Title

Planktivorous Fish Link Coral Reef and Oceanic Food Webs: Causes and Consequences of Landscape-Scale Patterns in Fish Behavior, Diet and Growth

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Publication Date

2011-12-01

UNIVERSITY OF CALIFORNIA, SAN DIEGO

Planktivorous Fish Link Coral Reef and Oceanic Food Webs: Causes and Consequences of Landscape-Scale Patterns in Fish Behavior, Diet and Growth

A dissertation submitted in partial satisfaction of the requirements for the degree
Doctor of Philosophy

in

Oceanography

by

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2011

The Dissertation of Katharine Mary Winston Hanson is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2011

DEDICATION

I dedicate this dissertation to my parents, Gene Paul Hanson and Mary Winston Hanson, to my daughter, Eva Marie Karaköylü, and to Dr. Peter Franks for supporting me in big ways and in small and encouraging me when I needed it the most.

EPIGRAPH

“C’est une merveille de voir chacun de ces atollons, environné d’un grand banc de pierre tout autour, n’y ayant point d’artifice humain.”

-François Pyrard de Laval, 1605

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ACKNOWLEDGEMENTS

And suppose that you lived in that forest in France,
where the average young person just hasn't a chance
to escape from the perilous pants-eating-plants!
But your pants are safe! You're a fortunate guy.
And you ought to be shouting, "How lucky am I!"

- Dr. Seuss

How lucky am I? Needless to say, some people are 'much more…oh, ever so much more…oh muchly much-much more' unlucky than I. This dissertation is the culmination of a sequence of serendipitous life events and fortunate encounters, but to ascribe my good fortune to 'luck' is an injustice to the teachers, mentors, family and friends that have helped me at each turn.

First and foremost, thank you to my family. To my parents, Gene and Mary, for their endless encouragement, support, and love. It is a blessing to be able to share my own daughter with them. Becoming a parent has brought me such a deeper understanding of the opportunities my parents have given me, and I hope I can pass on to Eva the love of learning that I inherited from them. To my younger brother, A.J., and my baby sister, Annie, for swiftly out-cooling me by both becoming rock stars – literally! What's a gal got to do to earn points for coolest profession in the family? The competition continues…. Thank you to Erdem for taking me to that forest in France, you are more than the average young person and I hadn't a chance. Thank you to Nuri and Meral for so lovingly accepting me into their family, and their endless support of and love for Eva.

Thank you to my high school biology teacher Mrs. O'Dwyer for taking us out of the classroom and into the ocean. I still fondly remember the magic of counting fish while diving through blue-green waves at the Jersey shore. Thank you to Dr. Gadebeku and Dr. Purcell for their frequent injections of fun into the science classroom, and to all of the educators at Oak Knoll for giving me a very loving first academic family.

Thank you to Dr. Bill Hamner, Dr. Rick Vance, Dr. Peggy Fong, Dr. Barney Schlinger, Dr. Dave Jacobs and Dr. Kimo Morris for amazing experiences at UCLA. In their company I have hunted for fossils on the side of Highway 405, spotted a monk seal, been entangled in a Portuguese man-of-war, spent hours pressing delicate algal samples, been reassured that the approaching lemon sharks were not interested in my fish-covered limbs, had truly heartfelt conversations about professional pathways, and taken some very questionable observational data while under the influence of Dramamine. The nature of those experiences should communicate how far beyond the lecture hall my experiences with these professors extended. I am so grateful for their willingness to bring UCLA students to the field and teach us marine science under water! My MBQ experiences continue to inspire my vision of a career in education. Thank you also to Frank DiCrisi and to the UCLA dive program for excellent training that was the beginning of many wonderful adventures on SCUBA. Fellow MBQ-ers you are the best!

Special thanks to Dr. Ian Tibbets and Dr. Michael Pool of the University of Queensland in Brisbane, Australia. These two professors gifted me with another incredible experience in field studies and memories and friendships that will last a lifetime. Dr. Pool led us on a wonderful, reflective discovery of Australian culture not to mention breathtaking hikes through forests fit for a fairy tale. Dr. Tibbets has created an amazing marine studies field program at UQ, and I am so grateful to have been a part of that maiden year. He is warm, incredibly humorous and I can't help but laugh out loud remembering the shenanigans and travels and wonderfully frightening night snorkels.

Thank you to Dr. Richard Strathmann and Dr. Richard Emlet for the amazing experience that is the Larval Biology course at Friday Harbor Labs. These professors brought overwhelming expertise and a sheer love of their research to the classroom. They worked shoulder-to-shoulder with us building crazy larval rearing contraptions in the shop, wading through mudflats, and nurturing hundreds and hundreds of beloved baby invertebrates. Thank you to our amazing teaching assistant Dawn Vaughan and to my fellow students for a magical summer. And thank you to the Mia Tegner award from the Biological Oceanography department at UCSD for affording the opportunity!

To Dr. Jameal Samhouri, Dr. Mark Steele, Dr. Clare Wormald, Dr. Kerry Nichols and Dr. Adrian Stier for giving me an introduction to field work that rang with laughter, had a hearty dose of quinine, smelled a little fishy, and was one of the best experiences of my life. Pants off to you! You are mentors, inspirations, dive buddies, colleagues and friends that I hope to have in my underwater Rolodex for many years to come. To my life partner Kerry, I can't wait to high-fives on the other side of this whole thing!

My experience at Scripps has been brightened by an incredible group of friends, peers, and mentors. First, many thanks to my advisor, Dr. Jim Leichter. Not all graduate students have the fortune to work side by side with their advisor in the field. It is impossible to catalogue everything that I learned during my time in the field with Jim. Through Jim's expertise I gained an understanding of the coastal oceanographic processes that are so integral to understanding the biology of coral reefs. Beyond his scientific influence, I also have Jim to thank for a wealth of knowledge about the ins and outs of working in the field– from learning how to live boat to building field equipment and so much in between. The sum of all of those experiences is the confidence I have to be able to start and run my own field programs. With Jim as an advisor, my graduate experience was an adventure, a grand challenge, and a whole lot of fun. I have him to thank for the opportunity to work in Moorea, and for many fond island memories. Thank you also to Dale Stokes for accompanying me on dives to collect samples even if that entailed descending to the disturbing depths of Pao Pao Bay, for sharing your amazing photos, and for plentiful Celebrity Jeopardy chortles.

While Moorea is a breathtaking island in its own right, my time in the field was so special largely because of the people I worked with. The staff of the UC Berkeley Gump Station become true friends to those of use fortunate enough to return year after year. Val, Irma, Loana, Jacque, Tony – thank you! Thank you to Frank Murphy and Neil Davies for the research support and the warm welcome to the island. My time in Moorea was also enhanced by my interactions with two programs – the Moorea Coral Reef LTER and the 3 Seas Field Biology program. My research literally would not have been possible without the financial and logistical support of the MCR LTER. More importantly, the MCR LTER provided a wonderful community of graduate students and scientists to interact with. Thank you to the principle investigators – Russ Schmitt, Sally Holbrook, Pete Edmunds and Bob Carpenter – for your encouragement and support of all of the MCR graduate students and their research. Bob Carpenter and Pete Edmunds very generously allowed me to tag along on their research dives, allowing me to collect samples around the island of Moorea – a feat I could not have pulled off on my own. Keith Seidel and Andy Brooks were incredibly helpful in teaching me the lay of the land (and the lab!) and introducing me to Moorea’s fish assemblages. Thank you to Alice Alldredge for sharing your wise words of advice and for sharing your incredible zooplankton expertise with me! Watching you and Jim working in the field was truly an inspiration –from your creativity in designing experiments to the superhuman efforts demanded by sampling such tiny organisms! Thank you for warmly welcoming me into your home to share dinners in Santa Barbara and in Moorea- both the cuisine and the conversations bring good memories. Thank you to all of the peers who kept me laughing through late nights in the lab and even underwater – Vinny “Vance” Moriatry, Tom Adam, Hollie Putnam, Stella Swanson, Annie Yau, Caitlin Cameron, Melissa Spitler, Abby Poray, Stephanie Talmage, Gerick Bergsma, Mai Maheigan, Nancy Muehllehner, Nicole Price, Hannah Stewart.

Thank you to our Stanford (and now Duke) colleagues Jim Hench and Joanna Rosman for your friendship, technical advice, Pipe Wrap, help in the field, and for giving me the most hilarious, unforgettable day in the Pao Pao River. You are inspiring role models, great field scientists, and wonderful people. Thank you to Steve Monismith for helping to spear fish and the wonderful reminder of how joyful it is to spend time underwater.

As Jim's student, I was also blessed with being able to participate in a long-standing field biology program – Notheastern University's East/West or 3 Seas Field Program. I had the great fortune to be a teaching fellow for this program for three years. The opportunity gave me an amazing teaching experience and funded the majority of my field work. This dissertation would not have been possible without the 3 Seas support. Thank you to the program's director, Salvatore Genovese, for giving me this incredibly opportunity and for giving so much of himself to the program. Sal's bright personality, enthusiasm and support for the students are a large part of the program's success. The 3 Seas course is truly unique and is an amazing experience for the students that participate. It was an equally amazing experience as a TA. I am humbled by the wonderful faculty members who teach for the program and with whom I was able to spend time – Mark Steele, Andy Brooks, Pete Edmunds, Ruth Gates, Jim Leichter, Brian Helmuth, Dan Bisaccio, Rich Aronson, Bill Precht and Gretchen Hoffman. These faculty put an incredible amount of passion and energy into teaching incredibly hands-on field courses and they truly artful educators and a whole lot of fun. Endless thanks to my fellow TAs and partners in crime – Mike Murray, Adrian Stier, Liz Bentley, Maggie Johnson, Will Goldenheim, Jackie Padillo-Gamiño, Zach Boudreau, David Combosch. So many laughs, so many robots, so many dock evenings, dance parties, so much engulfed in flames, heavy metal, priests, pirates, pomplemousse, cagey caging, tiny bubbles, wha'ha'pon...it's far too much to list and

far too much to ever forget. Adrian and Mike – I literally could not have survived the experience without you. Adrian you are a science rock star and I hope you are prepared to give us all jobs one day. You are entwined in every part of this research, and I am so grateful to have you as mon ami.

Whew...seven pages in and I haven't even arrived at my SIO acknowledgements! First, thank you to my wonderful dissertation committee. Mark Ohman has added so much to my experience at Scripps. I don't think any student can walk out of his course on marine zooplankton without a deep love for the remarkable creatures. The fascinating plankters can take some of the credit, but Mark's enthusiasm for and expertise in the subject is what truly makes the love for zooplankton and pelagic ecology impossible to escape. Mark welcomed me into his lab meetings and I have him to thank for a second, wonderful lab family – Celli, Jesse, Alison, Miriam, Linsey, Christian – thank you for your feedback, intellectually stimulating Friday afternoons and a hearty dose of laughter. Mark has given me feedback and advice at every step of the dissertation process. Chapter 3 of this dissertation, the study on selective feeding, was inspired by Mark and greatly improved by his input. Mark also helped me though some of the lowest, darkest, most difficult points of my graduate experience. The fact that I have a completed dissertation for which to compose an acknowledgements section is largely to his credit. Mark has also given me some of the brightest moments in my graduate experience during numerous research cruises he invited me to join, and it has been great fun to join him on the high seas. Mark – thank you for your unending mentorship and support, and for constantly challenging me to do my best.

Lisa, thank you for the wonderful courses you offer the graduate students at SIO. I know that as students we can only imagine a fraction of the time and effort required to orchestrate taking an entire class to sea or reviewing 20 student proposals in the course of a few weeks. Your feedback in committee meetings and individual meetings has strengthened this research and challenged me to put my own work into a broader ecological context. The entire dissertation has improved as a result, and I thank you for your perspective.

Thank you to Lihini for patiently listening while I worried over mixing models, and for bringing truly constructive feedback to every committee meeting. Your suggestions were not only always helpful, but always communicated in the most positive manner - thank you!

Thank you to Ian for patiently listening to even more worry over statistical analyses. Every meeting we had was marked by enjoyable conversation, no matter how dry the subject matter I brought to you. Even in just a few conversations a year, I came away impressed by the breadth of your interests and your true scholarship.

This dissertation is also in large part a credit to Peter Franks, whose support of not just me but of my family has pulled me through to the end. I have Peter to thank for wonderful experiences at sea, my first lab group family, lots of delicious pho, and the encouragement to carry on!

Thank you to the professors and fellow students of the CBMC IGERT program for a wonderful start to my experience here at Scripps and an inspiring commitment to conservation science. Thank you to Nancy Knowlton, Jeremy Jackson and Dick Norris for your leadership of the program and to Penny Dockery for your support of all of the

CMBC students. Thank you to my IGERT peers – Octavio Aburto-Oropeza, Katie Cramer, Geoff Cook, Davie Kline, Kristen Marhaver, Megan McKenna, Loren McClenachan, Jason Murray, Flavia Nunes, Melissa Roth, Sheila Walsh, Christine Whitcraft, Lorraine Anglin, Andy Balendy, Amy Broulik, Fernanda Mazzillo, Morgan Richie, Greg Wells.

Thank you to my Leichter/ Dayton / Ritter Hall lab peers – Cynthia Button, Talina Konotchick, Marco Hatch, Damien Cie, Christian Anderson, Marcel Croon. Thank you to Paul Dayton for sharing many lab parties and most of all for your amazing natural history course which must rank as one of the most valued educational experiences for anyone who has been lucky enough to participate. I am grateful to have been part of that wonderful legacy here at SIO.

Thank you to all of the many SIO staff who have given me support – the Scripps Library, the IOD business office, the machine shop, Doug Alden and the Hydraulics Lab, Christian McDonald and Rich Walsh of the SIO dive program, Denise Darling, Alice Zheng, Becky Burrola, Josh Reeves, Krystle Shertz and Cerise Maue in the SIO Grad Office.

Thank you to my “Mamas & Papas” support crew – Tali, Satch, Jude, Renee, Marco, Marin, Rachel, Steve, Avi, Jerry, Andrea, Zoe, Jean, Julia, Elsa. What would I have done with out you? Probably gone stark raving mad. Instead of madness there was baby yoga, breeders’ brunches, playground antics, lots of sand eating, zen gardens, so many generous dinner invitations and not at all least the deep belly laughter that comes only from the shared experience of extreme lack of sleep, the hilarious secret lives of babies, and the struggle to keep all of the balls in the air and at least half of the family in clean clothes.

To my three amigas – Melissa, Celli and Monique. You have been there through the thick and the thin, by land and by sea, weathered my drops from the radar, spoken the words “till death do you part”, shared travel adventures, crazy life changes and much, much more. I love you!

Chapter 2 is in preparation for submission to *Ecology* and is presented as part of this dissertation with the acknowledgement of the study co-author, James J. Leicther. The dissertation author was the primary investigator and is the primary author of this material.

Chapter 3 is in preparation for submission to *Marine Ecology Progress Series* and is presented as part of this dissertation with the acknowledgement of the study co-authors, Emilie L. Schnarr and Mark D. Ohman. The dissertation author was the primary investigator and is the primary author of this material.

Chapter 4 is in preparation for submission to the *Journal of Experimental Marine Biology and Ecology* and is presented as part of this dissertation with the acknowledgement of the study co-authors, Adrian C. Stier and James J. Leicther. The dissertation author was the primary investigator and is the primary author of this material.

Satellite images used in Chapter 3 were taken from Google Earth and are © 2011 Digital Globe.

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Leichter, JJ, Paytan A, Wankel S, **Hanson K,** Miller S, Altabet MA (2007) Nitrogen and oxygen isotopic signatures of subsurface nitrate seaward of the Florida Keys reef tract. Limnology and Oceanography **52**:1258-1267

ABSTRACT OF THE DISSERTATION

Planktivorous Fish Link Coral Reef and Oceanic Food Webs: Causes and Consequences of Landscape-Scale Patterns in Fish Behavior, Diet and Growth

by

Katharine Mary Winston Hanson

Doctor of Philosophy in Oceanography

University of California, San Diego, 2011

Professor James J. Leichter, Chair

Coral reefs support an abundance of organisms despite being surrounded by oceanic waters characterized by low nutrient levels. Over more than a century of research, scientists have debated whether life on coral reefs is self-sustaining or whether reef organisms extract nutrients from the open ocean that in turn subsidize organic production within the reef system. This dissertation focuses on one guild of coral reef consumers - fish that feed on zooplankton from the water column. Pairing two independent metrics of fish diet - gut content analysis and stable isotope analysis followed by a mass-balance mixing model - I provide direct evidence that zooplankton

from the open ocean comprise a significant proportion of the diet of fish inhabiting both offshore and nearshore reefs.

In a study of feeding behavior of the planktivorous fish *Dascyllus flavicaudu*s, I document that this species feeds selectively on certain taxa within the zooplankton assemblage. Oceanic copepods (Oncaeidae and Corycaeidae) were over-represented in fish gut contents relative to their abundance in environmental zooplankton samples. Non-random feeding by *D. flavicaudus* resulted in a 2 to 6-fold increase in the contribution of oceanic prey to fish diet beyond that expected under random feeding.

The natural spatial variability in the zooplankton assemblage on coral reefs has the potential to affect not only fish diet but fish growth. I examined the relationship between zooplankton abundance, fish feeding and fish growth using a field experiment where juvenile fish were transplanted to reef habitats spanning a range of ambient zooplankton densities. The resulting spatial patterns in fish growth support the hypothesis that spatial variability in the abundance of zooplankton prey can significantly affect fish growth. Fish transplanted to locations with turbid waters exhibited low growth rates, suggesting that changes in land use practices which alter water quality may have deleterious effects on planktivorous reef fishes and that factors such as turbidity can act to de-couple fish growth from zooplankton abundance.

This dissertation provides a landscape-scale perspective of planktivorous fish as links between oceanic and coral reef food webs and highlights the effects of fish behavior and reef habitat on cross-ecosystem exchange.

CHAPTER 1

Introduction

In one of my favorite examples of scientific writing, limnologist and visionary ecologist G. Evelyn Hutchinson concludes, “It is likely that something very important is involved here, but for the present what it may be is a mystery, a very good thing with which to end a discourse” (Hutchinson 1953, Ballard 1977). I venture that a mystery is also a very good thing with which to begin a discourse, and so I begin this dissertation by reviewing a mystery that is central to the history of scientific investigation of coral reefs.

THE CORAL REEF PARADOX:

... an oasis in a desert ocean
- Odum 1971

A voyage across the center of the tropical Pacific Ocean can be hypnotic in its visual homogeneity - thousands of kilometers of empty blue water with sparse and intermittent biological diversions. Suddenly, an expanse of emerald green water or a change in the color of the sky and at once you are confronted with a coral atoll teeming with life, sitting upon a great cement wall. The contrast between the relatively barren tropical oceans and a teeming coral reef is analogous to happening upon Las Vegas in the middle of the Nevada desert. Understandably, encountering coral reefs in the middle of a ‘desert ocean’ astounded early explorers. What was the origin of these structures? What processes allowed these unique pockets of life to thrive amidst barren oceans? These questions came to be known as the great ‘coral reef paradox’ and the contradiction between coral reefs and their surrounding oceans has inspired more than a century of research on reefs. Through revolutions in travel, media and even hobby aquariums, coral reefs have today become familiar ‘household’ ecosystems. The threats that overfishing, pollution, and a changing climate pose for reefs have turned our concern to the loss of life from these ecosystems rather than the origin of reef life. Decades of coral reef science have illuminated biological and physical aspects of both reefs and the surrounding tropical oceans that explain or dull the paradoxical contrast between the neighboring ecosystems. Nevertheless, continued exploration of the processes that create, maintain, and change life on reefs is an essential component of the efforts to conserve these ecologically and economically valuable habitats.

To channel the spirit of mystery that has motivated the past century of coral reef research, I find it helpful to revisit a more recent scientific discovery that challenged our understanding of life in the oceans. Oceanography in the 1960s was revolutionized by the theory of plate tectonics. This theory described the earth’s crust as a set of adjoining plates that, rather than being fixed and permanent, moved around the earth’s surface and were continually degraded and rebuilt. Cracks in this evolving seafloor afforded the potential for hot water from below to emerge in great plumes. The existence of such hot springs had exciting implications for the geology and chemistry of the oceans, and scientists clamored to find, map, sample and explore areas where these features were likely to occur. In 1977, scientists aboard the R/V *Knorr* departed the Panama Canal as part of the Galápagos Hydrothermal Expedition.

The scientific party of the expedition was comprised of geologists and chemists excited by their mission to explore the location where a prior cruise had identified likely hotspots. These scientists were to witness the discovery of an ecosystem so novel and unpredicted that it amazed the entire oceanographic community. In a video interview (WHOI 2002) given on the occasion of the 25th anniversary of the discovery, Marvin Lilley of the University of Washington describes:

> We were all so naïve I think. At the point at which the cruise was actually happening… the ship was full of a mixture of geologists and chemists, none of whom had any concept that these springs might harbor the rich biological communities that were actually found. The first indication that we had from the sub[mersible vehicle] that something exciting was going on on the seafloor was when Jack Corliss called up and asked if the seafloor wasn't supposed to be a biological desert. And when people standing around confirmed "yah", that was the general consensus, Jack said basically that he was sitting in the middle of a biological oasis and was completely surrounded by a vast animal community.

Interviewed on the same occasion, Dick Von Herzen of the Woods Hole Oceanographic Institution adds:

> Suddenly after the first few dives the report was that they saw some strange biology right at the ridge axis. These were reported back to the ship and we didn't know what to make of it because that was not our interest and we had no biologists on board who could tell us anything about it. When we radioed the information back to the biologists at Woods Hole they thought we were kind of crazy – I mean what were we talking about out here? They had never heard of such a thing.

A quote from a retrospective article by oceanographer Robert Ballard summarizes why the discovery of abundant life at the hydrothermal vents was so perplexing and unanticipated: “What were the organisms eating? They were living on solid rock in total darkness” (e.g. Ballard 1977).

Corals and coral reefs also live on solid rock though they exist not in total darkness but bathed in light within tropical latitudes. The enigma of the hydrothermal vent animals was that they existed without energy from the sun to drive primary production that could supply food for the animal community. Coral reefs have plenty of sunlight, but they seem to exist in the near absence of another ingredient vital for the production and maintenance of life – nutrients, namely nitrogen and phosphorus. Coral reefs are found in some of the most oligotrophic (nutrient-poor) areas of the world’s oceans. Darwin is often credited as the first to speculate on this paradox of abundant life in nutrient-poor oceans (Rougerie et al. 1992), although Darwin paid more attention the geological questions of the formation and foundation of coral atolls than to the ecological mystery of what sustained the broad diversity of reef life (Darwin 1842). In the early twentieth century, questions of the degree to which coral reefs were self-sustaining became understandably intertwined with questions about the balance between heterotrophy and autotrophy on the scale of individual coral colonies. Researchers debated whether primary production by zooxanthellae – microscopic single-celled algae that live as endosymbionts within coral tissues – could satisfy the metabolic demands of host corals. Some researchers suggested conclusions that were drawn for coral colonies could be extrapolated to the scale of whole coral islands. In addition to studying the carbon metabolism of corals, researchers began tracking changes in dissolved oxygen levels in reef waters as a method of tracking whole-reef metabolism (Sargent and Austin 1949). Efforts to quantify rates of primary production and respiration on reefs were joined by studies of fluxes of dissolved nitrogen and phosphorus across reefs. And what was the result of these decades of intense study? To be fair a great deal was learned about coral reefs and coral themselves, though without a clear consensus on the 'answer' to the great nutrient paradox of coral reefs which continued to be the subject for scientific debate. The mindset of the coral reef scientific community over this period can be characterized by a chronological journey through excerpts from the primary literature:

> On the other hand, the polypifers [corals] in their turn must prey on some other organic beings; the decrease of which from any cause, would cause a proportionate destruction of the living coral. The relations therefore, which determine the formation of reefs on any shore, by the vigorous growth of the efficient kinds of coral must be very complex, and with our imperfect knowledge quite inexplicable.
>
> \- Charles Darwin 1842
>
> \----
>
> The picture of the reef as a self-supporting community, depending on the current only for dissolved nutrients (in a broad sense), and not for particulate or dissolved organic matter, is reasonably clear cut.
>
> \- Sargent and Austin 1954
>
> \----
>
> The reef does not derive a net gain from the larger components of plankton in the water crossing the reef under stress of the trade winds. Whether a dissolved organic-matter gain is obtained is still uncertain.
>
> \- Odum and Odum 1955
>
> \----
>
> We suspect that the controversy concerning the relative importance of symbiotic algae and external food sources in coral nutrition may turn out to be a false issue and that further research will show that both are indispensable to reef-building corals.
>
> \- Johannes et al. 1970
>
> \----
>
> Perhaps the most important conclusion to emerge from recent work is that not only is some direct organic feeding necessary to sustain growth in reef corals, but there is almost certainly an under-recognized need of a similar kind for the reef as a whole. Thus, the popular concept of both corals and reefs as magnificent demonstrations of almost total

> autotrophic self-sufficiency is likely to prove to be an oversimplification.
>
> - Lewis et al. 1985

> In overall conclusion, it seems fair to say that the more detail that has appeared in the literature on the subject of the movement of organics through reef systems, the more confused has become any possible hypothesis concerned with the overall trophic balance of the system. However, it is clear that import, creation and redistribution and export of dissolved and particulate (living and detrital) organic matter is proving to be of the greatest possible importance to any complete study of system level carbon flux and trophic balance in coral reefs. Our earlier tendency to assume that a coral reef could be trophically characterized by consideration of its community metabolism was much too simplistic.
>
> - Kinsey 1985

After more than a century of research on coral reef nutrient and energy budgets, the following broad points are clear:

(1) Coral reefs harbor numerous examples of organisms that have evolved symbiotic relationships that facilitate and are adapted to life in low-nutrient conditions. Most notable among these relationships is that between stony or reef-building corals and their endosymbiotic algae (Muscatine and Porter 1977). The carbon fixed by these endosymbionts is utilized by and provides most if not all of the carbon demand of the coral host (Muscatine et al. 1981). Nevertheless, heterotrophic feeding on zooplankton is an important source of nutrients for corals and in some situations also represents a significant source of carbon (Porter 1976, Grottoli et al. 2006).

(2) Various pathways for the recycling of organic matter exist in coral reef ecosystems. Materials such as coral mucous, the production of which is partially fueled by the carbon fixed via photosynthesis by symbiotic zooxanthellae, often aggregate within shallow lagoons and can be remineralized within the lagoon sand and sediment (Wild et al. 2004). Such recycling of primary and secondary production on reefs represents a local source of nutrients to consumers and reduces the demand for nutrients imported from the open ocean.

(3) The biology and ecology of coral reefs are strongly influenced by physical processes including those driving the flow of water through reefs (Atkinson and Bilger 1992, Roberts et al. 1992, Sebens et al. 1997). A greater understanding of typical water velocities on coral reefs and the interaction of the reef matrix with incoming waves and currents have revealed that fluxes of nutrients to reefs may be high even though standing stocks are low (Atkinson and Bilger 1992).

(4) Coral reefs receive inputs of nutrients from a variety of sources including nitrogen-fixing cyanobacteria, terrestrial runoff, upwelling, and sub-thermocline waters brought to shallow reefs by breaking internal waves (Leichter et al. 1996, Sammarco et al. 1999). These nutrient sources represent both dissolved and particulate nutrient inputs. Zooplankton comprise a significant proportion of the particulate nutrients available to reef consumers, but their trophic importance to the reef has been alternately dismissed and emphasized (Odum and Odum 1955, Hamner et al. 1988).

Research on the trophic importance of zooplankton to coral reef ecosystems often proceeded from a coral-centric perspective. While corals do feed on zooplankton, a host of invertebrate and vertebrate reef organisms are also filter or particulate feeders. The small, colorful planktivorous fishes that swarm over reefs are some of the most abundant particle feeders on coral reefs. Researchers who studied zooplankton on reefs identified planktivorous fish as a main trophic pathway by which zooplankton, and the energy and nutrients they represent, enter the reef system:

> Our contention that zooplankton are a major source of nutrition for coral reef systems is in contrast to the conclusions of most prior investigators … Future investigations on reef nutrition that seek to determine precisely how much food is extracted from the waters that flow over reefs should relate the fine-scale distributions of zooplankton and fine-scale hydrography to detailed energy budgets of individual species of planktivorous fish.
>
> \- Hamner et al. 1988

Planktivorous fish are also abundant in rocky reef and kelp forest ecosystems. The zooplankton consumed by fish represent oceanic resources that are brought by waves and currents to consumers in these benthic ecosystems. Answering questions such as ‘How much zooplankton do planktivorous fish consume?’ has identified these fish as important agents of cross-ecosystem trophic exchange between the open-ocean and both rocky reef and kelp forest ecosystems (Bray et al. 1981, Pinnegar and Polunin 2006). Coral reef zooplankton assemblages contain both transient organisms that are swept in from the open ocean as well as zooplankton that reside in or originate from the reef system (Alldredge and King 1977, Hobson and Chess 1986, Carleton and Hamner 2007). Only the oceanic zooplankton represent an addition of new nutrients to the reef system. Thus, distinguishing the relative contribution of oceanic versus reef resources to fish diet is essential to evaluating planktivorous fish as agents of cross-ecosystem trophic exchange between oceanic and coral reef ecosystems and to our understanding of coral reef food-webs.

This dissertation was inspired in equal parts by the legacy of the great coral reef paradox, by a fascination with the marvelous, colorful coral reef zooplankton, and by the scientific mentors who first introduced me to coral reef ecology. It has been a true pleasure to come to know these organisms and this ecosystem in the process of my scientific training.

OVERVIEW OF THE DISSERTATION:

This dissertation includes three empirical data chapters. Each of the chapters is intended to stand alone as a publishable unit, and as a result there is some redundancy in the introductory sections and description of research methods. Below I give an overview of the dissertation and outline the research objectives of and hypotheses tested by each chapter.

Chapter 2: The contribution of oceanic and reef food sources to the diet and secondary production of planktivorous coral reef fishes

Motivation:

Planktivorous fishes on coral reefs have been described as a "wall of mouths" (Hamner et al. 1988). Measurements of the filtering efficiency of reef planktivores have revealed waters flowing off of reefs to be depleted in zooplankton by 55% (Johannes and Gerber 1974), 60% (Glynn 1973) and 61% (Tranter and George 1969) relative to waters arriving at the reef crest. This "wall of mouths" intercepts not only zooplankton swept in from the open ocean but eggs and larvae spawned by corals, fishes and crustaceans living on the reef. Numerous researchers (e.g. Emery 1968, Hamner et al. 1988) have described planktivorous reef fish as a link between oceanic and reef food webs, and suggested that by feeding on oceanic zooplankton this guild of fishes facilitates a large transfer of new nutrients into the reef system. However, planktivorous fish also feed on eggs, larvae and zooplankton resident to the reef. These food sources represent energy and nutrients that have been produced within the reef and thus do not represent a subsidy of new materials. To date, the relative importance of oceanic versus reef-associated zooplankton to the diet of these reef fishes has not been quantified.

Objectives:

2.1. To quantify the contribution of oceanic and reef-associated food sources to the diet and secondary production of planktivorous coral-reef fish using two independent metrics of fish diet: gut content analysis and stable isotope analysis.

2.2. To test the relative contribution of imported (allochthonous, oceanic) and local (autochthonous, reef-associated) food sources to the diet of fish in three reef habitats: the forereef, backreef and fringing reef.

Hypotheses:

2.1. Oceanic zooplankton constitute larger proportions of the diet of fish inhabiting offshore reefs than those inhabiting nearshore reefs.

2.2. Offshore fish will have depleted carbon isotope ratios relative to nearshore fish, reflecting differences in both prey type and carbon sources.

Chapter 3: Selective feeding increases the contribution of oceanic zooplankton to the diet of planktivorous coral reef fish

Motivation:

Most organisms are selective feeders – they consume and utilize only a fraction of the food resources available in the environment. Selective feeding in an organism can be assessed by comparing the composition of the organism's diet with the composition of food sources in the environment. An over- or under- representation of food types in the diet relative to the environment is indicative of selective feeding.

Our own human experience is a testament to the significance of feeding behavior. What and how we eat has great implications for our own survival and reproduction, affects our interactions with other humans and has enormous impacts on our environment. Selective feeding can have important consequences for predator-prey interactions within an ecosystem. Selective feeding can alter interactions between species that compete for similar food types. Changes in the feeding behavior of an abundant consumer can influence the flow of energy and resources through an entire food web.

Fishes that feed on zooplankton are known to be selective feeders (Lazzaro 1987). Selective feeding in zooplanktivorous fishes has been documented in a variety of freshwater and marine habitats but has not been explored in diurnal coral reef fishes. To assess zooplanktivorous fishes as links between oceanic and coral reef food webs, we must understand how the feeding behavior of these fishes influences their use of oceanic and reef-based food sources.

Objectives:

3.1. To determine whether the diet of the reef planktivore *Dascyllus flavicaudus* is influenced by selective (non-random) feeding.

3.2. To quantify departures from non-random feeding (positive or negative electivity) for specific zooplankton prey types.

3.3. To examine the effects of the feeding behavior of *D. flavicaudus* on dietary breadth and the contribution of oceanic zooplankton groups to fish diet.

Hypotheses:

Chapter 3 examines the following null hypotheses:

3.1. *Dascyllus flavicaudus* feeds randomly on the available zooplankton prey.

3.2. The distribution of prey items among 16 prey categories (i.e. dietary breadth) does not differ between environmental samples and gut content samples.

3.3. The proportion of oceanic zooplankton in fish guts mirrors the proportion of oceanic groups in the ambient zooplankton assemblage.

Chapter 4: Variation in the growth of a planktivorous coral reef fish (*Dascyllus flavicaudus*, Pomacentridae) in relation to food availability and prey consumption

Motivation:

Recent studies of coral reef fish populations have revealed that the same species of fish inhabiting neighboring reefs can have significantly different growth rates, sizes and life spans (Fowler and Doherty 1992, Choat and Axe 1996, Hart and Russ 1996, Newman and Williams 1996). These results were somewhat surprising in that the adjacent reefs were in close proximity (hundreds of km and less) and thus differences in temperature could not be used to explain the observed demographic variability. Scientists studying herbivorous and planktivorous fishes on coral reefs have proposed that differences in food availability or quality among reefs could be driving the observed patterns (Kingsford and Hughes 2005, Ruttenberg et al. 2005, Figueira et al. 2008, Paddack et al. 2009). In the study reported in Chapter 4, I conduct a transplant experiment with juvenile reef fish and examine the direct link between zooplankton abundance, fish gut fullness, and fish growth.

Understanding processes that regulate growth is particularly important for fishes. Fish populations are typically size-structured, meaning that key life-history transitions and vital rates are a function of an individual's size rather than age (Parker and Larkin 1959, Gerking and Raush 1979, Sogard 1997). Growth rates can affect the reproductive contribution of a subpopulation by altering local fish biomass and fecundity as well as by governing the time to size at sexual maturity and thus the number of reproductive individuals in a subpopulation (Jones 1987, Forrester 1990, Booth 1995). In this manner, energetic processes (Jones and McCormick 2002) that affect growth in fishes have the potential to influence population-level dynamics even though they may not directly alter the local number of individuals .

Objectives:

4.1. To examine growth rates in planktivorous fish across naturally occurring spatial variability in zooplankton abundance.

Hypotheses:

4.1. Fish growth rates are highest in habitats with the greatest ambient zooplankton densities.

4.2. Fish growth is positively correlated to the number of zooplankton prey items consumed.

4.3. Fish growth varies significantly among the three reef habitats that span gradients in physical characteristics (flow, turbidity, water column height) and biological factors (zooplankton and predator densities) that likely influence the feeding biology of planktivorous fishes.

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CHAPTER 2

The contribution of oceanic and reef food sources to the diet and secondary production of planktivorous coral reef fish

ABSTRACT:

The relative contribution of imported versus locally sourced energy and nutrients to secondary production on coral reefs has been actively debated for decades. Zooplankton dominate the particulate nutrients imported to reefs from the adjacent open ocean. Reef organisms that consume zooplankton represent trophic pathways through which allochthounous, oceanic resources can contribute to reef productivity. Here we examine the relative importance of oceanic versus reef-associated zooplankton in the diet of planktivorous reef fishes. Data on prey biomass in fish guts and stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$) sampled from both fish tissue and zooplankton prey were used to quantify the relative contribution of oceanic versus reef-associated resources to secondary production in reef planktivores. Sampling across three dominant reef habitats (fore, back and fringing reefs), we examine landscape-scale patterns in fish diet. Oceanic zooplankton, predominantly copepods from the families Oncaeidae and Corycaeidae, comprise 60 % to > 90 % of the diet of fish inhabiting the forereef habitat. The dominance of oceanic plankton in the diet of forereef fish results in relatively depleted carbon isotope ratios in tissues of the reef fish *Dascyllus flavicaudus* (mean $\delta^{13}C = -16.4$ ‰) indicating the contribution of pelagic carbon sources. Conspecifics inhabiting the shallow backreef and fringing reef have more enriched isotope ratios (mean $\delta^{13}C$ = -14.9 ‰) indicating an increased contribution of benthic carbon sources. Reef-associated zooplankton including fish eggs, larval decapods and benthic harpacticoid copepods accounted for significant proportions of the gut contents collected from fish inhabiting shallow nearshore reefs. Extensive sampling of *D. flavicaudus* confirmed that the cross-shore patterns in fish diet were temporally and spatially consistent within a species. Muscle isotope ratios ($\delta^{13}C$) collected from eight additional planktivorous species exhibited the same pattern of offshore depletion/ onshore enrichment sampled in *D. flavicaudus*. Oceanic zooplankton contribute substantially to the diet and secondary production of coral reef fishes across biologically and physically distinct reef habitats, though the dominance of oceanic versus reef-associated resources in fish diet is habitat-dependant. This study provides a spatially explicit view of allochthonous subsidies to coral reef planktivores. Our methodological approach can be applied across reef types to explore how variables such as reef geomorphology affect the role of oceanic plankton and planktivorous fishes within coral reef food webs.

INTRODUCTION:

The boundaries between adjacent ecosystems are permeable to fluxes of nutrients and organic material. Imported nutrients can stimulate local primary production while inputs of organic carbon can directly fuel secondary production within the recipient ecosystem. Inputs of allochthonous (distantly sourced) trophic resources have been shown to influence food web and community dynamics in a broad range of terrestrial and aquatic ecosystems. Allochthonous resources support populations of consumers in marine ecosystems such as seamounts (Genin 2004) and the deep sea (Smith & Baco 2003), freshwater ecosystems including lakes, streams and rivers (Fisher & Likens 1972, Carpenter et al. 2005), as well in coastal ecosystems such as sandy beaches (Colombini & Chelazzi 2003) and low-productivity islands (Polis & Hurd 1996).

The maintenance of coral reef ecosystems within nutrient-poor oceanic realms has intrigued explorers and scientists for more than a century (Darwin 1842, Dana 1872, Gardiner 1898). The pioneering studies of Sargent and Austin (1949, 1954) were the first quantitative attempts to understand productivity on the scale of the entire reef community. Questions of the self-sustaining nature of coral reefs and reef metabolism paralleled simultaneous research and debate over the importance of autotrophy versus heterotrophic feeding for the growth of individual coral colonies (reviewed in Lewis 1977, Ferrier-Pages et al. 2011). These scientific efforts examined the contribution of dissolved nutrients (e.g. Johannes et al. 1972) as well particulate nutrients in the form of plankton (e.g. Sargent & Austin 1949) and detritus (e.g. Glynn 1973) to primary and secondary production on reefs. Many of these studies were conducted on coral islands where the flow of water over reefs was primarily unidirectional (von Arks 1948), allowing questions of nutrient import and export to be examined by comparing measurements taken upstream and downstream of the reef (e.g. Odum & Odum 1955).

Studies of changes in zooplankton abundance as water flows over reefs have documented that reef planktivores can remove up to 60 % of the zooplankton from incoming oceanic waters (Tranter & George 1972, Glynn 1973). Much of this depletion is attributable to diurnal planktivorous fishes that form a “wall of mouths” on the slopes of deep coral reefs (Davis & Birdsong 1973, Hobson & Chess 1978, Hamner et al. 1988). These and similar findings have argued against claims of the insignificance of planktonic inputs to coral reef ecosystems as judged by the requirements of the reef corals (Sargent & Austin 1949, Johannes et al. 1970). However, coral reef zooplankton assemblages are not comprised solely of oceanic zooplankton advected onto the reef. Resident holoplanktonic taxa (Sale et al. 1976), demersal and hyperbenthic taxa (Emery 1968, Alldredge & King 1977, Carleton & Hamner 2007), and the eggs and larvae of reef corals, crustaceans and fishes can dominate zooplankton assemblages within the reef system. In some reef systems, these reef-associated forms are so abundant that zooplankton densities within the reef lagoon are greater than those in adjacent oceanic waters (Leborgne et al. 1989, LeBorgne et al. 1997). In addition to cross-shore gradients in zooplankton density and composition, strong vertical zooplankton gradients have been measured over coral reefs (Yahel et al. 2005, Alldredge & King 2009, Heidelberg et al. 2010).

Planktivorous fish species often feed within specific vertical strata of the water column (Hobson & Chess 1978). Many planktivorous fishes on coral reefs shelter within corals to avoid predation and thus are limited to feeding within a few meters of the reef surface (Davis & Birdsong 1973). Thus, both vertical and horizontal zooplankton gradients are likely to influence the type of prey consumed by reef planktivores. The relative importance of reef-associated versus oceanic zooplankton to the diet of planktivorous coral reef fishes has not been resolved (Williams et al. 1988). Similarly, although we know that planktivorous fish are an important prey source for larger coral reef fishes (St John et al. 2001) and contribute feces and excreta that are utilized by a variety of fishes and invertebrates (Robertson 1982, Cleveland et al. 2011), the role that planktivorous fishes play as a link between oceanic nutrients and the larger food web is not as resolved in coral reef ecosystems as it is in rocky reefs (Bray et al. 1981, Pinnegar & Polunin 2006) or seamounts (Genin 2004).

Current research on the role of allochthonous zooplankton in coral reef ecosystems is aided by the maturation of the disciplines of food web ecology and landscape ecology (Paine 1980, Turner 1989). Research at the intersection of these disciplines has proliferated, and subsequent reviews have clarified the fundamental research objectives critical to understanding food web and population-level consequences of allochthonous inputs (Polis et al. 2004). Taking a landscape approach to the study of such subsidies, we must investigate spatial and temporal variation in the magnitude and type of material exchanged as well as in the physical processes and biological agents that mediate the exchange (Vanni et al. 2004).

Investigating the relative contributions of oceanic versus reef-associated resources to the diet of reef fishes is aided by taxonomic distinctions between oceanic and reef zooplankton. Meroplanktonic forms such as coral and decapod larvae are inherently reef-associated. In reef systems with relatively small lagoons and short residence times, sharp onshore decreases in the density of particular zooplankton taxa can be indicative of their oceanic origin (Renon 1979, Lefevre 1986). The transition from ocean to reef also represents a gradient in the dominant primary producers from pelagic phytoplankton to benthic algae (including endosymbiotic zooxanthellae). In photosynthetic aquatic ecosystems, the carbon content of pelagic primary producers is characteristically lower in ^{13}C relative to ^{12}C as compared to benthic primary producers (France 1995, Figure 2.1, Appendix 2A). This contrast in stable carbon isotope ratios has been used to trace the contribution of pelagic versus benthic primary production to littoral ecosystems (Jennings et al. 1997, Pinnegar & Polunin 2000), lakes (Vander Zanden & Vadeboncoeur 2002), seagrass beds and coral reefs (Fry et al. 1982). Carbon isotope ratios have also been used to investigate ontogenetic changes in fish diets, for example in the diet of the coral reef fish *Mulloidchthys flavolineatus* (Mullidae) (Kolasinski et al. 2009). This species transitions from a pelagic larval phase to become a benthic carnivore feeding on meiofauna as juveniles and larger invertebrates as adults. The ontogenetic shift in diet was reflected by a transition from depleted muscle tissue carbon isotope ratios in juveniles to enriched ratios measured in juveniles and adults.

In this study we combine gut content and stable isotope analyses to quantify the contribution of oceanic and reef-associated food sources to the diet and secondary production of planktivorous coral-reef fishes. Sampling fish along gradients in the reef landscape, we test the relative contribution of imported (oceanic) and local (reef-associated) food sources to the diet of fish in three reef habitats: the forereef, backreef and fringing reef. We hypothesized that oceanic zooplankton constitute larger proportions of the diet of fish inhabiting offshore reefs than those inhabiting nearshore reefs. Therefore, we also hypothesized that offshore fish will have depleted carbon isotope ratios relative to nearshore fish, reflecting differences in both prey type and carbon sources. We examine whether oceanic or reef food sources provide the majority of the diet of reef planktivores based on prey biomass as well as a mass-balance model of carbon isotope ratios. Together these data provide a spatially explicit view of planktivorous reef fishes as consumers that utilize and assimilate oceanic energy and nutrients that are subsequently distributed within the larger coral reef food web.

MATERIALS AND METHODS:

Study site and species

Fish and zooplankton were collected from reefs surrounding Moorea, a high volcanic island in the Society Archipelago of French Polynesia (17°32’S, 149°50’W) (Figure 2.2). Three distinct reef habitats form concentric bands around the island. Coral cover on the fringing reef, the habitat closest to shore, extends to ~ 20 m depth (Fig 2.3a). A system of sand-filled lagoons separates fringing reefs from the backreef platform. The backreef habitat is shallow (< 3 m depth) and is characterized by a network of patch reefs and isolated coral heads separated by bare sand. Waves breaking on the reef crest delineate the seaward boundary of the backreef; the forereef habitat slopes offshore from the reef crest with coral cover extending to > 40 m depth. Circulation of water within Moorea’s reef system is strongly influenced by wave action: surface waves break on the reef crest and drive predominantly unidirectional currents across the backreef where water empties into the lagoon and circulates back to the ocean through a series of twelve deep (~ 30 m) reef passes (Hench et al. 2008). The islands of French Polynesia are located near an amphidromic point, and tidal amplitudes in the region do not exceed 0.3 m (Delesalle & Sournia 1992). During seasons of high wave activity, wind- and wave-driven flow dominate tidal influences and the resulting unidirectional flow renders the forereef habitat effectively ‘upstream’ of the backreef and fringing reef habitats.

We chose the yellowtail damselfish *Dascyllus flavicaudus* (Pomacentridae) as a model species for investigation of the diet of zooplanktivorous reef fishes. This species is common to Moorea’s reefs and can be found in all three habitats (forereef, backreef and fringing reef). *D. flavicaudus* exhibits feeding behaviors common to small-bodied, diurnal planktivorous reef fishes. During the day individuals hover over coral colonies to feed on zooplankton which they visually detect in the water column (Allen 1991). At night and when threatened, fish retreat to shelter within the coral. Because of this strong reliance on coral shelter, *D. flavicaudus* and similar reef fish species are described as “site-attached” in that their movements are restricted by the need to maintain proximity to the reef and individuals often return to a specific coral head each night. The home range of site-attached planktivorous reef fish is known to increase with fish size and to be larger in areas of continuous, versus patchy, coral cover (Godwin 1995). In this study, it is assumed that fish collected in a given location have been residing and feeding in that location. This assumption is robust on the timescale of the gut content analysis, which provides snapshots of fish diet over ≤ 12 hours. The response rate of fish muscle tissue isotope ratios to changes in diet composition is driven both by metabolic turnover and by the addition of new biomass through growth and varies with both fish size and temperature (Hesslein et al. 1993, Bosley et al. 2002). Our fish collections targeted fish that were ~ 10 g – 50 g (wet weight). Data on water temperatures collected between August 2005 and September 2007 recorded variation in sea surface temperature near Moorea as well as temperatures within the reef lagoon between ~ 26.5 °C and 30 °C (Edmunds et al. 2010). Laboratory studies of isotopic turnover in muscle tissue of similarly sized fish (5.38 – 9.87 g) raised at slightly lower temperatures (21 °C – 23 °C) measured carbon isotope half-lives of 21 to 29 days. Thus, the stable isotope values of small-bodied planktivorous fishes in Moorea are likely to integrate inputs from fish diet over a period of < 2 months (Suzuki et al. 2005, Weidel et al. 2011), and potentially a shorter period given the higher temperatures of tropical waters. Within reef habitats, our sampling locations were separated by > 500 m and physical barriers (reef crest, lagoon, expanses of bare sand) divided the three habitat types. Therefore, we believe that our assumption of residency within the collection location is also valid for site-attached reef planktivores over time scales relevant to the stable isotope analysis.

To explore the generality of the results obtained from *D. flavicaudus*, we extended our cross-shore sampling to include eight additional planktivorous species from the family Pomacentridae and a planktivorous trigger fish, *Odonus niger* (Balistidae). The species studied are nine of 47 fish species in Moorea that are classified as planktivores (Froese & Pauly 2010). The suite of species studied here (with the exception of the large-bodied balistid *O. niger*) is a subset of the 22 planktivorous fish species in Moorea that are small-bodied, diurnal zooplanktivores (Appendix 2B: Table 2B.1).

Sample collection: fish

Sampling of the focal species, *D. flavicaudus*, was conducted at two spatial scales (Figure 2.2). Island-wide sampling spanned Moorea's ~ 60 km perimeter with samples collected from six study sites established by the Moorea Coral Reef Long Term Ecological Research (MCR LTER) program. Fish were also collected from nine sites spanning 12 km on Moorea's north shore. Adjacent sites on the north shore were separated by > 500 m. At both spatial scales, fish were collected from the forereef, backreef and fringing reef habitats at each site. To examine temporal variability in fish diet, individuals from one site on the north shore (LTER site 1) were collected in four periods spanning three years (2007 – 2009). Collection of the additional planktivorous fish species occurred primarily on the north shore. Collections for all species targeted adult size classes to avoid ontogenetic bias in fish diet.

Fish were collected by SCUBA divers with hand-held microspears (Randall 1967) and euthanized in chilled seawater. Fish sampled for gut content analysis were kept on ice and dissected within 12 hours of collection. While *D. flavicaudus* does not have a true stomach, the anterior portion of the intestine in this species is extended into a pouch-like structure. Gut contents were removed from this pouch, preserved in 1.8 % buffered formaldehyde in seawater and later enumerated using a dissecting microscope. Dorsal white muscle tissue was sampled from fish, rinsed in de-ionized water and dried at 50°C for 24 hours. Dried tissue was ground to a homogenous powder for subsequent isotopic analysis using a mortar and pestle. Powdered tissue (~ 1 mg) was measured into pre-weighted tin capsules for isotopic analysis.

Fish not included in gut content analysis (including the additional planktivore species) were frozen (-20°C) and later dissected for muscle tissue collection. All fish were measured (total and standard lengths) and weighed before dissection or freezing.

Sample collection: zooplankton

Zooplankton samples for isotope analysis were collected using three approaches. Bulk zooplankton samples were collected with replicate oblique net tows (220 µm mesh) taken at two stations: an oceanic station located 5 km seaward of the reef crest and a reef station located within the lagoon on Moorea's north shore. Zooplankton prey were also sampled from the guts of *D. flavicaudus* by emptying the foregut pouch. Gut contents sampled for isotope analysis were not enumerated but were scored for the presence and abundance of dominant taxonomic groups. Samples from bulk net tows and gut contents were rinsed with de-ionized water over a 100 µm mesh screen, dried at 50°C for 24 hours and ground to a homogenous powder. Powdered samples (~ 1 mg) were transferred to tin capsules. Samples of specific zooplankton taxa were collected from additional net tows by sorting bulk tow contents under a dissecting microscope and selecting individuals from two taxonomic groups: (1) the copepods *Corycaeus* spp. and (2) zoea-stage larvae from mixed decapod species. Individual organisms were rinsed in de-ionized water, placed in pre-weighed tin capsules and dried at 50°C for 24 hours. In order to compile sufficient tissue for isotopic analysis, tens (zoea) to one hundred (*Corycaeus* spp.) individuals were placed in each capsule to achieve sample dry weights of approximately 1 mg.

Gut content analysis

Formaldehyde-preserved gut content samples (n = 50) were enumerated under a dissecting microscope. Zooplankton prey were categorized into twelve prey groups (Table 2.1). The count data for each zooplankton group were converted to prey biomass using published data on the carbon content (μg C individual^{-1}) of various zooplankton prey types (Appendix 2C: Table 2C.1).

The origin (oceanic vs. reef-associated) of zooplankton prey groups was ascribed on the basis of cross-shore distribution, life history, or both factors (Table 2.1, Figure 2.3). Prey groups such as decapod and coral larvae are intrinsically reef-associated, as they are offspring of benthic coral reef adults rather than pelagic, oceanic organisms. Data on the cross-shore distribution of zooplankton sampled from Moorea (Renon 1979) were used to identify taxa that are abundant in oceanic samples and rare or absent from reef samples (oceanic indicator taxa) and taxa that are abundant within the reef systems relative to oceanic samples (reef indicator taxa) (Figure 2.3b,c).

Stable isotope analysis

Dried fish muscle and zooplankton samples (~ 1 mg dry weight) were measured into tin capsules (Costech Analytical Technologies, Inc., Valencia, CA, USA) and submitted to the UC Davis Stable Isotope Facility for analysis. Samples were combusted in an on-line elemental analyzer (ANCA-GSL, PDZ Europa, Sercon Ltd., Cheshire, UK). Dual measurements of carbon and nitrogen stable isotope ratios were taken using continuous flow isotope ratio mass spectrometry (PDZ Europa 20-20 mass spectrometer, Sercon Ltd., Cheshire, UK). Isotope ratios are expressed relative to international standards for nitrogen (N_2 air) and carbon (Peedee Belemnite) using the following notation:

$$\delta X = [(R_{sample} - R_{standard})/ R_{standard}) \times 1000 \quad (‰)$$

where *X* is the heavy isotope (^{13}C or ^{15}N) and *R* is the ratio of heavy to light isotope (^{13}C:^{12}C or ^{15}N:^{14}N). Raw isotope ratios were corrected using laboratory working standards composed of a mixture of sucrose and ammonium sulfate (δ^{13}C = -24.44‰, δ^{15}N = 1.33‰) or nylon (δ^{13}C = -27.72, -27.86‰, δ^{15}N = -9.77, -9.96‰) (Appendix 2D: Table 2D.1). Working standards were interspersed with samples in each run; analytical precision was $\leq$ 0.10 ‰ for carbon and $\leq$ 0.18 ‰ for nitrogen. Aliquots of muscle tissue from seven individual *D. flavicaudus* were included in each run as internal standards to provide an estimate of error associated with the sample material. The standard deviations of replicate measurements of the internal standards were $\leq$ 0.16 ‰ for δ^{13}C and $\leq$ 0.53 ‰ for δ^{15}N (Appendix 2D: Table 2D.2).

Mass balance isotope mixing model of fish diet

We used a four-source mass balance model to estimate the contribution of oceanic and reef food sources to the diet of *D. flavicaudus* based on δ^{13}C of fish muscle tissue and of zooplankton prey. The four source values used in this model reflect end-members that bound the range of values measured in oceanic and reef-associated zooplankton samples. With one isotope and four sources, our model does not allow for the calculation of unique solutions. We used the software program IsoSource v. 1.3 (Phillips & Gregg 2003) to calculate distributions of feasible solutions for the percent contribution of the four food sources to the diet of fish consumers. This approach is based on isotopic mass balance equations that are iteratively solved for all possible percent contributions of each source value (0-100%). The model steps through percent contribution scores for each food source at a userdefined interval; we chose an interval of 1%. The distribution of feasible solutions for each modeled consumer $\delta^{13}C$ value is restricted to source combinations which result in a calculated consumer $\delta^{13}C$ that falls within a tolerance range of the measured consumer $\delta^{13}C$ value. Our chosen mass-balance tolerance threshold of 0.05‰ was informed both by the standard deviation of replicate fish muscle tissue samples (for $\delta^{13}C$) and the isotopic separation of oceanic and reef prey sources (Phillips & Gregg 2003). After calculating the distributions of feasible solutions, we summed the contributions of the two oceanic and two reef end-members to yield estimates of the percent contribution of all oceanic and all reef food sources to the diet of *D. flavicaudus*, an approach that has been used in previous applications of isotope mixing models (Newsome et al. 2004, Phillips et al. 2005). By choosing end-members that bound the range of values measured from both prey groups and by utilizing *a posteriori* aggregation, our model estimates of oceanic and reef contribution are mathematically identical to model scenarios which include multiple oceanic and reef source values interspersed within each set of bounds. This mixing model approach is an appropriate method for characterizing uncertainty in our study system, which involves consumers (zooplanktivorous reef fish) that feed on multiple sources (zooplankton types). The food sources utilized by fish in this study span a range of $\delta^{13}C$ values but have similar elemental composition, unlike applications involving, for example, a mixture of plant and animal food sources where the discrepancy in elemental composition among food sources necessitates the use of concentration-dependant models (Phillips & Koch 2002).

Statistical analyses

Welch's ANOVA was used to analyze the effect of reef habitat on the percent contribution of oceanic and reef zooplankton groups to the diet of *D. flavicaudus*. Welch's ANOVA (Welch 1951) is a variance-weighted one-way test and was chosen because it is robust to heterogeneous variances among groups (here the three reef habitats). The relationship between carbon and nitrogen isotope ratios measured in fish muscle tissue was examined using Spearman's rank correlation (Hollander & Wolfe 1973). This correlation method does not assume that the data come from a bivariate normal distribution.

RESULTS:

Quantifying fish diet using gut content analysis

The 50 fish guts sampled contained an average of 893.9 prey items (± 521.9 SD). This large number of prey items per gut sample allowed robust determinations of the contribution of abundant prey groups that had medians of >40 individuals per gut (Appendicularia, Corycaeidae, Oncaeidae, Calanoida, fish eggs) (Appendix 2E: Table 2E.1). The large number of prey items per fish also increased the likelihood of sampling rare prey groups with median abundances of fewer than ten individuals per gut sample (Harpacticoida, other Copepoda, Oithonidae, Decapoda, Ostracoda, Cladocera, coral larvae). The thirteen zooplankton prey groups identified fell into three main categories: crustaceans (copepods, ostracods and cladocerans), appendicularians, and meroplankton (eggs and larvae) (Figure 2.4). Crustaceans dominated fish gut contents, with a median 70 % contribution to total prey items. The copepod groups Calanoida, Corycaeidae, and Oncaeidae comprised the majority of this prey category (median = 88 % of total crustacean component). The median contributions of appendicularians and meroplankton to total prey items were 15.4 % and 8.6 %, respectively.

The percent contribution of oceanic and reef indicator taxa to total gut contents varied as a function of reef habitat (Figure 2.5). For all three oceanic indicator taxa, average percent contributions to fish diet were similar in the forereef and backreef habitats and dropped substantially in gut content samples from fringing reef fish. The average percent contribution of the copepods Oncaeidae varied significantly with reef habitat (Figure 2.5a, Welch's ANOVA, $F_{2, 30.48} = 15.50$, $p < 0.001$). The average percent contributions of Oncaeidae to samples from the forereef (33.3 %) and backreef (32.9 %) were three times larger than the average contribution of this group to fringing reef guts (10.7 %). Similarly, the average contribution of the copepods Corycaeidae to forereef (16.4 %) and backreef (21.7 %) samples were more than two-fold greater than the average contribution of this group to fringing reef samples (7.9 %) (Figure 2.5b,Welch's ANOVA, $F_{2, 23.5} = 12.40$, $p < 0.001$). The third oceanic indicator taxon, the copepod family Oithonidae, was rare in gut content samples from the forereef and backreef habitats where average contributions were < 0.1 % of total prey items. Oithonidae were not found in any fringing reef gut samples (Appendix 2E: Table 2E.1, Figure 2.5c).

Among the three reef indicator taxa, fish eggs comprised substantial proportions of fish gut contents while cladocerans and benthic harpacticoid copepods were absent from many samples and found in low numbers when present. The percent contribution of fish eggs to total prey items varied independently of reef habitat, comprising averages of 10.1 %, 12.5 % and 15.7 % of gut contents in forereef, backreef and fringing reef samples, respectively (Figure 2.5d, Welch's ANOVA,$F_{2, 21.76} = 0.99$, $p = 0.387$). Cladocerans were absent from forereef gut samples and found in only one of 13 fringing reef guts but comprised an average of 1.4 % of the gut contents in backreef fish (Appendix 2E: Table 2E.1, Figure 2.5e). Benthic Harpacticoida were more common in backreef and fringing reef samples than forereef samples but were rare (average contribution < 2.5 %) in samples from all habitats (Appendix 2E: Table 2E.1, Figure 2.5f).

Two prominent prey groups, calanoid copepods and appendicularians, were considered 'mixed-origin' as their cross-shore patterns of abundance did not unambiguously support assignment as either oceanic or reef indicator taxa. The average contribution of appendicularians to fish gut contents varied significantly among habitats (Figure 2.6a, Welch's ANOVA, $F_{2, 18.25} = 14.59$, $p < 0.001$) and was highest in samples from the fringing reef (53.7 %) and lowest in backreef samples (14.3 %). The average contribution of calanoid copepods to fish gut contents decreased onshore from the forereef (13.2 %) to the backreef (8.0 %) and fringing reef (5.8 %) though the effect of reef habitat was not significant at the chosen level of $\alpha = 0.05$ (Figure 2.6b, Welch's ANOVA, $F_{2, 21.22} = 3.27$, $p = 0.058$).

The shoreward decrease in the percent contribution of individual oceanic indicator taxa to total prey items translated to a shoreward decrease in the contribution of summed oceanic taxa to calculated total prey biomass (as μg C, Figure 2.7a). The average contribution of oceanic taxa to total prey biomass was three times higher on the forereef (36.8 %) and backreef (37.3 %) than on the fringing reef (10.2 %) (Figure 2.7a,Welch's ANOVA, $F_{2, 29.15} = 23.10$, $p < 0.001$). The average contribution of summed reef taxa was lowest on the forereef (24.6 %) and highest on the fringing reef (39.9 %) but the effect of reef habitat was not significant (Figure 2.7b, Welch's ANOVA, $F_{2, 20.25} = 2.45$, $p = 0.112$). The average 'undetermined' portion of prey biomass (comprised of mixed origin taxa) varied significantly among reef habitats (Figure 2.7c, Welch's ANOVA, $F_{2, 17.31} = 7.72$, $p = 0.005$), accounting for half (49.9 %) of the prey biomass in fringing reef samples, 38.6 % of prey biomass in forereef samples and 26.9 % of biomass in backreef samples. Because large proportions of prey biomass were of undetermined origin, the average contribution of both summed oceanic and summed reef taxa are minimum estimates of the importance of these food sources to the diet of *D. flavicaudus*. The contribution of oceanic zooplankton to total prey items dominated that of reef zooplankton in samples from forereef and backreef habitats but the two contributions were on the whole equivalent in fringing reef samples (Figure 2.8 a). When considered in terms of prey biomass, ratios of oceanic to reef zooplankton in forereef and backreef samples have median values near 1 while reef zooplankton dominate fringing reef samples (Figure 2.8b).

Habitat-dependent stable isotope ratios in Dascyllus flavicaudus

Dascyllus flavicaudus sampled from the forereef habitat had muscle tissue carbon isotope ratios ($\delta^{13}C$ ‰) that were distinct from and depleted in ^{13}C relative to those of backreef and fringing reef fish. This pattern of depleted carbon isotope ratios in offshore (forereef) fish compared to nearshore (back and fringing reef) fish was consistent across three years of sampling (Figure 2.9) and spatially consistent at two sampling scales: among reef locations sampled around the island's ~ 60 km perimeter (Figure 2.10a) as well among locations spanning ~ 12 km on the island's north shore (Figure 2.10b).

The most enriched carbon isotope ratios measured were associated with fringing reef fish. In the time series measurements as well as in some sampling locations (LTER sites 1, 2 and 5; north shore sites 7, 8 and 9) isotope ratios measured in fringing reef fish were distinctly enriched relative to backreef fish (Figs. 2.9, 2.10). However, this pattern was reversed at some locations (LTER site 4; north shore sites 3 and 6) and at other locations there was no clear distinction between backreef and fringing reef fish (north shore sites 4, 5). Carbon isotope ratios measured from fringing reef fish ranged 3.69 ‰ (-16.24 ‰ to -12.55 ‰) across the three datasets (island-scale, north shore and time series). Backreef fish exhibited a similar 3.3 ‰ range in carbon isotope ratios (-16.64 ‰ to -13.34). Isotope ratios measured in forereef fish were constrained to a 1.12 ‰ range (-16.84 ‰ to -15.72) across the datasets. We combined these three datasets to examine the overall effect of reef habitat on fish $\delta^{13}C$ by calculating average values for fish at each time point and collection location, yielding 19 average values for the both the forereef and the backreef habitats and 16 for the fringing reef (Figure 2.11). A one-way ANOVA on these averages highlights the significant dependence of fish muscle $\delta^{13}C$ on reef habitat (Welch's ANOVA, $F_{2, 26.3} = 93.55$, $p < 0.001$).

The nitrogen isotope ratios measured in fish muscle tissue were not consistent through time (Figure 2.12). Fish collected in all three habitats in 2009 had muscle $\delta^{15}N$

values that were ~2 ‰ higher than values measured in fish collected between December 2006 and March 2008. In contrast to carbon isotope ratios, there were no clear patterns in nitrogen isotope ratios among reef habitats that were consistent at either the island-wide (Figure 2.13a) or North shore (Figure 2.13b) spatial sampling scales. However, within the island-wide samples (collected in austral summer 2007), isotope ratios were distinct among the three reef habitats at certain locations (LTER sites 4, 5 and 6). In these locations, muscle tissue from forereef fish was enriched in ^{15}N relative to muscle tissue collected from fish inhabiting the back and fringing reefs. Isotope ratios from three north shore sampling locations (sites 7, 8 and 9 sampled in austral summer 2009) displayed the same trend of offshore enrichment in ^{15}N.

There was a significant negative correlation between fish muscle tissue carbon and nitrogen isotope ratios within samples collected during Austral summer 2007 (Figure 2.14a, Spearman's rho = -0.35, d.f = 87, $p < 0.001$) and within samples from summer 2009 (Figure 2.14d, Spearman's rho = -0.67, d.f. =121, $p < 0.001$). Fish muscle $\delta^{15}N$ values spanned 2.26 ‰ in summer 2007 and 3.01 ‰ in summer 2009. The summer 2007 dataset corresponds to the island-wide sampling (Figure 2.13a) and the summer 2009 dataset to the north shore sampling (Figure 2.13b). Fish muscle tissue carbon and nitrogen isotope ratios were not significantly correlated within the two remaining sampling periods: winter 2007 (Figure 2.14b, Spearman's rho = 0.27, d.f. = 21, p = 0.291) and summer 2008 (Figure 2.14c, Spearman's rho = -0.18, d.f. = 25, p = 0.374). These two time periods represent fish samples collected from one location (LTER site 1).

Habitat-dependent stable isotope ratios in a suite of planktivorous fishes

The pattern of offshore depletion in fish muscle tissue $\delta^{13}C$ measured in *D. flavicaudus* was paralleled in eight other diurnal planktivorous fish species. Of the eight species only two, *Chromis iomelas* and *C. margaritifer*, are common to all three reef habitats. In both species, individuals collected from the forereef had muscle $\delta^{13}C$ values with magnitudes and a range (-16.99 ‰ to -16.4 ‰) similar to those of *D. flavicaudus* sampled from the forereef (Figure 2.15). Muscle samples from backreef and fringing reef fish were distinctly enriched relative to forereef individuals, and again the range of values in the two *Chromis* species (-16.09 ‰ to -13.72 ‰) mirrored the magnitude and range of *D. flavicaudus* sampled from nearshore habitats. Muscle $\delta^{15}N$ sampled in *C. margaritifer* and *C. iomelas* ranged from 8.27 ‰ to 10.47 ‰, consistent with the magnitude and range of values measured in *D. flavicaudus* samples collected during the same time period (summer 2008). Carbon and nitrogen isotope ratios were not correlated within samples from *C. iomeals* (Figure 2.15a, Spearman's rho = 0.20, d.f. = 19, p = 0.409) but exhibited a significant, positive correlation in *C. margaritifer* (Figure 2.15b, Spearman's rho = 0.50, d.f. = 18 , p = 0.028).

Taking the data from all nine planktivore species together, fish sampled from the forereef across multiple species were distinctly depleted in ^{13}C relative to back and fringing reef fish, with $\delta^{13}C$ values of ~ 15.8 ‰ demarking the transition between offshore and nearshore individuals (Figure 2.16). Pooling data across all nine species, carbon and nitrogen isotope ratios were not significantly correlated (Spearman's rho = -0.18, d.f. = 120, p = 0.052).

Isotope mass balance model of fish diet

Carbon isotope ratios sampled from individual zooplankton taxa, bulk zooplankton samples, and bulk fish gut contents informed the selection of four end-members used with the IsoSource mass-balance model. These end-members bound the lower and upper range of δ^{13}C values for oceanic zooplankton (-20.9 ‰ to -18.35 ‰) and for reef zooplankton (-17.55 ‰ to -14.98 ‰) (Figure 2.17). The offsets between isotope ratios measured in gut contents and those in muscle tissue (*D. flavicaudus,* n = 93 fish) provide evidence of trophic enrichment in both δ^{13}C and δ^{15}N in fish muscle relative to zooplankton prey (gut contents) (Figure 2.18a). The average (± 95 % CI) offset in δ^{13}C between gut contents and muscle tissue (both sampled from the same individual fish) was 2.35 ‰ ± 0.15 ‰ and the average difference in δ^{15}N was 3.45 ‰ ± 0.11 ‰ (Figure 2.18b). Based on these data, we chose a carbon trophic enrichment factor of 2 ‰ and adjusted fish muscle tissue δ^{13}C values by this factor before running the mass balance model.

The IsoSource model and subsequent *a posteriori* aggregation of sources yielded a distribution of feasible solutions for each fish muscle δ^{13}C value modeled (stepping in increments of 0.1 ‰ from -16.8 ‰ to -12.8 ‰) (Figure 2.19). The range (5th to 95th percentile) of feasible solutions for the percent contribution of oceanic sources varied across modeled fish values. Modeled solutions were highly constrained for the most enriched fish values and reached a minimum of 0 % oceanic contribution at fish muscle values of 12.9 ‰. For fish values of -16 ‰ and lower, the minimum feasible contribution of oceanic food sources exceeded 50 %. The largest feasible contribution of oceanic food sources (90% of fish diet) was associated with a fish muscle $\delta^{13}C$ value of -16.8 ‰.

Solutions for depleted muscle $\delta^{13}C$ values were less constrained than solutions for the enriched fish values, though were still limited to a range of ~ 20 % contribution.

We generated percent contribution solutions for the 50 fish used in the gut content analysis. The modeled percent contributions of both oceanic and reef sources to the diet of forereef fish were substantially higher and more constrained than estimates based on gut contents (Figure 2.20 a, d). The minimum and maximum modeled solutions for oceanic groups in the diet of backreef fish fell within the range of proportional contributions estimated from gut contents (Figure 2.20b), but the modeled solutions for reef food sources exceeded the gut content estimates (Figure 2.20 e). The modeled solutions for fringing reef fish exhibited a dominance of reef over oceanic zooplankton that mirrored the gut content estimates (Figure 2.20 c, f). The modeled minimum and maximum feasible contributions of oceanic zooplankton to fringing reef fish diet were similar to estimates from gut content analysis, but the modeled solutions for the contributions of reef food sources to fish diet were larger than the gut content estimates. The discrepancy between modeled solutions and gut content estimates for forereef and fringing reef fish was not surprising given the large proportion of mixed-origin prey in the guts of fish in these habitats (Figure 2.5, 2.6c). We re-calculated fish diet composition from prey biomass under the assumptions that (a) 100 % of the mixed-origin prey biomass in the guts of forereef fish was oceanic in origin, (b) 50% of the mixed-origin biomass in backreef guts was oceanic in origin and 50 % reef associated, and (c) 100 % of the mixed origin prey biomass in fringing reef guts was reef associated. Correcting the prey biomass calculations using these assumptions aligned diet source estimates from gut contents analysis with those from the mass balance isotope model (Figure 2.21). With the corrected calculations, the mean percent contribution calculated using prey biomass fell between mean values based on minimum and maximum modeled solutions for three estimates: the contribution of oceanic zooplankton to the diet of forereef fish (Figure 2.21a, biomass = 75 %, model min. = 62 %, model max. = 88 %), the contribution of oceanic zooplankton to the diet of backreef fish (Figure 2.21b, biomass = 51%, model min. = 43 %, model max. = 66%), and the contribution of reef zooplankton to the diet of fringing reef fish (Figure 2.21f, biomass = 90 %, model min. = 85 %, model max. = 95 %). For the remaining three estimates, the mean percent contribution based on corrected prey biomass slightly fell slightly below mean contributions based on modeled values: the contribution of reef zooplankton to the diet of forereef fish (Figure 2.21d, biomass = 25 %, model min. = 37 %, model max. = 61 %), the contribution of reef zooplankton to the diet of backreef fish (Figure 2.21 e, biomass = 49 %, model min. = 57 %, model max. = 81 %), and the contribution of oceanic zooplankton to the diet of fringing reef fish (Figure 2.21 f, biomass = 10 %, model min. = 15 %, model max = 25 %).

Having established that the IsoSource mass balance model solutions bounded (forereef and backreef) or were similar to (fringing reef) estimates based on prey biomass, we used the IsoSource mass balance model to solve for the percent contribution of oceanic zooplankton to the diet of all 289 *D. flavicaudus* individuals sampled (Figure 2.22). Using the mass balance model, we calculated the average contribution of oceanic zooplankton to the diet of forereef, backreef and fringing reef fish based on both minimum and maximum feasible solutions. Oceanic zooplankton comprise an average of 60 % - 86 % of the diet of forereef fish (Figure 2.22 a,b). Oceanic food sources comprise an average of one-third to approximately half of the diet of backreef (34 % - 55 %) and fringing reef (26 % - 42 %) fish (Figure 2.22, c-f).

DISCUSSION:

Combining gut content analysis and stable isotope analysis, this study provides a spatially explicit view of the relative importance of allocthonous (imported) versus autocthonous (local) food sources to secondary production in planktivorous reef fish. Oceanic zooplankton contribute substantially to the diet of planktivores in all three of Moorea's reef habitats, and the relative importance of oceanic- versus reef-associated food sources in fish diet is habitat-dependent. A mass balance isotope model provided minimum and maximum feasible values for the contribution of oceanic and reef resources to fish diet. Median values for the minimum feasible contribution of oceanic resources of the diet of 289 sampled *Dascyllus flavicaudus* ranged from 60 % for fish collected from the forereef to 33 % for backreef fish and 27 % for fringing reef fish.

The comparison of two independent metrics of fish diet for a subset (n = 50) of the total sampled *Dascyllus flavicaudus* showed broad agreement between estimates of reef and oceanic contributions to fish diet based on prey biomass and those resulting from the mass-balance model of fish tissue carbon isotope ratios. The analysis of fish gut contents allowed identification of the specific zooplankton taxa that represented both oceanic and reef contributions to fish diet. Stable isotope analysis provided an independent metric of fish diet and the expanded sampling confirmed that the cross-shore gradient in oceanic contributions to fish diet is stable through time, coherent at ecologically relevant spatial scales, and consistent across a suite of planktivorous fish species. The isotope mixing model approach used to assess oceanic versus reef-associated contributions to fish diet constrains the feasible contribution of both prey categories. This type of 'min-max' mixing model approach (Phillips & Gregg 2003) is appropriate for our application involving consumers that feed on a variety of prey types spanning a continuum of carbon isotope ratios. Though the food sources and corresponding mixing model endpoints in our system span a range of carbon isotope ratios of only 5 ‰, the use of *a posteriori* aggregation of sources (Phillips et al. 2005) and the distinct spatial patterns within sampled fishes result in source contribution estimates that are sufficiently constrained to be ecologically informative.

Previous studies of zooplankton assemblages surrounding the island of Moorea (Lefevre 1986, Renon 1989) identified specific copepod groups that were abundant in oceanic waters but largely absent from the reef lagoon. These groups can, therefore, be considered oceanic in origin rather than residents of or reproducing within the reef system. The relative abundance of oceanic indicator taxa in fish gut contents decreased from offshore samples collected on the forereef to nearshore samples collected on the fringing reef. Two of the oceanic copepods groups, the families Oncaeidae and Corycaeidae, were found in all *D. flavicaudus* guts sampled in this study and together comprised up to 80 % of zooplankton prey biomass in the guts of forereef fish. These copepod groups account for the majority of oceanic contributions to fish diet in all three reef habitats. While these copepod families are common to coral reef ecosystems, strong cross-shore gradients in abundance and thus the utility of these families or genera therein as oceanic indicator taxa do not appear to be broadly consistent among reefs (Johnson 1954, Leis 1982, Binet 1984, Williams et al. 1988). Local knowledge of the cross-shore distribution of zooplankton groups is required before appropriate taxa can be selected as oceanic indicators in a given setting. The reef-indicator zooplankton prey utilized by *D. flavicaudus* were a mixture of meroplankton (fish eggs, decapod and coral larvae) as well as benthic (or hyperbenthic, Carleton & Hamner 2007) harpacticoid copepods. These groups are inherently tied to the reef, and will function as reef-indicator taxa in other systems.

Based on the depleted carbon isotope ratios ($\delta^{13}C$) of primary producers supporting oceanic zooplankton and the generally enriched $\delta^{13}C$ of the benthic algae that dominate primary production within the reef system, we predicted that a shoreward decrease in the relative importance of oceanic zooplankton in fish diet might manifest as a nearshore enrichment in the $\delta^{13}C$ of muscle tissue sampled from planktivorous fishes. This prediction was generally supported- muscle tissue samples from fish collected on the forereef were consistently depleted in ^{13}C (by 1 ‰ to 2 ‰) relative to muscle tissue sampled from fish inhabiting the shallow back and fringing reefs with little overlap in $\delta^{13}C$ values between offshore and nearshore individuals. Across the suite of eight planktivorous fish species sampled, 95 % of the 137 individuals sampled from the forereef had muscle tissue $\delta^{13}C$ values less than -16 ‰. In contrast, only 6 % of the 273 individuals sampled from backreef and fringing reefs had muscle tissue $\delta^{13}C$ values less than -16 ‰. Planktivorous fish inhabiting the forereef are characterized by depleted muscle tissue C isotope ratios relative to fish inhabiting nearshore reefs, reflecting the larger percent contribution of oceanic resources to the diet of forereef fish.

The current study significantly expands the available data on C and N stable isotope ratios measured from planktivorous coral reef fishes (Fry et al. 1982, Mill 2007, Carassou et al. 2008, Frederich et al. 2009, Greenwood et al. 2010, Wyatt et al. 2010). The $\delta^{13}C$ and $\delta^{15}N$ data for *Dascyllus flavicaudus* quantify isotopic variability among individuals collected within a sampling location (< 50 m^2 reef) as well as within and between reef habitats with replicate sampling at the whole-island scale. The result is a multi-scale perspective of fish diet and diet variability – a perspective unattainable from existing datasets on reef planktivores which are limited to sample sizes of < 20 individuals per species and while they may include several sampling locations, do not include replication among reef habitats (Fry et al. 1982, Carassou et al. 2008, Frederich et al. 2009, Greenwood et al. 2010, Wyatt et al. 2010). The previous isotopic studies of planktivorous coral reef fishes provide data on isotope trophic discrimination factors (Wyatt et al. 2010), size-based changes in diet (Mill 2007, Greenwood et al. 2010), and resource partitioning among fish species (Mill 2007, Carassou et al. 2008, Frederich et al. 2009). Though predictable cross-shore gradients in zooplankton abundance and species composition have been documented for many coral reefs (Glynn 1973, Renon 1979, Leis 1982, Hamner et al. 1988, Williams et al. 1988), the present study is the first to assess habitat dependence in the diet of reef planktivores and to employ stable isotopes to assess the contribution of pelagic/oceanic versus benthic/reef food sources to secondary production in reef fishes.

The magnitude and range of δ^{13}C values measured in zooplanktivorous fishes from Moorea (- 17.58 ‰ to – 11.86 ‰) are similar to those sampled from planktivorous fishes on other coral reef locations: Western Australia (δ^{13}C ~ -18 ‰ to -14 ‰, Wyatt et al. 2010); Solomon Islands (δ^{13}C ~ -18 ‰ to -14 ‰, Greenwood et al. 2010); New Caledonia (δ^{13}C ~ -18 ‰ to -12 ‰, Carassou et al. 2008); Madagascar (δ^{13}C ~ -19 ‰ to -11 ‰, Frederich et al. 2009), and the Gulf of Oman (δ^{13}C ~ -19.5 ‰ to -15 ‰, Mill 2007). Similarly the δ^{13}C values measured in ocean-associated zooplankton samples in this study (- 20.9 ‰ to -18.35 ‰) mirrored pelagic zooplankton carbon isotope ratios from other coral reef locations (δ^{13}C ~ -20 ‰ to -18 ‰) (Carassou et al. 2008, Frederich et al. 2009) including the Gulf of Oman (δ^{13}C ~ -22 ‰ to -17 ‰) where seasonal upwelling was hypothesized to drive periodic enrichment δ^{13}C of phyto- and zooplankton (Mill 2007). These similarities suggest that, in general, secondary production in planktivorous fishes on coral reefs are supported by a combination of oceanic and reef-associated carbon sources. The sampling approach taken in the present study could be used to elucidate variation in the relative importance of allocthonous versus autocthonous food sources among fish species and habitats in spanning geographically and geomorphologically diverse coral reef settings.

Nitrogen stable isotope ratios (δ^{15}N) measured in a consumer's tissues are influenced by the organism's trophic level (Minagawa & Wada 1984) and by the ratio of ^{15}N:^{14}N in the diet (Deniro & Epstein 1981). The present measurements of isotope ratios in the muscle tissue of planktivorous fishes document variability in δ^{15}N both within and among species. However, within a given sampling period, variation in δ^{15}N was < 3 ‰ among conspecifics and < 4 ‰ across the eight fish species sampled. The magnitude of this variation in $\delta^{15}N$ is smaller than the expected isotopic enrichment between successive trophic levels based on both the average N trophic fractionation sampled from a range of aquatic species (3.4 ‰, Vander Zanden & Rasmussen 2001) and on the average difference in $\delta^{15}N$ between fish gut contents and muscle tissue (3.45 ‰) measured in this study. While $\delta^{15}N$ and $\delta^{13}C$ were correlated within certain sampling locations and sampling periods, overall the cross-shore patterns in $\delta^{13}C$ measured in fish muscle tissue were not associated with corresponding shifts in $\delta^{15}N$. Thus, there is no evidence that the offshore depletion/ onshore enrichment of fish tissue carbon isotope ratios is associated with changes in the sampled fishes' trophic level across the three reef habitats.

Our measurements of fish tissue isotope ratios come from samples collected across a three-year period (December 2006 – March 2009). The magnitude and variability of $\delta^{15}N$ measured in muscle from *Dascyllus flavicaudus* was stable across the first three sampling periods (Austral summer 2007, winter 2007 and summer 2008) but $\delta^{15}N$ measured in fish from all three reef habitats increased by ~ 2 ‰ in March 2009. This temporal variation in fish $\delta^{15}N$ values likely reflects regional-scale changes in the nitrogen sources supporting zooplankton production.

Seasonal fluctuations in $\delta^{15}N$ of zooplankton of a similar magnitude have been reported in oligotrophic waters in the North Pacific Subtropical Gyre as well as in the Red Sea (Hannides et al. 2009, Aberle et al. 2010). In both studies, $\delta^{15}N$ values from individual copepod species were higher or more enriched during the winter and became depleted during the summer months. In the subtropical North Pacific (Station

ALOHA, 22.45°N, 158 °W), the average difference between summer and winter $\delta^{15}N$ was 2.4 ‰ for mixed zooplankton (1-2 mm size fraction) and up to 5.6 ‰ for certain copepod groups (Hannides et al. 2009). Concurrent isotope analysis on individual amino acids confirmed that these seasonal shifts in bulk $\delta^{15}N$ were not related to a change in the trophic position of the zooplankton (Hannides et al. 2009). In both the North Pacific and South Pacific, temporal (Dore et al. 2002) and spatial (Saino & Hattori 1987, Raimbault et al. 2008) changes in the nitrogen isotope ratios of particulate organic matter reflect fluctuations in the contribution of deep-water NO_3^- ($\delta^{15}N$ = 5 - 6 ‰ in the central Pacific, Cline & Kaplan 1975) versus biologically-fixed N_2 ($\delta^{15}N$ = 0 ‰) to biological production. The temporal changes in $\delta^{15}N$ that we measured in *D. flavicaudus* may have been driven by similar changes in nitrogen sources supporting secondary production within the South Pacific Gyre. However, the oceanographic mechanisms controlling nitrogen sources at the base of pelagic food webs in the central South Pacific Ocean are likely different than those operating in the subtropical North Pacific and the Red Sea (Moutin et al. 2008).

Aspects of Moorea's landscape likely influence cross-ecosystem trophic exchange. Archipelagos such as the Society Islands and Tuamotu Islands span gradients of geomorphologies ranging from high volcanic islands to low-lying atolls. Across these gradients, the residence time of waters within reef lagoons ranges from as short as a few hours to an extreme of multiple years (Delesalle & Sournia 1992, Hench et al. 2008). The isolation of the reef lagoon from oceanic waters encourages the establishment and reproduction of resident pelagic zooplankton communities (Carleton & Doherty 1998). Changes in island morphology and lagoon size also influence the structure of reef fish assemblages (Mellin et al. 2006). Thus, coral reef archipelagos offer an opportunity to explore the effect of reef geomorphology on the flux of oceanic energy and nutrients to reef food webs via zooplankton/ planktivore interactions. The relative spatial extent of deep forereef versus lagoon habitat in coral reefs might be analogous to the ratio of habitat edge to interior area in systems such as grasslands or forests. Ratios of habitat perimeter to habitat area are known to determine the magnitude of allocthonous inputs to a variety of terrestrial and marine ecosystems (Forman & Gordon 1986, Turner 1989, Polis et al. 1997). Characteristics of the boundary between the reef lagoon and the open ocean, such as the number and depth of reef passes, are also likely to influence cross-ecosystem exchange. The influence of boundary characteristics on cross-ecosystem exchange as has been demonstrated in other ecosystems (Wiens et al. 1985, Cadenasso et al. 2004).

Planktivorous fishes are abundant and productive components of coral reef ecosystems worldwide. This guild of fishes maintains numerous connections to the larger coral reef food web via pathways involving both predation and excretion. Planktivorous fishes consume oceanic resources in the form of zooplankton prey and thus represent an important pathway by which allocthonous energy and nutrients enter the reef system. As we have documented on the reefs surrounding Moorea, these oceanic resources can fuel a significant proportion of the secondary production of planktivorous fish biomass. Progress toward a landscape-scale understanding of energetic processes in coral reef ecosystems will be enhanced by continued investigation of both zooplankton and planktivorous fishes with specific consideration of the roles of reef geomorphology in mediating habitat connectedness and residence time.

Acknowledgements:

Chapter 2 is in preparation for submission to Ecology and is presented as part of this dissertation with the acknowledgement of the study co-author, James J. Leichter. The dissertation author was the primary investigator and is the primary author of this material.

We thank A. Stier, M. Murray, W. Goldenheim, and J. Padilla-Gamiño for their assistance collecting samples and the staff of the Richard B. Gump South Pacific Research Station for logistical support. We are grateful to T. Bramhill, M. Fuentes, E. Reed, N. Roberts, O. Stens and M. Ryder for their work processing fish tissue samples. Comments from L. Aluwihare, L. Levin and M. Ohman improved the manuscript. A. Hartman contributed unpublished data on coral larvae used in the prey biomass conversions. This research was funded by awards from the NSF Moorea Coral Reef LTER program to J. Leichter, a 3 Seas Teaching Fellowship to K. Hanson, and a PADI grant (KH). The collection of fish for this study was approved by French Polynesian research permits as well as by the UCSD Institutional Animal Care and Use Committee (Protocol # S06369). Stable isotope analysis was performed by the UC Davis Stable Isotope Facility.

Table 2.1. The habitat association of 12 zooplankton prey groups that comprise the diet of the reef fish *D. flavicaudus*. Prey groups are determined to be either oceanic in origin or associated with the reef system based on cross-shore patterns of abundance (Lefevre 1986, Renon 1989). Mixed-origin groups could not be decisively classified as either oceanic or reef on the basis of cross-shore distribution or life history.

Prey Group	**Association**
Oncaeidae	oceanic
Corycaeidae	oceanic
Oithonidae	oceanic
pelagic Harpacticoida	oceanic
Appendicularia	oceanic
Ostracoda	reef
benthic Harpacticoida	reef
Cladocera	reef
coral larvae	reef
Decapoda	reef
Calanoida	mixed-origin
fish eggs	mixed-origin

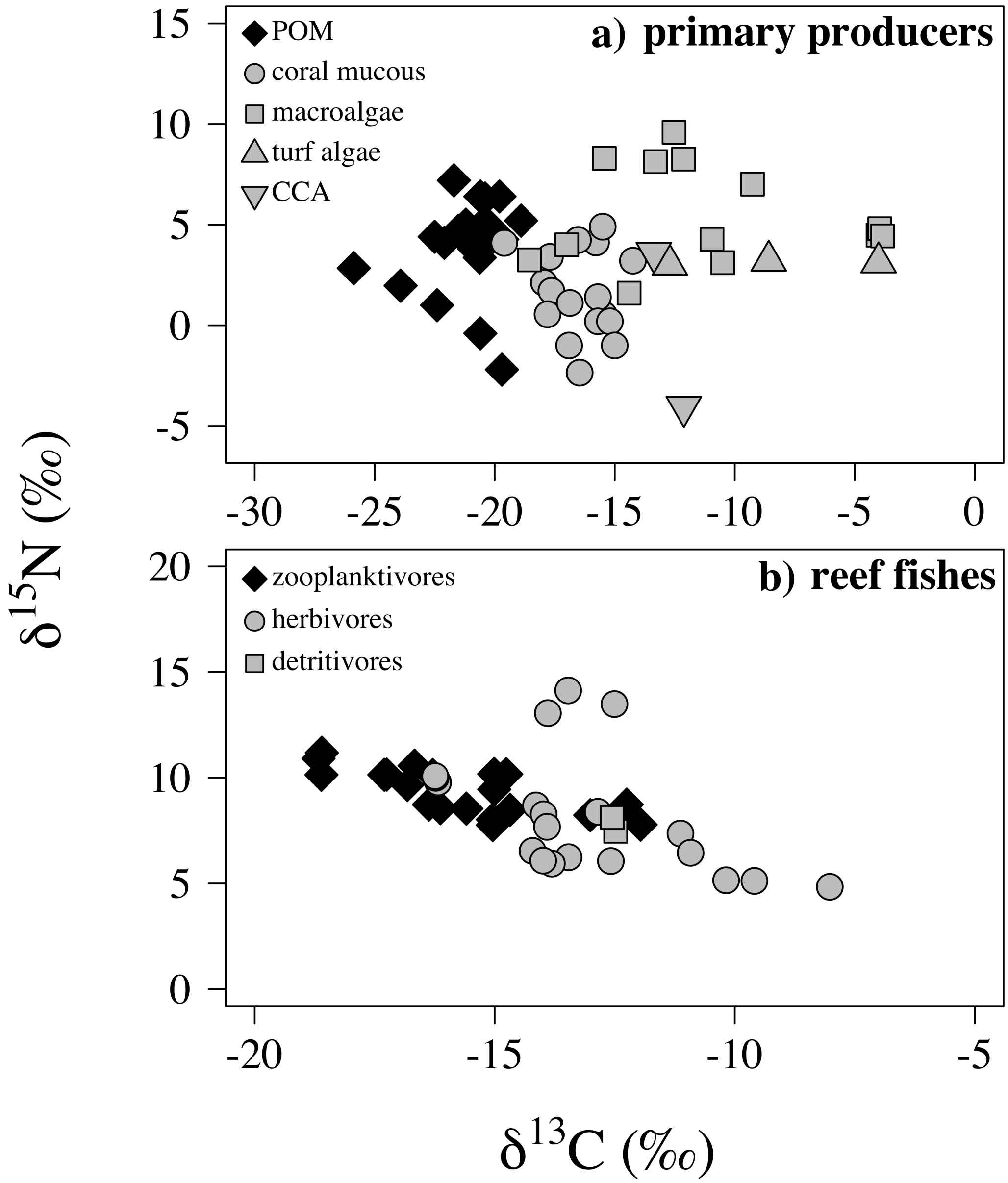

Figure 2.1. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios measured in coral reef organisms. Points represent average values reported in published studies representing a range of geographic locations (see Apppendix 2A). **a)** Samples associated with coral reef primary producers including particulate organic matter (POM) as a phytoplankton proxy as well as crustose coralline algae (CCA) **b)** Samples from three guilds of primary reef consumers (fishes)**.** Measurements from pelagic sources and pelagic-feeding consumers are shown in black with measurements from benthic primary producers and benthic-feeding fishes in grey.

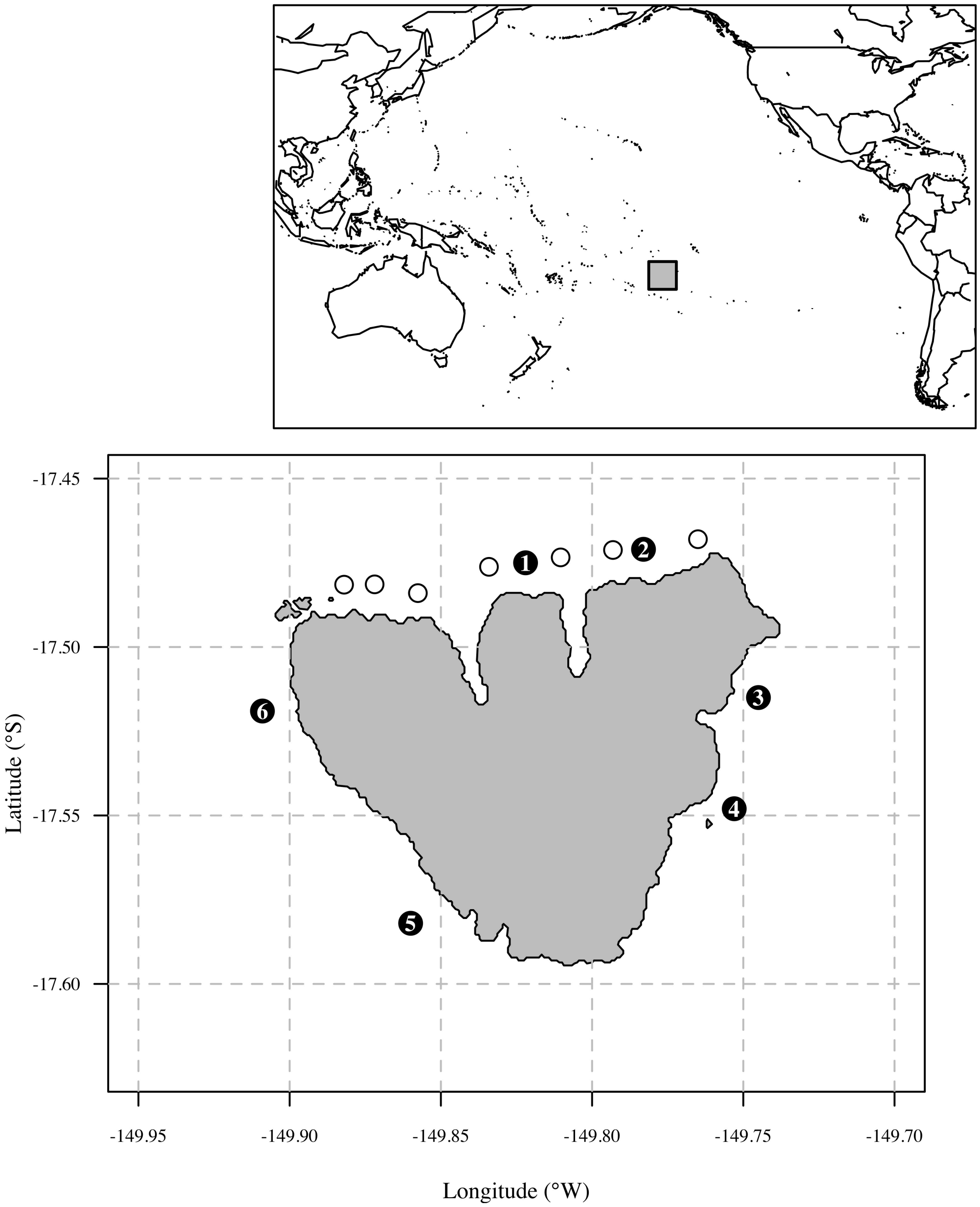

Figure 2.2. Map of the island of Moorea, French Polynesia (bottom panel) and the island's regional location in the South Pacific (top panel). Numbered circles indicate the locations of long-term monitoring stations established by the MCR LTER and used in the present study for island-wide sampling. North shore sampling included LTER sites 1 and 2 as well as seven additional sites (open circles). Sampling for the three-year time series was conducted at LTER site 1.

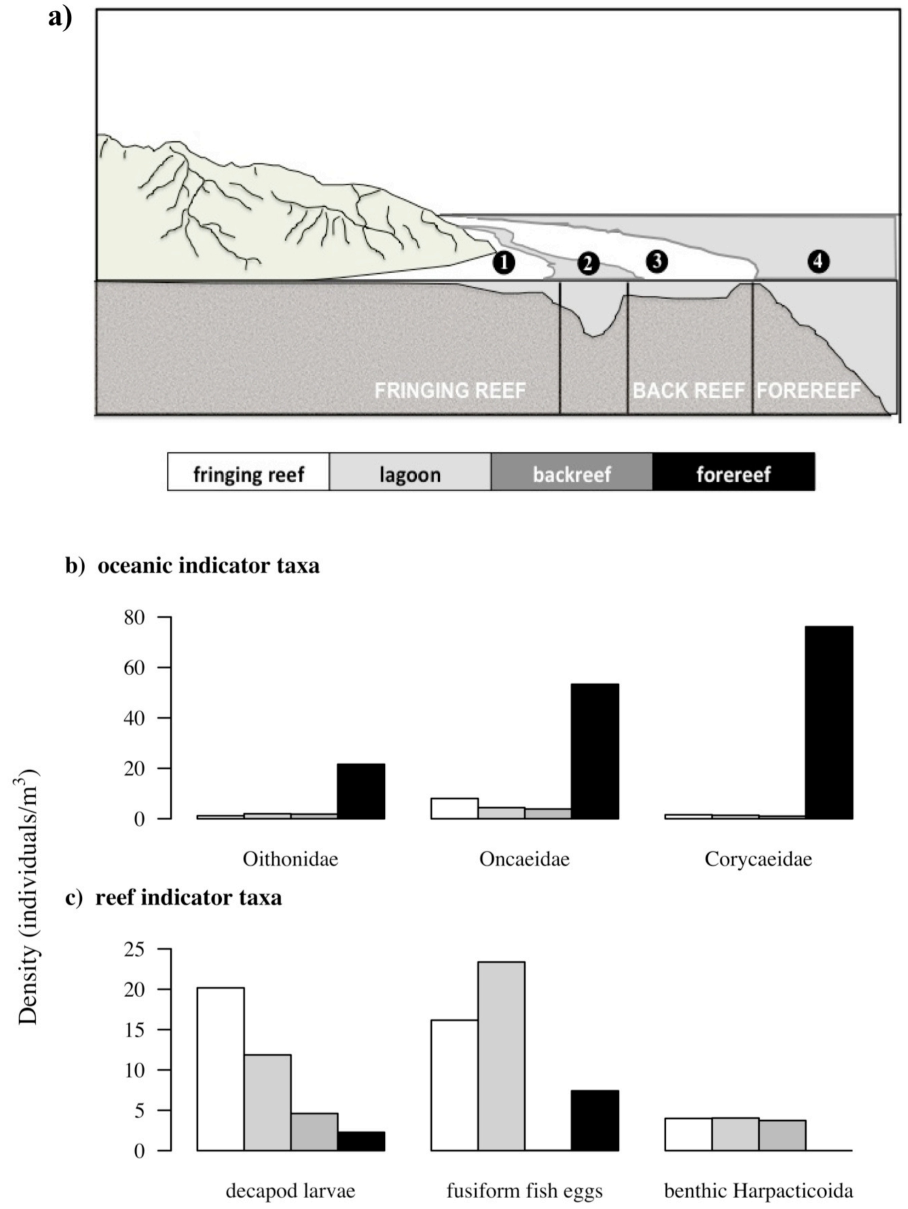

Figure 2.3. a) Schematic of the dominant reef habitats in Moorea. **b – c)** Cross-shore patterns of density for three oceanic indicator zooplankton taxa **(b)** and three reef indicator taxa **(c).** Numbered circles in panel **a** demonstrate the cross-shore position of samples depicted in panels **b** and **c**. Data are mean densities for samples collected from the fringing reef (n = 10), lagoon (n = 14), backreef (n = 7) and an oceanic station 200 m offshore of the reef crest (n = 12). Data are taken from Renon (1989); variance estimates were not included in the original publication.

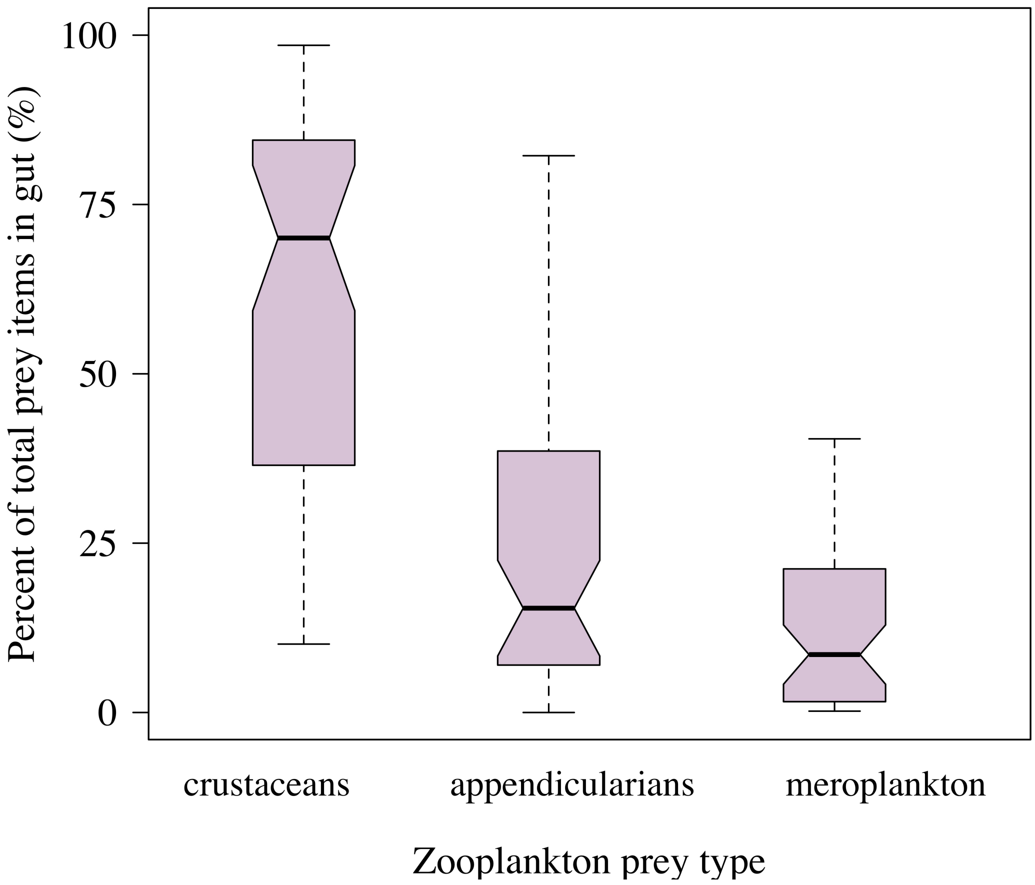

Figure 2.4. Percent contribution of three major zooplankton prey types to total prey items sampled from guts of *D. flavicaudus* (n = 50 fish). Boxes extend from 25th to 75th percentiles; whiskers to 1.5 times the interquartile range. Horizontal bars indicate medians. Notches extend from medians to ± (1.58 • interquartile range • $n^{-0.5}$) and approximate 95% confidence intervals for the difference between medians.

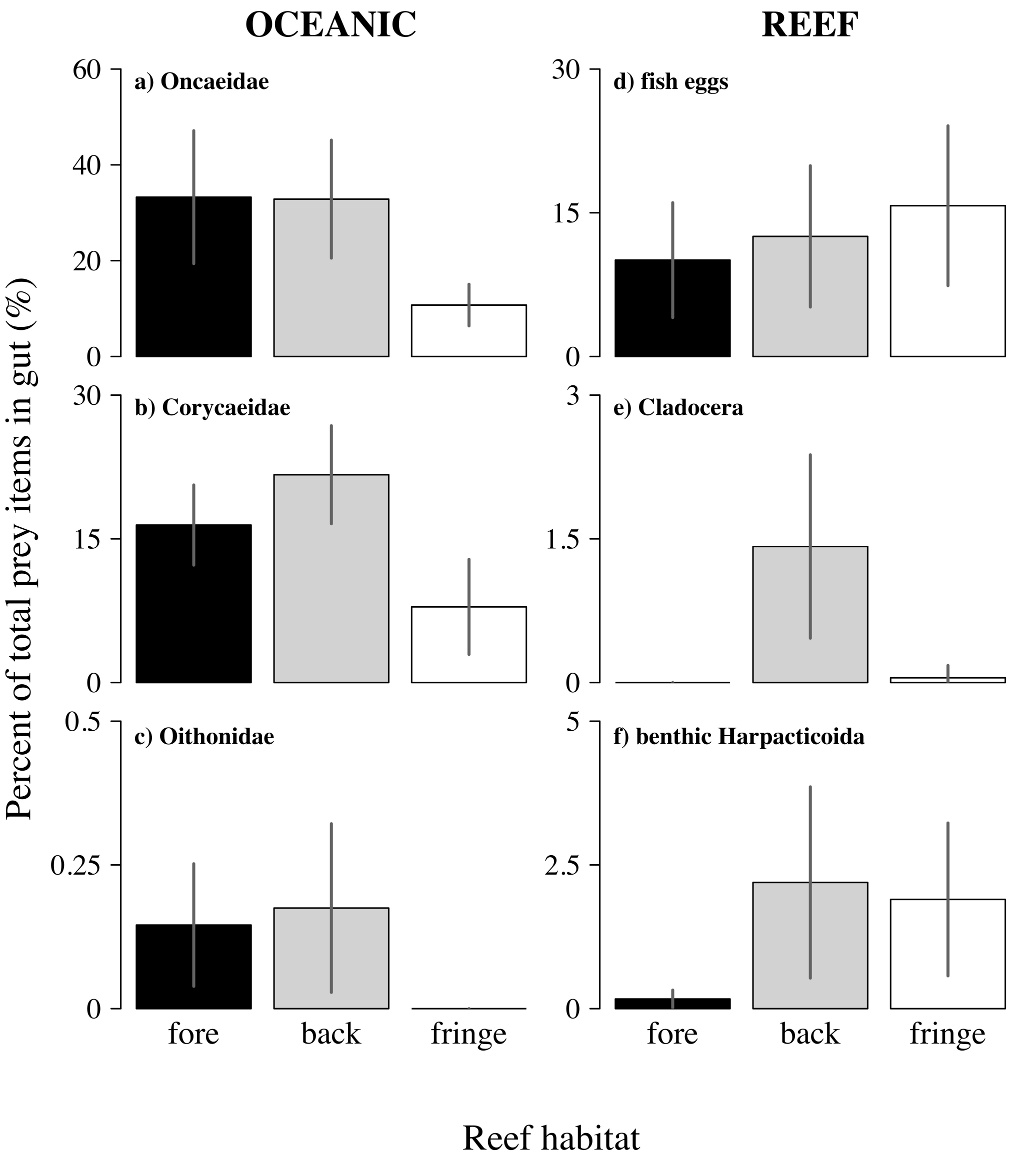

Figure 2.5. The percent contribution of zooplankton prey groups to total gut contents sampled from *D. flavicaudus*. Data are plotted separately for fish sampled from the forereef (in black,n = 22), backreef (grey, n = 20) and fringing reef (white, n = 8). **a-c)** Oceanic indicator taxa. **d-f)** Reef indicator taxa. Bar heights are habitat means, error bars represent 95 % confidence intervals on group means. Note variation in y-axis scale.

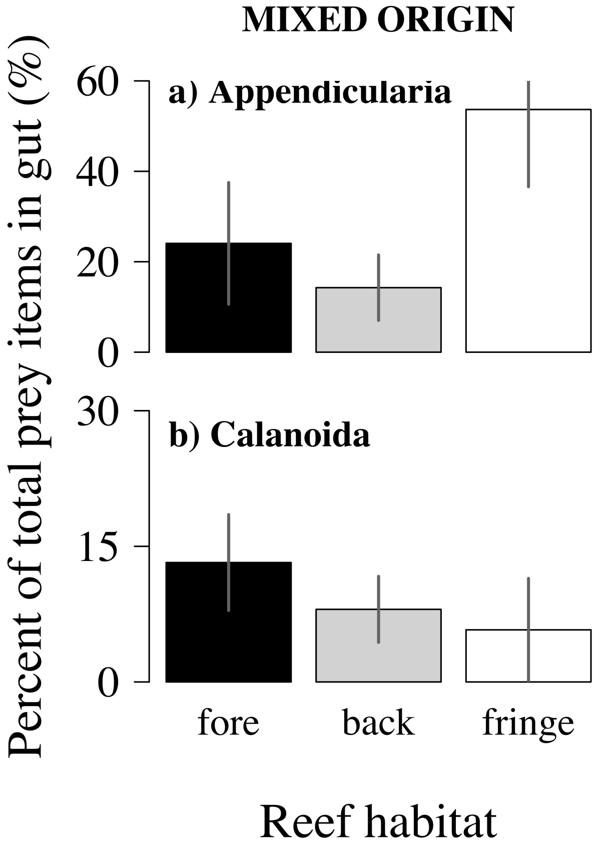

Figure 2.6. The relative contribution of mixed origin zooplankton prey groups to total gut contents sampled from *D. flavicaudus*. Data are plotted separately for fish sampled from the forereef (in black,n = 22), backreef (grey, n = 20) and fringing reef (white, n = 8). **a)** Appendicularia. **b)** Calanoida. Bar heights are habitat means, error bars represent 95 % confidence intervals on group means.

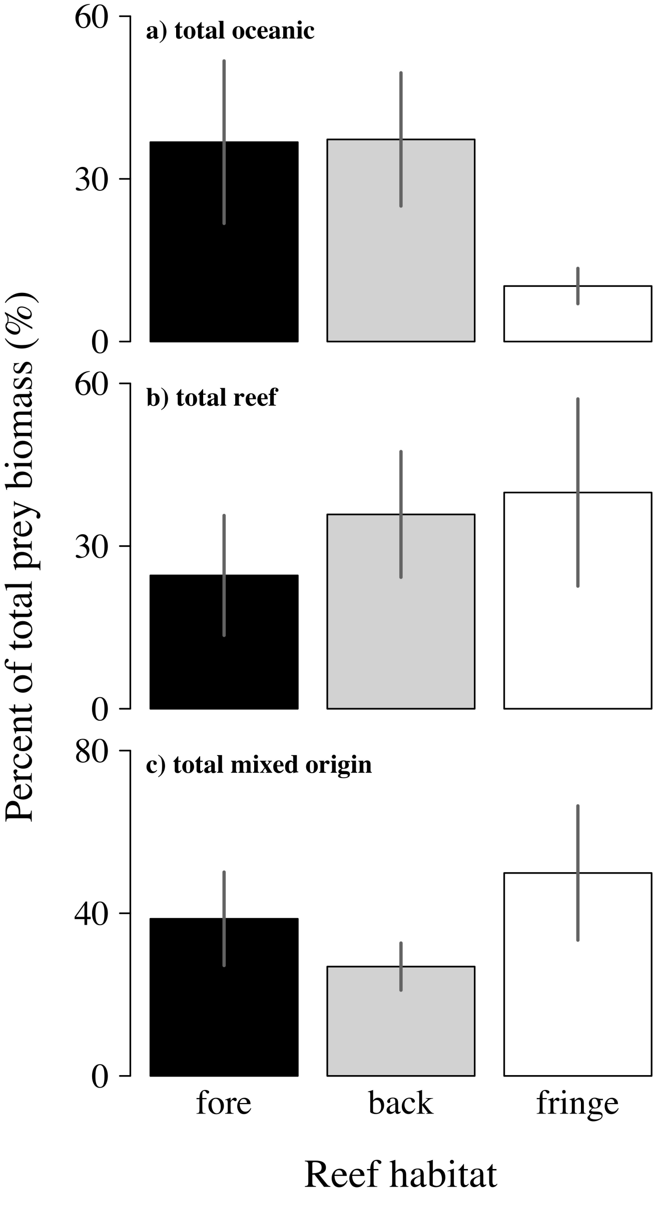

Figure 2.7. The relative contribution of **a)** summed oceanic indicator taxa, **b)** summed reef indicator taxa and **c)** summed mixed origin taxa to the calculated biomass of prey in fish guts. Data are plotted separately for fish sampled from the forereef (in black,n = 22), backreef (grey, n = 20) and fringing reef (white, n = 8). Bar heights are habitat means, error bars represent 95 % confidence intervals on group means.

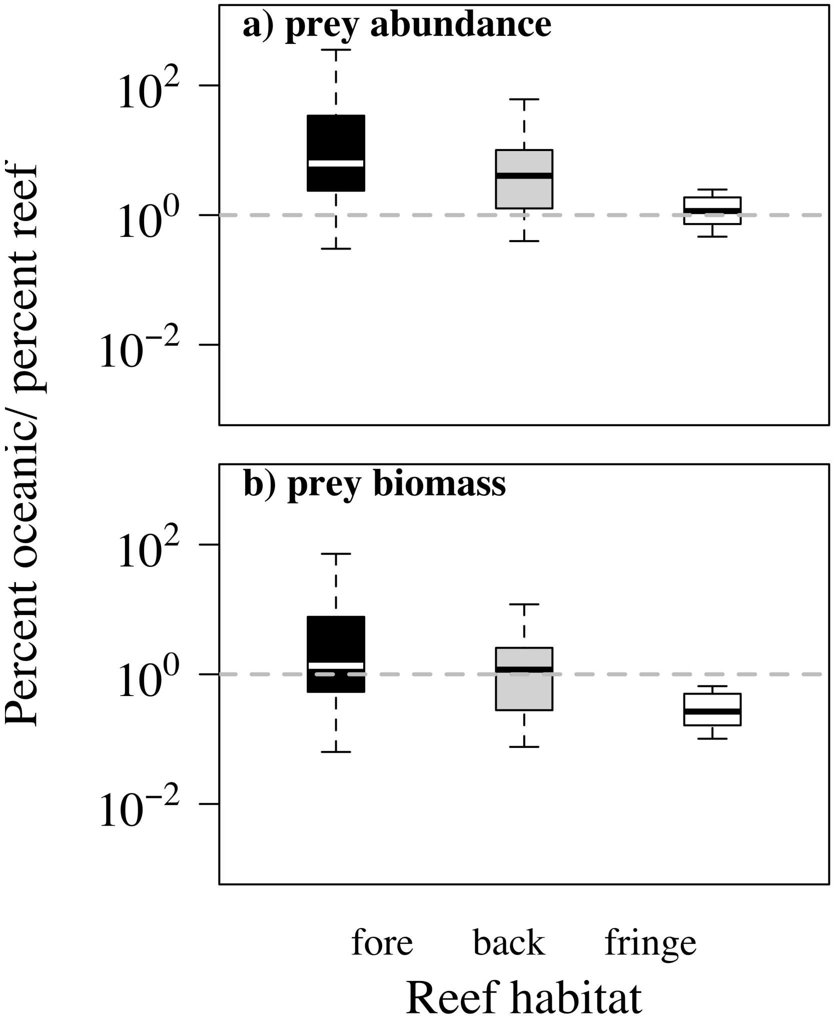

Figure 2.8. Ratios of the summed oceanic to reef indicator taxa in fish gut content samples, calculated using **(a)** prey abundance and **(b)** prey biomass (µg C).

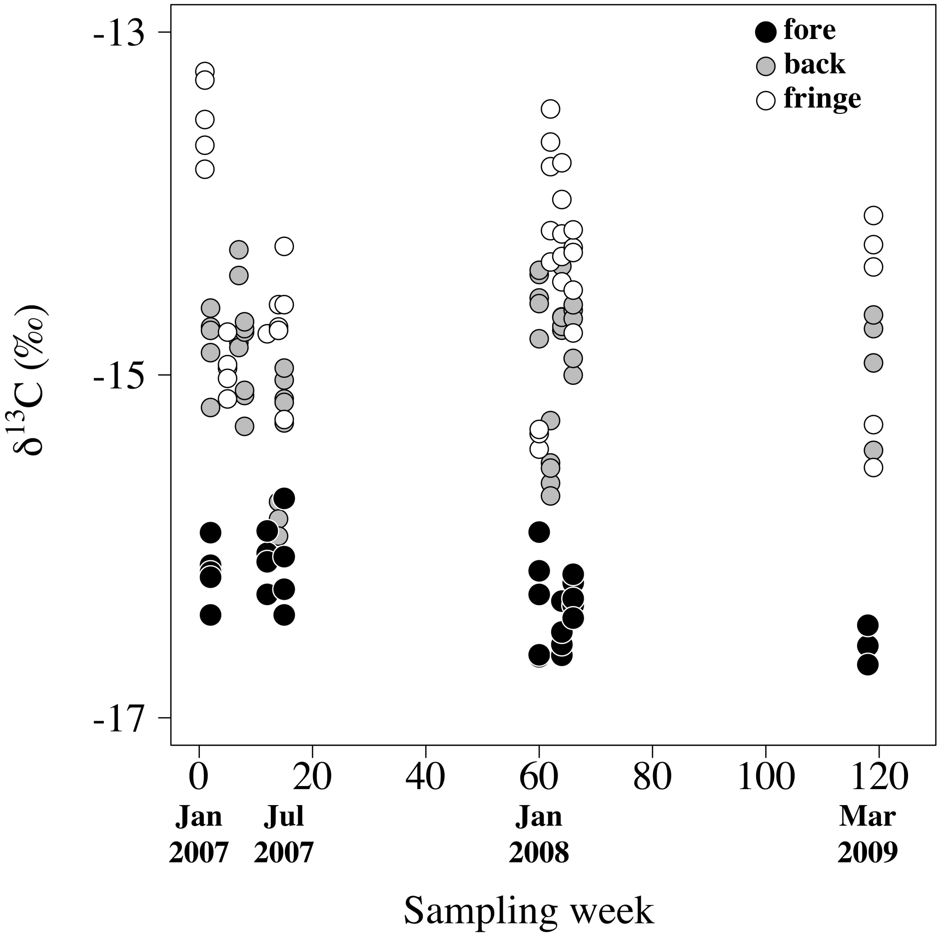

Figure 2.9. Time series of carbon isotope ratios (δ^{13}C ‰) measured in white muscle tissue from *D. flavicaudus*. Points represent individual fish collected from the forereef (black), backreef (grey) and fringing reef (white). Samples were collected at LTER site 1.

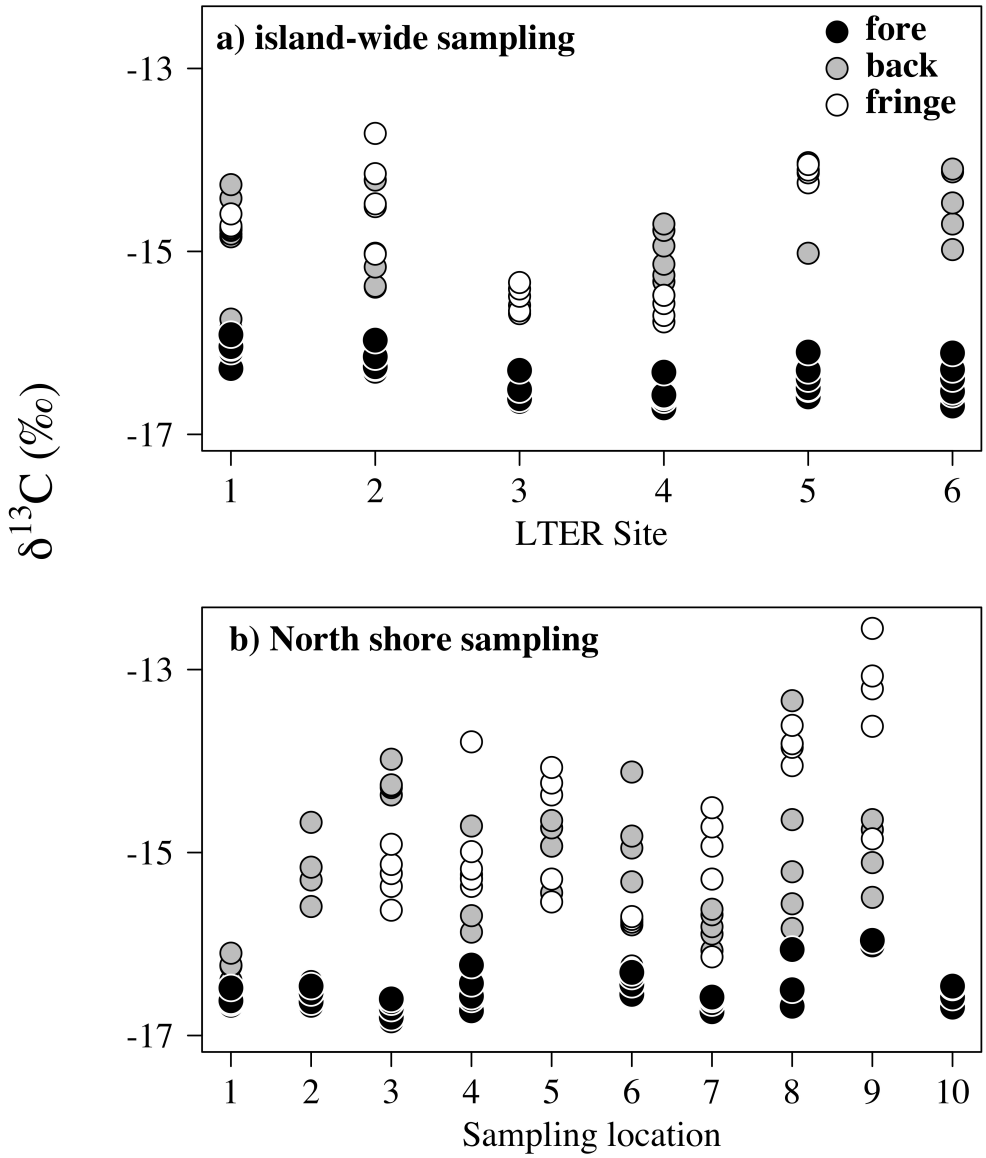

Figure 2.10. Carbon isotope ratios ($\delta^{13}C$ ‰) measured in white muscle tissue of *D. flavicaudus* collected at 2 spatial scales. **(a)** Island-wide sampling at 6 LTER sites. **(b)** Sampling at 7 sites on Moorea's north shore. Points represent individual fish collected from the forereef (black), backreef (grey) and fringing reef (white).

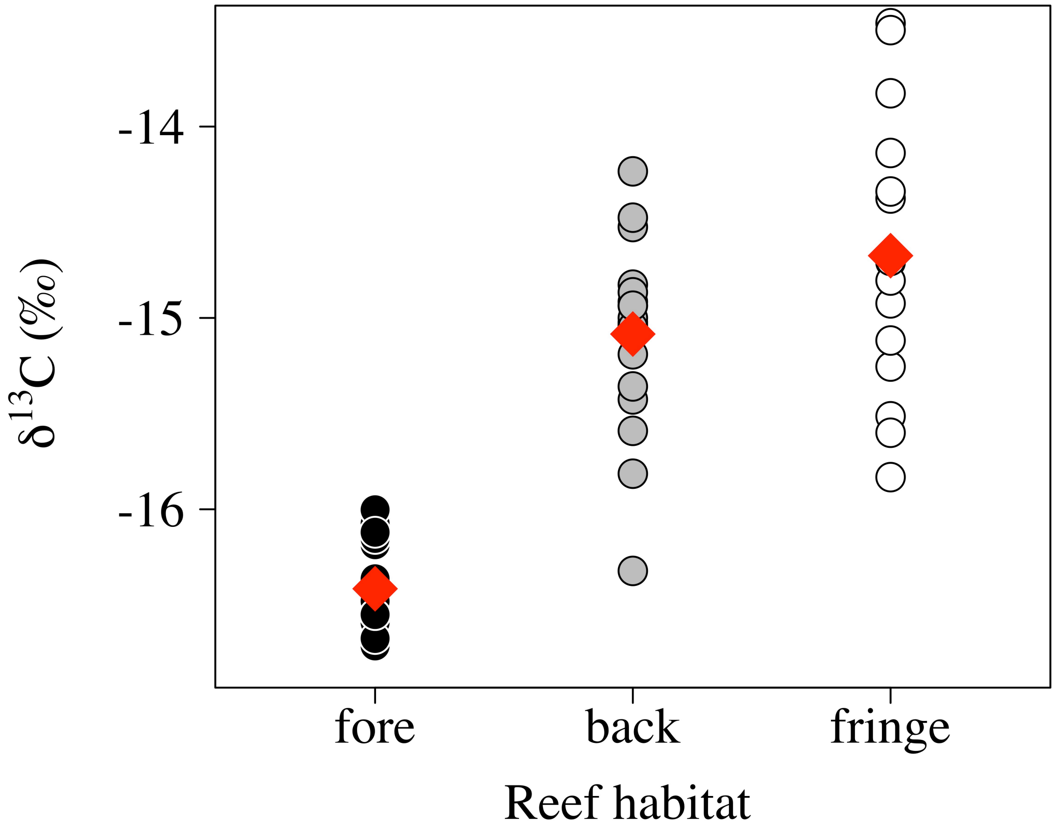

Figure 2.11. Carbon isotope ratios ($\delta^{13}C$ ‰) measured in white muscle tissue of *D. flavicaudus* collected from three reef habitats. Diamonds represent averages of individual values from collections made at distinct times or in distinct sampling locations. Diamonds indicate group means.

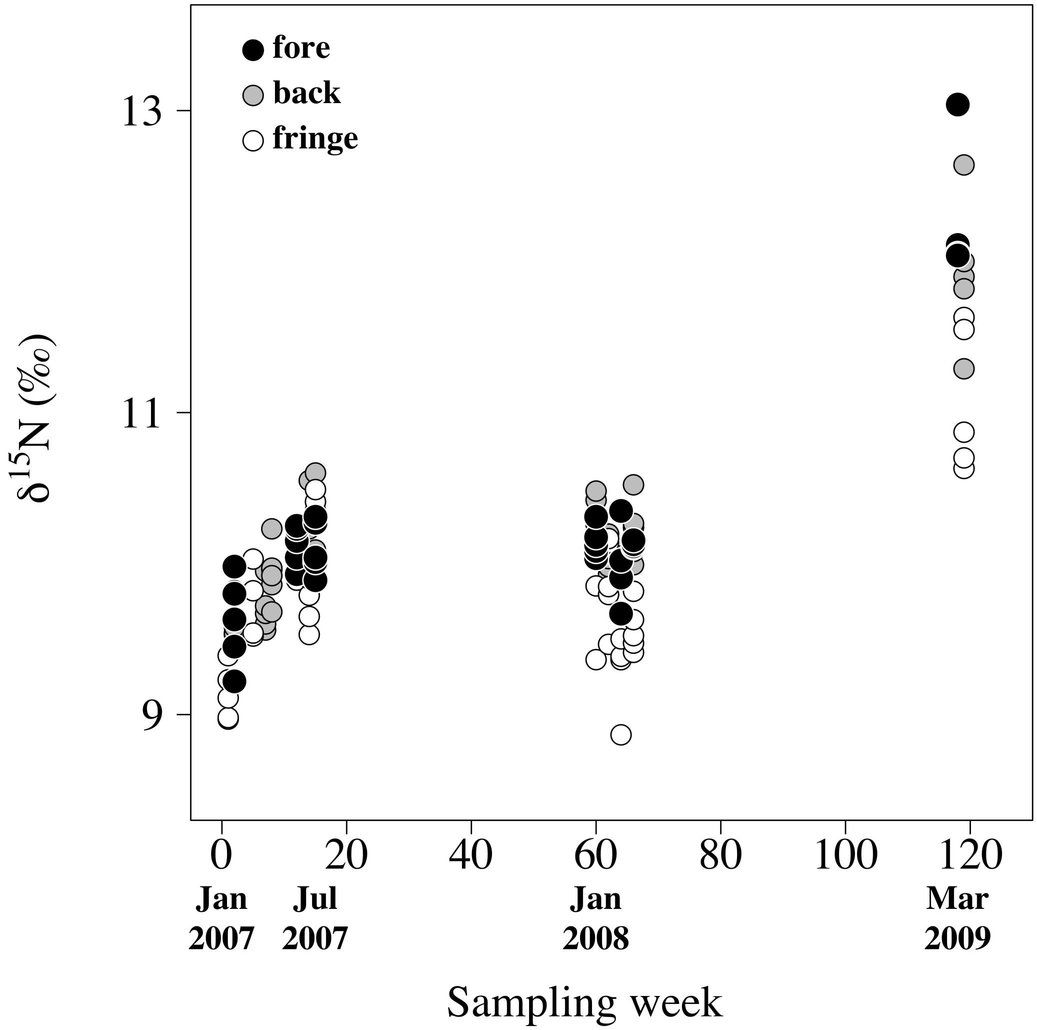

Figure 2.12. Time series of nitrogen isotope ratios (δ^{15}N ‰) measured in white muscle tissue from *D. flavicaudus*. Points represent individual fish collected from the forereef (black), backreef (grey) and fringing reef (white). Samples were collected at LTER site 1.

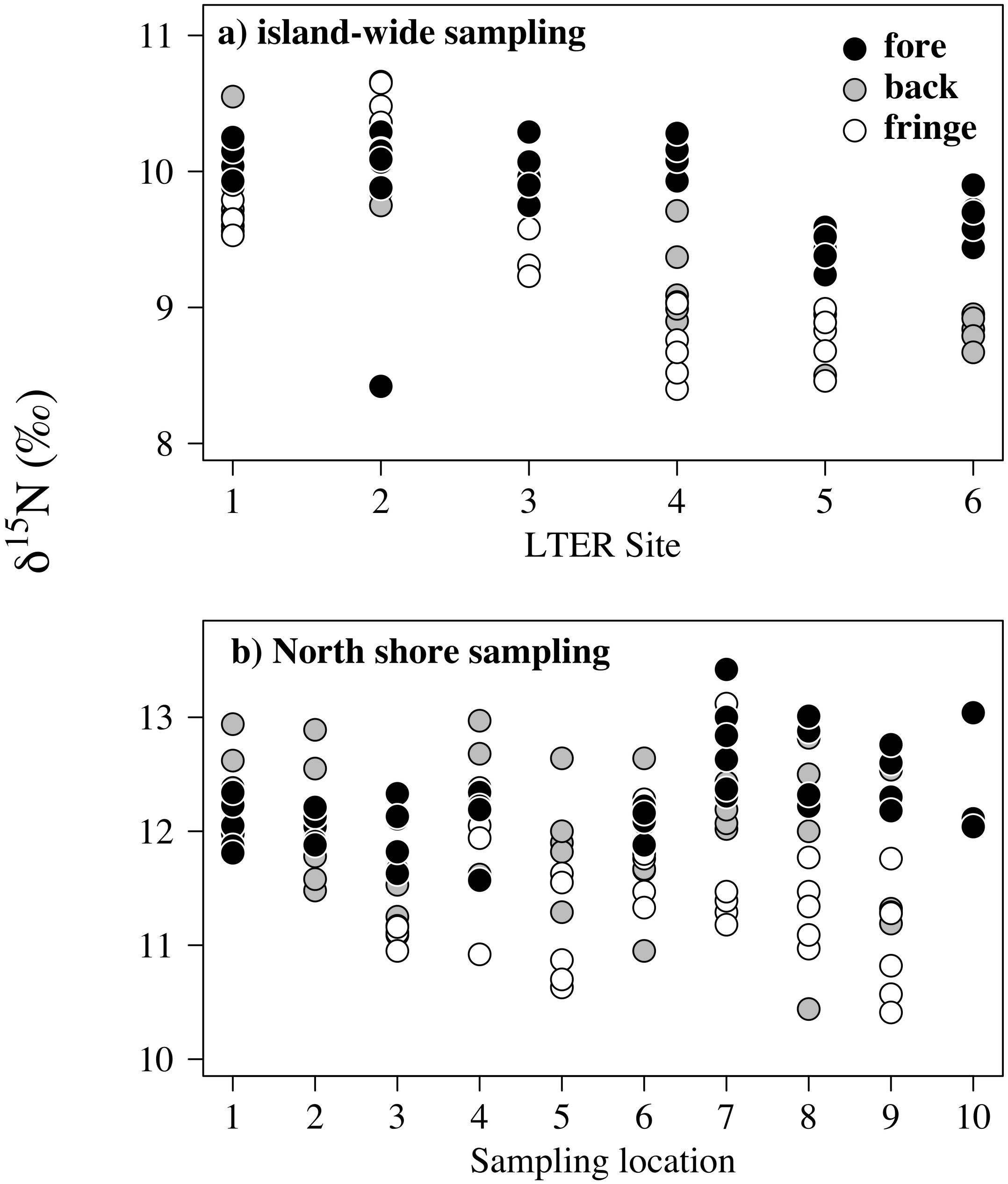

Figure 2.13. Nitrogen isotope ratios ($\delta^{15}N$ ‰) measured in white muscle tissue of *D. flavicaudus* collected at 2 spatial scales. **(a)** Island-wide sampling at 6 LTER sites. **(b)** Sampling at 7 sites on Moorea's north shore. Points represent individual fish collected from the forereef (black), backreef (grey) and fringing reef (white).

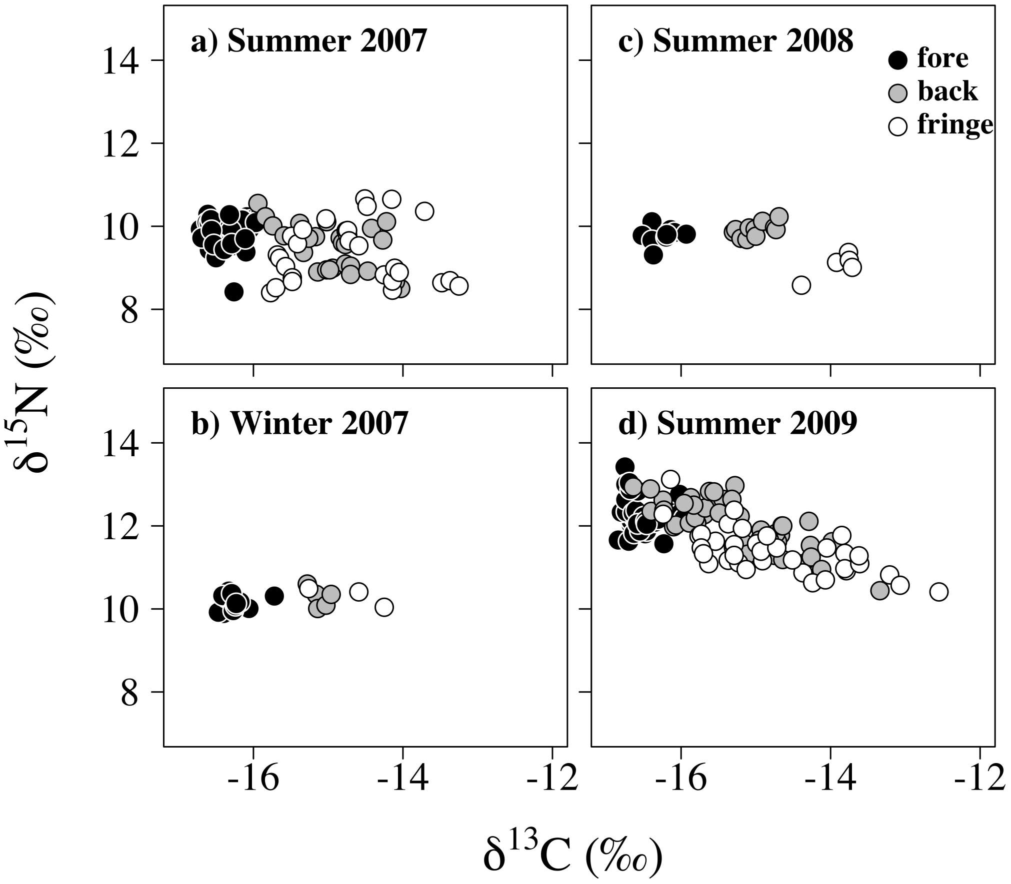

Figure 2.14. Biplots of carbon ($\delta^{13}C$ ‰) and nitrogen ($\delta^{15}N$ ‰) isotope measurements of white muscle tissue collected from *D. flavicaudus* during four time periods: **a)** summer 2007 (n = 88), **b)** winter 2007 (n = 22), **c)** summer 2008 (n = 26), **d)** summer 2009 (n = 122). Seasons refer to austral summer/winter. Points represent individual fish collected from the forereef (black), backreef (grey) and fringing reef (white).

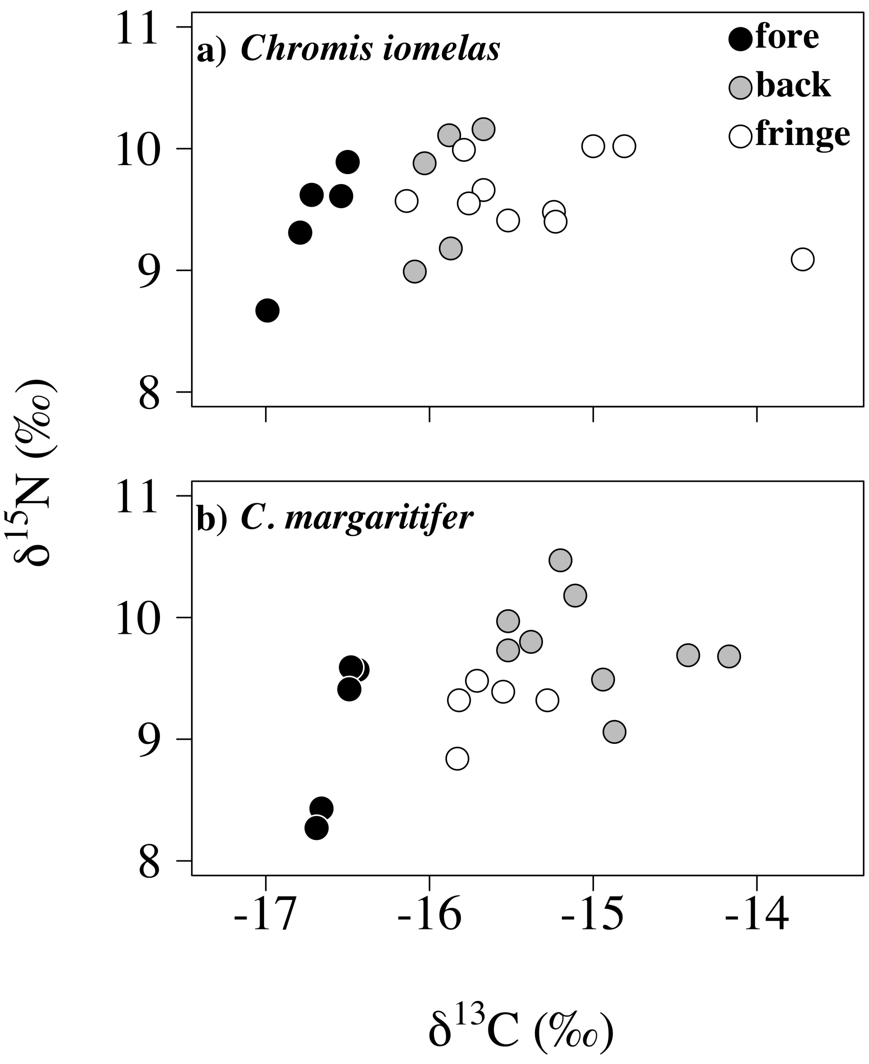

Figure 2.15. White muscle carbon and nitrogen isotope ratios sampled from two zooplanktivorous fish species common to the island of Moorea: **a)** *Chromis iomelas* and **b)** *C. margaritifer*. Points represent individual fish collected from the forereef (black), backreef (grey) and fringing reef (white).

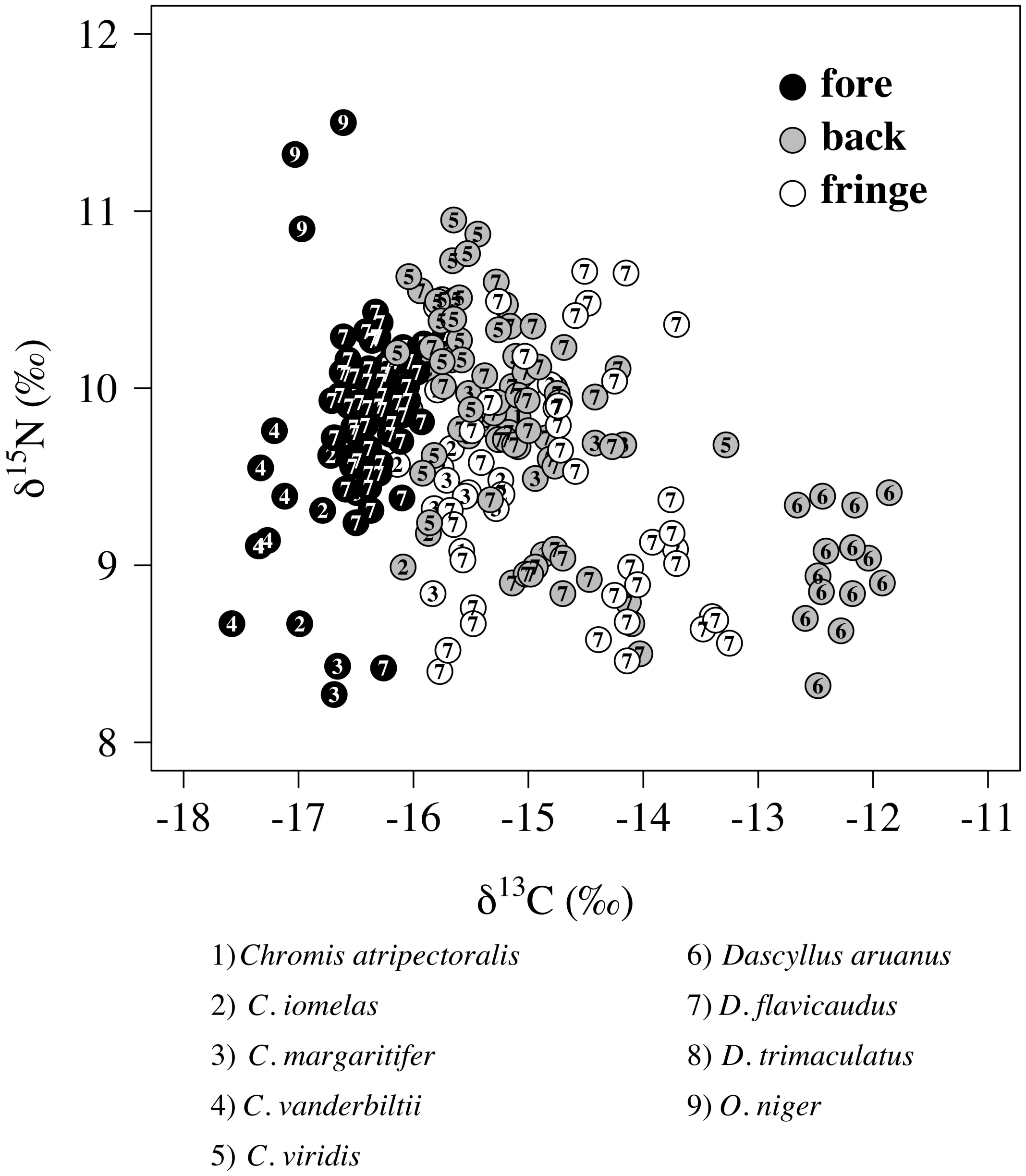

Figure 2.16. White muscle carbon and nitrogen isotope ratios sampled from nine zooplanktivorous fish species. Data for *D. flavicaudus* are limited to samples collected prior to 2009. Points represent individual fish collected from the forereef (black), backreef (grey) and fringing reef (white). Numbers indicate species identification.

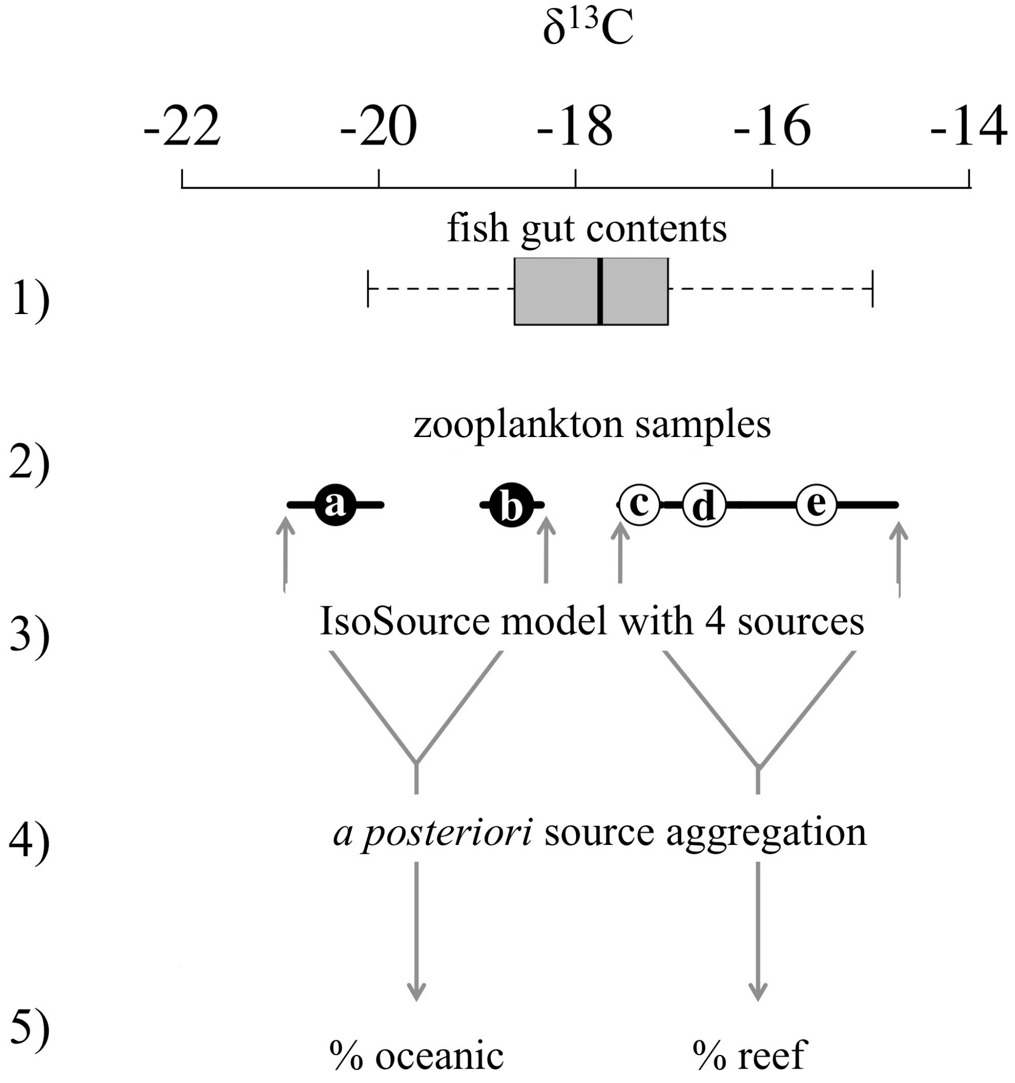

Figure 2.17. Conceptual diagram of the mass-balance 'min-max' approach used to model the contribution of ocean and reef food sources to the diet of planktivorous fish. The choice of two oceanic and two reef end members was informed by **1)** The distribution of δ^{13}C values measured in bulk fish gut content samples and **2)** δ^{13}C values measured in a**)** the copepod *Corycaeus* spp., **b)** bulk zooplankton collected 5 km seaward of the reef crest, **c)** bulk zooplankton collected within the reef lagoon, **d)** larval decapods, and **e)** fish gut samples dominated by fish eggs and larval decapods. The points represent average ratios (with 95% CI) from oceanic (in black) and reef-associated (in white) samples. **3)** Minimum and maximum values from both oceanic and reef zooplankton were chosen as end members which were used in the IsoSource model. **4)** The model solutions for both oceanic and both reef end-members were summed post-hoc to yield one modeled value for the percent contribution of oceanic sources and one value for reef sources for each model iteration **(5)**.

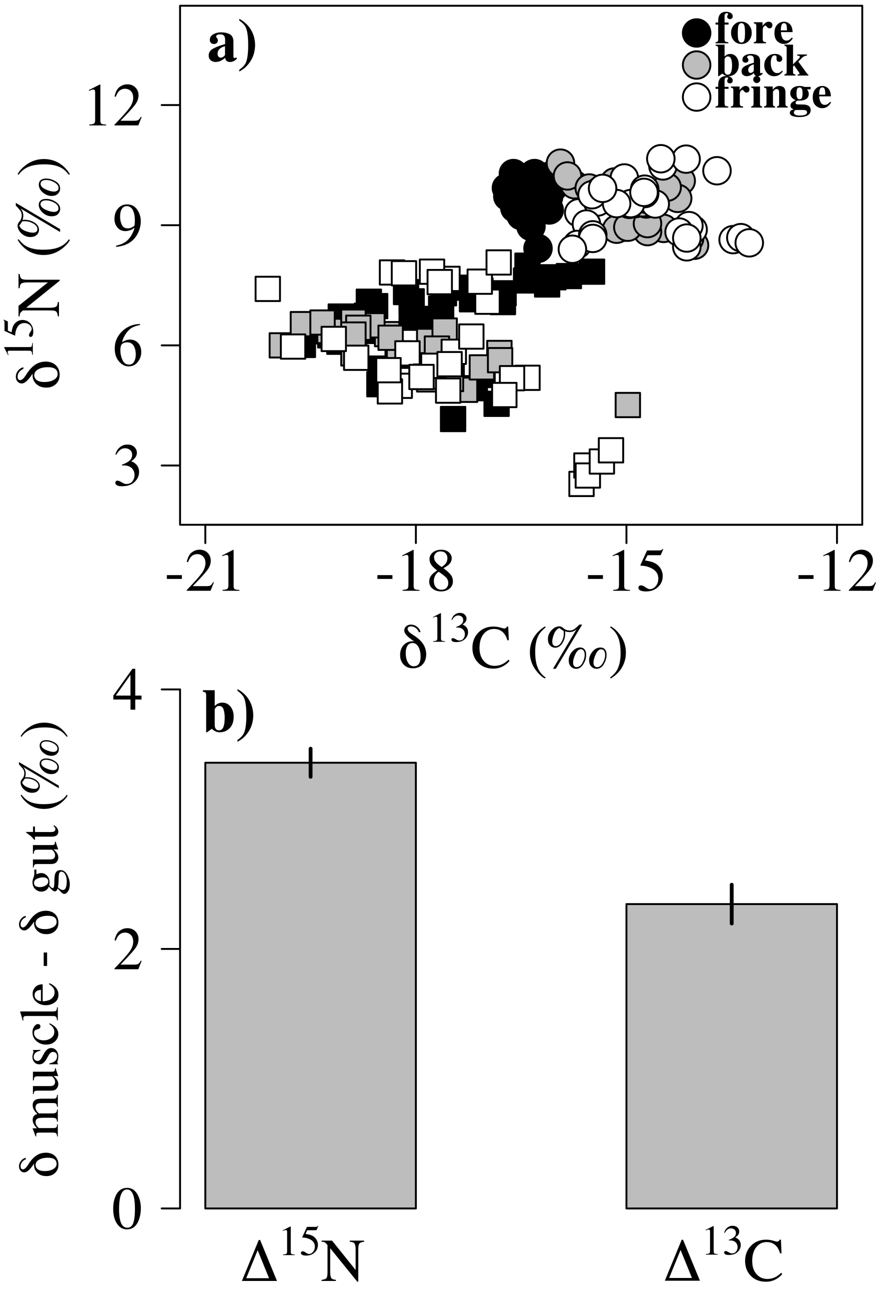

Figure 2.18. a) Carbon and nitrogen isotope ratios measured in muscle tissue (circles) and gut contents (squares) of *D. flavicaudus*. Points represent samples from individual fish collected from forereef (black), backreef (grey) and fringing reef (white) habitats. **b)** Barplot of the difference between isotope ratios ($\delta^{13}C$ or $\delta^{15}N$) measured in fish muscle tissue and isotope ratios measured in gut contents sampled from the same individual (n = 93 fish). Bar heights are means, error bars represent 95% confidence intervals on group means.

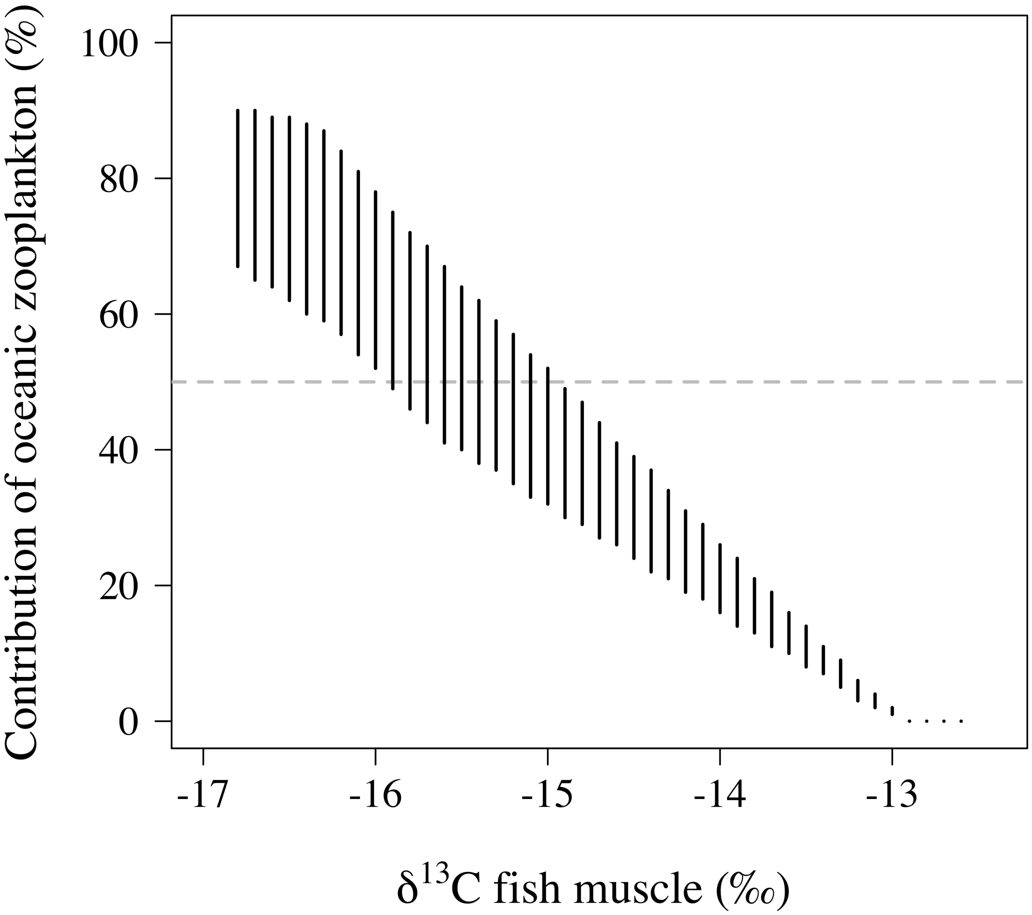

Figure 2.19. Modeled contribution of oceanic zooplankton to reef fish diet based on carbon isotope ratios measured in fish muscle tissue. Bars represent model solutions calculated at 0.1 ‰ intervals across the range of fish muscle $\delta^{13}C$ values measured. The length of the bars extends from the minimum (5th percentile) to maximum (95th percentile) feasible contribution of oceanic zooplankton to reef fish diet.

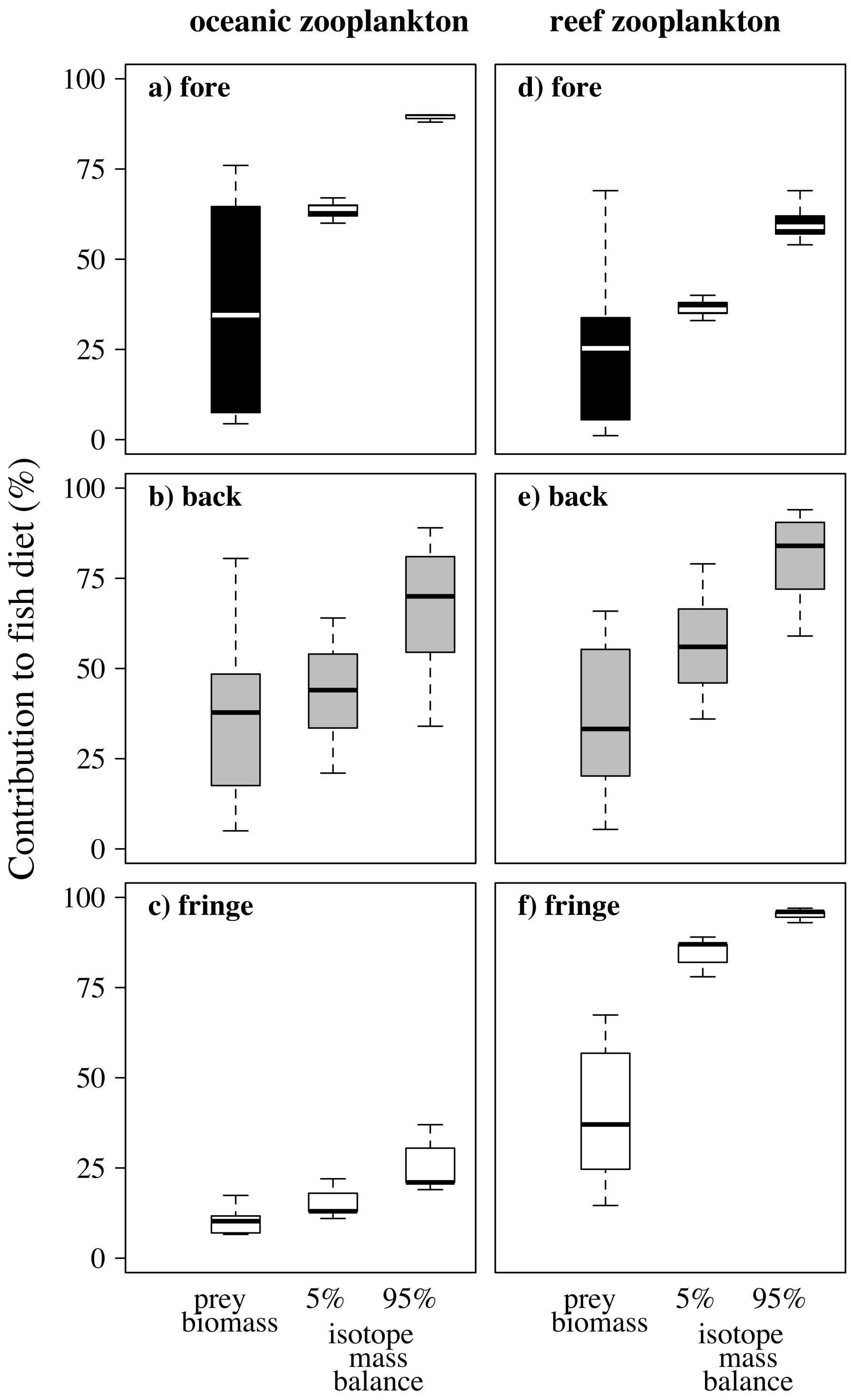

Figure 2.20. The calculated percent contribution of oceanic and reef zooplankton to the diet of *D. flavicaudus*. Calculations contributions are plotted separately for fish from the forereef **(a, d)**, backreef **(b, e)** and fringing reef **(c, f)**. Three calculations are shown for each habitat and prey type: calculations based on prey biomass as well as minimum (5th percentile) and maximum (95th percentile) feasible contributions generated by the IsoSource mass balance model.

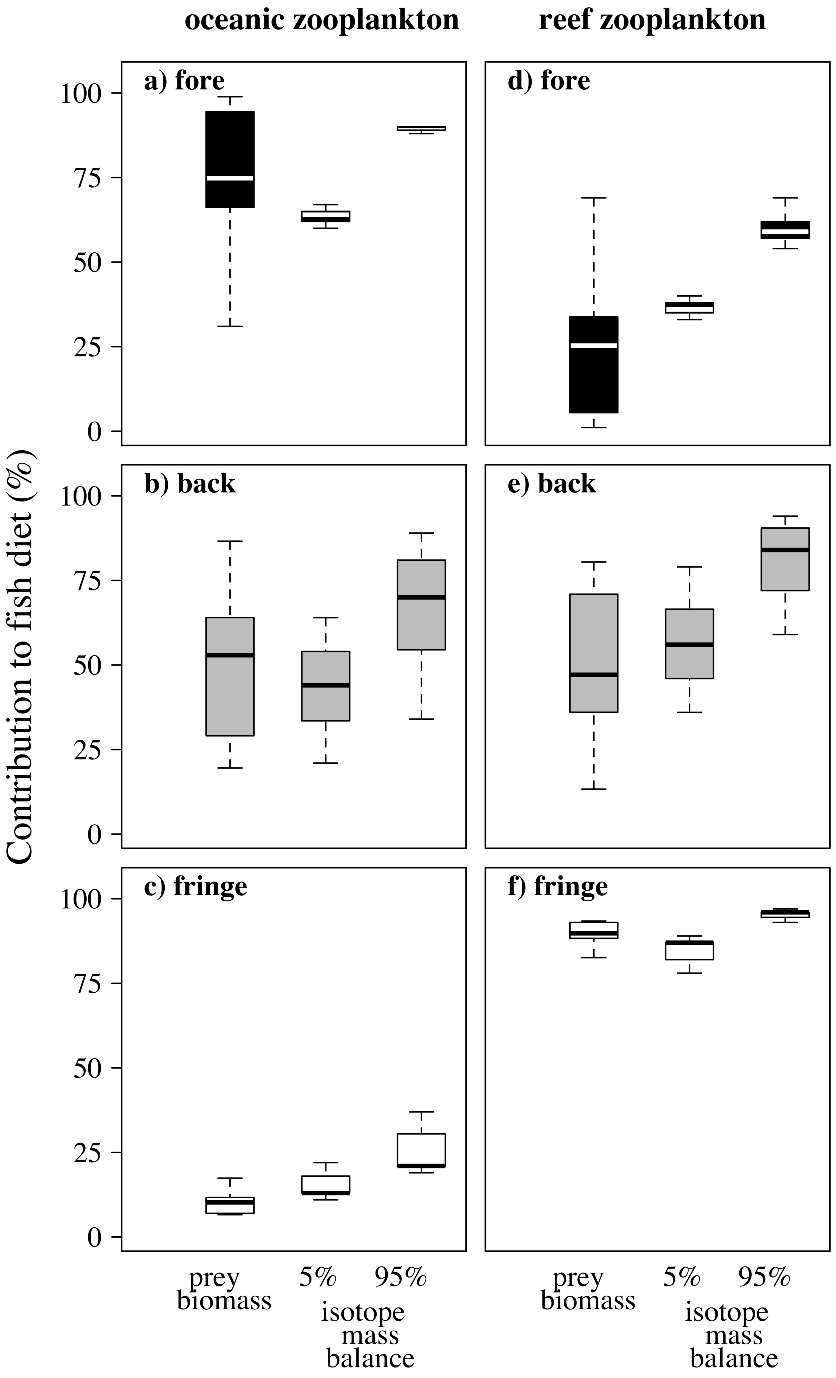

Figure 2.21. Corrected calculations of the percent contribution of oceanic and reef zooplankton to the diet of *D. flavicaudus* (see text for details). Calculations contributions are plotted separately for fish from the forereef **(a, d)**, backreef **(b, e)** and fringing reef **(c, f)**. Three calculations are shown for each habitat and prey type: calculations based on prey biomass as well as minimum (5th percentile) and maximum (95th percentile) feasible contributions generated by the IsoSource mass balance model.

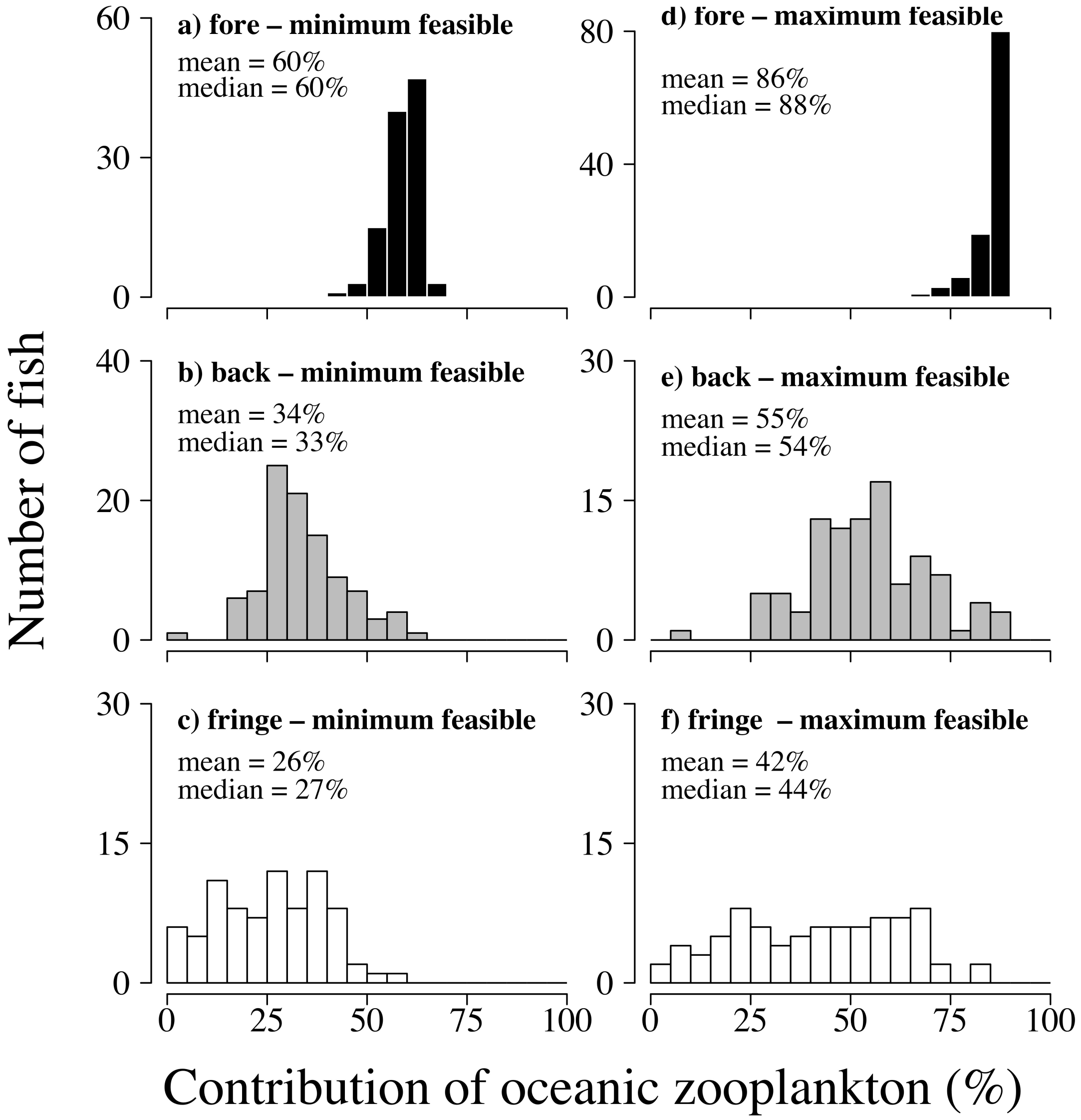

Figure 2.22. Distributions of the percent contribution of oceanic zooplankton to the diet of *D. flavicaudus* sampled from forereef (n = 109), backreef (n = 99) and fringing reef (n = 81) habitats. Data are minimim **(a-c)** and maximum **(d-f)** feasible contributions of oceanic zooplankton to fish diet generated by the IsoSource mass balance model.

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Appendix 2A. Published data on carbon and nitrogen stable isotope ratios measured in coral reef organisms.

Table 2A.1. Details of carbon and nitrogen stable isotope data for primary producers collected from published studies of coral reef ecosystems. The data are primarily reported averages and in a few instances measurements from one sample. Data not reported in text or tables was acquired using the software program WebPlotDigitizer (Rohatgi 2011).

Affiliation	Sample Type	Description	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Source
pelagic	POM	particulate organic matter	-20.63	3.37	Carassou et al. 2008
pelagic	POM		-19.68	4.27	Carassou et al. 2008
pelagic	POM		-20.13	4.32	Carassou et al. 2008
pelagic	POM		-22.5	4.4	Kolasinki et al. 2008
pelagic	POM		-19.8	6.4	Parmentier & Das 2004
pelagic	POM		-20.4	6.3	Burns et al. 2004
pelagic	POM		-20.2	4.9	Burns et al. 2004
pelagic	POM		-20.6	6.4	Burns et al. 2004
pelagic	POM		-20.6	4.9	Burns et al. 2004
pelagic	POM		-21.7	7.2	Burns et al. 2004
pelagic	POM		-21.2	5	Burns et al. 2004
pelagic	POM		-20.86	3.81	van Duyl et al. 2011
pelagic	POM		-23.92	1.97	van Duyl et al. 2011
pelagic	POM		-25.87	2.84	van Duyl et al. 2011
pelagic	POM		-21.52	4.69	van Duyl et al. 2011
pelagic	POM		-18.9	5.2	Naumann et al. 2010
pelagic	POM		-19.7	-2.2	Naumann et al. 2010
pelagic	POM		-22.4	1	Naumann et al. 2010
pelagic	POM		-22.1	4.1	Naumann et al. 2010
pelagic	POM		-20.6	-0.4	Haas et al. 2010
reef	macroalgae	*Turbinaria* sp.	-9.26	7.01	Mill et al. 2007
reef	macroalgae	*Dictyopteris* sp.	-15.43	8.3	Mill et al. 2007
reef	macroalgae	*Gracilaria* sp.	-12.13	8.26	Mill et al. 2007
reef	macroalgae	*Hypnea pannosa*	-13.30	8.13	Mill et al. 2007
reef	macroalgae	*Sarconema filiforme*	-12.13	8.26	Mill et al. 2007
reef	macroalgae	*Ulva lactuca*	-12.13	8.26	Mill et al. 2007
reef	macroalgae	*Pterocladia* sp.	-12.53	9.59	Mill et al. 2007
reef	macroalgae	Lobophora	-10.95	4.27	Carassou et al. 2008
reef	turf algae		-8.58	3.21	Carassou et al. 2008
reef	turf algae		-12.70	3.00	Carassou et al. 2008
reef	turf algae		-4.01	3.12	Carassou et al. 2008
reef	macroalgae	brown_macroalgae	-10.5	3.11	Carassou et al. 2008
reef	macroalgae	crustose coralline algae	-13.37	3.6	van Duyl et al. 2011
reef	macroalgae	crustose coralline algae	-12.12	-4.05	van Duyl et al. 2011
reef	coral mucous	*Montastrea annularis*	-15.46	0.54	van Duyl et al. 2011
reef	coral mucous	*Montastrea annularis*	-15.78	4.12	van Duyl et al. 2011
reef	coral mucous	*Montastrea annularis*	-16.46	-2.35	van Duyl et al. 2011
reef	coral mucous	*Montastrea annularis*	-14.24	3.21	van Duyl et al. 2011
reef	coral mucous	*Montastrea mirabilis*	-17.95	2.12	van Duyl et al. 2011

Table 2A.1. cont'd.

Affiliation	**Sample Type**	**Description**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**Source**
reef	coral mucous	*Montastrea annularis*	-15.78	4.12	van Duyl et al. 2011
reef	coral mucous	*Montastrea annularis*	-16.46	-2.35	van Duyl et al. 2011
reef	coral mucous	*Montastrea annularis*	-14.24	3.21	van Duyl et al. 2011
reef	coral mucous	*Montastrea mirabilis*	-17.95	2.12	van Duyl et al. 2011
reef	coral mucous	*Montastrea mirabilis*	-16.53	4.24	van Duyl et al. 2011
reef	coral mucous	*Montastrea mirabilis*	-17.64	1.71	van Duyl et al. 2011
reef	coral mucous	*Siderastrea siderea*	-17.8	0.55	van Duyl et al. 2011
reef	coral mucous	*Porites asteroides*	-16.87	1.11	van Duyl et al. 2011
reef	coral mucous	Fungia	-15.7	1.4	Naumann et al. 2010
reef	coral mucous	Acropora	-15.7	0.2	Naumann et al. 2010
reef	coral mucous	Fungia	-15.2	0.2	Naumann et al. 2010
reef	coral mucous	Fungia	-19.6	4.1	Naumann et al. 2010
reef	coral mucous	Acropora	-17.7	3.4	Naumann et al. 2010
reef	coral mucous	Fungia	-15.5	4.9	Naumann et al. 2010
reef	coral mucous	Pocillopora	-16.9	-1	Naumann et al. 2010
reef	coral mucous	Stylophora	-15	-1	Naumann et al. 2010
reef	macroalgae	exudate	-14.4	1.6	Haas et al. 2010

Table 2A.2. Details of carbon and nitrogen stable isotope data for fishes collected from published studies of coral reef ecosystems. Here sample type refers to the feeding guild of each fish species (D = detritivore, H = herbivore, Z = zooplanktivore). The data are primarily reported averages and in a few instances measurements from one sample. Data not reported in text or tables were acquired using the software program WebPlotDigitizer (Rohatgi 2011).

Affiliation	**Sample Type**	**Description**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	**Source**
benthic	D	*Amblygobius phalaena*	-12.48	7.47	Wyatt et al. 2010
benthic	D	*Gobiodon histrio*	-12.55	8.12	Wyatt et al. 2010
benthic	H	*Pomacentrus arabicus*	-13.47	14.129	Mill et al. 2007
benthic	H	*Acanthurus sohal*	-12.505	13.486	Mill et al. 2007
benthic	H	*Zebrasoma xanthurum*	-13.892	13.057	Mill et al. 2007
benthic	H	*Chrysiptera unimaculata*	-16.18	9.78	Wyatt et al. 2010
benthic	H	*Stegastes fasciolatus*	-16.23	10	Wyatt et al. 2010
benthic	H	*Stegastes nigricans*	-16.24	10.08	Wyatt et al. 2010
benthic	H	*Acanthurus nigrofuscus*	-11.13	7.36	Carassou et al. 2008
benthic	H	*Ctenochaetus striatus*	-10.92	6.45	Carassou et al. 2008
benthic	H	*Pomacentrus adelus*	-13.46	6.24	Carassou et al. 2008
benthic	H	*Scarus niger*	-14.21	6.54	Carassou et al. 2008
benthic	H	*Centropyge tibiscens*	-14.14	8.69	Carassou et al. 2008
benthic	H	*Cirripectes stigmaticus*	-13.81	5.94	Carassou et al. 2008
benthic	H	*Ctenochaetus striatus*	-12.58	6.06	Carassou et al. 2008
benthic	H	*Stegastes nigricans*	-13.98	8.27	Carassou et al. 2008
benthic	H	*Scarus niger*	-10.18	5.15	Carassou et al. 2008
benthic	H	*Scarus schlegeli*	-9.59	5.12	Carassou et al. 2008
benthic	H	*Chlorurus sordidus*	-8.02	4.84	Carassou et al. 2008
benthic	H	*Stegastes nigricans*	-13.91	7.68	Carassou et al. 2008
benthic	H	*Zebrasoma scopas*	-13.99	6.08	Carassou et al. 2008
benthic	H	*Acanthurus triostegus*	-12.85	8.39	Wyatt et al. 2010
pelagic	Z	*Abudefduf sexfasciatus*	-16.67	10.57	Wyatt et al. 2010
pelagic	Z	Chromis cinerascens	-18.67	10.91	Wyatt et al. 2010
pelagic	Z	*Chromis virides*	-17.3	10.14	Wyatt et al. 2010
pelagic	Z	*Dascyllus aruanus*	-15.01	10.18	Wyatt et al. 2010
pelagic	Z	*Pomacentrus albicaudautus*	-14.76	10.17	Wyatt et al. 2010
pelagic	Z	*Pomacentrus chrysurus*	-18.6	11.18	Wyatt et al. 2010
pelagic	Z	*Pomacentrus coelestis*	-18.61	10.14	Wyatt et al. 2010
pelagic	Z	*Pomacentrus moluccensis*	-16.29	10.13	Wyatt et al. 2010
pelagic	Z	*Pterocaesio tile*	-17.25	10.15	Wyatt et al. 2010
pelagic	Z	*Ostorhinchus doederleini*	-12.25	8.73	Carassou et al. 2008
pelagic	Z	*Caesio caerulaurea*	-16.13	8.56	Carassou et al. 2008
pelagic	Z	*Chrysiptera notialis*	-15.04	7.76	Carassou et al. 2008
pelagic	Z	*Abudefduf sexfasciatus*	-16.37	8.73	Carassou et al. 2008
pelagic	Z	*Ostorinchus doederleini*	-11.96	7.78	Carassou et al. 2008
pelagic	Z	*Chromis viridis*	-16.82	9.66	Carassou et al. 2008
pelagic	Z	*Dascyllus aruanus*	-15.01	9.45	Carassou et al. 2008
pelagic	Z	*Pomacentrus moluccensis*	-14.68	8.48	Carassou et al. 2008
pelagic	Z	*Abudefduf sexfasciatus*	-15.04	8.02	Carassou et al. 2008
pelagic	Z	*Caesio caerulaurea*	-15.59	8.54	Carassou et al. 2008
pelagic	Z	*Dascyllus aruanus*	-13.01	8.23	Carassou et al. 2008

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Appendix 2B. Diurnal zooplanktivorous fishes common to the island of Moorea.

Table 2B.1. Taxonomy and maximum reported total length of the twenty-two small-bodied, diurnal zooplanktivorus fish species known from Moorea's reefs. References for maximum reported species length are listed. The list is a subset of species identified by the Moorea Coral Reef LTER as part of an annual census of fishes.

Species	Maximum TL (mm)	Reference
Abudefduf sexfasciatus	160	Allen 1991
Amphiprion chrysopterus	170	Fautin and Allen 1992
Chromis acares	40	Allen 1991
C. agilis	75	Allen 1991
C. atripectoralis	120	Allen 1991
C. iomelas	80	Allen 1991
C. margaritifer	90	Allen 1991
C. vanderbilti	45	Allen 1991
C. viridis	80	Allen 1991
C. xanthura	150	Allen 1991
Cirrhilabrus exquisitus	120	Randall 1992
Dascyllus aruanus	100	Randall and Allen 1977
D. flavicaudus	120	Allen 1991
D. trimaculatus	110	Allen 1991
Nemateleotris magnifica	90	Randall et al. 1990
Pomacentrus pavo	85	Allen 1991
Pomachromis fuscidorsalis	60	Allen 1991
Pseudanthias mooreanus	72	Heemstra and Randall 1999
P. olivaceus	88	Heemstra and Randall 1999
P. pascalus	200	Randall et al. 1990
Ptereleotris evides	140	Randall and Hoese 1985
P. monoptera	120	Randall and Hoese 1985

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Appendix 2C. Data on the biomass of twelve zooplankton prey groups.

Table 2C.1. Published data on the carbon content (POC, ug C animal^{-1}) of various zooplankton types. The published data guided the values selected to transform count data to estimates of zooplankton biomass in the present study. The values used in this study were adjusted or selected from a range of values reported in the literature according to the body size of individuals sampled from fish guts in Moorea relative to the body size of reference organisms used in the published studies.

Zooplankton prey group	POC (µg C animal^{-1})	Size (mm)	Reference organism	Reference	Value used
Appendicularia	3.5 ± SD 0.2	0.4 - 1.5	appendicularians	Alldredge and King 2009	3.5
Corycaeidae	0.37 - 4.65	0.28 - 1.0	*Corycaeus* spp.	Satapoomin 1999	2.5
Oncaeidae	0.38 - 5.26	0.3 - 0.74	*Oncaea* spp.	Satapoomin 1999	2.8
Calanoida	0.81 - 12.23	0.59 - 1.2	*Centropages furcatus*	Satapoomin 1999	6.52
pelagic Harpacticoida	0.21 - 1.39	0.36 - 1.18	*Macrosetella gracilis*	Satapoomin 1999	0.8
benthic Harpacticoida	1.74 ± SD 0.22	0.838	*Amphiascoides atopus*	Baguley et al. 2004	1.74
Oithonidae	0.5	0.8	*Oithona similis*	Logerwell and Ohman 1999	0.5
Ostracoda	15.6 ± SD 3.4	0.2 - 1.2	ostracods	Alldredge and King 2009	15.6
Cladocera	15.6 ± SD 3.4	0.2 - 1.2	ostracods	Alldredge and King 2009	15.6
fish eggs	17.52 ± SD 1.40	1.003 ± SD 0.024	*Solea senegalensis*	Yúfera et al. 1999	8.76
coral larvae	42.4 ± SD 13.3	n/a	*Acropora humilis*	A. Hartman, unpublished data	20
Decapoda	17.9 ± SD 9.0	1.1 - 3.0	decapod larvae	Alldredge and King 2009	17.9

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Appendix 2D. Analytical precision and error related to stable isotope analysis of zooplankton and fish muscle tissue samples. Isotope analyses were performed by the UC Davis Stable Isotope Facility.

Table 2D.1. Analytical precision of the working standards used in stable isotope analysis.

Date	Run	Working Standard	n	Reference	$\delta^{15}N$ (‰) Average	SD	Reference	$\delta^{13}C$ (‰) Average	SD
June 2007	1	$(NH_4)_2SO_4$ & $C_{12}H_{22}O_{11}$	19	1.33	1.33	0.13	-24.44	-24.42	0.04
	2	$(NH_4)_2SO_4$ & $C_{12}H_{22}O_{11}$	18	1.33	1.33	0.03	-24.44	-24.42	0.05
	3	$(NH_4)_2SO_4$ & $C_{12}H_{22}O_{11}$	19	1.33	1.33	0.06	-24.44	-24.41	0.05
	4	$(NH_4)_2SO_4$ & $C_{12}H_{22}O_{11}$	12	1.33	1.33	0.12	-24.44	-24.37	0.07
May 2008	5	$(NH_4)_2SO_4$ & $C_{12}H_{22}O_{11}$	22	1.33	1.28	0.18	-24.44	-24.47	0.10
October 2009	6	Nylon	19	-9.96	-9.96	0.10	-27.72	-27.72	0.05
December 2009	7	Nylon	18	-9.96	-9.96	0.06	-27.72	-27.72	0.08
December 2009	8	Nylon	40	-9.77	-9.77	0.08	-27.86	-27.86	0.05
March 2010	9	Nylon	20	-9.77	-9.77	0.09	-27.86	-27.86	0.07

Table 2D.1. cont'd.

Notes:

$(NH_4)_2SO_4$ = ammonium sulfate
$C_{12}H_{22}O_{11}$ = sucrose

Working standards calibrated against NIST Standard Reference Materials (IAEA-N1, IAEA-N2, IAEA-N3, USGS-40, and USGS-41).

Table 2D.2. Precision of isotope ratios ($\delta^{15}N$, $\delta^{13}C$) and elemental composition ($C:N_{atomic}$) measured in replicate aliquots of muscle tissue sampled from individual *Dascyllus flavicuadus.* Replicate aliquots were analyzed over the course of three years.

		$\delta^{15}N$ (‰)		**$\delta^{13}C$ (‰)**		**C:N atm**	
Sample ID	**n**	**Average**	**SD**	**Average**	**SD**	**Average**	**SD**
DF 151	8	10.44	0.18	-16.07	0.16	3.67	0.16
DF 153	10	9.97	0.47	-16.10	0.07	3.69	0.20
DF 155	10	10.11	0.44	-16.04	0.05	3.63	0.18
DF 190	8	10.41	0.53	-16.28	0.05	3.65	0.19
DF 210	8	10.37	0.14	-16.62	0.09	3.67	0.15
DF 28	4	9.18	0.35	-16.19	0.06	3.40	0.07
DF 62	8	10.22	0.14	-15.51	0.06	3.68	0.16

CHAPTER 2

Selective feeding increases the contribution of oceanic zooplankton to the diet of planktivorous coral-reef fish

ABSTRACT:

Combining gut content analysis and sampling of ambient zooplankton assemblages, we examine departures from random feeding in the planktivorous coral-reef fish *Dascyllus flavicaudus*. This fish's diet is dominated by four zooplankton prey groups (two poecilostomatoid copepod families, appendicularians and calanoid copepods). *D. flavicaudus* exhibits strong positive electivity for the copepod families Oncaeidae and Corycaeidae as well as *Candacia* spp. and consistent negative electivity for the cylcopoid *Oithona* spp. and calanoid copepods. Categorizing the zooplankton prey groups as oceanic in origin, reef-associated, or mixed-origin, we explore the effects of this non-random feeding on the origin of prey in the diet of *D. flavicaudus*. Oceanic prey groups contribute 25 % to 76 % of total zooplankton biomass in fish diets, a 2 to 6-fold increase of the contribution of oceanic groups relative to expectations under random feeding. Selective feeding by *D. flavicaudus* also led to a significantly more even distribution of prey items among prey categories than expected from ambient prey abundance. The zooplankton prey groups for which *D. flavicaudus* exhibits strong positive electivity are characterized by distinctive body pigmentation. Prey groups showing negative electivity are characterized by relative transparency, inconspicuous swimming motions or the ability for rapid escape

responses. Non-random feeding likely influences the role *D. flavicaudus* plays linking the larger coral reef food web to oceanic energy and nutrients as oceanic zooplankton prey are converted to fish biomass and excreta subsequently utilized by other reef consumers.

INTRODUCTION:

Organisms generally utilize a subset of the available food resources in their environment. Theoretical and empirical studies of how and why organisms select this subset of available resources have proliferated over the past half-century, in part because such findings are of interest to a wide range of sub-disciplines including behavioral, evolutionary, population, and community ecology (Hughes 1993). Diet selection studies can have implications for conservation biology strategies, as exemplified by research on the vulnerability of specialist predators to habitat change (Laurance 1991, Ferrer & Negro 2004). Research on selective feeding has also made important contributions to the study of food webs, highlighting the effects of non-random feeding on the incorporation of resources by and flow of nutrients among various trophic levels (Pastor & Naiman 1992, Katechakis et al. 2002).

A predator's diet is determined by characteristics of the prey assemblage, qualities intrinsic to each prey type, encounter rates, and behavioral feeding preferences of the predator. Beyond properties inherent to predator or prey, the interactions between predator and prey are dynamic. These dynamic interactions can be described in terms of feeding 'electivity'. Initially defined by Scott (1920) (cited in Pearre 1982), electivity is the proportion of distinct food types in a consumer's diet relative to the proportion of available food types in the environment. Singer (2000) emphasized that electivity is a product of predator-prey interactions and not simply a function of a predator's preference for certain food types. Unlike preference, electivity will vary with changes in the environment such as prey density and prey distribution (Singer 2000) as well as with physical or biological factors that influence the predation cycle (sensu Holling 1966) from search and encounter through eating and digestive pause. In this sense, feeding electivity is central to the question of realized or actual trophic niche, and determines the subset of the resources available in a given setting that a consumer will utilize.

Planktivorous fish are ubiquitous components of coral reef ecosystems, accounting for up to 40 % of total fish biomass in some reef systems (Williams & Hatcher 1983, DeMartini et al. 2008). While the standing biomass of planktivorous fish can be substantial, static measurements such as biomass and abundance do not account for turnover associated with recruitment and predation and likely underestimate the contribution of planktivores to secondary production on reefs. In a study from the Great Barrier Reef, pomacentrids (many of which are planktivores) had the highest estimated rates of biomass production among fish families (0.57 g m^{-2} wk^{-1} ± SE 0.17), contributing 30 % of the estimated weekly biomass production despite accounting for only 15 % of the standing biomass (Depczynski et al. 2007). Planktivorous fish are consumed by piscivorous coral reef fish and can be dominant components of the diet of large piscivores such as serranids (groupers) (St John et al. 2001, Beukers-Stewart & Jones 2004), carangids (jacks) and lutjanids (snappers). Planktivorous fish also contribute to coral reef food webs in the form of feces and excreted ammonium. Robertson (1982) documented that 62 % - 98 % of feces produced by zooplanktivores feeding > 1 m above the reef surface were consumed by other fish species. Plantktivore feces that fall to the reef substrate are consumed by detritivores, including mobile species such as hermit crabs and shrimp (Rothans & Miller 1991). Resident planktivorous fish (Pomacentridae) inhabiting anemones excrete ammonium that is subsequently taken up by both the cnidarian hosts as well as by the anemones' endosymbiotic zooxanthellae (Roopin et al. 2008, Cleveland et al. 2011). Indirect evidence suggests that similar exchanges likely occur between planktivorous fish and corals (Holbrook et al. 2008). Thus, through combined contributions via predation, coprophagy, and uptake of excreted nutrients, planktivorous coral reef fish are an important link between pelagic particulate nutrients (in the form of zooplankton prey) and benthic coral reef consumers. Similar trophic relationships have been documented for planktivorous damselfish in rocky subtidal habitats (Bray et al. 1981, Pinnegar & Polunin 2006).

The consumption of zooplankton by planktivorous fish is one of the most common forms of predation in coral reef ecosystems. Particle-feeding planktivorous fish detect their zooplankton prey visually, and a large number of studies have documented their selective feeding (reviewed in Lazzaro 1987). Particle-feeding planktivorous fish often exhibit size-selective feeding, consuming large zooplankton disproportionately to small zooplankton (O'Brien et al. 1976, O'Brien 1979). Predation in particle-feeding planktivores can also be visibility-selective, with feeding rates influenced by the pigmentation and behavior of zooplankton prey as well as by the visual acuity of the fish predator (Arthur 1976, Hessen 1985). Feeding selectivity has been studied in the nocturnal coral-reef planktivorous fish *Apogon annularis* (Apogonidae) (Holzman & Genin 2005) as well as in larval stages of coral reef fish (Sampey et al. 2007, Carassou et al. 2009, Llopiz & Cowen 2009), but has not been previously documented in diurnal planktivorous fish on coral reefs.

The objective of this study is to determine whether selective feeding influences the diet of the reef fish *Dascyllus flavicaudus*. We quantify the taxonomic composition of zooplankton sampled from both fish gut contents and the ambient zooplankton assemblage. We combine these data (1) to test the null hypothesis that *D. flavicaudus* feeds randomly on the available zooplankton prey and (2) to quantify departures from non-random feeding (positive or negative electivity) for specific zooplankton prey types. We divide the zooplankton prey into oceanic and reef-associated constituents and find that non-random feeding in *D. flavicaudus* results in a more taxonomically even diet with a larger contribution of oceanic zooplankton groups than would be expected under random feeding. Thus, the importance of autochthonous (reef-associated) versus allochthonous (oceanic) food sources for the coral-reef fish *D. flavicaudus* is directly influenced by feeding behavior.

MATERIALS AND METHODS:

Study location and species

Fish and zooplankton were collected from reefs surrounding Moorea, a high volcanic island in the Society Archipelago of French Polynesia (17°32’S, 149°50’W). Three distinct reef habitats (forereef, backreef, and fringing reef) form concentric bands around the island. The fringing reef directly borders the island and extends to depths of ~20 m before terminating in sand-filled lagoons. The backreef habitat is shallow (< 3 m depth) and is characterized by a network of patch reefs and isolated coral heads separated by bare sand. The forereef habitat slopes offshore from the reef crest with coral cover extending to at least 60 m depth. The yellowtail damselfish *Dascyllus flavicaudus* is common to Moorea's reefs and can be found in all three habitats. *D. flavicaudus* exhibits feeding behaviors characteristic of small-bodied, diurnal planktivorous reef fish – during the day individuals hover over coral colonies to feed on zooplankton which they detect visually in the water column (Allen 1991).

Prey use

To identify the zooplankton prey groups used by *D. flavicaudus*, we analyzed the gut contents of fish collected from three locations in the forereef habitat and three backreef locations (n = 6 sampling locations; Figure 3.1). The six sampling locations were situated on Moorea's north shore and were separated by approximately 400 m. Five fish were sampled at each of the six locations. Fish were collected by SCUBA divers using hand-held microspears (Randall 1963) and euthanized in chilled seawater. Gut contents were removed from the anterior intestine, which in this species extends to a pouch-like structure. Gut content samples were rinsed over a 100 μm mesh screen with filtered seawater. The portions ≥ 100 μm were retained, preserved in 1.8 % buffered formaldehyde in seawater and later enumerated under a dissecting microscope as follows.

Zooplankton prey items were classified into 16 groups of varying taxonomic specificity (Appendix 3A: Tables 3A.1, 3A.2). Prey types (e.g. coral and polychaete larvae) that occurred in guts of only a few individual fish were grouped with unidentifiable organisms and categorized as ‘other’ zooplankton prey. These ‘other’ organisms were included in the calculation of log-likelihood statistics and forage ratios, but were not included in biomass calculations (see below).

The entire gut contents were enumerated for an initial subsample of fish (n = 18). Due to the large number of sampled prey items (Figure 3.2), the remaining gut content samples were split into 4 sub-samples using a Folsom plankton splitter (McEwen et al. 1954). Zooplankton prey were then counted from the subsamples. Rare taxa (< 100 individuals total, Appendix 3B: Table 3B.1) were counted from the entirety of the sample. Numerically dominant taxa (> 100 individuals total, Appendix 3B: Table 3B.2) were counted from one or more aliquots until 100 individuals were counted. Subsample counts were multiplied by the number of aliquots enumerated to yield an estimate of total abundance per fish gut.

Prey availability

Environmental zooplankton samples were collected at each of the six study locations by a SCUBA diver swimming with a plankton net (153 µm mesh net and cod end, 30 cm diameter) at a height of 1 m above the reef. Tows were conducted immediately following and in the vicinity (10 – 20 m) of fish collections. The volume of water sampled by environmental tows was estimated using a mechanical flow meter outfitted with a low velocity rotor (model 1030R6 General Oceanics Inc., Miami, FL, USA). The zooplankton tows sampled an average of 9.2 m^3 ± SD 2.4 of water. Environmental zooplankton samples were fixed in 1.8 % buffered formaldehyde in seawater and later enumerated under a dissecting microscope. All environmental zooplankton samples were split prior to enumeration.

Examining random feeding

Log-likelihood goodness-of-fit tests (Manly et al. 1993) were used to evaluate two null hypotheses: (1) The occurrence of zooplankton prey groups in fish gut contents does not vary among individual fish and (2) *Dascyllus flavicaudus* feed randomly on available zooplankton such that the relative contribution of zooplankton groups to fish gut contents does not differ from the relative abundance of zooplankton types in the environment. Both hypotheses were tested for across the six collection locations. The first hypothesis was evaluated by calculating the log-likelihood statistic X_{L1}^2 as:

$$X_{L1}^2 = 2 \sum_{j=1}^{n} \sum_{i=1}^{I} u_{ij} \ln \left[u_{ij} / E(u_{ij}) \right] \tag{1}$$

for $i = 1$ to I prey groups and $j = 1$ to n fish . Here u_{ij} is the observed count of prey group i in the stomach of fish j. $E(u_{ij})$ is the expected number of prey i in the gut of the j^{th} individual assuming that the j^{th} individual feeds in the same manner as the other fish sampled. $E(u_{ij})$ is calculated as:

$$E(u_{ij}) = [(u_{i+}\, u_{+j})/u_{++}] \tag{2}$$

where u_{i+} is the sum of individuals of prey group *i* across *n* fish, u_{+j} is the sum of all prey types for fish *j* and u_{++} is the grand sum of all prey enumerated in *n* gut contents samples (notation follows Manly et al. 1993). The significance of the resulting test statistic (X_{L1}^2) was evaluated against the critical value from the χ^2 distribution with ($I - 1)(n$-1) degrees of freedom and a Bonferroni-corrected significance level (0.05/*N*) where *N* is the number of simultaneous significant tests conducted. In this case, the test statistic was calculated for each collection location, thus $N = 6$. X_{L1}^2 values exceeding critical χ^2 values indicate that the relative proportions of zooplankton prey groups in fish gut contents vary significantly among fish collected from a given location. To evaluate the hypothesis that *Dascyllus flavicaudus* exhibit random feeding, a second log-likelihood statistic (X_{L2}^2) was calculated, this time including counts from the zooplankton tow sample as if this environmental sample was another individual fish (yielding n +1 total observations). The difference between these two statistics:

$$D = X_{L2}^2 - X_{L1}^2 \tag{3}$$

is distributed as a chi-square random variable with $DF_{L2} – DF_{L1}$ degrees of freedom. A calculated value of *D* that exceeds the χ^2 critical value indicates non-random feeding (Manly et al. 1993).

Feeding electivity

We quantified the feeding electivity exhibited by *Dascyllus flavicaudus* for each zooplankton group by calculating a forage ratio (w_i) that compares the proportion of prey group i in fish gut contents to the proportion of group i in the environmental sample. Our sampling design allows for measurement of prey use by individual fish, which are considered individual, random samples. While *D. flavicaudus* often live in large groups on single coral heads, we intentionally collected fish from separate coral heads (separated by > 2 m) in each location to minimize the possibility of feeding interference among individuals within each sample. The corresponding zooplankton tows are used as estimates of prey availability at each collection location. A forage ratio (w_i) was calculated for each zooplankton prey group from each of the 6 reef locations as:

$$w_i = (u_{i+}/u_{++}) / \pi_{\mathrm{i}} \qquad (4)$$

where u_{i+} is the sum of counts of prey group i across n fish and u_{++} is the grand sum of all prey groups enumerated in n gut content samples (notation follows Manly et al. 1993). π_i is the proportion of prey type i within the environmental zooplankton sample. Confidence intervals (95%) for w_i were calculated according to Manly (1993) and adjusted using a Bonferonni correction for $I = 16$ prey groups. The expected value of w_i under random feeding is 1, indicating that fish feed on zooplankton prey groups in direct proportion to their availability in the environment. Zooplankton groups with forage ratios ($w_i \pm$ CI) that exceeded 1 were associated with positive electivity, while groups with forage ratios ($w_i \pm$ CI) less than 1 were associated with negative electivity. Forage ratios ($w_i \pm$ CI) that overlapped 1 indicated that feeding on prey group i was indistinguishable from random feeding.

Influence of feeding electivity on fish diet

The influence of feeding electivity on the diet of *Dascyllus flavicaudus* was analyzed through (a) the taxonomic evenness of fish diet and (b) the relative contribution of oceanic zooplankton groups to total fish diet. To calculate the contribution of oceanic zooplankton to total fish diet, we distinguished zooplankton prey groups that are oceanic in origin from prey groups that are reef-associated using published data on cross-shore distributions of zooplankton abundance sampled in Moorea (Lefevre 1986, Renon 1989) (Table 3.1). Count data from zooplankton tow and fish gut samples were transformed to biomass estimates using published data on the carbon content (µg C individual^{-1}) of various zooplankton prey types (Appendix 3C: Table 3C.1). The environmental zooplankton samples from each collection location were used to calculate expected dietary evenness and percent contribution of oceanic groups to fish diet under a model of random feeding in which gut contents are a random sample of the ambient prey field. At each collection location, these expected values were compared with values calculated using the observed gut contents data. Zooplankton counts were summed across all fish within a collection location before calculating observed evenness and percent oceanic contribution, resulting in one pair of expected and observed measurements for each collection location. Paired t-tests were used to examine the null hypothesis of zero mean difference between observed and expected values.

A modified version (E_D) of Simpson's diversity index (D_S) was used to assess the taxonomic breadth of fish diet. Simpson's diversity index (also known as Levin's index of diet width) is calculated as:

$$D_S = 1 / \Sigma p_j^2 \qquad (5)$$

where p_j is the proportion of prey type j in the diet of a consumer (Levin 1968). This index (D_S) can be expressed as an evenness index (E_D) where values of D_S for each sample are scaled to the maximum possible value of D_S according to:

$$E_D = D_S / D_{S\,max} = 1 / \Sigma p_j^2 \times 1/S \qquad (6)$$

Here p_j is the proportion of prey type j in the diet of a consumer and S is the total number of species or prey types and ($1/S$) is the maximum value of D_S representing a sample with an equal number of all species. The equitability index ranges between 0 and 1. In our samples, the number of possible prey types remains constant ($S = 16$), as defined by the taxonomic resolution of the gut contents analysis. The contribution of oceanic zooplankton groups to total fish diet was determined by summing the estimated biomass of all oceanic zooplankton groups relative to the total zooplankton biomass for both environmental (expected) and fish gut contents (observed) samples. Carbon biomass was determined from the product of the number of prey type i and the estimated C content of each prey type (Appendix 3C: Table 3C.1).

RESULTS:

Prey use

The sampled fish guts contained large numbers of zooplankton prey items (median = 987 prey items per fish, Figure 3.2). The large sample size of prey items per fish suggests that gut content samples of *D. flavicaudus* are robust estimates of the diet of individual fish over short time scales (hours). Four zooplankton prey groups were dominant in fish gut samples: copepods from the families Oncaeidae and Corycaeidae, appendicularians, and calanoid copepods (Figure 3.3). Together these dominant groups comprised 33 % to 97 % of total gut contents sampled from individual fish. The remaining taxa typically comprised < 20 % of gut contents with some groups contributing <1 % of total prey enumerated. The combined contribution of these non-dominant groups to the gut contents of individual fish ranged from 0.8 % to 40 % of total prey items. The four dominant zooplankton groups occurred in all fish gut contents sampled (Table 3.2). Some non-dominant prey groups (fish eggs, pelagic harpacticoid copepods, *Oithona* spp.) occurred in greater than 60 % of all sampled fish guts, while other groups were both non-dominant and occurred in less than 10 % of guts samples (copepod nauplii, amphipods) (Table 3.1). Two groups, benthic harpacticoid copepods and cladocerans, were rare or absent from guts of forereef fish but occurred in > 90% of guts sampled from backreef fish (Table 3.1).

Prey availability

The composition of zooplankton groups in fish gut contents did not mirror the proportional contribution of zooplankton groups to the environmental samples (Figs. 3.3, 3.4). Three of the zooplankton groups that were numerically dominant in gut samples (Oncaeidae, Corycaeidae and appendicularians) each accounted for less than 20 % of zooplankton counted in environmental samples. In contrast, calanoid copepods and *Oithona* spp. dominated the environmental samples and together comprised 49 % - 78 % of the total zooplankton counts. Nevertheless, the combined contribution of these groups to fish gut contents ranged from as low as 1 % to a maximum of 20 % of total prey items.

Non-random feeding in Dascyllus flavicaudus

At each of the six collection locations, the relative contribution of zooplankton prey types to fish gut contents varied significantly among individual fish, evidenced by large log-likelihood statistics (X_{L1}^2) which were 2 to 10 fold greater than critical values (Table 3.3, Appendix 3D: Tables 3D.1 – 3D.12). With the inclusion of the environmental sample (zooplankton tow) at each location, the dissimilarity among samples increased, further inflating the second log-likelihood statistics (X_{L2}^2). At each reef location, the difference between these two statistics (D) was large, reflecting the disparity between fish gut contents and environmental zooplankton samples and indicating non-random feeding in *Dascyllus flavicaudus*.

Feeding electivity

Non-random feeding by *Dascyllus flavicaudus* resulted in both over- and underrepresentation of zooplankton groups in fish gut contents relative to the composition of the ambient zooplankton assemblage (Figure 3.5). Fish exhibited strong positive electivity for copepods from the family Oncaeidae. At all six locations sampled, the forage ratio (w_i ± CI) calculated for this group was significantly greater than 1 (Table 3.4, Appendix 3E: Tables 3E.1 – 3E.6). Oncaeidae was the only prey group with consistent evidence of positive electivity across all reef locations.

Electivity was positive for copepods from the family Corycaeidae in five of the six locations sampled and for the calanoid *Candacia* spp. at four locations; there was no evidence for non-random feeding on these copepods at the remaining two sites. Forage ratios for the copepod *Oithona* spp. and calanoid copepods indicated consistent negative electivity for these groups across sampled locations. Both of these copepod groups were present in large numbers in each environmental sample, but were infrequent in fish guts (Fig 3.3, Appendix 3B: Tables 3B.1- 3B.6). Evidence for negative electivity was also found for the 'other' copepod prey category. The forage ratios for the remaining eleven prey groups varied among reef locations with no consistent evidence for positive or negative electivity.

Influence of feeding electivity on fish diet

Non-random feeding in *Dascyllus flavicaudus* led to a significant difference between the expected (based on environmental samples) and observed taxonomic evenness of fish diet (Figure 3.6, $t = 3.121$, $df = 5$, $p = 0.0262$). Environmental samples exhibited low evenness values ranging from 0.106 to 0.191 (maximum $E_D = 1$). Prey items were more evenly distributed among zooplankton prey groups in fish gut contents samples, with evenness scores ranging from 0.169 to 0.411. Oceanic zooplankton groups (Table 3.1) comprised a significantly larger proportion of fish gut contents samples than expected from their abundance in environmental samples (Figure 3.7, $t = 5.048$, $df = 5$, $p = 0.00394$). The oceanic contribution to ambient zooplankton assemblages was low and similar among sampling locations (13.2 % ± 1.9 SD**).** In contrast, oceanic groups contributed up to 76 % of the zooplankton biomass in fish gut contents samples (54.3 % ± 20.9 SD), with greater variance among collection locations. Non-random feeding by *D. flavicaudus* resulted in a 2 to 6-fold increase of the contribution of oceanic groups to the total zooplankton biomass in fish diet beyond that expected under random feeding (Figure 3.7). The discrepancy between observed and expected percent contribution of oceanic prey to fish diet was driven largely by the positive electivity for the oceanic copepod groups Oncaeidae and Corycaeidae (Figure 3.5, Table 3.4).

DISCUSSION:

Dascyllus flavicaudus exhibits strong electivity (both positive and negative) for certain zooplankton prey groups, resulting in fish diets that differ significantly from the proportional composition of available prey in the environment. Fish feeding on three copepod groups (Oncaeidae, Corycaeidae and *Candacia* spp.) was associated with strong positive electivity scores; these groups comprised proportions of fish gut contents up to 50 times greater than their fractional contributions to environmental samples. Conversely, *D. flavicaudus* fed on the copepods *Oithona* spp. and calanoid copepods at much lower proportions than expected from their relative abundance in the environmental samples and thus these two prey groups are associated with strong negative electivity scores.

Though there was no consistent evidence for positive or negative electivity for Appendicularia, this group was found in all fish guts sampled and accounted for as much as 60 % of prey items sampled from individual fish. Appendicularians are known to be important prey in the diet of a broad range of adult, juvenile and larval fish worldwide (Purcell et al. 2007). Appendicularians can be an important food source for coral reef fish during their pelagic larval phase (Young & Davis 1990, Sampey et al. 2007, Llopiz et al. 2010), and are known to be prey for juvenile and adult diurnal planktivores on coral reefs (Hobson & Chess 1978, Hamner et al. 1988). As a food source, appendicularians can be nutritionally equivalent to small copepods in terms of biomass (Purcell et al. 2007, Alldredge & King 2009). As prey items for reef fish, appendicularians and other pelagic tunicates are unique among zooplankton groups as they provide a link between pico- and nanno-planktonic (including bacterial) carbon sources and fish predators (Alldredge & Madin 1982).

The 'selective' feeding in the reef fish *Dascyllus flavicaudus* described here is more appropriately termed electivity. Selective feeding implies that the consumer actively chooses among several available prey types, sizes of prey, etc. Feeding patterns (and forage ratios) similar to those calculated in the present study can also arise in the absence of active choice as a function of differential encounter rates among available zooplankton prey (Holzman & Genin 2005). Opportunities for selective feeding (either passive or active) can occur at each of the stages of the predation cycle outlined by Holling (1966): search, encounter, pursuit, capture, eating and digestive pause. *D. flavicaudus* is considered a 'particulate feeder' in that fish visually select and pursue individual zooplankton from the water column (Lazzaro 1987), and they rely on suction to ingest their particulate prey (Frederich et al. 2008). Prey detection in particulate-feeding zooplanktivorous fish and prey encounter rates are influenced by parameters of the physical environment (e.g. light intensity, flow speed), characteristics of the prey (e.g. actual or perceived size, pigmentation, swimming behavior) as well as by the visual acuity of fish predators (eye diameter, spectral sensitivities) (Lazzaro 1987, Kiflawi & Genin 1997). Evidence for active selection by a consumer and direct determination of the characteristics that drive active or passive selection (e.g. prey size or visibility) require field or laboratory experiments in which prey abundance and the distribution of prey characteristics can be manipulated (Hessen 1985, Holzman & Genin 2005). Documenting feeding 'preferences' of a consumer requires further controlled experimentation (Silva et al. 2010). The appropriate experimental design for studies of true consumer preference is subject to the operational definition of the term 'preference' as well as the specific hypotheses being tested (Underwood & Clarke 2007). The apparent selectivity documented here for *D. flavicaudus* provides the necessary groundwork for future experimental examination of active choice and/or feeding preferences in diurnal, planktivorous coral-reef fish.

Two of the copepod groups for which *D. flavicaudus* consistently exhibited positive electivity (Oncaeidae and Corycaeidae) are both brightly pigmented and females carry large, pigmented egg sacs. Copepods from these two families are known to have punctuated, jerky swimming motions (Yen 1988, Hwang & Turner 1995), which may make them more conspicuous to fish predators (Ware 1973, Wright & O'Brien 1982). The third prey taxon associated with positive electivity, the copepod *Candacia* spp., is the largest bodied among the copepod groups consumed by *D. flavicaudus*. This genus is characterized by dark pigmentation on the swimming legs and some species have a 'saddle' of black pigment across their prosome. Highly pigmented zooplankton are known to be more susceptible than transparent zooplankton to predation by visual planktivores (Luecke & O'Brien 1981). In planktivorous fish, the reaction distance (i.e. the maximum distance at which a predator responds to a prey item) and the probability of prey detection increase with increasing zooplankton prey size (Confer & Blades 1975) and with increasing zooplankton pigmentation (Utne-Palm 1999).

Aspects of swimming behavior are also likely to influence the negative electivity scores associated with the copepod groups *Oithona* spp. and calanoid copepods. Relative to other copepods, swimming in *Oithona* spp. is characterized by long periods where individuals remain motionless in the water column (Gauld 1966). On the basis of swimming behaviors as well as coloration, Paffenhöfer (1993) predicted that Oncaeaidae should be far more vulnerable to vertebrate predators than Oithonidae. Calanoid copepods generally exhibit relatively smooth, gliding swimming pattern (Brooks & Dodson 1965). Combined with their ability to execute powerful escape ‘jumps’(Kiorboe et al. 2010), these swimming behaviors may contribute to the low proportion of other calanoids in *D. flavicaudus* guts relative to their large proportional contribution to the available zooplankton assemblage.

The agreement of our data on the feeding behavior of *D. flavicaudus* with predictions based on attributes of copepod prey types emphasizes that feeding electivity reflects characteristics of the prey as well as dynamics of the predator-prey interaction. As such, the patterns of apparent selectivity we document for *D. flavicaudus* may predict the feeding behavior of other diurnal planktivorous fish on coral reefs. Similar patterns of predation on various copepod groups have also been documented for an invertebrate planktivore. A study of the scleractinian coral

Meandrina meandrites on reefs in St. Croix found that *Oithona sp*. contributed only 18.5 % of the prey items sampled from coral coelentera while this copepod accounted for 75.1 % of individuals enumerated from zooplankton tows (Johnson & Sebens 1993). Such patterns of prey use (e.g. apparent negative selectivity for Oithonidae) exhibited by multiple types of planktivores could significantly affect mortality rates of prey taxa. In a study of copepod carcasses (the result of predation by invertebrate and vertebrate planktivores) among zooplankton near the reefs of Eilat, Israel, Genin and colleagues (1995) found that the proportion of carcasses to live copepods was lower for cyclopoids than for calanoid copepods, suggesting lower predation rates on the former. In that study, the poecilostomatoid families Oncaeidae and Corycaeidae were included in counts of cyclopoid carcasses and no mention is made of the genus *Oithona*, although this group is found in the Gulf of Aqaba (Echelman & Fishelson 1990). A study of mortality in *Oithona similis* sampled from the North Sea documented low mortality rates (< 0.001 d^{-1}) for this species across life stages with the exception of the first two naupliar stages, indicating that the vast majority of individuals that survive stages N1 and N2 will also survive through adulthood (Eiane & Ohman 2004). This mortality pattern suggests that *Oithona* may generally exhibit hydrodynamically quiescent swimming behavior (Eiane & Ohman 2004) that, together with small body size and relative transparency, results in very low encounter rates and predation risk, a trend in agreement with the consistent negative electivity scores we calculated for *D. flavicaudus* feeding on *Oithona* spp.

Studies of coral reef zooplankton and diets of planktivorous reef organisms often provide little detailed taxonomic information for copepods even though copepods dominate reef zooplankton assemblages, the diet of planktivores and that of most larval fish (though see Sampey et al. 2007, Llopiz & Cowen 2009). Improvements to the taxonomic knowledge base available for coral reef zooplankton will permit future studies of the diet of zooplanktivorous coral reef fish to identify copepods to the higher taxonomic resolution.

The present study is the first to document strong non-random feeding in a diurnal, planktivorous coral-reef fish. These patterns of non-random feeding may significantly influence resource partitioning among competing zooplanktivorous fish, many of which live in large mixed-species groups that share coral habitat. The larval forms of tropical and sub-tropical fish species show strong apparent selectivity for subsets of the available zooplankton assemblage (Sampey et al. 2007, Llopiz & Cowen 2009, Llopiz et al. 2010), and such apparent resource partitioning could reduce competition among larval fish.

The non-random feeding exhibited by *Dascyllus flavicaudus* influences the proportional representation of oceanic zooplankton within fish diet. Oceanic zooplankton accounted for significantly greater proportions of fish diet than anticipated from environmental availability. This result was driven primarily by the strong positive electivity demonstrated for two oceanic copepod groups (Oncaeidae and Corycaeidae). Fish that eat zooplankton provide an important pathway for pelagic energy and nutrients to enter littoral reef systems in the form of accumulated fish biomass as well as waste products (Bray et al. 1981, Pinnegar & Polunin 2006). Our findings suggest that feeding behavior amplifies the role that *D. flavicaudus* plays as a vector for allochthonous (oceanic) material into coral reef food webs. Furthermore, agreement between our findings and previous studies of both reef consumers and zooplankton assemblages suggests that certain copepod taxa (specifically Oncaeidae and Corycaeidae) make more significant contributions to coral reef food webs than would be predicted from their numerical abundance alone, while taxa such as *Oithona* spp. make smaller contributions to reef food webs despite their numerical abundance within zooplankton assemblages.

***Acknowledgements*:**

Chapter 3 is in preparation for submission to Marine Ecology Progress Series and is presented as part of this dissertation with the acknowledgement of the study co-authors Emilie L. Schnarr, James J. Leichter and Mark D. Ohman. The dissertation author was the primary investigator and is the primary author of this material.

We thank A. Stier, L. Bentley, D. Combosch and W. Boudreau for their assistance collecting samples and the staff of the Richard B. Gump South Pacific Research Station for logistical support. This research was funded by mini-grant awards from the NSF Moorea Coral Reef LTER program to J. Leichter, a 3 Seas Teaching Fellowship to K. Hanson and an NSF REU fellowship to E. Schnarr via the California Current Ecosystem LTER. The collection of fish for this study was approved by French Polynesian research permits as well as by the UCSD Institutional Animal Care and Use Committee (Protocol # S06369).

Table 3.1. The habitat association of 16 zooplankton prey groups that comprise the diet of the reef fish *Dascyllus flavicaudus*. Prey groups are determined to be either oceanic in origin or associated with the reef system based on cross-shore patterns of abundance (Lefevre 1986, Renon 1989) and life history characteristics. Mixed origin groups could not be confidently assigned as either oceanic or reef associated.

Prey Group	**Association**
Oncaeidae	oceanic
Corycaeidae	oceanic
Appendicularia	oceanic
pelagic Harpacticoida	oceanic
Oithona spp.	oceanic
Ostracoda	reef
benthic Harpacticoida	reef
Cladocera	reef
fusiform fish eggs	reef
Decapoda	reef
round fish eggs	mixed origin
Calanoida	mixed origin
Candacia spp.	mixed origin
other Copepoda	mixed origin
Copepoda nauplii	mixed origin
Amphipoda	mixed origin

Table 3.2. The occurrence of 16 zooplankton prey groups in the diet of the reef fish *Dascyllus flavicaudus*. Data are shown for fish collected from the forereef (n = 15) and backreef (n = 14) habitats. Occurrence indicates the percentage of sampled guts that contained prey group *x*. Zooplankton prey groups are ordered from top to bottom by decreasing median percent contribution to total fish diet (see Fig. 3.3).

	% Occurrence	
Prey Group	**Forereef**	**Backreef**
Oncaeidae	100	100
Corycaeidae	100	100
Appendicularia	100	100
Calanoida	100	100
fusiform fish eggs	100	100
round fish eggs	80	100
other Copepoda	87	93
Candacia spp.	87	86
pelagic Harpacticoida	73	100
benthic Harpacticoida	27	100
Cladocera	0	93
Decapoda	47	29
Oithona spp.	67	79
Copepoda nauplii	7	0
Amphipoda	7	7
Ostracoda	20	29

Table 3.3. Log-likelihood statistics for goodness-of-fit tests of random feeding in *Dascyllus flavicaudus*. The test statistics are calculated for collections from 6 reef locations under 2 conditions: (a) based solely on gut contents counts (X_{L1}^2) and (b) including environmental zooplankton abundance from zooplankton tows (X_{L2}^2). The test statistic D is the difference between these two models. The critical χ^2 value shown is based on the degrees of freedom (DF) for each collection and $\alpha = 0.008$ (Bonferroni correction for $N = 6$ simultaneous tests).

Collection location	**Gut contents**			**Gut contents + environmental abundance**			$D = X_{L1}^2 - X_{L2}^2$		
	DF	X_{L1}^2	χ^2_{crit}	**DF**	X_{L2}^2	χ^2_{crit}	**DF**	D	χ^2_{crit}
forereef A	60	212	90	75	6934	108	15	6722	31
forereef B	60	512	90	75	2400	108	15	1888	31
forereef C	60	180	90	75	4215	108	15	4035	31
backreef A	60	952	90	75	6270	108	15	5318	31
backreef B	45	165	71	60	3250	90	15	3085	31
backreef C	60	396	90	75	4456	108	15	4060	31

Table 3.4. Electivity designations calculated for 16 zooplankton prey groups sampled from gut contents of *Dascyllus flavicaudus* collected at six reef locations. The numbers shown are forage ratios (with 95 % CI in parentheses) calculated for each prey group at each collection location (Appendix 3E: Tables 3E.1 – 3E.6). Calculated lower confidence limits resulting in negative values have been adjusted to zero. Positive electivity (+, in blue) indicates prey groups with forage ratio scores (w_i ± 95% CI) greater than 1, negative electivity (-, in red) indicates groups with forage ratio scores (w_i ± 95% CI) less than 1. Groups with forage ratio scores (w_i ± 95% CI) that overlapped 1 (in black) had similar relative abundances in fish guts and environmental samples. Fish feeding on these groups could not be distinguished from random feeding on the ambient zooplankton assemblage. Zooplankton groups with a forage ratio of zero and no corresponding confidence interval were not present in fish guts collected from a given sampling location.

Electivity	Zooplankton prey group	Forereef			Backreef		
		Site A	Site B	Site C	Site A	Site B	Site C
all +	Oncaeidae	25.44 (23.41 – 27.47)	1.85 (1.07 – 2.63)	54.43 (43.41 – 65.46)	8.29 (5.76 – 10.82)	2.43 (1.98 – 2.89)	3.01 (2.43 – 3.59)
majority +	Corycaeidae	2.20 (1.74 – 2.67)	0.96 (0.77 – 1.16)	7.40 (6.12 – 8.68)	2.22 (1.39 – 3.04)	3.97 (3.35 – 4.59)	3.36 (2.27 – 4.46)
	Candacia spp.	2.29 (1.29 – 3.29)	7.83 (4.06 – 11.61)	0.82 (0 – 1.97)	1.54 (0 – 3.27)	16.57 (4.08 – 29.07)	347.5 (125.13 – 569.87)
all -	*Oithona* spp.	0.01 (0 – 0.02)	0.01 (0.009 – 0.011)	0	0.03 (0.01 – 0.04)	0.01 (0 – 0.02)	0.05 (0.01 – 0.09)
	Calanoida	0.16 (0.13 – 0.19)	0.38 (0.22 – 0.53)	0.08 (0.02 – 0.15)	0.05 (0.02 – 0.07)	0.12 (0.11 – 0.13)	0.16 (0.09 – 0.23)
majority -	Copepoda	0.15 (0 – 0.39)	0.02 (0.01 – 0.04)	0.02 (0.01 – 0.03)	0.54 (0.26 – 0.81)	2.81 (1.45 – 4.17)	0.24 (0 – 0.48)
mixed	Appendicularia	0.64 (0.38 – 0.91)	5.89 (4.56 – 7.22)	0.79 (0.38 – 1.19)	2.37 (0.88 – 3.85)	8.39 (4.12 – 12.66)	1.06 (0.71 – 1.41)
	pelagic Harpacticoda	6.57 (4.67 – 8.46)	0.51 (0 – 1.43)	1.01 (0 – 2.48)	4.06 (2.00 – 6.11)	5.80 (3.87 – 7.73)	0.67 (0.52 – 0.81)
	benthic Harpacticoida	0	0.01 (0 – 0.03)	0.76 (0 – 1.87)	0.47 (0.18 – 0.76)	1.95 (0.49 – 3.41)	0.31 (0.10 – 0.51)
	Copepoda nauplii	0.02 (0 – 0.05)	0	0	0	0.83 (0 – 2.89)	0
	Ostracoda	0.15 (0 – 0.43)	0	0.14 (0 – 0.43)	0.09 (0 – 0.20)	0	0
	Cladocera	0	0	0	2.53 (1.71 – 3.34)	2.63 (1.22 – 4.03)	0.04 (0.01 – 0.08)
	round fish eggs	0.08 (0 – 0.19)	5.82 (2.90 – 8.75)	0.29 (0 – 0.58)	0.05 (0 – 0.10)	1.39 (1.22 – 1.55)	5.26 (3.23 – 7.30)
	fusiform fish eggs	1.56 (0 – 3.46)	1.16 (0.65 – 1.66)	4.55 (1.69 – 7.42)	0.72 (0.41 – 1.03)	2.65 (0.70 – 4.60)	63.44 (34.03 – 92.85)
	Decapoda	0.92 (0 – 2.21)	1.99 (1.32 – 2.66)	0	0.21 (0 – 0.67)	0.66 (0 – 1.93)	2.29 (0 – 6.12)
	other	0.53 (0.04 – 1.01)	0.82 (0 – 1.92)	0.20 (0 – 0.50)	0	4.97 (0 – 10.97)	1.47 (0 – 3.20)

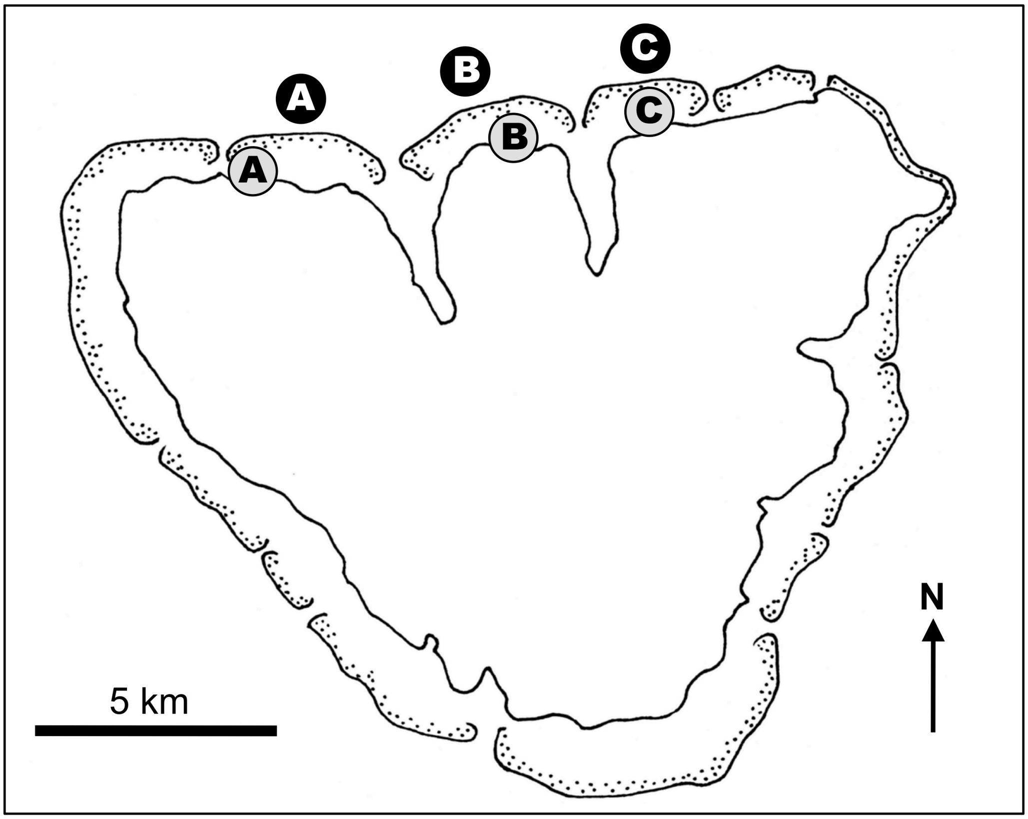

Figure 3.1. Map of the island of Moorea, French Polynesia showing the location of the six collection sites. The black symbols denote foreereef sites; backreef sites are indicated in grey.

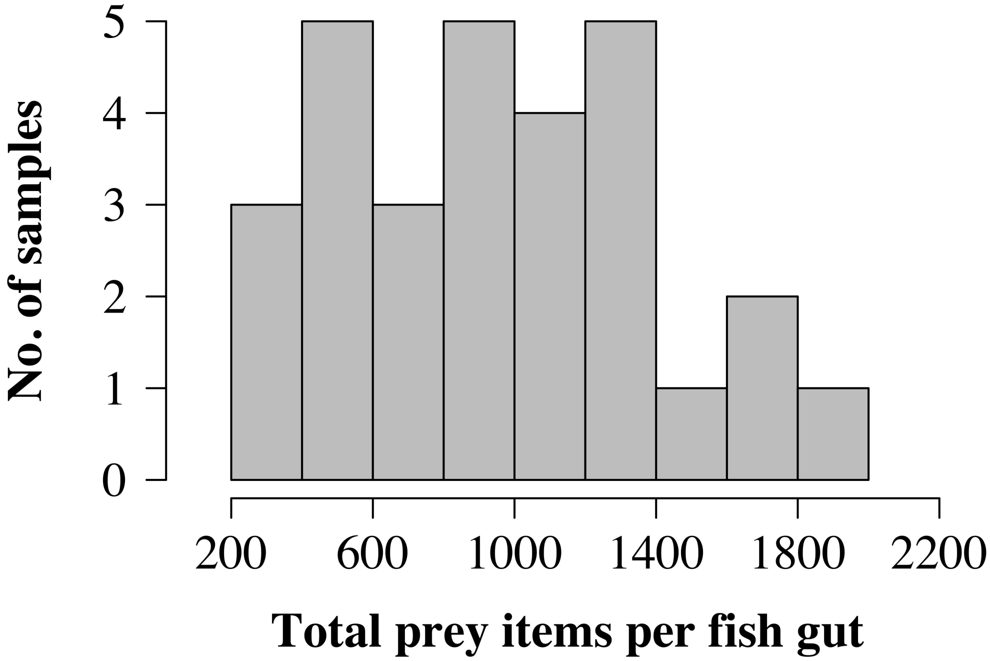

Figure 3.2. Frequency distribution of the number of total prey items in gut contents sampled from the reef fish *Dascyllus flavicaudus*.

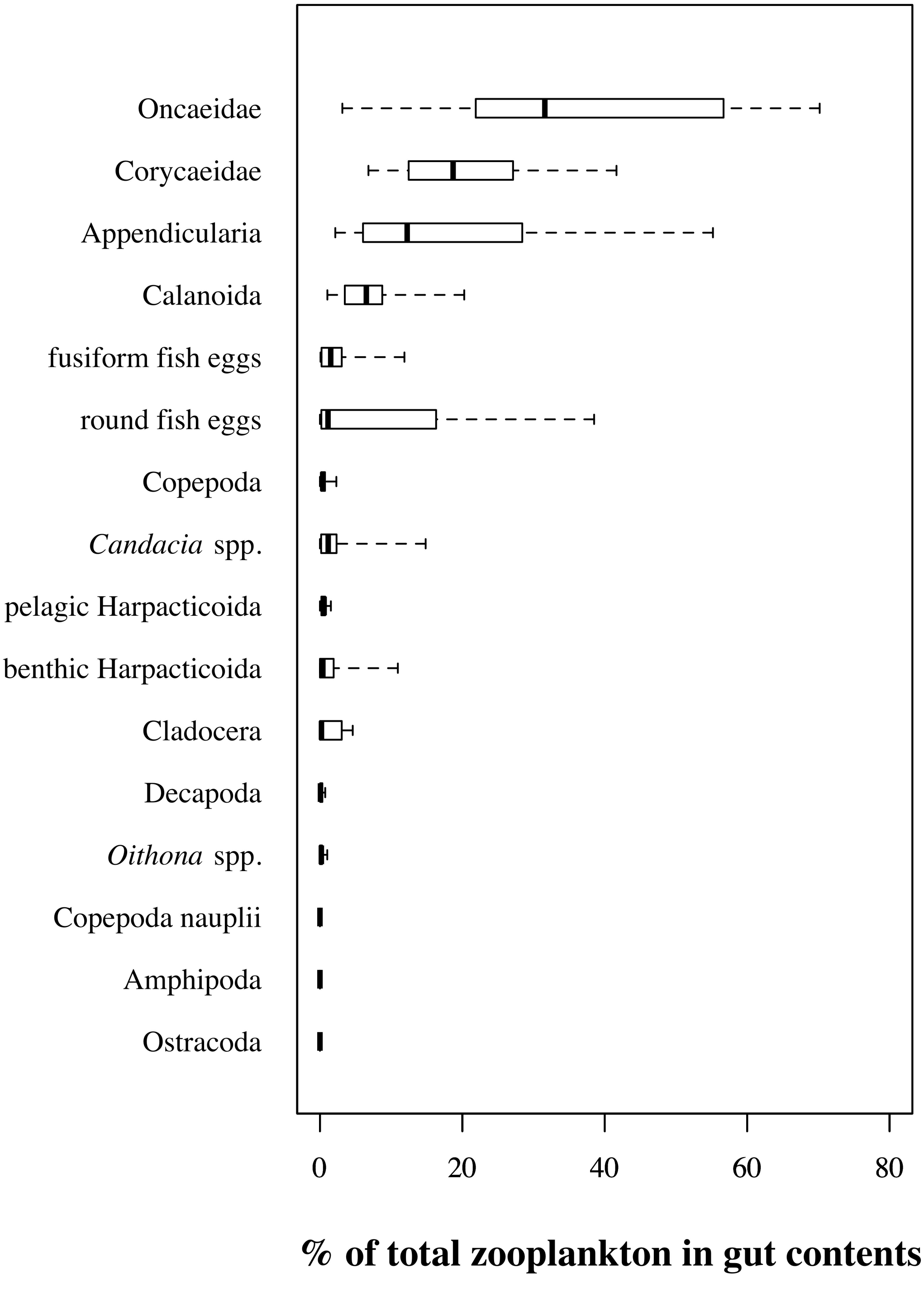

Figure 3.3. The percent contribution of zooplankton groups to total fish gut contents (n = 29 fish). Boxes extend from 25th to 75th percentile, whiskers to extreme data points. Black bars indicate median values. Prey groups are shown from top to bottom in order of decreasing median percent contribution to fish gut contents.

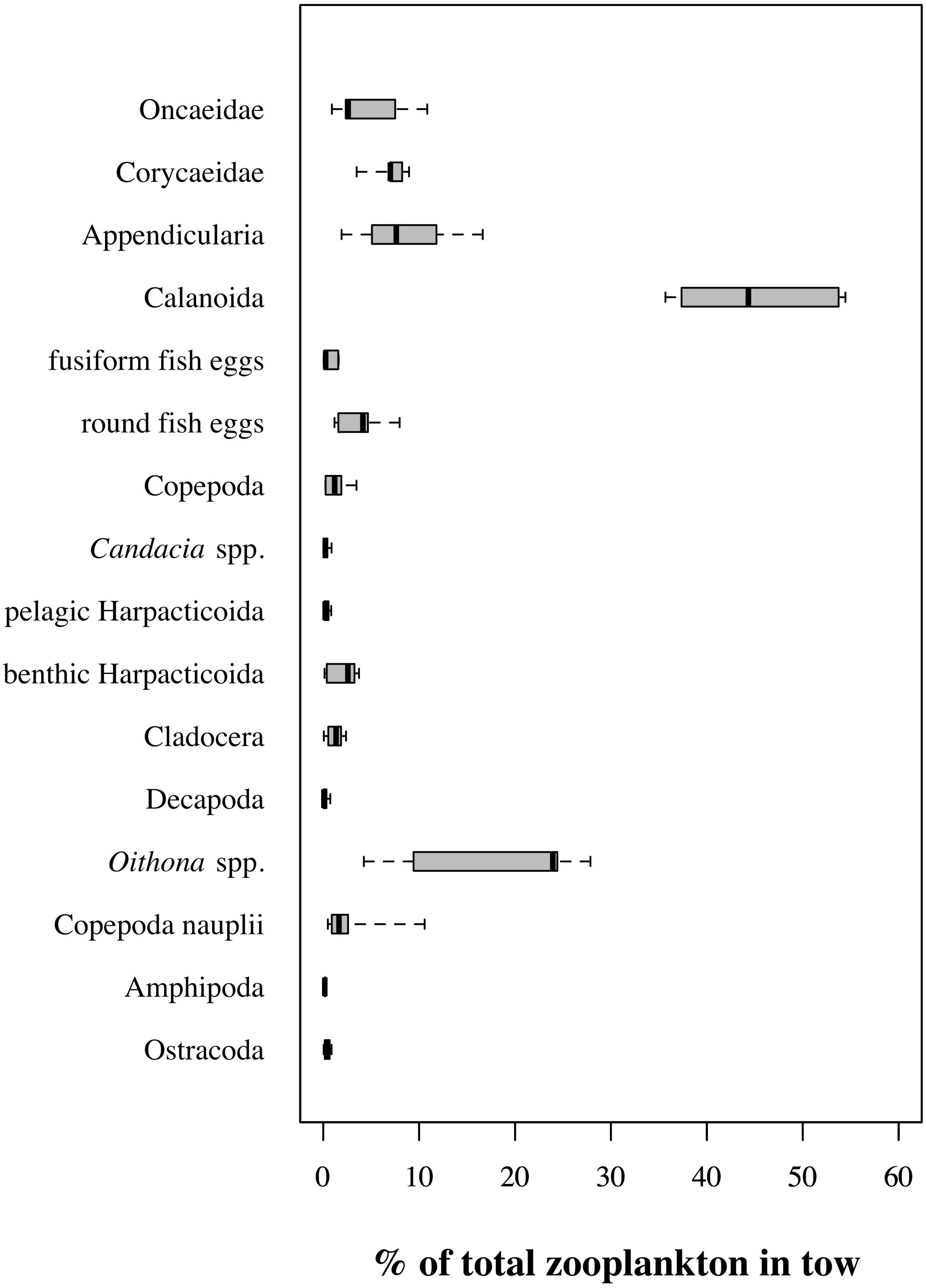

Figure 3.4. The percent contribution of zooplankton groups to total zooplankton collected in net tows at n = 6 reef locations. Boxes extend from 25th to 75th percentile, whiskers to extreme data points. Black bars indicate median values. Prey groups are shown from top to bottom in order of decreasing median percent contribution to fish gut contents (see Figure 3.3).

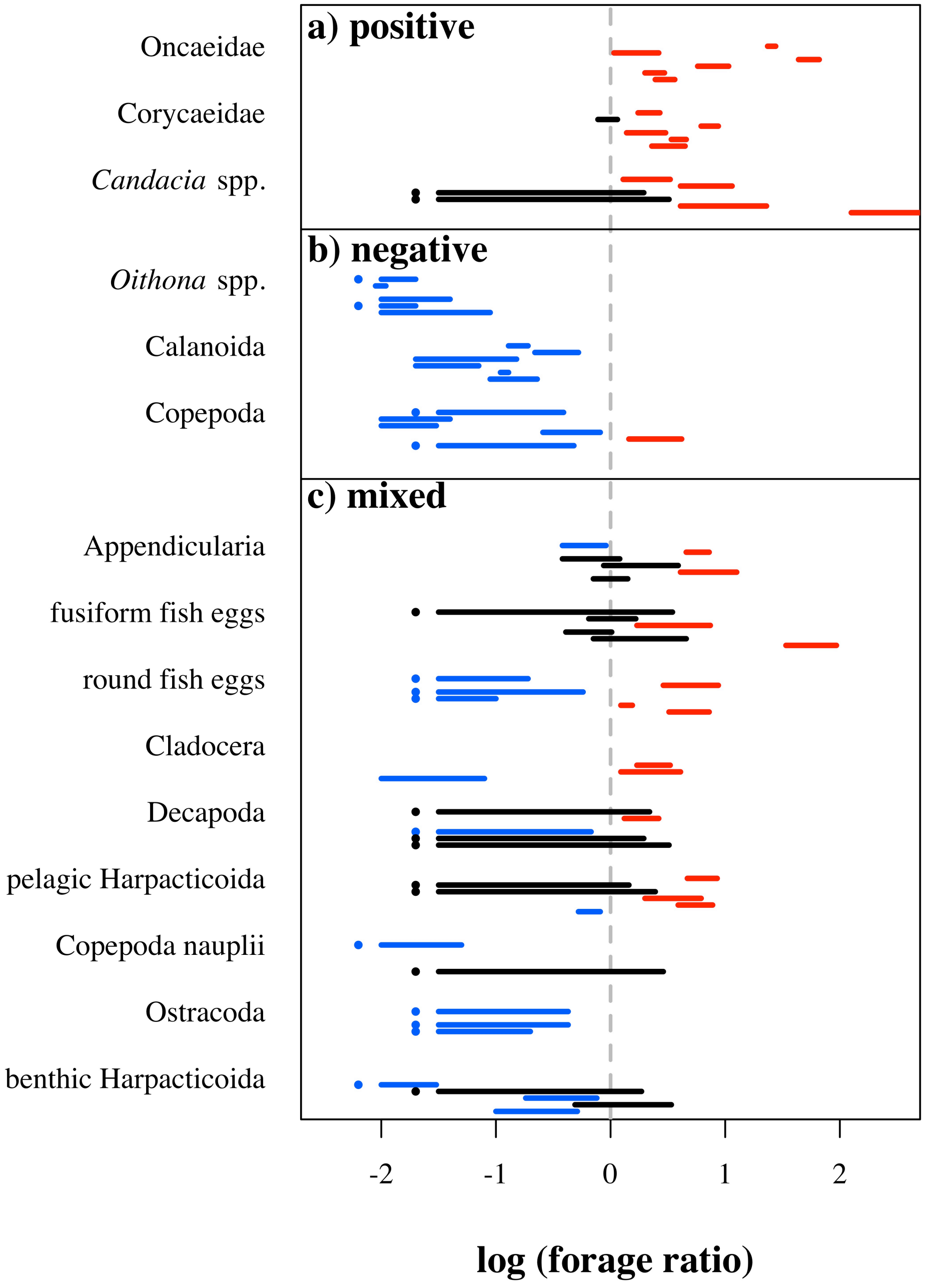

Figure 3.5. 95% confidence intervals on forage ratios calculated for 16 zooplakton taxa sampled from the guts of *D. flavicaudus.* Data are shown here as $\log_{10}$(forage ratio, w_i). Red lines indicate prey taxa associated with positive electivity, blue lines mark taxa associated with negative electivity. Black lines demark groups that can not be distinguished from random feeding. Circles indicate confidence intervals with that extend to $w_i = 0$ ($\log_{10} w_i \rightarrow -\infty$). **a)** Zooplankton groups associated with positive electivity at most sampling locations. **b)** Zooplankton groups associated with negative electivity at most sampling locations. **c)** Zooplankton groups with inconsistent electivity associations among sampling locations.

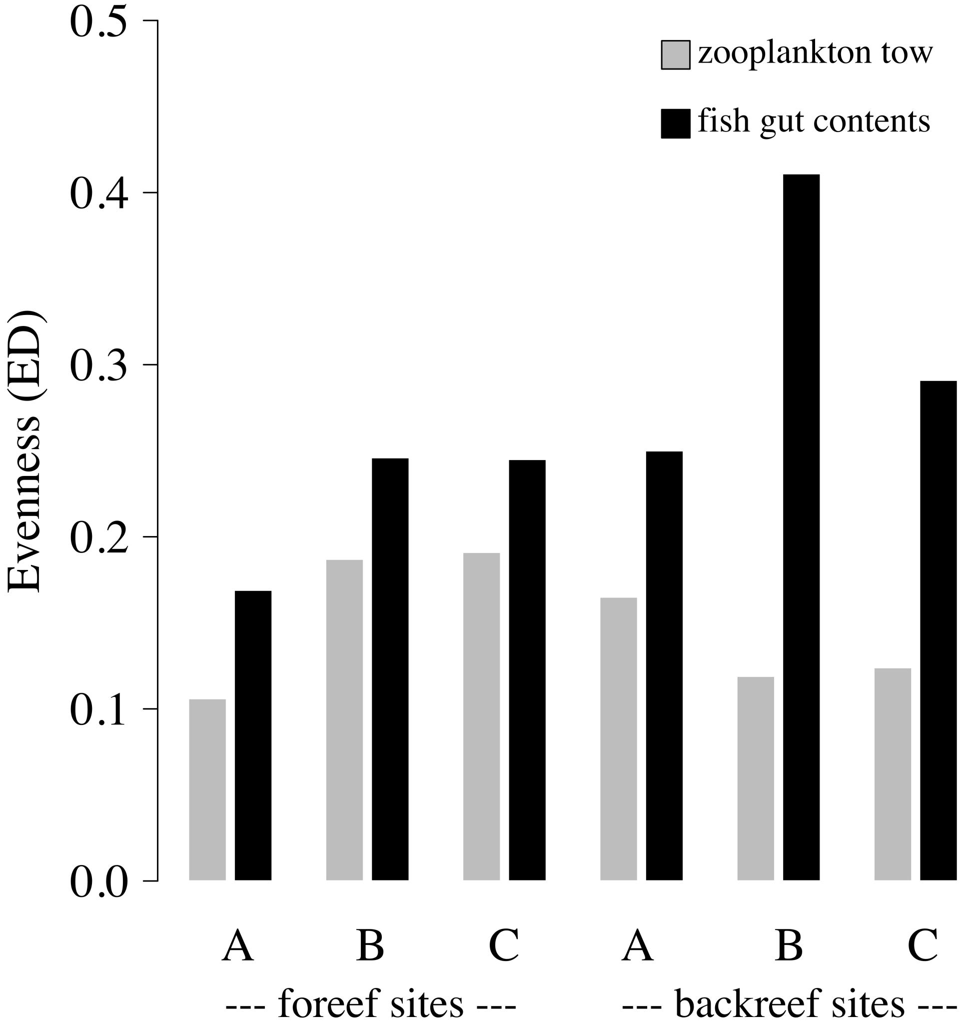

Figure 3.6. Evenness (E_D) of zooplankton carbon biomass sampled from zooplankton tows (grey bars) and fish gut contents (black bars). The data are paired by collection location.

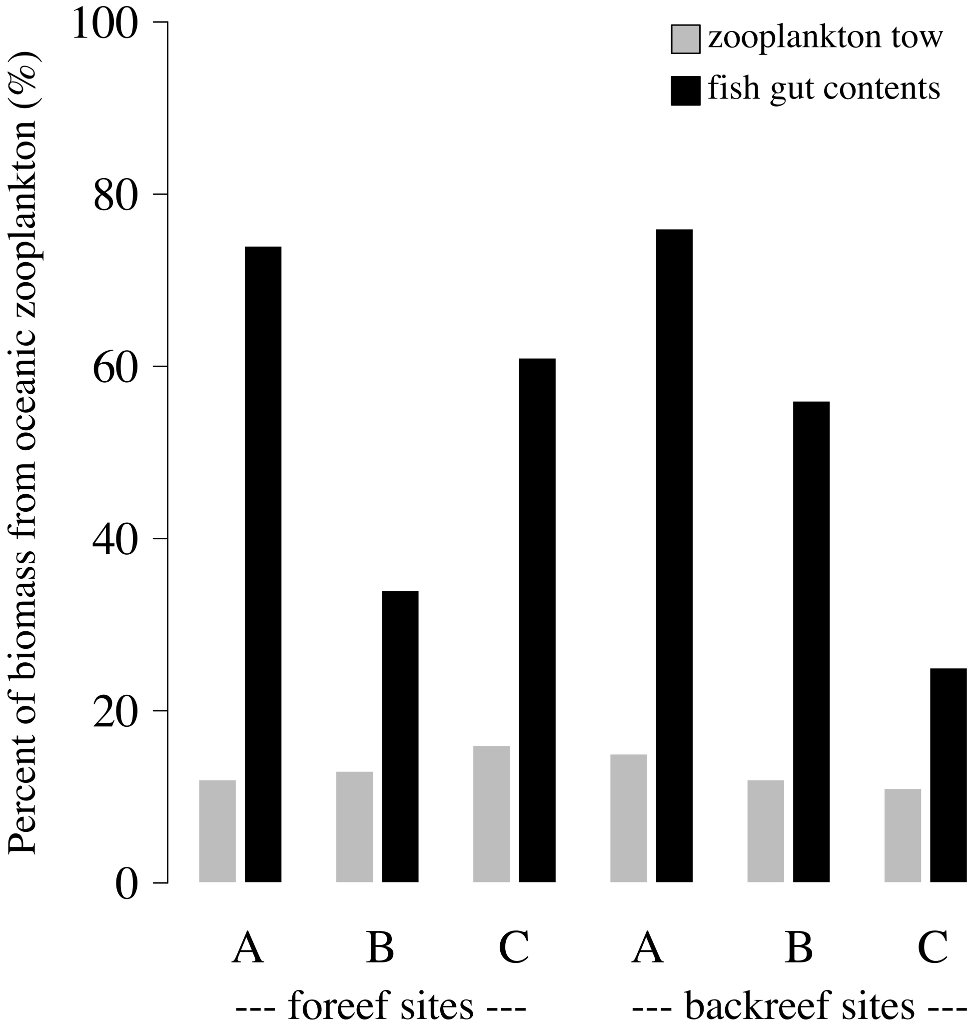

Figure 3.7. The percent contribution of oceanic groups to zooplankton carbon biomass sampled from zooplankton tows (grey bars) and fish gut contents (black bars). The data are paired by collection location.

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Appendix 3A: Taxonomic detail of prey groups used in the study of the diet of *Dascyllus flavicaudus*

Table 3A.1. Zooplankton associated with prey groups used in the current study. Species identifications are taken from a study conducted in Moorea, French Polynesia (Lefevre 1986).

Prey group	**Components**	**Source**
Appendicularia	*Oikopleura cophocera*	Lefevre (1986)
	O. longicauda	Lefevre (1986)
Cladocera	*Evadne* spp.	
Ostracoda	*Cypridina cf. serrata*	Lefevre (1986)
Decapoda	brachyuran larvae	
	anomuran larvae	
	natantian larvae	
fusiform fish eggs	*Chlorurus* spp.	Leis & Trnski (1989)
	Scarus spp.	Leis & Trnski (1989)
round fish eggs	mixed species	
other	coral larvae	
	polychaete larvae	
	pelagic amphipods	
	unidentifiable forms	

Table 3A.2. Copepods associated with zooplankton prey groups used in the current study. Species identifications are taken from two studies conducted in Moorea, French Polynesia (Lefevre 1986, Renon 1989).

Prey group	**Associated species**	**Source**
Corycaeidae	*Corycaeus agilis*	Lefevre (1986)
	C. latus	Lefevre (1986)
	C. limbatus	Lefevre (1986)
	C. robustus	Lefevre (1986)
	C. speciosus	Lefevre (1986)
	Farranula gracilis	Renon (1989)
	F. gibbula	Lefevre (1986)
Oncaeidae	*Lubbockia squillimana*	Lefevre (1986)
	Oncaea conifera	Lefevre (1986)
.	*O. mediterranea*	Lefevre (1986)
	O. venusta	Lefevre (1986)
Oithona spp.	*Oithona nana*	Lefevre (1986), Renon (1989)
	O. oculata	Renon (1989)
	O. plumifera	Lefevre (1986), Renon (1989)
	O. rigida	Renon (1989)
Candacia spp.	*Candacia aethiopica*	Renon (1989)
	C. catula	Lefevre (1986)
	C. simplex	Lefevre (1986)
	C. truncata	Lefevre (1986)

Table 3A.2. (cont'd) Copepods associated with zooplankton prey groups used in the current study. Species identifications are taken from two studies conducted in Moorea, French Polynesia (Lefevre 1986, Renon 1989).

Prey group	**Associated species**	**Source**
Calanoida	*Acartia danae*	Renon (1989)
	A. fossae	Lefevre (1986), Renon (1989)
	A. negligens	Renon (1989)
	Acrocalanus spp.	Renon (1989)
	Calanopia minor	Renon (1989)
	C. sewell	Lefevre (1986)
	Calocalanus pavo	Lefevre (1986)
	C. plumulosus	Lefevre (1986)
	Canthocalanus pauper	Renon (1989)
	Centropages furcatus	Lefevre (1986)
	C. gracilis	Lefevre (1986), Renon (1989)
	Clausocalanus spp.	Renon (1989)
	Labidocera bataviae	Renon (1989)
	Nannocalanus minor	Renon (1989)
	Paracalanus spp.	Renon (1989)
	Pleuromamma gracilis	Lefevre (1986), Renon (1989)
	Undinula vulgaris	Renon (1989)

Table 3A.2. (cont'd) Copepods associated with zooplankton prey groups used in the current study. Species identifications are taken from two studies conducted in Moorea, French Polynesia (Lefevre 1986, Renon 1989).

Prey group	**Associated species**	**Source**
pelagic Harpacticoida	*Euterpina acutifrons*	Lefevre (1986)
	Macrosetella gracilis	Renon (1989)
	Microsetella spp.	Lefevre (1986)
benthic Harpacticoida	*Metis* spp.	Renon (1989)
Copepoda	*Saphirella spp.*	Lefevre (1986), Renon (1989)
	Sapphirina auronitens	Lefevre (1986)
	S. gastrica	Lefevre (1986)
	S. nigromaculata	Lefevre (1986)
Copepoda nauplii	mixed species	

Appendix 3B: The abundance of zooplankton groups in gut content samples and environmental samples as related to sub-sampling and enumeration methodology.

Table 3B.1. Qualitative abundance of zooplankton groups in gut content samples. Rare taxa (< 100 individuals total) were counted from the entirety of the sample. Numerically dominant groups (> 100 individuals total) were counted from one or more aliquots until 100 individuals were counted. Subsample counts were multiplied by the number of aliquots enumerated to yield an estimate of total abundance.

Abundance designation	Prey group
Rare (<100 individuals) in 100% of samples	Calanoida
	Candacia spp.
	fusiform fish eggs
	Copepoda
	pelagic Harpacticoida
	benthic Harpacticoida
	Cladocera
	Decapoda
	Oithona spp.
	Copepoda - nauplii
	Ostracoda
Abundance varied among samples	Oncaeidae
	Corycaeidae
	Appendicularia
	round fish egg

Table 3B.2. Qualitative abundance of zooplankton groups in zooplankton tow samples. Rare taxa (< 100 individuals total) were counted from the entirety of the sample. Numerically dominant groups (> 100 individuals total) were counted from one or more aliquots until 100 individuals were counted. Subsample counts were multiplied by the number of aliquots enumerated to yield an estimate of total abundance.

Abundance designation	**Prey group**
Rare (<100 individals) in 100% of samples	Oncaeaidae
	fusiform fish eggs
	Candacia spp.
	pelagic Harpacticoida
	Decapoda
	Ostracoda
Abundant (>100 individals) in 100% of samples	Calanoida
	Oithona spp.
Abundance varied among samples	Corycaeidae
	Appendicularira
	round fish eggs
	Copepoda
	benthic Harpacticoida
	Cladocera
	Copepoda nauplii

Appendix 3C: Details of biomass conversions used to calculate the contribution of oceanic food sources to the diet of *Dascyllus flavicaudus.*

Table 3C.1. Published data on the carbon content (POC, μg C animal^{-1}) of various zooplankton types, together with the values selected to transform count data to zooplankton biomass in the present study. The values used in this study were adjusted or selected from a range of values reported in the literature according to the body size of individuals sampled from fish guts in Moorea relative to the body size of reference organisms used in the published studies.

Zooplankton prey group	POC (μg C animal^{-1})	Size (mm)	Reference organism	Reference	Value used (μg C animal^{-1})
Appendicularia	3.5 ± SD 0.2	0.4 - 1.5	appendicularians	Alldredge and King (2009)	3.5
Corycaeidae	0.37 - 4.65	0.28 - 1.0	*Corycaeus* spp.	Satapoomin (1999)	2.5
Oncaeidae	0.38 - 5.26	0.3 - 0.74	*Oncaea* spp.	Satapoomin (1999)	2.8
Calanoida	0.81 - 12.23	0.59 - 1.2	*Centropages furcatus*	Satapoomin (1999)	6.52
Candacia spp.	0.81 - 12.23	0.59 - 1.2	*Centropages furcatus*	Satapoomin (1999)	12.24
pelagic Harpacticoida	0.21 - 1.39	0.36 - 1.18	*Macrosetella gracilis*	Satapoomin (1999)	0.8
benthic Harpacticoida	1.74 ± SD 0.22	0.838	*Amphiascoides atopus*	Baguley et al. (2004)	1.74
Oithona spp.	0.5	0.8	*Oithona similis*	Logerwell and Ohman (1999)	0.5
Copepoda	4.6 ± SD 0.3	0.4 - 1.2	pooled copepods	Alldredge and King (2009)	4.6
Copepoda nauplii	0.068 ± SE 0.001	0.127	*Oithona davisae*	Almeda et al. (2011)	0.07
Ostracoda	15.6 ± SD 3.4	0.2 - 1.2	ostracods	Alldredge and King (2009)	15.6
Cladocera	15.6 ± SD 3.4	0.2 - 1.2	ostracods	Alldredge and King (2009)	15.6
round fish eggs	17.52 ± SD 1.40	1.003 ± 0.024	*Solea senegalensis*	Yúfera et al. (1999)	8.76
fusiform fish eggs	17.52 ± SD 1.40	1.003 ± 0.024	*Solea senegalensis*	Yúfera et al. (1999)	17.52
Decapoda	17.9 ± SD 9.0	1.1 - 3.0	decapod larvae	Alldredge and King (2009)	17.9

Appendix 3D: Details of the calculation of log-likelihood statistics used to evaluate the hypothesis of random feeding in *Dascyllus flavicaudus*.

Table 3D.1. Calculation of the test statistic X_{L1}^2 using gut contents data from *D. flavicaudus* collected at forereef site A.

	i **=Zooplankton prey group**	**Gut contents counts (u_{ij})**					**Total (u_{i+})**	**u_{ij} * ln[u_{ij} * (u_{++} / (u_{i+} * u_{+j}))]**				
		j = 1	**j = 2**	**j = 3**	**j = 4**	**j = 5**		**j = 1**	**j = 2**	**j = 3**	**j = 4**	**j = 5**
1	Appendicularia	68	94	113	50	19	344	-12.42	11.61	50.01	-12.30	-15.41
2	Corycaeidae	210	243	210	222	196	1081	-42.02	-17.43	-17.36	22.13	73.98
3	Oncaeidae	1196	1152	924	860	504	4636	99.97	32.85	-52.70	-1.76	-67.56
4	Calanoida	111	121	140	105	68	545	-16.96	-10.18	27.54	3.76	0.25
5	*Candacia* spp.	30	22	36	18	33	139	-2.84	-9.30	7.38	-6.51	21.35
6	pelagic Harpacticoida	10	16	11	9	11	57	-3.02	2.41	-0.98	-1.47	4.84
7	benthic Harpacticoida	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
8	*Oithona* spp.	3	10	3	3	5	24	-1.92	5.45	-1.57	-1.19	2.58
9	Copepoda	0	0	2	2	0	4	0.00	0.00	1.73	1.98	0.00
10	Copepoda nauplii	0	0	1	0	0	1	0.00	0.00	1.56	0.00	0.00
11	Ostracoda	0	0	0	2	1	3	0.00	0.00	0.00	2.55	0.99
12	Cladocera	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
13	round fish eggs	0	0	3	3	1	7	0.00	0.00	2.13	2.51	0.14
14	fusiform fish eggs	3	5	4	1	14	27	-2.28	-1.33	-1.41	-1.61	19.99
15	Decapoda	1	0	1	0	0	2	0.75	0.00	0.86	0.00	0.00
16	other	2	0	5	5	4	16	-1.28	0.00	1.96	2.60	2.79
	Column total (u_{+j})	**1634**	**1663**	**1453**	**1280**	**856**	**u_{++} = 6886**				**X_{L1}^2 =**	**212**

Table 3D.2. Calculation of the test statistic X_{L2}^2 using gut contents data from *D. flavicaudus* collected at forereef site A.

i =Zooplankton prey group		Gut contents counts (u_{ij})					ZP tow	Total (u_{i+})	u_{ij} * ln[u_{ij} * (u_{++} / (u_{i+} * u_{+j}))]					
		j = 1	j = 2	j = 3	j = 4	j = 5			j = 1	j = 2	j = 3	j = 4	j = 5	ZP tow
1	Appendicularia	68	94	113	50	19	246	590	-23.33	-3.47	31.89	-20.32	-18.46	68.58
2	Corycaeidae	210	243	210	222	196	226	1307	-2.28	28.56	22.38	64.13	111.07	-135.91
3	Oncaeidae	1196	1152	924	860	504	84	4720	531.87	448.86	280.97	308.80	114.44	-241.51
4	Calanoida	111	121	140	105	68	1560	2105	-124.88	-127.82	-108.57	-98.32	-65.86	1332.15
5	*Candacia* spp.	30	22	36	18	33	28	167	3.02	-4.99	14.42	-2.99	27.80	-17.70
6	pelagic Harpacticoida	10	16	11	9	11	4	61	0.09	7.39	2.44	1.33	8.26	-6.28
7	benthic Harpacticoida	0	0	0	0	0	12	12	0.00	0.00	0.00	0.00	0.00	13.84
8	*Oithona* spp.	3	10	3	3	5	900	924	-11.74	-27.26	-11.39	-11.01	-13.78	1014.53
9	Copepoda	0	0	2	2	0	12	16	0.00	0.00	-0.29	-0.04	0.00	10.39
10	Copepoda nauplii	0	0	1	0	0	30	31	0.00	0.00	-1.50	0.00	0.00	33.62
11	Ostracoda	0	0	0	2	1	9	12	0.00	0.00	0.00	0.54	-0.02	7.79
12	Cladocera	0	0	0	0	0	2	2	0.00	0.00	0.00	0.00	0.00	2.31
13	round fish eggs	0	0	3	3	1	38	45	0.00	0.00	-2.32	-1.94	-1.34	37.41
14	fusiform fish eggs	3	5	4	1	14	8	35	-1.92	-0.73	-0.94	-1.49	21.67	-2.58
15	Decapoda	1	0	1	0	0	1	3	0.72	0.00	0.84	0.00	0.00	0.05
16	other	2	0	5	5	4	14	30	-1.78	0.00	0.72	1.35	1.80	5.48
	Column total (u_{+j})	**1634**	**1663**	**1453**	**1280**	**856**	**3174**	**u_{++} = 10060**					**X_{L2}^2 =**	**6934**

Table 3D.3 Calculation of the test statistic X_{L1}^2 using gut contents data from *D. flavicaudus* collected at forereef site B.

i =Zooplankton prey group		Gut contents counts (u_{ij})					Total (u_{i+})	u_{ij} * ln[u_{ij} * (u_{++}/(u_{i+} * u_{+j}))]				
		j = 1	j = 2	j = 3	j = 4	j = 5		j = 1	j = 2	j = 3	j = 4	j = 5
1	Appendicularia	296	400	452	632	504	2284	-65.95	-49.29	-66.95	151.59	68.12
2	Corycaeidae	92	82	121	89	69	453	20.83	-7.39	18.36	-9.13	-16.25
3	Oncaeidae	67	41	51	36	33	228	39.92	-3.97	-1.31	-11.56	-9.46
4	Calanoida	135	67	184	232	120	738	16.45	-52.28	15.25	85.25	-20.42
5	*Candacia* spp.	9	17	14	21	31	92	-4.54	-1.18	-5.75	1.00	17.31
6	pelagic Harpacticoida	11	2	0	0	2	15	16.61	-0.79	0.00	0.00	-0.74
7	benthic Harpacticoida	0	1	0	0	0	1	0.00	1.62	0.00	0.00	0.00
8	*Oithona* spp.	3	3	3	2	3	14	0.84	0.24	-0.21	-0.84	0.32
9	Copepoda	1	4	3	1	2	11	-0.58	2.43	0.52	-0.87	-0.12
10	Copepoda nauplii	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
11	Ostracoda	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
12	Cladocera	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
13	round fish eggs	216	402	332	108	207	1265	11.44	189.99	44.55	-101.09	-33.92
14	fusiform fish eggs	15	16	20	13	31	95	-0.38	-2.60	-1.73	-6.04	16.32
15	Decapoda	4	4	10	9	8	35	-1.39	-2.20	2.19	1.50	1.36
16	other	2	2	16	1	3	24	-1.33	-1.73	17.06	-1.65	-1.30
	Column total (u_{+j})	**851**	**1041**	**1206**	**1144**	**1013**	**u_{++} = 5255**				**X_{L1}^2 =**	**512**

Table 3D.4 Calculation of the test statistic X_{L2}^2 using gut contents data from *D. flavicaudus* collected at forereef site B.

i =Zooplankton prey group		Gut contents counts (u_{ij})					ZP tow	Total (u_{i+})	u_{ij} * ln[u_{ij} * (u_{++} / u_{i+} * u_{+j})]					
		j = 1	j = 2	j = 3	j = 4	j = 5			j = 1	j = 2	j = 3	j = 4	j = 5	ZP tow
1	Appendicularia	296	400	452	632	504	66	**2350**	-27.83	2.23	-8.74	232.98	133.03	-108.58
2	Corycaeidae	92	82	121	89	69	80	**533**	20.34	-7.83	17.72	-9.61	-16.62	2.47
3	Oncaeidae	67	41	51	36	33	21	**249**	44.56	-1.13	2.22	-9.07	-7.17	-11.46
4	Calanoida	135	67	184	232	120	334	**1072**	-12.72	-66.75	-24.51	35.12	-46.35	254.26
5	*Candacia* spp.	9	17	14	21	31	2	**94**	-3.31	1.13	-3.85	3.85	21.52	-3.85
6	pelagic Harpacticoida	11	2	0	0	2	5	**20**	15.18	-1.05	0.00	0.00	-1.00	2.71
7	benthic Harpacticoida	0	1	0	0	0	23	**24**	0.00	-1.40	0.00	0.00	0.00	43.35
8	*Oithona* spp.	3	3	3	2	3	214	**228**	-7.06	-7.66	-8.10	-6.11	-7.58	398.90
9	Copepoda	1	4	3	1	2	76	**87**	-2.49	-5.21	-5.21	-2.78	-3.94	136.21
10	Copepoda nauplii	0	0	0	0	0	8	**8**	0.00	0.00	0.00	0.00	0.00	15.42
11	Ostracoda	0	0	0	0	0	6	**6**	0.00	0.00	0.00	0.00	0.00	11.56
12	Cladocera	0	0	0	0	0	1	**1**	0.00	0.00	0.00	0.00	0.00	1.93
13	round fish eggs	216	402	332	108	207	37	**1302**	39.19	241.63	87.19	-87.22	-7.33	-60.43
14	fusiform fish eggs	15	16	20	13	31	14	**109**	-0.08	-2.28	-1.33	-5.78	16.93	-1.75
15	Decapoda	4	4	10	9	8	3	**38**	-1.09	-1.90	2.94	2.17	1.96	-1.83
16	other	2	2	16	1	3	5	**29**	-1.39	-1.80	16.55	-1.69	-1.40	0.85
	Column total (u_{+j})	**851**	**1041**	**1206**	**1144**	**1013**	**895**	**u_{++} = 6150**					**X_{L2}^2 =**	**2400**

Table 3D.5 Calculation of the test statistic X_{L1}^2 using gut contents data from *D. flavicaudus* collected at forereef site C.

i =Zooplankton prey group		Gut contents counts (u_{ij})					Total (u_{i+})	$u_{ij} * \ln[u_{ij} * (u_{++} / u_{i+} * u_{+j})]$				
		j = 1	j = 2	j = 3	j = 4	j = 5		j = 1	j = 2	j = 3	j = 4	j = 5
1	Appendicularia	40	62	61	51	43	257	9.01	37.93	-3.66	5.19	-27.02
2	Corycaeidae	46	59	122	96	184	507	-14.46	-6.92	-5.65	5.27	26.85
3	Oncaeidae	121	96	286	133	332	968	0.74	-26.61	45.46	-35.35	29.68
4	Calanoida	5	12	12	22	8	59	-1.91	5.29	-2.57	16.12	-6.71
5	*Candacia* spp.	3	0	0	3	1	7	3.71	0.00	0.00	2.62	-0.79
6	pelagic Harpacticoida	1	2	1	0	0	4	0.70	2.68	-0.01	0.00	0.00
7	benthic Harpacticoida	1	0	0	0	1	2	1.39	0.00	0.00	0.00	0.47
8	*Oithona* spp.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
9	Copepoda	1	0	1	1	1	4	0.70	0.00	-0.01	0.33	-0.23
10	Copepoda nauplii	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
11	Ostracoda	0	0	0	0	1	1	0.00	0.00	0.00	0.00	1.16
12	Cladocera	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
13	round fish eggs	0	1	3	4	1	9	0.00	-0.16	0.84	3.63	-1.04
14	fusiform fish eggs	26	24	9	42	43	144	9.72	5.81	-12.55	20.45	-2.11
15	Decapoda	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
16	other	0	1	0	0	1	2	0.00	1.34	0.00	0.00	0.47
	Column total (u_{+j})	**244**	**257**	**495**	**352**	**616**	**u_{++} = 1964**				**X_{L1}^2 =**	**180**

Table 3D.6 Calculation of the test statistic X_{L2}^2 using gut contents data from *D. flavicaudus* collected at forereef site C.

	i =Zooplankton prey group	Gut contents counts (u_{ij})					ZP tow	Total (u_{i+})	u_{ij} * ln[u_{ij} * (u_{++} / (u_{i+} * u_{+j}))]					
		j = 1	j = 2	j = 3	j = 4	j = 5			j = 1	j = 2	j = 3	j = 4	j = 5	ZP tow
1	Appendicularia	40	62	61	51	43	496	753	2.96	28.54	-12.90	-2.53	-33.53	43.89
2	Corycaeidae	46	59	122	96	184	104	611	19.44	36.56	84.27	76.03	162.46	-131.53
3	Oncaeidae	121	96	286	133	332	27	995	109.17	59.41	301.74	83.83	327.18	-83.72
4	Calanoida	5	12	12	22	8	1064	1123	-12.03	-18.98	-26.84	-28.38	-22.89	480.95
5	*Candacia* spp.	3	0	0	3	1	13	20	3.34	0.00	0.00	2.24	-0.91	0.98
6	pelagic Harpacticoida	1	2	1	0	0	6	10	0.71	2.70	0.00	0.00	0.00	-0.03
7	benthic Harpacticoida	1	0	0	0	1	4	6	1.22	0.00	0.00	0.00	0.29	0.40
8	*Oithona* spp.	0	0	0	0	0	728	728	0.00	0.00	0.00	0.00	0.00	368.36
9	Copepoda	1	0	1	1	1	347	351	-2.85	0.00	-3.56	-3.22	-3.78	171.60
10	Copepoda nauplii	0	0	0	0	0	49	49	0.00	0.00	0.00	0.00	0.00	24.79
11	Ostracoda	0	0	0	0	1	11	12	0.00	0.00	0.00	0.00	-0.40	4.61
12	Cladocera	0	0	0	0	0	1	1	0.00	0.00	0.00	0.00	0.00	0.51
13	round fish eggs	0	1	3	4	1	47	56	0.00	-1.07	-1.87	0.01	-1.94	15.55
14	fusiform fish eggs	26	24	9	42	43	48	192	26.25	21.07	-6.83	47.16	25.23	-42.25
15	Decapoda	0	0	0	0	0	22	22	0.00	0.00	0.00	0.00	0.00	11.13
16	other	0	1	0	0	1	15	17	0.00	0.12	0.00	0.00	-0.75	5.71
	Column total (u_{+j})	**244**	**257**	**495**	**352**	**616**	**2982**	**u_{++} = 4946**					**X_{L2}^2 =**	**4215**

Table 3D.7 Calculation of the test statistic X_{L1}^2 using gut contents data from *D. flavicaudus* collected at backreef site A.

	i =Zooplankton prey group	Gut contents counts (u_{ij})					Total (u_{i+})	$u_{ij} * \ln[u_{ij} * (u_{++} / (u_{i+} * u_{+j}))]$				
		j = 1	j = 2	j = 3	j = 4	j = 5		j = 1	j = 2	j = 3	j = 4	j = 5
1	Appendicularia	358	155	117	460	748	1838	6.16	-125.72	-126.39	217.37	292.52
2	Corycaeidae	157	292	266	75	320	1110	-47.53	95.34	65.27	-62.77	14.82
3	Oncaeidae	592	708	728	424	572	3024	13.19	148.67	181.96	-45.30	-214.56
4	Calanoida	44	13	13	26	41	137	22.76	-9.01	-8.85	5.09	3.43
5	*Candacia* spp.	1	6	1	0	3	11	-0.74	6.33	-0.72	0.00	-0.03
6	pelagic Harpacticoida	2	9	4	6	8	29	-2.04	4.43	-1.23	1.69	0.02
7	benthic Harpacticoida	28	14	34	10	15	101	10.37	-4.40	19.90	-4.55	-9.25
8	*Oithona* spp.	2	1	1	2	1	7	0.80	-0.28	-0.27	1.21	-0.66
9	Copepoda	13	8	17	2	14	54	2.98	-1.98	8.81	-2.88	-0.84
10	Copepoda nauplii	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
11	Ostracoda	0	2	2	1	0	5	0.00	1.49	1.52	0.25	0.00
12	Cladocera	58	38	44	15	68	223	17.77	-4.09	2.24	-12.62	6.97
13	round fish eggs	2	1	4	2	15	24	-1.66	-1.52	-0.47	-1.25	12.30
14	fusiform fish eggs	2	1	2	3	4	12	-0.28	-0.82	-0.24	1.41	0.77
15	Decapoda	0	0	0	0	1	1	0.00	0.00	0.00	0.00	1.29
16	other	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
	Column total (u_{+j})	**1259**	**1248**	**1233**	**1026**	**1810**	**u_{++} = 6576**				**X_{L1}^2 =**	**952**

Table 3D.8 Calculation of the test statistic X_{L2}^2 using gut contents data from *D. flavicaudus* collected at backreef site A.

i =Zooplankton prey group		Gut contents counts (u_{ij})					ZP tow	Total (u_{i+})	u_{ij} * ln[u_{ij} * (u_{++} / (u_{i+} * u_{+j}))]					
		j = 1	j = 2	j = 3	j = 4	j = 5			j = 1	j = 2	j = 3	j = 4	j = 5	ZP tow
1	Appendicularia	358	155	117	460	748	326	2164	73.13	-96.73	-104.51	303.42	432.44	-219.70
2	Corycaeidae	157	292	266	75	320	210	1320	-19.73	147.05	112.37	-49.48	71.48	-130.07
3	Oncaeidae	592	708	728	424	572	153	3177	191.37	361.77	401.08	82.32	-42.39	-277.60
4	Calanoida	44	13	13	26	41	1224	1361	-62.85	-34.30	-34.15	-45.49	-76.34	1362.08
5	*Candacia* spp.	1	6	1	0	3	3	14	-0.64	6.99	-0.61	0.00	0.30	-0.96
6	pelagic Harpacticoida	2	9	4	6	8	3	32	-1.54	6.69	-0.22	3.20	2.03	-3.44
7	benthic Harpacticoida	28	14	34	10	15	90	191	2.33	-8.41	10.15	-7.42	-13.56	41.98
8	*Oithona* spp.	2	1	1	2	1	117	124	-4.25	-2.81	-2.80	-3.84	-3.18	135.81
9	Copepoda	13	8	17	2	14	42	96	0.05	-3.78	4.98	-3.33	-3.99	16.47
10	Copepoda nauplii	0	0	0	0	0	292	292	0.00	0.00	0.00	0.00	0.00	355.92
11	Ostracoda	0	2	2	1	0	24	29	0.00	-1.32	-1.30	-1.16	0.00	24.71
12	Cladocera	58	38	44	15	68	37	260	29.19	3.39	10.90	-9.67	20.35	-27.04
13	round fish eggs	2	1	4	2	15	220	244	-5.60	-3.48	-8.35	-5.19	-17.23	245.38
14	fusiform fish eggs	2	1	2	3	4	7	19	-0.50	-0.93	-0.45	1.09	0.33	1.54
15	Decapoda	0	0	0	0	1	2	3	0.00	0.00	0.00	0.00	0.54	1.63
16	other	0	0	0	0	0	9	9	0.00	0.00	0.00	0.00	0.00	10.97
	Column total (u_{+j})	**1259**	**1248**	**1233**	**1026**	**1810**	**2759**	**u_{++} = 9335**					**X_{L2}^2 =**	6270

Table 3D.9 Calculation of the test statistic X_{L1}^2 using gut contents data from *D. flavicaudus* collected at backreef site B.

	i =Zooplankton prey group	Gut contents counts (u_{ij})					Total (u_{i+})	u_{ij} * ln[u_{ij} * (u_{++} / (u_{i+} * u_{+j}))]				
		j = 1	j = 2	j = 3	j = 4	j = 5		j = 1	j = 2	j = 3	j = 4	j = 5
1	Appendiculariaa	216	93	40	51		400	67.70	2.38	-29.41	-14.69	
2	Corycaeidae	302	183	152	177		814	-18.70	-1.47	-16.82	43.49	
3	Oncaeidae	234	171	160	93		658	-24.40	23.41	24.54	-17.21	
4	Calanoida	68	36	34	24		162	4.18	-0.71	0.21	-3.31	
5	*Candacia* spp.	3	4	3	0		10	-0.82	2.27	1.09	0.00	
6	pelagic Harpacticoida	12	4	8	4		28	0.99	-1.85	2.52	-0.70	
7	benthic Harpacticoida	39	13	57	37		146	-15.23	-12.15	35.73	14.76	
8	*Oithona* spp.	2	0	2	0		4	0.47	0.00	1.75	0.00	
9	Copepoda	17	6	13	3		39	1.69	-2.32	6.09	-2.38	
10	Copepoda nauplii	0	1	0	0		1	0.00	1.48	0.00	0.00	
11	Ostracoda	0	0	0	0		0	0.00	0.00	0.00	0.00	
12	Cladocera	19	24	16	6		65	-5.71	11.71	2.65	-3.67	
13	round fish eggs	63	29	34	27		153	2.67	-5.18	2.15	1.00	
14	fusiform fish eggs	5	1	1	1		8	2.30	-0.60	-0.51	-0.31	
15	Decapoda	2	0	0	0		2	1.86	0.00	0.00	0.00	
16	other	2	0	0	1		3	1.05	0.00	0.00	0.67	
	Column total (u_{+j})	**984**	**565**	**520**	**424**		**u_{++} = 2493**				**X_{L1}^2 =**	**165**

Table 3D.10 Calculation of the test statistic X_{L2}^2 using gut contents data from *D. flavicaudus* collected at backreef site B.

i =Zooplankton prey group		Gut contents counts (u_{ij})					ZP tow	Total (u_{i+})	u_{ij} * ln[u_{ij} * (u_{++} / (u_{i+} * u_{+j}))]					
		j = 1	j = 2	j = 3	j = 4	j = 5			j = 1	j = 2	j = 3	j = 4	j = 5	ZP tow
1	Appendicularia	216	93	40	51		79	479	239.88	76.51	2.48	25.96		-105.08
2	Corycaeidae	302	183	152	177		340	1154	171.06	113.51	78.69	154.70		-254.98
3	Oncaeidae	234	171	160	93		448	1106	82.79	101.73	97.83	25.39		-193.37
4	Calanoida	68	36	34	24		2220	2382	-112.15	-62.29	-57.95	-44.37		891.68
5	*Candacia* spp.	3	4	3	0		1	11	1.82	5.80	3.74	0.00		-1.93
6	pelagic Harpacticoida	12	4	8	4		8	36	9.70	1.06	8.33	2.21		-8.26
7	benthic Harpacticoida	39	13	57	37		124	270	-1.09	-7.43	56.40	28.17		-37.95
8	*Oithona* spp.	2	0	2	0		632	636	-7.71	0.00	-6.43	0.00		294.37
9	Copepoda	17	6	13	3		23	62	10.42	0.76	12.77	-0.84		-11.95
10	Copepoda nauplii	0	1	0	0		2	3	0.00	1.36	0.00	0.00		0.13
11	Ostracoda	0	0	0	0		20	20	0.00	0.00	0.00	0.00		9.44
12	Cladocera	19	24	16	6		41	106	3.57	23.43	10.46	-0.74		-19.59
13	round fish eggs	63	29	34	27		183	336	14.68	0.35	8.64	6.15		-24.80
14	fusiform fish eggs	5	1	1	1		5	13	4.76	-0.10	-0.02	0.18		-2.42
15	Decapoda	2	0	0	0		5	7	1.31	0.00	0.00	0.00		0.68
16	other	2	0	0	1		1	4	2.43	0.00	0.00	1.36		-0.91
	Column total (u_{+j})	**984**	**565**	**520**	**424**		**4132**	**u_{++} = 6625**					**X_{L2}^2 =**	**3250**

Table 3D.11 Calculation of the test statistic X_{L1}^2 using gut contents data from *D. flavicaudus* collected at backreef site C.

i =Zooplankton prey group		Gut contents counts (u_{ij})					Total (u_{i+})	u_{ij} * ln[u_{ij} * (u_{++} / (u_{i+} * u_{+j}))]				
		j = 1	**j = 2**	**j = 3**	**j = 4**	**j = 5**		**j = 1**	**j = 2**	**j = 3**	**j = 4**	**j = 5**
1	Appendiculariaa	52	43	34	13	60	202	5.94	-9.34	-0.58	-8.63	20.91
2	Corycaeidae	156	262	84	154	226	882	-40.73	30.37	-49.27	51.51	45.37
3	Oncaeidae	180	183	144	128	212	847	-13.95	-37.05	-1.02	24.33	37.59
4	Calanoida	45	129	56	43	56	329	-23.32	50.76	-0.33	1.93	-11.66
5	*Candacia* spp.	92	36	95	11	70	304	25.39	-28.93	57.16	-13.63	6.57
6	pelagic Harpacticoida	6	5	3	2	5	21	1.31	-0.53	-0.54	-0.54	0.64
7	benthic Harpacticoida	9	5	4	10	15	43	-0.83	-4.11	-2.44	6.21	7.64
8	*Oithona* spp.	5	3	2	0	8	18	0.95	-1.39	-0.86	0.00	6.01
9	Copepoda	0	2	1	0	1	4	0.00	1.27	0.38	0.00	0.18
10	Copepoda nauplii	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
11	Ostracoda	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
12	Cladocera	1	1	1	1	0	4	0.08	-0.06	0.38	0.69	0.00
13	round fish eggs	290	266	185	77	103	921	91.54	23.36	29.54	-30.95	-64.72
14	fusiform fish eggs	13	39	20	22	17	111	-8.75	11.07	1.02	10.15	-5.34
15	Decapoda	0	0	0	1	1	2	0.00	0.00	0.00	1.39	0.87
16	other	0	4	4	0	1	9	0.00	2.08	3.82	0.00	-0.63
	Column total (u_{+j})	**849**	**978**	**633**	**462**	**775**	**u_{++} = 3697**				**X_{L1}^2 =**	**396**

Table 3D.12 Calculation of the test statistic X_{L2}^2 using gut contents data from *D. flavicaudus* collected at backreef site C.

i =Zooplankton prey group		Gut contents counts (u_{ij})					ZP tow	Total (u_{i+})	u_{ij} * ln[u_{ij} * (u_{++} / (u_{i+} * u_{+j}))]					
		j = 1	j = 2	j = 3	j = 4	j = 5			j = 1	j = 2	j = 3	j = 4	j = 5	ZP tow
1	Appendicularia	52	43	34	13	60	218	420	7.51	-8.04	0.45	-8.23	22.73	-5.94
2	Corycaeidae	156	262	84	154	226	300	1182	32.50	153.37	-9.84	123.81	151.47	-222.80
3	Oncaeidae	180	183	144	128	212	322	1169	65.25	43.48	62.35	80.65	130.88	-212.79
4	Calanoida	45	129	56	43	56	2336	2665	-83.15	-120.76	-74.79	-55.25	-86.12	1160.41
5	*Candacia* spp.	92	36	95	11	70	1	305	95.21	-1.61	129.26	-5.29	59.70	-5.09
6	pelagic Harpacticoida	6	5	3	2	5	36	57	-0.11	-1.71	-1.25	-1.02	-0.54	6.08
7	benthic Harpacticoida	9	5	4	10	15	160	203	-7.94	-8.06	-5.60	-1.69	-4.21	62.48
8	*Oithona* spp.	5	3	2	0	8	404	422	-11.01	-8.56	-5.65	0.00	-13.13	236.31
9	Copepoda	0	2	1	0	1	19	23	0.00	-0.70	-0.61	0.00	-0.81	8.31
10	Copepoda nauplii	0	0	0	0	0	111	111	0.00	0.00	0.00	0.00	0.00	69.77
11	Ostracoda	0	0	0	0	0	7	7	0.00	0.00	0.00	0.00	0.00	4.40
12	Cladocera	1	1	1	1	0	102	106	-2.43	-2.57	-2.14	-1.82	0.00	60.18
13	round fish eggs	290	266	185	77	103	200	1121	255.60	173.84	134.21	12.61	-6.45	-219.03
14	fusiform fish eggs	13	39	20	22	17	2	113	0.92	40.10	15.91	26.52	7.32	-6.81
15	Decapoda	0	0	0	1	1	1	3	0.00	0.00	0.00	1.74	1.23	-0.47
16	other	0	4	4	0	1	7	16	0.00	2.82	4.56	0.00	-0.45	-1.39
	Column total (u_{+j})	**849**	**978**	**633**	**462**	**775**	**4226**	**u_{++} = 7923**					**X_{L2}^2 =**	**4456**

Appendix 3E: Details of the calculation of forage ratios used to evaluate the selective random feeding in *Dascyllus flavicaudus.*

Table 3E.1 Calculation of forage ratios (w_i) for each of 16 zooplankton prey types using gut contents data from *D. flavicaudus* collected at forereef site A.

		Zooplankton tow		Gut contents counts (u_{ij})								Bonferroni 95% CI	
i = Zooplankton prey group		count	proportion (π_i)	$j = 1$	$j = 2$	$j = 3$	$j = 4$	$j = 5$	Total (u_{i+})	w_i	se (w_i)	Lower	Upper
1	Appendicularia	246	0.0775	68	94	113	50	19	344	0.64	0.097	0.38	0.91
2	Corycaeidae	226	0.0712	210	243	210	222	196	1081	2.20	0.171	1.74	2.67
3	Oncaeidae	84	0.0265	1196	1152	924	860	504	4636	25.44	0.745	23.41	27.47
4	Calanoida	1560	0.4915	111	121	140	105	68	545	0.16	0.010	0.13	0.19
5	*Candacia* spp.	28	0.0088	30	22	36	18	33	139	2.29	0.367	1.29	3.29
6	pelagic Harpacticoida	4	0.0013	10	16	11	9	11	57	6.57	0.695	4.67	8.46
7	benthic Harpactidcoida	12	0.0038	0	0	0	0	0	0	0	-	-	-
8	*Oithona* spp.	900	0.2836	3	10	3	3	5	24	0.01	0.003	0	0.02
9	Copepoda	12	0.0038	0	0	2	2	0	4	0.15	0.086	0	0.39
10	Copepoda nauplii	30	0.0095	0	0	1	0	0	1	0.02	0.014	0	0.05
11	Ostracoda	9	0.0028	0	0	0	2	1	3	0.15	0.101	0	0.43
12	Cladocera	2	0.0006	0	0	0	0	0	0	0	-	-	-
13	round fish eggs	38	0.0120	0	0	3	3	1	7	0.08	0.040	0	0.19
14	fusiform fish eggs	8	0.0025	3	5	4	1	14	27	1.56	0.697	0	3.46
15	Decapoda	1	0.0003	1	0	1	0	0	2	0.92	0.471	0	2.21
16	other	14	0.0044	2	0	5	5	4	16	0.53	0.177	0.04	1.01
	Total	**3174**	**1.0000**	**1634**	**1663**	**1453**	**1280**	**856**	**u_{++} = 6886**				

Table 3E.2 Calculation of forage ratios (w_i) for each of 16 zooplankton prey types using gut contents data from *D. flavicaudus* collected at forereef site B.

i = Zooplankton prey group		Zooplankton tow		Gut contents counts (u_{ij})								Bonferroni 95% CI	
		count	**proportion (π_i)**	$j = 1$	$j = 2$	$j = 3$	$j = 4$	$j = 5$	**Total (u_{i+})**	w_i	**se (w_i)**	**Lower**	**Upper**
1	Appendicularia	66	0.0737	296	400	452	632	504	2284	5.89	0.487	4.56	7.22
2	Corycaeidae	80	0.0894	92	82	121	89	69	453	0.96	0.071	0.77	1.16
3	Oncaeidae	21	0.0235	67	41	51	36	33	228	1.85	0.284	1.07	2.63
4	Calanoida	334	0.3732	135	67	184	232	120	738	0.38	0.057	0.22	0.53
5	*Candacia* spp.	2	0.0022	9	17	14	21	31	92	7.83	1.383	4.06	11.61
6	pelagic Harpacticoida	5	0.0056	11	2	0	0	2	15	0.51	0.337	0	1.43
7	benthic Harpactidcoida	23	0.0257	0	1	0	0	0	1	0.01	0.007	0	0.03
8	*Oithona* spp.	214	0.2391	3	3	3	2	3	14	0.01	0.001	0.01	0.01
9	Copepoda	76	0.0849	1	4	3	1	2	11	0.02	0.006	0.01	0.04
10	Copepoda nauplii	8	0.0089	0	0	0	0	0	0	0.00	-	-	-
11	Ostracoda	6	0.0067	0	0	0	0	0	0	0.00	-	-	-
12	Cladocera	1	0.0011	0	0	0	0	0	0	0.00	-	-	-
13	round fish eggs	37	0.0413	216	402	332	108	207	1265	5.82	1.071	2.90	8.75
14	fusiform fish eggs	14	0.0156	15	16	20	13	31	95	1.16	0.185	0.65	1.66
15	Decapoda	3	0.0034	4	4	10	9	8	35	1.99	0.246	1.32	2.66
16	other	5	0.0056	2	2	16	1	3	24	0.82	0.406	0	1.92
	Total	**895**	**1.0000**	**851**	**1041**	**1206**	**1144**	**1013**	**u_{++} = 5255**				

Table 3E.3 Calculation of forage ratios (w_i) for each of 16 zooplankton prey types using gut contents data from *D. flavicaudus* collected at forereef site

i = Zooplankton prey group		Zooplankton tow		Gut contents counts (u_{ij})								Bonferroni 95% CI	
		count	proportion (π_i)	$j = 1$	$j = 2$	$j = 3$	$j = 4$	$j = 5$	Total (u_{i+})	w_i	se (w_i)	Lower	Upper
1	Appendicularia	496	0.1663	40	62	61	51	43	257	0.79	0.148	0.38	1.19
2	Corycaeidae	104	0.0349	46	59	122	96	184	507	7.40	0.468	6.12	8.68
3	Oncaeidae	27	0.0091	121	96	286	133	332	968	54.43	4.037	43.41	65.46
4	Calanoida	1064	0.3568	5	12	12	22	8	59	0.08	0.024	0.02	0.15
5	*Candacia* spp.	13	0.0044	3	0	0	3	1	7	0.82	0.421	0.00	1.97
6	pelagic Harpacticoida	6	0.0020	1	2	1	0	0	4	1.01	0.538	0.00	2.48
7	benthic Harpactidcoida	4	0.0013	1	0	0	0	1	2	0.76	0.408	0.00	1.87
8	*Oithona* spp.	728	0.2441	0	0	0	0	0	0	0.00	-	-	-
9	Copepoda	347	0.1164	1	0	1	1	1	4	0.02	0.004	0.01	0.03
10	Copepoda nauplii	49	0.0164	0	0	0	0	0	0	0.00	-	-	-
11	Ostracoda	11	0.0037	0	0	0	0	1	1	0.14	0.107	0.00	0.43
12	Cladocera	1	0.0003	0	0	0	0	0	0	0.00	-	-	-
13	round fish eggs	47	0.0158	0	1	3	4	1	9	0.29	0.106	0.00	0.58
14	fusiform fish eggs	48	0.0161	26	24	9	42	43	144	4.55	1.051	1.69	7.42
15	Decapoda	22	0.0074	0	0	0	0	0	0	0.00	-	-	-
16	other	15	0.0050	0	1	0	0	1	2	0.20	0.108	0.00	0.50
	Total	**2982**	**1.0000**	**244**	**257**	**495**	**352**	**616**	**$u_{++} = 1964$**				

Table 3E.4 Calculation of forage ratios (w_i) for each of 16 zooplankton prey types using gut contents data from *D. flavicaudus* collected at backreef site A.

		Zooplankton tow		Gut contents counts (u_{ij})								Bonferroni 95% CI	
i = Zooplankton prey group		**count**	**proportion (π_i)**	**$j = 1$**	**$j = 2$**	**$j = 3$**	**$j = 4$**	**$j = 5$**	**Total (u_{i+})**	**w_i**	**se (w_i)**	**Lower**	**Upper**
1	Appendicularia	326	0.1182	358	155	117	460	748	1838	2.37	0.543	0.88	3.85
2	Corycaeidae	210	0.0761	157	292	266	75	320	1110	2.22	0.302	1.39	3.04
3	Oncaeidae	153	0.0555	592	708	728	424	572	3024	8.29	0.926	5.76	10.82
4	Calanoida	1224	0.4436	44	13	13	26	41	137	0.05	0.009	0.02	0.07
5	*Candacia* spp.	3	0.0011	1	6	1	0	3	11	1.54	0.635	0	3.27
6	pelagic Harpacticoida	3	0.0011	2	9	4	6	8	29	4.06	0.754	2.00	6.11
7	benthic Harpacticoida	90	0.0326	28	14	34	10	15	101	0.47	0.107	0.18	0.76
8	*Oithona* spp.	117	0.0424	2	1	1	2	1	7	0.03	0.005	0.01	0.04
9	Copepoda	42	0.0152	13	8	17	2	14	54	0.54	0.101	0.26	0.81
10	Copepoda nauplii	292	0.1058	0	0	0	0	0	0	0.00	-	-	-
11	Ostracoda	24	0.0087	0	2	2	1	0	5	0.09	0.039	0	0.20
12	Cladocera	37	0.0134	58	38	44	15	68	223	2.53	0.299	1.71	3.34
13	round fish eggs	220	0.0797	2	1	4	2	15	24	0.05	0.018	0.00	0.10
14	fusiform fish eggs	7	0.0025	2	1	2	3	4	12	0.72	0.113	0.41	1.03
15	Decapoda	2	0.0007	0	0	0	0	1	1	0.21	0.170	0	0.67
16	other	9	0.0033	0	0	0	0	0	0	0.00	-	-	-
	Total	**2759**	**1.0000**	**1259**	**1248**	**1233**	**1026**	**1810**	**$u_{++} = 6576$**				

Table 3E.5 Calculation of forage ratios (w_i) for each of 16 zooplankton prey types using gut contents data from *D. flavicaudus* collected at backreef site B.

i = Zooplankton prey group		Zooplankton tow		Gut contents counts (u_{ij})								Bonferroni 95% CI	
		count	**proportion (π_i)**	$j = 1$	$j = 2$	$j = 3$	$j = 4$	$j = 5$	**Total (u_{i+})**	w_i	**se (w_i)**	**Lower**	**Upper**
1	Appendicularia	79	0.0191	216	93	40	51	n/a	400	8.39	1.564	4.12	12.66
2	Corycaeidae	340	0.0823	302	183	152	177	n/a	814	3.97	0.227	3.35	4.59
3	Oncaeidae	448	0.1084	234	171	160	93	n/a	658	2.43	0.166	1.98	2.89
4	Calanoida	2220	0.5373	68	36	34	24	n/a	162	0.12	0.004	0.11	0.13
5	*Candacia* spp.	1	0.0002	3	4	3	0	n/a	10	16.57	4.578	4.08	29.07
6	pelagic Harpacticoida	8	0.0019	12	4	8	4	n/a	28	5.80	0.707	3.87	7.73
7	benthic Harpacticoida	124	0.0300	39	13	57	37	n/a	146	1.95	0.535	0.49	3.41
8	*Oithona* spp.	632	0.1530	2	0	2	0	n/a	4	0.01	0.004	0.00	0.02
9	Copepoda	23	0.0056	17	6	13	3	n/a	39	2.81	0.497	1.45	4.17
10	Copepoda nauplii	2	0.0005	0	1	0	0	n/a	1	0.83	0.753	0.00	2.89
11	Ostracoda	20	0.0048	0	0	0	0	n/a	0	0.00	0.000	0.00	0.00
12	Cladocera	41	0.0099	19	24	16	6	n/a	65	2.63	0.514	1.22	4.03
13	round fish eggs	183	0.0443	63	29	34	27	n/a	153	1.39	0.060	1.22	1.55
14	fusiform fish eggs	5	0.0012	5	1	1	1	n/a	8	2.65	0.713	0.70	4.60
15	Decapoda	5	0.0012	2	0	0	0	n/a	2	0.66	0.464	0.00	1.93
16	other	1	0.0002	2	0	0	1	n/a	3	4.97	2.198	0.00	10.97
	Total	**4132**	**1.0000**	**984**	**565**	**520**	**424**		u_{++} **= 2493**				

Table 3E.6 Calculation of forage ratios (w_i) for each of 16 zooplankton prey types using gut contents data from *D. flavicaudus* collected at backreef site C.

		Zooplankton tow		Gut contents counts (u_{ij})								Bonferroni 95% CI	
	i = Zooplankton prey group	count	proportion (π_i)	*j* = 1	*j* = 2	*j* = 3	*j* = 4	*j* = 5	Total (u_{i+})	w_i	se (w_i)	Lower	Upper
1	Appendicularia	218	0.0516	52	43	34	13	60	202	1.06	0.129	0.71	1.41
2	Corycaeidae	300	0.0710	156	262	84	154	226	882	3.36	0.401	2.27	4.46
3	Oncaeidae	322	0.0762	180	183	144	128	212	847	3.01	0.212	2.43	3.59
4	Calanoida	2336	0.5528	45	129	56	43	56	329	0.16	0.026	0.09	0.23
5	*Candacia* spp.	1	0.0002	92	36	95	11	70	304	347.50	81.455	125.13	569.87
6	pelagic Harpacticoida	36	0.0085	6	5	3	2	5	21	0.67	0.053	0.52	0.81
7	benthic Harpacticoida	160	0.0379	9	5	4	10	15	43	0.31	0.075	0.10	0.51
8	*Oithona* spp.	404	0.0956	5	3	2	0	8	18	0.05	0.015	0.01	0.09
9	Copepoda	19	0.0045	0	2	1	0	1	4	0.24	0.087	0	0.48
10	Copepoda nauplii	111	0.0263	0	0	0	0	0	0	0.00	-	-	-
11	Ostracoda	7	0.0017	0	0	0	0	0	0	0.00	-	-	-
12	Cladocera	102	0.0241	1	1	1	1	0	4	0.04	0.012	0.01	0.08
13	round fish eggs	200	0.0473	290	266	185	77	103	921	5.26	0.745	3.23	7.30
14	fusiform fish eggs	2	0.0005	13	39	20	22	17	111	63.44	10.772	34.03	92.85
15	Decapoda	1	0.0002	0	0	0	1	1	2	2.29	1.404	0	6.12
16	other	7	0.0017	0	4	4	0	1	9	1.47	0.632	0	3.20
	Total	**4226**	**1.0000**	**849**	**978**	**633**	**462**	**775**	**u_{++} = 3697**				

CHAPTER 4

The influence of food availability and habitat quality on growth in a planktivorous coral reef fish

ABSTRACT:

Food availability has been hypothesized as a driver of variability in growth rates of coral-reef fish at local scales. In this study, we conduct a transplant experiment with juvenile planktivorous reef fish *Dascyllus flavicaudus* (Pomacentridae) to examine the relationship between fish growth, zooplankton density and the amount of zooplankton prey consumed by juvenile fish. Over the course of 50 days, fish transplanted to the reef habitat with the highest long-term average zooplankton abundance (fringing reef) exhibited the greatest growth. The mean total length of fish transplanted to the fringing reef was 6.6 mm (15 %) greater than that of fish transplanted to the forereef where average zooplankton density was lower. The growth of transplanted fish was positively correlated with the number of zooplankton prey consumed, and the number of prey consumed by juvenile fish also varied significantly between reef habitats. An expanded shore-wide transplant experiment documented significant variation in fish growth within the fringing reef habitat. Lower growth rates in certain fringing reef locations and in an eutrophic nearshore bay were associated with increased turbidity levels, suggesting that variation in water quality can de-couple planktivore feeding rates from ambient prey densities. Human activities

that lead to increased turbidity may significantly impact the feeding and growth of planktivorous coral reef fishes.

INTRODUCTION:

Many tropical fish species have broad geographic distributions, inhabiting reef locations that span hundreds to thousands of kilometers. The demography and life history of tropical fish species are known to vary at these regional scales (Choat and Robertson 2002), and are often correlated with environmental gradients such as latitudinal changes in temperature (Meekan et al. 2001, Robertson et al. 2005, Ruttenberg et al. 2005, Trip et al. 2008). Variation in average size, asymptotic size, and growth rates can also occur at local spatial scales with significant differences among subpopulations separated by as little as tens of kilometers (Fowler and Doherty 1992, Choat and Axe 1996, Hart and Russ 1996, Newman and Williams 1996). These local demographic patterns cannot be explained by borad-scale changes in the physical environment such as gradients in ambient temperature. Researchers studying herbivorous and planktivorous reef fishes have hypothesized the observed demographic patterns are related to food availability or quality (Kingsford and Hughes 2005, Ruttenberg et al. 2005, Figueira et al. 2008, Paddack et al. 2009), and some studies have documented positive correlations between algal or zooplankton density and fish growth (Clifton 1995, Nemeth 1997, Gust et al. 2002).

The hypothesis that food availability drives patterns of growth in zooplanktivorous fishes relies on two assumptions – an assumption that planktivorous coral reef fishes are food limited and that higher zooplankton densities translate to higher feeding rates. The assumption of food limitation is supported by numerous studies involving both natural and artificial food supplementation experiments that have shown significant, positive effects of increased food on growth in planktivorous reef fishes (Jones 1986, Forrester 1990, Booth and Alquezar 2002, Kavanagh 2005). Far fewer data are available to evaluate the assumption that higher zooplankton densities result in higher feeding rates. In a controlled laboratory study of the reef planktivore *Chromis caerulea* (Pomacentridae), Kiflawi and Genin (1997) measured a 230 % increase in fish feeding rate with a three-fold increase in prey density. Studying the damselfish *Chromis chrysurus,* Noda et al. (1992) documented high feeding rates within patches of elevated copepod densities and demonstrated that both feeding rates and gut fullness tracked temporal patterns in zooplankton densities. Nevertheless, we currently lack field data on feeding rates and gut fullness for coral reef planktivores on spatial and temporal scales that are relevant to the question of local-scale demographic variability.

On coral reefs, multiple mechanisms may act to decouple planktivore feeding rates from local prey densities. Both increased turbidity and increased flow can depress feeding rates by making prey more difficult to detect visually, reducing the reactive volume of the fish predator, or inhibiting fish from foraging altogether (Hobson and Chess 1978, Kiflawi and Genin 1997, Stuart-Smith et al. 2004, Johansen et al. 2008). Interspecific and intraspecific competition and predation pressure have all been shown to affect the foraging behaviors of planktivorous coral reef fish (Coates 1980, Forrester 1990, Sackley and Kaufman 1996, Webster and Hixon 2000). There are strong vertical gradients* in zooplankton densities over coral reefs (Yahel et al.

2005, Alldredge and King 2009, Heidelberg et al. 2010), suggesting that surface or mid-water zooplankton tows may not accurately characterize the prey field available to planktivorous fishes that feed only in close proximity to the coral habitat. Physical and biological factors vary considerably across dominant reef habitat types, such as deep forereef slopes, shallow reef flats and fringing reefs. While isolating the ultimate mechanism driving fish feeding rates among habitats (e.g. prey density vs. water velocity or competition strength) may be difficult, fish feeding and growth may exhibit consistent spatial patterns across the reef landscape.

The objective of this study is to examine growth rates in planktivorous fish across naturally occurring spatial variability in zooplankton abundance. Using juveniles of the site-attached planktivorous damselfish *Dascyllus flavicaudus*, we conduct transplant experiments in which fish from a common collection site are distributed to coral heads in three physically and biologically distinct reef habitats (fore, back and fringing reefs) as well as to an eutrophic bay. We ask whether fish growth rates are highest in habitats with the greatest long-term average zooplankton densities. Moving beyond the comparison of fish growth and ambient zooplankton abundance, we examine the relationship between growth and the number of zooplankton prey found in guts juvenile fish at the terminal day of the transplant experiment. Finally, we ask whether fish growth varies consistently among the three reef habitats that span gradients in physical characteristics (flow, turbidity, depth) and biological factors (zooplankton and predator densities) that likely influence the feeding biology of planktivorous fishes. Our results suggest that natural variability in food availability can drive significant variation in growth rates of juvenile fishes.

Furthermore, environmental characteristics, namely water column turbidity, can de-couple fish growth from zooplankton abundance, resulting in lower growth rates than would be predicted from local zooplankton densities. Thus, changes in water quality related to land use and management practices may impact the growth and survival of site-attached planktivorous fishes in addition to threatening the coral shelter on which these species depend.

METHODS:

Study site and species:

Moorea (17°32’S, 149°50’W) is a high volcanic island in the Society Archipelago of French Polynesia. Three reef habitat types can be distinguished in Moorea – a deep sloping forereef with high and continuous coral cover, a shallow backreef or barrier reef where networks of coral patches are interspersed with bare sand, and a fringing reef directly adjacent to shore (Galzin and Pointier 1985). These three reef types are representative of habitat divisions found in many high volcanic coral reef islands (Stoddart 1969). *Dascyllus flavicaudus*, a zooplanktivorous damselfish (Family Pomacentridae), is found in each of the three reef habitats in Moorea. Fish settle to live coral heads (primarily *Pocillopora* spp.) at ~ 10 mm total length (TL) (Schmitt and Holbrook 1999a). In Moorea, settlement occurs in monthly pulses centered on the quarter moon phases (Schmitt and Holbrook 1997). The size at sexual maturity for this species is estimated at ~70 mm TL (Godwin 1995, Allsop and West 2003). The maximum size reported for this species is 120 mm TL (Lieske and Myers 1994). *D. flavicaudus* exhibits feeding behaviors common to small-bodied, diurnal planktivorous reef fishes. During the day individuals hover over coral colonies to feed on zooplankton which they detect visually in the water column (Allen 1991). At night and when threatened, fish retreat to shelter within the coral. Because of this strong reliance on coral shelter, *D. flavicaudus* and similar reef fish species are described as "site-attached" in that their movements are restricted by the need to maintain proximity to the reef and individuals often return to a specific coral head each night. The home range of site-attached planktivorous reef fish is known to increase with fish size and to be larger in areas of continuous, versus patchy, coral cover (Godwin 1995).

Fish growth and long-term zooplankton abundance

Data on zooplankton abundance in four reef locations (forereef, backreef, fringing reef and Pao Pao Bay) were provided by the Moorea Coral Reef Long Term Ecological Research project (MCR LTER). Samples were collected over the course of five years (2005 – 2009). At each station, samples were collected twice yearly – once during the austral summer and again during austral winter. Samples from the three reef habitats (forereef, backreef and fringing reef) were collected by diver-swum net tows positioned 1 m above the reef floor. Samples in Pao Pao Bay were collected as vertical net hauls (0 - 20 m depth). Tows were conducted using a 153 μm mesh net and cod end with 150 μm mesh; the net mouth measured 30 cm in diameter. All samples were collected during daylight hours. For our analysis, we excluded zooplankton types that are not eaten by juvenile or adult *Dascyllus flavicaudus* (pteropods, gastropod larvae, *Amphioxus*) from the estimates of total zooplankton densities.

To assess fish growth in the four zooplankton collection areas, we conducted a transplant experiment in which juvenile *Dascyllus flavicaudus* were collected from the backreef and transplanted to standardized experimental coral heads on the fore, back and fringing reefs as well as in Pao Pao Bay. Replicate standardized experimental shelters were constructed by attaching single live coral heads (*Pocillopora* spp., primarily *P. eydouxi*, ~30 cm wide × 25 cm high) to cement blocks using marine epoxy (Z-Spar^{TM} Splash Zone Compound A-788, Kop-Coat, Inc., Pennsylvania, USA). Five shelters were deployed in each of four study sites. The five replicate shelters within each location (forereef, backreef, fringing reef and Pao Pao Bay) were separated by ~20 m. Shelters deployed to the forereef were situated at 15 - 17 m depth, those in the backreef at 3 - 4 m, in the fringing reef at 9.5 - 14 m, and in Pao Pao Bay at 5.8 – 6.4 m depth. At each deployment location, shelters were placed on sand or rubble and were > 5 m from natural coral structure. Juvenile *D. flavicaudus* (20 - 40 mm TL) were collected from an approximately 0.12 km^2 in the backreef habitat on Moorea's north shore. Collected fish were transported to aquaria with running seawater and binned into two size classes: 20 – 30 mm TL and > 30 – 40 mm TL. Fish were distributed into twenty experimental cohorts of ten individuals, with each cohort receiving seven 20 – 30 mm TL fish and three >30 – 40 mm TL fish. Five cohorts were then randomly assigned to experimental shelters within each of the four study sites. The density of juvenile *D. flavicaudus* transplanted to experimental coral shelters was representative of naturally occurring groups of juveniles and settlers of this species. Coral heads of the size used to construct the experimental shelters typically receive 15 or fewer post-larval fish during a single monthly settlement pulse, although as densities up to 45 settlers per coral head have been observed (Schmitt and Holbrook 1999b).

Individual fish were marked with subcutaneous color tags using biocompatible elastomer (Visible Implant Elastomer (VIE), Northwest Marine technology, Washington, USA). This tagging technique has been successfully used with a variety of small-bodied coral reef fishes spanning the size range of individuals in the present study with no detectable impact on fish growth rate, mortality or susceptibility to predators (Buckley et al. 1994, Frederick 1997a, Malone et al. 1999). The color and placement (upper or lower dorsal on right or left side) were varied such that within each of the four study areas juvenile fish from each replicate coral head had unique tags, but tags were not unique for individual fish. Tagged juveniles were transplanted to experimental shelters in late January 2008 and recovered 50 days later using clove oil anesthetic and hand nets. Upon recovery, fish were immediately euthanized in chilled seawater and kept on ice. Within 12 hours of collection, fish were weighed (blotted wet weight to 0.01 g) and measured (TL to 0.1 mm) and subsequently frozen.

Fish growth, consumption of zooplankton prey, and reef habitat

In 2009, a second transplant experiment was conducted at sites spanning Moorea’s north shore. As in the 2008 transplant, juvenile fish were collected from one area on the backreef and transplanted to replicate coral heads, although the 2009 deployment did not include Pao Pao Bay. Nine shelters were deployed in each of the three reef habitats. The nine replicate shelters within each habitat were separated by >500 m, spanning 11.6 km of Moorea’s north shore (Figure 4.1). Shelters deployed to the forereef were situated at 12.8-19.2 m depth, those in the backreef at 1.8-2.7 m and in the fringing reef at 5.2-13.7 m. At each deployment location, shelters were placed on sand or rubble and were > 5 m from natural coral structure.

Juvenile *D. flavicaudus* (19 - 44 mm total length, TL) were collected from ~0.12 km^2 backreef area, transported to aquaria with running seawater, and binned into 5-mm size classes. Two fish from each size class were distributed to each of 27 holding tanks, resulting in experimental cohorts of ten individuals per tank. Tanks were randomly assigned to experimental shelters in each of three reef habitat treatments (forereef, backreef and fringing reef). The initial length (TL) of tagged juveniles did not differ among reef habitats ($F_{2,24} = 0.3232$, $p = 0.7270$). Fish were tagged with subcutaneous elastomer tags, with unique tags for each individual fish within each reef habitat. Tagged fish were weighed (wet weight to 0.01 g), photographed, and kept in aquaria for a 24-hour recovery period before being deployed to experimental shelters on the reef. Tagged juveniles were transplanted to experimental shelters in late January 2009 and recovered 45-47 days later using clove oil anesthetic and hand nets.

Upon recovery, fish were immediately euthanized in chilled seawater and kept on ice. The collection of tagged juveniles at the end of the experiment was conducted in the late afternoon (3 to 5 PM) on three consecutive days to minimize variation in foraging time that might confound the comparison of gut contents among reef habitats. Fish were weighed (blotted wet weight to 0.01 g) and photographed. Tag color and position were noted to confirm individual identities and fish were subsequently frozen.

Subsequently, the foreguts of frozen juvenile fish were removed and the entire gut contents identified and enumerated under a dissecting microscope. Initial and final sizes of tagged juveniles were measured to 0.1 mm from digital photographs using the image analysis software ImageJ (Rasband 1997-2009). Total length was measured from the tip of the snout to the tip of the longest lobe of the caudal fin; body length was measured from the tip of the snout to the beginning of the caudal peduncle, and body depth was measured from the base of the first dorsal spine to base of the pelvic fin (Appendix 4A, Figure 4A.1).

Statistical analysis

Prior to the comparison of mean fish growth in the 2008 transplant experiment, data were assessed for homogeneity of variance using the robust Brown-Forsythe Levene-type test, and Shapiro-Wilks tests were used to examine normality (Brown and Forsythe 1974, Royston 1995). Linear least-squares regressions were used to compare the various metrics of fish size and growth. Where data did not follow bivariate normal distributions, Spearman’s rank correlation was used to examine relationships in fish growth (Hollander and Wolfe 1973).

The analysis of growth among reef habitats was treated as a mixed linear model ANOVA with coral head considered a random factor nested within reef habitat. The ANOVA is an F-test on best linear unbiased predictors (BLUPs) of fish growth for each replicate coral head (Robinson 1991). These predictors were generated using a restricted maximum-likelihood approach (Harville 1977). This approach performs well for unbalanced and small samples. The result is a significance value for the main, fixed effect of reef habitat and a description of the proportion of total variance attributed to the random effect of coral head.

RESULTS:

Fish growth and long-term zooplankton abundance

Zooplankton densities, representing 10 – 15 samples per station over 5 years, increased from the offshore forereef (mean = 56.8 ind. m^{-3}, median = 44 ind. m^{-3}), to the nearshore backreef (mean = 105.2 ind. m^{-3}, median = 81.1 ind. m^{-3}) and fringing reef (mean = 143.7 ind. m^{-3}, median = 91.3 ind. m^{-3}) (Figure 4.2a). Zooplankton densities sampled from the eutrophic Pao Pao Bay (mean = 819.29 ind. m^{-3}, median = 648 ind. m^{-3}) exceeded plankton densities in the three reef habitats by more than five-fold. Growth in the transplanted juvenile fish also varied significantly across this gradient ($F_{3,146} = 5.14$, $p = 0.002$, Figure 4.2a). Average zooplankton density did not predict patterns in fish growth across all four habitats, as the final size (TL) of juveniles transplanted to Pao Pao Bay did not differ significantly from juveniles transplanted to the three reef habitats ($p > 0.05$, Tukey HSD) and was lower than the average TL attained by fringing reef fish.

Nevertheless, within the three reef habitats, average TL attained by transplanted juvenile fish did increase following the progressive shoreward increase in average zooplankton density (fore < back < fringe, Fig 4.2b). Among the three reef habitats, the single significant pair-wise comparison was that between fish growth on the forereef and on the fringing reef ($p < 0.001$). Average TL attained by fish transplanted to these two habitats differed by 6.57 mm (95 % CL = 2.45 mm – 10.68

mm). This difference in size between forereef and fringing reef fish was preserved when the random effect of coral head was accounted for in a one-way ANOVA using mean TL from each coral head ($F_{2,11} = 5.85$, $p = 0.019$, Tukey's HSD for fore vs. fringe: $p = 0.017$).

Comparing metrics of fish growth

Juveniles from the 2009 transplant were given unique tags, allowing a comparison of initial and final measurements and calculations of growth rates for each individual fish. Total length (Appendix 4A, Figure 4A.1) was an excellent predictor of body length ($BL = 0.67*TL – 0.75$, $r^2 = 0.99$, Appendix 4D, Figure 4D.1) and was chosen for use in the comparative analyses of fish growth. As expected from the relationship between fish TL and weight (Appendix 4A, Figure 4A.2,$Wt = 2.65e^{-5} \times TL^3$), increases in TL of as little as ~ 5 mm lead to a doubling in fish weight, and fish that experienced the greatest absolute change in TL experienced close to a 400% change in weight (Figure 4.3). *Dascyllus flaviaudus* is a deep-bodied fish with a circular rather than streamlined profile. Accordingly, juvenile fish gained 0.5 mm in body depth for every 1 mm gained in body length ($\Delta BD = 0.51 \times \Delta TL – 0.52$, $r^2 = 0.91$, $n = 125$, Figure 4.4). The absolute growth experienced by juvenile was variable among individuals, with some individuals exhibititing no measurable growth over the course of the experiment (Figure 4.5). The median absolute change in total length (6.5 mm), body depth (3.9 mm), and weight (2.64 g) corresponded to daily growth rates of 0.141 mm d^{-1}, 0.085 mm d^{-1}, and 0.014 g d^{-1}, respectively (Figure 4.5). Juveniles that exhibited the greatest gain in size over the course of the experiment experienced changes in TL and BD that were 2.5-fold greater than the median values, and weight gain that was four-fold greater than the median.

Fish growth and gut fullness

Copepods accounted for the majority of zooplankton sampled from guts of juvenile *Dascyllus flavicaudus,* with a median contribution of 86.4 % of prey items per fish gut (Figure 4.6a). Pelagic copepods from the families Corycaeidae and Oncaeidae and benthic harpacticoid copepods (including *Metis* spp.) were dominant among the copepods in fish guts. Appendicularia were found in 20 of the 46 gut samples, though they comprised < 5% of total prey items in the majority of gut samples (Figure 4.6b). Fish eggs, cladocerans, decapod larvae, coral larvae and unidentifiable zooplankton comprised the remaining prey items sampled. These ‘other’ zooplankton also contributed < 5 % to the gut contents in the majority of fish sampled (Figure 4.6c).

The average (± SE) carbon content of copepods (4.6 ± 0.3 μg C animal^{-1}) and appendicularians (3.5 ± 0.2 μg C) sampled from Moorea’s reefs are similar and both have considerably less organic carbon per individual than groups such as decapod larvae (17.9 ± 9 μg C) (Alldredge and King 2009). We calculated the biomass of zooplankton prey in the fish gut samples using the average values measured by Alldredge and King (2009) for copepods and appendicularians and applying the value for decapods to all of the ‘other’ zooplankton to estimate their maximum potential contribution to prey biomass. Because copepods overwhelmingly dominated the gut samples, prey number and prey biomass were highly correlated (Figure 4E.2, Spearman's $\rho = 0.99$, $p < 0.001$, $n = 46$), and we chose to use prey number in the subsequent analyses of fish growth.

Gut fullness appeared to increase exponentially with fish size (Appendix 4E, Figure 4E.1) , and due to this we limited our analysis of the relationship between growth and gut fullness to fish that had attained a final TL of ≥ 40 mm. As a result fish transplanted to the forereef were not included in the analysis. Focusing on the larger juveniles alleviated potential bias driven by a relationship between proportional growth and final size. For this subset of large juveniles, there was no significant relationship between the proportional change in TL experienced over the course of the transplant experiment and the final TL attained (Spearman's $\rho = -0.16$, $p = 0.5158$, $n = 19$). In contrast, there was a significant, positive relationship between relative change in TL and gut fullness (Figure 4.7a, Spearman's $\rho = 0.59$, $p = 0.0089$, $n = 19$). Fish that grew more over the course of the experiment had fuller guts than fish that experienced lower growth rates. Within the group of large juveniles analyzed, fish transplanted to the fringing reefs had significantly more prey items in their guts at the time of collection than fish transplanted to the backreef (Figure 4.7b, $F_{1,17} = 6.62$, $p = 0.020$). The average number (± 95 % CI) of zooplankton prey items in guts from fringing reef fish (714.4 ± 250) was twice the average number of prey in guts from backreef fish (321.9 ± 168). Fringing reef fish also experienced greater relative change in TL than did backreef fish, though the difference was less pronounced than the contrast in gut fullness ($F_{1,17} = 4.41$, $p = 0.051$).

Fish growth and reef habitat

Recovery rates of juvenile fish from forereef coral heads were significantly lower in the 2009 shore-wide transplant than the forereef recovery rates experienced during the 2008 transplant experiment. Only 13 of the 90 fish (14 %) transplanted to the forereef in 2009 were recovered, in contrast to a 76 % recovery rate from this habitat in 2008 (Appendix 4B, Table 4B.1). The low recovery rates of fish transplanted to the forereef led to small sample sizes within and among coral heads, and as a consequence we limited the analysis of habitat-dependant fish growth to the backreef and fringing reef habitats. The growth of juvenile fish varied both within and among replicate coral heads within each reef habitat (Figure 4.8). Fish growth varied more among coral heads in the fringing reef than among coral heads in the backreef, and the random effect of coral head was associated with 72.5 % of the overall variance in the linear mixed model. The main effect of reef habitat was not significant ($F_{1,\ 13.98} = 0.0131$, $p = 0.9107$). Within the fringing reef, fish transplanted to coral heads at sites 1, 2, 4 and 8 experienced the lowest growth rates, while fish transplanted to sites 5, 6, and 7 exhibited the greatest amount of growth across replicate coral heads from all three habitats (Figure 4.8c).

DISCUSSION:

This study provides two lines of evidence to support the hypothesis that local-scale variation in demographic rates of planktivorous coral reef fishes is driven by spatial patterns in food availability. The growth rates of transplanted juvenile *Dascyllus flavicaudus* varied significantly among three reef habitats and were highest in the reef habitat (fringing reef) where the long-term average zooplankton abundance was the greatest. The juvenile fish that exhibited the greatest proportional change in size over the course of the transplant also had more zooplankton prey items in their guts than fish that experienced lower rates of growth. Comparisons of gut fullness between zones agreed with patterns in fish growth – fish on the fringing reef had more prey items in their guts than fish on the backreef. The degree to which habitat-dependant growth in planktivorous fishes is predictable at ecologically relevant scales (e.g. across the island of Moorea) is likely influenced by the physical and biological homogeneity of the reef habitats. In our study, transplant locations on the fringing reef spanned considerable variation in local environmental characteristics such as turbidity, while the sites on the backreef and forereef were more homogenous. This environmental variability may explain why the random factor of coral head, or transplant location, was associated with a higher proportion of the overall variance in the fringing reef as compared to locations on the backreef.

The growth rates (as change in TL) measured for juvenile *Dascyllus flavicaudus* in this study (average = 0.152 mm day^{-1}, maximum = 0.363 mm day^{-1}), fall within the range of values (< 0.1 – 0.6 mm/day) measured for similarly sized juveniles of other planktivorous reef species (Thresher 1985, Forrester 1990, Pitcher 1992, Booth and Beretta 2004, Feary et al. 2009). The individuals that exhibited highest growth experienced a > 50 % change in total length over the 45 – 47 day experiment. Thus, it is unlikely that stress resulting from the collection and tagging significantly lowered the growth rates of juvenile *Dascyllus flavicaudus* in the transplant experiment. *D. flavicaudus* is a deep-bodied species, and as such fish that grew in TL grew proportionally in body depth. The resulting increase in cross-sectional area may mean that incremental growth in this species allows fish to reach a size refuge from gape-limited predators more quickly than planktivores, such as those in the genus *Chromis*, with a fusiform body shape. A study of the planktivorous damselfish *Pomacentrus amboinensis* on the Great Barrier Reef documented that differences in fish length of only 1 mm can significantly alter predation rates on newly settled reef fish (Holmes and McCormick 2006). Nevertheless, if high growth rates in juvenile fish are associated with 'riskier' foraging habits, faster-growing individuals may actually experience greater mortality rates than slow-growing conspecifics (Johnson and Hixon 2010).

Average zooplankton densities, measured over the course of five years, increased shoreward from the forereef to the fringing reef. Zooplankton densities within the nearshore Pao Pao Bay were two to six-fold higher than densities in the three reef habitats. The long-term average zooplankton density in the bay (819 ind. m^{-3}) is higher than typical daytime values for coral reef ecosystems (Sorokin 1990), though representative of reef areas on high volcanic islands or continental margins that receive significant terrestrial inputs fueling local zooplankton production (Hoover et al. 2006). The zooplankton samples from Pao Pao Bay were collected using vertical hauls between 20 m depth and the surface, while collections in the three reef habitats were made by divers swimming nets 1 m above the reef surface. Alldredge and King (2009) documented strong vertical gradients in zooplankton densities above Moorea's reefs. Samples taken during the day on the forereef documented a decrease from densities of ~ 400 ind. m^{-3} near the surface to about 100 ind. m^{-3} 1 m above the reef floor. Assuming a similar four-fold vertical decrease in zooplankton density still yields a long-term average for the bay (205 ind. m^{-3}) that exceeds the fringing reef average, and thus near-reef zooplankton abundances would also likely have predicted high fish growth rates in this area.

Fish transplanted to reefs in Pao Pao Bay did not grow as fast as predicted from the high ambient zooplankton densities. The bay is consistently more turbid than backreef and forereef habitats, and this effect is exaggerated during the rainy Austral summer when large amounts of terrestrial sediment are washed into the bay (Figure 4.9).

The increased turbidity within the bay may explain why the growth rates of juvenile fish transplanted to this area did not exceed growth rates of fish transplanted to the three reef habitats. Spatial variability in water quality may also have contributed to the within-habitat variation in growth rates measured in fish transplanted to the fringing reef. Three of the transplant locations on the fringing reef (Sites 1,2,8) were close to areas that received significant amounts of terrestrial input (Figure 4.10 a-c). At these sites, turbidity was noticeably higher than at well-flushed fringing reef sites. Three of the fastest growing fish cohorts had been transplanted to fringing reef sites with relatively clear waters (Figure 4.10 d-f).

In a study on the Great Barrier Reef, Kingsford and Hughes (2005) found that the asymptotic length of the planktivorous damselfish *Acanthochromis polyacanthus* was lowest on inner-shelf reefs characterized by high zooplankton abundances and increased turbidity compared to mid- and outer-shelf reefs. Turbidity is known to lower the feeding rates and alter feeding behaviors of planktivorous fishes (Engstrom-

Ost and Mattila 2008). The reactive distance of planktivorous fishes decreases with lower light levels, and the cessation and initiation of feeding in diurnal coral reef planktivorous fish occurs as a function of changes in ambient light (Rickel and Genin 2005).

Changes in land-use patterns can amplify the gradients in terrestrial input and turbidity that naturally occur between nearshore and offshore reefs. Sediment cores collected from the neighboring island, Tahiti, and reflecting the period between 1865 and 1965 showed drastic changes in sediment composition around the year 1957 and an increase in terrestrially-derived phosphorus over the course of the century (Fichez et al. 2005). These changes in the sediment record paralleled rapid increases in the human population on the island and related increases in erosion as mountainous terrain was graded and developed. A study conducted in Tasmania on lake-dwelling brown trout, *Salmo trutta*, provides a striking example of the biological implications of changes in water quality for planktivorous fishes. Fish stomach contents were monitored over a six-year period during which turbidity increased from 26 to 141 NTU (Nephelometric Turbidity Units) (Stuart-Smith et al. 2004). The volume of zooplankton prey found in fish guts decreased six-fold over the corresponding period along with changes in the diversity of prey ingested. This interaction between water quality and fish feeding behavior suggests that human activities which lead to increased runoff and sedimentation may have deleterious effects on reef fish beyond the threat posed to the coral in which fish shelter.

The transplant experiment conducted in this study demonstrates that over short time periods (months) spatial variation in the growth of juvenile reef fish is related to variability in zooplankton density and fish gut fullness. Many of the studies of demographic variability in reef fishes use otolith aging techniques where data on age-at-size are collected from adult fish and pooled to fit growth curves for a local population (Choat and Robertson 2002). Thus, a strict interpretation of the resulting spatial patterns is that fish that live as adults in a given location grew faster/slower than fish that live as adults in another location. While many of the planktivorous species studied can be considered site-attached as juveniles or on short time scales (Forrester 1990, Frederick 1997b), migration of small-bodied planktivorous fishes between and within reef habitats is not impossible. This leaves open the possibility that certain reef areas promote rapid growth in juvenile fishes, and that larger individuals subsequently migrate to areas selected for higher food availability or reduced competition. Furthermore, fish inhabiting reefs locations where corals exhibit mass-spawning receive enormous inputs of lipid-rich food over a short time period (Pratchett et al. 2001). Planktivorous fish have been shown to exhibit compensatory growth, and thus periodic inputs of food may compensate for lower long-term food availability (Kavanagh 2005). Longer-term studies are needed to track the implications of short-term variability in growth rates over the lifespan of fish or through growth to the size at sexual maturity.

Acknowledgements:

Chapter 4 is in preparation for submission to the *Journal of Experimental Marine Biology and Ecology* and is presented as part of this dissertation with the acknowledgement of the study co-authors, Adrian C. Stier and James J. Leicther. The

dissertation author was the primary investigator and is the primary author of this material.

I thank L. Bentley, D. Combosch and W. Boudreau for their assistance collecting samples and the staff of the Richard B. Gump South Pacific Research Station for logistical support. I am grateful to E. Schnarr for her contribution to the gut content analysis. N. Beeler and J. Tran assisted in the analysis of digital photos. Comments from I. Abramson and M. Ohman improved the analyses and manuscript. This research was funded by awards from the NSF Moorea Coral Reef LTER program to J. Leichter, a 3 Seas Teaching Fellowship to K. Hanson, and a PADI grant (KH). The collection of fish for this study was approved by French Polynesian research permits as well as by the UCSD Institutional Animal Care and Use Committee (Protocol # S06369). Satellite images were taken from Google Earth and are © 2011 Digital Globe.

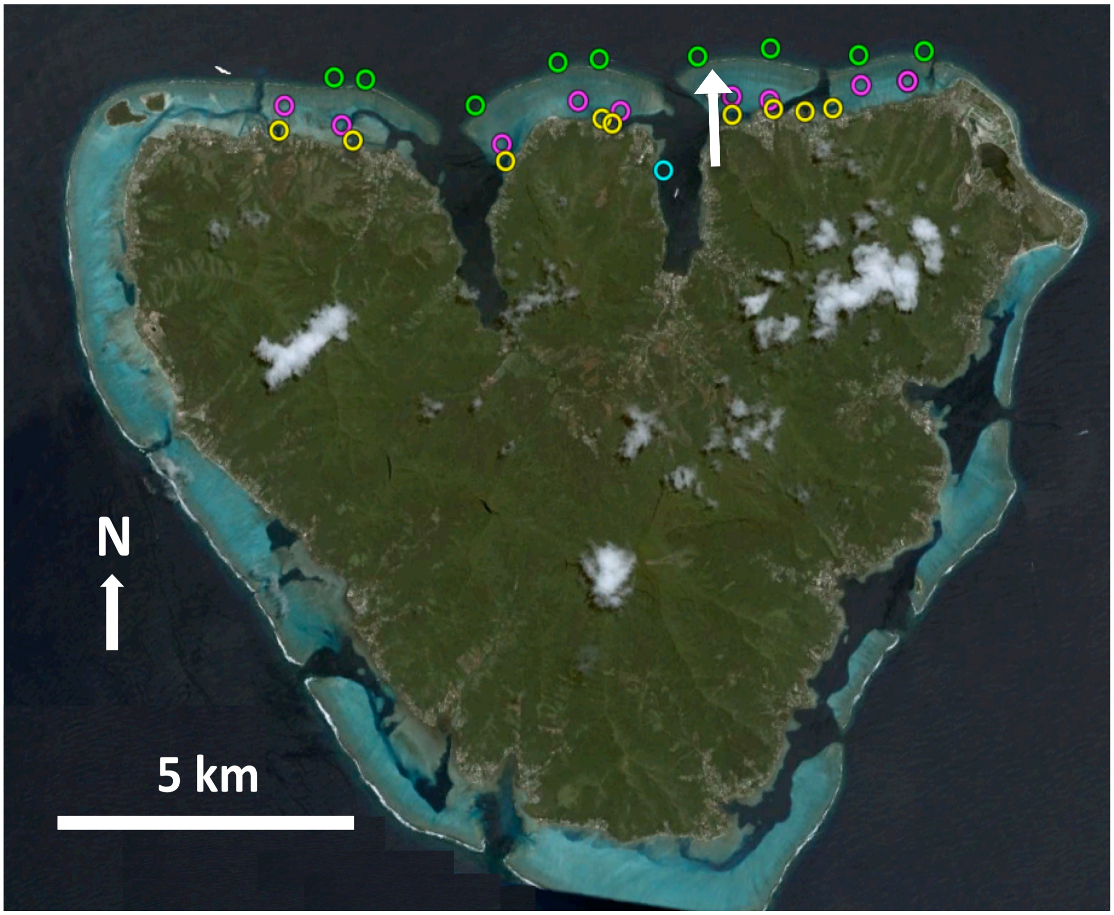

Figure 4.1. Map of the island of Moorea, French Polynesia (17°30’S, 149°50’W). The arrow indicates the backreef location where juvenile fish were collected. Circles indicate locations were juvenile fish were transplanted within the fringing reef (yellow), backreef (pink), forereef (green) and in Pao Pao Bay (blue). Satellite image is taken from Google Earth, © 2011 Digital Globe.

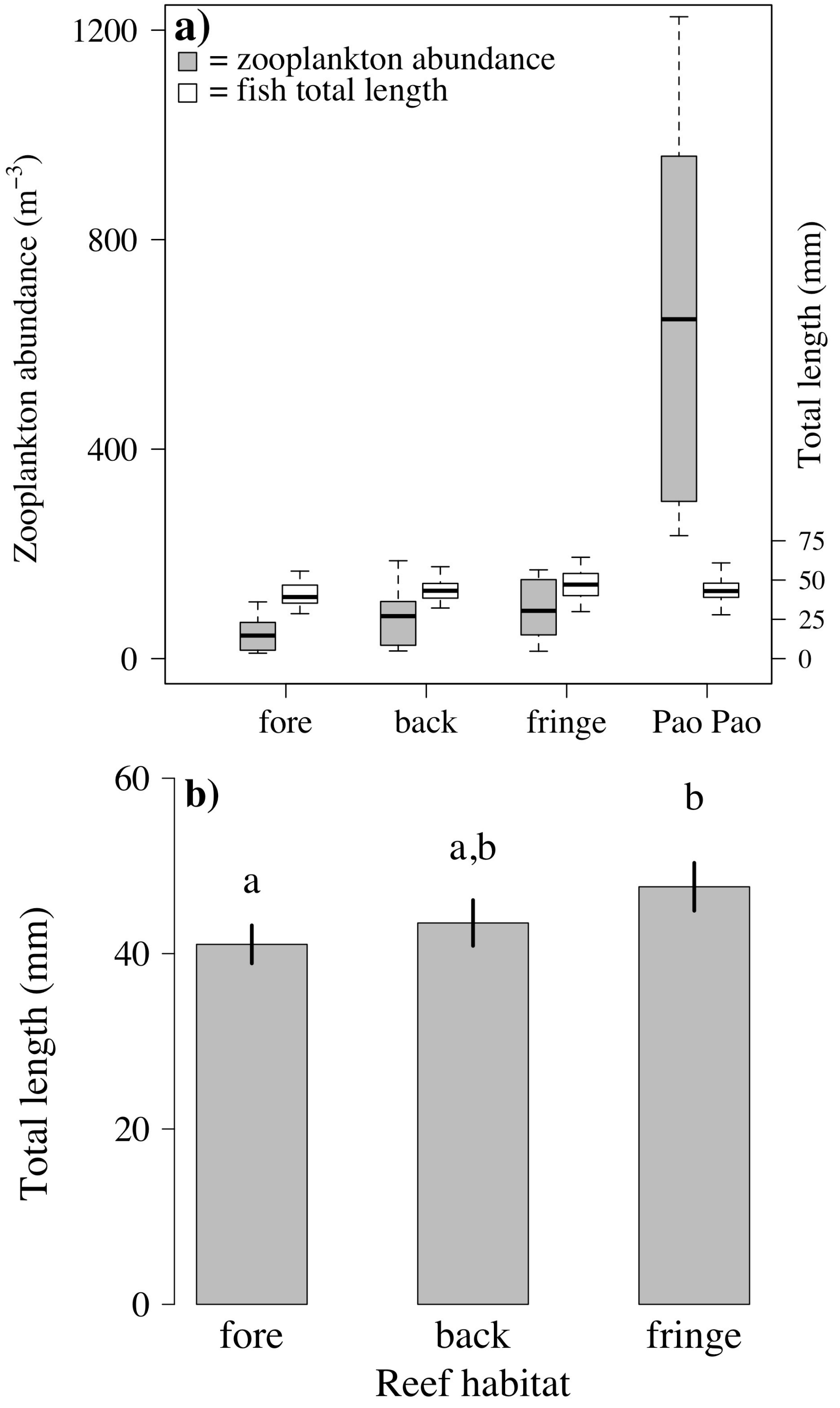

Figure 4.2. a) Boxplots of the final length (TL) attained by fish transplanted to four habitats – fore (n = 41 fish), back (n = 31) and fringing (n = 41) reefs as well as Pao Pao Bay (n = 37). Fish size data are paired with measurements of zooplankton density collected in each location over the course of five years (n = 10-15 samples per habitat). Boxes extend from 25th to 75th percentiles; whiskers to 1.5 times the interquartile range. **b)** Mean (± 95 % CI) total length achieved by fish transplanted to the three reef habitats. Letters indicate groupings from Tukey's HSD post-hoc comparisons.

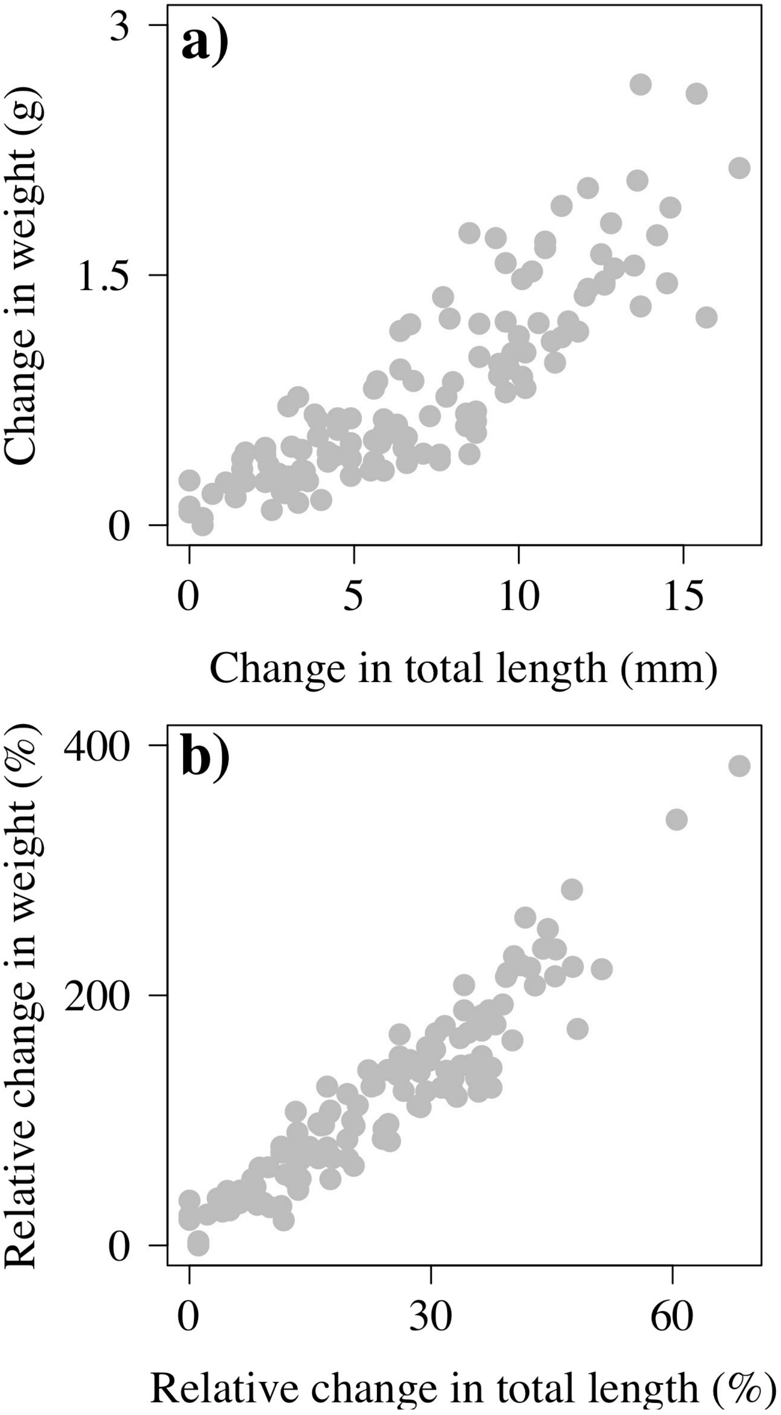

Figure 4.3. Comparison of growth in size and change in weight for juvenile *Dascyllus flavicaudus:* **a)** absolute growth. **b)** relative growth.

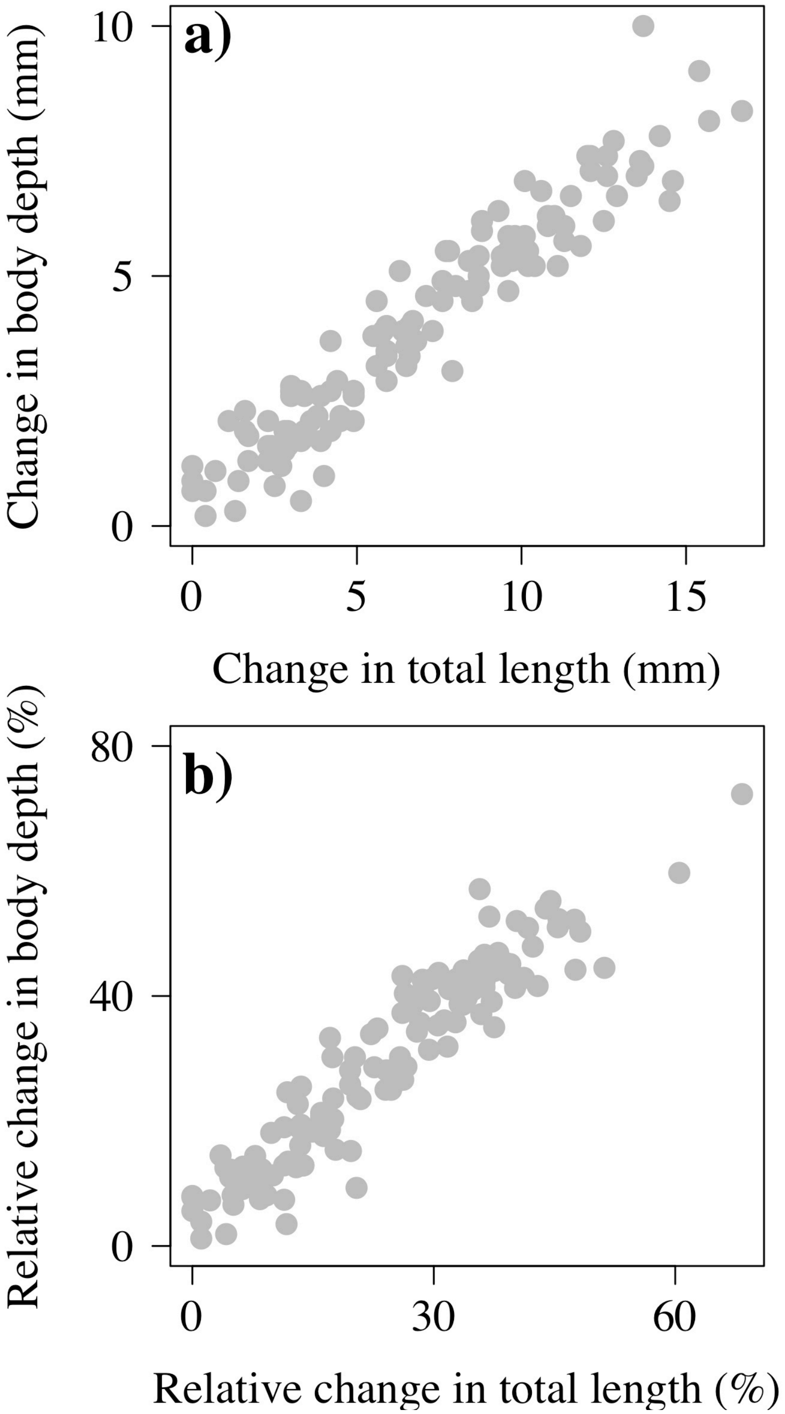

Figure 4.4. Comparison of growth in body length (TL) and body depth for juvenile *Dascyllus flavicaudus:* **a)** absolute growth. **b)** relative growth.

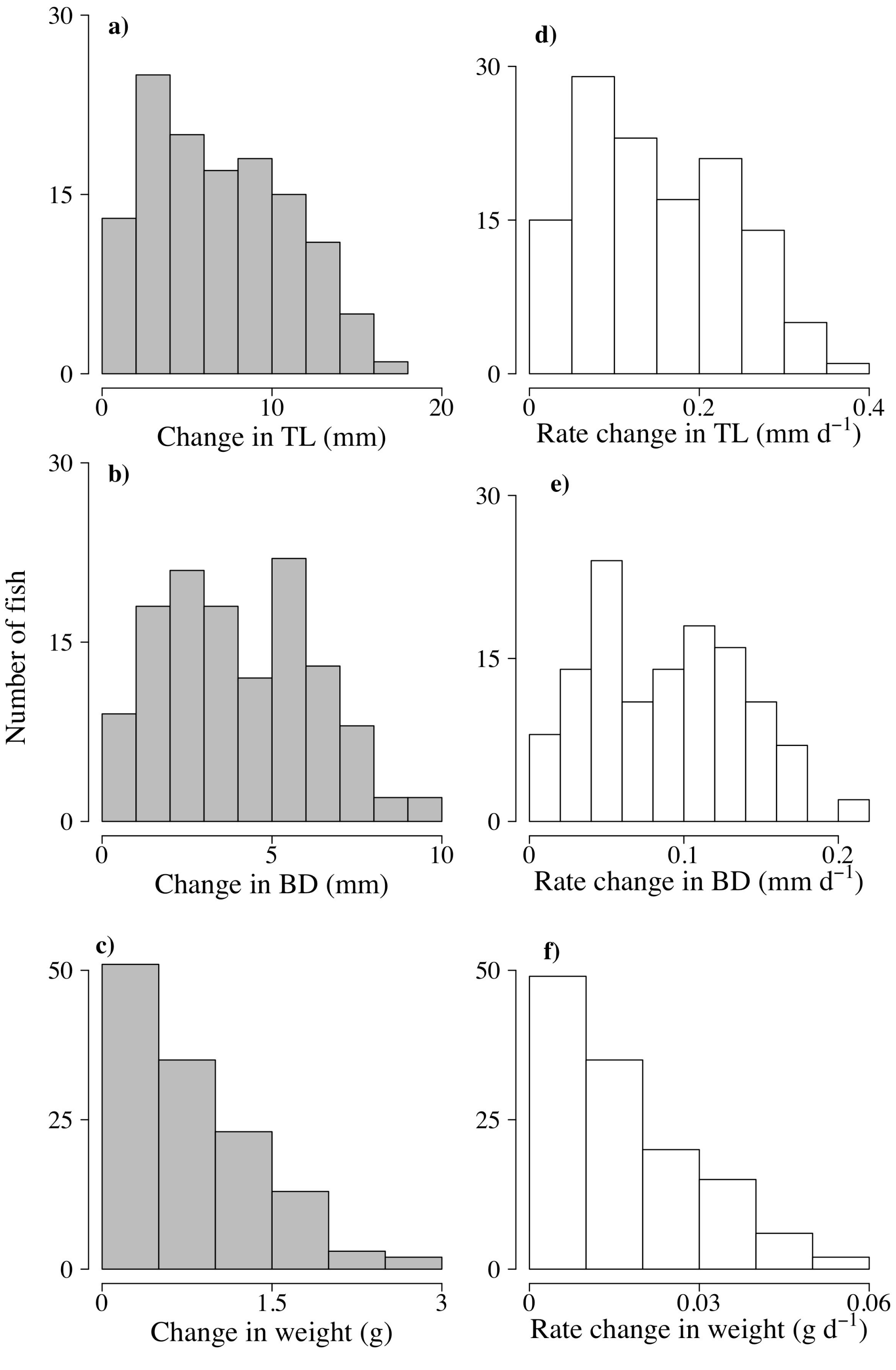

Figure 4.5. Frequency distributions of absolute growth **(a-c)** experienced by juvenile *Dascyllus flavicaudus* (n = 123 fish) as well as the rate of daily growth **(d-f)**.

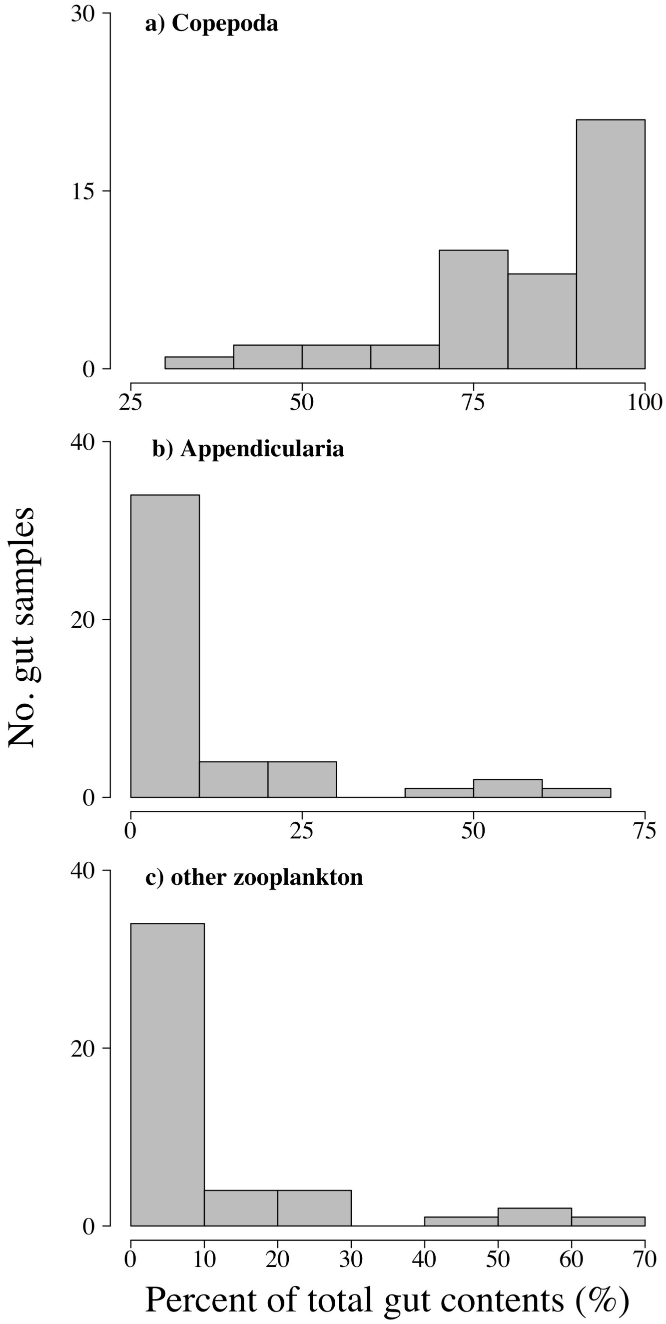

Figure 4.6. Frequency distributions of the percent contribution of copepods (a), appendicualrians (b) and other zooplankton groups (c) to gut contents sampled from juvenile *Dascyllus flavicaudus* (n = 46 fish).

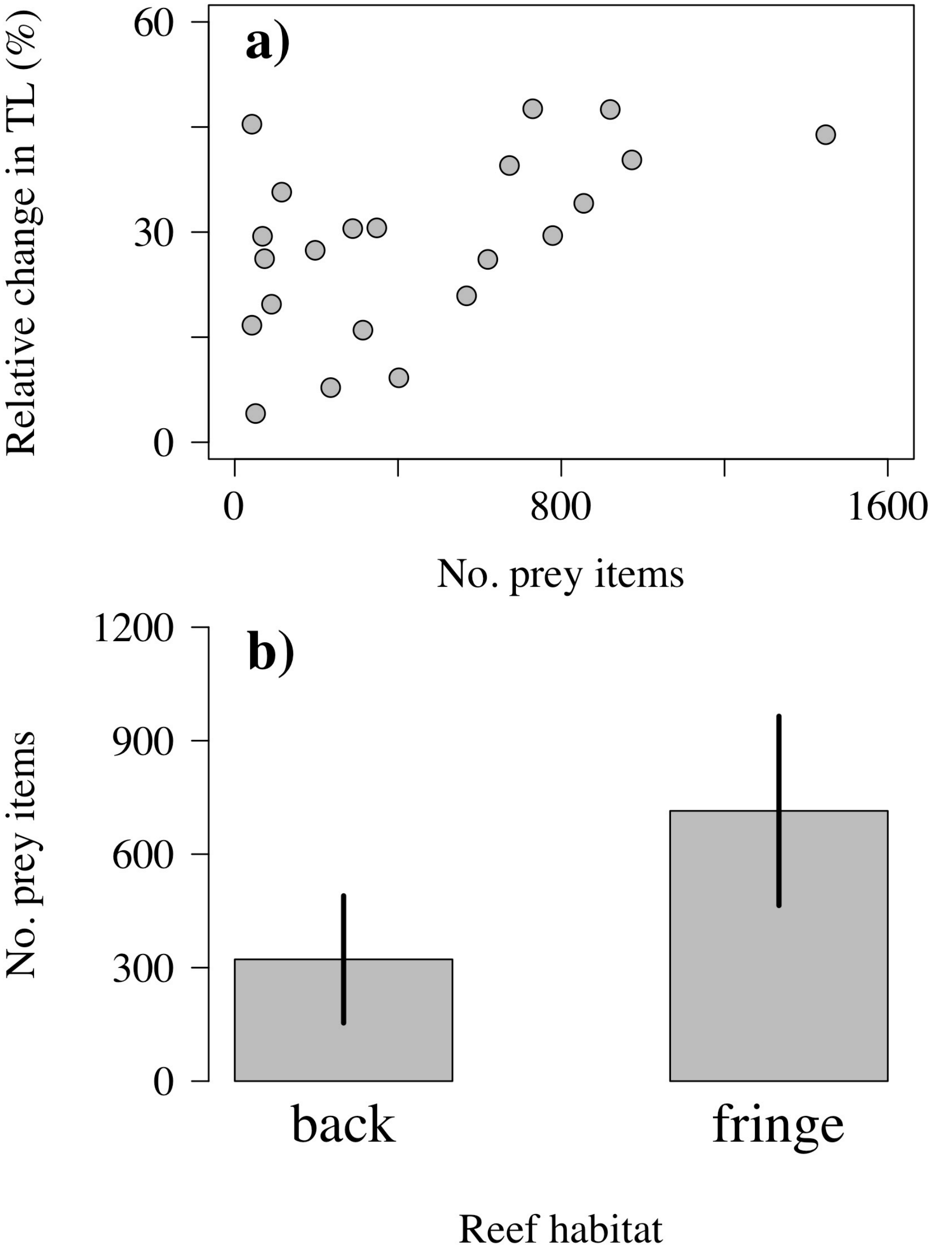

Figure 4.7. a) The relationship between the relative growth (TL) of juvenile fish and the number of zooplankton items found in fish guts**. b)** Comparison of the average number of prey items sampled from guts of fish transplanted to the backreef and to the fringing reef. Error bars are 95 % CI.

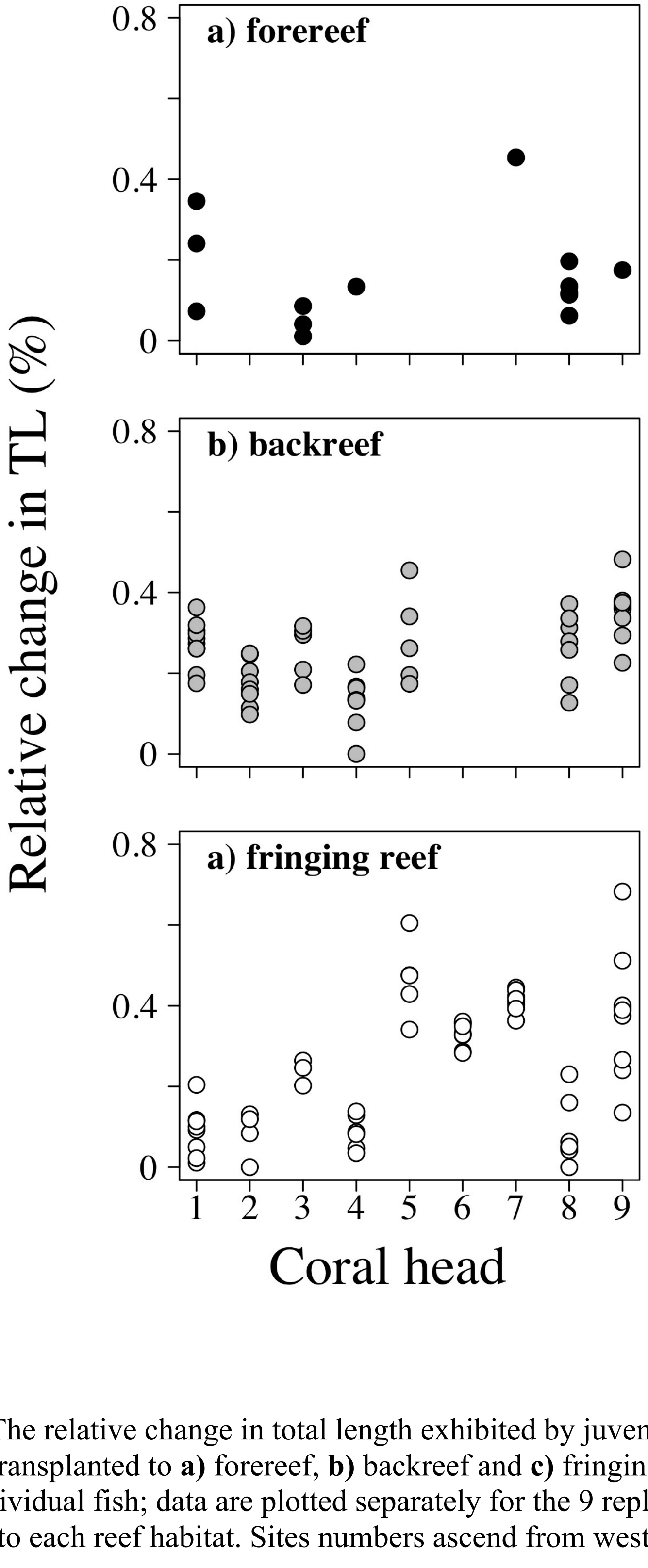

Figure 4.8. The relative change in total length exhibited by juvenile *Dascyllus flavicaudus* transplanted to **a)** forereef, **b)** backreef and **c)** fringing reef habitats. Points represent individual fish; data are plotted separately for the 9 replicate coral heads transplanted to each reef habitat. Sites numbers ascend from west to east (see Fig. 4.1).

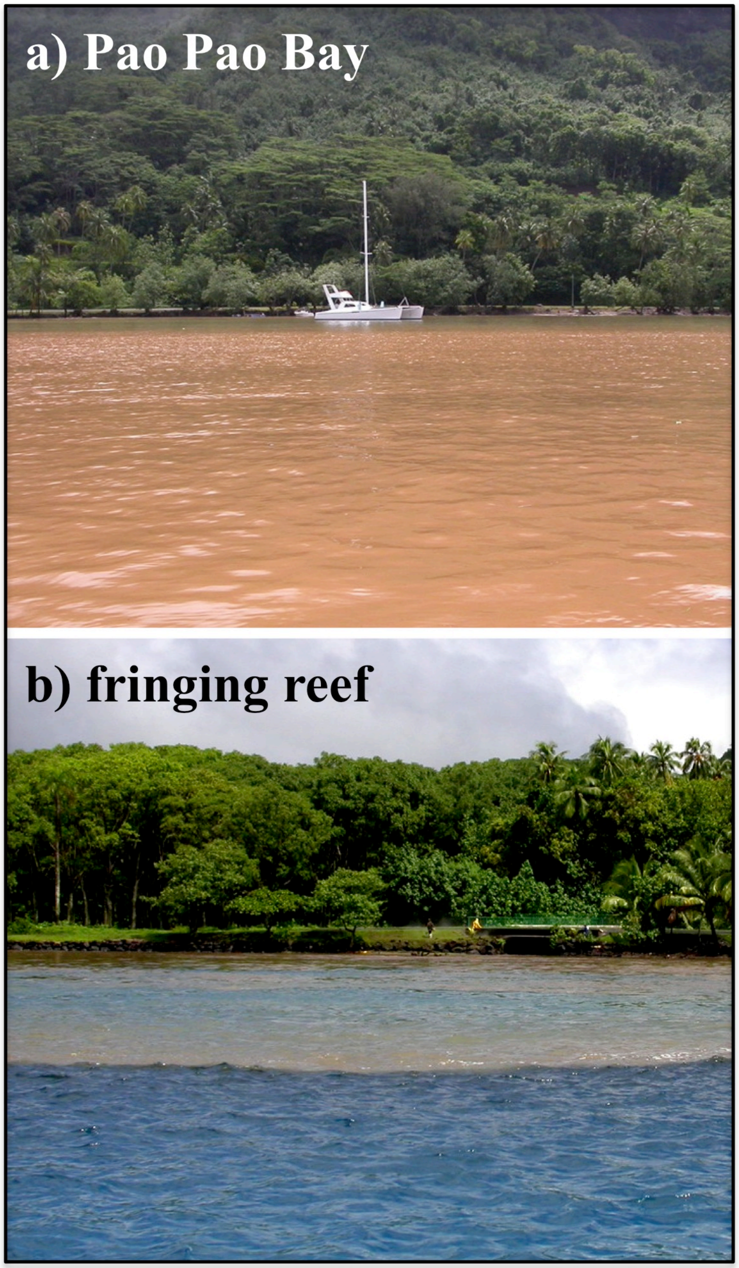

Figure 4.9. a) Muddied waters within Pao Pao Bay following a large rainstorm. **b)** Muddy water from a nearby stream lingers over the fringing reef.

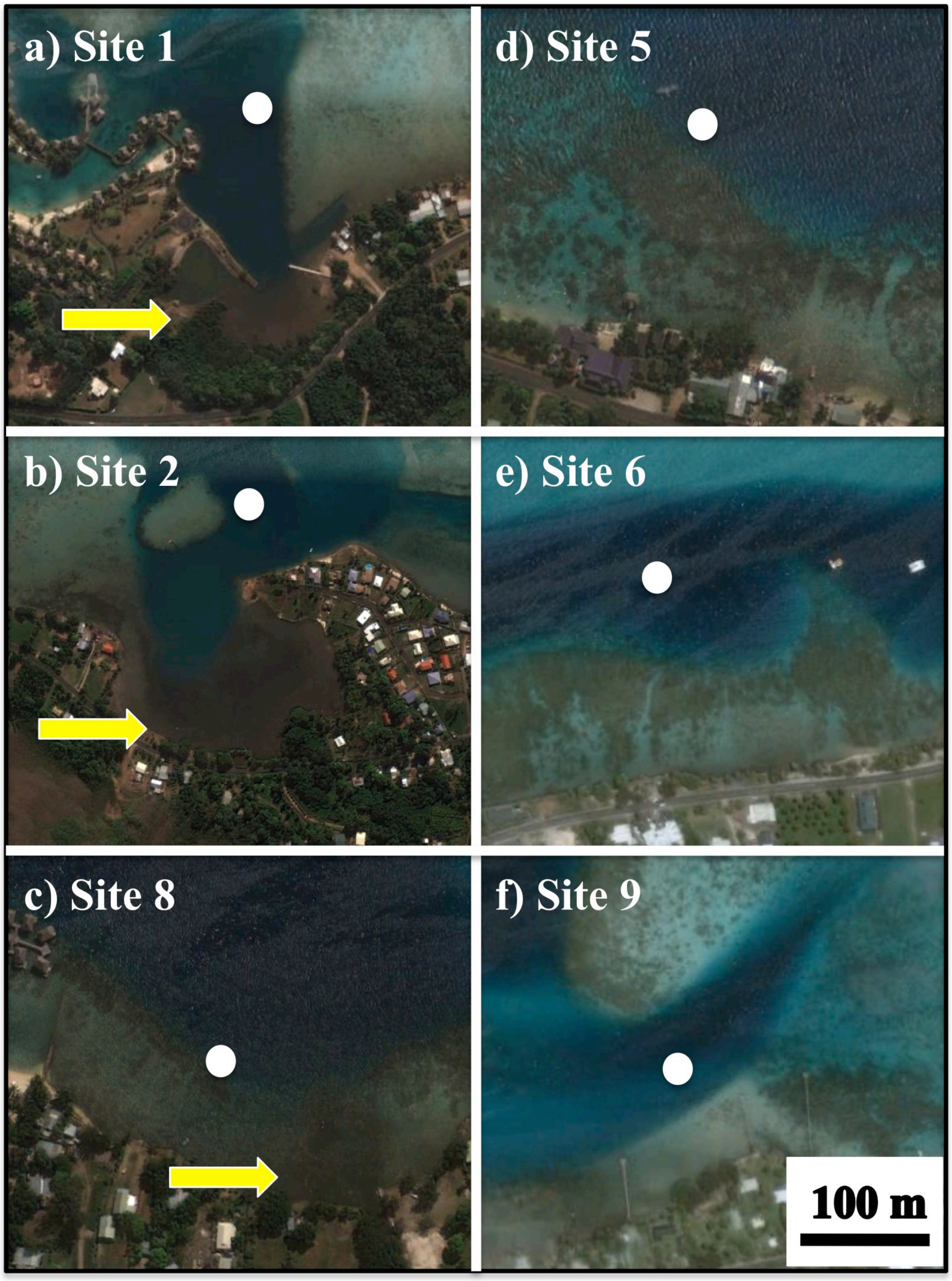

Figure 4.10. Aerial view of six of the nine fringing reef transplant locations utilized in 2009. White dots indicate the locations of transplanted coral heads and juvenile fish. **a-c)** Three sites characterized by turbid waters. Arrows indicate areas of shallow water with large amounts of terrestrial sediment **(a,b)** and the outflow of a small river **(c)**. **d-f)** Three sites with relatively high water clarity. Satellite images are taken from Google Earth, © 2011 ImageEye and © 2011 Digital Globe.

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Appendix 4A. Details of size metrics measured from juvenile fish.

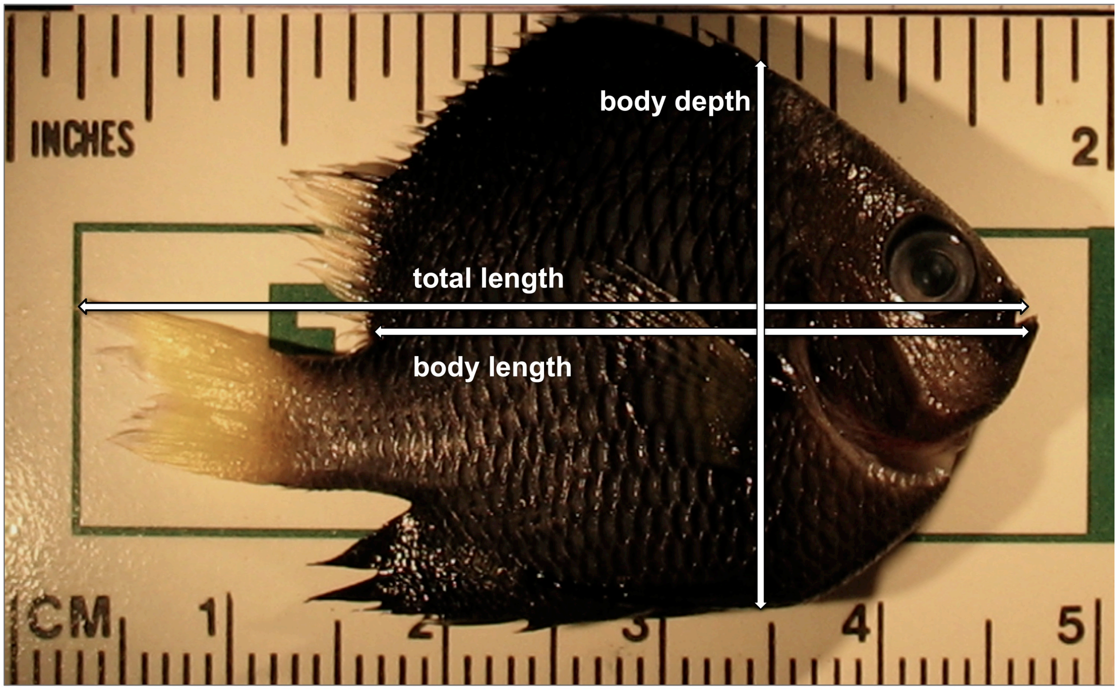

Figure 4A.1. Illustration of the three body size measurements taken on each juvenile *Dascyllus flavicaudus* from the regional-scale transplant experiment: total length (TL), body length (BL) and body depth (BD). Measurements were taken from digital photographs using the image analysis software ImageJ with measurements scaled to the ruler included in each photo.

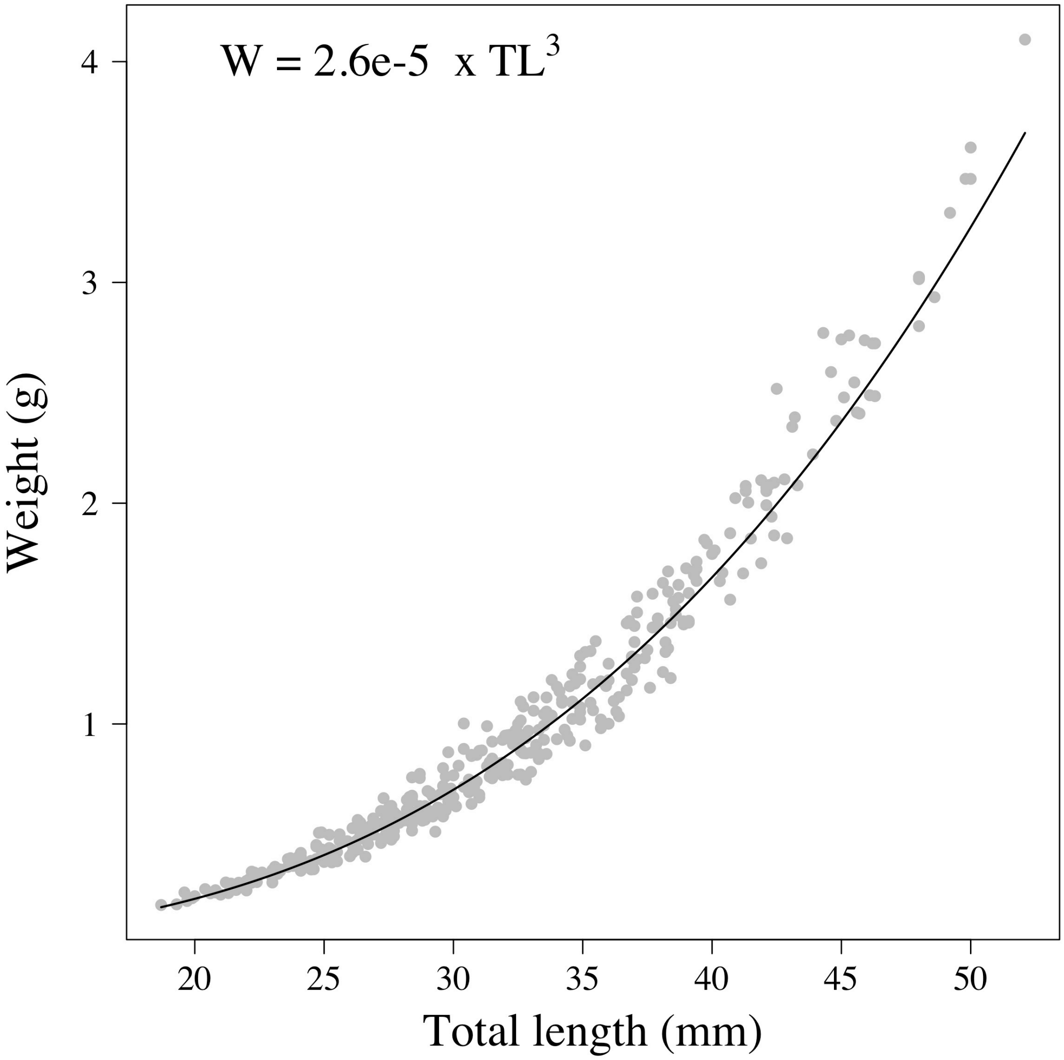

Figure 4A.2. Length-weight relationship for juvenile *Dascyllus flavicaudus* collected in Moorea, French Polynesia. The fitted equation was parameterized using a linear regression of ln(weight) on ln(total length).

Appendix 4B. Details of recovery rates for the 2008 and 2009 transplant experiments.

Table 4B.1. Recovery rates of tagged juvenile *Dascyllus flavicaudus* from replicate coral heads. Each coral head initially received 10 juvenile fish. Coral head numbers for the 2009 experiment correspond to locations spanning Moorea's north shore (see Fig. 4.1). Sites in each reef habitat are numbered increasing from east to west. Coral heads in the 2008 experiment were transplanted to Pao Pao Bay and to the fringing, back and forereef directly north of the bay. Replicates coral heads in the 2008 experiment were separated by approximately 20 m.

		Replicate coral shelter								
Year	**Habitat**	**1**	**2**	**3**	**4**	**5**				
2008	Forereef	8	10	7	7	6				
	Backreef	3	5	8	8	5				
	Fringing Reef	8	7	9	10	7				
	Pao Pao Bay	10	7	10	7	2				
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
2009	Forereef	3	0	3	1	0	0	1	5	1
	Backreef	10	8	5	8	5	0	0	7	9
	Fringing Reef	8	4	4	6	5	10	8	7	9

Appendix 4C. Time series of zooplankton abundance sampled from four locations on Moorea's north shore.

Table 4C.1. The total density of zooplankton sampled from Pao Pao Bay and stations in three reef habitats (fore, back and fringing reefs) north of the bay. Data were collected by the Moorea Coral Reef LTER.

Location	Latitude (°S)	Longitude (°W)	Date	Time	Volume sampled (L)	Total ZP (ind. m^{-3})
Pao Pao Bay	17.4931	149.7887	2005-08-09	11:00	2121	1225.6
			2005-12-06	17:00	3365	959.4
			2006-08-29	16:00	2055	528.6
			2006-12-13	10:25	2087	234.8
			2007-03-25	9:30	2030	858.9
			2007-08-20	9:30	2570	287.1
			2008-01-12	9:30	2282	767.4
			2008-08-25	9:15	2097	497.3
			2009-01-10	9:50	1888	2521.6
			2009-07-27	9:55	1892	300.2
Fringing reef	17.4852	149.8337	2005-08-04	15:00	5375	86.1
			2005-08-07	16:00	8865	35.7
			2006-03-29	16:00	13759	31.4
			2006-06-21	9:50	11534	54.9
			2006-08-21	17:25	11456	14.1
			2006-12-19	16:00	11273	169.5
			2007-03-17	16:30	7954	93.1
			2007-08-11	15:30	11149	104.0
			2008-01-07	9:00	20030	568.5
			2008-08-30	16:00	10845	89.4
			2009-01-18	10:00	9056	345.4
			2009-07-22	10:00	6216	132.2

Table 4C.1. cont'd

Location	Latitude (°S)	Longitude (°W)	Date	Time	Volume sampled (L)	Total ZP (m^{-3})
Backreef	17.4785	149.8419	2005-08-04	15:00	4558	18.6
			2005-08-04	16:00	7103	16.2
			2005-08-06	16:00	10459	80.9
			2005-08-10	9:00	9971	14.6
			2005-08-13	10:00	8546	88.3
			2005-08-13	10:00	11334	118.6
			2006-04-01	10:00	19467	81.1
			2006-04-01	10:50	23234	60.2
			2006-06-19	17:00	10236	509.6
			2006-06-24	10:00	17022	97.0
			2006-08-21	16:50	12827	21.0
			2006-12-21	16:00	11619	186.9
			2007-03-19	9:15	11127	99.5
			2008-01-10	9:30	23809	155.4
			2008-08-31	16:00	6615	29.9
Forereef	17.4750	149.8371	2005-08-05	8:00	11205	20.7
			2005-08-10	8:50	9522	10.4
			2006-03-30	9:00	12254	52.3
			2006-06-22	15:00	12099	12.7
			2006-08-23	9:50	13609	48.2
			2006-12-20	9:75	7632	14.8
			2007-03-20	9:00	9874	17.2
			2007-08-13	8:30	14884	86.0

Table 4C.2. The density of individual zooplankton taxa in samples from Pao Pao Bay and stations in three reef habitats (fore, back and fringing reefs) north of the bay. Data were collected by the Moorea Coral Reef LTER.

Site	Date	Abundance (ind. m^{-3})										
		Copepods	Ostracods	Decapod larvae	Amphipods	Isopods	Mysids	Polychaetes	Polychaete larvae	Larvaceans	Fish eggs	Tanaids
PP	2005-08-09	967.5	118.8	2.1	0.7	0.0	0.0	0.7	0.0	135.8	0.0	0.0
	2005-12-06	595.6	360.2	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	2006-08-29	294.0	222.0	9.7	0.0	1.0	0.0	0.0	0.0	0.0	1.9	0.0
	2006-12-13	136.7	65.4	9.2	0.0	1.7	0.0	1.7	0.0	11.7	8.4	0.0
	2007-03-25	781.2	22.4	19.2	0.8	0.8	0.0	5.6	0.0	28.8	0.0	0.0
	2007-08-20	105.1	129.0	19.8	0.6	0.0	0.0	0.6	0.0	0.6	31.5	0.0
	2008-01-12	697.9	49.1	8.2	0.0	0.0	0.0	2.0	0.0	2.0	8.2	0.0
	2008-08-25	410.8	81.1	2.7	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0
	2009-01-10	1296.8	84.1	12.0	12.0	48.0	0.0	288.2	0.0	744.5	36.0	0.0
	2009-07-27	237.9	9.5	22.2	1.1	3.2	1.1	10.6	0.0	5.3	9.5	0.0
FR	2005-08-04	70.7	0.0	0.0	0.2	0.0	1.7	0.7	0.0	0.0	12.7	0.2
	2005-08-07	19.8	0.0	0.0	12.2	0.2	0.2	0.3	0.0	0.5	2.5	0.0
	2006-03-29	16.6	0.0	0.1	0.0	0.1	0.0	0.9	0.0	4.9	8.8	0.0
	2006-06-21	34.8	0.0	0.0	0.0	0.0	0.0	3.3	0.0	0.3	16.6	0.0
	2006-08-21	3.8	0.0	0.0	0.2	0.3	0.3	0.0	0.0	0.0	9.4	0.0
	2006-12-19	127.2	0.0	1.7	0.0	1.1	0.0	1.1	0.0	6.0	30.7	1.7
	2007-03-17	61.9	0.0	2.4	0.4	0.4	0.0	0.8	0.0	6.8	20.0	0.4
	2007-08-11	65.7	0.0	0.0	0.0	8.8	0.0	6.0	0.0	0.0	23.0	0.5
	2008-01-07	496.7	0.0	0.0	0.0	0.0	0.0	9.0	0.0	23.5	39.3	0.0
	2008-08-30	63.3	1.0	0.3	0.0	2.0	0.0	5.9	0.0	0.5	16.3	0.0
	2009-01-18	255.3	0.0	0.0	0.0	7.5	0.0	5.0	0.0	20.0	50.1	7.5

Table 4C.2. cont'd.

Site	Date	Abundance (ind. m^{-3})										
		Copepods	Ostracods	Decapod larvae	Amphipods	Isopods	Mysids	Polychaetes	Polychaete larvae	Larvaceans	Fish eggs	Tanaids
BR	2005-08-04	14.9	0.4	0.2	0.0	0.9	0.0	0.4	0.4	1.1	0.2	0.0
	2005-08-04	12.4	0.0	0.0	0.0	0.1	0.0	0.0	0.0	2.0	1.7	0.0
	2005-08-06	65.4	8.0	0.3	0.0	0.0	0.0	0.1	0.0	2.2	4.9	0.0
	2005-08-10	9.2	3.0	0.2	0.0	0.5	0.0	0.6	0.0	1.2	0.0	0.0
	2005-08-13	75.8	0.0	1.1	0.0	0.0	0.0	1.6	9.5	0.0	0.2	0.2
	2005-08-13	95.3	0.0	1.1	0.0	1.1	0.0	2.1	19.1	0.0	0.0	0.0
	2006-04-01	75.0	0.0	3.0	0.0	1.2	0.0	1.8	0.0	0.0	0.0	0.0
	2006-04-01	56.8	0.0	2.5	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
	2006-06-19	482.5	0.0	5.1	0.0	0.0	0.6	11.4	0.0	0.3	9.7	0.0
	2006-06-24	86.3	0.8	0.3	0.4	0.0	0.0	6.8	0.0	0.0	2.4	0.0
	2006-08-21	9.1	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	11.2	0.0
	2006-12-21	159.0	0.0	17.0	1.0	0.0	0.0	1.0	0.0	0.0	8.8	0.0
	2007-03-19	80.5	1.2	0.0	0.0	0.0	0.0	0.0	0.0	13.8	4.0	0.0
	2008-01-10	102.4	9.3	5.6	0.0	1.9	0.0	3.7	0.0	2.8	29.8	0.0
	2008-08-31	19.0	2.3	0.9	0.0	0.0	0.5	0.5	0.0	0.0	6.8	0.0
		0.0										
FR	2005-08-05	17.4	0.0	0.0	1.5	0.3	0.9	0.1	0.0	0.0	0.5	0.0
	2005-08-10	6.3	0.2	0.0	0.2	0.0	0.0	0.0	0.0	3.8	0.0	0.0
	2006-03-30	38.0	0.5	1.4	0.5	0.5	0.0	0.0	0.0	9.5	1.9	0.0
	2006-06-22	10.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.1	2.3	0.0
	2006-08-23	45.4	0.3	0.4	0.0	0.1	0.1	0.0	0.0	0.1	1.5	0.1
	2006-12-20	10.6	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	4.0	0.0

Appendix 4D. Total length as a metric of fish growth.

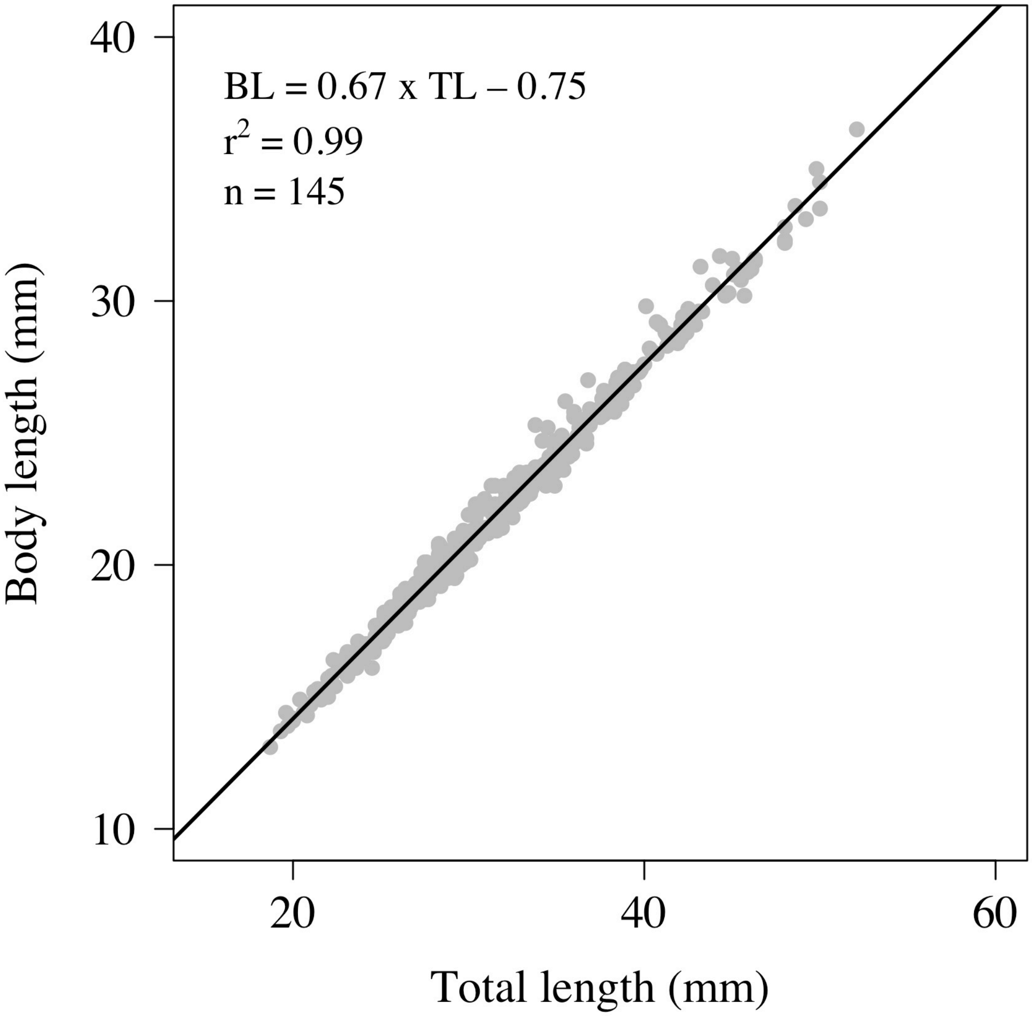

Figure 4D.1. Linear fit of the relationship between measured body length and measured total length for juveniles of the reef fish *Dascyllus flavicaudus* collected in Moorea, French Polynesia. See Appendix 4A for photo of length measurements.

Appendix 4E. Details of the gut content analysis for *Dascyllus flavicaudus*.

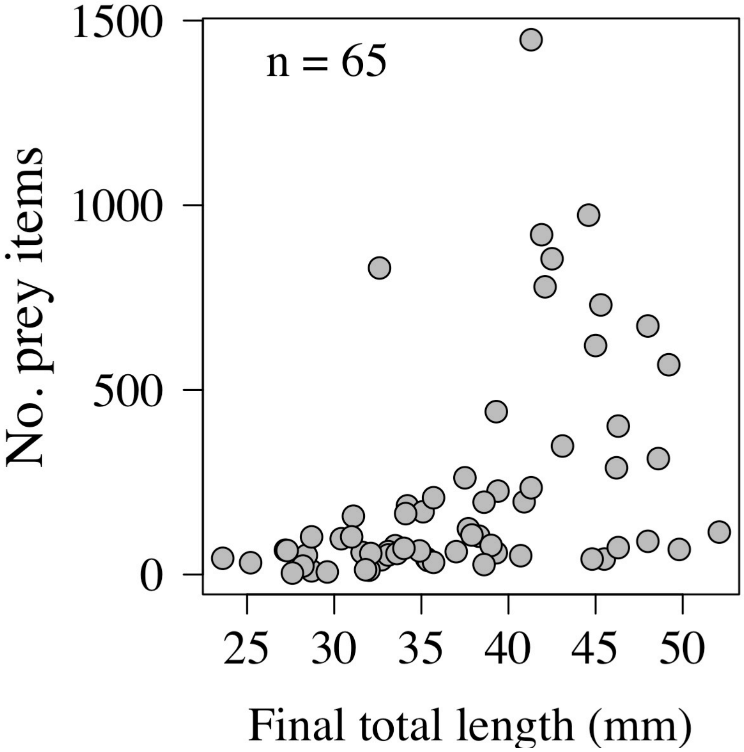

Figure 4E.1. The number of prey items sampled from guts of juvenile *Dascyllus flavicaudus* on the terminal day of the transplant experiment in relation to the final size (total length) of juvenile fish.

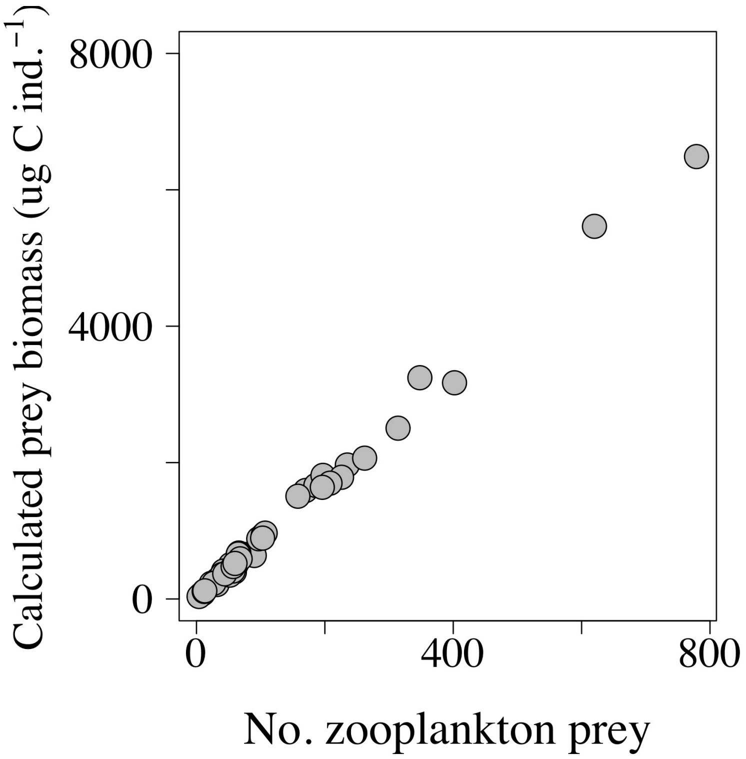

Figure 4E.2. The relationship between number of prey items sampled from guts of individual *Dascyllus flavicaudus* juveniles and calculated prey biomass.

CHAPTER 5

Summary of the Dissertation

The overarching objective of this dissertation was to explore the relative importance of oceanic food sources to coral reef food webs. To meet this objective, I chose to focus on one subset of coral reef consumers – diurnal fishes that prey on zooplankton in the water column. To summarize this dissertation, I review the hypotheses examined and main findings of the three empirical data chapters. I conclude with suggestions for future avenues of research on planktivorous fish in coral reef food webs.

REVIEW OF HYPOTHESES AND MAIN FINDINGS:

Chapter 2. The contribution of oceanic and reef food sources to the diet and secondary production of planktivorous coral reef fishes

In Chapter 2, I paired two independent metrics of fish diet – gut content analysis and stable isotope analysis – to quantify the contribution of oceanic and reef-associated food sources to secondary production in planktivorous fishes. The relative importance of imported (oceanic) and local (reef-associated) food sources was compared among Moorea's three reef habitats – fore, back and fringing reefs.

Oceanic zooplankton comprised larger proportions of the diet of fish inhabiting the deep forereef than of fish inhabiting nearshore reefs. This gradient in the relative importance of oceanic zooplankton to fish diet was mirrored by a pattern of offshore depletion/ nearshore enrichment of $^{13}C:^{12}C$ in the muscle tissue of planktivorous reef fishes. Though the role of imported versus local food sources to fish diet was habitat-dependant, planktivorous fishes in all reef locations ingested and incorporated significant amounts of oceanic zooplankton and thus carbon sourced from pelagic, oceanic primary production.

The design of the study reported in Chapter 2 was inspired by a growing body of research from the intersection of the fields of landscape ecology and food web ecology. Broadly, landscape ecology describes a body of research characterized by a focus on spatial heterogeneity in the biotic and abiotic environment, exploring implications of this heterogeneity for physical and biological interactions within an ecosystem (Turner 1989). As described by Turner in her review of the field, the rise of landscape ecology over the course of the twentieth century marked a shift from interest in the processes that create pattern to the influence of pattern on process. As ecologists continued to develop this landscape view, the field's approach to the study of species interactions was also changing. The concept of a 'food chain' is credited to British zoologist Charles Elton (1927). Elton's idea presented a novel way to partition a community of organisms by sorting them into a diet-based hierarchy. This led to a new language with which scientists could summarize and explore ecosystem complexity and species relationships (Paine 1980). The food chain concept, and later the food web concept, significantly shaped the way ecosystem dynamics and stability were modeled and studied in the following decades (Lindeman 1942, MacArthur 1955). Food web studies of coral reef ecosystems that focus on the transfer of energy between various trophic groups are broadly analogous to mid-twentieth century scientific efforts to construct carbon, nitrogen and phosphorus budgets for reef ecosystems.

The research in Chapter 2 answers two questions that are fundamental to landscape-scale food web studies and investigations of cross-ecosystem trophic exchange (Vanni et al. 2004). First, what organisms serve as links between adjacent ecosystems? Planktivorous fishes are an obvious candidate within coral reef ecosystems – zooplankton prey are essentially bundles of particulate energy, nutrients and minerals. In systems such as rocky reefs and kelp forests, planktivorous fishes are appreciated as conduits through which particulate nutrients from the pelagic reach benthic consumers and in these systems the influence of planktivorous fishes on nutrient flux to the benthos has been quantified (Bray et al. 1981, Pinnegar and Polunin 2006). Such investigations in rocky littoral areas and kelp beds are simplified by the fact that the zooplankton in question are known to be tied to pelagic, oceanic or offshore food webs. In coral reefs, however, similar questions are complicated by the nature of reef zooplankton assemblages. The zooplankton on coral reefs is a mixture of transient, oceanic taxa that originate offshore, resident groups that feed and reproduce on reefs and within lagoons, and pelagic life stages of benthic coral reef organisms. Only the transient, oceanic taxa represent subsidies of new nutrients into the reef system. Thus, an understanding of planktivorous fishes as agents of cross-ecosystem exchange was not possible without knowing whether these fishes feed primarily on reef-associated or oceanic zooplankton. The research I present on a suite of nine planktivorous species confirms that this guild of fishes promotes cross-ecosystem exchange and is an entry point for new, oceanic energy and nutrients that contribute to productivity in coral reef ecosystems.

Having identified zooplanktivores as 'agents' of cross-ecosystem exchange, I assess spatial and temporal variability in oceanic subsidies to reef fish production. Within this study, spatial patterns in the diet of reef planktivores inhabiting the forereef, backreef and fringing reef are consistent around the island of Moorea, stable through time, and occur across a suite of nine planktivorous species. Such knowledge of the spatial and temporal variability of cross-ecosystem exchange is an essential component of landscape-level food web studies.

Following the insights gained in Chapter 2, Chapter 3 pursued a third primary question of food web studies: What are the biological processes that mediate cross-ecosystem exchange? In Chapter 3, I examined the feeding behavior of planktivorous reef fishes as a potential process mediating reef-ocean exchange.

Chapter 3: Selective feeding increases the contribution of oceanic zooplankton to the diet of planktivorous coral reef fish

In Chapter 3, I focused on the feeding biology of the coral reef planktivore *Dascyllus flavicaudus* and asked whether selective feeding in this species affects the contribution of oceanic versus reef zooplankton to fish diet. By comparing the taxonomic composition of fish gut contents with that of the ambient prey assemblage, I rejected the null hypothesis that the diet of *D. flavicaudus* represents a random selection of prey items from the environment. The forage ratios calculated for each prey group suggest that *D. flavicaudus* feeds selectively on highly-pigmented, erratically swimming copepods such as those from the families Oncaeidae and Corycaeidae. Calanoid copepods, the dominant component of environmental zooplankton samples, were highly underrepresented in fish guts, which may reflect highly developed escape responses by this prey group. The copepods for which *D. flavicaudus* exhibited positive electivity were oceanic species while those underrepresented in the diet (with the exception of Oithonidae) were known or are likely to be reef-associated. Non-random feeding by *D. flavicaudus* resulted in oceanic prey groups contributing 25 to 76 % of total zooplankton biomass in fish diets, a 2 to 6-fold increase beyond that expected under a model of random feeding.

This study was, to my knowledge, the first to explore selective feeding in a diurnal planktivorous coral reef fish, and the first to examine the implications of such feeding behavior for the exchange of nutrients between oceanic and coral reef food webs. The taxonomic resolution of the data was an improvement on many previous studies that have considered all copepods as one prey type. By increasing taxonomic resolution within the copepod prey, I was able to quantify the importance of families such as Oncaeidae and Corycaediae to fish diet. These cosmopolitan families are ubiquitous to tropical oceans. However, due to their relatively small body sizes they have been chronically under-sampled and their importance in pelagic food webs underestimated (Paffenhofer 1993, Turner 2004). The abundance and production of small-bodied copepods in coral reef ecosystems is also likely underestimated (Hopcroft et al. 1998). My research suggests that these copepod families may be important and even dominant prey items for a suite of zooplanktivorus reef fishes.

Chapter 4: Variation in the growth of a planktivorous coral reef fish (*Dascyllus flavicaudus*, Pomacentridae) in relation to food availability and prey consumption

In Chapter 4, I move from a focus on the food web implications of fish diet to examine the consequences of spatial patterns in diet for the growth of a zooplanktivorous fish. This chapter builds upon a growing body of research that has documented local-scale (100's of km and less) demographic variability within reef fishes. As planktivorous coral reef fishes are known to be food limited, and the abundance of zooplankton prey can vary considerably across the reef, it is logical to propose that spatial patterns in food abundance may drive spatial patterns in fish growth. However, the feeding rate of zooplanktivorous fishes is not a simple function of ambient prey density but is influenced by a suite of physical and biological factors including water velocity and competitive interactions with other fishes. As Moorea's three reef habitats are distinct in many aspects associated with fish feeding, I hypothesized that the growth rates of juvenile fish would vary predictably with reef habitat.

The growth rates of transplanted juvenile *Dascyllus flavicaudus* were highest in the reef habitat (fringing reef) where the long-term average zooplankton abundance was the greatest. However, when I extended the transplant experiment to span Moorea's north shore, the significant effect of reef habitat on fish growth was not upheld. The substantial loss of juvenile fish from the forereef in the shore-wide transplant experiment precluded a robust comparison of fish growth across the three habitats at this scale. I can not comment on whether fish growth on the forereef would have differed substantially enough from the nearshore reefs to result in a significant habitat effect, as it did in the more localized 2008 experiment. Nevertheless, the shore-wide experiment did offer support for the hypothesized association between food availability and fish growth. The juvenile fish that exhibited the greatest proportional change in size over the course of the transplant also had more zooplankton in their guts on the terminal day of the experiment than fish that experienced lower rates of growth.

Furthermore, the spatial expansion of the 2009 transplant experiment resulted in the distribution of replicate coral heads and fish cohorts across within-habitat environmental patchiness. This heterogeneity was most pronounced in the fringing reef habitat, where some transplant sites were characterized by low visibility and turbid water. Fish growth rates at three markedly turbid fringing reef locations were the lowest in this habitat. Similarly, despite high zooplankton densities in Pao Po Bay, the growth of fish transplanted to this relatively turbid location fish was not significantly different than growth in the three reef habitats even though median zooplankton abundances in the bay were six to fourteen times greater than those on the reef.

Water quality and turbidity levels in Moorea's bays have surely changed over the past century with the development of upslope areas for agriculture, the initiation of a ferry service, and other anthropogenic impacts on the environment. There are no data available that document the quality of reefs in the bays prior to this time, or follow changes in the reef communities here through time. Today, the mounding corals that cover shallow ledges at the edge of Pao Pao Bay are predominantly dead. However, the walls of the bay are covered with dense thickets of the finger coral *Porites rus*.

This coral species appears to be more tolerant of turbid, high-sediment environments than other reef corals, and as a result the walls of the Pao Pao Bay provide ample habitat for coral-dependent reef fishes. These thickets of *P. rus* inside the bay are, however, largely empty of planktivorous fishes. In contrast, seemingly identical *P. rus* thickets that are common to Moorea's fringing reefs are teeming with planktivorous fishes. The discrepancy may be driven by low delivery rates of fish larvae to coral habitat within the bay regardless of water quality, but it is plausible that the lack of planktivorous fishes in the bay is related to the high turbidity.

FUTURE RESEARCH ON PLANKTON AND PLANKTIVORES IN CORAL REEF ECOSYSTMS:

As discussed in Chapter 1, most studies that have examined nutrient budgets and energy pathways on coral reefs have focused on the demands of corals and of primary producers within the reef system. Far fewer studies have examined the relative importance of allochthonous versus autochthonous resources for the many non-coral filter feeders and particulate feeders on reefs; yet, these vertebrates and invertebrates are ubiquitous components of the reef assemblage with an enormous capacity to 'biofilter' passing organic matter. Particle-feeding fishes are of special interest because of their connections to higher trophic level predators. Unlike particle feeders such as gorgonians, cryptic sponges, and even corals themselves, planktivorous fishes are directly preyed upon by a broad array of fish predators. In addition to their fecal contribution to the detrital pool, planktivorus fishes represent an efficient conduit for oceanic energy and nutrients to support secondary production in higher trophic levels.

Recent settlers and young recruits of most coral reef fishes also serve this role, as much of their biomass has been gained during their pelagic larval phase and thus reflects the contribution of oceanic resources.

In this dissertation I provide new, direct evidence that oceanic zooplankton are a significant component of the diet of planktivorus coral reef fishes, with oceanic resources comprising 60 - 90% of the diet of forereef fish. Estimating the fate of this ocean-subsidized reef fish biomass is challenging due to the paucity of taxonomically-resolved data on the diet of piscivorous reef fish and on mortality rates for juvenile and adult planktivores. Nevertheless, it is likely that oceanic resources support an ecologically significant proportion of the biomass of piscivorous reef fishes. Whether directly or indirectly (via planktivorous fish), zooplankton also support the majority of the lagoon fish biomass consumed by human populations in Polynesia. Table 5.1 presents data on landings of reef fish by artisanal fisheries on two Polynesian islands. These data come from a study of fish landings on Moorea in 2001 (Yonger 2002) and a study of landings on Tikehau, an atoll in the Tuamotu Archipelago, in the years 1983 – 1987 (Caillart et al. 1994). Using data on the diet and food items reported for the fished species (Froese and Pauly 2010), I classified each species according to their connection to a zooplankton prey base. Fish that are labeled ‘direct’ are those that feed directly on zooplankton. Species that feed on fishes are considered to have an indirect connection to zooplankton, as zooplanktivorous fishes are likely prey items for these reef piscivores. Fish that feed on algae or benthic invertebrates are considered to have no link to the zooplankton (even though invertebrates likely benefit from plankton-derived inputs to the detrital food web). The remaining fish were identified in the primary studies as ‘miscellaneous marine fishes’ with no further taxonomic detail. It is likely that the majority of these unidentified species are either zooplanktivores or piscivores and thus linked to zooplankton, though to be conservative I have labeled them separately as ‘unknown.’

Summing across the various species’ yield, I calculate that 65 % of the artisanal fish catch on Moorea and 61 % of the catch on Tikehau is linked to a zooplankton prey base. As mentioned earlier, it is difficult to estimate relative contribution of planktivores (versus herbivores or invertivores) to the diet of piscivorous fish, the ‘indirect link’ category. Nevertheless, 55 % of the total catch in Moorea and 8 % of the total catch in Tikehau is comprised of fish that feed *directly* on zooplankton. In Moorea this result is driven by large landings of the bigeye scad *Selar crumenopthalamus*.

Zooplankton are a rich source of food that directly or indirectly fuel a significant amount of the fish biomass on reefs. This fish biomass is passed up the food web to top predators as well as extracted from the lagoon for human consumption. More research is needed to understand the role that oceanic versus reef zooplankton play in supporting this total fish biomass. The results of this dissertation suggest that oceanic zooplankton likely make an ecologically significant contribution at the whole-reef scale, and may dominate the zooplanktonic contribution to the forereef habitat. The vast majority of reef studies to date focus on shallow, well-lit portions of the reef when in reality many coral reefs have a significant ‘mesophotic’ region that extends beyond 30 m depth (Lesser et al. 2009, Hinderstein et al. 2010). The absolute density of planktivorous fishes can be higher on mesophotic reefs than on shallow reefs, and planktivores can also represent a higher proportion of the fish assemblage on deep reefs (Kahng et al. 2010). To my knowledge, the diet of planktivorous fish inhabiting mesophotic reefs has not been examined. Planktivorous fish inhabiting mesophotic reefs may be an important food source for piscivorous species that migrate periodically or ontogenetically between deep and shallow reef areas. Our understanding of the trophic importance of planktivorous fishes in coral reef food webs may underestimated due to the bias toward sampling easily accessible shallow portions of the reef.

With the hindsight of seven years of study focused on plankton and planktivores in coral reef ecosystems, I present the following research suggestions for young, enthusiastic, spearfish-loving, compressed-air-breathing, planktophillic students of coral reef ecology. For your consideration….

(1) How do spatial patterns in the diet of nocturnal planktivorous reef fish compare to patterns in diet for diurnal reef planktivores? Does the migration of nocturnal fish that feed on the forereef and return to shelter in backreef coral drive an increased flux of oceanic nutrients to nearshore reefs?

(2) Does the contribution of oceanic zooplankton to the diet of nearshore fish vary predictably with lagoon size? For reefs where the tides drive a large portion of reef circulation, do reef-associated zooplankton swept from the shallows comprise a significant proportion of the diet of forereef fish?

(3) What is the contribution of oceanic carbon sources to the diet of piscivorous reef fishes? Do planktivorous fishes inhabiting mesophotic reefs contribute to the diet of mobile piscivorous species?

Revisiting the coral reef paradox, viewed through a ‘fisheye’ lens, promises to add novel insight to our understanding of coral reef ecosystems and the processes that promote and maintain their vibrant biological communities.

Table 5.1. Landings of artisanal lagoon fisheries on the islands of Moorea (2001) and Tikehau (1983-1987). Data are taken from Yonger (2002) and Caillart (1994). ZP = zooplankton.

Location	Species	Common name	Catch (kg)	Diet	ZP Link
Moorea	*Selar crumenopthalamus*	bigeye scad	26762	zooplankton	direct
	Myripristis spp.	soldierfish	6056	zooplankton	direct
	Naso unicornis	bluespine unicornfish	3700	zooplankton	direct
	Scarus oviceps	dark capped parrotfish	3246	detritus	weak
	Epinephalus merra	honeycomb grouper	2508	fish	indirect
	Ctenochaetus striatus	striated surgeonfish	1848	algae	none
	Caranx melampygus	bluefin tevally	1613	fish	indirect
	Misc. marine fishes	--	20115	--	unknown
Tikehau	*Lethrinus miniatus*	trumpet emperor	129679	benthic invertebrates	weak
	Lutjanus gibbus	humpback red snapper	68251	fish	indirect
	Caranx melampygus	bluefin trevally	67116	fish	indirect
	Slear crumenopthalamus	bigeye scad	55734	fish	indirect
	Epinephelus microdon	camogflage grouper	55075	fish	indirect
	Lutjanus fulvus	blacktail snapper	47932	fish	indirect
	Naso brevirostrus	spotted unicornfish	40002	zooplankton	direct
	Mulloides spp.	goatfish	34524	benthic invertebrates	weak
	Albula vulpes	bonefish	31671	benthic invertebrates	weak
	Upeneus vittatus	yellowstriped goatfish	17627	benthic invertebrates	weak
	Sphyraena forsteri	bigeye barracuda	12709	fish	indirect
	Acanthurus xanthopterus	yellowfin surgeonfish	10282	algae	none
	Myripristis spp.	soldierfish	8816	zooplankton	direct
	Decapterus pinnulatus	mackeral scad	8781	zooplankton	direct
	Misc. marine fishes	--	74322	--	unknown

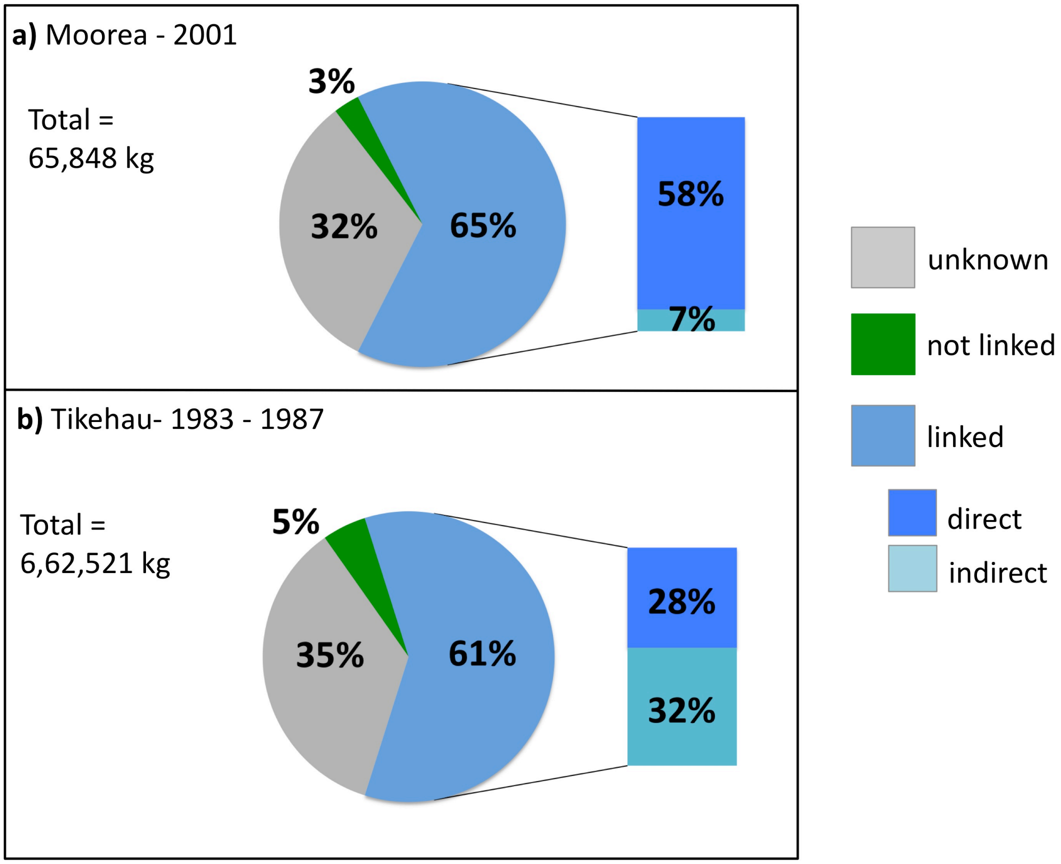

Figure 5.1. Landings of artisanal lagoon fisheries on the Polynesian islands of **a)** Moorea and **b)** Tikehau. Using the species composition of the landings, the total yield is divided according to the association to a zooplankton prey base. The stacked bars show the 'linked' category further divided into direct (via zooplanktivores) and indirect (via piscivores) planktonic contributions to fishery yields.

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