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### Editorial on Adaptations of nutrient supply organs that fuel the fire of life

In this special edition of *Comparative Biochemistry and Physiology A*, we bring together 18 articles on digestion and metabolism that advance the field of nutritional physiology by integrating diverse perspectives on how the gut helps organisms meet their metabolic needs. The larger suite of redox reactions that compose the main thoroughfare of metabolism (Glycolysis, Citric Acid Cycle, Electron Transport Chain, and Chemiosmosis) have many tributaries that must be fed from the alimentary canal. Although digestion has been somewhat well-studied in biomedical models (e.g., rodents, humans), and in animals we grow for human consumption, the general principles of the digestive process, and the perturbations that can disrupt that process, require more investigation. The perspectives acquired from examining many different organisms aids in this process with implications for numerous fields.

The papers in this edition span seven main themes: the energetics of digestion, particularly in the face of global change (including dietary shifts and rising temperatures), how hormones of the gut respond to changes in gut function due to a meal, dietary impacts on ecomorphology and function, particularly of the gut, how the enteric microbiome responds to perturbations and potential consequences of this for the host, how gut size scales with body sizes spanning orders of magnitude, maintenance of gastrointestinal gas and acid-base balance in response to challenges, and how the loss of the stomach generates expectations for agastric fishes. Thus, the authors dig deep into a diverse array of topics that help us better understand the general principles of digestion in a changing world.

### 1. The energetics of digestion

da Mota Araujo et al. (2022) lead this section by examining what fuels the rapid response of the digestive system to a meal in an infrequent feeding snake, Boa constrictor. Although the Burmese python (Python bivittatus) has been given considerable attention in this context, boas have not. Hence, the authors examined how the Boa gut (and metabolic fuels) respond to a feeding event. They found that feeding had profound effects on gut morphology and substrate usage. They observed that plasma glucose concentrations shot up after feeding, but normalized within two days of the feeding event, whereas plasma protein and lipid did not change significantly over the measured time period. The authors took this to mean that the snake has enough reserves on hand to fuel the transition from fasting to the post-prandial state. Nevertheless, lipid droplets quickly accumulated in enterocytes following feeding, showing the importance of absorbed nutrients in the short-term energy balance of the animal. Enzymes involved in gluconeogenesis were most active about six days after feeding, as opposed to after months of fasting, showing that glycogen stores were replenished more from feeding bouts

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Available online 13 January 2023 1095-6433/© 2023 Elsevier Inc. All rights reserved. than from endogenous substrate conversion. Glycogen accumulation matched this pattern as well. This is an interesting finding that concurs with what is known about other infrequent feeding animals (e.g., Secor et al., 1994).

Another major theme in digestive physiology is understanding what is known as the "heat increment of feeding", "dietary induced thermogenesis", or the more ambiguously termed "specific dynamic action", each of which describe the elevated metabolic rate that follows consumption of a meal. Much of the increase in metabolic rate has been tied to the upregulation of protein synthesis and modifications that happen in response to the influx of nutrients in the gut and the bloodstream. In this special edition, Bury (2022) asked the question of whether intestinal upregulation was a sufficient explanatory variable for the large uptick in metabolic rate observed during dietary induced thermogenesis. They used existing datasets on infrequent feeding snakes, coming to the conclusion that increases in intestinal mass following feeding are indeed positively correlated with increased metabolic rate. However, increases in other aspects of the gut, like microvillar length, are not also correlated with this metabolic upregulation. So, yes, an increase in the mass of the intestinal organs do happen at the same time as an increase in metabolic rate following meal consumption, but that isn't the only explanation for the increased metabolic demand. Bury (2022) makes the call for more datasets so that the role of the gut itself can be determined in the quest to understand dietary induced thermogenesis.

Mendoza et al. (2022) investigated how changing the polysaccharide component of feeds for juvenile turtles (*Chelonoidis carbonaria*) affects their digestibility and growth. By reducing the amount of fiber and increasing the amount of starch in the diet, the authors showed that digestibility of many metrics in the diet increased, and that the turtles grew faster and achieved larger sizes when eating more soluble polysaccharides as opposed to insoluble ones. Interestingly, they observed that the turtles ate more food when it is was enriched with starch as opposed to fiber (usually it would be the other way around since the excess fiber essentially dilutes the nutrient load of the food, thus requiring higher intake). Many of the variables they measured showed that with more digestible nutrients present, the gut can provide more for the growing animal, which is key for culturing species.

Frederick et al. (2022) focused their work on abalone, which are large, gastropods that are important food items historically for indigenous human populations, and also currently for the broader population. Red abalone (California) and pāua (New Zealand) are each cultured for their meat in their respective regions in opposite hemispheres, and each have affinities for cold water habitats. Thus, as conditions warm on abalone farms, will the abalone gut be able to keep up with increased energy demand? Frederick and colleagues clearly showed that both species of abalone experienced the expected increased metabolic rates with warmer conditions, but the animals were able to eat more and the gut was able to keep pace with this increased demand (i.e., no reduction in organic matter digestibility with increased intake). Interestingly, the adjustments made to the gut were not the same, as the abalone showed species-specific responses in terms of what digestive enzymes were elevated in response to the increased metabolic demand and food intake. Thus, there is encouraging results that abalone can keep up with warming in an aquaculture setting, but it is intriguing that the animals can do this in different ways, perhaps due to their different evolutionary histories.

Rounding out this section is a review of digestibility studies in reptiles. Wehrle and German (2023) explore the concept of digestibility, especially from a methodological standpoint, with an emphasis on lizards. The authors compiled a large list of studies from which to draw knowledge on the topic. Following critical reviews challenging the use of ratios in digestibility analyses, Wehrle and German (2023) echo the cautionary tale that ratio-based calculations should only likely be used in limited circumstances (e.g., Beaupre and Dunham, 1995). They do take a limited swath of data that was available to examine the impacts of temperature on digestibility in lizards, finding that the impact of temperature on digestion in reptiles is not a universal one. Overall, this review leads to a call for more detail in data collection of digestibility data to better understand how reptiles use different resources. More detail needs to be part of the experimental planning itself to provide the variables needed to understand digestive efficiency. Such data has implications in livestock management, conservation and ecosystem management.

### 2. Hormonal signaling during digestion

de Figueiredo et al. (2022) examined the metabolic responses of feeding in Boa constrictor, focusing on metabolic rate, corticosterone concentrations, and immune cell distribution. They found that, concomitant with an increase in metabolic rate, corticosterone levels do indeed spike up after feeding, and this correlates with a change in immune cell distribution (calculated as the heterocyte/lymphocyte ratio). Thus, with such an increase in metabolic demand, feeding is also somewhat of a stressful event that could leave the animal vulnerable to predation, or pathogenic attack from an ingested meal. The animal, therefore, ramps up the stress response, which has far ranging impacts on immune response (increase heterocyte/lymphocyte ratio) and metabolism at large. The authors argue that a ramping up of the hypothalmic-pituitary-adrenal axis may be a broadly observed phenomenon, but that it may be more pronounced in infrequently feeding snakes, like Boa. Hormonal signaling plays a wide range of roles in animal physiology, but particularly in response to feeding.

# 3. Dietary impacts on ecomorphology and function, particularly of the gut

Taverne et al. (2022) examined jaw kinematics in two populations of the lizard *Podarcis siculus* from Croatia. Nevo et al. (1972) moved five breeding pairs of *P. siculus* from the island of Pod Kopište to Pod Mrčaru; *P. siculus* previously didn't exist on the latter island. The lizards thrived on Pod Mrčaru as they expanded their territory. Thirty six years later, Herrel et al. (2008) found that the Pod Mrčaru lizards were larger, had stronger bite force, and were omnivorous (Pod Kopište lizards were, and remain, carnivorous). This new "generalist" feeding habit resulted in numerous changes to gut morphology (Herrel et al., 2008) and gut function (Wehrle et al., 2020) in the *P. siculus* from Pod Mrčaru. Taverne et al. (2022), took *P. siculus* from the two populations into the laboratory and reared them on a cricket-only diet for a year and a half, yet found demonstrable differences in jaw kinematics in how they responded to immobile (mealworms) and mobile (crickets) prey. Since these animals had a considerable acclimation period, the authors concluded that the prey capture and behavioral differences observed among the lizards from the two populations are likely genetically hardwired. Hence, they provide yet another example of rapid changes in prey capture ability that has occurred in these two *P. siculus* populations as they continue to diverge. When animals start consuming new resources, the flexibility of nearly every aspect of their food intake and digestive process must accommodate the new resources, and Taverne et al. (2022) show that this starts with the oral cavity and how prey are acquired.

Ruthsatz et al. (2022) examined whether microplastics act like dietary fiber, essentially diluting consumed food with something that is recalcitrant to digestion. Thus, they compared gut mass, length, and diameter in *Xenopus laevis* tadpoles that were fed standard fish feed, those with feed containing microplastics, and those with feed supplemented with cellulose (i.e., natural fiber). They observed that the tadpole guts were longer and heavier in the plastic- and fibersupplemented diets, consistent with the higher intake required to meet nutritional demand in a diet diluted by an indigestible component. Tadpoles are not known to have elevated gastrointestinal fermentation indicative of fiber digestion (Pryor and Bjorndal, 2005), so this is an excellent system in which to examine the general principle of microplastics acting as a dietary diluent. Ruthsatz and colleagues add to the growing literature on how microplastics impact gut structure and function.

Yawitz et al. (2022) examined gut morphological and enzymatic differences among five closely-related species of mice in the genus Peromyscus. They found clear phylogenetic signals for foregut mass and small intestine length, suggesting that species sharing common ancestry share similarities in these traits, which very much impact diet and digestion. What's more is that they didn't examine these traits in wildcaught individuals consuming their natural foods, but in animals that had been held in captivity under common garden conditions for several generations at this point. Hence, the observed differences were evolved differences present in the examined populations and not just arising from proximal diet. Yawitz et al. (2022) also found differences in small intestine aminopeptidase activities, further accentuating the evolutionary differences in digestive tract structure and function among the examined species. Few studies examine so many species at once, particularly in those that have been held in captivity, so this study highlights potential adaptations among the species for their natural diets. These results help us better understand dietary specialization in rodents and beyond.

Closing out this section, Oguchi et al. (2022) tested the Adaptive Modulation Hypothesis (AMH), which, based on economic principles, predicts that there should be a match between ingestion of a particular nutrient and the digestive enzyme activities needed to digest that nutrient in the gut. They did this by feeding northern bobwhites and chickens (juveniles and adults) diets of varying carbohydrate, protein, and lipid amounts and measuring the activity levels of maltase, sucrase, and aminopeptidase N in the intestines of the birds. Although the birds consuming high-carbohydrate diets generally had heavier intestines, resulting in greater summed disaccharidase activities for the whole intestine, the mass-specific activities for these enzymes really only showed suppression in response to high-lipid diets in the northern bobwhites. The chickens actually showed support for the AMH with disaccharidases. In terms of protein, the juvenile chickens and the northern bobwhites showed increased aminopeptidase N activity in response to increased dietary protein, supporting the AMH, whereas adult chickens did not. Hence, any pattern of enzyme modulation varies among species, and even ontogenetic stage. A broader phylogenetic analysis showed that not all Galliformes (or broader groups of birds) show the same responses in terms of the AMH; most birds show some response of enzyme activities in response to nutrient intake, but some specialists do not. Thus, the gut remains a tunable instrument in the quest to acquire sufficient nutrients from variable diets, and Oguchi et al. (2022) clarify some of the general principles of digestion in birds, and vertebrates more generally.

# 4. Responses of hosts and their enteric microbiomes to perturbations

Stevenson et al. (2022) lead off this section with an impressive examination of the enteric microbial diversity of the marine herbivorous fish species, Kyphosus sydneyanus. The authors used 16 s rDNA sequencing and metagenomics to examine community diversity and potential function. Stevenson and colleagues showed that there were three levels to the microbial diversity in this fish's gut: radially, comparing the intestinal lumen to the mucosal lining of the intestine, axially, showing differences moving anterior to posterior along the intestine, and among individuals of the same fish species. The radial and axial differences make sense because there are different selective environments along these gradients, and there are different substrates available for degradation as one moves along the intestine towards the hindgut. The intraspecific variation is intriguing, but the authors used the metagenomic sequencing to show that although there were community differences among the individual fish, the microbial metabolic pathways represented in the enteric microbial communities were similar. Thus, the selective forces of the gut environment don't necessarily select for individual bacterial species, but for some amalgam of metabolic pathways represented in the community of microbes. Of course, the metabolic pathways need to provide some function for the microbial community and the host, and the authors did a thorough job of dissecting the pathways needed to completely breakdown the more recalcitrant portions of the brown algae consumed by this fish species. Each of the pathways was represented in the metagenomic sequencing performed. This may be one of the most thorough and interesting examinations of a marine herbivorous fish microbiome to date, and helps answer broad questions about digestive physiology of herbivorous fish, and even vertebrates at large.

Leigh et al. (2022) took advantage of a laboratory population of zebrafish to ask what happens to an animal's microbiome when it first switches to a new diet? Zebrafish that had been consuming a commercial feed for hundreds of generations were switched to foods with varying protein and fiber concentrations: 40:10, 30:30, and 10:60 (protein to fiber ratio). They followed the fish to the F<sub>1</sub> generation consuming the different diets and examined digestive physiology and the enteric microbial community using 16 s rDNA sequencing. The laboratory diets elicited different microbiomes, as the microbial community was different on each diet (especially compared to the fish consuming the ancestral diet). Since these were laboratory animals, the authors observed that the communities changed mostly through change of abundance of the same microbes, as opposed to new taxa appearing in the communities. Thus, the bacterial communities still resembled that of other published zebrafish microbiomes, but with different ratios of species, and a butyrate producing member of the phylum Bacillota (Clostridium butyricum) becoming more abundant in the fish consuming the high-fiber diet. Digestive enzyme activities were generally most elevated in the 30:30 protein:fiber diet fish, but the 10:60 protein:fiber diet fish had the longest guts to go along with the butyrate producing bacteria, which agrees with observations that more butyrate production by enteric microbes leads to more enterocyte proliferation (and more gut tissue). Hence, this is one of the few studies to follow what happens with diet switching across multiple generations and leads to hypotheses for how animals may respond to changing resources in a changing world.

MacPherson et al. (2022) used antibiotics and fasting treatments to show that nitrogen recycling is likely occurring via the intestinal microbiome in spiny dogfish. The authors observed that when fed animals were treated with antibiotics, plasma urea levels dropped significantly, as did urea and ammonia excretion in the antibiotic-treated animals in comparison to fed controls. Fasted animals showed little difference in these parameters, suggesting a role of the enteric microbiome in participating in recycling nitrogen via urease activity in the gut, particularly following a meal. Moreover, the control animals lost about 5-fold less weight than the antibiotic treated animals during the experiment, again hinting that the microbiome plays an important role in nitrogen metabolism of this shark species. This is the first such observation in a shark species and allows further hypothesis formation about the roles of intestinal microbes in nitrogen homeostasis in carnivorous fishes.

Closing out this section, Perez-Marron et al. (2022) examined the gut microbiome of Alligator mississippiensis from the oral cavity to the hindgut. They observed that the oral microbial community establishes early and diversifies over time, consistent with other oral microbiome studies in terrestrial vertebrates. Applying metagenomic sequencing to the microbial genetic material in the proximal and distal intestines shows that the community structure, membership, and function likely changes moving from proximal to distal along the intestine. Indeed, the hindgut microbiome contains a lot of usual denizens in the Bacillota, Bacteriodota, and Pseudomonodota (formerly Firmicutes, Bacteroidetes, and Proteobacteria, respectively), but is dominated by Pseudomonodota, as is usual for carnivorous animals (e.g., Egerton et al., 2018). Interestingly, the authors observed that microbes found in the human microbiome, like Clostridiodes difficile, are also found in the A. mississippiensis gut. They also observed that antibiotic resistant microbes do take residence in the alligator gut, thus providing a heretofore unconsidered reservoir for antibiotic resistance. Finally, with the examination of potential metabolic pathways present in the metagenome, the authors identify potential targets for new antibiotics. Thus, a detailed examination of the alligator microbiome reveals that they have an active enteric microbial community that likely contributes to the metabolism of the host, but also provides a new habitat to explore for biomedically-relevant studies. Such findings further support the notion that all animals are worth studying on multiple levels because one never knows what they may find, including new antibiotics, or emerging pathogens.

#### 5. Scaling of gut structure and function with size

Munn et al. (2022) examined the ontogenetic scaling of the mass of gastrointestinal contents with increasing body size in different gut regions of the western grey kangaroo (Macropus fuliginosus melanops). Although an increase in intestinal content mass would be predicted with increasing body mass, the authors observed that the rate of that increase changed when the animals emerged from the pouch and began to consume more plant material. Notably, the foregut and caecum content masses disproportionately represented more of the relative content mass as the animals grew, showing the importance of gastrointestinal fermentation in this species. This relationship began while the young were still at least partially (if not fully) consuming milk, showing that a reliance on enteric microbes in the digestive process begins early in this marsupial species. The work presented in this paper shows the importance of taking a wide range of sizes into account in ontogenetic analyses of morphological scaling since aspects of the relationship changed as the animals transitioned from juveniles to adults. Overall, the gut changed to fit a higher-fiber diet, and the changes appeared to be hardwired, occurring before true dietary shifts occurred.

## 6. Maintenance of gastrointestinal gas and acid-base balance in response to challenges

Jung et al. (2022) explored the gas and acid-base balance of the digestive tract and blood in freshwater acclimated rainbow trout (*Oncorhynchus mykiss*) and marine English sole (*Parophrys vetulus*). Their own previous work on freshwater acclimated *O. mykiss* had suggested the extreme  $CO_2$  concentrations observed in the gut could be absorbed into the splanchnic circulation, thus influencing the  $O_2$  delivery from the blood to the digestive tissues (via the Bohr and Root effects). However, the authors didn't find any effects of the extreme gaseous environment of the intestinal lumen on venous blood conditions in either species. In fact, the lack of change in  $PO_2$  or  $PCO_2$  following feeding in both species

suggests a mechanism other than respiratory compensation to account for acid-base balance following a meal, essentially suggesting fishes respond differently than terrestrial animals to such conditions. Moreover, Jung and colleagues challenge the notion that freshwater fishes have more elevated intestinal bicarbonate than marine fishes, finding elevated bicarbonate in both taxa. The differences among *O. mykiss* and *P. vetulus*, especially diet and phylogenetic unrelatedness, lead to calls for more work in this area using conspecifics acclimated to fresh- and salt water and fed a constant diet to discern any differences in bicarbonate in the intestinal environment. Overall, the study generates new, testable hypotheses for how fishes manage the intestinal and blood environments during feeding in fresh and salt water.

Quijada-Rodriguez et al. (2022) examined how the green shore crab (Carcinus maenas) responded to a meal in terms of acid-base balance and nitrogen metabolism. They found that gastric fluid pH was unaffected by the presence of digesta, but that the crab experienced a respiratory acidosis after feeding. Hemolymph ammonia concentrations were elevated after feeding, and about 1/3 of this was converted to urea, perhaps to detoxify the circulating ammonium. Ammonia excretion appeared to be the primary mechanism of acid-base balance, as bicarbonate did not change over the course of the experiment. Interestingly, gill urease activity was elevated as the crab was excreting large amounts of ammonia, suggesting that urea degradation to ammonia provided another mechanism for the crab to dump nitrogen into the environment and help with N and acid-base balance. Each of these responses is different from how the animal responds to hypercapnia or emersion, which typically results in more bicarbonate production. Hence, the green shore crab responds differently following a meal than they do to environmental challenges, and the response is mediated through the gut and gills. More detailed studies are needed to elucidate what this means for the broader physiology of this species and perhaps other crustaceans.

### 7. Trait loss and digestive physiology

Esfandiyari et al. (2022) investigated whether members of the fish order Gobiiformes have truly lost their ability to secrete gastric acid and the acidic protease, pepsin. The evolution of the acidic stomach is a hallmark of vertebrate evolution, arising in the ancestor of cartilaginous and boney fishes and being present in subsequent lineages. However, the stomach itself, with the phenotype of acid and pepsin secretion, as been lost more than a dozen times, mostly in boney fishes. This loss is usually accompanied by a pseudogenation of the genes encoding the subunits of the  $H^+/K^+$  -ATPase gastric proton pump, as well as the pepsin genes (Castro et al., 2014). The absence of acidic pH and peptic activity are also easily confirmable in taxa missing a gastric stomach (e.g., members of the family Cyprinidae). Although cited numerous times, the evidence of stomach-loss in the Gobiiformes is weak, and in need of a more detailed examination. Thus, Esfandiyari et al. (2022) used immunohistochemistry, RT-PCR, and genomic analyses to confirm the presence of the  $H^+/K^+$  -ATPase gastric proton pump. Indeed, all of the Gobiiforms (representing to the two major families in the order) they examined retained the active proteins in what appear to be gastric glands of the anterior gastrointestinal tract. Furthermore, the genes for these proteins are expressed, and the full coding genes are present in the genomes of all the fishes. Hence, the Gobiiformes do not appear to be a true agastric lineage like some other groups of fishes. The stomach has been lost in some goby species, but those losses cannot be traced to the common ancestor of the whole order. When studying fish evolution, stomach loss is one of the most intriguing aspects of phenotype loss, since the gastric stomach appears to be so important to digestion and immunity in many taxa (including terrestrial vertebrates). The deep analysis by Esfandiyari et al. (2022) provides a blueprint for how to investigate whether a trait has actually been lost, which it clearly has not in all gobies.

### 8. Conclusions

Overall, we assembled a diverse group of researchers and topics investigating form and function of the digestive system. Spanning from the oral cavity, through gastric compartments, the intestine, into the body, and even following excretion. Studies in this volume considered responses of the animal, as well as the microbes inhabiting their alimentary canals, to a variety of changes. The gut, and indeed, animals themselves, must be able to respond to a wide variety of changes. The papers represented here provide new data and new ways forward for studying how animals acquire the resources to fuel the fire of life.

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