by including species identity as a random effect (but not study identity, as very few studies quantified gut passage time for multiple species). For absorption efficiency, we included both species identity and study identity as random effects. For gut length we were unable to include species identity as a random effect because it impeded our ability to calculate model weights (see Supporting Information Appendix S1), and so restricted our analysis to one estimate of gut length per species. We did include study identity and phylogenetic order (to account for influence of body shape on gut length; Karachle & Stergiou, 2010b) as random effects. We note that although we modelled unadjusted gut length in all of our analyses, relative gut length (gut length/body length; RGL) is also presented in our results to facilitate comparison between groups. Differences in the nutrient concentrations of plants and animals were analysed using only diet (plant or animal) as a predictor variable. Due to limited sample sizes, we did not differentiate between specific diet types (e.g. diatoms versus macroalgae).

To determine which model best described each response variable, we used Pareto-smoothed importance sampling leave-one-out (PSIS-LOO) cross-validation ('loo' package; Vehtari et al., 2017). We then used PSIS-LOO estimates to compare models against one another and calculate both LOO and stacked model weights (Vehtari et al., 2017; Yao et al., 2018). LOO model weights represent a form of model selection that assigns probabilities describing the likelihood that each candidate model best predicts the data out of a model set. In contrast, stacked model weights represent a form of model averaging that jointly optimizes model weights to describe the combination of models that best describe the data. We reran each set of models 10–12 times to calculate averages and standard errors of model weights.

Below we present the best model for each response variable as selected by PSIS-LOO cross-validation. A more detailed explanation of the statistical analyses and the full output of all models tested are available in Supporting Information Appendix S1.

3 | RESULTS

3.1 | Gut passage time

Decreasing temperature was associated with an overall increase in gut passage time for fishes across all diet types, but the rate of increase in gut passage time was greater for macroalgivores than carnivores consuming fish or invertebrates (Figure 2). Model selection found the strongest support for the diet*temperature interaction model ($89 \pm 2\%$ SE of LOO weight; $80 \pm 1\%$ SE of stacked weight) out of the three competing models. The model predicted that gut passage time

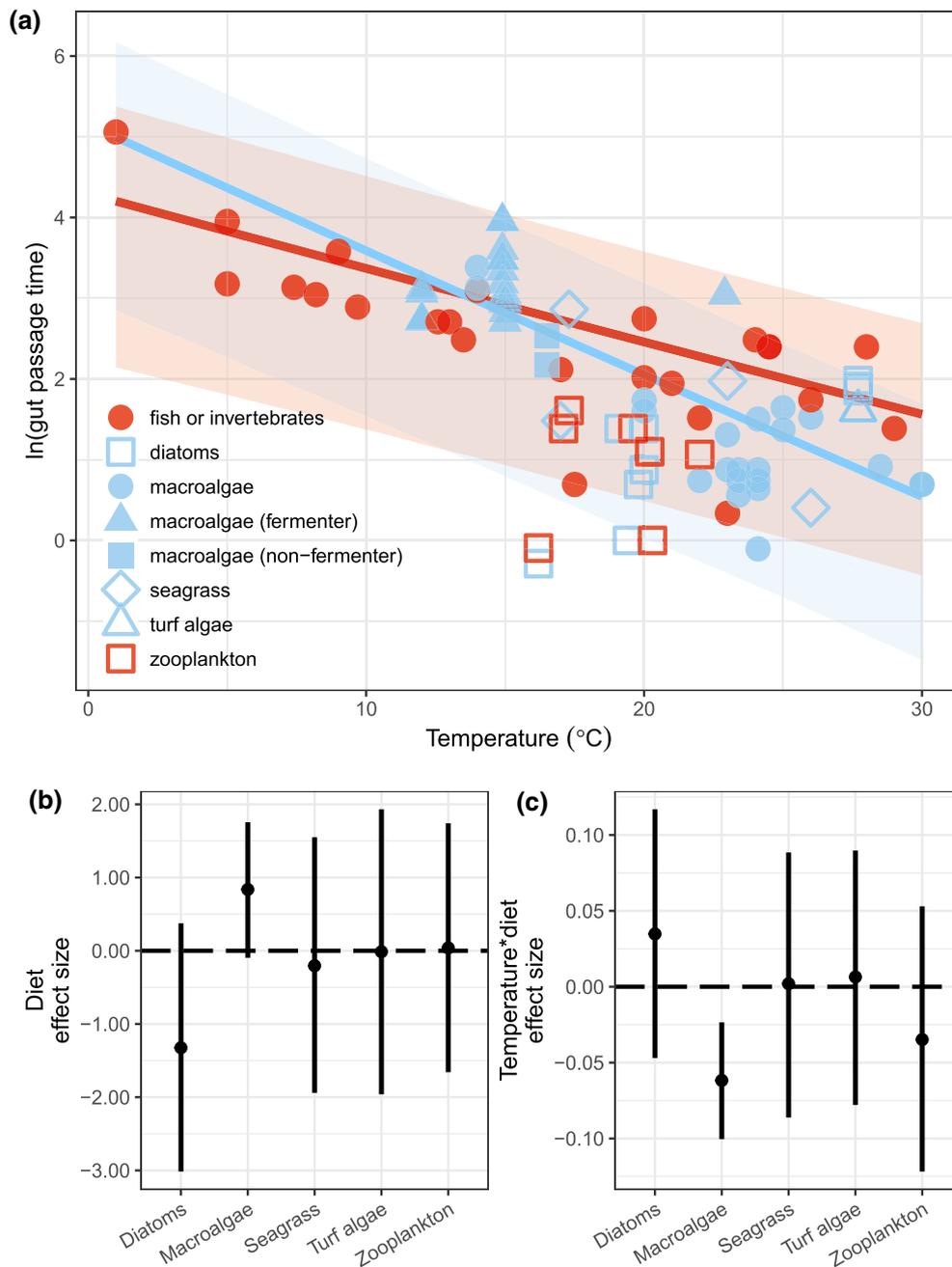


FIGURE 2 Gut passage time of marine fishes (40 species, $n = 89$) as it relates to temperature and diet. Estimates and 95% credibility intervals (CIs) in all three panels are from the best supported model describing gut passage time ($\ln(\text{gut passage time}) \sim \text{diet} * \text{temperature}$). All values of gut passage time and effect sizes are \ln -transformed. (a) Gut passage time against temperature. Lines and shaded areas show means and 95% CIs, respectively, of gut passage time for carnivores consuming fish or invertebrates (red) and macroalgiivores (blue) as predicted by the model. Macroalgiivores that are known to ferment or not ferment their food are distinguished. (b) Estimated effect of diet on gut passage time and 95% CIs. The y axis represents the difference between the gut passage time of each diet type and the gut passage time of carnivores consuming fish or invertebrates (the model intercept). Diet did not have an independent effect on gut passage time, as shown by overlapping 95% CIs for all categories. (c) Estimated diet*temperature interaction effects and 95% CIs. The y axis represents the estimated differences between the effect of temperature on the gut passage time of carnivores consuming fish or invertebrates and the effect of temperature on other diet types. The figure shows that the gut passage time of macroalgiivorous fishes responded more strongly to changes in temperature than did the gut passage time of carnivores [Colour figure can be viewed at wileyonlinelibrary.com]

increased with decreasing temperature at similar rates for carnivorous fishes ($n = 24$) and fishes consuming diatoms ($n = 10$), seagrass ($n = 4$), turf algae ($n = 2$) and zooplankton ($n = 7$; 2c). However, the available data for these diet categories were considerably more limited than for

macroalgiivores ($n = 42$). The model detected no independent diet effects (Figure 2b), predicting that gut passage time did not differ consistently among macroalgiivores, carnivores, or any other group based on diet alone, but was instead temperature dependent.

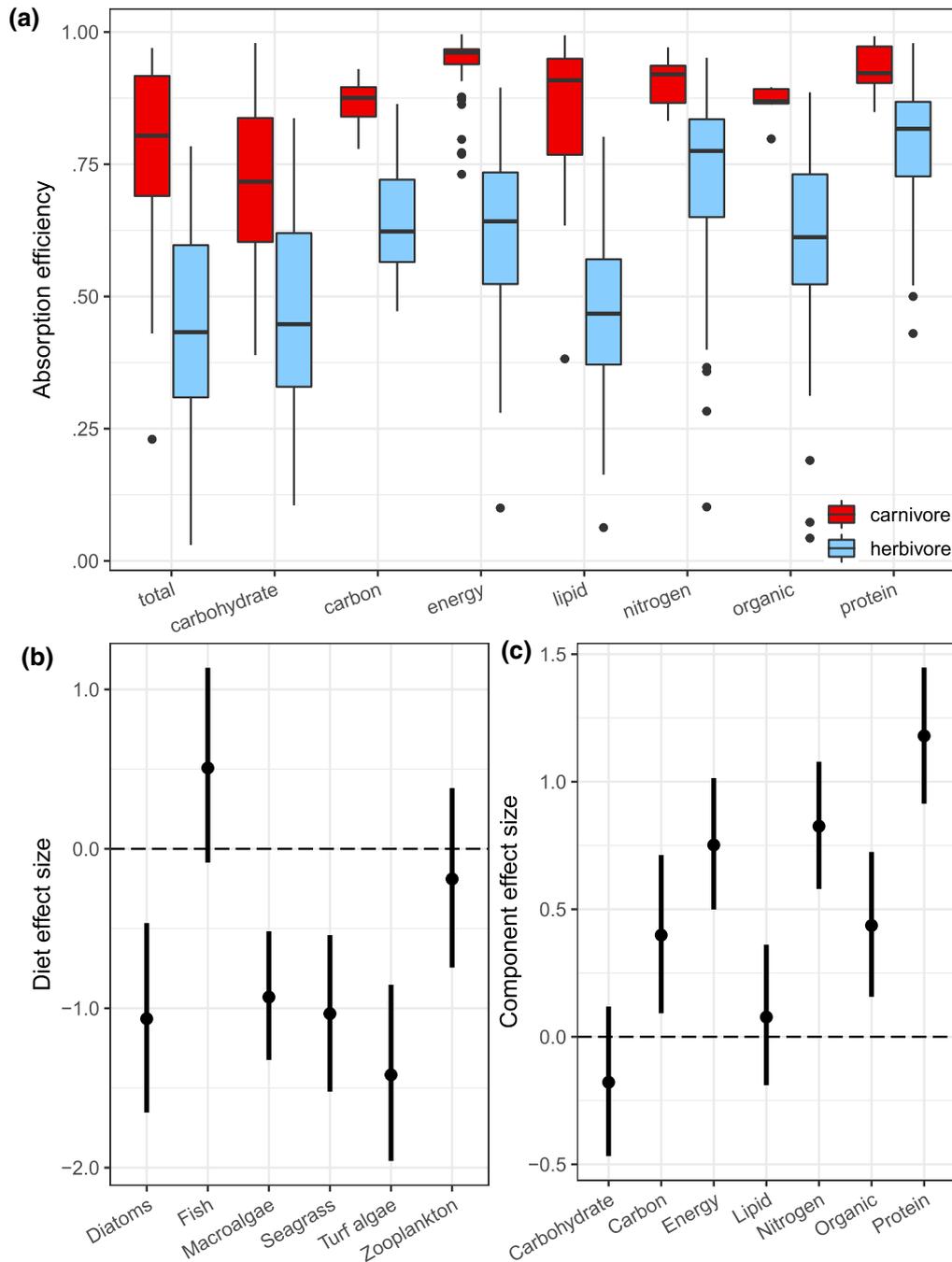


FIGURE 3 Absorption efficiency of marine fishes (50 species, $n = 500$) as it relates to diet and component absorbed. Estimates and 95% credibility intervals (CIs) in bottom two panels are from the best supported model describing absorption efficiency (absorption efficiency \sim diet + component). All effect size estimates and 95% CIs are logit-transformed. (a) Absorption efficiencies of carnivores (red) and herbivores (blue). (b) Estimated effect of diet on absorption efficiency. The y axis represents the estimated difference between the absorption efficiency of each diet type and the absorption efficiency of invertivores (the model intercept). Figure shows that absorption efficiency was lower for all herbivorous diet types. (c) Estimated effect of component on absorption efficiency. The y axis represents the difference between the absorption efficiency of different food components and total absorption efficiency (the model intercept). Figure shows that carbon, energy, nitrogen, organic material, and protein absorption efficiencies were greater than total absorption efficiency [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Absorption efficiency

Model selection did not support an effect of temperature on absorption efficiency; model selection assigned the most support to the diet-only model ($48 \pm 2\%$ SE of LOO weight, $83 \pm 4\%$ SE of stacked weight), and the 95% credibility intervals of temperature and

temperature*diet interaction effects in non-selected models consistently overlapped with 0. Absorption efficiency was consistently lower for herbivores than carnivores (Figure 3a,b) but all herbivores had similar absorption efficiencies whether they consumed diatoms, macroalgae, seagrass or turf algae; likewise, carnivores had similar absorption efficiencies regardless of diet. Across all trophic groups

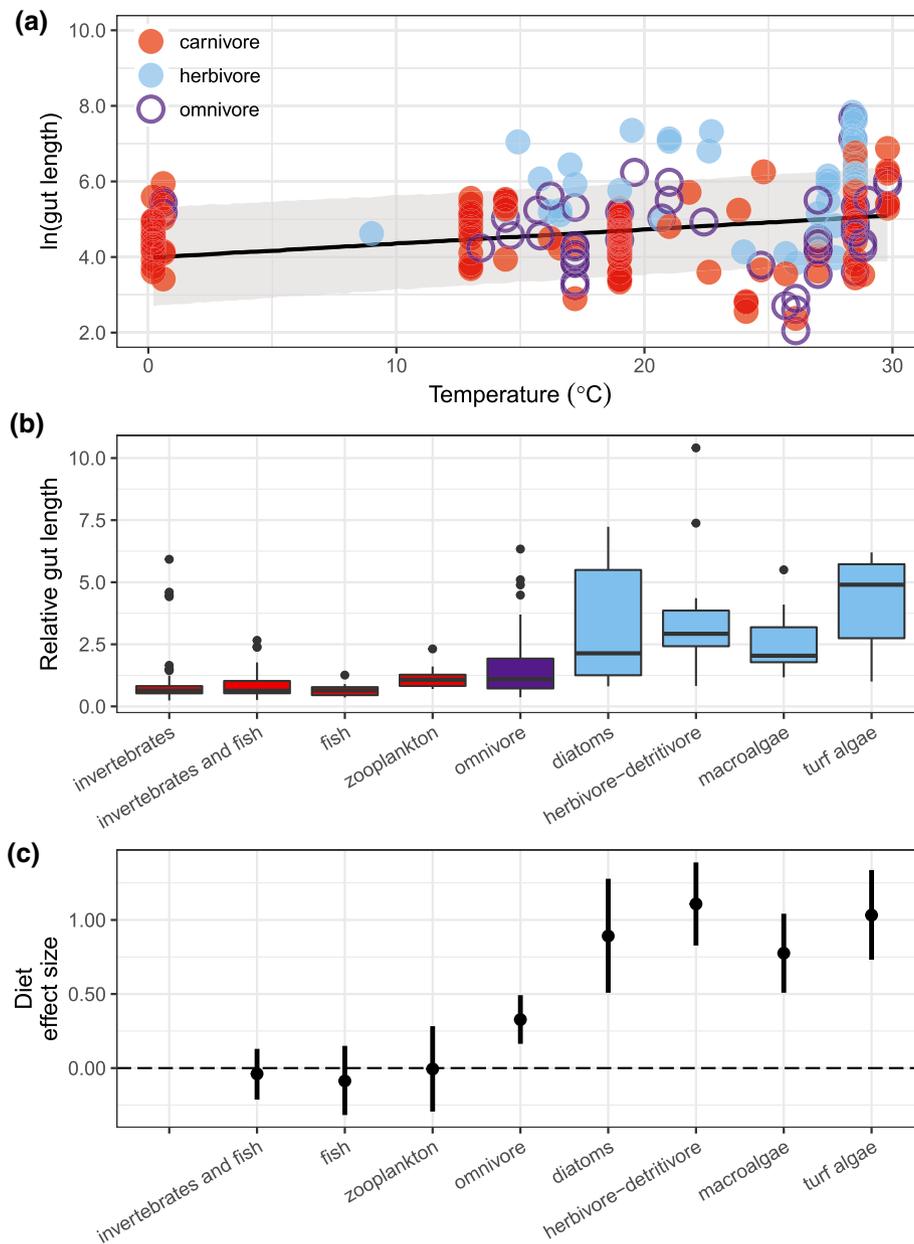


FIGURE 4 Gut length of marine fishes (249 species, $n = 249$) as it relates to temperature and diet. Estimates and 95% credibility intervals (CIs) in panels (a) and (c) are from the best supported model describing ln-transformed gut length (gut length \sim ln(body length) + temperature + diet). All effect size estimates and 95% CIs are ln-transformed. (a) Gut lengths (uncorrected for body length) of carnivores (red), omnivores (purple) and herbivores (blue). Line and shaded areas show mean and 95% CI of the gut length of invertivores across temperature, respectively. (b) Relative gut length (gut length/body length; RGL) of fishes consuming different diets. (c) Estimated effect of diet on gut length with 95% CIs. The y axis represents the difference between the gut length of invertivores (the model intercept) and other diet types. Figure shows that omnivores and all herbivorous diet types had longer guts than invertivores [Colour figure can be viewed at wileyonlinelibrary.com]

and diets, several compounds were absorbed at much higher proportions relative to total absorption efficiency ($58 \pm 25\%$ SD; Figure 3c), particularly nitrogen ($76 \pm 18\%$ SD), protein ($84 \pm 13\%$ SD) and energy ($86 \pm 18\%$ SD).

3.3 | Gut length

Gut length decreased in association with decreasing temperature at similar rates for fishes across all diet types (Figure 4a). Model selection

assigned the most weight to the temperature + diet model ($74 \pm 2\%$ SE of LOO weight, $76 \pm 3\%$ SE of stacked weight). Carnivorous fishes had shorter guts than omnivorous and herbivorous fishes (Figure 4b,c). Relative gut length (gut length/body length; RGL) for carnivores was 0.9 ± 0.8 SD, for omnivores 1.6 ± 1.4 SD and for herbivores 3.4 ± 2.0 SD. Within carnivores, gut length was not credibly different among the four diet types (invertebrates: 0.9 RGL ± 0.9 SD; invertebrates and fish: 0.9 RGL ± 0.6 SD; fish: 0.6 RGL ± 0.2 SD; zooplankton: 1.2 RGL ± 0.5 SD). Among herbivores, there was no credible difference in gut length between herbivore-detrivores (3.5

RGL \pm 2.1 SD), macroalgivores (2.6 RGL \pm 1.2 SD), and consumers of turf algae (4.3 RGL \pm 1.8 SD) or diatoms (3.3 \pm 2.8 SD).

3.4 | Nutrient concentrations

Plants fed to herbivorous fishes in our analysis were nutrient-poor compared to animal prey fed to carnivores (Figure 5). Plants had significantly lower concentrations of energy, nitrogen, carbon, protein and lipids than animal prey. Notably, there was a large difference in protein content between plant (8.0 \pm 4.7% SD) and animal (57.9 \pm 15.7% SD) material, as well as nitrogen content (plant: 2.4 \pm 1.0% SD; animal: 9.3 \pm 1.8% SD) and energy content (plant: 11.1 \pm 3.7 kJ/g SD; animal: 18.7 \pm 3.4 kJ/g SD).

4 | DISCUSSION

Using a global database of 304 marine fish species and 99 studies (Figure 1), we tested potential mechanisms thought to be the basis

for the temperature constraint hypothesis, that is, whether the relatively low abundance and diversity of herbivorous fishes at high latitudes can be explained by inhibited plant digestion at low temperatures. Our analyses of gut passage time, absorption efficiency and gut length reveal that currently available data offer little support for the temperature constraint hypothesis. We demonstrate that decreasing temperature slows down digestion more for macroalgivores than carnivores (Figure 2); however, it is unclear whether this disproportionate increase in gut passage time reflects a true disadvantage to herbivorous fishes or rather results from an increase in the representation of herbivorous fishes that use microbial fermentation to digest their food (Clements et al., 2014). Temperature does not drive a systematic difference in absorption efficiency between herbivorous and carnivorous fishes (Figure 3), which excludes reduced absorption efficiency at low temperatures as a possible explanation for the temperature constraint hypothesis. Finally, we show that gut length decreases with decreasing temperature for all trophic groups (Figure 4), which could indicate a re-allocation of resources for other somatic growth and/or reproduction, benefitting all trophic groups similarly.

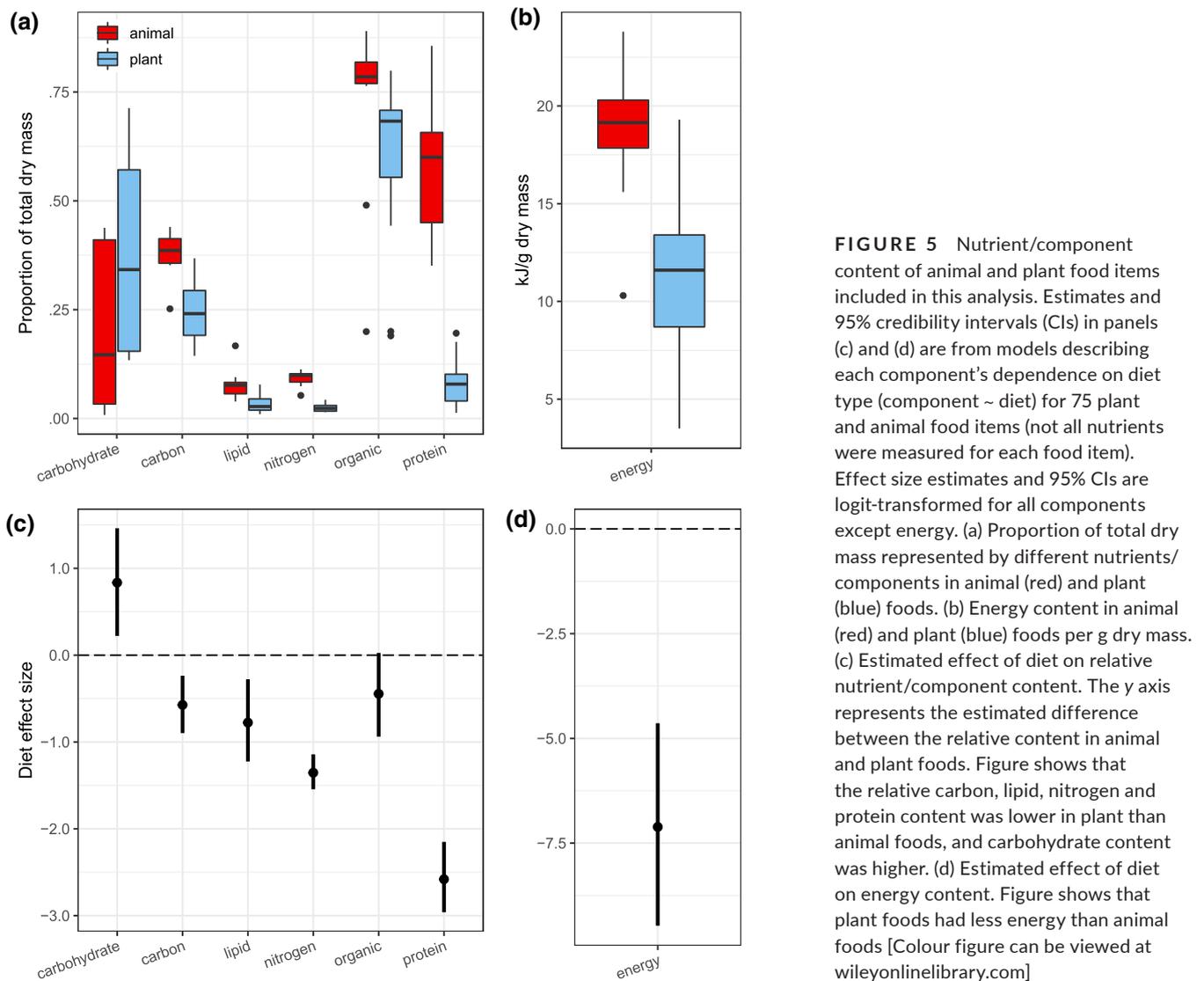


FIGURE 5 Nutrient/component content of animal and plant food items included in this analysis. Estimates and 95% credibility intervals (CIs) in panels (c) and (d) are from models describing each component's dependence on diet type (component \sim diet) for 75 plant and animal food items (not all nutrients were measured for each food item). Effect size estimates and 95% CIs are logit-transformed for all components except energy. (a) Proportion of total dry mass represented by different nutrients/components in animal (red) and plant (blue) foods. (b) Energy content in animal (red) and plant (blue) foods per g dry mass. (c) Estimated effect of diet on relative nutrient/component content. The y axis represents the estimated difference between the relative content in animal and plant foods. Figure shows that the relative carbon, lipid, nitrogen and protein content was lower in plant than animal foods, and carbohydrate content was higher. (d) Estimated effect of diet on energy content. Figure shows that plant foods had less energy than animal foods [Colour figure can be viewed at wileyonlinelibrary.com]

Our analysis of gut passage times shows that decreasing temperature slows digestion in macroalgalivorous fishes more than in carnivorous fishes (Figure 2). Although longer gut passage times at low temperatures could represent a disadvantage for herbivorous fishes by limiting feeding rates, as predicted by the temperature constraint hypothesis, this pattern could alternatively be explained by the latitudinal distribution of herbivorous fishes that rely on microbial fermentation to digest their food. Species with high levels of microbial fermentation are associated with longer gut passage times than fishes relying primarily on endogenous enzymes (Clements et al., 2014). Microbial fermentation has been recorded in both tropical (Clements & Choat, 1995) and temperate fishes (Clements & Choat, 1997), but the relative representation of fermenting and non-fermenting fishes across latitudes is unknown. Levels of fermentation have been quantified in very few marine herbivores (too few to include as a predictor in our analyses), and use of fermentation is inconsistent even within families (German et al., 2015). However, microbial fermentation appears to be a requirement for fishes that consume brown algae such as kelps, as endogenous enzymes cannot break down storage compounds such as mannitol (White et al., 2010). Thus, if fermenting herbivores are better represented at low temperatures within our dataset, it could explain why our models detected a greater increase in gut passage time with decreasing temperature among fishes consuming macroalgae.

It may be that herbivorous fishes relying on fermentation still suffer a disadvantage due to increased gut passage times. However, at least one example suggests this is not the case: the temperate, fermenting herbivore *Odax pullus* reaches high abundances even in the coldest part of its range, and exhibits patterns of growth and distribution that mirror those of the related carnivore *Notolabrus fucicola* (Trip et al., 2014). Clements et al. (2009) have proposed that eukaryotic symbionts in the hindgut, such as nematodes, consume and digest fermenting microbes, then excrete amino acids that are available for host uptake. Fish hindguts also support symbiotic spirochaetes that have been identified as nitrogen fixers in other animals (Clements et al., 2009; Lilburn et al., 2001). This suggests that microbial fermentation offers nutritional benefits to fishes that offset the cost of increased gut passage time. However, further research is needed to clarify the nutritional relationships between herbivorous fishes and their gut symbionts.

Our analysis revealed that decreasing temperature does not decrease absorption efficiency in herbivorous fishes (Figure 3). Absorption efficiency is temperature-independent across all trophic groups likely because increased gut passage times maintain rates of nutrient absorption at low temperatures. We observed that absorption efficiency in herbivores is generally lower than in carnivores. This is consistent with previous work showing that total absorption efficiency is correlated with the nitrogen content of the food ingested (Pandian & Marian, 1985); nitrogen content in plant material in our analysis was substantially lower than in animal prey (Figure 5). Furthermore, we found absorption efficiencies are highest for nitrogen, energy and protein, supporting previous suggestions that herbivorous fishes optimize feeding and digestion to fulfil protein or

energy requirements, as herbivorous fishes typically consume protein- and energy-poor foods (Bowen et al., 1995; Fris & Horn, 1993; Horn et al., 1995; Horn et al., 1986; Johnson et al., 2017).

Decreasing temperature was associated with decreased gut length among all trophic groups (Figure 4), contradicting the prediction that gut length in herbivores would increase to offset the negative effects of low temperatures on plant digestion. This surprising finding might not be caused by a direct temperature effect on gut length, but by an increase in diet quality at low temperatures. Fishes consuming a nutrient-rich diet are predicted to have shorter guts because enzymatic reaction rates and consequently nutrient uptake are faster at high nutrient concentrations, allowing for a shorter gut to meet an individual's nutritional demands (Horn & Messer, 1992). The palatability and nitrogen concentration of marine plants increases with decreasing temperature and increasing latitude (Borer et al., 2013; Brey et al., 2010; Vergés et al., 2018), which should increase rates of nutrient uptake and allow for a shorter gut among herbivores. In contrast, the nitrogen content of marine animals decreases with decreasing temperature in favour of increased carbon and possibly increased lipid content (Brey et al., 2010). This shift in nutrient composition may favour cold-water carnivorous fishes and allow for a shorter gut: a review of the nutritional requirements of cultured fish found that cold-water species tend to have lower protein requirements and higher lipid requirements than warm-water species (Bowyer et al., 2013). Similarly, increases in diet quality with decreasing temperature could explain reductions in the gut length of omnivores. However, multiple omnivorous species have been shown to increase consumption of animal prey at low temperatures (Behrens & Lafferty, 2007, 2012; González-Bergonzoni et al., 2016; Vejříková et al., 2016), which have higher protein, nitrogen and energy concentrations than plant material (Figure 5). Therefore, we cannot exclude the possibility that this phenomenon contributes to latitudinal gradients in gut length.

The interpretation of our results requires a consideration of the data that were available for analysis. Researchers tend to work with locally abundant organisms for both ecological and logistical reasons, and so have likely selected study organisms that are locally successful and have strong digestive performance. Thus, although our meta-analysis was able to elucidate general relationships between temperature and aspects of fish digestion, a strong negative effect of low temperatures on a specific clade or functional group of fishes may have been underestimated in our analysis because poorly performing species would likely be passed over when selecting focal species in the original studies. Similarly, the thermal range over which data are available for the digestive performance of herbivores (9–30°C) is smaller than for carnivores (0.2–30°C), presumably due to the rarity of herbivores at lower temperatures. We also found that very few studies have explicitly quantified digestive performance in a given species at multiple temperatures. Future work could quantify the effects of temperature on different types of digestive mechanisms (e.g. the use of fermentation versus endogenous enzymes, acid lysis versus mechanical grinding, etc.), to determine if some types of digestive mechanisms are more effective and/or prevalent

at low temperatures than others. Although the relative distribution of herbivorous fishes with latitude has been documented in multiple studies (Ferreira et al., 2004; Floeter et al., 2004, 2005; Gaines & Lubchenco, 1982; Meekan & Choat, 1997), relatively little is known about the distribution of digestive mechanisms. Altogether, pursuing these lines of inquiry should contribute to a more comprehensive understanding of how temperature affects different types of herbivorous fishes and contributes to broader patterns of diversity.

Given the lack of support for a general constraint on the digestion of plant material at low temperatures, why are herbivorous fishes relatively rare at high latitudes? As both our analyses and previous work have shown, herbivory is overall energetically inefficient relative to carnivory independent of temperature (Horn, 1989; Pandian & Vivekanandan, 1985), as it entails lower absorption efficiencies (Figure 3), longer guts (Figure 4) and lower quality food (Figure 5). It has been proposed that because of these disadvantages, the evolution of herbivory is more strongly favoured in species-rich environments such as coral reefs, where competition for high quality, easily digestible animal prey is intense (Harmelin-Vivien, 2002). In contrast, relatively low species diversity and high resource availability in temperate environments would render transitions to herbivory less likely. Thus, the relatively low diversity and abundance of herbivorous fishes at low temperatures may be due less to physiological constraints, and more to competition over evolutionary time-scales at low latitudes. Recent work on the phylogeography of herbivorous fishes (e.g. Egan et al., 2018; Knudsen et al., 2019) provides a promising avenue for exploring alternatives to the temperature constraint hypothesis and identifying the processes driving latitudinal gradients in the evolution and distribution of herbivorous fishes.

Our findings also have key implications concerning ongoing range expansions of herbivorous fishes, which can have transformative impacts on biogenic habitats such as kelp forests and sea-grass meadows (Hyndes et al., 2016; Vergés et al., 2014, 2016, 2019; Zarco-Perello et al., 2017, 2020). First, our results suggest that herbivorous fishes colonizing new habitats are not subject to unique thermal constraints as would be expected if low temperatures imposed a general disadvantage on plant digestion. Therefore, herbivorous species should be able to expand their ranges at similar rates as their carnivorous counterparts. However, the effects of herbivorous species' range expansions on biogenic ecosystems depend not only on a species' presence or abundance, but also its per capita consumption rates of plant material (Heck et al., 2015; O'Connor, 2009; Vergés et al., 2018). Given that higher individual consumption rates have been linked to shorter gut passage times and stronger impacts on ecosystem function (Heck et al., 2015), our finding that gut passage time can vary as much as 10-fold between species at a given temperature (Figure 2a) has substantial implications. As herbivorous fishes continue to expand their ranges poleward, understanding individual species' digestive physiology could provide valuable insights as to their likely ecological impact on affected biogenic ecosystems and the diverse communities they support.

5 | CONCLUSIONS

Our global analysis of the effects of temperature on digestive performance and investment in marine fishes runs counter to predicted mechanisms of the temperature constraint hypothesis, which claims that low temperatures disadvantage plant digestion by fishes. Across species, the gut passage time of macroalgivores increases at a greater rate with decreasing temperature than carnivores. However, we hypothesize that this relationship results from increased representation of fishes that depend on microbial fermentation rather than an outright negative effect of low temperatures. Other metrics of digestive performance and investment (absorption efficiency and gut length) do not support the temperature constraint hypothesis. Thus, we conclude that if low temperatures have a negative effect on plant digestion, those negative effects are likely confined to specific phylogenetic or functional groups of fishes. Our analysis of the currently available data on temperature and digestion in marine fishes points to several lines of future research, namely (a) investigating the effects of temperature on the performance and distribution of fishes employing specific digestive mechanisms, (b) developing and testing evolutionary hypotheses that could explain gradients in herbivorous fish diversity, and (c) investigating the relationship between herbivores' digestive physiology and their ecological impact on warming marine ecosystems.

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DATA AVAILABILITY STATEMENT

All data used in our analyses are publicly available through Dryad (<https://doi.org/10.5061/dryad.g1jwstqq1>), and all data and code are publicly available through GitHub (<https://github.com/nicoleknigh0/meta-analysis-fish-digestion>).

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BIOSKETCHES

Nicole Knight studies the effects of temperature on trophic interactions and species' distributions across marine ecosystems.

Frédéric Guichard is interested in how the environment and ecological interactions affect the dynamics of species abundance and ecosystem functions.

Andrew Altieri researches how marine ecosystems respond to the interaction between global environmental factors and local ecological processes.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX

DATA SOURCES

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