Ecology and Trophic Relationships Among Fishes and Invertebrates in the Hawaiian Archipelago: Insights from Fatty Acid Signatures Analysis

by

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Department of Biology

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ABSTRACT

Healthy coral reefs have become increasingly rare, and their continuous degradation has serious implications for loss of marine biodiversity. There is an urgent need to assess the strength of top-down versus bottom-up effects on reef communities, to better understand how food web alterations can change the structure and function of these vulnerable marine systems. In this study, I used fatty acid (FA) analysis to investigate the trophic and ecological relationships among potential key forage species of the critically endangered monk seal in the Hawaiian archipelago.

A series of multivariate tests performed on groups of closely related and ecologically equivalent species of fishes and invertebrates using a restricted number of FAs revealed that FA differences among groups primarily reflected diet, but could also be related to habitat and ecology. The same groups were subsequently analysed using an alternate method in quantitative FA signature analysis (QFASA) simulations, which allowed for the effects of using various subsets of FAs to be evaluated. Overall, species groups were relatively well characterized using both methods. When present, overlap in FA composition principally occurred among groups with similar diet/ecology, and were more prominent at higher trophic levels. A last set of analyses which combined the multivariate and QFASA simulation methods revealed that despite taxonomical relatedness and similarities in trophic ecology, individual species of carnivorous fish could be reliably distinguished using FAs. Therefore, while increasing the number of FAs used in the analyses might be useful to refine the resolution of distinctions, using a restricted number of FAs can also result in reliable differentiation among species. My results suggested that despite tremendous diversity, finer scale variations in FA composition could be detected among groups, and among species which shared the same diet and trophic ecology. These findings have important implications for the study of food web interactions in the Hawaiian archipelago, as they provide the foundation for using the same species groups in diets estimations of monk seal, as well as other top predators in this ecosystem. Moreover, they provide a framework for using multiple approaches to link FA patterns to the foraging ecology of individual species.

LIST OF ABBREVIATIONS USED

ANOVA	Analysis of variance
cm	Centimeter
CSM	Cross Seamount
D	Dietary fatty acid set
DFA	Discriminant function analysis
DHA	Docosahexaenoic acid
DNA	Deoxyribonucleic acid
ED	Extended dietary fatty acid set
EDS1	Extended dietary subset 1
EDS2	Extended dietary subset 2
EPA	Eicosapentaenoic acid
FA	Fatty acid
FFS	French Frigate Shoals
FID	Flame ionization detector
g	Gram
GBR	Great Barrier Reef
GC	Gas chromatograph
GP	Gardner Pinnacles
ha	Hectare
HE	Hawaiian-Emperor
M1	Modified extended dietary fatty acid subset 1
M2	Modified extended dietary fatty acid subset 2
MANOVA	Multivariate analysis of variance
MHI	Main Hawaiian Islands
MR	Maro Reef
NOAA	National Oceanic and Atmospheric Administration
NPSG	North Pacific Subtropical Gyre
NWHI	Northwestern Hawaiian Islands
PUFA	Polyunsaturated fatty acid
QFASA	Quantitative fatty acid signature analysis
Smt 11	Mid-Pacific Seamount 11
t	Metric ton
Unk	Unknown collection location
µm	Micrometer

ACKNOWLEDGEMENTS

This has been a long journey and as I am writing this, I can’t help but reflect on how humbling this entire experience was, and how truly grateful I am to the many people who have made this thesis possible. First, I would like to express my earnest gratitude to my supervisor Sara Iverson for her guidance, astute insight, and support throughout this adventure. I am also thankful to Frank Parrish whose thoughts and expertise have without doubt greatly influenced the evolution of this thesis work. I am grateful to Jeff Hutchings for his encouragement and assistance in difficult times. I would also like to thank Shelley Lang and current and past members of the Iverson Lab for extensive assistance with sample processing and lab analyses. Wade Blanchard, thank you for your continued patience during our stat sessions. Bud Antonelis, Charles Littnan and Robert Dollar; it was always a pleasure to work with you guys. Tatiana and Grigori, I thank you for your words of wisdom and moral support. To my dear friends Sarah, Angela, Boss, Claudia, Camille, Antonin, and Jeri thank you for listening and keeping up with the emotional rollercoaster. And last but not least, a special thank you to my brother Bruno, who has many times saved the day, even from afar.

CHAPTER 1 INTRODUCTION

1.1 USING BIOCHEMICAL TRACERS IN THE STUDY OF MARINE FOOD WEBS

Traditional approaches to understanding ecological interactions in marine ecosystems, such as direct observation and analysis of gut contents, possess unquestionable strengths such as the ability to provide valuable taxonomic information on the prey consumed by a predator, but also have a number of well-recognized associated biases and limitations (reviewed in Tollit et al. 2010). For example, differential rates of digestion can lead to the underestimation of soft-bodied and/or smaller prey items, and the digesta recovered only provide information on the most recent meal consumed. Thus there is a need for the development of methods which allow a more accurate estimation of the type and proportion of prey species taken by a given predator, and the assessment of variation in diets over larger time scales. More recently, alternative methods have been developed to help decipher the nutritional ecology of marine predators which employ various types of biochemical tracers such as stable isotope (SI), the molecular identification of prey using DNA, and fatty acids (FAs). These methods are have proven especially useful in marine environment since direct observation of predators foraging at sea, such as seabirds and marine mammals, is often not possible.

1.1.1 ISOTOPIC AND MOLECULAR ANALYSES

SI analyses are based on the premises that isotopic ratios in the proteins of consumers reflect those of the proteins of their prey, and that the relative abundance of the heavier to lighter isotopes changes across trophic levels in a predictable manner

(Bearhop et al. 2004, Tollit et al. 2010). Isotopic measurements are most commonly performed using isotopes of carbon, nitrogen, hydrogen and oxygen (Newsome et al. 2010). Variations in isotopic ratios can provide useful information on dietary guilds due to the selective retention of the heavier isotope in higher trophic levels, and on foraging location as they can allow, for instance, the determination of whether fishes or invertebrates occupy benthic versus pelagic ecological zones (Miller et al. 2010). At higher trophic levels, SI analyses have also been used to study the trophic ecology of seabirds in temperate, polar, and tropical regions and can provide critical information on the trophic level of the consumer and their prey as well as the region of feeding (e.g. Jaeger et al. 2010). Isotopic analyses have also been successfully employed in the study of the foraging ecology, habitat use, migration, and physiology of marine mammals (reviewed in Newsome et al. 2010). However, SI analyses generally do not allow for detailed evaluation of differences among diets of ecologically similar species or to actually estimate species composition of diets.

Molecular identification of prey recovered from fecal samples using DNA analyses has also been applied in the study of marine mammal diets (e.g. Deagle et al. 2005) and allowed for a greater resolution in prey detection and identification. However this method remains somewhat dependant on the recovery of hard body parts which have not been severely degraded by digestion, prey DNA is not extractable from all samples, and prey identification is conditional to the previous existence of prey genetic primer (reviewed in Tollit et al. 2010).

1.1.2 FATTY ACID ANALYSES

One of the most promising of the newer biochemical tracer approaches is the use of fatty acids (FAs) to study aspects of food web dynamics (Dalsgaard et al. 2003, Iverson 2009). FAs obtained through the diet can be followed through their integration in the tissues of consumers at different trophic levels, and can therefore be used as diet indicators to gain a detailed understanding of trophic interactions within ecosystems (e.g. Budge et al. 2002, Iverson et al. 2002, Iverson et al. 2004). In fishes and marine invertebrates (and in any higher animals), only a limited number of FAs can be synthesized *de novo*; thus, most FAs are obtained through the diet (Sargent et al. 1989, Cook 1991). Nevertheless, some FAs can arise in animals by biosynthesis from carbohydrates or proteins consumed in excess of requirements. However, such FAs are mostly limited to the n-9 and n-7 families of FAs, and biosynthesis is *inhibited* by diets that contain high levels of FAs (Sargent et al. 1989) or when the consumer is in a fasting state (Iverson et al. 1993). Thus, FAs and families of FAs that are abundant in marine ecosystems, such as those with n-3 and n-6 double bonds, as well as many others, can only arise in the consumer from dietary intake (Sargent et al. 1989).

Numerous validation studies have been conducted which demonstrate the direct and quantitative effect of dietary FAs on the lipid stores of consumers, including mammals (Iverson et al. 2004, Tucker et al. 2009), fishes (Kirsch et al. 1998, Stowasser et al. 2009), and invertebrates (Silina & Zhukova 2009, Spilmont et al. 2009). In marine environments, many FAs originate in photosynthetic primary producers; unicellular algae are particularly rich in n-3 polyunsaturated FAs (PUFAs), as well as n-6 PUFAs, which can account for up to 50% of their total lipid composition (Sargent et al. 1989). For that reason, n-3 and n-6 FAs tend to dominate the lipid composition of marine organisms, as FAs get propagated through marine food webs.

FA signatures (the quantitative array of all FAs in the tissue of a consumer) have been shown to differ among members of pelagic and benthic food webs (Sargent et al. 1989, Budge et al. 2002). In pelagic environments, the major consumers of primary producers are crustacean zooplankton species, such as copepods and euphausiids (Sargent et al. 1989). Thus, zooplanktivorous fishes contain particularly high quantities of 20:1n-9 and 22:1n-11, derived from the consumption of copepod wax esters (Sargent et al. 1989, Budge et al. 2002). In turn, the FA signatures of piscivorous fishes (e.g. gadoids, cod, and haddock) feeding on these zooplanktivores will also have varying levels of 20:1n-9 and 22:1n-11, reflecting their diet (Sargent et al. 1989). In contrast, organisms belonging to marine food webs in which copepod consumption does not occur or occurs at lower levels can be expected to differ significantly with regard to these particular FAs (Sargent et al. 1989, Budge et al. 2002). FA signatures can also differ greatly between ecosystems as a result of differing levels and types of primary production. For instance, levels of certain isomers of long-chain monounsaturates differ greatly between the North Atlantic and the North Pacific, and ratios of n-6/n-3 fatty acids are far greater in tropical versus temperate ecosystems (Dalsgaard et al. 2003, Iverson 2009).

Most of the FA research undertaken to investigate various aspects of marine food webs has targeted temperate and arctic systems, however their use in complex and more diverse ecosystems such as tropical and subtropical coral reefs has remained largely unexplored. Healthy coral reefs have become exceedingly rare. It is imperative that we improve our knowledge of how remaining intact reef ecosystems are constructed and structured, in terms of species and species interactions, to better understand the short and long term impact of anthropogenic disturbances and global climate change on these vulnerable systems (Hughes et al. 2003, Bellwood et al. 2004).

1.1.3 THE STRENGTH OF USING MULTIPLE APPROACHES

Given that each of these newer biochemical tracer approaches possess various strengths and weaknesses, the greatest potential of these methodologies lies in using them in combination with other complementary methods to provide a detailed and more complete picture of trophic relationships and food web interactions (see Tollit et al. 2010). For example, SI analyses have most recently been advanced to compound-specific isotopic analyses which have been employed for example to investigate shifts in dietary FA sources (planktonic versus benthic) in marine fish (Koussoroplis et al. 2010). The emergent use of legacy contaminants as biomarkers, used in conjunction with FA and SI analyses, represents a promising tool which has allowed further understanding of the processes responsible for bioaccumulations of toxins across trophic levels in marine food webs (e.g. Hebert et al. 2009, Lavoie et al. 2010). The most detailed information pertaining to the foraging ecology and trophic relationships of Hawaiian fishes and invertebrates has relied heavily on the work of a few authors which have performed comprehensive in situ observation over various temporal and spatial scale (e.g. Hobson 1974, Randall 1996). However, published information on the diet and ecology of these species remains scarce and in some instances contradictory. Thus, there is a need to develop complementary trophic biomarker approaches in the context of coral reef food web studies to further our understanding of the processes structuring these complex yet fragile ecosystems.

1.2 TOPOGRAPHY AND TROPHIC STRUCTURE IN THE HAWAIIAN ARCHIPELAGO

The Hawaiian-Emperor (HE) chain is composed of over 100 volcanoes which stretches over 6000 km across the Pacific Ocean (Grigg 1997). It is the longest, oldest volcanic chain in the world. This chain originates from the north-westward movement of the Pacific tectonic plate over a thermal plume which melts and uplifts the earth's crust, and creates a linear trail of islands. The combined action of subsidence and erosion gradually reduce the emergent land surface. The islands become smaller, lower and more eroded until they reach sea level and form atolls (Grigg 1997). Coral growth on atoll perimeter reefs temporarily counterbalance the effect of subsidence and erosion and keep the islands at sea level, as the plate continues to move to the northwest. Upon reaching higher latitudes, coral growth becomes insufficient and islands sink to become seamounts, guyots, and banks. Such complex topographic structure has led to the creation of an ecosystem which offers a mosaic of habitats to its constituent marine species.

The Hawaiian archipelago is located at the southeastern end of the HE chain, and is comprised of 18 islands and atolls which together constitute the most remote large-scale coral reef ecosystem in the world (Maragos & Gulko 2002). Located in the center of the North Pacific Subtropical Gyre (NPSG), the archipelago is further isolated from neighbouring ecosystems by wind-driven geostrophic circulation leading to surface waters convergence (Karl 1999). Such isolation has led to the evolution of many endemic species, which today comprise 25% of all Hawaiian reef species. The Northwestern Hawaiian Islands (NWHI; 25-30°N, 175°E-165°W) ecosystem is comprised of 10 atolls and islets extending 2,000 km northwest of the Main Hawaiian Islands (MHI; Figure 1.1;

Maragos & Gulko 2002). The early implementation of precocious protection measures has allowed for the NWHI to persist in a fairly unaffected state; it is now considered to be one of the last healthy reef ecosystem of the world (Parrish & Boland 2004). The designation of the NWHI as a National Marine Monument in June 2006 further emphasizes the ecological and cultural importance of this unique ecosystem, and illustrates the desire to protect and preserve it.

As a consequence of their protected status, the NWHI have been subjected to extremely light fishing pressure (Maragos & Gulko 2002). Moreover, the islands and atolls in that system are virtually uninhabited, thus limiting the direct deleterious impact of urbanisation and pollution. The opposite situation is encountered in the MHI where most of the large economically important species have been overfished, and where overexploitation led to population collapses and/or the alteration of life histories in remaining species (Pauly et al. 1998, Carr et al. 2002, Dulvy et al. 2004). As a result, striking differences exist among the trophic structure and reef fish assemblage of the NWHI relative to the MHI (Friedlander & DeMartini 2002). The overall fish biomass of shallow reef systems across the archipelago is far greater in the NWHI (2.4 t ha^{-1}) relative to the MHI (0.67 t ha^{-1}), and species at any trophic level are generally larger in the NWHI than are their MHI counterparts. Perhaps the most remarkable difference among the NWHI and MHI however, resides at the level of the abundance of top predators in both ecosystems. In the NWHI, apex predators such as jacks, sharks, and snappers comprise 54% of the fish biomass, while at a mere 3%, they are virtually absent from the MHI ecosystem. The healthy condition of the NWHI, which is reflected through its unique trophic structure, makes it an ideal environment to conduct research on food web dynamics in a complex subtropical marine ecosystem.

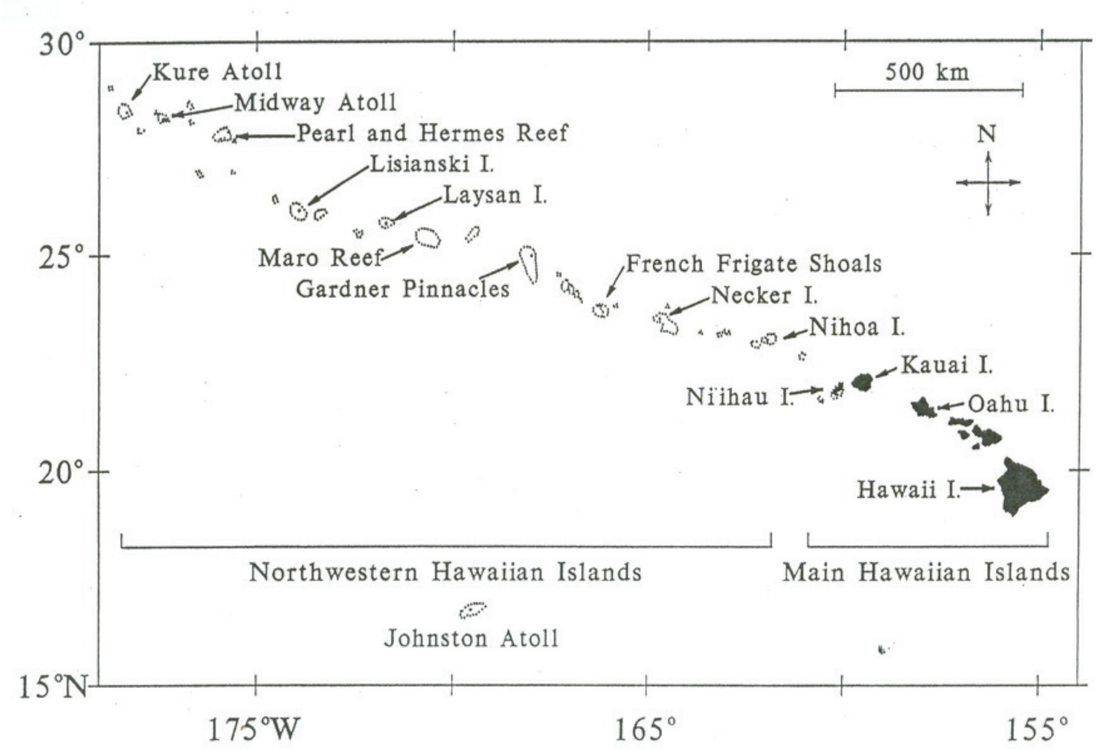

Figure 1.1 Map of the Hawaiian archipelago (from Johanos & Baker 2004).

1.3 THESIS OVERVIEW

The overall aim of this thesis, which includes 5 chapters, is to use FA signature analysis to define more explicitly the trophic and ecological relationships among forage species of fishes and invertebrates of the Hawaiian archipelago through the distinctions and overlaps in their FA composition. I begin in Chapter 2 by contrasting habitat complexity and species composition in temperate versus tropical reef ecosystems, and by discussing some of the major ecological mechanisms which have been brought forward to explain community structure of tropical coral reefs with an emphasis on predatory and competitive interactions and their effect as drivers of biodiversity. I also discuss several problems/biases associated with a number of methods commonly used in ecological studies conducted on coral reef ecosystems, and how the development of novel methods, such as FA signature analysis, have the potential to address these issues.

In Chapter 3, I explore ways to collapse the vast number of forage species to be analyzed into ecologically meaningful groups to allow for the greatest number of species to be included in the FA analyses. I subsequently investigate to what degree these groups can be differentiated on the basis of their FA signature using a subset of dietary derived FAs.

In Chapter 4 I evaluate the same species groups across various FA subsets in a different mathematical model using quantitative fatty acid signature (QFASA) simulations to determine numbers and combinations of species groups and FAs that best differentiate these subtropical forage species. While QFASA simulations have been used in previous studies specifically in the context of modeling predator diets, I use them here as a tool to further investigate FA overlaps and distinctions among species groups in the context of understanding ecological and trophic relationships. Assessment of these simulation procedures forms the basis for fully addressing trophic relationships among *individual* species using a different format of QFASA simulations (Chapter 5).

Finally, after careful consideration of the degree of distinction among the FA composition of groups of closely related and ecologically equivalent species (Chapter 3), the performance of species groups in QFASA simulations, as well as the number/combination of FAs yielding the most accurate estimates (Chapter 4), and an overall understanding of which species groups need to be better defined by further increasing the resolution of FA analyses, I evaluate in Chapter 5 the extent to which individual species of carnivorous fishes across and within ecological depth zones can be differentiated on the basis of their FA composition. I perform two main sets of analyses in this chapter: first to investigate whether ecologically equivalent species feeding on similar resources at depth versus in the shallows possess similar FA signatures, and second to evaluate to what degree sand-associated species can be differentiated on the basis of their FA composition. These studies provide information not only about this subtropical reef ecosystem, but serve as a template for other studies linking FAs and the elucidation of trophic structure in a marine ecosystem.

1.4 PUBLICATIONS ARISING FROM THE THESIS

At this time, one publication has arisen from this thesis (Chapter 3).

Piché J, Iverson SJ, Parrish FA, Dollar R (2010) Characterization of forage fish and invertebrates in the Northwestern Hawaiian Islands using fatty acid signatures: species and ecological groups, MEPS 418: 1-15.

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CHAPTER 2 POPULATION DYNAMICS AND COMMUNITY STRUCTURE OF TROPICAL REEF ECOSYSTEMS

2.1 INTRODUCTION

Despite covering less than 1% of the Earth's surface, coral reefs contribute greatly to the tropical marine biodiversity of the world's oceans (Crossland et al. 1991, Sala & Knowlton 2006). They are the largest biologically constructed features known, and they support more species per unit area than any other marine ecosystem (Wood 1999). However, the regulatory processes structuring coral reef communities remain poorly understood, and thus the mechanisms underlying the establishment and maintenance of high diversity remain unclear (Bellwood et al. 2004).

Population regulation is one of the foundational concepts in ecology (Hixon et al. 2002). Ecologists have long debated whether population dynamics in tropical ecosystems are principally controlled by density-dependent or density-independent factors (e.g. Connell 1978). Here I discuss several key ecological mechanisms brought forward to explain community structure with a primary focus on the relative strengths of top-down versus bottom-up population control, and how they can help explain tropical reef community structure. To do this I will use several conceptual models to examine the evidence for the roles of competition and predation in shaping reef biodiversity. Invertebrate species are undeniably an important component of coral reef communities. However, the literature seldom provides detailed information on the ecological processes regulating coral reef invertebrate populations. Given that relationships among reef fish species have been studied more intensively, reef fish population dynamics will be the main focus of this synthesis.

I first contrast how tropical and temperate reefs are structurally different in terms of habitat complexity and species composition to introduce the theories on the maintenance of high diversity of tropical coral reef ecosystems and the influence of density-dependent versus density independent effects on community structure. I then review the evidence in support of the major hypotheses brought forward to explain the primary limiting agent in reef population regulation. I conclude with a discussion on the various problems associated with current approaches used in the study of competitive and predatory relationships on tropical reefs and potential ways to address these issues in future research.

2.2 CORAL REEFS

Marked differences exist in the biogeographical range, structure, and species composition of reefs developing in tropical versus temperate waters (Bellwood et al. 2004). The distribution of tropical coral reefs is restricted within 30°N and 30°S latitudes. Tropical reefs are self-supporting systems organised for maximum retention and recycling of resources as they subsist in nutrient deserts (Parrish 1989). Open tropical oceans are oligotrophic areas where warm waters are permanently stratified and subjected to little mixing. Animal-plant symbioses are favoured in nutrient depleted environments, as organisms have to evolve ways to optimize the use of limited resources (Hughes et al. 1992). The evolution of photosymbiosis allowed hermatypic (reef-building) corals to invade the previously unexploited warm tropical waters (Wood 1995). Up to 90% of the organic carbon produced photosynthetically by the zooxanthellae symbiont is directly transferred to the polyp host (Davies 1984). Combined with filter feeding exerted by the polyps, this dual capture of energy is sufficient to sustain life despite the low ambient nutrient levels. The algal symbionts are also responsible for the restricted range of hermatypic corals as they require light to carry out their photosynthetic activities, and are very sensitive to increased water temperatures which can cause coral bleaching (Falkowski et al. 1984). Therefore, hermatypic corals are usually restricted to the euphotic zone (< 50 m), where seawater temperatures seldom drop below 20°C during the winter (Edmunds 2008). Major tropical reef complexes do not develop in nutrient rich waters, or waters subjected to seasonal patterns of nutrient availability, even if the temperatures are sufficiently high (Wood 1999). High nutrient concentrations reduce water clarity and consequently the amount of light reaching the coral. High sedimentation rates can also suffocate the coral polyp. In addition, hermatypic corals can be outcompeted by fast-growing macroalgae under a nutrient rich regime (Hughes 1994). Tropical coral reefs are highly complex ecosystems which can be divided into a wide array of zones, habitat types and ecological subsystems (e.g. Parrish & Boland 2004). The increased spatial heterogeneity brought about by the coral matrix also provides a wide array of microhabitats and refuges from predation (Ebeling & Hixon 1991).

Temperate reefs occur poleward of the 20°C isotherm for the coldest months of the year, as this isotherm delimit the boundary between tropical and temperate seas (Ebeling & Hixon 1991). Water temperature in these systems may vary annually and, in regions subjected to strong upwelling, temperature changes can occur within a few hours (Ebeling & Hixon 1991). Temperate reefs are subjected to seasonal pulses of high nutrient influx; resident species therefore have adapted to periods of food shortage, while maximizing growth rates and reproduction during periods of nutrient influx. Under these variable environmental conditions, fast-growing opportunistic species with rapid population turn-over are favoured (Wood 1993, Garrison & Link 2000). Moreover, temperate reef systems are structurally different from tropical reefs. They consist of various kinds of rock substrates and are commonly subdivided in three principal habitat types: shallow mixed algae zones, rocky substrata dominated by crustose coralline algae, and kelp forests dominated by laminarian species (Babcock et al. 1999). Kelp canopies have an important impact on the diversity and local distribution of species as they provide refuge from predation and wave action while trapping planktonic prey (Perez-Matus et al. 2007).

High structural complexity has been shown to be correlated with increased species diversity (Huston 1979, Eriksson et al. 2006) and tropical reef systems are indeed remarkably more structurally complex and diverse than their temperate counterparts. A classic theoretical model often used to depict the establishment and maintenance of high diversity in the tropics stipulates that species co-exist in equilibrium communities as explained by the predation/competition equations of Lotka-Volterra (Sale 1977). The conditions leading to this equilibrium state would involve competitive interactions leading to specialization and resource partitioning. This model however does not take into consideration density-independent disturbances or habitat patchiness, which are both commonly encountered on coral reef ecosystems (Connell 1978). Consequently whether coral reefs can be considered to be equilibrium communities is still unclear (Sale 1977, Connell 1978).

Many reef ecosystems tend to undergo a transition to an alternate state rather than regenerating following a disturbance (Bellwood et al. 2004). One of the most familiar and well documented examples of phase shift in tropical reef systems is the situation encountered on many Caribbean reefs where the combined effect of natural and human induced disturbances have led to a shift of dominance from coral to fleshy macroalgae (Knowlton 1992, Hughes 1994, Scheffer et al. 2001, Bellwood et al. 2004). First, increased nutrient loading from land runoffs, paired with intensive fishing, promoted algal growth and a shift from fish-dominated to echinoid-dominated herbivory (Bellwood et al. 2004). Second, a disease outbreak decimated the sea urchin (*Diadema antillarum*) populations, and corals were rapidly overgrown by macroalgae. This closely interlinked sequence of ecological events has led to the collapse of many Caribbean reefs.

Since most of the classic theoretical models explaining high diversity were constructed from field experiments on trees (e.g. Hubbell 1979), birds (e.g. Lack 1942, MacArthur 1958) and insects (e.g. Murdoch et al. 1972, Lawton & Strong 1981), some authors have in the past questioned the adequacy of their application to define diversity in marine environments (Pianka 1966, Schoener 1974). The collapse of reef ecosystems could likely be predicted and perhaps prevented to a certain degree, provided that the precursor signs of degradation through the alteration of community structure could be recognized. While the dynamics of competitive and predatory relationships among reef species continue to be actively studied, the mechanisms responsible for the maintenance of high diversity on tropical coral reefs remains unexplained.

2.3 DENSITY DEPENDENCE AND POPULATION REGULATION

Density-dependent (competition, predation, recruitment) and density- independent (abiotic disturbances) processes act on the structure of local populations at various spatial and temporal scales. In the context of coral reefs, density-dependent effects might be more easily detectable at smaller scales (e.g. local reefs) while large-scale observations (e.g. regional cluster of reefs) can provide important insight on global patterns of population changes (Caley 1993). Local population dynamics are directly dependent on four interconnected demographic rates: birth, death, immigration and emigration (reviewed in Hixon 1998). In the context of coral reef population studies, 'birth' relates to the time of settlement of the pelagic larvae on the reef. Death can occur as a result of density-dependent factors such as predation and starvation (competition), and from density-independent disturbances. Given that coral reefs are considered to be open populations interconnected demographically by larval dispersal (Booth & Beretta 1994), immigration and emigration are believed to have a direct impact on the composition of local species assemblages (Swearer et al. 1999) and on the persistence of co-existing species through larval replenishment (Forrester 1995, Jones et al. 1999).

Density-dependent effects resulting from predation can occur in several ways. First, an increase in prey populations can instigate an increase in predator populations. Second, a shift can occur in the local distribution of predators toward areas where higher densities of prey can be found. Evidence for shifts in transient predator populations as a function of prey abundance has been documented for reef fishes (Stewart & Jones 2001). Third, predators can change their foraging patterns as a function of prey densities; if the favoured prey population becomes so scarce that the energy cost of foraging is higher than the gain, predators will target more abundant prey (Beukers-Stewart & Jones 2004). Density-dependent effects can also lead to compensatory mortality in co-existing species with similar requirements. Compensatory mortality occurs when the most abundant competitor is subjected to higher mortality rates relative to the other species, and its population size is reduced allowing for competitively inferior species to flourish (Huston 1979). In his seminal work on food webs and species diversity of rocky shore communities, Paine (1966) demonstrated that upon predator removal, the successive replacement of species led to an assemblage ultimately dominated by one or two species. Diversity would then be directly related to the capacity of a predator to prevent resource monopolization by a single species (Paine 1966). Feeding on the most successful competitor therefore exerts a regulatory effect on prey populations consequently promoting local diversity through the suppression of dominant species (e.g. Connell 1961). However, there seems to be little evidence that compensatory mortality occurs in reef fishes (reviewed in Hixon 1998). Resource monopolization in coral reef ecosystems could alternatively be prevented by density-independent factors such as environmental disturbances (e.g. Woodley et al. 1981). Density-independent factors act on several levels. They can directly cause mortality or a shift in population structure as local species have different tolerance to disturbances (Woodley et al. 1981). In addition, changes in environmental conditions can favour new species as being the superior competitor (Connell et al. 1997).

2.4 COMMUNITY STRUCTURE

There are currently three main hypotheses with respect to the major processes structuring communities of coral reef fishes: 1) The Competition Hypothesis: resources are limiting in coral reefs so competition is the primary limiting agent which controls local diversity and abundance, 2) The Recruitment Limitation Hypothesis: pre-settlement mortality (eggs and larvae) prevents adult populations to reach levels at which resources would become limiting and competitive interactions would occur and 3) The Predation Hypothesis: post-settlement mortality determines adult patterns of abundance (Hixon 1991). An extensive body of work has been and continues to be dedicated to understanding the effect of biotic and abiotic factors on recruitment rates and the dynamics of larval dispersal of reef fishes (Caley et al. 1996, Syms & Jones 2000). Here, I only briefly discuss the premises associated with the Recruitment Limitation Hypothesis; evidence in support of this hypothesis are reviewed in depth elsewhere (e.g. Hixon et al. 2002). For the sake of brevity, I will focus on the competition and the predation hypotheses; these theories are more directly related to the goals of my thesis work of defining trophic and ecological relationships to better understand the complex network of interactions structuring a coral reef ecosystem. The two aforesaid hypotheses will therefore be discussed and contrasted in the context of coral reef ecosystems in the following sections.

2.4.1 THE COMPETITION HYPOTHESIS

Understanding what constitutes the requirements for the co-existence of ecologically similar species has been a central theme in ecological sciences. How similar competing species can be, and how they can co-exist in an enduring community have been the motivation behind early studies aimed at elucidating what determines the stability and structure of multi-species communities (Hutchinson 1959, May & MacArthur 1972). The **Competition** or **Niche Diversification Hypothesis** was first proposed to explain the mechanisms responsible for the co-existence of closely related or ecologically similar species (MacArthur 1958, Pianka 1974). Based on the premise that resources are limiting, this hypothesis stipulates that each species is a superior competitor for a specific resource or range of resources. Modifications in the morphology/behaviour of weaker competitors would therefore result in high levels of specialisation and allow for large numbers of species to co-exist. Density independent factors such as environmental fluctuation also play an important role in determining which species has the competitive advantage (e.g. Kettlewell 1955). Competition among species with largely overlapping requirements would ultimately lead to either character displacement or competitive exclusion (e.g. Connell 1961). As its main premise, the competitive exclusion principle prohibits the co-existence of species with identical requirements (May & MacArthur 1972). Character displacement is more commonly defined as "the measurable phenotypic difference existing between two species which has arisen as a result of the selective pressures on one or both species to avoid competition with the other" (Townsend et al. 2000). This implies that character displacement is genetically based as individuals exhibiting behavioral, morphological, or ecological modifications become favored over evolutionary time by natural selection (Nursall 1974). Character displacement and niche diversification resulting from interspecific competition has been demonstrated in many animal taxa including birds (MacArthur 1958, Schluter et al. 1985), mammals (Dayan & Simberloff 1998), and fishes (Robinson & Wilson 1994, Swanson et al. 2003). If tropical reef populations are primarily limited by resource availability, is there any evidence that the patterns of resource utilization results from competitive interactions among co-existing species?

Resource partitioning studies have the common goal of defining the limits that interspecific competition places on the number of species that can coexist (Schoener 1974). Despite a few exceptions (e.g. territoriality), the absence of obvious competitive interactions among reef species has led many to assume that factors other than resource limitation are responsible for population regulation on tropical reefs. Past studies abound in this sense by providing evidence that reef fishes tend to be generalist feeders exhibiting broadly overlapping diets (Sale 1977, Sale & Williams 1982). Conversely, a few well-known members of reef fish communities may render the niche diversification hypothesis particularly conceivable. The beak of parrotfishes seemingly implies that they have evolved this specialized morphological structure to feed exclusively by scraping algae off corals, a resource not commonly used by other species. Similarly, the evolution of a high tolerance to toxins in clownfishes has allowed them to dwell within anemones, a habitat space inaccessible to other species. Recent investigations of this hypothesized link between specialized morphology and specialized diet/habitat have revealed that morphological adaptations encountered in coral reef species do not necessarily imply strict specialization in resource use (Bellwood et al. 2006). For example, a study investigating the trophic diversity of nine sympatric cardinalfish species (Family Apogonidae) from the Great Barrier Reef (GBR) revealed that morphology was of limited utility in predicting dietary groupings (Barnett et al. 2006). Species were originally classified in three groupings based on the morphology of the feeding apparatus. However, it was established from stomach content analyses that while two species had predominantly piscivorous diets, the seven other species of cardinalfish were hardly distinguishable and displayed overlapping generalist diets. An important point raised by Barnett et al. (2006) is that while morphology is strongly linked to the feeding mode, it does not inevitably restrict resource use. Therefore, a specialized morphology alone is insufficient to infer specialization in resource partitioning.

Niche shift resulting from competitive interactions have been demonstrated in coral reef fishes. By contrasting their study with other published results, Anderson et al. (1981) hypothesized that changes in chaetodontid-pomacentrid community structure across Pacific reef complexes (GBR, Fiji, Society Islands, Hawaii) are responsible for a gradient in chaetodontid diversity and an associated dietary niche shift. On the GBR, pomacentrids are dominant planktivores whereas sympatric chaetodontid species belong to one of four trophic categories: hard coral eater, soft coral eater, non-coralline benthic invertebrate eaters, or generalist feeder which combines the three aforementioned categories. However, while the total number of chaetodontid species declines from GBR to Hawaii, the proportion of planktivorous chaetodontids *increases*. The authors correlate this trend with a drastic *decrease* in the number of planktivorous pomacentrid species, from 47 species on GBR to 9 in Hawaii. With a reduction in the competitive interactions associated with planktivory, chaetodontids which are normally the weaker competitor are re-established as dominant planktivores.

Territoriality. Competitive interactions resulting from territoriality have important implications on community structure and the spatial patterns of distribution of species (Fretwell & Lucas 1970, Smith & Parker 1976, Choat 1991). This is especially true in the case of tropical coral reefs, where the defended territories of herbivorous fish can often account for more than 70% of the reef substratum (Choat 1991). Tropical herbivores thus have a great influence on the distribution of the sessile biota on which they feed (Choat & Bellwood 1985). The territorial behavior of damselfishes (Family Pomacentridae) and surgeonfishes (Family Acanthuridae) is particularly well documented (e.g. Nursall 1974, Sale 1975, Choat 1991). Territoriality has an impact on both the relationships among heterospecific individuals, and among conspecifics. Interspecific hierarchy has been reported in multi-species communities of territorial pomacentrids; while pomacentrids defending territories exhibit the same behavior toward intra or inter-specific transgressors, the level of aggressiveness of the response varies among species (Nursall 1974). Such responses might include darting toward the invader, nipping, and exposing various brightly colored morphological parts such as the belly or underside of fins as a warning signal. The better competitor is also the most aggressive and has a higher success in interspecific confrontations. Within single species groups, variation in territorial behavior can be influenced by the spatial position of the defended territory of an individual within the group. Individuals positioned at the center of the group are larger than those on the edge, and exhibit higher fitness since less energy is devoted to interspecific competition, and more is diverted toward growth and reproduction (Meadows 2001). Hence not only does territoriality play an important role in the local distribution of species, but it can also have a direct impact on the fitness of individuals.

Fish Guilds. Mixed-species aggregations have been described in birds and mammals (reviewed in Morse 1977), and in fishes (e.g. Aronson & Sanderson 1987). Group foraging has a great impact on the fitness of the individuals (Viscido et al. 2004). In reef fishes, it can play a determinant role in foraging success given that a group is more likely to succeed in invading defended territories to access resources (Robertson et al. 1976). Foraging in a single or multi-species aggregation also reduces the risk of predation as an individual is less likely to be specifically targeted by a predator when it aggregates with others (Morse 1977). The term ‘guild’ was formulated to describe a group of species using the same class of resource (e.g. food, habitat or space) in similar ways (Root 1967). The most commonly observed feeding guilds on a reef are composed of herbivorous species, although carnivorous foraging aggregations do exist but are poorly documented (Aronson & Sanderson 1987). The three main components of feeding niche separation are usually prey type, prey size, and foraging habitat (Schoener 1974, Gladfelter & Johnson 1983). Based on the premise that two species with identical niches cannot co-exist (competitive exclusion principle), one could assume that resource utilisation among reef fish foraging in a mixed species guild should be partitioned along those axes. Interestingly, previous work on tropical reef surgeonfish (Family Acanthuridae) provided evidence of high degrees of dietary and habitat overlap among species within guilds which is not consistent with competition and resource partitioning as being the main factors allowing for co-existence of multiple species (Robertson & Gaines 1986). Contrastingly, a study on tropical squirrelfish (F. Holocentridae) by Gladfelter & Johnson (1983) has revealed little overlap in food and foraging microhabitat (position within a reef zone) among species within foraging guilds. It is also noteworthy to mention that there is a diverse range of described multi-species fish foraging associations. The two main categories are shoaling associations and attendant associations, the latter being further subdivided into 4 types: following and scavenging, interspecific joint hunting, hunting by riding, and aggressive mimicry (Lukoschek & McCormick 2000). In most experiments on resource partitioning among guild members, the authors do not discuss the potential implications of different foraging guild types (e.g. perhaps the level of dietary/habitat overlap differs in facultative versus obligate associations), and the results are often generalized toward corroborating or falsifying the niche diversification hypothesis.

Caution should be made in considering the ecological factors linked with each type of foraging guild before drawing simplified conclusions which might not be applicable to all foraging aggregations.

Another point to note with respect to resource partitioning studies in which published results are contrasted, is the variety of different techniques used to determine the degree of overlap in food utilization among members of a guild: in situ observations of foraging behaviour (e.g. Pratchett 2005), stomach content (e.g. Zekeria et al. 2002), and calculation of niche breath using various similarity indices (e.g. Gladfelter & Johnson 1983, Longenecker 2007). One must wonder to what extent the results of these studies are directly comparable, and to what extent generalities can be drawn from such a wide range of results.

Inherent to the elucidation of the mechanisms underlying co-existence of species with similar requirements, is the question of how much niche overlap is too much overlap. In other words, when does competition lead to competitive exclusion? The competitive exclusion principle is based on the premise that two sympatric noninterbreeding species occupying the same ecological niche cannot coexist on limiting resources, and one species will outcompete the other over time (Hardin 1960). The theory of limiting similary is an outgrowth from the competitive exclusion principle and stipulates that there must be a quantifiable limit to how similar two species can be with regards to resource utilization before one competitively excludes the other (Hutchinson 1959, Abrams 1983). There is evidence that competitive exclusion is occurring in reef species. In a study aimed at evaluating the effect of fishing on the diversity, abundance, and pattern of fish assemblages, McClanahan (1994) compared the community structure of a reef protected from fishing to an unprotected reef and a transition reef subjected to intermediate levels of management. The authors suggest that the poor recovery of the parrotfish population on the transition reef can be interpreted as evidence of competitive exclusion of parrotfish by sea urchins who are superior competitors for the same resources.

2.4.2 THE RECRUITMENT LIMITATION HYPOTHESIS

Most coral reef fishes and invertebrates are broadcast-spawning species which possess a dispersive larval stage prior settlement on the reef substratum (Robertson 1991). Although adults are largely reef-associated species, widespread larval dispersal increases the chance of settlement upon free suitable space despite the high risk of mortality associated with this reproductive strategy (Doherty & Fowler 1994). **The Recruitment Limitation Hypothesis** stipulates that high pre-settlement mortality results in low larval supply which prevents local populations to reach densities at which resource would become limiting (Jones 1991). When this hypothesis was first formulated, it was deemed revolutionary given that the general belief at the time was that reef populations where regulated by post-settlement processes (reviewed in Hixon 1998). However, the importance of properly defining recruitment became evident in the following decades when discrepancies in the sampling methodologies started to emerge; to avoid confusing the effect of pre and post-settlement mortality on population structure, recruitment censuses should be conducted as close as possible to the time planktonic larvae settle on the reef substratum (Hixon 1998). Another problem encountered in studying the effect of recruitment on a local population is the confounding effect of migration of individuals away from the site of recruitment with that of mortality. This is the reason why permanently reef-associated (sedentary) species like damselfishes have been particularly well studied (Doherty 1991).

A central issue associated with the recruitment hypothesis is whether recruitment is independent of resident adult populations or to what extent the larval pool is representative of local populations (Jones 1991). If coral reefs are open ecosystems connected by larval dispersal, does it imply that a) the greater the distance between two sites, the less chances of exchange of larvae through dispersal, or b) that dispersive larvae assemble in a common homogeneous pool in which species would have equal chances of colonizing newly freed space, and thus local resident fish species assemblage would represent a random sample from that pool (e.g. space lottery of Peter Sale, 1977)? Given that coral reef systems exhibit high levels of within- and among-reef patchiness, it has been suggested that habitat heterogeneity among local coral reef patches might result in a differential rate of settlement depending on substrate quality (Anderson et al. 1981, Choat & Bellwood 1991). Based on these premises, the local distribution of species would be attributable to selective settlement of new recruits, and not necessarily to the abundance or distribution of resident species. Because of substrate preference and difference in habitat structure on various scales, the local distribution of species thus could not be expected to be random (Anderson et al. 1981).

2.4.3 THE PREDATION HYPOTHESIS

Predation and herbivory determine many aspects of modern coral reef community structure. Piscivorous predators are keystone species and major shifts in trophic structure and species assemblages have been reported in systems where apex predator populations are declining (Friedlander & DeMartini 2002). Upon the decline of herbivore populations, coral reefs can rapidly become dominated by macroalgae which limits the light available for the coral polyps and can ultimately lead to the death of the reef because macroalgae cropping by grazing herbivores allows coral recruits to settle in spaces that would otherwise be occupied by their fast growing algal competitors (Wood 1993, Hughes et al. 1999).

The Predation Hypothesis stipulates that if predation pressure is the primary limiting factor on population growth on coral reefs, prey population densities/abundance would be maintained below the levels at which competitive interactions and resource partitioning would occur (Hixon 1991). The role of predation in structuring reef communities should be reflected through a) morphological and/or behavioural adaptations minimizing the risk of predation and b) predictable shifts over time or space in prey species abundance and distribution with fluctuations in predator densities or prey refuge (Hixon 1991). The theoretical models depicting predator prey relationships often imply that the mortality rate in prey species is a direct function of the local abundance/density of the predator (Hixon 1991). These models thus undermine the effect of predation as a selective force, and the role played by antipredatory mechanisms in prey survival (Abrams 1993). When antipredatory mechanisms are considered in prey death rate estimations, increased predator densities do not necessarily result in increased prey mortality (Abrams 1993). Examples of morphological and chemical antipredatory mechanisms in reef fishes include: structure of the body (e.g. spine, tough skin), coloration patterns (e.g. camouflage, mimicry), and the production of toxins (e.g. tetraodontiformes; Hixon 1991). Behavioral antipredatory mechanisms are also common and include schooling and modifications in daily activity patterns to avoid peak predator foraging time. Dusk and dawn are transitory periods during which diurnal and nocturnal prey species are particularly vulnerable given that their specialized visual systems become ineffective for detecting predators; diurnal and nocturnal reef fishes therefore remain sheltered in the coral matrix at twilight to avoid predators (Hixon 1991).

2.5 COMPETITION, PREDATION, AND THE SPECIALIZATION DEBATE

Central to the literature addressing the processes structuring coral reef species assemblages is certainly the issue of whether these communities are primarily regulated a) through competitive interactions which allows populations to be maintained near an equilibrium state, or b) by the effect of predation and abiotic disturbances which renders the composition of reef species assemblages unpredictable and therefore not maintained in an equilibrium state. Moreover, this question tends to be posed in a way that seemingly implies that reef species have to either be generalists or specialists with regards to resource utilisation. One could argue that the specialization debate tends to exclude the fact that perhaps a combination of factors are regulating coral reef community structure, and that the network of interactions among reef species is possibly much more complex than originally thought. Moreover, there is a need for a methodology that can accommodate tracking the sum of all these interacting processes. It is unlikely that the effects of competition and predation are completely dissociable. There is evidence of specialization in some species but it would be reasonable to assume that others would be unspecialized opportunistic omnivores. Under low predation pressure, a species might feed on resources that would not be consumed in the presence of predators. In addition, some species foraging in aggregations would not have access to certain resources if it wasn’t for this association with other species within guilds.

It has recently been argued that the competition hypothesis, i.e. that food is the primary limiting agent to population growth of tropical reef species, was never falsified *per se* and therefore should merit more attention before alternate hypotheses such as the predation hypothesis are brought forward (Longenecker 2007). I find that this argument is poorly substantiated. One of the studies cited as evidence of food limitation (Jones 1986) demonstrates enhanced growth rate of a planktivorous pommacentrid (*Pomacentrus amboinensis*) with food supplementation. However, the potential effect of predation on the foraging behaviour of *P. amboinensis* is not discussed, thus the extent to which the reported enhanced growth rate implies that fish would eat more if there was more food when subjected to natural risk of predation is unclear. The utilization of stomach content analyses to draw inferences about resource partitioning among co-existing species is also a source of criticism amongst the proponents of the niche diversification hypothesis. Several researchers employing this method have reached the conclusion that reef fishes are generalists with regards to diet (e.g. Hiatt & Strasburg 1960, Hobson 1974), but these results are now being contested on the basis of the lack of taxonomic resolution of prey items recovered (Longenecker 2007). The analyses of stomach/gut contents often prevent identification of prey to the species level. As a result diet items are categorized into broad taxonomic groupings which would lead to potential feeding specialization being overlooked. However, the biases associated with stomach content analyses are widely recognized and one could assume that they are accounted for in the interpretation of the results by researchers employing this method.

Increasing the taxonomical resolution of prey items would undeniably provide a more accurate picture of diets, but the improvement of this method alone would not be sufficient to resolve the issue at stake. For one thing, utilizing gut content analysis alone to define diets of reef species over their entire life span would require a gigantic sampling effort. Combining stomach content analysis and *in situ* observations with other methods to investigate the effect of competition/resource partitioning and predation on coral reef community structure would seem a more advisable approach. However, there are also problems associated with current alternative methodologies. For example, visual censuses of small schooling species and cryptic species can be difficult to conduct (e.g. Talbot et al. 1978). The complexity of the coral matrix provides a wide array of shelter where some species hide diurnally and others nocturnally. To ensure that sampling truly reflects the population, censuses would have to involve around the clock observations and a very thorough examination of every hole and crevice, which is not feasible. Inherent to most investigations on the effect of predation on reef communities are artifacts associated with the use of exclusion cages which renders the results of these studies extremely hard to interpret as cage effect and predatory effect become impossible to distinguish (reviewed in Steele 1996). Thus, there is a definite need for a method or methods that can assess the level of integration from different food sources within a coral reef ecosystem.

Recently, methods have been developed which employ various biochemical tracers and DNA analyses to understand predator-prey relationships. Of these, fatty acid (FA) signature analysis may have the greatest potential for furthering our knowledge of the processes structuring coral reef communities. Because FAs are conserved through food webs, they have already been proven to be an efficient tool which can be employed to gain a detailed understanding of trophic interactions within an ecosystem (e.g. Budge et al. 2002, Iverson et al. 2002). The use of FAs is especially powerful in marine environments where their complexity allows for specific FAs to be followed through their integration in the tissue of consumers at different trophic levels (Dalsgaard et al. 2003, Dalsgaard & St John 2004). Numerous validation studies have been conducted which demonstrate the direct and quantitative effect of dietary FAs on the lipid stores of consumers, including mammals, seabirds, fishes, and invertebrates (reviewed in Dalsgaard et al. 2003, Budge et al. 2006, Iverson 2009). Although FA signature analysis has recently been advanced to quantitatively estimate diets of higher mammalian and avian predators (Iverson et al. 2004, 2007, Thiemann et al. 2008, Tucker et al. 2009) in both marine and terrestrial ecosystems, this technique has not yet been developed for fishes and invertebrates. Nevertheless, the characterization of FA signatures and their overlap among species of reef fishes and invertebrates can provide information about their habitat, feeding ecology, resource use, and behavior (Piché et al. 2010). It is expected that FA signatures, in combination with ecological information and results gathered using the methods previously discussed in this review, should allow a greater resolution in understanding the complex network of interactions underlying coral reef ecosystem structure.

CHAPTER 3 CHARACTERIZATION OF FORAGE FISHES AND INVERTEBRATES IN THE NORTHWESTERN HAWAIIAN ISLANDS USING FATTY ACID SIGNATURES: SPECIES AND ECOLOGICAL GROUPS

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3.1 INTRODUCTION

Marine ecosystems are complex, diverse, and understanding the trophic interactions and energy flow through them is a tremendous challenge (Steele 1996). Increasingly bottom-up and top-down impacts on predator and prey populations are evaluated to understand species distributions, population dynamics, and ecosystem structure and change. Traditional methods to study aspects of predator-prey relationships and marine food webs have relied on prey remains recovered from predator stomachs and feces. However, newer methods such as biochemical tracers and DNA analyses have emerged as a means to determine such relationships (Deagle et al. 2005). One of the most promising of these approaches is the use of fatty acids (FAs) to study food web structure and potentially to estimate the types and proportion of prey consumed by a predator (*reviewed in* Dalsgaard et al. 2003, Iverson et al. 2004, Budge et al. 2006, Iverson 2009). Given the diversity of FAs in marine ecosystems and their conservation through food chains, FAs can be used to gain a powerful understanding of trophic interactions within ecosystems (e.g. Budge et al. 2002, Iverson et al. 2002, Parrish et al. 2002, Dalsgaard et al. 2003, Dalsgaard & St John 2004, Stowasser et al. 2009).

Most recently, FA signature analysis has been advanced to quantitatively estimate diets of higher predators such as seabirds and mammals (quantitative FA signature analysis, QFASA; Iverson et al. 2004, 2006, Beck et al. 2007, Iverson et al. 2007, Nordstrom et al. 2008, Thiemann et al. 2008, Tucker et al. 2009). These diet estimations have been conducted in northern temperate to Arctic ecosystems (and/or captivity) using a small (3-9) to relatively moderate (≤ 28) number of prey types. However, in more highly complex food webs, multiple prey species thriving in the same habitat and feeding on similar resources may become more difficult to differentiate based on FA signature alone. Additionally, statistical problems arise when the number of potential prey increases and numerically exceeds the number of FAs used in the QFASA estimation procedures.

Coral reefs are the largest biological features on earth and support more species per unit area than any other marine ecosystem (Wood 1999). The Northwestern Hawaiian Islands (NWHI) ecosystem (25-30°N, 175°E-165°W) constitutes the most remote large-scale coral reef ecosystem in the world (Maragos & Gulko 2002), with its 10 atolls and islets extending 2,000 km northwest of the Main Hawaiian Islands (MHI). The subtropical communities of this region varies with the depth and habitat found on the upper slopes of the Hawaiian ridge. The peaks support coral reefs or banks of algal meadows. In contrast the flanks of the ridge experience less photosynthesis and grow little biotic substrate where the slopes extend into the abyss. Because of its vertical nature the trophic structure of the NWHI is extremely diverse and unique, with an overall fish biomass in the shallow reefs of 2.4 t ha^{-1}, comprised of 27% herbivores, 18% low-level carnivores, and dominated (54%) by apex predators (Friedlander & DeMartini 2002). The diversity and biomass of fish communities subsequently diminishes with depth to levels as low as 0.0035 t ha^{-1} in the subphotic (301-500m) zone (Parrish & Abernathy 2006). A key top predator in the NWHI ecosystem is the Hawaiian monk seal (*Monachus* *schauinslandi*), which is the only non-migratory phocid seal relying entirely on subtropical insular ecosystems for subsistence (Ragen & Lavigne 1999). Monk seal populations have experienced severe declines over the past several decades and are listed as critically endangered. Thus, understanding their foraging ecology and the prey species upon which they depend is a central issue in assessing management and recovery plans. However, estimating their diet using FA signatures is problematic as they inhabit an extremely diverse ecosystem comprising a multitude of potential prey species.

Thus, the NWHI represents an ideal platform to investigate the use of FAs as a tool to investigate trophic relationships in an extremely complex and subtropical ecosystem. To use FAs to understand trophic interactions both among forage species, and also eventually at the top of the food web in the NWHI, it is necessary to first characterize FA patterns and their variation in the prey assemblage. Given the great diversity of potential prey species in the NWHI, a critical step for eventual quantitative predator analysis must be to reduce the vast number of species into ecologically relevant groups. The objectives of this study were to 1) determine the FA composition of NWHI fish and invertebrate species that are potential prey of the Hawaiian monk seal, 2) explore meaningful ways to collapse a high number of representative prey species into relevant groups that are biologically and ecologically meaningful to allow the largest number of species to be incorporated in trophic analyses, and 3) determine to what degree these species/groups of species can be characterized on the basis of their FA signatures.

3.2 MATERIALS AND METHODS

3.2.1 SAMPLE COLLECTION

A collection program was established as part of a study of the diet of the Hawaiian monk seal at the NOAA Pacific Islands Fisheries Science Center. Fish and invertebrate species were sampled across the eastern end of the NWHI archipelago and the MHI, from 1997 through 2005. The bulk of specimens were collected from four main NWHI islands/reef areas: Necker Island, French Frigate Shoals (FFS), Gardner Pinnacles, & Maro Reef (see Appendix 3.1). Over 85% of the total samples originated from these four locations, and more than 50% of those were collected at FFS. Reasons for concentrating collection effort at FFS included that the atoll provided the only logistical support base with infrastructure on the eastern half of the NWHI, it was restricted from any commercial/recreational activities, and there was an extensive apparent abundance of potential monk seal prey items available. Moreover, FFS has the largest monk seal subpopulation but the worst cohort survival rate among the youngest age classes, making it an important location to study foraging habitat, food availability, and other potential ecological implications which may be affecting their survival rates (R. Dollar, pers. obs.). Early collections were focused on shallow reef species based upon evidence from analysis of scat and spews (Goodman-Lowe 1998, Goodman-Lowe et al. 1999), and later collections were focused on obtaining slope and subphotic species based on feeding behavior observed in animal-borne imaging studies (“Crittercam”)(Parrish et al. 2000a, Parrish et al. 2002). The broad range of habitats that the monk seal feeds across (reefs to subphotic depths) made for a very diverse collection of fish and invertebrate species sampled between depths of 10 - 500 m. Upon capture, all fish and invertebrate specimens were frozen in airtight plastic bags with detailed records of location and habitat prior to being shipped to Dalhousie for analysis. Specimens were stored at -20°C and processed within 6 months. A total of 2,190 specimens representing 100 species was analyzed for this study. An average sample size of 21 individuals per species was used to generate the fatty acid signature of each species with the exception of the spiny lobster, slipper lobster, and Panther flounder where 71, 72, and 75 specimens were used respectively.

3.2.2 FATTY ACID ANALYSIS

Individual fishes and invertebrates were thawed and measured; fork length or carapace width was measured to the nearest 0.1 cm, and body mass (i.e. wet weight, WW) was measured to the nearest 0.1 g. Each whole individual was then homogenized in a food processor. Stomach contents of individuals were not removed prior to homogenization given that we treated them as prey eaten whole by consumers. Lipids were quantitatively extracted from each individual specimen in duplicate aliquots using a modified Folch method (Folch et al. 1957, Iverson et al. 2001); fat content (WW) is expressed as the average of the two duplicates. FAs were converted to FA methyl esters by acidic transesterification and analyzed using temperature-programmed gas liquid chromatography according to Budge et al. (2002), and Iverson et al. (2002), on a Perkin Elmer Autosystem II Capillary FID gas chromatograph (GC) fitted with a 30 m x 0.25 mm i.d. column coated with 50% cyanopropyl polysiloxane (0.25 μm film thickness; J&W DB-23; Folsom, CA) and linked to a computerized integration system (Turbochrome 4.1 software, PE Nelson). Identification of FAs and isomers were determined from the following sources: known standard mixtures (Nu Check Prep., Elysian, MN), silver-nitrate (argentation) chromatography, and GC-mass spectrometry.

All sample chromatograms and FA identifications were individually examined for accuracy in identification and integration of peak areas, and corrected and reintegrated if necessary. FAs are named as A:Bn-X, where A is the number of carbon atoms, B is the number of double bonds in the carbon chain, and n-X represents the position of the first double bond relative to the methyl terminal end. FAs are expressed as mean wet mass percent of total FAs ± SEM.

3.2.3 ECOLOGICAL ASSESSMENTS AND SPECIES GROUPING PROCEDURES

Due to the large number of species analyzed, the fact that some species were of key commercial or ecological importance, and the constraints of sample collection that led to small sample sizes for some species (e.g. n = 4 for *Octopus ornatus*), I explored meaningful ways to create groups of species. Although grouping species on the basis of taxonomical proximity alone might seem intuitive, closely related species (e.g. belonging to the same family, genus) can have very different diets and ecology, which will greatly influence their FA composition. For example, if I was to simply group all snapper species by that taxon (i.e., as "snappers"), I would be grouping both shallow reef feeders with deep subphotic feeders, creating a different FA signature than found in any individual species. Therefore, a thorough analysis of the ecology of each species was performed, and a synthesis of the following factors was used to assign species to groups: taxonomy, diet, ecological subsystem (reef, bank, slope, or subphotic), habitat (live reef, isolated rock, sand, or carbonate substrate) and commercial interest. The diet of each species was estimated through a comparative study of published data (Hobson 1974, Parrish et al. 1986, Parrish 1989, Moffitt & Parrish 1992, Seki & Somerton 1994, Randall 1996, Hoover 1998, Humphreys 2000, Parrish & Boland 2004, Parry 2006, Froese & Pauly

2009, Palomares & Pauly 2010). Crustaceans were classified as benthic carnivores that feed on the mix of bottom productivity and detritus. For fish, diet categories were assigned to each species following the model of trophic community composition suggested by J.D. Parrish (1989): benthic herbivore (browser, grazer), planktivore (algal planktivore, zooplanktivore), benthic carnivore (corallivore, invertebrate feeder), piscivore, or detritivore/omnivore. Cephalopods were divided into an octopus group that feed on benthic crustaceans and squid that feed on fish.

After an in depth analysis of all data gathered, the 100 species investigated were assigned to 47 groups composed of closely related *and* ecologically similar species. The number of species incorporated within a group ranged from 1 to 8 species. Some key species of particular economic (fisheries) or ecological importance were treated individually and thus were not grouped with others (Polovina & Mitchum 1992, Coffman & Kim 2009, Kittinger et al. 2010). Species of commercial interest included the three species of snappers (*Etelis carbunculus*, *Pristipomoides filamentosus*, *P. zonatus*) and the spiny lobsters (*Panulirus marginatus*), which were all analyzed separately. In some instances, species which were the only representatives of their family and/or possessed distinctive ecology were not grouped with others.

3.2.4 STATISTICAL ANALYSES

FA data were analyzed using hierarchical cluster analysis, multivariate analysis of variance (MANOVA), and discriminant function analysis (DFA) using the stepwise method to assess which FAs accounted for most of the variance in group separation on the first two discriminant functions. I used the 15 dietary FAs (n-1 of the smallest species group sample size) that were either the most abundant and/or exhibited the greatest variance across all species, accounting for approximately 86 mass% of total FAs identified. These FAs included 14:0, 16:0, 16:1n-7, 18:0, 18:1n-9, 18:1n-7, 18:2n-6, 20:1n-9, 20:4n-6, 20:5n-3, 22:1n-11, 22:4n-6, 22:5n-6, 22:5n-3, and 22:6n-3. Hierarchical cluster analysis was used to evaluate the degree of similarity in FA signatures by sequentially merging the 47 groups into clusters, from the most to the least similar, with each cluster being nested within the next. The distance among clusters was computed by an agglomerative method using average linkage between groups and Euclidean distance measures. While this method did not require a reduction in the number of FAs to be used (total 74 FAs), the cluster analysis was conducted using the same 15 dietary FAs that were used in all MANOVAs and DFAs to render all results directly comparable. Percentage values for FAs were transformed into log ratios prior to DFA (*see* Budge et al. 2002 and Iverson et al. 2002): the values for the 15 FAs were first re-normalized over 100%, then each re-normalized value was divided by the value for 18:0, a reference FA. The rationale for selecting 18:0 as the reference FA is that this FA is ubiquitous in the ecosystem of study, it is found in all samples, and exhibits variability. Given that the log of zero cannot be taken, a value of 0.005% was added to any zero values, the 15 ratios were log transformed, and the resulting log ratios were used in DFA. All data analyses were performed using SPSS version 11.5 (SPSS Inc., Chicago IL) and R version 2.6.2. Wilk's Lambda was used to assess the power of the discrimination among species/groups; the smaller the value, the more significant the difference. The percent of group cases correctly classified into their assigned groups were used to evaluate the performance of the classification function, and the classifications were cross-validated using leave-one-out cross validation procedure. The predicted group membership of each species/group of species was examined for any consistent misclassification. The statistical approach used could thus be summarized as follows: hierarchical cluster analysis on 47 groups using 15 FAs → DFA among 47 groups using 15 FAs → individual DFA within four major functional groups using 15 FAs.

3.3 RESULTS

The fat content and FA composition (FAs used in analyses) of the 100 species analyzed (n = 2,190 individuals) are presented in Appendix 3.2. The ecological habitat and diet guild of each of these species was summarized (Appendix 3.3) and based upon these evaluations, species were grouped into 47 groups, composed of closely related and ecologically similar species (Appendix 3.3; Table 3.1), for subsequent analyses.

3.3.1 HIERARCHICAL CLUSTER ANALYSIS

For the 47 groups the 15 FAs generally separated species according to the variables of diet and ecological subsystems (i.e. depth; Fig. 3.1). The first node isolated one of the subphotic fish, the armorhead, from all the other groups. The second node grouped together four of the five groups of herbivore. The third node separated the cephalopods from all remaining groups. The fourth node separated the deep-water groups (subphotic and slope) from the other groups. The fifth node clustered together the crustaceans, except the shrimps which were affiliated with the deep-water species. The sixth node grouped the carnivores (which encompassed the benthic carnivores, piscivores, planktivores, and omnivores).

3.3.2 DISCRIMINANT ANALYSIS AMONG SPECIES GROUPS

DFA performed on the 47 species groups revealed separation primarily among herbivores, planktivores, carnivores, crustaceans and cephalopods (Fig. 3.2). Fourteen significant discriminant functions were generated (Wilk's Lambda 0.518, $p < 0.001$) and groups were separated with 75.8% of cross-validated group cases; 1,659 of 2,190 individuals were correctly classified to their group. The FA which accounted for most of the variance in the separation of the 47 groups was 18:1n-9 (higher in deep-water species), followed by 16:0 (higher in herbivores and planktivores). A plot of the group centroids on the first two discriminant functions revealed that individuals with similar FA composition associated into three distinct clusters; all benthic herbivores ($n = 310$) were situated in the upper left quadrant, crustaceans ($n = 352$) were mainly distributed in the upper right quadrant, and all carnivorous fishes which included benthic carnivores, omnivores/detritivores, and piscivores ($n = 1281$) were predominantly scattered in the lower left and right quadrants (Fig. 3.2). The two groups of cephalopods ($n = 55$) were both positioned in the upper right quadrant but were spatially distinct from one another. Most planktivores ($n = 172$) were located at the interface of the herbivore and carnivore cluster, with the exception of the planktivorous armorhead *Pseudopentaceros wheeleri* ($n = 20$); armorheads were tightly clustered in the lower right quadrant, and this group was spatially isolated from all others on the first two discriminant functions. Figure 3.2 also revealed separation among groups as a function of habitat/ecological subsystem. The majority of the deep-water species were located in the lower right quadrant: armorhead (3; *P. wheeleri*), beardfish (4; *Polymixia berndti*), cutthroat/snake eel (10; *Meadia abyssalis* & *Ophichthus kunaloa*), squirrelfish snapper (25; *Etelis carbunculus*), flower snapper (28; *Pristipomoides zonatus*), shrimp (40; *Heterocarpus ensifer* & *H. laevigatus*), and duckbill (47; *Bembrops filifera*), suggesting that species living at depth have distinct and somewhat characteristic FA signatures.

The proportion of individuals correctly classified was high in the majority of the 47 groups analyzed (Table 3.2); the angelfish (1), armorhead (3), scorpionfish (24) and shrimp (40) groups had 100% of cross-validated grouped cases correctly classified and more than half of the groups (27/47) exhibited a classification success > 80% (1, 2, 3, 6, 9, 10, 13, 14, 17, 18, 19, 20, 21, 23, 24, 25, 28, 31, 32, 35, 36, 38, 39, 40, 42, 46, 47). However, five groups were classified poorly, with < 60% individuals correctly classified: the chromis/dascyllus (12), the box crab (41), the conger eel (7), the knife/razorfish (34), and the *Parupeneus* goatfish (16) groups (see Table 3.2 for details). However, most misclassifications occurred among groups with similar diet and/or ecology. Classification success was high in the two cephalopod groups. The few misclassified octopuses were classified as squids and vice versa. Interestingly, cephalopods did not cluster together in this DFA analysis, which suggest substantial differences in their FA composition despite their taxonomical relatedness.

3.3.3 FAT CONTENT AND FATTY ACID COMPOSITION AMONG FUNCTIONAL GROUPS

The average FA composition (mean ± SD) for each individual functional group (i.e. herbivores, planktivores, carnivores, crustaceans and cephalopods) and for each of the 47 species groups is presented in Appendix 3.4. Average fat content varied significantly across functional groups (ANOVA, F=838.65, Tukey HSD post hoc test, $p < 0.001$). Fat contents among herbivores and planktivores were comparable at 3.7% and 3%

fat, respectively. Crustaceans had the lowest percentage of fat (1.2%), while cephalopods and carnivores were similar at 1.4% and 2% fat, respectively. The armorhead exhibited drastically higher fat contents at 27% fat.

The 15 FAs used in the analyses were significantly different across the six functional groups at 0.05 significance level (Wilk’s Lambda 0.032, Tukey HSD post hoc test, $p < 0.001$). I will focus on the 5 most abundant FAs which accounted for approximately 60% of total FA in NWHI species: 16:0, 18:1n-9, 20:4n-6, 20:5n-3, and 22:6n-3. On average, herbivores had the highest proportion of 16:0 at 30%, while 16:0 levels in other functional groups ranged from 26% in planktivores to 14% in crustaceans (Appendix 3.4). Armorhead contained a markedly higher level of 18:1n-9 at 26.5%, while cephalopods contained the lowest (4%). Levels of 20:4n-6 were noticeably lower in armorheads at 0.6%, and were the highest on average in crustaceans (11%). Cephalopods and crustaceans contained the highest proportion of 20:5n-3 at 10% and 9% respectively, in comparison with herbivores (7%), carnivores and planktivores (5%) and armorhead (4.5%). Cephalopods also exhibited the highest proportion of 22:6n-3 at 26.5%, followed by carnivores (18%), planktivores (14%), armorheads (13%), crustaceans (11%), and herbivores (5%).

3.3.4 DISCRIMINANT ANALYSES WITHIN FUNCTIONAL GROUPS

To increase the resolution of my investigation and evaluate variation in FA composition among groups in more detail, subsequent DFAs were conducted using the selected 15 FAs on each of the four major functional groups separately (herbivores, planktivores, carnivores, and crustaceans). The FA signatures of the two cephalopod groups were also analyzed and contrasted.

Herbivores. DFA performed on the 5 groups of herbivores (n = 310; angelfish (1), parrotfish (21), chub (23), tang/surgeonfish (31), unicornfish (32)) yielded a cross-validated classification success of 97.7%. Four significant discriminant functions were generated (Wilk's Lambda 0.345, $p < 0.001$). All groups contained an extremely high proportion of correctly classified individuals, with classification success ranging from 95-100% (Table 3.2). A plot of the discriminant scores and group centroids on the first two discriminant functions (Fig. 3.3), revealed that parrotfishes (21) had a more distinct FA signature as they clustered by themselves in the lower left quadrant. The unicornfish (27) and chub (18) groups, as well as the angelfish and tang/surgeonfish groups formed two separate clusters that partially overlapped (Fig. 3.3). Nevertheless, the four aforementioned groups all had a high number of individuals correctly classified (see Table 3.2), indicating that they would likely be separated on the remaining discriminant functions, and that they are distinguishable on the basis of their FA signatures.

Differences in FA levels were significant across the five groups of herbivores (Wilk's Lambda 0.002, $p < 0.001$). Tang/surgeonfishes (26) had high levels of 16:0 at 32%, and chubs (18) had the lowest (25%). Unicornfishes (27) exhibited the highest proportion of 18:1n-9 at 11.5%, relative to the other groups of herbivores (6-10%). Parrotfishes (16) had higher levels of 20:4n-6 at 12.5%, while tang/surgeonfishes (26) and unicornfishes (27) had the lowest (7% and 6.5% respectively). Tang/surgeonfishes exhibited the highest levels of 20:5n-3 at 8%. Levels of 22:6n-3 where the highest in chubs (18) at 9% relative to the other herbivores (3-5%).

Planktivores. The planktivorous armorheads clearly separated from all other planktivores and clustered tightly by themselves in the DFA on the 47 groups (Fig. 3.2).

Armorheads are thus readily distinguishable from the other groups of planktivores, as well as from all the other species groups analyzed. As such they are treated and discussed separately in an upcoming section. DFA conducted on the remaining 5 groups of planktivores (n = 172; cardinalfish (2), pennantfish (9), sergeant (11), chromis/dascyllus (12), triggerfish M (35)) yielded a cross-validated classification success of 87.2%. Four significant functions were generated (Wilk's Lambda 0.204, $p < 0.001$). A plot of the scores and group centroids on the first and second discriminant functions revealed that *Melichthys niger* triggerfishes (35) and *Heniochus diphreutes* pennantfishes (9) were spatially isolated from the other planktivores (Fig. 3.3). *M. niger* had the lowest levels of 14:0 and this FA accounted for most of the variance in the separation along the first discriminant function. *H. diphreutes* had the lowest proportion of 18:1n-9, the FA which accounted for most of the variance on the second function. Moreover, *M. niger* and *H. diphreutes* had the highest (9.7%) and lowest (2%) levels of 20:4n-6 respectively. Classification success was high (> 80%) for all groups of planktivores, with the exception of the chromis/dascyllus group (12) for which 19.5% individuals were misclassified as sergeant (11; see Table 3.2). Conversely, the classification success of chromis/dascyllus was much lower in the DFA conducted on all 47 groups (43.9%), which indicates that these fishes can be distinguished from other planktivores.

Carnivores. DFA performed on the 28 groups encompassed in the carnivore cluster (n = 1,281; beardfish (4), bigeye (5), cusk eel (6), conger eel (7), butterfly/forcepfish (8), cutthroat/snake eel (10), dragonet (13), gurnard (14), goatfish M (15), goatfish P (16), flounder (17), lizard/snakefish (18), sandperch (19), moray (20), toby (22), scorpionfish (24), squirrelfish snapper (25), bluestripe snapper (26), pink snapper (27), flower snapper (28), soldierfish (29), squirrelfish (30), tilefish (33), knife/razorfish (34), triggerfish S (36), wrasse/hogfish/coris (37), boarfish (46), and duckbill (47)) yielded a cross-validated classification success of 75.5%. Fourteen significant discriminant functions were generated (Wilk's Lambda 0.790, $p < 0.001$). For more than half of the carnivores (17/28), classification success was ≥ 80% (Table 3.2). Three groups were poorly classified (< 60% individuals correctly classified), and most misclassifications occurred among groups with similar diet/ecology. A plot of the group centroids on the first two discriminant functions (Fig. 3.3) showed that groups thriving at subphotic depths (4, 10, 47) and all deep-water groups living on the slope (25, 27, 28) assembled together in the upper right quadrant. Nine groups inhabiting bank summits (5, 6, 7, 14, 17, 18, 19, 24, 34) were located in the lower right quadrant, along with the bluestripe snapper (26), which occurs in shallow reef lagoons but also on outer reef slopes, and the duckbill (46) which are subphotic fishes with a flexible depth range (Appendix 3.3). The remaining eleven groups, consisting of seven reef (8, 15, 16, 20, 29, 36, 37) and four bank (13, 22, 30, 33) groups, were scattered in the lower and upper left quadrant. Thus, carnivorous deep-water species (i.e. species thriving on the slopes and at subphotic depths), were differentiated from species living at shallower depths on the basis of their FA signatures. Correspondingly, carnivores living on bank summits and coral reefs associated more closely on the plot and thus had more similar FA composition.

MANOVA conducted on the 15 FAs used in the DFA showed that variations in FA composition among groups of carnivores were significant (Wilk's Lambda 0.001, $p < 0.001$). The six groups of deep-water species located in the upper right quadrant (4, 10, 25, 27, 28, 47) exhibited on average the highest levels of 18:1n-9 at 15%, relative to 9%

in groups thriving at moderate depths (banks) and in the shallows (reefs). The butterfly/forceptfishes (8) were the only group spatially isolated from the other carnivores; they exhibited the highest levels of 22:4n-6 (5%) relative to ~2% in the other groups. The butterfly/forcepfish (8), moray eel (20), and toby (22) groups had the lowest levels of 20:5n-3 (2.8% on average), while levels of 20:5n-3 reached 7.6% in knife/razorfish (34). The average proportion of 20:4n-6 in deep water groups (3%) was less than half of the average proportion encountered in reef and bank groups (7%). Levels of 22:6n-3 were higher in deep-water carnivores at 23% relative to the reef/bank groups (15%).

Crustaceans. DFA performed on the 6 groups of crustaceans (n = 352; shrimp (40), box crab (41), swimming crab (42), pebble crab (43), slipper lobster (44), spiny lobster (45)) yielded a cross-validated classification success of 81.5%. Five significant discriminant functions were generated (Wilk's Lambda 0.447, $p < 0.001$). A plot of individual scores and group centroids on the first two discriminant functions (Fig. 3.3) showed that shrimps (40) were clearly separated from the 5 other crustacean groups. Classification success was high in the shrimps (40), swimming crabs (42), and slipper lobsters (44), which suggested that these three groups have more distinct FA signatures (Table 2). Some overlap was detected among the remaining crab (41, 43) and spiny lobster (45) groups. For example, the box crabs *Calappa spp.* (41) and spiny lobsters *P. marginatus* (45) were consistently misclassified as one another: 25.4% of box crabs were classified as spiny lobster, and 17% of spiny lobsters were incorrectly classified as box crabs. This indicates a fairly high degree of similarity among the FA composition of these two groups, which renders these crustaceans harder to distinguish on the basis of the 15 FAs used in this analysis.

Significant differences in FA composition (15 FAs) were detected among crustaceans (Wilk's Lambda 0.016, $p < 0.001$). On average, swimming crabs (42) and pebble crab (43) had the highest levels of 16:0 at approximately 16%. Shrimps (40) had high levels of 18:1n-9 (18%), relative to 12% on average in the other groups. Spiny lobsters (45), box crabs (41), and swimming crabs (42) all high levels of 20:4n-6 (~15%), while shrimps (40) comparatively had low levels (3.6%). Shrimps (40) however exhibited a high proportion of 20:5n-3 at 11% relative to 9% in the other groups. Levels of 22:6n-3 were also the highest in shrimps (40) at 14.5% relative to approximately 11% in the crab and lobster groups (41-45).

Cephalopods. DFA performed on the 47 groups of species showed that octopus (38) and squid (39) possessed distinct FA compositions with high classification success (Table 3.2) as these cephalopods did not associate closely on the first two discriminant functions (Fig. 3.2; Appendix 3.3). Significant differences in FA levels among octopus (38) and squid (39) were detected (MANOVA, Wilk's Lambda 0.057, $p < 0.001$). Specifically, octopuses had particularly high levels of 20:4n-6 (13.5%) relative to squid (~3%). Squid on the other hand had high levels 18:1n-9 (~7%) and very high levels of 22:6n-3 (~34%), while these FAs were present in lower proportion in octopus (~3% and ~24% respectively). Of all the species group analyzed, squid had the highest levels of 22:6n-3.

Armorheads. Planktivorous armorheads had 100% correctly classified individuals in the DFA on the 47 groups, and were spatially distinct from all groups. Armorheads had very high levels of 18:1n-9 at 26.54% which is atypical not only of planktivores, but also of any species group in this system. Armorheads also exhibited very low levels of 20:4n-6 at ~0.6% which was also uncommon in NWHI species.

Table 3.1 Summary of groupings of 100 species of Northwestern Hawaiian Islands (NWHI) and Main Hawaiian Islands (MHI) fishes and invertebrates into 47 groups based on taxonomy, diet, and ecological evaluation from the literature (see Appendix 3.3).

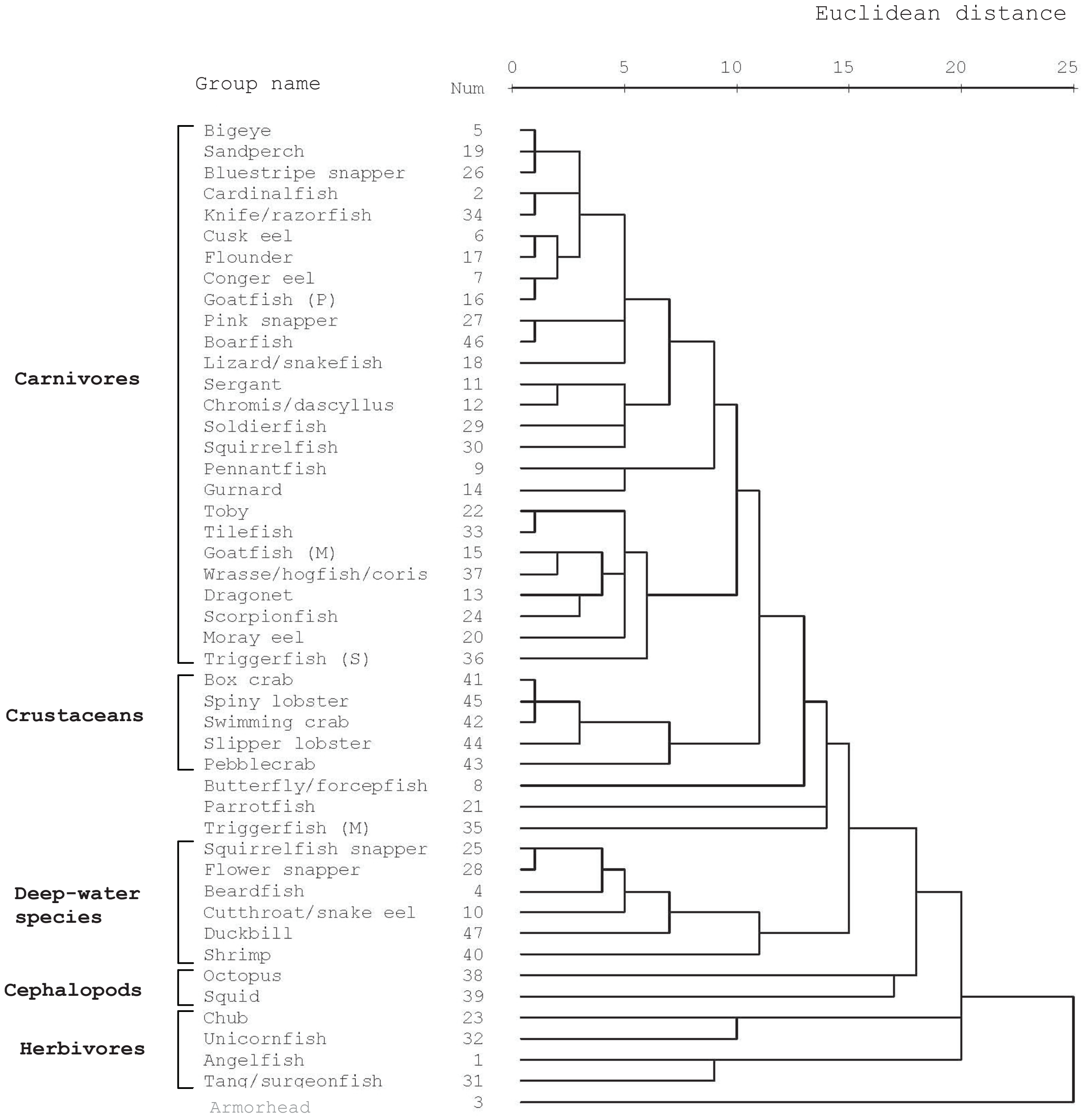
Group	Number of Species	Number of Individuals (n)	Diet guild
1. Angelfish	1	20	Benthic herbivore
2. Cardinalfish	1	18	Planktivore
3. Armohead	1	20	Planktivore
4. Beardfish	1	20	Piscivore
5. Bigeye	2	40	Piscivore
6. Cusk eel	1	20	Piscivore
7. Conger eel	2	46	Piscivore
8. Butterfly/forcepfish	6	134	Benthic carnivore
9. Pennantfish	1	36	Planktivore
10. Cutthroat/snake eel	2	39	Piscivore
11. Sergeant	3	57	Planktivore
12. Chromis/dascyllus	2	41	Planktivore
13. Dragonet	1	20	Benthic carnivore
14. Gurnard	1	24	Benthic carnivore
15. Goatfish (M*)	2	41	Benthic carnivore
16. Goatfish (P**)	4	77	Benthic carnivore
17. Flounder	3	116	Benthic carnivore
18. Lizard/snakefish	3	59	Piscivore
19. Sandperch	1	18	Benthic carnivore
20. Moray eel	7	135	Piscivore
21. Parrotfish	3	60	Benthic herbivore
22. Toby	4	80	Benthic carnivore
23. Chub	2	38	Benthic herbivore
24. Scorpionfish	1	19	Benthic carnivore
25. Squirrelfish snapper	1	21	Benthic carnivore
26. Bluestripe snapper	1	22	Omnivore
27. Pink snapper	1	24	Benthic carnivore
28. Flower snapper	1	19	Omnivore
29. Soldierfish	1	20	Benthic carnivore
30. Squirrelfish	1	21	Benthic carnivore

Table 3.1 *end*

Group	Number of Species	Number of Individuals (n)	Diet guild
31. Tang/surgeonfish	8	154	Benthic herbivore
32. Unicornfish	2	38	Benthic herbivore
33. Tilefish	1	16	Benthic carnivore
34. Knife/razorfish	3	57	Benthic carnivore
35. Triggerfish (M***)	1	20	Planktivore
36. Triggerfish (S****)	1	19	Benthic carnivore
37. Wrasse/hogfish/coris	7	135	Benthic carnivore
38. Octopus	3	40	Benthic carnivore
39. Squid	1	15	Piscivore
40. Shrimp	2	70	Benthic carnivore
41. Box crab	2	59	Benthic carnivore
42. Swimming crab	1	29	Benthic carnivore
43. Pebblecrab	1	21	Benthic carnivore
44. Slipper lobster	2	102	Benthic carnivore
45. Spiny lobster	1	71	Benthic carnivore
46. Boarfish	2	20	Benthic carnivore
47. Duckbill	1	19	Benthic carnivore
Total:	100	2190	

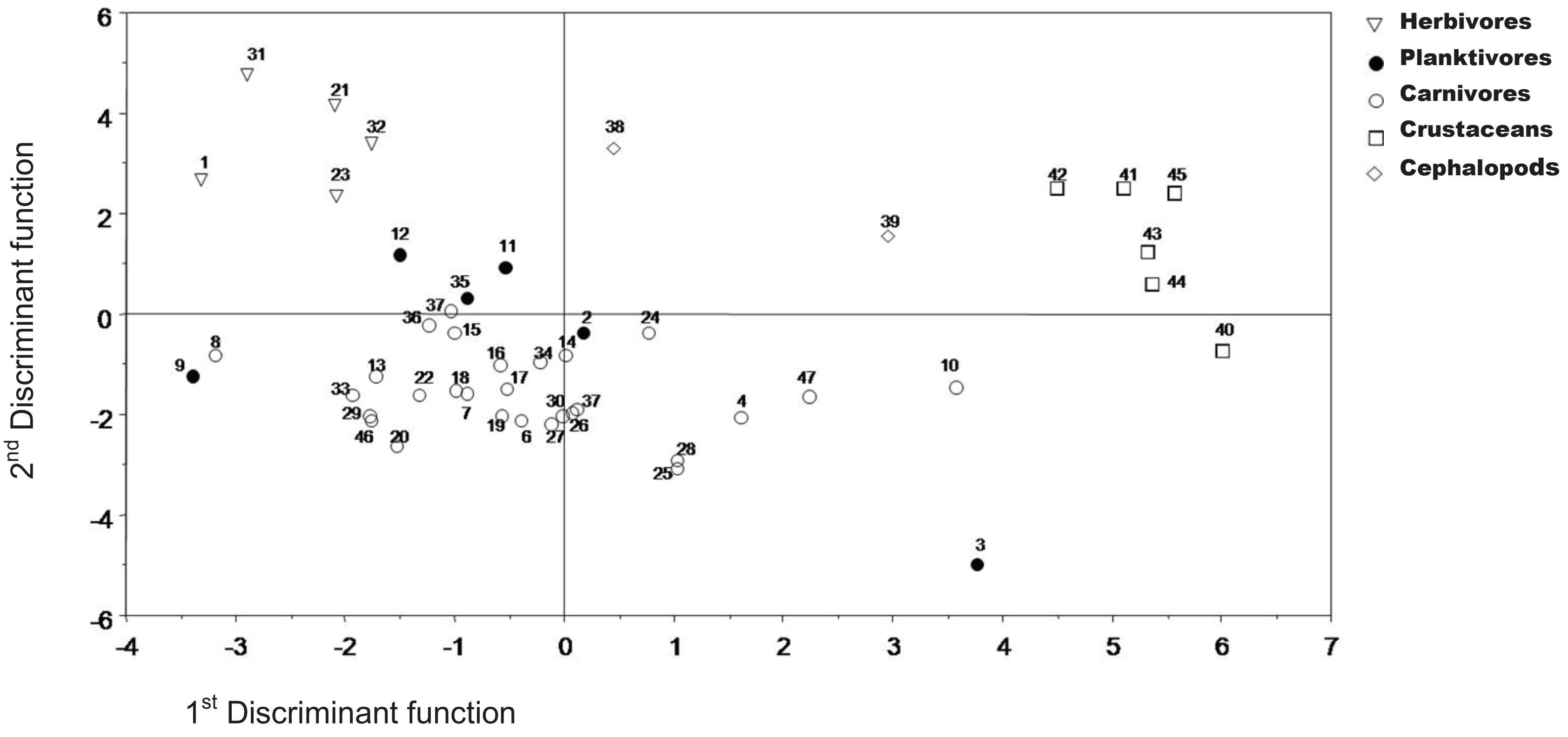
* *Mulloidichthys* spp
***Parupeneus* spp
****Melichthys spp*
*****Sufflamen spp*

Figure 3.1 Hierarchical cluster dendrogram of the degree of similarity in the fatty acid (FA) composition of the 47 species groups (see Table 3.1 for species/group sample size); similar groups were merged into 5 main clusters: carnivores (also including piscivores, planktivores, omnivores), crustaceans, deep-water species (slope and subphotic), cephalopods, and herbivores. Each cluster was nested into the next, from the most to the least similar. Armorheads did not cluster with any other groups. Goatfish (P): *Parupeneus* spp. Goatfish (M): *Mulloidichthys* spp. Triggerfish (S): *Sufflamen bursa*. Triggerfish (M): *Melichthys niger*.



Euclidean distance
0
5
10
15
20
25
Group name
Num
Carnivores
Crustaceans
Deep-water species
Cephalopods
Herbivores
Bigeye 5
Sandperch 19
Bluestripe snapper 26
Cardinalfish 2
Knife/razorfish 34
Cusk eel 6
Flounder 17
Conger eel 7
Goatfish (P) 16
Pink snapper 27
Boarfish 46
Lizard/snakefish 18
Sergant 11
Chromis/dascyllus 12
Soldierfish 29
Squirrelfish 30
Pennantfish 9
Gurnard 14
Toby 22
Tilefish 33
Goatfish (M) 15
Wrasse/hogfish/coris 37
Dragonet 13
Scorpionfish 24
Moray eel 20
Triggerfish (S) 36
Box crab 41
Spiny lobster 45
Swimming crab 42
Slipper lobster 44
Pebblecrab 43
Butterfly/forcepfish 8
Parrotfish 21
Triggerfish (M) 35
Squirrelfish snapper 25
Flower snapper 28
Beardfish 4
Cutthroat/snake eel 10
Duckbill 47
Shrimp 40
Octopus 38
Squid 39
Chub 23
Unicornfish 32
Angelfish 1
Tang/surgeonfish 31
Armorhead 3

Figure 3.2 Discriminant function analysis (DFA) of fatty acid (FA) signatures among the 47 species groups. Group centroids (within group mean for each discriminant function) for the first and second (of 14 significant) discriminant functions, which accounted for 49% of total variance, for DFA performed on the 47 species groups (n = 2,190; see Table 3.1 for species/group sample sizes) using the 15 FAs that exhibited the greatest average variance, abundance, and reflection of diet. The two FAs which accounted for most of the variance in group separation on the first two discriminant functions were 18:1n-9 and 16:0. **1**: angelfish, **2**: cardinalfish, **3**: armorhead, **4**: beardfish, **5**: bigeye, **6**: cusk eel, **7**: conger eel, **8**: butterfly/forcepfish, **9**: pennantfish, **10**: cutthroat/snake eel, **11**: sergeant, **12**: chromis/dascyllus, **13**: dragonet, **14**: gurnard, **15**: goatfish M (*Mulloidichthys spp*), **16**: goatfish P (*Parupeneus spp*), **17**: flounder, **18**: lizard/snakefish, **19**: sandperch, **20**: moray eel, **21**: parrotfish, **22**: toby, **23**: chub, **24**: scorpionfish, **25**: squirrelfish snapper, **26**: bluestripe snapper, **27**: pink snapper, **28**: flower snapper, **29**: soldierfish, **30**: squirrelfish, **31**: tang/surgeonfish, **32**: unicornfish, **33**: tilefish, **34**: knife/razorfish, **35**: triggerfish M (*Melichthys niger*), **36**: triggerfish S (*Sufflamen bursa*), **37**: wrasse/hogfish/coris, **38**: octopus, **39**: squid, **40**: shrimp, **41**: box crab, **42**: swimming crab, **43**: pebble crab, **44**: slipper lobster, **45**: spiny lobster, **46**: boarfish, **47**: duckbill.


▽ Herbivores
● Planktivores
○ Carnivores
□ Crustaceans
◇ Cephalopods
2nd Discriminant function
1st Discriminant function
6
4
2
0
-2
-4
-6
-4
-3
-2
-1
0
1
2
3
4
5
6
7
31
21
32
1
23
38
12
11
35
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19
6
30
37
26
27
28
25
4
47
10
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43
44
40
3

Table 3.2 Predicted group membership for discriminant function analyses (DFAs) among the 47 group of species, and within the 4 main functional groups: herbivores, planktivores, crustaceans, and carnivores (including piscivores and omnivores). The armorhead and cephalopod groups were excluded from the within functional group analyses. The number and proportion of individuals correctly classified, and the major missclafications for groups with less than 60 % individuals correctly classified are reported. * *Melichthys niger*; ** *Mulloidichthys* spp; *** *Parupeneus* spp; ****Sufflamen bursa*.

Functional Group	**Group of Species**	**Number of Individuals (n)**	**DFA among 47 groups**		**DFA within 4 functional groups**	
			Count	%	Count	%
Herbivores	1. Angelfish	20	20	100.0	19	95.0
	21. Parrotfish	60	57	95.0	60	100.0
	23. Chub	38	32	84.2	38	100.0
	31. Tang/surgeonfish	154	138	89.6	150	97.4
	32. Unicornfish	38	36	94.7	36	94.7
Planktivores	2. Cardinalfish	18	15	83.3	17	94.4
	3. Armorhead	20	20	100.0	N/A	N/A
	9. Pennantfish	36	32	88.9	35	97.2
	11. Sergeant	57	32	56.1	48	84.2
	12. Chromis/dascyllus	41	18	**43.9**[1]	30	73.2
	35. Triggerfish (M*)	20	18	90.0	20	100.0
Carnivores	4. Beardfish	20	15	75.0	16	80.0
	5. Bigeye	40	29	72.5	30	75.0
	6. Cusk eel	20	17	85.0	16	80.0
	7. Conger eel	46	17	**37.0**[2]	15	**32.6**[6]
	8. Butterfly/forcepfish	134	91	67.9	109	81.3
	10. Cutthroat/snake eel	39	37	94.9	37	94.9
	13. Dragonet	20	17	85.0	18	90.0
	14. Gurnard	24	20	83.3	20	83.3
	15. Goatfish (M**)	41	28	68.3	28	68.3
	16. Goatfish (P***)	77	32	**41.6**[3]	34	**44.2**[7]
	17. Flounder	116	94	81.0	98	84.5
	18. Lizard/snakefish	59	49	83.1	45	76.3
	19.Sandperch	18	15	83.3	15	83.3
	20. Moray eel	135	111	82.2	110	81.5
	22. Toby	80	63	78.8	58	72.5
	24. Scorpionfish	19	19	100.0	19	100.0

Table 3.2 *end*

Functional Group	Group of Species	Number of Individuals (n)	DFA among 47 groups		DFA within 4 functional groups	
			Count	%	Count	%
Carnivores	25. Squirrelfish snapper	21	19	90.5	19	90.5
	26. Bluestripe snapper	22	14	63.6	14	63.6
	27. Pink snapper	24	16	66.7	17	70.8
	28. Flower snapper	19	18	94.7	18	94.7
	29. Soldierfish	20	15	75.0	17	85.0
	30. Squirrelfish	21	14	66.7	14	66.7
	33. Tilefish	16	12	75.0	14	87.5
	34.Knife/razorfish	57	30	**52.6** [4]	33	**57.9** [8]
	36. Triggerfish (S****)	19	18	94.7	17	89.5
	37. Wrasse/hogfish/coris	135	82	60.7	96	71.1
	46. Boarfish	20	19	95.0	19	95.0
	47. Duckbill	19	17	89.5	17	89.5
Crustaceans	40. Shrimp	70	70	100.0	70	100.0
	41. Box crab	59	24	**40.7** [5]	33	**55.9** [9]
	42. Swimming crab	29	24	82.8	27	93.1
	43. Pebblecrab	21	15	71.4	16	76.2
	44. Slipper lobster	102	79	77.5	89	87.3
	45. Spiny lobster	71	49	69.0	51	71.8
Cephalopods	38. Octopus	40	38	95.0	N/A	N/A
	39. Squid	15	14	93.3	N/A	N/A
	Total:	2190				

Major misclassifications (%, group name (group #)) for DFA on 47 groups:

[1] 17.1% tang/surgeonfish (31); 14.6% sergeant (11); 7.3% gurnard (14)

[2] 21.7% moray (20); 17.4% lizard/snakefish (18); 13.0% knife/razorfish (34)

[3] 18.2% sandperch (19); 9.1% scorpionfish (24); 7.8% *Mulloidichthys* goatfish (15); 5.2% cusk eel (6); 5.2% cardinalfish (2)

[4] 14.0% *Parupeneus* goatfish (16); 14.0% cardinalfish (2); 5.3% lizard/snakefish (18); 5.3% cusk eel (6)

[5] 30.5% spiny lobster (45); 10.2% pebble crab (43); 6.8% swimming crab (42); 5.1% Slipper lobster

Major misclassifications (%, group name (group #)) for DFAs within functional groups:

[6] 21.7% moray (20); 15.2% knife/razorfish (34); 15.2% lizard/snakefish (18)

[7] 19.5% sandperch (19); 10.4% scorpionfish (24); 5.2% *Mulloidichthys* goatfish (15); 6.5% cusk eel (6)

[8] 15.8% *Parupeneus* goatfish (16); 8.8% scorpionfish (24); 5.3% lizard/snakefish (18); 5.3% cusk eel (6)

[9] 23.7% spiny lobster (45); 8.5% slipper lobster (44); 6.8% pebble crab (43); 5.1% swimming crab (42)

Figure 3.3 Discriminant scores and group centroids (within group mean for each discriminant function) for the discriminant function analyses (DFAs) conducted on the four functional groups: herbivores (n = 310), planktivores (n = 172), carnivores (n = 1281), and crustaceans (n = 352). The armorhead group (*Pseudopentaceros wheeleri*, n = 20) is excluded from the DFA performed on planktivores. For clarity purposes, only the group centroids are presented for the carnivores DFA (see Table 3.2 for species/group names). The first two discriminant functions accounted for 85%, 90%, 54.3%, and 84.4% of the total variance in herbivores, planktivores, carnivores, and crustaceans respectively. The two FAs which accounted for most of the variance on the first two discriminant functions were 20:1n-9 and 16:0 in herbivores, 14:0 and 18:1n-9 in planktivores, 18:1n-9 and 22:4n-6 in carnivores, and 18:1n-9 and 20:5n-3 in crustaceans. Triggerfish M: *Melichthys niger*, Goatfish M: *Mulloidichthys spp*, Goatfish P: *Parupeneus spp*. Triggerfish S: *Sufflamen bursa*.

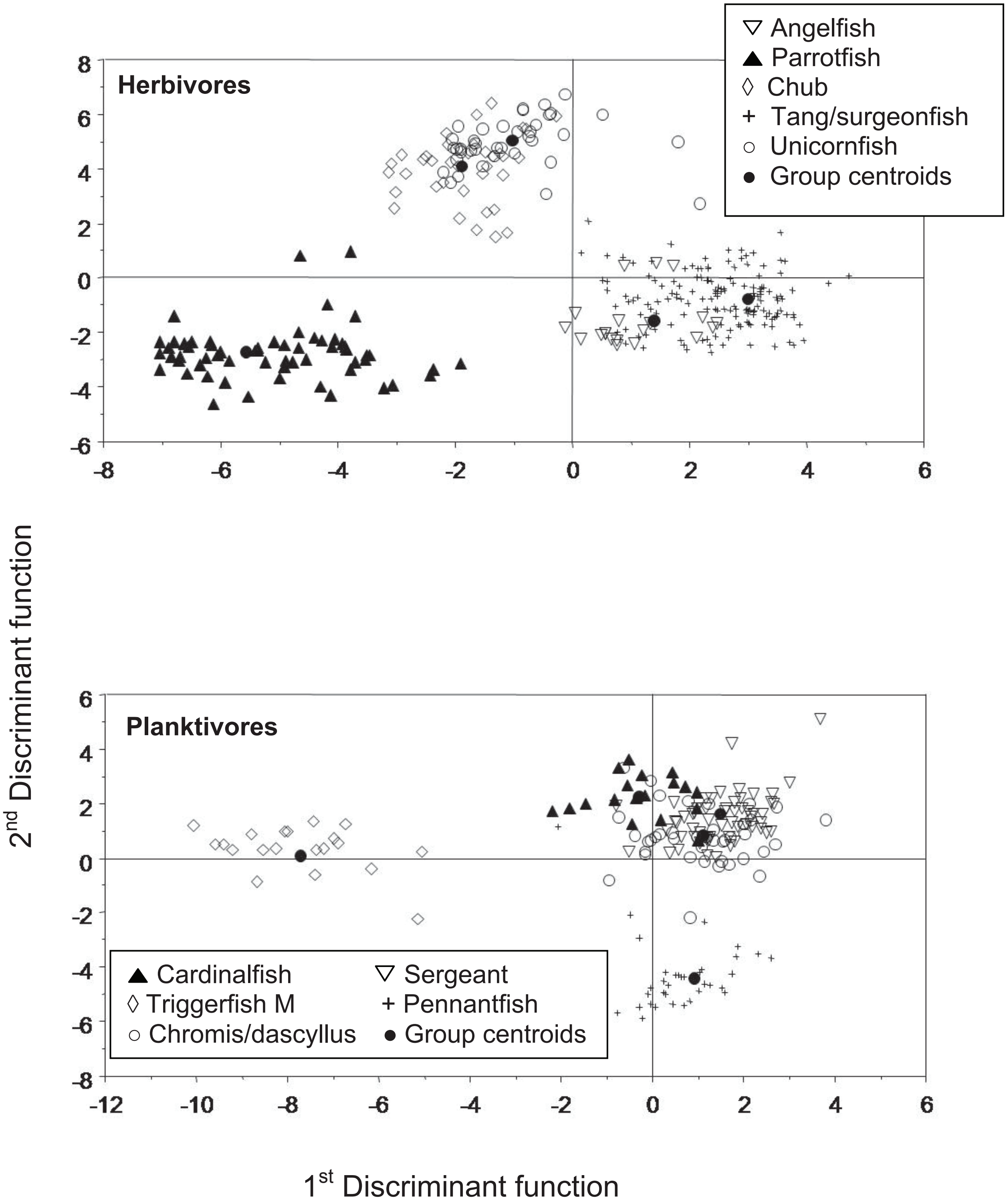
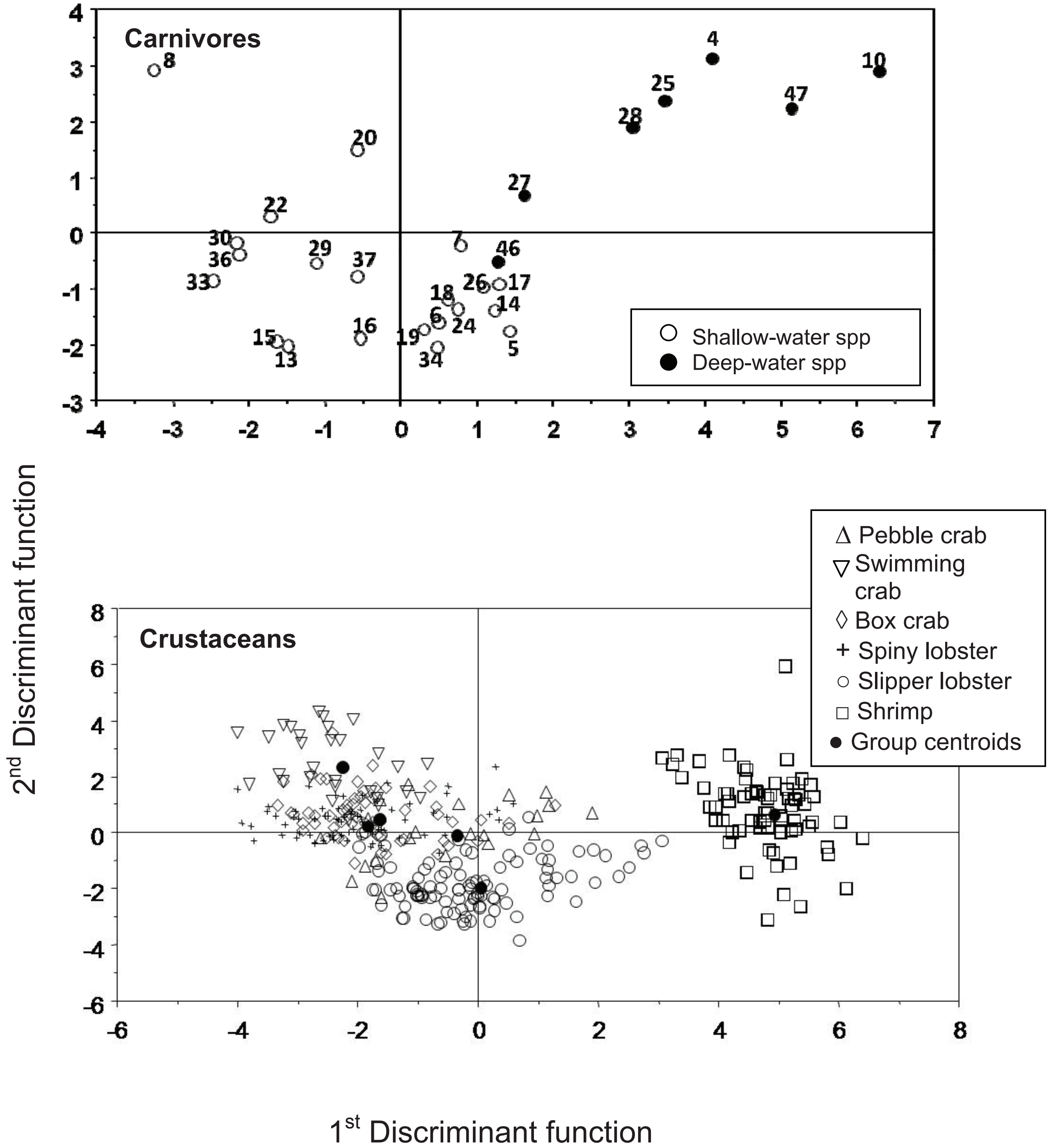

Angelfish
Parrotfish
Chub
Tang/surgeonfish
Unicornfish
Group centroids
Herbivores
8
6
4
2
0
-2
-4
-6
-8
-6
-4
-2
0
2
4
6
2nd Discriminant function
Planktivores
6
4
2
0
-2
-4
-6
-8
Cardinalfish
Sergeant
Triggerfish M
Pennantfish
Chromis/dascyllus
Group centroids
-12
-10
-8
-6
-4
-2
0
2
4
6
1st Discriminant function

Figure 3.3 *end*



3.4 DISCUSSION

The results of this study indicate that NWHI fishes and invertebrates, grouped by closely related and ecologically equivalent species, can be separated into broad functional groups, within which individual species groups can be further distinguished from one another on the basis of their FA composition. FA trophic markers have long been recognized as efficient tools in studies of marine food webs (Sargent et al. 1989, Budge et al. 2002, Dalsgaard et al. 2003, Budge et al. 2006). Recent studies have demonstrated that FAs can be successfully used to elucidate feeding ecology and trophic relationships of marine fish (Drazen et al. 2009, Stowasser et al. 2009) and invertebrates (Silina & Zhukova 2009, Spilmont et al. 2009). However, northern/temperate and abyssal marine ecosystems have been the focus of most research efforts, and FA data regarding trophic interactions in tropical marine ecosystems are scarce (reviewed in Dalsgaard et al. 2003). The present study is, to my knowledge, the first to employ FA analysis to investigate trophic and ecological relationships in a highly complex subtropical reef ecosystem while also integrating such a large number of species in the analysis. The prey database is comprised of a wide array of species, from different trophic levels/depth/habitat, which allows investigations to be conducted at various scales to ultimately provide a better picture of interactions occurring at the ecosystem level. Compared to their more temperate counterparts, most NWHI prey species contained very low levels of long-chain monounsaturated FA isomers (e.g. 20:1 and 22:1) which are typical of North Atlantic and North Pacific prey (Iverson 2009). They also exhibited much higher levels of n-6 polyunsaturated FAs (PUFA), a characteristic previously reported in tropical marine prey species (Dalsgaard et al. 2003, Iverson 2009).

3.4.1 DISCRIMINANT ANALYSIS AMONG SPECIES GROUPS

DFA performed on the 47 species groups showed that diet played a primary role in discriminating among herbivorous fishes, crustaceans reliant on heterotrophic benthos, and carnivorous fishes (Fig. 3.2). Planktivorous fishes were generally less well defined as an independent trophic group (except for the armorhead), consistent with the fact that they eat planktonic animals and larvae that feed directly on primary productivity; as such their FA signature possesses attributes of both herbivorous and carnivorous diet. Cephalopods were spatially distinct from other groups but were also reliably differentiated from each other, despite their taxonomical relatedness. All deep-water species groups were scattered together in the lower right quadrant, while herbivores and planktivores were further separated from the crustaceans and cephalopods (Fig. 3.2). Overall, despite a relatively broad overlap, 27 of 47 groups were reasonably well classified at >80% success. In many cases, misclassified individuals were classified into groups of closely related species and/or groups of species with similar diet and/or ecology. For example box crabs were misclassified as other crustaceans (crabs and lobsters) which also feed on mollusks and benthic invertebrates.

The low levels of total body fat we found among most prey are common in species inhabiting a tropical environment, or an environment subjected to little fluctuation in food availability where there is no need to accumulate large energy reserves (Dalsgaard et al. 2003). However, the armorhead *P. wheeleri* was composed of an astounding 27% fat. This can be explained by the life history of *P. wheeleri*, as juvenile armorheads undergo a 2+ year epipelagic pre-recruitment phase in the subarctic and transitional waters of the Northeast Pacific and Gulf of Alaska, building their fat reserves before returning to the Southern Emperor-Northern Hawaiian Ridge seamounts in the temperate central North Pacific to settle and begin maturation (Seki & Somerton 1994, Humphreys 2000). Moreover, armorheads possessed high levels of 18:1n-9 (27%), a marker of animal production, which is consistent with a diet of planktonic fishes and invertebrates (Dalsgaard et al. 2003; see Appendix 3.3 for detailed diet). Herbivores exhibited the highest levels of 16:0, a FA known to be more abundant in individuals feeding directly on primary production (Dalsgaard et al. 2003). Carnivores were lower in 20:5n-3 (eicosapentaenoic acid or EPA) relative to 22:6n-3 (docosahexaenoic acid or DHA), while the opposite situation was encountered in herbivores. This is in agreement with reports that EPA/DHA ratio values become smaller at higher trophic levels and thus can be used as an index of carnivory (Dalsgaard et al. 2003).

3.4.2 DISCRIMINANT ANALYSES WITHIN FUNCTIONAL GROUPS

Classification success of a number of species groups increased upon conducting DFAs separately on each functional group. This indicates that finer scale variations in FA composition are detectable when a DFA is applied on groups sharing the same diet/ecology.

Herbivores. Herbivores play a key structural role in benthic coral reef communities (Hixon & Brostoff 1996). They are a chief link between benthic primary productivity and higher trophic levels. Moreover, by the consistent and differential removal of algae and/or exhibiting territorial behavior which prevents excessive corallivore predation, herbivorous fish also promote local diversity on coral reefs (Hixon & Brostoff 1996, Gochfeld 2010). Classification success was very high for the DFA conducted on the five groups of herbivores, and all individual groups had high proportions of individuals correctly classified (Fig. 3.3; Table 3.2). This indicates that angelfishes, parrotfishes, chubs, tang/surgeonfishes, and unicornfishes in this system can be accurately differentiated from one another on the basis of their FA composition. These results are consistent with previous findings that herbivorous reef fishes are selective feeders, and thus occupy narrower trophic niches (Cvitanovic & Bellwood 2009, Hoey & Bellwood 2009). For example, a study conducted on Lizard Island, Great Barrier Reef has shown that a single species of unicornfish (*Naso unicornis*) was the dominant consumer of adult macroalgae of the genus *Sargassum* (Hoey & Bellwood 2009). These feeding patterns are further understandable from a morphological and physiological standpoint as some herbivorous reef fish species have evolved specialized digestive tracts and/or tolerance for algal chemical defense allowing them to feed on specific algae types (Stachowicz & Hay 1999, Fox et al. 2009). All of the specimens in the herbivore group were collected from roughly the same depth range (<20 m) which contrasts with the range of specimens in the carnivore and crustacean groups; this could in part be responsible for preventing segregation of species along a depth gradient in this cluster.

Planktivores. Despite lacking spatial definition as a functional group on the original DFA analysis, the majority of planktivores were accurately classified on the basis of their FA composition. *H. diphreutes* pennantfishes were collected from lobster traps on bank summits which is likely why they differed from planktivores collected at shallower depths. *M. niger* triggerfishes mostly feed on zooplankton but can also consume benthic algae (Froese & Pauly 2009) which might explain their high levels of 20:4n-6, a known marker of benthic productivity (e.g. Cooper et al. 2009). While the proportion of correctly classified chromis/dascyllus individuals increased substantially in the within-planktivore DFA (Table 3.2), this group still had the lowest classification success of all planktivores. Misclassified individuals however were mostly classified as sergeants, another group of planktivores exhibiting similar foraging ecology (see Appendix 3.3). This indicates potential overlap in FA composition among these species.

Carnivores. Trophic relationships become less clear with increasing trophic levels as the FA signatures of consumers may originate from a greater variety of dietary sources (Dalsgaard et al. 2003, Iverson 2009). Examining trophic relations in carnivores, omnivores, and piscivores thus becomes more complex as the within-carnivores DFA illustrates. The effect on FA composition in species that feed in deep-water was noticeable, as these groups (subphotic and slope) were separated from groups of species thriving at shallower depth (bank summits and reef flats) on the first two discriminant functions (Fig. 3.3). Classification success was highly variable among the 28 groups of carnivores. However, misclassifications generally occurred among closely related groups or groups with similar diet/ecology. Conger eels were mostly misclassified as moray eels which have similar diets/habitat, or as cryptic benthic carnivores which possess the same burrowing habits (Table 3.2; Appendix 3.3). *Parupeneus* goatfishes were most commonly misclassified as sandperches and scorpionfishes, with all three groups possessing both overlapping depth range and diets (benthic crustaceans; Appendix 3.3). Knife/razorfishes were mostly misclassified as other burrowing or sand dwelling species such as *Parupeneus* goatfishes who probe the sand with their barbells to find benthic invertebrates.

The butterfly/forcepfishes (Chaetodontidae) were spatially isolated from all other groups of carnivores. Chaetodontids encompass 61% of all corallivorous reef fish species (Bellwood et al. 2010). Among all the species group analyzed, the butterfly/forcepfishes were the only group which included fish primarily feeding on live corals (e.g. *C. multicinctus, C. ornatissimus, C. quadrimaculatus*), and this group appeared to have a more distinct FA composition relative to all other carnivores.

Crustaceans. High proportions of correctly classified individuals (Table 3.2) for shrimps, swimming crabs, and slipper lobsters indicate that these groups/species of crustaceans can be readily distinguished by their FA signatures. Furthermore, the spatial distribution of groups/species in the crustaceans DFA (Fig. 3.3) suggested there was an influence of depth on FA signatures in species thriving in deep water, as the subphotic shrimps clearly separated from the other crustaceans. The remaining crab and lobster groups were more problematic; pebble crabs (*Carpilius convexus*) and spiny lobsters (*P. marginatus*) were reasonably well classified but the classification success of the box crabs remained poor (Table 3.2). Overlap in FA signatures among crabs and lobsters could be due to commonalities in diets as these two groups of decapods reportedly feed on a mixture of mollusks, snails, and other benthic invertebrates (Appendix 3.3).

Cephalopods. Cephalopods associated together in the hierarchical cluster analysis, but separated more distinctly on the DFA performed on the 47 groups. Thus, despite their taxonomical relatedness, other factors such as diet and ecology have a great effect on their FA composition. Both squids and octopuses were found to have characteristic FA compositions, and both were low in fat (on average 1.4%). Some authors have suggested that findings of low total lipid proportions in squid are erroneous, and argued that these values must be derived from using partial versus whole specimens for lipid extraction (Phillips et al. 2002). However, that is not the case in the present study, nor in some other analyses of whole cephalopods (e.g. Kirsch et al. 1998, Iverson et al. 2002).

On average, octopuses and squids exhibited noticeably higher levels of 22:6n-3 relative to herbivores, planktivores, carnivores, and crustaceans (Appendix 3.4), which has been found previously in the NWHI as well as other marine ecosystems (e.g. Goodman-Lowe et al. 1999, Budge et al. 2002, Iverson et al. 2002). Octopuses were sampled from shallow reef and bank depths (<40 m) and were more closely associated with prey that depend on the benthic productivity of the algal beds. Markers of benthic productivity (e.g. high levels of 20:4n-6) obtained through a diet of filter feeding mollusks and other benthic invertebrates which feed directly on primary production are strongly conserved in octopuses. Contrastingly, prey base surveys found the squid *Sthenoteuthis oualaniensis* at subphotic depths and they were more closely associated with heterotrophs that rely much more on the detrital food web. The diet of the squid *S. oualaniensis* reportedly consists mostly of myctophid fishes, and other cephalopods (Parry 2006). Myctophids are pelagic fish primarily feeding on planktonic crustaceans (Shreeve et al. 2009). Marked differences in dietary sources among the two groups of cephalopods are thus reflected at the level of their FA signature.

3.4.3 VARIATIONS AMONG ECOLOGICAL SUBSYSTEMS

Results of DFAs on the 47 groups, on the carnivores, and on the crustaceans respectively demonstrated that deep-water species in the NWHI had distinctive FA characteristics. In general, species living at subphotic depths (301-500 m) or on the slope

(51-300 m) exhibited higher levels of 18:1n-9. Deep-water species groups readily distinguishable on the basis of their FA composition included armorheads, beardfishes, cutthroat/snake eels, squirrelfish snappers, pink snappers, flower snappers, shrimps, and duckbills. This interesting pattern should be addressed in future analyses.

3.5 CONCLUSION

The present study clearly demonstrates that despite some existing overlap among FA signatures, differences in the FA composition of diverse fish and invertebrate species inhabiting the NWHI allows groups of closely related and ecologically similar species to be characterized. These differences in FA composition primarily reflect diet, which can also be related to the habitat and ecology of these species. These results are promising as they demonstrate that in spite of tremendous diversity, FA analyses could improve our understanding of the complex network of interactions structuring tropical coral reef ecosystems. These findings also provide the foundation for using the same species groups/FAs in QFASA simulations and diet estimation of a key top predator in this ecosystem, the endangered Hawaiian monk seal. Moreover, the patterns identified in the prey community model will enhance the resolution at which use of the prey base by monk seals can be evaluated, which in turn will be useful in determining seal survivorship limitations in conjunction with tagging and diving studies. Future studies of the prey base should focus on increasing the resolution of these analyses by investigating differences in FA patterns among individual species, and incorporating a higher number of FAs in the analyses, as well as evaluating the effects of species misclassifications in actual estimates of monk seal diets.

CHAPTER 4 QUANTIFYING OVERLAP AMONG ECOLOGICAL GROUPS OF SUBTROPICAL FISHES AND INVERTEBRATES USING QUANTITATIVE FATTY ACID SIGNATURE ANALYSIS (QFASA)

4.1 INTRODUCTION

Understanding the trophic dynamics of complex marine ecosystems containing extreme species diversity represents a huge challenge, as does determining the contribution of a given prey species to a consumer's diet. In recent years, the use of fatty acids (FAs) has significantly expanded as a promising means by which not only trophic relationships can be elucidated but also the integration of different food sources (i.e. prey types and proportions) consumed by a predator can be quantitatively estimated (reviewed in Dalsgaard et al. 2003, Iverson et al. 2004, Budge et al. 2006, Iverson 2009). Because FAs are conserved through food webs, FA trophic markers have long been recognized as powerful tools in studies of marine food webs, where their complexity allows for specific FA patterns to be followed through their incorporation in consumer tissue at different trophic levels (e.g., Budge et al. 2002, Iverson et al. 2002, Dalsgaard & St John 2004). Recent studies have shown that FAs can be successfully used to infer the feeding ecology and trophic relationships of marine fish (Drazen et al. 2009, Stowasser et al. 2009) and invertebrates (Drazen et al. 2008, Silina & Zhukova 2009). However, most of these trophic studies have been focused on fishes and invertebrates belonging to northern/temperate and abyssal food webs, containing a relatively limited number of species. Few studies using FAs have been conducted in tropical or subtropical marine systems (reviewed in Dalsgaard et al. 2003).

The Hawaiian archipelago represents the most remote large-scale subtropical coral reef ecosystem in the world (Maragos & Gulko 2002), and contains an extremely rich and diverse assemblage of fish and invertebrate species. Hence the ability to use FAs to characterize trophic relationships represents a unique challenge. Piché et al. (2010; *see Chapter 3*) conducted an initial investigation of trophic relationships among 100 species of fishes and invertebrates from the Northwestern Hawaiian Islands (NWHI) and Main Hawaiian Islands (MHI) using multivariate techniques such as discriminant function analysis (DFA) and hierarchical cluster analysis. Results showed that the large number of forage species in the NWHI and MHI ecosystem could be reduced into a smaller number of ecologically meaningful species groups, as required for analyses, and that these groups could generally be characterized by their FA profiles, or signatures. Differences in FA signatures were primarily attributed to diet, but also linked to habitat and ecology. For example, FA patterns revealed segregation of species along a depth gradient. However, although roughly 70 FAs are indentified and quantified in such marine samples, only 15 FAs could be used in these studies due to restrictions on the number of variables that can be used in DFA according to the smallest group sample size (n-1). Whether poor classification success found in some species groups could be attributed to using less information (i.e. the small number of FAs used) was not evaluated. Additionally, these types of multivariate statistical analyses are limited in the questions they can be used to answer about the quantitative separation of (prey) species for investigating higher trophic levels.

Quantitative FA signature analysis (QFASA; Iverson et al. 2004) was developed to estimate the diets of predators by determining the proportional mixture of prey species signatures that most closely resembles that of the predator's fat stores after accounting for predator FA metabolism effects. An important feature of the QFASA model was the introduction of prey simulation studies. QFASA simulations were aimed at evaluating prey FA signature overlap in a similar fashion to how QFASA performs actual diet estimation procedures, prior to estimating the predator's diet. Hence simulation studies could potentially be a more powerful quantitative means than techniques such as DFA or cluster analysis for assessing the reliability with which prey can be differentiated or exhibit overlap as used in QFASA, and also allow for a much larger set of FAs to be used in the analyses.

The objectives of this study were to develop a novel use of QFASA simulations as a tool to further investigate trophic relationships and quantify overlaps and distinctions among forage fishes and invertebrates in the Hawaiian archipelago. My aims were to evaluate which number/combination of FAs would allow the best characterization of Hawaiian fish and invertebrate species, to determine how some further species groupings affects QFASA simulation results, and to examine the effects of sequentially removing misclassified species/groups from the simulation set as a means to better understand distinctions and trophic overlap. Through these simulations, I aimed to push the limits of QFASA by testing complex mixtures of selected species across a large number of species groups. The results of such studies will also be of central importance to the eventual application of QFASA to estimating the diets of the critically endangered Hawaiian monk seal (*Monachus schauinslandi*), which is a key top predator in the NWHI ecosystem.

4.2 MATERIALS AND METHODS

4.2.1 SAMPLE COLLECTION

A collection program was established at the NOAA Pacific Islands Fisheries Science Center as part of a study of the diet of the Hawaiian monk seal. Fish and invertebrate species were collected across the eastern end of the NWHI archipelago and the MHI, from 1997 through 2005 (*see* Piché et al. 2010, *Chapter 3*, for details). Specimens were sampled from all habitats, ranging from shallow reefs to deep water talus slopes. At collection, specimens were frozen in airtight plastic bags with detailed records of location and habitat. Frozen samples were stored at -20°C and processed within 6 months. A total of 2,190 specimens representing 100 species was analyzed for this study.

4.2.2 FATTY ACID ANALYSIS

Individual fishes and invertebrates were thawed and measured (fork length or carapace width to the nearest 0.1 cm, body mass to the nearest 0.1 g). Each individual was then homogenized in a food processor. Lipids were quantitatively extracted from each individual specimen in duplicate aliquots using a modified Folch method (Folch et al. 1957, Iverson et al. 2001) and FAs were analyzed using temperature-programmed gas liquid chromatography using a highly polar capillary column (*see* Budge et al. 2002, Iverson et al. 2002, Piché et al. 2010, *Chapter 3*). FAs are named as A:Bn-X, where A is the number of carbon atoms, B is the number of double bonds in the carbon chain, and n-X represents the position of the first double bond relative to the methyl terminal end. FAs are expressed as mean mass percent of total FAs ± SEM.

4.2.3 SPECIES GROUPINGS

The large number of species analyzed (n=100) and the constraints of sample collection that led to small sample sizes for some species (e.g. n=4) required the creation of groups for many analyses and to assure we were not modeling on vastly more species than FAs used in analyses. A grouping procedure was developed and led to the formation of 47 groups (containing 1 to 8 species), based on a range of factors including taxonomy, diet, ecological subsystem, habitat, and commercial interest (Table 4.1; see Piché et al. 2010, *Chapter 3* for details).

4.2.4 QFASA SIMULATION PROCEDURES

The model. The QFASA model (Iverson et al. 2004) involves two components: simulations and modeling (estimation of predator diets). Simulations are a means within the model to first investigate prey FA signature overlap before the actual modeling of the predator takes place, using the same mathematical procedures used in QFASA (statistical software R version 2.6.2). In the basic simulation procedure, a proportional "pseudo" diet of a predator is first specified summing to 1 (or 100%; e.g., 20% species X, 30% species Y and 50% species Z) and from this a pseudo predator signature is created; the model then proceeds as in QFASA by determining what proportional mixture of all species (A through Z) in the prey database yields a FA signature which is closest to the specified pseudo predator signature (Iverson et al. 2004). This tests the ability to estimate a true mixture diet based solely on differentiating and quantifying prey species by their FA signatures. In the present study, I used the combination of pseudo signatures and simulation procedures as a tool to further investigate distinction of FA signatures, trophic relationships, and trophic overlaps across 47 groups of fish and invertebrate species in the subtropical reef ecosystem of the Hawaiian archipelago (Table 4.1). The procedures for each trial (see Fig. 4.1) were as follows:

1. A pseudo signature was created by first specifying a mixture of 4, or 6 species/species groups and the proportion of the signature that each group represents (with all proportions totaling 1).
2. For each species/species group specified above, the sample (e.g. n = 40) of individuals was randomly split into two equal sets: a simulation set (n = 20) and a modeling set (n = 20).
3. The pseudo signature was computed from the simulation set of FA signatures, in the proportions specified for each species/group.
4. This pseudo signature was then fitted on the modeling set of the specified species/groups and all other groups in the database.
5. These procedures (2-4, the splitting into two sets and fitting on the database) were repeated 1,000 times to generate an error measure.

FA selection. Although 65-74 FAs are routinely identified in prey and predators in the NWHI and MHI, not all of these FAs provide information about diet. I thus tested four subsets of FAs in simulations to determine which performed best in differentiating Hawaiian fish and invertebrate species. The first two FA subsets were based on those specified in Iverson et al. (2004): one contained 31 FAs which were strictly dietary in origin (“Dietary” set, D), and the second was comprised of 39 FAs which were derived mostly from diet but could also be biosynthesized to some degree (“Extended Dietary” set, ED; Table 4.2). These FA sets were used as the initial basis for testing species separations. However, given that these analyses would eventually be conducted in parallel with monk seal diet investigations, two additional sets were then tested. A third set of FAs (n=33) was created largely following more recent work in QFASA ("Modified ED 1" set, M1; S.J. Iverson unpublished data). The fourth set of FAs (n=34), was constructed from the ED set, but where FAs with an mean of less than 0.01% mass percent or were routinely zeros in many NWHI and MHI species were removed ("Modified ED 2" set, M2).

4.2.5 SIMULATION TRIALS

A number of trials were conducted to test the effects of the mixture of species groups used in the specified pseudo signature, appropriateness of species groupings, FA subset used, and removal of misidentified species (Fig. 4.2). If no overlap existed in the FA signatures among the groups specified, each species should be identified in simulation results in the proportion originally specified in the pseudo signature. If a species was significantly over- or underestimated, data were further analyzed to determine where the misclassifications occurred (i.e. which species were misclassified as others).

Exploration of species mixtures. Simulation trials were first conducted using five different pseudo signatures (Trials 1-5) which were each created using a mixture of either 4 or 6 groups (selected from the 47 groups specified in Piché et al. 2010, *Chapter 3*) specified in various proportions. The groups used to generate the pseudo signatures as well as the proportion that each group occupied in the species mixes represented a mixture of various fish, cephalopod and crustacean species of importance to the Hawaiian reef ecosystem, and species potentially important to diets of a key predator, the monk seal

(Goodman-Lowe 1998, Goodman-Lowe et al. 1999, Parrish et al. 2000a, Parrish et al. 2002). These pseudo signatures were first analyzed using two FA subsets, D and ED (Table 4.2).

Assessment of species groupings. In the next set of simulations (Trials 6-8), several separate groups of closely related species were combined to evaluate how it would impact the simulation results for species that exhibited poor classification success. In the initial five analyses above, the four species of snappers (*E. carbunculus, L. kasmira, P. filamentosus, P. zonatus*) were considered separately, because some snappers are of significant economical importance and/or because of some differences in their diet and ecology (shallow- versus deep-water species). However, in this set of analyses, all four species were combined into a single “snapper” group. The same procedure was followed for species from two genera of goatfishes (*Mulloidichthys* and *Parupeneus* spp), which were first treated separately but were combined into a single “goatfish” group for this set of simulations trials. These simulations were performed as above using FA subsets D and ED (see Table 4.2). The effect of using a large proportion of snapper or goatfish in the specified pseudo signature (paired with minor amounts of one well-estimated species group) was also investigated to see if simulation results would provide more information on the species/group for which these poorly estimated groups were misidentified.

Evaluation of FA subsets and sequential removal of species groups. To further test the effects of using different FA subsets, this set of simulations used the two pseudo signatures (mixtures of species/groups) which yielded the most accurate estimations from Trials 1 and 3 above, but compared the original results of using the D and ED FA sets with two additional modified FA sets (M1 and M2, Table 4.2). It was previously found (Iverson et al. 2004) that sequentially removing misclassified species arising in pseudo signature estimates and then re-running the model can be quite informative. The newly estimated pseudo signature can then be used to determine which species are substituted for the missing species and therefore allow a deeper understanding of species overlap. Thus, following the first simulations of these two pseudo signatures using four FA subsets, misclassified species groups which represented ≥ 0.02% of the estimated pseudo signature were then sequentially removed. Simulations were re-run after each exclusion to examine whether the estimated pseudo signature would provide further insight into species distinction and overlap.

4.3 RESULTS

The fat content and FA composition (n=39 for the largest FA subset used in analyses) of the 100 species analyzed (n = 2,190 individuals) is presented in Appendix 4.1. The number of species and individuals encompassed in each of the 47 groups are listed in Table 4.1 (see Piché et al. 2010, *Chapter 3*). Tabulated results for the values of all simulation trials are summarized in Appendix 4.2, where the specified pseudo signature is listed for each trial, with the average classification success (i.e. proportions of individuals correctly estimated for each group) across the simulations for each trial. Selected simulation results are presented visually in boxplots (Figs 4.3 and 4.4). In all plots, "a" denotes the proportion specified for each of the prey species groups chosen for the pseudo signature. The box plots indicate the median (middle horizontal bar), the 25th (lower bar) and the 75th (top bar) percentiles of the data distribution (i.e., the box contains 50% of the data). Dots represent outliers, defined as being any value greater (or less) than 1.5 times the interquartile range (75th percentile – 25th percentile) above the 75th (or below the 25th) percentile.

4.3.1 INITIAL SET OF SIMULATIONS: EXPLORATION OF VARIOUS SPECIES MIXTURES

The pseudo signature of **Trial 1** (n = 4 groups) was composed of 0.15 spiny lobster, 0.15 pink snapper, 0.35 moray eel and 0.35 wrasse/hogfish/coris. Spiny lobster, moray eel and wrasse/hogfish/coris were estimated at 72-84%, 91-97% and 65-76% of the levels specified, respectively, (Fig. 4.3a, App. 4.2A). However, pink snapper was poorly estimated, appearing at only 35-45% of specified. Groups not specified in the pseudo signature but appearing in the estimated pseudo signature in significant amounts included primarily scorpionfish, but also toby and tilefish to a lesser extent, as well as trace-minor amounts of other groups.

In **Trial 2** (n = 6 groups)**,** the specified pseudo signature was 0.15 box crab, 0.30 cusk eel, 0.15 flounder, 0.15 flower snapper, 0.15 spiny lobster and 0.10 squid. Box crab (69-89% of specified), cusk eel (80-81%), spiny lobster (73-76%), and squid (86-94%) were all reasonably well-differentiated (App. 4.2A). The flounder group was somewhat underestimated, at 43-63% specified. However, the flower snapper was very poorly estimated at only 10-24% specified. Misidentified groups appearing in the estimated pseudo signature included a mixture of species, but primarily lizard/snakefish, squirrelfish snapper, swimming crab, and duckbill.

The pseudo signature of **Trial 3** (n = 6 groups) was composed of 0.20 parrotfish, 0.15 scorpionfish, 0.15 spiny lobster, 0.15 squirrelfish snapper, 0.30 triggerfish M (*Melichthys niger*), and 0.05 octopus. Parrotfish (88-92% of that specified), scorpionfish

(59-71%), spiny lobster (80-89%), triggerfish M (89-97%), and octopus (68-70%) were all fairly well estimated (Fig. 4.4a, App. 4.2A). However, again the snapper species (squirrelfish snapper) remained poorly differentiated, with only 25-28% correctly estimated. Groups not included in the pseudo signature but represented in the estimated pseudo signature included primarily swimming crab, lizard/snakefish, moray eel, duckbill, and beardfish.

The pseudo signatures simulated in **Trial 4** (n = 4 groups) and **Trial 5** (n = 6 groups) contained the greatest number and percentages of misidentified individuals totaling up to 53% (App. 4.2A). In Trial 4 (0.15 angelfish, 0.35 goatfish M (*Mulloidichthys spp*), 0.35 bluestripe snapper, and 0.15 pebble crab), the angelfish group and goatfish M group were estimated at 79-85% and 62-71% of that specified, while pebble crab was estimated at 58-59% (App. 4.2A). Similar to the other snappers in Trials 1-3, the bluestripe snapper was poorly differentiated at only 12-14% of that specified. In Trial 5, (0.20 butterfly/forcepfish, 0.20 chromis/dascyllus, 0.15 duckbill, 0.15 lizard/snakefish, 0.20 slipper lobster, and 0.10 swimming crab), only the butterfly/forcepfish (74-80% of specified) and lizard/snakefish (61-71%) groups were fairly well-estimated. Poorer differentiation occurred for the chromis/dascyllus (32% of specified), duckbill (48-51%), slipper lobster (43-48%) and especially the swimming crab (7-9% of specified). In both Trials 4 and 5, other crustaceans (lobsters and crabs) were misidentified in proportions that could have accounted for most of the underestimation of pebble crab (Trial 4) and both slipper lobster and swimming crab (Trial 5, App. 4.2A).

4.3.2 SECOND SET OF SIMULATIONS: ASSESSMENT OF SNAPPER AND GOATFISH GROUPINGS

***Snappers*.** The initial set of simulations identified several problematic species/groups in their ability to be differentiated. First, simulation results (Trials 1-4 App. 4.2A) indicated that the four species of snappers (squirrelfish, bluestripe, pink, and flower snapper), represented variously only 10-45% of the specified proportions. This was consistent with results of previous discriminant function analyses (DFAs) conducted on the same 47 groups of species using 15 of the most abundant/variable FAs across all species (Piché et al. 2010, *Chapter 3*), which indicated that *Pristipomoides* snappers in the Hawaiian archipelago exhibit similarities in FA signatures; DFA results showed that pink snappers were consistently misclassified as flower snapper (J. Piché *unpublished data*). In order to determine whether the four snapper species should be grouped together for subsequent simulations, all snappers were combined and considered as one group in this second set of simulations (App. 4.2B).

***Goatfishes*.** Two genera of goatfishes (*Mulloidichthys* and *Parupeneus* spp) were originally considered as two different species groups because of different taxonomy/ecology. However, classification results of previous DFA revealed that individual goatfishes of the two genuses were consistently misidentified as one another (Piché et al. 2010, *Chapter 3, and unpublished data*). In addition, the results of Trial 4 (*Parupeneus* goatfish appeared in the estimated pseudo signature while only *Mulloidichthys* goatfish was specified) suggested that there might be an overlap in the FA signature of the two groups of goatfishes. The two goatfish groups were therefore combined and treated as a single group for this second set of simulations (App. 4.2B).

The pseudo signature in **Trial 6** (n = 4 groups) included the combined snapper and goatfish groups (0.35 each), mixed with two other groups which had performed well in previous simulations: angelfish and moray eel (at 0.15 each). Angelfish and moray eel were again well-estimated at 72-83% and 92-98% of specified, respectively. However, snappers (34-37% of specified) and especially goatfishes (17-27%), each combined as a group, were poorly differentiated (App. 4.2B). Estimates thus remained low and combining groups did not substantially improve results from treating the four snapper species and the two goatfish genera separately.

Trial 7 was constructed to investigate which group(s) the combined snapper group was misclassified for by simplifying the species mixture to only two groups. For this trial, the majority of the pseudo signature specified consisted of the combined snapper group (0.90), with only a small proportion of moray eel (0.10, which was well differentiated in other trials and thus could be expected to have a fairly distinct FA signature). The moray eel was estimated at 81-85% of that specified. While the snappers appeared to be better differentiated at 73% of that specified, this cannot be interpreted as an indicator that snappers are better distinguished as a single group given the proportion of snapper specified in the pseudo signature and the fact that the species "mixture" contained only two species groups. Misidentified species largely indicated overlap among the FA signatures of snappers and the FA signature of other carnivores in the NWHI ecosystem, such as duckbill, lizard/snakefish, sandperch , and beardfish (App. 4.2B).

Trial 8 was constructed in a similar manner as Trial 7 to assess which species/groups the combined goatfish group was getting misclassified for. Goatfish was thus the dominant group in the pseudo signature (0.90), and moray eel occupied the remaining 0.10. The goatfish were estimated at 49-60% of that specified, which remained lower than the 62-71% correctly estimated goatfish M in Trial 4 (App. 4.2A). Moray eels however were underestimated for the first time across all trials, at 24-25% of that specified. Species misidentified in this trial included primarily tilefish and cardinalfish, but also triggerfish S, gurnard, scorpionfish, squirrelfish and bigeye (App. 4.2B).

Overall, combining species groups did not substantially improve their differentiation; if the four species of snappers and/or the two genuses of goatfishes had exhibited overlap in FA signature among themselves, grouping these closely related species should have improved the simulation estimates. Thus I reverted back to considering these as separate species/groups in subsequent trials.

4.3.3. THIRD SET OF SIMULATIONS: EVALUATION OF FA SUBSETS

The first two sets of simulations were conducted using the two sets of FAs (D and ED, Table 4.2) from Iverson et al. (2004) and yielded in general fairly well estimated proportions and differentiation of most major species/groups in simulated pseudo signatures out of all 47 groups. However, some species groups (especially snappers) were consistently underestimated and there were clearly species/groups misidentified. In an attempt to further determine the influence of specific FA sets on the model, and to assess which set would allow the most accurate species separations/estimations, two additional sets of FAs were used in this third set of simulations: the M1 set (n = 34) and M2 set (n = 33; Table 4.2). I used the pseudo signatures from Trials 1 and 3 (App. 4.2A), which yielded the simulation results with the lowest proportion of misclassified individuals to compare all four FA subsets. In both **Trials 9** and **10**, the D and M1 sets yielded the most accurate simulation results, correctly estimating species/groups at an average of 80-83% of that specified, except for the two snappers (only about 30% each) and averaging a total proportion of misclassified individuals of 23-24% (App. 4.2C).

4.3.4 FOURTH SET OF SIMULATIONS: SEQUENTIAL REMOVAL OF SPECIES GROUPS

Given the results of Trials 1-5 (App. 4.2A), and Trials 9 and 10 (App. 4.2C), Trials 1 and 3 and FA sets D and M1 were used in the final set of simulations. In Trial 1, three major groups of misclassified individuals (≥ 2.0%) were identified in the estimated pseudo signature: scorpionfish, toby and tilefish. Thus, in **Trial 11**, these groups were sequentially removed and each time simulations were re-run. The correct estimation of species/groups increased sequentially from an average initially of 71-73% to 75-77% of that specified (Fig. 4.3b, App. 4.2D). Moray eel became overestimated upon the removal of scorpionfish (and subsequently toby and tilefish) but this was accounted for in calculating the overall proportions of correctly estimated individuals reported above. The pink snapper which originally represented 40-45% of that specified remained relatively poorly estimated at 44-49% (App. 4.2D).

The major groups with which misclassifications had occurred in Trial 3 (i.e. swimming crab, lizard/snakefish, moray, duckbill, and beardfish) were sequentially removed in **Trial 12** and through the process, the overall proportion of correctly estimated individuals increased from 70-72% to 83-84% (Fig. 4.4b, App. 4.2D). In this case, the effect of removing misclassified species groups on the outcome of the estimations was evident in certain species specified in the pseudo signature. For example, removing the swimming crab predominantly improved the proportion of correctly estimated spiny lobster (from 81-89% to 93-98%). Similarly, while the removal of lizard/snakefish had already increased the proportion of correctly estimated scorpionfish from 58-70% to 71-80%, the subsequent removal of moray further improved it (from 75-83% to 83-93%). Also, removing both the duckbill and beardfish from the simulation process noticeably augmented the proportion of correctly estimated squirrelfish snappers, which increased from 31-33% to 41-47% upon the removal of the first, and from 44-49% to 53-55% with the removal of the second.

Table 4.1 Summary of groupings of 100 species of Northwestern Hawaiian Islands (NWHI) and Main Hawaiian Islands (MHI) fishes and invertebrates into 47 groups based on taxonomy, diet, and ecological evaluation from the literature (from Piché et al. 2010, *Chapter 3*).

Group	Number of Species	Number of Individuals (n)	Diet guild
1. Angelfish	1	20	Benthic herbivore
2. Cardinalfish	1	18	Planktivore
3. Armohead	1	20	Planktivore
4. Beardfish	1	20	Piscivore
5. Bigeye	2	40	Piscivore
6. Cusk eel	1	20	Piscivore
7. Conger eel	2	46	Piscivore
8. Butterfly/forcepfish	6	134	Benthic carnivore
9. Pennantfish	1	36	Planktivore
10. Cutthroat/snake eel	2	39	Piscivore
11. Sergeant	3	57	Planktivore
12. Chromis/dascyllus	2	41	Planktivore
13. Dragonet	1	20	Benthic carnivore
14. Gurnard	1	24	Benthic carnivore
15. Goatfish (M*)	2	41	Benthic carnivore
16. Goatfish (P**)	4	77	Benthic carnivore
17. Flounder	3	116	Benthic carnivore
18. Lizard/snakefish	3	59	Piscivore
19. Sandperch	1	18	Benthic carnivore
20. Moray eel	7	135	Piscivore
21. Parrotfish	3	60	Benthic herbivore
22. Toby	4	80	Benthic carnivore
23. Chub	2	38	Benthic herbivore
24. Scorpionfish	1	19	Benthic carnivore
25. Squirrelfish snapper	1	21	Benthic carnivore
26. Bluestripe snapper	1	22	Omnivore
27. Pink snapper	1	24	Benthic carnivore
28. Flower snapper	1	19	Omnivore
29. Soldierfish	1	20	Benthic carnivore
30. Squirrelfish	1	21	Benthic carnivore

Table 4.1 *end*

Group	Number of Species	Number of Individuals (n)	Diet guild
31. Tang/surgeonfish	8	154	Benthic herbivore
32. Unicornfish	2	38	Benthic herbivore
33. Tilefish	1	16	Benthic carnivore
34. Knife/razorfish	3	57	Benthic carnivore
35. Triggerfish (M***)	1	20	Planktivore
36. Triggerfish (S****)	1	19	Benthic carnivore
37. Wrasse/hogfish/coris	7	135	Benthic carnivore
38. Octopus	3	40	Benthic carnivore
39. Squid	1	15	Piscivore
40. Shrimp	2	70	Benthic carnivore
41. Box crab	2	59	Benthic carnivore
42. Swimming crab	1	29	Benthic carnivore
43. Pebblecrab	1	21	Benthic carnivore
44. Slipper lobster	2	102	Benthic carnivore
45. Spiny lobster	1	71	Benthic carnivore
46. Boarfish	2	20	Benthic carnivore
47. Duckbill	1	19	Benthic carnivore
Total:	100	2190	

* *Mulloidichthys* spp
***Parupeneus* spp
****Melichthys spp*
*****Sufflamen spp*

Figure 4.1 Graphic depiction of quantitative fatty acid signature analysis (QFASA) simulation studies. In this example, the pseudo signature composition specified was 0.35 moray eel, 0.15 lobster, 0.35 wrasse, and 0.15 pink snapper. For each of these species groups, the individuals sampled are randomly split into equal halves: a simulation set and a modeling set. The pseudo signature is created from the simulation set, and then modeled with the other half of the individuals of those groups and all other species groups in the database (modeling set). The procedures of splitting the specified prey, creating the pseudo signature, and modeling that signature are each repeated 1,000 times for each stipulated diet. This allows for overlap among species groups to be characterized; if there is no overlap, the simulation results will reflect the species group proportions specified in the pseudo signature. See Iverson et al. (2004) for further details.

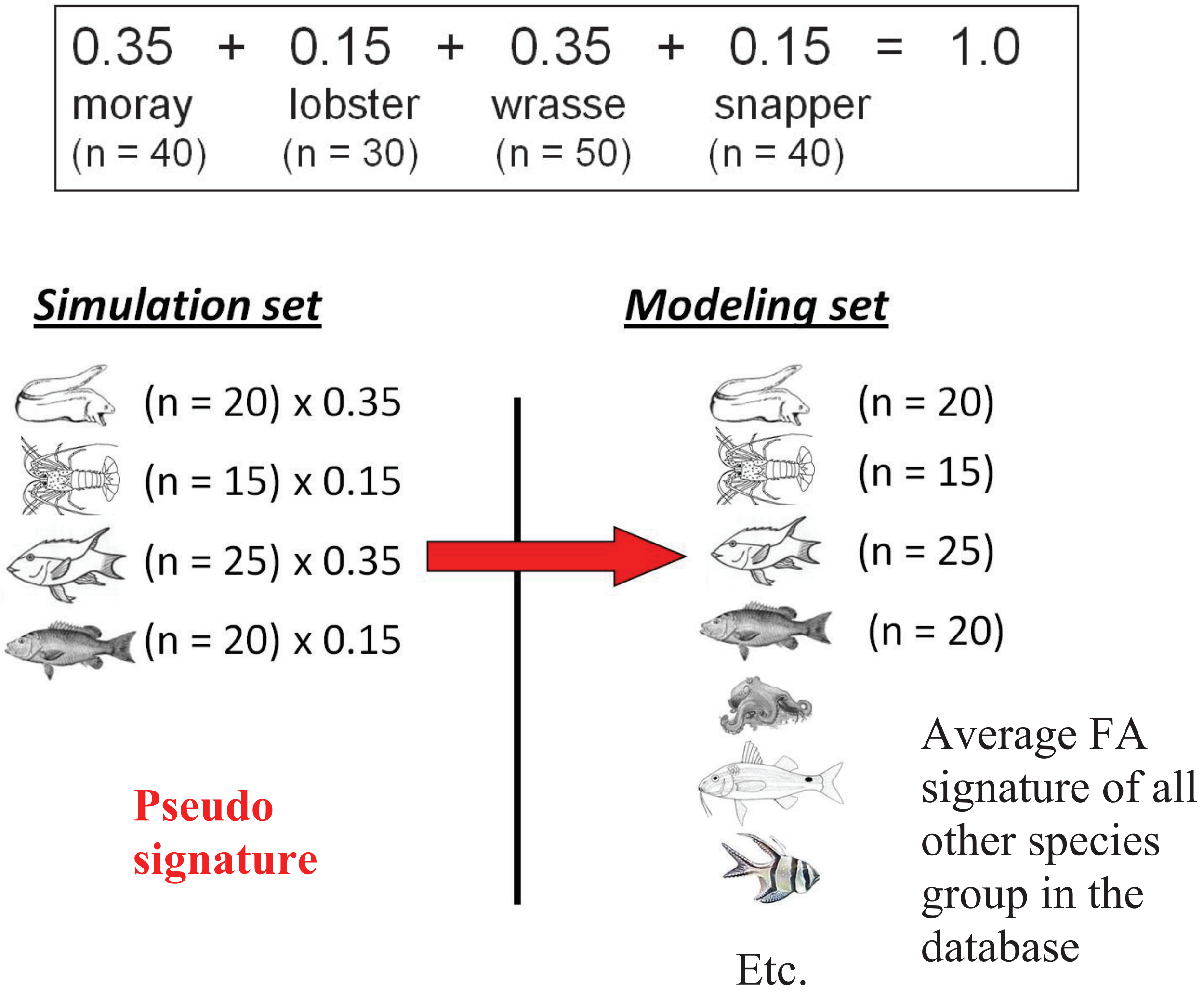

0.35 + 0.15 + 0.35 + 0.15 = 1.0
moray
(n = 40)
lobster
(n = 30)
wrasse
(n = 50)
snapper
(n = 40)
Simulation set
(n = 20) x 0.35
(n = 15) x 0.15
(n = 25) x 0.35
(n = 20) x 0.15
Pseudo signature
Modeling set
(n = 20)
(n = 15)
(n = 25)
(n = 20)
Average FA signature of all other species group in the database
Etc.

Table 4.2 List of all 65 fatty acids (FAs) quantified in fishes and invertebrates in the Northwestern Hawaiian Islands (NWHI) and Main Hawaiian Islands (MHI), and the 4 FA subsets used in simulations. Dietary (D) and extended dietary (ED) subsets were based on those specified in Iverson et al. (2004); modified ED 1 and 2 (M1 and M2) removed or included FAs as described in text.

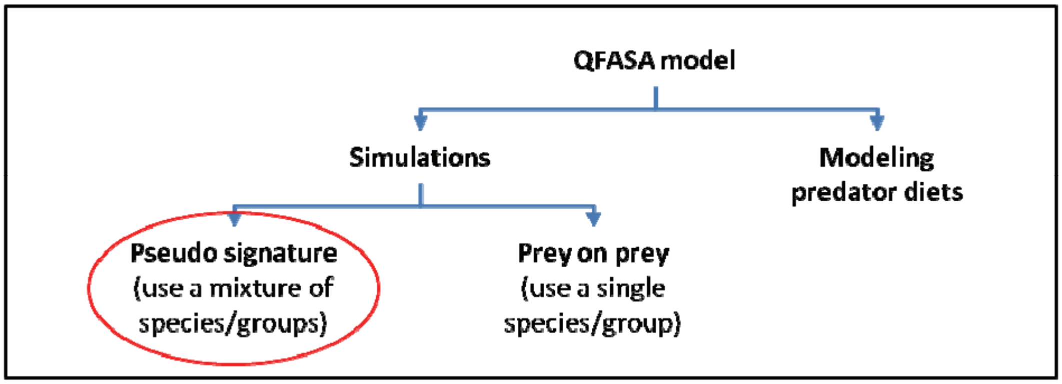
Fatty Acids	**Dietary (D)**	**Extended Dietary (ED)**	**Modified ED 1 (M1)**	**Modified ED 2 (M2)**
12:0				
13:0				
Iso14				
14:0		√	√	√
14:1n-9				
14:1n-7				
14:1n-5				
Iso15				
Anti15				
15:0				
15:1n-8				
15:1n-6				
Iso16				
16:0		√	√	√
16:1n-11				
16:1n-9				
16:1n-7		√		√
7Me16:0				
16:1n-5				
16:2n-6	√	√		
Iso17				
16:2n-4	√	√	√	√
16:3n-6	√	√	√	√
17:0		√		√
16:3n-4	√	√	√	√
17:1				
16:3n-1				
16:4n-1	√	√	√	
18:0		√	√	√
18:1n-13				
18:1n-11				
18:1n-9		√	√	√
18:1n-7		√	√	√
18:1n-5			√	
18:2d511				
18:2n-7				
18:2n-6	√	√	√	√
18:2n-4	√	√	√	√
18:3n-6	√	√	√	√
18:3n-4	√	√	√	√

Table 4.2 *end*

Fatty Acids	**Dietary (D)**	**Extended Dietary (ED)**	**Modified ED 1 (M1)**	**Modified ED 2 (M2)**
18:3n-3	√	√	√	√
18:3n-1	√	√	√	√
18:4n-3	√	√	√	√
18:4n-1	√	√		
20:0				
20:1n-11	√	√	√	√
20:1n-9	√	√	√	√
20:1n-7	√	√	√	√
20:2n-6	√	√	√	√
20:3n-6	√	√		√
20:4n-6	√	√	√	√
20:3n-3	√	√	√	√
20:4n-3	√	√	√	√
20:5n-3	√	√	√	√
22:1n-11	√	√	√	√
22:1n-9	√	√	√	√
22:1n-7	√	√		√
22:2n-6	√	√		
21:5n-3	√	√	√	√
22:4n-6	√	√	√	√
22:5n-6	√	√	√	√
22:4n-3	√	√	√	
22:5n-3		√	√	√
22:6n-3	√	√	√	√
24:1n-9				
Total:	**31**	**39**	**33**	**34**

Figure 4.2 Conceptual chart of quantitative fatty acid signature analysis (QFASA) simulation procedures to assess species differentiation and overlap. Within the QFASA model are two components: simulations and subsequent modeling of predator diets. Modeling is used to estimate the diet of a predator by determining which mixture of prey FA signatures comes closest to matching the signature of a given predator after accounting for metabolism effects. Simulations are used to quantify overlap in FA signatures among the ‘prey’ species themselves prior to modeling, by identifying which species/groups are sufficiently similar that they can be misclassified as one another. Also presented are the various steps undertaken during the present exploratory procedures, aimed at developing the application of QFASA simulations for the study of the ecology and trophic interactions among fishes and invertebrates in the Hawaiian archipelago.

Overview of QFASA Procedures


QFASA model

Simulations

Modeling predator diets

Pseudo signature (use a mixture of species/groups)

Prey on prey (use a single species/group)

Pseudo Signature Simulations: Exploratory Procedures

Which mix of species groups (pseudo signature) performs best in the model?
Five trials conducted with different pseudo signatures , all composed of either 4 or 6 species/groups, and simulated using two sets of FAs.

⬇

Does combining problematic groups improve simulation results?
Some groups of closely related species were consistently poorly represented in the simulation results. To validate species grouping, the effect of combining these groups was explored.

⬇

Which FA set best differentiates NWHI fish and invertebrates?
Simulations were performed using four FA sets (n = 31, 33, 34, 39).

⬇

How does the sequential removal of misclassified groups impact the simulation results?

Figure 4.3 Boxplots of quantitative fatty acid signature analysis (QFASA) simulation results for the pseudo signature of Trial 1 (0.15 Spiny lobster, 0.15 Pink snapper, 0.35 Moray eel, and 0.35 wrasse/hogfish/coris) performed on the 47 species groups using the M1 FA set (n=33); **a.** original simulation results (App. 4.2D, Trial 11; total proportion of misclassified individuals = 23%), **b.** simulation results upon the removal of all major misidentified species/group accounting for ≥2% of the estimated pseudo signature (i.e. Scorpionfish, Toby and Tilefish; total proportion of misclassified individuals = 19%). 1000 iterations. In all plots, "a" denotes the proportion specified for each of the prey species groups chosen for the pseudo signature. Simulation results are represented in the box plots as the median (middle horizontal bar), the 25th (lower bar) and the 75th (top bar) percentiles of the data distribution (i.e., the box contains 50% of the data). Dots represent outliers defined as being any value greater (or less) than 1.5 times the interquartile range (75th percentile – 25th percentile) above the 75th (or below the 25th) percentile.

Figure 4.3 a

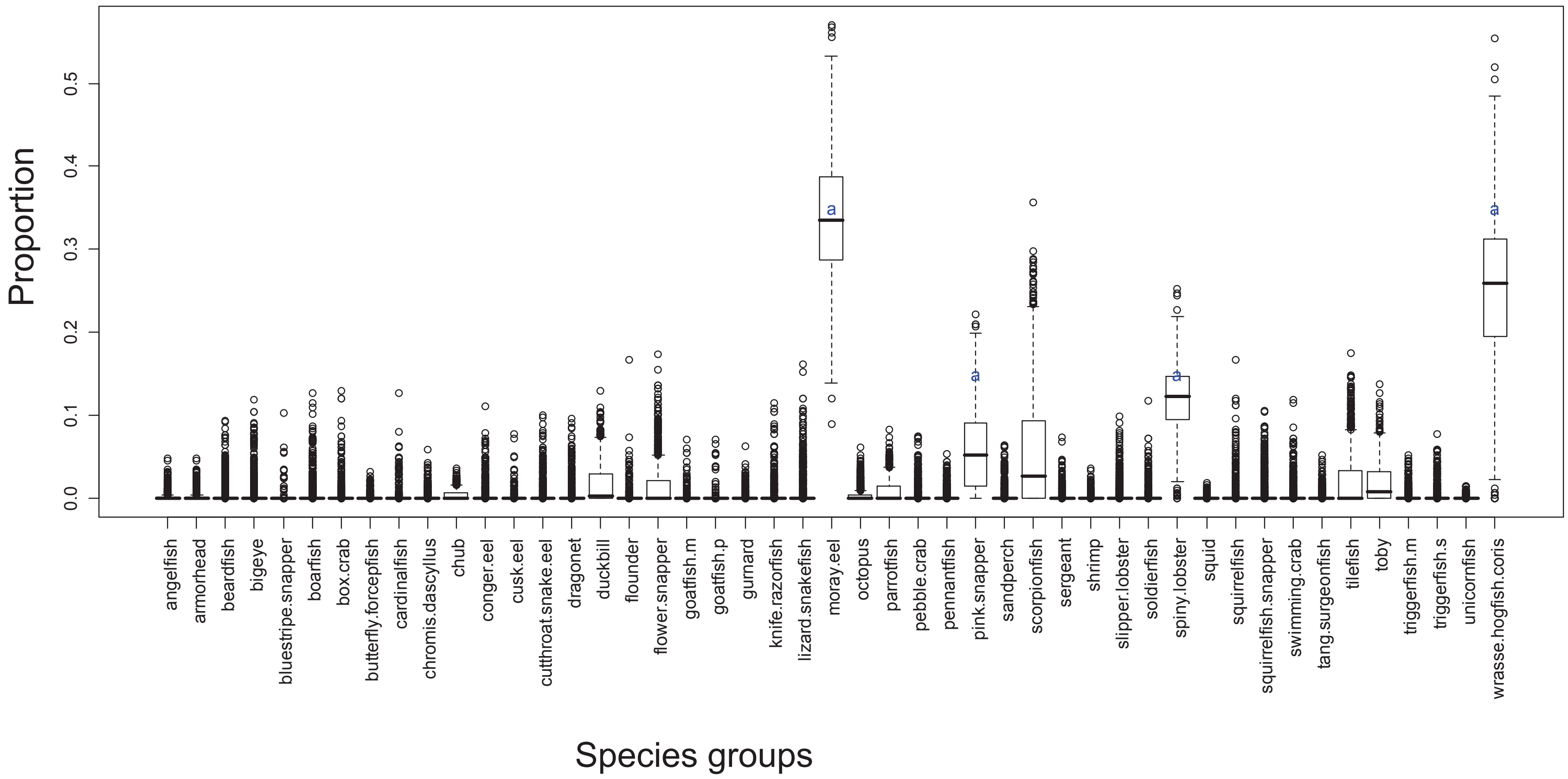
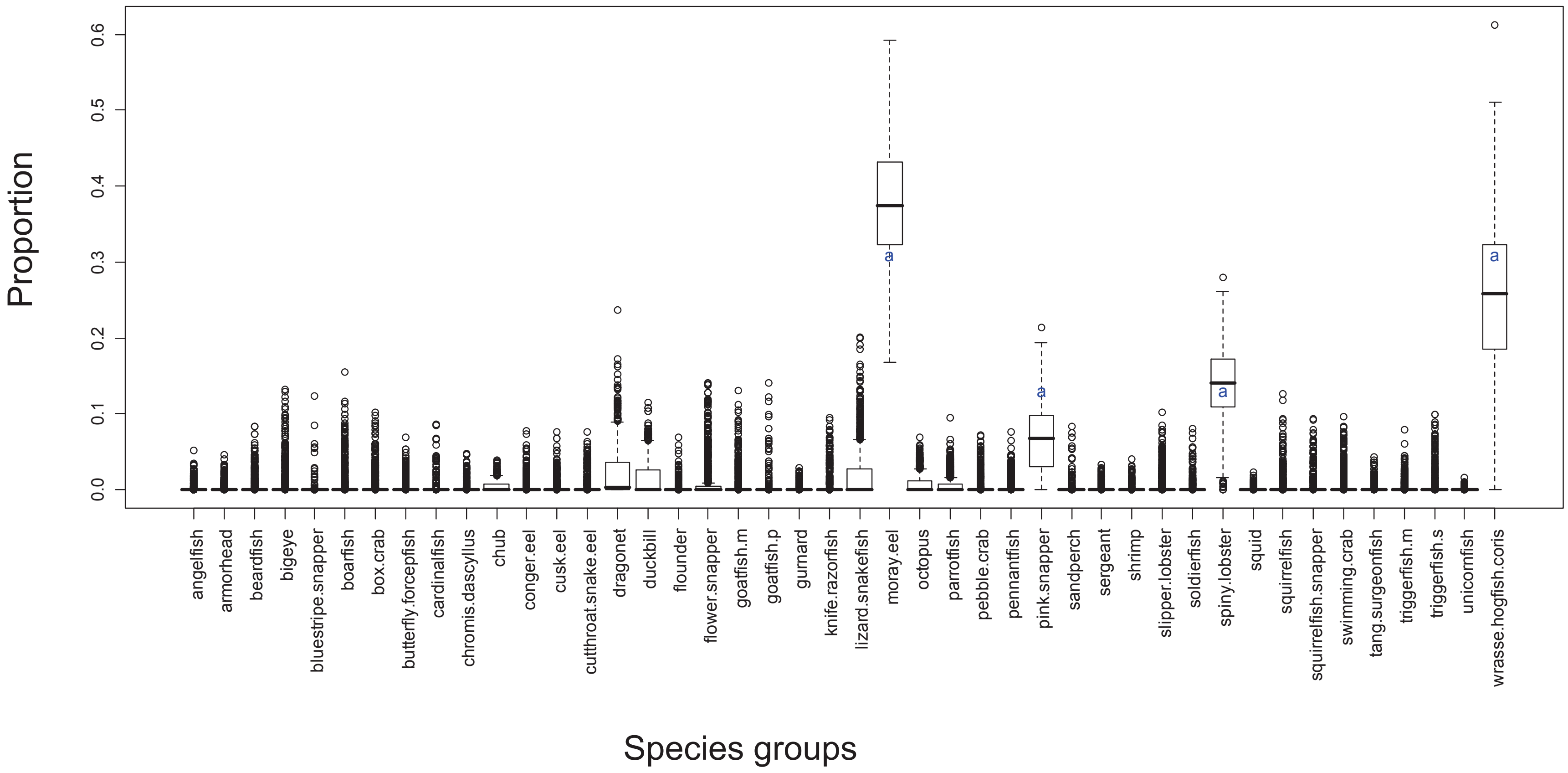

Proportion
0.0
0.1
0.2
0.3
0.4
0.5
a
a
a
a
angelfish
armorhead
beardfish
bigeye
bluestripe.snapper
boarfish
box.crab
butterfly.forcepfish
cardinalfish
chromis.dascyllus
chub
conger.eel
cusk.eel
cutthroat.snake.eel
dragonet
duckbill
flounder
flower.snapper
goatfish.m
goatfish.p
gurnard
knife.razorfish
lizard.snakefish
moray.eel
octopus
parrotfish
pebble.crab
pennantfish
pink.snapper
sandperch
scorpionfish
sergeant
shrimp
slipper.lobster
soldierfish
spiny.lobster
squid
squirrelfish
squirrelfish.snapper
swimming.crab
tang.surgeonfish
tilefish
toby
triggerfish.m
triggerfish.s
unicornfish
wrasse.hogfish.coris
Species groups

Figure 4.3 b


Proportion
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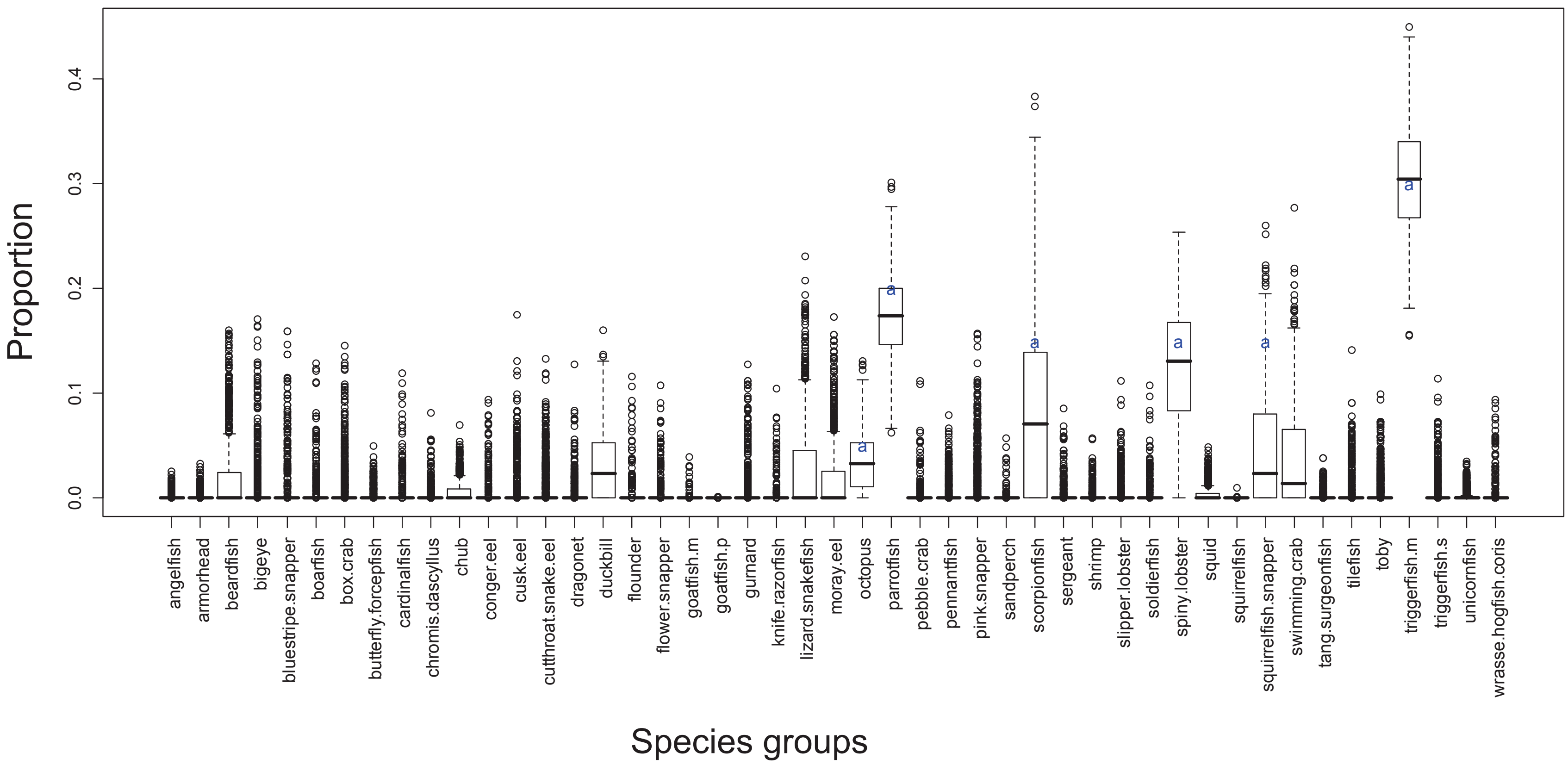
cardinalfish
chromis.dascyllus
chub
conger.eel
cusk.eel
cutthroat.snake.eel
dragonet
duckbill
flounder
flower.snapper
goatfish.m
goatfish.p
gurnard
knife.razorfish
lizard.snakefish
moray.eel
octopus
parrotfish
pebble.crab
pennantfish
pink.snapper
sandperch
sergeant
shrimp
slipper.lobster
soldierfish
spiny.lobster
squid
squirrelfish
squirrelfish.snapper
swimming.crab
tang.surgeonfish
triggerfish.m
triggerfish.s
unicornfish
wrasse.hogfish.coris
Species groups

Figure 4.4 Boxplots of quantitative fatty acid signature analysis (QFASA) simulation results for the pseudo signature of Trial 3 (0.20 Parrotfish, 0.15 Scorpionfish, 0.15 Spiny lobster, 0.15 Squirrelfish snapper, 0.30 Triggerfish M, 0.05 Octopus) using the M1 FA set (n=33); **a.** original simulation results (App. 4.2D, Trial 12; total proportion of misclassified individuals = 24%), **b.** simulation results upon the removal of all major misidentified species/group accounting for ≥2% of the estimated pseudo signature (i.e. Swimming crab, Lizard/snakefish, Duckbill, Moray eel, and Beardfish; total proportion of misclassified individuals = 14%). 1000 iterations. See Fig. 4.3 legend for description of plots.

Figure 4.4 a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tilefish
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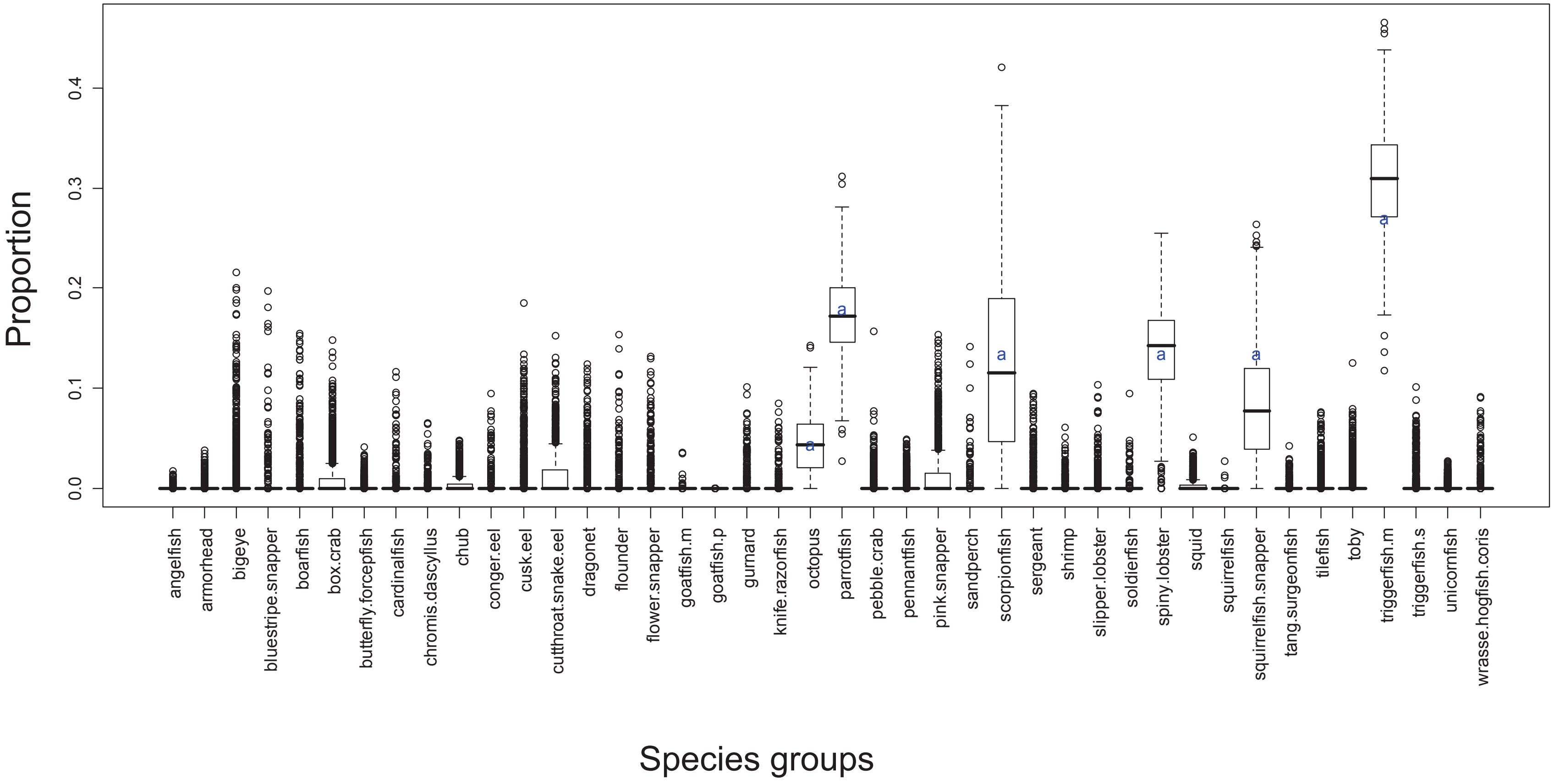
wrasse.hogfish.coris

Figure 4.4 b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squirrelfish.snapper
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Species groups

4.4 DISCUSSION

QFASA was originally developed to allow the quantitative estimation of predator diets, integrated over time, from the FA signatures of their lipid stores and a comprehensive prey database. The aims of the present study were to use QFASA simulations in a novel context as a tool to quantify overlaps and distinctions in the investigation of trophic relationships among groups of forage species. This new application of QFASA represents a departure from the various statistical techniques previously employed (e.g. MANOVA, cluster analyses, and DFA) to analyze and compare FA composition among prey species. The model allows for a wider array of FAs to be used which could potentially provide more refined information on the distinction among species. QFASA simulations could prove to be particularly useful in the study of food webs in complex and remote marine ecosystems such as coral reefs, where sampling logistics remain a challenge, and direct observation often provides an incomplete picture of relationships among species. The present study is, to my knowledge, the first attempt to use QFASA simulations to investigate overlap among FA signatures of such a vast number of species, and interpret the results in the context of the trophic ecology of the species analyzed. While caution must be used in interpreting some of the patterns revealed through the simulation process, comparison of simulation outcomes with the results of previous DFA analyses (Piché et al. 2010, *Chapter 3*) allowed species/groups which are either distinguished well or difficult to differentiate on the basis of their FA signature to be identified, and potential explanations for the observed overlap to be proposed.

***Lutjanidae* (snappers).** Deep-water snappers such as the squirrelfish *E. carbunculus*, pink *P. filamentosus* and flower snapper *P. zonatus* are greatly valued game fishes which have long been commercially exploited in the Hawaiian Islands (Haight et al. 1993a). However, until the introduction of the bluestripe snapper *L. kasmira* in the late 1950s, snappers were completely absent from the shallow reef species assemblages of the Hawaiian archipelago (Morales-Nin & Ralston 1990). *L. kasmira* was long believed to represent a threat to indigenous deep-water snapper populations by dislodging them from their preferred habitat, by feeding on the same resources and even cannibalizing their young (Parrish et al. 2000b). Given the economic and ecological importance of these four snapper species, they were first analyzed separately (App. 4.2A). Similarities in the FA signatures among deep- and shallow-water snapper species would also seem to be counterintuitive considering that prey species assemblages, and consequently the influence of diet on FA signatures, can be expected to differ at depth relative to the shallows. However, all snapper species were poorly identified in the first set of simulations. The effect of combining all four species as a single group was investigated in the second set of trials based on the possibility that while snapper species differ in depth range their prey may not. That is, snappers are considered to be opportunistic benthic predators which consume a wide array of fishes and invertebrates, many of which have broad and potentially overlapping foraging depth ranges (Parrish 1987). However, the proportion of correctly estimated snappers remained very low (34-37%, App. 4.2B Trial 6). Moreover, both deep- and shallow-water species groups appeared as misidentified groups in the simulation results, consistent with overlap mostly occurring among snappers and other fish thriving within the same depth zone (App 4.2B Trial 7). Hence, despite their poor classification success, it was considered most appropriate to continue to treat snapper species separately (App. 4.2A, C, D) .

Simulation results revealed that the FA composition of the bluestripe snapper did not resemble any of the three deep-water snappers, as none arose as a misidentified group in the estimated pseudo signature (App. 4.2, Trial 4). This poor estimation was likely due to similarities in its FA composition with sand-dwelling fishes such as knife/razorfish (Labridae) and sandperch (Pinguipedidae), and with the reef-associated soldierfish (Holocentridae), each of which accounted for > 5% of misclassifications in the estimated pseudo signatures. *L. kasmira* aggregates close to the reef substratum during the day, and disperse over sandy areas at night to forage (Friedlander et al. 2002). Bluestripe snappers feed predominantly on benthic invertebrates, but small fishes and pelagic invertebrates can also be taken (Parrish et al. 2000b). The three species encompassed in the knife/razorfish group (*C. lecluse*, *I. pavo*, *I umbrilatus*), as well as the sandperch *P. schauinslandii,* live in close association with sand bottoms and primarily feed on benthic invertebrates (Froese & Pauly 2010, Randall 1996). Soldierfish (holocentrids) also target invertebrate prey, however some species are bottom feeders while others are known to forage higher in the water column. Hobson (1975) described the soldierfish genus *Myripristis* spp as belonging to the latter category, while Hiatt and Strasburg (1960) reported that some species within that same genus consumed sand-dwelling invertebrates such as polychaetes. The potential FA overlap detected among the bluestripe snapper, the knife/razorfish, the sandperch, and the soldierfish species groups could thus be related to similarities in foraging behaviour and/or diets among their constituent species.

In contrast, the consistently low proportion of correctly estimated individuals for the flower snapper and squirrelfish snapper may be explained by similarities at the level of their FA composition with other deep-water species in this ecosystem. When these two snappers were integrated in the mixtures of species specified in the pseudo signature, other deep-water species such as duckbill (*Bemprops filifera*) and beardfish (*Polymixia berndti*) appeared in the simulation results (e.g. App. 4.2A, Trials 2 and 3). Moreover, upon the sequential removal of these misidentified deep-water species from the simulation process, the proportion of accurately estimated squirrelfish snapper substantially increased (App. 4.2D, Trial 12). Previous FA analyses (Piché et al. 2010) revealed that deep-water species in this ecosystem possess distinctive FA signatures, characterized by high levels of 18:1n-9, which renders them readily distinguishable from other species/groups, across and within trophic levels. Interestingly, although the pink snapper was also routinely underestimated in the simulation trials, its inclusion in the specified pseudo signature did not result in any other deep-water species emerging in the simulation results (App 4.2A, Trial 1). The diet of the pink snapper in this system can be dominated by zooplankton while some of the other deep-water snappers (e.g. squirrelfish snapper) prey mostly on fish (Haight et al. 1993b). Given that 18:1n-9 is a marker of animal productivity, it would thus be less abundant in species feeding at lower trophic levels.

***Mullidae* (goatfish).** Simulation results indicated potential overlap among the two groups of goatfishes, as a small proportion of *Mulloidichthys* goatfishes were wrongfully estimated as being *Parupeneus* goatfishes (App 4.2A, Trial 4). Past DFA results demonstrated that *Mulloidichthys* (yellowstripe *M. flavolineatus* and yellowfin *M.*

vanicolensis) goatfishes were better defined on the basis of their FA composition (using15 FAs) than the closely related *Parupeneus* goatfishes (doublebar *P. bifasciatus,* yellowbarbell *P. chrysonemus,* manybar *P. multifasciatus,* and sidespot *P. pleurostigma*) which were among the species groups most poorly classified (Piché et al. 2010, *Chapter 3*, Table 3.2). In addition, the previous investigations revealed that FA signatures also appeared to be somewhat overlapping as members of the two genera were misclassified for one another. However, combining all goatfishes into a single group drastically lowered the proportion of correctly estimated individuals, from 62-71% (App. 4.2A, Trial 4) to 17-27% (App 4.2B, Trial 6), which confirmed that *Mulloidichthys* and *Parupeneus* goatfishes should be considered separately. It is noteworthy to mention that Trial 8 (0.90 combined goatfish, and 0.10 moray eel) was the only trial in which moray eel was greatly underestimated (24-25% of that specified). Morays are voracious predators of fishes and are known to prey on members of the Mullidae (goatfishes) and Apogonidae (cardinalfishes, i.e., the second most important misidentified group) families (Hobson 1974, Parrish et al. 1986); the large proportion of goatfishes specified in the pseudo signature might have affected their distinction from other species group in this trial.

Sandperch (*Parapercis schauinslandii*) and knife/razorfish (Labridae spp) routinely appeared as major misidentified groups in the simulation results of trials using goatfishes (e.g. App. 4.2A Trial 4 and App. 4.2B Trial 6). Knife/razorfishes were also poorly characterized using 15 FAs in previous DFAs, and a majority of misclassified individuals were classified as *Parupeneus* goatfishes (Piché et al. 2010, *Chapter 3*, Table 3.2). Goatfishes probe the sand in search of prey, while knife/razorfish and sandperch burrow/dive in the sand to escape predation, however all the aforementioned species groups feed primarily on benthic invertebrates living in close association with soft-bottom sediments (Randall 1996, Froese & Pauly 2010). Overlapping signatures among these sand-dwelling carnivores could therefore signify that species thriving on the sandy fields of Hawaiian banks can be harder to differentiate on the basis of FA composition alone, given that they share very similar foraging ecology/diets.

Crustaceans. Crabs and lobsters appeared to exibit various degrees of overlap with one another depending on the species/group, as crustaceans other than the one(s) specified in the pseudo signatures were consistently represented in the simulation results (App. 4.2A, C and D). In addition, the proportion of correctly estimated spiny lobsters (*Panulirus marginatus*) was markedly improved (from 81-89% to 93-98%) upon the removal of swimming crabs (*Charybdis hawaiiensis*) from the simulation process (App. 4.2D, Trial 12). Crustaceans in this ecosystem have recently been shown to possess relatively distinct FA signatures relative to species belonging to other functional groups (i.e. herbivores, planktivores, carnivores, cephalopods; Piché et al. 2010, *Chapter 3*). However, pebble crab (*Carpilius convexus*), spiny lobster, and especially box crabs (*Calappa spp*) were consistently misclassified as other crustaceans foraging on similar benthic prey species (Piché et al. 2010, *Chapter 3*). The results of the present study are consistent with previous results and present additional evidence that Hawaiian decapods sharing similar feeding habits are more difficult to differentiate from one another on the basis of their FA composition.

Planktivores. Across all simulations performed, Trial 5 yielded the poorest proportion of accurately estimated individual (45-48%) which is suspected to be partly due to the inclusion of slipper lobster (*Scyllarides* spp) and swimming crab in the pseudo signature; both groups of crustaceans were poorly differentiated in the simulation (43-48% and 7-9% respectively) and the major misidentified group was spiny lobster (App. 4.2A). However, the chromis/dascyllus group which encompassed planktivorous damselfishes (oval chromis *C. ovalis* and Hawaiian dascyllus *D. albisella*) was also poorly differentiated with on average only 32% of individuals correctly estimated. Interestingly, two other groups of planktivores, the sergeant (*Abudefduf* spp) and pennantfish (*H. diphreutes*), also appeared in the simulation results as major misidentified groups which might be indicative of overlap among planktivorous fishes. Bigeyes (*P. alalaua* and *P. meeki*) also appeared in the simulation results as a misclassified group, and this suggests further evidence that these fishes are indeed planktivores (Randall 1996, Sandin & Williams 2010) and not piscivores as had previously reported (Froese & Pauly 2010).

4.5 CONCLUSION

In the present study, I used QFASA simulations as a novel tool to further investigate trophic relationships among NWHI and MHI fish and invertebrate species, and demonstrated the type of iterations which can be performed to characterize FA distinctions and overlaps among the FA signatures of a wide array of species groups. Most of the species groups analyzed were relatively well estimated, despite the huge complexity of this prey database and ecosystem. However, potential overlap was also detected in some species/groups with similar diet and/or ecology, especially among some deep-water species, among some sand-dwelling carnivores, and among crustaceans. Comparison of simulations results with previous analyses conducted on the same species groups using other statistical methods, as well as using published information on the trophic ecology of Hawaiian fish and invertebrate species, has allowed for a more thorough interpretation of species characteristics and overlaps. These studies also have important implications for studying food web interactions in the subtropical reef ecosystem of the Hawaiian archipelago at higher trophic levels, especially for use in eventually estimating diets of predators such as the critically endangered monk seal.

CHAPTER 5 TROPHIC ECOLOGY OF CARNIVOROUS FISHES FROM THE HAWAIIAN ARCHIPELAGO: INSIGHTS FROM FATTY ACID SIGNATURES ANALYSIS

5.1 INTRODUCTION

Despite persistent research effort brought about by the precarious state of coral reefs in the face of climate change, habitat destruction and fishing pressure, studies of coral reef ecosystems have for the most part targeted shallow water reef communities and/or large conspicuous species which are deemed more relevant from an ecological/economical standpoint (Rooney et al. 2010). There is a vital need to further our knowledge of the processes structuring coral reefs and of the trophic/ecological relationships among their constituent species to better understand the repercussions of overfishing and mortality of keystone species on the ecosystem as a whole. Unfortunately, the tools which can be used to elucidate trophic relationships in such complex and extremely diverse systems are limited, especially as direct observation is rarely possible.

Some of the most promising approaches to understanding food webs in marine and aquatic ecosystems employ the use of various types of biomarkers or trophic tracers, such as fatty acids (FAs) and stable isotopes (e.g. Post 2002, Dalsgaard et al. 2003, West et al. 2006). But while stable isotopes can generally only identify trophic levels, FAs may provide greater resolution and insight into trophic relationships among species (e.g. Iverson 2009). Although FAs constitute the majority of all lipids, only a limited number of FAs can be biosynthesized by animals and the remaining must be obtained through the diet. It is therefore possible to distinguish between dietary and non-dietary FAs. Moreover, ingested FAs remain largely intact through digestion and are consequently conserved through food webs (Dalsgaard et al. 2003, Iverson 2009). This is especially true in marine environments where their complexity and diversity can allow for specific FAs to be followed through their integrations in the tissues of consumers across different trophic levels. The quantitative array of all FAs in the tissue of a consumer, also known as the FA signature, can thus provide a detailed and time integrated picture of its diet.

Recent studies have demonstrated that FAs can be used successfully as a tool to elucidate various aspects of the trophic ecology of mammals (Thiemann et al. 2009), seabirds (Iverson et al. 2007, Williams & Buck 2010), fish (Budge et al. 2002, Iverson et al. 2002, Dalsgaard & St John 2004) and invertebrates (Stowasser et al. 2006, Silina & Zhukova 2009) in a number of marine ecosystems. Spatial, temporal and size-related variations in species FA patterns associated with fluctuations in prey species assemblages and/or ontogenetic changes in diet have been reported, but inter-specific variability generally remains greater than intra-specific variability which has allowed species to be differentiated regardless of their trophic level. Nonetheless, the majority of these FA investigations have been performed on simple to moderately complex food webs in arctic, sub-arctic, and temperate marine systems. In contrast, only a few studies have been performed on the dynamics of FAs in tropical and/or subtropical marine regions (e.g. Saito et al. 1999, Wilson et al. 2001, also reviewed in Dalsgaard et al. 2003). Recently, Piché et al. (2010) explored the FA compositions of coral reef fishes and invertebrates from the Hawaiian archipelago, and demonstrated that differences in FA composition across a broad range of grouped taxa can be primarily attributed to diet, which is also linked to habitat (e.g. depth) and foraging ecology. However, groups of carnivorous fishes were shown to present a higher degree of overlap among FA signatures, which rendered them more difficult to differentiate using a fairly limited number of FAs (n=15). Nevertheless, the degree to which FAs could be used to provide finer scale resolution of trophic relationships among individual species that share close taxonomical relatedness and similar diet guilds has not been investigated.

The Hawaiian archipelago constitutes the most remote large-scale coral reef ecosystem in the world (Maragos & Gulko 2002). Due to the unique geomorphology and bottom topography of the Hawaiian Ridge, the structure of subtropical reef communities and composition of the associated ichthyofauna has been shown to vary across a depth gradient (e.g. Gosline 1965, Chave & Mundy 1994, Friedlander et al. 2010, Rooney et al. 2010). Four distinct ecological depth zones have been defined: shallow reefs (<30 m), banks (30-50 m), slopes (51-300 m) and subphotic depths (301-500 m; Parrish & Abernathy 2006). Within each zone, variations occur at the level of geomorphology, bottom cover, and preponderance of major taxa (Maragos & Gulko 2002). Depth associated changes in reef fish community structure also involve a reduction in fish biomass/diversity with increasing depth, as well as a shift toward carnivory related to the decline of light-dependent primary producer populations supporting herbivorous species (Thresher & Colin 1986). As such, carnivores (which can broadly encompass planktivores, benthic carnivores, and piscivores) are the only functional group that is well-represented across all ecological subsystems. Because of this broad vertical range, the reefs of the Hawaiian archipelago represent an ideal environment to conduct FA studies aimed at investigating distinctions in FA patterns among individual species of carnivorous reef fish, within and across ecological depth zones.

The bulk of the information currently available on the ecology of coral reef fishes mainly focuses on large and/or conspicuous species thriving in the shallows, or species which are or have been exploited commercially at some point in time. Despite supporting an important community of predators, energy flow at depth in coral reef ecosystems is not well-understood. Similarly, small, cryptic, and/or secretive species which constitute an important part of coral reef food webs remain understudied and as such poorly understood (DeFelice & Parrish 2003). The ecological relevance of sand-dwelling populations can be grossly underestimated using visual census techniques (Ackerman & Bellwood 2000, Willis 2001). However, studies in which rotenone is used have revealed a surprisingly rich assemblage of small sand-associated species (< 5 cm, also referred to as cryptobenthic species) which would otherwise have been overlooked (e.g. Smith-Vaniz et al. 2006). FA analyses therefore could potentially assist in improving the current understanding of coral reef benthic food webs.

The objectives of this study were to 1) increase the resolution of FA investigations by performing analyses on individual species of carnivorous fish using a greater number of FAs, 2) compare the FA composition of species sharing similar diet and foraging ecology across ecological depth zones, and 3) explore to what extent carnivorous species living in close association with the sand within the same ecological subsystem can be differentiated on the basis of their FA signatures.

5.2 MATERIALS AND METHODS

5.2.1 SAMPLE COLLECTION

A collection program established by the NOAA Pacific Islands Fisheries Science Center allowed fish and invertebrate species to be sampled across the eastern end of the Hawaiian archipelago, from 1997 through 2005 (see Piché et al. 2010 for detailed descriptions). Collection efforts targeted potential prey species of the critically endangered Hawaiian monk seal (*Monachus schauinslandi*), which have a surprisingly broad vertical foraging range (e.g. Goodman-Lowe et al. 1999, Parrish et al. 2002). This allowed for an extremely diverse array of species to be sampled between the depths of 10-500m; species assemblages of the shallow reefs and banks on the upper slope of the Hawaiian ridge, as well as those of the lower slope extending to subphotic depths, were therefore equally represented. Upon capture, all specimens were frozen in airtight plastic bags with detailed records of location and habitat prior to being shipped to Dalhousie for analysis. Specimens were stored at -20°C and processed within 6 months. A total of 2,190 fish and invertebrate specimens representing 100 species was analyzed through this collection program (see Piché et al. 2010 for FA data on all species). In the present study, I focused on a subset of 25 carnivorous fish species (n= 544 individuals), six of which are endemic to the Hawaiian Islands (*Ariosoma marginatum*, *Dascyllus albisella*, *Gymnothorax steindachneri*, *Callionymus decoratus*, *Cymolutes lecluse*, *Iniistius umbrilatus*). A sample size of 10-26 individuals per species was used to generate the FA signature of each species, with the exception of the Panther flounder (*Bothus pantherinus*) where 75 specimens were used.

5.2.2 FATTY ACID ANALYSIS

Individual fishes were thawed and measured; fork length was measured to the nearest 0.1 cm, and body mass was measured to the nearest 0.1 g. Each whole individual was then homogenized in a food processor. Stomach contents of individuals were not removed prior to homogenization given that we treated them as prey eaten whole by consumers. Lipids were quantitatively extracted from each individual specimen in duplicate aliquots using a modified Folch method (Folch et al. 1957, Iverson et al. 2001); fat content is expressed as the average of the two duplicates. FAs were converted to FA methyl esters by acidic transesterification and analyzed using temperature-programmed gas liquid chromatography according to Budge et al. (2002), and Iverson et al. (2002), on a Perkin Elmer Autosystem II Capillary FID gas chromatograph (GC) fitted with a 30 m x 0.25 mm i.d. column coated with 50% cyanopropyl polysiloxane (0.25 µm film thickness; J&W DB-23; Folsom, CA) and linked to a computerized integration system (Turbochrome 4.1 software, PE Nelson). Identification of FAs and isomers were determined from the following sources: known standard mixtures (Nu Check Prep., Elysian, MN), silver-nitrate (argentation) chromatography, and GC-mass spectrometry. All sample chromatograms and FA identifications were individually examined for accuracy in identification and integration of peak areas, and corrected and reintegrated if necessary. FAs are named as A:Bn-X, where A is the number of carbon atoms, B is the number of double bonds in the carbon chain, and n-X represents the position of the first double bond relative to the methyl terminal end. FAs are expressed as mean mass percent of total FAs ± SEM.

5.2.3 SPECIES SELECTION

Paired foraging equivalents across depth zones. Five subphotic species were identified for investigation: beardfish (*Polymixia berndti*), abyssal eel (*Meadia abyssalis*), snake eel (*Ophichthus kunaloa*), boarfish (*Antigonia eos*), and duckbill (*Bembrops filifera*). The subphotic armorhead *Pseudopentaceros wheeleri* was not used in these analyses due to its unique FA signature and high fat content (~27%), both consequences of an unusual life history spent far outside of the Hawaiian ecosystem, which renders comparison with other species in this ecosystem not meaningful (see Piché et al. 2010 for details). Each of these subphotic species was paired with a shallow reef species (<30 m) with otherwise similar ecology on the basis of the following criteria: diet, foraging habit/behaviour, average size (cm), general morphology, and overall sample size. This allowed for 5 pairs (n = 188 individuals) of ecologically equivalent species living at both ends of the depth gradient to be studied.

Sand-dwelling communities. Sixteen species (n = 376 individuals) were identified as being closely associated with the sand fields of banks (30-50 m) on the peaks of the Hawaiian ridge. These fishes are relatively small (11 cm on average), and some species actively forage for prey by probing the sand, while others are ambush predators lying on or buried in the sand. All species are benthic carnivores/piscivores and most have restricted mobility to render them less easily detectable on the exposed substrate.

5.2.4 STATISTICAL ANALYSES

The FA data for the “paired foraging equivalents across depth zones” and “sand-dwelling” trials were analyzed separately using hierarchical cluster analysis, multivariate analysis of variance (MANOVA), and discriminant function analysis (DFA). All data analyses were performed using SPSS version 11.5 (SPSS Inc., Chicago IL) and R version 2.6.2. Hierarchical cluster analyses were conducted to investigate how individual species in both trials would be situated relative to one another on the basis of selected FA subsets; an agglomerative method was used to compute the average linkage between species through an Euclidean distance measure. DFAs were performed to assess which FAs accounted for most of the variance in the separation of individual species on the first two discriminant functions. Wilk's Lambda was used to assess the power of the discrimination among species; the smaller the value, the more significant the difference. The percent of cases accurately classified into their assigned species were used to evaluate the performance of the classification function, and the classifications were cross-validated using leave-one-out cross validation procedure. Quantitative FA signature analysis (QFASA) simulations (see below) were subsequently performed to further investigate patterns and overlap among individual species.

FA subsets. To comply with the requirements of the statistical method used (n-1 of smallest sample size), as well as to make use of the greater flexibility of the QFASA model which allows for a higher number of FAs to be incorporated in the analyses, three different FA subsets were used in this study: the large extended dietary set (n=39; from Iverson et al. 2004) was used in all QFASA simulations, which encompassed FAs that are strictly or mostly dietary in origin and which exhibited the greatest abundance/variance across all species analyzed. Given the requirements for reduced FAs used in DFA analyses, the extended dietary subset 1 (EDS1, n=15) was used in the "sand-dwelling" DFA, and the extended dietary subset 2 (EDS2, n=10) was used in the "paired foraging equivalents across depth zones" DFA (Table 5.1), based on the appropriate number of FAs that exhibited the greatest abundance/variance. On average, the selected FAs accounted for 93, 87, and 82 mass% of the total FAs identified for the extended dietary set, EDS1, and EDS2 respectively.

Prior to cluster and DFA analyses, percentage values for FAs were transformed into log ratios (*see* Budge et al. 2002 and Iverson et al. 2002): the values for the 10 (or 15) FAs were first re-normalized over 100%, then each re-normalized value was divided by the value for 18:0 (a reference FA). Given that the log of zero cannot be taken, a value of 0.005% was added to any zero values, the ratios were log transformed, and the resulting log ratios were used in DFA.

5.2.5 QFASA SIMULATIONS

Simulations were performed on the "paired foraging equivalents" and "sand-dwelling" species separately using the 39 FAs (Table 5.1). In QFASA simulations (conducted using R), the FA signature of a subset of a given species is compared across the signatures of its other subset and all the other species selected for the simulation, to estimate the degree to which individual species are correctly estimated as themselves against all other species investigated. First, the tested species sample is randomly split into two halves of equal sample size: set A and set B. The average FA signature of set A is then fitted on the average FA signature of set B and all other species using the QFASA model. This simulation procedure is repeated 500 times to generate an error measure, and the splitting process (each individual species divided equally into set A and set B) is repeated for each iteration. If a species has a distinct FA signature, it would be 100%

correctly estimated as itself in the simulation results. However, if the species is poorly estimated and other species are instead identified in substantial proportions (e.g. ≥ 5%) in the simulation results, this would indicate overlap in FA signatures with those species. These potential overlaps were then examined further to determine whether they could be related to similarities in diet and/or ecology, or whether some species could be feeding on others.

5.3 RESULTS

The fat content and FA composition (FA used in the analyses; mean ± SEM) of the 25 fish species analyzed (n=564 individuals) are presented in Appendix 5.1. The parameters used to create five pairs of ecologically equivalent deep versus shallow water fish are listed in Appendix 5.2. The key ecological/behavioural traits unifying or differentiating the 16 sand-dwelling species analyzed are detailed in Appendix 5.3. To compare DFA and simulation results more directly, results for both type of analyses have been tabulated together.

5.3.1 PAIRED FORAGING EQUIVALENTS ACROSS DEPTH ZONES

Hierarchical cluster analysis. The 10 FAs clearly separated the 10 species into two major nodes: shallow versus deep water species (Fig. 5.1). Within the shallow-water node, the dascyllus and goatfish were separated from the other species, while the two moray eels associated more closely together and with the lizardfish. Within the deep-water node, boarfish was isolated from all other species, and the two species of eels (abyssal and snake eel) were also tightly associated to one another. None of the paired species were closely associated.

Discriminant function analysis. DFA performed on the 10 species using 10 FAs generated nine significant discriminant functions (Wilk's Lambda 0.000, $p < 0.001$) and individual species were separated with 90% of cross-validated group cases correctly classified (Table 5.2). The two FAs which accounted for most of the variance on the first two discriminant functions were 18:1n-9 and 16:0. Species were spatially distributed into 3 clusters: the three morays/goatfish, the three dascyllus/lizardfish/boarfish, and the remaining four deep-water species (Fig. 5.2). The dashed lines connect each shallow water species to their deep-water analogue (contained within the ellipse, except for the boarfish; Fig. 5.2). The dascyllus *D. albisella* and the boarfish *A. eos* were the only (shallow/deep) pair that associated more tightly on the first two functions. The remaining four deep-water species were spatially separated from their corresponding shallow-water species. Abyssal eel and boarfish were 100% correctly classified. Of the remaining species, five had ≥90% of individuals accurately classified: duckbill, lizardfish, snake eel, beardfish, goatfish (Table 5.2). The large moray eel *G. steindachneri* had a classification success of 84% with 3 individuals (total 25) misclassified as *G. eurostus*, a smaller species of moray. Conversely, 1 (of 14) *G. eurostus* moray was misclassified as *G. steindachneri*. The lowest classification success was for the dascyllus (80%) where 4 of 20 individuals were misclassified as lizardfish *S. lobeli*.

The 10 FAs used in the analyses varied significantly across the 10 species (Wilk's Lambda 0.000, Tukey HSD post hoc test, $p < 0.001$). The FA which accounted for most of the variance (55.7% of total variance) on the first two DFA functions was 18:1n-9.

With the exception of the boarfish *A. eos*, all deep-water species had high levels of 18:1n-9, ranging from 14.5% in the duckbill to 20% in abyssal eel; this is approximately twice as much as found in shallow-water species at 8% on average. In the case of the boarfish however, the level of 18:1n-9 (i.e. 9%) was more easily comparable to levels in shallow water species. The goatfish *M. flavolineatus* had the lowest proportion of 18:1n-9 of all species at 6%. The second most important FA in the separation of the 10 species was 16:0, which accounted for 19.8% of the total variance. The dascyllus *D. albisella* had on average high levels of 16:0 (28.7%) relative the other 4 shallow water species (~19%) and the 5 deep-water species (also ~19%). The morays and goatfish all exhibited higher levels of 20:4n-6 (~9%), relative to the other shallow-water species (~5%), and deep-water species (~3%).

Simulations. QFASA simulations performed using 39 FAs demonstrated that most of the species analyzed were reliably identified as themselves on the basis of their FA composition: > 80% individuals were correctly estimated in seven out of ten species (Table 5.2). The beardfish *P. berndti* yielded the lowest proportion of correctly estimated individuals (57%). This is somewhat surprising considering that 90% of the beardfish were accurately classified in the DFA previously performed using 10 FAs (Table 5.2). In the simulations, 30% of misclassified beardfish were identified as abyssal eel (*M. abyssalis*), another deep-water species. The smaller moray species (*G. eurostus*) had 68% of individuals accurately estimated, with 16% of the misclassified individuals identified as the larger species from the same genus *G. steindachneri*, and 5% as the goatfish *M. flavolineatus*. While the proportion of correctly classified *G. eurostus* was higher in the DFA (86%), misclassifications occurred among the same species (i.e. larger moray and goatfish). The classification success of the abyssal eel *M. abyssalis* decreased from 100% in the DFA to 79% of individuals correctly in the simulations. However, all misclassified individuals were categorized as other deep-water species: 8% beardfish, and 6% snake eel.

5.3.2 SAND-DWELLING COMMUNITIES

Hierarchical cluster analysis. The 15 FAs separated the 16 individual sand-dwelling species into 3 main nodes (Fig. 5.3). In general, species belonging to the same genus (e.g. *Synodus* spp, *Iniistius* spp) were more closely associated with one another, with the exception of the flowery flounder (*Bothus mancus*) which separated from the two other *Bothus* spp and belonged to an entirely different node.

Discriminant function analysis. DFA performed on the 16 species using 15 FAs generated 14 significant discriminant functions (Wilk's Lambda 0.516, $p < 0.001$), and yielded a cross-validated classification success of 82% (Fig. 5.4). The two FAs accounting for most of the variance on the first two discriminant functions were 22:4n-6 and 18:1n-9. Most species with a flatfish body form (i.e. 7 out of 9 species) clustered together on the plot of the first two discriminant functions, with the exception of the flowery flounder *B. mancus* and the dragonet *C. decoratus* (Fig. 5.4). Species with an eel or fish body form (i.e. 5 out of 7 species) were also more tightly associated with one another, except for the puffer *T. florealis* and the tilefish *M. breviostris,* which appeared to be spatially distinct from all other species. Overall, ≥ 80% individuals were correctly classified in half of the species (Table 5.3). The one species with a very poor classification success (27%) was the lizardfish *Iniistius pavo*. However, 33% of misclassified individuals were classified as *I. umbrilatus*, another species of the same genus.

The 15 FAs used in the DFA varied significantly across the 16 sand-dwelling species analyzed (Wilk's Lambda 0.000, Tukey HSD post hoc test, $p < 0.001$). The FA 22:4n-6 explained most (31.2%) of the variance on the first discriminant function despite accounting for only ~1% of total lipids in most species. However, four species exhibited higher levels of 22:4n-6: *T. florealis* (puffer) 1.9%, *B. mancus* (flounder F) 2.2%, *C. decoratus* (dragonet) 2.4%, and *M. brevirosis* (tilefish) 4.5%. These four species also contained higher levels of 20:4n-6 (puffer = 8%, dragonet = 9%, tilefish and flounder F both = 10%), which accounted for approximately 5% of total lipids in the other species. Dragonet and tilefish also had the lowest levels of 18:1n-9 at 6% and 7% respectively versus 9% on average in other species.

Simulations. Half of the 16 species performed well in QFASA simulations conducted using 39 FAs, with ≥ 80% individuals correctly estimated (Table 5.3). While *I. pavo* (razorfish P) remained the most problematic species with 53% of individuals accurately estimated, it performed better in the simulation than in the DFA using 15 FAs (27% individuals correctly classified). However, misclassifications consistently occurred among the same species in both statistical analyses: *I. umbrilatus* (razorfish U), *C. lecluse* (knifefish), and *T. myops* (snakefish). Similarly, in the lizardfish *S. variegatus*, misclassifications occurred as snakefish in both DFA and simulations (Table 5.3). Overall, performing simulations using 39 FAs yielded an improved classification success for four species: *B. mancus* (flounder F, ↑ 10%), *D. orientalis* (gurnard, ↑ 10%), *I. pavo* (razorfish P, ↑ 20%), and *S. lobeli* (lizardfish L, ↑ 10%). However, it significantly decreased the proportion of correctly estimated individuals by ~20% for *M. brevirostris* (tilefish) and *S. variegatus* (lizardfish V), and by ~10% for *C. decoratus* (dragonet) and *T. florealis* (puffer).

Table 5.1 List of all 65 fatty acids (FAs) quantified in the signature of Hawaiian reef fishes, and of the 3 FA subsets used in the analyses; the extended dietary set was used in all QFASA simulations, the extended dietary subset 1 (EDS1) was used in the "sand-dwelling communities" DFA, and the extended dietary subset 2 (EDS2) was used in the "paired foraging equivalents" DFA.

Fatty Acids	Extended Dietary Set	Extended Dietary Subset 1	Extended Dietary Subset 2
12:0			
13:0			
Iso14			
14:0	√	√	√
14:1n-9			
14:1n-7			
14:1n-5			
Iso15			
Anti15			
15:0			
15:1n-8			
15:1n-6			
Iso16			
16:0	√	√	√
16:1n-11			
16:1n-9			
16:1n-7	√	√	√
7Me16:0			
16:1n-5			
16:2n-6	√		
Iso17			
16:2n-4	√		
16:3n-6	√		
17:0	√	√	
16:3n-4	√		
17:1			
16:3n-1			
16:4n-1	√		
18:0	√	√	√
18:1n-13			
18:1n-11			
18:1n-9	√	√	√
18:1n-7	√	√	√

Table 5.1 *end*

Fatty Acids	Extended Dietary Set	Extended Dietary Subset 1	Extended Dietary Subset 2
18:1n-5			
18:2d511			
18:2n-7			
18:2n-6	√	√	
18:2n-4	√		
18:3n-6	√		
18:3n-4	√		
18:3n-3	√		
18:3n-1	√		
18:4n-3	√		
18:4n-1	√		
20:0			
20:1n-11	√		
20:1n-9	√	√	
20:1n-7	√		
20:2n-6	√		
20:3n-6	√		
20:4n-6	√	√	√
20:3n-3	√		
20:4n-3	√		
20:5n-3	√	√	√
22:1n-11	√		
22:1n-9	√		
22:1n-7	√		
22:2n-6	√		
21:5n-3	√		
22:4n-6	√	√	
22:5n-6	√	√	
22:4n-3	√		
22:5n-3	√	√	√
22:6n-3	√	√	√
24:1n-9			
Total:	**39**	**15**	**10**

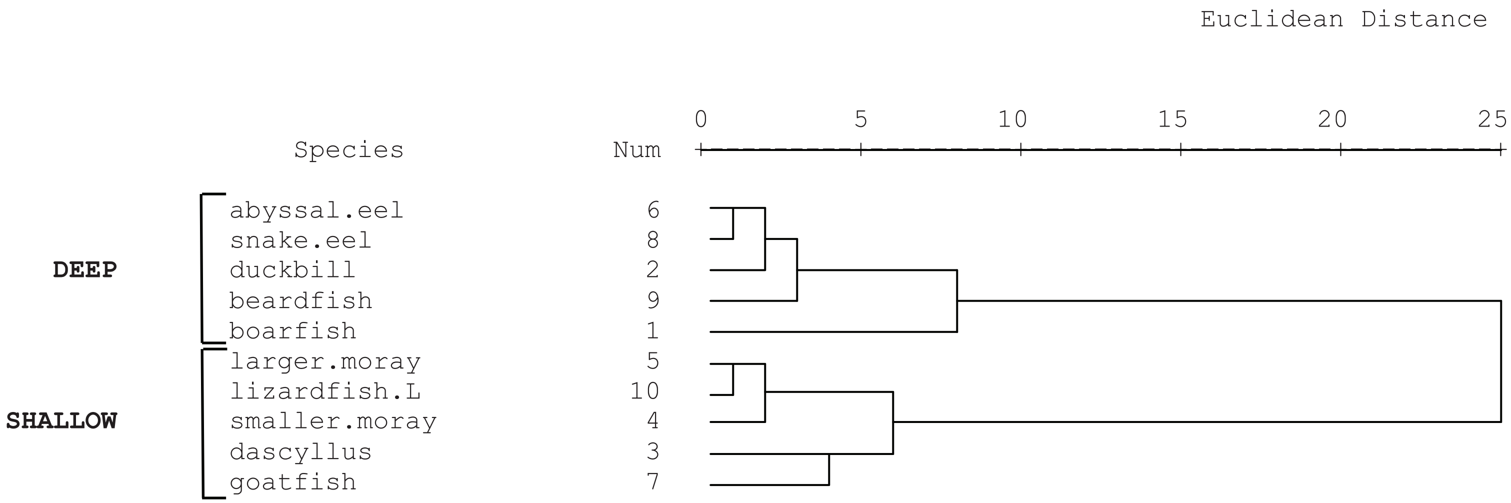
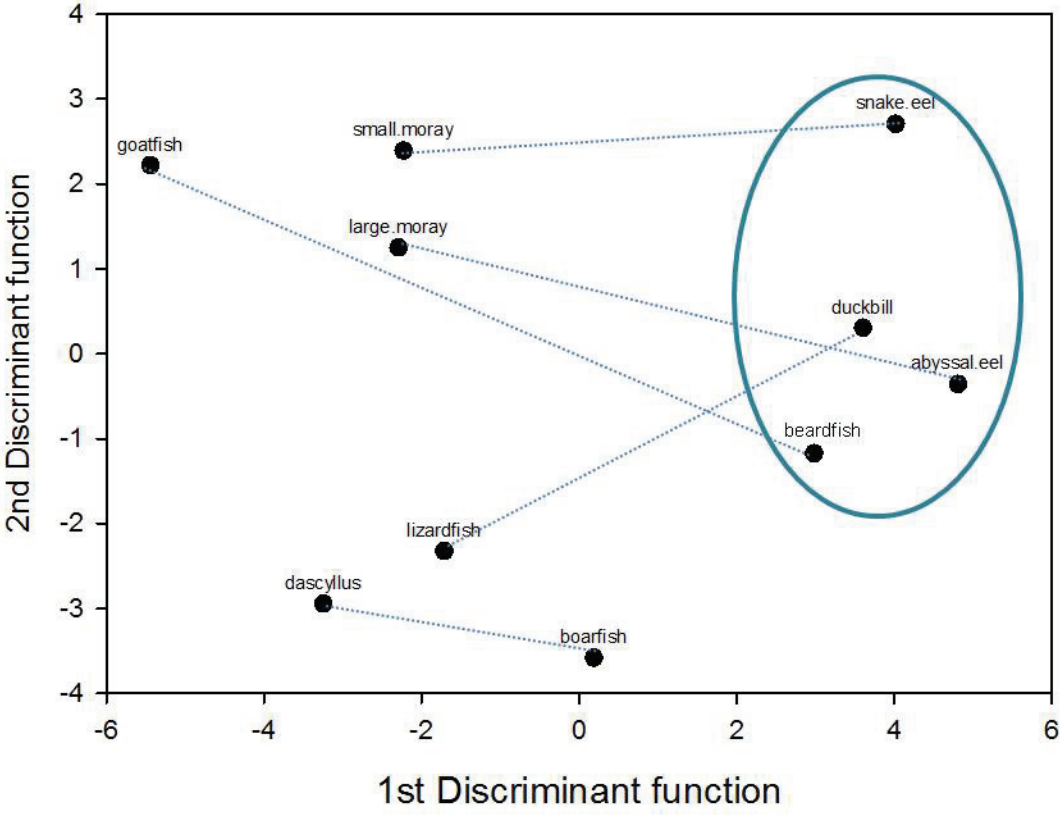


Figure 5.1 Hierarchical cluster dendrogram of the degree of similarity in the fatty acid composition of the 10 species used in the paired ecological equivalents analyses. Species (see Appendix 5.2 for sample size) were separated into two major nodes: the shallow (reef, < 30 m) versus deep water (subphotic, 301-500 m) species. Each node (left to right) was nested into the next, from the most to the least similar. boarfish = *A. eos*, duckbill = *B. filifera*, dascyllus = *D. albisella*, small.moray = *G. eurostus*, large.moray = *G steindachneri*, abyssal eel = *M. abyssalis*, goatfish = *M. flavolineatus*, snake eel = *O. Kunaloa*, beardfish = *P. berndti*, lizardfish.L = *S. lobeli*.

Table 5.2 Discriminant function analysis (DFA) and simulation results for the paired foraging equivalents across depth zones investigations. Results of DFA performed on 10 species (total n=188) using 10 fatty acids (FAs, see Table 5.1); misclassifications (%, species) that accounted for ≥ 5% of the number of individuals are listed for each species. Results of quantitative fatty acid signature analysis (QFASA) simulations performed using 39 FAs (see Table 5.1); misclassifications (%, species) that accounted for ≥ 5% of the number of individuals estimated are listed for each species.

	DFA (10 FAs)		**Simulation (39 FAs)**	
Species	**Correctly classified**	**Misclassified (≥ 5%)**	**Correctly estimated**	**Misclassified (≥ 5%)**
Deep				
Antigonia eos (boarfish)	100%		92%	
Bembrops filifera (duckbill)	95%	5% *M. abyssalis*	83%	6% *O. kunaloa*, 5% *S. lobeli*
Meadia abyssalis (abyssal eel)	100%		79%	8% *P. berndti*, 6% *O. kunaloa*
Ophichthus kunaloa (snake eel)	90%	5% *P.berndti*, 5% *B. filifera*	86%	6% *M. abyssalis*
Polymixia berndti (beardfish)	90%	5% *M. abyssalis*, 5% *B. filifera*	57%	30% *M. abyssalis*, 8% *S. lobeli*
Shallow				
Dascyllus albisella (dascyllus)	80%	20% *S. lobeli*	85%	5% *A. eos*
Gymnothorax eurostus (smaller moray)	86%	7% *G. steindachneri*, 7% *M. flavolineatus*	68%	16% *G. steindachneri*, 6% *D. albisella*, 5% *M. flavolineatus*
Gymnothorax steindachneri (larger moray)	84%	12% *G. eurostus*	90%	
Mulloidichthys flavolineatus (goatfish)	91%	9% *D. albisella*	89%	5% *D. albisella*
Synodus lobeli (lizardfish)	91%	9% *D. albisella*	90%	

Figure 5.2 Discriminant function analysis (DFA) of fatty acid (FA) signatures among paired ecological equivalents across depth zones. Group centroids (within group mean for each discriminant function) for the first and second (of 9 significant) discriminant functions, which accounted for 75.5% of total variance for DFA performed on the 10 species (n = 188; see Appendix 5.2 for species sample sizes) using the 10 FAs that exhibited the greatest average variance, abundance, and reflection of diet. The dashed lines connect the deep-water species to their shallow-water analogue. The ellipse encompasses all deep-water species, with the exception of the boarfish. Species names: boarfish = *A. eos*, duckbill = *B. filifera*, dascyllus = *D. albisella*, small.moray = *G. eurostus*, large.moray = *G steindachneri*, abyssal eel = *M. abyssalis*, goatfish = *M. flavolineatus*, snake eel = *O. Kunaloa*, beardfish = *P. berndti*, lizardfish.L = *S. lobeli*.


snake.eel
small.moray
goatfish
large.moray
duckbill
abyssal.eel
beardfish
lizardfish
dascyllus
boarfish
4
3
2
1
0
-1
-2
-3
-4
2nd Discriminant function
-6
-4
-2
0
2
4
6
1st Discriminant function

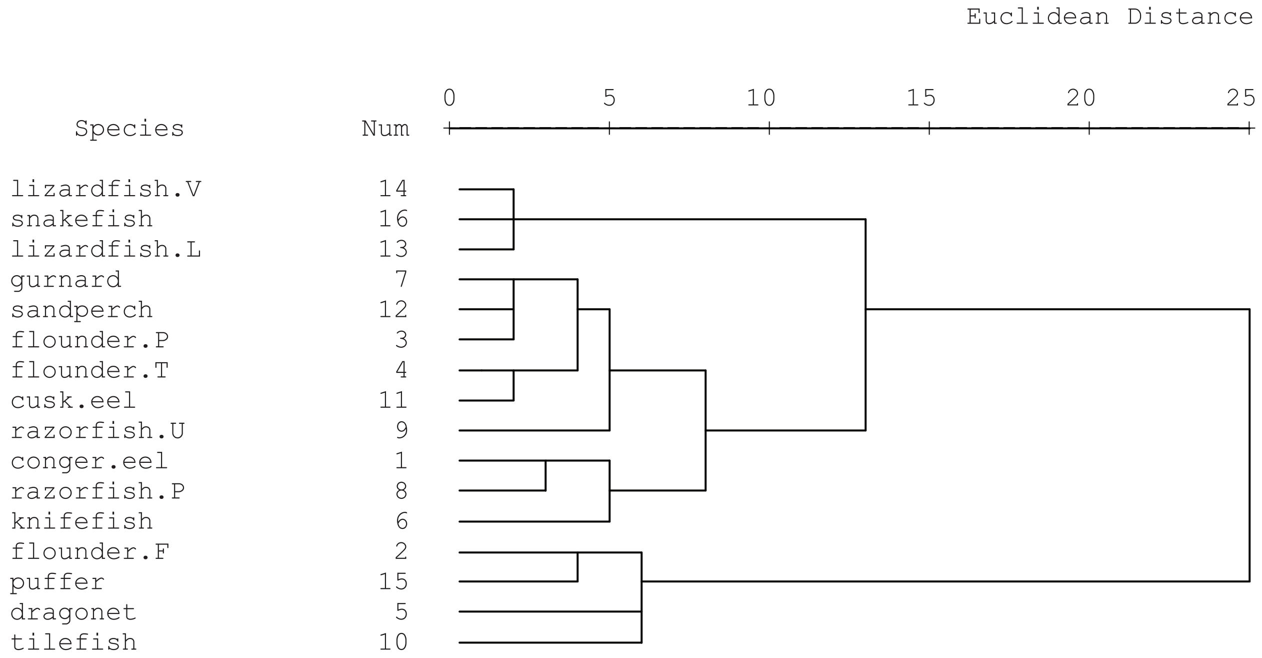


Figure 5.3 Hierarchical cluster dendrogram of the degree of similarity in the fatty acid (FA) composition of the 16 sand-dwelling species analyzed (see Appendix 5.3 for species sample sizes). Each node (left to right) was nested into the next, from the most to the least similar. Species names: conger eel = *A. marginatum*, flounder F = *B. mancus*, flounder P = *B. pantherinus*, flounder T = *B. thompsoni*, dragonet = *C. decoratus*, knifefish = *C. lecluse*, gurnard = *D. orientalis*, razorfish P = *I. pavo*, razorfish U = *I. umbrilatus*, tilefish = *M. brevirostris*, cusk eel = *O. Muraenolepsis*, sandperch = *P. schauinslandi*, lizardfish L = *S. lobeli*, lizardfish V = *S. variegatus*, puffer = *T. florealis*, snakefish = *T. myops*.

Figure 5.4 Discriminant function analysis (DFA) of fatty acid (FA) signatures among 16 species of carnivorous sand-dwelling fishes. Group centroids (within group mean for each discriminant function) for the first and second (of 14 significant) discriminant functions, which accounted for 50.9% of total variance for DFA performed on 16 sand-dwelling species (n = 376; see Appendix 5.3 for species sample sizes) using the 15 FAs that exhibited the greatest average variance, abundance, and reflection of diet. The blue ellipse at top right identifies 7 of 9 species with a flatfish body type (except flounder F and dragonet) and the red ellipse at the bottom right of the plot encompasses 5 of 7 species with a fish (except puffer and tilefish) or eel body type. Species names: conger eel = *A. marginatum*, flounder F = *B. mancus*, flounder P = *B. pantherinus*, flounder T = *B. thompsoni*, dragonet = *C. decoratus*, knifefish = *C. lecluse*, gurnard = *D. orientalis*, razorfish P = *I. pavo*, razorfish U = *I. umbrilatus*, tilefish = *M. brevirostris*, cusk eel = *O. Muraenolepsis*, sandperch = *P. schauinslandi*, lizardfish L = *S. lobeli*, lizardfish V = *S. variegatus*, puffer = *T. florealis*, snakefish = *T. myops*.

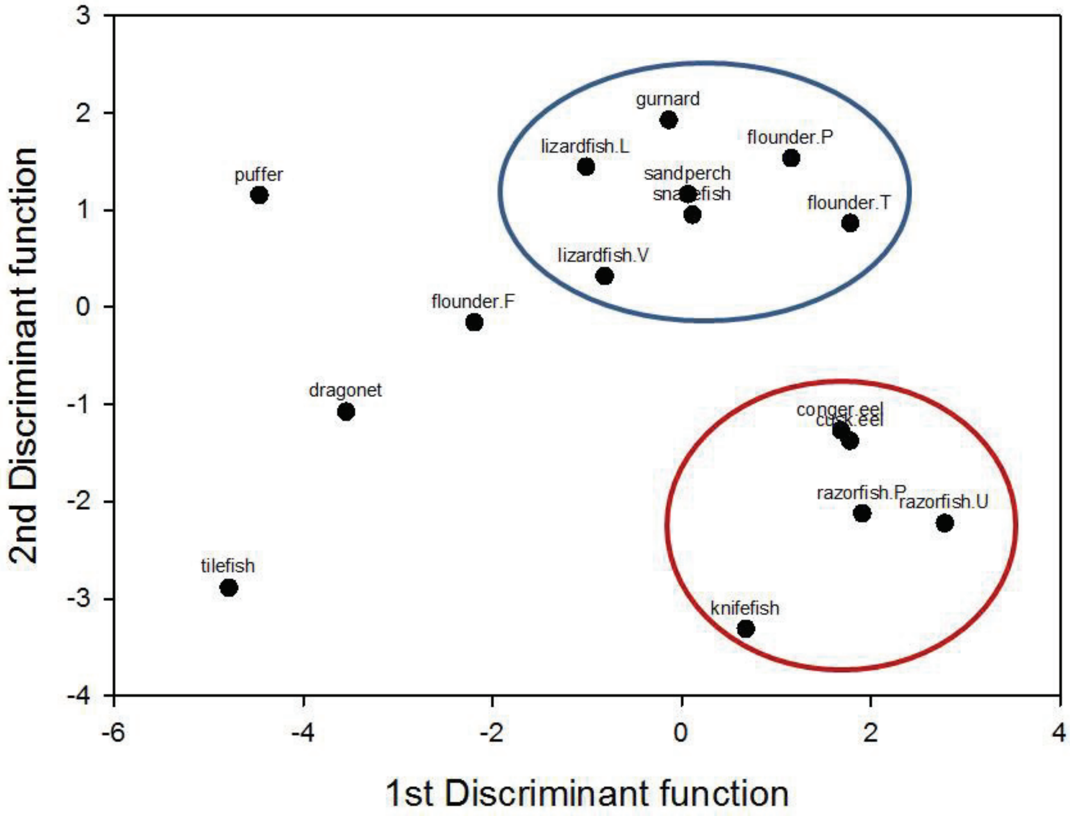

gurnard
lizardfish.L
flounder.P
sandperch
snakefish
flounder.T
puffer
lizardfish.V
flounder.F
dragonet
conger.eel
cusk.eel
razorfish.P
razorfish.U
tilefish
knifefish
3
2
1
0
-1
-2
-3
-4
-6
-4
-2
0
2
4
2nd Discriminant function
1st Discriminant function

Table 5.3 Discriminant function analysis (DFA) and simulations results for sand-dwelling communities investigations. Results of DFA performed on 16 species (total n=376) using 15 fatty acids (FAs, see Table 5.1); misclassifications (%, species) that accounted for ≥ 5% of the number of individuals are also listed for each species. Results of QFASA simulations performed using 39 FAs (see Table 5.1); misclassifications (%, species) that accounted for ≥ 5% of the number of individuals estimated are also listed for each species.

	DFA (15 FAs)		**Simulation (39 FAs)**	
Species	**Correctly classified**	**Misclassified (≥ 5%)**	**Correctly estimated**	**Misclassified (≥ 5%)**
Ariosoma marginatum (conger eel)	77%	11% *B. tompsoni*, 7.7% *C. lecluse*	71%	7% *C. lecluse*, 5% *B. pantherinus*, 5% *T. myops*
Bothus mancus (flounder F)	75%	12.5% *B. pantherinus*, 12.5% *T. florealis*	85%	5% *M. brevirostris*
Bothus pantherinus (flounder P)	97%		93%	
Bothus thompsoni (flounder T)	76%	8% *A. marginatum*	78%	7% *D. orientalis*
Callionymus decoratus (dragonet)	90%	5% *M. brevirostris*, 5% *T. florealis*	80%	8% *M. brevirostris*
Cymolutes lecluse (knifefish)	83%	9% *A. marginatum*	82%	6% *I. umbrilatus*
Dactyloptena orientalis (gurnard)	83%		91%	5% *S. lobeli*
Iniistius pavo (razorfish P)	27%	33% *I. umbrilatus*, 20% *C. lecluse*, 20% *T. myops*	53%	15% *I. umbrilatus*, 11% *C. lecluse*, 8% *T. myops*
Iniistius umbrilatus (razorfish U)	79%	10% *I. pavo*, 5% *C. lecluse*, 5% *O. muraenolepsis*	80%	6% *C. lecluse*, 5% *I. pavo*
Malacanthus brevirostris (tilefish)	100%		81%	7% *B. mancus*
Ophidion muraenolepis (cusk eel)	80%	10% *C. lecluse*, 5% *I. pavo*, 5% *B. thompsoni*	75%	5% *D. orientalis*
Parapercis schauinslandii (sandperch)	94%	6% *S. variegatus*	80%	7% *D. orientalis*, 5% *S. lobeli*

Table 5.3 *end*

Species	DFA (15 FAs) Correctly classified	Misclassified (≥ 5%)	Simulation (39 FAs) Correctly estimated	Misclassified (≥ 5%)
Synodus lobeli (lizardfish L)	60%	25% *P. schauinslandii* , 10% *S. variegatus* , 5% *T. myops*	71%	13% *T. myops* , 5% *P. schauinslandi*
Synodus variegatus (lizardfish V)	79%	10% *T. myops* , 5% *P. schauinslandii* , 5% *B. mancus*	60%	18% *T. myops* , 9% *S. lobeli*
Torquigener florealis (puffer)	90%	5% *D. orientalis* , 5% *B. pantherinus*	77%	6% *M. brevirostris*
Trachinocephalus myops (snakefish)	70%	10% *S. variegatus* , 5% *S. lobeli* , 5% *D. orientalis* , 5% *C. decoratus* , 5% *B. pantherinus*	75%	8% *S. Lobeli* , 8% *S. Variegatus*

5.4 DISCUSSION

The results of this study indicate that in general, despite close taxonomical relatedness and/or comparable diet guilds, individual species of carnivorous fishes from the Hawaiian Islands can be reliably distinguished on the basis of their FA signatures both across and within ecological subsystems. Dietary FAs have a direct and quantitative effect on the FA composition of a consumer (reviewed in Iverson 2009). My results demonstrate that paired carnivorous species exhibiting similar foraging ecology, but occupying deep- vs shallow-water, most closely resembled the other species within the same ecological depth zone. My results also revealed that sand-dwelling carnivorous species exhibiting flatfish body form and ambusher feeding tactics have more similar FA profiles, compared to species with eel and fish body forms. These results are consistent with previous investigations of sand communities in marine (Hobson & Chess 1986) and freshwater ecosystems (Zuanon et al. 2006), which have emphasized the importance of predator-prey interactions as a driver for morphological and behavioural adaptations to life on the exposed substrate. The present study is, to my knowledge, the first to use FAs as a tool to make inferences about FA patterns and the ecology of individual species in a subtropical reef ecosystem.

5.4.1 PAIRED FORAGING EQUIVALENTS ACROSS DEPTH ZONES

DFA performed on five pairs of ecologically equivalent species from opposite ecological zones showed that with the exception of boarfish (*A. eos*), deep-water species were more closely associated with one another rather than with their shallow-water reef counterparts (Fig 5.2). Individuals of all 10 species were ≥ 80% correctly classified and misclassifications mostly occurred among closely related species, and/or species with similar trophic ecology thriving within the same depth range. However, in several instances, detected overlaps in FA signatures could be interpreted as indicators of trophic linkages among individual species.

Damselfish and lizardfish. DFA results revealed that 20% of the dascyllus were misclassified as lizardfishes, and 9% of lizardfish were misclassified as dascyllus (Table 5.2). Damselfishes of the genus *Dascyllus* are site-attached planktivores which actively forage during daytime and seek shelter within the coral matrix at night and/or to escape predators (Mann & Sancho 2007). Damselfishes, like other planktivores, are a critical link between primary productivity and higher trophic levels in coral reef ecosystems (Hobson 1991). Energy transfer can occur directly through piscivory, but also indirectly through coprophagy (Robertson 1982). For example, due to the increased feeding rates of planktivores during zooplankton blooms, zooplankters are passed almost intact in the fecal pellets to the reef trophic system as they are consumed by fish while sinking, or upon reaching the ocean floor (Hobson 1991). However, coprophagy is most commonly encountered in herbivores and detritivores (Robertson 1982) and is an unlikely explanation for the potential overlap detected between damselfish and lizardfish. A direct trophic link is more plausible, as lizardfish, which are well-camouflaged ambush predators of small fish, are also known to prey on recently settled juvenile damselfish (Sweatman 1984, Parrish et al. 1986).

Moray eels. Both moray eel species were consistently misclassified as one another, which can be attributed to taxonomical relatedness and comparable foraging ecology (Table 5.2, Appendix 5.2). However, *G. eurostus* (small moray) also exhibited similarities in FA signature with the goatfish *M. flavolineatus*, which also associated more closely with the morays on the DFA plot (Fig. 5.2). Goatfish and moray eels contained higher levels of 20:4n-6 (~9%) relative to the other shallow reef species (~5%), and deep-water species (~3%) in this set of analyses (see Appendix 5.1). A known marker of benthic productivity (Dalsgaard et al. 2003), 20:4n-6 has been shown to be particularly abundant in this ecosystem in some species of invertebrates (e.g. crustaceans and octopus) and fish (e.g. parrotfish, triggerfish) living in close association with the benthos (see Piché et al. 2010). Moray eels and goatfish both target prey which are closely associated with the substrate: morays forage across the reef in search of prey sheltered in holes or crevices, while goatfish probe the substrate with sensory barbells to uncover buried or hidden prey (Hobson 1974, Krajewski et al. 2006). High levels of 20:4n-6 could thus be explained by the fact that all three species are feeding on prey in which markers of benthic productivity are strongly conserved. The FA overlap detected among *G. eurostus* and *M. flavolineatus* suggests that the former might be feeding on the latter, an assumption further supported by previous reports of predation of Muranenidae on Mullidae (Parrish et al. 1986).

Goatfish. DFA and simulation results revealed a potential overlap in FA signatures among the goatfish *M. flavolineatus* and the damselfish *D. albisella* (Table 5.2). *M. flavolineatus* is a nocturnal or crepuscular benthic carnivore that feeds on crustaceans, mollusks, worms, urchins and foraminiferans while damselfish is a planktivore (Randall 1996, Froese & Pauly 2010). Therefore, a direct trophic link between the two species is unlikely. However, incidences of goatfish feeding off drifting crustaceans and/or forming mixed foraging aggregations with damselfish have been reported (Krajewski & Bonaldo 2006). Based on these observations, it has been argued that some members of the Mullidae family could in fact be facultative planktivores (e.g. Krajewski & Bonaldo 2006). The similarities identified among the FA signatures of *M. flavolineatus* and *D. albisella* would thus be in accordance with this idea.

Deep-water species. All deep-water species contained very high proportions of 18:1n-9 (~18%) relative to shallow water species (~8%), except for the boarfish *A. eos* (~9%). As 18:1n-9 is a marker of animal production, it would necessarily be more abundant in fish feeding at higher trophic levels. Beardfish, duckbill, snake eel and abyssal eel are benthic carnivores or piscivores (see Appendix 5.2), while boarfish is a planktivore relying on zooplankton migrating vertically in the water column and/or planktonic invertebrates being brought about horizontally by currents (Benoit-Bird et al. 2008). Diel migration of zooplankters up the water column during the night renders surface productivity available at depth when they migrate back to the mesophotic zone (Steinberg et al. 2008). This may be why boarfish associated more closely with its shallow-water analogue, the Hawaiian dascyllus *D. albisella* (Fig. 5.2), despite possessing a FA signature which clearly allowed them to be characterized as a deep-water species. This is further supported by simulation results where 5% of the damselfish were misclassified as boarfish.

QFASA simulations. When compared with the DFA results, the simulations performed using an increased number of FAs (10 → 39FAs) overall yielded a reduced proportion of correctly classified individuals for most species, especially in the case of *G. eurostus* (smaller moray), *M. abyssalis* (abyssal eel), and *P. berndti* (beardfish). These three species all performed well in the DFA, with classification successes of 86%, 100%, and 90% respectively. While increasing the number of FAs in the analyses can certainly be useful in refining the discrimination among species, the 10 species in this set of analyses were already very well differentiated using 10 FAs in DFAs. It is not clear whether using more FAs or a different statistical method (simulations) was the cause of this reduced distinction among the signature of closely related species and/or species living in the same ecological subsystem. In simulations, the smaller moray (*G. eurostus*) was mostly misclassified as the larger species of moray *G. steindachneri*, and abyssal eel (*M. abyssalis)* and boarfish (*P. berndti)* were more frequently misclassified as other deep-water species. The differences between the two statistical procedures would clearly be important to account for in QFASA diet estimation procedures for predators of these fishes (e.g., Iverson et al. 2004).

5.4.2 SAND-DWELLING COMMUNITIES

DFA performed on 16 sand dwelling species using 15 FAs separated species into two main groups on the basis of general morphology: species with a flatfish body form (n= 7), and species with eel (n=2) or fish (n=3) body forms (Fig. 5.4). Individuals of half of the species were ≥ 80% correctly classified, and 14 of 16 species had a classification success ≥ 70% (Table 5.3). Body form, evasion guild, and foraging behaviour are intrinsically linked (Webb 1984). Predation pressure leads to the development of morphological-ecological relationships aimed at maximizing fitness (e.g. Hobson 1975). Thus species living on exposed sand field often adopt cryptic and/or burrowing behaviour to avoid detection from both predator and prey (Hobson & Chess 1986). Sand-dwellers with flatfish body form are generally well-camouflaged ambush predators which often lay motionless on or in the substrate. In contrast, while they remain closely associated with the bottom, sand-dwelling species with eel or fish body forms tend to actively search for their prey and burrow in the sand as a predator avoidance mechanism, or during their resting period (Zuanon et al. 2006). Both DFA and simulation results revealed that some misclassifications which occurred among closely related species could be attributed to similar foraging ecology, but in other cases they could be interpreted as potential predatory interactions.

Bothidae. Of the three flounder species analyzed, all performed relatively well in the DFA and simulations but the panther flounder *B. pantherinus* appeared to have the most distinct FA signature (Table 5.3). The flowery flounder *B. mancus* was misclassified as *B. pantherinus* which indicates similarities in their FA signatures. However, panther flounders were the smallest sand-dwellers analyzed and it is unlikely that they would feed on the same prey type as the larger *B. mancus* (see Appendix 5.3 for size ranges). *B. mancus* is a cryptic benthic carnivore that feeds primarily on fish (Hobson 1974) and it is therefore possible that *B. pantherinus* constitutes one of its prey. Thompson's flounder *B. thompsoni* and the large-eye conger *A. marginatum* were also misclassified for one another. However, the former is a benthic carnivore feeding on small fish and crustaceans (Randall 1996) while *A. marginatum* is a piscivore. Differences in diet guild as well as size ranges suggest that the conger eel might consume *B. thompsoni*.

Labridae. Misclassifications occurred among the three species of wrasse, the knifefish *C. lecluse*, and the razorfishes *I. pavo* and *I. umbrilatus* (Table 5.3). Of all species, *I. pavo* had a very low proportion of individuals correctly classified in both the DFA and simulations, which indicates that FA overlap is great among some of the labrids analyzed. *I. pavo* also exhibited overlap in FA signature with the piscivorous synodontid snakefish *T. myops*. Most wrasses, including *I. pavo*, are known to feed predominantly on hard-shelled invertebrates by using their well-developed pharyngeal teeth (Hiatt & Strasburg 1960, Hobson 1974). Therefore, *C. lecluse* is somewhat unusual in being a benthic carnivore that reportedly preys mostly on fish (Froese & Pauly 2010). *I. umbrilatus* is also a benthic carnivore, but its diet has not yet been described (Froese & Pauly 2010). More research is clearly needed to unravel the detailed foraging ecology of these species. However, previous authors have argued that some wrasses are opportunistic feeders that are greatly influenced by prey availability which might complicate the elucidation of their diet (Hiatt & Strasburg 1960). The cusk eel *O. muraenolepis* exhibited apparent similarities at the level of their FA signature with that of wrasses (Table 5.3). However, as the diet and foraging habits of *O. muraenolepis* have not yet been documented, it is difficult to draw any inference from the FA patterns detected.

Synodontidae. Synodontids (*S. lobeli*, *S. variegatus*, and *T. myops*) were consistently misclassified for one another in the DFA and simulations (Table 5.3). Lizardfishes and snakefishes are known to be voracious ambush predators of small fishes, although crustaceans can also occasionally be taken (Hiatt & Strasburg 1960, Hobson 1974). It is therefore possible that these three piscivorous species feed on a wide array of prey which renders their FA signatures harder to differentiate. Possible overlap in FA composition was also detected among the sandperch *P. schauinslandii* and the lizardfishes. This is interesting because the mouth construction, dentition, and feeding ecology of both families is reportedly very similar (Hiatt & Strasburg 1960). One could thus conclude that these common morphological and behavioural traits indicate that sandperches and lizardfishes target similar prey species. However, sandperches are benthic carnivores which primarily feed on crustaceans, and occasionally on small fishes (Hiatt & Strasburg 1960). Perhaps the similarities detected at the level of FA composition indicate that the trophic categories attributed to each species needs to be revisited, as they all appear to be opportunistic ambush predators of a broad range of prey which include both small fishes and benthic crustaceans.

Unusual FA patterns. Four of the species analyzed exhibited particularly high levels of n-6 FAs: tilefish (*M. brevirostris*), puffer (*T. florealis*), and to a lesser extent dragonet (*C. decoratus*) and flounder F (*B. mancus*). These four species were unusually high in 20:4n-6 (8-10%) relative to the other sand-dwelling species (~5%). *M. brevirostris*, the only species with 100% of individuals correctly classified, also possessed high level of this 22:4n-6 (~5% relative to 1-2% in other species) which was also the FA accounting for most of the variance on the first two discriminant functions. Moreover, misclassified individuals in all four species were mostly attributed to another n-6 rich species. *M. brevirostris*, *T. florealis*, *C. decoratus*, and *B. mancus* are benthic carnivores and all feed to a certain degree on crustaceans and/or other benthic invertebrates which are known to be particularly high in 20:4n-6 FA in this ecosystem (Piché et al. 2010). However, interpreting the results in more detail is difficult as there is little published information on the ecology of these species, as well as on the prey species assemblages they might be feeding on.

5.5 CONCLUSION

Discriminating among groups of carnivores on the basis of their FA composition has been shown to be problematic in comparison to herbivores, planktivores, and crustaceans in this ecosystem (Piché et al. 2010). Specific FA patterns become increasingly difficult to detect in higher trophic levels because dietary FA can be obtained through a wider variety of food source (Dalsgaard et al. 2003, Iverson 2009). However, the present study clearly demonstrates that individual species of carnivorous fishes can be reliably distinguished using FAs despite taxonomical relatedness and similarities in trophic ecology. Results show that while increasing the number of FA used in the analyses might be useful to refine the resolution of distinctions, using a restricted number of FAs can also result in reliable ability to differentiate among species. These findings demonstrate that FA analyses, used in conjunction with other methods, represent an important tool which can help to decifer the foraging ecology of species living in complex ecosystems, such as coral reefs. Future studies should focus on further exploring which dietary FA subset(s) best defines species in this ecosystem to pursue investigations at the level of individual species. Additional work could also focus on obtaining FA data of primary producers/consumers in this ecosystem to elucidate the origins of high levels of n-6 in some species.

CHAPTER 6 CONCLUSIONS

Despite persistent research effort brought about by their vulnerable status, the mechanisms underlying the establishment and maintenance of high biodiversity in tropical coral reef ecosystems, and more specifically the relative contribution of top-down versus bottom-up effects on community structure and the composition of prey species assemblage remains poorly understood (Bellwood et al. 2004). In Chapter 2 I have reviewed some of the major hypotheses currently in place to explain the potential importance of competitive and predatory relationships in structuring tropical reef communities. However, the various approaches currently in use to study food webs and trophic relationships in such complex marine systems possess a number of biases and limitations, and there is a need to develop methods which would allow the level of integration from the different food sources making up a coral reef ecosystem to be assessed. The overall aim of my thesis was to determine whether fatty acid (FA) analyses could be used to increase the resolution of trophic investigations among forage species in a complex subtropical reef ecosystem, the Hawaiian archipelago, and to explore how FA distinctions and overlaps can be interpreted in the context of the ecology of the species studied.

I began in Chapter 3 by investigating to what extent fish and invertebrate species from the Northwestern Hawaiian Islands (NWHI) and Main Hawaiin Islands (MHI), selected as a function of their potential importance to monk seal diets, could be differentiated on the basis of their FA composition by analyzing groups of closely related and ecologically equivalent species using a restricted number of the most abundant/variable FAs across all species. I found that diet played a primary role in distinguishing among species groups, as they separated into five broad functional groups: herbivores, planktivores, carnivores, crustaceans and cephalopods. Within these functional groups, I discovered that some of the detected FA patterns could further be related to habitat/ecological subsystem (i.e. depth) and foraging ecology. For example, deep-water species/groups, whether fishes or crustaceans, could readily be distinguished from their shallow-water counterparts on the basis of their FA composition. Also, the unique life history of the pelagic armorhead was reflected through its very distinct FA signature which differed from all others. Overall, most species groups could be reliably characterized by their FA signature, and overlaps principally occurred among groups with analogous diet and/or ecology, such as among eels, among goatfishes, and among crustaceans. In Chapter 4, I used quantitative FA signature analysis (QFASA) simulations to further investigate overlaps and distinctions among the same species groups, to determine whether this tool, which allows for a greater number of FAs to be analyzed, would increase the resolution of differences among groups and in a manner that could eventually be used for estimating predator diets. After a first set of simulations, potential overlap among closely related species prompted me to revisit the species groupings, but to no avail, thus original groups were conserved in subsequent simulations. By evaluating the effect of using various FA subsets and of sequentially removing major misidentified species, I found that species groups were generally well estimated but that some overlap occurred especially among deep-water fish species, among sand-associated carnivores, and among crustaceans. This is consistent with the findings of Chapter 3 which targeted the same species groups using different procedures and fewer FAs. Most of the deep-water carnivorous fish species analyzed can therefore be readily distinguished the basis of their FA composition from fishes thriving at shallower depths regardless of their trophic level (Chapter 3), however QFASA simulations revealed that they can also be difficult to differentiate from one another. Sand-associated carnivorous fishes were also problematic in routinely exhibiting various degrees of overlap among one another regardless of the statistical method used. It is true that considering the complexity of the Hawaiian archipelago reef ecosystem, overlap would be expected to occur among at least some predators feeding at the same trophic level within the same ecological zone, given that their FA signature would integrate FAs arising from similar dietary sources (Dalsgaard et al. 2003, Iverson 2009).

In Chapter 5 I aimed to address the consistent overlap among groups of carnivorous fishes identified in Chapters 3 and 4 by further increasing the resolution of FA investigations and performing analyses on *individual* species using methods which allowed for differences to be detected across both a restricted and increased number of FAs. I found that when treated individually, species of carnivorous fish can be reliably distinguished using FAs despite close taxonomical relatedness and similar foraging ecology. I demonstrated that pairs of deep versus shallow-water carnivores with similar foraging ecology, when contrasted across depth zones, more closely resembled other species thriving in the same ecological depth zone despite exhibiting differences in diet and/or foraging habits. Within the same ecological subsystem, sand-associated species on Hawaiian banks separated as a function of body form which is intrinsically linked to foraging tactics and therefore to the type of prey consumed, which is reflected at the level of their FA signature. In some instances, published information about the diet and ecology of species/families allowed me to interpret overlapping FA composition as a possible trophic linkage among species.

Overall, these investigations are, to my knowledge, the first to use FAs as a tool to study trophic and ecological relationships among species in a complex subtropical reef ecosystem. These analyses have yielded promising results as they provide evidence that despite tremendous species diversity, FAs can be employed to investigate the diet and ecology of Hawaiian fish and invertebrate species/groups, among and within trophic guilds. Moreover, these studies have illustrated the strength of using multiple approaches (DFA, QFASA, and ecological information from the literature) to link FA patterns to the foraging ecology of individual species. These findings have important implications for the study of food web interactions in the Hawaiian archipelago at higher trophic levels, as they provide the foundation for using the same species groups in diet estimations of the critically endangered monk seal, as well as other top predators in this ecosystem. Moreover, the types of iterations performed in QFASA provide a framework for using the model as an ecological tool and performing similar studies in other ecosystems.

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APPENDIX 3.1 Collection location for the 100 species of fish and invertebrate analyzed. MHI: Main Hawaiian Islands, FFS: French Frigate Shoals, GP: Gardner Pinnacles, MR: Maro Reef, Smt 11: Mid-Pacific Seamount 11 (18.49°N, 177.99°W), CSM: Cross Seamount (18.7°N, 158.3°W), Unk: unknown collection location (from Piché et al. 2010).

Species Name	Common Name	Family	MHI	Niihau	Nihoa	Necker	FFS	GP	MR	Laysan	Midway	Smt 11	CSM	Unk	Total
Abudefduf abdominalis	Hawaiian sergeant	Pomacentridae					11				9				**20**
Abudefduf sordidus	Blackspot sergeant	Pomacentridae				6	15								**21**
Abudefduf vaigiensis	Indo-Pacific sergeant	Pomacentridae					16								**16**
Acanthurus achilles	Achilles tang	Acanthuridae					20								**20**
Acanthurus dussumieri	Eyestripe surgeonfish	Acanthuridae					16								**16**
Acanthurus leucopareius	Whitebar surgeonfish	Acanthuridae				9	13								**22**
Acanthurus nigroris	Bluelined surgeonfish	Acanthuridae					14				6				**20**
Acanthurus olivaceus	Orangeband surgeonfish	Acanthuridae				10	10								**20**
Acanthurus triostegus	Convict tang	Acanthuridae					15				5				**20**
Anampses cuvier	Pearl wrasse	Labridae					16				4				**20**
Antigonia capros	Boarfish	Pentacerotidae	10												**10**
Antigonia eos	Boarfish	Pentacerotidae	10												**10**
Apogon maculiferus	Spotted cardinalfish	Apogonidae				11	4		3						**18**
Ariosoma marginatum	Big-eye conger	Congridae					11	13			2				**26**

APPENDIX 3.1 *continued*

Species Name	Common Name	Family	MHI	Niihau	Nihoa	Necker	FFS	GP	MR	Laysan	Midway	Smt 11	CSM	Unk	Total
Bembrops filifera	Duck-billed bembropsid	Percophidae	19												**19**
Bodianus bilunulatus	Hawaiian hogfish	Labridae				6	14								**20**
Bothus mancus	Flowery flounder	Bothidae					15				1				**16**
Bothus pantherinus	Panther flounder	Bothidae					39	36							**75**
Bothus thompsoni	Thompson's flounder	Bothidae					19		6						**25**
Calappa bicornis	Two-horned box crab	Calappidae				10			13						**23**
Calappa calappa	Smooth box crab	Calappidae				16	8	12							**36**
Callionymus decoratus	Longtail dragonet	Callionymidae					1	19							**20**
Canthigaster coronata	Crown toby	Tetraodontidae			2	2	13		3						**20**
Canthigaster jactator	Hawaiian whitespotted	Tetraodontidae				10	7		7						**24**
Canthigaster rivulata	Maze toby	Tetraodontidae			2		8	6							**16**
Carpilius convexus	Convex pebble crab	Xanthidae				8	9		4						**21**
Centropyge potteri	Potter's angelfish	Pomacanthidae					19		1						**20**
Chaetodon fremblii	Bluestripe butterflyfish	Chaetodontidae				12	7		3						**22**

APPENDIX 3.1 *continued*

Species Name	Common Name	Family	MHI	Niihau	Nihoa	Necker	FFS	GP	MR	Laysan	Midway	Smt 11	CSM	Unk	Total
Chaetodon miliaris	Milletseed butterflyfish	Chaetodontidae				18	9								**27**
Chaetodon multicinctus	Multiband butterflyfish	Chaetodontidae					19								**19**
Chaetodon ornatissimus	Ornate butterflyfish	Chaetodontidae					20								**20**
Chaetodon quadrimaculatus	Four spot butterflyfish	Chaetodontidae					20								**20**
Charybdis hawaiiensis	Hawaiian swimming crab	Portunidae				9	5	10	5						**29**
Chlorurus perspicillatus	Spectacled parrotfish	Scaridae					22								**22**
Chlorurus sordidus	Bullethead parrotfish	Scaridae					19								**19**
Chromis ovalis	Oval chromis	Pomacentridae					17		4						**21**
Conger cinereus	Moustache conger	Congridae				13	1		6						**20**
Coris ballieui	Lined coris	Labridae		9	1	6									**16**
Coris flavovittata	Yellow striped coris	Labridae					20								**20**
Ctenochaetus strigosus	Goldring surgeonfish	Acanthuridae					16								**16**
Cymolutes lecluse	Hawaiian knifefish	Labridae		2			10				11				**23**
Dactyoptena orientalis	Helmut gurnard	Dactylopteridae					4	20							**24**

APPENDIX 3.1 *continued*

Species Name	Common Name	Family	MHI	Niihau	Nihoa	Necker	FFS	GP	MR	Laysan	Midway	Smt 11	CSM	Unk	Total
Dascyllus albisella	Hawaiian dascyllus	Pomacentridae				3	14				3				**20**
Etelis carbunculus	Squirrelfish snapper	Lutjanidae				10	9		2						**21**
Forcipiger flavissimus	Forcepfish	Chaetodontidae					26								**26**
Gymnothorax albimarginatus	Whitemargin moray	Muraenidae				11			9						**20**
Gymnothorax berndti	Berndt's moray	Muraenidae				8	2	9	1						**20**
Gymnothorax eurostus	Stout moray	Muraenidae				7	1		4		2				**14**
Gymnothorax flavimarginatus	Yellow margin moray	Muraenidae					11		8						**19**
Gymnothorax meleagris	Whitemouth moray	Muraenidae				10	7	1							**18**
Gymnothorax steindachneri	Steindachner's moray	Muraenidae				12		6	7						**25**
Gymnothorax undulatus	Undulated moray	Muraenidae				5	5		9						**19**
Heniochus diphreutes	Pennantfish	Chaetodontidae				12	12		12						**36**
Heterocarpus ensifer	Two-spined shrimp	Pandalidae				11			20						**31**
Heterocarpus laevigatus	Red-tipped shrimp	Pandalidae				19		20							**39**
Iniistius pavo	Peacock razorfish	Labridae		4	4		2				5				**15**

APPENDIX 3.1 *continued*

Species Name	Common Name	Family	MHI	Niihau	Nihoa	Necker	FFS	GP	MR	Laysan	Midway	Smt 11	CSM	Unk	Total
Iniistius umbrilatus	Blackside razorfish	Labridae		9	9		1								**19**
Kyphosus bigibbus	Gray chub	Kyphosidae					19								**19**
Kyphosus vaigiensis	Low fin chub	Kyphosidae					19								**19**
Lutjanus kasmira	Bluestripe snapper	Lutjanidae				15	7								**22**
Malacanthus brevirostris	Flagtail tilefish	Malacanthidae		3			11	2							**16**
Meadia abyssalis	Abyssal cutthroat eel	Synaphobranchidae										19			**19**
Melichthys niger	Black triggerfish	Balistidae					20								**20**
Mulloidichthys flavolineatus	Yellow stripe goatfish	Mullidae					19				2				**21**
Mulloidichthys vanicolensis	Yellow fin goatfish	Mullidae				1	19								**20**
Myripristis berndti	Bigscale soldierfish	Holocentridae				2	16		2						**20**
Naso lituratus	Orangespine unicornfish	Acanthuridae					19								**19**
Naso unicornis	Bluespine unicornfish	Acanthuridae				1	18								**19**
Octopus cyanea	Hawaiian day octopus	Octopodidae				3	7		3						**13**
Octopus ornatus	Ornate octopus	Octopodidae				2	2								**4**

APPENDIX 3.1 *continued*

Species Name	Common Name	Family	MHI	Niihau	Nihoa	Necker	FFS	GP	MR	Laysan	Midway	Smt 11	CSM	Unk	Total
Octopus sp.	Unidentified octopus	Octopodidae	1			1	15	5	1						**23**
Ophichthus kunaloa	Snake eel	Ophichthidae											20		**20**
Ophidion muraenolepis	Black edged cusk eel	Ophidiidae					11	6	3						**20**
Oxycheilinus unifasciatus	Ringtail wrasse	Labridae					19								**19**
Panulirus marginatus	Spiny lobster	Palinuridae	5			23	6	10			16				**60**
Panulirus marginatus	Spiny lobster - tails only	Palinuridae							11						**11**
Parapercis schauinslandii	Redspotted sandperch	Pinguipedidae					1	17							**18**
Parupeneus bifasciatus	Doublebar goatfish	Mullidae				3	16								**19**
Parupeneus chrysonemus	Yellow barbel goatfish	Mullidae						19							**19**
Parupeneus multifasciatus	Manybar goatfish	Mullidae				11	9								**20**
Parupeneus pleurostigma	Sidespot goatfish	Mullidae				12	2	1	3		1				**19**
Polymixia berndti	Berndt's beardfish	Polymixiidae					15	5							**20**
Priacanthus alalaua	Forskal's bigeye	Priacanthidae	11			7		1	1						**20**
Priacanthus meeki	Hawaiian bigeye	Priacanthidae					20								**20**

APPENDIX 3.1 *continued*

Species Name	Common Name	Family	MHI	Niihau	Nihoa	Necker	FFS	GP	MR	Laysan	Midway	Smt 11	CSM	Unk	Total
Pristipomoides filamentosus	Pink snapper	Lutjanidae				16	8								**24**
Pristipomoides zonatus	Flower snapper	Lutjanidae				6		13							**19**
Pseudopentaceros wheeleri	Armorhead	Pentacerotidae										20			**20**
Sargocentron xantherythrum	Hawaiian squirrellfish	Holocentridae				10	1	6	4						**21**
Scarus dubius	Regal parrotfish	Scaridae					15				4				**19**
Scyllarides haanii	Ridgeback slipper lobster	Scyllaridae				10	6	10			4				**30**
Scyllarides squammosus	Common slipper lobster	Scyllaridae				31	12	10	8		11				**72**
Sebastapistes ballieui	Spotfin scorpionfish	Scorpaenidae				4			15						**19**
Stenoteuthis oualaniensis	Neon flying squid	Ommastrephidae	2			1								12	**15**
Sufflamen bursa	Lei triggerfish	Balistidae					19								**19**
Synodus lobeli	Lobel's lizardfish	Synodontidae					20								**20**
Synodus variegatus	Reef lizardfish	Synodontidae				2	14				3				**19**
Thalassoma ballieui	Blacktail wrasse	Labridae				3	14		2		1				**20**
Thalassoma duperry	Saddle wrasse	Labridae					18				2				**20**

APPENDIX 3.1 *end*

Species Name	Common Name	Family	MHI	Niihau	Nihoa	Necker	FFS	GP	MR	Laysan	Midway	Smt 11	CSM	Unk	Total
Torquigener florealis	Floral puffer	Tetraodontidae	6				1	10	3						**20**
Trachinocephalus myops	Snakefish	Synodontidae	3		2		7	8							**20**
Zebrasoma flavescens	Yellow tang	Acanthuridae					20								**20**
		Total	**67**	**27**	**20**	**418**	**1037**	**275**	**183**	**0**	**92**	**39**	**20**	**12**	**2190**

APPENDIX 3.2 Fat content and fatty acid (FA) composition (mass %) of the 100 species of NWHI and MHI fishes and invertebrates analyzed (n = 2,190). Values are means ± SEM of 15 FAs (out of 74) which were the most abundant and/or exhibited the greatest variance across all species (from Piché et al. 2010).

Fishes

Group	11	11	11	31	31	31	31	31
Species name	*Abudefduf abdominalis*	*Abudefduf sordidus*	*Abudefduf vaigiensis*	*Acanthurus achilles*	*Acanthurus dussumieri*	*Acanthurus leucopareius*	*Acanthurus nigroris*	*Acanthurus olivaceus*
Common name	(Hawaiian sergeant)	(Blackspot sergeant)	(Indo-Pacific sergeant)	(Achilles tang)	(Eyestripe surgeonfish)	(Whitebar surgeonfish)	(Bluelined surgeonfish)	(Orangeband surgeonfish)
	n=20	n=21	n=16	n=20	n=16	n=22	n=20	n=20
Length (cm)	18.78 ± 1.06	15.84 ± 2.73	15.39 ± 1.20	15.93 ± 2.93	17.84 ± 3.98	15.60 ± 3.92	18.71 ± 2.01	18.05 ± 4.54
Mass (g)	209.17 ± 33.42	191.22 ± 71.18	129.23 ± 25.37	136.08 ± 66.53	227.31 ± 110.18	182.56 ± 108.99	193.26 ± 57.15	190.90 ± 127.49
Lipid content (%)	2.03 ± 0.84	2.44 ± 1.13	3.42 ± 2.33	4.41 ± 2.88	2.19 ± 0.77	3.61 ± 1.91	4.22 ± 1.22	2.98 ± 2.16
Saturated FA								
14:0	4.33 ± 1.12	2.45 ± 0.65	5.73 ± 1.36	3.74 ± 0.79	7.53 ± 3.70	7.86 ± 3.40	7.67 ± 2.56	7.38 ± 2.86
16:0	25.39 ± 4.31	27.25 ± 4.69	28.02 ± 4.06	40.56 ± 4.97	27.09 ± 2.55	30.50 ± 3.77	31.79 ± 3.23	27.58 ± 2.43
18:0	6.93 ± 0.97	8.07 ± 1.91	7.54 ± 1.53	6.15 ± 0.83	6.10 ± 1.78	4.82 ± 0.83	4.27 ± 0.66	4.72 ± 1.41
subtotal:	36.65 ± 4.63	37.77 ± 3.27	41.29 ± 3.70	50.46 ± 4.88	40.72 ± 2.88	43.18 ± 2.63	43.73 ± 2.35	39.68 ± 3.36
Monounsaturated FA								
16:1n-7	4.46 ± 1.44	5.19 ± 2.04	4.71 ± 1.52	3.50 ± 1.22	7.45 ± 2.06	5.40 ± 1.79	6.98 ± 1.52	8.05 ± 3.89
18:1n-9	9.09 ± 1.84	8.85 ± 2.19	8.05 ± 0.95	8.37 ± 0.76	3.73 ± 0.49	6.50 ± 1.11	6.29 ± 1.01	4.41 ± 1.27
18:1n-7	1.93 ± 0.42	2.50 ± 0.43	2.06 ± 0.46	2.23 ± 0.23	1.80 ± 0.50	1.69 ± 0.34	2.14 ± 0.48	1.60 ± 0.38
20:1n-9	1.20 ± 0.62	0.78 ± 0.31	0.80 ± 0.17	1.80 ± 0.61	0.40 ± 0.07	0.83 ± 0.44	0.86 ± 0.38	0.31 ± 0.21
22:1n-11	0.71 ± 0.76	0.34 ± 0.24	0.18 ± 0.11	0.03 ± 0.03	2.43 ± 3.17	0.12 ± 0.16	1.44 ± 2.54	5.47 ± 6.40
subtotal:	17.39 ± 3.03	17.66 ± 3.99	15.81 ± 2.59	15.93 ± 2.52	15.82 ± 2.25	14.54 ± 1.40	17.71 ± 1.49	19.84 ± 3.93
Polyunsaturated FA								
18:2n-6	1.44 ± 0.30	3.03 ± 1.20	1.62 ± 0.13	0.94 ± 0.19	1.53 ± 0.29	1.58 ± 0.29	1.60 ± 0.25	1.48 ± 0.39
20:4n-6	4.21 ± 1.63	7.58 ± 3.48	2.72 ± 1.24	6.18 ± 2.31	8.92 ± 2.24	7.23 ± 1.49	5.61 ± 1.13	8.81 ± 4.81
22:4n-6	0.66 ± 0.21	1.98 ± 1.36	0.58 ± 0.21	1.87 ± 0.62	1.65 ± 0.46	2.42 ± 0.39	1.78 ± 0.39	1.40 ± 0.74
20:5n-3	4.76 ± 0.71	5.42 ± 1.77	4.51 ± 0.56	7.68 ± 1.62	5.91 ± 1.58	7.81 ± 1.74	7.12 ± 1.14	5.44 ± 2.20
22:5n-6	1.38 ± 0.50	0.87 ± 0.35	1.19 ± 0.56	0.52 ± 0.28	1.31 ± 0.42	0.93 ± 0.31	0.78 ± 0.22	1.26 ± 0.63
22:5n-3	1.95 ± 0.60	2.97 ± 1.21	1.74 ± 0.35	3.18 ± 0.62	2.36 ± 0.68	3.17 ± 0.79	2.77 ± 0.70	2.19 ± 0.76
22:6n-3	18.25 ± 3.15	6.06 ± 1.89	17.94 ± 5.24	2.94 ± 1.47	5.29 ± 2.78	3.93 ± 1.81	2.88 ± 0.82	5.10 ± 2.44
subtotal:	32.66 ± 4.30	27.93 ± 6.62	30.30 ± 7.20	23.30 ± 5.90	26.96 ± 4.47	27.07 ± 4.78	22.53 ± 1.95	25.68 ± 6.64
Total:	86.70 ± 1.13	83.35 ± 1.96	87.40 ± 1.59	89.68 ± 1.43	83.49 ± 2.70	84.79 ± 2.27	83.97 ± 2.23	85.20 ± 3.01

APPENDIX 3.2 *continued*

	Fishes							
Group	31	37	46	46	2	7	47	37
Species name	*Acanthurus triostegus*	*Anampses cuvier*	*Antigonia capros*	*Antigonia eos*	*Apogon maculiferus*	*Ariosoma marginatum*	*Bembrops filifera*	*Bodianus bilunulatus*
Common name	(Convict tang)	(Pearl wrasse)	(Boarfish)	(Boarfish)	(Spotted cardinalfish)	(Large-eye conger)	(Duck-billed bembropsid)	(Hawaiian hogfish)
	n=20	n=20	n=10	n=10	n=18	n=26	n=19	n=20
Length (cm)	14.75 ± 2.20	22.03 ± 5.55	6.33 ± 0.39	6.65 ± 0.39	7.32 ± 1.42	18.68 ± 7.12	17.37 ± 5.39	24.25 ± 6.24
Mass (g)	90.90 ± 47.74	274.78 ± 162.14	6.44 ± 1.38	9.82 ± 1.24	9.06 ± 5.63	23.15 ± 28.18	40.04 ± 27.98	392.08 ± 305.14
Lipid content (%)	2.35 ± 1.70	3.39 ± 1.47	1.37 ± 0.37	2.37 ± 0.81	2.19 ± 0.77	1.65 ± 0.47	1.83 ± 1.40	1.49 ± 0.55
Saturated FA								
14:0	5.65 ± 1.43	4.12 ± 1.48	1.53 ± 0.25	4.70 ± 0.87	3.71 ± 0.84	2.68 ± 1.03	1.83 ± 0.77	3.53 ± 1.54
16:0	31.60 ± 5.88	21.99 ± 1.37	18.53 ± 0.57	20.36 ± 1.01	22.18 ± 3.00	20.44 ± 1.45	17.89 ± 1.04	20.48 ± 1.27
18:0	4.69 ± 1.74	8.99 ± 0.76	8.92 ± 0.41	6.78 ± 0.40	9.40 ± 1.65	8.66 ± 1.39	5.49 ± 0.97	10.08 ± 0.79
subtotal:	41.94 ± 5.32	35.10 ± 2.27	28.98 ± 0.57	31.84 ± 1.40	35.29 ± 4.90	31.78 ± 1.83	25.21 ± 0.98	34.08 ± 2.14
Monounsaturated FA								
16:1n-7	4.69 ± 2.01	3.36 ± 0.54	2.83 ± 0.14	5.03 ± 0.60	3.19 ± 0.61	3.36 ± 1.03	4.74 ± 1.85	2.63 ± 0.56
18:1n-9	7.53 ± 0.90	9.81 ± 1.79	9.79 ± 0.62	8.91 ± 1.16	9.02 ± 1.32	9.71 ± 1.58	14.52 ± 3.03	9.48 ± 1.27
18:1n-7	1.41 ± 0.21	3.53 ± 0.55	2.09 ± 0.10	2.49 ± 0.14	2.81 ± 0.45	3.19 ± 0.64	2.95 ± 0.82	2.24 ± 0.26
20:1n-9	0.67 ± 0.30	0.73 ± 0.19	1.21 ± 0.22	0.79 ± 0.22	0.92 ± 0.29	0.42 ± 0.12	1.26 ± 0.25	0.54 ± 0.17
22:1n-11	0.00 ± 0.01	0.18 ± 0.08	0.19 ± 0.04	0.31 ± 0.09	0.22 ± 0.15	0.14 ± 0.07	0.10 ± 0.03	0.40 ± 0.22
subtotal:	14.29 ± 1.92	17.62 ± 1.35	16.12 ± 0.90	17.53 ± 1.66	16.16 ± 1.95	16.82 ± 2.69	23.58 ± 5.47	15.29 ± 1.83
Polyunsaturated FA								
18:2n-6	1.51 ± 0.31	1.59 ± 0.14	1.00 ± 0.08	1.46 ± 0.11	1.28 ± 0.15	1.32 ± 0.19	0.92 ± 0.18	1.80 ± 0.24
20:4n-6	8.37 ± 2.92	9.14 ± 1.34	4.23 ± 0.12	1.77 ± 0.35	5.34 ± 2.02	5.45 ± 1.40	3.88 ± 0.98	12.48 ± 2.01
22:4n-6	2.74 ± 0.54	2.86 ± 0.64	0.96 ± 0.12	0.59 ± 0.10	1.01 ± 0.46	1.01 ± 0.61	0.64 ± 0.13	2.43 ± 0.53
20:5n-3	10.87 ± 2.12	8.69 ± 1.12	4.29 ± 0.37	4.76 ± 0.34	7.70 ± 1.73	6.45 ± 1.25	4.53 ± 1.61	4.36 ± 0.86
22:5n-6	0.60 ± 0.24	1.13 ± 0.34	2.93 ± 0.18	1.81 ± 0.28	1.08 ± 0.20	1.56 ± 0.31	2.42 ± 0.33	1.54 ± 0.48
22:5n-3	4.40 ± 0.68	2.54 ± 0.49	2.90 ± 0.50	3.40 ± 0.40	1.92 ± 0.49	2.03 ± 0.62	2.62 ± 0.35	3.20 ± 0.85
22:6n-3	4.54 ± 2.15	6.97 ± 1.19	26.10 ± 1.03	22.04 ± 3.36	18.09 ± 5.44	21.28 ± 4.38	24.92 ± 4.00	9.55 ± 3.46
subtotal:	33.04 ± 6.09	32.92 ± 3.13	42.41 ± 1.17	35.82 ± 3.68	36.43 ± 5.48	39.10 ± 3.34	39.93 ± 6.10	35.36 ± 5.16
Total:	89.27 ± 1.12	85.64 ± 1.77	87.51 ± 0.46	85.19 ± 1.16	87.87 ± 1.06	87.70 ± 2.21	88.71 ± 1.52	84.73 ± 2.37

APPENDIX 3.2 *continued*

	Fishes							
Group	17	17	17	13	22	22	22	1
Species name	*Bothus mancus*	*Bothus pantherinus*	*Bothus thompsoni*	*Callionymus decoratus*	*Canthigaster coronata*	*Canthigaster jactator*	*Canthigaster rivulata*	*Centropyge potteri*
Common name	(Flowery flounder)	(Panther flounder)	(Thompson's flounder)	(Longtail dragonet)	(Crown toby)	(Hawaiian whitespotted toby)	(Maze toby)	(Potter's angelfish)
	n=16	n=75	n=25	n=20	n=20	n=24	n=16	n=20
Length (cm)	12.69 ± 2.89	5.48 ± 0.84	9.10 ± 2.38	11.39 ± 3.25	7.95 ± 1.86	6.42 ± 0.87	7.78 ± 1.87	8.31 ± 1.72
Mass (g)	44.77 ± 24.66	3.45 ± 1.58	9.33 ± 6.17	5.06 ± 2.60	24.49 ± 16.06	9.79 ± 4.01	14.04 ± 10.51	25.89 ± 13.25
Lipid content (%)	1.07 ± 0.26	2.11 ± 0.76	2.02 ± 0.95	1.19 ± 0.16	1.48 ± 0.65	1.59 ± 0.69	0.97 ± 0.73	4.30 ± 1.14
Saturated FA								
14:0	1.38 ± 0.47	3.58 ± 1.22	5.53 ± 2.48	2.50 ± 1.27	0.77 ± 0.25	0.95 ± 0.26	0.89 ± 0.23	7.68 ± 1.10
16:0	18.50 ± 1.51	20.46 ± 1.74	19.57 ± 2.24	18.88 ± 1.62	19.98 ± 4.88	21.71 ± 2.95	16.17 ± 2.75	29.57 ± 1.95
18:0	10.12 ± 1.22	7.80 ± 1.23	7.45 ± 1.12	11.40 ± 2.24	11.56 ± 1.51	11.40 ± 2.23	13.99 ± 1.23	6.60 ± 0.76
subtotal:	30.00 ± 1.31	31.84 ± 2.24	32.55 ± 3.64	32.79 ± 3.75	32.31 ± 4.84	34.06 ± 3.27	31.05 ± 2.55	43.86 ± 2.36
Monounsaturated FA								
16:1n-7	1.99 ± 0.52	3.47 ± 0.61	3.66 ± 0.85	2.70 ± 0.58	1.68 ± 0.66	2.17 ± 0.87	1.88 ± 0.60	7.84 ± 1.16
18:1n-9	9.62 ± 1.29	9.71 ± 2.03	9.62 ± 2.27	6.18 ± 0.83	7.07 ± 1.86	7.79 ± 0.92	7.20 ± 1.05	6.81 ± 0.85
18:1n-7	2.34 ± 0.51	2.17 ± 0.24	2.38 ± 0.35	2.89 ± 0.40	3.09 ± 0.46	3.07 ± 0.33	2.79 ± 0.46	2.48 ± 0.20
20:1n-9	0.52 ± 0.13	0.60 ± 0.11	0.69 ± 0.22	0.37 ± 0.08	0.57 ± 0.19	0.32 ± 0.05	0.68 ± 0.13	0.25 ± 0.06
22:1n-11	0.09 ± 0.08	0.20 ± 0.11	0.34 ± 0.16	0.25 ± 0.07	0.36 ± 0.27	0.42 ± 0.21	0.48 ± 0.15	1.45 ± 2.14
subtotal:	14.56 ± 1.25	16.16 ± 1.83	16.69 ± 1.79	12.39 ± 1.32	12.78 ± 2.36	13.78 ± 1.66	13.03 ± 1.61	18.84 ± 1.45
Polyunsaturated FA								
18:2n-6	0.99 ± 0.15	1.18 ± 0.08	1.22 ± 0.07	1.05 ± 0.19	1.05 ± 0.45	1.22 ± 0.23	0.88 ± 0.21	1.66 ± 0.18
20:4n-6	10.43 ± 2.51	3.33 ± 0.66	3.55 ± 1.49	8.92 ± 1.57	11.23 ± 3.02	11.08 ± 2.05	12.34 ± 3.11	5.28 ± 0.73
22:4n-6	2.16 ± 0.59	0.68 ± 0.20	0.64 ± 0.31	2.38 ± 0.81	3.90 ± 0.93	4.29 ± 0.97	4.14 ± 0.72	1.36 ± 0.33
20:5n-3	4.71 ± 1.17	5.08 ± 0.89	5.38 ± 0.93	4.75 ± 0.63	2.38 ± 0.72	2.99 ± 1.02	3.09 ± 0.82	6.45 ± 1.77
22:5n-6	2.04 ± 0.67	1.74 ± 0.20	1.67 ± 0.31	2.49 ± 0.38	3.41 ± 1.84	1.76 ± 0.56	3.57 ± 1.09	0.82 ± 0.43
22:5n-3	4.25 ± 0.86	2.69 ± 0.67	2.30 ± 0.31	2.68 ± 0.41	3.70 ± 1.35	4.24 ± 1.10	4.24 ± 1.36	2.59 ± 0.51
22:6n-3	20.09 ± 3.40	24.28 ± 2.24	20.99 ± 2.53	19.94 ± 4.05	13.00 ± 5.05	9.83 ± 2.88	13.78 ± 3.19	2.94 ± 1.24
subtotal:	44.68 ± 2.56	38.98 ± 2.33	35.75 ± 2.94	42.22 ± 4.97	38.67 ± 7.92	35.40 ± 4.63	42.05 ± 5.27	21.10 ± 2.01
Total:	89.23 ± 1.65	86.97 ± 0.95	84.99 ± 2.58	87.40 ± 1.42	83.76 ± 2.41	83.24 ± 2.04	86.13 ± 2.19	83.80 ± 1.81

APPENDIX 3.2 *continued*

	Fishes							
Group	8	8	8	8	8	21	21	12
Species name	*Chaetodon fremblii*	*Chaetodon miliaris*	*Chaetodon multicinctus*	*Chaetodon ornatissimus*	*Chaetodon quadrimaculatus*	*Chlorurus perspicillatus*	*Chlorurus sordidus*	*Chromis ovalis*
Common name	(Bluestripe butterflyfish)	(Milletseed butterflyfish)	(Multiband butterflyfish)	(Ornate butterflyfish)	(Fourspot butterflyfish)	(Spectacled parrotfish)	(Bullethead parrotfish)	(Oval chromis)
	n=22	n=27	n=19	n=20	n=20	n=22	n=19	n=21
Length (cm)	9.80 ± 1.86	9.55 ± 2.69	9.44 ± 1.24	15.24 ± 3.47	12.33 ± 1.03	20.61 ± 5.94	17.96 ± 5.53	10.93 ± 1.67
Mass (g)	28.25 ± 13.41	27.64 ± 17.94	25.09 ± 7.98	145.12 ± 70.88	63.33 ± 11.45	275.15 ± 229.20	198.38 ± 176.32	47.77 ± 17.41
Lipid content (%)	4.35 ± 2.28	3.06 ± 1.87	3.41 ± 1.70	3.38 ± 2.05	4.67 ± 2.72	1.75 ± 1.22	2.10 ± 0.79	4.56 ± 2.06
Saturated FA								
14:0	2.64 ± 0.57	3.34 ± 1.43	1.87 ± 0.54	1.66 ± 0.33	2.71 ± 0.79	3.03 ± 1.37	3.51 ± 1.23	5.03 ± 1.98
16:0	26.10 ± 2.59	24.68 ± 2.85	26.11 ± 3.14	23.67 ± 1.84	31.53 ± 2.48	26.60 ± 2.28	29.80 ± 2.50	28.59 ± 2.28
18:0	9.02 ± 1.42	7.76 ± 1.67	10.84 ± 1.17	11.55 ± 0.60	9.86 ± 0.64	7.21 ± 1.32	7.34 ± 0.54	6.93 ± 1.80
subtotal:	37.76 ± 2.64	35.78 ± 2.75	38.83 ± 2.86	36.88 ± 2.32	44.09 ± 2.26	36.84 ± 2.49	40.66 ± 3.13	40.55 ± 2.52
Monounsaturated FA								
16:1n-7	2.10 ± 0.31	2.74 ± 1.06	1.48 ± 0.45	1.08 ± 0.16	2.74 ± 0.59	2.93 ± 1.63	3.47 ± 1.31	5.21 ± 1.61
18:1n-9	8.56 ± 1.77	9.88 ± 1.54	10.02 ± 1.20	8.21 ± 0.92	9.24 ± 1.48	6.62 ± 0.96	6.19 ± 0.58	7.51 ± 1.56
18:1n-7	2.91 ± 0.51	2.53 ± 0.35	0.99 ± 0.21	0.76 ± 0.09	1.29 ± 0.16	3.48 ± 0.62	3.60 ± 0.26	1.79 ± 0.36
20:1n-9	0.97 ± 0.58	1.00 ± 0.45	1.90 ± 0.66	2.50 ± 0.75	1.26 ± 0.29	0.20 ± 0.10	0.19 ± 0.04	0.53 ± 0.16
22:1n-11	1.08 ± 1.77	2.43 ± 2.73	0.10 ± 0.13	0.03 ± 0.05	0.11 ± 0.11	0.12 ± 0.17	0.05 ± 0.05	1.56 ± 3.38
subtotal:	15.61 ± 2.46	18.58 ± 3.70	14.49 ± 1.40	12.57 ± 1.31	14.64 ± 1.63	13.35 ± 1.75	13.49 ± 1.52	16.60 ± 2.73
Polyunsaturated FA								
18:2n-6	1.17 ± 0.40	1.02 ± 0.30	0.60 ± 0.10	0.54 ± 0.08	0.69 ± 0.14	2.98 ± 0.96	3.76 ± 0.78	1.42 ± 0.22
20:4n-6	8.49 ± 2.28	5.90 ± 2.77	10.69 ± 1.85	9.03 ± 0.83	6.86 ± 1.18	14.74 ± 2.57	13.82 ± 2.66	5.63 ± 4.01
22:4n-6	3.54 ± 0.79	2.43 ± 1.39	8.72 ± 1.67	9.97 ± 1.30	5.24 ± 1.02	1.44 ± 0.33	1.35 ± 0.32	0.82 ± 0.36
20:5n-3	4.34 ± 0.74	3.23 ± 0.66	1.75 ± 0.45	1.73 ± 0.54	2.73 ± 0.56	7.01 ± 1.88	4.84 ± 0.91	6.50 ± 2.65
22:5n-6	1.15 ± 0.39	1.52 ± 0.61	0.17 ± 0.11	0.15 ± 0.07	0.73 ± 0.64	1.19 ± 0.43	1.20 ± 0.29	1.05 ± 0.31
22:5n-3	3.45 ± 0.79	2.77 ± 0.76	3.28 ± 0.59	3.11 ± 0.35	5.71 ± 2.24	2.41 ± 0.88	2.36 ± 0.44	1.84 ± 0.66
22:6n-3	8.45 ± 2.39	14.32 ± 4.26	6.43 ± 2.80	7.67 ± 3.85	4.69 ± 1.21	6.45 ± 2.92	4.42 ± 1.65	11.11 ± 6.88
subtotal:	30.59 ± 3.57	31.19 ± 6.82	31.64 ± 3.81	32.20 ± 3.45	26.64 ± 2.35	36.23 ± 5.49	31.76 ± 4.48	28.37 ± 4.22
Total:	83.96 ± 1.32	85.55 ± 1.54	84.96 ± 1.25	81.66 ± 1.58	85.37 ± 1.30	86.42 ± 2.03	85.91 ± 1.30	85.52 ± 2.33

APPENDIX 3.2 *continued*

Fishes

Group	7	37	37	31	34	14	12	25
Species name	*Conger cinereus*	*Coris ballieui*	*Coris flavovittata*	*Ctenochaetus strigosus*	*Cymolutes lecluse*	*Dactyloptena orientalis*	*Dascyllus albisella*	*Etelis carbunculus*
Common name	(Mustache conger)	(Lined coris)	(Yellow striped coris)	(Goldring surgeonfish)	(Hawaiian knifefish)	(Helmut gurnard)	(Hawaiian dascyllus)	(Squirrelfish snapper)
	n=20	n=16	n=20	n=16	n=23	n=24	n=20	n=21
Length (cm)	100.46 ± 29.34	18.01 ± 3.02	23.80 ± 8.57	13.84 ± 2.41	8.53 ± 3.53	8.25 ± 1.28	9.53 ± 1.58	30.85 ± 4.27
Mass (g)	1741.48 ± 939.59	82.80 ± 43.98	332.01 ± 388.24	100.30 ± 45.03	13.08 ± 15.49	14.40 ± 4.47	31.90 ± 10.44	500.57 ± 217.41
Lipid content (%)	2.04 ± 1.05	1.84 ± 0.99	1.10 ± 0.39	6.66 ± 4.11	2.14 ± 0.85	1.90 ± 0.71	3.29 ± 2.55	2.08 ± 0.74
Saturated FA								
14:0	3.79 ± 1.06	3.34 ± 1.13	1.94 ± 0.87	10.25 ± 1.04	3.30 ± 1.12	4.65 ± 1.47	3.22 ± 1.23	2.50 ± 0.31
16:0	24.81 ± 2.61	20.04 ± 1.27	20.08 ± 1.05	27.89 ± 1.97	19.29 ± 1.89	22.44 ± 2.23	28.65 ± 5.26	19.97 ± 0.80
18:0	7.84 ± 0.67	9.00 ± 1.00	9.90 ± 0.48	3.38 ± 0.89	9.29 ± 1.19	8.98 ± 1.46	9.20 ± 1.05	6.19 ± 0.45
subtotal:	36.45 ± 3.21	32.38 ± 2.46	31.92 ± 1.65	41.53 ± 2.01	31.88 ± 2.47	36.07 ± 2.23	41.07 ± 5.29	28.66 ± 0.92
Monounsaturated FA								
16:1n-7	4.72 ± 1.19	3.13 ± 0.62	2.17 ± 0.58	12.19 ± 1.39	4.03 ± 1.31	5.05 ± 1.52	4.51 ± 1.76	4.31 ± 0.71
18:1n-9	12.24 ± 1.50	10.07 ± 1.11	7.21 ± 1.05	4.33 ± 0.75	9.26 ± 0.77	7.29 ± 1.04	7.40 ± 1.01	14.91 ± 1.90
18:1n-7	2.94 ± 0.29	2.51 ± 0.37	2.60 ± 0.33	2.38 ± 0.34	3.63 ± 0.93	2.97 ± 0.38	2.95 ± 1.36	2.85 ± 0.30
20:1n-9	0.66 ± 0.12	0.59 ± 0.12	0.55 ± 0.27	0.64 ± 0.35	0.55 ± 0.14	1.03 ± 0.39	0.97 ± 0.27	1.42 ± 0.19
22:1n-11	0.37 ± 0.46	0.24 ± 0.14	0.45 ± 0.26	0.03 ± 0.04	0.14 ± 0.05	0.10 ± 0.14	0.19 ± 0.29	0.27 ± 0.10
subtotal:	20.92 ± 2.42	16.53 ± 1.35	12.98 ± 1.59	19.59 ± 1.62	17.60 ± 2.08	16.44 ± 1.74	16.03 ± 3.60	23.77 ± 2.72
Polyunsaturated FA								
18:2n-6	1.14 ± 0.32	1.37 ± 0.16	1.67 ± 0.39	1.48 ± 0.11	1.21 ± 0.20	1.24 ± 0.23	1.35 ± 0.17	0.91 ± 0.08
20:4n-6	6.29 ± 1.47	6.49 ± 1.80	15.66 ± 3.46	3.43 ± 1.71	6.37 ± 1.69	3.17 ± 1.04	5.01 ± 1.81	2.61 ± 0.46
22:4n-6	2.40 ± 0.48	1.27 ± 0.35	3.94 ± 0.73	0.87 ± 0.22	1.66 ± 0.34	0.55 ± 0.16	1.22 ± 0.26	0.63 ± 0.10
20:5n-3	2.64 ± 0.52	6.20 ± 0.94	5.09 ± 0.83	7.02 ± 1.12	8.05 ± 1.49	5.56 ± 0.69	4.25 ± 0.92	3.39 ± 0.39
22:5n-6	1.39 ± 0.25	1.65 ± 0.27	1.97 ± 0.42	0.66 ± 0.21	1.35 ± 0.34	1.61 ± 0.30	1.26 ± 0.62	1.88 ± 0.18
22:5n-3	3.21 ± 0.40	1.85 ± 0.40	3.37 ± 0.76	1.65 ± 0.31	2.19 ± 0.43	2.03 ± 0.27	2.35 ± 0.55	2.72 ± 0.18
22:6n-3	14.01 ± 3.75	18.45 ± 4.09	9.62 ± 3.57	3.26 ± 1.49	14.61 ± 3.96	21.39 ± 3.66	14.62 ± 5.95	24.65 ± 2.34
subtotal:	31.08 ± 4.75	37.28 ± 4.07	41.31 ± 5.14	18.37 ± 3.91	35.45 ± 3.87	35.56 ± 4.24	30.05 ± 8.06	36.79 ± 2.71
Total:	88.44 ± 1.48	86.19 ± 1.22	86.20 ± 3.38	79.48 ± 2.57	84.93 ± 2.46	88.07 ± 0.76	87.15 ± 1.83	89.22 ± 0.84

APPENDIX 3.2 *continued*

	Fishes							
Group	8	20	20	20	20	20	20	20
Species name	*Forcipiger flavissimus*	*Gymnothorax albimarginatus*	*Gymnothorax berndti*	*Gymnothorax eurostus*	*Gymnothorax flavimarginatus*	*Gymnothorax meleagris*	*Gymnothorax steindachneri*	*Gymnothorax undulatus*
Common name	(Forcepfish)	(Whitemargin moray)	(Berndt's moray)	(Stout moray)	(Yellow margin moray)	(Whitemouth moray)	(Steindachner's moray)	(Undulated moray)
	n=26	n=20	n=20	n=14	n=19	n=18	n=25	n=19
Length (cm)	14.46 ± 14.01	89.48 ± 9.31	79.13 ± 8.39	41.32 ± 8.79	93.81 ± 24.04	75.31 ± 15.33	49.93 ± 10.60	72.60 ± 23.97
Mass (g)	30.05 ± 16.31	728.65 ± 218.42	660.83 ± 349.47	189.95 ± 126.07	966.69 ± 1160.0	1148.55 ± 709.39	327.81 ± 185.86	999.38 ± 818.33
Lipid content (%)	3.62 ± 2.06	0.84 ± 0.41	1.41 ± 0.74	1.42 ± 0.81	1.67 ± 1.03	1.50 ± 0.80	0.85 ± 0.37	1.83 ± 1.47
Saturated FA								
14:0	3.25 ± 0.94	2.45 ± 1.26	2.24 ± 0.91	2.25 ± 1.03	3.54 ± 1.64	3.37 ± 1.27	1.59 ± 0.59	2.76 ± 1.23
16:0	30.21 ± 4.76	19.23 ± 2.65	19.92 ± 1.18	19.99 ± 2.35	23.57 ± 3.62	23.68 ± 2.51	18.34 ± 1.16	22.51 ± 4.11
18:0	9.78 ± 1.91	10.92 ± 1.39	9.33 ± 1.30	9.93 ± 1.19	10.44 ± 1.08	9.61 ± 1.36	10.70 ± 0.82	9.24 ± 1.66
subtotal:	43.24 ± 3.86	32.60 ± 3.03	31.48 ± 1.74	32.17 ± 2.53	37.56 ± 4.66	36.67 ± 2.88	30.63 ± 1.70	34.51 ± 3.86
Monounsaturated FA								
16:1n-7	2.11 ± 0.60	2.58 ± 0.82	3.15 ± 0.83	2.91 ± 1.16	3.93 ± 1.54	3.19 ± 1.13	1.71 ± 0.64	3.78 ± 1.56
18:1n-9	7.60 ± 1.78	10.76 ± 1.41	11.82 ± 3.15	10.27 ± 1.48	9.87 ± 1.55	9.12 ± 1.00	9.22 ± 0.85	10.13 ± 1.22
18:1n-7	2.00 ± 0.44	2.53 ± 0.42	2.77 ± 0.43	3.09 ± 0.55	3.02 ± 0.43	2.58 ± 0.30	2.50 ± 0.43	2.91 ± 0.32
20:1n-9	2.17 ± 1.05	0.81 ± 0.44	1.31 ± 0.47	0.73 ± 0.27	0.87 ± 0.28	0.92 ± 0.35	0.81 ± 0.21	0.87 ± 0.33
22:1n-11	0.38 ± 0.22	0.27 ± 0.41	0.45 ± 0.43	0.37 ± 0.29	0.24 ± 0.23	0.33 ± 0.35	0.16 ± 0.20	0.21 ± 0.22
subtotal:	14.25 ± 2.09	16.94 ± 2.63	19.50 ± 4.43	17.36 ± 2.03	17.92 ± 2.92	16.14 ± 1.21	14.40 ± 1.82	17.89 ± 2.22
Polyunsaturated FA								
18:2n-6	0.88 ± 0.33	0.72 ± 0.11	0.76 ± 0.21	1.06 ± 0.24	1.17 ± 0.23	1.04 ± 0.17	0.66 ± 0.19	0.95 ± 0.30
20:4n-6	4.41 ± 1.98	10.21 ± 3.33	6.47 ± 2.94	8.88 ± 1.75	8.94 ± 3.40	6.74 ± 2.20	9.76 ± 2.69	7.51 ± 3.03
22:4n-6	2.76 ± 1.39	4.42 ± 1.25	2.08 ± 0.78	3.02 ± 0.65	3.03 ± 0.72	3.33 ± 0.95	2.85 ± 0.83	3.71 ± 1.03
20:5n-3	2.16 ± 0.79	1.53 ± 1.62	2.25 ± 0.53	3.32 ± 1.73	2.39 ± 0.58	2.58 ± 1.15	2.96 ± 1.07	2.15 ± 0.80
22:5n-6	0.79 ± 0.28	1.96 ± 0.33	2.01 ± 0.40	1.47 ± 0.24	1.32 ± 0.39	1.72 ± 0.37	1.67 ± 0.19	1.60 ± 0.27
22:5n-3	2.72 ± 0.81	2.40 ± 0.74	2.66 ± 0.48	3.03 ± 0.55	2.56 ± 0.41	3.76 ± 0.44	1.94 ± 0.42	3.75 ± 1.32
22:6n-3	11.86 ± 5.66	16.37 ± 2.48	23.22 ± 4.30	17.35 ± 3.63	11.91 ± 4.86	16.09 ± 3.02	22.88 ± 3.04	16.03 ± 4.85
subtotal:	25.58 ± 4.98	37.61 ± 4.29	39.45 ± 5.29	38.13 ± 3.56	31.32 ± 7.38	35.27 ± 3.59	42.72 ± 2.99	35.70 ± 6.05
Total:	83.07 ± 4.68	87.15 ± 1.30	90.43 ± 1.37	87.66 ± 1.21	86.80 ± 2.31	88.07 ± 1.06	87.75 ± 1.06	88.10 ± 1.73

APPENDIX 3.2 *continued*

Fishes

Group	9	34	34	23	23	26	10	7
Species name	*Heniochus diphreutes*	*Iniistius pavo*	*Iniistius umbrilatus*	*Kyphosus bigibbus*	*Kyphosus vaigiensis*	*Lutjanus kasmira*	*Malacanthus brevirostris*	*Meadia abyssalis*
Common name	(Pennantfish)	(Peacock razorfish)	(Blackside razorfish)	(Gray chub)	(Low fin chub)	(Bluestripe snapper)	(Flagtail tilefish)	(Abyssal cutthroat eel)
	n=36	n=15	n=19	n=19	n=19	n=22	n=16	n=19
Length (cm)	4.39 ± 0.86	11.02 ± 4.69	9.22 ± 3.28	24.67 ± 4.75	20.27 ± 5.62	12.15 ± 7.70	11.71 ± 3.92	50.58 ± 9.98
Mass (g)	2.69 ± 1.55	37.91 ± 45.21	27.28 ± 30.74	409.37 ± 175.34	257.97 ± 175.16	89.37 ± 117.58	16.29 ± 17.52	134.70 ± 74.18
Lipid content (%)	3.94 ± 1.66	1.81 ± 0.89	2.59 ± 0.93	1.68 ± 1.15	1.43 ± 0.71	2.68 ± 1.04	1.55 ± 0.51	2.64 ± 0.97
Saturated FA								
14:0	5.38 ± 1.69	3.74 ± 2.32	5.22 ± 1.65	3.84 ± 1.60	3.48 ± 1.73	3.08 ± 1.01	1.60 ± 1.15	2.69 ± 0.95
16:0	28.21 ± 5.33	19.24 ± 1.24	20.86 ± 1.93	24.77 ± 4.38	24.64 ± 2.28	21.14 ± 2.75	18.34 ± 1.95	19.82 ± 1.21
18:0	8.11 ± 1.04	9.65 ± 0.94	8.47 ± 0.64	8.52 ± 1.54	8.93 ± 1.58	9.61 ± 0.96	11.56 ± 0.80	4.47 ± 0.59
subtotal:	41.71 ± 6.50	32.63 ± 2.51	34.55 ± 2.68	37.13 ± 4.77	37.04 ± 2.34	33.83 ± 3.18	31.50 ± 3.20	26.98 ± 1.28
Monounsaturated FA								
16:1n-7	5.18 ± 1.47	2.86 ± 1.17	3.58 ± 0.54	1.82 ± 0.70	1.73 ± 0.84	3.61 ± 0.89	1.84 ± 0.81	3.54 ± 1.02
18:1n-9	4.89 ± 1.22	9.47 ± 1.26	8.87 ± 1.43	10.10 ± 1.04	9.56 ± 0.92	10.30 ± 2.87	6.97 ± 0.95	20.23 ± 3.52
18:1n-7	2.54 ± 0.32	2.98 ± 0.98	2.41 ± 0.28	1.38 ± 0.63	1.20 ± 0.50	2.83 ± 0.21	2.82 ± 0.30	2.84 ± 0.26
20:1n-9	0.89 ± 0.38	0.58 ± 0.33	0.65 ± 0.28	1.10 ± 0.53	0.84 ± 0.47	0.82 ± 0.34	0.48 ± 0.17	1.87 ± 0.63
22:1n-11	0.06 ± 0.05	0.10 ± 0.04	0.17 ± 0.06	0.02 ± 0.03	0.04 ± 0.03	0.18 ± 0.14	0.33 ± 0.23	0.45 ± 0.27
subtotal:	13.55 ± 1.71	16.00 ± 2.72	15.69 ± 1.64	14.41 ± 1.64	13.37 ± 1.50	17.75 ± 3.76	12.44 ± 1.68	28.93 ± 4.63
Polyunsaturated FA								
18:2n-6	1.29 ± 0.23	1.07 ± 0.15	1.17 ± 0.13	2.61 ± 0.67	2.60 ± 0.83	1.20 ± 0.32	1.11 ± 0.12	0.88 ± 0.09
20:4n-6	1.86 ± 1.54	5.55 ± 1.40	4.89 ± 1.27	9.51 ± 3.54	10.09 ± 3.68	4.02 ± 2.23	10.36 ± 3.31	3.32 ± 1.12
22:4n-6	0.68 ± 0.29	0.90 ± 0.30	0.89 ± 0.32	2.96 ± 0.56	2.46 ± 0.82	0.92 ± 0.73	4.50 ± 1.39	0.34 ± 0.10
20:5n-3	3.45 ± 0.95	7.19 ± 2.25	7.36 ± 1.13	4.48 ± 1.08	5.61 ± 1.26	5.11 ± 1.49	4.56 ± 0.51	5.01 ± 1.96
22:5n-6	1.58 ± 0.62	1.73 ± 0.53	1.48 ± 0.21	0.88 ± 0.41	1.06 ± 0.65	1.57 ± 0.31	2.11 ± 0.52	1.06 ± 0.22
22:5n-3	4.99 ± 1.48	1.51 ± 0.34	1.39 ± 0.26	3.67 ± 0.51	3.76 ± 0.74	2.24 ± 0.36	3.76 ± 0.50	1.53 ± 0.22
22:6n-3	17.34 ± 4.32	20.64 ± 6.98	17.94 ± 3.18	7.94 ± 4.75	9.62 ± 6.26	20.60 ± 4.04	16.58 ± 3.84	20.90 ± 4.00
subtotal:	31.19 ± 6.16	38.58 ± 5.73	35.11 ± 3.20	32.05 ± 7.59	35.19 ± 5.84	35.67 ± 5.85	42.98 ± 6.35	33.05 ± 5.06
Total:	86.45 ± 1.66	87.22 ± 1.77	85.35 ± 1.74	83.59 ± 2.42	85.60 ± 3.18	87.25 ± 1.14	86.92 ± 2.51	88.96 ± 0.81

APPENDIX 3.2 *continued*

	Fishes							
Group	35	15	15	29	32	32	10	6
Species name	*Melichthys niger*	*Mulloidichthys flavolineatus*	*Mulloidichthys vanicolensis*	*Myripristis berndti*	*Naso lituratus*	*Naso unicornis*	*Ophichthus kunaloa*	*Ophidion muraenolepis*
Common name	(Black triggerfish)	(Yellow stripe goatfish)	(Yellow fin goatfish)	(Bigscale soldierfish)	(Orangespine unicornfish)	(Bluespine unicornfish)	(Snake eel)	(Black edged cusk eel)
	n=20	n=21	n=20	n=20	n=19	n=19	n=20	n=20
Length (cm)	20.23 ± 3.85	22.18 ± 3.16	19.50 ± 4.13	17.61 ± 4.20	26.72 ± 2.09	22.20 ± 5.72	39.79 ± 2.50	13.54 ± 2.61
Mass (g)	288.65 ± 119.58	198.08 ± 96.99	162.29 ± 90.18	199.65 ± 122.44	468.46 ± 130.04	286.06 ± 191.30	33.96 ± 7.30	19.74 ± 13.82
Lipid content (%)	1.61 ± 1.43	1.86 ± 1.10	2.31 ± 1.21	3.39 ± 1.74	7.44 ± 6.11	4.29 ± 3.31	2.37 ± 0.80	1.74 ± 0.71
Saturated FA								
14:0	0.78 ± 0.23	2.31 ± 0.87	2.79 ± 0.81	4.80 ± 0.43	5.52 ± 0.62	3.90 ± 0.80	3.08 ± 1.02	3.52 ± 1.40
16:0	25.68 ± 3.87	19.36 ± 4.07	22.45 ± 2.76	26.40 ± 2.50	31.43 ± 2.90	31.90 ± 4.54	16.32 ± 0.68	18.34 ± 2.24
18:0	10.38 ± 1.21	11.35 ± 1.77	10.30 ± 0.79	9.41 ± 0.91	6.01 ± 1.18	7.34 ± 1.60	5.33 ± 1.32	8.01 ± 1.05
subtotal:	36.85 ± 3.35	33.02 ± 4.32	35.55 ± 3.11	40.61 ± 2.38	42.96 ± 2.10	43.14 ± 3.79	24.73 ± 1.25	29.87 ± 2.72
Monounsaturated FA								
16:1n-7	1.78 ± 0.67	3.09 ± 0.80	3.94 ± 0.95	4.62 ± 0.78	1.95 ± 0.65	2.34 ± 0.72	6.51 ± 1.90	3.01 ± 0.76
18:1n-9	9.54 ± 1.62	5.99 ± 1.75	8.25 ± 1.06	9.50 ± 1.18	11.37 ± 1.21	11.57 ± 2.25	18.30 ± 3.11	9.49 ± 1.51
18:1n-7	4.49 ± 0.62	3.47 ± 0.55	3.16 ± 0.82	2.57 ± 0.23	1.71 ± 0.47	2.42 ± 0.50	3.19 ± 0.35	2.47 ± 0.52
20:1n-9	0.27 ± 0.10	0.61 ± 0.42	0.52 ± 0.17	0.96 ± 0.15	4.51 ± 1.13	3.24 ± 1.60	1.62 ± 0.37	0.68 ± 0.10
22:1n-11	0.07 ± 0.04	0.36 ± 0.20	0.21 ± 0.14	0.44 ± 0.62	0.00 ± 0.00	0.04 ± 0.11	0.22 ± 0.10	0.33 ± 0.42
subtotal:	16.15 ± 1.92	13.51 ± 1.83	16.08 ± 1.42	18.10 ± 2.02	19.54 ± 3.09	19.61 ± 4.13	29.85 ± 4.58	15.98 ± 1.23
Polyunsaturated FA								
18:2n-6	1.85 ± 0.43	1.29 ± 0.41	1.50 ± 0.50	1.29 ± 0.12	2.95 ± 0.39	2.47 ± 0.62	1.02 ± 0.26	1.18 ± 0.20
20:4n-6	9.66 ± 2.83	8.70 ± 1.59	6.73 ± 2.06	2.47 ± 0.47	5.88 ± 1.81	7.22 ± 3.11	3.95 ± 1.69	3.92 ± 1.79
22:4n-6	1.60 ± 0.48	3.13 ± 0.77	2.03 ± 0.85	1.04 ± 0.60	3.14 ± 1.29	3.00 ± 1.13	0.46 ± 0.23	1.20 ± 0.62
20:5n-3	7.30 ± 1.22	6.13 ± 1.32	6.84 ± 1.53	4.33 ± 0.76	3.93 ± 0.89	3.72 ± 1.10	5.40 ± 1.74	6.80 ± 1.22
22:5n-6	0.85 ± 0.31	1.71 ± 0.64	1.46 ± 0.39	1.19 ± 0.26	0.40 ± 0.16	0.74 ± 0.53	1.32 ± 0.32	1.82 ± 0.41
22:5n-3	3.08 ± 0.56	2.73 ± 0.43	2.66 ± 0.90	2.96 ± 0.50	2.03 ± 0.74	2.03 ± 0.52	1.97 ± 0.37	2.26 ± 0.36
22:6n-3	10.34 ± 4.41	11.25 ± 4.48	13.14 ± 5.76	14.21 ± 2.30	1.73 ± 0.93	3.61 ± 4.26	17.70 ± 2.48	24.97 ± 3.58
subtotal:	34.69 ± 4.74	34.94 ± 5.81	34.36 ± 4.83	27.50 ± 2.37	20.06 ± 4.66	22.78 ± 7.20	31.82 ± 3.97	42.15 ± 3.23
Total:	87.68 ± 1.07	81.48 ± 2.87	85.99 ± 2.74	86.21 ± 1.12	82.56 ± 1.67	85.53 ± 1.86	86.40 ± 0.65	88.00 ± 0.99

APPENDIX 3.2 *continued*

Fishes

Group	37	19	16	16	16	16	4	5
Species name	*Oxycheilinus unifasciatus*	*Parapercis schauinslandii*	*Parupeneus chrysonemus*	*Parupeneus bifasciatus*	*Parupeneus multifasciatus*	*Parupeneus pleurostigma*	*Polymixia berndti*	*Priacanthus alalaua*
Common name	(Ringtail wrasse)	(Redspotted sandperch)	(Yellow barbel goatfish)	(Doublebar goatfish)	(Manybar goatfish)	(Sidespot goatfish)	(Berndt's beard fish)	(Forskal's bigeye)
	n=19	n=18	n=19	n=19	n=20	n=19	n=20	n=20
Length (cm)	21.23 ± 4.85	6.78 ± 2.05	9.71 ± 0.86	16.65 ± 4.91	16.43 ± 3.02	16.49 ± 3.97	15.61 ± 4.66	11.29 ± 4.05
Mass (g)	235.54 ± 178.59	7.61 ± 6.71	18.98 ± 5.02	107.11 ± 85.16	86.15 ± 43.23	102.27 ± 97.99	121.13 ± 91.00	30.79 ± 22.55
Lipid content (%)	1.21 ± 0.57	1.94 ± 0.79	3.40 ± 1.16	1.40 ± 1.23	1.51 ± 1.18	2.69 ± 1.77	2.00 ± 0.90	2.64 ± 1.91
Saturated FA								
14:0	3.64 ± 1.36	4.18 ± 1.15	4.68 ± 0.80	2.94 ± 0.97	2.57 ± 1.05	3.28 ± 1.15	3.00 ± 1.15	2.56 ± 1.29
16:0	22.44 ± 1.73	20.81 ± 1.39	22.61 ± 1.30	22.33 ± 1.72	19.61 ± 1.99	20.58 ± 3.84	20.70 ± 1.41	20.14 ± 3.21
18:0	9.67 ± 0.86	9.33 ± 1.29	9.29 ± 0.62	10.54 ± 0.88	10.42 ± 0.82	9.64 ± 1.03	6.16 ± 0.87	8.97 ± 0.96
subtotal:	35.74 ± 2.26	34.32 ± 1.59	36.58 ± 1.78	35.81 ± 2.45	32.60 ± 2.89	33.51 ± 4.69	29.86 ± 1.48	31.68 ± 3.59
Monounsaturated FA								
16:1n-7	3.16 ± 1.42	3.74 ± 0.84	4.78 ± 0.59	3.49 ± 1.10	2.80 ± 0.97	3.49 ± 1.09	3.09 ± 0.56	2.57 ± 0.92
18:1n-9	9.62 ± 0.69	8.32 ± 1.06	9.57 ± 0.83	9.12 ± 1.95	8.10 ± 0.82	7.75 ± 0.69	17.48 ± 4.02	11.28 ± 1.49
18:1n-7	2.15 ± 0.32	2.63 ± 0.27	2.73 ± 0.27	2.98 ± 0.65	2.76 ± 0.49	2.88 ± 0.50	2.49 ± 0.58	1.93 ± 0.26
20:1n-9	0.46 ± 0.15	0.76 ± 0.17	0.76 ± 0.12	0.77 ± 0.41	0.52 ± 0.12	0.61 ± 0.24	2.16 ± 1.07	0.69 ± 0.28
22:1n-11	0.24 ± 0.20	0.25 ± 0.09	0.29 ± 0.15	0.21 ± 0.12	0.26 ± 0.19	0.43 ± 0.39	0.66 ± 1.61	0.15 ± 0.11
subtotal:	15.63 ± 1.59	15.71 ± 1.76	18.13 ± 1.31	16.58 ± 2.18	14.43 ± 1.83	15.15 ± 2.12	25.87 ± 5.98	16.63 ± 1.92
Polyunsaturated FA								
18:2n-6	1.30 ± 0.27	1.28 ± 0.11	1.26 ± 0.07	1.63 ± 0.32	1.50 ± 0.39	1.41 ± 0.26	0.65 ± 0.17	1.10 ± 0.19
20:4n-6	8.69 ± 1.28	3.16 ± 0.73	2.68 ± 0.57	8.11 ± 2.09	7.57 ± 1.82	6.31 ± 2.16	3.28 ± 0.92	3.08 ± 1.30
22:4n-6	2.26 ± 0.27	0.68 ± 0.16	0.68 ± 0.10	2.00 ± 0.70	1.88 ± 0.48	2.24 ± 0.93	0.45 ± 0.12	0.47 ± 0.32
20:5n-3	4.05 ± 0.77	4.50 ± 0.55	5.49 ± 0.43	7.74 ± 1.86	5.78 ± 1.13	5.77 ± 1.52	4.88 ± 1.41	5.47 ± 1.48
22:5n-6	2.01 ± 0.40	2.20 ± 0.50	1.48 ± 0.21	1.19 ± 0.34	1.87 ± 0.52	1.72 ± 0.65	1.44 ± 0.36	2.00 ± 0.54
22:5n-3	2.83 ± 0.34	1.74 ± 0.20	1.72 ± 0.16	2.20 ± 0.45	2.29 ± 0.41	2.13 ± 0.35	1.68 ± 0.22	1.28 ± 0.40
22:6n-3	16.65 ± 4.31	23.60 ± 2.86	19.33 ± 2.07	12.46 ± 4.30	19.44 ± 6.20	18.34 ± 7.61	22.72 ± 5.04	26.86 ± 5.09
subtotal:	37.79 ± 4.88	37.17 ± 3.59	32.64 ± 2.41	35.34 ± 4.42	40.34 ± 5.74	37.92 ± 7.51	35.09 ± 6.60	40.27 ± 5.91
Total:	89.16 ± 1.33	87.19 ± 0.89	87.35 ± 0.53	87.72 ± 1.78	87.37 ± 1.35	86.57 ± 1.77	90.83 ± 1.79	88.57 ± 1.43

APPENDIX 3.2 *continued*

	Fishes							
Group	5	27	28	3	30	21	24	36
Species name	*Priacanthus meeki*	*Pristipomoides filamentosus*	*Pristipomoides zonatus*	*Pseudopentaceros wheeleri*	*Sargocentron xantherythrum*	*Scarus dubius*	*Sebastapistes ballieui*	*Sufflamen bursa*
Common name	(Hawaiian bigeye)	(Pink snapper)	(Flower snapper)	(Armorhead)	(Hawaiian squirrelfish)	(Regal parrotfish)	(Spotfin scorpionfish)	(Lei triggerfish)
	n=20	n=24	n=19	n=20	n=21	n=19	n=19	n=19
Length (cm)	21.67 ± 5.88	51.86 ± 10.62	35.68 ± 2.88	30.33 ± 1.70	9.38 ± 2.24	21.96 ± 6.15	8.54 ± 1.60	15.24 ± 1.40
Mass (g)	217.06 ± 117.18	2888.37 ± 1318.84	1276.95 ± 262.88	614.51 ± 88.29	19.89 ± 10.69	330.04 ± 339.77	17.46 ± 7.98	103.11 ± 17.93
Lipid content (%)	1.67 ± 1.21	2.01 ± 2.10	2.28 ± 0.99	27.13 ± 4.62	4.06 ± 3.24	4.44 ± 2.16	1.19 ± 0.42	3.53 ± 2.23
Saturated FA								
14:0	3.68 ± 1.02	2.48 ± 0.88	3.57 ± 1.15	4.20 ± 0.35	4.48 ± 1.52	5.04 ± 1.15	1.76 ± 0.58	1.34 ± 0.32
16:0	20.86 ± 2.07	20.34 ± 1.13	20.21 ± 0.87	17.56 ± 0.69	23.73 ± 5.21	30.46 ± 3.47	18.14 ± 1.36	24.01 ± 2.47
18:0	8.73 ± 1.01	7.89 ± 0.59	6.74 ± 0.44	5.17 ± 0.39	10.53 ± 1.26	5.68 ± 0.82	10.23 ± 0.66	10.63 ± 0.69
subtotal:	33.27 ± 2.13	30.70 ± 1.49	30.52 ± 1.02	26.94 ± 0.67	38.74 ± 5.64	41.19 ± 3.33	30.14 ± 1.39	35.98 ± 2.35
Monounsaturated FA								
16:1n-7	3.58 ± 0.93	2.86 ± 1.09	5.25 ± 1.13	4.40 ± 0.43	3.23 ± 0.53	6.23 ± 1.53	2.40 ± 0.43	2.90 ± 0.63
18:1n-9	11.51 ± 2.71	12.03 ± 4.23	15.53 ± 3.79	26.54 ± 2.11	9.20 ± 1.43	6.48 ± 0.81	9.35 ± 0.48	8.75 ± 0.79
18:1n-7	2.41 ± 0.37	2.10 ± 0.32	2.91 ± 0.30	2.92 ± 0.22	2.93 ± 0.61	3.35 ± 0.63	2.36 ± 0.33	4.24 ± 0.40
20:1n-9	0.66 ± 0.28	1.11 ± 0.32	1.54 ± 0.32	2.65 ± 0.24	1.09 ± 0.26	0.27 ± 0.10	0.69 ± 0.23	0.51 ± 0.11
22:1n-11	0.20 ± 0.12	0.33 ± 0.23	0.48 ± 0.34	1.96 ± 0.80	0.70 ± 0.65	0.09 ± 0.19	0.23 ± 0.05	0.21 ± 0.12
subtotal:	18.36 ± 3.68	18.42 ± 5.87	25.70 ± 4.29	38.47 ± 1.78	17.17 ± 1.35	16.42 ± 1.17	15.03 ± 0.65	16.62 ± 1.24
Polyunsaturated FA								
18:2n-6	1.32 ± 0.20	1.08 ± 0.21	0.97 ± 0.18	0.83 ± 0.09	1.13 ± 0.14	2.47 ± 0.66	1.27 ± 0.08	1.49 ± 0.22
20:4n-6	3.63 ± 1.46	3.29 ± 1.01	2.96 ± 0.62	0.64 ± 0.05	5.48 ± 2.67	8.54 ± 3.16	10.13 ± 2.74	8.81 ± 2.05
22:4n-6	0.73 ± 0.44	0.65 ± 0.18	0.73 ± 0.22	0.11 ± 0.01	2.80 ± 1.39	0.99 ± 0.59	1.78 ± 0.59	3.74 ± 0.62
20:5n-3	5.31 ± 1.12	3.64 ± 0.79	3.19 ± 0.57	4.50 ± 0.41	4.45 ± 0.92	5.82 ± 1.00	5.86 ± 0.92	7.02 ± 1.00
22:5n-6	1.82 ± 0.43	2.92 ± 0.98	2.03 ± 0.38	0.36 ± 0.03	1.20 ± 0.32	0.82 ± 0.26	1.89 ± 0.22	1.02 ± 0.22
22:5n-3	1.55 ± 0.33	2.43 ± 0.49	2.28 ± 0.31	1.55 ± 0.13	2.61 ± 0.57	2.67 ± 0.44	1.77 ± 0.21	3.59 ± 0.68
22:6n-3	21.32 ± 4.07	26.03 ± 4.57	19.71 ± 2.45	13.29 ± 0.71	12.96 ± 4.20	4.06 ± 2.21	19.90 ± 1.83	7.63 ± 2.88
subtotal:	35.69 ± 4.91	40.04 ± 6.87	31.88 ± 3.79	21.27 ± 1.15	30.62 ± 6.10	25.36 ± 3.99	42.60 ± 2.85	33.28 ± 4.27
Total:	87.32 ± 1.23	89.17 ± 1.21	88.10 ± 1.44	86.68 ± 1.16	86.53 ± 1.58	82.98 ± 2.27	87.77 ± 1.56	85.88 ± 1.41

APPENDIX 3.2 *continued*

	Fishes						
Group	18	18	37	37	22	18	31
Species name	*Synodus lobeli*	*Synodus variegatus*	*Thalassoma ballieui*	*Thalassoma duperry*	*Torquigener florealis*	*Trachinocephalus myops*	*Zebrasoma flavescens*
Common name	(Lobel's lizardfish)	(Reef lizardfish)	(Blacktail wrasse)	(Saddle wrasse)	(Floral puffer)	(Snakefish)	(Yellow tang)
	n=20	n=19	n=20	n=20	n=20	n=20	n=20
Length (cm)	8.54 ± 1.64	12.18 ± 6.54	22.45 ± 5.11	11.77 ± 2.62	9.77 ± 6.80	13.07 ± 6.15	10.53 ± 3.72
Mass (g)	6.82 ± 4.62	39.34 ± 61.38	224.18 ± 154.29	31.89 ± 18.44	48.58 ± 63.50	45.17 ± 55.58	53.60 ± 40.81
Lipid content (%)	1.26 ± 0.48	0.95 ± 0.65	1.46 ± 0.75	1.56 ± 0.57	2.23 ± 1.45	0.93 ± 0.27	6.35 ± 3.02
Saturated FA							
14:0	1.92 ± 1.49	2.23 ± 0.77	3.15 ± 1.23	2.64 ± 0.76	1.62 ± 0.37	1.78 ± 0.58	4.82 ± 1.38
16:0	19.70 ± 1.58	20.88 ± 1.47	21.84 ± 2.42	21.51 ± 2.24	16.86 ± 2.42	19.61 ± 1.24	37.20 ± 4.11
18:0	9.94 ± 0.66	9.29 ± 0.74	9.50 ± 1.33	9.55 ± 0.74	12.06 ± 1.87	8.59 ± 0.64	4.53 ± 2.14
subtotal:	31.56 ± 1.60	32.39 ± 1.58	34.49 ± 3.51	33.70 ± 2.43	30.54 ± 1.31	29.98 ± 1.41	46.55 ± 3.21
Monounsaturated FA							
16:1n-7	2.17 ± 0.97	2.15 ± 0.62	3.03 ± 0.78	2.53 ± 0.79	2.73 ± 1.22	2.13 ± 0.47	4.32 ± 1.39
18:1n-9	7.71 ± 0.65	7.75 ± 0.87	10.75 ± 1.53	8.76 ± 0.91	9.12 ± 2.57	8.48 ± 1.24	8.36 ± 0.84
18:1n-7	2.59 ± 0.35	2.51 ± 0.31	2.55 ± 0.54	2.54 ± 0.38	2.86 ± 0.52	2.42 ± 0.40	1.91 ± 0.20
20:1n-9	0.45 ± 0.20	0.40 ± 0.13	0.60 ± 0.27	0.69 ± 0.27	0.94 ± 0.47	0.39 ± 0.10	1.55 ± 0.79
22:1n-11	0.28 ± 0.27	0.12 ± 0.24	0.30 ± 0.26	0.34 ± 0.26	0.34 ± 0.18	0.10 ± 0.14	0.00 ± 0.01
subtotal:	13.20 ± 1.27	12.94 ± 1.14	17.23 ± 2.28	14.85 ± 1.02	15.99 ± 4.18	13.52 ± 1.54	16.14 ± 2.85
Polyunsaturated FA							
18:2n-6	1.08 ± 0.11	1.32 ± 0.10	1.56 ± 0.34	1.50 ± 0.28	0.96 ± 0.26	1.11 ± 0.15	1.37 ± 0.34
20:4n-6	5.49 ± 1.89	5.39 ± 1.87	9.87 ± 3.02	9.87 ± 1.53	8.14 ± 2.74	5.52 ± 2.16	6.49 ± 2.56
22:4n-6	0.74 ± 0.20	0.96 ± 0.56	1.97 ± 0.44	2.96 ± 0.55	1.95 ± 0.73	0.92 ± 0.75	2.98 ± 0.57
20:5n-3	4.04 ± 0.54	4.43 ± 0.89	4.39 ± 0.81	4.88 ± 0.61	3.97 ± 0.65	4.11 ± 0.74	10.55 ± 1.98
22:5n-6	2.27 ± 0.35	2.62 ± 0.45	1.42 ± 0.41	1.46 ± 0.31	2.94 ± 1.14	2.45 ± 0.35	0.37 ± 0.32
22:5n-3	1.95 ± 0.26	1.94 ± 0.58	2.74 ± 0.27	3.13 ± 0.62	3.76 ± 0.48	1.75 ± 0.51	3.14 ± 0.38
22:6n-3	28.24 ± 3.78	26.28 ± 4.32	13.89 ± 4.17	13.74 ± 3.16	17.90 ± 3.11	29.30 ± 4.01	3.55 ± 2.85
subtotal:	43.82 ± 3.75	42.94 ± 2.54	35.84 ± 4.80	37.54 ± 3.53	39.62 ± 5.12	45.15 ± 2.40	28.45 ± 5.41
Total:	88.59 ± 1.78	88.28 ± 1.06	87.56 ± 1.25	86.10 ± 2.22	86.15 ± 1.71	88.66 ± 1.06	91.14 ± 1.13

APPENDIX 3.2 *continued*

	Invertebrates							
Group	41	41	43	42	40	40	38	38
Species name	*Calappa bicornis*	*Calappa calappa*	*Carpilius convexus*	*Charybdis hawaiiensis*	*Heterocarpus ensifer*	*Heterocarpus laevigatus*	*Octopus cyanea*	*Octopus ornatus*
Common name	(Two-horned box crab)	(Smooth box crab)	(Convex pebble crab)	(Hawaiian swimming crab)	(Two-spined shrimp)	(Red-tipped shrimp)	(Hawaiian day octopus)	(Ornate octopus)
	n=23	n=36	n=21	n=29	n=31	n=39	n=13	n=4
Length (cm)	5.79 ± 1.96	7.41 ± 2.94	6.73 ± 2.21	5.93 ± 1.27	9.55 ± 0.95	13.50 ± 1.60	17.63 ± 2.58	58.20 ± 8.39
Mass (g)	37.64 ± 18.20	129.11 ± 73.64	108.06 ± 44.96	70.88 ± 28.13	13.45 ± 3.69	39.78 ± 11.09	832.60 ± 938.95	266.91 ± 198.16
Lipid content (%)	0.53 ± 0.35	0.81 ± 0.46	0.95 ± 0.48	0.75 ± 0.40	2.57 ± 0.94	1.93 ± 0.74	1.12 ± 0.43	0.66 ± 0.39
Saturated FA								
14:0	1.63 ± 0.71	1.36 ± 0.67	2.20 ± 1.01	1.20 ± 0.56	2.73 ± 0.67	2.41 ± 0.56	0.93 ± 0.41	0.74 ± 0.20
16:0	13.63 ± 2.75	14.14 ± 3.56	15.96 ± 2.96	16.50 ± 2.52	16.64 ± 1.46	15.04 ± 1.41	17.66 ± 1.72	15.55 ± 0.82
18:0	9.19 ± 1.62	9.07 ± 1.55	8.24 ± 1.93	8.95 ± 0.94	4.83 ± 0.57	4.90 ± 0.62	11.28 ± 1.67	11.92 ± 0.62
subtotal:	24.45 ± 2.08	24.57 ± 2.73	26.39 ± 2.39	26.65 ± 2.75	24.20 ± 2.17	22.35 ± 2.04	29.87 ± 1.87	28.21 ± 0.54
Monounsaturated FA								
16:1n-7	3.48 ± 0.96	5.76 ± 2.78	4.36 ± 0.98	3.07 ± 1.03	5.78 ± 1.27	5.85 ± 1.25	0.83 ± 0.62	0.70 ± 0.39
18:1n-9	9.96 ± 2.22	7.64 ± 2.60	12.01 ± 3.39	9.33 ± 0.92	16.10 ± 2.39	19.33 ± 4.06	3.08 ± 1.70	2.57 ± 0.73
18:1n-7	2.84 ± 0.68	3.00 ± 0.99	3.26 ± 0.83	2.54 ± 0.42	4.84 ± 0.53	4.46 ± 0.67	2.04 ± 0.41	1.84 ± 0.24
20:1n-9	1.17 ± 0.42	0.89 ± 0.20	1.39 ± 0.48	0.88 ± 0.34	1.71 ± 0.44	2.65 ± 0.94	1.97 ± 0.59	2.03 ± 0.34
22:1n-11	0.70 ± 0.54	0.42 ± 0.20	1.48 ± 1.96	0.50 ± 0.51	1.30 ± 1.12	0.96 ± 0.73	0.13 ± 0.10	0.11 ± 0.08
subtotal:	18.15 ± 3.40	17.72 ± 2.64	22.50 ± 3.83	16.32 ± 2.13	29.72 ± 2.44	33.25 ± 5.06	8.05 ± 3.01	7.25 ± 1.33
Polyunsaturated FA								
18:2n-6	2.07 ± 0.33	1.54 ± 0.62	1.68 ± 0.25	2.22 ± 0.43	0.98 ± 0.11	0.79 ± 0.18	0.82 ± 0.21	0.85 ± 0.32
20:4n-6	14.07 ± 4.49	15.85 ± 3.57	8.76 ± 4.07	14.33 ± 2.89	3.12 ± 1.77	3.88 ± 0.95	17.92 ± 4.49	17.96 ± 0.88
22:4n-6	1.03 ± 0.41	1.72 ± 0.80	0.62 ± 0.36	1.32 ± 0.79	0.23 ± 0.16	0.34 ± 0.18	2.10 ± 0.72	2.41 ± 0.37
20:5n-3	10.64 ± 1.54	8.03 ± 2.23	8.37 ± 2.32	9.63 ± 1.75	12.20 ± 1.68	9.70 ± 1.94	7.37 ± 1.64	7.73 ± 1.43
22:5n-6	0.85 ± 0.31	0.95 ± 0.21	0.69 ± 0.19	0.62 ± 0.13	0.62 ± 0.23	0.89 ± 0.27	1.65 ± 0.24	1.47 ± 0.18
22:5n-3	1.80 ± 0.41	1.79 ± 1.02	1.47 ± 0.42	1.56 ± 0.36	1.58 ± 0.29	1.62 ± 1.24	1.34 ± 0.27	1.61 ± 0.55
22:6n-3	10.62 ± 1.82	7.90 ± 3.77	10.64 ± 2.42	11.86 ± 2.53	14.93 ± 2.29	14.14 ± 3.43	20.31 ± 3.62	19.03 ± 4.24
subtotal:	41.09 ± 4.74	37.76 ± 6.19	32.22 ± 3.58	41.55 ± 5.42	33.66 ± 2.44	31.36 ± 4.39	51.50 ± 3.15	51.06 ± 3.71
Total:	83.69 ± 1.78	80.05 ± 2.77	81.11 ± 3.28	84.52 ± 2.07	87.58 ± 1.42	86.95 ± 1.49	89.42 ± 2.66	86.51 ± 2.28

APPENDIX 3.2 *end*

	Invertebrates				
Group	38	45	44	44	39
Species name	*Octopus sp.*	*Panulirus marginatus*	*Scyllarides haanii*	*Scyllarides squammosus*	*Sthenoteuthis oualaniensis*
Common name	(Octopus spp)	(Spiny lobster)	(Ridgeback slipper lobster)	(Common slipper lobster)	(Neon flying squid)
	n=23	n=71	n=30	n=72	n=15
Length (cm)	N/A	22.65 ± 6.45	25.79 ± 7.04	20.35 ± 3.63	30.77 ± 7.40
Mass (g)	334.73 ± 776.91	414.80 ± 333.97	604.94 ± 397.39	287.53 ± 120.01	307.21 ± 338.03
Lipid content (%)	1.56 ± 0.84	1.17 ± 0.46	0.99 ± 0.58	0.91 ± 0.42	1.67 ± 0.36
Saturated FA					
14:0	1.22 ± 0.64	1.18 ± 0.39	1.55 ± 0.61	1.33 ± 0.50	1.53 ± 0.63
16:0	18.29 ± 1.67	13.15 ± 1.97	13.23 ± 2.08	13.47 ± 1.95	18.43 ± 0.80
18:0	10.10 ± 0.88	9.73 ± 1.13	8.29 ± 0.79	9.51 ± 1.00	6.63 ± 0.95
subtotal:	29.61 ± 1.54	24.06 ± 1.81	23.08 ± 2.24	24.30 ± 1.98	26.59 ± 1.39
Monounsaturated FA					
16:1n-7	0.95 ± 0.52	3.92 ± 1.06	4.85 ± 3.35	3.25 ± 1.00	1.37 ± 0.78
18:1n-9	2.94 ± 1.00	10.23 ± 2.52	13.74 ± 3.89	12.84 ± 2.27	6.62 ± 2.97
18:1n-7	1.69 ± 0.25	2.63 ± 0.49	3.33 ± 1.90	2.05 ± 0.70	1.36 ± 0.29
20:1n-9	1.82 ± 0.33	0.90 ± 0.31	2.05 ± 0.69	1.19 ± 0.24	4.46 ± 0.81
22:1n-11	0.11 ± 0.08	0.36 ± 0.53	0.58 ± 0.38	0.37 ± 0.43	0.19 ± 0.08
subtotal:	7.50 ± 1.69	18.05 ± 3.87	24.55 ± 6.60	19.69 ± 3.19	14.01 ± 3.22
Polyunsaturated FA					
18:2n-6	0.68 ± 0.15	2.02 ± 0.47	1.18 ± 0.39	1.86 ± 0.30	0.38 ± 0.14
20:4n-6	10.19 ± 4.74	16.88 ± 4.26	9.49 ± 3.77	9.93 ± 2.73	2.75 ± 0.27
22:4n-6	1.10 ± 0.73	1.41 ± 0.57	0.69 ± 0.29	1.25 ± 0.51	0.16 ± 0.02
20:5n-3	10.43 ± 2.31	9.24 ± 2.36	7.92 ± 2.27	7.76 ± 1.47	11.30 ± 1.44
22:5n-6	1.53 ± 0.29	0.85 ± 0.24	0.99 ± 0.36	1.17 ± 0.33	1.02 ± 0.17
22:5n-3	1.40 ± 0.28	1.74 ± 0.65	1.14 ± 0.47	1.30 ± 0.70	0.68 ± 0.16
22:6n-3	26.64 ± 3.80	8.48 ± 2.45	13.27 ± 3.92	12.84 ± 2.69	33.57 ± 3.33
subtotal:	51.97 ± 2.55	40.63 ± 4.80	34.67 ± 6.80	36.11 ± 4.40	49.86 ± 2.61
Total:	89.08 ± 2.38	82.74 ± 2.36	82.30 ± 3.81	80.11 ± 2.84	90.47 ± 0.69

APPENDIX 3.3 Groupings of 100 species of NWHI and MHI fishes and invertebrates into 47 groups based on ecological evaluation from the literature; species used and evaluated were based on expected importance to monk seal diets (from Piché et al. 2010)**.**

Group	Order	Family	Species Name	n	Ecological Subsystem	Habitat	Habitat (details)	Diet Guild	Diet Items	Ecology & Behavior
1. Angelfish	Perciformes	Pomacanthidae	*Centropyge potteri* (Potter's angelfish)	20	BANK	ROCK	Inhabit rock, coral, or rubble areas of seaward reefs (1)	Benthic Herbivores (2; 6)	Mostly filamentous benthic algae and organic detritus (2). Other minor items: diatoms, sponges and copepods (2)	Diurnal, behave more like damselfish (2); limits mouvement to restricted well defined location close/among Porites coral (2); ENDEMIC
2. Cardinalfish	Perciformes	Apogonidae	*Apogon maculiferus* (Spotted cardinalfish)	18	BANK	ROCK	N/A	Planktivores	Larger animals of the plankton (9)	Nocturnal, under ledges or in caves by day (1)
3. Armohead	Perciformes	Pentacerotidae	*Pseudopentaceros wheeleri* (slender armorhead)	20	SUBPHOTIC	CARBONATE	Deep-water (9); Associated with the summits and upper slopes of the Southern Emperor-Northern Hawaiian Ridge seamounts (4); Exposed to temperate conditions distinct from tropical environment encountered throughout the Hawaiian archipelago (4)	Planktivores [1]	Zooplankton, nekton (1) ; Micronektonic fishes (myctophids, sternoptychids, and astronesthids), crustaceans (euphausiids, sergestids, caridean shrimps, and mysids), and most importantly, pelagic tunicates, namely pyrosomes and salps (11)	Lenghty epipelagic pre-recruitment phase in subarctic North Pacific waters (4)
4. Beardfish	Polymixiiformes	Polymixiidae	*Polymixia berndti* (Berndt's beardfish)	20	SUBPHOTIC	CARBONATE	Deep-water species (18-585 m), reef associated (1)	Piscivores	Nekton & zoobenthos (1)	N/A
5. Bigeye	Perciformes	Priacanthidae	*Priacanthus alalaua* (Forskal's bigeye)	20	BANK	ROCK	Rocky bottoms although many specimens have been trawled from open waters (1); Depth range 9-275m but occurs mostly at depths of 100m or more (1); Has also been captured at night at shallower depths (9-46 m) (1)	Piscivores [2]	Larger animals of the zooplankton: larval fishes, crustacean larvae, larval worms (9); Nekton: finfish (1)	Nocturnal (9); More common around islands (1)
5. Bigeye	Perciformes	Priacanthidae	*Priacanthus meeki* (Hawaiian bigeye)	20	BANK	ROCK	Inhabits clear lagoon and seaward reefs (1); Depth range 3-50m (1)	Piscivores [2]	Same as above	Nocturnal, found under ledges during the day (1) ENDEMIC
6. Cusk eel	Ophidiiformes	Ophidiidae	*Ophidion muraenolepis* (Black edged cusk eel)	20	BANK	SAND	Demersal, found in the deep shelf and upper slope (1); Depth range 80-370m (1)	Piscivores	N/A	Nocturnal (9)
7. Conger eel	Anguilliformes	Congridae	*Conger cinereus* (Mustache conger)	20	BANK	ROCK	Common on reef flats and seagrass beds of shallow lagoons, depth range 0-80m (1)	Piscivores (7)	Mostly finfish, sometimes crustacean (9); Fishes from the Apogonidae, Labridae, Pomacentridae families (7)	Nocturnal (9)
7. Conger eel	Anguilliformes	Congridae	Ariosoma marginatum (Large-eye conger)	26	BANK	SAND	Sand-dwelling in the shallows to 490 m (1)	Piscivores	N/A	Nocturnal, can be seen at night with head protruding obliquely from the sand (9); ENDEMIC
8. Butterfly/forcepfish	Perciformes	Chaetodontidae	*Chaetodon fremblii* (Bluestripe butterflyfish)	22	REEF	REEF	Inhabit areas with rock or coral (1)	Benthic Carnivores (6)	Tentacles of tubeworms and other invertebrates (9)	Diurnal, take cover in the reef at night (7); ENDEMIC
8. Butterfly/forcepfish	Perciformes	Chaetodontidae	*Chaetodon miliaris* (Milletseed butterflyfish)	27	REEF	REEF	Inhabit shallow reef flats, also on shallow seamounts (1); Depth range 0-250m (1)	Planktivores (6)	Mainly zooplankton (9), also benthic invertebrates (1)	Diurnal, form schools at midwater to forage (9); Take cover in the reef at night (9); ENDEMIC

APPENDIX 3.3 *continued*

Group	Order	Family	Species Name	n	Ecological Subsystem	Habitat	Habitat (details)	Diet Guild	Diet Items	Ecology & Behavior
8. Butterfly/forcepfish	Perciformes	Chaetodontidae	*Chaetodon multicinctus* (Multiband butterflyfish)	19	REEF	REEF	Depth range 5-30m (1)	Benthic Carnivores (6)	Mainly coral polyps, also polychaete worms and small shrimps (1)	Diurnal, take cover in the reef at night (9); Usually seen in pairs (9); ENDEMIC
8. Butterfly/forcepfish	Perciformes	Chaetodontidae	*Chaetodon ornatissimus* (Ornate butterflyfish)	20	REEF	REEF	Most common on seaward reefs but can also occur in coral-rich areas of lagoon (1); Depth range 1-36m (1)	Benthic Carnivores	Coral tissue (1)	Diurnal, take cover in the reef at night (9); Occurs in pairs (1); (9)
8. Butterfly/forcepfish	Perciformes	Chaetodontidae	*Chaetodon quadrimaculatus* (Fourspot butterflyfish)	20	REEF	REEF	Almost exclusively on exposed seaward reefs (1); Depth range 2-15 m (1)	Benthic Carnivores	Mainly coral polyps (9)	Diurnal, take cover in the reef at night (9); Frequently seen in pair (9)
8. Butterfly/forcepfish	Perciformes	Chaetodontidae	*Forcipiger flavissimus* (Forcepfish)	26	REEF	REEF	Day: over coral reef, night: close among rock/coral (2); Common in exposed seaward reefs but also found in lagoon reefs (1); Depth range 1-114 m (1)	Benthic Carnivores	Hydroids, fish eggs, small crustaceans but prefers tube feet of echinoderms, pedicilaria of sea urchins, and polychaete tentacles (1; 9)	Diurnal, occurs singly or in groups of up to 5 individuals (1); Tears pieces of large benthic animals with their elongated snout/mouth (2)
9. Pennantfish	Perciformes	Chaetodontidae	*Heniochus diphreutes* (Pennantfish)	36	BANK	ROCK	Along outer reef slopes, in current channels (1); Depth range 15-210 m (1)	Planktivores	Zooplankton (9)	Adults form large schools well above the bottom (1; 9)
10. Cutthroat/snake eel	Anguilliformes	Synaphobranchidae	*Meadia abyssalis* (Abyssal cutthroat eel)	19	SUBPHOTIC	CARBONATE	Deep-water, depth range 100-329 m (1)	Piscivores	N/A	N/A
10. Cutthroat/snake eel	Anguilliformes	Ophichthidae	*Ophichthus kunaloa* (Snake eel)	20	SUBPHOTIC	CARBONATE	Deep-water, depth range 220-382 m (1); Benthic on hard substrata with crevices (1)	Piscivores	Diet of the family Ophichthidae: small fishes and crustaceans (1)	N/A
11. Sergeant	Perciformes	Pomacentridae	*Abudefduf abdominalis* (Hawaiian sergeant)	20	REEF	REEF	Occurs inshore in calm bays and in deeper water on exposed coasts (9); Found in quiet waters with rocky bottoms in inshore and offshore reefs (1); Depth range 1-50 m (1)	Planktivores	Mainly zooplankton, but algae also eaten (9)	Diurnal, form feeding aggregation during the day to feed in the water column, descend to the reef at night (2)
11. Sergeant	Perciformes	Pomacentridae	*Abudefduf sordidus* (Blackspot sergeant)	21	REEF	REEF	Inshore on rocky bottoms where the surge is strong (9); Rocky lagoons, reef flat shorelines and piers subject to mild surge, depth range 0-3m (1)	Planktivores [3] (7)	Benthic algae, crabs, sponges, polychaete worms (9); Algae, diatoms, detritus (2)	Diurnal, generally solitary (2); Highly territorial (1)
11. Sergeant	Perciformes	Pomacentridae	*Abudefduf vaigiensis* (Indo-Pacific sergeant)	16	REEF	REEF	Upper edge of outer reef slopes and inshore rocky reefs; depth range 0-15m (1)	Planktivores	Zooplankton, benthic algae, and small invertebrates (1)	Form foraging aggregations (1)
12. Chromis/dascyllus	Perciformes	Pomacentridae	*Chromis ovalis* (Oval chromis)	21	REEF	REEF	Depth range 6-46m (1)	Planktivores (6)	Mainly calanoid and cyclopoid copepods, but also tunicates, mysids, euphausids, crustacean larvae, larval worms, and fish eggs (1)	Diurnal, form foraging aggregations 2-5m above the reef during the day, descend back to the reef at night (2; 9); ENDEMIC
12. Chromis/dascyllus	Perciformes	Pomacentridae	*Dascyllus albisella* (Hawaiian dascyllus)	20	REEF	ROCK	Found in very shallow, protected water, over coral and rocky bottoms (1); Depth range 1-50m (1)	Planktivores (6)	Zooplankton, benthic invertebrates, and algae (1); Shrimp and crab larvae, mysids, and calanoid copepods (2)	Diurnal, form foraging aggregations in the water column during the day, descend back to the reef at night (2); ENDEMIC

APPENDIX 3.3 *continued*

Group	Order	Family	Species Name	n	Ecological Subsystem	Habitat	Habitat (details)	Diet Guild	Diet Items	Ecology & Behavior
13. Dragonet	Perciformes	Callionymidae	*Callionymus decoratus* (Longtail dragonet)	20	BANK	SAND	Found in lagoons and bays to well offshore, usually on fine sand substrata not disturbed by surge (1); On sand in the shallows to 110m (9); Depth range 1-134m (1)	Benthic Carnivores	N/A	N/A
14. Gurnard	Scorpaeniformes	Dactylopteridae	*Dactyloptena orientalis* (Helmut gurnard)	24	BANK	SAND	Inhabits coastal waters with sandy substrates (1); Depth range 0-100m (1)	Benthic Carnivores	Crustaceans, clams, and small fish (1); Crustaceans and small mollusks (9)	Solitary, well-camouflaged, slow-moving, bottom-dwelling (1); Use anterior pectoral rays to dig into the sand looking for prey (9)
15. Goatfish (M)	Perciformes	Mullidae	*Mulloidichthys flavolineatus* (Yellowstripe goatfish)	21	REEF	REEF	Shallow sandy areas of lagoon and seaward reefs (1); Depth range 5-35m (1)	Benthic Carnivores	Crustaceans, mollusks, worms, heart urchins and foraminiferans (1)	Schooling during the day, disperse at night to feed (9)
15. Goatfish (M)	Perciformes	Mullidae	*Mulloidichthys vanicolensis* (Yellowfin goatfish)	20	REEF	REEF	Sandy bottoms of reef flats, lagoons, and seaward reefs (1); Depth range 5-113m (1)	Benthic Carnivores (7)	Small worms and crustaceans (1)	Schooling during the day, disperse at night to forage (9); Sometimes form mix-species aggregation with bluestripe snapper, Lutjanus kasmira, and shows blue stripes (1)
16. Goatfish (P)	Perciformes	Mullidae	*Parupeneus bifasciatus* (Doublebar goatfish)	19	REEF	REEF	Inhabits lagoon and seaward reefs, adults tend to occur around rocky or coralline areas of high vertical relief (1); Depth range 1-80m (1)	Benthic Carnivores (7)	Day: crabs and shrimps, night: fishes and megalops (2); Feeds on crabs, shrimps, other crustaceans, octopuses, small fishes and worms (9)	Active both day & night (2)
16. Goatfish (P)	Perciformes	Mullidae	*Parupeneus chrysonemus* (Yellowbarbel goatfish)	19	REEF	REEF	Generally found at depths greater than 60 meters, but occurs at diving depths in NWHI (9); Depth range 20-183m (1)	Benthic Carnivores	N/A	N/A
16. Goatfish (P)	Perciformes	Mullidae	*Parupeneus multifasciatus* (Manybar goatfish)	20	REEF	REEF	Occurs over sand patches and consolidated limestone, or coral bottowm from reef flats and shallows (1)	Benthic Carnivores (6; 7)	Benthic crustaceans (2); Feed primarily on small crabs and shrimps, but demersal fish eggs, mollusks, and foraminiferans are also taken (1)	Diurnal, probe cracks, crevices & sand/debris pockets w their barbels (2)
16. Goatfish (P)	Perciformes	Mullidae	*Parupeneus pleurostigma* (Sidespot goatfish)	19	REEF	REEF	In seagrass beds; over sand, rubble, or coral and rock bottoms of shallow lagoon and seaward reefs to depths up to 46m (1)	Benthic Carnivores	Crabs, polychaetes, shrimps, heart urchins, gastropods, foraminiferans, brittle stars, and fishes (1)	N/A
17. Flounder	Pleuronectiformes	Bothidae	*Bothus mancus* (Flowery flounder)	16	BANK	SAND	Most numerous lying immobile in areas where rocks are interspersed with small patch of sand (2); Occasionally rests on bare rock (1) ; Depth range 0-150m (1)	Benthic Carnivores [4]	Small fishes, crabs, shrimps (1); Small fishes (2)	Mostly active during the day, well-camouflaged (2); On sand, frequently buried except for its eyes (2)

APPENDIX 3.3 *continued*

Group	Order	Family	Species Name	n	Ecological Subsystem	Habitat	Habitat (details)	Diet Guild	Diet Items	Ecology & Behavior
17. Flounder	Pleuronectiformes	Bothidae	*Bothus pantherinus* (Panther flounder)	76	BANK	SAND	Sandy or silty sand, and muddy bottoms (1); In areas surrounding coral reefs, but not within reef environment (9); 0-150m (1)	Benthic Carnivores	Small fishes and crustaceans (9)	N/A
17. Flounder	Pleuronectiformes	Bothidae	*Bothus thompsoni* (Thompson's flounder)	25	BANK	SAND	Sandy and muddy areas of the shelf (1)	Benthic Carnivores	Small fishes and crustaceans (9)	N/A
18. Lizard/snakefish	Aulopiformes	Synodontidae	*Synodus lobeli* (Lobel's lizardfish)	20	BANK	SAND	Found on sand bottoms (1); Depth range 0-32m (1)	Piscivores (7)	N/A	N/A
18. Lizard/snakefish	Aulopiformes	Synodontidae	*Synodus variegatus* (Reef lizardfish)	19	BANK	SAND	Rest motionless and fully exposed on sand patches, rock, or coral (2); Prefers resting on hard surface (1); Depth range 4-91m (1)	Piscivores	Small fishes eg.wrasse (2)	Active both day and night (2); Partially buried in sand with only eyes & tip of snout exposed (2)
18. Lizard/snakefish	Aulopiformes	Synodontidae	*Trachinocephalus myops* (Snakefish)	20	BANK	SAND	Rest on, or more often burrows into sand leaving eyes exposed (9); Depth range shallows-400m (9)	Piscivores	Mostly fishes but also small crustaceans (1)	Partially buried in sand (2)
19. Sandperch	Perciformes	Pinguipedidae	*Parapercis schauinslandii* (Redspotted sandperch)	18	BANK	SAND	Usually on open sand and rubble substrates near reefs (1); Depth range shallows -50m (1)	Benthic carnivores (6)	Mainly benthic crustaceans & occasionally small fishes (9)	Adults have lyre-tail and may swim high above the substrate (1)
20. Moray eel	Anguilliformes	Muraenidae	*Gymnothorax albimarginatus* (Whitemargin moray)	20	REEF	REEF	Coastal reef sand slopes (1)	Piscivores (7)	Reef fish (9)	Secretive in reefs during the day, over sand at night to hunt (1)
20. Moray eel	Anguilliformes	Muraenidae	*Gymnothorax berndti* (Berndt's moray)	20	REEF	REEF	Prefers rock and sponge areas (1); Deep-water species, depth range 30-300m (1)	Piscivores (7)	Finfish (1)	N/A
20. Moray eel	Anguilliformes	Muraenidae	*Gymnothorax eurostus* (Stout moray)	14	REEF	REEF	Inshore reef species (1)	Piscivores (7)	Finfish (1); Crustaceans: caridean shrimps & xanthid crabs (2); Fishes of Labridae family (7)	Most common inshore moray in Hawaii (1)
20. Moray eel	Anguilliformes	Muraenidae	*Gymnothorax flavimarginatus* (Yellowmargin moray)	19	REEF	REEF	Occurs in coral or rocky areas of reef flats and protected shorelines to seaward reefs, along drop-offs (1); Depth range 1-150m (1)	Piscivores (7)	Cephalopods, fishes, crustaceans (1); Fishes (2)	Mostly diurnal, they are sensitive to stimuli emanating from an injured fish (2); Most numerous of large muraenids in Hawaii (2)
20. Moray eel	Anguilliformes	Muraenidae	*Gymnothorax meleagris* (Whitemouth moray)	18	REEF	REEF	Coral-rich areas of lagoon and seaward reefs; Prefers very shallow depth (1); Depth range 1-36m (1)	Piscivores (7)	Small fishes (e.g. Abudefduf spp) and crustaceans (e.g. xanthid crab) (2)	Active both day and night (2); Protrudes head from crevices during the day (2)
20. Moray eel	Anguilliformes	Muraenidae	*Gymnothorax steindachneri* (Steindachner's moray)	25	REEF	REEF	Shallow seaward reefs to over 30 m (1); In holes or crevices at the base of corals or rocks (1)	Piscivores (7)	Finfish (1); Fishes of Mullidae family (7)	N/A
20. Moray eel	Anguilliformes	Muraenidae	*Gymnothorax undulatus* *(Undulated moray)*	19	REEF	REEF	On reef flats among rocks, rubble, or debris, and in lagoons and seaward reefs (1)	Piscivores (7)	Fishes, octopi, and probably crustaceans (1); Fishes of the Apogonidae and Mullidae families (7)	Nocturnal, cavernicolous (2)

APPENDIX 3.3 *continued*

Group	Order	Family	Species Name	n	Ecological Subsystem	Habitat	Habitat (details)	Diet Guild	Diet Items	Ecology & Behavior
21. Parrotfish	Perciformes	Scaridae	*Chlorurus perspicillatus* (Spectacled parrotfish)	22	REEF	REEF	Clear lagoon and seaward reefs, depth range 1-71m (1)	Benthic Herbivores	N/A	Food triturated in pharyngeal mill; major producer of sand in coral reef areas (9)
21. Parrotfish	Perciformes	Scaridae	*Chlorurus sordidus* (Bullethead parrotfish)	19	REEF	REEF	Both coral rich and open pavement areas of shallow reef flats and lagoon and seaward reefs as well as along drop-offs, depth range 3-50 m (1)	Benthic Herbivores	Feeds on benthic algae (1)	Diurnal, juveniles form large groups that migrate great distances between feeding and sleeping grounds (1)
21. Parrotfish	Perciformes	Scaridae	*Scarus dubius* (Regal parrotfish)	19	REEF	REEF	Inhabits seaward reefs, depth range 1-20m (1)	Benthic Herbivores (6)	Grazes on benthic algae (1)	ENDEMIC
22. Toby	Tetraodontiformes	Tetraodontidae	*Canthigaster coronata* (Crown toby)	20	BANK	ROCK	Found on sand or rubble bottoms of seaward reefs, usually at depth greater than 20m (9)	Benthic Carnivores (6)	Gastropods, sponges, algae, bivalves, polychaetes, tunicates, crabs, sea urchins, heart urchins, brittle stars, bryozoans, peanut worms, small crustaceans and foraminiferans (1)	N/A
22. Toby	Tetraodontiformes	Tetraodontidae	*Canthigaster jactator* (Hawaiian whitespotted toby)	24	BANK	ROCK	Shallow-water reef fish (9); Found on lagoon and seaward reefs (1); Depth range 1-30m (1)	Benthic Carnivores[5] (6)	Feeds on sponges, algae, detritus, tunicates, polychaetes, bryozoans, sea urchins, brittle stars, crabs, peanut worms, shrimps, zoanthids, fishes, amphipods and foraminiferans (1; 9); Coralline algae and hard-bodied benthic invertebrates (2)	Diurnal (2); ENDEMIC
22. Toby	Tetraodontiformes	Tetraodontidae	*Canthigaster rivulata* (Maze toby)	16	BANK	ROCK	Deep-water species (9); Depth range 30.5- 357m (9); Inhabits rocky areas and coral reefs (1)	Benthic Carnivores	N/A	N/A
22. Toby	Tetraodontiformes	Tetraodontidae	*Torquigener florealis* (Floral puffer)	20	BANK	SAND	Occurs over sand bottoms (9); Depth range usually 90-128m (1)	Benthic Carnivores	N/A	N/A
23. Chub	Perciformes	Kyphosidae	*Kyphosus bigibbus* (Gray chub)	19	REEF	REEF	Found around exposed seaward reefs of isolated high islands (1)	Benthic Herbivores	Benthic algae (9)	Diurnal, often occurs in foraging aggregations where the group is able to overwhelm the defenses of
23. Chub	Perciformes	Kyphosidae	*Kyphosus vaigiensis* (Lowfin chub)	19	REEF	REEF	Aggregates over hard, algal coated bottoms of exposed surf-swept outer reef flats, lagoons, and seaward reefs to a depth of at least 24m (1)	Benthic Herbivores	Mainly algae (9); Diet changes depending on life cycle and season: juveniles feed on small crustaceans and adults are carnivorous during summer, and herbivorous during winter (1)	May occur as solitary fish or in schools (9)
24. Scorpionfish	Scorpaeniformes	Scorpaenidae	*Sebastapistes ballieui* (Spotfin scorpionfish)	19	BANK	REEF	Reef-associated, depth range 1-11m (1)	Benthic Carnivores	Ambush predators of fishes and crustaceans (9)	ENDEMIC; mostly nocturnal (3)
25. Squirrelfish snapper	Perciformes	Lutjanidae	*Etelis carbunculus* (Squirrelfish snapper)	21	SLOPE	CARBONATE	Inhabits rocky bottoms (1); Deep-water species, depth range 90-400m (1)	Benthic Carnivores	Ambush predators of fishes and crustaceans (9); Mostly feeds on fishes and invertebrates such as squids, shrimps and crabs (1)	N/A
26. Bluestripe snapper	Perciformes	Lutjanidae	*Lutjanus kasmira* (Bluestripe snapper)	22	REEF	REEF	Inhabits coral reefs, occurring in both shallow lagoons and on outer reef slopes (1); Occurs from the shallows to 275m (9)	Omnivores	Feeds on fishes, shrimps, crabs, stomatopods, cephalopods, planktonic crustaceans, and also takes a variety of algae (1)	Introduced from French Polynesia and has become extremely abundant (9); Frequently found in large aggregations around coral formation, caves or wrecks during the day (1); Disperse to feed at night (9)
27. Pink snapper	Perciformes	Lutjanidae	*Pristipomoides filamentosus* (Pink snapper)	24	SLOPE	CARBONATE	Occurs over rocky bottoms (1); Deep-water species: depth range 40-400m (1)	Benthic Carnivores	Feeds on small fishes, shrimps, crabs, amphipods, ascidians and salps (1)	Nocturnal: at night, it migrates vertically to the upper part of its habitat to feed (1)

APPENDIX 3.3 *continued*

Group	Order	Family	Species Name	n	Ecological Subsystem	Habitat	Habitat (details)	Diet Guild	Diet Items	Ecology & Behavior
28. Flower snapper	Perciformes	Lutjanidae	*Pristipomoides zonatus* (Flower snapper)	19	SLOPE	CARBONATE	Occurs over rocky bottoms (1); Deep-water species: depth range 70-300m (1)	Omnivores	Feeds on fishes, shrimps, crabs, cephalopods, miscellaneous benthic invertebrates and pelagic organisms, including urochordates (1)	N/A
29. Soldierfish	Beryciformes	Holocentridae	*Myripristis berndti* (Bigscale soldierfish)	20	REEF	REEF	Inhabits caves and hides under ledges of subtidal reef flats, channels and margins to outer reef slopes (1); Depth range 1-50m (1)	Benthic Carnivores (7)	Feeds mainly on plankton such as crab larvae (1)	Nocturnal (9); Occurs in loose aggregations (1), Water-column feeders (2)
30. Squirrelfish	Beryciformes	Holocentridae	*Sargocentron xantherythrum* (Hawaiian squirrelfish)	21	BANK	ROCK	Common near caves and ledges (1); depth-range 1-217m (1)	Benthic Carnivores (6)	Benthic crustaceans (9)	Nocturnal, hide in caves and under ledges during the day and disperse to forage at night (9); Bottom feeders (2); ENDEMIC
31. Tang/surgeonfish	Perciformes	Acanthuridae	*Acanthurus achilles* (Achilles tang)	20	REEF	REEF	On clear seaward reefs, depth range 0-10m (1); Inhabits surf zone (9)	Benthic Herbivores	Feeds on filamentous and small fleshy algae (1)	Usally occur in groups (1); Agressively territorial (9)
31. Tang/surgeonfish	Perciformes	Acanthuridae	*Acanthurus dussumieri* (Eyestripe surgeonfish)	16	REEF	REEF	Seaward reefs & outer reef walls, deep shipwreck, depth range 4-131m (1)	Benthic Herbivores	Feeds on surface film of fine green and blue-green algae, diatoms, and detritus covering sand (1)	Diurnal, schooling species (1)
31. Tang/surgeonfish	Perciformes	Acanthuridae	*Acanthurus leucopareius* (Whitebar surgeonfish)	22	REEF	REEF	Boulder-strewn areas of surge zone, depth range 1-85m (1)	Benthic Herbivores	Browse on filamentous algae (1)	Often in schools (1); Form foraging aggregations to overwhelm territorial herbivorous damselfishes, and may accompany schools of convict tang *Acanthurus triostegus* (9)
31. Tang/surgeonfish	Perciformes	Acanthuridae	*Acanthurus nigroris* (Bluelined surgeonfish)	20	REEF	REEF	Clear lagoon and seaward reefs, often in areas with mixed coral, pavement, rubble and sand substrates, depth range 1-90m (1)	Benthic Herbivores (6)	Feeds on filamentous algae, diatoms and fine algal film of compacted sand (1)	N/A
31. Tang/surgeonfish	Perciformes	Acanthuridae	*Acanthurus olivaceus* (Orangeband surgeonfish)	20	REEF	REEF	Seaward reefs, in areas of bare rock or mixed rubble and sand, depth range 9-46m (1); Usually seen over sand substrata near reefs (9)	Benthic Herbivores (6)	Feed on surface film of detritus, diatoms, and fine filamentous algae covering sand and bare rock (1)	Can occur in small groups (9)
31. Tang/surgeonfish	Perciformes	Acanthuridae	*Acanthurus triostegus* (Convict tang)	20	REEF	REEF	Lagoon and seaward reefs with hard substrate, depth range 0-90m (1)	Benthic Herbivores	Benthic algae (9); filamentous algae (1)	Form large foraging aggregations to overwhelm territorial herbivorous damselfishes (9)
31. Tang/surgeonfish	Perciformes	Acanthuridae	*Ctenochaetus strigosus* (Goldring surgeonfish)	16	REEF	REEF	Abundant among Finger Corals as well as shallow reefs (9); Depth range 1-113 (1)	Benthic Herbivores (6)	Feeds on detritus by whisking its comb-like teeth over the bottom as it closes its mouth (1)	Diurnal, solitary (1)
31. Tang/surgeonfish	Perciformes	Acanthuridae	*Zebrasoma flavescens* (Yellow tang)	20	REEF	REEF	Coral-rich areas of lagoon and seaward reefs, depth range 2-46m (1)	Benthic Herbivores (6)	Browses on filamentous algae (1)	N/A

APPENDIX 3.3 *continued*

Group	Order	Family	Species Name	n	Ecological Subsystem	Habitat	Habitat (details)	Diet Guild	Diet Items	Ecology & Behavior
32. Unicornfish	Perciformes	Acanthuridae	*Naso lituratus* (Orangespine unicornfish)	19	REEF	REEF	Found in areas of coral, rock, or rubble of lagoon and seaward reefs, depth range 0-90m (1)	Benthic Herbivores	Feeds upon leafy seaweed (9)	N/A
32. Unicornfish	Perciformes	Acanthuridae	*Naso unicornis* (Bluespine unicornfish)	19	REEF	REEF	Inhabits channels, moats, lagoon and seaward reefs with strong surge, depth range 1-180m (1)	Benthic Herbivores (6)	Feeds upon leafy brown algae (9)	Diurnal, typically occurring in small groups (1)
33. Tilefish	Perciformes	Malacanthidae	*Malacanthus brevirostris* (Flagtail tilefish)	16	BANK	SAND	Inhabits barren, open areas of outer reef slopes, depth range 5-50m (1); Found over rocks or sandy areas adjacent to reefs (9)	Benthic Carnivores	Feed upon worms and crustaceans (9)	Usually live in a burrow of their own construction, often under a surface rock on sand (1)
34. Knife/razorfish	Perciformes	Labridae	*Cymolutes lecluse* (Hawaiian knifefish)	23	BANK	SAND	Occurs over open sand bottom (9)	Benthic Carnivores	Feeds on fishes (1)	Dive into sand with the approach of danger (9); ENDEMIC
34. Knife/razorfish	Perciformes	Labridae	*Iniistius pavo* (Peacock razorfish)	15	BANK	SAND	Lagoon and seaward reef areas with fine to loose, coarse sand bottoms (1)	Benthic Carnivores	Feeds on hard-shelled invertebrates, including mollusks and crustaceans (1)	Dives into the sand when threatened (1)
34. Knife/razorfish	Perciformes	Labridae	*Iniistius umbrilatus* (Blackside razorfish)	19	BANK	SAND	Inhabits sandy bottoms beyond the reef (1)	Benthic Carnivores	N/A	ENDEMIC
35. Triggerfish (M)	Tetraodontiformes	Balistidae	*Melichthys niger* (Black triggerfish)	20	REEF	REEF	Found on inner and outer reef crests, usually near the slope or drop-off to deeper water, depth range 0-75m (1)	Planktivores ^{6} (9)	Calcareous algae, zooplankton and phytoplankton (1); Foliose algae, coralline algae (2)	May form large aggregations (9)
36. Triggerfish (S)	Tetraodontiformes	Balistidae	*Sufflamen bursa* (Lei triggerfish)	19	REEF	REEF	Inner and outer reef habitats from exposed algae reef flats to deep along drop-offs, 1-90m (1).	Benthic Carnivores (6)	Crabs, bivalves, gastropods, algae, echinoids, tunicates, worms, eggs, and detritus (1)	N/A
37. Wrasse/hogfish/coris	Perciformes	Labridae	*Anampses cuvier* (Pearl wrasse)	20	REEF	REEF	Over rocky substrate of inshore areas, tide pools, and relatively deeper water 0-26m (1)	Benthic Carnivores	Crustaceans, sipunculids, gastropods, chitons, ophiuroids and echinoids, tunicates, algae, foraminifera, and fish material (1)	ENDEMIC
37. Wrasse/hogfish/coris	Perciformes	Labridae	*Bodianus bilunulatus* (Hawaiian hogfish)	20	REEF	REEF	Occurs on deep reef slopes rich with invertebrates such as sponges and seawhips (1)	Benthic Carnivores (6; 7)	N/A	ENDEMIC
37. Wrasse/hogfish/coris	Perciformes	Labridae	*Coris ballieui* (Lined coris)	16	BANK	ROCK	Occurs below 60 ft on mixed sand and rock bottom (9)	Benthic Carnivores (6)	N/A	N/A
37. Wrasse/hogfish/coris	Perciformes	Labridae	*Coris flavovittata* (Yellowstriped coris)	20	REEF	REEF	N/A	Benthic Carnivores (6)	N/A	N/A
37. Wrasse/hogfish/coris	Perciformes	Labridae	*Oxycheilinus unifasciatus* (Ringtail wrasse)	19	REEF	REEF	Occurs at depths of 10-165m (9)	Benthic Carnivores	Mostly fishes (65% of diet), but also crabs, brittle star, sea urchin (9)	N/A
37. Wrasse/hogfish/coris	Perciformes	Labridae	*Thalassoma ballieui* (Blacktail wrasse)	20	REEF	REEF	N/A	Benthic Carnivores (7)	Mainly sea urchins, crabs and small fishes (9); Fishes from the Apogonidae, Labridae, Mullidae, Pomacentridae families (7)	N/A

APPENDIX 3.3 *continued*

Group	Order	Family	Species Name	n	Ecological Subsystem	Habitat	Habitat (details)	Diet Guild	Diet Items	Ecology & Behavior
38. Octopus	Octopoda	Octopodidae	*Octopus cyanea* (Hawaiian day octopus)	13	BANK	SAND	Reef, shallows to depths of more than 45m (3)	Benthic Carnivores	Mostly crabs, in deeper waters may take mollusks and occasionally fishes (3)	Diurnal, most frequently seen Hawaiian octopus (3)
38. Octopus	Octopoda	Octopodidae	*Octopus ornatus* (Ornate octopus)	4	BANK	SAND	N/A	Benthic Carnivores	N/A	Nocturnal, usually found flattened against bottom (3)
38. Octopus	Octopoda	Octopodidae	*Octopus sp.*	23	BANK	SAND	N/A	Benthic Carnivores	N/A	N/A
39. Squid	Teuthoida	Ommastrepidae	*Sthenoteuthis oualaniensis* (Neon flying squid)	15			Open water, depths of 0-1000m (10)	Piscivores	Fishes and cephalopods (8); Benthic crustaceans, cephalopods, finfish (10)	N/A
40. Shrimp	Decapoda	Pandalidae	*Heterocarpus ensifer* (Two-spined shrimp)	31	SUBPHOTIC	CARBONATE	Range of maximum abundance: 450-550m (5)	Benthic Carnivores	N/A	Smaller than H. laevigatus, aggregates around benthic relief over sandy bottom (5)
40. Shrimp	Decapoda	Pandalidae	*Heterocarpus laevigatus* (Red-tipped shrimp)	39	SUBPHOTIC	CARBONATE	Range of maximum abundance: 550-675m (5)	Benthic Carnivores	N/A	Solitary; found at higher densities on volcanic substrate (5)
41. Box crab	Decapoda	Calappidae	*Calappa bicornis* (Two-horned box crab)	23	BANK	SAND	N/A	Benthic Carnivores	Mostly marine snails (3)	N/A
41. Box crab	Decapoda	Calappidae	*Calappa calappa* (Smooth box crab)	36	BANK	SAND	Occurs on sandy bottoms from the shallows to depths of 50ft or more (3)	Benthic Carnivores	Mostly marine snails (3)	N/A
42. Swimming crab	Decapoda	Portunidae	*Charybdis hawaiiensis* (Hawaiian swimming crab)	29	BANK	SAND	N/A	Benthic Carnivores	N/A	N/A
43. Pebble crab	Decapoda	Carpiliidae	*Carpilius convexus* (Convex pebble crab)	21	BANK	ROCK	N/A	Benthic Carnivores	N/A	N/A
44. Slipper lobster	Decapoda	Scyllaridae	*Scyllarides haanii* (Ridgeback slipper lobster)	30	BANK	CARBONATE	Benthic, hard-substrate	Benthic Carnivores	N/A	Largest Hawaiian slipper lobster; nocturnal; hide in crevices and holes during day (3)
44. Slipper lobster	Decapoda	Scyllaridae	*Scyllarides squammosus* (Common slipper lobster)	72	BANK	SAND	Reef; often encountered on roofs of caves where orange cup coral abundant (3)	Benthic Carnivores	Bivalve mollusk (3)	N/A
45. Spiny lobster	Decapoda	Palinuridae	*Panulirus marginatus* (Spiny lobster)	60	REEF	REEF	Few feets to 600ft, inhabit crevices and caves (3)	Benthic Carnivores	N/A	ENDEMIC; Nocturnal (3)

APPENDIX 3.3 *end*

Group	Order	Family	Species Name	n	Ecological Subsystem	Habitat	Habitat (details)	Diet Guild	Diet Items	Ecology & Behavior
46. Boarfish	Perciformes	Caproidae	*Antigonia eos* (Boarfish)	10	SUBPHOTIC	CARBONATE	N/A	Benthic Carnivores	Feeds on small molluscs and crustaceans	N/A
46. Boarfish	Perciformes	Caproidae	*Antigonia capros* (Boarfish)	10	SUBPHOTIC	CARBONATE	N/A	Benthic Carnivores	N/A	N/A
47. Duckbill	Perciformes	Percophidae	*Bembrops filifera* (Duck-billed bembropsid)	20	SUBPHOTIC	CARBONATE	N/A	Benthic Carnivores	N/A	N/A

Discrepancies: [1] may be benthic carnivore (9); [2] may be planktivore (7, 9); [3] may be omnivore (2)· [4] may be piscivore (2, 7); [5] may be omnivore (2); [6] may be benthic herbivore (2) or benthic carnivore (7)

References: (1) FishBase (Froese & Pauly 2009); (2) Hobson 1974; (3) Hoover 1998; (4) Humphreys 2000; (5) Moffitt & Parrish 1992; (6) Parrish & Boland 2004; (7) Parrish et al. 1986; (8) Parry 2006; (9) Randall 1996; (10) SeaLifeBase (Palomares & Pauly 2010); (11) Seki & Somerton 1994

Ecological subsystem categories (from Parrish & Abernathy, 2006):
Reef= shallow reef (<30m)
Bank= algal beds and sand fields (30-50m)
Slope= talus, sand, rubble, carbonate (51-300m)
Subphotic= carbonate, manganese, basalt, sand, precious coral (301-500m)

APPENDIX 3.4 Average (mean ± SD) fatty acid (FA) composition (15 FAs used in the analyses) for the 5 functional groups, and for the 47 groups of species (from Piché et al. 2010).

Functional Group	Group	(n)	14:0	16:0	16:1n-7	18:0	18:1n-9	18:1n-7	18:2n-6	20:1n-9	20:4n-6	20:5n-3	22:1n-11	22:4n-6	22:5n-6	22:5n-3	22:6n-3
Herbivores	1. Angelfish	20	7.69 ± 1.10	29.58 ± 1.95	7.84 ± 1.16	6.61 ± 0.76	6.82 ± 0.85	2.48 ± 0.20	1.66 ± 0.18	0.26 ± 0.06	5.28 ± 0.73	6.46 ± 1.77	1.46 ± 2.14	1.36 ± 0.33	0.82 ± 0.43	2.59 ± 0.51	2.95 ± 1.24
	21. Parrotfish	60	3.82 ± 1.51	28.84 ± 3.23	4.15 ± 2.07	6.77 ± 1.22	6.44 ± 0.81	3.48 ± 0.54	3.07 ± 0.96	0.22 ± 0.09	12.49 ± 3.88	5.95 ± 1.63	0.09 ± 0.15	1.27 ± 0.47	1.08 ± 0.38	2.48 ± 0.64	5.05 ± 2.55
	23. Chub	38	3.66 ± 1.65	24.71 ± 3.44	1.78 ± 0.77	8.72 ± 1.55	9.83 ± 1.01	1.29 ± 0.57	2.61 ± 0.74	0.97 ± 0.51	9.81 ± 3.57	5.05 ± 1.29	0.04 ± 0.03	2.71 ± 0.74	0.97 ± 0.54	3.72 ± 0.63	8.78 ± 5.55
	31. Tang/ surgeonfish	154	6.77 ± 2.99	31.98 ± 5.90	6.39 ± 3.22	4.84 ± 1.58	6.31 ± 1.93	1.89 ± 0.46	1.44 ± 0.35	0.90 ± 0.67	6.92 ± 3.07	7.87 ± 2.52	1.18 ± 3.21	2.01 ± 0.83	0.80 ± 0.47	2.91 ± 0.99	3.92 ± 2.20
	32. Unicornfish	38	4.71 ± 1.08	31.67 ± 3.77	2.14 ± 0.71	6.68 ± 1.54	11.47 ± 1.79	2.07 ± 0.60	2.71 ± 0.57	3.88 ± 1.51	6.55 ± 2.60	3.83 ± 0.99	0.02 ± 0.08	3.07 ± 1.20	0.57 ± 0.42	2.03 ± 0.63	2.67 ± 3.19
	Total	**310**	**5.63 ± 2.75**	**30.29 ± 5.34**	**4.96 ± 3.17**	**6.03 ± 1.98**	**7.43 ± 2.46**	**2.18 ± 0.85**	**2.07 ± 0.91**	**1.10 ± 1.30**	**8.20 ± 3.94**	**6.57 ± 2.51**	**0.70 ± 2.39**	**2.04 ± 0.98**	**0.85 ± 0.48**	**2.80 ± 0.94**	**4.52 ± 3.42**
Planktivores	2. Cardinalfish	18	3.71 ± 0.84	22.18 ± 3.00	3.19 ± 0.61	9.41 ± 1.65	9.02 ± 1.32	2.81 ± 0.45	1.29 ± 0.15	0.92 ± 0.29	5.34 ± 2.02	7.71 ± 1.73	0.23 ± 0.15	1.01 ± 0.46	1.08 ± 0.20	1.93 ± 0.49	18.09 ± 5.44
	9. Pennantfish	36	5.38 ± 1.69	28.21 ± 5.33	5.18 ± 1.47	8.12 ± 1.04	4.89 ± 1.22	2.54 ± 0.32	1.29 ± 0.23	0.89 ± 0.39	1.86 ± 1.54	3.45 ± 0.95	0.06 ± 0.05	0.68 ± 0.29	1.59 ± 0.62	4.99 ± 1.48	17.34 ± 4.32
	11. Sergeant	57	4.03 ± 1.69	26.81 ± 4.45	4.80 ± 1.71	7.52 ± 1.58	8.72 ± 1.81	2.18 ± 0.50	2.08 ± 1.05	0.93 ± 0.46	5.04 ± 3.14	4.94 ± 1.23	0.43 ± 0.52	1.13 ± 1.06	1.14 ± 0.51	2.27 ± 0.99	13.67 ± 6.81
	12. Chromis/ dascyllus	41	4.15 ± 1.87	28.62 ± 3.97	4.87 ± 1.70	8.04 ± 1.86	7.46 ± 1.31	2.36 ± 1.14	1.39 ± 0.20	0.75 ± 0.31	5.33 ± 3.11	5.40 ± 2.28	0.89 ± 2.49	1.02 ± 0.37	1.15 ± 0.49	2.09 ± 0.66	12.83 ± 6.61
	35. Triggerfish (M)	20	0.78 ± 0.23	25.69 ± 3.87	1.78 ± 0.67	10.39 ± 1.21	9.54 ± 1.62	4.50 ± 0.62	1.85 ± 0.43	0.27 ± 0.10	9.66 ± 2.83	7.30 ± 1.22	0.07 ± 0.04	1.60 ± 0.48	0.86 ± 0.31	3.09 ± 0.56	10.34 ± 4.42
	Total	**172**	**3.93 ± 2.01**	**26.92 ± 4.70**	**4.38 ± 1.83**	**8.30 ± 1.77**	**7.74 ± 2.20**	**2.63 ± 0.98**	**1.64 ± 0.72**	**0.80 ± 0.42**	**5.01 ± 3.45**	**5.30 ± 2.05**	**0.40 ± 1.28**	**1.05 ± 0.73**	**1.20 ± 0.53**	**2.86 ± 1.50**	**14.32 ± 6.35**
	3. Armorhead	20	4.21 ± 0.35	17.56 ± 0.69	4.41 ± 0.43	5.18 ± 0.39	26.54 ± 2.11	2.92 ± 0.22	0.83 ± 0.09	2.65 ± 0.24	0.64 ± 0.05	4.51 ± 0.41	1.97 ± 0.80	0.11 ± 0.01	0.36 ± 0.02	1.55 ± 0.13	13.29 ± 0.71
Carnivores	4. Beardfish	20	3.00 ± 1.15	20.71 ± 1.41	3.09 ± 0.56	6.16 ± 0.87	17.48 ± 4.02	2.49 ± 0.58	0.65 ± 0.17	2.17 ± 1.07	3.28 ± 0.92	4.88 ± 1.41	0.66 ± 1.61	0.46 ± 0.12	1.44 ± 0.36	1.68 ± 0.22	22.72 ± 5.04
	5. Bigeye	40	3.12 ± 1.28	20.50 ± 2.69	3.08 ± 1.05	8.85 ± 0.98	11.40 ± 2.16	2.17 ± 0.40	1.21 ± 0.22	0.68 ± 0.28	3.36 ± 1.39	5.39 ± 1.30	0.18 ± 0.12	0.60 ± 0.40	1.91 ± 0.49	1.42 ± 0.39	24.09 ± 5.35
	6. Cusk eel	20	3.52 ± 1.41	18.35 ± 2.24	3.01 ± 0.76	8.01 ± 1.05	9.50 ± 1.51	2.47 ± 0.52	1.18 ± 0.20	0.68 ± 0.10	3.93 ± 1.79	6.80 ± 1.22	0.34 ± 0.42	1.20 ± 0.62	1.83 ± 0.41	2.26 ± 0.36	24.97 ± 3.58
	7. Conger eel	46	3.16 ± 1.17	22.34 ± 2.97	3.96 ± 1.28	8.31 ± 1.20	10.81 ± 1.99	3.08 ± 0.53	1.25 ± 0.27	0.52 ± 0.17	5.82 ± 1.48	4.79 ± 2.15	0.24 ± 0.33	1.62 ± 0.89	1.49 ± 0.30	2.54 ± 0.79	18.12 ± 5.47
	8. Butterfly/ forcepfish	134	2.66 ± 1.08	27.06 ± 4.21	2.09 ± 0.86	9.68 ± 1.84	8.90 ± 1.73	1.82 ± 0.85	0.84 ± 0.34	1.61 ± 0.90	7.33 ± 2.86	2.70 ± 1.11	0.78 ± 1.67	5.11 ± 3.16	0.81 ± 0.65	3.44 ± 1.45	9.33 ± 5.01

APPENDIX 3.4 *continued*

Functional Group	Group	(n)	14:0	16:0	16:1n-7	18:0	18:1n-9	18:1n-7	18:2n-6	20:1n-9	20:4n-6	20:5n-3	22:1n-11	22:4n-6	22:5n-6	22:5n-3	22:6n-3
	10. Cutthroat/ snake eel	39	2.89 ± 0.99	18.03 ± 2.02	5.07 ± 2.14	4.91 ± 1.11	19.24 ± 3.42	3.02 ± 0.35	0.95 ± 0.20	1.75 ± 0.52	3.64 ± 1.46	5.21 ± 1.83	0.33 ± 0.24	0.40 ± 0.19	1.19 ± 0.30	1.76 ± 0.38	19.26 ± 3.64
	13. Dragonet	20	2.50 ± 1.27	18.89 ± 1.62	2.70 ± 0.58	11.40 ± 2.24	6.18 ± 0.83	2.89 ± 0.40	1.06 ± 0.19	0.37 ± 0.08	8.93 ± 1.57	4.75 ± 0.63	0.25 ± 0.07	2.38 ± 0.81	2.49 ± 0.38	2.68 ± 0.41	19.94 ± 4.05
	14. Gurnard	24	4.65 ± 1.47	22.44 ± 2.23	5.05 ± 1.52	8.98 ± 1.46	7.30 ± 1.05	2.98 ± 0.38	1.25 ± 0.23	1.03 ± 0.39	3.18 ± 1.04	5.57 ± 0.69	0.10 ± 0.14	0.56 ± 0.16	1.61 ± 0.30	2.03 ± 0.27	21.39 ± 3.65
	15. Goatfish (M)	41	2.55 ± 0.86	20.87 ± 3.79	3.51 ± 0.96	10.84 ± 1.46	7.09 ± 1.84	3.32 ± 0.71	1.39 ± 0.47	0.57 ± 0.32	7.74 ± 2.07	6.48 ± 1.45	0.29 ± 0.19	2.60 ± 0.98	1.59 ± 0.54	2.70 ± 0.69	12.17 ± 5.17
	16. Goatfish (P)	77	3.36 ± 1.27	21.26 ± 2.67	3.63 ± 1.19	9.98 ± 0.98	8.63 ± 1.38	2.84 ± 0.50	1.45 ± 0.31	0.66 ± 0.27	6.19 ± 2.75	6.19 ± 1.59	0.30 ± 0.24	1.71 ± 0.86	1.57 ± 0.52	2.09 ± 0.42	17.42 ± 6.09
	17. Flounder	116	3.70 ± 1.94	20.00 ± 1.94	3.31 ± 0.84	8.05 ± 1.46	9.68 ± 1.98	2.24 ± 0.33	1.17 ± 0.12	0.61 ± 0.15	4.36 ± 2.74	5.09 ± 0.95	0.22 ± 0.14	0.88 ± 0.60	1.77 ± 0.35	2.82 ± 0.87	23.00 ± 3.03
	18. Lizard/snakefish	59	1.97 ± 1.03	20.05 ± 1.52	2.15 ± 0.71	9.27 ± 0.87	7.99 ± 1.00	2.51 ± 0.35	1.17 ± 0.16	0.41 ± 0.15	5.47 ± 1.94	4.19 ± 0.74	0.17 ± 0.23	0.87 ± 0.55	2.44 ± 0.40	1.88 ± 0.47	27.97 ± 4.16
	19. Sandperch	18	4.18 ± 1.15	20.81 ± 1.39	3.74 ± 0.84	9.33 ± 1.29	8.32 ± 1.05	2.63 ± 0.27	1.29 ± 0.12	0.76 ± 0.17	3.16 ± 0.73	4.51 ± 0.55	0.26 ± 0.09	0.68 ± 0.16	2.20 ± 0.50	1.74 ± 0.20	23.60 ± 2.86
	20. Moray eel	135	2.56 ± 1.31	20.91 ± 3.33	2.98 ± 1.33	10.07 ± 1.40	10.15 ± 1.86	2.75 ± 0.46	0.89 ± 0.28	0.91 ± 0.38	8.42 ± 3.12	2.44 ± 1.22	0.28 ± 0.32	3.20 ± 1.13	1.69 ± 0.39	2.81 ± 0.94	17.98 ± 5.40
	22. Toby	80	1.06 ± 0.43	18.96 ± 4.04	2.14 ± 0.95	12.13 ± 2.02	7.83 ± 1.87	2.97 ± 0.45	1.05 ± 0.33	0.61 ± 0.34	10.64 ± 3.06	3.10 ± 1.00	0.40 ± 0.21	3.58 ± 1.27	2.83 ± 1.41	3.99 ± 1.12	13.43 ± 4.68
	24. Scorpionfish	19	1.76 ± 0.58	18.15 ± 1.36	2.41 ± 0.43	10.23 ± 0.65	9.35 ± 0.48	2.37 ± 0.33	1.27 ± 0.08	0.69 ± 0.23	10.13 ± 2.74	5.87 ± 0.92	0.23 ± 0.05	1.78 ± 0.59	1.90 ± 0.22	1.78 ± 0.21	19.90 ± 1.83
	25. Squirrelfish snapper	21	2.50 ± 0.31	19.97 ± 0.80	4.31 ± 0.71	6.19 ± 0.45	14.92 ± 1.90	2.86 ± 0.30	0.91 ± 0.08	1.42 ± 0.19	2.62 ± 0.46	3.39 ± 0.39	0.27 ± 0.10	0.64 ± 0.10	1.88 ± 0.18	2.72 ± 0.18	24.65 ± 2.34
	26. Bluestripe snapper	22	3.08 ± 1.01	21.15 ± 2.75	3.61 ± 0.89	9.62 ± 0.96	10.30 ± 2.87	2.83 ± 0.21	1.20 ± 0.32	0.83 ± 0.34	4.02 ± 2.23	5.12 ± 1.49	0.18 ± 0.14	0.92 ± 0.73	1.57 ± 0.31	2.25 ± 0.36	20.61 ± 4.04
	27. Pink snapper	24	2.48 ± 0.88	20.34 ± 1.13	2.86 ± 1.09	7.89 ± 0.59	12.03 ± 4.23	2.10 ± 0.32	1.09 ± 0.21	1.11 ± 0.32	3.29 ± 1.01	3.65 ± 0.79	0.33 ± 0.23	0.65 ± 0.18	2.92 ± 0.98	2.43 ± 0.49	26.03 ± 4.57
	28. Flower snapper	19	3.58 ± 1.15	20.21 ± 0.87	5.25 ± 1.13	6.75 ± 0.44	15.53 ± 3.79	2.91 ± 0.30	0.97 ± 0.18	1.55 ± 0.32	2.96 ± 0.62	3.19 ± 0.57	0.48 ± 0.34	0.74 ± 0.22	2.03 ± 0.38	2.28 ± 0.31	19.71 ± 2.45
	29. Soldierfish	20	4.80 ± 0.43	26.40 ± 2.50	4.62 ± 0.78	9.42 ± 0.91	9.51 ± 1.18	2.57 ± 0.23	1.29 ± 0.12	0.96 ± 0.15	2.48 ± 0.47	4.34 ± 0.76	0.45 ± 0.62	1.04 ± 0.60	1.19 ± 0.26	2.96 ± 0.49	14.22 ± 2.30
	30. Squirrelfish	21	4.49 ± 1.52	23.74 ± 5.21	3.24 ± 0.53	10.53 ± 1.26	9.21 ± 1.43	2.94 ± 0.62	1.13 ± 0.14	1.09 ± 0.26	5.48 ± 2.67	4.45 ± 0.92	0.70 ± 0.65	2.80 ± 1.39	1.21 ± 0.32	2.62 ± 0.57	12.96 ± 4.20
	33. Tilefish	16	1.60 ± 1.15	18.34 ± 1.95	1.84 ± 0.81	11.56 ± 0.80	6.98 ± 0.95	2.82 ± 0.31	1.11 ± 0.12	0.48 ± 0.17	10.36 ± 3.31	4.56 ± 0.51	0.33 ± 0.23	4.50 ± 1.39	2.11 ± 0.52	3.76 ± 0.50	16.58 ± 3.85
	34. Knife/razorfish	57	4.06 ± 1.85	19.80 ± 1.88	3.58 ± 1.16	9.11 ± 1.07	9.19 ± 1.16	3.05 ± 0.94	1.16 ± 0.17	0.59 ± 0.25	5.66 ± 1.60	7.59 ± 1.64	0.14 ± 0.06	1.21 ± 0.50	1.49 ± 0.39	1.75 ± 0.51	17.31 ± 5.26

APPENDIX 3.4 *end*

Functional Group	Group	(n)	14:0	16:0	16:1n-7	18:0	18:1n-9	18:1n-7	18:2n-6	20:1n-9	20:4n-6	20:5n-3	22:1n-11	22:4n-6	22:5n-6	22:5n-3	22:6n-3
	36. Triggerfish (S)	19	1.34 ± 0.31	24.02 ± 2.47	2.91 ± 0.63	10.63 ± 0.69	8.76 ± 0.79	4.24 ± 0.40	1.49 ± 0.22	0.51 ± 0.11	8.81 ± 2.05	7.02 ± 1.00	0.21 ± 0.12	3.74 ± 0.62	1.02 ± 0.22	3.59 ± 0.68	7.63 ± 2.88
	37. Wrasse/ hogfish/coris	135	3.19 ± 1.38	21.22 ± 1.89	2.85 ± 0.88	9.55 ± 0.94	9.37 ± 1.62	2.60 ± 0.58	1.55 ± 0.31	0.60 ± 0.23	10.44 ± 3.47	5.37 ± 1.74	0.31 ± 0.23	2.57 ± 0.92	1.59 ± 0.47	2.84 ± 0.72	12.50 ± 5.12
	46. Boarfish	20	3.12 ± 1.74	19.45 ± 1.23	3.93 ± 1.21	7.85 ± 1.16	9.35 ± 1.01	2.29 ± 0.23	1.23 ± 0.25	1.00 ± 0.30	3.00 ± 1.29	4.53 ± 0.42	0.26 ± 0.09	0.78 ± 0.22	2.37 ± 0.62	3.15 ± 0.51	24.07 ± 3.19
	47. Duckbill	19	1.83 ± 0.77	17.89 ± 1.04	4.75 ± 1.85	5.49 ± 0.97	14.52 ± 3.03	2.95 ± 0.82	0.92 ± 0.18	1.26 ± 0.25	3.88 ± 0.98	4.54 ± 1.61	0.10 ± 0.03	0.64 ± 0.13	2.42 ± 0.33	2.62 ± 0.35	24.92 ± 4.00
	Total	**1,281**	**2.91 ± 1.52**	**21.22 ± 3.69**	**3.16 ± 1.34**	**9.26 ± 2.02**	**9.87 ± 3.19**	**2.64 ± 0.69**	**1.15 ± 0.35**	**0.87 ± 0.59**	**6.58 ± 3.59**	**4.58 ± 1.93**	**0.33 ± 0.64**	**2.17 ± 1.93**	**1.72 ± 0.77**	**2.66 ± 1.03**	**17.72 ± 7.07**
Crustaceans	40. Shrimp	70	2.56 ± 0.63	15.75 ± 1.63	5.82 ± 1.25	4.87 ± 0.59	17.90 ± 3.77	4.63 ± 0.64	0.87 ± 0.18	2.23 ± 0.89	3.55 ± 1.42	10.81 ± 2.21	1.11 ± 0.93	0.30 ± 0.18	0.77 ± 0.28	1.60 ± 0.94	14.49 ± 2.99
	41. Box crab	59	1.47 ± 0.69	13.94 ± 3.25	4.88 ± 2.51	9.12 ± 1.56	8.55 ± 2.69	2.94 ± 0.88	1.75 ± 0.58	1.01 ± 0.34	15.16 ± 4.01	9.05 ± 2.36	0.53 ± 0.40	1.45 ± 0.75	0.91 ± 0.25	1.79 ± 0.83	8.96 ± 3.41
	42. Swimming crab	29	1.20 ± 0.56	16.50 ± 2.52	3.07 ± 1.04	8.95 ± 0.94	9.33 ± 0.92	2.54 ± 0.42	2.22 ± 0.43	0.88 ± 0.34	14.33 ± 2.89	9.63 ± 1.75	0.50 ± 0.51	1.33 ± 0.79	0.62 ± 0.13	1.56 ± 0.36	11.86 ± 2.53
	43. Pebble crab	21	2.20 ± 1.01	15.96 ± 2.96	4.36 ± 0.98	8.24 ± 1.93	12.01 ± 3.39	3.26 ± 0.83	1.68 ± 0.25	1.39 ± 0.48	8.76 ± 4.07	8.37 ± 2.32	1.48 ± 1.96	0.62 ± 0.36	0.69 ± 0.19	1.47 ± 0.42	10.64 ± 2.43
	44. Slipper lobster	102	1.40 ± 0.54	13.40 ± 1.98	3.72 ± 2.11	9.15 ± 1.09	13.10 ± 2.85	2.43 ± 1.32	1.67 ± 0.45	1.45 ± 0.58	9.80 ± 3.06	7.81 ± 1.73	0.43 ± 0.42	1.09 ± 0.52	1.12 ± 0.35	1.25 ± 0.64	12.97 ± 3.09
	45. Spiny lobster	71	1.18 ± 0.40	13.16 ± 1.97	3.93 ± 1.06	9.73 ± 1.13	10.23 ± 2.52	2.64 ± 0.49	2.03 ± 0.47	0.90 ± 0.31	16.88 ± 4.26	9.24 ± 2.36	0.37 ± 0.53	1.42 ± 0.57	0.85 ± 0.24	1.74 ± 0.65	8.49 ± 2.45
	Total	**352**	**1.63 ± 0.79**	**14.32 ± 2.59**	**4.36 ± 1.94**	**8.34 ± 2.11**	**12.34 ± 4.33**	**3.05 ± 1.22**	**1.64 ± 0.60**	**1.37 ± 0.74**	**11.19 ± 5.79**	**9.09 ± 2.35**	**0.64 ± 0.82**	**1.05 ± 0.70**	**0.89 ± 0.32**	**1.55 ± 0.75**	**11.47 ± 3.72**
Cephalopods	38. Octopus	40	1.08 ± 0.56	17.81 ± 1.79	0.88 ± 0.54	10.67 ± 1.34	2.95 ± 1.23	1.82 ± 0.34	0.74 ± 0.20	1.89 ± 0.43	13.48 ± 5.83	9.17 ± 2.50	0.12 ± 0.09	1.56 ± 0.87	1.57 ± 0.27	1.40 ± 0.31	23.82 ± 4.97
	39. Squid	15	1.53 ± 0.63	18.43 ± 0.80	1.37 ± 0.78	6.63 ± 0.95	6.63 ± 2.97	1.36 ± 0.29	0.38 ± 0.14	4.46 ± 0.81	2.75 ± 0.27	11.30 ± 1.44	0.20 ± 0.08	0.16 ± 0.02	1.02 ± 0.17	0.68 ± 0.16	33.58 ± 3.33
	Total	**55**	**1.20 ± 0.61**	**17.98 ± 1.60**	**1.02 ± 0.64**	**9.57 ± 2.20**	**3.95 ± 2.47**	**1.70 ± 0.38**	**0.65 ± 0.25**	**2.59 ± 1.28**	**10.55 ± 6.91**	**9.75 ± 2.44**	**0.14 ± 0.09**	**1.18 ± 0.97**	**1.42 ± 0.34**	**1.21 ± 0.42**	**26.48 ± 6.32**

APPENDIX 4.1 Fat content and fatty acid (FA) composition (mass %) of the 100 species of NWHI and MHI fishes and invertebrates analyzed (n = 2,190). Values are means ± SEM of 39 FAs (out of 74) which were the most abundant and/or exhibited the greatest variance across all species.

Fishes

Group	11	11	11	31	31	31
Species name	*Abudefduf abdominalis*	*Abudefduf sordidus*	*Abudefduf vaigiensis*	*Acanthurus achilles*	*Acanthurus dussumieri*	*Acanthurus leucopareius*
Common name	(Hawaiian sergeant)	(Blackspot sergeant)	(Indo-Pacific sergeant)	(Achilles tang)	(Eyestripe surgeonfish)	(Whitebar surgeonfish)
	n=20	n=21	n=16	n=20	n=16	n=22
Length (cm)	18.78 ± 1.06	15.84 ± 2.73	15.39 ± 1.20	15.93 ± 2.93	17.84 ± 3.98	15.60 ± 3.92
Mass (g)	209.17 ± 33.42	191.22 ± 71.18	129.23 ± 25.37	136.08 ± 66.53	227.31 ± 110.18	182.56 ± 108.99
Fat content (%)	2.03 ± 0.84	2.44 ± 1.13	3.42 ± 2.33	4.41 ± 2.88	2.19 ± 0.77	3.61 ± 1.91
Saturated FA						
14:0	4.33 ± 1.12	2.45 ± 0.65	5.73 ± 1.36	3.74 ± 0.79	7.53 ± 3.70	7.86 ± 3.40
16:0	25.39 ± 4.31	27.25 ± 4.69	28.02 ± 4.06	40.56 ± 4.97	27.09 ± 2.55	30.50 ± 3.77
17:0	1.04 ± 0.10	1.27 ± 0.39	1.08 ± 0.10	0.95 ± 0.15	0.59 ± 0.29	0.82 ± 0.34
18:0	6.93 ± 0.97	8.07 ± 1.91	7.54 ± 1.53	6.15 ± 0.83	6.10 ± 1.78	4.82 ± 0.83
subtotal:	37.69 ± 4.60	39.03 ± 3.12	42.37 ± 3.70	51.40 ± 4.75	41.30 ± 2.70	44.00 ± 2.48
Monounsaturated FA						
16:1n-7	4.46 ± 1.44	5.19 ± 2.04	4.71 ± 1.52	3.50 ± 1.22	7.45 ± 2.06	5.40 ± 1.79
18:1n-9	9.09 ± 1.84	8.85 ± 2.19	8.05 ± 0.95	8.37 ± 0.76	3.73 ± 0.49	6.50 ± 1.11
18:1n-7	1.93 ± 0.42	2.50 ± 0.43	2.06 ± 0.46	2.23 ± 0.23	1.80 ± 0.50	1.69 ± 0.34
20:1n-11	0.30 ± 0.25	0.44 ± 0.39	0.11 ± 0.05	0.05 ± 0.03	0.05 ± 0.04	0.06 ± 0.04
20:1n-9	1.20 ± 0.62	0.78 ± 0.31	0.80 ± 0.17	1.80 ± 0.61	0.40 ± 0.07	0.83 ± 0.44
20:1n-7	0.15 ± 0.05	0.24 ± 0.12	0.11 ± 0.03	0.17 ± 0.03	0.08 ± 0.03	0.12 ± 0.04
22:1n-11	0.71 ± 0.76	0.34 ± 0.24	0.18 ± 0.11	0.03 ± 0.03	2.43 ± 3.17	0.12 ± 0.16
22:1n-9	0.26 ± 0.18	0.18 ± 0.15	0.12 ± 0.03	0.12 ± 0.05	0.11 ± 0.07	0.12 ± 0.05
22:1n-7	0.08 ± 0.03	0.17 ± 0.13	0.12 ± 0.05	0.05 ± 0.02	0.05 ± 0.03	0.03 ± 0.02
subtotal:	18.18 ± 3.39	18.69 ± 4.08	16.27 ± 2.57	16.33 ± 2.59	16.10 ± 2.21	14.87 ± 1.40
Polyunsaturated FA						
16:2n-6	0.07 ± 0.03	0.23 ± 0.19	0.09 ± 0.04	0.02 ± 0.01	0.59 ± 0.61	0.42 ± 0.49
16:2n-4	0.38 ± 0.10	0.31 ± 0.12	0.34 ± 0.05	0.01 ± 0.02	0.07 ± 0.03	0.25 ± 0.19
16:3n-6	0.24 ± 0.10	0.25 ± 0.11	0.37 ± 0.11	0.02 ± 0.01	0.63 ± 0.27	0.45 ± 0.28
16:3n-4	0.08 ± 0.04	0.37 ± 0.21	0.07 ± 0.03	0.10 ± 0.02	0.86 ± 0.37	0.74 ± 0.49
16:4n-1	0.03 ± 0.02	0.09 ± 0.09	0.03 ± 0.01	0.02 ± 0.02	0.21 ± 0.20	0.24 ± 0.18
18:2n-6	1.44 ± 0.30	3.03 ± 1.20	1.62 ± 0.13	0.94 ± 0.19	1.53 ± 0.29	1.58 ± 0.29
18:2n-4	0.07 ± 0.02	0.06 ± 0.01	0.08 ± 0.02	0.02 ± 0.01	0.08 ± 0.03	0.05 ± 0.01
18:3n-6	1.19 ± 0.76	1.11 ± 0.47	0.96 ± 0.46	0.39 ± 0.12	1.71 ± 0.59	1.38 ± 0.51
18:3n-4	0.07 ± 0.04	0.07 ± 0.03	0.05 ± 0.01	0.10 ± 0.02	0.05 ± 0.03	0.06 ± 0.01
18:3n-3	0.49 ± 0.14	2.12 ± 1.28	0.65 ± 0.20	0.34 ± 0.08	1.18 ± 1.37	0.87 ± 0.38
18:3n-1	0.10 ± 0.01	0.09 ± 0.05	0.12 ± 0.02	0.00 ± 0.01	0.03 ± 0.02	0.03 ± 0.02
18:4n-3	0.68 ± 0.25	1.01 ± 0.46	0.75 ± 0.24	0.20 ± 0.07	2.87 ± 0.75	2.65 ± 0.99
18:4n-1	0.01 ± 0.02	0.01 ± 0.01	0.00 ± 0.01	0.02 ± 0.02	0.01 ± 0.01	0.01 ± 0.01
20:2n-6	0.34 ± 0.06	0.43 ± 0.10	0.29 ± 0.04	0.19 ± 0.04	0.18 ± 0.06	0.24 ± 0.10
20:3n-6	0.37 ± 0.14	0.63 ± 0.12	0.36 ± 0.14	1.07 ± 0.20	0.88 ± 0.25	1.11 ± 0.15
20:4n-6	4.21 ± 1.63	7.58 ± 3.48	2.72 ± 1.24	6.18 ± 2.31	8.92 ± 2.24	7.23 ± 1.49
20:3n-3	0.09 ± 0.02	0.19 ± 0.06	0.09 ± 0.03	0.09 ± 0.03	0.11 ± 0.09	0.11 ± 0.08
20:4n-3	0.24 ± 0.06	0.22 ± 0.05	0.32 ± 0.06	0.34 ± 0.07	0.37 ± 0.08	0.53 ± 0.13
20:5n-3	4.76 ± 0.71	5.42 ± 1.77	4.51 ± 0.56	7.68 ± 1.62	5.91 ± 1.58	7.81 ± 1.74
22:2n-6	0.02 ± 0.01	0.03 ± 0.03	0.01 ± 0.01	0.01 ± 0.01	0.16 ± 0.26	0.15 ± 0.25
21:5n-3	0.12 ± 0.05	0.12 ± 0.07	0.15 ± 0.06	0.10 ± 0.04	0.18 ± 0.09	0.08 ± 0.05
22:4n-6	0.66 ± 0.21	1.98 ± 1.36	0.58 ± 0.21	1.87 ± 0.62	1.65 ± 0.46	2.42 ± 0.39
22:5n-6	1.38 ± 0.50	0.87 ± 0.35	1.19 ± 0.56	0.52 ± 0.28	1.31 ± 0.42	0.93 ± 0.31
22:4n-3	0.03 ± 0.02	0.04 ± 0.01	0.02 ± 0.01	0.09 ± 0.05	0.19 ± 0.14	0.16 ± 0.06
22:5n-3	1.95 ± 0.60	2.97 ± 1.21	1.74 ± 0.35	3.18 ± 0.62	2.36 ± 0.68	3.17 ± 0.79
22:6n-3	18.25 ± 3.15	6.06 ± 1.89	17.94 ± 5.24	2.94 ± 1.47	5.29 ± 2.78	3.93 ± 1.81
subtotal:	37.26 ± 3.78	35.31 ± 5.84	35.04 ± 6.57	26.45 ± 6.36	37.33 ± 3.87	36.59 ± 3.80
Total	93.14 ± 0.80	93.04 ± 1.29	93.68 ± 0.82	94.19 ± 1.06	94.73 ± 2.45	95.46 ± 1.21

Appendix 4.1 *continued*

	Fishes					
Group	31	31	31	37	46	46
Species name	*Acanthurus nigroris*	*Acanthurus olivaceus*	*Acanthurus triostegus*	*Anampses cuvier*	*Antigonia capros*	*Antigonia eos*
Common name	(Bluelined surgeonfish)	(Orangeband surgeonfish)	(Convict tang)	(Pearl wrasse)	(Boar fish)	(Boar fish)
	n=20	n=20	n=20	n=20	n=10	n=10
Length (cm)	18.71 ± 2.01	18.05 ± 4.54	14.75 ± 2.20	22.03 ± 5.55	6.33 ± 0.39	6.65 ± 0.39
Mass (g)	193.26 ± 57.15	190.90 ± 127.49	90.90 ± 47.74	274.78 ± 162.14	6.44 ± 1.38	9.82 ± 1.24
Fat content (%)	4.22 ± 1.22	2.98 ± 2.16	2.35 ± 1.70	3.39 ± 1.47	1.37 ± 0.37	2.37 ± 0.81
Saturated FA						
14:0	7.67 ± 2.56	7.38 ± 2.86	5.65 ± 1.43	4.12 ± 1.48	1.53 ± 0.25	4.70 ± 0.87
16:0	31.79 ± 3.23	27.58 ± 2.43	31.60 ± 5.88	21.99 ± 1.37	18.53 ± 0.57	20.36 ± 1.01
17:0	0.72 ± 0.24	0.48 ± 0.17	0.64 ± 0.07	1.70 ± 0.23	1.15 ± 0.08	1.21 ± 0.15
18:0	4.27 ± 0.66	4.72 ± 1.41	4.69 ± 1.74	8.99 ± 0.76	8.92 ± 0.41	6.78 ± 0.40
subtotal:	44.45 ± 2.31	40.17 ± 3.38	42.58 ± 5.31	36.81 ± 2.27	30.13 ± 0.60	33.05 ± 1.53
Monounsaturated FA						
16:1n-7	6.98 ± 1.52	8.05 ± 3.89	4.69 ± 2.01	3.36 ± 0.54	2.83 ± 0.14	5.03 ± 0.60
18:1n-9	6.29 ± 1.01	4.41 ± 1.27	7.53 ± 0.90	9.81 ± 1.79	9.79 ± 0.62	8.91 ± 1.16
18:1n-7	2.14 ± 0.48	1.60 ± 0.38	1.41 ± 0.21	3.53 ± 0.55	2.09 ± 0.10	2.49 ± 0.14
20:1n-11	0.04 ± 0.02	0.03 ± 0.03	0.01 ± 0.03	0.91 ± 0.40	0.22 ± 0.05	0.20 ± 0.06
20:1n-9	0.86 ± 0.38	0.31 ± 0.21	0.67 ± 0.30	0.73 ± 0.19	1.21 ± 0.22	0.79 ± 0.22
20:1n-7	0.14 ± 0.05	0.07 ± 0.03	0.08 ± 0.03	0.26 ± 0.05	0.29 ± 0.04	0.18 ± 0.03
22:1n-11	1.44 ± 2.54	5.47 ± 6.40	0.00 ± 0.01	0.18 ± 0.08	0.19 ± 0.04	0.31 ± 0.09
22:1n-9	0.08 ± 0.02	0.06 ± 0.04	0.11 ± 0.04	0.07 ± 0.03	0.31 ± 0.03	0.18 ± 0.04
22:1n-7	0.08 ± 0.05	0.03 ± 0.02	0.03 ± 0.03	0.07 ± 0.02	0.15 ± 0.01	0.09 ± 0.01
subtotal:	18.03 ± 1.48	20.04 ± 3.95	14.52 ± 1.98	18.94 ± 1.35	17.08 ± 0.96	18.17 ± 1.76
Polyunsaturated FA						
16:2n-6	0.24 ± 0.08	0.21 ± 0.08	0.10 ± 0.04	0.07 ± 0.02	0.02 ± 0.01	0.04 ± 0.01
16:2n-4	0.46 ± 0.58	0.16 ± 0.19	0.11 ± 0.05	0.19 ± 0.05	0.69 ± 0.06	0.30 ± 0.03
16:3n-6	0.67 ± 0.32	0.72 ± 0.47	0.14 ± 0.05	0.22 ± 0.06	0.06 ± 0.01	0.59 ± 0.10
16:3n-4	0.90 ± 0.43	0.90 ± 0.59	0.20 ± 0.07	0.18 ± 0.06	0.02 ± 0.01	0.05 ± 0.05
16:4n-1	0.47 ± 0.13	0.18 ± 0.21	0.23 ± 0.10	0.03 ± 0.03	0.16 ± 0.13	0.11 ± 0.06
18:2n-6	1.60 ± 0.25	1.48 ± 0.39	1.51 ± 0.31	1.59 ± 0.14	1.00 ± 0.08	1.46 ± 0.11
18:2n-4	0.06 ± 0.01	0.05 ± 0.01	0.02 ± 0.01	0.09 ± 0.02	0.08 ± 0.01	0.16 ± 0.02
18:3n-6	1.48 ± 0.56	1.37 ± 0.31	0.74 ± 0.15	0.47 ± 0.15	0.40 ± 0.02	0.36 ± 0.02
18:3n-4	0.07 ± 0.04	0.04 ± 0.02	0.08 ± 0.03	0.14 ± 0.05	0.06 ± 0.01	0.06 ± 0.02
18:3n-3	1.13 ± 0.36	1.02 ± 0.62	0.89 ± 0.34	0.87 ± 0.33	0.30 ± 0.10	1.01 ± 0.15
18:3n-1	0.03 ± 0.01	0.02 ± 0.02	0.00 ± 0.01	0.04 ± 0.01	0.22 ± 0.20	0.17 ± 0.03
18:4n-3	2.55 ± 0.85	2.50 ± 1.36	0.79 ± 0.26	0.60 ± 0.11	0.20 ± 0.07	0.94 ± 0.14
18:4n-1	0.02 ± 0.01	0.01 ± 0.01	0.00 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
20:2n-6	0.20 ± 0.06	0.18 ± 0.06	0.17 ± 0.04	0.79 ± 0.11	0.43 ± 0.03	0.37 ± 0.04
20:3n-6	0.98 ± 0.15	0.68 ± 0.14	1.14 ± 0.18	0.58 ± 0.05	0.18 ± 0.02	0.20 ± 0.02
20:4n-6	5.61 ± 1.13	8.81 ± 4.81	8.37 ± 2.92	9.14 ± 1.34	4.23 ± 0.12	1.77 ± 0.35
20:3n-3	0.10 ± 0.04	0.07 ± 0.03	0.07 ± 0.02	0.22 ± 0.07	0.10 ± 0.02	0.23 ± 0.04
20:4n-3	0.50 ± 0.12	0.35 ± 0.16	0.30 ± 0.07	0.34 ± 0.09	0.25 ± 0.02	0.90 ± 0.11
20:5n-3	7.12 ± 1.14	5.44 ± 2.20	10.87 ± 2.12	8.69 ± 1.12	4.29 ± 0.37	4.76 ± 0.34
22:2n-6	0.05 ± 0.07	0.09 ± 0.11	0.02 ± 0.03	0.02 ± 0.01	0.04 ± 0.01	0.03 ± 0.00
21:5n-3	0.20 ± 0.05	0.19 ± 0.08	0.04 ± 0.03	0.19 ± 0.08	0.14 ± 0.02	0.11 ± 0.01
22:4n-6	1.78 ± 0.39	1.40 ± 0.74	2.74 ± 0.54	2.86 ± 0.64	0.96 ± 0.12	0.59 ± 0.10
22:5n-6	0.78 ± 0.22	1.26 ± 0.63	0.60 ± 0.24	1.13 ± 0.34	2.93 ± 0.18	1.81 ± 0.28
22:4n-3	0.18 ± 0.07	0.13 ± 0.06	0.08 ± 0.02	0.04 ± 0.01	0.05 ± 0.01	0.16 ± 0.03
22:5n-3	2.77 ± 0.70	2.19 ± 0.76	4.40 ± 0.68	2.54 ± 0.49	2.90 ± 0.50	3.40 ± 0.40
22:6n-3	2.88 ± 0.82	5.10 ± 2.44	4.54 ± 2.15	6.97 ± 1.19	26.10 ± 1.03	22.04 ± 3.36
subtotal:	32.81 ± 2.82	34.54 ± 4.19	38.15 ± 6.15	37.98 ± 3.09	45.83 ± 1.24	41.62 ± 3.43
Total	95.29 ± 0.60	94.75 ± 0.69	95.24 ± 1.10	93.72 ± 0.83	93.04 ± 0.33	92.84 ± 0.51

Appendix 4.1 *continued*

	Fishes					
Group	2	7	47	37	17	17
Species name	*Apogon maculiferus*	*Ariosoma marginatum*	*Bembrops filifera*	*Bodianus bilunulatus*	*Bothus mancus*	*Bothus pantherinus*
Common name	(Spotted cardinalfish)	(Large-eye conger)	(Duck-billed bembropsid)	(Hawaiian hogfish)	(Flowery flounder)	(Panther flounder)
	n=18	n=26	n=19	n=20	n=16	n=75
Length (cm)	7.32 ± 1.42	18.68 ± 7.12	17.37 ± 5.39	24.25 ± 6.24	12.69 ± 2.89	5.48 ± 0.84
Mass (g)	9.06 ± 5.63	23.15 ± 28.18	40.04 ± 27.98	392.08 ± 305.14	44.77 ± 24.66	3.45 ± 1.58
Fat content (%)	2.19 ± 0.77	1.65 ± 0.47	1.83 ± 1.40	1.49 ± 0.55	1.07 ± 0.26	2.11 ± 0.76
Saturated FA						
14:0	3.71 ± 0.84	2.68 ± 1.03	1.83 ± 0.77	3.53 ± 1.54	1.38 ± 0.47	3.58 ± 1.22
16:0	22.18 ± 3.00	20.44 ± 1.45	17.89 ± 1.04	20.48 ± 1.27	18.50 ± 1.51	20.46 ± 1.74
17:0	1.49 ± 0.19	1.46 ± 0.34	0.83 ± 0.17	1.65 ± 0.24	1.32 ± 0.42	1.36 ± 0.19
18:0	9.40 ± 1.65	8.66 ± 1.39	5.49 ± 0.97	10.08 ± 0.79	10.12 ± 1.22	7.80 ± 1.23
subtotal:	36.78 ± 4.97	33.25 ± 1.77	26.03 ± 0.89	35.73 ± 2.35	31.33 ± 1.43	33.20 ± 2.41
Monounsaturated FA						
16:1n-7	3.19 ± 0.61	3.36 ± 1.03	4.74 ± 1.85	2.63 ± 0.56	1.99 ± 0.52	3.47 ± 0.61
18:1n-9	9.02 ± 1.32	9.71 ± 1.58	14.52 ± 3.03	9.48 ± 1.27	9.62 ± 1.29	9.71 ± 2.03
18:1n-7	2.81 ± 0.45	3.19 ± 0.64	2.95 ± 0.82	2.24 ± 0.26	2.34 ± 0.51	2.17 ± 0.24
20:1n-11	0.23 ± 0.08	0.26 ± 0.21	0.27 ± 0.08	0.91 ± 0.42	0.14 ± 0.08	0.20 ± 0.06
20:1n-9	0.92 ± 0.29	0.42 ± 0.12	1.26 ± 0.25	0.54 ± 0.17	0.52 ± 0.13	0.60 ± 0.11
20:1n-7	0.20 ± 0.05	0.31 ± 0.11	0.21 ± 0.07	0.19 ± 0.06	0.19 ± 0.04	0.27 ± 0.08
22:1n-11	0.22 ± 0.15	0.14 ± 0.07	0.10 ± 0.03	0.40 ± 0.22	0.09 ± 0.08	0.20 ± 0.11
22:1n-9	0.13 ± 0.05	0.09 ± 0.03	0.17 ± 0.05	0.11 ± 0.04	0.08 ± 0.03	0.11 ± 0.04
22:1n-7	0.10 ± 0.04	0.08 ± 0.03	0.08 ± 0.05	0.12 ± 0.05	0.15 ± 0.04	0.14 ± 0.04
subtotal:	16.81 ± 2.02	17.56 ± 2.77	24.30 ± 5.41	16.61 ± 2.16	15.11 ± 1.30	16.87 ± 1.94
Polyunsaturated FA						
16:2n-6	0.05 ± 0.05	0.05 ± 0.05	0.01 ± 0.01	0.03 ± 0.01	0.05 ± 0.05	0.08 ± 0.04
16:2n-4	0.24 ± 0.10	0.65 ± 0.21	0.71 ± 0.29	0.29 ± 0.06	0.34 ± 0.27	0.78 ± 0.11
16:3n-6	0.24 ± 0.08	0.11 ± 0.04	0.07 ± 0.04	0.10 ± 0.03	0.04 ± 0.01	0.23 ± 0.09
16:3n-4	0.08 ± 0.05	0.04 ± 0.03	0.03 ± 0.01	0.09 ± 0.03	0.04 ± 0.02	0.05 ± 0.02
16:4n-1	0.05 ± 0.05	0.01 ± 0.02	0.24 ± 0.09	0.08 ± 0.03	0.01 ± 0.02	0.00 ± 0.00
18:2n-6	1.28 ± 0.15	1.32 ± 0.19	0.92 ± 0.18	1.80 ± 0.24	0.99 ± 0.15	1.18 ± 0.08
18:2n-4	0.12 ± 0.04	0.16 ± 0.05	0.08 ± 0.02	0.06 ± 0.01	0.07 ± 0.02	0.19 ± 0.04
18:3n-6	0.42 ± 0.10	0.34 ± 0.08	0.28 ± 0.06	0.55 ± 0.16	0.41 ± 0.11	0.41 ± 0.05
18:3n-4	0.08 ± 0.03	0.11 ± 0.04	0.09 ± 0.03	0.08 ± 0.03	0.08 ± 0.03	0.12 ± 0.04
18:3n-3	0.55 ± 0.15	0.27 ± 0.11	0.25 ± 0.06	0.54 ± 0.18	0.18 ± 0.09	0.36 ± 0.15
18:3n-1	0.07 ± 0.03	0.20 ± 0.06	0.33 ± 0.09	0.06 ± 0.02	0.08 ± 0.07	0.20 ± 0.02
18:4n-3	0.52 ± 0.15	0.14 ± 0.08	0.07 ± 0.04	0.36 ± 0.14	0.11 ± 0.07	0.47 ± 0.24
18:4n-1	0.00 ± 0.01	0.00 ± 0.01	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
20:2n-6	0.48 ± 0.06	0.45 ± 0.12	0.34 ± 0.05	0.75 ± 0.13	0.55 ± 0.16	0.44 ± 0.06
20:3n-6	0.26 ± 0.09	0.30 ± 0.07	0.15 ± 0.05	0.62 ± 0.11	0.33 ± 0.10	0.17 ± 0.04
20:4n-6	5.34 ± 2.02	5.45 ± 1.40	3.88 ± 0.98	12.48 ± 2.01	10.43 ± 2.51	3.33 ± 0.66
20:3n-3	0.15 ± 0.03	0.12 ± 0.04	0.09 ± 0.02	0.15 ± 0.04	0.16 ± 0.06	0.17 ± 0.03
20:4n-3	0.27 ± 0.06	0.51 ± 0.19	0.31 ± 0.11	0.22 ± 0.04	0.23 ± 0.09	0.50 ± 0.09
20:5n-3	7.70 ± 1.73	6.45 ± 1.25	4.53 ± 1.61	4.36 ± 0.86	4.71 ± 1.17	5.08 ± 0.89
22:2n-6	0.02 ± 0.02	0.00 ± 0.00	0.02 ± 0.01	0.04 ± 0.03	0.00 ± 0.00	0.00 ± 0.00
21:5n-3	0.13 ± 0.08	0.12 ± 0.05	0.07 ± 0.05	0.16 ± 0.10	0.09 ± 0.02	0.15 ± 0.03
22:4n-6	1.01 ± 0.46	1.01 ± 0.61	0.64 ± 0.13	2.43 ± 0.53	2.16 ± 0.59	0.68 ± 0.20
22:5n-6	1.08 ± 0.20	1.56 ± 0.31	2.42 ± 0.33	1.54 ± 0.48	2.04 ± 0.67	1.74 ± 0.20
22:4n-3	0.04 ± 0.01	0.09 ± 0.04	0.04 ± 0.01	0.05 ± 0.01	0.09 ± 0.03	0.10 ± 0.02
22:5n-3	1.92 ± 0.49	2.03 ± 0.62	2.62 ± 0.35	3.20 ± 0.85	4.25 ± 0.86	2.69 ± 0.67
22:6n-3	18.09 ± 5.44	21.28 ± 4.38	24.92 ± 4.00	9.55 ± 3.46	20.09 ± 3.40	24.28 ± 2.24
subtotal:	40.20 ± 5.53	42.79 ± 3.16	43.12 ± 5.80	39.59 ± 4.64	47.54 ± 2.25	43.40 ± 2.09
Total	93.78 ± 0.92	93.59 ± 1.49	93.45 ± 1.14	91.93 ± 1.39	93.98 ± 1.15	93.47 ± 0.53

Appendix 4.1 *continued*

	Fishes					
Group	17	13	22	22	22	1
Species name	*Bothus thompsoni*	*Callionymus decoratus*	*Canthigaster coronata*	*Canthigaster jactator*	*Canthigaster rivulata*	*Centropyge potteri*
Common name	(Thompson's flounder)	(Longtail dragonet)	(Crown toby)	(Hawaiian whitespotted toby)	(Maze toby)	(Potter's angelfish)
	n=25	n=20	n=20	n=24	n=16	n=20
Length (cm)	9.10 ± 2.38	11.39 ± 3.25	7.95 ± 1.86	6.42 ± 0.87	7.78 ± 1.87	8.31 ± 1.72
Mass (g)	9.33 ± 6.17	5.06 ± 2.60	24.49 ± 16.06	9.79 ± 4.01	14.04 ± 10.51	25.89 ± 13.25
Fat content (%)	2.02 ± 0.95	1.19 ± 0.16	1.48 ± 0.65	1.59 ± 0.69	0.97 ± 0.73	4.30 ± 1.14
Saturated FA						
14:0	5.53 ± 2.48	2.50 ± 1.27	0.77 ± 0.25	0.95 ± 0.26	0.89 ± 0.23	7.68 ± 1.10
16:0	19.57 ± 2.24	18.88 ± 1.62	19.98 ± 4.88	21.71 ± 2.95	16.17 ± 2.75	29.57 ± 1.95
17:0	1.25 ± 0.18	1.59 ± 0.38	2.48 ± 0.46	2.04 ± 0.45	2.14 ± 0.42	0.92 ± 0.39
18:0	7.45 ± 1.12	11.40 ± 2.24	11.56 ± 1.51	11.40 ± 2.23	13.99 ± 1.23	6.60 ± 0.76
subtotal:	33.80 ± 3.80	34.38 ± 3.94	34.79 ± 5.00	36.10 ± 3.39	33.19 ± 2.72	44.78 ± 2.16
Monounsaturated FA						
16:1n-7	3.66 ± 0.85	2.70 ± 0.58	1.68 ± 0.66	2.17 ± 0.87	1.88 ± 0.60	7.84 ± 1.16
18:1n-9	9.62 ± 2.27	6.18 ± 0.83	7.07 ± 1.86	7.79 ± 0.92	7.20 ± 1.05	6.81 ± 0.85
18:1n-7	2.38 ± 0.35	2.89 ± 0.40	3.09 ± 0.46	3.07 ± 0.33	2.79 ± 0.46	2.48 ± 0.20
20:1n-11	0.18 ± 0.07	0.48 ± 0.16	1.02 ± 0.77	0.89 ± 0.47	1.35 ± 0.47	0.13 ± 0.12
20:1n-9	0.69 ± 0.22	0.37 ± 0.08	0.57 ± 0.19	0.32 ± 0.05	0.68 ± 0.13	0.25 ± 0.06
20:1n-7	0.47 ± 0.16	0.28 ± 0.09	0.32 ± 0.12	0.22 ± 0.07	0.48 ± 0.11	0.12 ± 0.06
22:1n-11	0.34 ± 0.16	0.25 ± 0.07	0.36 ± 0.27	0.42 ± 0.21	0.48 ± 0.15	1.45 ± 2.14
22:1n-9	0.16 ± 0.03	0.07 ± 0.03	0.11 ± 0.06	0.09 ± 0.05	0.16 ± 0.04	0.08 ± 0.03
22:1n-7	0.22 ± 0.09	0.22 ± 0.04	0.19 ± 0.09	0.25 ± 0.17	0.25 ± 0.06	0.07 ± 0.03
subtotal:	17.72 ± 1.83	13.43 ± 1.34	14.42 ± 2.83	15.22 ± 1.98	15.27 ± 1.93	19.24 ± 1.52
Polyunsaturated FA						
16:2n-6	0.03 ± 0.01	0.17 ± 0.09	0.03 ± 0.01	0.07 ± 0.08	0.03 ± 0.04	0.23 ± 0.04
16:2n-4	0.63 ± 0.10	0.69 ± 0.17	0.71 ± 0.25	0.91 ± 0.30	0.63 ± 0.14	0.19 ± 0.14
16:3n-6	0.21 ± 0.08	0.10 ± 0.03	0.04 ± 0.01	0.09 ± 0.04	0.04 ± 0.03	0.85 ± 0.27
16:3n-4	0.02 ± 0.03	0.15 ± 0.06	0.09 ± 0.05	0.12 ± 0.07	0.04 ± 0.05	1.08 ± 0.37
16:4n-1	0.01 ± 0.05	0.00 ± 0.00	0.12 ± 0.08	0.07 ± 0.07	0.00 ± 0.01	0.17 ± 0.12
18:2n-6	1.22 ± 0.07	1.05 ± 0.19	1.05 ± 0.45	1.22 ± 0.23	0.88 ± 0.21	1.66 ± 0.18
18:2n-4	0.19 ± 0.06	0.11 ± 0.05	0.11 ± 0.03	0.09 ± 0.03	0.12 ± 0.03	0.17 ± 0.04
18:3n-6	0.17 ± 0.15	0.65 ± 0.12	0.58 ± 0.29	0.61 ± 0.21	0.47 ± 0.28	1.27 ± 0.19
18:3n-4	0.07 ± 0.02	0.07 ± 0.03	0.12 ± 0.04	0.10 ± 0.04	0.08 ± 0.04	0.31 ± 0.09
18:3n-3	0.35 ± 0.13	0.25 ± 0.09	0.41 ± 0.58	0.50 ± 0.37	0.16 ± 0.11	0.74 ± 0.14
18:3n-1	0.24 ± 0.04	0.17 ± 0.06	0.28 ± 0.09	0.18 ± 0.06	0.24 ± 0.06	0.04 ± 0.03
18:4n-3	0.50 ± 0.21	0.26 ± 0.09	0.18 ± 0.10	0.31 ± 0.12	0.15 ± 0.08	1.96 ± 0.58
18:4n-1	0.01 ± 0.01	0.01 ± 0.04	0.01 ± 0.02	0.00 ± 0.01	0.00 ± 0.00	0.09 ± 0.02
20:2n-6	0.46 ± 0.06	0.46 ± 0.08	0.74 ± 0.20	0.46 ± 0.09	0.64 ± 0.15	0.28 ± 0.10
20:3n-6	0.19 ± 0.02	0.33 ± 0.05	0.42 ± 0.14	0.43 ± 0.11	0.27 ± 0.06	1.02 ± 0.21
20:4n-6	3.55 ± 1.49	8.92 ± 1.57	11.23 ± 3.02	11.08 ± 2.05	12.34 ± 3.11	5.28 ± 0.73
20:3n-3	0.17 ± 0.05	0.07 ± 0.03	0.25 ± 0.26	0.12 ± 0.06	0.15 ± 0.08	0.07 ± 0.02
20:4n-3	0.53 ± 0.15	0.18 ± 0.05	0.17 ± 0.11	0.19 ± 0.06	0.12 ± 0.06	0.91 ± 0.14
20:5n-3	5.38 ± 0.93	4.75 ± 0.63	2.38 ± 0.72	2.99 ± 1.02	3.09 ± 0.82	6.45 ± 1.77
22:2n-6	0.00 ± 0.00	0.02 ± 0.02	0.03 ± 0.02	0.02 ± 0.04	0.00 ± 0.00	0.02 ± 0.04
21:5n-3	0.11 ± 0.04	0.05 ± 0.03	0.22 ± 0.13	0.08 ± 0.08	0.04 ± 0.03	0.30 ± 0.06
22:4n-6	0.64 ± 0.31	2.38 ± 0.81	3.90 ± 0.93	4.29 ± 0.97	4.14 ± 0.72	1.36 ± 0.33
22:5n-6	1.67 ± 0.31	2.49 ± 0.38	3.41 ± 1.84	1.76 ± 0.56	3.57 ± 1.09	0.82 ± 0.43
22:4n-3	0.10 ± 0.03	0.05 ± 0.03	0.08 ± 0.06	0.08 ± 0.02	0.10 ± 0.16	0.09 ± 0.05
22:5n-3	2.30 ± 0.31	2.68 ± 0.41	3.70 ± 1.35	4.24 ± 1.10	4.24 ± 1.36	2.59 ± 0.51
22:6n-3	20.99 ± 2.53	19.94 ± 4.05	13.00 ± 5.05	9.83 ± 2.88	13.78 ± 3.19	2.94 ± 1.24
subtotal:	39.73 ± 2.67	46.01 ± 4.85	43.23 ± 7.57	39.83 ± 4.74	45.34 ± 5.04	30.89 ± 2.30
Total	91.25 ± 3.02	93.83 ± 0.86	92.44 ± 1.16	91.15 ± 1.45	93.80 ± 1.50	94.91 ± 1.66

Appendix 4.1 *continued*

	Fishes					
Group	8	8	8	8	8	21
Species name	*Chaetodon fremblii*	*Chaetodon miliaris*	*Chaetodon multicinctus*	*Chaetodon ornatissimus*	*Chaetodon quadrimaculatus*	*Chlorurus perspicillatus*
Common name	(Bluestripe butterflyfish)	(Milletseed butterflyfish)	(Multiband butterflyfish)	(Ornate butterflyfish)	(Fourspot butterflyfish)	(Spectacled parrotfish)
	n=22	n=27	n=19	n=20	n=20	n=22
Length (cm)	9.80 ± 1.86	9.55 ± 2.69	9.44 ± 1.24	15.24 ± 3.47	12.33 ± 1.03	20.61 ± 5.94
Mass (g)	28.25 ± 13.41	27.64 ± 17.94	25.09 ± 7.98	145.12 ± 70.88	63.33 ± 11.45	275.15 ± 229.20
Fat content (%)	4.35 ± 2.28	3.06 ± 1.87	3.41 ± 1.70	3.38 ± 2.05	4.67 ± 2.72	1.75 ± 1.22
Saturated FA						
14:0	2.64 ± 0.57	3.34 ± 1.43	1.87 ± 0.54	1.66 ± 0.33	2.71 ± 0.79	3.03 ± 1.37
16:0	26.10 ± 2.59	24.68 ± 2.85	26.11 ± 3.14	23.67 ± 1.84	31.53 ± 2.48	26.60 ± 2.28
17:0	1.18 ± 0.34	0.98 ± 0.24	0.52 ± 0.09	0.52 ± 0.07	0.61 ± 0.29	1.03 ± 0.25
18:0	9.02 ± 1.42	7.76 ± 1.67	10.84 ± 1.17	11.55 ± 0.60	9.86 ± 0.64	7.21 ± 1.32
subtotal:	38.94 ± 2.73	36.76 ± 2.69	39.35 ± 2.83	37.41 ± 2.33	44.70 ± 2.22	37.87 ± 2.55
Monounsaturated FA						
16:1n-7	2.10 ± 0.31	2.74 ± 1.06	1.48 ± 0.45	1.08 ± 0.16	2.74 ± 0.59	2.93 ± 1.63
18:1n-9	8.56 ± 1.77	9.88 ± 1.54	10.02 ± 1.20	8.21 ± 0.92	9.24 ± 1.48	6.62 ± 0.96
18:1n-7	2.91 ± 0.51	2.53 ± 0.35	0.99 ± 0.21	0.76 ± 0.09	1.29 ± 0.16	3.48 ± 0.62
20:1n-11	1.03 ± 0.53	0.26 ± 0.15	0.08 ± 0.09	0.04 ± 0.04	0.15 ± 0.10	0.02 ± 0.02
20:1n-9	0.97 ± 0.58	1.00 ± 0.45	1.90 ± 0.66	2.50 ± 0.75	1.26 ± 0.29	0.20 ± 0.10
20:1n-7	0.25 ± 0.07	0.16 ± 0.08	0.07 ± 0.03	0.06 ± 0.01	0.14 ± 0.05	0.18 ± 0.08
22:1n-11	1.08 ± 1.77	2.43 ± 2.73	0.10 ± 0.13	0.03 ± 0.05	0.11 ± 0.11	0.12 ± 0.17
22:1n-9	0.31 ± 0.14	0.32 ± 0.19	0.35 ± 0.15	0.59 ± 0.18	0.30 ± 0.06	0.06 ± 0.04
22:1n-7	0.19 ± 0.10	0.13 ± 0.09	0.03 ± 0.04	0.04 ± 0.02	0.15 ± 0.09	0.07 ± 0.03
subtotal:	17.39 ± 2.57	19.46 ± 3.67	15.02 ± 1.42	13.31 ± 1.45	15.37 ± 1.60	13.68 ± 1.78
Polyunsaturated FA						
16:2n-6	0.14 ± 0.13	0.05 ± 0.04	0.02 ± 0.02	0.03 ± 0.01	0.05 ± 0.02	0.07 ± 0.06
16:2n-4	0.42 ± 0.12	0.36 ± 0.11	0.94 ± 0.21	0.85 ± 0.15	0.65 ± 0.16	0.40 ± 0.21
16:3n-6	0.08 ± 0.04	0.35 ± 0.30	0.01 ± 0.02	0.01 ± 0.01	0.07 ± 0.08	0.17 ± 0.10
16:3n-4	0.08 ± 0.05	0.09 ± 0.07	0.02 ± 0.02	0.04 ± 0.01	0.11 ± 0.12	0.13 ± 0.09
16:4n-1	0.06 ± 0.08	0.11 ± 0.09	0.03 ± 0.05	0.02 ± 0.03	0.06 ± 0.06	0.09 ± 0.06
18:2n-6	1.17 ± 0.40	1.02 ± 0.30	0.60 ± 0.10	0.54 ± 0.08	0.69 ± 0.14	2.98 ± 0.96
18:2n-4	0.06 ± 0.01	0.14 ± 0.06	0.00 ± 0.01	0.01 ± 0.01	0.02 ± 0.03	0.04 ± 0.01
18:3n-6	0.77 ± 0.25	0.67 ± 0.24	1.58 ± 0.58	2.03 ± 0.61	1.34 ± 0.30	1.04 ± 0.36
18:3n-4	0.08 ± 0.04	0.06 ± 0.02	0.03 ± 0.02	0.05 ± 0.03	0.04 ± 0.04	0.12 ± 0.06
18:3n-3	0.82 ± 0.55	0.57 ± 0.45	0.05 ± 0.04	0.03 ± 0.01	0.13 ± 0.08	1.56 ± 0.60
18:3n-1	0.09 ± 0.03	0.08 ± 0.03	0.19 ± 0.05	0.24 ± 0.07	0.13 ± 0.04	0.02 ± 0.02
18:4n-3	0.76 ± 0.41	0.81 ± 0.54	0.53 ± 0.18	1.09 ± 0.34	0.66 ± 0.16	0.99 ± 0.53
18:4n-1	0.00 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.01	0.01 ± 0.01	0.00 ± 0.01
20:2n-6	0.53 ± 0.10	0.36 ± 0.08	0.64 ± 0.08	0.60 ± 0.10	0.38 ± 0.09	0.48 ± 0.12
20:3n-6	1.21 ± 0.67	0.80 ± 0.51	1.49 ± 0.57	1.84 ± 0.28	1.39 ± 0.23	0.78 ± 0.13
20:4n-6	8.49 ± 2.28	5.90 ± 2.77	10.69 ± 1.85	9.03 ± 0.83	6.86 ± 1.18	14.74 ± 2.57
20:3n-3	0.26 ± 0.15	0.12 ± 0.04	0.02 ± 0.02	0.06 ± 0.06	0.05 ± 0.03	0.19 ± 0.03
20:4n-3	0.60 ± 0.17	0.65 ± 0.23	0.40 ± 0.11	0.69 ± 0.22	0.70 ± 0.14	0.51 ± 0.26
20:5n-3	4.34 ± 0.74	3.23 ± 0.66	1.75 ± 0.45	1.73 ± 0.54	2.73 ± 0.56	7.01 ± 1.88
22:2n-6	0.04 ± 0.05	0.06 ± 0.05	0.02 ± 0.02	0.02 ± 0.03	0.01 ± 0.02	0.01 ± 0.01
21:5n-3	0.06 ± 0.02	0.17 ± 0.07	0.06 ± 0.06	0.08 ± 0.02	0.07 ± 0.04	0.07 ± 0.04
22:4n-6	3.54 ± 0.79	2.43 ± 1.39	8.72 ± 1.67	9.97 ± 1.30	5.24 ± 1.02	1.44 ± 0.33
22:5n-6	1.15 ± 0.39	1.52 ± 0.61	0.17 ± 0.11	0.15 ± 0.07	0.73 ± 0.64	1.19 ± 0.43
22:4n-3	0.12 ± 0.04	0.12 ± 0.04	0.10 ± 0.04	0.30 ± 0.09	0.11 ± 0.03	0.05 ± 0.02
22:5n-3	3.45 ± 0.79	2.77 ± 0.76	3.28 ± 0.59	3.11 ± 0.35	5.71 ± 2.24	2.41 ± 0.88
22:6n-3	8.45 ± 2.39	14.32 ± 4.26	6.43 ± 2.80	7.67 ± 3.85	4.69 ± 1.21	6.45 ± 2.92
subtotal:	36.76 ± 3.77	36.76 ± 5.76	37.78 ± 3.46	40.18 ± 2.47	32.63 ± 2.57	42.94 ± 3.77
Total	93.09 ± 0.99	92.99 ± 0.56	92.14 ± 1.04	90.90 ± 0.63	92.70 ± 0.69	94.49 ± 0.35

Appendix 4.1 *continued*

	Fishes					
Group	21	12	7	37	37	31
Species name	*Chlorurus sordidus*	*Chromis ovalis*	*Conger cinereus*	*Coris ballieui*	*Coris flavovittata*	*Ctenochaetus strigosus*
Common name	(Bullethead parrotfish)	(Oval chromis)	(Mustache conger)	(Lined coris)	(Yellow striped coris)	(Goldring surgeonfish)
	n=19	n=21	n=20	n=16	n=20	n=16
Length (cm)	17.96 ± 5.53	10.93 ± 1.67	100.46 ± 29.34	18.01 ± 3.02	23.80 ± 8.57	13.84 ± 2.41
Mass (g)	198.38 ± 176.32	47.77 ± 17.41	1741.48 ± 939.59	82.80 ± 43.98	332.01 ± 388.24	100.30 ± 45.03
Fat content (%)	2.10 ± 0.79	4.56 ± 2.06	2.04 ± 1.05	1.84 ± 0.99	1.10 ± 0.39	6.66 ± 4.11
Saturated FA						
14:0	3.51 ± 1.23	5.03 ± 1.98	3.79 ± 1.06	3.34 ± 1.13	1.94 ± 0.87	10.25 ± 1.04
16:0	29.80 ± 2.50	28.59 ± 2.28	24.81 ± 2.61	20.04 ± 1.27	20.08 ± 1.05	27.89 ± 1.97
17:0	1.31 ± 0.20	0.84 ± 0.35	0.94 ± 0.17	1.59 ± 0.35	1.46 ± 0.36	0.46 ± 0.09
18:0	7.34 ± 0.54	6.93 ± 1.80	7.84 ± 0.67	9.00 ± 1.00	9.90 ± 0.48	3.38 ± 0.89
subtotal:	41.96 ± 3.24	41.39 ± 2.70	37.39 ± 3.25	33.97 ± 2.78	33.38 ± 1.93	41.99 ± 1.99
Monounsaturated FA						
16:1n-7	3.47 ± 1.31	5.21 ± 1.61	4.72 ± 1.19	3.13 ± 0.62	2.17 ± 0.58	12.19 ± 1.39
18:1n-9	6.19 ± 0.58	7.51 ± 1.56	12.24 ± 1.50	10.07 ± 1.11	7.21 ± 1.05	4.33 ± 0.75
18:1n-7	3.60 ± 0.26	1.79 ± 0.36	2.94 ± 0.29	2.51 ± 0.37	2.60 ± 0.33	2.38 ± 0.34
20:1n-11	0.04 ± 0.02	0.08 ± 0.06	0.29 ± 0.18	0.50 ± 0.17	0.94 ± 0.51	0.03 ± 0.03
20:1n-9	0.19 ± 0.04	0.53 ± 0.16	0.66 ± 0.12	0.59 ± 0.12	0.55 ± 0.27	0.64 ± 0.35
20:1n-7	0.17 ± 0.04	0.10 ± 0.10	0.15 ± 0.07	0.23 ± 0.06	0.21 ± 0.08	0.19 ± 0.05
22:1n-11	0.05 ± 0.05	1.56 ± 3.38	0.37 ± 0.46	0.24 ± 0.14	0.45 ± 0.26	0.03 ± 0.04
22:1n-9	0.03 ± 0.01	0.10 ± 0.04	0.10 ± 0.03	0.09 ± 0.03	0.10 ± 0.07	0.11 ± 0.05
22:1n-7	0.05 ± 0.02	0.03 ± 0.03	0.07 ± 0.02	0.09 ± 0.04	0.10 ± 0.05	0.04 ± 0.03
subtotal:	13.77 ± 1.51	16.90 ± 2.67	21.53 ± 2.58	17.44 ± 1.37	14.33 ± 1.84	19.96 ± 1.71
Polyunsaturated FA						
16:2n-6	0.07 ± 0.03	0.14 ± 0.10	0.04 ± 0.03	0.04 ± 0.01	0.11 ± 0.09	0.36 ± 0.07
16:2n-4	0.44 ± 0.12	0.13 ± 0.07	0.29 ± 0.07	0.47 ± 0.21	0.34 ± 0.05	0.08 ± 0.02
16:3n-6	0.23 ± 0.16	0.47 ± 0.25	0.18 ± 0.08	0.16 ± 0.06	0.09 ± 0.04	1.45 ± 0.33
16:3n-4	0.18 ± 0.09	0.42 ± 0.61	0.11 ± 0.07	0.07 ± 0.02	0.08 ± 0.04	2.26 ± 0.54
16:4n-1	0.03 ± 0.02	0.28 ± 0.41	0.09 ± 0.09	0.07 ± 0.04	0.02 ± 0.03	1.49 ± 0.30
18:2n-6	3.76 ± 0.78	1.42 ± 0.22	1.14 ± 0.32	1.37 ± 0.16	1.67 ± 0.39	1.48 ± 0.11
18:2n-4	0.05 ± 0.01	0.08 ± 0.02	0.10 ± 0.01	0.10 ± 0.02	0.05 ± 0.01	0.07 ± 0.02
18:3n-6	1.16 ± 0.14	2.01 ± 1.30	0.49 ± 0.18	0.48 ± 0.09	0.49 ± 0.18	1.29 ± 0.19
18:3n-4	0.13 ± 0.06	0.05 ± 0.02	0.10 ± 0.04	0.12 ± 0.03	0.06 ± 0.03	0.05 ± 0.02
18:3n-3	1.87 ± 0.42	0.74 ± 0.19	0.41 ± 0.22	0.54 ± 0.17	0.61 ± 0.23	1.65 ± 0.52
18:3n-1	0.03 ± 0.01	0.02 ± 0.03	0.06 ± 0.03	0.15 ± 0.05	0.06 ± 0.02	0.02 ± 0.03
18:4n-3	0.82 ± 0.25	1.90 ± 1.52	0.26 ± 0.18	0.54 ± 0.18	0.30 ± 0.12	4.20 ± 0.84
18:4n-1	0.01 ± 0.01	0.00 ± 0.01	0.01 ± 0.01	0.01 ± 0.02	0.01 ± 0.02	0.02 ± 0.01
20:2n-6	0.47 ± 0.09	0.27 ± 0.11	0.47 ± 0.08	0.70 ± 0.24	0.86 ± 0.29	0.20 ± 0.02
20:3n-6	0.75 ± 0.12	0.66 ± 0.31	0.60 ± 0.25	0.29 ± 0.07	0.51 ± 0.11	0.43 ± 0.09
20:4n-6	13.82 ± 2.66	5.63 ± 4.01	6.29 ± 1.47	6.49 ± 1.80	15.66 ± 3.46	3.43 ± 1.71
20:3n-3	0.20 ± 0.04	0.07 ± 0.03	0.13 ± 0.05	0.19 ± 0.09	0.16 ± 0.05	0.10 ± 0.03
20:4n-3	0.50 ± 0.19	0.46 ± 0.18	0.54 ± 0.18	0.30 ± 0.05	0.21 ± 0.06	0.41 ± 0.05
20:5n-3	4.84 ± 0.91	6.50 ± 2.65	2.64 ± 0.52	6.20 ± 0.94	5.09 ± 0.83	7.02 ± 1.12
22:2n-6	0.01 ± 0.01	0.03 ± 0.07	0.02 ± 0.01	0.04 ± 0.04	0.03 ± 0.02	0.01 ± 0.01
21:5n-3	0.10 ± 0.04	0.17 ± 0.09	0.12 ± 0.06	0.16 ± 0.07	0.12 ± 0.10	0.25 ± 0.06
22:4n-6	1.35 ± 0.32	0.82 ± 0.36	2.40 ± 0.48	1.27 ± 0.35	3.94 ± 0.73	0.87 ± 0.22
22:5n-6	1.20 ± 0.29	1.05 ± 0.31	1.39 ± 0.25	1.65 ± 0.27	1.97 ± 0.42	0.66 ± 0.21
22:4n-3	0.05 ± 0.01	0.05 ± 0.04	0.07 ± 0.02	0.03 ± 0.01	0.03 ± 0.02	0.09 ± 0.03
22:5n-3	2.36 ± 0.44	1.84 ± 0.66	3.21 ± 0.40	1.85 ± 0.40	3.37 ± 0.76	1.65 ± 0.31
22:6n-3	4.42 ± 1.65	11.11 ± 6.88	14.01 ± 3.75	18.45 ± 4.09	9.62 ± 3.57	3.26 ± 1.49
subtotal:	38.86 ± 3.79	36.32 ± 3.79	35.16 ± 4.72	41.75 ± 3.54	45.45 ± 4.34	32.80 ± 3.02
Total	94.60 ± 0.74	94.62 ± 0.96	94.07 ± 1.06	93.16 ± 0.87	93.15 ± 1.90	94.74 ± 0.39

Appendix 4.1 *continued*

	Fishes					
Group	34	14	12	25	8	20
Species name	*Cymolutes lecluse*	*Dactyoptena orientalis*	*Dascyllus albisella*	*Etelis carbunculus*	*Forcipiger flavissimus*	*Gymnothorax albimarginatus*
Common name	(Hawaiian knifefish)	(Helmut gurnard)	(Hawaiian dascyllus)	(Squirrelfish snapper)	(Forcepfish)	(Whitemargin moray)
	n=23	n=24	n=20	n=21	n=26	n=20
Length (cm)	8.53 ± 3.53	8.25 ± 1.28	9.53 ± 1.58	30.85 ± 4.27	14.46 ± 14.01	89.48 ± 9.31
Mass (g)	13.08 ± 15.49	14.40 ± 4.47	31.90 ± 10.44	500.57 ± 217.41	30.05 ± 16.31	728.65 ± 218.42
Fat content (%)	2.14 ± 0.85	1.90 ± 0.71	3.29 ± 2.55	2.08 ± 0.74	3.62 ± 2.06	0.84 ± 0.41
Saturated FA						
14:0	3.30 ± 1.12	4.65 ± 1.47	3.22 ± 1.23	2.50 ± 0.31	3.25 ± 0.94	2.45 ± 1.26
16:0	19.29 ± 1.89	22.44 ± 2.23	28.65 ± 5.26	19.97 ± 0.80	30.21 ± 4.76	19.23 ± 2.65
17:0	1.72 ± 0.27	1.63 ± 0.15	1.14 ± 0.27	0.96 ± 0.12	1.51 ± 0.54	0.66 ± 0.23
18:0	9.29 ± 1.19	8.98 ± 1.46	9.20 ± 1.05	6.19 ± 0.45	9.78 ± 1.91	10.92 ± 1.39
subtotal:	33.60 ± 2.43	37.69 ± 2.32	42.21 ± 5.27	29.62 ± 0.97	44.75 ± 3.43	33.26 ± 3.20
Monounsaturated FA						
16:1n-7	4.03 ± 1.31	5.05 ± 1.52	4.51 ± 1.76	4.31 ± 0.71	2.11 ± 0.60	2.58 ± 0.82
18:1n-9	9.26 ± 0.77	7.29 ± 1.04	7.40 ± 1.01	14.91 ± 1.90	7.60 ± 1.78	10.76 ± 1.41
18:1n-7	3.63 ± 0.93	2.97 ± 0.38	2.95 ± 1.36	2.85 ± 0.30	2.00 ± 0.44	2.53 ± 0.42
20:1n-11	0.49 ± 0.30	0.11 ± 0.06	0.19 ± 0.19	0.19 ± 0.04	1.42 ± 0.61	0.15 ± 0.13
20:1n-9	0.55 ± 0.14	1.03 ± 0.39	0.97 ± 0.27	1.42 ± 0.19	2.17 ± 1.05	0.81 ± 0.44
20:1n-7	0.30 ± 0.15	0.22 ± 0.03	0.16 ± 0.08	0.16 ± 0.03	0.30 ± 0.14	0.12 ± 0.07
22:1n-11	0.14 ± 0.05	0.10 ± 0.14	0.19 ± 0.29	0.27 ± 0.10	0.38 ± 0.22	0.27 ± 0.41
22:1n-9	0.10 ± 0.05	0.23 ± 0.06	0.13 ± 0.04	0.21 ± 0.05	0.34 ± 0.14	0.17 ± 0.10
22:1n-7	0.13 ± 0.04	0.14 ± 0.06	0.10 ± 0.06	0.08 ± 0.01	0.13 ± 0.07	0.06 ± 0.03
subtotal:	18.62 ± 2.20	17.14 ± 1.76	16.60 ± 3.83	24.40 ± 2.72	16.44 ± 1.99	17.44 ± 2.76
Polyunsaturated FA						
16:2n-6	0.10 ± 0.06	0.05 ± 0.02	0.05 ± 0.03	0.01 ± 0.01	0.05 ± 0.03	0.03 ± 0.06
16:2n-4	0.23 ± 0.07	0.20 ± 0.06	0.38 ± 0.10	0.80 ± 0.10	0.61 ± 0.30	0.41 ± 0.18
16:3n-6	0.17 ± 0.10	0.53 ± 0.23	0.23 ± 0.23	0.14 ± 0.02	0.05 ± 0.02	0.08 ± 0.11
16:3n-4	0.14 ± 0.10	0.03 ± 0.01	0.06 ± 0.03	0.03 ± 0.01	0.03 ± 0.02	0.10 ± 0.09
16:4n-1	0.01 ± 0.01	0.00 ± 0.00	0.02 ± 0.02	0.02 ± 0.03	0.02 ± 0.04	0.09 ± 0.16
18:2n-6	1.21 ± 0.20	1.24 ± 0.23	1.35 ± 0.17	0.91 ± 0.08	0.88 ± 0.33	0.72 ± 0.11
18:2n-4	0.10 ± 0.03	0.24 ± 0.07	0.09 ± 0.06	0.11 ± 0.02	0.04 ± 0.02	0.06 ± 0.04
18:3n-6	0.46 ± 0.07	0.39 ± 0.04	1.07 ± 0.87	0.27 ± 0.10	0.97 ± 0.40	0.38 ± 0.07
18:3n-4	0.15 ± 0.06	0.06 ± 0.01	0.05 ± 0.02	0.10 ± 0.01	0.06 ± 0.03	0.04 ± 0.02
18:3n-3	0.56 ± 0.46	0.46 ± 0.17	0.56 ± 0.33	0.23 ± 0.03	0.17 ± 0.05	0.10 ± 0.08
18:3n-1	0.07 ± 0.03	0.07 ± 0.03	0.10 ± 0.03	0.18 ± 0.03	0.13 ± 0.07	0.08 ± 0.04
18:4n-3	0.51 ± 0.24	0.49 ± 0.22	0.56 ± 0.32	0.17 ± 0.04	0.33 ± 0.22	0.10 ± 0.19
18:4n-1	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.01	0.00 ± 0.00	0.01 ± 0.02
20:2n-6	0.61 ± 0.19	0.55 ± 0.05	0.40 ± 0.06	0.30 ± 0.03	0.51 ± 0.13	0.34 ± 0.09
20:3n-6	0.42 ± 0.10	0.19 ± 0.01	0.62 ± 0.19	0.18 ± 0.02	2.24 ± 1.32	0.37 ± 0.11
20:4n-6	6.37 ± 1.69	3.17 ± 1.04	5.01 ± 1.81	2.61 ± 0.46	4.41 ± 1.98	10.21 ± 3.33
20:3n-3	0.17 ± 0.08	0.21 ± 0.04	0.15 ± 0.05	0.14 ± 0.03	0.08 ± 0.07	0.07 ± 0.03
20:4n-3	0.34 ± 0.13	0.40 ± 0.13	0.50 ± 0.18	0.48 ± 0.07	0.58 ± 0.27	0.20 ± 0.10
20:5n-3	8.05 ± 1.49	5.56 ± 0.69	4.25 ± 0.92	3.39 ± 0.39	2.16 ± 0.79	1.53 ± 1.62
22:2n-6	0.01 ± 0.01	0.06 ± 0.03	0.02 ± 0.03	0.00 ± 0.01	0.02 ± 0.02	0.02 ± 0.03
21:5n-3	0.16 ± 0.08	0.10 ± 0.02	0.13 ± 0.07	0.09 ± 0.01	0.09 ± 0.09	0.10 ± 0.09
22:4n-6	1.66 ± 0.34	0.55 ± 0.16	1.22 ± 0.26	0.63 ± 0.10	2.76 ± 1.39	4.42 ± 1.25
22:5n-6	1.35 ± 0.34	1.61 ± 0.30	1.26 ± 0.62	1.88 ± 0.18	0.79 ± 0.28	1.96 ± 0.33
22:4n-3	0.04 ± 0.02	0.07 ± 0.02	0.09 ± 0.19	0.05 ± 0.01	0.09 ± 0.03	0.05 ± 0.03
22:5n-3	2.19 ± 0.43	2.03 ± 0.27	2.35 ± 0.55	2.72 ± 0.18	2.72 ± 0.81	2.40 ± 0.74
22:6n-3	14.61 ± 3.96	21.39 ± 3.66	14.62 ± 5.95	24.65 ± 2.34	11.86 ± 5.66	16.37 ± 2.48
subtotal:	39.72 ± 2.96	39.66 ± 3.71	35.12 ± 7.33	40.10 ± 2.66	31.67 ± 3.34	40.23 ± 4.01
Total	91.94 ± 1.61	94.49 ± 0.27	93.93 ± 1.05	94.12 ± 0.56	92.86 ± 3.02	90.93 ± 1.76

Appendix 4.1 *continued*

	Fishes					
Group	20	20	20	20	20	20
Species name	*Gymnothorax berndti*	*Gymnothorax eurostus*	*Gymnothorax flavimarginatus*	*Gymnothorax meleagris*	*Gymnothorax steindachneri*	*Gymnothorax undulatus*
Common name	(Berndt's moray)	(Stout moray)	(Yellow margin moray)	(Whitemouth moray)	(Steindachner's moray)	(Undulated moray)
	n=20	n=14	n=19	n=18	n=25	n=19
Length (cm)	79.13 ± 8.39	41.32 ± 8.79	93.81 ± 24.04	75.31 ± 15.33	49.93 ± 10.60	72.60 ± 23.97
Mass (g)	660.83 ± 349.47	189.95 ± 126.07	966.69 ± 1160.0	1148.55 ± 709.39	327.81 ± 185.86	999.38 ± 818.33
Fat content (%)	1.41 ± 0.74	1.42 ± 0.81	1.67 ± 1.03	1.50 ± 0.80	0.85 ± 0.37	1.83 ± 1.47
Saturated FA						
14:0	2.24 ± 0.91	2.25 ± 1.03	3.54 ± 1.64	3.37 ± 1.27	1.59 ± 0.59	2.76 ± 1.23
16:0	19.92 ± 1.18	19.99 ± 2.35	23.57 ± 3.62	23.68 ± 2.51	18.34 ± 1.16	22.51 ± 4.11
17:0	0.92 ± 0.19	0.97 ± 0.25	1.00 ± 0.19	1.00 ± 0.21	0.94 ± 0.20	0.83 ± 0.25
18:0	9.33 ± 1.30	9.93 ± 1.19	10.44 ± 1.08	9.61 ± 1.36	10.70 ± 0.82	9.24 ± 1.66
subtotal:	32.41 ± 1.86	33.14 ± 2.60	38.56 ± 4.79	37.67 ± 2.97	31.57 ± 1.85	35.34 ± 3.87
Monounsaturated FA						
16:1n-7	3.15 ± 0.83	2.91 ± 1.16	3.93 ± 1.54	3.19 ± 1.13	1.71 ± 0.64	3.78 ± 1.56
18:1n-9	11.82 ± 3.15	10.27 ± 1.48	9.87 ± 1.55	9.12 ± 1.00	9.22 ± 0.85	10.13 ± 1.22
18:1n-7	2.77 ± 0.43	3.09 ± 0.55	3.02 ± 0.43	2.58 ± 0.30	2.50 ± 0.43	2.91 ± 0.32
20:1n-11	0.19 ± 0.11	0.21 ± 0.11	0.31 ± 0.16	0.31 ± 0.18	0.23 ± 0.21	0.23 ± 0.15
20:1n-9	1.31 ± 0.47	0.73 ± 0.27	0.87 ± 0.28	0.92 ± 0.35	0.81 ± 0.21	0.87 ± 0.33
20:1n-7	0.15 ± 0.06	0.18 ± 0.10	0.15 ± 0.06	0.15 ± 0.04	0.11 ± 0.06	0.15 ± 0.06
22:1n-11	0.45 ± 0.43	0.37 ± 0.29	0.24 ± 0.23	0.33 ± 0.35	0.16 ± 0.20	0.21 ± 0.22
22:1n-9	0.33 ± 0.13	0.16 ± 0.13	0.15 ± 0.07	0.16 ± 0.07	0.16 ± 0.08	0.16 ± 0.07
22:1n-7	0.13 ± 0.09	0.09 ± 0.03	0.06 ± 0.03	0.08 ± 0.03	0.05 ± 0.04	0.07 ± 0.04
subtotal:	20.29 ± 4.54	18.00 ± 2.23	18.59 ± 3.12	16.84 ± 1.30	14.95 ± 2.03	18.50 ± 2.42
Polyunsaturated FA						
16:2n-6	0.02 ± 0.03	0.06 ± 0.05	0.08 ± 0.07	0.06 ± 0.06	0.01 ± 0.01	0.05 ± 0.06
16:2n-4	0.50 ± 0.12	0.23 ± 0.09	0.44 ± 0.22	0.29 ± 0.08	0.29 ± 0.08	0.23 ± 0.11
16:3n-6	0.09 ± 0.04	0.13 ± 0.07	0.15 ± 0.08	0.18 ± 0.16	0.06 ± 0.06	0.11 ± 0.08
16:3n-4	0.07 ± 0.10	0.20 ± 0.14	0.16 ± 0.14	0.15 ± 0.19	0.04 ± 0.04	0.10 ± 0.12
16:4n-1	0.03 ± 0.05	0.15 ± 0.12	0.06 ± 0.07	0.09 ± 0.11	0.13 ± 0.08	0.07 ± 0.08
18:2n-6	0.76 ± 0.21	1.06 ± 0.24	1.17 ± 0.23	1.04 ± 0.17	0.66 ± 0.19	0.95 ± 0.30
18:2n-4	0.09 ± 0.03	0.08 ± 0.02	0.09 ± 0.02	0.09 ± 0.03	0.08 ± 0.03	0.08 ± 0.03
18:3n-6	0.25 ± 0.24	0.48 ± 0.15	0.44 ± 0.27	0.51 ± 0.24	0.23 ± 0.17	0.29 ± 0.18
18:3n-4	0.08 ± 0.03	0.10 ± 0.04	0.10 ± 0.05	0.10 ± 0.06	0.03 ± 0.03	0.11 ± 0.07
18:3n-3	0.19 ± 0.13	0.27 ± 0.18	0.35 ± 0.15	0.30 ± 0.17	0.14 ± 0.08	0.34 ± 0.29
18:3n-1	0.14 ± 0.05	0.03 ± 0.02	0.06 ± 0.04	0.06 ± 0.03	0.07 ± 0.03	0.05 ± 0.04
18:4n-3	0.09 ± 0.09	0.26 ± 0.20	0.29 ± 0.21	0.30 ± 0.26	0.11 ± 0.14	0.18 ± 0.13
18:4n-1	0.00 ± 0.01	0.00 ± 0.01	0.01 ± 0.02	0.01 ± 0.04	0.01 ± 0.01	0.01 ± 0.02
20:2n-6	0.36 ± 0.09	0.51 ± 0.11	0.51 ± 0.07	0.44 ± 0.11	0.52 ± 0.09	0.48 ± 0.09
20:3n-6	0.19 ± 0.05	0.43 ± 0.12	0.62 ± 0.24	0.58 ± 0.17	0.22 ± 0.08	0.53 ± 0.24
20:4n-6	6.47 ± 2.94	8.88 ± 1.75	8.94 ± 3.40	6.74 ± 2.20	9.76 ± 2.69	7.51 ± 3.03
20:3n-3	0.12 ± 0.06	0.12 ± 0.04	0.13 ± 0.05	0.11 ± 0.03	0.11 ± 0.03	0.12 ± 0.06
20:4n-3	0.34 ± 0.12	0.26 ± 0.12	0.41 ± 0.15	0.40 ± 0.14	0.18 ± 0.08	0.43 ± 0.27
20:5n-3	2.25 ± 0.53	3.32 ± 1.73	2.39 ± 0.58	2.58 ± 1.15	2.96 ± 1.07	2.15 ± 0.80
22:2n-6	0.01 ± 0.02	0.01 ± 0.01	0.02 ± 0.02	0.03 ± 0.04	0.02 ± 0.03	0.04 ± 0.06
21:5n-3	0.06 ± 0.06	0.10 ± 0.08	0.07 ± 0.05	0.09 ± 0.06	0.08 ± 0.10	0.06 ± 0.04
22:4n-6	2.08 ± 0.78	3.02 ± 0.65	3.03 ± 0.72	3.33 ± 0.95	2.85 ± 0.83	3.71 ± 1.03
22:5n-6	2.01 ± 0.40	1.47 ± 0.24	1.32 ± 0.39	1.72 ± 0.37	1.67 ± 0.19	1.60 ± 0.27
22:4n-3	0.04 ± 0.02	0.06 ± 0.02	0.07 ± 0.03	0.09 ± 0.04	0.05 ± 0.04	0.09 ± 0.06
22:5n-3	2.66 ± 0.48	3.03 ± 0.55	2.56 ± 0.41	3.76 ± 0.44	1.94 ± 0.42	3.75 ± 1.32
22:6n-3	23.22 ± 4.30	17.35 ± 3.63	11.91 ± 4.86	16.09 ± 3.02	22.88 ± 3.04	16.03 ± 4.85
subtotal:	42.12 ± 5.14	41.63 ± 3.00	35.37 ± 6.66	39.14 ± 3.15	45.09 ± 2.49	39.07 ± 5.29
Total	94.82 ± 0.59	92.77 ± 1.12	92.52 ± 2.28	93.66 ± 1.07	91.61 ± 0.97	92.91 ± 1.16

Appendix 4.1 *continued*

	Fishes					
Group	9	34	34	23	23	26
Species name	*Heniochus diphreutes*	*Iniistius pavo*	*Iniistius umbrilatus*	*Kyphosus bigibbus*	*Kyphosus vaigiensis*	*Lutjanus kasmira*
Common name	(Pennantfish)	(Peacock razorfish)	(Blackside razorfish)	(Gray chub)	(Low fin chub)	(Bluestripe snapper)
	n=36	n=15	n=19	n=19	n=19	n=22
Length (cm)	4.39 ± 0.86	11.02 ± 4.69	9.22 ± 3.28	24.67 ± 4.75	20.27 ± 5.62	12.15 ± 7.70
Mass (g)	2.69 ± 1.55	37.91 ± 45.21	27.28 ± 30.74	409.37 ± 175.34	257.97 ± 175.16	89.37 ± 117.58
Fat content (%)	3.94 ± 1.66	1.81 ± 0.89	2.59 ± 0.93	1.68 ± 1.15	1.43 ± 0.71	2.68 ± 1.04
Saturated FA						
14:0	5.38 ± 1.69	3.74 ± 2.32	5.22 ± 1.65	3.84 ± 1.60	3.48 ± 1.73	3.08 ± 1.01
16:0	28.21 ± 5.33	19.24 ± 1.24	20.86 ± 1.93	24.77 ± 4.38	24.64 ± 2.28	21.14 ± 2.75
17:0	1.12 ± 0.28	1.46 ± 0.35	1.95 ± 0.28	0.77 ± 0.26	0.87 ± 0.28	1.43 ± 0.22
18:0	8.11 ± 1.04	9.65 ± 0.94	8.47 ± 0.64	8.52 ± 1.54	8.93 ± 1.58	9.61 ± 0.96
subtotal:	42.82 ± 6.50	34.10 ± 2.51	36.50 ± 2.56	37.89 ± 4.73	37.91 ± 2.36	35.27 ± 3.27
Monounsaturated FA						
16:1n-7	5.18 ± 1.47	2.86 ± 1.17	3.58 ± 0.54	1.82 ± 0.70	1.73 ± 0.84	3.61 ± 0.89
18:1n-9	4.89 ± 1.22	9.47 ± 1.26	8.87 ± 1.43	10.10 ± 1.04	9.56 ± 0.92	10.30 ± 2.87
18:1n-7	2.54 ± 0.32	2.98 ± 0.98	2.41 ± 0.28	1.38 ± 0.63	1.20 ± 0.50	2.83 ± 0.21
20:1n-11	0.19 ± 0.10	0.37 ± 0.28	0.45 ± 0.21	0.07 ± 0.05	0.07 ± 0.04	0.22 ± 0.16
20:1n-9	0.89 ± 0.38	0.58 ± 0.33	0.65 ± 0.28	1.10 ± 0.53	0.84 ± 0.47	0.82 ± 0.34
20:1n-7	0.18 ± 0.07	0.25 ± 0.15	0.23 ± 0.10	0.11 ± 0.06	0.08 ± 0.06	0.20 ± 0.07
22:1n-11	0.06 ± 0.05	0.10 ± 0.04	0.17 ± 0.06	0.02 ± 0.03	0.04 ± 0.03	0.18 ± 0.14
22:1n-9	0.21 ± 0.07	0.09 ± 0.05	0.13 ± 0.05	0.22 ± 0.10	0.15 ± 0.11	0.19 ± 0.06
22:1n-7	0.08 ± 0.02	0.09 ± 0.05	0.12 ± 0.04	0.03 ± 0.04	0.04 ± 0.03	0.11 ± 0.05
subtotal:	14.21 ± 1.72	16.81 ± 3.08	16.61 ± 1.74	14.83 ± 1.79	13.70 ± 1.66	18.47 ± 3.85
Polyunsaturated FA						
16:2n-6	0.05 ± 0.02	0.06 ± 0.05	0.08 ± 0.02	0.03 ± 0.03	0.03 ± 0.01	0.04 ± 0.02
16:2n-4	0.74 ± 0.18	0.44 ± 0.22	0.42 ± 0.11	0.21 ± 0.12	0.26 ± 0.25	0.52 ± 0.15
16:3n-6	0.21 ± 0.15	0.11 ± 0.06	0.20 ± 0.04	0.05 ± 0.03	0.07 ± 0.06	0.21 ± 0.13
16:3n-4	0.05 ± 0.03	0.06 ± 0.03	0.08 ± 0.03	0.06 ± 0.05	0.10 ± 0.02	0.03 ± 0.02
16:4n-1	0.04 ± 0.04	0.05 ± 0.05	0.02 ± 0.03	0.08 ± 0.09	0.04 ± 0.05	0.03 ± 0.03
18:2n-6	1.29 ± 0.23	1.07 ± 0.15	1.17 ± 0.13	2.61 ± 0.67	2.60 ± 0.83	1.20 ± 0.32
18:2n-4	0.08 ± 0.04	0.09 ± 0.05	0.12 ± 0.05	0.03 ± 0.02	0.04 ± 0.03	0.15 ± 0.08
18:3n-6	0.91 ± 0.33	0.35 ± 0.13	0.52 ± 0.09	0.71 ± 0.15	0.81 ± 0.27	0.37 ± 0.05
18:3n-4	0.04 ± 0.03	0.11 ± 0.03	0.18 ± 0.06	0.05 ± 0.03	0.06 ± 0.02	0.10 ± 0.04
18:3n-3	0.43 ± 0.21	0.41 ± 0.19	0.49 ± 0.14	1.01 ± 0.43	1.14 ± 0.56	0.47 ± 0.25
18:3n-1	0.16 ± 0.04	0.15 ± 0.11	0.15 ± 0.05	0.02 ± 0.04	0.05 ± 0.05	0.12 ± 0.04
18:4n-3	0.62 ± 0.26	0.39 ± 0.25	0.51 ± 0.10	1.22 ± 0.46	1.25 ± 0.55	0.50 ± 0.34
18:4n-1	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.00 ± 0.00
20:2n-6	0.40 ± 0.09	0.63 ± 0.17	0.71 ± 0.19	0.43 ± 0.11	0.44 ± 0.15	0.45 ± 0.13
20:3n-6	0.88 ± 0.32	0.22 ± 0.05	0.23 ± 0.03	1.70 ± 0.52	1.38 ± 0.62	0.21 ± 0.07
20:4n-6	1.86 ± 1.54	5.55 ± 1.40	4.89 ± 1.27	9.51 ± 3.54	10.09 ± 3.68	4.02 ± 2.23
20:3n-3	0.13 ± 0.05	0.18 ± 0.08	0.19 ± 0.09	0.21 ± 0.08	0.19 ± 0.06	0.15 ± 0.04
20:4n-3	0.71 ± 0.26	0.29 ± 0.09	0.31 ± 0.10	2.40 ± 1.15	1.67 ± 0.90	0.49 ± 0.25
20:5n-3	3.45 ± 0.95	7.19 ± 2.25	7.36 ± 1.13	4.48 ± 1.08	5.61 ± 1.26	5.11 ± 1.49
22:2n-6	0.01 ± 0.02	0.00 ± 0.01	0.02 ± 0.02	0.01 ± 0.02	0.02 ± 0.02	0.05 ± 0.06
21:5n-3	0.09 ± 0.04	0.12 ± 0.04	0.14 ± 0.03	0.03 ± 0.04	0.04 ± 0.04	0.14 ± 0.04
22:4n-6	0.68 ± 0.29	0.90 ± 0.30	0.89 ± 0.32	2.96 ± 0.56	2.46 ± 0.82	0.92 ± 0.73
22:5n-6	1.58 ± 0.62	1.73 ± 0.53	1.48 ± 0.21	0.88 ± 0.41	1.06 ± 0.65	1.57 ± 0.31
22:4n-3	0.13 ± 0.05	0.03 ± 0.03	0.04 ± 0.02	0.44 ± 0.22	0.34 ± 0.20	0.06 ± 0.02
22:5n-3	4.99 ± 1.48	1.51 ± 0.34	1.39 ± 0.26	3.67 ± 0.51	3.76 ± 0.74	2.24 ± 0.36
22:6n-3	17.34 ± 4.32	20.64 ± 6.98	17.94 ± 3.18	7.94 ± 4.75	9.62 ± 6.26	20.60 ± 4.04
subtotal:	36.87 ± 6.07	42.27 ± 5.64	39.52 ± 3.29	40.76 ± 5.54	43.12 ± 4.35	39.76 ± 5.81
Total	93.91 ± 1.53	93.17 ± 0.87	92.63 ± 0.84	93.49 ± 1.61	94.74 ± 1.23	93.50 ± 0.54

Appendix 4.1 *continued*

	Fishes					
Group	10	7	35	15	15	29
Species name	*Malacanthus brevirostris*	*Meadia abyssalis*	*Melichthys niger*	*Mulloidichthys flavolineatus*	*Mulloidichthys vanicolensis*	*Myripristis berndti*
Common name	(Flagtail tilefish)	(Abyssal cutthroat eel)	(Black triggerfish)	(Yellow stripe goatfish)	(Yellow fin goatfish)	(Bigscale soldierfish)
	n=16	n=19	n=20	n=21	n=20	n=20
Length (cm)	11.71 ± 3.92	50.58 ± 9.98	20.23 ± 3.85	22.18 ± 3.16	19.50 ± 4.13	17.61 ± 4.20
Mass (g)	16.29 ± 17.52	134.70 ± 74.18	288.65 ± 119.58	198.08 ± 96.99	162.29 ± 90.18	199.65 ± 122.44
Fat content (%)	1.55 ± 0.51	2.64 ± 0.97	1.61 ± 1.43	1.86 ± 1.10	2.31 ± 1.21	3.39 ± 1.74
Saturated FA						
14:0	1.60 ± 1.15	2.69 ± 0.95	0.78 ± 0.23	2.31 ± 0.87	2.79 ± 0.81	4.80 ± 0.43
16:0	18.34 ± 1.95	19.82 ± 1.21	25.68 ± 3.87	19.36 ± 4.07	22.45 ± 2.76	26.40 ± 2.50
17:0	1.59 ± 0.29	0.80 ± 0.10	1.56 ± 0.12	2.60 ± 0.75	1.55 ± 0.25	1.53 ± 0.16
18:0	11.56 ± 0.80	4.47 ± 0.59	10.38 ± 1.21	11.35 ± 1.77	10.30 ± 0.79	9.41 ± 0.91
subtotal:	33.09 ± 3.44	27.78 ± 1.34	38.40 ± 3.31	35.62 ± 4.04	37.10 ± 3.17	42.14 ± 2.41
Monounsaturated FA						
16:1n-7	1.84 ± 0.81	3.54 ± 1.02	1.78 ± 0.67	3.09 ± 0.80	3.94 ± 0.95	4.62 ± 0.78
18:1n-9	6.97 ± 0.95	20.23 ± 3.52	9.54 ± 1.62	5.99 ± 1.75	8.25 ± 1.06	9.50 ± 1.18
18:1n-7	2.82 ± 0.30	2.84 ± 0.26	4.49 ± 0.62	3.47 ± 0.55	3.16 ± 0.82	2.57 ± 0.23
20:1n-11	0.89 ± 0.48	0.43 ± 0.16	0.11 ± 0.04	1.39 ± 0.66	0.60 ± 0.43	0.50 ± 0.39
20:1n-9	0.48 ± 0.17	1.87 ± 0.63	0.27 ± 0.10	0.61 ± 0.42	0.52 ± 0.17	0.96 ± 0.15
20:1n-7	0.36 ± 0.16	0.17 ± 0.04	0.18 ± 0.03	0.65 ± 0.33	0.31 ± 0.27	0.22 ± 0.06
22:1n-11	0.33 ± 0.23	0.45 ± 0.27	0.07 ± 0.04	0.36 ± 0.20	0.21 ± 0.14	0.44 ± 0.62
22:1n-9	0.10 ± 0.05	0.33 ± 0.10	0.08 ± 0.03	0.10 ± 0.06	0.09 ± 0.04	0.16 ± 0.03
22:1n-7	0.15 ± 0.09	0.05 ± 0.02	0.14 ± 0.06	0.23 ± 0.13	0.13 ± 0.04	0.11 ± 0.04
subtotal:	13.94 ± 2.16	29.91 ± 4.72	16.65 ± 1.93	15.89 ± 1.79	17.22 ± 1.74	19.08 ± 2.26
Polyunsaturated FA						
16:2n-6	0.07 ± 0.06	0.02 ± 0.02	0.06 ± 0.08	0.05 ± 0.04	0.06 ± 0.03	0.05 ± 0.02
16:2n-4	0.41 ± 0.09	0.61 ± 0.08	0.43 ± 0.10	0.27 ± 0.09	0.27 ± 0.19	0.56 ± 0.15
16:3n-6	0.05 ± 0.04	0.10 ± 0.11	0.07 ± 0.08	0.11 ± 0.06	0.22 ± 0.08	0.22 ± 0.05
16:3n-4	0.04 ± 0.03	0.06 ± 0.12	0.10 ± 0.05	0.13 ± 0.07	0.12 ± 0.05	0.04 ± 0.02
16:4n-1	0.01 ± 0.03	0.24 ± 0.24	0.06 ± 0.06	0.05 ± 0.04	0.07 ± 0.12	0.01 ± 0.02
18:2n-6	1.11 ± 0.12	0.88 ± 0.09	1.85 ± 0.43	1.29 ± 0.41	1.50 ± 0.50	1.29 ± 0.12
18:2n-4	0.09 ± 0.04	0.10 ± 0.04	0.23 ± 0.16	0.06 ± 0.02	0.09 ± 0.02	0.13 ± 0.02
18:3n-6	0.36 ± 0.16	0.19 ± 0.03	0.75 ± 0.29	0.67 ± 0.12	0.51 ± 0.09	0.70 ± 0.57
18:3n-4	0.12 ± 0.04	0.14 ± 0.03	0.05 ± 0.02	0.10 ± 0.05	0.09 ± 0.04	0.08 ± 0.02
18:3n-3	0.25 ± 0.15	0.23 ± 0.07	0.87 ± 0.24	0.51 ± 0.33	0.84 ± 0.54	0.48 ± 0.10
18:3n-1	0.13 ± 0.03	0.23 ± 0.04	0.08 ± 0.04	0.07 ± 0.02	0.08 ± 0.08	0.13 ± 0.03
18:4n-3	0.12 ± 0.07	0.23 ± 0.31	0.55 ± 0.15	0.45 ± 0.59	0.48 ± 0.18	0.55 ± 0.10
18:4n-1	0.00 ± 0.00	0.02 ± 0.04	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.05	0.00 ± 0.01
20:2n-6	0.65 ± 0.10	0.37 ± 0.05	0.33 ± 0.07	0.66 ± 0.18	0.66 ± 0.16	0.56 ± 0.12
20:3n-6	0.42 ± 0.06	0.14 ± 0.03	0.57 ± 0.21	0.50 ± 0.28	0.37 ± 0.10	0.30 ± 0.05
20:4n-6	10.36 ± 3.31	3.32 ± 1.12	9.66 ± 2.83	8.70 ± 1.59	6.73 ± 2.06	2.47 ± 0.47
20:3n-3	0.14 ± 0.04	0.18 ± 0.07	0.10 ± 0.02	0.14 ± 0.05	0.19 ± 0.07	0.17 ± 0.04
20:4n-3	0.26 ± 0.08	0.47 ± 0.10	0.34 ± 0.07	0.32 ± 0.39	0.29 ± 0.07	0.45 ± 0.11
20:5n-3	4.56 ± 0.51	5.01 ± 1.96	7.30 ± 1.22	6.13 ± 1.32	6.84 ± 1.53	4.33 ± 0.76
22:2n-6	0.01 ± 0.03	0.02 ± 0.01	0.06 ± 0.11	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.01
21:5n-3	0.14 ± 0.10	0.09 ± 0.12	0.09 ± 0.07	0.18 ± 0.10	0.11 ± 0.04	0.15 ± 0.07
22:4n-6	4.50 ± 1.39	0.34 ± 0.10	1.60 ± 0.48	3.13 ± 0.77	2.03 ± 0.85	1.04 ± 0.60
22:5n-6	2.11 ± 0.52	1.06 ± 0.22	0.85 ± 0.31	1.71 ± 0.64	1.46 ± 0.39	1.19 ± 0.26
22:4n-3	0.08 ± 0.03	0.03 ± 0.01	0.08 ± 0.02	0.05 ± 0.04	0.03 ± 0.02	0.07 ± 0.04
22:5n-3	3.76 ± 0.50	1.53 ± 0.22	3.08 ± 0.56	2.73 ± 0.43	2.66 ± 0.90	2.96 ± 0.50
22:6n-3	16.58 ± 3.84	20.90 ± 4.00	10.34 ± 4.41	11.25 ± 4.48	13.14 ± 5.76	14.21 ± 2.30
subtotal:	46.34 ± 5.78	36.54 ± 5.24	39.51 ± 4.55	39.28 ± 4.81	38.90 ± 4.26	32.17 ± 2.15
Total	93.37 ± 1.12	94.23 ± 0.49	94.57 ± 1.23	90.79 ± 2.05	93.22 ± 1.85	93.39 ± 0.86

Appendix 4.1 *continued*

	Fishes					
Group	32	32	10	6	37	19
Species name	*Naso lituratus*	*Naso unicornis*	*Ophichthus kunaloa*	*Ophidion muraenolepis*	*Oxycheilinus unifasciatus*	*Parapercis schauinslandii*
Common name	(Orangespine unicornfish)	(Bluespine unicornfish)	(Snake eel)	(Black edged cusk eel)	(Ringtail wrasse)	(Redspotted sandperch)
	n=19	n=19	n=20	n=20	n=19	n=18
Length (cm)	26.72 ± 2.09	22.20 ± 5.72	39.79 ± 2.50	13.54 ± 2.61	21.23 ± 4.85	6.78 ± 2.05
Mass (g)	468.46 ± 130.04	286.06 ± 191.30	33.96 ± 7.30	19.74 ± 13.82	235.54 ± 178.59	7.61 ± 6.71
Fat content (%)	7.44 ± 6.11	4.29 ± 3.31	2.37 ± 0.80	1.74 ± 0.71	1.21 ± 0.57	1.94 ± 0.79
Saturated FA						
14:0	5.52 ± 0.62	3.90 ± 0.80	3.08 ± 1.02	3.52 ± 1.40	3.64 ± 1.36	4.18 ± 1.15
16:0	31.43 ± 2.90	31.90 ± 4.54	16.32 ± 0.68	18.34 ± 2.24	22.44 ± 1.73	20.81 ± 1.39
17:0	0.45 ± 0.09	0.60 ± 0.63	0.72 ± 0.11	1.37 ± 0.19	1.07 ± 0.14	1.46 ± 0.12
18:0	6.01 ± 1.18	7.34 ± 1.60	5.33 ± 1.32	8.01 ± 1.05	9.67 ± 0.86	9.33 ± 1.29
subtotal:	43.41 ± 2.05	43.74 ± 3.44	25.45 ± 1.30	31.24 ± 2.81	36.81 ± 2.29	35.78 ± 1.66
Monounsaturated FA						
16:1n-7	1.95 ± 0.65	2.34 ± 0.72	6.51 ± 1.90	3.01 ± 0.76	3.16 ± 1.42	3.74 ± 0.84
18:1n-9	11.37 ± 1.21	11.57 ± 2.25	18.30 ± 3.11	9.49 ± 1.51	9.62 ± 0.69	8.32 ± 1.06
18:1n-7	1.71 ± 0.47	2.42 ± 0.50	3.19 ± 0.35	2.47 ± 0.52	2.15 ± 0.32	2.63 ± 0.27
20:1n-11	0.08 ± 0.03	0.14 ± 0.35	0.40 ± 0.18	0.13 ± 0.05	0.21 ± 0.09	0.18 ± 0.04
20:1n-9	4.51 ± 1.13	3.24 ± 1.60	1.62 ± 0.37	0.68 ± 0.10	0.46 ± 0.15	0.76 ± 0.17
20:1n-7	0.18 ± 0.05	0.23 ± 0.20	0.30 ± 0.09	0.19 ± 0.07	0.11 ± 0.04	0.23 ± 0.06
22:1n-11	0.00 ± 0.00	0.04 ± 0.11	0.22 ± 0.10	0.33 ± 0.42	0.24 ± 0.20	0.25 ± 0.09
22:1n-9	0.49 ± 0.12	0.36 ± 0.23	0.26 ± 0.06	0.20 ± 0.10	0.09 ± 0.03	0.16 ± 0.03
22:1n-7	0.02 ± 0.02	0.05 ± 0.10	0.08 ± 0.03	0.16 ± 0.14	0.11 ± 0.04	0.17 ± 0.05
subtotal:	20.31 ± 3.24	20.39 ± 4.08	30.88 ± 4.58	16.67 ± 1.29	16.14 ± 1.65	16.45 ± 1.76
Polyunsaturated FA						
16:2n-6	0.03 ± 0.01	0.03 ± 0.01	0.03 ± 0.02	0.05 ± 0.03	0.07 ± 0.05	0.05 ± 0.03
16:2n-4	0.14 ± 0.13	0.41 ± 0.19	0.81 ± 0.11	0.83 ± 0.25	0.34 ± 0.08	0.56 ± 0.09
16:3n-6	0.04 ± 0.01	0.04 ± 0.04	0.17 ± 0.12	0.18 ± 0.09	0.19 ± 0.12	0.29 ± 0.08
16:3n-4	0.05 ± 0.02	0.03 ± 0.03	0.21 ± 0.16	0.04 ± 0.03	0.22 ± 0.15	0.05 ± 0.02
16:4n-1	0.03 ± 0.04	0.02 ± 0.02	0.38 ± 0.15	0.00 ± 0.00	0.10 ± 0.04	0.00 ± 0.00
18:2n-6	2.95 ± 0.39	2.47 ± 0.62	1.02 ± 0.26	1.18 ± 0.20	1.30 ± 0.27	1.28 ± 0.11
18:2n-4	0.01 ± 0.01	0.02 ± 0.03	0.11 ± 0.04	0.17 ± 0.08	0.06 ± 0.03	0.17 ± 0.04
18:3n-6	0.90 ± 0.17	0.72 ± 0.17	0.35 ± 0.09	0.37 ± 0.11	0.62 ± 0.24	0.52 ± 0.09
18:3n-4	0.06 ± 0.03	0.03 ± 0.04	0.16 ± 0.03	0.07 ± 0.03	0.08 ± 0.01	0.07 ± 0.01
18:3n-3	1.21 ± 0.35	1.04 ± 0.31	0.31 ± 0.16	0.36 ± 0.12	0.35 ± 0.14	0.38 ± 0.09
18:3n-1	0.03 ± 0.01	0.02 ± 0.06	0.37 ± 0.07	0.17 ± 0.05	0.13 ± 0.03	0.13 ± 0.03
18:4n-3	3.28 ± 1.15	2.00 ± 0.77	0.43 ± 0.36	0.30 ± 0.14	0.49 ± 0.25	0.44 ± 0.13
18:4n-1	0.01 ± 0.01	0.00 ± 0.00	0.03 ± 0.04	0.00 ± 0.00	0.01 ± 0.02	0.00 ± 0.00
20:2n-6	0.63 ± 0.19	0.44 ± 0.16	0.39 ± 0.07	0.42 ± 0.07	0.40 ± 0.07	0.39 ± 0.05
20:3n-6	1.74 ± 0.42	1.62 ± 0.55	0.17 ± 0.04	0.26 ± 0.05	0.61 ± 0.20	0.23 ± 0.04
20:4n-6	5.88 ± 1.81	7.22 ± 3.11	3.95 ± 1.69	3.92 ± 1.79	8.69 ± 1.28	3.16 ± 0.73
20:3n-3	0.20 ± 0.05	0.16 ± 0.04	0.23 ± 0.10	0.13 ± 0.05	0.08 ± 0.02	0.11 ± 0.02
20:4n-3	2.21 ± 0.24	1.80 ± 0.61	0.42 ± 0.18	0.67 ± 0.32	0.28 ± 0.12	0.60 ± 0.14
20:5n-3	3.93 ± 0.89	3.72 ± 1.10	5.40 ± 1.74	6.80 ± 1.22	4.05 ± 0.77	4.50 ± 0.55
22:2n-6	0.06 ± 0.04	0.02 ± 0.03	0.04 ± 0.01	0.02 ± 0.02	0.03 ± 0.02	0.01 ± 0.01
21:5n-3	0.05 ± 0.04	0.04 ± 0.08	0.05 ± 0.02	0.11 ± 0.03	0.13 ± 0.04	0.09 ± 0.02
22:4n-6	3.14 ± 1.29	3.00 ± 1.13	0.46 ± 0.23	1.20 ± 0.62	2.26 ± 0.27	0.68 ± 0.16
22:5n-6	0.40 ± 0.16	0.74 ± 0.53	1.32 ± 0.32	1.82 ± 0.41	2.01 ± 0.40	2.20 ± 0.50
22:4n-3	0.28 ± 0.06	0.20 ± 0.06	0.04 ± 0.02	0.09 ± 0.03	0.04 ± 0.02	0.08 ± 0.02
22:5n-3	2.03 ± 0.74	2.03 ± 0.52	1.97 ± 0.37	2.26 ± 0.36	2.83 ± 0.34	1.74 ± 0.20
22:6n-3	1.73 ± 0.93	3.61 ± 4.26	17.70 ± 2.48	24.97 ± 3.58	16.65 ± 4.31	23.60 ± 2.86
subtotal:	31.04 ± 4.73	31.42 ± 6.93	36.53 ± 4.16	46.37 ± 2.79	42.01 ± 3.83	41.35 ± 3.43
Total	94.76 ± 0.87	95.55 ± 1.34	92.86 ± 0.62	94.28 ± 0.38	94.96 ± 0.39	93.58 ± 0.50

Appendix 4.1 *continued*

	Fishes					
Group	16	16	16	16	4	5
Species name	*Parupeneus chrysonemus*	*Parupeneus bifasciatus*	*Parupeneus multifasciatus*	*Parupeneus pleurostigma*	*Polymixia berndti*	*Priacanthus alalaua*
Common name	(Yellow barbel goatfish)	(Doublebar goatfish)	(Manybar goatfish)	(Sidespot goatfish)	(Berndt's beard fish)	(Forskal's bigeye)
	n=19	n=19	n=20	n=19	n=20	n=20
Length (cm)	9.71 ± 0.86	16.65 ± 4.91	16.43 ± 3.02	16.49 ± 3.97	15.61 ± 4.66	11.29 ± 4.05
Mass (g)	18.98 ± 5.02	107.11 ± 85.16	86.15 ± 43.23	102.27 ± 97.99	121.13 ± 91.00	30.79 ± 22.55
Fat content (%)	3.40 ± 1.16	1.40 ± 1.23	1.51 ± 1.18	2.69 ± 1.77	2.00 ± 0.90	2.64 ± 1.91
Saturated FA						
14:0	4.68 ± 0.80	2.94 ± 0.97	2.57 ± 1.05	3.28 ± 1.15	3.00 ± 1.15	2.56 ± 1.29
16:0	22.61 ± 1.30	22.33 ± 1.72	19.61 ± 1.99	20.58 ± 3.84	20.70 ± 1.41	20.14 ± 3.21
17:0	1.51 ± 0.10	1.52 ± 0.27	1.35 ± 0.21	1.47 ± 0.36	0.77 ± 0.16	1.31 ± 0.44
18:0	9.29 ± 0.62	10.54 ± 0.88	10.42 ± 0.82	9.64 ± 1.03	6.16 ± 0.87	8.97 ± 0.96
subtotal:	38.09 ± 1.84	37.33 ± 2.63	33.95 ± 3.06	34.98 ± 4.98	30.63 ± 1.56	32.98 ± 4.01
Monounsaturated FA						
16:1n-7	4.78 ± 0.59	3.49 ± 1.10	2.80 ± 0.97	3.49 ± 1.09	3.09 ± 0.56	2.57 ± 0.92
18:1n-9	9.57 ± 0.83	9.12 ± 1.95	8.10 ± 0.82	7.75 ± 0.69	17.48 ± 4.02	11.28 ± 1.49
18:1n-7	2.73 ± 0.27	2.98 ± 0.65	2.76 ± 0.49	2.88 ± 0.50	2.49 ± 0.58	1.93 ± 0.26
20:1n-11	0.25 ± 0.03	0.36 ± 0.27	0.31 ± 0.15	0.58 ± 0.42	0.51 ± 1.16	0.18 ± 0.08
20:1n-9	0.76 ± 0.12	0.77 ± 0.41	0.52 ± 0.12	0.61 ± 0.24	2.16 ± 1.07	0.69 ± 0.28
20:1n-7	0.20 ± 0.04	0.22 ± 0.07	0.18 ± 0.08	0.26 ± 0.11	0.17 ± 0.06	0.18 ± 0.06
22:1n-11	0.29 ± 0.15	0.21 ± 0.12	0.26 ± 0.19	0.43 ± 0.39	0.66 ± 1.61	0.15 ± 0.11
22:1n-9	0.13 ± 0.03	0.10 ± 0.04	0.07 ± 0.03	0.06 ± 0.02	0.35 ± 0.18	0.12 ± 0.02
22:1n-7	0.12 ± 0.03	0.08 ± 0.04	0.08 ± 0.02	0.09 ± 0.02	0.08 ± 0.04	0.12 ± 0.03
subtotal:	18.83 ± 1.32	17.34 ± 2.23	15.07 ± 2.02	16.13 ± 2.34	26.99 ± 7.00	17.22 ± 2.00
Polyunsaturated FA						
16:2n-6	0.05 ± 0.02	0.04 ± 0.02	0.02 ± 0.02	0.02 ± 0.02	0.03 ± 0.02	0.03 ± 0.02
16:2n-4	0.44 ± 0.07	0.23 ± 0.14	0.24 ± 0.05	0.29 ± 0.10	0.78 ± 0.19	0.63 ± 0.08
16:3n-6	0.33 ± 0.05	0.19 ± 0.10	0.17 ± 0.09	0.24 ± 0.13	0.09 ± 0.09	0.17 ± 0.14
16:3n-4	0.07 ± 0.03	0.09 ± 0.04	0.07 ± 0.04	0.04 ± 0.03	0.07 ± 0.10	0.03 ± 0.01
16:4n-1	0.00 ± 0.00	0.03 ± 0.02	0.03 ± 0.04	0.02 ± 0.03	0.00 ± 0.00	0.19 ± 0.10
18:2n-6	1.26 ± 0.07	1.63 ± 0.32	1.50 ± 0.39	1.41 ± 0.26	0.65 ± 0.17	1.10 ± 0.19
18:2n-4	0.18 ± 0.03	0.07 ± 0.03	0.09 ± 0.03	0.13 ± 0.04	0.09 ± 0.04	0.09 ± 0.03
18:3n-6	0.47 ± 0.06	0.31 ± 0.09	0.53 ± 0.12	0.43 ± 0.10	0.25 ± 0.06	0.43 ± 0.05
18:3n-4	0.10 ± 0.02	0.09 ± 0.02	0.06 ± 0.03	0.08 ± 0.03	0.11 ± 0.04	0.10 ± 0.03
18:3n-3	0.47 ± 0.08	0.67 ± 0.24	0.49 ± 0.22	0.52 ± 0.25	0.17 ± 0.10	0.39 ± 0.15
18:3n-1	0.12 ± 0.02	0.05 ± 0.04	0.07 ± 0.02	0.08 ± 0.03	0.18 ± 0.04	0.25 ± 0.08
18:4n-3	0.60 ± 0.09	0.57 ± 0.13	0.42 ± 0.18	0.45 ± 0.22	0.20 ± 0.29	0.44 ± 0.34
18:4n-1	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.01	0.01 ± 0.01
20:2n-6	0.49 ± 0.06	0.64 ± 0.10	0.60 ± 0.11	0.68 ± 0.16	0.28 ± 0.06	0.37 ± 0.07
20:3n-6	0.20 ± 0.03	0.48 ± 0.18	0.40 ± 0.12	0.33 ± 0.10	0.11 ± 0.02	0.13 ± 0.06
20:4n-6	2.68 ± 0.57	8.11 ± 2.09	7.57 ± 1.82	6.31 ± 2.16	3.28 ± 0.92	3.08 ± 1.30
20:3n-3	0.13 ± 0.02	0.16 ± 0.05	0.13 ± 0.04	0.15 ± 0.05	0.16 ± 0.08	0.19 ± 0.12
20:4n-3	0.34 ± 0.06	0.26 ± 0.10	0.21 ± 0.05	0.31 ± 0.11	0.31 ± 0.10	0.22 ± 0.08
20:5n-3	5.49 ± 0.43	7.74 ± 1.86	5.78 ± 1.13	5.77 ± 1.52	4.88 ± 1.41	5.47 ± 1.48
22:2n-6	0.01 ± 0.01	0.01 ± 0.02	0.01 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01
21:5n-3	0.12 ± 0.02	0.10 ± 0.03	0.12 ± 0.06	0.11 ± 0.06	0.09 ± 0.05	0.15 ± 0.04
22:4n-6	0.68 ± 0.10	2.00 ± 0.70	1.88 ± 0.48	2.24 ± 0.93	0.45 ± 0.12	0.47 ± 0.32
22:5n-6	1.48 ± 0.21	1.19 ± 0.34	1.87 ± 0.52	1.72 ± 0.65	1.44 ± 0.36	2.00 ± 0.54
22:4n-3	0.06 ± 0.01	0.05 ± 0.04	0.03 ± 0.01	0.04 ± 0.02	0.05 ± 0.01	0.02 ± 0.01
22:5n-3	1.72 ± 0.16	2.20 ± 0.45	2.29 ± 0.41	2.13 ± 0.35	1.68 ± 0.22	1.28 ± 0.40
22:6n-3	19.33 ± 2.07	12.46 ± 4.30	19.44 ± 6.20	18.34 ± 7.61	22.72 ± 5.04	26.86 ± 5.09
subtotal:	36.81 ± 2.28	39.38 ± 3.98	44.03 ± 5.01	41.85 ± 6.78	38.08 ± 6.40	44.11 ± 5.34
Total	93.73 ± 0.28	94.05 ± 1.42	93.06 ± 0.68	92.96 ± 0.95	95.70 ± 0.60	94.31 ± 0.51

Appendix 4.1 *continued*

	Fishes					
Group	5	27	28	3	30	21
Species name	*Priacanthus meeki*	*Pristipomoides filamentosus*	*Pristipomoides zonatus*	*Pseudopentaceros wheeleri*	*Sargocentron xantherythrum*	*Scarus dubius*
Common name	(Hawaiian bigeye)	(Pink snapper)	(Flower snapper)	(Armorhead)	(Hawaiian squirrelfish)	(Regal parrotfish)
	n=20	n=24	n=19	n=20	n=21	n=19
Length (cm)	21.67 ± 5.88	51.86 ± 10.62	35.68 ± 2.88	30.33 ± 1.70	9.38 ± 2.24	21.96 ± 6.15
Mass (g)	217.06 ± 117.18	2888.37 ± 1318.84	1276.95 ± 262.88	614.51 ± 88.29	19.89 ± 10.69	330.04 ± 339.77
Fat content (%)	1.67 ± 1.21	2.01 ± 2.10	2.28 ± 0.99	27.13 ± 4.62	4.06 ± 3.24	4.44 ± 2.16
Saturated FA						
14:0	3.68 ± 1.02	2.48 ± 0.88	3.57 ± 1.15	4.20 ± 0.35	4.48 ± 1.52	5.04 ± 1.15
16:0	20.86 ± 2.07	20.34 ± 1.13	20.21 ± 0.87	17.56 ± 0.69	23.73 ± 5.21	30.46 ± 3.47
17:0	1.37 ± 0.20	1.13 ± 0.15	1.04 ± 0.19	0.64 ± 0.04	1.59 ± 0.27	1.37 ± 0.37
18:0	8.73 ± 1.01	7.89 ± 0.59	6.74 ± 0.44	5.17 ± 0.39	10.53 ± 1.26	5.68 ± 0.82
subtotal:	34.64 ± 2.23	31.83 ± 1.48	31.57 ± 1.09	27.58 ± 0.66	40.33 ± 5.61	42.56 ± 3.28
Monounsaturated FA						
16:1n-7	3.58 ± 0.93	2.86 ± 1.09	5.25 ± 1.13	4.40 ± 0.43	3.23 ± 0.53	6.23 ± 1.53
18:1n-9	11.51 ± 2.71	12.03 ± 4.23	15.53 ± 3.79	26.54 ± 2.11	9.20 ± 1.43	6.48 ± 0.81
18:1n-7	2.41 ± 0.37	2.10 ± 0.32	2.91 ± 0.30	2.92 ± 0.22	2.93 ± 0.61	3.35 ± 0.63
20:1n-11	0.24 ± 0.10	0.18 ± 0.06	0.31 ± 0.07	1.04 ± 0.43	0.77 ± 0.47	0.09 ± 0.05
20:1n-9	0.66 ± 0.28	1.11 ± 0.32	1.54 ± 0.32	2.65 ± 0.24	1.09 ± 0.26	0.27 ± 0.10
20:1n-7	0.17 ± 0.05	0.19 ± 0.04	0.22 ± 0.03	0.54 ± 0.07	0.19 ± 0.08	0.19 ± 0.04
22:1n-11	0.20 ± 0.12	0.33 ± 0.23	0.48 ± 0.34	1.96 ± 0.80	0.70 ± 0.65	0.09 ± 0.19
22:1n-9	0.10 ± 0.05	0.22 ± 0.08	0.35 ± 0.11	1.30 ± 0.37	0.20 ± 0.08	0.05 ± 0.05
22:1n-7	0.08 ± 0.02	0.10 ± 0.04	0.09 ± 0.03	0.15 ± 0.05	0.09 ± 0.04	0.04 ± 0.02
subtotal:	18.95 ± 3.75	19.11 ± 5.98	26.68 ± 4.33	41.50 ± 1.21	18.41 ± 1.41	16.80 ± 1.18
Polyunsaturated FA						
16:2n-6	0.04 ± 0.03	0.02 ± 0.01	0.02 ± 0.01	0.06 ± 0.02	0.01 ± 0.01	0.16 ± 0.10
16:2n-4	0.59 ± 0.13	0.56 ± 0.11	0.73 ± 0.18	0.49 ± 0.05	0.41 ± 0.11	0.39 ± 0.24
16:3n-6	0.25 ± 0.14	0.12 ± 0.04	0.15 ± 0.02	0.05 ± 0.00	0.14 ± 0.09	0.36 ± 0.11
16:3n-4	0.06 ± 0.04	0.05 ± 0.04	0.05 ± 0.03	0.02 ± 0.00	0.04 ± 0.02	0.30 ± 0.11
16:4n-1	0.02 ± 0.04	0.08 ± 0.05	0.06 ± 0.03	0.02 ± 0.00	0.03 ± 0.03	0.04 ± 0.05
18:2n-6	1.32 ± 0.20	1.08 ± 0.21	0.97 ± 0.18	0.83 ± 0.09	1.13 ± 0.14	2.47 ± 0.66
18:2n-4	0.13 ± 0.04	0.10 ± 0.02	0.11 ± 0.02	0.04 ± 0.00	0.07 ± 0.02	0.07 ± 0.01
18:3n-6	0.33 ± 0.16	0.47 ± 0.08	0.38 ± 0.05	0.16 ± 0.01	0.35 ± 0.18	1.12 ± 0.21
18:3n-4	0.10 ± 0.03	0.11 ± 0.03	0.12 ± 0.05	0.07 ± 0.01	0.09 ± 0.02	0.13 ± 0.06
18:3n-3	0.51 ± 0.24	0.27 ± 0.08	0.24 ± 0.04	0.45 ± 0.06	0.39 ± 0.07	1.81 ± 0.64
18:3n-1	0.16 ± 0.04	0.22 ± 0.05	0.28 ± 0.07	0.18 ± 0.02	0.09 ± 0.03	0.05 ± 0.04
18:4n-3	0.54 ± 0.20	0.24 ± 0.09	0.23 ± 0.04	0.82 ± 0.19	0.40 ± 0.14	1.43 ± 0.55
18:4n-1	0.00 ± 0.01	0.03 ± 0.02	0.00 ± 0.00	0.02 ± 0.01	0.00 ± 0.01	0.02 ± 0.01
20:2n-6	0.53 ± 0.15	0.34 ± 0.06	0.34 ± 0.06	0.52 ± 0.07	0.62 ± 0.27	0.44 ± 0.10
20:3n-6	0.17 ± 0.07	0.19 ± 0.08	0.20 ± 0.03	0.12 ± 0.01	0.36 ± 0.09	0.68 ± 0.16
20:4n-6	3.63 ± 1.46	3.29 ± 1.01	2.96 ± 0.62	0.64 ± 0.05	5.48 ± 2.67	8.54 ± 3.16
20:3n-3	0.16 ± 0.07	0.17 ± 0.10	0.12 ± 0.05	0.23 ± 0.06	0.14 ± 0.05	0.21 ± 0.06
20:4n-3	0.32 ± 0.10	0.48 ± 0.15	0.46 ± 0.09	0.70 ± 0.11	0.31 ± 0.11	1.04 ± 0.33
20:5n-3	5.31 ± 1.12	3.64 ± 0.79	3.19 ± 0.57	4.50 ± 0.41	4.45 ± 0.92	5.82 ± 1.00
22:2n-6	0.01 ± 0.01	0.03 ± 0.04	0.05 ± 0.03	0.05 ± 0.01	0.02 ± 0.02	0.05 ± 0.09
21:5n-3	0.11 ± 0.04	0.10 ± 0.04	0.08 ± 0.01	0.23 ± 0.02	0.11 ± 0.03	0.10 ± 0.06
22:4n-6	0.73 ± 0.44	0.65 ± 0.18	0.73 ± 0.22	0.11 ± 0.01	2.80 ± 1.39	0.99 ± 0.59
22:5n-6	1.82 ± 0.43	2.92 ± 0.98	2.03 ± 0.38	0.36 ± 0.03	1.20 ± 0.32	0.82 ± 0.26
22:4n-3	0.04 ± 0.02	0.05 ± 0.02	0.05 ± 0.02	0.05 ± 0.01	0.05 ± 0.02	0.08 ± 0.02
22:5n-3	1.55 ± 0.33	2.43 ± 0.49	2.28 ± 0.31	1.55 ± 0.13	2.61 ± 0.57	2.67 ± 0.44
22:6n-3	21.32 ± 4.07	26.03 ± 4.57	19.71 ± 2.45	13.29 ± 0.71	12.96 ± 4.20	4.06 ± 2.21
subtotal:	39.76 ± 4.62	43.67 ± 7.04	35.54 ± 4.06	25.54 ± 1.48	34.25 ± 6.02	33.84 ± 3.04
Total	93.36 ± 0.95	94.61 ± 0.59	93.79 ± 0.94	94.62 ± 0.12	93.00 ± 0.97	93.20 ± 1.80

Appendix 4.1 *continued*

	Fishes					
Group	24	36	18	18	37	37
Species name	*Sebastapistes ballieui*	*Sufflamen bursa*	*Synodus lobeli*	*Synodus variegatus*	*Thalassoma ballieui*	*Thalassoma duperry*
Common name	(Spotfin scorpionfish)	(Lei triggerfish)	(Lobel's lizardfish)	(Reef lizardfish)	(Blacktail wrasse)	(Saddle wrasse)
	n=19	n=19	n=20	n=19	n=20	n=20
Length (cm)	8.54 ± 1.60	15.24 ± 1.40	8.54 ± 1.64	12.18 ± 6.54	22.45 ± 5.11	11.77 ± 2.62
Mass (g)	17.46 ± 7.98	103.11 ± 17.93	6.82 ± 4.62	39.34 ± 61.38	224.18 ± 154.29	31.89 ± 18.44
Fat content (%)	1.19 ± 0.42	3.53 ± 2.23	1.26 ± 0.48	0.95 ± 0.65	1.46 ± 0.75	1.56 ± 0.57
Saturated FA						
14:0	1.76 ± 0.58	1.34 ± 0.32	1.92 ± 1.49	2.23 ± 0.77	3.15 ± 1.23	2.64 ± 0.76
16:0	18.14 ± 1.36	24.01 ± 2.47	19.70 ± 1.58	20.88 ± 1.47	21.84 ± 2.42	21.51 ± 2.24
17:0	1.40 ± 0.27	2.04 ± 0.20	1.44 ± 0.27	1.20 ± 0.19	1.10 ± 0.36	1.33 ± 0.31
18:0	10.23 ± 0.66	10.63 ± 0.69	9.94 ± 0.66	9.29 ± 0.74	9.50 ± 1.33	9.55 ± 0.74
subtotal:	31.54 ± 1.63	38.03 ± 2.44	33.00 ± 1.71	33.59 ± 1.67	35.59 ± 3.79	35.04 ± 2.54
Monounsaturated FA						
16:1n-7	2.40 ± 0.43	2.90 ± 0.63	2.17 ± 0.97	2.15 ± 0.62	3.03 ± 0.78	2.53 ± 0.79
18:1n-9	9.35 ± 0.48	8.75 ± 0.79	7.71 ± 0.65	7.75 ± 0.87	10.75 ± 1.53	8.76 ± 0.91
18:1n-7	2.36 ± 0.33	4.24 ± 0.40	2.59 ± 0.35	2.51 ± 0.31	2.55 ± 0.54	2.54 ± 0.38
20:1n-11	0.31 ± 0.09	0.81 ± 0.26	0.17 ± 0.13	0.10 ± 0.08	0.37 ± 0.18	0.74 ± 0.29
20:1n-9	0.69 ± 0.23	0.51 ± 0.11	0.45 ± 0.20	0.40 ± 0.13	0.60 ± 0.27	0.69 ± 0.27
20:1n-7	0.15 ± 0.05	0.22 ± 0.05	0.22 ± 0.23	0.14 ± 0.05	0.13 ± 0.07	0.19 ± 0.06
22:1n-11	0.23 ± 0.05	0.21 ± 0.12	0.28 ± 0.27	0.12 ± 0.24	0.30 ± 0.26	0.34 ± 0.26
22:1n-9	0.11 ± 0.02	0.06 ± 0.02	0.16 ± 0.11	0.08 ± 0.04	0.09 ± 0.09	0.09 ± 0.03
22:1n-7	0.08 ± 0.03	0.06 ± 0.03	0.11 ± 0.07	0.07 ± 0.03	0.04 ± 0.02	0.10 ± 0.04
subtotal:	15.68 ± 0.71	17.77 ± 1.38	13.87 ± 1.60	13.33 ± 1.24	17.86 ± 2.33	15.97 ± 1.24
Polyunsaturated FA						
16:2n-6	0.02 ± 0.02	0.08 ± 0.05	0.02 ± 0.01	0.04 ± 0.02	0.06 ± 0.05	0.05 ± 0.03
16:2n-4	0.32 ± 0.09	0.38 ± 0.04	0.66 ± 0.15	0.79 ± 0.23	0.28 ± 0.10	0.23 ± 0.06
16:3n-6	0.07 ± 0.04	0.10 ± 0.03	0.09 ± 0.07	0.12 ± 0.06	0.14 ± 0.09	0.17 ± 0.18
16:3n-4	0.04 ± 0.04	0.11 ± 0.02	0.03 ± 0.02	0.06 ± 0.04	0.07 ± 0.05	0.07 ± 0.02
16:4n-1	0.04 ± 0.09	0.01 ± 0.02	0.03 ± 0.05	0.07 ± 0.04	0.13 ± 0.10	0.08 ± 0.08
18:2n-6	1.27 ± 0.08	1.49 ± 0.22	1.08 ± 0.11	1.32 ± 0.10	1.56 ± 0.34	1.50 ± 0.28
18:2n-4	0.09 ± 0.02	0.13 ± 0.03	0.11 ± 0.04	0.11 ± 0.05	0.07 ± 0.04	0.06 ± 0.01
18:3n-6	0.46 ± 0.06	0.50 ± 0.11	0.44 ± 0.07	0.40 ± 0.12	0.45 ± 0.15	0.62 ± 0.23
18:3n-4	0.09 ± 0.03	0.15 ± 0.03	0.06 ± 0.04	0.10 ± 0.02	0.10 ± 0.03	0.08 ± 0.04
18:3n-3	0.32 ± 0.10	0.60 ± 0.14	0.23 ± 0.08	0.31 ± 0.11	0.45 ± 0.17	0.50 ± 0.20
18:3n-1	0.10 ± 0.04	0.08 ± 0.01	0.27 ± 0.05	0.28 ± 0.12	0.05 ± 0.04	0.05 ± 0.04
18:4n-3	0.29 ± 0.13	0.46 ± 0.14	0.24 ± 0.12	0.32 ± 0.17	0.34 ± 0.14	0.41 ± 0.21
18:4n-1	0.02 ± 0.04	0.00 ± 0.00	0.01 ± 0.02	0.01 ± 0.01	0.02 ± 0.03	0.00 ± 0.01
20:2n-6	0.63 ± 0.14	0.79 ± 0.15	0.47 ± 0.11	0.39 ± 0.09	0.58 ± 0.14	0.69 ± 0.13
20:3n-6	0.26 ± 0.03	0.45 ± 0.11	0.26 ± 0.05	0.26 ± 0.23	0.60 ± 0.23	0.93 ± 0.34
20:4n-6	10.13 ± 2.74	8.81 ± 2.05	5.49 ± 1.89	5.39 ± 1.87	9.87 ± 3.02	9.87 ± 1.53
20:3n-3	0.16 ± 0.05	0.11 ± 0.03	0.14 ± 0.07	0.20 ± 0.08	0.11 ± 0.03	0.13 ± 0.03
20:4n-3	0.23 ± 0.08	0.30 ± 0.07	0.30 ± 0.18	0.34 ± 0.08	0.34 ± 0.12	0.32 ± 0.07
20:5n-3	5.86 ± 0.92	7.02 ± 1.00	4.04 ± 0.54	4.43 ± 0.89	4.39 ± 0.81	4.88 ± 0.61
22:2n-6	0.01 ± 0.02	0.03 ± 0.02	0.00 ± 0.01	0.03 ± 0.02	0.02 ± 0.03	0.02 ± 0.03
21:5n-3	0.08 ± 0.03	0.10 ± 0.02	0.14 ± 0.06	0.14 ± 0.06	0.08 ± 0.08	0.09 ± 0.07
22:4n-6	1.78 ± 0.59	3.74 ± 0.62	0.74 ± 0.20	0.96 ± 0.56	1.97 ± 0.44	2.96 ± 0.55
22:5n-6	1.89 ± 0.22	1.02 ± 0.22	2.27 ± 0.35	2.62 ± 0.45	1.42 ± 0.41	1.46 ± 0.31
22:4n-3	0.03 ± 0.01	0.04 ± 0.02	0.03 ± 0.03	0.04 ± 0.02	0.04 ± 0.04	0.04 ± 0.01
22:5n-3	1.77 ± 0.21	3.59 ± 0.68	1.95 ± 0.26	1.94 ± 0.58	2.74 ± 0.27	3.13 ± 0.62
22:6n-3	19.90 ± 1.83	7.63 ± 2.88	28.24 ± 3.78	26.28 ± 4.32	13.89 ± 4.17	13.74 ± 3.16
subtotal:	45.87 ± 2.35	37.71 ± 3.91	47.36 ± 3.41	46.96 ± 2.16	39.77 ± 4.58	42.09 ± 3.17
Total	93.08 ± 1.12	93.50 ± 0.84	94.22 ± 1.05	93.88 ± 0.72	93.22 ± 0.81	93.10 ± 1.61

Appendix 4.1 *continued*

	Fishes			Invertebrates		
Group	22	18	31	41	41	43
Species name	*Torquigener florealis*	*Trachinocephalus myops*	*Zebrasoma flavescens*	*Calappa bicornis*	*Calappa calappa*	*Carpilius convexus*
Common name	(Floral puffer)	(Snakefish)	(Yellow tang)	(Two-horned box crab)	(Smooth box crab)	(Convex pebble crab)
	n=20	n=20	n=20	n=23	n=36	n=21
Length (cm)	9.77 ± 6.80	13.07 ± 6.15	10.53 ± 3.72	5.79 ± 1.96	7.41 ± 2.94	6.73 ± 2.21
Mass (g)	48.58 ± 63.50	45.17 ± 55.58	53.60 ± 40.81	37.64 ± 18.20	129.11 ± 73.64	108.06 ± 44.96
Fat content (%)	2.23 ± 1.45	0.93 ± 0.27	6.35 ± 3.02	0.53 ± 0.35	0.81 ± 0.46	0.95 ± 0.48
Saturated FA						
14:0	1.62 ± 0.37	1.78 ± 0.58	4.82 ± 1.38	1.63 ± 0.71	1.36 ± 0.67	2.20 ± 1.01
16:0	16.86 ± 2.42	19.61 ± 1.24	37.20 ± 4.11	13.63 ± 2.75	14.14 ± 3.56	15.96 ± 2.96
17:0	1.45 ± 0.22	1.28 ± 0.28	0.73 ± 0.11	1.34 ± 0.28	1.52 ± 0.24	1.21 ± 0.33
18:0	12.06 ± 1.87	8.59 ± 0.64	4.53 ± 2.14	9.19 ± 1.62	9.07 ± 1.55	8.24 ± 1.93
subtotal:	31.98 ± 1.38	31.26 ± 1.47	47.27 ± 3.13	25.79 ± 2.02	26.09 ± 2.78	27.61 ± 2.50
Monounsaturated FA						
16:1n-7	2.73 ± 1.22	2.13 ± 0.47	4.32 ± 1.39	3.48 ± 0.96	5.76 ± 2.78	4.36 ± 0.98
18:1n-9	9.12 ± 2.57	8.48 ± 1.24	8.36 ± 0.84	9.96 ± 2.22	7.64 ± 2.60	12.01 ± 3.39
18:1n-7	2.86 ± 0.52	2.42 ± 0.40	1.91 ± 0.20	2.84 ± 0.68	3.00 ± 0.99	3.26 ± 0.83
20:1n-11	0.77 ± 0.34	0.11 ± 0.09	0.03 ± 0.03	0.65 ± 0.29	0.88 ± 0.48	1.49 ± 1.16
20:1n-9	0.94 ± 0.47	0.39 ± 0.10	1.55 ± 0.79	1.17 ± 0.42	0.89 ± 0.20	1.39 ± 0.48
20:1n-7	0.37 ± 0.21	0.15 ± 0.06	0.13 ± 0.03	0.29 ± 0.13	0.36 ± 0.19	0.42 ± 0.13
22:1n-11	0.34 ± 0.18	0.10 ± 0.14	0.00 ± 0.01	0.70 ± 0.54	0.42 ± 0.20	1.48 ± 1.96
22:1n-9	0.18 ± 0.07	0.07 ± 0.03	0.11 ± 0.05	0.22 ± 0.10	0.26 ± 0.12	0.31 ± 0.17
22:1n-7	0.15 ± 0.06	0.07 ± 0.03	0.05 ± 0.05	0.13 ± 0.07	0.15 ± 0.06	0.31 ± 0.22
subtotal:	17.46 ± 4.12	13.92 ± 1.58	16.46 ± 2.88	19.43 ± 3.62	19.37 ± 2.90	25.02 ± 4.24
Polyunsaturated FA						
16:2n-6	0.06 ± 0.04	0.04 ± 0.03	0.06 ± 0.03	0.04 ± 0.03	0.09 ± 0.05	0.04 ± 0.03
16:2n-4	0.50 ± 0.15	0.97 ± 0.30	0.11 ± 0.04	0.22 ± 0.11	0.25 ± 0.11	0.34 ± 0.30
16:3n-6	0.11 ± 0.11	0.08 ± 0.05	0.12 ± 0.02	0.17 ± 0.11	0.09 ± 0.08	0.22 ± 0.16
16:3n-4	0.09 ± 0.05	0.03 ± 0.02	0.08 ± 0.03	0.14 ± 0.12	0.09 ± 0.07	0.15 ± 0.11
16:4n-1	0.03 ± 0.03	0.02 ± 0.04	0.03 ± 0.02	0.10 ± 0.10	0.07 ± 0.06	0.18 ± 0.17
18:2n-6	0.96 ± 0.26	1.11 ± 0.15	1.37 ± 0.34	2.07 ± 0.33	1.54 ± 0.62	1.68 ± 0.25
18:2n-4	0.13 ± 0.06	0.11 ± 0.04	0.03 ± 0.00	0.11 ± 0.04	0.09 ± 0.06	0.11 ± 0.06
18:3n-6	0.63 ± 0.15	0.37 ± 0.12	0.57 ± 0.10	0.48 ± 0.10	0.28 ± 0.23	0.42 ± 0.18
18:3n-4	0.09 ± 0.04	0.07 ± 0.03	0.06 ± 0.03	0.09 ± 0.03	0.15 ± 0.05	0.20 ± 0.13
18:3n-3	0.28 ± 0.27	0.23 ± 0.08	0.60 ± 0.32	0.48 ± 0.10	0.58 ± 0.77	0.48 ± 0.15
18:3n-1	0.16 ± 0.07	0.29 ± 0.09	0.00 ± 0.00	0.11 ± 0.04	0.09 ± 0.04	0.09 ± 0.04
18:4n-3	0.20 ± 0.23	0.19 ± 0.10	0.40 ± 0.18	0.37 ± 0.23	0.18 ± 0.12	0.63 ± 0.57
18:4n-1	0.00 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.04	0.01 ± 0.02	0.05 ± 0.03
20:2n-6	0.62 ± 0.12	0.33 ± 0.07	0.20 ± 0.04	1.21 ± 0.33	1.66 ± 0.30	0.94 ± 0.42
20:3n-6	0.21 ± 0.03	0.21 ± 0.08	1.25 ± 0.11	0.35 ± 0.12	0.38 ± 0.19	0.41 ± 0.24
20:4n-6	8.14 ± 2.74	5.52 ± 2.16	6.49 ± 2.56	14.07 ± 4.49	15.85 ± 3.57	8.76 ± 4.07
20:3n-3	0.19 ± 0.07	0.10 ± 0.04	0.10 ± 0.05	0.20 ± 0.06	0.23 ± 0.09	0.15 ± 0.03
20:4n-3	0.24 ± 0.14	0.29 ± 0.09	0.35 ± 0.10	0.23 ± 0.12	0.18 ± 0.12	0.27 ± 0.15
20:5n-3	3.97 ± 0.65	4.11 ± 0.74	10.55 ± 1.98	10.64 ± 1.54	8.03 ± 2.23	8.37 ± 2.32
22:2n-6	0.05 ± 0.02	0.01 ± 0.02	0.01 ± 0.02	0.01 ± 0.02	0.02 ± 0.03	0.01 ± 0.01
21:5n-3	0.07 ± 0.04	0.11 ± 0.03	0.03 ± 0.04	0.20 ± 0.11	0.10 ± 0.11	0.23 ± 0.15
22:4n-6	1.95 ± 0.73	0.92 ± 0.75	2.98 ± 0.57	1.03 ± 0.41	1.72 ± 0.80	0.62 ± 0.36
22:5n-6	2.94 ± 1.14	2.45 ± 0.35	0.37 ± 0.32	0.85 ± 0.31	0.95 ± 0.21	0.69 ± 0.19
22:4n-3	0.09 ± 0.03	0.06 ± 0.03	0.12 ± 0.03	0.03 ± 0.02	0.04 ± 0.02	0.03 ± 0.02
22:5n-3	3.76 ± 0.48	1.75 ± 0.51	3.14 ± 0.38	1.80 ± 0.41	1.79 ± 1.02	1.47 ± 0.42
22:6n-3	17.90 ± 3.11	29.30 ± 4.01	3.55 ± 2.85	10.62 ± 1.82	7.90 ± 3.77	10.64 ± 2.42
subtotal:	43.35 ± 4.73	48.68 ± 2.52	32.59 ± 5.62	45.64 ± 4.40	42.34 ± 6.35	37.15 ± 3.31
Total	92.80 ± 1.00	93.86 ± 0.75	96.32 ± 0.56	90.86 ± 1.68	87.80 ± 2.09	89.78 ± 3.05

Appendix 4.1 *continued*

	Invertebrates					
Group	42	40	40	38	38	38
Species name	*Charybdis hawaiiensis*	*Heterocarpus ensifer*	*Heterocarpus laevigatus*	*Octopus cyanea*	*Octopus ornatus*	*Octopus sp.*
Common name	(Hawaiian swimming crab)	(Two-spined shrimp)	(Red-tipped shrimp)	(Hawaiian day octopus)	(Ornate octopus)	(Octopus spp)
	n=29	n=31	n=39	n=13	n=4	n=23
Length (cm)	5.93 ± 1.27	9.55 ± 0.95	13.50 ± 1.60	17.63 ± 2.58	58.20 ± 8.39	N/A
Mass (g)	70.88 ± 28.13	13.45 ± 3.69	39.78 ± 11.09	832.60 ± 938.95	266.91 ± 198.16	334.73 ± 776.91
Fat content (%)	0.75 ± 0.40	2.57 ± 0.94	1.93 ± 0.74	1.12 ± 0.43	0.66 ± 0.39	1.56 ± 0.84
Saturated FA						
14:0	1.20 ± 0.56	2.73 ± 0.67	2.41 ± 0.56	0.93 ± 0.41	0.74 ± 0.20	1.22 ± 0.64
16:0	16.50 ± 2.52	16.64 ± 1.46	15.04 ± 1.41	17.66 ± 1.72	15.55 ± 0.82	18.29 ± 1.67
17:0	1.71 ± 0.36	0.71 ± 0.11	0.73 ± 0.15	1.55 ± 0.26	1.62 ± 0.44	1.84 ± 0.29
18:0	8.95 ± 0.94	4.83 ± 0.57	4.90 ± 0.62	11.28 ± 1.67	11.92 ± 0.62	10.10 ± 0.88
subtotal:	28.36 ± 2.77	24.91 ± 2.17	23.08 ± 2.08	31.42 ± 1.87	29.83 ± 0.53	31.45 ± 1.71
Monounsaturated FA						
16:1n-7	3.07 ± 1.03	5.78 ± 1.27	5.85 ± 1.25	0.83 ± 0.62	0.70 ± 0.39	0.95 ± 0.52
18:1n-9	9.33 ± 0.92	16.10 ± 2.39	19.33 ± 4.06	3.08 ± 1.70	2.57 ± 0.73	2.94 ± 1.00
18:1n-7	2.54 ± 0.42	4.84 ± 0.53	4.46 ± 0.67	2.04 ± 0.41	1.84 ± 0.24	1.69 ± 0.25
20:1n-11	0.67 ± 0.42	0.66 ± 0.66	0.57 ± 0.35	0.47 ± 0.09	0.52 ± 0.12	0.39 ± 0.09
20:1n-9	0.88 ± 0.34	1.71 ± 0.44	2.65 ± 0.94	1.97 ± 0.59	2.03 ± 0.34	1.82 ± 0.33
20:1n-7	0.19 ± 0.11	0.42 ± 0.15	0.96 ± 1.11	0.11 ± 0.05	0.10 ± 0.05	0.14 ± 0.05
22:1n-11	0.50 ± 0.51	1.30 ± 1.12	0.96 ± 0.73	0.13 ± 0.10	0.11 ± 0.08	0.11 ± 0.08
22:1n-9	0.19 ± 0.09	0.43 ± 0.10	0.76 ± 0.32	0.51 ± 0.16	0.55 ± 0.13	0.41 ± 0.08
22:1n-7	0.12 ± 0.06	0.17 ± 0.04	0.22 ± 0.06	0.07 ± 0.04	0.13 ± 0.14	0.06 ± 0.03
subtotal:	17.49 ± 2.41	31.39 ± 2.53	35.77 ± 6.04	9.19 ± 3.17	8.54 ± 1.24	8.51 ± 1.72
Polyunsaturated FA						
16:2n-6	0.07 ± 0.06	0.05 ± 0.02	0.06 ± 0.03	0.04 ± 0.06	0.02 ± 0.02	0.04 ± 0.05
16:2n-4	0.26 ± 0.12	0.26 ± 0.07	0.49 ± 0.14	0.11 ± 0.15	0.05 ± 0.04	0.16 ± 0.14
16:3n-6	0.07 ± 0.06	0.33 ± 0.15	0.15 ± 0.10	0.03 ± 0.04	0.01 ± 0.01	0.04 ± 0.05
16:3n-4	0.11 ± 0.09	0.22 ± 0.11	0.14 ± 0.08	0.04 ± 0.04	0.00 ± 0.00	0.04 ± 0.02
16:4n-1	0.09 ± 0.07	0.31 ± 0.18	0.16 ± 0.10	0.01 ± 0.01	0.02 ± 0.04	0.01 ± 0.02
18:2n-6	2.22 ± 0.43	0.98 ± 0.11	0.79 ± 0.18	0.82 ± 0.21	0.85 ± 0.32	0.68 ± 0.15
18:2n-4	0.10 ± 0.04	0.16 ± 0.03	0.12 ± 0.03	0.04 ± 0.02	0.04 ± 0.03	0.08 ± 0.03
18:3n-6	0.40 ± 0.20	0.23 ± 0.02	0.24 ± 0.05	0.18 ± 0.08	0.16 ± 0.06	0.19 ± 0.10
18:3n-4	0.10 ± 0.05	0.16 ± 0.06	0.26 ± 0.06	0.04 ± 0.03	0.07 ± 0.05	0.06 ± 0.03
18:3n-3	0.74 ± 0.21	0.42 ± 0.10	0.27 ± 0.08	0.14 ± 0.05	0.22 ± 0.24	0.15 ± 0.08
18:3n-1	0.07 ± 0.04	0.09 ± 0.02	0.11 ± 0.04	0.02 ± 0.04	0.07 ± 0.05	0.04 ± 0.04
18:4n-3	0.29 ± 0.18	0.83 ± 0.38	0.30 ± 0.26	0.05 ± 0.03	0.08 ± 0.08	0.09 ± 0.09
18:4n-1	0.01 ± 0.01	0.09 ± 0.04	0.07 ± 0.08	0.01 ± 0.02	0.07 ± 0.06	0.01 ± 0.01
20:2n-6	1.35 ± 0.24	0.39 ± 0.16	0.37 ± 0.07	1.08 ± 0.23	0.99 ± 0.07	0.86 ± 0.19
20:3n-6	0.36 ± 0.15	0.14 ± 0.03	0.13 ± 0.03	0.24 ± 0.15	0.20 ± 0.14	0.13 ± 0.04
20:4n-6	14.33 ± 2.89	3.12 ± 1.77	3.88 ± 0.95	17.92 ± 4.49	17.96 ± 0.88	10.19 ± 4.74
20:3n-3	0.20 ± 0.04	0.17 ± 0.07	0.20 ± 0.12	0.28 ± 0.09	0.40 ± 0.24	0.67 ± 0.36
20:4n-3	0.21 ± 0.09	0.36 ± 0.10	0.20 ± 0.07	0.10 ± 0.04	0.12 ± 0.05	0.17 ± 0.13
20:5n-3	9.63 ± 1.75	12.20 ± 1.68	9.70 ± 1.94	7.37 ± 1.64	7.73 ± 1.43	10.43 ± 2.31
22:2n-6	0.05 ± 0.12	0.00 ± 0.01	0.00 ± 0.01	0.05 ± 0.06	0.01 ± 0.01	0.03 ± 0.06
21:5n-3	0.14 ± 0.10	0.26 ± 0.10	0.10 ± 0.07	0.07 ± 0.03	0.05 ± 0.03	0.13 ± 0.05
22:4n-6	1.32 ± 0.79	0.23 ± 0.16	0.34 ± 0.18	2.10 ± 0.72	2.41 ± 0.37	1.10 ± 0.73
22:5n-6	0.62 ± 0.13	0.62 ± 0.23	0.89 ± 0.27	1.65 ± 0.24	1.47 ± 0.18	1.53 ± 0.29
22:4n-3	0.03 ± 0.02	0.03 ± 0.01	0.02 ± 0.01	0.03 ± 0.01	0.01 ± 0.01	0.06 ± 0.03
22:5n-3	1.56 ± 0.36	1.58 ± 0.29	1.62 ± 1.24	1.34 ± 0.27	1.61 ± 0.55	1.40 ± 0.28
22:6n-3	11.86 ± 2.53	14.93 ± 2.29	14.14 ± 3.43	20.31 ± 3.62	19.03 ± 4.24	26.64 ± 3.80
subtotal:	46.17 ± 5.33	38.15 ± 2.39	34.76 ± 4.52	54.06 ± 2.97	53.63 ± 3.41	54.92 ± 2.34
Total	92.02 ± 1.73	94.46 ± 1.02	93.61 ± 0.68	94.67 ± 2.66	91.99 ± 3.04	94.88 ± 2.67

Appendix 4.1 *end*

Invertebrates

Group	45	44	44	39
Species name	*Panulirus marginatus*	*Scyllarides haanii*	*Scyllarides squammosus*	*Sthenoteuthis oualaniensis*
Common name	(Spiny lobster)	(Ridgeback slipper lobster)	(Common slipper lobster)	(Neon flying squid)
	n=71	n=30	n=72	n=15
Length (cm)	22.65 ± 6.45	25.79 ± 7.04	20.35 ± 3.63	30.77 ± 7.40
Mass (g)	414.80 ± 333.97	604.94 ± 397.39	287.53 ± 120.01	307.21 ± 338.03
Fat content (%)	1.17 ± 0.46	0.99 ± 0.58	0.91 ± 0.42	1.67 ± 0.36
Saturated FA				
14:0	1.18 ± 0.39	1.55 ± 0.61	1.33 ± 0.50	1.53 ± 0.63
16:0	13.15 ± 1.97	13.23 ± 2.08	13.47 ± 1.95	18.43 ± 0.80
17:0	1.42 ± 0.29	1.18 ± 0.45	1.88 ± 0.45	1.14 ± 0.14
18:0	9.73 ± 1.13	8.29 ± 0.79	9.51 ± 1.00	6.63 ± 0.95
subtotal:	25.48 ± 1.85	24.26 ± 2.40	26.18 ± 2.06	27.73 ± 1.47
Monounsaturated FA				
16:1n-7	3.92 ± 1.06	4.85 ± 3.35	3.25 ± 1.00	1.37 ± 0.78
18:1n-9	10.23 ± 2.52	13.74 ± 3.89	12.84 ± 2.27	6.62 ± 2.97
18:1n-7	2.63 ± 0.49	3.33 ± 1.90	2.05 ± 0.70	1.36 ± 0.29
20:1n-11	1.01 ± 0.48	0.94 ± 0.55	1.29 ± 0.43	0.42 ± 0.19
20:1n-9	0.90 ± 0.31	2.05 ± 0.69	1.19 ± 0.24	4.46 ± 0.81
20:1n-7	0.29 ± 0.11	1.32 ± 1.99	0.38 ± 0.25	0.13 ± 0.04
22:1n-11	0.36 ± 0.53	0.58 ± 0.38	0.37 ± 0.43	0.19 ± 0.08
22:1n-9	0.14 ± 0.08	0.44 ± 0.18	0.14 ± 0.07	0.23 ± 0.04
22:1n-7	0.14 ± 0.11	0.20 ± 0.24	0.11 ± 0.14	0.03 ± 0.02
subtotal:	19.63 ± 4.16	27.45 ± 8.25	21.61 ± 3.36	14.82 ± 3.30
Polyunsaturated FA				
16:2n-6	0.08 ± 0.13	0.06 ± 0.09	0.10 ± 0.15	0.02 ± 0.03
16:2n-4	0.27 ± 0.08	0.33 ± 0.17	0.52 ± 0.21	0.37 ± 0.20
16:3n-6	0.08 ± 0.07	0.12 ± 0.11	0.11 ± 0.10	0.12 ± 0.11
16:3n-4	0.06 ± 0.06	0.05 ± 0.05	0.08 ± 0.11	0.12 ± 0.11
16:4n-1	0.14 ± 0.13	0.11 ± 0.05	0.15 ± 0.08	0.11 ± 0.04
18:2n-6	2.02 ± 0.47	1.18 ± 0.39	1.86 ± 0.30	0.38 ± 0.14
18:2n-4	0.08 ± 0.04	0.09 ± 0.06	0.08 ± 0.03	0.10 ± 0.05
18:3n-6	0.54 ± 0.24	0.30 ± 0.25	0.46 ± 0.20	0.23 ± 0.06
18:3n-4	0.09 ± 0.07	0.09 ± 0.07	0.08 ± 0.08	0.15 ± 0.06
18:3n-3	0.59 ± 0.26	0.44 ± 0.21	0.55 ± 0.25	0.17 ± 0.08
18:3n-1	0.08 ± 0.03	0.11 ± 0.04	0.14 ± 0.05	0.11 ± 0.04
18:4n-3	0.25 ± 0.13	0.37 ± 0.30	0.48 ± 0.26	0.27 ± 0.22
18:4n-1	0.01 ± 0.02	0.02 ± 0.03	0.02 ± 0.03	0.12 ± 0.03
20:2n-6	1.19 ± 0.23	0.71 ± 0.41	0.79 ± 0.25	0.42 ± 0.06
20:3n-6	0.31 ± 0.18	0.21 ± 0.13	0.16 ± 0.06	0.08 ± 0.03
20:4n-6	16.88 ± 4.26	9.49 ± 3.77	9.93 ± 2.73	2.75 ± 0.27
20:3n-3	0.17 ± 0.08	0.18 ± 0.16	0.10 ± 0.04	1.22 ± 0.29
20:4n-3	0.17 ± 0.06	0.23 ± 0.10	0.19 ± 0.08	0.20 ± 0.05
20:5n-3	9.24 ± 2.36	7.92 ± 2.27	7.76 ± 1.47	11.30 ± 1.44
22:2n-6	0.04 ± 0.05	0.03 ± 0.03	0.01 ± 0.03	0.01 ± 0.01
21:5n-3	0.25 ± 0.15	0.23 ± 0.18	0.37 ± 0.15	0.12 ± 0.08
22:4n-6	1.41 ± 0.57	0.69 ± 0.29	1.25 ± 0.51	0.16 ± 0.02
22:5n-6	0.85 ± 0.24	0.99 ± 0.36	1.17 ± 0.33	1.02 ± 0.17
22:4n-3	0.01 ± 0.02	0.02 ± 0.04	0.02 ± 0.02	0.01 ± 0.01
22:5n-3	1.74 ± 0.65	1.14 ± 0.47	1.30 ± 0.70	0.68 ± 0.16
22:6n-3	8.48 ± 2.45	13.27 ± 3.92	12.84 ± 2.69	33.57 ± 3.33
subtotal:	45.05 ± 4.68	38.38 ± 7.23	40.52 ± 4.21	53.79 ± 2.32
Total	90.16 ± 1.35	90.08 ± 1.91	88.32 ± 1.92	96.34 ± 0.21

APPENDIX 4.2 QFASA Simulation Summaries.

A) Initial set of simulations. Summary of the first simulation results examining five mixtures of species/groups (i.e. pseudo signatures) and two fatty acid (FA) subsets: a set of 31 FAs (D) and a set of 39 FAs (ED, Table 4.2);1000 iterations were computed for each trial. Percentages represent the average proportion that each species/group were specified in the pseudo signatures, and in the average estimated pseudo signature (i.e. in the simulation results). Misidentified species/groups that appeared at ≥ 2.0% in an estimated pseudo signature are also listed (**); the remaining misidentifications are combined under the 'others' category. 'Total' represents the total proportions of misclassified individuals in the estimated pseudo signature.

Trial 1. Pseudo signature, 4 groups: Spiny lobster, Pink snapper, Wrasse/hogfish/coris and Moray eel.

	Specified	**D**	**ED**
Spiny lobster	15%	12.6%	10.8%
Pink snapper	15%	6.7%	5.3%
Moray eel	35%	33.8%	32%
Wrasse/hogfish/coris	35%	22.6%	26.7%
Scorpionfish **		6.9%	6.9%
Toby**		2.6%	2.0%
Tilefish**		2.2%	2.3%
Others**		12.6%	14.3%
Total**		24.3%	25.5%

Trial 2. Pseudo signature, 6 groups: Box crab, Cusk eel, Flounder, Flower snapper, Spiny lobster and Squid.

	Specified	**D**	**ED**
Box crab	15%	10.3%	13.4%
Cusk eel	30%	24.3%	23.9%
Flounder	15%	6.4%	9.4%
Flower snapper	15%	1.5%	3.6%
Spiny lobster	15%	11.4%	11.0%
Squid	10%	9.4%	8.6%
Lizard/snakefish**		4.0%	1.2%
Squirrelfish snapper**		3.7%	2.8%
Swimming crab**		3.2%	1.0%
Duckbill**		3.0%	3.3%
Octopus**		2.3%	1.9%
Beardfish**		2.1%	1.1%
Pink snapper**		2.0%	1.2%
Slipper lobster**		2.0%	1.0%
Cutthroat/snake eel**		1.4%	2.1%
Others**		13.2%	14.0%
Total**		36.9%	29.6%

APPENDIX 4.2 *continued*

Trial 3. Pseudo signature, 6 groups: Parrotfish, Scorpionfish, Spiny lobster, Squirrelfish snapper, Triggerfish M and Octopus.

	Specified	D	ED
Parrotfish	20%	18.4%	17.7%
Scorpionfish	15%	10.7%	8.8%
Spiny lobster	15%	13.4%	12%
Squirrelfish snapper	15%	3.8%	4.2%
Triggerfish M	30%	26.6%	29%
Octopus	5%	3.4%	3.5%
Swimming crab**		2.8%	3.9%
Lizard/snakefish**		2.8%	3.0%
Moray**		2.3%	1.7%
Duckbill**		2.7%	3.4%
Beardfish**		2.1%	1.7%
Others**		11.3%	10.8%
Total**		24.0%	24.5%

Trial 4. Pseudo signature, 4 groups: Angelfish, Goatfish M, Bluestripe snapper and Pebble crab.

	Specified	D	ED
Angelfish	15%	11.9%	12.7%
Goatfish M	35%	21.8%	24.7%
Bluestripe snapper	35%	4.3%	4.9%
Pebble crab	15%	8.9%	8.7%
Knife/razorfish**		7.0%	3.1%
Sandperch**		5.8%	4.7%
Soldierfish**		5.2%	5.1%
Slipper lobster**		3.7%	3.3%
Gurnard**		3.3%	4.3%
Squirrelfish**		2.6%	1.4%
Dragonet**		2.2%	1.5%
Goatfish P**		2.2%	1.6%
Triggerfish M**		2.0%	2.4%
Others**		19.4%	21.8%
Total**		53.0%	49.2%

Trial 5. Pseudo signature, 6 groups: Butterfly/forcepfish, Chromis/ dascyllus, Duckbill, Lizard/snakefish, Slipper lobster and Swimming crab.

	Specified	D	ED
Butterfly/forcepfish	20%	16.0%	17.0%
Chromis/dascyllus	20%	6.4%	8.8%
Duckbill	15%	7.2%	8.6%
Lizard/snakefish	15%	10.7%	13.7%
Slipper lobster	20%	9.5%	12.0%
Swimming crab	10%	0.7%	2.9%
Spiny lobster**		9.1%	4.5%
Bigeye**		3.9%	2.7%
Sergeant**		3.4%	3.3%
Pennantfish**		3.2%	0.9%
Tang/surgeonfish**		2.8%	1.9%
Scorpionfish**		2.8%	2.4%
Pink snapper**		2.2%	1.7%
Pebble crab**		2.2%	3.0%
Others**		19.8%	16.5%
Total**		49.4%	36.9%

APPENDIX 4.2 *continued*

B) Assessment of snapper and goatfish groupings. Summary of the simulation results examining three mixtures of species/groups (i.e. pseudo signatures), but combining all four species of snappers (*E. carbunculus* , *L. kasmira* , *P. filamentosus* , and *P. zonatus*) into a single group and both groups of goatfishes (*Mulloidichthys* spp and *Parupeneus* spp) into a single group. Two FA subsets (D and ED, Table 4.2) were used;1000 iterations were computed for each trial. Percentages represent the average proportion that each species/group were specified in the pseudo signatures, and in the average estimated pseudo signature (i.e. in the simulation results). Misidentified species/groups that appeared at ≥ 2.0% in an estimated pseudo signature are also listed (**); the remaining misidentifications are combined under the 'others' category. ‘Total’ represents the total proportions of misclassified individuals in the estimated pseudo signature.

Trial 6. Pseudo signature, 4 groups: Angelfish, Snapper, Goatfish, and Moray eel.

	Specified	D	ED
Angelfish	15%	10.8%	12.4%
Snapper	35%	12.0%	12.8%
Goatfish	35%	6.1%	9.4%
Moray eel	15%	14.7%	13.8%
Sandperch**		7.8%	5.0%
Bigeye**		6.8%	4.2%
Knife/razorfish**		3.9%	3.0%
Gurnard**		3.2%	4.6%
Squirrelfish**		3.1%	2.7%
Triggerfish S**		2.8%	2.5%
Conger eel**		2.8%	3.3%
Tilefish**		2.5%	2.0%
Toby**		2.2%	2.1%
Others**		20.5%	22.0%
Total**		55.6%	51.4%

Trial 7. Pseudo signature, 2 groups: Snapper and Moray eel.

	Specified	D	ED
Snapper	90%	65.9%	65.6%
Moray eel	10%	8.5%	8.1%
Duckbill**		5.5%	5.9%
Lizard/snakefish**		4.4%	4.5%
Sandperch**		3.2%	1.7%
Beardfish**		3.1%	2.4%
Others**		9.1%	11.7%
Total**		25.3%	26.2%

Trial 8. Pseudo signature, 2 groups: Goatfish and Moray eel.

	Specified	D	ED
Goatfish	90%	53.9%	60.7%
Moray	10%	2.5%	3.3%
Tilefish**		9.0%	5.5%
Cardinalfish**		6.1%	2.3%
Triggerfish S**		3.9%	3.4%
Gurnard**		3.6%	4.4%
Scorpionfish**		2.7%	3.3%
Squirrelfish**		2.3%	3.0%
Bigeye**		2.3%	1.6%
Others**		13.6%	12.2%
Total**		43.5%	35.7%

APPENDIX 4.2 *continued*

C) Evaluation of FA subsets. Summary of the simulation results examining the two mixtures of species/groups (i.e. pseudo signatures) from Trials 1 and 3 (see A above), but comparing results of the original two FA subsets (D, n = 31 FAs, and ED, n = 39 FAs) with two additional FA subsets (M1, n = 33FAs, and M2, n = 34 FAs, Table 4.2);1000 iterations were computed for each trial. Percentages represent the average proportion that each species/group were specified in the pseudo signatures, and in the average estimated pseudo signature (i.e. in the simulation results). Misidentified species/groups that appeared at ≥ 2.0% in an estimated pseudo signature are also listed (**); the remaining misidentifications are combined under the 'others' category. 'Total' represents the total proportions of misclassified individuals in the estimated pseudo signature. Boxes represent the trials with the lowest proportion of misclassifications.

Trial 9. Pseudo signature (from original Trial 1), 4 groups: Spiny lobster, Pink snapper, Wrasse/hogfish/coris and Moray eel.

	Specified	**D**	**ED**	**M1**	**M2**
Spiny lobster	15%	12.6%	10.8%	11.7%	10.7%
Pink snapper	15%	6.7%	5.3%	5.9%	5.2%
Moray eel	35%	33.8%	32%	33.2%	32.0%
Wrasse/ hogfish/coris	35%	22.6%	26.7%	25.6%	26.4%
Scorpionsfish **		6.9%	6.9%	6.0%	7.4%
Toby**		2.6%	2.0%	1.8%	2.0%
Tilefish**		2.2%	2.3%	1.9%	2.0%
Others**		12.6%	14.3%	13.7%	14.6%
Total**		24.3%	25.5%	23.4%	26.0%

Trial 10. Pseudo signature (from original Trial 3), 6 groups: Parrotfish, Scorpionfish, Spiny lobster, Squirrelfish snapper, Triggerfish M and Octopus.

	Specified	**D**	**ED**	**M1**	**M2**
Parrotfish	20%	18.4%	17.7%	17.3%	17.5%
Scorpionfish	15%	10.7%	8.8%	8.4%	8.3%
Spiny lobster	15%	13.4%	12%	12.2%	12.2%
Squirrelfish snapper	15%	3.8%	4.2%	4.5%	3.4%
Triggerfish M	30%	26.6%	29%	30.3%	29.6%
Octopus	5%	3.4%	3.5%	3.3%	3.3%
Swimming crab**		2.8%	3.9%	3.7%	3.4%
Lizard/ snakefish**		2.8%	3.0%	3.3%	3.0%
Duckbill**		2.7%	3.4%	2.8%	4.0%
Moray**		2.3%	1.7%	1.8%	1.8%
Beardfish**		2.1%	1.7%	2.0%	1.6%
Others**		11.3%	10.8%	10.2%	11.8%
Total**		24.0%	24.5%	23.8%	25.6%

APPENDIX 4.2 *continued*

D) Effect of sequential removal of misidentified groups. Summary of the simulation results examining the two mixtures of species/groups (i.e. pseudo signatures) from Trials 9 and 10 (see C above), using the best-performing two FA subsets (D and M1) and sequentially removing groups in subsequent simulations;1000 iterations were computed for each trial. Percentages represent the average proportion that each species/group were specified in the pseudo signatures, and in the average estimated pseudo signature (i.e. in the simulation results). Misidentified species/groups that appeared at ≥ 2.0% in an estimated pseudo signature are also listed (**): these groups were then sequentially removed to examine the impact on simulation results. The remaining groups are combined under the 'others' category. 'Total' represents the total proportions of misclassified individuals in the estimated pseudo signature.

Trial 11. Pseudo signature (from original Trial 1), 4 groups: Spiny lobster, Pink snapper, Wrasse/hogfish/coris and Moray eel.

		Original		Scorpionfish removed		Scorpionfish and toby removed		Scorpionfish, toby, tilefish removed	
		n = 47		n = 46		n = 45		n = 44	
	Specified	**D**	**M1**	**D**	**M1**	**D**	**M1**	**D**	**M1**
Spiny lobster	15%	12.6%	11.7%	14.4%	13.5%	14.5%	13.9%	14.6%	13.9%
Pink snapper	15%	6.7%	5.9%	8.0%	6.9%	8.2%	7.4%	7.3%	6.6%
Moray eel	35%	33.8%	33.2%	35.8%	35.2%	36.4%	36.1%	38.0%	37.8%
Wrasse/hogfish/coris	35%	22.6%	25.6%	22.9%	25.3%	23.2%	24.3%	24.4%	25.3%
Scorpionfish		6.9%	6.0%						
Toby		2.6%	1.8%	2.0%	1.6%				
Tilefish		2.2%	1.9%	2.3%	2.3%	3.0%	3.1%		
Others		12.6%	13.7%	12.7%	15.3%	14.8%	15.3%	15.9%	16.3%
Total		24.3%	23.4%	19.0%	19.2%	17.8%	18.4%	15.9%	16.3%

APPENDIX 4.2 *end*

Trial 12. Pseudo signature (from original Trial 3), 6 groups: Parrotfish, Scorpionfish, Spiny lobster, Squirrelfish snapper, Triggerfish M and Octopus.

		Original		Swimming crab removed		Swimming crab and lizard/snakefish removed		Swimming crab, lizard/snakefish, and duckbill removed		Swimming crab, lizard/snakefish, duckbill, and moray removed		Swimming crab, lizard/snakefish, duckbill, moray, and beardfish removed	
		n = 47		n = 46		n = 45		n = 44		n = 43		n = 42	
	Specified	**D**	**M1**	**D**	**M1**	**D**	**M1**	**D**	**M1**	**D**	**M1**	**D**	**M1**
Parrotfish	20%	18.4%	17.3%	18.7%	17.6%	18.9%	17.9%	18.7%	17.5%	18.6%	17.4%	18.4%	17.3%
Scorpionfish	15%	10.7%	8.4%	10.5%	8.7%	12.0%	10.7%	12.4%	11.3%	13.9%	12.4%	13.6%	12.2%
Spiny lobster	15%	13.4%	12.2%	14.7%	14.0%	14.2%	13.2%	14.6%	13.8%	13.9%	13.3%	14.4%	13.7%
Squirrelfish snapper	15%	3.8%	4.5%	4.5%	4.7%	4.7%	4.9%	6.2%	7.0%	6.6%	7.3%	7.9%	8.2%
Triggerfish M	30%	26.6%	30.3%	27.1%	30.6%	26.7%	30.5%	27.0%	30.9%	26.9%	30.7%	27.1%	30.8%
Octopus	5%	3.4%	3.3%	3.5%	3.8%	3.8%	4.4%	3.7%	4.2%	3.8%	4.3%	3.9%	4.3%
Swimming crab		2.8%	3.7%	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Lizard/snakefish		2.8%	3.3%	2.9%	3.5%	▨	▨	▨	▨	▨	▨	▨	▨
Duckbill		2.7%	2.8%	2.2%	2.7%	2.5%	3.2%	▨	▨	▨	▨	▨	▨
Moray eel		2.3%	1.8%	2.1%	1.7%	1.9%	1.4%	1.9%	1.3%	▨	▨	▨	▨
Beardfish		2.1%	2.0%	2.2%	2.0%	2.0%	1.7%	2.2%	1.8%	2.0%	1.7%	▨	▨
Others		11.3%	10.2%	11.8%	10.5%	12.9%	12.1%	13.3%	12.2%	14.1%	13.0%	15.1%	13.3%
Total		24.0%	23.8%	21.2%	20.4%	19.3%	18.4%	17.4%	15.3%	16.1%	14.7%	15.1%	13.3%

APPENDIX 5.1 Fat content and fatty acid (FA) composition (mass %) of the 25 carnivorous species of NWHI and MHI fish analyzed (n = 564). Values are means ± SEM of 39 FAs (out of 74) which were the most abundant and/or exhibited the greatest variance across all species.

Species name	*Antigonia eos*	*Ariosoma marginatum*	*Bembrops filifera*	*Bothus mancus*	*Bothus pantherinus*	*Bothus thompsoni*
Common name	(Boarfish)	(Large-eye conger)	(Duckbill)	(Flowery flounder)	(Panther flounder)	(Thompson's flounder)
	n=10	n=26	n=19	n=16	n=75	n=25
Length (cm)	6.65 ± 0.39	18.68 ± 1.40	17.37 ± 5.39	12.69 ± 2.89	5.48 ± 0.84	9.10 ± 2.38
Mass (g)	9.82 ± 1.24	23.15 ± 5.53	40.04 ± 27.98	44.7 ± 24.66	3.45 ± 1.58	9.33 ± 6.17
Lipid content (%)	2.37 ± 0.81	1.65 ± 0.47	1.83 ± 1.40	1.07 ± 0.26	2.11 ± 0.76	2.02 ± 0.95
Saturated FA						
14:0 *●	4.70 ± 0.87	2.68 ± 1.03	1.83 ± 0.77	1.38 ± 0.47	3.58 ± 1.22	5.53 ± 2.48
16:0 *●	20.36 ± 1.01	20.44 ± 1.45	17.89 ± 1.04	18.50 ± 1.51	20.46 ± 1.74	19.57 ± 2.24
17:0 *	1.21 ± 0.15	1.46 ± 0.34	0.83 ± 0.17	1.32 ± 0.42	1.36 ± 0.19	1.25 ± 0.18
18:0 *●	6.78 ± 0.40	8.66 ± 1.39	5.49 ± 0.97	10.12 ± 1.22	7.80 ± 1.23	7.45 ± 1.12
subtotal:	33.05 ± 1.53	33.25 ± 1.77	26.03 ± 0.89	31.33 ± 1.43	33.20 ± 2.41	33.80 ± 3.80
Monounsaturated FA						
16:1n-7 *●	5.03 ± 0.60	3.36 ± 1.03	4.74 ± 1.85	1.99 ± 0.52	3.47 ± 0.61	3.66 ± 0.85
18:1n-9 *●	8.91 ± 1.16	9.71 ± 1.58	14.52 ± 3.03	9.62 ± 1.29	9.71 ± 2.03	9.62 ± 2.27
18:1n-7 *●	2.49 ± 0.14	3.19 ± 0.64	2.95 ± 0.82	2.34 ± 0.51	2.17 ± 0.24	2.38 ± 0.35
20:1n-11	0.20 ± 0.06	0.26 ± 0.21	0.27 ± 0.08	0.14 ± 0.08	0.20 ± 0.06	0.18 ± 0.07
20:1n-9 *	0.79 ± 0.22	0.42 ± 0.12	1.26 ± 0.25	0.52 ± 0.13	0.60 ± 0.11	0.69 ± 0.22
20:1n-7	0.18 ± 0.03	0.31 ± 0.11	0.21 ± 0.07	0.19 ± 0.04	0.27 ± 0.08	0.47 ± 0.16
22:1n-11	0.31 ± 0.09	0.14 ± 0.07	0.10 ± 0.03	0.09 ± 0.08	0.20 ± 0.11	0.34 ± 0.16
22:1n-9	0.18 ± 0.04	0.09 ± 0.03	0.17 ± 0.05	0.08 ± 0.03	0.11 ± 0.04	0.16 ± 0.03
22:1n-7	0.09 ± 0.01	0.08 ± 0.03	0.08 ± 0.05	0.15 ± 0.04	0.14 ± 0.04	0.22 ± 0.09
subtotal:	18.17 ± 1.76	17.56 ± 2.77	24.30 ± 5.41	15.11 ± 1.30	16.87 ± 1.94	17.72 ± 1.83
Polyunsaturated FA						
16:2n-6	0.04 ± 0.01	0.05 ± 0.05	0.01 ± 0.01	0.05 ± 0.05	0.08 ± 0.04	0.03 ± 0.01
16:2n-4	0.30 ± 0.03	0.65 ± 0.21	0.71 ± 0.29	0.34 ± 0.27	0.78 ± 0.11	0.63 ± 0.10
16:3n-6	0.59 ± 0.10	0.11 ± 0.04	0.07 ± 0.04	0.04 ± 0.01	0.23 ± 0.09	0.21 ± 0.08
16:3n-4	0.05 ± 0.05	0.04 ± 0.03	0.03 ± 0.01	0.04 ± 0.02	0.05 ± 0.02	0.02 ± 0.03
16:4n-1	0.11 ± 0.06	0.01 ± 0.02	0.24 ± 0.09	0.01 ± 0.02	0.00 ± 0.00	0.01 ± 0.05
18:2n-6 *	1.46 ± 0.11	1.32 ± 0.19	0.92 ± 0.18	0.99 ± 0.15	1.18 ± 0.08	1.22 ± 0.07
18:2n-4	0.16 ± 0.02	0.16 ± 0.05	0.08 ± 0.02	0.07 ± 0.02	0.19 ± 0.04	0.19 ± 0.06
18:3n-6	0.36 ± 0.02	0.34 ± 0.08	0.28 ± 0.06	0.41 ± 0.11	0.41 ± 0.05	0.17 ± 0.15
18:3n-4	0.06 ± 0.02	0.11 ± 0.04	0.09 ± 0.03	0.08 ± 0.03	0.12 ± 0.04	0.07 ± 0.02
18:3n-3	1.01 ± 0.15	0.27 ± 0.11	0.25 ± 0.06	0.18 ± 0.09	0.36 ± 0.15	0.35 ± 0.13
18:3n-1	0.17 ± 0.03	0.20 ± 0.06	0.33 ± 0.09	0.08 ± 0.07	0.20 ± 0.02	0.24 ± 0.04
18:4n-3	0.94 ± 0.14	0.14 ± 0.08	0.07 ± 0.04	0.11 ± 0.07	0.47 ± 0.24	0.50 ± 0.21
18:4n-1	0.00 ± 0.00	0.00 ± 0.01	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01
20:2n-6	0.37 ± 0.04	0.45 ± 0.12	0.34 ± 0.05	0.55 ± 0.16	0.44 ± 0.06	0.46 ± 0.06
20:3n-6	0.20 ± 0.02	0.30 ± 0.07	0.15 ± 0.05	0.33 ± 0.10	0.17 ± 0.04	0.19 ± 0.02
20:4n-6 *●	1.77 ± 0.35	5.45 ± 1.40	3.88 ± 0.98	10.43 ± 2.51	3.33 ± 0.66	3.55 ± 1.49
20:3n-3	0.23 ± 0.04	0.12 ± 0.04	0.09 ± 0.02	0.16 ± 0.06	0.17 ± 0.03	0.17 ± 0.05
20:4n-3	0.90 ± 0.11	0.51 ± 0.19	0.31 ± 0.11	0.23 ± 0.09	0.50 ± 0.09	0.53 ± 0.15
20:5n-3 *●	4.76 ± 0.34	6.45 ± 1.25	4.53 ± 1.61	4.71 ± 1.17	5.08 ± 0.89	5.38 ± 0.93
22:2n-6	0.03 ± 0.00	0.00 ± 0.00	0.02 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
21:5n-3	0.11 ± 0.01	0.12 ± 0.05	0.07 ± 0.05	0.09 ± 0.02	0.15 ± 0.03	0.11 ± 0.04
22:4n-6 *	0.59 ± 0.10	1.01 ± 0.61	0.64 ± 0.13	2.16 ± 0.59	0.68 ± 0.20	0.64 ± 0.31
22:5n-6 *	1.81 ± 0.28	1.56 ± 0.31	2.42 ± 0.33	2.04 ± 0.67	1.74 ± 0.20	1.67 ± 0.31
22:4n-3	0.16 ± 0.03	0.09 ± 0.04	0.04 ± 0.01	0.09 ± 0.03	0.10 ± 0.02	0.10 ± 0.03
22:5n-3 *●	3.40 ± 0.40	2.03 ± 0.62	2.62 ± 0.35	4.25 ± 0.86	2.69 ± 0.67	2.30 ± 0.31
22:6n-3 *●	22.04 ± 3.36	21.28 ± 4.38	24.92 ± 4.00	20.09 ± 3.40	24.28 ± 2.24	20.99 ± 2.53
subtotal:	41.62 ± 3.43	42.79 ± 3.16	43.12 ± 5.80	47.54 ± 2.25	43.40 ± 2.09	39.73 ± 2.67
Total	92.84 ± 0.51	93.59 ± 1.49	93.45 ± 1.14	93.98 ± 1.15	93.47 ± 0.53	91.25 ± 3.02

* : indicates the 15 FAs used in the sand-dwelling DFA

● : indicates the 10 FAs used in the paired foraging equivalents DFA

APPENDIX 5.1 *continued*

Species name	*Callionymus decoratus*	*Cymolutes lecluse*	*Dactyoptena orientalis*	*Dascyllus albisella*	*Gymnothorax eurostus*	*Gymnothorax steindachneri*
Common name	(Longtail dragonet)	(Hawaiian knifefish)	(Helmut gurnard)	(Hawaiian dascyllus)	(Stout moray)	(Steindachner's moray)
	n=20	n=23	n=24	n=20	n=14	n=25
Length (cm)	11.39 ± 3.25	8.53 ± 3.53	8.25 ± 1.28	9.53 ± 1.58	41.32 ± 8.79	49.93 ± 10.60
Mass (g)	5.06 ± 2.60	13.08 ± 15.49	14.40 ± 4.47	31.90 ± 10.44	189.95 ± 126.07	327.81 ± 185.86
Lipid content (%)	1.19 ± 0.16	2.14 ± 0.85	1.90 ± 0.71	3.29 ± 2.55	1.42 ± 0.81	0.85 ± 0.37
Saturated FA						
14:0 *●	2.50 ± 1.27	3.30 ± 1.12	4.65 ± 1.47	3.22 ± 1.23	2.25 ± 1.03	1.59 ± 0.59
16:0 *●	18.88 ± 1.62	19.29 ± 1.89	22.44 ± 2.23	28.65 ± 5.26	19.99 ± 2.35	18.34 ± 1.16
17:0 *	1.59 ± 0.38	1.72 ± 0.27	1.63 ± 0.15	1.14 ± 0.27	0.97 ± 0.25	0.94 ± 0.20
18:0 *●	11.40 ± 2.24	9.29 ± 1.19	8.98 ± 1.46	9.20 ± 1.05	9.93 ± 1.19	10.70 ± 0.82
subtotal:	34.38 ± 3.94	33.60 ± 2.43	37.69 ± 2.32	42.21 ± 5.27	33.14 ± 2.60	31.57 ± 1.85
Monounsaturated FA						
16:1n-7 *●	2.70 ± 0.58	4.03 ± 1.31	5.05 ± 1.52	4.51 ± 1.76	2.91 ± 1.16	1.71 ± 0.64
18:1n-9 *●	6.18 ± 0.83	9.26 ± 0.77	7.29 ± 1.04	7.40 ± 1.01	10.27 ± 1.48	9.22 ± 0.85
18:1n-7 *●	2.89 ± 0.40	3.63 ± 0.93	2.97 ± 0.38	2.95 ± 1.36	3.09 ± 0.55	2.50 ± 0.43
20:1n-11	0.48 ± 0.16	0.49 ± 0.30	0.11 ± 0.06	0.19 ± 0.19	0.21 ± 0.11	0.23 ± 0.21
20:1n-9 *	0.37 ± 0.08	0.55 ± 0.14	1.03 ± 0.39	0.97 ± 0.27	0.73 ± 0.27	0.81 ± 0.21
20:1n-7	0.28 ± 0.09	0.30 ± 0.15	0.22 ± 0.03	0.16 ± 0.08	0.18 ± 0.10	0.11 ± 0.06
22:1n-11	0.25 ± 0.07	0.14 ± 0.05	0.10 ± 0.14	0.19 ± 0.29	0.37 ± 0.29	0.16 ± 0.20
22:1n-9	0.07 ± 0.03	0.10 ± 0.05	0.23 ± 0.06	0.13 ± 0.04	0.16 ± 0.13	0.16 ± 0.08
22:1n-7	0.22 ± 0.04	0.13 ± 0.04	0.14 ± 0.06	0.10 ± 0.06	0.09 ± 0.03	0.05 ± 0.04
subtotal:	13.43 ± 1.34	18.62 ± 2.20	17.14 ± 1.76	16.60 ± 3.83	18.00 ± 2.23	14.95 ± 2.03
Polyunsaturated FA						
16:2n-6	0.17 ± 0.09	0.10 ± 0.06	0.05 ± 0.02	0.05 ± 0.03	0.06 ± 0.05	0.01 ± 0.01
16:2n-4	0.69 ± 0.17	0.23 ± 0.07	0.20 ± 0.06	0.38 ± 0.10	0.23 ± 0.09	0.29 ± 0.08
16:3n-6	0.10 ± 0.03	0.17 ± 0.10	0.53 ± 0.23	0.23 ± 0.23	0.13 ± 0.07	0.06 ± 0.06
16:3n-4	0.15 ± 0.06	0.14 ± 0.10	0.03 ± 0.01	0.06 ± 0.03	0.20 ± 0.14	0.04 ± 0.04
16:4n-1	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.02 ± 0.02	0.15 ± 0.12	0.13 ± 0.08
18:2n-6 *	1.05 ± 0.19	1.21 ± 0.20	1.24 ± 0.23	1.35 ± 0.17	1.06 ± 0.24	0.66 ± 0.19
18:2n-4	0.11 ± 0.05	0.10 ± 0.03	0.24 ± 0.07	0.09 ± 0.06	0.08 ± 0.02	0.08 ± 0.03
18:3n-6	0.65 ± 0.12	0.46 ± 0.07	0.39 ± 0.04	1.07 ± 0.87	0.48 ± 0.15	0.23 ± 0.17
18:3n-4	0.07 ± 0.03	0.15 ± 0.06	0.06 ± 0.01	0.05 ± 0.02	0.10 ± 0.04	0.03 ± 0.03
18:3n-3	0.25 ± 0.09	0.56 ± 0.46	0.46 ± 0.17	0.56 ± 0.33	0.27 ± 0.18	0.14 ± 0.08
18:3n-1	0.17 ± 0.06	0.07 ± 0.03	0.07 ± 0.03	0.10 ± 0.03	0.03 ± 0.02	0.07 ± 0.03
18:4n-3	0.26 ± 0.09	0.51 ± 0.24	0.49 ± 0.22	0.56 ± 0.32	0.26 ± 0.20	0.11 ± 0.14
18:4n-1	0.01 ± 0.04	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.01	0.01 ± 0.01
20:2n-6	0.46 ± 0.08	0.61 ± 0.19	0.55 ± 0.05	0.40 ± 0.06	0.51 ± 0.11	0.52 ± 0.09
20:3n-6	0.33 ± 0.05	0.42 ± 0.10	0.19 ± 0.01	0.62 ± 0.19	0.43 ± 0.12	0.22 ± 0.08
20:4n-6 *●	8.92 ± 1.57	6.37 ± 1.69	3.17 ± 1.04	5.01 ± 1.81	8.88 ± 1.75	9.76 ± 2.69
20:3n-3	0.07 ± 0.03	0.17 ± 0.08	0.21 ± 0.04	0.15 ± 0.05	0.12 ± 0.04	0.11 ± 0.03
20:4n-3	0.18 ± 0.05	0.34 ± 0.13	0.40 ± 0.13	0.50 ± 0.18	0.26 ± 0.12	0.18 ± 0.08
20:5n-3 *●	4.75 ± 0.63	8.05 ± 1.49	5.56 ± 0.69	4.25 ± 0.92	3.32 ± 1.73	2.96 ± 1.07
22:2n-6	0.02 ± 0.02	0.01 ± 0.01	0.06 ± 0.03	0.02 ± 0.03	0.01 ± 0.01	0.02 ± 0.03
21:5n-3	0.05 ± 0.03	0.16 ± 0.08	0.10 ± 0.02	0.13 ± 0.07	0.10 ± 0.08	0.08 ± 0.10
22:4n-6 *	2.38 ± 0.81	1.66 ± 0.34	0.55 ± 0.16	1.22 ± 0.26	3.02 ± 0.65	2.85 ± 0.83
22:5n-6 *	2.49 ± 0.38	1.35 ± 0.34	1.61 ± 0.30	1.26 ± 0.62	1.47 ± 0.24	1.67 ± 0.19
22:4n-3	0.05 ± 0.03	0.04 ± 0.02	0.07 ± 0.02	0.09 ± 0.19	0.06 ± 0.02	0.05 ± 0.04
22:5n-3 *●	2.68 ± 0.41	2.19 ± 0.43	2.03 ± 0.27	2.35 ± 0.55	3.03 ± 0.55	1.94 ± 0.42
22:6n-3 *●	19.94 ± 4.05	14.61 ± 3.96	21.39 ± 3.66	14.62 ± 5.95	17.35 ± 3.63	22.88 ± 3.04
subtotal:	46.01 ± 4.85	39.72 ± 2.96	39.66 ± 3.71	35.12 ± 7.33	41.63 ± 3.00	45.09 ± 2.49
Total	93.83 ± 0.86	91.94 ± 1.61	94.49 ± 0.27	93.93 ± 1.05	92.77 ± 1.12	91.61 ± 0.97

* : indicates the 15 FAs used in the sand-dwelling DFA

● : indicates the 10 FAs used in the paired foraging equivalents DFA

APPENDIX 5.1 *continued*

Species name	*Iniistius pavo*	*Iniistius umbrilatus*	*Malacanthus brevirostris*	*Meadia abyssalis*	*Mulloidichthys flavolineatus*	*Ophichthus kunaloa*
Common name	(Peacock razorfish)	(Blackside razorfish)	(Flagtail tilefish)	(Abyssal cutthroat eel)	(Yellow stripe goatfish)	(Snake eel)
	n=15	n=19	n=16	n=19	n=21	n=20
Length (cm)	11.02 ± 4.69	9.22 ± 3.28	11.71 ± 3.92	50.58 ± 9.98	22.18 ± 3.16	39.79 ± 2.50
Mass (g)	37.91 ± 45.21	37.91 ± 45.21	16.29 ± 17.52	134.70 ± 74.18	198.08 ± 96.99	33.96 ± 7.30
Lipid content (%)	1.81 ± 0.89	2.59 ± 0.93	1.55 ± 0.51	2.64 ± 0.97	1.86 ± 1.10	2.37 ± 0.80
Saturated FA						
14:0 *●	3.74 ± 2.32	5.22 ± 1.65	1.60 ± 1.15	2.69 ± 0.95	2.31 ± 0.87	3.08 ± 1.02
16:0 *●	19.24 ± 1.24	20.86 ± 1.93	18.34 ± 1.95	19.82 ± 1.21	19.36 ± 4.07	16.32 ± 0.68
17:0 *	1.46 ± 0.35	1.95 ± 0.28	1.59 ± 0.29	0.80 ± 0.10	2.60 ± 0.75	0.72 ± 0.11
18:0 *●	9.65 ± 0.94	8.47 ± 0.64	11.56 ± 0.80	4.47 ± 0.59	11.35 ± 1.77	5.33 ± 1.32
subtotal:	34.10 ± 2.51	36.50 ± 2.56	33.09 ± 3.44	27.78 ± 1.34	35.62 ± 4.04	25.45 ± 1.30
Monounsaturated FA						
16:1n-7 *●	2.86 ± 1.17	3.58 ± 0.54	1.84 ± 0.81	3.54 ± 1.02	3.09 ± 0.80	6.51 ± 1.90
18:1n-9 *●	9.47 ± 1.26	8.87 ± 1.43	6.97 ± 0.95	20.23 ± 3.52	5.99 ± 1.75	18.30 ± 3.11
18:1n-7 *●	2.98 ± 0.98	2.41 ± 0.28	2.82 ± 0.30	2.84 ± 0.26	3.47 ± 0.55	3.19 ± 0.35
20:1n-11	0.37 ± 0.28	0.45 ± 0.21	0.89 ± 0.48	0.43 ± 0.16	1.39 ± 0.66	0.40 ± 0.18
20:1n-9 *	0.58 ± 0.33	0.65 ± 0.28	0.48 ± 0.17	1.87 ± 0.63	0.61 ± 0.42	1.62 ± 0.37
20:1n-7	0.25 ± 0.15	0.23 ± 0.10	0.36 ± 0.16	0.17 ± 0.04	0.65 ± 0.33	0.30 ± 0.09
22:1n-11	0.10 ± 0.04	0.17 ± 0.06	0.33 ± 0.23	0.45 ± 0.27	0.36 ± 0.20	0.22 ± 0.10
22:1n-9	0.09 ± 0.05	0.13 ± 0.05	0.10 ± 0.05	0.33 ± 0.10	0.10 ± 0.06	0.26 ± 0.06
22:1n-7	0.09 ± 0.05	0.12 ± 0.04	0.15 ± 0.09	0.05 ± 0.02	0.23 ± 0.13	0.08 ± 0.03
subtotal:	16.81 ± 3.08	16.61 ± 1.74	13.94 ± 2.16	29.91 ± 4.72	15.89 ± 1.79	30.88 ± 4.58
Polyunsaturated FA						
16:2n-6	0.06 ± 0.05	0.08 ± 0.02	0.07 ± 0.06	0.02 ± 0.02	0.05 ± 0.04	0.03 ± 0.02
16:2n-4	0.44 ± 0.22	0.42 ± 0.11	0.41 ± 0.09	0.61 ± 0.08	0.27 ± 0.09	0.81 ± 0.11
16:3n-6	0.11 ± 0.06	0.20 ± 0.04	0.05 ± 0.04	0.10 ± 0.11	0.11 ± 0.06	0.17 ± 0.12
16:3n-4	0.06 ± 0.03	0.08 ± 0.03	0.04 ± 0.03	0.06 ± 0.12	0.13 ± 0.07	0.21 ± 0.16
16:4n-1	0.05 ± 0.05	0.02 ± 0.03	0.01 ± 0.03	0.24 ± 0.24	0.05 ± 0.04	0.38 ± 0.15
18:2n-6 *	1.07 ± 0.15	1.17 ± 0.13	1.11 ± 0.12	0.88 ± 0.09	1.29 ± 0.41	1.02 ± 0.26
18:2n-4	0.09 ± 0.05	0.12 ± 0.05	0.09 ± 0.04	0.10 ± 0.04	0.06 ± 0.02	0.11 ± 0.04
18:3n-6	0.35 ± 0.13	0.52 ± 0.09	0.36 ± 0.16	0.19 ± 0.03	0.67 ± 0.12	0.35 ± 0.09
18:3n-4	0.11 ± 0.03	0.18 ± 0.06	0.12 ± 0.04	0.14 ± 0.03	0.10 ± 0.05	0.16 ± 0.03
18:3n-3	0.41 ± 0.19	0.49 ± 0.14	0.25 ± 0.15	0.23 ± 0.07	0.51 ± 0.33	0.31 ± 0.16
18:3n-1	0.15 ± 0.11	0.15 ± 0.05	0.13 ± 0.03	0.23 ± 0.04	0.07 ± 0.02	0.37 ± 0.07
18:4n-3	0.39 ± 0.25	0.51 ± 0.10	0.12 ± 0.07	0.23 ± 0.31	0.45 ± 0.59	0.43 ± 0.36
18:4n-1	0.00 ± 0.00	0.00 ± 0.01	0.00 ± 0.00	0.02 ± 0.04	0.00 ± 0.00	0.03 ± 0.04
20:2n-6	0.63 ± 0.17	0.71 ± 0.19	0.65 ± 0.10	0.37 ± 0.05	0.66 ± 0.18	0.39 ± 0.07
20:3n-6	0.22 ± 0.05	0.23 ± 0.03	0.42 ± 0.06	0.14 ± 0.03	0.50 ± 0.28	0.17 ± 0.04
20:4n-6 *●	5.55 ± 1.40	4.89 ± 1.27	10.36 ± 3.31	3.32 ± 1.12	8.70 ± 1.59	3.95 ± 1.69
20:3n-3	0.18 ± 0.08	0.19 ± 0.09	0.14 ± 0.04	0.18 ± 0.07	0.14 ± 0.05	0.23 ± 0.10
20:4n-3	0.29 ± 0.09	0.31 ± 0.10	0.26 ± 0.08	0.47 ± 0.10	0.32 ± 0.39	0.42 ± 0.18
20:5n-3 *●	7.19 ± 2.25	7.36 ± 1.13	4.56 ± 0.51	5.01 ± 1.96	6.13 ± 1.32	5.40 ± 1.74
22:2n-6	0.00 ± 0.01	0.02 ± 0.02	0.01 ± 0.03	0.02 ± 0.01	0.02 ± 0.01	0.04 ± 0.01
21:5n-3	0.12 ± 0.04	0.14 ± 0.03	0.14 ± 0.10	0.09 ± 0.12	0.18 ± 0.10	0.05 ± 0.02
22:4n-6 *	0.90 ± 0.30	0.89 ± 0.32	4.50 ± 1.39	0.34 ± 0.10	3.13 ± 0.77	0.46 ± 0.23
22:5n-6 *	1.73 ± 0.53	1.48 ± 0.21	2.11 ± 0.52	1.06 ± 0.22	1.71 ± 0.64	1.32 ± 0.32
22:4n-3	0.03 ± 0.03	0.04 ± 0.02	0.08 ± 0.03	0.03 ± 0.01	0.05 ± 0.04	0.04 ± 0.02
22:5n-3 *●	1.51 ± 0.34	1.39 ± 0.26	3.76 ± 0.50	1.53 ± 0.22	2.73 ± 0.43	1.97 ± 0.37
22:6n-3 *●	20.64 ± 6.98	17.94 ± 3.18	16.58 ± 3.84	20.90 ± 4.00	11.25 ± 4.48	17.70 ± 2.48
subtotal:	42.27 ± 5.64	39.52 ± 3.29	46.34 ± 5.78	36.54 ± 5.24	39.28 ± 4.81	36.53 ± 4.16
Total	93.17 ± 0.87	92.63 ± 0.84	93.37 ± 1.12	94.23 ± 0.49	90.79 ± 2.05	92.86 ± 0.62

* : indicates the 15 FAs used in the sand-dwelling DFA

● : indicates the 10 FAs used in the paired foraging equivalents DFA

APPENDIX 5.1 *end*

Species name	*Ophidion muraenolepis*	*Parapercis schauinslandii*	*Polymixia berndti*	*Synodus lobeli*	*Synodus variegatus*	*Torquigener florealis*	*Trachinocephalus myops*
Common name	(Black edged cusk eel)	(Redspotted sandperch)	(Berndt's beard fish)	(Lobel's lizardfish)	(Reef lizardfish)	(Floral puffer)	(Snakefish)
	n=20	n=18	n=20	n=20	n=19	n=20	n=20
Length (cm)	13.54 ± 2.61	6.78 ± 2.05	15.61 ± 4.66	8.54 ± 1.64	12.18 ± 6.54	9.77 ± 6.80	13.07 ± 6.15
Mass (g)	19.74 ± 13.82	7.61 ± 6.71	121.13 ± 91.00	6.82 ± 4.62	39.34 ± 61.38	48.58 ± 63.50	45.17 ± 55.58
Lipid content (%)	1.74 ± 0.71	1.94 ± 0.79	2.00 ± 0.90	1.26 ± 0.48	0.95 ± 0.65	2.23 ± 1.45	0.93 ± 0.27
Saturated FA							
14:0 *●	3.52 ± 1.40	4.18 ± 1.15	3.00 ± 1.15	1.92 ± 1.49	2.23 ± 0.77	1.62 ± 0.37	1.78 ± 0.58
16:0 *●	18.34 ± 2.24	20.81 ± 1.39	20.70 ± 1.41	19.70 ±	20.88 ± 1.47	16.86 ± 2.42	19.61 ± 1.24
17:0 *	1.37 ± 0.19	1.46 ± 0.12	0.77 ± 0.16	1.44 ± 0.27	1.20 ± 0.19	1.45 ± 0.22	1.28 ± 0.28
18:0 *●	8.01 ± 1.05	9.33 ± 1.29	6.16 ± 0.87	9.94 ± 0.66	9.29 ± 0.74	12.06 ± 1.87	8.59 ± 0.64
subtotal:	31.24 ± 2.81	35.78 ± 1.66	30.63 ± 1.56	33.00 ± 1.71	33.59 ± 1.67	31.98 ± 1.38	31.26 ± 1.47
Monounsaturated FA							
16:1n-7 *●	3.01 ± 0.76	3.74 ± 0.84	3.09 ± 0.56	2.17 ± 0.97	2.15 ± 0.62	2.73 ± 1.22	2.13 ± 0.47
18:1n-9 *●	9.49 ± 1.51	8.32 ± 1.06	17.48 ± 4.02	7.71 ± 0.65	7.75 ± 0.87	9.12 ± 2.57	8.48 ± 1.24
18:1n-7 *●	2.47 ± 0.52	2.63 ± 0.27	2.49 ± 0.58	2.59 ± 0.35	2.51 ± 0.31	2.86 ± 0.52	2.42 ± 0.40
20:1n-11	0.13 ± 0.05	0.18 ± 0.04	0.51 ± 1.16	0.17 ± 0.13	0.10 ± 0.08	0.77 ± 0.34	0.11 ± 0.09
20:1n-9 *	0.68 ± 0.10	0.76 ± 0.17	2.16 ± 1.07	0.45 ± 0.20	0.40 ± 0.13	0.94 ± 0.47	0.39 ± 0.10
20:1n-7	0.19 ± 0.07	0.23 ± 0.06	0.17 ± 0.06	0.22 ± 0.23	0.14 ± 0.05	0.37 ± 0.21	0.15 ± 0.06
22:1n-11	0.33 ± 0.42	0.25 ± 0.09	0.66 ± 1.61	0.28 ± 0.27	0.12 ± 0.24	0.34 ± 0.18	0.10 ± 0.14
22:1n-9	0.20 ± 0.10	0.16 ± 0.03	0.35 ± 0.18	0.16 ± 0.11	0.08 ± 0.04	0.18 ± 0.07	0.07 ± 0.03
22:1n-7	0.16 ± 0.14	0.17 ± 0.05	0.08 ± 0.04	0.11 ± 0.07	0.07 ± 0.03	0.15 ± 0.06	0.07 ± 0.03
subtotal:	16.67 ± 1.29	16.45 ± 1.76	26.99 ± 7.00	13.87 ± 1.60	13.33 ± 1.24	17.46 ± 4.12	13.92 ± 1.58
Polyunsaturated FA							
16:2n-6	0.05 ± 0.03	0.05 ± 0.03	0.03 ± 0.02	0.02 ± 0.01	0.04 ± 0.02	0.06 ± 0.04	0.04 ± 0.03
16:2n-4	0.83 ± 0.25	0.56 ± 0.09	0.78 ± 0.19	0.66 ± 0.15	0.79 ± 0.23	0.50 ± 0.15	0.97 ± 0.30
16:3n-6	0.18 ± 0.09	0.29 ± 0.08	0.09 ± 0.09	0.09 ± 0.07	0.12 ± 0.06	0.11 ± 0.11	0.08 ± 0.05
16:3n-4	0.04 ± 0.03	0.05 ± 0.02	0.07 ± 0.10	0.03 ± 0.02	0.06 ± 0.04	0.09 ± 0.05	0.03 ± 0.02
16:4n-1	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.05	0.07 ± 0.04	0.03 ± 0.03	0.02 ± 0.04
18:2n-6 *	1.18 ± 0.20	1.28 ± 0.11	0.65 ± 0.17	1.08 ± 0.11	1.32 ± 0.10	0.96 ± 0.26	1.11 ± 0.15
18:2n-4	0.17 ± 0.08	0.17 ± 0.04	0.09 ± 0.04	0.11 ± 0.04	0.11 ± 0.05	0.13 ± 0.06	0.11 ± 0.04
18:3n-6	0.37 ± 0.11	0.52 ± 0.09	0.25 ± 0.06	0.44 ± 0.07	0.40 ± 0.12	0.63 ± 0.15	0.37 ± 0.12
18:3n-4	0.07 ± 0.03	0.07 ± 0.01	0.11 ± 0.04	0.06 ± 0.04	0.10 ± 0.02	0.09 ± 0.04	0.07 ± 0.03
18:3n-3	0.36 ± 0.12	0.38 ± 0.09	0.17 ± 0.10	0.23 ± 0.08	0.31 ± 0.11	0.28 ± 0.27	0.23 ± 0.08
18:3n-1	0.17 ± 0.05	0.13 ± 0.03	0.18 ± 0.04	0.27 ± 0.05	0.28 ± 0.12	0.16 ± 0.07	0.29 ± 0.09
18:4n-3	0.30 ± 0.14	0.44 ± 0.13	0.20 ± 0.29	0.24 ± 0.12	0.32 ± 0.17	0.20 ± 0.23	0.19 ± 0.10
18:4n-1	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.01	0.01 ± 0.02	0.01 ± 0.01	0.00 ± 0.01	0.00 ± 0.00
20:2n-6	0.42 ± 0.07	0.39 ± 0.05	0.28 ± 0.06	0.47 ± 0.11	0.39 ± 0.09	0.62 ± 0.12	0.33 ± 0.07
20:3n-6	0.26 ± 0.05	0.23 ± 0.04	0.11 ± 0.02	0.26 ± 0.05	0.26 ± 0.23	0.21 ± 0.03	0.21 ± 0.08
20:4n-6 *●	3.92 ± 1.79	3.16 ± 0.73	3.28 ± 0.92	5.49 ± 1.89	5.39 ± 1.87	8.14 ± 2.74	5.52 ± 2.16
20:3n-3	0.13 ± 0.05	0.11 ± 0.02	0.16 ± 0.08	0.14 ± 0.07	0.20 ± 0.08	0.19 ± 0.07	0.10 ± 0.04
20:4n-3	0.67 ± 0.32	0.60 ± 0.14	0.31 ± 0.10	0.30 ± 0.18	0.34 ± 0.08	0.24 ± 0.14	0.29 ± 0.09
20:5n-3 *●	6.80 ± 1.22	4.50 ± 0.55	4.88 ± 1.41	4.04 ± 0.54	4.43 ± 0.89	3.97 ± 0.65	4.11 ± 0.74
22:2n-6	0.02 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.00 ± 0.01	0.03 ± 0.02	0.05 ± 0.02	0.01 ± 0.02
21:5n-3	0.11 ± 0.03	0.09 ± 0.02	0.09 ± 0.05	0.14 ± 0.06	0.14 ± 0.06	0.07 ± 0.04	0.11 ± 0.03
22:4n-6 *	1.20 ± 0.62	0.68 ± 0.16	0.45 ± 0.12	0.74 ± 0.20	0.96 ± 0.56	1.95 ± 0.73	0.92 ± 0.75
22:5n-6 *	1.82 ± 0.41	2.20 ± 0.50	1.44 ± 0.36	2.27 ± 0.35	2.62 ± 0.45	2.94 ± 1.14	2.45 ± 0.35
22:4n-3	0.09 ± 0.03	0.08 ± 0.02	0.05 ± 0.01	0.03 ± 0.03	0.04 ± 0.02	0.09 ± 0.03	0.06 ± 0.03
22:5n-3 *●	2.26 ± 0.36	1.74 ± 0.20	1.68 ± 0.22	1.95 ± 0.26	1.94 ± 0.58	3.76 ± 0.48	1.75 ± 0.51
22:6n-3 *●	24.97 ± 3.58	23.60 ± 2.86	22.72 ± 5.04	28.24 ±	26.28 ± 4.32	17.90 ± 3.11	29.30 ± 4.01
subtotal:	46.37 ± 2.79	41.35 ± 3.43	38.08 ± 6.40	47.36 ± 3.41	46.96 ± 2.16	43.35 ± 4.73	48.68 ± 2.52
Total	94.28 ± 0.38	93.58 ± 0.50	95.70 ± 0.60	94.22 ±	93.88 ± 0.72	92.80 ± 1.00	93.86 ± 0.75

* : indicates the 15 FAs used in the sand-dwelling DFA

● : indicates the 10 FAs used in the paired foraging equivalents DFA

APPENDIX 5.2 Ecological, behavioural, and morphological parameters considered in the selection and pairing of deep- versus shallow-water species for the paired ecological equivalents analyses. Ten species were selected for pairing (total n = 188). Lined up species represent a pair. Evasion guild: H = hide, C = camouflage, F = flee, B = burrow. Note: main reference for deep-water fish species = Chave & Mundy 1994.

Deep-water					Shallow-water					Common biological characteristics				
Species	**Common name**	**(n)**	**Lenght (cm)**		**Species**	**Common name**	**(n)**	**Lenght (cm)**		**Diet**	**Evasion guild**	**Feeding behavior**	**Body shape**	**Sources**
			Min	**Max**				**Min**	**Max**					
Antigonia eos	boarfish	10	6.1	7.1	*Dascyllus albisella*	dascyllus	20	6.0	11.6	Planktivores	H	Hover over substrate and wait for food to blow by in the current.	fish	Mann et al 2007
Bembrops filifera	duckbill	19	7.7	24.0	*Synodus lobeli*	lizardfish	20	5.4	12.0	Benthic carnivores	C	Ambush predators.	fish	Hiatt & Strasburg 1960
Polymixia berndti	beardfish	20	9.0	21.7	*Mulloidichthys flavolineatus*	goatfish	21	18.0	30.0	Benthic carnivores	F	Probe sand with their barbels.	fish	Froese & Pauly 2010, Hobson 1974,1975
Ophichthus kunaloa	snake eel	20	35.7	43.4	*Gymnothorax eurostus*	stout moray	14	29.1	58.2	Piscivores	B/H	Head protruding from burrow/crevice during the day, venture out to hunt at night. *	eel	Hiatt & Strasburg 1960
Meadia abyssalis	abyssal eel	19	31.3	68.2	*Gymnothorax steindachneri*	Steindachner's moray	25	32.2	65.0	Piscivores	H	Head protruding from crevice during the day, venture out to hunt at night. **	eel	Hiatt & Strasburg 1960

* Pair of smaller eels

** Pair of larger eels

APPENDIX 5.3 Ecological, behavioural, and morphological parameters used in the selection of the 16 species (total n = 376) used in the sand-dwelling communities analyses. Evasion guilds (from Parrish et al. 2005): H = hide, C = camouflage, F = flee, B = burrow, S = shelter. Diet Guild: P = piscivores, BC = benthic carnivores.

Species Name	**Common Name**	**(n)**	**Lenght (cm)**		**Evasion Guild**	**Diet**		**Foraging behavior**	**Body shape**	**Sources**
			Min	Max		Guild	Items			
Ariosoma marginatum	Large-eye conger	**26**	11.5	34.5	B	P	N/A	In sand, can be seen at night with head protuding form the sand.	eel	Randall 1996
Bothus mancus	Flowery flounder	**16**	6.3	17.4	C	BC	Small fishes, crabs, shrimps	On sand, frequently burried except for the eyes.	flatfish	Hobson 1974, Hiatt & Strasburg 1960
Bothus pantherinus	Panther flounder	**75**	4.0	7.4	C	BC	Small fishes, crustaceans	On sand and muddy bottoms.	flatfish	Randall 1996
Bothus thompsoni	Thompson's flounder	**25**	6.2	14.0	C	BC	Small fishes, crustaceans	On sandy and muddy areas.	flatfish	Randall 1996
Callionymus decoratus	Longtail dragonet	**20**	7.9	20.8	C	BC	Small benthic invertebrates	On sand.	flatfish	Froese & Pauly 2010 (Family Callionymidae)
Cymolutes lecluse	Hawaiian knifefish	**23**	4.3	15.6	B	BC	Fishes	Over open sand bottom. Dives into the sand when threatened.	fish	Froese & Pauly 2010, Randall 1996
Dactyloptena orientalis	Helmut gurnard	**24**	6.6	12.1	C	BC	Crustaceans, mollusks, small fishes	Well-camouflaged, slow-moving, bottom-dwelling. Use anterior pectoral rays to dig into the sand looking for prey.	flatfish	Froese & Pauly 2010, Randall 1996

APPENDIX 5.3 *end*

Species Name	Common Name	(n)	Lenght (cm)		Evasion Guild	Diet		Foraging behavior	Body shape	Sources
			Min	Max		Guild	Items			
Malacanthus brevirostris	Flagtail tilefish	**16**	7.5	20.5	B	BC	Worms, crustaceans	Live in a burrow used to evade predators; are not ambush predators given that they enter their burrow head first and exit tail first.	fish	Able et al. 1982
Ophidion muraenolepis	Black edge cusk eel	**20**	7.9	18.0	B	P	N/A	Buried in the sand during the day, probe sand barbel-like pelvic fins at night.	eel	Hobson & Chess 1986
Parapercis schauinslandii	Redspotted sandperch	**18**	3.5	10.1	C	BC	Mainly crustaceans	On open sand substrates.	flatfish	Randall 1996
Synodus lobeli	Lobel's lizarfish	**20**	5.4	12.0	C	P	Small fishes	On sand.	flatfish	Hiatt & Srasburg 1960 (lizardfishes)
Synodus variegatus	Reef lizardfish	**19**	6.2	28.0	C	P	Small fishes	On sand, motionless, and fully exposed.	flatfish	Hobson 1974
Torquigener florealis	Floral puffer	**20**	2.4	21.0	S	BC	N/A	On sand.	fish	Randall 1996
Trachinocephalus myops	Snakefish	**20**	3.9	25.5	C	P	Mainly fishes	On sand, or burrowed in sand with only eyes exposed.	flatfish	Hiatt & Srasburg 1960 (lizardfishes)

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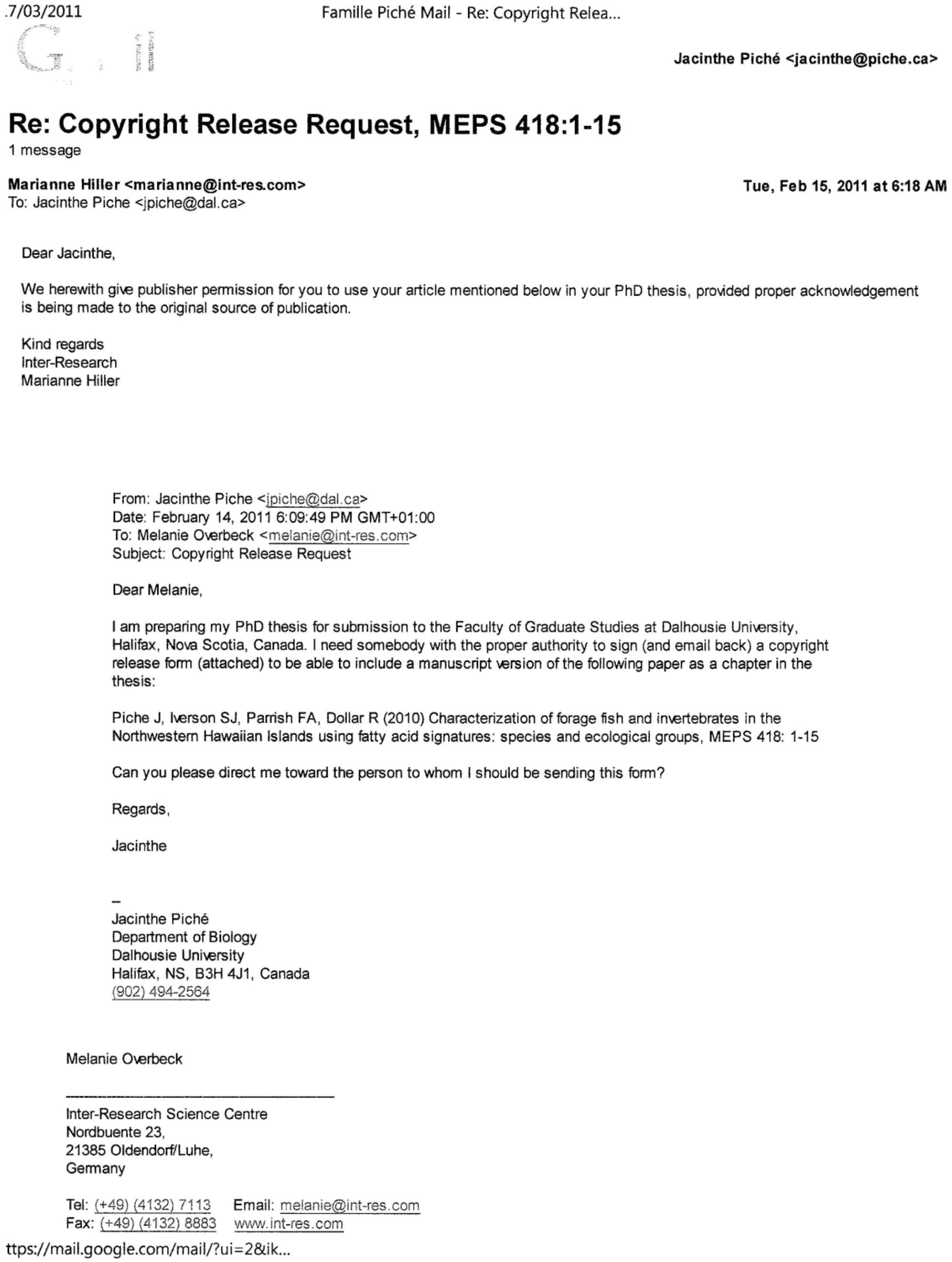

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Jacinthe Piché <jacinthe@piche.ca>

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1 message

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Regards,

Jacinthe

–
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