Elucidating coral reef predator trophodynamics across an oceanic atoll

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Abstract

Coral reef food webs are complex, vary spatially and temporally, and remain poorly understood. Predators on reefs may play major roles linking ecosystems and maintaining ecosystem integrity. In addition, there is increasing evidence of inter- and intra-specific variation in marine predator resource use. Given the high biomass and diversity of predator populations on coral reefs, sympatric predators may vary in their resource use to facilitate coexistence. Knowledge of predator trophodynamics and resource partitioning is important for predicting how reef communities will respond to environmental change and fluctuations in available prey. Using a combination of underwater visual census and baited remote underwater video survey methods, reef predator (e.g. Carangidae, Lutjanidae, Serranidae) populations were quantified across North Malé Atoll (Maldives), which includes outer edge forereefs as well as inner lagoonal reefs. Bulk $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ stable isotopes revealed that predators' isotopic niches varied substantially spatially and interspecifically, with minimal overlap in isotopic niches among species. Furthermore, within populations, there was evidence of intraspecific variation in resource use. Bayesian stable isotope mixing models revealed that all predators were heavily reliant on planktonic production sources, and this planktonic reliance extended to predators inside atoll lagoons. Compound-specific $\delta^{13}C$ stable isotope analysis of essential amino acids further indicated that the planktonic subsidies that played an important role in sustaining both outer forereef and lagoonal reef grouper biomass likely originated from mesopelagic plankton communities rather than nearshore plankton communities. Various statistical modelling techniques (e.g. distance-based linear models and structural equation models) highlighted the importance of live coral and reef structural complexity in driving reef predator assemblages. Lagoonal and forereef predators are equally at risk from anthropogenic and climate-induced changes, which may impact the energetic linkages they construct. This highlights the need for management plans that employ a multiscale seascape approach by integrating findings and strategies across disciplines and ecosystem boundaries.

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All published articles are appended to the thesis.

With the exception of the pelagic samples of *Decapterus macarellus* and *Uroteuthis duvauceli*, the primary consumer compound-specific isotope data used in Chapter 5 were processed by Dr Mike Zhu during his PhD: Zhu, Y. (2019) Studies in the stable isotope ecology of coral reef-fish food webs. Newcastle University PhD Thesis.

All other work was done by Christina Skinner.

Contents

Appendices

List of Figures

List of Tables

> *The ocean throwing its waters over the broad reef appears an invincible, all-powerful enemy; yet we see it resisted, and even conquered, by means which at first seem most weak and inefficient.”*
>
> *– Charles Darwin*

Chapter 1 General introduction

1.1 Ecosystem resilience

Ecosystems (Tansley, 1935; Willis, 1997) are dynamic entities comprising a community of organisms, influenced by both internal and external factors. Over the past few decades, ecosystems have been subjected to increasing stress from climate change and other anthropogenic activities. As humans are reliant on ecosystems for many services, the stability of ecosystems and their resilience has been a subject of increasing research. A resilient ecosystem is one that has the capacity to retain its structure and function and continue to develop, even when under external stress (Holling, 1973; Costanza and Mageau, 1999). As such, ecosystem functioning and resilience are tightly coupled. While the term “function” is widely used in ecosystem studies, only recently has a formal definition been proposed for its application to coral reef systems. Bellwood *et al.* (2019) define “function” as “the movement or storage of energy or material”, so ecosystem functioning relies heavily on the constant supply and cycling of energy and nutrients (Hyndes *et al.*, 2014).

1.2 Connectivity

Connectivity is an important ecological concept yet there is no clear consensus on its definition or how it should be measured (Calabrese and Fagan, 2004). Definitions are separated into two groups: 1) *structural connectivity* is the connectivity between the landscape/seascape structure and 2*) functional connectivity* relates to the behaviour of organisms in their response to the landscape/seascape (Kindlmann and Burel, 2008), and is closely tied to the definition of “function” proposed by Bellwood et al. (2019) (see above Section 1.1). Functional connectivity includes situations where organisms may move across habitat boundaries (Kindlmann and Burel, 2008), and is the focus of this review.

1.2.1 *Ecosystem connectivity*

Terrestrial and marine ecosystems differ markedly, partly due to fundamental differences in their physical structure. Marine ecosystems are inextricably linked by water (Ogden, 1997), so their “openness” leads to many important exchanges across their boundaries (Carr *et al.*, 2003). However, until recently species interactions and nutrient transfer occurring across ecosystem boundaries (e.g. transition zones between defined adjacent habitats) and the impact of species declines beyond individual ecosystems were seldom considered (Lundberg and Moberg, 2003; Barbier *et al.*, 2011; Berkström *et al.*, 2012). Increasingly, ecologists are realising that ecosystems are not isolated systems, but linked by the flow of organisms (trophic) and energetic material (spatial) (Polis and Strong, 1996; Huxel and McCann, 1998; Bellwood *et al.*, 2019). However, identifying the trophodynamics (flows of energy) (Lindeman, 1942) of food webs is challenging, particularly when they may span across multiple ecosystems (Hyndes *et al.*, 2014). Although the idea of trophodynamics began in aquatic systems, applications of the concept to marine ecosystems did not occur for several decades (Libralato *et al.*, 2014). From this point on, this review will focus predominantly on aquatic systems.

1.2.2 Mobile link species

Connectivity between ecosystems may enhance the capacity of an ecosystem to restore itself after a disturbance; for example, organisms that cross ecosystem boundaries are thought to play a key role in ecosystem resilience (Holling, 1973; Mills *et al.*, 1993; Lundberg and Moberg, 2003; Staddon *et al.*, 2010). These organisms are referred to as "mobile link species"; they exert a substantial influence on ecosystem function and have the capacity to impact two distinct systems (Huxel and McCann, 1998; Lundberg and Moberg, 2003). Mobile link species have been categorised depending on their ecological connectivity role into: 1) genetic linkers that carry materials such as pollen and eggs, 2) process linkers that provide or support essential processes, e.g. cross-system foragers, and 3) resource linkers that transport energetic resources such as nutrients and minerals (Lundberg and Moberg, 2003; Berkström *et al.*, 2012).

In tropical seascapes, many fish species are resource linkers which connect adjacent ecosystems by using resources across a mosaic of interlinked patches (Clark *et al.*, 2009). Migrating herbivorous grunts (*Haemulon* spp) in the Caribbean transfer important nutrients to primary producers on coral reefs through excretion. Coral reefs are nutrient-poor environments so faecal material rich in nitrogen (in the form of NH4+) and phosphorus provides a significant supplement, adding nutrients and energy to the benthic community (Meyer and Schultz, 1985). Similarly, faeces of the planktivorous damselfish *Chromis chromis* provide an important flux of nitrogen and phosphorus to Mediterranean reefs while simultaneously linking pelagic and littoral food webs (Pinnegar and Polunin, 2006).

Damselfish are small-bodied and highly site-attached (Fishelson, 1998), so the latter case demonstrates that species may create linkages even when they are less mobile. Where food webs overlap geographically, such as coral reefs and the adjacent pelagic ocean, species may be able to take advantage of multiple food webs with minimal movement, playing an important ecological coupling role.

Nutrient transfer by mobile link species does not just occur within land- or seascapes however, but also across adjacent marine, riverine and terrestrial ecosystems. Brown bears, *Ursos arctos*, are an important vector of Pacific salmon-derived N to forest ecosystems in Alaska, and white spruce*, Picea glauca*, derived 15.5-17.8% of their total N from salmon (Hilderbrand *et al.*, 1999). On island systems off Mexico, nutrient-rich, ocean-derived seabird guano subsidizes terrestrial food webs, transferring large amounts of energetic material from sea to land (Stapp *et al.*, 1999). Similarly in the Chagos archipelago, animal-mediated nutrient flows were identified between pelagic, coral reef and island ecosystems. On islands that were free of invasive predatory rats, seabird densities and nitrogen deposits were significantly greater, leading to increased nitrogen in the soil, macroalgae, turf algae and reef fish. Furthermore, damselfish on the reefs grew faster and reef fish biomass was 48% greater overall compared to rat-infested islands where seabird densities were lower (Graham *et al.*, 2018). Ecological processes such as these can substantially alter species diversity and abundance in connected habitats (Lundberg and Moberg, 2003), highlighting the importance of identifying and considering energetic linkages across adjacent ecosystems (Stapp *et al.*, 1999) when assessing ecosystem function and resilience.

Some fish undergo diurnal or crepuscular (twilight) migrations which can provide ecological coupling between ecosystems by translocating biomass through predator-prey interactions (Kneib, 2002). Their larger home ranges mean they may feed on prey in adjacent habitats (Nagelkerken *et al.*, 2008a), transferring carbon which fuels neighbouring food webs (Layman *et al.*, 2011; Hyndes *et al.*, 2014). Transient top predators which move between various nearshore and open ocean systems can also have considerable effects through predation (Blaber, 2000). Pelagic predators accounted for 37% of prey biomass transport between coral reef and adjacent seagrass habitats in the Caribbean (Clark *et al.*, 2009). As these pelagic species have larger home ranges (Cartamil *et al.*, 2003), these frequent transboundary movements broaden the spatial context of ecological connectivity (Clark et al., 2009), creating linkages between oceanic and coastal ecosystems and providing evidence that transient species can influence community structure (Estes et al., 1998).

1.3 Food web science

Identifying and understanding these cross-system linkages is important for effectively managing ecosystems and the species that live in them. Furthermore, knowledge of food chain length and the primary production sources sustaining food webs is also vital for predicting how systems will respond to change. There are several approaches and methodologies used to understand and quantify such fluxes.

1.3.1 Stomach content analysis (SCA)

Traditionally, food web studies used SCA to investigate resource use and food web energy flow. There are several employed methods; 1) occurrence: the number of sampled stomachs that contain one or more individuals of each food category; 2) numerical: the number of individuals in each food category recorded across all stomachs; 3) volumetric: the total volume of each food category; 4) gravimetric: the weight of each food item; and 5) subjective: the contribution of each food category is estimated by eye (Hyslop, 1980). There are inherent limitations to using SCA including, but not limited to: difficulties in accurately identifying easily digested or smaller food sources such as plankton or detritus, an increased necessity for lethal sampling, a shorter temporal scale (as SCA only provides diet samples of recently ingested items) and increased data uncertainty due to consumption of non-dietary components (Table 1.1) (Hyslop, 1980; Pinnegar and Polunin, 1999; Greenwood *et al.*, 2010).

1.3.2 Stable isotope analysis (SIA)

Stable isotopes are two or more forms of the same element which have the same number of protons in their nuclei but a different number of neutrons. They occur naturally in biological material and are an important tool used to study food webs. Isotopic composition is reported in terms of δ values, defined as parts per thousand (‰) different from a known standard (Peterson and Fry, 1987). Three isotopes are commonly employed in food web science: carbon (ratio of $^{13}C/^{12}C$ expressed as $\delta^{13}C$), nitrogen (ratio of $^{15}N/^{14}N$ expressed as $\delta^{15}N$), and sulfur (ratio of $^{34}S/^{32}S$ expressed as $\delta^{32}S$). $\delta^{13}C$ determines the primary production

Table 1.1. Advantages and disadvantages of stomach contents analysis (SCA), bulk, amino acid (AA), and fatty acid (FA) compound-specific stable isotope analyses (SIA) for elucidating the trophic relationships of consumers. Table adapted from Polunin and Pinnegar (2002).

Information	SCA	Bulk SIA	CSIA
Resolution of principal trophic pathways in food web	Can be good where individual sources are identifiable (e.g. indigestible hard parts)	Can be good if pathways well distinguished by $\delta^{13}C$ of basal materials, poor if > two pathways	Good as distinct separation in AA of major primary producers
Connectance (proportion of linkages that are realised)	Good but only for individual sources that are identifiable	Poor because only broad categories distinguishable as a rule	Poor as only broad categories of resources distinguishable
Measure of nutritional role of different dietary items	Poor because diet, not actual absorption, quantified	Can be good because isotopes are in materials that have been assimilated	Good because AA and FA are in materials that have been assimilated
Measure of short-term differences in diet	Potentially good because data are only short term	Can be good if use tissues that have fast turnover rates (e.g. plasma)	Could be good, but little information on isotopic incorporation rates
Measure of spatial differences in diet	Will be good where major items identifiable	Will be good where shifts in items with distinct $\delta^{13}C$ and/or in trophic level	Could be good, but few studies have spatially compared primary producer AA and FA values
Measure of trophic level	Often inaccurate because diet incompletely described	Can be accurate if basal materials are identified, and change in $\delta^{15}N$ per trophic level validated	Good, can be determined from a single consumer tissue sample
Measure of feeding strategies within populations (i.e. variance)	Poor, may be overestimated as diet only snapshot	Good as isotopes represent consistent assimilated prey items	Good as isotopes represent consistently assimilated prey items

sources responsible for the energy flow in the system while $\delta^{15}N$ indicates the trophic position occupied in the food web (Post, 2002). $\delta^{34}S$ can serve as an additional tracer to help discriminate between two producers when there are difficulties using only $\delta^{13}C$ and $\delta^{15}N$ (Connolly *et al.*, 2004), although there are some questions over its effectiveness given the variation in producer sulfur signatures (Stribling *et al.*, 1998).

Animals will take on the isotopic composition of the food that they eat with a small enrichment, known as the trophic discrimination factor (TDF or Δ: the difference in isotope ratio between consumer and diet). During metabolic reactions, lighter isotopes are discriminated against so consumer tissues become greater in the ratio of heavy:light isotopes (^{13}C or ^{15}N enriched) with increasing trophic level compared to their diet (Peterson and Fry, 1987). $\delta^{13}C$ increases by 0.0-0.4% per trophic level, $\delta^{15}N$ increases by 3-5%, and $\delta^{34}S$ shows little to no change and is therefore considered a good indicator of source composition (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Peterson and Howarth, 1986; Fry, 1988; Post, 2002). The ratio of stable isotopes in animal tissues can therefore be used to trace energy flow in the food web, although different tissues have different enrichment factors. Each tissue has a different turnover rate depending on how metabolically active it is, meaning some tissues may take longer than others to come to isotopic equilibrium following a change in diet (Libby *et al.*, 1964; Tieszen *et al.*, 1983). Tissues with fast turnover rates represent the short-term diet (e.g. plasma, liver) while tissues with slower turnover rates represent the long-term diet (e.g. bone, muscle) (Vander Zanden *et al.*, 2015; Carter *et al.*, 2019). In the gag grouper (*Mycteroperca microlepis*), $\delta^{13}C$ turnover rates were primarily influenced by metabolic rate although it varied among individuals (Nelson et al. 2011). It is also important to consider relationships between isotopic signature and body size (Arim *et al.*, 2007). As organisms grow larger, they may change their diet, which can lead to different $\delta^{13}C$ and $\delta^{15}N$ values. Indeed, a review of the literature revealed that there are shifts in $\delta^{13}C$ and $\delta^{15}N$ values with increasing body size for many coral reef fish, which is linked to size-based feeding and possibly changes in production source (Greenwood *et al.*, 2010).

Different compounds can affect the stable isotope values obtained during analysis. Lipid content of tissues significantly alters the observed $\delta^{13}C$ values (Nelson *et al.*, 2011); tissues with a higher lipid content are depleted in ^{13}C (Tieszen *et al.*, 1983). Inclusion of lipids could thus result in unreliable stable isotope data for some species (Post, 2002) but chemical lipid extraction may alter $\delta^{15}N$ values, requiring separation of $\delta^{13}C$ and $\delta^{15}N$ analyses. Instead, mathematical corrections of bulk tissue data can be made using a mass balance arithmetic correction applied after the $\delta^{13}C$ and $\delta^{15}N$ values have been obtained, which negates the need to run separate analyses (Sweeting *et al.*, 2006). Currently, there is no clear consensus in the scientific community on the correct protocol to follow regarding tissue lipid extractions so each study must be assessed on a case-specific basis. Urea is another compound which may alter stable isotope values, particularly in elasmobranchs. Elasmobranch tissues retain urea to keep osmotic balance but a high concentration of urea can skew ecological interpretations, so removal from tissues is recommended prior to SIA (Kim *et al.*, 2012). In order to accurately interpret the isotope data and interpret trophodynamics, it is thus crucial to know the species-specific and tissue-specific turnover rates, the appropriate sample treatment and the correct TDF (Tieszen *et al.*, 1983; Shiffman *et al.*, 2012).

SIA has become an important technique to elucidate food web dynamics. It can provide greater resolution of data, incorporate temporal variability in diet and typically requires a lower sampling effort than SCA (Wyatt *et al.*, 2012b). In addition, SIA only represents prey material that has been assimilated to consumer tissue and it enables food chain length and the trophic level of consumers to be calculated (Pinnegar and Polunin, 1999; Polunin and Pinnegar, 2002). Furthermore, due to their slow turnover in some tissues (Tieszen *et al.*, 1983), isotopes may be more reliable at showing individual foraging variability within the population as they represent consistent long-term assimilated resources (Araújo *et al.*, 2007). However, limitations of SIA include the uncertainty of the predatory impact (i.e. lack of information on actual predation events and volume of prey consumed), the lack of species-specific diet data and that, although the importance of different food sources is identified, there is limited insight into the amount of carbon being transferred by the organisms (Table 1.1) (Hyndes *et al.*, 2014). There can also be significant inter-instrument differences in $\delta^{13}C$ and $\delta^{15}N$ values of the same individual sample, suggesting care needs to be taken when directly comparing stable isotope values between studies (Mill *et al.*, 2008).

1.3.3 Compound-specific SIA (CSIA)

SIA techniques are constantly progressing and recent advances include the SIA of individual compounds. This approach combines gas or liquid chromatography with an isotope-ratio mass spectrometer (IRMS) and is known as CSIA. Currently, the two compounds that are focussed on in food web science are amino acids (AA) and fatty acids (FA). In short, for elucidation of food web energy pathways using AA, this technique analyses the stable isotope content of “source” essential amino acids (e.g. leucine and phenylalanine) which higher trophic level consumers cannot synthesize “de novo”. AA-CSIA is advantageous over traditional bulk tissue SIA as the “source” amino acids retain the isotopic composition of the base of the food web with little to no fractionation as they move up the food chain, providing greater resolution. Furthermore, bulk SIA can be highly variable where consumers are sustained by multiple resources with varying isotopic compositions. CSIA more accurately traces resource use as there is distinct separation in the essential amino acids of major primary consumers (Table 1.1) (Larsen *et al.*, 2013; Nielsen and Winder, 2015; Ishikawa, 2018). They can thus act as a unique “fingerprint” identifying the production sources at the base of the food web (Larsen *et al.*, 2013; McMahon *et al.*, 2013). However, few studies have investigated how these fingerprints vary spatially and temporally and at what taxonomic scale they become indistinguishable (Whiteman *et al.*, 2019).

One major advantage of CSIA is that trophic position can be estimated from the consumer tissue alone (Nielsen *et al.*, 2015; Papastamatiou *et al.*, 2015). Other advantages are that only a small sample size is needed, that isotope information is available at the biochemical building block level, and that there is a greater understanding of the metabolic processes that affect the isotope values of single compounds than bulk tissues (Table 1.1) (Boecklen *et al.*, 2011). Disadvantages are that the process of extracting the compounds is much more costly and time consuming, with sample preparation taking several days. The subsequent CSIA of an individual sample can then take hours, while bulk tissues now only take minutes (Boecklen *et al.*, 2011). Regardless, CSIA is an increasingly popular technique that will continue to advance as the technology improves.

1.3.4 SIA for tracing energy flow

SIA is one of the main techniques employed to trace energy fluxes across ecosystem boundaries and reveal nutrient links that are often not immediately apparent. For example, in billabongs (a blind channel leading out from a river), the primary energy source in the food web was not the most visually dominant macrophyte, but instead an inconspicuous alga found outside the sampled habitat (Bunn and Boon, 1993). Similarly, organisms inhabiting seagrass meadows in Corsica were supported by energy from planktonic carbon rather than carbon from one of the most abundant seagrass species *Posidonia* (Dauby, 1989; Pinnegar and Polunin, 2000). On coral reefs, energetic materials from adjacent mangroves and seagrass beds were major production sources for sampled fish in the Gulf of Mexico (Carreón-Palau *et al.*, 2013), while benthic primary production contributed ~65% to consumer production in the Papahānaumokuākea Marine National Monument food web (Hilting *et al.*, 2013). Finally, the purple-striped jellyfish, *Pelagia noctiluca*, although collected in nearshore waters, was dependent on autochthonous rather than terrigenous organic matter, suggesting it may link pelagic and nearshore ecosystems (Malej *et al.*, 1993). These studies highlight the complexities of food webs and underline the importance of considering energy and nutrient transfer from other habitats when investigating trophodynamics.

Sampling the tissues of more mobile species can also reveal vital information about their movements and distributions. Dolphin populations off the coast of Florida were easily distinguished by their different $\delta^{34}S$ signatures, as the values were much lower in individuals feeding from nearshore coastal food sources compared to those foraging offshore (Barros *et al.*, 2010). Australian sharpnose shark, *Rhizoprionodon taylori*, were found not to forage more than 100 km away from their capture location, suggesting this species does not make large regional movements but remains in adjacent bays (Munroe *et al.*, 2015). Food webs are inherently complex but a better understanding of how organisms interact with each other can be obtained by tracking animal movements using identified energy pathways (McMahon *et al.*, 2013; Nielsen *et al.*, 2015).

1.3.5 SIA data analysis

Ecological niches are multidimensional spaces where the axes represent different environmental conditions and resources, determining the unique survival requirements of an organism (Hutchinson, 1957). In ecological studies, stable isotope data can help to understand these characteristics of community structure and resource use. Isotope data are presented on a bi-plot using the isotope values (δ-values) as coordinates. The area (δ-space) of these coordinates is determined to be the animal's isotopic niche and provides an understanding of their diet (Newsome *et al.*, 2007). The size of the niche and position of the individual coordinates is then used to infer intraspecific variation in resource use, known as the niche width (Bearhop *et al.*, 2004). Community-wide metrics, e.g. ranges in $\delta^{15}N$ and $\delta^{13}C$ values which highlight the vertical structure/trophic levels and food web basal resources respectively, can also be applied to further elucidate trophic diversity and redundancy (Layman *et al.*, 2007a). However, these metrics are sensitive to sample size and do not account for inherent natural variability occurring among systems. As such, the R package SIBER (Stable Isotope Bayesian Ellipses in R) was developed to robustly statistically compare these metrics among communities using Bayesian inference techniques (Jackson *et al.*, 2011).

Stable isotope mixing models use the stable isotope values of consumers and their potential prey to estimate the likely contribution of various food sources to an animal's assimilated diet. In recent years, their capabilities have advanced substantially and they are now a key component of stable isotope food web studies. Previously, mixing models could not cope with more than two or three food sources characterised by one or two isotope values (Phillips and Gregg, 2003). Now, however, several Bayesian mixing models have been developed that can incorporate uncertainties such as a large number of sources, a small number of samples, or variability in an animal's diet (Phillips, 2012; Stock *et al.*, 2018). Although the ease of running these Bayesian mixing models is increasing, the authors of these models caution that the underlying isotope data must be robust, with clear questions laid out and strong sampling designs (Phillips *et al.*, 2014).

1.3.6 Ecosystem modelling

Ecosystem models are increasingly being used to simulate ecosystem dynamics and better understand complex food webs. Ecological relationships are determined and combined to form a simulation of the study ecosystem. Many models are widely available but one of the most commonly used for the marine environment is Ecopath with Ecosim (Colléter *et al.*, 2013), which allows construction of mass balanced models (Heymans *et al.*, 2016). Models allow researchers to study large systems and carry out experiments with no need for funding or ethical considerations. Moreover, they can provide more information and identify issues which single-species models may not (Fulton *et al.*, 2003). However, they do rely on data which has been gathered in the field and furthermore, where model complexity is high, predictions may be highly uncertain (Duplisea, 2000). In addition, ease of use and a lack of best practice guidelines means model quality may be compromised through misuse by inexperienced users (Heymans *et al.*, 2016).

1.4 Predators

Predators are typically larger bodied animals occupying the top of the food web. Coral reefs support a large number of predators that vary in their movements and reef usage, ranging from transient, mobile species to more reef-attached. Here, reef predators are mostly piscivore, top predators occupying the upper level of the food chain at trophic positions 3.4 and above (Table 1.2).

1.4.1 Predator-prey relationships

As larger bodied, higher trophic level animals, predators are widely considered to alter the structure of food webs through direct (predation) and indirect (changing prey behaviour) actions. Predator-prey relationships are complicated and vary between species and even individuals, as they are influenced by characteristics such as body size, diet and home range (Roff *et al.*, 2016). Predators can exert significant influence over prey communities; the peacock grouper, *Cephalopholis argus*, reduced prey abundance on reefs by up to 50% and prey diversity by 45% (Stier *et al.*, 2014), and even transient fish predators reduced prey densities on patch reefs that they visited fairly infrequently (Harborne *et al.*, 2017).

Table 1.2 Top predator families found on coral reefs and their general movement patterns.

Family	Common name	Movements
Aulostomidae	Trumpetfish	Reef-attached
Belonidae	Needlefish	Reef-attached
Carangidae	Trevally	Transient
Carcharhinidae	Requiem sharks	Transient
Fistulariidae	Cornetfish	Reef-attached
Haemulidae	Grunts	Reef-attached
Lethrinidae	Emperor	Reef-attached
Lutjanidae	Snapper	Reef-attached
Scombridae	Tuna	Transient
Scorpaenidae	Scorpionfish	Reef-attached
Serranidae	Groupers	Reef-attached
Sphyraenidae	Barracuda	Transient

Prey communities also have the ability to influence predators and their movements. Growth rates and local abundances of the chocolate grouper *C. boenak* were strongly linked to their prey, increasing when prey abundances were high. Furthermore, 31% of monitored individuals moved from areas of low to high prey density (Beukers-Stewart *et al.*, 2011). Similarly, biomass of planktivores was determined to be the key driver of reef shark abundances in the British Indian Ocean Territory Marine Reserve and data-driven statistical models identified it as a greater predictor than habitat variables such as depth and coral cover (Tickler *et al.*, 2017). These findings underline the notion that prey availability is inextricably linked to predator spatial distributions and, in some cases, is more important than available habitat. However, predator-prey relationships are not always intuitive. Predator fish productivity was highest on reefs with intermediate complexity (i.e. habitat structure), as when it increased, so did prey refuge space. Consequently predation levels dropped, causing declines in predator growth (Rogers *et al.*, 2018).

Trophic cascades may occur when top predators significantly alter their prey densities, resulting in the release of trophic levels below the prey from predation (or in some cases herbivory). There are several classical examples of top down trophic cascades in aquatic ecosystems (Carpenter *et al.*, 1985; Power, 1990). One of the best documented is in the North Pacific kelp ecosystem, where sea otters exerted top down control of urchin populations, allowing kelp forests, where other invertebrates resided, to proliferate (Estes and Duggins, 1995). In 1990 the sea otter population collapsed from killer whale predation, a new predator-prey relationship arising from a change in killer whale feeding habits, subsequently releasing the urchin communities and causing the disappearance of the kelp forests (Estes *et al.*, 2004). Although this is an oversimplification of the many trophic links in this system, it demonstrates the role that predator-prey relationships can have in ecosystem dynamics and community structure.

There has been substantial debate over whether sharks cause trophic cascades. Some studies argue that they do (Myers *et al.*, 2007; Burkholder *et al.*, 2013; Ruppert *et al.*, 2013), while others find no evidence of it (Roff *et al.*, 2016; Casey *et al.*, 2017). On coral reefs, sharks are considered apex predators, but most reef sharks feed at the same trophic level and have a similar diet to large mesopredatory fish. This suggests that reef sharks (e.g. blacktips, *Carcharhinus melanopterus*, whitetips, *Triaenodon obesus*), should be reassigned to high level mesopredators and the apex predators are the “other” sharks (e.g. tiger, *Galeocerdo cuvier*, lemon, *Negaprion brevirostris*) that visit reefs infrequently (Figure 1.1) (Frisch *et al.*, 2016). There is currently little evidence of other apex teleost predators causing trophic cascades on reefs (Mumby *et al.*, 2012). The functional redundancy existing among reef sharks and large piscivores could explain why evidence of cascades on reefs is rare.

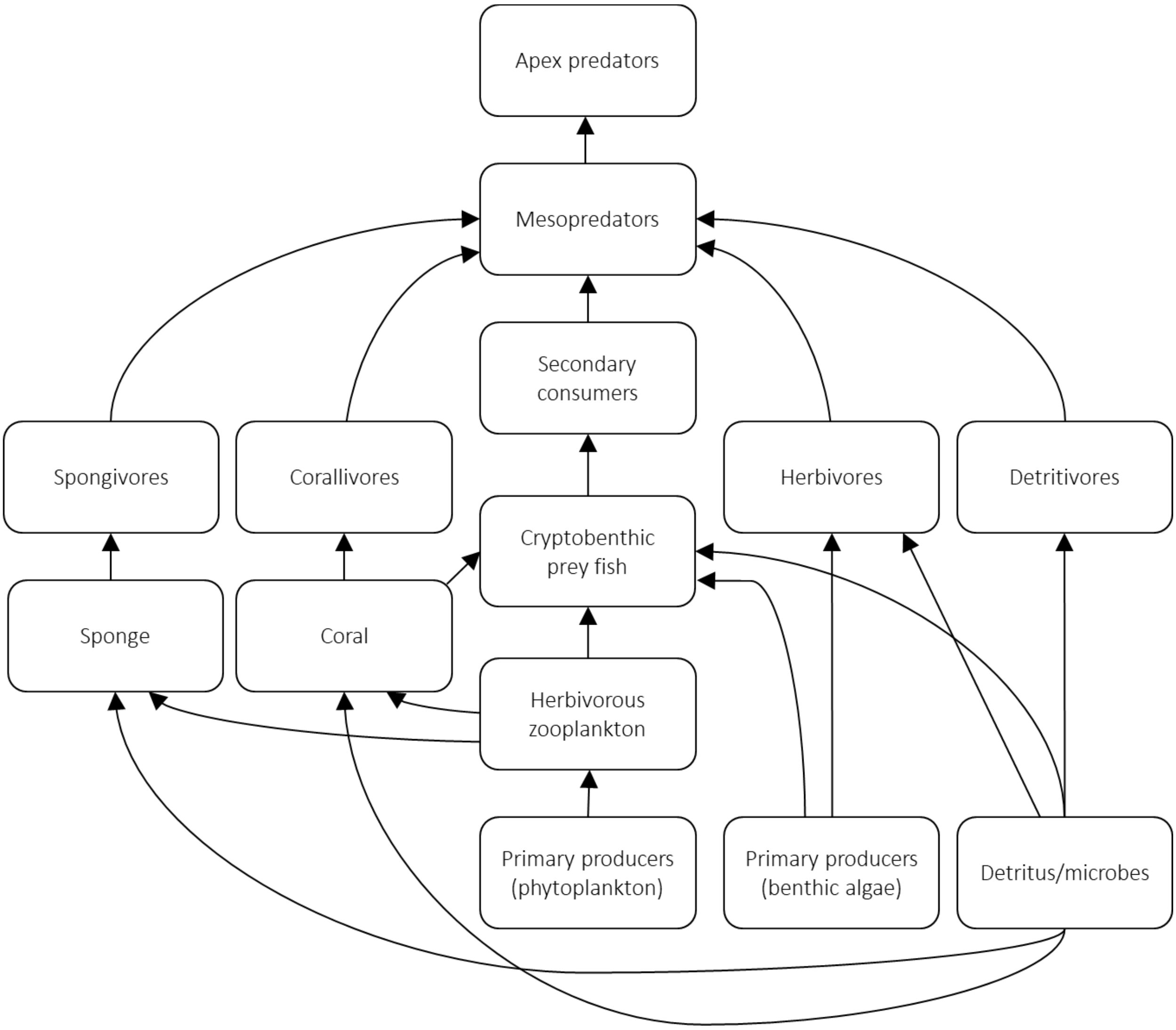


Figure 1.1. Simplified model of a coral reef food web where arrows indicate the flow of energy and predator/prey relationships.

1.4.2 Resource partitioning

While predator-prey relationships are being increasingly well documented, an area lacking in study is how ecologically similar predators co-occur and partition often limited, shared resources in the same location. The Atlantic tarpon *Megalops atlanticus* and the bull shark *Carcharhinus leucas* occupy the same trophic niche and have similar prey, but the tarpon avoided productive feeding habitats when bull shark abundances were high, a behaviour interpreted as avoiding greater danger (Hammerschlag *et al.*, 2012). In Hawaii, three species of jack (*Caranx ignobilis*, *C. orthogrammus* and *C. melampygus*) had only minor dietary overlap despite being caught in the same bay, indicating clear interspecific differences in resource acquisition (Meyer *et al.*, 2001). Similarly, two sympatric species of coral trout that co-occur on reefs, *Plectropomus laevis* and *P. leopardus*, had different target prey and resource uses from each other. Within the *P. laevis* population, there were also two distinct colour phases, which had different feeding regimes and hence dietary niches (Matley *et al.*, 2017). Dietary specialisation of predators does not occur in all systems or between all species (Gallagher *et al.*, 2017) but it warrants further study, particularly in systems where resources are limited or fluctuating.

1.4.3 Predators as mobile link species

Being more mobile, predators have greater opportunity to feed on multiple species in multiple habitats, playing an important ecological role connecting distinct food webs (Barnett *et al.*, 2012; Espinoza *et al.*, 2015). Nutrient transfer is well documented for lower trophic level planktivorous fish (Hamner *et al.*, 1988; Pinnegar and Polunin, 2006) but less so for marine predators. However, there is growing evidence that reef predators may influence nutrient cycling by transferring energetic materials (Schmitz *et al.*, 2010), often between reef and adjacent pelagic ocean. In the remote Central Pacific Palmyra Atoll, blacktip reef sharks, *C. melanopterus*, grey reef sharks, *C. amblyrhynchos*, and red snapper, *Lutjanus bohar*, relied on production sources from outside their primary habitats, playing a key role providing ecological coupling as cross-system foragers (McCauley *et al.*, 2012c). Using telemetry data and network theory, this energetic link was quantified. It was estimated that *C. amblyrhynchos* deposited 94.5 kg of nitrogen across the atoll each day, 86% of which derived from pelagic production sources (Williams *et al.*, 2018b), creating an important link between reef and pelagic systems. Linkages have also been identified across depth ranges as Galapagos sharks, *Carcharhinus galapagensis*, and giant trevally, *Caranx ignobilis*, foraged in both shallow and deep water mesophotic reef habitats, transporting nutrients between them (Papastamatiou *et al.*, 2015). Although there are certainly many energetic connections that have not yet been identified, understanding this connectivity is crucial. These linkages contribute to ecosystem resilience and stability (Bascompte *et al.*, 2005; Osgood and Baum, 2015), which is particularly timely for species and systems that are adapting in the face of global climate change (Roessig *et al.*, 2004; Munday *et al.*, 2009).

1.5 Environmental change

1.5.1 Climate change and anthropogenic stressors

Since the 1880s, it is estimated that human activities have increased the global temperature by 1°C (Hartmann *et al.*, 2013). By 2050-2100, it is predicted that the global temperature will increase by 2°C, carbon dioxide emissions will exceed 500 ppm and the human population will have surpassed 9 billion (Hoegh-Guldberg *et al.*, 2007). Land and seascapes are under increasing pressure of global changes and other anthropogenic stressors such as habitat degradation and deforestation, coastal development, oil and chemical spills, nutrient runoff, pollution, and resource overexploitation.

Coral reef ecosystems are particularly vulnerable to these threats. Ocean warming and acidification, coupled with overfishing, habitat loss, and decrease in oceanic productivity mean there are no pristine reefs left (Pandolfi *et al.*, 2003). Increased water temperatures are causing coral reefs worldwide to bleach, with bleaching events now occurring as often as every six years (Hughes *et al.*, 2018a). Furthermore, projected annual severe bleaching conditions, where reefs change and recovery will be limited, will affect >75% reefs worldwide before 2070 under emissions scenario RCP4.5 (van Hooidonk *et al.*, 2016). These events have caused declines in structural complexity, coral biodiversity, and the abundance and diversity of reef-associated fishes (Jones *et al.*, 2004; Carpenter *et al.*, 2008; Pratchett *et al.*, 2018).

Although the direct impacts of continued coral reef degradation may be apparent, species do not react to environmental change uniformly, indicating that further change of reef communities and loss of species richness may arise through indirect pathways that we have yet to identify. For example, in degraded coral habitats, while the Nagasaki damselfish, *Pomacentrus nagasakiensis*, could still recognise predators through alarm cue conditioning and transfer this information to conspecifics, the Ambon damselfish, *Pomacentrus amboinensis*, could not (Chivers *et al.*, 2016). This has negative implications for their predator avoidance ability and underlines that even species of the same genus will have different traits or adaptations rendering them more or less successful in these changing environments. Discrepancies in survivorship are even more evident when looking at coral species. Lower relief massive corals such as the Poritidae are frequently found to be more thermally tolerant and able to resist or survive bleaching than structurally complex and fast growing corals such as *Acropora* and *Pocillopora* that have suffered unprecedented global losses (Loya *et al.*, 2001; Hughes *et al.*, 2017b; Hughes *et al.*, 2018b).

Interactions between human society and reefs are shifting due to unprecedented changes in reef structure (Williams and Graham, 2019). Consequently, in addition to the environmental and biological impacts of this degradation (e.g. loss of coastal defences and biodiversity), there are economic consequences of a change or reduction in reef services (Woodhead *et al.*, 2019). Loss of habitat structural complexity is predicted to cause a 3-fold reduction in fishery productivity (Rogers *et al.*, 2014), while a global reduction in coral cover of 1% would result in a loss of US$3.95 - 23.78 billion annually (Chen *et al.*, 2015). Not only will reductions in live coral cover affect those relying on reefs for their livelihoods at the local scale, but it will also have significant global repercussions. Moving forward, a better understanding of coral reef ecosystem function is required that addresses their complex socio-ecological nature (Williams and Graham, 2019).

1.5.2 Decline of ecosystem capacity

Connectivity and movements across ecosystem boundaries help shape the food web structure of ecosystems, leading to increased energy flow and promoting ecosystem resilience (Sheaves, 2009; Hammerschlag *et al.*, 2012; O'Leary *et al.*, 2017). Human disturbances may alter this energy flow through fragmentation, arising from the loss and degradation of habitats or by building developments that interfere with connectivity (Berkström *et al.*, 2012; Crook *et al.*, 2015). An analysis of global forest cover across five continents found that habitat fragmentation led to a 13 to 75% reduction in biodiversity, declines in biomass and altered nutrient cycles, suggesting key ecosystem functions were seriously impaired (Haddad *et al.*, 2015). In addition, the loss of mobile link species from overexploitation will disrupt their energy transfer movements, irreversibly altering their ecological connectivity role (Hyndes *et al.*, 2014). In short, ecosystem function, stability and resilience are reliant on the energetic connections existing between adjacent habitats, which stand to be altered through a range of impacts.

Knowledge of species distributions, migrations, and food web dynamics is thus essential for understanding the impact climate change will have on ecosystem function (White *et al.*, 2013; Hunt *et al.*, 2015). Current management strategies focus on the conservation of key species or habitats, often in the form of marine reserves, but rarely consider the seascape perspective (Berkström *et al.*, 2012). A recent study assessing the efficacy of marine reserves found that only reserves in areas of low human impact were able to sustain top predators. Although the reserves in areas of high human impact still had increased fish biomass compared to fished areas, the lack of predators suggests they are not able to maintain full ecosystem function (Cinner *et al.*, 2018). Consequently, in order to sustain ecosystem function and resilience, managers must consider ecological patterns and processes across ecosystem boundaries, spatial scales and scientific disciplines (Lundberg and Moberg, 2003).

1.5.3 Decline of predator populations

Over the past few decades, marine predator populations have declined worldwide due to a combination of anthropogenic stressors such as overexploitation and habitat degradation (Graham *et al.*, 2010; Williams *et al.*, 2015; Roff *et al.*, 2016), with model estimates putting the global predatory fish biomass loss at two-thirds over the last 100 years (Figure 1.2) (Christensen *et al.*, 2014). Due to their greater mobility and low density, predator populations are often inadequately monitored and managed (White *et al.*, 2013), causing uncertainty about their status. Furthermore, predator life history traits, including slow growth and late sexual maturation, render them increasingly vulnerable and susceptible to fishery-driven declines (Myers and Worm, 2003; Dulvy *et al.*, 2008). It is unsurprising, therefore, that numerous studies are reporting substantial and rapid worldwide declines in sharks, rays and other reef-associated predator populations from overexploitation (Friedlander and DeMartini, 2002b; Robbins *et al.*, 2006; Davidson *et al.*, 2016; Spaet *et al.*, 2016), even far from human population centres (Graham *et al.*, 2010). Recovery of these populations to pre-disturbance, pristine levels is predicted to take decades, large areas closures, and a cessation of human and environmental impacts (Myers and Worm, 2005; Robbins *et al.*, 2006).

The effects of predator loss are uncertain but will vary among species and systems (Stevens *et al.*, 2000). At fished sites in the northern Line Islands there were no clear trends in prey abundances with lower densities of predators, but there were increases in prey longevity and maximum sizes, suggesting predator impacts on fish communities are not always obvious (Ruttenberg *et al.*, 2011). Although the verdict on shark-driven trophic cascades on reefs is still unclear, sharks and other teleost reef predators can exert significant influence over prey communities. Indeed, in food web models, 48% of the trophic chains with strong interactions involved sharks (Bascompte *et al.*, 2005), suggesting their ecological role is an important one.

Figure 1.2. Global biomass trends for predatory fish over 100 years from 1910 to 2010, predicted from ecosystem models run by the authors. Modified from Christensen *et al.* (2014). Solid line: median values, dotted lines: upper and lower 95% confidence intervals.

When determining the ecological consequences of predator declines, it is important that both direct consumptive effects and indirect non-consumptive risk effects be taken into consideration, as prey are not behaviourally inert (Heithaus *et al.*, 2009). Prey behaviours and morphological traits may evolve or change in response to declines in predation pressure. Following declines in active predators at two atolls, nocturnal prey were found to increase diurnally in density and biomass by eight times and six times respectively, suggesting a temporal niche shift arising from an anticipated reduced predation risk (McCauley *et al.*, 2012b). Furthermore, on reefs depleted of sharks in northwestern Australia, the eyes and caudal fins of several species of prey were smaller than on undepleted reefs. Large eyes and caudal fins are two morphological traits associated with predator avoidance - they aid with early predator detection and rapid escape. This suggests there may have been morphological changes in several prey species arising from predator depletions, which in turn may change how they use their energetic resources (Hammerschlag *et al.*, 2018).

Some predators are also adapting to changing environmental conditions. Significant reductions in live coral cover and changes in dominant prey fish species on the Great Barrier Reef led to a shift in the main carbon pathway on the reef, from pelagic plankton to benthic algae. The $\delta^{13}C$ value of the mesopredatory coral grouper *Plectropomus maculatus* shifted accordingly from more pelagic to more benthic, suggesting a dietary adaptation response to the prey community fluctuations (Hempson *et al.*, 2017b). However, overall declines in the *P. maculatus* population suggest that while a diet switch may be beneficial in the short-term, it might not prevent the long-term negative effects of habitat degradation (Hempson *et al.*, 2017b).

Similar concerns surrounding predator resource use arise from predicted decreases in global oceanic production (Asch *et al.*, 2018). Increasing evidence that predators rely on energy fluxes from multiple pathways (McCauley *et al.*, 2012c; Frisch *et al.*, 2016; Zgliczynski *et al.*, 2019) underlines the impact that pelagic production declines may have on their populations. Reef based energy pathways may be no more resilient to change. Corals with high thermal tolerance that may dominate future coral assemblages are characterised by lower structural complexity and prey fish assemblages on reefs dominated by these corals were less diverse and abundant, due to the reduced available habitat space (Loya *et al.*, 2001). Furthermore, chocolate grouper, *Cephalopholis boenak*, muscle tissue lipid content was lower on reefs with more thermally tolerant, less structurally complex corals, which has negative implications for their fecundity, growth and survivorship (Hempson *et al.*, 2017a). These studies have significant implications for the future of predator populations in the face of climate change and suggest that both pelagic and reef energy pathways may be substantially altered.

1.6 Oceanic-reef systems

Almost 200 years ago, Charles Darwin observed the paradox that tropical waters are oligotrophic yet coral reef ecosystems support a large amount of life (Darwin, 1842; Lowe and Falter, 2015; Gove *et al.*, 2016). The surrounding ocean may provide a major source of nutrition to coral reef communities (Munk and Sargent, 1954; Williams *et al.*, 2015), with an increase in phytoplankton biomass of up to 86% near islands and atolls, a phenomenon termed the "Island Mass Effect" (Doty and Oguri, 1956; Gove *et al.*, 2016). This suggests that there is more pelagic production available to reef communities than previously recognised (Hamner *et al.*, 2007). Phytoplankton is an essential energy source that drives marine ecosystems. An increased biomass may play a significant role in reef trophodynamics, increasing reef fish biomass, cover of calcifying benthic organisms, and vertical and horizontal movements of pelagic and mesopelagic fish communities (Wyatt *et al.*, 2010a; Wyatt *et al.*, 2012b; Gove *et al.*, 2016). However, the quantity of potential food available and its circulation onto the reef is subject to significant spatial and temporal variation (Wyatt *et al.*, 2012b; Wyatt *et al.*, 2013). It is determined by a wide range of transient hydrodynamic processes and physical drivers, such as wind, waves, tides, coastal upwelling and reef height morphology (Figure 1.3) (Hamner *et al.*, 2007; Lowe and Falter, 2015). These natural physical processes drive nutrients and plankton onto the forereef where schools of planktivorous fish form a "wall of mouths" and efficiently recycle them (Hamner *et al.*, 1988; Hamner *et al.*, 2007; Clark *et al.*, 2009; Wyatt *et al.*, 2010a). Planktivores are a key component of coral reef food webs, supporting other groups through excretion and when preyed upon (Williams *et al.*, 2015). Water depleted of prey, with zooplankton biomass up to seven times lower, then moves to the lagoon across reef crests (Hamner *et al.*, 2007). On the ebb tide, lagoon waters enriched with fish eggs spawned on the reef and other reef particulate organic matter (POM) advect offshore (Wyatt *et al.*, 2010a).

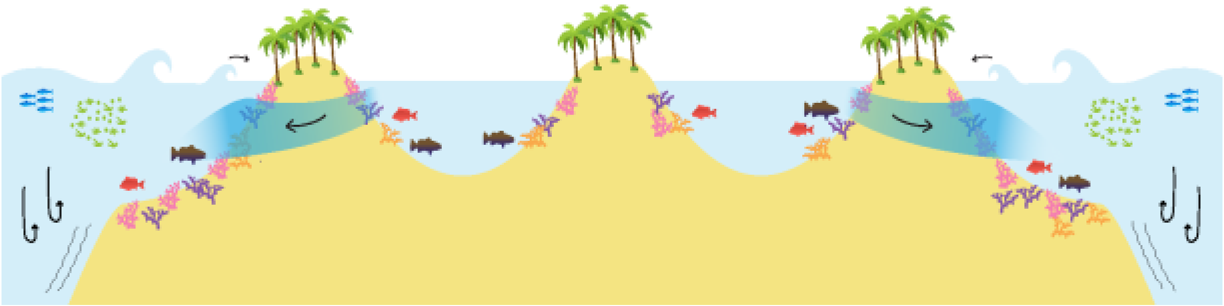


Figure 1.3. An illustration of an atoll-reef ecosystem showing both outer edge reefs and shallow inner lagoonal habitats. Arrows indicate water movement. Waves drive water over reef crests and into the atoll lagoon. Lagoonal water is flushed out of deep channels. Coastal upwelling occurs adjacent to outer reef slopes. Fish pictured on reefs are examples of coral reef predators (Lutjanidae and Serranidae), while those in the water column are planktivores.

Mobile link species are key to the integration of these nutrients across reef zones and adjacent pelagic habitats. Stable isotope values of herbivores and carnivores on the reef slope show evidence of reliance on oceanic resources (Wyatt *et al.*, 2012b), while conversely planktivorous transient megafauna aggregate close to reef slopes to feed on reef derived POM (Wyatt *et al.*, 2013). Pelagic predators found in the upper 100-200 m, such as albacore and yellowfin tuna, also forage on reef prey, often in the form of eggs found floating in the open ocean (Allain *et al.*, 2012), reinforcing the notion that energetic materials are transferred regularly across reef and adjacent pelagic habitats.

1.7 The Maldives

Although globally there are no pristine reefs remaining (Pandolfi *et al.*, 2003), the Maldives is estimated to have one of the most underexploited fisheries (Newton *et al.*, 2007), partly due to a small human population spread over many islands (Naseer and Hatcher, 2004). As such, reef fish biomass is still relatively high and top predators are abundant (Cinner *et al.*, 2018). The Maldives are thus a prime location to explore the role that higher trophic level predators play in food web trophodynamics.

The Maldives is a country composed of 22 atolls which run from north to south across the equator, forming a single chain which becomes double in the central part of the archipelago (Anderson *et al.*, 2011). They have an estimated coral reef area of 8920 km^2 (Spalding *et al.*, 2001) while the pelagic ocean within their Exclusive Economic Zone covers almost 1 million km^2 (FAO, 2006). Their north-south extent cuts across the equator and is subject to equatorial currents that change with the season. During the northeast monsoon (November to March), the Indian North Equatorial Current flows to the west from the south of the Indonesian islands, while during the southwest monsoon (April to October) the Counter Equatorial Current flows east. These currents transport high concentrations of nutrients, making the Maldives unique location. As one of the key Small Island Developing States affected by climate change there is an urgent need to analyse how a semi-pristine oceanic system sustains high abundances of marine predators. To fully understand the impact climate change may have on the system and its connectivity, and to maintain the integrity of these linkages for those reliant on them, it is crucial to understand how dependent the reefs are on oceanic production.

1.7.1 Marine management in the Maldives

Coral reefs are important to the local population (~420,000 people) as they provide livelihoods and services in the form of fisheries and, increasingly, tourism (> 1 million visitors annually) (Ministry Of Tourism, 2018). The primary fishery, with 70-75% of recorded landings, is the tuna fishery which is predominantly caught using the traditional live bait pole-and-line method (Adam and Sinan, 2013). Consequently, live bait is the most important reef fish resource. Accordingly in 2004, the main fishery export was tuna (89%) while reef fishery exports (live grouper, aquarium fish and sea cucumbers) comprised only 11% (Adam, 2006; McClanahan, 2011). However, as there is a growing demand for food for both tourists and locals alike, artisanal reef fisheries targeting large piscivores such as serranids (groupers), lutjanids (snappers), lethirinids (breams), and carangids (jacks) are becoming increasingly important. Indeed, estimated reef fishery annual catches increased from 2006 – 2014 (Sattar *et al.*, 2014) and further expansion and diversification of the fisheries sector and associated marine products was named as a key priority in the 2009-2013 Strategic Action Plan (Adam and Sinan, 2013). From 2013-2017 the annual number of tourists (2013: 1,125,202 tourists; 2017: 1,389,542 tourists) and growth rate of tourist arrivals increased (7.8% growth) (Cowburn *et al.*, 2018; Ministry Of Tourism, 2018). As the reef fishery was close to its Maximum Sustainable Yield in 2014 (Sattar *et al.*, 2014) it is almost certainly now overexploited. Currently, management of the Maldivian reef fishery is minimal, although size restrictions on grouper landings and exports were recently implemented following declines in their abundances (Marine Research Centre and Marine Conservation Society, 2011) and a nationwide shark fishing ban was introduced in March 2010 (Ushan *et al.*, 2012).

1.8 Thesis justification

Predators are an important component of coral reef communities, playing an ecological role structuring reef fish assemblages (Roff *et al.*, 2016). Predator distributions often vary spatially, with abundance, species richness, and biomass thought to be greater on outer reef slopes with greater proximity to deeper water (Dale *et al.*, 2011; Richards *et al.*, 2012). There is increasing evidence that reef sharks on outer edge reefs are heavily reliant on oceanic nutrients due to their proximity to the open ocean (Papastamatiou *et al.*, 2010; McCauley *et al.*, 2012c). However, the extent of this reliance across key teleost reef predators and inside lagoonal habitats is largely unknown.

While several older studies carried out extensive work analysing reef predator stomach contents to elucidate their resource use (Harmelin-Vivien and Bouchon, 1976; Shpigel and Fishelson, 1989), more recent research using stable isotopes to explore niche partitioning and resource use has focussed on sharks and pelagic teleosts (Gallagher *et al.*, 2017; Shipley *et al.*, 2018; Shiffman *et al.*, 2019). As a result, there is little isotopic information on how sympatric reef predators are able to co-exist in such high densities on coral reefs. Feeding specialisations may allow co-occurring species to partition resources to reduce competition and it is more likely to occur where resource diversity and population densities are higher (Araújo *et al.*, 2011). There is increasing evidence of intraspecific dietary specialisations in many large marine predators (Matich *et al.*, 2011; Patrick *et al.*, 2014; Bodey *et al.*, 2018), but, to my knowledge, no one has investigated this phenomenon among coral reef teleost predators, even though coral reefs are a prime location for it to occur. There is also increasing evidence that suggests that species resource use can vary substantially spatially (Matley *et al.*, 2017; Shiffman *et al.*, 2019), but this aspect is often not considered when investigating reef trophodynamics.

Reef predators are dominant components of the reef fishery (Sattar *et al.*, 2014), which provides livelihoods and food to millions globally (Pauly *et al.*, 2002). A range of anthropogenic and climate-induced stressors currently threaten coral reefs (Cinner *et al.*, 2016; Hughes *et al.*, 2017b) and reef predator populations are declining worldwide (Friedlander and DeMartini, 2002a; DeMartini *et al.*, 2008), but we still do not fully understand their ecological roles or how these may vary at an individual or spatial scale. In order to understand the ecosystem-wide implications of their declines, we need to identify the ecological linkages they may construct. Furthermore, for environmental managers to adequately protect and manage these species, detailed information on their resource and habitat usage is required.

1.9 Thesis outline

This thesis is a comprehensive study of coral reef predator trophodynamics. The overall aims of this research were, across an oceanic atoll:

1) to investigate predator distributions and identify the drivers of their community structure;
2) to compare inter- and intra-specific patterns of their resource use;
3) to identify the origin of the carbon supporting their biomass.

The **first data chapter** uses a combination of underwater visual census and baited remote underwater videos to assess reef predator distributions across an oceanic atoll. The relative importance of both outer edge reef slopes and inner lagoonal habitats in terms of reef predator communities was quantified. This raised the question of how these sympatric species could coexist at such high densities and partition resources. The **second data chapter** used bulk $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ stable isotope data derived from white muscle tissue of dominant fishery target reef predators to investigate how their resource use varied both inter- and intra-specifically and spatially. In the **third data chapter**, Bayesian stable isotope mixing models using bulk $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ stable isotope data aimed to determine the likely principal food sources (represented by primary consumers) supporting these reef predator species. This approach was then further developed in the **fourth data chapter** by using $\delta^{13}C$ stable isotope values of essential amino acids of four grouper species. This method provides greater resolution than bulk stable isotope data, offering additional insight into the origin of the carbon supporting the reef food web. In the **final data chapter**, a structural equation model was constructed to disentangle potential biotic and abiotic drivers of predator biomass and test whether the same carbon pathways identified as important through stable isotope analysis were drivers of observed predator biomass. In the **final chapter**, the thesis findings are reviewed and the contributions to the field of ecology are discussed. Recommendations for future research and the implications for management are also suggested.

Note: the final published paper from this chapter is appended to the thesis.

Chapter 2 The importance of oceanic atoll lagoons for coral reef predators

2.1 Introduction

Coral reef predators play an important role in structuring reef fish communities (Clark *et al.*, 2009; Roff *et al.*, 2016). They regulate the composition and dynamics of prey communities, directly through predation and indirectly through the modification of prey behaviour (Ceccarelli and Ayling, 2010; Roff *et al.*, 2016). Locally abundant teleosts such as snappers, emperors and groupers are an important part of the reef predator assemblage, making regular movements between hard and adjacent soft bottom habitats (Berkström *et al.*, 2012; Green *et al.*, 2015). They also substantially contribute to coral reef fishery yields, providing livelihoods to millions of people globally. Currently, populations of sharks and other reef fishes are experiencing worldwide declines (Graham *et al.*, 2010; Roff *et al.*, 2016), but their removal can result in community-wide impacts which may destabilise the food web (Bascompte *et al.*, 2005).

In both terrestrial and marine systems, predators show a preference for edge habitats (Phillips *et al.*, 2004; Heithaus *et al.*, 2006), such as forest grassland edges (Svobodová *et al.*, 2011), forereef ledges (Papastamatiou *et al.*, 2009) and deep water shelf areas (Cappo *et al.*, 2007). As such, reef predators may increase in density and diversity from shallow, lagoonal habitats to outer reef slopes (Friedlander *et al.*, 2010; Dale *et al.*, 2011). Outer reef habitats could provide a greater availability of resources; for example they host aggregations of planktivorous fish (Hamner *et al.*, 1988; Hamner *et al.*, 2007) which take advantage of increased plankton prey abundances (Wyatt *et al.*, 2013) and sustain reef predators (Frisch *et al.*, 2014; Matley *et al.*, 2018).

In the Maldives, atolls are characterised by oceanic outer reef slopes with deep channels separating inner shallow, lagoonal reefs from the adjacent open ocean. A range of hydrodynamic processes such as equatorial currents and local upwelling facilitate water mixing within the Maldivian archipelago (Sasamal 2007), enhancing biological production. Consequently, unlike more closed systems, nutritional resources are available throughout the atolls and into the lagoons due to extensive water circulation (Radice *et al.*, 2019). Furthermore, tourist resort islands, often located inside atoll lagoons, act as refuges for reef fish communities because fishing is prohibited there. As such, resort islands support a higher diversity of commercial fish species, such as groupers, than other permanently inhabited islands (Moritz *et al.*, 2017). Inner lagoonal reef habitats may thus be equally as important to reef predator assemblages as outer edge reefs (Skinner et al. 2019).

Fisheries in the Maldives traditionally focussed on tuna, but the annual reef fishery catch has increased (Sattar *et al.*, 2014) due to a growing demand for reef fish from tourists (Ministry Of Tourism, 2018). Moreover, the 2009-2013 Maldives Strategic Action Plan identified expansion and diversification of the fisheries sector as a national priority (Adam and Sinan, 2013), signifying further development and exploitation of the reef fishery. Although the Maldives was classified as one of the most underexploited fisheries in the Indian Ocean (Newton *et al.*, 2007; MacNeil *et al.*, 2015), there are no unfished or historically "pristine" coral reef ecosystems in the region (McClanahan, 2011). In addition, current estimates suggest that the reef fishery is approaching the limit of its maximum sustainable yield (Sattar *et al.*, 2014) and prior to 1998 sharks were intensively fished (Ushan *et al.*, 2012). There is thus an urgent need to assess abundances and distributions of reef predator populations to determine which atoll habitats are important.

All survey methods for assessing abundances of fish have their strengths and weaknesses. Because of this, multiple methods to assess predator populations are desired that take into inherent interspecific differences in body size, habitat association, aggregative or schooling behaviour, mobility (particularly in the case of elasmobranchs), or the response to the presence of divers or various types of equipment (Kulbicki, 1988; Willis and Babcock, 2000; White *et al.*, 2013). Underwater visual census (UVC) allows a comprehensive sampling of smaller, resident species that are harder to detect, however time underwater is limited and high replication is required to detect rarer (or more mobile) species (Dulvy *et al.*, 2003). Conversely, baited remote underwater video (BRUV) offers a non-invasive and non-destructive technique that can cover a wide geographic area, depth range and number of habitats and is particularly useful in assessing occurrences of larger, more mobile species (Willis and Babcock, 2000; Cappo *et al.*, 2003; Harvey *et al.*, 2012; White *et al.*, 2013). However, it can be difficult and time consuming to identify species from footage and there is a potential bias arising from attracting species to the bait (Willis and Babcock, 2000; Cappo *et al.*, 2003; Harvey *et al.*, 2012; Espinoza *et al.*, 2014). By combining these two survey methodologies, a more comprehensive estimate of reef predator abundances and distributions can be achieved.

This study aimed to assess coral reef predator assemblages across an oceanic atoll using both BRUV and UVC. We sought to determine if there were 1) differences in the abundance, size, biomass, and diversity of predators between the inner and outer atoll, and 2) what habitat characteristics help explain the differences?

2.2 Materials and Methods

2.2.1 Study site

The Maldives is an archipelago of 16 atolls and is the historical archetype of a coral reef province (Naseer and Hatcher, 2004). The coral reef area is 8920 km^2 (Spalding *et al.*, 2001) while the EEZ covers almost 1 million km^2 (FAO, 2006). The north-south extent cuts across the equator and is subject to equatorial currents transporting high concentrations of nutrients (Sasamal, 2007). Fieldwork was conducted in North Malé atoll (4°18'34.5"N, 73°25'26.4"E) from January to April 2017. North Malé Atoll is located in the centre of the double chain of the Maldivian archipelago, on the eastern side. It has an atoll perimeter of 161 km, 117.9 km of which is shallow edge reef while 43.1 km is deeper channels (Beetham and Kench, 2014), promoting water exchange between the adjacent open ocean and the atoll lagoon. The atoll has 189 reef platforms, covering 22.3% of its surface area (Naseer and Hatcher 2004). The atoll was divided into two areas: 1) inner: enclosed lagoonal reef platform sites, and 2) outer: outer reef slope sites.

2.2.2 Underwater visual census (UVC)

UVC was carried out at 40 sites, 20 in the inner atoll and 20 in the outer atoll (Figure 2.1). A total of 200 transects were surveyed, 100 within each atoll area. At each site five 50 x 5 m transects were laid parallel to the forereef habitat at 2.5 - 15 m depth. A minimum of 5 m was left between transects to ensure independence. Abundances and sizes to the nearest centimetre of all reef predator species were recorded (here predators at assumed trophic levels 3.5 and above, species list in Appendix Table A1). Predators were characterised as either mobile and highly visible or cryptic and site attached based on their behaviour (Brock, 1982). Two observers recorded the predatory fish assemblage. The first observer laid the transect while recording all mobile, highly-visible predators and the second searched the benthos for cryptic, site-attached predators. Percent cover of branching, massive and table coral, and macroalgae was estimated for each transect in the following categories: 0% = Absent, >0 and <25% = Low, >25 and <50% = Fair, >50 and <75% = Good, >75 % = Excellent (Chou *et al.*, 1994). Reef habitat structural complexity was visually assessed on a 6-point scale from 0 to 5, where 0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex, 4 = very complex and 5 = exceptionally complex (Polunin and Roberts, 1993). Abundances of the crown of thorns (*Acanthaster plancii*) and pin cushion (*Culcita novaguineae*) starfish, both coral predators, were also recorded by the second observer. The same observers were used throughout the surveys to prevent observer bias (Willis and Babcock, 2000). A training period was carried out prior to data collection to ensure accurate species identification and size estimates (Wilson *et al.*, 2007).

2.2.3 Baited remote underwater video (BRUV)

Overall, 205 BRUVs were deployed, 102 in the inner atoll and 103 in the outer atoll (Fig 1). BRUV deployments were restricted to depths of 2.5 to 15 m to sample the same habitat as the UVC surveys and set ≥ 600 m apart (Cappo *et al.*, 2003). GoPro Hero 4 cameras with red filters were attached to stainless steel frames with detachable bait arms holding a bait bag. Bait bags were made out of 12 mm wire mesh encased in 15 mm plastic mesh. These were attached to 160 cm lengths of 22 mm plastic PVC pipe using cable ties and a metal pin. Bait consisted of ~1 kg of guts and discards from a range of oily fish species: bonito (*Sarda orientalis*), rainbow runner (*Elagatis bipinnulata*) and great barracuda (*Sphyraena barracuda*). BRUVs were deployed with 6 mm polypropylene ropes and surface marker buoys and set manually on coral rubble or sand. For each BRUV, the time deployed and the depth were recorded. Cameras were only deployed during daylight hours (09:00 - 17:00) to avoid bias from changes in feeding behaviour (Willis and Babcock, 2000) and left to record for approximately 70 minutes to ensure 60 min of analysable footage.

During video processing, 25 deployments were excluded from analysis as i) the field of view was blocked by upright substrate or ii) the camera angle had moved and was facing straight up or straight down (Asher *et al.*, 2017). Consequently, only 180 deployments were included, 90 from each atoll area. Habitat was classified into one of nine categories: 1) aggregate reef, 2) dead boulder coral/rock, 3) entirely reef rubble, 4) rubble/reef, 5) rubble/sand, 6) sand

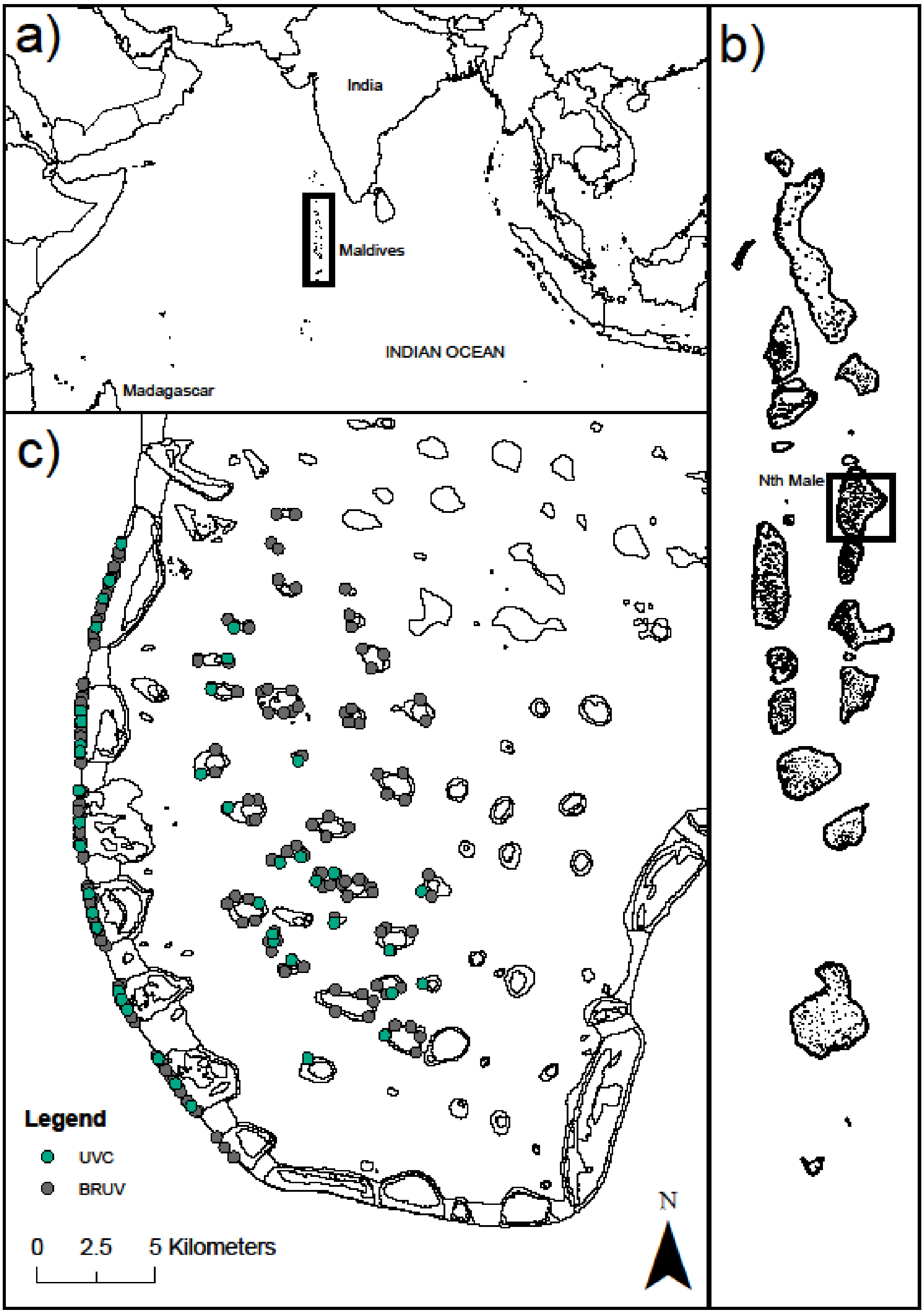


Figure 2.1. Location of the underwater visual census (UVC) and baited remote underwater video (BRUV) locations. a) Maldives location in the north Indian Ocean (3.2028° N, 73.2207° E), b) North Malé Atoll in the central Maldives archipelago (4.4167° N, 73.5000° E), and c) the UVC and BRUV inner and outer survey locations in North Malé Atoll.

flat, 7) sand with reef in view, 8) sand with scattered coral/rock and 9) spur and groove, the first habitat type being the most dominant of the two identified (Asher *et al.*, 2017).Reef habitat structural complexity was visually assessed on a 6-point scale (see above) (Polunin and Roberts 1993). Analysis of footage was focused solely on upper trophic level fish predators i.e. all shark, Aulostomidae, Carangidae, Fistulariidae, Scombridae and Serranidae species and larger bodied, more mobile Lutjanidae and Lethrinidae species (see Table A1 for full species list). Predators were identified to the lowest taxonomic level of species in most cases, but where species could not be identified, individuals were pooled at the genus level (Espinoza *et al.*, 2014). For each species, the maximum number seen at any one time on the whole video (MaxN) was recorded (Harvey *et al.*, 2012). Video analysis began after a settlement period (min 02:00 – max 08:00 minutes) had elapsed (Kiggins *et al.*, 2018). The settlement period was characterised as over when all sand or sediment had settled and visibility returned to normal and at least a minute had passed since the BRUV was moved or repositioned.

2.2.4 Data Analysis

The following statistical procedures were carried out for both UVC and BRUV data using PRIMER 6 (v. 6.1.15) with the add-on PERMANOVA+ (v. 1.0.5) (Anderson et al. 2008) and R version 3.5.2 (R Core Team, 2017) linked with RStudio version 1.1.463 (RStudio Team, 2012).

Species richness for each dataset was determined using the species accumulation curve in the vegan R package (Oksanen *et al.*, 2018). Curves were generated using 100 permutations and the “exact” method, which finds the expected mean species richness. 95% confidence intervals were calculated from standard deviations. Only individuals identified to species level were included.

Spatial variation in predator populations

UVC assemblage data were analysed at the transect level and BRUV assemblage data at the BRUV level. Where BRUV sites were repeat sampled on different days each deployment was counted as an independent sample. Predator abundance data were square root transformed to reduce right skewness from large outliers and because square root transformation can be applied to zero values. A resemblance matrix was created based on Bray-Curtis similarity measures. Using the R vegan package (Oksanen *et al.*, 2018), data were graphically compared using non-metric multi-dimensional scaling (nMDS) with a Kruskal fit scheme set to 3 and a minimum stress level of 0.01. If there were clear outliers, these were removed and an additional nMDS plot was carried out on a subset of the data (see supplemental material for all nMDS plots; Figure A1 and A2). Significantly correlated species were extracted and overlaid on the nMDS plots as vectors. Differences in the predator assemblage occurring between atoll areas and among sites were investigated using a nested model in PERMANOVA+ (Type III Sum of Squares, under a reduced model with 9999 permutations), where site (UVC: 40 levels and BRUV: 39 levels) was a random factor nested within the fixed factor area (2 levels). Species contributing to between-area dissimilarity and within-area similarity were identified using the SIMPER function (Clarke and Warwick, 2001).

UVC predator biomass data was calculated using length-weight relationships available on FishBase (http://fishbase.org) with the exception of *Aethaloperca rogaa* where length-weight relationships were taken from Mapleston et al. (2009). Spatial differences in UVC predator biomass were investigated using a Generalized Linear Model (GLM) with transect level biomass as the response variable and site nested within area as the predictor variables. Model normality and homogeneity assumptions were assessed by plotting predicted values against residuals, predicted values against standardised residuals, and qqplots of standardised residuals. Biomass data were log transformed to satisfy model assumptions. An analysis of variance (ANOVA) was applied to determine whether effects were significant ($p < 0.05$). A second GLM was run with the same parameters but without the nurse shark, *Nebrius ferrugineus*, as three large (1.9 – 2.5 m) individuals were recorded on only one transect in the inner atoll.

Variation in predator body size between atoll areas was investigated for each predator family individually using a linear mixed effects model with the R package lme4 (Bates *et al.*, 2015). Body size (cm) was the response variable, area was a fixed effect and species was a random effect. Model assumptions were checked as above and data were log transformed to meet assumptions when necessary. When the predator family only had one recorded species (Aulostomidae, Carcharhinidae, Scorpaenidae), an ANOVA with body size (cm) as the response variable and area as the predictor variable was used. Size data were checked for normality and homogeneity of variances using a Shapiro-Wilks test and a Levene's test respectively. When data did not conform to these parameters, a non-parametric Kruskal-Wallis test was used. Although two species of Carangidae were recorded, *C. ignobilis* was only observed once in the inner atoll. This observation was removed from analysis and an

ANOVA was used. Fistulariidae and Ginglymostomatidae were only recorded in the inner atoll so no size-based comparisons were made.

Correlation with environmental variables

Using PRIMER, environmental data were normalised as they were measured on different scales. For each entry of a variable, the mean of the variable is subtracted and the value is divided by the standard deviation for that variable (Clarke and Gorley, 2006). UVC environmental variables consisted of depth, complexity, branching coral cover (BC), massive coral cover (MC), table coral cover (TC), algal cover (AC), abundance of crown of thorns starfish (COTS) and abundance of pin cushion starfish (PIN) while BRUV environmental variables consisted of depth, complexity and habitat type. Variables were assessed for collinearity using pairs plots and by calculating the variance inflation factor (VIF) using the vifstep method in the usdm R package (Naimi *et al.*, 2014). VIF quantifies the severity of collinearity between predictor variables. The vifstep method calculates VIF for all variables in a stepwise fashion. It excludes the variable with a VIF > specified threshold, repeating the process until no variables have a VIF > specified threshold. Here, the VIF threshold was set to 3 (Zuur *et al.*, 2010). Data were compared using Principal Coordinates Analysis (PCO) based on Euclidean distance similarity measures with overlaid vectors of Pearson's correlated environmental variables. Differences in environmental variables between inner and outer atoll were investigated using a nested model in PERMANOVA+ (Type III Sum of Squares, under a reduced model with 9999 permutations), where site (UVC: 40 levels and BRUV: 39 levels) was a random factor nested within the random factor area (2 levels).

To investigate the relationships between the predator assemblage and the respective environmental variables (Table A2), the RELATE function in PRIMER 6 (v. 6.1.15) with a Spearman's Rank Correlation coefficient and 9999 permutations (Clarke and Warwick 2001) was used. These correlations were further tested using a distance-based multiple linear regression model (DISTLM) in PERMANOVA+ (v. 1.0.5) (Clarke and Gorley, 2006), which models the relationship between a multivariate distance-based dataset, as described by a resemblance matrix, and the variables (Clarke and Gorley, 2006) using distance based redundancy analysis (dbRDA) (Clarke and Gorley, 2006). Relationships were first analysed using marginal tests. The Best selection procedure was used as it incorporates and examines the selection criterion for all possible combinations of predictor variables, with an AICc selection criterion and 9999 permutations of the raw data to obtain p-values for each individual predictor variable (Clarke and Gorley, 2006). AICc values indicate the goodness of a model fit to the data and the model with the lowest AICc value was considered the most parsimonious (Symonds and Moussalli, 2011).

2.3 Results

A total of 6524 predators of 47 species and ten families were recorded from the 200 transects that surveyed 50,000 m^2 of reef (Figure 2.2A) and the 10,800 minutes of examined footage from 180 BRUVs (90 in each area) (Figure 2.2B). Species accumulation plots showed similar patterns and indicated that the sampling effort of each method was sufficient to record most of the predators occurring in the area surveyed (Figure 2.3). However, both methods showed higher predator species richness in the inner atoll compared to the outer atoll, and this difference was greatest for the BRUVs.

2.3.1 Spatial variation in predator populations

Similar numbers of individuals and species were recorded in each atoll area (
Table 2.1). Five species were only recorded in the inner atoll (*Carcharhinus falciformis*, *Elagatis bipinnulata*, *Epinephelus ongus*, *Lethrinus harak* and *Lethrinus microdon*) while seven species were only recorded in the outer atoll (*Carcharhinus amblyrhynchos*, *Epinephelus malabaricus*, *Epinephelus tauvina*, *Lutjanus decussatus*, *Lutjanus fulvus*, *Macolor macularis* and *Negaprion acutidens*; Table A1).

Table 2.1. Summary of collected reef predator data in inner and outer atoll areas by underwater visual census (UVC) and baited remote underwater video (BRUV).

	Inner			Outer		
	UVC	**BRUV**	**Total**	**UVC**	**BRUV**	**Total**
Individuals	1786	1527	3313	2339	872	3211
Species	33	34	39	33	31	41
Species unique to method	5	6		10	8	
Families	10	8	10	8	8	10

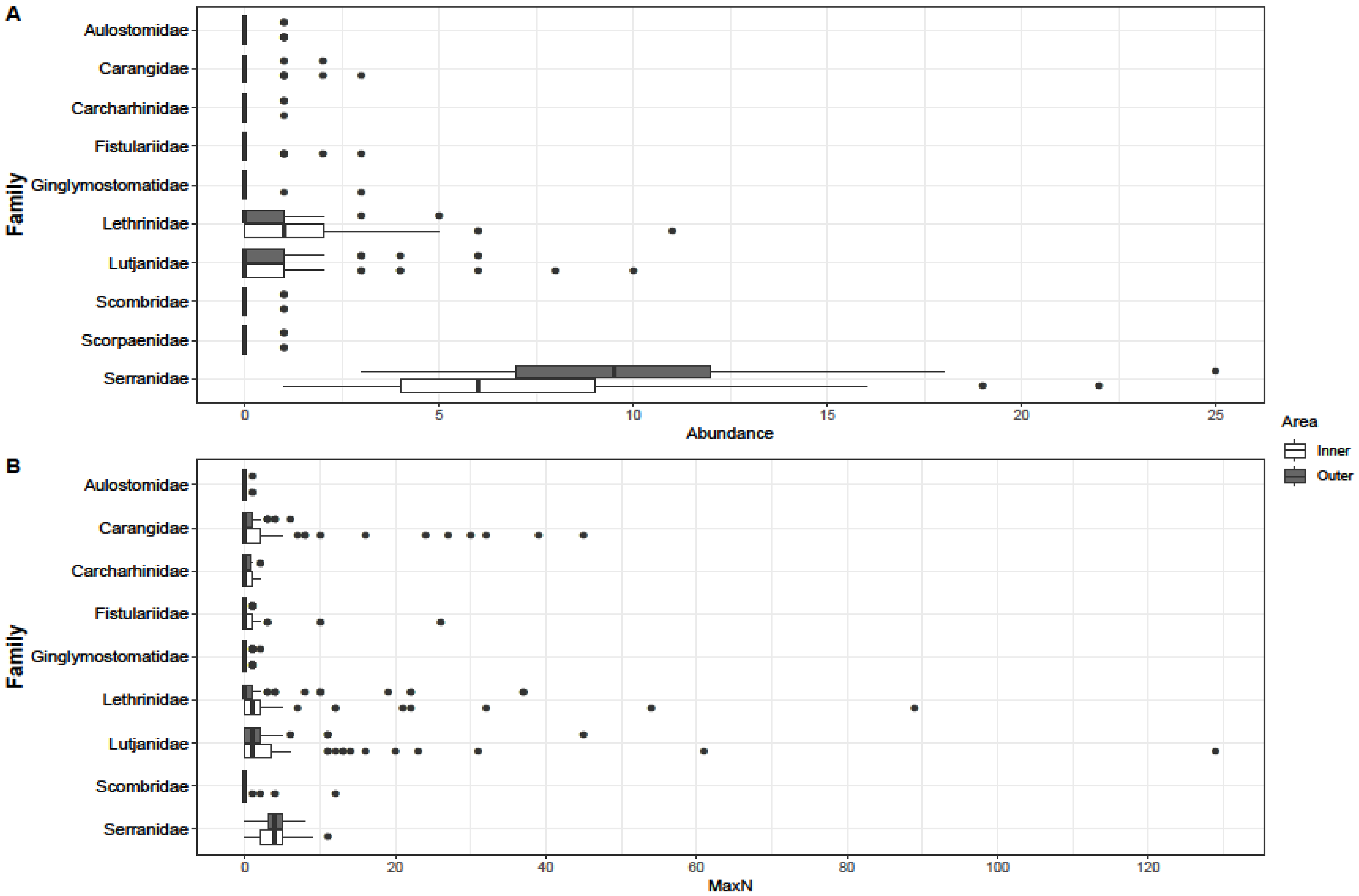


Figure 2.2. A) Abundance from underwater visual census (UVC) and B) MaxN from baited remote underwater video (BRUV) of predator families in inner and outer atoll. Individual points are A) 250 m2 transects and B) BRUV deployments.

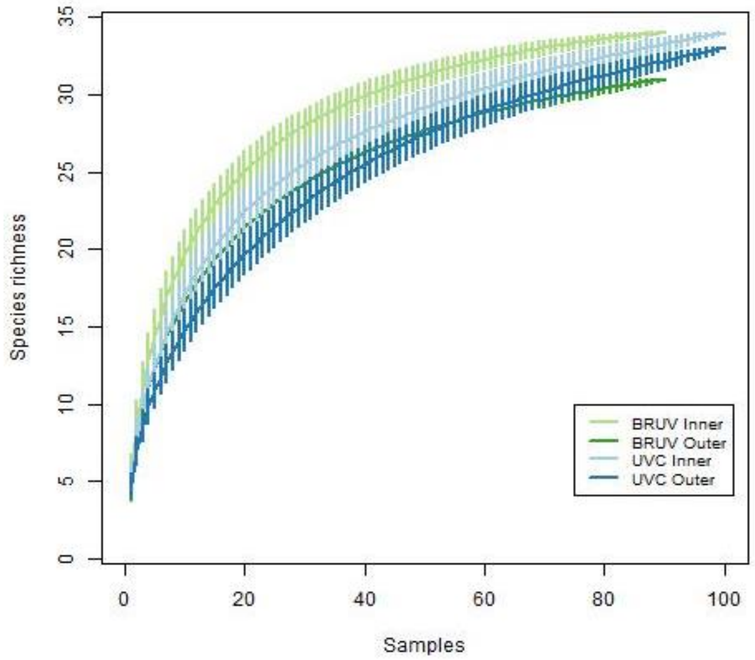


Figure 2.3. Species accumulation curves derived from the cumulative number of UVC transects and BRUV deployments in both inner and outer atoll. Bars represent 95% confidence intervals derived from standard deviation.

Total recorded predator biomass was 0.29 t ha^{-1} in the inner atoll and 0.25 t ha^{-1} in the outer atoll. The biomass of Carcharinidae, Lethrinidae, Lutjanidae and Serranidae were greater in the outer atoll while biomasses of Aulostomidae, Carangidae and Scombridae were greater in the inner atoll (Figure 2.4). There was no significant difference in total predator biomass between areas (ANOVA, $p < 0.05$) but there was a highly significant difference in biomass among sites within areas (ANOVA, $F_{1,39} = 2.08$, $p = <0.001$). When *Nebrius ferrugineus* was removed from biomass calculations, total predator biomass was significantly greater in the outer atoll (ANOVA, $F_1 = 4.51$, $p = <0.05$) and there were still significant differences among sites within each area (ANOVA, $F_{1,39} = 1.82$, p = $p < 0.05$).

The size of Aulostomidae (ANOVA, $p > 0.05$), Carcharinidae (ANOVA, $p > 0.05$) and Scorpaenidae (Kruskal-Wallis, $p > 0.05$) did not differ between atoll areas but Carangidae were larger in the outer atoll (mean inner: 28.56 cm; outer: 39.75 cm; ANOVA, $F_{1,11} = 12.68$, $p = < 0.001$). Linear mixed effects models suggested no difference in mean size of Scombridae between atoll areas (mean inner: 49.67 cm; outer: 49.00 cm), but Lethrinidae (mean inner 21.79 cm; outer: 24.74 cm), Lutjanidae (mean inner: 23.04 cm; outer: 30.46 cm), and Serranidae (mean inner: 18.81 cm; outer: 18.99 cm) were all significantly larger in the outer atoll (Table 2.2; Figure 2.5).

Table 2.2. Differences in predator body size between inner and outer atoll areas as determined by linear mixed effects models. Separate models were run on each individual family.

Formula: Size ~ Area + (1 | Species)

	Estimate	SE	df	*t*	*p*-value	
Lethrinidae						
(Intercept)	21.87	1.32	1.51	16.56	0.01	*
Area	2.96	0.78	174.66	3.79	0.00	***
Lutjanidae						
(Intercept)	25.69	2.61	4.43	9.83	0.00	***
Area	6.39	1.59	129.76	4.01	0.00	***
Scombridae						
(Intercept)	45.76	12.48	1.08	3.67	0.16	
Area	-2.62	4.51	4.00	-0.58	0.59	
Serranidae						
(Intercept)	20.28	1.72	11.98	11.77	0.00	***
Area	2.30	0.28	1631.84	8.13	0.00	***

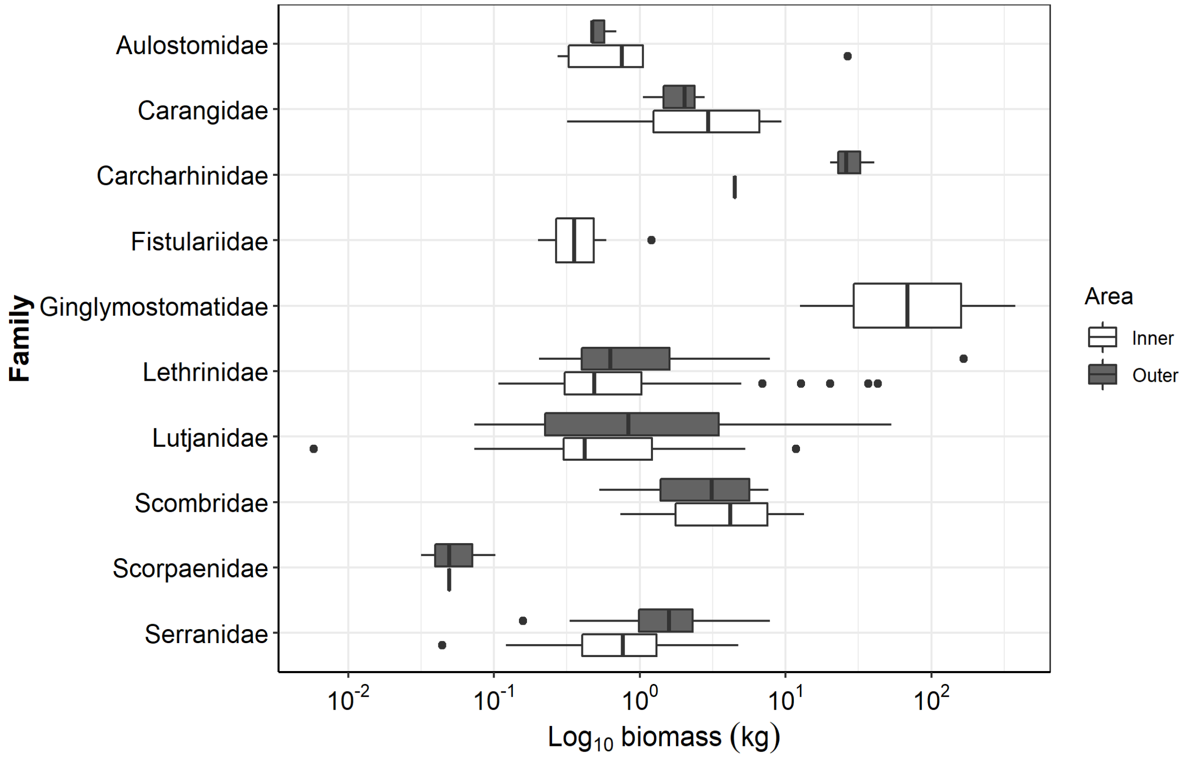


Figure 2.4. Biomass (kg) of predator families recorded by underwater visual census (UVC). Values are on a log10 scale.

The nMDS plot of the UVC predator data suggested different inner and outer atoll predator assemblages, while that of the BRUV data suggested greater overlap between areas (Figure 2.6). There were highly significant differences in the predator assemblage between atoll areas (Nested PERMANOVA, UVC = $F_1 = 17.57$, p = <0.001; BRUV = $F_1 = 4.07$, p = <0.001) and among sites (Nested PERMANOVA, UVC = $F_{38} = 2.21$, p = <0.001; BRUV = $F_{37} = 1.40$, p = <0.001). SIMPER analysis revealed a high level of dissimilarity in biota between atoll areas (SIMPER UVC = 63.94%, driven by *Cephalopholis leopardus*, C. argus, and *Anyperodon leucogrammicus*; BRUV = 74.11%, driven by *Caranx melampygus* and *C. argus*; Table 2.3). Within areas, similarity of predator assemblages recorded using UVC was moderate (SIMPER, inner: 41.10%, driven by *C. argus*, *A. leucogrammicus*, and *Monotaxis grandoculis*; outer: 49.12%, driven by *C. argus* and *C. leopardus*), while similarity of those recorded using BRUV was low (SIMPER, inner: 29.07%, driven by *Aethaloperca rogaa*, *Lutjanus bohar*, and *C. argus*; outer: 33.37%, driven by *C. argus*, *A. rogaa*, and *L. bohar*; (Table 2.3).

Table 2.3. Main species contributing to between-area dissimilarity and within-area similarity using both UVC and BRUV abundance data. Species contributing below 9% are not shown.

	Dissimilarity between	Similarity within area	
Species	**Areas**	**Inner**	**Outer**
UVC			
C. leopardus	13.73%	-	30.41%
C. argus	11.22%	34.62%	40.56%
A. leucogrammicus	10.04%	18.44%	-
A. rogaa	9.97%	15.39%	12.39%
M. grandoculis	9.17%	19.35%	-
BRUV			
C. melampygus	9.95%	-	-
C. argus	9.08%	12.07%	32.23%
A. rogaa	-	30.63%	17.64%
L. bohar	-	20.86%	14.67%
M. grandoculis	-	10.30%	-
C. nigripinnis	-	-	12.31%

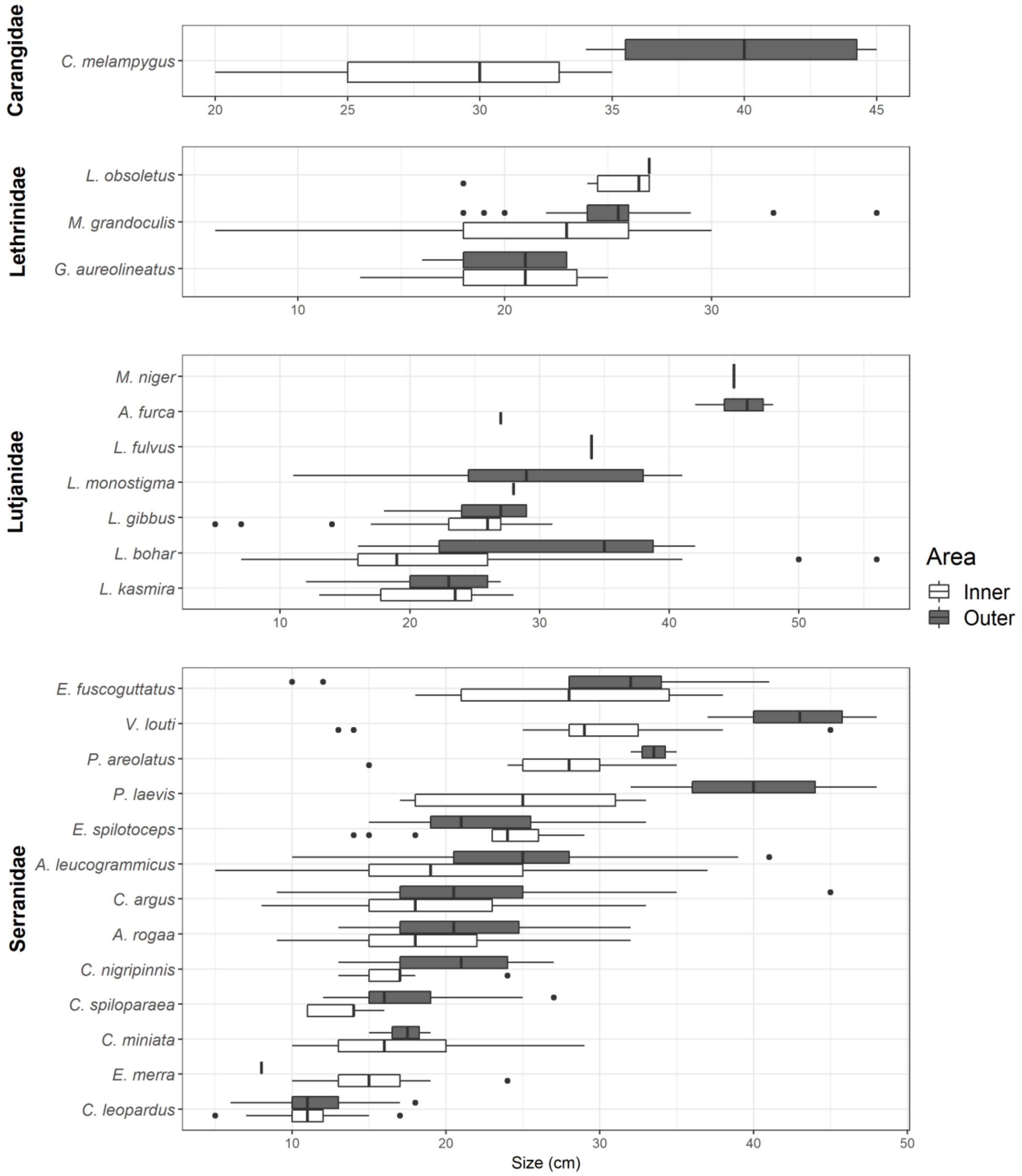


Figure 2.5. Total length (cm) of predators belonging to four families where there were significant differences between inner and outer atoll, as indicated by ANOVA and linear mixed effects models. Vertical bars represent the median.

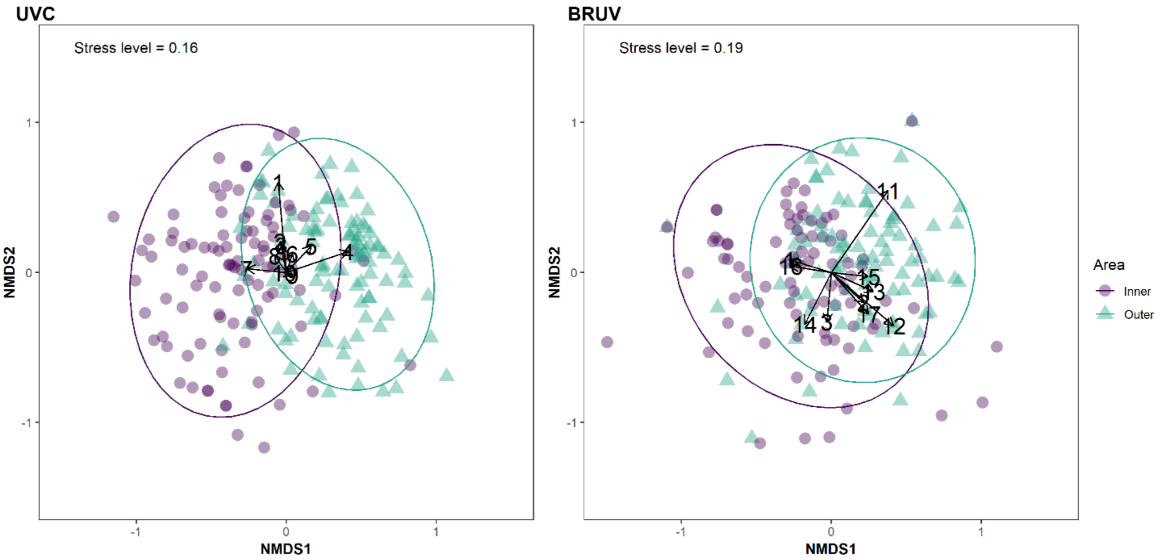


Figure 2.6. Non-metric multidimensional scaling (nMDS) of predator abundance data from A) underwater visual census (UVC) and B) baited remote underwater video (BRUV). Species that are significantly correlated (p < 0.05) are overlaid. UVC (1-10) and BRUV (1-3, 11-17): 1: *Aethaloperca rogaa*; 2: *Aprion virescens*; 3: *Caranx melampygus*; 4: *Cephalopholis spiloparea*; 5: *Epinephelus fasciatus*; 6: *Epinephelus malabaricus*; 7: *Epinephelus merra*; 8: *Gnathodentex aureolineatu;* 9: *Macolor niger;* 10: *Pterois antennata*; 11: *Cephalopholis argus*; 12: *Cephalopholis leopardus*; 13: *Cephalopholis nigripinnis*; 14: *Cephalopholis* spp; 15: *Epinephelus spilotoceps*; 16: *Lutjanus bohar*; 17: *Nebrius ferrugineus*.

2.3.2 Correlation with environmental variables

None of the UVC or BRUV environmental predictor variables were collinear. Environmental data varied significantly between areas (Nested PERMANOVA, UVC = F_1 = 11.95, p = <0.001; BRUV = F_1 = 15.99, p = <0.001) and among sites (Nested PERMANOVA, UVC = F_{38} = 5.89, p = <0.001; BRUV = F_{37} = 1.58, p = <0.05). The first two axes of a PCO explained 82.88% of the total variation in the BRUV environmental data and showed areas to be relatively separate. There was similar separation between atoll areas in the UVC environmental data but the first two axes of the PCO only explained 43.1% of the total variation in the data and the points were more clustered.

The predator assemblage was correlated with the environmental data collected using UVC (RELATE, Rho = 0.115, p <0.05) and BRUV (RELATE, Rho = 0.157, p <0.05). With the UVC data, marginal tests showed depth (Pseudo-F = 25.73, p <0.001, Prop. variation = 0.12), BC

(Pseudo-*F* = 7.10, p <0.001, Prop. variation = 0.3), MC (Pseudo-*F* = 8.12, p <0.001, Prop. variation = 0.04), TC (Pseudo-*F* = 2.73, p <0.05, Prop. variation = 0.01), complexity (Pseudo-*F* = 3.57, p <0.005, Prop. variation = 0.02) and PIN (Pseudo-*F* = 5.18, p <0.001, Prop. variation = 0.03) had a significant interaction with the predator assemblage. The most parsimonious model included depth, BC, MC and complexity (DISTLM; AICc = 1479.1), which when visualised using a dBRDA explained 87.2% of the variation in the fitted data but only 13.6% of the total variation in the data (Figure 2.7A). For the BRUV data, marginal tests showed complexity (Pseudo-*F* = 3.18, p <0.005, Prop. variation = 0.02), depth (Pseudo-*F* = 3.26, p <0.001, Prop. variation = 0.02) and habitat type (Pseudo-*F* = 2.31, p <0.05 Prop. variation = 0.01) as having a highly significant correlation with the predator assemblage, but the final best model included only depth and complexity (DISTLM; AICc = 1377.8). Results visualised using a dbRDA explained 100% of the variation in the fitted data but only 3.7% of the total variation in the data (Figure 2.7B).

2.4 Discussion

There were several distinct differences between the inner lagoonal and outer edge reef habitats. In contrast to previous studies, density and diversity of predators were similar between the inner lagoonal and outer forereef slopes (Friedlander *et al.*, 2010; Dale *et al.*, 2011), but there were significant differences in species composition. Furthermore, when the rarely recorded *Nebrius ferrugineus* was omitted, biomass was significantly greater along the outer reef slopes. Lethrinidae, Lutjanidae, and Serranidae, were also significantly larger in the outer atoll, so despite being more numerically abundant in the inner atoll, their mean biomass was greater along the outer reef slopes. Schooling species belonging to these families (e.g. *Gnathodentex aureolineatus* and *Lutjanus kasmira*) were more frequently recorded in the outer atoll (Table A1) and several large bodied species of Lutjanidae and Serranidae were also uniquely recorded in the outer atoll (e.g. *Epinephelus malabaricus*, *Lutjanus decussatus*, *Lutjanus fulvus*, and *Macolor macularis*).

These findings are consistent with ontogenetic shifts in habitat use. Although teleost reef predators often have smaller home ranges (Nash *et al.*, 2015), some species of Lutjanidae, Lethrinidae and Serranidae may move tens to hundreds of kilometres between habitat types as they undergo ontogenetic shifts, moving from juvenile nurseries such as mangroves and seagrasses to their adult habitat on coral reefs (Williams, 1991; Green *et al.*, 2015).

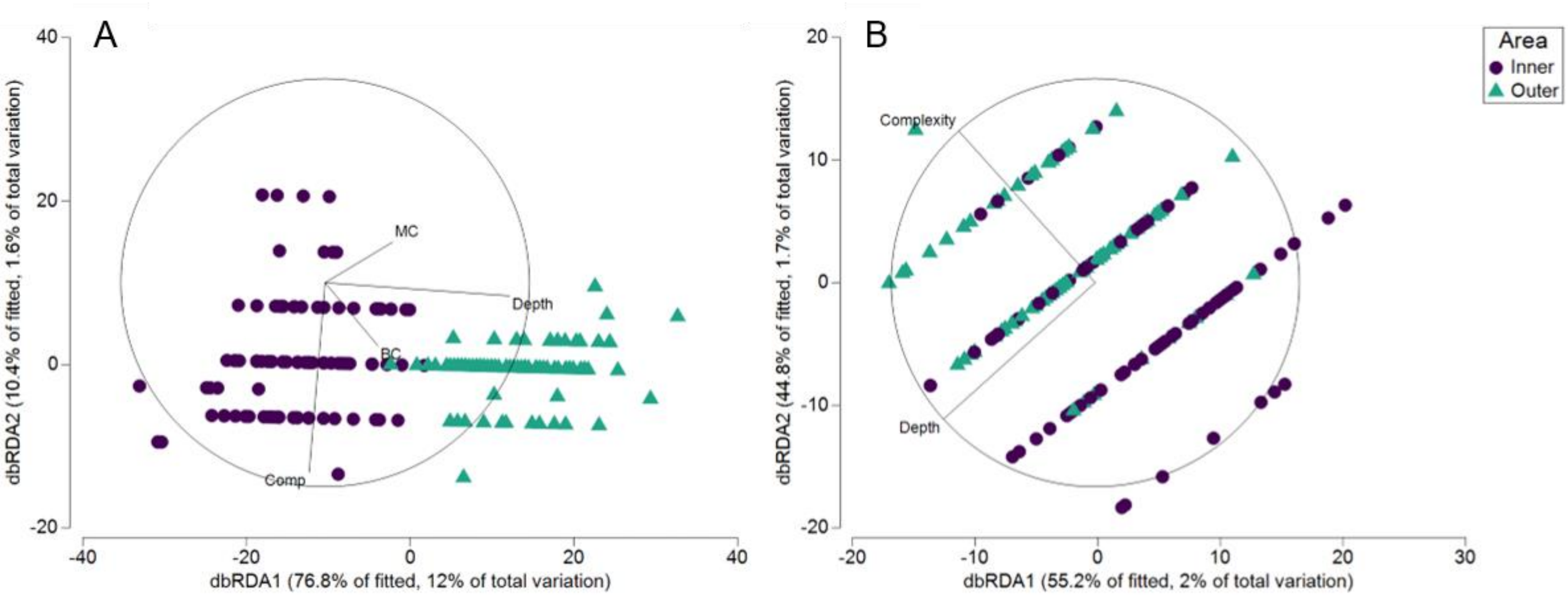


Figure 2.7. Distance-based redundancy analysis (dbRDA) of Bray-Curtis dissimilarities calculated from square-root transformed abundances of reef predator species vs. environmental predictor variables. The most parsimonious model was chosen using the AICc selection criterion and included A) complexity, depth, branching coral (BC), and massive coral (MC) for the underwater visual census (UVC) predator data, and B) depth and complexity for the baited remote underwater video (BRUV) predator data.

The presence of juvenile nursery habitats close to coral reefs increases adult biomass (Mumby *et al.*, 2004; Nagelkerken, 2007) while a lack of nursery habitats has been linked to lower adult densities and the absence of some species (Olds *et al.*, 2012; Wen *et al.*, 2013). The significant differences in predator sizes and abundances between inner and outer atoll found here are consistent with ontogenetic habitat shifts, and indicate that the inner atoll lagoon may be an important nursery habitat for many of these predator species. In the British Virgin Islands, nearly half the reef fishes exhibited ontogenetic shifts between lagoons and forereefs and almost all species were significantly larger in the reef habitat than in the lagoon (Gratwicke *et al.*, 2006). Furthermore, even isolated nursery habitats are utilized by juvenile emperors, suggesting that ontogenetic migrations of these species act to connect adult and juvenile habitats (Nakamura *et al.*, 2009). In North Malé Atoll, the proximity of the edge and lagoonal reefs to each other, in addition to the relatively shallow nature of the lagoon, may facilitate a high degree of mobility and connectivity between inner and outer atoll (Berkström *et al.*, 2013).

Differences in the reef habitat between atoll areas may also play a role. The outer reef slopes provide a larger, more continuous reef area compared to the shallow inner reefs, where soft bottom habitat is extensive. Large piscivorous fish are more abundant in areas of higher live coral cover with greater habitat structural complexity (Connell and Kingsford, 1998) and growth rates and abundances of predatory fishes tend to be higher when prey densities are greater (Beukers-Stewart *et al.*, 2011). Higher prey availability is also a key driver of ontogenetic emigrations of snappers and emperors from nearshore to coral reef habitats (Kimirei *et al.*, 2013). The larger body sizes and school sizes in the outer atoll, in addition to the unique occurrence of several of these species, suggest that this habitat may be of a higher quality, providing sufficient food and space to fit the requirements of these predator species. However, only a detailed assessment of the available habitat and prey assemblages will help determine the factors influencing predator distributions.

Several families had a greater biomass in the inner atoll, including Aulostomidae, Carangidae, Fistulariidae and Ginglymostomatidae. Aulostomidae were rarely recorded along the outer edge reefs although their habitat preferences include reefs extending to the continental slope (Bowen *et al.*, 2001). Competition from the greater numbers of Lutjanidae and Serranidae may play a role in limiting their numbers in the outer atoll. Higher numbers of the bluefin trevally, *C. melampygus*, were the main contribution to the greater biomass of

Carangidae. *C. melampygus* is an important mobile predator that is prominent in nearshore waters (Hobson, 1979; Sancho, 2000). Their diet consists of diurnally active prey, predominantly from shallow-water habitats (Sudekum *et al.*, 1991), which suggests they may enter the lagoon during the day to hunt. The lagoon may also represent an important nursery ground for this species, as juvenile *C. melampygus* occupy shallow-water protected environments such as lagoons and estuaries (Smith and Parrish, 2002). As no UVC surveys or BRUV deployments were conducted at night, it is not certain whether their numbers would increase along the outer edge reefs after dark. Fistulariidae and Ginglymostomatidae had a greater biomass in the inner atoll, but only because biomass estimates were derived solely from UVC. Fistulariidae prefer coastal areas with soft bottoms (Fritzsche, 1976) and were recorded in both atoll areas with BRUVs, but the UVC surveys were conducted solely on hard reef substrate. Ginglymostomatidae were frequently recorded in both inner and outer atoll on BRUVs but biomass estimates came from the occurrence of several large *N. ferrugineus* on two transects in the inner atoll, while none were recorded during UVC in the outer atoll. Future work would benefit from the inclusion of biomass estimates from several survey methods and from conducting surveys at night.

Several species were recorded solely in one atoll area. Two of the species unique to the outer atoll were the grey reef shark, *Carcharhinus amblyrhynchos*, and the lemon shark, *Negaprion acutidens*. Grey reef sharks prefer forereef habitats over lagoons (Papastamatiou *et al.*, 2018) and although juvenile lemon sharks are atoll lagoon residents (Filmalter *et al.*, 2013), adults move to deeper coastal reef habitats (Compagno, 1984). Conversely, the silky shark, *Carcharhinus falciformis*, and the rainbow runner, *Elagatis bipinnulata*, were recorded exclusively in the inner atoll by the BRUVs. These are not typically reef-associated species (Bonfil, 1993) but the BRUVs were effective in recording their use of the deep water channels between the shallow inner reefs. Channels act as important habitat corridors, enhancing connectivity between the inner lagoonal and outer reef slopes, with energy moving from one area to another through a range of hydrodynamic processes (Sasamal, 2007; Rogers *et al.*, 2017; Green *et al.*, 2019). These corridors also facilitate movement of mobile marine species, with marine predators taking advantage of them for foraging (Hastie *et al.*, 2016). The thumbprint, *L. harak,* and smalltooth, *L. microdon*, emperors were also only observed in the inner atoll on BRUVs. Emperors forage extensively over sandy bottoms where they predate on less mobile prey (Kulbicki *et al.*, 2005). While the BRUVs were deployed over a range of hard and soft bottom substrates, the UVC surveys were conducted solely on hard bottom reef substrate. In addition, BRUVs will attract these species to the bait while UVC typically requires high replication to record such species (Dulvy *et al.*, 2003). These discrepancies between the survey methods may explain the absence of the emperors from the UVC dataset. Moreover, these species are not necessarily exclusive to one area. The one-hour BRUV soak time and lack of long term and night time sampling are likely to lead to underrepresentation or absence of rarer species (Asher *et al.*, 2017).

The asymptotes of the species accumulation plots indicated that the BRUV and UVC surveys were sufficient to obtain an accurate measure of species richness and, although actual values varied, predator family abundance patterns were similar for both methods between areas. However, several species uniquely recorded with either UVC or BRUV underline the importance of using more than one survey methodology when assessing fish populations. For example, sharks were almost exclusively recorded with BRUVs. The teleost predators identified through the BRUV footage have small home ranges (Nash *et al.*, 2015) and will not travel far in response to a bait plume, but sharks, being more mobile, may follow bait plumes to investigate the origin of the scent. This is one of the biases of this methodology (Willis and Babcock 2000; Cappo et al. 2003; Harvey et al. 2012) but it is also why BRUVs are effective in tandem with UVC, which underrepresents more mobile, transient species (MacNeil *et al.*, 2008). In contrast, the species recorded solely during UVC, such as the strawberry grouper, *Cephalopholis spiloparaea*, the honeycomb grouper, *Epinephelus merra* and the spotfin lionfish, *Pterois antennata*, are more cryptic and wary. These species may be near the BRUV but their cryptic nature, the habitat complexity and the angle of the camera mean they may be missed.

Our analysis found a clear interaction of the predator assemblage data with live branching and massive coral cover, which accords with previous studies (Bell and Galzin, 1984; Komyakova *et al.*, 2013). Depth and complexity were important variables for models of both the UVC and the BRUV assemblage data. Structural complexity on reefs provides important habitat structure and refuge for prey communities. It is linked to increased fish biomass and abundance, and declines are predicted to significantly reduce fisheries productivity (Rogers *et al.*, 2014). However, predator growth rates decrease at reefs of higher complexity as increased refuge space allows more prey to hide, reducing available food, so reefs with intermediate complexity are most productive in terms of predator communities (Rogers *et* *al.*, 2018). The relationship between predator assemblage data and structural complexity is complicated, but its inclusion in both models reinforces its importance in structuring predator assemblages (Ferrari *et al.*, 2017). Depth was the second predictor included in both models. Reef fish communities vary dramatically with depth (Friedlander *et al.*, 2010; Schultz *et al.*, 2014; Jankowski *et al.*, 2015) as predator abundances and species compositions change (Asher *et al.*, 2017; Tuya *et al.*, 2017). Its inclusion in both models is further evidence that it plays a key role in structuring predator communities.

Total biomass of all recorded predators (inner atoll 0.29 t ha^{-1}, outer atoll 0.25 t ha^{-1}) was similar to that found at other remote but inhabited and exploited atolls (Kiritimati ~0.2 t ha^{-1}, Tabuaeran ~0.3 t ha^{-1} (Sandin *et al.*, 2008)), and it was considerably lower than at unfished, uninhabited atolls and islands (Palmyra ~1.8 t ha^{-1}, Kingman ~5.2 t ha^{-1} (Sandin *et al.*, 2008); Chagos Archipelago ~3 – 7.75 t ha^{-1} (Graham *et al.*, 2013)). Although the Maldives are considered underexploited (Newton et al. 2007), this indicates that these predator species are likely overfished. Reef fisheries provide an important source of food to both tourists and increasingly locals, and the rise in reef fish catch is evidence of a growing demand for these resources (Sattar *et al.*, 2014). Reef predators typically dominate the reef fish catch with fishermen targeting Carangidae, Lutjanidae and Serranidae using handlines (Sattar *et al.*, 2011; Sattar *et al.*, 2012; Sattar *et al.*, 2014). Although more recent information on the status of the reef fishery is lacking, significant declines in the mean length of the ten most exploited grouper species (Sattar *et al.*, 2011) and of key target species *Lutjanus bohar* and *L. gibbus* (Sattar et al. 2014) suggest the fishery is already overexploited.

While predators were recorded throughout the sites surveyed, the relatively low total biomass recorded here is indicative of an exploited system (Friedlander *et al.*, 2010). Recovery of exploited systems to pristine conditions and a high biomass of apex predators is estimated to take decades and involve large area closures (Myers and Worm, 2003; Robbins *et al.*, 2006). While this may be unrealistic to achieve, careful management of the reef fish populations in the Maldives is required to prevent irreversible loss of these key predatory species. Nonetheless, the total number of predator species recorded was higher than several other studies assessing reef fish communities in remote or semi-pristine areas, a probable outcome given that the Indian Ocean is a region of moderately high species richness (Roberts *et al.*, 2002).

Globally, reef predator populations are declining and species richness is being lost due to climate change and a range of direct anthropogenic stressors (Friedlander and DeMartini, 2002b; Hempson *et al.*, 2017b; Hughes *et al.*, 2017a). To date, little information exists on reef predator communities and their distributions in the Maldives. Evidently, lagoonal reefs are important habitats hosting diverse and abundant reef predator populations, which may have been previously undervalued. Predator communities are important in terms of biodiversity and available resources, so there is an urgent need to manage them carefully in the face of climate change, rapidly increasing tourism, and fisheries expansion to prevent future declines.

Note: the final published paper from this chapter is appended to the thesis.

Chapter 3 Novel tri-isotope ellipsoid approach reveals dietary variation in sympatric predators

3.1 Introduction

Trophic interactions are key regulators of community dynamics and ecosystem function. Food web and population dynamics are driven by resource availability, with sympatric species often in direct competition with each other (Schoener, 1983). Resource partitioning often occurs among co-occurring species to reduce inter- and intraspecific competition when resources are limited (Schoener, 1974). Often linked to body size or ontogeny (Werner and Gilliam, 1984), increasing evidence suggests that individuals may vary in their resource usage compared to conspecifics of the same age and size (Araújo *et al.*, 2011). As trophic energy dissipates up food webs, food resource scarcity is likely to be an important driver of foraging behaviour in large predators. Consumers may alter their foraging to include underutilised resources when competition is high, leading to dietary specialisations within populations (Bolnick *et al.*, 2003).

Predators (here referring to upper trophic level sharks and teleosts) are thought to play an important role in structuring communities. Through their foraging, they may alter prey behaviour (Lima and Dill, 1990) and, being more mobile, may couple distinct food chains (McCauley *et al.*, 2012c), altering energy flows and stabilising food webs (McCann *et al.*, 2005; Rooney *et al.*, 2006). Feeding specialisations have been extensively documented in upper trophic level vertebrate populations, particularly fishes (Bolnick *et al.*, 2003; Araújo *et al.*, 2011). While marine predators are often considered to be dietary generalists (Costa, 1993; Gallagher *et al.*, 2017), they may vary significantly in their trophic ecology at both the individual and species levels. Such specialisations can alter community dynamics (Bolnick *et al.*, 2011), so species-level assessments of trophodynamics will not account for differing ecological roles (Matich *et al.*, 2011).

Stable isotope ratios in animal tissues provide unique dietary perspectives and reveal important facets of resource use (Bearhop *et al.*, 2004) as they reflect assimilation of prey material into consumer bodies over time (Post, 2002). Carbon (δ^{13}C) and sulfur (δ^{34}S) isotope data help elucidate the production sources responsible for the energy flow in the food web, while nitrogen (δ^{15}N) suggests the relative trophic position at which an animal is feeding

(Minagawa and Wada, 1984; Pinnegar and Polunin, 1999; Connolly *et al.*, 2004; Croisetière *et al.*, 2009). Different animal tissues have different turnover rates (Tieszen *et al.*, 1983) with fast turnover tissues (e.g. plasma or liver) representing short-term diet while slow turnover tissues (e.g. muscle) represent long-term diet (Carter *et al.*, 2019). Consequently, muscle tissue can help identify consistent patterns in predator resource use (Vander Zanden *et al.*, 2015; Carter *et al.*, 2019).

Studies of vertebrate marine predator trophic niches and dietary specialisations have focussed on elasmobranchs (Matich *et al.*, 2011; Gallagher *et al.*, 2017; Shipley *et al.*, 2018; Shiffman *et al.*, 2019) and birds (Patrick *et al.*, 2014; Bodey *et al.*, 2018), with most studies focussing on only a few co-occurring species. There is a lack of isotopic information on resource partitioning among co-occurring teleost predators (Matley *et al.*, 2017), particularly in the tropics (Cameron *et al.*, 2019). This is despite the fact that coral reefs often support a high biomass and diversity of sympatric teleost predators (Stevenson *et al.*, 2007; Friedlander *et al.*, 2010), a factor thought to increase the occurrence of dietary specialisation (Araújo *et al.*, 2011). Coral reefs, along with their predator populations, are currently experiencing unprecedented worldwide declines due to a range of anthropogenic and climate-related stressors (Friedlander and DeMartini, 2002b; Hughes *et al.*, 2017a). Given their potential stabilising roles in food web dynamics, knowledge of sympatric reef predator trophodynamics and resource partitioning is important for predicting how reef communities will respond to change (Matich *et al.*, 2011).

To our knowledge, no study to date has considered the isotopic niche partitioning of teleost coral reef predators across multiple, co-occurring families. Greater understanding of spatial and intraspecific variation in predator feeding patterns is essential to predict how species will respond to fluctuations in resource availability as environments change (Matley *et al.*, 2017; Shiffman *et al.*, 2019). Here, we use a tri-isotope ellipsoid approach to examine the isotopic niches of seven key teleost coral reef predator species to determine whether predator resource use varies 1) spatially and/or 2) intraspecifically, and 3) whether their isotopic niches overlap.

3.2 Materials and Methods

3.2.1 Study site and sample collection

Fieldwork was conducted in North Malé Atoll, Republic of the Maldives (N 04°26.154’, E 73° 29.902’) from January to April 2017. Sampling occurred at sites across two distinct reef areas: 1) inner: enclosed lagoonal reef platforms (hereafter ‘inner atoll’) and 2) outer: outer reef slopes (hereafter ‘outer atoll’) (Figure A3).

In each area seven reef predator species belonging to three families were sampled opportunistically: groupers (Serranidae: *Aethaloperca rogaa*, redmouth; *Anyperodon leucogrammicus*, slender; *Cephalopholis argus*, peacock; *Cephalopholis miniata*, coral hind), snappers (Lutjanidae: *Lutjanus bohar*, red; *Lutjanus gibbus*, humpback), and jack (*Caranx melampygus*, bluefin trevally). Predators (trophic level ≥ 3.5) were chosen for sampling based on their status as key fishery target species (Sattar *et al.*, 2014) and being dominant components of the predator assemblage biomass in both inner and outer atoll areas (first author, unpublished data). Predators were caught using rod and reel, handlines and pole spears. For each individual, the total length (cm) was recorded and then a sample of dorsal white muscle tissue (1-2 g wet mass) was removed. Sampling was conducted non-lethally where possible using a 4 mm biopsy punch. All tissue sampling was carried out in compliance with UK Home Office Scientific Procedures (Animals) Act Requirements and approved by the Newcastle University Animal Welfare and Ethical Review Body (Project ID No: 526). Only adults (>15 cm) were sampled to limit possible ontogenetic dietary shifts.

Tissue samples were oven dried at 50°C for 24 hours, redried using a freeze drier, and then ground to a fine homogenous powder using a pestle and mortar. Subsamples of 2.5 mg of tissue were weighed into 3 x 5 mm tin capsules and sequentially analysed for δ^{15}N, δ^{13}C, and δ^{34}S using a PyroCube elemental analyser (Elementar, Hanau, Germany) interfaced with an Elementar VisION isotope ratio mass spectrometer at the East Kilbride (UK) node of the Natural Environment Research Council Life Sciences Mass Spectrometry Facility in August 2017. Stable isotope ratios are reported using the delta (δ) notation which for δ^{13}C, δ^{15}N, or δ^{34}S is: $[(R_{sample}/R_{standard}) - 1]$, where *R* is the ratio of the heavy to light isotope (e.g. ^{13}C/^{12}C), and measured values are expressed in per mil (‰).

International reference materials were placed at the start and end of each N/C/S run (~140-150 samples) to correct for accuracy and drift. Materials used were USGS40 (glutamic acid) for δ^{13}C and δ^{15}N (analytical precision (s.d) δ^{13}C = 0.07; δ^{15}N = 0.16) and silver sulfide standards IAEA- S1, S2 and S3 for δ^{34}S (analytical precision (s.d.) = 0.17, 0.59 and 1.46 respectively). Internal reference materials were placed every ten samples. Materials used were MSAG2 (a solution of methanesulfonamide and gelatin), M2 (a solution of methionine, gelatin, glycine) and ^{15}N-enriched alanine and SAAG2 (a solution of sulfanilamide, gelatin and ^{13}C-enriched alanine) (Table A3). A randomly spaced study-specific reference was also used (one mature individual [TL = 41.4 cm] of *A. leucogrammicus*, analytical precision (s.d.) δ^{13}C = 0.14, δ^{15}N = 0.27 and δ^{34}S = 0.73 respectively, n = 31) (Table A3).

High lipid content in fish muscle tissue can skew carbon isotope data interpretations as lipids are depleted in ^{13}C relative to proteins (Focken and Becker, 1998). Carbon stable isotope data were lipid corrected arithmetically when the C:N ratio of the muscle tissue was > 3.7 using the mass balance equation from Sweeting *et al.* (2006):

$$(1) \qquad \delta^{13}\mathrm{C}_{\mathrm{protein}} = \frac{\left(\delta^{13}\mathrm{C}_{\mathrm{sample}}\ \mathrm{x}\ \mathrm{C{:}N}_{\mathrm{sample}}\right) + \left(7\ \mathrm{x}\ \left(\mathrm{C{:}N}_{\mathrm{sample}} - \mathrm{C{:}N}_{\mathrm{protein}}\right)\right)}{\mathrm{C{:}N}_{\mathrm{sample}}}$$

Here, C:N protein was 3.7 determined by Fry *et al.* (2003) from shrimp muscle protein C:N.

3.2.2 Ellipsoid Metrics

The “SIBER” package in *R* (Jackson *et al.* 2011) provides methods for analysing bivariate stable isotope data although such methods are applicable to any bivariate normally distributed data. We extend these methods to the three-dimensional case in order to apply ellipsoids to trivariate data and calculate their overlap.

Ellipsoid volume can be estimated analytically from the sample covariance matrix by decomposition into their respective Eigenvalues and Eigenvectors. In the three-dimensional case, the square root of the Eigenvalues represents the three orthogonal axes, one semi-major and two semi-minor (a, b and c respectively), that describe the standard ellipsoid, synonymous to the 2-dimensional standard ellipse (Jackson *et al.*, 2011). The standard ellipsoid captures approximately 20% of the data (Fox *et al.*, 2007), which can be subsequently rescaled to capture any desired proportion of data. The volume of the ellipsoid is then taken to be $\frac{4}{3}\pi abc$ which we denote SEV (standard ellipsoid volume). As with SEA (standard ellipse area), SEV is biased to underestimation of volume when sample sizes are small (Jackson *et al.*, 2011). A small sample size correction for degrees of freedom following Fox *et al.* (2007) can be applied to correct for such bias giving SEV_C, equivalent to SEAc (Jackson *et al.*, 2011), only here the correction factor is $\frac{n-1}{n-3}$ as the ellipsoids are in three dimensions.

To quantify uncertainty in SEV estimates, a Bayesian framework was developed by generalising code in the SIBER package to the *n*-dimensional case (Jackson *et al.*, 2011). Data are assumed to be well described by the multivariate normal distribution and Bayesian posteriors of the mean and covariance structures estimated using JAGS (Just Another Gibbs Sampler) via the R package RJAGS (Plummer, 2018). Ellipsoid volume can subsequently be estimated from each covariance draw to provide a posterior estimate of SEV, which we denote SEV_B. Sensitivity analysis indicates that this Bayesian approach slightly underestimates population SEV at small sample sizes (approximately $n \leq 8$, see Figure A4).

To estimate the degree of overlap between two ellipsoids, we used a numerical approach, utilising the packages “rgl” (Adler *et al.*, 2018) and “geometry” (Habel *et al.*, 2019). Ellipsoids were approximated by three-dimensional meshes: a series of vertices that lie on the ellipsoid surface forming quadrilateral faces. The intersection of these two meshes is then approximated by a third mesh, the convex hull of which estimates the ellipsoid overlap volume. This method underestimates volumes as convex surfaces are approximated by planar faces, however this bias is reduced as the number of vertices used to represent the ellipsoids increases, which can be iteratively increased by subdividing faces (see Figure A5). As with estimating SEV_B, we use a Bayesian approach to estimate data covariance structures and calculate overlap for each paired posterior draw to provide a posterior estimate of overlap. Functions for estimating SEV, SEV_C, SEV_B and overlap posteriors are provided in the supporting information to the online publication (https://doi.org/10.1002/ece3.5779).

3.2.3 Data Analysis: Application

The ranges in carbon (*CR*), nitrogen (*NR*) and sulfur (*SR*) isotope values for each predator were calculated (Layman *et al.*, 2007b). Using the MVN R Package (Korkmaz *et al.*, 2014), multivariate normality was checked using Mardia’s test (Mardia, 1970) as it can calculate a corrected version of skewness for small sample sizes (< 20). All species in each area conformed to multivariate normality ($p > 0.05$) with the exception of *L. gibbus* and *L. bohar* in the inner atoll. Both had normal kurtosis ($p > 0.05$) but were non-normally skewed ($p < 0.05$). Univariate normality tests showed that δ^{34}S was normally distributed for both species, δ^{15}N was only normally distributed for *L. gibbus*, and both had non-normally distributed δ^{13}C. The non-normality was driven by one *L. gibbus* with a more positive δ^{13}C and two *L. bohar* that had more positive δ^{13}C and lower δ^{15}N respectively. As all the other data conformed to multivariate normality and these data points represent individuals with differing resource uses (Jackson *et al.*, 2011), data were considered well described by the multivariate normal distribution for all further analysis.

For each species in each area, Bayesian estimates for the multivariate normal distribution of the data were calculated (15000 iterations with a burn in of 10000 and a thinning factor of 25). Bayesian ellipsoids were fit to 75% of the data (EV_B) and their median volume and interquartile range (25 – 75 %) was determined. The degree of ellipsoid overlap between species within each area was calculated based on EV_B where Bayesian posteriors were determined from 7500 iterations with a burn in of 5000 and a subdivision value of 4. Overlap was expressed as a median percentage with 95% credible intervals where 100% indicates completely overlapping ellipsoids and 0% indicates entirely distinct ellipsoids. When the overlap between two species was ≥ 60%, niche overlap was considered significant (Matley *et al.*, 2017). Outer atoll *L. bohar* were excluded as only one fish was caught.

Individual body size may also influence trophic interactions; we tested for this using Mixed-Effects Models with the R package lme4 (Bates *et al.*, 2015). The δ^{13}C, δ^{15}N or δ^{34}S stable isotope value was the response variable, with area (inner/outer) and total length (mm) (and their interaction) as fixed effects, and total length (mm) nested within species as a random effect. Model normality and homogeneity assumptions were checked by plotting model residuals. Significant effects were determined using the R package lmerTest (Kuznetsova *et al.*, 2017) which provides p-values for lmer model fits via Satterthwaite's degrees of freedom method. Statistical power to detect size-related effects was determined using the simr R package (Green and MacLeod, 2016). All analyses were carried out in R Statistical Software version 3.5.2 (R Core Team, 2017) and RStudio version 1.1.383 (RStudio Team, 2012).

3.3 Results

There were substantial differences in the isotope values among the seven species sampled in both areas (Table 3.1). δ^{13}C ranged from -18.00 (*Aethaloperca rogaa*, outer) to -10.11 (*Lutjanus bohar*, inner), δ^{15}N ranged from 10.11 (*L. bohar*, inner) to 14.59 (*Lutjanus gibbus*, outer), and δ^{34}S ranged from 17.06 (*Caranx melampygus*, inner) to 21.02 (*A. rogaa*, outer).

In the inner atoll, the median niche volume of *L. bohar* (25.62) was five times larger than the niches of the other predators. Excluding *L. bohar*, *C. miniata* median niche volume (3.22) was half the size of the niches of the other predators, while that of *C. argus* was double the size (8.10). *C. melampygus* and *L. gibbus* had median niche volumes that were of a similar size (4.21 and 4.76 respectively) and *A. rogaa* and *A. leucogrammicus* had niches of a similar size (6.22 and 5.53 respectively) (Table 3.2; Figure 3.1). In the outer atoll, the median niche volume of *L. gibbus* (20.63) was five times larger than the niches of the other predators. The niche volumes of all the other predators were of similar size (6.45– 7.96), except for *C. argus* which had the smallest median niche volume (4.32) (Table 3.2; Figure 3.2).

All predators had larger median isotopic niche volumes in the outer atoll than in the inner atoll, except for *C. argus* (inner: 8.10; outer: 4.32) (Table 3.2; Figure 3.1 and Figure 3.2). Median niche volume of *L. gibbus* in the outer atoll (20.63) was four times larger than the niche volume of their inner atoll conspecifics (4.76). *C. miniata* had a median niche volume twice as large in the outer atoll (inner: 3.22; outer: 7.06), while the niches of *A. leucogrammicus* and *C. melampygus* were only 1.5 times larger in the outer atoll (Table 3.2; Figure 3.1 and Figure 3.2).

There were no effects of body size or area on predator δ^{15}N and δ^{34}S values (Table A4) but statistical power was low (Median (95% CI) δ^{15}N: 9% (4–16) and δ^{34}S: 14% (8–22). Statistical power to detect size effects was highest for δ^{13}C (Median (95% CI) δ^{13}C: 70% (60 – 77)) but there were no overall size effects on predator δ^{13}C values. However, they were significantly more negative in the outer atoll ($p < 0.01$) and there was a significant effect of size interacting with area ($p < 0.05$) (Table A4).

Table 3.1. Summary information for the predators in inner and outer atoll. Mean δ^{13}C, δ^{15}N, and δ^{34}S values are in per mil (‰) with SE in brackets. CR: δ^{13}C range, NR: δ^{15}N range, SR: δ^{34}S range.

Family	Species	Area	n	Size (mm)	δ^{13}C (‰)	*CR*	δ^{15}N (‰)	*NR*	δ^{34}S (‰)	*SR*
Carangidae	*Caranx melampygus*	Inner	10	248-410	-16.47 (0.22)	3.50	12.39 (0.17)	0.48	18.12 (0.15)	1.20
		Outer	6	372-461	-15.80 (0.02)	0.93	12.44 (0.20)	1.48	18.25 (0.16)	1.29
Lutjanidae	*Lutjanus bohar*	Inner	12	210-370	-15.36 (0.63)	7.06	12.36 (0.29)	2.94	18.59 (0.18)	0.70
		Outer	1	185	-14.87 (0.00)		12.97 (0.00)		17.94 (0.00)	
	Lutjanus gibbus	Inner	13	244-357	-16.36 (0.15)	2.96	12.58 (0.08)	0.02	19.14 (0.17)	1.51
		Outer	9	287-420	-16.26 (0.60)	7.84	12.99 (0.32)	3.54	18.96 (0.33)	2.84
Serranidae	*Aethaloperca rogaa*	Inner	11	164-278	-16.08 (0.26)	2.72	12.77 (0.07)	0.14	19.49 (0.17)	0.99
		Outer	11	148-336	-17.11 (0.17)	4.02	12.99 (0.16)	0.96	19.79 (0.18)	1.95
	Anyperodon leucogrammicus	Inner	10	238-346	-15.60 (0.19)	1.91	12.94 (0.11)	0.11	19.49 (0.17)	0.79
		Outer	10	262-426	-15.61 (0.04)	3.37	12.81 (0.15)	0.42	19.28 (0.01)	0.17
	Cephalopholis argus	Inner	11	186-342	-15.46 (0.23)	2.81	12.77 (0.08)	0.01	19.32 (0.26)	1.78
		Outer	10	190-345	-16.14 (0.19)	2.42	12.29 (0.08)	0.72	19.58 (0.14)	0.53
	Cephalopholis miniata	Inner	11	160-320	-16.92 (0.10)	2.87	12.73 (0.06)	0.21	19.73 (0.17)	1.47
		Outer	10	161-298	-16.88 (0.22)	4.23	12.64 (0.10)	1.26	19.55 (0.20)	0.52

Table 3.2. Bayesian 75% ellipsoid volume (EVB) estimates for predators sampled in inner and outer atoll, given as median with interquartile range (IQR, 25th and 75th percentile).

	Inner		**Outer**	
Species	Median	IQR	Median	IQR
A. rogaa	6.22	3.95, 6.89	6.45	4.39, 7.22
A. leucogrammicus	5.53	3.78, 6.30	7.96	5.27, 9.06
C. melampygus	4.21	2.85, 4.87	6.78	3.61, 7.51
C. argus	8.10	5.13, 8.92	4.32	2.77, 4.69
C. miniata	3.22	1.98, 3.45	7.06	4.36, 7.65
L. bohar	25.62	18.15, 29.14		
L. gibbus	4.76	3.30, 5.30	20.63	12.58, 22.67

There were few instances of significant niche overlap among the predators in the inner atoll. *A. leucogrammicus* had a niche that significantly overlapped with *C. argus* (median overlap: 63%) and *L. gibbus* had a niche that significantly overlapped with *L. bohar* (median overlap: 74%) (Table 3.3). There were no instances of significant niche overlap among predators in the outer atoll (Table 3.3).

3.4 Discussion

This study is the first to investigate how resource use varies intraspecifically and spatially for multiple sympatric coral reef predators across an atoll at a scale of tens of kilometres. To date, studies of reef predator trophodynamics in the tropics have focussed on single species or genera, despite the multispecies nature of many coral reef fisheries (Newton *et al.*, 2007). We reveal considerable spatial variation in predator resource use inferred from variability in isotopic composition, suggesting differences within and among species.

3.4.1 Is there intraspecific variation in predator resource use?

Although considered to be generalist predators, the large variation in isotope niche volumes, as determined by the 75% Bayesian ellipsoid volume (EV_B), suggests differences in resource utilisation among species. The niches of *L. bohar* (inner atoll) and *L. gibbus* (outer atoll) were estimated to be larger than those of the other predators. For both these species, larger EV_B were driven by two individuals that differed considerably in isotope values from the rest (higher δ^{13}C, lower δ^{15}N, and δ^{34}S), despite being of similar sizes to their conspecifics. As stable isotope values represent assimilated food items, the less negative δ^{13}C of these individuals indicates feeding on more benthic prey. It also suggests that prey from a range of production sources are available to the predators across the atoll seascape. This hypothesis is supported by isotope values of primary consumers, which had large but similar ranges in both atoll areas (Inner δ^{13}C -18.26 to -11.93; δ^{15}N 6.70 to 12.39; δ^{34}S 18.14 to 22.40; Outer δ^{13}C -17.49 to -11.77; δ^{15}N 6.24 to 11.74; δ^{34}S 18.79 to 20.42) (Skinner *et al.*, 2019).

There is little published information on the movements of *L. bohar* and *L. gibbus* specifically; snappers generally have high site fidelity, but this can vary spatially (Farmer and Ault, 2011; Pittman *et al.*, 2014). As such, these isotope data give insight into their foraging behaviours in the absence of spatial tracking methods to assess resource partitioning. In the Bahamas, δ^{13}C values of *Lutjanus griseus* and *Lutjanus apodus* indicated consistent intraspecific variability in space and resource use, with some individuals exploiting different areas of a creek and more marine-based resources, while others did not (Hammerschlag-Peyer and Layman, 2010). In our Maldives data, some individuals of *L. bohar* and *L. gibbus* appeared to be feeding on more benthic prey (less negative δ^{13}C) at lower trophic levels (lower δ^{15}N). Stomach contents data indicate that both *L. bohar* and *L. gibbus* are capable of feeding on a range of prey, foraging predominantly on reef-associated fish but also partly on crustaceans (Randall and Brock, 1960; Talbot, 1960; Wright *et al.*, 1986). The isotopic differences among individuals sampled within the same area suggests they may have alternative feeding strategies focusing on different prey. This specialisation within populations may explain how coral reefs can support a high density of co-occurring predators.

3.4.2 Is there spatial variation in predator resource use?

Community-wide isotope metrics (Layman *et al.*, 2007a) suggested that all four grouper species (*A. rogaa*, *A. leucogrammicus*, *C. argus* and *C. miniata*) varied in their resource use spatially. All four had larger NR values in the outer atoll, and with the exception of *C. argus*, they all had larger CR values in the outer atoll. Although δ^{15}N values of a corallivore, *Chaetodon meyeri*, and a nocturnal planktivore, *Myripristis violacea*, were significantly higher in the outer atoll, the differences in mean values were small (~1‰) and isotopic values of all other prey species were similar between areas (Skinner *et al.*, 2019). Furthermore, δ^{13}C and δ^{15}N values of coral host and particulate organic matter (POM) are consistent around the Maldives and do not vary between inner and outer atoll (Radice *et al.*, 2019). This suggests that the differences in predator CR and NR ranges are a direct result of feeding on different combinations of prey, rather than differences in baseline isotope values.

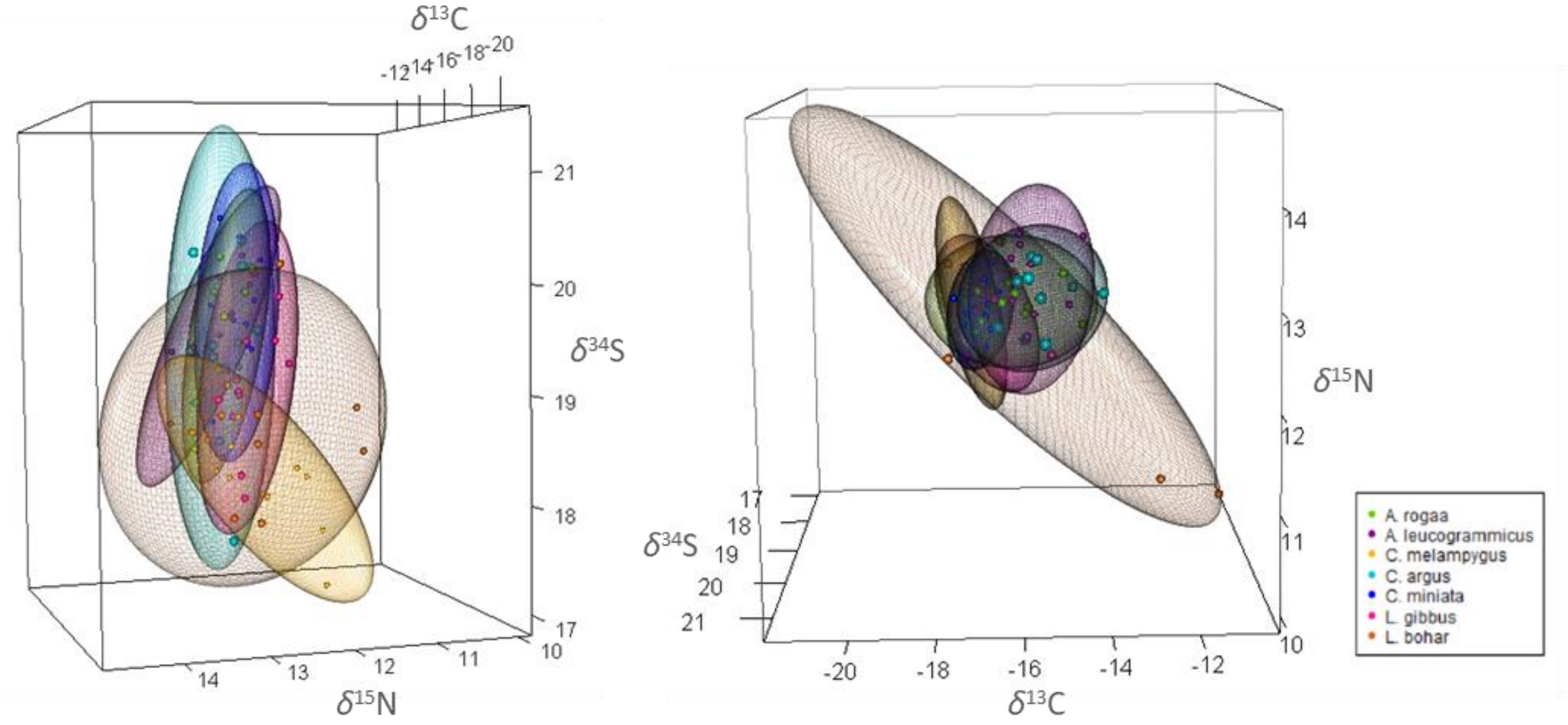


Figure 3.1. 75% ellipsoids corrected for small sample size generated using $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ data for predators in the inner atoll. See rotating GIF in supporting information with online publication (https://doi.org/10.1002/ece3.5779).

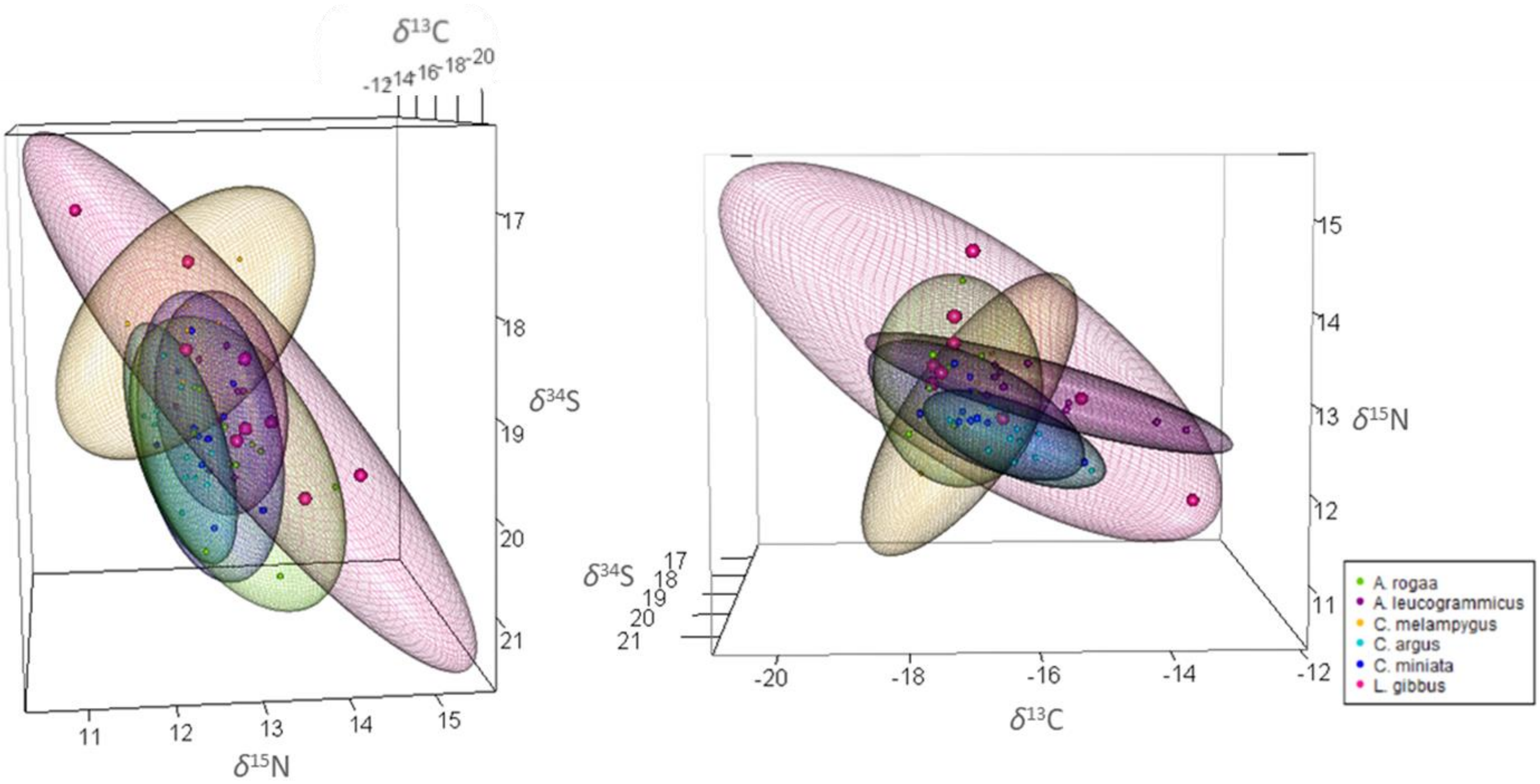


Figure 3.2. 75% ellipsoids corrected for small sample size generated using δ^{13}C, δ^{15}N and δ^{34}S data for predators in the outer atoll. See rotating GIF in supporting information with online publication (https://doi.org/10.1002/ece3.5779).

Stomach contents data show that *A. rogaa*, *C. argus*, and *C. miniata* feed primarily on reef-associated fish from a range of families that are sustained by multiple production sources (Harmelin-Vivien and Bouchon, 1976; Shpigel and Fishelson, 1991; Dierking *et al.*, 2011). While no stomach contents data was available for *A. leucogrammicus*, it occupies the same reef habitat as the other groupers (Sluka and Reichenbach, 1995), so likely has a similar diet. The larger CR and NR of these species could indicate that their prey rely on a wide range of production sources. Where benthic and pelagic food webs overlap such as here, predators might have access to prey from two food webs (i.e. planktivores and herbivores) while remaining in the same habitat (Matich *et al.*, 2011). Furthermore, *C. argus* in particular displays extensive foraging plasticity allowing it to take advantage of small scale fluctuations in prey availability (Karkarey *et al.*, 2017), a behaviour possibly reflected in the larger CR and NR ranges.

Interestingly, and in contrast to the patterns identified with the CR and NR ranges, *A. leucogrammicus* and *C. miniata* had larger SR ranges (δ^{34}S: 18.60-20.29 and 18.70-20.65 respectively) in the inner atoll, despite having smaller CR and NR ranges and isotopic niches there. The δ^{34}S isotope values revealed that these two species may be feeding on prey reliant on a range of production sources, including more benthic-sustained detritivores (mean ± s.d. δ^{34}S: 18.14 ± 0.22) and herbivores (mean ± s.d. δ^{34}S: 19.66 ± 0.22) (Skinner *et al.*, 2019). Assessing the resource use of these two predators in the inner atoll based solely on δ^{13}C and δ^{15}N values may have missed this intricacy, as the δ^{13}C and δ^{15}N values were indicative of feeding on more pelagic prey from higher trophic levels (evidenced by lower δ^{13}C and higher δ^{15}N). In food web studies, δ^{34}S is often overlooked, despite its ability to help distinguish between different marine producers (Connolly *et al.*, 2004) and reveal resource usage intricacies and pathways (Croisetière *et al.*, 2009; Gajdzik *et al.*, 2016) that may be masked using only δ^{13}C or δ^{15}N. The primary reason for this is that measuring δ^{34}S is typically more challenging, and thus more costly, than measuring δ^{13}C or δ^{15}N. However, recent technological advances and new instruments mean that δ^{13}C, δ^{15}N and δ^{34}S can be measured from the same sample aliquot with a high level of precision (Fourel *et al.*, 2015). Given these advances and the relative ease of now measuring δ^{34}S, we strongly suggest that more studies incorporate δ^{34}S to employ the tri-isotope ellipsoid approach that we present here.

With the exception of *C. argus*, all predators had larger isotopic niches in the outer atoll. Given the similarity in prey and primary producer isotope values between atoll areas (Radice *et al.*, 2019; Skinner *et al.*, 2019), it seems likely that this spatial variation in resource use is linked to variations in resource availability (Araújo *et al.*, 2011). The oceanic rim reefs of the outer atoll had higher live branching coral and habitat structural complexity following the 2016 bleaching event compared to inner atoll reefs (first author, unpublished data). Coral cover is strongly linked to fish species richness (Komyakova *et al.*, 2013) and reefs with higher complexity and coral cover support greater densities of smaller-bodied (<20 cm) fish (Alvarez-Filip *et al.*, 2011). Although prey fish biomass was similar between atoll areas, densities of planktivores were greater along the outer edge reefs (first author, unpublished data). This may lead to increased specialisation and population niche size, a hypothesis supported by the larger isotopic niche volumes of the predator populations in the outer atoll.

Inner atoll *L. gibbus* had an isotopic niche volume (EV_B) a tenth the size of the outer atoll population. Spatial differences in *L. gibbus* feeding have previously been recorded; it has a crab dominated diet in Japan (Nanami and Shimose, 2013) but a forage fish (clupeid) dominated diet in Yemen (Ali *et al.*, 2016). Differential preferences for crabs, which are benthic, and clupeids, which are pelagic, may explain the differing range in $\delta^{13}C$ and $\delta^{34}S$ values between atoll areas found here. Furthermore, the smaller EV_B of the inner atoll population may mean individuals are consistently feeding on a similar but select group of prey. As isotope values of key prey species were similar in both atoll areas (Skinner *et al.*, 2019), this further supports the hypothesis that there is spatial variation in resource availability across the atoll.

Table 3.3. Median percentage overlap in ellipsoids (Bayesian 75% ellipsoid generated using δ^{13}C, δ^{15}N and δ^{34}S data) with 95% credible intervals showing the uncertainty in the overlap estimates between each pair of predator species. The table is to be read across each row: for example, in the inner atoll 46% of the *A. rogaa* ellipsoid overlapped with the *A. leucogrammicus* ellipsoid, and 53% of the *A. leucogrammicus* ellipsoid overlapped with the *A. rogaa* ellipsoid. Significant overlap (≥ 60%) is in bold. Overlap was only determined for predators in the same atoll area.

		A. rogaa	*A. leu*	*C. mel*	*C. argus*	*C. miniata*	*L. bohar*	*L. gibbus*
Inner	*A. rogaa*	-	46 (18 - 77)	1 (0 - 14)	57 (24 - 86)	30 (11 - 52)	39 (11 - 78)	31 (9 - 57)
	A. leu	53 (24 - 85)	-	0 (0 - 4)	**63 (33 - 95)**	12 (0 - 29)	18 (0 - 52)	16 (0 - 39)
	C. melampygus	2 (0 - 20)	0 (0 - 5)	-	0 (0 - 8)	5 (0 - 23)	57 (30 - 94)	29 (7 - 56)
	C. argus	45 (20 - 75)	42 (18 -70)	0 (0 - 4)	-	10 (0 - 26)	30 (8 - 64)	14 (0 - 31)
	C. miniata	57 (25 - 94)	21 (0 - 56)	6 (0 - 30)	27 (0 - 64)	-	46 (13 - 85)	53 (24 - 86)
	L. bohar	10 (2 - 23)	4 (0 - 12)	10 (3 - 20)	10 (2 - 23)	6 (1 - 14)	-	14 (5 - 26)
	L. gibbus	41 (15 - 70)	18 (0 - 42)	26 (6 - 50)	24 (0 - 50)	36 (12 - 61)	**74 (48 - 100)**	-
Outer	*A. rogaa*	-	29 (7 - 59)	10 (0 - 35)	20 (2 - 44)	47 (22 - 79)	-	56 (25 - 89)
	A. leu	23 (5 - 43)	-	9 (0 - 32)	16 (1 - 38)	26 (4 - 54)	-	51 (20 - 82)
	C. melampygus	10 (0 - 34)	12 (0 - 36)	-	3 (0 - 19)	17 (0 - 47)	-	34 (7 - 69)
	C. argus	31 (5 - 61)	31 (5 - 65)	5 (0 - 35)	-	55 (23 - 90)	-	29 (2 - 76)
	C. miniata	44 (17 - 76)	31 (4 - 60)	17 (0 - 43)	33 (11 - 65)	-	-	46 (9 - 85)
	L. gibbus	18 (5 - 36)	20 (6 - 42)	11 (2 - 27)	7 (0 - 17)	16 (4 - 32)	-	-

3.4.3 Do the isotopic niches of sympatric predators overlap?

The degree of niche overlap was low; there were only two occurrences of significant niche overlap in the inner atoll and none in the outer atoll. This might suggest that the level of competition among these species is low in both areas with predators feeding on a variety of different resources. Overlapping niches do not conclusively equate to increased competition for resources (Layman *et al.*, 2012; Gallagher *et al.*, 2017). All predators had a larger degree of niche overlap with *Lutjanus bohar* (inner) and *Lutjanus gibbus* (outer) due to the exceptionally large niches of these two species, but the level of direct competition may be lower. Predators could be feeding on prey over different spatiotemporal scales, which would reduce their direct competition. Alternatively, due to protein turnover and prey isotope signature integration into muscle tissue over time, predators may be feeding on ecologically different diets but still express similar isotope values, confounding interpretation of the level of competition existing in the community.

It is worth noting that not all predators caught in the same location necessarily derive their nutrition from that locality though. The bluefin trevally, *Caranx melampygus*, had a distinct isotopic niche which overlapped minimally with the niches of the other predators in both atoll areas. *C. melampygus* is a transient, midwater predator with an extensive territory (Holland *et al.*, 1996; Sancho, 2000) and is the most mobile of all the predators sampled. It regularly makes crepuscular migrations of 1-2 km between different habitats (Meyer and Honebrink, 2005). Furthermore, it was the only predator to occupy a similar isotopic niche in both areas, suggesting it may use resources from across the atoll. Stomach contents data indicate it feeds predominantly on nekton spanning multiple trophic levels, with little reliance on crustaceans or cephalopods (Meyer *et al.*, 2001). Consequently, this separation is likely attributable to differing habitat usage and prey encounters compared to the other more reef-associated and site-attached species (Sluka and Reichenbach, 1995).

Ontogenetic shifts in feeding strategies are well documented (Werner and Gilliam, 1984; Kimirei *et al.*, 2013), but adults may also vary in their resource use as a function of their size. Here, body size did not appear to drive niche variability; there was no relationship between body size and δ^{13}C, δ^{15}N, or δ^{34}S. Although there was a significant relationship between δ^{13}C and the interaction between area and body size, the effect was weak. However, statistical power was low and the ability to detect relationships may have been limited due to small sample sizes and limited size ranges; size-based shifts in feeding might have been observed with greater replication. While more depth is needed in these data, it seems size-based effects on adult predator resource use are absent or weak here (Layman *et al.*, 2005; Gallagher *et al.*, 2017; Matley *et al.*, 2017; Shipley *et al.*, 2018). Within the diverse food webs of coral reefs where prey sizes vary, strong relationships with body size may be masked as predators target large primary consumers (Layman *et al.*, 2005).

Predators are often thought to be dietary generalists but we show inter- and intra-specific differences in resource use with minimal significant niche overlap, highlighting how trophic resource use varies among sympatric reef predators at a scale of tens of kilometres. We did not specifically test for individual specialisation but several individuals of *Lutjanus* appeared to be feeding in completely different ways to their conspecifics. Individual specialisation is not ubiquitous in marine predator populations (Matich *et al.*, 2011), but small sample sizes of these predators means statistical power to detect potential differences was limited, thus underestimating intraspecific trophic variation. Feeding specialisations are linked to ecological opportunity, and are thought to be more common where resource diversity and density of competing individuals are greater (Araújo *et al.*, 2011). This makes coral reefs a prime location for predators to demonstrate vastly different individual feeding behaviours. Predators may provide stability to communities by linking separate food chains (McCann *et al.*, 2005; Rooney *et al.*, 2006), but individual dietary specialisations could alter this ecological linkage role (Matich *et al.*, 2011) with potential consequences for ecosystem resilience. Detailed information on individual predator resource use is required to identify their ecological role and help understand how they will respond to environmental change.

Note: the final published paper from this chapter is appended to the thesis.

Chapter 4 Prevalence of pelagic dependence among coral reef predators across an atoll seascape

4.1 Introduction

Until recently, species interactions and nutrient transfer across habitat boundaries and the impact of species declines beyond individual ecosystems were seldom considered (Lundberg and Moberg, 2003). However, ecosystems are now recognised to be linked by flows of organisms and energetic materials (Huxel and McCann, 1998) yet understanding the trophodynamics (the flow of energy) (Lindeman, 1942) of a food web is challenging, particularly for complex marine systems such as coral reefs where spatial variation can be high (Bierwagen *et al.*, 2018).

Once thought to be somewhat ecologically closed (Odum and Odum, 1955; Hamner *et al.*, 2007), coral reef ecosystems are subject to upwelling and tidal energy, which drive an exchange of plankton, water and nutrients with the ocean (Hamner *et al.*, 2007; Lowe and Falter, 2015). Upwelling often occurs through wind-driven wind-water interactions; surface water is displaced by the wind and replaced by colder nutrient-rich deeper waters. Phytoplankton, a bottom-up driver of ocean production, is often more abundant near islands and atolls (Doty and Oguri, 1956; Gove *et al.*, 2016). Since Darwin (1842) it has been hypothesised that the surrounding ocean provides a major source of nutrition to coral reef communities. Fish on outer reef edges can benefit from this exogenous source (Wyatt *et al.*, 2012a) but intense feeding by outer reef communities (Genin *et al.*, 2009) means the energetic material seaward of the reef is different from that in lagoons (Hamner *et al.*, 2007). Furthermore, various hydrodynamic processes such as breaking waves and tides are needed to deliver ocean water into the lagoons (Lowe *et al.*, 2009), suggesting lagoonal reef fish may not have access to the same resources.

Reef fish communities demonstrate increased reliance on oceanic production seaward of the reef but greater reliance on reef production inshore and into lagoons (Wyatt *et al.*, 2012b; Gajdzik *et al.*, 2016; Le Bourg *et al.*, 2017), indicating that the quantity and quality of food available to inner-reef fish varies substantially (Wyatt *et al.*, 2012b). Variation in nutrient availability and content to the inner and outer reef habitats may lead to spatial differences in reef communities. Indeed, planktivorous fish communities are more abundant with increasing proximity to the ocean (Friedlander *et al.*, 2010). Aggregations of these planktivorous fish, the “wall of mouths” (Hamner *et al.*, 1988), form on the outer edge of many reefs where they take advantage of increased plankton prey abundances (Wyatt *et al.*, 2013). The community structure of a coral reef is thus heavily influenced by the adjacent ocean (Letourneur, 1996; Garcia *et al.*, 2018). Oceanic production is a key driver of forereef fish biomass (Williams *et al.*, 2015; Robinson *et al.*, 2017) but quantitative estimates of its contribution to lagoonal reef fish biomass are lacking.

Highly mobile reef predators often rely on production sources from outside their primary habitat (McCauley *et al.*, 2012c; Papastamatiou *et al.*, 2015) and benefit from the aggregations of planktivores (Matley *et al.*, 2018). Some of these predators are partly reliant on oceanic energy fluxes (McCauley *et al.*, 2012c; Frisch *et al.*, 2014; Frisch *et al.*, 2016), while others are supported by benthic primary production (Hilting *et al.*, 2013). To date most of the understanding of these food web relationships comes from studies of reef sharks or from outer forereef slope communities (Papastamatiou *et al.*, 2010; McCauley *et al.*, 2012c; Frisch *et al.*, 2014; Frisch *et al.*, 2016). This raises the question of the ubiquity of planktonic reliance in reef fishery target predator communities and whether it extends to those in atoll lagoons.

With climate change, oceanic productivity is projected to decline, particularly at low latitudes, and reef predators could be affected. As surface waters warm and sea ice disappears, nutrients will be trapped and transferred to the deep ocean, leading to surface nutrient reductions and a decline in primary production and carbon export (Moore *et al.*, 2018). Yet the extent of coral reef fishery target species reliance on pelagic production, particularly inside atoll lagoons, is little known. Our study aimed to: 1) determine the level of contribution of planktonic production sources to fishery target reef predator biomass and 2) identify whether this varies between inner lagoonal and outer atoll edge reefs, and among species. In order to address 1) we had to assess fishery target predator species prevalence and biomass across the atoll. We hypothesise that planktonic reliance will be greater along outer edge reefs with reduced reliance in the lagoon where predators will rely more on reef-based production sources.

4.2 Materials and Methods

4.2.1 Study site

The Maldives consists of 16 atolls comprising ocean-facing edge reefs and enclosed lagoons with patch reefs (Naseer and Hatcher, 2004). The coral reef area is small (8920 km^2) (Spalding *et al.*, 2001) while the pelagic ocean area within the Exclusive Economic Zone covers ~1 million km^2 (FAO, 2006). Ocean current flow direction fluctuates with the monsoon. During the Northeast Monsoon, the current flows to the west increasing production on the west coast (Sasamal, 2007), while during the Southwest Monsoon currents flow to the east increasing primary production on the eastern side (Anderson *et al.*, 2011). Fieldwork was conducted in North Malé atoll (4°18'34.5"N, 73°25'26.4"E) which is located on the eastern side of the archipelago from January to April 2017 (NE monsoon). The atoll was divided into two areas: inner atoll/lagoon and outer atoll/edge reef (Figure 4.1).

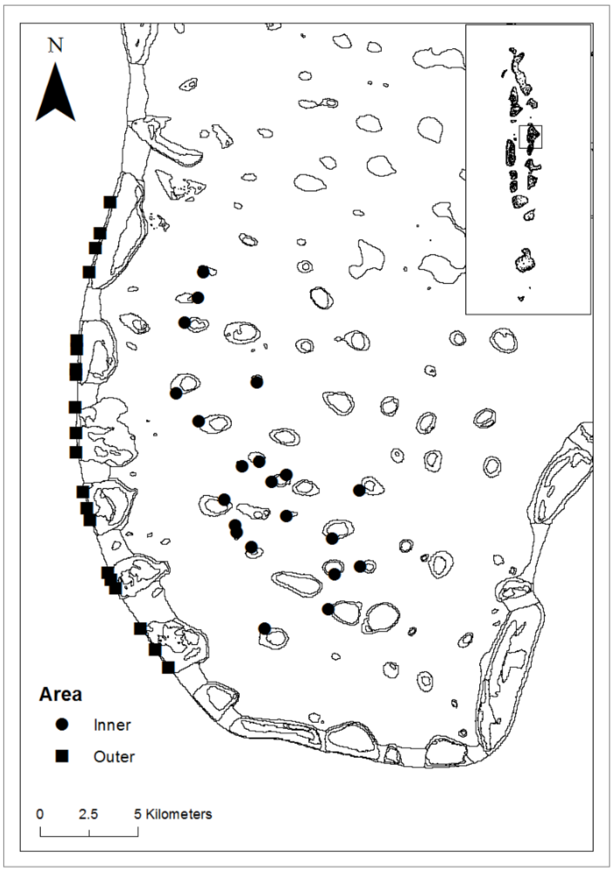


Figure 4.1. UVC sampling sites in inner lagoonal and outer edge reef areas of North Malé atoll.

4.2.2 Predator community assessments

Underwater visual census (UVC) was used to quantify fishery target predator biomass. UVC was conducted at 40 sites (20 in each area) covering 50,000 m^2. These reef fish predators (hereafter “predators”) were mostly piscivore apex predators occupying the upper level of the food chain at assumed trophic positions ≥3. Predators were classified as fishery target species based on current practice in the Maldives from visits to the Malé fish market (C. Skinner, personal observation) and from Sattar *et al.* (2014). Only forereef habitat was surveyed. At each site five 50 x 5 m transects were laid haphazardly (minimum 5 m apart) but parallel to the reef at 3 - 10 m depth. Abundance and size (cm) of all predators were recorded. Predators were characterised based on their behaviour as more mobile or more site-attached (Brock, 1982). Two observers recorded the predator assemblage; the first laid the transect and recorded mobile species and the second searched for cryptic, site-attached species, e.g. smaller Serranidae. The same observers were used throughout the surveys to prevent observer bias (Willis and Babcock, 2000). Site-level averages of fish biomass were calculated. All UVC fishery target predator biomass data were calculated using length-weight relationships available on FishBase (http://fishbase.org) with the exception of *Aethaloperca rogaa* where length-weight relationships were taken from Mapleston *et al.* (2009).

4.2.3 Fish collection

Fish were collected opportunistically from sites across inner and outer atoll areas for stable isotope analysis (Figure 4.1). Total length (cm) of each individual was recorded. Samples (1-2 g wet mass) of white muscle tissue from the dorsal musculature adjacent to the dorsal fin were removed. White dorsal muscle was used because it is less variable in δ^{13}C and δ^{15}N than other tissues (Pinnegar and Polunin, 1999).

Sampled predators were selected based on their prevalence in UVC data, presence in both inner and outer atoll areas, inclusion of species from the dominant fishery target families, and their high trophic position. Nine species belonging to four families were sampled: groupers (Serranidae: *Aethaloperca rogaa*, redmouth grouper, *n* = 22; *Anyperodon leucogrammicus*, slender grouper, *n* = 20; *Cephalopholis argus*, peacock grouper, *n* = 21; *Cephalopholis miniata*, coral hind, *n* = 21), snappers (Lutjanidae: *Aphareus furca*, jobfish, *n* = 8; *Lutjanus bohar*, red snapper, *n* = 13; *Lutjanus gibbus*, humpback snapper, *n* = 22;), emperors (Lethrinidae: *Lethrinus obsoletus*, orange-striped emperor, *n* = 5) and jacks (Carangidae: *Caranx melampygus*, bluefin trevally, *n* = 16). Predators were captured using rod and reel, handlines, and pole spears. Where possible (e.g. when caught using handlines), sampling was non-lethal using 4 mm biopsy punches (Henderson *et al.*, 2016).

Different primary producers vary in ratios of $\delta^{13}C$ and $\delta^{34}S$, with distinct values typically associated with benthic versus planktonic algae (France, 1995) and marine habitat types respectively. Food web analysis typically uses $\delta^{13}C$, but $\delta^{34}S$ helps to discriminate between different production pathways as there is often greater variability in mean S isotopic value of sources compared to C or N (Connolly *et al.*, 2004). Here, food sources were characterised through sampling a range of primary consumers that feed on specific food groups. Primary consumers can be used as a reference baseline for elucidating trophic positions in the food web with greater certainty than those of primary producers as they incorporate variability and have slower tissue turnover times (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999). Primary consumers were chosen based on dietary information from the published literature. Six energy pathways were represented: 1) benthic algae (*Acanthurus leucosternon*, powderblue surgeonfish, 6 inner, 11 outer (Robertson *et al.*, 1979)); 2) hard corals (*Chaetodon meyeri*, scrawled butterflyfish, 5 inner, 11 outer (Sano, 1989)); 3) detritus (*Pearsonothuria graeffei*, blackspotted sea cucumber, 7 inner, 8 outer (Purcell *et al.*, 2012)), 4) diurnal plankton (*Caesio xanthonota*, yellowback fusilier, 11 inner, 2 outer (Bellwood, 1988); *Caesio varilineata*, variable-lined fusilier, 12 inner (Bellwood, 1988); *Decapterus macarellus*, mackerel scad, 20 inner (Smith-Vaniz, 1995); *Pterocaesio pisang*, banana fusilier, 12 inner (Bellwood, 1988)); 5) nocturnal plankton (*Myripristis violacea*, lattice soldierfish, 11 inner, 6 outer (Hobson, 1991)) and 6) diel vertically migrating (DVM) plankton (*Uroteuthis duvaucelii*, Indian Ocean squid, 7 outer (Islam *et al.*, 2018)). Although an effort was made to consistently sample primary consumers, *U. duvaucelii* does not feed directly on DVM plankton but on small crustaceans and fishes (e.g. bottom dwelling sea robins, *Trigla* sp (Islam *et al.*, 2018)). However, they reside at depths of 30 – 170 m and feed primarily at night when they migrate to shallower waters, so they were considered a suitably representative proxy for DVM plankton. Several species of planktivores were sampled to control for the greater variability occurring across plankton communities. Primary consumer species were collected using pole spears or from Malé fish market.

4.2.4 Stable isotope analysis

Tissue samples were oven dried at 50°C for 24 hours and then freeze dried before grinding to a homogenous powder using a pestle and mortar. Approximately 2.5 mg was weighed into 3 x 5 mm tin capsules and analysed for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ using a PyroCube elemental analyser (Elementar, Hanau, Germany) interfaced with an Elementar VisION IRMS at the NERC Life Sciences Mass Spectrometry Facility, East Kilbride, UK. Four international reference materials were used at the start and end of each C/N/S run and three internal reference materials every ten samples to ensure accuracy and correct for drift (Table A3). Analytical precision (s.d.) for international standard USGS40 was 0.1 and 0.2 for $\delta^{13}C$ and $\delta^{15}N$ respectively, and for IAEA- S1, S2, and S3 it was 0.2, 0.6 and 1.5 for $\delta^{34}S$ respectively. Analytical precision (s.d.) for internal reference materials M2, MSAG2, and SAAG2 was 3.2, 0.1, and 0.1 for $\delta^{13}C$, 3.2, 0.2, and 0.1 for $\delta^{15}N$ and 1.7, 0.5, and 0.5 for $\delta^{34}S$ respectively. Accuracy between runs was assessed using a randomly spaced study-specific reference (mature *Anyperodon leucogrammicus,* TL = 41.4 cm). Analytical precision (s.d.) was 0.1 for $\delta^{13}C$, 0.3 for $\delta^{15}N$, and 0.7 for $\delta^{34}S$.

Carbon stable isotope data were lipid corrected arithmetically when the C:N ratio of the muscle tissue was > 3.7 using the mass balance equation of Sweeting *et al.* (2006):

$$\delta_{protein} = \frac{\left(\delta_{sample}\ x\ C{:}N_{sample}\right) + \left(7\ x\ \left(C{:}N_{sample} - C{:}N_{protein}\right)\right)}{C{:}N_{sample}} \tag{1}$$

Lipid corrections were applied to only 20 predator samples (*A. rogaa*, *C. melampygus*, C. *miniata*, *L. gibbus*) and 12 primary consumer samples (exclusively *P. graeffei*). Mean (s.d.) differences in $\delta^{13}C$ values after correction were 1.2 (1.0) and 1.0 (0.9) respectively.

4.2.5 Data analysis

All analyses were carried out using R Statistical Software version 3.5.1 (R Core Team, 2017) and RStudio version 1.1.383 (RStudio Team, 2012).

Predator abundance data were square root transformed and a Bray-Curtis similarity matrix was made. Using the “vegan” R package (Oksanen *et al.*, 2018), differences in predator abundances between areas were assessed using a PERMANOVA with 999 permutations. Species contributing to these differences were identified using SIMPER analysis.

Bayesian stable isotope mixing models were run using the R package "MixSIAR" (Stock and Semmens, 2016a) to ascertain the predators' principal food sources. Each model was run using three tracers ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) with area (inner/outer) as a fixed factor and species as a random factor. The error term Residual * Process was selected as residual error incorporates potential variation involving consumers e.g. differences in metabolic rate or digestibility, while process error incorporates variation related to the sampling process (e.g. *L. bohar* n = 1 sample size in the outer atoll) (Stock and Semmens, 2016b). Models were run using the "very long" MCMC parameters. Model convergence was assessed using the trace plots and the Gelman-Rubin and Geweke diagnostic tests.

Source contribution estimates can be highly uncertain when there are too many sources (Ward *et al.*, 2011). For the best separation of source contributions, it is recommended that sources are combined prior to analysis based on biological knowledge and similar isotopic values (*a priori*) or, where source isotope values differ, estimated proportional contributions are combined following analysis (*a posteriori*) (Phillips *et al.*, 2005). Here, sources were represented by the sampled primary consumer species. Sources were combined *a priori* when they were 1) the same species or represented the same food source and 2) there were no significant differences in their isotope values. $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values of the 1) primary consumer species sampled in both inner and outer atoll areas and 2) the four diurnal planktivore species were compared using ANOVAs or, where data did not conform to normality or homeoscedascity, Kruskal-Wallis tests. In some cases, source isotope values may be statistically different even when they have similar isotope values. When this occurred, the mean isotope values of each source were calculated. If the difference in the mean values was small (~1‰), they were combined *a priori* (Phillips *et al.*, 2014).

A mean isotopic value and standard deviation was determined for each group to represent the different sources in the mixing models. Several sources were then combined *a posteriori*. This approach allows each individual source to be included in the running of the model while combining sources after may provide a narrower combined distribution with greater biological relevance (Phillips *et al.*, 2005; Phillips *et al.*, 2014). Differences in the $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values of the reef-based group and planktonic source group were assessed using a Kruskal-Wallis test.

Trophic discrimination factors (TDF, Δ) vary depending on many factors and inappropriate TDF can result in misinterpretations. Because of this, four models were run using different TDF. TDFs were chosen as they were calculated based on white muscle tissue from upper trophic level predatory fish in marine environments and when plotted, the consumer data were inside the polygon made by the source data. **Model 1** used in situ values field estimated from Palmyra Atoll for $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$: +1.2 (SD ± 1.9) and +2.1 (SD ± 2.8) respectively (McCauley *et al.* 2012b). Little published information is available on $\Delta\delta^{34}S$ but it is thought to be around 0‰ (Peterson and Fry, 1987). In a feeding study of European sea bass (*Dicentrarchus labrax*), Barnes and Jennings (2007) calculated $\Delta\delta^{34}S$ to be -0.53 (SD ± 0.04) but it ranged from -1.59 to +0.26. Therefore $\Delta\delta^{34}S$ SD was increased to 1.0 to incorporate this variability and provide additional model parameter space. **Model 2** used the $\Delta\delta^{13}C$ = +0.4 (SD ± 0.2) and $\Delta\delta^{15}N$ = +2.3 (SD ± 0.3) for aquatic environments from McCutchan Jr *et al.* (2003) and the same $\Delta\delta^{34}S$ as model 1. **Model 3** used values from (Vander Zanden *et al.*, 1999) for carnivores, $\Delta\delta^{13}C$ = +0.9 (SD ± 1.0) and $\Delta\delta^{15}N$ = +3.2 (SD ± 0.4) and the same $\Delta\delta^{34}S$ as model 1. **Model 4** used $\Delta\delta^{13}C$ +1.2 (SD ± 1.9) and $\Delta\delta^{15}N$ +2.1 (SD ± 2.8) from McCauley *et al.* (2012c) and a $\Delta\delta^{34}S$ of +1.9 (SD ± 0.51) for aquatic environments from McCutchan Jr *et al.* (2003), however the model did not converge and the consumer source data were outside the source mixing polygon.

The predictive accuracy of the different models was compared using the R package “loo” (Vehtari *et al.*, 2018) (Table A8). LOO (leave-one-out-cross-validation) assesses Bayesian model prediction accuracy (Vehtari *et al.*, 2017). The model with the lowest LOO value and the highest Akaike weight was **Model 1,** which is presented in the results (Stock *et al.*, 2018).

4.3 Results

Of 30 fishery target species in five families recorded by UVC, nine in four families were sampled for stable isotope analysis in both inner and outer atoll areas (Figure 4.1). The average predator biomass (± s.d.) across the study sites was 127.9 ± 107.9 kg ha^{-1} (100.3 ± 78.7 kg ha^{-1} inner; 155.5 ± 126.9 kg ha^{-1} outer). The sampled species constituted 58% of the predator assemblage (60% or 60.6 ± 39.8 kg ha^{-1} inner; 55% or 84.8 ± 66.2 kg ha^{-1} outer). The predator assemblages differed between atoll areas (perMANOVA, 999 permutations, $p < 0.01$) but only one of the sampled predators, *A. leucogrammicus*, contributed significantly to this (SIMPER, $p < 0.01$) and it was more abundant in the inner atoll. Mean $\delta^{13}C$ values (± s.e.) ranged from -17.1 ± 0.2 to -13.3 ± 1.4 (*A. rogaa*, outer atoll to *L. obsoletus*, inner atoll), $\delta^{15}N$ from 12.1 ± 0.4 to 13.4 ± 0.1 (*L. obsoletus*, inner atoll to *L. obsoletus*, outer atoll) and $\delta^{34}S$ from 16.2 ± 0.7 to 19.8 ± 0.2 (*L. obsoletus*, inner atoll to *A. rogaa*, outer atoll) (Figure 4.2; Table A5).

There were significant differences in isotopes of three primary consumer species between atoll areas: *Chaetodon meyeri* (hard coral) (ANOVA, $\delta^{15}N$: $F_{1,14} = 6.5$, $p < 0.05$), *Myripristis violacea* (nocturnal plankton) (Kruskal-Wallis, $\delta^{15}N$: $\chi^2_{1,15} = 4.5$, $p < 0.05$), and *Pearsonothuria graeffei* (detritus) (ANOVA, $\delta^{15}N$: $F_{1,13} = 4.7$, $p < 0.05$; $\delta^{13}C$: $F_{1,13} = 14.9$, $p < 0.05$; and $\delta^{34}S$: $F_{1,13} = 8.0$, $p < 0.05$) Table A6). These differences were small (~1‰) so these sources were combined *a priori* (Table A7; Figure A6). There were no significant differences in values between areas for the remaining primary consumer species (ANOVA or Kruskal-Wallis, $p > 0.05$). $\delta^{15}N$ and $\delta^{34}S$ values did not differ significantly among diurnal planktivores *Caesio varilineata* (mean ± s.e.: $\delta^{15}N$ 11.5 ± 0.1; $\delta^{34}S$ 19.1 ± 0.2), *Caesio xanthonota* (mean ± s.e.: $\delta^{15}N$ 11.6 ± 0.3; $\delta^{34}S$ 18.9 ± 0.3), *Decapterus macarellus* (mean ± s.e.: $\delta^{15}N$ 11.7 ± 0.2; $\delta^{34}S$ 19.2 ± 0.2) or *Pterocaesio pisang* (mean ± s.e.: $\delta^{15}N$ 11.5 ± 0.1; $\delta^{34}S$ 18.9 ± 0.3) (ANOVA, $p > 0.05$) but $\delta^{13}C$ values did (Kruskal-Wallis, $\delta^{13}C$: $\chi^2_{1,53} = 30.1$, $p < 0.01$), Table A6). As the differences in $\delta^{13}C$ values were small (~1‰) these species were combined into one food source group (hereafter "Diurnal planktivores" (Table A7; Figure A6).

A posteriori, the food sources (represented by primary consumers) benthic algae, coral and detritus were combined into one "reef" source group (hereafter "reef" sources) while nocturnal plankton, diurnal plankton and DVM plankton were combined into one "plankton" source group. The $\delta^{13}C$ and $\delta^{15}N$ values of the reef-based and planktonic-based primary consumers were highly significantly different ($\delta^{13}C$: Kruskal-Wallis, $\chi^2_1 = 80.6$, $p < 0.01$ and $\delta^{15}N$: $\chi^2_1 = 67.9$, $p < 0.01$ respectively) (Figure 4.2a; Figure A6a). Planktonic primary consumers all had more negative $\delta^{13}C$ signatures while reef primary consumers had less negative $\delta^{13}C$, indicating benthic energy pathways (Figure 4.2a, Figure A6a). The reef-based and plankton-based $\delta^{34}S$ scarcely differed ($\chi^2_1 = 1.9$, $p > 0.05$) (Figure 4.2b, Figure A6b).

Of the four Bayesian stable isotope mixing models, models 3 and 4 had a 0% probability of being the best model so they were not included in the results (Table A8). Model 1 had a 55% probability of being the best model and model 2 had a 45% probability of being the best model (Figure 4.3; Table A8). While both model 1 and 2 showed the same trends (Figure 4.3), the output from model 1 is presented here as it had the highest weight (Table A8).

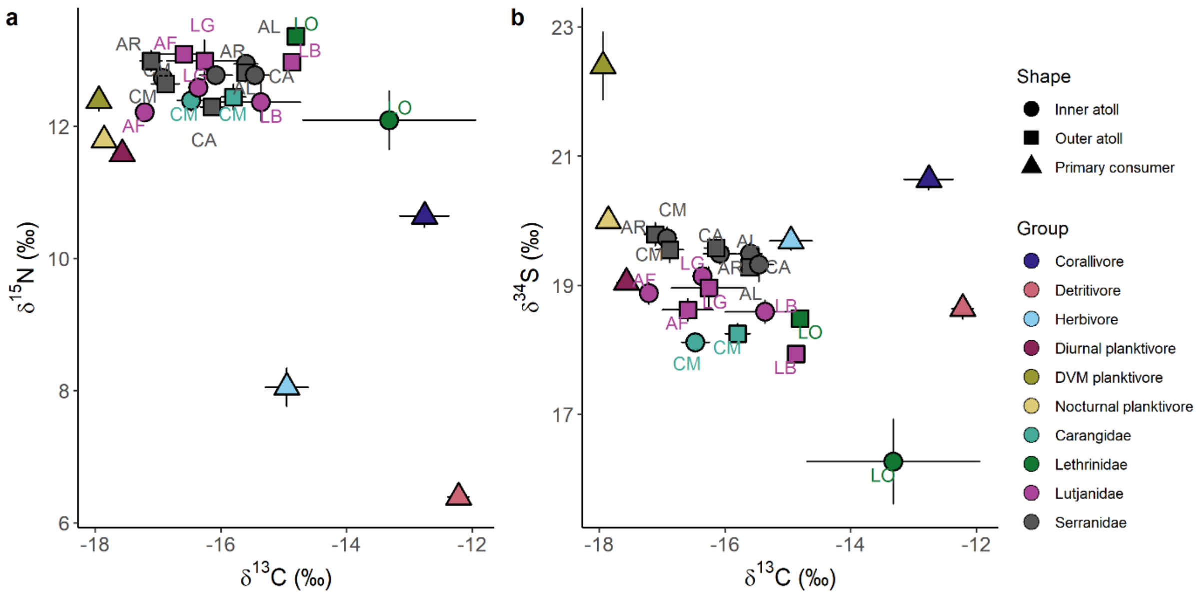


Figure 4.2. Mean isotope values (± SE) of a) $\delta^{13}C$ and $\delta^{15}N$ and b) $\delta^{13}C$ and $\delta^{34}S$ of combined primary consumers (triangles) sampled to represent end-members and reef predators sampled in inner (circle) and outer (square) atoll. Predator species labelled in group order are: CM = *Caranx melampygus*, LO = *Lethrinus obsoletus*, AF = *Aphareus furca*, LB = *Lutjanus bohar*, LG = *Lutjanus gibbus*, AL = *Anyperodon leucogrammicus,* AR = *Aethaloperca rogaa*, CA = *Cephalopholis argus*, CM = *Cephalopholis miniata*.

All nine predators were predominantly (65 – 88%) sustained by planktonic food sources in both inner and outer atoll (Figure 4.3; Table A9). Median plankton reliance was highest for *L. obsoletus* in the inner atoll (88%) and lowest for *C. argus* in the outer atoll (65%). Differences in reliance between areas for each species were small and ranged from 0.1-11%.

Groupers in both areas derived 65-80% of their biomass from planktonic food sources while reef sources contributed only 20-35%. Between areas, contributions did not vary by more than 6%. *A. rogaa* had higher median planktonic reliance in the outer atoll (80% outer, 74% inner), while *C. argus* had higher median reliance in the inner atoll (70% inner, 65% outer). Median values for *A. leucogrammicus* and *C. miniata* were equal in both atoll areas (75% both; 72% inner, 73% outer respectively). Credible intervals were similar for all groupers.

The snapper, emperor and jack median planktonic reliance range was 68-88%. Both *A. furca* and *L. gibbus* had higher median planktonic reliance in the outer atoll than in the inner atoll (75% outer, 68% inner; 84% outer, 73% inner respectively), whereas *L. bohar* had a slightly higher median reliance on plankton in the inner atoll (77% inner, 73% outer). *L. obsoletus* had almost equal median planktonic reliance in both areas (86% inner, 88% outer). Of all the predators, *L. gibbus* had the biggest difference in median reliance between atoll areas (11%). Credible intervals for *L. gibbus* were small while those for *L. obsoletus* and outer atoll *L. bohar* were largest. *C. melampygus* had greater median plankton reliance in the inner atoll (73% inner, 69% outer) and credible intervals were similar to the groupers. There was substantial overlap in the proportional planktonic contribution estimates of all the predators in both areas.

4.4 Discussion

Planktonic production was the primary contributor to reef fishery target predator biomass regardless of proximity to the open ocean. These results add to growing evidence (McCauley *et al.*, 2012c; Wyatt *et al.*, 2012b; Frisch *et al.*, 2014) that oceanic production is crucial for sustaining the biomass of many coral reef fish communities; this planktonic dependence is prevalent among the main predators and in the present case it clearly extends to lagoonal reefs. These identified linkages are not necessarily ubiquitous to coral reef systems however. In the Northwestern Hawaiian Islands, over 90% of apex predator biomass was sustained by benthic primary production (Hilting *et al.*, 2013), highlighting how trophodynamics may vary substantially spatially, even among similar systems.

Plankton was the predominant contributor to biomass for all of the predators sampled. These predator families have a known reliance on nekton (Kulbicki *et al.*, 2005). Given the high diversity and biomass of planktivores on Maldivian reefs (McClanahan, 2011; Moritz *et al.*, 2017) and the relatively small home ranges of the sampled predators (Sluka and Reichenbach, 1995; Sattar, 2009; Karkarey *et al.*, 2017), we hypothesise that they link adjacent pelagic and reef ecosystems by primarily feeding on planktivorous prey. Cross-system linkages, similar to those found here, are increasingly being documented. In the Solomon Islands, the piscivorous coral trout *Plectropomus leopardus* is sustained by feeding on planktivorous fish (Greenwood *et al.*, 2010). In Palmyra atoll, a circuitous ecological interaction chain was discovered where $\delta^{15}N$ from seabird guano over preferred

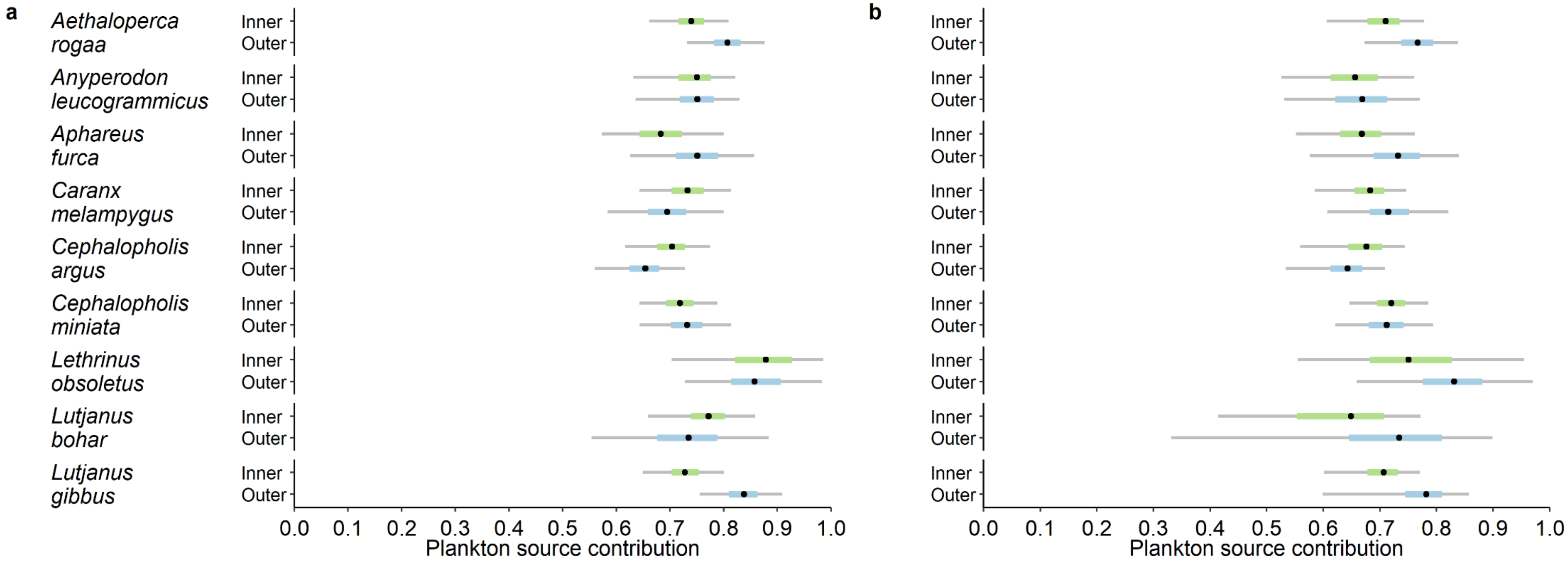


Figure 4.3. Results of two Bayesian mixing models with applied trophic discrimination factors, which determined the plankton source contribution to the nine reef predators in both inner and outer atoll. Thick bars represent credible intervals 25-75% while thin bars represent 2.5-97.5%. Black dots represent the medians (50%). a: Model 1 had a 55% probability of being the best model; b: model 2 had a 45% probability of being the best model.

native forests led to increased abundances and biomasses of zooplankton in adjacent waters (McCauley *et al.*, 2012a). Similarly in the Chagos Archipelago, on islands free of invasive rats, seabird densities were higher, leading to increased N deposition from offshore foraging, increasing reef fish community biomass (Graham *et al.*, 2018). These semi-pristine environments provide an opportunity to identify these linkages and determine how anthropogenic and climate-induced impacts may affect them.

The high degree of planktonic dependence in predators on lagoonal reefs suggests that planktonic resources are readily available across both atoll areas. Similarly, coral host and POM $\delta^{13}C$ and $\delta^{15}N$ did not differ between inner and outer reefs in the central Maldives (Radice *et al.*, 2019). Although there is little published information on the internal hydrodynamics of North Malé atoll, these results suggest that lagoonal waters are providing planktonic subsidies to inner reef communities, but it is unclear whether they come from outside the atoll or from internal hydrodynamic characteristics of the lagoon. In Palmyra atoll, inner and outer regions are well connected by a range of hydrodynamic processes (Rogers *et al.*, 2017). Mixing inside lagoons arises from wave forcing over reef crests, and vortices (generated from the wake of flow separation from currents hitting the atoll) help to redistribute water to different regions (Rogers *et al.*, 2017). Internal waves and surface downwelling are also key distributors of particulate rich waters (Williams *et al.*, 2018a). However, these findings are in contrast to Ningaloo, Western Australia and Mo'orea, French Polynesia, where $\delta^{13}C$ and fatty acids of reef fish (Wyatt *et al.*, 2012b) and the $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ of damselfish (Gajdzik *et al.*, 2016) respectively showed a gradient in oceanic reliance, decreasing into the lagoons. While the lagoons of both Ningaloo and Mo'orea are fairly constricted, North Malé lagoon is substantially more open. We hypothesise that the porosity and open nature of the atoll render lagoonal conditions similar to the open ocean. Future work to identify how nutrients circulate and enter into the lagoons would allow this transfer of energetic materials to be better understood.

The Maldives experiences substantial monsoonal fluctuations in production (Radice *et al.*, 2019). As such, timing and location of sampling may influence the degree of planktonic reliance. Here, sampling occurred on the eastern side of the archipelago during the NE season, i.e. when production is supposedly lower. Additionally, due to the double chain nature of the Maldivian archipelago, the outer atoll sites surveyed were adjacent to other atolls, rather than to the pelagic ocean. Despite this, planktonic production was the predominant contributor to predator biomass. This further supports the hypothesis that the porosity of the atoll allows oceanic resources to permeate, and as a result, Maldivian coral reefs are heavily influenced by the open ocean regardless of location and season.

Although interspecific differences in plankton reliance were apparent, median values were high and similar between areas for each species. *L. obsoletus* had the highest plankton reliance in both areas (~87%). Emperors often forage over soft bottom habitats where they feed on prey such as molluscs and crustaceans (Kulbicki *et al.*, 2005). Many of these may reflect planktonic signatures as they feed on plankton via filter feeding (Jørgensen, 1966) or in the water column at night (McMahon *et al.*, 2016). *Lethrinus nebulosus* on Ningaloo reef slopes also relies on oceanic production but in the lagoon it is sustained by reef-based production (Wyatt *et al.*, 2012b), perhaps further indication that variation in lagoonal hydrodynamics may influence food web structure. However, inner atoll *L. obsoletus* mean $\delta^{13}C$ values were closer to the reef-based primary consumers, and both inner and outer atoll *L. obsoletus* source contributions had large credible intervals. While these were likely confounded by small sample size (n = inner 3, outer 2), they may also reflect variability in the range of isotope values. Inner atoll *L. obsoletus* isotope values covered a broader range (range $\delta^{13}C$: 4.8‰, $\delta^{15}N$: 1.5‰, $\delta^{34}S$: 2.3‰) than in the outer atoll (range $\delta^{13}C$: 0.2‰; $\delta^{15}N$: 0.2‰; $\delta^{34}S$: 0.3‰), indicating that individuals in the lagoon have a larger isotopic niche than their forereef conspecifics. Niche width depends on the diversity of resources available (Araújo *et al.*, 2011) and so the greater availability of soft bottom habitat in the lagoon may offer a wider range of prey.

Outer atoll *C. argus* had the lowest plankton reliance (65%). *C. argus* are generalist predators that prey on a wide range of reef-associated fish (Harmelin-Vivien and Bouchon, 1976; Dierking *et al.*, 2011), so greater benthic reliance is probable. However, the median value of 65% indicates that two thirds of their biomass is supported by planktonic subsidies, higher than expected given previous dietary studies. *C. argus* can exhibit foraging plasticity (Karkarey *et al.*, 2017) and readily switch prey groups (Shpigel and Fishelson, 1989). As such, they may be opportunistically foraging on planktivores, a dominant component of Maldivian reefs (McClanahan, 2011). Similarly on the Great Barrier Reef, *Plectropomus* species primarily foraged on the most abundant prey families, Pomacentridae and Caesionidae, indicating that they were opportunistic generalists (Matley *et al.*, 2018). The ability of *C. argus* to switch prey may confer a competitive advantage, allowing them to survive fluctuations in prey communities resulting from environmental change (Karkarey *et al.*, 2017).

The predator assemblage differed significantly between areas, but only one of the sampled predators, *A. leucogrammicus,* contributed significantly. Evidently, the sampled predators constitute an important part of the assemblage and are key components of the biomass in each area. Furthermore, irrespective of minor differences in median plankton reliance, all the predators had substantially overlapping credible intervals. Even *L. gibbus*, where median plankton reliance differed most between areas (inner 75%, outer 86%), had credible intervals which overlapped considerably with the other species. This may indicate a degree of interspecific competition, raising the question of how they partition resources. Further investigation of their dietary niches is the recommended next step for this work.

UVC has been the main method for assessing reef fish populations but it can under-sample more mobile species (Willis and Babcock, 2000; White *et al.*, 2013). To account for such shortcomings, 50 m transects (a total of 1250 m^2 surveyed reef at each site from five transects) were used to increase the likelihood of encountering mobile predators (McCauley *et al.*, 2012c), while baited underwater video deployed in the same areas (C. Skinner *et al*. unpublished data) identified the same fish species as the most prevalent.

Multiple primary consumers were sampled to attempt to comprehensively characterise the potential production sources at the base of the reef food web. Planktivorous primary consumers may differ isotopically due to differing preferences among the diverse plankton taxa, so several planktivorous primary consumers were sampled. Although the primary consumers representing “reef” and “plankton” separated out isotopically, future studies would benefit from validating each primary consumer by characterising the food source they represent and including multiple primary consumers to represent each end member, e.g. bristle-toothed surgeonfish *Ctenochaetus striatus* as an alternate detritivore (Tebbett *et al.*, 2018) or chevron butterflyfish *Chaetodon trifascialis* as an alternate corallivore (McMahon *et al.*, 2012).

Reef predators are important fishery targets, providing food security and ecosystem services to millions globally (Cinner *et al.*, 2018). Herein, they are found to play an important ecological role linking adjacent ecosystems (McCauley *et al.*, 2012c). Projected declines in oceanic productivity, particularly at low latitudes (Bopp *et al.*, 2013; Moore *et* *al.*, 2018), may severely impact these Maldivian predators and the linkages they construct. Marine protected areas (MPAs) are widely used in coral reef conservation but reliance of many reef fish on non-reef production sources suggests the protection MPAs offer is susceptible to climate-induced changes. To adequately address these potential impacts on coral reef food webs, managers need to move towards management plans that transcend the boundaries of these threatened ecosystems.

Chapter 5 Carbon isotopes of essential amino acids highlight pelagic subsidies to predators on oceanic coral reefs

5.1 Introduction

Coral reefs are considered to be productive hotspots in oligotrophic deserts (Darwin, 1842) but their food webs are complex (Bierwagen *et al.*, 2018) and the mechanisms through which they maintain exceptionally high diversity and biomass remain poorly understood. There is increasing evidence that oceanic production sources are fundamentally important in sustaining reef fish communities (McCauley *et al.*, 2012c; Frisch *et al.*, 2014; Frisch *et al.*, 2016; Matley *et al.*, 2018; Skinner *et al.*, 2019), particularly on degraded forereef slopes (Morais and Bellwood, 2019). One mechanism of this may be through small benthic fish (<50 mm in length) which drive the productivity of coral reefs; an abundant and continuous supply of larvae connect adjacent pelagic and reef systems while adults provide fodder for a range of predators (Brandl *et al.*, 2019).

Bulk stable isotope data have been important in exploring these reef-pelagic linkages but they lack resolution, for example co-occurring sources may not be isotopically distinct (Skinner *et al.*, 2019; Whiteman *et al.*, 2019), preventing accurate separation. The isotopic data that characterise food-web baselines will also vary with environmental conditions (Boecklen *et al.*, 2011; Larsen *et al.*, 2013), requiring robust sampling of dietary sources to compare data across spatial and temporal scales (Hadwen *et al.*, 2010; Liew *et al.*, 2019). Furthermore, as macromolecules are often not directly routed to consumer tissue, there is a trophic fractionation factor between consumer and diet (DeNiro and Epstein, 1978) which varies substantially among species (Wyatt *et al.*, 2010b).

Advances in technology now allow the profiling of specific biochemical compounds, such as amino acids. Amino acids are the building blocks of protein and they can be categorised as: essential (EAA, organisms cannot synthesize them *de novo*), conditionally essential (*de novo* synthesis requires specific physiological conditions), or non-essential (organism can synthesise them *de novo*) (Whiteman *et al.*, 2019). The $\delta^{13}C$ value of an individual amino acid ("^{13}C fingerprints") helps reveal its mode of carbon acquisition; it derives from the specific synthesis pathways involved (Larsen *et al.*, 2009). As organisms cannot synthesize EAAs *de* *novo*, fractionation between diet and consumer is minimal and the $\delta^{13}C$ values of consumer amino acids represent the primary producer sources of carbon (McMahon *et al.*, 2010). Even when bulk values vary, $\delta^{13}C$ primary producer fingerprints are robust to differing growth and environmental conditions (Vokhshoori *et al.*, 2014; Larsen *et al.*, 2015; McMahon *et al.*, 2015a) and broad patterns are consistent across studies and labs (Liew *et al.*, 2019).

In both terrestrial and aquatic systems (Larsen *et al.*, 2009; Larsen *et al.*, 2013; McMahon *et al.*, 2015a; McMahon *et al.*, 2016), EAAs show distinct separation among primary producers with different carbon origins. In fact, amino acid $\delta^{13}C$ values of aquatic primary producers are especially distinct (Arthur *et al.*, 2014; Wang *et al.*, 2018). In Chapter 4, Bayesian mixing models using bulk stable isotope data indicated that key fishery target reef predators were predominantly sustained by planktonic production sources, even inside atoll lagoons. However, due to the methodological constraints associated with the lower resolution of bulk stable isotopes and the inability to separate isotopically similar planktonic sources, the origin of this pelagic production remains unclear. Phytoplankton are primarily composed of amino acids (Nguyen and Harvey, 1997; Hedges *et al.*, 2002) and different plankton community regimes have previously been separated using $\delta^{13}C$ amino acid values (McMahon *et al.*, 2015a). This suggests that planktonic sources with different origins may have distinct $\delta^{13}C$ EAA values, providing additional resolution to disentangle the sources of planktonic carbon sustaining predators on reefs.

Bulk stable isotope data vary in their resolution of relationships between body size and trophic ecology (Layman *et al.*, 2005; Ou *et al.*, 2017; Dalponti *et al.*, 2018). Organisms may change their diets over time; larger body size allows a wider range of prey to be exploited (Scharf *et al.*, 2000), which would lead to changes in stable isotope values. Very few studies to date (e.g. McMahon *et al.*, 2012; Vane *et al.*, 2018) have used the greater power of EAA $\delta^{13}C$ data to investigate how resource use might change with increasing body size and how this might affect isotope values. To determine how consumers will respond to environmental change and fluctuations in resource availability, knowledge of their resource use and how it varies with increasing body size or spatially is needed.

Here, $\delta^{13}C$ values of EAAs were used to help trace the origin of the organic carbon sustaining predator biomass across an oceanic atoll. The main questions addressed were: 1) Do $\delta^{13}C_{EAA}$

values vary spatially or with body size? 2) Do primary consumers have distinct $\delta^{13}C_{EAA}$ values? 3) If so, are there differences in predator planktonic resource usage spatially?

5.2 Materials and Methods

5.2.1 Tissue sampling procedure

Sampling occurred across sites in both inner and outer atoll areas of North Malé Atoll, Maldives (Figure 4.1). Samples were collected from reef slopes between 7 - 25 m depth during the NE monsoonal period (January – April 2017 and December 2018) to avoid any seasonal fluctuations in production sources and their signatures.

Four grouper species were selected for sampling as they were the most abundant upper trophic level (assumed TL ≥ 4) groupers in both inner and outer atoll, reach a range of sizes allowing for comparison of resource use at different lengths, and are a key component of the local reef fishery (Sattar *et al.*, 2014). Samples of white dorsal muscle tissue (~1g wet mass) were removed from the redmouth (*Aethaloperca rogaa*), slender (*Anyperodon leucogrammicus*), peacock (*Cephalopholis argus*), and coral hind (*Cephalopholis miniata*). Fish were sampled from both inner and outer atoll using a pole spear and across a large size range relative to their maximum body size (*A. rogaa* 148 – 342 mm; *A. leucogrammicus* 166 – 426 mm; *C. argus* 186 – 345 mm; *C. miniata* 152 – 320 mm). Care was taken not to sample juveniles (< 15 cm) to control for dietary changes related to ontogeny. All tissue sampling was carried out in compliance with UK Home Office Scientific Procedures (Animals) Act Requirements.

Samples were collected from primary consumer species to represent end-member food sources. Six energy pathways were identified: 1) benthic algae: powderblue surgeonfish, *Acanthurus leucosternon* (samples n = 7 inner, 6 outer) (Robertson *et al.*, 1979); 2) detritus: bristletooth surgeonfish, *Ctenochaetus striatus* (n = 7 inner, 6 outer) (McMahon *et al.*, 2016); 3) coral: scrawled butterflyfish, *Chaetodon meyeri* (n = 3 inner, 6 outer) (Sano, 1989), 4) diurnal reef plankton: variable-lined fusilier, *Caesio varilineata* (n = 2 inner, 4 outer), yellowback fusilier, *Caesio xanthonota,* (n = 1 inner, 7 outer) (Bellwood, 1988; Hamner *et al.*, 1988; Russ *et al.*, 2017); 5) nocturnal reef plankton: lattice soldierfish, *Myripristis violacea* (n = 6 inner, 6 outer) (Hobson, 1991); 6) pelagic plankton: mackerel scad, *Decapterus* *macarellus* (n = 7 outer) (Smith-Vaniz, 1995), Indian Ocean squid, *Uroteuthis duvauceli* (n = 7 outer) (Islam *et al.*, 2018).

5.2.2 Amino acid (AA) derivatisation and stable isotope analysis

Amino acid derivatisation followed the protocol devised by Corr *et al.* (2007). Muscle tissue was oven dried at 50°C for 48 hours and then ground to a fine powder using a pestle and mortar. An aliquot of ground tissue (~1.5 mg) was added to a culture tube together with 50 µl of internal standard norleucine (400 µg/mL), then hydrolysed with 6M HCl (100°C for 24 hours) under N_2 gas to displace any oxygen present. Hydrolysed samples were dried using a stream of N_2 whilst being heated on a block at 70°C, then resuspended in 0.1M HCl and stored in a freezer until ready for the next stage.

Using ion-exchange chromatography, the AA fraction was isolated with Dowex® 50WX8 hydrogen form resin (200 - 400 mesh). Resin was prepared by soaking overnight in 3M $NaOH_{aq}$, then washing five times with Milli-Q® water before storing in 6M HCl. Approximately 1mL of prepared resin was added to a glass flash column and washed six times with 2 ml of MilliQ water, then the sample was added to the column. Salts were eluted by adding 5 ml of MilliQ water. The AA fraction was eluted by adding 5 ml of 2M NH_4OH, collecting it in a clean tube and drying it using a stream of N_2 (70°C). Esterification of the AA fraction was carried out by adding 0.25 ml of a 4:1 mixture of isopropanol and acetyl chloride to the AA fraction and heating for 1 hour (100°C). The reaction was then quenched by placing the culture tubes in a freezer for at least 15 minutes, before removing the reagents under a gentle stream of N_2 (40°C). To ensure all residual solvent was removed, the sample was twice re-dissolved in 0.25 ml of dichloromethane (DCM) and then dried under a gentle steam of N_2 (40°C).

Acetylation was achieved by adding 1 ml of a mixture of acetone:triethylamine:acetic anhydride (5:2:1) to each sample and heating for 10 minutes (60°C). Reagents were evaporated under a very gentle stream of N_2 at room temperature. Liquid-liquid separation was then performed to isolate the derivatised amino acid fraction by adding 2 ml of ethyl acetate and 1 ml of saturated NaCl to each sample and vortexing then leaving to settle. Once the layers had separated, the top layer was drawn off and collected into a clean vial. This was repeated three times. All organic phases were combined and dried under a very gentle stream of N_2 (room temperature). Any residual water was removed with two successive 1 ml aliquots of DCM and evaporated under a very gentle stream of N_2 (ice bath). Samples were then stored in a freezer until they could be screened.

For screening, the derivatised AAs were resuspended in ethyl acetate and analysed using gas chromatography with an Agilent 7890 gas chromatograph with flame ionization detection (GC/FID), fitted with a DB-35 column 30m x 0.32mm x 0.5µm (Agilent), and an Agilent G4513A autosampler (Agilent Technologies, Santa Clara, CA, USA). The GC oven temperature was set to the following program: 70°C (hold 2 minutes) to 150°C at 15°C min^{-1}, then to 210°C at 2°C min^{-1}, then to 270°C at 8°C min^{-1}. The injection mode was Cold on Column (COC) and the injection volume was 1 µl with helium carrier gas at a flow rate of 2.00 ml/minute.

The $\delta^{13}C$ isotopic compositions of the AAs were analysed using a GC/IRMS. A Thermo Scientific (Bremen, Germany) Delta V Plus isotope-ratio mass spectrometer (IRMS) was fitted with a Trace GC Ultra Oven, GC Isolink, and a ConFlo 4 for interface. The GC was fitted with a DB-35 column 30m x 0.32mm x 0.5µm (Agilent). The oven was set as follows: 40°C (hold 5 minutes) to 120°C at 15°C min^{-1}, then to 180°C at 3°C min^{-1}, then to 210°C at 1.5°C min^{-1}, then to 270°C at 5°C (hold 7 minutes).

Pulses of reference gas (CO_2) were introduced into the IRMS instrument during the analysis giving rise to peaks with known $\delta^{13}C$ values (^{13}C:^{12}C ratio relative to Pee Dee Belemnite). These reference pulses were used to calculate the analyte peaks in each chromatogram. Identification of the derivatised amino acids was achieved by matching the peak elution times with those from a mixed amino acid standard (derivatised) containing (alanine [Ala], glycine [Gly], valine [Val], leucine [Leu], norleucine [Nle], threonine [Thr], serine [Ser], proline [Pro], aspartic acid [Asp], glutamic acid [Glu], hydroxyproline [Hyd], phenylalanine [Phe], lysine [Lys] and tyrosine [Tyr]). All GC/FID work and GC/IRMS work was carried out at the Bristol Node of the NERC Life Sciences Mass Spectrometry Facility, UK.

To account for the change in measured values arising from the addition of carbon atoms during the derivatisation process, a correction factor was determined for each amino acid (Table A10). The correction factor calculation was:

1) $$\frac{\big((cd\ x\ measured\ value\ of\ standard) - (c\ x\ underivatised\ 13C\ value)\big)}{d}$$

where *c* is the number of carbon atoms in the amino acid*, d* is the number of carbons added during the derivatisation process, and *cd* is the total number of carbon atoms in the derivative group. The correction factor for each amino acid was then applied to the raw measured values of the samples using the following equation:

2) $$\frac{((cd\ x\ measured\ value\ of\ standard) - (d\ x\ underivatised\ 13C\ value))}{c}$$

All primary consumer data (except for the pelagic primary consumers *D. macarellus* and *U. duvauceli*) were derivatised and analysed by Zhu (2019).

5.2.3 Data analysis

Isotopic signatures were derived from the five EAAs: leucine (Leu), lysine (Lys), phenylalanine (Phe), threonine (Thr), and valine (Val). Analyses were carried out in R 3.5.2 (R Core Team, 2017) interfaced with RStudio 1.1.463 (RStudio Team, 2012).

Essential amino acid $\delta^{13}C$ values were normalised to their respective sample means (denoted as $\delta^{13}C_{EAAn}$). For each sample, the mean value of all five EAAs was calculated and then subtracted from the absolute EAA $\delta^{13}C$ values (denoted as $\delta^{13}C_{EAAa}$). Normalising the individual $\delta^{13}C_{EAA}$ values to the mean removes natural variability in $\delta^{13}C$ values of the individual amino acids arising from differing environmental (Larsen *et al.*, 2013; Larsen *et al.*, 2015; McMahon *et al.*, 2015a) or laboratory or study conditions (Liew *et al.*). Using this method, trends in $\delta^{13}C$ fingerprints are consistent and data across studies is compatible, allowing the major carbon sources of the predators to be investigated.

As groupers were sampled during two different time periods, differences in their $\delta^{13}C_{EAA}$n values between years were investigated using permutation tests with the R package coin (Hothorn *et al.*, 2008). For each grouper species in each area, permutation tests of independence with 9999 resamples were conducted to identify whether $\delta^{13}C_{EAAn}$ values of each amino acid varied between years. Following this, linear mixed effects models were run using the package lme4 (Bates *et al.*, 2015) to investigate spatial and body size effects on grouper $\delta^{13}C_{EAAn}$ values. The $\delta^{13}C_{EAAn}$ value was the response variable with grouper species as a random effect and area (inner/outer) and body size (mm) as fixed effects. All model assumptions were checked by plotting the model residuals using histograms and qqplots, and plotting residuals vs fitted values. Wald tests were used to determine significant effects.

Primary consumers were collected from both inner and outer atoll so spatial differences in their $\delta^{13}C_{EAAn}$ values were investigated using permutation tests of independence with 9999 resamples with the coin package (Hothorn *et al*., 2008). Where two primary consumer species were collected to represent the same food source, permutation tests of independence determined whether there were any differences in their $\delta^{13}C_{EAAn}$ values.

Multivariate signatures of the $\delta^{13}C_{EAAn}$ values were visualised with principal component analysis (PCA) for the a) groupers, b) primary consumers, and c) groupers and primary consumers using the covariance matrices.

To quantify the contribution of the different food sources to the four grouper species in both inner and outer atoll, a Bayesian stable isotope mixing model was run for each species using the MixSIAR package (Stock and Semmens, 2016a). Primary consumer $\delta^{13}C_{EAAn}$ values were separated into representative source groups using k-medoids clustering analysis based on the PAM (partitioning around medoids) algorithm (Kaufman and Rousseeuw, 1990). A medoid is a point in the cluster for which the average dissimilarity between it and all the other points in the cluster is minimal. K-medoids clustering is thus less sensitive to outliers than k-means clustering, which uses the mean of points in the cluster. Clustering was carried out using the cluster package (Maechler *et al.*, 2018) and the factoextra package (Kassambara and Mundt, 2017). The optimal number of clusters was determined using the gap statistic which compares output values of clustering with different numbers of groups to output values from clustering under a reference null distribution of the data (Tibshirani *et al.*, 2001). The optimal number of clusters is that with the largest gap statistic, meaning the clustering structure is far from a random distribution of points. Mean and s.d. values were calculated for each cluster to represent source means in the mixing models.

The trophic discrimination factor was set to 0.1 ± 1.0 % as essential AAs undergo minimal fractionation up the food chain (McMahon *et al.*, 2016). A larger standard deviation value was included to provide the model with additional parameter space. Consumer data were individual grouper $\delta^{13}C_{EAAn}$ values. For each model, area (inner/outer) was included as a fixed factor and body size (mm) was included as a continuous variable. Each model was run with process x residual error terms to incorporate any variation in consumer digestibility or variation related to the sampling process (Stock and Semmens, 2016b). Model MCMC parameters were set to short (chain length = 50000, burn = 25000, thin = 25, chains = 3). Model convergence was assessed using two diagnostics: Gelman-Rubin and Geweke. The Gelman-Rubin diagnostic provides a convergence summary based on multiple chains. Model parameters with a German-Rubin diagnostic > 1.1 are considered to have not converged. The Geweke diagnostic assesses convergence by comparing means from the first and last part of a Markov chain. If the samples are drawn from a stationary part of the chain then the two means are equal and the Geweke statistic has a standard normal distribution. Here, models were considered converged when no variables had a Gelman-Rubin diagnostic > 1.05 and based on the Geweke diagnostic less than 5% of the variables were outside the 95% CI. Differences in the relative contribution of the dominant food source to groupers between atoll areas was tested for using a permutation test of independence (9999 permutations).

5.3 Results

In total, $\delta^{13}C_{EAAn}$ values from 72 samples of four species of grouper and 67 samples of eight primary consumer species from both inner and outer atoll were analysed (Table 5.1). The range in Thr and Phe $\delta^{13}C_{n}$ values was greatest (12.86 and 12.07 respectively), followed by Leu (6.45), Val (6.43) and Lys (6.37).

Only inner atoll *Anyperodon leucorgrammicus* Phe $\delta^{13}C_{EAAn}$ values and outer atoll *Cephalopholis miniata* Leu $\delta^{13}C_{EAAn}$ values differed significantly between sampling years (Permutation tests of independence, 9999 resamples, p = 0.046 and p = 0.049 respectively). As a result, all groupers from both sampling years were combined for all subsequent analyses. Atoll area and body size had no significant effect on any of the grouper $\delta^{13}C_{EAAn}$ values (Table 5.2).

There were no significant differences in any of the $\delta^{13}C_{EAAn}$ values of *Acanthurus leucosternon*, *Caesio varilineata*, *Caesio xanthonota*, or *Myripristis violacea* between inner and outer atoll (Permutation tests of independence, 9999 resamples, p > 0.05), so samples from both atoll areas were pooled for each species (Table A11). *Chaetodon meyeri* Leu and Lys $\delta^{13}C_{EAAn}$ values differed significantly between atoll areas (Permutation tests of independence, 9999 resamples, p = 0.038 and p = 0.034 respectively) and *Ctenochaetus striatus* Phe $\delta^{13}C_{EAAn}$ values differed significantly between areas (Permutation tests of independence, 9999 resamples, p = 0.047), so samples from each area were not pooled.

Table 5.1. Summary data of $\delta^{13}C_{EAA}$ absolute values for individual primary consumer and grouper species.

Species	Code	Group	Area	n	Leu	Lys	Phe	Thr	Val
Acanthurus leucosternon	AcLeu	PC: benthic algae	Inner	7	-17.82 ± 1.16	-17.28 ± 0.90	-16.59 ± 0.99	-16.01 ± 1.29	-20.07 ± 1.09
			Outer	6	-18.27 ± 2.18	-18.29 ± 2.29	-16.04 ± 1.51	-15.73 ± 1.64	-21.43 ± 2.36
Aethaloperca rogaa	AeRog	Predator	Inner	9	-21.38 ± 1.31	-14.74 ± 1.31	-23.61 ± 1.19	-6.56 ± 1.88	-20.33 ± 2.13
			Outer	9	-21.98 ± 0.77	-14.76 ± 0.77	-24.46 ± 1.35	-6.18 ± 1.05	-21.39 ± 1.14
Anyperodon leucogrammicus	AnyLeu	Predator	Inner	9	-20.51 ± 0.91	-14.43 ± 0.83	-23.65 ± 1.77	-6.29 ± 1.75	-19.99 ± 1.18
			Outer	9	-20.45 ± 1.30	-13.75 ± 1.62	-23.37 ± 1.62	-5.70 ± 1.79	-19.63 ± 1.18
Caesio varilineata	CaVa	PC: reef plankton	Inner	2	-24.96 ± 1.13	-18.84 ± 0.18	-21.47 ± 0.40	-13.91 ± 0.24	-25.70 ± 0.17
			Outer	4	-24.48 ± 1.34	-18.95 ± 1.17	-21.89 ± 1.02	-14.60 ± 1.62	-25.71 ± 2.54
Caesio xanthonota	CaXa	PC: reef plankton	Inner	1	-23.81 ± 0.00	-18.17 ± 0.00	-21.10 ± 0.00	-12.91 ± 0.00	-24.49 ± 0.00
			Outer	7	-22.92 ± 1.19	-18.13 ± 1.36	-21.23 ± 1.26	-12.97 ± 1.99	-23.15 ± 1.83
Cephalopholis argus	CeAr	Predator	Inner	9	-20.21 ± 1.24	-13.62 ± 1.26	-23.02 ± 0.97	-5.60 ± 1.70	-19.60 ± 1.39
			Outer	9	-21.30 ± 1.48	-14.58 ± 1.23	-24.56 ± 0.91	-7.08 ± 1.98	-20.36 ± 2.69
Cephalopholis miniata	CeMin	Predator	Inner	9	-21.31 ± 0.68	-15.43 ± 1.14	-23.34 ± 1.53	-5.93 ± 1.09	-20.58 ± 1.62
			Outer	9	-21.69 ± 0.42	-15.20 ± 1.10	-25.00 ± 1.56	-7.02 ± 1.66	-20.23 ± 0.89
Chaetodon meyeri	ChMe	PC: coral	Inner	3	-21.78 ± 1.15	-13.55 ± 0.41	-16.12 ± 1.18	-10.24 ± 2.03	-22.71 ± 0.63
			Outer	6	-18.73 ± 0.84	-12.48 ± 1.33	-14.48 ± 0.64	-7.45 ± 0.67	-20.33 ± 1.45
Ctenochaetus striatus	CtSt	PC: detritus	Inner	6	-19.24 ± 1.89	-17.00 ± 1.17	-17.24 ± 1.41	-14.75 ± 1.35	-19.20 ± 2.17
			Outer	6	-19.02 ± 2.74	-16.73 ± 1.76	-15.00 ± 2.01	-13.61 ± 2.13	-19.23 ± 3.28
Decapterus macarellus	DeMa	PC: pelagic plankton	Outer	4	-22.91 ± 1.06	-15.69 ± 0.94	-24.62 ± 1.42	-7.96 ± 0.92	-22.20 ± 0.88
Myripristis violacea	MyVi	PC: nocturnal plankton	Inner	6	-22.95 ± 0.25	-17.74 ± 0.15	-21.30 ± 1.16	-13.01 ± 0.69	-23.69 ± 1.23
			Outer	6	-23.69 ± 2.04	-18.08 ± 0.92	-20.84 ± 1.19	-12.94 ± 1.03	-23.70 ± 2.29
Uroteuthis duvaucelii	UrDe	PC: pelagic plankton	Outer	4	-23.79 ± 0.61	-16.82 ± 0.86	-24.92 ± 0.79	-9.01 ± 0.86	-23.25 ± 0.99

Table 5.2. Atoll area and body size effects on grouper $\delta^{13}C_{EAAn}$ values. N =72 for each amino acid.

Formula: $\delta^{13}C_{EAAn} \sim Area * Size + (1|Species)$

	Leucine		Lysine		Phenylalanine		Threonine		Valine	
Intercept	-3.50 (0.44)	***	2.07 (0.53)	***	-6.41 (0.83)	***	10.23 (0.78)	***	-2.33 (0.80)	**
Area	-0.58 (0.59)		1.09 (0.70)		-1.17 (1.10)		0.83 (1.03)		0.05 (1.07)	
Size	-0.00 (0.00)		0.00 (0.00)		0.00 (0.00)		0.00 (0.00)		-0.00 (0.00)	
Area * Size	0.00 (0.00)		-0.00 (0.00)		0.00 (0.00)		-0.00 (0.00)		0.00 (0.00)	
AIC	157.26		181.23		242.14		233.58		238.37	
Log Likelihood	-72.63		-84.62		-115.07		-110.79		-113.19	
Var: species (Intercept)	0.02		0.06		0		0.01		0	
Var: Residual	0.30		0.42		1.10		0.96		1.04	

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

There were no significant differences in any of the $\delta^{13}C_{EAAn}$ values between the two pelagic primary consumers *Decapterus macarellus* and *Uroteuthis duvauceli* (Permutation tests of independence, 9999 resamples, $p > 0.05$), so these two species were hereafter considered as one "pelagic plankton" source group. Between the caesionids, *Caesio varilineata* and *C. xanthonota*, there were significant differences in the Phe and Val $\delta^{13}C_{EAAn}$ values (Permutation tests of independence, 9999 resamples, $p = 0.032$ and $p = 0.033$ respectively) so these two species were not combined (Table A11).

The first two axes of the PCA of the grouper $\delta^{13}C_{EAAn}$ values explained 69.2% of the variation and showed no clear grouping of species or atoll area (Figure 5.1; Table 5.3). The PCA of the primary consumers showed separation of the different groups, particularly axis one, which explained 68.1% of the variation, while the second principal component axis explained 21.4% of the variation (Figure 5.1Figure 5.2A; Table 5.3). The separation along PC1 appeared to split the primary consumers into three distinct groups: 1) pelagic plankton, 2) reef plankton, nocturnal plankton, coral, and 3) benthic algae and detritus. A third PCA visualised the associations between the groupers and the primary consumers and the groupers were closest to the pelagic plankton group (Figure 5.2B; Table 5.3).

Table 5.3. Eigenvectors and variance explained (%) for the four principal components (PC) of the PC analysis used to visualise the $\delta_{13}C_{EAAn}$ values of 1) groupers, 2) primary consumers, and 3) groupers and primary consumers plotted together from both inner and outer atoll.

	PC1	PC2	PC3	PC4
1) Groupers				
Leu	0.81	0.21	-0.22	0.49
Lys	-0.08	0.62	0.78	-0.02
Phe	-0.66	0.43	-0.61	-0.10
Thr	-0.60	-0.72	0.25	0.23
Val	0.87	-0.32	-0.01	-0.38
Variance	44.40	24.83	21.75	9.02
2) Primary consumers				
Leu	0.90	0.13	-0.40	0.12
Lys	-0.91	-0.06	0.04	0.40
Phe	0.69	-0.69	0.20	-0.01
Thr	-0.95	0.15	-0.09	-0.26
Val	0.61	0.74	0.27	0.05
Variance	68.09	21.44	5.58	4.88

	PC1	PC2	PC3	PC4
3) Groupers and primary consumers				
Leu	0.87	0.28	0.28	-0.30
Lys	-0.88	-0.15	0.42	0.14
Phe	0.84	-0.51	-0.05	0.18
Thr	-0.95	0.12	-0.19	-0.21
Val	0.17	0.96	-0.02	0.23
Variance	63.51	25.88	5.83	4.78

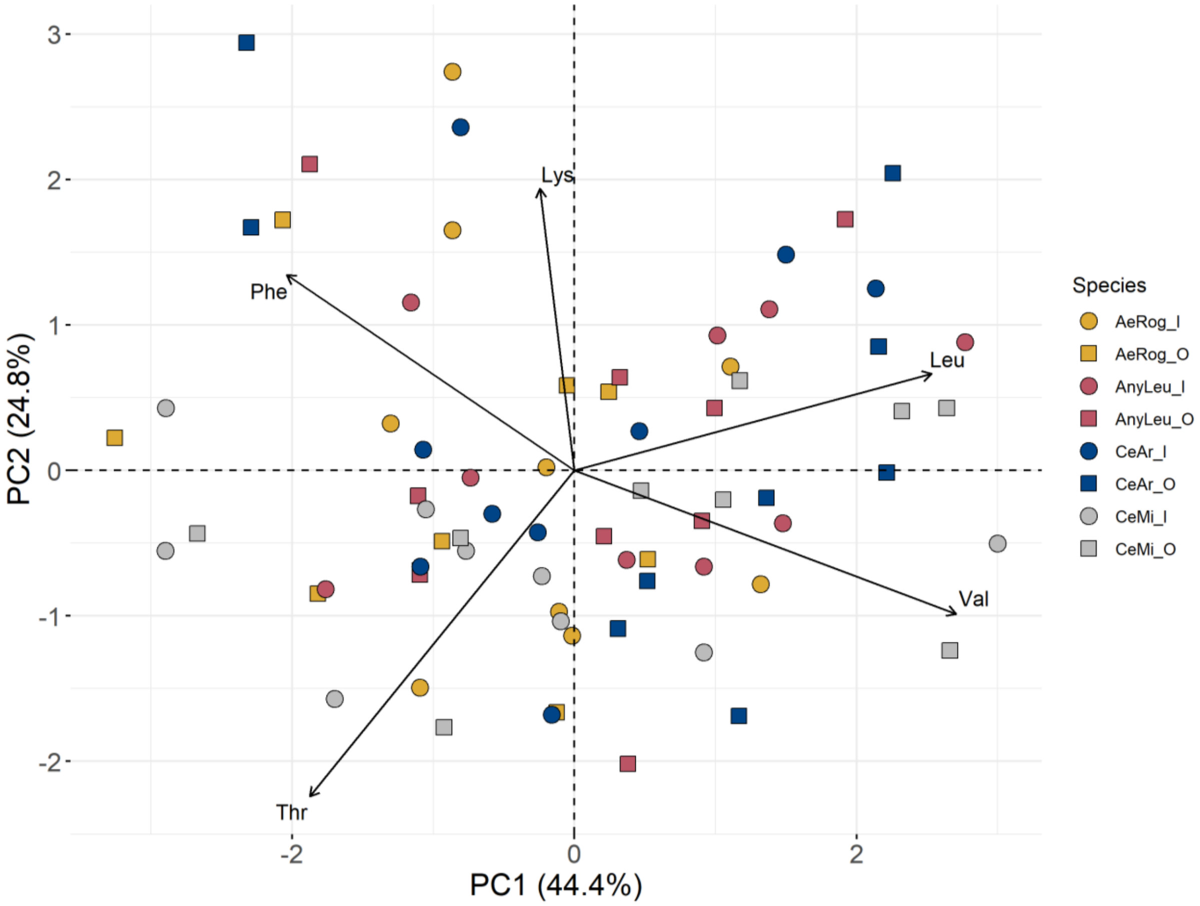


Figure 5.1. Principal components analysis (PCA) of the $\delta^{13}C_{EAAn}$ values of four groupers in both inner and outer atoll. Arrows show the direction and magnitude of the eigenvectors for each essential amino acid. PC1 (x-axis) and PC2 (y-axis) explain 69.2% of the variation in the data. I = inner atoll; O = outer atoll. AeRog = *Aethaloperca rogaa*; AnyLeu = *Anyperodon leucogrammicus*; CeAr = *Cephalopholis argus*; CeMi = *Cephalopholis miniata*.

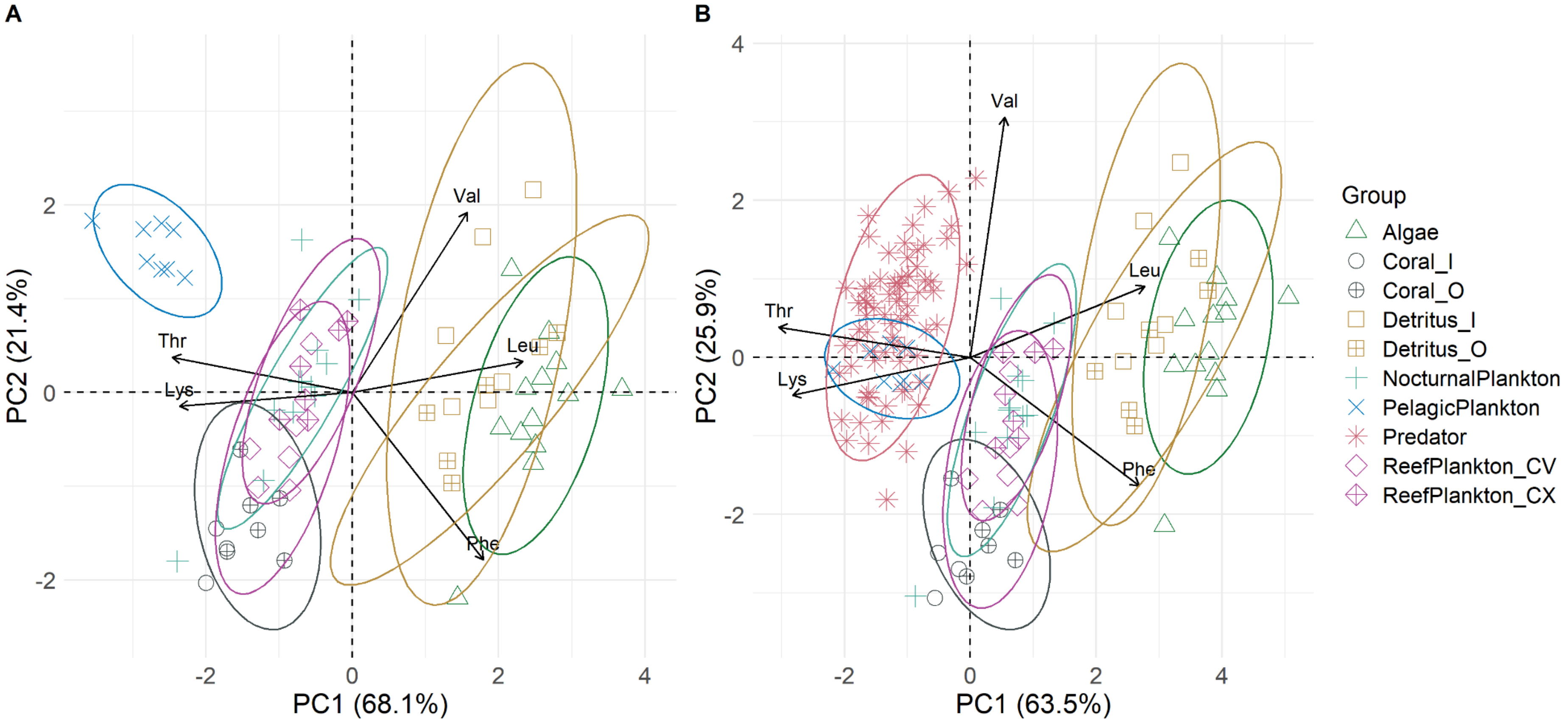


Figure 5.2. Principal components analysis (PCA) of the $\delta^{13}C_{EAAn}$ values of A) only primary consumers and B) primary consumers with predators (pink stars) added. Arrows show the direction and magnitude of the eigenvectors for each essential amino acid. I: inner atoll; O: outer atoll; CV: *Caesio varilineata*, variable-lined fusilier; CX: *Caesio xanthonota*, yellowback fusilier.

Based on the gap statistic and the k-medoids cluster analysis (Figure 5.3), the primary consumers were split into four groups, representing: 1) algae/detritus, 2) coral, 3) reef plankton, and 4) pelagic plankton. When running Bayesian isotope mixing models, sources can be combined *a posteriori* based on biological knowledge (Phillips *et al.*, 2005; Phillips *et al.*, 2014). Here, after the mixing models had run, the source groups representing coral and algae/detritus were combined into one group named "Reef Benthic".

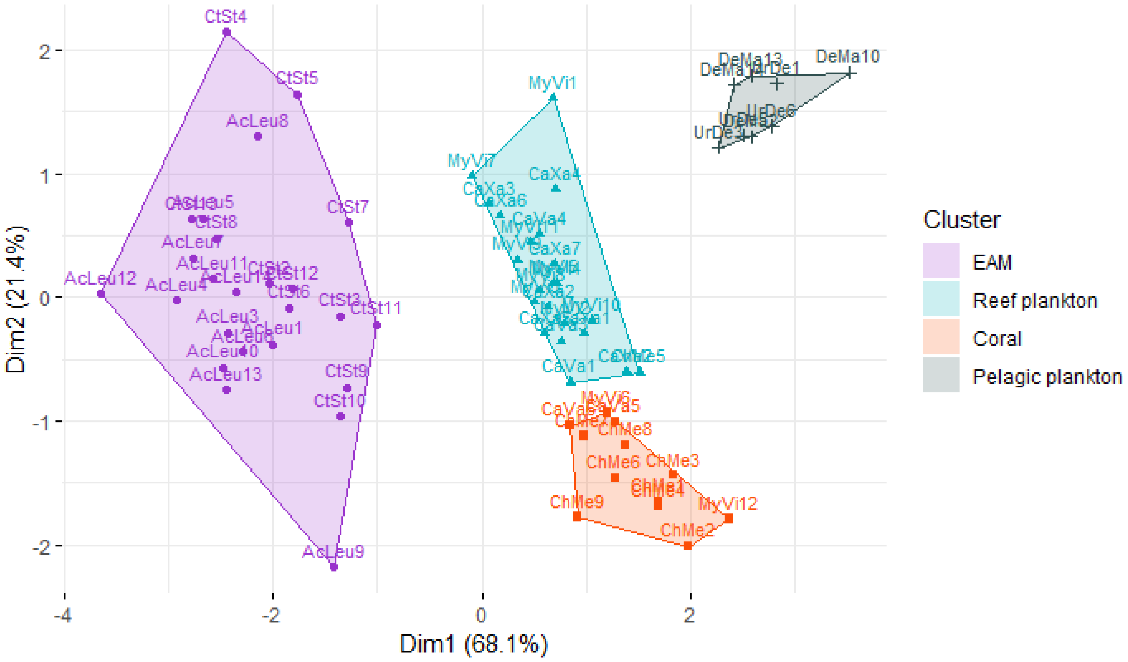


Figure 5.3. K-medoids cluster analysis of primary consumer species sampled to represent food sources. Clustering was based on the normalised δ^{13}C values of essential amino acids Leu, Lys, Phe, Thr and Val. EAM: epilithic algal matrix. Species codes are in Table 5.1.

The mixing models indicated that all four groupers derived the majority (95-99%) of their food from pelagic production sources in both inner and outer atoll (Figure 5.4). Median pelagic source reliance was significantly greater in the outer atoll (98-99%) than in the inner atoll (95-97%) (Permutation test of independence, 9999 resamples, Z = -2.38, p =0.028). Patterns in pelagic reliance were consistent between atoll areas among the groupers. Of all four groupers, *Aethaloperca rogaa* consistently had the highest median pelagic reliance, followed by *Cephalopholis miniata*, *Anyperodon leucogrammicus* and *C. argus*. Median reliance on benthic reef and reef plankton sources was higher in the inner atoll (1.5-3% and 1-1.6% respectively) than in the outer atoll (0.4-1% and 0.3-0.6% respectively). Credible intervals were consistently larger for groupers in the inner atoll than in the outer atoll.

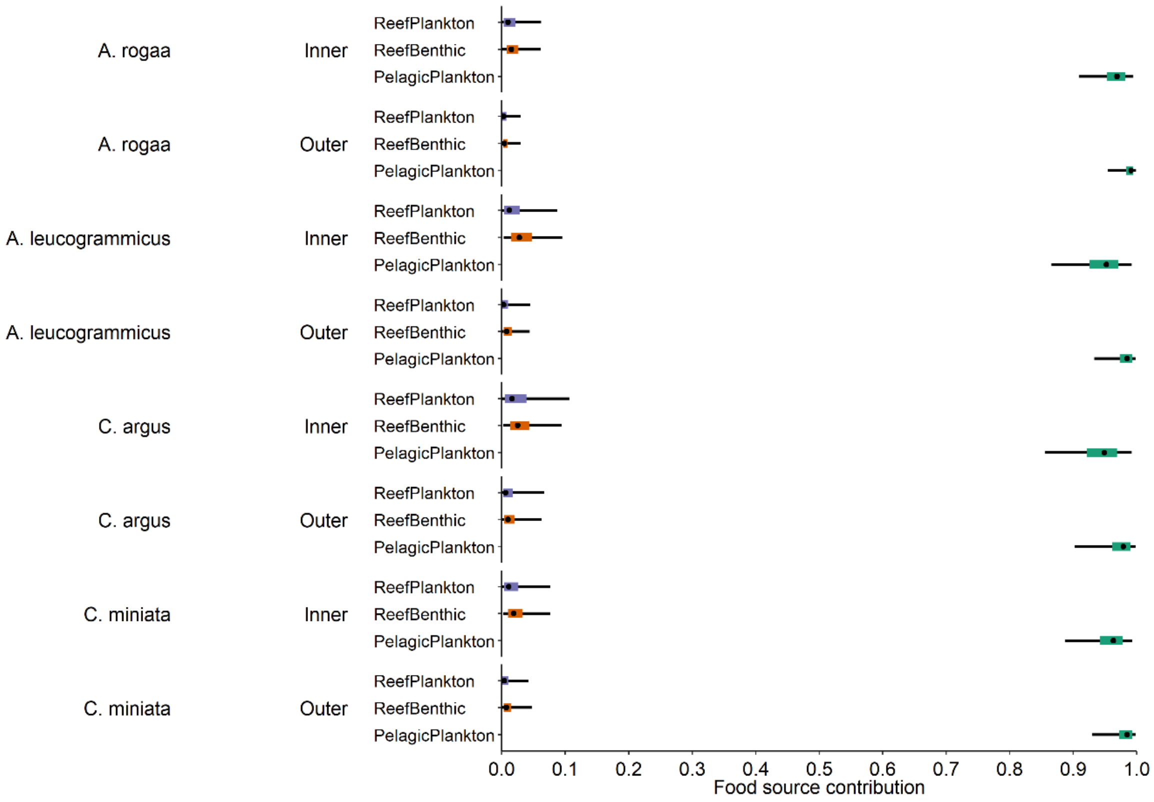


Figure 5.4. Food source contributions for four grouper species in inner and outer atoll, as determined by Bayesian isotope mixing models. Black bars represent 95% credible intervals (2.5–97.5%), coloured bars represent interquartile ranges (25-75%) and black dots represent the median (50%). Green = pelagic plankton, orange = reef benthic, purple = reef plankton.

5.4 Discussion

Primary consumer $\delta^{13}C$ values of essential amino acids showed good discrimination among clusters broadly representing benthic algae/detritus, coral, reef plankton (diurnal and nocturnal) and pelagic plankton. The proximity of benthic algae and detritus to each other is not surprising. Although the powderblue surgeonfish, *Acanthurus leucrosternon*, is classified as a herbivore (Robertson *et al.*, 1979) and the lined bristletooth, *Ctenochaetus striatus*, is classified as a detritivore (McMahon *et al.*, 2016), it is likely that they are not strictly feeding on a single homogenous production source. Furthermore, much of the detrital material they are feeding on may have been of algal origin; the epilithic algal matrix (Wilson *et al.*, 2003). Diurnal and nocturnal reef plankton and coral were also isotopically similar to each other, perhaps indicative of coral heterotrophy, with the fusiliers (*Caesio varilineata* and *C. xanthonota*), soldierfish (*Myripristis vittata*) and corals feeding on localised reef-based plankton that are supported by the same phytoplankton sources (Hamner *et al.*, 1988; Hobson, 1991; Alldredge and King, 2009). A novel finding here is that the $\delta^{13}C_{EAA}$ values of the reef plankton and the pelagic plankton primary consumers were distinct from one another. Mackerel scad, *Decapterus macarellus*, and Indian Ocean squid, *Uroteuthis duvauceli*, are found in deeper oceanic waters and *U. duvauceli* come to the surface to feed at night (Smith-Vaniz, 1986; Islam *et al.*, 2018). Their $\delta^{13}C_{EAA}$ values may be a proxy for a pelagic, deep-water vertically migrating plankton community (Hays, 2003) that is distinct from the localised reef plankton community comprised predominantly of copepods (Alldredge and King, 2009).

Pelagic plankton, rather than reef plankton, primarily sustained all groupers. This linkage likely arises through a range of mechanisms. Oceanic atolls, like those in the Maldives, have an enhanced biomass of mesopelagic prey such as lanternfish and euphausiids (Bradbury *et al.*, 1970; Letessier *et al.*, 2016) which migrate to the surface waters to feed at night. In addition, surface slicks (convergence of surface waters forming above internal waves) accumulate pelagic marine organisms close to shore; in slicks half (50.1%) the larval fish are pelagic compared to 26.4% in ambient waters, and densities of deep-water mesopelagic larval fish are 2.7-fold higher in slicks compared to ambient waters (Gove *et al.*, 2019). Furthermore, particularly in the Indian Ocean, small benthic reef fish larvae are a key component of the ichthyoplankton and connect the reef-pelagic interface. Juveniles and adults provide 60% of consumed biomass on reefs, a contribution until now overlooked (Brandl *et al.*, 2019). The combination of enhanced mesopelagic prey and consistently available cryptobenthic fauna suggests these reefs may be a sink of pelagic energy (Letessier *et al.*, 2016; Brandl *et al.*, 2019). Conversely, on the Great Barrier Reef, open ocean water-column pathways supported only 57% of reef fish productivity on forereef slopes, however this contribution was expected to be higher on oceanic reefs (Morais and Bellwood, 2019). Currently, little information exists on $\delta^{13}C_{EAA}$ incorporation rates or the timeframe that they may represent, however I hypothesise that the predominantly pelagic $\delta^{13}C_{EAA}$ values of the groupers is indicative of an atoll-wide food web fuelled by pelagic subsidies.

Even inside the atoll lagoons, groupers were almost exclusively reliant on pelagic production sources. Extensive mixing of oceanic waters renders lagoonal conditions in the Maldives reefs akin to the open ocean (Rogers *et al.*, 2017), contributing to the consistently high pelagic reliance across the atoll. These findings correlate with the bulk isotope data (Chapter

4, Skinner *et al.*, 2019) and previous research that found no difference in coral host and POM $\delta^{13}C$ and $\delta^{15}N$ between inner and outer reefs in the Maldives (Radice *et al.*, 2019), providing further evidence of a well-mixed system where oceanic nutrients are available throughout. In contrast, several studies have found an increasing reliance of consumers on oceanic nutrients with proximity to the open ocean (Wyatt *et al.*, 2012b; Gajdzik *et al.*, 2016). In the Red Sea, foraging by the snapper *Lutjanus ehrenbergii* was more benthic on shelf reefs and more planktonic on oceanic reefs (as identified by $\delta^{13}C_{EAA}$ values), but it was unclear whether this difference arose from a reliance on different food items in each location or from differing levels of planktonic inputs to the same food webs (McMahon *et al.*, 2016). Similarly, here, while oceanic nutrients are clearly available throughout, it is uncertain whether the groupers are consistently selecting pelagic-derived prey or all the food webs across the atoll are supported by pelagic inputs. Gut contents data or feeding observations in this locale may provide important additional information which could help tease apart these two hypotheses.

Grouper $\delta^{13}C_{EAAn}$ suggest all four species derive their carbon from the same pathways regardless of size. Previous research indicates $\delta^{13}C_{EAA}$ values remain consistent across taxa (McMahon *et al.*, 2016) and differing growth rates (Larsen *et al.*, 2015), although the latter study investigated this for the marine diatom, *Thalassiosira weissflogii*, only so how this varies among upper level consumers is unknown. While growth rate is partly dependent on food availability, pelagic reef fish have higher growth rates as they exploit adjacent pelagic prey (Morais and Bellwood, 2018). *A. rogaa,* which had the greatest pelagic reliance, also has the highest reported growth rate, while *C. argus,* which had the lowest pelagic reliance, also has the lowest reported growth rate (Mapleston *et al.*, 2009). Future work would benefit from including a greater number of predator samples across all sizes to investigate size effects on $\delta^{13}C_{EAA}$ with greater statistical power. However, due to time constraints associated with the derivatisation process and the high cost of processing samples for compound-specific stable isotope analysis this was beyond the scope of this study. Although the number of studies utilising $\delta^{13}C$ of amino acids is increasing, the incorporation rates of AA from diet to consumer are scarcely known; there is substantial variation among amino acids (Bradley *et al.*, 2014; Downs *et al.*, 2014; Whiteman *et al.*, 2018) and how this varies among taxa is uncertain (Whiteman *et al.*, 2019). Consequently, the dietary timeframe represented by these values is unclear.

This is the first study to characterise multiple planktonic sources for reefs using $\delta^{13}C_{EAA}$ values. Previous research on reefs in the Red Sea used calanoid copepods to represent pelagic plankton signatures (McMahon *et al.*, 2016). The Red Sea is a relatively enclosed, oligotrophic body of water, with limited exchanges with the adjacent Indian Ocean (Racault *et al.*, 2015), but planktonic primary production and N_2 fixation differ between open water and nearshore reef settings (Tilstra *et al.*, 2018). Furthermore, POM increases to the South with increased proximity to nutrient-rich Indian Ocean water (Kürten *et al.*, 2016). Consequently, the pelagic plankton signature derived from reef-based calanoid copepods (McMahon *et al.*, 2016) may have been similar to that of the nearshore reef plankton of this study. Additional sampling of plankton from the open water and further South nearer to the Indian Ocean may have resulted in a distinct and separate pelagic plankton isotopic signature such as that found here.

As with all emerging technologies, there is still much that is unknown about $\delta^{13}C_{EAA}$ data. Firstly, fractionation of EAA stable isotopes between diet and consumer is thought to be minimal (McMahon *et al.*, 2010), but this may not be the case. Increasing evidence suggests that EAAs may not be directly routed from dietary material but instead are assimilated from symbiotic gut microbes (Newsome *et al.*, 2011). Alternatively, EAAs may undergo extensive catabolism when absorbed by cells lining the gut (Metges, 2000). Both of these phenomena would lead to non-zero fractionation factors but are as yet relatively unexplored (Whiteman *et al.*, 2019). Here, despite using a small fractionation factor for the mixing models, a larger standard deviation value was used to provide additional model parameter space (0.1 ± 1.0 %) in the absence of accurate fractionation factors. However, if the $\delta^{13}C_{EAA}$ fractionation values are similar to that for non-essential amino acids (-0.5 – 2.4‰) (McMahon *et al.*, 2015b), the mixing model may have been too constrained to find an appropriate solution. Consequently, this may expound the rigidity and lack of variation in the food source contribution estimates presented here. As compound-specific stable isotope analysis becomes a more popular tool to investigate trophodynamics, a greater understanding of the mechanisms through which EAAs are integrated by consumers will be required, and is the recommended next step for future work.

Secondly, all the primary consumer samples (with the exception of the pelagic *U. duvauceli* and *D. macarellus*) were derivatised and analysed separately to the pelagic primary consumers and the groupers. The strong pelagic reliance of the groupers may be influenced by differences in $\delta^{13}C_{EAA}$ values between studies arising from: 1) derivatising with different batches of reagents, and 2) the calibration settings of the GC/IRMS at different times (Zhang *et al.*, 2012), causing the groupers to be closest isotopically to the pelagic primary consumers run at the same time as them. However, by using consistent laboratory standards and normalising the $\delta^{13}C_{EAA}$ data to the mean, values should be comparable between studies (Larsen *et al.*, 2013; Larsen *et al.*, 2015; McMahon *et al.*, 2015a; Liew *et al.*, 2019), especially when samples were collected in the field at the same time and run on the same GC/IRMS. As such, it is unlikely that the strong pelagic signature arises solely from differences in $\delta^{13}C_{EAA}$ values, but future research should focus on how varying lab or GC/IRMS conditions may influence $\delta^{13}C_{EAA}$ values and their ecological interpretation. In addition, several grouper samples were collected at a different time to the others. However, not only were they caught during the same monsoonal season in the same location and no significant differences in values were identified, but $\delta^{13}C_{EAA}$ values are thought to be robust to seasonal fluctuations (Larsen *et al.*, 2015) and $\delta^{13}C_{EAAn}$ values show even less variability (McMahon *et al.*, 2015a).

Finally, while fusiliers are classic reef planktivores, due to their highly mobile nature (Russ *et al.*, 2017), they may not have been the most appropriate proxy for localised reef plankton in this context. Moreover, as groupers are typically more reef-associated it is uncertain to what degree they would predate on them, perhaps explaining the lack of reliance on reef plankton sources. Sampling of other more site-attached planktivores such as balistids (*Odonus niger*), pomacentrids (*Chromis* spp) and serranids (*Pseudanthias* spp), which are all frequently found in grouper stomach contents (Shpigel and Fishelson, 1989; St John, 1999; Dierking *et al.*, 2011; Meyer and Dierking, 2011), is the recommended next step for this work.

While coral reefs worldwide are experiencing unprecedented losses of live coral cover (Hughes *et al.*, 2017b), fish productivity on those that rely on pelagic subsidies may be more resilient to coral bleaching than previously thought (Morais and Bellwood, 2019). Groupers are a fundamental component of the Maldivian reef fishery (Sattar *et al.*, 2014) and their exceptionally high pelagic reliance found here suggests that fishery predictions based solely on reef-associated habitat loss may be misleading (Robinson *et al.*, 2019b).

Chapter 6 Disentangling the drivers of coral reef food webs

6.1 Introduction

Understanding food web dynamics and the drivers of community structure is a central goal in ecology. But food webs are complex, with vast numbers of species connected via multiple linkages, so disentangling the trophic interactions driving community composition can be complicated (Polis and Strong, 1996). In marine systems, predator-prey interactions are well studied (Hobson, 1979; Baum and Worm, 2009; Allain *et al.*, 2012) but the key drivers of predator distributions and how prey assemblages influence predators is often unclear. Predator survival is reliant on access to food so investigating predator-prey species distributions across spatial scales may offer insight into the biotic and abiotic factors that drive predator community structure (Beukers-Stewart *et al.*, 2011; Sandom *et al.*, 2013). Identifying the drivers of community structure is important to determine how communities may respond to changing environments, and a better understanding of predator-prey relationships may facilitate this. Furthermore, knowledge of carbon pathways and energetic linkages is fundamental in assessing food web function and resilience.

On coral reefs, site-attached piscivorous reef predators (lutjanids, serranids) play an important role in structuring prey communities (Boaden and Kingsford, 2015) and contributing to ecosystem integrity and resilience by maintaining biodiversity (McCann *et al.*, 2005; Rooney *et al.*, 2006; Ceccarelli and Ayling, 2010). The bulk and compound-specific stable isotope data presented in Chapters 4 and 5 indicated that the sampled reef predators were all primarily sustained by planktonic production sources. This ecological linkage is likely generated through feeding on planktivores (Matley *et al.*, 2018; Skinner *et al.*, 2019), a dominant component of the Maldivian reef fish biomass (Moritz *et al.*, 2017), and there was little contribution from other prey fish groups. This suggests that there may be a relationship between predator and planktivore abundance, with biomass of one influenced by the other. However, findings from previous research investigating the relationships between reef predators and their prey are unclear. Strong positive relationships were identified between abundances of reef predators and their prey on the Great Barrier Reef (Stewart and Jones, 2001; Beukers-Stewart *et al.*, 2011) and prey biomass was considered an important driver of reef-associated shark abundances in the Chagos archipelago (Tickler *et al.*, 2017). In contrast, a longer-term study in the US Virgin Islands identified a negative correlation between predator abundance and the maximum number of co-occurring prey, and no overall relationship between predator and prey abundances (Hixon and Beets, 1993). This latter case may be the result of wrongly assuming “prey” of the predators in some instances.

In addition to predator and prey densities, environmental variables such as depth and structural complexity are also important in explaining relationships between these groups. Structural habitat complexity provides refuge for prey from predation, with higher levels of complexity detrimental to predator growth rates, potentially altering food web dynamics (Graham and Nash, 2013; Rogers *et al.*, 2018). Furthermore, species compositions of both predator and prey fish communities change with depth (Jankowski *et al.*, 2015; Asher *et al.*, 2017). However, due to the indirect nature of these variables, relationships are challenging to interpret and often overlooked using traditional predator prey models. Consequently, how all these variables interact and which are most important in driving predator biomass is unknown.

Studies investigating community structure often rely on modelling techniques (e.g. general linear models) that examine the impact of a few variables on a single biological endpoint response, such as abundance, diversity or biomass (Lefcheck and Freckleton, 2016; Bruder *et al.*, 2019). These approaches do not account for the fact that ecosystems are networks comprised of multiple interlinked multitrophic biotic interactions, further influenced by a range of environmental factors (Seibold *et al.*, 2018; Bruder *et al.*, 2019). As such, fully understanding the relationships between predators, their prey, and the surrounding habitat can prove complicated. Structural equation models (SEMs) can incorporate multiple interrelated predictor and response variables (Lefcheck and Freckleton, 2016), making them a useful method for understanding complex systems with both direct and indirect linkages (Shipley, 2002; Grace, 2006; Grace *et al.*, 2010). Hypothetical pathways between variables are identified *a priori* and are expressed in equation form, with response variables driven by one or multiple predictor variables. These response variables then become predictors for other variables, forming a sequence of causal relationships (Fan *et al.*, 2016; Lefcheck and Freckleton, 2016). Hence, in complex systems such as coral reefs, SEMs can more accurately estimate the importance of multiple interlinked biotic and abiotic factors in structuring reef predator biomass than other multivariate or linear modelling techniques.

The data generated in this thesis offer the unique chance to test whether fish community structure is primarily driven by 1) habitat structural complexity or 2) food (prey) availability. Using SEMs, I examine which biotic or abiotic variables are most important in driving site-attached piscivorous reef predator biomass and whether the carbon pathways identified with stable isotopes in previous chapters are evident. I hypothesise that structural complexity will be the most important driver of all prey groups as it provides refuge from predation (Graham and Nash, 2013) and planktivore biomass will be the key driver of predator biomass demonstrated by the stable isotope data in Chapters 4 and 5.

6.2 Materials and Methods

6.2.1 Site selection

All fieldwork was conducted in North Malé Atoll, Maldives (N 04° 25′ 46.2″, E 73° 30′ 4.3″). Surveys were split between two areas: the inner lagoonal reefs (hereafter “Inner”), and the outer edge reefs (hereafter “Outer”).

6.2.2 Underwater Visual Census (UVC)

UVC was conducted at a total of 40 sites, 20 in each atoll area between March to April 2018 (Figure 6.1). At each site, two 30 x 5 m transects were randomly surveyed parallel to the forereef slope between depths of 3 – 15 m. All transects were a minimum of 10 m apart to reduce overlap. The entire fish community of all sizes was recorded to genus or species level depending on their diet and body morphometries (Table A12 and A13: full species list and classifications). When members of the same genus all consumed the same diet and had a similar body shape they were only recorded to genus, however when diet or body shape differed within the genus, fish were recorded to species level. Blennies were split into two groups depending on whether they were sabretooth blennies or not, and gobies were separated into either reef gobies or sand gobies (Kuiter, 2014). All UVC surveys were conducted by the same two observers who were fully trained in fish identification and size estimations. The fish community was split into larger, more mobile species (Acanthuridae, Lutjanidae, Lethrinidae) and smaller, cryptic site-attached species (Blenniidae, Gobiidae, Pomacanthidae). The first observer swam while reeling out the transect and recording all the mobile fish that would be disturbed, while the second observer swept one side of the transect first and then the second side, searching all the holes and refuges for hidden fish.

Along the transect, the benthic substrate type was recorded every 50 cm. Complexity was measured by draping a fine-link chain along a 10 m section of the transect tape from 10 – 20 m. The place the chain reached on the transect tape was then recorded. Complexity was calculated using equation 1, where a number closer to 1 signified a flat, low relief reef while a number closer to 0 indicated a reef of high complexity.

Eqn 1) $Reef\ complexity = \frac{chain\ measurement}{10}\ x\ 100$

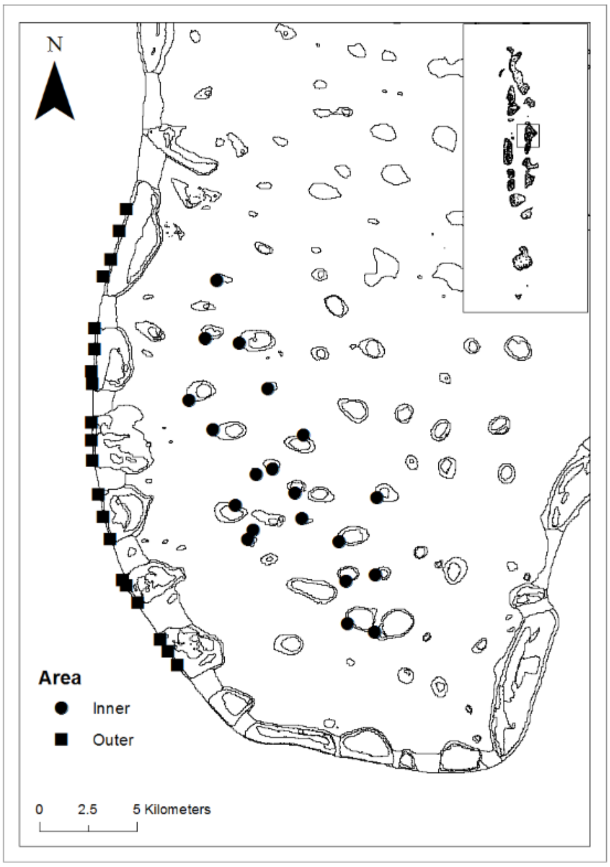


Figure 6.1. Sites (40) on North Malé Atoll where underwater visual census (UVC) was conducted.

6.2.3 Data analysis

Data were analysed in R statistical software version 3.5.2 (R Core Team, 2017). Fish biomass was calculated using published length-weight relationship data on Fishbase (Froese and Pauly, 2018). When only the genus was recorded, the length-weight data for the most common species (C Skinner, unpublished data) on the reefs was used. Fish were categorised into six functional feeding groups based on the literature and FishBase: predator, benthic carnivore, corallivore, EAMvore (epilithic algal matrix-vores), omnivore or planktivore (Table

A12 and A13). All prey fish > 20 cm were removed from further analysis as it was assumed they were too large to be fed on by the predators (St John, 1999; Dunic and Baum, 2017). As the focus of the stable isotope work in previous chapters has been on fishery target, reef-associated predators, all transient (*Elagatis bipinnulata* and *Gymnosarda unicolor*) and non-target predator species (*Aulostomus chinensis*, *Fistularia commersonii*, *Gnathodentex aureolineatus*, *Monotaxis grandoculis*, *Pterois antennata* and *P. volitans*) were removed from further analysis.

Structural Equation Modelling (SEM) and path analysis were used to explore the relationships between the predators, their prey and their environment. SEM uses a variance-covariance matrix to test the relationship between pathways. Models are fit using maximum-likelihood estimation, which continually refines parameter value estimates to minimise differences between the observed and expected variance-covariance matrices (Lefcheck and Freckleton, 2016). A full conceptual model was developed to explore which biotic and abiotic variables influence reef predator biomass (Figure 6.2). Depth and atoll area were considered predictors of the benthic habitat. Benthic habitat and underlying geology determines structural complexity but atoll location (e.g. inner or outer atoll) may also have an influence. Benthic habitat and structural complexity were considered to be variables that structure biomass of all prey fish groups. Finally, biomass of all prey fish groups and structural complexity were considered predictors of predator biomass.

At each site, benthic cover, prey and predator biomass data were averaged across both transects. Benthic habitat and fish biomass data were first explored separately to visualise patterns in the community structure. Principal Component Analysis (PCA) was used to capture and simplify the complex nature of the multivariate benthic community data using the FactoMineR package (Le *et al.*, 2008) and the FactoExtra package (Kassambara and Mundt, 2017). PCA generates a two dimensional ordination which helps to visualise patterns and reduce dimensionality when using many quantitative variables. The multivariate homogeneity of group dispersions was subsequently calculated for each atoll area group on a Euclidean distance matrix of the data to determine the mean distance-to-centroid of the sites using the vegan package (Oksanen *et al.*, 2018). The scores for the first two PC orthogonal axes for each site were subsequently extracted and used as explanatory variables for the benthic habitat in the SEM. The mean structural complexity and biomass of each fish functional group at each site were plotted onto the extracted PC1 and PC2 coordinates of the benthic variables to further visualise relationships in fish and benthic community structure.

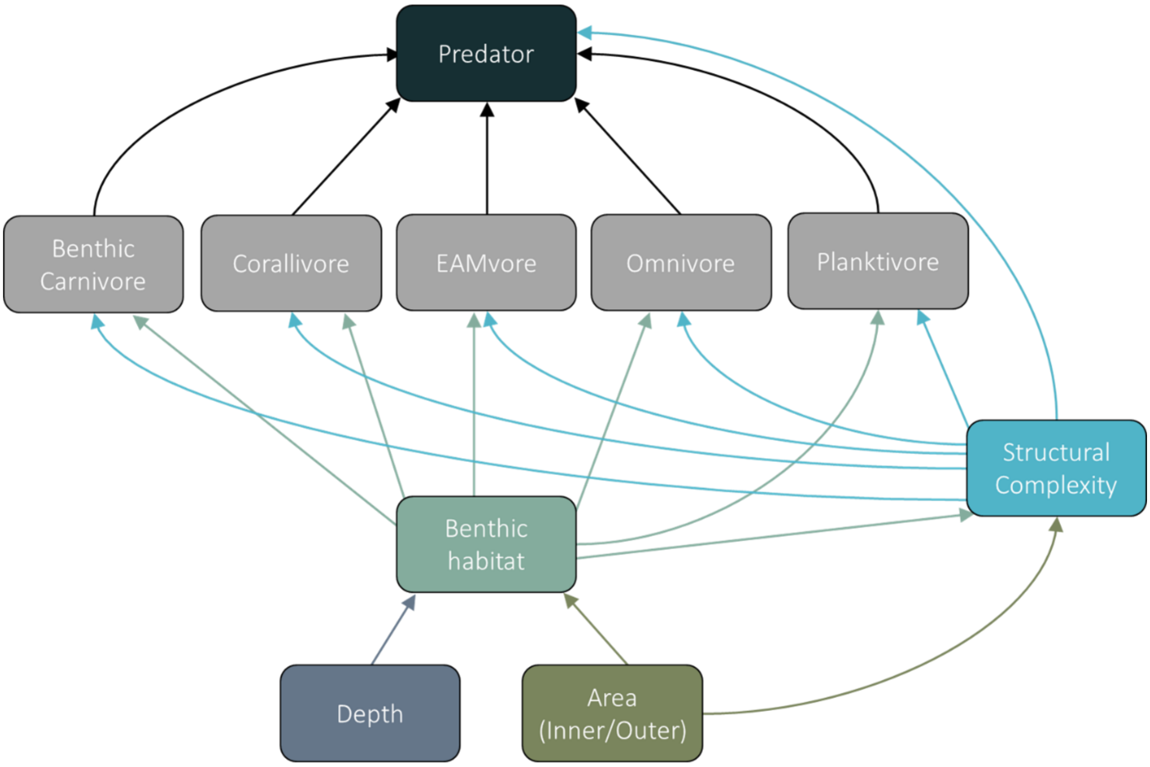


Figure 6.2. Conceptual pathway model of the biotic and abiotic variables influencing reef predator biomass.

Before testing the SEM model, pairwise plots were used to inspect outliers and to assess collinearity between variables. All variables were checked for normality using a Shapiro-Wilks test and fish biomass data and depth were log-transformed. Some variables remained non-normal after transformation. To account for this, a bootstrapping approach based on 1000 draws was used to estimate the model test-statistics and the standard errors for the SEM parameter estimates (Rosseel, 2012). Using the lavaan package (Rosseel, 2012), the conceptual full model was fit with all predicted pathways. Following this, non-significant pathways were removed until the most parsimonious model was achieved. Standardised coefficients were used to assess the importance of predictor variable paths as they can be used to compare variables measured on different scales (Kwan and Chan, 2011). Model fit was assessed by looking at the root mean square error of approximation (RMSEA), the comparative fit index (CFI), the Bayes Information Criterion (BIC) and the standard errors of the parameter estimates. Models with an RMSEA < 0.08 (Browne and Cudeck, 1992) and a CFI > 0.95 (Hu and Bentler, 1998) are considered a reasonable fit for SEM models, i.e. the model is able to reproduce the variance-covariance matrix of the data. The most parsimonious model was the model with the greatest number of significant pathways, the lowest RMSEA and BIC, and the highest CFI.

6.3 Results

6.3.1 Benthic and fish community data

In total, fish from 31 families were identified to either family level (Apogonidae, Mullidae, Synodontidae), genus (33 genera) or species (90 species) and classified based on their feeding behaviours (Table A12).

A PCA revealed substantial separation in the benthic variables between areas along PC axis 1 explaining 29.7% of the variation in the data (Figure 6.3). Sites in the outer atoll were more clustered than those in the inner atoll; average distance to median was 21.23 for inner atoll sites and 14.48 for outer atoll sites. The variables driving the outer atoll sites were live coral, crustose coralline algae (CCA) and algae (i.e. turf and macroalgae), while the variables contributing most to the inner atoll sites were sand, rock and rubble. The PCA separated sites by whether they had more biotic or abiotic substrate along the first axis and by whether they had more coral or algal cover along the second axis.

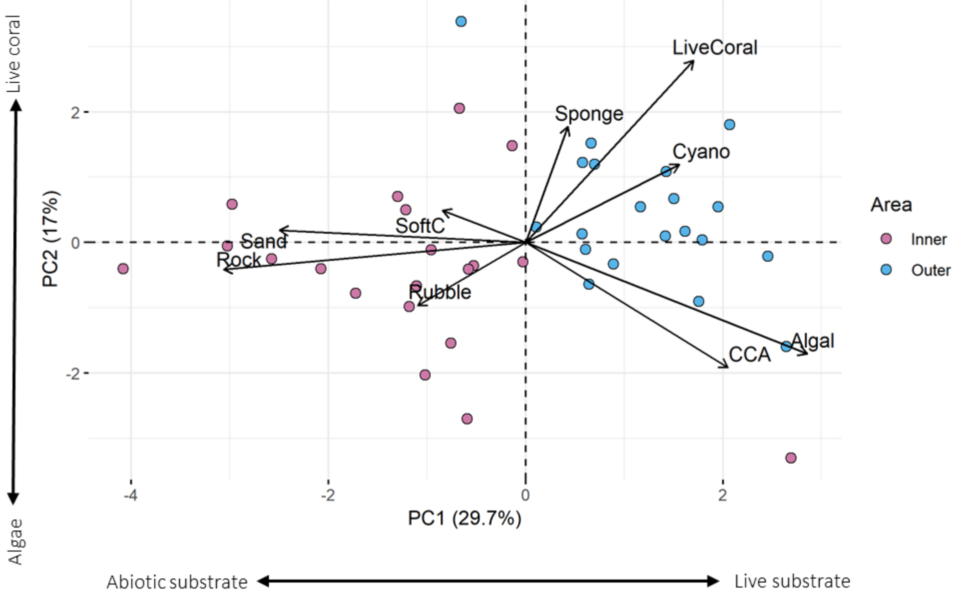


Figure 6.3. Principal components analysis (PCA) of the benthic community with eigenvectors overlaid showing the benthic categories contributing to the PC1 and PC2 axes, which explain 46.7% of the variation in the data.

Structural complexity was similar between inner (mean ± s.d. = 0.66 ± 0.08) and outer atoll sites (mean ± s.d. = 0.70 ± 0.05) with plots on the PC1 and PC2 coordinates revealing no clear patterns (Figure 6.4). Plots of the fish biomass on the PC1 and PC2 coordinates indicated that the distribution of predator biomass (Figure 6.5a) across all sites was similar to that of the corallivores (Figure 6.5b) and planktivores (Figure 6.5f), all of which had greater biomass in the outer atoll.

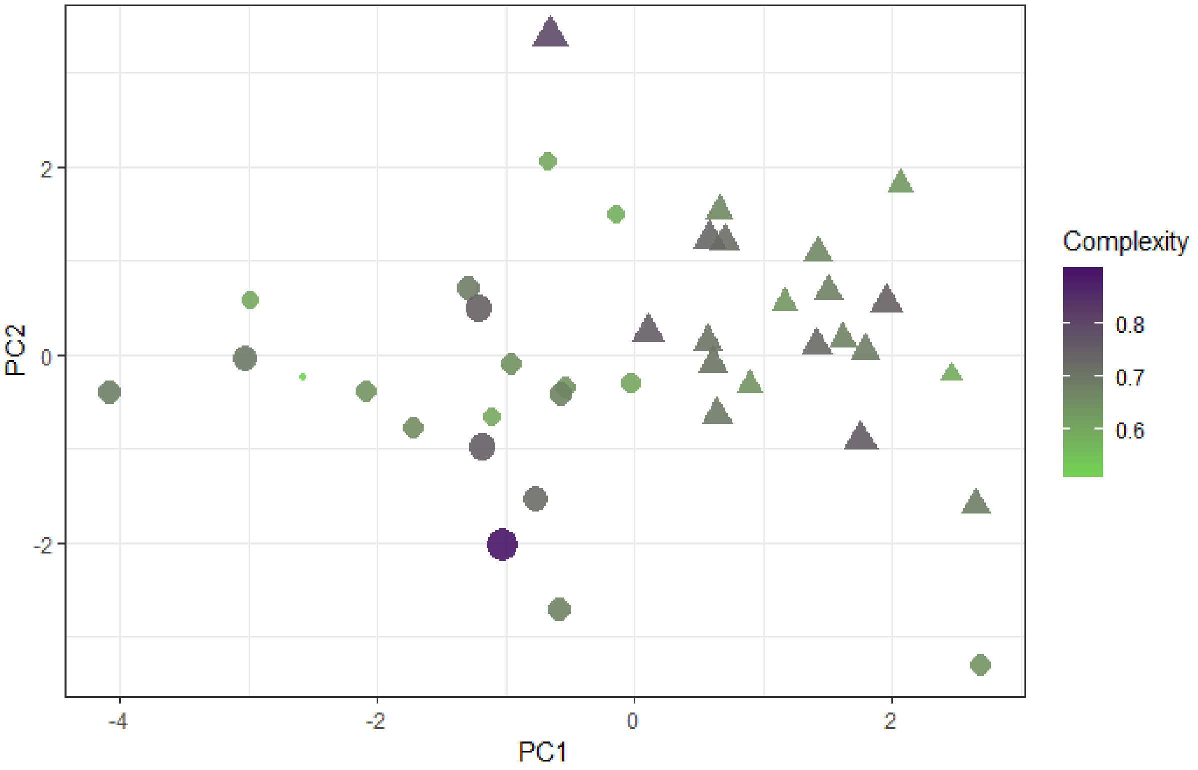


Figure 6.4. Mean site-level structural complexity plotted on the PC1 and PC2 coordinates for each site. A number closer to 1 signifies a flat, low relief reef while a number closer to 0 indicates a reef of high complexity. Points are scaled to values, with larger points indicating values closer to 1 (low relief) while smaller points indicate values closer to 0 (high relief). Circles = inner atoll, triangle = outer atoll.

6.3.2 SEM model

Full model

The mean RMSEA for the full (null) model was 0.138 and the CFI was 0.71, both of which indicate a poor fit (Figure 6.6). The chi square was significant (χ^2 = 45.76, d.f. = 26, p = 0.01) suggesting that the predictive model did differ from the observed data. The BIC was 692.70.

Parsimonious model

All pathways involving depth, complexity, benthic carnivores and omnivores were non-significant and removal improved model fit. The mean RMSEA from 1000 bootstrap draws for the final model was 0.056 and the CFI score was 0.967, both of which indicate a good fit (Figure 6.7). Moreover, the chi square was non-significant (χ^2 = 14.65, d.f. = 13, p = 0.329) suggesting that the predictive model did not differ from the observed data. The BIC was 474.07.

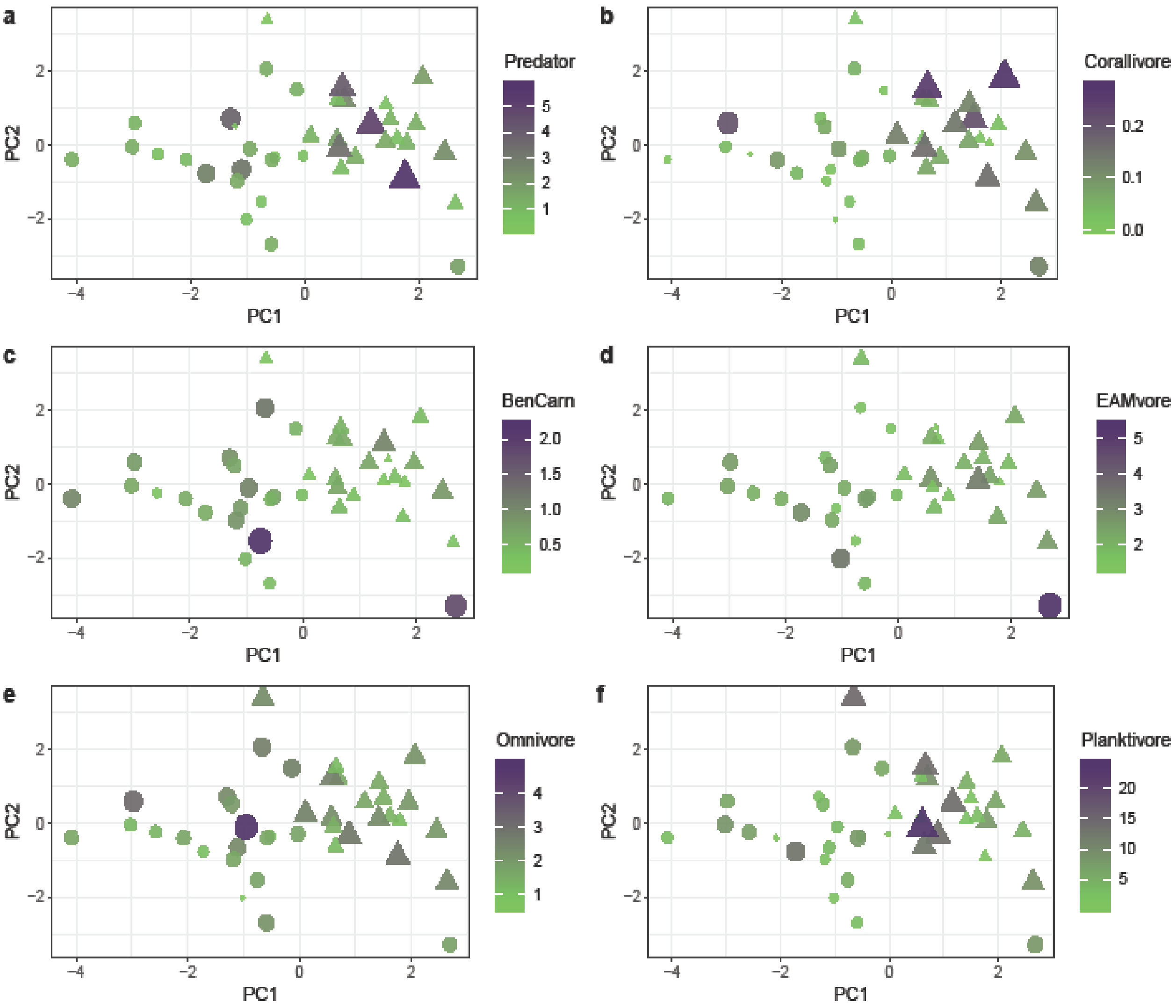


Figure 6.5. Mean site-level predator (a) and prey (b-f) biomass (kg/150 m^2) plotted on the PC1 and PC2 coordinates for each site. Note the difference in scales on the different panels. Points are scaled to values, with larger points indicating larger values (higher biomass) while smaller points indicate lower values (low biomass). BenCarn = benthic carnivores. Circles = inner atoll, triangles = outer atoll.

6.3.3 Pathways

Full model

In the full (null) model (Figure 6.6), only three pathways were significant (Table 6.1): atoll area significantly influenced both PC1 and complexity and PC2 significantly influenced the EAMvores (Table 6.1).

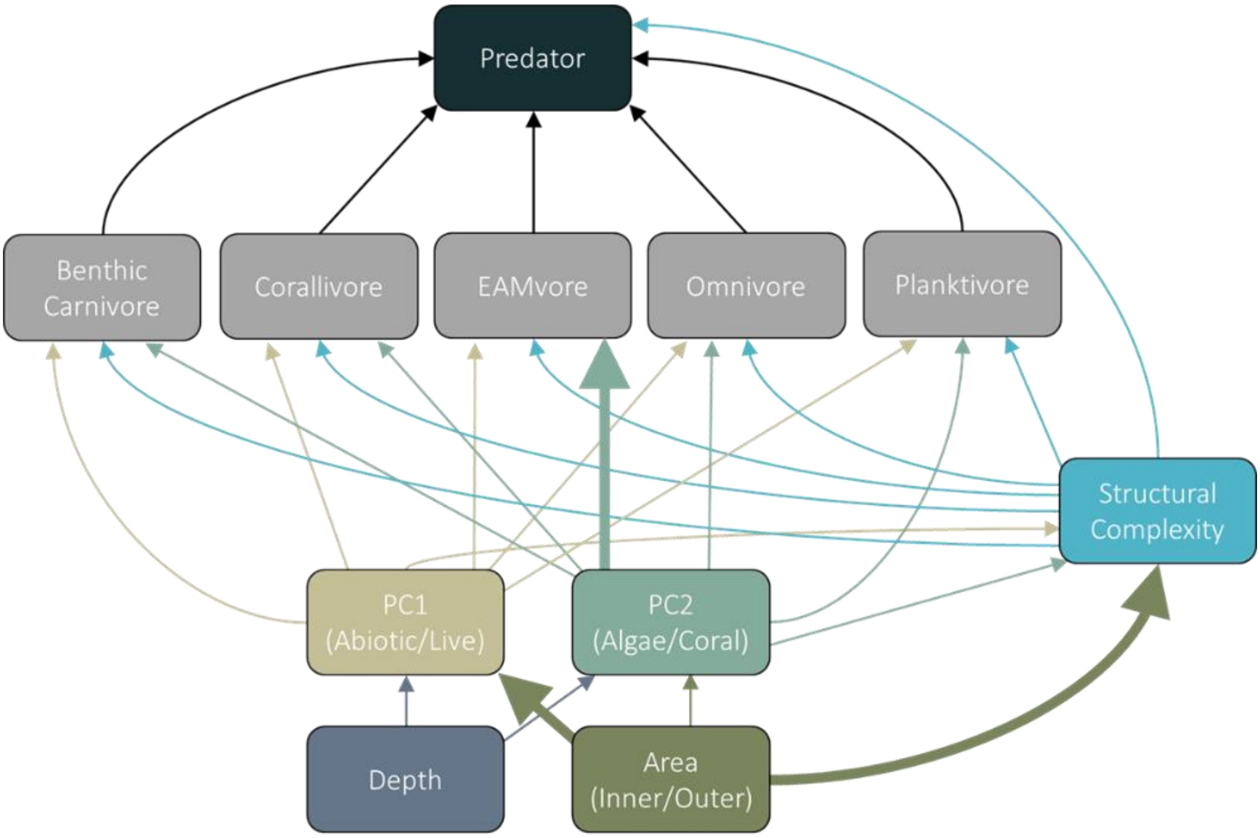
Parsimonious model

Not all pathways retained in the most parsimonious model (Figure 6.7) were significant (Table 6.2), but they all improved model fit (Figure A7). Area significantly predicted PC1 and PC2. PC1 significantly influenced corallivore biomass and PC2 significantly influenced EAMvore biomass. Predator biomass was driven by corallivore and planktivore biomass, but the latter relationship was not significant. Predator and EAMvore biomass covaried. The pathways between area and PC2, PC1 and corallivore, and predator and corallivore, were not significant in the full model but became so in the parsimonious model after other pathways had been removed.

Table 6.1. Parameter estimates for the SEM involving analysis of all pathways in the full (null) model. Significant pathways ($p < 0.05$) are in bold.

From	To	Estimate	SE	Z-value	P-value
PC1 ~	Depth	-0.041	0.336	-0.503	0.615
PC1 ~	Area	0.758	0.387	6.389	**0.000**
PC2 ~	Depth	0.015	0.582	0.082	0.935
PC2 ~	Area	0.350	0.476	1.820	0.069
Complexity ~	PC1	-0.347	0.010	-1.441	0.149
Complexity ~	PC2	-0.274	0.012	-1.239	0.215
Complexity ~	Area	0.584	0.026	3.042	**0.002**
Corallivore ~	PC1	0.360	0.175	1.943	0.052
Corallivore ~	PC2	0.135	0.150	1.126	0.260
Corallivore ~	Complexity	-0.131	4.968	-0.611	0.541
Planktivore ~	PC1	0.142	0.089	0.954	0.340
Planktivore ~	PC2	0.183	0.109	1.325	0.185
Planktivore ~	Complexity	-0.099	2.338	-0.615	0.538
BenthicCarnivore ~	PC1	-0.229	0.057	-1.389	0.165
BenthicCarnivore ~	PC2	-0.199	0.095	-0.955	0.340
BenthicCarnivore ~	Complexity	-0.134	1.520	-0.748	0.454
EAMvore ~	PC1	0.117	0.026	0.734	0.463
EAMvore ~	PC2	-0.438	0.045	-2.082	**0.037**
EAMvore ~	Complexity	0.114	0.602	0.756	0.449

Omnivore ~	PC1	0.094	0.036	0.624	0.533
Omnivore ~	PC2	0.207	0.043	1.483	0.138
Omnivore ~	Complexity	-0.219	1.204	-1.048	0.294
Predator ~	BenthicCarnivore	0.092	0.219	0.516	0.606
Predator ~	EAMvore	-0.117	0.428	-0.714	0.475
Predator ~	Omnivore	-0.035	0.365	-0.175	0.861
Predator ~	Corallivore	0.258	0.079	1.468	0.142
Predator ~	Planktivore	0.124	0.151	0.588	0.557
Predator ~	Complexity	-0.108	2.372	-0.477	0.633



RMSEA = 0.138, CFI = 0.71, BIC = 692.70

Figure 6.6. The full (null) model of path analysis results exploring the abiotic and biotic drivers of reef predator biomass. Single arrows indicate causal paths. Thick arrows indicate significant relationships and thin arrows denote a non-significant relationship. Model fit was assessed using the root mean square error of approximation (RMSEA), the comparative fit index (CFI) and the Bayes Information Criterion (BIC). Models are considered a good fit when RMSEA < 0.08 and CFI > 0.95.

Table 6.2. Parameter estimates for the structural equation model involving analysis of all pathways in the parsimonious model. Significant pathways ($p < 0.05$) are in bold.

From	To	Estimate	SE	Z-value	P-value
PC1 ~	Area	0.730	0.359	6.647	**0.000**
PC2 ~	Area	0.360	0.367	2.431	**0.015**
Corallivore ~	PC1	0.356	0.163	2.030	**0.042**
EAMvore	PC2	-0.466	0.044	-2.321	**0.020**
Predator ~	Corallivore	0.291	0.056	2.408	**0.016**
Predator ~	Planktivore	0.139	0.132	0.767	0.443
Covariances					
Predator ~~	EAMvore	-0.224	0.026	-1.400	0.162

6.4 Discussion

The final parsimonious SEM provides a unique insight into the structuring of the atoll coral reef food web. This approach has allowed the complex and indirect linkages driving predator biomass to be further explored, pathways which traditional linear modelling techniques might overlook. The parsimonious model revealed significant linkages between predators, prey and the habitat, with carbon pathways seemingly flowing up the food web from primary producers to the predators via their prey. This highlights the extent of connectivity in these systems, with indirect associations likely equally important drivers of predator community structure.

Atoll location (inner/outer) was a significant driver of the benthic cover (PC1 and PC2); inner and outer atoll sites were almost entirely distinct from one another indicating substantial spatial variation. This is consistent with other studies that have recorded differences in reef habitat between lagoons and outer edge reefs (Brown *et al.*, 2018), particularly in the Maldives (Morri *et al.*, 2015; Pisapia *et al.*, 2016). While sites in the inner atoll were characterised by sand, rock and rubble due to the greater availability of soft bottom habitat, outer atoll sites had a higher percentage of live coral cover (inner = 15.61% ± 10.43; outer = 28.24% ± 6.31). This difference in live coral cover between inner and outer atoll sites may be related to their degree of exposure. Being adjacent to the open ocean, the outer atoll sites are subject to strong oceanic currents that could help alleviate temperature stress, reducing the level of bleaching-induced coral morality (Safaie *et al.*, 2018; Pisapia *et al.*, 2019).

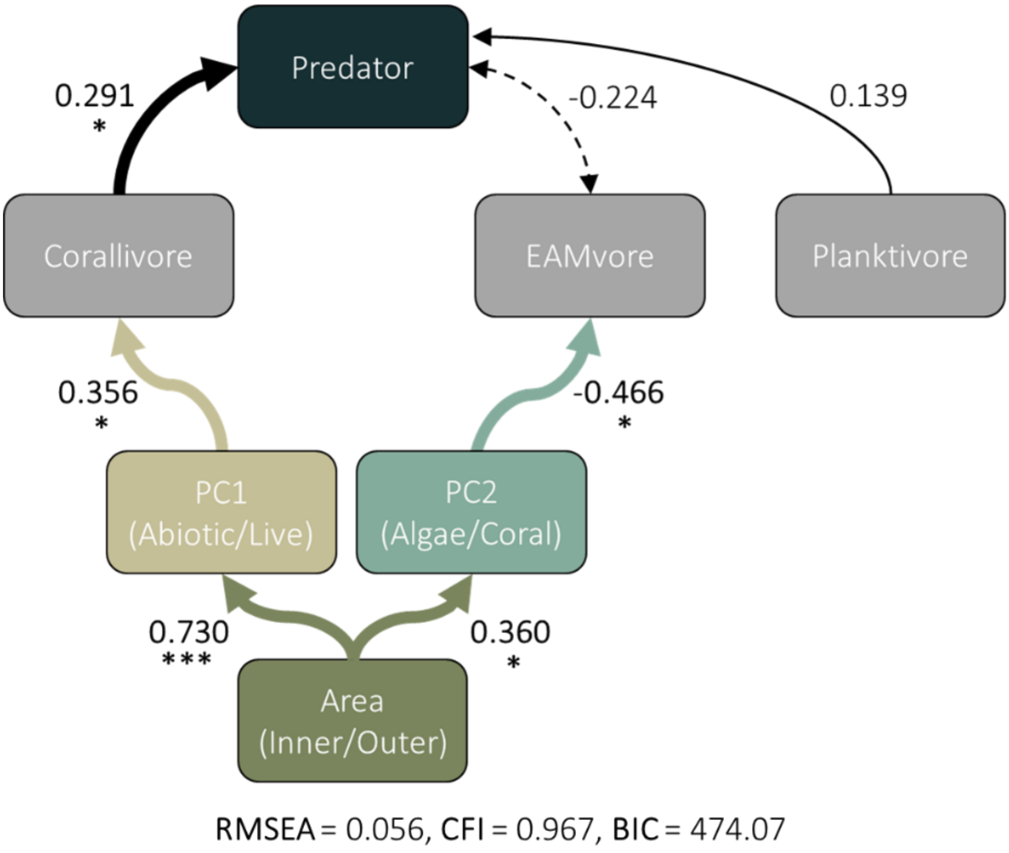


Figure 6.7. The parsimonious model of path analysis results exploring the abiotic and biotic drivers of reef predator biomass. Single arrows indicate causal paths with standardised path coefficients. Thick arrows indicate significant relationships with stars showing the significance level (* = $p < 0.05$, *** = $P < 0.001$). Thin arrows indicate a non-significant relationship and dotted arrows signify covariance. Model fit was assessed using the root mean square error of approximation (RMSEA), the comparative fit index (CFI) and the Bayes Information Criterion (BIC). Models are considered a good fit when RMSEA < 0.08, CFI > 0.95.

Several of the prey groups were significantly linked to the benthic habitat. Positive relationships have been recorded between fish functional groups and the abundance of their preferred food type (Floeter *et al.*, 2007), suggesting food availability is a key driver of their populations. Live coral cover (represented by PC1), rather than complexity or depth, was a significant positive driver of corallivore biomass. Numerous studies have identified positive relationships between corallivores and live coral cover (Bell and Galzin, 1984; Bouchon-Navaro and Bouchon, 1989; Jennings *et al.*, 1996; Darling *et al.*, 2017), with substantial declines recorded following mass coral bleaching events (Wilson *et al.*, 2006; Robinson *et al.*, 2019a), even when reef structural complexity is maintained (Benkwitt *et al.*, 2019). This suggests that food availability may be more important for maintaining corallivore populations than habitat structure. Recently the Maldives has experienced significant declines in live coral cover due to mass bleaching (Pisapia *et al.*, 2019). Given the relationship identified here and in previous studies, and the obligate nature of their feeding, corallivores may be seriously impacted following the loss of live coral from successive bleaching events. Algal cover (represented by PC2) was a significant positive driver of EAMvore biomass. Although turf and macroalgae were combined into one group for the analyses, macroalgae cover was low across the atoll (inner: 4.02% ± 5.57; outer = 2.01% ± 3.07) so this relationship was likely driven by turf algae cover (inner: 21.72% ± 11.85; outer = 33.20% ± 10.20). Positive relationships between herbivores and turf algae are common, as fish tend to aggregate in zones of highest food availability (Williams and Polunin, 2001; Russ, 2003). However, at higher levels of wave exposure, while algal turf increases, herbivore biomass decreases (Williams *et al.*, 2013; Heenan *et al.*, 2016), signifying that there is a wave exposure threshold beyond which this positive relationship is decoupled.

No significant relationships were identified for the benthic carnivores, omnivores, or planktivores. There are several possible explanations for this. Firstly, food source data were absent for these prey groups. Benthic carnivores and omnivores often feed on invertebrates, while planktivores feed on plankton, but these food sources were not recorded during the surveys. Furthermore, these prey items may not be strongly associated with the habitat variables that were measured here. Consequently, trophic interactions arising between these prey groups and their environment would have been overlooked. Secondly, these groups are dietary generalists, which may preclude the model from identifying any strong relationships. Future work would benefit from including measures of all potential food items to accurately investigate all potential trophic interactions. Thirdly, although each species has been classified based on their feeding behaviour as reported in the literature, increasing evidence (e.g. isotope data in Chapter 3) suggests that there is substantial individual and spatial variation within populations. Categorising feeding behaviours at the species level may mask the individual dietary intricacies so common in nature. Finally, while previous studies have identified live coral cover and structural complexity as important variables driving planktivore communities (Darling *et al.*, 2017; Russ *et al.*, 2017), no significant relationships were identified in the final model presented here. Many planktivore species are highly mobile so population estimates during UVC are susceptible to substantial temporal variation

(McClanahan *et al.*, 2007; MacNeil *et al.*, 2008). Consequently, detection of significant relationships may have occurred had the data been collected at a different time.

Corallivores were the only prey group to significantly influence predator biomass, despite being the group with the lowest overall biomass and the smallest species richness. Carangidae, Lutjanidae and Serranidae predate on a range of reef-associated fish species but corallivores are not considered a major component of their diet (Meyer *et al.*, 2001; Dierking *et al.*, 2011; Ali *et al.*, 2016; Dance *et al.*, 2018). However, as corallivores are driven by food availability and are strongly associated with the habitat (Boaden and Kingsford, 2015), their biomass may be a proxy for a healthier reef state characterised by a greater percentage of live coral cover, which in turn supports a greater biomass of predators. In contrast, reductions in live coral cover have been linked to both declines in corallivore (Rice *et al.*, 2019) and reef predator (Sandin *et al.*, 2008) populations. Although the pathway between planktivores and predators was not significant, its inclusion in the final model substantially improved model fit. Numerous studies indicate that reef predators are sustained by planktivores (Ali *et al.*, 2016; Matley *et al.*, 2018; Skinner *et al.*, 2019) confirming that this relationship is an important one. As discussed above, planktivore populations experience substantial spatial and temporal variability (Kingsford, 1989; Malcolm *et al.*, 2007) which may have precluded a significant relationship from being identified with this dataset.

Depth and complexity were not included in the most parsimonious model. Unlike previous studies (Graham and Nash, 2013; Rogers *et al.*, 2014; Schultz *et al.*, 2014; Jankowski *et al.*, 2015; Ferrari *et al.*, 2017), they did not appear to be important variables structuring either the predator or prey community. However, the gradients in complexity and depth recorded here may not be comparable to the studies where they were identified as important. For example, here, all transects were conducted on the upper forereef slope in a relatively narrow depth range (3 – 15m), so depth-related changes in community biomass may have been missed. Furthermore, mean complexity was similar between atoll locations (mean ± s.d.: inner 0.66 ± 0.08; outer 0.70 ± 0.05) with a relatively narrow gradient (inner 0.52 – 0.89; outer 0.60 – 0.79), possibly linked to a flattening of the reefs following the 2016 bleaching event (Newman *et al*., 2015; Pisapia *et al*., 2019). While atoll area was a significant driver of structural complexity in the full model, no complexity pathways were included in the parsimonious model. It is possible that inherent variability in structural complexity and depth between inner and outer atoll was represented by, and incorporated into, the atoll area variable. Area was subsequently identified as an important driver of differences between sites while any influence of depth or complexity was masked, precluding their incorporation in the final model. Moreover, the complexity measure used here may not offer any different information compared to the benthic PC axes. For example, measures of live coral cover or rubble, here interpreted in terms of food availability, also intrinsically provide habitat for refuge. Consequently, the relationship between the benthic habitat and the prey community may also include an inherent refuge influence. Future work would benefit from incorporating measures of refuge availability (e.g. hole size and abundance) into models, while surveying transects across a greater range of depths and levels of complexity.

Reef food webs are complex with many interrelating trophic interactions. Although the underwater visual surveys were extensive, not all energy pathways were investigated during this study, most notably those involving invertebrates. Arriving at robust solutions with a SEM requires a lot of data as the model is evaluating multiple hypotheses simultaneously (Grace, 2006; Lefcheck and Freckleton, 2016). Although the final model was a good fit, additional insight into the predator-prey-habitat relationships occurring on these reefs might have been achieved with a larger dataset, or with the inclusion of additional parameters such as invertebrate biomass, primary production or temperature. Despite this, the final model gives a reasonable representation of the reef food web and a better understanding of the interactions occurring between organisms. It does contrast with the stable isotope data in Chapters 4 and 5 though, suggesting that the pathways that are important to the food web may not necessarily structure it or the biomass of predators. Food availability, rather than abiotic variables such as reef structural complexity or depth, appears to be the primary driver of predator-prey relationships in this system. However, as benthic composition and structural complexity are interrelated, the PCA may inherently include some habitat refuge information, which warrants further study. The distinct spatial structuring of the benthic cover also highlights the importance of incorporating spatial variation into analyses, as reefs vary considerably at the local and global scale. Ultimately, although SEMs provide a unique tool to gain insight into systems with many complex processes, capturing all predator-prey-habitat relationships is impossible. However, the model presented here offers a novel perspective on the importance of food availability in structuring reef communities, and rather challenges the contention (Chapters 4 and 5) that planktonic feeding is driving predator biomass.

Chapter 7 General discussion

7.1 Overview

This thesis provided a unique perspective on reef predator assemblages and their complex trophodynamics, advancing our current knowledge of coral reef food webs. One of the strengths of this thesis has been the use of multiple statistical and survey methodologies to investigate these energetic linkages, which allowed greater insight into the complex interactions on these reefs. The combination of both underwater visual census (UVC) and baited remote underwater video (BRUV) identified the primary drivers of reef predator community structure (**aim one**), while bulk and compound-specific stable isotope analysis determined the origin of the carbon sustaining their biomass (**aim three**). Bulk stable isotope data also identified inter- and intraspecific variations in predator resource use (**aim two**). The implications of these findings are discussed below.

7.2 Reef-pelagic connectivity and coral reef resilience

One of the major findings of this thesis is that planktonic subsidies are a key contributor to reef predator biomass (Chapter 4, Skinner *et al.*, 2019), and that it is likely that these subsidies are of a deep-water, mesopelagic origin (Chapter 5). While the importance of planktonic inputs to reef communities is now being realised (McCauley *et al.*, 2012c; Frisch *et al.*, 2014; Matley *et al.*, 2018), the origin of this material has not been fully considered. The data in this thesis offer the opportunity to revisit how we view coral reef communities. Rather than being isolated ecosystems somehow teeming with life, it is evident that the adjacent pelagic ocean exerts a substantial influence and mesopelagic subsidies may play a vital role sustaining reef food webs. However, the characteristics, origins and delivery mechanisms of these inputs remain to be explored. While the compound-specific stable isotope analysis here offers new insight, it also raises questions. Specifically, where is this material coming from and how is it being incorporated into the food chain? What drives it and what does it contain? Can it be better characterised and traced? There are also questions regarding the interpretation of the $\delta^{13}C$ essential amino acid (EAA) data, as mechanisms are not yet fully understood. For example, are EAAs routed directly to consumer tissue from their diet or are there transformative interactions with the gut microbiome? What is the integration rate and turnover time of EAA to consumer tissues? How do animal activity levels and body size affect these mechanisms? Do these mechanisms vary inter- and intraspecifically and among EAAs? These questions are at the forefront of the emerging field of compound-specific stable isotope analysis and represent an exciting new era in food web studies. Currently, answers to these questions are lacking. However, a first step might involve sampling mesopelagic prey from around the atolls to determine their $\delta^{13}C_{EAA}$ signature or attaining a better understanding of the flow dynamics and water circulation (i.e. presence and frequency of internal waves) of the archipelago. Both these areas of research would provide important information that could help characterise and measure these allochthonous inputs.

This work was carried out in the central Maldives, where seasonally alternating equatorial currents determine the degree of primary production available to reef communities (Sasamal, 2007; Anderson *et al.*, 2011). However, conducting the same work across the more northern or southern parts of the Maldivian archipelago, or elsewhere in the Indian Ocean or around the world, might have yielded different results. Spatial fluctuations in primary production and differences in atoll physiography (e.g. being more enclosed or more open) might both influence the degree of planktonic reliance of a reef food web. Several studies have demonstrated increased reliance of reef communities on oceanic nutrients with increasing proximity to the open ocean (i.e. from inner lagoons to outer shelf reefs) (Wyatt *et al.*, 2012b; Gajdzik *et al.*, 2016; McMahon *et al.*, 2016; Le Bourg *et al.*, 2017). To date, there has been little research on how planktonic reliance might vary globally across gradients of primary production or in relation to the degree of water circulation. However, stable isotope $\delta^{15}N$ values of several coral reef fish species were closely linked to gradients in oceanic primary production and species had larger dietary niche widths where primary production was greater (Miller *et al.*, 2019; Zgliczynski *et al.*, 2019). This suggests that reef trophodynamics do vary spatially and in relation to available primary production, and this warrants further study.

The role of coprophagy (feeding on faeces) in connecting the reef-pelagic interface must also be considered. While fish from all trophic levels excrete material regularly, diurnal planktivores that dominate the water column (e.g. caesionids, damselfishes), produce substantial amounts of low-density faeces. The majority of this material is ingested by other fish, primarily herbivores and detritivores (Robertson, 1982), representing an important energetic subsidy to the reef food web (Hobson, 1991). Furthermore, the faecal material may be enriched in $\delta^{15}N$ compared to various benthic algal groups, leading to the herbivores and detritivores that readily consume it having higher $\delta^{15}N$ values (Zgliczynski *et al.*, 2019). Here, bulk stable isotope $\delta^{15}N$ values of the herbivore *Acanthurus leucosternon* and the detritivore *Pearsonothuria graeffei* were consistently low ($\delta^{15}N$ mean ± sd: 6.24 ± 0.16 to 8.30 ± 0.81; Table A7). Furthermore, $\delta^{13}C$ values of essential amino acids of *A. leucosternon* and the detritivore *Ctenochaetus striatus* showed relatively clear separation from the reef planktivores *Caesio varilineata* and *C. xanthanota* (Figure 5.2), suggesting coprophagy may not be a dominant component of the diet of these species. Regardless, given the huge biomass of planktivores on Maldivian reefs (Figure 7.1) and the amount of material that they excrete, coprophagy likely plays an important role providing energetic subsidies to reef food webs here, and sampling other herbivore or detritivore species might evidence this.

Ocean-reef connectivity may have implications for coral reef resilience. Globally, coral reefs are under threat from a range of anthropogenic and climate-related stressors. Successive coral bleaching events have caused significant declines in live coral cover worldwide (Hughes *et al.*, 2017b; Pisapia *et al.*, 2019), resulting in persistent shifts in coral (Hughes *et al.*, 2018b) and reef fish assemblages (Robinson *et al.*, 2019a). The vulnerability and the resilience (the capacity to recover from a disturbance) of individual reefs to these threats is not uniform however, as the natural carrying capacity of coral reefs varies across environmental gradients (Heenan *et al.*, 2019). Consequently, coral reef food webs supported by planktonic production sources may be more resilient to bleaching-induced coral mortality than reefs that are more reliant on benthic production sources. However, climate change is also predicted to cause declines in ocean production (e.g. from increased stratification, light limitation) (Asch *et al.*, 2018), which would have serious ramifications for reefs that are primarily supported by oceanic inputs. Furthermore, results of a DISTLM (Chapter 2) and a SEM (Chapter 6) indicated that live coral cover and corallivores respectively were important significant drivers of the predator assemblage, suggesting that loss of live coral cover might influence reef predators despite the lack of a direct association (i.e. stable isotope evidence).

Interactions with, and the influence of, reef structural complexity should be considered when determining what structures the predator assemblage. While structural complexity was not included in the final SEM (Chapter 6), it is likely that it did exert some influence given that benthic cover and structural complexity are interrelated. Multiple studies have highlighted its importance in structuring reef fish assemblages by providing refuge and supporting fish productivity (Chapter 2, Graham and Nash, 2013; Rogers *et al.*, 2014;

Newman *et al.*, 2015; Rogers *et al.*, 2018). It also facilitates pelagic coupling by mediating the ability of planktivores to trap plankton on reefs (Morais and Bellwood, 2019). As such, structural complexity is an intrinsic component of reefs and continued reef flattening will surely affect reef food webs worldwide (Graham *et al.*, 2006; Newman *et al.*, 2015), regardless of whether they are sustained by benthic or pelagic inputs.

Predicting how these fish communities will respond to environmental change remains a challenge, however, this thesis highlights how current views of coral reef systems need to change. The extent of connectivity with the open ocean, regardless of exposure or level of degradation (Morais and Bellwood, 2019), shows how coral reef management plans must transcend ecosystem boundaries. Localised management efforts involving the setup of MPAs may not be sufficient for reef communities reliant on oceanic production. Future work should investigate the complex interactions between live coral cover, structural complexity, primary production and water circulation, to better understand how coral reefs worldwide may respond to changing environmental conditions.

7.3 Nature is complicated

Investigating an animal's resource use and foraging patterns can help determine its functional role within an ecosystem. This is important in identifying how it might respond to change, which facilitates appropriate management. The bulk stable isotope data (Chapter 3) highlighted how predator resource use can vary both spatially and among and within species, regardless of body size. Predators may couple adjacent food webs through their foraging, constructing linkages which provide stability to ecosystems (McCann *et al.*, 2005), but variations in their resource use indicate these linkages are not identical, and in some cases may be entirely absent. Consequently, their ecological roles may be vastly different, but species-level categorisations will hide this. However, these intra-specific feeding specialisations may help promote population resilience to environmental change, as individuals are reliant on a wider range of resources. Occurrences of feeding specialisations are greater where resource diversity is high (Araújo *et al.*, 2011), suggesting coral reefs are a prime location for them to occur. Coral reef fish that show variations in their resource use may therefore be more resilient to environmental change than previously thought.

Ecologists attempt to categorise functional traits to better understand ecosystem function, but this conflicts with the natural variability inherent in complex systems such as coral reefs.

This is evident in Chapter 6, where interactions between several of the prey groups (benthic carnivores, omnivores, and planktivores) and any biotic or abiotic factors proved too complicated to disentangle. It is possible that the absence of significant relationships involving these groups was an artefact of the broad categorisations of species into various prey functional groups, which did not account for any individual differences in resource use. For example, 20 individual species, seven genera, and two whole groups (sand and reef gobies) were classified as omnivores based on the literature. Omnivores, by definition, forage on a range of food sources, so it is perhaps not surprising that no clear relationships were identified with the measures of benthic cover. However, they are an important part of the fish assemblage on these reefs; they had the third greatest biomass behind planktivores and EAMvores (Figure 7.1). Attempting to neatly classify species into discrete categories based on their functional traits may overlook important processes occurring in these ecosystems, particularly as many assumed “functions” lack empirical evidence (Bellwood *et al.*, 2019). However, to accurately assess ecosystem function, these energetic linkages must be identified before they disappear.

What are the implications of this for studies of ecosystem function globally? Here, considerable variation in species resource use was recorded at a scale of tens of kilometres within the same atoll. This signifies that care should be taken in extrapolating species-specific information on resource use to other locations, even within the same geographic region, particularly as resource variability also varies at these scales. Individual assessments of species resource usage across different spatial scales and at different body sizes may be required for an accurate interpretation of their functional roles. Furthermore, dietary intricacies were discovered here despite relatively few select species being investigated, suggesting that dietary variation may be more prevalent. The degree of dietary specialisation across other trophic levels and amongst other functional groups remains little explored. Management approaches that make species-level assumptions from spatially restricted samples or use strategies based on body size (e.g. the Maldivian grouper fishery; Sattar *et al.*, 2014), might overlook these differences in feeding behaviours. Accounting for this variation will help to accurately understand how species will respond to change, but investigating intraspecific variations in resource use across large spatial scales is a monumental task.

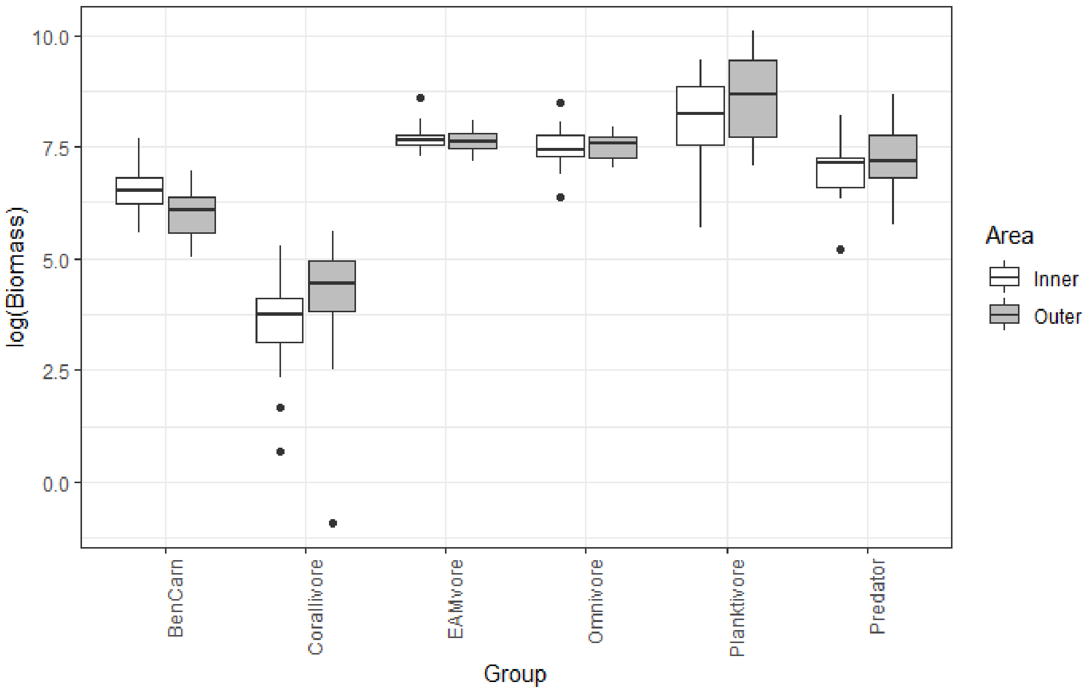


Figure 7.1. Log transformed biomass data of fish functional groups in both inner and outer areas of North Malé atoll, Maldives. BenCarn: benthic carnivore, EAM: epilithic algal matrix. Note low corallivore biomass due to post-bleaching reef state.

7.4 Declining predators, increasing tourists: the Maldivian experience

The present extensive underwater survey data indicate that the Maldives has diverse and ubiquitous reef predator populations, found not only along the outer edge reefs but also inside the atoll lagoon (Chapter 2; Chapter 6). Overall biomass was low compared to other uninhabited, unfished reefs (e.g. Palmyra atoll in the Northern Line Islands and the Chagos archipelago; Sandin *et al.*, 2008; Graham *et al.*, 2013), suggesting population declines might have occurred relative to unfished levels. However, coral reefs have varying natural carrying capacities and reef fish biomass distributions are scale dependent. Alternatively, Maldivian reefs may represent “middle-driven” systems, where the greatest biomass occurs at intermediate consumer levels (i.e. planktivores), rather than being top-heavy (Heenan *et al.*, 2019), a hypothesis supported by the data collected for Chapter 6. Regardless, tourists, and increasingly locals, are relying on reef fish for food, and reef predators (e.g. snappers and groupers), are an important part of the catch (Sattar *et al.*, 2014). Since tourism began in the Maldives in the 1970s the sector has continued to grow (Domroes, 2001), with tourist arrivals increasing by an average of 7.8% each year from 2013 to 2017 (Ministry Of Tourism, 2018). As the number of tourists continues to grow, the demand for reef fish will increase with it. Although islands that host tourist resorts do not allow fishing on their house reefs (Moritz *et al.*, 2017; Cowburn *et al.*, 2018), guest fishing trips to nearby reefs occur on an almost daily basis (Skinner, pers. obs.). Currently, recording of resort landings data is voluntary (Sattar *et al.*, 2014) so the impact of these trips has not been quantified, even though they occur at the national scale. Given the continued expansion of the tourism sector and the increasing number of resorts, it is highly recommended that these exploitative activities be monitored and incorporated into the Maldives reef fishery management plan.

Loss of reef habitat from bleaching-induced coral mortality (Pisapia *et al.*, 2019) may also be having an impact on reef predator assemblages. The last mass bleaching event in the Maldives occurred in 2016 (Pisapia *et al.*, 2019), the year before the first surveys were conducted (Chapter 2). Consequently, the surveys in 2017 and 2018 may have documented reef predator assemblages as they experienced habitat-related declines. In support of this hypothesis, despite surveying almost identical sites in 2017 (Chapter 2) and 2018 (Chapter 6), there were stark differences in the species composition between years (Table 7.1).

Several of the species contributing to these differences were highly mobile. They were likely not recorded in consecutive years because of 1) their transient nature and 2) differences in transect lengths between years (50 m in 2017; 30 m in 2018). Several site-attached grouper species were also not recorded in consecutive years, probably because their cryptic behaviour made them harder to detect. However, as several species of *Epinephelus* were still unique to each year, there appeared to be a continued presence, albeit a shift in species composition. Most striking, however, was the complete absence of emperors (*Lethrinus obsoletus*) and four species of snapper (*Lutjanus decussatus*, *L. fulvus*, *L. monostigma*, and *Macolor niger*) from the surveys in 2018. Although purely speculative, this might suggest that these reef-associated and relatively site-attached predators (Nash *et al.*, 2015) are in decline following the loss of suitable reef habitat and steadily increasing exploitation (Sattar *et al.*, 2012; Sattar *et al.*, 2014). As water temperatures continue to rise, a fourth global bleaching event is likely within the next decade (Hughes *et al.*, 2017b). This indicates that reef fish assemblages in the Maldives will be subjected to an unprecedented level of impact from a combination of stressors. The long-term effects of this are unknown, but will surely result in continued declines in reef predator populations if adequate management measures (e.g. mandatory reporting of resort catch, minimum landing sizes) are not in place.

Table 7.1. Reef predator species recorded by underwater visual census conducted on reefs in North Malé atoll in 2017 and 2018. † indicates a transient species.

Both years	Only 2017	Only 2018
Aethaloperca rogaa	*Carangoides ferdau* †	*Cephalopholis sexmaculata*
Anyperodon leucogrammicus	*Caranx ignobilis* †	*Diploprion bifasciatum*
Aphareus furca	*Epinephelus fuscoguttatus*	*Elagatis bipinnulata* †
Aprion virescens	*Epinephelus malabaricus*	*Epinephelus longispinis*
Aulostomus chinensis	*Epinephelus ongus*	*Epinephelus macrospilos*
Caranx melampygus	*Gymnosarda unicolor* †	*Epinephelus polyphekadion*
Cephalopholis argus	*Lethrinus obsoletus*	
Cephalopholis leopardus	*Lutjanus decussatus*	
Cephalopholis miniata	*Lutjanus fulvus*	
Cephalopholis nigripinnis	*Lutjanus monostigma*	
Cephalopholis spiloparaea	*Macolor niger*	
Epinephelus fasciatus	*Sarda orientalis* †	
Epinephelus merra	*Triaenodon obesus* †	
Epinephelus spilotoceps		
Fistularia commersonii		
Gnathodentex aureolineatus		
Lutjanus bohar		
Lutjanus gibbus		
Lutjanus kasmira		
Macolor macularis		
Monotaxis grandoculis		
Plectropomus areolatus		
Plectropomus laevis		
Pterois antennata		
Variola louti		

7.5 Concluding remarks

This thesis highlights the extent of connectivity between coral reefs and the surrounding ocean, providing evidence that coral reef food webs are heavily subsidised by pelagic inputs. These inputs are likely mesopelagic in origin, identifying an important energetic link between nutrient-rich deeper waters and shallow reef communities, potentially established via local wind-driven upwelling and internal waves. While this may signify increased resilience of these reef communities to a loss of live coral cover from mass bleaching, they will be at an increased risk from climate-induced declines in oceanic primary production.

These data also provide evidence that predator resource use varies considerably both spatially and within populations. Rather than being generalists, some predators have individual feeding behaviours that are entirely different from their conspecifics. This highlights how care must be taken when classifying a species' functional role, as species-level assumptions will overlook these intricacies. Food availability rather than habitat structure may be the primary driver of fish assemblages on these reefs, suggesting fluctuations in prey arising from loss of suitable reef habitat may have serious ramifications for reef predator communities.

While it might appear that there are no winners, with most reef communities at risk in some way, this thesis provides much needed insight into the complex trophic interactions of coral reefs. This will enable managers to make informed decisions that take into account the resource requirements of these predator species that are a dominant component of coral reef fish assemblages. Clearly, coral reefs are not isolated ecosystems but inextricably linked with the surrounding ocean. Management strategies should focus on a seascape approach that incorporates ecology and oceanography, integrating findings across disciplines and spatial scales, and transcending the boundaries of these threatened ecosystems.

“In nature we never see anything isolated, but everything in connection with something else which is before it, beside it, under it and over it.”

Johann Wolfgang von Goeth

Appendices

A.1 Appendix for Chapter 2

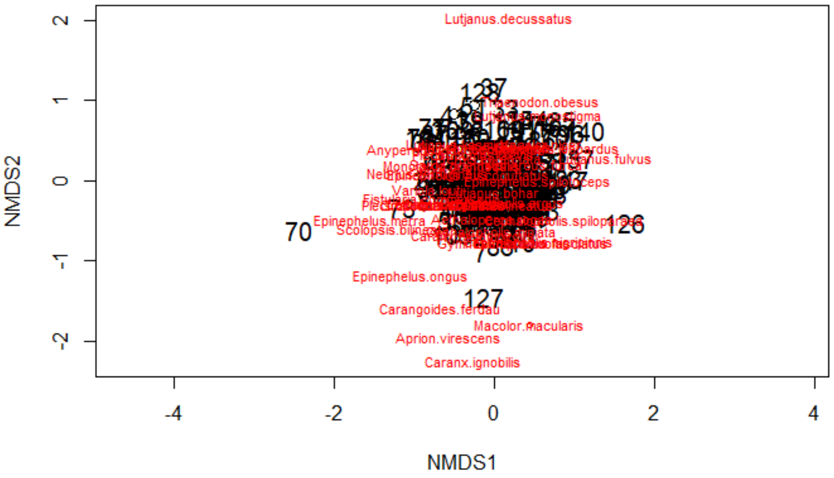


Figure A1. Non-metric multidimensional scaling (MDS) plot of UVC data with outliers of transects 70, 126 and 127. Transect 70 had no recorded predators except five *Epinephelus merra*, a rare species. Transect 126 and 127 were from the same inner atoll site that had high abundances of C. *spilopar*ea and *C. nigripinnis* compared to other transects.

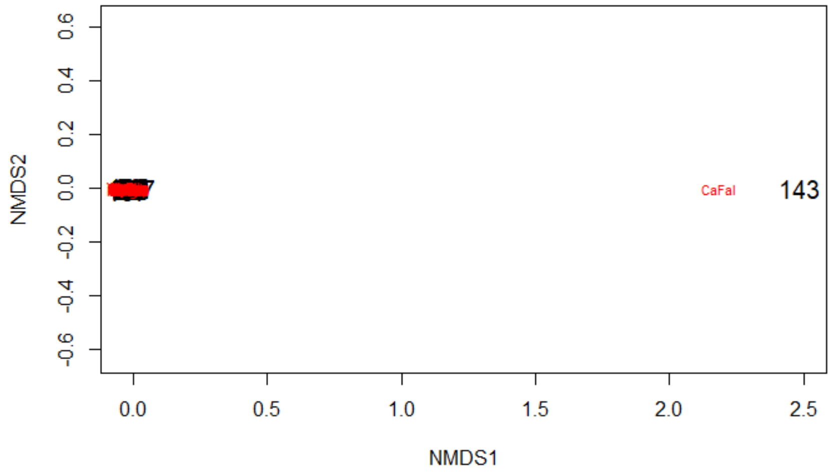


Figure A2. Non-metric multidimensional scaling (MDS) plot of BRUV data showing an outlier of BRUV 143. This video had no recorded predators for the entirety of the video footage except one *C. falciformis*, a rare species only recorded twice during all deployments.

Table A1. Total number of individual predators recorded in inner and outer atoll with UVC and BRUV. 1 = species only recorded during UVC, 2 = species only recorded during BRUV, * = aggregating/schooling species.

Family	Species	Inner		Outer	
		UVC	BRUV	UVC	BRUV
Aulostomidae	*Aulostomus chinensis*	26	2	3	1
Carangidae	*Carangoides ferdau*	1	2	-	-
	Caranx ignobilis	1	7	-	6
	Caranx melampygus	46	281	4	63
	Elagatis bipinnulata[2]	-	8	-	-
Carcharhinidae	*Carcharhinus amblyrhynchos*[2]	-	-	-	2
	Carcharhinus falciformis[2]	-	2	-	-
	Carcharhinus melanopterus[2]	-	17	-	11
	Carcharhinus spp	-	-	-	1
	Negaprion acutidens[2]	-	-	-	1
	Triaenodon obesus	1	15	3	10
Fistulariidae	*Fistularia commersonii*	17	75	-	12
Ginglymostomatidae	*Nebrius ferrugineus*	4	16	-	19
Lethrinidae	*Gnathodentex aureolineatus**	651	210	734	117
	Lethrinus harak[2]	-	1	-	-
	Lethrinus microdon[2]	-	9	-	-
	Lethrinus obsoletus	6	3	1	5
	Lethrinus spp	-	5	-	7
	Monotaxis grandoculis	148	82	91	87
Lutjanidae	*Aphareus furca*	1	1	5	3
	Aprion virescens	2	5	-	8
	Lutjanus bohar	49	125	71	80
	Lutjanus decussatus[1]	-	-	1	-
	Lutjanus fulvus[1]	-	-	1	-
	*Lutjanus gibbus**	76	224	95	9
	*Lutjanus kasmira**	36	114	255	66
	Lutjanus monostigma[1]	1	-	7	-
	Macolor macularis[1]	-	-	2	-
	Macolor niger	-	-	1	1
Scombridae	*Gymnosarda unicolor*	6	4	6	-
	Sarda orientalis	3	15	1	-
Scorpaenidae	*Pterois antennata*	3	-	3	-
Serranidae	*Aethaloperca rogaa*	124	98	130	71
	Anyperodon leucogrammicus	134	15	47	2
	Cephalopholis argus	234	67	367	128
	Cephalopholis leopardus	54	24	289	42
	Cephalopholis miniata	44	8	4	4
	Cephalopholis nigripinnis	9	14	23	69
	Cephalopholis spiloparaea[1]	5	-	53	-
	Cephalopholis spp	-	24	-	9

Epinephelus fasciatus	-	2	16	5
Epinephelus fuscoguttatus	8	7	9	1
Epinephelus malabaricus[1]	-	-	1	-
Epinephelus merra[1]	43	-	1	-
Epinephelus ongus[1]	2	-	-	-
Epinephelus spilotoceps	13	2	107	10
Epinephelus spp	-	5	-	2
Epinephelus tauvina[2]	-	-	-	2
Plectropomus areolatus	11	8	2	1
Plectropomus laevis	9	10	2	3
Plectropomus spp	-	4	-	4
Variola louti	18	15	4	10
Variola spp	-	1	-	-

Table A2. Description of the predictor variables used to investigate the structure of the predator assemblages.

Dependent variable	Description	Survey method	Mean ± s.d.	Range	Reference
Depth	BRUV deployment or UVC transect depth in metres	UVC	7.72 ± 2.96 m	2.5 – 14.8 m	(Friedlander *et al.*, 2010; Schultz *et al.*, 2014; Jankowski *et al.*, 2015)
		BRUV	7.90 ± 2.03 m	2.5 – 12.40 m	
Complexity	Visually assessed on a 6 point scale (Polunin and Roberts, 1993)	UVC	2.14 ± 0.78	0 - 4	(Rogers *et al.*, 2014; Rogers *et al.*, 2018)
		BRUV	1.78 ± 0.83	0 - 4	
Habitat type	Visually assessed from video footage into 9 categories (Asher *et al.*, 2017)	BRUV			(Espinoza *et al.*, 2014)
Live branching coral	Percentage cover visually assessed into five categories (Chou *et al.*, 1994)	UVC		0 - 2	(Bell and Galzin, 1984; Komyakova *et al.*, 2013; Boaden and Kingsford, 2015)
Live massive coral				0 - 2	
Live table coral				0 - 1	
Algal cover				0 - 2	
PIN	Pin cushion starfish abundance	UVC	0.53 ± 0.85	0 - 4	(Bruckner and Coward, 2019)
COTS	Crown of thorn starfish abundance	UVC	0.68 – 1.88	0 - 16	(Kayal *et al.*, 2012)

A.2 Appendix for Chapter 3

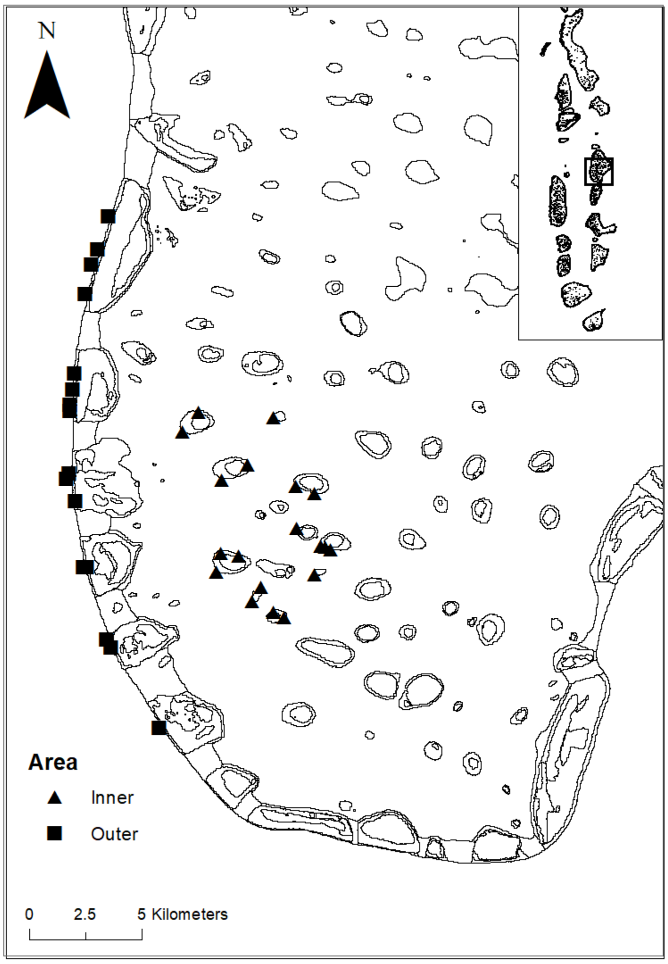


Figure A3. Fish tissue sampling sites in North Malé atoll, Republic of the Maldives. Fish sampling sites were located in either the inner lagoonal reefs (inner) or along the outer edge reefs (outer).

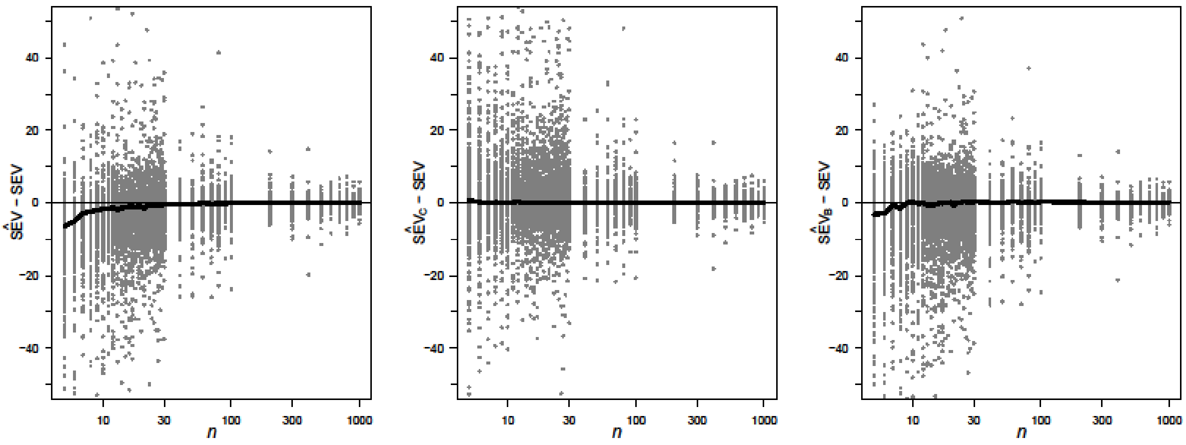


Figure A4. Bias estimation plots for population standard ellipsoid volume (SEV) as a function of sample size (n, on log scale) based on $\widehat{SEV}$ (left hand plot), after small sample size correction $\widehat{SEV}_C$ (middle plot), and the Bayesian estimation $\widehat{SEV}_B$ taken as the median posterior value (right hand plot) following methods described by Jackson *et al.* (2011). Note that the y-axis is restricted for clarity leaving some extreme values outside the depicted boundaries. Grey point are the results of 10000 total simulations, with heavy black line the median value for a given n. Thin black line shows perfect estimate of y = 0. Populations were defined by drawing from a Wishart distribution with degrees of freedom ρ = 3 and the scale matrix $V = \begin{bmatrix} 2 & 0 & 0 \\ 0 & 2 & 0 \\ 0 & 0 & 2 \end{bmatrix}$ using the MASS' package in *R* (Venables and Ripley, 2002; R Core Team, 2017). Bayesian posteriors were determined from 15000 iterations with a burn in of 10000 and a thinning factor of 25.

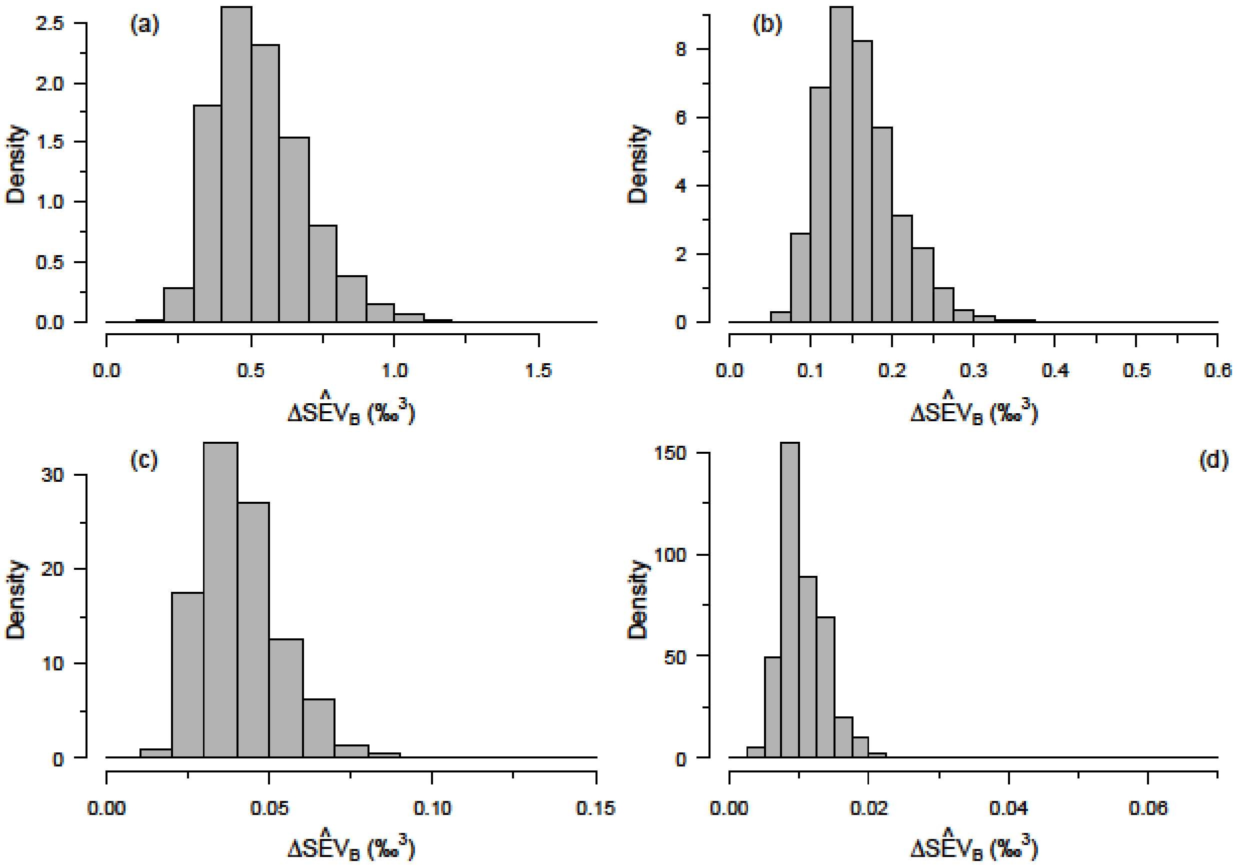


Figure A5. Density histograms of difference in overlap volume calculated from 75% $\widehat{SEV}_B$ for *A. rogaa* and *A. leucogrammicus* data (15000 iterations with a burn in of 10000 and a thinning factor of 25) with increasing number of subdivisions used for mesh approximation of ellipsoids: 1 to 2 (a); 2 to 3 (b); 3 to 4 (c); and 4 to 5 (d). Differences rapidly converge to zero beyond 4 subdivisions. Note that both the x and y axes differ for each plot. Mesh construction and overlap approximation done using the packages 'rgl' (Adler *et al.*, 2018) and 'geometry' (Habel *et al.*, 2019) respectively in *R* (R Core Team, 2017), see code provided in supplement to paper online (https://doi.org/10.1002/ece3.5779).

Table A3. Accepted and measured values ± SD of the international, internal and study-specific reference materials used during the stable isotope analyses. International standards were USGS40 (glutamic acid) for δ^{13}C and δ^{15}N (Qi *et al.*, 2003) and silver sulfide standards IAEA- S1, S2 and S3 for δ^{34}S (Coplen and Krouse, 1998). The internal reference materials were MSAG2 (a solution of methanesulfonamide and gelatin), M2 (a solution of methionine, gelatin, glycine and ^{15}N-enriched alanine) and SAAG2 (a solution of sulfanilamide, gelatin and ^{13}C-enriched alanine). The selected internal references cover a large range of isotopic composition and are in solution form, so easily dispensed by syringe.

			Accepted values				Measured values		
Reference	Material		δ^{15}N	δ^{13}C	δ^{34}S	n	δ^{15}N	δ^{13}C	δ^{34}S
International	IAEA-S1	Mean			-0.3	11			0.01
		SD			*				0.17
International	IAEA-S2	Mean			22.62	12			22.16
		SD			0.20				0.59
International	IAEA-S3	Mean			-32.49	12			-31.61
		SD			0.20				1.46
International	USGS40	Mean	-4.5	-26.39		12	-4.52	-26.37	
		SD	0.1	0.04			0.16	0.07	
Internal	M2	Mean	32.70	-34.28	14.43	78	32.33	-33.82	13.92
		SD	0.27	0.11	0.46		3.19	3.24	1.67
Internal	MSAG2	Mean	2.24	-21.23	6.18	116	2.21	-21.36	6.20
		SD	0.09	0.12	0.43		0.23	0.09	0.53
Internal	SAAG2	Mean	4.55	-5.78	0.04	65	4.64	-5.67	0.38
		SD	0.06	0.12	0.36		0.10	0.10	0.52
Study-specific	*Anyperodon leucogrammicus*	Mean				31	12.53	-13.40	19.80
		SD					0.27	0.14	0.73

* = exact value defining scale

Table A4. Linear mixed effects models of differences in predator δ^{13}C, δ^{15}N and δ^{34}S isotope values with body size and between atoll areas. The number presented is the model coefficient with the standard error in brackets. Significance level is denoted using asterisks where *** = p < 0.001, ** = p < 0.01 and * = p < 0.05.

Formula: Isotope ~ Size + Area + Area * Size + (1 + Size | Species)

	δ^{13}C	**δ^{15}N**	**δ^{34}S**
(Intercept)	-14.63 (0.67)***	12.19 (0.38)***	18.51 (0.42)***
Size	-0.01 (0.00)	0.00 (0.00)	0.00 (0.00)
Area	-2.25 (0.85)**	-0.30 (0.43)	0.04 (0.53)
Size:Area	0.01 (0.00)*	0.00 (0.00)	-0.00 (0.00)
AIC	435.74	254.56	315.78
Num. obs.	135	135	135

A.3 Appendix for Chapter 4

Table A5. Mean (± S.E) body length (mm) and stable isotope ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) values (‰) for each reef predator species sampled in both inner and outer atoll.

Family	Species	Area	n	Length (mm)	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
Carangidae	*Caranx melampygus*	Inner	10	327.30 ± 23.58	-16.47 ± 0.22	12.39 ± 0.17	18.12 ± 0.15
		Outer	6	414.83 ± 14.27	-15.80 ± 0.20	12.44 ± 0.20	18.25 ± 0.16
Lethrinidae	*Lethrinus obsoletus*	Inner	3	377.33 ± 19.33	-13.32 ± 1.37	12.09 ± 0.45	16.27 ± 0.66
		Outer	2	332.00 ± 4.00	-14.81 ± 0.09	13.36 ± 0.07	18.49 ± 0.12
Lutjanidae	*Aphareus furca*	Inner	6	325.16 ± 8.86	-17.21 ± 0.05	12.21 ± 0.08	18.88 ± 0.17
		Outer	2	479.00 ± 55.00	-16.59 ± 0.40	13.09 ± 0.07	18.62 ± 0.18
	Lutjanus bohar	Inner	12	304.41 ± 13.65	-15.36 ± 0.63	12.36 ± 0.29	18.59 ± 0.18
		Outer	1	185.00 ± 0.00	-14.87 ± 0.00	12.97 ± 0.00	17.94 ± 0.00
	Lutjanus gibbus	Inner	13	287.92 ± 9.75	-16.36 ± 0.15	12.58 ± 0.08	19.14 ± 0.17
		Outer	9	318.88 ± 13.32	-16.26 ± 0.60	12.99 ± 0.32	18.96 ± 0.33
Serranidae	*Aethaloperca rogaa*	Inner	11	227.81 ± 10.12	-16.08 ± 0.26	12.77 ± 0.07	19.49 ± 0.17
		Outer	11	265.90 ± 17.96	-17.11 ± 0.17	12.99 ± 0.16	19.79 ± 0.18
	Anyperodon leucogrammicus	Inner	10	275.55 ± 12.65	-15.60 ± 0.19	12.94 ± 0.11	19.49 ± 0.17
		Outer	10	331.70 ± 17.47	-15.61 ± 0.04	12.81 ± 0.15	19.28 ± 0.01
	Cephalopholis argus	Inner	11	260.81 ± 14.95	-15.46 ± 0.23	12.77 ± 0.08	19.32 ± 0.26
		Outer	10	257.80 ± 13.75	-16.14 ± 0.19	12.29 ± 0.08	19.58 ± 0.14
	Cephalopholis miniata	Inner	11	269.63 ± 12.50	-16.92 ± 0.10	12.73 ± 0.06	19.73 ± 0.17
		Outer	10	232.00 ± 13.11	-16.88 ± 0.22	12.64 ± 0.10	19.55 ± 0.20

Table A6. Summary of ANOVAs comparing $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values between inner and outer atoll areas and between species. † = data did not conform to normality so a non-parametric Kruskal-Wallis test was used instead. Significance is denoted by '*'. Following these statistical tests Caesio varilineata, Caesio xanthanota, Decapterus macarellus and Pterocaesio pisang were combined into one group named "Diurnal planktivores".

			$\delta^{13}C$		$\delta^{15}N$		$\delta^{34}S$		
	Species	df	F	p-value	F	p-value	F	p-value	Combined
Inner and Outer	*Acanthurus leucosternon*	1, 15	$1.980^{\dagger}$	0.159	$0.646^{\dagger}$	0.421	$0.364^{\dagger}$	0.547	Y
	Caesio xanthanota	1, 11	$1.914^{\dagger}$	0.167	$0.010^{\dagger}$	0.921	$0.623^{\dagger}$	0.430	Y
	Chaetodon meyeri	1, 14	$3.088^{\dagger}$	0.079	6.494	**0.023***	4.525	0.052	Y
	Myripristis violacea	1, 15	$3.289^{\dagger}$	0.070	$4.471^{\dagger}$	**0.034***	0.318	0.582	Y
	Pearsonothuria graeffei	1, 13	14.861	**0.003***	4.752	**0.048***	8.044	**0.014***	Y
Species groups	*Caesio varilineata, Caesio xanthonota, Decapterus macarellus, Pterocaesio pisang*	1, 53	$30.052^{\dagger}$	**0.000***	0.467	0.706	0.414	0.744	Y

Table A7. Mean (± S.E) stable isotope ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) values (‰) for each primary consumer species sampled in both inner and outer atoll. Bold indicates statistical differences in isotope values of the samples species were found between areas using ANOVA or Kruskal-Wallis tests. When differences in the mean were small (~1‰), samples from each area were combined for each group.

Source	Species	Area	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
Coral	*Chaetodon meyeri*	Inner	-11.93 ± 0.46	**11.22 ± 0.24**	21.11 ± 0.23
Coral	*Chaetodon meyeri*	Outer	-13.14 ± 0.49	**10.37 ± 0.20**	20.42 ± 0.19
Detritus	*Pearsonothuria graeffei*	Inner	**-12.67 ± 0.23**	**6.70 ± 0.14**	**18.14 ± 0.22**
Detritus	*Pearsonothuria graeffei*	Outer	**-11.77 ± 0.12**	**6.24 ± 0.16**	**18.93 ± 0.17**
Diurnal plankton	*Caesio varilineata*	Inner	**-18.26 ± 0.08**	11.46 ± 0.09	19.01 ± 0.18
Diurnal plankton	*Caesio xanthonota*	Inner	**-17.05 ± 0.34**	11.55 ± 0.32	18.92 ± 0.35
Diurnal plankton	*Caesio xanthonota*	Outer	**-17.49 ± 0.00**	11.74 ± 0.49	18.79 ± 0.41
Diurnal plankton	*Decapterus macarellus*	Inner	**-17.19 ± 0.27**	11.71 ± 0.15	19.22 ± 0.19
Diurnal plankton	*Pterocaesio pisang*	Inner	**-18.02 ± 0.17**	11.48 ± 0.10	18.94 ± 0.33
DVM plankton	*Uroteuthis duvauceli*	Inner	-17.94 ± 0.01	12.39 ± 0.17	22.40 ± 0.53
Benthic algae	*Acanthurus leucosternon*	Inner	-13.65 ± 0.67	8.30 ± 0.81	19.66 ± 0.17
Benthic algae	*Acanthurus leucosternon*	Outer	-14.16 ± 0.37	7.92 ± 0.13	19.71 ± 0.21
Nocturnal plankton	*Myripristis violacea*	Inner	-16.76 ± 0.18	**11.91 ± 0.11**	20.04 ± 0.15
Nocturnal plankton	*Myripristis violacea*	Outer	-17.04 ± 0.08	**11.58 ± 0.07**	19.91 ± 0.13

Table A8. Comparison of mixing models fit using MixSIAR on the reef predator diet data using four different trophic discrimination factors. dLOOic = difference in LOOic between each model and the model with the lowest LOOic (Stock *et al.*, 2018). The model with the lowest LOOic and the highest weight was presented in the results. Model 1 had a 55% probability of being the best model while model 2 had a 45% probability of being the best model suggesting both are equally good. * indicates the model did not converge.

Model	$\Delta\delta^{13}C$	$\Delta\delta^{15}N$	$\Delta\delta^{34}S$	LOOic	SE (LOOic)	dLOOic	SE (dLOOic)	Weight
1	1.2 ± 1.9	2.1 ± 2.8	-0.53 ± 1.00	609	61.7	0	-	0.55
2	0.4 ± 0.2	2.3 ± 0.3	-0.53 ± 1.00	609.4	60.5	0.4	14.3	0.45
3	0.9 ± 1.0	3.2 ± 0.4	-0.53 ± 1.00	665.8	63	56.8	16.3	0
4*	1.2 ± 1.9	2.1 ± 2.8	1.9 ± 0.51	824	75.7	215	22.4	0

Table A9. Credible intervals of plankton source contribution for two three-source ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) Bayesian stable isotope mixing models with different trophic discrimination factors (TDF, Δ), run to ascertain likely food source contributions for nine reef predator species. Model 1: $\Delta\delta^{13}C$ +1.2 (SD ± 1.9), $\Delta\delta^{15}N$ +2.1 (SD ± 2.8), $\Delta\delta^{34}S$ -0.53 (SD ± 1.00) and Model 2: $\Delta\delta^{13}C$ +0.4 (SD ± 0.2), $\Delta\delta^{15}N$ +2.3 (SD ± 0.3), $\Delta\delta^{34}S$ -0.53 (SD ± 1.00).

Species	Area	Q_0.025	Q_0.25	Q_0.5	Q_0.75	Q_0.975
Model 1						
Aethaloperca rogaa	Inner	0.661	0.716	0.740	0.764	0.809
Aethaloperca rogaa	Outer	0.732	0.782	0.807	0.832	0.877
Anyperodon leucogrammicus	Inner	0.632	0.716	0.750	0.776	0.822
Anyperodon leucogrammicus	Outer	0.636	0.718	0.751	0.782	0.830
Aphareus furca	Inner	0.573	0.644	0.683	0.722	0.800
Aphareus furca	Outer	0.626	0.711	0.751	0.790	0.857
Caranx melampygus	Inner	0.643	0.703	0.733	0.763	0.814
Caranx melampygus	Outer	0.584	0.659	0.695	0.731	0.800
Cephalopholis argus	Inner	0.616	0.676	0.704	0.728	0.775
Cephalopholis argus	Outer	0.560	0.625	0.654	0.680	0.728
Cephalopholis miniata	Inner	0.643	0.693	0.719	0.743	0.789
Cephalopholis miniata	Outer	0.644	0.702	0.732	0.760	0.814
Lethrinus obsoletus	Inner	0.703	0.821	0.879	0.928	0.986
Lethrinus obsoletus	Outer	0.728	0.814	0.858	0.907	0.983
Lutjanus bohar	Inner	0.659	0.739	0.772	0.802	0.859
Lutjanus bohar	Outer	0.554	0.676	0.735	0.788	0.884
Lutjanus gibbus	Inner	0.649	0.703	0.728	0.754	0.801
Lutjanus gibbus	Outer	0.755	0.810	0.838	0.863	0.910
Model 2						
Aethaloperca rogaa	Inner	0.606	0.678	0.710	0.735	0.778
Aethaloperca rogaa	Outer	0.673	0.738	0.767	0.794	0.838
Anyperodon leucogrammicus	Inner	0.526	0.613	0.656	0.697	0.761
Anyperodon leucogrammicus	Outer	0.531	0.622	0.669	0.713	0.771
Aphareus furca	Inner	0.552	0.63	0.668	0.702	0.762
Aphareus furca	Outer	0.576	0.689	0.732	0.771	0.840
Caranx melampygus	Inner	0.585	0.655	0.683	0.708	0.747
Caranx melampygus	Outer	0.607	0.682	0.715	0.752	0.821
Cephalopholis argus	Inner	0.559	0.644	0.676	0.704	0.744
Cephalopholis argus	Outer	0.533	0.613	0.643	0.669	0.709
Cephalopholis miniata	Inner	0.646	0.695	0.720	0.744	0.786
Cephalopholis miniata	Outer	0.621	0.680	0.712	0.742	0.794
Lethrinus obsoletus	Inner	0.555	0.682	0.751	0.827	0.955
Lethrinus obsoletus	Outer	0.659	0.776	0.831	0.881	0.970
Lutjanus bohar	Inner	0.414	0.554	0.649	0.707	0.772
Lutjanus bohar	Outer	0.332	0.645	0.734	0.809	0.899
Lutjanus gibbus	Inner	0.601	0.678	0.707	0.732	0.771
Lutjanus gibbus	Outer	0.599	0.745	0.782	0.810	0.857

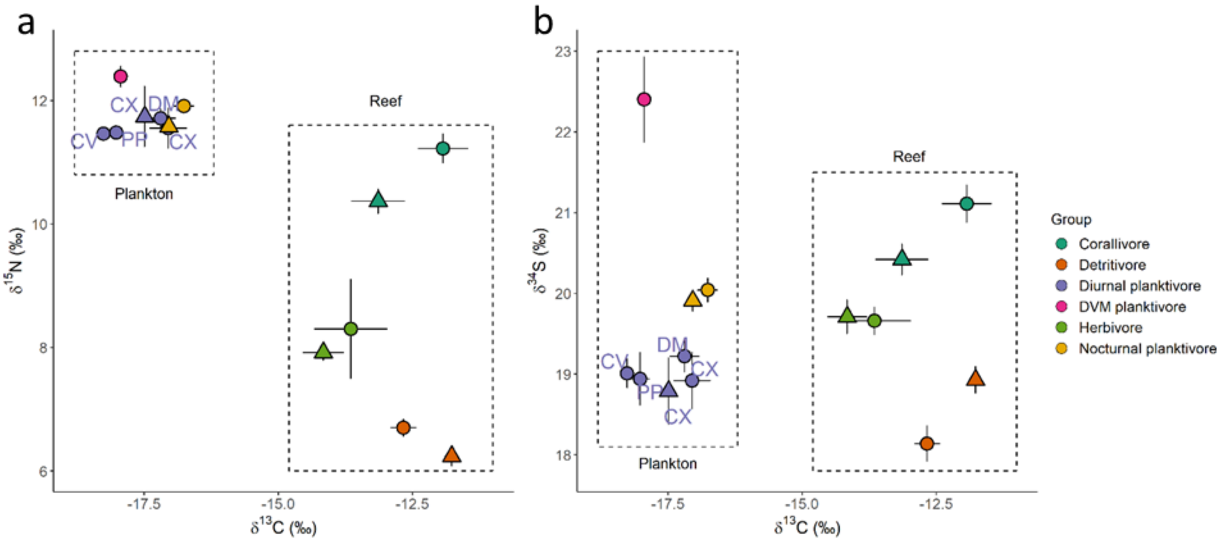


Figure A6. Mean isotope values (± SE) of a) δ^{13}C and δ^{15}N and b) δ^{13}C and δ^{34}S of all primary consumers sampled to represent different end-members in both inner (●) and outer (▲) atoll before they were combined *a priori*. Boxes show *a posteriori* groupings. Four species of diurnal planktivores were sampled: CV: *Caesio varilineata*, CX: *Caesio xanthanota*, DM: *Decapterus macarellus* and PP: *Pterocaesio pisang*.

A.4 Appendix for Chapter 5

Table A10. The number of carbon atoms involved in the amino acid derivatisation process which are used to calculate a correction factor for each amino acid.

Amino Acid	No. C atoms (c)	No. C atoms added in derivative group (d)	Total C atoms in derivative group (cd)	Underivatised ^{13}C value	Average GC/C/IRMS value	Correction Factor
Alanine	3	5	8	-26.11	-35.46	-41.07
Aspartic acid	4	8	12	-7.69	-34.91	-48.52
Glutamic acid	5	8	13	-13.3	-30.32	-40.95
Glycine	2	5	7	-40.99	-39.70	-39.18
Hydroxyproline	5	7	12		-34.97	
Luecine	6	5	11	-22.53	-32.75	-45.02
Lysine	6	7	13	-22.24	-34.52	-45.05
Norluecine	6	5	11		-34.92	
Phenylalanine	9	5	14	-30.27	-36.87	-48.74
Proline	5	5	10	-10.64	-25.67	-40.70
Serine	3	7	10	-36.5	-43.09	-45.91
Threonine	4	7	11	-30.56	-42.53	-49.38
Tyrosine	9	7	16	-16.94	-31.34	-49.86
Valine	5	5	10	-26.17	-36.61	-47.05

Table A11. Summary of permutation tests of independence investigating differences in normalised $\delta^{13}C$ values of essential amino acids of primary consumers between inner and outer atoll area and between species. Significant differences ($p < 0.05$) are highlighted in bold.

		Leucine		**Lysine**		**Pheylalanine**		**Threonine**		**Valine**	
Test	**Species**	*Z*	p-value	*Z*	p-value	*Z*	p-value	*Z*	p-value	*Z*	p-value
Area	*Acanthurus leucosternon*	0.126	0.909	1.245	0.320	-1.655	0.090	-1.347	0.229	1.529	0.131
Area	*Chaetodon meyeri*	-1.780	**0.038**	1.924	**0.034**	1.390	0.172	-1.109	0.295	-0.413	0.765
Area	*Ctenochaetus striatus*	1.081	0.309	1.278	0.228	-1.972	**0.047**	-0.908	0.398	1.287	0.246
Area	*Myripristis violacea*	1.132	0.293	0.650	0.554	-0.962	0.396	-0.528	0.647	-0.148	0.898
Area	*Caesio varilineata*	-1.403	0.134	-0.084	1.000	0.682	0.734	1.258	0.330	-0.188	0.934
Area	*Caesio xanthonota*	-0.793	0.432	0.716	0.717	0.800	0.713	0.614	0.720	-1.420	0.141
Species	*C. varilineata* & *C. xanthonota*	-0.886	0.413	1.795	0.059	2.112	**0.032**	-0.214	0.840	-2.089	**0.033**
Species	*U. duvauceli* & *D. macarellus*	-0.018	1.000	0.497	0.632	-1.553	0.119	0.835	0.456	0.600	0.593

A.5 Appendix for Chapter 6

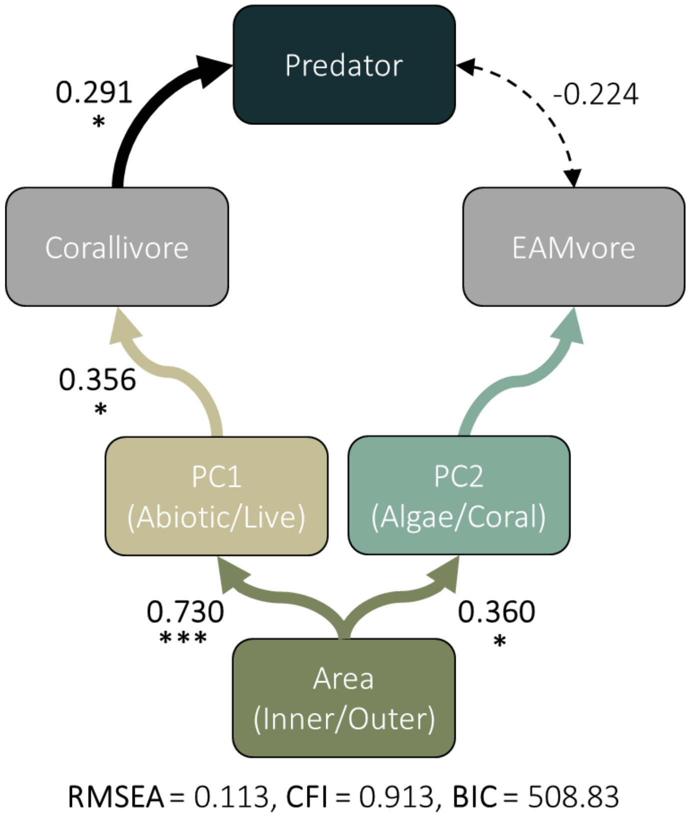


Figure A7. The model of path analysis results exploring the abiotic and biotic variables influencing reef predator biomass without the planktivore pathway. This model was a poorer fit than the model presented in the results (Figure 6.7). Single arrows indicate indicate causal paths with standardised path coefficients. Thick arrows indicate significant relationships with stars denoting the significance level (* = p < 0.05, ** = p < 0.01, *** = P < 0.001) and dotted arrows signify covariance.

Table A12. List of all prey species recorded during underwater visual census and their functional groups.

Family	Species	Functional group	Reference
Acanthuridae	*Acanthurus auranticavus*	E	(Robertson, 1982)
	Acanthurus leucocheilus	E	(Green and Bellwood, 2009)
	Acanthurus leucosternon	E	(Green and Bellwood, 2009)
	Acanthurus mata	E	(Hiatt and Strasburg, 1960)
	Acanthurus nigricauda	E	(Choat *et al.*, 2002)
	Acanthurus nigrofuscus	E	(Green and Bellwood, 2009)
	Acanthurus thompsoni	P	(Hobson, 1974)
	Acanthurus tristis	E	(Green and Bellwood, 2009)
	Ctenochaetus striatus	E	(Choat *et al.*, 2002)
	Ctenochaetus truncatus	E	(Eggertsen *et al.*, 2019)
	Naso brevirostris	O	(Choat *et al.*, 2002)
	Naso elegans	E	(Green and Bellwood, 2009)
	Naso hexacanthus	P	(Choat *et al.*, 2002)
	Naso thynnoides	P	(Durville *et al.*, 2003)
	Zebrasoma desjardinii	E	(Choat, 1991)
	Zebrasoma scopas	E	(Choat *et al.*, 2002)
Apogonidae		B	(Hobson, 1974)
Balistidae	*Balistapus undulatus*	O	(Hiatt and Strasburg, 1960)
	Balistoides conspicillum	B	(Patankar *et al.*, 2018)
	Melichthys indicus	O	(Patankar *et al.*, 2018)
	Odonus niger	P	(Patankar *et al.*, 2018)
	Sufflamen bursa	O	(Patankar *et al.*, 2018)
Blenniidae	Blennies	E	(Durville *et al.*, 2003)
	Sabretooth blennies	B	(Durville *et al.*, 2003)
Caesionidae	*Caesio* spp	P	(Russ *et al.*, 2017)
	Pterocaesio spp	P	(Russ *et al.*, 2017)
Chaetodontidae	*Chaetodon auriga*	O	(Hobson, 1974)
	Chaetodon collare	C	(Allen *et al.*, 1998)
	Chaetodon falcula	B	(Narayani *et al.*, 2015)
	Chaetodon guttatissimus	O	(Durville *et al.*, 2003)
	Chaetodon kleinii	O	(Sano, 1989)
	Chaetodon madagaskariensis	O	(Durville *et al.*, 2003)
	Chaetodon melannotus	O	(Sano, 1989)
	Chaetodon meyeri	C	(Sano, 1989)
	Chaetodon triangulum	C	(Chandler *et al.*, 2016)
	Chaetodon trifasciatus	C	(Narayani *et al.*, 2015)
	Chaetodon xanthocephalus	O	(Durville *et al.*, 2003)
	Forcipiger flavissimus	O	(Hobson, 1974)
	Forcipiger longirostris	B	(Hobson, 1974)
	Hemitaurichthys zoster	O	(Hobson, 1974)
	Heniochus pleurotaenia	P	(Lieske and Myers, 2009)
Cirrhitidae	*Paracirrhites* spp	O	(Hobson, 1974)

Diodontidae	*Diodon liturosus*	B	(Patankar *et al.*, 2018)
Gobiidae	Reef gobies	O	(Hiatt and Strasburg, 1960)
	Sand gobies	O	(Hiatt and Strasburg, 1960)
Haemulidae	*Plectorhinchus* spp	O	(Durville *et al.*, 2003)
Holocentridae	*Myripristis* spp	P	(Hobson, 1974)
	Neoniphon spp	B	(Durville *et al.*, 2003)
	Sargocentron spp	B	(Durville *et al.*, 2003)
Labridae	*Anampses meleagrides*	B	(Durville *et al.*, 2003)
	Bodianus spp	B	(Hobson, 1974)
	Cheilinus spp	B	(Hobson, 1974)
	Cheilio inermis	B	(Ormond, 1980)
	Cirrhilabrus exquisitus	B	(Durville *et al.*, 2003)
	Coris spp	B	(Hobson, 1974)
	Epibulus spp	B	(Hiatt and Strasburg, 1960)
	Gomphosus caeruleus	B	(Hobson, 1974)
	Halichoeres spp	B	(Hobson, 1974)
	Hemigymnus spp	B	(Hiatt and Strasburg, 1960)
	Hologymnosus spp	B	(Durville *et al.*, 2003)
	Labrichthys unilineatus	C	(Westneat, 2001)
	Labroides spp	B	(Hiatt and Strasburg, 1960)
	Macropharyngodon bipartitus	B	(Hobson, 1974)
	Novaculichthys taeniourus	B	(Hiatt and Strasburg, 1960)
	Oxycheilinus digramma	B	(Durville *et al.*, 2003)
	Pseudocheilinus spp	B	(Hobson, 1974)
	Stethojulis albovittata	B	(Hiatt and Strasburg, 1960)
	Thalassoma amblycephalum	P	(Hobson, 1974)
	Thalassoma spp	B	(Hobson, 1974)
	Wetmorella spp	B	(Westneat, 2001)
Microdesmidae	*Ptereleotris evides*	P	(Durville *et al.*, 2003)
Monacanthidae	*Amanses scopas*	C	(Durville *et al.*, 2003)
	Oxymonacanthus longirostris	C	(Patankar *et al.*, 2018)
	Paraluteres prionurus	O	(Cornic, 1987)
Mullidae		B	(Hobson, 1974)
Nemipteridae	*Scolopsis* spp	B	(Hiatt and Strasburg, 1960)
Ostraciidae	*Ostracion meleagris*	O	(Patankar *et al.*, 2018)
Pempheridae	*Parapriacanthus ransonneti*	P	(Durville *et al.*, 2003)
	Pempheris vanicolensis	P	(Durville *et al.*, 2003)
Pinguipedidae	*Parapercis* spp	B	(Hiatt and Strasburg, 1960)
Pomacanthidae	*Apolemichthys trimaculatus*	O	(Durville *et al.*, 2003)
	Centropyge multispinis	O	(Alwany, 2009)
	Pomacanthus imperator	B	(Alwany, 2009)
	Pygoplites diacanthus	O	(Alwany, 2009)
Pomacentridae	*Abudefduf vaigiensis*	P	(Frédérich *et al.*, 2009)
	Amblyglyphidodon spp	O	(Durville *et al.*, 2003)
	Amphiprion spp	O	(Durville *et al.*, 2003)
	Chromis spp	P	(Hobson, 1974)
	Dascyllus spp	O	(Frédérich *et al.*, 2009)
	Plectroglyphidodon spp	E	(Frédérich *et al.*, 2009)

	Pomacentrus caeruleus	P	(Frédérich *et al.*, 2009)
	Pomacentrus chrysurus	E	(Allen, 1991)
	Pomacentrus indicus	O	(Durville *et al.*, 2003)
	Pomacentrus pavo	O	(Frédérich *et al.*, 2008)
	Pomacentrus philippinus	O	(Durville *et al.*, 2003)
Priacanthidae	*Priacanthus hamrur*	B	(Hobson, 1974)
Scaridae	*Cetoscarus* spp	E	(Plass-Johnson *et al.*, 2013)
	Chlorurus spp	E	(Green and Bellwood, 2009)
	Hipposcarus spp	E	(Green and Bellwood, 2009)
	Scarus spp	E	(Hobson, 1974)
Serranidae	*Pseudanthias* spp	P	(Durville *et al.*, 2003)
Siganidae	*Siganus* spp	E	(Hiatt and Strasburg, 1960)
Synodontidae		O	(Hiatt and Strasburg, 1960)
Tetraodontidae	*Arothron* spp	O	(Hobson, 1974)
	Canthigaster spp	O	(Hobson, 1974)
Zanclidae	*Zanclus cornutus*	B	(Hobson, 1974)

Table A13. List of all fishery target, reef-associated teleost predators recorded on underwater visual census.

Genus	Species
Carangidae	*Caranx melampygus*
Lutjanidae	*Aphareus furca*
	Aprion virescens
	Lutjanus bohar
	Lutjanus gibbus
	Lutjanus kasmira
	Macolor macularis
Serranidae	*Aethaloperca rogaa*
	Anyperodon leucogrammicus
	Cephalopholis argus
	Cephalopholis leopardus
	Cephalopholis miniata
	Cephalopholis nigripinnis
	Cephalopholis sexmaculata
	Cephalopholis spiloparaea
	Epinephelus fasciatus
	Epinephelus longispinis
	Epinephelus macrospilos
	Epinephelus merra
	Epinephelus polyphekadion
	Epinephelus spilotoceps
	Plectropomus areolatus
	Plectropomus laevis
	Variola louti

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ORIGINAL PAPER

The importance of oceanic atoll lagoons for coral reef predators

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Abstract

Predators on coral reefs play an important ecological role structuring reef fish communities and are important fishery targets. It is thought that reef predator assemblages increase in density and diversity from inner lagoonal to outer edge reefs. Oceanic atolls may differ though, as nutrients are available throughout. Reef predator populations are declining, but there is little known about how their distributions may vary across oceanic atolls. Using a combination of underwater visual census and baited remote underwater video, this study aimed to compare reef predator populations between inner and outer reefs of North Malé Atoll (Maldives) and determine which reef metrics may drive any differences in assemblage structure. We found that predator assemblages were significantly different between inner and outer atoll. Body sizes of several predator families were consistently larger in the outer atoll, however, abundance, biomass and species richness were similar between outer edge reefs and inner lagoonal reefs suggesting atoll lagoons may be undervalued habitats. Depth and complexity were consistently important predictors of the predator assemblage. Inner atoll lagoonal habitat is equally as important for reef predator assemblages as outer reef slopes, although the dominant species differ. This study provides important information on reef predator populations in the Maldives, where detailed assessments of the reef predator assemblage are lacking but the reef fishery is thriving and annual catch will continue to increase.

Introduction

Coral reef predators play an important role in structuring reef fish communities (Clark et al. 2009; Roff et al. 2016). They regulate the composition and dynamics of prey assemblages, directly through predation and indirectly through the modification of prey behaviour (Ceccarelli and Ayling 2010; Roff et al. 2016). Locally abundant teleosts such as snappers, emperors and groupers are an important part of the reef predator assemblage, making regular movements between hard and adjacent soft bottom habitats (Berkström et al. 2012; Green et al. 2015). They also substantially contribute to coral reef fishery yields, providing livelihoods to millions of people globally. Currently, populations of sharks and other reef fishes are experiencing worldwide decline (Graham et al. 2010; Roff et al. 2016), but their removal can result in community-wide impacts which may destabilise the food web (Bascompte et al. 2005).

In both terrestrial and marine systems, predators show a preference for edge habitats (Phillips et al. 2004; Heithaus et al. 2006), such as forest grassland edges (Svobodová et al. 2011), forereef ledges (Papastamatiou et al. 2009) and outer shelf areas (Cappo et al. 2007). Consequently, reef predators may increase in density and diversity from shallow, lagoonal habitats to outer reef slopes (Friedlander et al. 2010; Dale et al. 2011). Outer reef habitats may provide a greater availability of resources, for example they host aggregations of planktivorous fishes (Hamner et al. 1988, 2007) that take advantage of increased plankton prey abundance (Wyatt et al. 2013) and sustain reef predators (Frisch et al. 2014; Matley et al. 2018).

In the Maldives, atolls are characterised by an oceanic outer reef slope with deep channels separating inner shallow, lagoonal reefs from the adjacent open ocean. A range of hydrodynamic processes such as equatorial currents and

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local upwelling facilitate water mixing within the Maldivian archipelago (Sasamal 2007), enhancing biological productivity. Consequently, unlike more closed systems, nutritional resources are available throughout the atolls and into the lagoons due to the extensive water circulation (Radice et al. 2019). Furthermore, tourist resort islands, often located inside atoll lagoons, act as refuges for reef fish communities, because fishing is often prohibited there. As such, resort islands support a higher diversity of commercial fish species, such as groupers, than other permanently inhabited islands (Moritz et al. 2017). Inner lagoonal reef habitats may thus be equally as important to reef predator assemblages as outer edge reefs (Skinner et al. 2019).

Fisheries in the Maldives traditionally focused on tuna, but the annual reef fishery catch has increased (Sattar et al. 2014) due to a growing demand for reef fish from tourists (Ministry of Tourism 2018). Moreover, the 2009–2013 Maldives Strategic Action Plan identified expansion and diversification of the fisheries sector as a national priority (Adam and Sinan 2013), signifying further development and exploitation of the reef fish fishery. Although the Maldives was classified as one of the most underexploited fisheries in the Indian Ocean (Newton et al. 2007; MacNeil et al. 2015), there are no unfished or historically "pristine" coral reef ecosystems in the region (McClanahan 2011). In addition, current estimates suggest that the reef fishery is approaching the limit of its maximum sustainable yield (Sattar et al. 2014) and prior to 1998 sharks were intensively fished (Ushan et al. 2012). There is thus an urgent need to assess abundance and distribution of reef predator populations to determine which atoll habitats are important.

All survey methods for assessing abundances of fishes have their strengths and weaknesses, so, to accurately assess predator populations, multiple methods are desired that take into account inherent interspecific differences in body size, habitat association, aggregative or schooling behaviour, mobility (particularly in the case of elasmobranchs), or the response to the presence of divers or various types of equipment (Kulbicki 1988; Willis and Babcock 2000; White et al. 2013). Underwater visual census (UVC) allows a comprehensive sampling of smaller, resident species that are harder to detect, however time underwater is limited and high replication is required to detect rarer (or more mobile) species (Dulvy et al. 2003). Conversely, baited remote underwater video (BRUV) offers a non-invasive and non-destructive technique that can cover a wide geographic area, depth range and number of habitats (Harvey et al. 2013). BRUV is particularly useful in assessing occurrences of larger, more mobile species (Willis and Babcock 2000; Cappo et al. 2003; Harvey et al. 2012; White et al. 2013). However, it can be difficult and time consuming to identify species from the video footage and there is a potential bias arising from attracting species to the bait (Willis and Babcock 2000; Cappo et al. 2003; Harvey et al. 2012; Espinoza et al. 2014). By combining these two survey methodologies, a more comprehensive estimate of reef predator abundances and distributions can be achieved.

This study aimed to assess coral reef predator assemblages across an oceanic atoll using both BRUV and UVC. We sought to determine if there were: (1) differences in the abundance, size, biomass, and diversity of predators between the inner and outer atoll, and (2) what habitat characteristics help explain the differences?

Materials and methods

Study site

The Maldives is an archipelago of 16 atolls and is the historical archetype of a coral reef province (Naseer and Hatcher 2004). The coral reef area is 8920 km^2 (Spalding et al. 2001), while the EEZ covers almost 1 million km^2 (FAO 2006). The north–south extent cuts across the equator and is subject to equatorial currents transporting high concentrations of nutrients (Sasamal 2007). Fieldwork was conducted in North Malé Atoll (4°18′34.5 N, 73°25′26.4 E) from January to April 2017. North Malé Atoll is located in the centre of the double chain of the Maldivian archipelago, on the eastern side. It has an atoll perimeter of 161 km, 117.9 km of which is shallow edge reef while 43.1 km is deeper channels (Beetham and Kench 2014), promoting water exchange between the adjacent open ocean and the atoll lagoon. The atoll has 189 reef platforms, covering 22.3% of its surface area (Naseer and Hatcher 2004). The atoll was divided into two areas: (1) inner: enclosed lagoonal reef platform sites, and (2) outer: outer reef slope sites.

Underwater visual census (UVC)

UVC was carried out at 40 sites, 20 in the inner atoll and 20 in the outer atoll (Fig. 1). A total of 200 transects were surveyed, 100 within each area. At each site, five 50 × 5 m transects were laid parallel to the forereef habitat at 2.5–15 m depth. A minimum of 5 m was left between transects. Abundance and size to the nearest centimetre of all reef predator species were recorded (here predators at assumed trophic levels 3.5 and above, species list in Appendix Table S1). Predators were characterised as either mobile and highly visible or cryptic and site attached based on their behaviour (Brock 1982). Two observers recorded the predatory fish assemblage. The first observer laid the transect while recording all mobile, highly visible predators, and the second searched the benthos for cryptic, site-attached predators. Percent cover of branching, massive and table coral, and algae was estimated for each transect in the

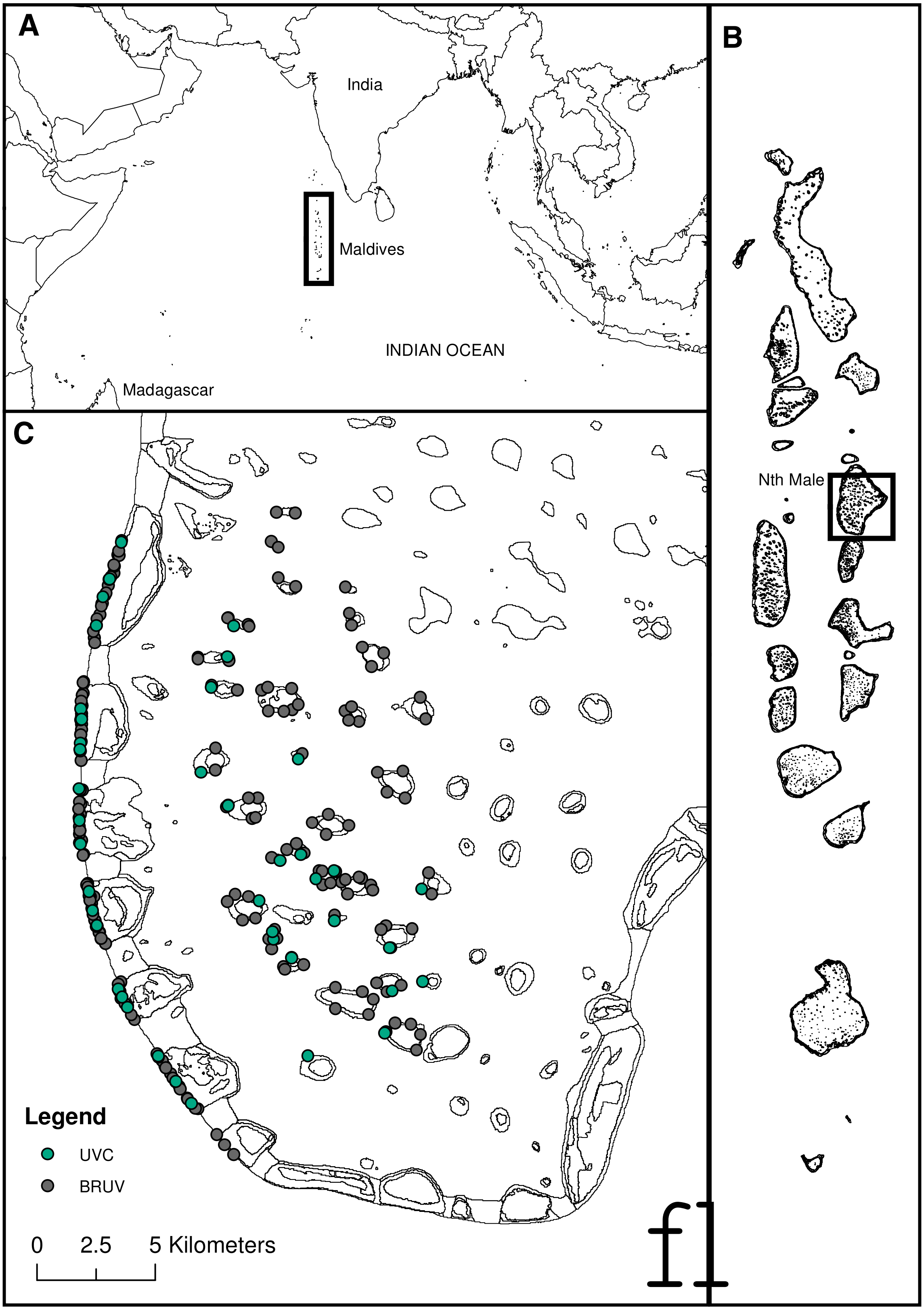

Fig. 1 Underwater visual census (UVC) and baited remote underwater video (BRUV) survey locations. **a** Maldives location in the north Indian Ocean (3.2028° N, 73.2207° E), **b** North Malé Atoll in the central Maldives archipelago (4.4167° N, 73.5000° E), and **c** the UVC and BRUV inner and outer survey locations in North Malé Atoll

following categories: 0% = absent, > 0 and < 25% = low, > 25 and < 50% = fair, > 50 and < 75% = good, > 75% = excellent (Chou et al. 1994). Reef habitat structural complexity was visually assessed on a 6-point scale from 0 to 5, where 0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex, 4 = very complex and 5 = exceptionally complex (Polunin and Roberts 1993). Abundance of crown of thorns (*Acanthaster planci*) and pin cushion starfish (*Culcita novaguineae*) starfish were also recorded by the second observer. The same observers were used throughout the surveys to prevent observer bias (Willis and Babcock 2000). A training period was carried out prior to data collection to ensure accurate species identification and size estimates (Wilson et al. 2007).

Baited remote underwater video (BRUV)

Overall, 205 BRUVs were deployed, 102 in the inner atoll and 103 in the outer atoll (Fig. 1). BRUV deployments were restricted to depths of 2.5–15 m to sample the same habitat as the UVC surveys and set ≥ 600 m apart (Cappo et al. 2003). For each BRUV, a single GoPro Hero 4 camera with a red filter was attached to a stainless steel frame with a detachable bait arm holding a bait bag. Bait bags were made out of 12 mm wire mesh encased in 15 mm plastic mesh. These were attached to 160 cm lengths of 22 mm plastic PVC pipe using cable ties and a metal pin. Bait consisted of ~ 1 kg of guts and discards from a range of oily fish species: bonito (*Sarda orientalis*), rainbow runner (*Elagatis bipinnulata*) and great barracuda (*Sphyraena barracuda*). BRUVs were deployed with 6 mm polypropylene ropes and surface marker buoys and set manually on coral rubble or sand. For each BRUV, the time deployed and the depth were recorded. Cameras were only deployed during daylight hours (09:00–17:00) to avoid bias from changes in feeding behaviour (Willis and Babcock 2000) and left to record for approximately 70 min to ensure there was 60 min of analysable footage.

During video processing, 25 deployments were excluded from analysis as (1) the field of view was blocked by upright substrate or (2) the camera angle had moved and was facing straight up or straight down (Asher et al. 2017). Consequently, only 180 deployments were included, 90 from each atoll area. Habitat was classified into one of nine categories: (1) aggregate reef, (2) dead boulder coral/rock, (3) entirely reef rubble, (4) rubble/reef, (5) rubble/sand, (6) sand flat, (7) sand with reef in view, (8) sand with scattered coral/rock and (9) spur and groove, the first habitat type being the most dominant of the two identified (Asher et al. 2017). Reef habitat structural complexity was visually assessed using the same 6-point scale of vertical relief as for the UVC surveys (see above) (Polunin and Roberts 1993). Analysis of footage was focused solely on fish predators, i.e. all sharks, Aulostomidae, Carangidae, Fistulariidae, Scombridae and Serranidae species and larger bodied, more mobile Lutjanidae and Lethrinidae species (see Table S1 for full species list). Predators were identified to the lowest taxonomic level of species in most cases, but where species could not be identified, individuals were pooled at the genus level (Espinoza et al. 2014). For each species, the maximum number seen at any one time on the whole video (MaxN) was recorded (Harvey et al. 2012). Video analysis began after a settlement period (min 02:00–max 08:00 min) had elapsed (Kiggins et al. 2018). The settlement period was characterised as over when all sand or sediment had settled and visibility returned to normal and at least a minute had passed since the BRUV was moved or repositioned.

Data analysis

The following statistical procedures were carried out for both UVC and BRUV data using PRIMER 6 (v. 6.1.15) with the add-on PERMANOVA+ (v. 1.0.5) (Anderson et al. 2008) and R version 3.5.2 (R Core Team 2017) linked with R Studio version 1.1.463 (RStudio Team 2012).

Species richness for each dataset was determined using the species accumulation curve in the vegan R package (Oksanen et al. 2018). Curves were generated using 100 permutations and the "exact" method, which finds the expected mean species richness. 95% confidence intervals were calculated from standard deviations. Only individuals identified to species level were included.

Spatial variation in predator populations

UVC assemblage data were analysed at the transect level and BRUV assemblage data at the BRUV level. Where BRUV sites were repeat sampled on different days, each deployment was counted as an independent sample. Predator abundance data were square root transformed and a resemblance matrix was created based on Bray–Curtis similarity measures. Using the R vegan package (Oksanen et al. 2018), data were graphically compared using non-metric multidimensional scaling (nMDS) with a Kruskal fit scheme set to 3 and a minimum stress level of 0.01. If there were clear outliers that were entirely distinct from the other points, these were removed and an additional nMDS plot was carried out on a subset of the data (see supplemental material for all MDS plots, Fig S1 and S2). Significantly correlated species were extracted and overlaid on the nMDS plots as vectors. Differences in the predator assemblage occurring between atoll areas and among sites were investigated using a nested model in PERMANOVA+ (Type III sum of squares, under a reduced model with 9999 permutations), where site (UVC: 40 levels and BRUV: 39 levels) was a random factor nested within the fixed factor area (two levels). Species contributing to between-area dissimilarity and within-area similarity were identified using the SIMPER function (Clarke and Warwick 2001).

UVC predator biomass data were calculated using length–weight relationships available on FishBase (https://fishbase.org) with the exception of *Aethaloperca rogaa* where length–weight relationships were taken from Mapleston et al. (2009). Spatial differences in UVC predator biomass were investigated using a generalized linear model (GLM) with transect level biomass as the response variable and site nested within area as the predictor variable. Model normality and homogeneity assumptions were assessed by plotting predicted values against residuals, predicted values against standardised residuals, and q–q plots of standardised residuals. Biomass data were $\log_{10}$ transformed to satisfy model assumptions. An analysis of variance (ANOVA) was applied to determine whether effects were significant ($p<0.05$). A second GLM was run with the same parameters but without the nurse shark, *Nebrius ferrugineus*, as three large (1.9–2.5 m) individuals were recorded on only one transect in the inner atoll.

Variation in predator body size between atoll areas was investigated for each predator family individually using a linear mixed effects model with the R package lme4 (Bates et al. 2015). Body size (cm) was the response variable, area was a fixed effect and species was a random effect. Model assumptions were checked as above and data were log transformed to meet assumptions when necessary. When the predator family only had one recorded species (Aulostomidae, Carcharhinidae, Scorpaenidae), an ANOVA with body size (cm) as the response variable and area as the predictor variable was used. Size data were checked for normality and homogeneity of variances using a Shapiro–Wilk's test and a Levene's test, respectively. When data did not conform to these parameters, a non-parametric Kruskal–Wallis test was used. Although two species of Carangidae were recorded, *Caranx ignobilis* was only observed once in the inner atoll. This observation was removed from analysis and an ANOVA was used. Fistulariidae and Ginglymostomatidae were only recorded in the inner atoll so no size-based comparisons were made.

Correlation with environmental variables

Using PRIMER, environmental data were normalised. For each entry of a variable, the mean of the variable is subtracted and the value is divided by the standard deviation for that variable (Clarke and Gorley 2006). UVC environmental variables consisted of depth, complexity (Comp), branching coral cover (BC), massive coral cover (MC), table coral cover (TC), algal cover (AC), abundance of crown of thorns starfish (COTS) and abundance of pin cushion starfish (PIN), while BRUV environmental variables consisted of depth, complexity and habitat type. Data were compared using principal coordinate analysis (PCO) based on Euclidean distance similarity measures with overlaid vectors of Pearson's correlated environmental variables. Differences in environmental variables between inner and outer atoll were investigated using a nested model in PERMANOVA+ (Type III sum of squares, under a reduced model with 9999 permutations), where site (UVC: 40 levels and BRUV: 39 levels) was a random factor nested within the fixed factor area (two levels).

To investigate the relationships between the predator assemblage and the respective environmental variables (Table S2), the RELATE function in PRIMER 6 (v. 6.1.15) with a Spearman's rank correlation coefficient and 9999 permutations (Clarke and Warwick 2001) was used. These correlations were further tested using a distance-based multiple linear regression model (DISTLM) in PERMANOVA+ (v. 1.0.5) (Anderson et al. 2008), which models the relationship between a multivariate distance-based dataset, as described by a resemblance matrix, and the variables (Anderson et al. 2008) using distance-based redundancy analysis (dbRDA) (Legendre and Anderson 1999). Relationships were first analysed using marginal tests. No starting terms were specified for the model. The Best selection procedure was used as it incorporates and examines the selection criterion for all possible combinations of predictor variables, with an AICc selection criterion and 9999 permutations of the raw data to obtain *p* values for each individual predictor variable (Anderson et al. 2008). AICc values indicate the goodness of a model fit to the data and the model with the lowest AICc value was considered the most parsimonious (Symonds and Moussalli 2011).

Results

A total of 6524 predators of 47 species and ten families were recorded from the 200 transects that surveyed 50,000 m^2 of reef (Fig. 2a) and the 10,800 min of examined footage from 180 BRUVs (90 in each area) (Fig. 2b). Species accumulation plots showed similar patterns and indicated that the sampling effort of each method was sufficient to record most of the predators occurring in the area surveyed (Fig. 3). However, both methods showed higher predator species richness in the inner atoll compared to the outer atoll, and this difference was greatest for the BRUVs.

Spatial variation in predator populations

Similar numbers of species were recorded in each atoll area (Table 1), although five species were only recorded in the inner atoll (*Carcharhinus falciformis*, *Elagatis bipinnulata*, *Epinephelus ongus*, *Lethrinus harak* and *Lethrinus microdon*),

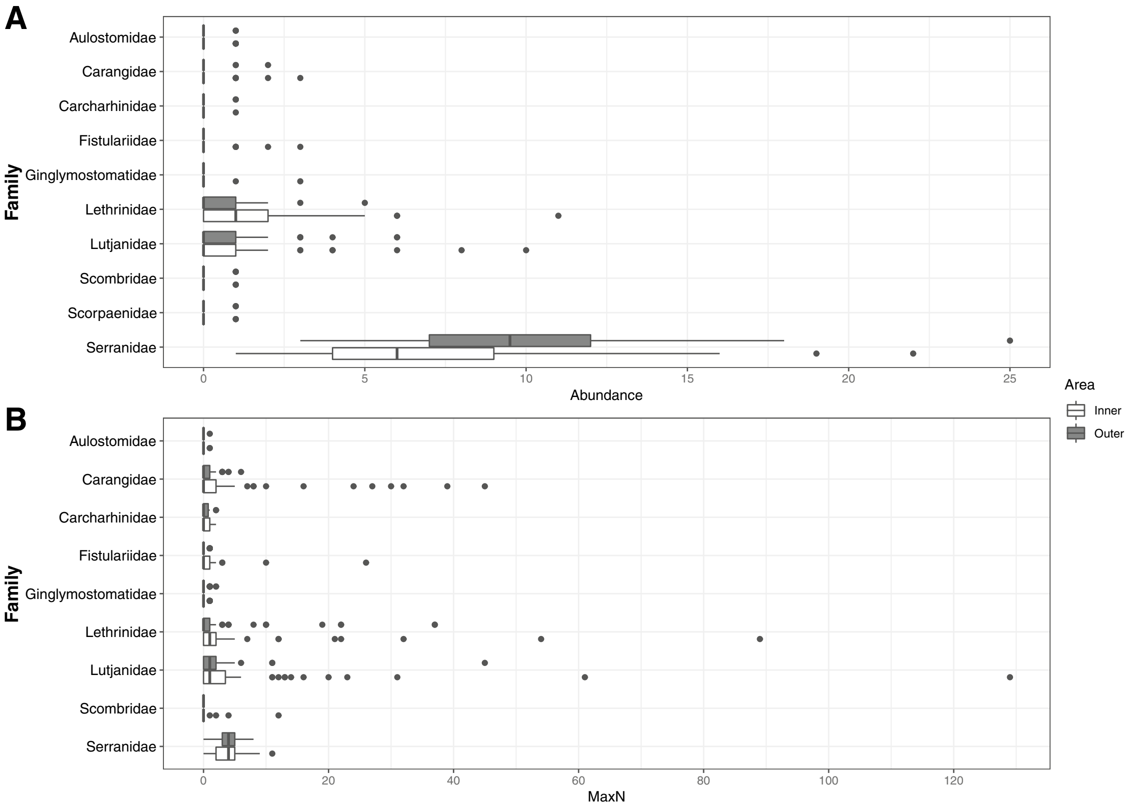

Fig. 2 **a** Abundance from underwater visual census (UVC) and **b** MaxN from baited remote underwater video (BRUV) of predator families in inner and outer atoll. Individual points are **a** 250 m^2 transects and **b** BRUV deployments

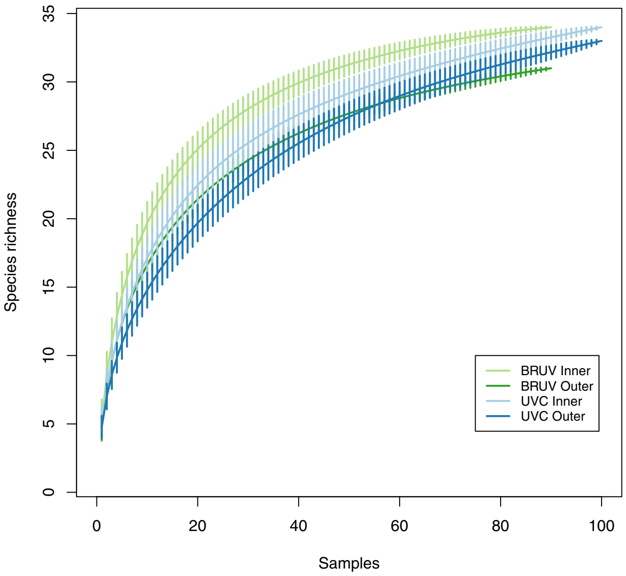

Fig. 3 Species accumulation curves derived from the cumulative number of underwater visual census (UVC) transects and baited remote underwater video (BRUV) deployments in both inner and outer atoll. Bars represent 95% confidence intervals derived from standard deviation

while seven species were only recorded in the outer atoll (*Carcharhinus amblyrhynchos*, *Epinephelus malabaricus*, *Epinephelus tauvina*, *Lutjanus decussatus*, *Lutjanus fulvus*, *Macolor macularis* and *Negaprion acutidens*; Table S1).

Total recorded predator biomass was 0.29 t ha^{-1} in the inner atoll and 0.25 t ha^{-1} in the outer atoll. The biomass of Carcharhinidae, Lethrinidae, Lutjanidae and Serranidae was greater in the outer atoll, while biomasses of Aulostomidae, Carangidae and Scombridae were greater in the inner atoll (Fig. 4). There was no significant difference in total predator biomass between areas (ANOVA, $p < 0.05$), but there was a highly significant difference in biomass among sites within areas (ANOVA, F (1,39) = 2.08, $p \leq 0.001$). When *Nebrius ferrugineus* was removed from biomass calculations, total predator biomass was significantly greater in the outer atoll (ANOVA, F (1) = 4.51, $p \leq 0.05$) and there were still significant differences among sites within each area (ANOVA, F (1,39) = 1.82, $p \leq 0.05$).

The size of Aulostomidae (ANOVA, $p > 0.05$), Carcharinidae (ANOVA, $p > 0.05$) and Scorpaenidae (Kruskal–Wallis, $p > 0.05$) did not differ between atoll areas, but Carangidae were larger in the outer atoll (mean inner: 28.56 cm; outer: 39.75 cm; ANOVA, F (1,11) = 12.68, $p \leq 0.001$). Linear mixed effects models suggested no difference in mean size of Scombridae between atoll areas (mean inner: 49.67 cm; outer: 49.00 cm), but Lethrinidae (mean inner 21.79 cm; outer: 24.74 cm), Lutjanidae (mean inner: 23.04 cm; outer: 30.46 cm), and Serranidae (mean inner: 18.81 cm; outer: 18.99 cm) were all significantly larger in the outer atoll (Table 2; Fig. 5).

The nMDS plot of the UVC predator data revealed relatively distinct inner and outer atoll predator assemblages, while that of the BRUV data suggested greater

Table 1 Summary of recorded predator data

	Inner			Outer		
	UVC	BRUV	Both	UVC	BRUV	Both
Individuals (mean ± sd)	9.56 ± 6.01	16.97 ± 24.72	13.07 ± 17.90	10.81 ± 4.04	9.69 ± 10.42	10.28 ± 7.75
Species	33	34	39	33	31	41
Species unique to method	5	6		10	8	
Families	10	8	10	8	8	10

Summary of collected reef predator data in inner and outer atoll areas by underwater visual census (UVC) and baited remote underwater video (BRUV)

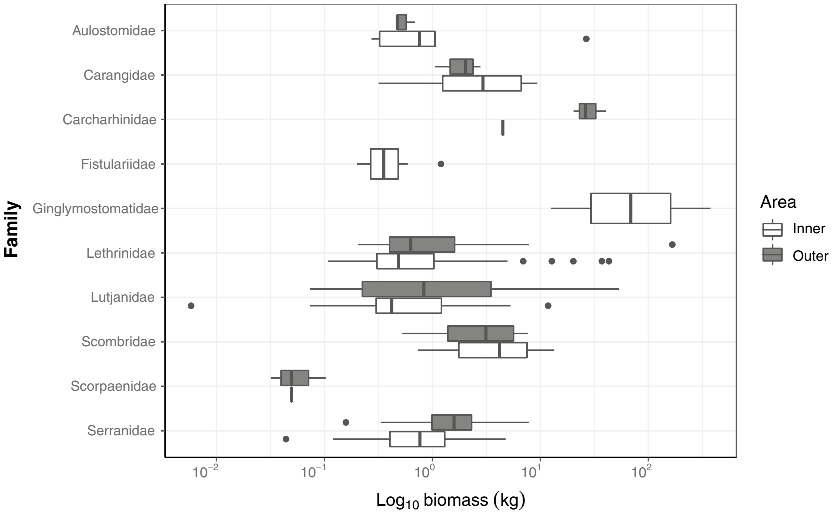

Fig. 4 Biomass (kg) of predator families recorded by underwater visual census (UVC). Values are on a $\log_{10}$ scale

Table 2 Linear mixed effects model of differences in predator body sizes between areas

Formula: size − area + (1 | species)			*df*	*t*	*p* value	
	Estimate	SE				
Lethrinidae						
Intercept	21.87	1.32	1.51	16.56	0.01	*
Area	2.96	0.78	174.66	3.79	0.00	***
Lutjanidae						
Intercept	25.69	2.61	4.43	9.83	0.00	***
Area	6.39	1.59	129.76	4.01	0.00	***
Scombridae						
Intercept	45.76	12.48	1.08	3.67	0.16	
Area	-2.62	4.51	4.00	-0.58	0.59	
Serranidae						
Intercept	20.28	1.72	11.98	11.77	0.00	***
Area	2.30	0.28	1631.84	8.13	0.00	***

Separate models were run on each individual family with body size as the response variable, area as a fixed factor and species as a random factor

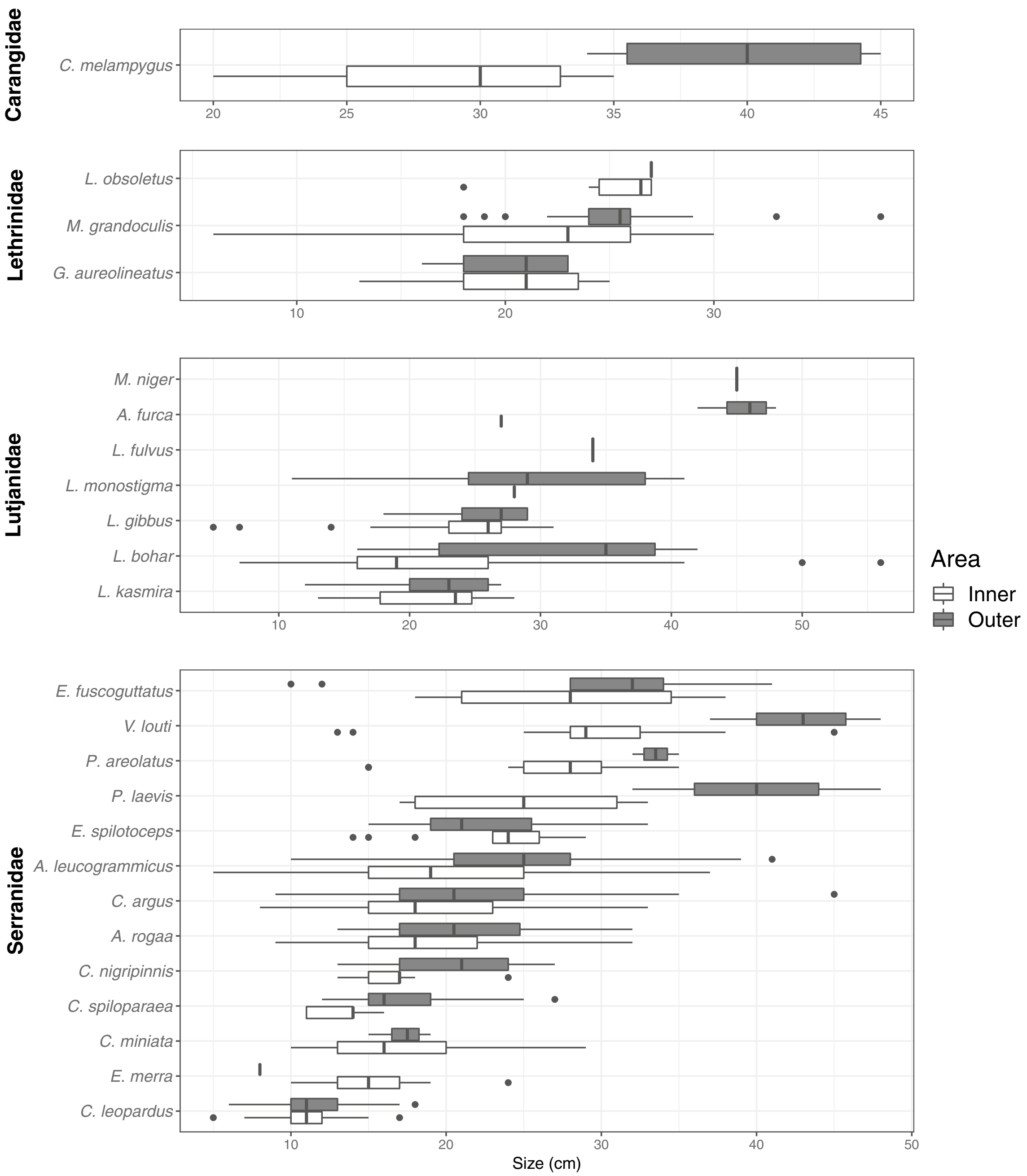

Fig. 5 Total length (cm) of predators belonging to four families where there were significant differences between inner and outer atoll, as indicated by ANOVA and linear mixed effects models. Vertical bars represent the median

overlap between areas (Fig. 6). There were highly significant differences in the predator assemblage between atoll areas (Nested PERMANOVA, UVC = $F(1) = 17.57$, $p \leq 0.001$; BRUV = $F(1) = 4.07$, $p \leq 0.001$) and among sites (Nested PERMANOVA, UVC = $F(38) = 2.21$, $p \leq 0.001$; BRUV = $F(37) = 1.40$, $p \leq 0.001$). SIMPER analysis revealed a high level of dissimilarity in biota between atoll areas (SIMPER UVC = 63.94%, driven by *Cephalopholis leopardus*, *C. argus*, and *Anyperodon leucogrammicus*; BRUV = 74.11%, driven by *Caranx melampygus* and *C. argus*; Table 3). Within areas, similarity of predator assemblages recorded using UVC was moderate (SIMPER, inner: 41.10%, driven by *C. argus*, *A. leucogrammicus*, and *Monotaxis grandoculis*; outer: 49.12%, driven by *C. argus* and *C. leopardus*), while similarity of those recorded using BRUV was low (SIMPER, inner: 29.07%, driven by *Aethaloperca rogaa*, *Lutjanus bohar*, and *C. argus*; outer: 33.37%, driven by *C. argus*, *A. rogaa*, and *L. bohar*; Table 3).

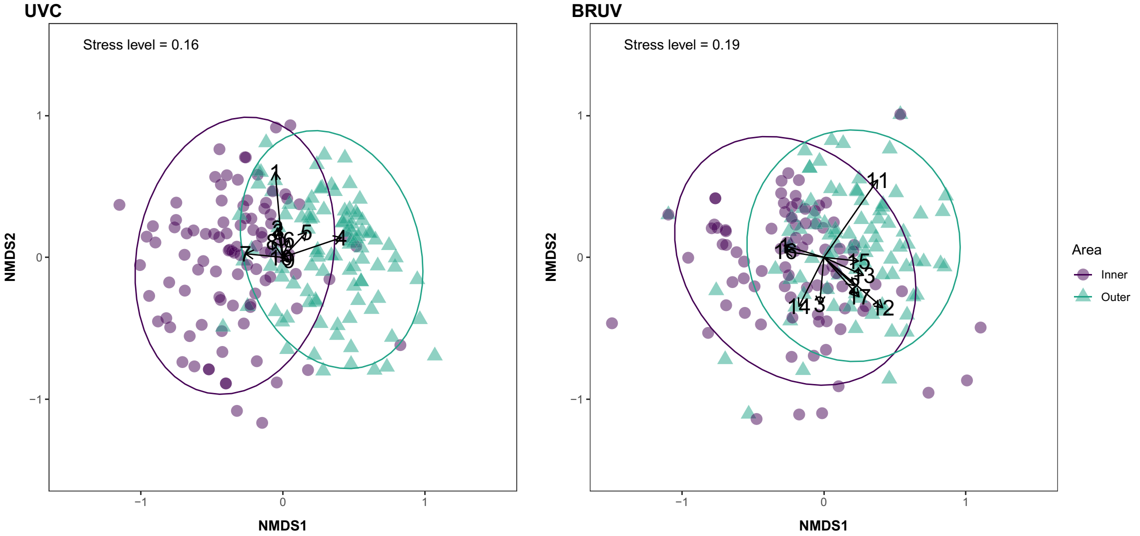

Fig. 6 Non-metric multidimensional scaling (nMDS) of predator abundance data from **a** underwater visual census (UVC) and **b** baited remote underwater video (BRUV). Species that are significantly correlated ($p<0.05$) are overlaid as vectors. UVC (1–10) and BRUV (1–3, 11–17): 1: *Aethaloperca rogaa*; 2: *Aprion virescens*; 3: *Caranx melampygus*; 4: *Cephalopholis spiloparaea*; 5: *Epinephelus fasciatus*; 6: *Epinephelus malabaricus*; 7: *Epinephelus merra*; 8: *Gnathodentex aureolineatus;* 9: *Macolor niger;* 10: *Pterois antennata*; 11: *Cephalopholis argus*; 12: *Cephalopholis leopardus*; 13: *Cephalopholis nigripinnis*; 14: *Cephalopholis* spp.; 15: *Epinephelus spilotoceps*; 16: *Lutjanus bohar*; 17: *Nebrius ferrugineus*

Table 3 Main species contributing to between area and within area dissimilarity using both UVC and BRUV abundance data. Species contributing below 9% are not shown

Species	Dissimilarity between	Similarity within	
	Areas (%)	Inner (%)	Outer (%)
UVC			
Cephalopholis leopardus	13.73	–	30.41
Cephalopholis argus	11.22	34.62	40.56
Anyperodon leucogrammicus	10.04	18.44	–
Aethaloperca rogaa	9.97	15.39	12.39
Monotaxis grandoculis	9.17	19.35	–
BRUV			
Caranx melampygus	9.95	–	–
Cephalopholis argus	9.08	12.07	32.23
Aethaloperca rogaa	–	30.63	17.64
Lutjanus bohar	–	20.86	14.67
Monotaxis grandoculis	–	10.30	–
Cephalopholis nigripinnis	–	–	12.31

Correlation with environmental variables

Environmental data varied significantly between areas (Nested PERMANOVA, UVC = $F(1)=11.95$, $p<0.001$; BRUV = $F(1)=15.99$, $p<0.001$) and among sites (Nested PERMANOVA, UVC = $F(38)=5.89$, $p<0.001$; BRUV = $F(37)=1.58$, $p<0.05$). The first two axes of a PCO explained 82.88% of the total variation in the BRUV environmental data and showed areas to be relatively distinct (Fig. S3). There was similar separation between atoll areas in the UVC environmental data, but the first two axes of the PCO only explained 43.1% of the total variation in the data and the points were more clustered (Fig. S3).

The predator assemblage was correlated with the environmental data collected using UVC (RELATE, $Rho=0.115$, $p<0.05$) and BRUV (RELATE, $Rho=0.157$, $p<0.05$). With the UVC data, marginal tests showed that depth (Pseudo-$F=25.73$, $p<0.001$, Prop. variation = 0.12), BC (Pseudo-$F=7.10$, $p<0.001$, Prop. variation = 0.3), MC (Pseudo-$F=8.12$, $p<0.001$, Prop. variation = 0.04), TC (Pseudo-$F=2.73$, $p<0.05$, Prop. variation = 0.01), complexity (Pseudo-$F=3.57$, $p<0.005$, Prop. variation = 0.02) and PIN (Pseudo-$F = 5.18$, $p < 0.001$, Prop. variation $= 0.03$) had a significant interaction with the predator assemblage. The most parsimonious model included depth, BC, MC and complexity (DISTLM; AICc $= 1479.1$), which when visualised using a dbRDA explained 87.2% of the variation in the fitted data but only 13.6% of the total variation in the data (Fig. 7a). For the BRUV data, marginal tests showed that complexity (Pseudo-$F = 3.18$, $p < 0.005$, Prop. variation $= 0.02$), depth (Pseudo-$F = 3.26$, $p < 0.001$, Prop. variation $= 0.02$) and habitat type (Pseudo-$F = 2.31$, $p < 0.05$ Prop. variation $= 0.01$) had a highly significant correlation with the predator assemblage, but the final best model included only depth and complexity (DISTLM; AICc $= 1377.8$). Results visualised using a dbRDA explained 100% of the variation in the fitted data but only 3.7% of the total variation in the data (Fig. 7b).

Discussion

There were several distinct differences between the inner lagoonal and outer edge reef habitats. In contrast to previous studies, density and diversity of predators were similar between the inner lagoonal and outer forereef slopes (Friedlander et al. 2010; Dale et al. 2011), but there were significant differences in species composition. Furthermore, when the rarely recorded *Nebrius ferrugineus* was omitted, biomass was significantly greater along the outer reef slopes. Lethrinidae, Lutjanidae, and Serranidae, were also significantly larger in the outer atoll, so despite being more numerically abundant in the inner atoll, their mean biomass was greater along the outer reef slopes. Schooling species belonging to these families (e.g. *Gnathodentex aureolineatus* and *Lutjanus kasmira*) were more frequently recorded in the outer atoll (Table S1) and several large bodied species of Lutjanidae and Serranidae were also uniquely recorded in the outer atoll (e.g. *Epinephelus malabaricus, Lutjanus decussatus, Lutjanus fulvus*, and *Macolor macularis*).

These findings are consistent with shifts in habitat usage related to ontogeny. Although teleost reef predators often have relatively small home ranges (Nash et al. 2015), some species of Lutjanidae, Lethrinidae and Serranidae may move tens to hundreds of kilometres between habitat types as they undergo ontogenetic shifts, moving from juvenile nurseries such as mangroves and seagrasses to their adult habitat on coral reefs (Williams 1991; Green et al. 2015). The presence of juvenile nursery habitats close to coral reefs increases adult biomass (Mumby et al. 2004; Nagelkerken 2007), while a lack of nursery habitats has been linked to lower adult densities and the absence of some species (Olds et al. 2012; Wen et al. 2013). The significant differences in predator sizes and abundances between inner and outer atoll found here are consistent with ontogenetic habitat shifts, and indicate that the inner atoll lagoon may be an important nursery habitat for many of these predator species. In the British Virgin Islands, nearly half the reef fishes exhibited ontogenetic shifts between lagoons and forereefs and almost all species were significantly larger in the reef habitat than in the lagoon (Gratwicke et al. 2006). Furthermore, even isolated nursery habitats are utilized by juvenile emperors, suggesting that ontogenetic migrations of these species act to connect adult and juvenile habitats (Nakamura et al. 2009). In North Malé Atoll, the proximity of the edge and lagoonal reefs to each other, in addition to the relatively shallow nature of the lagoon, may facilitate a high degree of mobility and connectivity between inner and outer atoll (Berkström et al. 2013).

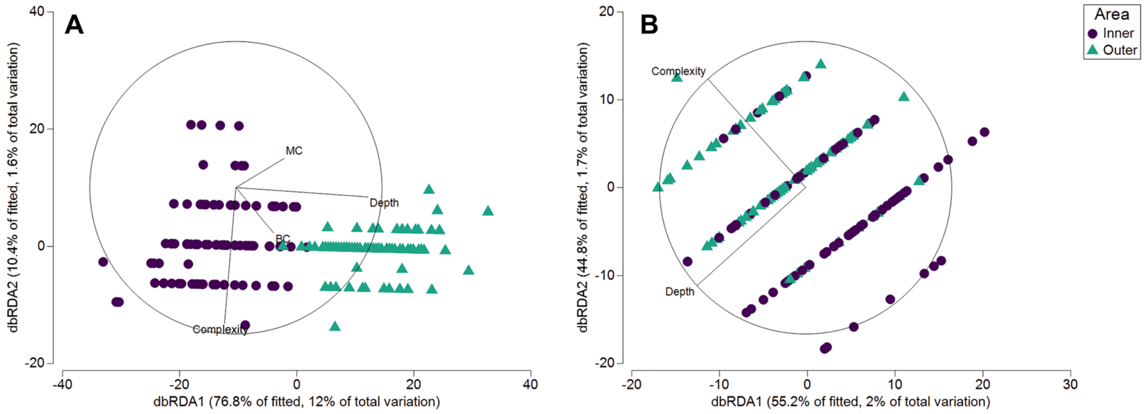

Fig. 7 Distance-based redundancy analysis (dbRDA) of Bray–Curtis dissimilarities calculated from square root transformed abundance of reef predator species vs. environmental predictor variables. The most parsimonious model was chosen using the AICc selection criterion and included **a** complexity, depth, branching coral (BC), and massive coral (MC) for the underwater visual census (UVC) predator data, and **b** depth and complexity for the baited remote underwater video (BRUV) predator data

Differences in the reef habitat between atoll areas may also play a role. The outer reef slopes provide a larger, more continuous reef area compared to the shallow inner reefs, where soft bottom habitat is extensive. Large piscivorous fish are more abundant in areas of higher live coral cover with greater habitat structural complexity (Connell and Kingsford 1998), and growth rates and abundances of predatory fishes tend to be higher when prey densities are greater (Beukers-Stewart et al. 2011). Higher prey availability is also a key driver of ontogenetic emigrations of snappers and emperors from nearshore to coral reef habitats (Kimirei et al. 2013). The larger body sizes and school sizes in the outer atoll, in addition to the unique occurrence of several of these species, suggest that this habitat may be of a higher quality, providing sufficient food and space to fit the requirements of these predator species. However, only a detailed assessment of the available habitat and prey assemblages will help determine the factors influencing predator distributions.

Several families had a greater biomass in the inner atoll, including Aulostomidae, Carangidae, Fistulariidae and Ginglymostomatidae. Aulostomidae were rarely recorded along the outer reef slopes, although their habitat preferences include reefs extending to the continental slope (Bowen et al. 2001). Competition from the greater numbers of Lutjanidae and Serranidae may play a role in limiting their numbers in the outer atoll. Higher numbers of the bluefin trevally, *Caranx melampygus*, were the main contribution to the greater biomass of Carangidae. *C. melampygus* is an important mobile predator that is prominent in nearshore waters (Hobson 1979; Sancho 2000). Their diet consists of diurnally active prey, predominantly from shallow-water habitats (Sudekum et al. 1991), which suggests they may enter the lagoon during the day to hunt. The lagoon may also represent an important nursery ground for this species, as juvenile *C. melampygus* occupy shallow-water protected environments, such as lagoons and estuaries (Smith and Parrish 2002). As no UVC surveys or BRUV deployments were conducted at night, it is not certain whether their numbers would increase along the outer reef slopes after dark. Fistulariidae and Ginglymostomatidae had a greater biomass in the inner atoll, but only because biomass estimates were derived solely from UVC. Fistulariidae prefer coastal areas with soft bottoms (Fritzsche 1976) and were recorded in both atoll areas with BRUVs, but the UVC surveys were conducted solely on hard reef substrate. Ginglymostomatidae were frequently recorded in both inner and outer atoll on BRUVs, but biomass estimates came from the occurrence of several large *N. ferrugineus* on two transects in the inner atoll, while none were recorded during UVC in the outer atoll. Future work would benefit from the inclusion of biomass estimates from several survey methods and from conducting surveys at night.

Several species were recorded solely in one atoll area. Two of the species unique to the outer atoll were the grey reef shark, *Carcharhinus amblyrhynchos*, and the lemon shark, *Negaprion acutidens*. Grey reef sharks prefer forereef habitats over lagoons (Papastamatiou et al. 2018) and although juvenile lemon sharks are atoll lagoon residents (Filmalter et al. 2013), adults move to deeper coastal reef habitats (Compagno 1984). Conversely, the silky shark, *Carcharhinus falciformis*, and the rainbow runner, *Elagatis bipinnulata*, were recorded exclusively in the inner atoll by the BRUVs; these are not typically reef-associated species (Bonfil 1993) but the BRUVs were effective in recording their use of the channels between the shallow inner reefs. Channels act as important habitat corridors, enhancing connectivity between the inner lagoonal and outer reef slopes, with energy moving from one area to another through a range of hydrodynamic processes (Sasamal 2007; Rogers et al. 2017; Green et al. 2019). These corridors also facilitate movement of mobile marine species, with marine predators taking advantage of them for foraging (Hastie et al. 2016). The thumbprint, *Lethrinus harak,* and smalltooth, *L. microdon*, emperors were also only observed in the inner atoll on BRUVs. Emperors forage extensively over sandy bottoms where they predate on less mobile prey (Kulbicki et al. 2005). While the BRUVs were deployed over a range of hard and soft bottom substrates, the UVC surveys were conducted solely on hard bottom reef substrate. In addition, BRUVs will attract these species to the bait, while UVC typically requires high replication to record such species (Dulvy et al. 2003). These discrepancies between the survey methods may explain the absence of the emperors from the UVC dataset. Moreover, these species are not necessarily exclusive to one area. The 1-h BRUV soak time and lack of long-term and night time sampling are likely to lead to underrepresentation or absence of rarer species (Asher et al. 2017).

The asymptotes of the species accumulation plots suggested that the BRUV and UVC surveys were sufficient to obtain an accurate measure of species richness and, although actual values varied, predator family abundance patterns were similar for both methods between areas. However, several species uniquely recorded with either UVC or BRUV underline the importance of using more than one survey methodology when assessing fish populations. For example, sharks were almost exclusively recorded with BRUVs. BRUVs are more effective at recording carnivores (Langlois et al. 2010) and heavily exploited species that are wary of divers (Lindfield et al. 2014). The teleost predators identified through the BRUV footage have small home ranges (Nash et al. 2015) and will not travel far in response to a bait plume, but sharks, being more mobile, may follow bait plumes to investigate the origin of the scent. This is one of the biases of this methodology (Willis and Babcock 2000; Cappo et al.

2003; Harvey et al. 2012), but it is also why BRUVs are effective in tandem with UVC, which underrepresents more mobile, transient species (MacNeil et al. 2008). In contrast, the species recorded solely during UVC, such as the strawberry grouper, *Cephalopholis spiloparaea*, the honeycomb grouper, *Epinephelus merra* and the spotfin lionfish, *Pterois antennata*, are more cryptic and wary. These species may be near the BRUV but their cryptic nature, the habitat complexity and the angle of the camera mean they may be missed.

Our analysis found a clear interaction of the predator assemblage data with live branching and massive coral cover, which accords with previous studies (Bell and Galzin 1984; Komyakova et al. 2013). Depth and complexity were important variables for models of both the UVC and the BRUV assemblage data. Structural complexity on reefs provides important habitat structure and refuge for prey assemblages and is linked to increased fish biomass and abundance (Rogers et al. 2014). While structural complexity is also important for predator assemblages, reefs of intermediate complexity are most suitable for their productivity, as the increased refuge space on higher complexity reefs allows more prey to hide, thereby reducing available food (Rogers et al. 2018). The relationship between predator assemblage data and structural complexity is complicated, but its inclusion in both models reinforces its importance in structuring predator assemblages (Ferrari et al. 2017). Depth was the second predictor included in both models. Reef fish communities vary dramatically with depth (Friedlander et al. 2010; Schultz et al. 2014; Jankowski et al. 2015), as predator abundances and species compositions change (Asher et al. 2017; Tuya et al. 2017). Its inclusion in both models is further evidence that it also plays a key role in structuring predator assemblages.

Total biomass of all recorded predators (inner atoll 0.29 t ha^{-1}, outer atoll 0.25 t ha^{-1}) was similar to that found at other remote but inhabited and exploited atolls (Kiritimati ~ 0.2 t ha^{-1}, Tabuaeran ~ 0.3 t ha^{-1} (Sandin et al. 2008)), and it was considerably lower than at unfished, uninhabited atolls and islands (Palmyra ~ 1.8 t ha^{-1}, Kingman ~ 5.2 t ha^{-1} (Sandin et al. 2008); Chagos Archipelago ~ 3–7.75 t ha^{-1} (Graham et al. 2013)). Although the Maldives are considered underexploited (Newton et al. 2007), this indicates that these predator species are likely overfished. Reef fisheries provide an important source of food to both tourists and increasingly locals, and the rise in reef fish catch is evidence of a growing demand for these resources (Sattar et al. 2014). Reef predators typically dominate the reef fish catch with fishermen targeting Carangidae, Lutjanidae and Serranidae using handlines (Sattar et al. 2011, 2012, 2014). Although more recent information on the status of the reef fishery is lacking, significant declines in the mean length of the ten most exploited grouper species (Sattar et al. 2011) and of key target species *Lutjanus bohar* and *L. gibbus* (Sattar et al. 2014) suggest the fishery is already overexploited.

In addition to the outer reef slopes, reef fisherman in Baa Atoll, North and South Ari Atoll, and Vaavu Atoll target patch reef edges and small isolated submerged reefs (locally known as *thila*) in the lagoon, but there is little information available on which habitats fishers target in North Malé Atoll (Sattar et al. 2012). Furthermore, although resort islands within atoll lagoons often prohibit fishing on their house reefs (Domroes 2001; Moritz et al. 2017), they organise regular recreational fishing trips to reefs nearby. Catches from these recreational trips are also dominated by upper level reef predators (e.g. *C. melampygus*, *Cephalopholis miniata*, *L. bohar*, *L. gibbus*, *Lethrinus olivaceus*), with an estimated 68,000 individuals caught on an annual basis, often of a small size (Sattar et al. 2014). Currently, recording of resort landings data is voluntary (Sattar et al. 2014), so the full impact of these trips has not been accurately quantified, despite the fact that they occur at a national scale. Given the consistent removal of reef predators through both commercial and recreational fishing, it is likely that lagoonal reefs are being substantially exploited yet their predator populations are largely unstudied. While predators were recorded throughout the sites surveyed, the relatively low total biomass recorded here is indicative of an exploited system (Friedlander et al. 2010). Recovery of exploited systems to intact (or nearly intact) conditions and a high biomass of apex predators is estimated to take decades and involve large area closures (Myers and Worm 2003; Robbins et al. 2006). While this may be unrealistic to achieve, careful management of the reef fish populations in the Maldives is required to prevent irreversible loss of these key predatory species.

Globally reef predator populations are declining and species richness is being lost due to climate change and a range of direct anthropogenic stressors (Friedlander and DeMartini 2002; Hempson et al. 2017; Hughes et al. 2017). To date, little information exists on reef predator assemblages and their distributions in the Maldives. Evidently, lagoonal reefs are important habitats hosting diverse and abundant reef predator populations which may have been previously undervalued. Predator assemblages are important in terms of biodiversity and available resources, so there is an urgent need to manage them carefully in the face of climate change, rapidly increasing tourism, and fisheries expansion to prevent future declines in their populations.

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Author contributions CS, ACM, SPN and NVCP conceived the ideas and designed the methodology. CS and SNA collected the data and CS processed and analysed the data. CS wrote the first draft of the manuscript and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability The datasets collected and analysed during the current study are available in the Marine Data Archive repository, https://doi.org/10.14284/388.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All work was conducted under research permit no: (OTHR)30-D/INDIV/2016/515 granted by the Republic of the Maldives Ministry of Fisheries and Agriculture. Newcastle University Animal Welfare and Ethical Review Body approved the project (Project ID: 526). CS was supported by a Newcastle University Faculty of Science, Agriculture and Engineering Doctoral Training Award studentship and a cooperative agreement with Banyan Tree.

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ORIGINAL RESEARCH

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Novel tri-isotope ellipsoid approach reveals dietary variation in sympatric predators

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Abstract

Sympatric species may partition resources to reduce competition and facilitate coexistence. While spatial variation and specialization in feeding strategies may be prevalent among large marine predators, studies have focussed on sharks, birds, and marine mammals. We consider for the first time the isotopic niche partitioning of co-occurring, teleost reef predators spanning multiple families. Using a novel tri-isotope ellipsoid approach, we investigate the feeding strategies of seven of these species across an atoll seascape in the Maldives. We demonstrate substantial spatial variation in resource use of all predator populations. Furthermore, within each area, there was evidence of intraspecific variation in feeding behaviors that could not wholly be attributed to individual body size. Assessing species at the population level will mask these intraspecific differences in resource use. Knowledge of resource use is important for predicting how species will respond to environmental change and spatial variation should be considered when investigating trophic diversity.

KEYWORDS
coral reef, foraging, individual specialization, stable isotopes

1 | INTRODUCTION

Trophic interactions are key regulators of community dynamics and ecosystem function. Food web and population dynamics are driven by resource availability, with sympatric species often in direct competition with each other (Schoener, 1983). Resource partitioning often occurs among co-occurring species to reduce inter- and intraspecific competition when resources are limited (Schoener, 1974). Often linked to body size or ontogeny (Werner & Gilliam, 1984), increasing evidence suggests that individuals may vary in their resource usage compared with conspecifics of the same age and size (Araújo, Bolnick, & Layman, 2011). As trophic energy dissipates up food webs, food resource scarcity is likely to be an important driver of foraging behavior in large predators. Consumers may alter their foraging to include underutilized resources when competition is high, leading to dietary specializations within populations (Bolnick et al., 2003).

Predators (here referring to upper trophic level sharks and teleosts) are thought to play an important role in structuring communities. Through their foraging, they may alter prey behavior (Lima & Dill, 1990) and, being more mobile, may couple distinct food chains (McCauley et al., 2012), altering energy flows and stabilizing food webs (McCann, Rasmussen, & Umbanhowar, 2005; Rooney, McCann, Gellner, & Moore, 2006). Feeding specializations have been extensively documented in upper trophic level vertebrate populations, particularly fishes (Araújo et al., 2011; Bolnick et al., 2003). While marine predators are often considered to be dietary generalists (Costa, 1993; Gallagher, Shiffman, Byrnes, Hammerschlag-Peyer,

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& Hammerschlag, 2017), they may vary significantly in their trophic ecology at both the individual and species levels. Such specializations can alter community dynamics (Bolnick et al., 2011), so species-level assessments of trophodynamics will not account for differing ecological roles (Matich, Heithaus, & Layman, 2011).

Stable isotope ratios in animal tissues provide unique dietary perspectives and reveal important facets of resource use (Bearhop, Adams, Waldron, Fuller, & Macleod, 2004) as they reflect assimilation of prey material into consumer bodies over time (Post, 2002). Carbon (δ^{13}C) and sulfur (δ^{34}S) isotope data help elucidate the production sources responsible for the energy flow in the food web, while nitrogen (δ^{15}N) suggests the relative trophic position at which an animal is feeding (Connolly, Guest, Melville, & Oakes, 2004; Croisetière, Hare, Tessier, & Cabana, 2009; Minagawa & Wada, 1984; Pinnegar & Polunin, 1999). Different animal tissues have different turnover rates (Tieszen, Boutton, Tesdahl, & Slade, 1983) with fast turnover tissues (e.g., plasma or liver) representing short-term diet while slow turnover tissues (e.g., muscle) represent long-term diet (Carter, Bauchinger, & McWilliams, 2019). Consequently, muscle tissue can help identify consistent patterns in predator resource use (Carter et al., 2019; Vander Zanden, Clayton, Moody, Solomon, & Weidel, 2015).

Studies of vertebrate marine predator trophic niches and dietary specializations have focussed on elasmobranchs (Gallagher et al., 2017; Matich et al., 2011; Shiffman, Kaufman, Heithaus, & Hammerschlag, 2019; Shipley et al., 2018) and birds (Bodey et al., 2018; Patrick et al., 2014), with most studies focussing on only a few co-occurring species. There is a lack of isotopic information on resource partitioning among co-occurring teleost predators (Matley, Tobin, Simpfendorfer, Fisk, & Heupel, 2017), particularly in the tropics (Cameron et al., 2019). This is despite the fact that coral reefs often support a high biomass and diversity of sympatric teleost predators (Friedlander, Sandin, DeMartini, & Sala, 2010; Stevenson et al., 2007), a factor thought to increase the occurrence of dietary specialization (Araújo et al., 2011). Coral reefs, along with their predator populations, are currently experiencing unprecedented worldwide declines due to a range of anthropogenic and climate-related stressors (Friedlander & DeMartini, 2002; Hughes et al., 2017). Given their potential stabilizing roles in food web dynamics, knowledge of sympatric reef predator trophodynamics and resource partitioning is important for predicting how reef communities will respond to change (Matich et al., 2011).

To our knowledge, no study to date has considered the isotopic niche partitioning of teleost coral reef predators across multiple, co-occurring families. Greater understanding of spatial and intraspecific variation in predator feeding patterns is essential to predict how species will respond to fluctuations in resource availability as environments change (Matley et al., 2017; Shiffman et al., 2019). Here, we use a tri-isotope ellipsoid approach to examine the isotopic niches of seven key teleost coral reef predator species to determine whether predator resource use varies 1) spatially and/or 2) intraspecifically, and 3) whether their isotopic niches overlap.

2 | MATERIALS AND METHODS

2.1 | Study site and sample collection

Fieldwork was conducted in North Malé atoll, Republic of the Maldives (N 04°26.154′, E 73°29.902′) from January to April 2017. Sampling occurred at sites across two distinct reef areas, the inner lagoonal reefs (hereafter "inner atoll") and atoll-rim outer reef slopes (hereafter "outer atoll") atoll (Figure S1).

In each area, seven reef predator species belonging to three families were sampled opportunistically: groupers (Serranidae: *Aethaloperca rogaa*, redmouth; *Anyperodon leucogrammicus*, slender; *Cephalopholis argus*, peacock; *Cephalopholis miniata*, coral hind), snappers (Lutjanidae: *Lutjanus bohar*, red; *Lutjanus gibbus*, humpback), and jack (*Caranx melampygus*, bluefin trevally). Predators (trophic level ≥ 3.5) were chosen for sampling based on their status as key fishery target species (Sattar, Wood, Islam, & Najeeb, 2014) and being dominant components of the predator assemblage biomass in both inner and outer atoll areas (first author, unpublished data). Predators were caught using rod and reel, handlines and pole spears. For each individual, the total length (cm) was recorded, and then, a sample of dorsal white muscle tissue (1–2 g wet mass) was removed. Sampling was conducted nonlethally where possible using a 4 mm biopsy punch. All tissue sampling was carried out in compliance with UK Home Office Scientific Procedures (Animals) Act Requirements and approved by the Newcastle University Animal Welfare and Ethical Review Body (Project ID No: 526). Only adults were sampled to limit possible ontogenetic dietary shifts.

Tissue samples were oven-dried at 50°C for 24 hr, redried using a freeze drier, and then ground to a fine homogenous powder using a pestle and mortar. Subsamples of 2.5 mg of tissue were weighed into 3 × 5 mm tin capsules and sequentially analyzed for δ^{15}N, δ^{13}C, and δ^{34}S using a PyroCube elemental analyser (Elementar, Hanau, Germany) interfaced with an Elementar VisION isotope ratio mass spectrometer at the East Kilbride (UK) node of the Natural Environment Research Council Life Sciences Mass Spectrometry Facility in August 2017. Stable isotope ratios are reported using the delta (δ) notation which for δ^{13}C, δ^{15}N, or δ^{34}S is: $[(R_{\text{sample}}/R_{\text{standard}}) - 1]$, where R is the ratio of the heavy to light isotope (e.g., $^{13}C/^{12}C$), and measured values are expressed in per mil (‰).

International reference materials were placed at the start and end of each N/C/S run (~140–150 samples) to correct for accuracy and drift. Materials used were USGS40 (glutamic acid) for δ^{13}C and δ^{15}N (analytical precision (*SD*) $\delta^{13}C = 0.07$; $\delta^{15}N = 0.16$) and silver sulfide standards IAEA-S1, S2, and S3 for δ^{34}S (analytical precision (*SD*) = 0.17, 0.59, and 1.46, respectively). Internal reference materials were placed every 10 samples. Materials used were MSAG2 (a solution of methanesulfonamide and gelatin), M2 (a solution of methionine, gelatin, glycine), and ^{15}N-enriched alanine and SAAG2 (a solution of sulfanilamide, gelatin, and ^{13}C-enriched alanine) (Table S1). A randomly spaced study-specific reference was also used (one mature individual [TL = 41.4 cm] of *A. leucogrammicus*, analytical precision (*SD*) $\delta^{13}C = 0.14$, $\delta^{15}N = 0.27$, and $\delta^{34}S = 0.73$, respectively, $n = 31$) (Table S1).

High lipid content in fish muscle tissue can skew carbon isotope data interpretations as lipids are depleted in ^{13}C relative to proteins (Focken & Becker, 1998). Carbon stable isotope data were lipid corrected arithmetically when the C:N ratio of the muscle tissue was > 3.7 using the mass balance equation from Sweeting, Polunin, and Jennings (2006):

$$\delta^{13}C_{\text{protein}} = \frac{(\delta^{13}C_{\text{sample}} \times C{:}N_{\text{sample}}) + (7 \times (C{:}N_{\text{sample}} - C{:}N_{\text{protein}}))}{C{:}N_{\text{sample}}} \quad (1)$$

Here, C:N protein was 3.7 determined by Fry et al. (2003) from shrimp muscle protein C:N.

2.2 | Ellipsoid metrics

The "SIBER" package in *R* (Jackson, Inger, Parnell, & Bearhop, 2011) provides methods for analyzing bivariate stable isotope data although such methods are applicable to any bivariate normally distributed data. We extend these methods to the three-dimensional case in order to apply ellipsoids to trivariate data and calculate their overlap.

Ellipsoid volume can be estimated analytically from the sample covariance matrix by decomposition into their respective eigenvalues and eigenvectors. In the three-dimensional case, the square root of the eigenvalues represents the three orthogonal axes, one semimajor and two semiminor (a, b, and c, respectively), that describe the standard ellipsoid, synonymous to the two-dimensional standard ellipse (Jackson et al., 2011). The standard ellipsoid captures approximately 20% of the data (Friendly 2007), which can be subsequently rescaled to capture any desired proportion of data. The volume of the ellipsoid is then taken to be $(4/3)\pi abc$ which we denote SEV. As with SEA, SEV is biased to underestimation of volume when sample sizes are small (Jackson et al., 2011). A small sample size correction for degrees of freedom following Friendly (2007) can be applied to correct for such bias giving SEV_C, equivalent to SEAc (Jackson et al., 2011), and only here, the correction factor is $(n-1)/(n-3)$ as the ellipsoids are in three dimensions.

To quantify uncertainty in SEV estimates, a Bayesian framework was developed by generalizing code in the SIBER package to the *n*-dimensional case (Jackson et al., 2011). Data are assumed to be well described by the multivariate normal distribution and Bayesian posteriors of the mean and covariance structures estimated using JAGS via the R package RJAGS (Plummer, 2018). Ellipsoid volume can subsequently be estimated from each covariance draw to provide a posterior estimate of SEV, which we denote SEV_B. Sensitivity analysis indicates that this Bayesian approach slightly underestimates population SEV at small sample sizes (approximately $n \le 8$, see Figure S2).

To estimate the degree of overlap between two ellipsoids, we used a numerical approach, utilizing the packages "rgl" (Adler et al., 2018) and "geometry" (Habel, Grasman, Gramacy, Mozharovskyi, & Sterratt, 2019). Ellipsoids were approximated by three-dimensional meshes: a series of vertices that lie on the ellipsoid surface forming quadrilateral faces. The intersection of these two meshes is then approximated by a third mesh, the convex hull of which estimates the ellipsoid overlap volume. This method underestimates volumes as convex surfaces are approximated by planar faces; however, this bias is reduced as the number of vertices used to represent the ellipsoids increases, which can be iteratively increased by subdividing faces (see Figure S3). As with estimating SEV_B, we use a Bayesian approach to estimate data covariance structures and calculate overlap for each paired posterior draw to provide a posterior estimate of overlap. Functions for estimating SEV, SEV_C, SEV_B, and overlap posteriors are provided in an R script in the supplementary.

2.3 | Data analysis: application

The ranges in carbon (CR), nitrogen (NR), and sulfur (SR) isotope values for each predator were calculated (Layman, Quattrochi, Peyer, & Allgeier, 2007). Using the MVN R Package (Korkmaz, Goksuluk, & Zararsiz, 2014), multivariate normality was checked using Mardia's test (Mardia, 1970) as it can calculate a corrected version of skewness for small sample sizes (<20). All species in each area conformed to multivariate normality ($p > .05$) with the exception of *L. gibbus* and *L. bohar* in the inner atoll. Both had normal kurtosis ($p > .05$) but were non-normally skewed ($p < .05$). Univariate normality tests showed that $\delta^{34}S$ was normally distributed for both species, $\delta^{15}N$ was only normally distributed for *L. gibbus*, and both had non-normally distributed $\delta^{13}C$. The non-normality was driven by one *L. gibbus* with a more positive $\delta^{13}C$ and two *L. bohar* that had more positive $\delta^{13}C$ and lower $\delta^{15}N$, respectively. As all the other data conformed to multivariate normality and these data points represent individuals with differing resource uses (Jackson et al., 2011), data were considered well described by the multivariate normal distribution for all further analysis.

For each species in each area, Bayesian estimates for the multivariate normal distribution of the data were calculated (15,000 iterations with a burn-in of 10,000 and a thinning factor of 25). Bayesian ellipsoids were fit to 75% of the data (EV_B), and their median volume and interquartile range (25%–75%) were determined. The degree of ellipsoid overlap between species within each area was calculated based on EV_B where Bayesian posteriors were determined from 7,500 iterations with a burn-in of 5,000 and a subdivision value of 4. Overlap was expressed as a median percentage with 95% credible intervals where 100% indicates completely overlapping ellipsoids and 0% indicates entirely distinct ellipsoids. When the overlap between two species was ≥60%, niche overlap was considered significant (Matley et al., 2017). Outer atoll *L. bohar* were excluded as only one fish was caught.

Individual body size may also influence trophic interactions; we tested for this using mixed-effects models with the R package lme4 (Bates, Maechler, Bolker, & Walker, 2015). The $\delta^{13}C$, $\delta^{15}N$, or $\delta^{34}S$ stable isotope values were the response variable, with area (inner/outer)

TABLE 1 Summary information for the predators in inner and outer atoll

Family	Species	Area	*n*	Size (mm)	δ^{13}C (‰)	CR	δ^{15}N (‰)	NR	δ^{34}S (‰)	SR
Carangidae	*Caranx melampygus*	Inner	10	248–410	−16.47 (0.22)	3.50	12.39 (0.17)	0.48	18.12 (0.15)	1.20
		Outer	6	372–461	−15.80 (0.02)	0.93	12.44 (0.20)	1.48	18.25 (0.16)	1.29
Lutjanidae	*Lutjanus bohar*	Inner	12	210–370	−15.36 (0.63)	7.06	12.36 (0.29)	2.94	18.59 (0.18)	0.70
		Outer	1	185	−14.87 (0.00)		12.97 (0.00)		17.94 (0.00)	
	Lutjanus gibbus	Inner	13	244–357	−16.36 (0.15)	2.96	12.58 (0.08)	0.02	19.14 (0.17)	1.51
		Outer	9	287–420	−16.26 (0.60)	7.84	12.99 (0.32)	3.54	18.96 (0.33)	2.84
Serranidae	*Aethaloperca rogaa*	Inner	11	164–278	−16.08 (0.26)	2.72	12.77 (0.07)	0.14	19.49 (0.17)	0.99
		Outer	11	148–336	−17.11 (0.17)	4.02	12.99 (0.16)	0.96	19.79 (0.18)	1.95
	Anyperodon leucogrammicus	Inner	10	238–346	−15.60 (0.19)	1.91	12.94 (0.11)	0.11	19.49 (0.17)	0.79
		Outer	10	262–426	−15.61 (0.04)	3.37	12.81 (0.15)	0.42	19.28 (0.01)	0.17
	Cephalopholis argus	Inner	11	186–342	−15.46 (0.23)	2.81	12.77 (0.08)	0.01	19.32 (0.26)	1.78
		Outer	10	190–345	−16.14 (0.19)	2.42	12.29 (0.08)	0.72	19.58 (0.14)	0.53
	Cephalopholis miniata	Inner	11	160–320	−16.92 (0.10)	2.87	12.73 (0.06)	0.21	19.73 (0.17)	1.47
		Outer	10	161–298	−16.88 (0.22)	4.23	12.64 (0.10)	1.26	19.55 (0.20)	0.52

Note: Mean δ^{13}C, δ^{15}N, and δ^{34}S values are in per mil (‰) with *SE* in brackets.
Abbreviations: CR: δ^{13}C range, NR: δ^{15}N range, SR: δ^{34}S range.

TABLE 2 Bayesian 75% ellipsoid volume (EV_B) estimates for predators sampled in inner and outer atoll, given as median with interquartile range (IQR, 25th and 75th percentile)

	Inner		Outer	
Species	Median	IQR	Median	IQR
Aethaloperca rogaa	6.22	3.95, 6.89	6.45	4.39, 7.22
Anyperodon leucogrammicus	5.53	3.78, 6.30	7.96	5.27, 9.06
Caranx melampygus	4.21	2.85, 4.87	6.78	3.61, 7.51
Cephalopholis argus	8.10	5.13, 8.92	4.32	2.77, 4.69
Cephalopholis miniata	3.22	1.98, 3.45	7.06	4.36, 7.65
Lutjanus bohar	25.62	18.15, 29.14		
Lutjanus gibbus	4.76	3.30, 5.30	20.63	12.58, 22.67

and total length (mm) (and their interaction) as fixed effects and total length (mm) nested within species as a random effect. Model normality and homogeneity assumptions were checked by plotting model residuals. Significant effects were determined using the R package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017) which provides *p*-values for lmer model fits via Satterthwaite's degrees of freedom method. Statistical power to detect size-related effect was determined using the simr R package (Green & MacLeod, 2016). All analyses were carried out in R Statistical Software version 3.5.2 (R Core Team, 2017) and RStudio version 1.1.383 (RStudio Team, 2012).

3 | RESULTS

There were substantial differences in the isotope values among the seven species sampled in both areas (Table 1). δ^{13}C ranged from −18.00 (*A. rogaa*, outer) to −10.11 (*Lutjanus bohar*, inner), δ^{15}N ranged from 10.11 (*L. bohar*, inner) to 14.59 (*L. gibbus*, outer), and δ^{34}S ranged from 17.06 (*C. melampygus*, inner) to 21.02 (*A. rogaa*, outer).

In the inner atoll, the median niche volume of *L. bohar* (25.62) was five times larger than the niches of the other predators. Excluding *L. bohar*, *C. miniata* median niche volume (3.22) was half the size of the niches of the other predators, while that of *C. argus* was double the size (8.10). *C. melampygus* and *L. gibbus* had median niche volumes that were of a similar size (4.21 and 4.76, respectively), and *A. rogaa* and *A. leucogrammicus* had niches of a similar size (6.22 and 5.53, respectively) (Table 2; Figure 1).

In the outer atoll, the median niche volume of *L. gibbus* (20.63) was five times larger than the niches of the other predators. The niche volumes of all the other predators were of similar size (6.45–7.96), except for *C. argus* which had the smallest median niche volume (4.32) (Table 2; Figure 2).

All predators had larger median isotopic niche volumes in the outer atoll than in the inner atoll, except for *C. argus* (inner: 8.10; outer: 4.32) (Table 2; Figures 1 and 2). Median niche volume of *L. gibbus* in the outer atoll (20.63) was four times larger than the niche volume of their inner atoll conspecifics (4.76). *C. miniata* had a median niche volume twice as large in the outer atoll (inner: 3.22; outer:

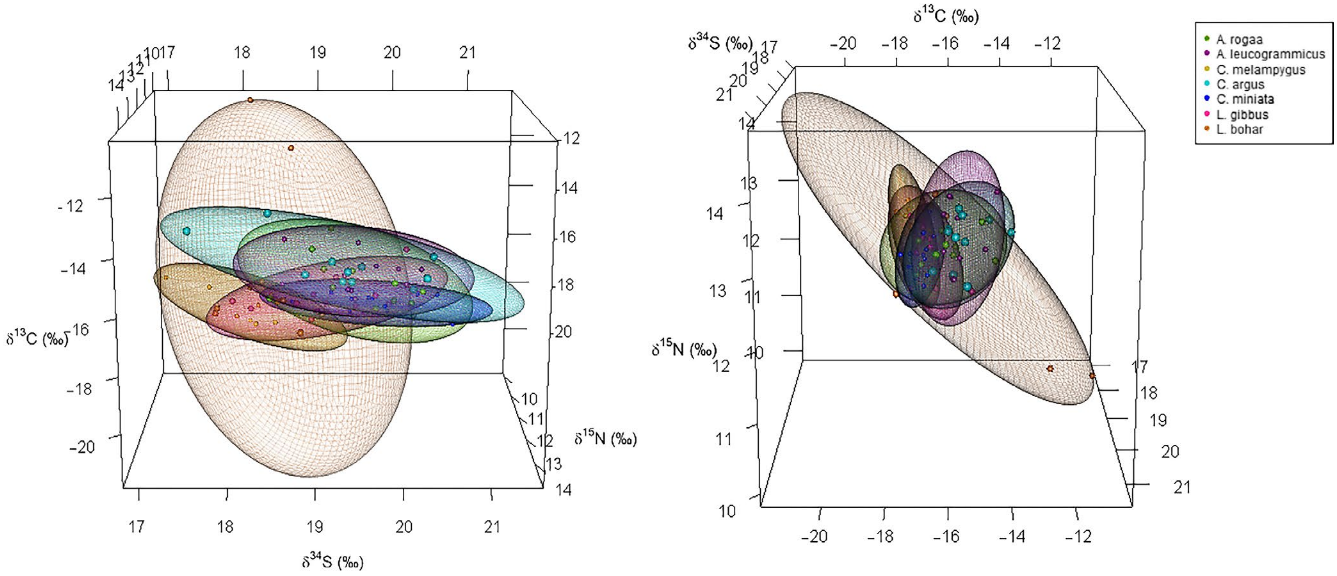

FIGURE 1 75% ellipsoids corrected for small sample size generated using δ^{13}C, δ^{15}N, and δ^{34}S data for predators in the inner atoll

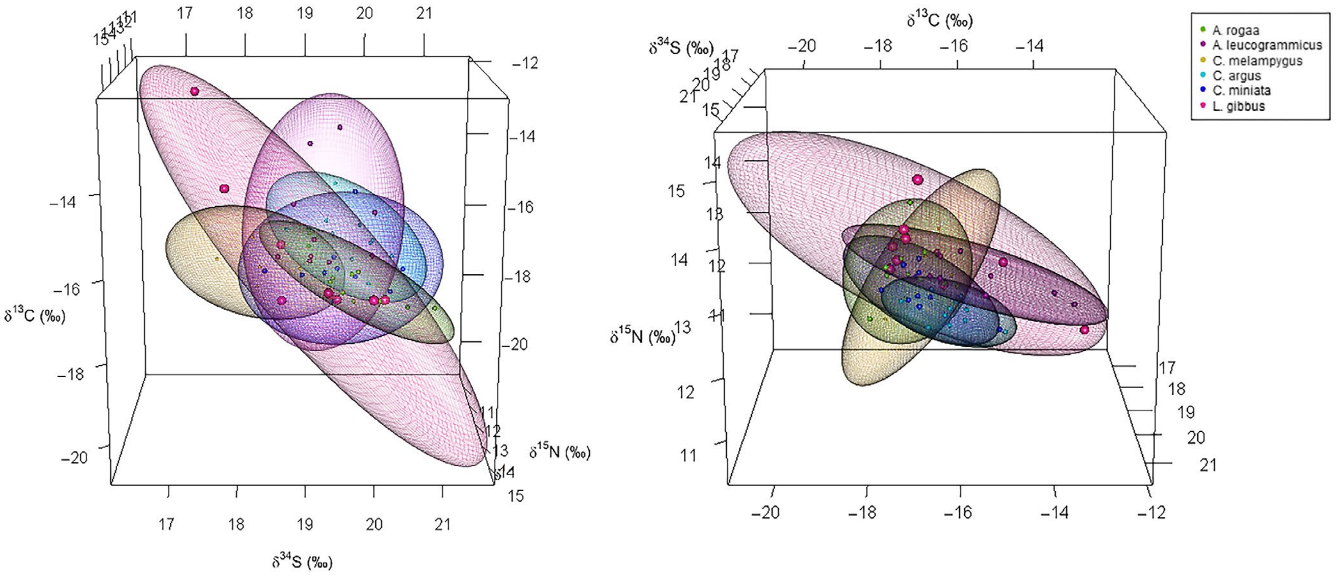

FIGURE 2 75% ellipsoids corrected for small sample size generated using δ^{13}C, δ^{15}N, and δ^{34}S data for predators in the inner atoll

7.06), while the niches of *A. leucogrammicus* and *C. melampygus* were only 1.5 times larger in the outer atoll (Table 2; Figures 1 and 2).

There were no effects of body size or area on predator δ^{15}N and δ^{34}S values (Table S2) but statistical power was low (Median [95% CI] δ^{15}N: 9% [4–16] and δ^{34}S: 14% [8–22]). Statistical power to detect size effects was highest for δ^{13}C (Median (95% CI) δ^{13}C: 70% (60 – 77)) but there were no overall size effects on predator δ^{13}C values. However, they were significantly more negative in the outer atoll ($p < .01$) and there was a significant effect of size interacting with area ($p < .05$) (Table S2).

There were few instances of significant niche overlap among the predators in the inner atoll. *A. leucogrammicus* had a niche that significantly overlapped with *C. argus* (median overlap: 63%), and *L. gibbus* had a niche that significantly overlapped with *L. bohar* (median overlap: 74%) (Table 3). There were no instances of significant niche overlap among predators in the outer atoll (Table 3).

4 | DISCUSSION

This study is the first to investigate how resource use varies intraspecifically and spatially for multiple sympatric coral reef predators across an atoll seascape. To date, most studies of reef predator trophodynamics in the tropics have focussed on single species or genera, despite the multispecies nature of many coral reef fisheries (Newton, Cote, Pilling, Jennings, & Dulvy, 2007). We reveal considerable spatial

TABLE 3 Median percentage overlap in ellipsoids (Bayesian 75% ellipsoid generated using δ^{13}C, δ^{15}N, and δ^{34}S data) with 95% credible intervals showing the uncertainty in the overlap estimates between each pair of predator species

		A. rogaa	*A. leu*	*C. mel*	*C. argus*	*C. miniata*	*L. bohar*	*L. gibbus*
Inner	*A. rogaa*	—	46 (18–77)	1 (0–14)	57 (24–86)	30 (11–52)	39 (11–78)	31 (9–57)
	A. leu	53 (24–85)	—	0 (0–4)	**63 (33–95)**	12 (0–29)	18 (0–52)	16 (0–39)
	C. melampygus	2 (0–20)	0 (0–5)	—	0 (0–8)	5 (0–23)	57 (30–94)	29 (7–56)
	C. argus	45 (20–75)	42 (18–70)	0 (0–4)	—	10 (0–26)	30 (8–64)	14 (0–31)
	C. miniata	57 (25–94)	21 (0–56)	6 (0–30)	27 (0–64)	—	46 (13–85)	53 (24–86)
	L. bohar	10 (2–23)	4 (0–12)	10 (3–20)	10 (2–23)	6 (1–14)	—	14 (5–26)
	L. gibbus	41 (15–70)	18 (0–42)	26 (6–50)	24 (0–50)	36 (12–61)	**74 (48–100)**	—
Outer	*A. rogaa*	—	29 (7–59)	10 (0–35)	20 (2–44)	47 (22–79)	—	56 (25–89)
	A. leu	23 (5–43)	—	9 (0–32)	16 (1–38)	26 (4–54)	—	51 (20–82)
	C. melampygus	10 (0–34)	12 (0–36)	—	3 (0–19)	17 (0–47)	—	34 (7–69)
	C. argus	31 (5–61)	31 (5–65)	5 (0–35)	—	55 (23–90)	—	29 (2–76)
	C. miniata	44 (17–76)	31 (4–60)	17 (0–43)	33 (11–65)	—	—	46 (9–85)
	L. gibbus	18 (5–36)	20 (6–42)	11 (2–27)	7 (0–17)	16 (4–32)	—	—

Note: The table is to be read across each row: for example, in the inner atoll 46% of the *Aethaloperca rogaa* ellipsoid overlapped with the *Anyperodon leucogrammicus* ellipsoid, and 53% of the *A. leucogrammicus* ellipsoid overlapped with the *A. rogaa* ellipsoid. Significant overlap (≥60%) is in bold. Overlap was only determined for predators in the same atoll area.

variation in predator resource use inferred from variability in isotopic composition, suggesting differences within and among species.

4.1 | Is there intraspecific variation in predator resource use?

Although considered to be generalist predators, the large variation in isotope niche volumes, as determined by the 75% Bayesian ellipsoid volume (EV_B), suggests differences in resource utilization among species. The niches of *L. bohar* (inner atoll) and *L. gibbus* (outer atoll) were estimated to be larger than those of the other predators. For both these species, larger EV_B was driven by two individuals that differed considerably in isotope values from the rest (higher δ^{13}C, lower δ^{15}N, and δ^{34}S), despite being of similar sizes to their conspecifics. As stable isotope values are time-integrated indicators of assimilated food items, the less negative δ^{13}C of these individuals indicates consistent feeding on more benthic prey. It also suggests that prey from a range of production sources are available to the predators across the atoll seascape. This hypothesis is supported by isotope values of primary consumers, which had large but similar ranges in both atoll areas (Inner δ^{13}C −18.26 to −11.93; δ^{15}N 6.70 to 12.39; δ^{34}S 18.14 to 22.40; Outer δ^{13}C −17.49 to −11.77; δ^{15}N 6.24 to 11.74; δ^{34}S 18.79 to 20.42) (Skinner, Newman, Mill, Newton, & Polunin, 2019b).

There is little published information on the movements of *L. bohar* and *L. gibbus* specifically; snappers generally have high site fidelity, although this can vary spatially (Farmer & Ault, 2011; Pittman et al., 2014). As such, these isotope data give insight in to their foraging behaviors in the absence of spatial tracking methods to assess resource partitioning. In the Bahamas, δ^{13}C values of *Lutjanus griseus* and *Lutjanus apodus* indicated consistent intraspecific variability in space and resource use, with some individuals exploiting different areas of a creek and more marine-based resources, while others did not (Hammerschlag-Peyer & Layman, 2010). In our Maldives data, some individuals of *L. bohar* and *L. gibbus* appeared to be feeding on more benthic prey (less negative δ^{13}C) at lower trophic levels (lower δ^{15}N). Stomach content data indicate that both *L. bohar* and *L. gibbus* are capable of feeding on a range of prey, foraging predominantly on reef-associated fish but also partly on crustaceans (Randall & Brock, 1960; Talbot, 1960; Wright, Dalzell, & Richards, 1986). The isotopic differences among individuals sampled within the same area suggest they may have alternative feeding strategies focusing on different prey. This specialization within populations may explain how coral reefs can support a high density of co-occurring predators.

4.2 | Is there spatial variation in predator resource use?

Community-wide isotope metrics (Layman, Arrington, Montan, & Post, 2007) suggested that all four grouper species (*A. rogaa*, *A. leucogrammicus*, *C. argus*, and *C. miniata*) varied in their resource use spatially. All four had larger NR values in the outer atoll, and with the exception of *C. argus*, they all had larger CR values in the outer atoll. Although δ^{15}N values of a corallivore, *Chaetodon meyeri*, and a nocturnal planktivore, *Myripristis violacea*, were significantly higher in the outer atoll, the differences in mean values were small (~1‰) and isotopic values of all other prey species were similar between areas (Skinner et al., 2019b). Furthermore, δ^{13}C and δ^{15}N values of coral host and particulate organic matter (POM) are consistent around the Maldives and do not vary between inner and outer atoll (Radice et al., 2019). This suggests that the differences in predator CR and NR ranges are a direct result of feeding on different combinations of prey, rather than differences in baseline isotope values.

Stomach content data show that *A. rogaa*, *C. argus*, and *C. miniata* feed primarily on reef-associated fish from a range of families that are sustained by multiple production sources (Dierking, Williams, & Walsh, 2011; Harmelin-Vivien & Bouchon, 1976; Shpigel & Fishelson, 1991). While no stomach content data were available for *A. leucogrammicus*, it likely has a similar diet to the other groupers. The larger CR and NR of these species could indicate that their prey rely on a wide range of production sources. Where benthic and pelagic food webs overlap such as here, predators might have access to prey from two food webs (i.e., planktivores and herbivores) while remaining in the same habitat (Matich et al., 2011). Furthermore, *C. argus* in particular displays extensive foraging plasticity allowing it to take advantage of small scale fluctuations in prey availability (Karkarey, Alcoverro, Kumar, & Arthur, 2017), a behavior possibly reflected in the larger CR and NR ranges.

Interestingly, and in contrast to the patterns identified with the CR and NR ranges, *A. leucogrammicus* and *C. miniata* had larger SR ranges (δ^{34}S: 18.60–20.29 and 18.70–20.65, respectively) in the inner atoll, despite having smaller CR and NR ranges and isotopic niches there. The δ^{34}S isotope values revealed that these two species may be feeding on prey reliant on a range of production sources, including more benthic-sustained detritivores (mean ± *SD* δ^{34}S: 18.14 ± 0.22) and herbivores (mean ± *SD* δ^{34}S: 19.66 ± 0.22) (Skinner et al., 2019b). Assessing the resource use of these two inner atoll predators solely based on δ^{13}C and δ^{15}N values may have missed this intricacy, as the δ^{13}C and δ^{15}N values were indicative of feeding on more pelagic prey from higher trophic levels (evidenced by lower δ^{13}C and higher δ^{15}N). In food web studies, δ^{34}S is often overlooked, despite its ability to help distinguish between different marine producers (Connolly et al., 2004) and reveal resource usage intricacies and pathways (Croisetière et al., 2009; Gajdzik, Parmentier, Sturaro, & Frédérich, 2016) that may be masked using only δ^{13}C or δ^{15}N. The primary reason for this is that measuring δ^{34}S is typically more challenging, and thus more costly, than measuring δ^{13}C or δ^{15}N. However, recent technological advances and new instruments mean that δ^{13}C, δ^{15}N, and δ^{34}S can be measured from the same sample aliquot with a high level of precision (Fourel, Lécuyer, & Balter, 2015). Given these advances and the relative ease of measuring δ^{34}S, we strongly suggest that more studies incorporate δ^{34}S to employ the tri-isotope ellipsoid approach that we present here.

With the exception of *C. argus*, all predators had larger isotopic niches in the outer atoll. Given the similarity in prey and primary producer isotope values between atoll areas (Radice et al., 2019; Skinner et al., 2019b), it seems likely that this spatial variation in resource use is linked to variations in resource availability (Araújo et al., 2011). The oceanic rim reefs of the outer atoll had higher live branching coral and habitat structural complexity following the 2016 bleaching event compared with inner atoll reefs (first author, unpublished data). Coral cover is strongly linked to fish species richness (Komyakova, Munday, & Jones, 2013), and reefs with higher complexity and coral cover support greater densities of smaller-bodied (<20 cm) fish (Alvarez-Filip, Gill, & Dulvy, 2011). Although prey fish biomass was similar between atoll areas, densities of planktivores were greater along the outer edge reefs (first author, unpublished data). This may lead to increased specialization and population niche size, a hypothesis supported by the larger isotopic niche volumes of the predator populations in the outer atoll.

Inner atoll *L. gibbus* had an isotopic niche volume (EV_B) a tenth the size of the outer atoll population. Spatial differences in *L. gibbus* feeding have previously been recorded; it has a crab-dominated diet in Japan (Nanami & Shimose, 2013) but a forage fish (clupeid)-dominated diet in Yemen (Ali, Belluscio, Ventura, & Ardizzone, 2016). Differential preferences for crabs, which are benthic, and clupeids, which are pelagic, may explain the differing range in δ^{13}C and δ^{34}S values between atoll areas found here. Furthermore, the smaller EV_B of the inner atoll population may mean individuals are consistently feeding on a similar but select group of prey. As isotope values of key prey species were similar in both atoll areas (Skinner et al., 2019b), this further supports the hypothesis that there is spatial variation in resource availability across the atoll.

4.3 | Do the isotopic niches of sympatric predators overlap?

The degree of niche overlap was low; there were only two occurrences of significant niche overlap in the inner atoll and none in the outer atoll. This might suggest that the level of competition among these species is low in both areas with predators feeding on a variety of different resources. Overlapping niches do not conclusively equate to increased competition for resources (Gallagher et al., 2017; Layman et al., 2012). All predators had a larger degree of niche overlap with *Lutjanus bohar* (inner) and *L. gibbus* (outer) due to the exceptionally large niches of these two species, but the level of direct competition may be lower. Predators could be feeding on prey over different spatiotemporal scales, which would reduce their direct competition. Alternatively, due to protein turnover and prey isotope signature integration into muscle tissue over time, predators may be feeding on ecologically different diets but still express similar isotope values, confounding interpretation of the level of competition existing in the community.

It is worth noting that not all predators caught in the same location necessarily derive their nutrition from that locality though. The bluefin trevally, *C. melampygus*, had a distinct isotopic niche which overlapped minimally with the niches of the other predators in both atoll areas. *C. melampygus* is a transient, midwater predator with an extensive territory (Holland, Lowe, & Wetherbee, 1996; Sancho, 2000) and is the most mobile of all the predators sampled. It regularly makes crepuscular migrations of 1–2 km between different habitats (Meyer & Honebrink, 2005). Furthermore, it was the only predator to occupy a similar isotopic niche in both areas, suggesting it may use resources from across the atoll. Stomach content data indicate it feeds predominantly on nekton spanning multiple trophic levels, with little reliance on crustaceans or cephalopods (Meyer, Holland, Wetherbee, & Lowe, 2001). Consequently, this separation is likely attributable to differing habitat usage and prey encounters compared to the other more reef-associated and site-attached species (Sluka & Reichenbach, 1995).

Ontogenetic shifts in feeding strategies are well documented (Kimirei et al., 2013; Werner & Gilliam, 1984), but adults may also vary in their resource use as a function of their size. Here, body size did not appear to drive niche variability; there was no relationship between body size and $\delta^{13}C$, $\delta^{15}N$, or $\delta^{34}S$. Although there was a significant relationship between $\delta^{13}C$ and the interaction between area and body size, the effect was weak. However, statistical power was low and the ability to detect relationships may have been limited due to small sample sizes and limited size ranges; size-based shifts in feeding might have been observed with greater replication. While more depth is needed in these data, it seems size-based effects on adult predator resource use are absent or weak here (Gallagher et al., 2017; Layman, Winemiller, Arrington, & Jepsen, 2005; Matley et al., 2017; Shipley et al., 2018). Within the diverse food webs of coral reefs where prey sizes vary, strong relationships with body size may be masked as predators target large primary consumers (Layman et al., 2005).

Predators are often thought to be dietary generalists but we show inter- and intraspecific differences in resource use with minimal significant niche overlap, highlighting how trophic resource use varies among sympatric reef predators at a scale of tens of kilometers. We did not specifically test for individual specialization but several individuals of *Lutjanus* appeared to be feeding in completely different ways to their conspecifics. Individual specialization is not ubiquitous in marine predator populations (Matich et al., 2011), but small sample sizes of these predators mean statistical power to detect potential differences was limited, thus underestimating intraspecific trophic variation. Feeding specializations are linked to ecological opportunity and are thought to be more common where resource diversity and density of competing individuals are greater (Araújo et al., 2011). This makes coral reefs a prime location for predators to demonstrate vastly different individual feeding behaviors. Predators may provide stability to communities by linking separate food chains (McCann et al., 2005; Rooney et al., 2006), but individual dietary specializations could alter this ecological linkage role (Matich et al., 2011) with potential consequences for ecosystem resilience. Detailed information on individual predator resource use is required to identify their ecological role and help understand how they will respond to environmental change.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

CS, ACM, SPN, and NVCP conceived the ideas, all authors designed the methodology, CS collected the data, CS and JN processed the samples, CS and MRDC analyzed the data, CS led the writing of the manuscript, and all authors contributed to revisions.

DATA AVAILABILITY STATEMENT

Data used in this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.7jj53hb (Skinner, Newman, Mill, Newton, & Polunin, 2019a).

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SUPPORTING INFORMATION

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

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RESEARCH ARTICLE

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Prevalence of pelagic dependence among coral reef predators across an atoll seascape

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Abstract

1. Coral reef food webs are complex, vary spatially and remain poorly understood. Certain large predators, notably sharks, are subsidized by pelagic production on outer reef slopes, but how widespread this dependence is across all teleost fishery target species and within atolls is unclear.
2. North Malé Atoll (Maldives) includes oceanic barrier as well as lagoonal reefs. Nine fishery target predators constituting ca. 55% of the local fishery target species biomass at assumed trophic levels 3–5 were selected for analysis. Data were derived from carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulphur ($\delta^{34}S$) stable isotopes from predator white dorsal muscle samples, and primary consumer species representing production source end-members.
3. Three-source Bayesian stable isotope mixing models showed that uptake of pelagic production extends throughout the atoll, with predatory fishes showing equal planktonic reliance between inner and outer edge reefs. Median plankton contribution was 65%–80% for all groupers and 68%–88% for an emperor, a jack and snappers.
4. Lagoonal and atoll edge predators are equally at risk from anthropogenic and climate-induced changes, which may impact the linkages they construct, highlighting the need for management plans that transcend the boundaries of this threatened ecosystem.

KEYWORDS
climate change, connectivity, foraging, plankton, stable isotopes, trophic ecology, trophodynamics

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1 | INTRODUCTION

Until recently, species interactions and nutrient transfer across habitat boundaries and the impact of species declines beyond individual ecosystems were seldom considered (Lundberg & Moberg, 2003). However, ecosystems are now recognized to be linked by flows of organisms and energetic materials (Huxel & McCann, 1998), yet understanding the trophodynamics (the flow of energy) (Lindeman, 1942) of a food web is challenging, particularly for complex marine systems such as coral reefs where spatial variation can be high (Bierwagen, Heupel, Chin, & Simpfendorfer, 2018).

Once thought to be somewhat ecologically closed (Hamner, Colin, & Hamner, 2007; Odum & Odum, 1955), coral reef ecosystems are subject to upwelling and tidal energy, which drive an exchange of plankton, water and nutrients with the ocean (Hamner et al., 2007; Lowe & Falter, 2015). Phytoplankton, a bottom-up driver of ocean productivity, is often more abundant near islands and atolls (Doty & Oguri, 1956; Gove et al., 2016). Since Darwin (1842), it has been hypothesized that the surrounding ocean provides a major source of nutrition to coral reef communities. Fish on outer reef edges can benefit from this exogenous source (Wyatt, Falter, Lowe, Humphries, & Waite, 2012), but intense feeding by outer reef communities (Genin, Monismith, Reidenhbach, Yahel, & Koseff, 2009) means the energetic material seaward of the reef is different from that in lagoons (Hamner et al., 2007). Furthermore, various hydrodynamic processes are needed to deliver ocean water into the lagoons (Lowe, Falter, Monismith, & Atkinson, 2009), suggesting lagoonal reef fish may not have access to the same resources.

Reef fish communities demonstrate increased reliance on oceanic production seaward of the reef but greater reliance on reef production inshore and into lagoons (Le Bourg et al., 2017; Gajdzik, Parmentier, Sturaro, & Frédérich, 2016; Wyatt, Waite, & Humphries, 2012), indicating that the quantity and quality of food available to inner reef fish varies substantially (Wyatt, Waite, et al., 2012). Variation in nutrient availability and content to the inner and outer reef habitats may lead to spatial differences in reef communities. Indeed, planktivorous fish communities are more abundant with increasing proximity to the ocean (Friedlander, Sandin, DeMartini, & Sala, 2010). Aggregations of these planktivorous fish, the "wall of mouths" (Hamner, Jones, Carleton, Hauri, & Williams, 1988), form on the outer edge of many reefs where they take advantage of increased plankton prey abundances (Wyatt, Lowe, Humphries, & Waite, 2013). The community structure of a coral reef is thus heavily influenced by the adjacent ocean (Garcia, Pelletier, Carpentier, Roman, & Bockel, 2018; Letourneur, 1996; Lowe & Falter, 2015). Oceanic productivity is a key driver of fore-reef fish biomass (Robinson et al., 2017; Williams et al., 2015), but quantitative estimates of its contribution to lagoonal reef fish biomass are lacking.

Highly mobile reef predators often rely on production sources from outside their primary habitat (McCauley, Young, et al., 2012; Papastamatiou, Meyer, Kosaki, Wallsgrove, & Popp, 2015) and benefit from the aggregations of planktivores (Matley et al., 2018). Some of these predators are partly reliant on oceanic energy fluxes (Frisch, Ireland, & Baker, 2014; Frisch et al., 2016; McCauley, Young, et al., 2012), while others are supported by benthic primary production (Hilting, Currin, & Kosaki, 2013). To date, most of the understanding of these food web relationships comes from studies of reef sharks or from outer forereef slope communities (Frisch et al., 2014, 2016; McCauley, Young, et al., 2012; Papastamatiou, Friedlander, Caselle, & Lowe, 2010). This raises the question of the ubiquity of planktonic reliance in reef fishery target predator communities and whether it extends to those in atoll lagoons.

With climate change, oceanic productivity is projected to decline particularly at low latitudes (Moore et al., 2018) and reef predators could be affected. Yet, the extent of coral reef fishery target species reliance on pelagic production, particularly inside atoll lagoons, is little known. Our study aimed to: (1) determine the level of contribution of planktonic production sources to fishery target reef predator biomass and (2) identify whether this varies between inner lagoonal and outer atoll edge reefs, and among species. In order to address (1), we had to assess fishery target predator species prevalence and biomass across the atoll. We hypothesize that planktonic reliance will be greater along outer edge reefs with reduced reliance in the lagoon where predators will rely more on reef-based production sources.

2 | MATERIALS AND METHODS

2.1 | Study site

The Maldives consists of 16 atolls comprising ocean-facing edge reefs and enclosed lagoons with patch reefs (Naseer & Hatcher, 2004). The coral reef area is small (8,920 km^2) (Spalding, Ravilious, & Green, 2001), while the pelagic ocean area within the Exclusive Economic Zone covers ~1 million km^2 (FAO, 2006). Ocean current flow direction fluctuates with the monsoon. During the Northeast Monsoon, the current flows to the west increasing productivity on the west coast (Sasamal, 2007), while during the Southwest Monsoon, the currents flow to the east increasing primary productivity on the eastern side (Anderson, Adam, & Goes, 2011). Fieldwork was conducted in North Malé Atoll (4°18′34.5″N, 73°25′26.4″E), which is located on the eastern side of the archipelago from January to April 2017 (NE Monsoon). The atoll was divided into two areas: inner atoll/lagoon and outer atoll/edge reef.

2.2 | Predator community assessments

Underwater visual census (UVC) was used to quantify fishery target predator biomass. Underwater visual census was conducted at 40 sites (20 in each area) covering 50,000 m^2. These reef fish predators (hereafter "predators") were mostly piscivore apex predators occupying the upper level of the food chain at assumed trophic positions ≥3. Predators were classified as fishery target species based on current practice in the Maldives from visits to the Malé fish market (C. Skinner, personal observation) and from Sattar, Wood, Islam, and Najeeb

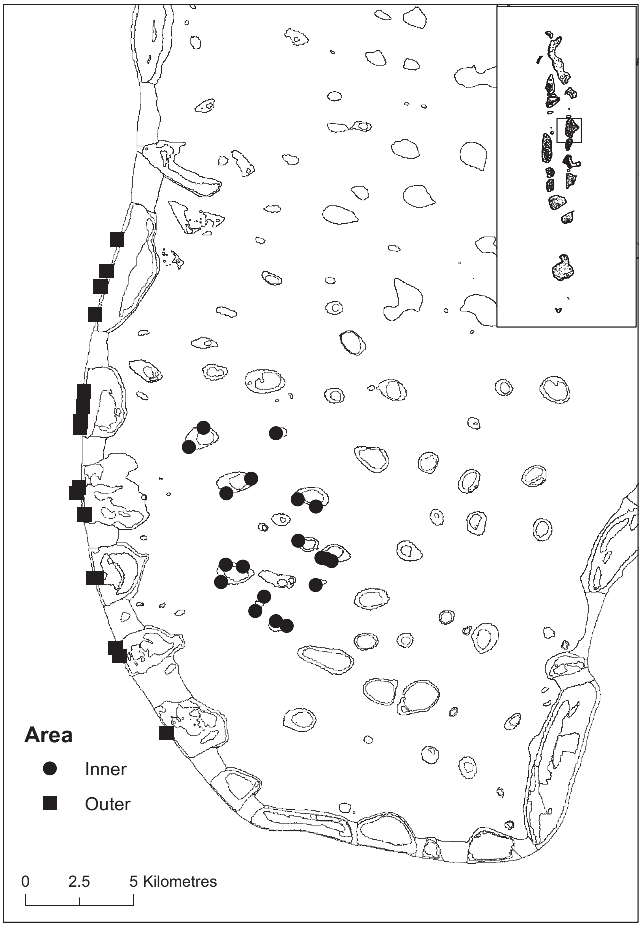

FIGURE 1 Fish sampling sites in inner lagoonal and outer edge reef areas of North Malé Atoll. Inset is Republic of the Maldives

(2014). Only forereef habitat was surveyed. At each site, five 50 × 5 m transects were laid haphazardly (minimum 5 m apart) but parallel to the reef at 3–10 m depth. Abundance and size (cm) of all predators were recorded. Predators were characterized based on their behaviour as more mobile or more site-attached (Brock, 1982). Two observers recorded the predator assemblage; the first laid the transect and recorded mobile species, and the second searched for cryptic, site-attached species, for example smaller Serranidae. The same observers were used throughout the surveys to prevent observer bias (Willis & Babcock, 2000). Site-level averages of fish biomass were calculated. All UVC fishery target predator biomass data were calculated using length–weight relationships available on FishBase (http://fishbase.org) with the exception of *Aethaloperca rogaa* where length–weight relationships were taken from Mapleston et al. (2009).

2.3 | Fish collection

Fish were collected opportunistically from sites across inner and outer atoll areas for stable isotope analysis (Figure 1). Total length (cm) of each individual was recorded. Samples (1–2 g wet mass) of white muscle tissue from the dorsal musculature adjacent to the dorsal fin were removed. White dorsal muscle was used because it is less variable in δ^{13}C and δ^{15}N than other tissues (Pinnegar & Polunin, 1999).

Sampled predators were selected based on their prevalence in UVC data, presence in both inner and outer atoll areas, inclusion of species from the dominant fishery target families, and their high trophic position. Nine species belonging to four families were sampled: groupers (Serranidae: *A. rogaa*, redmouth grouper, *n* = 22; *Anyperodon leucogrammicus*, slender grouper, *n* = 20; *Cephalopholis argus*, peacock grouper, *n* = 21; *Cephalopholis miniata*, coral hind, *n* = 21), snappers (Lutjanidae: *Aphareus furca*, jobfish, *n* = 8; *Lutjanus bohar*, red snapper, *n* = 13; *Lutjanus gibbus*, humpback snapper, *n* = 22), emperors (Lethrinidae: *Lethrinus obsoletus*, orange-striped emperor, *n* = 5) and jacks (Carangidae: *Caranx melampygus*, bluefin trevally, *n* = 16). Predators were captured using rod and reel, handlines and pole spears. Where possible (e.g. when caught using handlines), sampling was non-lethal using 4-mm biopsy punches (Henderson, Stevens, & Lee, 2016).

Different primary producers vary in ratios of δ^{13}C and δ^{34}S, with distinct values typically associated with benthic versus planktonic algae (France, 1995) and marine habitat types, respectively. Food web analysis typically uses δ^{13}C, but δ^{34}S helps to discriminate between different production pathways as there is often greater variability in mean S isotopic value of sources compared to C or N (Connolly, Guest, Melville, & Oakes, 2004). Here, food sources were characterized through sampling a range of primary consumers that feed on specific food groups. Primary consumers can be used as a reference baseline for elucidating trophic positions in the food web with greater certainty than those of primary producers as they incorporate variability and have slower tissue turnover times (Cabana & Rasmussen, 1996; Vander Zanden & Rasmussen, 1999). Primary consumers were chosen based on dietary information from the published literature. Six energy pathways were represented: (a) benthic algae (*Acanthurus leucosternon*, powderblue surgeonfish, 6 inner, 11 outer (Robertson, Polunin, & Leighton, 1979)); (b) hard corals (*Chaetodon meyeri*, scrawled butterflyfish, 5 inner, 11 outer (Sano, 1989)); (c) detritus (*Pearsonothuria graeffei*, blackspotted sea cucumber, 7 inner, 8 outer (Purcell, Samyn, & Conand, 2012)); (d) diurnal plankton (*Caesio xanthonota*, yellowback fusilier, 11 inner, 2 outer (Bellwood, 1988); *Caesio varilineata*, variable-lined fusilier, 12 inner (Bellwood, 1988); *Decapterus macarellus*, mackerel scad, 20 inner (Smith-Vaniz, 1995); *Pterocaesio pisang*, banana fusilier, 12 inner (Bellwood, 1988)); (e) nocturnal plankton (*Myripristis violacea*, lattice soldierfish, 11 inner, 6 outer (Hobson, 1991)); and (f) diel vertically migrating (DVM) plankton (*Uroteuthis duvaucelii*, Indian Ocean squid, 7 outer (Islam, Hajisamae, Pradit, Perngmak, & Paul, 2018)). Although an effort was made to consistently sample primary consumers, *U. duvaucelii* does not feed directly on DVM plankton but on small crustaceans and fishes (e.g. bottom-dwelling sea robins, *Trigla* sp. (Islam et al., 2018)). However, they reside at depths of 30–170 m and feed primarily at night when they migrate to shallower waters, so they were considered a suitably representative proxy for DVM plankton. Several species of planktivores were sampled to control for the greater variability occurring across plankton communities.

Primary consumer species were collected using pole spears or from Malé fish market.

2.4 | Stable isotope analysis

Tissue samples were oven-dried at 50°C for 24 hr and then freeze-dried before grinding to a homogenous powder using a pestle and mortar. Approximately 2.5 mg was weighed into 3 × 5 mm tin capsules and analysed for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ using a PyroCube elemental analyser (Elementar) interfaced with an Elementar VisION IRMS at the NERC Life Sciences Mass Spectrometry Facility, East Kilbride, UK. Stable isotope ratios are reported using the delta (δ) notation with measured values expressed in per mil (‰), where δ is $[(R_{sample}/R_{standard}) - 1] \times 1000$ and R is the ratio of heavy to light isotope (e.g. $^{13}C/^{12}C$). Four international reference materials were used at the start and end of each C/N/S run and three internal reference materials every ten samples to ensure accuracy and correct for drift (Table S1). Analytical precision (*SD*) for international standard USGS40 was 0.1 and 0.2 for $\delta^{13}C$ and $\delta^{15}N$, respectively, and for IAEA-S1, IAEA-S2 and IAEA-S3, it was 0.2, 0.6 and 1.5 for $\delta^{34}S$, respectively. Analytical precision (*SD*) for internal reference materials M2, MSAG2 and SAAG2 was 3.2, 0.1 and 0.1 for $\delta^{13}C$, 3.2, 0.2 and 0.1 for $\delta^{15}N$ and 1.7, 0.5 and 0.5 for $\delta^{34}S$, respectively. Accuracy between runs was assessed using a randomly spaced study-specific reference (mature *A. leucogrammicus*, TL = 41.4 cm). Analytical precision (*SD*) was 0.1 for $\delta^{13}C$, 0.3 for $\delta^{15}N$ and 0.7 for $\delta^{34}S$.

Carbon stable isotope data were lipid-corrected arithmetically when the C:N ratio of the muscle tissue was >3.7 using the mass balance equation of Sweeting, Polunin, and Jennings (2006):

$$\delta_{\mathrm{protein}} = \frac{(\delta_{\mathrm{sample}} \times \mathrm{C{:}N}_{\mathrm{sample}}) + (7 \times (\mathrm{C{:}N}_{\mathrm{sample}} - \mathrm{C{:}N}_{\mathrm{protein}}))}{\mathrm{C{:}N}_{\mathrm{sample}}} \quad (1)$$

Lipid corrections were applied to only 20 predator samples (*A. rogaa*, *C. melampygus*, *C. miniata*, *L. gibbus*) and 12 primary consumer samples (exclusively *P. graeffei*). Mean (*SD*) differences in $\delta^{13}C$ values after correction were 1.2 (1.0) and 1.0 (0.9), respectively.

2.5 | Statistical analyses

All analyses were carried out using R Statistical Software version 3.5.1 (R Development Core Team, 2010) and RStudio version 1.1.383 (RStudio Team, 2012).

Predator abundance data were square-root-transformed, and a Bray–Curtis similarity matrix was made. Using the "VEGAN" R package (Oksanen et al., 2018), differences in predator abundances between areas were assessed using a perMANOVA with 999 permutations. Species contributing to these differences were identified using SIMPER analysis.

Bayesian stable isotope mixing models were run using the R package "MIXSIAR" (Stock & Semmens, 2016a) to ascertain the predators' principal food sources. Each model was run using three tracers ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) with area (inner/outer) as a fixed factor and species as a random factor. The error term Residual * Process was selected as residual error incorporates potential variation involving consumers, for example differences in metabolic rate or digestibility, while process error incorporates variation related to the sampling process (e.g. *L. bohar n* = 1 sample size in the outer atoll) (Stock & Semmens, 2016b). Models were run using the "very long" MCMC parameters. Model convergence was assessed using the trace plots and the Gelman–Rubin and Geweke diagnostic tests.

Source contribution estimates can be highly uncertain when there are too many sources (Ward, Semmens, Phillips, Moore, & Bouwes, 2011). For the best separation of source contributions, it is recommended that sources are combined prior to analysis based on biological knowledge and similar isotopic values (a priori) or, where source isotope values differ, that estimated proportional contributions are combined following analysis (a posteriori) (Phillips, Newsome, & Gregg, 2005). Here, sources were represented by the sampled primary consumer species. Sources were combined a priori when (a) they were the same species or they represented the same food source and (b) there were no significant differences in their isotope values. $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values of the (a) primary consumer species sampled in both inner and outer atoll areas and (b) the four diurnal planktivore species were compared using ANOVAs or, where data did not conform to normality or homoscedasticity, Kruskal–Wallis tests. In some cases, source isotope values may be statistically different even when they have similar isotope values. When this occurred, the mean isotope values of each source were calculated. If the difference in the mean values was small (~1‰), they were combined a priori (Phillips et al., 2014).

A mean isotopic value and standard deviation was determined for each group to represent the different sources in the mixing models. Several sources were then combined a posteriori. This approach allows each individual source to be included in the running of the model while combining sources after may provide a narrower combined distribution with greater biological relevance (Phillips et al., 2014, 2005). Differences in the $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values of the reef-based group and planktonic source group were assessed using a Kruskal–Wallis test.

Trophic discrimination factors (TDF, Δ) vary depending on many factors, and inappropriate TDF can result in misinterpretations. Because of this, four models were run using different TDFs. Trophic discrimination factors were chosen as they were calculated based on white muscle tissue from upper trophic level predatory fish in marine environments, and when plotted, the consumer data were inside the polygon made by the source data. **Model 1** used in situ values field-estimated from Palmyra Atoll for $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$: +1.2 (*SD* ± 1.9) and +2.1 (*SD* ± 2.8), respectively (McCauley, Young, et al., 2012). Little published information is available on $\Delta\delta^{34}S$, but it is thought to be around 0‰ (Peterson & Fry, 1987). In a feeding study of European sea bass (*Dicentrarchus*

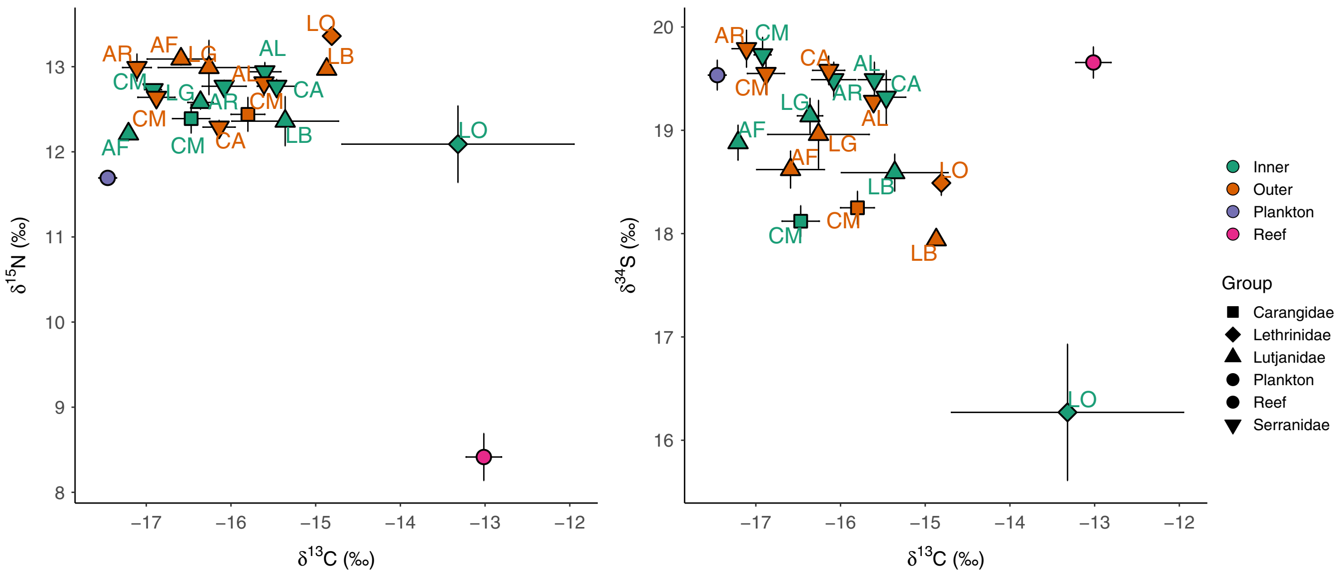

FIGURE 2 Mean isotope values (±*SE*) of (a) δ^{13}C and δ^{15}N and (b) δ^{13}C and δ^{34}S of combined "reef" and "plankton" primary consumer groups (circles) sampled to represent different end-members and reef predators sampled in inner atoll and outer atoll. Predators in group order: CM = *Caranx melampygus*, LO = *Lethrinus obsoletus*, AF = *Aphareus furca*, LB = *Lutjanus bohar*, LG = *Lutjanus gibbus*, AL = *Anyperodon leucogrammicus*, AR = *Aethaloperca rogaa*, CA = *Cephalopholis argus*, CM = *Cephalopholis miniata*

labrax), Barnes and Jennings (2007) calculated $\Delta\delta^{34}$S to be −0.53 (*SD* ± 0.04), but it ranged from −1.59 to +0.26. Therefore, $\Delta\delta^{34}$S *SD* was increased to 1.0 to incorporate this variability and provide additional model parameter space. **Model 2** used the $\Delta\delta^{13}$C = +0.4 (*SD* ± 0.2) and $\Delta\delta^{15}$N = +2.3 (*SD* ± 0.3) for aquatic environments from McCutchan, Lewis, Kendall, and McGrath (2003) and the same $\Delta\delta^{34}$S as model 1. **Model 3** used values from Vander Zanden, Casselman, and Rasmussen (1999) for carnivores, $\Delta\delta^{13}$C = +0.9 (*SD* ± 1.0) and $\Delta\delta^{15}$N = +3.2 (*SD* ± 0.4) and the same $\Delta\delta^{34}$S as model 1. **Model 4** used $\Delta\delta^{13}$C + 1.2 (*SD* ± 1.9) and $\Delta\delta^{15}$N + 2.1 (*SD* ± 2.8) from McCauley, Young, et al. (2012) and a $\Delta\delta^{34}$S of +1.9 (*SD* ± 0.51) for aquatic environments from McCutchan et al. (2003); however, the model did not converge and the consumer source data were outside the source mixing polygon.

The predictive accuracy of the different models was compared using the R package "LOO" (Vehtari, Gabry, Yao, & Gelman, 2018) (Table S5). Leave-one-out-cross-validation (LOO) assesses Bayesian model prediction accuracy (Vehtari, Gelman, & Gabry, 2017). The model with the lowest LOO value and the highest Akaike weight was **model 1,** which is presented in the results (Stock et al., 2018). However, the same patterns remained with the different TDFs (Figure S2). Although median values of plankton contributions vary, the fundamental concepts are consistent: (a) planktonic reliance is a significant contributor to fishery target reef predator biomass, and (b) this reliance extends into inner atoll areas.

3 | RESULTS

Of 30 fishery target species in five families recorded by UVC, nine in four families were sampled for stable isotope analysis in both inner and outer atoll areas (Figure 1). The average predator biomass (±*SD*) across the study sites was 127.9 ± 107.9 kg/ha (100.3 ± 78.7 kg/ha inner; 155.5 ± 126.9 kg/ha outer). The sampled species constituted 58% of the predator assemblage (60% or 60.6 ± 39.8 kg/ha inner; 55% or 84.8 ± 66.2 kg/ha outer). The predator assemblages differed between atoll areas (perMANOVA, 999 permutations, $p < .01$), but only one of the sampled predators, *A. leucogrammicus*, contributed significantly to this (SIMPER, $p < .01$) and it was more abundant in the inner atoll. Mean δ^{13}C values (±*SE*) ranged from −17.1 ± 0.2 to −13.3 ± 1.4 (*A. rogaa*, outer atoll, to *L. obsoletus*, inner atoll), δ^{15}N from 12.1 ± 0.4 to 13.4 ± 0.1 (*L. obsoletus*, inner atoll, to *L. obsoletus*, outer atoll) and δ^{34}S from 16.2 ± 0.7 to 19.8 ± 0.2 (*L. obsoletus*, inner atoll, to *A. rogaa*, outer atoll; Figure 2a,b; Table S2).

There were significant differences in isotopic data of three primary consumer species between atoll areas: *C. meyeri* (hard coral) (ANOVA, δ^{15}N: $F_{1,14} = 6.5$, $p < .05$); *M. violacea* (nocturnal plankton) (Kruskal–Wallis, δ^{15}N: $\chi^2_{1,15} = 4.5$, $p < .05$); and *P. graeffei* (detritus) (ANOVA, δ^{15}N: $F_{1,13} = 4.7$, $p < .05$; δ^{13}C: $F_{1,13} = 14.9$, $p < .05$; and δ^{34}S: $F_{1,13} = 8.0$, $p < .05$; Table S3). These differences were small (~1‰) so these sources were combined a priori (Table S4; Figure S3). There were no significant differences between the areas for the remaining primary consumer species (ANOVA or Kruskal–Wallis, $p > .05$). δ^{15}N and δ^{34}S values did not differ significantly among diurnal planktivores *C. varilineata* (mean ± *SE*: δ^{15}N 11.5 ± 0.1; δ^{34}S 19.1 ± 0.2), *C. xanthonota* (mean ± *SE*: δ^{15}N 11.6 ± 0.3; δ^{34}S 18.9 ± 0.3), *D. macarellus* (mean ± *SE*: δ^{15}N 11.7 ± 0.2; δ^{34}S 19.2 ± 0.2) or *P. pisang* (mean ± *SE*: δ^{15}N 11.5 ± 0.1; δ^{34}S 18.9 ± 0.3) (ANOVA, $p > .05$) but δ^{13}C values did (Kruskal–Wallis, δ^{13}C: $\chi^2_{1,53} = 30.1$, $p < .01$; Table S3). As the differences in δ^{13}C values were small (~1‰), these species were combined into one food source group (hereafter "Diurnal planktivores" [Table S4; Figure S3]).

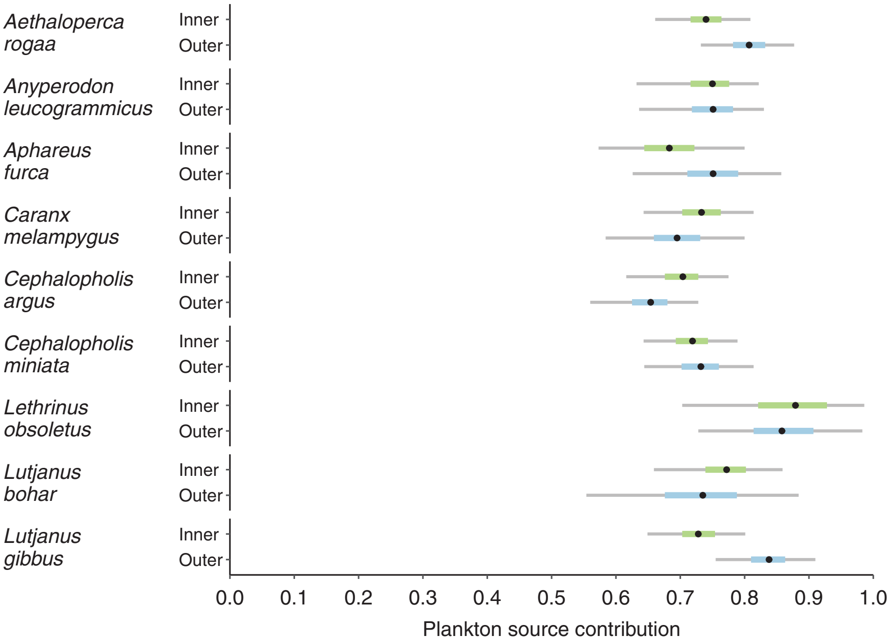

FIGURE 3 Results of Bayesian mixing model with applied trophic discrimination factors, which determined the plankton source contribution to the nine reef predators in both inner and outer atolls. Thick bars represent credible intervals 25%–75%, while thin bars represent 2.5%–97.5%. Black dots represent the medians (50%)

A posteriori, the food sources (represented by the primary consumers) benthic algae, coral and detritus were combined into one "reef" food source group (hereafter "reef" sources), while nocturnal plankton, diurnal plankton and DVM plankton were combined into one "plankton" food source group. The δ^{13}C and δ^{15}N values of the reef-based and planktonic-based primary consumer end-members were highly significant different (δ^{13}C: Kruskal–Wallis, χ^2_1 = 80.6, $p < .01$; and δ^{15}N: χ^2_1 = 67.9, $p < .01$, respectively; Figure 2a; Figure S3a). Planktonic primary consumers all had more negative δ^{13}C signatures, while reef-based primary consumers had less negative δ^{13}C, indicating benthic energy pathways (Figure 2a; Figure S3a). The reef-based and plankton-based δ^{34}S scarcely differed (χ^2_1 = 1.9, $p > .05$; Figure 2b; Figure S3b).

Mixing models indicated that all nine predators were predominantly (65%–88%) sustained by planktonic food sources in both inner and outer atolls (Figure 3; Table S6). Median plankton reliance was highest for *L. obsoletus* in the inner atoll (88%) and lowest for *C. argus* in the outer atoll (65%). Differences in reliance between areas for each species were small and ranged from 0.1% to 11%.

Groupers in both areas derived 65%–80% of their biomass from planktonic food sources, while reef sources contributed only 20%–35%. Between areas, contributions did not vary by more than 6%. *A. rogaa* had higher median planktonic reliance in the outer atoll (80% outer, 74% inner), while *C. argus* had higher median reliance in the inner atoll (70% inner, 65% outer). Median values for *A. leucogrammicus* and *C. miniata* were equal in both atoll areas (75% both; 72% inner, 73% outer, respectively). Credible intervals were similar for all four grouper species.

The median planktonic reliance range of snappers, emperor and jack was 68%–88%. Both *A. furca* and *L. gibbus* had higher median planktonic reliance in the outer atoll than in the inner atoll (75% outer, 68% inner; 84% outer, 73% inner, respectively), whereas *L. bohar* had a slightly higher median reliance on plankton in the inner atoll (77% inner, 73% outer). *Lethrinus obsoletus* had almost equal median planktonic reliance in both areas (86% inner, 88% outer). Of all the predators, *L. gibbus* had the biggest difference in median reliance between atoll areas (11%). Credible intervals for *L. gibbus* were small, while those for *L. obsoletus* and outer atoll *L. bohar* were largest. *Caranx melampygus* had greater median plankton reliance in the inner atoll (73% inner, 69% outer), and credible intervals were similar to the groupers. There was substantial overlap in the proportional planktonic contribution estimates of all the predators in both areas.

4 | DISCUSSION

Planktonic production was the primary contributor to reef fishery target predator biomass regardless of proximity to the open ocean. These results add to growing evidence (Frisch et al., 2014; McCauley, Young, et al., 2012; Wyatt, Waite, et al., 2012) that oceanic productivity is crucial for sustaining the biomass of many coral reef fish communities; this planktonic dependence is prevalent among the main predators, and in the present case, it clearly extends to lagoonal reefs. These identified linkages are not necessarily ubiquitous to coral reef systems, however. In the Northwestern Hawaiian Islands, over 90% of apex predator biomass was sustained by benthic primary production (Hilting et al., 2013), highlighting how trophodynamics may vary substantially spatially, even among similar systems.

Plankton was the predominant contributor to biomass for all of the predators sampled. These predator families have a known reliance on nekton (Kulbicki et al., 2005). Given the high diversity and biomass of planktivores on Maldivian reefs (McClanahan, 2011; Moritz et al., 2017) and the relatively small home ranges of the sampled predators (Karkarey, Alcoverro, Kumar, & Arthur, 2017; Sattar, 2009; Sluka & Reichenbach, 1995), we hypothesize that they link adjacent pelagic and reef ecosystems by primarily feeding on planktivorous prey. Cross-system linkages, similar to those found here, are increasingly being documented. In the Solomon Islands, the piscivorous coral trout *Plectropomus leopardus* is sustained by feeding on planktivorous fish (Greenwood, Sweeting, & Polunin, 2010). In Palmyra Atoll, a circuitous ecological interaction chain was discovered where δ^{15}N from seabird guano over preferred native forests led to increased abundances and biomasses of zooplankton in adjacent waters (McCauley, Desalles, et al., 2012). Similarly in the Chagos Archipelago, on islands free of invasive rats, seabird densities were higher, leading to increased N deposition from offshore foraging, increasing reef fish community biomass (Graham et al., 2018). These semi-pristine environments provide an opportunity to identify these linkages and determine how anthropogenic and climate-induced impacts may affect them.

The high degree of planktonic dependence in predators on lagoonal reefs suggests that planktonic resources are readily available across both atoll areas. Similarly, coral host and POM δ^{13}C and δ^{15}N did not differ between inner and outer reefs in the central Maldives (Radice et al., 2019). Although there is little published information on the internal hydrodynamics of North Malé Atoll, these results suggest that lagoonal waters are providing planktonic subsidies to inner reef communities, but it is unclear whether they come from outside the atoll or from internal hydrodynamic characteristics of the lagoon. In Palmyra Atoll, inner and outer regions are well connected by a range of hydrodynamic processes (Rogers, Monismith, Fringer, Koweek, & Dunbar, 2017). Mixing inside lagoons arises from wave forcing over reef crests and vortices, generated from the wake of flow separation from currents hitting the atoll, help to redistribute water to different regions (Rogers et al., 2017). Internal waves and surface downwelling are also key distributors of particulate-rich waters (Williams et al., 2018). However, these findings are in contrast to Ningaloo, Western Australia, and Mo'orea, French Polynesia, where δ^{13}C and fatty acids of reef fish (Wyatt, Waite, et al., 2012) and the δ^{13}C, δ^{15}N and δ^{34}S of damselfish (Gajdzik et al., 2016), respectively, showed a gradient in oceanic reliance, decreasing into the lagoons. While the lagoons of both Ningaloo and Mo'orea are fairly constricted, North Malé lagoon is substantially more open. We hypothesize that the porosity and open nature of the atoll render lagoonal conditions similar to the open ocean. Future work to identify how nutrients circulate and enter into the lagoons would allow this transfer of energetic materials to be better understood.

The Maldives experiences substantial monsoonal fluctuations in productivity (Radice et al., 2019). As such, timing and location of sampling may influence the degree of planktonic reliance. Here, sampling occurred on the eastern side of the archipelago during the NE season, that is when productivity is supposedly lower. Additionally, due to the double chain nature of the Maldivian archipelago, the outer atoll sites surveyed were adjacent to other atolls, rather than to the pelagic ocean. Despite this, planktonic production was the predominant contributor to predator biomass. This further supports the hypothesis that the porosity of the atoll allows oceanic resources to permeate, and as a result, Maldivian coral reefs are heavily influenced by the open ocean regardless of location and season.

Although interspecific differences in plankton reliance were apparent, median values were high and similar between areas for each species. *Lethrinus obsoletus* had the highest plankton reliance in both areas (~87%). Emperors often forage over soft bottom habitats where they feed on prey such as molluscs and crustaceans (Kulbicki et al., 2005). Many of these may reflect planktonic signatures as they feed on plankton via filter feeding (Jørgensen, 1966) or in the water column at night (McMahon, Thorrold, Houghton, & Berumen, 2016). *Lethrinus nebulosus* on Ningaloo reef slopes also relies on oceanic productivity, but in the lagoon, it is sustained by reef-based production (Wyatt, Waite, et al., 2012), perhaps further indication that variation in lagoonal hydrodynamics may influence food web structure. *Lethrinus obsoletus* also had larger credible intervals. While these were likely confounded by small sample size (*n* = inner 3, outer 2), they may also reflect variability in the range of isotope values. Inner atoll *L. obsoletus* isotope values covered a broader range (range δ^{13}C: 4.8‰; δ^{15}N: 1.5‰; and δ^{34}S: 2.3‰) than in the outer atoll (range δ^{13}C: 0.2‰; δ^{15}N: 0.2‰; and δ^{34}S: 0.3‰), indicating that individuals in the lagoon have a larger isotopic niche than their forereef conspecifics. Niche width depends on the diversity of resources available (Araújo, Bolnick, & Layman, 2011). The greater availability of soft bottom habitat in the lagoon may offer a wider range of prey.

Outer atoll *C. argus* had the lowest plankton reliance (65%). *Cephalopholis argus* are generalist predators that prey on a wide range of reef-associated fish (Dierking, Williams, & Walsh, 2011; Harmelin-Vivien & Bouchon, 1976), so greater benthic reliance is probable. However, the median value of 65% indicates that two thirds of their biomass is supported by planktonic subsidies, higher than expected given previous dietary studies. *Cephalopholis argus* can exhibit foraging plasticity (Karkarey et al., 2017) and readily switch prey groups (Shpigel & Fishelson, 1989). As such, they may be opportunistically foraging on planktivores, a dominant component of Maldivian reefs (McClanahan, 2011). Similarly on the Great Barrier Reef, *Plectropomus* species primarily foraged on the most abundant prey families, Pomacentridae and Caesionidae, indicating that they were opportunistic generalists (Matley et al., 2018). The ability of *C. argus* to switch prey may confer a competitive advantage, allowing them to survive fluctuations in prey communities resulting from environmental change (Karkarey et al., 2017).

The predator assemblage differed significantly between areas, but only one of the sampled predators, *A. leucogrammicus*, contributed significantly. Evidently, the sampled predators constitute an important part of the assemblage and are key components of the biomass in each area. Furthermore, irrespective of minor differences in median plankton reliance, all the predators had substantially overlapping credible intervals. Even *L. gibbus*, where median plankton reliance differed most between areas (inner 75%, outer 86%), had credible intervals, which overlapped considerably with the other species. This may indicate a degree of interspecific competition, raising the question of how they partition resources. Further investigation of their dietary niches is the recommended next step for this work.

Underwater visual census has been the main method for assessing reef fish populations, but it can undersample more mobile species (White, Simpfendorfer, Tobin, & Heupel, 2013; Willis & Babcock, 2000). To account for such shortcomings, 50-m transects (a total of 1,250 m^2 surveyed reef at each site from five transects) were used to increase the likelihood of encountering mobile predators (McCauley, Young, et al., 2012), while baited underwater video deployed in the same areas (C. Skinner et al. unpublished data) identified the same fish species as the most prevalent.

Multiple primary consumers were sampled to attempt to comprehensively characterize the potential production sources at the base of the reef food web. Planktivorous primary consumers may differ isotopically due to differing preferences among the diverse plankton taxa, so several planktivorous primary consumers were sampled. Although the primary consumers representing “reef” and “plankton” separated out isotopically, future studies would benefit from validating each primary consumer by characterizing the food source they represent and including multiple primary consumers to represent each end-member, for example bristle-toothed surgeonfish *Ctenochaetus striatus* as an alternate detritivore (Tebbett, Goatley, Huertas, Mihalitsis, & Bellwood, 2018) or chevron butterflyfish *Chaetodon trifascialis* as an alternate corallivore (McMahon, Berumen, & Thorrold, 2012).

Reef predators are important fishery targets, providing food security and ecosystem services to millions globally (Cinner et al., 2018). Herein, they are found to play an important ecological role linking adjacent ecosystems (McCauley, Young, et al., 2012). Projected declines in oceanic productivity, particularly at low latitudes (Bopp et al., 2013; Moore et al., 2018), may severely impact these Maldivian predators and the linkages they construct. Marine protected areas (MPAs) are widely used in coral reef conservation, but reliance of many reef fish on non-reef production sources suggests the protection MPAs offer is susceptible to climate-induced changes. To adequately address these potential impacts on coral reef food webs, managers need to move towards management plans that transcend the boundaries of these threatened ecosystems.

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AUTHORS' CONTRIBUTIONS

All persons who qualify under authorship criteria are listed as authors, and all take responsibility for the content of the article. C.S., S.P.N. and N.V.C.P. formulated the ideas; C.S., S.P.N., A.C.M. and N.V.C.P. developed methodology; C.S. conducted fieldwork; C.S. and J.N. processed samples; A.C.M. and C.S. analysed the data; C.S. wrote the manuscript; and all authors edited the manuscript.

DATA AVAILABILITY STATEMENT

Data used in this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.7jj53hb (Skinner, Newman, Mill, Newton, & Polunin, 2019).

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SUPPORTING INFORMATION

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