Linking the feeding ecology of marine consumers to patterns of distribution across scales

Nicole Katherine Sutts Knight

Department of Biology, Faculty of Science

McGill University, Montréal

August 2023

A thesis submitted to McGill University in partial fulfilment of the requirements of the degree of

Doctor of Philosophy

Abstract

Patterns of distribution result from individuals interacting with the environment and other organisms. In this thesis, I seek to improve our understanding of when and how the environmentally-driven variation in the ecology and physiology of individuals can explain patterns at higher levels of ecological organization. I focus primarily on the effects of the environment on feeding and digestion, which underpins the ability of individuals to survive, grow and reproduce. In my second chapter, I test the longstanding Temperature Constraint Hypothesis (TCH), which proposes that herbivorous fishes are less abundant and diverse at high latitudes because low temperatures impede the digestion of plant material. By analyzing a global dataset of the effects of temperature on digestive performance, I show that there is currently little evidence to support the TCH. In my third chapter, I combine physiological and distribution data to test the effects of seasonal upwelling on tropical damselfishes. I first quantify how seasonal upwelling impacts damselfish feeding, digestion, and body condition, then test whether patterns of damselfish distribution along a regional upwelling gradient are consistent with the effects of upwelling on damselfish physiology. I found that both the performance and biomass of two of my focal species responded positively to upwelling, whereas the performance and biomass of the third species did not exhibit a strong response to upwelling. Altogether, my findings are consistent with the hypothesis that performance can predict patterns of distribution, but shows that these relationships are contingent on species characteristics including diet and plasticity. In my fourth chapter, I use high-resolution biomass and diet data from cryptic, coral-associated invertebrates to explore relationships between habitat degradation and the biomass of different trophic groups. I show that trophic groups respond differently to the loss of coral habitat, with the strongest effects on grazers and predators. Overall, my thesis demonstrates how combining information on processes occurring at the individual level with patterns of distribution can improve our understanding of the ecology of species and communities, and that incorporating species- and environment-specific context can further this goal.

Résumé

Les motifs de distribution résultent de l'interaction des individus avec l'environnement abiotique et d'autres organismes. Dans cette thèse, je cherche à améliorer notre compréhension de quand et comment l'écologie et la physiologie des individus peuvent expliquer des modèles à des niveaux plus élevés d'organisation écologique. Je me concentre principalement sur les effets de l'environnement sur l'alimentation et la digestion, qui étayent la capacité des individus à survivre, grandir et se reproduire. Dans mon deuxième chapitre, je teste l’hypothèse de contrainte de température (TCH), qui propose depuis longtemps que les poissons herbivores sont moins abondants et moins diversifiés aux latitudes élevées car les basses températures entravent la digestion du matériel végétal. En analysant un ensemble de données globales sur les effets de la température sur les performances digestives, je montre qu'il existe actuellement peu de preuves pour soutenir le TCH. Dans mon troisième chapitre, je combine des données physiologiques et de distribution pour tester les effets de l'upwelling saisonnier sur les demoiselles tropicales. Je quantifie d'abord l'impact de l'upwelling saisonnier sur l'alimentation, la digestion et l'état corporel des demoiselles, puis je teste si les modèles de distribution des demoiselles à travers d'un gradient régional d'upwelling sont cohérents avec les effets de l'upwelling sur la physiologie des demoiselles. J'ai constaté que les performances et la biomasse de deux de mes

espèces focales répondaient positivement à l'upwelling, tandis que les performances et la biomasse de la troisième espèce ne présentaient pas de réponse forte à l'upwelling. En général, mes résultats sont cohérents avec l'hypothèse selon laquelle la performance peut prédire les motifs de distribution, mais montre que ces relations dépendent des caractéristiques de l'espèce, notamment le régime alimentaire et la plasticité. Dans mon quatrième chapitre, j'utilise des données à haute résolution sur la biomasse et le régime alimentaire d'un paysage marin tropical pour explorer les relations entre la dégradation de l'habitat et la biomasse de différents groupes trophiques. Je montre que les groupes trophiques réagissent différemment à la perte d'habitat corallien, avec les effets les plus forts sur les brouteurs et les prédateurs. Tous ensemble, ma thèse démontre comment la combinaison d'informations sur les processus se produisant au niveau individuel avec des modèles de distribution peut améliorer notre compréhension de l'écologie des espèces et des communautés, et que l'intégration du contexte spécifique aux espèces et à l'environnement peut favoriser cet objectif.

Table of Contents

List of Figures

Figure 2.1. 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).

Figure 2.2. 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 (gut passage time) ~ diet*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 macroalgivores (blue) as predicted by the model. Macroalgivores 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 macroalgivorous fishes responded more strongly to changes in temperature than did the gut passage time of carnivores.

Figure 2.3. 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 ~ 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.

Figure 2.4. 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 ~ 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.

Figure 2.5. 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 ~ 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.

Figure S2.1. Absorption efficiency estimates (n = 500) for the 50 species of marine fish included in this analysis across temperature. Data are separated by diet and the type of component absorbed. 0 is no nutrient absorbed during digestion, 1 is complete absorption of the nutrient during digestion.

Figure 3.1. Maps of Central America and the Tropical Eastern Pacific (TEP) showing (a) the mesh used in all distribution models (grey lines), with Reef Life Survey sites (points) distinguished by region, (b) our fish collection sites in Las Islas Perlas (star) and STRI SST monitoring sites (blue diamonds), (c) annual minimum sea surface temperature in the TEP, and (d) annual maximum net primary productivity in the TEP.

Figure 3.2. Seasonal variation in a) Sea surface temperature and b) chlorophyll at Las Islas Perlas. Data collected by the authors during the study period shown in black. Historical mean daily values shown by grey dots. In a), dark and light shaded areas represent the historical mean daily values ± 1 SD and 2 SD, respectively. Historical data were provided by the Physical Monitoring program at the Smithsonian Tropical Research Institute. Images shown in c) and d) are of benthic algal growth in Las Islas Perlas during the non-upwelling and upwelling seasons, respectively. Photo credit: Nicole Knight.

Figure 3.3. Diet data from three species of damselfish collected from Isla Pacheca and Islote Saboga during the non-upwelling and upwelling seasons. a) Isotope signatures from white muscle tissue of damselfish and three food sources. Ellipses include data pooled across sites and seasons. b) Principal components analysis of presence/absence stomach content data from damselfish. Each point represents the stomach contents of one fish. Ellipses include data pooled across sites and separated by season.

Figure 3.4. Damselfish ln-transformed gut length (GL; a-c), digesta mass (DM; d-f), and gut-removed body mass (BM; g-i) during the non-upwelling (light blue) and upwelling (green) seasons against ln-transformed standard length (SL). *Abudefduf troschelii* is represented in panels a, d, and g; *Microspathodon dorsalis* in panels b, e,

and h; *Stegastes flavilatus* in panels c, f, and i. Points show real data from Isla Pacheca (circles) and Islote Saboga (triangles); lines show the model projected means for Pacheca (solid) and Saboga (dashed); shaded areas show the 95% credibility intervals.

Figure 3.5. Parameter estimate distributions generated by the full R-INLA models (including all fixed effects and a random spatial effect). Distributions reflect associations between standardized environmental predictors on biomass (yellow) and probability of presence (pink). Effects with 95% credibility intervals that do not overlap 0 are indicated by an asterisk.

Figure 3.6. Heat maps with contour lines showing ln-transformed predicted damselfish biomass across combinations of environmental variables. Heat maps generated from posterior values of INLA2 models (models including credible environmental predictors and a random spatial effect) a-b) *M. dorsalis*, c) *Abudefduf troschelii*, d) *S. flavilatus*.

Figure 3.7. Heat maps with contour lines showing probability of *M. dorsalis* presence across combinations of environmental variables. Heat maps generated from posterior values of INLA2 models (models including credible environmental predictors and a random spatial effect).

List of Tables

Table 2S3.1. Gut passage time model definitions. All models include species ID as a random effect.

Table 2S3.2. Prior definitions for all gut passage time models.

Table 2S3.3. Results of leave-one-out pareto-smoothed importance sampling (LOO-PSIS) model evaluations for gut passage time. GP.2 was selected as the best fitting model. All models include species ID as a random effect. elpd_loo is the expected log predictive density, p_loo is the effective number of parameters, and loo_ic is the LOO information criterion. All bracketed values are standard error estimates. Guidelines for interpreting these criteria is available at https://mc-stan.org/loo/reference/loo-glossary.html.

Table 2S3.4. Parameter estimates for the three models describing gut passage time of marine fishes. Square brackets indicate 95% confidence intervals.

Table 2S4.1. Absorption efficiency model definitions. All models include species ID and study ID as random effects.

Table 2S4.2. Prior definitions for all absorption efficiency models.

Table 2S4.3. Results of leave-one-out Pareto-smoothed importance sampling (LOO-PSIS) model evaluations for the absorption efficiency of marine fishes. AE.1

was selected as the best fitting model. All models include component and method as fixed effects and species ID as a random effect. elpd_loo is the expected log predictive density, p_loo is the effective number of parameters, and loo_ic is the LOO information criterion. All bracketed values are standard error estimates. Guidelines for interpreting these criteria is available at https://mc-stan.org/loo/reference/loo-glossary.html.

Table 2S4.4. Parameter estimates for the four models describing absorption efficiency of marine fishes. Square brackets indicate 95% confidence intervals.

Table 2S5.1. Gut length model definitions. All models include study ID and phylogenetic order as random effects.

Table 2S5.2. Prior definitions for all gut length models.

Table 2S5.3. Results of leave-one-out pareto-smoothed importance sampling (LOO-PSIS) model evaluations for the gut length of marine fishes. GL.2 was selected as the best fitting model. All models include ln(length) as a fixed effect and phylogenetic order as a random effect. elpd_loo is the expected log predictive density, p_loo is the effective number of parameters, and loo_ic is the LOO information criterion. All bracketed values are standard error estimates. Guidelines for interpreting these criteria is available at https://mc-stan.org/loo/reference/loo-glossary.html.

Table 2S5.4 Parameter estimates for the four models describing gut length of marine fishes. Square brackets indicate 95% confidence intervals.

Table 2S6.1. Prior definitions for all food composition models.

Table 2S5.4 Parameter estimates for the four models describing differences in nutrient concentration between animal (intercept) and plant food items. Square brackets indicate 95% confidence intervals. Each row represents a separate model. Estimates for all components except energy are logit-transformed.

Table 3.1. Sample sizes (n) and average body size (TL = total length, SL = standard length, wet mass) of fish collected during the upwelling and non-upwelling seasons in Las Perlas Archipelago, Panama. Standard deviations given in brackets.

Table 3.2. Estimated WAIC, AUC, and RMSE values for the INLA models built to describe occupancy and biomass of *Abudefduf troschelii*, *Stegastes flavilatus*, and *Microspathodon dorsalis* across the Tropical Eastern Pacific. INLA0 has no random spatial effect and the full set of fixed effects, INLA1 has a random spatial effect and the full set of fixed effects, and INLA2 has a random spatial effect and predictors that were identified as important in the INLA1 models. Improved model fit is indicated by lower WAIC scores, higher AUC scores, and lower RMSE scores. Only biomass was modelled for *S. flavilatus*, so no AUC score is presented.

Table 3.A.1. Frequency of occurrence (%) of food items consumed by damselfishes collected during the non-upwelling (N-UP) and upwelling (UP) seasons.

List of abbreviations

AUC – area under receiver curve
BM – body mass
DM – digesta mass
GL – gut length
INLA – Integrated nested Laplace approximation
LOO-CV – leave-one-out cross validation
LOO-PSIS – leave-one-out pareto-smoothed importance sampling
NPP – net primary productivity
RLS – Reef Life Survey
SST – sea surface temperature
TCH – Temperature constraint hypothesis
TEP – Tropical Eastern Pacific

Acknowledgements

I wish to acknowledge that this thesis was conducted on the traditional lands of indigenous peoples from across the Americas, including the Bokota, the Kanien'kehà:ka, and the Musqueam, among others. I am deeply grateful for the opportunity to experience and better understand the natural systems in these lands.

I thank my supervisors, Andrew Altieri and Frédéric Guichard, for their unwavering support, patience, and kindness throughout my doctoral degree. Andrew and Fred, you’re both incredible scientists, and I’m deeply grateful that I got to learn from both of you. I look forward to transitioning from your delinquent student who never sends you drafts on time to your esteemed collaborator who never sends you drafts on time.

I also want to thank my committee members, Lauren Chapman and Andrew Hendry, who provided valuable feedback, encouragement, and advice over the many years of this program.

I thank the wonderful organizers of and participants in the McGill Graphos program, which helped me immeasurably throughout the process of writing this thesis. I particularly want to acknowledge Alexandra Bacopoulos-Viau, whose kindness, support, and wisdom made my thesis and my thesis-writing life bearable.

Mary O’Connor, you were the first person to give me the chance to be a scientist, and the first person to show me what it means to do great science. You helped to set me on this path, and I can never thank you enough.

Angela Choi, it’s a gift to have a friend that I love and admire as much as you. I look forward to a lifetime of being doctors together.

Viky Frühling, thank you for all of your help and friendship- you made every day of work more fun.

Katie Grabowski, your friendship and support has meant the world to me these past few years. Here’s to many more years of friendship and science.

Suni Hope-Johnston, I could not have done this without your constant kindness, support, and friendship. You have been such a source of strength, and I am so grateful.

Amy and Scott Hughes, I’m so grateful for your continued love and support, no matter how far apart we are or how bad I am at promptly returning text messages. You are my lifelong friends, and I love you both.

Chantal Hutchinson- your kindness, empathy and courage helped me more than I can say. I am forever grateful.

Matthieu Leray, mi abuelito, thank you for your incredible generosity, wisdom, and silliness over the years. Your work ethic and scientific vision inspire me.

Tracy Luong, you've been my dear friend for almost twenty years now. I can't imagine getting through this process without you, and I can't imagine my life without you. I look forward to retiring in Tofino together, so we can kayak with sea lions.

Tess Morelli, I'm so grateful for all of your help and for the chance to work with you. You're an amazing person and researcher, and I can't wait to see what you do next.

Tianna Peller, may we have many, many years of discussing science over a pitcher of Cheval Blanc. You're as wonderful a friend as you are a scientist.

Andrew Sellers, you are the weirdest, most delightful person to work with. My thesis and I wouldn't be the same without your expertise, field skills, or friendship.

Sara Swaminathan, collaborating with you has been a true joy. I hope we continue to be friends and colleagues for many years to come.

To all of my fellow grad students over the years- Marisol, Anne-Sophie, Léa, Ananda, Betzi, José, Brandon, Perry, Nicole, Adrienne, Lucía, Patrick, Kaleigh, Maggie, Alex, Félix, Brendon, Jake, Julien, Max, and many more wonderful people than I can list here- your friendship and support have made this long process bearable. I hope to have many more opportunities to work with you all.

I want to thank the kind and helpful administrative and support staff at McGill University, the Smithsonian Tropical Research Institute, the University of Florida, and the University of British Columbia. None of this research would have been possible without you.

To my aunties Patty Canil and Diane Adamo, I hope you know how much your love and support mean to me. Thank you for the calls, the e-mails, the visits and the wisdom. I'm so grateful that you are my family.

To my grandfather, Clifford N. Sutts, thank you for always believing in me and cheering me on. I love you.

To my grandparents who are no longer with us- Joyce Knight, Maurice Knight, and Mary Sutts- I have carried your love and memories with me throughout this difficult process, and I am so grateful for our time together. You are missed every day.

To my beloved dogs, Lucy and Gracie: you barked, ate my furniture, and crawled on my laptop in a series of valiant efforts to prevent me from writing. I probably could have submitted my thesis six months earlier without you. I love you.

Cassandra Knight, thank you for your love, support, and jokes. You're a wonderful sister, and I'm truly grateful to have you in my life. That said, I expect you to read this thesis in full, and will be quizzing you on it later.

Finally, Jordan and Roland Knight. I don't know how to thank you in just a few lines, or how to express my gratitude for everything that you've done for me. So instead, I dedicate my thesis to you- because not a word of it could have been written without your unconditional love and support.

Preface

Thesis format and style

This is a manuscript-based thesis. It contains a general introduction, connecting statements, and a general discussion and conclusions to show each chapter contributes to a unified whole. The literature review for this thesis is incorporated into both the general introduction (~10 pages) and the three manuscripts listed here (~12 pages):

1) A global meta-analysis of temperature effects on marine fishes' digestion across trophic groups
2) Damselfish performance predicts distribution across a tropical upwelling mosaic
3) Coral degradation differentially affects invertebrate trophic functional groups

The first manuscript was published in *Global Ecology and Biogeography.* The second manuscript is in preparation for submission to *Ecography.* The third manuscript is in preparation for submission to *Coral Reefs.*

Contribution to original knowledge

Contributions from Chapter 2

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

- I conducted the first systematic, global test of the Temperature Constraint Hypothesis (TCH), which proposes that herbivorous fishes are rare at high latitudes because low temperatures impede plant digestion.
- I show that existing evidence to support the TCH is weak, despite the frequency with which it is invoked as an explanation for large-scale patterns in fish biodiversity.
- To my knowledge, I demonstrate for the first time that fish species in coldwater ecosystems have shorter guts than species in warmwater ecosystems, and that this pattern is likely driven by latitudinal differences in diet quality.

Contributions from Chapter 3

Damselfish performance predicts distribution across a tropical upwelling mosaic

- I test for the first time how seasonal upwelling influences the feeding ecology and physiology of tropical fishes, and whether the effects of upwelling on individual fishes predict patterns of distribution.

- I demonstrate that seasonal upwelling generally benefits tropical damselfishes, and that digestive plasticity plays a role in allowing individuals to benefit from seasonal variation in temperature and resource availability.
- I show that the physiological effects of upwelling predict patterns of distribution across species.

Contributions from Chapter 4

Coral degradation differentially affects invertebrate trophic functional groups

- I characterized trophic composition of coral-associated invertebrate assemblages using one of the highest resolution datasets of which I am aware
- I demonstrate how the biomass of different trophic groups is associated with overall reef health
- I reveal associations between niche breadth and patterns of distribution, and how these associations vary across trophic groups.

Contributions of co-authors

This thesis is the product of research that I led throughout its development, execution, and write-up. I am the primary author for all chapters of the thesis. My supervisors, Andrew Altieri and Frédéric Guichard, contributed to each stage of this research by helping develop the initial research questions, plan and troubleshoot study design and data collection, and analyze, interpret, and write up the data. Each research chapter was accomplished with the help of additional co-authors; their contributions are listed below.

Chapter 2: I developed the research questions and analyses in this chapter with Andrew Altieri and Frédéric Guichard. I collected and analyzed the data used in this chapter, and Andrew Altieri and Frédéric Guichard provided feedback on the execution and interpretation of all statistical analyses. I wrote the first draft of this chapter, and Andrew Altieri and Frédéric Guichard contributed substantially to all of the many, many, many, subsequent drafts.

Chapter 3: The research questions associated with this chapter were initially developed with Andrew Sellers, with substantial input from Andrew Altieri and Frédéric Guichard. The fieldwork was conducted primarily by myself and Andrew Sellers, and the laboratory work was planned and conducted by myself, Andrew Sellers, and Matthieu Leray. Mark Torchin provided feedback and guidance on the field and laboratory work. I conducted the statistical analyses, and all co-authors provided feedback and assistance with interpretation. I wrote the first draft of the chapter, and all co-authors contributed to subsequent drafts.

Chapter 4: The research questions associated with this chapter were first developed with Matthieu Leray, and subsequently refined and improved in discussions with Andrew Altieri and Frédéric Guichard. Matthieu Leray was the primary leader of the field work associated with collecting invertebrate abundance and biomass data; I was responsible for assisting with this field work and collecting samples of invertebrate tissues for isotope analysis. I conducted the isotope analyses under the supervision and guidance of David M. Baker. I conducted a literature review of invertebrate species' feeding ecology with Tess Morelli. I designed and implemented all statistical analyses. All co-authors provided feedback on the implementation and interpretation of all statistical analyses. I wrote the first draft of this chapter, and all co-authors contributed to subsequent drafts.

Chapter 1: General introduction and literature review

Humans have sought to understand the distribution of living organisms for hundreds of years (Buffon & Smellie, 1785; Humboldt & Bonpland, 1805; Linné, 1781; Lomolino et al., 2004; Wallace, 1876). These efforts have led to crucial insights about natural selection and evolution (Darwin, 1859; Darwin et al., 1858), how individuals relate to their environment (Grinnell, 1917), and coexistence and community assembly (Cody & Diamond, 1975; Hutchinson, 1959). Patterns of distribution, whether of genes, traits, populations, or species, provide opportunities to develop, test, and refine hypotheses in virtually every area of ecological and evolutionary research *because* they reflect the integrated outcomes of many ecological and evolutionary processes. Conversely, disentangling the relationships between species' ecology, evolutionary history, and distribution is a fraught undertaking that requires the careful collection and synthesis of evidence across scales of organization.

Patterns of distribution originate from individuals interacting with their local environment and other organisms. This idea was presented in the early 20th century by Joseph Grinnell, who in a series of papers systematically compared the ecological requirements of several species with the characteristics of the environments in which those species were or were not found (Grinnell, 1904, 1917b, 1917a). Grinnell noted that a wide range of ecological factors may limit the distribution of a species, including available habitat and food, temperature, competition, and predation, and that these factors are complex and interrelated (Grinnell, 1917a). The concept that arose from Grinnell's work, the ecological niche, has been variously defined and revised (Chase & Leibold, 2009; R. H. Johnson, 1910), but from here on I refer to the niche sensu Hutchinson, i.e., as an n-dimensional hypervolume describing the conditions that allow a species to persist indefinitely in the absence of a competing species (Hutchinson, 1957).

The niche as defined above encompasses a broad range of conditions, including favourable conditions under which a species is able to maintain high abundance, and less favourable conditions under which it is able to persist, but at much lower abundances (Brown, 1984; Hutchinson, 1978; Weber et al., 2017). This variation in abundance reflects the complex responses of individuals to their environment, including local food resources, climate, and habitat availability (M. Kearney & Porter, 2009; Soberon & Nakamura, 2009), as well as other biotic interactions such as competition, predation, and facilitation (Araujo & Rozenfeld, 2014; Boulangeat et al., 2012; Chave et al., 2002). It is expected that individuals living under highly suitable conditions will have improved performance, which may include increased rates of survival, resource uptake, growth, and reproduction, and that this improved performance results in increased local abundance (Brambilla & Ficetola, 2012; Duncan et al., 2020; Lee-Yaw et al., 2016; Lunghi et al., 2018; Melis et al., 2010; Polis & Hurd, 1995). However, it may be difficult to identify a) the effects of environmental and biotic variation on different aspects of individual performance, and b) what aspects of individual performance determine patterns of local abundance.

A crucial aspect of individual performance is the uptake and digestion of resources. For a species to persist in a given environment in the absence of immigration, individuals of that species must take up enough resources to meet their demands for respiration, growth, and reproduction. Whether individuals can meet these demands is determined by interactions between their physiology and the local environment. Consumers must be able to locate, subdue, and digest available resources, and environmental conditions such as temperature and habitat complexity can modify the success of these activities (Grabowski et al., 2008; Grady et al., 2019; Voigt & Hovel, 2019). Consumers that are well-adapted to their environment and can meet or exceed their resource demands can have increased rates of survival, growth, and reproduction, resulting in increased abundance (Brambilla & Ficetola, 2012; Lunghi et al., 2018; Polis & Hurd, 1995; Weber et al., 2017).

In this introduction, I explore several topics that pertain to patterns of feeding, performance, and distribution in marine consumers. First, I discuss how broad-scale oceanographic processes affect virtually all aspects of marine invertebrate ecology, and the advantages of assessing the impacts of these processes at different scales. I then review some strengths and weaknesses of species distribution models (and similar techniques), and why physiological data may improve our inference from these models. I review the importance of temperature and biogenic habitat availability to the performance and distribution of consumers. Finally, I provide a brief overview of this thesis.

Oceanographic processes set patterns of distribution in marine ecosystems

Broad-scale oceanographic processes spanning tens to thousands of kilometers modify a broad suite of environmental conditions, including temperature, resource availability, salinity, oxygen saturation, and patterns of circulation (Kämpf & Chapman, 2016; Peller et al., 2021; Stewart, 2009). These environmental conditions have profound effects on the physiology and distribution of organisms, modifying spatial patterns of resource uptake and demand, reproduction, stress, and dispersal (Camargo-Cely & Collin, 2019; Gaylord & Gaines, 2000; Guzmán-Agüero et al., 2013; M. D. Johnson et al., 2021; Kroeker et al., 2016; McCabe & Navarrete, 2018; Menge et al., 2003, 2004; Morgan, 2014; Robertson, 1990; Salo et al., 2014; Sanford, 2002). Unsurprisingly, environmental variation driven by these oceanographic processes is also strongly associated with patterns of distribution of marine organisms (Grady et al., 2019; Sunday et al., 2012; Waldock et al., 2019). However, understanding the links between oceanographic processes, individual physiology, and species' distributions is difficult for several reasons, including a) the enormous spatial scales over which oceanographic processes occur, b) the complex effects of environmental variation on different aspects of individual performance, and c) complicating factors at the local scale, such as phenotypic plasticity and biotic interactions.

We can test the mechanisms linking broad-scale oceanographic processes and patterns of species distribution at different scales, with different advantages and disadvantages to each. Working at the local scale typically allows for more complex, higher-resolution data collection, either through observations or experimental work. However, it is likely that the transferability of these findings to other sites or regions is limited, because broad-scale variation modifies local processes. For example, the relative importance of predation and recruitment as determinants of the distribution of sessile filter feeders in the Gulf of Maine depends on levels of wave exposure and differences in the coastal oceanography of the northern and southern Gulf of Maine (Bryson et al., 2014). In contrast, larger-scale studies have their own limitations, including logistical difficulties, low replication, and an inability to manipulate certain factors (Menge et al., 2004). However, by combining small- and large-scale perspectives, we can make new, more powerful inferences about the factors shaping species' distributions (Brown, 1995; Eme & Bennett, 2008; Knight et al., 2021; Lunghi et al., 2018; Sellers et al., 2021).

The successes and limitations of species distribution models

“Regression is indeed an oracle, but a cruel one. It speaks in riddles and delights in punishing us for asking bad questions.” -Richard McElreath (2020)

A common suite of large-scale techniques to understand the spatial distribution of species tests for associations between species’ occupancy, abundance, and local environmental conditions. These techniques, including species distribution models (SDMs), ecological niche models (ENMs), and habitat suitability models (HSMs), can contribute meaningfully to a variety of goals, such as understanding the environmental drivers that shape species’ ranges and patterns of abundance (Duncan et al., 2020; Lunghi et al., 2018; Waldock et al., 2019; Young & Carr, 2015), assessing the likely effects of climate change on species’ distributions (Braschler et al., 2020; M. R. Kearney et al., 2010; Sunday et al., 2015), developing management plans for species recovery and restoration (Evans et al., 2015; Regan et al., 2008), or predicting the likely spread of invasive species or diseases (DeVaney et al., 2009; Petitpierre et al., 2017).

However, the success of SDMs and similar techniques to meet these goals depends, to varying degrees, on making accurate inferences about species’ niches

(Guisan et al., 2017; Peterson & Soberón, 2012). There are many reasons why an SDM may not reflect a species' niche, including the coarse scale of broadly available environmental data, unidentified causal relationships involving model predictors, the existence of sink populations, or dispersal limitations (Lee-Yaw et al., 2022). These confounding effects can make it difficult both to make ecological inferences and to predict species' occurrence or abundance at new sites (Bahn & McGill, 2007; Elith & Graham, 2009; Elith & Leathwick, 2009; Lee-Yaw et al., 2022). One promising avenue to disentangle these relationships is to integrate physiological or ecological data, which can provide more direct and accurate understandings of species' niches, with patterns of species distributions. For example, transplant experiments that test individual performance in different environments can distinguish between niche and dispersal constraints on species' range limits (Hargreaves et al., 2014; Lee-Yaw et al., 2016). Similarly, lab estimates of thermal tolerance have been combined with characterizations of the sub-lethal effects of low temperatures to better understand what sets geographic limits in range-expanding fishes (Beck et al., 2016; Booth et al., 2018).

The importance of temperature in marine ecosystems

Among marine ectotherms, the thermal environment is one of the most impactful constraints on individual performance (Ashton et al., 2022; Barneche et al., 2009; Dell et al., 2014; Knight et al., 2021; O'Connor, 2009) and distribution

(Grady et al., 2019; Sunday et al., 2010; Waldock et al., 2019). Ectotherms cannot regulate their temperature physiologically, and subtidal species have few opportunities for behavioural thermoregulation, e.g., basking, so their metabolism is set by the temperature of the surrounding water. Furthermore, the temperature dependence of autecological rates scales up to impact higher levels of ecological organization, including interspecific interactions (Dell et al., 2014; Kordas et al., 2011; O'Connor, 2009; Sellers et al., 2021), population dynamics (Bernhardt et al., 2018; Liebhold et al., 2004), and patterns of species distribution (Grady et al., 2019; Sunday et al., 2012; Waldock et al., 2019). However, increasing complexity with scale can make the effects of temperature at higher levels of organization weaker and less predictable.

The effects of temperature on a physiological process such as respiration are typically very predictable: rates increase at a near-exponential rate with increasing temperature up to a peak, then decline rapidly (Brown & Sibly, 2012). However, the effects of temperature on different physiological processes occurring within the same organism may exhibit different responses, leading to effects on performance that may not be easily predicted (e.g., Floeter et al., 2005; Lemoine & Burkepile, 2012; Marshall et al., 2011). For example, over the range of normal temperatures experienced by *L. variegatus*, respiration rate increases exponentially with temperature, but feeding rate exhibits a unimodal relationship, and absorption efficiency is temperature-invariant (Lemoine & Burkepile, 2012). These parameters, when combined to estimate ingestion efficiency, show a substantial decrease in ingestion efficiency at high temperatures, at which respiration rates are high and feeding rates are low (Lemoine & Burkepile, 2012). A meta-analysis from this same study showed that thermal dependencies of ingestion efficiency are likely common, but the strength and direction of these dependencies can vary (Lemoine & Burkepile, 2012).

Consumers depend on biogenic habitats

Many marine ecosystems are defined by the availability of biogenic habitats, including corals, seagrasses, mangroves, and mussels, which support productive and diverse consumer assemblages (Knight et al., 2015; Nguyen et al., 2020; Paquette et al., 2019; Saldana et al., 2021; Thomsen et al., 2018; Vaslet et al., 2012; Whippo et al., 2018). Consumer survival and performance improves in these biogenic habitats because they provision both food and shelter (Kuempel & Altieri, 2017; Lewis & Smith, 2019; Sides & Woodley, 1985), they typically also support higher consumer biomass and diversity than structurally simple habitats (Nelson et al., 2016; Saldana et al., 2021). However, as these habitats are degraded or lost, the effects on the recruitment, abundance, and diversity of consumer communities vary depending on both the type of habitat and the nature of its relationship to consumers (Byrnes et al., 2011; Campbell et al., 2018; Nelson et al., 2016; Saldana et al., 2021; Tomas et al., 2015). Given the rapid rate of loss of biogenic foundation species around the globe, understanding how this loss affects the performance and distribution of consumer communities is becoming increasingly urgent.

Thesis overview

In this thesis, I seek to explain how environmental variation in temperature, resource availability, and habitat quality impact the feeding ecology, performance, and abundance of marine ectotherms. I then test whether these effects scale up to impact higher levels of ecological organization, including the global distribution of herbivorous fishes (Chapter 2), the distribution of tropical damselfishes in a highly seasonal, heterogeneous environment (Chapter 3), and the functional composition of coral-associated invertebrates (Chapter 4). Across all three chapters, I show how environmental variation shapes the ecology and physiology of marine species, and how we can leverage this variation to better understand patterns of distribution and community structure.

In the second chapter of my thesis, I tested the temperature constraint hypothesis, which proposes that herbivorous fishes are rare at high latitudes because low temperatures impede the digestion of plant material (Gaines & Lubchenco, 1982; Trip et al., 2014). To test this hypothesis, I collected and analyzed a dataset of 99 published studies to quantify the relationship between temperature and the gut passage time, absorption efficiency, and gut length of fishes consuming different diets. I found that although the gut passage time of herbivorous fishes is disproportionately long for species in cold environments, this relationship appears to be driven by the high representation of fish that rely on hindgut fermentation in temperate ecosystems, which typically have longer gut passage times (Clements et al., 2014). Because herbivorous fishes that use hindgut fermentation have symbioses that likely provide nutritional benefits to the host (Clements et al., 2009; Lilburn et al., 2001), this increase in gut passage time at low temperatures may not constitute a disadvantage, but rather a trade-off. However, it is unclear whether fermentation is the only digestive mechanism that performs well at low temperatures, as the digestive strategies of most herbivorous fishes have not been clearly documented. Understanding the geographic distribution and performance of different digestive strategies, as well as the phylogeography of herbivory, may constitute a promising avenue to explain the global distribution of herbivorous fishes.

The third chapter of my thesis tests whether and how understanding environmental controls on species' feeding and digestive performance can inform species distribution models. Specifically, I test how seasonal upwelling influences the feeding, digestion, body condition and distribution of three tropical damselfish species consuming different diets. I predicted that upwelling could improve damselfishes' physiological condition because increased resource availability and decreased metabolic demands would allow individuals to accumulate more mass; alternatively, I predicted that upwelling would cause damselfishes to have worse physiological condition due to cold stress and slow rates of digestion. I further predicted that species that exhibited improved physiological performance under upwelling conditions would exhibit increased probability of occupancy and biomass under strong upwelling conditions. My results reveal that damselfish are generally able to take advantage of increased resource availability during seasonal upwelling, in part by lengthening their guts and increasing their digestive capacity. Further, my distributional models showed that species that performed well under upwelling conditions had higher probability of occupancy and biomass under strong upwelling conditions, consistent with the hypothesis that more favourable environmental conditions lead to increased abundance.

In the fourth chapter of my thesis, I characterized how the functional composition of coral-associated invertebrate assemblages changes along a gradient of habitat degradation, and estimated dominance and niche breadth (using isotopic data) in common invertebrate consumers. My results show that the biomass of trophic functional groups responds differently to the degradation of coral reef habitat, likely due to the different ways they depend on coral. All functional groups tended to be dominated by a small number of species, but this tendency was particularly pronounced in deposit feeders and grazers. Altogether, these findings suggest that as Caribbean coral habitats continue to degrade, the relative representation of different functional groups will change. Further, the relative dominance of only a handful of species of consumers indicates that some functions provided by these assemblages (algal consumption, detrital consumption) are particularly vulnerable to species loss.

References

Araujo, M. B., & Rozenfeld, A. (2014). The geographic scaling of biotic interactions. *ECOGRAPHY*, *37*(5), 406–415. https://doi.org/10.1111/j.1600-0587.2013.00643.x

Ashton, G. V., Freestone, A. L., Duffy, J. E., Torchin, M. E., Sewall, B. J., Tracy, B., Albano, M., Altieri, A. H., Altvater, L., Bastida-Zavala, R., Bortolus, A., Brante, A., Bravo, V., Brown, N., Buschmann, A. H., Buskey, E., Barrera, R. C., Cheng, B., Collin, R., … Ruiz, G. M. (2022). *Predator control of marine communities increases with temperature across 115 degrees of latitude*.

Bahn, V., & McGill, B. J. (2007). Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography*, *16*(6), 733–742. https://doi.org/10.1111/j.1466-8238.2007.00331.x

Barneche, D. R., Floeter, S. R., Ceccarelli, D. M., Frensel, D. M. B., Dinslaken, D. F., Mário, H. F. S., & Ferreira, C. E. L. (2009). Feeding macroecology of territorial damselfishes (Perciformes: Pomacentridae). *Marine Biology*, *156*(3), 289–299. https://doi.org/10.1007/s00227-008-1083-z

Beck, H. J., Feary, D. A., Fowler, A. M., Madin, E. M. P., & Booth, D. J. (2016). Temperate predators and seasonal water temperatures impact feeding of a range expanding tropical fish. *Marine Biology*, *163*(4), 70. https://doi.org/10.1007/s00227-016-2844-8

Bernhardt, J. R., Sunday, J. M., Thompson, P. L., & O'Connor, M. I. (2018). Nonlinear averaging of thermal experience predicts population growth rates in a thermally variable environment. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1886), 20181076. https://doi.org/10.1098/rspb.2018.1076

Booth, D. J., Beretta, G. A., Brown, L., & Figueira, W. F. (2018). Predicting Success of Range-Expanding Coral Reef Fish in Temperate Habitats Using Temperature-Abundance Relationships. *Frontiers in Marine Science*, *5*. https://doi.org/10.3389/fmars.2018.00031

Boulangeat, I., Lavergne, S., Van Es, J., Garraud, L., & Thuiller, W. (2012). Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. *JOURNAL OF BIOGEOGRAPHY*, *39*(1), 204–214. https://doi.org/10.1111/j.1365-2699.2011.02581.x

Brambilla, M., & Ficetola, G. F. (2012). Species distribution models as a tool to estimate reproductive parameters: A case study with a passerine bird species. *Journal of Animal Ecology*, *81*(4), 781–787. https://doi.org/10.1111/j.1365-2656.2012.01970.x

Braschler, B., Duffy, G. A., Nortje, E., Kritzinger-Klopper, S., du Plessis, D., Karenyi, N., Leihy, R. I., & Chown, S. L. (2020). Realised rather than fundamental thermal niches predict site occupancy: Implications for climate change forecasting. *Journal of Animal Ecology*, *89*(12), 2863–2875. https://doi.org/10.1111/1365-2656.13358

Brown, J. H. (1984). On the Relationship between Abundance and Distribution of Species. *The American Naturalist*, *124*(2), 255–279.

Brown, J. H. (1995). *Macroecology*. University of Chicago Press.

Brown, J. H., & Sibly, R. M. (2012). The Metabolic Theory of Ecology and Its Central Equation. In *Metabolic Ecology* (pp. 21–33). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781119968535.ch2

Bryson, E. S., Trussell, G. C., & Ewanchuk, P. J. (2014). Broad-scale geographic variation in the organization of rocky intertidal communities in the Gulf of Maine. *Ecological Monographs*, *84*(4), 579–597. https://doi.org/10.1890/13-1106.1

Buffon, G. L. L., & Smellie, W. (1785). *Natural history, general and particular* (2nd ed., pp. 1–550). Printed for W. Strahan and T. Cadell. https://doi.org/10.5962/bhl.title.32809

Byrnes, J. E., Reed, D. C., Cardinale, B. J., Cavanaugh, K. C., Holbrook, S. J., & Schmitt, R. J. (2011). Climate-driven increases in storm frequency simplify kelp forest food webs: CLIMATE CHANGE AND KELP FOREST FOOD WEBS. *Global Change Biology*, *17*(8), 2513–2524. https://doi.org/10.1111/j.1365-2486.2011.02409.x

Camargo-Cely, A., & Collin, R. (2019). Combined effects of temperature, salinity, and diet simulating upwelling and nonupwelling seasons alter life-history characteristics of a tropical invertebrate. *Ecology and Evolution*, *9*(24), 14368–14378. https://doi.org/10.1002/ece3.5873

Campbell, J. E., Altieri, A. H., Johnston, L. N., Kuempel, C. D., Paperno, R., Paul, V. J., & Duffy, J. E. (2018). Herbivore community determines the magnitude and mechanism of nutrient effects on subtropical and tropical seagrasses. *Journal of Ecology*, *106*(1), 401–412. https://doi.org/10.1111/1365-2745.12862

Chase, J. M., & Leibold, M. A. (2009). Ecological Niches: Linking Classical and Contemporary Approaches. In *Ecological Niches*. University of Chicago Press. https://doi.org/10.7208/9780226101811

Chave, J., Muller-Landau, H. C., & Levin, S. A. (2002). Comparing classical community models: Theoretical consequences for patterns of diversity. *AMERICAN NATURALIST*, *159*(1), 1–23. https://doi.org/10.1086/324112

Clements, K. D., Angert, E. R., Montgomery, W. L., & Choat, J. H. (2014). Intestinal microbiota in fishes: What's known and what's not. *Molecular Ecology*, *23*(8), 1891–1898. https://doi.org/10.1111/mec.12699

Clements, K. D., Raubenheimer, D., & Choat, J. H. (2009). Nutritional ecology of marine herbivorous fishes: Ten years on. *Functional Ecology*, *23*(1), 79–92. https://doi.org/10.1111/j.1365-2435.2008.01524.x

Cody, M., & Diamond, J. (1975). *Ecology and Evolution of Communities:* Belknap Press.

Darwin, C. (1859). *On the origin of species by means of natural selection*. London : J. Murray.

Darwin, C., Gray, A., & Wallace, A. R. (1858). *On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection.* Linnean Society. https://catalog.hathitrust.org/Record/012453015

Dell, A. I., Pawar, S., & Savage, V. M. (2014). Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *The Journal of Animal Ecology*, *83*(1), 70–84. https://doi.org/10.1111/1365-2656.12081

DeVaney, S. C., McNyset, K. M., Williams, J. B., Peterson, A. T., & Wiley, E. O. (2009). A Tale of Four "Carp": Invasion Potential and Ecological Niche Modeling. *PLOS ONE*, *4*(5), e5451. https://doi.org/10.1371/journal.pone.0005451

Duncan, M. I., James, N. C., Potts, W. M., & Bates, A. E. (2020). Different drivers, common mechanism; the distribution of a reef fish is restricted by local-scale oxygen and temperature constraints on aerobic metabolism. *Conservation Physiology*, *8*(1), coaa090. https://doi.org/10.1093/conphys/coaa090

Elith, J., & Graham, C. H. (2009). Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography*, *32*(1), 66–77. https://doi.org/10.1111/j.1600-0587.2008.05505.x

Elith, J., & Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Eme, J., & Bennett, W. A. (2008). Low temperature as a limiting factor for introduction and distribution of Indo-Pacific damselfishes in the eastern United States. *Journal of Thermal Biology*, *33*(1), 62–66. https://doi.org/10.1016/j.jtherbio.2007.10.003

Evans, T. G., Diamond, S. E., & Kelly, M. W. (2015). Mechanistic species distribution modelling as a link between physiology and conservation. *Conservation Physiology*, *3*(1), cov056. https://doi.org/10.1093/conphys/cov056

Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddack, M. J., & Horn, M. H. (2005). Geographical gradients of marine herbivorous fishes: Patterns and processes. *Marine Biology*, *147*(6), 1435–1447. https://doi.org/10.1007/s00227-005-0027-0

Gaines, S., & Lubchenco, J. (1982). A Unified Approach to Marine Plant-Herbivore Interactions .2. Biogeography. *Annual Review of Ecology and Systematics*, *13*, 111–138. https://doi.org/10.1146/annurev.es.13.110182.000551

Gaylord, B., & Gaines, S. D. (2000). Temperature or Transport? Range Limits in Marine Species Mediated Solely by Flow. *The American Naturalist*, *155*(6), 769–789. https://doi.org/10.1086/303357

Grabowski, J. H., Hughes, A. R., & Kimbro, D. L. (2008). Habitat Complexity Influences Cascading Effects of Multiple Predators. *Ecology*, *89*(12), 3413–3422. https://doi.org/10.1890/07-1057.1

Grady, J. M., Maitner, B. S., Winter, A. S., Kaschner, K., Tittensor, D. P., Record, S., Smith, F. A., Wilson, A. M., Dell, A. I., Zarnetske, P. L., Wearing, H. J., Alfaro, B., & Brown, J. H. (2019). Metabolic asymmetry and the global diversity of marine predators. *Science*, *363*(6425). https://doi.org/10.1126/science.aat4220

Grinnell, J. (1917). Field Tests of Theories Concerning Distributional Control. *The American Naturalist*, *51*(602), 115–128. https://doi.org/10.1086/279591

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat Suitability and Distribution Models: With Applications in R*. Cambridge University Press. https://doi.org/10.1017/9781139028271

Guzmán-Agüero, J. E., Nieves-Soto, M., Hurtado, M. Á., Piña-Valdez, P., & Garza-Aguirre, M. del C. (2013). Feeding physiology and scope for growth of the oyster Crassostrea corteziensis (Hertlein, 1951) acclimated to different conditions of temperature and salinity. *Aquaculture International*, *21*(2), 283–297. https://doi.org/10.1007/s10499-012-9550-4

Hargreaves, A. L., Samis, K. E., & Eckert, C. G. (2014). Are Species' Range Limits Simply Niche Limits Writ Large? A Review of Transplant Experiments beyond the Range. *The American Naturalist*, *183*(2), 157–173. https://doi.org/10.1086/674525

Humboldt, A. von, & Bonpland, A. (1805). *Essai sur la géographie des plantes: Accompagné d'un tableau physique des régions équinoxiales, fondé sur des mesures exécutées, depuis le dixième degré de latitude boréale jusqu'au dixième degré de latitude australe, pendant les années 1799, 1800, 1801, 1802 et 1803 ([Reprod.]) / par Al. de Humboldt et A. Bonpland ; préf. réd. par Al. de Humboldt*. https://gallica.bnf.fr/ark:/12148/bpt6k977938

Hutchinson, G. E. (1959). Homage to Santa Rosalia or Why Are There So Many Kinds of Animals? *The American Naturalist*, *93*(870), 145–159. https://doi.org/10.1086/282070

Hutchinson, G. E. (1978). *An introduction to population ecology*. Yale University Press.

Johnson, M. D., Scott, J. J., Leray, M., Lucey, N., Bravo, L. M. R., Wied, W. L., & Altieri, A. H. (2021). Rapid ecosystem-scale consequences of acute deoxygenation on a Caribbean coral reef. *Nature Communications*, *12*(1), Article 1. https://doi.org/10.1038/s41467-021-24777-3

Johnson, R. H. (1910). *Determinate evolution in the color-pattern of the lady-beetles*. Washington, Carnegie Inst. http://archive.org/details/determinateevolu00johnuoft

Kämpf, J., & Chapman, P. (2016). *Upwelling Systems of the World*. Springer International Publishing. https://doi.org/10.1007/978-3-319-42524-5

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*(4), 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Kearney, M. R., Wintle, B. A., & Porter, W. P. (2010). Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, *3*(3), 203–213. https://doi.org/10.1111/j.1755-263X.2010.00097.x

Knight, N. S., Guichard, F., & Altieri, A. H. (2021). A global meta-analysis of temperature effects on marine fishes' digestion across trophic groups. *Global Ecology and Biogeography*, *30*(4), 795–810. https://doi.org/10.1111/geb.13262

Knight, N. S., Prentice, C., Tseng, M., & O'Connor, M. I. (2015). A comparison of epifaunal invertebrate communities in native eelgrass Zostera marina and non-native Zostera japonica at Tsawwassen, BC. *Marine Biology Research*, *11*(6), 564–571. https://doi.org/10.1080/17451000.2014.985230

Kordas, R. L., Harley, C. D. G., & O'Connor, M. I. (2011). Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. *Journal of Experimental Marine Biology and Ecology*, *400*(1), 218–226. https://doi.org/10.1016/j.jembe.2011.02.029

Kroeker, K. J., Sanford, E., Rose, J. M., Blanchette, C. A., Chan, F., Chavez, F. P., Gaylord, B., Helmuth, B., Hill, T. M., Hofmann, G. E., McManus, M. A., Menge, B. A., Nielsen, K. J., Raimondi, P. T., Russell, A. D., & Washburn, L. (2016). Interacting environmental mosaics drive geographic variation in mussel performance and predation vulnerability. *Ecology Letters*, *19*(7), 771–779. https://doi.org/10.1111/ele.12613

Kuempel, C. D., & Altieri, A. H. (2017). The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Scientific Reports*, *7*(1), Article 1. https://doi.org/10.1038/srep39670

Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergo, A. M., Noreen, A. M. E., Li, Q., Schuster, R., & Angert, A. L. (2016). A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters*, *19*(6), 710–722. https://doi.org/10.1111/ele.12604

Lee-Yaw, J. A., L. McCune, J., Pironon, S., & N. Sheth, S. (2022). Species distribution models rarely predict the biology of real populations. *Ecography*, *2022*(6), e05877. https://doi.org/10.1111/ecog.05877

Lemoine, N. P., & Burkepile, D. E. (2012). Temperature-induced mismatches between consumption and metabolism reduce consumer fitness. *Ecology*, *93*(11), 2483–2489. https://doi.org/10.1890/12-0375.1

Lewis, L. S., & Smith, J. E. (2019). Functional diversity among herbivorous sea urchins on a coral reef: Grazing rate, dietary preference, and metabolism. *Marine Ecology Progress Series*, *625*, 71–87. https://doi.org/10.3354/meps13038

Liebhold, A., Koenig, W. D., & Bjornstad, O. N. (2004). Spatial synchrony in population dynamics. *ANNUAL REVIEW OF ECOLOGY EVOLUTION AND SYSTEMATICS*, *35*, 467–490. https://doi.org/10.1146/annurev.ecolsys.34.011802.132516

Lilburn, T. G., Kim, K. S., Ostrom, N. E., Byzek, K. R., Leadbetter, J. R., & Breznak, J. A. (2001). Nitrogen fixation by symbiotic and free-living spirochetes. *Science (New York, N.Y.)*, *292*(5526), 2495–2498. https://doi.org/10.1126/science.1060281

Linné, C. von. (1781). *Select Dissertations from the Amoenitates Academicae: A Supplement to Mr. Stillingfleet's Tracts Relating to Natural History*. G. Robinson, ... and J. Robson.

Lomolino, M. V., Sax, D. F., & Brown, J. H. (Eds.). (2004). *Foundations of Biogeography: Classic Papers with Commentaries*. University of Chicago Press. https://press.uchicago.edu/ucp/books/book/chicago/F/bo3635862.html

Lunghi, E., Manenti, R., Mulargia, M., Veith, M., Corti, C., & Ficetola, G. F. (2018). Environmental suitability models predict population density, performance and body condition for microendemic salamanders. *Scientific Reports*, *8*(1), Article 1. https://doi.org/10.1038/s41598-018-25704-1

Marshall, D. J., Dong, Y., McQuaid, C. D., & Williams, G. A. (2011). Thermal adaptation in the intertidal snail Echinolittorina malaccana contradicts current theory by revealing the crucial roles of resting metabolism. *Journal of Experimental Biology*, *214*(21), 3649–3657. https://doi.org/10.1242/jeb.059899

McCabe, M. K., & Navarrete, S. A. (2018). Reproductive investment in rocky intertidal mussels: Spatiotemporal variability and environmental determinants. *Marine Ecology Progress Series*, *599*, 107–124. https://doi.org/10.3354/meps12608

Melis, C., Herfindal, I., Kauhala, K., Andersen, R., & Hogda, K.-A. (2010). Predicting animal performance through climatic and plant phenology variables: The case of an omnivore hibernating species in Finland. *Mammalian Biology*, *75*(2), 151–159. https://doi.org/10.1016/j.mambio.2008.12.001

Menge, B. A., Blanchette, C., Raimondi, P., Freidenburg, T., Gaines, S., Lubchenco, J., Lohse, D., Hudson, G., Foley, M., & Pamplin, J. (2004). Species Interaction Strength: Testing Model Predictions Along an Upwelling Gradient. *Ecological Monographs*, *74*(4), 663–684. https://doi.org/10.1890/03-4060

Menge, B. A., Lubchenco, J., Bracken, M. E. S., Chan, F., Foley, M. M., Freidenburg, T. L., Gaines, S. D., Hudson, G., Krenz, C., Leslie, H., Menge, D. N. L., Russell, R., & Webster, M. S. (2003). Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proceedings of the National Academy of Sciences*, *100*(21), 12229–12234. https://doi.org/10.1073/pnas.1534875100

Morgan, S. G. (2014). Behaviorally Mediated Larval Transport in Upwelling Systems. *Advances in Oceanography*, *2014*, 1–17. https://doi.org/10.1155/2014/364214

Nelson, H. R., Kuempel, C. D., & Altieri, A. H. (2016). The resilience of reef invertebrate biodiversity to coral mortality. *Ecosphere*, *7*(7), e01399. https://doi.org/10.1002/ecs2.1399

Nguyen, B. N., Shen, E. W., Seemann, J., Correa, A. M. S., O’Donnell, J. L., Altieri, A. H., Knowlton, N., Crandall, K. A., Egan, S. P., McMillan, W. O., & Leray, M. (2020). Environmental DNA survey captures patterns of fish and invertebrate diversity across a tropical seascape. *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-63565-9

O’Connor, M. I. (2009). Warming strengthens an herbivore–plant interaction. *Ecology*, *90*(2), 388–398. https://doi.org/10.1890/08-0034.1

Paquette, L., Archambault, P., & Guichard, F. (2019). From habitat geometry to ecosystem functions in marine mussel beds. *Marine Ecology Progress Series*, *608*, 149–163. https://doi.org/10.3354/meps12808

Peller, T., Andrews, S., Leroux, S., & Guichard, F. (2021). From Marine Metacommunities to Meta-ecosystems: Examining the Nature, Scale and Significance of Resource Flows in Benthic Marine Environments. *Ecosystems*, *24*, 1–14. https://doi.org/10.1007/s10021-020-00580-x

Peterson, A., & Soberón, J. (2012). Species Distribution Modeling and Ecological Niche Modeling: Getting the Concepts Right. *Natureza e Conservação*, *10*, 1–6. https://doi.org/10.4322/natcon.2012.019

Petitpierre, B., Broennimann, O., Kueffer, C., Daehler, C., & Guisan, A. (2017). Selecting predictors to maximize the transferability of species distribution models: Lessons from cross-continental plant invasions. *Global Ecology and Biogeography*, *26*(3), 275–287. https://doi.org/10.1111/geb.12530

Polis, G. A., & Hurd, S. D. (1995). Extraordinarily high spider densities on islands: Flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences*, *92*(10), 4382–4386. https://doi.org/10.1073/pnas.92.10.4382

Regan, H. M., Hierl, L. A., Franklin, J., Deutschman, D. H., Schmalbach, H. L., Winchell, C. S., & Johnson, B. S. (2008). Species prioritization for monitoring and management in regional multiple species conservation plans. *Diversity and Distributions*, *14*(3), 462–471. https://doi.org/10.1111/j.1472-4642.2007.00447.x

Robertson, R. (1990). Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes. *Journal of Experimental Marine Biology and Ecology*, *144*(1), 49–62. https://doi.org/10.1016/0022-0981(90)90019-9

Saldana, P., Alford, S., Mainella, A., Crotty, S., Prince, K., Sullivan, C., Earl, K., Angelini, C., & Altieri, A. (2021). *Grateful for the dead: The widespread importance of dead foundation species for biodiversity, ecosystem function, and resilience.* [Preprint]. Preprints. https://doi.org/10.22541/au.163252121.17081433/v1

Salo, T., Pedersen, M. F., & Boström, C. (2014). Population specific salinity tolerance in eelgrass (Zostera marina). *Journal of Experimental Marine Biology and Ecology*, *461*, 425–429. https://doi.org/10.1016/j.jembe.2014.09.010

Sanford, E. (2002). The feeding, growth, and energetics of two rocky intertidal predators (Pisaster ochraceus and Nucella canaliculata) under water temperatures simulating episodic upwelling. *Journal of Experimental Marine*

Biology and Ecology, *273*(2), 199–218. https://doi.org/10.1016/S0022-0981(02)00164-8

Sellers, A. J., Leung, B., Altieri, A., Glanz, J., Turner, B., & Torchin, M. (2021). Seasonal upwelling reduces herbivore control of tropical rocky intertidal algal communities. *Ecology*, *102*. https://doi.org/10.1002/ecy.3335

Sides, E. M., & Woodley, J. D. (1985). Niche separation in three species of Ophiocoma (Echinodermata: Ophiuroidea) in Jamaica, West Indies. *Bulletin of Marine Science*, *36*(3), 701–715.

Soberon, J., & Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*, *106*, 19644–19650. https://doi.org/10.1073/pnas.0901637106

Stewart, R. H. (2009). *Introduction to Physical Oceanography*. University Press of Florida.

Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2010). Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1713), 1823–1830. https://doi.org/10.1098/rspb.2010.1295

Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, *2*(9), Article 9. https://doi.org/10.1038/nclimate1539

Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R. A., Smale, D. A., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thompson, P. A., & Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, *18*(9), 944–953. https://doi.org/10.1111/ele.12474

Thomsen, M. S., Altieri, A. H., Angelini, C., Bishop, M. J., Gribben, P. E., Lear, G., He, Q., Schiel, D. R., Silliman, B. R., South, P. M., Watson, D. M., Wernberg, T., & Zotz, G. (2018). Secondary foundation species enhance biodiversity. *Nature Ecology & Evolution*, *2*(4), Article 4. https://doi.org/10.1038/s41559-018-0487-5

Tomas, F., Martínez-Crego, B., Hernán, G., & Santos, R. (2015). Responses of seagrass to anthropogenic and natural disturbances do not equally translate to its consumers. *Global Change Biology*, *21*(11), 4021–4030. https://doi.org/10.1111/gcb.13024

Trip, E. D. L., Clements, K. D., Raubenheimer, D., & Choat, J. H. (2014). Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient. *Journal of Animal Ecology*, *83*(4), 866–875. https://doi.org/10.1111/1365-2656.12183

Vaslet, A., Phillips, D. L., France, C., Feller, I. C., & Baldwin, C. C. (2012). The relative importance of mangroves and seagrass beds as feeding areas for resident and transient fishes among different mangrove habitats in Florida and Belize: Evidence from dietary and stable-isotope analyses. *Journal of Experimental Marine Biology and Ecology*, *434–435*, 81–93. https://doi.org/10.1016/j.jembe.2012.07.024

Voigt, E. P., & Hovel, K. A. (2019). Eelgrass structural complexity mediates mesograzer herbivory on epiphytic algae. *Oecologia*, *189*(1), 199–209. https://doi.org/10.1007/s00442-018-4312-2

Waldock, C., Stuart-Smith, R. D., Edgar, G. J., Bird, T. J., & Bates, A. E. (2019). The shape of abundance distributions across temperature gradients in reef fishes. *Ecology Letters*, *22*(4), 685–696. https://doi.org/10.1111/ele.13222

Wallace, A. R. (1876). *The geographical distribution of animals, with a study of the relations of living and extinct faunas as elucidating the past changes of the earth's surface.* Macmillan and Co. https://catalog.hathitrust.org/Record/006221857

Weber, M. M., Stevens, R. D., Diniz-Filho, J. A. F., & Grelle, C. E. V. (2017). Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography*, *40*(7), 817–828. https://doi.org/10.1111/ecog.02125

Whippo, R., Knight, N., Prentice, C., Cristiani, J., Siegle, M., & O'Connor, M. (2018). Epifaunal diversity patterns within and among seagrass meadows suggest landscape-scale biodiversity processes. *Ecosphere*, *9*, e02490. https://doi.org/10.1002/ecs2.2490

Young, M., & Carr, M. H. (2015). Application of species distribution models to explain and predict the distribution, abundance and assemblage structure of nearshore temperate reef fishes. *Diversity and Distributions*, *21*(12), 1428–1440. https://doi.org/10.1111/ddi.12378

Chapter 2: A global meta-analysis of temperature effects on marine fishes' digestion across trophic groups

Authors: Nicole S. Knight[1,2,3], Frédéric Guichard[1], Andrew H. Altieri[2,3]

[1] Department of Biology, McGill University, Montréal, QC, Canada

[2] Smithsonian Tropical Research Institute, Ancón, Panamá

[3] Department of Environmental Engineering, University of Florida, Gainesville, FL, USA

Status: This chapter was published in the journal *Global Ecology and Biogeography*, January 31, 2021:

Knight, N. S., Guichard, F., & Altieri, A. H. (2021). A global meta-analysis of temperature effects on marine fishes' digestion across trophic groups. *Global Ecology and Biogeography*, 30(4), 795–810. https://doi.org/10.1111/geb.13262

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

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; BarreraOro & 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 pro cesses 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 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.

Methods

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 2.1, Appendix, Supporting Information Appendix 2S1). 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).

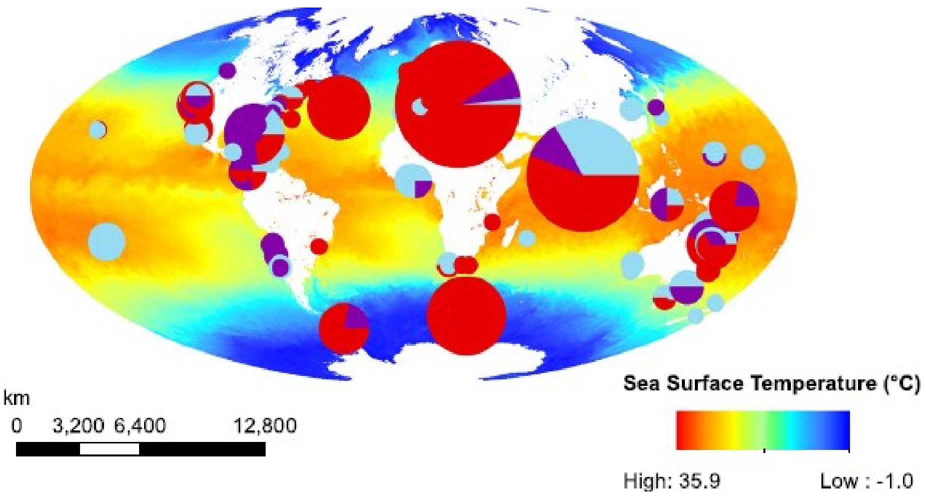

Figure 2.1. World map (Aitoff's projection) showing the locations of all studies included in the analysis. The size of each point is proportional to the number of species in each study (range: 1–56 species), and colours show the proportion of herbivorous (blue),omnivorous (purple) and carnivorous (red) 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).

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.

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 compete 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.

Results

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 2.2). Model selection found the strongest support for the diet*temperature interaction model (89 ± 2% SE of LOO weight; 80 ± 1% SE of stacked weight) out of the three competing models. The model predicted that gut passage time 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 macroalgivores (n = 42). The model detected no independent diet effects (Figure 2.2b), predicting that gut passage time did not differ consistently among macroalgivores, carnivores, or any other group based on diet alone, but was instead temperature dependent.

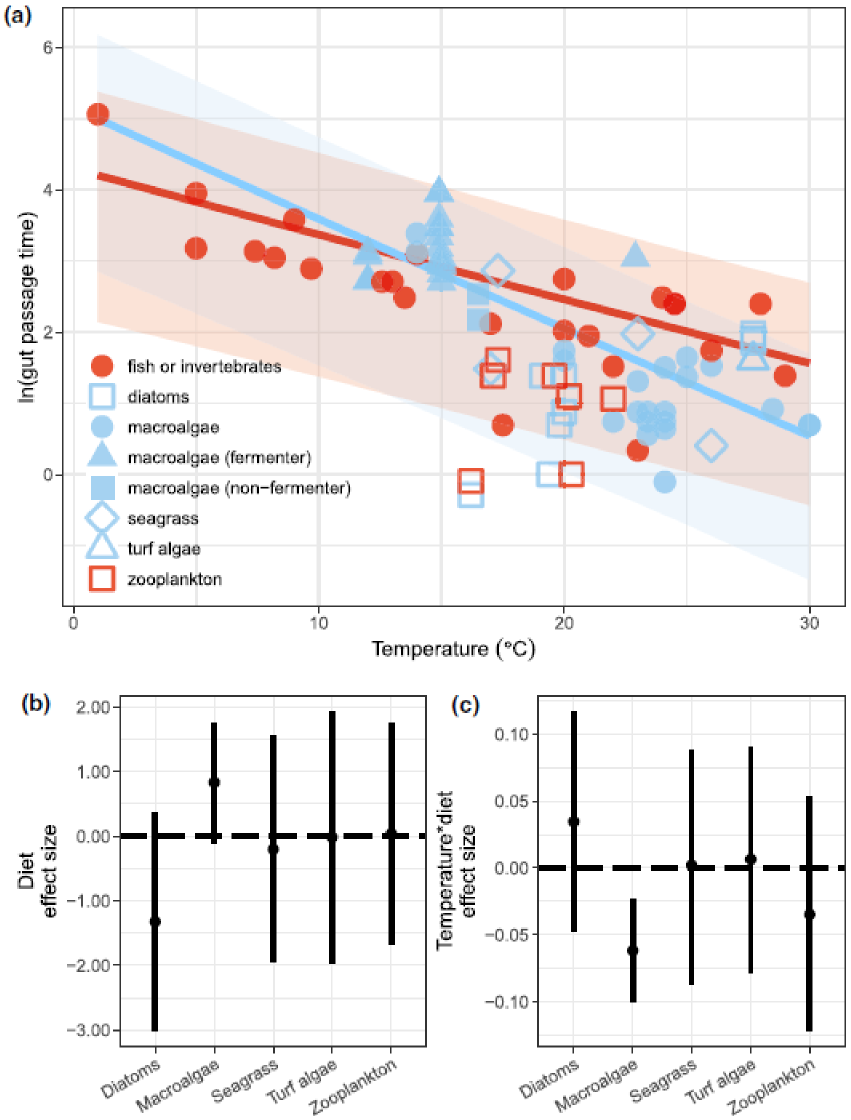

Figure 2.2. Gut passage time of marine fishes (40 species, n = 89) as it relates to temperature and diet. Estimates and 95% credibility intervals (CIs) in all three panels are from the best supported model describing gut passage time (ln (gut passage time) ~ diet*temperature). All values of gut passage 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 macroalgivores (blue) as predicted by the model. Macroalgivores 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 macroalgivorous fishes responded more strongly to changes in temperature than did the gut passage time of carnivores.

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 ± 2% SE of LOO weight, 83 ± 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 2.3a,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 and diets, several compounds were absorbed at much higher proportions relative to total absorption efficiency (58 ± 25% SD; Figure 2.3c), particularly nitrogen (76 ± 18% SD), protein (84 ± 13% SD) and energy (86 ± 18% SD).

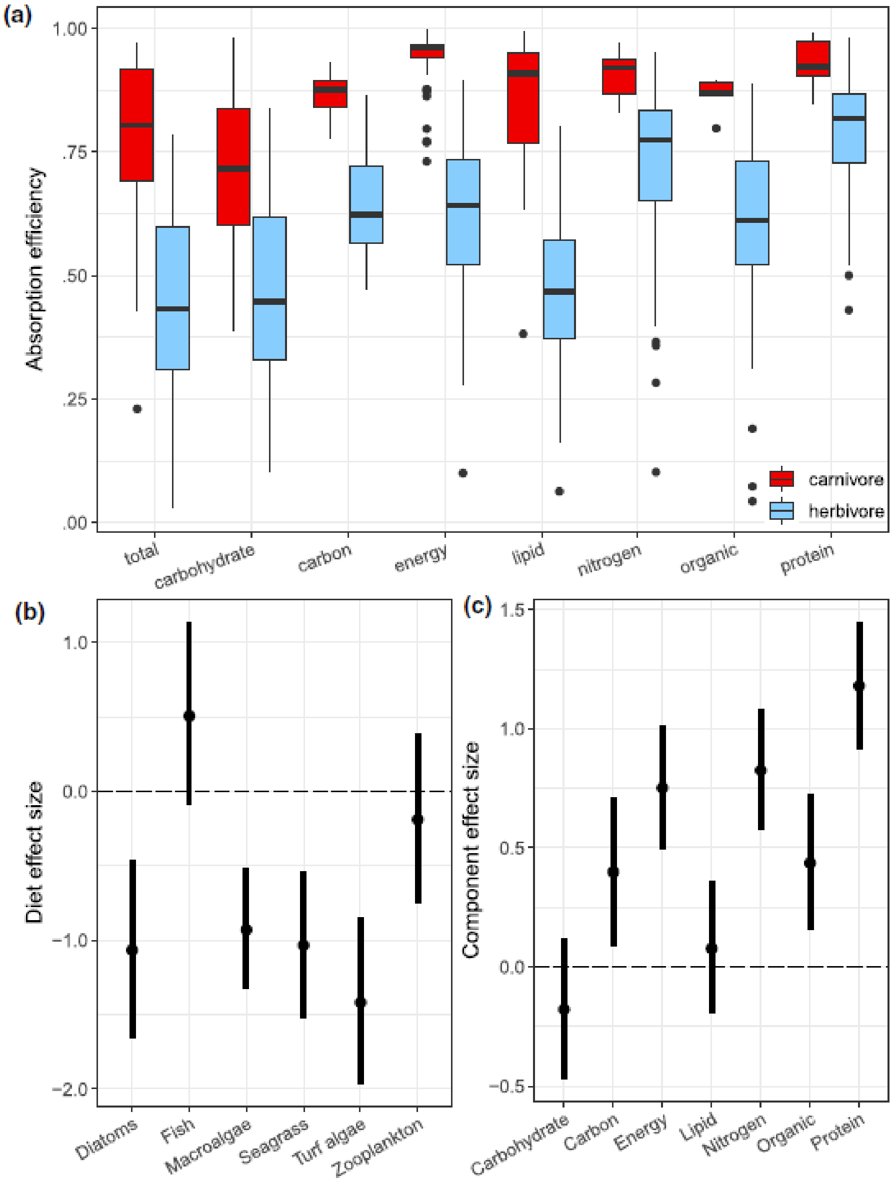

Figure 2.3. Absorption efficiency of marine fishes (50 species, n = 500) as it relates to diet and component absorbed. Estimates and 95% credibility intervals (CIs) in bottom two panels are from the best supported model describing absorption efficiency (absorption efficiency ~ diet + component). All 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.

Gut length

Gut length decreased in association with decreasing temperature at similar rates for fishes across all diet types (Figure 42.4a). Model selection assigned the most weight to the temperature + diet model (74 ± 2% SE of LOO weight, 76 ± 3% SE of stacked weight). Carnivorous fishes had shorter guts than omnivorous and herbivorous fishes (Figure 2.4b,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-detritivores (3.5 RGL ± 2.1 SD), macroalgivores (2.6 RGL ± 1.2 SD), and consumers of turf algae (4.3 RGL ± 1.8 SD) or diatoms (3.3 ± 2.8 SD).

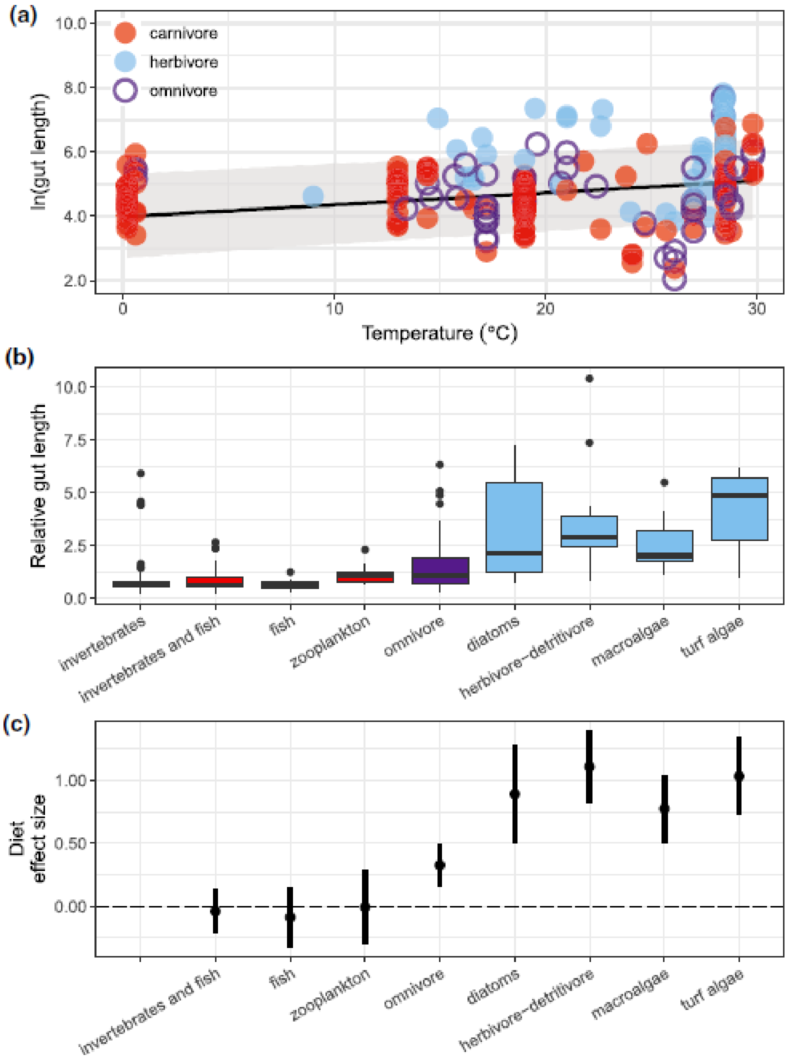

Figure 2.4. Gut length of marine fishes (249 species, n = 249) as it relates to temperature and diet. Estimates and 95% credibility intervals (CIs) in panels (a) and (c) are from the best supported model describing ln-transformed gut length (gut length ~ ln(body length) + temperature + diet). All effect 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.

Nutrient concentrations

Plants fed to herbivorous fishes in our analysis were nutrient-poor compared to animal prey fed to carnivores (Figure 2.5). 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 ± 4.7% SD) and animal (57.9 ± 15.7% SD) material, as well as nitrogen content (plant: 2.4 ± 1.0% SD; animal: 9.3 ± 1.8% SD) and energy content (plant: 11.1 ± 3.7 kJ/g SD; animal: 18.7 ± 3.4 kJ/g SD).

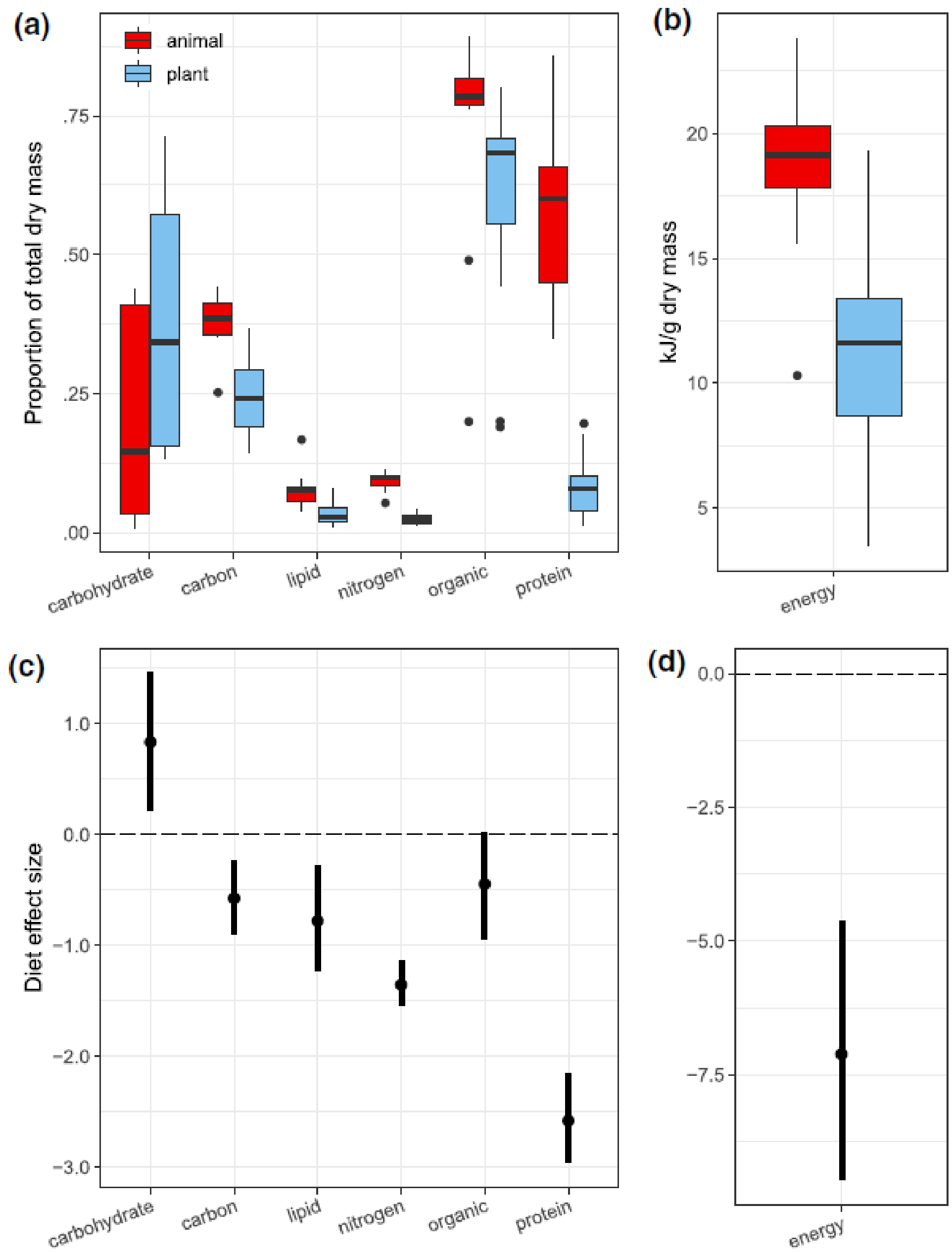

Figure 2.5. Nutrient/component content of animal and plant food items included in this analysis. Estimates and 95% credibility intervals (CIs) in panels (c) and (d) are from models describing each component's dependence on diet type (component ~ diet) for 75 plant and animal food items (not all nutrients 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.

Discussion

Using a global database of 304 marine fish species and 99 studies (Figure 2.1), 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 2.2); 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 2.3), 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 2.4), which could indicate a re-allocation of resources for other somatic growth and/or reproduction, benefitting all trophic groups similarly.

Our analysis of gut passage times shows that decreasing temperature slows digestion in macroalgivorous fishes more than in carnivorous fishes (Figure 2.2). 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 2.3). 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 2.5). 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 2.4), 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 2.5). 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 2.3), longer guts (Figure 2.4) and lower quality food (Figure 2.5). 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 seagrass 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 2.2a) 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.

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.

Acknowledgements

The authors thank Andrew Sellers, Lauren Chapman and Andrew Hendry for their discussion, which improved earlier versions of this manuscript, as well as three anonymous referees for their constructive comments and suggestions. Sea surface temperature data were obtained from the COBE-SST2 database provided by the National Oceanic and Atmospheric Administration Earth Science Research Lab in Boulder, Colorado, from their website at https://www.esrl.noaa.gov/psd/. N.S.K. was funded by National Sciences and Engineering Research Council of Canada (NSERC) Postgraduate Scholarships (Master's and Doctoral Program), an NSERC Collaborative Research and Training Experience Program Grant in Biodiversity, Ecosystem Services and Sustainability, a Short-Term Fellowship from the Smithsonian Tropical Research Institute (STRI), and additional funding from McGill University and STRI.

Data availability statement

All data used in our analyses are publicly available through Dryad (https://doi.org/10.5061/dryad.g1jws tqq1), and all data and code are publicly available through GitHub (https://github.com/nicoleknight0/meta-analysis-fish-digestion).

ORCID

Nicole S. Knight https://orcid.org/0000-0001-9256-242X

Frédéric Guichard https://orcid.org/0000-0002-7369-482X

Andrew H. Altieri https://orcid.org/0000-0001-7439-8742

References

Barrera-Oro, E., & Casaux, R. J. (1990). Feeding selectivity in *Notothenia neglecta*, Nybelin, from Potter Cove, South Shetland Islands, Antarctica. *Antarctic Science*, 2, 207–213.

Barrera-Oro, E. (2002). The role of fish in the Antarctic marine food web: Differences between inshore and offshore waters in the southern Scotia Arc and west Antarctic Peninsula. *Antarctic Science*, 14, 293–309.

Behrens, M. D., & Lafferty, K. D. (2012). Geographic variation in the diet of opaleye (*Girella nigricans*) with respect to temperature and habitat. *PloS One*, 7(9), e45901.

Behrens, M. D., & Lafferty, K. D. (2007). Temperature and diet effects on omnivorous fish performance: Implications for the latitudinal diversity gradient in herbivorous fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 867–873.

Benavides, A. G., Cancino, J. M., & Ojeda, F. P. (1994). Ontogenetic Changes in Gut Dimensions and Macroalgal Digestibility in the Marine Herbivorous Fish, *Aplodactylus punctatus*. *Functional Ecology*, 8(1), 46.

Borer, E. T., Bracken, M. E. S., Seabloom, E. W., Smith, J. E., Cebrian, J., Cleland, E. E., Elser, J. J., Fagan, W. F., Gruner, D. S., Harpole, W. S., Hillebrand, H., Kerkhoff, A. J., & Ngai, J. T. (2013). Global biogeography of autotroph chemistry: Is insolation a driving force? *Oikos*, 122(8), 1121–1130.

Bowen, S. H., Lutz, E. V., & Ahlgren, M. O. (1995). Dietary Protein and Energy as Determinants of Food Quality: Trophic Strategies Compared. *Ecology*, 76(3), 899–907.

Bowyer, J. N., Qin, J. G., & Stone, D. A. J. (2013). Protein, lipid and energy requirements of cultured marine fish in cold, temperate and warm water. *Reviews in Aquaculture*, 5(1), 10–32.

Brey, T., Mueller-Wiegmann, C., Zittier, Z. M. C., & Hagen, W. (2010). Body composition in aquatic organisms—A global data bank of relationships between mass, elemental composition and energy content. *Journal of Sea Research*, 64(3), 334–340.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789.

Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, 80(1), 1–28.

Casaux, R., Barrera-Oro, E., Baroni, A., & Ramón, A. (2003). Ecology of inshore notothenioid fish from the Danco Coast, Antarctic Peninsula. *Polar Biology*, 26, 157–165.

Chown, S. L., Gaston, K. J., & Robinson, D. (2004). Macrophysiology: Large-scale patterns in physiological traits and their ecological implications. *Functional Ecology*, 18(2), 159–167.

Clarke, A., & Johnston, I. A. (1996). Evolution and adaptive radiation of Antarctic fishes. *Trends in Ecology & Evolution*, 11(5), 212–218.

Clements, K. D., & Choat, J. H. (1995). Fermentation in Tropical Marine Herbivorous Fishes. *Physiological Zoology*, 68(3), 355–378.

Clements, K. D., & Choat, J. H. (1997). Comparison of herbivory in the closely-related marine fish genera *Girella* and *Kyphosus*. *Marine Biology*, 127(4), 579–586.

Clements, K. D., Angert, E. R., Montgomery, W. L., & Choat, J. H. (2014). Intestinal microbiota in fishes: What's known and what's not. *Molecular Ecology*, 23(8), 1891–1898.

Clements, K.D., Raubenheimer, D., & Choat, J. H. (2009). Nutritional ecology of marine herbivorous fishes: Ten years on. *Functional Ecology*, 23(1), 79–92.

Edwards, D. J. (1971). Effect of temperature on rate of passage of food through the alimentary canal of the plaice *Pleuronectes platessa* L. *Journal of Fish Biology*, 3(4), 433–439.

Egan, J., Bloom, D., Kuo, C.-H., Hammer, M., Tongnunui, P., Iglésias, S., Sheaves, M., Grudpan, C., & Simons, A. (2018). Phylogenetic analysis of trophic niche evolution reveals a latitudinal herbivory gradient in Clupeoidei (herrings, anchovies, and allies). *Molecular Phylogenetics and Evolution*, 124.

Espinoza, R. E., Wiens, J. J., & Tracy, C. R. (2004). Recurrent evolution of herbivory in small, cold-climate lizards: Breaking the ecophysiological rules of reptilian herbivory. *Proceedings of the National Academy of Sciences of the United States of America*, 101(48), 16819–16824.

Ferreira, C. E. L., Floeter, S. R., Gasparini, J. L., Ferreira, B. P., & Joyeux, J. C. (2004). Trophic structure patterns of Brazilian reef fishes: A latitudinal comparison. *Journal of Biogeography*, 31(7), 1093–1106.

Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddack, M. J., & Horn, M. H. (2005). Geographical gradients of marine herbivorous fishes: Patterns and processes. *Marine Biology*, 147(6), 1435–1447.

Floeter, S. R., Ferreira, C. E. L., Dominici-Arosemena, A., & Zalmon, I. R. (2004). Latitudinal gradients in Atlantic reef fish communities: Trophic structure and spatial use patterns. *Journal of Fish Biology*, 64(6), 1680–1699.

Fris, M. B., & Horn, M. H. (1993). Effects of diets of different protein content on food consumption, gut retention, protein conversion, and growth of *Cebidichthys violaceus* (Girard), an herbivorous fish of temperate zone marine waters. *Journal of Experimental Marine Biology and Ecology*, 166(2), 185–202.

Gaines, S., & Lubchenco, J. (1982). A Unified Approach to Marine Plant-Herbivore Interactions .2. Biogeography. *Annual Review of Ecology and Systematics*, 13, 111–138.

German, D. P., Nagle, B. C., Villeda, J. M., Ruiz, A. M., Thomson, A. W., Contreras Balderas, S., & Evans, D. H. (2010). Evolution of Herbivory in a Carnivorous Clade of Minnows (Teleostei: Cyprinidae): Effects on Gut Size and Digestive Physiology. *Physiological and Biochemical Zoology*, 83(1), 1–18.

German, D. P., Sung, A., Jhaveri, P., & Agnihotri, R. (2015). More than one way to be an herbivore: Convergent evolution of herbivory using different digestive strategies in prickleback fishes (Stichaeidae). *Zoology*, 118(3), 161–170.

González-Bergonzoni, I., Jeppesen, E., Vidal, N., Teixeira-de Mello, F., Goyenola, G., López-Rodríguez, A., & Meerhoff, M. (2016). Potential drivers of seasonal shifts in fish omnivory in a subtropical stream. *Hydrobiologia*, 768(1), 183–196.

Grady, J. M., Maitner, B. S., Winter, A. S., Kaschner, K., Tittensor, D. P., Record, S., Smith, F. A., Wilson, A. M., Dell, A. I., Zarnetske, P. L., Wearing, H. J., Alfaro, B., & Brown, J. H. (2019). Metabolic asymmetry and the global diversity of marine predators. *Science*, 363(6425).

Harmelin-Vivien, M. (2002). Energetics and Fish Diversity on Coral Reefs. In P.F. Sale (Ed.), *Coral Reef Fishes.* Cambridge, MA: Academic Press.

Heck, K., Fodrie, F., Madsen, S., Baillie, C., & Byron, D. (2015). Seagrass consumption by native and a tropically associated fish species: Potential impacts of the tropicalization of the northern Gulf of Mexico. Marine Ecology Progress Series, 520, 165–173.

Horn, M. H. (1989). Biology of marine herbivorous fishes. In *Oceanography and Marine Biology An Annual Review* (Vol. 27 pp. 134-221). Aberdeen, Scotland: Aberdeen University Press.

Horn, M. H., & Gibson, R. N. (1990). Effects of temperature on the food processing of three species of seaweed-eating fishes from European coastal waters. *Journal of Fish Biology*, 37(2), 237–247.

Horn, M. H., Mailhiot, K. F., Fris, M. B., & McClanahan, L. L. (1995). Growth, consumption, assimilation and excretion in the marine herbivorous fish

Cebidichthys violaceus (Girard) fed natural and high protein diets. *Journal of Experimental Marine Biology and Ecology*, 190(1), 97–108.

Horn, M. H., & Messer, K. S. (1992). Fish guts as chemical reactors: A model of the alimentary canals of marine herbivorous fishes. *Marine Biology*, 113(4), 527–535.

Horn, M. H., Neighbors, M. A., & Murray, S. N. (1986). Herbivore responses to a seasonally fluctuating food supply: Growth potential of two temperate intertidal fishes based on the protein and energy assimilated from their macroalgal diets. *Journal of Experimental Marine Biology and Ecology*, 103(1–3), 217–234.

Hyndes, G. A., Heck, K. L., Vergés, A., Harvey, E. S., Kendrick, G. A., Lavery, P. S., McMahon, K., Orth, R. J., Pearce, A., Vanderklift, M., Wernberg, T., Whiting, S., & Wilson, S. (2016). Accelerating Tropicalization and the Transformation of Temperate Seagrass Meadows. *BioScience*, 66(11), 938–948.

Iken, K., Barrera-Oro, E. R., Quartino, M. L., Casaux, R. J., & Brey, T. (1997). Grazing by the Antarctic fish *Notothenia coriiceps*: Evidence for selective feeding on macroalgae. *Antarctic Science*, 9(04).

Ireland, C. D., & Horn, M. H. (1991). Effects of macrophyte secondary chemicals on food choice and digestive efficiency of *Cebidichthys violaceus* (Girard), an herbivorous fish of temperate marine waters. *Journal of Experimental Marine Biology and Ecology*, 153(2), 179–194.

Johnson, J. S., Raubenheimer, D., Bury, S. J., & Clements, K. D. (2020). Does temperature constrain diet choice in a marine herbivorous fish? *Marine Biology*, 167(7), 99.

Karachle, P. K., & Stergiou, K. I. (2010a). Intestine morphometrics of fishes: A compilation and analysis of bibliographic data. *Acta Ichthyologica et Piscatoria*, 40(1).

Karachle, Paraskevi K., & Stergiou, K. I. (2010b). Gut length for several marine fish: Relationships with body length and trophic implications. *Marine Biodiversity Records*, 3:e106.

Knudsen, S. W., Choat, J. H., & Clements, K. D. (2019). The herbivorous fish family Kyphosidae (Teleostei: Perciformes) represents a recent radiation from higher latitudes. *Journal of Biogeography*, 46(9), 2067–2080.

Lilburn, T. G., Kim, K. S., Ostrom, N. E., Byzek, K. R., Leadbetter, J. R., & Breznak, J. A. (2001). Nitrogen fixation by symbiotic and free-living spirochetes. Science (New York, N.Y.), 292(5526), 2495–2498.

Lobato, F. L., Barneche, D. R., Siqueira, A. C., Liedke, A. M. R., Lindner, A., Pie, M. R., Bellwood, D. R., & Floeter, S. R. (2014). Diet and Diversification in the Evolution of Coral Reef Fishes. *PLOS ONE*, 9(7), e102094.

Mazumder, S. K., Das, S. K., Rahim, S. M., & Ghaffar, M. A. (2018). Temperature and diet effect on the pepsin enzyme activities, digestive somatic index and relative gut length of Malabar blood snapper (*Lutjanus malabaricus* Bloch & Schneider, 1801). *Aquaculture Reports*, 9, 1–9.

Meekan, M. G., & Choat, J. H. (1997). Latitudinal variation in abundance of herbivorous fishes: A comparison of temperate and tropical reefs. *Marine Biology*, 128(3), 373–383.

Montgomery, W. L., & Gerking, S. D. (1980). Marine macroalgae as foods for fishes: An evaluation of potential food quality. *Environmental Biology of Fishes*, 5(2), 143–153.

Naval Oceanographic Office. (2008). K10 Global 10km Analyzed SST data set. Ver. 1.0. PO.DAAC, CA, USA. Dataset accessed [2020-12-23] at https://doi.org/10.5067/GHK10-41N01

O’Connor, M. I. (2009). Warming strengthens an herbivore–plant interaction. *Ecology*, 90(2), 388–398.

Pandian, T. J., & Marian, M. P. (1985). Nitrogen content of food as an index of absorption efficiency in fishes. *Marine Biology*, 85(3), 301–311.

Pandian, T. J., & Vivekanandan, E. (1985). Energetics of Feeding and Digestion. In P. Tytler & P. Calow (Eds.), *Fish Energetics: New Perspectives* (pp. 99–124). Springer Netherlands.

Pillans, R. D., Franklin, C. E., & Tibbetts, I. R. (2004). Food choice in *Siganus fuscescens*: Influence of macrophyte nutrient content and availability. *Journal of Fish Biology*, 64(2), 297–309.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Sardain, A., Sardain, E., & Leung, B. (2019). Global forecasts of shipping traffic and biological invasions to 2050. *Nature Sustainability*, 2(4), 274–282.

Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R. A., Smale, D. A., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thompson, P. A., & Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, 18(9), 944–953.

Tummers, B. (2006). DataThief III. <https://datathief.org/>

Trip, E. D. L., Clements, K. D., Raubenheimer, D., & Choat, J. H. (2014). Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient. *Journal of Animal Ecology*, 83(4), 866–875.

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27(5), 1413–1432.

Vejříková, I., Vejřík, L., Syväranta, J., Kiljunen, M., Čech, M., Blabolil, P., Vašek, M., Sajdlova, Z., Chung, S., Šmejkal, M., Frouzova, J., & Peterka, J. (2016). Distribution of Herbivorous Fish Is Frozen by Low Temperature. *Scientific Reports*, 6, 39600.

Vergés, A., Doropoulos, C., Czarnik, R., McMahon, K., Llonch, N., & Poore, A. G. B. (2018). Latitudinal variation in seagrass herbivory: Global patterns and explanatory mechanisms. *Global Ecology and Biogeography*, 27(9), 1068–1079.

Vergés, A., Doropoulos, C., Malcolm, H. A., Skye, M., Garcia-Pizá, M., Marzinelli, E. M., Campbell, A. H., Ballesteros, E., Hoey, A. S., Vila-Concejo, A., Bozec, Y.-M., & Steinberg, P. D. (2016). Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proceedings of the National Academy of Sciences*, 113(48), 13791–13796.

Vergés, A., McCosker, E., Mayer-Pinto, M., Coleman, M. A., Wernberg, T., Ainsworth, T., & Steinberg, P. D. (2019). Tropicalisation of temperate reefs: Implications for ecosystem functions and management actions. *Functional Ecology*, 33(6), 1000–1013.

Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L., Booth, D. J., Coleman, M. A., Feary, D. A., Figueira, W., Langlois, T., Marzinelli, E. M., Mizerek, T., Mumby, P. J., Nakamura, Y., Roughan, M., van Sebille, E., Gupta, A. S., … Wilson, S. K. (2014). The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*, 281(1789), 20140846.

White, W. L., Coveny, A. H., Robertson, J., & Clements, K. D. (2010). Utilisation of mannitol by temperate marine herbivorous fishes. *Journal of Experimental Marine Biology and Ecology*, 391(1–2), 50–56.

Yao, Y., Vehtari, A., Simpson, D., & Gelman, A. (2018). Using Stacking to Average Bayesian Predictive Distributions (with Discussion). *Bayesian Analysis*, 13(3), 917–1007.

Zarco-Perello, S., Carroll, G., Vanderklift, M., Holmes, T., Langlois, T. J., & Wernberg, T. (2020). Range-extending tropical herbivores increase diversity, intensity and extent of herbivory functions in temperate marine ecosystems. Functional Ecology.

Zarco-Perello, S., Wernberg, T., Langlois, T. J., & Vanderklift, M. A. (2017). Tropicalization strengthens consumer pressure on habitat-forming seaweeds. *Scientific Reports*, 7(1), 820.

Appendix 1: Data Sources

Aldana M., Pulgar J.M., Ogalde F., & Ojeda F.P. (2002). Morphometric and parasitological evidence for ontogenetic and geographical dietary shifts in intertidal fishes. *Bulletin of Marine Science*, 70(1), 55-74.

Anderson, T. A. (1988). The effect of feeding frequency on utilization of algal nutrients by the marine herbivore, the luderick, *Girella tricuspidata* (Quoy and Gaimard). *Journal of Fish Biology*, 32(6), 911–921.

Baker, E. J. C., Clauss, M., & Clements, K. D. (2016). Selection and intake of algal species in butterfish (*Odax pullus*; Labridae). Marine Biology, 163(6).

Baker, E (2011). The Nutritional Ecology of *Odax pullus*. MSc thesis. University of Auckland.

Baker, E. J. C., Clauss, M., & Clements, K. D. (2016). Selection and intake of algal species in butterfish (*Odax pullus*; Labridae). *Marine Biology*, 163(6).

Barry, J. P., & Ehret, M. J. (1993). Diet, food preference, and algal availability for fishes and crabs on intertidal reef communities in southern California. *Environmental Biology of Fishes*, 37(1), 75–95.

Benavides, A. G., Cancino, J. M., & Ojeda, F. P. (1994). Ontogenetic Changes in Gut Dimensions and Macroalgal Digestibility in the Marine Herbivorous Fish, *Aplodactylus punctatus*. *Functional Ecology*, 8(1), 46.

Berumen, M.L., Pratchett, M.S. & Goodman, B.A. (2011). Relative gut lengths of coral reef butterflyfishes (Pisces: Chaetodontidae). *Coral Reefs,* 30: 1005.

Beumer, J. P. (1978). Feeding ecology of four fishes from a mangrove creek in north Queensland, Australia. *Journal of Fish Biology*, 12(5), 475–490.

Blaxter, J.H., Holliday, F.G.T (1958). Herring (*Clupea harengus* L.) in aquaria: II. Feeding*. Scottish Home Department Marine Research* 6.

Boerger, C. M. (2011). Life History, diet and production of an herbivorous temperate marine fish, *Medialuna californiensis* (Family: Kyphosidae) (Thesis, California State University, Northridge). Retrieved from http://dspace.calstate.edu/handle/10211.2/824.

Boettcher, A. A., & Targett, N. M. (1993). Role of Polyphenolic Molecular Size in Reduction of Assimilation Efficiency in *Xiphister mucosus*. *Ecology*, 74(3), 891–903.

Boyce, S. (2000). Digestion rate, gut passage time and absorption efficiency in the Antarctic spiny plunderfish. *Journal of Fish Biology*, 57(4), 908–929.

Bruggemann, J., Begeman, J., Bosma, E., Verburg, P., & Breeman, A. (1994). Foraging by the Stoplight-Parrotfish *Sparisoma viride* .2. Intake and Assimilation of Food, protein and energy. *Marine Ecology Progress Series*, 106(1-2), 57–71.

Bray R.N., & Ebeling A.W. (1975). Food, activity, and habitat of three “picker-type” microcarnivorous fishes in the kelp forests off Santa Barbara, California. *Fishery Bulletin*, 73(4), 815-829.

Bryan, P. (1975). Food-Habits, Functional Digestive Morphology, and Assimilation Efficiency of Rabbitfish *Siganus spinus* (Pisces, Siganidae) on Guam. *Pacific Science*, 29(3), 269–277.

Buckle, E. C., & Booth, D. J. (2009). Ontogeny of space use and diet of two temperate damselfish species, *Parma microlepis* and *Parma unifasciata*. *Marine Biology*, 156(7), 1497–1505.

Caceres, C. W., & Ojeda, F. P. (2000). Patrones de forrajeo en dos especies de peces intermareales herbívoros de las costas de Chile: Efecto de la abundancia y composición química del alimento. *Revista Chilena de Historia Natural*, 73(2), 253–260.

Carrassón, M., & Matallanas, J. (1994). Morphometric characteristics of the alimentary tract of deep-sea Mediterranean teleosts in relation to their feeding habits. *Marine Biology*, 118(2), 319–322.

Chao, L.N. (1973). Digestive system and feeding habits of the cunner, *Tautogolabrus adspersus*, a stomachless fish. *Fishery Bulletin,* 71(2), 565-586.

Choat, J. H., Robbins, W. D., & Clements, K. D. (2004). The trophic status of herbivorous fishes on coral reefs. *Marine Biology*, 145(3), 445–454.

Clements, K. D., & Choat, J. H. (1993). Influence of season, ontogeny and tide on the diet of the temperate marine herbivorous fish *Odax pullus* (Odacidae). *Marine Biology*, 117(2), 213–220.

Cleveland, A., & Montgomery, W. (2003). Gut characteristics and assimilation efficiencies in two species of herbivorous damselfishes (Pomacentridae: *Stegastes dorsopunicans* and *S. planifrons*). *Marine Biology*, 142(1), 35–44.

Cockcroft, A. C., & Du Preez, H. H. (1989). Nitrogen and energy loss via nonfaecal and faecal excretion in the marine teleost *Lithognathus lithognathus*. *Marine Biology*, 101(3), 419–425.

Cockcroft, A. C., & Du Preez, H. H. (1990). Nitrogen and energy loss in the marine teleost *Lithognathus mormyrus* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 140(3), 159–171.

Conacher, M. J., W. J. R. Lanzing, and A. W. D. Larkum. (1979). Ecology of Botany Bay. II. Aspects of the Feeding Ecology of the Fanbellied Leatherjacket, *Monacanthus chinensis* (Pisces : Monacanthidae), in *Posidonia australis* Seagrass Beds in Quibray Bay, Botany Bay, New South Wales. *Marine and Freshwater Research* 30(3):387–400.

Crossman, D. J., Choat, J. H., & Clements, K. D. (2005). Nutritional ecology of nominally herbivorous fishes on coral reefs. *Marine Ecology Progress Series*, 296, 129–142.

Dankwa, H. R., Jr, J. B., & Yankson, K. (2005). Food and feeding habits of grey Mullets (Pisces: Mugilidae) in two estuaries in Ghana. *West African Journal of Applied Ecology*, 8(1).

Day, R. D., German, D. P., & Tibbetts, I. R. (2011). Why can't young fish eat plants? Neither digestive enzymes nor gut development preclude herbivory in the young of a stomachless marine herbivorous fish. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, 158(1), 23–29.

Depczynski, M., & Bellwood, D. (2003). The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series*, 256, 183–191.

Drazen, J. C., Reisenbichler, K. R., & Robison, B. H. (2007). A comparison of absorption and assimilation efficiencies between four species of shallow- and deep-living fishes. *Marine Biology*, 151(4), 1551–1558.

Du Preez, H. H., & Cockroft, A. C. (1988). Nonfaecal and faecal losses of *Pomadasys commersonni* (Teleostei: Pomadasyidae) feeding on the surf clam, *Donax serra*. *Comparative Biochemistry and Physiology Part A: Physiology*, 90(1), 63–70.

Du Preez, H. H., & Cockroft, A. C. (1988). Nonfaecal and faecal losses of the marine teleost, *Lichia amia* (Linnaeus, 1758), feeding on live southern mullet, *Liza richardsonii* (Smith, 1846). *Comparative Biochemistry and Physiology Part A: Physiology*, 90(1), 71–77.

Durbin, E. G., & Durbin, A. G. (1981). Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). Fishery Bulletin - United States, National Marine Fisheries Service (USA). Retrieved from http://agris.fao.org/agris-search/search.do?recordID=US8231194

Edwards, D. J. (1971). Effect of temperature on rate of passage of food through the alimentary canal of the plaice *Pleuronectes platessa* L. *Journal of Fish Biology*, 3(4), 433–439.

Edwards, R. R. C., Finlayson, D. M., & Steele, J. H. (1972). An experimental study of the oxygen consumption, growth, and metabolism of the cod (*Gadus morhua* L.). *Journal of Experimental Marine Biology and Ecology*, 8(3), 299–309.

Edwards, T. W., & Horn, M. H. (1982). Assimilation efficiency of a temperate-zone intertidal fish (*Cebidichthys violaceus*) fed diets of macroalgae. *Marine Biology*, 67(3), 247–253.

Emery, A. R. (1973). Comparative Ecology and Functional Osteology of Fourteen Species of Damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. *Bulletin of Marine Science*, 23(3), 649–770.

Fris, M. B., & Horn, M. H. (1993). Effects of diets of different protein content on food consumption, gut retention, protein conversion, and growth of *Cebidichthys violaceus* (Girard), an herbivorous fish of temperate zone marine waters. *Journal of Experimental Marine Biology and Ecology*, 166(2), 185–202.

Galetto, M. J., & Bellwood, D. R. (1994). Digestion of algae by *Stegastes nigricans* and *Amphiprion akindynos* (Pisces: Pomacentridae), with an evaluation of methods used in digestibility studies. *Journal of Fish Biology*, 44(3), 415–428.

Gammanpila, M., Upali S. Amarasinghe, & Wijeyaratne, M.J.S. (2017). Morphological Correlates with Diet of Fish Assemblages in Brush Park Fisheries of Tropical Estuaries. *Environmental Biology of Fishes* 100(10), 1285–99.

Garner, J.G. (2017). Gut throughput rate and satiation of the invasive lionfish (*Pterois volitans*) and its potential impact on an endemic, endangered labrid fish *Halichoeres socialis*. MSc Thesis. Boston University. Retrieved from https://open.bu.edu/handle/2144/24082

Gerking, S. D. (1984). Fish as Primary Consumers. *Transactions of the American Fisheries Society*, 113(3), 378–387.

German, D. P., Sung, A., Jhaveri, P., & Agnihotri, R. (2015). More than one way to be an herbivore: convergent evolution of herbivory using different digestive strategies in prickleback fishes (Stichaeidae). *Zoology*, 118(3), 161–170.

Goldenberg, S. U., & Erzini, K. (2014). Seagrass feeding choices and digestive strategies of the herbivorous fish *Sarpa salpa*. *Journal of Fish Biology*, 84(5), 1474–1489.

Goldschmid, A., Kotrschal, K., & Wirtz, P. (1984). Food and gut length of 14 Adriatic blenniid fish (Blenniidae; Percomorpha; Teleostei). *Zoologischer Anzeiger - A Journal of Comparative Zoology*, 213, 145–150.

Hernaman, V., Probert, P. K., & Robbins, W. D. (2009). Trophic ecology of coral reef gobies: Interspecific, ontogenetic, and seasonal comparison of diet and feeding intensity. *Marine Biology*, 156(3), 317–330.

Horn, M. H., & Gibson, R. N. (1990). Effects of temperature on the food processing of three species of seaweed-eating fishes from European coastal waters. *Journal of Fish Biology*, 37(2), 237–247.

Horn, M. H., & Neighbors, M. A. (1984). Protein and nitrogen assimilation as a factor in predicting the seasonal macroalgal diet of the monkeyface prickleback. *Transactions of the American Fisheries Society*, 113(3), 388–396.

Horn, M. H., Gawlicka, A. K., German, D. P., Logothetis, E. A., Cavanagh, J. W., & Boyle, K. S. (2006). Structure and function of the stomachless digestive system in three related species of New World silverside fishes (Atherinopsidae) representing herbivory, omnivory, and carnivory. *Marine Biology*, 149(5), 1237–1245.

Horn, M. H., Mailhiot, K. F., Fris, M. B., & McClanahan, L. L. (1995). Growth, consumption, assimilation and excretion in the marine herbivorous fish *Cebidichthys violaceus* (Girard) fed natural and high protein diets. *Journal of Experimental Marine Biology and Ecology*, 190(1), 97–108.

Horn, M. H., Neighbors, M. A., & Murray, S. N. (1986). Herbivore responses to a seasonally fluctuating food supply: Growth potential of two temperate intertidal fishes based on the protein and energy assimilated from their macroalgal diets. *Journal of Experimental Marine Biology and Ecology*, 103(1–3), 217–234.

James, A. G., Probyn, T., & Seiderer, L. J. (1989). Nitrogen excretion and absorption efficiencies of the Cape anchovy *Engraulis capensis* Gilchrist fed upon a variety of plankton diets. *Journal of Experimental Marine Biology and Ecology*, 131(2), 101–124.

Kaiser, M. J., Westhead, A. P., Hughes, R. N., & Gibson, R. N. (1992). Are digestive characteristics important contributors to the profitability of prey? *Oecologia*, 90(1), 61–69.

Kanda, M., & Yamaoka, K. (1994). Tooth and Gut Morphology in Relation to Feeding in Three Girellid Species (Perciformes, Girellidae) From Southern Japan. *Netherlands Journal of Zoology*, 45(3–4), 495–512.

Kanda, M., & Yamaoka, K. (1997). Positional relationship between the ovary and intestine in *Girella mezina* (Perciformes, Girellidae). *Ichthyological Research*, 44(2), 316–318.

Karachle, P. K., & Stergiou, K. I. (2010). Gut length for several marine fish: Relationships with body length and trophic implications. *Marine Biodiversity Records*, 3.

Klumpp, D., & Nichols, P. (1983). Nutrition of the southern sea garfish *Hyporhamphus melanochir*: Gut passage rate and daily consumption of two food types and assimilation of seagrass components. *Marine Ecology Progress Series*, 12, 207–216.

Kotrschal, K., & Lindquist, D. G. (1986). The Feeding Apparatus in four Pacific Tube Blennies (Teleostei: Chaenopsidae): *Marine Ecology*, 7(3), 241–253.

Lambert, T. C. (1985). Gastric emptying time and assimilation efficiency in Atlantic mackerel (*Scomber scombrus*). *Canadian Journal of Zoology*, 63(4), 817–820.

Lassuy, D. R. (1984). Diet, intestinal morphology, and nitrogen assimilation efficiency in the damselfish, *Stegastes lividus*, in Guam. *Environmental Biology of Fishes*, 10(3), 183–193.

Laur, D. R., & Ebeling, A. W. (1983). Predator-prey relationships in surfperches. *Environmental Biology of Fishes*, 8(3), 217–229.

Lemos, D., Netto, B., & Germano, A. (2006). Energy budget of juvenile fat snook *Centropomus parallelus* fed live food. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 144(1), 33–40.

Liedke, A. M. R., Barneche, D. R., Ferreira, C. E. L., Segal, B., Nunes, L. T., Burigo, A. P., Carvalho, J. A., Buck, S., Bonaldo, R. M., & Floeter, S. R. (2016). Abundance, diet, foraging and nutritional condition of the banded butterflyfish (*Chaetodon striatus*) along the western Atlantic. *Marine Biology*, 163(1), 6.

Lison De Loma, T., Harmelin-Vivien, M., Naim, O., & Fontaine, M.-F. (2000). Algal food processing by *Stegastes nigricans*, an herbivorous damselfish: Differences between an undisturbed and a disturbed coral reef site (La Réunion, Indian Ocean). *Oceanologica Acta*, 23(7), 793–804.

Lobel, P. S., & Ogden, J. C. (1981). Foraging by the herbivorous parrotfish *Sparisoma radians*. *Marine Biology*, 64(2), 173–183.

Logothetis, E. (2001). Gut morphology and function in *Atherinops affinis* (Teleostei: Atherinopsidae), a stomachless omnivore feeding on macroalgae. *Journal of Fish Biology*, 59(5), 1298–1312.

Manjakasy, J. M., Day, R. D., Kemp, A., & Tibbetts, I. R. (2009). Functional morphology of digestion in the stomachless, piscivorous needlefishes *Tylosurus gavialoides* and *Strongylura leiura* ferox (Teleostei: Beloniformes). *Journal of Morphology*, 270(10), 1155–1165.

Marnane, M. J., & Bellwood, D. R. (1997). Marker technique for investigating gut throughput rates in coral reef fishes. *Marine Biology*, 129(1), 15–22.

Mazlan, A. G., & Grove, D. J. (2003). Gastric digestion and nutrient absorption along the alimentary tract of whiting (*Merlangius merlangus* L.) fed on natural prey. *Journal of Applied Ichthyology*, 19(4), 229–238.

Menzel, D. W. (1960). Utilization of food by a Bermuda reef fish, *Epinephelus guttatus*. *ICES Journal of Marine Science*, 25(2), 216–222.

Montgomery, W. L. (1977). Diet and Gut Morphology in Fishes, with Special Reference to the Monkeyface Prickleback, *Cebidichthys violaceus* (Stichaeidae: Blennioidei). Copeia, 1977(1), 178–182.

Montgomery, J. L. M., & Targett, T. E. (1992). The nutritional role of seagrass in the diet of the omnivorous pinfish *Lagodon rhomboides* (L.). *Journal of Experimental Marine Biology and Ecology*, 158(1), 37–57.

Montgomery, W. L., & Gerking, S. D. (1980). Marine macroalgae as foods for fishes: an evaluation of potential food quality. *Environmental Biology of Fishes*, 5(2), 143–153.

Moreira, E., Novillo, M., Eastman, J. T., & Barrera-Oro, E. (2020). Degree of herbivory and intestinal morphology in nine notothenioid fishes from the western Antarctic Peninsula. *Polar Biology*, 43(5), 535–544.

Muñoz, A. A., & Ojeda, F. P. (2000). Ontogenetic changes in the diet of the herbivorous *Scartichthys viridis* in a rocky intertidal zone in central Chile. *Journal of Fish Biology*, 56(4), 986–998.

Nakamura, E. L. (1962). Observations on the Behavior of Skipjack Tuna, *Euthynnus pelamis*, in Captivity. Copeia, 1962(3), 499–505.

Ojeda, P.F. (1986). Morphological characterization of the alimentary tract of Antarctic fishes and its relation to feeding habits. *Polar Biology*, 5(2), 125–128.

Pillans, R. D., Franklin, C. E., & Tibbetts, I. R. (2004). Food choice in *Siganus fuscescens*: influence of macrophyte nutrient content and availability. *Journal of Fish Biology*, 64(2), 297–309.

Pinnegar, J. K., & Polunin, N. V. C. (2006). Planktivorous damselfish support significant nitrogen and phosphorus fluxes to Mediterranean reefs. *Marine Biology*, 148(5), 1089–1099.

Pogoreutz, C., & Ahnelt, H. (2014). Gut morphology and relative gut length do not reliably reflect trophic level in gobiids: A comparison of four species from a tropical Indo-Pacific seagrass bed. *Journal of Applied Ichthyology*, 30(2), 408–410.

Polunin, N. V. C. (1988). Efficient uptake of algal production by a single resident herbivorous fish on the reef. *Journal of Experimental Marine Biology and Ecology*, 123(1), 61–76.

Polunin, N. V. C., Harmelin-Vivien, M., & Galzin, R. (1995). Contrasts in algal food processing among five herbivorous coral-reef fishes. *Journal of Fish Biology*, 47(3), 455–465.

Randall, J. E. (1961). Contribution to the Biology of the Convict Surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*. Pacific Science, 15(2), 215-272.

Raubenheimer, D., Zemke-White, W. L., Phillips, R. J., & Clements, K. D. (2005). Algal Macronutrients and Food Selection by the Omnivorous Marine Fish *Girella Tricuspidata*. *Ecology*, 86(10), 2601–2610.

Reshma, K. J., Sumithra, T. G., Nair, A. V., Stefi Raju, V., Kishor, T. G., Sreenath, K. R., & Sanil, N. K. (2018). An insight into the gut microbiology of wild-caught Mangrove Red Snapper, *Lutjanus argentimaculatus* (Forsskal, 1775). *Aquaculture*, 497, 320–330.

Rimmer, D. W. (1986). Changes in diet and the development of microbial digestion in juvenile buffalo bream, *Kyphosus cornelii*. *Marine Biology*, 92(3), 443–448.

Rimmer, D. W., & Wiebe, W. J. (1987). Fermentative microbial digestion in herbivorous fishes. *Journal of Fish Biology*, 31(2), 229–236.

Robertson, A. I., & Klumpp, D. W. (1983). Feeding Habits of the Southern Australian Garfish *Hyporhamphus melanochir*: A Diurnal Herbivore and Nocturnal Carnivore. *Marine Ecology Progress Series*, 10(2), 197-201.

Rosenthal, H., & Paffenhöffer, G.A. (1972). On the digestion rate and calorific content of food and feces in young gar fish. *Naturwissenschaften*, 59(6), 274-275.

Smith, K. L. (1973). Energy transformations by the sargassum fish, *Histrio histrio* (L.). *Journal of Experimental Marine Biology and Ecology*, 12(3), 219–227.

Smith, R. L., & Paulson, A. C. (1974). Food Transit Times and Gut pH in Two Pacific Parrotfishes. Copeia, 1974(3), 796–799.

Sturm, E. A., & Horn, M. H. (1998). Food habits, gut morphology and pH, and assimilation efficiency of the zebraperch *Hermosilla azurea*, an herbivorous kyphosid fish of temperate marine waters. *Marine Biology*, 132(3), 515–522.

Targett, N. M., Boettcher, A. A., Targett, T. E., & Vrolijk, N. H. (1995). Tropical marine herbivore assimilation of phenolic-rich plants. *Oecologia*, 103(2), 170–179.

Targett, T. E. (1979). The effect of temperature and body size on digestive efficiency in *Fundulus heteroclitus* (L.). *Journal of Experimental Marine Biology and Ecology*, 38(2), 179–186.

Targett, T. E., & Targett, N. M. (1990). Energetics of food selection by the herbivorous parrotfish *Sparisoma radians*: roles of assimilation efficiency, gut evacuation rate, and algal secondary metabolites. *Marine Ecology Progress Series*, 66, 13–21.

van der Lingen, C. (1998). Nitrogen excretion and absorption efficiencies of sardine *Sardinops sagax* fed phytoplankton and zooplankton diets. *Marine Ecology Progress Series*, 175, 67–76.

Wallace, J. C. (1973). Observations on the relationship between the food consumption and metabolic rate of *Blennius pholis* L. *Comparative Biochemistry and Physiology Part A: Physiology*, 45(2), 293–306.

Weisberg, S. B., & Victor A., L. (1982). Ingestion, egestion, excretion, growth, and conversion efficiency for the mummichog, *Fundulus heteroclitus* (L.). *Journal of Experimental Marine Biology and Ecology*, 62(3), 237–249.

Yiu, B. A., Booth, D. J., Fowler, A. M., & Feary, D. A. (2019). Macroalgal resource use differences across age and size classes in the dominant temperate herbivorous fish *Aplodactylus lophodon* (Aplodactylidae). *Marine and Freshwater Research*, 70(4), 531–540.

Appendix 2 : Data collection and analysis

All data are available at Dryad under [doi:10.5061/dryad.g1jwstqq1].

All analyses were conducted using R version 3.6.1 Action of the Toes (R Core Team, 2019).

This document contains model output and model comparisons for all candidate models, but not the results of prior and posterior predictive checks. A reproducible script for all models, plots, and prior and posterior checks is available at https://github.com/nicoleknight0/meta-analysis-fish-digestion

1. Literature search and data collection

1.1 Eligibility criteria

For an estimate of gut passage time, absorption efficiency or gut length to be included in our meta-analysis it had to have the following characteristics:

1) Taken from marine or estuarine fish species
2) Taken from non-larval individuals
3) Not taken from species that are strictly detritivorous or corallivorous
4) Not taken from individuals fed an artificial diet with optimized composition for nutrient uptake/digestion (i.e., as found in many aquaculture studies)
5) Not taken from individuals force-fed food items not typically consumed in the wild

and

6) In the case of gut length, reported some metric of body length or size.

We note that there exists a large body of literature on the “gastric evacuation rates” (the rate at which food leaves the stomach and enters the hindgut) of carnivores, which was developed as a method for indirectly estimating feeding rates by quantifying the minimum amount of time required for stomach clearance between meals (Bromley, 1994). We chose not to include this data in our analysis because: a) almost no data on gastric evacuation rates exists for herbivores so we could not make valid comparisons between trophic groups, and b) gastric evacuation rates have been estimated using a wide range of methods and models, and it is unclear under what circumstances comparisons between such models is meaningful (Bromley, 1994). Gut passage time has been quantified for both herbivores and carnivores and is a more easily comparable metric.

1.2 Information sources and search

We searched Web of Science, JSTOR, and Google Scholar. 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 relevant papers found incidentally. Altogether, we included papers published between 1958 and March 2020. All search term combinations included marine and fish, as well as the following combinations of additional search terms (but not all search term combinations were used for all databases): assim*, assimilation eff*, absorption, absorption eff*, “absorption efficiency”, “assimilation efficiency”, excret*, egest*, conversion, “gut length”, “gut morphology”, gut passage, gut transit, “gut passage time”, “gut transit time”, digest*, digest* + temperature. We initially excluded studies if their titles or abstracts were not relevant, then checked the remaining studies for data that met the eligibility criteria described above. By the end of this process, 99 studies were eligible for inclusion in the meta-analysis.

1.3 Data collection

Data were extracted from text, tables, and figures in the accepted studies. We collected temperature and diet as predictor variables, as well as body length, since many biological traits scale with size (Brown et al., 2004). However, metrics of body size in reported in collected studies varied widely. Metrics included standard length, total length, and fork length, these were further divided into average values, median values, maximum/minimum values, or no reported values. Whenever possible, we used the average body size; if this was not provided, we used the mid-range (maximum – minimum / 2) body size provided. We did not distinguish between standard, total and fork length. If fish mass but not length was reported, we used published length-weight relationships for the species in question to calculate fish length. These instances are noted in the raw data.

Ambient temperature was likewise not always included in all the studies included in our dataset, particularly for estimates of gut length. We supplemented these datasets by extracting the date and location of data collection from the study and used that data to find the local sea surface temperature (SST) at the time of sampling from the COBE SST data provided by NOAA/OAR/ESRL PSD via http://www.esrl.noaa.gov/psd/. On the rare occasion that the specific collection period was not included in the publication, we took the average temperature of the location for five years preceding publication of the data. These instances are noted in the data.

1.4 Risks of bias across studies

We identified two potential sources of bias across the studies in our dataset: the method used to calculate absorption efficiency (marker method or total collection), and the method used to calculate gut length (from esophagus to anus or pylorus to anus). We specifically address these sources of bias and how they were handled analytically in our descriptions of our analyses for each variable (*Section 4.1 Calculations of absorption efficiency*, *Section 5.1 Measurement of gut length*).

2. Data analysis strategy

The primary goal of our analyses was to test whether the digestive performance of marine herbivorous fishes is more negatively affected by low temperatures than carnivorous fishes. To achieve this goal, we analyzed data from four response variables (gut passage time, absorption efficiency and gut length) using a Bayesian framework as implemented by the R package 'brms' (Bürkner, 2018) to analyze our data. For each response variable (except nutrient concentrations), we competed several models against one another to test whether temperature, diet, and a temperature-diet interaction effect were meaningful predictors of the data.

For all models, we chose weakly regularizing priors for all regression coefficients. Uninformative, weakly regularizing priors reduce the risk of overfitting but can increase the probability of not detecting small effect sizes (McElreath, 2016). To check that our priors were reasonable, we ran prior predictive checks following Gabry et al. (2019). To generate posterior probability distributions for each model, we ran four chains of 8,000 iterations each (including 4,000 warm-up iterations). To determine that models converged appropriately we checked for high effective sample sizes, R-hat values of 1, trace plots and low Pareto-K values (using the 'loo' package; Vehtari et al. 2019). Following convention, we calculated 95% credibility intervals for all parameters. We also ran posterior predictive checks.

We used several tools to determine which models best described the data. First, we ran Pareto smoothed importance sampling leave-one-out cross-validation

(PSIS-LOO) to a) check the performance of individual models, and b) calculate model weights (where model weight estimates the probability that the candidate model best describes the data out of the competing set of models; Vehtari et al. 2019). We also used model stacking as an alternative form of model evaluation: model stacking assumes that the true data-generating model may not be included as a candidate model, and so jointly optimizes model weights to maximize predictive power across the entire set of models (Yao et al. 2018). This process has the effect of down-weighting models that make similar predictions (for examples, see https://cran.r-project.org/web/packages/loo/vignettes/loo2-weights.html). Because model weights calculated using PSIS-LOO can vary for models with relatively small sample sizes (Yao et al. 2018), we reran models and model weighting 10 – 12 times to estimate the standard error associated with all model weights. Finally, to evaluate the importance of individual predictors, we considered the magnitude of the estimated effect size of each explanatory variable and the position of its 95% credibility interval relative to zero.

3. Gut passage time

3.1 Model structure and priors

We modelled gut passage time following a gamma distribution (which is often used to model the duration of an event) with a ln link. All models were fitted using 89 estimates of gut passage time from 40 species. Only temperature, diet, and a temperature-diet interaction are included as fixed effects (Table 2S3.1); earlier versions of the models included ln(body length) as a fixed effect, but it was later removed because its parameter estimates were consistently centered on 0. We included species as a random effect to account for repeat sampling, but not study ID, as very few studies (4/33) tested multiple species. Prior definitions are shown in Table 2S3.2.

Table 2S3.1. Gut passage time model definitions. All models include species ID as a random effect.

Model	Model definition
GP.0	gut passage time ~ temperature
GP.1	gut passage time ~ temperature + diet
GP.2	gut passage time ~ temperature * diet

Table 2S3.2. Prior definitions for all gut passage time models.

Coefficient	Prior	Notes
Intercept	Normal(5, 1)	Corresponds to the log-transformed longest recorded gut passage time (estimated at 1°C)
Slope	Normal(0, 1)	For fixed effects

Standard deviation	Exponential(1)	For random effects
Shape parameter (φ)	Gamma(0.01, 0.01)	*brms* default; appears to behave well

3.2 Model performance

LOO-PSIS cross validation revealed that all models had a large number of observations with high Pareto K values, which indicate influential observations. Although high Pareto-K values can indicate that a model has been misspecified, in this case it is more likely that many observations are influential because many species are represented by only one estimate of gut passage time (see https://rdrr.io/github/stan-dev/loo/man/loo-glossary.html under "Pareto-K estimates"). Posterior predictive checks of all models (LOO-PIT, density overlay) indicate that the model estimates fit the data well, but the model estimates of "group" or "random" effects may be sensitive to new data.

3.3 Results

Our models support a temperature-diet interaction effect on the gut passage time of marine fishes (Table 2S3.3, S3.4). Model selection assigned the bulk of model weight (89 ± 2% SE of LOO weight; 80 ± 1% SE of stacking weight) to the temperature-diet interaction model (Table 2S3.3), followed by the temperature only model (7 ± 1% SE LOO weight; 20 ± 1% SE stacking weight) and the temperature + diet model (2% LOO weight, 0% stacking weight). The temperature-diet interaction model estimated that with decreasing temperature, digestion slows more for fishes consuming macroalgae than for carnivores consuming fish or invertebrates. However, a similar effect was not detected for fishes consuming diatoms, seagrass, or turf algae, though the available data for these categories (N = 10; 4; 2, respectively) were considerably more limited than for macroalgae (N = 42).

Table 2S3.3. Results of leave-one-out pareto-smoothed importance sampling (LOO-PSIS) model evaluations for gut passage time. GP.2 was selected as the best fitting model. All models include species ID as a random effect. elpd_loo is the expected log predictive density, p_loo is the effective number of parameters, and loo_ic is the LOO information criterion. All bracketed values are standard error estimates. Guidelines for interpreting these criteria is available at https://mc-stan.org/loo/reference/loo-glossary.html.

Model	Effects tested	elpd_loo	p_loo	loo_ic	LOO weight (%)	Stacked weight (%)
GP.0	temperature	-246.9 (10.8)	41.8 (5.0)	493.8 (21.6)	7 (1)	20 (1)

GP.1	diet + temperature	-248.4 (11.1)	45.6 (5.4)	496.8 (22.2)	4 (1)	0 (0)
GP.2	diet * temperature	-245.1 (11.8)	47.8 (6.2)	490.2 (23.5)	89 (2)	80 (1)

Table 2S3.4. Parameter estimates for the three models describing gut passage time of marine fishes. Square brackets indicate 95% confidence intervals.

Parameter	GP.0 (temperature)	GP.1 (diet + temperature)	GP.2 (diet * temperature)
Species	0.83 [0.64, 1.08]	0.83 [0.63, 1.08]	0.77 [0.56, 1.03]
Intercept	4.21 [3.67, 4.74]	4.46 [3.88, 5.06]	4.03 [3.42, 4.65]
Diet: diatoms	na	-0.58 [-1.21, 0.07]	-1.33 [-3.01, 0.37]
Diet: macroalgae	na	-0.42 [-0.96, 0.11]	0.84 [-0.10, 1.75]
Diet: seagrass	na	-0.08 [-0.68, 0.55]	-0.19 [-1.94, 1.55]
Diet: turf algae	na	0.22 [-0.87, 1.31]	-0.01 [-1.96, 1.93]
Diet: zooplankton	na	-0.53 [-1.14, 0.11]	0.04 [-1.66, 1.74]
Temperature	-0.11 [-0.13, -0.09]	-0.11 [-0.13, -0.09]	-0.09 [-0.11, -0.07]
Temperature-diatoms	na	na	0.04 [-0.05, 0.12]

Temperature-macroalgae	na	na	-0.06 [-0.10, -0.02]
Temperature-seagrass	na	na	0.00 [-0.09, 0.09]
Temperature-turf algae	na	na	0.01 [-0.08, 0.09]
Temperature-zooplankton	na	na	-0.03 [-0.12, 0.05]

4. Absorption efficiency

4.1 Calculation of absorption efficiency

In the primary literature, absorption efficiency was calculated as a percentage of the nutrient or component absorbed during digestion, where an absorption efficiency of 0% means all of the nutrient was egested, and 100% means all of the nutrient or component was absorbed for use by the fish. These estimates were calculated using either the total collection method, in which the quantities of nutrient in the food and feces were directly compared (Eq. 1):

$$(Eq. 1) \quad absorption\ efficiency = \frac{nutrient\ in\ food - nutrient\ in\ feces}{nutrient\ in\ food}$$

or using the ash-marker method, in which it assumed that ash is not absorbed by the fish during digestion and can thus be used to standardize nutrient absorption (Eq. 2):

$$(Eq. 2) \quad absorption\ efficiency = \left(1 - \frac{\%\ ash\ in\ food}{\%\ ash\ in\ feces} x \frac{\%\ nutrient\ in\ feces}{\%\ nutrient\ in\ food}\right) x\ 100$$

However, absorption efficiencies calculated using the ash marker method are typically lower than those using the total collection method (Galetto & Bellwood 1994, Pandian & Marian 1995), so “method” was included as an effect in all of our analyses.

4.2 Model structure and priors

We modelled absorption efficiency following a beta distribution, which is appropriate for double-bounded data (Smithson & Shou 2020). All models were fitted using 500 estimates of absorption efficiency across 50 species. Data were transformed using a logit link. All models include "component" (what is being absorbed, e.g., protein or organic material or energy) and "method" (marker or total collection, see above) as population-level or “fixed” effects (Table 2S4.1). Earlier versions of the models included ln(body length) as a fixed effect, but ln(body length) was later removed because estimates of this parameter were consistently centered on 0. All models included species ID and study ID as group-level or "random" effects to account for repeat sampling. Prior definitions are shown in Table 2S4.2.

Table 2S4.1. Absorption efficiency model definitions. All models include species ID and study ID as random effects.

Model	Model definition
AE.0	absorption efficiency ~ component + method
AE.1	absorption efficiency ~ diet + component + method
AE.2	absorption efficiency ~ temperature + diet + component + method
AE.3	absorption efficiency ~ temperature * diet + component + method

Table 2S4.2. Prior definitions for all absorption efficiency models.

Coefficient	Prior	Notes
Intercept	Normal(0, 1)	Corresponds to logit-transformed 50% efficiency

Slope	Normal(0, 1)	For fixed effects
Standard deviation	Exponential(1)	For random effects
Precision parameter (φ)	Exponential(1)	*brms* default was too wide

4.3 Results

Our models support an effect of diet but not temperature on absorption efficiency in fishes (Table 2S4.3; Figure S4.1). Model selection assigned 48 ± 2% SE of LOO weight (83 ± 4% SE stacked weight) to the diet-only model (Table 2S4.3), followed by the temperature-diet interaction model (22 ± 1% SE LOO; 17 ± 4% SE stacked) and the temperature + diet model (30 ± 2% SE LOO; 0 ± 0% SE stacked). The diet-only model estimated that absorption efficiencies are lower for herbivores than carnivores, but estimates of absorption efficiency were similar for herbivores consuming different diets (e.g., macroalgae vs. diatoms) and carnivores consuming different diets (Table 2S4.4). Absorption efficiencies quantified using the total collection method are on average 23% higher than those quantified using the ash marker method, but the estimated 95% CI of this effect overlapped 0 (mean 0.29, 95% CI: [-0.07, 0.62]), likely due to the inclusion of one study (Boyce et al. 2000) which provided estimates of total absorption that were considerably lower than those using an ash marker method.

Table 2S4.3. Results of leave-one-out Pareto-smoothed importance sampling (LOO-PSIS) model evaluations for the absorption efficiency of marine fishes. AE.1 was selected as the best fitting model. All models include component and method as fixed effects and species ID as a random effect. elpd_loo is the expected log predictive density, p_loo is the effective number of parameters, and loo_ic is the LOO information criterion. All bracketed values are standard error estimates. Guidelines for interpreting these criteria is available at https://mc-stan.org/loo/reference/loo-glossary.html.

Model	Effects tested	elpd_loo	p_loo	loo_ic	LOO weight (%)	Stacked weight (%)
AE.0	none	357.3 (19.2)	47.1 (3.7)	-714.5 (38.4)	0 (0)	0 (0)
AE.1	diet	369.8 (19.9)	47.2 (4.0)	-739.6 (39.7)	48 (2)	83 (4)
AE.2	diet + temperature	369.0 (19.9)	47.9 (4.0)	-738.1 (39.8)	30 (2)	0 (0)
AE.3	diet * temperature	369.2 (20.0)	49.4 (4.1)	-738.4 (40.0)	22 (1)	17 (4)

Table 2S4.4. Parameter estimates for the four models describing absorption efficiency of marine fishes. Square brackets indicate 95% confidence intervals.

Parameter	AE.0 (null)	AE.1 (diet)	AE.2 (diet + temperature)	AE.3 (diet * temperature)
Species	0.50 [0.18, 0.79]	0.37 [0.13, 0.57]	0.37 [0.15, 0.57]	0.34 [0.08, 0.56]
Study ID	0.47 [0.14, 0.81]	0.27 [0.03, 0.50]	0.27 [0.04, 0.51]	0.30 [0.05, 0.55]
Intercept	0.34 [0.00, 0.70]	0.99 [0.59, 1.40]	0.97 [0.43, 1.52]	0.93 [0.35, 1.55]
Diet: diatoms	na	-1.06 [-1.65, -0.47]	-1.06 [-1.67, -0.46]	0.11 [-1.76, 1.98]
Diet: fish	na	0.51 [-0.09, 1.14]	0.51 [-0.08, 1.14]	0.68 [-0.51, 1.88]
Diet: macroalgae	na	-0.93 [-1.32, -0.52]	-0.93 [-1.33, -0.51]	-1.01 [-1.85, -0.12]
Diet: seagrass	na	-1.03 [-1.52, -0.54]	-1.04 [-1.54, -0.54]	-0.75 [-2.39, 0.91]
Diet: turf algae	na	-1.41 [-1.96, -0.85]	-1.42 [-2.00, -0.85]	-0.00 [-1.89, 1.90]
Diet: zooplankton	na	-0.19 [-0.74, 0.38]	-0.19 [-0.75, 0.38]	0.81 [-0.60, 2.18]

Component: carbohydrate	-0.20 [-0.50, 0.11]	-0.18 [-0.47, 0.12]	-0.18 [-0.47, 0.12]	-0.16 [-0.46, 0.14]
Component: carbon	0.33 [0.01, 0.65]	0.40 [0.09, 0.71]	0.40 [0.09, 0.71]	0.41 [0.10, 0.72]
Component: energy	0.79 [0.53, 1.06]	0.75 [0.50, 1.01]	0.75 [0.49, 1.02]	0.75 [0.50, 1.01]
Component: lipid	0.09 [-0.19, 0.38]	0.08 [-0.19, 0.36]	0.08 [-0.20, 0.36]	0.09 [-0.19, 0.37]
Component: nitrogen	0.74 [0.48, 1.00]	0.83 [0.58, 1.08]	0.82 [0.57, 1.07]	0.83 [0.58, 1.09]
Component: organic	0.37 [0.07, 0.66]	0.44 [0.16, 0.72]	0.43 [0.15, 0.71]	0.44 [0.16, 0.72]
Component: protein	1.13 [0.85, 1.40]	1.18 [0.91, 1.45]	1.18 [0.91, 1.45]	1.19 [0.92, 1.46]
Method: total collection	0.52 [0.05, 0.94]	0.31 [-0.04, 0.64]	0.31 [-0.05, 0.62]	0.24 [-0.13, 0.59]
Temperature	na	na	0.00 [-0.02, 0.02]	0.01 [-0.02, 0.04]
Temperature-diatoms	na	na	na	-0.07 [-0.18, 0.03]

Temperature-fish	na	na	na	-0.02 [-0.08, 0.05]
Temperature-macroalgae	na	na	na	-0.01 [-0.05, 0.04]
Temperature-seagrass	na	na	na	-0.02 [-0.09, 0.05]
Temperature-turf algae	na	na	na	-0.07 [-0.14, 0.01]
Temperature-zooplankton	na	na	na	-0.06[-0.13, 0.01]

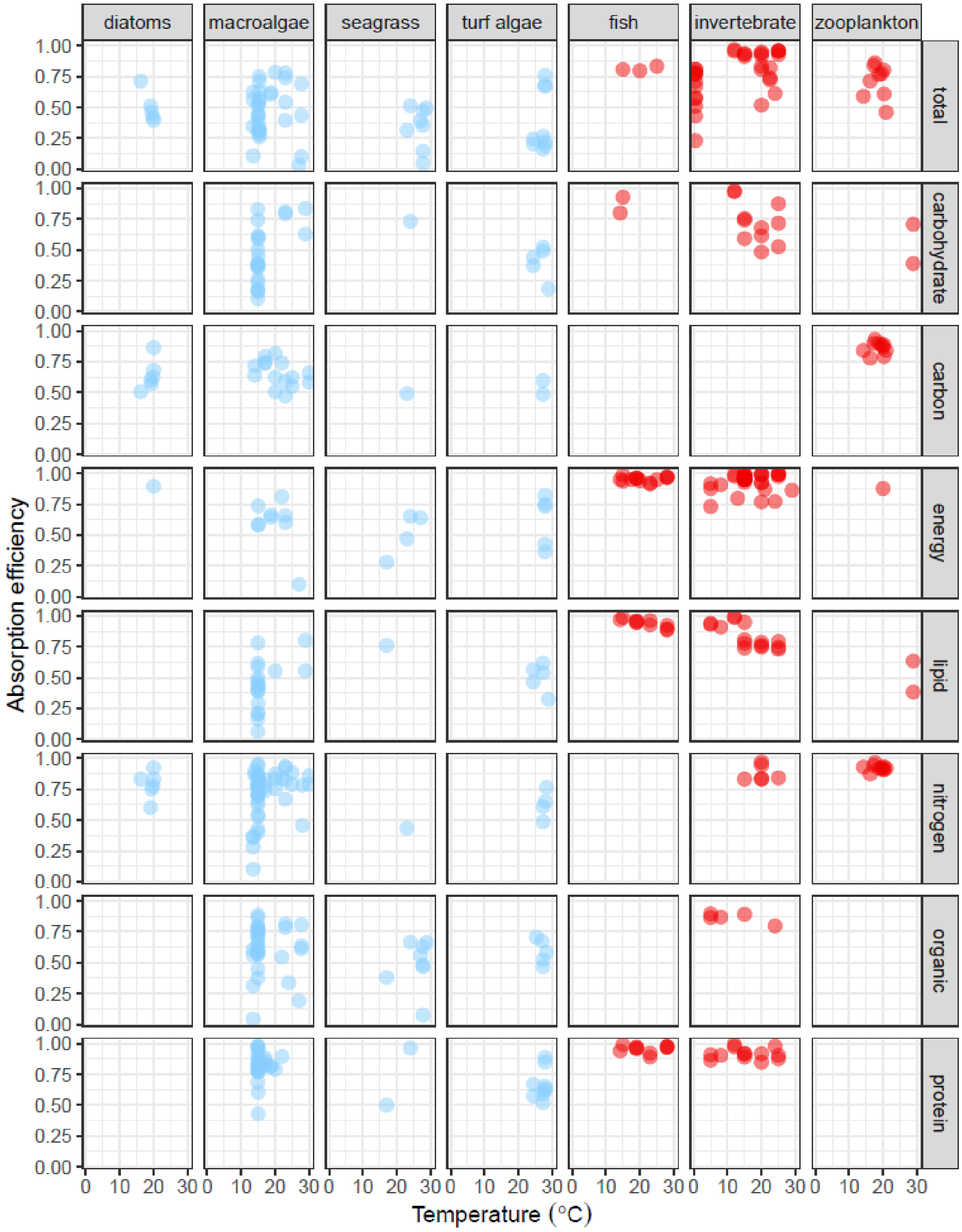

Figure 2S2.1. Absorption efficiency estimates (n = 500) for the 50 species of marine fish included in this analysis across temperature. Data are separated by diet and the type of component absorbed. 0 is no nutrient absorbed during digestion, 1 is complete absorption of the nutrient during digestion.

5. Gut length

5.1 Measurement of gut length

We only accepted gut length data from individuals that were collected from the field and immediately dissected, or immediately preserved after collection and later dissected to preclude effects of captivity or diet manipulation on gut morphology. Gut length was measured one of two ways. Researchers either a) dissected out the entire length of the digestive tract (from esophagus to anus), or b) dissected out just the intestinal portion of the digestive tract (from pylorus to anus). We recorded which method was used, and initially accounted for it in our models by including an additional parameter for calculation type. However, the model predicted that the intestine-only measurements were higher than the entire gut measurements, suggesting that species selected for intestine-only measurements tended to have longer guts, and so this parameter was dropped from subsequent models.

5.2 Model structure and priors

We modelled gut length following a lognormal distribution to account for the allometric relationship between gut length and body length (Table 2S5.1; Kerkhoff &

Enquist 2009). All models were fitted using 249 estimates of gut length across 249 species. Data were transformed using a ln link. All models include ln-transformed body length as a fixed effect and phylogenetic order as a random effect (as general body form can affect gut length; Karachle & Stergiou 2010). Species was not included as a random effect because many species were represented only once in the dataset, causing many estimates to have Pareto-K estimates exceeding 0.7 and slowing leave-one-out cross validation to the point of impracticality. Thus, we restricted our analysis to one estimate of gut length per species. For species with multiple estimates of gut length, we first excluded reports of poorer quality (e.g., no reported temperature), then randomly selected from the remaining estimates. Study ID was included as a random effect. Prior definitions are shown in Table 2S5.2.

Table 2S5.1. Gut length model definitions. All models include study ID and phylogenetic order as random effects.

Model	Model definition
GL.0	gut length ~ ln(body length)
GL.1	gut length ~ diet + ln(body length)
GL.2	gut length ~ temperature + diet + ln(body length)
GL.3	gut length ~ temperature * diet + ln(body length)

Table 2S5.2. Prior definitions for all gut length models.

Coefficient	Prior	Notes
Intercept	Normal(0, 2)	Gives a gut length of 1 mm at 1mm body length.
Slope	Normal(0, 1)	For fixed effects
Standard deviation	Exponential(1)	For random effects
Variance (σ)	Exponential(1)	

5.3 Model performance

LOO-PSIS cross validation revealed that all models had several observations with high Pareto K values, which indicate influential observations. Although high Pareto-K values can indicate that a model has been misspecified, in this case it is likely that many observations are influential because many studies are represented by only one estimate of gut passage time (see https://rdrr.io/github/stan-dev/loo/man/loo-glossary.html under "Pareto-K estimates"). Posterior predictive checks of all models (LOO-PIT, density overlay) indicate that the model estimates fit the data well, but the model estimates of group effects may be sensitive to new data.

5.4 Results

The best selected model supports an effect of temperature and diet on gut length in fishes (Table 2S5.3). Model selection assigned 74 ± 2% SE of LOO weight (76 ± 3% SE of stacked weight) to the temperature + diet model (Table 2S5.3). The selected model predicted that gut length decreases with decreasing temperature and is greater for fishes consuming herbivorous diets. Gut length was similar across fishes consuming different types of herbivorous diets, and within fishes consuming different types of carnivorous diets (Table 2S5.4).

Table 2S5.3. Results of leave-one-out pareto-smoothed importance sampling (LOO-PSIS) model evaluations for the gut length of marine fishes. GL.2 was selected as the best fitting model. All models include ln(length) as a fixed effect and phylogenetic order as a random effect. elpd_loo is the expected log predictive density, p_loo is the effective number of parameters, and loo_ic is the LOO information criterion. All bracketed values are standard error estimates. Guidelines for interpreting these criteria is available at https://mc-stan.org/loo/reference/loo-glossary.html.

Model	Effects tested	elpd_loo (SE)	p_loo (SE)	loo_ic (SE)	LOO weight (%)	Stacked weight (%)
GL.0	-	-1389.4 (23.8)	42.2 (3.8)	2778.8 (47.6)	0 (0)	5 (0)

GL.1	diet	-1340.5 (25.1)	52.0 (5.4)	2681.1 (50.1)	4 (1)	0 (0)
GL.2	temperature + diet	-1337.5 (25.0)	49.9 (5.2)	2675.0 (49.9)	74 (2)	76 (3)
GL.3	temperature *diet	-1338.6 (24.7)	53.4 (5.3)	2677.1 (49.4)	21 (2)	19 (3)

Table 2S5.4 Parameter estimates for the four models describing gut length of marine fishes. Square brackets indicate 95% confidence intervals.

Parameter	GL.0 (null)	GL.1 (diet)	GL.2 (diet + temperature)	GL.3 (diet * temperature)
Phylogenetic order	0.49 [0.32, 0.71]	0.29 [0.15, 0.46]	0.31 [0.17, 0.48]	0.29 [0.15, 0.45]
Study ID	0.62 [0.46, 0.81]	0.51 [0.38, 0.68]	0.43 [0.31, 0.59]	0.43 [0.31, 0.59]
Intercept	-0.56 [-1.34, 0.21]	-0.76 [-1.37, -0.16]	-1.74 [-2.54, -0.93]	-1.54 [-2.39, -0.66]
ln(body length)	1.17 [1.03, 1.32]	1.14 [1.02, 1.25]	1.18 [1.06, 1.30]	1.18 [1.06, 1.30]
Diet: diatoms	na	0.99 [0.60, 1.37]	0.89 [0.51, 1.28]	1.25 [0.21, 2.27]
Diet: fish	na	-0.08 [-0.32, 0.16]	-0.09 [-0.32, 0.15]	-0.20 [-0.79, 0.39]
Diet: herbivore-detritivore	na	1.14 [0.86, 1.41]	1.11 [0.83, 1.39]	-0.14 [-2.04, 1.74]

Diet: invertebrates and fish	na	-0.03 [-0.21, 0.14]	-0.04 [0.21, 0.13]	-0.42 [-0.95, 0.11]
Diet: macroalgae	na	0.79 [0.51, 1.06]	0.78 [0.51, 1.04]	0.59 [-0.35, 1.51]
Diet: omnivore	na	0.34 [0.18, 0.51]	0.33 [0.16, 0.49]	-0.06 [-0.61, 0.48]
Diet: turf algae	na	1.07 [0.76, 1.38]	1.03 [0.73, 1.34]	0.96 [-0.39, 2.29]
Diet: zooplankton	na	0.01 [-0.28, 0.31]	-0.01 [-0.29, 0.28]	0.85 [-0.39, 2.08]
Temperature	na	na	0.04 [0.02, 0.06]	0.03 [0.01, 0.05]
Temperature-diatoms	na	na	na	-0.02 [-0.07, 0.03]
Temperature-fish	na	na	na	0.00 [-0.03, 0.03]
Temperature-HD	na	na	na	0.05 [-0.02, 0.12]
Temperature-I/F	na	na	na	0.02 [-0.01, 0.04]
Temperature-macroalgae	na	na	na	0.01 [-0.04, 0.05]
Temperature-omnivore	na	na	na	0.02 [-0.01, 0.04]
Temperature-turf algae	na	na	na	0.00 [-0.05, 0.06]

Temperature-zooplankton	na	na	na	-0.04 [-0.09, 0.02]

6. Nutrient composition

6.1 Model structure and priors

We modelled food composition data in two different ways. For percent composition data, we used the beta distribution with a logit link for the same reasons as described for the absorption efficiency data. For the energy content data, which was not expressed as a percentage but as *kJ energy / g dry mass*, we used the Gaussian distribution. We built models to test each of the following dietary components separately, to avoid unwanted correlations (as nutrient concentrations must sum to 100%, they are inevitably interdependent, organic content and ash content must also sum to 100%). We tested for an effect of food type (plant or animal) on the dry mass concentration of the following dietary components: nitrogen, carbon, protein, carbohydrates, lipid, organic, ash and energy. We did not test across more specific diet classifications (e.g., diatoms, macroalgae, zooplankton) because of small sample sizes. Priors are shown in Table 2S6.1.

Table 2S6.1. Prior definitions for all food composition models.

Coefficient	Prior	Notes
Percent composition		
Intercept	Normal(0, 1)	Corresponds to 50% of food content
Slope	Normal(0, 1)	For fixed effects
Precision parameter (φ)	Gamma(0.01, 0.01)	*brms* default; appears to behave well
Energy		
Intercept	Normal(13.9, 5)	Corresponds to the average energy content of food in the dataset
Slope	Normal(0, 5)	For fixed effects
Variance	Exponential(1)	

6.2 Results

The plant food items fed to herbivorous fishes in our analysis were nutrient-poor compared to food items fed to carnivores (Table 2S5.4). Plant food items had significantly lower concentrations of energy, nitrogen, carbon, protein, and lipids than animal food items. Notably, there was a large difference in protein content between plant and animal material, as well as nitrogen content and energy content (Table 2S5.4).

Table 2S5.4 Parameter estimates for the four models describing differences in nutrient concentration between animal (intercept) and plant food items. Square brackets indicate 95% confidence intervals. Each row represents a separate model. Estimates for all components except energy are logit-transformed.

Nutrient/component	Intercept	Diet
Carbohydrate	-1.39 [-1.94, -0.85]	0.84 [0.22, 1.46]
Carbon	-0.53 [-0.81, -0.25]	-0.57 [-0.90, -0.24]
Energy	18.40 [16.44, 20.34]	-7.09 [-9.47, -4.64]
Lipid	-2.44 [-2.79, -2.09]	-0.77 [-1.22, -0.28]
Nitrogen	-2.29 [-2.42, -2.16]	-1.35 [-1.54, -1.14]
Organic	0.92 [0.50, 1.36]	-0.45 [-0.94, 0.03]
Protein	0.29 [-0.01, 0.60]	-2.57 [-2.96, -2.15]

References

Bromley, P. J. (1994). The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. *Reviews in Fish Biology and Fisheries*, 4(1), 36–66.

Bürkner, P. (2018). Advanced Bayesian Multilevel Modeling with the R Package brms. *The R Journal*, 10(1), 395-411.

Elliott, J. P., & Bellwood, D. R. (2003). Alimentary tract morphology and diet in three coral reef fish families. *Journal of Fish Biology*, 63(6), 1598–1609.

Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in Bayesian workflow. *Journal of the Royal Statistical Society: Series A (Statistics in Society)*, 182(2), 389–402.

Galetto, M. J., & Bellwood, D. R. (1994). Digestion of algae by *Stegastes nigricans* and *Amphiprion akindynos* (Pisces: Pomacentridae), with an evaluation of methods used in digestibility studies. *Journal of Fish Biology*, 44(3), 415–428.

Karachle, P. K., & Stergiou, K. I. (2010). Gut length for several marine fish: Relationships with body length and trophic implications. *Marine Biodiversity Records*, 3.

Kerkhoff, A. J., & Enquist, B. (2009). Multiplicative by nature: Why logarithmic transformation is necessary in allometry. *Journal of Theoretical Biology*, 257(3), 519–521.

McElreath, R. (2015). Statistical Rethinking: A Bayesian Course with Examples in R and Stan. Boca Raton, UNITED STATES: Chapman and Hall/CRC.

Pandian, T. J., & Marian, M. P. (1985). Nitrogen content of food as an index of absorption efficiency in fishes. *Marine Biology*, 85(3), 301–311.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Smithson, M., & Shou, Y. (2020). Generalized Linear Models for Bounded and Limited Quantitative Variables. Sage Publishing.

Vehtari A., Gabry J., Magnusson M., Yao Y., Gelman A. (2019). loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.2.0, https://mc-stan.org/loo.

Yao, Y., Vehtari, A., Simpson, D., & Gelman, A. (2018). Using Stacking to Average Bayesian Predictive Distributions (with Discussion). *Bayesian Analysis*, 13(3), 917–1007.

Connecting statement: from global to regional patterns of performance and distribution

The meta-analysis I conduct in Chapter 2 took a documented pattern of distribution (herbivorous fishes are less common at high latitudes), and tested a physiological hypothesis that sought to explain it (digesting plant material is more difficult at low temperatures). In Chapter 3, I examine a system in which we expect seasonal upwelling to have strong physiological effects, and test for links between those physiological effects and patterns of distribution across a highly heterogeneous region. Chapter 2 limited its focus to the effects of a single environmental predictor (temperature) on the digestive performance of individuals across a broad spatial scale, and Chapter 3 expands on this work by considering the interactive effects of both temperature and resource availability.

The results from Chapter 2 explicitly inform the questions I test in Chapter 3. My finding that the strength of the temperature dependence of digestion varies with the type of resource consumed led me to test how temperature variation associated with seasonal upwelling impacts resource uptake by tropical damselfishes consuming different diets. Similarly, my finding that interspecific variation in species’ gut lengths is associated with temperature impelled me to consider whether seasonal variation in temperature and resource availability could cause differences in optimal gut length. Altogether, Chapter 3 allowed me to test, at a higher resolution, relationships hinted at in Chapter 2.

Chapter 3: Damselfish performance predicts distribution across a tropical upwelling mosaic

Nicole S. Knight, Andrew J. Sellers, Frédéric Guichard, Matthieu Leray, Mark E. Torchin, Andrew H. Altieri

Abstract

Local abiotic conditions, through their control of individual performance, are expected to drive large-scale patterns of species abundance. In coastal systems upwelling leads to declines in temperature and increases in resource availability, but it is unclear whether these changes consistently benefit resident fish consumers, and the extent to which these physiological effects predict regional patterns of distribution. We tested how upwelling in the Tropical Eastern Pacific affects the physiology and distribution of three damselfish species (*Abudefduf troschelii*, *Microspathodon dorsalis*, and *Stegastes flavilatus*) common to the region. We tested for physiological effects by collecting fishes from Las Islas Perlas during the upwelling and non-upwelling seasons. We found that the body condition of two of our focal species (*M. dorsalis* and *S. flavilatus*) improved during seasonal upwelling, likely due to increased resource availability, but the body condition of *A. troschelii* did not measurably change. Increased resource uptake during the upwelling season appears to have been facilitated by plasticity in species' diets and digestive physiology. To test whether damselfish distribution is correlated with upwelling-driven productivity maxima and thermal minima, we built spatially explicit species distribution models. We found that the two species with improved body condition under upwelling had increased biomass and probability of occurrence under stronger upwelling conditions, whereas the species that had unchanged body condition did not. Altogether, our results suggest that the physiological effects of upwelling affect patterns of damselfish distribution, and demonstrate how information across scales can be combined to improve ecological inference.

Introduction

Classic ecological theory predicts that species abundance and occupancy are shaped by individual performance as a function of local abiotic conditions (Brown, 1984; Grinnell, 1917; Hutchinson, 1957, 1978). These general expectations are supported by accumulating evidence showing that individual performance (measured as resource uptake relative to demand, growth rates, and reproductive output) is positively associated with patterns of occupancy and abundance (Brambilla & Ficetola, 2012; Duncan et al. 2020; Lee-Yaw et al., 2016; Lunghi et al., 2018; Melis et al., 2010). However, this association is not absolute, and may be overridden by other factors (Dallas et al., 2017). Individual performance and species abundance may become decoupled in the presence of strong biotic interactions including competition, herbivory and predation (Campbell et al., 2018; Jones et al., 2013; Polis & Hurd 1995; Unglaub et al., 2018). These relationships can also be complicated by local adaptation and plasticity (Conover & Present, 1990; Sackett et al., 2013), increasing the difficulty of predicting species' responses across broad geographic regions. Thus, substantiating whether relationships between environment, performance, and abundance as put forth by foundational theory requires renewed efforts to collect information at different ecological scales to mechanistically link individual performance to patterns of species abundance.

In marine systems, oceanographic processes control local abiotic conditions and consequently can have strong effects on individual performance (Catry et al., 2013; Kroeker et al., 2016; Lester et al., 2007; Sanford, 2002). This is perhaps best exemplified by upwelling, a phenomenon in which surface waters are pushed offshore allowing deeper waters to rise to the surface, causing decreased temperature and increased resource availability in coastal ecosystems (D'Croz & O'Dea, 2007; Palacios et al., 2013; Thiel et al., 2007). These environmental changes typically benefit pelagic and extratropical species: increased resource availability under upwelling conditions increases growth rates, speeds up the onset of reproduction, and improves body condition (Aldana et al., 2017; Brosset et al., 2015;

Fuentes et al., 2017; Pulgar et al., 2013; Zuloaga et al., 2023). In turn, fish abundance is commonly greater in upwelling regions (Rykaczewski & Checkley, 2008; Schilling et al., 2022; Ware & Thomson, 1991).

Despite these examples, it is not clear whether increased productivity under upwelling conditions benefits all fishes. The effects of upwelling on primary productivity and temperature varies substantially within and across upwelling regions (Kämpf & Chapman, 2016; Patti et al., 2008). Coastal habitats may experience relatively large declines in temperature but limited increases in primary productivity, or vice-versa, depending on local conditions (Kämpf & Chapman, 2016). The duration of upwelling can also impact the availability of different types of resources. Plankton concentrations tend to be higher under intermittent rather than persistent upwelling regimes (Menge & Menge, 2013); similarly, different upwelling regimes can favour different types of benthic algae (Nielsen & Navarrete, 2004; Sellers et al., 2021). Thus, fishes consuming different diets, e.g., fishes feeding from planktonic vs. benthic sources, may not benefit to the same degree under different upwelling regimes.

Temperature may also limit the ability of fishes to benefit from increased resource availability under upwelling conditions (Sato et al., 2018). As temperatures decrease, rates of feeding and digestion slow (Barneche et al., 2009; Brown et al., 2004; Clarke & Johnston, 1999; Knight et al., 2021; Smith, 2008). If resource uptake declines faster with decreasing temperature than resource demand, consumers may experience energetic deficits and impaired performance (Brodersen et al., 2011; Floeter et al., 2005; Lemoine & Burkepile, 2012). This phenomenon has been observed in tropical fishes, which slow or cease feeding at temperatures approaching their critical thermal minimum (CTMin) (Beck et al., 2016; Eme & Bennett, 2008; Figueira et al., 2009). However, the feeding and digestive physiology of fishes are plastic in response to variation in resource quality, availability, and temperature (Caceres et al., 1994; Horn et al., 1986; Logothetis, 2001; Moran et al., 2019; Rowe et al., 2018; Sepulveda & Moeller, 2020). Fishes could compensate for the expected decreases in feeding and digestion rate due to low temperatures if they are able to feed on higher-quality food, or lengthen their guts to increase their maximum digestive capacity.

In the Tropical Eastern Pacific (TEP), seasonal upwelling events lasting several months each year cause annual resource booms and drive down sea surface temperatures (SST; D'Croz & O'Dea, 2007; Stuhldreier et al., 2015). The effects of upwelling on fishes in the region likely vary across species: thermal lows during the upwelling season overlap with the CTMin of some species, but not others (Graham, 1971, 1972; Mora & Ospina, 2002). Similarly, low temperatures during the upwelling season lead to increased reproductive activity for some species, and decreased activity for others (Foster, 1987; Robertson, 1990). Independent of their direct effects on organisms' physiologies, upwelling may have complex effects on predation (Meekan et al., 2001; Menge & Menge, 2013; Witman et al., 2010), habitat availability (Enochs et al., 2021; Pérez-Matus et al., 2017) and recruitment (Borja et al., 1998; Schilling et al., 2022), potentially obscuring associations between individual performance and patterns of fish biomass and occupancy.

Given this complexity, we suggest that these predictions are best tested by synthesizing individual performance data with broad-scale distribution models. This approach, in a system characterized by strong environmental forcing and ecologically distinct fishes presents an opportunity to test not only for interspecific variation in the relationship between upwelling and fish performance, but whether this relationship is strong enough to measurably impact patterns of distribution. In this study, we tested two research questions with an integrated approach that included both in situ fish sampling and models of species' abundance and occupancy with three species of tropical damselfish (*Abudefduf troschelii*, *Microspathodon dorsalis*, *Stegastes flavilatus*; Family Pomacentridae) found across the TEP in regions with different intensities of seasonal upwelling:

First, how does seasonal upwelling affect resource uptake by our three focal species? To answer our first research question, we collected damselfish from Las Islas Perlas during both the non-upwelling and upwelling seasons, and quantified changes in their diet, digestive morphology, and body condition (gutless body mass standardized to length) (Jakob et al., 1996; Rennie & Verdon, 2008). We predicted that plastic changes in diet and digestion across seasons could help damselfishes cope with low temperatures by allowing them to consume more or higher-quality food. We also predicted that if resource uptake exceeds demand, body condition would improve during the seasonal upwelling season.

Second, how does spatial variation in upwelling conditions influence patterns of damselfish distribution? To answer our second research question, we built spatially explicit species' distribution models (SDMs) to test whether damselfish biomass or occupancy are associated with variation in upwelling conditions across the TEP. We expected that seasonal temperature and resource availability changes associated with upwelling would have opposing effects on damselfish biomass: we predicted that damselfish biomass would increase with maximum annual primary productivity, and decrease with decreasing minimum annual temperature. As an alternative to our upwelling-centric hypotheses, we predicted that damselfish biomass would increase with minimum annual productivity.

We found that our integrative approach both allowed us to test a pattern expected by classic ecological theory, while at the same time explaining apparent discrepancies between the individual- and population-level responses to environmental drivers.

Methods

Study system

Along the Pacific coast of Central America, seasonal upwelling occurs in the Gulfs of Tehuantepec, Papagayo, and Panama, where topographic depressions in the Central American cordillera permit the passage of strong winds across the isthmus during boreal winter (D'Croz & O'Dea, 2007; Xie et al., 2005) . These winds push surface waters offshore and cause deep waters to well up, resulting in several months of decreased water temperature and increased nutrient availability (Figure 3.1; D'Croz & O'Dea, 2007; Sellers et al., 2021). In contrast, adjacent regions that experience no or minimal seasonal upwelling are relatively warm, nutrient-poor, experience little seasonal variation, and have markedly different community structure and dynamics from upwelling regions (D'Croz & O'Dea, 2007; Sellers et al., 2021). To test whether the strength of seasonal upwelling impacts damselfish distribution, we analyzed patterns of damselfish biomass and occupancy (with a species distribution model described below) along the Pacific coast of Central

America, from Panama to southern Nicaragua (the region over which data were available from Reef Life Survey; Figure 3.1). This area encompasses two regions that experience strong seasonal upwelling, Panamá and Rivas, which are separated by Chiriquí, Puntarenas and Guanacaste.

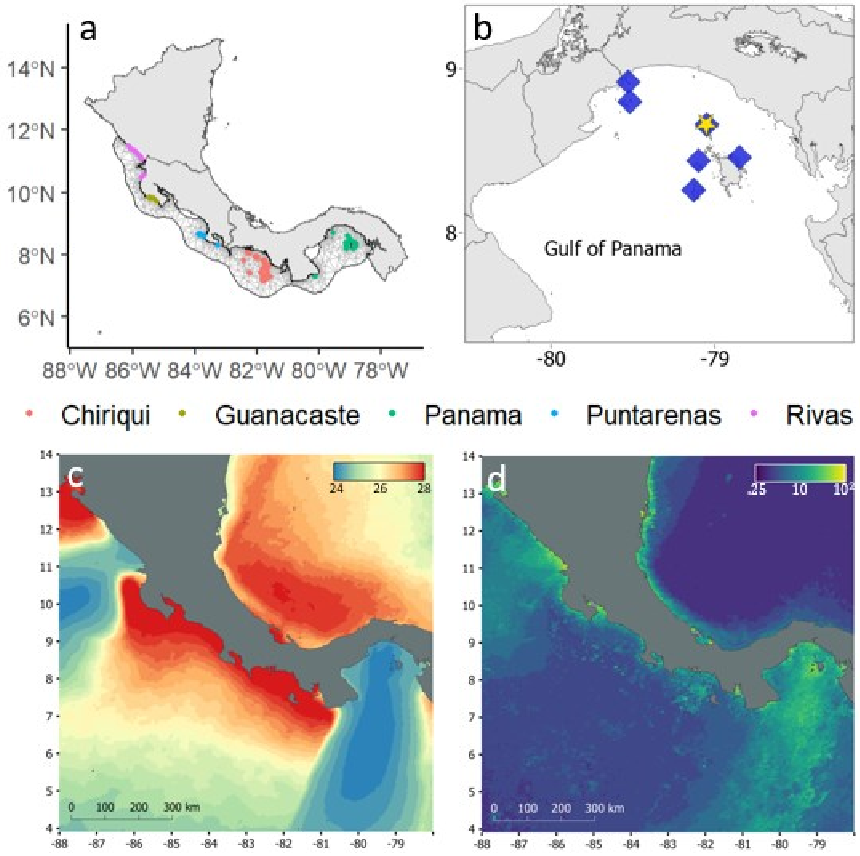

Figure 3.1. Maps of Central America and the Tropical Eastern Pacific (TEP) showing (a) the mesh used in all distribution models (grey lines), with Reef Life Survey sites (points) distinguished by region, (b) our fish collection sites in Las Islas Perlas (star) and STRI SST monitoring sites (blue diamonds), (c) annual minimum sea surface

temperature in the TEP, and (d) annual maximum net primary productivity in the TEP.

To quantify the effects of seasonal upwelling on the physiology of damselfishes, we collected three species of damselfish (*Abudefduf troschelii*, *Microspathodon dorsalis*, and *Stegastes flavilatus*) from Las Islas Perlas in the Gulf of Panama, which experiences strong seasonal upwelling from December to April of each year. We chose to sample fishes from within the Pomacentridae family to constrain phylogenetic variation, while still capturing variation in diet and behaviour. We collected fish during the non-upwelling (November to early December 2018) and upwelling (March to early April 2019) seasons from two reefs, at Isla Pacheca and Islote Saboga. Both sites were characterized by rocky reefs with *Pocillopora* corals on the surrounding sand flats.

Testing how seasonal upwelling impacts fish performance

To characterize seasonal upwelling in the Gulf of Panama, we measured temperature and chlorophyll-α concentrations at both sites during each sampling trip (6 trips during the non-upwelling season, 9 trips during the upwelling season) We measured temperature at the surface, 1m below the surface, and 5m below the surface using a YSI Pro-Plus (upwelling: n = 26; non-upwelling: n = 16). To measure chlorophyll-α, we used an AquaFlash fluorometer on five replicate water samples collected from the surface and five replicate samples from ~1m above the seafloor by a diver. These five replicates were averaged to calculate the value of each sample. We compared these environmental data collected during our study periods with historical data collected at Isla Pacheca from 1995 – 2018 (temperature) and 2017-2019 (chlorophyll), provided by the Physical Monitoring program at the Smithsonian Tropical Research Institute. The work derived from these data do not represent the original data or documentation provided by STRI, and we refer the reader to https://biogeodb.stri.si.edu/physical_monitoring/ for more information.

We collected the observed food sources of damselfishes (turf algae and plankton) during the non-upwelling season (on three different trips) and the upwelling season (on five different trips) to quantify their $\delta^{15}N$ and $\delta^{13}C$ signatures as well as their percent carbon and nitrogen (%C and %N). By quantifying $\delta^{15}N$ and $\delta^{13}C$, %C, and %N, we were able to characterize the contribution of different food sources to each damselfish species' diet and assess diet quality. To collect turf algae, we haphazardly scraped samples (several cm^2) from the benthos (n = 6 in each season). To collect plankton from the reef, a SCUBA diver towed an 80 µm plankton net 1-2 meters directly above the reef for five minutes (non-upwelling n = 4, upwelling n = 8). We also collected plankton further offshore (up to several hundred meters away from the site) by towing the same net from the boat (non-upwelling n = 3, upwelling n = 4) to estimate the $\delta^{13}C$ signature of pelagic food sources. All samples were stored in opaque bottles in a cooler with ice until returning to the lab.

In the lab, environmental samples were rinsed in deionized water, and any large debris or macrofauna were removed. In our samples of turf algae, we did not remove small invertebrates (e.g., amphipods and copepods < 2mm), which would likely be consumed incidentally by grazing fish. Samples were then dried at 60°C, powdered, and loaded into tin capsules for analysis. We measured $\delta^{15}N$ and $\delta^{13}C$ using a Thermo Electron deltaV Advantage isotope ratio mass spectrometer coupled with a ConFlo IV interface linked to a Thermo IsoLink Elemental Analyzer. Percent carbon and nitrogen were measured using a Carlo Erba NA1500 elemental analyzer. L-glutamic acid (USGS40 and USGS41) was used as a reference material.

Las Perlas fish collections and dissections

We collected fish from the shallow subtidal (<10m depth) at Isla Pacheca and Islote Saboga early in the day (8:30AM – 1:30PM), when our focal species were observed feeding (Table 3.1). After returning to the boat, we immediately stored the fish on ice; upon returning to the lab, they were frozen until dissection.

Table 3.1. Sample sizes (n) and average body size (TL = total length, SL = standard length, wet mass) of fish collected during the upwelling and non-upwelling seasons in Las Perlas Archipelago, Panama. Standard deviations given in brackets.

	Non-upwelling season				**Upwelling season**			
Species	**n**	**TL (mm)**	**SL (mm)**	**Mass (g)**	**n**	**TL (mm)**	**SL (mm)**	**Mass (g)**
A. troschelii	46	165 (12)	125 (9)	104 (24)	31	161 (13)	122 (10)	104 (23)
M. dorsalis	33	251 (32)	179 (23)	334 (108)	33	254 (28)	179 (19)	370 (106)
S. flavilatus	48	146 (8)	117 (8)	86 (23)	34	146 (9)	116 (7)	90 (18)

We dissected fish to estimate gut length, gut content mass, and body condition (gutless mass standardized to standard length), which is an indicator of fishes' nutritional status (Jakob et al., 1996; Rennie & Verdon, 2008). After dissecting out and weighing the full gut, we measured the length of the fully extended gut from esophagus to anus. We then emptied the gut of all digesta and reweighed the empty gut to calculate gut content mass. For our estimate of body condition, we reweighed fish after removing the gut, to prevent seasonal variation in gut mass and food content mass from affecting our estimates.

We quantified diet in three ways. First, to identify the foods consumed by each species during the non-upwelling and upwelling seasons, we analyzed stomach contents using light microscopy to identify food items to broad categories (e.g., algae: green filamentous, red branching; animals: copepod, amphipod). We quantified each species' gut contents as frequency of occurrence data (number of guts in which an item was observed divided by the total number of guts) due to the practical and analytical concerns with collecting accurate volumetric data (Baker et al., 2014). Second, to estimate the nutritional value of species' diets, we homogenized and dried each individual's gut contents to measure percent carbon and nitrogen content. Third, to characterize the long-term diet of each species, we took samples of white muscle tissue to measure $\delta^{15}N$ and $\delta^{13}C$ ratios. Isotope and percent carbon and nitrogen samples were processed following the same procedures described above in *Environmental measurements*.

Las Perlas data analysis

We conducted all statistical analyses in R Version 4.2.1, Funny-Looking Kid (R Core Team 2019). All models testing univariate responses (temperature, chlorophyll-α, $\delta^{15}N$, $\delta^{13}C$, gut length, gut content mass, and body condition) were built using the R package *brms* (Bürkner 2018). For response variables that did not follow the normal distribution, we built generalized linear models using the appropriate underlying distribution and data transformations. For all models testing fish dissection data (body mass, gut length, and digesta mass), we used model selection and 95% credibility intervals to identify important predictor variables (candidate variables: ln-transformed body size, season, site, and a site*season interaction). Model selection was conducted using leave-one-out cross validation (loo package; Vehtari et al. 2017) to calculate model weights, where the model with the highest weight is most likely out of the candidate models to best predict future data.

Tropical Eastern Pacific distribution data

We obtained occurrence (presence/absence) and biomass data for our three focal species from Reef Life Survey (RLS), a citizen science program that employs a diver-based visual fish survey following a standardized protocol to collect fish community composition and size data from coral and rocky reefs around the world (Edgar & Stuart-Smith, 2014) (https://reeflifesurvey.com/survey-data/). Our dataset included 356 surveys from 158 sites (surveys from the same site were conducted at multiple depths). All surveys were conducted between 2006 and 2016 during the non-upwelling season, when visibility is substantially better.

Tropical Eastern Pacific environmental covariates

We included three environmental predictors in our models of damselfish occupancy and biomass: minimum sea surface temperature (minSST), maximum net primary productivity (maxNPP), and minimum net primary productivity (minNPP). minSST and maxNPP are both strongly impacted by seasonal upwelling

(D’Croz & O’Dea, 2007; Sellers et al., 2021), and correspond to our predictions that tropical fishes will be negatively affected by decreased temperatures and positively affected by increased resource availability. We included minNPP to represent the alternative prediction that periods of low resource availability predict patterns of damselfish distribution better than the effects of seasonal upwelling. We obtained daily SST estimates from the GHRSST (Group for High Resolution Sea Surface Temperature) Level 4 MUR (Multiscale Ultrahigh Resolution) Global Foundation Sea Surface Temperature Analysis (v4.1) (NASA/JPL, 2010), which estimates SST at a spatial resolution of 0.01° of latitude and longitude (ERDDAP dataset ID: jplMURSST41). Because of the large size of this dataset, we downloaded SST day from every third day. We obtained monthly NPP estimates from Aqua MODIS (Moderate Resolution Imaging Spectroradiometer) at a spatial resolution of 0.0125° (Behrenfeld & Falkowski, 1997). Datasets for both variables were downloaded from the ERDDAP data server (Simons, 2022). We used the data to estimate the average SST and NPP for each site and calendar month over the 10-year period that fish surveys were conducted (2006-2016), then extracted minimum SST (minSST), minimum NPP (minNPP) and maximum NPP (maxNPP).

Tropical Eastern Pacific distribution models

Occurrence and biomass data tend to be spatially autocorrelated (Miller, 2012), due to both endogenous factors (e.g., dispersal) and exogenous factors (e.g., environmental covariates that are not included in the model), leading to biased model estimates (Dormann, 2007). To account for this, we built all distribution models using the R-INLA package, which explicitly models spatial autocorrelation (Bakka et al., 2018). R-INLA uses integrated nested Laplace approximation (INLA) to estimate parameters in a computationally efficient manner, and can model response variables that are not normally distributed (Bakka et al., 2018).

To model the occurrence and biomass of *Abudefduf troschelii* and *Microspathodon dorsalis* , we used a hurdle-gamma distribution (Martínez-Minaya et al., 2018). In a hurdle-gamma model, occurrence is modelled following the Bernoulli distribution (where 0 = absence, 1 = presence), and biomass is modelled following the gamma distribution. For *Stegastes flavilatus*, which was present in all but four surveys, we only modelled biomass, and so we used a gamma model following the structure of the gamma portion of the hurdle-gamma model described below. The distribution of each species was modelled separately.

We modelled occurrence and biomass using an equation adapted from Quiroz et al. (2015):

$$\pi(y_i|p_i,\mu_i,\theta_i) = (1-p_i)\delta_0 + p_i h(y_i|\mu_i,\theta_i) I_{[y_i>0]}$$

$$\begin{aligned} logit(p_i) = {} & \beta_1{}^{(1)} + \beta_2{}^{(1)} minSST_i + \beta_3{}^{(1)} maxNPP_i + \beta_4{}^{(1)} minNPP_i + \beta_5{}^{(1)}(minSST_i \\ & * maxNPP_i) + \beta_6{}^{(1)}(minSST_i * minNPP_i) + \beta_7{}^{(1)}(Guanacaste) \\ & + \beta_8{}^{(1)}(Panama) + \beta_9{}^{(1)}(Puntarenas) + \beta_{10}{}^{(1)}(Rivas) + f_1{}^{(1)}(depth) \\ & + u_i{}^{(1)} \end{aligned}$$

$$\begin{aligned} log(\mu_i) = {} & \beta_1{}^{(2)} + \beta_2{}^{(2)} minSST_i + \beta_3{}^{(2)} maxNPP_i + \beta_4{}^{(2)} minNPP_i + \beta_5{}^{(2)}(minSST_i \\ & * maxNPP_i) + \beta_6{}^{(2)}(minSST_i * minNPP_i) + \beta_7{}^{(2)}(Guanacaste) \\ & + \beta_8{}^{(2)}(Panama) + \beta_9{}^{(2)}(Puntarenas) + \beta_{10}{}^{(2)}(Rivas) + f_1{}^{(2)}(depth) \\ & + u_i{}^{(2)} \end{aligned}$$

$$u_i \sim GMRF(0, \Sigma)$$

Where π_i is a probability distribution function (PDF) describing the probability of our focal species' having a given biomass (y_i) at reef i, p_i is the probability of a species' presence at reef i, and $1 - p_i$ is the probability of a species' absence at reef i. δ_0 is the Dirac delta function, which evaluates to 1 at $y_i = 0$ and 0 everywhere else; similarly, $I_{[y_i>0]}$ is an indicator function, which evaluates to 1 at $y_i > 1$ and 0 everywhere else. Here $h(y_i|\mu_i,\theta_i)$ is assigned as the gamma PDF, which performed better than the log-normal PDF in model comparisons. In the model above, separate coefficients are estimated for occupancy and biomass, i.e., ${\beta_1}^{(1)}$ and ${\beta_1}^{(2)}$ are not equivalent and may have different values. Further, $logit(p_i)$ and $log(\mu_i)$ need not be modelled with the same set of predictors.

In each equation, β_1 is an intercept term representing the probability of a species' presence, or species biomass, respectively, in the region of Chiriquí (our intercept level) under average values of minimum sea surface temperature (minSST), maximum net primary productivity (maxNPP), and minimum net primary productivity (minNPP). β_2-β_6 are coefficients associated with our standardized environmental covariates and their interactions, and β_7-β_{10} are coefficients associated with dummy variables indicating the region in which each survey was conducted, which we included to account for factors we were unable to describe explicitly in the model (e.g., regional patterns of circulation). f_1 is a smooth function describing the effect of depth. u_i is a random spatial effect, modelled in R-INLA as a Gaussian Markov Random Field (GMRF) with a mean of zero and a covariance matrix Σ defined using the Matérn covariance function. All predictors were assigned weakly regularizing priors to prevent model overfitting (McElreath, 2020).

In addition to fitting the full model, we fitted a model with all of our fixed predictors but no spatial random effect, as well as a model that included a spatial random effect and the most important predictors of damselfish distribution as identified by the full model. We compared model performance by estimating the Widely Applicable Information Criterion (WAIC) values for each model, as well as Area Under the receiver operating characteristic Curve (AUC; for occupancy), the coefficient of determination (R^2, for biomass).

Results

Environmental effects of upwelling in Las Islas Perlas

Our environmental samples demonstrated that mean SST during the non-upwelling season (Figure 3.2a) was similar at Isla Pacheca (28.4 ± 0.2°C SD) and Islote Saboga (28.6 ± 0.1°C SD). Mean SST decreased during the upwelling season to 19.6 (± 1.2°C SD) at Isla Pacheca and to 22.0 (± 1.1°C SD) at Islote Saboga (Figure 3.2a). Chlorophyll-α concentrations during the non-upwelling season averaged 2.5 (± 0.3 µg/L SD) at Isla Pacheca and 2.4 (± 0.5 µg/L SD) at Islote Saboga (Figure 3.2b). During the upwelling season, chlorophyll-α increased to 7.4 (± 2.7 µg/L SD) at Isla Pacheca and 8.4 (± 2.7 µg/L SD) at Islote Saboga (Figure 3.2b). The values that we observed during the non-upwelling and upwelling seasons were similar to historical values collected by the Smithsonian Tropical Research Institute's Physical Monitoring program (Figure 3.2).

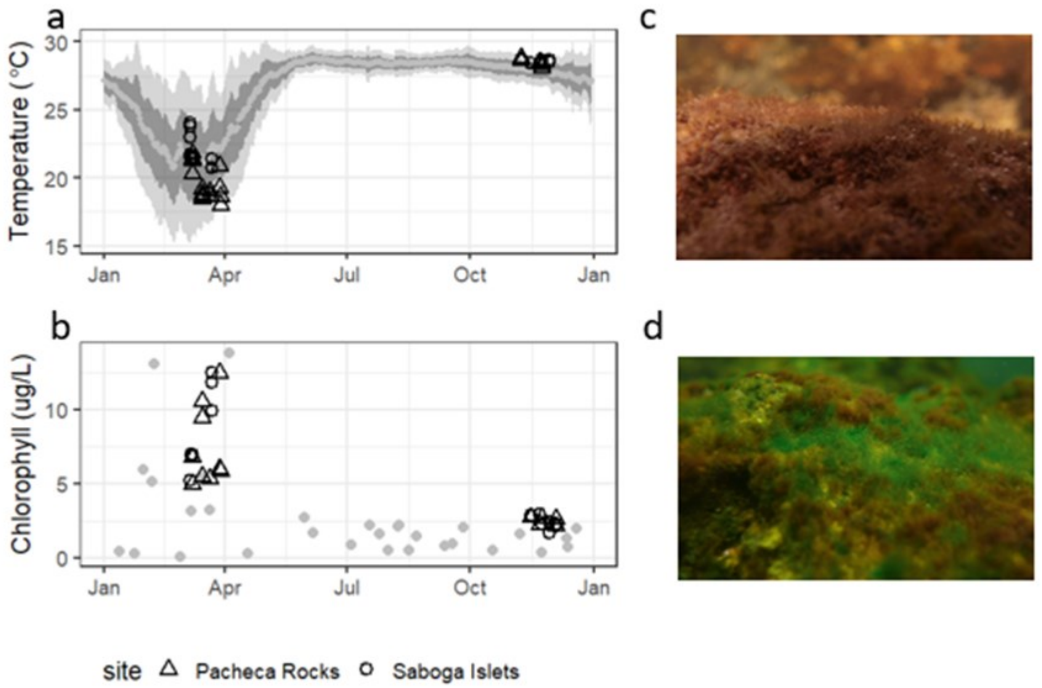

Figure 3.2. Seasonal variation in a) Sea surface temperature and b) chlorophyll at Las Islas Perlas. Data collected by the authors during the study period shown in black. Historical mean daily values shown by grey dots. In a), dark and light shaded areas represent the historical mean daily values ± 1 SD and 2 SD, respectively. Historical data were provided by the Physical Monitoring program at the Smithsonian Tropical Research Institute. Images shown in c) and d) are of benthic algal growth in Las Islas Perlas during the non-upwelling and upwelling seasons, respectively. Photo credit: Nicole Knight.

Damselfish diets

Our diet analysis revealed that *Abudefduf troschelii* and *Stegastes flavilatus* are both omnivores that consume benthic algae, small invertebrates, and zooplankton, whereas *Microspathodon dorsalis* is an herbivore that primarily feeds on diatoms, turf algae and sediment (Appendix). Of the three species, *A. troschelii* consumes the most animal prey; accordingly, its gut contents were richer in nitrogen (8±2% SD of dry mass) and carbon (4±7% SD of dry mass) than those of *S. flavilatus* (N: 6±2% SD of dry mass; C: 33±6% SD of dry mass) and *M. dorsalis* (N: 5±2% SD of dry mass; C: 28±6% SD of dry mass). δ^{13}C signatures suggest that *A. troschelii* feeds primarily from sources in the water column, whereas *S. flavilatus* feeds from the water column and benthos, and *M. dorsalis* feeds primarily from the benthos (Figure 3.3a). The diets of all three species shifted during the upwelling season (Figure 3.3b). All three species were more frequently observed consuming green algae (Appendix), which was more prevalent during the upwelling season (Figure 3.2c-d).

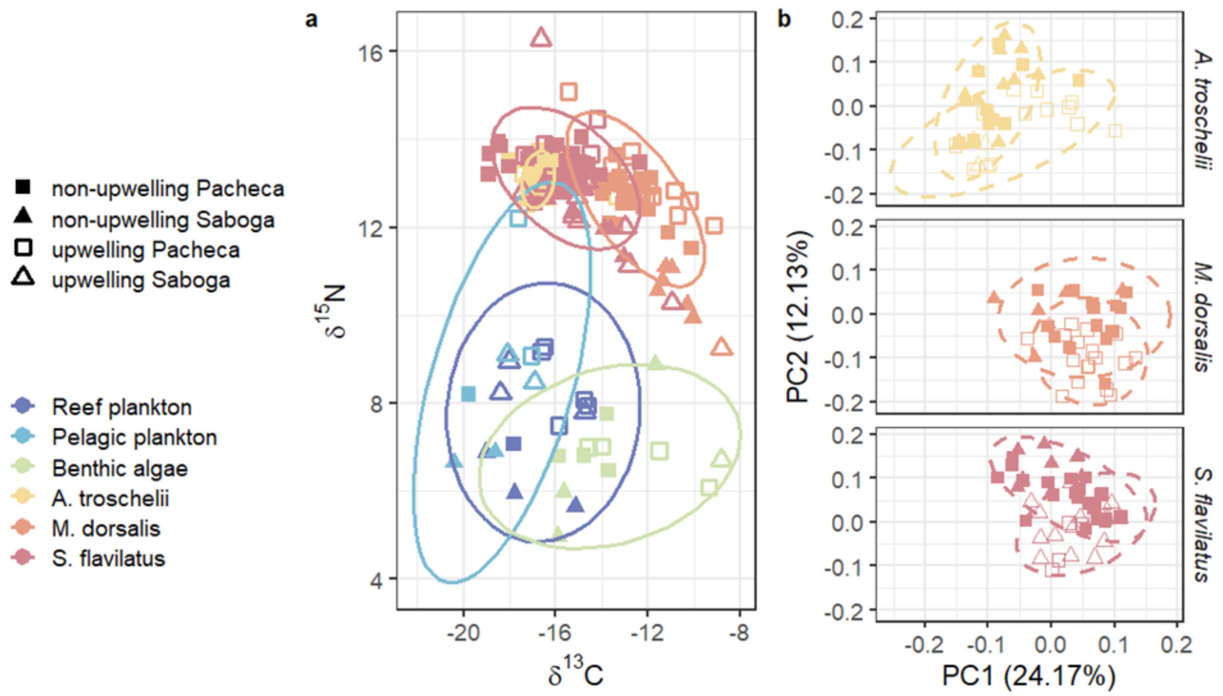

Figure 3.3. Diet data from three species of damselfish collected from Isla Pacheca and Islote Saboga during the non-upwelling and upwelling seasons. a) Isotope signatures from white muscle tissue of damselfish and three food sources. Ellipses include data pooled across sites and seasons. b) Principal components analysis of presence/absence stomach content data from damselfish. Each point represents the stomach contents of one fish. Ellipses include data pooled across sites and separated by season.

Damselfish morphology

The gut length of *A. troschelii* increased during the upwelling season (upwelling ES: 0.10; 95%CI: -0.01, 0.21; Figure 3.4a), as did digesta mass (upwelling ES: 0.25, 95%CI: -0.02, 0.52; Figure 3.4d). There was weak evidence that *A. troschelii* body mass relative to length (i.e., body condition) increased during the upwelling season: the best model included an upwelling term (model weight: 0.99), but the effect of upwelling overlapped zero (upwelling ES: 0.03, 95%CI: -0.03, 0.09; Figure 3.4g), giving an 84% posterior probability that body condition improved during the upwelling season. The gut length of *M. dorsalis* increased during the upwelling season (upwelling ES: 0.10; 95%CI: 0.03, 0.17); the best model (weight: 0.67) suggested that this increase was greater in larger individuals (upwelling * body size ES: 0.05; 95%CI: -0.02, 0.12; Figure 3.4b). The best model of *M. dorsalis* digesta mass supported an effect of upwelling (model weight: 0.75); this effect overlapped 0 (upwelling ES: 0.35, 95%CI: -0.07, 0.75), but gave a 95% posterior probability that digesta mass was greater during the upwelling season (Figure 3.4). The body condition of *M. dorsalis* improved during the upwelling season (upwelling ES: 0.09, 95%CI: 0.00, 0.18). The gut length of *S. flavilatus* increased during the upwelling season (upwelling ES: 0.13; 95% CI: 0.07, 0.20). The digesta mass of *S. flavilatus* also increased during upwelling, but this increase was greater at Isla Pacheca (upwelling ES: 0.84; 95%CI: 0.62, 1.07) than Islote Saboga (upwelling * Saboga ES: -0.54, 95%CI: -0.87, -0.20). The body condition of *S. flavilatus* improved during the upwelling season (upwelling ES: 0.10, 95%CI: 0.01, 0.18).

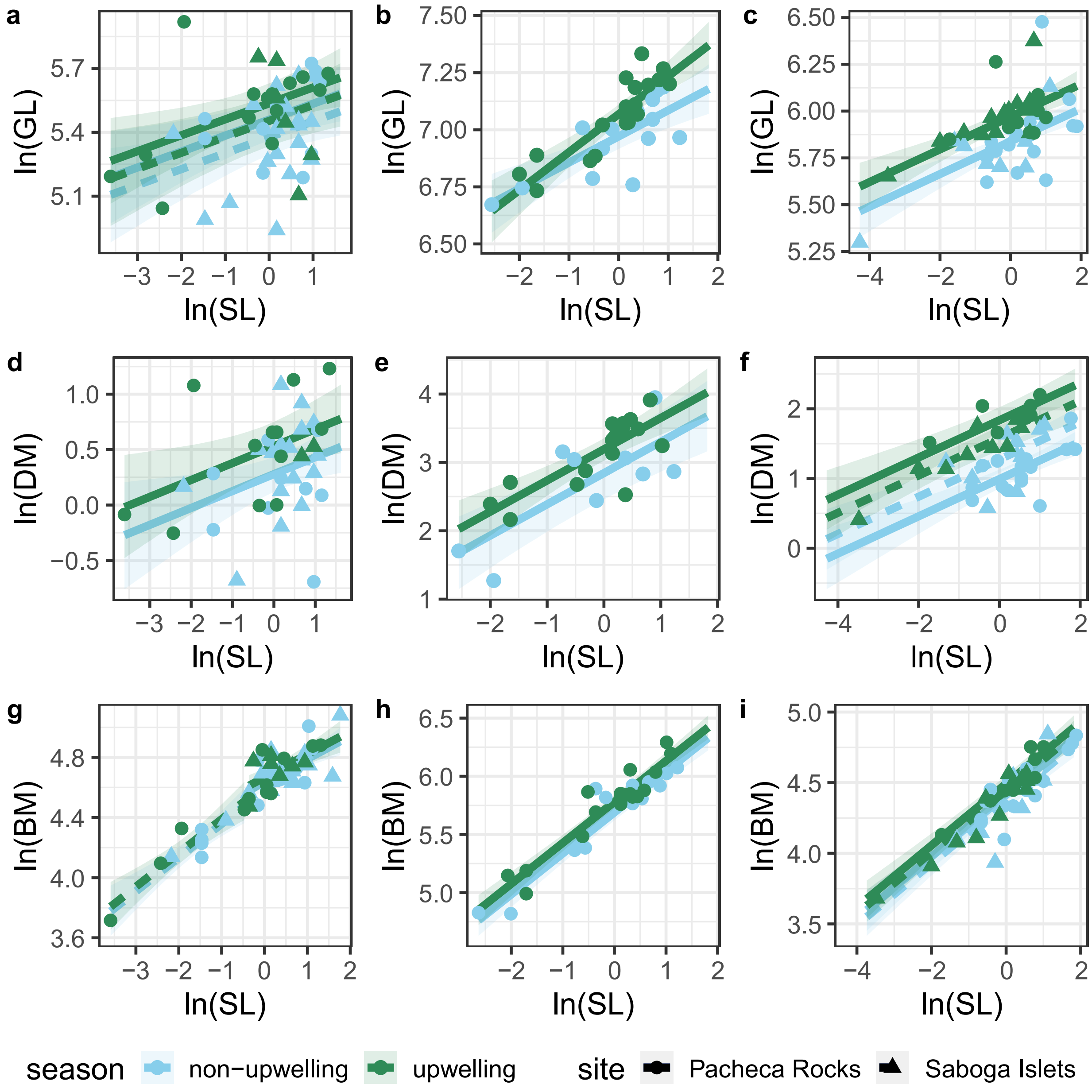

Figure 3.4. Damselfish ln-transformed gut length (GL; a-c), digesta mass (DM; d-f), and gut-removed body mass (BM; g-i) during the non-upwelling (light blue) and upwelling (green) seasons against ln-transformed standard length (SL). *Abudefduf troschelii* is represented in panels a, d, and g; *Microspathodon dorsalis* in panels b, e, and h; *Stegastes flavilatus* in panels c, f, and i. Points show real data from Isla

Pacheca (circles) and Islote Saboga (triangles); lines show the model projected means for Pacheca (solid) and Saboga (dashed); shaded areas show the 95% credibility intervals.

Damselfish distribution models

Our models revealed that environmental predictors associated with seasonal upwelling influence the distribution of all three damselfish species (Figures 5, 6). The biomass of *A. troschelii* was predicted by minNPP, minSST, and a minNPP*minSST interaction (Figure 3.5b). Biomass of *A. troschelii* generally increased with increasing minSST and minNPP (Figure 3.6e). *Abudefduf troschelii* was present in 179 of 354 surveys, but patterns of occupancy corresponded only to spatial, not environmental, predictors. Models built to predict *A. troschelii* occupation performed reasonably but not exceptionally well, with AUC scores ranging from 0.74-0.78 (Table 3.1). The biomass of *M. dorsalis* was predicted by minNPP, maxNPP, minSST, minNPP*minSST and maxNPP*minSST (Figure 3.5a). *Microspathodon dorsalis* had high probability of occurrence and biomass at reefs with low minSST and high minNPP and maxNPP (Figure 3.6a-d); at reefs with high minSST *M. dorsalis* was more likely to be present if minNPP was low (Figure 3.6a). *Microspathodon dorsalis* was present in 179 of 354 surveys, and an AUC score of 0.88 indicates excellent model performance (Table 3.2). *Stegastes flavilatus* was present under virtually all environmental conditions surveyed (350 of 354 surveys), but its biomass increased with decreasing minSST and increasing maxNPP (Figures 5c, 6f). Including a spatial random effect improved model performance for all three species (Table 3.2).

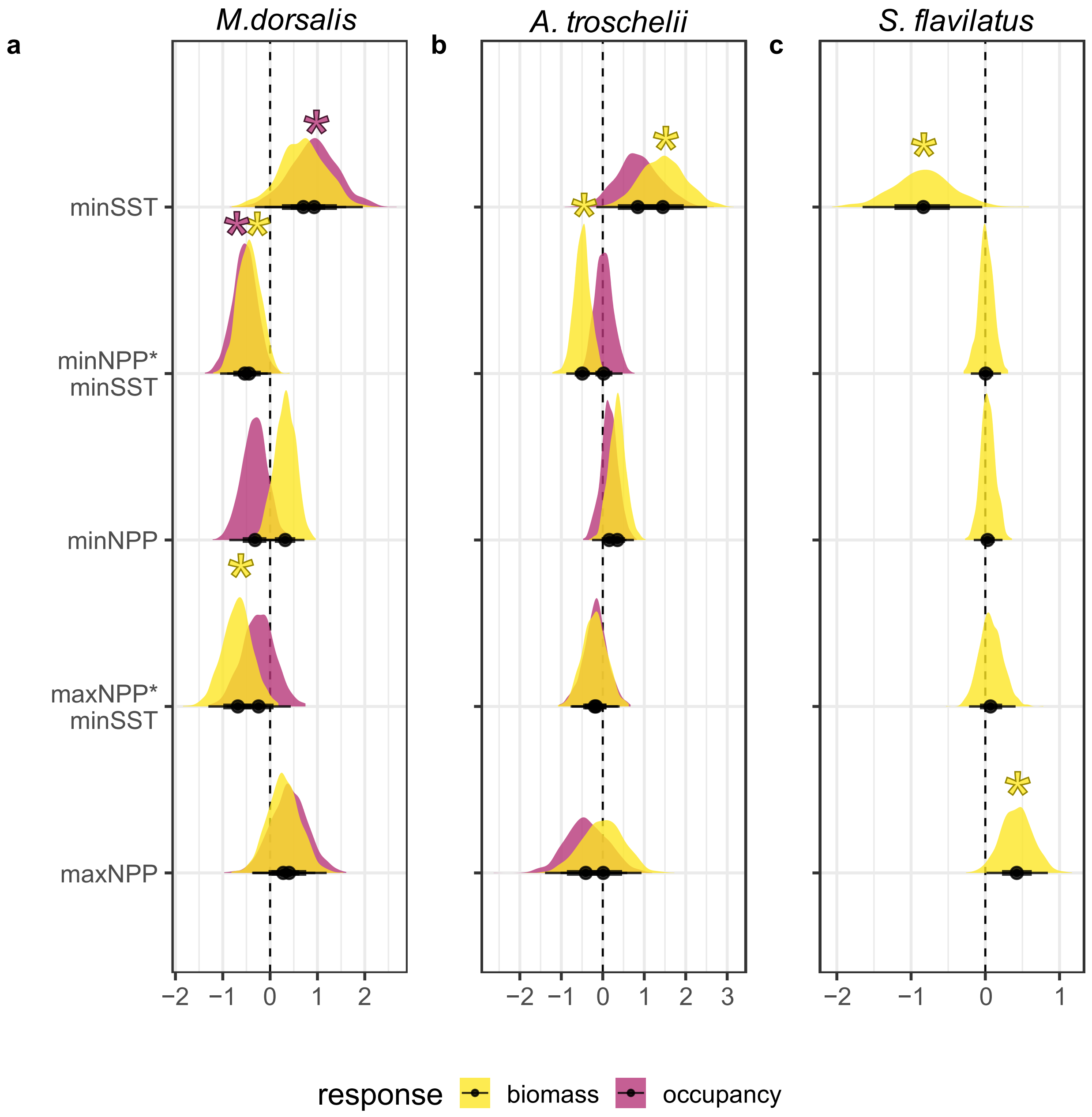

Figure 3.5. Parameter estimate distributions generated by the full R-INLA models

(including all fixed effects and a random spatial effect). Distributions reflect associations between standardized environmental predictors on biomass (yellow) and probability of presence (pink). Effects with 95% credibility intervals that do not overlap 0 are indicated by an asterisk.

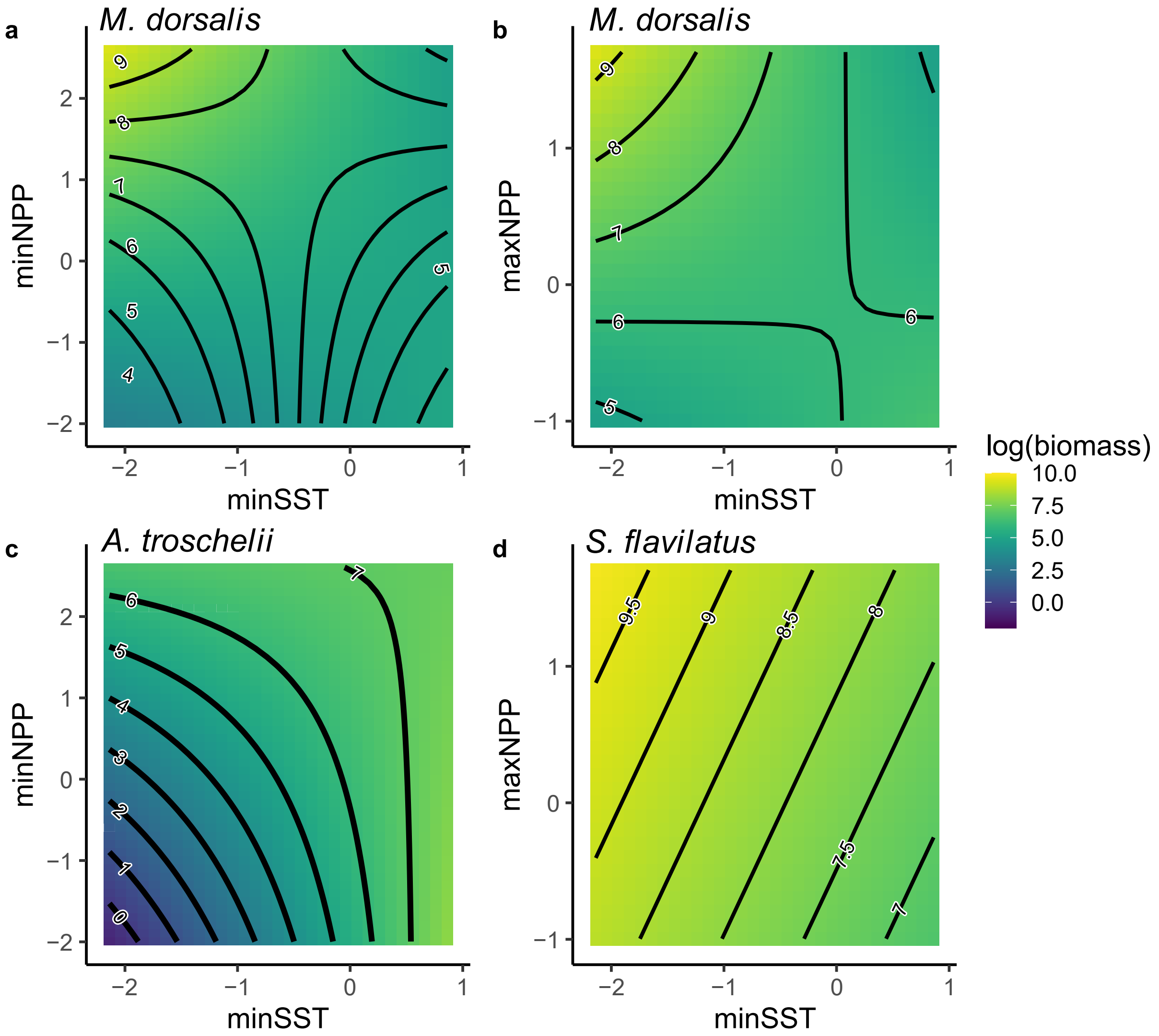

Figure 3.6. Heat maps with contour lines showing ln-transformed predicted damselfish biomass across combinations of environmental variables. Heat maps

generated from posterior values of INLA2 models (models including credible environmental predictors and a random spatial effect) a-b) *M. dorsalis*, c) *Abudefduf troschelii*, d) *S. flavilatus*.

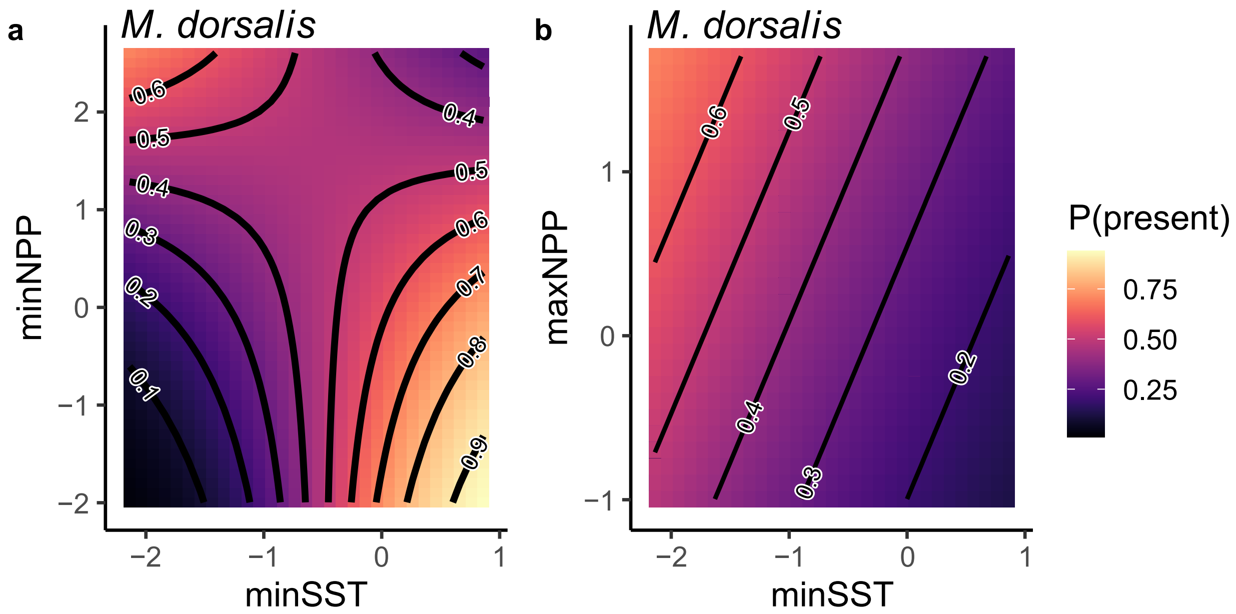

Figure 3.7. Heat maps with contour lines showing probability of *M. dorsalis* presence across combinations of environmental variables. Heat maps generated from posterior values of INLA2 models (models including credible environmental predictors and a random spatial effect).

Table 3.2. Estimated WAIC, AUC, and RMSE values for the INLA models built to describe occupancy and biomass of *Abudefduf troschelii*, *Stegastes flavilatus*, and *Microspathodon dorsalis* across the Tropical Eastern Pacific. INLA0 has no random spatial effect and the full set of fixed effects, INLA1 has a random spatial effect and the full set of fixed effects, and INLA2 has a random spatial effect and predictors that were identified as important in the INLA1 models. Improved model fit is indicated by lower WAIC scores, higher AUC scores, and lower RMSE scores. Only biomass was modelled for *S. flavilatus*, so no AUC score is presented.

	A. troschelii			*S. flavilatus*		*M. dorsalis*		
Model	WAIC	AUC	RMSE	WAIC	RMSE	WAIC	AUC	RMSE
INLA0	3481	0.74	2610	5594	1399	3677	0.74	7508
INLA1	3459	**0.78**	**2529**	5560	**1231**	**3579**	**0.89**	**4313**
INLA2	**3451**	0.77	2545	**5558**	1239	3581	**0.89**	4363

Discussion

Seasonal upwelling impacts the ecology of our three focal damselfish species across scales, from individual performance to patterns of regional distribution. Damselfishes' physiological responses to seasonal upwelling were qualitatively similar: all three species exhibited increased gut length and digesta mass, and the body condition (gutless mass standardized to length) of *Microspathodon dorsalis* and *Stegastes flavilatus* improved. However, patterns of damselfish biomass and occupancy responded differently to variation in temperature and productivity associated with upwelling strength. *Stegastes flavilatus* biomass exhibited a clear positive association with upwelling strength; its biomass increased with increasing maximum NPP and decreasing SST. *Microspathodon dorsalis* biomass and occupancy were highest under high maximum NPP and low minimum SST, but in contrast to *S. flavilatus*, biomass was substantially lower at sites where low temperatures were not accompanied by high maximum productivity. The distribution of *A. troschelii* was not clearly associated with upwelling conditions: *A. troschelii* biomass was predicted by minSST and minNPP, but these associations may be mediated by exposure, rather than upwelling. Here we discuss how by combining individual performance data with broad-scale distribution models, we can make novel insights into the ecology of these common tropical fishes.

All three species exhibited longer guts and more digesta during the upwelling season, reflecting the importance of digestive plasticity in allowing fishes to succeed during the upwelling season. Digestion is energetically expensive (Huang et al., 2018; Tsuboi et al., 2015), and so individuals should optimize gut length to maximize nutrient uptake but minimize investment in digestive tissues (Penry & Jumars, 1986). During the warm, resource-poor non-upwelling season, fishes' preferred foods are expected to be more limited, and so a shorter gut should be optimal. With upwelling, resource availability increases, but digestive rates slow as temperatures decline (Knight et al., 2021). Slow digestion can limit resource uptake as the gut becomes full, potentially leading to energetic deficits (Brodersen et al., 2011; Floeter et al., 2005; Lemoine & Burkepile, 2012). Thus, under cold upwelling conditions a longer gut may be beneficial.

Although *A. troschelii* had a longer gut and more digesta mass during the upwelling season, its body condition did not measurably improve. It's possible that the body condition of *A. troschelii* did not improve simply because it was directing excess resources elsewhere: the reproductive efforts of *A. troschelii* increase during upwelling (Foster, 1987), whereas reproduction by *S. flavilatus*, which did have improved body condition during upwelling, decreases (Robertson, 1990). Alternatively, it may be that at Las Perlas, *A. troschelii* benefitted less from increased resource availability during the upwelling season: *A. troschelii* relies to a greater extent on pelagic food sources than *M. dorsalis* and *S. flavilatus* (Figure 3.3; Montgomery, 1980; Olivier et al., 2019). *Abudefduf troschelii* primarily consumed zooplankton during the non-upwelling season, but increased its uptake of benthic green algae during the upwelling season (Appendix S1). This increase could indicate that *A. troschelii* is supplementing its preferred diet of zooplankton with benthic algae, with diminished benefits.

Similarly, our distributional analyses showed that the biomass of *M. dorsalis* and *S. flavilatus* increases with maximum NPP, but the biomass of *A. troschelii* does not. There are several possible explanations for this disparity. First, it may be that seasonal upwelling simply doesn't benefit *A. troschelii* to the same extent that it does *M. dorsalis* and *S. flavilatus*, as indicated by our analyses of body condition. However, it is also possible that maximum NPP is a poor predictor of zooplankton availability. Zooplankton have highly patchy distributions, which do not necessarily exhibit strong correlations with phytoplankton abundance (Grémillet et al., 2008; Messié & Chavez, 2017). Moreover, the best model of *A. troschelii* occupancy did not include any environmental predictors, and with an AUC score of 0.78, did not perform as well as that of *M. dorsalis* (AUC = 0.89). Our best model of *A. troschelii* biomass did include minimum NPP and minimum SST (and their interaction) as predictors, but this may not reflect a direct physiological relationship. The CTMin of *A. troschelii* (11.2°C; Graham, 1971) is substantially lower than the typical range of thermal minima associated with seasonal upwelling in the TEP (16-18°C; D'Croz & O'Dea, 2007); further, the association between temperature and biomass weakened with increasing minimum NPP. We suggest that instead that minimum NPP and minimum SST are correlated with exposure in this system, which can affect the supply of planktonic foods (Sellers et al., 2021).

Upwelling appears to favour both *Stegastes flavilatus* and *M. dorsalis*, but with some differences. *Stegastes flavilatus* appeared to benefit from seasonal upwelling to a greater extent than *M. dorsalis*: its biomass increases independently with increasing productivity or decreasing temperature, whereas *M. dorsalis* biomass only increased with decreasing minimum temperature if productivity (minimum or maximum) was high (Figure 3.6). We suggest that *M. dorsalis* is more vulnerable to the effects of decreasing temperature on resource uptake and digestion than *S. flavilatus* , and consequently depends to a greater extent on increased resource availability in cold conditions. Similarly, *Microspathodon dorsalis* was present in far fewer surveys than *S. flavilatus* (179/354 and 350/354 surveys, respectively), indicating that its environmental tolerance is less broad than that of *S. flavilatus*. Seasonal upwelling may also provide a particular benefit to the small-bodied *S.*

flavilatus: *S. flavilatus* has a dramatically shortened maximum lifespan the Gulf of Panama (4 years, vs. 19 years in Baja California), likely due to intense predation (Meekan et al., 2001). A crucial refuge from predation among fishes is increased size (Ahti et al., 2020); thus, *S. flavilatus* may especially benefit from directing excess resources acquired during upwelling to increased growth.

Predicting the effects of broad-scale oceanographic processes is difficult, as multiple environmental variables may change simultaneously and have both positive and negative effects on different aspects of individual performance (Menge et al., 2004) This difficulty emphasizes the added value of SDMs, which can identify the net impact of large-scale environmental variation when environmental changes impact some individual rates positively and others negatively. For example, although upwelling improved the body condition of *S. flavilatus* (Figure 3.4), prior work shows that its reproductive output and recruitment decrease with decreasing temperature during upwelling (Robertson, 1990). Considering these results on their own, it is unclear whether seasonal upwelling benefits *S. flavilatus*, as both reproductive output and body condition can impact survival and fitness (Berumen et al., 2005; Lloret-Lloret et al., 2022; Shima et al., 2020). However, our finding that *S. flavilatus* biomass increases under strong upwelling conditions suggest that the positive effects of upwelling outweigh documented negative effects.

Conclusions

Although prior work has largely demonstrated positive effects of upwelling on fish performance and biomass (Aldana et al., 2017; Brosset et al., 2015; Fuentes et al., 2017; Pulgar et al., 2013; Rykaczewski & Checkley, 2008; Schilling et al., 2022; Ware & Thomson, 1991; Zuloaga et al., 2023), we found that not all species benefit equally from seasonal upwelling, possibly due to differences in their reliance on benthic and pelagic resources. Further, our combined physiological and distributional analyses support the hypothesis that species that do benefit from seasonal upwelling exhibit increases in biomass, consistent with classic ecological theory (Brown, 1984; Grinnell, 1917; Hutchinson, 1978).

Acknowledgements

We thank Alexis Lam, Friederike Clever, Carmen Schloeder, Carlos Vega, and Maycol Madrid for their assistance in the field and laboratory. We also thank Lauren Chapman and Andrew Hendry for comments that improved previous versions of this work. This work was supported by a STRI Ernst Mayr Fellowship for NK, a MITACs Research training award for NK, a NEO Grant-in-Aid from McGill University for NK, an NSERC PGSD for NK, and a McGill Writing Year Award for NK. All collections were conducted under permit No. SC/A-19-18 provided by the Ministerio de Ambiente del Gobierno de la Republica de Panamá.

References

Ahti, P. A., Kuparinen, A., & Uusi-Heikkilä, S. (2020). Size does matter—The eco-evolutionary effects of changing body size in fish. *Environmental Reviews*, *28*(3), 311–324. https://doi.org/10.1139/er-2019-0076

Aldana, M., García-Huidobro, M. R., Pulgar, V. M., & Pulgar, J. (2017). Upwelling promotes earlier onset and increased rate of gonadal development of four coastal herbivores. *Bulletin of Marine Science*, *93*(3), 671–688. https://doi.org/10.5343/bms.2016.1063

Barneche, D. R., Floeter, S. R., Ceccarelli, D. M., Frensel, D. M. B., Dinslaken, D. F., Mário, H. F. S., & Ferreira, C. E. L. (2009). Feeding macroecology of territorial damselfishes (Perciformes: Pomacentridae). *Marine Biology*, *156*(3), 289–299. https://doi.org/10.1007/s00227-008-1083-z

Beck, H. J., Feary, D. A., Fowler, A. M., Madin, E. M. P., & Booth, D. J. (2016). Temperate predators and seasonal water temperatures impact feeding of a range expanding tropical fish. *Marine Biology*, *163*(4), 70. https://doi.org/10.1007/s00227-016-2844-8

Berumen, M. L., Pratchett, M. S., & McCormick, M. I. (2005). Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). *Marine Ecology Progress Series*, *287*, 217–227. https://doi.org/10.3354/meps287217

Borja, A., Uriarte, A., Egaña, J., Motos, L., & Valencia, V. (1998). Relationships between anchovy (*Engraulis encrasicolus*) recruitment and environment in the Bay of Biscay (1967–1996). *Fisheries Oceanography*, *7*(3–4), 375–380. https://doi.org/10.1046/j.1365-2419.1998.00064.x

Brambilla, M., & Ficetola, G. F. (2012). Species distribution models as a tool to estimate reproductive parameters: A case study with a passerine bird species. *Journal of Animal Ecology*, *81*(4), 781–787. https://doi.org/10.1111/j.1365-2656.2012.01970.x

Brodersen, J., Rodriguez-Gil, J. L., Jönsson, M., Hansson, L.-A., Brönmark, C., Nilsson, P. A., Nicolle, A., & Berglund, O. (2011). Temperature and Resource Availability May Interactively Affect Over-Wintering Success of Juvenile Fish in a Changing Climate. *PLOS ONE*, *6*(10), e24022. https://doi.org/10.1371/journal.pone.0024022

Brosset, P., Menard, F., Fromentin, J.-M., Bonhommeau, S., Ulses, C., Bourdeix, J.-H., Bigot, J.-L., Van Beveren, E., Roos, D., & Saraux, C. (2015). Influence of environmental variability and age on the body condition of small pelagic fish in the Gulf of Lions. *Marine Ecology Progress Series*, *529*, 219–231. https://doi.org/10.3354/meps11275

Brown, J. H. (1984). On the Relationship between Abundance and Distribution of Species. *The American Naturalist*, *124*(2), 255–279.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Caceres, C. W., Fuentes, L. S., & Ojeda, F. P. (1994). Optimal feeding strategy of the temperate herbivorous fish *Aplodactylus punctatus*: The effects of food availability on digestive and reproductive patterns. *Oecologia*, *99*(1), 118–123. https://doi.org/10.1007/BF00317091

Catry, T., Ramos, J. A., Catry, I., Monticelli, D., & Granadeiro, J. P. (2013). Inter-annual variability in the breeding performance of six tropical seabird species: Influence of life-history traits and relationship with oceanographic parameters. *Marine Biology*, *160*(5), 1189–1201. https://doi.org/10.1007/s00227-013-2171-2

Clarke, A., & Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, *68*(5), 893–905. https://doi.org/10.1046/j.1365-2656.1999.00337.x

Dallas, T., Decker, R. R., & Hastings, A. (2017). Species are not most abundant in the centre of their geographic range or climatic niche. *Ecology Letters*, *20*(12), 1526–1533. https://doi.org/10.1111/ele.12860

D'Croz, L., & O'Dea, A. (2007). Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll.

Estuarine Coastal and Shelf Science, 73(1–2), 325–340. https://doi.org/10.1016/j.ecss.2007.01.013

Duncan, M. I., James, N. C., Potts, W. M., & Bates, A. E. (2020). Different drivers, common mechanism; the distribution of a reef fish is restricted by local-scale oxygen and temperature constraints on aerobic metabolism. Conservation Physiology, 8(1), coaa090. https://doi.org/10.1093/conphys/coaa090

Eme, J., & Bennett, W. A. (2008). Low temperature as a limiting factor for introduction and distribution of Indo-Pacific damselfishes in the eastern United States. *Journal of Thermal Biology*, *33*(1), 62–66. https://doi.org/10.1016/j.jtherbio.2007.10.003

Enochs, I. C., Toth, L. T., Kirkland, A., Manzello, D. P., Kolodziej, G., Morris, J. T., Holstein, D. M., Schlenz, A., Randall, C. J., Mate, J. L., Leichter, J. J., & Aronson, R. B. (2021). Upwelling and the persistence of coral-reef frameworks in the eastern tropical Pacific. *Ecological Monographs*, *91*(4), e01482. https://doi.org/10.1002/ecm.1482

Figueira, W. F., Biro, P., Booth, D. J., & Valenzuela, V. C. (2009). Performance of tropical fish recruiting to temperate habitats: Role of ambient temperature and implications of climate change. *Marine Ecology Progress Series*, *384*, 231–239. https://doi.org/10.3354/meps08057

Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddack, M. J., & Horn, M. H. (2005). Geographical gradients of marine herbivorous fishes: Patterns and processes. *Marine Biology*, *147*(6), 1435–1447. https://doi.org/10.1007/s00227-005-0027-0

Foster, S. A. (1987). Diel and lunar patterns of reproduction in the Caribbean and Pacific sergeant major damselfishes *Abudefduf saxatilis* and *A. troschelii. Marine Biology*, *95*(3), 333–343. https://doi.org/10.1007/BF00409563

Fuentes, E. N., Zuloaga, R., Almarza, O., Mendez, K., Valdés, J. A., Molina, A., & Pulgar, J. (2017). Upwelling-derived oceanographic conditions impact growth performance and growth-related gene expression in intertidal fish. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *214*, 12–18. https://doi.org/10.1016/j.cbpb.2017.09.001

Graham, J. B. (1971). Temperature Tolerances of Some Closely Related Tropical Atlantic and Pacific Fish Species. *Science*, *172*(3985), 861–863. https://doi.org/10.1126/science.172.3985.861

Graham, J. B. (1972). Low-Temperature Acclimation and the Seasonal Temperature Sensitivity of Some Tropical Marine Fishes. *Physiological Zoology*, *45*(1), 1–13. https://doi.org/10.1086/physzool.45.1.30155921

Grémillet, D., Lewis, S., Drapeau, L., Van Der Lingen, C. D., Huggett, J. A., Coetzee, J. C., Verheye, H. M., Daunt, F., Wanless, S., & Ryan, P. G. (2008). Spatial match–

mismatch in the Benguela upwelling zone: Should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology*, *45*(2), 610–621. https://doi.org/10.1111/j.1365-2664.2007.01447.x

Grinnell, J. (1917). Field Tests of Theories Concerning Distributional Control. *The American Naturalist*, *51*(602), 115–128. https://doi.org/10.1086/279591

Horn, M. H., Neighbors, M. A., & Murray, S. N. (1986). Herbivore responses to a seasonally fluctuating food supply: Growth potential of two temperate intertidal fishes based on the protein and energy assimilated from their macroalgal diets. *Journal of Experimental Marine Biology and Ecology*, *103*(1), 217–234. https://doi.org/10.1016/0022-0981(86)90142-5

Huang, C. H., Yu, X., & Liao, W. B. (2018). The Expensive-Tissue Hypothesis in Vertebrates: Gut Microbiota Effect, a Review. *International Journal of Molecular Sciences*, *19*(6), 1792. https://doi.org/10.3390/ijms19061792

Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Hutchinson, G. E. (1978). *An introduction to population ecology*. Yale University Press.

Kämpf, J., & Chapman, P. (2016). Comparison, Enigmas and Future Research. In J. Kämpf & P. Chapman (Eds.), *Upwelling Systems of the World: A Scientific Journey* *to the Most Productive Marine Ecosystems* (pp. 395–424). Springer International Publishing. https://doi.org/10.1007/978-3-319-42524-5_10

Knight, N. S., Guichard, F., & Altieri, A. H. (2021). A global meta-analysis of temperature effects on marine fishes' digestion across trophic groups. *Global Ecology and Biogeography*, *30*(4), 795–810. https://doi.org/10.1111/geb.13262

Kroeker, K. J., Sanford, E., Rose, J. M., Blanchette, C. A., Chan, F., Chavez, F. P., Gaylord, B., Helmuth, B., Hill, T. M., Hofmann, G. E., McManus, M. A., Menge, B. A., Nielsen, K. J., Raimondi, P. T., Russell, A. D., & Washburn, L. (2016). Interacting environmental mosaics drive geographic variation in mussel performance and predation vulnerability. *Ecology Letters*, *19*(7), 771–779. https://doi.org/10.1111/ele.12613

Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergo, A. M., Noreen, A. M. E., Li, Q., Schuster, R., & Angert, A. L. (2016). A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters*, *19*(6), 710–722. https://doi.org/10.1111/ele.12604

Lemoine, N. P., & Burkepile, D. E. (2012). Temperature-induced mismatches between consumption and metabolism reduce consumer fitness. *Ecology*, *93*(11), 2483–2489. https://doi.org/10.1890/12-0375.1

Lester, S. E., Gaines, S. D., & Kinlan, B. P. (2007). Reproduction on the Edge: Large-Scale Patterns of Individual Performance in a Marine Invertebrate. *Ecology*, *88*(9), 2229–2239. https://doi.org/10.1890/06-1784.1

Lloret-Lloret, E., Albo-Puigserver, M., Giménez, J., Navarro, J., Pennino, M. G., Steenbeek, J., Bellido, J. M., & Coll, M. (2022). Small pelagic fish fitness relates to local environmental conditions and trophic variables. *Progress in Oceanography*, *202*, 102745. https://doi.org/10.1016/j.pocean.2022.102745

Logothetis, E. (2001). Gut morphology and function in *Atherinops affinis* (Teleostei: Atherinopsidae), a stomachless omnivore feeding on macroalgae. *Journal of Fish Biology*, *59*(5), 1298–1312. https://doi.org/10.1006/jfbi.2001.1740

Lunghi, E., Manenti, R., Mulargia, M., Veith, M., Corti, C., & Ficetola, G. F. (2018). Environmental suitability models predict population density, performance and body condition for microendemic salamanders. *Scientific Reports*, *8*(1), Article 1. https://doi.org/10.1038/s41598-018-25704-1

McElreath, R. (2020). *Statistical Rethinking, 2nd Edition*. https://learning.oreilly.com/library/view/statistical-rethinking-2nd/9780429639142/

Meekan, M., Ackerman, J., & Wellington, G. (2001). Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. *Marine Ecology Progress Series*, *212*, 223–232. https://doi.org/10.3354/meps212223

Melis, C., Herfindal, I., Kauhala, K., Andersen, R., & Hogda, K.-A. (2010). Predicting animal performance through climatic and plant phenology variables: The case of an omnivore hibernating species in Finland. *Mammalian Biology*, *75*(2), 151–159. https://doi.org/10.1016/j.mambio.2008.12.001

Menge, B. A., Blanchette, C., Raimondi, P., Freidenburg, T., Gaines, S., Lubchenco, J., Lohse, D., Hudson, G., Foley, M., & Pamplin, J. (2004). Species Interaction Strength: Testing Model Predictions Along an Upwelling Gradient. *Ecological Monographs*, *74*(4), 663–684. https://doi.org/10.1890/03-4060

Menge, B. A., & Menge, D. N. L. (2013). Dynamics of coastal meta-ecosystems: The intermittent upwelling hypothesis and a test in rocky intertidal regions. *Ecological Monographs*, *83*(3), 283–310. https://doi.org/10.1890/12-1706.1

Messié, M., & Chavez, F. P. (2017). Nutrient supply, surface currents, and plankton dynamics predict zooplankton hotspots in coastal upwelling systems. *Geophysical Research Letters*, *44*(17), 8979–8986. https://doi.org/10.1002/2017GL074322

Montgomery, W. L. (1980). The impact of non-selective grazing by the giant blue damselfish, *Microspathodon dorsalis*, on algal communities in the Gulf of California, Mexico. *Bulletin of Marine Science*, *30*(1), 290–303.

Mora, C., & Ospina, A. (2002). Experimental effect of cold, La Niña temperatures on the survival of reef fishes from Gorgona Island (eastern Pacific Ocean). *Marine Biology*, *141*(4), 789–793. https://doi.org/10.1007/s00227-002-0862-1

Moran, C. J., Carlowicz, R. M., & Gerry, S. P. (2019). A temperate labrid fish demonstrates compensatory mechanisms to feed at torpor-inducing temperatures. *Journal of Zoology*, *307*(2), 125–130. https://doi.org/10.1111/jzo.12624

Nielsen, K., & Navarrete, S. (2004). Mesoscale regulation comes from the bottom-up: Intertidal interactions between consumers and upwelling. *Ecology Letters*, *7*, 31–41. https://doi.org/10.1046/j.1461-0248.2003.00542.x

Olivier, D., Lepoint, G., Aguilar-Medrano, R., Díaz, A. H. R., Sánchez-González, A., & Sturaro, N. (2019). Ecomorphology, trophic niche, and distribution divergences of two common damselfishes in the Gulf of California. *Comptes Rendus Biologies*, *342*(9), 309–321. https://doi.org/10.1016/j.crvi.2019.11.001

Palacios, D. M., Hazen, E. L., Schroeder, I. D., & Bograd, S. J. (2013). Modeling the temperature-nitrate relationship in the coastal upwelling domain of the California Current. *Journal of Geophysical Research-Oceans*, *118*(7), 3223–3239. https://doi.org/10.1002/jgrc.20216

Patti, B., Guisande, C., Vergara, A. R., Riveiro, I., Maneiro, I., Barreiro, A., Bonanno, A., Buscaino, G., Cuttitta, A., Basilone, G., & Mazzola, S. (2008). Factors responsible for the differences in satellite-based chlorophyll a concentration between the major global upwelling areas. *Estuarine, Coastal and Shelf Science*, *76*(4), 775–786. https://doi.org/10.1016/j.ecss.2007.08.005

Penry, D., & Jumars, P. (1986). Chemical Reactor Analysis and Optimal Digestion. *Bioscience*, *36*(5), 310–313. https://doi.org/10.2307/1310235

Pérez-Matus, A., Carrasco, S. A., Gelcich, S., Fernandez, M., & Wieters, E. A. (2017). Exploring the effects of fishing pressure and upwelling intensity over subtidal kelp forest communities in Central Chile. *Ecosphere*, *8*(5), e01808. https://doi.org/10.1002/ecs2.1808

Polis, G. A., & Hurd, S. D. (1995). Extraordinarily high spider densities on islands: Flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences*, 92(10), 4382–4386. https://doi.org/10.1073/pnas.92.10.4382

Pulgar, J., Poblete, E., Alvarez, M., Morales, J. P., Aranda, B., Aldana, M., & Pulgar, V. M. (2013). Can upwelling signals be detected in intertidal fishes of different trophic levels? *Journal of Fish Biology*, *83*(5), 1407–1415. https://doi.org/10.1111/jfb.12220

Robertson, R. (1990). Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes. *Journal of Experimental Marine Biology and Ecology*, *144*(1), 49–62. https://doi.org/10.1016/0022-0981(90)90019-9

Rowe, C. E., Figueira, W., Raubenheimer, D., Solon-Biet, S. M., & Machovsky-Capuska, G. E. (2018). Effects of temperature on macronutrient selection, metabolic and swimming performance of the Indo-Pacific Damselfish (*Abudefduf vaigiensis*). *Marine Biology*, *165*(11), 178. https://doi.org/10.1007/s00227-018-3435-7

Rykaczewski, R. R., & Checkley, D. M. (2008). Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proceedings of the National Academy of Sciences*, *105*(6), 1965–1970. https://doi.org/10.1073/pnas.0711777105

Sanford, E. (2002). The feeding, growth, and energetics of two rocky intertidal predators (*Pisaster ochraceus* and *Nucella canaliculata*) under water temperatures simulating episodic upwelling. *Journal of Experimental Marine Biology and Ecology*, *273*(2), 199–218. https://doi.org/10.1016/S0022-0981(02)00164-8

Sato, M., Barth, J. A., Benoit-Bird, K. J., Pierce, S. D., Cowles, T. J., Brodeur, R. D., & Peterson, W. T. (2018). Coastal upwelling fronts as a boundary for planktivorous fish distributions. *Marine Ecology Progress Series*, *595*, 171–186. https://doi.org/10.3354/meps12553

Schilling, H. T., Hinchliffe, C., Gillson, J. P., Miskiewicz, A. G., & Suthers, I. M. (2022). Coastal winds and larval fish abundance indicate a recruitment mechanism for southeast Australian estuarine fisheries. *Fisheries Oceanography*, *31*(1), 40–55. https://doi.org/10.1111/fog.12561

Sellers, A. J., Leung, B., Altieri, A., Glanz, J., Turner, B., & Torchin, M. (2021). Seasonal upwelling reduces herbivore control of tropical rocky intertidal algal communities. *Ecology*, *102*. https://doi.org/10.1002/ecy.3335

Sepulveda, J., & Moeller, A. H. (2020). The Effects of Temperature on Animal Gut Microbiomes. *Frontiers in Microbiology*, *11*. https://www.frontiersin.org/articles/10.3389/fmicb.2020.00384

Shima, J. S., Osenberg, C. W., Alonzo, S. H., Noonburg, E. G., Mitterwallner, P., & Swearer, S. E. (2020). Reproductive phenology across the lunar cycle: Parental decisions, offspring responses, and consequences for reef fish. *ECOLOGY*, *101*(8). https://doi.org/10.1002/ecy.3086

Smith, T. B. (2008). Temperature effects on herbivory for an Indo-Pacific parrotfish in Panamá: Implications for coral–algal competition. *Coral Reefs*, *27*(2), 397–405. https://doi.org/10.1007/s00338-007-0343-6

Stuhldreier, I., Sánchez-Noguera, C., Rixen, T., Cortés, J., Morales, A., & Wild, C. (2015). Effects of Seasonal Upwelling on Inorganic and Organic Matter Dynamics in the Water Column of Eastern Pacific Coral Reefs. *PLOS ONE*, *10*(11), e0142681. https://doi.org/10.1371/journal.pone.0142681

Thiel, M., Macaya, E. C., Acuna, E., Arntz, W. E., Bastias, H., Brokordt, K., Camus, P. A., Castilla, J. C., Castro, L. R., Cortes, M., Dumont, C. P., Escribano, R., Fernandez, M., Gajardo, J. A., Gaymer, C. F., Gomez, I., Gonzalez, A. E., Gonzalez, H. E., Haye, P. A., … Vega, J. M. A. (2007). The Humboldt Current System of northern and central Chile. In R. N. Gibson, R. J. A. Atkinson, & J. D. M. Gordon (Eds.), *Oceanography and Marine Biology, Vol 45* (Vol. 45, pp. 195–344). Crc Press-Taylor & Francis Group. https://www.webofscience.com/wos/woscc/full-record/WOS:000252476600006

Tsuboi, M., Husby, A., Kotrschal, A., Hayward, A., Buechel, S. D., Zidar, J., Løvlie, H., & Kolm, N. (2015). Comparative support for the expensive tissue hypothesis: Big brains are correlated with smaller gut and greater parental investment in Lake Tanganyika cichlids. *Evolution; International Journal of Organic Evolution*, *69*(1), 190–200. https://doi.org/10.1111/evo.12556

Ware, D. M., & Thomson, R. E. (1991). Link Between Long-Term Variability in Upwelling and Fish Production in the Northeast Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(12), 2296–2306. https://doi.org/10.1139/f91-270

Witman, J. D., Brandt, M., & Smith, F. (2010). Coupling between subtidal prey and consumers along a mesoscale upwelling gradient in the Galápagos Islands. *Ecological Monographs*, *80*(1), 153–177. https://doi.org/10.1890/08-1922.1

Zuloaga, R., Varas, O., Ahrendt, C., Pulgar, V. M., Valdés, J. A., Molina, A., Duarte, C., Urzúa, Á., Guzmán-Rivas, F., Aldana, M., & Pulgar, J. (2023). Revealing coastal upwelling impact on the muscle growth of an intertidal fish. *Science of The Total Environment*, *858*, 159810. https://doi.org/10.1016/j.scitotenv.2022.159810

<u>Appendix 1.</u> Fish diet data.

Table 3.A.1. Frequency of occurrence (%) of food items consumed by damselfishes collected during the non-upwelling (N-UP) and upwelling (UP) seasons.

Species	***A. troschelii***		***M. dorsalis***		***S. flavilatus***	
Season	**N-UP**	**UP**	**N-UP**	**UP**	**N-UP**	**UP**
Algae						
Green filamentous	50.0	63.2	95.0	87.0	97.3	64.0
Green foliose	0.0	57.9	10.0	78.3	24.3	84.0
Green branching	9.4	0.0	25.0	4.3	35.1	24.0
Red branching	37.5	21.1	70.0	65.2	91.9	72.0
Red filamentous	12.5	26.3	55.0	60.9	59.5	72.0
Red calcareous	3.1	10.5	50.0	30.4	51.4	88.0
Diatoms	0.0	5.3	100.0	100.0	0.0	0.0
Animal prey						
Copepod	53.1	52.6	30.0	39.1	2.7	12.0
Amphipod	43.8	63.2	10.0	21.7	8.1	36.0

Fish eggs	37.5	0.0	15.0	0.0	16.2	0.0
Fish larvae	0.0	5.3	0.0	0.0	0.0	0.0
Gastropod	9.4	0.0	5.0	13.0	5.4	12.0
Nematode	0.0	0.0	0.0	0.0	0.0	0.0
Polychaete	3.1	21.1	0.0	0.0	10.8	4.0
Anemone	0.0	0.0	5.0	0.0	5.4	0.0
Shrimp	3.1	26.3	0.0	0.0	2.7	4.0
Mite	0.0	0.0	20.0	13.0	0.0	0.0
Tubeworm	0.0	0.0	0.0	0.0	2.7	0.0
Brittle star	0.0	0.0	0.0	0.0	0.0	4.0
Hydroid	0.0	0.0	5.0	0.0	2.7	0.0
Unknown animal tissue	3.1	0.0	0.0	0.0	24.3	16.0
Other						
Sediment	3.1	15.8	90.0	95.7	48.6	72.0
Detritus	0.0	5.3	0.0	34.8	0.0	12.0

Sample size	**32**	**19**	**20**	**23**	**37**	**25**

Connecting statement: considering the effects of habitat on consumer abundance

In Chapters 2 and 3, I tested how environmental variation in temperature and resource availability impacts the feeding, digestive physiology and distribution of marine fishes. However, I did not explicitly consider the effects of habitat quality on consumers. Many consumer species depend on biogenic habitat, including corals, seagrasses, mangroves and mussels, and the distribution of biogenic habitat plays a definitive role in controlling the distribution of marine consumers at the local and seascape scales.

In Chapter 4, I seek to understand patterns of distribution in hyper-diverse invertebrate assemblages found on dead corals in Caribbean Panama. However, instead of testing for the impact of abiotic factors on abundance (as in Chapter 3), I tested whether different trophic groups respond differently to coral degradation. Further, because I operated on a much smaller scale (tens of kilometers) than Chapters 2 and 3 (thousands of kilometers), I was able to document extremely high-resolution patterns of biomass, to collect information on the feeding ecology of 53 coexisting consumer taxa.

Chapter 4: Coral degradation differentially affects invertebrate trophic functional groups

Nicole S. Knight, Andrew H. Altieri, Frédéric Guichard, Tess Morelli, Joan Antaneda, Gustav Paulay, David M. Baker, Bryan Nguyen, François Michonneau, Robert Lasley, Matthieu Leray

Abstract

Cryptic invertebrate consumers are a crucial link in benthic marine ecosystems, but as coral reefs decline, the biomass, diversity, and composition of these communities can change. However, it remains unclear how coral degradation impacts the functional composition of associated invertebrate assemblages. In this study, we sampled 12 coral reefs across Bahía Almirante, Caribbean Panama to characterize different aspects of invertebrate function. We first quantified variation in the biomass and diversity of different trophic functional groups across a gradient of coral degradation. We then estimated the isotope signatures, niche breadths, and niche overlap of dominant consumers, to better understand how these consumers contribute to ecosystem function. Our results reveal that trophic functional groups responded differently to habitat degradation; grazer and predator biomass declined with decreasing live coral cover, whereas deposit- and suspension-feeding organisms were unaffected. Invertebrate diversity was not affected by any of our environmental predictors. Our analyses of niche breadth varied by approximately an order of magnitude; but niche overlap was typically low within trophic groups, suggesting strong niche complementarity and low functional redundancy. Altogether, our findings demonstrate the cryptic invertebrate communities are vulnerable to the effects of habitat degradation, and further, that consumer species are not functionally interchangeable and so may not be easily replaced.

Introduction

In benthic marine habitats, consumers exert strong control over ecosystem function (Burkepile & Hay, 2006; Duffy, 2002; Hillebrand et al., 2007; O'Connor et al., 2017; Shurin et al., 2002). Ecosystem function, defined in this context as "the movement or storage of energy or material within an ecosystem", following Bellwood et al. (2019), is particularly dependent on consumers that take up primary production and detritus. These consumers facilitate foundation species including corals and seagrasses by removing their algal competitors (Altman-Kurosaki et al., 2018; Brandl et al., 2019; Duffy et al., 2003), recycle detritus (Emery et al., 2021; Williamson et al., 2021), and serve as prey to higher-order predators, supporting complex food webs (Casey et al., 2019). However, the overall ecosystem function of consumer assemblages varies substantially, and depend on the identities (Bagur et al., 2014; Campbell et al., 2018; Emery et al., 2021; Laigle et al., 2018), diversity (Duffy et al., 2003), and abundance (Moksnes et al., 2008; Spiers & Frazer, 2023) of constituent species.

How consumer loss impacts ecosystem function depends on the relative importance of dominance and niche complementarity in the system. When ecosystem function is highly dependent on a single dominant species, the loss of that species is expected to cause large declines in function (Lessios, 1988; Treplin et al., 2013; Winfree et al., 2015). In contrast, when species contributing to ecosystem function exhibit high niche complementarity (the differential uptake of resources), ecosystem function should decline gradually with decreasing species richness (Adam et al., 2015; Duffy et al., 2003; Karlson et al., 2010; Lewis & Smith, 2019; Wong & Dowd, 2021). Regardless of the relative importance of dominance and complementarity in a given system, ecosystem function may be maintained despite species loss if that function can be replaced by similar species (i.e., there are species that are functionally redundant) (Bellwood et al., 2006; Campbell et al., 2018; Elmqvist et al., 2003); however, in many cases ecosystem function is characterized by low redundancy (Bellwood et al., 2006; Henderson et al., 2020; Reich et al., 2012).

In the Caribbean, many large herbivorous fishes have been removed by overfishing (Hughes, 1994; Jackson et al., 2014; Loh et al., 2015; Shantz et al., 2020), and the formerly dominant grazer, the large generalist urchin *Diadema antillarum*, has been marginalized by a disease outbreak (Hewson et al., 2023; Hylkema et al., 2023; Lessios, 1988). In Bahía Almirante, Caribbean Panama, this function appears to have been replaced by small-bodied and cryptic herbivores (Kuempel & Altieri, 2017; Sangil & Guzman, 2016), a potentially important but underexplored pool of functional diversity (Glynn & Enochs, 2011; Nelson et al., 2016; Nguyen, 2020; Nguyen et al., 2020). These invertebrate assemblages also include suspension and deposit feeders that provide a suite of benefits, such as incorporating nutrients from the water column and nearby seagrass and mangrove habitats (Granek et al., 2009; Heck et al., 2008; Ribes et al., 2003; Williamson et al., 2021). However, various events have led to the loss of coral in the region that mirror declines in the broader Caribbean (Altieri et al., 2017; Alvarez-Filip et al., 2009; Cramer et al., 2012; Seemann et al., 2014), putting the functional fate of these communities into question.

In this study, we tested how the degradation of coral habitat contributes to changes in the functional composition of cryptic invertebrate consumers. We did this by destructively sampling dead *Agaricia tenuifolia* from 12 reefs in Bahía

Almirante to estimate invertebrate biomass and composition. We then characterized the diets, niche breadths, and niche overlap of common consumers, using a combination of isotope data and a literature search. We tested the following research questions: first, do functional groups respond differently to changes in biomass and diversity in response to the degradation of coral habitat? Second, what is the relative importance of dominance, niche complementarity, and functional redundance in these trophic groups? Our results reveal that the functional composition of invertebrate communities changes with habitat degradation; the biomass of herbivores and predators declines with decreasing live coral cover whereas deposit and suspension feeders are unaffected. Further, grazers and deposit feeders tend to be dominated by one or two species, but across all groups, niche overlap is low, suggesting low functional redundancy.

Methods

Study system

Bahía Almirante is a semi-enclosed lagoonal system located in Bocas del Toro, Caribbean Panama (Figure 4.1). Water flows into the lagoon primarily between Isla Colón and the mainland, carrying in sediments from the Ríos Changuinola and Sixaola (Saric, 2005). Water flows out of two outlets, between Islas Colón and Bastimentos and Islas Bastimentos and Popa (Figure 4.1; blue arrows); but water exchange in the lagoon is limited, contributing to local temperature increases and oxygen depletion (Adelson et al., 2022; Seemann et al., 2014).Over the past few decades the lagoon has been impacted by a variety of anthropogenic activities, including increased sedimentation, nutrification, heavy metal loading, boat traffic, and overfishing (Seemann et al., 2014). These environmental changes, as well as various bleaching and hypoxic events, have led to substantial declines in coral cover and diversity across a spatial gradient in the lagoon (Altieri et al., 2017; Seemann et al., 2014).

Agaricia tenuifolia, the thin-leaf lettuce coral, is one of the more abundant and widespread corals across Bahía Almirante (Seemann et al., 2014), and is composed of thin, flat, irregular, upright fronds, giving colonies substantial structural complexity. This structural complexity allows both live and dead *A. tenuifolia* to support diverse, abundant assemblages of cryptic invertebrates (Nelson et al., 2016).

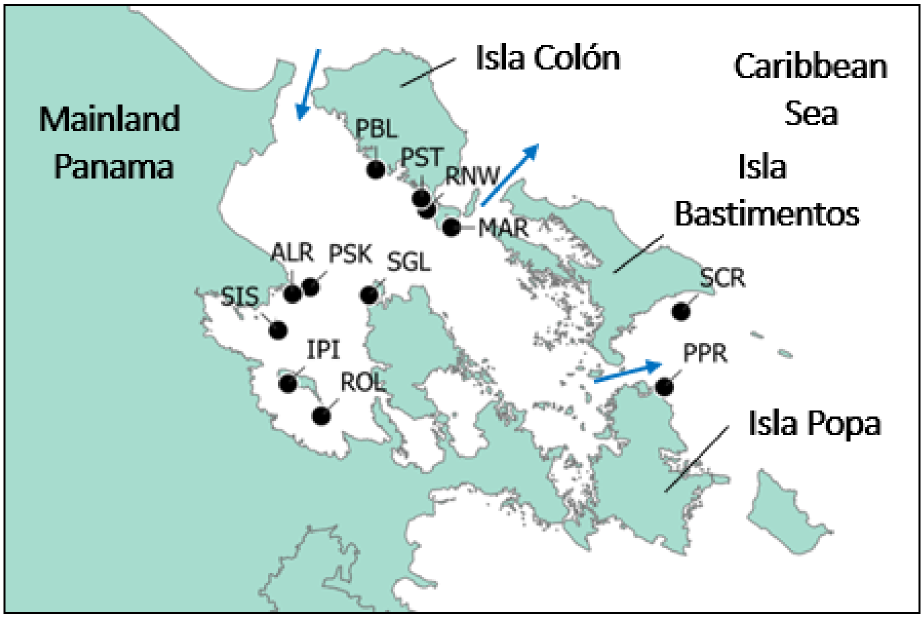

Figure 4.1. Collection sites in Bahía Almirante, Caribbean Panama. Blue arrows show channels through which water flows into and out of the lagoon. Site abbreviations are as follows: ROL = Cayo Roldan, IPI = Isla Pastores, SIS = Cayo Hermanas, ALR = Almirante, PSK = Ponsak, SGL = Seagal, PBL = Punta Puebla, PST = Punta STRI, RNW = Runway, MAR = Marina, SCR = Salt Creek, PPR = Popa Reef.

Community sampling

We quantified the composition and biomass of invertebrate assemblages associated with dead colonies of *Agaricia tenuifolia* in June 2016. A team of divers collected *A. tenuifolia* from 12 reefs across Bahía Almirante (Figure 4.2). We standardized our sampling efforts by haphazardly selecting three 0.25m^2 quadrats of dead *A. tenuifolia* from each reef. For each quadrat, we detached every dead coral colony from the substrate (excavating to the sandy bottom or cemented reef platform) and immediately enclosed them within a heavy-duty plastic bag while still underwater. Although it is likely some large, motile organisms were lost during this process, the diversity and abundance of motile species that we observed in our samples suggest that any loss was minimal and consistent across locations. The bags were transported to the boat, where they were placed into large, aerated bins of seawater until processing later that day. We also sampled plankton by towing a 0.80 µm plankton net (0.5 m diameter) for 5 min per reef, and we collected 5 to 10 blades of the turtle seagrass *Thalassia testudinum* per reef, for stable isotope analysis.

In the laboratory, we transferred dead coral substrate (and associated sponges) to large sorting trays containing 45µm filtered seawater. We broke corals and sponges into small, planar pieces, then shook them in the seawater to dislodge any motile organisms. We filtered the water from all trays and bins through 2mm sieves and placed the contents in a tray. We sorted and counted specimens retained by the 2mm sieve to morphospecies (smaller size fractions were saved and analyzed, but these data are not included in this paper). One to a few individuals from each morphospecies were photographed alive (Paulay et al. 2017), preserved in 80% ethanol, and catalogued in the Florida Museum of Natural History invertebrate collection as reference vouchers. All coral skeleton was saved and weighed to estimate coral mass within each plot.

Other invertebrates grouped into morphospecies were dried at 60°C overnight to measure dry weight and then incinerated at 400°C for four hours in a combustion furnace to estimate ash-free dry weight. We collected and weighed the sponge tissue within each plot in the same way. Finally, to characterize the trophic niches of common species, we opportunistically set aside individuals from each plot that appeared to constitute a large portion of that plot's biomass due to either high abundance or large body size. Because we conducted this sampling prior to knowing the full biomass distribution of taxa, our coverage of the highest-biomass species was not complete, but did include 33 high-biomass taxa.

Reef benthic cover

We conducted surveys of benthic cover at each site during May and June of 2016. We placed three 20m transects parallel to the shore 2-4m deep, and photographed 100cm x 70cm quadrats, each spaced 2m apart (n = 30 per site). We analyzed all photos in the CoralNet platform (Beijbom et al., 2015). We employed a stratified random sampling design, in which we divided each image into a 10x10 grid of cells, then randomly sampled 1 point in each cell (n = 100 per image). Points were assigned to one of the following categories: live hard coral, dead hard coral, live soft coral, sponge, zoanthid, other invertebrates, seagrass, grazable substrate, macroalgae, rubble, sand, shade and “unknown”. We trained the CoralNet algorithm by manually scoring the first 15 photos; the remaining photos were scored automatically using the algorithm. We later verified the assignments made by CoralNet. Finally, the mean benthic cover of each category was estimated per reef. However, only live hard coral, dead hard coral, rubble, and sand were included in our analyses.

Stable isotope analysis

Our isotopic analyses were designed to a) estimate the mean and variance of each taxon’s $\delta^{15}N$ and $\delta^{13}C$ values, b) test whether trophic designations from the literature were consistent with observed estimates of $\delta^{15}N$ and $\delta^{13}C$, and c) estimate the isotopic niche breadth and niche overlap of common consumer species. To measure $\delta^{15}N$ and $\delta^{13}C$ isotope ratios, we set aside individuals from 33 consumer taxa (N = 339, range of samples per species = 1 - 76) and 2 potential food sources (turtle grass, n = 6; plankton, n = 24). Data for an additional potential food source collected in Bocas del Toro, particulate organic matter, was provided by Chris Freeman (unpublished). All individuals from consumer taxa sampled for isotope analysis were weighed then dried at 60°C overnight. For taxa with shells, carapaces, or tests, we dissected out soft tissues prior to drying. We then ground each sample into a fine powder, weighed it on a microbalance, and packed it into tin capsules. Samples from taxa containing calcium carbonate ($CaCO_3$) that could not be easily separated from other tissues (e.g., brittle stars) were packed into silver capsules, weighed, then acidified using previously sealed ampoules of hydrochloric acid to prevent $CaCO_3$ from interfering with our estimates of isotope ratios and percent carbon (Jacob et al., 2005). Samples were processed in an EA3028 Elemental Analyser (Eurovector, Italy), and analyzed by a Perspective Isotope Ratio Mass Spectrometer (Nu, United Kingdom) using iACET as a standard reference material. We use δ notation for isotope ratios: values of $\delta^{15}N$ and $\delta^{13}C$ are calculated as $\frac{R_{sample}}{R_{standard}} - 1$ where R is the heavy/light isotope ratio (e.g., $\delta^{15}N/\delta^{14}N$). Measured values are reported in per mil (‰).

Trophic classifications

To quantify the trophic composition of the invertebrate assemblages associated with each plot, we first identified the species with the most biomass across the pooled assemblage. We searched the literature for information on diet and feeding mechanism for each of these species. Because of the difficulty of obtaining sufficient diet data, we classified species according to their feeding mechanism as suspension feeders, deposit feeders, grazers, or predators (Table 4.1). Some species were recorded to engage in multiple types of feeding, in these cases, all types were recorded but we classified the species following its dominant type of feeding. We then checked these literature classifications against the $\delta^{15}N$ signatures of species for which we collected isotope data.

Table 4.1. Trophic group definitions used throughout this manuscript.

Trophic group	**Description**	**Examples**
Suspension feeder	Consume food (plankton, bacteria, detritus) suspended in the surrounding water. Includes filter feeders	*Ctenoides scaber,* *Ophiothrix oerstedii*
Deposit feeder	Consume organic particles in sediment	*Holothuria impatiens*, *Ophionereis reticulata*
Grazer	Consume algae or plant material by scraping, biting, etc.	*Echinometra viridis*, *Lithopoma tectum*
Predator	Consumes animal prey	*Fasciolara tulipa*, *Baseodiscus*

Statistical analyses

All statistical analyses were conducted in R version 4.2.1, *Funny-Looking Kid* (R Core Team, 2021) using RStudio version 2022.7.2.576, *Spotted Wakerobin* (RStudio Team, 2022).

We first analyzed variation in the coral structure and benthic cover of reefs across Bahía Almirante using a Principal Component Analysis, which allowed us to better understand spatial variation in reef characteristics. To test how live coral cover (reef scale) and coral mass (plot scale) impact the biomass and diversity of different functional groups (both estimated at the plot level) across Bahía Almirante, we built generalized linear models (GLM) using the Bayesian modelling package *brms* (Bürkner, 2017). We ln-transformed biomass and modelled it using the student distribution; we modelled diversity (Gini-Simpson index; GS index) using the beta distribution with a logit link. We chose to use the GS index as our diversity response because our data exclude small and rare species, and the GS weights species evenness more heavily than other indices such as species richness or Shannon's diversity (Chao et al., 2014; Whittaker, 1965). All models initially included a random effect of reef ID, given that we expected plots from the same reef to be more similar. To test which predictor best explained variation in invertebrate biomass and diversity, we competed the models against each other using model selection, compared effect sizes, and ran posterior predictive checks to ensure reasonable model fit.

Although the isotopic data we collected for all 33 taxa are presented in the results section to increase the available data for these species, only taxa with $n > 5$ in at least one site were included in our statistical analyses. To model $\delta^{15}N$ and $\delta^{13}C$, we built GLMs following the student distribution, which provides better estimates for data with outliers than the normal distribution. $\delta^{15}N$ and $\delta^{13}C$ were modelled separately. In each of our two models, we included trophic group (Table I) as a fixed effect, and site ID nested within taxon ID as a random effect. We structured our random effect this way because the isotopic signatures of taxa may vary across sites interactively (e.g., species A might have higher $\delta^{13}C$ at site X than site Y, whereas species B might have lower $\delta^{13}C$ at site X than site Y). In these models, we also included two predictors of variance (σ): trophic classification as a fixed effect, and taxon ID as a random effect. Including these two effects allowed us to assess whether trophic or taxonomic identity were better determinants of the variability of a taxon's isotopic niche.

We also assessed the variability of a taxon's isotopic niche (i.e., niche breadth) using the *SIBER* package (A. L. Jackson et al., 2011). *SIBER* estimates a taxon's isotopic niche by jointly modelling $\delta^{15}N$ and $\delta^{13}C$ following a multivariate normal distribution, which it uses to calculate the standard ellipse area (SEA). Because variation in diet across sites inflates estimates of SEA (Jackson et al., 2011), if a species had n > 5 at multiple sites, isotope data from each site were analyzed separately. We also corrected our estimates of SEA for low sample sizes (corrected estimates are denoted SEA_c). For the model we ran a total of 20,000 iterations, including 1,000 burn-in iterations, across two chains. Iterations were thinned by a factor of 10. We used our estimates of isotopic niche position and breadth to calculate niche overlap between common consumer species using the formula $\frac{Overlap}{SEA_c} * 100\%$.

Results

Reef attributes

Coral reef habitats across Bahía Almirante vary substantially in both coral structure and benthic cover, but reefs closer together have more similar characteristics (Figure 4.2). Reefs near the mainland, in the most sheltered part of the bay (ROL, IPI, SIS; Figure 4.1), had relatively low cover of both live and dead hard coral, high cover of coral rubble and bare sand, low dead coral mass within plots, and high sponge mass (Tables 4S1 and 4S2). Of the sites located in the main portion of Bahía Almirante, southern sites (ALR, PSK, SGL) were characterized by a mix of live and dead hard coral, with some rubble and bare sand. Sites along the southwest coast of Isla Colón (PBL, PST, RNW) had virtually no live coral cover, but high dead coral cover and coral rubble, with relatively low sponge mass. MAR, located next to the Bocas Marina, was more similar to reefs exposed to the open Caribbean (SCR and PPR); all three sites had relatively high live coral cover.

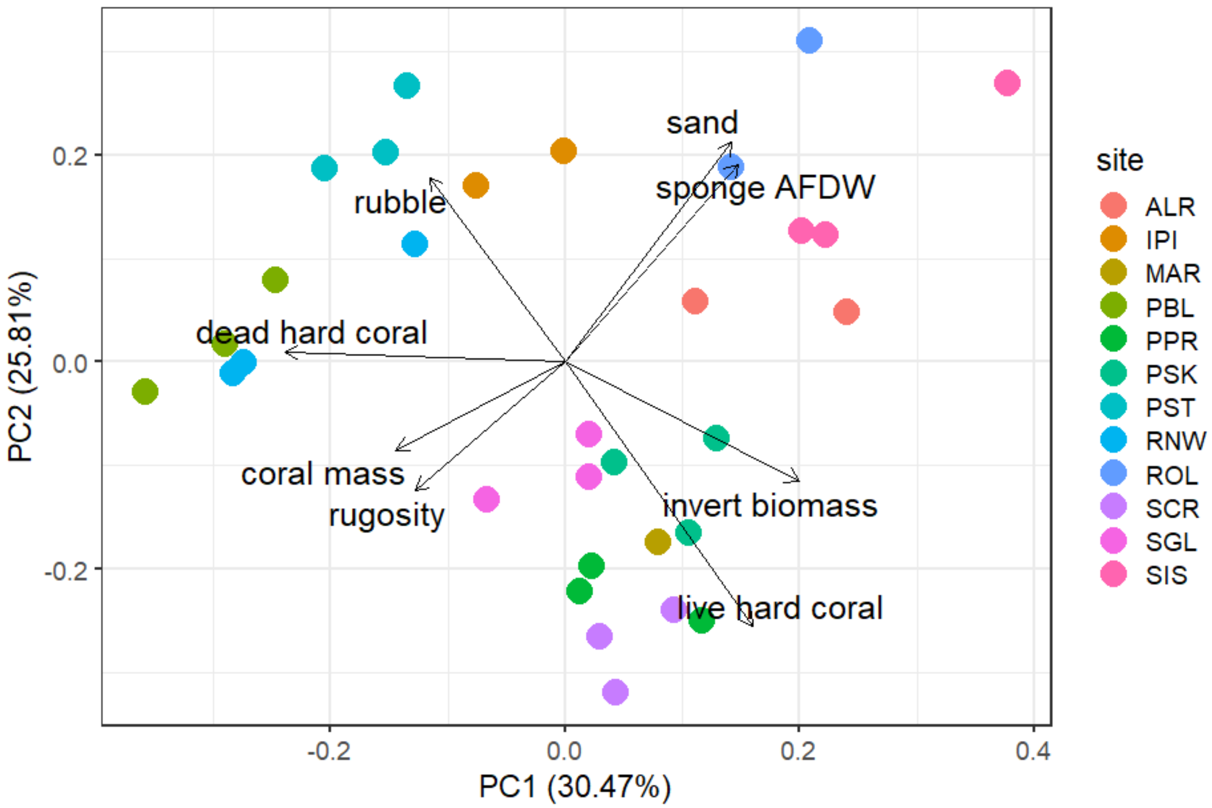

Figure 4.2. Characteristics of 12 coral reefs in Bahía Almirante, Caribbean Panama. Each point in the principle components analysis (PCA) represents the values associated with one plot of dead *Agaricia tenuifolia*; colours denote the site at which each plot was collected. Coral mass, rugosity, and sponge AFDW were all measured

at the plot level; live hard coral and dead hard coral (% cover) were measured at the reef level (i.e., values are identical for plots within a given site).

Across 36 plots of dead *Agaricia tenuifolia*, we observed a total of 24,765 individuals from 505 invertebrate taxa. We collected biomass estimates for 117 taxa that represented 84% of all individuals sampled; the taxa that were not included were generally too small and rare to contribute substantially to invertebrate biomass. Of the 117 taxa for which we collected biomass estimates, we were able to find trophic classifications for 53 taxa, representing 94% of all recorded biomass. Of these 53 taxa, we positively identified 21 as suspension feeders, 15 as predators, 13 as grazers, and 6 as deposit feeders.

Consumer summary

Total invertebrate dry mass averaged 254g per 0.25m^2 plot (±128g SD), but varied sevenfold across plots (range 85 - 622g). Invertebrate biomass varied across trophic groups: suspension feeders constituted the most invertebrate biomass on average (78±75g), followed by grazers (65±32g), predators (54±48g), and deposit feeders (42±55g). Grazer biomass was positively associated with live coral cover (reef level) and coral mass (plot level); predator biomass was positively associated with live coral cover only (Table 4.2). Neither suspension nor deposit feeder biomass was predicted by any environmental variables, except for site, which was included as a random effect (Table 4.2).

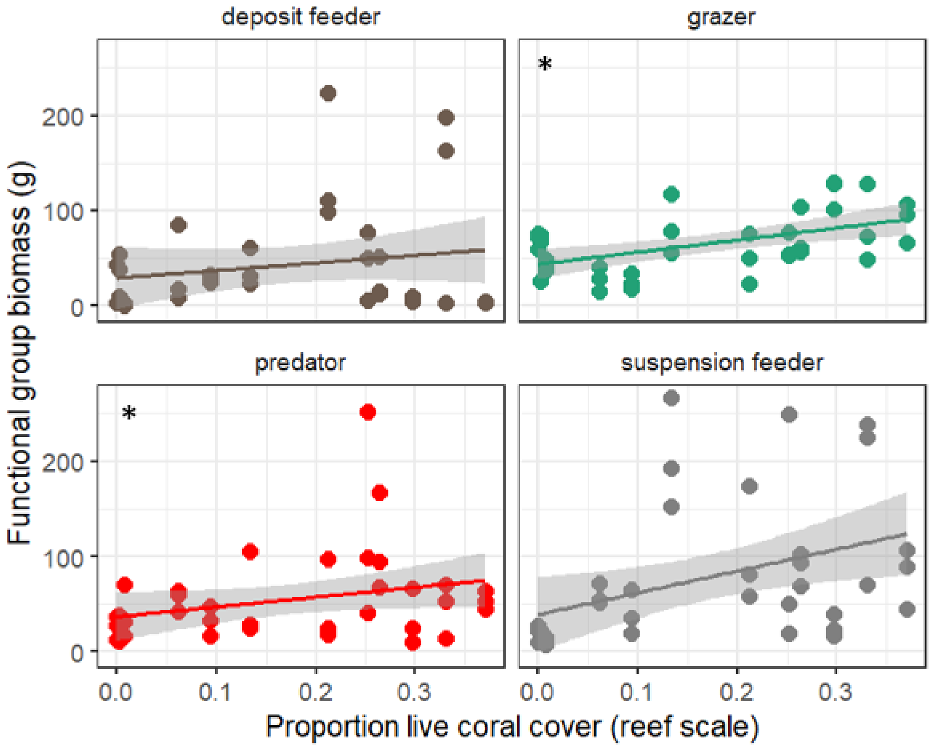

Figure 4.3. Changes in functional group biomass across the proportion of the reef that is covered in live coral. Each point represents a single plot from one of twelve reefs. Stars represent functional groups for which the relationship between biomass and coral cover was significant (grazers and predators).

Table 4.2. Predictors from the best selected models describing the biomass of different trophic functional groups. Live coral cover and Coral mass are fixed predictors, measured at the reef and plot level respectively, and Site is a random predictor. The best models for each group were selected using leave-one-out cross validation, and validated using posterior predictive checks.

Group	**Predictor**	**Median and 95% CI**
Grazer	Coral mass	0.03 [-0.01, 0.07]
	Live coral cover	0.02 [0.00, 0.04]
	Site	0.35 [0.06, 0.68]
Predator	Live coral cover	1.75 [-0.16, 3.67]
Suspension feeder	Site	0.99 [0.59, 1.63]
Deposit feeder	Site	1.17 [0.47, 2.07]

Invertebrate diversity, quantified using the inverse Simpson index, averaged 0.86 per plot (±0.07). Predators and suspension feeders exhibited the highest average diversity (0.65±0.15 and 0.64±0.16, respectively), followed by grazers (0.47±0.23), and deposit feeders (0.25±0.18). However, because not all taxa are included in our analyses, our diversity estimates should be considered as minimum values. Variation in invertebrate diversity across functional groups was not explained by any of our environmental predictors.

Assemblages of deposit feeders and grazers exhibited the greatest tendency to be dominated by one or two taxa: the polychaete Terebellidae sp. and the sea cucumber *Holothuria impatiens* constituted an average of 46.2 and 42.8% (respectively) of overall deposit-feeder biomass, but represented as much as 95.6 and 90.5% (respectively) of site-level deposit-feeder biomass (Figure 4.4). Similarly, the urchin *Echinometra viridis* represented 50% of all grazer biomass, and represented up to 92.8% of site-level grazer biomass. The next most dominant grazer was the snail *Cerithium litteratum*, representing only 12.7% of all grazer biomass. Assemblages of predators and suspension feeders were less prone to domination by a single taxon: the highest-biomass predator, the brittle star *Ophioderma appressum* constituted 27.9% of all predator biomass, (site-level maximum: 55.3%). The highest-biomass suspension feeder, the brittle star *Ophiocoma wendtii*, only constituted 17.3% of all biomass (site-level maximum: 20.5%).

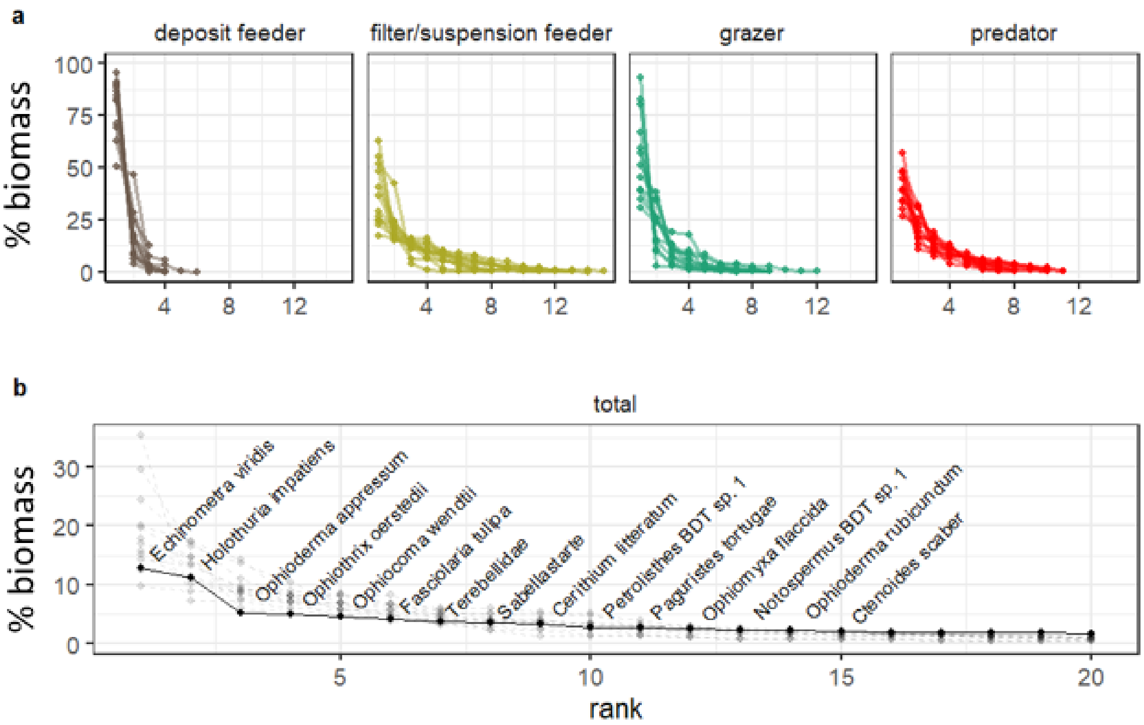

Figure 4.4. Rank biomass curves describing invertebrate assemblages associated with dead *Agaricia tenuifolia* in Bahía Almirante, Caribbean Panama. The y-axis gives the percent biomass contributed by each species. Each line represents a site. Panel a) shows rank abundance curves for each trophic group, and panel b) shows rank abundance curves including the 20 taxa constituting the most biomass in the entire invertebrate assemblage. In panel b), light lines represent pooled data from each site, and the dark line represents the entire pooled dataset. Labels denote the 15 taxa with the highest biomass in the entire dataset. Appendix I gives the biomass contributions of each species to their trophic group.

Isotope analyses

Our analyses reveal that trophic level, taxon identity, and collection site all impact values of consumer $\delta^{15}N$ and $\delta^{13}C$ (Figures 4.5, 4.6). $\delta^{15}N$ values, which indicate trophic level, were indistinguishable between species classified in the literature as predators (7.03‰, 95%CI: 6.09, 7.97) and deposit feeders (7.14‰, 95%CI: 6.74, 7.52), but lower for species classified as suspension feeders (4.16‰, 95% CI: 3.74, 4.57) or grazers (3.75‰, 95%CI: 3.29, 4.23). $\delta^{13}C$ values, which in marine systems indicate the relative contributions of terrestrial (high $\delta^{13}C$) and marine (low $\delta^{13}C$) carbon, were highest for predators (-14.3‰, 95%CI: -15.1, -13.6) and grazers (-14.6‰, 95%CI: -15.4, -13.8) and lower for deposit feeders (-16.37‰, 95%CI: -17.93, -14.86) and suspension feeders (-17.6‰, 95%CI: -18.3, -16.9). Model selection assigned the most support to models containing a nested taxon ID:site ID random effect for both $\delta^{15}N$ (0.72, 95%CI: 0.50, 0.98; 85% of model weight) and $\delta^{13}C$ (1.17, 95%CI: 0.73, 1.70; 83% of model weight). Although some taxa were not included in our statistical analyses due to insufficient sample sizes, they have been included in Figure 5 for reference.

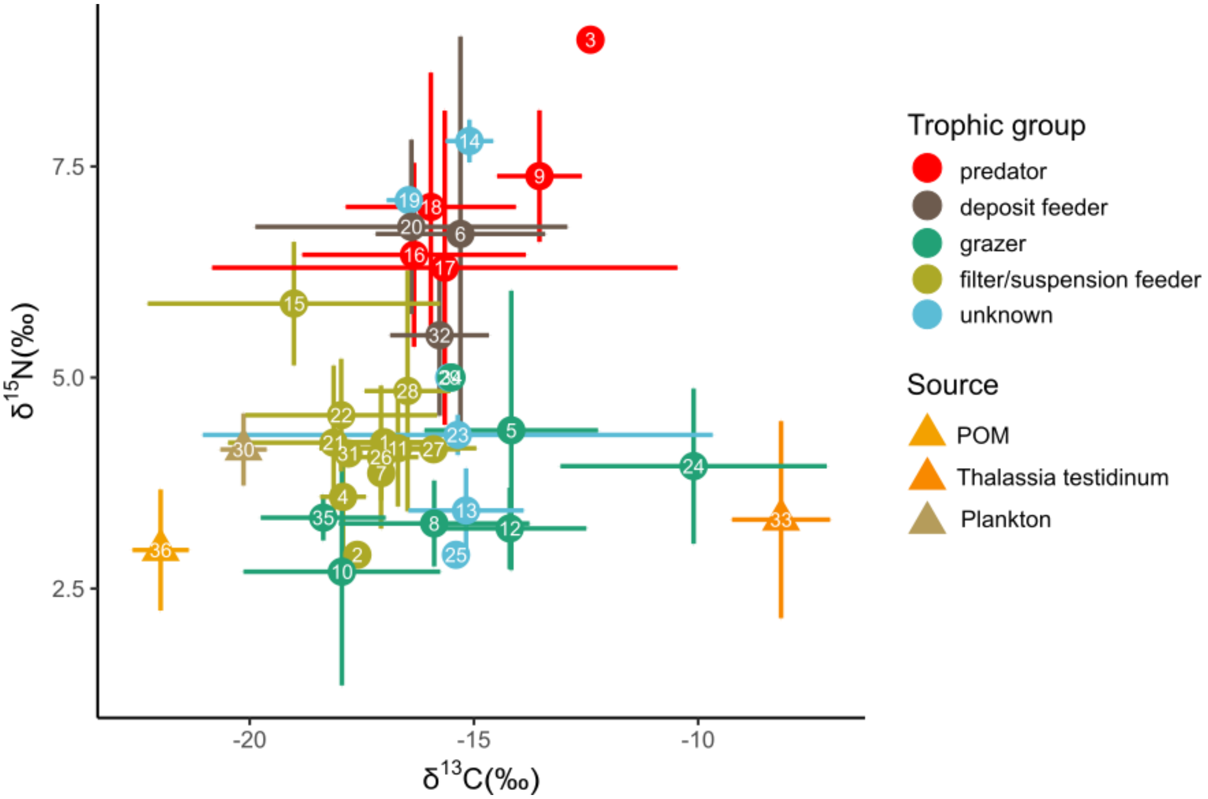

Figure 4.5. δ^{15}N and δ^{13}C signatures (mean ± SD) of invertebrate consumer taxa (circles) and possible diet sources (triangles) collected from Almirante Bay, Panama. Colours are assigned based on primary trophic designation from literature (Appendix 1). Each point represents the mean signature of one taxon, and is marked with a number corresponding to the taxon identity, as follows: 1) *Antillipecten antillarum*, 2) Arcidae, 3) *Baseodiscus* sp., 4) *Ctenoides scaber*, 5) *Echinometra viridis*, 6) *Holothuria impatiens*, 7) *Limaria pellucida*, 8) *Lithopoma tectum*, 9) *Lysmata jundalini*, 10) *Lytechinus williamsi*, 11) *Malleus candeanus*, 12) *Mithraculus forceps*, 13) *Mithrax*, 14) *Odontozona* n. sp. aff. rubra, 15) *Ophiocoma wendtii*, 16)

Ophioderma appressum, 17) *Ophioderma rubicundum*, 18) *Ophiomyxa flaccida*, 19) Ophiomyxidae sp., 20) *Ophionereis reticulata*, 21) *Ophiothrix oerstedii*, 22) *Ophiothrix* sp., 23) *Paguristes* sp., 24) *Paguristes tortugae*, 25) Paguroidea sp., 26) Pectinidae sp., 27) *Petrolisthes* sp., 28) *Petrolisthes* BDT sp. 1, 29) Pilumnidae sp., 30) Plankton, 31) *Sabellastarte* sp., 32) Terebellidae sp., 33) *Thalassia testudinum*, 34) *Thor manningi*, 35) *Turbo* sp., 36) Particulate organic matter (POM values provided by Chris Freeman)

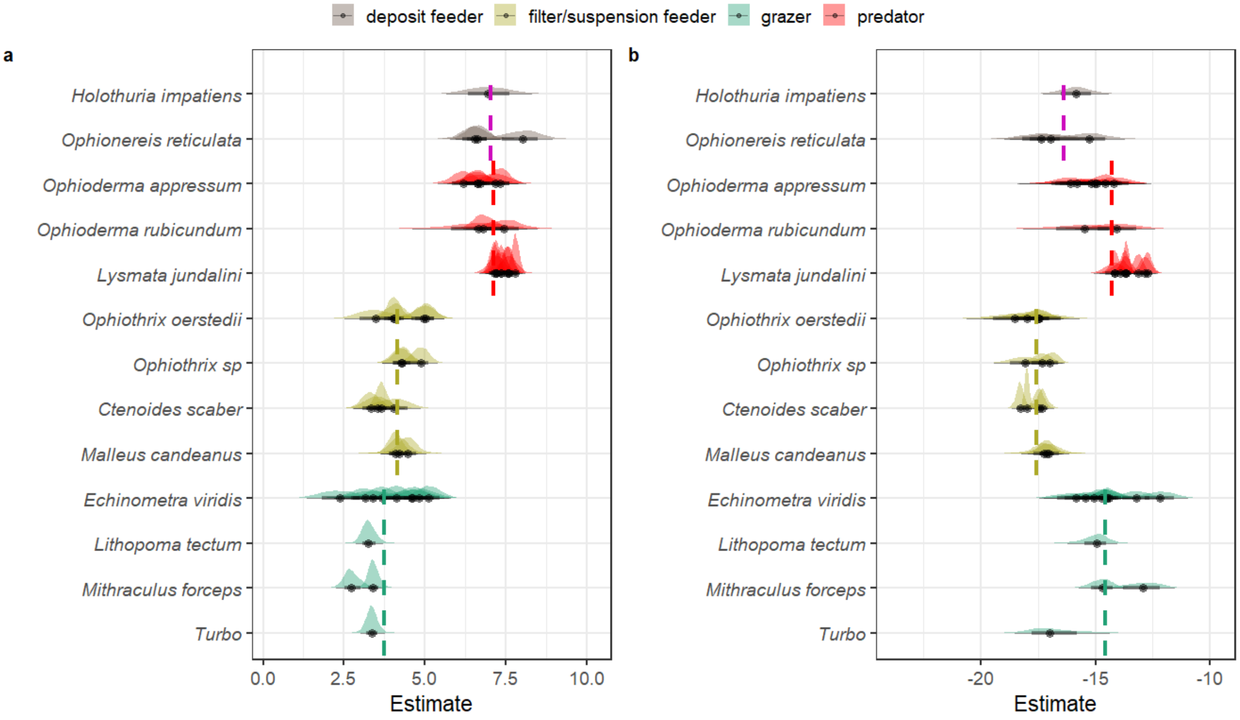

Figure 4.6. Model estimates of the δ^{15}N (a) and δ^{13}C (b) signatures of 13 common consumers collected from dead *Agaricia tenuifolia* across Bahía Almirante, Panama. Filled area represents distribution of all posterior draws, black lines represent the range of values over which we observe the middle 95% of posterior draws. Dashed

vertical lines represent the median estimate of δ^{15}N and δ^{13}C for each trophic group combined. Multiple distributions for a single species represent estimates of δ^{15}N and δ^{13}C from different sites.

Estimates of isotopic niche breadth (SEA$_c$) varied by more than an order of magnitude across consumer taxa (*Lysmata jundalini:* 0.28‰^{2}, *Ophionereis reticulata:* 8.3‰^{2}; Figure 4.7, asterisks). Species that were widely sampled (e.g., *Echinometra viridis*, *Lysmata jundalini*, and *Ophionereis reticulata*) exhibited similar niche breadths across reefs (Figure 4.7), although isotopic signatures across sites differed (Figure 4.6). Niche overlap within and across trophic groups was generally low but ranged from 0%-70% (Table 4.3).

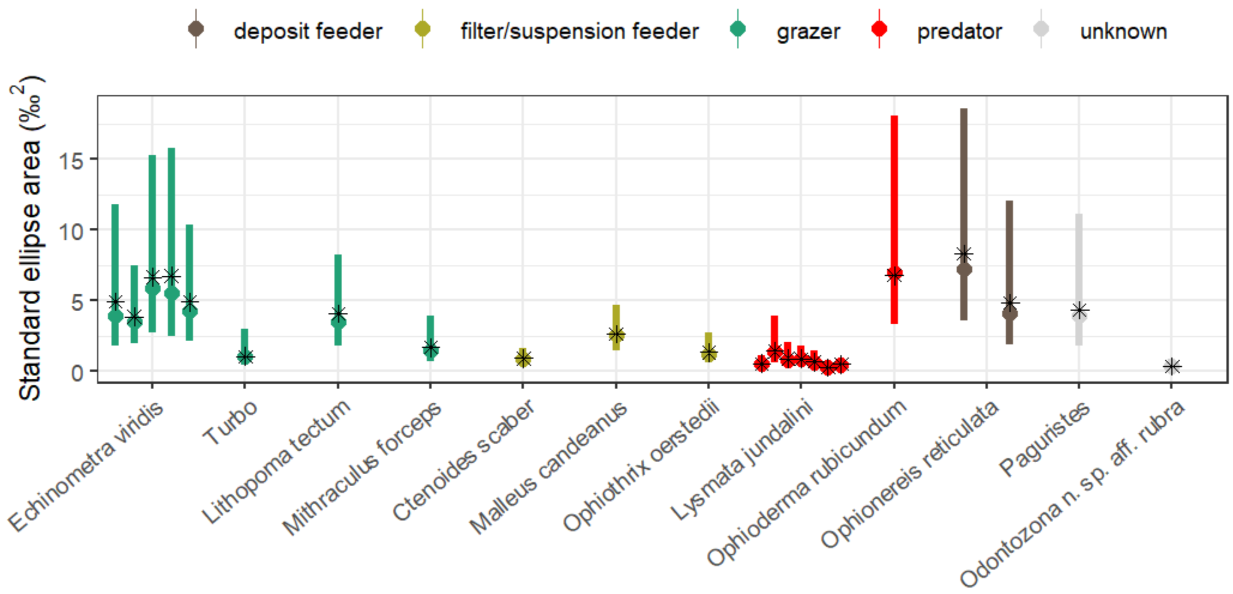

Figure 4.7. Trophic niche breadths of 12 taxa collected from Bocas del Toro,

Panama, as estimated by standard ellipse area (SEA). Points show median SEA estimate at a given site, lines show 95% credibility intervals, and black asterisks indicate SEA estimates corrected for small sample size (SEA_c). Three species have SEA estimates from multiple sites (*E. viridis*, *L. jundalini* and *Ophionereis reticulata*) that were estimated independently and are represented by separate lines.

Table 4.3. Isotopic niche overlaps (% of the total area that overlaps) calculated from δ^{15}N and δ^{13}C signatures. Values show overlap between niche of taxon in each row with the niche of taxon in each column. Taxon comparisons are only made between taxa collected from the same site (blank cells indicate no comparison made). Values marked with a star are the average niche overlap calculated from multiple site pairs. Taxon codes: EV = *Echinometra viridis*, TU = *Turbo* sp., LT = *Lithopoma tectum*, MF = *Mithraculus forceps*, CS = *Ctenoides scaber*, MC = *Malleus candeanus*, OO = *Ophiothrix oerstedii*, LJ = *Lysmata jundalini*, ORu = *Ophioderma rubicundum*, ORe = *Ophionereis reticulata*, PA = *Paguristes* sp., OD = *Odontazona n. sp. aff. rubra*. Colours indicate trophic group, and correspond to colors in Figure 2. Interior coloured cells represent niche overlap estimates for taxa within a given trophic group.

	EV	TU	LT	MF	CS	MC	OO	LJ	ORu	ORe	PA	OD
EV				10.7	4.5		0.0	22.0*		34.9		

TU			26.3									
LT		1.6										
MF	34.4				0.1	0.0		29.9			48.2	
CS	34.3			0.1		70.1		0.3			59.0	
MC				0.0	27.9						47.4	
OO	0.0							6.0				
LJ	53.5*			23.4	0.0		1.6					37.1
ORu												35.5
ORe	29.7											
PA				10.5	6.0	11.9						
OD								34.8	15.7			

Discussion

Dead *Agaricia tenuifolia* in Bahía Almirante support highly diverse assemblages of invertebrate consumers (505 taxa) that contribute to various ecosystem functions, including grazing, detrital recycling, and water filtration.

Despite high species richness, only 50 species constituted 96% of recorded biomass, suggesting that the majority of species contribute little to overall ecosystem function. The loss of live coral cover at the reef scale was associated with declines in the biomass of herbivores and predators, but not suspension or deposit feeders. None of our environmental predictors explained variation in the diversity of different trophic groups. Our isotope analyses revealed substantial variation in niche size among common reef consumers and little niche overlap, even within trophic groups. Altogether, our findings suggest that only a handful of species dominate ecosystems contributed by cryptobenthic communities, and moreover, that many species within a given trophic group are not functionally interchangeable. This suggests that in the event of further species losses in the Caribbean, species' functional contributions may not be easily replaced.

Species depend on the structure provided by corals for different reasons, perhaps contributing to the variation in the response of different trophic groups to coral loss. Many species depend on coral structure for protection from predators, and having available structure on the surrounding reef is likely particularly important for highly motile species, such as brittle stars (Pomory, 2001; Shulman, 2020; Sides & Woodley, 1985). Further, grazing invertebrates depend on coral as substrate for algal growth (Kuempel & Altieri, 2017; Nelson et al., 2016; Sangil &

Guzman, 2016), potentially explaining why grazers are susceptible to declines in coral mass (Table II). In contrast, the suspension and deposit feeders did not depend on live coral cover or coral mass. Bivalve suspension feeders likely benefit from coral substrate as a hard surface on which to attach, but may have lower recruitment rates on live coral, which predate on larvae (Hutchings, 2008; Nelson et al., 2016). Furthermore, both suspension- and deposit-feeding organisms feed on resources that do not depend on coral substrate, and that can originate from nearby ecosystems such as seagrasses and mangroves (Granek et al., 2009; Heck et al., 2008; Ribes et al., 2003).

Both grazing and deposit-feeding assemblages were more likely to be dominated by one or two species, whereas suspension-feeding and predator assemblages were more even and diverse (Table 4.2, Figure 4.3). Our analyses of niche breadth show that both the dominant grazer *Echinometra viridis* and the deposit-feeding *Ophionereis reticulata* have substantially broader isotopic niches than other common consumer species (Figure 4.7). The broad trophic niche of *E. viridis*, which apparently reflects an opportunistic feeding strategy, likely contributes to the high biomass of *E. viridis*, given that hundreds of algal species are present in Caribbean Panama (Wysor & Clerck, 2003; Wysor & Kooistra, 2003). Many grazers are limited in the algae they can consume due to algal defenses, digestibility, and physical accessibility (Cruz-Rivera & Paul, 2006; Lewis & Smith, 2019; Rasher et al., 2013), and so have a competitive disadvantage. Consistent with this pattern, we found that some of the less dominant grazers had much narrower niches than *E. viridis*, with little niche overlap (Figure 4.7; Table 4.3). Deposit feeding assemblages were similarly uneven (Figure 4.4) with low species richness, but we suggest that the relative digestibility of detrital matter contributes to these low-diversity assemblages. Although detritus comes from a wide variety of sources and so is inherently heterogeneous, likely contributing to the broad isotopic signature of *O. reticulata*, it typically has fewer impediments to consumption (such as chemical defenses) than live algae, and so requires less specialization (Moore et al., 2004; Wilson et al., 2003).

In contrast, both suspension feeders and predators were more diverse trophic groups than grazers or deposit feeders (Figure 4). Our low estimates of SEA_c for these taxa (Figure 7; excluding *Ophioderma rubicundum,* which also feeds on detritus; Warner, 1982) suggest that niche specialization and complementarity likely contribute to their high diversity, as has been observed in other systems (Casey et al., 2019; Leray et al., 2015; Richoux et al., 2014; Sánchez González et al., 2023; Wing & Jack, 2012). As a functional group, suspension feeders are defined by the fact that they feed from the water column (Table I), but encompass species that selectively feed from a wide range of sources, including plankton, bacteria, and detritus, leading to high niche complementarity (Lefebvre et al., 2009; Sánchez González et al., 2023; Tallis, 2009; Tran & Ackerman, 2019; Wing & Jack, 2012). Similarly, predators are limited in their prey selection by both size and their ability to overcome various physical and chemical defenses (Blackmon & Valentine, 2022; Meredith et al., 2007; Muller et al., 2020; Wainwright, 1988). Thus, many coral reef predators exhibit definite dietary preferences and niche partitioning (Casey et al., 2019; Leray et al., 2015).

Our analyses demonstrate that coral-associated invertebrate assemblages are a highly diverse group that are dominated by a relatively small number of taxa. The susceptibility of these invertebrates to the degradation of coral habitat appears to depend on trophic group, possibly because some groups depend on different aspects of coral structure or to different degrees. Further, the relative importance of dominance and complementarity appears to vary across trophic groups, likely due in part to physical and chemical differences in the foods consumed by each group. Different trophic groups also appear to be differentially susceptible to species loss: grazer and deposit feeder biomass are largely concentrated in one or two taxa, suggesting large declines in function if these particular species are lost. In contrast, suspension-feeding and predatory invertebrates appear to be more diverse with narrow isotopic niches, suggesting they are susceptible to a gradual decline in functionality with decreasing species richness.

Acknowledgements

We thank Nancy Knowlton, James O'Donnell, Lyle McMillan, Moises Bernal, Natasha Hinojosa, Owen MacMillan, Valerie MacMillan, Michael Hynes, Clare Fieseler, Nasir Alimardani and Ines Galtieri d'Auriac for their help in the field. We further thank the staff at the Bocas del Toro, Naos Island, and Hong Kong University's Stable Isotope Laboratory. All collections were conducted in accordance with permit SE/A-44-16 issued by the Ministerio de Ambiente.

References

Adam, T. C., Kelley, M., Ruttenberg, B. I., & Burkepile, D. E. (2015). Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. *Oecologia*, *179*(4), 1173–1185. https://doi.org/10.1007/s00442-015-3406-3

Adelson, A. E., Altieri, A. H., Boza, X., Collin, R., Davis, K. A., Gaul, A., Giddings, S. N., Reed, V., & Pawlak, G. (2022). Seasonal hypoxia and temperature inversions in a tropical bay. *Limnology and Oceanography*, *67*(10), 2174–2189. https://doi.org/10.1002/lno.12196

Altieri, A. H., Harrison, S. B., Seemann, J., Collin, R., Diaz, R. J., & Knowlton, N. (2017). Tropical dead zones and mass mortalities on coral reefs. *Proceedings of the National Academy of Sciences*, *114*(14), 3660–3665. https://doi.org/10.1073/pnas.1621517114

Altman-Kurosaki, N. T., Priest, M. A., Golbuu, Y., Mumby, P. J., & Marshell, A. (2018). Microherbivores are significant grazers on Palau’s forereefs. *Marine Biology*, *165*(4), 74. https://doi.org/10.1007/s00227-018-3327-x

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., & Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: Region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 3019–3025. https://doi.org/10.1098/rspb.2009.0339

Bagur, M., Gutiérrez, J., Arribas, L., & Palomo, M. (2014). Endolithic invertebrate communities and bioerosion rates in southwestern Atlantic intertidal consolidated sediments. *Marine Biology*, *161*, 2279–2292. https://doi.org/10.1007/s00227-014-2505-8

Beijbom, O., Edmunds, P. J., Roelfsema, C., Smith, J., Kline, D. I., Neal, B. P., Dunlap, M. J., Moriarty, V., Fan, T.-Y., Tan, C.-J., Chan, S., Treibitz, T., Gamst, A., Mitchell, B. G., & Kriegman, D. (2015). Towards Automated Annotation of Benthic Survey Images: Variability of Human Experts and Operational Modes of

Automation. *PLOS ONE*, *10*(7), e0130312. https://doi.org/10.1371/journal.pone.0130312

Bellwood, D. R., Hughes, T. P., & Hoey, A. S. (2006). Sleeping functional group drives coral-reef recovery. *Current Biology*, *16*(24), 2434–2439. https://doi.org/10.1016/j.cub.2006.10.030

Blackmon, D. C., & Valentine, J. F. (2022). Predator-Induced Nocturnal Benthic Emergence: Field and Experimental Evidence for an Unknown Behavioral Escape Mechanism along the Coral Reef-Seagrass Interface. *Diversity-Basel*, *14*(9), 762. https://doi.org/10.3390/d14090762

Brandl, S. J., Rasher, D. B., Côté, I. M., Casey, J. M., Darling, E. S., Lefcheck, J. S., & Duffy, J. E. (2019). Coral reef ecosystem functioning: Eight core processes and the role of biodiversity. *Frontiers in Ecology and the Environment*, *17*(8), 445–454. https://doi.org/10.1002/fee.2088

Burkepile, D. E., & Hay, M. E. (2006). Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. *Ecology*, *87*(12), 3128–3139. https://doi.org/10.1890/0012-9658(2006)87[3128:hvncom]2.0.co;2

Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, *80*(1), Article 1. https://doi.org/10.18637/jss.v080.i01

Campbell, J. E., Altieri, A. H., Johnston, L. N., Kuempel, C. D., Paperno, R., Paul, V. J., & Duffy, J. E. (2018). Herbivore community determines the magnitude and mechanism of nutrient effects on subtropical and tropical seagrasses. *Journal of Ecology*, *106*(1), 401–412. https://doi.org/10.1111/1365-2745.12862

Casey, J. M., Meyer, C. P., Morat, F., Brandl, S. J., Planes, S., & Parravicini, V. (2019). Reconstructing hyperdiverse food webs: Gut content metabarcoding as a tool to disentangle trophic interactions on coral reefs. *Methods in Ecology and Evolution*, *10*(8), 1157–1170. https://doi.org/10.1111/2041-210X.13206

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Cramer, K. L., Jackson, J. B. C., Angioletti, C. V., Leonard-Pingel, J., & Guilderson, T. P. (2012). Anthropogenic mortality on coral reefs in Caribbean Panama predates coral disease and bleaching. *Ecology Letters*, *15*(6), 561–567. https://doi.org/10.1111/j.1461-0248.2012.01768.x

Cruz-Rivera, E., & Paul, V. J. (2006). Feeding by coral reef mesograzers: Algae or cyanobacteria? *Coral Reefs*, *25*(4), 617–627. https://doi.org/10.1007/s00338-006-0134-5

Duffy, J. E. (2002). Biodiversity and ecosystem function: The consumer connection. *Oikos*, *99*(2), 201–219. https://doi.org/10.1034/j.1600-0706.2002.990201.x

Duffy, J. E., Paul Richardson, J., & Canuel, E. A. (2003). Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters*, *6*(7), 637–645. https://doi.org/10.1046/j.1461-0248.2003.00474.x

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, *1*(9), 488–494. https://doi.org/10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2

Emery, K. A., Dugan, J. E., Bailey, R. A., & Miller, R. J. (2021). Species identity drives ecosystem function in a subsidy-dependent coastal ecosystem. *Oecologia*, *196*(4), 1195–1206. https://doi.org/10.1007/s00442-021-05002-w

Glynn, P. W., & Enochs, I. C. (2011). Invertebrates and Their Roles in Coral Reef Ecosystems. In Z. Dubinsky & N. Stambler (Eds.), *Coral Reefs: An Ecosystem in Transition* (pp. 273–325). Springer Netherlands. https://doi.org/10.1007/978-94-007-0114-4_18

Granek, E. F., Compton, J. E., & Phillips, D. L. (2009). Mangrove-Exported Nutrient Incorporation by Sessile Coral Reef Invertebrates. *Ecosystems*, *12*(3), 462–472. https://doi.org/10.1007/s10021-009-9235-7

Heck, K. L., Carruthers, T. J. B., Duarte, C. M., Hughes, A. R., Kendrick, G., Orth, R. J., & Williams, S. W. (2008). Trophic Transfers from Seagrass Meadows Subsidize Diverse Marine and Terrestrial Consumers. *Ecosystems*, *11*(7), 1198–1210. https://doi.org/10.1007/s10021-008-9155-y

Henderson, C. J., Gilby, B. L., Schlacher, T. A., Connolly, R. M., Sheaves, M., Maxwell, P. S., Flint, N., Borland, H. P., Martin, T. S. H., & Olds, A. D. (2020). Low redundancy and complementarity shape ecosystem functioning in a low-diversity ecosystem. *Journal of Animal Ecology*, *89*(3), 784–794. https://doi.org/10.1111/1365-2656.13148

Hewson, I., Ritchie, I. T., Evans, J. S., Altera, A., Behringer, D., Bowman, E., Brandt, M., Budd, K. A., Camacho, R. A., Cornwell, T. O., Countway, P. D., Croquer, A., Delgado, G. A., DeRito, C., Duermit-Moreau, E., Francis-Floyd, R., Gittens, S., Henderson, L., Hylkema, A., … Breitbart, M. (2023). A scuticociliate causes mass mortality of Diadema antillarum in the Caribbean Sea. *Science Advances*, *9*(16), eadg3200. https://doi.org/10.1126/sciadv.adg3200

Hillebrand, H., Gruner, D. S., Borer, E. T., Bracken, M. E. S., Cleland, E. E., Elser, J. J., Harpole, W. S., Ngai, J. T., Seabloom, E. W., Shurin, J. B., & Smith, J. E. (2007). Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the*

National Academy of Sciences, *104*(26), 10904–10909. https://doi.org/10.1073/pnas.0701918104

Hughes, T. P. (1994). Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. *Science*, *265*(5178), 1547–1551. https://doi.org/10.1126/science.265.5178.1547

Hutchings, P. (2008). Role of polychaetes in bioerosion of coral substrates. In M. Wisshak & L. Tapanila (Eds.), *Current Developments in Bioerosion* (pp. 249–264). Springer. https://doi.org/10.1007/978-3-540-77598-0_13

Hylkema, A., Kitson-Walters, K., Kramer, P. R., Patterson, J. T., Roth, L., Sevier, M. L. B., Vega-Rodriguez, M., Warham, M. M., Williams, S. M., & Lang, J. C. (2023). The 2022 Diadema antillarum die-off event: Comparisons with the 1983-1984 mass mortality. *Frontiers in Marine Science*, *9*. https://www.frontiersin.org/articles/10.3389/fmars.2022.1067449

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*(3), 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson, J., Donovan, M., Cramer, K., & Lam, V. (2014). *Status and trends of Caribbean coral reefs: 1970-2012*. Gland, Switzerland: Global Coral Reef Monitoring

Network; International Union for the Conservation of Nature (IUCN). https://bvearmb.do/handle/123456789/590

Jacob, U., Mintenbeck, K., Brey, T., Knust, R., & Beyer, K. (2005). Stable isotope food web studies: A case for standardized sample treatment. *Marine Ecology Progress Series*, *287*, 251–253. https://doi.org/10.3354/meps287251

Karlson, A. M. L., Nascimento, F. J. A., Näslund, J., & Elmgren, R. (2010). Higher diversity of deposit-feeding macrofauna enhances phytodetritus processing. *Ecology*, *91*(5), 1414–1423. https://doi.org/10.1890/09-0660.1

Kuempel, C. D., & Altieri, A. H. (2017). The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Scientific Reports*, *7*(1), Article 1. https://doi.org/10.1038/srep39670

Laigle, I., Aubin, I., Digel, C., Brose, U., Boulangeat, I., & Gravel, D. (2018). Species traits as drivers of food web structure. *Oikos*, *127*(2), 316–326. https://doi.org/10.1111/oik.04712

Lefebvre, S., Marín Leal, J. C., Dubois, S., Orvain, F., Blin, J.-L., Bataillé, M.-P., Ourry, A., & Galois, R. (2009). Seasonal dynamics of trophic relationships among co-occurring suspension-feeders in two shellfish culture dominated ecosystems. *Estuarine, Coastal and Shelf Science*, *82*(3), 415–425. https://doi.org/10.1016/j.ecss.2009.02.002

Leray, M., Meyer, C. P., & Mills, S. C. (2015). Metabarcoding dietary analysis of coral dwelling predatory fish demonstrates the minor contribution of coral mutualists to their highly partitioned, generalist diet. *Peerj*, *3*, e1047. https://doi.org/10.7717/peerj.1047

Lessios, H. A. (1988). Mass Mortality of Diadema Antillarum in the Caribbean: What Have We Learned? *Annual Review of Ecology and Systematics*, *19*, 371–393.

Lewis, L. S., & Smith, J. E. (2019). Functional diversity among herbivorous sea urchins on a coral reef: Grazing rate, dietary preference, and metabolism. *Marine Ecology Progress Series*, *625*, 71–87. https://doi.org/10.3354/meps13038

Loh, T.-L., McMurray, S. E., Henkel, T. P., Vicente, J., & Pawlik, J. R. (2015). Indirect effects of overfishing on Caribbean reefs: Sponges overgrow reef-building corals. *PeerJ*, *3*, e901. https://doi.org/10.7717/peerj.901

Meredith, T. L., Cowart, J. D., Henkel, T. P., & Pawlik, J. R. (2007). The polychaete *Cirriformia punctata* is chemically defended against generalist coral reef predators. *Journal of Experimental Marine Biology and Ecology*, *353*(2), 198–202. https://doi.org/10.1016/j.jembe.2007.08.023

Moksnes, P.-O., Gullström, M., Tryman, K., & Baden, S. (2008). Trophic cascades in a temperate seagrass community. *Oikos*, *117*(5), 763–777. https://doi.org/10.1111/j.0030-1299.2008.16521.x

Moore, J. C., Berlow, E. L., Coleman, D. C., de Ruiter, P. C., Dong, Q., Hastings, A., Johnson, N. C., McCann, K. S., Melville, K., Morin, P. J., Nadelhoffer, K., Rosemond, A. D., Post, D. M., Sabo, J. L., Scow, K. M., Vanni, M. J., & Wall, D. H. (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters*, *7*(7), 584–600. https://doi.org/10.1111/j.1461-0248.2004.00606.x

Muller, E., de Gier, W., ten Hove, H. A., van Moorsel, G. W. N. M., & Hoeksema, B. W. (2020). Nocturnal Predation of Christmas Tree Worms by a Batwing Coral Crab at Bonaire (Southern Caribbean). *Diversity*, *12*(12), Article 12. https://doi.org/10.3390/d12120455

Nelson, H. R., Kuempel, C. D., & Altieri, A. H. (2016). The resilience of reef invertebrate biodiversity to coral mortality. *Ecosphere*, *7*(7), e01399. https://doi.org/10.1002/ecs2.1399

Nguyen, B. N. (2020). *Sequencing Tropical Marine Biodiversity* [George Washington University]. https://scholarspace.library.gwu.edu/concern/gw_etds/c534fp62z?locale=en

Nguyen, B. N., Shen, E. W., Seemann, J., Correa, A. M. S., O'Donnell, J. L., Altieri, A. H., Knowlton, N., Crandall, K. A., Egan, S. P., McMillan, W. O., & Leray, M. (2020). Environmental DNA survey captures patterns of fish and invertebrate diversity across a tropical seascape. *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-63565-9

O'Connor, M. I., Gonzalez, A., Byrnes, J. E. K., Cardinale, B. J., Duffy, J. E., Gamfeldt, L., Griffin, J. N., Hooper, D., Hungate, B. A., Paquette, A., Thompson, P. L., Dee, L. E., & Dolan, K. L. (2017). A general biodiversity–function relationship is mediated by trophic level. *Oikos*, *126*(1), 18–31. https://doi.org/10.1111/oik.03652

Pomory, C. M. (2001). An escape response behaviour in the brittle star *Ophiopteris papillosa* (Echinodermata: Ophiuroidea). *Marine and Freshwater Behaviour and Physiology*, *34*(3), 171–180. https://doi.org/10.1080/10236240109379070

R Core Team. (2021). *R: A Language and Environment for Statistical Computing* [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Rasher, D. B., Hoey, A. S., & Hay, M. E. (2013). Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology*, *94*(6), 1347–1358. https://doi.org/10.1890/12-0389.1

Reich, P. B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S. E., Flynn, D. F. B., & Eisenhauer, N. (2012). Impacts of Biodiversity Loss Escalate Through Time as Redundancy Fades. *Science*, *336*(6081), 589–592. https://doi.org/10.1126/science.1217909

Ribes, M., Coma, R., Atkinson, M. J., & Iii, R. A. K. (2003). Particle removal by coral reef communities: Picoplankton is a major source of nitrogen. *Marine Ecology Progress Series*, *257*, 13–23. https://doi.org/10.3354/meps257013

Richoux, N. B., Vermeulen, I., & Froneman, P. W. (2014). Stable isotope ratios indicate differential omnivory among syntopic rocky shore suspension-feeders. *Marine Biology*, *161*(5), 971–984. https://doi.org/10.1007/s00227-013-2358-6

RStudio Team. (2022). *RStudio: Integrated Development Environment for R* (2022.7.2.576) [Computer software]. RStudio, PBC.

Sánchez González, I., Hopper, G. W., Bucholz, J. R., Kubala, M. E., Lozier, J. D., & Atkinson, C. L. (2023). Niche specialization and community niche space increase with species richness in filter-feeder assemblages. *Ecosphere*, *14*(5), e4495. https://doi.org/10.1002/ecs2.4495

Sangil, C., & Guzman, H. M. (2016). Assessing the herbivore role of the sea-urchin Echinometra viridis: Keys to determine the structure of communities in disturbed coral reefs. *Marine Environmental Research*, *120*, 202–213. https://doi.org/10.1016/j.marenvres.2016.08.008

Saric, M. B. (2005). *Sedimentologie und Geobiologie von Riffassoziationen in der Bahia Almirante (Archipel von Bocas del Toro, Panamá)* [Text.PhDThesis, Ludwig-Maximilians-Universität München]. https://edoc.ub.uni-muenchen.de/4491/

Seemann, J., González, C. T., Carballo-Bolaños, R., Berry, K., Heiss, G. A., Struck, U., & Leinfelder, R. R. (2014). Assessing the ecological effects of human impacts on coral reefs in Bocas del Toro, Panama. *Environmental Monitoring and Assessment*, *186*(3), 1747–1763. https://doi.org/10.1007/s10661-013-3490-y

Shantz, A. A., Ladd, M. C., & Burkepile, D. E. (2020). Overfishing and the ecological impacts of extirpating large parrotfish from Caribbean coral reefs. *Ecological Monographs*, *90*(2), e01403. https://doi.org/10.1002/ecm.1403

Shulman, M. J. (2020). Echinometra sea urchins on Caribbean coral reefs: Diel and lunar cycles of movement and feeding, densities, and morphology. *Journal of Experimental Marine Biology and Ecology*, *530–531*, 151430. https://doi.org/10.1016/j.jembe.2020.151430

Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D., & Halpern, B. S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, *5*(6), 785–791. https://doi.org/10.1046/j.1461-0248.2002.00381.x

Sides, E. M., & Woodley, J. D. (1985). Niche separation in three species of *Ophiocoma* (Echinodermata: Ophiuroidea) in Jamaica, West Indies. *Bulletin of Marine Science*, *36*(3), 701–715.

Spiers, L. J., & Frazer, T. K. (2023). How herbivores reshape a macroalgal community on a Little Cayman coral reef: The role of herbivore type and density. *Journal* *of Experimental Marine Biology and Ecology*, *562*, 151884. https://doi.org/10.1016/j.jembe.2023.151884

Tallis, H. (2009). Kelp and rivers subsidize rocky intertidal communities in the Pacific Northwest (USA). *Marine Ecology Progress Series*, *389*, 85–96. https://doi.org/10.3354/meps08138

Tran, K., & Ackerman, J. D. (2019). Mussels partition resources from natural waters under flowing conditions. *The Science of the Total Environment*, *696*, 133870. https://doi.org/10.1016/j.scitotenv.2019.133870

Treplin, M., Pennings, S. C., & Zimmer, M. (2013). Decomposition of Leaf Litter in a U.S. Saltmarsh is Driven by Dominant Species, Not Species Complementarity. *Wetlands*, *33*(1), 83–89. https://doi.org/10.1007/s13157-012-0353-1

Wainwright, P. C. (1988). Morphology and Ecology: Functional Basis of Feeding Constraints in Caribbean Labrid Fishes. *Ecology*, *69*(3), 635–645. https://doi.org/10.2307/1941012

Warner, G. (1982). Food and Feeding Mechanisms: Ophiuroidea. In *Echinoderm Nutrition*. CRC Press.

Whittaker, R. H. (1965). Dominance and Diversity in Land Plant Communities. *Science*, *147*(3655), 250–260. https://doi.org/10.1126/science.147.3655.250

Williamson, J. E., Duce, S., Joyce, K. E., & Raoult, V. (2021). Putting sea cucumbers on the map: Projected holothurian bioturbation rates on a coral reef scale. *Coral Reefs*, *40*(2), 559–569. https://doi.org/10.1007/s00338-021-02057-2

Wilson, S. K., Bellwood, D. R., Choat, J. H., & Furnas, M. J. (2003). Detritus in the epilithic algal matrix and its use by coral reef fishes. In R. N. Gibson & R. J. A. Atkinson (Eds.), *Oceanography and Marine Biology, Vol 41* (Vol. 41, pp. 279-+). Taylor & Francis Ltd. https://www.webofscience.com/wos/woscc/full-record/WOS:000185182700006

Winfree, R., W. Fox, J., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, *18*(7), 626–635. https://doi.org/10.1111/ele.12424

Wing, S., & Jack, L. (2012). Resource specialisation among suspension-feeding invertebrates on rock walls in Fiordland, New Zealand, is driven by water column structure and feeding mode. *Marine Ecology Progress Series*, *452*, 109–118. https://doi.org/10.3354/meps09588

Wong, M. C., & Dowd, M. (2021). Functional trait complementarity and dominance both determine benthic secondary production in temperate seagrass beds. *Ecosphere*, *12*(11), e03794. https://doi.org/10.1002/ecs2.3794

Wysor, B., & Clerck, O. D. (2003). *An Updated and Annotated List of Marine Brown Algae (Phaeophyceae) of the Caribbean Coast of the Republic of Panama*. *46*(2), 151–160. https://doi.org/10.1515/BOT.2003.016

Wysor, B., & Kooistra, W. H. C. F. (2003). An annotated list of marine Chlorophyta from the Caribbean coast of the Republic of Panama. *Nova Hedwigia*, *77*(3–4), 487–523. https://doi.org/10.1127/0029-5035/2003/0077-0487

Appendix

Table 4S1. Attributes of dead *Agaricia tenuifolia* plots sampled in Bahía Almirante, Caribbean Panama. Three plots were sampled at each site. Standard deviations given in brackets.

Site	Invertebrate biomass (g)	Coral mass (kg)	Sponge AFDW (g)	Rugosity
ROL	138.9 (38.2)	9.7 (1.6)	77.8 (26.2)	1.6 (0.2)
IPI	187.3 (54.4)	13.4 (1.0)	17.3 (21.2)	1.7 (0.3)
SIS	387.6 (79.9)	12.8 (3.2)	49.8 (78.5)	2.0 (0.4)
ALR	353.4 (123.1)	14.0 (0.8)	41.4 (11.6)	1.6 (0.1)
PSK	354.7 (118.9)	16.1 (2.2)	21.8 (13.3)	2.0 (0.3)
SGL	210.1 (56.3)	13.6 (0.5)	4.6 (7.9)	2.4 (0.4)
PBL	134.3 (45.4)	18.0 (5.7)	4.9 (4.1)	2.2 (0.5)
PST	155.2 (14.5)	22.5 (4.1)	28.1 (12.4)	2.1 (0.4)
RNW	115.9 (34.6)	18.7 (3.4)	16.1 (15.0)	2.3 (0.2)
MAR	313.9 (54.7)	18.5 (3.1)	3.0 (-)	2.3 (0.3)

SCR	249.7 (57.9)	16.6 (1.5)	2.5 (1.8)	2.3 (0.3)
PPR	450.2 (149.1)	21.3 (2.9)	9.0 (6.3)	2.0 (0.3)

Table 4S2. Benthic cover of 12 coral reefs sampled in Bahía Almirante, Caribbean Panama. All values given as percent cover of 25m transects.

Site	Live hard coral (%)	Dead hard coral (%)	Coral rubble (%)	Bare sand (%)
ROL	9.4	7.1	11.9	19.9
IPI	6.2	9.0	34.3	11.7
SIS	13.3	2.4	12.6	35.6
ALR	21.2	22.8	7.3	22.1
PSK	25.2	16.6	9.2	9.9
SGL	29.7	22.8	13.8	14.3
PBL	0	53.6	16.8	4.6
PST	0.3	21.4	32.9	20.8
RNW	0.8	45.3	10.7	10.5
MAR	26.3	9.0	4.0	20.1
SCR	37.1	4.4	7.1	0.3
PPR	22	18.4	14.3	5.0

Chapter 5: Discussion

Throughout this thesis, I sought to explain how environmental variation impacts the feeding ecology, performance, and distribution of marine ectotherms. In the second chapter of my thesis, I tested whether a documented biogeographical pattern (herbivorous fishes are rarer at high latitudes) could be explained by systematic differences in fish physiology (digestion of plant material is less efficient at low temperatures). In the third chapter, I tested whether seasonal variation in temperature and resource availability impacted the feeding ecology, digestive physiology, and distribution of tropical damselfishes, and whether the effects of upwelling on distribution were concordant with our expectations from the effects of upwelling on damselfish performance. In the fourth chapter of my thesis, I demonstrate how taxa consuming different resources exhibit variation in niche breadth and patterns of biomass within diverse communities. In this final chapter, I review themes that recur across these manuscripts, the limitations inherent to the different analytical approaches that I employed (meta-analyses, field studies, and distribution models), and directions for future research in the field.

Linking physiological processes to geographical patterns: successes and limitations of different approaches

Ecological processes occurring at different scales- individual performance, population dynamics, ecosystem function, and so on- are profoundly interdependent (O'Connor et al., 2020). To fully disentangle the processes that generate various ecological patterns, including patterns of distribution, we must account for the interplay of these processes by considering and synthesizing evidence from multiple scales. This is a goal I have sought to achieve throughout my thesis, with some successes, and some limitations.

In the first chapter of my thesis, I conducted a meta-analysis to test how temperature affects digestion across trophic groups (Knight et al., 2021). A strength of this approach was that for the first time, a physiological hypothesis concerning global patterns in a tremendously diverse taxonomic group was tested using a broad set of physiological data (99 studies including hundreds of species), whereas previous work had primarily focused on a single or several species (e.g., Floeter et al., 2005; Horn & Gibson, 1990). In addition to demonstrating that existing studies did not provide strong evidence supporting the temperature constraint hypothesis (TCH), I was able to identify that a particular digestive strategy (symbiosis with a fermenting gut microbiome) might be more common in coldwater herbivores, and suggest a new line of inquiry into the distribution of adaptations to herbivory across latitudes.

Of course, an inevitable limitation on meta-analyses are the available data. If herbivorous fishes do not exist in certain thermal environments, then estimates of their performance cannot be included in a meta-analysis. So how can an ecologist understand why certain species do not exist? Perhaps they can’t. But there are questions that can be asked and tested that may help shed some light on the matter. For example, plenty of invertebrate species such as krill and amphipods (Everson, 2008; Werner & Auel, 2005) are highly successful feeding on algae and phytoplankton in the world’s coldest waters. What are the digestive mechanisms used by these species? To what extent do they differ from those found in fishes? Similarly, what are the thermal dependencies of the various digestive mechanisms that *are* used by herbivorous fishes, such as acid lysis, enzymatic digestion, and fermentation? Are these dependencies linear, or exponential, or do they exhibit some sort of threshold behaviour? Taxa are limited by their biochemistry, and variations in biochemistry can generate surprising patterns of distribution at broad scales (e.g., Clarke & Johnston, 1996; Espinoza et al., 2004; Grady et al., 2019). Fortunately, however, these are questions for a different dissertation.

In the second chapter of my thesis, I again used a broad-scale, publicly available dataset collected by other researchers (distribution data from Reef Life Survey and environmental data collected by STRI and NOAA), but combined it with diet and physiological data that I collected myself. There were several benefits to this approach. Whereas meta-analyses necessarily sacrifice context for the chance to ask questions at broad phylogenetic and geographical scales, by working with researchers familiar with upwelling in the Gulf of Panama, I was able to test questions that were targeted and region-appropriate. Further, the data I collected provided context to the patterns of distribution that we observed, adding to a growing body of literature that combines physiological and distributional data to increase confidence in our inferences about broad-scale patterns (Duncan et al., 2020; Hargreaves et al., 2014; Kroeker et al., 2016; Lunghi et al., 2018; Menge et al., 2004; Sunday et al., 2015).

The final manuscript in my thesis reflects one of the fundamental trade-offs in experimental design: I participated in a team that was able to obtain high-resolution data describing how habitat degradation impacts the distribution of different trophic groups, but at a much smaller spatial scale (a dozen reefs in a single bay). Although I was able to show that different trophic groups respond differently to coral degradation, the relatively small scale of this project suggests that the transferability of my results to other reefs in the Caribbean or beyond may be limited by differences in consumer identities, the degree of coral decline, or other idiosyncrasies. However, many processes that shape the distribution of consumers occur at local and regional scales (Byrnes et al., 2022; Menge et al., 2004; Whippo et al., 2018), and these processes are often unexplained by broad-scale distribution models, which may be better at predicting upper limits on species abundance rather than local variation in species abundance (VanDerWal et al., 2009).

Individual performance predicts distribution (sometimes)

All three of my manuscripts explored, to different degrees, the idea consumer performance can reasonably be linked to broader scale patterns of distribution (Brown, 1984; Grinnell, 1917; Hutchinson, 1957, 1978). In the second chapter of my thesis, I concluded that was little evidence to support a direct link between the effects of temperature on algal digestion and the latitudinal decline in herbivorous fishes. However, this chapter did leave open the possibility that herbivory in fishes evolved more frequently in the tropics because high species richness and intense competition made it more advantageous to consume plant material, thus suggesting an indirect relationship between performance and distribution, albeit over evolutionary timelines (Bellwood et al., 2017; Egan et al., 2018; Harmelin, 2002; Knudsen et al., 2019). Further, I discovered that in the available data, herbivores that depend on fermentation are overrepresented at high latitudes, possibly indicating a general trend in the distribution of digestive mechanisms across latitudes.

The third chapter of my thesis was the most direct test of a link between individual performance and distribution. It was the only chapter that included both analyses of the effects of environmental variation on individual performance as well as data on the distribution of different species along an environmental gradient. It was also the chapter that provided the clearest support for a link between individual performance and distribution: the two species that had improved body condition during seasonal upwelling also exhibited increased biomass at sites that experience strong seasonal upwelling. I cannot conclusively state that improved individual performance drives higher species' biomass under upwelling conditions, as I did not test the effects of upwelling on intermediate links between performance and distribution (e.g., fitness, dispersal, recruitment). However, my findings represent the most comprehensive assessment of the effects of seasonal upwelling on tropical fishes to date, and provide leads for future research.

In the fourth chapter of my thesis, I demonstrated that different trophic groups respond differently to the loss of coral habitat, likely due to differences in why and how much these trophic groups depend on the structural complexity provided by corals. I did not directly measure the effects of coral availability on individual performance, but a review of the existing literature provided ample support for the hypothesis that invertebrate performance depends, to differing degrees, on coral availability and structural complexity (Fabricius et al., 2014; Glynn, 2004; Glynn & Enochs, 2011; Nelson et al., 2016; Saldana et al., 2021; Sides & Woodley, 1985). The functional contributions of cryptic coral invertebrates are still poorly understood relative to those of other consumers such as fishes and invertebrate macrofauna (Brandl et al., 2019; Edmunds & Carpenter, 2001; Francis et al., 2019; Levitan et al., 2023), but this chapter makes a unique contribution to understanding these relationships.

The physical and chemical characteristics of resources affect feeding and digestion

Differences in the physical, chemical and nutritional characteristics of resources affect virtually all aspects of the feeding ecology and digestive physiology of consumers (Choat & Clements, 1998; Karasov et al., 2011). For example, in the second chapter of my thesis, I explore the effects of a lower-quality diet (plant material) on the digestive physiology of fishes. Ecological stoichiometry postulates that not all resources are equally efficient at meeting species' nutritional demands, as the ratios of nutrients in different foods are often imbalanced relative to consumer needs (Simpson & Raubenheimer, 2012; Sterner, 2002). As I demonstrate in the second chapter of my thesis, this problem is particularly pronounced for herbivores, which consume diets that are much lower in protein and energy and other key nutrients than do predators (Choat & Clements, 1998; Knight et al., 2021) I demonstrate that as a consequence of these nutrient imbalances, herbivores exhibit longer guts and lower absorption efficiencies than carnivores. Further, the thermal dependence of digestion is stronger among macroalgivorous fishes, possibly because at low temperatures fishes require special adaptations to herbivory, i.e., a well-developed gut microbiome.

It has been suggested that the hypothesis I tested in my second chapter, i.e., that the difficulties of digesting a herbivorous diet are exacerbated at low temperatures, is not restricted to fishes (Clarke & O'Connor, 2014; Espinoza et al., 2004; Floeter et al., 2004, 2005; Gaines & Lubchenco, 1982; Gonzalez-Bergonzoni et al., 2016; Vejrikova et al., 2016; Zimmerman & Tracy, 1989). Herbivory is more common among endotherms than ectotherms (Karasov & Martínez del Rio, 2007), and herbivorous mammals and birds have higher internal body temperatures than their carnivorous counterparts (Clarke & O'Connor, 2014). Further, ectothermic herbivores tend to be more common in the tropics, or in areas where behavioural thermoregulation is possible (Espinoza et al., 2004; Floeter et al., 2004, 2005; Gaines & Lubchenco, 1982; Zimmerman & Tracy, 1989). However, the extent to which low temperatures disadvantage herbivory in other species remains unclear.

In the fourth chapter of my thesis, I find data that support the hypothesis that differences in the nature of resource availability affect niche breadth and coexistence. Niche breadth among suspension feeders, predators, and grazers (with the exception of the generalist urchin *Echinometra viridis*) were typically low, but likely for different reasons. Among predators and grazers, limited niche breadths are likely due in large part to the vast array of resource defenses. Animal prey often have hard shells and carapaces, spines, or exhibit fleeing and hiding behaviour to avoid predation (Aronson, 1988; Dunn et al., 2018; Pomory, 2001; Wainwright, 1987), which demand certain adaptations from their predators, such as a strong jaw to crush shells (Wainwright, 1988). Similarly, algal resources exhibit a wide range of chemical defenses such as diterpenes and phlorotannins, which are not digestible by all herbivores (Amsler, 2008; Rasher et al., 2013; Stachowicz & Hay, 1999).

In contrast, high niche specialization and complementarity among suspension feeders may be due to the fact that suspension feeders as a group are so broadly defined, and include zooplanktivores, phyto-planktivores, detritivores, and bacterivores (Lefebvre et al., 2009; Sánchez González et al., 2023; Tallis, 2009; Tran & Ackerman, 2019; Wing & Jack, 2012). It is unclear the extent to which suspension feeders are limited by the physical or chemical characteristics of their prey, though some constraints exist: for example, filter feeders can only take up particles that exceed the mesh size of their filters (Filella et al., 2008). It has been shown that increased species richness can lead to greater niche specialization and partitioning in suspension feeders, suggesting that competition, rather than physical constraints, limit niche breadth (Sánchez González et al., 2023). However, to my knowledge, this has not been tested in coral reefs.

Final conclusion and summary

Throughout this thesis, I sought to test how environmental variation in temperature, resource availability, and habitat lead to differences in the feeding ecology, performance, and distribution of marine organisms. I tested these questions in a variety of coastal systems and across myriad fish and invertebrate taxa. I further employed a variety of techniques that synthesized information across a broad range of spatial scales. Several key insights include that herbivorous fishes are not limited by their ability to digest plant material at low temperatures (Chapter 2), that seasonal upwelling improves the performance of tropical fishes and that this improved performance translates to increases in biomass, and that degradation in coral ecosystems is likely to lead to different responses across key trophic groups. Despite their limitations, these chapters demonstrate the value of developing a cross-scale, holistic understanding of different species and systems, and identify promising avenues for future work.

References

Amsler, C. D. (Ed.). (2008). *Algal Chemical Ecology*. Springer. https://doi.org/10.1007/978-3-540-74181-7

Aronson, R. B. (1988). Palatability of Five Caribbean Ophiuroids. *Bulletin of Marine Science*, *43*(1), 93–97.

Bellwood, D. R., Goatley, C. H. R., & Bellwood, O. (2017). The evolution of fishes and corals on reefs: Form, function and interdependence. *Biological Reviews*, *92*(2), 878–901. https://doi.org/10.1111/brv.12259

Brandl, S. J., Rasher, D. B., Côté, I. M., Casey, J. M., Darling, E. S., Lefcheck, J. S., & Duffy, J. E. (2019). Coral reef ecosystem functioning: Eight core processes and the role of biodiversity. *Frontiers in Ecology and the Environment*, *17*(8), 445–454. https://doi.org/10.1002/fee.2088

Brown, J. H. (1984). On the Relationship between Abundance and Distribution of Species. *The American Naturalist*, *124*(2), 255–279.

Byrnes, J., Brown, A., Sheridan, K., Peller, T., Lawlor, J., Beaulieu, J., Z, J. M., Hesketh, A., Pereira, A., Knight, N. S., Super, L., Bledsoe, E., Burant, J., Dijkstra, J., & Benes, K. (2022). *Notes from the Past Show How Local Variability can Stymie Urchins and the Rise of the Reds in the Gulf of Maine*. EcoEvoRxiv. https://doi.org/10.32942/osf.io/u6exy

Choat, J. H., & Clements, K. D. (1998). Vertebrate herbivores in marine and terrestrial environments: A nutritional ecology perspective. *Annual Review of Ecology and Systematics*, *29*, 375–403. https://doi.org/10.1146/annurev.ecolsys.29.1.375

Clarke, A., & Johnston, I. A. (1996). Evolution and adaptive radiation of antarctic fishes. *Trends in Ecology & Evolution*, *11*(5), 212–218. https://doi.org/10.1016/0169-5347(96)10029-x

Duncan, M. I., James, N. C., Potts, W. M., & Bates, A. E. (2020). Different drivers, common mechanism; the distribution of a reef fish is restricted by local-scale oxygen and temperature constraints on aerobic metabolism. *Conservation Physiology*, *8*(1), coaa090. https://doi.org/10.1093/conphys/coaa090

Dunn, R. P., Altieri, A. H., Miller, K., Yeager, M. E., & Hovel, K. A. (2018). Contrasting behavioral responses to predatory risk cues reflect different foraging strategies in two Caribbean sea urchins. *Marine Ecology Progress Series*, *604*, 187–198. https://doi.org/10.3354/meps12733

Edmunds, P. J., & Carpenter, R. C. (2001). Recovery of Diadema antillarum reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Sciences*, *98*(9), 5067–5071. https://doi.org/10.1073/pnas.071524598

Egan, J. P., Bloom, D. D., Kuo, C.-H., Hammer, M. P., Tongnunui, P., Iglésias, S. P., Sheaves, M., Grudpan, C., & Simons, A. M. (2018). Phylogenetic analysis of trophic niche evolution reveals a latitudinal herbivory gradient in Clupeoidei (herrings, anchovies, and allies). *Molecular Phylogenetics and Evolution*, *124*, 151–161. https://doi.org/10.1016/j.ympev.2018.03.011

Espinoza, R. E., Wiens, J. J., & Tracy, C. R. (2004). Recurrent evolution of herbivory in small, cold-climate lizards: Breaking the ecophysiological rules of reptilian herbivory. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(48), 16819–16824. https://doi.org/10.1073/pnas.0401226101

Everson, I. (2008). *Krill: Biology, Ecology and Fisheries*. John Wiley & Sons.

Fabricius, K. E., De'ath, G., Noonan, S., & Uthicke, S. (2014). Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1775), 20132479. https://doi.org/10.1098/rspb.2013.2479

Filella, M., Rellstab, C., Chanudet, V., & Spaak, P. (2008). Effect of the filter feeder Daphnia on the particle size distribution of inorganic colloids in freshwaters. *Water Research*, *42*(8), 1919–1924. https://doi.org/10.1016/j.watres.2007.11.021

Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddack, M. J., & Horn, M. H. (2005). Geographical gradients of marine herbivorous fishes: Patterns and processes. *Marine Biology*, *147*(6), 1435–1447. https://doi.org/10.1007/s00227-005-0027-0

Francis, F. T., Filbee-Dexter, K., Yan, H. F., & Côté, I. M. (2019). Invertebrate herbivores: Overlooked allies in the recovery of degraded coral reefs? *Global Ecology and Conservation*, *17*, e00593. https://doi.org/10.1016/j.gecco.2019.e00593

Glynn, P. W. (2004). High complexity food webs in low-diversity eastern Pacific reef-coral communities. *Ecosystems*, *7*(4), 358–367. https://doi.org/10.1007/s10021-004-0184-x

Glynn, P. W., & Enochs, I. C. (2011). Invertebrates and Their Roles in Coral Reef Ecosystems. In Z. Dubinsky & N. Stambler (Eds.), *Coral Reefs: An Ecosystem in Transition* (pp. 273–325). Springer Netherlands. https://doi.org/10.1007/978-94-007-0114-4_18

Grady, J. M., Maitner, B. S., Winter, A. S., Kaschner, K., Tittensor, D. P., Record, S., Smith, F. A., Wilson, A. M., Dell, A. I., Zarnetske, P. L., Wearing, H. J., Alfaro, B., & Brown, J. H. (2019). Metabolic asymmetry and the global diversity of marine predators. *Science*, *363*(6425). https://doi.org/10.1126/science.aat4220

Grinnell, J. (1917). Field Tests of Theories Concerning Distributional Control. *The American Naturalist*, *51*(602), 115–128. https://doi.org/10.1086/279591

Hargreaves, A. L., Samis, K. E., & Eckert, C. G. (2014). Are Species' Range Limits Simply Niche Limits Writ Large? A Review of Transplant Experiments beyond the Range. *The American Naturalist*, *183*(2), 157–173. https://doi.org/10.1086/674525

Harmelin, M. (2002). *Energetics and Fish Diversity on Coral Reefs* (pp. 265–274). https://doi.org/10.1016/B978-012615185-5/50016-5

Horn, M. H., & Gibson, R. N. (1990). Effects of temperature on the food processing of three species of seaweed-eating fishes from European coastal waters. *Journal of Fish Biology*, *37*(2), 237–247.

Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Hutchinson, G. E. (1978). *An introduction to population ecology*. Yale University Press.

Karasov, W. H., Martinez del Rio, C., & Caviedes-Vidal, E. (2011). Ecological Physiology of Diet and Digestive Systems. In D. Julius & D. E. Clapham (Eds.), *Annual Review of Physiology, Vol 73* (Vol. 73, pp. 69–93). Annual Reviews.

Knight, N. S., Guichard, F., & Altieri, A. H. (2021). A global meta-analysis of temperature effects on marine fishes' digestion across trophic groups. *Global Ecology and Biogeography*, *30*(4), 795–810. https://doi.org/10.1111/geb.13262

Knudsen, S. W., Choat, J. H., & Clements, K. D. (2019). The herbivorous fish family Kyphosidae (Teleostei: Perciformes) represents a recent radiation from higher latitudes. *Journal of Biogeography*, *46*(9), 2067–2080. https://doi.org/10.1111/jbi.13634

Kroeker, K. J., Sanford, E., Rose, J. M., Blanchette, C. A., Chan, F., Chavez, F. P., Gaylord, B., Helmuth, B., Hill, T. M., Hofmann, G. E., McManus, M. A., Menge, B. A., Nielsen, K. J., Raimondi, P. T., Russell, A. D., & Washburn, L. (2016). Interacting environmental mosaics drive geographic variation in mussel performance and predation vulnerability. *Ecology Letters*, *19*(7), 771–779. https://doi.org/10.1111/ele.12613

Lefebvre, S., Marín Leal, J. C., Dubois, S., Orvain, F., Blin, J.-L., Bataillé, M.-P., Ourry, A., & Galois, R. (2009). Seasonal dynamics of trophic relationships among co-occurring suspension-feeders in two shellfish culture dominated ecosystems. *Estuarine, Coastal and Shelf Science*, *82*(3), 415–425. https://doi.org/10.1016/j.ecss.2009.02.002

Levitan, D. R., Best, R. M., & Edmunds, P. J. (2023). Sea urchin mass mortalities 40 y apart further threaten Caribbean coral reefs. *Proceedings of the National Academy of Sciences*, *120*(10), e2218901120. https://doi.org/10.1073/pnas.2218901120

Lunghi, E., Manenti, R., Mulargia, M., Veith, M., Corti, C., & Ficetola, G. F. (2018). Environmental suitability models predict population density, performance and body condition for microendemic salamanders. *Scientific Reports*, *8*(1), Article 1. https://doi.org/10.1038/s41598-018-25704-1

Menge, B. A., Blanchette, C., Raimondi, P., Freidenburg, T., Gaines, S., Lubchenco, J., Lohse, D., Hudson, G., Foley, M., & Pamplin, J. (2004). Species Interaction Strength: Testing Model Predictions Along an Upwelling Gradient. *Ecological Monographs*, *74*(4), 663–684. https://doi.org/10.1890/03-4060

Nelson, H. R., Kuempel, C. D., & Altieri, A. H. (2016). The resilience of reef invertebrate biodiversity to coral mortality. *Ecosphere*, *7*(7), e01399. https://doi.org/10.1002/ecs2.1399

O'Connor, M. I., Barneche, D. R., González, A. L., & Messier, J. (2020). Editorial: Unifying Ecology Across Scales: Progress, Challenges and Opportunities. *Frontiers in Ecology and Evolution*, *8*. https://www.frontiersin.org/articles/10.3389/fevo.2020.610459

Pomory, C. M. (2001). An escape response behaviour in the brittle star ophiopteris papillosa (echinodermata: Ophiuroidea). *Marine and Freshwater Behaviour and Physiology*, *34*(3), 171–180. https://doi.org/10.1080/10236240109379070

Rasher, D. B., Hoey, A. S., & Hay, M. E. (2013). Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology*, *94*(6), 1347–1358. https://doi.org/10.1890/12-0389.1

Saldana, P., Alford, S., Mainella, A., Crotty, S., Prince, K., Sullivan, C., Earl, K., Angelini, C., & Altieri, A. (2021). *Grateful for the dead: The widespread importance of dead foundation species for biodiversity, ecosystem function, and resilience.* [Preprint]. Preprints. https://doi.org/10.22541/au.163252121.17081433/v1

Sánchez González, I., Hopper, G. W., Bucholz, J. R., Kubala, M. E., Lozier, J. D., & Atkinson, C. L. (2023). Niche specialization and community niche space increase with species richness in filter-feeder assemblages. *Ecosphere*, *14*(5), e4495. https://doi.org/10.1002/ecs2.4495

Sides, E. M., & Woodley, J. D. (1985). Niche separation in three species of Ophiocoma (Echinodermata: Ophiuroidea) in Jamaica, West Indies. *Bulletin of Marine Science*, *36*(3), 701–715.

Simpson, S. J., & Raubenheimer, D. (2012). The nature of nutrition: A unifying framework. *Australian Journal of Zoology*, *59*(6), 350–368. https://doi.org/10.1071/ZO11068

Stachowicz, J. J., & Hay, M. E. (1999). Mutualism and Coral Persistence: The Role of Herbivore Resistance to Algal Chemical Defense. *Ecology*, *80*(6), 2085–2101. https://doi.org/10.2307/176680

Sterner, R. Warner. (2002). *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press,.

Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R. A., Smale, D. A., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thompson, P. A., & Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, *18*(9), 944–953. https://doi.org/10.1111/ele.12474

Tallis, H. (2009). Kelp and rivers subsidize rocky intertidal communities in the Pacific Northwest (USA). *Marine Ecology Progress Series*, *389*, 85–96. https://doi.org/10.3354/meps08138

Tran, K., & Ackerman, J. D. (2019). Mussels partition resources from natural waters under flowing conditions. *The Science of the Total Environment*, *696*, 133870. https://doi.org/10.1016/j.scitotenv.2019.133870

VanDerWal, J., Shoo, L. P., Johnson, C. N., & Williams, S. E. (2009). Abundance and the Environmental Niche: Environmental Suitability Estimated from Niche Models Predicts the Upper Limit of Local Abundance. *American Naturalist*, *174*(2), 282–291. https://doi.org/10.1086/600087

Wainwright, P. C. (1987). Biomechanical limits to ecological performance: Mollusc-crushing by the Caribbean hogfish, Lachnolaimus maximus (Labridae).

Journal of Zoology, *213*(2), 283–297. https://doi.org/10.1111/j.1469-7998.1987.tb03704.x

Wainwright, P. C. (1988). Morphology and Ecology: Functional Basis of Feeding Constraints in Caribbean Labrid Fishes. *Ecology*, *69*(3), 635–645. https://doi.org/10.2307/1941012

Werner, I., & Auel, H. (2005). Seasonal variability in abundance, respiration and lipid composition of Arctic under-ice amphipods. *Marine Ecology Progress Series*, *292*, 251–262. https://doi.org/10.3354/meps292251

Whippo, R., Knight, N., Prentice, C., Cristiani, J., Siegle, M., & O’Connor, M. (2018). Epifaunal diversity patterns within and among seagrass meadows suggest landscape-scale biodiversity processes. *Ecosphere*, *9*, e02490. https://doi.org/10.1002/ecs2.2490

Wing, S., & Jack, L. (2012). Resource specialisation among suspension-feeding invertebrates on rock walls in Fiordland, New Zealand, is driven by water column structure and feeding mode. *Marine Ecology Progress Series*, *452*, 109–118. https://doi.org/10.3354/meps09588